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STRAY NOTES ON ACARIDA (ARACHNIDA) I

by

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Since 1964 I have been publishing a series of extensive descriptions and morphological studies of various groups of mites. Although this type of work is rather time-devouring, it enlarges our knowledge considerably as to structures hitherto generally neglected. At the same time, however, we must not lose our broader view on the Acarida as a whole: the analytical investigations should be supplemented by synthetic work. For this reason, I used to add to my descriptions a number of remarks on subjects of general importance. It now appears that this way of publishing does not keep pace with the development of my views. A number of stray observations and opinions did not come off, and had to wait a long time before being included in an appropriate study. For this reason, the present series of notes is started, which has the advantage that it can be composed in restricted spaces of time, and which is meant to fill up the gaps left by the larger studies. The first part of the series, which is published here, deals already with various subjects; these subjects relate to practically al orders of mites.

A. Preliminary redescription of *Allothyrus constrictus* (Domrow)

In 1961, in a study of the Holothyrida, I created the genus *Allothyrus* with *Holothyrus constrictus* Domrow as type. Although at that time I had not yet seen the species, the original description sufficiently demonstrated its separate systematic position. In a survey of relationships and differences between Opilioacarida, Holothyrida, and Gamasida (Van der Hammen, 1966), I pointed to the necessity of a redescription of the type-species of *Allothyrus*, because several important characters of this interesting genus

were still unknown. Shortly afterwards, Dr. R. Domrow (Queensland Institute of Medical Research, Brisbane, Australia) kindly offered me to send three specimens of the species for study. It is a pleasure to me to express hereby my sincere thanks to Dr. Domrow for the valuable opportunity to study the species, and for his permission to completely dissect one of the three specimens. Although I had not yet enough time for a complete redescription, it appeared useful to study a number of details, and to publish a description of those characters of which the knowledge is of immediate importance to the classification of mites. I hope to publish a more complete redescription in my series of Further Notes on the Holothyrida.

Material, locality, and date. — Mt. Nebo, S.E. Queensland, Australia, October 1964; rain-forest humus; leg. Dr. R. Domrow: two males, one female. The present description is based mainly on the female, which is nearly completely dissected.

Habitus and colour. — In dorsal view, the species has more or less the habitus of a Gamasid mite. In ventral view, it is at once recognizable as Holothyrid because of (a) the projecting dorsal shield and the bordering plicature band, (b) the sternum presenting a sternal groove, (c) the concave epiandrium of the male, (d) the presence of taenidium I and 2, and (e) the presence of stigma 2 which is situated in a concave area.

The colour is rather light-brown; there is no trace of subcuticular pigment grains. The small setae are whitish; part of them (e.g. the dorsals) are papilliform.

Cerotegument. — When a species is observed on a carbon block, a rather large quantity of white, fine-grained cerotegument appears to be present on the ventral surface. Dorsally, this layer is of irregular thickness and mixed with some adhering dirt. On the legs, rather large quantities are present in the terminal part.

Cuticle. — When studied on a carbon block, the sculpture of the cuticle appears to consist of irregularly distributed tubercles and granulate interspaces. Each tubercle bears a small, whitish papilla. There are numerous pores between the tubercles. In transparent light, the lower layer of the cuticle (the lower layer of the ectostracum, or the endostracum) appears to be porous; the structure appears as a punctate layer under the superficial sculpture. In the male, there are a dorsal and a holoventral shield. In the female the ventral surface consists of sternal, ventral, and exopodal shield.

Dorsal shield. — The dorsal shield presents, at the level of legs III and IV, two oval, rather large, slightly concave areas without tubercles or setae. These are probably muscle attachments of the chelicerae.

Lateral view. — The region of stigmata and tracheae is represented in fig. 1A. Stigma 1 (st. 1) is situated rather far posteriorly, above the anterior part of coxa IV. It has a large taenidium or peritreme (t. 1) which extends in anterior and posterior direction; this taenidium is relatively broader and shorter than in *Holothyrus*. The bottom of the taenidium is covered by a thick layer of cerotegument of special structure, as represented in fig. 1A. Taenidium 2 (t. 2) is similar to that in *Holothyrus*; it runs dorsally of, and parallel to taenidium 1. Stigma 2 (st. 2) is very small.

