A REVISED CLASSIFICATION OF THE MITES (ARACHNIDEA, ACARIDA) WITH DIAGNOSES, A KEY, AND NOTES ON PHYLOGENY

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With 1 text-figure

INTRODUCTION

In 1961 I published a paper on a species of the genus *Holothyrus*, in which I paid also some attention to the general classification of the mites. Before that time I had chiefly studied Oribatid mites, and I was surprised by the neglect of important discoveries made in the field of Oribatid morphology by specialists of other groups. I realized that a comparative study of acarid morphology was badly needed, and that this could be the only base for a satisfactory general classification.

I continued and developed this idea, and in the course of ten years I investigated, in a more or less detailed way, representatives of all groups of mites. In this way I published papers on Opilioacarida (Van der Hammen, 1966, 1968a, 1968b, 1969b, 1971), Holothyrida (1961, 1965, 1968a), Gamasida (1964a), Ixodida (1964), Oribatida (1968), Actinedida (1968a, 1969), Tarsonemida (1970), and Acaridida (1968a). In the same period I published a series of papers on general problems in the field of comparative morphology, ontogeny, phylogeny, and classification (Van der Hammen, 1962, 1963, 1964b, 1968a, 1968c, 1970a, 1970b, 1970c). In addition a small paper was published dealing with some morphological problems in Palpigradida (Van der Hammen, 1969a).

The results of this period of comparative study were summarized in a paper read at the Third International Congress of Acarology (Van der Hammen, 1972). In the present paper the subject is treated at greater length, especially by adding detailed diagnoses; the addition of a key for the identification of superorders and orders (although still in its experimental stage) will contribute to the practical value of the system of classification.

The present paper is composed in the following way. In a first section the important problem of mono- or polyphyletic origin of the mites is dealt with. This is followed by sections on the distinguishing characters of the two superorders, on the systematic position of the Opilioacarida, and on affinities with other groups of Arachnidea. The subdivision of the two superorders is treated in two sections. Subsequently, the nomenclature of superorders and orders is discussed. The phylogeny of the mites is also dealt with in a separate section. The paper is concluded with diagnoses, a key, a summary, and a list of literature cited in the text.

The problem of mono- or polyphyletic origin

The problem of classification and phylogeny of the mites starts with the problem of their monophyletic or polyphyletic origin. In order to solve this first problem we must begin with a reconsideration of the characters by which the mites as a group, a subclass, are distinguished. This concerns only two characters: the presence of a gnathosoma, and the occurrence of a larva with only three pairs of legs. The latter character is not present in all mites, because the number of legs can (in rare cases) be further reduced, whilst in Holothyrida the larva appears to be still unknown. Apart from mites, a hexapod larva is also known from Ricinuleida, in which group this character has certainly developed by parallel evolution. The absence of a fourth pair of legs in the larva must be regarded as a regression of the posterior part of the prosoma, and is comparable with the regression of the number of posterior opisthosomatic segments in Actinotrichida. It is possibly connected with the small size of the larva, and could in the two superorders of mites, recognized here, have developed by parallel evolution.

In order to arrive at a more definitive conclusion on mono- or polyphyletic origin, it will evidently be necessary to consider the gnathosoma. In a recent study on the phylogeny of the Opilioacarida and their affinities with other groups of mites (Van der Hammen, 1971: 472), I pointed to a very important difference between Anactinotrichida and Actinotrichida (the two superorders into which the mites are subdivided here). In Actinotrichida, the gnathosomatisation (i.e. the development, in the course of evolution, of a gnathosoma) is connected with the development of a podocephalic canal (originally external, but in some groups secondarily internal) which runs from the podosoma to the dorsal surface of the infracapitulum, ventrally of the bases of the chelicerae. This canal carries the products of several glands, among which some can apparently be characterized as coxal [1] (cf. Grandjean, 1968; Prasse, 1968). In Opilioacarida, i.e. in primitive Anactinotrichida, the coxal glands (cf. With, 1904) debouch into a pair of sternal taenidia (in the sternal region of the first pair of legs) which unite between the sternapo-

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[1] The coxal glands mentioned by Wainstein (1965) for Hydrachnei (= Hydrachnellae) debouch in the epimera.

physes, and continue into the sternal taenidium of the infracapitulum (a groove which generally has been called deutosternum or hypostome).

When we compare the phylogenies of podocephalic canal and sternal taenidia, we must arrive at the conclusion that in a theoretical common ancestor of Anactinotrichida and Actinotrichida, sternal taenidia as well as podocephalic canal must both have been absent; this, however, at the same time means that the gnathosoma of this (theoretical) ancestor was still at the beginning of its evolution, and this ancestor itself still at the very beginning of its evolution as a mite. This leads to the conclusion that, in reality, the gnathosoma of mites is the result of parallel evolution, which means that the two groups of mites have, independently, developed a gnathosoma out of homologous parts. In a recent study of the phylogeny of the gnathosoma (Van der Hammen, 1970c), I have indeed demonstrated that this phylogeny must have been different in the two superorders, especially as to the phylogeny of the tegulum which in Anactinotrichida extends more or less horizontally in forward direction. Evidently, the subclass of the mites is not of monophyletic origin, and a further study of the distinguishing characters of the two superorders will underline its biphyletic nature.

DISTINGUISHING CHARACTERS OF THE TWO SUPERORDERS OF MITES

Anactinotrichida can be distinguished from Actinotrichida by a number of characters, of which I mention here the following.

