COMPARATIVE STUDIES IN CHELICERATA II. EPIMERATA (PALPIGRADI AND ACTINOTRICHIDA)

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With 31 text-figures

ABSTRACT

A comparative study is made of two groups of Chelicerata (Palpigradi and Actinotrichid mites, together constituting the Epimerata, a chelicerate class), and models of the evolution of epimerate characters are prepared. The study is based on the same methods and principles as the first part of the present series, and the same terminology has been used. The models of the evolution of characters constitute the epimerate archetype and the standard of epimerate classification.

CONTENTS

I. INTRODUCTION

The name Epimerata was introduced by me in 1977, and refers to a chelicerate class, comprising two subclasses (Palpigradi and Actinotrichida); a short diagnosis of the class was given in the same publication (Van der Hammen, 1977: 316). Before that time, I had already pointed to the relationship of the two groups (Van der Hammen, 1972a: 279; 1973: 278).

In the present paper my previous views are studied in more detail. The paper is a continuation of my study of the Cryptognomae (Van der Hammen, 1979a), and is based on similar methods and principles. Since the publication of the first part of the present series, I published the general part of the Glossary of Acarological Terminology (Van der Hammen, 1980), a paper on Type Concept, higher Classification and Evolution (Van der Hammen, 1981), and a paper on Numerical Changes and Evolution in Actinotrichid Mites (Van der Hammen, 1981a). The results of these three fundamental publications constitute also the theoretical base of the present paper. It may be remarked here that two morphological terms used in the present paper, viz., "telson" and "endite", must be regarded as "neutral" descriptive terms, indicating structures which are, as yet, not completely understood.

In the course of time, the views on the relationships of Palpigradi and Actinotrichida with other chelicerate groups have varied. These views are summarized in chapters II and III respectively. In chapter VI the relationships between the two groups, and the affinities with other Chelicerates, are further discussed.

II. PALPIGRADI

A representative of the Palpigradi was first discovered and described by the Italian zoologist Grassi (1885, 1886) who, in 1883, had become Professor of zoology and comparative anatomy at Catania (Sicily). He studied the morphology, the internal anatomy and the affinities of a species collected under rocks near Catania, and which he named *Koenenia mirabilis*. Grassi compared it with Uropygi, Schizomida, Amblypygi, Solifugae and Opilionida, and regarded it as a representative of a new order (Microthelyphonida).

Thorell (1888: 358) replaced the name Microthelyphonida by Palpigradi, a name considered by him more appropriate. Pocock (1893: 9), in his study of Arachnid morphology and classification, could not add further data on the group; although he discussed its affinities, it could not be included in his classification.

Hansen & Sörensen (1897) published a detailed morphological study of *Koenenia mirabilis*, in which attention was paid also to the systematic position (they pointed to a relationship with Schizomida). Börner (1901, 1902, 1904) and Hansen (1901) continued the study of the morphology of the Palpigradi. Börner (1902, 1904) classified the Palpigradi with the Pedipalpi. Hansen (1930) dealt with the comparative morphology of the walking legs.

In the mean time, Wheeler and Rucker had discovered interesting palpigrade species in Texas, of which the external morphology, the internal anatomy and part of the postembryonic development was described in a series of papers (Wheeler, 1900; Rucker, 1901, 1903, 1903a).

Versluys & Demoll (1921: 750-751; 1922: 134, 141-148, 158, 163, 165, 372, 375), in their discussion of the relationship of Merostomata and other groups of Chelicerata, also dealt with the Palpigradi. They enumerated a series of ancestral and derived character states present in Palpigradi, but not in Scorpionida, and pointed to the fact that Palpigradi cannot be descendants of Scorpion-like ancestors (Arachnid ancestors, moreover, cannot have been Merostomata-like).

Kaestner (1932, 1955, 1956) and Roewer (1934) published useful summaries of the knowledge on Palpigradi. New details, especially with reference to internal anatomy, were described and summarized by Millot (1942, 1943, 1949).

Snodgrass (1948: 19-22, fig. 6) summarized the knowledge with reference to the palpigrade mouthparts. Petrunkevitch (1955: 116-118, figs. 82, 83) classified the Palpigradi with the arachnid subclass Cauligastra (including also Uropygi, Amblypygi, Araneida, Solifugae and Ricinulei); in this subclass they constituted the superorder Latisterna.

Condé (1965) described a species belonging to the interstitial microfauna of the Farasan Islands in the southern Red Sea. Monniot (1966) described a species belonging to the interstitial microfauna of Pointe Noire, Congo Brazzaville (she collected several specimens of the species); she made also a study (Monniot, 1970) of the fine structure of tegument and phaneres in *Eukoenenia mirabilis.*

Savory (1935: 90-95, figs. 43-46; 1964: 142-147, figs. 61-65; 1971: 27-28, 30-32, 35, 38-39, 41, fig. 8; 1974: 43-45; 1977: 125-131, figs. 33-37) published several summaries, and observations about phylogeny; he pointed to the possibility of a palpigrade evolution different and separate from that of other Chelicerates.

Van der Hammen (1969a, 1977, 1977a) studied the morphology of the mouthparts and the appendages, and classified the Palpigradi, together with the Actinotrichida, in a new chelicerate subclass, the Epimerata.

Firstman (1973: 6-8, 46, 49-50, figs. 3, 4, 35) investigated the palpigrade arterial system and endosternite; he characterized the endosternite as the most primitive of all the known extant Chelicerata.

Weygoldt & Paulus (1979, 1979a) and Weygoldt (1980) studied the phylogeny of the Chelicerata and introduced a cladistic classification. They regarded the presence of a flagellum and three-segmented chelicerae in Palpigradi as primitive characters, and mentioned the following derived characters: reduction of size; subdivision of the prosoma; absence of eyes, lyrifissures and respiratory organs; the occurrence in fissures of the soil. The cladistic classification of these authors is based on a hypothesis about the origin of the Chelicerata, and the interpretation of character states is adapted to this view.

Alberti (1979) investigated the structure of sperm and the spermiocytogenesis in *Prokoenenia wheeleri* (Rucker), which appeared to present special derived characters. He pointed to the isolated position of the Palpigrades as far as the morphology of the sperm is concerned.

Rowland & Sissom (1980) described a fossil Palpigrade from the Tertiary, and prepared a review of the morphology and systematics, as well as a complete bibliography, of the Palpigradi.

In the course of nearly a century, about fifty Palpigrade species have been described by some fifteen authors.

The present discussion of palpigrade morphology is, for the greater part, based on original studies; it is supplemented with data from literature. The chapter is subdivided into three parts: a survey of the material, a descriptive part, and additional remarks.

A. Material

The original part of the present chapter is based on the study of *Eukoenenia mirabilis* (Grassi). The material of this species was collected for me at Banyuls-sur-Mer, France (a classical locality), in the period 1962-1978, by my friends and colleagues Dr. J. Travé and Dr. Y. Coineau (at that time both working at the Laboratoire Arago, Banyuls-sur-Mer)¹). When I started the present study, I had already completely dissected part of this material for previous investigations. The results of these earlier studies (cf. Van der Hammen, 1969a, 1977a) are included here. Figs. 1-3 and 5-6 of the present paper (among which three figures of the general aspect) are all prepared after one and the same specimen (an adult female). With the help of figs. 1-3 (the specimen in dorsal, ventral and lateral view respectively), a three-dimensional image of the species can be built up. The material used for the present paper has been studied in cavity slides, in diluted lactic acid. In this medium, it becomes very soft and can be easily deformed. The outlines of figs. 1, 3 consequently present slight differences to one another, although the figures are based on the same specimen.

B. Descriptive part

Habitus. — Palpigradi are small, elongate, whitish and delicate Chelicerata with a long, narrow, fragile flagellus, and long, thin appendages. The movements of living specimens are rapid and vivid; opisthosoma and flagellum can be actively elevated and even bent to the front.

Divisions of the body, tagmata and segmentation. — The palpigrade body is divided into two tagmata: prosoma and opisthosoma. The dorsal surface of the prosoma (prodorsum or aspidosoma) is subdivided into a propeltidium, a small paired mesopeltidium (often undistinguishable) and a metapeltidium, separated by soft skin. The border of these sclerites is not distinct, and they apparently represent pseudosclerites (cf. Grandjean, 1965: 557-558). The epimeral regions of palp and leg I are fused, those of legs II-IV are separated by soft skin. The soft skin between pro- and metapeltidium, between metapeltidium and opisthosoma, and between the epimera, permit of opisthosomatic movements in the vertical as well as in the horizontal plane²). The opisthosoma is subdivided into eleven segments (VII-XVII) and a flagellum. The segments are separated by intersegmental furrows, distinct in the dorsal region, partly less distinct in the ventral region.

Cuticle. — The chitinous tegument is thin, flexible and whitish. The borders between pseudoscleritic parts (cf. Van der Hammen, 1980: 131) and soft skin are indistinct. The cuticle presents a papillate microsculpture closely resembling

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¹) I am greatly indebted to Drs. Travé and Coineau for placing this rare material at my disposal.

²) The movability is not restricted to a single interval of soft skin, as in the case of dichoidy or ptychoidy in Oribatid mites (cf. Van der Hammen, 1980: 45, 131-132), but is attributable to two dorsal and probably three or four ventral intervals (figs. 1A, 2A, 3A).

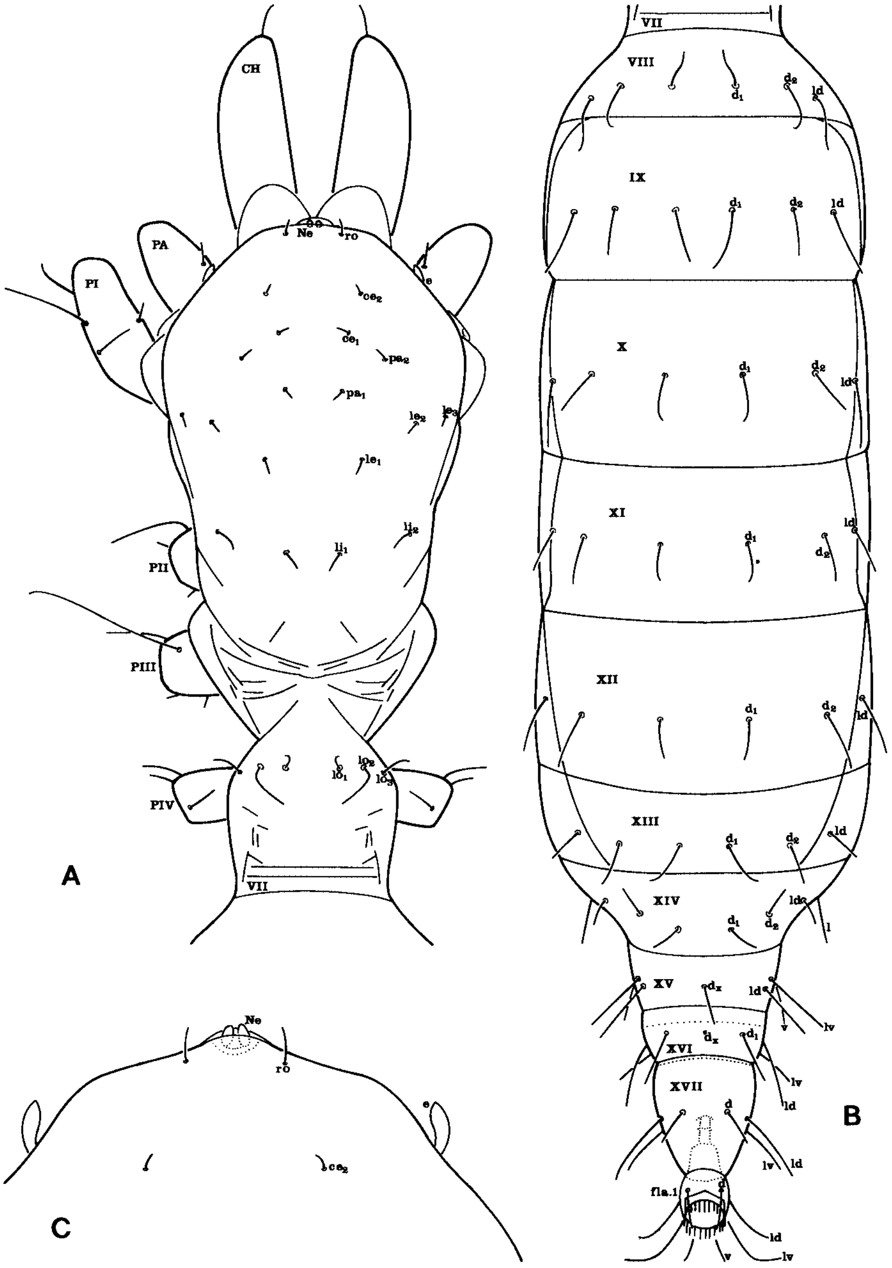

Fig. 1. *Eukoenenia mirabilis* (Grassi), adult female, dorsal view; A, prosoma and anterior part of opisthosoma; B, opisthosoma (greater part of flagellum omitted); C, rostral region; A, B, × 245; C, × 458.

a pubescence (cf. Monniot, 1970: 559, fig. B); it bears various types of phaneres. There are no lyrifissures. Respiration is supposed to be cutaneous, and one of the functions of the cuticle must consequently pertain to gaseous interchange.

Aspidosoma. — Four pseudosclerites are present, separated by soft skin: a propeltidium, a paired mesopeltidium and a metapeltidium. The soft skin is striate.The borders of the pseudosclerites are not distinct (figs. 1A, C, 3A, 8A). All specimens at my disposal presented an elevated rostral part, which is said to be an artificial condition caused by the preservation medium (alcohol); it could, however, also represent a relaxed condition (cf. Van der Hammen, 1969a: 42). The shape of living specimens appears to correspond with fig. 8A. There are no eyes. The frontal organ has more or less the shape of a pair of partly fused setae (figs. 1A, C, 3A, 4A, C, 6E). In *Leptokoenenia* the two elements are globular, with echinulate microsculpture and terminal point (fig. 8C). In living specimens, the frontal organ is hidden under the rostral part of the aspidosoma (fig. 8A). The frontal organ resembles, on the one hand, the lateral organ (the supracoxal seta *e*), and could, consequently represent the supracoxal setae of the chelicerae. It is, on the other hand, because of its position, also reminescent of the actinotrichid naso (also a frontal organ, which can sometimes present an inferior bilobate eye). The two hypotheses (which could both be valid) are simultaneously expressed in the notation (*Ne*). Apart from the frontal and lateral organ (the latter will be dealt with in the paragraph on the lateral aspect of the podosoma), there are thirteen pairs of aspidosomatic setae: ten pairs on the propeltidium (*ro*, ce_1, ce_2, pa_1, pa_2, le_1, le_2, le_3, li_1, li_2) and three pairs on the metapeltidium (lo_1, lo_2, lo_3). This number appears to be constant in all extant species of Palpigradi in which it is described in a reliable way (genera *Eukoenenia*, *Prokoenenia*, *Leptokoenenia*).

Dorsal and laterodorsal regions of opisthosoma. — The dorsal and laterodorsal regions of the opisthosomatic segments are perhaps partly pseudoscleritic. The intersegmental furrows are distinct. The posterior three segments (XV-XVII) are movable with respect to each other; they are slightly telescoping, and constitute a pygidium which can be slightly elevated with respect to segment XIV. The numbers of dorsal and laterodorsal opisthosomatic setae of the segments VIII-XIV (figs. 1B, 3B) appear to be constant in all species of Palpigradi in which it is described in a reliable way (genera *Eukoenenia*, *Prokoenenia*, *Leptokoenenia*); there are, on each of these segments, three pairs of dorsal and laterodorsal setae: d_1, d_2, and *ld*. The number is less constant in the posterior narrowed part of the opisthosoma (the segments XV-XVII, constituting the pygidium), in which, moreover, an unpaired dorsal seta d_x (or a vestige of it) can be present; the unpaired seta probably represents a fused pair. In the figured specimen (cf. figs. 1B, 3B), the dorsal and laterodorsal setae of segments XV-XVII are the following: XV, d_x, *ld*; XVI, d_x (vestige), d_1, *ld*; XVII, *d*, *ld*.

Flagellum. — The flagellum is movable: its basal piece articulates with an articular tooth inside segment XVII; it can be actively elevated and depressed by a set of antagonistic muscles (figs. 1B, 2B, 3B). In my specimens the flagellum was

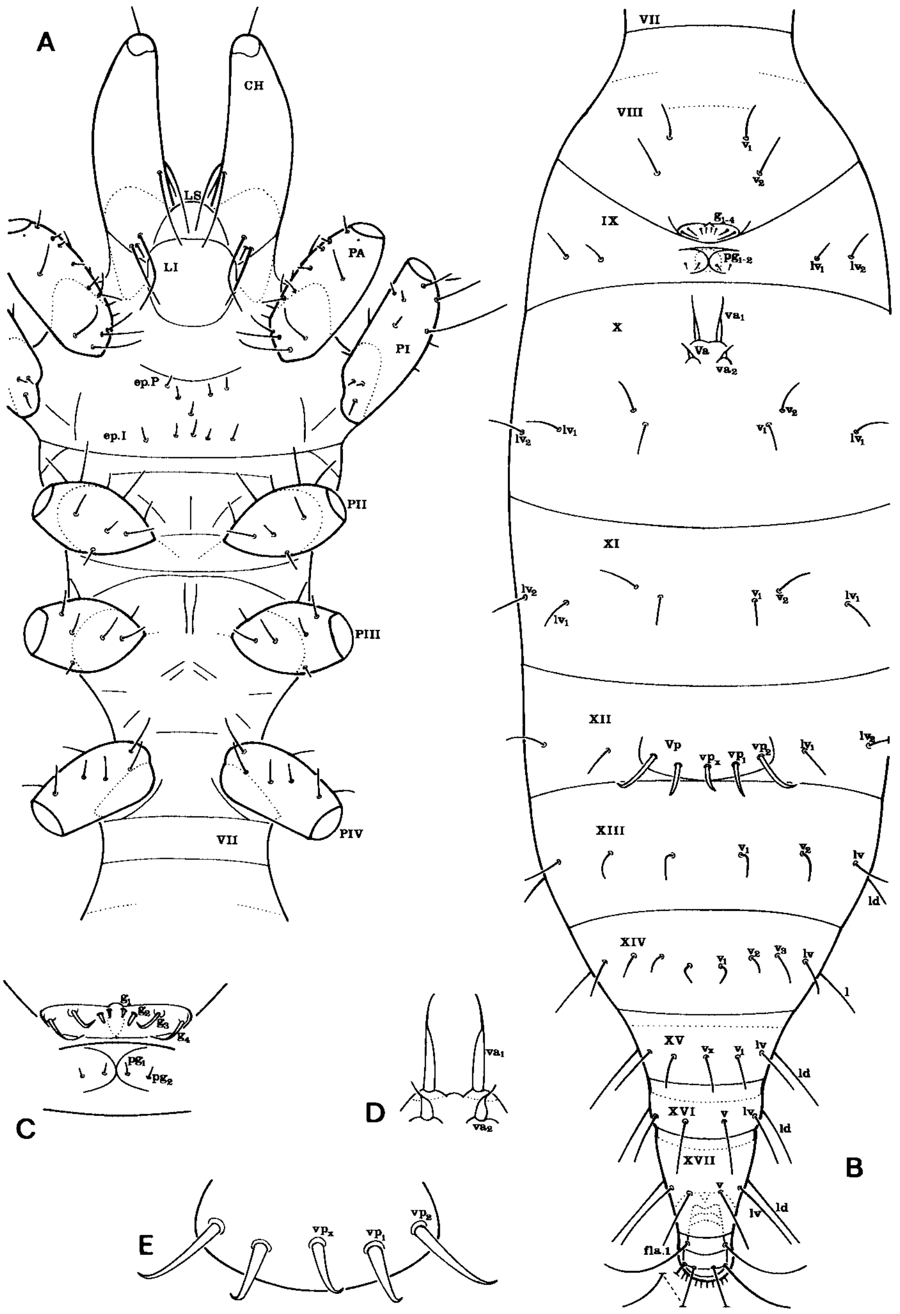

Fig. 2. *Eukoenenia mirabilis* (Grassi), adult female, ventral view; A, prosoma (and anterior part of opisthosoma); B, opisthosoma (greater part of flagellum omitted); C, genital region of segments VIII and IX; D, ventral verruca of segment X (anterior ventral opisthosomatic verruca); E, ventral verruca of segment XII (posterior ventral opisthosomatic verruca); A, B, x 245; C-E, x 458.

broken off, with the exception of the proximal segment. According to data in literature (fig. 8E) it is composed of a variable number of flagellar segments (often fourteen or fifteen, apart from the basal piece). The flagellar segments present verticils of 6-8 setae; some of the segments present moreover a terminal whorl of spines. The distalmost segment of the flagellum presents a terminal whorl of some seven setae. The flagellum is generally regarded as representing the telson, its presence constituting a primitive character. Although the presence of a telson must indeed be regarded as primitive, its segmented condition certainly constitutes a derived character state.

Ventral and lateroventral region of opisthosoma. — Ventrally, the intersegmental furrows of the opisthosoma can be less distinct, particularly in the anterior part. The ventral regions of the opisthosomatic segments are of unequal length, particularly because of the ventral shortening of segment IX, and the ventral lengthening of segment X. The segments can present ventral and lateroventral setae, lobes, verrucae and invaginable papillae. Segments VIII and IX of the female can be produced in the shape of one lobe (segment VIII) or two lobes (segment IX) (figs. 2B, C, 3B, C). In the male (fig. 8D) segments VIII and IX both present two lobes which can be subdivided. The lobes bear setae, some of which contain the ducts and orifices of glands. In *Prokoenenia*, segments X-XII each present a pair of invaginable papillae, reminiscent of the genital papillae of Actinotrichida. In *Eukoenenia mirabilis*, the ventral region of segments X and XII presents an unpaired wart-like structure with setae, here called anterior and posterior verruca (*Va*, respectively *Vp*; cf. figs. 2B, D, E, 3B); some of the setae of the verrucae contain the ducts and orifices of glands. The anterior and posterior verrucae could be homologous with a pair of papillae (they resemble the sternal and genital verrucae of Opilioacarida, which are supposed to be homologous with endites or exites of appendages). The anus has a ventral position in the distal part of segment XVII; it is best visible in lateral view (fig. 3B). The number of ventral and lateroventral opisthosomatic setae is more variable than the number of dorsal and laterodorsal setae; in literature, mention is made of sexual dimorphism pertaining to the number of ventral setae. In the figured specimen (cf. figs. 2B, 3B), the ventral and lateroventral setae are the following (there are no setae inserted on segment VII): VIII, $g_{1\text{-}4}$, $v_{1\text{-}2}$; IX, $pg_{1\text{-}2}$, $lv_{1\text{-}2}$; X-XI, $v_{1\text{-}2}$, $lv_{1\text{-}2}$; XII, vp_{x}, $vp_{1\text{-}2}$, $lv_{1\text{-}2}$; XIII, $v_{1\text{-}2}$, *lv*; XIV, $v_{1\text{-}3}$, *lv*, *l*; XV, v_{x}, v_{1}, *lv*; XVI-XVII, *v*, *lv*.

Ventral aspect of podosoma. — The coxisternal part of the podosoma (the palpigrade podosoma includes the coxisternal region of the palp) is constituted by epimera, separated by intersegmental intervals of soft skin (fig. 2A). The epimera are partly or completely pseudosclerotized (data published until now are contradictory); a detailed comparative study of the pseudoscleritization in various Palpigrade genera, after staining with Chlorazol Black (cf. Coineau, 1974), will be interesting. The epimera of palp and leg I are fused to a single pseudosclerite (figs. 2A, 4B). Epimera II and III of *Leptokoenenia* (cf. Monniot, 1966: 48, fig. 4) each consist of several pseudosclerites; fig. 2A of the present

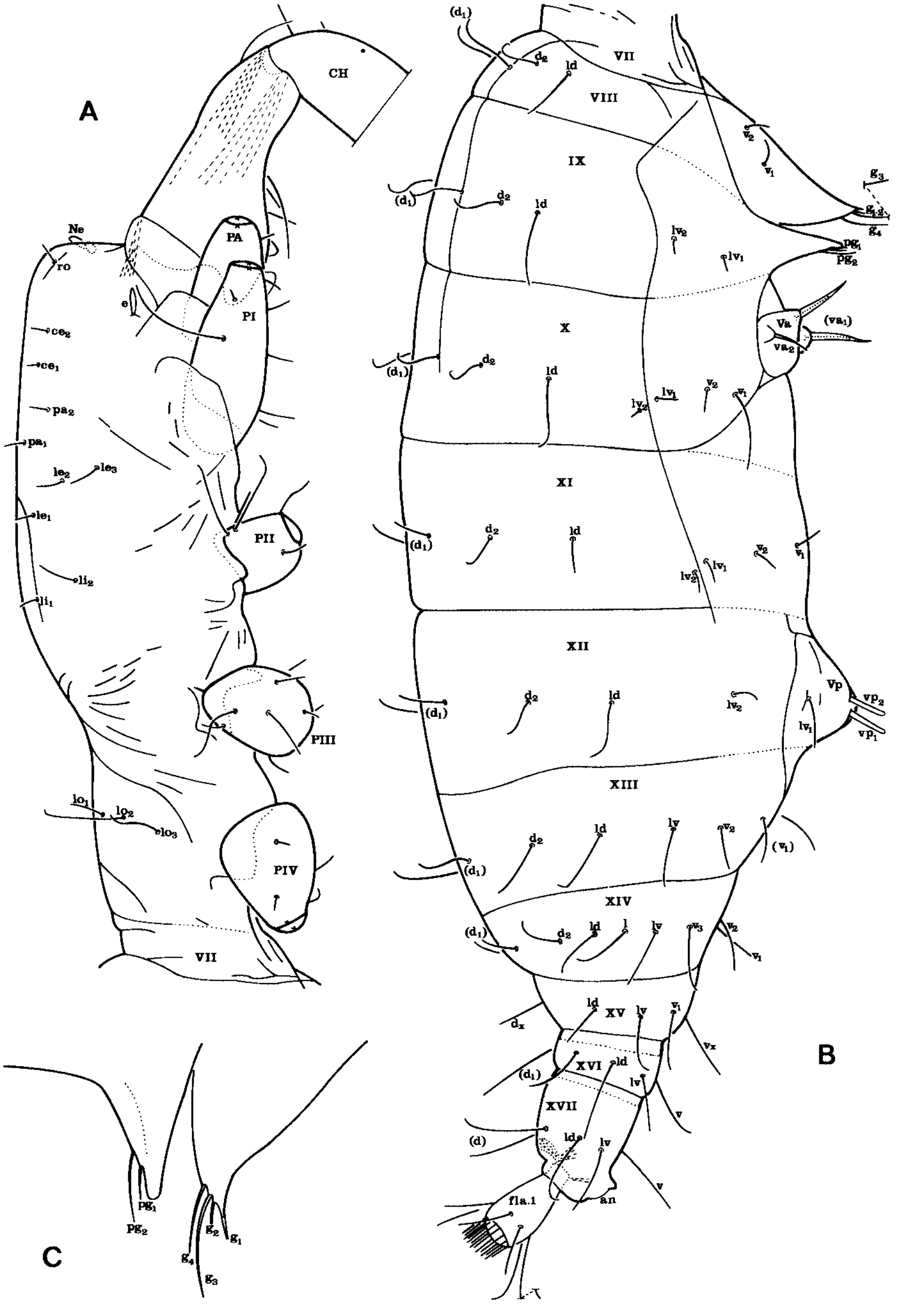

Fig. 3. *Eukoenenia mirabilis* (Grassi), adult female, lateral view; A, prosoma (with anterior part of opisthosoma); B, opisthosoma (greater part of flagellum omitted); C, genital region; A, B, × 245; C, × 458.