Ventral face. — Above, I mentioned already that the ventral surface of the male consists of a holoventral shield; the epiandrium is distinctly concave. After warming in lactic acid, the female ventral surface can easily be separated into a sternal, an exopodal, and a ventral shield. The sternum is divided by intersegmental areas into three segments. These areas are characterized by the absence of setae; they are nearly not sculptured. Intersegmental area 1, situated between coxae I and II, is concave, and corresponds with the sternal groove of Holothyrus. Intersegmental area 2, situated between coxae II and III, is hardly concave; it shows a pair of lyrifissures. Intersegmental area 3 (posteriorly of coxae III) partly borders the genital area. The segments are characterized by the presence of numerous setae. A study of the internal face of the sternal shield demonstrates that the intersegmental areas correspond with transverse, internal lamellae or ridges; these, consequently, are apodemes. There are two sternapophyses (fig. 2A: SA), just as in Opilioacarus. They are inserted separately in the soft skin, just anteriorly of the sternal shield. In ventral view, the place of insertion is difficult to distinguish, because of a difference of level: the shield is slightly higher (in ventral view) than the soft skin. The sternapophyses lack setae; their shape is long, narrow, and tapering.

Posteriorly, the female exopodal shield presents a narrow fusion with the ventral shield. The female genital area consists of four rather large shields; these are represented by Domrow (1955: fig. 1A).

The ventral shield is especially interesting because of the presence, at both sides, of a remarkable structure, described by Domrow (1955: 160,

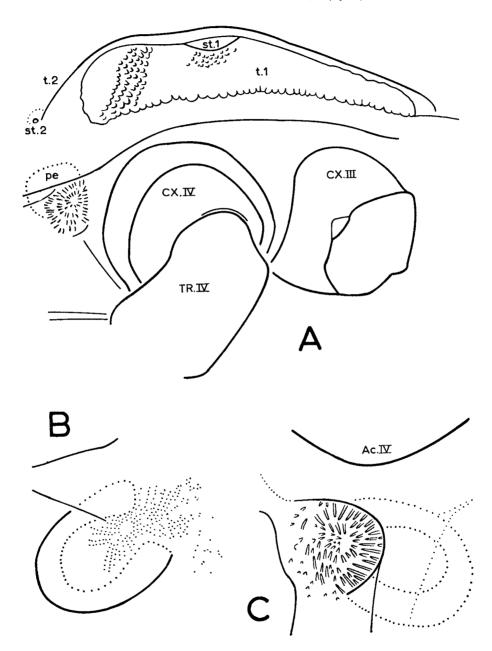


Fig. 1. Allothyrus constrictus (Domrow), female; A, lateral part of idiosoma with taenidia and stigmata, and parts of legs III and IV; B, right peridium, internal view; C, right peridium, ventral view; A, \times 235; B, C, \times 490.

fig. 1K) as "a sub-spherical pit with aperture guarded by heavy brush of fine setae". This structure is represented by me in various orientations in fig. 1A-C. It appears that it consists of a chitinous sac attached to the ventral shield, and distinctly protruding into the body cavity. The sac is named here peridium (pe). The wall of the peridium is remarkably heavy; the orifice is rather wide. Orifice as well as surrounding part of ventral shield are beset with numerous papillae. The function of the two peridia is completely unknown; they occur in both sexes. Although their position is slightly different (just posteriorly of coxa IV, instead of paraxially), they remind of the genital papillae of Opilioacarus (cf. Van der Hammen, 1966), of which the function is also unknown; they lack, however, the cover (genital verruca), instead of which they present an aperture with numerous papillae. The position of the sac reminds of the position of the stigmata in Ixodidae (not in Argasidae); the function, however, cannot be respiratory because of the heavy wall. For the same reason the sac is certainly also no gland. A study of the contents, as well as a further comparison with Opilioacarus, will be interesting.

Gnathosoma. — A ventral view of the gnathosoma in retracted position in the camerostome is represented in fig. 2A. Mentum and genae are not separated. A distinct subcapitular groove is present. There are many more infracapitular setae than in Holothyrus. In the figured specimen the number of these is 26; the setae are not all symmetrically arranged. It is not easy to compare them with the setae of Holothyrus or Opilioacarus. The adaptation of the Holothyrus notation to Allothyrus should be considered provisional. The following setae are distinguished in the figured specimen: $va_1, va_2, lva, vm_1, vm_2, vm_3^*, lvm, vp_1, vp_2, lvp_1, lvp_2, lvp_3, lvp_4, lvp_5^*$ (an asterisk points to the presence at one side only). The corniculi are rather long; they lack the lateral tooth characteristic of Holothyrus. The ventral part of the lateral lips, i.e. the laciniae, are a continuation of the anterior part of the genae. They are rather long and tapering, and beset with rather long papillae; consequently, they are strongly different from the laciniae in Holothyrus. Laterally, the infracapitulum presents a rounded apophysis (β) corresponding with an apophysis (α) on the trochanter of the palp. After separation of the gnathosoma from the idiosoma, it appears that a subcapitular apodeme is indeed present in Allothyrus; it consists of a pair of lateral pieces, pointed in the posterior part, which are easily separated from the mentum, a large tendon is attached to their posterior border. The apodeme apparently has no median part. A subcapitular apodeme should be considered homologous with an apodeme I (attached to

