COMPARATIVE STUDIES IN CHELICERATA I. THE CRYPTOGNOMAE (RICINULEI, ARCHITARBI AND ANACTINOTRICHIDA)

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With 31 figures

ABSTRACT

A comparative study is made of three groups of Chelicerata: Ricinulei, Architarbi and Anactinotrichid mites. Ricinulid terminology is revised, and a partly new interpretation of Ricinulid structure is given. Models are prepared of the evolution of Cryptognomic characters. Classification of the three groups is based on a cladistic analysis.

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I. INTRODUCTION

The name Cryptognomae was introduced by me in 1977, in a paper on a new classification of Chelicerata (Van der Hammen, 1977a: 316, 318, tab. 3). The group (a class) comprised Anactinotrichid mites and Ricinulei, whilst the extinct Architarbi were added with a question-mark. The classification of mites, and the recognition of Anactinotrichida as a separate group, has been discussed on several occasions (cf. Van der Hammen, 1961, 1972a); in the last-mentioned paper (on p. 278) I pointed to a possible relationship of Anactinotrichida with Ricinulei and Opilionida.

Before the classical study by Hansen & Sørensen (1904), Ricinulei were classified with Opilionida (generally placed between Cyphophthalmi and Trogulidae), although Karsch (1892) regarded the group as an offshoot of the extinct Anthracomarti. Generally, the extinct Architarbi (cf. Petrunkevitch, 1955) have been regarded as related to Opilionida (especially Cyphophthalmi).

The present paper is the first of a series in which my 1977 model of Chelicerate classification will be worked out in detail. It is a sequel to my work on classification and terminology of mites, and at the same time a logical development of it, especially since mites are classified in two separate groups of Chelicerata, with different affinities.

The base of the present study is constituted by my previous studies on Anactinotrichid morphology. Consequently, terminology and conventions (notations, orientation of figured structures) are those previously used and explained in my glossary of acarological terminology (Van der Hammen, 1976). A list of the notations used in figs. 1-30 of the present paper is given in chapter VIII.

An important part of the present paper is devoted to the study of Ricinulid morphology. In the chapter on Anactinotrichida reference is made to previous studies of this group. A survey of the present paper is given in the table of contents.

Thanks are due to Dr. Y. Coineau (Banyuls-sur-Mer, France), Dr. G. O. Evans (Dublin, Ireland), Dr. T. van der Hammen (Amsterdam, The Netherlands) and Dr. H. Schubart (Manaus, Brazil) for contributing rare Ricinulid material to the present study.

II. RICINULEI

Comparative Ricinulid morphology was founded by Hansen & Sørensen in 1904, when they published their classic work on two orders of Arachnida. Little had changed by 1932 when Kästner published his chapter on Ricinulei in Kükenthal's Handbuch. Segmentation, supposed primitiveness, and internal anatomy were subsequently studied by Millot (1945, 1946, 1947), and at the time when the chapter on Ricinulei in Grassé's Traité de Zoologie was published (Millot, 1949) important progress was made.

From about 1967 onwards, our knowledge of Ricinulei has again considerably increased. Cooke (1967) studied the biology of Ricinulei (among which sperm transfer); Kennaugh (1968) made an examination of the cuticle; Brignoli (1973) studied the female genital apparatus. Extensive comparative morphological papers were published by Pittard & Mitchell (1972), Dumitresco & Juvara-Bals (1973, 1976, 1977, 1977a) and Legg (1976). Tuxen (1974) studied the systematics of the African Ricinulei. Several authors published descriptions of new species of American Ricinulei.

The present study is not a summary of previous literature. It is for the greater part an original study of those characters relevant to a comparative study of the Cryptognomae. Besides original observations, important data from the literature are, however, also mentioned. As mentioned above, this study is based on previous studies of Anactinotrichida, and the greater part of the terminology used here is that of the second volume of my glossary of acarological terms (Van der Hammen, 1976). It might be remarked that only a small number of the terms used here refer to Ricinulei only.

In the present study several new data are introduced, e.g. with reference to the articulation of the appendages, the structure of the mouthparts, the numbering of the body segments, the homology of appendicular segments, and the interpretation of phaneres. Several terms used by previous authors are replaced by the standard terminology introduced in the glossary. In this way the paper constitutes a contribution to the development of a general chelicerate terminology.

The present chapter is divided into three parts: a survey of the material used here, a descriptive part, and additional remarks.

A. Material

In the course of the present investigation four species of Ricinulei have been studied by me, viz., *Ricinoides karschii* (Hansen & Sørensen), *Ricinoides sjoestedtii* (Hansen & Sørensen), *Cryptocellus foedus* Westwood, and *Heteroricinoides magnus* (Ewing). The greater part of the drawings have been prepared after the relatively rich material of the first-mentioned species, of which I could study larva, protonymph, deutonymph, tritonymph, and adult female. A survey of the material at my disposal (with remarks on identity and geographical distribution) is given below.

Ricinoides karschii (Hansen & Sørensen, 1904)

Cryptostemma westermanni, Karsch, 1892: 25-32, pl. 4.
Cryptostemma Karschii Hansen & Sørensen, 1904: 153-154, pl. 8 fig. 4a, b, pl. 9 fig. 1a-l.
Ricinoides karschi, Tuxen, 1974: 100, figs. 29-33.

Material. — Gabon, Forest of the M'Passa plateau, 15 km from Makokou, collected in the months December and January of the years 1971-1978 by Dr. Y. Coineau: 1 larva, 1 protonymph, 5 deutonymphs, 9 tritonymphs, and 1 adult female.

Remark. — The original description was based on material from Kribi, S.W. Cameroon. Hansen & Sørensen studied also material from Benita river, Congo (probably Rio Benito, now Equatorial Guinea). The locality in Gabon is about 400 km from Kribi and about 350 km from Rio Benito.

Ricinoides sjoestedtii (Hansen & Sørensen, 1904)

Cryptostemma Sjöstedtii Hansen & Sørensen, 1904: 151-153, pl. 8 fig. 3a-m.
Ricinoides sjostedti, Tuxen, 1974: 98-100, figs. 24-28.

Material. — S. Nigeria, Nko Obubra div., 3 July 1930, Percy Sladen Trust Expedition, collected by I. T. Sanderson: 3 tritonymphs, 1 adult female.

Remark. — The species is known from Cameroon and the adjoining part of South Nigeria.

Cryptocellus foedus Westwood, 1874

Cryptocellus foedus Westwood, 1874: 201, pl. 37 fig. 5.
Cryptocellus foedus, Hansen & Sørensen, 1904: 155-156, pl. 9 fig. 2a-e.
Cryptocellus Simonis Hansen & Sørensen, 1904: 156-157, pl. 9 fig. 3a-i.
Cryptocellus foedus, Beck & Schubart, 1968: 75-76, figs. 1, 6, 7, 13, 18.

Material. — Brazil, Belém, 3 August 1966, collected by Dr. H. Schubart: one adult male.

Remarks. — The species is known from the Amazon Basin in Brazil. *Cryptocellus foedus* is the type species of the genus *Cryptocellus* Westwood.

Heteroricinoides magnus (Ewing, 1929)

Cryptocellus magnus Ewing, 1929: 589, fig. 1.
Cryptocellus manni Ewing, 1929: 591, figs. 2, 5, 8.
Cryptocellus magnus, Platnick & Shadab, 1976: 5-7, figs. 1-15.

Material. — N. Colombia, Magdalena Department, Sierra Nevada de Santa Marta, Ecoandes transecto Alto Buritaca, altitude 900 m, July-September 1977, collected by Dr. T. van der Hammen and his collaborators: one adult male.

Remarks. — The species is known from various localities in the Magdalena Department, Northern Colombia. As mentioned by Dumitresco & Juvara-Bals (1976: 148) the species is related to *Heteroricinoides bordoni* Dumitresco & Juvara-Bals, type of the genus *Heteroricinoides* Dumitresco & Juvara-Bals. The species is transferred here to the last-mentioned genus. *H. bordoni* was described from Maracaibo, N.E. Venezuela.

B. Descriptive part

Habitus. — Ricinulei are clumsy, rather slow-moving animals, medium-sized (adults not exceeding 10 mm), flattened, with a movable flap (cucullus) attached to the front edge of the body. They rapidly sham death when alarmed.

Divisions of the body (fig. 1). — The body is divided into prosoma and opisthosoma. The prosoma is constituted by the precheliceral metameres and the segments I-VI. The opisthosoma is here regarded as constituted by the segments VII-XIX (partly fused), the segments VII and VIII constituting a "pedicel" which enables coupling of prosoma and opisthosoma. Part of the anterior prosomatic segments constitute a movable gnathosoma (the mouth parts) which is located in a camerostome. An abjugal furrow separates a dorsal region of the prosoma (the aspidosoma) from the podosoma. Details on the present interpretation are given below.

Cuticle. — The cuticle is extraordinary thick and more of less leathery; it is very hard, and difficult to section. It presents lyrifissures, several types of tubercles, granulations and pits, several types of setae, "scales", and other phaneres (solenidia, coronidia), etc. There are no trichobothria. Details on the cuticular organs are discussed below, in the relevant sections.

Aspidosoma (fig. 1A). — The anterior part of the aspidosoma constitutes the cucullus (fig. 5A), a movable hood which can be raised to a horizontal plane, and lowered to a vertical position (covering the camerostome). Although the cucullus has been observed to assist in several activities (capture of prey, egg carrying), the original function certainly pertains to the concealment of the mouthparts and to the protection of the camerostome. Its presence constitutes a specialized (derived) character of the Ricinulei.

The surface of the aspidosoma presents various types of tubercles, various phaneres (setae), and pits (with tubercles); the pits probably represent sigilla. In many species of Ricinulei, the aspidosoma presents, at each side, a light area, above coxa II. In my specimen of *Heteroricinoides magnus* it is removed from the lateral border of the aspidosoma, and slightly bilobate at the paraxial border. It occupies the same position as the eyes of Opilioacarida, and is here regarded as a vestige of two eyes. Because the lenses and the dark pigment are lacking light sensitivity will certainly be reduced.

Pedicel and associated regions (figs. 2, 3A, C). — The anterior, narrowed (but not very narrow) part of the opisthosoma constitutes the pedicel. It comprises the segments VII and VIII. The genital region of the pedicel (segment VIII) is dealt with below; the sclerite situated in females anteriorly of the genital opening, is attributed here to segment VII.

Apart from the small sclerites, the cuticle of the pedicel is soft. It can be folded when prosoma and opisthosoma are coupled (it bears a slight resemblance to a concertina-passage in a corridor-train). In a locked position, the pedicel is completely concealed. The locking device (fig. 3A, C) involves a posterodorsal ridge of the aspidosoma corresponding with an anterodorsal groove of the opisthosoma, and a pair of anteroventral opisthosomatic sockets corresponding with coxae IV and its posterior keels.

The pedicel is strongly different from that in other groups of Chelicerata, not only because it comprises segment VIII, but also because of its function. Its main function is to enable coupling of prosoma and opisthosoma, in which condition genital opening and stigmata are concealed and protected. The position of the single pair of stigmata is apparently prosomatic; it is dealt with below.

Opisthosoma (figs. 1, 3B, D). — The opisthosoma is divided into the pedicel (dealt with above), a main body, and the pygidium (dealt with below). The pedicel is constituted by two segments (VII and VIII), the pygidium by three. The "segments" of the main body are relatively very long; they are regarded here as fusions of respectively the following segments: IX + X, XI + XII, XIII + XIV, and XV + XVI (cf. chapter VI). The pygidium is constituted by three segments, viz., the numbers XVII, XVIII and XIX. According to this interpretation, the number of segments is the same as in Opilioacarids. The cuticle of the opisthosomatic body presents tubercles, setae and sigilla.

Pygidium (fig. 3B, D). — The narrow pygidium is constituted by the segments XVII-XIX. The anal opening is situated in segment XIX. The segments can be withdrawn, each into the preceding segment, like a telescope, and then retracted into the opisthosomatic body. It may be remarked here that in Opilioacarids segment XIX is retractable.

Genital region (fig. 4A, B). — The female genital region is represented in fig. 4A, B. It is constituted by a genital shield (segment VIII), situated posteriorly of the pregenital shield, segment VII). When studied from the inside, the structure of the vulva (segment VIII; at the inside of the genital shield) becomes visible. It has been studied by Brignoli (1973: 154-155, fig. 1A-D), Legg (1976: 37-39, fig. 28A), Platnick & Shadab (1976: 2, figs. 14, 16, 17), and especially by Dumitrescu & Juvara-Bals (1976: 160-165, figs. 6-8; 1977: 259-261, fig. 1). In all genera there are a pair of supposed spermathecae (simple or with a diverticulum); in the genus *Ricinoides* a number of sac-like structures is also present (in our specimen of *Ricinoides sjoestedtii* the number is six). Millot (1947) interpreted the so-called spermathecae as glands; because of their thick wall and narrow lumen, I am inclined to support his view. The function of the sac-like structures is unknown.

The male genital region was described in detail by Pittard & Mitchell (1972: 13, figs, 42, 46-48) and Dumitresco & Juvara-Bals (1973: 268, fig. 7B). It is much smaller than that of the female. It is characterized by the presence of a conical, sclerotized, projecting piece bearing the genital opening at the postero-ventral side. The structure is not a penis or a spermatopositor. Its composition of two segments (as supposed by Pittard & Mitchell) is not evident. The male presents no separate pregenital sclerite.

Podosoma (figs. 1C, 5B, C). — The podosoma extends from the subcapitular furrow (the border of the gnathosoma) to the disjugal furrow (the anterior border of the pedicel). Laterally it is bordered by the abjugal furrow (at the lateral border of the aspidosoma). The sternal region of the podosoma is reduced; its place is taken by the enlarged coxae of the legs. Coxae I-III are fixed; only coxae IV are movable. The small sternal sclerite of segment III (the segment of legs I) presents two or three sternapophyses (fig. 5C), similar in shape to those of the genus *Allothyrus* (Holothyrida), and homologous with the sternapophyses of Anactinotrichida.

Paraxially of coxa I, or between coxae I and II (fig. 5C), the orifice of the coxal glands is present (just as in Opilioacarids). It is supposed here that the products of these glands are transported to the subcapitular gutter (as in Opilioacarids). Just as in Anactinotrichida, the Riniculid sternapophyses are associated with the subcapitular gutter.

The stigma is generally supposed to belong to the prosoma (cf. chapter VI). It is situated above coxae III or IV, close to the border of the pedicel.

Gnathosoma (figs. 5C, 6, 7, 9D). — The gnathosoma is situated in a camerostome (fig. 5C); it is movable with respect to the idiosoma. Just as in Anactinotrichida, two parts can be distinguished: a cheliceral frame (the dorsal part) and an infracapitulum. The membraneous cheliceral frame constitutes the body wall between the infracapitulum and the aspidosoma; the chelicerae are movably attached to it. In comparison with Anactinotrichida, the Ricinulid infracapitulum is rather primitive (the cervix is small; there are no lateral lips; the mouth presents two commissures only, and is consequently crescent-shaped; and there is a capitular as well as a subcapitular apodeme), although it presents a specialization particular to Ricinulei only, viz., the enlarged coxal regions of the palp. The labrum (or upper lip) is large; its dorsal surface presents long setae (fig. 6A). After removal of the labrum, the labium (or under lip) becomes visible (fig. 6B); its surface is covered with radula-like teeth. The labium is completely incorporated in the mentum (the coxisternal region of the palpal segment).

The mouth (fig. 7C) has two commissures (*J* and *J'*). There is a capitular apodeme (the internal continuation of the cervix; it starts from the border of segments I and II), with a pair of tendons (*tc*); and a subcapitular apodeme (the internal continuation of the mentum; it starts from the border of segments II and III), also with a pair of tendons (*tsc*) (figs. 6A, D, 7A, E). It may be remarked here that a subcapitular apodeme is present in Holothyrida, whilst a capitular apodeme is found in many other Anactinotrichida.

The coxal regions of the palp (there is no indication that there has been a free palpal coxa in the ancestors of Ricinulei) are much enlarged in paraxial direction (figs. 6D, 7A, C), although the subcapitular gutter has remained open (fig. 6D). The characteristic two pairs of setae, situated at both sides of the subcapitular gutter (fig. 6D, E) are here interpreted as laterocoxal setae (*e*) (cf. chapter VI and Van der Hammen, 1977b: 13-15). The palpal acetabulum (fig. 9D) has an advanced position (fig. 7B, D).

Chelicera (fig. 8). — The chelicerae are composed of two segments: the body of the chelicera (including the fixed jaw) and the apotele (= the movable jaw); there is no separate trochanter. The fixed jaw is much smaller than the movable jaw. The base of the movable jaw presents the usual insertions of two tendons (t_s and t_i). The position of the chelicerae has changed; the jaws operate in a plane parallel to the infracapitulum (not perpendicular to it). The chelicerae are beset with numerous long setae; they present many orifices of cuticular glands.

Palp (figs. 9-13). — The palp is composed of the following segments (figs. 9, 10A): trochanter, femur, genu, tibiotarsus and apotele (= claw-segment); as will be demonstrated below, the second segment is not a trochanter 2. The terminal part of the tibiotarsus (the fixed jaw) and the apotele (the movable jaw) constitute a chela. The articulation of the palpal trochanter with the infracapitulum (fig. 9) is bidesmatic and bicondylar. The articulation between trochanter and femur (fig. 11A-D) is also bidesmatic and bicondylar (the femur is relatively very short). The articulation between femur and genu (fig. 11A, E-F) is monodesmatic and monocondylar; the tendon insertion has developed a superior position. Because of the monodesmatic distal articulation, the segment distinctly represents a femur and not a trochanter 2. The articulation between genu and tibiotarsus (fig. 12) is bicondylar; a superior tendon is inserted at the base of the tibiotarsus, whilst one of the tendons of the apotele is also involved in the articulation. The genu/tibiotarsus joint permits of active flexion and extension. The articulation between tibiotarsus and apotele (fig. 13) is bicondylar and bidesmatic (as usual); the position of the apotele is superior instead of inferior. The cuticle of the palp (fig. 10 B-D) presents various types of tubercles ("corrugated", "saucer-shaped", and "mushroom-shaped"), lyrifissures, orifices of cuticular glands, and various types of phaneres (some of which associated with pits). The phaneres associated with pits are probably solenidia. The long and narrow tubercles in the distal part of the palp of *Ricinoides karschii* (fig. 13A) are characterized by the presence of a line (lengthwise) and a central canal. They could represent transformed lyrifissures. There is a gradual transition from the long and narrow tubercles to the saucer-shaped. For this reason a comparative investigation of the ultrastructure of lyrifissures and tubercles could be interesting.

Legs (figs. 14-23). — Legs I and II are composed of the following eudesmatic segments (fig. 14A): coxa, trochanter, femur, genu, tibia, tarsus, and apotele; leg III and IV present moreover a trochanter 2. Coxae I-III are fixed, whilst coxa IV is movable. All tarsi of the legs are divided into a basi- and a telotarsus (an ancestral, adesmatic division), whilst telotarsi II-IV present a number of adesmatic divisions (a derived character of the Ricinulei). The number of adesmatic telotarsal segments of the adult is five in the case of legs II and IV (telotarsi 1-5), four in the case of leg III (telotarsi 1-4). The number of immature telotarsal segments will be dealt with below.

The articulation between coxa IV and the body is bidesmatic (figs. 25E, 27A) and apparently monocondylar. The articulation between coxa and trochanter (fig. 15) is bidesmatic and bicondylar, just as the articulation between trochanter 1 and trochanter 2 of legs III and IV (fig. 21C, E-G). The articulation between trochanter and femur of legs I and II (fig. 16) and between trochanter 2 and femur of legs III and IV is also bicondylar and bidesmatic.

The articulation femur/genu (patella) is a complicated hinge joint (fig. 17). It presents (in the case of leg I, investigated here) two superior condyles (representing the enlarged single, superior condyle of ancestral Cryptognomae) and several inferior tendons (viz., a tendon inserted, distally of the articulation points, on the genu, and some three tendons inserted on a sclerite at the base of the genu). A large tendon (apparently t_{i}, one of the tendons of the apotele) continues into the femur.

The articulation genu (patella)/tibia (fig. 18) is a hinge joint of which the axis of rotation is nearly vertical instead of horizontal. It is bicondylar (the two condyles, which are antiaxial in leg I, represent the enlarged single condyle of the ancestral hinge joint) and bidesmatic (the two tendons, which are paraxial in leg I, take the place of the single tendon of the ancestral hinge joint). One of the tendons of the apotele apparently continues into the genu (and the femur).

The articulation tibia/basitarsus (fig. 19) is a hinge joint. It is bicondylar (the two superior condyles take the place of the ancestral single condyle). In the case of leg I there is apparently one paraxial tendon (*tta*), inserted on a basal sclerite, whilst one of the tendons of the apotele (apparently t_{i}) continues into the tibia (and even as far as the femur).

The adesmatic articulation between basi- and telotarsus (fig. 20A-C), and between the various telotarsi, are worked by the two tendons of the apotele, which are guided by openings situated superiorly, resp. inferiorly of the axis of rotation of the joints in question.

