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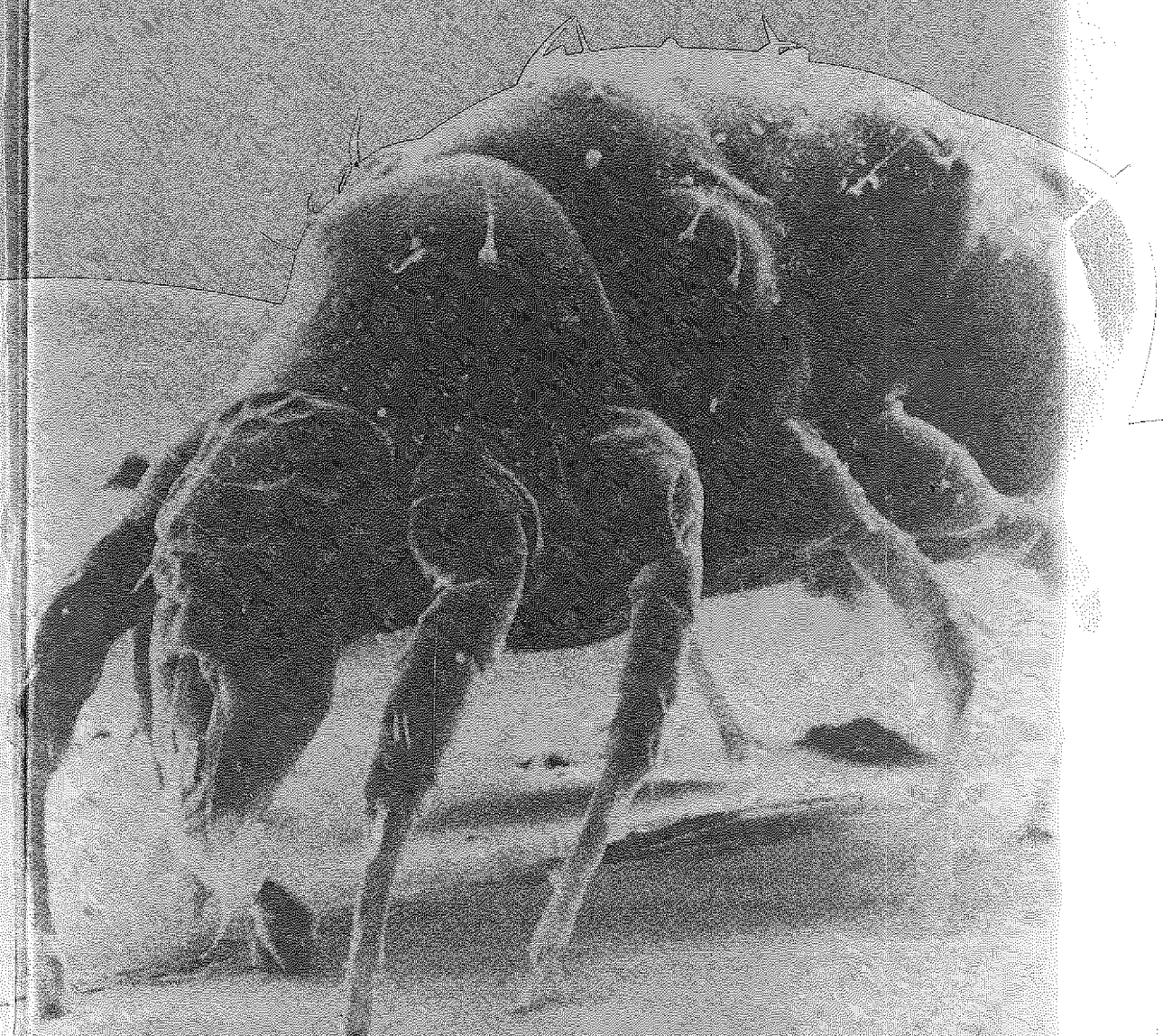
ACAROLOGY VI

volume 1

edited by
D.A. Griffiths and C.E. Bowman



ACAROLOGY VI

Volume 1

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Table of Contents

Preface

Acarology VI represents the proceedings of the VI International Congress of Acarology held 5–11 September 1982 in the historic seat of learning, Edinburgh University Scotland. It includes within its two volumes the contents of the Congress symposia together with the contributions to all other sessions, presented either as submitted papers or as posters.

Acarologists from thirty-nine countries attended, fifteen more countries than the total for the first congress held in 1963. More significantly, an analysis of the membership shows a seven-fold increase in members who practise their science in the third world.

For much of its history the study of mites was nurtured and developed by individuals or small groups of scientists following narrow specialisms, isolated one from another by geographic and linguistic barriers. The need to break down these frontiers, to pursue closer scientific relationships so that acarology might develop into a cohesive discipline, was realized and it resulted in the inauguration of the first congress.

When the programme for the sixth was considered it was deemed a propitious time to pause and survey progress by commissioning world authorities in specific relevant fields to present, in a series of symposia, a synthesis of the research completed during the interim twenty years. These valuable and timely contributions are published as chapters one to four of this volume. They illustrate how the science of acarology has achieved the status of an integrated discipline with the ability to relate and debate with those of other arthropod groups.

The thirteen submitted paper sessions together with the posters reflect current research and opinion on an international level. They range from basic treatises on systematics and physiology to the description of practical techniques for the treatment and control of a wide range of economically important ticks and mites.

Special thanks should go to the people who assisted in the organisation of the meeting in Edinburgh (in alphabetical order): Anne Baker; Diane Bowman; Gwilym Evans; Ian Jeffery; Don Macfarlane; Joan Macfarlane; Olive Welland.

Our thanks should also go to the sectional chairmen and vice-chairmen at Edinburgh (in alphabetical order): G. Alberti; W. T. Atyeo; J. Boczek; J. E. M. H. van Bronswijk; G. P. ChannaBasavanna; Y. Coineau; D. R. Cook; M. Costa; R. O. Drummond; N. G. Emmanouel;

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Diverse people have assisted in the preparation of these volumes. Our thanks should go to (in alphabetical order); Diane Bowman; Walter E. Bowman; Joan Macfarlane; Fred Sowan (Editor-in-Chief, Ellis Horwood Ltd); the Staff of the British Museum (Natural History) Arachnida Section – Anne Baker, Paul Hillyard, Keith Hyatt, Keiran Martyn, Fred Wanless; the Staff of the British Museum (Natural History) General and Zoological Libraries; the Staff of the Commonwealth Institute of Entomology – Chris Hamilton (Librarian), Don Macfarlane, Reg Sims; the Staff of Slough Laboratory – John Chambers, Sonia Donaghy, Corinne Ferguson, Christine George, Bernadette Higgins, Jagdish Tailor, Olive Welland; the Staff of Slough Laboratory Library – Tim Cullen, Sylvia Ingram Parkinson.

Editing these volumes has been a taxing task, and we have tried our best to fully understand the material submitted. Nevertheless, all responsibility for published opinions, facts, and figures rests entirely with the authors of each edited contribution.

D. A. GRIFFITHS
C. E. BOWMAN

Slough, Berkshire

Presidential address

Gwilym O. Evans†

In his Presidential Address to the 2nd International Congress of Acarology at Sutton Bonington in 1967, T. E. Hughes discussed some of the possible future trends in acarological research. His observations were profound and stimulating and, after a lapse of fifteen years, I feel it is opportune to reflect on some of the advances made in the interim and to consider the current problems confronting researchers in selected branches of acarology. My comments will, of necessity, be brief especially since some of the topics will be the subject of review papers read at the Symposia.

The availability of elegant techniques in the fields of biochemistry, physiology, and morphology has been the basis of much of the advancement in our knowledge of the physiology and structure of the Acari. Some of the recent works on the nervous system and sense organs, on the integument, and on the structure and function of gland systems have rivalled comparable work on insects in their detail and sophistication. The ultrastructure of acarine mechanoreceptors and chemoreceptors, for example, is amazing in its variety and complexity, and if variety of structure reflects variety in function it is not surprising that the Acari respond to a wide array of environmental stimuli as has been shown in *Ixodes ricinus* by Lees and in *Ophionyssus natricis* by Camin. Minute size does not seem to be an insuperable barrier to sensory perception in the Acari – the high incidence of dual-functioning sensilli†† usually having combined mechanoreceptive and chemoreceptive functions, permits of maximum perception in minimal space. At present, functions of sensilli are largely inferred from their structure and location, and it is desirable that future work should emphasize the more functional approach using the techniques of electrophysiology. The study of structure without regard to function can be a sterile as well as a frustrating exercise.

All these studies have demonstrated the overwhelming similarity in the basic structure of acarines to other terrestrial arthropods, although many novel features are evident. This should come as no surprise to the majority, but to those of us, mainly taxonomists, who tend to treat the Acari as a special creation for our various amusements, this fact is too often overlooked, much to the detriment of the science.

Notwithstanding the recent significant contributions to physiology and fine structure, however, our exploration of acarine structure and function is still in its infancy, and the elabor-

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††There is considerable confusion over the spelling of this word. I follow those who consider it to be a diminutive form of *sensus*, so that the correct word is *sensillus*, plural *sensilli*.

ate terminology for many structures conceals our ignorance of their function. This was brought home to me in no uncertain way when I was recently looking at the detailed surface structure of the chelicerae and coxae of the Mesostigmata.

The presence of two sensilli on the fixed digit of the chelicera of free-living gamasine mites is well established, and they have been termed the 'Dorsal seta' and '*pilus dentilis*' (Plate 1C: 1 and 2). The occurrence of a 'placoid' sensillus apically or subapically on the digit appears to have been overlooked (Plate 1A, C: 3). The relative positions and form of the sensilli show considerable variety (Plate 1A–D). Of particular interest is the replacement of the trichoid-like sensillus (*pilus dentilis*) by a placoid sensillus in such widely different taxa as *Eviphis* and *Dinychus* and the migration of the sensilli to the external face of the digit. Both taxa have extremely long cheliceral shafts, and the similarity in their sensory receptors probably reflects similarity in the function of the trophic appendages. Nothing is known of the specific function of the sensilli or of their innervation. Their external form and location would appear to provide useful taxonomic characters.

Scanning electron microscope (S.E.M.) studies of the coxae of the first pair of legs of the Gamasina have revealed the consistent presence of three distinct openings of gland systems on the ventral surface of each coxa in the female. An opening occurs internally on the coxa, and the other two occur together, usually in a depression, externally (Plate 1E). An additional opening occurs internally on the coxa of male parasitids. In common with other Arachnida, one of these openings may belong to a coxal gland system, but this is pure speculation. Unlike other Acari the coxae of the first pair of legs in the Mesostigmata are located in a common cavity with the gnathosoma and the secretions of the coxal gland complex probably debouch into this cavity where the tritosternum functions in a fluid transport system. The two openings externally on the coxa show a range of form and, as in the case of the cheliceral sensilli, could provide taxonomic criteria at generic and specific levels (Plate 1F–H).

These examples suggest the wealth of structure which will be revealed by detailed S.E.M. studies of the surface topography of the acarines. The definition of surface structure leads in the inquiring researcher to the investigation of internal structure and function. Functional studies of such minute animals are limited, at present, by the lack of techniques, but this is surely only a temporary phenomenon.

Although there has been renewed interest in the behavioural studies of the Acari during the last fifteen years, particularly in relation to predator–prey interaction, chemical communication, and mating behaviour, progress in this fascinating field has been fragmentary. The impetus for many of the predator–prey studies derives from the economic importance of the prey species and the potential role of the predator in a biological control system. The early investigation of the *Cheyletus–Acarus* interaction remains a classic, and there is little doubt that the work of

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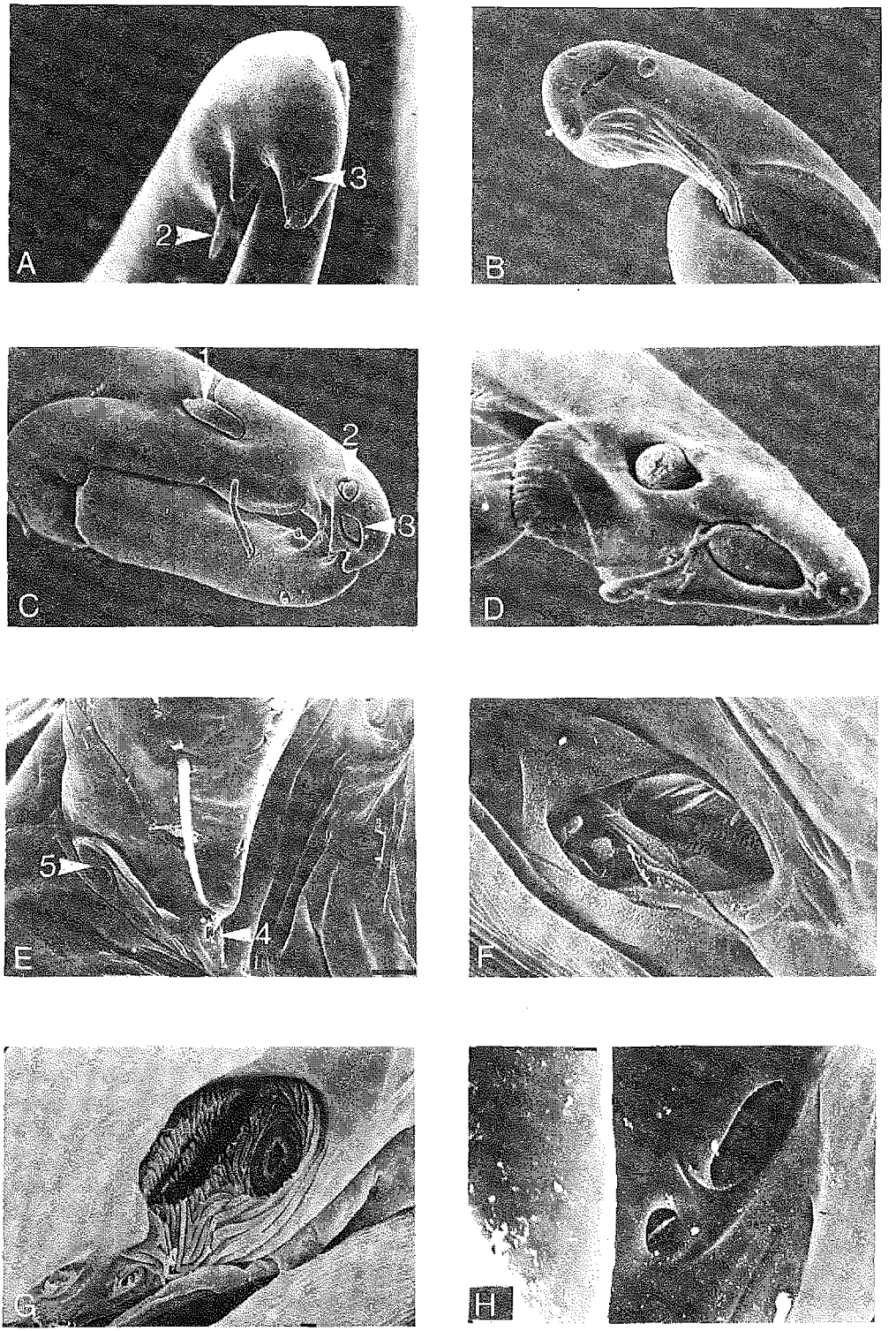
Plate 1

Scanning Electron Microscope investigations of cheliceral sensilli and coxal 'gland' openings in the Mesostigmata.

A–D, sensilli in the distal region of the fixed digit of the chelicerae of females of four species of mesostigmatic mites: A, *Parasitus* (× 1400); B, *Veigaia* (× 2785); C, *Eviphis* (× 1500); D, *Dinychus* (× 4175).

E–G, 'gland' openings ventrally on coxae I of females of four species of mesostigmatic mites. E, location of the openings in *Hypoaspis* (× 640); F–H, form of the openings on the external face of coxae I, in F, *Pergamasus* (× 2550); G, *Parasitus* (× 2550); H, *Rhodacarus* (× 4175).

1, dorsal 'seta'; 2, *Pilus dentilis*; 3, apical placoid sensillus; 4, internal gland opening; 5, external gland openings. ▷


A
2
3
B
C
1
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D
E
5
4
F
G
H

Sabelis with its sophisticated modelling will set an example and a standard for future studies. The present concentration on the phytoseiid/tetranychid system is understandable for economic and academic reasons – not least of which is the fact that it provides ideal postgraduate projects – but it is hoped that future studies will feature more euedaphic predator–prey systems including mite–nematode and mite–collembolan interactions which may also be of economic significance. Certainly the possible role of chemical cues and the nature of the sensory mechanisms involved should not be overlooked in the studies.

From the standpoint of chemical communication, there seems little doubt that pheromones will be found to be important in the biology of free-living and symbiotic Acari as they are in the Insects. Recent work has established the existence of sex attractants and arrestants, and of alarm and assembly pheromones, but relatively little is known of their chemistry or source. Recently, allelochemicals have been shown to play a role in prey location by phytoseiid mites and in repelling competitor species in acarids. The utilization of pheromones and allelochemicals in pest management deserves investigation.

The Acari are unique in the diversity of the methods of insemination they display. Although other chelicerates have stalked spermatophores (scorpions, false scorpions, and amblypygids), use their mouthparts to transport sperm material to the female gonopore (Solifugae and spiders), or practise direct copulation (Opiliones), and have evolved elaborate pairing behaviour, it is only in the Acari that we find all of these methods practised. In fact, each of the other major taxa typically have only a single method of insemination. The evolutionary significance of this diversity in the Acari has received little attention. More detailed studies of both direct and indirect methods of insemination may provide valuable information for elucidating relationships within and between higher taxa.

In another field of acarology, namely embryology, progress during the last fifteen years has been slow and disappointing. No comparable detailed studies to those on ticks by Aeschlimann and Anderson have been forthcoming on mites and our knowledge of their embryology is fragmentary. For example, details of the formation of the germ band are lacking, and the extent and significance of the differences in the position of the germ band in early embryonic development between the Mesostigmata and other Acari remain problematical. We have no information on the embryology of the opilioacarids or holothyrids. Embryology could well provide information on the phylogenetic relationships of the Acari. To this end our ignorance of embryological development in the Palpigradi and Ricinulei which are considered to be key groups in elucidating the phylogeny of the Acari, is particularly significant.

Problems of systematics

The most problematical area in acarology at the present time is probably systematics. Three topics, in particular, are sources of contention and confusion. Firstly, the phylogenetic relationships of the three major acarine taxa, secondly, system(s) of classification, and thirdly, terminology.

Phylogeny

One of the most significant contributions to acarine classification was made by Zachvatkin in 1952 when he postulated a diphyletic origin of the Acari within the Chelicerata. Surprisingly, no critical appraisal of Zachvatkin's classification has been forthcoming from arachnologists; Savory, for example, does not even refer to Zachvatkin's work in either of the two editions of his book on the Arachnida. Further, it was not until 1969 that Grandjean referred in any detail to Zachvatkin's work and then questioned only one of a number of criteria presented by

the Russian author in support of his classification. This referred to the presence of actinopilin in the setae of non-acarine chelicerates – Grandjean suggesting that in this group birefringence may be due to 'une substance axiopileuse' and not to true actinopilin.

This diphyletic concept was adopted by Sheals, Macfarlane, and myself in 1961 and later in 1968 by van der Hammen who has subsequently proposed a radically new classification of the Chelicerata. This aligns the Acariformes with the Palpigradi in a taxon Epimerata while the remaining groups of the Acari are considered to be most closely related to the Ricinulei and are together included in the taxon Cryptognomae. The interpretation, selection, and weighting of the major classificatory criteria used by van der Hammen require critical reappraisal, as do those criteria presented by Zachvatkin in support of his classification.

One important fact, however, should be borne in mind when discussing the phylogeny of the Arachnida and especially when assigning the term 'primitive' to certain morphological features of extant forms. That is, the probable occurrence of major phylogenetic ramifications within this group of aquatic origin before its transition or transitions to a terrestrial way of life. Features indicating such ramifications have undoubtedly been obscured by subsequent terrestrial adapations, and this adds considerably to the difficulty of reaching clear-cut conclusions on the relationships between the major taxa of the Arachnida. Grandjean gave an excellent piece of advice in relation to the higher classification of the Acari – 'qu'il est préférable de laisser du jeu entre les pièces du puzzle que nous assemblons sous le nom de classification naturelle'. Such flexibility is certainly desirable in the present state of our knowledge of the Arachnida.

Classification

The diverse opinions of the classification of the Acari are not surprising when one considers the diversity in contemporary approaches to animal classification. Several different concepts of relationships exist within the field of systematics. The earlier omnispective approach emphasized the practical approach to classification based on phenotypic similarity of the taxa and on consideration of their evolutionary history – albeit without phylogenetic analysis. This has, to some extent, given way to the phenetic and cladistic approaches to classification. Both have generated lively discussion and each, in turn, has been considered a panacea for the defects in other classificatory methods.

The phenetic approach is based strictly on the overall resemblance between taxa, with no phylogenetic assumptions. Contributions on this subject at one of the symposia during the 1967 Congress created considerable interest, but subsequently the potential of phenetics as a tool in taxonomy does not seem to have been fully realized. The methodology is somewhat laborious and its philosophy debatable. In my opinion the major practical contribution made by phenetics has been the emphasis on the examination of a wide range of criteria. This feature has been adopted by the more traditional taxonomists even when the entirely phenetic approach to classification has been rejected. A modification of the phenetic method to include characters selected and weighted according to their supposed phylogenetic significance – so called panphenetics – has found some support.

