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Previous volumes (2010-2017): 250 € / year (4 issues)
Acarologia, CBGP, CS 30016, 34988 MONTFERRIER-sur-LEZ Cedex, France

The digitalization of Acarologia papers prior to 2000 was supported by Agropolis Fondation under the reference ID 1500-024 through the « Investissements d’avenir » programme (Labex Agro: ANR-10-LABX-0001-01)

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THE PRETARSI OF ASTIGMATID MITES

BY

Warren T. Atyeo

ABSTRACT

A comparative study of pretarsal modifications of approximately 350 supraspecific taxa of feather mites and representatives of over 50 genera of non-feather mites is presented; inter- and intragroup comparisons are made. A hypothetical pretarsus is developed and two major lines of ambulacral types are suggested; these lines indicate that certain historical divisions of the parasitic Astigmata based on host preferences need re-examination.

RESUME

Une étude des modifications du prépétare d'environ 350 taxons supraspécifiques d'Acariens plumicoles et de représentants de plus de 50 genres d'Astigmates non plumicoles est présentée; des comparaisons sont faites à l'intérieur de différents groupes et entre les groupes. Un prépétare hypothétique est présenté et deux principales directions de types ambulacraires sont suggérées. Ces données montrent que certaines divisions historiques des Astigmatides parasites, basées sur les préférences d'hôtes demandent un nouvel examen.

INTRODUCTION

A long term study of the feather mites has included the comparison of the pretarsal elements within and between approximately 250 named and 100 new supraspecific taxa. During the study it became obvious that certain pretarsal structures were homologous within the super-familial Analgoidea (s.l.). The questions remained as to whether some of these structures were homologous to the empodial and/or true claws and whether homologies could be made with mites of other astigmatic superfamilies.

The study was expanded to include representatives of over 50 genera of the Astigmata other than feather mites. Fortunately within the collection there was a long series of Canestriniidae from Brazil and the South Pacific. This series allowed me to speculate on possible evolu-

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3. I would like to thank Donald E. Johnston (Ohio State University) for reviewing the manuscript and for his most generous loans of determined non-feather mite material. Without these loans the study would have been restricted to the feather mites.
4. I would also like to thank Barry M. O'Connor (Cornell University) for determining the Canestriniidae.

tionary steps necessary to evolve the simple empodial claw of the Anoetoidea, Acaroidea and Ewingioidea to the elaborate pretarsi of other superfamilies. The study showed that within the Analgioidea (s.l.) the pretarsi of the suprageneric taxa are remarkably constant and the pretarsal modifications can be used in defining the higher categories. In the same vein, the study demonstrated that the division of the Psoroptoidea and the Analgioidea on the basis of host preference should be re-examined as there are many types of pretarsi within the same psoroptoid families. Recommendations for realignment of the included taxa of the Psoroptoidea are not being proposed because of the limitations of the study material; however, apparent discrepancies in the current classification(s) will be noted. An exhaustive literature survey was not done as even the better illustrations of astigmatic mites usually have stylized pretarsi and details critical to this study are not included.

The current investigation will be presented in sections, the first being a review of the tarsal and pretarsal investigations of Grandjean (1941, 1943) and how they relate to the Astigmata, second will be a series of pretarsi of the Canestriniidae demonstrating modifications from a claw to an ambulacral disc, third will be a hypothetical pretarsus of the disc type, and finally, a review of the pretarsal types of the astigmatic superfamilies.

Oribatei and Acaridae

Grandjean (1941) demonstrated that pretarsal structures of the Oribatei are essentially the same in all groups (Fig. 1). The claw(s) (modified setae) is implanted on a basilar piece which is moved by levator and depressor tendons in conjunction with a pair of condylophores articulated with lateral acetabula on the basilar piece and mesally with dorsolateral apices of the tarsus. The origins of the muscles for the levator and depressor tendons are in the tarsi and tibiae for the levators, only the tibiae for the depressors. Insertions of the tendons are on the dorsal and ventral surfaces of the basilar piece near the junction of the conjunctiva. The extent of the conjunctiva differs between groups, but there is always an area of flexibility between the rigid tarsus and movable elements of the pretarsus.