The articulation between tarsus and apotele (fig. 20E-F) is a pivot joint (bicondylar, bidesmatic). In the case of leg I, investigated here, one of the tendons continues as far as the femur.

The cuticle of the legs presents: lyrifissures (fig. 21D: the lyrifissures $ibt_{1\text{-}2}''$ of the basitarsus occupy the same position as *ibt''* in Opilioacarida); several types of tubercles (fig. 14C), just as on body and palp; compound phaneres (fig. 14C, 21A, B), i.e. ordinary tubercles surmounted by a corrugated tubercle; and various other types of phaneres, such as solenidia (often associated with pits) (fig. 14C, D), coronidia (dorsally on tibia and basitarsus, just as in Opilioacarids) (fig. 21A), "treelike" setae (fig. 14B), and "ordinary" setae (fig. 14C, D). As will be dealt with below, the compound phaneres of Ricinulei and the compound and mucronate setae of Opilioacarids could be homologous organs. Coronidia and solenidia have also been described from Opilioacarida. The "treelike" setae could be homologous with the bifid seta of Opilioacarida, on telotarsus 2 (acrotarsus) of leg II; they could represent famuli. Solenidia associated with pits are known also from Anactinotrichida.

Leg III of the adult male (figs. 22, 23) is a gonopod. The segments involved in sperm transfer are basitarsus, telotarsus 1 and telotarsus 2. The male basitarsus presents a relatively large apophysis (the basitarsal process) and a depression in which telotarsus 1 recedes. The male telotarsus 1 presents two or three processes, viz., a fixed process (here called falcicula), the so-called accessory piece (here called rastellum), and a small process (here called docidium); all three processes are present in our male specimen of *Heteroricinoides magnus*, whilst the docidium is lacking in our male specimen of *Cryptocellus foedus*. The male telotarsus 2 presents a so-called lamina cyathiformis (here called spathula), in which the telotarsal processes fit. In *Cryptocellus foedus* trochanter 2, tibia and basitarsus of the male gonopod (fig. 23A) each present a distal apophysis; in the male leg I of this species apophyses are present on femur and tibia (fig. 23B), whilst trochanter I of the male leg IV also presents an apophysis (fig. 23C).

Internal anatomy. — The internal anatomy of Ricinulei has been studied by Millot (1947). He made observations on the central nervous system (all ganglia fused to a solid mass pierced by the oesophagus), the respiratory system (each stigma gives entrance into an atrium from which numerous tracheal tubules are starting), the circulatory system (reduced), the alimentary canal (mouth, pharynx, oesophagus, midgut and caeca, hindgut and anus), the excretory system (Malpighian tubes, coxal glands), the prosomatic glands, the musculature, and the genital organs. Firstman (1973: 16-18, fig. 11) subsequently studied the arterial system (characterized as typically apulmonate) and the endosternite (vestigial).

Postembryonic development (figs. 24-27). — The immature stases differ from the adults by several characters, among which the wider separation of opisthosomatic tergites and sternites, the incomplete development of genital region (fig. 27A) and gonopods, and a smaller number of telotarsal segments (except in the tritonymph). The telotarsal formulae, from larva to adult, or (in the case of leg IV) from protonymph to adult, are the following: leg I, 1-1-1-1-1; leg II, 2-4-5-5-5; leg III, 2-3-4-4-4; leg IV, 2-4-5-5. A case of supposed regeneration is shown in fig. 27E: in a tritonymph of *Ricinoides karschii*, the right leg III presented the abnormal number of two telotarsi, whilst the corresponding left leg (fig. 27D) presented the normal number of four; it is supposed that the right telotarsus was broken off in a preceding stase. Leg IV of the larva is vestigial (fig. 24D, E). In the case of *Ricinoides karschii* it is present as a pair of stumps. A qualification as leg buds is not correct (it is a case of regression). A prelarva is not yet known from Ricinulei, but could be present as a calyptostase or an elattostase (cf. Van der Hammen, 1978).

Sperm transfer. — Cooke (1967) has made observations on sperm transfer. After an initial phase of courtship behaviour, the male mounts the female, collects a spermatophore (a globule with an apparently hardened surface), from his genital opening, in one of the gonopods (leg III) and applies it to the genital opening of the female; it takes some time to introduce the spermatophore (or its contents) into the vulva.

C. Remarks

The distribution of extant Ricinulei is essentially Gondwanian. Species are now known from West Africa (from former Portuguese Guinea to Gabon) and from part of the Americas (from southern Texas to Brazil). Two extinct families of the group (Poliocheridae and Curculioididae) are known from the Carboniferous of Europe and North America (cf. Petrunkevitch, 1955). Evidently, the group at that time had a different and much larger distribution.

Of the two fossil families, the family Poliocheridae is closest to extant Ricinulei, whilst the family Curculioididae is especially different by the presence of a single, dorsal, opisthosomatic shield (longitudinally divided) and the presence of divided opisthosomatic sternites.

Fossil and extant Ricinulei must be characterized as highly specialized Chelicerates. Specialization seems to be linked with a special kind of protection: all openings (mouth, stigmata, genital opening, anus) can be concealed; the arthrodial membranes of the appendicular articulations are protected by complicated joints; the cuticle is extraordinary thick and hard. In spite of the highly specialized joints of the legs, locomotion seems to be slow. Extant species are known to sham death in case of danger.

Nothing seems to be known about the enemies of Ricinulei. Protective specialization seems to be excessive, and other hypotheses with reference to its adaptive value could perhaps be introduced (e.g. protection against harmful radiation, during the early period of terrestrial life). The colonization by Ricinulei of Mexican and Central American caves seems to be a recent, favourable development in the evolution of the group.

III. ARCHITARBI

The extinct Architarbi are known from the Carboniferous of Europe and North America only. Three families are distinguished: Architarbidae (with a dozen genera), Opiliotarbidae (with one genus), and Heterotarbidae (with one genus). My brief summary of the main characters and my interpretations are based on the monographs by Petrunkevitch (1913, 1949, 1955).

Architarbi are Chelicerates of medium size (generally smaller than 2 cm). The body is divided into prosoma and opisthosoma, which are broadly joined. The opisthosoma is constituted by at least ten or eleven segments; the anterior five or six segments are abbreviated (as segments VII-XII in Opilioacarida). Gnathosoma probably present.

The aspidosoma is entire. Eyes are absent or present (one sessile pair, or three pairs on a flat tubercle).

The abbreviated anterior opisthosomatic segments are longitudinally bisected by a median line. The number of opisthosomatic sternites is smaller than that of tergites. Anal opening ventral, although sometimes better visible in dorsal view; for this reason, a retractable pygidium (as in Ricinulei) could be present. The structures described as a pair of round genital openings, and one to four pairs of ventral sacs, could represent invaginated opisthosomatic appendages (comparable with the genital papillae of Opilioacarids).

Sternum absent or small (in the last-mentioned case consisting of three or four sclerites). Coxae much enlarged in paraxial direction.

Mouth concealed. Coxal region of palp generally hidden from view by the coxae of leg I. There is probably a gnathosoma, located in a camerostome, and an infracapitulum with a subcapitular gutter.

Chelicerae three-jointed, chelate, small. Palpi short and slender, apparently with five free segments and a coxal region (apotele apparently unknown).

Legs I and II with coxa, trochanter, femur, genu, tibia, and tarsus (apotele apparently unknown). Tarsus apparently subdivided into adesmatic segments. Legs III and IV of Opiliotarbidae with two trochanters, in other families similar to legs I and II. Leg I can be long and slender (as in Opilioacarida).

IV. ANACTINOTRICHIDA

Some years ago I dealt with the classification of mites in general, as well as with that of Anactinotrichida (Van der Hammen, 1972a). Besides, several important Anactinotrichid characters have been discussed in a series of introductory papers (Van der Hammen, 1968b, 1970, 1970a, 1970b, 1972). Species of the four orders of Anactinotrichida have moreover been described (sometimes in great detail) in the following papers: Opilioacarida, Van der Hammen, 1966, 1968a, 1969, 1971, 1977 (see also Van der Hammen, 1976); Holothyrida, Van der Hammen, 1961, 1965, 1968; Gamasida, Van der Hammen, 1964a; Ixodida, Van der Hammen, 1964. The present chapter is based on these studies, although some additional details are added, based on a reinvestigation of the same material. Besides, details from other papers are also mentioned. The present chapter constitutes a concise, general introduction to comparative Anactinotrichid morphology, adapted to the purpose of the present paper; generally, no reference is made to the structure of highly specialized (e.g. parasitic) groups.

Habitus. — Anactinotrichida constitute a group of animals which are generally rather small (rarely medium-sized, such as some Holothyrida and Ixodida) and of widely divergent habitus. The general shape varies from hemispherical to flat, and from nearly round to elongate and narrow.

Divisions of the body. — The original subdivision into prosoma and opisthosoma is still recognizable in Opilioacarida, but has gone lost in all other Anactinotrichida. A separate gnathosoma is present in all groups. An aspidosoma is present in Opilioacarida. A podosoma is more or less distinctly defined in all Anactinotrichida. Segmentation is distinctly present in Opilioacarida only [1]). The subdivision of the dorsal shield of many Gamasida, by a notomeristic scissure (Van der Hammen, 1970: 8-9) into two parts, is certainly not homologous with the original subdivision, by the disjugal furrow, into prosoma and opisthosoma. In comparison with Opilioacarida and Architarbi, the notomeristic scissure takes the place of the border of segments XII and XIII, and could be homologous with this intersegmental furrow.

Cuticle. — In Opilioacarida the cuticle is leathery and faintly sclerotized (but remarkably tough when sectioned). In *Holothyrus* it is hard and leathery, and remarkably thick. In Gamasida and Ixodida, variously constituted sclerites are found, separated by soft skin.

Eyes. — Two or three pairs of eyes are present in Opilioacarida, one or

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[1]) Traces of segmentation are present in a Holothyrid discovered by Dr. J. B. Kethley (Chicago); the description of this important species is in preparation.

two pairs in some Ixodida. Eyes are not present in Holothyrida, Gamasida and part of the Ixodida.

Phanerotaxy. — In Opilioacarida many types of phaneres are found, viz., papilliform or lobate setae, compound setae, mucronate setae, solenidia, coronidia, various types of ordinary setae (generally hollow), etc. Compound setae consist of an ornate base, surmounted by a striate distal part; they could represent a tubercle surmounted by a sensory phanere. Mucronate setae probably represent compound setae of which the distal part has become very small. On the Opilioacarid opisthosoma, lyrifissures can take the place of papilliform setae.

The number of types of phaneres is reduced in other groups of Anactinotrichida; compound and mucronate setae are apparently not known from Holothyrida, Gamasida and Ixodida. All Anactinotrichida are characterized by the absence of trichobothria.

The evolution of Anactinotrichid chaetotaxy (Van der Hammen, 1975) is supposed to start with an atactotrichous primordiotrichy (as in Opilioacarida and Holothyrida), from which an idionymous arrangement of setae (idiotrichy) has developed. Idiotrichy is, however, also found in larval Opilioacarida; in the smallest Holothyrid nymph known to me (a larva is unknown from Holothyrida), leg chaetotaxy seems to be idiotrichous.

Anal region. — The anus is terminal in Opilioacarida. In this group, the anal segment (*XIX*) is retractable.

Genital region. — The transverse genital orifice of Opilioacarida is flanked by a pair of genital verrucae and invaginable papillae; they are considered homologous with exite and endite of an opisthosomatic appendage (Van der Hammen, 1976). In adult females of Opilioacarida a large ovipositor is present. It is an invaginable tube, the wall of which is a continuation of the vagina. The structure of the Opilioacarid ovipositor is very simple (no segmentation, no terminal lobes); it is the most primitive ovipositor known from Chelicerata.

Podosoma. — A sternum or sternal region is present in all Anactinotrichida. The basal segment of the legs is a coxa. Sternapophyses are known from Opilioacarida and Holothyrida (a pair), and Gamasida (a fused pair). Coxal glands debouching near coxa I are known from Opilioacarida; the orifice is connected by sternal taenidia with the subcapitular gutter. Sternapophyses are associated with the subcapitular gutter.

Gnathosoma. — The gnathosoma consists of a cheliceral frame and an infracapitulum. In most Gamasida, the cheliceral frame has developed a limbus, constituting a supracheliceral vault. The infracapitulum consists of a dorsal cervix, a ventral mentum, a pair of large lateral ridges, and a pair of malapophyses (of which the ventral surface is called gena; the paired genae are a continuation of the mentum). The mouth is surrounded by three lips: the labrum or upper lip, and a pair of lateral lips; an underlip is no more recognizable. The mouth presents three commissures. The ventral surface of the infracapitulum presents (in Opilioacarida, Holothyrida and Gamasida) a subcapitular gutter which is associated with the sternapophyses.

The base of the infracapitulum is characterized by the presence of apodemes. A subcapitular apodeme is now known from Holothyrida, whilst a capitular apodeme is now known from Opilioacarida and Gamasida. A further study of these apodemes (especially in primitive Gamasida, but also in other Anactinotrichida), and of the way of retraction and articulation of the gnathosoma is, however, badly needed.

Chelicera. — The chelicera is three-segmented (belonging to the prehensile type) in Opilioacarida, Holothyrida and Gamasida, much transformed in Ixodida. There are originally a dorsal and an antiaxial lyrifissure.

Palp. — There are originally six free palpal segments: trochanter, femur, genu, tibia, tarsus and apotele. The apotele is terminal in Opilioacarida; in Holothyrida and Gamasida its position is paraxial (near the base of the tarsus). In Opilioacarida, Holothyrida and Gamasida the border of tarsus and tibia is oblique (the paraxial surface is longer than the antiaxial). In Ixodida the number of palpal segments is reduced. The Anactinotrichid palp has no free coxa; the infracapitulum presents, however, a coxal region at the base of the palp. In Gamasida, this coxal region presents a laterocoxal seta (*e*). The articulation between genu and tibia of the Anactinotrichid palp is represented in fig. 28. In Opilioacarida (fig. 28A) it is a bicondylar and bidesmatic joint, permitting of active flexion and extension. In Holothyrida, Gamasida and Ixodida (fig. 28B-E) it is also bicondylar, although it is apparently functioning as a hinge joint (permitting of active flexion). In Gamasida it does, however, not look like a normal hinge articulation, especially in dorsal view (cf. Van der Hammen, 1964a: 25, fig. 14). The genu/tibia joint of the Anactinotrichid palp should be subject of detailed investigations on a large scale.

Legs. — The ancestral number of Anactinotrichid eudesmatic leg segments is seven or eight: coxa, trochanter, femur, genu, tibia, tarsus and apotele in the case of leg I and II, whilst leg III and IV of Opilioacarida present two trochanters (trochanter 1 and trochanter 2). The disappearance of trochanter 2 is due to suppression, as appears from a study of postembryonic development. It is absent (by ascendant regression) in larva and protonymph (where a normal basifemur is present), and incompletely developed in the deutonymph (where the basal segment of the femur presents characters of a basifemur as well as of a trochanter 2 (Van der Hammen, 1977: 64, fig. 11C); in tritonymph and adult, trochanter 2 and basifemur are both present (normally developed). The apotele of leg I can be absent in Gamasida; this is also due to suppression.

The articulation between the coxa and the body is apparently acondylar and polydesmatic. The articulation between coxa and trochanter is bi- or monocondylar and bidesmatic. The articulation between trochanter 1 and 2, and between trochanter or trochanter 2 and femur is bicondylar and bidesmatic. The articulations between femur and genu, genu and tibia, and tibia and tarsus are mono- or bicondylar hinge joints. The articulation between tarsus and apotele is bicondylar and bidesmatic.

The femur comprises two adesmatic segments, viz., basi- and telofemur, separated by the basifemoral ring. The articulation permits of little or no movement. It is found at the place of the bend at the base of the femur, and is characterized by the presence of lyrifissures. The tarsus comprises at least two adesmatic segments (apart from the pretarsus), viz., basi- and telotarsus, separated by a basitarsal ring or scissure; in Opilioacarida the telotarsus of legs II-IV is subdivided into two adesmatic segments.

The Anactinotrichid telotarsus I presents several types of sensory phaneres associated with pits or capsules, varying from the telotarsal organ in Opilioacarida (a pit with two sunken solenidia) to Haller's organ in ticks.

Internal anatomy. — Recent summaries of the internal anatomy were given by T. E. Hughes (1959) and Legendre (1967, 1968). The endosternite was studied by Firstman (1973). A study of the internal anatomy of a species of Opilioacarida, by Coineau & Legendre, is in course of preparation. The following is only a brief outline.

The central nervous system is concentrated to a single mass, situated in the prosoma, and pierced by the oesophagus.

The respiratory system of Opilioacarida comprises four pairs of opisthosomatic stigmata and tracheae which partly continue into the prosoma. Two pairs of stigmata are described from Holothyrida [1]. One pair of stigmata is present in Gamasida and Ixodida; it is homologous with the anterior pair of Holothyrida (although the single pair of stigmata of the family Ixodidae could be homologous with a pair of opisthosomatic appendages; cf. Van der Hammen, 1968: 273). The anterior pair of stigmata of Holothyrida, and the single pair of stigmata of Gamasida and Argasidae (Ixodida) were supposed to be homologous with one of the pairs of opisthosomatic stigmata (probably

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[1] According to Dr. J. B. Kethley, Chicago (unpublished observation) several pairs of stigmata are present in a species of Holothyrid of which the description is in course of preparation.

stigma 2) of Opilioacarida. It occupies, however, the same position as the single pair of prosomatic stigmata of Ricinulei. I return to the problem in chapter VI.

The circulatory system is lacunar; a heart is present. The alimentary canal comprises pharynx, oesophagus, midgut and caeca, and hindgut. The excretory system comprises the Malpighian tubes and the coxal glands (in Opilioacarida connected with the subcapitular gutter by means of sternal taenidia). There are various prosomatic glands associated with the gnathosoma. The genital organs belong to the arachnidean type. A primitive ovipositor is known from Opilioacarida (described above) and Ixodida. An endosternite is present.

Postembryonic development. — In Opilioacarida the postembryonic development comprises six stases (prelarva, larva, protonymph, deutonymph, tritonymph and adult). The hexapod prelarva is a calyptostase (nearly an elattostase); the larva is characterized by the presence of vestiges of leg IV (as in Ricinulei). The life-cycle of Holothyrida is incompletely known: a prelarva and a hexapod larva are unknown, whilst there are at least three nymphs. The prelarva of Gamasida is unknown; the Gamasid life-cycle comprises a hexapod larva and apparently two nymphs. The postembryonic development of Ixodida comprises a larva and one nymph. The evolutionary phenomena with reference to the evolution of the Anactinotrichid life-cycle are the following (cf. Van der Hammen, 1978): protelattosis (regression of prelarva and larva), plethomorphosis (formation of isophena at the level of the nymph in Argasid ticks), and perhaps neoteny(in the case of one or two instead of three nymphs).

Sperm transfer. — Sperm transfer is unknown from Opilioacarida and Holothyrida. In Gamasida the male chelicera is functioning as a gonopod (a spermatophore is transferred). In Ixodida a spermatophore, attached before to the female genital opening, is pushed inside by the male gnathosoma.

V. Diagnostic characters

Starting from the descriptions given in the preceding chapters, the following diagnoses of Cryptognomae, Ricinulei, Architarbi and Anactinotrichida have been prepared. Provisionally the rank of class is attributed to the Cryptognomae.

Cryptognomae

Small to medium-sized Chelicerates of which the body is originally composed of precheliceral metameres and nineteen segments. There are two tagmata: prosoma and opisthosoma. The mouthparts constitute a movable gnathosoma, originally located in a camerostome. Trichobothria absent. Eyes absent or present (one to three pairs). One to four pairs of stigmata. Anal segment(s) sometimes retractable. Sternapophyses generally present, associated with the subcapitular gutter. Coxal glands in some groups also associated with the subcapitular gutter [1]). Palp without free coxa; the genu/tibia joint sometimes constitutes a flexor-extensor articulation. The palpal tibia and tarsus tend to constitute one segment (tibiotarsus). Legs originally with free coxae (associated with a sternum). Legs III and IV originally (in all three groups) with two trochanters; trochanter 2 is, however, suppressed in many Anactinotrichida and Architarbi. All legs with basi- and telotarsus. Apotele originally with two claws. Legs in some groups (Ricinulei and Opilioacarida) with coronidia. Life-cycle originally with six stases. Larva hexapod (a vestige of leg IV is present in the larva of Ricinulei and Opilioacarida; a larva is not known from Architarbi).

