STUDIES ON OPILIOACARIDA (ARACHNIDA) I. DESCRIPTION OF OPILIOACARUS TEXANUS (CHAMBERLIN & MULAIK) AND REVISED CLASSIFICATION OF THE GENERA

by

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With 21 text-figures

In a comparative morphological investigation of all groups of mites, a detailed study of the interesting Opilioacarida must be of primary importance. Regarded as partly primitive and isolated, they present on the one hand an important series of characters in common with Anactinotrichida, on the other a somewhat shorter list of characters found also in Actinotrichida. A revaluation of these relationships appeared at this moment highly desirable.

According to our present knowledge, Opilioacarida are rare, and the area of distribution is discontinuous. Species are now known from such widely separated localities as Algeria, Sicily, Corfu, Aden, Asiatic Russia, Ivory Coast, Angola, Tanzania (new record), Madagascar (new record), Uruguay, The Argentine, Puerto Rico, Texas, and Arizona. The gaps can partly be attributed to the fact that, as a rule, Opilioacarids must be collected by hand, under stones, etc., a method generally not applied to mites. Besides, adult Opilioacarida are in the field probably often mistaken for immature Arthropods. Certain data (to be published in the following number of the present series) point, however, also to a very localized occurrence.

Recently, various contributors have placed valuable material at my disposal, in that way enabling me to start the present series of investigations. Because these materials consist of species that belong to two genera, the extent of the series is provisionally estimated at two papers.

The first part of my study on Opilioacarid morphology is connected with my very interesting travel to the United States of America in 1963. While visiting the Department of Entomology of the University of Kansas, Lawrence, Dr. J. H. Camin promised me some material of *Neocarus texanus* Chamberlin & Mulaik for morphological research. Soon after my return, he could send me indeed five specimens which had been collected by Dr. R. E. Beer in southern Texas. The material consisted of two females, one male, and two nymphs, a number sufficient for an orientating study; the observations published here are completely founded on it.

I appreciate reminding here also my very pleasant stay with Dr. R. W. Strandtmann in Lubbock (Texas) in 1963, and the beautiful excursions made in the surrounding country. Although we looked in vain for Opilioacarids, we visited an area where Dr. Strandtmann on one occasion had collected a specimen. In this way, I received a very good impression of the interesting semi-arid region where the species is found.

It is a pleasure to me to express hereby my sincere thanks to Drs. Beer, Camin, and Strandtmann for their gracious hospitality extended to me during my stay in America, and for their valuable contributions to my experience and investigation.

Neocarus texanus was described by Chamberlin & Mulaik in 1942 after material collected in Texas, U.S.A. The authors considered the species to be a representative of a new genus and a new family (Neocaridae), because of a different disposition of the stigmata. According to their interpretation, stigmata 2-4 would be situated in one segment (instead of in separate segments), and an additional, unpaired stigma (not observed in other Opilioacarida) would be present in one of the anterior furrows (apparently the disjugal, according to my 1963 nomenclature). In the same paper, the authors added a concise description of a second species, collected in Arizona. This form is apparently very closely related to the species from Texas.

Anticipating the results of the present paper, I can as well inform here that the stigmata of *N. texanus* in reality are situated in separate segments (just as in other species of Opilioacarida), whilst I could not discover the unpaired disjugal stigma. A detailed study leads to the conclusion that *Neocarus* is a synonym of *Opilioacarus*, and that, consequently, the family name Neocaridae must be rejected.

Because the differences between *texanus* and *arizonicus* are not evident (they refer mainly to colour), and because only one incomplete specimen of *arizonicus* is known, the latter name is placed here provisionally in the synonymy of *texanus*.

Although I could not compare my specimens with the type of *texanus* (I asked in vain for the loan of this material), the identity appears to be certain. The original diagnosis contains sufficient data, e.g. on measurements (very important for the specific identification of an *Opilioacarus*), to justify my conclusion.

The present study has been carried out in the same manner as my previous morphological investigations (Van der Hammen, 1964, 1965). My way of approach implies that, during the first series of descriptions, many problems will arise which can only be mentioned by the way. It implies also that there is room for theoretical, often speculative views. Hypotheses will necessarily be introduced as starting-point for further investigations. Because special attention is paid to possible homologies, readers will often be troubled with the introduction of a partly new terminology. In my opinion, however, a comparative acarid morphology can be built up only by following a way of constant reorientation, along careful observation, thorough comparison, and stimulating hypotheses. This uncertain way has its special charm for one who knows to appreciate adventures in the field of science.

I may add here that in my opinion two things are of basic importance for a thorough study of the morphology of very small Arthropods. The first of these is the training of ones ability to orientate an object (even when it is extremely small) in any required position under the microscope. The second is a clear comprehension of the relation between ontogeny and phylogeny, and the contribution of a separate phylogeny to each stase, in this way allowing a correct interpretation of a change taking place in the course of post-embryonic development. Exercises in orientation, as well as learning to comprehend an ontogeny, should be fundamental parts of any acarological education.

The composition of the present paper is similar to that of my previous studies. It consists for an important part of a detailed description, which is followed by general remarks on various subjects. A preliminary revision, and a key to genera and species of Opilioacarida will facilitate future work in the group. Some attention is paid also to internal structures, such as they were visible in transparent slides. These are, as a rule, only mentioned by the way. The structures should, of course, be studied mainly in sections.

The use of the paper is facilitated by the addition of a glossary of terms, and an alphabetic list of abbreviations. In a summary at the end, the main results of my investigation are enumerated.

Opilioacarus texanus (Chamberlin & Mulaik, 1942)

Locality and date. — Big Bend National Park (near Rio Grande), Texas, U.S.A.; under rocks; April 11, 1963.

Material. — Two females, one male, and two nymphs, collected by Dr. R. E. Beer, and sent by Dr. J. H. Camin; one of the nymphs certainly is a subadult specimen, because it is only slightly smaller than the adults.

Description. — I have studied my complete material in order to prepare the present description. Four specimens (viz., females, male, and subadult) appeared to be needed in order to execute fig. 1-21. The relation between figures and specimens is the following: fig. 1-3, 4A-D, F-H, 6F, 7-12 have been drawn after female 1; fig. 4E, 5A, 6A-E, 13, 16, 20B-D, 21 after female 2; fig. 14 after the male; and fig. 5B, 15, 17-19, 20A after the subadult specimen. Although I should have preferred to draw the legs of an adult female, the subadult appeared to be the only specimen that, in the course of the investigation, still presented a complete, nearly undamaged series of appendages. The single male was the first specimen used for study; later on it appeared no more suited for the preparation of figures, except of the palp.

A number of five specimens is indeed too small for a detailed study of a delicate animal like *Opilioacarus*. After some time, specimens get damaged, fragments become colourless and often are very difficult to recover. More material is for instance required to study the variability in number and shape of the setae of the legs, an interesting and probably important question which is indicated below. A special section is therefore added (remark 10), summarizing the problems that are deserving of further investigation.

Females are easily recognizable by the presence of ovipositor and eggs; they have, moreover, one pair of pregenital setae. My single male is characterized by the presence of five pregenital setae, just as in *O. segmentatus* (cf. Grandjean, 1936:435). The juvenile specimens are recognizable by the presence of a small fold at the place of the genital orifice, instead of a transverse slit, and by the absence of a genital sclerite.

I may remark that Opilioacarids should be studied in cold, diluted lactic acid (one part of lactic acid and one part of distilled water), at least during the greater part of the study. In this way, specimens become sufficiently clear, without getting deformed; muscles remain visible for weeks. Afterwards, further material can be warmed in less diluted lactic acid (two parts of lactic acid, one part of distilled water). During the last-mentioned process, the idiosoma and the segments of the legs risk to get damaged; the specimens become, however, completely transparent and loose all of their colour.

In the present paper, much attention is especially paid to the segmentation of the idiosoma (including a close examination of muscle attachments and lyrifissures), to the gnathosoma, and to the articulation of the appendages. Techniques applied are the same as described in my paper on *Glyptholaspis* (Van der Hammen, 1964). A wide range of cavity slides is required to study *Opilioacarus*: a depth of 2 mm for the first observations of the complete animal, 0.2 mm for detailed studies of pretarsus and apotele. All figured structures are orientated according to the directions given by me in the above-mentioned paper; drawings are executed with the aid of a camera lucida.

Measurements. — In the following records, the gnathosoma is supposed to be orientated as in fig. 3, i.e. inclined. The length is measured from the tip of the labrum to that of the anal tubercle.

Adult: length 1.60-1.70 mm; breadth 0.65-0.75. Subadult nymph: length 1.55; breadth 0.62. Smaller nymph: length 1.25; breadth 0.58.

The legs of the subadult have been carefully measured; data on separate segments are given below. The total lengths (coxa not included) are the following: I 2.20; II 1.09; III 1.04; IV 1.56. The sequence of the legs (according to decreasing length) consequently is I, IV, II, III. Leg I is nearly one and a half times as long as the body, leg IV just as long, and leg II and III both about two-thirds.

Habitus and colour. — The species has a superficial resemblance to a very small harvestman; as a mite it is, however, relatively large. When studied on a carbon block, it appears that a prodorsal region is distinctly marked off by lateral and posterior furrows; this prodorsum presents a small, curved furrow in the posterior median part, and several deepened areas (e.g. in front of the eyes) at the places of muscle attachments. The opisthosoma shows dorsally a number of transverse furrows; the anterior three, especially the first one, are rather deep. Ventrally, there is a distinct furrow at the level of the greatest width of the idiosoma. The composite setae of the ventral surface (sternal and genital region), i.e. the setae consisting of a broad base and a narrow, pointed distal part (cf. the paragraphs in question), are also easily recognizable when a specimen is studied in a dry condition.

The ground colour of the species is pale yellowish brown. The prodorsum bears two pairs of eyes, surrounded by blackish eye-patches; anteriorly and laterally there are blue stripes; there is a vague median blue band. With the exception of the anal valves, each segment of the opisthosoma presents dorsally and laterally a bluish band, separated from neighbouring bands by pale interspaces.

The following parts of the legs are blue. Leg I: nearly completely. Leg II: femur, genu, tibia. Leg. III: femur, genu, tibia, basitarsus. Leg IV: distal part of telofemur, genu, tibia, proximal part of basitarsus.

Just as in other Opilioacarida, the colours are partly cuticular, partly caused by pigment grains under the cuticle (probably in the hypodermis). The pigment grains are bluish or violet, and relatively widely separate, except in the eye-patches where they are clustered closely together so that the patches appear to be black. The colour of the pigment grains, as well as the blue cuticular colour, disappear rather rapidly in lactic acid.

Food. — The gut of four of my specimens contained large masses of pollen grains; sometimes these belonged to one plant-species only, on one occasion distinctly to several. The pollen ocurred as the only content, mixed with some small brown balls of probably vegetable origin, or mixed with very few fragments of Arthropod appendages; only in one case (a female) the gut contained a mass of small, dark-brown fragments which could be pieces of chitin. Apparently, the diet of the species, at least in April (the time of collecting), especially consists of pollen grains. It is evident that Opilioacarida are not as exclusively carnivorous as is supposed in literature. I recall, however, that With (1904: 163, pl. 6 fig. 11) already discovered round bodies in the intestine, which he showed to botanists who regarded them as pollen grains or spores of fungi. The occurrence of the species under rocks must be a diurnal habit; at night, *O. texanus* will probably be found climbing plants.

Cerotegument. — This matter is difficult to recognize in *Opilioacarus*. On a carbon block, the cuticle has a slightly frosted appearance; probably a very thin, finely granulated layer of cerotegument is indeed present.

Cuticle. — The cuticle is leathery and faintly sclerotized; it is easily deformed, but sectioning with a razor blade is thwarted by a remarkable resistance. The sculpture consists of numerous small cones or knobs. The chitinous tegument covers the idiosoma nearly completely; there are only interruptions of soft skin in the genital region (cf. the paragraph in question) and at the base of the anal tubercle. Although the anal valves are nearly colourless and without sculpture, the surface is rather smooth, not wrinkled, and probably does not represent soft skin. This nearly uninterrupted cuticle, which is not subdivided into well-defined shields, makes a remarkable character of the Opilioacarida.

Idiosoma. — In dorsal view we can easily distinguish two main parts of the body: an anterior with setae, but without lyrifissures; and a posterior in which setae are only present in the anal region, and in which a large number of lyrifissures can be observed. These two parts are dorsally and laterally separated by a deep furrow. In my opinion they represent prosoma and opisthosoma, which hypothesis is supported by a study of the traces of segmentation. The deep furrow consequently is the disjugal furrow (cf. Van der Hammen, 1963).

The segmentation of the opisthosoma can be reconstructed by a study of furrows, lyrifissures, and muscle attachments together. It is necessary to investigate dorsal, ventral, and lateral views (fig. 1-3), and to combine

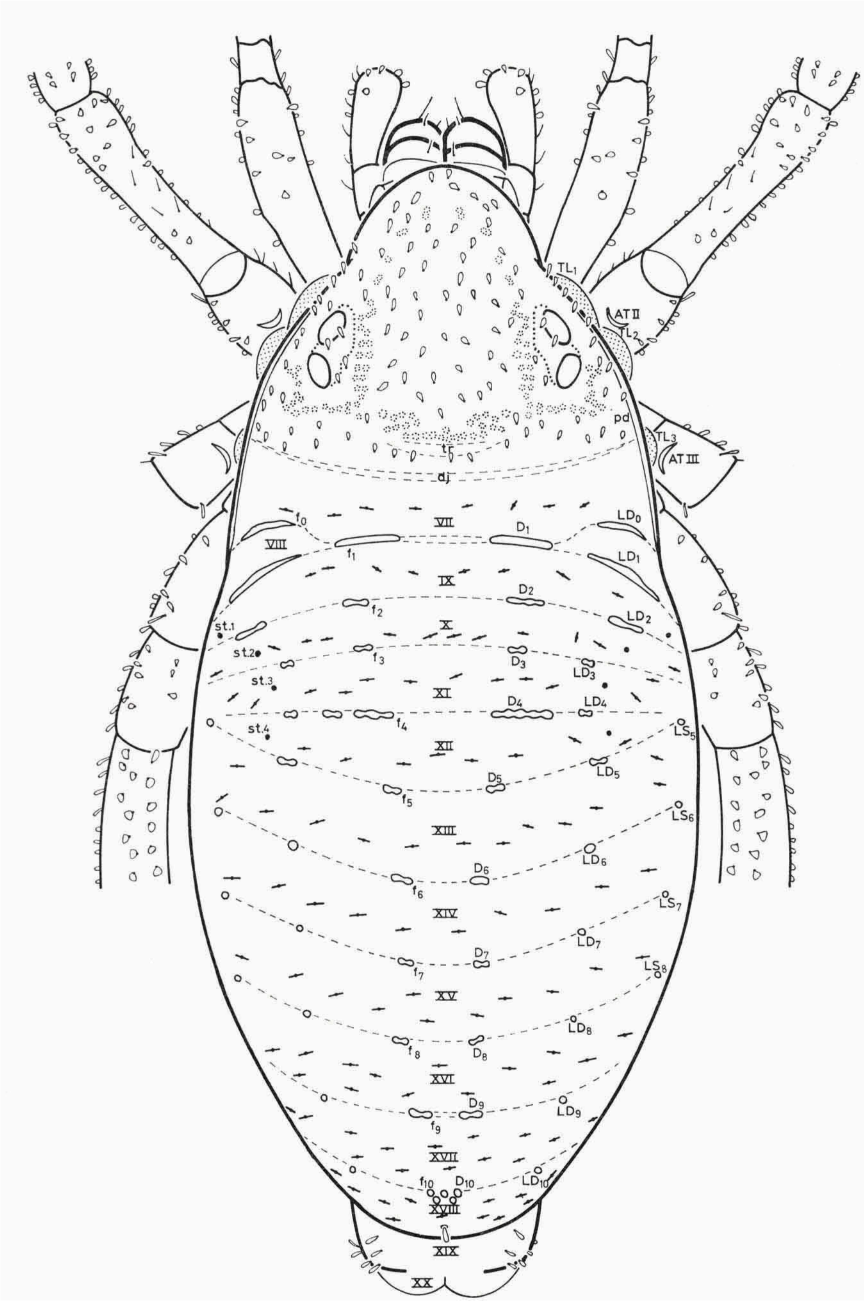

Fig. 1. *Opilioacarus texanus* (Chamberlin & Mulaik), dorsal view of female; × 92.

these aspects in order to arrive at a clear three-dimensional image of the species. Muscle attachments are situated in the furrows, when these are present; otherwise, they are arranged in distinct, more or less transverse rows. In connecting the attachments of each transverse row by lines, segmentation can be clearly established. It appears that a segment bears one or two rows of lyrifissures that generally are orientated parallel to its borders. In my opinion, the anal tubercle consists of two segments: a basal segment and the segment of the valves. After a first study of dorsal and ventral view, thirteen segments can be recognized in this way. An investigation of the lateral aspect reveals, however, that segments have been partly pushed up in backward direction, resulting in an obscuration of several pleural parts. Because the dorsal part of one segment has disappeared (it is wedged off by the first and "second" opisthosomatic "tergite"), whilst a ventral part of another segment (in front of the genital orifice) is not to trace with certainty, we arrive at a total number of fourteen opisthosomatic segments. Taking into account that in Arachnida the genital orifice is situated in segment VIII, and that in *Opilioacarus* at least a dorsal part of the pregenital segment is present, the fourteen opisthosomatic segments are the numbers VII-XX. The wedged-off "tergite" is part of segment VIII.

The prosoma probably consists of a rostral lobe (i.e. the precheliceral segment), the segments of chelicera and palp (I and II), and the segments of the legs (III-VI). Possibly, the tergites of III-VI are reduced to a small area.

Prodorsum. — An anterior dorsal part of the idiosoma (fig. 1), bordered by distinct, deep, posterior and lateral furrows, is named here prodorsum. As mentioned above, the posterior furrow is considered here the disjugal (*dj*), the lateral is named prodorsal furrow (*pd*): The last-mentioned furrow is best visible in lateral view. The outline of the prodorsum is rounded in the anterior part; it suddenly broadens in front of the first pair of legs, and reaches its greatest width at the posterior border. In lateral view (fig. 3, 9), the anterior part appears to be elevated, forming a distinct rostral lobe. Although it is much broader, this lobe reminds of the frontal protuberance of the Endeostigmata. The cheliceral frame is dorsally attached to the internal anterior (i.e. ventral) border of the lobe, which points to the precheliceral origin of the latter.

In the posterior part of the prodorsum, there is a transverse furrow (*tr*) which is slightly curved forward (procurved). It is short, but distinct and rather broad; in the lateral part, it is obscured. The narrow area bordered anteriorly by furrow *tr*, and posteriorly by furow *dj*, may represent:

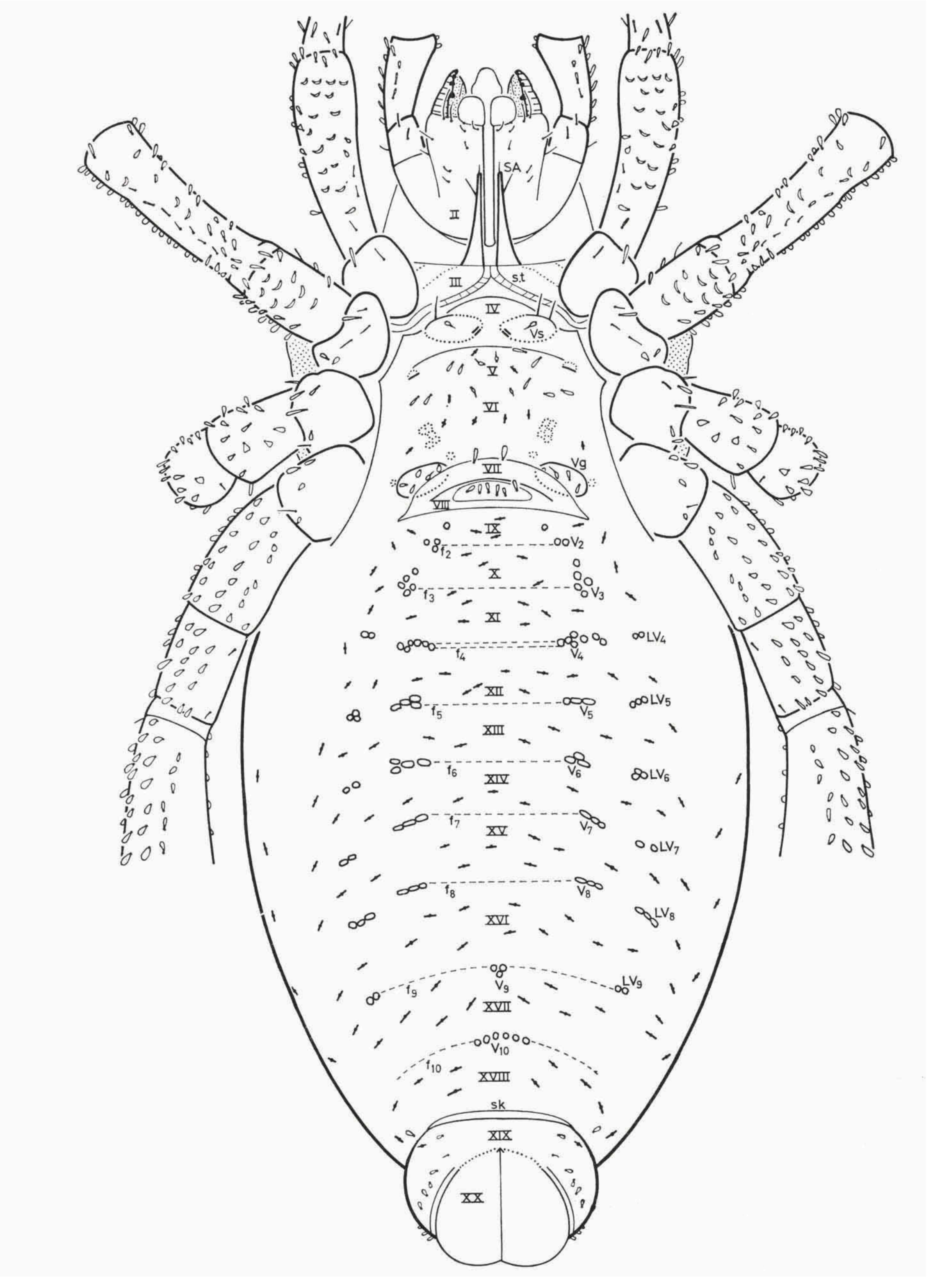

Fig. 2. *Opilioacarus texanus* (Chamberlin & Mulaik), ventral view of female; × 92.

(1) tergite VI only; (2) the dorsal part of the metapodosoma (tergites V-VI); or (3) the dorsal part of the entire podosomatic region (III-VI). Just as in other Arachnida, the dorsal part of the podosoma will be reduced.

There are two pairs of eyes, situated in two blackish pigment spots (fig. 1, 4A). I point here to the presence of a pair of circular spots (*RE*), situated laterally of the rostral lobe (fig. 7, 9). These are slightly concave, and posteriorly bordered by a semi-circular excavation of the prodorsum. They appear as white spots, partly surrounded by dark pigment. They can represent rudiments of rostral eyes, parts of other photo-sensitive organs, or simply muscle attachments. A histological study must solve this interesting question.

The prodorsum presents numerous setae, but no lyrifissures. The setae are papilliform; some of the posterior region are represented in fig. 4C. There are numerous muscle attachments, mainly in front of furrow *tr*, and laterally at both sides of the eyes. The attachments are small, round, smooth spots, easily recognizable in the sculptured surface (fig. 4B). A concentration of muscles is attached in a region running from in front of the eyes to the excavations laterally of the rostrum.

Opisthosoma. — In this paragraph, dorsal, ventral, and lateral aspects of the opisthosoma will be fully described with the exception of anal tubercle and genital region, which are dealt with below.

In dorsal view (fig. 1), the outline of the opisthosoma is more or less oval; it is suddenly curved outward at the border of segments VII and VIII; the greatest breadth is between segments XIII and XIV. The disjugal furrow is slightly curved forward (procurved). The posterior borders of segments VII-X are curved backward (recurved). The border of segments XI and XII is straight. All remaining opisthosomatic segments are procurved when studied in dorsal view. Segment VIII has no dorsal part; it is wedged off by segments VII and IX; its lateral parts are, however, still rather easily visible in dorsal view, because they are bordered by deep furrows. The intersegmental furrows are indicated in fig. 1-3 as f_{0-10}. The deep furrows are f_0 and f_1; f_{2-5} and f_{10} are still rather distinct in the centro-dorsal part; the remaining dorsal furrows are faint, or only recognizable by means of the muscle attachments.

In ventral view (fig. 2), the opisthosoma presents twelve postgenital segments, of which the posterior two belong to the anal tubercle. The intersegmental furrow between XI and XII is distinct; the remaining ventral borders of the segments are best recognizable by a study of the muscle attachments.

