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NOTES ON THE COMPARATIVE MORPHOLOGY OF TICKS (ANACTINOTRICHIDA: IXODIDA)

by

L. VAN DER HAMMEN

Rijksmuseum van Natuurlijke Historie, Leiden

With 23 text-figures

Abstract

A study is made of the comparative morphology of Ticks, based on the principles and methods set down in the author's previous studies in Mites and other Chelicerates, and in his Glossary of Acarological Terminology. Special attention is paid to the morphology of gnathosoma and appendages.

Introduction

Ticks or Ixodida constitute a separate order of the subclass Anactinotrichida, now classified by me with the Cryptognomae, a Chelicerate class (Van der Hammen, 1972, 1977a, 1979). They present several typical Anactinotrichid characters, such as the presence of pedal coxae and a sternum, the absence of a sejugal furrow or interval, the absence of actinopilin, the absence of trichobothria, the subdivision of femora I-IV (by a basifemoral ring associated with lyrifissures) into basi- and telofemur, the subdivision of tarsi II-IV (by a basitarsal ring, associated with lyrifissures) into basi- and telotarsus, and the absence of a podocephalic canal.

Ticks are characterized by their relatively large size, the specialized shape of the lateral lips (presenting recurved teeth), the presence of lateral teeth on the movable jaw of the chelicerae, the presence of Haller's organ (a sensory area) on tarsus I, and the presence of lateral stigmata without sinuous peritreme.

Ticks are, with few exceptions, parasitic on Vertebrates (mainly on Mammals, Birds and Reptiles). The total number of described species was recently estimated at 800 (Krantz, 1978).

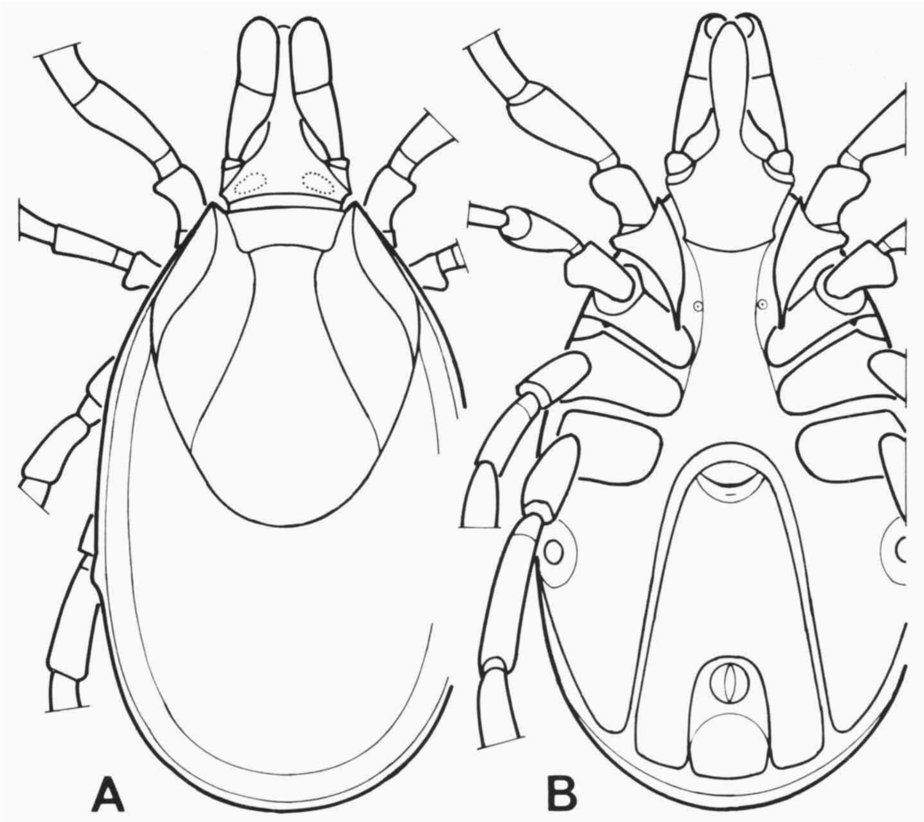

Fig. 1. *Ixodes ricinus* (Linnaeus), adult female; A, dorsal view; B, ventral view (slightly schematized); A, B, × 32.

According to Camicas & Morel (1977) the order Ixodida is subdivided into two suborders: Ixodina and Argasina. The suborder Ixodina includes two superfamilies: Ixodoidea (with the families Ixodidae and Amblyommidae) and Nuttallielloidea (with the family Nuttalliellidae, based on one incompletely known species). The suborder Argasina includes the superfamily Argasoidea (with the single family Argasidae).

Ixodina (hard ticks) are generally characterized by the presence of a dorsal scutum, whilst the gnathosoma is visible from above; in nymphs and adults a pair of stigmata is present, posteriorly of coxa IV.

Argasina (soft ticks) are characterized by the absence of a dorsal scutum (the cuticle is leathery or wrinkled), whilst in nymphs and adults the gnathosoma is not visible from above; the pair of stigmata is situated, in nymphs and adults, near coxa III.

As far as known, the Ixodid postembryonic development is characterized

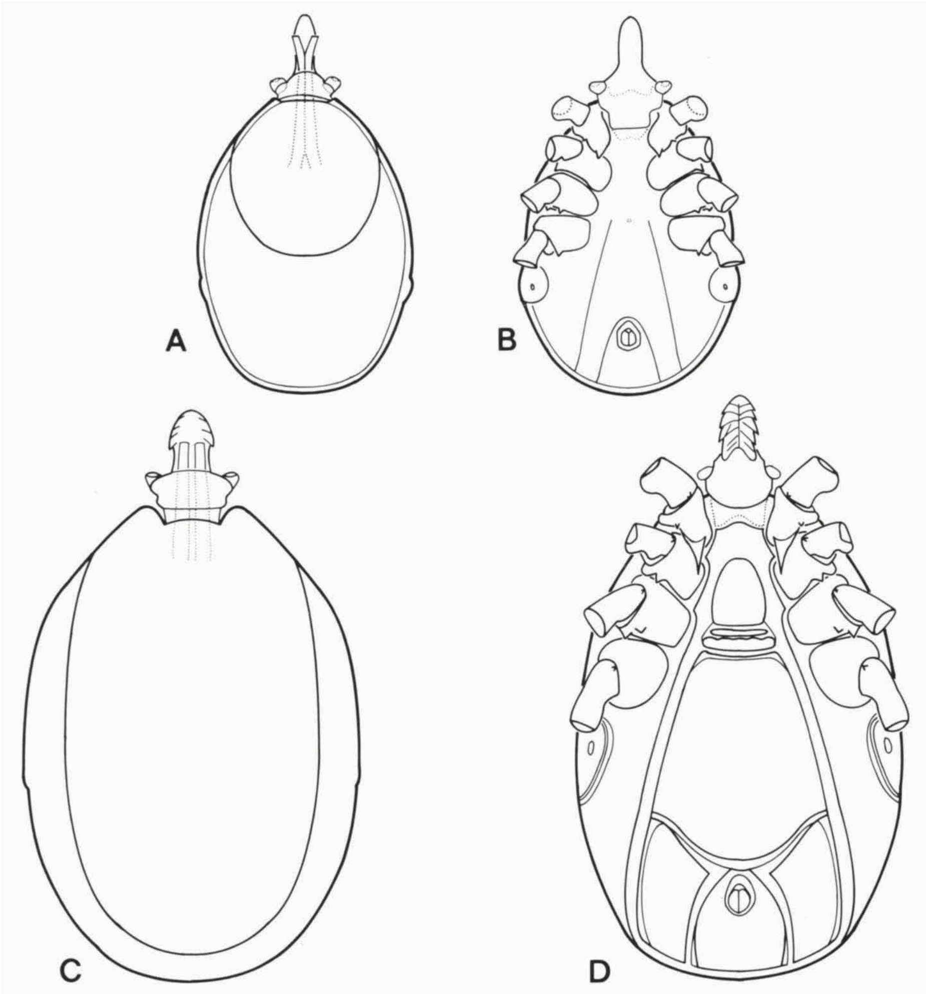

Fig. 2. *Ixodes ricinus* (Linnaeus); A, B, nymph; A, dorsal view; B, ventral view; C, D, adult male; C, dorsal view; D, ventral view (slightly schematized); A–D, × 32.

by the presence of three stases: larva, nymph and adult. In Argasidae the nymph can undergo growing- or repetition-moults (the subsequent nymphal forms constitute isophena of the nymph; they do not represent different stases).

Larvae (fig. 3) are characterized by the presence of three pairs of legs (leg IV being absent). Nymphs (fig. 2A, B) are characterized by the absence of the genital opening. In Ixodoidea the male (fig. 2C, D) is characterized by the presence of a large scutum, occupying the entire dorsal surface of the idiosoma; in the Ixodoid female (fig. 1) the scutum is restricted to the anterior part.

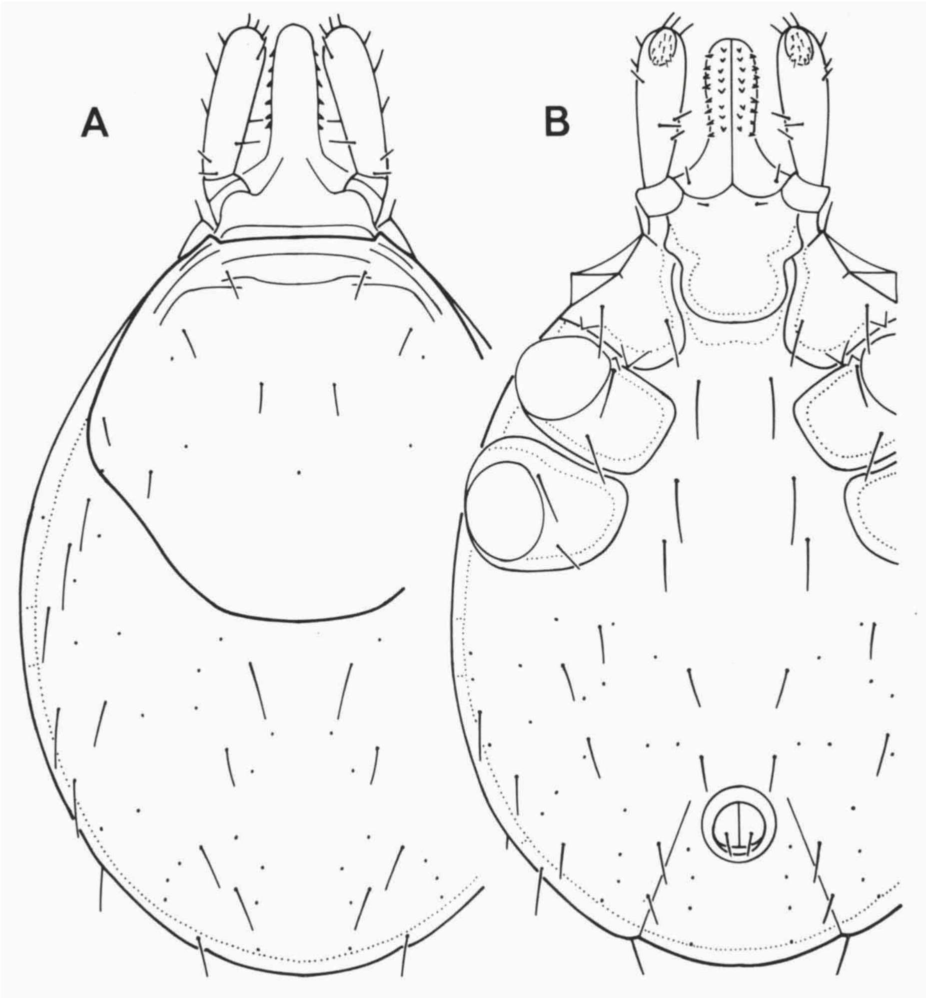

Fig. 3. *Ixodes ricinus* (Linnaeus), larva; A, dorsal view; B, ventral view; A, B, × 161.

In Argasidae the male genital region has the shape of a horseshoe; in females it is more or less oval (fig. 5A, B).

Although the morphology of ticks has been treated at great length in literature (e.g. André, 1949; Arthur, 1946, 1951, 1953, 1953a, 1956, 1956a, 1957, 1962; Babos, 1964; Bertram, 1939; Hughes, 1959; Nuttal, Cooper & Robinson, 1908, 1908a, 1908b; Pagenstecher, 1861; Robinson & Davidson, 1913, 1913a, 1914; Ruser, 1933; Schulze, 1932, 1935, 1941, 1942; Snodgrass, 1948; Vitzthum, 1931, 1940, 1941, 1942, 1943; Zebrowsky, 1926), the facts as known until now cannot easily be included in a more general review. The aim of the present paper is to integrate the study of Ixodid morphology into the general study of Acarid and Chelicerate comparative morphology, by the application of the methods and principles of my previous studies of Anactinotrichid and Cryptognomic morphology (Van der Hammen, 1961, 1964, 1964a, 1965, 1966, 1968, 1968a, 1969, 1977, 1979), and by using the terminology of the Glossary of Acarological Terminology (Van der Hammen, 1976, 1980).