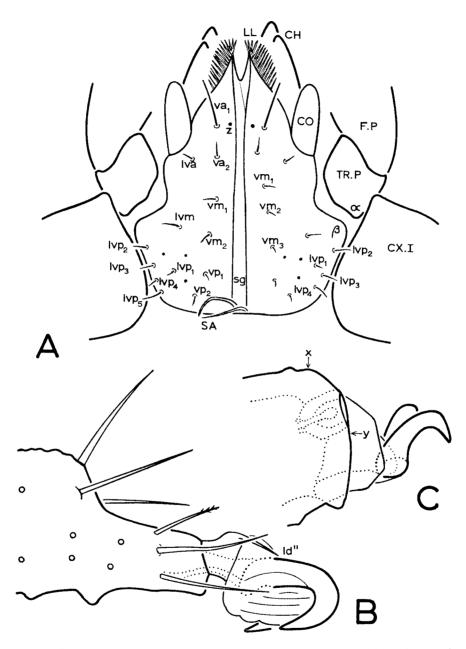


Fig. 2. Allothyrus constrictus (Domrow), female; A, ventral view of gnathosoma in camerostome; B, distal part of tarsus and apotele of one of the posterior legs, lateral view; C, lateral (antiaxial) view of distal part of right leg I (setae omitted); A, \times 235; B, C, \times 490.

the idiosoma); the first apodeme of the sternal shield in *Allothyrus* is apodeme 2. The presence of a subcapitular apodeme is probably connected with the fact that the gnathosoma does not turn along a basal transverse axis, but can be extended (protracted) as a whole. This is apparently a special character of the Holothyrida.

The labrum is not radula-shaped as in *Holothyrus*, but long and tapering, and beset with papillae. There is a laterodorsal infracapitular seta *ldm*, just as in *Holothyrus* and *Opilioacarus*; it is strong and curved. There is a pair of dorsal orifices of infracapitular glands in the cervix, posterolaterally of the base of the labrum; consequently these have the same position as in *Opilioacarus* and Oribatida. The two cheliceral grooves are separated by a ridge which, above the base of the labrum, ends in a point. There are apparently no paralabral teeth.

Chelicera. — The chelicerae bear two dorsal setae, situated in segment 2; consequently, they differ from the chelicerae of *Holothyrus*, which present only one dorsal seta. A dorsal lyrifissure *id* is situated between the two setae; there is also an antiaxial lyrifissure *ia*. The jaws of the chelicerae have one anterior tooth and a pair of posteriors.

Palp. — The palp has no fringed seta on the genu, and no paraxial group or comb of stiff setae on the tibia. The tarsus presents a dorsal area of hollow setae; the terminal sensory seta (u according to my 1961 notation) is curved, and flattened in the terminal part. The apotele bears a tripartite "claw".

Legs. — Leg I is remarkable for more than one reason. It is not divided into basi- and telotarsus, but it presents a terminal secondary segment which reminds of the terminal segment of the palp in Ixodidae. The subdivision is complete. The secondary segment is named here apicotarsus; its presence is apparently a unique character of *Allothyrus*. The apicotarsus is represented in fig. 2C. The terminal part of the main, basal division, here named bathrotarsus, presents two sensory areas. There is one area with a great number of hollow setae, which in fig. 2C (the setae are not drawn) extends from x to y. These hollow sensory setae, which occur dorsally and antiaxially, are differently shaped; several are long and curved. Close to the dorsal sensory area, there is an antilaterodorsal capsule of which the orifice is in the terminal part of the bathrotarsus. It contains one clavate solenidion, whilst two sensory setae are inserted on the border of its orifice. These two sensory setae have a broadened distal part; one of them is dorsal and slightly paraxial, the other ventrally of the orifice and slightly antiaxial. The capsule reminds of the capsule of the ticks. Below, in section B, I return to the phylogeny of the two sensory areas.

Legs II-IV present basi- and telotarsus; there is also a short pretarsus with a strong and remarkably curved inferior tendon t_1 of the apotele, and one pair of laterodorsal pretarsal setae (*ld*) (fig. 2B). These laterodorsals (probably mainly consisting of an epiostracum) are reduced; an alveolus, a central core, and a basal bulb are not distinctly recognizable, and it is only by comparison with *Holothyrus* and *Opilioacarus* that we can interpret them as setae. I return to this important observation in section C of this paper.

Diagnostic characters of the genus *Allothyrus.* — No subcuticular pigment grains. Sternal region of the segment of leg I with two separate sternapophyses. Ventral shield with a pair of peridia, posteriorly of coxa IV. Infracapitulum with a great number of infracapitular setae, among which more than one pair of va, vm, vp, and lvp. Corniculi without lateral tooth. The ventral part of the lateral lips has the shape of a pair of laciniae. Subcapitular apodeme consisting of a pair of separate lateral, posteriorly pointed chitinous pieces. Labrum not radula-shaped, but tapering, and beset with papillae. Paralabral teeth apparently absent. Chelicerae with two dorsal setae. Palp without fringed seta on genu, and without paraxial group or comb of stiff setae on tibia. Leg I divided into bathrotarsus and apicotarsus; bathrotarsus with two terminal sensory areas, of which one consists of a capsule with a hidden solenidion. Pretarsi II-IV with a pair of reduced laterodorsal setae.