Ricinulei

Medium-sized Cryptognomae. Prosoma with a cucullus and with vestiges of (two pairs of) eyes. One pair of prosomatic stigmata. Anterior part of opisthosoma (segments VII and VIII) constituting a pedicel. Prosoma and opisthosoma can be coupled by locking devices. Posterior three opisthosomatic segments (XVII-XIX) constituting a retractable pygidium. Coxae enlarged in paraxial direction; sternum reduced. Two or three sternapophyses associated with the subcapitular gutter. Orifices of coxal glands near coxae I, associated with subcapitular gutter. Mouthparts constituting a movable gnathosoma (with capitular and subcapitular apodeme), located in a camerostome. Mouth with two commissures; upper lip large, under lip incorporated in mentum. Chelicerae chelate, without trochanter. Palp without free coxa; composed of trochanter, femur, genu, tibiotarsus and apotele; the terminal part of the tibiotarsus, and the apotele constitute a chela. Coxa IV movable; coxae I-III fixed. Legs III and IV with two trochanters. Telotarsi II-IV subdivided. Leg III of the male constitutes a gonopod (basitarsus, telotarsus 1 and telotarsus 2 are involved in sperm transfer). Legs with various types of phaneres, among which coronidia (dorsally on tibia and basitarsus). Life-cycle with at least five stases (larva, three nymphs, and adult). Larva with vestiges of leg IV.

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[1]) In Epimerata (Palpigradi and Actinotrichida) the orifice of the coxal glands is originally postero-dorsally of the base of leg I. In Actinotrichida it is generally associated with a podocephalic canal (originally external and extending to the dorsal surface of the infracapitulum); the original function of the canal appears to be osmoregulation.

Architarbi

Medium-sized, extinct Cryptognomae, known from the Carboniferous. Prosoma and opisthosoma broadly joined. Eyes absent or present (one sessile pair or three pairs on low tubercle). Anterior opisthosomatic segments abbreviated. A retractable pygidium is not known, but could be present. Anus ventral. Gnathosoma probably present. Coxae enlarged in paraxial direction; sternum small or absent. Chelicerae three-jointed, chelate. Palpi short and slender. Legs III and IV of Opiliotarbidae with two trochanters.

Anactinotrichida

Small or medium-sized Cryptognomae. Prosoma and opisthosoma broadly joined. Segmentation lost, except in Opilioacarida. Eyes absent or present (one, two or three pairs). One to four pairs of stigmata. Anus originally terminal; anal segment retractable in Opilioacarida. Podosoma with sternum or sternal region. One pair of sternapophyses (often fused), associated with subcapitular gutter. Coxal glands in Opilioacarida associated with subcapitular gutter. Gnathosoma with capitular or subcapitular apodeme. Mouth with three commissures, bordered by an upper lip and a pair of lateral lips. Infracapitulum originally consisting of cervix, mentum, large lateral ridges and malapophyses. Chelicerae originally prehensile, three-jointed, chelate; cheliceral body generally with two lyrifissures (*id*, *iα*). Palp generally with apotelic claws. Border between palpal tibia and tarsus oblique; the two segments have the shape of a single tibiotarsus. Legs with free coxae. Legs III and IV of Opilioacarida with two trochanters. Femora subdivided by a basifemoral ring into basi- and telofemur. In Opilioacarida, telotarsi II-IV are subdivided. A pretarsus (sometimes with setae or vestiges of setae) is often present. Life-cycle of Opilioacarida with six stases (prelarva, larva, three nymphs and adult); number of stases reduced in Gamasida and Ixodida.

VI. Evolution of Cryptognomic characters

As a result of the present study, characters or groups of characters of the three groups can be compared, and hypothetic models can be constructed with reference to their evolution. The present chapter deals with the evolution of body, eyes, respiratory system, genital organs and reproduction, mouthparts and ingestion (including chelicerae and palp), legs, phanerotaxy, and the life-cycle.

Constitution of the body. — The body of all Chelicerata is originally composed of two tagmata: prosoma and opisthosoma. All Cryptognomae (although it is not known with certainty from the extinct Architarbi) have developed a gnathosoma: an anterior, movable division of the body (not a tagma) with mouth and two pairs of appendages (chelicerae and palps). The ancestral number of segments (apart from the precheliceral metameres) is supposed to be nineteen, the number still found in Opilioacarida. In the last-mentioned group, the anterior opisthosomatic segments (segments VII-XII) are slightly shortened, whilst the lateral parts of these segments have disappeared (cf. Van der Hammen, 1966: 10, fig. 3; 1970: 6, fig. 1B). It is supposed here that this anterior opisthosomatic region corresponds with the region of the narrowed segments in Architarbi, whilst the border between segments XII and XIII is supposed to correspond with the notomeristic furrow of many Gamasida. With the exception of Opilioacarida, nearly all traces of segmentation (including the division into prosoma and opisthosoma) have disappeared in Anactinotrichida. It is supposed here that the ancestral number of nineteen segments has remained the same in Ricinulei and Architarbi. The large segments of Ricinulei (indeed with double rows of sigilla) are supposed to represent fusions of two segments. Segment XIX of Opilioacarida constitutes a retractable anal tubercle. This tendency has been further developed in Ricinulei, in which group segments XVII, XVIII and XIX constitute a retractable pygidium. It is supposed here that a retractable pygidium was also present in the extinct Architarbi (the anal opening is often better visible in dorsal view). My interpretations of the constitution of the body in Cryptognomae are summarized and compared in fig. 29.

Eyes. — Three pairs of eyes are known from *Paracarus*, a genus of Opilioacarida (cf. Van der Hammen, 1968a: 60, fig. 1A, C), and from several genera of Architarbi. In *Paracarus* a group of three eyes is found at both sides of the aspidosoma; in the genera of Architarbi with six eyes, these are found on a flat, trifoliate tubercle situated in the anterior, median part of the aspidosoma. Two pairs of (lateral) eyes are known from the remaining Opilioacarida and from some Ixodida, whilst a vestige of two pairs of lateral eyes is found in Ricinulei. One pair of sessile eyes with an anterior, median position is found in some genera of Architarbi. Eyes are absent in the remaining Architarbi and Anactinotrichida. The presence of three pairs of eyes (with lateral position) is supposed to represent the ancestral condition (cf. Van der Hammen, 1971: 467, fig. 2), whilst concentration on a tubercle, the presence of two or one pair, and the absence of eyes are regarded as derived conditions.

Respiratory system. — In a provisional classification of respiratory organs in mites (Van der Hammen, 1968: 273), the Anactinotrichid stigmata (with exception of those of the family Ixodidae) were supposed to be of opisthosomatic origin. Four pairs are known from Opilioacarida, two pairs from Holothyrida (an undescribed species discovered by Dr. J. B. Kethley, Chicago, presents more than two pairs of stigmata), and one pair from Gamasida and Ixodida. The single pair of stigmata of Ricinulei seems to be prosomatic (situated above coxa IV); it resembles the anterior pair of Holothyrida, and the single pair of Gamasida and Argasidae. Two hypotheses can now be introduced: (1) the single pair of stigmata of Ricinulei, Gamasida and Argasidae (Ixodida), and the anterior pair of Holothyrida are all of prosomatic origin; (2) the pair of Ricinuleid stigmata is of opisthosomatic origin (the anterior position, in the prosoma, but close to the base of the pedicel, being the result of shifting). A study of the species of Holothyrid discovered by Dr. J. B. Kethley, and a study of Ricinulid embryology could both supply arguments in favour of one of these hypotheses. It should, however, be borne in mind that, even in the case of homology and homonomy, this can only be the result of parallel evolution, because the evolution of stigmata and trachea (as an adaptation to terrestrial life), certainly did not start until the groups were already separated by very important discontinuities.

Genital organs and reproduction. — Mention must be made here of the presence of a primitive ovipositor in Opilioacarida and Ixodida, which probably is the result of an independent development in each group. Sperm transfer is unknown from Opilioacarida, Holothyrida and the extinct Architarbi. In the remaining Anactinotrichida, and in Ricinulei, sperm transfer is nearly direct, and one of the appendages is functioning as a gonopod (in Gamasida the chelicera is functioning as a gonopod, in Ricinulei leg III). In Ixodida chelicerae and lateral lips apparently collaborate in sperm transfer. In all known cases sperm is transferred in the shape of a spermatophore.

Mouthparts and ingestion. — As far as known all Cryptognomae are characterized by the presence of a gnathosoma. The most primitive gnathosoma is found in Ricinulei. It presents a capitular and a subcapitular apodeme, both with tendons. In Holothyrida a subcapitular apodeme only is present, in Opilioacarida and Gamasida (as far as known) a capitular. The apodemes and tendons, as well as articulation and/or retraction of the gnathosoma, should be subject of a study on a larger scale; it will be especially important to investigate the possible existence of a subcapitular apodeme in primitive Gamasida.

A primitive crescent-shaped mouth with two commissures (*J*, *J'*) is present in Ricinulei. In Anactinotrichida it is trifid, with three commissures (*Js*, *Js'*, *Ji*). Two lips (labrum and labium) are present in Ricinulei, three lips are known from Anactinotrichida (labrum and a pair of lateral lips; a labium is not present in Anactinotrichida) [1]. The Ricinulid labium, although distinctly differentiated, is completely incorporated in the mentum (the epimeral region of the palp). The considerable extension of the mentum is a character of all Cryptognomae; the disappearance of the labium in Anactinotrichida is certainly a further development of this evolution.

In Ricinulei, Opilioacarida, *Allothyrus* and Gamasida, the subcapitular gutter (on the ventral surface of the infracapitulum) is known to be associated with the sternapophyses; in Opilioacarida and Ricinulei, the gutter is, moreover, known to be associated with the coxal glands. This adaptation must have been part of the adaptation to terrestrial life; the subcapitular gutter could be associated with osmoregulation. I may refer to two entries in the general part of the Glossary of Acarological Terminology (Van der Hammen, 1980), viz., podocephalic canal, and subcapitular gutter.

The coxal regions of the Ricinulid palps are considerably enlarged: the ventral borders nearly meet in the median plane, nearly covering the subcapitular gutter (and the sternapophyses). The laterocoxal setae *e* of the Ricinulid palp have moved to a position close to the border of the gutter [2]. The result of the coxal extension in Ricinulei clearly demonstrates that the palpal coxae cannot have been involved in the evolution of the Anactinotrichid mentum and tegulum.

The ingestion of food has been dealt with in my paper on a new classification of Chelicerata (Van der Hammen, 1977a: 312-313). Ingestion of solid food certainly was the normal way of ingestion in Cryptognomic ancestors; it is still known from Opilioacarida. Probably, the ancestral chelicera had not only a prehensile function, but participated also in fragmentation of the

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[1] In Holothyrida and Gamasida (not in Opilioacarida) the pharynx is characterized by a quadrangular section. A pharynx with quadrangular section is usually associated with the presence of four lips. Apparently, the Holothyrid and Gamasid labium is completely incorporated in the mentum.

[2] Latero- or supracoxal setae are characterized topographically: they are found above the base of the legs (in Epimerata) or on the lateroventral side of the coxae. They can be morphologically different from neighbouring setae; they can show several degrees of regression (loss of root and central core). Ancestrally one seta is associated with one coxa or coxal region; in the course of evolution the setae can be multiplied (as is the case in Ricinulei). Latero- or supracoxal setae are now mentioned from the coxal regions or coxae of palp, leg I and leg II of species of Epimerata and Cryptognomae. The pair of supracoxal setae of the chelicerae could still be present in Palpigradi. The homology and homonomy of these latero- or supracoxal setae is still hypothetical, and a study of the ultrastructure of the setae could be interesting (cf. Van der Hammen, 1977b: 13-15, fig. 2B, C, F-L).

food. The ancestral three-segmented type of prehensile chelicera is still found in most Anactinotrichida and is also known from the extinct Architarbi. In Ricinulei the basal segment (the trochanter) has disappeared.

In the palp of some Anactinotrichida (Opilioacarida) and Ricinulei the genu/tibia articulation permits of active flexion and extension, and consequently differs from that of the legs. This could be an indication that the Cryptognomic palp did not arise as an ambulatory appendage, but indeed as a palpal appendage. The joint in question should, however, be studied on a much larger scale. In most Anactinotrichida (Opilioacarida, Holothyrida, Gamasida) the palpal tarsus is a direct continuation of the palpal tibia; both segments seem to constitute one segment. In Ricinulei the palpal tibia and tarsus have fused and constitute a single tibiotarsus.

Legs. — The ancestral Cryptognomic legs are here supposed to have been composed of: free coxa, trochanter (or trochanter 1 and 2 in the case of legs III and IV), femur, genu (patella), tibia, basitarsus, telotarsus and apotele; the adesmatic basi- and telotarsus constitute the eudesmatic tarsus. A model of the evolution of the Cryptognomic legs (based on the case of leg III) is represented in fig. 30. The free coxa has become an enlarged fixed coxa in Ricinulei and Architarbi ¹) although the enlarged coxa IV of Ricinulei is movable. Trochanter 2 is suppressed in all Anactinotrichida except Opilioacarida, and in all Architarbi except Opiliotarbidae ²). In all Anactinotrichida a basifemoral ring (an adesmatic joint of very little or no movability) has developed, dividing the femur in a small basifemur and a larger telofemur. In legs II-IV of Opilioacarida and Ricinulei, the single ancestral telotarsus has been subdivided in the course of evolution; telotarsal segments can, moreover, be added as a result of a cosmiotactic evolution. The apotele of leg I can be suppressed in Gamasida. In fig. 30 a survey is

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¹) A similar evolutionary phenomenon is found in Arachnidea s. str. (according to my 1977a concept). In this group the coxae have remained free in Araneida, whilst they have become fixed in Amblypygi and Uropygi (including Schizomida). A comparative analysis of this parallel evolution (especially viewed from the angle of functional morphology) could be interesting.

In several groups of Chelicerata, the possession of enlarged, fixed coxae is associated with the adaptation to one special way of life. Most extinct groups had enlarged, fixed coxae. The possession of free coxae apparently permits of a much greater variety of adaptations (Spiders, Anactinotrichid mites; the absence of coxae in Actinotrichid mites apparently permitted of a similar variety of adaptations). The only example of a group of Chelicerata with enlarged, fixed coxae, characterized by adaptation to various ways of life, is constituted by Opilionida; this fact could be connected with the presence, in the Opilionid legs, of rocking joints at unusual places (trochanter/femur, patella/tibia).

²) Femur 1 and femur 2 of Epimerata are integrated; the integration is anergastic (the joint gradually disappears).

also given of the evolution of the joints. The pivot joint between coxa and trochanter has become a rocking joint in many Anactinotrichida. Hinge joints can become complicated by flattening of the dorsal surface and the development of two main articulation points. In Ricinulei the genu/tibia articulation has been subject to a torsion of 90°.

Of all Cryptognomic legs, those of Opilioacarida have the greatest number of ancestral characters. Apart from the increased length, the subdivision of telotarsus II-IV, and the subdivision of tibia I (not mentioned above), the Opilioacarid legs could indeed be characterized as prototypes of the Cryptognomic legs.

Phanerotaxy. — Ancestral Cryptognomic chaetotaxy is supposed to have been primordiotrichous (cf. Van der Hammen, 1975: 379-381, fig. 2), from which condition idionymous chaetotaxy could have evolved. In the long legs of Opilioacarida the number of verticils of setae is supposed to have increased by cosmiotrichy (the secondary formation of setae, in a simple and recognizable arrangement, by multiplication of setae previously present in the same area).

Cryptognomic chaetotaxy is characterized by the absence of trichobothria (present in most Chelicerata, but also absent in Opilionida). Apparently the constitution of the Cryptognomic setae (mostly hollow) prevented the evolution of trichobothria. The constitution of papilliform, lobate, compound and mucronate setae in Opilioacarida suggests that part of the phaneres arose from tubercles surmounted by a sensory phanere. The relation of these phaneres to lyrifissures should be subject of further research.

Life-cycle. — The ancestral life-cycle of six stases (prelarva, larva, protonymph, deutonymph, tritonymph and adult) is still present in Opilioacarida. A prelarva is unknown from Ricinulei, but could be represented by a calyptostase. The number of stases is reduced in Gamasida and Ixodida (the life-cycle of Holothyrida is incompletely known). The evolutionary phenomena with reference to the Cryptognomic life-cycle (cf. Van der Hammen, 1978: 49-52, fig. 6) refer to: protelattosis (regression of the first stases), plethomorphosis (the formation of isophena at the level of the nymph in Argasid ticks), and probably also neoteny (in cases with one or two nymphs instead of three).

Ancestral Cryptognomae. — Of all Cryptognomae now known to us, Opilioacarida have preserved the greatest number of ancestral characters; Ricinulei as well as the remaining Anactinotrichida are all much higher developed. A reconstruction of the Cryptognomic prototype would resemble Opilioacarida in many characters; it would, however, be medium-sized, present a more primitive gnathosoma (without lateral lips, and with capitular and subcapitular apodemes), and shorter and more primitive legs (as mentioned above), but in other characters it would be nearly exactly similar to an Opilioacarid (with three pairs of eyes as in *Paracarus*, and with an opisthosoma presenting setae as in *Panchaetes* and *Salfacarus*).

VII. Cryptognomic phylogeny

The results of an analysis of characters and character states and their distribution can be synthesized in the cladogram of fig. 31. The basic dichotomy in the Cryptognomae appears to be between Anactinotrichida on the one hand, and Architarbi and Ricinulei on the other. The first-mentioned group is especially characterized by the possession of a specialized gnathosoma and basifemoral rings. The last-mentioned two groups are especially characterized by the possession of enlarged coxae and a reduced sternum. The cladogram includes the fossil Architarbi which are much more primitive than Ricinulei. Architarbi present, however, an interesting derived character state: the ventral position of the anus. For this reason, the ancestors of the Ricinulei, although certainly very similar to Architarbi, cannot be identified with the last-mentioned group.

Because I have preferred a strictly subordinated higher classification, Architarbi and Ricinulei are classified here in a subclass Schizotergida, which constitutes the sister group of the Anactinotrichida. The name refers to the segmentary arrangement of dorsal opisthosomatic sclerites in nearly all representatives of the group (except some extinct Ricinulei); the only example of opisthosomatic segmentation in Anactinotrichida (Opilioacarida) is not characterized by the occurrence of separate sclerites. Schizotergida are characterized by the presence of a primitive gnathosoma (without lateral lips), enlarged coxae and a reduced sternum, and undivided femora. The rank of subclass is given to Anactinotrichida and Schizotergida, the rank of superorder to the four groups of Anactinotrichida and to Architarbi and Ricinulei.

A few words must be added here on a possible relationship of Cryptognomae and Opilionida. Both groups are characterized by the absence of trichobothria. As mentioned above, this absence is probably connected with the constitution of the phaneres. Compound phaneres consisting of a basal tubercle surmounted by a sensory phanere are present in Opilionida and some groups of Cryptognomae. Because of the fundamental differences in the articulation of the legs, a possible relationship must be remote, and refer to lobopod marine ancestors (possibly with palp), which could be estimated to have lived in the Cambrium, I return to this subject in the third paper of the present series, in which the Opilionidea will be dealt with. Evidently, Chelicerate phylogeny should be reconsidered after the completion of the last paper of the present series.

VIII. LIST OF NOTATIONS

AN, anal opening.
AP, apotele.
BF, basifemur.
bp, basitarsal process.
BTA, basitarsus.
c, *c'*, *c''*, condyle, articulation point.
c_i, inferior condyle.
c_s, superior condyle.
CU, cucullus.
CX, coxa.
CX. III, *CX. IV*, coxae III-IV.
disj, disjugal furrow.
do, docidium.
e, laterocoxal seta of palp.
F, femur.
fa, falcicula.
GE, genu (patella).
gl, gland.
$ibt_{1\text{-}2}''$, proximal, posterolaterodorsal lyrifissures of basitarsus.
J, commissure of mouth.
LI, labium (under lip).
LS, labrum (upper lip).
og, orifice of coxal gland.
ol', *ol''*, ungues.
PA, palp.
PI-IV, legs I-IV.
ra, rastellum.
SA, sternapophyses.
scl, sclerite.
sg, subcapitular gutter.
ss, sac-like structures of female genital region.
st, stigma.
t_i, inferior tendon of apotele.

t_s, superior tendon of apotele.
tc, tendon of capitular apodeme.
tf_s, superior tendon of femur.
TF, telofemur.
tf′, *tf″*, tendons of femur.
tg, $tg_{1\text{-}3}''$, tendons of genu.
TI, tibia.
TITA, tibiotarsus (of palp).
tr_i, inferior tendon of trochanter 2.
tr_s, superior tendon of trochanter 2.
TR, trochanter.
TR.1, trochanter 1.
TR.2, trochanter 2.
tsc, tendon of subcapitular apodeme.
tta, tendon of tarsus.
TTA, telotarsus.
TTA.1, telotarsus 1.
tti, *tti″*, tendons of tibia.
tti_i, inferior tendon of tibia.
tti_s, superior tendon of tibia.
ttr′, *ttr″*, tendons of trochanter (or trochanter 1).
2, *3*, *4*, *5*, telotarsi 2-5.
VII-XIX, opisthosomatic segments VII-XIX.
′ (prime), anterior face of appendage.
″ (double prime), posterior face of appendage.

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[1] The correct date of publication of Cook's paper is not 1800 (which is certainly a printer's error) but 1899. The error has been copied by at least one author.