Material

The present study is based on three species of ticks, viz., *Ixodes ricinus* (Linnaeus) (family Ixodidae), *Hyalomma dromedarii* C. L. Koch (family Amblyommidae), and *Ornithodoros savignyi* (Audouin) (family Argasidae). The material of *Ixodes ricinus* originates from the following localities in The Netherlands: Hagenau (Gelderland), 16 September 1959 (represented in figs. 1–2); Wilp (Gelderland), July 1967 (represented in fig. 3); and Formerum (Terschelling), 29 June 1974 (represented in figs. 4C, 5D, E, 6–9, 12A–C, 15–20). The material of *Hyalomma dromedarii* originates from Abu Rawash, Imbaba, Giza Governorate, Egypt, 8 February 1962. The material of *Ornithodoros savignyi* originates from Mansuriya, Imbaba, Giza Governorate, Egypt, 7 February 1962. I am most grateful to Dr. Harry Hoogstraal (U.S. Naval Medical Research Unit No. 3, Cairo, Egypt) who, at my request, sent me the Egyptian ticks described here.

Descriptive part

Constitution of the body. — The Ixodid body is divided into two pseudotagmata: gnathosoma and idiosoma. The original subdivision into prosoma and opisthosoma is no more recognizable. The podosoma is restricted to a small sternal area and the circumpedal regions.

Tegument. — According to data in literature (Pagenstecher, 1861; Nordenskiöld, 1908; Arthur, 1962; Babos, 1964; Nathanson, 1967), the skin consists of a living layer (hypodermis) and several non-living layers which are secreted by the hypodermis. Generally, three non-living layers can be distinguished: chitonostracum or procuticle (the thickest layer) and epiostracum or epicuticle (together constituting the cuticle; the epiostracum represents the superficial cuticular layer) and the cerotegument (consisting of a lipid layer with wax blooms and, in Argasidae, an outer cement layer, both developed by exuda-

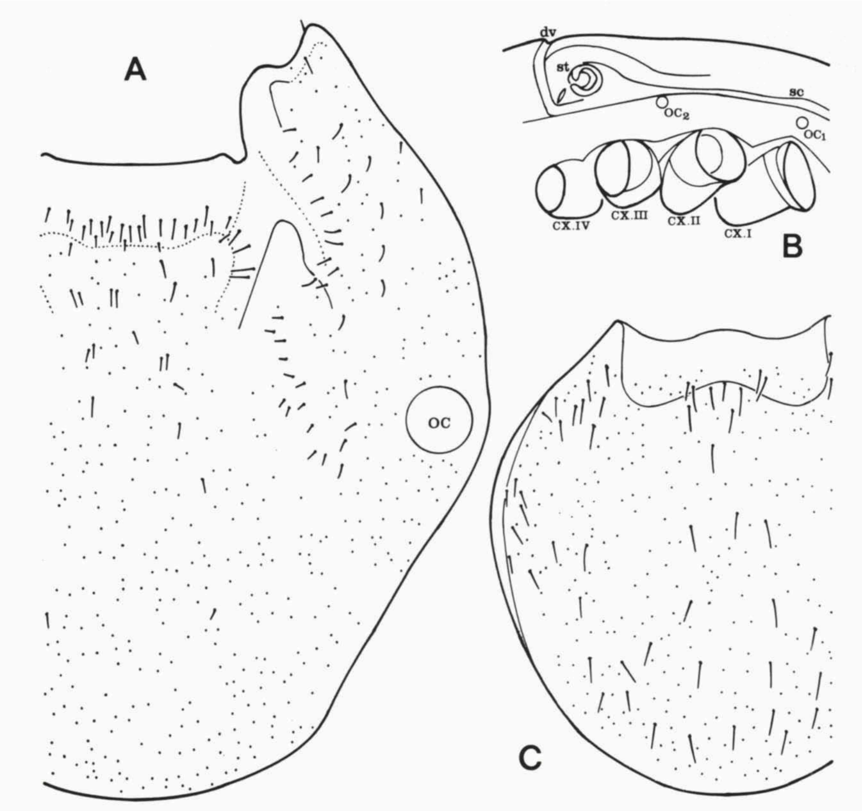

Fig. 4. A, *Hyalomma dromedarii* C. L. Koch, female, dorsal view of scutum; B, *Ornithodoros savignyi* (Audouin), female (not engorged), lateral view of "pleural" region; C, *Ixodes ricinus* (Linnaeus), female, dorsal view of scutum; A, C, × 44; B, × 8.

tion through pores in the cuticle). The chitonostracum generally consists of three layers: ectostracum, endostracum and Schmidt's layer. The cuticle can be soft or sclerotized; it contains numerous pore canals extending from the hypodermis to the epiostracum. The soft cuticle has the ability to stretch enormously during engorgement. The tegument contains tegumentary glands and various types of tegumentary sense organs. Setae and other sensory phaneres are inserted on the tegument.

Chaetotaxy. — Larval chaetotaxy (fig. 3) appears to be idionymous (setae being capable of receiving an individual designation). Numbers of setae generally increase progressively in nymphs and adults (fig. 4A, C), and chaetotaxy becomes adelonymous (setae being no more capable of receiving an individual designation).

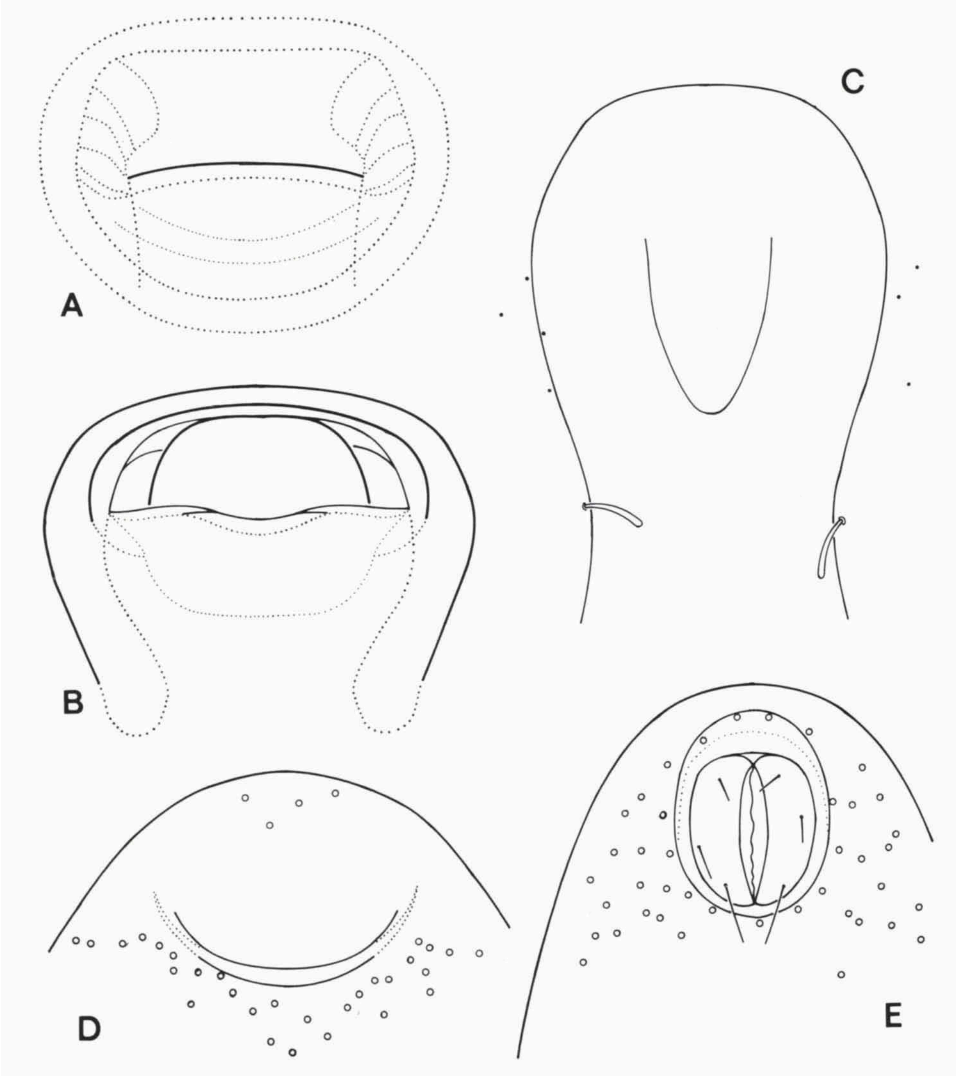

Fig. 5. A, B, *Ornithodoros savignyi* (Audouin), ventral view of genital region; A, female; B, male; C, *Hyalomma dromedarii* C. L. Koch, female, ventral view of genital region; D, E, *Ixodes ricinus* (Linnaeus), female; D, ventral view of genital region; E, ventral view of anal region; A, × 44; B, × 88; C, × 186; D, E, × 141.

Eyes. — Eyes are either absent (fig. 4C), or there are on both sides one or two eyes. In Ixodoidea the eyes are situated, in the female, close to the lateral border of the scutum (fig. 4A) and, in the male, in a corresponding position. In Argasidae the eyes, in case they are present, have a lateral, supracoxal posi-

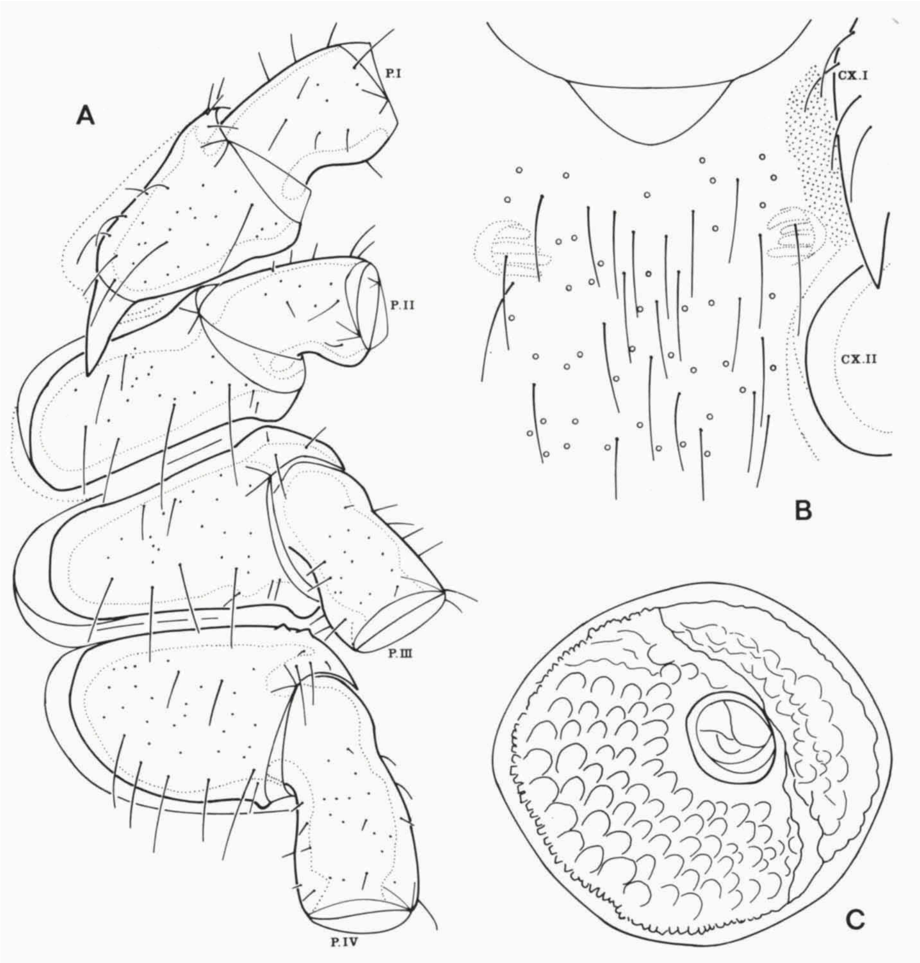

Fig. 6. *Ixodes ricinus* (Linnaeus), adult female; A, coxae and trochanteres of left legs I–IV, ventral view; B, anterior part of sternal region, ventral view; C, right peritreme and stigma, ventral (slightly oblique) view; A, × 77; B, × 118; C, × 155.

tion (fig. 4B). Eyes, in ticks, are simple ocelli that consist of a rounded, transparent part of the cuticle, functioning as a lens, and sensory cells.

Dorsal aspect of idiosoma. — As mentioned above, the dorsal side of the idiosoma of Ixodoidea presents a scutum (large, occupying the entire surface in the male; small, restricted to the anterior part, in the female and the immature stases); in Argasidae the dorsal side is leathery or wrinkled. Grooves (cervical, lateral, posteromedian, paramedian, accessory, marginal, etc.) apparently correspond with muscle insertions. The festoons along the posterior border of Amblyommidae, and the paired foveae dorsales of the same group, constitute sensory organs.

Ventral aspect of idiosoma. — Apart from the podosoma, the respiratory organs, the genital region and the anal region, which are dealt with in separate paragraphs, the ventral side of the idiosoma presents several grooves (postanal median, anal, genital, etc.). The ventral side of males of the genus *Ixodes* presents a number of ventral sclerites (fig. 2D).