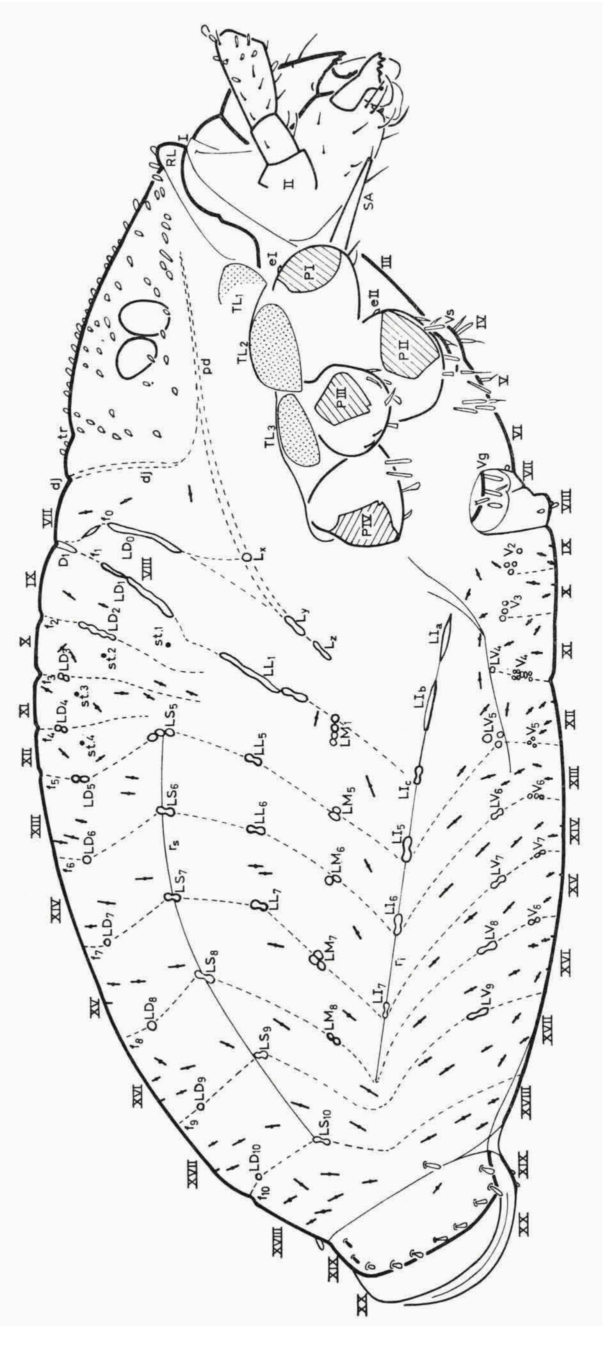

Fig. 3. *Opilioacarus texanus* (Chamberlin & Mulaik), lateral view of female; × 92.

The lateral parts of all opisthosomatic segments (fig. 3) have apparently been pushed up in backward direction, as was already mentioned above. This is especially distinct in the case of segments XIII-XVII. The lateral parts of IX-XII are apparently fused whilst it is difficult to establish with certainty the lateral borders of segments VII and VIII.

The sculpture of the opisthosoma (fig. 4F) consists of small cones which appear as knobs when studied from above. They are arranged in rows that run more or less parallel to the borders of the segments (although slightly winding); at the same time, although in a less distinct way, the cones are also part of a more or less longitudinal system of rows.

The opisthosoma presents numerous muscle attachments. Externally, these are recognizable because they appear as smooth, slightly concave spots in the sculptured cuticle; the spots (at least the dorsals) are surrounded by granules which are much smaller than the cones (fig. 4D). The small granules are not present around the muscle attachments of the prosoma. When a specimen, freshly prepared in cold, diluted lactic acid, is studied in transmitted light, the muscles are easily visible; the greater part of the dorsals are running in latero-ventral direction, but part of the posteriors run backward.

Apart from their intersegmental position, the muscle attachments are also arranged in distinct longitudinal rows. In dorsal view, three pairs of rows are visible: a pair of dorsal rows, a pair of latero-dorsals, and a pair of laterals. In fig. 1 these are indicated as follows: $D_{1\text{-}10}$ (dorsals), $LD_{0\text{-}10}$ (latero-dorsals), $LS_{5\text{-}8}$ (laterals). D_1, LD_0, and LD_1 are elongate, relatively large, and situated in rather deep furrows. D_2, LD_2, and D_4 are also relatively large; the remaining dorsal muscle attachments are smaller. The shape of the attachments varies according to the position; $D_{2\text{-}9}$ and $LD_{3\text{-}5}$ are more or less ∞-shaped; D_4 and sometimes LD_2 are composite. The remaining muscle attachments visible in dorsal view are small and more or less circular; D_{10} is not a pair, but a median group of about five.

The ventral muscle attachments (fig. 2) are arranged in four rows: one pair of ventrals ($V_{2\text{-}8}$), and one pair of latero-ventrals ($LV_{4\text{-}9}$). The posterior border of segment XVI presents a small unpaired group of median attachments (V_9) instead of a pair; the posterior border of XVII presents an unpaired transverse row (V_{10}). All ventral muscle attachments consist of groups of round or oval spots.

In lateral view (fig. 3), six rows of lateral muscle attachments are visible: $LD_{0\text{-}10}$, $LS_{5\text{-}10}$, $LL_{1,5\text{-}7}$, $LM_{1,5\text{-}8}$, $LI_{\text{a-c}, 5\text{-}7}$, $LV_{4\text{-}9}$; three muscle attachments ($L_{\text{x-z}}$) have a separate position in segments VII or VIII. $LS_{5\text{-}10}$ and $LI_{\text{a-c}, 5\text{-}7}$ are situated on distinct ridges (r_s, respectively r_i). The number

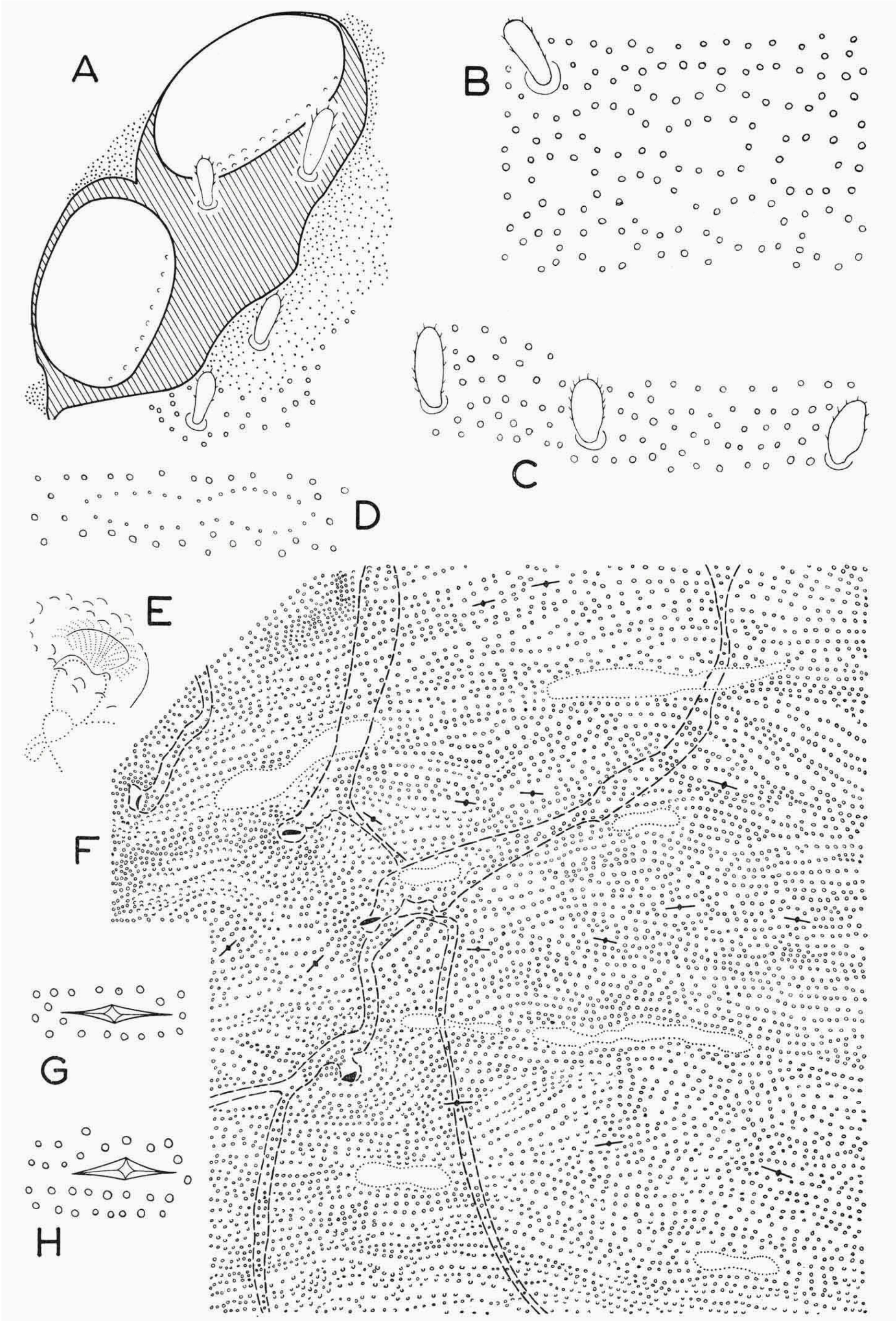

Fig. 4. *Opilioacarus texanus* (Chamberlin & Mulaik), female; A, left pair of eyes; B, muscle attachments in the posterior part of the prosoma; C, dorsal setae of the posterior part of the prosoma; D, muscle attachments between fourth and fifth opisthosomatic segments; E, lateral view of stigma 2; F, dorsal (slightly oblique) view of left region of stigmata 1-4; G, H, dorsal lyrifissures of the fifth opisthosomatic segment; A, × 550; B-D, G, H, × 720; E, × 565; F, × 295.

of groups of muscle attachments on the dorsal, ventral, and lateral surfaces of the opisthosoma totals in such a way 119. Owing to different angles of vision, the shape of some lateral attachments can vary according to the orientation of the animal in the slide.

Each segment presents a rather large number of lyrifissures. Dorsally, these are generally arranged in one transverse row to a segment; only in segments XVI, XVII, and XVIII they are distinctly in two dorsal rows. According to the figured specimen, the numbers visible in dorsal view in segments VII, IX-XVIII are respectively the following: 8-8-12-12-8-13-10-11-14-14-12. There appears to be a rather definitive, more or less symmetric arrangement of the lyrifissures. Two lyrifissures are represented in fig. 4G, H.

The ventral area, enclosed by the muscle attachments *V* and *LV* shows (in the figured specimen) the following disposition of the lyrifissures in segments IX-XVIII respectively: 3-4-8-10-8-7-8-9-8-6. The lyrifissures in segments IX-XI are apparently irregularly scattered; those in segments XIII and XIV are arranged in one row; the remaining segments present, more or less distinctly, two rows.

Laterally, the rows of lyrifissures follow the backward moving up of the segments. Between muscle attachments *LD* and *LV*, there are at each side about 35 lateral lyrifissures, arranged in some six rows. In consequence of this, the total number of opisthosomatic lyrifissures amounts to 263 (the lyrifissures of the genital capsules not counted). The distribution of the lyrifissures in the figured specimen is represented in the following table.

	VII	VIII	IX	X	XI	XII	XIII	XIV	XV	XVI	XVII	XVIII	Total
dorsals	8	0	8	12	12	8	13	10	11	14	14	12	122
laterals	2	0	← 24 →				6	10	8	8	8	4	70
ventrals		0	3	4	8	10	8	7	8	9	8	6	71
Total	10	0	±19	±22	±24	±24	27	27	27	31	30	22	263

There are four pairs of stigmata (fig. 4F). I repeat here that I could not discover the unpaired disjugal stigma described by Chamberlin & Mulaik (1942); possibly these authors have observed an artefact. Each pair of stigmata is situated in a separate segment: stigma 1 in IX, stigma 2 in X, stigma 3 in XI, stigma 4 in XII. Grandjean (1935: 207, fig. 3A) pointed to the disposition of the stigmata in connection with the neighbouring lyrifissures, each stigma being situated in a segmental row of fissures. He framed the interesting hypothesis that stigmata and tracheae originate from lyrifissures by specialization. The disposition in the present species excellently suits this view (fig. 4F). Part of the tracheal system is also represented in fig. 4F. As mentioned by Grandjean (1935), the stigmata are unprotected; the shape is slightly irregular, depending on the angle of vision; stigma 2 is represented separately in fig. 4E.

Stigmata 1-4 are also easily visible in lateral view; it appears that stigma 1 has a more ventral position than 2-4. It is interesting that the segments of the stigmata (IX-XII) are at the same time the segments of which the pleural parts have fused.

With the exception of the anal tubercle and the XVIIIth segment, the opisthosoma is completely without setae. Segment XVIII presents a small, unpaired dorsal seta and one pair of laterals; these are papilliform.

Anal tubercle. — The exact position of the anal tubercle is best visible in lateral view (fig. 3): it is directed not only backwards, but also slightly downwards. There is a crossband of soft skin, ventrally at the base of the tubercle (fig. 2:*sk*). It is possible that this area permits of a further downward bending, or even of a partial retraction of the tubercle.

As mentioned above, the anal tubercle consists of two parts: a sculptured basal part with setae, and a smooth (although sclerotized) terminal part consisting of the anal valves. These two parts are regarded here as representing two segments: XIX and XX. Segment XIX presents ten pairs of small, more or less papilliform setae (fig. 1-3), viz., eight pairs of laterodistals, one pair of dorso-proximals, and one pair of ventro-proximals. The anal valves are completely without setae. There is one pair of lateral lyrifissures, situated in segment XIX (fig. 2, 3); I do not know whether a number of indistinct marks in the same segment represent further lyrifissures.

Genital region. — This region is regarded here as consisting of the genital orifice, the areas in front and posteriorly of it, and the so-called genital capsules. Because my material consists of females, one male, and nymphs, a few notes on juvenile and secondary sexual characters will be added here.

The adult genital orifice (fig. 2, 3, 5A, 6F:*og*) is a recurved slit, more or less situated in a fold; in my two nymphs, a small fold only is present at this place (fig. 5B). Posteriorly of the adult orifice, an elongate, oval sclerite, separated by a small area of soft skin from the remaining sclerotized ventral surface, is distinctly recognizable. It bears a variable number of papilliform setae, viz., six or five setae arranged in one transverse row in my two females, and ten setae arranged in two rows (3 + 7) in the male. In my specimens, this genital sclerite is situated on an extending fold (fig. 3, 6F); its surface is sculptured as the neighbouring sclerotized areas. The genital sclerite is absent in my two nymphs (fig. 5B).

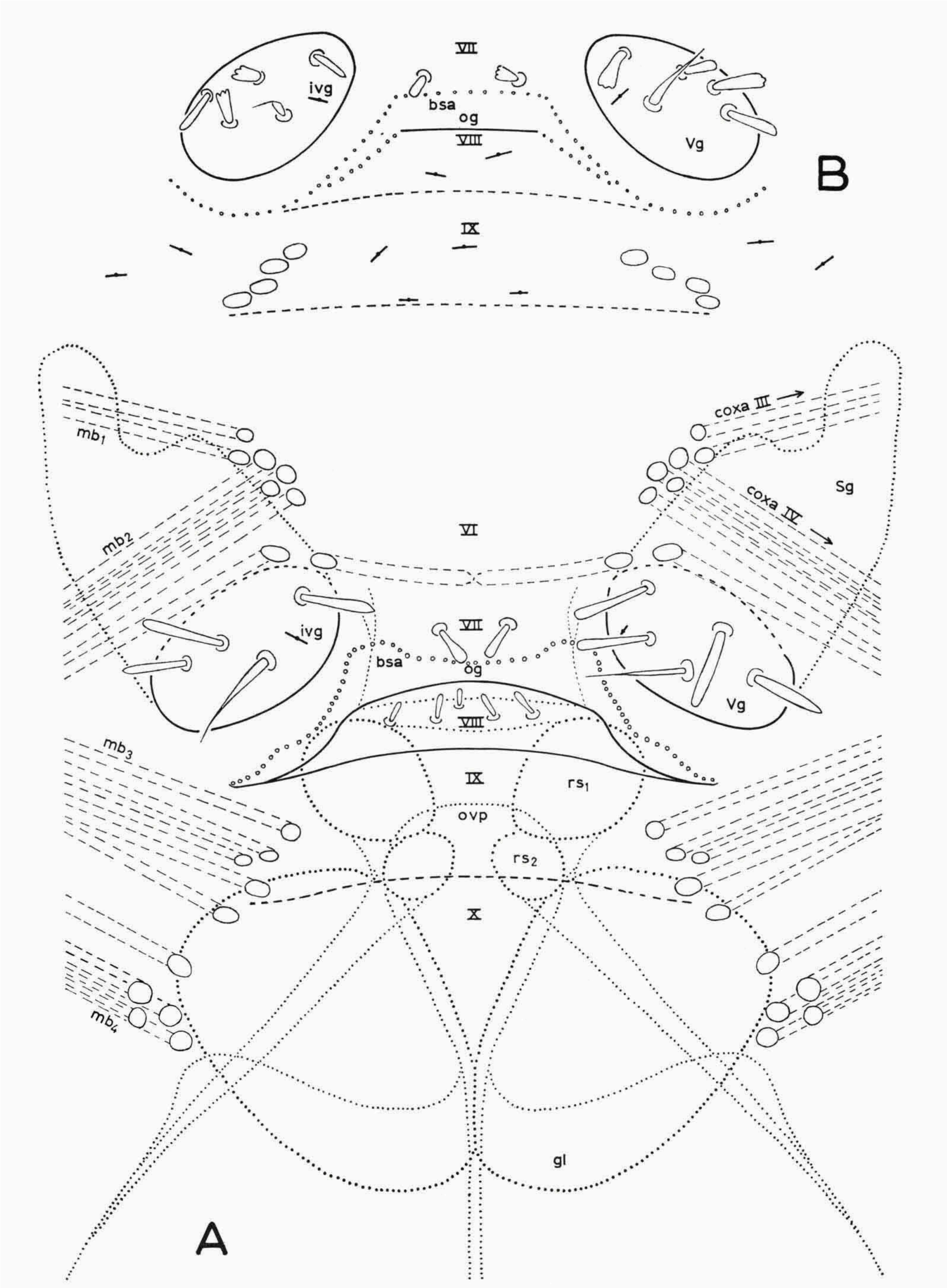

Fig. 5. *Opilioacarus texanus* (Chamberlin & Mulaik); A, female genital region; B, genital region of subadult specimen; A, B, × 370.

The area in front of the genital orifice can also be folded; sometimes (fig. 2) this fold can partly cover the genital capsules. The pregenital area is different in the two sexes, as was already described in *Opilioacarus segmentatus* by Grandjean (1936:435). In the male specimen, it presents the same sculpture as the remaining part of the idiosoma, whilst the female shows a trapezoid smooth area of which the border is indicated in fig. 5A (*bsa*). The female presents two pregenital papilliform setae (situated in a pair), the male five (irregularly scattered). According to Grandjean (1936: 435), the female pregenital area of *O. segmentatus* has no setae and no trapezoid outline; these differences will probably constitute useful specific characters.

The pregenital capsules are wart-like valves that can open by a posterior, paraxial slit. This slit continues into a long, internal sac (fig. 5A:*Sg*) which extends to the coxal region. The sac is also present in the male. The function of the capsule and its remarkable sac is unknown. It has apparently no internal connection with the genital orifice. It is not impossible that the sacs can be protruded; they remind of the genital verrucae or papillae of Actinotrichida. In the paragraph on the sternal region, I return to this interesting question. Below, and in the figures I have already indicated the capsules as genital verrucae (*Vg*).

Each genital verruca presents one lyrifissure, one composite seta (consisting of a long, narrow tip and a broader base), and a number of papilliform setae (three to four in the females, five to six in the male). According to Naudo (1963: 18-20, fig. 6), the males of *Panchaetes dundoensis* from Angola lack the composite seta of the capsules, as well as the internal sac. This does not correspond with the condition in *Opilioacarus*; possibly there is a wide range of secondary sexual characters in the Opilioacarida.

In fig. 2 and 5, an attempt is made to establish the segmentation of the genital region. The genital sclerite certainly belongs to segment VIII, the genital segment of all Arachnida. I am inclined to regard the pregenital area presenting two or five setae (in female and male respectively) as segment VII, the pregenital segment. It is, however, difficult to decide whether the genital verrucae belong to segments VI, VII, or VIII; below, I shall return to the question of their homology.

In fig. 5A I have represented part of the internal structures such as they were visible (by transparency) in a female in lactic acid. The muscles running from the ventral attachments in latero-dorsal directions are figured at the same time (mb_{1-4}). Posteriorly of the genital orifice, two pairs of probably chitinous vesicles can be observed, viz., a small posterior pair, and a larger anterior; these are possibly receptacula seminis (rs_1, rs_2). Two large glands

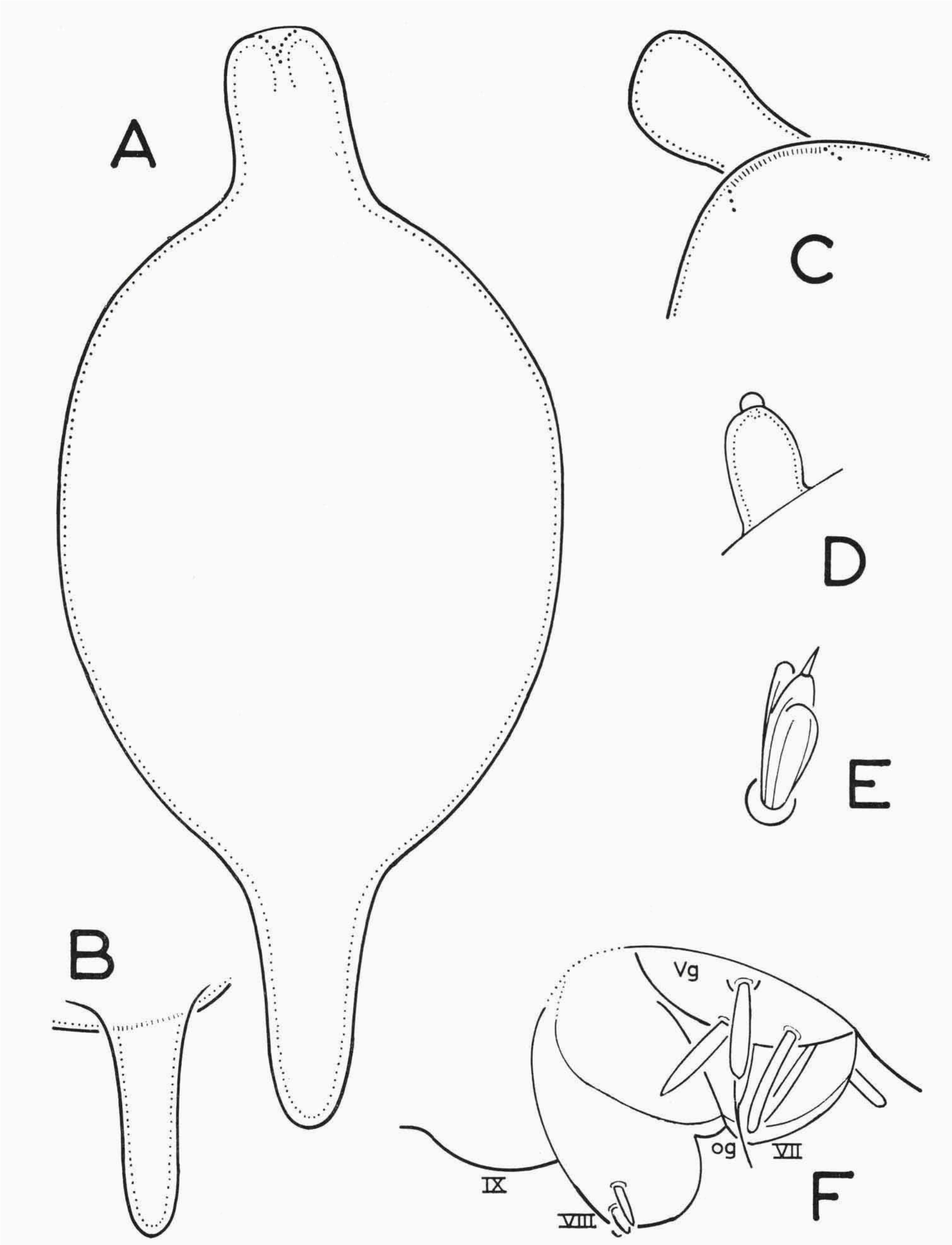

Fig. 6. *Opilioacarus texanus* (Chamberlin & Mulaik); A, egg; B, C, details (elongate, resp. blunt process) of a smaller egg, orientated obliquely; D, latero-coxal seta *eII*; E, distal seta *l'* of right basitarsus III; F, lateral view of female genital region; A-C, × 490; D-E, × 1750; F, × 490.

(*gl*) and the ovipositor (*ovp*) are also easily recognizable. The receptacula slightly resemble the structures figured by With (1904: pl. 6 fig. 18) as male glands. My specimen is, however, distinctly a female because of the presence of ovipositor and a large number of eggs.

Eggs, removed from a female, are represented in fig. 6A-C. They have a remarkable shape which appeared to be constant in all eggs studied by me; probably, this shape is not due to the action of lactic acid. All eggs presented two processes: a blunt one, and a narrow, elongate. The wall of these is slightly thicker than the wall of the remaining egg; at the base of the processes, the wall of the egg is apparently partly porous (fig. 6B, C). In the largest egg present (fig. 6A), the blunt process shows a remarkable internal structure, reminding of an orifice and a connected canal; as long as nothing is known about the egg-laying habits of the species, any interpretation of this structure will, however, be utterly unfounded.

Sternal region of the podosoma. — The sclerotized part of the sternal region has a more or less pentagonal appearance (fig. 2); the greatest breadth is posteriorly of coxa IV. Laterally, it is bordered by a faint ridge, showing salient angles between coxae I and II, and between coxae II and III.

The sternal region of the segment of leg I consists for the greater part of soft skin. It bears a remarkable pair of apophyses which have been named labial appendages by With (1904: pl. 6 fig. 3), and tritosternum by Grandjean (1936). Recently (Van der Hammen, 1964), I abandoned the name tritosternum and introduced the term furca for its specialized shape in the Gamasina. The paired structure in Opilioacarida necessitates the creation of a new term. I introduce here the name sternapophyses, which term can also be used as a collective noun for all apophyses of this type. As mentioned already by Grandjean (1936: 441), these can be present in various segments in various groups of Arachnida, viz., in the segment of the palp (as lateral lips), in segments III, IV, and perhaps V, and even in the ventral region of the opisthosoma; in remark 3, I return to this important question.

In my alcohol material, the sternapophyses of *O. texanus* (fig. 2, 3, 8, 9:*SA*) are orientated nearly parallel to the ventral surface of the infracapitulum; they bear a latero-ventral (antiaxial) seta, and a terminal one. Just as the furca of the Gamasina, they are close to the subcapitular groove. From between the bases of the sternapophyses, a pair of open grooves run in latero-posterior directions, and disappear between coxa I and II. They present a small tectum near coxa I (not figured). These open grooves certainly are taenidia (here named sternal taenidia: *s.t*). I could, however, not discover with certainty the glands debouching into it; possibly, these are coxal glands. Anteriorly, the united taenidia are connected with the subcapitular groove; this connection points to the possibility of the latter also being a taenidium.