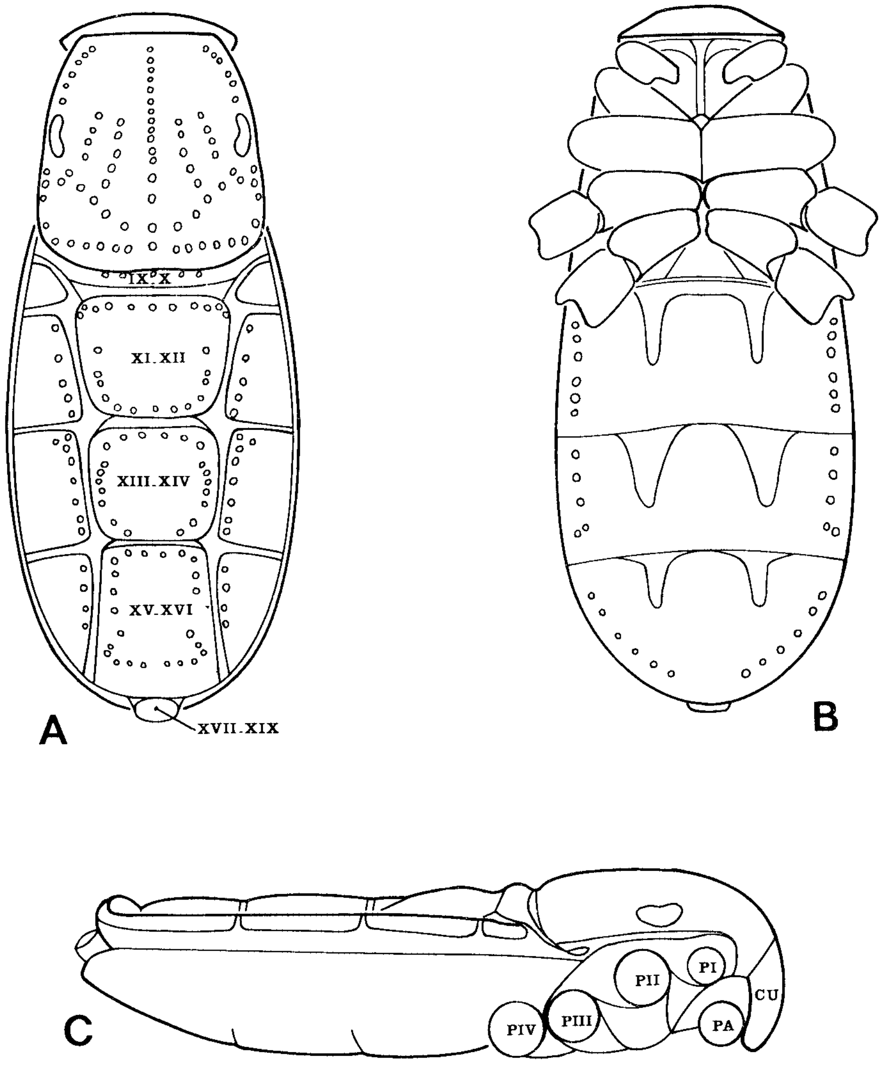

Fig. 1. *Heteroricinoides magnus* (Ewing), male; A, dorsal view; B, ventral view; C, lateral view (podosoma schematized); A-C, × 12.5.

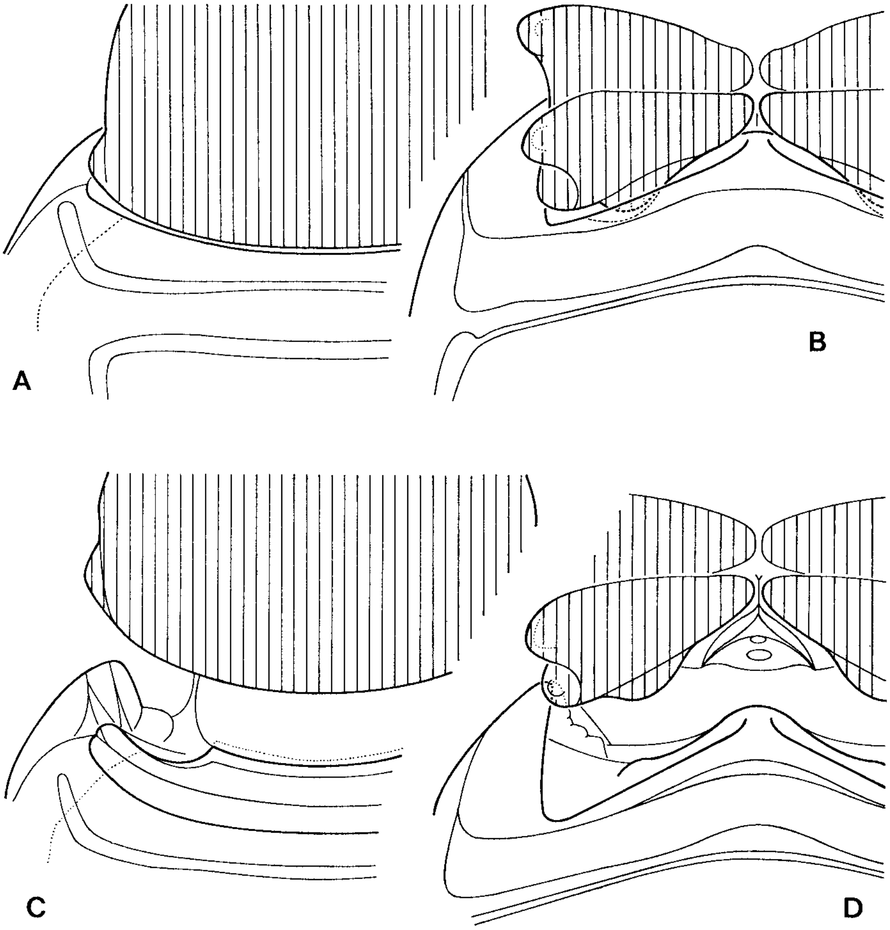

Fig. 2. *Ricinoides karschii* (Hansen & Sørensen), deutonymph; pedicel and associated regions of prosoma and opisthosoma (the prosoma is hatched); A, B, locked position (pedicel concealed); C, D, uncoupled; A, C, dorsal view; B, D, ventral view; A-D, × 37.

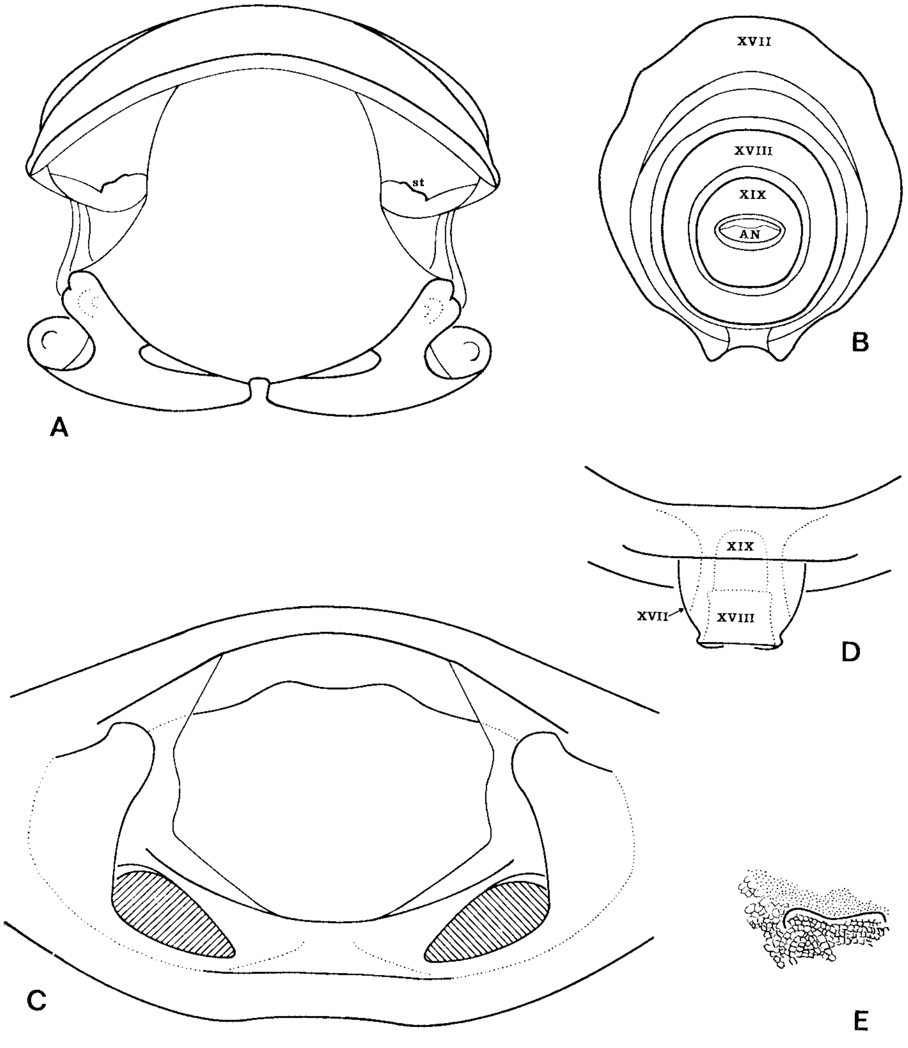

Fig. 3. *Ricinoides karschii* (Hansen & Sørensen), deutonymph; A, posterior view of prosoma; B, posterior view of pygidium (segments XVIII and XIX retracted); C, anterior view of opisthosoma (without pedicel); D, dorsal view of pygidium (segments XVIII and XIX retracted); E, posterior view of left stigma; A, C, D, × 37; B, E, × 118.

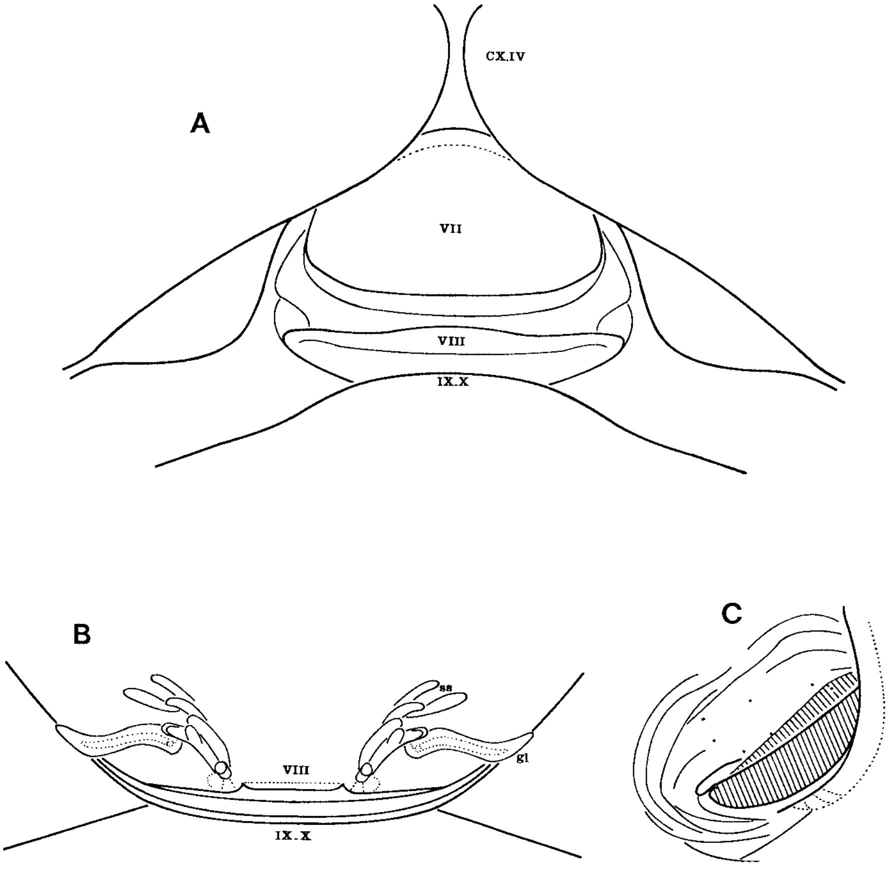

Fig. 4. *Ricinoides sjoestedtii* (Hansen & Sørensen), female; A, ventral view of genital region; B, vulva, viewed from inside; C, posterior view of left stigma (the opening is between the two hatched parts); A, × 73; B, C, × 118.

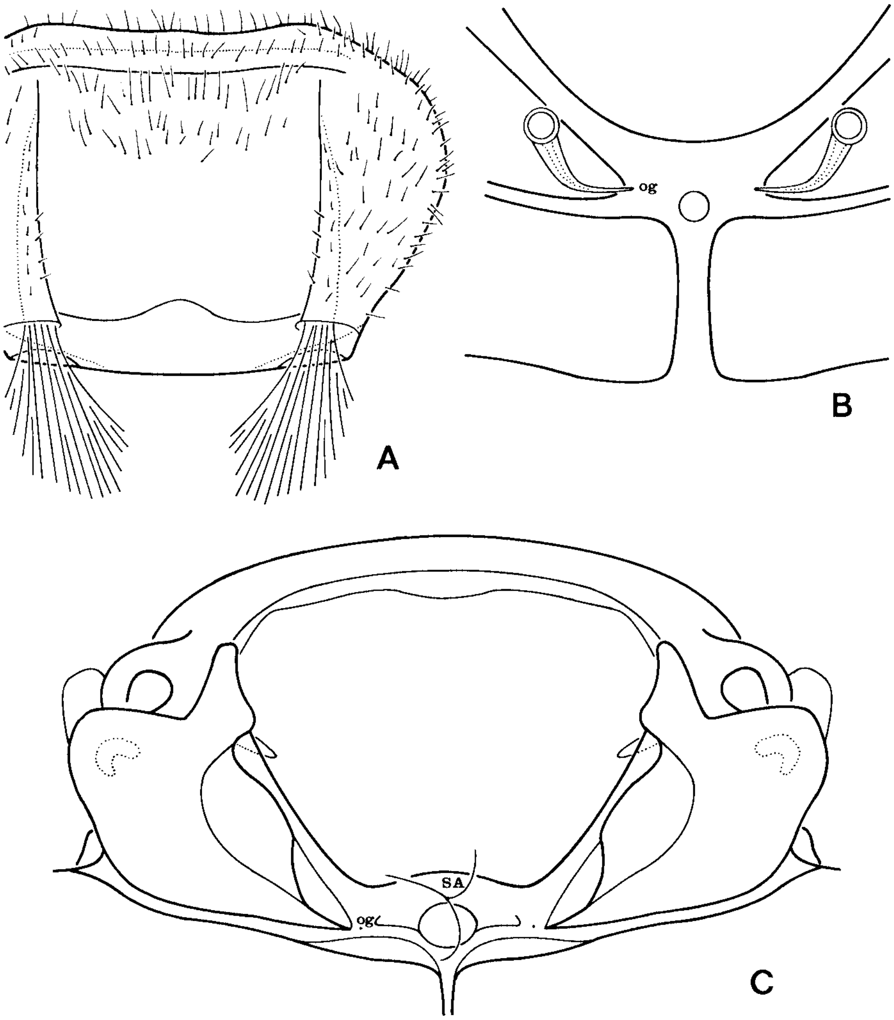

Fig. 5. *Ricinoides karschii* (Hansen & Sørensen), tritonymph; A, ventral view of cucullus; B, coxal and sternal regions of segments III and IV (with pair of excretory canals of coxal glands), viewed from interior; C, ventral view of camerostome and coxal and sternal regions of segment III (gnathosoma and cucullus removed); A-C, × 44.

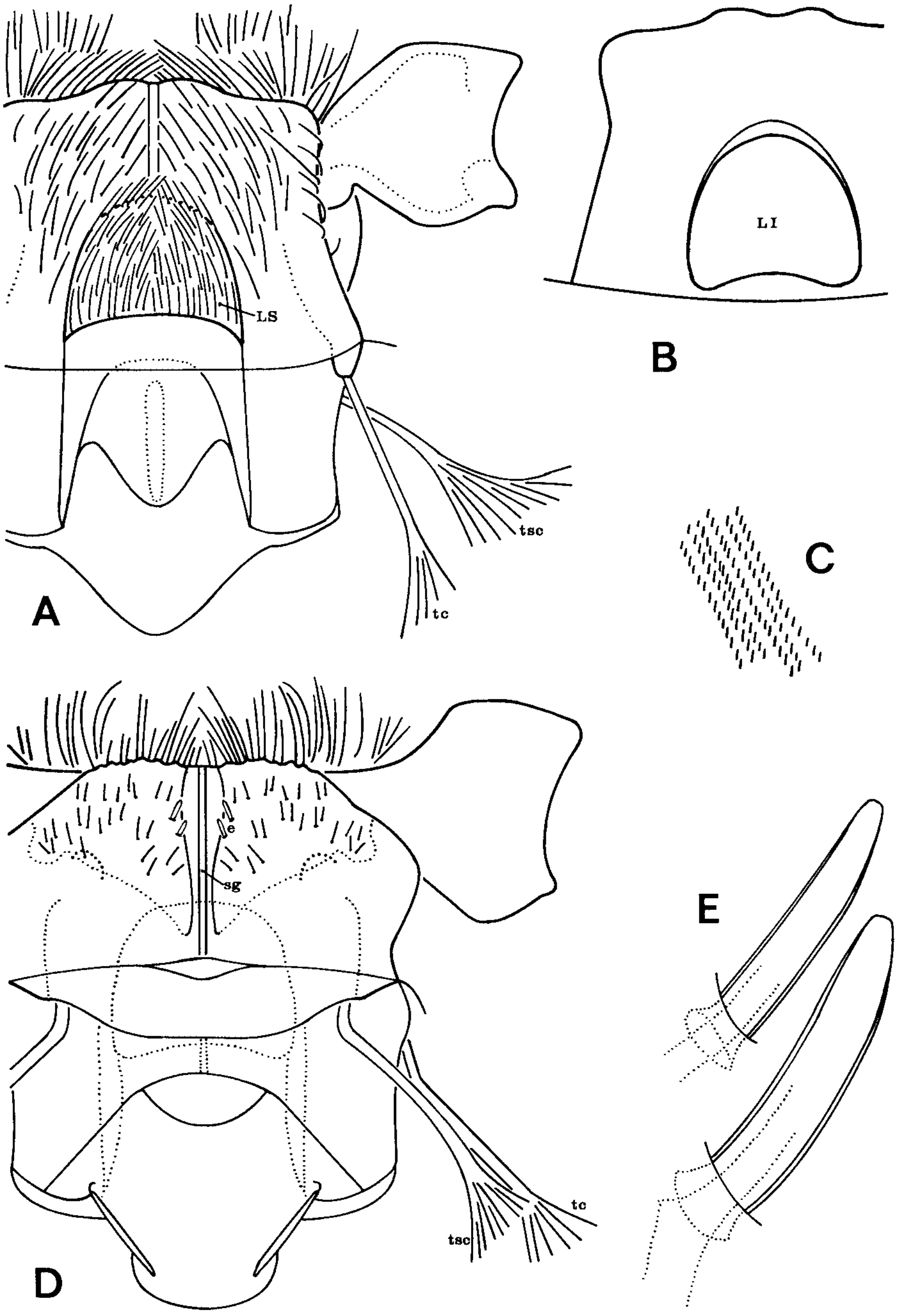

Fig. 6. *Ricinoides karschii* (Hansen & Sørensen), infracapitulum of tritonymph; A, dorsal view; B, dorsal view after removal of the labrum, showing the labium; C, fragment of radula-like surface of labium; D, ventral view; E, laterocoxal setae of the right side; A, B, D, × 55; C, × 368; D, × 687.

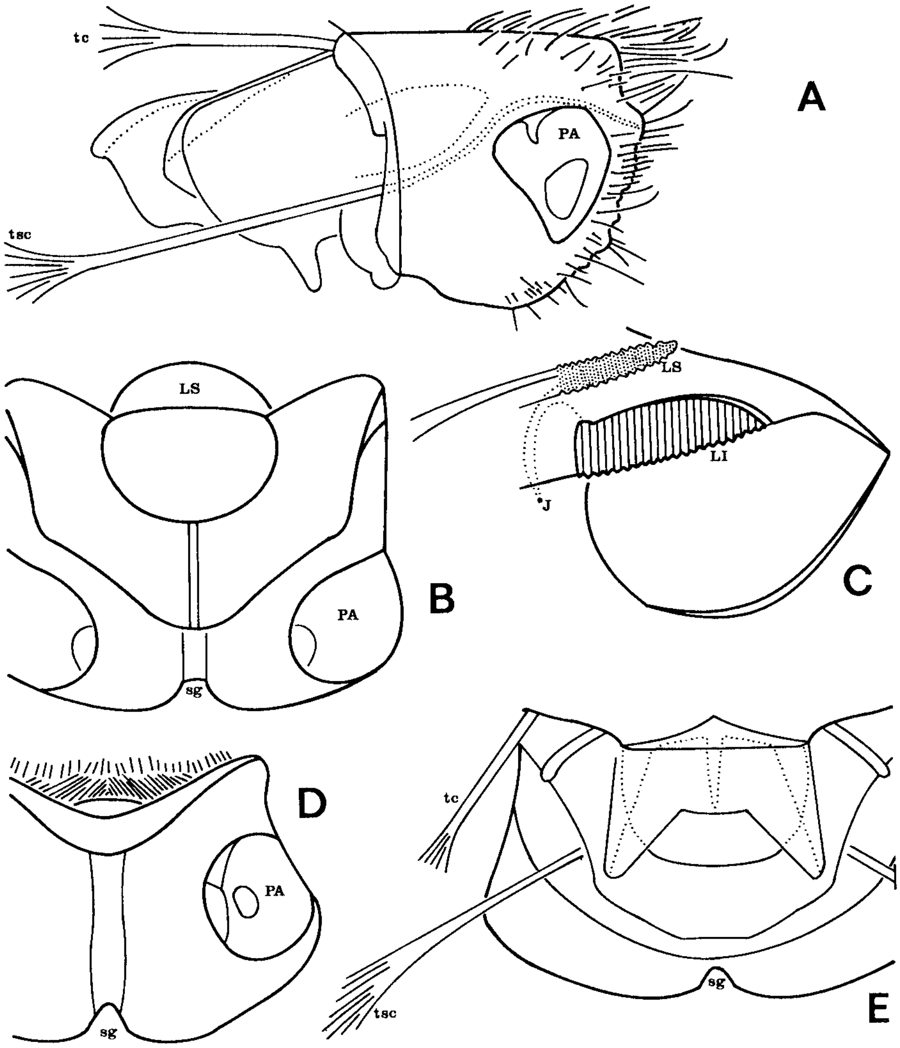

Fig. 7. *Ricinoides karschii* (Hansen & Sørensen), infracapitulum of tritonymph; A, lateral view; B, frontal view (obliquely from above); C, sagittal section through anterior part, viewed from the paraxial side; D, frontal view; E, posterior view; A-E, × 55.