The most recently introduced concept of relationship which has created considerable interest and debate originates from Hennig's 'phylogenetic systematics'. The restriction of the meaning of phylogenetic, in this context, to relationships based solely on branching sequences in evolution is unacceptable to the majority of systematists who now refer to Hennig's system as cladistics. It is based on branching lineages but ignores evolutionary divergence. All taxa are considered to be monophyletic in Hennig's sense. Publications by acarologists adopting this

systematic concept show a refreshingly new approach to classification. The method encourages, if not demands, the examination of broader spectra of animal groups in constructing lineages, and this must be to the benefit of systematics. The procedure is not without its problems, among which the determination of character states is the most significant.

Terminology

The need for a concise and unambiguous terminology in any science is unquestionable. The general acceptance of one term for each structure in descriptive taxonomy and anatomy is the ideal which is rarely attainable; the existence of two terms for the same feature is manageable, but the present position in acarology, where there is often a plethora of terms for the same structure, is totally unacceptable. This situation, which is particularly evident in descriptive taxonomy, not only leads to confusion within the discipline but has led during the last forty years to its fragmentation into taxonomic areas which are becoming increasingly isolated within their specific terminologies. This is particularly evident, for example, in those specializing in the Mesostigmata and the Cryptostigmata. Certain of the terminology lacks logic; for example, there is a general agreement to suppress 'capitulum' in favour of 'gnathosoma', but a ready acceptance of the terms 'infra-' or 'sub-capitulum' – which in the absence of a capitulum are meaningless. Surely, a term should be descriptive of the form, function, or location of a structure. Recently, there has been an attempt to reject ordinal names with the suffix 'stigmata' on the basis that not *all* members of a particular taxon exhibit the characteristic implied by its name. Some of the proposed replacement names apparently have the sole merit, and I quote, 'that they are without sense'. One can only wonder at the attitude of entomologists to a change in the ordinal names of insects, such as Diptera and Hemiptera, for the same reason. This approach is symptomatic of the 'nominamania' prevalent in acarology at the present time.

My observations are perhaps somewhat hypercritical but, nevertheless, those who have the task of introducing students to acarology will appreciate the counterproductive effects of unnecessarily complex terminologies on attitudes to learning, and the resulting frustration of the teacher in attempting to generate enthusiasm for his subject. One of my students summarized the essential requirements for the study of the Acari to be: a good microscope and technique, a comprehensive literature, and a classical education to decipher the terminology!

Turning the pages of the proceedings of the 1st Congress of Acarology at Fort Collins in 1963, I noticed that the topic of terminology loomed large at that time, and there was an effort to initiate the compilation of an illustrated glossary of morphological terms. Unfortunately little or no progress was made. Is it time to reconsider the matter? The subsequent publication of van der Hammen's compilation of terms could form the basis of a comprehensive reappraisal of terminology. This deserves the serious consideration of our Executive Committee who could provide the stimulus and organize the task. The objective is not necessarily the standardization of terminology but its rationalization.

The future

The points I have raised in my address have been selective and reflect many of my own interests in acarology. Time does not permit me to refer to the progress in or potential for research in the field of soil ecology which for many of us provided our first introduction to the mites. Those of us who have delved ever deeper into their taxonomy and biology never cease to wonder at their diversity and adaptability. The rapid progress during the last twenty years in the study of various aspects of the biology of acarines, particularly in ecology, physiology, and

ultrastructure, and the considerable recruitment of non-taxonomists to acarology, are certain to change the course of this once taxonomy-dominated science and augurs well for the future.

Finally, let us be determined that even in the event of the fragmentation of the Acari taxonomically, the unity of acarology in the sense of Berlese, Michael, Oudemans, Vitzthum, and Grandjean will be maintained, and that its expression will be through the Congress of Acarology.

SYMPOSIA

1 Speciation and evolution in Acari

1.1 PARALLEL HOST-PARASITE EVOLUTION IN THE SARCOPTIDAE AND THE LISTROPHOROIDEA (Acarina: Astigmata)

A. Fain†

INTRODUCTION

My paper will be divided into two parts. In the first part I will deal with parallel host–parasite evolution in the family Sarcoptidae and in the four families of the Listrophoroidea, all of which belong to the Astigmata. In the second part I will discuss the possible relationships existing between certain hosts, according to the similarity of their mite fauna.

PARALLEL HOST–PARASITE EVOLUTION

Before dealing with evolution in parasitic mites it is necessary to recall some general phenomena in relation to parasitism in acarines (Fain 1968, 1979).

Parasitism by mites is probably very ancient, and one may surmise that in some groups these parasites are almost as old as their hosts.

Host specificity in parasitic mites is variable and depends on the degree of permanency of the parasite. Mites which remain on their host during all stages of their development are more specific than those that leave their hosts periodically. Specificity is particularly strict in the fur mites such as the Myobiidae and Listrophoroidea.

Phylogenetic evolution in parasitic mites is always of the regressive type, which is also true for other parasitic arthropods and parasitic worms. That means that a parasite living on an evolved host is more regressed than one living on a primitive host. Regression may involve all the external organs, especially the cuticular shields, claws, legs, and chaetotaxy. The regression

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of the legs begins with the fusion of some segments, generally the tarsus, with the tibia. In the most primitive genera all the segments of the legs are free. In the evolved genera some or all of the legs show a fusion of the tibia and tarsus, and more rarely of the other segments. Some of these structures may disappear completely during the process of regression. The mites that fix to the hair of their hosts have developed constructive structures required for attachment to their host. These adaptive or specialized structures are secondary formations without phylogenetic significance. As a rule phylogenetic regression is more marked in endoparasitic mites, while constructive adaptation or specialization is more evident in ectoparasites (Fain 1969).

There is generally a good correlation between the degree of the regression of the parasite and the degree of evolution of the host. The host and its parasite follow a parallel evolution, but they go in opposite directions.

The cause or mechanism of the regressive evolution in parasites is not known. I have suggested that the reduction of the external structures in the parasites is related to the immunological reaction of the host which tends to reject the parasite (Fain 1979b, 1982c).

EVOLUTION IN THE SARCOPTIDAE

Some groups of mites are particularly suitable for the study of the evolution of host and parasite. This is the case in the prostigmatic fur mites of the family Myobiidae. These myobiids live on marsupials, insectivora, bats, and rodents and are strictly permanent; this renders them particularly interesting for the study of evolution. I have reported on these mites in previous papers. I will show now that parallel host–parasite evolution is also well marked in other groups of mites and specially in the Sarcoptidae and in the Listrophoroidea, both in the Astigmata.

The Sarcoptidae live in the corneous layers of the skin. They are permanent parasites and are important producers of mange in man and animals. The family Sarcoptidae is composed, at present, of four subfamilies. The most primitive is the subfamily Caenolestocoptinae, which contains only a single genus and species living on *Lestoros inca,* a Peruvian marsupial. In this species all the tarsi are free in both sexes and the male possesses large adanal suckers, which is a unique character of this family (Fain & Lukoschus 1976). Another primitive subfamily is the Diabolicoptinae, in which all the tarsi are free as in the Caenolestocoptinae, but the male has no adanal suckers. This subfamily contains two genera, *Diabolicoptes* and *Satanicoptes,* represented by three species living on Australian dasyurid polyprotodont marsupials (Fain & Domrow 1974b, Fain & Lawrence 1975).

In the other two, more evolved, subfamilies, Notoedrinae and Sarcoptinae, the tarsi III and IV of the female are fused with the corresponding tibiae, and the males always lack the adanal suckers. In the Notoedrinae tarsus IV in the male is free, while in the Sarcoptinae this tarsus is fused with the tibia (Fain 1968).

The Notoedrinae contain, at present, six genera, most of which live on bats; others are found on insectivores, carnivores, lagomorphs, and rodents.

The Sarcoptinae, the most evolved of the family contain six genera, of which three are endemic to monkeys of the family Cercopithecidae, two live on rodents, and one, the genus *Sarcoptes,* is found on numerous domestic animals and on man.

It appears from this comparative study that the most primitive Sarcoptidae live on marsupials, the most evolved on primates. Forms, intermediate in evolution, are found on other mammals such as bats, carnivores, lagomorphs, and rodents.

One may conclude that parallel host–parasite evolution is particularly well marked in the mites of the family Sarcoptidae (Fain 1976).

Moreover, the species living on the South American marsupial is more primitive than those infecting Australian dasyurid marsupials. This could be an argument that Australian marsupials are more recent than South American marsupials.

Among the six genera composing the Notoedrinae five obviously belong to the same evolutionary line. The most primitive is *Nycteridocoptes,* in which the hysteronotum bears five pairs of *d* setae, five pairs of *l* setae, and two pairs of anals. This genus is represented by nine species living on Megachiroptera and by four species living on Microchiroptera, all from the Old World. In another genus, *Chirnyssoides,* more evolved, two pairs of setae have disappeared (*d2* and *ae*). This genus is represented by eight species endemic on bats of the family Phyllostomatidae which is restricted to the New World. A third genus, *Chirnyssus*, resembles *Chirnyssoides* except that two other pairs of setae (*d3* and *l2*) have also disappeared. This genus is represented by two species living on Old World Microchiroptera. The most evolved genus of the series is *Notoedres.* It has the same chaetotaxy as *Chirnyssus* but the dorsal shields of the male are more reduced and the epimeres have a more evolved structure.

Notoedres is represented by numerous species on Old and New World Microchiroptera and on rodents. There are also a few species on carnivores and one species on a prosimian. The species of *Notoedres* parasitizing rodents, carnivores, and the prosimian, obviously have been derived from the more primitive forms living on bats. The first ancestor of the Notoedrinae is probably the genus *Nycteridocoptes* living on Megachiroptera.

Nycteridocoptes is however, not the most primitive genus of the family Sarcoptidae. The three genera living on marsupials are distinctly more primitive and are therefore probably the first ancestors of this family of mites.

The genus *Sarcoptes,* the most important in the family from the medical and veterinary point of view, has a very special position among the parasitic mites. In a study of the variability of *Sarcoptes scabiei* I have shown that the genus *Sarcoptes* contains only one very variable species. This species is able to infect not only man but also different hosts belonging to 17 families and seven orders of mammals. Almost all these hosts are domestic animals. This species is very rare in wild animals living in their natural habitat. No other permanent parasitic mite is able to parasitize such a large variety of hosts. The great variability observed in *S. scabiei* suggests that this species is not yet completely adapted to any of these hosts but remains in a continuous adapting process in all of them. The variability of this species is the result of the permanent interbreeding of the strains infesting man and domestic animals.

I have proposed the hypothesis that the genus *Sarcoptes* is derived from one of the three genera of Sarcoptinae parasitizing monkeys. Man is probably the primary host for *S. scabiei,* and from man the mite has passed to domestic animals. The frequent interbreeding of the mite in a variety of hosts has not only prevented speciation but has provided new characters which have increased the variability enabling the mite to adapt to very different hosts (Fain 1968, 1978).

EVOLUTION IN THE SUPERFAMILY LISTROPHOROIDEA

A further group of fur mites, the Listrophoroidea, are permanent and highly specific parasites. This superfamily is divided into four families according to the mode of attachment to the host and the shape of the clasping organs.

In the Listrophoridae the ventral surface of the propodosoma bears a pair of large chitinous membranes which envelop the hair of the host and serve to maintain it in position. The anterior legs contribute to the fixation of the mite to the hair of the host by pressing the membranes together. All the legs are normal.

In the Chirodiscidae the anterior legs are strongly modified and bear large chitinous membranes which are firmly pressed to the hair of the host.

In the Myocoptidae the fixation to the hair of the host is realized by means of the posterior legs which are modified into powerful claspers. The anterior part of the body is normal and does not bear chitinous membranes.

In the Atopomelidae there are no chitinous membranes on the body or the legs, and the posterior legs are not modified into claspers. The anterior legs are slightly modified and they fix to the hair of the host by encircling it.

The most reliable character for evaluating the evolution in the Listrophoroidea is the degree of development of the dorsal shields, especially the postscapular shield. In some families the prescapular shield and the tarsal suckers are also reduced and provide additional characters of evolution.

Evolution in the Listrophoridae

The family Listrophoridae contains 20 genera and about 120 species. It is represented in the Holarctic, Nearctic, and Oriental regions, but is completely absent in Australia, New Guinea, and Madagascar, except for one species, *Leporacarus gibbus,* a parasite of the domestic rabbit, which has been imported into Australia with its host. The Listrophoridae are particularly well represented on rodents, which harbour about 10 genera and 90 species.

In the genus *Afrolistrophorus,* one of the most primitive of the family, there is a large postscapular shield covering the median and the lateral parts of the body. This genus is represented by 22 species on the Afrotropical and Oriental rodents and by one species on each of the following hosts: a neotropical marsupial (*Lestoros inca*), a primitive nearctic rat, a palaerctic murine, and the cosmopolitan *Mus musculus*.

The genus *Geomylichus* contains 13 species, all from Nearctic rodents of the families Geomyiidae, Heteromyidae, and Cricetidae (Hesperomyinae). This genus is closely related to *Afrolistrophorus* but more specialized.

The third important genus, *Prolistrophorus,* is distinctly more evolved than the two preceding and is intermediate between *Afrolistrophorus* and *Listrophorus.* The postscapular shield presents a median oval area where the sclerotization is replaced by soft cuticle. This genus is represented by 12 species, of which three live on Nearctic Cricetidae and nine on Neotropical Cricetidae or Echimyidae.

The genus *Listrophorus* is more regressed and thus more evolved than *Prolistrophorus.* The median part of the postscapular shield is replaced by soft striated cuticle, and only the lateral parts of this shield are conserved. This genus is represented in the Nearctic region by 13 species of which 12 live on Microtidae and one on a Cricetidae. Among the 12 species from Microtidae, six live on the musk rat *Ondatra zibethica.* On the same musk rat we find in the Palearctic region four of the species already represented in North America, and on Microtidae five other endemic species. The genus *Listrophorus* is completely absent in the Afrotropical and Oriental regions, in Madagascar, and in Australia.

In addition to these four main genera, the rodents harbour several other genera living on Sciuridae, Spalacidae, etc . . .

Parallel-evolution is well marked in the Listrophoridae parasitic on rodents. In America the most evolved genus, *Listrophorus,* is found almost exclusively on Microtidae which are also the most evolved rodents. *Prolistrophorus,* a more primitive genus, is common on South American Cricetidae and Echimyidae, which are more primitive rodents. The ancestor of the group, *Afrolistrophorus*, is found only on primitive South American rodents and on a marsupial *Lestoros inca.* The origin of *Afrolistrophorus* is probably not in South America but in Africa where we find the most primitive species. Perhaps this genus has been introduced from Africa with hystricomorph rodents, probably by rafting in the early Eocene.

The Listrophoridae are also represented on Insectivora, Carnivora, and Lagomorpha. Curiously enough they are completely absent in bats where they are replaced by another family, the Chirodiscidae.

The Insectivora harbour 11 species forming four genera (*Asiochirus, Echinosorella, Dubininetta, Olistrophorus*), which have a large postscapular shield as in the genus *Afrolistrophorus.* All the species are endemic for Insectivora except one species of the genus *Olistrophorus* which parasitizes a primitive rodent (*Platacanthomys*).

The genus *Lagomorpha* supports four species of the genus *Leporacarus.* This is a primitive genus but with some specialized characters. One species lives on the rabbit (*L. gibbus*); the three others live on hares, either in Europe (*L. brevicauda*), South Africa (*L. leporicolus*) or North America (*L. sylvilagi*).

The Carnivora are parasitized by four genera and 10 species. These genera are very unequally evolved. The most primitive is *Hemigalichus,* which lives on an oriental viverrid. Another genus, slightly more evolved, is *Lynxacarus* with nine species, of which five are specialized for Carnivora, three for *Tupaia*, and one for a rodent. A third genus, *Lutracarus*, has a median postscapular shield as in *Lynxacarus* but the male lacks genital suckers, indicating a more evolved condition. It is represented by a single species living on *Lutra canadensis.* In a fourth genus, *Carnilistrophorus,* the postscapular shield has completely disappeared. It is the most evolved genus of the family Listrophoridae. It contains three species endemic for Afrotropical Carnivora, one species living on a Macroscelididae and one species living on a rodent *Myospalax*.

Evolution in the Chirodiscidae

The family Chirodiscidae is composed of four subfamilies: Labidocarpinae, Chirodiscinae, Schizocoptinae, and Lemuroeciinae. I will deal here only with the Labidocarpinae, which is the most numerous and includes mostly parasites of bats.

The Labidocarpinae from bats is divided into 15 genera and 150 species (Fain 1982d,e). Several characters may be used to evaluate the degree of evolution of the different genera. The most reliable are the degree of reduction of the postscapular shields, the reduction of the tarsal suckers on the posterior legs, and the reduction of the idiosomal chaetotaxy.

These characters have not always evolved in a parallel way. In some genera (such as *Olabidocarpus, Dentocarpus, Adentocarpus,* and *Asiolabidocarpus*) the reduction of the tarsal suckers has preceded that of the postscapular shield. The opposite has occurred in some species of the genus *Paralabidocarpus* in which the postscapular shield is strongly reduced or absent while the tarsal suckers are normally developed. The genus *Labidocarpoides* is intermediate between the two former groups. All the other genera lack the tarsal suckers, but some such as *Labidocarpus* have retained the peduncle of the sucker. The most evolved genus is *Alabi-*

docarpus, in which the postscapular shield and the tarsal suckers and peduncles are completely absent and the dorsal chaetotaxy is strongly reduced.

Curiously, the most primitive genera are not found on Megachiroptera as would be expected but on the Microchiroptera. A similar situation exists for another family of fur mites parasitic on bats, the Myobiidae. These exceptions to the rule for parallel evolution indicate that at least some families living on bats have arisen from the Microchiroptera and from there have passed to the Megachiroptera.

In the Microchiroptera parallel evolution of host and parasite is generally well marked except for the genus *Alabidocarpus,* the most evolved of the family, which is found on Megachiroptera and on a number of Microchiropteran genera.

Evolution in the Atopomelidae

The Atopomelidae, a large family almost entirely tropical, is divided into two subfamilies, the Atopomelinae represented in Neotropical, Afrotropical, Oriental, and Australian regions, and the Centetesiinae represented by two genera endemic on Insectivora of Madagascar.

The Atopomelinae are particulary well represented in Australian and Neotropical marsupials. In Australia and New Guinea the marsupials harbour 20 endemic genera and 98 species. The endemic rodents of these regions are parasitized by two endemic genera and 23 species. In the Neotropical region the marsupials are parasitized by five endemic genera and 23 species, and the hystricomorph rodents, mostly Echimyidae, by nine endemic genera and 20 species. In the Afrotropical region this family is represented by four genera. In the Oriental region there is only one genus, *Listrophoroides,* which is also present in the Afrotropical region. This genus is divided into 16 subgenera and 159 species. In Madagascar the two subfamilies are represented by one and two genera respectively.

In the genera living on Australian and New Guinean marsupials (Fain 1972) parallel evolution of host and parasite is not always clear except in, for instance, the genus *Cytostethum,* which is divided into two unequally evolved subgenera. In the typical subgenus there is a large shield on the anterior part of the hysteronotum. The other subgenus *Metacytostethum* is lacking this shield. The subgenus *Cytostethum,* the most primitive, contains all the species from potoroine marsupials, while the subgenus *Metacytostethum* contains a few species from potoroine and all the species living on macropodine marsupials. Since the potoroines are considered more primitive than the macropodines, it appears that the parasites have evolved in parallel with their hosts.

Multiple speciation can occur in the parasites of marsupials. The most remarkable example is that of the long-nosed kangaroo-rat also called the potoroo, which lives in eastern Australia including Tasmania. This animal harbours 21 species belonging to the same subgenus (*Cytostethum*) (Fain & Domrow 1974a).

In South America the marsupials are parasitized by a diverse fauna of Atopomelidae. If we use the degree of development of the postscapular shield as a criterion of evolution, we can establish the following list of genera.

The most primitive genus is *Dromiciolichus* living on a small marsupial, *Dromiciops,* from Patagonia. Another genus, *Prodidelphoecius,* is slightly more evolved, having a reduction of the prescapular shield. It lives on *Monodelphis.* In a third genus, *Didelphoecius,* the regression of the shields is more marked: this genus contains 17 species living on *Monodelphis, Didelphis, Caluromys,* and *Marmosa.* The most evolved genus, *Didelphilicus,* lives on the genera *Philander* and *Didelphis.*

The Atopomelidae from South American marsupials resemble in their general aspect those living on Australian marsupials, but no genus is represented in both groups of marsupials. The genera which are the closest to each other are *Didelphoecius*, widespread in the American Didelphidae, and *Dasyurochirus*, well represented in the Australian Dasyuridae. The two genera, however, are sufficiently distinct to remain separate. These two familes of Marsupials harbour also closely related genera of Myobiidae, which confirms the affinities existing between these two families of marsupials.

The genus Listrophoroides

The rodents of tropical Africa and Asia are parasitized by the genus *Listrophoroides* which contains at present 16 subgenera and 159 species (Fain 1981a). The genus is completely absent in Europe. In America it is represented only by *Listrophoroides cucullatus* living on *Rattus rattus* imported from tropical Asia. In Australia it is represented by *L. cucullatus* and by an endemic species. This genus is practically confined to the Afro-asiatic region. It contains 53 species in the Oriental region (New-Guinea included), 56 species in the Afrotropical region, and 49 species in Madagascar.

In Asia, almost all the species are living on Murinae. In Africa this genus infests different and more primitive families of rodents and a primate (*Galago*). In Madagascar it infests not only the endemic rodents of the family Nesomyidae but also insectivores of the family Tenrecidae and primates of the family Lemuridae.