Anal region. — The anus is constituted by a median longitudinal split in the posterior part of the ventral region. It is bordered by the anal valves (or paraprocts) which can be surrounded by a sclerotized ring (fig. 5E). The valves bear one or more setae; the number of anal setae can increase in the course of postembryonic development. In several taxa the anal chaetotaxy could be neotrichous.

Genital region. — The genital opening appears, in the course of postembryonic development, in the adult stase. It has an advanced position at the level of coxae III and IV, and is constituted by a transverse, more or less rounded slit. In Argasidae the male genital region has the shape of a horseshoe; in females it is more or less oval (fig. 5A, B). In Ixodina the genital region is more or less oval and can be surrounded, anteriorly and laterally, by the genital groove (figs. 1B, 2D, 5C, D).

Respiratory organs. — The paired stigmata, which are of postlarval (nymphal) origin, are situated posteriorly of coxa IV (Ixodina; figs. 1A, 2B, D) or laterally, above coxae III-IV (Argasina; fig. 4B). The split-shaped stigmata are surrounded by a so-called peritreme (fig. 6C), a taenidium with a characteristic microsculpture (which microsculpture is apparently mainly attributable to the microsculpture of the cerotegument).

Lateral aspect of idiosoma. — Unengorged ticks are flat, and the lateral part of the idiosoma is narrow. The lateral region includes the stigmata (described above) and the lateral part of the podosoma (described below). In Argasina the eyes have a lateral position above the coxae, close to a lateral (supracoxal) fold (fig. 4B).

Podosoma. — The podosoma consists of a sternal and a circumcoxal region. The sternal region extends from the base of the gnathosoma to the genital region, and laterally to the circumcoxal region (fig. 1B). In males of the genus *Ixodes* there is a small sternal shield (fig. 2D). The sternal region presents numerous setae and "pores" (fig. 6B). The circumcoxal region (fig. 6A) is not sclerotized. Legs II-IV do not possess a coxa/body articulation, although muscles are inserted on the base of the coxae. The coxae can possibly be moved because of the flexibility of the circumcoxal tegument.

Gnathosoma (figs. 7—11). — In all Anactinotrichida the gnathosoma consists (as in Actinotrichida) of two parts: cheliceral frame and infracapitulum. The cheliceral frame constitutes the body wall between the rostral region of the idiosoma and the dorsal part of the infracapitulum; it includes the tegulum (the dorsal part of the so-called basis capituli; in ticks extensor muscles are apparently inserted on its base). The cheliceral frame is attached to the dorsal part of the infracapitulum according to the line *at* (fig. 10A, C, D). The cheliceral sheaths are movably attached to the cheliceral frame. In adult females, the tegulum presents a pair of areae porosae (fig. 7).

The infracapitulum consists of a ventral region (mentum), a small dorsal region (cervix), and the large lateral ridges (including the coxal vaults or cavities, and the acetabula of the palps). It bears the lips and the palpi, and contains mouth and pharynx. The mentum (figs. 8, 9A, B) presents several infracapitular setae; flexor muscles are inserted on its internal prolongation (the subcapitular apodeme; fig. 11B). There are three lips (fig. 10): a labrum (upper lip) and the paired lateral lips. The lateral lips present a ventral and a dorsal part. The ventral part constitutes the so-called hypostome (with a denticulate ventral surface, and a membraneous dorsal wall; cf. figs. 7, 8, 9A, B, D). In *Ornithodoros* (Argasina; cf. fig. 10C, D) the paired labella (which constitute the dorsal part of the lateral lips) have the shape of a pair of laterodorsal lobes. In *Hyalomma* (Ixodina; cf. fig. 10A, B) the paired labella have fused (in literature they have erroneously been regarded as part of the cheliceral sheaths), and constitute an anterior prolongation of the cervix, completely covering the sunken labrum (in literature the labrum has been referred to as tongue-like process or flap); there is a distinct longitudinal ridge in the median part. The more or less triangular opening between the lateral lips constitutes the entrance to the preoral cavity. The labral sclerite is associated with the lateral walls of the pharynx, probably constituting part of a suctorial apparatus (figs. 10A, 11A). (The architecture of this part of the infracapitulum can only be studied after removal of the tegulum and the chelicerae by dissection). The posterior border of the cervix is indicated by the line *at*; anteriorly the cervix passes into the labella. Laterally the cervix is bordered by the lateral walls of the gnathosoma, and the large lateral ridges. A section of the pha-

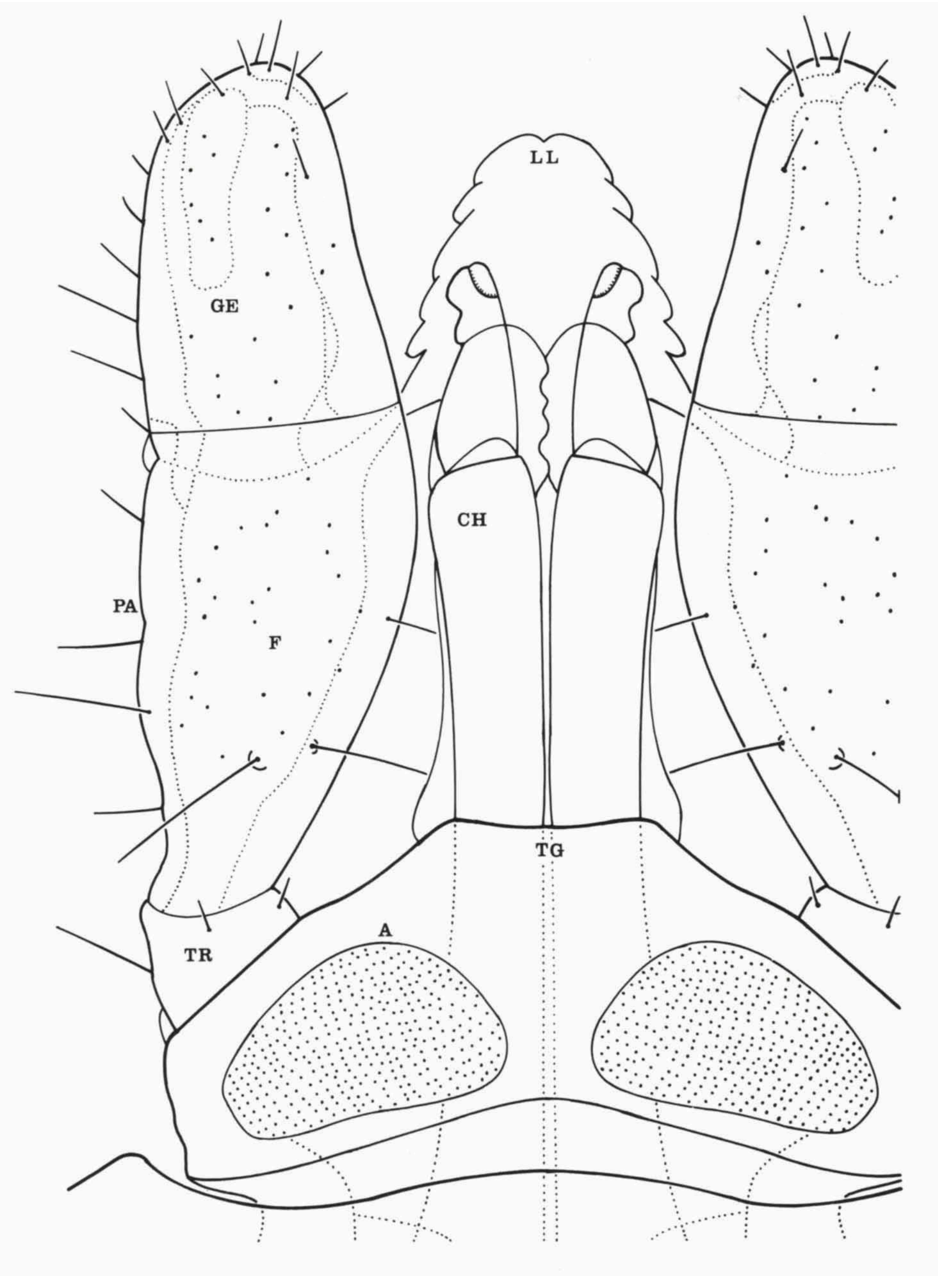

Fig. 7. *Ixodes ricinus* (Linnaeus), adult female, dorsal view of gnathosoma; × 176.

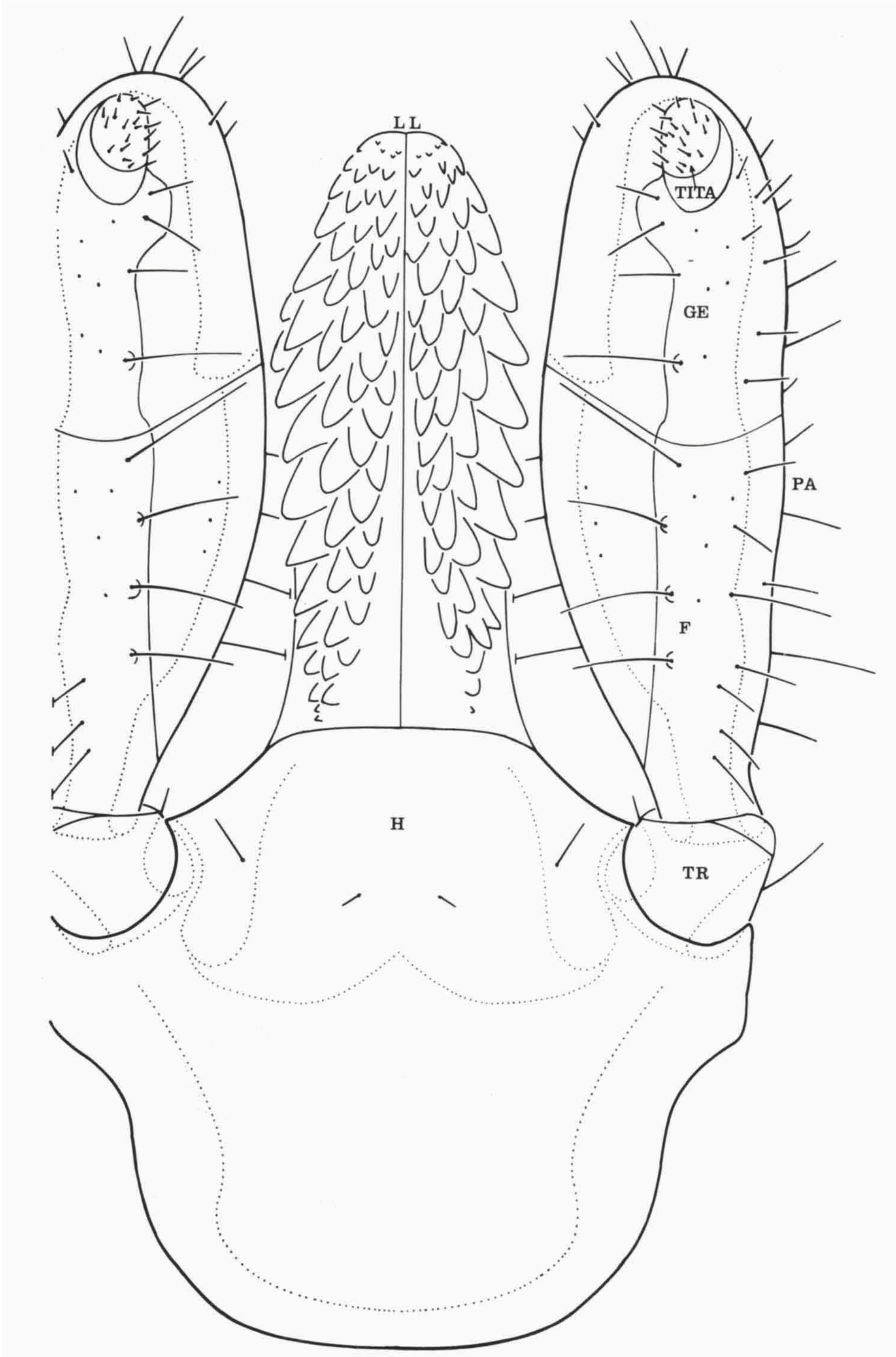

Fig. 8. *Ixodes ricinus* (Linnaeus), adult female, ventral view of gnathosoma; × 176.