(1) The stigmata belong to a homologous opisthosomatic series: four pairs in Opilioacarida, two or three pairs in Holothyrida (two pairs is the general number for this group but, according to unpublished investigation by Mrs. Athias-Henriot, a third pair is present in a New Zealand species of *Allothyrus*), and one pair in Gamasida and Ixodida.

(2) The setae present no birefringent axis of actinopilin.

(3) The genital opening consists of a transverse fissure that secondarily can be covered by a number of shields.

(4) A sternum and free coxae are generally present.

(5) There is no sejugal furrow or interval separating legs II and III.

(6) There are often sternapophyses (or their homologues) situated in the sternal region of the first pair of legs.

(7) Primitively the coxal glands debouch into sternal taenidia; there is no podocephalic canal.

(8) The chelicera generally presents a dorsal lyrifissure beside an antiaxial.

(9) The palp often presents apotelic claws or homologues of apotelic claws.

(10) There are apparently no trichobothria.

(11) The femur of the legs is generally subdivided into two parts (basi- and telofemur) by a secondary articulation associated with lyrifissures.

(12) The tarsus of the legs often presents secondary articulations. Generally, there is a basi- and a telotarsus, although this subdivision is often lacking in the case of leg I. (It may be remarked, however, that a number of Prostigmata present also a secondary subdivision of the tarsus).

(13) The legs present several lyrifissures besides those associated with secondary articulations.

(14) The pretarsus sometimes presents setae or rudiments of setae.

Actinotrichida, when compared with Anactinotrichida, differ by the following characters.

(1) The tracheae (when present) belong to two groups: (a) there are genital trachea in some representatives of three of the four orders in which the superorder is subdivided here; and (b) there are often tracheae, in several regions of the body, which have probably developed from porose areas of the cuticle.

(2) The setae present an actinopilinous axis.

(3) Originally, there are six pairs of prodorsal setae.

(4) The primary genital opening is trifid; it often debouches into a progenital chamber which extends over three segments; in that case, the secondary genital opening is longitudinal.

(5) There is a podocephalic canal into which primitively debouch three pairs of glands.

(6) There are no free coxae and no sternum, but generally there are epimera or coxisternal regions.

(7) There is a sejugal furow or interval.

(8) The chelicera presents no dorsal lyrifissure.

(9) The palp presents no apotelic claw (and no apotele).

(10) There are often trichobothria on idiosoma and appendages.

(11) In case the femur consists of two parts, this concerns primary segments, connected by a primary articulation which is not associated with lyrifissures.

(12) The legs present a characteristic basic chaetotaxic pattern which, in principle, permits of the recognition of a number of homologues in all four orders.

(13) There is a maximum of one lyrifissure on each of the appendages.

(14) Regressive stases (calyptostases as well as elattostases) are rather common.

When we compare these two lists now, we can easily see that they are nearly exclusively composed of characters which cannot be arranged in pairs of homologous origin. Evidently, this means that the fundamental differences in the two groups of mites concern differences between groups of a high category, differences referring to strongly diverging evolutions of the general plan of construction of the Arachnidea.

THE SYSTEMATIC POSITION OF THE OPILIOACARIDA

The Opilioacarida, here classified with the Anactinotrichida, are still regarded as a separate (third) group by several authors. It will be important to deal here in short with their relationships. Opilioacarida have a number of characters in common with Actinotrichida, which are rarely or not found in other groups of Anactinotrichida. This concerns: (1) the soft cuticle; (2) the presence of pigment grains under the cuticle (although these also occur in species of *Holothyrus*); (3) the presence of a rostral lobe (although different from a naso); (4) the presence of a disjugal furrow; (5) the shape of one of the paralabial setae, which functionally is a rutellum, although it is homologous with the corniculus of Holothyrida and Gamasida; (6) the position of the paired orifice of the infracapitular glands in the cervix, just as in some Actinotrichida; (7) the birefringency of some tarsal setae, although their true nature has not been studied; (8) the rapid backward gait, when trying to escape danger; (9) the occurrence of autotomy.

As mentioned before, some of these characters indeed occur in some other Anactinotrichida (or are homologous with other Anactinotrichid characters); others (such as autotomy and rapid backward gait) are functional characters which can be the result of convergence, or are of uncertain value (such as the birefringency or some setae). The remaining characters are ancestral ones which have no decisive value in a classification, the primary importance being that of shared possession of secondary characters.

Special value is attributed here to the important series of characters which Opilioacarida share with Holothyrida; of these characters I mention the following: (1) the infracapitular setae are numerous; although they are slightly variable in number, the basic pattern is in all cases the same, so that the same notation can be applied to both groups, a notation different from that of other Anactinotrichida; of special value is the occurrence of laterodorsal infracapitular setae, unknown from other groups of mites; (2) the tegulum is not prolonged into a supracheliceral limb (i.e. into a structure generally named tectum or epistome) (but this structure is also absent in *Uropodella*, a primitive genus of Gamasida); (3) the large lateral lips surround the preoral cavity ventrally as well as laterally and partly dorsally; they are hardly subdivided into specialized parts (only a dorsal labellum can be recognized); (4) the apotelic claw of the palp is easily recognizable as such; (5) the palpal tarsus is characterized by the presence of a dorsal area with hollow setae; (6) the pretarsus bears one or two pairs of true setae.