In his second series on the ambulacra, Grandjean (1943) compared the pretarsi of the Oribatei with Acarus farris (Oudemans) [= Tyroglyphus farinae (L.) sensu Grandjean] (Fig. 2). The structures observed in A. farris agreed with the structures of the Oribatei even though they were greatly reduced in size. Grandjean could not see the insertions of the tendons but he assumed that the insertions were similar to those of the Oribatei. He did propose that the insertions could be on the conjunctiva near the empodial claw (as in Fig. 2), but even then the movement of the pretarsus would be essentially the same. After examining numerous acaroid species, I can not add additional information as the insertions of the tendons have never been observed.

Throughout the 1941 and 1943 papers Grandjean does not morphologically limit the tarsus, pretarsus and ambulacrum; even in 1952 when he coined the term "apotele", it was defined as the apical segment of an appendage. His only definitive statement was that the condylophores represent the apex of the tarsus because of their articulations with the basilar piece which is moved by tendons originating in the tarsus and tibia. Beyond this, he made such statements as the ambulacrum is distinguished from the tarsus because it is not rigid, ambulacra may not be totally homologous between groups as the deformable areas (articulating membranes) may be differently formed, and the articulating membrane could not be modified as an ambulacral disc as it is of tarsal origin. Even in his discussions of the various types of cuticle there are never specific limits placed for the ambulacrum, tarsus or pretarsus. I can understand
Figs. 1-6. Lateral aspects of pretarsus and tarsal apex of *Camisia segnis* (Hermann) modified from Grandjean (1941) (1) and *Acarus farris* (Ouds.) [= *Tyroglyphus farinae* (L.) sensu Grandjean (1943)] (2); canestrinid species illustrating pretarsal modifications (3-6): tritonymph, n. g., n. sp. (3), *Grandiella* sp. female (4), (?)*Phobia* sp., male (5), *Grandiella* sp., female (6). *ac*, acetabulum; *bp*, basilar piece; *cd*, condylophore; *cj*, conjunctiva; *dt*, *tt*, depressor and levator tendons; *fl*, flange. Scales: A: 4, 6; B: 3, 5.
his dilemma as the problem is really the extent and origin(s) of the articulating membrane (flexible conjunctiva). In taxa with an empodial claw there is probably no satisfactory definition, but in those taxa with ambulacral discs, the terms referring to the terminal complexes of the leg can be defined.

In groups with well-defined discs supporting variously developed sclerites, the junction between the pretarsal (or ambulacral) stalk and the disc proper is on the dorsomesal surface of the disc, the same location as the articulations of the condylophores and the basilar piece. Hence, in the disc bearing groups the ambulacrum = the pretarsus = the apotele, and the external limit of the tarsus is the flexible extension of the tarsus through which runs the condylophores, ligaments and tendons. Internally, the articulations of the condylophores to the basilar piece will be the point for differentiating the tarsus and the pretarsus. Hencefore, in this paper, the ambulacra of these mites will be referred to as ambulacral discs and the flexible extension of the tarsus will be the ambulacral stalk.

In those groups with an empodial claw (i.e., most Acaridia), such distinctions cannot be made as the articulating points are within an articulating membrane which probably includes portions of the tarsus and pretarsus. For these species, the flexible articulating membrane could be referred to as the caruncle even though the caruncles of one family might only be analogous to the caruncles of another family, for example, Acaridae and Saproglyphidae (Figs 2, 15-16).

**Empodial claw to ambulacral disc**

One major puzzle has been the relation of the pretarsi having distinct empodial claws to those with ambulacral discs in which are often incorporated distinct plates or sclerites. Thus the interest in undetermined species of Canestriniidae from the South Pacific and Brazil, species in which there are varying degrees of elaboration of the pretarsal elements. The character states could represent possible evolutionary trends and they certainly illustrate possibilities of evolving a complex ambulacrum from a simple claw and basilar piece.

In each of the canestriniid species (Figs. 3-6) the tarsus is attached to the dorsomesal surface of the pretarsus; the basic structures in each are the claw, the basilar piece, the paired condylophores and the membranous pretarsal envelope. The basic trend appears to be the development of strengthening devices (e.g., sclerites) in the dorsal surface of the ambulacral envelope as the envelope increases in diameter.