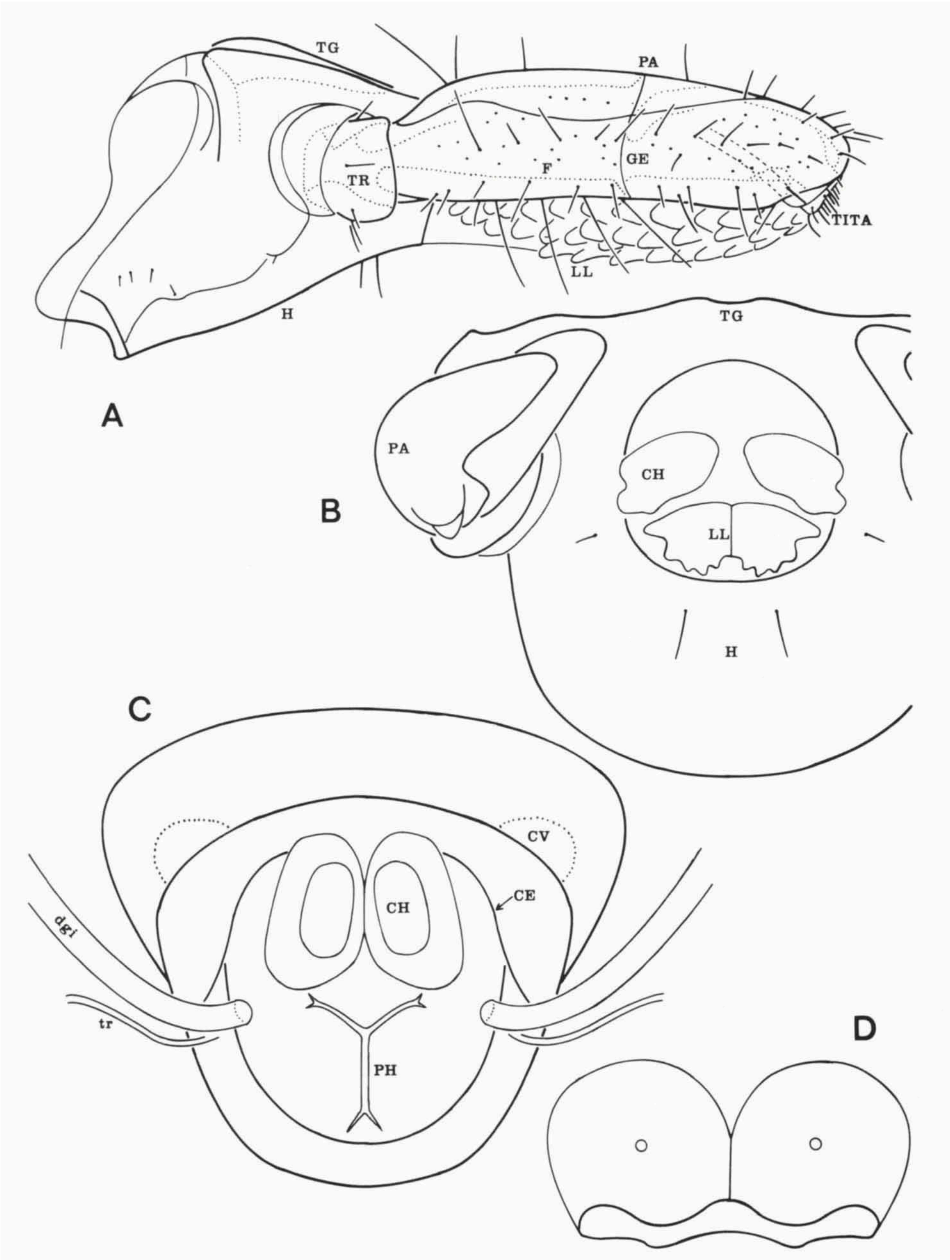

Fig. 9. *Ixodes ricinus* (Linnaeus), adult female; A, lateral view of gnathosoma; B, frontal view of gnathosoma; C, posterior (oblique) view of gnathosoma; D, transverse section (near the base) of the lateral lips; A, × 92; B, × 141; C, × 108; D, × 224.

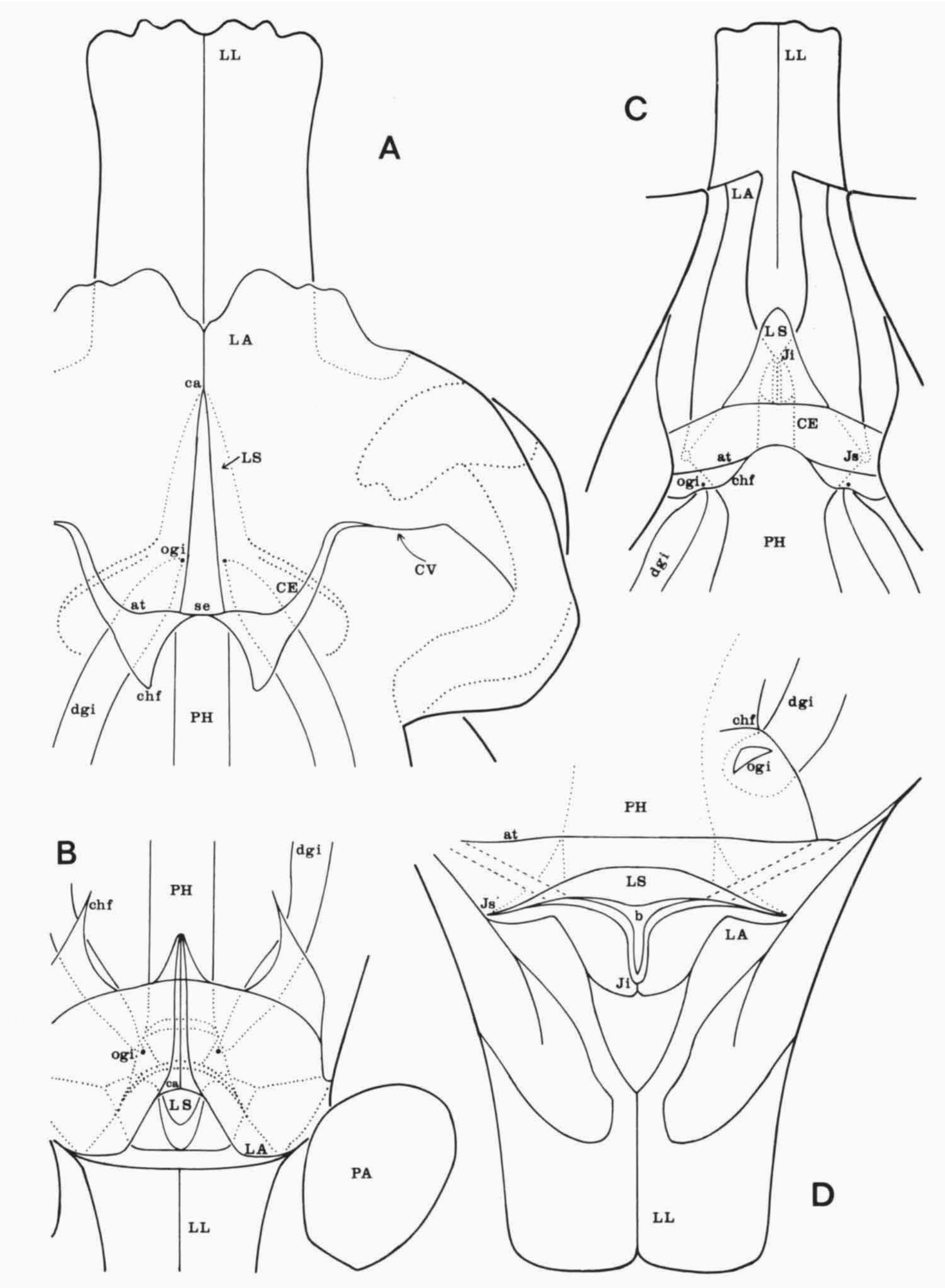

Fig. 10. A, B, *Hyalomma dromedarii* C. L. Koch, gnathosoma of adult female (tegulum and chelicerae removed); A, dorsal view; B, dorsofrontal view; C, D, *Ornithodoros savignyi* (Audouin), gnathosoma of adult female (tegulum and chelicerae removed); C, dorsal view; D, frontal view; A–C, × 88; D, × 141.

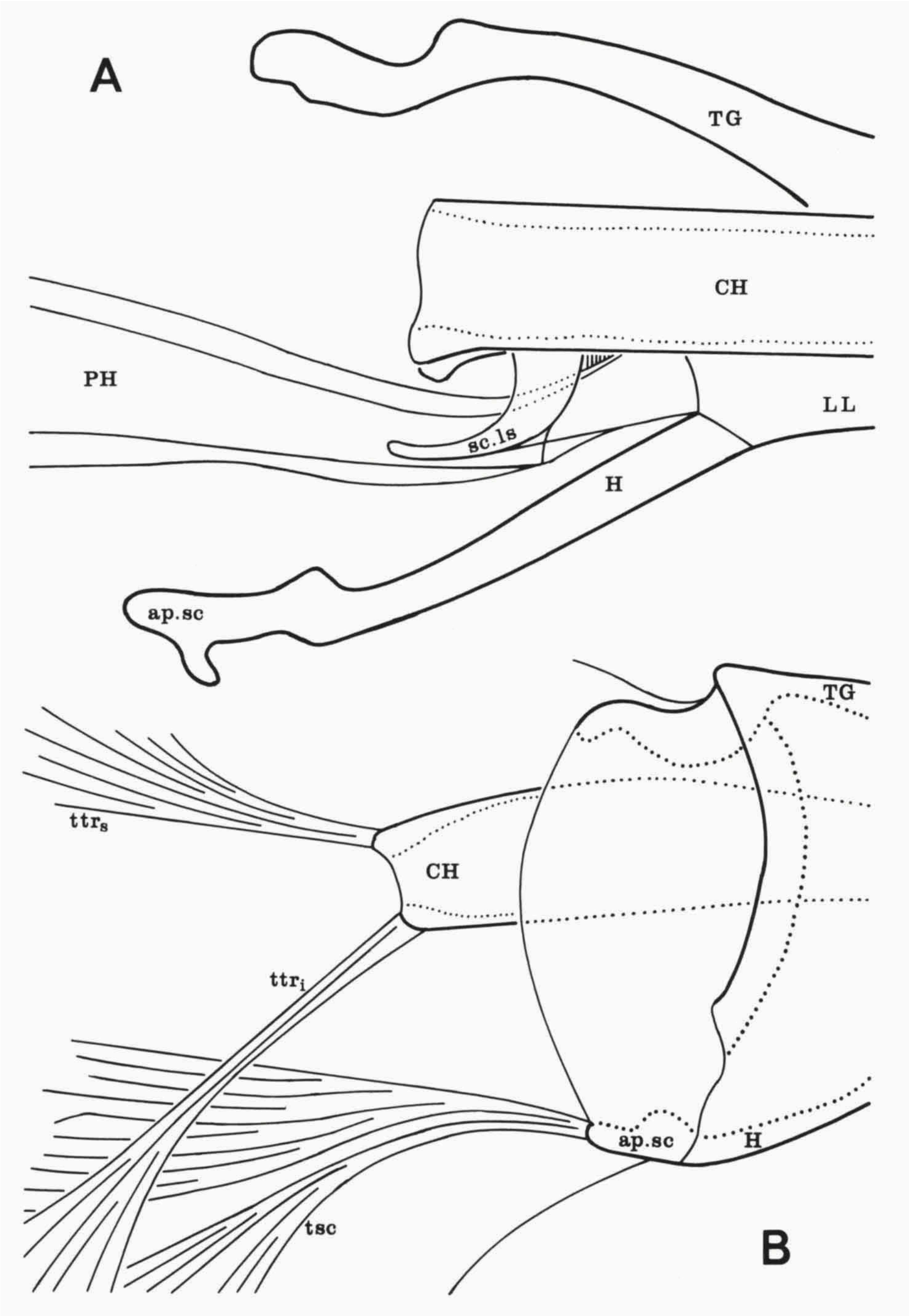

Fig. 11. *Hyalomma dromedarii* C. L. Koch, basal part of gnathosoma of adult female; A, longitudinal section, close to pharynx (basal part of chelicera removed); B, lateral view of entire base; A, × 132; B, × 90.

rynx is trifid, each of the three branches being split again near the end (fig. 9C). The ducts of the paired infracapitular glands enter the infracapitulum (fig. 9C) and debouch in the cheliceral frame close to the line *at* (*Ornithodoros*; cf. fig. 10C, D), or in the cervix (*Hyalomma;* cf. fig. 10A, B).

Chelicera. — The paired chelicerae consist of three segments: trochanter, body of chelicera and apotele (fig. 12D); the exact limits of these are not easily distinguishable; muscles are inserted on the base of the trochanter (fig. 11B: ttr_s, ttr_i). Trochanter and body of chelicera are apparently incompletely separated by an area of soft tegument with more or less dorsal position (fig. 12D). The shape of the chela is considerably different from that in other groups of Anactinotrichida (figs. 7, 8, 12A—C). It consists of a so-called hood, which represents the fixed jaw of other Anactinotrichida, and a so-called digit representing the apotele or movable jaw. The apotele is operated by the usual two tendons (t_s and t_i). The digit consists of a so-called internal article and a so-called external article. The tendons are inserted on the internal article which articulates with the body of the chelicera. The external article articulates with the internal article. A so-called dorsal process, or third apophysis, is found in the distal part of the internal article.

Palp. — The Ixodid palp (figs. 7, 8, 9, 13, 14) consists of four segments: trochanter, femur, genu and tibiotarsus. In Opilioacarida, Holothyrida and Gamasida the tarsus of the palp is relatively small, whilst tibia and tarsus together have the shape of a single segment; in Ixodina tibia and tarsus have apparently been integrated into a single tibiotarsus. There is no palpal apotele. In Argasidae (fig. 14) the shape of the palp resembles that of a leg. In Ixodoidea (fig. 13) the palp has a specialized shape: it is flattened and presents a paraxial concavity, adapted to the shape of the lateral lips (cf. fig. 9B). In Argasidae the tibiotarsus has the shape of a normal terminal segment. In Ixodoidea the tibiotarsus is relatively very small and has shifted to a ventrodistal position. The articulation between gnathosoma and trochanter is constituted by a rocking joint, the trochanter/femur articulation by a pivot joint. The articulation between femur and genu allows of little mobility (the segments have been integrated in the case of the larvae). The articulation between genu and tibiotarsus is constituted by a hinge joint with flexor muscles. The palp presents setae and other phaneres (eupathidia-like phaneres are found in the distal part of the tibiotarsus). In Ixodoidea setae of the paraxial side can constitute a comb extending over femur and genu; the comb is apparently associated with the lateral lips. "Pores" can be found in all segments.