In my opinion the distinct relationship between Opilioacarida and Holothyrida justifies the classification of the former with Anactinotrichida. Opilioacarida constitute in fact the most primitive group of this superorder, a group of which the morphology is of considerable value for the comprehension of Holothyrida, Gamasida and Ixodida.

Affinities with other groups of Arachnidea

A better comprehension of the biphyletic origin of the mites could be obtained by comparison with other groups of Arachnidea. Data in literature, however, are not sufficient for this purpose, because many details need reinvestigation. I point, for instance, to the problem of the identity of the first segment of the appendages; it is very important for us to know whether this is a coxa or a trochanter. In one case recently reinvestigated by me (Van der Hammen, 1969a: 44), that of chelicera and palp of the Palpigradida, the first segment appeared to be a trochanter, although it had been named coxa in literature. In some groups of Arachnidea the occurrence of free coxae and a sternum has become complicated because of the secondary enlargement of the coxae in medial direction, at the cost of the sternum. This process has, by many authors, been misunderstood as the only process of sclerotization of the ventral surface. In reality it has not occurred in mites. Other important problems in this connection are: (1) the possible homology of the sternapophyses with certain apophyses in Scorpionida, Amblypygi, and Opilionida; (2) the formation, in some higher developed groups, of a chitinous tube at the base of the acetabula, which does not represent the original coxa 1); (3) the recognition of laterocoxal setae, which are often reduced and can often only be understood in a comparative study 2). It seems that

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1) These tubes, absent in primitive species, are apparently connected with shifting of their circumtrochanteric opening.

2) Latero- or supracoxal setae (cf. Grandjean, 1962: 401) are known from all groups of Actinotrichida. They were discovered in Opilioacarida by Grandjean (1936: 430, fig. 4); I paid special attention to them in my study of *Opilioacarus texanus* (cf. Van der Hammen, 1966: 38-40, 57-58, figs. 3, 6D). This case is very important because, although the setae are reduced to a very small, thin and flat structure (probably consisting nearly exclusively of epiostracum, and probably without root), they are still distinctly

such groups as Ricinuleida and Opilionida are more related to Anactinotrichida, whilst Palpigradida could be related to Actinotrichida. It seems that Actinotrichida are more strongly different from most other groups of Arachnidea than is the case with Anactinotrichida. This, however, are merely opinions. What we need, in reality, is a new comparative morphological investigation of all groups of Arachnidea. In fact, comparative Arachnid morphology is our fundamental problem, the study of which is the condition for further conclusions on Acarid morphology.

Subdivision of the Anactinotrichida

After these observations on the two superorders of mites, we shall now proceed with the subdivision of each of these groups. As mentioned before the Anactinotrichida are subdivided here into four orders: Opilioacarida, Holothyrida, Gamasida, and Ixodida. It appears that any attempt to arrange these four orders into two groups, is artificial. Opilioacarida constitute the group with the greatest number of ancestral characters; as mentioned above, they are at the same time distinctly related to Holothyrida. *Allothyrus*, a genus of Holothyrida, shows even more close relationships with Opilioacarida (it is characterized by the presence of a pair of sternapophyses, more than one pair of setae on the principal cheliceral segment, several infracapitular setae which are lacking in *Holothyrus*, and in the New Zealand species three pairs of stigmata). On the other hand, *Allothyrus* shows distinct relationships with Gamasida (because of the development of the lateral lips). According to recent, unpublished investigations by Mrs. Athias-Henriot, some striking correspondences exist between Holothyrida or Opilioacarida, and Ichthyostomastogasteridae, a family of Gamasida, mainly South American in distribution; of these I mention the absence of a supracheliceral limb (*Uropodella*), and the presence of a rutellum-shaped corniculus together with the ingestion of solid food (*Asternolaelaps*). Evidently the four orders of Anactinotrichida are all distinctly related, although separated from each other by distinct discontinuities.

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mucronate, by which their setal nature is proved. Their position is the base for homologization of laterocoxal setae in Gamasida (Van der Hammen, 1964a). Evans & Till (1965: 201) disputed this interpretation on account of their discoveries in Dermanyssidae. A generalization of data observed in highly specialized and parasitic species only is not in accordance with the principles of comparative morphology. At the same time these authors did not mention the most important argument, i.e. the presence of distinct laterocoxal setae in Opilioacarida.

Supracoxal setae were also described from Palpigradida (Van der Hammen, 1969a: 42, 44, fig. 1 A, C); in this case, a fused pair of supracoxal setae was recognized above the base of the chelicerae; it is the only known case of supracoxal setae of the chelicerae; beside these, supracoxal setae were found in this group above the base of the palp.

The four orders of Anactinotrichida are very unequal in size. Opilioacarida comprise only one family Opilioacaridae. I now distinguish two families of Holothyrida, viz., Holothyridae and Allothyridae fam. nov. [1]). Gamasida are here subdivided, according to data published and communicated by Mrs. Athias-Henriot (1968, 1969, 1969a, 1971), into six suborders. Antennophorina, Liroaspina, Uropodina, Zerconina, Parasitina, and Dermanyssina. The order Ixodida is subdivided here into two suborders: Ixodina and Argasina.