The anterior part of the sternal region, which apparently belongs to the segment of leg II (segment IV), presents a pair of warts similar in shape to the genital capsules. In ventral view, the anterior border of the warts is especially distinct; in various lateral orientations, the more or less hemispherical shape is easily visible (fig. 3). Just as the capsules, they present a lyrifissure and setae; there are one or two spiniform setae at the anterior border, and one composite seta posteriorly of it. Because of the wart-like shape, the structures are named here sternal verrucae (*Vs*). When sternal and genital verrucae are indeed homologous structures, and when the genital verrucae would, moreover, appear to be homologous with the genital papillae of Actinotrichida, there would be some evidence to homologize the sternal verrucae with Claparède's organ, now only known from prelarvae and larvae of Actinotrichida. I return to this problem in remark 3.

The sternal region posteriorly of the verrucae is apparently composed of segments V and VI. It presents concentrations of muscle attachments, which are represented in fig. 2 and, in detail, in fig. 5A. The last-mentioned figure shows also the muscle bundles mb_{1-2}, running to coxae III and IV. A pair of transverse muscles in front of the pregenital area appear to be attached to an unknown internal, exactly median structure. There are two irregular rows of lyrifissures in the sternal region of segments V and VI; the anterior row, consisting of two large and two small lyrifissures, probably belongs to segment V; the posterior row, consisting of six small lyrifissures, probably to segment VI. There are also a number of setae in this area, viz., four composite setae arranged in a trapezoid, and ten or nine (respectively in female 1 and 2) to thirteen (male) papilliform setae arranged in two irregular rows; in the nymphs the number of papilliform setae is smaller.

Lateral region of the podosoma. — In fig. 3, a female is represented of which the legs (with the exception of the coxae) have been removed. The coxae are free, movable segments, which will be dealt with in the paragraph on the legs. The lateral region of the podosoma is characterized by the presence of lobes dorsally of the anterior three pairs of legs. These lobes are partly also visible in dorsal and ventral view (fig. 1, 2). According to Chamberlin & Mulaik (1942: 128, pl. 2 fig. 12), the posterior two (they did not observe the anterior) articulate with dorsal processes (*AT*II, *AT*III) on trochanteres II and III. In my opinion this is only part of the function of the lobes, the main function certainly being a protection of the basal parts of the legs. The lobes are named here pedotectal lobes ($TL_{1\text{-}3}$). I may remark that trochanter I lacks a dorsal processus corresponding to the anterior pedotectal lobe (TL_1).

Gnathosoma. — The entire gnathosoma has more or less the shape of a cone, the broadest part being attached to the idiosoma. In my material, this buccal cone is generally inclined at an angle of about 45 degrees with the longitudinal axis of the idiosoma. According to Grandjean (1936: 421), who observed a living specimen of *O. segmentatus,* the gnathosoma is, however, very mobile, being able of movements in the vertical plane, as well

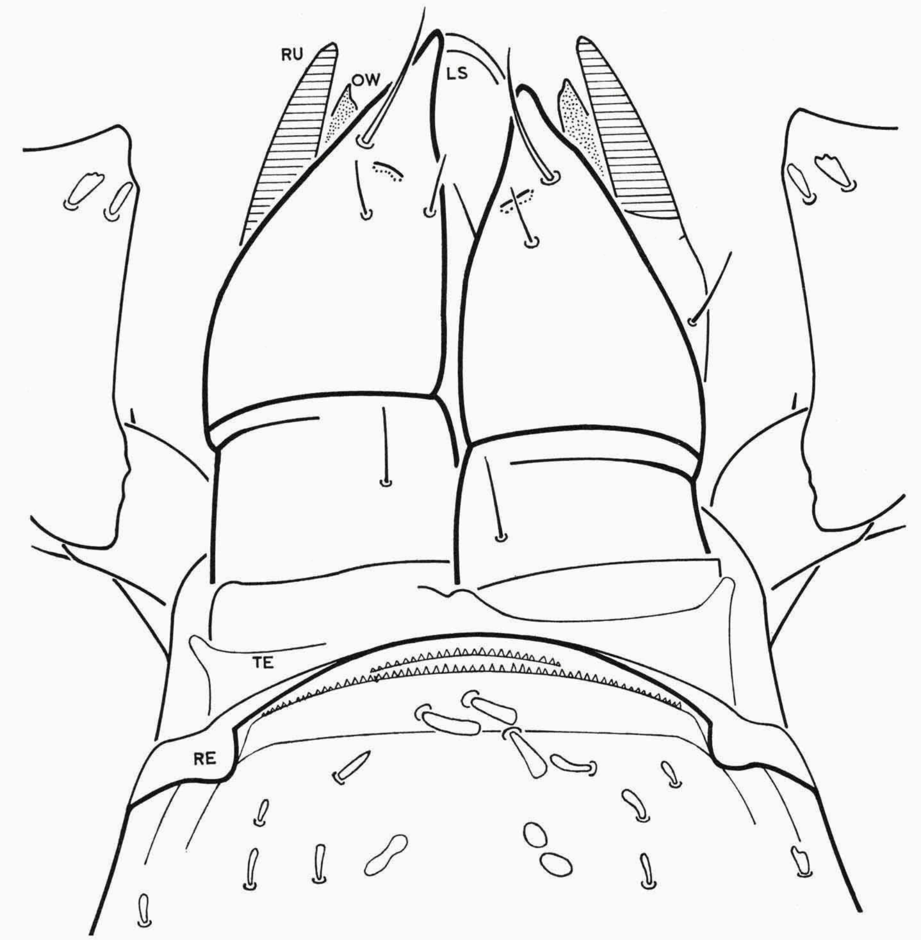

Fig. 7. *Opilioacarus texanus* (Chamberlin & Mulaik), female; dorsal view of gnathosoma and anterior part of idiosoma; × 370.

as of slighter movements from left to right (or the reverse). Probably the buccal cone can also be extended.

Just as in other mites, the gnathosoma is composed of cheliceral frame and infracapitulum. It will be described here in dorsal, ventral, lateral, frontal, and posterior view. Sectioning appeared not to be necessary for a first orientation, because preparations in lactic acid of the entire gnathosoma are sufficiently clear to see the internal structures. In the course of the investigation, the chelicerae must, however, be removed in order to establish the exitence of a cheliceral vault, and to study the dorsal aspect of the infracapitulum.

When the entire gnathosoma is studied in dorsal orientation (fig. 7), it appears that the greater part is hidden from view by the relatively large chelicerae. The cheliceral sheaths pass proximally into a tectum which can only be recognized with certainty after removal of the chelicerae, and

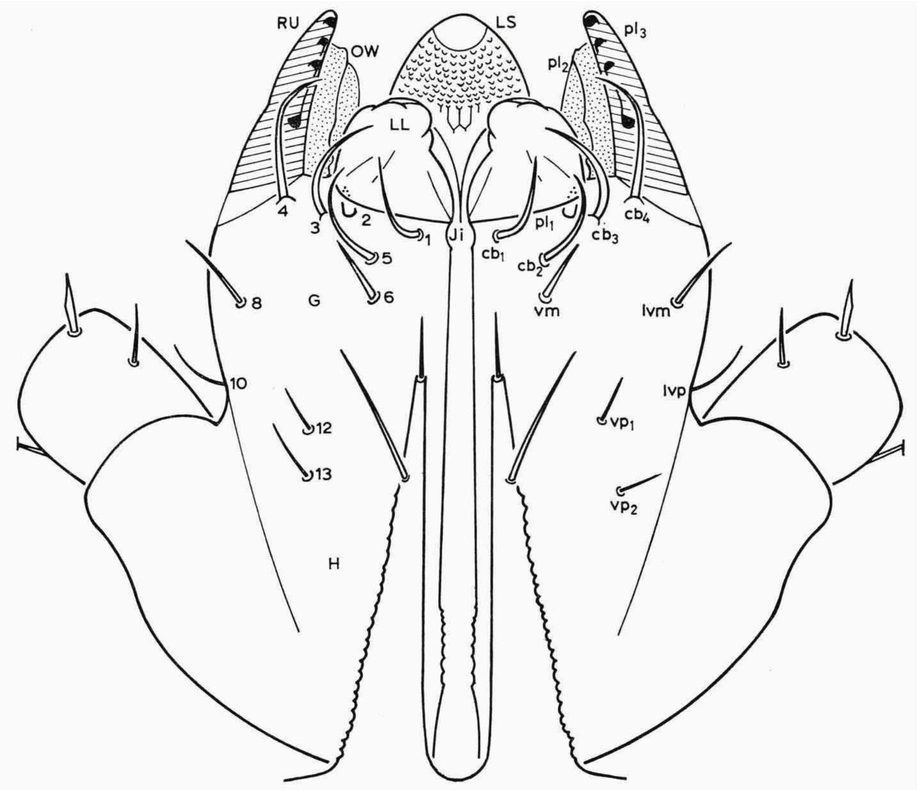

Fig. 8. *Opilioacarus texanus* (Chamberlin & Mulaik), female; ventral view of gnathosoma and sternapophyses; × 370.

consequently will be described below. Part of the rutella (*RU*), With's organs (*OW*) and labrum (*LS*) are also visible in this orientation.

A ventral view of the gnathosoma (fig. 8) presents the following characters. Mentum (*H*) and genae (*G*) are not separated by a labio-genal articulation; the infracapitulum consequently is anarthric (cf. Grandjean, 1957a: 261). There is a distinct subcapitular groove running from the lateral lips and the ventral commissure (*Ji*) of the mouth to the posterior border of the infracapitulum, where it continues in the soft skin of the podosoma, and joins the pair of taenidia which start from between the sternapophyses. In the paragraph on the sternal region of the podosoma, I pointed already to the possibility of the subcapitular groove being a taenidium; this would be a definite proof of the subcapitular groove not representing a separate sternum. The genae are fused in the median part in both sexes. In ventral orientation, the lateral lips appear as thick lobes which meet in the ventral commissure of the mouth.

I have made an attempt to classify the large number of infracapitular setae. When we consider With's organ and the rutellum as hypertrophied setae, we can distinguish a row of three pairs of specialized setae, viz., (1) a small horn-like spine, close to the ventral border of the lateral lips (partly covered by them in ventral view), (2) With's organ, (3) rutellum. These are named here paralabial setae ($pl_{1\text{-}3}$). The small spine which is found in *O. segmentatus* close to the rutellum (cf. Grandjean, 1936: fig. 1), is apparently absent in *O. texanus*; it is regarded here as a fourth paralabial seta (pl_4). The paralabials 1) are the only infracapitular setae which are not hollow; they are very interesting because they are still numerous in Opilioacarida. Some paralabial setae appear to be in regression: pl_1 and pl_4 probably are reduced in size; pl_2 (With's organ) is apparently subject to an ascendant regression (according to observations by Naudo, 1963, it is lacking in small nymphs). In all other groups of mites the series has been reduced to one pair (either rutella or corniculi). Paralabial seta pl_1 indeed resembles a small corniculus.

Posteriorly of the paralabial setae, but very close to them, is a series of four pairs of curved setae, here named circumbuccal setae ($cb_{1\text{-}4}$). Apparently, these have a special function, because each is in close relation to a special part of the gnathosoma: cb_1 and cb_2 are bent over the lateral lips; cb_3 over With's organ, and cb_4 over the rutellum. Probably they control certain movements of these organs. I shall return to the circumbuccal setae in remark 4. After having distinguished paralabial and circumbuccal setae,

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1) Possibly with exception of the rutellum; in Oribatid mites rutella present a central cavity.

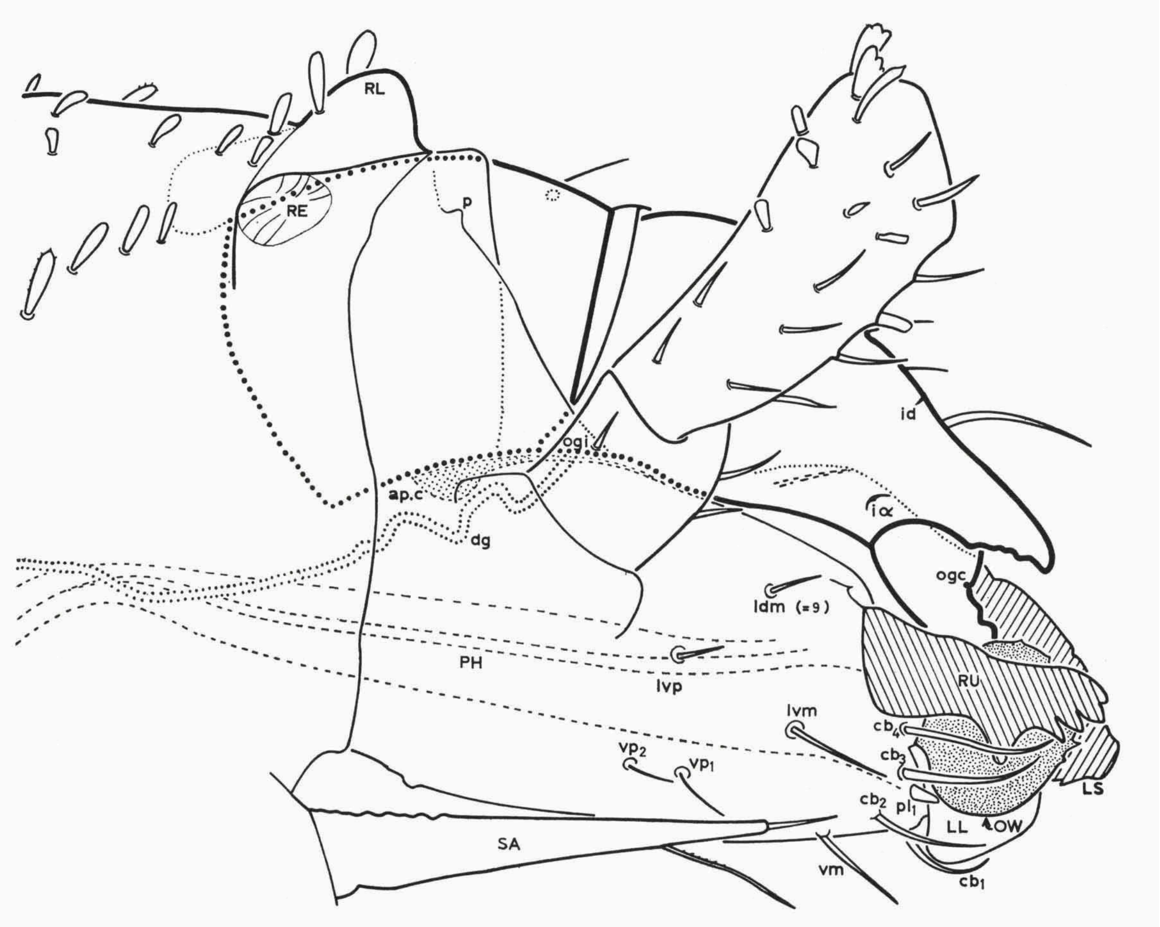

Fig. 9. *Opilioacarus texanus* (Chamberlin & Mulaik), female; lateral view of gnathosoma and anterior part of idiosoma; × 370.

the remaining setae are rather easy to classify according to the system introduced by me in my papers on *Holothyrus* (Van der Hammen, 1961, 1965). Ventrally there are two pairs of median setae (*vm, lvm*), and three pairs of posteriors (vp_1, vp_2, *lvp*).

In fig. 8 I have added Grandjean's 1936 notation at the left side. The relation between his numbers and my notations are easy to establish. According to Grandjean, his numbers 10-11 (both *lvp*), and 12-13 (both *vp*) appeared sometimes to be replaced by one seta, whilst his seta 14 (vp_3) was mostly absent. In my material of *O. texanus,* 11 and 14 are not present. Grandjean's seta 7 (vm_2), constantly occurring in *O. segmentatus,* is also absent in *O. texanus.*

According to Grandjean's classification (1957a: 252), the rutellum of *Opilioacarus* belongs to the category of the ordinary atelebasic rutella (occurring, for instance, in primitive Oribatid mites like *Parhypochthonius, Camisia,* and *Hermannia*); this type of rutellum is not primitive and narrow (as in *Heterochthonius* or *Eniochthonius*), but nevertheless has no broad base reaching to the median groove of the infracapitulum.

Grandjean (1957a: 273) is of the opinion that With's organ probably is a second rutellum. It is remarkable because it can expand enormously under the influence of lactic acid, so that it is difficult to represent its exact shape.

The labrum is easily visible in ventral orientation; it presents numerous teeth at the ventral surface.

Several parts of the gnathosoma can best be studied in lateral view. In fig. 9, a lateral membrane is distinctly visible; it was named synaptic tectum by Grandjean (1936: 427). Dorsally, it is apparently attached to the cheliceral tectum; a rounded prominence (*p*) is visible at its anterior latero-dorsal border. Ventrally, the synaptic tectum is attached to the infracapitulum. The shape of labrum, With's organ, and rutellum is easily recognizable in lateral view. With's organ appears as a more or less rounded disk with irregularly dentate or serrate anterior and dorsal border. The rutellum is large with five ventral teeth, of which the proximal one is the largest. The rutellum presents an internal core which extends into the genae as a root. Apart from the ventral infracapitular setae, a latero-dorsal pair appears also to be present, just as in *Holothyrus*; it is indicated here as *ldm* (corresponding with Grandjean's seta 9). In lateral view, the pharynx is visible by transparency, together with the efferent duct (*dg*) of an infracapitular gland, which debouches ventrally of the chelicerae.

There appear to be a pair of these infracapitular (probably salivary) glands: two ducts and two orifices (*ogi*) are present. These are best visible when the chelicerae have been removed (fig. 10). The position of *ogi* exactly corresponds with the position of foramen and orifice of subcapitular gland in Oribatid mites, such as these were described and represented by Grandjean (1957: 88, fig. 1) for *Xenillus clypeator* Robineau-Desvoidy. The removal of the chelicerae should be executed with the utmost care, otherwise the small cheliceral tectum (fig. 10: *TE*) risks to get damaged or lost. Up to now, this tectum was supposed to be absent in Opilioacarida. According to my observations, it resembles the cheliceral tectum of *Holothyrus,* although it is still smaller; in both groups, the cheliceral tectum is characterized by the absence of an anterior dorsal prolongation.

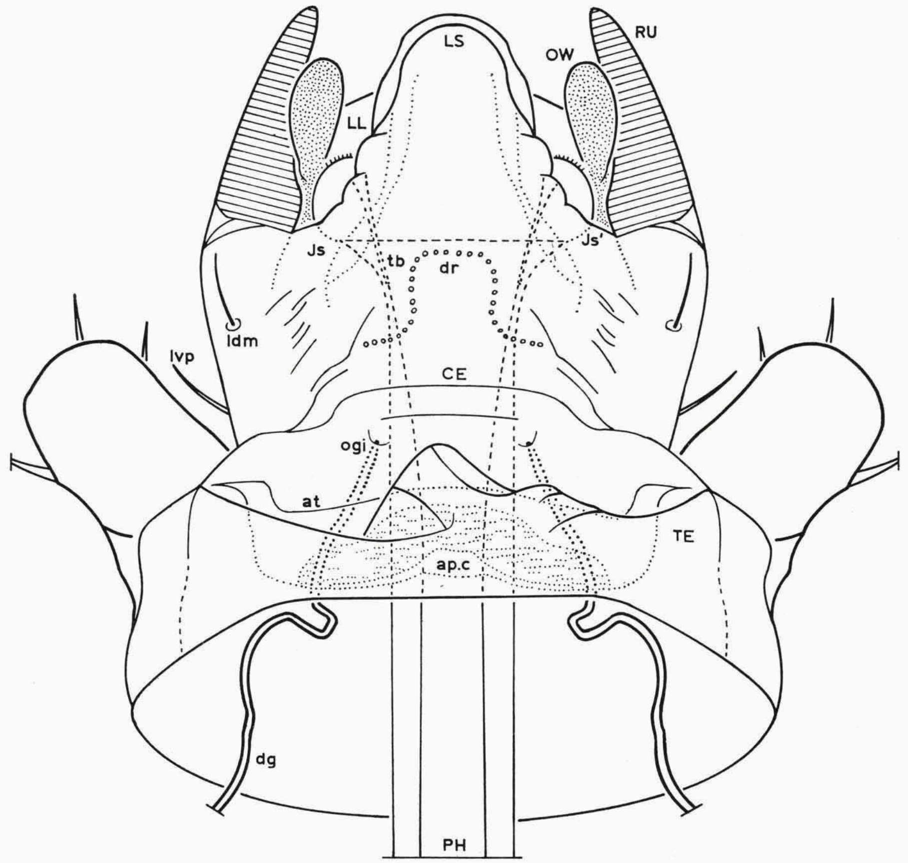

Fig. 10. *Opilioacarus texanus* (Chamberlin & Mulaik), female; dorsal (oblique) view of gnathosoma without chelicerae; × 370.

Apart from the orifices *ogi,* the dorsal surface of the infracapitulum presents the following characters. The labrum has a very broad base. The dorsal commissures of the mouth, *Js* and *Js'* (where labrum and lateral lips meet), are easily visible. A pair of muscles (*tb*) run from the labrum in posterior direction, and are apparently attached to the pharynx, just at the place where the latter forms a pair of latero-dorsal folds. With's organ, rutellum, and the dorsal infracapitular seta *ldm* are easily visible. The cervix is vaulted; the median elevated part (*dr*) is sculptured. There is no latero-coxal seta of the palp. The ventral part of the cheliceral sheaths is attached to the cervix according to a line *at*; this line represents the epimeric furrow situated between segments I and II, i.e. the segments of chelicera and palp. The distinctly thickened area behind *at*, is the capitular apodeme (*ap.c*), which was already visible in lateral view (fig. 9); the capitular apodeme internally separates segments I and II.

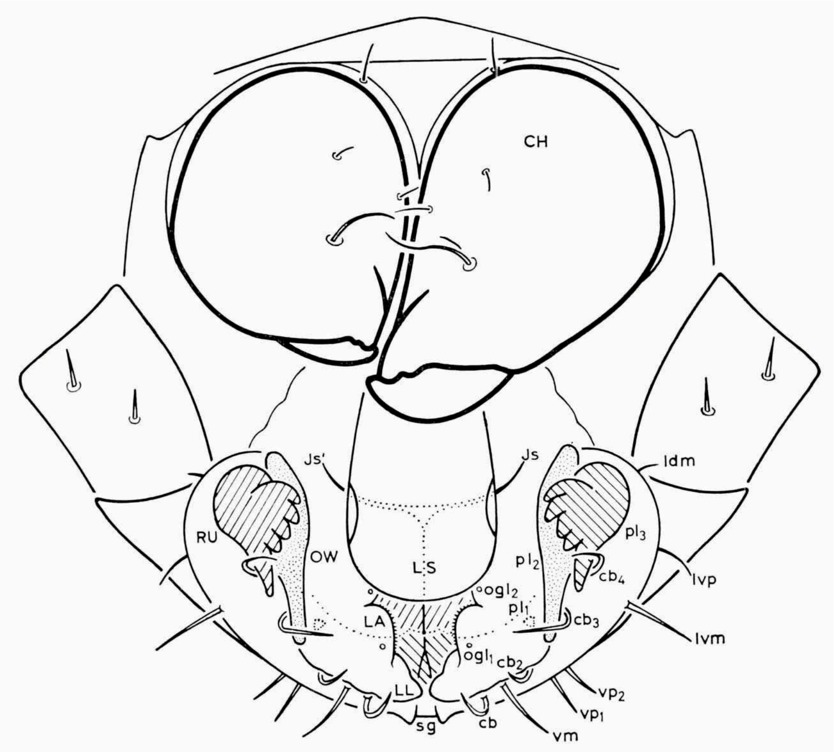

Fig. 11. *Opilioacarus texanus* (Chamberlin & Mulaik), female; frontal view of gnathosoma; × 370.

The triangular shape of the mouth is visible by transparency when the gnathosoma is studied in frontal view. In fig. 11, I have indicated the dorsal commissures *Js* and *Js'*; *Ji* is visible in the pre-oral cavity. The figure shows that the lateral lips are remarkably thick lobes, ventrally and laterally surrounding the pre-oral cavity. The latero-dorsal part of the lateral lips is more or less separated; it shows the beginning of a specialization as a pair of small labella (*LA*). These labella are beset with small teeth which correspond with the teeth in the ventral part of the labrum. Two pairs of glands debouch in the latero-dorsal part of the lateral lips; the orifices (ogl_1, ogl_2) as well as the ducts are easy to observe. The glands are named here labial glands. The curved shape of the circumbuccal setae ($cb_{1\text{-}4}$) is excellently visible in this orientation; as mentioned above, these setae are supposed here to control the movements of lateral lips, With's organ and rutellum. Other noteworthy characters represented in fig. 11 are the latero-dorsal position of seta *ldm*, and the profile of the subcapitular groove (*sg*).

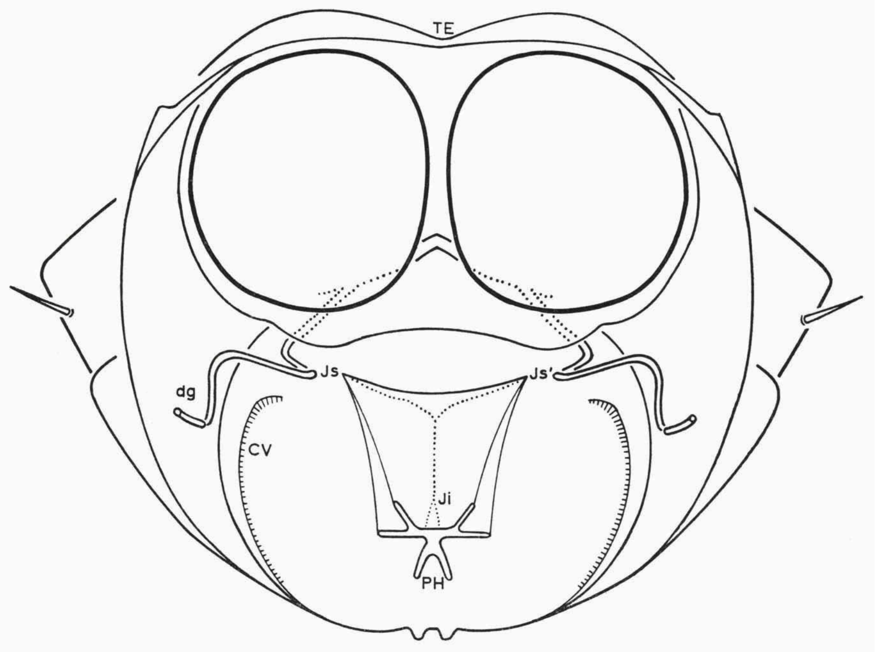

Fig. 12. *Opilioacarus texanus* (Chamberlin & Mulaik), female; posterior view of gnathosoma; × 370.