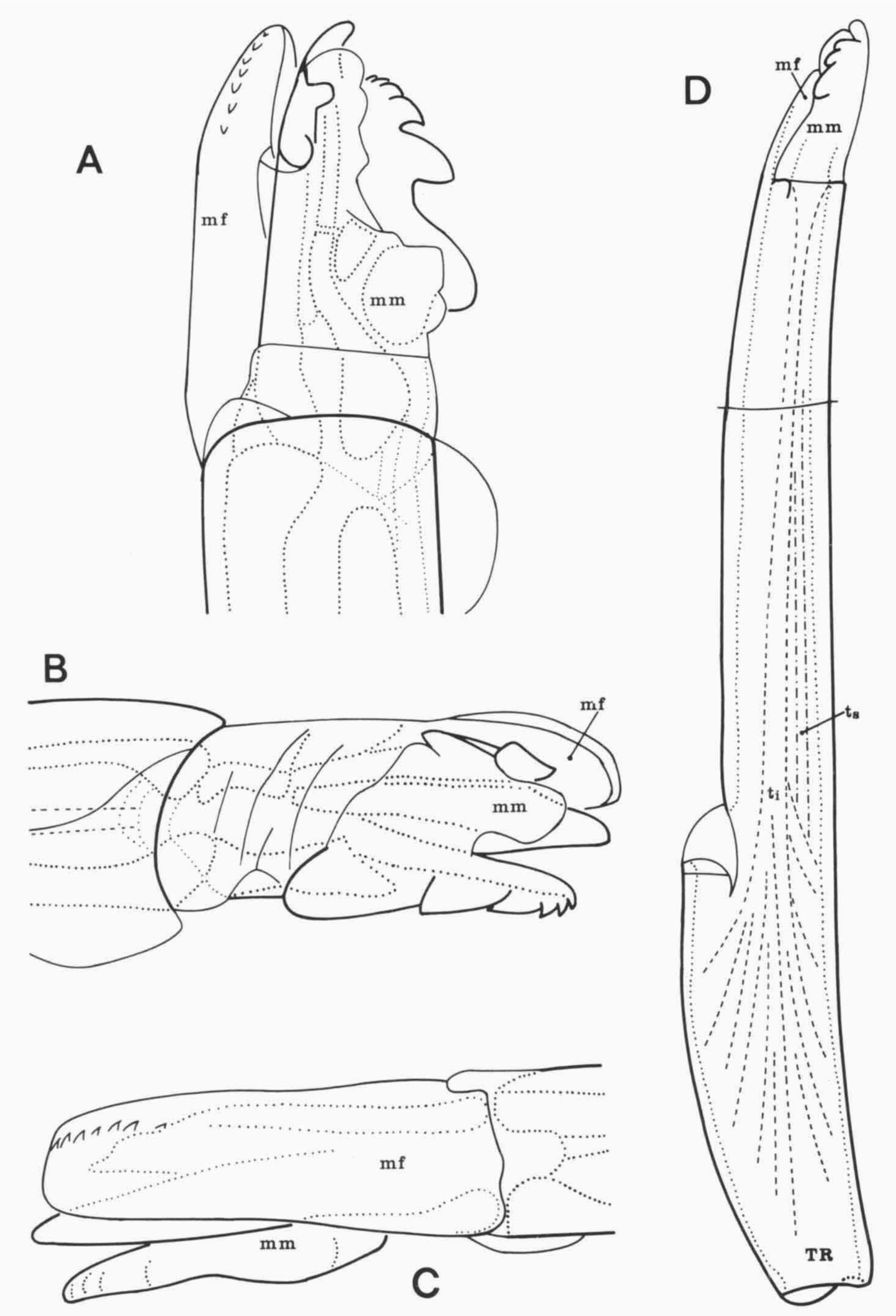

Fig. 12. A–C, *Ixodes ricinus* (Linnaeus), distal part of right chelicera of adult female; A, dorsal (slightly oblique) view of chelicera in situ; B, lateral (antiaxial) view; C, lateral (paraxial) view; D, *Hyalomma dromedarii* C. L. Koch, right chelicera of adult female, lateral (antiaxial) view; A–C, × 368; D, × 110.

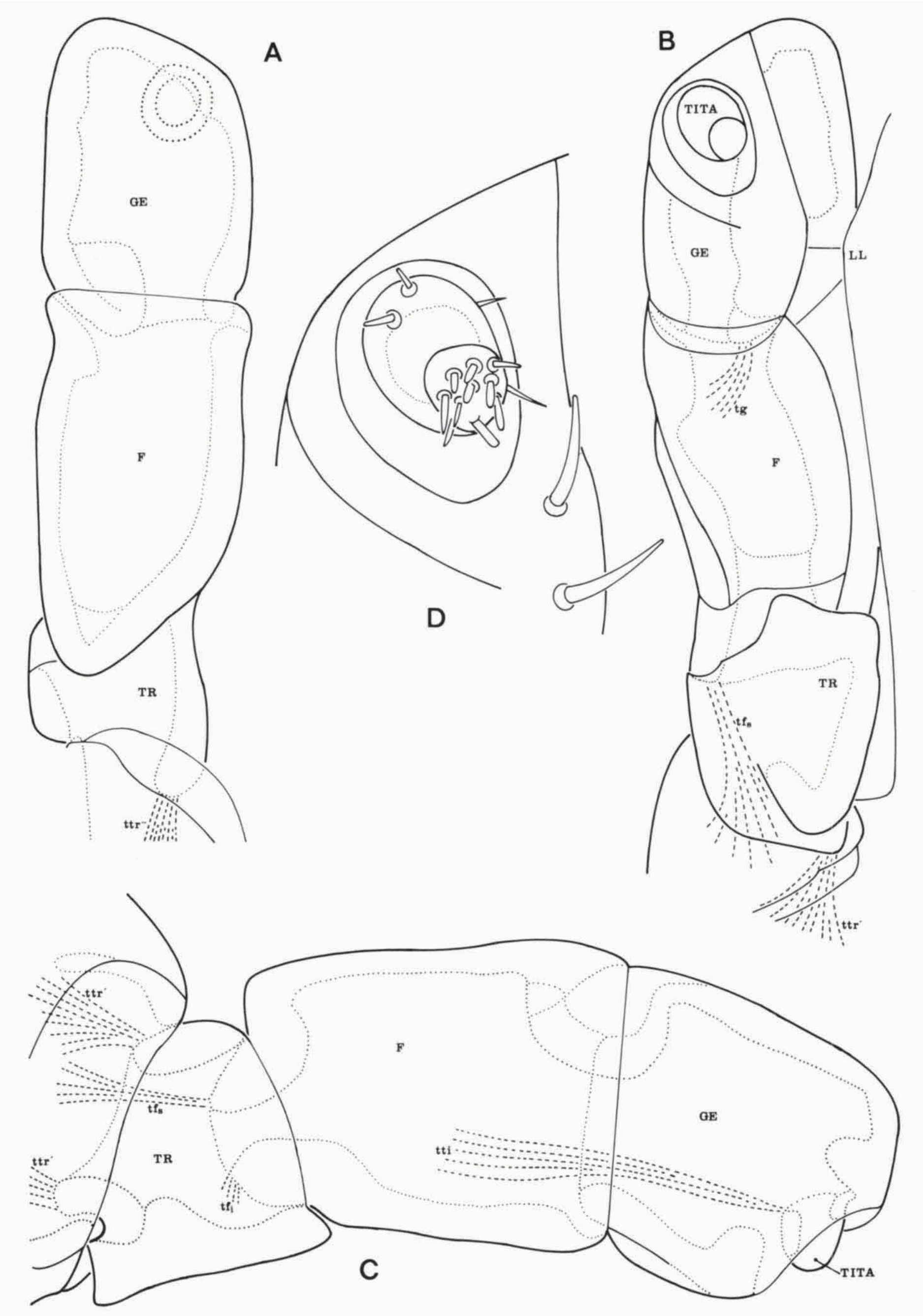

Fig. 13. *Hyalomma dromedarii* C. L. Koch, right palp of adult female; A, dorsal view; B, ventral view; C, lateral (antiaxial) view (in figs. A–C all phaneres are omitted); D, ventral view of terminal part; A–C, × 118; D, × 246.

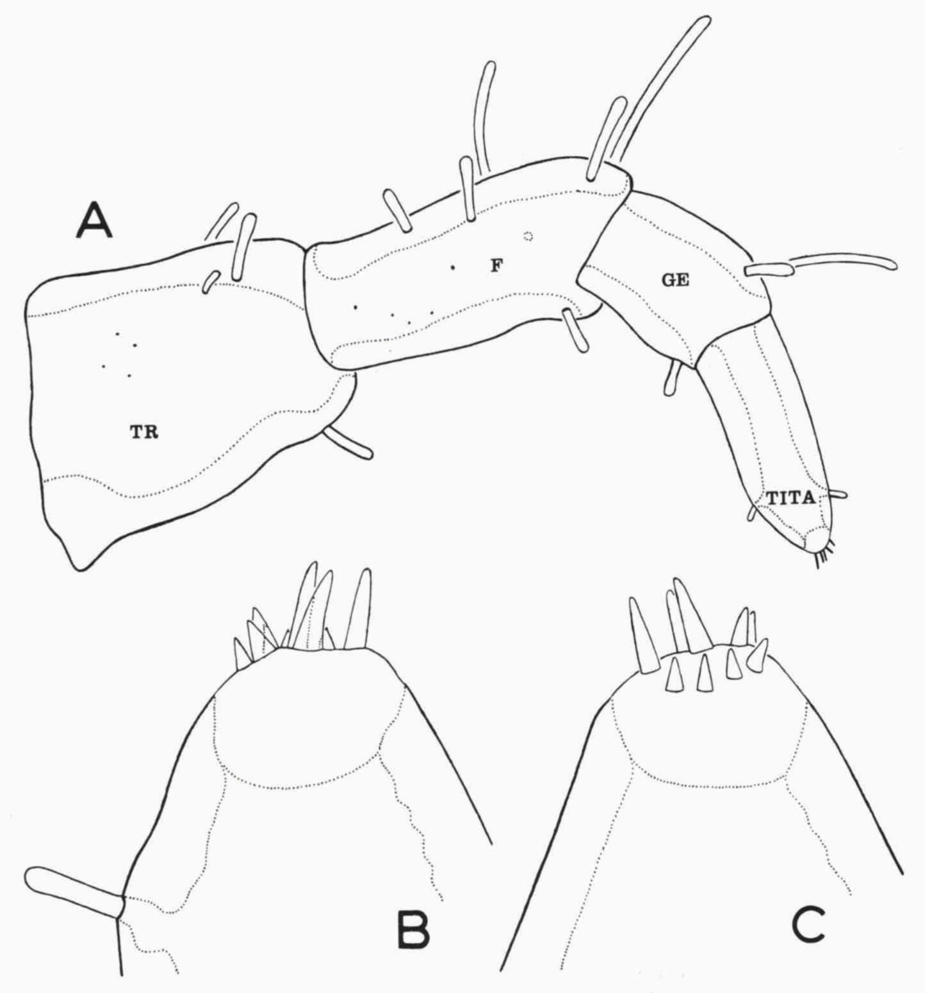

Fig. 14. *Ornithodoros savignyi* (Audouin), right palp of adult female; A, lateral (antiaxial) view; B, C, distal part of tibiotarsus; B, lateral (antiaxial) view; C, lateral (paraxial) view; A, × 120; B, C, × 830. (After Van der Hammen, 1964).

Legs (figs. 15—23). — The legs of Ixodina and Argasina consist of seven eudesmatic segments: coxa, trochanter, femur, genu, tibia, tarsus and apotele (figs. 15A, 17A, 18A, 19A, B, 21, 22). The femur of legs I—IV (figs. 16A, 17B, 18B, 19C) is subdivided by a basifemoral ring into two adesmatic segments: basifemur and telofemur (the adesmatic articulation allows of very little mobility). The tarsus of legs II—IV (figs. 17F, 18E, 19F) is subdivided by a basitarsal ring into two adesmatic segments: basitarsus and telotarsus (the adesmatic articulation allows of very little mobility).