The multiplicity of subgenera and species found in Madagascar and the diversity of hosts parasitized are arguments for the antiquity of the genus *Listrophoroides* in Madagascar, it seems probable that it originated in Madagascar, probably, on the Tenrecidae.

In continental Africa the genus is represented by the subgenus *Alistrophorus* which is also represented in Madagascar.

In Asia most of the species belong to the typical subgenus which is also represented in continental Africa by a few species. The passage of the group to Asiatic Muridae probably happened by means of this typical subgenus, whose success on the Muridae of the Oriental region can be explained by the great development of the genus *Rattus* in this region.

We can conclude that the parallel host-parasite evolution is well marked in the Sarcoptidae and in the Listrophoroidea.

RELATIONSHIPS BETWEEN CERTAIN HOSTS AS SUGGESTED BY THE SIMILARITY OF THEIR MITE FAUNA

Relations between Hystricomorph rodents and Primates

In a previous paper dealing with parasitic mites of the family Rhyncoptidae (Fain 1965) I have drawn attention to the curious relationship which seems to exist between the Afrotropical hystricomorph rodents and some African or South American primates. Such a relationship was suggested by the discovery in these two groups of hosts of highly specialized mites very similar in morphology and belonging to the same genus or at least to a closely related genus. Some of these similarities could be explained by convergence, but convergence alone could not lead to such a degree of resemblance. These observations have been made for three different families of mites each belonging to a different order. (Fain 1982a).

(1) The family Rhyncoptidae (Astigmata) contains only one genus, *Rhyncoptes* (Lawrence 1956, with four species. These mites have a very particular morphology, probably relative to their mode of life. They have anterior parts of their body deeply sunk in the pilous follicle, the rest of the body being free. They are maintained in this position by means of their anterior legs which are strongly inflated and bear powerful hooks.

The typical species of this genus is *Rhyncoptes recurvidens* Lawrence, described from the South African porcupine *Hystrix africaeaustralis.* Three other species of the same genus from monkeys were described by me: *Rhyncoptes anastosi* was discovered in several South American monkeys (*Tamarinus, Leontocebus,* and *Oedipomidas*). A total of more than 20 specimens of this mite were discovered. The second species is *R. cebi,* discovered in the hair follicles of *Cebus albifrons* from Venezuela. The third species is *R. cercopitheci,* found in the hair follicles of *Cercopithecus mona campbelli* from West Africa.

(2) A similar situation exists in the family Halarachnidae (Mesostigmata) composed of several genera living in the respiratory tract of mammals, mainly Primates. One of these genera, *Rhinophaga,* is represented by six species parasitizing the nasal cavities and sinuses. Two of these species live in Afrotropical monkeys (*Cercopithecus* or *Papio*), one in a *Macacus* from Indonesia, one in the Organ-Outan, and two in *Atherurus africanus,* an hystricomorph rodent from Central Africa.

(3) The third family of mites found in similar conditions is that of the Psorergatidae, which live in the corneous layer of the the skin of mammals. Among the three genera described in the genus, one *Psorobia,* contains five species, each endemic for a different group of hosts. One lives on cattle, one on sheep, one on a Mustelidae, one on an Hystricomorph rodent, *Hystrix africaeaustralis,* and one on *Cercopithecus aethiops pygerythrus,* the two last hosts coming from South Africa.

These three examples suggest the existence of relationships between the African hystricomorph rodents and certain Afrotropical or Neotropical monkeys, the exact nature of which is unknown. We also ignore how some of these parasites have passed from Africa to South America, probably by the rafting of their hosts, in the early Eocene.

RELATIONS BETWEEN AFROTROPICAL AND NEOTROPICAL PRIMATES

Here follows a list of the families of mites which are represented in Primates of the Old World and the New World by either the same genus or by closely related genera (Fain 1982b).

(1) I have already dealt with the genus *Rhyncoptes* represented in South American and in Afrotropical monkeys.

(2) Another family of mites, the Lemurnyssidae, living in the nasal cavities, is represented in an African Lorisidae by one species of the genus *Lemurnyssus* (Astigmata) and in South American monkeys by three species of the genus *Mortelmansia,* which is very close to the former.

(3) The family Psoroptidae (Astigmata) consists at present of 10 subfamilies living on the skin of various mammals and producing mange. The subfamily Cebalginae, with six genera and seven species is endemic on South American monkeys. The Cebalginae are closely related to the Paracoroptinae, another subfamily of Psoroptidae which live on Afrotropical monkeys (Cercopithecides, Colobes, Chimpanze, Gorilla). They differ from the former mostly in some specialized characters.

SUMMARY

Evolution and parallel-evolution of host and parasite are considered in the acarines of the families Sarcoptidae, Listrophoridae, Chirodiscidae, and Atopomelidae, parasitic on mammals.

Phylogenetic evolution in the parasites is always of the regressive type. The mites which possess the most regressed external characters (dorsal shields, chaetotaxy, tarsal suckers, etc.) or with reduced legs by fusion of some segments, are the most evolved. As a rule the most regressed mites are found on the most evolved hosts.

The presence of some closely related mites on both South American and African monkeys and on African hystricomorph rodents suggests that these parasites have passed from Africa to South America with the hystricomorph rodents, probably by rafting in the Early Eocene.

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1.2 PHYLOGENETIC RELATIONSHIPS AMONG HIGHER TAXA IN THE ACARIFORMES, WITH PARTICULAR REFERENCE TO THE ASTIGMATA

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INTRODUCTION

Although the order Acariformes has been recognized as a natural group by most contemporary acarologists, relationships among the higher taxa within the Acariformes have been the subject of much controversy. This grouping of taxa under the equivalent inclusive names 'Trombidisarcoptiformes' (Oudemans 1931), Actinochitinosi (Grandjean 1935), Acariformes (Zachvatkin 1952), or Actinotrichida (Hammen 1972), has united certain taxa which have been hypothesized to be natural groups. The subgroups most generally recognized in recent classifications are the Prostigmata (=Actinedida), Oribatei, and Astigmata (=Acaridiae, Acaridida).

A phylogenetic analysis of the higher category relationships among acariform groups was undertaken for two reasons. Firstly, during an analysis of relationships within the Astigmata (OConnor 1981, 1982) it was realized that a well-supported hypothesis as to the relationships of the Astigmata, as a group, to other acariform lineages was required in order to properly use the method of outgroup comparisons to determine the within group character state polarities. Secondly, such an analysis will produce testable hypotheses of relationships (cladograms) which attempt to mirror the evolutionary history of the group. Such hypotheses will be of more use in both within group character analysis (Hammen 1981) and studies of higher order relationships (Hammen 1977) than the present vague or unsound hypotheses.

Previous workers have suggested several hypotheses of the relationships among the Prostigmata, Oribatei, and Astigmata, usually in the form of classifications. Whilst these classifications may not have been originally proposed as hypotheses of phylogenetic relationships, they may be treated as such, and tested using the methods of phylogenetic systematics (cladistics). Berlese (1897) regarded the Astigmata and Oribatei as closely related, specifically with the Astigmata as ancestors of the Oribatei. This inclusive group was regarded as the sister-group of the Prostigmata. Thor (1929) considered the Astigmata as ancestral to both Oribatei and Prostigmata. Oudemans (1923) placed the Oribatei and Astigmata as sister-groups, terming the inclusive group 'Sarcoptiformes', thus following Reuter (1909). He further regarded the Sarcoptiformes as the sister-group of the 'Trombidiformes' (=Prostigmata). This hypothesis has been accepted in many subsequent treatments, including those of Vitzthum, Baker & Wharton, Zachvatkin, and Hirschmann. An alternative hypothesis was suggested by Grandjean (1937, 1954), who rejected a close relationship between the Astigmata and Oribatei. He proposed that the Oribatei and Prostigmata were nearest relatives ('connected' by the Endeostigmata which he considered lay within the Prostigmata), and that this group was only distantly related to the Astigmata. This view is similar to that of Thor (1929) and has been adopted by T. E. Hughes and Evans *et al.* in their works on the British Acari. More recently, van der Hammen (1972) has suggested a relationship between the Astigmata and Tarsonemina, with this inclusive group as the sister-group of the Oribatei and the Prostigmata. This last hypothesis was clearly shown to be untrue

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by Lindquist (1976) regarding the position of the Tarsonemina, thus leaving the remainder of the hypothesis equivalent to that proposed by Grandjean.

METHODS

Phylogenetic systematics (cladistics) is a method used for developing hypotheses of evolutionary relationships based on ancestor–descendant relationships. This method is I believe, different from the methods used by previous workers cited above because the hypothesized relationships are based upon the sharing among taxa of *derived* character states, inherited from a common ancestor, in which the states first appeared through mutation or recombination. It hypothesizes relationships based on known evolutionary processes, as opposed to the older, more intuitive or subjective methods of analysis. They tended to accentuate differences rather than to stress relationships between groups.

The methods used here may be summarized briefly according to the following principles (Wiley 1981). First, all natural taxa must be hypothesized as monophyletic. That is, any natural group, whether named or not, must consist of hypothesized ancestral species together with all of its descendants. Groups consisting of descendants from different ancestors (polyphyletic groups) or groups consisting of only some of the descendants of a common ancestor (paraphyletic groups) are rejected as unnatural, arbitrary, and human constructs. Secondly, all monophyletic groups must be defined with respect to another monophyletic group (sister-group) with which it shares a most recent common ancestor. These two principles enable the construction of a nested set of phylogenetic hypotheses, usually presented in the form of a cladogram, from which a completely phylogenetic, natural classification may be derived. In practice, each taxon is defined by two sets of character states: derived character states hypothesized to have been present in the common ancestor of the taxon, and ancestral character states which have been modified in the sister-group of the taxon in question.

The problem of how one determines the ancestral versus the derived states of any character has been addressed by a number of recent workers. The general agreement has been that the only valid method for determining the direction of such morphoclines is the so-called 'outgroup' method, which requires a pre-existing phylogenetic hypothesis (Watrous & Wheeler 1981). In this method, a character state occurring in groups related to the group under study (on the basis of other hypothesized derived character states) is hypothesized to be ancestral within that group under study. The other state of the character, occurring only within the group under study, is hypothesized as the derived state.

In the present study, it was apparent from the outset that with the exception of the Astigmata, the major subdivisions of the Acariformes, generally accepted by previous workers, were not natural, monophyletic groups. The inclusion of the 'Endeostigmata' in the Prostigmata was based apparently on the mistaken idea that the podocephalic canals and their openings were homologous with the tracheae and stigmata of the 'Prostigmata' *sensu stricto*. Although this error was recognized early on by Grandjean, he continued to recognize the 'Endeostigmata' as part of the 'Prostigmata' on the basis of what now appear to be ancestral character states which provide no phylogenetic information.

To remedy this problem and to generate a new hypothesis of relationships within the Acariformes, I have analysed 64 characters having 286 character states in the following groups (all hypothesized to be monophyletic): each named family in the 'Endeostigmata' listed by

Kethley (1982); the Prostigmata (including all groups possessing stigmatic openings on the gnathosoma or anterior hysterosoma); the Astigmata; and each group within the Oribatei listed by Grandjean (1954, 1969) with some updating.

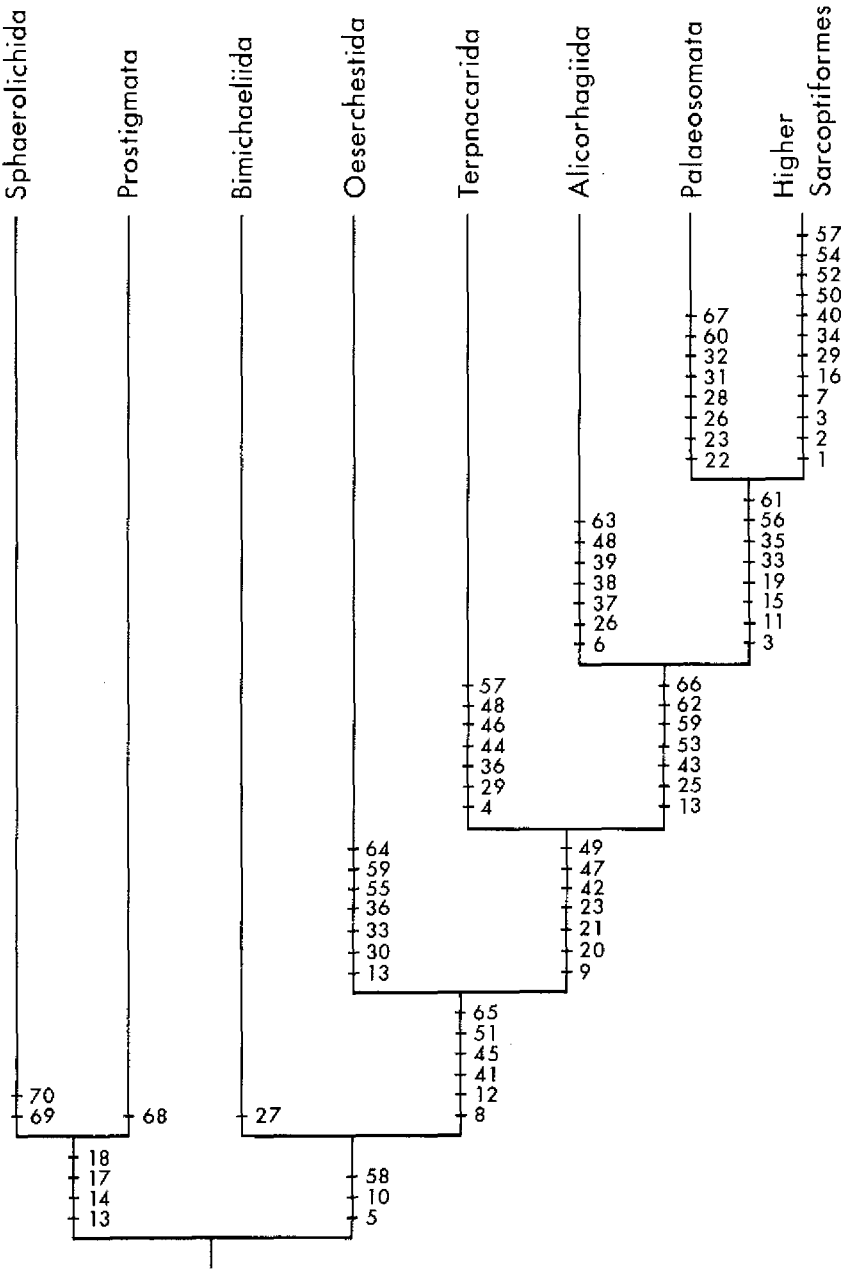

Fig. 1 – Cladogram of relationships among early derivative groups in the Acariformes. Derived character states listed by number in the Appendix.

RESULTS

The cladogram presented in Fig. 1 represents an hypothesis of the evolution of early derivative groups within the Acariformes. Further analysis of the group here termed 'higher Sarcoptiformes' has been completed; but present space limitations preclude a detailed discussion. The basic division of the Acariformes into two subgroups as defined by the first branching point of the cladogram represents a significant departure from previous hypotheses. It may be used in a phylogenetic classification to divide the order into two suborders. I retain the traditional names 'Trombidiformes' and 'Sarcoptiformes' for these groups since the present concepts conform generally to the traditional groupings under these names. They differ only in the reallocation of taxa formerly included in the paraphyletic Endeostigmata.

The present concept of the Trombidiformes is defined by the derived character states of the loss of primary segmentation, the loss of the anamorphic segments AN and PA, and the reduction to fewer than four pairs of setae on opisthosomal segment C and fewer than three pairs on segments D and E. With respect to its sister-group, the Trombidiformes ancestrally retain a setiform rutellum, an undifferentiated prodorsum, and solenidia on tarsus IV. This concept of the Trombidiformes includes the Prostigmata as a more restricted subgroup which is equivalent to the Prostigmata *sensu* Kethley (1982) less the Endeostigmata *sensu* Kethley (1982). The Trombidiformes also includes two families from the former Endeostigmata, the Sphaerolichidae and Lordalychidae. These two families present a number of shared derived character states indicating that the two form a monophyletic group for which I propose the infraordinal rank Sphaerolichida. Major taxa within the Prostigmata may also be ranked as infraorders in sequence with the Sphaerolichida (see Lindquist 1976) for phylogenetic hypotheses concerning the groups within the Prostigmata). I propose to sequence the taxa in both suborders at infraordinal rank to eliminate the use of the rank 'cohort' and its derivatives in acarine classification. These ranks are used by other zoologists to denote levels between class and order in Linnaean hierarchies. Although the use of these ranks between suborder and superfamily is of long standing in acarine classification, it appears to be of greater utility to bring acarine classification in line with that of other groups in terms of the Linnaean hierarchy.

The suborder Sarcoptiformes as here defined includes the remaining acariform groups. The suborder may be defined by the possession of a toothed rutellum, differentiated prodorsal region, and the loss of solenidia from tarsus IV (derived states). While retaining (in early derivative groups) primary segmentation, normal anamorphic addition of segments AN and PA, and the ancestral number of four pairs of dorsal opisthosomal setae on segment C and three on segments D and E. Derived character states for each monophyletic group within the Sarcoptiformes (through the Palaeosomata) are indicated on the cladogram (Fig. 1) and enumerated in the Appendix. The new taxa here recognized at infraordinal rank are the following: Bimichaeliida, including the families Bimichaeliidae (=Pachygnathidae and Alycidae of authors) and Nanorchestidae; Oeserchestida, including the Oeserchestidae and Grandjeanicidae; Terpnacarida, with the single family Terpnacaridae; Alicorhagiida, with the single family Alicorhagiidae; and Palaeosomata, including several superfamilial groups as defined by Grandjean (1954, 1969). Additional infraordinal taxa within the Sarcoptiformes should be recognized (OConnor 1981); however, these will not be discussed here owing to space limitations.

A major conclusion of this study with respect to the higher categories formerly recognized has been the introduction of a new hypothesis of relationships between the Astigmata and Oribatei. The analysis of these characters indicates that the Astigmata is not a group of early derivative acariform mites as envisioned by most prior workers. Instead, it is proposed here that

the Astigmata has its closest relationship with several groups of relatively advanced 'oribatid' mites. Of the 'oribatid' groups analysed in this study, the Astigmata share a number of derived character states with the Brachypilina, Holosomata, Perlohmanniidae, Collohmanniidae, Phthiracaroidea, and Epilohmanniidae. These character states include presence of the lateral opisthosomal glands, the elongation of the tibial solenidia, and the reduction or loss of the setae from opisthosomal segment F. The first of these character states is also shared with the Parhypochthonioidea. These are derived states not shared with any of the groups mentioned earlier in this paper nor with the Enarthronota, Lohmanniidae, or Eulohmanniidae.

At this point, it is necessary to discuss some particular characters which have been previously cited as not supporting a relationship between the Astigmata and oribatid groups. The absence of a rutellum is often cited as a character state of the Astigmata. If the gnathosoma of most Astigmata is analysed in detail, it becomes apparent that not only is a rutellum present, but it is of a similar form (atelebasic to pantelebasic form of Grandjean) to that found in the 'oribatid' groups cited above as sharing other derived character states. This type of rutellum consists of the ancestral shaft with apical teeth and an enlarged median lobe which is more or less fused with the ventral apex of the subcapitulum. Akimov (1979) illustrates this region of the gnathosoma of the Acaridae and refers to the lateral, toothed portion as a rutellum, but not the continuous median lobe. In the Astigmata, the median rutellar lobes are completely fused to the subcapitulum, covering the median subcapitular lobes.

The opisthosomal chaetotaxy of the Astigmata has been the subject of much debate; however, adoption of the system of chaetotactic designations based on ancestral segmentation developed by Grandjean for the 'oribatid' mites, enables homologies to be hypothesized with little room for doubt. The loss of a row of setae from the ancestral pattern found in early derivative Sarcoptiformes is apparent throughout ontogeny in the Astigmata. That this lost row is homologous with that of segment F, the reduced or lost row in the more derived 'oribatid' groups, is demonstrated by two pieces of evidence. In the Astigmata, as in the other groups with reduced setae on row F, the cupule *ip* retains its ancestral position laterad of the missing setal row, that is, the cupule is positioned *between* two setal rows (E and H). Secondly, in early derivative Astigmata, notably some Histiostomatidae, there appears a structure medial to cupule *ip* which has been interpreted as a 'pore' or even an extra cupule. That this 'pore' is a vestige of the absent seta f_2 is clear from its position and morphological similarity to the setal vestiges present on segment F in such groups as the Perlohmanniidae.

The remaining problem characters of the Astigmata fall into two categories. In the first group are the autapomorphies, or unique derived character states of the Astigmata. Grandjean (1937) cited a number of these as evidence that the Astigmata and Oribatei could not be closely related. However, autapomorphies such as the modifications of the deutonymph in the Astigmata and changes in the genitalia due to the evolution of direct copulation, are useful in phylogenetic analysis only in the sense that they define monophyletic groups. Such states are of no use in determining relationships within a group so defined, or in determining relationships of the group to others.

The other character states pose more difficult questions. The absence of body sclerotization in the majority of astigmatid taxa has often been cited as an ancestral character state. I believe this character state reflects a general pattern of neoteny in the Astigmata which can be demonstrated by a large series of characters. In the 'oribatid' groups cited above, as sharing derived character states with the Astigmata, the body is generally well-sclerotized in the adult. The pre-adult instars, however, are not sclerotized. Similar ontogenetic changes occur in such characters as stegasimy of the prodorsum, addition of setae in the adoral, subcapitular, palpal,

coxal, pedal, genital, aggenital, and paraproctal regions, addition of pedal solenidia, addition of the true pretarsal claws, and development of the female ovipositor. In these characters, the Astigmata generally exhibit character states found in pre-adult instars of the cited 'oribatid' groups. That these character states are not necessarily ancestral is supported by comparisons with the early derivative sarcoptiform groups such as the Bimichaeliida, etc.