Systematic position. — Without doubt, *Allothyrus* is a representative of the Holothyrida. Apart from its general habitus, especially in ventral view, the following characters point to this relationship: the absence of specialized sternal setae; the presence of two pairs of stigmata and two pairs of taenidia; the shape of male and female genital area; the presence of numerous anal setae; the presence of a subcapitular apodeme; the shape of some terminal setae of the palp.

The genus has also a number of characters in common with both *Holo*thyrus and *Opilioacarus*. I point to the presence of a great number of infracapitular setae; the presence of infracapitular seta *ldm*; the shape of the tegulum (i.e. the structure formerly named cheliceral tectum; cf. Van der Hammen, 1968) which is anteriorly not produced; the presence of an area with hollow setae on the dorsal surface of the palpal tarsus; the presence of distinct pretarsal setae. Allothyrus has the following characters in common with Opilioacarus only: the presence of a pair of sternapophyses; the presence of more than six pairs of infracapitular setae; the presence of more than one pair of setae on the principal cheliceral segment. Besides, the bathrotarsal capsule is possibly homologous with the telotarsal organ, the peridium with the pregenital sac.

The genus Allothyrus reminds of the Gamasida because of the shape of laciniae and labrum.

A comparison between *Holothyrus* and *Allothyrus* on the one hand, and Ixodida on the other, should be subject of further studies. The presence of Haller's organ, and several other characters point to a distinct relationship between the two groups.

Summarizing our data, our conclusion is that *Allothyrus* is a characteristic representative of the Holothyrida, which demonstrates (sometimes even more clearly than *Holothyrus*) distinct relationships with Opilioacarida on the one hand, and Gamasida and Ixodida on the other.

B. THE PHYLOGENY OF HALLER'S ORGAN IN ANACTINOTRICHIDA

Above, in the section on Allothyrus constrictus (Domrow), I described two sensory areas in the terminal part of the bathrotarsus. One of these sensory areas is a capsule with a hidden, clavate solenidion, and two sensory setae near the entrance; the other a dorsal group of hollow setae. The capsule is antiaxial; it reminds on the one hand of the telotarsal organ of Opilioacarus, on the other of the capsule of the ticks. In Opilioacarus, the telotarsal organ consists of an antiaxial cavity or capsule with two solenidions, of which one is clavate and completely hidden, the other setiform and partly extending. Opilioacarus has, moreover, a dorsal area of sensory setae in the terminal part of the tarsus (cf. Van der Hammen, 1966: 40, fig. 15E, 16A, C). When comparing fig. 2C of the present study with fig. 16C of my 1966 paper, it is obvious to suppose that the capsules of Opilioacarus and Allothyrus are homologous, just as the dorsal sensory areas, and that only the mutual position of the two areas has changed: in Allothyrus the capsule has advanced in distal direction; it is now situated close to the dorsal sensory area. In Holothyrus (cf. Van der Hammen, 1961: 192, fig. 8a, b; 1965: 269, fig. 9C, D) the two sensory areas have apparently both become dorsal.

The condition in *Holothyrus* is distinctly recognizable as Haller's organ, as was already mentioned by me in 1961. This throws a new light on the phylogeny of Haller's organ in ticks. It appears plausible to suppose that in Ixodida, this organ consists of two parts of different origin. The capsule

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could be derived from a telotarsal organ, the trough from the original dorsal sensory area. Prolonged investigations in this field would be very interesting, just as a further study of the sensory area of leg I in Gamasida.

C. On the origin of the paradactyli of Macrochelidae and other Gamasida

The presence of pretarsal setae is considered a special character of Opilioacarida and Holothyrida (cf. Van der Hammen, 1966: 61); two pairs of pretarsal setae are found in *Opilioacarus* (cf. Van der Hammen, 1966: fig. 21A-C), one pair in *Holothyrus* (cf. Van der Hammen, 1961: fig. 9a-c). Pretarsal setae have been thought to be absent in Gamasida and Ixodida.