Subdivision of the Actinotrichida

In the course of several morphological investigations of groups of Actinotrichida, I arrived at a recognition of four orders which I named Actinedida, Oribatida, Acaridida, and Tarsonemida. Although authors nowadays use to classify Tarsonemida with Trombidiformes or Prostigmata, I have recently separated them from this group (Van der Hammen, 1970: 23). (The remainder of Trombidiformes or Prostigmata corresponds with my Actinedida). The presence of ambulacra with primitively two claws and a pulvillus, the small number of opisthosomatic segments (VII-XII), and the presence of a single pair of stethosomatic stigmata, constitute characters which remove Tarsonemida from Actinedida and Oribatida. The Tarsonemid ambulacrum reminds of that of many Acaridida because of its pulvillus, whilst the number of opisthosomatic segments apparently is the larval number of Acaridida (as far as this is known). The shape of some Tarsonemid solenidia reminds of that of several Acaridida. Unpublished stereoscan micrographs of the palp of a Tarsonemid recently described by me show a striking similarity to the palp of the Acaridida.

Actinedida and Oribatida constitute two groups which are for the greater part very distinctly and very widely separated; some of their primitive representatives, on the contrary, are very closely related. Sometimes it seems even difficult to delimit the two groups at their bases. Within each group, however, the species show distinct relationships, so that there can be no doubt as to their classification. In a recent paper (Van der Hammen, 1969: 193) I enumerated a number of characters which serve to distinguish primitive Actinedida from Oribatida. Some of these characters apply to all or nearly all Actinedida, others have only a restricted validity; all of them, however, can serve to distinguish Actinedida from Oribatida. It concerns the following characters: (1) a rostral tectum is absent, and the naso (if present) extends

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[1]) Allothyridae fam. nov. This family consists of the genus *Allothyrus* only, and its diagnosis is that of the genus; the distinguishing characters, among which the number of stigmata, are here considered of fundamental importance.

unprotected between the chelicerae; (2) the prodorsum often has two pairs of bothridial setae; (3) although there can be opisthosomatic microsclerites, a notogaster or gastronotal sclerite is not present; (4) the femora can present solenidia; (5) the claws can present tenent hairs; (6) the median claw can, in some or in all stases, be replaced by an empodium; (7) the number of nymphs tends to be reduced.

The four orders of Actinotrichida could be arranged in two cohorts: one comprising Actinedida and Oribatida, the other comprising Acaridida and Tarsonemida. I have not named these groups here because, in my opinion, it is still too early for it.

Actinedida are preliminarily subdivided here into six suborders: Alycina (= Endeostigmata), Bdellina (Eupodoidea, Tydeoidea, Cunaxoidea, Halacaroidea), Labidostommina (Labidostommidae), Anystina (Caeculoidea, Anystoidea; Raphignathoidea, Tetranychoidea, Cheyletoidea), Phytoptina (= Tetrapodili), Trombidina (Trombidei = Parasitengona, Hydrachnei). The subdivision of the Oribatida is dealt with by Grandjean (1954, 1965, 1969). I have not yet studied the subdivision of Acaridida and Tarsonemida; a classification of the former was published by Yunker (1955).

NOMENCLATURE OF THE SUPERORDERS AND ORDERS

A few words must be added on the nomenclature used here for the superorders and orders. These names are not submitted to the Code of Zoological Nomenclature. Nevertheless, the names chosen here partly represent the oldest available names. This concerns the names Holothyrida Thon (1905), Gamasida Leach (1815), Ixodida Leach (1815), Oribatida Dugès (1833), Acaridida Latreille (1802), Tarsonemida Canestrini & Fanzago (1877): of these names, the original endings only have partly been corrected. The name Opilioacarida Zakhvatkin (1952) is preferred here instead of Notostigmata With (1904) for the sake of uniformity. The name Actinedida was recently introduced by me (Van der Hammen, 1968b: 405) for two reasons: (1) for the sake of uniformity, and (2) in order to avoid misunderstanding (the group having received a new interpretation, without Tarsonemida). Because of the great variety within the group, I have looked for a name without any sense. I have chosen the generic name *Actineda* as root, which just as *Oribata* (the root of Oribatida) is no more in use, and of which the translation has not much meaning. As far as ordinal names are concerned, I have rejected the names ending with stigmata. When these names were reintroduced (Evans, Sheals & Macfarlane, 1961), they were for the greater part no more in general use; they are also far from being the oldest available names, and they include several incorrect meanings (some

Tetrastigmata have six stigmata; several Prostigmata have no stigmata or they have genital tracheae; many Cryptostigmata have no stigmata; and some Astigmata have genital tracheae). In fact this nomenclature has numerous disadvantages, and not a single advantage.

As to the names Anactinochaeta and Actinochaeta, sometimes used instead of Anactinotrichida and Actinotrichida, these must be regarded as incorrect when applied to mites only, because Zakhvatkin (1952) introduced the name Actinochaeta for a group of Arachnid orders, among which Actinotrichida.