The claw, which appears to be hollow, is apically exposed and curved downward over the distal margin of the ambulacral membrane. In all species, this relationship is the same even though the claw may vary in length and thickness. At the base of the claw in the simplest of the pretarsi (Figs. 3, 4) there is a U-shaped basilar piece which is directed under the claw base; the basilar piece appears to be articulated rather than fused to the claw. From this state, there are broad distal expansions of the basilar piece which fuse with ventrolateral, platelike flanges of the claw to form a large U-shaped basilar piece (Fig. 5) or are continuous with the ventral surface of the claw and lateral flanges (Fig. 6). Regardless of the condition of the basilar piece, these flanges are identifiable as discrete units in the Canestriniiidae; in other superfamilies they are seldom recognizable.

The condylophores are similar in all species. Each is distally expanded and appears to be articulated with the mesal surface of the basilar piece. The mesal terminations of the condylophores are articulated with the dorsal surfaces of the tarsus. Tendons are not observable.
Visualizing the ambulacral stalk joining the dorsomesal surface of the ambulacrum at an oblique angle, the mesal portion of the ambulacral disc is free and ventral to the stalk. The relative development of this section of the disc is correlated with what might be called accessory plates or sclerites to give rigidity to the free margin of the disc. In figures 3-6, there are different degrees of disc and sclerite development. In the smaller discs, the accessory sclerites are small and independent; in the larger discs, the sclerites are fused to form one broad plate beneath the ambulacral stalk; occasionally irregular sclerites are lateral to the claw. In other superfamilies, there is a pair of unguiform sclerites which articulate to the basilar piece; sometimes the unguiform sclerites are independent, sometimes they are joined ventral to the stalk in a fashion similar to the canestriniids; whether the accessory and unguiform sclerites are homologous is unknown, but as the accessory sclerites do not articulate with the basilar piece, it is doubtful.

As mentioned, it is doubtful whether all structures in the canestriniid pretarsi are homologous to the more complicated pretarsi of feather and fur mites. Besides, in the latter groups there are structures which apparently have no counterparts in the canestriniids. To better illustrate the complexity of many of the pretarsi of mites ectoparasitic on vertebrates, a hypothetical ambulacrum of the disc type has been developed.

**Hypothetical Ambulacral Disc**

The disc-type of ambulacrum must be developed for considerable movement. In the fully extended state, the structure is convex dorsally, concave ventrally, and all sclerites are "imprinted" on the dorsal surface. With the contraction of the levator and/or depressor muscles with concomitant reduction of hydrostatic pressure, the ambulacrum collapses in a series of folds along predetermined lines. Major folds occur along the lines of articulation between major sclerites; minor folds may be present, but differ between major taxa.

In selecting terminology for the various parts of the pretarsus, Grandjean (1941, 1943) has been used extensively. Names for the thickenings of the pretarsal envelope (i.e., plates or sclerites) have topographical bases. To diagrammatically illustrate the pretarsus, various aspects or levels through the pretarsus have been created to show relative positions of the component parts.

In the hypothetical pretarsus the dorsal (external) surface (Fig. 7) a line approximately parallels the disc edge on either side; this line separates the lateral membranous flange from the pretarsus proper. The dorsal surface is connected to the membranous extension of the tarsal cylinder through which run maximally six structures: dorsally, a pair of condylophores and the levator tendon; ventrally, two retainer ligaments and the depressor tendon. The tendons and ligaments are dotted at their distal extremities as insertions have not been satisfactorily observed. In scanning electron micrographs, various sclerites are outlined against the dorsal surface indicating they are thickenings of this surface; ventrally the micrographs show the ambulacrum as having a smooth, concave surface.

The pretarsal sclerites (Fig. 8) are typically dominated by the large central sclerite, the indistinguishably fused basilar piece and empodial claw to which are inserted the levator and depressor tendons and to which are articulated the condylophores (Fig. 10). The unguiform and lateral sclerites appear are articulated respectively to the basilar piece and the expanded section of the claw. The unguiform sclerites are not believed to be remnants of the true claws, but simply strengthening devices on the dorsal surface of the pretarsus around the tarsal-pretarsal connection. Often the unguiform sclerites are expanded completely around the mesal apex.
FIGS. 7-9. Hypothetical pretarsus, dorsal aspect (7), pretarsal sclerites (8), composite of all aspects (9).
of the ambulacral stalk, analogous to the conditions of the Canestriniidae (Figs. 4, 6). The
condylophore guide, when present, is U-shaped with the arms of the U directed dorsal where
the arms are in close connection with the internal margins of the unguiform sclerites. The body
of the guide is bent ventral and all of the connecting structures passing through the tarsal stalk pass over the condylophore guide.