This view, however, has become less probable because of the presence in *Allothyrus* of pretarsal setae (one pair of laterodorsals; the position corresponds with that in *Holothyrus*) which apparently lack a central core, a basal bulb, and a corresponding alveolus. The pretarsal setae evidently can become reduced (just as the laterocoxal setae). It may be wondered therefore whether the structures described by me as paradactyli in *Glyptholaspis confusa* (Foà) (cf. Van der Hammen, 1964: 32, fig. 19A-D) and apparently present in various other Gamasida are also reduced and specialized setae (the anterior and posterior paradactyli would be part of one laterodorsal seta). This would mean that the occurrence of pretarsal setae is not a special character of Opilioacarida and Holothyrida, but of Opilioacarida and Anactinotrichida. The problem should be subject of further studies; especially observations on ticks will be very important.

D. The genital tracheae of the female of *Gohieria fusca* (Oudemans)

Oudemans (1928: 348) was the first to mention the occurrence of tracheae in *Ferminia fuscus* (now *Gohieria fusca*). According to his concise note, he observed two unbranched trunks; in his opinion these did not originate from the "pseudostigmatic organ", but he was inclined to believe that they represented genital tracheae. From the text it is not evident whether the two trunks represent two tracheae of one pair, or two tracheae of one side. However, according to an unpublished drawing (no. 1580, apparently prepared about 1928, and now present in the Rijksmuseum van Natuurlijke Historie, Leiden), Oudemans supposed to observe two pairs of tracheae: one running in anterior direction, another in posterior, the latter extending

to the genital region (although its exact relation to this region is not drawn).

Grandjean (1937: 280) cited the supposed existence of genital tracheae in *Ferminia fuscus*, although he remarked that he had not studied the species himself.

Apparently, A. M. Hughes (1948: 70, fig. 95) was the first to mention with certainty the occurrence of genital tracheae in the female (not in the male) of *Gohieria fusca*. Later (1961: 137, fig. 186), she repeated her description and drawing, and added a new observation: in fresh specimens the tracheae are full of air. This observation was published shortly before by T. E. Hughes (1959: 200, pl. 52 fig. 5). According to the last-mentioned author, Grandjean (1934a) should be of the opinion that the genital tracheae of *Gohieria* are no true tracheae; Hughes refers to this paper under a wrong title. In the study in question, however, mention is made only of the genital tracheae of *Haplochthonius, Cosmochthonius*, and *Cyta*, but not of *Gohieria*; the tracheae are considered true tracheae. T. E. Hughes's remark evidently is without any foundation.

Description and figure by A. M. Hughes, nor those by T. E. Hughes are very distinct as to the orifice of the tracheae. Their figure (a specimen in dorsal view, in which the tracheae are visible by transparency) shows the bases of the tracheae as nearly contiguous, debouching into a very small common slit. According to the drawing there is also a transverse connection between the two tracheae, in the posterior part of the opisthosoma.

In order to represent the genital tracheae of *Gohieria fusca* in a way that enables a comparison with the condition in Cosmochthoniidae, Haplochthoniidae, and Bdellidae, a new figure is prepared here after material kindly put at my disposal by Dr. D. A. Griffiths, Pest Infestation Laboratory, Slough, Buckinghamshire, England; this material originates from a culture. It is a pleasure to me to express hereby my sincere thanks to Dr. Griffiths for his valuable contribution to my investigation.

In fig. 3A, B the tracheae are represented. Fig. 3A (the genital region in ventral view) demonstrates that there is one pair of genital tracheae, debouching into the pregenital chamber. Each trachea branches into an anterior part (which ends in a large caecum) and a long, winding posterior part which gradually narrows towards the end. The posterior parts cross, and this probably led A. M. Hughes to the drawing of a mutual connection. The crossing of the two tracheae (tr, tr') is represented in fig. 3A as well as in fig. 3B (a lateral view of the tracheae). Fig. 3B shows also the characteristic bend of the anterior branch.

The figure demonstrates that the genital tracheae of Gohieria correspond

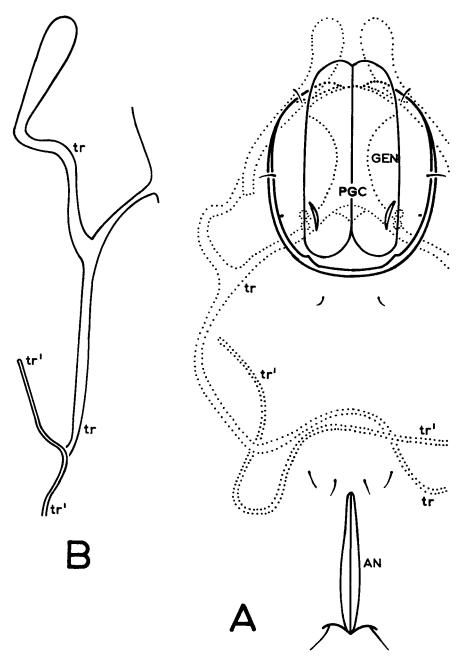


Fig. 3. Gohieria fusca (Oudemans), female; A, ventral view of genital region with genital tracheae and anal orifice; B, lateral view of genital tracheae; A. B, \times 350.

with the posterior pair of tracheae (tr.p) of Haplochthonius and Cosmochthonius. It is remarkable that in Haplochthoniidae and Cosmochthoniidae the posterior trachea tends to become reduced. In cases where only one pair of tracheae exists (Amnemochthonius, Bdellidae), it is the anterior which has persisted. In Gohieria no trace of an anterior trachea is present, although the pregenital chamber is widened in the anterior part. This is an interesting difference between Gohieria and the other groups mentioned above.