The ontogenetic *patterns* themselves are useful as characters, and in many cases, support the hypothesis that the Astigmata are derived from a relatively advanced 'oribatid' group. One hypothesis suggesting the neoteny of the Astigmata relates to the strong metamorphosis which takes place between the protonymph and deutonymph. Many ontogenetic patterns are similar to the ancestral patterns of the Sarcoptiformes, especially in the early derivative astigmatid groups such as the Schizoglyphidae. The reverse metamorphosis at the tritonymphal moult in most Astigmata entails a return to a basically protonymphal morphology. For example, the median suckers of the attachment organ in the astigmatid deutonymph are homologues of setae an_1, an_2, and an_3, setae which appear ancestrally in the deutonymph. In most Astigmata, these setae are then suppressed in the tritonymph, in most cases reappearing only in the adult female.

Further evidence of neoteny in the Astigmata involves two trends. One is additional neoteny, ultimately resulting in completely larviform adults whose only ontogenetic addition is that of functional genitalia. This trend is found in several groups of parasitic Astigmata, notably in the Knemidokoptidae, Sarcoptidae (=Teinocoptidae), and Apionacaridae. Secondly, neotenic trends are apparently reversed in several independent groups of Astigmata, resulting in strongly sclerotized, stegasime adults with well-sclerotized coxal fields, genital valves, and legs. These groups include some Glycyphagidae, Algophagidae, and Histiostomatidae.

SUMMARY

A phylogenetic analysis of relationships among the higher taxa in the order Acariformes results in a hypothesis of relationships quite different from prior conceptions. The order is divided into two suborders, for which the names Trombidiformes (including the Prostigmata and Sphaerolichida) and Sarcoptiformes (including the Astigmata, oribatid groups, and remaining endeostigmatid groups) are retained. The Astigmata are proposed to have had a most recent common ancestor with oribatid groups possessing the lateral opisthosomal gland, elongate tibial solenidia, and reduced setation on opisthosomal segment F. Apparently, ancestral character states in the Astigmata all relate to neotenous trends already present in the related oribatid groups. In a truly phylogenetic classification, the Oribatei is seen as a paraphyletic group (excluding some descendants of a common ancestor, the Astigmata) and must be rejected as a formal group. The suborder Sarcoptiformes, as presently defined, is a natural group and should serve to replace Oribatei, particularly as several early derivative lineages formerly considered in the Trombidiformes are now placed with their nearest sarcoptiform relatives.

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APPENDIX

Derived character states used to develop phylogenetic hypothesis of relationships among early derivative taxa in the Acariformes (Fig. 1).

1. Cheliceral trochanter reduced or absent.
2. Ventral subcapitular lobe absent.
3. Dorsal subcapitular lobe with denticles.
4. Lateral subcapitular lobes with one larval and one protonymphal setal pairs.
5. Rutellum of a simple shaft with teeth.
6. Two pairs of larval and one pair of protonymphal subcapitular setae.
7. Palpal tarsus with three eupathidial setae.
8. Naso broad with median eye.
9. Lateral eyes absent.
10. Prodorsum differentiated but unsclerotized.
11. Prodorsum sclerotized in adult.
12. Rostral setae no longer as trichobothria.
13. Hysterosoma without primary segmentation.
14. Anamorphic segments AN and PA not added in ontogeny.
15. Adult hysterosoma with numerous sclerites per ancestral segment.
16. Adult hysterosoma with at most one sclerite per ancestral segment.
17. Hysterosomal segment C with fewer than four pairs of setae.
18. Hysterosomal segments D and E with fewer than two pairs of setae.

19. Hysterosomal segment F with fewer than three pairs of setae.
20. Hysterosomal segment H with four pairs of larval setae, transcupular pair lost in post-larval ontogeny.
21. Hysterosomal segment PS with four pairs of larval setae, transcupular pair lost in post-larval ontogeny.
22. Hysterosomal segment PS with five to seven pairs of larval setae, transcupular pair lost in post-larval ontogeny.
23. Hysterosomal segment AD with four pairs of setae in protonymph, transcupular pair lost in post-protonymphal ontogeny.
24. Hysterosomal segment AD with five to six pairs of setae throughout post-larval ontogeny.
25. Hysterosomal segment PA with one pair of setae throughout post-deutonymphal ontogeny.
26. Hysterosomal segment PA without setae.
27. All hysterosomal segments neotrichous.
28. Hysterosomal cupules *iad* and *ian* absent.
29. Coxal fields I with three fundamental setal pairs throughout ontogeny.
30. Coxal fields I with one fundamental setal pair throughout ontogeny.
31. Coxal fields II with one fundamental and one or more accessory setal pairs.
32. Coxal fields III with two fundamental and one or more accessory setal pairs.
33. Coxal fields IV with one fundamental and four accessory setal pairs.
34. Coxal fields IV with one fundamental and two to three accessory setal pairs.
35. Genital valves sclerotized in adult.
36. Genital valves with one pair of protonymphal setae, three deutonymphal setae, and at least one additional pair added in tritonymph or adult.
37. Eugenital setae absent in adult.
38. Ovipositor absent in female.
39. Obligate parthenogenesis, males never found.
40. Femora of adults not divided.
41. Femoral solenidia absent.
42. Genu I with three fundamental solenidia.
43. Genu II with one fundamental solenidion throughout ontogeny.
44. Genu II without solenidia.
45. Genu III with one fundamental solenidion, adult maximum two.
46. Genu III without solenidia.
47. Genu IV with no fundamental and one accessory solenidion.
48. Genu IV without solenidia.
49. Tibia I with two fundamental solendia, adult maximum four.
50. Tibia I with two fundamental solenidia, adult maximum three.
51. Tibia II with two fundamental solenidia throughout ontogeny.
52. Tibia II with one fundamental solenidion throughout ontogeny.
53. Tibia III with one fundamental solendion.
54. Tarsus I with one fundamental solenidion, adult maximum three.
55. Tarsus I hypersolenidious.
56. Tarsus I with solenidion omega-3 tritonymphal.
57. Tarsus II with one fundamental solenidion, adult maximum two.
58. Tarsus IV without solenidia.
59. Famulus II absent.
60. Setation of adult trochanters 0-1-2-2.

61. Genua with 3-3-2-0 fundamental setae.
62. True claws claw-like, with rays or setules, absent in larva.
63. True claws absent on pretarsus I only.
64. True claws absent on all pretarsi throughout ontogeny.
65. Empodium claw-like, with setules.
66. Empodium claw-like, without setules.
67. Hysterosomal setae non-birefringent.
68. Tracheal system opening via anterior 'prostigmata'.
69. Opisthosomal dorsum strongly arched.
70. Legs IV modified for jumping.

1.3 CURRENT THEORIES ON THE EVOLUTION OF MAJOR GROUPS OF ACARI AND ON THEIR RELATIONSHIPS WITH OTHER GROUPS OF ARACHNIDA, WITH CONSEQUENT IMPLICATIONS FOR THEIR CLASSIFICATION

Evert E. Lindquist†

INTRODUCTION

Various authors (Main 1972, Lindquist 1975, Weygoldt & Paulus 1979a,b) have noted that, owing to the great age and early divergence of major arachnid groups, there are profound differences in structure, development, and ways of life between extant groups. There appears to have been an early major adaptive radiation during mid-Palaeozoic (Silurian-Devonian) times followed by an arrestment that has persisted since the late Palaeozoic, such that representatives of most arachnid orders look essentially the same today as they did 250 million years ago. Even in some mites, fossils from the Devonian show family-level similarities with extant representatives of relatively 'primitive' (early derivative) endeostigmatic and oribatid mites (Hirst 1923, Dubinin 1962, Rolfe 1982).

The mites, however, are singularly exceptional to this general arrestment of adaptive radiation that persisted in other arachnid groups, since remarkable secondary radiations occurred apparently during late Mesozoic and early Cenozoic times. Among the mites, there is no question that subgroups have repeatedly and independently broken out of the restraints of predatory, scavenging, and fungivorous ways of life to evolve as plant feeders, and parasites and commensals of invertebrate and vertebrate animals. Some mite groups, even at the *family* level, continue to undergo such diversification (e.g. Laelapidae, Tydeidae, Tarsonemidae), wheras others have become locked orthoselectively into one or another way of life long ago (e.g. Eriophyoidea as plant parasites, Parasitengona as protelian parasites of animals).

There is also little question that virtually *all* of these secondary radiations began *within* the major groups of mites – Parasitiformes and Acariformes – that is, well *after* the evolution of the ancestral stocks of these two groups. The question that I would like to address here is: During the earlier, primary adaptive radiation(s) of the major arachnid groups, was there an early initial and single evolution of an ancestral lineage of mites *prior* to their diversification into two or more major groups, *or* were there two or more lineages of mite-like arachnids which evolved independently from separate ancestors and which, though they came to resemble each other to a considerable extent through convergence, continued to diversify as separate groups? In other words, are the mites a natural, monophyletic group or are they an artificial, paraphyletic or diphyletic assemblage? It is important to consider paraphyly and diphyly as separate alternatives. If paraphyly seems to be the more probable of the two, then a case could be made for retaining 'Acari' as a natural group by redefining it more extensively so as to change it to a monophyletic group. For example, if Anactinotrichida is shown to be the sister-group of the Ricinulei, and Acariformes the out-group, then the Acari could be redefined to embrace all three of these groups.

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In the following discussions, I use 'Anactinotrichida' for one major acarine group comprising the Opilioacarida, Holothyrida, Ixodida, and Gamasida. I use 'Parasitiformes' to indicate anactinotrichid mites *excluding* the Opilioacarida, but *including* the Holothyrida (except in Table 1 where Holothyrida is also treated separately). 'Actinotrichida' is used interchangeably with 'Acariformes' for the second major group comprising the Actinedida (or Prostigmata), Oribatida, and Acaridida. The current cladistic terms used herein are defined adequately by OConnor in this volume (paper 1.2).

CRITICAL REVIEW OF CURRENT THEORIES

During the first half of this century, the Acari was generally considered, without serious question, as a 'natural' group (whatever that meant). The earlier literature on phylogeny of mites was reviewed by Woolley (1961), and will not be considered here. Some of the observations of Grandjean (1935a, 1936, 1954) focused on fundamental differences between the two major groups of Acari, for which he proposed 'Actinochitinosi' and 'Anactinochitinosi' in 1935. He stopped short, however, of suggesting that either of these groups was more closely related to another order of Arachnida than to each other. This tempers the statements by Woolley (1961) that Grandjean 'considered a polyphyletic origin for the Acarina', and by Krantz (1978) that Grandjean 'and others believe the Acari to be of diphyletic origin'. André & Lamy (1937 – not seen by the author) apparently proposed that the Parasitiformes arose from an Opiliones-like ancestor, separately from other mites. On the other hand, Vitzthum (1941–43) related the Parasitiformes to the Ricinulei based on their sharing a six-legged larva and a pair of lateral prosomal stigmata. Baker & Wharton (1952) alluded to the obscurity of phylogenetic relationships of mites, and to the idea of their polyphyletic origin being topical. However, no comprehensive presentation on polyphyly was advanced. During the same period the distinctiveness of the Acari as a whole, based on the presence of a gnathosoma, the undivided nature of the prosoma, and the absence of a prosomal-opisthosomal constriction and of an external opisthosomal segmentation, was emphasized (Snodgrass 1952, Petrunkevitch 1949, Baker & Wharton 1952).

Thoughts on the origin of mites have diversified dramatically during the second half of this century. In a pioneering and challenging paper, Zachvatkin (1952) pointed out the seemingly near impossibility of a general definition of Acari as a natural group, in contrast to other orders of Arachnida which were readily definable both morphologically and biologically. He made the first serious attempt to recognize a polyphyletic nature in the mites, to relate their major groups to different higher groupings of arachnids, and to propose a 'natural' higher classification of the arachnid and other chelicerate orders (Table 2). He was first to coin the term 'Acariformes' (equivalent to Grandjean's earlier 'Actinochitinosi') for the Trombidiformes + Sarcoptiformes assemblage, and related this group most closely to the Solifugae and Palpigradi in his new superorder the Actinochaeta. He placed the Parasitiformes and Opilioacariformes in another new superorder, the Actinoderma. Note that he not only treated these mite groups as separate orders, but he proposed each as being more closely related to another order of arachnids than to each other. Even within the Actinoderma, Parasitiformes was related as closest to the Ricinulei, and Opilioacariformes as closest to the Opiliones.

It is difficult to disagree with Zachvatkin regarding the distinctiveness of his three major groupings of mites. Indeed, this was more eloquently presented previously by Grandjean (1936). But the problem with Zachvatkin's scheme of relationships and classification, as we shall see later in this presentation, is that it is based largely on the degree and nature of reciprocal *differences*

rather than on the presence of shared derived character states, no matter how few they may be. To his defence, he would not have been aware of the phylogenetic systematic methodology of Hennig (1950), which was probably unknown to him during the time of preparing his 1952 paper (which was in fact completed after his death in December, 1950 by A. B. Lange).

During the last twenty years, various authors (e.g. van der Hammen 1972, 1977a,b, Athias-Henriot 1971, 1975) have followed Zachvatkin (1952) in recognizing the mites as diphyletic or polyphyletic in origin, to the point where at present this is almost taken for granted in some modern introductory texts, manuals, and references (e.g., Evans & Till 1979, Krantz 1978, Johnston 1982). Other authors, however, have reasserted the hypothesis that mites comprise a natural group – the Acari (Dubinin 1959, 1962, Sitnikova 1978, Weygoldt & Paulus 1979a,b). Of particular interest is that the arguments given by proponents of either school – monophyly or polyphyly – do not support each other closely. For example, the diphyletic classification of mites of Zachvatkin (1952) and of van der Hammen (1977a,b) are discordant. Similarly, but more suprisingly, the arguments for a monophyletic Acari by Sitnikova (1978) and Weygoldt & Paulus (1979a,b) have little in common. One reason for discord in both camps lies in the differing methodologies of phylogenetic assessment. Only in the study of Weygoldt & Paulus is a concerted effort made to apply the cladistic methodology of Hennig (1950, 1966); and even in that study, the establishment of character state polarities (or transformation series) was not fully presented. Authors such as van der Hammen have applied certain terms used in cladistics, but they have not applied the methodology in a convincing manner.

At this point, then, it is imperative to review the major characters considered by various authors as important to supporting their cases for polyphyly or monophyly in mites. In doing so, I have also considered some other characters that were not used in previous phylogenetic analysis. A few characters are omitted from this review because their presence and homology in other arachnid orders is not determined, e.g., presence of supracoxal setae, famuli, mucronate and coronidial setae, etc.

The rigorous exercise of proposing polarities or transformation series for states of homologous characters – and thus in laying one's cards out on the table, so to speak – is the most important preliminary step in cladistic analysis; yet too often this is not presented in detail sufficient for critical evaluation by others. My discussions for each of the 40 characters and their primitive and derived states are given in the Appendix to this paper. A summary is given in Table 1, which in part indicates character state polarities. Note that for each taxon, the character state indicated is ancestral and does not indicate possible further transformation of the character within derivative subgroups of the taxon; for example, trichobothria (character nr. 20) are indicated as present in Acariformes even though they are lost secondarily in more derivative subgroups of Acariformes. In all cases, decisions made on polarities are based on the out-group comparison method advocated by cladistic methodology. Some of these decisions are obvious; others are more problematic (see Appendix).

A brief review of the current phylogenetic and higher classificatory schemes proposed by various authorities for the mites follows, succeeded by a tentative conclusion based on the characters discussed in the Appendix and listed in Table 1.

The scheme of Zachvatkin (1952) is shown in Table 2. Of the 9 characteristics given for the Actinochaeta, the 6th, 7th, and parts of the 2nd (lack of a complete sternum), 3rd (pregenital segment not reduced), and 5th (empodium clawlike) are plesiomorphies. The 4th and part of the 3rd (opisthosomal segments not abruptly reduced) are not distinctive, at least among the major groups of mites. The 1st and 2nd include misinterpretation of dorsal shielding as far as the Acariformes is concerned, since this group retains the basic prosomal-opisthosomal body

Table 1

Summary of analysis of character state polarites

ORDERS / CHARACTERS	Parasitiformes	Holothyrida	Opilioacarida	Acariformes	Ricinulei	Opiliones	Solifugae	Pseudoscorpiones	Palpigradi	Araneae	Amblypygi	Uropygi
1. Embryo inversion	–	?	?	?	?	–	+	–	?	+	+	+
2. Number opisth. segments embryo.	6	?	?	6?	?	9	11	12	?	12	?	12
3. Larval legs IV.	–	–	–	–	–	+	+	+	+	+	+	+
4. Number stases.	4	6?	6	6	6?	5–9	9–10	5	?	3–15	6–9	6
5. Number opisth. (+ anamorphic) segments.	10?	10?	13?	7 (+3)	13	11	11	12	13	12	12	13
6. Larval caudal bend.	+	?	–	+	–	–	–	–	–	–	–	–
7. Prosomal tagma.	–	–	+	+	+	+	+	+	+	+	+	+
8. Limb tissue regression.	–	–	–	+	–	–	–	–	–	–	–	–
9. Gnathosoma	+	+	+	+	+	–	–	–	–	–	–	–
10. Labrum.	+	+	+	+	+	?	+	?	?	?	?	?
11. Lateral lips.	al	al	a	a	–	–	–	–	–	–	–	–
12. Rutella	+	+	+	+	–	–	–	–	–	–	–	–
13. Larval subcapitular setae	2	2?	2	5	∞	..	..	..	..	..	..	..
14. Cheliceral setae.	1–2	1–2	4	2	∞	6+	∞	∞	6–7	∞	∞	∞
15. Cheliceral lyrifissures	2	2	2	1	1?	1?	?	3+	0	∞	?	?
16. Gnathotectum	+	+	?	–	–	..	..	..	..	..	..	..
17. Palpal apotele.	scl	scl	cl	–	ch	cl	ad	ch	cl	cl	rcl	rcl
18. Integument pigment.	–	+	+	+	–	?	?	–	?	–	–	–
19. Actinopilin.	–	–	–	+	–	–	?	?	–	?	?	?
20. Trichobothria	–	–	–	+	–	–	+	+	+	+	?	?
21. Solenidia.	+?	+	+	+	+	+	+	?	–	?	?	?
22. Idiosomal lyrifissure reduction	al	al	a	a2	–	–	?	?	0	–	–	–
23. Eye pairs medial	0	0	0	1	0	0	1	0	0	1	1	1
23. Eye pairs lateral.	0–1	0	2–3	2	2?	1–2	1–2	1–2	0	3	3	3

Table 1

Summary of analysis of character state polarites

CHARACTERS \ ORDERS	Parasitiformes	Holothyrida	Opilioacarida	Acariformes	Ricinulei	Opiliones	Solifugae	Pseudoscorpiones	Palpigradi	Araneae	Amblypygi	Uropygi
24. Stigmata: no. pairs	1	1	4	0	1	1	3	2	0?	2L	2L	2L
24. Stigmata: seg. no.	?	?	9–12	–	6?	8	5,9–11	9–10	?	8–9	8–9	8–9
25. Coxal glands	vI	vI	vI	dI	vI	v3	vP	v3	vI	vI,3	vI,3	vI
26. Tritosternum	+	+	+	–	+	–	–	–	–	–	+	–
27. Sternal setae reduction.	++	++	++	+	–	–	–	–	–	–	–	–
28. Claparède organs larval (embryonic).	–	–	–	+	–	(?)	+	–	(?)	–	(+)	(+)
29. Genital verrucae, segment no.	–	–	8?	8–10	–	–	–	–	8–11	–	–	–
30. Eversible ovipositor.	–	–	+	+	–	+	?	?	+	–	?	?
31. Larval postanal seta.	+	+?	+	–	–	?	..	..	..	..	..	..
32. Leg coxae free.	+	+	+	–	–	–	–	–	+I	–	–	–
33. Trochanters III-IV divided.	–	–	a1	–	a	–	a	–	–	–	–	–
34. Femora divided.	2_0	2_0	2_0	1_0	–	–	–	1_0	–	–	–	–
35. Tarsi divided.	2_0	2_0	1_0	–	1_0	1_0	1_0	1_0	1_0	1_0	1_0	1_0
36. Acrotarsus: I	+	+	+	–	+	+	+	–	+	–	+	+
36. Acrotarsus: II-IV	–	–	+	–	+	+	+	–	+	–	+	+
37. Pretarsal setal pairs	1	1	2	0	0	0	1–4?	0	0	0?	0	0
38. Empodium	–	–	–	+	–	+	–	+	+	±	+?	+?
39. Spermatozoan structure.	a2	?	a2	a3	a1?	–	a3?	–	–	a	a	a
40. Ingestion of solids.	+	?	+	+	–	+?	–	–	–	–	–	–

Symbols: –, lacking or not formed; +, present; . ., structure not applicable in taxon; ∞, many; ch, chelate; cl, clawed; rcl, raptorial-clawed; scl, subterminal-clawed; ad, adhesive; L, lungs; vI, v3, vP, opening ventrally in region of leg I, III, palp, respectively; dI, opening dorsally above leg I; I_0, primary; 2_0, secondary; a, a1–3, apomorphies 1 to 3, respectively. Horizontal underlining brackets indicate synapomorphies. See Appendix for further clarification.

plan. Parts of the 5th also include misinterpretation, since a well-formed palptarsus is primitively present in Acariformes, as is the genual segment of all the legs; lack of a genual segment in the Solifugae, Palpigradi, and Pseudoscorpionida may be a matter of incorrect homologies of leg segments. The 8th (true anamorphosis) and 9th (true actinopilin), characteristic of the Acariformes, have not been confirmed in other orders of Arachnida. In referring to the general presence of paired, metameric, ventral organs such as Claparède's organ and genital verrucae, the 6th characteristic is plesiomorphic; the form, ontogeny, and function of these organs may be modified in apomorphic ways as in the Acariformes, but this is not shared with any of the other arachnid orders. We are left with no synapomorphic evidence for the Actinochaeta as a monophyletic grouping of orders, or for the Acariformes being more closely related phylogenetically to any of the orders in that grouping than it is to the Opilioacarida and Parasitiformes.