PHYLOGENY OF THE MITES

My views on the phylogeny of the mites are illustrated by the dendrogram of fig. 1. This scheme represents the mites as biphyletic. The dotted vertical line in the centre of the drawing represents the archetype (i.e. a synthetic

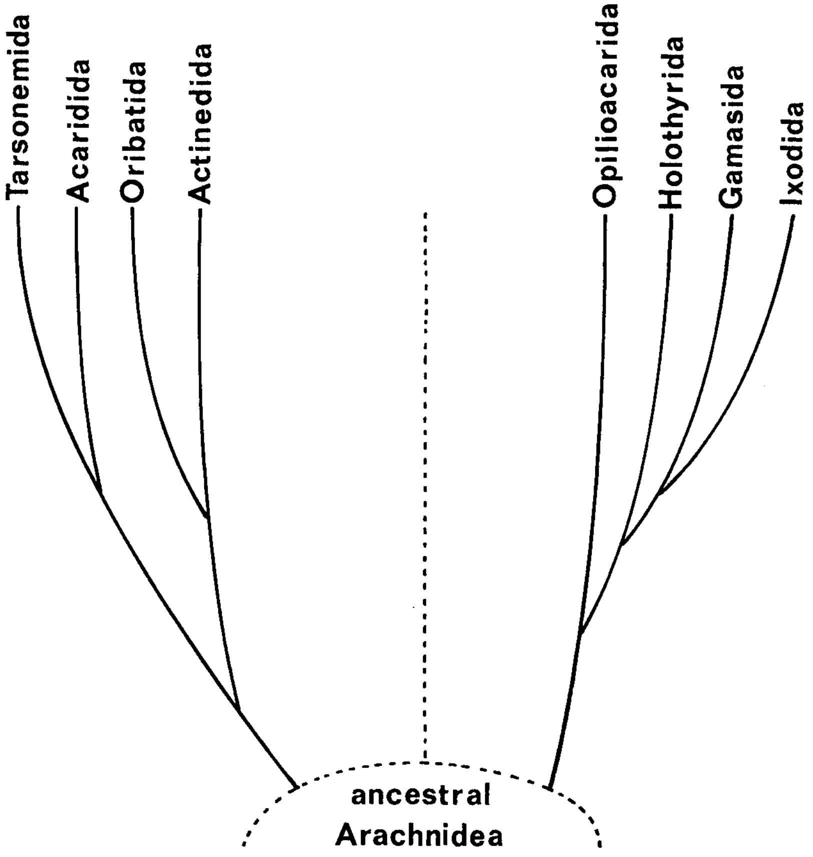

Fig. 1. Dendrogram representing the phylogeny of the mites.

combination of ancestral characters), used here as standard of reference. Because comparative Arachnid morphology is still insufficiently known, the archetypical values and the average divergence of the orders are mere estimations. In a further stage of the investigation, this will pre-eminently be a numerical problem. The Opilioacarida are supposed (in the dendrogram) to have not very much diverged from the ancestor of the Anactinotrichida. I have supposed that Gamasida and Ixodida can be derived from the ancestral line of the Holothyrida. The distribution of Opilioacarida and Holothyrida is more or less Gondwanian. The closest representatives among the Gamasida, according to unpublished investigations by Mrs. Athias-Henriot (as mentioned above), are species belonging to the Ichthyostomastogasteridae, a family of which the main centre is in South America. Consequently, the origin of the Anactinotrichida could be Gondwanian. As to the phylogeny of the Actinotrichida, the recognition of two groups is also represented in the dedrogram. It is supposed that primitive Actinedida are closest to the common ancestor of the Actinotrichida.

The dendrogram illustrates at the same time schematically the present state of my investigations of evolution and comparative morphology. It represents only a stage in the development of acarology. As mentioned before, one of the most important subjects is now the study of comparative Arachnid morphology. Besides, a further elaboration of Acarid morphology, especially a study of Ixodida and Acaridida in comparison with other groups of mites, is also a subject with a high priority. Our glossary of acarological terms, which is now in an advanced state, will certainly be an important contribution to this comparative study. The results of all these subjects together, will close a first round in the study of classification and phylogeny.

DIAGNOSES OF SUPERORDERS AND ORDERS

The distinguishing characters of the two superorders and of the eight orders are summarized in the following diagnoses.

Superorder Anactinotrichida

The stigmata (one to four pairs) belong to a homonomous opisthosomatic series. The ordinary setae have no birefringent axis of actinopilin. The idiosoma can present a considerable number of lyrifissures or their derivates. The genital opening is a transverse fissure that secondarily can be covered with a number of sclerites. As a rule there are free coxae and a sternum. There is no sejugal furrow or interval; the distance between the pairs of legs II and III is not larger than the distance between I and II, and III and IV. The sternal region of leg I presents in many cases a pair of sternapophyses or an unpaired sternapophysis which is the result of a fusion of the two (sternapophyses are not known from the genus *Holothyrus*, and from Ixodida). Beside a lateral (antiaxial) lyrifissure, the chelicera has also a dorsal one. The palpal tarsus (when present) is relatively small; palpal tarsus and tibia together often have the shape of one segment, or have fused. The palp often presents apotelic claws or homologues of these. There are no trichobothria. Generally, the femur of the legs is (sometimes indistinctly) subdivided into two parts (basi- and telofemur) by a secondary articulation associated with compound lyrifissures. As a rule the tarsus of the legs presents one or more secondary articulations; generally there is a basitarsus and a telotarsus, although in numerous cases this subdivision can be absent in leg I. The legs present several lyrifissures beside those associated with secondary articulations. Sometimes, the pretarsus bears setae or their homologues. As a rule the ambulacrum presents a pulvillus; generally it has two claws.