In section E, I return to the possible origin of the genital tracheae.

E. PROVISIONAL CLASSIFICATION OF RESPIRATORY ORGANS IN MITES

Recently, in a paper on *Opilioacarus*, I introduced the hypothesis that the four pairs of stigmata of Opilioacarida, the two pairs of Holothyrida, and the single pair of Gamasida and Ixodida are parts of one homologous series (cf. Van der Hammen, 1966: 52, 62); this series is opisthosomatic. Consequently, the condition in Anactinotrichida would be a simple and surveyable one. In contradistinction to this, the condition in Actinotrichida is much more complicated and heterogeneous, because various types of stigmata are present in the three suborders. For a clear comprehension of the relationships between the large groups of mites, and even between these groups and other orders of Arachnida, a general survey of respiratory organs would be an important contribution. For that purpose the following provisional classification is introduced here.

1. Opisthosomatic series. The stigmata are supposed to have developed from lyrifissures (cf. Grandjean, 1935: 207, fig. 3A; Van der Hammen, 1966: 16, fig. 4F). The greatest number is present in Opilioacarida (four pairs, with a dorsal or laterodorsal position).

Two pairs are present in Holothyrida: one pair of large, oval stigmata above coxa III (*Holothyrus*) or coxa IV (*Allothyrus*); and one small, round stigma posteriorly of coxa IV. Both stigmata are lateral, although stigma 2 is situated in the dorsal shield. Stigma 1 is connected with a tracheal trunk, stigma 2 with a system of sacculi.

One pair of stigmata is present in Gamasida and Ixodida. These stigmata are generally situated laterally, above coxa II, III or IV (Gamasida, Argasidae); in Ixodidae, however, they have a ventral position, posteriorly of coxa IV. Stigma I of Holothyrida and the single pair of stigmata of Gamasida and Argasidae are undoubtedly homologous. The homology of the pair of stigmata of the Ixodidae is, however, doubtful; above (in section A) I pointed to the remarkable fact that the peridium of *Allothyrus* has nearly exactly the same position.

2. Genital tracheae. Oudemans (1906) was the first to discover the presence of genital tracheae; his observations were based on *Cyta*. Genital tracheae are now known from several Bdellidae (cf. Grandjean, 1938: 6); from *Cosmochthonius* (cf. Grandjean, 1962: 408, fig. 3D), *Haplochthonius* (cf. Grandjean, 1947: 231, fig. 2B, 3A, F), *Amnemochthonius* (cf. Grandjean, 1948: 33, fig. 1B, C, D, 2A); and from *Gohieria*. These tracheae consequently occur in all three orders of Actinotrichida. There can be two pairs (an anterior and a posterior) or one pair. The conditions in Bdellidae and Enarthronota are related: when one pair is reduced or has disappeared, it is always the posterior pair. In *Gohieria*, however, only a posterior pair is present.

Apparently, the genital tracheae are segmentally arranged organs. They are supposed here to originate from accessory glands. In Pseudoscorpionida segmentally arranged accessory glands can develop into trachea-like organs (cf. Vachon, 1938: 58, 108; Grandjean, 1944: 168). Possibly, a similar evolution has given rise to the genital tracheae in Actinotrichida.

3. Various respiratory organs supposed to originate from porose areas; this series can be subdivided into the following groups.

a. An axillary series (a name suggested by Prof. Grandjean during our annual conference in Genève in 1966). The stigmata are on the line of articulation of the appendages and their coxal region; their position is paraxial. They are found at the base of the chelicerae (Prostigmatida; cf. Grandjean, 1938a), at the base of the palp (*Eupelops*; a brachytrachea, cf. Grandjean, 1936: 91, fig. 10A), and in the acetabula of a number of legs (the higher Oribatid mites).

b. Respiratory organs starting from superficial parts of the cuticle. This group consists of sacculi, brachytracheae, and tracheae, on notogaster and legs.

c. Respiratory organs starting from hidden depressions of the surface, such as bothridia, preanal fold, apodemes.

The respiratory organs of section 3 are described in detail by Grandjean (1934); those of groups b and c apparently occur only in Oribatid mites. It will be interesting to prepare a survey of the postembryonic ontogeny of all respiratory organs mentioned above. The respiratory organs of the Tarsonemini are not included in the above-mentioned classification. Apparently they do not fit into one of the sections. I have not yet studied a representative of this group; the existing descriptions do not permit of a definite interpretation.