Of the 9 characterisitcs given for Zachvatkin's Actinoderma, the 1st (incorrect for the Parasitiformes), 2nd, 4th, 5th, 8th, and 9th are plesiomorphies. The 3rd and 7th do not hold for the Opilioacarida, nor does the 3rd for the Parasitiformes. The 6th represents losses of metameric structures, primarily of the opisthosoma, that have probably occurred repeatedly and independently among several orders of the Arachnida. This is an example of homoplasy, and at best, might be used as secondary evidence to support a relationship between the Opilioacarida, Parasitiformes, and perhaps the Ricinulei and Opiliones. Again, we are left with no sound synapomorphic evidence for the Actinoderma as a monophyletic grouping of orders, or for the Opilioacarida and Parasitiformes being more closely related phylogenetically to any of the orders in this grouping than they are to the Acariformes.

The scheme of van der Hammen (1977a,b, 1979a) is shown in Table 3. Of the 9 characteristics given for the Epimerata (=Acoxata), the 1st, 4th, 6th, and 7th are plesiomorphies. The 2nd and 3rd involve uncertain leg segment homologies. In the Palpigradi, the basal free segment may be a free coxa, in which case there is only one femoral segment, as in most other arachnid orders; also, a primarily divided femur is not an autapomorphy of this group, since it is present in the Pseudoscorpionida, which is excluded from this group. The condition of an entire tarsus in the Acariformes excludes a basi- and telo-tarsal division, whereas the tarsus subdivided into 2 or more segments on all legs in the Palpigradi does not exclude a basi- and telo-tarsal division. The 5th involves uncertain homology of famulus-like structures; this also is not autapomorphic for this group, since a famulus is present on tarsi I to IV of the Ricinulei, which is excluded from this group. We are left with no synapomorphic evidence for the Epimerata as a monophyletic group, or for the Acariformes (Actinotrichida) being more closely related phylogenetically to the Palpigradi than it is to the Opilioacarida and Parasitiformes.

Of the approximately 16 characteristics given for van der Hammen's Cryptognomae, the 4th, 5th, and 11th are plesiomorphies. The 1st, 2nd, 3rd, 8th, 10th, and 12th are not autapomorphic for this group, since a hexapod larva, six postembryonic stases, and a movable gnathosoma are present in the Acariformes, the lack of trichobothria is characteristic of the Opiliones, and the subdivision of trochanters III-IV and loss of the empodial claw occur in the Solifugae. The 6th, 13th, 14th, and 15th involve structures of uncertain homology: homologies of stigmata are problematic, and segmental location of those in the Opilioacarida is similar to that of the Solifugae and Pseudoscorpionida, which are excluded from this group; the sunken tarsal sensilla of the Ricinulei are probably not homologous with those of the Haller's organ cluster of the Opilioacarida, Holothyrida, and Ixodida, since they are of different form and arrangement, and are not restricted to tarsus I; mucronate setae and coronidia or solenidiform setae of legs may be subject to homoplasy: they are not necessarily homologous between the Ricinulei and Opilioacarida, and their occurrence in other arachnid orders outside of this group-

Table 2

Scheme of Zachvatkin (1952): Classification of chelicerate orders, and characteristics of Actinochaeta versus Actinoderma Class Chelicerata

Superorder 1. Merostomata superord. nov.
- Synziphosura
- Xiphosura

Superorder 2. Holactinochitinosi superord. nov.
- Scorpiones
- Thelyphones (=Holopeltidia)

Superorder 3. Actinochaeta superord. nov.
- Palpigradi
- Solifugae
- Acariformes ord. nov (=Actinochitinosi)
- Tartarides (=Schizopeltidia, =Uropygi)
- Chelonethi (=Pseudoscorpiones)

Superorder 4. Actinoderma superord. nov.
- Phrynides (=Amblypygi)
- Araneae
- Ricinulei
- Parasitiformes (=Anactinochitinosi)
- Opiliones
- Opilioacarina (=Notostigmata)
- Anthracomarti

Arachnida-Actinochaeta (Actinotrichida)	Arachnida-Actinoderma (Anactinotrichida)
1. Body divided into proterosoma and hysterosoma.	• Body divided into prosoma and opisthosoma.
2. Head covered above by primitive propeltidium; meso- and meta-peltidium distinct. Undivided sternum absent.	• Prosoma covered by single carapace with little or no indication of peltidial divisions. Undivided sternum usually present.
3. Pregenital segment hardly reduced. Abdominal segments gradually diminishing posteriorly, not forming anal macrosomite.	• Pregenital segment strongly reduced, forming waist. Last 3 abdominal segements forming abrupt, reduced anal macrosomite.
4. Coxae regularly arranged, usually converged along midline.	• Coxae radially arranged, usually well separated by sternum.
5. Femora divided, genua absent. Palpi lacking distinct pretarsus. Empodium often clawlike.	• Femora usually entire, genua present. Palpi usually with distinct pretarsus. Empodium rarely clawlike.
6. Coxal organs present, sometimes richly developed (Palpigradi).	◦ Coxal organs lacking.
7. External female genitalia a trilobed cone or a short vulva with usually longitudinal slit.	• External female genitalia a transverse slit covered by skin folds or by an unpaired valve.
8. Development epimorphic with traces of anamorphosis.	◦ Development purely epimorphic.
9. Setae and derivatives with actino-chitinous core.	• Setae lacking actinochitinous core.

Table 3

Scheme of van der Hammen (1977–79): classification of chelicerate orders and characteristics of Epimerata versus Cryptognomae

Classification of Chelicerata

1. Epimerata	Palpigradi
	Actinotrichida
2. Cryptognomae	Anactinotrichida
	Ricinulei
	?Architarbi
3. Opilionidea	Opilionida
4. Apatellata	Solifugae
	?Kustarachnae
	Pseudoscorpionida
5. Arachnidea	Schizomida
	Uropygi
	Amblypygi
	Araneida
	Trigonotarbi
?	Haptopoda
	Anthracomarti
6. Merostomata	Xiphosura
	Eurypterida
7. Scorpionidea	Scorpionida

Epimerata (Acoxata)	Cryptognomae
1. Leg coxae lacking, e.g., coxisterna.	1. Larvae with 3 pairs legs.
2. Leg femora subdivided.	2. 6 postembryonic stases.
3. Legs lack basitarsus.	3. Movable gnathosoma.
4. Supracoxal seta present.	4. Tritosternum present.
5. Leg tarsi with famulus.	5. Coxal glands associated with subcapitular gutter.
6. Trichobothria present on legs.	6. Stigmata present, 4 to 1 pairs.
7. Legs with empodial claw.	7. Tendency, immovable palpal tibia & tarsus.
8. Stigmata lacking, original respiration cuticular.	8. Trichobothira lacking.
9. Ingestion & internal digestion of solid food.	9. Leg coxae free, associated with with sterna.
	10. Legs III–IV with 2 trochanters.
	11. Legs with basi- & telo-tarsus.
	12. Leg apoteles 2-clawed, empodium lacking.
	13. Tarsus I often with sunken organs.
	14. Legs with mucronate setae.
	15. Legs with coronidia (solenidiform).
	16. Chelicerae often with ventral oncophysis (elaborated arthrodial membrane).

ing is inadequately explored (I have observed mucronate setae on tarsi I and II of Opiliones). The 9th and 16th do not hold for the Ricinulei, nor does the 16th for the Opilioacarida. The 7th represents a tendency towards a tibio-tarsal fusion of the palpal segments, which is not well manifested in some Opilioacarida. This may be another example of homoplasy, and at best, might be used as secondary evidence to support a relationship between the Ricinulei and Anactinotrichida. We are again left without sound synapomorphic evidence for the Cryptognomae as a monophyletic group, or for the Anactinotrichida being more closely related phylogenetically to the Ricinulei than it is to the Acariformes.

In Dubinin's (1957, 1959, 1962) scheme, the mites are considered as a natural group, the Acaromorpha, based on 8 characteristics (Table 4). Of these characteristics, the 6th is plesiomorphic. The 1st, 7th, and 8th are not autapomorphic since they are present in the Ricinulei. The 2nd, 3rd, and 5th are essentially tendencies that do not hold for mites as a whole: external segmental structure with a maximal number of opisthosomal segments is retained in opilioacarids, which also do not have a caudal bend to the body. The 4th, reduction of the sternum, if found in various orders of the Arachnida, and is an example of homoplasy. As defined, the grouping is not well supported.

Dubinin considered the Solifugae to be the out-group of the Acaromorpha, whereas the Ricunulei was allied to the Pedipalpides in the Scorpionomorpha, and the Opiliones to the Araneae in the Arachnida. A relationship between the Acari and Solifugae was based on the palpi not being chelate, and on the so-called 'rhagoid' body form of palaeacaroid mites being similar to that of solpugids. However, neither characteristic is synapomorphic or based on homologous structures. The palpi of solpugids terminate with a specialized, suckerlike structure, whereas those of mites terminate with paired claws, or an apotele is entirely lacking. Palaeacaroid mites retain a prosomal plate that is not equivalent to the propeltidium of solpugids, and they have no other prosomal plate equivalent to the postpeltidial structures of solpugids. Also, the body form of Palaeacaroidea is not demonstrably typical of the ancestral acarine stock.

Earlier, Grandjean (1936, 1954) had also considered the possibility of a common ancestry between the Acariformes mites and Solifugae, based on similarities of cheliceral structure, a prelarval Claparéde's organ, pretarsal structure, solenidia, and structure of the prodorsal shield. Alberti (1980b) recently noted some intriguing apomorphic similarities in sperm structure between the Solifugae and Acariformes, in exclusion of the Anactinotrichida. Counter to this, there are also similarities between the Solifugae and the anactinotrichid Opilioacarida, including the presence of comparably-located stigmata and of divided trochanters on legs III and IV. Clearly then, the Solifugae, along with the Ricinulei, Opiliones, and Palpigradi, should be kept in mind during an out-group analysis of arachnid groups, as was done to some extent recently by Weygoldt & Paulus (1979a,b).

Only passing reference will be made to the phylogenetic and classificatory scheme of Savory (1971, 1977) (Table 5). In it, the Acari was apparently assumed to be a natural group. Savory's brief diagnosis of the Acari did not include *one* characteristic, derived or otherwise, that clearly distinguished the group from other orders of the Arachnida, although inconspicuous somatic segmentation was mentioned in other discussions. The Acari and Opiliones *sensu lato* were regarded as sister-groups because of the 'conspicuous resemblances' (1971) and 'close relationships' (1977) evident between 'primitive' groups of each order – the Opilioacarida and the Cyphophthalmi. No concise elaboration of these resemblances was made other than casual mention of a few characteristics (the lack of eyes, unusual colours, shortened abdomen without a telson, subdivided tarsi, and 6-legged nymph), which supposedly also indicated the Ricinulei as the out-group of the Acari and Opiliones. Not one of these characteristics, whether primitive

or specialized, holds for the two, or the three, orders considered. A comprehensive refutation of Savory's concepts, especially as they refer to the relationships of the Cyphophthalmi to the Ricinulei and Opiliones, was given by Shear (1980) based on cladistic analysis.

Table 4

Scheme of Dubinin (1957, 1959, 1962): classification of chelicerate orders, and characteristics of Acaromorpha (=Acari)

Class Merostomata
- Order Limulida

Class Scorpionomorpha
- Subclass Holactinochitinosi
  - Order Eurypterida
  - Order Scorpionida
- Subclass Pedipalpides
  - Order Uropygi
  - Order Amblypygi
  - Order Palpigradi
  - Order Pseudoscorpionodea
  - Order Ricinulei

Class Solifugomorpha
- Order Solifugae

Class Acaromorpha
- Order Acariformes
- Order Parasitiformes
- Order Opilioacarina

Class Arachnida
- Subclass Opiliomorphae
  - Order Opiliones
- Subclass Soluta
  - Order Trigononotarbi
- Subclass Araneae
  - Order Liphistiomorphae
  - Order Mygalomorphae
  - Order Araneomorphae

Acaromorphia
1. Development of a gnathosoma.
2. Segmentation of idiosoma weakly expressed or effaced.
3. Tendency towards reduction of number of opisthosomal segments.
4. Lack of an entire sternum.
5. Longitudinal axis of body bent posteroventrally – caudal bend.
6. Female genitalia developed as a trilobate cone.
7. Six postembryonic stases.
8. Hexapod larva.

Table 5
Scheme of Savory (1971, 1977): classification of terrestrial chelicerate orders

Class Arachnida

Subclass Scorpionmorphae
Order Scorpiones
Subclass Arachnomorphae
Infraclass Palpigradoidea
Order Palpigradi
Infraclass Arachnoidea
Cohort Uropygaceae
Superorder Uropygoides
Order Uropygi
Order Schizomida
Cohort Aranaceae
Superorder Aranoides
Order Amblypygi
Order Araneae
Superorder Kustarachnoides
Order Kustarachnae
Subclass Opilionomorphae
Infraclass Trigonotarboidea
Superorder Trigonotarboides
Superorder Anthracmartoides
Infraclass Opilionoidea
Cohort Ricinuliaceae
Order Ricinulei
Cohort Opilionaceae
Superorder Opilionoides
Order Opiliones
Order Cyphophthalmi
Superorder Acaroides
Order Acari
Cohort Architarbaceae
Order Architarbi
Subclass Chelonethomorphae
Order Pseudoscorpiones
Order Solifugae

In a study by Sitnikova (1978) the Acari was considered as a monophyletic group based on 7 characteristics (Table 6). Of these, none is plesiomorphic. However, the 5th and possibly the 6th are not autapomorphic since the 5th and possibly the 6th are present in the Ricinulei (data on the embryology and a prelarva are not yet available). The 1st, 2nd, 3rd, and 7th are trends that are not sufficiently demonstrable for an ancestral acarine stock as a whole; the 1st and 2nd have already been discussed for Dubinin's scheme; and the 3rd and 7th do not apply as apomorphies of discrete structures or attributes of the Acari as a whole in distinction to other

Table 6

Characteristics of a monophyletic Acari – Sitnikova (1978)

1. Trend towards reduction of number of body segments, including initial dorsal reduction of genital segment (VII).
2. Development of a caudal body bend, beginning during embryogenesis.
3. Similar reductive modifications of internal structures.
4. Similar embryonic development.
5. Reduction of leg IV, leading to hexapod condition of prelarva and larva.
6. Embryonization of prelarva.
7. Trends toward shortening of life cycle and attaining sexual maturity rapidly.

Table 7

Scheme of Weygoldt & Paulus (1979b): classification of chelicerate orders, based on cladogram of phylogenetic relationships. (Names in parentheses refer to similar usages by previous authors – see Tables 3–5).

Chelicerata
- Aglaspida
- Euchelicerata
  - Xiphosurida
  - Metastomata
    - Eurypterida
    - Arachnida
      - Ctenophora (Pectinifera)
        - Scorpiones
      - Lipoctena (Epectinata)
        - Megoperculata (Arachnidea Hammen, Arachnoidea Savory)
          - Uropygi
            - Thelyphonida
            - Schizomida
          - Labellata (Aranoides Savory)
            - Amblypygi
            - Araneae
        - Apulmonata
          - Palpigradi
        - Holotracheata
          - Haplocnemata (Apatellata Hammen, Chelonethomorphae Savory)
            - Solifugae
            - Pseudoscorpiones (Chelonethi)
          - Cryptoperculata (Opilionomorphae Savory)
            - Acarinomorpha
            - Ricinulei
            - Acari (Acaromorpha Dubinin)
            - Opiliones
- Pantopoda
  - Pycnogonida

arachnid orders. The 4th is also imprecise, and embryological data are not yet available for such critical groups as the Ricinulei, Opilioacarida, and Holothyrida. As presented, then, the monophyly of Acari is not convincing.

In the cladistic analysis of Weygoldt & Paulus (1979a,b) (Table 7), the Acari was proposed as a monophyletic group based essentially on *one* characteristic – presence of a gnathosoma. This grouping is seriously weakened by the authors' not having accounted for a similarly-formed structure in the Ricinulei. The Acari and Ricinulei were proposed as sister-groups comprising the 'Cryptoperculata' (or 'Opilionomorphae' of Savory (1977)), based on three nymphal instars. Curiously, they did not augment this autapomorphy with that of the gnathosoma. In turn, the Opiliones was proposed as the out-group of the Acari + Ricinulei, together comprising the 'Cryptoperculata' (or 'Opilionomorphae' of Savory (1977), based on three characteristics: (1) the trend toward use of legs *II* as tactile rather than ambulatory appendages; (2) the extensive effacing of limits between the prosoma and opisthosoma, with an anterior shift of the genital opening to between legs IV; (3) spermatozoa aflagellate and indented, with the acrosome on the concave side. This grouping is tenuous: legs II are not tactile in nature in early-derivative groups of mites; the genital opening in the Ricinulei and many Acariformes is located little or no more anteriorly than in some other orders of the Arachnida – in fact in some of the early-derivative Prostigmata and Oribatei, it is located more *posteriorly* than in other arachnids; their data on spermatozoa are insufficient in the absence of observations in the Ricinulei and Holothyrida, and are not supported by the more comprehensive recent studies on fine structure of spermatozoa by Alberti (1980a,b). Alberti's studies did not add further support for the Acari being a monophyletic group as a whole, but neither did they suggest different sister-groups for either of the Anactinotrichida or Actinotrichida. In the scheme of Weygoldt & Paulus, then, we are left with a supportable grouping of Acari + Ricinulei, but with an unconvincing case for Acari as a monophyletic group.

Based on the cases put forth by advocates of either a polyphyletic or a monophyletic origin for mites, we are left in an inconclusive position. However, on the basis of a greater variety of developmental, gnathosomal, and idiosomal characteristics, I propose that the case for Acari as a monophyletic group can be strengthened considerably. This is based primarily on further consideration of data discussed in the Appendix and summarized in Table 1, from which the following apomorphic states are evident (Table 8).

Table 8

Apomorphic characteristics of Acari
(Parenthetical numbers refer to characters as numbered in Table 1 and Appendix)

1. A pair of subcapitular rutella (12).
2. A pair of subcapitular, bilobate lateral lips flanking mouth ventrolaterally (11).
3. Larva with at most 5 fundamental pairs of subcapitular setae, 2 pairs of which adoral (13).
4. Reduction of sternal lyrifissures to fundamental maximum of 3 pairs (22).
5. Reduction of prodorsal *id* lyrifissures to fundamental maximum of 3 pairs (22).
6. Idiosoma primitively faintly sclerotized, lacking well-formed tergites and sternites on opisthosoma.
7. Violet pigment in hypodermis of idiosoma (18).
8. Ingestion, and further internal digestion, of solid food particles (40).
9. Presence of a hexapodal prelarva (see 3).
10. Second (femoro-genual-tibial) segment of chelicerae with at most 2 or 3 setae (14).
11. Chelicerae with only 1 or 2 lyrifissures, antiaxial one constant (15).

The 1st, 2nd, 3rd, 4th, and possibly the 5th, 6th, 7th, and 8th characteristics are autapomorphic for the Acari among extant arachnid orders. The 7th has been observed in the Opilioacarida, Holothyrida, and some Endeostigmata (van der Hammen 1961, 1966, 1969). The 8th, known to occur in the Opilioacarida and various groups of the Acariformes, including early-derivative groups, is known otherwise among chelicerates only in the Xiphosura in a marine milieu (van der Hammen 1977b); among terrestrial-feeding arachnids, this is clearly of secondary, independent origin in the ancestral stock of the Acari, rather than an ancestral condition as suggested by van der Hammen. The 9th is either another autapomorphy or, if found to occur in the Ricinulei, a synapomorphy that should be deleted from this list and added to the one for Acari + Ricinulei below. The 10th and 11th are reductive apomorphies that possibly may have arisen independently in 1 or 2 other arachnid orders, and are of lesser value cladistically. Another possible autapomorphy may be a unique degree of reduction in the number of *embryonic* opisthosomal segments to six (or five plus a telson as discussed by Aeschlimann (paper 3.3 in the present volume)).

That the Acari and Ricinulei are sister-groups, is based on the following four synapomorphies (Table 9). This is a short list of characteristics, but the 1st and 2nd are uniquely constructive modifications of great significance. The 3rd is also a possible autapomorphy of the Acari + Ricinulei, but more data are required on labral structures in other arachnid orders to assess this. The 4th is conjectural in a transformation series: subdivided trochanters are confirmed otherwise only in the Solifugae, and if this is the case amidst an undivided trochanter for all other arachnid orders, then the divided condition is a probable apomorphy derived independently in the Solifugae and in the Ricinulei + Acari, and apparently underwent suppression early in the ancestral acarines, as evidenced by its retention only in the Opilioacarida, in which it is repressed until the third nymphal instar.