The shape of the pharynx can best be studied in posterior view (fig. 12). A transverse section just behind the infracapitulum appears to be hexagonal. The mouth is, however, triangular (fig. 11; also represented in fig. 12). This change of shape can partly be explained in the following way. As mentioned above, a pair of muscles (fig. 10: *tb*) are attached to the pharynx, just behind

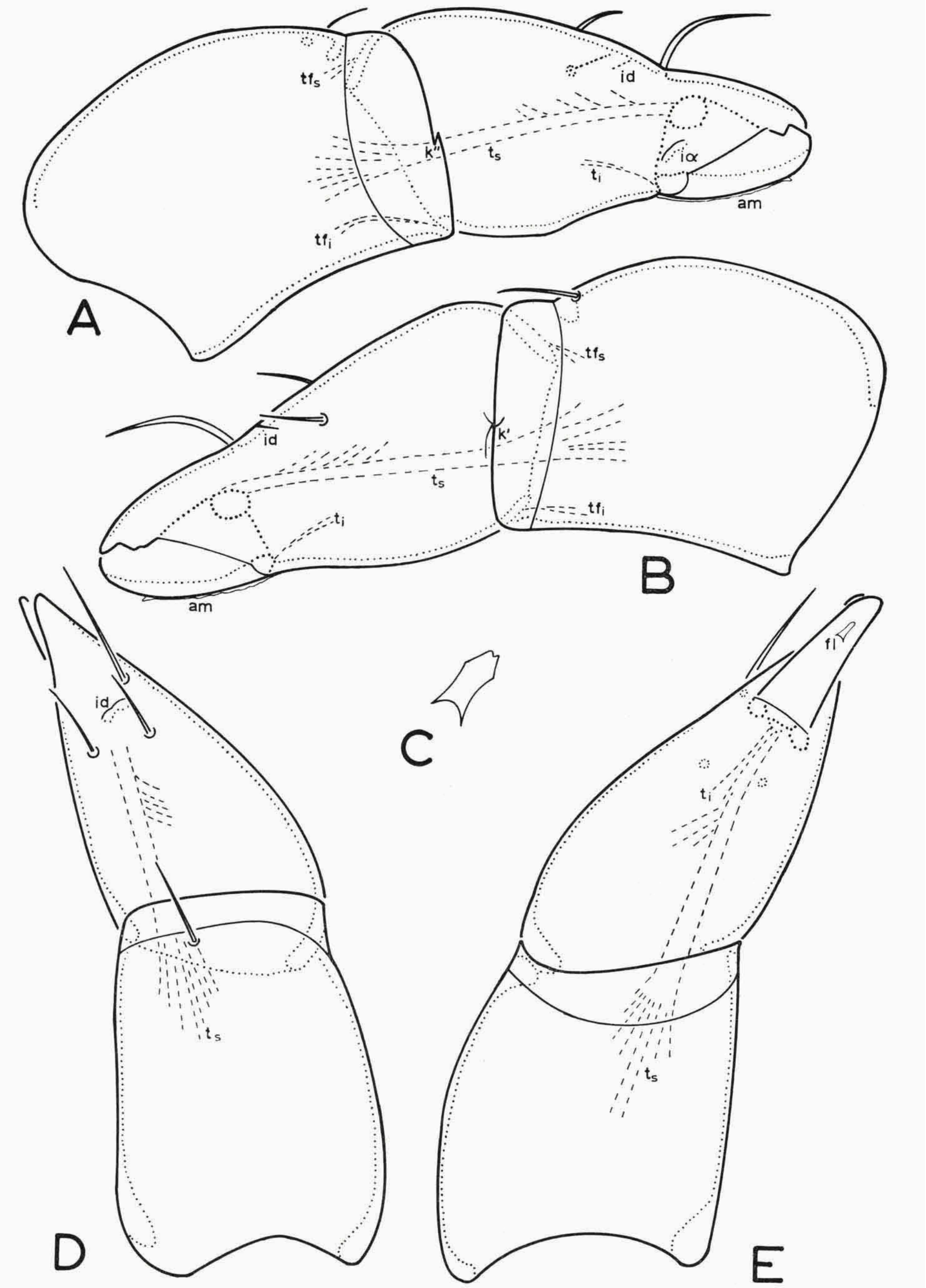

Fig. 13. *Opilioacarus texanus* (Chamberlin & Mulaik), right chelicera of female; A, lateral (antiaxial) face; B, lateral (paraxial) face; C, ventral arthrodial flap of movable bit; D, dorsal face; E, ventral face; A-B, D-E, × 370; C, × 1315.

the mouth. At this place, the latero-dorsal lobes of the pharynx (reference is made here to the "closed" pharynx) are doubled, in such a way giving rise to two pairs of folds. The ventral fold of the pharynx possibly is in connection with a boss in the ventral wall of the infracapitulum, just as in *Holothyrus*. I could, however, not clearly establish the existence of this boss. The single longitudinal section prepared by me, was not suited to be represented here. According to this section, the muscles encircling the pharynx continue as far as the dorsal commissures (*Js, Js'*) of the mouth; apparently they do not extend to *Ji*.

Fig. 12 represents also the infracapitular vault (i.e. the room enclosed by the infracapitulum), the entrance to the coxal vaults (*CV*), the ducts of the infracapitular glands (*dg*), and the cheliceral tectum (*TE*).

Summarizing the main characters of the gnathosoma of *Opilioacarus texanus*, I point to: (1) the presence of a very small cheliceral tectum; (2) the presence (at each side) of rutellum, With's organ, a small horn-like paralabial spine, and ten hollow infracapitular setae (including a latero-dorsal one); (3) the lobe-shaped lateral lips and the orifices of labial glands; (4) the absence of latero-coxal setae; (5) the efferent ducts and the orifices of the infracapitular glands; (6) the triangular mouth; and (7) the partly hexagonal pharynx.

Chelicera. — The chelicerae (fig. 13A-E) consist of three segments, viz., segment 1, segment 2, and apotele. They are not very long, but rather high in comparison with the breadth. The antiaxial surface is distinctly curved.

Segments 1 and 2 articulate by means of a pair of medio-lateral condyles (fig. 13A, B: *k', k"*). The border of the segments is rather faintly sclerotized, so that the exact shape of the condyles is difficult to establish. Two small tendons are attached to segment 2, viz., a superior (tf_s) and an inferior (tf_i). In comparison with the legs (cf. the paragraph below), the articulation functions as an articulation between trochanter and femur; it seems plausible to suppose that this analogy points indeed to a homology of the segments in question.

The articulation of movable and fixed bit functions also by means of two tendons (t_s, t_i). The superior tendon (t_s) is very strong, and extends into segment 1. The movable bit is considered in all mites to be the apotele.

Segment 1 bears one dorsal seta. The distal part is less sclerotized. Segment 2 bears three setae (one dorsal, two latero-dorsals), and two lyrifissures, viz., a dorsal (*id*) and an antiaxial (*iα*). When segment 1 is indeed the trochanter, segment 2 must be a fusion of femur, genu, tibia, and tarsus.

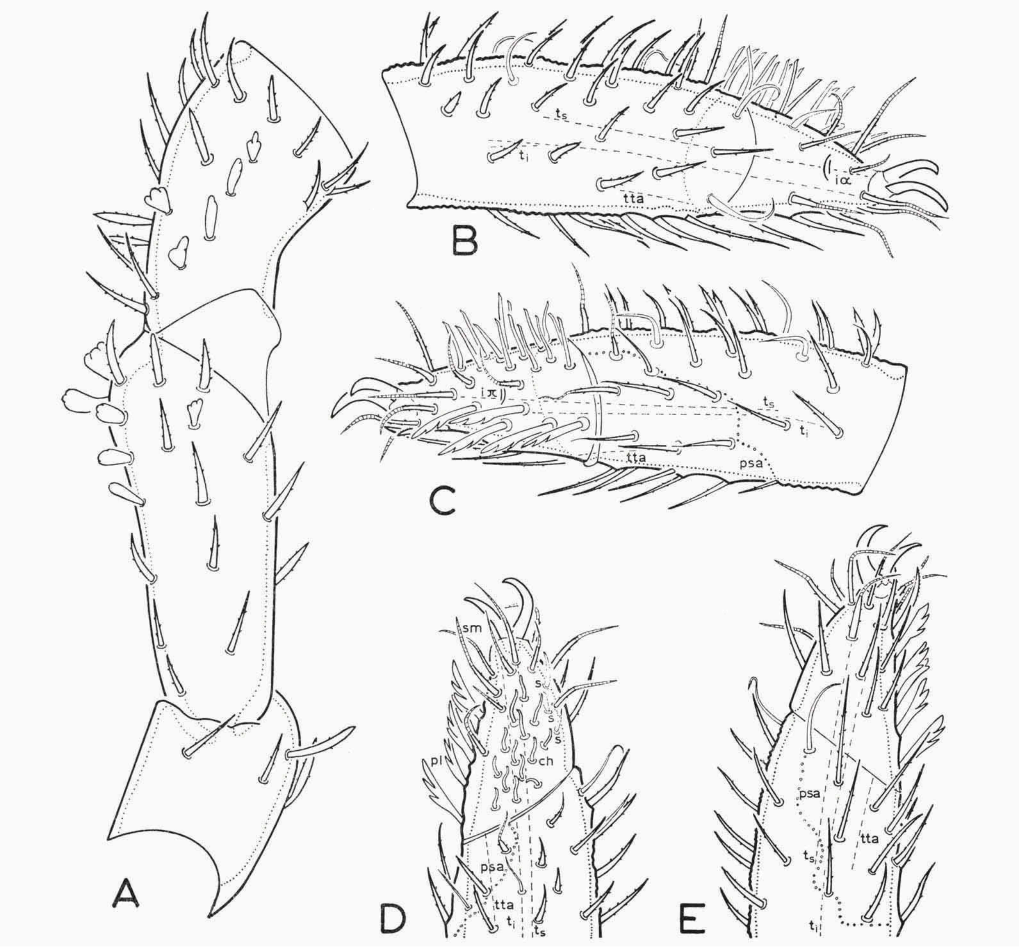

Fig. 14. *Opilioacarus texanus* (Chamberlin & Mulaik), right palp of male; A, lateral (antiaxial) view of trochanter, femur, and genu; B, C, tibia, tarsus, and apotele; B, lateral (antiaxial) face; C, lateral (paraxial) face; D, E, distal part of tibia, tarsus, and apotele; D, dorsal view; E, ventral view; A-E, × 295.

The chela is represented opened in fig. 9, and closed in fig. 13. Fixed and movable bit have both about three irregularly shaped teeth. The movable bit bears a rather distinct mark (fig. 9: *ogc*) at the base of the proximal tooth; this probably represents the orifice of a cheliceral gland.

The arthrodial membrane of the articulation between segment 2 and apotele extends to the distal third part of the last-mentioned segment. This is especially visible in lateral view (13A, B: *am*). It ends in a small flap or ligule, best visible in ventral view (fig. 13E: *fl*). The ligule is represented to a larger scale in fig. 13C. It is difficult to establish the exact latero-ventral border of the arthrodial membrane.

Palp. — There are six palpal segments, viz., trochanter, femur, genu, tibia, tarsus, and apotele. They are represented in fig. 14A-E. Just as in *Holothyrus*, tibia and tarsus have the shape of one large segment. Trochanter, femur, and genu (fig. 14A) bear ordinary setae; on the last-mentioned two segments, a number of papilliform setae also occur. Tibia, and especially tarsus present a variety of setae (fig. 14B-E). The tibia bears a great number of more or less lanceolate, barbed setae, mixed with composite setae (i.e. setae composed of a relatively broad base and a thin, solenidion-like terminal part) and setae which are strongly curved (probably solenidions).

The tarsus presents five types of setae, arranged in the following way: (1) a dorsal area of 14 hollow setae (*ch*) with more or less truncated tip; (2) a paraxial group of leaf-shaped setae (*pl*); (3) three latero-dorsal (slightly antiaxial) setae, probably representing solenidions (*s*); (4) composite setae (*sm*), especially in the terminal part; (5) barbed setae in the ventral region. The tarsus is, moreover, provided with an antiaxial and a paraxial lyrifissure ($i\alpha$, $i\pi$).

In dorsal and ventral view, the border of tarsus and tibia appears to be oblique: the paraxial surface of the tarsus is distinctly longer than the antiaxial. The tendon of the tarsus has a paraxial position (fig. 14D, E:*tta*). A flexed tarsus consequently can be directed slightly outwards. The apotele is movable by means of two tendons, a superior and an inferior (fig. 14B-E:t_s, t_i). The distal paraxial part of the tibia presents a smooth area without sculpture; its border (*psa*) is represented in fig. 14C-E. The tarsus is completely without sculpture.

Legs. — The legs are inserted laterally. The coxae of the first three pairs are dorsally protected by pedotectal lobes (fig. 3); coxae II-IV are close to the lateral border of the sternal area (fig. 2). Acetabula are rather indistinct when the coxae are not removed. In my material legs I-II are directed forward, legs III-IV backward. Leg I is distinctly longer and more slender, its claws are much thinner; papilliform setae are less numerous than in legs II-IV. According to observations by Grandjean (1936: 420) on *O. segmentatus*, leg I has only a restricted ambulatory function; its main function will be sensory. Part of the cuticle of telotarsus I is smooth (in fig. 15A, *tsa* is the posterior border of the smooth area).

As mentioned above, the sequence of the legs (according to decreasing length) is I, IV, II, III. They consist of a different number of segments, connected by primary or secondary articulations. The segments are named here: coxa, trochanter (trochanter 1 and 2 in legs III-IV), femur (basi- and telofemur in leg I), genu, tibia (basi- and telotibia in leg I), basitarsus, telotarsus (telo- and acrotarsus in legs II-IV), pretarsus (only in legs II-IV), and apotele. The term acrotarsus is introduced here for the first time; the segment in question was still unnamed. The prefixes "basi" and "telo" are joined here only to names of segments connected by secondary articulations (without muscles). The two trochanteres of leg III and IV are named trochanter 1 and 2; they are connected by primary articulations (with muscles).

The legs of the subadult specimen have been measured in detail (with exception of the coxae). The lengths are represented in the following table.

Length in mm of the segments of the legs (measured along the middle)

		leg I	leg II	leg III	leg IV
trochanter	trochanter 1	0.25	0.12	0.09	0.14
	trochanter 2			0.06	0.12
femur	telofemur	0.05	0.29	0.23	0.38
	basifemur	0.48			
genu		0.36	0.13	0.11	0.19
tibia	basitibia	0.31	0.14	0.14	0.25
	telotibia	0.25			
basitarsus		0.24	0.16	0.16	0.21
telotarsus	telotarsus	0.26	0.17	0.17	0.19
	acrotarsus		0.06	0.06	0.06
pretarsus + apotele			0.02	0.02	0.02
Total		2.20	1.09	1.04	1.56

It is interesting to compare the length of homologous segments in leg II and III. These legs resemble each other, and have nearly the same total length; leg III presents, however, two trochanteres. It appears that the trochanter of leg II is smaller than trochanteres 1 + 2 of leg III. Femur and genu of leg II are, however, both longer than the corresponding segments of leg III. The exceptional length of leg I (when compared with leg IV) is especially caused by the lengths of femur, genu, and tibia.

The segments of the legs are movably connected by means of different types of articulations. The coxae have no condyles, but are movable in various directions by means of muscles. The articulation between coxa and trochanter has one tendon (*ttr*); according to Grandjean (1936: 430) it is autotomic. A retrotectum protecting this articulation is visible in the figures of leg I (fig. 15B: *te*) and leg IV (fig. 19A: *te*); I do not know whether this tectum is present in legs II and III.

Trochanter 1 and 2, and trochanter and femur articulate by means of a pair of condyles (*k'*, *k''*) situated medio-laterally; there are a dorsal and a ventral tendon, to which elevator, respectively depressor muscles are attached.

These tendons are indicated as tr_s and tr_i in the case of trochanter 2, and as tf_s and tf_i in the case of the femur.

The articulation between basifemur and telofemur of leg I is a secondary articulation of very restricted movability. The suture separating both parts is complete and passes through an important number of lyrifissures (three antiaxials and some paraxials) of which the canals are distinct. In legs II-IV there are two large lyrifissures at the place of this articulation, an anterior (*if'*) and a posterior (*if''*).

The articulations between femur and genu, and between genu and tibia each have one tendon (*tg*, respectively *tti*), to which flexor muscles are attached.

The articulation between basitibia and telotibia of leg I is a secondary articulation of very restricted movability; it is situated halfway the tibia. The two parts are separated ventrally by a large lyrifissure, dorsally by a fold; laterally, the sclerotized cuticle is not interrupted. I may recall here that according to Grandjean (1936: 430), tibia I is completely divided in the adults of *O. segmentatus.*

The articulation between tibia and basitarsus has one tendon (*tta*) to which flexor muscles are attached.

The secondary articulation between basitarsus and telotarsus is different in leg I and in legs II-IV. Basi- and telotarsus of leg I (fig. 15E) are separated ventrally by two lyrifissures which have the shape of cupules. Dorsally and laterally, the segments are separated by soft skin. The ventral part of the articulation functions probably as a hinge.

Basitarsus and telotarsus of legs II-IV (fig. 17, 18, 19E) are completely separated by soft skin; a medio-lateral part *t* of the telotarsal cuticle is, however, salient and certainly functions as an articulation-point. This remarkable articulation is represented in detail in fig. 20B-D. The basitarsus presents dorsally a pair of knobs (*k'*, *k''*), corresponding with a pair of dorsal cavities (*c'*, *c''*) in the telotarsus. When the telotarsus is elevated, the cavities rest against the knobs. In front of each telotarsal cavity is a lyrifissure (*ite'*, *ite''*). Ventrally, just behind the articulation, the basitarsus presents a large lyrifissure (*ibv*).

Telotarsus and acrotarsus (in legs II-IV) are dorsally and laterally separated from each other by soft skin (cf. fig. 17, 18). The articulation permits of flexing in ventral direction.

The apotele is movable by means of two tendons, a superior (t_s) and an inferior (t_i), to which elevator, respectively depressor muscles are attached. The superior tendon (t_s) passes pretarsus, acrotarsus (in the case of legs II-IV), and telotarsus, and continues into the basitarsus. The inferior

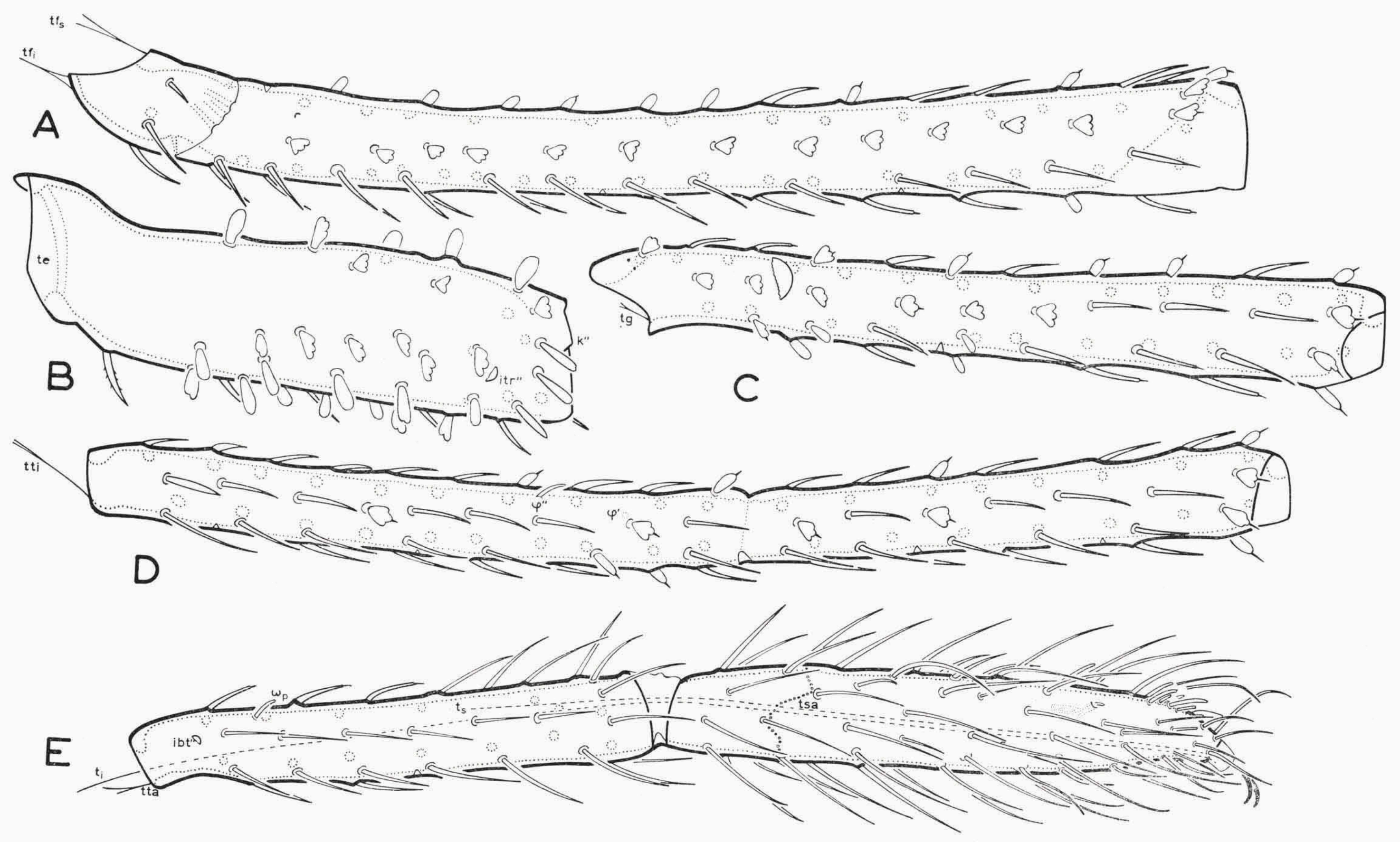

Fig. 15. *Opilioacarus texanus* (Chamberlin & Mulaik); lateral (antiaxial) face of right leg I of subadult specimen; A, femur; B, trochanter; C, genu; D, tibia; E, tarsus and apotele; A-E, × 295.

tendon (t_i) passes pretarsus, acrotarsus, telotarsus, and basitarsus, and continues into the tibia.

The pretarsus of legs II-IV (fig. 21A-C) presents an internal skeleton, consisting of two ventral bars which articulate distally with the apotele, proximally with a knob in the acrotarsus. I may remark here that the small terminal part of telotarsus I, characterized by the thin wall and the absence of setae, possibly is homologous with a pretarsus.

The two tendons t_s and t_i have apparently an important part in the articulation of the complex of apotele and tarsal segments. Pulling t_s will result in elevating the claws, elevating the pretarsus, extending the acrotarsus, and elevating the telotarsus. Pulling t_i will result in depressing claws, pretarsus, and telotarsus; the acrotarsus is possibly flexed by means of hydrostatic pressure. I could not discover highly specialized structures guiding the tendons, just as they were described by Grandjean (1952) in the case of *Tarsolarkus*. In fig. 20A I have nevertheless shown that tendon t_i is more or less guided by an internal boss (*B*) of the ventral wall of the basitarsus. This figure demonstrates also the functioning of the articulation of tibia and basitarsus. When the muscles pull at the tendon *tta*, the ventral basal part of the basitarsus and the arthrodial membrane (*am*) are retracted into the tibia. The thickened dorsal parts of tibia and basitarsus function as a hinge. The hinge consists of two types of chitin; possibly one of these is more elastic than the other. The basitarsus is probably extended by hydrostatic pressure as well as by the elasticity of the hinge.

The legs present an important number of lyrifissures, apart from those connected with articulations. I have observed ventral lyrifissures in all segments of the legs, with the exception of coxa, acrotarsus, pretarsus, and apotele; they are only partly represented in fig. 15, 17, 18, 19. There is a considerable variation in size of the ventral lyrifissures. A distinct posterior lyrifissure *ibt″* is present in the proximal part of the basitarsus; it is situated latero-dorsally (antiaxially in legs I-II, and paraxially in legs III-IV). Trochanter I presents an antiaxial lyrifissure (*itr″*) in the distal part.

All legs bear two claws and a pulvillus. The claws of leg I are very thin and the pulvillus is reduced (fig. 16A-C). The pulvilli of legs II-IV are distinct, but not very large. Pulvillus III is represented in various orientations in fig 21A-C; it has the shape of a little cushion under the claws. The pretarsus of legs II-IV has two pairs of setae: a pair of pectinate lateral setae (*l′*, *l″*), and a pair of curved latero-dorsals (*ld′*, *ld″*).