F. On the classification of Prostigmatida

Recently, on account of my study of the podocephalic canal (cf. Van der Hammen, 1968), Grandjean wrote to me that it would be interesting to prepare a general table of the Actinotrichida, dividing the groups into two categories according to the external or internal condition of the podocephalic canal. This would indeed be an important study, of particular interest to the classification of the Prostigmatida, an order regarded as heterogeneous, and subdivided in an unsatisfactory way. Other generally neglected characters, very important for the subdivision of this group, would be the numbers of active stases and calvptostases or elattostases which form part of a postembryonic ontogeny. A third group of characters, up to now apparently not used in studies on Prostigmatid classification, is found in the number of segments that are paraproctal in the course of a postembryonic ontogeny, especially in the number of postlarval segments. In many Prostigmatida the anal orifice is bordered by the pseudanal segment PS (of larval origin); in more primitive species, however, the protonymph can add an adanal AD, the deutonymph an anal AN, and the tritonymph even a peranal segment PA. One or more posterior opisthosomatic segments consequently can have disappeared by vertical evolution.

On account of the above-mentioned characters, the Prostigmatida can be arranged in the following groups.

Group I. Endeostigmata. Larva, protonymph, deutonymph, tritonymph, and adult are active stases; one of the nymphal stases, however, can be absent (*Alicorhagia fragilis* Berlese, and some *Bimichaelia* species, according to Grandjean, 1942b: 134). The podocephalic canal is external. According to data published by Grandjean (1939: 17), there are three postlarval opisthosomatic segments (Terpnacaridae and some Pachygnathidae) or two (*Alicorhagia, Pachygnathus trichotus* Grandjean); the adult anal orifice is consequently bordered by PA or AN.

The Endeostigmata apparently constitute a heterogeneous group, showing transitions to groups 2 and 3.

Group 2. Bdellidae, Tydeidae, Caeculidae, Anystidae. Larva, protonymph, deutonymph, tritonymph, and adult are active stases. The podocephalic canal is external or internal (but attached to the tegument). The adult anal orifice is bordered by PS (Tydeidae, cf. Grandjean, 1938b: 1856), or AD (Caeculidae, Anystidae, Bdellidae ad part.; cf. resp.: Coineau, 1963: 207; Grandjean, 1943: 71; 1938: 21); the occurrence of AN in some Bdellidae is uncertain (cf. Grandjean, 1938: 21).

The present group is certainly heterogeneous.

Group 3. Raphignathoidea, Tetranychoidea, Cheyletoidea. Larva, two nymphs, and adult are active stases; a third nymph is apparently absent. The podocephalic canal is superficial. The adult anal orifice is in some cases known to be bordered by PS (cf. Grandjean, 1944a: 110); possibly, this is a general condition of the group.

The three superfamilies are apparently related.

Group 4. Labidostommidae. The larva is an elattostase; protonymph, deutonymph, tritonymph, and adult are active stases. The podocephalic canal is internal. The adult anal orifice is probably bordered by *PS*, although this is not certain because the anal region of the larva is glabrous (cf. Grandjean, 1942: fig. 1B; 1942a: fig. D-F): deuto- and tritonymph at least do not add further segments.

Group 5. Parasitengona. Larva, deutonymph, and adult are active stases; protonymph and tritonymph are calyptostases. The podocephalic canal is internal. It is as yet impossible to interpret the ontogeny of the paraproctal segments.

In this survey, the Tarsonemini and Tetrapodili are not taken into consideration. In the first-mentioned group, only larva and adult are active stases. The post-embryonic development of the Tetrapodili is still more complicated. None of the characters mentioned above is clearly investigated in the two groups. It is, moreover, doubtful whether the Tarsonemini can be classified with the Prostigmatida; possibly they constitute a separate order Tarsonemida.

A comparison of existing classifications and the present grouping, together with a further investigation of the above-mentioned characters in related families, will probably result in a more satisfactory classification of the Prostigmatida. Although the suborder as a whole appears to be rather heterogeneous, all of its groups (Tarsonemini excepted) appear to be related to each other in one way or another. Actinotrichida should be considered a superorder of which the orders (or at least two of them) are very closely related as to their primitive representatives. The evolution of these orders, however, has proceeded in distinctly different directions; consequently, they represent different groups of evolutionary trends.

G. On the systematic position of the Opilioacarida

As mentioned above in section A, a study of the genus *Allothyrus* clearly demonstrates the distinct relationship between Opilioacarida on the one hand, and Holothyrida, Gamasida, and Ixodida on the other. In

section B, I have demonstrated that the telotarsal organ of *Opilioacarus* is probably homologous with the capsule of Haller's organ in *Allothyrus* and ticks. In section C, I pointed to a possible homology of the paradactyli of the Macrochelidae and other Gamasida with pretarsal setae. These observations add a number of important characters to the list of those characters which Opilioacarida have in common with Anactinotrichida (cf. Van der Hammen, 1966: 60-64).