Table 9

Synapomorphic characteristics of Acari and Ricinulei
(Parenthetical numbers refer to characters as numbered in Table 1 and Appendix)

1. A hexapod larva, followed by 3 octopod nymphal instars (3, 4).
2. A movable gnathosoma, separated by a circumcapitular suture from the idiosoma (9).
3. A roughened, scaly or denticulate labrum above mouth (10).
4. Trochanters of legs III and IV divided into 2 articulating segments (33).

Based on the following 11 synapomorphies, a reasonably convincing case can be made for the Opilioacarida being the sister-group of the Parasitiformes (Holothyrida + Gamasida + Ixodida), and together constituting the Anactinotrichida (Table 10). The 1st, 2nd, 3rd, 4th, and possibly the 5th and 6th characteristics are autapomorphic for this group. The 6th has been observed in the Opilioacarida, Ixodida, and several early-derivative groups of the Gamasida (Uropodina, Epicriidae, Zerconidae) by Alberti (1980a); data for the Holothyrida are not yet available. The 8th, 9th, 10th, and 11th are reductive apomorphies that appear to have arisen independently in other arachnid orders and are of lesser value cladistically. The 7th has arisen independently in the Palpigradi but in a different way: together with the palpal coxae, coxae I are freely movable, but coxae II to IV have relatively little mobility. A possible 12th characteristic may be autapomorphic for this group if it is demonstrated more convincingly that a gnathosomal tectum is present, albeit weakly, in the Opilioacarida.

Table 10

Apomorphic characteristics of Anactinotrichida
(Parenthetical numbers refer to characters as numbered in Table 1 and Appendix)

1. Larva with only 2 pairs of subcapitular setae, both of which are of adoral (circumbuccal) origin (13).
2. Larva with an unpaired postanal seta (31).
3. Femora of all legs with secondary, nonarticulated division (basifemoral ring) (34).
4. Tarsus I with dorsal cluster of solenidiform setae subdistally, which may become further elaborated into Haller's organ.
5. Pretarsi of legs II to IV with 1 or 2 pairs of setae (37).
6. Spermatozoa aflagellate, primitively containing a large vacuole (39).
7. Coxae of all legs movable (32).
8. Losses of Claparédes organs and of genital verrucae (28, 29).
9. Loss of all trichobothria (20).
10. Loss of median eyes (23).
11. Loss of empodium on all leg tarsi (38).

Within the Parasitiformes, sister-group relationships between the Holothyrida, Ixodida, and Gamasida require elucidation; but the grouping of these three suborders together is strongly defined by at least 14 apomorphies, as follows (Table 11). The 1st, 2nd, 3rd, 4th, 5th, and possibly the 6th and 7th characteristics are autapomorphic for this group – called the Parasitiformes herein. The 8th, 9th, 10th, 11th, 12th, 13th and 14th are purely reductive apomorphies, most of which have also arisen independently in other arachnid orders and are of lesser value cladistically.

Table 11

Apomorphic characteristics of Parasitiformes
(Parenthetical numbers refer to characters as numbered in Table 1 and Appendix)

1. Loss of dorsosejugal suture and effacement of primary division between pro- and opisthosoma (7).
2. 1 pair of stigmata, located in region of legs III or IV (24).
3. Lateral lips of subcapitulum fimbriated, often produced into attenuated laciniae (secondarily reduced in some parasitic taxa) (11).
4. Palpal apotele sub-basal and paraxial on tarsus (17).
5. Tarsi of all legs with secondary, nonarticulated division (basitarsal ring) (35).
6. A gnathosomal tectum forming a supracheliceral vault (9).
7. Tarsi II to IV with intercalary sclerite which primitively bears 2 setae.
8. Effacement of external evidence of, and reduction in number of, opisthosomal segments to apparently 10 (5).
9. Reduction in numbers of opisthosomal lyrifissures to fundamental, designatable pairs on larva (22).
10. Pretarsal setae reduced to maximally 1 pair on legs II to IV (37).
11. Paired sternapophyses fused into single tritosternum (26).
12. Trochanters of legs III–IV not divided (33).
13. Lack of acrotarsus on legs II to IV (36).
14. Lateral eyes reduced to 1 poorly-developed pair or lacking (23).

This leaves us with the Acariformes (Actinotrichida) as the sister-group of the Opiliocarida + Parasitiformes (Anactinotrichida). The Acariformes is strongly definable apomorphically, as follows (Table 12). The 1st, 2nd, 3rd, 4th, 5th, and possibly the 6th, 7th, and 8th characteristics are autapomorphic for this group. In the 6th, disappearance of the nuclear envelope during spermiocytogenesis was noted as a distinctive characteristic shared by a wide variety of the Actinotrichida, including early-derivative representatives (Alberti 1980b). The 9th, 10th, 11th, 12th, 13th, and 14th are simple reductive apomorphies which have arisen independently in other arachnid orders and are of lesser value cladistically.

Table 12

Apomorphic characteristics of Acariformes (Actinotrichida)
(Parenthetical numbers refer to characters as numbered in Table 1 and Appendix)

1. Anamorphosis – postlarval addition of opisthosomal segments (5).
2. Prior to moulting, formation of new legs completed inside body rather than within old leg hulls (8).
3. Prodorsum with 6 fundamental pairs of setae.
4. Body lyrifissures restricted to dorsolateral face of opisthosoma, with a maximum of 7 pairs (22).
5. Coxal glands debouch dorsally via podocephalic canals in prosoma to bases of chelicerae (25).
6. Spermatozoa aflagellate, primitively with a fully-formed acrosome complex (including vacuole and filament), but lacking at least part of the nuclear envelope (39).
7. Genital verrucae modified to papilliform or disclike osmoregulatory structures (29).
8. Setae and setigenous structures with actinopilin (19).
9. Loss of primary stigmata originating from opisthosomal segments (24).
10. Loss of dorsal cheliceral lyrifissure (15).
11. Loss of palptarsal apotele (17).
12. Loss of tritosternum (26).
13. Tarsi of legs I to IV not divided into basi- and telo-tarsus (35).
14. Tarsi of legs II to IV lacking an acrotarsus (36).

The data given above support the hypothesis maintained by Grandjean (1936, 1970) for over 30 years, that the two major acarine lineages have a remote but common ancestry, and that no other order of the Arachnida is nearly as closely related to either one of them as they are to each other. Support of Grandjean's opinion on the basis of shared derived character states is ironic, because Grandjean (1970, p. 814) did not agree with the cladistic principle of not using primitive character states in the reconstruction of phylogenetic relationships.

That the division or separation of the two major lineages of the Acari is profound, is supported by two considerations. First, of the 10 or more apomorphies listed above for each lineage, some in each case do not relate to those of the other: anamorphosis and podocephalic canals of the Actinotrichida do not relate readily to an alternative condition in the Anactinotrichida any more than an unpaired postanal seta and Haller's organ of the latter relate readily to any condition in the former. This was noted by van der Hammen (1973) in his argument for divergent evolution from unrelated ancestral groups. Second, the fossil record clearly shows that readily recognizable and diverse forms of early-derivative endeostigmatic and oribatid

acariform mites already existed during late Devonian times (Hirst 1923, Dubinin 1962, Rolfe 1982). One must infer from this that the sister lineage was already separated by this time, and that the common, ancestral acarine stock must have arisen in the late Silurian period, over 400 million years ago. Dubinin (1962) was of the same opinion regarding the late Silurian as the time during which the acarine lineage evolved from a more ancestral chelicerate stock. The Acari therefore may be one of the earliest lineages of terrestrial arachnids, and this may preclude serious consideration of certain other orders of the Arachnida from having sister- or out-group relationships with the Acari if there is strong doubt that thier lineages extend back into Silurian times.

The question, of whether the opilioacarid-like Anactinotrichida or the endeostigmatic-like Actinotrichida is more 'primitive' or closer to the ancestral acarine stock, is a red herring, a distraction. Theoretically, as sister-groups, neither is more early derivative than the other. Not surprisingly, 'primitive' members of both groups retain a considerable variety of plesiomorphic characteristics. Comparison of the *number* of plesiomorphies retained in early-derivative members of each group is *not* necessarily a reliable index of degree of primitiveness according to cladistic methodology.

The implications on classification of the Acari, as a monophyletic group as presented above, are straightforward. First, we can mercifully continue to use 'Acari' and 'mites' as meaningful names denoting the entire subclass as a natural group. Second, we can recognize the two major lineages by continuing to use Actinotrichida (or Acariformes) for the one and Anactinotrichida for the other; the latter includes the Opilioacarida along with the Holothyrida, Ixodida and Gamasida. Third, we can apply the name Parasitiformes to the major grouping *within* the Anactinotrichida that *excludes* the Opilioacarida. Note that this concept of Parasitiformes *includes* the Holothyrida along with the Ixodida and Gamasida, in contrast to a more traditional use of this name for just the latter two suborders as found in general works of the 1950s, e.g. André (1949), Hughes (1959). In fact, this suggested usage of Parasitiformes goes back to Reuter's (1909) original concept of the group, which included the Holothyrida but excluded Opilioacarida.

The implications of a diphyletic classification of mites would be more confusing and unsettling. 'Acari' could not be used readily alone for either assemblage, and we would see further use of 'true mites' for Acariformes, and perhaps 'other mites' for Anactinotrichida. 'Acari' would then refer to a polyphyletic or paraphyletic group in much the same way as we continue to conceptualize 'reptiles'.

The hypothesis of monophyly of the Acari will be subject to further testing as additional critical data become available, especially embryonic, early postembryonic (e.g., prelarval and larval), and fine structural data from key groups such as the Palpigradi, Ricinulei, Opilioacarida, and Holothyrida. More careful recognition, description, and homologization of structures, such as lyrifissures, solenidia, actinopilinous setae, leg segments, ventral opisthosomal structures, ovipositor, male reproductive organs, and lateral (Claparéde) organs, done in a comparative way among all arachnid orders, is indispensable.

In closing, I would like to pay tribute to Zachvatkin and to van der Hammen for having proposed their stimulating hypotheses on a diphyletic origin of mites. I can only echo van der Hammen (1966) in saying that there is always '. . . room for theoretical, often speculative views', and that hypotheses are '. . . necessarily introduced as starting-points for further investigation'. 'This uncertain way has its special charm for one who knows (how) to appreciate adventures in the field of science'. As Shear (1980) pointed out for the Opiliones, so there remains much to be learned about mites and related arachnids: in examining hypotheses of

relationship, we reject or support them based only on *'what we know now'*. In offering evidence and a viewpoint that does not support a diphyletic origin of Acari, I leave the door wide open for further, and, I hope, more conclusive, investigations on the origin and evolution of mites.

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† *See also* Additional references from Appendix.

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APPENDIX

Discussion of characters and character state polarities (transformations) summarized in Table 1

EMBRYONIC DEVELOPMENT

A variety of embryonic charactersitics are available for comparison between major arachnid groups, but observations are lacking for such critical groups as the Palpigradi, Ricinulei, Opilioacarida, Holothyrida, and some early-derivative Acariformes. This hinders meaningful comparative analysis at present. Nevertheless, the following observations reviewed by Anderson (1973) and Aeschlimann (paper 3.3 in this volume) are of interest.

1. *Inversion of embryonic opisthosoma.* Relatively early-derivative parasitiform mites retain relatively large (350–1000 nm diameter) eggs containing much cytoplasmic yolk and a thin periplasm below the surface of the egg; translocation of the yolk mass from a dorsal position on the prosoma to a ventral position on the opisthosoma, accompanied by inversion of the opisthosoma (a downward and forward flexure between the prosomal limbs) has not been observed. This simple mode of embryonic development appears similar to that in the Opiliones, and in distinction to that shared by spiders, uropygids, amblypygids, and perhaps solpugids, in which there is striking yolk translocation and embryo inversion. The latter is considered to be

more specialized by Anderson (1973). On the basis of out-group comparison, however, I would consider yolk translocation and embryo inversion to be plesiomorphic among orders of the Arachnida. Various acariform mites produce relatively small (100–150 nm) eggs showing evidence of secondary reduction in yolk content and apparently lacking a periplasm; translocation of the reduced yolk mass is not evident, but there may be some inversion, with both anterior and posterior extremities of the embryo flexed ventrally.

2. *Number of embryonic opisthosomal segments.* During embryonic development, Anderson (1973) and Aeschlimann (paper 3.3 in this volume) observed that ticks show 6 opisthosomal segments (i.e., 5 segments plus telson). This is the same number of segments as retained in *larval* Acariformes, and it may be that the mites of both major groups have the same complement of embryonic opisthosomal segments prior to emergence from the egg. This is clearly fewer than the 9 opisthosomatic segments reported for embryos of the Opiliones, and the 11 or 12 for those of the Araneida, Uropygi, and Solifugae (Anderson 1973). Embryological observations of other early-derivative acarines may indicate whether a maximum of 6 opisthosomal segments is characteristic and apomorphic for the Acari as a whole.

POSTEMBRYONIC DEVELOPMENT

3. *Suppression of legs IV* in the larva and prelarva, with partial effect back into embryonic development, is a derived characteristic common to all major groups of mites. During embryonic development, mites of both major groups have 4 pairs of limb buds of which the fourth pair is characteristically reduced in size. Vestiges of legs IV persist in the larvae of, Opilioacarida and of a number of early-derivative Acariformes (reviewed in Travé 1976) but, so far as is known, they do not persist in the prelarva. Apparently, then, this suppression began in the *prelarval* stase where its effect has been the most complete. The fact, that the Ricinulei also have a hexapod larva with vestiges of legs IV, does not in itself refute (as suggested by van der Hammen (1972)) the condition in mites from being a synapomorphy. This may be a case of parallel or convergent evolution (homoplasy), or this may be an indicator (autapomorphy) of common ancestry for the Acari and Ricinulei. Observations on prelarvae and embryonic development in the Ricinulei have not been made.

4. *Number of postembryonic stases* (instars) is primitively 6 in both major groups of mites: prelarva, larva, 3 nymphs, adult. This number is retained in the Opilioacarida (Coineau & van der Hammen 1979) and in a variety of taxa in the Acariformes. It is generally assumed that a prelarva is lacking in the Parasitiformes, but data are lacking for the early-derivative Holothyrida. In addition, Sitnikova (1978) felt that not all of the references to an 'embryonic' (prelarval) moult in some ticks and gamasid mites may be in error. In particular, she and Bregetova (1979) cited observation of 3 nymphal stases in a species of Sejina by Lange (1970) and in some Uropodina by Camin (1953) and Krasinskaya (1961). However, the observations by F. Athias (1975) that two deutonymphal morphs, one phoretic and one not, may occur in the Uropodina, is the probable explanation of a 'tritonymph' in this group. Presence of a tritonymph may be considered a primitive characteristic of all Acari including the Parasitiformes, since 3 nymphs are retained in the Holothyrida (Johnston 1982, from personal communication with J. B. Kethley). Whether Ricinulei are also characterized by 6 stases is uncertain, since observations on a prelarva are lacking; they do have a larval and 3 nymphal stases, however. Reduction of stase number to 6 has also occurred in the Pseudoscorpionida (2 calyptostases and 3 nymphs), and the Uropygi and Schizomida (1 elattostase and 4 nymphs). These reductions are probably independent from those of the Acari and Ricinulei, since the sister-groups of these orders of

the Arachnida are characterized by primitively having more than 6 stases (reviewed in van der Hammen 1973), and since none of these groups is itself an apparent sister-group of the Acari (Weygoldt & Paulus 1979a,b). The sequence of stases in Palpigradi is, unfortunately, not known. A transformation series for this character is:

p – 6–10 stases, the 1st typically an elattostase: Amblypygi, Araneida, Solifugae, Opiliones.

a_1 – 6 stases, the 1st an elattostase or calyptostase: Uropygi, Schizomida, Pseudoscorpionida, ?Ricinulei, Acari-Opilioacarida, ?Holothyrida (condition of 1st stase unknown), Acariformes.

a_2 – 4 stases, the 1st calyptostase and last nymphal stase lost: Acari-Parasitiformes, excluding Holothyrida.

5. *The number of segments constituting the opisthosoma* of mites depends, in part, on whether segments are added by anamorphosis during postembryonic development. There appear to be independent trends in reduction of number of opisthosomal segments in the Anactinotrichida on the one hand and the Actinotrichida on the other. Opilioacarida retain the greatest number of opisthosomal segments – 11 according to Sitnikova (1978, table 1), 13 according to van der Hammen (1979a, Fig. 29) – of which none is added anamorphically; apparently all are present in the larval stase. Certain early-derivative Acariformes retain 8 or 9 segments according to Sitnikova, or 10 according to van der Hammen; the number of primary body segments is not so much of concern here as the fact that 3 segments are still added anamorphically. Within the Acariformes there are repeated trends of partial to total elimination of anamorphosis, such that adults of many subgroups retain the larval complement, which includes apparently only 6 opisthosomal segments but actually 7 or 8 if the first segment, C, is compounded of 2 or 3 primitive segments including dorsal vestiges of genital segments VII–VIII. In the Parasitiformes external evidence of body segmentation, including the division between prosoma and opisthosoma, has disappeared. One can use idiosomal chaetotaxy and sigillotaxy to reconstruct probable segmentation (Athias–Henriot 1971), but a satisfactory homology of parasitiform with acariform segments has not yet been accomplished. Parasitiform mites appear to retain a moderately large number of opisthosomal segments – 8 according to Sitnikova and perhaps 2 more, or 10, according to van der Hammen's interpretation; and there is no anamorphosis during postembryonic development in these mites. These 10 segments may be homologous with the maximal 10 opisthosomal segments of adult Acariformes.

Since anamorphosis is not known otherwise among the orders of the Arachnida, and since a maximum of 19 segments (13 opisthosomal) is characteristic for the soma of the Arachnida in general (Millot 1949, Weygoldt & Paulus 1979a), I regard the condition of somal segmentation in the Opilioacarida as plesiomorphic, and typical of the epimorphic development generally found among larger arachnids of other orders (Sitnikova 1978). This means that anamorphosis is apomorphic for the ancestral stock of the Acariformes, and that further apomorphy has occurred with suppression of anamorphosis, concomitant with the reduction in number of the opisthosomal segments within various, more derivative, groups of the Acariformes. Reference to 'traces of anamorphosis' in the Palpigradi by Zachvatkin (1952) refers only to sequential appearance of ventral organs on segments already present, similar to the appearance of genital acetabula in the Acariformes. That opisthosomal segmentation is completed during embryonic development in the Palpigradi, was admitted by Zachvatkin in the same discussion (p. 39).

6. *A caudal bend* or posteroventral curvature of the opisthosoma caudally, is characteristic of the larva of most early-derivative mites, as discussed by Sitnikova (1978). The absence of a caudal bend in larval and nymphal Opilioacarida is regarded as retention of a primitive condition as found in other orders of the Arachnida. Development of a caudal bend is readily evident in

larvae of both the Parasitiformes and Acariformes, and may be retained through postlarval development in many groups where location of the anus on the ventral surface is characteristic of many acarine adults. Development of a caudal bend may be correlated with the reduction in the number of opisthosomal segments, which together lead to reduction in body size. This may also be correlated with the position of the anal growth zone in embryos of the Parasitiformes and Acariformes, i.e., ventrally on the soma behind the rudiments of legs IV. Transformation reversal to the primitive, orthosomatic, state is found among some smaller mites of more derivative groups of the Acariformes, in which anamorphosis is suppressed and the anus is located terminally, e.g. the Eleutherengona and Heterostigmata.

7. *Tagmata.* Despite great diversity in body form among the orders of the Arachnida, there is retained a fundamental division of the arachnid body into prosoma and opisthosoma (Millot 1949, Savory 1977). This division is still distinct dorsally in the Acariformes and Opilioacarida, in which a prodorsal region is delineated from the opisthosoma by a dorsosejugal or disjugal furrow. This condition is considered plesiomorphic in the Acari. The condition in the Parasitiformes, in which the disjugal furrow is obliterated by the presence of a larger podonotal shield in all postlarval instars, is apomorphic. It is notable that tick embryos still retain a distinction between prosoma and opisthosoma that becomes obliterated during further development (Anderson 1973). Zachvatkin (1952), followed by Sitnikova (1978), attempted to demonstrate that the typical podonotal shield of the Gamasida incorporates dorsal elements of the cheliceral and pedipalpal segments. It is more probable instead that this shield incorporates dorsal elements of several of the most anterior opisthosomal segments, possibly the first 5 as indicated schematically by van der Hammen (1979a). If the latter scheme is correct, the partial subdivision of the podonotal shield retained in moderately early-derivative rhodacarids may possibly reflect, in part, the disjugal boundary.

8. *Limb tissue regression.* Prior to moulting by one postembryonic stase to the next, apolysis in the Opilioacarida and Parasitiformes is comparatively fast and renders these mites inactive for only a brief time. The leg epidermis separates from the old cuticle, and a new cuticle is formed inside the hull of the old one. This process is similar to that found in other orders of the Arachnida (van der Hammen 1964, Woodring 1969) and is, therefore, regarded as plesiomorphic. In the Acariformes, a more extensive limb tissue regression occurs, such that formation of the new legs is completed inside the idiosoma rather than within the old leg hulls. This condition, not known from other arachnid orders, is considered an apomorphy of the Acariformes. According to Woodring (1969), a more complete limb tissue regression is found in more derivative groups within the Acariformes, e.g. Astigmata and Parasitengona.