All coxae (fig. 2, 3) bear a number of papilliform and ordinary setae. Coxae I and II present moreover a latero-coxal seta (*eI*, resp. *eII*), situated in nearly exactly the same position as described by me in the case of *Glyptho-*

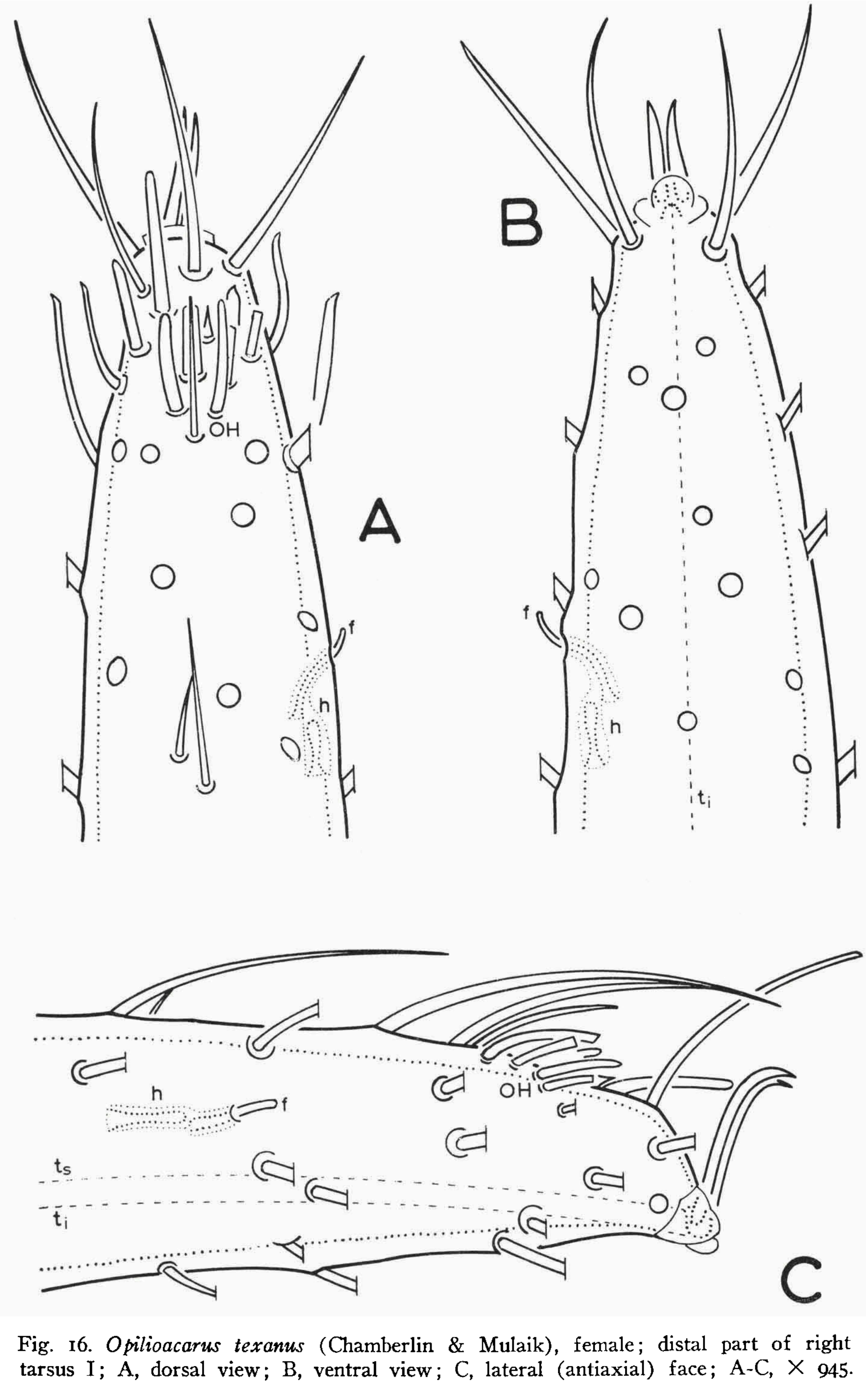

Fig. 16. *Opilioacarus texanus* (Chamberlin & Mulaik), female; distal part of right tarsus I; A, dorsal view; B, ventral view; C, lateral (antiaxial) face; A-C, × 945.

laspis (Gamasina), i.e. paraxially. The two latero-coxal setae are exactly similar in shape. Although they are reduced in several respects, they still distinctly belong to the mucronate type: there is a relatively broad, hollow basal part, and a small, hollow, distinctly separated tip; both parts are connected by a canal (fig. 6D).

There is an important difference in the chaetotaxy of leg I and legs II-IV, especially in the terminal part. This is certainly connected with the specialized sensory function of the first leg.

Telotarsus I (fig. 15) presents a great number of long, smooth setae. An anterior dorsal area is striking because of a number of smaller setae of different shapes. This area is represented to a larger scale, in different orientations, in fig. 16A, C (*OH*). Ten hollow setae are easily visible; they are broad and blunt, pointed, nearly rectangular in outline, or mucronate. Laterally of this area, two pairs of setae are present with obliquely truncated tip. I regard this area as homologous with Haller's organ in *Holothyrus*, which has exactly the same position. The name Haller's organ can, however, not be applied to *Opilioacarus* because the setae are not inserted in a hollow area. Several setae of the telotarsus adhere to each other, certainly by means of some secretion (cf. fig. 16A, C).

The distal, antiaxial part of the telotarsus bears an interesting organ, already discovered by Grandjean (1936: 433, fig. 5B, C) in *O. segmentatus*. It consists of a small cavity with two hollow setae, probably solenidions. One of these solenidions (*h*), which is clavate, is completely hidden; the other solenidion (*f*), which is setiform, is partly extending. The organ is represented in dorsal, ventral, and lateral view in fig 15A-C. It was named Haller's organ by Grandjean (1936). According to Grandjean's present opinion (in litt.) this statement is, however, incorrect (cf. Van der Hammen, 1961: 192), because hidden solenidions are found in several groups of mites. As mentioned above, an area truly homologous with Haller's organ is found in *Opilioacarus* in the dorsal terminal part of telotarsus I. The two solenidions resemble the hidden solenidions of several Prostigmata. I do not know whether they are found also in Anactinotrichida. In the course of the present investigation I have established that they are absent in *Holothyrus coccinella*. The cavity and the two hidden solenidions together are named here provisionally telotarsal organ.

The greater part of the setae of basitarsus I resemble those of the telotarsus. Some of the dorsal setae are, however, mucronate; they have the shape of an ordinary elongate seta with a distinctly separated point. The proximal part of basitarsus I presents a small latero-dorsal (antiaxial) hollow seta, probably a solenidion (ω_p).

Tibia I presents a great number of ordinary setae, mixed with some papilliforms which are provided with a distinct terminal point; the complete terminal verticil consists of papilliform setae. The basitibia presents in its distal part, antiaxially as well as paraxially, a small hollow seta, probably a solenidion (fig. 15D: φ', φ'').

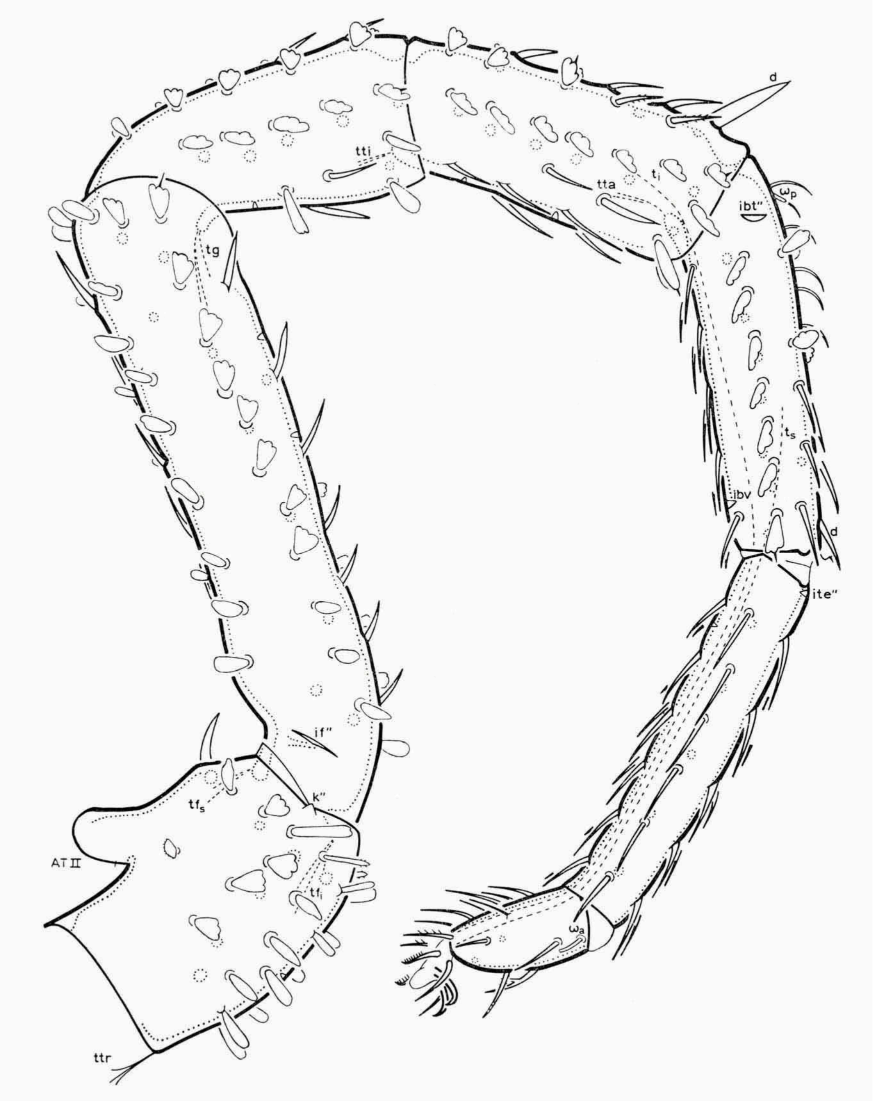

Fig. 17. *Opilioacarus texanus* (Chamberlin & Mulaik); lateral (antiaxial) face of right leg II of subadult specimen; × 295.

In genu I, papilliform setae are somewhat more numerous than ordinary setae; part of the dorsals and laterals, and all of the terminal verticil are provided with a distinct point. All ordinary setae are mucronate.

Femur I has also somewhat more papilliform than ordinary setae. Part of the dorsal and terminal setae are provided with a point. The setae of the

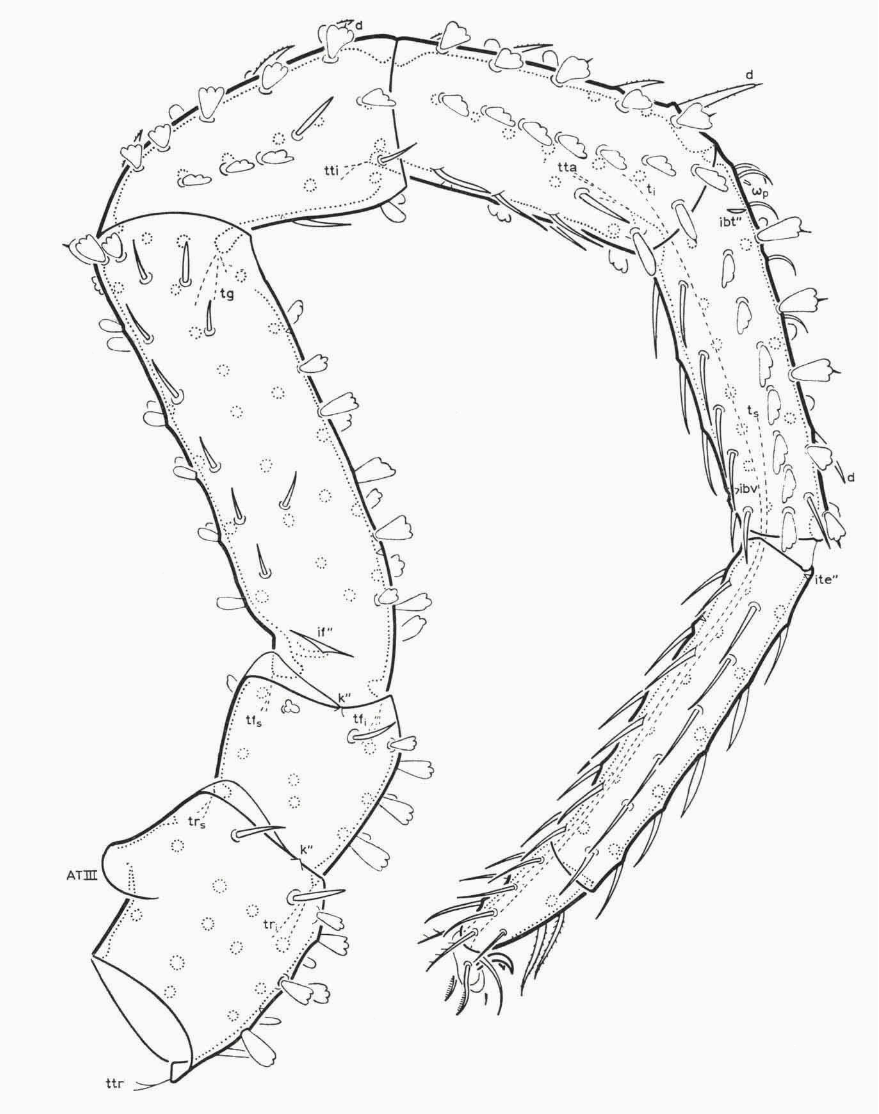

Fig. 18. *Opilioacarus texanus* (Chamberlin & Mulaik); lateral (paraxial) face of right leg III of subadult specimen; × 295.

trochanter are for the greater part papilliform; they occur mainly ventrally and antiaxially.

Trochanter II (fig. 17) presents a great number of papilliform setae, situated mainly antiaxially and ventrally. There is a large, dorsal, spoon-shaped process which, according to Chamberlin & Mulaik (1952: 128, pl. 2 fig. 12), articulates with pedotectal lobe II.

Femur II presents a row of dorsal setae (*d*), two rows of latero-dorsals (*ld*), two rows of laterals (*l*), and two rows of ventrals (*v*). The greater part of the setae is papilliform, but part of the *d* series, two l', and all v'' are ordinary setae. The ventral seta of the terminal verticil (probably v'', but it has a higher position) is papilliform; it is provided with a point.

Genu II presents a row of ordinary *d* setae, two rows of papilliform *ld* and *l* setae, and a number of irregularly inserted ventral setae of papilliform or ordinary shape; l'' of the terminal verticil is provided with a point. Nearly the same description applies to tibia II; the terminal *d* seta is, however, mucronate and strikingly large; one of the ld'' setae, and the terminal v'' are provided with a point.

Basitarsus II is characterized by the presence in the proximal part of a number of dorsal setae which have exactly the shape of a quarter of a circle. They are probably solenidions, just as the smaller, straight, dorsal seta (ω_p) in the proximal part. There are some mucronate dorsal setae, ordinary and papilliform latero-dorsals, papilliform laterals (the terminal with a point), and ordinary ventrals.

Telotarsus II presents six rows of ordinary setae (*ld, l, v*). Acrotarsus II is characterized by the presence of a latero-dorsal (antiaxial) seta (ω_a; probably a solenidion), a bifid seta (probably ld'), a composite seta (probably *d*), a number of ordinary setae, and a pair of latero-ventral terminal setae (*lv*) with four bristles of equal length.

Leg III (fig. 18) resembles leg II in many respects. The number of posterior setae of trochanter 1 and 2 and femur is, however, small in comparison with the number of anteriors because the posterior surface is paraxial in leg III and the segments in question touch the idiosoma. The dorsal spoon-shaped process belongs to trochanter 1. The paraxial ld'' and l'' of the femur are ordinary setae. Genu and tibia III show a strong resemblance to the corresponding segments of leg II; the terminal *d* of the tibia is also mucronate and strikingly large. The basitarsus presents the same dorsal "solenidions" as basitarsus II, including ω_p. The terminal part of the basitarsus (fig. 20C) shows a small, rounded dorsal seta (ω_d), which probably represents also a solenidion. Seta ld' of the acrotarsus is not bifid; the terminal (*lv*) have four bristles.

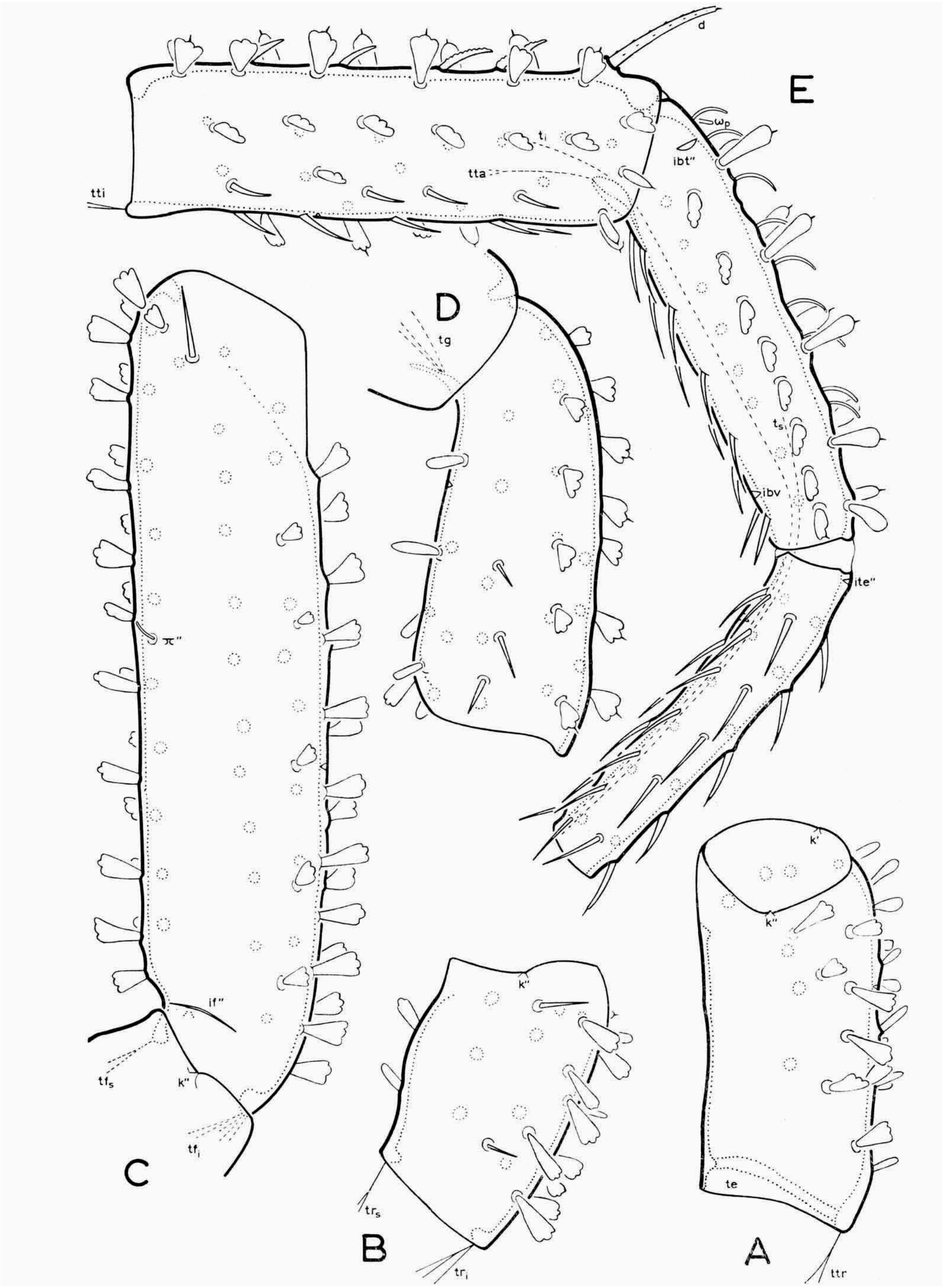

Fig. 19. *Opilioacarus texanus* (Chamberlin & Mulaik); lateral (paraxial) face of right leg IV of subadult specimen; A, trochanter 1; B, trochanter 2; C, distal part of trochanter 2, and femur; D, distal part of femur, and genu; E, tibia, basitarsus, and telotarsus; acrotarsus, pretarsus, and apotele omitted; A-E, × 295.

The chaetotaxy of leg IV (fig. 19) resembles that of leg III in many respects. The number of posterior (paraxial) setae of the femur is strongly reduced; latero-dorsally, just in the middle of the segment, a small, paraxial, solenidion-like seta (π'') is, however, present. Trochanter 1 has no dorsal spoon-shaped process. The number of paraxial setae of the genu is reduced.

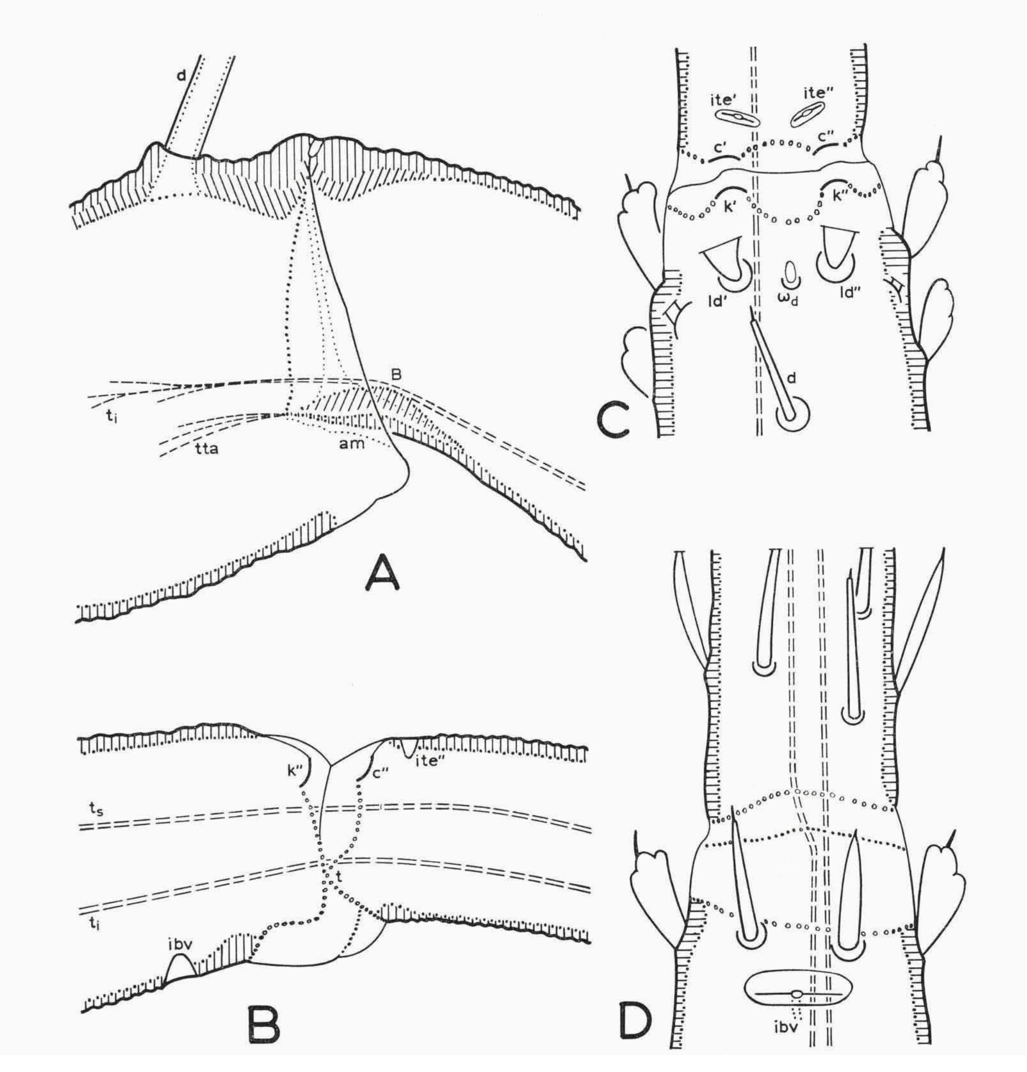

Fig. 20. *Opilioacarus texanus* (Chamberlin & Mulaik); A, lateral (paraxial) aspect of articulation between tibia and basitarsus of right leg IV of subadult specimen (all setae omitted, except part of the large dorso-distal seta of the tibia); B-D, articulation between basi- and telotarsus of right leg III of female; B, lateral (paraxial) aspect (setae omitted); C, dorsal view; D, ventral view; A-D, × 710.

The terminal seta *d* of the tibia is mucronate and longer than in leg II and III. The dorsal, solenidion-like setae of the basitarsus, which have the shape of a quarter of a circle, occur in the greater part of the segment; they are only absent in the distal region; the solenidion ω_p is present. The greater part of the dorsal and terminal papilliform setae of genu, tibia, and basitarsus are provided with a point. All dorsal setae of the telotarsus are mucronate.

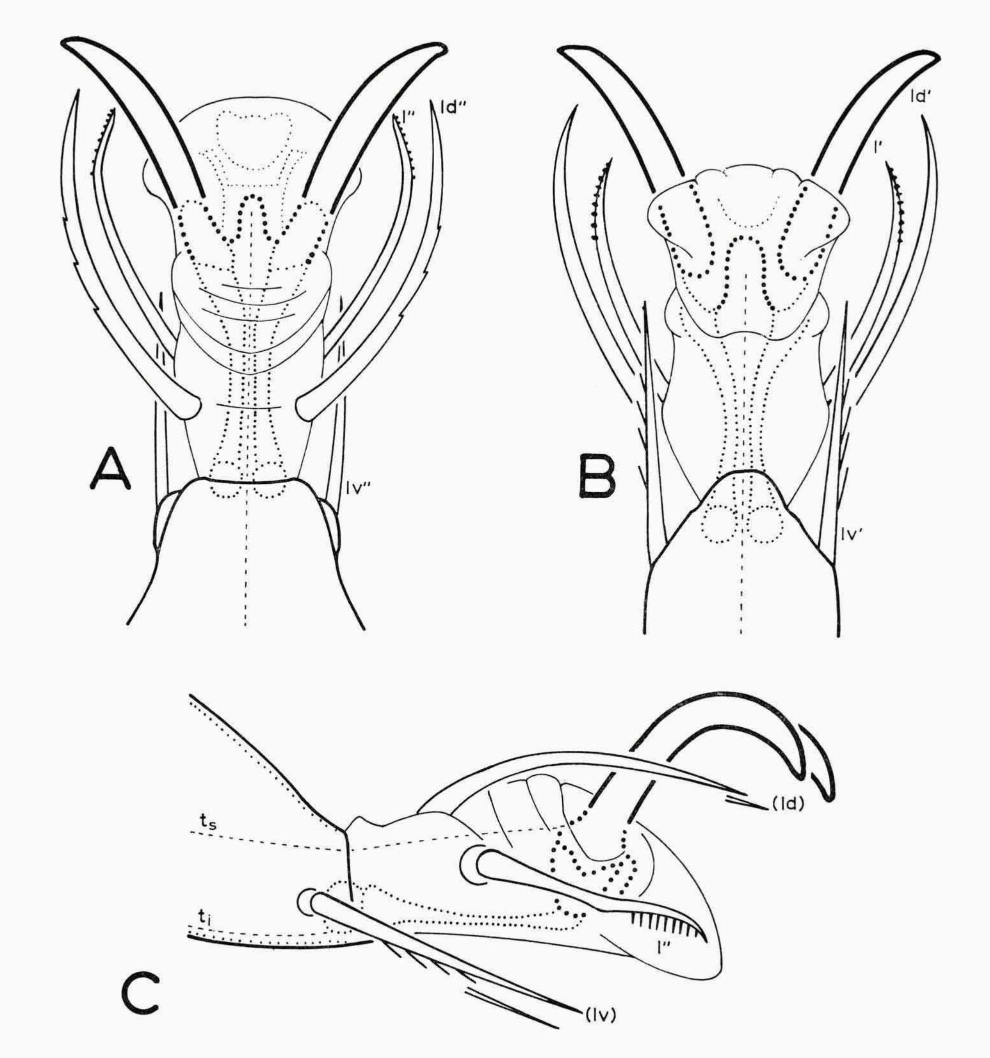

Fig. 21. *Opilioacarus texanus* (Chamberlin & Mulaik), female; distal part of acrotarsus, pretarsus, and apotele of right leg III; A, dorsal view; B, ventral view; C, lateral (paraxial) face; A-C, × 1530.