The differences between Opilioacarida and Actinotrichida are considered more important since my study of the podocephalic canal (Van der Hammen, 1968). The presence of this canal is an essential character of the lastmentioned group. *Opilioacarus* has no podocephalic canal, but the coxal glands debouch into sternal taenidia which are connected with the subcapitular groove.

As mentioned in section E (cf. also Van der Hammen, 1966: 52, 62), the respiratory system of *Opilioacarus* is thoroughly different from the various types found in Actinotrichida.

When we consider the list of characters in common between Opilioacarida and Actinotrichida, we must conclude that the greater part of it refers to primitive characters. Because no really primitive species are known among Gamasida and Ixodida, the list consequently can be misleading. For this reason, the following characters of Opilioacarida should now be regarded as probably primitive, and not demonstrating a relationship with Actinotrichida: the soft cuticle; the presence of pigment grains under the cuticle; the presence of a rostral lobe, a disjugal furrow, and one or two pairs of rutella; the position of the pair of orifices of infracapitular glands.

From this it follows that the position of the Opilioacarida as separate group, showing relationships with Anactinotrichida as well as with Actinotrichida, is no longer maintainable. In my opinion, Opilioacarida should henceforth be classified with the Anactinotrichida, in which superorder they have an outstanding position because of their important number of primitive characters.

Alphabetic	LIST	OF	ABBREVIATIONS	USED	IN	FIG.	1-3
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Ac. IV, acetabulum IV.	LL, lateral lips.			
AN, anal orifice.	lva, anterior lateroventral infracapitular			
CH, chelicera.	seta.			
CO, corniculus.	lvm, median lateroventral infracapitular			
CX.I-IV, coxa I-IV.	seta.			
F.P, femur of palp.	lvp_{1-5} , posterior lateroventral infra-			
GEN, genital valves	capitular setae.			
ld", posterior laterodorsal seta (of	pe, peridium.			
pretarsus).	PGC, pregenital chamber.			

SA, sternapophyses.

sg, subcapitular groove.

st. 1-2, stigmata 1-2.

- t. 1-2, taenidia 1-2.
- tr, tr', right, resp. left (genital) trachea.

TR. P, trochanter of palp.

TR. IV, trochanter IV.

- va₁₋₂, anterior ventral infracapitular setae.
- vm_{1-3} , median ventral infracapitular setae.

 vp_{1-2} , posterior ventral infracapitular setae.

- x, y, posterior, resp. anterior border of sensory area of tarsus I.
- z, supposed vestige of infracapitular seta.
- α , apophysis (condyle) of palpal trochanter.
- β , lateral apophysis (condyle) of infracapitulum.

Summary

The present paper is the first part of a series of stray notes on various acarological problems. In this first part the following subjects are dealt with, and the following conclusions are drawn.

I. A redescription is given of *Allothyrus constrictus* (Domrow), an Australian representative of the Holothyrida. This species is characterized by the presence of a chitinous sac (named here peridium) of unknown function, posteriorly of coxa IV. It is further characterized by the presence of sternapophyses, of a great number of infracapitular setae, and of two dorsal cheliceral setae. Leg I is subdivided into a bathrotarsus and a very small terminal apicotarsus. Haller's organ is present in the dorsal terminal part of the bathrotarsus. *Allothyrus constrictus* demonstrates relationships to Opilioacarida as well as to Gamasida and Ixodida.

2. In a section on the phylogeny of Haller's organ, the hypothesis is framed that the two parts of this organ are of different origin, one part (the capsule) being homologous with a telotarsal organ, the other part (the trough) with a dorsal sensory area.

3. The paradactyli of the Macrochelidae and other Gamasida are supposed to be homologous with laterodorsal pretarsal setae.

4. A description is given of the genital tracheae of *Gohieria fusca* (Oudemans), of which the exact connection with the pregenital chamber was still unknown.

5. The respiratory organs of mites are provisionally classified according to homology; three groups are recognized: (1) an opisthosomatic series, (2) genital tracheae, and (3) respiratory organs originating from porose areas; the last mentioned group is subdivided into (a) an axillary series, (b) respiratory organs starting from superficial parts of the cuticle, and (c) respiratory organs starting from hidden depressions of the surface.

6. In a contribution to the classification of the Prostigmatida, the families are arranged according to the condition of the podocephalic canal; to the number of active stases and calyptostases or elattostases forming part of a postembryonic ontogeny; and to the number of segments that are paraproctal in the course of a postembryonic ontogeny.

7. The systematic position of the Opilioacarida is discussed anew. This group is now regarded as definitely belonging to the Anactinotrichida.

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