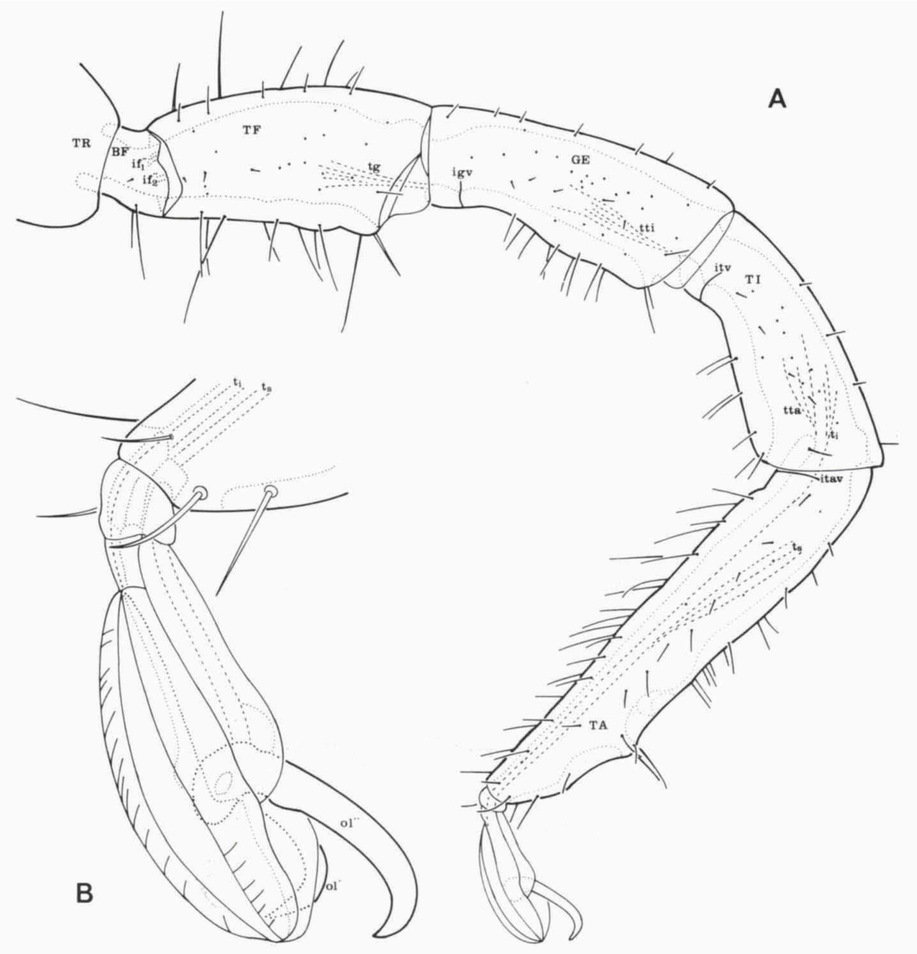

Fig. 15. *Ixodes ricinus* (Linnaeus), adult female, lateral (antiaxial = posterior) view of right leg I; A, distal part of trochanter, femur, genu, tibia, tarsus and apotele; B, distal part of tarsus and apotele; A, × 77; B, × 246.

The articulation coxa I/body allows of some mobility. There is no articulation between the body and coxae II–IV, but (as mentioned in the paragraph on the podosoma) the elasticity of the circumcoxal tegument probably allows of some coxal movability by the muscles inserted on the base of the coxa. The eudesmatic articulation between coxa and trochanter is apparently a bidesmatic rocking joint. The eudesmatic trochanter/femur articulation is constituted by a bidesmatic bicondylar pivot joint with levator and depressor muscles. The femur/genu, genu/tibia, and tibia/tarsus articulations are constituted by hinge joints with broadened and flattened superior hinge; they present infe-

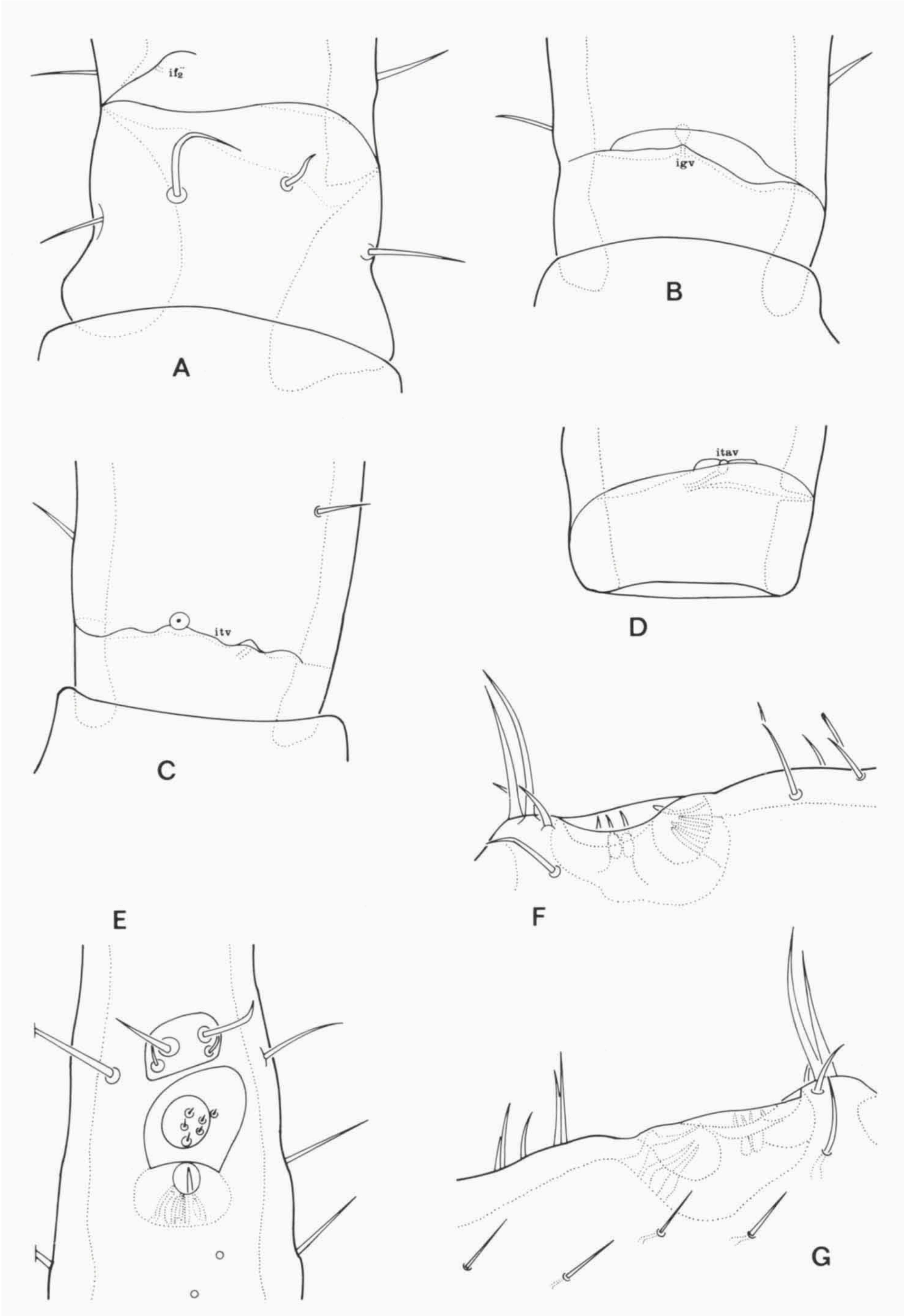

Fig. 16. *Ixodes ricinus* (Linnaeus), details of right leg I of adult female; A, basal part of femur, ventral view; B, basal part of genu, ventral view; C, basal part of tibia, ventral view; D, basal part of tarsus, ventral view; E–G, Haller's organ; E, dorsal view; F, lateral (paraxial = anterior) view; G, lateral (posterior) view; A–G, × 246.

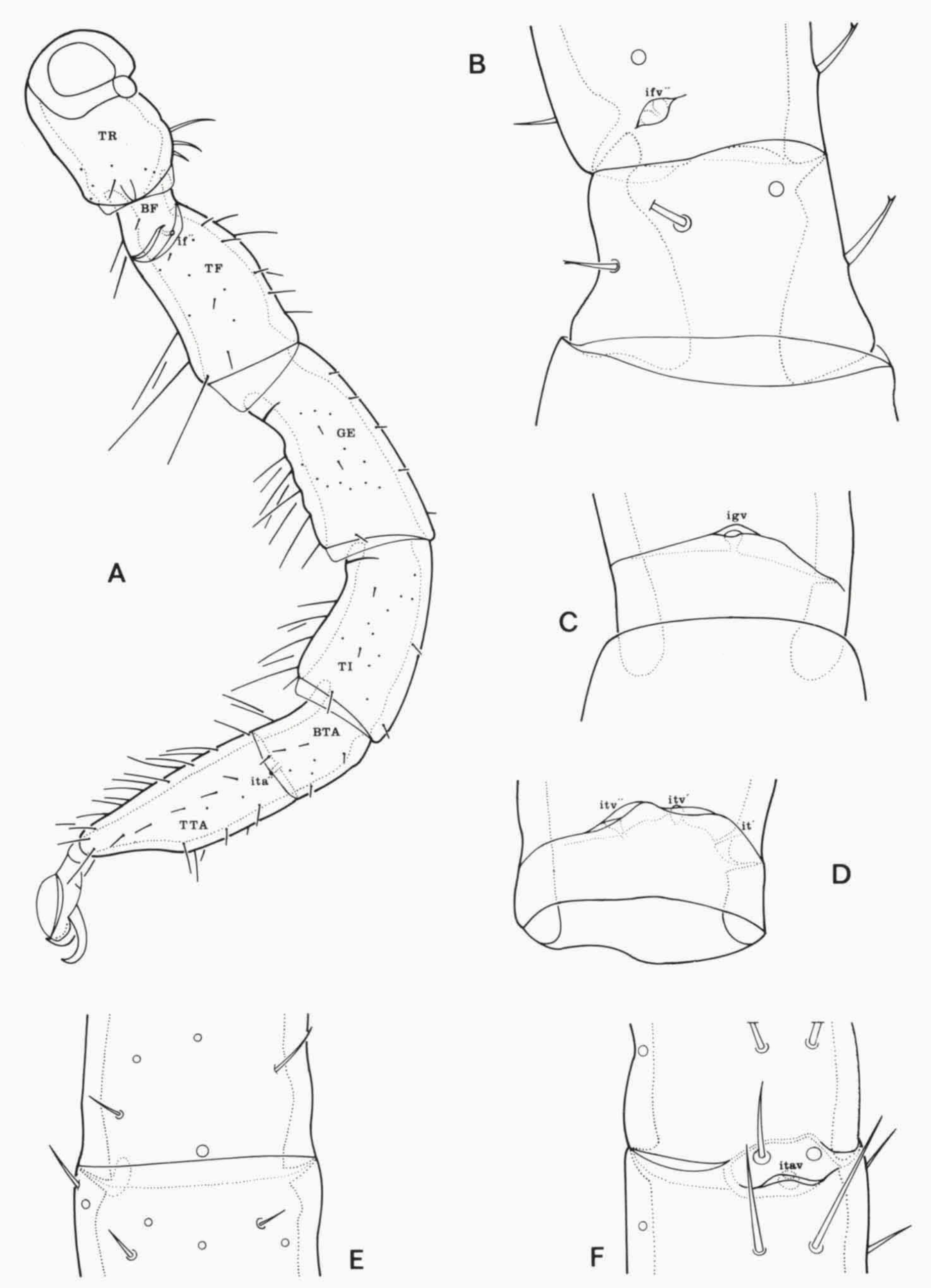

Fig. 17. *Ixodes ricinus* (Linnaeus), right leg II of adult female; A, lateral (posterior) view of trochanter, femur, genu, tibia, tarsus and apotele; B, basal part of femur, ventral view; C, basal part of genu, ventral view; D, basal part of tibia, ventral view; E, F, basitarsal ring; E, dorsal view; F, ventral view; A, × 77; B–F, × 246.