Acrotarsus IV has the same number of setae as in leg III; the dorsal seta *d* is mucronate.

Part of the terminal setae of the legs are birefringent. An investigation of leg III in polarized light revealed that birefringency is strong in the case of the claws (including their basal part), but that the median process of the apotele (between the claws) is isotropic; consequently it cannot be regarded as a vestige of the central claw. The four pretarsal setae (laterals and latero-dorsals) are all strongly birefringent. The setae of the acrotarsus are birefringent in various degrees: distinctly in the ventrals, faintly in the laterals, and apparently not in the dorsal and latero-dorsals. Birefringency is also exhibited by the distal v' of the telotarsus.

Apart from the setae, the cuticle is also distinctly birefringent. A faint degree of birefringency can be observed in the tendons of the apotele: distinct in t_1, rather indistinct in t_8.

I have made no efforts to establish whether the birefringency of the setae is indeed due to actinopilin. The intensity resembles that observed in Actinotrichida. Staining with iodine, treating with basic hypochlorites, and investigations of the optical properties will be important parts of further research.

According to Grandjean (1936: 437), X ($= N_p = \alpha$) is perpendicular to the surface in the case of the cuticle, which is rather exceptional.

Development. — As mentioned above, my material contains two nymphs of different size (lengths respectively 1.25 and 1.55 mm); these certainly represent different stases. They are recognizable as juvenile specimens by the only partly developed genital orifice: a small fold (fig. 5B) is present at the place of the large transverse slit of the adults; a genital sclerite and genital setae are still absent. No special attention is paid here to differences in juvenile and adult leg chaetotaxy, although the nymphs present distinctly less verticils. My material is, however, too small, and the number of setae at the same time too high to allow of reliable data on variability.

Apart from differences in size, the two nymphs present also distinct differences in other characters. These relate to the chaetotaxy of sternal region and genital region. All setae of the sternal verrucae (one or two spiniform setae, and one composite seta), and the complete sternal trapezoid of four composite setae are present in both nymphs. The number of remaining sternal setae is, however, smaller than in the adult: five in the smallest nymph, eight in the large, instead of nine to thirteen in the adult.

The pregenital area of the smallest nymph has no setae; the largest nymph has two setae, just as in the female. Apart from the composite seta (present in both nymphs), the genital verrucae present three or four setae in the smallest nymph, four setae in the largest (four to six in the adult).

Leg III and IV have in both nymphs two trochanteres and an undivided tibia, just as in the adult. A fusion of trochanter 2 and basifemur (when present) will be restricted to the younger stases (cf. remark 8).

Both of my nymphs have four pairs of stigmata.

The largest nymph presents only small differences in size as well as in chaetotaxy in comparison with the adults; without doubt, it is a subadult specimen. Because the other nymph is still rather large, at least three nymphal stases will be present, apart from a hexapod larva. Up to now nothing is known about the occurrence of a prelarva in Opilioacarida. The probable occurrence of three nymphal stases approaches the condition in Actinotrichida, and differs from Anactinotrichida (i.e. from Gamasina). My juvenile material of *Holothyrus* points with some probability to at least the same number of stases, although the larva is still unknown to me.

PRELIMINARY REVISION OF THE SPECIES OF OPILIOACARIDA

Eight species and one variety are recognized here as representatives of the Opilioacarida. They are classified by me in four genera. A new genus *Adenacarus* is created for *Eucarus arabicus* With, because of important differences dealt with below. The subgenus *Panchaetes* is raised here to generic rank. *Paracarus* is considered a valid genus. As mentioned above, *Neocarus* is placed in the synonymy of *Opilioacarus,* and *N. arizonicus* is regarded as a synonym of *O. texanus.* Diagnostic characters of the genera are given in the following survey.

Panchaetes Naudo, 1963

All opisthosomatic segments with papilliform setae. Proximal tooth of rutellum not longer than remaining teeth.

Type: *Opilioacarus hexophthalmus* Redikorzev, 1937.

Remark: The occurrence of setae on all opisthosomatic segments is considered here of sufficient importance to justify the raising of *Panchaetes* from subgeneric to generic rank.

Paracarus Chamberlin & Mulaik, 1942

Three pairs of eyes: two large ones and a small intermediate which is situated slightly higher. Prosoma smooth, opisthosoma sculptured. Segmentation pronounced; segment XX possibly absent. Stigmata 3 and 4 with a dorsal position. Rutellum with six teeth. Leg III as long as the body; all remaining legs longer.

Type: *Opilioacarus hexophthalmus* Redikorzev, 1937.

Remark: Dr. Nina Bregetova (Leningrad) kindly gave me the following valuable information on the type-material [1]. Three specimens of the species (among which the type) are still present in Leningrad. Redikorzev's third eye is not a clear spot, but indeed an eye. Stigmata 3 and 4 have probably indeed a dorsal position. Judging from Redikorzev's description, opisthosomatic setae are present; these could, however, not be observed by Dr. Bregetova.

Adenacarus nov. gen.

Opisthosoma with distinct intersegmental furrows. Sternapophyses with four setae. Proximal tooth of rutellum with secondary basal tooth. With's organ apparently absent. Legs II and III longer than the body.

Type: *Eucarus* [2] *arabicus* With, 1904.

Remark: Some of the above-mentioned characters (pronounced segmentation, rutellum with six teeth, absence of With's organ, leg II and III longer than the body) point to a close relationship wiht *Paracarus*.

Opilioacarus With, 1902

Segments VII-XVIII without papilliform setae. Sternapophyses with two setae. Proximal tooth of rutellum distinctly stronger than the remaining teeth.

Type: *Opilioacarus segmentatus* With, 1902.

The species of Opilioacarida described up to now, are enumerated in the following list which contains also a survey of the geographic distribution.

1. *Panchaetes papillosus* (André, 1947) (Ivory Coast).
2. *Panchaetes dundoensis* Naudo, 1963, and *P. dundoensis* var. *condensus* Naudo, 1963 (Angola).

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[1] I wish to express here my sincere thanks to Dr. Nina Bregetova for her kind assistance in the present investigation.

[2] *Eucarus* was created by With (1904) to replace the "badly chosen" name *Opilioacarus* With, 1902. It must be placed in the synonymy of the last-mentioned generic name.

3. *Paracarus hexophthalmus* (Redikorzev, 1937) (Asiatic Russia).
4. *Adenacarus arabicus* (With, 1904) (Aden).
5. *Opilioacarus segmentatus* With, 1902 (Algeria, Corfu, Ivory Coast).
6. *Opilioacarus italicus* (With, 1904) (Sicily).
7. *Opilioacarus platensis* Silvestri, 1905 (Uruguay, The Argentine).
8. *Opilioacarus texanus* (Chamberlin & Mulaik, 1942) (Texas, Arizona).

In this list is not included the very interesting Opilioacarid collected by T. Tibbetts in Puerto Rico, and mentioned by Camin, Clark & Gorirossi Bourdeau (1958: 903, fig. 2); this species is officially still undescribed. Probably it represents a new genus.

A new species of *Panchaetes* from Madagascar will be described in the second part of the present series; I have seen also an undescribed species of *Panchaetes* (in the collection of Prof. Dr. M. André) originating from Tanzania. These data illustrate the vaste distribution of the genus in the African region.

The above-mentioned eight valid species can be identified by means of the following key.

KEY TO THE GENERA AND SPECIES OF OPILIOACARIDA

1. Three pairs of eyes, viz., two large ones, and a small intermediate . . . . *Paracarus hexophthalmus* (Redikorzev)
— Two pairs of eyes 2

2. Segments VII-XVII with papilliform setae (*Panchaetes*) 3
— Segments VII-XVII without papilliform setae 4

3. Papilliform setae of the idiosoma relatively short (20-25 μ), with smooth ribs and without denticles at the tip . . . . . . *Panchaetes papillosus* (André)
— Papilliform setae of the idiosoma longer and more elongate, with barbed ribs and denticulate tip . . *Panchaetes dundoensis* Naudo (+ var. *condensus* Naudo)

4. Sternapophyses with four setae; rutellum with six teeth (i.e. the proximal one of a row of five with a basal secondary tooth). . . . *Adenacarus arabicus* (With)
— Sternapophyses with two setae; rutellum with five teeth (*Opilioacarus*) . 5

5. All legs longer than the body 6
— Legs II and III shorter than the body 7

6. Idiosoma 2.5 × as long as broad . . . . *Opilioacarus italicus* With
— Idiosoma 1.8 × as long as broad . . . . *Opilioacarus platensis* Silvestri

7. Idiosoma 2 × as long as broad; leg I 1.3 × as long as the body . . . . *Opilioacarus segmentatus* With
— Idiosoma 2.3-2.5 × as long as broad; leg I nearly 1.5 × as long as the body . . . . . *Opilioacarus texanus* (Chamberlin & Mulaik)

REMARKS

REMARK I. THE NUMBER OF SEGMENTS AND THE SUBDIVISION OF THE IDIOSOMA

The number of segments established in the present paper, is the highest number now known in Arachnida. Recently (Van der Hammen, 1963: 445), I mentioned that this number generally varies from 17-19. In regarding the anal valves of *Opilioacarus* as representing a separate segment, this number has increased to 20, one segment more than in Scorpionida. Possibly, this points again to the partly primitive character of Opilioacarida.

The intersegmental arrangement of muscle attachments, together with the occurrence of a prosoma without lyrifissures and an opisthosoma with lyrifissures, confirm the hypothesis recently framed by me (Van der Hammen, 1963) that the idiosoma of mites is primarily composed of prosoma and opisthosoma, and not of propodosoma and hysterosoma. The data illustrate my views in a magnificent way, because the backward moving up of the lateral region distinctly demonstrates that dorsal and ventral parts of the opisthosoma have partly penetrated the prosoma. Possibly, this moving up is connected with a regression of the podosomatic tergites.

Considering the undoubted relationship between Opilioacarida and Anactinotrichida, the above-mentioned data throw a new light on the composition of the Gamasine dorsal shield. Judging from my description of *Glyptholaspis confusa* (cf. Van der Hammen, 1964), this dorsal shield has a small anterior part without pores, and a much larger posterior part with pores. In order to stimulate further morphological investigation in Gamasina, I introduce here the following two hypotheses. (1) Only the small anterior part of the Gamasine dorsal shield, without pores, belongs to the prosoma, the remaining part to the opisthosoma. (2) Originally, each opisthosomatic segment presented one transverse row of setae and one transverse row of lyrifissures or pores (the pores do not necessarily represent the borders of the segments, as mentioned by me in 1964). According to these hypotheses, the terms podonotal and opisthonotal shield are not correct, because podonotal shield would partly refer to the opisthosoma. It will, however, certainly be very difficult (if not impossible) to reduce the chaetotaxy of the Gamasine idiosoma to the original segmented condition. I do not know if any primitive species are known. Parasitic species must of course be excluded from a first study. Prototaxy, orthotaxy, neotaxy, plethotaxy, ideotaxy, and oligotaxy (cf. Grandjean, 1965: 714-717) should be thoroughly taken into account. In the case of *Glyptholaspis confusa* e.g., about nine or ten transverse rows of setae and pores could in this way be supposed to be of opisthosomatic origin. This is, however, mentioned here solely by the way, as a suggestive example without any further evidence. Investigation in this field should be continued.

It is useful to point here at the same time to the stigmata of *Opilioacarus*, which are situated also segmentally in the opisthosoma. These stigmata are subject to a regression which started with stigma 4, and subsequently attacked all pairs. Two pairs of stigmata are still present in *Holothyrus*, one in Gamasina. A third hypothesis can therefore be introduced here, stating that stigmata in Opilioacarida and Anactinotrichida are parts of a homologous series. As a consequence of this, the pair of Gamasine stigmata would be also of opisthosomatic origin. Evidently, the stigmata of Actinotrichida have developed in a different way.

REMARK 2. THE TEGUMENT OF *OPILIOACARUS* IN COMPARISON WITH OTHER ACARIDA

Opilioacarus is remarkable because of its nearly uninterruptedly sclerotized cuticle which envelops the idiosoma completely. Although the degree of sclerotization is not very high, sectioning meets a remarkable resistance. The same difficulty, although much more pronounced, is found in *Holothyrus*; in this group, the cuticle is also nearly uninterrupted. A histological comparison of the tegument of Opilioacarida and Holothyrina appears to be very important.

It is interesting that an apparently rather primitive group like Opilioacarida presents no segmental interruptions of the sclerotized cuticle. The question arises now whether scissures (a translation of the french "coupures"), when these occur in higher developed Acarida, represent indeed borders of segments or tagmata. It appears advisable to be extremely careful in the interpretation of shields in specialized groups. As mentioned above, it is for instance evident that the scissure between the so-called podonotal and opisthonotal shields in Gamasina has nothing to do with the border between prosoma and opisthosoma. Probably, more examples of this kind will be discovered.

The presence of pigment grains under the cuticle, apparently in the hypodermis, is a remarkable character of Opilioacarida. It is also found in a number of Holothyrina and Actinotrichida (several Prostigmata). The occurrence of the grains is not always connected with a thin or faintly sclerotized cuticle, because the cuticle of *Holothyrus* is relatively very thick. It will be interesting to know exactly in which groups they occur and whether it is a primitive character. Apparently the grains are not found in

Acaridei and Oribatid mites (the racemiform spots found in the last-mentioned group are apparently situated below the hypodermis). Are they also absent in Gamasina and Ixodina? In my opinion the possible presence of pigment grains will be an important subject for further study.

REMARK 3. THE VENTRAL PROTUBERANCES OF ARACHNIDA, PARTICULARLY OF ACARIDA

Many Arachnida demonstrate a disposition to develop excrescences of different shape in the coxisternal region of gnathosoma and prosoma, and even in the ventral region of the opisthosoma. These excrescences can be lobate, conical, papilliform, wart-like, with or without setae, erect or close to the surface of the body. They are restricted to segments II-V of the prosoma, and segments VII-XII of the opisthosoma. Because it is still difficult to conclude with certainty whether these excrescences are homologous structures, further investigations in this field will be very important. Up to now, the protuberances in mites have been attributed to two different series: a series of endopodites (Claparède's organ and genital verrucae), and a series of sternal protuberances (lateral lips, and sternapophyses or furca).

Considering the conditions in *Opilioacarus*, the question arises, however, whether these excrescences do not belong to only one series of homologous structures. Fig. 2 distinctly demonstrates that lateral lips, sternapophyses, sternal verrucae, and genital verrucae are situated in a pair of longitudinal rows. Sternal and genital verrucae in *Opilioacarus* are similar in shape; the same applies to Claparède's organ and the genital papillae in Actinotrichida. The situation of these structures is in both groups exactly the same, with the only exception that in Actinotrichida three pairs of genital papillae can be present. The most plausible inference seems to be that the sternal verrucae of *Opilioacarus* are homologous with Claparède's organ of Actinotrichida, up to now only known from prelarvae and larvae. The homology of the capsules or genital verrucae of *Opilioacarus* with the genital papillae of many Actinotrichida is a logical consequence of this conclusion. It means that the capsules are indeed part of the opisthosoma.

Below, in remark 9, the relationship between Opilioacarida and other groups of mites will be further discussed.

REMARK 4. THE INFRACAPITULAR SETAE OF *OPILIOACARUS*

Above, in the section on the gnathosoma, the infracapitular setae (including With's organ and rutellum) are classified in four rows or groups. The first of these consists of the paralabial setae ($pl_{1\text{-}4}$), the second of the circumbuccals (cb_{1-4}), the third of the medians (*vm, lvm, ldm* in *O. texanus*), and the fourth of the posteriors (vp_1, vp_2, *lvp* in *O. texanus*). With's organ (pl_2) is, according to Grandjean (1957a: 273), probably a second rutellum; pl_1, although rather small, has all morphological characters of a corniculus; pl_4, present in *O. segmentatus*, must be subject of a further study. Consequently, the first group (comprizing the paralabial setae) is remarkable because it consists of three or four pairs of specialized or hypertrophied setae of different character. All other groups of mites have retained at most one of these: corniculus or rutellum.

The circumbuccal setae are characterized by the distinctly curved shape. Assuming that four is the primitive number, two setae of this series have apparently persisted in *Holothyrus* (*va, lva*). Are they still present in other groups of mites? Grandjean (during our annual conference in Geneva in 1965) set up the hypothesis that they have persisted in Actinotrichida as adoral setae. I am inclined to enlarge this hypothesis and regard cb_{1-4} as possibly homologous with the adoral setae (or_{1-3}) and the anterior setae (*a*) of the genae in Actinotrichida. From this it would follow that in Gamasina the series is reduced to only one seta, viz., the anterior seta (*a*) of the genae (cf. Van der Hammen, 1964). A further comparison of this hypothesis with the condition in different groups of mites will be very interesting.

The median setae (*vm, lvm, ldm* in *O. texanus*) are certainly homologous with the median setae (also *vm, lvm, ldm*) of *Holothyrus*; they have nearly exactly the same position. It must be considered highly important that a latero-dorsal infracapitular seta (*ldm*) is found exclusively in Opilioacarida and Holothyrina.

The posterior setae (vp_1, vp_2, *lvp* in *O. texanus*; *vp, lvp* in *Holothyrus*) also have nearly the same position in both groups; they differ, however, in number. According to Grandjean (1936: 425), there is even intraspecific variability: the number in *O. segmentatus* varies from two (*vp, lvp*) to five (vp_1, vp_2, vp_3, lvp_1, lvp_2).

Both median and posterior infracapitular setae of Opilioacarida and Holothyrina take the place of the median setae (*m*) of other groups of mites. None of these can be homologized with the pair of setae (*h*) of the mentum.

REMARK 5. PRIMARY SEGMENTS OF THE APPENDAGES, FUSION, SECONDARY SUBDIVISION, AND ARTICULATION

Coxa, trochanter 1 and 2, femur, genu, tibia, tarsus, and apotele are considered here primary segments, movable by means of their own tendons. In legs III and IV these are all present; in the remaining appendages the number is smaller because of deficiency or fusion of various segments.

A free coxa is absent in chelicera and palp, although specialized coxal regions can be recognized here. I may remark that coxal regions are certainly homologous with free coxae, because in some mites both present latero-coxal setae in corresponding positions. It appears, however, impossible to decide whether the presence of free coxae is the primitive condition and the presence of fixed coxal regions the secondary, or the reverse. According to Grandjean (1936: 427) the cheliceral sheaths must be regarded as the coxal region of the chelicerae. In *Opilioacarus,* a coxal region is distinctly differentiated at the base of the palp; this part presents no latero-coxal setae.

As mentioned in the description, segment 1 of the chelicerae is functionally a trochanter. I am inclined to attach much importance to the articulation between this segment and segment 2, and to regard it indeed as a true trochanter. Segment 2 of the chelicerae consequently is a fusion of femur, genu, tibia, and tarsus.

At the place of trochanter 1 and 2 of legs III and IV, legs I and II present only one segment; there are no arguments in support of a hypothesis that the trochanter of palp and legs I and II is the result of a fusion of two trochanteres. Trochanter 2 of legs III and IV tends, on the contrary, to fuse with the femur by ascendant evolution; basifemur I and the basal part of femur II are, however, too small to contain parts of a second trochanter.

Femur, genu, tibia, tarsus, and apotele of palp and legs are free segments. Although tibia and tarsus of the palp have the shape of one large segment, they are movably articulated, and the tarsus has its own tendon. The movable bit of the chelicerae is the apotele; just as the apotele of palp and legs, it can be depressed and elevated by means of two tendons.

The primary segments (with the exception of coxa and trochanter) are connected by two types of articulations. The first type is characterized by a dorsal hinge, and one ventral tendon. The second type has a mediolateral hinge, consisting of an antiaxial and a paraxial "condyle", and a ventral as well as a dorsal tendon. The two types are preliminarily named here monovalent and bivalent. Bivalent articulations occur between trochanter 1 and 2, between trochanter and femur, between segment 1 and 2 of the chelicera, and between tarsus and apotele. Monovalent articulations occur between femur and genu, genu and tibia, and tibia and tarsus. The articulation between coxa and trochanter has apparently also one tendon; the structure is, however, complicated, and probably permits of movements in more than one plane; it should be studied in detail after new material. The articulation between coxa and idiosoma is more or less universal and permits of movements in various directions (although probably mainly about a longitudinal axis).

The primary articulations of the legs can be classified as indicated in

Table 1. — The primary articulations in the legs of *Opilioacarus*.

primary articulations	universal (probably mainly more or less longitudinal)		idiosoma/coxa
	complicated, as yet not sufficiently clear (one tendon, one articular tooth)		coxa/trochanter
	mainly transversal	bivalent	trochanter 1/trochanter 2
			trochanter/femur
			tarsus/apotele
		monovalent	femur/genu
			genu/tibia
			tibia/tarsus

table 1; this survey demonstrates at the same time the gaps in our knowledge on the subject.

Femora, tibia I, and tarsi of the legs are subdivided by secondary articulations which are together characterized by the absence of individual tendons, but which are quite different in comparison with each other: the secondary division passes through lyrifissures or not, and the movability varies from very restricted to "bivalent". In this way several types of secondary articulations have developed.

A basifemur is distinctly separated by a suture in femur I; this suture passes through three antiaxial and a number of paraxial lyrifissures. A basifemur is not completely separated in femur II-IV; at the place of the secondary "articulation" two large lyrifissures are present: an anterior *if′* (paraxial in leg II, and antiaxial in leg III-IV) and a posterior *if″* (antiaxial in leg II, and paraxial in legs III-IV).

The articulation between basi- and telotibia I passes through a ventral lyrifissure; dorsally is presents a fold. In *O. texanus* the two parts are laterally not distinctly separated; the movability will consequently be restricted.

Tarsus I is subdivided into a basitarsus and a telotarsus; these are ventrally separated by two lyrifissures, laterally and dorsally by soft skin. Telotarsus I will flex and extend by means of hydrostatic pressure and the tendons of the apotele.

Tarsi II-IV consist of basitarsus, telotarsus, acrotarsus, and pretarsus. Basi- and telotarsus have developed a secondary bivalent articulation: the telotarus can be elevated as well as depressed, mainly by the tendons of the apotele. The articulation between telo- and acrotarsus resembles that between basi- and telotarsus I; lyrifissures are, however, absent; flexion will probably take place by hydrostatic pressure, and extension by the tendon t_8 of the apotele. The pretarsus is elevated and depressed by the tendons of the apotele;

Table 2. — The secondary articulations in the legs of *Opilioacarus*.

secondary articulations	articulations passing through lyrifissures	lyrifissures laterally	two lyrifissures suture absent	basifemur/telofemur II-IV
			many lyrifissures, suture complete	basifemur/telofemur I
		lyrifissures ventrally	one lyrifissure, dorsal fold	basitibia/telotibia I
			two lyrifissures, laterally and dorsally soft skin	basitarsus/telotarsus I
	articulations not passing through lyrifissures	monovalent	articulation ventrally	telotarsus/acrotarsus II-IV
		bivalent	articulation externally	basitarsus/telotarsus II-IV
			articulation internally	acrotarsus/pretarsus II-IV

the articulation takes place between a pair of chitinous pieces in the pretarsus and a pair of condyles in the acrotarsus.

Fig. 17 and 18, representing complete appendages (without coxae), clearly demonstrate the close relation between various types of articulations on the one hand, and the position of the legs and the function of the segments on the other.

The secondary articulations can be classified, according to increasing degree of movability, as indicated in table 2.

REMARK 6. THE LATERO-COXAL SETAE

The latero-coxal setae in *Opilioacarus* are interesting because they distinctly belong to the mucronate type; this is indeed a proof of their setal origin. Without any doubt they are homologous with *eI* and *eII* in *Glyptholaspis* (Gamasina) and Actinotrichida.

A comparison of various groups of Actinotrichida makes it clear that latero-coxal setae disappear from posteriorly to anteriorly, starting with *eII*; the list of priority in this case is *e*, *eI*, *eII*. Opilioacarida demonstrate another evolutionary trend because *e* (the latero-coxal seta of the palp) is absent, whilst *eI* and *eII* are both present. Apparently we are concerned here with a regression which starts anteriorly by suppressing *e*, although we can regard it as a continuation of a trend which already suppressed the latero-coxal setae of the chelicerae.

The above-mentioned data demonstrate that presence and absence of latero-coxal setae are distinctly subject to general laws, which emphasizes the value of *e*, *eI*, and *eII* for comparative morphology and classification.