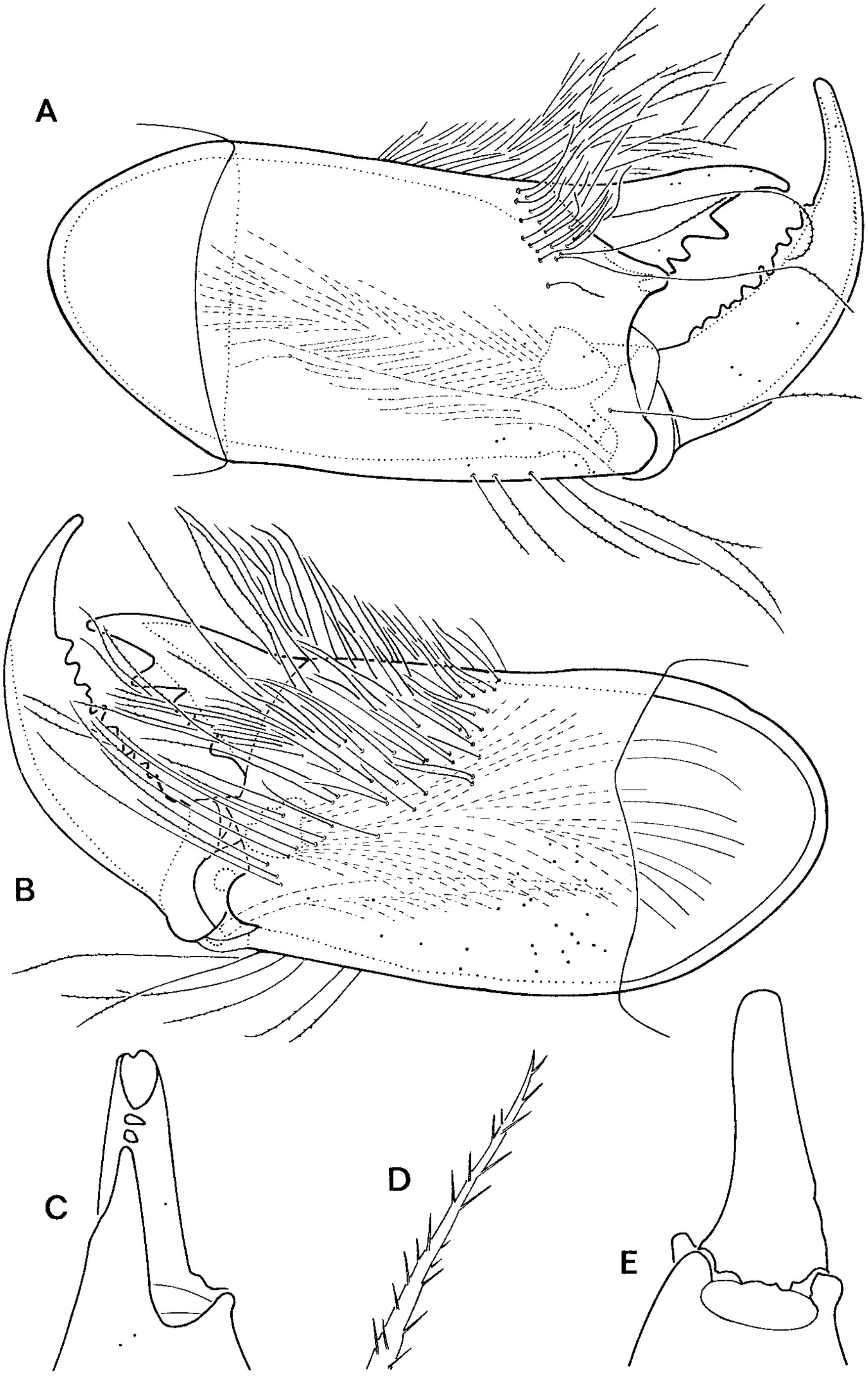

Fig. 8. *Ricinoides karschii* (Hansen & Sørensen), right chelicera of tritonymph; A, dorsal view; B, ventral view; C, lateral (paraxial) view (setae omitted); D, distal part of seta of the ventral surface; E, lateral (antiaxial) view (setae omitted); A-C, E, × 92; D, × 550.

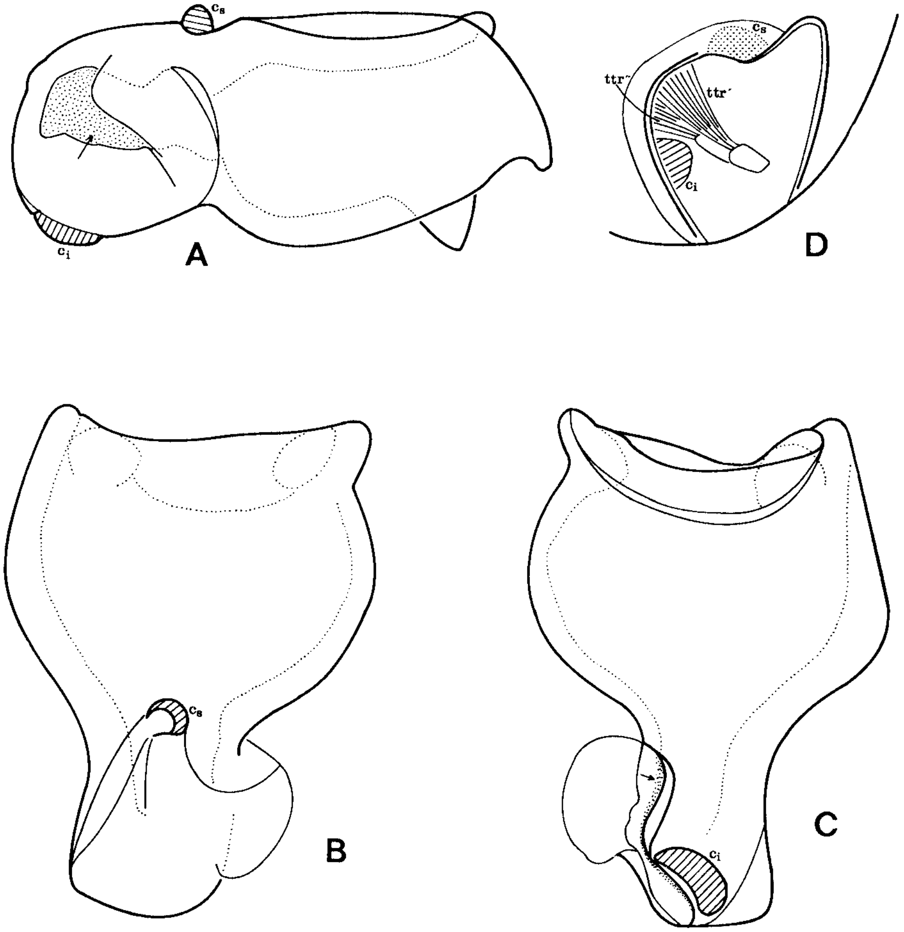

Fig. 9. *Ricinoides karschii* (Hansen & Sørensen), tritonymph; A-C, trochanter of right palp (the arrows in figs. A and C indicate the proximal internal opening); D, acetabulum of right palp; A, lateral (posterior) view; B, dorsal view; C, ventral view; D, latero-frontal view; A-D, × 88.

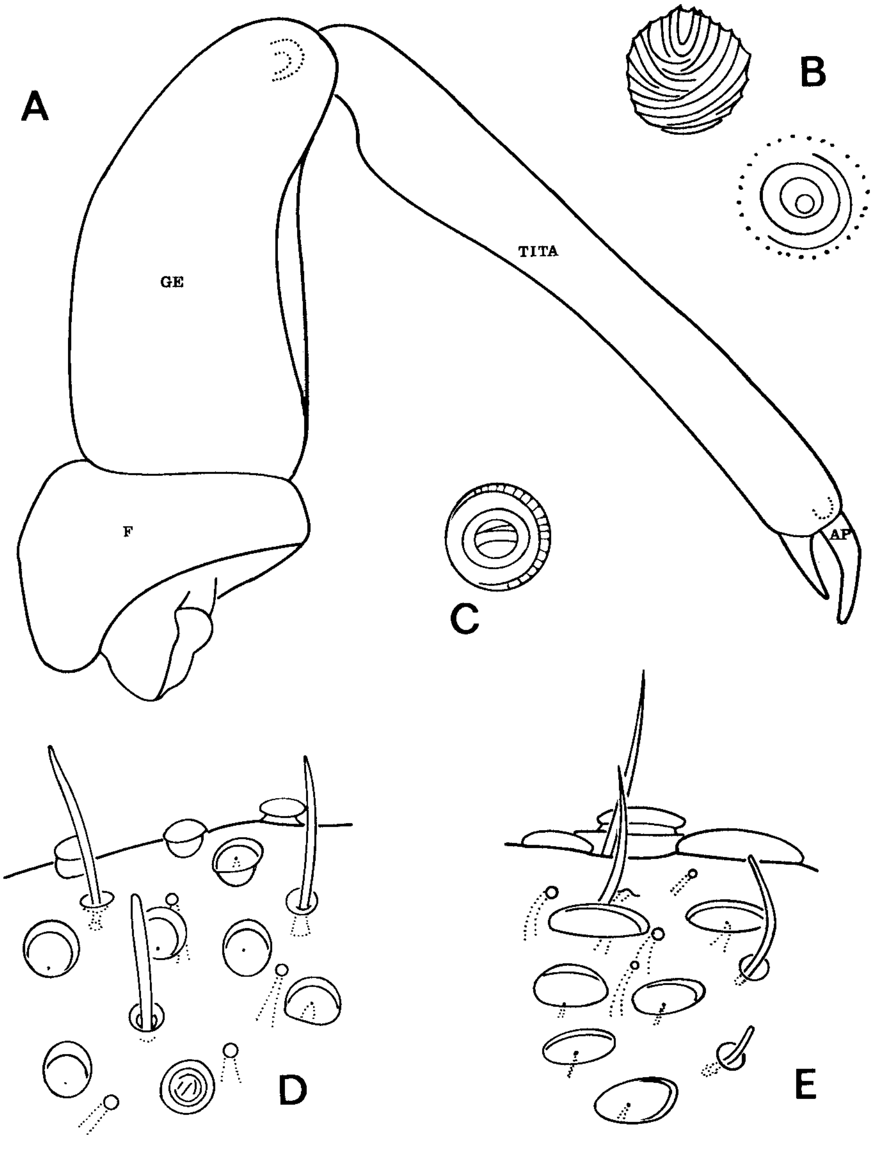

Fig. 10. *Ricinoides karschii* (Hansen & Sørensen), antiaxial face of right palp of female; A, femur, genu, tibiotarsus and apotele; B, "corrugated tubercle" and "saucer-shaped tubercle" of femur; C, "saucer-shaped tubercle" of the base of the tibiotarsus; D, basal part of tibiotarsus with phaneres, tubercles and orifices of cuticular glands; E, median part of tibiotarsus with phaneres, tubercles and orifices of cuticular glands; A, × 55; B, C, × 687; D, E, × 368.

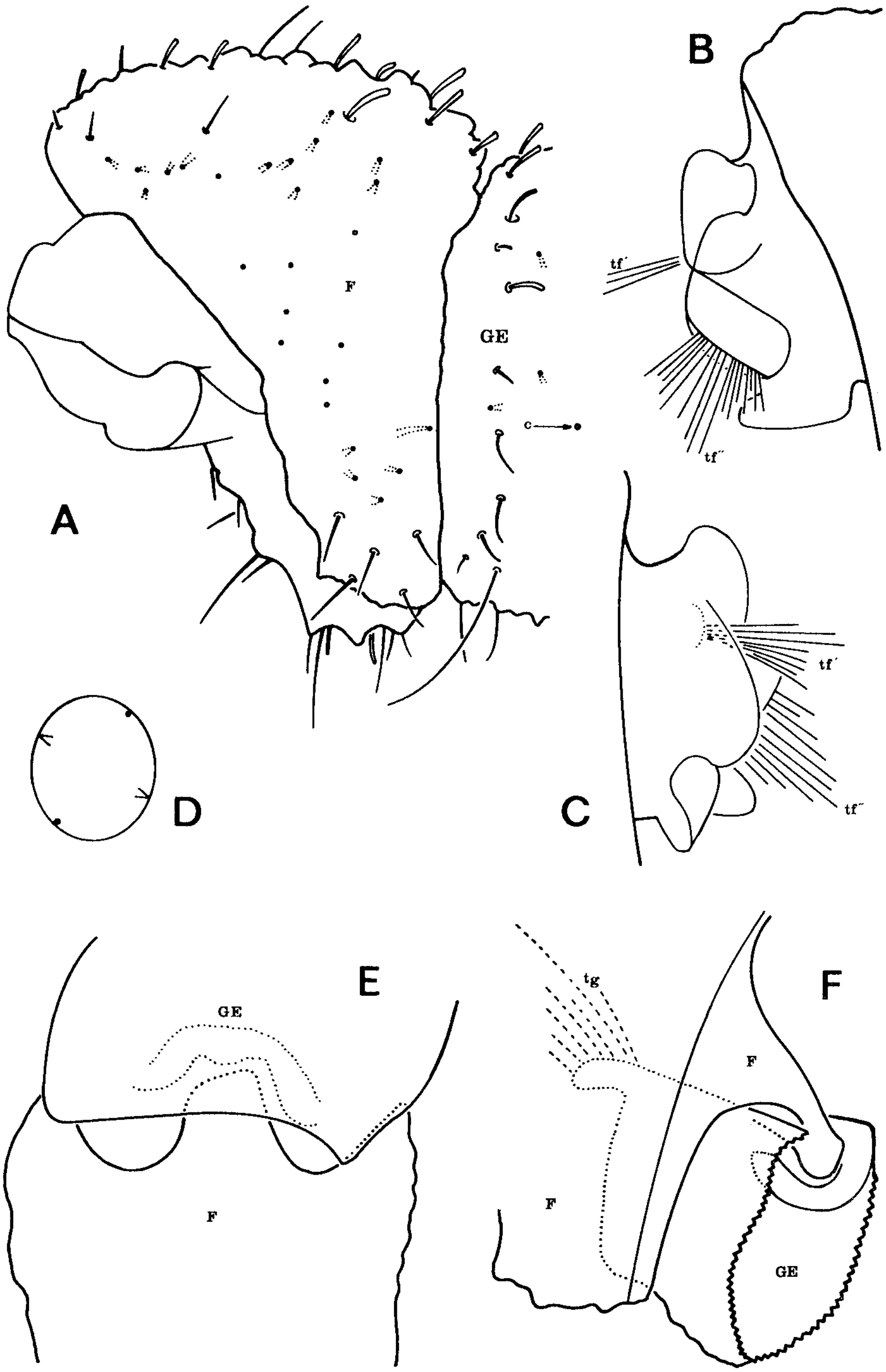

Fig. 11. *Ricinoides karschii* (Hansen & Sørensen), fragments of right palp of female; A, femur and proximal part of genu (patella), lateral (antiaxial) view; B, C, basal part of femur; B, lateral (antiaxial) view; C, lateral (paraxial) view; D, schematic representation of the articulation between trochanter and femur; E, F, distal part of femur and proximal part of genu (patella); E, dorsal view; F, lateral (antiaxial) view; A-C, E, F, × 110.

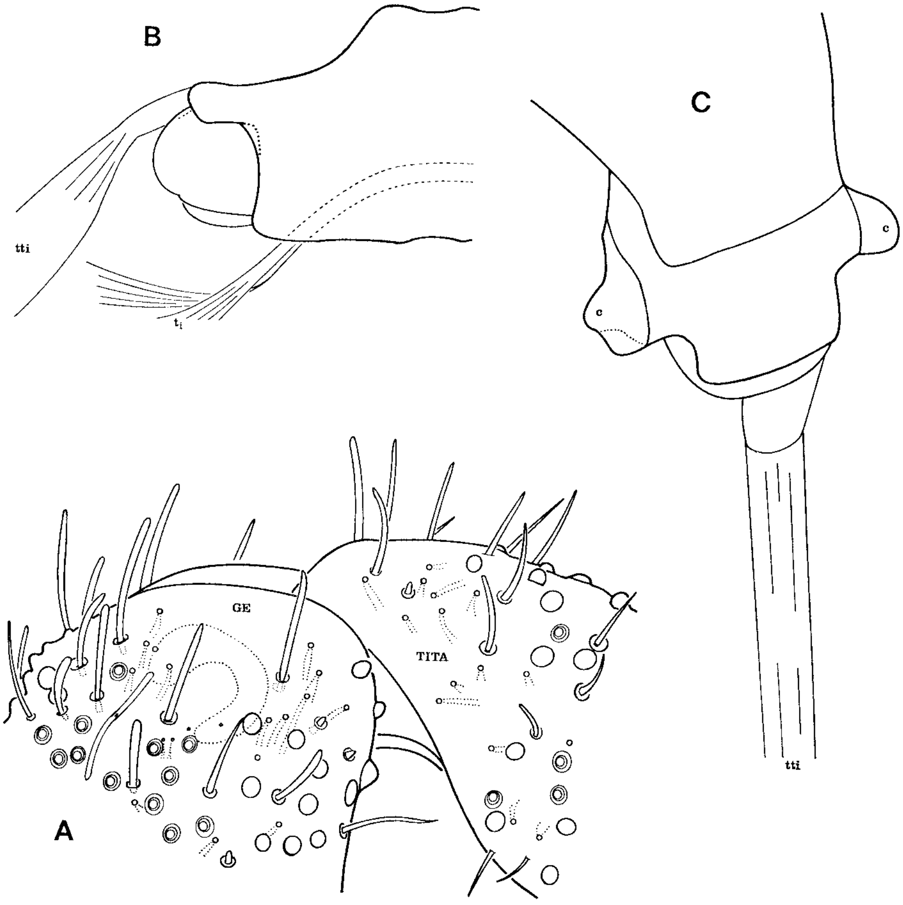

Fig. 12. *Ricinoides karschii* (Hansen & Sørensen), fragments of right palp of female; A, distal part of genu (patella) and proximal part of tibiotarsus, lateral (antiaxial) view; B, C, base of tibiotarsus, separated from genu (patella); B, lateral (antiaxial) view; C, dorsal view; A, C, × 155.