GNATHOSOMAL STRUCTURES

9. *Gnathosomatization.* Formation of the gnathosoma, as an anterior movable structure separated by a circumcapitular suture from the rest of the prosoma, is characteristic of the Acari as a whole and of the Ricinulei. Evidence given by van der Hammen (1970, 1972a), ostensibly showing that gnathosomal formation 'certainly is the result of parallel evolution' separately in acariform and parasitiform mites, is not convincing in the absence of embryological observations, like those of Anderson (1973) for ticks, for the Ricinulei, Opilioacarida, Holothyrida, and early-derivative Acariformes. One could just as readily suggest that gnathosomal formation is the result of parallel or convergent evolution in the Ricinulei separately from the Acari. Furthermore, even if there were some divergence in gnathosomal composition during later stages of embryonic differentiation in the acariform versus the parasitiform mites, and in

the ricinuleids, this would not nullify the hypothesis of apomorphic formation of a more generalized (less differentiated) gnathosoma in a single ancestral stock of mite-like arachnids, which might be evident slightly earlier during embryogenesis. From a such basic gnathosoma, further embryonic differentiation, reflecting further specialization of gnathosomal formation within each of the major groups, would be expected.

10. *Labrum.* A dorsal subcapitular lobe, apparently homologous with the labrum, is present in early-derivative mites of all major groups and in the Ricinulei, and is of similar structure. The labrum is prominent, with a roughened scaly surface in the Opilioacarida; it is also well developed and beset with numberous fine denticles, or is fringed, in the Holothyrida and Parasitiformes. The labrum is short but similarly fringed in the Ricinulei (Pittard & Mitchell 1972). A denticulate, fringed, or striated labrum is also present in early-derivative acariform mites, though it is lost secondarily in most of the Prostigmata. The presence and form of the labrum is possibly synapomorphic for the Acari and Ricinulei.

11. *Lateral lips.* In early-derivative groups of all major groups of the Acari, a pair of membranous bilobate lateral lips or lobes project from the ventral apex of the subcapitulum and flank the mouth ventrolaterally. The lateral lips in the Opilioacarida are relatively unmodified lobes similar to those in some of the Endeostigmata and early-derivative Oribatei. In the Holothyrida, they are more differentiated into dorsal, and conspicuously fringed ventral, lobes (mistakenly denoted as the labrum in Fig. 9–2 of Krantz (1978)); and in the holothyrids (e.g., *Allothyrus*) the ventral fringed lobes are long, tapering, typical laciniae like those characteristic of the Gamasida (van der Hammen 1968). In the Gamasida, the dorsal lobes of the lateral lips may be further differentiated as fimbrillae, according to van der Hammen (1964); these may be elaborations of the laterodorsal lobes, termed 'labella' by van der Hammen (1966), of the Opilioacarida. Lateral lips are not developed in other orders of the Arachnida, including the Ricinulei as noted by van der Hammen (1979a). Their development is considered here as apomorphic for the Acari in general, with further, separate apomorphic trends evident in the Acariformes and Parasitiformes. In parasititic groups such as the Ixodida, the lateral lips may be lost secondarily.

12. *Rutella.* In the Acariformes, the rutella of the subcapitulum are known to be of setigenous origin, in part because they are optically birefringent and in part because they have retained a primitively setiform state in some early-derivative taxa (some Endeostigmata and Bdellidae). Although they have become lost in nearly all the Prostigmata, they have acquired a thickened, toothed aspect and rigidity by losing their alveolar socket in the Oribatei and Acaridiae. Similar, robust and toothed rutella are manifest in the Opilioacarida. And similar, toothed or entire structures, called *corniculi,* are present in the Holothyrida and remain well developed in free-living forms throughout the Parasitiformes. There is little doubt that we are considering homologous structures, be they called rutella or corniculi, and that these are apomorphic structures peculiar to the Acari. Van der Hammen (1968) considered the presence of rutella as primitive. Grandjean (1970) considered them as derived, but acquired convergently in the Actino- and Anactino-trichida, indicating a more remote common ancestry of the two groups. The origin of rutella once, within an ancestral acarine stock, seems more probable. There is no sign of such structures in the Ricinulei or in other orders of the Arachnida.

13. *Subcapitular setae.* The subcapitulum of early-derivative Acariformes commonly has 6 or 7 pairs of setae, of which 2 of the usually 3 pairs of adorals are larval, and the third is protonymphal; 3 of the other 4 pairs of subcapitular setae are also larval, and the fourth is usually protonymphal. In the Opilioacarida, there may be 10 or more pairs of subcapitular setae, of which 2 of the 4 pairs of adorals, called 'circumbuccals' by van der Hammen (1966), are the only setae expressed in the larva; these may well be homologous with adorals or_{1-2} of the Acariformes. Apart from

the adorals, 2 other pairs of setae, *vm* and *lvm*, first expressed on the protonymph in the Opilioacarida (Coineau & van der Hammen 1979), may be homologous with larval setae *a* and *m* of the Acariformes. Larvae of ticks show a similar condition to those of the Opiliocarida, with only 2 pairs of subcapitular setae being present, and in an adoral position; an additional pair (in the Ixodidae) or several more pairs (in the Argasidae) may be added in the nymph. A similar state is anticipated to occur in larval Holothyrida. In the Parasitiformes other than the Ixodida and Holothyrida, the subcapitulum bears only 4 pairs of setae of which 2 are larval and 2 protonymphal; the two pairs of larval setae (*a* and m_2 of van der Hammen (1966), hyp_{1-2} of Evans & Till (1979)) are anterior in position and probably homologous with the two pairs of larval adorals of the Opilioacarida and Ixodida. It is evident that the subcapitulum in the Anactinotrichida and Actinotrichida bears a few pairs of fundamental setae which are first expressed in the larval stase and which are at least in part homologous between the two groups. In contrast, the subcapitulum of the Ricinulei has many small setae on larval and post-larval stases. The condition in the Acari may therefore be regarded as apomorphic. Van der Hammen (1964) also interpreted the subcapitular setae of the Gamasida as homologous with those of the Acariformes, though his homologies differ from mine, in part I suspect because he did not consider the ontogeny of these setae.

14. *Cheliceral setation.* The chelicerae retain 3 or 4 setae, including one on the trochanter, in the Opilioacarida; but no more than 2 setae, with none on the trochanter, are retained in other mites. This is in contrast to the presence of 6 to many setae on the chelicerae, a plesiomorphic condition, found in all other orders of the Arachnida (Millot 1949). Whether reduction in cheliceral setae is originally a single trend characteristic of the Acariformes and Parasitiformes as a whole, or is two or more independent trends (as has clearly continued within the Acariformes), is problematic. In the Gamasida, the distal cheliceral seta is reduced in size and displaced antiaxially to assume the position of a *pilus dentilis*. As a less parsimonious alternative, one could interpret the *pilus dentilis* as a *de novo* structure, formed independently of the loss of one of the two cheliceral setae. That the *pilus dentilis* is a tubular or grooved excresence of the cheliceral wall, called a 'stylus' by Athias-Henriot (1975), is doubtful. In either event, formation of a *pilus dentilis* is apomorphic.

15. *Cheliceral lyrifissures.* Two cheliceral lyrifissures, one dorsal and one antiaxial, are situated near the level of the origin of the fixed chela in the Opilioacarida, Holothyrida, and Gamasida. Loss of these stress organs in most groups of the Acariformes is apomorphic, with an intermediate condition, retention of the antiaxial lyrifissure, present in a few early-derivative taxa such as the Bdellidae (Grandjean 1935b). Data on the occurrence of cheliceral lyrifissures in other arachnid orders are incomplete. An antiaxial one is present in some of the Opiliones (Grandjean 1935b) and in the Ricinulei (personal observation). Several are evident in the Pseudoscorpionida (Vachon 1949) and many in the Araneida (Millot 1949), and probably these conditions occur in at least some of the other orders of the Arachnida. No cheliceral lyrifissures are apparent in the Palpigradi.

16. *Gnathosomal tectum.* In the Opilioacarida, a gnathotectum or epistome is questionably formed as a weak membranous dorsal extension covering a small part of the gnathosomal bases (Grandjean (1936) indicated that the membranous margin regarded by some authors as a weak cheliceral tectum is nothing more than a supple fold of the membranous coxal bases of the chelicerae, which disappears when the chelicerae are fully protracted). This strucuture *is* developed in the Holothyrida, and is more sclerotized and elaborated in the Gamasida, but is apparently lost secondarily in the Ixodida. It is also lacking in the Acariformes. A gnathotectum is apparently not formed in the Ricinulei. I regard the condition in the Ricinulei as plesiomorphic, that in the

Opilioacarida as a possible first apomorphic step, those in the Holothyrida and Gamasida as successively more apomorphic, and the absence in the Acariformes derivable from the state in the Opilioacarida or Ricinulei.

17. *Palpal segmentation.* The pedipalps of early-derivative members of all major groups of the Acari are 5-segmented excluding the coxal bases, a plesiomorphic condition found in other orders of the Arachnida (Millot 1949). In the Opilioacarida and Parasitiformes, the palp-tibia and -tarsus are immovably attached so as to function like one segment. This is a step towards, though perhaps independent from, the condition in the Ricinulei which have a fused palpal tibiotarsus. Although both of these states are found also among groups within the Acariformes, various early-derivative groups of the latter retain the 5 freely-articulating segments.

Opilioacarids have an apotele – a symmetrical pair of claws attached to the palptarsus distally. Holothyrid and other parasitiform mites have the homologous structure, but the claws are generally asymmetrical and reduced in size, and attached paraxially to the palptarsus, subdistally in the former and sub-basically in the latter. In all groups of the Acariformes, an apotele is lacking on the palptarsus. In the Ricinulei, the palpal tibiotarsus bears an apotele which forms a chela with the terminal part of the segment. This may be an autapomorphy of the Ricinulei, since other arachnid orders equipped with chelate palpi (Pseudoscorpions) or raptorial palpi (Uropygi, Amblypygi) are apparently distantly related to ricinuleids (Weygoldt & Paulus 1979b) and have the movable digit (the apotele) ventral instead of dorsal (Pittard & Mitchell 1972).

Proposing a transformation series for the nature of a palptarsal apotele among the Acari and Ricinulei is problematic, depending on whether one regards the clawed versus the chelate state as more plesiomorphic, and the absence of an apotele as even more primitive or as secondarily derived for the Acariformes stock. Possibly, the two small chelate digits of the palptarsal apotele of the Ricinulei are homologous and derived from a more plesiomorphic clawed condition similar to that retained in the Opilioacardia. I tentatively regard the absence of a palptarsal apotele in the Acariformes as secondary and apomorphic.

BODY SURFACE STRUCTURES

18. *Integumental pigmentation.* A peculiar violet pigment in the hypodermis of the idiosoma has been noted in early-derivative members of the major acarine groups, including the Opilioacarida, Holothyrida, and some Endeostigmata (van der Hammen 1961, 1966, 1969). A similar pigment also appears to be present in some early-derivative Prostigmata, such as the Rhagidiidae and Bdellidae. The nature and function of this pigment is unknown, but its presence has not been reported for members of other arachnid orders. This pigment is tentatively regarded here as autapomorphic for the Acari. However, search for a similar pigment should be made in other, relatively small and soft-bodied arachnids such as the Opiliones and Palpigradi.

19. *Birefringent structures.* The presence or absence of birefringent structures has been used by various authors as a key character in distinguishing arachnid orders ever since this phenomenon was discovered and named 'actinochitin' by Grandjean (1935) nearly 50 years ago. However, there has been considerable confusion, because a general cuticular birefringence has been reported in some arachnid orders, and a limited effect observed in a few thick structures of setigenous origin in others, including the Opilioacarida. Van der Hammen (1961) reviewed the *chemical,* as well as optical, distinctiveness of actinochitin as elaborated earlier by Grandjean, as did Grandjean (1970) himself later. Because this material is not chitinous in composition, these authors introduced the term 'actinopilin' for this iodophilic substance that resists dissolving

in alkaline hypochlorite or in boiling lactic acid solutions. As such, actinopilin is characteristic only of the Acariformes among the mites. As for the variably birefringent structures found in other mites and other orders of the Arachnida, Grandjean (1970) reviewed in detail that various chemically dissimilar structures can be birefringent, and that there possibly is more than one sort of actinopilin, perhaps even among the actinotrichid mites! He also discussed some obstacles that impede determination of actinopilin by ordinary observational methods. On these bases, he rightly doubted the significance of earlier observations by himself and by Zachvatkin (1952) regarding the presence of birefringent structures among other orders of the Arachnida as a reliable criterion for establishing relationships and classifications such as the Actinochaeta *sensu* Zachvatkin. Granting that there are basic differences between the presence or absence of actinopilin in setae, a more important distinction must be made in proposing which of these conditions is apomorphic relative to the other(s). Curiously, recent proponents of monophyly in mites have skirted this issue, whereas those of polyphyly have used this difference indiscriminately. Because of the lack of reliable data on actinopilin in orders of the Arachnida other than the Acari, a meaningful transformation series of this characteristic cannot be hypothesized at present.

20. *Trichobothria* are found on the appendages of members of Scorpiones, various orders of the Arachnida including the Palpigradi, Araneae, Pseudoscorpiones, and Solifugae (Millot 1949, Savory 1977), and of a few relatively early-deriviative families of the Acariformes. Therefore, I regard the presence of trichobothrial setae as the retention of a primitive character state in the Acariformes. Trichobothria are lacking on the appendages of the great majority of the Acariformes, and on the body and appendages in the Opilioacarida, Holothyrida, other Parasitiformes, and also the Ricinulei and Opiliones. The rare presence of trichoboth-like structures or 'trichocysts' in a few of the Gamasida apparently concerns non-homologous structures that are secondarily derived (Athias-Henriot 1969).

21. *Solenidia,* with their typically hollowed shaft and internally striated walls (Grandjean 1935c), are found on the palpi and legs of most of the Acariformes and also the Opilioacarida, Holothyrida, and Ricinulei. The striated nature of these phanéres is difficult to discern in opilioacarids and holothyrids, but is present (Grandjean 1936, van der Hammen 1965). Solenidia are stated to be generally absent in other Parasitiformes, but this is not entirely certain for tarsus I of some early-derivative groups including the Ixodida; they are stated to be present there by Grandjean (1935c), Athias-Henriot (1969) and, with less certainty, by van der Hammen (1964). I am uncertain as to the range of occurrence of solenidia in the arachnid orders other than the Acari and Ricinulei, but I have observed them in the Opilionida, and Grandjean (1936) observed them in the Opilionida and Solifugae. Their presence in the Acari is therefore considered plesiomorphic.

22. *Idiosomal lyrifissures.* Athias-Henriot (1975, 1979) pointed out that the condition of numerous, undesignatable cuticular glands (euneoadeny or primordioadeny) is always associated with the condition of numerous undesignatable setae (euneotrichy or primordiotrichy). Together, as a primitive state, the presence of numerous glands, lyrifissures, and setae together on the dorsal and ventral surfaces of the opisthosoma and on the sternal region can be regarded as primordiotaxy, since this is characteristic of most arachnid orders, including the Opiliones (Martens 1978), the Ricinulei (Pittard & Mitchell 1972, van der Hammen 1979a), and the Araneida, Amblypygi, and Uropygi (Millot 1949). Based on out-group comparison, then, the similar condition found on the opisthosoma of the Opilioacarida is plesiomorphic. However, reduction of sternal lyrifissures to a fundamental maximum of 3 pairs, as in the Opilioacarida and Parasitiformes, may be regarded as an apomorphy for the Acari as a whole. Similarly,

reduction of prodorsal *id* lyrifissures to a maximal 3 pairs (in the Opilioacarida, Holothyrida, Gamasida) or none (in the Acariformes) is a probable apomorphy for the Acari. Note that the podo*notal* shield or region in most of the Gamasida is more extensive than the prodorsal region in the Opilioacarida and Acariformes, so that the lyrifissure id_4 associated with seta s_5 of somal segment VII is excluded from consideration, as are various glandular pores, in distinction to lyrifissures (Athias-Henriot 1969), on any part of the podonotum. Retention of numerous undesignatable setae but designatable (though still peripherally abundant) opisthosomal lyrifissures appears to be an early apomorphy among the Holothyrida and early-derivative groups of the Gamasida such as the Uropodina, Sejina, and some Trigynaspida. A separate transformation occurred in the Acariformes: the setal complement became reduced to designatable series; the lyrifissures became reduced to maximally 7 pairs and restricted to the dorsolateral face of the opisthosoma (opisthosomal cupules are considered to be homologues of lyrifissures according to Grandjean (1935b) and to van der Hammen (1976)); and cuticular glands became similarly reduced. Hypertrichy, or neotrichy, in the presence of an already reduced and denotable set of pores and lyrifissures, is clearly of secondary origin. Exemplified by postlarval instars of the Haemogamasidae in the Parasitiformes and of the Trombidioidea in the Acariformes, and designated as epineotrichy by Athias-Henriot (1975, 1979), this phenomenon occurs well within major groupings of the Acari and is not of concern here.

23. *Prosomal eyes.* Arachnids of several orders (Amblypygi, Uropygi, Araneae) retain a pair of anteromedian eyes as well as 3 (sometimes 4 or 5) pairs of lateral eyes; in the Opiliones and Pseudoscorpiones, 1 or 2 pairs of lateral eyes are generally retained but the anteromedian eyes are lacking; and in the Palpigradi and Ricinulei, all eyes are lacking (Millot 1949, Savory 1977). The first state, which is plesiomorphic for the arachnid orders as a whole, is retained with little modification in some early-derivative taxa of acariform mites, in which the only apomorphic changes are loss of 1 of the 3 pairs of lateral eyes, and consolidation of the pair of anteromedian eyes into one unpaired structure; even then, a bilobed condition of the median eye is evident in some Endeostigmata and Palaeacaroidea (Grandjean 1958). A further early trend within the Acariformes is the continued reduction and loss of the median eye. Opilioacarid mites retain 2 pairs or rarely (in *Paracarus*) 3 pairs of lateral eyes, but lack the anteromedian eyes. Lateral as well as anteromedian eyes are lacking in the Parasitiformes other than retention of one lateral pair in some ixodoid ticks. An apomorphy of a hypothetical ancestral stock of the Acari may be the retention of 3 pairs of lateral eyes in the presence of a reduced and partly consolidated pair of anteromedian eyes.

24. *Stigmata* are considered to be primitively absent in the Acariformes lineage, as evidenced by the endeostigmatic and palaeacariform taxa (Grandjean 1939a, 1954). Prosomal respiratory systems characteristic of relatively early-derivative prostigmatic taxa and the Oribatei are clearly within-group specializations of the Acariformes. By contrast, stigmatic systems are primitively present in the Opilioacarida and Parasitiformes, and a transformation series is readily evident. The single-paired meso-or meta-stigmatic systems of the Ixodida and Gamasida probably derive from the pair of large stigmata above legs III or IV in the Holothyrida. Van der Hammen (1961, 1968) interpreted a pair of smaller openings situated posterolaterad of coxa IV as a second pair of respiratory stigmata in the Holothyrida, and he even referred to the presence of a third pair in a species of *Allothyrus* (van der Hammen 1972). Recent observations of Travé (in press) confirm the comprehensive early observations of Thon (1906) that the respiratory system of Holothyrida opens via only *one* pair of stigmata. The second, more posterior, pair of openings misinterpreted as respiratory stigmata by van der Hammen are apparently the openings of noxious secretory glands. The single pair of stigmata common to the Parasitiformes probably

derives from one of the four pairs of small stigmata in opilioacarids, of which all are in series above and slightly behind legs IV, and of which the second and third pairs appear first during ontogeny (protonymph) and lead to larger tracheal trunks in adults than do the first and fourth pairs (see Fig. 4F in van der Hammen 1966). On the opilioacarids, these structures arise on body segments IX to XII, i.e., they are opisthosomal, but they could readily be displaced more anteriorly above legs III–IV, along with other dorsolateral elements of segments VII–XII, subsequent to effacement of the disjugal and sejugal boundaries and the enlargement of the prodorsum or peltidium with 'podonotal' elements.

What is *not* so readily apparent are the structures present in out-group arachnid orders from which these acarine stigmatic systems may have been derived. Grandjean (1935b), followed by van der Hammen (1966), hypothesized that they arose from lyrifissures, since they are in serial alignment with transverse rows of the latter. Athias-Henriot (1969) suggested that stigmata of the Gamasida are derived from solenostomes (cuticular glands) since they are in series with two other peritremal solenostomes. Both of these hypotheses are very tenuous. The stigmata of segments IX to XII in opilioacarids may be more readily derived from similar structures developed earlier and still retain in part in other arachnid orders, e.g., stigmata on segments IX to XI in the Solifugae (Millot & Vachon 1949) and on segments IX and X in the Pseudoscorpionida (Millot 1949). More ancestral arachnids, like members of their out-group, the scorpions, may have retained respiratory organs on segments IX to XII.

25. *Coxal gland systems* consist of two fundamentally different types amongst the Acari. However, both types derive from a modified pair of nephridial organs associated with the bases of legs I (Alberti & Storch 1977). In the Acariformes, a pair of tubular glands debouches *dorsally,* above coxisterna I, into a pair of podocephalic canals which also take up the excretory or secretory ducts of one to three pairs of acinose glands before converging from either side of the prodorsum and debouching on the dorsal surface of the subcapitulum (Alberti & Storch 1977, Grandjean 1944). In the Opilioacarida and Parasitiformes, a pair of coxal glands debouch *ventrally* in the region of coxae I where the products may be conducted by a pair of taenidia in the Opilioacarida, or by a pair of grooves in the Parasitiformes (Bowman 1984, Evans 1984, respectively paper 6.9 and Presidential address, this volume), to the base of the tritosternum. Similar debouchment and conduction of products by way of a pair of grooves between coxisternal plates I and II to the base of the tritosternum apparently also occurs in the Ricinulei (Pittard & Mitchell 1972). The latter system is relatively plesiomorphic, since it is a modification of a ventrally-debouching nephridial system of widespread occurrence among orders of the Arachnida (Millot 1949). Derivation of dorsal debouchment via a podocephalic system in the Acariformes is less certain, but is very probably more apomorphic than, and possibly derivable from, the system of the Opilioacarida and Parasitiformes (Grandjean 1944).