REMARK 7. THE CHAETOTAXY OF THE LEGS IN *OPILIOACARUS*

The legs of *Opilioacarus* are interesting because unpaired dorsal setae (*d*) are still present in many segments. Although the number of these setae is apparently strongly reduced in leg I (probably in connection with the specialized function of this leg), many *d* setae are found in the remaining legs, especially in II-III. In these two legs, dorsal setae occur on femur, genu, tibia, basitarsus, and acrotarsus. Often they belong to the composite papilliform or to the mucronate type, i.e. in both cases a distinctly separated, hollow point is present. According to Grandjean (1936: 435), the mucronate setae are a transition to the *sm* setae which consist of an ornate base and a smooth, transversely striated distal part. The *sm* setae remind of the solenidiomorph setae of Opilionida. Solenidions could have originated by specialization from these solenidiomorphs. It is interesting to see that on basitarsus II and III a row of solenidions passes distally into a row of mucronate setae; in leg IV these solenidions have even taken the place of all dorsal mucronate setae. It is obvious to suppose that in leg II and III an original row of *sm* setae developed in the proximal part into solenidions (by disappearance of the ornate base), and in the distal part (by reduction of the tip to a small point) into mucronate setae.

It is interesting to observe moreover that a point is apparently more often present in dorsal and terminal setae, and in setae in the neighbourhood of secondary articulations; probably they still have some sensory function. Further investigations in this field are, however, badly needed.

Verticils in Opilioacarida apparently originally consisted of seven setae, viz., *d*, (*ld*), (*l*), and (*v*). Many complete, distinctly recognizable verticils are still present. All verticils of the telotarsus consist, however, of six setae because of the absence of *d*. The number of verticils is considerable, and increases during post-embryonic ontogeny.

A few words must be added here on the importance of the recognition of the unpaired dorsal seta *d*, even in groups where its occurrence has become rare. The evolution of number and position of the setae develops according to fixed laws; some of these laws are known and concern the regression of *d*. A notation neglecting the evolutionary trends can perhaps be practical for the identification and grouping of species, but probably risks not to lead to progress in understanding.

REMARK 8. THE POST-EMBRYONIC ONTOGENY OF OPILIOACARIDA

The development of Opilioacarida is only partly known. The number of stases is uncertain, and we can only start here from the supposition that it is probably five (larva, three nymphs, and adult). The most complete data are those published by Naudo (1963), whose description includes also the larva which, until recently, was unknown. It is interesting to summarize here the immature characters mentioned by him.

The larva of *Panchaetes dundoensis* Naudo (1963: 20, fig. 12-14) is characterized by the presence of only three pairs of legs; a vestige of leg IV appears, however, to be present. The capsules (genital verrucae) are visible, although the borders are indistinct; they do not bear setae. The opisthosoma presents only one dorsal seta situated in segment XVIII, and apparently one pair on the anal tubercle (segment XIX); the unpaired seta of segment XVIII is certainly homologous with the dorsal pre-anal seta in *Opilioacarus*. The number of sternal setae is small. The larva has no stigmata or tracheae; With's organ is also absent, and the rutellum is apparently reduced. The legs present secondary subdivisions of femur I (which consists of basifemur and telofemur), and of all tarsi (which consist of basitarsus and telotarsus); trochanter 2 and acrotarsus are not present as separate segments.

The smallest nymph described by Naudo (1963), probably a protonymph, has four pairs of legs, genital verrucae with one papilliform seta, an increased number of opisthosomatic setae, and two pairs of stigmata (stigma 1 and 2). Trochanter 2 and acrotarsus are not yet present as separate segments. With's organ is normally developed.

The second nymph in size presents genital verrucae with three papilliform setae; it has three pairs of stigmata (stigma 1, 2, and 3). Legs II-IV have separate acrotarsi; there is no separate trochanter 2.

A nymph belonging to *Panchaetes dundoensis* var. *condensus* Naudo probably represents a third nymph. This nymph is characterized by the presence of four pairs of stigmata (stigma 1-4); the genital verrucae have three or four papilliform setae; legs III and IV have a separate trochanter 2.

We can add to these data an observation by Grandjean, according to which a secondary subdivision of tibia I in *O. segmentatus* is present in the adult, but lacks in his smallest nymph. As mentioned above, With's organ is apparently absent in the adults of *Paracarus* and *Adenacarus* (the condition in the nymphs is unknown). According to my own data, the two largest nymphs of *O. texanus* (probably deuto- and tritonymph) both have legs III and IV with a separate trochanter 2, and four pairs of stigmata.

These data together demonstrate a number of evolutionary trends, of which some will be briefly mentioned here. Many more material is, however, required to study the trends in detail. They are interpreted here hypothetically in the following way.

(1) The dorsal pre-anal seta is personally excepted from the ascendant regression of the opisthosomatic setae; this regression is complete (segment XVIII and the anal tubercle excepted) in the larva of *Panchaetes*, and in all stases of *Opilioacarus*.

(2) The stigmata and tracheae are subject to an ascendant regression (because there is apparently no fixed base level for each stigma, the evolutions are not vertical). The number is zero in the larva, and eight pairs in the adult. The number in the nymphs possibly shows specific variation.

(3) With's organ is subject to an ascendant regression which in *Adenacarus* and probably also in *Paracarus* has reached the adult level.

(4) In larvae and a varying number of nymphs, trochanter 2 of legs III and IV is fused with the basifemur (cf. Naudo, 1963: 23, fig. 15-22). This is considered here a secondary condition, the primitive being the presence of two trochanteres (these have both their own tendons, in contradistinction to the secondary subdivisions of tibia and tarsus). The fusion is part of an ascendant evolution.

(5) The secondary subdivision of the tibia is part of a descendant evolution. It is present in the adult, but absent in a number of immature stases.

(6) Acrotarsi II-IV are present in the adult and in some nymphal stases; they are absent in the larva and the remaining nymphs. Apparently the secondary subsivision of the telotarsus is part of a descendant evolution.

Probably, many more characters in Opilioacarida (e.g. of the chaetotaxy of the infracapitulum) will show distinct evolutionary trends. It is worth while to study in detail the development of as many species as possible.

REMARK 9. THE RELATIONSHIPS OF OPILIOACARIDA WITH ANACTINOTRICHIDA AND ACTINOTRICHIDA

A detailed survey of the relationships of *Opilioacarus* with other groups of mites, was given by Grandjean (1936: 437). He published lists of characters in common with Anactinotrichida and Actinotrichida, and a list of characters special to *Opilioacarus*. The present investigation, together with my previous studies on Anactinotrichid morphology (Van der Hammen, 1961, 1964, 1965) necessitate, however, a revaluation of these affinities. For this reason I have compared here my collected data on Opilioacarida with characters now known from Holothyrina, the remaining Anactinotrichida, and Actinotrichida. It is still too early to prepare lists of characters in common with other Arachnida.

According to our present knowledge, Opilioacarida are recognizable by the following distinctive characters.

(1) The habitus is very special, and shows a superficial resemblance to a harvestman.

(2) The number of segments is large; it is here found to be 20.

(3) Four pairs of stigmata are present, situated in the opisthosoma (in segments IX-XII).

(4) The number of opisthosomatic lyrifissures is strikingly large.

(5) The opisthosomatic muscles are numerous; they are distinctly segmentally arranged.

(6) The anal orifice is situated on a separate anal tubercle.

(7) The genital region presents a pair of large, internal sacs, covered by capsules (genital verrucae).

(8) The infracapitulum presents at least three pairs of specialized or hypertrophied paralabial setae, including probably one pair of small corniculi and two pairs of rutella.

(9) Although the mouth is triangular, the pharynx soon develops a hexagonal section.

(10) The chelicera bears one seta on segment 1, and three setae on segment 2. In the remaining groups of mites this number is apparently distinctly smaller.

It is remarkable that the number of characters in common between Opilioacarida and Holothyrina (and for the greater part not found in other groups) is more important than would appear from the completely different habitus. They relate to the following important structures.

(1) The cuticle is nearly uninterrupted; only one or more genital sclerites or shields are separated.

(2) With few exceptions, pigment grains are present under the cuticle, probably in the hypodermis (according to our present knowledge, this character is only found again in some Prostigmata).

(3) The gnathosoma has a large number of infracapitular setae (at least seven pairs); one of these pairs has a latero-dorsal position.

(4) A small cheliceral tectum is present, which is anteriorly not produced (it is still unknown whether this condition is also found in Actinotrichida).

(5) The lateral lips are large; they surround the pre-oral cavity ventrally as well as laterally and partly dorsally; they are hardly subdivided into specialized parts.

(6) The claws of the palpal apotele are still easily recognizable as such.

(7) Tibia and tarsus of the palp together have the shape of one large segment. This character, although in a less pronounced way, is found again in Anactinotrichida.

(8) The tarsus of the palp is characterized by a dorsal area with hollow setae.

(9) The pretarsus bears one or two pairs of setae.

I may remark in this connection, that a redescription of a species of *Allothyrus* Van der Hammen, 1961, especially of *A. constrictus* (Domrow 1955) will be very important. Judging from Domrow's original description, *A. constrictus* is characterized by a great number of infracapitular setae (more than in *Holothyrus*), among which five *lvp*. In this respect it approaches more or less the condition in Opilioacarida, whilst a different shape of the lateral lips, and the presence of a furca are possibly characters that approach the condition in Gamasina. Apparently, the dorsal shield presents many lyrifissures.

The question arises now, whether the apparent relationships between Opilioacarida and Holothyrina justify a re-establishment of the suborder Onychopalpida. I may recall here that this suborder was created by Wharton (1947). It was diagnosed by Baker & Wharton (1952: 36) as presenting (1) a palp with claws, (2) a labium with a radula-like organ, and (3) at least two pairs of stigmata. Baker, Camin, Cunliffe, Woolley & Yunker (1958) added two further characters, viz., (4) the absence of a cheliceral tectum, and (5) the presence of numerous infracapitular setae (the accompanying illustration apparently refers to *Allothyrus*; the characterization of part of these setae as accessory, now appears not to be justified).

Of these five characters, the second is not valid: a radula-shaped labrum is restricted to *Holothyrus*; teeth are found on the ventral and lateral surfaces of the labrum of many species of mites. The fourth character is also not valid: above, I have demonstrated that a cheliceral tectum is distinctly present.

In order to estimate the value of the characters in common between Opilioacarida and Holothyrina, it is necessary to discuss the relationship of these groups with Anactinotrichida and Actinotrichida.

Opilioacarida have a lot of characters in common with Anactinotrichida. These are arranged here in the following list.

(1) Stigmata 1-4 of Opilioacarida, stigmata 1-2 of Holothyrina, and the single pair of stigmata of Gamasina and Ixodina are considered here parts of the same homologous series.

(2) A sternum is more or less distinctly present in Opilioacarida as well as in many Anactinotrichida.

(3) A sejugal furrow or interval is absent in both groups.

(4) The pair of taenidia running from between coxae I and II (apparently from the orifice of a coxal gland) to the subcapitular groove, is probably also present in several Anactinotrichida.

(5) The sternal region of the first pair of legs bears in Opilioacarida a pair of sternapophyses; this pair is undoubtedly homologous with the furca of *Allothyrus* and Gamasina.

(6) A subcapitular groove, probably representing a taenidium, is found in Opilioacarida, Holothyrina, and Gamasina.

(7) The coxae of Opilioacarida are free, just as in Holothyrina and Gamasina.

(8) The chelicerae have a dorsal lyrifissure as well as an antiaxial; only the latter is exceptionally found in Actinotrichida.

(9) As mentioned above, tibia and tarsus of the palp have, in Opilioacarida and Holothyrina, the shape of one large segment. This condition is found again, although less developed, in Gamasina.

(10) The palpal claws of Opilioacarida and Holothyrina are homologous with the "tined seta" of the Gamasina. Palpal claws are completely absent in Actinotrichida.

(11) Trichobothria do not occur in Opilioacarida and Anactinotrichida. They are found in many Actinotrichida (on the idiosoma as well as on the legs).

(12) A basifemur, separated by a suture (passing through lyrifissures) from the telofemur, is present in Opilioacarida and Anactinotrichida.

(13) Secondary articulations of the tarsi of the legs, although differently developed, are found in both groups.

(14) The legs present in both groups several lyrifissures. In Actinotrichida this number is reduced to at most one; the single lyrifissure is situated dorsally or antiaxially at the base of the tarsus.

The list of characters found in Opilioacarida as well as in Actinotrichida is shorter. Three of the characters mentioned in this connection by Grandjean (1936: 439) must be removed from the list of these relationships. It concerns: (1) the cheliceral vault which appears indeed to be present in Opilioacarida; (2) the efferent ducts of infracapitular glands, which are now also known from Gamasina (the position of the orifices, however, is still considered here of interest); (3) the latero-coxal setae which have also been discovered in the last-mentioned group. The revised list, to which some data are added, now comprises the following characters.

(1) The cuticle of Opilioacarida is soft, just as in many Prostigmata.

(2) Pigment grains under the cuticle, probably in the hypodermis, are also found in Prostigmata.

(3) A rostral lobe is present also in Endeostigmata.

(4) A disjugal furrow (synonym: dorso-sejugal furrow) is present in Opilioacarida and many Actinotrichida.

(5) Sternal and genital verrucae of the Opilioacarida are considered here possibly homologous with Claparède's organ, respectively genital papillae of many Actinotrichida; these are still unknown from Anactinotrichida.

(6) A rutellum is found in Opilioacarida, all Oribatid mites, and many Endeostigmata.

(7) The orifices (*ogi*) of the infracapitular glands have the same position as in some Actinotrichida.

(8) In Opilioacarida, a number of setae of the tarsi of the legs are distinctly birefringent. It will be interesting to investigate whether this really concerns actinopilin.

(9) The telotarsal organ resembles the hidden solenidions of some Prostigmata.

With the exception of the subcuticular pigment grains (which occur also in *Holothyrus*), these characters are not known from Anactinotrichida. No further resemblances appear to be present between Holothyrina and Actinotrichida. Consequently, this list clearly demonstrates the special position of the Opilioacarida.

In my opinion *Holothyrus* has too many characters in common with Gamasina and Ixodina to be separated from the Anactinotrichida. Our conclusion must be that Opilioacarida constitute a separate group, distinctly related to Anactinotrichida, but nevertheless presenting a number of interesting characters in common with Actinotrichida. A re-establishment of the suborder Onychopalpida would obscure the synthetic character of the Opilioacarida. The classification of the mites in three groups (Opilioacarida, Anactinotrichida, Actinotrichida) appears to be the most logic solution.

REMARK 10. SUMMARY OF THE MOST IMPORTANT REMAINING PROBLEMS

The small number of specimens studied by me, as well as the lack of observations in the field, have been the cause that the present description contains a number of unsatisfactory gaps. In order to stimulate continued research in Opilioacarida, a concise list is prepared here, summarizing the details that still deserve special attention.

(1) The occurrence of large masses of pollen grains in the gut of *Opilioacarus texanus* proves that the presence of the latter under rocks is only a diurnal habit. It will be very interesting to study the nocturnal life habits of the species. Data on activity and abundance can possibly be obtained by placing catch-boxes in an area where the species is known to occur. The presence of *O. texanus* on plants could be proved by sweeping at night with a net. The pollen grains in the gut can easily be identified by comparing them with pollen of the flowering plants in the area in question. It is probable that the species feeds on pollen in a special season only; in semi-arid regions flowering plants are mainly found in spring.

(2) It will be interesting to investigate the variability of length and broadth of the idiosoma in connection with sex and stase. My material did not show differences in measurements between male and females. The differences between the stases will, however, certainly be discontinuous. The relation length:broadth appears to be increasing from larva to adult. My smallest nymph is relatively broader than the adults. According to data published by Naudo (1963), this relation in *Panchaetes* increases from about 1 in the larva to about 1.9 in the adult (1.4 respectively 1.6 in two different nymphs).

(3) A histological study of the tegument of *Opilioacarus* will be very important. The faint degree of sclerotization results in a leathery cuticle; there are nearly no interruptions of soft skin. A comparison of the tegument of *Opilioacarus* with that of *Holothyrus* and other groups of mites will be interesting.

(4) According to my observations, the prosoma of *O. texanus* presents a rostral lobe. A histological study of this lobe will be very interesting, especially because it presents at both sides a concave light spot of unknown nature, which is partly surrounded by dark pigment.

(5) Differences between male and female genital region are given above. Because of the lack of sufficient material, the variability of these differences could not be taken into consideration. A detailed description of the ovipositor, and a comparison of it with the ovipositor of other groups of Arachnida in which this organ is present, will be very important. The function of the pair of sacs covered by capsules can only be established by the observation of living specimens.

(6) With (1904: 165) described a coxal gland of which the duct appeared to be directed towards the first or second pair of coxae. He could not discover its orifice. Probably, this is the gland which debouches into the system of taenidia running from between coxae I and II to the subcapitular groove. I could trace the taenidium up to the posterior surface of coxa I; probably, the orifice of the gland is indeed at this side. It will be interesting to verify my observation, and to prepare an exact description of the taenidia with their complicated structure of widenings, narrowings, uneven bottom, and tecta; a reinvestigation of the gland will also be important.

(7) The chaetotaxy of the legs presents a number of interesting characters of which some should be studied in detail with the help of more extensive material. I point here to the apparent substitution of papilliform setae by lanceolate, of which I observed a few cases.

Another interesting problem concerns the presence of a point on the papilliform setae. According to my observations, points are especially found on dorsal setae, and on those in the neighbourhood of primary or secondary articulations. A statistical investigation is required in order to demonstrate clearly whether a possible connection is indeed present.

A study of the variability in number and position of the setae will probably pave the way for a definitive notation.

(8) The articulation between coxa and trochanter is characterized here as complicated. The trochanter apparently has one tendon, the coxa presents one articular tooth. I do not think that the movements are only transversal. Further study of the morphology of the articulation, as well as observations on a living specimen will certainly be conclusive.

(9) It is very important to know whether the birefringency of a number of setae on tarsi II-IV (especially ventrals and laterals of pretarsus,

acrotarsus, and part of the telotarsus) is caused by actinopilin. For that purpose, both optical and chemical properties of the setae should be studied.

(10) Only a few data on the internal anatomy of *O. texanus* are mentioned here. Detailed descriptions (e.g. of the genital organs) will certainly be clarifying.

(11) Rearing will be inevitable in order to establish the exact number of stases in Opilioacarida. Pollen grains are possibly excellent food during captivity. In the laboratory, the function of the shape of the eggs will probably become clear. When the number of stases is known, a further study can be made of the development of the numbers of setae in the species.

REMARK II. SUMMARY OF THE HYPOTHESES INCLUDED IN THE PRESENT PAPER

Hypotheses have an important part in the development of a science, because they arrange data in a new way, and stimulate research along a different line. In morphology and systematics they can have the advantage that they open up new possibilities for the discovery of general laws governing evolution. On that account, a number of suppositions have been included in the present paper as bases for reasoning, and as starting-point for further investigation. These hypotheses are enumerated in the following list which must be considered a recapitulation of my various ways of approach.

(1) The parts of the opisthosoma, bordered by transverse furrows and rows of muscle attachments, are regarded here as segments. Little is known of the embryology of mites, and data on the embryology of *Opilioacarus* are completely wanting. The hypothesis is supported by the presence of transverse rows of lyrifissures (*Opilioacarus*) and setae (*Panchaetes*). The backward moving up of the lateral parts exactly suits hypothesis 2.

(2) The body of mites is regarded as consisting of prosoma and opisthosoma, primarily separated by a disjugal fold. This hypothesis is considered proved in Actinotrichida by the arguments published by me in 1963.

(3) The stigmata of Opilioacarida and Anactinotrichida are regarded here as belonging to one homologous series. This hypothesis is supported by the regression of the stigmata in the immature stases of Opilioacarida, and by the presence of still two pairs in *Holothyrus*.

(4) The ventral protuberances of segments II-IV and of the genital region are considered here parts of a homologous series. Further investigations in this field should be extended over various groups of Arachnida.

(5) The gnathosoma is regarded here as consisting of the ventral parts

of segment I (cheliceral frame) and segment II (infracapitulum). The dorsal parts are incorporated in the prosoma. This hypothesis is proved by the existence of a precheliceral rostral lobe in the prosoma, and an epimeric furrow and a capitular apodeme at the border of cheliceral frame and infracapitulum.

(6) The distinguishing of a row of paralabial setae (among which a pair of corniculi and two pairs of rutella) and a row of circumbuccal setae opens up new possibilities for a homologization of the infracapitular setae in various groups of mites.

(7) The occurrence of latero-coxal setae is considered here of much importance. In spite of several indications of reduction, the setal character has remained distinct in *Opilioacarus* because of the mucronate shape. The presence of latero-coxal setae in fixed coxal regions, as well as on free coxae, is a proof of the homology of these two. The regression of latero-coxal setae takes place according to fixed laws.

(8) A hypothesis homologizing segment 1 of the chelicerae with a trochanter, should give rise to a reinvestigation of these appendages in all groups of Arachnida.

(9) The presence of two trochanteres instead of one in legs III and IV is regarded here as a primitive character, the subdivision of tibia I and all tarsi as a secondary. These hypotheses should give rise to a study of the legs in other Arachnida.

(10) The setae of the appendages are regarded as originally belonging to verticils consisting of a number of paired setae and one unpaired dorsal. This dorsal seta has disappeared in many cases. The process of regression is apparently subject to fixed laws. Many setae *d* are still present in *Opilioacarus*. The hypothesis appears plausible and should be compared with the condition in other groups of Arachnida.

(11) On basitarsus II-III a dorsal row of solenidions passes into a dorsal row of mucronate setae, whilst on basitarsus IV the dorsal row consists of solenidions only. This supports the hypothesis that solenidions as well as mucronate setae in *Opilioacarus* originate from *sm* setae. It will be interesting to make a further study of the occurrence of solenidions and solenidiomorph setae in various groups of Arachnida.

GLOSSARY

The present glossary differs from the preceding glossaries published by me (Van der Hammen, 1964, 1965) in that it is divided into two parts. Because publications on Opilioacarida (twelve have been worked into the present paper) are mostly characterized by a divergent and deviating terminology, the first part contains a list of all those terms which are here regarded as synonyms of names used by me. The second part is a complete glossary of terms suggested here to be used henceforth in descriptions of Opilioacarida.

SYNONYMIC LIST

Abdomen (With; Chamberlin & Mulaik; Naudo) — opisthosoma without segment VII.
Abdomen (Redikorzev) — opisthosoma.
Anal hill (With) — anal tubercle.
Antennae (With) — chelicerae.
Appendices labiales (Silvestri) — sternapophyses.
Appendices labiaux (Naudo) — sternapophyses.
Basitrochanter (Grandjean) — trochanter 1.
Canal podocéphalique (Grandjean) — sternal taenidia.
Capitulum (Grandjean; Naudo) — gnathosoma.
Capsules (Grandjean) — genital verrucae.
Capsules copulatrices (Naudo) — genital verrucae.
Cephalothorax (With) — prosoma together with the first opisthosomatic segment (= segment VII).
Cephalothorax (Redikorzev) — prosoma.
Chitinous tube *tu* (With) — subcapitular groove.
Copulatory suckers (With) — genital verrucae.
Corniculus maxillaris (Redikorzev) — rutellum.
False segment at the base of the femur (Chamberlin & Mulaik) — basifemur.
Fan hair (With) — papilliform seta.
Fissure (Grandjean) — lyrifissure.
Fissure lyriforme (Grandjean) — lyrifissure.
Gouttière sternale du menton *g.ax.* (Grandjean) — subcapitular groove.
Gouttière *u* (Grandjean) — sternal taenidium.
Head + thorax (With; Chamberlin & Mulaik) — prosoma together with the first opisthosomatic segment (= segment VII).
Hysterosoma (Baker & Wharton) — opisthosoma (anterior border not precisely defined).
Hysterosoma (Naudo) — opisthosoma without segment VII.
Intercalary segment between trochanter and femur proper (Chamberlin & Mulaik) — basifemur.
Labial appendages (With) — sternapophyses.

Lateral lobes (With) — lateral lips.
Lobe maxillaire (Naudo) — rutellum.
Lobus maxillaris (Silvestri) — rutellum.
Lyriform area (With) — lyrifissure.
Lyriform fissure (With; Chamberlin & Mulaik) — lyrifissure.
Mandibule (Grandjean; André) — chelicera.
Maxilla (Chamberlin & Mulaik) — infracapitulum.
Maxillae (With; Silvestri) — infracapitulum.
Maxillary lobe (With) — rutellum.
Maxillary plate (With) — With's organ.
Maxillary spine (With) — paralabial seta 1 (corniculus).
Maxille (Grandjean) — rutellum.
Maxilles (Naudo) — infracapitulum.
Menton (Grandjean) — ventral surface of the infracapitulum (mentum + genae).
Metasoma (Silvestri) — opisthosoma (segment VII probably not included).
Metatarsus (With; Chamberlin & Mulaik) — basitarsus.
Métatarse (Naudo) — basitarsus.
Muscular spot (With) — muscle attachment.
Opisthosoma (Naudo) — opisthosoma without segment VII.
Organe adaxial (Naudo) — sternal taenidia + subcapitular groove 1).
Organe de Haller (Grandjean) — telotarsal organ.
Organe lyriforme (Grandjean) — lyrifissure.
Organe maxillaire (Grandjean) — rutellum.
Papille (André; Naudo) — papilliform seta.
Pars maxillaris gnathopodum (Silvestri) — infracapitulum.
Patella (With; Chamberlin & Mulaik) — genu.
Praetarsus (Redikorzev) — telotarsus or acrotarsus 2).
Presternal stylets (Chamberlin & Mulaik) — sternapophyses.
Pretarsus (Camin, Clark & Gorirossi Bourdeau) — apotele.

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1) I wish to express here my sincere thanks to Mr. M. H. Naudo who kindly sent me a definition of this term (it was not precisely explained in his text). In his letter, Mr. Naudo pointed to a curious similarity between his adaxial organ and the podocephalic canal of Bdellids and other Actinotrichida (cf. Grandjean, 1944:144). This canal runs, however, in the direction of the capitular epimeric furrow. The glands debouching into podocephalic canal and sternal taenidia should be thoroughly investigated and compared.

2) Redikorzev (1937:12) uses the terms "Praetarsus" and "Tarsus" in a concise description of leg I. Judging from his fig. 3, leg I consists of three segments, viz., basitarsus, telotarsus, and acrotarsus (a condition unknown in other Opilioacarida). For this reason, it is not impossible that his "Praetarsus" and "Tarsus" refer to acrotarsus and telotarsus respectively.