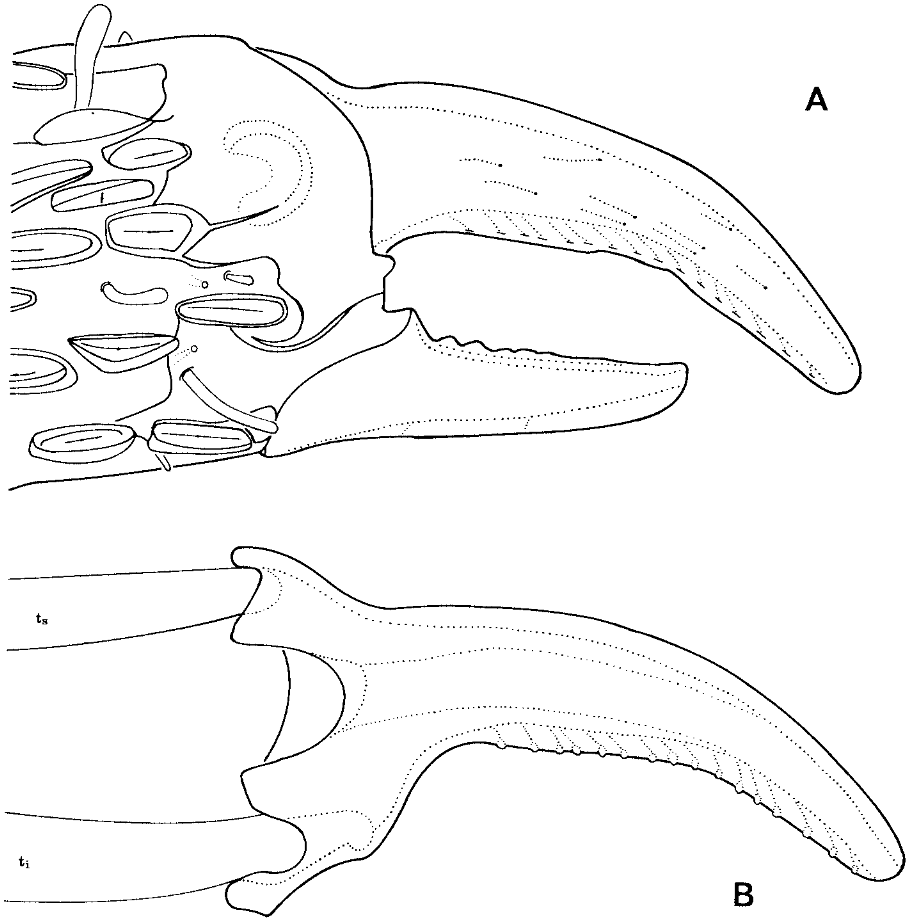

Fig. 13. *Ricinoides karschii* (Hansen & Sørensen), antiaxial face of fragment of right palp of female; A, distal part of tibiotarsus, and apotele; B, apotele (separated from tibiotarsus) with superior tendon t_s and inferior tendon t_i; A, B, × 295.

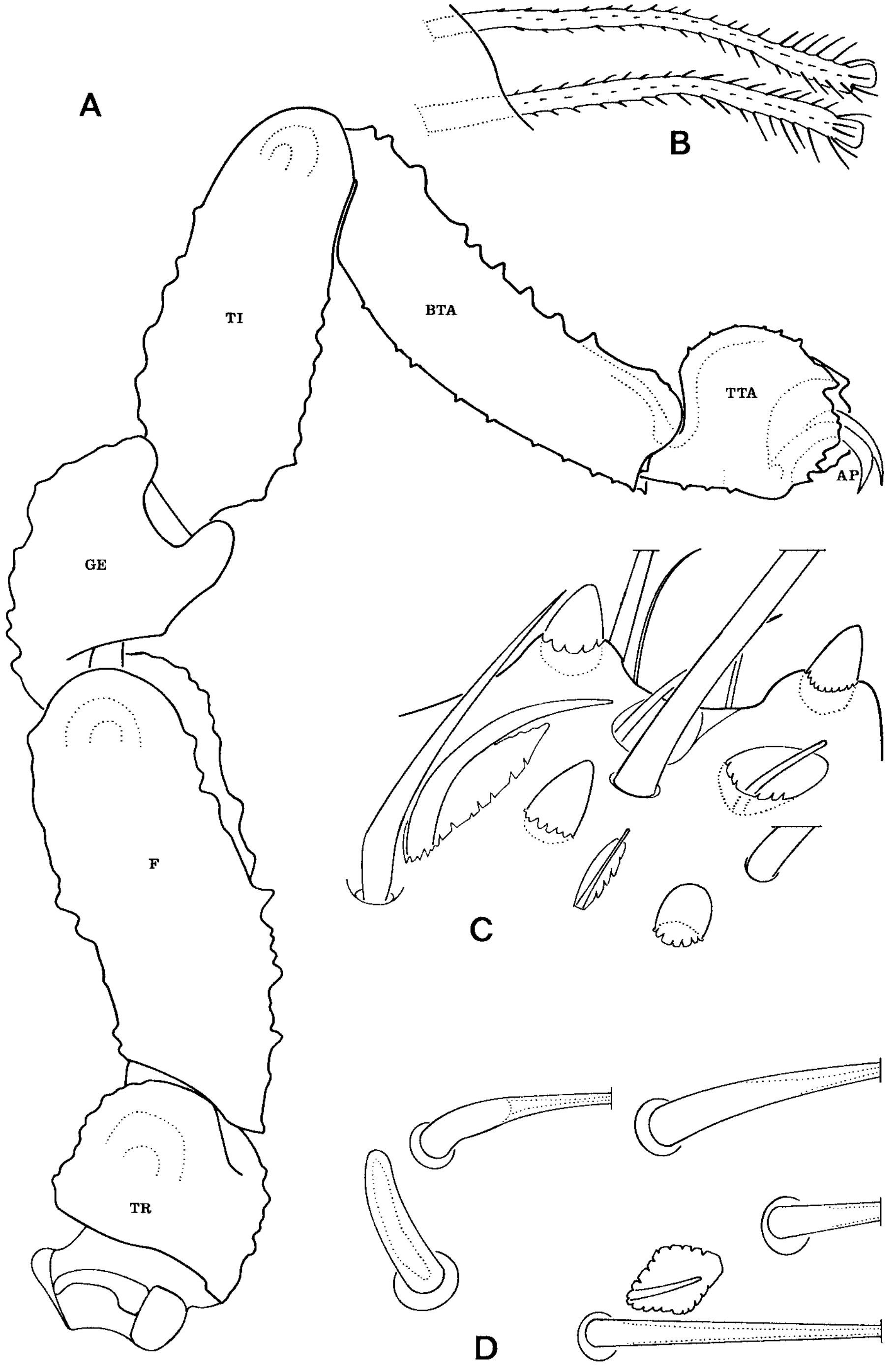

Fig. 14. *Ricinoides karschii* (Hansen & Sørensen), right leg I of female; A, antiaxial face of trochanter, femur, genu (patella), tibia, basitarsus, telotarsus and apotele; B, "tree-like setae" ("famuli") of telotarsus, antiaxial view; C, laterodorsal phaneres of telotarsus, antiaxial view; D, lateral phaneres of telotarsus, antiaxial view; A, × 44; B-D, × 550.

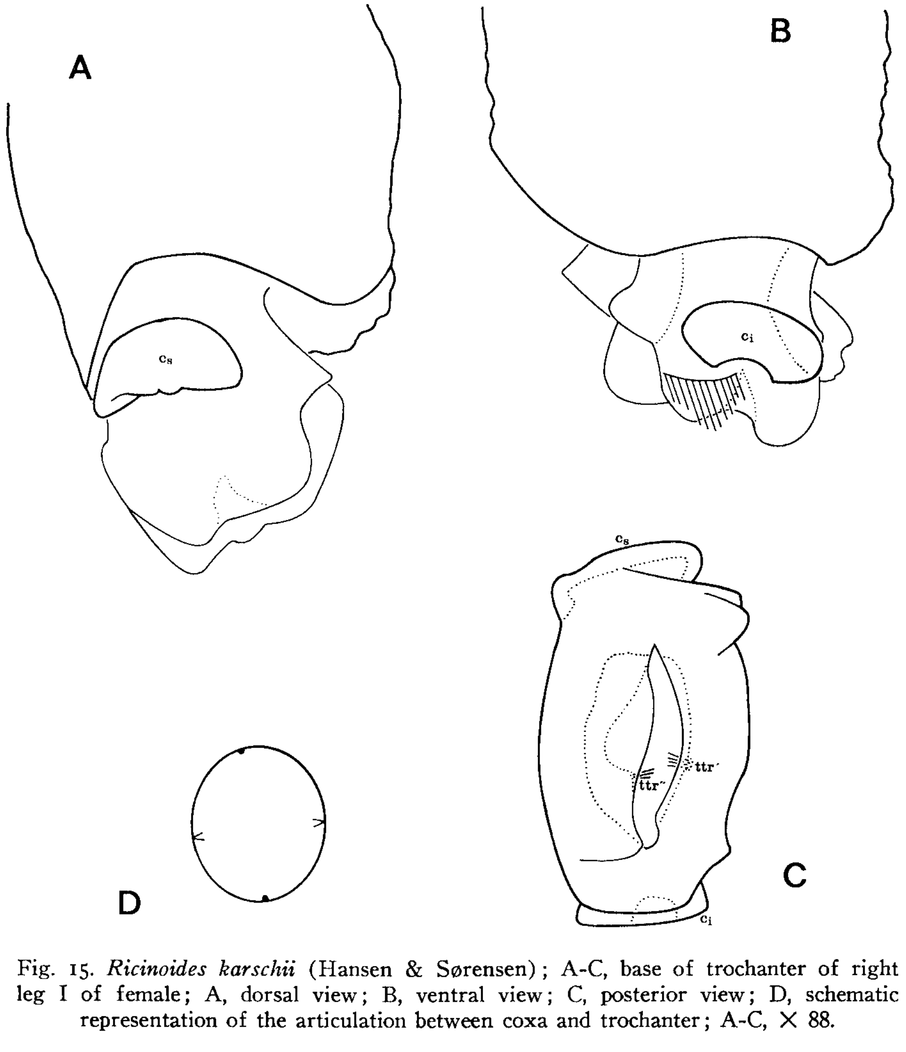

Fig. 15. *Ricinoides karschii* (Hansen & Sørensen); A-C, base of trochanter of right leg I of female; A, dorsal view; B, ventral view; C, posterior view; D, schematic representation of the articulation between coxa and trochanter; A-C, × 88.

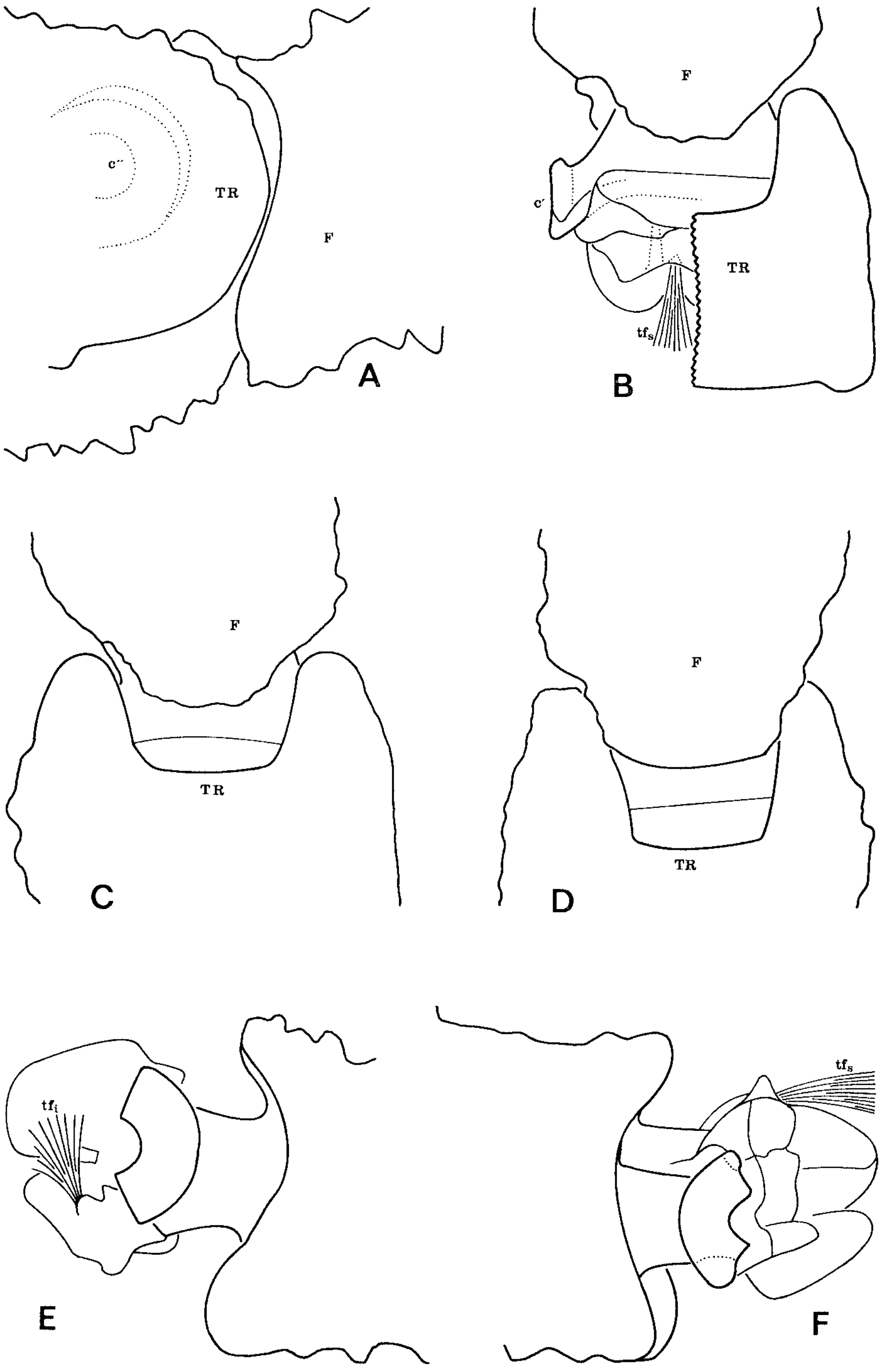

Fig. 16. *Ricinoides karschii* (Hansen & Sørensen), fragments of right leg I of female; A, distal part of trochanter and proximal part of femur, lateral (antiaxial) view; B, proximal part of femur and fragment of distal part of trochanter (paraxial half removed), dorsal view; C, D, articulation trochanter/femur; C, dorsal view; D, ventral view; E, F, base of femur; E, lateral (antiaxial) view; F, lateral (paraxial) view; A, × 92; B-F, × 88.

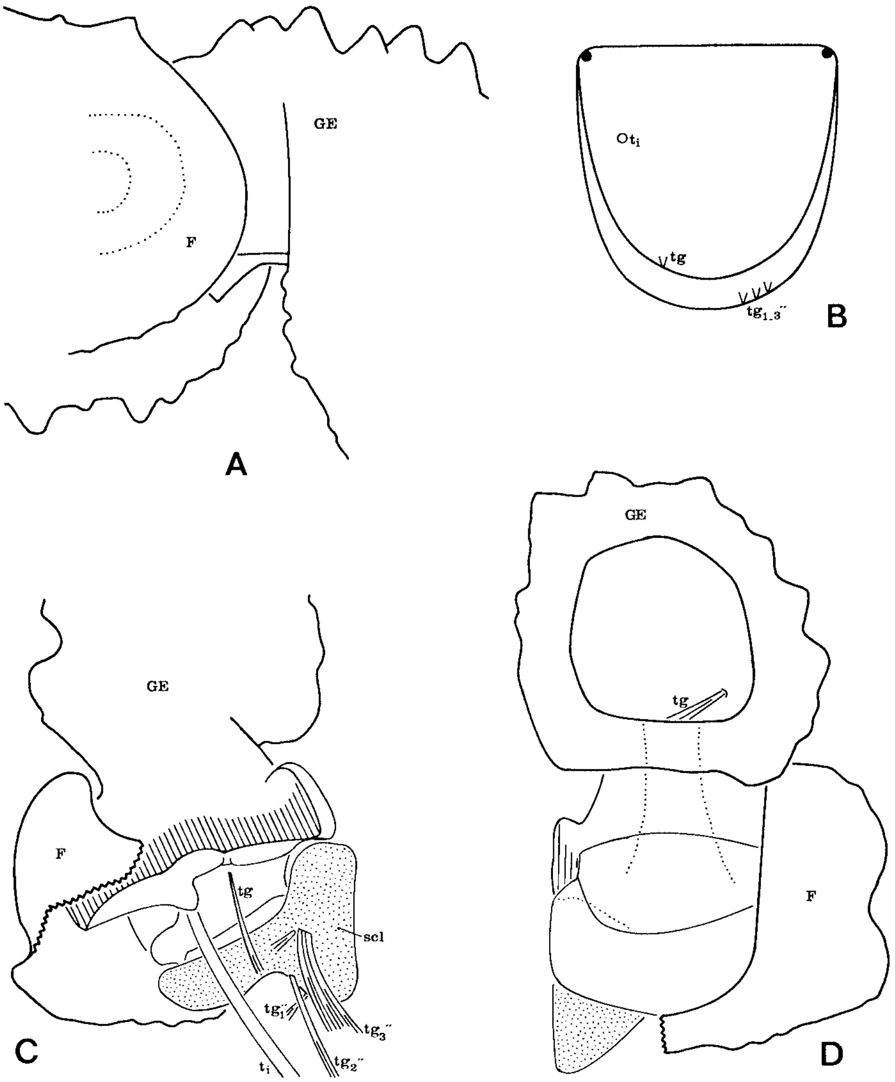

Fig. 17. *Ricinoides karschii* (Hansen & Sørensen), fragment of right leg I of female; A, distal part of femur and proximal part of genu (patella), lateral (antiaxial) view; B, schematic representation of the articulation between femur and genu (patella); C, D, proximal part of genu (patella), and fragment of distal part of femur (antiaxial half removed); C, dorsal view; D, ventral view; A, × 88; C, D, × 92.

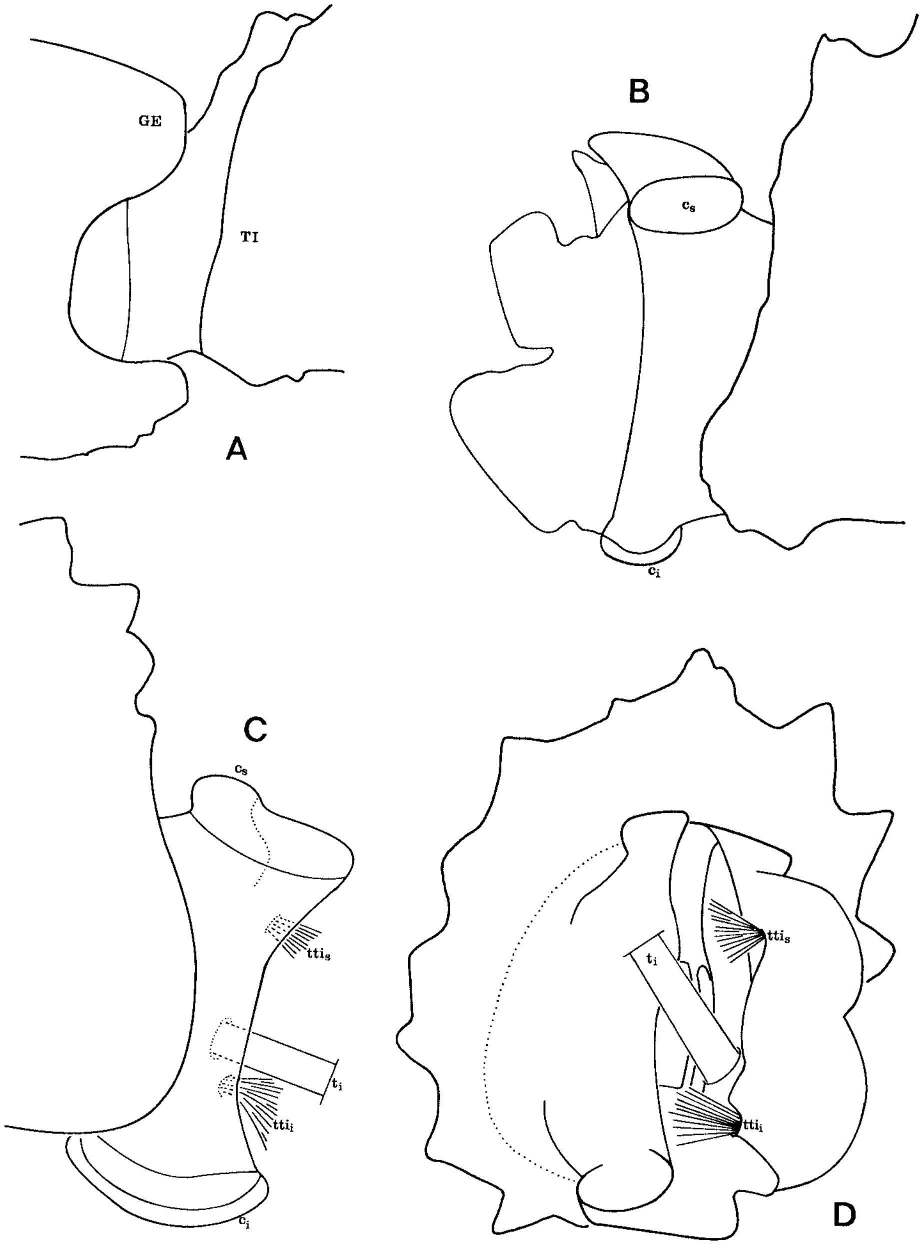

Fig. 18. *Ricinoides karschii* (Hansen & Sørensen), fragments of right leg I of female; A, articulation between genu (patella) and tibia, lateral (antiaxial) view; B-D, base of tibia (separated from genu); B, lateral (antiaxial) view; C, lateral (paraxial) view; D, posterior view; A, × 92; B-D, × 141.