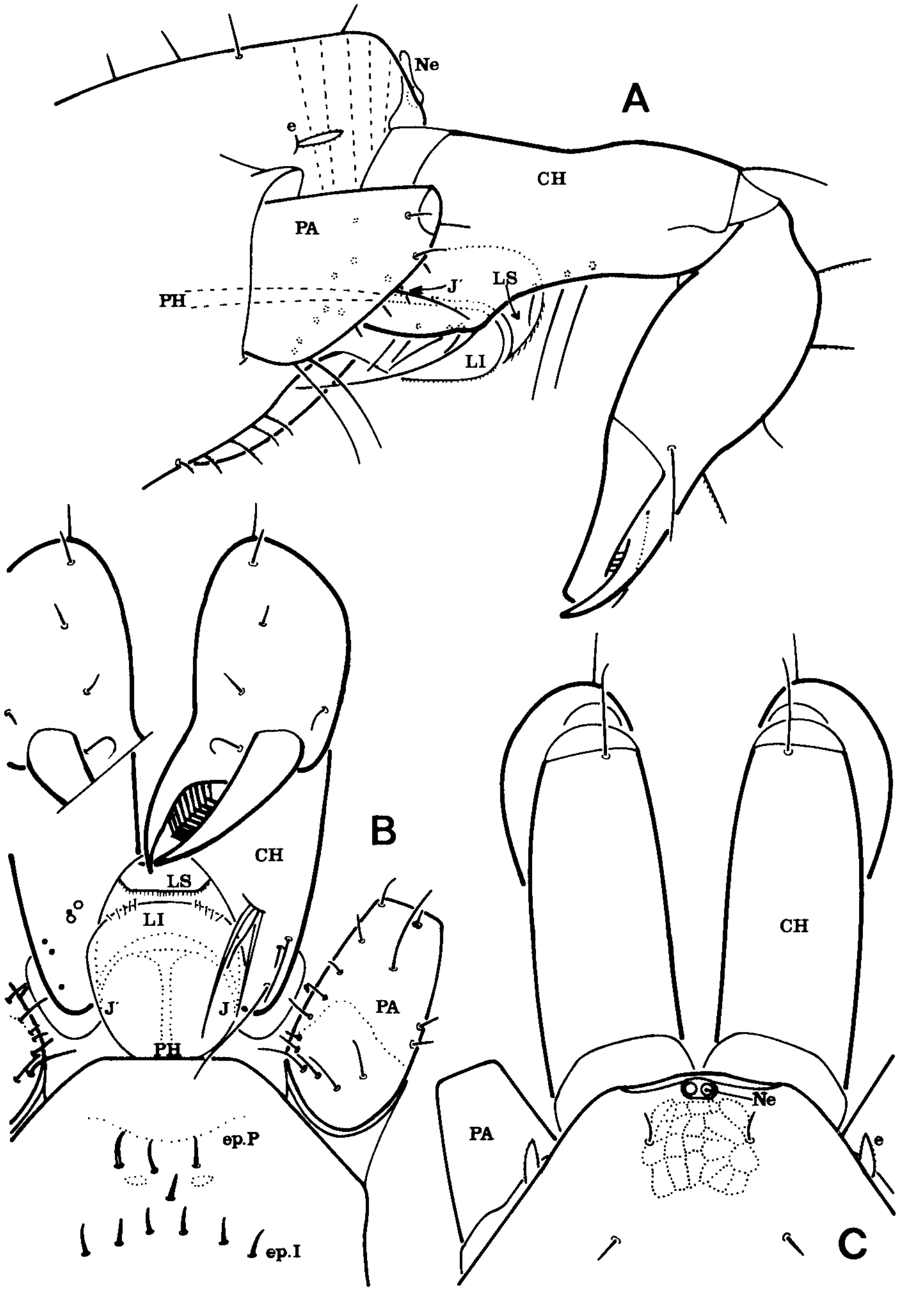

Fig. 4. *Eukoenenia mirabilis* (Grassi), female, anterior region of prosoma with mouthparts; A, lateral view; B, ventral view; C, dorsal view; A-C, × 368. (Redrawn after Van der Hammen, 1969a).

paper suggests that the same condition could be present in *Eukoenenia*. Epimeron IV consists of a single pseudosclerite. The intersegmental intervals are extensile; the normal condition in living specimens is represented in fig. 8B, whilst the specimen of fig. 2A is completely stretched out. The pseudosclerite constituting the epimera of palp and leg I presents epimeral setae, of which the number varies not only with sex and age, but shows also specific differences.

Lateral aspect of podosoma. — The supracoxal setae *e* of the palp are inserted in the lateral region of the podosoma, above the palpal acetabulum (figs. 3A, 4A, 6E); in Actinotrichida, supracoxal setae are also associated with the base of the appendages (cf. Van der Hammen, 1980: 153-154). The supracoxal setae can be multiplied; the numbers recorded in literature, for different species, vary from one to five (cf. fig. 8F-H). Multiplication of supracoxal setae is also known from Actinotrichida (cf. Van der Hammen, 1977a: 13-15, fig. 2F, H-L). The orifice of the coxal gland is above the acetabulum of leg I (cf. fig. 6E), as in Actinotrichida; the coxal gland itself was described by Millot (1942: 42-45, fig. 7). There could be a primitive podocephalic canal, extending from the orifice of the coxal gland to the mouth, although it could not be discerned by me with absolute certainty. At the base of palp and leg I, the prosoma is slightly extending, constituting a coxal region; the soft skin does not represent a coxa, nor does it exclusively represent an arthrodial membrane. The lateral aspect of the palpigrade prosoma resembles that of Actinotrichida in many respects.

Mouthparts. — In Palpigradi, the elements involved in food-intake comprise the labrum or upper lip, the labium or under lip, the mouth (and pharynx) and the chelicerae (fig. 4). The chelicerae are described below in a separate paragraph. The mouth is situated between the bases of the chelicerae. It is crescent-shaped; there are two oral commissures (*J* and *J'*), at the places of junction of labrum and labium. The bases of the two lips have fused[1]). The dorsal face of the labrum is convex. It overhangs the labium and is capable of closing the preoral cavity. Its anterodorsal surface presents numerous ciliae. The labium is rounded and swollen in its anterior part. According to Millot (1942: 36, fig. 2), it contains many glandular (mucous) cells.

Chelicera. — The first pair of appendages (figs. 4, 5A) is composed of trochanter, body of chelicera (the terminal part of which constitutes the fixed jaw), and apotele (the movable jaw); fixed jaw and movable jaw constitute the chela. The three segments are well developed and the chelicera is relatively large. The articulations between trochanter and body of chelicera, and between body of chelicera and apotele, are bidesmatic and bicondylar. The articulation between prosoma and chelicera (at the base of the trochanter) is apparently tridesmatic. At the base of the chelicera (as mentioned above, a similar condition is found at the bases of palp and leg I), the prosoma is slightly extending, constituting a coxal region; the soft skin does, however, not represent a coxa, nor

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[1]) The base of the labrum (i.e. the part which has fused with the labium) could, in reality, represent the cervix (cf. Van der Hammen, 1980: 28-29).

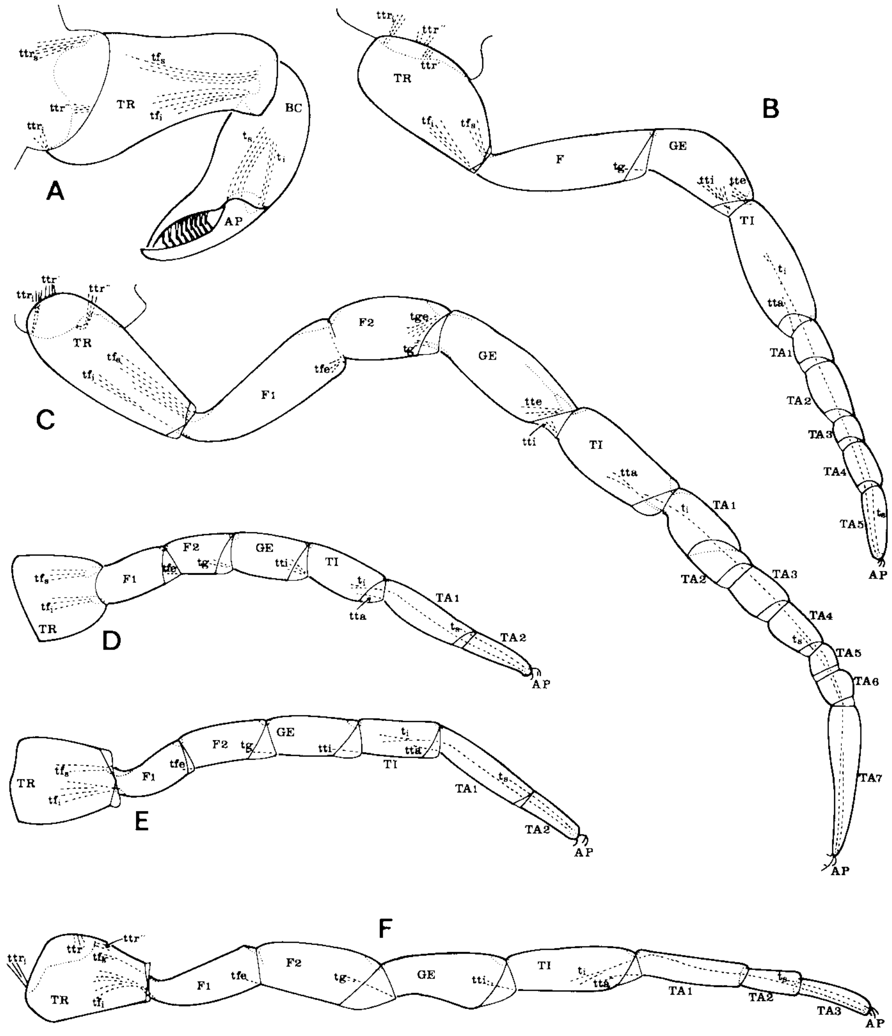

Fig. 5. *Eukoenenia mirabilis* (Grassi), adult female, segmentation and articulation of the appendages; A, lateral (antiaxial) view of right chelicera; B, lateral (antiaxial = posterior) view of right palp; C, lateral (antiaxial = posterior) view of right leg I; D, lateral (antiaxial = posterior) view of right leg II; E, lateral (paraxial = posterior) view of right leg III; F, lateral (antiaxial = anterior) view of left leg IV; A-F, × 245.

does it exclusively represent an arthrodial membrane. The plane of pseudosymmetry of the body of the chelicera has been subject to considerable torsion: the chela operates in a plane nearly perpendicular to the axis of the body; of the two jaws of the chela, the apotele (the movable jaw) is the antiaxial one. Both jaws of the chela present some nine oblique, narrow, pointed teeth. The cheliceral trochanter and the body of the chelicera present several setae; in *Eukoenenia mirabilis*, two groups of three ventral setae of the trochanter appear to be associated with the lips.

Palp and legs. — The segmentation and articulation of palp and legs is represented in fig. 5B-F. The segments of the palp are: trochanter, femur, genu (patella), tibia, tarsus 1-5, and apotele. All legs present the following segments: trochanter, femur 1, femur 2, genu (patella), tibia, a variable number of tarsal segments, and apotele. The adesmatic tarsal segments of the legs are the following: leg I, tarsus 1-7; legs II-III, tarsus 1-2; leg IV, tarsus 1-3. There is no evidence for an ancestral division of the tarsus into basi- and telotarsus. The articulation between trochanter and body (in the case of palp and legs) apparently constitutes a rocking joint (cf. also fig. 6A). The articulation between trochanter and femur (or femur 1) constitutes a bidesmatic, bicondylar, bivalent pivot joint, with levator and depressor muscles. The articulation between femur 1 and femur 2 of the legs (in the case of legs I and IV, the separation is incomplete at the posterior face) is constituted by a monodesmatic, monocondylar, monovalent hinge joint; the muscles of this articulation are distinctly present, although I did not discern them in 1977 (cf. Van der Hammen, 1977a: 13, fig. 1F, G). The articulation between femur and genu of the palp, and between femur 2 and genu of legs II-IV are also constituted by normal hinge joints. The articulations between femur 2 and genu of leg I, and between genu and tibia of palp and leg I, are constituted by bidesmatic, monocondylar hinge joints; the two sets of muscles of these joints are flexor and extensor muscles respectively. The extensor muscles are inserted just above the articulation point; in lateral view, they seem to pass through the condyle (fig. 6B, D). A hinge joint with extensor muscle is also found in the palp of some Cryptognomae (cf. Van der Hammen, 1979a: 25, figs. 12B, 28A). The occurrence of this type of joint in palpigrade palp and leg I is apparently not only associated with the palpal function of leg I, but also points to the palpal (not ambulatory) origin of the palp. The articulation between genu (patella) and tibia of legs II-IV is constituted by a hinge joint with flexor muscles only. The articulation between tibia and tarsus 1 of palp and legs is contituted by a monocondylar, monovalent hinge joint; one tendon is inserted on the base of the tarsus (*tta*), whilst the inferior tendon of the apotele (t_i) passes on into the tibia. The articulation between the tarsal segments is adesmatic; they are moved under the influence of the tendons of the apotele (t_s and t_i). The articulation between tarsus and apotele of palp and legs is bidesmatic, bicondylar and bivalent (fig. 6C). Palp and legs present various types of phaneres (fig. 7). Ordinary setae are present in all segments (the three claws of palp and legs I-IV are considered homonomous with ordinary setae). Trichobothria (also homonomous with ordinary setae) are found on genu (patella) and tarsi 1, 2, 4 and 6 of leg I (cf. 7A, D). The number of trichobothria on tarsi 1-7 of leg I in *Eukoenenia mirabilis* and *Leptokoenenia scurra* can be represented by the formula 2-2-0-1-0-1-0. Tarsi 2, 3, 5 and 7 of leg I (and tarsi 1 and 3 of leg IV in *Leptokoenenia scurra*) present moreover a different type of phanere (figs. 7D, E, 8I, J), which could be homonomous with

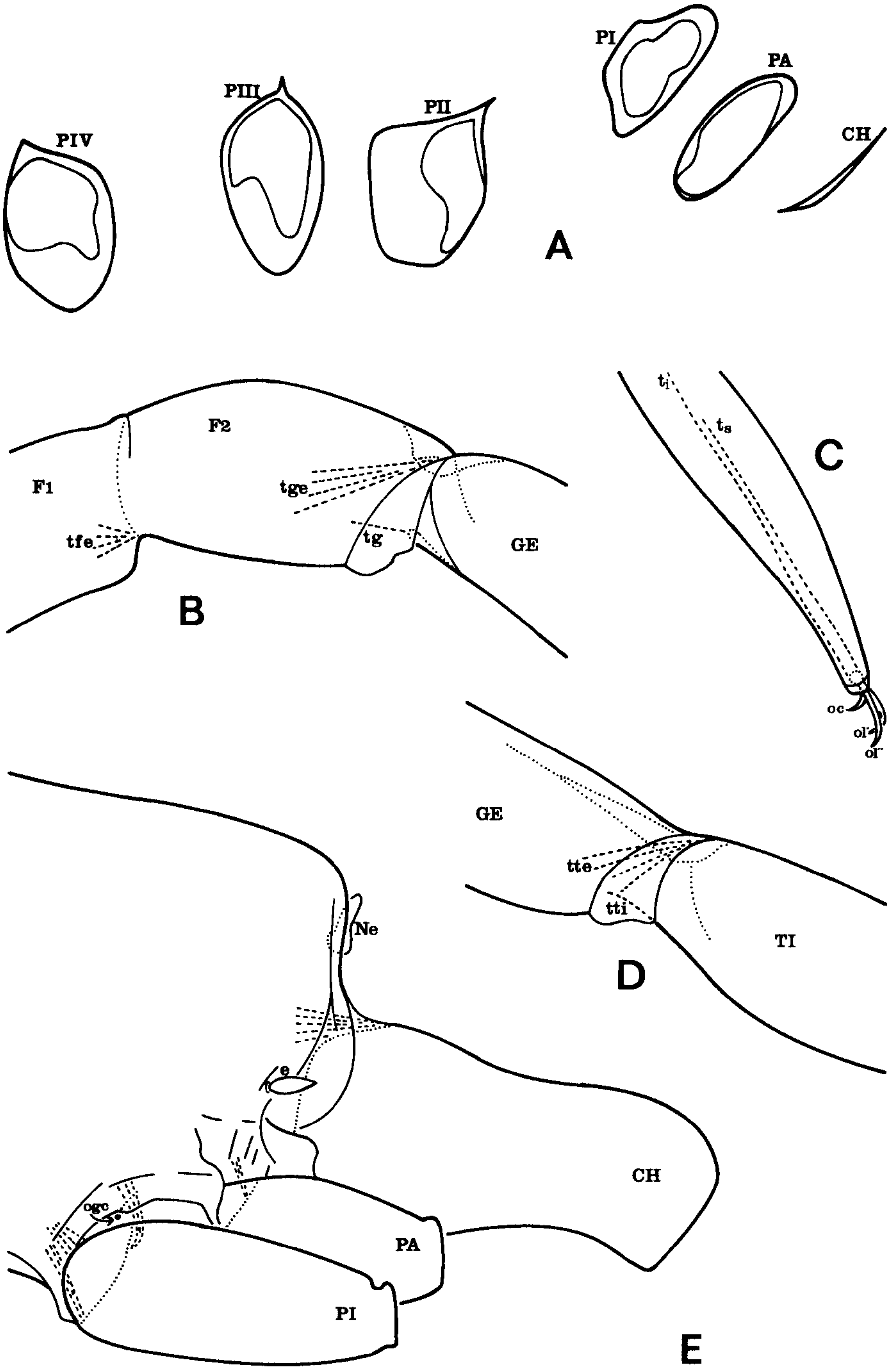

Fig. 6. *Eukoenenia mirabilis* (Grassi), adult female; A, base of the appendages of the left side, viewed from the interior (and slightly from below); B, distal part of femur 1, femur 2, and proximal part of genu of right leg I, lateral (antiaxial) view; C, distal part of tarsus 6, and apotele of right leg I, lateral view; D, distal part of genu, and proximal part of tibia of right leg I, lateral (antiaxial) view; E, anterior part of prosoma, lateral view (obliquely from above); A, × 368; B-D, × 687; E, × 470.

a solenidion (cf. Van der Hammen, 1980: 144); this type is long, stiff, flat, hollow, more or less reclining (i.e. bending toward, or applied to, the surface of the appendage), and often more or less blunt (i.e. without point). These stiff phaneres have a rectangular section, whilst each of the angles presents a longitudinal row of ciliae. A fourth type of phanere is constituted by the bifurcate phaneres occurring, for instance, on tarsus 4, 6 and 7 of leg I in *Eukoenenia mirabilis*, and apparently also on tarsus 5 of the palp in *Leptokoenenia scurra* (cf. figs. 7F, 8I, J); these bifurcate phaneres could be homonomous with the Actinotrichid famulus (cf. Van der Hammen, 1980: 62-63). The claws of palp and legs are tridactyl; the central claw represents a true claw (not an empodium).

Internal anatomy. — Important contributions to our knowledge of the internal anatomy were published by Rucker (1901, 1903), Börner (1904), Millot (1942, 1943), Firstman (1973) and Alberti (1979). Summaries were given by Kaestner (1932), Roewer (1934), Millot (1949) and Rowland & Sissom (1980). The following is a compendious survey. The alimentary canal consists of mouth, pharynx, oesophagus, midgut and caeca (one pair in the prosoma, six in the opisthosoma), hindgut (rectum) and anus. The excretory system comprises the coxal glands, and absorption cells in the gut; there are no Malpighian tubes, nor any other excretory organ. The palpigrade endosternite is more primitive than that of any other extant Chelicerate: there are six pairs of ventral suspensors, four pairs of dorsal suspensors, and five pairs of lateral suspensors. The circulatory system is very simple. The central nervous system consists of a relatively large supraoesophageal ganglion and a smaller suboesophageal ganglion; from the posterior end of the suboesophageal ganglion a nerve cord passes to the opisthosoma, in the anterior part of which there are three distinct ganglionic swellings. The male reproductive system comprises paired testes; palpigrade sperm and spermiocytogenesis present derived characters and are strongly different from other groups of Chelicerates. The female reproductive system comprises two ovaries and two oviducts which converge in the uterus. A pair of prosomatic glands of unknown function debouches posteriorly of leg II. Several opisthosomatic glands are associated with the genital lobes and the opisthosomatic verrucae; the orifice of these glands is in the terminal part of large setae. The opisthosomatic musculature consists of longitudinal (dorsal, lateral, ventral), oblique and dorsoventral muscles; there are five pairs of dorsoventrals (in segments VIII-XII).

Postembryonic development. — Our knowledge of the palpigrade life-cycle is based on the study by Rucker (1903) who described three immature instars and the adult of *Prokoenenia wheeleri*. The instars are, among others, distinctly different in size, chaetotaxy, development of the genital region, characters of the flagellum, and the number of opisthosomatic papillae (in segments X-XII). The behaviour of the papillae (they are known from *Prokoenenia* only) in the course of postembryonic development is interesting because it reminds us of the postembryonic development of the genital papillae in Actinotrichida (the normal development of the Actinotrichid papillae is the following: absent in prelarva and

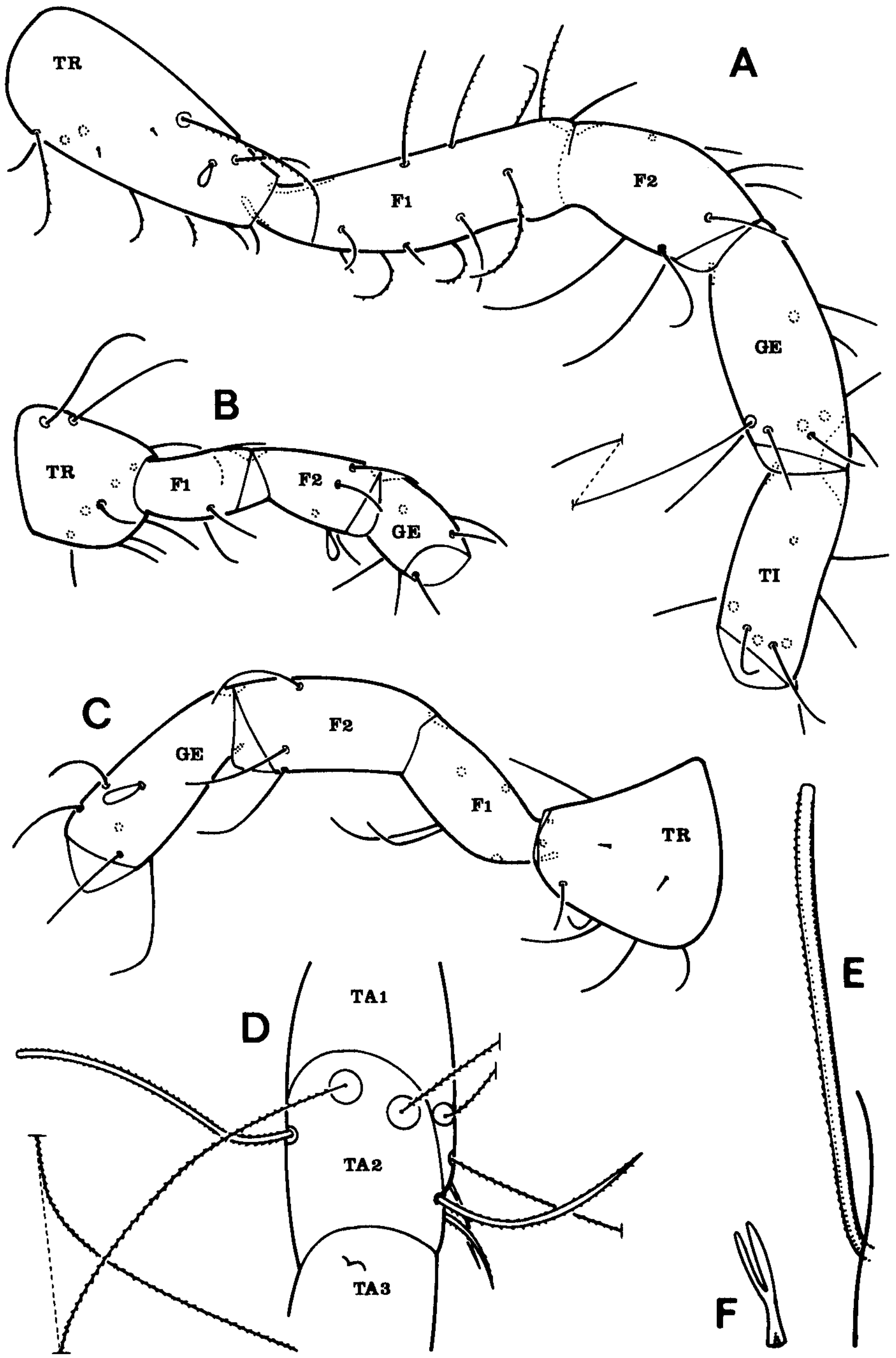

Fig. 7. ***Eukoenenia mirabilis*** (Grassi), adult female; A, trochanter, femur 1, femur 2, genu and tibia of right leg I, lateral (antiaxial) view; B, trochanter, femur 1, femur 2 and genu of right leg II, lateral (antiaxial) view; C, trochanter, femur 1, femur 2 and genu of right leg IV, lateral (antiaxial = anterior) view; D, distal part of tarsus 1, tarsus 2, and proximal part of tarsus 3 of right leg I, lateral (antiaxial) view; E, reclining phanere (supposed solenidion) of tarsus 7 of right leg I, ventral view; F, right "famulus" of tarsus 7 of right leg I, ventral view; A-C, × 368; D, × 707; E-F, × 1312. (Redrawn after Van der Hammen, 1977a).