Order Opilioacarida

The body is built up of nineteen segments (irrespective of prechelicerals), among which thirteen distinctly recognizable opisthosomatic segments; owing to this, and because of the relatively very long legs, Opilioacarida have a superficial resemblance to small harvestmen. There are two or three pairs of eyes, and four pairs of stigmata (in segments IX-XII); stigma 1 is of tritonymphal origin, stigmata 2 and 3 of protonymphal, and stigma 4 of deutonymphal. The number of opisthosomatic lyrifissures is sometimes considerable. The opisthosomatic segments are separated by furrows, at the interior side of which numerous muscles are attached. The anal opening is situated at the end of an anal tubercle which can be retracted. The genital region is characterized by the presence, laterally of the genital opening, of a pair of genital papillae which can be evaginated; at rest they are each covered with a vaulted cover (genital verruca). There is a pair of sternapophyses. The tegulum is not prolonged into a supracheliceral limb (a supracheliceral limb is a thin border situated above the chelicerae and functioning as protective roof). The infracapitulum presents, close to the anterior border, three pairs of paralabial setae which, as a rule, are specialized or hypertrophied: a small corniculus, With's organ (in *Paracarus* a forked seta), and a rutellum. Four pairs of circumbuccal setae and a rather great number of remaining infracapitulars (among which at least one pair of laterodorsals) are situated posteriorly of the paralabials. Although the mouth is triangular, the pharynx behind it soon develops an outline which is hexagonal in cross-section. The chelicera presents 0-1 seta on segment 1 (the trochanter) and 3-4 setae on segment 2 (in all remaining groups of mites this number is apparently smaller). The palpal tarsus presents a striking paradorsal area, closely beset with hollow setae. The legs present important numbers of setae, more or less arranged in verticils (linear cosmiotrichy). Two tarsal solenidia are sunken and constitute the telotarsal organ. Pretarsi II-IV each present two pairs of setae. Legs III and IV present two trochanters. The postembryonic development (as far as known) comprises five stases: larva, protonymph, deutonymph, tritonymph, and adult; the tritonymphs are sexed (male and female tritonymphs are distinctly recognizable).

Order Holothyrida

There are, as a rule, two pairs of stigmata, of which the anterior and larger one is connected with tracheae, the posterior smaller with a system of air sacs; each of the stigmata is connected with a lateral groove, a taenidium; according to Mrs. Athias-Henriot (in litt.), *Allothyrus australasiae* (Womersley) presents three pairs of stigmata. The idiosoma presents one dorsal shield covering the complete dorsal surface, and overlapping the ventral shield; the latter shield presents very small, irregularly scattered hairs. Eyes are not present. The anal shields present a good many (at any rate more than two) setae. The genital opening of the female is covered with four shields; that of the male is situated in a distinctly differentiated region (the epiandrium), and it is covered with two shields. There is a sternal groove in the anterior part of the sternum. There are no special sternal setae in a fixed number. Paired sternapophyses are present in *Allothyrus*. The gnathosoma is covered with a rostral tectum. The tegulum is not prolonged into a suprachelicerал limb. The infracapitulum has no capitular apodeme, but a subcapitular in the produced part of the mentum. There are many infracapitular setae, among which one pair of laterodorsals and one pair of corniculi. A cross section of the pharynx is quadrigonal. The chelicerae are long; they consist of three segments. The palp presents paraxially, at the base of the tarsus, a transformed bi- or tripartite apotelic claw. Palpal tarsus with a striking paradorsal area, closely beset with hollow setae. Legs with a great number of setae (neotrichy). The terminal part of tarsus I presents Haller's organ. Pretarsi II-IV with one pair of setae. The postembryonic development is still insufficiently studied; the larva is unknown, but there appear to be three nymphs; the largest nymphs are sexed (male and female nymphs are in these cases distinctly recognizable).

Order Gamasida

There is one pair of lateral stigmata (except in the larva) that, as a rule, is connected at both sides with a taenidium (the so-called peritreme). The subdivision of the body into prosoma and opisthosoma is completely lost. The idiosoma is dorsally covered with one or more shields. There are no eyes. The anal shields present each at the most one seta. The genital opening of the female is closed by three or four shields; that of the male by two. As a rule an unpaired sternapophysis is present (absent in strongly specialized, parasitic species). There are at the most four pairs of infracapitular setae (among which no laterodorsals) and one pair of corniculi. Generally the tegulum is anteriorly prolonged into a well-developed supracheliceral limb. The pharynx has a triangular or quadrangular cross-section. As a rule the palp consists of five free segments (coalescene of segments sometimes occurs) and an apotele (paraxially at the base of the palpal tarsus); the apotele bears a bi-, tri-, or quadripartite fork. The legs generally consist of seven segments (the apotele included); the ambulacrum of leg I is sometimes missing. The postembryonic development comprises four stases: larva, protonymph, deutonymph, and adult.

Order Ixodida

There is one pair of stigmata (except in the larva), situated posteriorly of coxa IV, or laterally above coxae II-III. A distinct subdivision of the body into prosoma and opisthosoma is lost. The idiosoma can present a dorsal shield (Ixodina) or a leathery cuticle (Argasina). One or two pairs of eyes can be present, or eyes are absent. The anal shields each bear one or more setae. There are no sternapophyses. The lateral lips are elongate; they are armed with recurved teeth. Posteriorly of the mouth, the pharynx is V-shaped; it then becomes quadrangular, and finally hexagonal (as in Opilioacarida). Tibia and tarsus of the palp have coalesced; the palpal apotele is lacking. The legs generally present seven primary segments, among which the apotele; the coxae generally are little or not movable. The tarsus of leg I presents Haller's organ. The postembryonic development of most ticks comprises three stases: larva, nymph and adult. In Argasina the nymphs pass through a series of moults; these possibly concern growing-moults, and no transformations to other nymphal stases.