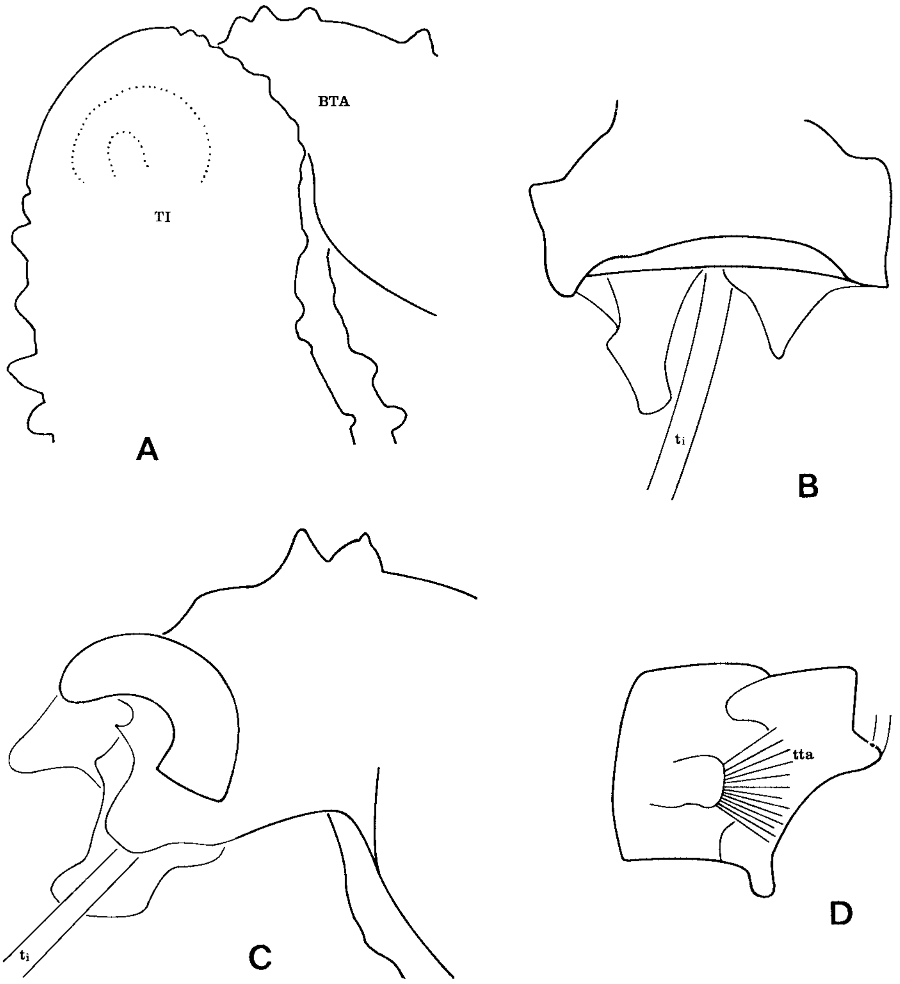

Fig. 19. *Ricinoides karschii* (Hansen & Sørensen), fragments of right leg I of female; A, articulation between tibia and basitarsus, lateral (antiaxial) view; B, C, base of basitarsus, separated from tibia (without basal sclerite); B, dorsal view; C, lateral (antiaxial) view; D, basal sclerite of basitarsus, posterior view; A, × 92; B-D, × 141.

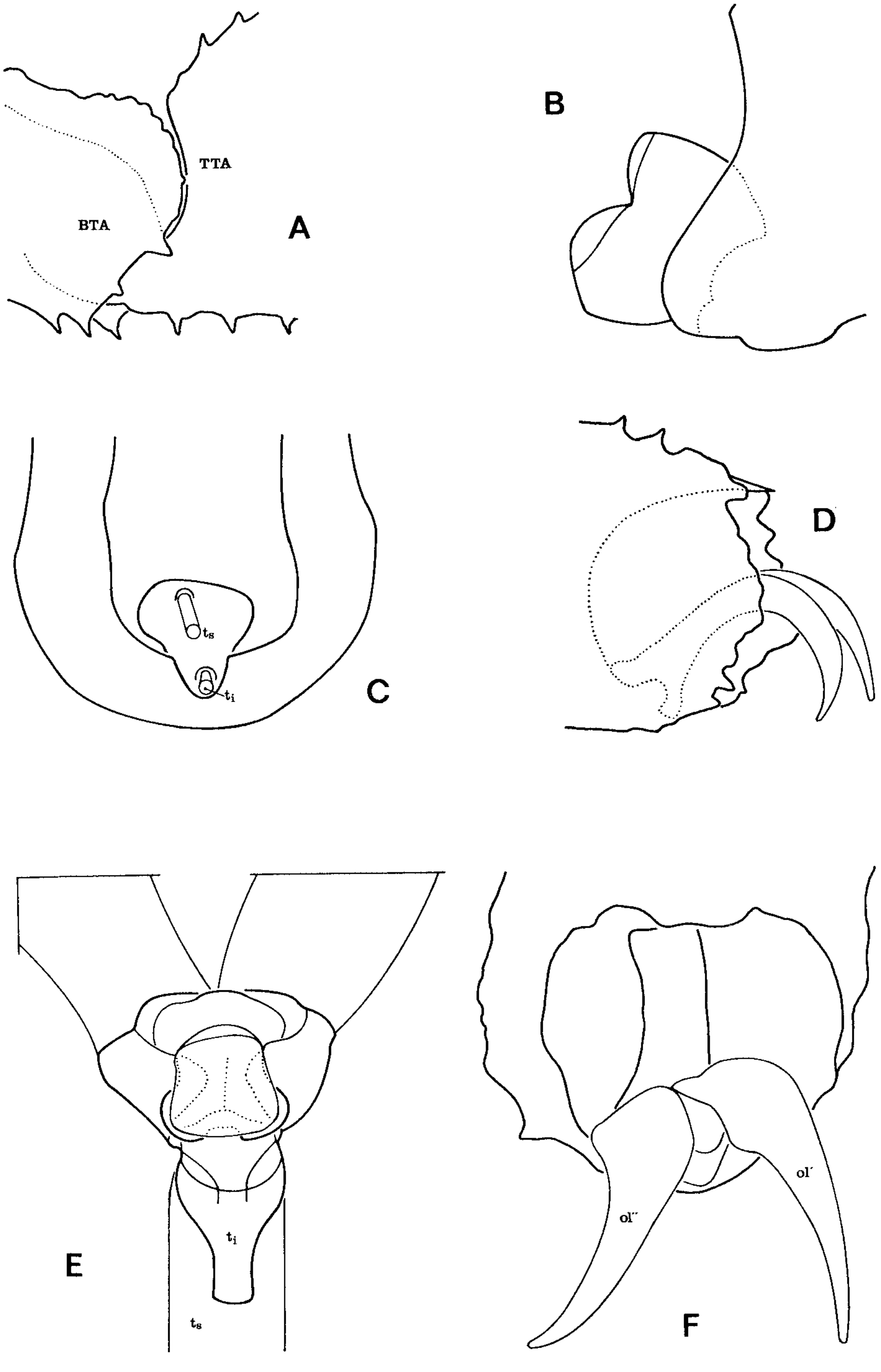

Fig. 20. *Ricinoides karschii* (Hansen & Sørensen), fragments of right leg I of female; A, articulation between basitarsus and telotarsus, lateral (antiaxial) view; B, basal part of telotarsus, lateral (antiaxial) view; C, transverse section through telotarsus, with the two guided tendons, viewed in the direction of the basitarsus; D, distal part of telotarsus, and apotele, lateral (antiaxial) view; E, apotele, separated from telotarsus, ventral view; F, distal part of telotarsus and apotele, frontal view; A, D, × 92; B, C, F, × 141; E, × 295.

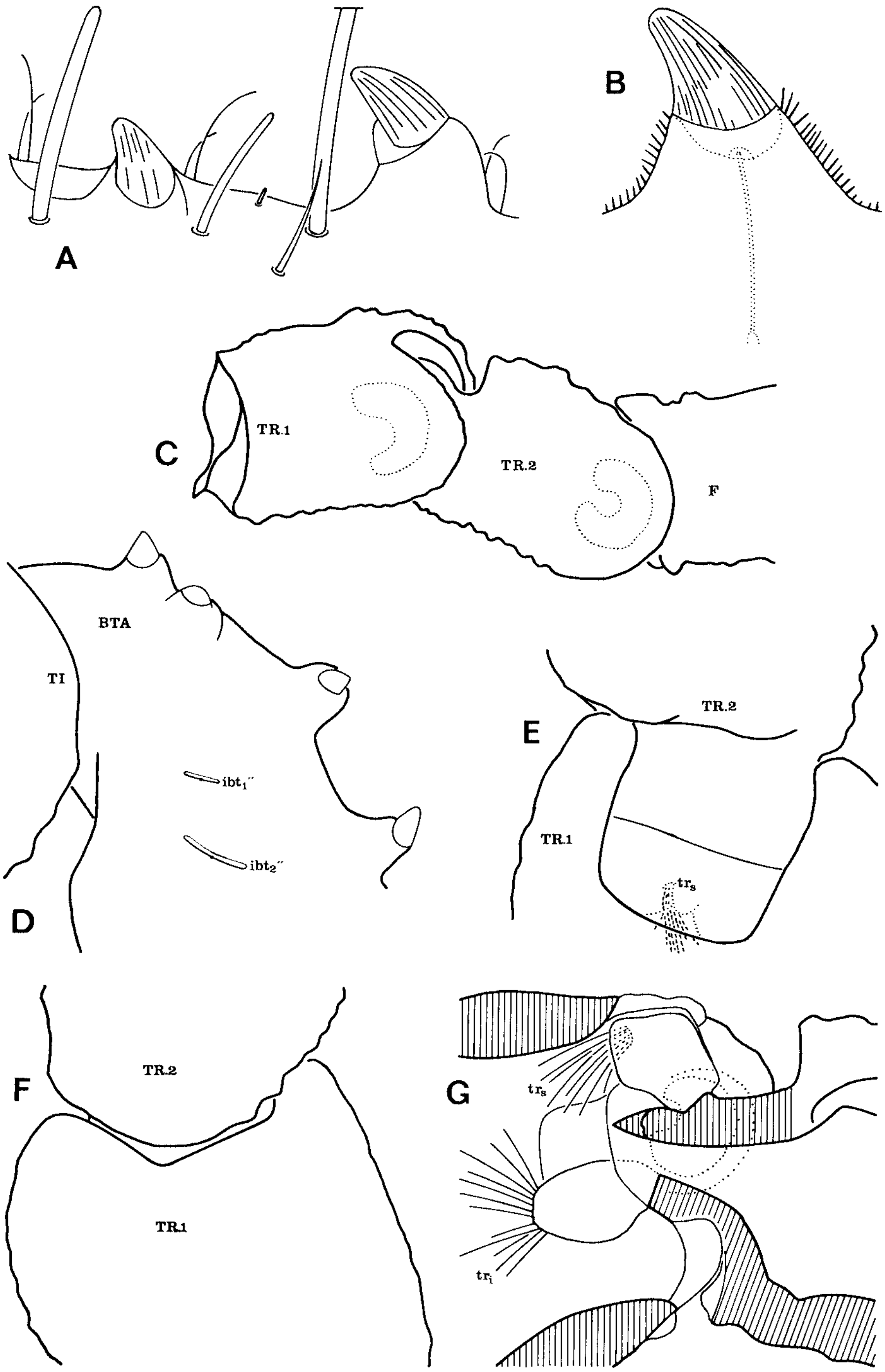

Fig. 21. *Ricinoides karschii* (Hansen & Sørensen), right leg IV of female; A, dorsal phaneres (hollow setae, mucronate tubercles, and coronidia) of the basitarsus, antiaxial view; B, dorsal mucronate tubercle of the basitarsus, antiaxial view; C, trochanter 1, trochanter 2, and base of femur, antiaxial view; D, base of basitarsus with lyrifissures ibt_1'' and ibt_2'', antiaxial view; E, F, articulation trochanter 1/trochanter 2; E, dorsal view; F, ventral view; G, sagittal section through the articulation trochanter 1/trochanter 2 (the paraxial "half" is viewed from the inside); A, × 295; B, × 550; C, × 44; D, × 141; E-G, × 88.

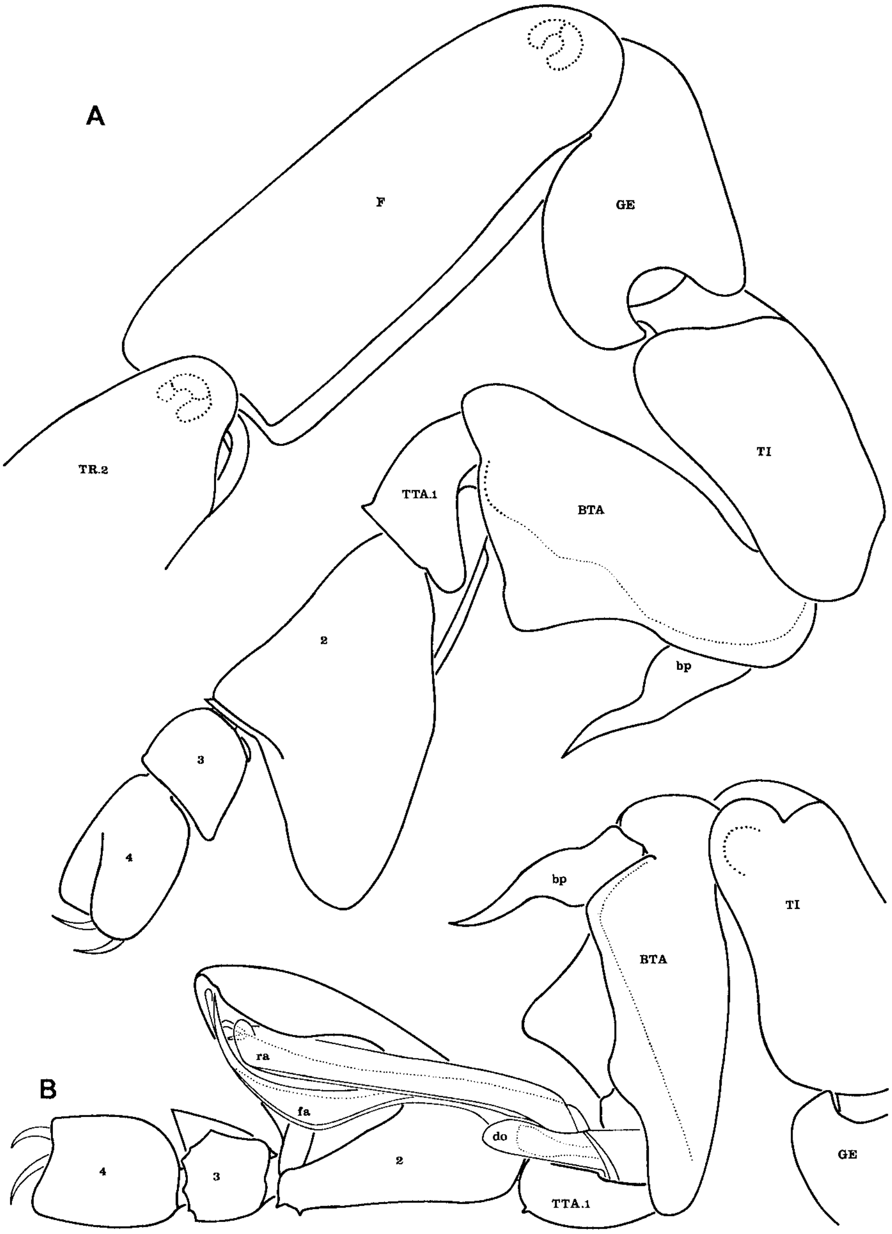

Fig. 22. *Heteroricinoides magnus* (Ewing), part of right leg III (gonopod) of male; A, approximately lateral (posterior) view; B, approximately lateral (anterior) view; A, B, × 37.

Fig. 23. *Cryptocellus foedus* Westwood, male; A, right leg III (gonopod), approximately lateral (anterior) view; B, part of right leg I (distal part of trochanter, femur, genu, tibia, proximal part of basitarsus), approximately lateral (posterior) view; C, coxa, trochanter 1 and part of trochanter 2 of right leg IV, approximately lateral (posterior) view; A-C, × 37.

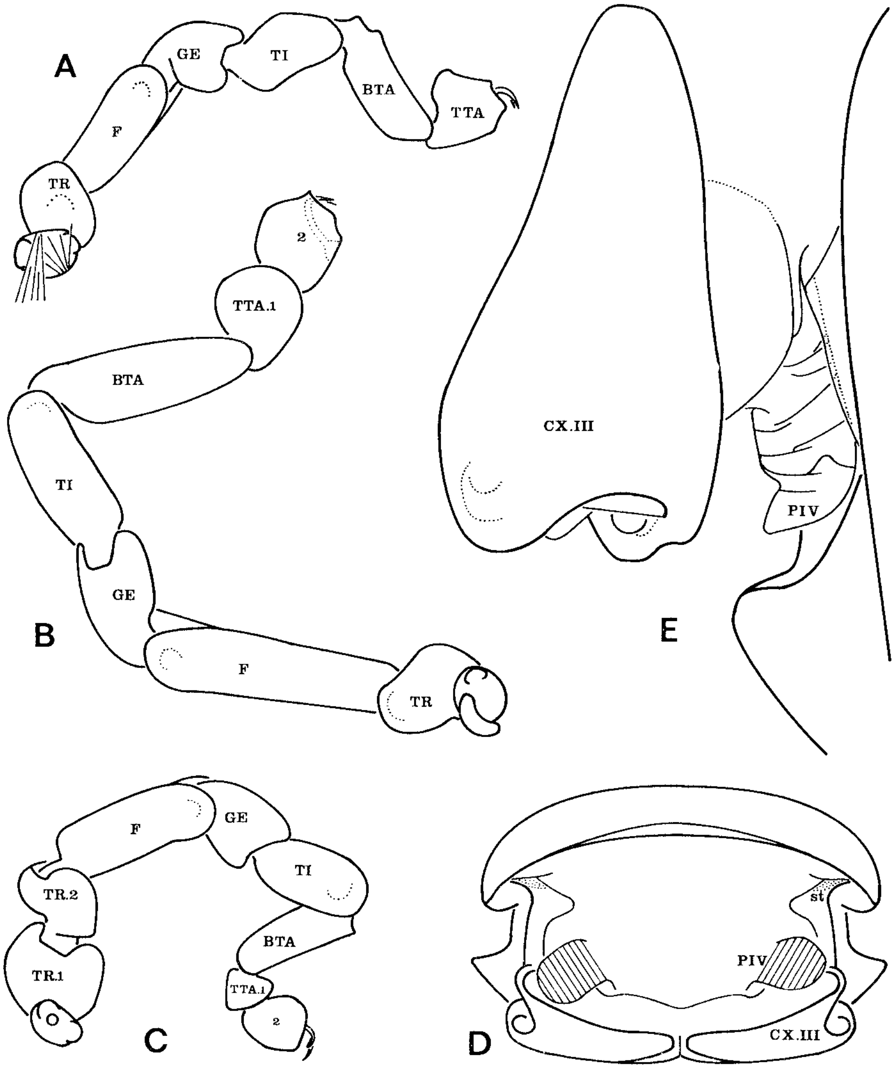

Fig. 24. *Ricinoides karschii* (Hansen & Sørensen), larva; A, right leg I, lateral (posterior) view; B, right leg II, lateral (posterior) view; C, right leg III, lateral (posterior) view; D, posterior view of prosoma with vestiges of leg IV (hatched parts); E, ventral view of posterior prosomatic region (with coxa III and vestige of leg IV), and anterior region of opisthosoma (right side); A-D, × 44; E, × 141.