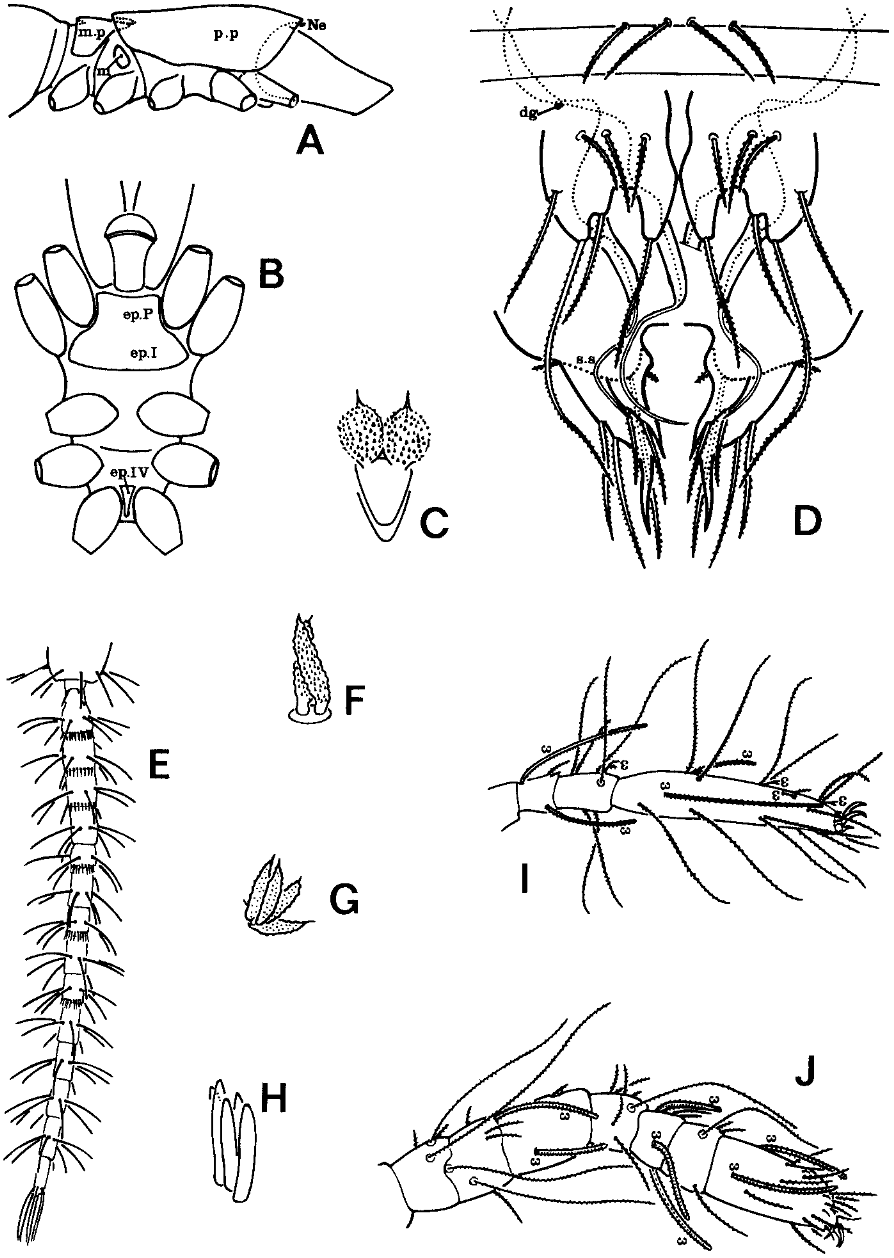

Fig. 8. Details of various Eukoeneniid species. A, B, *Eukoenenia mirabilis* (Grassi); A, lateral view of prosoma and anterior part of opisthosoma; B, ventral view of prosoma. C-F, *Leptokoenenia scurra* Monniot; C, frontal organ *Ne*; D, ventral view of male genital region; E, flagellum of female; F, supracoxal setae *e*. G, *Prokoenenia millotorum* Rémy, supracoxal setae *e*. H, *Eukoenenia pyrenaica* (Hansen), supracoxal setae *e*. I, *Eukoenenia mirabilis* (Grassi), lateral view of tarsi 5-7 and apotele of leg I. J, *Leptokoenenia scurra* Monniot, lateral view of tarsi 1-7 and apotele of leg I. A, B, about 75 × ; C, F, G, H, much enlarged; D, about 310 × ; E, about 125 × ; I, about 350 × ; J, about 300 × . (A, B, redrawn after Millot, 1949; C-F, J, redrawn after Monniot, 1966; G, redrawn after Rémy, 1950; H, redrawn after Hansen, 1926; I, redrawn after Börner, 1901).

larva, one pair in the protonymph, two pairs in the deutonymph, three pairs in the tritonymph and the adult). Rucker found no papillae in the first known instar of *Prokoenenia*, two pairs in the second known, and three pairs in the third known instar and the adult. There is an important gap between the sizes of Rucker's first and second known instar, and the occurrence of an instar of intermediate size, with one pair of papillae, seems highly probable. Judging from conditions known in Actinotrichida, the palpigrade life-cycle could include the following instars (stases): prelarva (probably an elattostase or a calyptostase), larva (Rucker's first known instar), protonymph, deutonymph (Rucker's second instar), tritonymph (Rucker's third instar), and adult. A schematic representation of the postembryonic development of the opisthosoma in the stases of this hypothetical life-cycle is given in fig. 9. A further discussion of postembryonic development and evolution of epimerate opisthosomatic papillae is given in the chapter on Actinotrichida, and in the chapter on evolution of epimerate characters.

C. Remarks

Species of Palpigradi are known from the tropical, subtropical or warm regions of Europe, Asia, Africa and America. It is interesting to mention, in this connection, the living palpigrade specimen collected by Grandjean near Périgueux (Dordogne), France, and recorded by me in the introduction to the second volume of his Complete Acarological Works (Van der Hammen, 1973a: v); this specimen now constitutes one of the northernmost records for the group.

An extinct species, supposed to constitute a separate palpigrade family, was described from the Jurassic of Germany (Haase, 1890: 11; 1890a: 653-657, pl. 31). A fossil Eukoeneniid is now known from the Tertiary of Arizona, U.S.A. (Rowland & Sissom, 1980). Extant palpigrade species apparently prefer the deeper layers of the soil, although they have also been found in litter and on the surface of the soil (after heavy rain). Two species are known from interstitial biotopes. According to Monniot (1966: 42), the behaviour of her interstitial Palpigradi in water was normal. It has been suggested that Palpigradi are of marine origin,and that, in the course of evolution, members of this group colonized the terrestrial soil, in passing the interstitial environment (Monniot, 1966; Van der Hammen, 1977). It is generally assumed that terrestrial life was not possible before the Silurian (because of the penetration of harmful radiation, owing to the low oxygen content of the atmosphere). Life in the deeper layers of the soil must, however, have been possible at an earlier moment in the history of the earth, and Palpigrades (together with Actinotrichida) could have been among the earliest terrestrial animals.

Although Palpigradi present a great number of primitive characters (they probably constitute the Chelicerate group with the most important number of ancestral characters), they have developed many derived characters, of which the following are mentioned here: the development of the "telson" into a many-

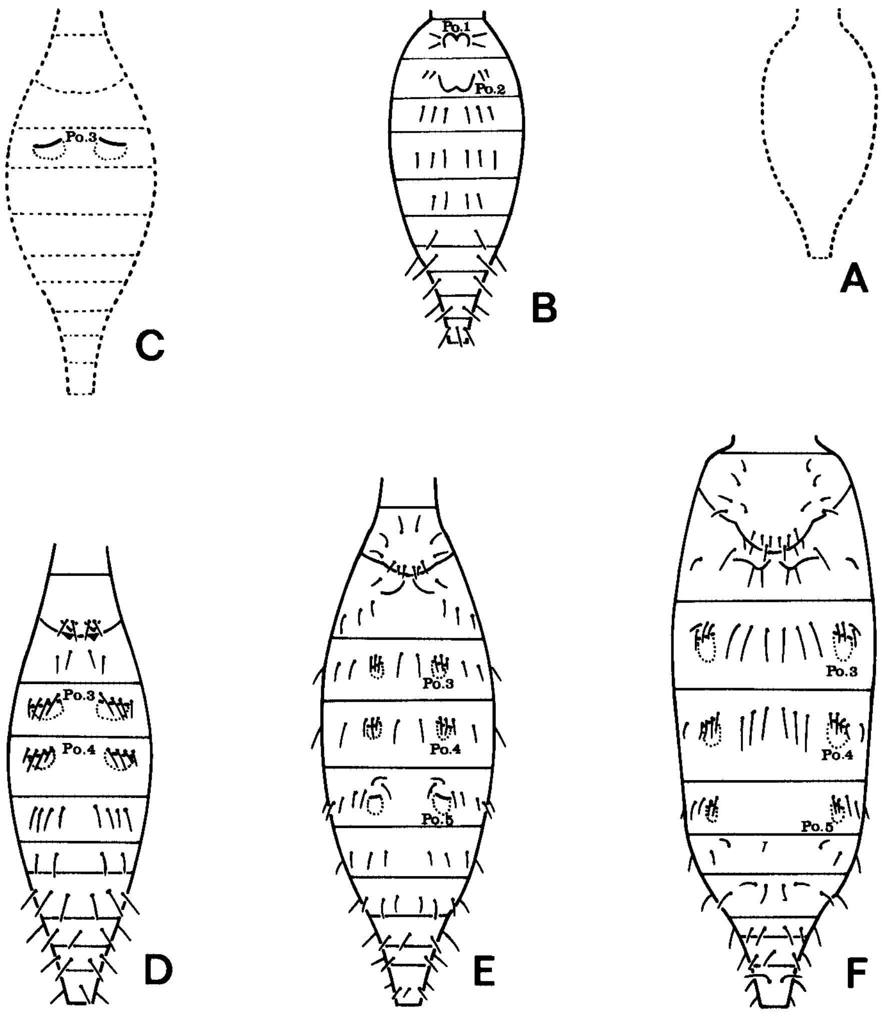

Fig. 9. Schematic representation of the postembryonic development of the opisthosoma (ventral view; flagellum omitted) in *Prokoenenia wheeleri* (Rucker). In this species (as in other Palpigradi) the life-cycle is still incompletely known, and the present representation is partly hypothetical. A, hypothetical first instar (prelarva); B, second instar or larva (representing the first instar now known to us), with evaginated papillae *Po1* and *Po2*; C, hypothetical third instar (protonymph), with invaginated opisthosomatic papillae *Po3*; D, deutonymph (representing the second instar now known to us), with invaginated opisthosomatic papillae *Po3* and *Po4*. E, female tritonymph (representing the third instar now known to us), with invaginated opisthosomatic papillae *Po3*, *Po4* and *Po5*; F, adult female, with invaginated opisthosomatic papillae *Po3*, *Po4* and *Po5*. A-F, about 90 ×. (B, D, E, F, based on Rucker, 1903).

segmented flagellum; the development of the opisthosomatic appendages into genital lobes, evaginable papillae and opisthosomatic verrucae; the specialized morphology of the sperm (possibly connected with the life habits in an environment close to the groundwater); the fusion of the epimera of palp and leg I; the multiplication of the supracoxal seta *e*, in many species; the association of setae of the cheliceral trochanter with the lips; the torsion in the body of the chelicera; the subdivision of the tarsus of palp and legs; the occurrence of extensor muscles in palp and leg I; and the presence of trichobothria.

Important contributions to the study of palpigrade evolution (and the interpretation of character states) could be produced by a comparative study of the postembryonic development (cf. Van der Hammen, 1981), as soon as the lifecycle of several species will be completely known.

III. ACTINOTRICHIDA

The mites, here classified with the subclass Actinotrichida, were first recognized as constituting a separate group (Trombidi-Sarcoptiformes) by Oudemans (1931: 318). Oudemans (1936: 3; 1940: 295) subsequently restricted the use of the name Acari to his Trombidi-Sarcoptiformes, and classified this group, together with Scorpionida, Pedipalpi, Anthracomarthi, Pseudoscorpionida, Solifugae, Opilionida and Ricinulei, with his Fixicoxata.

Grandjean (1935: 123-126; 1936: 84-85, 88-89) distinguished the same group of mites, which he named Actinochitinosi, and mentioned several of its characters. A more detailed study of the distinguishing characters and the affinities (Grandjean pointed to a certain resemblance to Solifugae) was published by him shortly afterwards (Grandjean, 1936a: 438-442). Later on (Grandjean, 1970: 800-807, 809-814), he reinvestigated and discussed the characters and affinities of the group.

Zakhvatkin (1952: 10-24, 44, figs. 1-15) replaced the name Actinochitinosi by Acariformes, and classified the group, together with Palpigradi, Solifugae, Schizomida and Pseudoscorpionida, with his Actinochaeta.

Van der Hammen (1961: 179; 1966: 63; 1968a: 277; 1968b: 403, 404; 1969: 194-196; 1972: 3, 36; 1972a: 274-279, 280-281, 283, 286-289; 1973: 275-278; 1977: 316) introduced the name Actinotrichida (proposed by Grandjean), and studied the distinguishing characters and affinities. He pointed, among many other characters, to the fundamental differences between the actinotrichid and the anactinotrichid gnathosoma (podocephalic canal in Actinotrichida; sternal taenidia and/or subcapitular gutter in Anactinotrichida)¹).

Weygoldt & Paulus (1979, 1979a) and Weygoldt (1980) returned to a classification of Actinotrichida with Acari (together with Anactinotrichida), although they were convinced of the polyphyletic origin of the group. They

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¹) Another fundamental difference is constituted by the incorporation of the labium in the anactinotrichid mentum (cf. Van der Hammen, 1979a: 24).

united Acari and Ricinulei as Acarinomorpha (supposing the Acari were different from Ricinulei by the possession of a gnathosoma, although a gnathosoma is also present in the last-mentioned group).

Alberti (1980a) investigated the fine structure of spermatozoa and spermiocytogenesis of Actinotrichida. He pointed to the fundamental differences (in this respect) from Anactinotrichida (including Opilioacarida; his study confirmed the monophyletic origin of the group), and pointed to the presence of interesting similarities between Actinotrichida and Solifugae, and the absence of striking similarities between Actinotrichida and Palpigradi (as far as sperm morphology and cytogenesis is concerned).

Actinotrichida are divided here into four orders: Actinedida, Oribatida, Tarsonemida and Acaridida. The present paper deals with representatives of all four orders, although preferably with free-living and more primitive representatives. It might be remarked here that the morphology of Acaridida is still insufficiently known; it will be the subject of a separate paper, in which the relationships of the four groups will be rediscussed.

A. Material

The present chapter is based on the study of several species, together representing the four Actinotrichid orders. These species are enumerated below, in a survey of the material, in which the systematic position is indicated. The survey includes the species of which I have made no original study, but of which a drawing is adopted from literature. References are given to the sources of these drawings (and also to my own papers, in case reference is made to an earlier study of the material by me).

Order Actinedida

Suborder Endeostigmata (= Alycina)

1. *Alycus roseus* C. L. Koch (family Alycidae) (figs. 11, 14A, 15G, 16, 19B, 21E).
   Locality and date: Arnhem, The Netherlands, 9 September 1965.
   Reference: Van der Hammen, 1969.

Suborder Anystina

2. *Tarsolarkus* spec. (family Anystidae) (fig. 22A, B).
   Locality and date: Mongaillard, Coulounieix (Dordogne), France; on low plants in a rather barren pasture, during the warm hours of the day, in the full sun, in July and August.
   Reference: Grandjean, 1952a.
3. *Tetranychus urticae* C. L. Koch (family Tetranychidae) (fig. 14G, E).
   Locality and date: Amsterdam, The Netherlands (culture), 22 November 1974.

4. *Cheyletus eruditus* (Schrank) (family Cheyletidae) (fig. 20C).
Locality and date: Zuidwijk, Wassenaar, The Netherlands, in a poultry-house, 3 September 1962.

Suborder Trombidina (= Parasitengona)

5. *Oecosmaris callitricha* Grandjean (family Smarididae) (fig. 15E).
Locality: Mongaillard, Coulounieix (Dordogne), France.
Reference: Grandjean, 1947.

Order Oribatida

Suborder Palaeosomata

6. *Aphelacarus acarinus* (Berlese) (family Aphelacaridae) (figs. 10, 14C, 15A, 21A-D).
Locality and date: Leiden, The Netherlands, in culture of *Liposcelis* killed before by heat, 28 January 1981.

Suborder Enarthronota

7. *Cosmochthonius lanatus* (Michael) (family Cosmochthoniidae) (fig. 19A).
Locality and date: Mongaillard, Coulounieix (Dordogne), France, in house, July 1924-September 1929.
Reference: Grandjean, 1947a (sub: *Cosmochthonius domesticus* Grandjean).

Suborder Mixonomata

8. *Eulohmannia ribagai* (Berlese) (family Eulohmanniidae) (figs. 15B, D, 22G).
Localities and dates: Warnsborn, Arnhem, The Netherlands, litter of oak, 18 June 1965. Menez Hom, near Châteaulin (Finistère), Britanny, France, June 1932.
Reference: Grandjean, 1939.
9. *Epilohmannia cylindrica* (Berlese) (family Epilohmanniida) (figs. 14B, 15C).
Locality and date: Mongaillard, Coulounieix (Dordogne), France, in the soil of a bush in a pasture, 3 September 1959.
10. *Phthiracarus laevigatus* (C. L. Koch) (family Phthiracaridae) (fig. 20B).
Locality and date: Surroundings of Regensburg, Bavaria, Germany (type-locality), July 1959 and June 1961.
Reference: Van der Hammen, 1963a.

Suborder Nothrina

11. *Hermannia convexa* (C. L. Koch) (family Hermanniidae) (figs. 14D, E, 15F, 17, 18, 19C, D, 20A, 21F, G, 23, 24).
Locality and date: Schwaighauser Forst, N. of Regensburg, Bavaria, Germany (type-locality), July 1959, June 1961. References: Van der Hammen, 1968, 1972.

12. *Archegozetes magna* (Sellnick) (family Trhypochthoniidae) (fig. 12).
    Locality and date: Oeriv, Padaido Islands, former Netherlands New Guinea, beach-forest (*Barringtonia* formation), litter, 3 March 1954.
    References: Van der Hammen, 1955, 1955a, 1981a.

Order Tarsonemida

13. *Tarsonemoides limbatus* Van der Hammen (family Tarsonemidae) (fig. 22C, D).
    Locality and date: Near Rû de Gally, Parc de Versailles, France (type-locality), wet moss in alder-marsh, 22 November 1961.
    Reference: Van der Hammen, 1970.

Order Acaridida

14. *Fusacarus* spec. (family Fusacaridae) (fig. 22E, F).
    Locality and date: Hammam Meskoutine, Algeria, litter, etc. in a hollow olive-tree, March 1935.
    Reference: Grandjean, 1953.

B. Descriptive part

Habitus (fig. 10). — Small or very small Chelicerata, rarely medium-sized (the length of the body of *Dinothrombium tinctorium* (L.), the largest known Actinotrichid mite, is up to 1.6 cm), exhibiting a great variety in facies, varying from narrow to semi-globular, from soft-skinned to heavily sclerotized, from hairy to nearly glabrous, and from pale to bright-coloured. The length of the legs varies from relatively short to relatively very long.

Divisions of the body, tagmata and segmentation. — The original division of the actinotrichid body is into a prosoma and an opisthosoma, the two being separated by the disjugal furrow. Incomplete segmentation of the opisthosoma is present in various species. In the course of evolution, the constitution of the actinotrichid body has been subject to important changes. Fusion of segments, shifting of the paraproctal region from a posterior terminal to a ventral position, changes in the genital region by the evolution of a progenital chamber (see below), and the evolution of pseudotagmata and other subdividions of the body (fig. 13A) considerably transformed the ancestral condition. Two furrows (circumcapitular and sejugal) can divide the body into four pseudotagmata: gnathosoma and idiosoma (separated by the circumcapitular furrow), and proterosoma and hysterosoma (separated by the sejugal furrow). The abjugal furrow separates a podosoma from an aspidosoma. Other divisions which can be distinguished are: epiprosoma (the prosoma without the podosoma), propodosoma and metapodosoma (anterior and posterior part of the podosoma, separated by the sejugal furrow), and stethosoma (the prosoma without the gnathosoma). Modern soma-terminology is the result of studies by Van der Hammen (1963, 1986b, 1969) and Grandjean (1970). References to the older

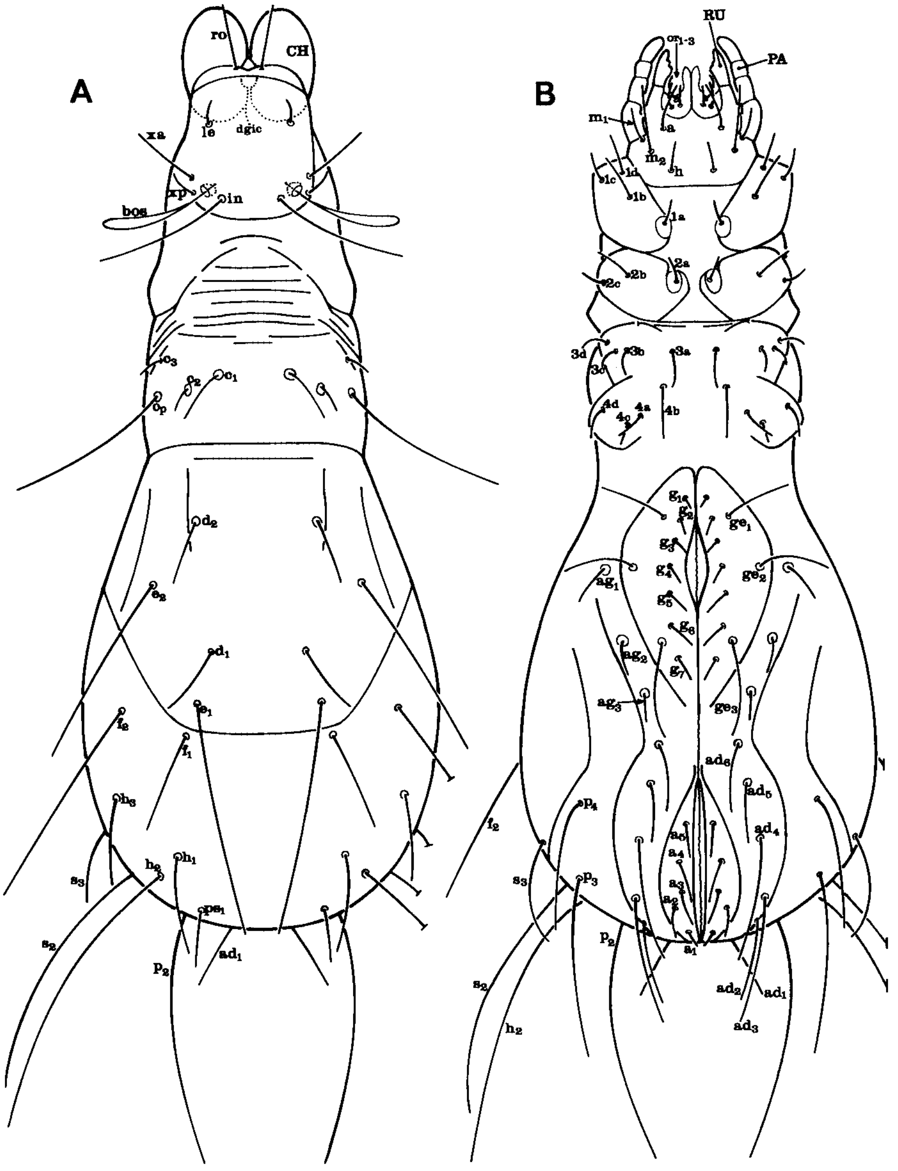

Fig. 10. *Aphelacarus acarinus* (Berlese), adult female; A, dorsal view; B, ventral view; A, B, × 295.

literature, including the first introductions of the terms, are given in the Glossary of Acarological Terminology (Van der Hammen, 1980). Generally, gnathosoma and idiosoma are movably connected (gnatho-idiosomatic articulation). The divisions of the actinotrichid idiosoma can be immovably connected (holoidy) or some can be movably joined. In the last-mentioned case, we can

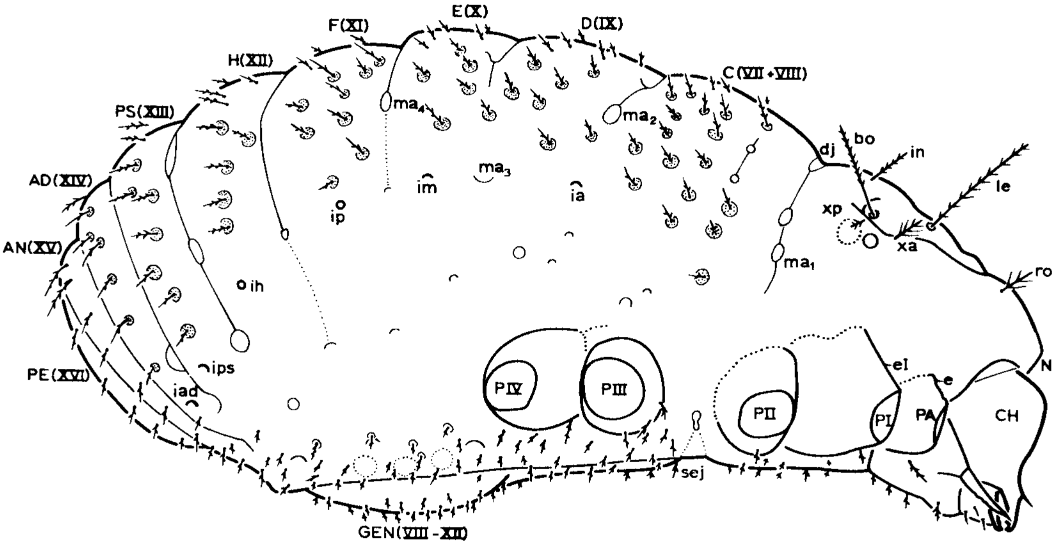

Fig. 11. *Alycus roseus* C. L. Koch, adult female, lateral view; × 233. (After Van der Hammen, 1969).

distinguish protero-hysterosomatic articulation or dichoidy (fig. 13B), known from many primitive Oribatid mites; and ptychoidy (the presence of a dorsal hinge between prosoma and opisthosoma, permitting the prosoma to be folded down and the legs to be concealed; cf. fig. 13C, D), known from several other groups of primitive Oribatid mites (Mesoplophoroidea, Protoplophoroidea, Euphthiracaroidea, Phthiracaroidea). Ptychoidy requires: (1) a complete separation, by soft skin, of the ventral part of the podosoma from the remaining part of the exoskeleton, (2) a completely sclerotized opisthosoma, and (3) an articulated coxisternal region, in the ancestors, at the stases at which the mites are now ptychoid (cf. Grandjean, 1969: 132-139).