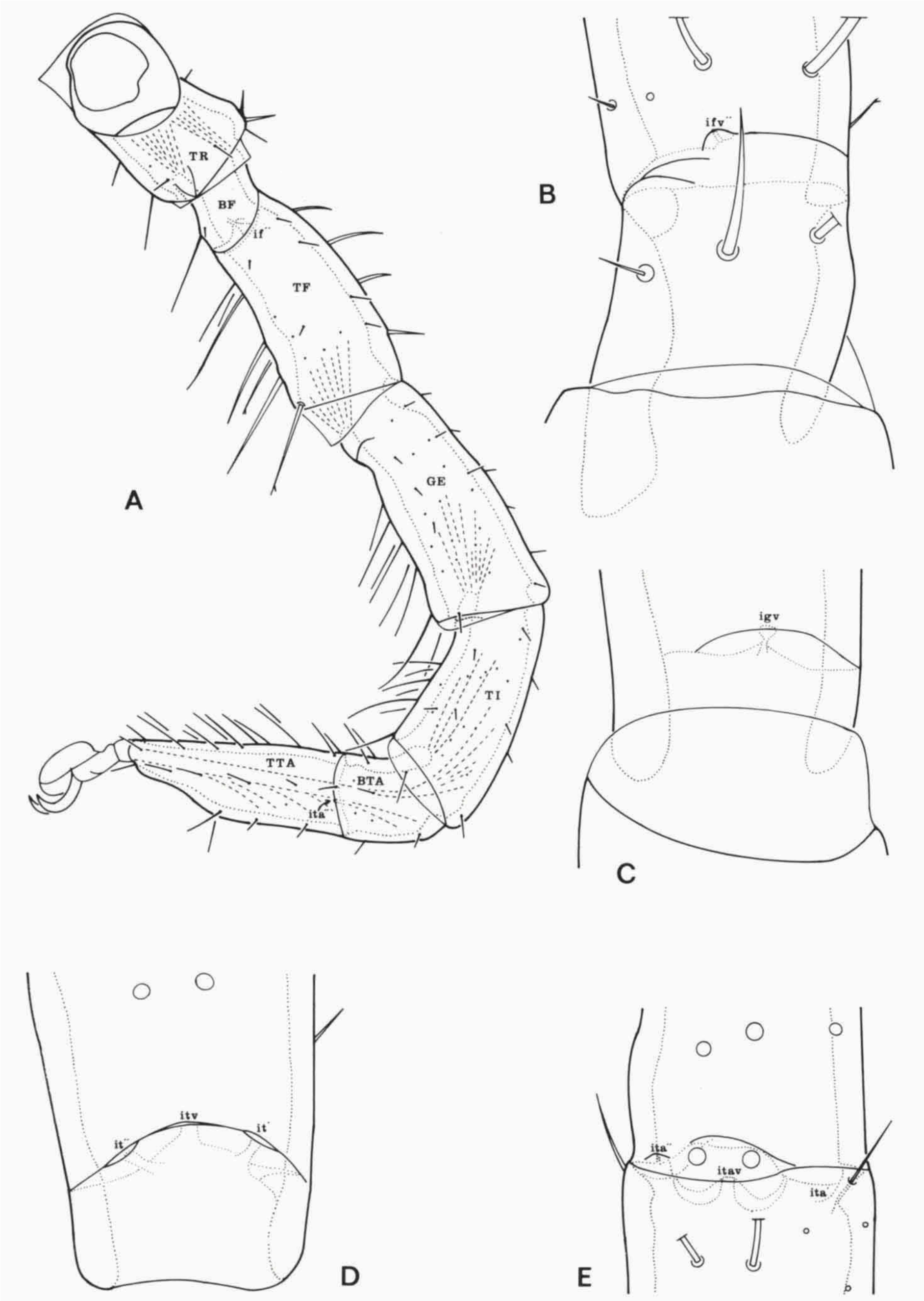

Fig. 18. *Ixodes ricinus* (Linnaeus), right leg III of adult female; A, lateral (posterior) view of trochanter, femur, genu, tibia, tarsus and apotele; B, basal part of femur, ventral view; C, basal part of genu, ventral view; D, basal part of tibia, ventral view; E, basitarsal ring, ventral view (in figs. B–E several setae are represented by their alveolus only); A, × 77; B–E, × 246.

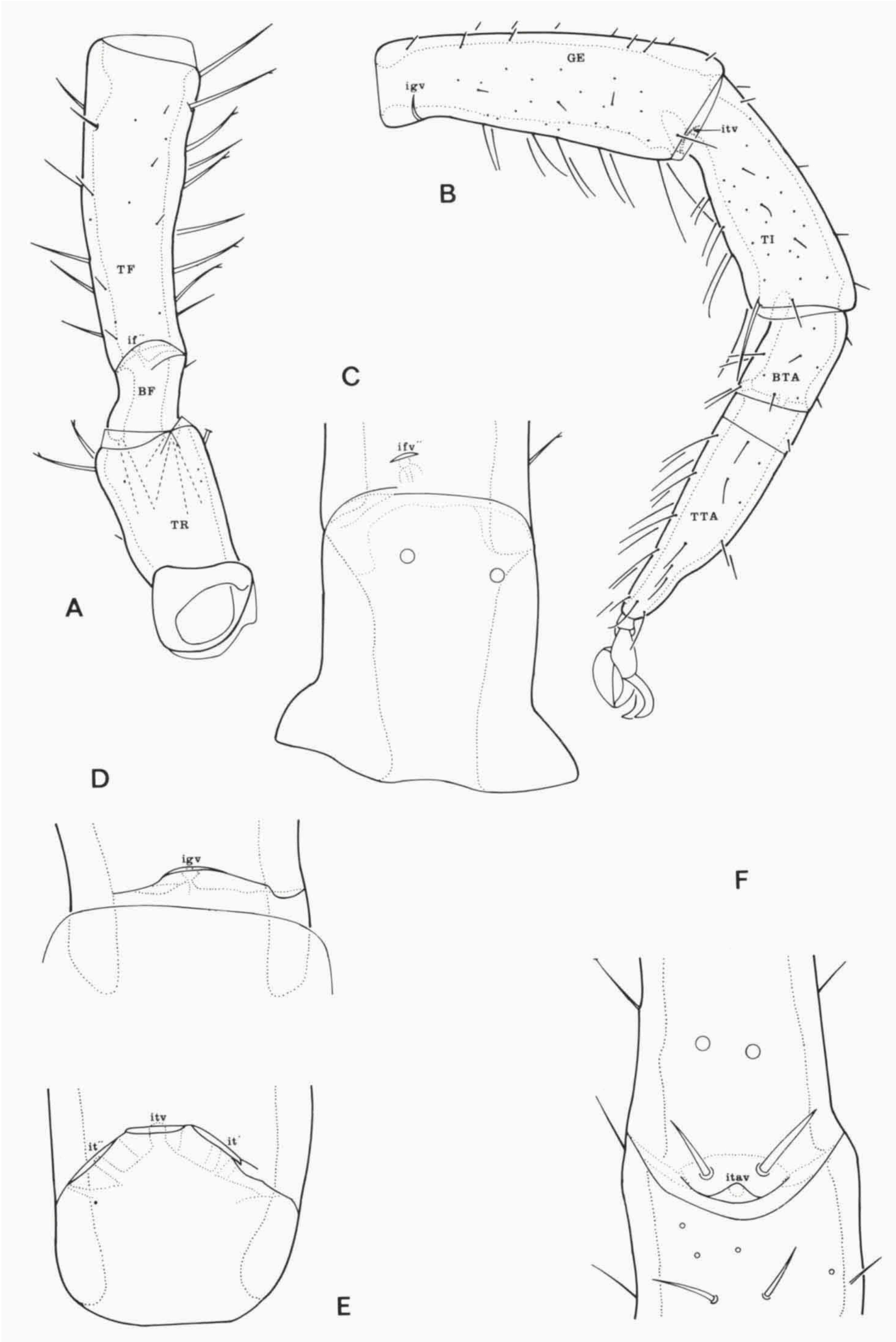

Fig. 19. *Ixodes ricinus* (Linnaeus), right leg IV of adult female; A, lateral (posterior) view of trochanter and femur; B, lateral (posterior) view of genu, tibia, tarsus and apotele; C, basal part of femur, ventral view; D, basal part of genu, ventral view; E, basal part of tibia, ventral view; F, basitarsal ring, ventral view; A, B, × 77; C–F, × 246.

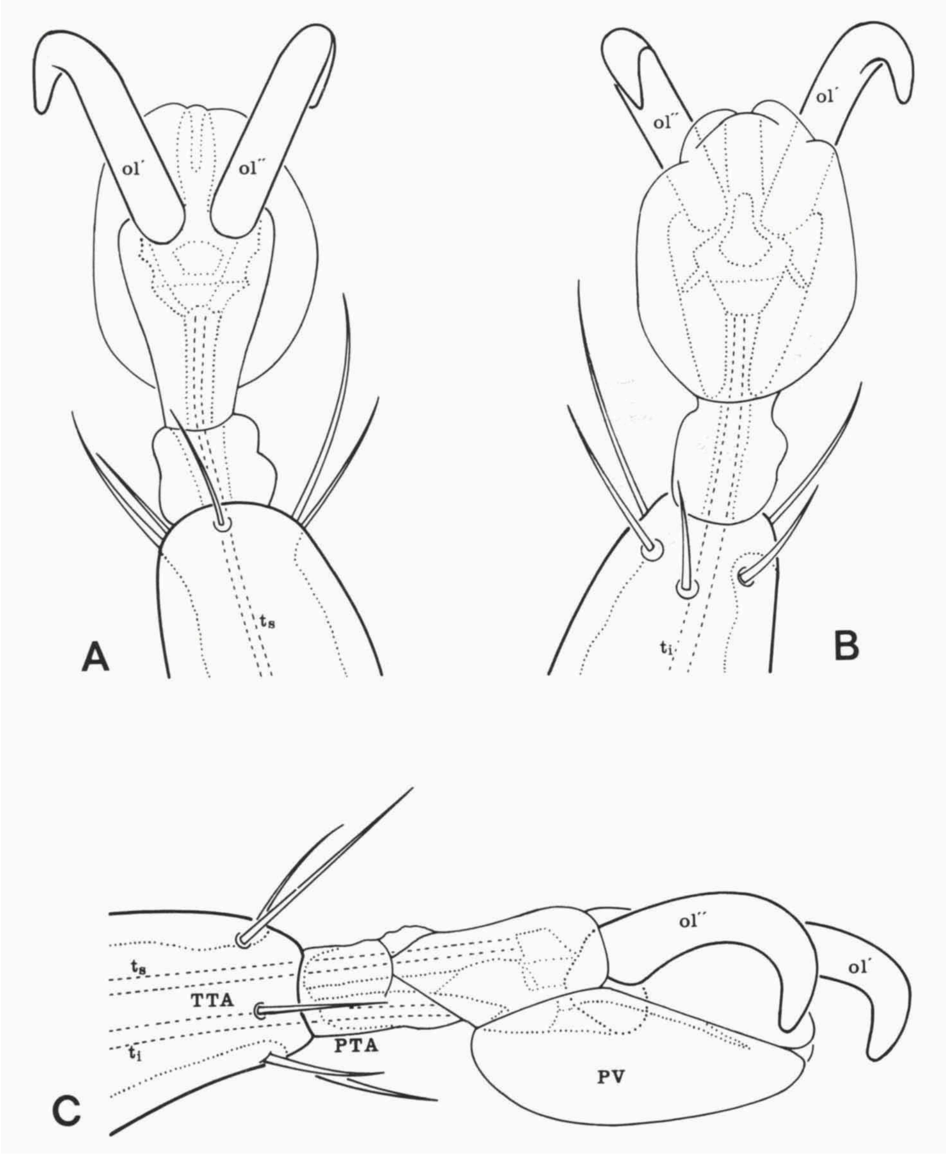

Fig. 20. *Ixodes ricinus* (Linnaeus), adult female, ambulacrum of right leg II; A, dorsal view; B, ventral view; C, lateral (posterior) view; A–C, × 368.

rior flexor muscles. The study of leg musculature is thwarted by the thick and dark cuticle of many ticks. In the case of *Hyalomma dromedarii*, in which species the cuticle of the appendages is less dark, I could establish the occurrence of extensor muscles associated with the femur/genu articulation (fig. 21); this

Fig. 21. *Hyalomma dromedarii* C. L. Koch, segmentation and articulation of right leg II of adult female, lateral (posterior) view (coxa not included; setae omitted); × 73.

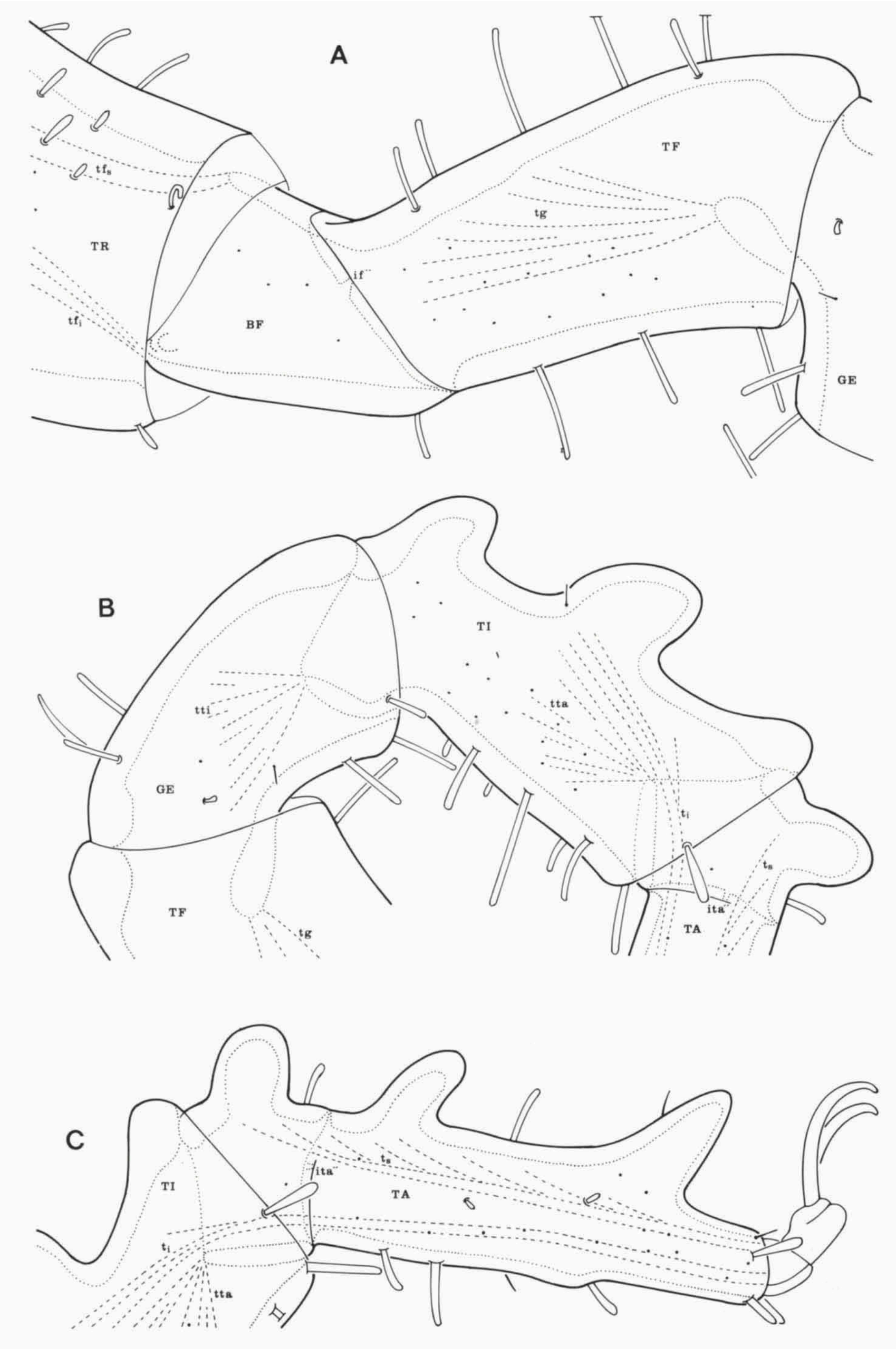

Fig. 22. *Ornithodoros savignyi* (Audouin), right leg III of adult female, lateral (posterior) view; A, distal part of trochanter, femur and basal part of genu; B, distal part of femur, genu, tibia and basal part of tarsus; C, distal part of tibia, tarsus and apotele; A–C, × 77.