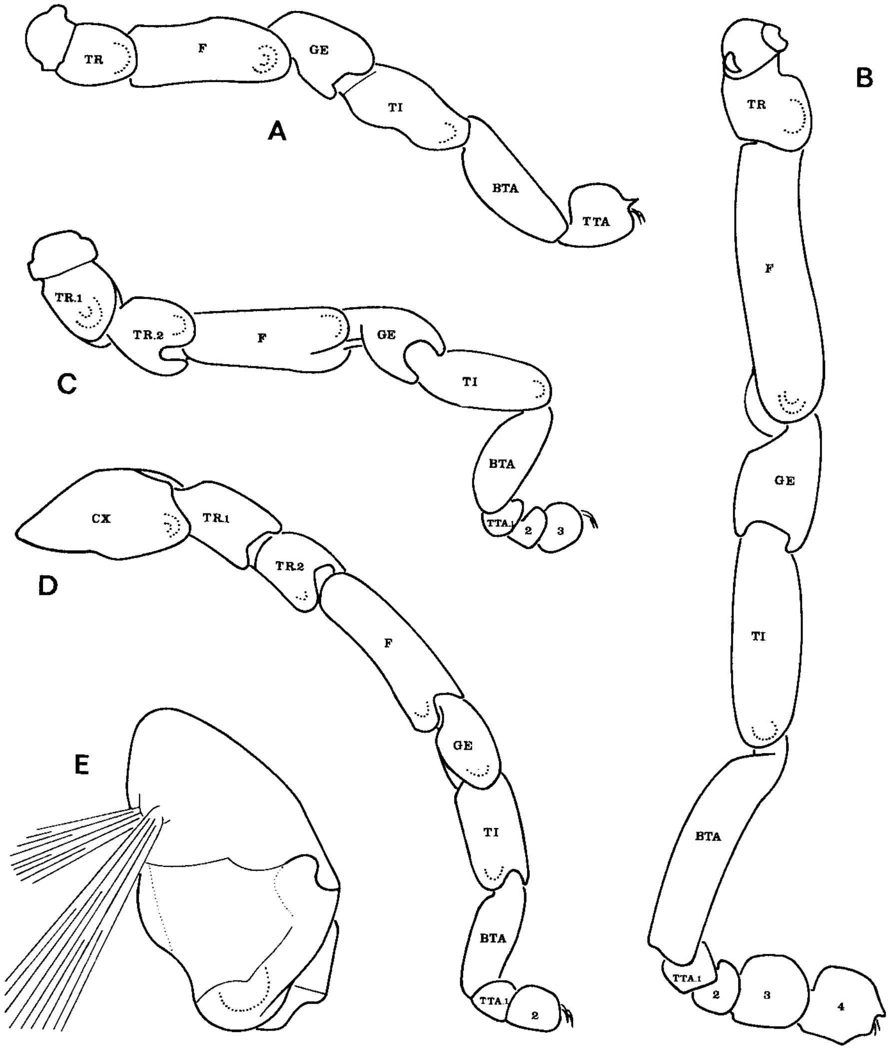

Fig. 25. *Ricinoides karschii* (Hansen & Sørensen), protonymph; A-D, right legs in lateral (posterior) view; A, leg I; B, leg II; C, leg III; D, leg IV (including the movable coxa); E, dorsal view of right coxa IV (separated from the prosoma); A-D, × 37; E, ×73.

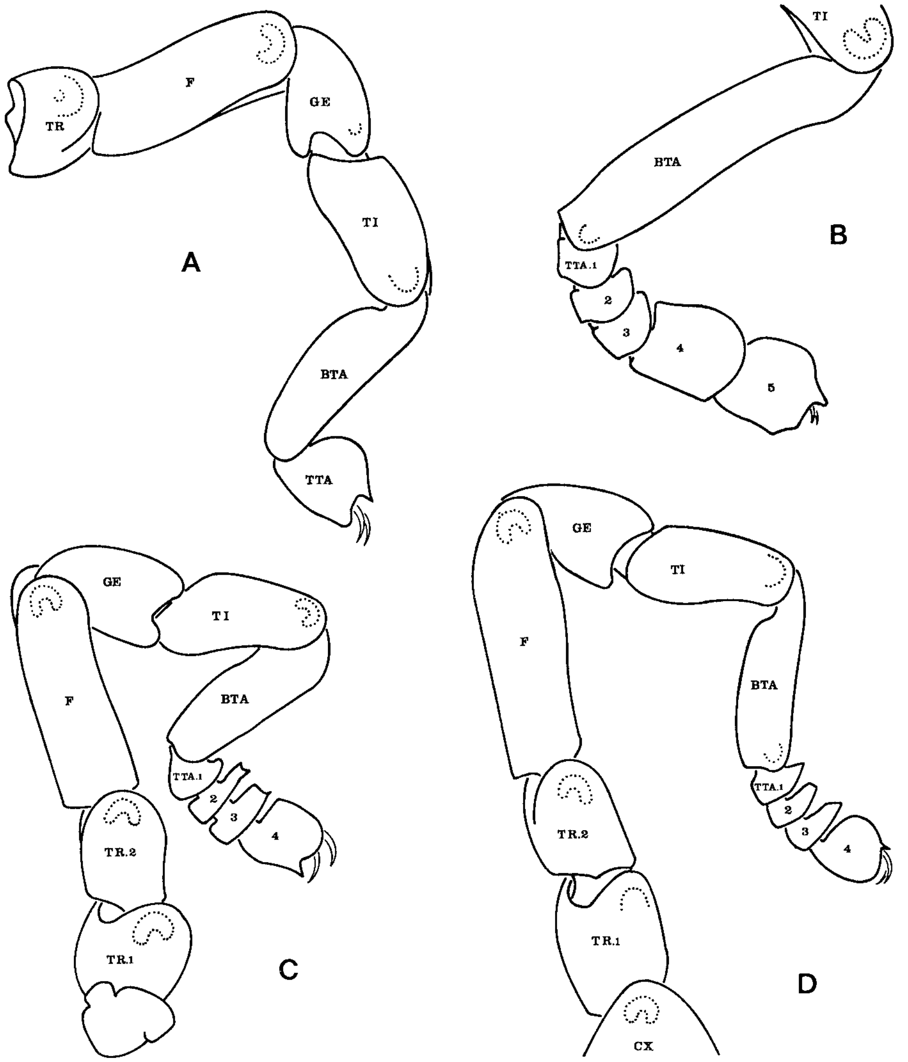

Fig. 26. *Ricinoides karschii* (Hansen & Sørensen), deutonymph; A-D, right legs in approximately lateral (posterior) view; A, leg I; B, terminal part of leg II; C, leg III; D, leg IV; A-D, × 37.

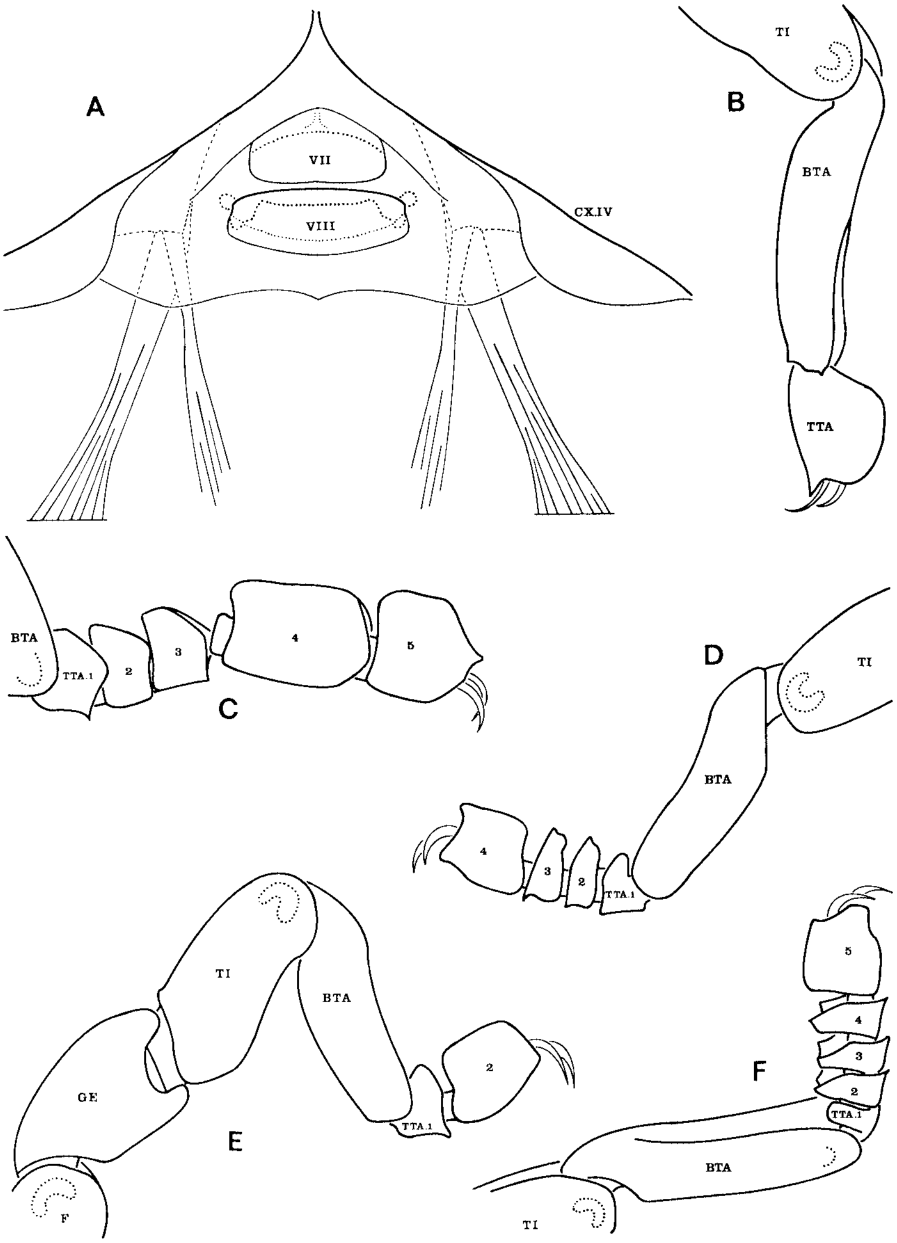

Fig. 27. *Ricinoides karschii* (Hansen & Sørensen), female tritonymph; A, ventral view of genital region (and posterior border of coxae IV); B-D, legs in approximately lateral (posterior) view; B, terminal part of right leg I; C, terminal part of right leg II (joint between telotarsi 3 and 4 dislocated); D, terminal part of left leg III; E, terminal part of abnormal right leg III (probably a case of regeneration; the corresponding normal left leg is represented in fig. D); F, terminal part of right leg IV; A, × 73; B-F, × 37.

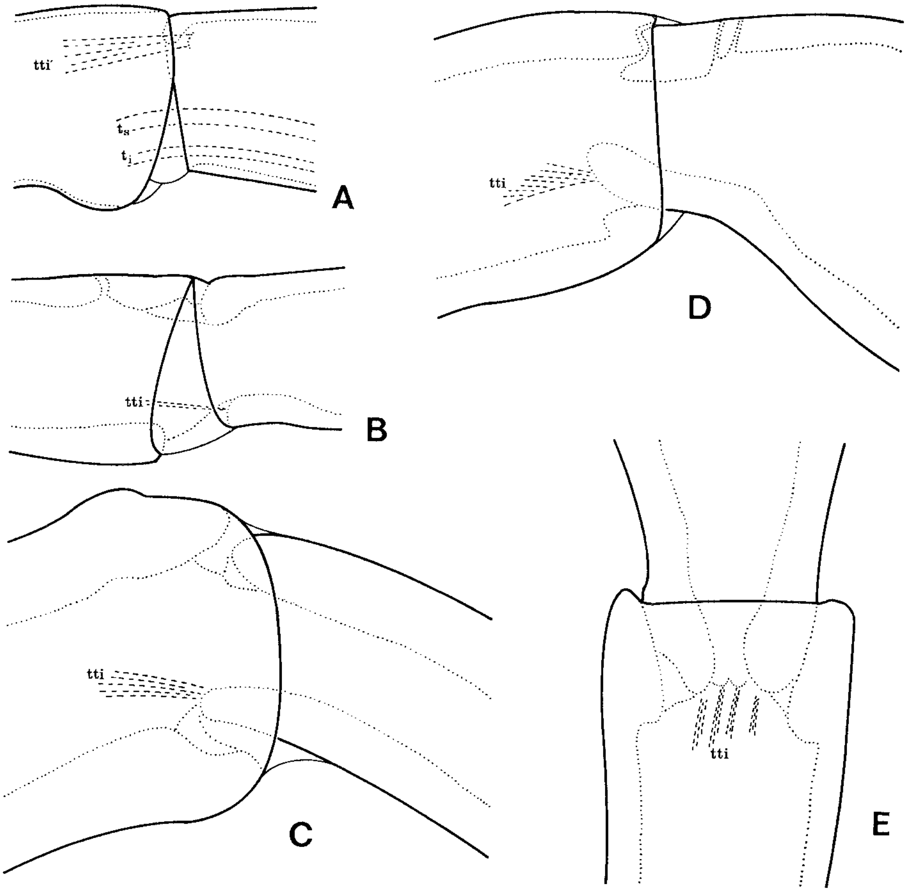

Fig. 28. The genu-tibia articulation of the female right palp in Anactinotrichida; A-D, lateral (antiaxial) view; E, dorsal view; A, *Opilioacarus platensis* Silvestri; B, *Glyptholaspis confusa* (Foà); C, *Ornithodoros savignyi* (Audouin); D, E, *Holothyrus coccinella* Gervais; A, C, × 295; B, × 550; D, E, × 186.

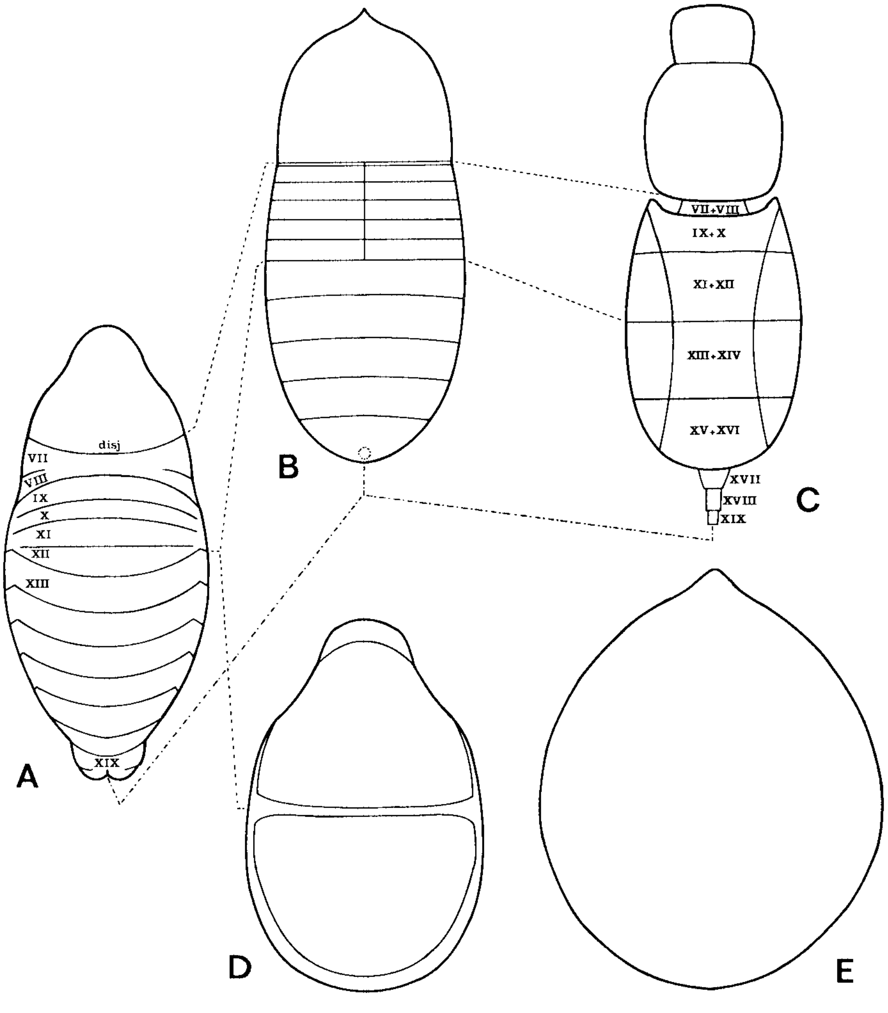

Fig. 29. Schematic representation of soma, tagmosis, segmentation and constitution of the body in the Cryptognomae; A, Opilioacarida (Anactinotrichida); B, Architarbi; C, Ricinulei; D, Gamasida (part) (Anactinotrichida); E, Holothyrida, Gamasida (part) (Anactinotrichida); the figures are not drawn to scale; corresponding parts are connected by dotted lines.

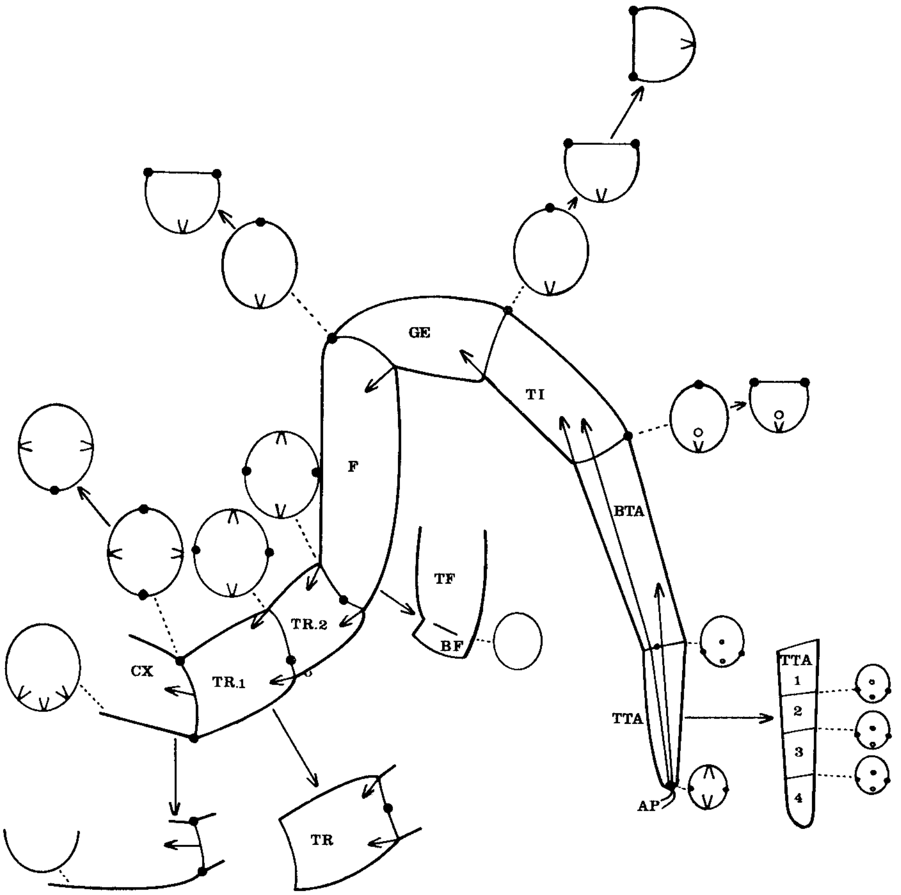

Fig. 30. Model of the evolution of leg III in Cryptognomae. The ancestral leg III is supposed to be composed of: free coxa, trochanter 1, trochanter 2, femur, genu (patella), tibia, basitarsus, telotarsus and apotele. In the figure of the entire leg, articulation-points are represented by dots, tendons by arrows. The model demonstrates the evolution of a fixed coxa, the suppression of trochanter 2, the evolution of a basifemur, and the evolution of four telotarsi. The model demonstrates also the evolution of the separate joints. The schematic sections of the ancestral joints are connected, by dotted lines, with the joints in question (in the figure of the entire leg). The direction of the evolution is indicated by an arrow. In the schematic sections an articulation point is represented by a dot, a tendon by a v-shaped symbol. The sections demonstrate the evolution of a rocking joint between coxa and trochanter, the evolution of hinge joints with flattened dorsal surface and two main articulation points, and the evolution of torsion in the genu/tibia articulation.

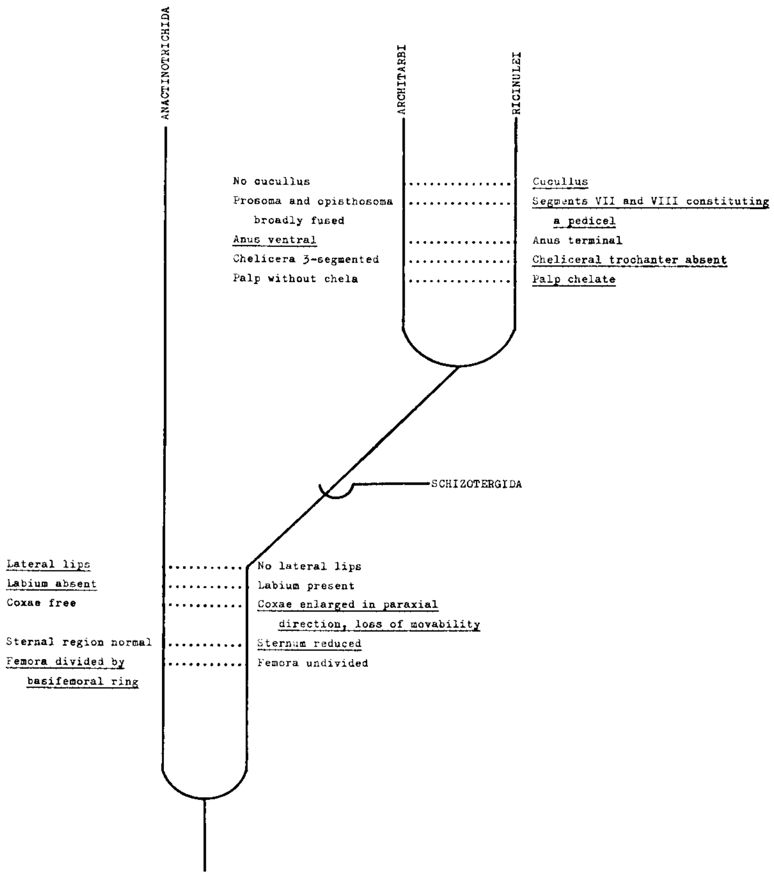

Fig. 31. Cladogram of the main Cryptognomic groups. Derived character states are underlined. Pairs of character states are connected by dotted lines.