Studies by Van der Hammen (1969, 1970a) have demonstrated that the body of primitive segmented Actinotrichid mites consists of a number of precheliceral metameres and the segments I-VI (prosoma) and VII-XVI (opisthosoma) (cf. fig. 11). In the course of embryonic development, the paraproctal segments (i.e. the segments XIII-XVI) are suppressed and can reappear in the course of postembryonic development (hysteromorphosis, cf. fig. 12). Each of these segments is eustasic (the ontophylogenetic harmony is vertical) and can reappear at a fixed level of the postembryonic development. The base levels of segments XIII-XVI are respectively: larval, protonymphal, deutonymphal and tritonymphal. When a certain paraproctal segment does not appear at its base level, it will not appear later on in ontogeny, nor will any of the segments which, in the plan of construction of the group, are posteriorly of it. In Tarsonemida, the paraproctal segment is constituted by segment XII (cf. Van der Hammen, 1970), and it is logical to suppose that the base level of this segment is, at least

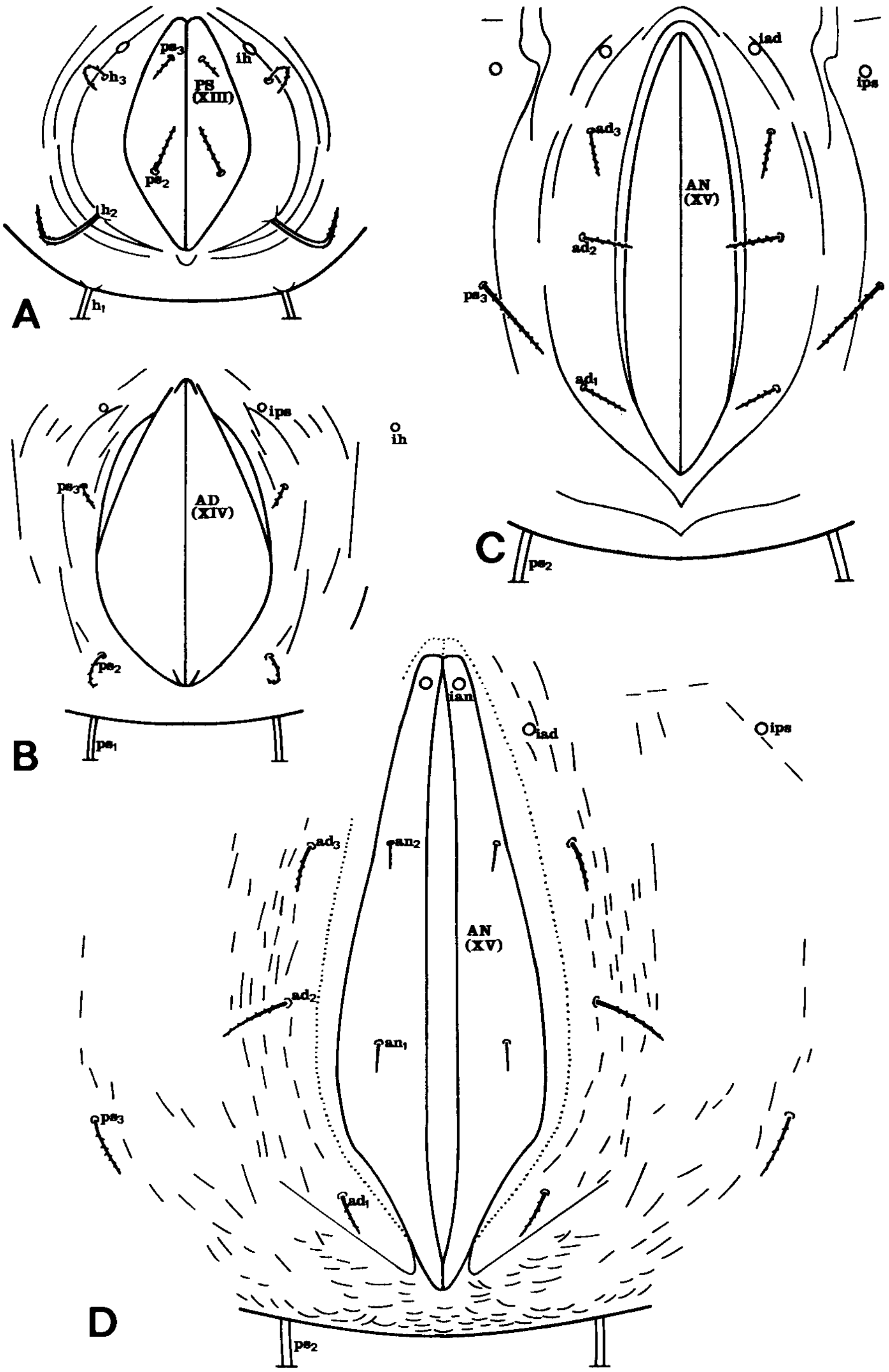

Fig. 12. Postembryonic development of the paraproctal region of *Archegozetes magna* (Sellnick); A, larva; B, protonymph; C, deutonymph; D, tritonymph; A-D, × 472. (After Van der Hammen, 1981a).

ancestrally, prelarval (the development of Tarsonemida is, however, insufficiently known; in extant Tarsonemida the life-cycle apparently includes larva and adult only). It is also logical to suppose that, in the Actinotrichid ancestors, segment XVII, with adult base level, must have been present; this segment is not known from extant Actinotrichida, but could be still present in some primitive species (especially primitive Actinedida). The presence of segment XVI (the peranal segment) is known from: Parhypochthoniidae, Brachychthoniidae and Pterochthoniidae (primitive Oribatida); and Terpnacaridae and some Pachygnathidae (primitive Actinedida). The anal segment (segment XV) remains the terminal paraproctal segment in most Oribatida. The adanal segment (segment XIV) remains the terminal paraproctal segment in several groups of Actinedida (Caeculidae, Anystidae). The pseudanal segment (segment XIII) remains the terminal paraproctal segment in many other Actinedida (Tydeidae, Raphignathoidea, Tetranychoidea, Cheyletoidea).

Tegument. — The actinotrichid tegument (or skin) generally consists of a living layer or hypodermis, and three non-living layers, viz., chitonostracum (procuticle), epiostracum (epicuticle) and cerotegument (cement and lipid layers, and wax blooms). The chitonostracum generally consists of three layers: Schmidt's layer, endostracum and ectostracum. Chitonostracum and epiostracum constitute the cuticle. The skin can be soft, or sclerotized and melanized; the highest degree of sclerotization is found in the ectostracum. Sclerites, when present, can be segmentally arranged. The cuticle can present various types of microsculpture: aciculate, alveolate, areolate, corniculate, costate, costulate, foveolate, granulate, plicate, punctate, reticulate, rugose, scabrous, shagreened, striate, striolate, sulcate, tuberculate, vermiculate, verrucose, etc. The cerotegument develops by exudation through pores in the cuticle; it can present various types of microsculpture. In many Actinotrichida, respiration is cutaneous, and the cuticle not heavily sclerotized. It is supposed here that, in Actinotrichid ancestors, the skin was soft.

Aspidosoma. — The aspidosoma is bordered laterally by the abjugal furrow, anteriorly by the circumcapitular furrow, and posteriorly by the disjugal furrow. The surface of the aspidosoma is constituted by the prodorsum; it can be scleritized (prodorsal shield), or not. The prodorsum can be transversely subdivided, by two furrows, into prostethidium, mesostethidium and metastethidum (fig. 11). The ancestral number of prodorsal setae is six pairs (figs. 10A, 11): rostral setae (*ro*), lamellar setae, or anterior trichobothria (*le*), interlamellar setae (*in*), trichobothria or sensilli, or posterior trichobothria (*bos*), anterior exobothridial setae (*exa*), posterior exobothridial setae (*exp*). A naso, or frontal protuberance (probably of precheliceral, and possibly acronal, origin), is present in many Actinedida and some Oribatida (e.g. Archeonothridae, Brachychthoniidae). It is unpaired and, when present, it is found at (or under) the rostral extremity of the aspidosoma, overhanging the chelicerae (fig. 15B, D, G); an eye (often bilobate) can be present at its ventral surface. The prodorsum can present an unpaired anterior, and one or two pairs of lateral eyes, but many

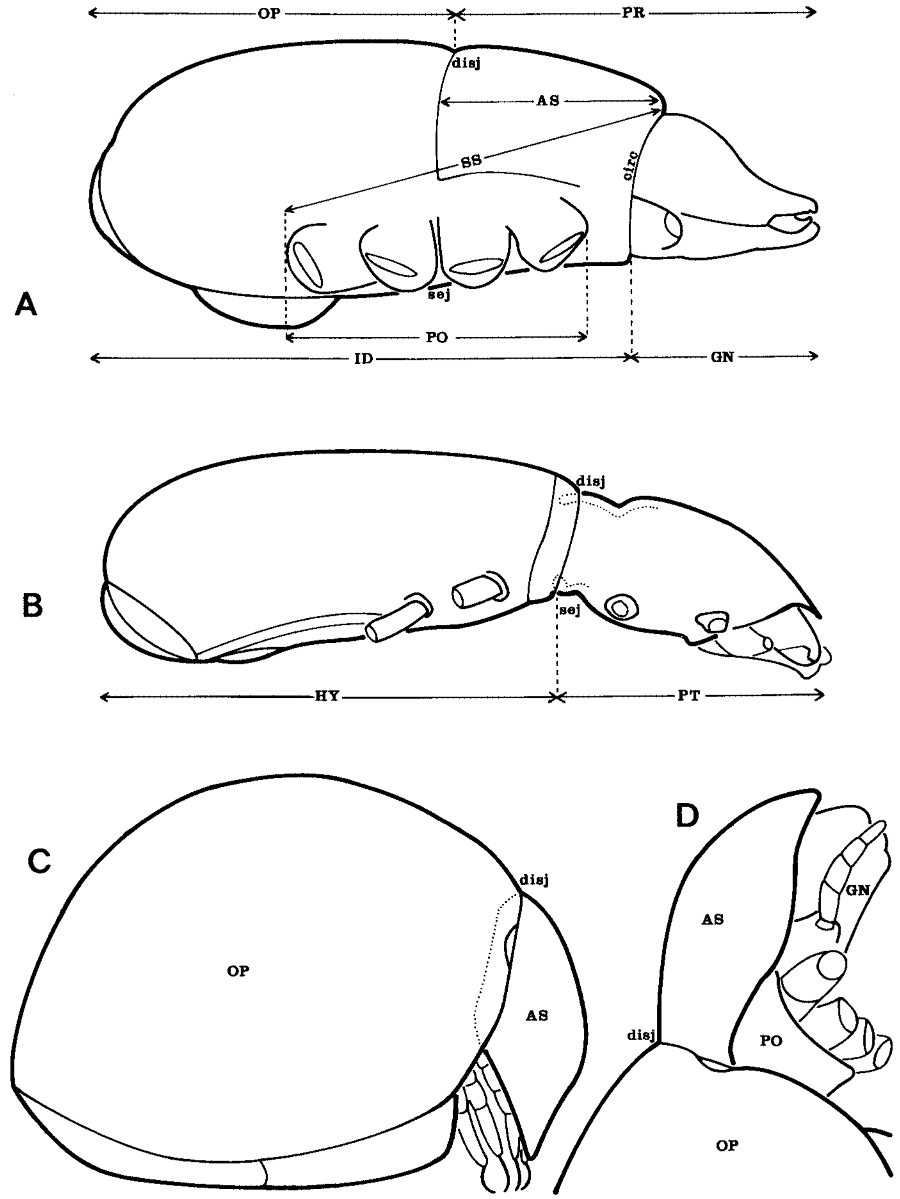

Fig. 13. Schematic representations (in lateral view) of the divisions of the actinotrichid body by furrows (circumcapitular, disjugal, sejugal, abjugal). A, normal condition, in which two tagmata (prosoma, opisthosoma), four pseudotagmata (gnathosoma, idiosoma, proterosoma, hysterosoma) and five further divisions (stethosoma, aspidosoma, podosoma, propodosoma, metapodosoma) can be distinguished. B, division into protero- and hysterosoma in the case of protero-hysterosomatic articulation (dichoidy), in which disjugal and sejugal furrows are continuous. C, D, division into prosoma and opisthosoma in the case of ptychoidy (in Euptyctima); the podosoma can be completely withdrawn, and the apidosoma folded down, by which the mite is closed up like an armadillo; C, specimen in partly closed up condition; D, anterior part of specimen in normal "opened" condition. (A, B, redrawn after Van der Hammen, 1972).

Actinotrichid mites (Acaridida, Tarsonemida, most Oribatid mites, several groups of Actinedida) have no eyes.

Opisthosoma (dorsal, laterodorsal and paraproctal regions). — The opisthosomatic cuticle can be soft or sclerotized. Segmentation can be indicated by furrows in the soft skin, or scissures in the scleritized cuticle. The paraproctal region has developed a ventral position; external traces of segmentation (when present) are, as a result of this dislocation, not continued in lateroventral direction. The ancestral number of opisthosomatic lyrifissures or cupules is seven pairs, attributed to the segments IX-XV (cf. Van der Hammen, 1969: 185, 198). Chaetotaxy can be primordiotrichous (primitive, adelonymous and chaotic), hypertrichous (primitive, idionymous and supernumerary), holotrichous (normal, idionymous), meritrichous (idionymous, reduced in number), or neotrichous (increased in number, idionymous or adelonymous).

Genital region. — The actinotrichid genital region is close to the anal region (the two regions are often even contiguous), not separated by a distance proportionate to the distance between segments VIII and XVI (figs. 10B, 11); it is also relatively very large. It is laterally bordered by the aggenital region which can present one or more pairs of setae. The ancestral condition is already highly complicated by the development of a secondary genital opening, and can be characterized in the following way. There is a secondary, longitudinal progenital opening, closed by a pair of progenital valves, giving entrance into a progenital chamber. This chamber contains (in the adult) three pairs of evaginable progenital papillae, a trifid eugenital opening, and eugenital setae (fig. 14A). The genital papillae represent opisthosomatic appendages; they can be segmented (fig. 14B). The postembryonic development of the genital papillae is interesting: there are one pair in the protonymph, two pairs in the deutonymph, and three pairs in the tritonymph and adult (a development very similar to the postembryonic development of the opisthosomatic papillae of segments X-XII in *Prokoenenia*). In Oribatida and several Actinedida, an invaginable ovipositor has developed as an outgrowth of the vagina (figs. 14C, E). The trifid eugenital orifice is found, in these cases, at the distal end of the ovipositor (fig. 14D); it is surrounded by three terminal lobes. An ovipositor is not present in Tarsonemida, Acaridida, and several groups of Actinedida (in the last-mentioned group the absence can be an ancestral or a derived character state). In Tetranychidae, genital region and ovipositor are quite different (fig. 14F, G): there is a single progenital valve, whilst the ovipositor arises by extension of the plicate tegument of the genital region.

The following interpretation of the ancestral Actinotrichid genital region is given here. The trifid eugenital opening is situated in, or between, the segments VIII and IX, and is surrounded by the opisthosomatic appendages of segment VIII (one pair) and the opisthosomatic appendages of segment IX (a fused pair); it might be remarked here that a similar condition, although reversed, is found in Palpigradi. The three pairs of genital papillae represent the opisthosomatic papillae of segments X-XII, which are included in the progenital chamber. Fig.

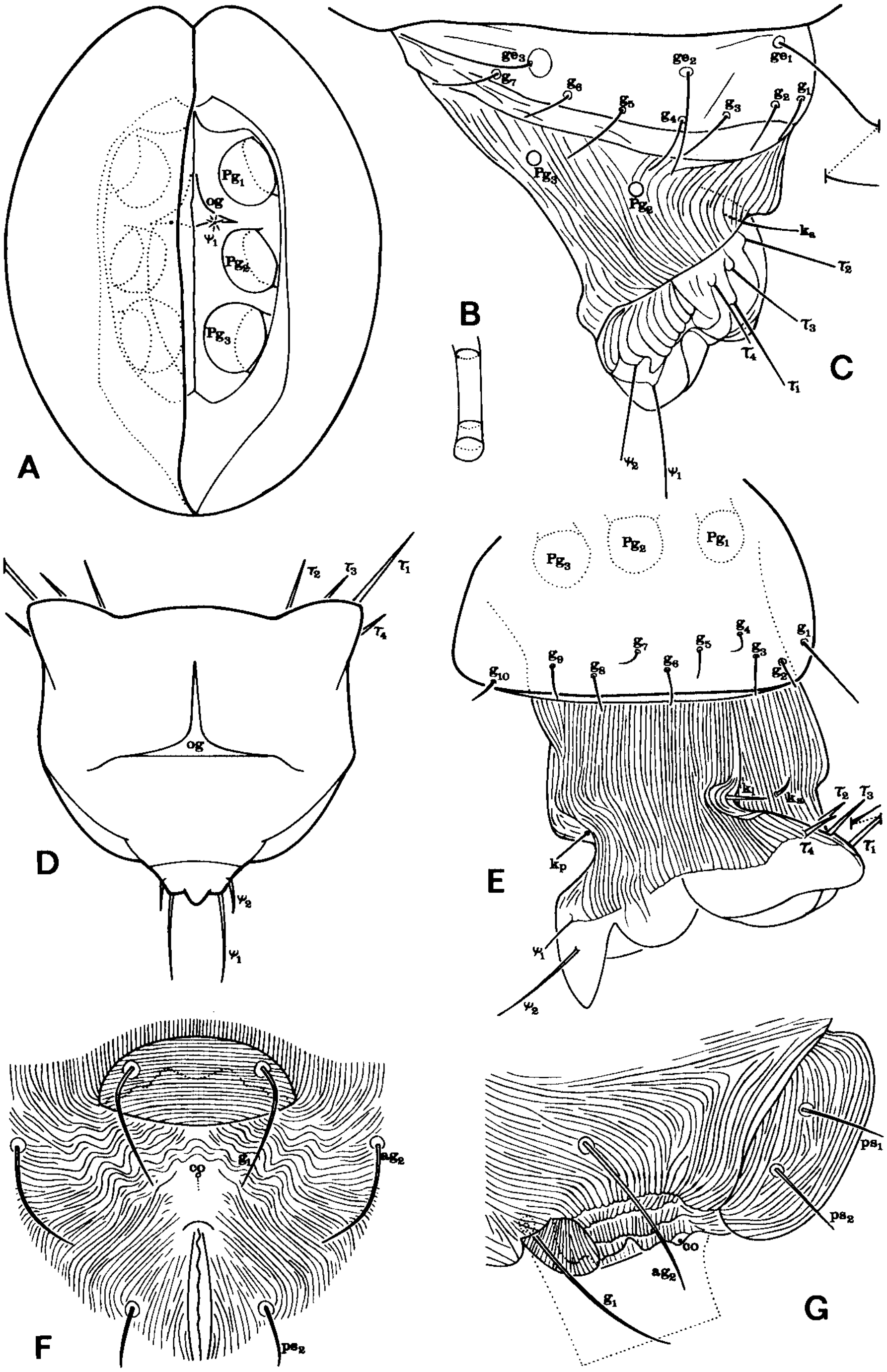

Fig. 14. Genital region of various species of Actinotrichida. A, *Alycus roseus* C. L. Koch, ventral view (left progenital lip removed). B, *Epilohmannia cylindrica* (Berlese), genital papilla *Pg3*, lateroventral view. C, *Aphelacarus acarinus* (Berlese), evaginated ovipositor, lateral view (right face). D, E, *Hermannia convexa* (C. L. Koch), evaginated ovipositor; D, distal view; E, lateral view (right face). F, G, *Tetranychus urticae* C. L. Koch; F, ventral view; G, lateral view (left face; the position of the protruded genital region, functioning as an ovipositor, is represented by a dotted line). A-C, F-G, × 550; D-E, × 186.

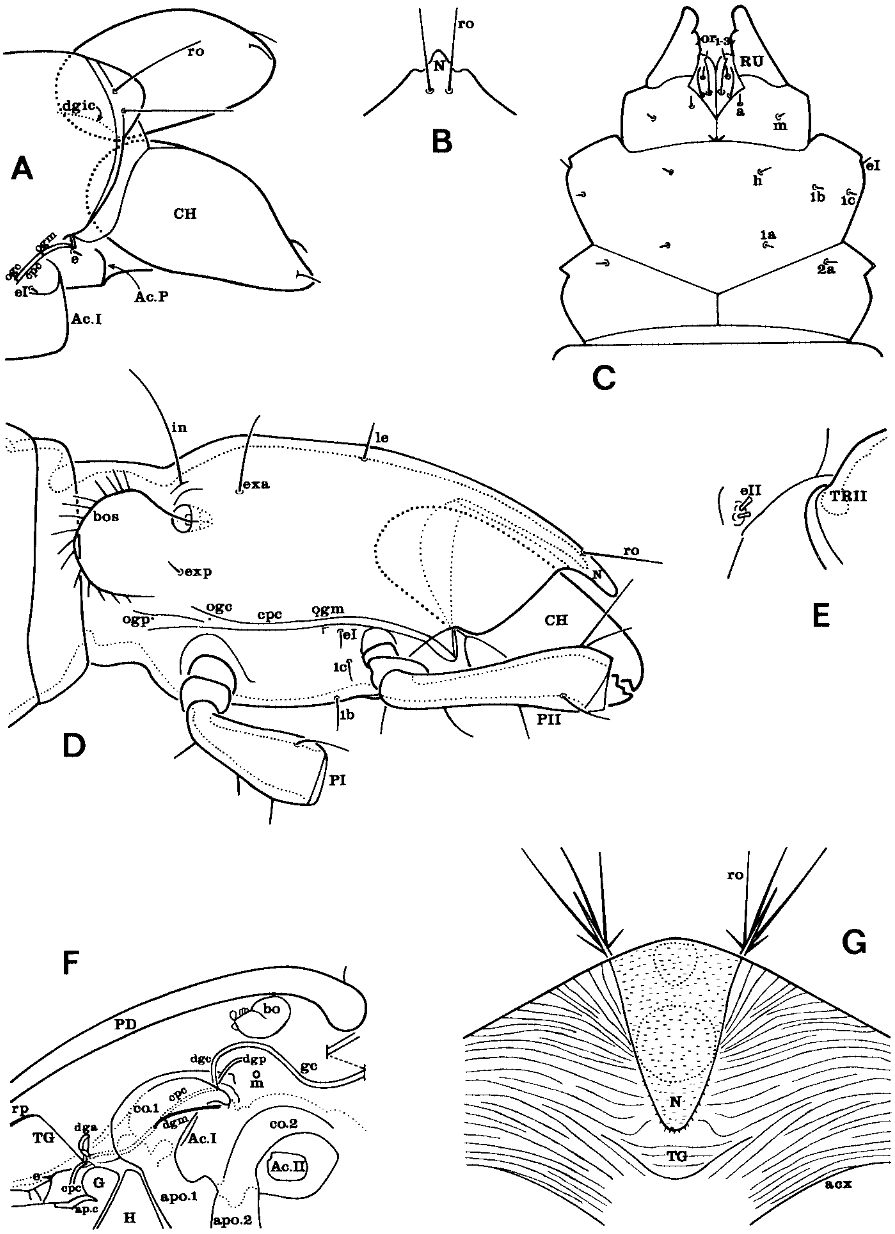

Fig. 15. Prosomatic regions of various species of Actinotrichida. A, *Aphelacrus acarinus* (Berlese), adult, laterodorsal view of anterior part of prosoma. B, *Eulohmannia ribagai* (Berlese), adult, dorsal view of rostrum. C, *Epilohmannia cylindrica* (Berlese), adult, ventral view of proterosoma and infracapitulum. D, *Eulohmannia ribagai* (Berlese), adult, lateral view of anterior part of prosoma. E, *Oecosmaris callitricha* Grandjean, adult, laterodorsal view of supracoxal setae *eII* (redrawn after Grandjean, 1947). F, *Hermannia convexa* (C. L. Koch), adult, internal view of part of the lateral prosomatic region (redrawn after Van der Hammen, 1968). G, *Alycus roseus* (C. L. Koch), adult female, ventral view of naso and adjoining parts of prosoma (redrawn after Van der Hammen, 1969). A, × 550; B, D, × 295; C, × 376; E, × 522; F, × 118; G, × 1050. (N.B. In fig. 15 D the sigla *PI* and *PII* have been shifted).