Superorder Actinotrichida

The body is originally composed of sixteen segments (irrespective of the prechelicerals); this number can be reduced to fifteen, fourteen, thirteen or twelve; in many cases there is still a naso (a protuberance of precheliceral origin). The secondary respiratory organs (when present) belong to two groups: (1) genital tracheae (in a restricted number of cases, especially in primitive species); (2) tracheae, etc., probably originating from areae porosae.

Originally there are six pairs of prodorsal setae. The setae of body and appendages present an axis of actinopilin. The number of lyrifissures is restricted; there is a maximum of seven lyrifissures on the idiosoma, and of one on each of the appendages. There is a pair of external or internal podocephalic canals, in each of which originally debouch three glands. The primary genital opening is trifid, and generally debouches into a progenital chamber that extends over three segments; the secondary genital opening is longitudinal (this condition is not recognizable in all cases). There are no free coxae and no sternum, but epimera or coxisternal regions. There is a sejugal furrow or interval. The chelicerae have no dorsal lyrifissure. The palp presents no apotelic claws. There are often trichobothria, on legs or body. In case two femora are present, the articulation between these is a primary one, not associated with lyrifissures. The tarsus can, in rare cases, present secondary articulations which, however, are never associated with lyrifissures. Originally each of the legs has three claws; the central claw, however, can be replaced by an empodium; one or both lateral claws can get lost by regression. In the postembryonic development, regressive stases (calyptostases or elattotases) can occur at various levels. Originally there are six stases: prelarva, larva, three nymphs, and adult; the prelarva (when present) is always a calyptostase.

Order Actinedida

The body of the adult is composed of 13-16 segments; they have partly or nearly completely fused. In numerous cases, the cuticle of the adult is little or not sclerotized; small or larger shields occur rather often, but a complete sclerotized armour is rare. As a rüle there is no rostral tectum. In case tracheae are present, these debouch at the base of the chelicerae (most Prostigmata), and (in rare cases) in the progenital chamber; tracheae are absent in many primitive Actinedida (Endeostigmata) and in Phytoptina. Prodorsal trichobothria are present in many cases (one or two pairs); sometimes trichobothria are found on the legs. The anus is sometimes replaced by an uroporus. The podocephalic canal is external or internal. A latero-abdominal gland is never present. The claws of the legs can present tenent hairs; the central claw can be replaced by an empodium. Solenidia can be present on femur, genu, tibia, and tarsus. Beside a calyptostasic prelarva, other calyptostases (protonymphal and tritonymphal) occur in various species; the larva of *Labidostomma* and *Rhagidia* is an elattostase. One of the three nymphal stases can be lacking (some Endeostigmata, Raphignathoidea, Tetranychoidea, Cheylethoidea); many Phytoptina appear to have only one nymphal sase.

Order Oribatida

The body of the adults is composed of 14-16 segments; these have partly or nearly completely fused. The cuticle of the adults (and sometimes also of the immatures) is partly or completely sclerotized. There is nearly always a rostral tectum. Tracheae are absent in many primitive Oribatids; the adults of the higher Oribatids are characterized by the presence of a tracheal system starting from acetabula and apodemes; beside these, various other types of tracheae occur. One pair of prodorsal trichobothria (never two pairs) is nearly always present; it consists of a bothridial seta (of specialized shape) and a strongly developed bothridium. The legs never present trichobothria. The podocephalic canal is external. In many cases (many primitive and all higher Oribatids) there is a latero-abdominal gland. The claws of the legs never bear tenent hairs; empodia are not found; pulvilli are rare. Solenidia occur on genu, tibia, and tarsus only. There are nearly always three nymphal stases. Beside the calyptostasic prelarva, no other calyptostases occur; there are no elattostases.

Order Acaridida

The body of the adults is possibly composed of 14 segments that have nearly completely fused. As a rule the cuticle is feebly sclerotized; sclerites can, however, occur. A rostral tectum is never present. Tracheae are nearly always absent. As far as known, one pair of genital tracheae is occurring in the female of *Gohieria fusca* (Oudemans) only. There are no prodorsal trichobothria. A paired latero-abdominal gland is present. The podocephalic canal is external. The palps are reduced; they are small and more or less flattened, and consist of two segments only. As a rule the legs present one apotelic claw and a pulvillus, although both can be lacking. There are three nymphal stases. As a rule the deutonymph is an elattostase (the hypopus) or is lacking; in rare cases the deutonymph is a calyptostase.

Order Tarsonemida

The body of the adults is probably composed of 12 segments; parts of this segmentation are still distinctly visible (in many cases the opisthosoma is subdivided into segments). The cuticle is distinctly, although slightly sclerotized, and often very shining. The female generally presents one pair of stigmata, originally situated in apodeme 1. The female presents, moreover, a latero-ventral, originally prodorsal, trichobothrium. The mouthparts are partly reduced; the palps are very small and recognizable with a high power magnification only. The gut is ending blindly; an uropore is found at the place of the anus (it is the outlet of an excretory organ). The legs originally present two claws and a pulvillus; sometimes, one or both claws and the pulvillus are absent. Solenidia occur on tibia and tarsus only. The number of legs can, also in the adults, sometimes be reduced (in the parasitic family Podapolipidae, the legs of the adult female can even be completely lost). Only two stases of the postembryonic development are known with certainty, viz., larva and adult.