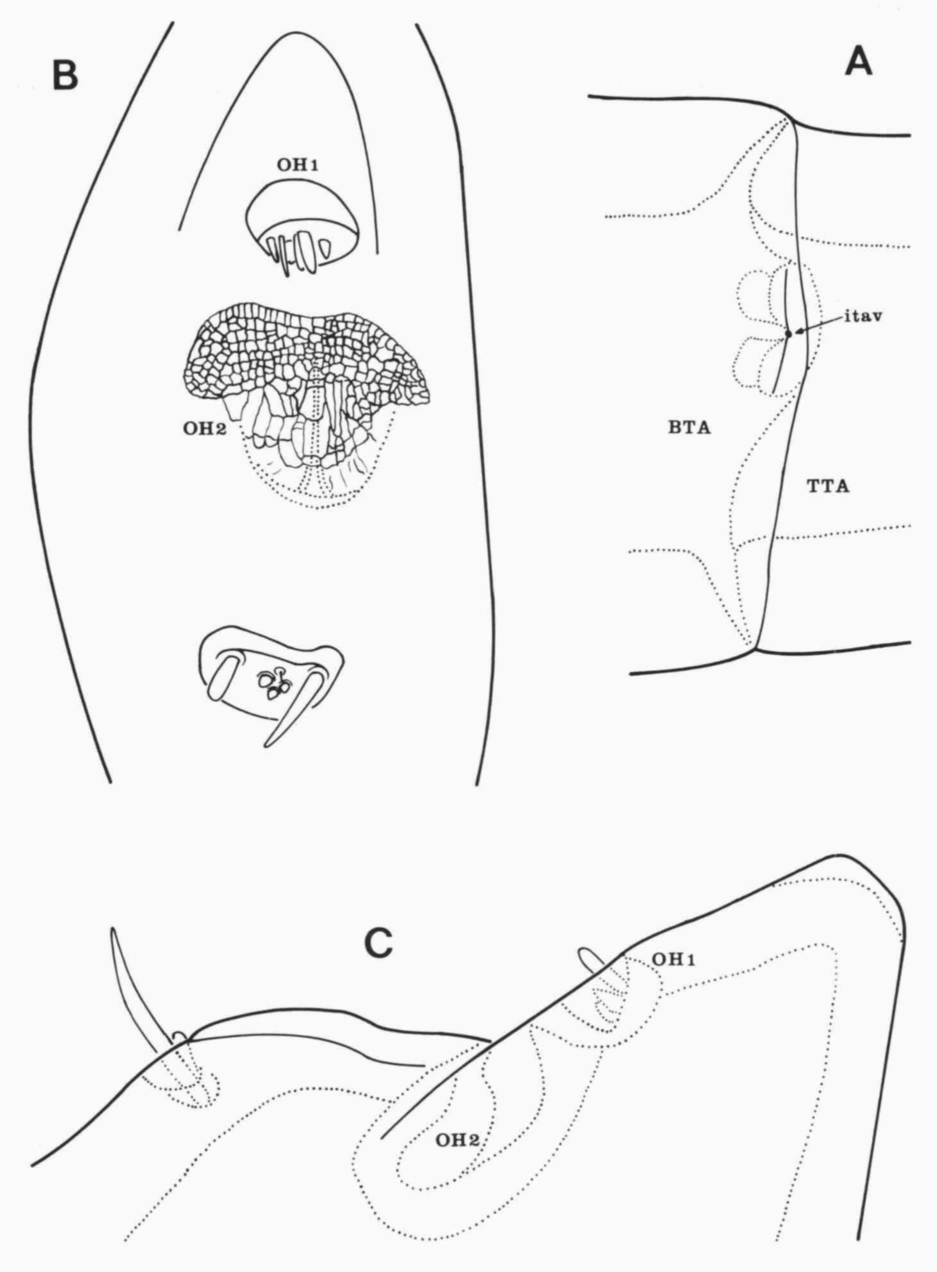

Fig. 23. *Ornithodoros savignyi* (Audouin), adult female; A, ventral view of basitarsal ring of right leg III; B, C, Haller's organ of right leg I; B, dorsal view; C, lateral (antiaxial = posterior) view; A, × 368; B–C, × 470.

extensor was already described by Ruser (1933; in her opinion, part of the flexor muscles could also function as extensors, which does not seem very probable). The tarsus/apotele articulation is constituted by a bidesmatic bicondylar pivot joint with levator and depressor muscles (there is a superior tendon t_s and an inferior tendon t_i).

The basifemoral ring is constituted by an external suture (corresponding with an internal cuticular fissure) associated with several (sometimes compound) lyrifissures. The basitarsal ring of legs II–IV is constituted by a suture corresponding with an internal cuticular fissure and associated with lateral and ventral lyrifissures. In Ixodoidea (not in Argasidae) the ventral lyrifissure *itav* is associated with a "sclerite" (with two setae) which is bordered by a suture (corresponding with an internal cuticular fissure). Externally the cuticle of the "sclerite" is continuous with that of the surrounding part of the tarsus; consequently, it does not constitute an "intercalary sclerite", as erroneously mentioned by Edwards & Evans (1967: 598, 601, fig. 2B). The function of the "sclerite" is probably associated with the sensory function of the ventral lyrifissure *itav* (apparently the detection of minute deformations in the exoskeleton).

Genu and tibia I–IV (figs. 16B, C, 17C, D, 18C, D, 19D, E) and tarsus I (fig. 16D) present one or more basiventral lyrifissures: one ventral lyrifissure (*igv*) in the case of the genu, three lyrifissures (*it″* or *itv″*, *itv*, *it′* or *itv′*) in the case of the tibia, and one ventral lyrifissure (*itav*) in the case of tarsus I.

The legs present setae and other sensory phaneres. Several types of sensory phaneres are concentrated in Haller's organ (in leg I); this organ consists of an anterior trough and a capsule (figs. 16E–G, 23B, C). Various types of "pores" are present in the cuticle of the legs.

The ambulacrum consists of a small pretarsus, an apotele with two claws, and a pulvillus (figs. 15B, 20). The pulvillus is reduced in the family Argasidae (fig. 22C).

Internal anatomy. — Summaries of data on the internal anatomy were published by Hughes (1959), Arthur (1962) and Babos (1964). Recently (Van der Hammen, 1979), I gave a concise summary of our knowledge on Cryptognomic and Anactinotrichid internal anatomy. The following summary is entirely based on data from literature.

The central nervous system is concentrated to a single mass, pierced by the oesophagus. The supraoesophageal mass consists of the cerebral and cheliceral ganglia. The pedipalpal ganglia lie level with the entry of the oesophagus in the brain (or somewhat lower). The suboesophageal nerve mass includes the four pairs of ganglia associated with the podosomatic segments. Posteriorly of the fourth pair of pedal ganglia, lie several pairs of opisthosomatic ganglia.

The respiratory system consists, at both sides, of a stigma, a subostial space, an atrium and tracheae. The circulatory system consists of a heart, a pair of ostia, an aorta, a periganglionic sinus, and arteries. The alimentary canal comprises pharynx, oesophagus, midgut and caeca, and hindgut. The excretory system comprises the paired Malpighian tubes (debouching into the terminal part of the hindgut) and the paired coxal glands (in fully engorged or ovigerous females they fulfil the function of the Malpighian tubes; the orifice is posteriorly of coxa I). A paired infracapitular gland is situated in the anterior part of the idiosoma; as mentioned above, the orifices are in the gnathosoma.

The male testes are elongate structures; narrow vasa deferentia arise from their frontal end, and join to form a common ejaculatory duct (accessory glands open, near the base of the ejaculatory duct, into the lumen). The paired female ovaria are tubular; the oviducts join to form a common oviduct which passes into the vagina (in some cases the oviducts pass into a bilobate uterus; the vagina can function as a primitive ovipositor).

According to Firstman (1973), the endosternite has a single pair of persistent transverse suspensors and three pairs of dorsoventral suspensors; it can be characterized as rather primitive.

Reproductive behaviour. — Reproduction in ticks is generally bisexual. Thelytokous parthenogenesis is sporadically found, in Argasina and Ixodina, in species which normally reproduce bisexually (Oliver, 1971: 291–294). Sperm transfer is nearly direct; the male implants a spermatophore in the female system by means of chelicerae and gnathosoma (this is a case of gonopody). Oviposition takes place by means of a primitive ovipositor.

Postembryonic development. — As far as known, the Ixodid life-cycle comprises three stases: larva, nymph and adult. A prelarva has not been found, although a calyptostasic prelarva could remain enclosed in the egg (a prelarva is known from Opilioacarida). The larva is hexapod. The single nymph could be homologous with the Opilioacarid protonymph (in that case the Ixodid adult would be neotenous). In Argasidae, the nymph can pass through growing- or repetition-moults; the forms which are the result of this type of moulting are not different from the preceding form (except in size), and are called isophena of the nymph.

Affinities. — The relatively large size, the presence of a subcapitular apodeme and a camerostome, the shape of Haller's organ, and the shape of the lateral lips constitute characters that could point to an affinity between Ixodida and Holothyrida (cf. Camicas & Morel, 1977: 412). Particularly important, for a phylogenetic classification of the four orders of Anactinotrichida (Opilioacarida, Holothyrida, Gamasida and Ixodida), will be a comparative morphological and phylogenetic study of gnathosoma movement in these groups.

LIST OF NOTATIONS

A, area porosa
ap.sc, subcapitular apodeme
at, line of attachment of the cheliceral frame to the infracapitulum

b, mouth
BF, basifemur
BTA, basitarsus

ca, carina
CE, cervix
CH, chelicera
chf, cheliceral frame
CV, coxal vault (cavity) of the infracapitulum
CXI–II, coxae I–II

dgi, duct of infracapitular gland
dv, dorsoventral groove

F, femur

GE, genu

H, mentum

if ″, if_1'', if_2'', posterolateral lyrifissures of basifemoral ring
ifv″, posteroventral lyrifissure of basisfemoral ring
igv, ventral lyrifissure of genu
it′, anterolateral lyrifissure of tibia
it″, posterolateral lyrifissure of tibia
ita′, anterolateral lyrifissure of basitarsal ring
ita″, posterolateral lyrifissure of basitarsal ring
itav, ventral lyrifissure of basitarsal ring
itv, ventral lyrifissure of tibia
itv″, posteroventral lyrifissure of tibia

Ji, inferior oral commissure
Js, *Js*′, superior oral commissures

LA, labellum
LL, lateral lips
LS, labrum

mf, fixed jaw of chelicera
mm, movable jaw of chelicera

OC, OC_1, OC_2, eyes
ogi, orifice of infracapitular gland
OH_1, anterior trough of Haller's organ
OH_2, capsule of Haller's organ
ol′, anterior lateral unguis
ol″, posterior lateral unguis

PA, palp
PH, pharynx
PTA, pretarsus
PV, pulvillus
PI–IV, legs I–IV

sc, supracoxal fold
sc.ls, labral sclerite
se, capitular saddle
st, stigma

t_i, inferior tendon of apotele
t_s, superior tendon of apotele
TA, tarsus
TF, telofemur
tf_i, inferior tendon of femur
tf_s, superior tendon of femur
tg, tendon (flexor) of genu
TG, tegulum
tge, tendon (extensor) of genu
TI, tibia
TITA, tibiotarsus

tr, trachea
TR, trochanter
tsc, tendon of subcapitular apodeme
tta, tendon of tarsus
TTA, telotarsus
tti, tendon of tibia
ttr_i, inferior tendon of trochanter
ttr_s, superior tendon of trochanter
ttr', anterior tendon of trochanter
ttr", posterior tendon of trochanter

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