11 demonstrates that the posterior border of the progenital opening indeed coincides with the posterior border of segment XII. The progenital valves could represent the exites of opisthosomatic appendages (possibly of segment VIII and IX). This new interpretation, which has gradually developed by way of previous hypotheses (Van der Hammen, 1963: 448-449; 1969: 198-199, fig. 7A; 1977: tab. 2; 1979: 429-430; 1981a: 28-31, fig. 11), finally explains all problems posed by the complicated morphology of the actinotrichid genital region.

Epimeral region. — The ventral region of the podosoma can be partly or completely scleritized (figs. 10B, 24B). In *Epilohmannia cylindrica* (Berlese), epimeron 1 has fused with the epimeral region of the palp (fig. 15C), as in Palpigradi. A sejugal furrow or interval is present between epimera 2 and 3. Epimeral chaetotaxy can be subject to numerical changes (multiplications and deficiencies); the number of epimeral setae generally increases in the course of postembryonic development, as in Palpigradi.

Lateral aspect of podosoma. — Supracoxal setae (*eI* and *eII*) (cf. Van der Hammen, 1977a: 13-15, fig. 2B, C, F-L; 1980: 153-154; 1981a: 26) can be present above the bases of legs I and II. Seta *eII* is the first supracoxal seta to disappear; it can also be subject to duplication (cf. fig. 15E). A podocephalic canal (fig. 15A, B, F) can be present, originally extending from above the base of leg I to the gnathosoma. The orifices of four podocephalic glands can be associated with the podocephalic canal, viz., those of anterior, median, coxal and posterior (lateral) gland. The number of glands can, however, be reduced, and the podocephalic canal can become internal (several Actinedida) (cf. Van der Hammen, 1968: 19-22, 29-30, figs. 1, 7-11; 1980: 120-121). In *Eulohmannia ribagai* (Berlese) (fig. 15B), the podocephalic canal extends from posteriorly of the base of leg II to the gnathosoma, and the orifice of the coxal gland is above the base of leg II; this could be a secondary condition, although it cannot be easily explained.

Gnathosoma. — The division of the body, anteriorly of the circumcapitular furrow, is called gnathosoma. It can be situated in a camerostome, a cavity sheltered dorsally and laterally by the aspidosoma (fig. 18). The gnathosoma bears two pairs of appendages: chelicerae and palps. Two principal parts can be distinguished: cheliceral frame and infracapitulum (figs. 16A, 18). The cheliceral frame consists of the membraneous tegument which constitutes the body-wall between the rostral region of the aspidosoma and the infracapitulum. The chelicerae are movably attached to the cheliceral frame by means of the cheliceral sheaths. The superior part of the cheliceral frame constitutes the tegulum.

The infracapitulum consists of a dorsal region or cervix (fig. 17), a ventral region or mentum (fig. 16B), a pair of large lateral ridges, and a pair of malapophyses, probably representing endites (of which the ventral surface, or gena, is a continuation of the mentum). The cervix presents an axial convexity, highest near the base of the labrum, which is called capitular saddle; it separates the two cheliceral grooves. The ventral surface of the infracapitulum presents in-

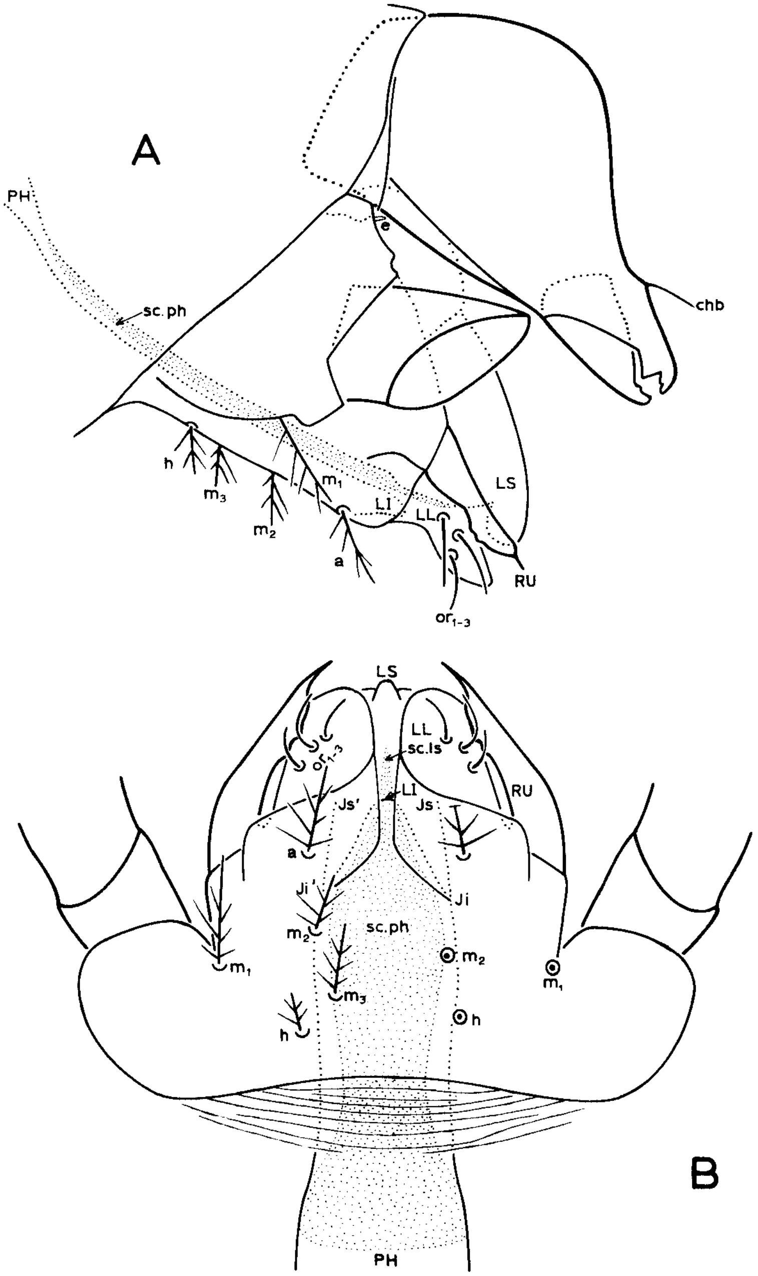

Fig. 16. *Alycus roseus* C. L. Koch, gnathosoma of adult female; A, lateral view (chelicera slightly raised); B, ventral view; A, B, × 708. (After Van der Hammen, 1969).

fracapitular setae. The infracapitulum contains mouth and pharynx. The mouth is surrounded by three or four lips: labrum, lateral lips, and labium. The lateral lips bear the adoral setae. The labium has disappeared in most Actinotrichid mites. When it is present, the mouth has four commissures and a quadrangular section; when the labium is absent, there are three commissures, and the section is triangular. The exoskeleton of the infracapitulum generally presents internal projections, or apodemes, on which several tendons can be inserted. A capitular apodeme, constituting the internal continuation of the cervix, is generally present (fig. 17); it separates, internally, the cheliceral frame and the infracapitulum. A subcapitular apodeme, constituting the internal continuation of the mentum, is, moreover, known from Caeculidae (Coineau, 1974a: 78, fig. 28); it separates, internally, the infracapitulum and the sternal region of segment III (epimera 1). The simultaneous presence of capitular and subcapitular apodeme constitutes a primitive character (it is also known from Ricinulei, a Cryptognomic subclass).

The evolution of the gnathosoma (gnathosomatization) in Actinotrichida, evidently, is closely connected with the evolution of the podocephalic canal (cf. the previous section, dealing with the lateral aspect of the podosoma).

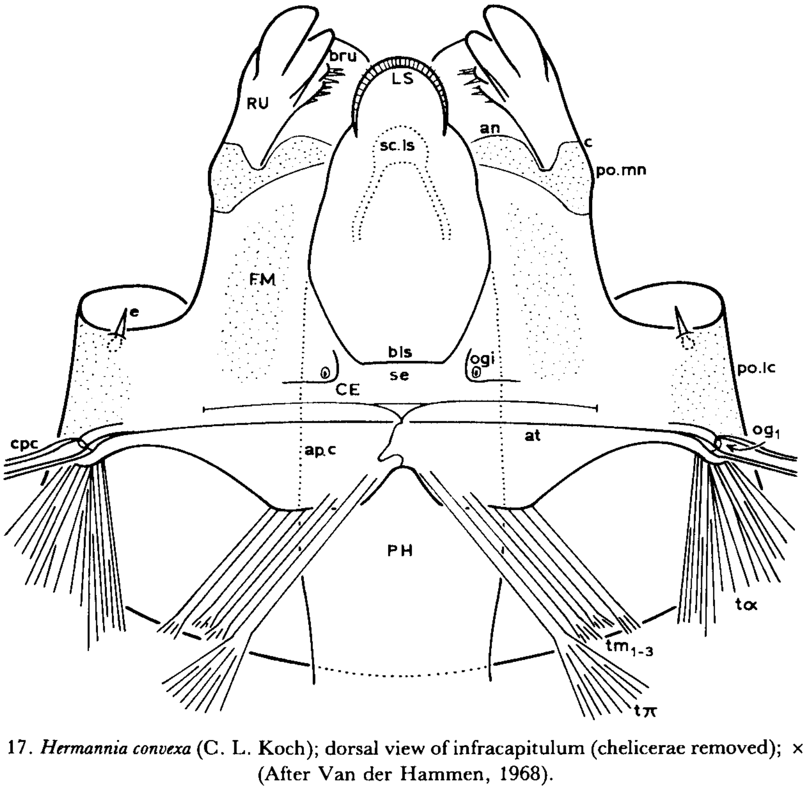

Fig. 17. *Hermannia convexa* (C. L. Koch); dorsal view of infracapitulum (chelicerae removed); x 368. (After Van der Hammen, 1968).

Papers of fundamental importance, dealing with the gnathosoma, have been published by Grandjean (1936a, 1957, 1957a) and Van der Hammen (1968, 1970c). Further literature on the gnathosoma is given, under various entries, in the Glossary of Acarological Terminology (Van der Hammen, 1980).

Chelicera. — The actinotrichid chelicera is originally composed of three segments: trochanter, body of chelicera, and apotele (fig. 19B-D). Generally, the actinotrichid cheliceral trochanter is reduced to a ventral or lateroventral element. The body of the chelicera represents femur, genu, tibia and tarsus. Its distal part constitutes the fixed jaw of the chela. Conditions in Endeostigmata and Enarthronota (cf. Grandjean, 1947a) demonstrate that the fixed jaw

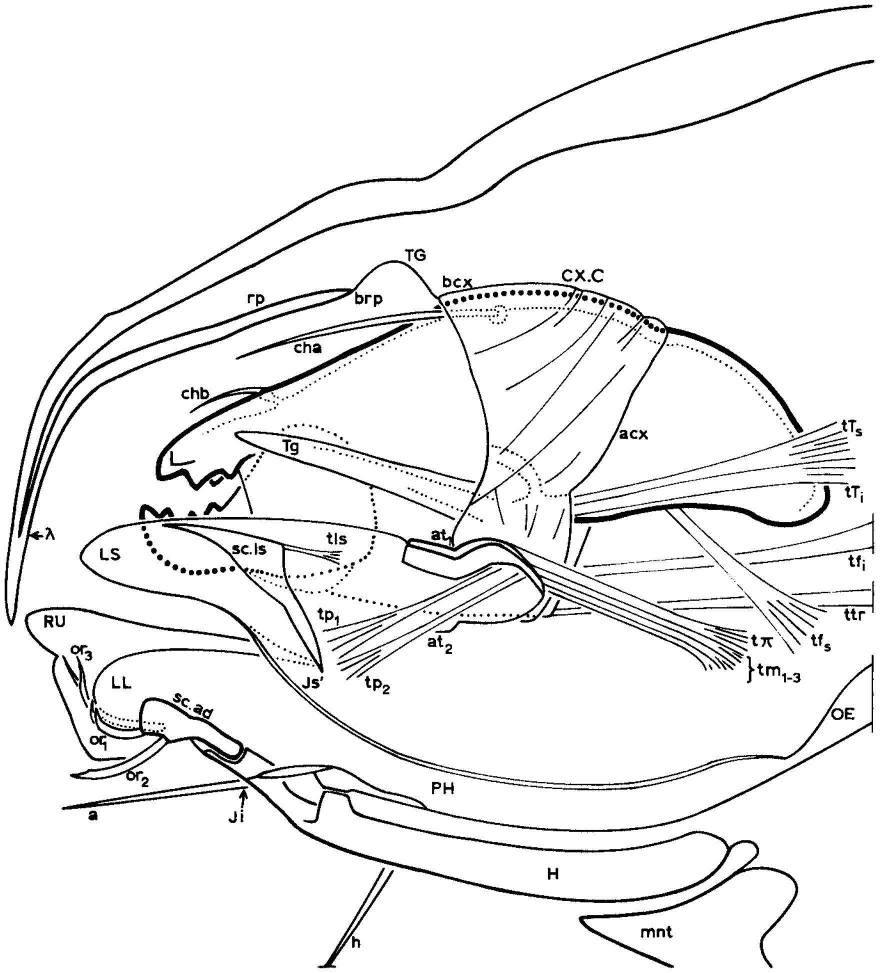

Fig. 18. *Hermannia convexa* (C. L. Koch); longitudinal (sagittal) section of gnathosoma in camerostome (chelicerae nearly completely retracted); x 368. (After Van der Hammen, 1968).

represents a hypertrophied seta or a group of coalesced setae (fig. 19A). The apotele constitutes the movable jaw of the chela. Various oncophyses, i.e. extensions of an arthrodial membrane, often in the shape of a hyaline intumescence, have been described from actinotrichid chelicerae. The ancestral function of the actinotrichid chelicera probably is partly prehensile; it could also have participated in the fragmentation of food (ingestion of solid food and internal digestion are known from extant Oribatida and Endeostigmata). In the course of evolution, the chelicera has developed several specialized functions (e.g. suctorial), by which, in several groups, the shape has been radically transformed. In Tarsonemida, e.g., the greater part of the chelicera is supposed to have fused with the cervix, whilst the apotele has remained free (it constitutes a stylet, situated inside the infracapitulum) (cf. Van der Hammen, 1970: 11-12, fig. 7A-B).

Palp. — The ancestral number of actinotrichid palpal segments is five (fig. 20A): trochanter, femur, genu, tibia and tarsus (a palpal apotele is not present in Actinotrichida). The articulations are originally similar to those in the corresponding joints of the legs (the genu/tibia articulation could, however, have extensor muscles, although I have not been able to discern them with certainty; cf. fig. 20A). The number of palpal segments is reduced in many Actinotrichid species; there are, for instance, four segments in *Eulohmannia ribagai* (Berlese) and *Cheyletus eruditus* (Scrank) (fig. 20C), three segments in *Phthiracarus laevigatus* (C. L. Koch) (fig. 20B), two segments in *Epilohmannia cylindrica* (Berlese). In many families of Actinedida (the so-called Dactylognatha) a thumb-claw complex is present (fig. 20C), consisting of a hypertrophied seta of the tibia (the tibial claw) and the palpal tarsus (the thumb); in these cases, the tarsus is reduced in shape, and has shifted to a ventrobasal position on the tibia. The main function of the actinotrichid palp is now sensory; in Dactylognatha it is, apparently, also prehensile. The palpal segments can present setae, the palpal tarsus also a solenidion; several of the tarsal setae can become eupathidia. A supracoxal seta *e* is generally inserted above the base of the palp. It might be remarked here that, in comparison with the legs, the actinotrichid palp (generally) is relatively small.

Legs. — The ancestral number of leg-segments is seven (fig. 21A-D): trochanter, femur 1, femur 2, genu, tibia, tarsus, and apotele (cf. Van der Hammen, 1970b). Two femora (fig. 21E) are present in some primitive Oribatida and in many Actinedida. In most Oribatida (fig. 21F) femur 1 and 2 have been integrated (by anergastic union) into a single femur (cf. Grandjean, 1954). In *Fusacarus* (fig. 22E-F), femur and genu of leg II have been integrated, by anchylosis, into a single femorogenu (cf. Grandjean, 1953). A femorogenu is also present in leg III of Tarsonemida (fig. 22D) (cf. Van der Hammen, 1970). Tibia and tarsus of the legs can be integrated into a single tibiotarsus (fig. 22C) (cf. Grandjean, 1954: 356). The apotele can disappear as a result of suppression. The number of tarsal segments can increase (fig. 22A-B), first by subdivision, thereupon by cosmiotaxy (tarsus 1, 2, etc.); these adesmatic subdivisions are rare in Actinotrichida (they are known from some Prostigmata). The actinotrichid tarsus does not consist of a basi- and a telotarsus.

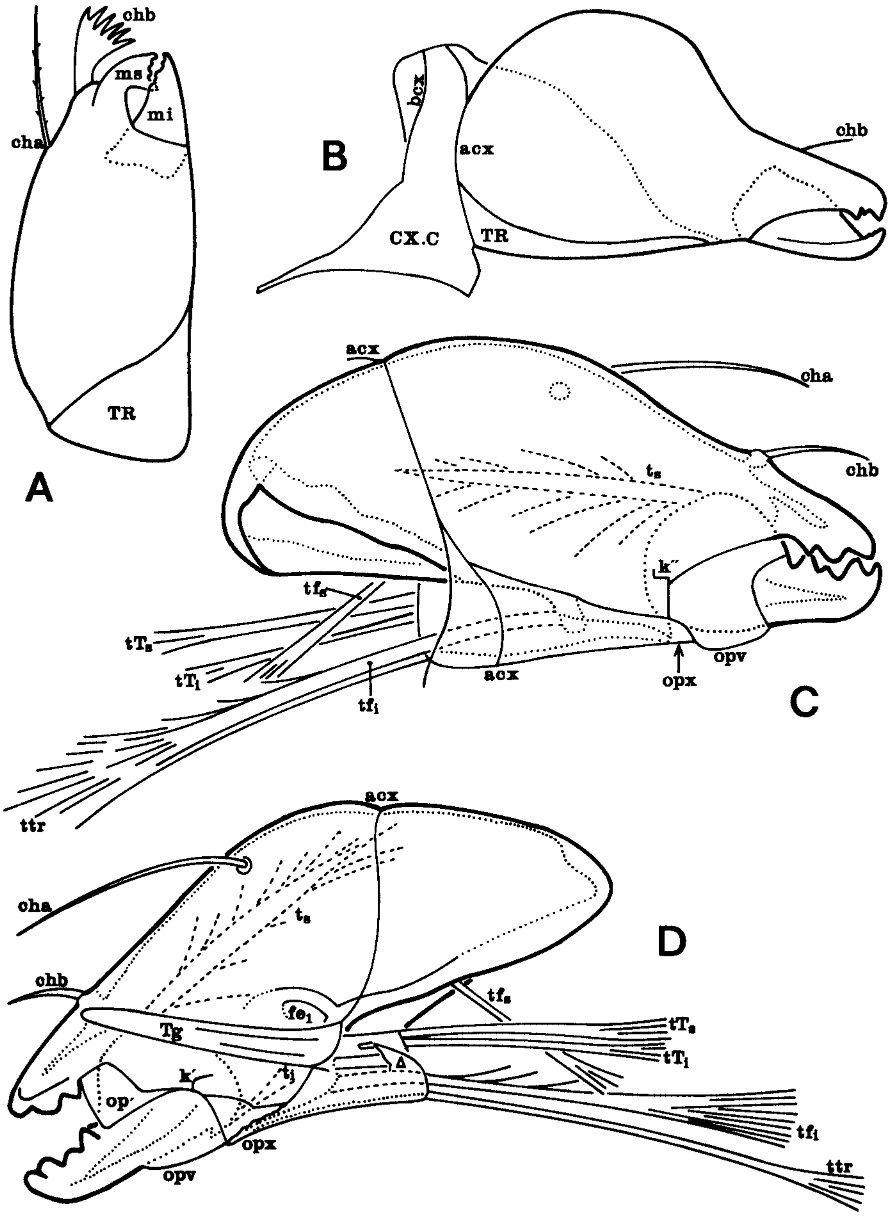

Fig. 19. Actinotrichid chelicerae. A, *Cosmochthonius lanatus* (Michael), lateral (antiaxial) view of right chelicera. B, *Alycus roseus* C. L. Koch, lateral (antiaxial) view of right chelicera (redrawn after Van der Hammen, 1969). C, D, *Hermannia convexa* (C. L. Koch); C, lateral (antiaxial) view of right chelicera; D, lateral (paraxial) view of right chelicera (C, D, redrawn after Van der Hammen, 1968). A, × 1312; B, × 707; C, D, × 368.

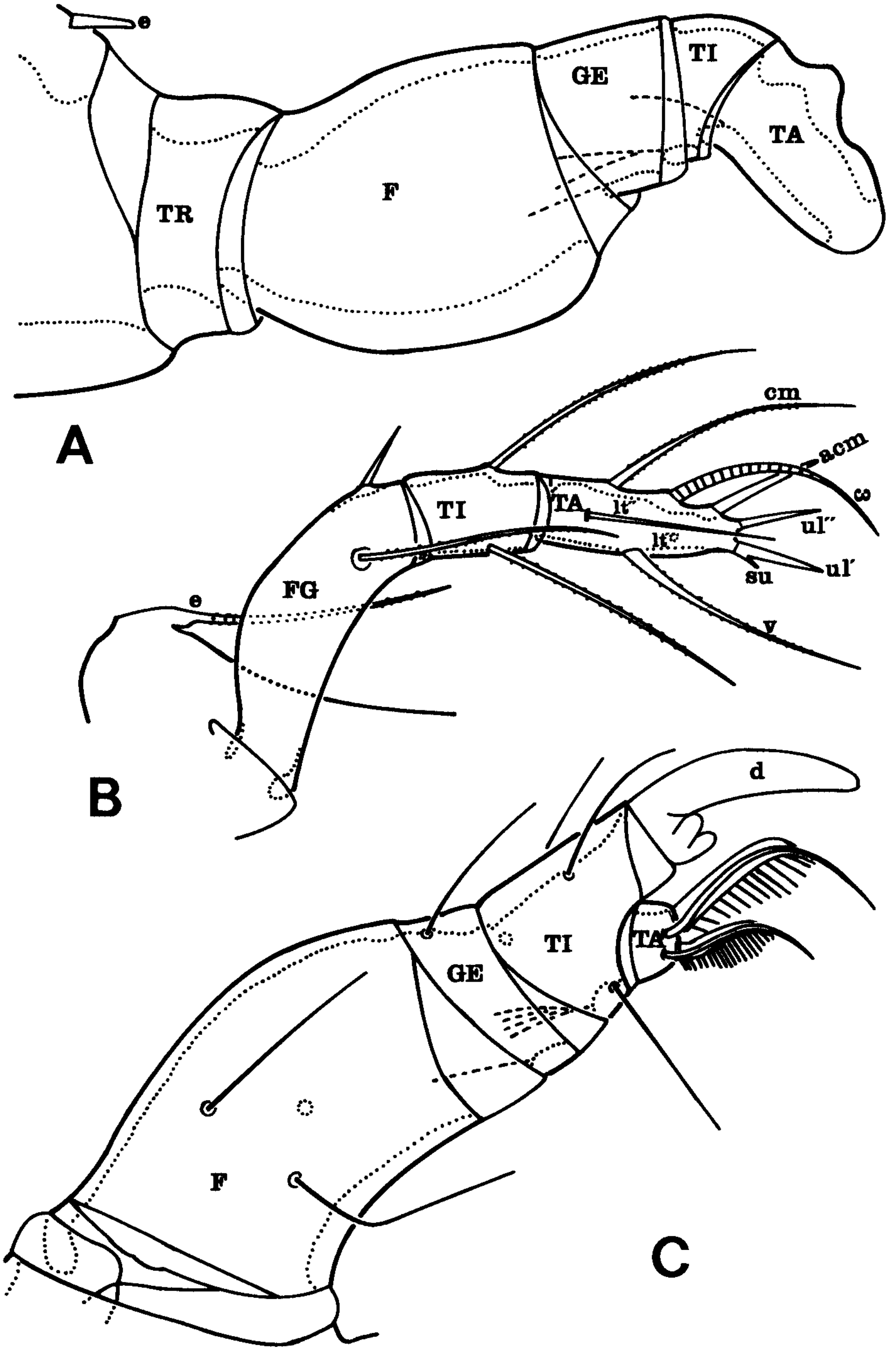

Fig. 20. Lateral (antiaxial) view of the right palp in the adult of three species of Actinotrichida; A, *Hermannia convexa* (C. L. Koch) (all palpal phaneres omitted); B, *Phthiracarus laevigatus* (C. L. Koch) (redrawn after Van der Hammen, 1963a); C, *Cheyletus eruditus* (Schrank); A, × 917; B, × 487; C, × 627.