Prosoma (Silvestri) — prosoma, probably together with the first opisthosomatic segment (= segment VII).
Prosoma (Naudo) — prosoma together with segment VII.
Proximal segment to femur (Chamberlin & Mulaik) — basifemur.
Pseudocapitulum (With; Chamberlin & Mulaik; Naudo) — gnathosoma.
Rostrum (With) — cheliceral tectum.
Rounded prominence on the lateral margin of the thorax (Chamberlin & Mulaik) — pedotectal lobe.
Salivary duct (With) — sternal taenidium.
Saugnäpfe (Redikorzev) — genital verrucae.
Sillon *s* (Grandjean) — disjugal furrow.
Sillon *u* (Grandjean) — sternal taenidium.
Stylets (Chamberlin & Mulaik) — sternapophyses.
Tarsus (With; Chamberlin & Mulaik) — telotarsus + acrotarsus.
Tarsus (Redikorzev) — basitarsus or telotarsus [1]).
Telotrochanter (Grandjean) — trochanter 2.
Transverse grooves on the ventral surface of the legs (Chamberlin & Mulaik) — lyrifissures.
Tritosternum (Grandjean; Baker & Wharton; Baker, Camin, Cunliffe, Woolley & Yunker) — sternapophyses.
Trochanterofémur (Naudo) — trochanter 2.

LIST OF TERMS USED IN THE PRESENT PAPER

ACCESSORY GLAND. — Relatively large, paired female gland, situated posteriorly of the receptacula seminis.

ACROTARSUS. — Subterminal secondary subdivision of tarsus II-IV, situated between telotarsus and pretarsus.

ACTINOPILIN. — Anisotropic matter with strong birefringence, optically uniaxial, negative, heterogeneous, with radial structure; in a transverse section of a seta the optic axis is everywhere a radius of the circle of section (cf. Van der Hammen, 1961:175).

ANAL TUBERCLE. — Posterior part of the opisthosoma, consisting of segments XIX and XX; it is distinctly separated from segment XVIII, and directed obliquely downward.

ANARTHRY. — The absence of labio-genal articulation; mentum and genae are not separated.

ANTIAXIAL. — Used here for the side of an appendage (and its structures) not facing the idiosoma. Opposite: paraxial. Antiaxial and paraxial should be used beside anterior and posterior. Both sets of terms are required to

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1) Compare note 2 on p. 69.

describe all phenomena exhibited by the legs (parallel homology, paraxial regression, etc.).

APOTELE. — The terminal segment of the appendages. In the case of palp and legs, it is reduced to a basal piece bearing the claws. The movable bit is the apotele of the chelicerae.

ARTHRODIAL MEMBRANE. — The membrane by which two segments are connected; it is retracted or extended by the movements of the articulation.

ASCENDANT EVOLUTION. — An evolution starting at a base level and successively attacking one or more following stases.

ATELEBASIC RUTELLUM. — A large rutellum of which the base does not reach the plane of symmetry.

BASIFEMUR. — The proximal secondary segment of the femur. In leg I of *Opilioacarus* it is separated from the telofemur by a suture and several lyrifissures. In legs II-IV the separation is incomplete, and consists of two large lyrifissures only.

BASITARSUS. — The proximal secondary segment of the tarsus.

BASITIBIA. — The proximal secondary segment of tibia I.

BIVALENT ARTICULATION. — An articulation permitting of elevating as well as depressing. It is characterized by the presence of two tendons (a superior and an inferior) and a pair of medio-lateral condyles.

CAPITULAR APODEME. — The internal border of segment I (cheliceral frame) and segment II (infracapitulum) consisting of a reinforced lamella.

CEROTEGUMENT. — The superficial cement- and wax-like layers of the tegument, developed by exsudation through the cuticle.

CERVIX. — The dorsal wall of the infracapitulum.

CHELICERAL FRAME. — The epimere of the cheliceral segment. It is reduced to the coxal region of the chelicerae (and its derivates).

CHELICERAL GLAND. — A gland which is supposed here to debouch in *Opilioacarus* in the movable bit of the chelicerae.

CHELICERAL SHEATHS. — The coxae of the chelicerae, of which the tegument has developed into a flexible membrane which can be invaginated as well as protracted.

CHELICERAL TECTUM. — The roof of the cheliceral vault. It is attached to the cheliceral sheaths; laterally it is connected with the synaptic tectum.

CHELICERAL VAULT. — The room between cheliceral tectum and cervix.

CIRCUMBUCCAL SETAE. — The four pairs of curved setae which apparently guide the movements of lateral lips, With's organ, and rutellum.

COMMISSURE OF THE MOUTH. — The external point of a commissural line where two lips meet.

COMPOSITE SETA. — A seta consisting of an ornate base and a striate, solenidion-like terminal part.

CORNICULUS. — A horn-shaped paralabial seta.

COXAL VAULT. — The coxal region of the palp which posteriorly passes into the infracapitular vault.

DEPRESSOR MUSCLES. — Muscles attached to inferior tendons of the appendages.

DESCENDANT EVOLUTION. — An evolution starting with the highest level concerned, and successively attacking a number of lower stases.

DISJUGAL FURROW. — The dorsal furrow separating prosoma and opisthosoma.

ELEVATOR MUSCLES. — The muscles attached to the superior tendons of the appendages.

FLEXOR MUSCLES. — The muscles attached to the tendons of trochanter, genu, tibia, and tarsus.

GENAE. — The paired prolongation of the mentum, anteriorly of the coxal region of the palp. In Opilioacarida the genae are separated in the plane of symmetry by the anterior part of the subcapitular groove.

GENITAL VERRUCAE. — The pair of wart-like capsules, covering the entrance of the pregenital sacs.

GNATHOSOMA. — The buccal cone; it consists of cheliceral frame and infracapitulum.

INFRACAPITULAR GLANDS. — Paired, probably salivary glands, debouching in the dorsal part of the infracapitulum.

INFRACAPITULAR SETAE. — The epimeric setae of the infracapitulum; they are distinguished here into paralabial, circumbuccal, latero-dorsal, median, and ventral setae.

INFRACAPITULAR VAULT. — The room between dorsal and ventral wall of the infracapitulum (i.e. between cervix and mentum). It has a pharyngeal chamber, and a pair of coxal vaults.

INFRACAPITULUM. — The epimere of the palpal segment, containing pharynx, mouth, and lips.

LABELLUM. — In Opilioacarida a dorsal specialized part of the lateral lips.

LABIAL GLANDS. — Glands of unknown character, of which two pairs of ducts and orifices are visible in the lateral lips.

LABIO-GENAL ARTICULATION. — The articulation generally starting from the commissure *Ji*, and separating mentum and genae. It is often incomplete or absent; it is not present in Opilioacarida.

LABRUM. — The upper lip; its ventral wall is a prolongation of the dorsal inner wall of the pharynx; its base is attached to the cervix.

LATERAL LIPS. — The lips of which the inner wall is a prolongation of the lateral walls of the pharynx. The base of the lateral lips is attached to the genae.

LATERO-COXAL SETAE. — Specialized, partly reduced setae of the coxal regions or the free coxae of the appendages.

LYRIFISSURES. — Fissures in the tegument, externally characterized by small depressions, but separated from the open air by an uninterrupted epiostracum. The fissures generally widen; often a distinct room is present. In lyrifissures associated with articulations, the room continues into a long canal. In some groups of Arachnida, lyrifissures can be arranged in groups (lyriform organs). In mites they occur only isolated; the number varies from a few to a great many. Part of the lyrifissures are probably stress-sensitive organs.

MENTUM. — A part of the ventral surface of the infracapitulum. Anteriorly it passes into the genae. In the case of anarthry mentum and genae are continuous; the imaginary line separating the two, passes just in front of the palpal acetabula.

MONOVALENT ARTICULATION. — An articulation permitting of flexing and extending, but not of elevating. It is characterized by the presence of one tendon.

MOUTH. — The entrance to the pharynx. It can be defined by commissures or commissural lines which indicate the places where labrum and lateral lips are connected.

MUCRONATE SETA. — A seta provided with a distinctly separated terminal point.

OPISTHOSOMA. — The posterior part of the idiosoma. In Opilioacarida it presents lyrifissures in the dorsal, lateral, as well as ventral parts; in that way the opisthosoma differs from the prosoma where lyrifissures are found only in the sternal region. Prosoma and opisthosoma are separated by the disjugal furrow.

PAPILLIFORM SETA. — A broad, rounded seta, often provided with lobes and ribs. Part of the papilliform setae have a terminal point; in this way they resemble the mucronate setae.

PARALABIAL SETAE. — The specialized, more or less hypertrophied setae in the terminal part of the genae, close to the lateral lips.

PARAXIAL. — Used here for the side of an appendage (and its structures) facing the idiosoma (cf. antiaxial).

PEDOTECTAL LOBES. — Lateral lobes of the podosoma, dorsally of acetabula I, II, and III.

PHARYNGEAL CHAMBER. — The central part of the infracapitulum, separated by lateral walls from the coxal vaults. Posteriorly the chamber passes into the infracapitular vault. In *Opilioacarus* the chamber is little developed.

Pharynx. — The anterior part of the gut, functioning as suctorial apparatus. It is provided with a muscular wall. A transverse section can be triangular, quadrangular, or (in Opilioacarida) hexagonal.

Pregenital sac. — The internal sac of which the orifice is covered by a genital verruca (capsule).

Pregenital setae. — The setae in front of the genital orifice.

Pre-oral cavity. — The room in front of the mouth, enclosed by labrum, genae, and lateral lips.

Pretarsus. — The terminal part of the tarsus, characterized by the presence of an internal chitinous skeleton, functioning as articulation of the apotele.

Primary articulation. — An articulation provided with its own tendon(s).

Procurved. — Curved forward (⌣).

Prodorsal furrows. — The furrows laterally bordering the prodorsum. In *O. texanus* they are posteriorly connected with the disjugal furrow; anteriorly they do not distinctly reach the rostrum.

Prodorsum. — The dorsal part of the prosoma, distinctly bordered by disjugal and prodorsal furrows.

Prosoma. — The anterior part of the idiosoma. In *Opilioacarus* it is characterized by the absence of lyrifissures in the dorsal and lateral regions. It is separated from the opisthosoma by the disjugal furrow.

Pulvillus. — A small cushion, situated under and between the claws; dorsally as well as laterally and ventrally it is connected with the pretarsus.

Recurved. — Curved backward (⌢).

Retrotectum. — A tectum at the base of a segment of a leg, which protects the terminal part of the preceding segment.

Rostral lobe. — A terminal lobe of the prosoma, probably representing the precheliceral segment.

Rutellum. — A hypertrophied seta (one of the paralabial setae) in the terminal part of the genae. In *Opilioacarus* its ventral border is provided with relatively large, rounded teeth.

Scissure. — A transverse, segmental interruption of soft skin in a sclerotized area ("coupure").

Secondary articulation. — An articulation not provided with an own tendon (i.e. a tendon attached to the distal one of the two segments in question).

Sejugal furrow. — The furrow separating the coxisternal regions of legs I and II from those of legs III and IV. The furrow is not present in Opilioacarida and Anactinotrichida.

SM SETAE. — Setae consisting of an ornate base and a smooth, transversely striated distal part.

SOLENIDION. — A hollow seta without basal bulb. In Actinotrichida it is easily recognizable by the absence of actinopilin. In the remaining groups of mites this criterion is lacking. Identification, although not conclusive, must be based on a comparative study of shape and structure.

STASE. — The interval between two moults, as well as the animal itself during this period. Larva, nymphs, and adult are stases of an Opilioacarid.

STERNAL TAENIDIA. — The pair of open canals running apparently from coxa I (probably from the orifice of a coxal gland) to the subcapitular groove.

STERNAL VERRUCAE. — A pair of wart-like excrescences in the sternal region of leg II.

STERNAPOPHYSES. — A pair of apophyses, provided with setae, in the sternal region of leg I. They are generally orientated more or less parallel to the subcapitular groove.

SUBCAPITULAR GROOVE. — A longitudinal groove in the sternal part of the infracapitulum. It passes the mentum and separates the genae. The subcapitular groove probably is a taenidium; it is connected with the sternal taenidia.

SUBCHELICERAL EPIMERIC FURROW. — The transverse furrow representing the external border separating cheliceral frame and infracapitulum. Posteriorly it passes into the capitular apodeme.

SYNAPTIC TECTUM. — The tectum laterally connecting infracapitulum and cheliceral frame.

TAENIDIUM. — Collective noun for open canals at the surface of the body, which are in relation with stigmata, glands, or the mouth.

TELOTARSAL ORGAN. — A cavity in the antiaxial part of telotarsus I, with one hidden and one projecting solenidion (known from *Opilioacarus* only).

TELOTARSUS. — The terminal subdivision of the tarsus in leg I of *Opilioacarus*; in leg II-IV it is the secondary segment between basitarsus and acrotarsus.

TELOTIBIA. — The distal secondary segment of tibia I.

TENDON. — Connective band between terminal parts of muscle and e.g. base of segment. A tendon consists of material resisting lactic acid, whilst muscles are dissolved in this medium.

TRANSVERSAL ARTICULATION. — An articulation of which the main movements take place in a transverse plane (generally more or less the plane of pseudosymmetry of the segments in question).

Trochanter 1, 2. — The two primary segments which, in legs III and IV, take the place of one trochanter.

Universal articulation. — An articulation without condyles, permitting of movements in various directions (not restricted to a transverse plane).

Vertical evolution. — An evolution which has attacked all levels concerned at the same time.

Verticil. — A whorl of setae of the appendages. It is considered the basic element of leg chaetotaxy. A primitive verticil is supposed here to consist of seven setae: one dorsal, two latero-dorsals, two laterals (or latero-ventrals), and two ventrals.

With's organ. — A hypertrophied seta (one of the paralabials) in the terminal part of the genae. It consists of a base and a main body which has more or less the shape of a disc.

As appears from the list of synonyms, an attempt is made to bring some uniformity in Opilioacarid terminology. In order to render it more complete and precise, seventeen new terms are introduced in the present paper, viz., prodorsal furrow, sternal taenidium, sternapophysis, sternal verruca, genital verruca, pregenital sac, scissure, pedotectal lobe, labial gland, paralabial setae, circumbuccal setae, acrotarsus, telotarsal organ, monovalent, bivalent, universal, and transversal articulation; these terms are defined in the text as well as in the glossary.

ALPHABETIC LIST OF ABBREVIATIONS USED IN FIG. 1-21

am, arthrodial membrane.
ap. c, capitular apodeme.
at, capitular epimeric furrow.
AT II-III, dorsal apophyses of trochanter II-III.
B, internal, ventral boss in basitarsus.
bsa, border of smooth pregenital area.
c', *c"*, basidorsal cavities in telotarsus.
cb_{1-4}, circumbuccal setae.
CE, cervix.
ch, dorsal area of truncated palpal setae.
CH, chelicera.
Coxa III, IV →, direction of muscle bundles.
CV, coxal vault.
d, dorsal seta of appendages.
D_{1-10}, dorsal opisthosomatic muscle attachments.
dg, duct of infracapitular gland.
dj, disjugal furrow.
dr, median elevated part of cervix.
eI, *eII*, latero-coxal setae of legs I-II.
f, projecting solenidion of telotarsal organ.
f_{0-10}, intersegmental opisthosomatic furrows.
fl, terminal flap of arthrodial membrane.
G, gena.
gl, female accessory gland.
h, hidden solenidion of telotarsal organ.
H, mentum.
ibt", latero-dorsal lyrifissure of basitarsus.
ibv, ventro-distal lyrifissure of basitarsus.
id, dorsal lyrifissure of chelicera.
if", posterior lyrifissure of femur.
ite', *ite"*, basi-dorsal lyrifissures of telotarsus.
itr", antiaxial lyrifissure of trochanter I.
ivg, lyrifissure of genital verruca.

iα, antiaxial lyrifissure of chelicera and palpal tarsus.

iπ, paraxial lyrifissure of palpal tarsus.

Ji, ventral commissure of mouth.

Js, *Js'*, dorsal commissures of mouth.

k', *k''*, condyles.

l', *l''*, lateral setae of the legs.

$L_{x\text{-}z}$, lateral opisthosomatic muscle attachments.

LA, labellum.

ld', *ld''*, latero-dorsal setae of the legs.

$LD_{0\text{-}10}$, latero-dorsal opisthosomatic muscle attachments.

ldm, latero-dorsal infracapitular seta.

$LI_{c\text{-}a,\ 5\text{-}7}$, ventro-lateral opisthosomatic muscle attachments.

LL, lateral lips.

$LL_{1,\ 5\text{-}7}$, lateral opisthosomatic muscle attachments.

$LM_{1,\ 5\text{-}8}$, medio-lateral opisthosomatic muscle attachments.

LS, labrum.

$LS_{5\text{-}10}$, dorso-lateral opisthosomatic muscle attachments.

lv', *lv''*, (*lv*), latero-ventral setae of the legs.

$LV_{4\text{-}9}$, latero-ventral opisthosomatic muscle attachments.

lvm, latero-ventral median infracapitular seta.

lvp, latero-ventral posterior infracapitular seta.

$mb_{1\text{-}4}$, ventral muscle bundles.

og, genital orifice.

ogc, supposed orifice of cheliceral gland.

ogi, orifice of infracapitular gland.

$ogl_{1\text{-}2}$, orifices of labial glands.

OH, dorsal sensory area of telotarsus I.

ovp, ovipositor.

OW, With's organ.

p, latero-dorsal prominence of synaptic tectum.

PI-IV, coxae of legs I-IV.

pd, prodorsal furrow.

PH, pharynx.

pl, leaf-shaped setae of palpal tarsus.

$pl_{1\text{-}3}$, paralabial setae.

psa, border of smooth area of palpal tibia.

r_i, ventro-lateral ridge of opisthosoma.

r_s, dorso-lateral ridge of opisthosoma.

RE, concave light spot, laterally of rostral lobe.

RL, rostral lobe.

$rs_{1\text{-}2}$, supposed receptacula seminis.

RU, rutellum.

s, supposed solenidions of palpal tarsus.

SA, sternapophysis.

sg, subcapitular groove.

Sg, internal pregenital sac.

sk, ventral crossband of soft skin at base of anal tubercle.

sm, composite setae of palpal tarsus.

s.t, sternal taenidium.

st. 1-4, stigmata 1-4.

t, articulation-point of telotarsus.

t_i, inferior tendon of apotele.

t_s, superior tendon of apotele.

tb, muscle attached to dorsal wall of pharynx.

te, retrotectum of trochanter I and IV.

TE, cheliceral tectum.

tf_i, inferior tendon of femur.

tf_s, superior tendon of femur.

tg, tendon of genu.

$TL_{1\text{-}3}$, pedotectal lobes.

tr, transverse prodorsal furrow.

tr_i, inferior tendon of trochanter 2.

tr_s, superior tendon of trochanter 2.

tsa, border of telotarsal smooth area (leg I).

tta, tendon of tarsus.

tti, tendon of tibia.

ttr, tendon of trochanter.

v', *v''*, ventral setae of appendages.

$V_{2\text{-}10}$, ventral opisthosomatic muscle attachments.

Vg, genital verruca.

vm, medio-ventral infracapitular seta.

$vp_{1\text{-}2}$, postero-ventral infracapitular setae.

Vs, sternal verruca.

π'', supposed solenidion of femur IV.

φ', *φ''*, supposed solenidions of tibia I.

ω_a, supposed solenidion of acrotarsus II.

ω_d, supposed solenidion in dorso-distal part of basitarsus III.

ω_p, supposed solenidion of basitarsus.

1-13, infracapitular setae (Grandjean's notation).

I-XX, segments of the idiosoma.

SUMMARY

In the present paper a detailed description is given of *Opilioacarus texanus*, a species which had not been redescribed since the publication of its concise original diagnosis. The study is part of a comparative morphological investigation of all groups of mites, according to the same methods and principles. Special attention is paid here to the preparation of a complete set of illustrations; 21 figures together are the elements of a three-dimensional image of the species. The application of my methods to *Opilioacarus* resulted in the observation of several unknown or insufficiently studied structures. The following list is a concise summary of the main results.

1. Males, females, and nymphs can be distinguished by characters of the genital region, viz., the condition of the genital orifice, the number of pregenital setae, the presence of a genital sclerite, and the number of genital setae.
2. *Opilioacarus* is not as exclusively carnivorous as is supposed in literature. An important part of the food of *O. texanus* apparently consists of pollen grains.
3. Prosoma and opisthosoma can easily be distinguished because the dorsal and lateral prosomatic surfaces do not present lyrifissures. The furrow separating the two tagmata is the disjugal furrow.
4. A rostral lobe (in the anterior part of the prosoma) possibly represents the precheliceral segment. Laterally, it bears a pair of very interesting round spots of unknown character.
5. The number of opisthosomatic muscle attachments and lyrifissures is considerable. Their disposition reveals that the opisthosoma consists of fourteen segments. The number of segments of the idiosoma consequently is twenty, the highest number observed in Arachnida.
6. The stigmata are situated in four different segments, viz., the numbers IX-XII. The hypothesis is framed that the stigmata in Opilioacarida and Anactinotrichida belong to the same homologous series.
7. The capsules are named here genital verrucae; they bear a distinct resemblance to a pair of warts in the sternal region, which are consequently named sternal verrucae. It is not impossible that sternal and genital verrucae are homologous with Claparède's organ and genital papillae of Actinotrichida.
8. The eggs separated from a female specimen have a remarkable shape; they present a narrow, elongate process, and a blunt one. The function of these processes is unknown.
9. A pair of apophyses in the sternal region of leg I are named here sternapophyses; they are undoubtedly homologous with the furca (tritosternum) of many Anactinotrichida. This homology is a proof of the non-sternal character of the so-called tritosternum.
10. The hypothesis is framed here that lateral lips, sternapophyses, sternal verrucae, and genital verrucae are parts of one homologous series of sternal protuberances.
11. The lobes in the lateral part of the podosoma are considered here protections of the bases of the legs, for which reason they are named pedotectal lobes.
12. A cheliceral tectum, although small, is distinctly present.

The infracapitular setae are distinguished here into paralabials (specialized, hypertrophied setae), circumbuccals (curved setae which probably have a guiding function), medians, a latero-dorsal, and posteriors. The row of paralabial setae consists of two rutella and a corniculus. The presence of a pair of latero-dorsal infracapitular setae is considered here very important; they are also found in *Holothyrus*.

The subcapitular groove is connected with a pair of sternal taenidia which run from between coxa I and II to the sternapophyses; these taenidia are apparently in connection with coxal glands. In all probability, the subcapitular groove is also a taenidium.

A pair of infracapitular (probably salivary) glands debouch at the dorsal surface of the infracapitulum.

A subcapitular epimeric furrow and a capitular apodeme are distinctly present; they are the external and internal ventral border of segments I and II.

Although the mouth is triangular, a transverse section of the pharynx soon becomes hexagonal, partly because of the attachment of a pair of dorsal muscles.

Two pairs of ducts and orifices of labial glands are present in the lateral lips.

13. The chelicerae are characterized by the presence of one seta on segment 1, and three setae on segment 2. Because the articulation between segment 1 and 2 presents two medio-lateral condyles and two tendons (tf_s and tf_i), segment 1 is supposed here to be the trochanter. Because the movable bit is the apotele, segment 2 consequently is a fusion of femur, genu, tibia, and tarsus.

14. The palp presents an apotele with two distinct claws. The tarsus of the palp presents a variety of setae belonging to five different types.

15. The primary segments of the leg are named here: coxa, trochanter (trochanter 1 and 2 in the case of leg III and IV), femur, genu, tibia, tarsus, apotele. The secondary segments are named: basifemur, telofemur; basitibia, telotibia (both in leg I only); basitarsus, telotarsus, acrotarsus (in leg II-IV only), pretarsus.

A survey is given of the various primary articulations. Three main types are distinguished here: universal (no condyles, several muscles), bivalent transversal (two condyles, two tendons), and monovalent transversal (one tendon).

There is a great variety of secondary articulations; a total of seven types are distinguished here. Primary and secondary articulations are surveyably arranged in two tables. A description is given of the supposed way of moving of apotele and secondary tarsal segments by the two tendons of the apotele.

The chaetotaxy of the legs presents still an important number of complete verticils of seven setae (one dorsal, two latero-dorsals, two laterals, and two ventrals).

The setae of the legs belong to different types: papilliform, mucronate, *sm* (ornate base, striate distal part), solenidions. It is not impossible that solenidions as well as mucronate setae originate from *sm* setae.

Part of the distal setae of the tarsus (especially a number of ventrals and laterals) are birefringent. Investigations in this field should be continued.

16. Because my two nymphs are still relatively large, it is probable that at least three nymphal stases are present.

17. In a survey of all known species of Opilioacarida, a new genus *Adenacarus* is created for *Eucarus arabicus* With; *Panchaetes* Naudo is raised from subgeneric to generic rank. In this way four genera are distinguished. The eight known species are compared, and a key will facilitate their identification.

18. A number of remarks explain and survey some general problems, viz., segmentation, subdivision of the body, tegument, ventral protuberances, infracapitular setae, primary and secondary segments of the appendages and articulation, latero-coxal setae, leg chaetotaxy, and post-embryonic ontogeny; the remarks illustrate my ways of approaching various problems.

19. The distinguishing characters of Opilioacarida are listed, and a survey is given of the characters which this group has in common with respectively *Holothyrus*, Anactinotrichida, and Actinotrichida. This survey results in the maintenance of a subdivision of the mites into three groups, although Opilioacarida demonstrate a closer relationship to Anactinotrichida (especially to *Holothyrus*).

20. A summary is given of the most important remaining problems in order to stimulate continued research in Opilioacarida.

21. A summary is also given of the various hypotheses which underly part of the present paper. Attention is called to the special importance of hypotheses in general for the development of a science.

22. All synonyms of morphological terms occurring in literature on Opilioacarida are listed, together with the names used in the present paper. A glossary contains the definitions of the terms suggested here to be used henceforth in descriptions of Opilioacarida; seventeen new terms are introduced.

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1) Although the journal is apparently issued in 1904, the reprint mentions 1903 as date of publication. Awaiting further evidence, the former date is cited in the present paper.