THE IDENTIFICATION OF SUPERORDERS AND ORDERS OF MITES

In order to promote the practical use of the system of classification here introduced, the following key for the identification of superorders and orders has been constructed. Key characters are of course the most useful and most clear out of a number of diagnostic characters; consequently the key is not, at the same time, a schematic representation of relationship and phylogeny.

KEY FOR THE IDENTIFICATION OF SUPERORDERS AND ORDERS

1. The legs present free coxae (in Ixodida and Spinturnicidae little movable, or coalesced at the base, but still recognizable as separate coxae), and there is nearly always a sternum (lacking in Ixodida). There is no sejugal furrow or sejugal interval . . . . (Anactinotrichida) 2

— The legs have no free coxae, and there is no sternum, but there are coxisternal regions (the epimera). There is a distinct sejugal furrow or sejugal interval (in some cases the number of legs is reduced, e.g. two pairs in Phytoptina, no legs in some Podapolipidae) . . . . (Actinotrichida) 5

2. The opisthosoma is distinctly segmented. At both sides of the genital opening, a pair of convex, wart-like capsules (genital verrucae) are present, functioning as covers of evaginable genital papillae. A pair of rutella is found in the distal part of the malapophyses . . . . Opilioacarida

— The opisthosoma is not segmented. There are no genital verrucae and no rutella (in rare cases the corniculi can present a resemblance to a rutellum) 3

3. Gnathosoma with a pair of characteristic lateral lips, armoured with striking, recurved teeth . . . . Ixodida

— Lateral lips without striking, recurved teeth 4

4. Infracapitulum, apart from a pair of corniculi, with a large number (at any rate more than four pairs) of setae, among which a pair of laterodorsals. Anal shields each with more than two (as a rule very small) setae. Tegulum not produced into a supracheliceral limb (the dorsal shield of the idiosoma, however, is produced into a small rostral tectum). Idiosoma with extremely small, irregularly scattered setae. Palpal tarsus with a striking dorsal area closely beset with hollow setae . . . . Holothyrida

— Infracapitulum, apart from a pair of corniculi, at the most with four pairs of setae, among which no laterodorsals. Anal shields each with at the most two setae. The tegulum is generally produced into a supracheliceral limb, covering part of the chelicerae. Idiosoma with a distinct, more or less regular, setation. Palpal tarsus without striking dorsal area closely beset with hollow setae . . . . Gamasida

5. Mouthparts strongly reduced. Palp very small, closely pressed against the gnathosoma; palpal segments not or nearly not recognizable. No sucker-plate at the ventral surface of the opisthosoma . . . . Tarsonemida

— Mouthparts as a rule well-developed; even in a relatively small gnathosoma, the component parts are still well visible. As a rule the palpi present a distinctly recognizable segmentation. In case the mouthparts are reduced, the ventral surface of the gnathosoma presents a distinct sucker-plate 6

6. Palp small, although distinctly recognizable, presenting only two segments. In case the mouthparts are reduced, the opisthosoma presents ventrally a sucker-plate. The ambulacrum of the legs is composed of one claw and a pulvillus, or of a stalked sucker. Prodorsum without trichobothria . . . . Acaridida

— Palpi generally with three to five segments, and relatively not small (in case they are relatively small, the opisthosoma is more or less vermiform). Ambulacra with one to three claws, but nearly always without pulvillus (sometimes claws are absent). Prodorsum in many cases with one to two pairs of trichobothria 7

7. Cuticle often little sclerotized. Generally there is no rostral tectum. In many cases there are one to two prodorsal, little specialized, trichobothria. Ambulacra often with an empodium at the place of a central claw; claws and empodia sometimes provided with tenent hairs. Anal opening sometimes replaced by an uropore. Infracapitulum rarely with a pair of rutella (in case a rutellum is present, adults are little or not sclerotized and do not present a rostral tectum) . . . . . . Actinedida

— Body of the adults (and often also of the immatures) completely or partly covered with sclerites. Rostral tectum generally present. In most cases there is one pair of prodorsal trichobothria (not more), of which the bothridium is generally strongly developed. Ambulacra never with an empodium; claws never with tenent hairs. Anal opening always with two valves. Infracapitulum with a pair of rutella . . . Oribatida

SUMMARY

In the present paper the classification of the mites is revised as a result of comparative investigations carried out in the period 1961-1971. The problem of mono- or polyphyletic origin is studied, and a reconsideration of the diagnostic characters has led to the conclusion that the mites are of biphyletic origin. Two superorders are distinguished: Anactinotrichida and Actinotrichida. The classification of Opilioacarida with Anactinotrichida is explained. It appears that a comparison with other groups of Arachnidea is now of essential importance. Anactinotrichida comprize: Opilioacarida, Holothyrida, Gamasida, and Ixodida. Actinotrichida comprize: Actinedida, Oribatida, Acaridida, and Tarsonemida. The subdivision of most of these groups is dealt with, and the classification of especially Holothyrida and Actinedida is revised (a new family Allothyridae is created, and Actinedida are subdivided into Alycina, Bdellina, Labidostommina, Anystina, and Trombidina). A discussion of the nomenclature of superorders and orders leads to a rejection of the names introduced by Evans, Sheals & Macfarlane (1961). A hypothetical reconstruction of phylogeny of the orders is given, which is illustrated by a dendrogram. The use of the present classification is facilitated by the addition of diagnoses of superorders and orders, and of a key.

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