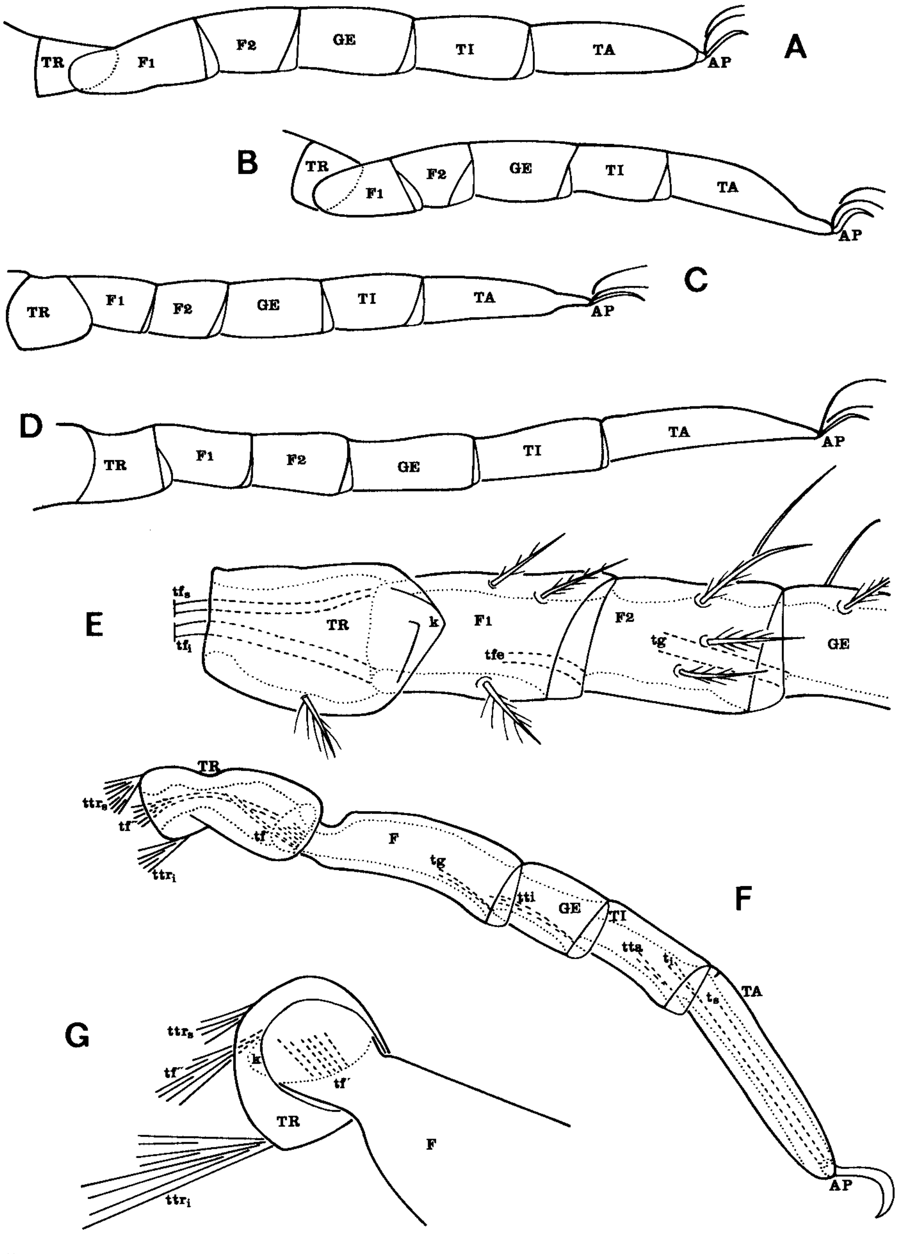

Fig. 21. Segmentation and articulation of actinotrichid legs (1). A-D, *Aphelacarus acarinus* (Berlese), lateral (antiaxial) view of legs I-IV; A, right leg I; B, right leg II; C, left leg III; D, left leg IV. E, *Alycus roseus* C. L. Koch, lateral (antiaxial) view of trochanter, femur 1, femur 2, and proximal part of genu of left leg IV. F, G, *Hermannia convexa* (C. L. Koch); F, lateral (antiaxial) view of left leg IV; G, lateral (antiaxial) view of trochanter and proximal part of femur of right leg I. A-D, x 550; E, x 566; F, G, x 295.

The ancestral types of articulation in the actinotrichid legs are the following (fig. 21E-G): the body/trochanter, trochanter/femur, and tarsus/apotele articulations constitute pivot joints; the femur 1/femur 2, femur/genu, genu/tibia, and tibia/tarsus articulations constitute hinge joints. In higher Oribatid mites, a rocking joint has developed between body and trochanter. Leg movements are complicated here by the pseudosymmetrical arrangement of the legs: legs I and II are directed to the front and the femur is elbowed; legs III and IV are directed backwards and the trochanter is elbowed (cf. Grandjean, 1952: 24-27); leg-rocking has not been analysed in detail in these cases.

The legs generally present a rising part, a knee-segment (genu), and a descending part. In higher Oribatid mites, the knee-segment is relatively small.

In the course of evolution, the main function of leg I can change from ambulatory to sensory. The evolution involves suppression of the apotelic claw, and the development of hexapodous stepping. It is, for instance, known from Tydeidae and Cheyletidae (Actinedida), and Staurobatidae (Oribatida) (cf. Grandjean, 1967: 720-721).

The actinotrichid tarsus generally presents one dorsal, proximal lyrifissure. Various types of phaneres can be present on the legs (fig. 23): ordinary setae (which can be present on all segments), trichobothria, eupathidia (modified setae, of which the solid axis and the root are pierced by a canal), famulus (a hollow phanere, inserted in the dorsal or antiaxial region of tarsus I and, rarely, tarsus II), and solenidia (hollow phaneres with thin wall and short, largely open root; they can be found on femur, genu, tibia and tarsus). Actinotrichid setae are characterized by the presence of an actinopilinous axis (cf. Van der Hammen, 1980: 10).

In many groups of Actinotrichida, the larva and the prelarva present a variously shaped, paired organ of unknown function, situated between epimera 1 and 2 (Claparède's organ). In its most primitive shape, it has the aspect of a relatively long, segmented appendage, with hemispherical distal part (fig. 22G). Its shape is similar to that of the genital papillae, and it is supposed to represent the endite of leg I or leg II.

Internal anatomy. — The literature on actinotrichid internal anatomy is summarized in the Glossary of Acarological Terminology (Van der Hammen, 1980), where detailed references are also given. The alimentary canal generally comprises: mouth (and gullet), pharynx, oesophagus, midgut (incl. stomach) and caeca, hindgut (rectum) and anus. The excretory system can comprise: Malphighian tubes, an unpaired excretory tube, a uroporus (an excretory pore at the place of the anus, in cases where the gut ends blindly), and coxal glands (originally debouching, dorsally of leg I, into the podocephalic canal). An endosternite is present in Actinotrichida, sometimes as a transverse band, sometimes more extensively developed (cf. Van der Hammen, 1969: 187, fig. 4A; Firstman, 1973: 12-14); it has not yet been studied in detail. The circulatory system is open; a dorsal vessel (heart), or its vestige, is apparently often present. Respiration is cutaneous, or by means of secondary respiratory organs

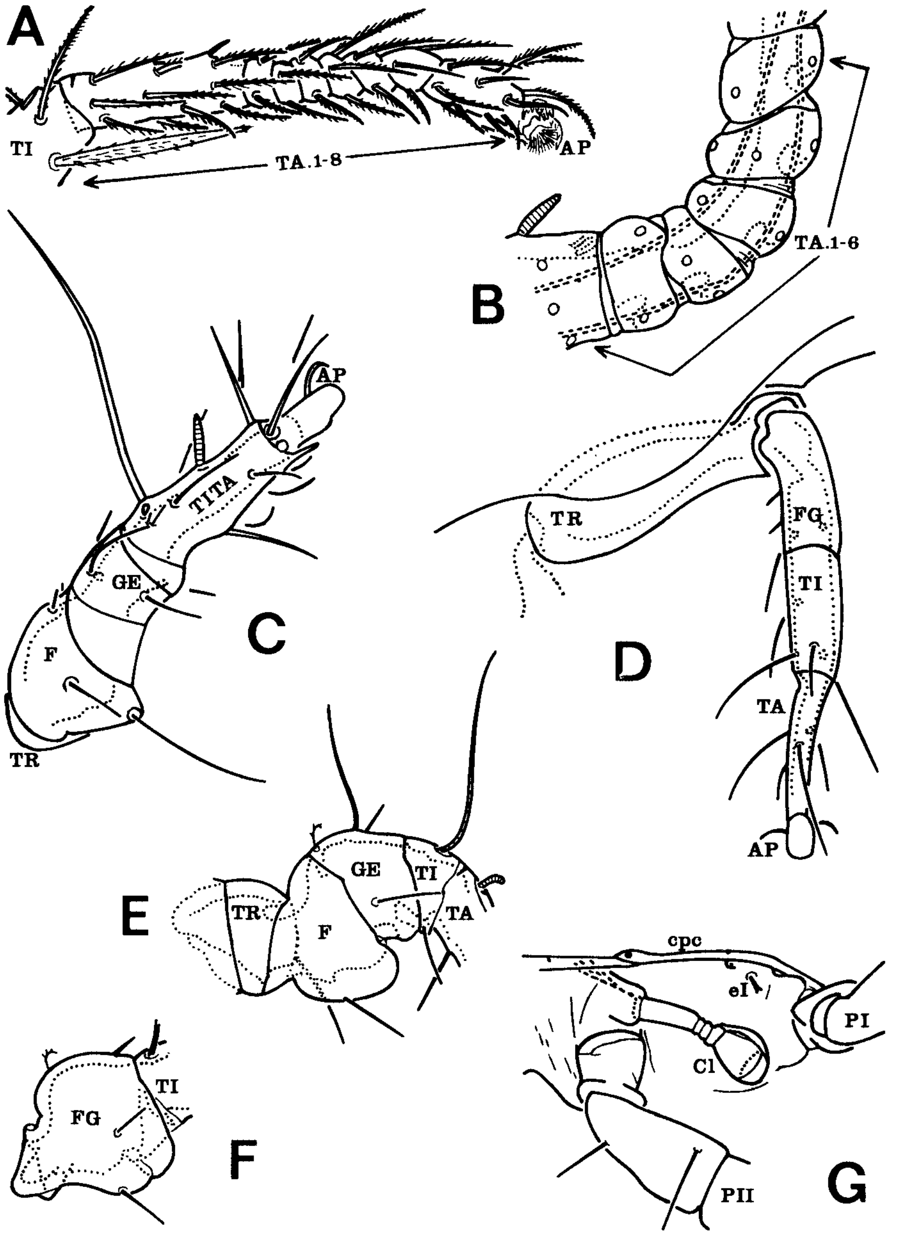

Fig. 22. Segmentation and articulation of actinotrichid legs (2). A, B, *Tarsolarkus* spec., lateral (antiaxial) view of right leg I (redrawn after Grandjean, 1952a); A, tarsus and ambulacrum; B, tarsus 1-7. C, D, *Tarsonemoides limbatus* Van der Hammen, female (redrawn after Van der Hammen, 1970); C, lateral (antiaxial) view of right leg I; D, lateral (antiaxial) view of left leg III. E, F, *Fusacarus* spec. (redrawn after Grandjean, 1953); E, lateral (antiaxial) view of right leg I (from the trochanter up to the base of the tarsus); F, lateral (antiaxial) view of the femorogenu of right leg II. G, *Eulohmannia ribagai* (Berlese), lateral view of the anterolateral part of the podosoma with Claparède's organ and the bases of legs I and II (redrawn after Grandjean, 1939). A, × 323; B, × 700; C, D, × 943; E, F, × 457; G, × 470.

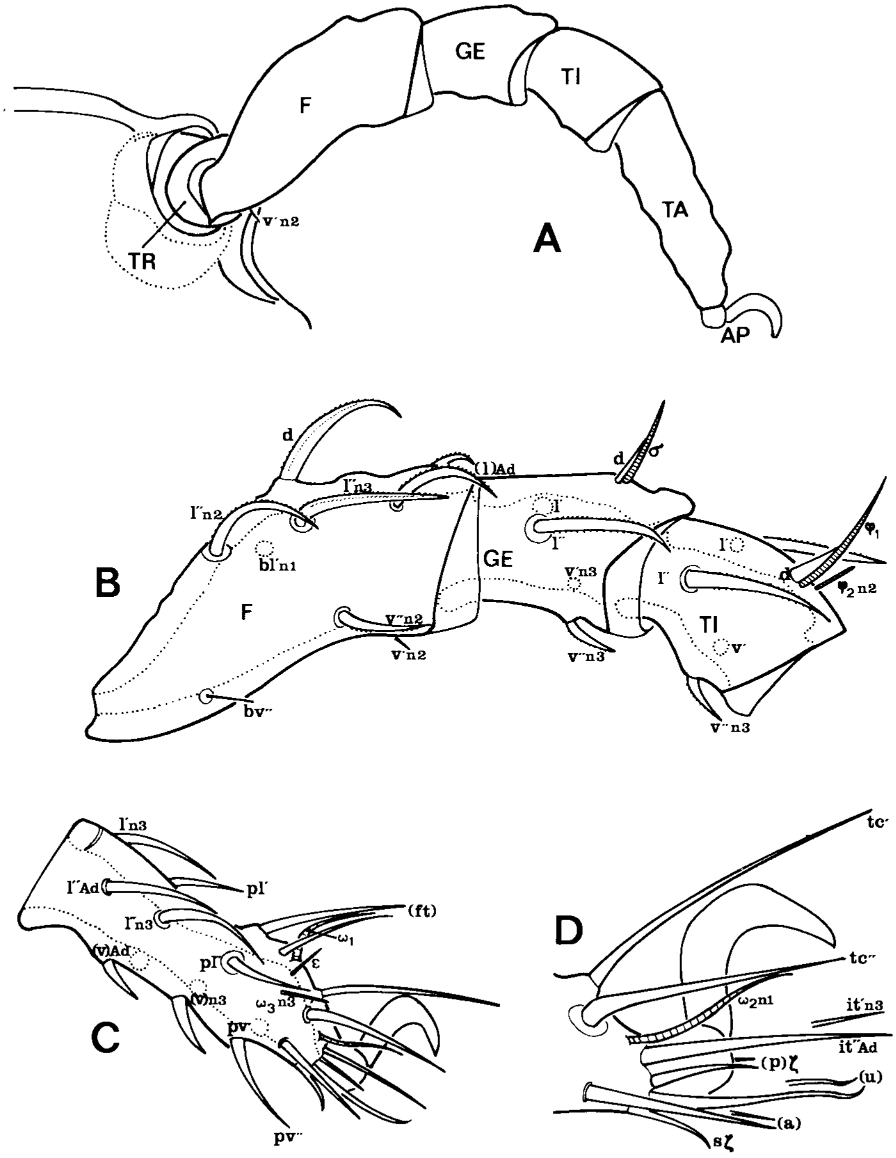

Fig. 23. *Platynothrus peltifer* (C. L. Koch), adult, lateral (antiaxial) view of right leg I; A, leg and acetabulum; B, femur, genu and tibia; C, tarsus and apotele; D, terminal part of tarsus, and apotele; A, x 232; B, C, x 368; D, x 687. (After Van der Hammen, 1981a).

(tracheae, etc.). Secondary respiratory organs can start from various superficial parts of the idiosomatic cuticle, from the progenital chamber, from the base of the appendages, and from hidden depressions of the surface (bothridium, preanal fold, apodemes). The central nervous system is concentrated to a solid mass in the prosoma, pierced by the oesophagus. Actinotrichid sensory organs (or supposed sensory organs) include: eyes and other photoreceptors, various phaneres, genital papillae and Claparède's organ, lyrifissures, etc. The male reproductive system can comprise: accessory glands, ductus ejaculatorius, penis or spermatopositor, testes, vasa deferentia and vesicula seminalis. Fine structure of actinotrichid spermatozoa, and spermiocytogenesis have been studied by Alberti (1980a); his results confirm the monophyletic character of the Actinotrichida, and demonstrate the absence of striking similarities between Actinotrichida, on the one hand, and Anactinotrichida (incl. Opilioacarida) or Palpigradi, on the other hand, whilst Actinotrichida and Solifugae appear to have some characters in common. The female reproductive system can comprise accessory glands (rarely), bursa copulatrix, ovarium, oviduct, ovipositor, receptaculum seminis, vagina and vulva. The glandular system comprises, among others, various prosomatic glands and various tegumentary glands. The opisthosomatic musculature consists, among others, of longitudinal and dorsoventral muscles; it has still to be studied, in detail, in a primitive species.

Reproduction. — Actinotrichid reproduction can be parthenogenetic or sexual. Reproductive behaviour involves sperm transfer (spermatophory, gonopody or copulation), often preceded by courtship behaviour. Oviposition can take place by means of an ovipositor. Actinotrichida are oviparous or ovoviviparous.

Postembryonic development. — The ancestral actinotrichid life-cycle comprises six stases: prelarva, larva, protonymph, deutonymph, tritonymph and adult (figs. 24, 25). The prelarva, when present, is a calyptostase or, rarely, an elattostase (cf. Coineau, 1977); a prelarva is not known for several groups. Generally, the larva is characterized by hexapody. In Trombidina, the proto- and tritonymph are calyptostasic; in Acaridida, the deutonymph can be elattostasic (hypopus). Neoteny could be present in groups with a reduced number of stases (several groups of Actinedida, Tarsonemida). Adult moults (and isophena) are mentioned for some species of Actinedida (Trombidina) and Acaridida (*Dermatophagoides*) (cf. Van der Hammen, 1980: 12).

C. Remarks

Actinotrichida represent one of the oldest extant Chelicerate groups. A representative (*Protacarus crani* Hirst) is known from the Devonian (cf. Hirst, 1923: 456-459, figs. 1-2, pl. 11 figs. a-b; Petrunkevitch, 1955: 97, fig. 1a-b); it represents a species of Eupodid, and does not present important differences from extant representatives of the family. Actinotrichida constitute one of the most successful Chelicerate groups: the diversity of extant species is considerable. Actinotrichid mites can be free-living or parasitic, aquatic or terrestrial, epigeous or hypogeous, xerophilous or hygrophilous, arboricolous, arenicolous, cavernicolous, epizoic, halophilous, muscicolous, saxicolous, etc.

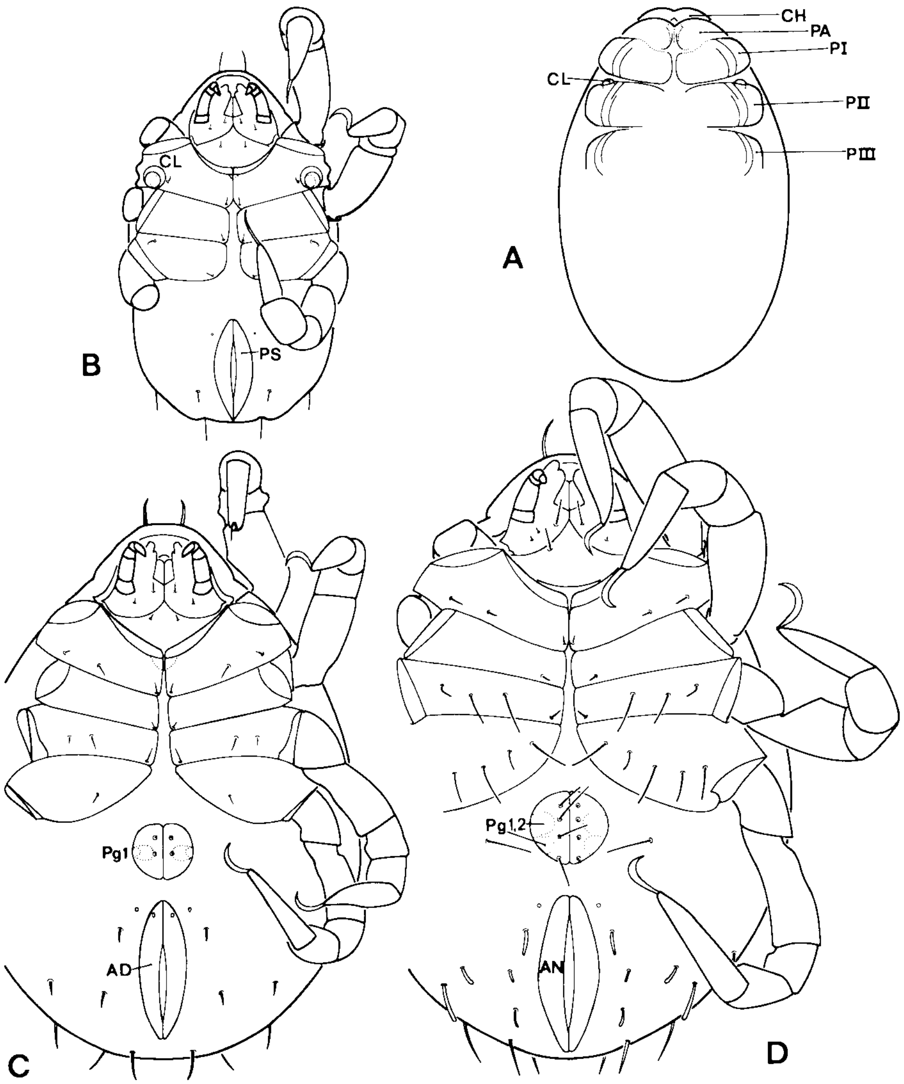

Fig. 24. Postembryonic development of *Hermannia convexa* (C. L. Koch) (1); ventral views of: A, prelarva; B, larva; C, protonymph; D, deutonymph; A-D, x 106. (After Van der Hammen, 1972).

Several species of Actinotrichid mites can be found at considerable depths in the soil. Nematalycidae are known from the interstitial (cf. Coineau, Fize & Delamare Deboutteville, 1967). Actinotrichid ancestors could indeed have colonized the terrestrial soil, long before the Silurian, by way of the interstitial environment.

Fig. 25. Postembryonic development of *Hermannia convexa* (C. L. Koch) (2); ventral views of: A, tritonymph; B, adult female; A-B, x 106. (After Van der Hammen, 1972).

IV. DIAGNOSTIC CHARACTERS

Starting from the descriptions given in the chapters II and III, the following diagnoses of Epimerata, Palpigradi and Actinotrichida have been prepared. The rank of class is attributed to Epimerata, the rank of subclass to Palpigradi and Actinotrichida.

Epimerata

Small or very small, rarely medium-sized, Chelicerata of which the body is originally composed of precheliceral metameres and seventeen segments. There are two tagmata: prosoma and opisthosoma. The genital opening is surrounded by the opisthosomatic appendages of segments VIII and IX. Trichobothria are often present on body and/or appendages. Coxal glands originally debouching dorsally or posterodorsally of the base of leg I. Podosoma with epimera. Supracoxal setae originally present. Legs without coxa, ancestrally with two femora and three claws; the tarsus is not subdivided into basi- and telotarsus, but can present a subdivision into tarsus 1, 2, etc. Ancestrally, the opisthosomatic appendages of segments X-XII are suppressed, and re-appear in the course of postembryonic development. The palpigrade life-cycle is incompletely known, but the ancestral epimerate life-cycle could be composed of six stases, as in Actinotrichida.

Palpigradi

Small, elongate Chelicerata, living in the soil. Prodorsum subdivided into propeltidium, mesopetidium and metapeltidium. No eyes. The opisthosoma is subdivided into eleven segments. Rostral region with frontal organ. Prodorsum with thirteen pairs of setae. Terminal flagellum with many segments. Anus, with ventrodistal position, in segment XVII. Postgenital region with opisthosomatic appendages in the shape of invaginable papillae or verrucae. The epimera of palp and leg I are fused and present epimeral setae. Supracoxal seta *e* present above the base of the palp; it can be multiplied. The mouth is surrounded by two lips: labrum and labium. Chelicerae 3-segmented; cheliceral trochanter relatively large. Palp with claws. The number of adesmatic tarsal segments in palp and legs I-IV (of the adult) is: 5-7-2-2-3. The articulation between femur 2 and genu of leg I, and between genu and tibia of palp and leg I, are constituted by bidesmatic hinge joints (with extensor muscles).

Actinotrichida

Small or very small, rarely medium-sized, Chelicerata. Mouthparts constituting a gnathosoma. Opisthosomatic segments XIII-XVII are suppressed in the course of embryonic development, and can re-appear (with the exception of segment XVII) in the course of postembryonic development. The trifid eugenital opening is situated in a progenital chamber which is closed by progenital valves; the opening between the valves is longitudinal (ancestral condition). The opisthosomatic appendages of segments X-XII (the genital papillae) are, ancestrally, included in the progenital chamber. Prodorsum ancestrally with six pairs of setae. A frontal protuberance or naso can be present in the rostral region. An unpaired anterior eye and one or two pairs of eyes can be present. Mouth originally surrounded by four lips (labrum, lateral lips and labium); the labium has disappeared in most species. Chelicera with reduced trochanter (or trochanter no more recognizable). Palp without apotele. Legs rarely with tarsal subdivisions (tarsus 1, 2, etc.). Anus with ventral position. Supracoxal setae *e*, *eI*, and *eII* can be present above the base of palp and legs I and II respectively; supracoxal seta *eII* can be multiplied.