26. *Tritosternum.* The condition of a tritosternum, as an unpaired structure basically present in the Holothyrida and Gamasida, is an apomorphic derivative of the pair of sternapophyses between the bases of legs I in Opilioacarida. Presence of such a structure in the Anactinotrichida is a plesiomorphy: an apparently homologous structure is found in the Ricinulei, Amblypygi, and Solifugae (Millot 1949, Millot & Vachon 1949), in which a fusion into an unpaired structure has arisen independently. Absence of paired sternapophyses or a tritosternum from the sternal region of somal segment III is considered apomorphic for the Acariformes.

27. *Sternal setation.* The complement of fundamental sternal setae and their ontogeny is closely similar between the Actino- and Anactino-trichida, indicating a possible synapomorphy of homologous structures for the Acari as a whole. In the Opilioacarida (Coineau & van der Hammen 1979) as in the Parasitiformes, sternal setal pairs 1, 2, and 3 are present on the larva,

the 5th or genital pair is added on the protonymph, and the 4th pair is added on the deutonymph; additional secondary sternal setae may also be added on the nymphs of the opilioacarids, holothyrids, and ixodids, but usually not of the gamasids. In the Acariformes, the most medial pairs of coxisternal setae are readily distinguishable as midventral or intercoxal setae in early derivative Acariformes, in which they are usually off of the coxal fields of each of legs I to III (OConnor 1982). Intercoxals 1*a*, 2*a* and 3*a* are present on the larva; the genital pair g_1 is added on the protonymph, and a metamerically comparable 4th pair of intercoxal setae, 4*b*, may be added on the deutonymph. A comparable condition of the presence and ontogeny of sternal setae is not known in other orders of the Arachnida.

28. *A pair of Claparèdes's organs* is primitively present between the bases of legs I and II in the prelarva and larva of acariform mites; in postlarval instars, they are lacking and are seemingly replaced by the first pair of genital verrucae of somal segment VIII. Whether Claparède's organs are associated fundamentally with somal segment III or with IV (legs I or II), is uncertain (Grandjean 1946). That the presence of these organs is a plesiomorphy in the Acariformes is indicated by the presence of apparently homologous 'lateral organs' during embryonic development in various orders of the Arachnida (Anderson 1973) and by their presence in the prelarva of the Solifugae (Grandjean 1936, Dawydoff 1949). A pair of so-called 'sternal verrucae' is present between the bases of legs I and II on the larva and postlarval instars of the Opilioacarida. Thought to be *metamerically* homologous with the pair of genital verrucae of somal segment VIII, they may also be homologues of Claparède's organs (van der Hammen 1966). However, the presence of the sternal verrucae in *postlarval* instars of the Opilioacarida argues against this. In either case, the *absence* of Claparède's organs is regarded as apomorphic for the Parasitiformes, and for the Anactinotrichida as a whole if verrucae are not homologous organs. I note that the pair of jugular plates, which bear the first pair of sternal lyrifissures and setae in adults of some relatively early-derivative taxa of the Sejina and Trigynaspida in the Parasitiformes, may be modified homologues of the sternal verrucae found in the Opilioacarida.

29. *Genital verrucae*. Correlated with the primitive presence of Claparède's organs in the prelarva and larva of acariform mites is the primitive presence of 2 or 3 pairs of perhaps metamerically homologous genital verrucae (papillae, acetabula, discs) in postlarval instars of the same individuals. The most anterior pair of genital verrucae is interpreted to originate on somal segment VIII (van der Hammen 1969), which is the basic genital segment of the arachnids (Millot 1949); being the first ontogenetically of the 2 or 3 pairs of verrucae to develop, in the protonymph, it may be regarded as the most fundamental pair. The genital papillae of acariform mites are thought to be derived from ventral eversible vesicles of the type found on opisthosomal segments II to IV (somal segments VIII to X) in the Palpigradi (OConnor 1982). The function of these vesicles in the Palpigradi is not known, but they are possible vestiges or modifications of the invaginated respiratory organs found in a similar position on somal segments VIII to XI in several other arachnid orders. If the genital papillae of acariform mites *are* derived from such formerly respiratory structures, it becomes intriguing to consider the genital tracheae found in a few early-derivative acariform groups (e.g., Bdellidae, Cosmochthonioidea) as remnants of such an earlier respiratory system rather than newly-evolved structures.

Although such organs are lacking in all stases of parasitiform mites, a pair of so-called 'genital verrucae' is present in the area between the bases of legs IV on larval and postlarval instars of the Opilioacarida. These organs are thought to originate from somal segment VIII, and to be homologous with the first pair of genital papillae of acariform mites (van der Hammen 1966). As such, their presence should be regarded as plesiomorphic, though details of their structure may be apomorphic. Their absence on the *larva* in the Acariformes is possibly a

suppression of the condition in the Opilioacarida and may be, therefore, an early apomorphic step in a transformation series that is further continued by postlarval suppression of these structures among various taxa within the Acariformes. Their absence in *all* postembryonic instars in the Parasitiformes is a separate transformation trend and apomorphy. However, it may be that the latigynial structures or plates, which bear a pair of lyrifissures and a variable number of setae on the adult female of relatively early-derivative trigynaspid taxa in the Parasitiformes, are modified homologues of the genital verrucae found in the Opilioacarida.

30. *An eversible ovipositor* is present in adult females of early derivative taxa throughout the Acariformes. This condition, found also in the Opiliones, is a plesiomorphy in the Acari. A similar structure is also found in the Opilioacarida but not in the Parasitiformes (Johnston 1982), and its loss in the latter group is considered an apomorphy. Even in the Opilioacarida the ovipositor does not retain all of the primitive characteristics as found in the Acariformes and described by Grandjean (1956), e.g., with apex clearly trilobate and bearing several pairs of eugenital setae.

31. *Anal setation.* In the Opilioacarida, a fundamental unpaired seta occurs dorsoposteriorly behind the anal opening of larvae. A similar unpaired seta occurs behind the anus in larvae of argasid, but not of ixodid, ticks. I lack data on presence of this seta in larvae of the Holothyrida, but I anticipate its presence there. This seta is probably homologous with the postanal seta found in the larval instar of trigynaspine, and in the larval and postlarval instars of monogynaspine, Gamasida. If so, then this character state is apomorphic for the Anactinotrichida. I have observed the presence of an unpaired dorsomedial seta on each opisthosomal segment in an early (first?) nymphal instar of some of the Opiliones; on opisthosomal segment X (apparently IX) this seta takes the position of a postanal seta dorsocaudad of the anal tubercle. Whether the postanal seta in anactinotrichid mites may be derived from such a seta is problematic. The absence of a postanal seta is probably correlated with anamorphosis and the suppression of terminal segments in the Acariformes, and is therefore considered a secondary loss and apomorphic in this group.

A pair of fundamental setae flank the anus in the larvae of the Opilioacarida, but they are on the anal valves and therefore are not homologous with the para-anal setae of the Gamasida. They may be homologous with the pair of euanal setae which are retained on the anal valves of larvae and sometimes of postlarval instars in the Parasitiformes. Euanal setae are apparently lost secondarily in ticks. Several pairs of euanal setae are present on the postlarval instars of the Holothyrida as in the Opilioacarida; but I have no data on the condition in larval Holothyrida. Again, because of anamorphosis and suppression of terminal body segments, homologous setae are absent secondarily in the Acariformes: setae *pa* expressed on the tritonymph and adult of some early-derivative Acariformes are not homologous with euanal setae because they are not fundamental larval setae and they are not associated with a homologous segment.

LEG STRUCTURES

32. *Coxae.* The origin and nature of the coxal region or segment of the appendages, particularly the legs, has been a controversial topic in the morphology of the Arachnida. A freely mobile coxa was regarded as ancestral by some authors (e.g., Hughes 1959), whereas at the other extreme, the *absence* of a coxa was hypothesized as ancestral by van der Hammen (1977a). An intermediate position was espoused by Grandjean (1936, 1952), who considered a coxal region to be present primitively, from which either greater mobility or more inflexible consolidity with the body wall could arise. Van der Hammen's (1977a,b) proposal for a group, named the

'Acoxata' in one paper and the 'Epimerata' in another, and based largely on the absence of coxae, is tenuous. To support this, he assumed, without evidence, that the supracoxal setae originate on the prosoma, and that they subsequently become located on the *trochanter* in the Acariformes but on the *coxa* in the Opilioacarida! His evidence for the absence of a coxa in the Palpigradi was based entirely on articulation characteristics of the basalmost leg segment: by his definition, if the terminal articulation of the first, basal segment has 2 condyles and 2 tendons interacting with the second segment, then the first segment must be a trochanter. However, Weygoldt & Paulus (1979a), using observations by Manton (1977) that joint characteristics are variable and changeable, doubted whether one can conclude from the type of joint that the first leg segment of the Palpigradi is a trochanter. Evans (personal communication 1983) has observed a functional correlation or need for the most basal free segment to have a similar vertical (promotor–remotor) movement, followed by a horizontal (levator–depressor) movement in the second segment, no matter whether the first is a coxa or a trochanter, and the second is a trochanter or a femur. Like Grandjean (1936), Weygoldt & Paulus (1979a) noted that the coxisternal region is a variable and not necessarily homologous area among the arachnid orders, and that free coxae correlated with separate sternal plating is probably a derived state. Evidence of the coxal region of the appendages having an originally unarticulated but partly movable condition is their function originally as gnathobases in trituration of food in early-derivative orders of Chelicerata. For these reasons, then, I consider the coxisternal condition in the Acariformes as plesiomorphic, and the movable condition in the Parasitiformes as an apomorphy that has probably arisen independently in the Palpigradi and Araneae. Within the Parasitiformes, a transformation reversal to less mobile coxae has occurred in the Ixodida, probably correlated with reduction of sternal plating in this group.

33. *Trochanters.* Weygoldt & Paulus (1979a) suggested considerable caution in interpretation and homologization of leg segments other than the coxa. Eudesmatic joints may become adesmatic or even disappear; and secondary joints may possibly become eudesmatic. In light of this variability, they doubted interpretations such as that by van der Hammen (1977a) of the presence of two femora and simultaneous absence of a genu in the Solifugae and Pseudoscorpionida.

The presence of two articulating trochanters on each of legs III and IV in the Opilioacarida was well supported by observations of Grandjean (1936) on its ontogeny. I regard the presence of two trochanters on legs III–IV, in contrast to an undivided condition on legs I–II, as a plesiomorphic retention of a specalized state that is present in all active instars of the Ricinulei and Solifugae. An undivided trochanter is found in all other arachnid orders (Millot 1949), and is therefore considered the most plesiomorphic state. In the absence of other synapomorphies indicating a sister-relationship between the Ricinulei and Solifugae, I consider the subdivision of trochanters III and IV to have arisen independently in these two groups and possibly as different adaptations, since ricinuleids are slow and defensive whereas solpugids are fast and aggressive. Suppression of this condition until the tritonymph is apomorphic for the Opilioacarida, and perhaps for the ancestral stock of the Acari as whole. Further transformation reversal to total suppression of a divided trochanter may have occurred twice within the Acari – once in the Acariformes and one in the Parasitiformes.

34. *Femora.* Two quite different states of subdivision of the leg femora are evident in the Acari. In the Acariformes, all leg femora are entire in the larva and protonymph of early-derivative taxa (the condition of divided femora in the larvae of some Parasitengona is interpreted here as a secondary, within-group transformation reversal); that of any or all of the legs may become primarily subdivided beginning with the deutonymph, and those of the other legs

similarly so with the tritonymph (Grandjean 1952, OConnor 1982). Within the Acariformes, suppression of subdivision occurs, starting first with legs I and II. The transformation continues, with a step in which only the adult retains sutural vestiges of subdivision on femora III and IV, as in most Heterostigmata. In more derived taxa within the Acariformes (e.g., the Raphignathoidea, Tetranychoidea, Astigmata, and Oribatei other than the Palaeacaroidea), the leg femora never divide in any stase. I agree with the interpretation of OConnor (1982), that this transformation series is an example of a regressive tendency that became established very early within the Acariformes, such that the divided state of the femora is plesiomorphic. This contrasts with the initial concept of Grandjean (1939), that an entire femur is a primitive condition; however, it is fully accordant with Grandjean's (1952) subsequent and eloquent argument that the divided state is primitive.

In the Opilioacarida and Parasitiformes, all leg femora are divided in a secondary fashion, in that an unarticulated suture ('peripodomeric fissure' of Evans & Till (1979)), which passes through one or more lyrifissures, separates a short basifemur from a long telofemur. This condition, found in the larval and postlarval instars, is not found elsewhere in the Arachnida. Therefore, I regard this condition as apomorphic. Whether this represents a secondary subdivision of primitively entire femora, or a secondary fusion of primarily divided femora, is uncertain. Derivation from the latter would imply a primitive condition of a primary articulated division of all leg femora in all active postembryonic instars. If this was the plesiomorphic condition of an ancestral acarine stock, then the condition found in the Anactinotrichida could be derived by secondary fusion of the two femoral segments, and that in the Actinotrichida by a gradual ontogenetic suppression of the subdivision. However, homologies of leg segments between the various orders of the Arachnida are uncertain, and misinterpretations and misnomers of these segments exist in the literature. Evidence for a primarily divided femur in legs I to IV in other orders of the Arachnida is not well documented.

35. *Tarsi.* Division of each of the leg tarsi into a movable basi- and telo-tarsus is a plesiomorphic condition found in most orders of the Arachnida (Millot 1949); the telotarsus is commonly subdivided further. This condition is retained on all legs in the Opilioacarida and on legs II to IV in the ixodid ticks. An apomorphic transformation shared by the Holothyrida, Gamasida, and argasid ticks is the fusion of these segments such that they are immovable but delineated by a mesotarsal ring or suture ('peripodomeric fissure' of Evans & Till (1979)) which runs through one or more lyrifissures. This condition is not found in other orders of the Arachnida. In the Acariformes, the tarsi of all legs are primitively entire: evidence of any previous division is entirely effaced in all active instars. This condition is regarded as apomorphic, and derived separately from that of the Parasitiformes, i.e., directly from the plesiomorphic condition.

36. *Acrotarsi.* In the Opilioacarida, legs II to IV of adults have the telotarsus subdivided, such that a distinct apical acrotarsus is evident. On leg IV, the acrotarsus first forms in the deutonymph, and on legs II and III, in the tritonymph. Vestige of an acrotarsal subdivision is sometimes evident on leg I of adult opilioacarids, e.g. *Paracarus* (see Fig. 4 in van der Hammen (1968)). An acrotarsus is retained on leg I in some holothyrids, and an internal-wall vestige of it is evident in other holothyrids and in some ixodid ticks. It is also retained on leg I in some early-derivative Gamasida. Tarsi II to IV lack an acrotarsus in all Holothyrida and the other Parasitiformes. As mentioned above, the tarsi of all legs are primitively undivided in the Acariformes.

The acrotarsus may be homologous with one of the several tarsomeres that are subdivided from the tarsus in some other arachnid orders. A notably similar condition is found in the Ricinulei, in which tarsomeres are 'added' on legs II to IV in the proto- and deuto-nymph (Pittard & Mitchell 1972). The condition in the Opilioacarida may be considered as apomorphic

in that the number of tarsomeres is reduced to one, and its appearance on legs II and III is retarded until the tritonymph. The condition found in some Holothyrida and early-derivative Gamasida is a further reductive apomorphic step leading to the complete loss of acrotarsi as found in most the Gamasida. The lack of acrotarsi in the Acariformes is viewed as an apomorphy independent from the trend in the Parasitiformes.

37. *Pretarsal setae.* The pretarsus, which is characteristically well developed on legs II to IV of anactinotrichid mites, bears 2 pairs of well-developed setae in the Opilioacarida (Grandjean 1936, van der Hammen 1966), of which 1 pair of small to moderate-sized setae remain in the Holothyrida (Grandjean 1936, van der Hammen 1961, 1968). Although lacking in the Ixodida, one pair of apparently the same structures persists as typically small to minute setiform processes at the bases of pretarsi II to IV in many of the Gamasida. These are not homologous with the so-called 'paradactyli' of the Gamasida, as suggested by van der Hammen (1968), which are closely associated with claws and are not apparently setigenous. Instead, the pretarsal pair of setae of the Gamasida are inserted in the area of attachment of the pretarsus to the tarsus, such that they appear as a pair of small, most dorsoapical setae of the tarsus itself. As suggested by van der Hammen (1968), the occurrence of pretarsal setae may be a special character of the Anactinotrichida. I have not found them in the Actinotrichida, Ricinulei, Palpigradi, and Opiliones. However, one to several pairs of setae are found on the so-called 'post-tarsus' of the Solifugae (Grandjean 1936, Millot & Vachon 1949). Whether the post-tarsus of solpugids is homologous with the pretarsus of anactinotrichid mites, is problematic.

38. *Empodium.* The presence of an unpaired, third or empodial claw is present and fundamental (larval) in the Acariformes, according to Grandjean (1939b, 1943). In the Opilioacarida, homologous structures of only the paired lateral claws, including their condylophores, are evident (Grandjean 1943); the paired claws in the Parasitiformes are similar to the condition in the Opilioacarida. Whether the 3-clawed state is derived, by secondary development of a clawlike empodium, from a 2-clawed state, *or* whether the latter is derived by secondary reduction of an empodium, is debatable: both transformations occur in subgroups within the Acariformes (e.g., the Tetranychoidea). I tentatively regard the 3-clawed state as basically plesiomorphic among the arachnid orders and in the ancestral acarine stock, because a state with paired claws and a usually smaller, clawlike empodium is found in several other orders (Uropygi, Palpigradi, Araneida), or the empodium may be a fleshy structure (Amblypygi, Pseudoscorpionida), or it may remain clawlike in the absence of the paired claws (Opiliones) (Millot 1949, Savory 1977). Loss of the empodium has occurred, apparently independently, in the Soifugae, Ricinulei, and Anactinotrichida. Because the direction of transformation of this character is so uncertain, and because homoplasy of it is demonstrable in the Acariformes, the presence or absence of an empodium is of little use in cladistic analysis.

OTHER CHARACTERS

39. *Structure of spermatozoa.* Data on fine structure of the spermatozoa are not available for a few critical arachnid groups such as the Ricinulei and Holothyrida. However, the excellent recent comparative studies of Alberti (1980a, b, 1984 (paper 8.7, this volume)) indicated that early-derivative mites of all major groups are characterized by having aflagellate spermatozoa with an acrosomal complex complete with chromatin body, acrosome filament (perforatorium), and vacuole. Weygoldt & Paulus (1979a,b) regarded the characteristically folded or ribbed surface (appearing 'cogwheel-like' in transverse section) of spermatozoa of various Acari as

apomorphic for the group as a whole; but Alberti's observations on a wider variety of mites, including the Opilioacarida, indicated this to be an over-generalization. Alberti's data did not reveal structural characteristics that are apomorphic for the Acari as a whole; they were also not conclusive in indicating whether either the Actinotrichida or Anactinotrichida is more closely related to another order of the Arachnida than to each other. His data did, however, indicate apomorphies for each of these major groups of mites. Spermatozoa of the Opilioacarida, Ixodida, and several early-derivative groups of the Gamasida are autapomorphic in containing an enlarged vacuole; though apomorphic for the Anactinotrichida as a whole, this state is plesiomorphic *within* the Anactinotrichida, since a more derived state (longitudinally-ribbed spermatozoa) is characteristic of the podospermous Monogynaspida. Spermatozoa of the Actinotrichida exhibit 3 major forms, but a synapomorphy of all of them is the partial or complete disappearance of the nuclear envelope during spermiogenesis. The primitive presence in actinotrichid spermatozoa of an acrosome filament that is coiled externally around the chromatin body, rather than penetrating the nuclear body as in the Anactinotrichida, is similar to a condition found in some other arachnid orders, and is therefore plesiomorphic.

40. *Ingestion.* Nearly all orders of terrestrial Chelicerata, other than the Acari, are characterized by preliminary external (extra-intestinal) digestion and subsequent ingestion of only liquefied substances of their food (van der Hammen 1977b). This may be correlated with terrestrial predatory habits, and regarded as an apomorphy for terrestrial arachnids as a whole, in contrast to the ingestion of particulate material, as found in Xiphosura, in a marine milieu (Weygoldt & Paulus 1979b). In various groups of mites, including the Opilioacarida and some of the early-derivative taxa of the Parasitiformes (uropodine Gamasida) and the Acariformes (some Endeostigmata, Oribatei, free-living Acaridiae), ingestion, followed by further internal digestion, of solid food particles in terrestrial milieux, is evident from behaviour and from observation of gut contents. This appears to be correlated, initially at least, with nonpredatory habits and the presence of well-formed, usually toothed, rutella. Among terrestrially-living arachnids, the ingestion of solid food is regarded here, as was also done by Weygoldt & Paulus (1979a), as a secondary, apomorphic specialization of the ancestral stock of the Acari, rather than as a primitive condition as interpreted by van der Hammen (1977b). The implication of this was noted earlier by Dubinin (1962): the feeding behaviour in an ancestral stock of the Acari might have been as free-living ominvores and saprophages rather than as obligate predators, much as in the Opiliones. Ingestion of solid food possibly also occurs in the Opiliones (Weygoldt & Paulus 1979a); in the absence of unequivocal observations on feeding in the Ricinulei, this is tentatively thought to be an independent specialization in the Opiliones.

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