V. EVOLUTION OF EPIMERATE CHARACTERS

In the present chapter models are prepared of the evolution of epimerate characters and groups of characters. The models constitute a first outline of an epimerate archetype (a standard of epimerate higher classification), developed according to the principles explained in my paper on Type Concept, higher Classification and Evolution (Van der Hammen, 1981: 35-41, figs. 4-7); they are, at the same time, a continuation (according to improved methods) of the chapter on the evolution of cryptognomic characters, in the first paper of the present series (Van der Hammen, 1979a: 21-27, figs. 29-30). The models demonstrate the incompleteness of our knowledge of comparative epimerate morphology, and the nearly complete lack of any knowledge, even hypothetical, with reference to evolutionary mechanisms.

Constitution of the body. — The epimerate body originally consists of prosoma and opisthosoma. A reconstruction of its ancestral (plesiotypic) condition should consider the following morphological data: (1) the presence, in Palpigradi, of seventeen segments and a telson (flagellum); (2) the suppression of segments in the course of actinotrichid embryonic development, and the addition of part of these segments in the course of postembryonic development (hysteromorphosis); (3) the necessity to derive dichoidy and ptychoidy from a common ancestor in which: (a) the epimeral region was separated from the aspidosoma by soft skin; and (b) the epimeral region presented articulations in the shape of transverse bands of soft skin (cf. Grandjean, 1969: 132-139). In the reconstruction of fig. 26A, all of these conditions are fulfilled; it is characterized by the presence of seventeen segments and a telson, a terminal anus, and interruptions of soft skin between the epimera and in the prodorsum (it presents, moreover, a frontal protuberance, three pairs of supracoxal setae, and a primitive podocephalic canal). A ventral view of this plesiotype is represented in fig. 26B; it presents five pairs of opisthosomatic appendages (in segments VIII-XII respectively). The ancestral palpigrade condition is only slightly different from the epimerate plesiotype: the telson has developed into a long, segmented flagellum; the opisthosomatic appendages of segments VIII and IX are associated with the genital opening, and the anterior pair has fused (fig. 26C); the supracoxal setae *eII* and *eI* have, moreover, disappeared. Important changes have taken place in the actinotrichid ancestral type (fig. 26D, E): the opisthosomatic appendages of segments X-XII are included in the progenital chamber; the opisthosomatic appendages of segments VIII and IX are associated with the eugenital opening (which is trifid), and the posterior pair has

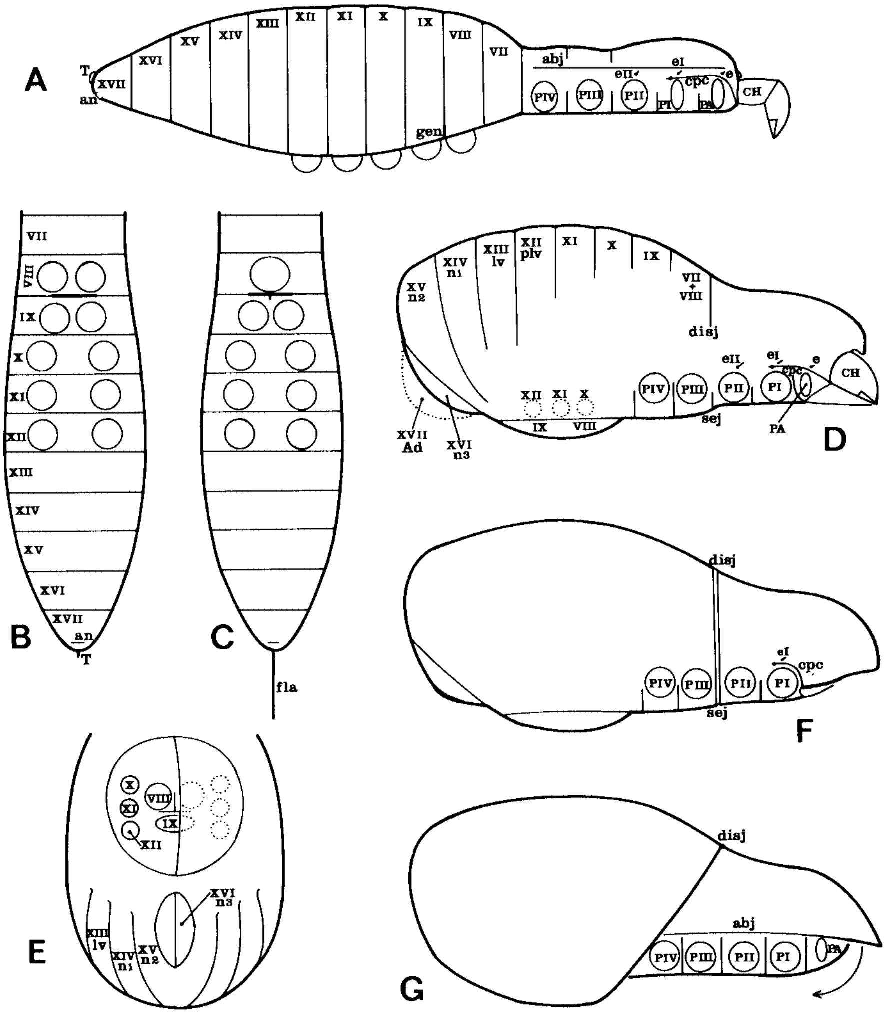

Fig. 26. Schematic representation of the constitution of the epimerate body; A, B, epimerate plesiotype; A, lateral view; B, ventral view of opisthosoma; C, palpigradid plesiotype, ventral view of opisthosoma; D, E, actinotrichid plesiotype; D, lateral view; E, ventral view of opisthosoma; F, actinotrichid dichoid type, lateral view; G, actinotrichid ptychoid type, lateral view.

fused; the anus has shifted to a ventral position, and the posterior segments are suppressed in the course of embryonic development and can be added (reappear) in the course of postembryonic development (the base levels are: larval (XIII), protonymphal (XIV), deutonymphal (XV) and tritonymphal (XVI); segment XVII, with supposed adult base level is not known from Actinotrichida; segment XII, with supposed prelarval base level, is paraproctal in Tarsonemida). The posterior part of the aspidosoma has disappeared in Actinotrichida, whilst a movable gnathosoma has developed. In dichoidy (fig. 26F), the ventrosejugal interval is continuous with the dorsodisjugal furrow. In ptychoidy (fig. 26G), the disjugal furrow permits of articulation; the soft skin between prosoma and aspidosoma, and between the epimera, permits of concealment.

Phanerotaxy. — Three types of phaneres can be found in Actinotrichida: setae, famuli and solenidia. These three types could also be present in Palpigradi (cf. Van der Hammen, 1977a: 15): the bifurcate phaneres of the palpigrade tarsi could represent famuli, the phaneres with quadrangular section and ciliate ribs could represent solenidia (the three types of phaneres could be present in all groups of Chelicerata, although a study of their fine structure will be indispensable for a definite conclusion). The actinotrichid setae (fig. 27A) present an actinopilinous axis. The presence of actinopilin, in setae, has not yet been demonstrated for Palpigradi, although Zakhvatkin (1952) found that the palpigrade setae are birefringent. Plesiotypically, setae are arranged in verticils and files (fig. 27H). Eupathidia (fig. 27B) and trichobothria (fig. 27C, D) represent specialized setae. Famuli are inserted on the tarsus (in Actinotrichida on tarsus I and, rarely, on tarsus II); the ancestral shape is represented in fig. 27E (fig. 27F, G represent derived shapes). Solenidia, i.e. hollow phaneres with open root and with numerous pores (cf. Vercammen-Grandjean, 1965), can be found on the actinotrichid femur, genu, tibia and tarsus of the legs, and the tarsus of the palp; they can present various shapes (fig. 27I-K). The evolutionary aspects of numerical changes in phanerotaxy have recently been discussed by Van der Hammen (1981a).

Respiratory system. — Respiration is apparently exclusively cutaneous in Palpigradi and many Actinotrichida (primitive Actinedida, primitive Oribatida, most Acaridida). Secondary respiratory organs (stigmata, tracheae, brachytracheae, tracheoles, etc.) have developed independently in many Actinotrichida. Actinedida (with the exception of primitive species) are prostigmatic: the stigmata are found at the base of the chelicerae. In higher Oribatid mites, tracheae start from acetabula and apodemata. In female Tarsonemida there is, at both sides, a stigma in apodeme 1. Other respiratory organs can start from various superficial parts of the cuticle, from hidden depressions of the surface, and from the progenital chamber.

Aspidosoma. — The palpigrade aspidosoma is schizopeltid. In primitive Actinedida (Actinotrichida), the prodorsum (with little or no scleritization) can be subdivided (by furrows and apodemes) into pro-, meso- and metastethidium. The presence of a subdivided prodorsum is regarded as a primitive character. Eyes are not present in Palpigradi, although there is a frontal protuberance. Actinotrichida can present two pairs of lateral eyes and an unpaired anterior eye; the actinotrichid naso (the frontal protuberance) can present an eye at its ventral surface (it is often bilobate). The actinotrichid naso and the palpigrade frontal protuberance could be homologous; the presence of a naso in Actinotrichida constitutes a primitive character. It is unknown whether palpigrade ancestors were in the possession of eyes. Eyes could have developed independently in Ac-

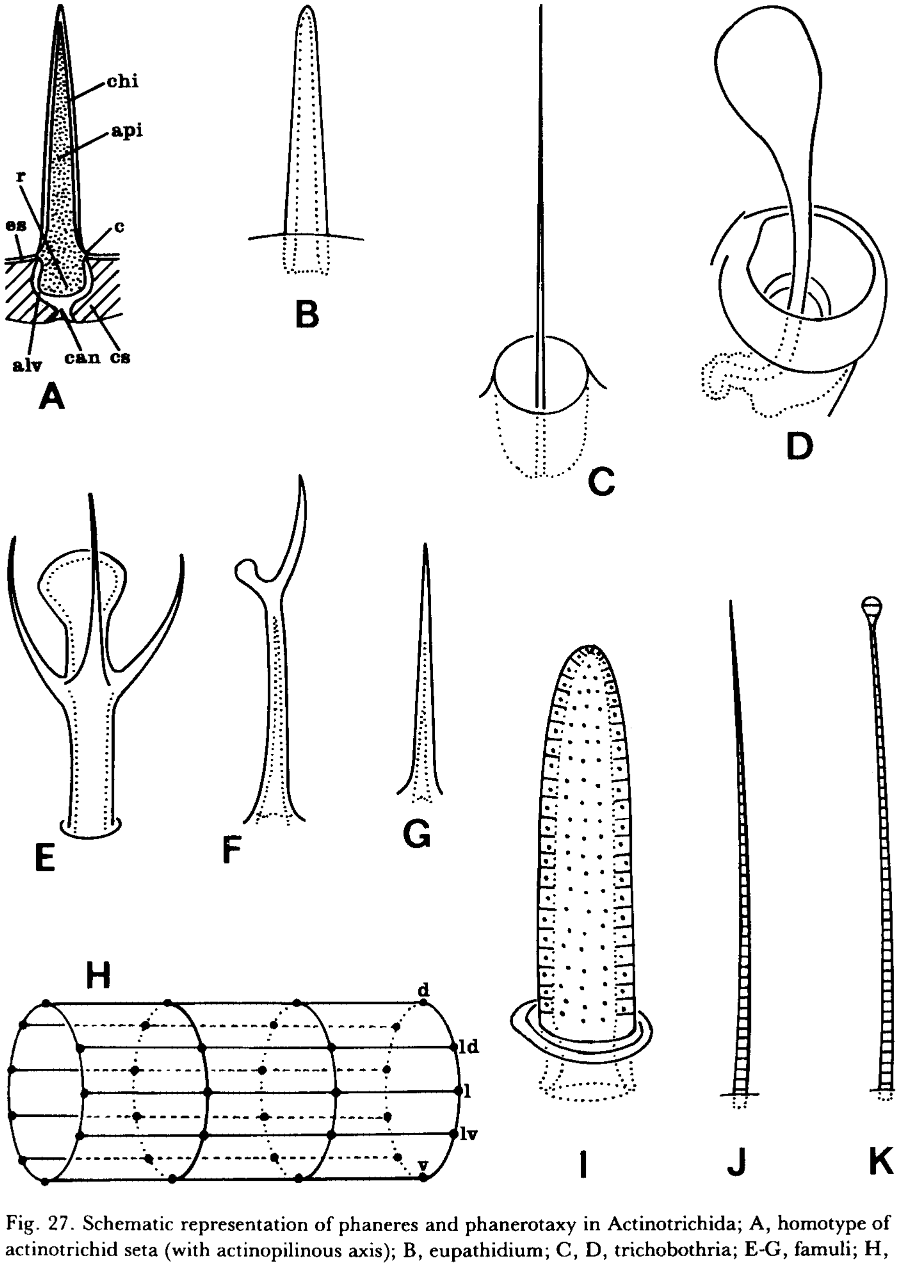

Fig. 27. Schematic representation of phaneres and phanerotaxy in Actinotrichida; A, homotype of actinotrichid seta (with actinopilinous axis); B, eupathidium; C, D, trichobothria; E-G, famuli; H, arrangement of setae in verticils and files; I-K. solenidia (I, based on Vercammen-Grandjean, 1965). Eupathidia and trichobothria represent modified setae; they have evolved from ordinary setae by: (1) the development of a canal in the solid setal axis (eupathidia); (2) the development of a bothridium at the place of insertion, and of various specialized setal shapes (bothridial setae). The ancestral shape of a famulus (sensory function unknown) is that of a globular head surrounded by bracteae, borne on a stalk. The solenidial sense could be chemical.

tinotrichida, although the absence of eyes in higher Actinotrichida apparently refers to a loss (i.e. a derived character state). The palpigrade prodorsum presents thirteen pairs of setae, whilst the primitive number in Actinotrichida is six pairs; Actinotrichida could have lost the seven posterior pairs present in Palpigradi (together with the posterior tergites of the prodorsum). Two pairs of actinotrichid prodorsal setae can become trichobothria.

Podosoma. — The podosoma of Palpigradi and Actinotrichida is characterized by the presence of epimera which can be separated by soft skin, or fuse in various ways (a fusion of the epimera of palp and leg I, present in Palpigradi, is also known from the Oribatid family Epilohmanniidae). The number of epimeral setae generally increases in the course of postembryonic development. The orifice of a coxal gland is ancestrally present above the base of leg I; the presence of a primitive external podocephalic canal could have been a (derived) character of all primitive terrestrial Epimerata. Supracoxal setae must, originally, have been present above the bases of palp (*e*), leg I (*eI*) and leg II (*eII*). Supracoxal seta *eII* is the weakest of the three; it is present in some Actinotrichida, and can be multiplied (a sign of weakness). Supracoxal seta *e* can be multiplied in Palpigradi (*eI* and *eII* are not present in this group).

Mouthparts and ingestion. — The differences between palpigrade and actinotrichid mouthparts are considerable. In Palpigradi, a labrum, a labium and a crescent-shaped mouth (situated between the bases of the chelicerae) are present, whilst Actinotrichida possess a complicated gnathosoma. Theoretically a gnathosoma can, however, be derived from a structure very similar to that in Palpigradi (cf. Van der Hammen, 1970c: 19-20, fig. 1). Fig. 28A represents a diagram of the mouthparts of a hypothetical epimerate ancestor, in which the position of a number of selected points (*a*, *b*, *c*, *d*, *e*, *f*, *g*) is indicated. In fig. 28B, a schematic representation of a primitive actinotrichid gnathosoma, the same points are indicated; this diagram demonstrates that the epimeron of segment II (*fg*), the palp, and the mouth have advanced, whilst the other points have, more or less, kept the same position. In Oribatid mites, in which the gnathosoma is situated in a camerostome, a further shifting of the points has taken place (fig. 28C): *a* and *b* cannot be indicated with certainty; *cd* has become mobile; *e*, *f*, *g*, the palp and the mouth have preserved about the same position as in the primitive actinotrichid type. Fig. 28D, E, F represent schematic sections of the mouth: a primitive chelicerate mouth with two lips (as in Palpigradi); a primitive actinotrichid mouth with four lips (as in some primitive Actinedida and Oribatida; the lateral lips are extensions of the ''endites'' of the palps); and the trifid mouth with three lips (as in most Actinotrichida).

Ingestion of fragmented solid food, and internal digestion have certainly been present in ancestral aquatic Epimerata; the chelicerae must have had here a prehensile as well as a masticatory function. The alimentation of extant Palpigradi is unknown, although the morphology of the chelicera demonstrates that its function will be prehensile and possibly also masticatory. In primitive

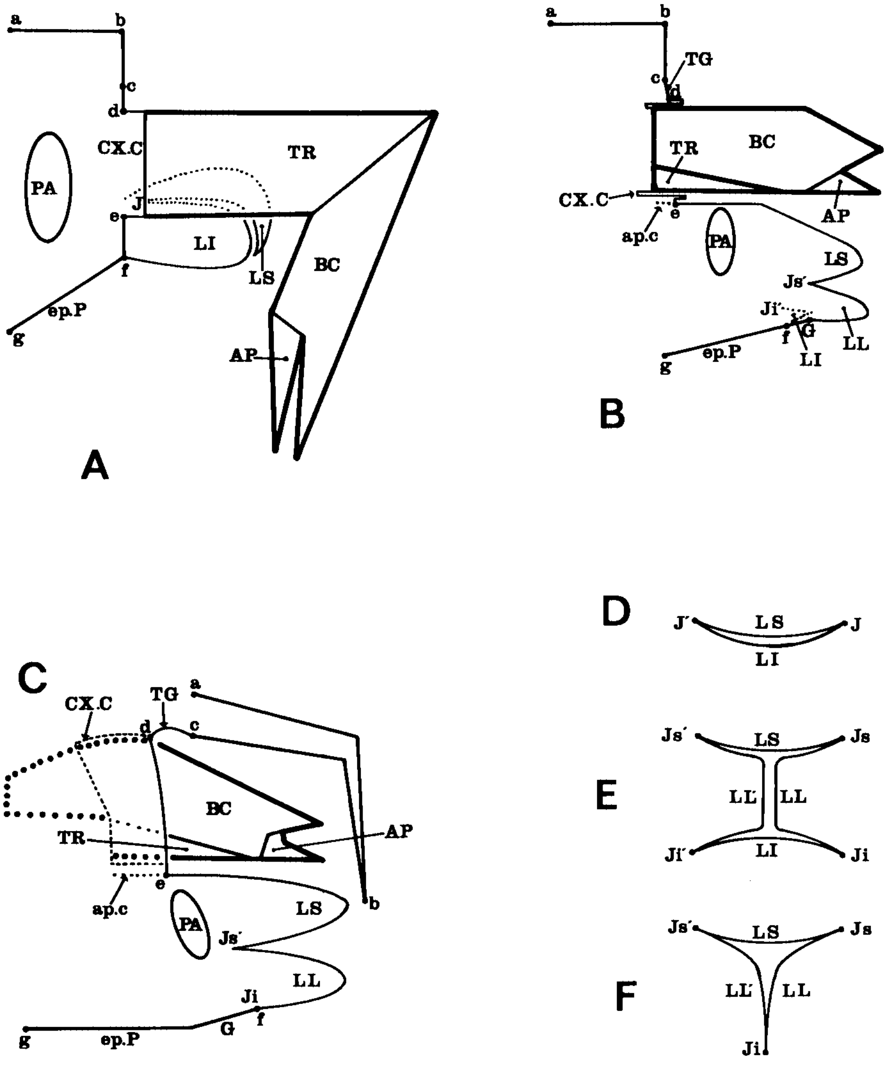

Fig. 28. Diagrams of epimerate mouthparts, showing the position of a number of selected points with respect to each other, and in different types; A, palpigrade type of mouthparts; B, primitive actinotrichid type of gnathosoma; C, oribatid type of gnathosoma; D-F, mouth viewed from in front; D, palpigrade type; E, primitive actinotrichid type; F, general actinotrichid type with three lips. (Redrawn after Van der Hammen, 1970c).

Actinotrichida, fragmented solid food is ingested, and internally digested. Various ways of ingestion and digestion are known from higher Actinotrichida.

Appendages. — The ancestral epimerate chelicera is supposed to have been three-segmented (trochanter, body of chelicera, apotele), with pivot joints between the segments (fig. 29A). In Palpigradi, the superior tendon of the

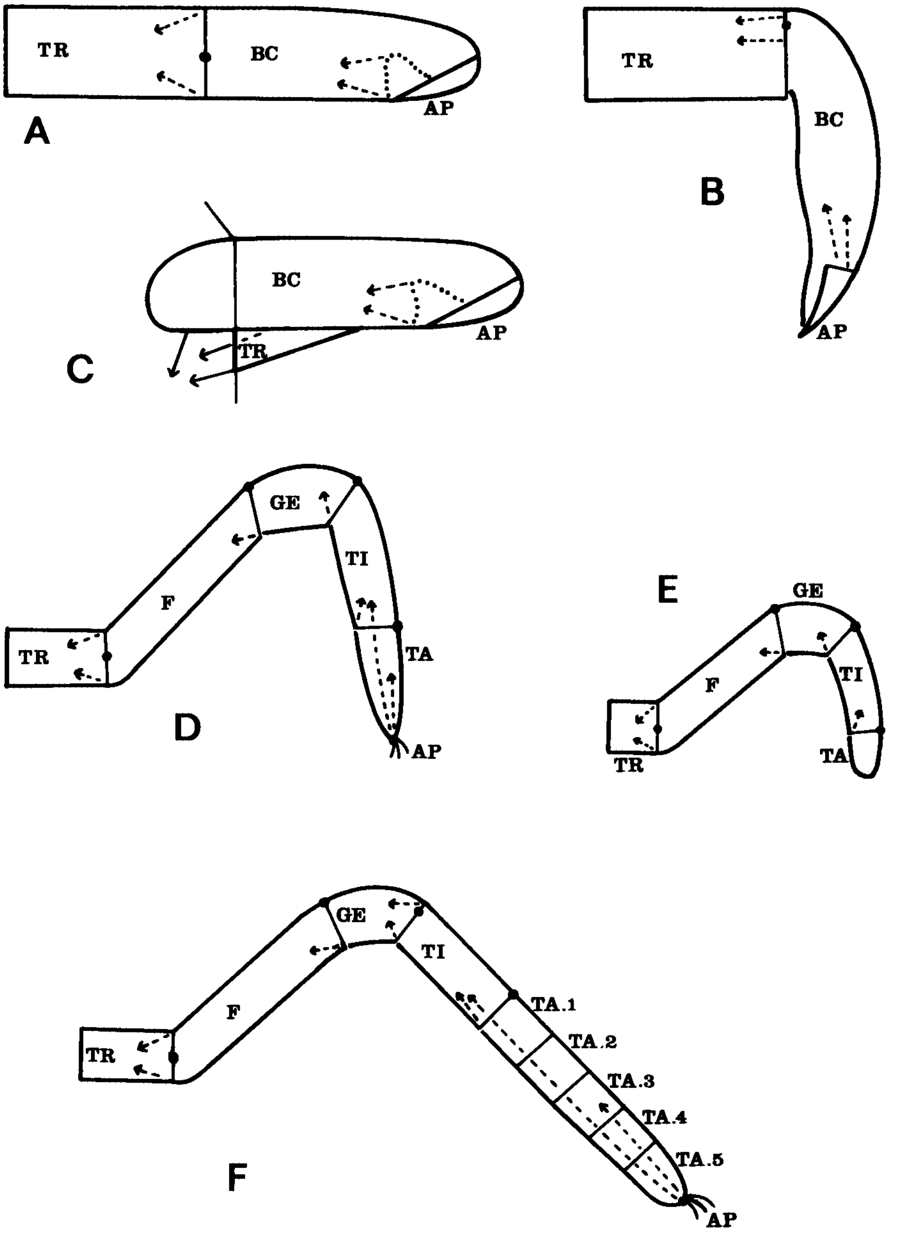

Fig. 29. Diagrammatic representation of segmentation and articulation of epimerate chelicerae and palps. A-C, chelicerae; A, hypothetical ancestral (plesiotypic) condition; B, palpigrade type; C, actinotrichid type. D-F, palps; D, hypothetical ancestral (plesiotypic) condition; E, actinotrichid type; F, palpigrade type.

trochanter/body-of-chelicera joint has the function of an extensor, whilst there has been torsion in the body of the chelicera (fig. 29B). In Actinotrichida, the trochanter has been subject to regression: it has become an element with lateroventral position (fig. 29C), or is no more discernible.

The ancestral condition of the palp is represented in fig. 29D; it consists of six segments (trochanter, femur, genu, tibia, tarsus and apotele). The palp of primitive Actinotrichida resembles this condition, with the exception of the suppression of the apotele (fig. 29E). Various palpal segments can have fused in Actinotrichida. The palpigrade palp (with ambulatory function) (fig. 29F) is characterized by the presence of five adesmatic tarsal segments, and of extensor muscles at the genu/tibia joint (apparently associated with a palpal function which has now completely or partly disappeared). The palpigrade palp presents an apotele with three claws.

The hypothetical ancestral condition of the epimerate legs is represented in fig. 30A. It presents seven segments: trochanter, femur 1, femur 2, genu, tibia, tarsus and apotele (with three claws). Palpigrade legs II-IV (leg IV is represented in fig. 30B) differ from the ancestral condition by the subdivision of the tarsus. Palpigrade leg I, with palpal function, is characterized by the presence of seven adesmatic tarsal segments, and extensor muscles at the femur 2/genu and genu/tibia joints (fig. 30C). The legs in primitive Actinotrichida resemble the hypothetical ancestral condition (fig. 30A). Part of the evolution of the legs in higher Actinotrichida is represented schematically in fig. 30D; it includes the development (by integration of segments) of femorogenu and tibiotarsus, and the evolution (by subdivision and multiplication) of tarsi 1, 2, etc. A palpal evolution of leg I in Actinotrichida is associated with the suppression of the apotele.

Reproduction. — Because nothing is known about palpigrade reproductive behaviour, few remarks can be made here on the evolution of epimerate reproduction. Fertilization must have been external in epimerate aquatic ancestors. Because of the great differences in sperm morphology and spermiocytogenesis, between Palpigradi and Actinotrichida, the evolution of sperm transfer in the two groups must have been separate from the beginning of their terrestrial life.

Life-cycle. — The ancestral life-cycle (fig. 31A), with six stases (in which the prelarva is elattostasic or calyptostasic), is still found in many Actinotrichida, and could also be present in Palpigradi. The evolution of the Actinotrichid life-cycle is represented in a series of ontophylogenetic diagrams (fig. 31; cf. also Van der Hammen, 1978). Neoteny, in which maturity is attained at one of the nymphal levels, is supposed to be present in many groups of Actinedida (fig. 31B) and Tarsonemida (fig. 31C). Progressive protelattosis (fig. 31D), in which the larva has become elattostasic, is known from some species of Actinedida (e.g. *Labidostomma* species). Metelattosis is known from Trombidina (fig. 31E: regressive stases are found at the level of proto- and tritonymph) and Acaridida (fig. 31F: hypopus formation at the level of the deutonymph). Plethomorphosis

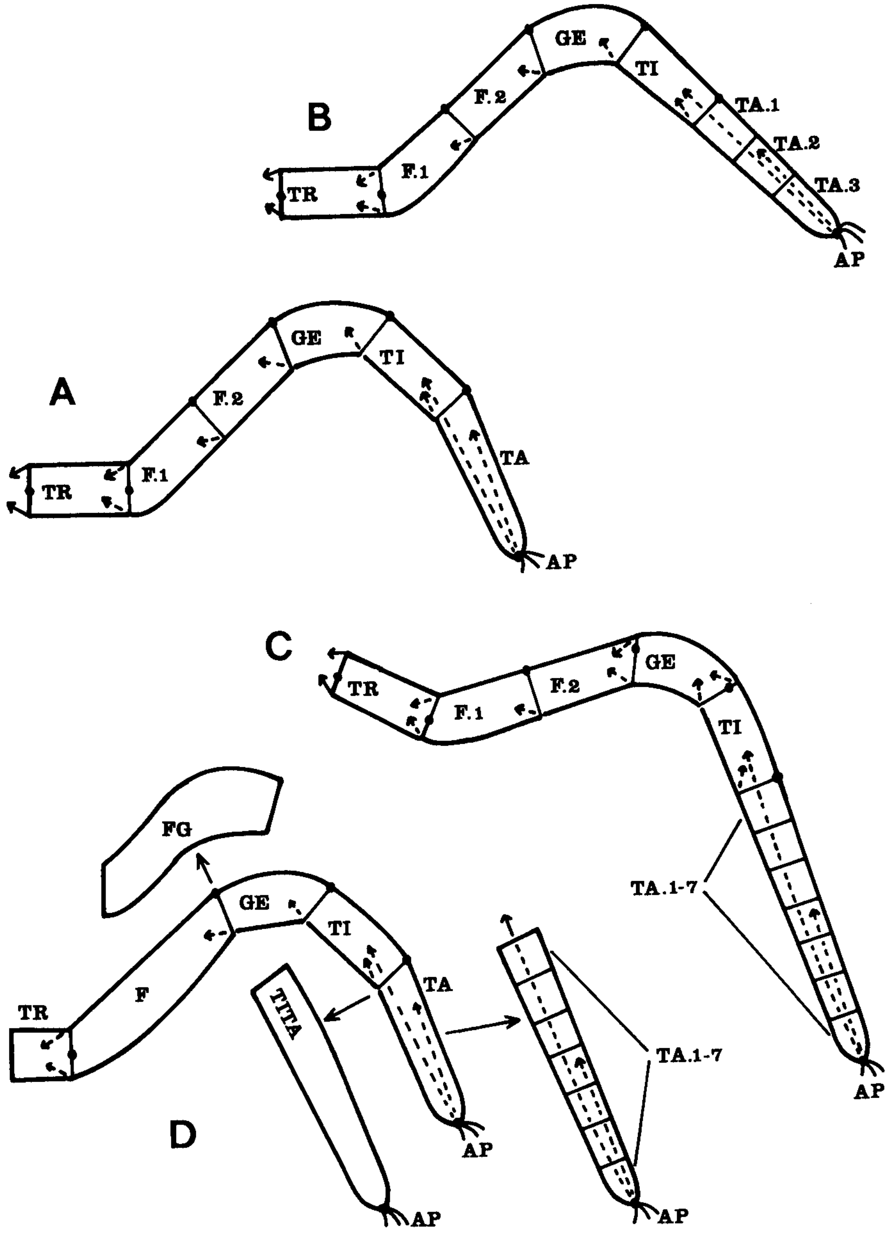

Fig. 30. Schematic representation of segmentation and articulation of the legs in Epimerata; A, plesiotype of the epimerate leg (with two femora); B, palpigrade leg IV (with tarsi 1-3); C, palpigrade leg I (with tarsi 1-7, and extensor muscles at the femur 2/genu and the genu/tibia articulations); D, diagram of the evolution of the legs in Actinotrichida, starting from species with integrated femora (the diagram represents the development, by fusion, of femorogenu and tibiotarsus; and the evolution, by subdivision and multiplication, of tarsi 1-7).

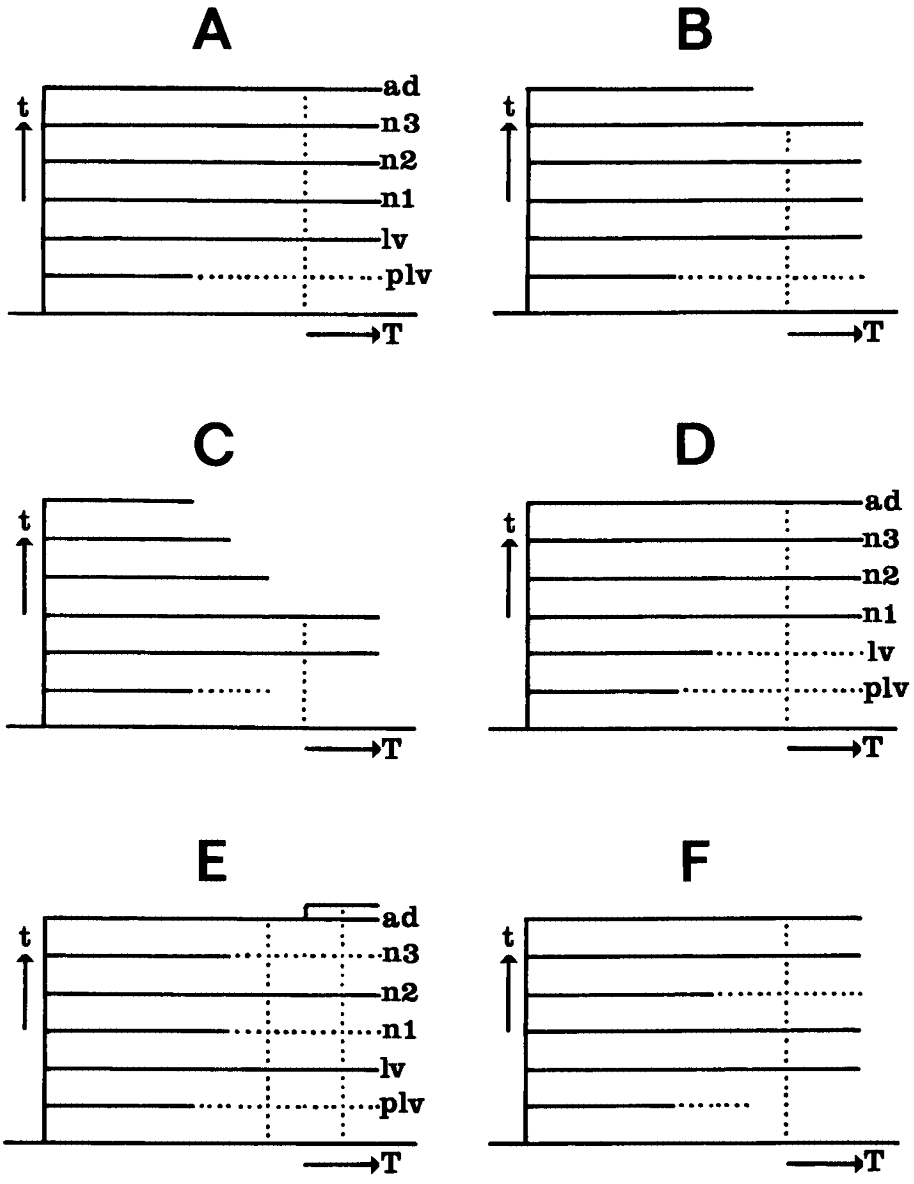

Fig. 31. Ontophylogenetic diagrams of the various types of postembryonic development present in Actinotrichida; the horizontal dotted lines represent regressive stases (elattostases or calyptostases); the vertical dotted lines represent the ontogeny of the group for which the type is characteristic. A, ancestral type, with six stases, of which the prelarva is elattostasic or calyptostasic (this type is present in Oribatida and many Actinedida, and could also be the palpigrade type). B, neotenous type, with two nymphs, in which maturity is supposed to have been attained at the tritonymphal level (this type is present in several groups of Actinedida). C, neotenous type with two stases (larva and adult); it is supposed that maturity is attained at the level of the protonymph (this type is found in Tarsonemida). D, type with progressive protelattosis, in which the larva has become elattostasic (it is present in some species of Actinedida). E, type with metelattosis at the level of proto- and tritonymph; in this type, plethomorphosis (the secondary formation of isophena by growing moults or repetition moults) can occasionally be present at the level of the adult (the type is characteristic for Trombidina). F, type with metelattosis at the level of the deutonymph (this type is present in Acaridida with hypopus-formation).

can occasionally be found at the level of the adult, e.g., in some species of Trombidina (fig. 31E).

Ancestral Epimerata. — Primitive Actinotrichida, and particularly Palpigradi, still present many ancestral characters. A reconstruction of the epimerate plesiotype resembles Palpigradi (especially *Prokoenenia*) in many characters (seventeen segments, five pairs of opisthosomatic appendages, cutaneous respiration, two lips and crescent-shaped mouth, chelicerae with three segments, palp with apotele and three claws, orifice of the coxal gland above the base of leg I, legs with two femora and three claws); it presents, however, undivided tarsi, supracoxal setae above the bases of legs I and II, and separated epimera of palp and leg I. This plesiotype is supposed to have lived in the deeper layers of the soil, and to have evolved before the Silurian. Actinotrichida (even primitive groups) are much more remote from this plesiotype than Palpigradi. The last-mentioned group constitutes indeed the most primitive group of extant Chelicerata.

VI. EPIMERATE RELATIONSHIPS

Palpigradi and Actinotrichida must have evolved separately from the beginning of the terrestrial life of both groups (supposed to have started before the Silurian). Epimerata could indeed represent the earliest terrestrial chelicerate group. They must already have been separated from other Chelicerata by the end of the Cambrium. Remote affinities with other groups of Chelicerata are certainly present, but are not yet clearly understood. Those characters, which had already developed before the period of terrestrial life had started, i.e. the prototactic number of seventeen body segments and the prototactic number of seven leg segments (trochanter, femur 1, femur 2, genu, tibia, tarsus, and an apotele with three claws), represent the most important grade in the hierarchy of characters. A very important character is also constituted by the ancestral position of the orifice of the coxal gland (above the base of leg I). The development of a segmented flagellum, in Palpigradi; and the regression of the cheliceral trochanter, the development of a gnathosoma, lateral lips, and a progenital chamber (including shifting of opisthosomatic segments), and the suppression of segment XVII (and the telson), in Actinotrichida, are among the fundamental characters separating the two groups. In Palpigradi and Actinotrichida, sperm morphology and spermiocytogenesis evolved in divergent directions, probably from the beginning of the terrestrial life of the groups.

Lehtinen (1980: 210) regarded the presence of an ovipositor in mites and harvestmen as an indication of affinity. An ovipositor, however, is present only in some groups of mites, and great differences in morphology (cf. fig. 14) indicate that it arose independently in these groups (it could, moreover, not have evolved before the period of terrestrial life). Evidently, the ovipositor found in Oribatida and Endeostigmata (with three terminal lobes homologous with the opisthosomatic appendages of segments VIII and IX), the segmented Opilionid ovipositor (with two terminal lobes), and the Opilioacarid ovipositor (a primitive unsegmented ovipositor without terminal lobes shaped like opisthosomatic appendages) are not at all "amazingly similar" (as stated by Lehtinen). It might be remarked here also that the actinotrichid genital papillae (opisthosomatic appendages of segments X-XII), and the opilioacarid genital papillae (opisthosomatic appendages of segment VIII) are not homologous but homonomous structures. The comparative study of sperm morphology and spermiocytogenesis in Opilioacarida and other Anactinotrichida, by Alberti (1980), has definitely demonstrated that the first-mentioned group must be classified with Anactinotrichida.

In the cladistic classification of Chelicerata, prepared by Weygoldt & Paulus (1979, 1979a) and Weygoldt (1980), Palpigradi, Solifugae, Pseudoscorpionida, Opilionida, Ricinulei and Acari constitute a single monophyletic group (Apulmonata), characterized by reduction of size, loss of booklungs, and reduction of the number of eyes (in the present paper, it is supposed that ancestral Epimerata were characterized by cutaneous respiration). Apulmonata are supposed, by Weygoldt & Paulus, to have split into Palpigradi and Holotracheata, because of the development of a simple coxisternal region in Palpigradi, on the one hand, and the loss of a flagellum in Holotrachata, on the other hand (the possession of a simple coxisternal region is, in fact, an ancestral character of Epimerata, whilst the development of a many-segmented flagellum from a telson is regarded here as a derived character). Among the Holotracheata, mites and Ricinulei constitute the Acarinomorpha, a group characterized by the occurrence of a hexapod larva, whilst mites and Ricinulei are supposed to be separated from each other by the development of a gnathosoma in mites. The comparative study of fine structure of the spermatozoa and spermiocytogenesis by Alberti (1980, 1980a) has now definitely confirmed the fundamental differences between Actinotrichida and Anactinotrichida. The comparative study of Anactinotrichida and Ricinulei (Van der Hammen, 1979a) has demonstrated the close affinities between the two groups, and the presence of a primitive gnathosoma in Ricinulei.

Little is known about the phylogeny of the four Actinotrichid orders. All of them appear to be related to Endeostigmata (primitive Actinedida), which group apparently closely resembles the actinotrichid ancestors. Fundamental differences, mentioned up to now, appear to refer to evolutionary programs, realized in different ways by the different representatives. Actinedida and Oribatida represent groups which are, for the greater part, very different from each other, although the primitive representatives are closely related. Evidently, the affinities and the phylogeny of the four actinotrichid orders should be reinvestigated.

VII. LIST OF NOTATIONS

a, anterior infracapitular seta.

a (fig. 28), point in the rostral region of the prosoma.

(*a*), antelateral setae of tarsus.
abj, abjugal furrow.
Ac.P, acetabulum of palp.
acx, line of attachment of cheliceral sheath to chelicera.
Ac.I, acetabulum of leg I.
Ac.II, acetabulum of leg II.
ad, adult.
Ad, adult base level.
AD, adanal segment (segment XIV).
$ad_{1\text{-}6}$, adanal setae.
$ag_{1\text{-}3}$, aggenital setae.
alv, alveolus.
an, anus.
an (fig. 17), anterior paraxial border of gena.
AN, anal segment (segment XV).
$an_{1\text{-}5}$, anal setae.
AP, apotele.
apc, actinopilinous core of seta.
ap.c, capitular apodeme.
apo.1-2, apodemata 1 and 2.
AS, aspidosoma.
at, at_1, at_2, line of attachment of cheliceral frame to infracapitulum.

b (fig. 28), point in the rostral region of the prosoma.
BC, body of chelicera.
bcx, base of cheliceral sheath.
bl′, anterior basilateral seta of femur.
bls, base of labrum.
bo, bothridium.
bos, bothridial seta.
brp, posterior border of rostrophragma.
bru, brush of rutellum.
bv″, posterior basiventral seta of femur.

c, collar.
c (fig. 28), point in the rostral region of the prosoma.
C, notogastral region attributed to segments VII and VIII.
$c_{1\text{-}3}$, c_{p}, notogastral setae of "segment" *C*.
can, canal.
$ce_{1\text{-}2}$, prodorsal setae attributed to segment I.
CE, cervix.
CH, chelicera.
cha, posterior seta of chelicera.
chb, anterior seta of chelicera.
chi, chitinous part of seta.

circ, circumcapitular furrow.
Cl, Claparède's organ.
cm, culminal seta of palpal tarsus.
co, copulatory orifice.
co.1, cotyloid wall of acetabulum I.
co.2, cotyloid wall of acetabulum II.
cpc, podocephalic canal.
cs, chitonostracum (procuticle).
CX.C, cheliceral sheath ("coxal" region of chelicera).

d, dorsal seta.
d (fig. 28), point in the frontal or tegular region of the prosoma.
D, notogastral region attributed to segment IX.
$d_{1\text{-}2}$ (Palpigradi), dorsal setae of opisthosoma.
$d_{1\text{-}2}$ (Actinotrichida), notogastral setae attributed to segment IX.
d_x, unpaired dorsal seta.
dg, duct of gland.
dga, duct of anterior podocephalic gland.
dgc, duct of coxal gland.
dgic, duct of intercheliceral gland.
dgm, duct of median podocephalic gland.
dgp, duct of posterior podocephalic gland.
disj, disjugal furrow.

e, supracoxal seta of palp.
e (fig. 28), point at the base of the chelicera.
E, notogastral region attributed to segment X.
$e_{1\text{-}2}$, notogastral setae attributed to segment X.
ep.P, epimeron of segment II (palpal segment).
ep.I, epimeron of segment III (segment of leg I).
es, epiostracum (epicuticle).
eI, supracoxal seta of leg I.
eII, supracoxal seta of leg II.

f (fig. 28), point at the base of the labium, or coinciding with inferior oral commissure.
F (opisthosoma), notogastral region attributed to segment XI.
F (appendages), femur.
$f_{1\text{-}2}$, notogastral setae attributed to segment XI.
FC, cheliceral groove.
fel, fenestrate area of body of chelicera.
FG, femorogenu.
fla, flagellum.
fla.1, first segment of flagellum.
(*ft*), fastigial setae of tarsus.

F1, femur 1.
F2, femur 2.
FI, femur of leg I.
FII, femur of leg II.

g (fig. 28), point at the posterior border of the epimeral region of the palp.
G, gena.
$g_{1\text{-}7}$,genital setae.
GE, genu.
$ge_{1\text{-}3}$, antiaxial genital setae.
gen, genital opening.
GEN, progenital opening.
GN, gnathosoma.

h, posterior infracapitular seta.
H (gnathosoma), mentum.
H (opisthosoma), notogastral region attributed to segment XII.
$h_{1\text{-}3}$, notogastral setae attributed to segment XII.
HY, hysterosoma.

ia, lyrifissure or cupule attributed to segment IX.
iad, lyrifissure or cupule of adanal segment (segment XIV).
ian, lyrifissure or cupule of anal segment (segment XV).
ID, idiosoma.
ih, lyrifissure or cupule attributed to segment XII.
im, lyrifissure or cupule attributed to segment X.
in, interlamellar seta.
ip, lyrifissure or cupule attributed to segment XI.
ips, lyrifissure or cupule of pseudanal segment (segment XIII).
it', *it"*, iteral setae of tarsus.

J, *J'*, oral commissures.
Ji, *Ji'*, inferior oral commissures.
Js, *Js'*, superior oral commissures.

k, *k'*, *k"*, condyles.
ka, *kl*, *kp*, setae of the constricted part of the ovipositor.

l, *l'*, *l"*, (*l*) lateral setae.
ld, laterodorsal seta.
le, lamellar seta.
$le_{1\text{-}3}$, prodorsal setae attributed to segment III.
LI, labium.
$li_{1\text{-}2}$, prodorsal setae attributed to segment IV.
LL, *LL'*, lateral lips.
$lo_{1\text{-}3}$, prodorsal setae of metapeltidium.
LS, labrum.

lt, lt″, lateral setae of palpal tarsus.
lv, larva, larval base level.
lv, lv_{1-2} (Palpigradi), lateroventral setae.

m, m_{1-3}, median infracapitular setae.
m (Palpigradi), mesopeltidium.
m (fig. 15F), lateral prodorsal mark.
ma_{1-4}, sigilla (external marks of muscle insertions).
mi, movable jaw of chelicera.
mnt, mentotectum.
m.p, metapeltidium.
ms, fixed jaw of chelicera.

N, naso.
Ne, frontal organ.
n1, protonymph, protonymphal base level.
n2, deutonymph, deutonymphal base level.
n3, tritonymph, tritonymphal base level.

OE, oesophagus.
og, eugenital opening.
og_1, orifice of anterior podocephalic gland.
ogc, orifice of coxal gland.
ogi, orifice of infracapitular gland.
ogm, orifice of median podocephalic gland.
ogp, orifice of posterior podocephalic gland.
op′, paraxial oncophysis of body of chelicera.
OP, opisthosoma.
opv, ventral oncophysis of body of chelicera.
opx, coxal oncophysis of chelicera.
or_{1-3}, adoral setae.

(*p*), proral setae of tarsus.
p_{2-4}, setae of segment XIII.
PA, palp.
pa_{1-2}, prodorsal setae attributed to segment II.
PD, prodorsum.
PE, peranal segment (segment XVI).
pg_{1-2}, postgenital setae.
Pg_{1-3}, genital papillae.
PH, pharynx.
pl′, *pl″*, primilateral setae of tarsus.
plv, prelarva, prelarval base level.
PO, podosoma.
po.lc, laterocoxal porose area of infracapitulum.
Po.1-5, opisthosomatic appendages.

po.mn, porose area of manubrium.
p.p, propeltidium.
PR, prosoma.
PS, pseudanal segment (segment XIII).
ps_{1-3}, setae of pseudanal segment.
PT, proterosoma.
pv′, *pv″*, primiventral setae of tarsus.
PI-IV, legs I-IV.

r, root of seta.
ro, rostral seta.
rp, rostrophragma.
RU, rutellum.

s, subungual seta of tarsus.
s_{2-3}, setae of segment XIII.
sc.ls, labral sclerite.
sc.ph, dorsal pharyngeal sclerite.
se, capitular saddle.
sej, sejugal interval or furrow.
ss, secretory seta.
SS, stethosoma.
su, subultimal seta of palpal tarsus.

t, ontogenetic time.
T (fig. 31), phylogenetic time.
T, telson.
t_i, inferior tendon of apotele.
t_s, superior tendon of apotele.
TA, tarsus.
TA1-8, tarsus 1-8.
tc′, *tc″*, tectal setae of tarsus.
tf_i, inferior tendon of femur.
tf_s, superior tendon of femur.
tf′, anterior tendon of femur.
tf″, posterior tendon of femur.
tfe, tendon of femur 2.
tg, tendon of genu.
Tg, Trägårdh's organ.
TG, tegulum.
tge, tendon of extensor muscle of genu.
TI, tibia.
TITA, tibiotarsus.
tls, tendons of labral sclerite.
tm_{1-3}, median tendons inserted on capitular apodeme.

$tp_{1\text{-}2}$, dorsal infracapitular tendons.
TR, trochanter.
TRII, trochanter of leg II.
tT_i, inferior tendon of Trägårdh's organ.
tT_s, superior tendon of Trägårdh's organ.
tta, tendon of tarsus.
tte, tendon of extensor muscle of tibia.
tti, tendon of tibia.
ttr, tendon of trochanter.
ttr_i, inferior tendon of trochanter.
ttr_s, superior tendon of trochanter.
ttr', anterior tendon of trochanter.
ttr'', posterior tendon of trochanter.
$t\alpha$, posterior antiaxial tendon of infracapitulum.
$t\pi$, paraxial tendon inserted on capitular apodeme.

(*u*), ungual setae of tarsus.
ul', ul'', ultimal setae of palpal tarsus.

v, v', v'', (v), $v_{1\text{-}3}$, ventral setae.
v_x, unpaired ventral seta.
Va, anterior opisthosomatic verruca (verruca of segment X).
$va_{1\text{-}2}$, setae of anterior opisthosomatic verruca.
Vp, posterior opisthosomatic verruca (verruca of segment XII).
vp_x, unpaired seta of posterior opisthosomatic verruca.
$vp_{1\text{-}2}$, setae of posterior opisthosomatic verruca.

xa, anterior exobothridial seta.
xp, posterior exobothridial seta.

Δ (delta), condyle.
ϵ (epsilon), famulus or supposed famulus.
ζ (zeta), eupathidium.
λ (lambda), base of rostral limbus.
σ (sigma), solenidion of genu.
τ, $\tau_{1\text{-}4}$ (tau), anterior eugenital setae.
$\varphi_{1\text{-}2}$ (phi), solenidia of tibia.
$\Psi_{1\text{-}2}$ (psi), posterior eugenital setae.
ω, $\omega_{1\text{-}3}$ (omega), solenidia (or supposed solenidia) of tarsus.

1a-d, epimeral setae of segment III.
2a-c, epimeral setae of segment IV.
3a-d, epimeral setae of segment V.
4a-d, epimeral setae of segment VI.

VII-XVII, segments of the body.

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

″ (double prime), posterior face of an appendage.

(), a pair.

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