The various lateral plates may be present or absent, may be well defined or irregular and
may be variously shaped. As in the Canestriniidae the development of these lateral plates are
usually correlated with the development of the ambulacral disc.

The retainer ligaments known to occur in the Analgoidea (s.s.) are believed to insert on the
unguiform sclerites. The function of the ligaments is presumably to maintain the proper level
of extension of the ambulacrum when hydrostatic pressure is high. In actuality, the retainer
ligaments are present in an obvious state only in families known to completely retract the pre-
tarsus into the tubular ambulacral stalk.

The condylophores occur in a variety of shapes and lengths; if an ambulacral stalk is present,
regardless of the presence or absence of an ambulacrum, the condylophores are also present (except possibly Ewingiidae). Typically the condylophores are articulated with thickenings on the
dorsolateral walls of the tarsal cylinder, only in the Freyanoidea is it probable that the articulating
surfaces are on the ventrolateral walls of the tarsus. As with other pretarsal structures, the
size (diameter) of a condylophore is strongly correlated with the size of the ambulacral disc.

Figure 9 is a composite of all levels of the hypothetical pretarsus. The central plate has
dorsal and ventral surfaces that are dissimilar, but the composite attempts to illustrate the total
effect of all parts. In reality, the condylophores are more approximate and this proximity
precludes the observation of the distal portion of the tendons and retainer ligaments.

**Pretarsi of the superfamilies**

In the presentation of the superfamilies, the groups with discrete empodial claws, the Anoe-
toidea, Acaroidea, Canestrinioida, and Ewingioidea will be first; next will be the feather mite
groups as there is a homogeneity of ambulacral types within each superfamily; following the
feather mites will be the mites adapted as internal, follicular and dermal parasites, the Cytoditoidea,
Rhynchoptoidea and Sarcoptoidea; lastly will be the Listrophoroidea and the heterogeneous
Psoroptoidea and Turbinoptidae.

**ANOETOIDEA**

Material. *Histiosoma* sp., *Anoetus hughesi* Hunter and Hunter, 1964; *A. gibsoni* (Nesbitt,
1954).

The *Histiosoma* specimens (Fig. 11) and the males of *Anoetus* are essentially the same as
*Acarus* with well-defined acetabula, heavy condylophores and distinct empodial claws. The
primary difference would be the proportion of exposed claw in relation to that covered by the
articulating membrane. The junction between the claw and the membrane (*collet of Grandjean*)
is near the distal claw termination in *Acarus* and near the acetabula in the Anoetidae. The
females of the *Anoetus* species examined (Fig. 12) are associated with pitcher plants (*Sarra-
cenia* spp.) and in each, the claw beyond the articulating membrane is long, thin and only slightly
curved; the articulating surfaces are similar to those of the male.
Acaroidea


Species of Acarus and Rhizoglyphus are similar to Acarus farris (Fig. 2), and the chaetodactylid deutonymphs have a characteristically large claw with well-developed condylophores. Major trends in pretarsal and tarsal modifications are the reduction in the size of the claw, reduction and often fusion of the condylophores to each other, and a lengthening of the ambulacral stalk beyond the insertions of the tarsal setae. Reduction in claw size culminates in the Hypodectidae in which the adults (Fig. 20) have only a modified disc without claw remnants and the deutonymphs lack all evidence of a pretarsus. Reduced condylophores are seen in the Carpoglyphidae-Saprogllyphidae series (Figs. 13-16); the condylophores are short and independent of the claw (as in the saproglyphids) or they may be fused. The trend for condylophore reduction is not seen in other large groups of the Astigmata.

The lengthening of the ambulacral stalk is common in non-avian ectoparasites. As in the Chortoglyphidae-Glycyphagidae-Hypodectidae group, there is a corresponding lengthening of the condylophores as the ambulacral stalks are lengthened. There also seems to be a disassociation of the condylophores from the claw as the paired structures are most often seen as being apically divergent and distant from the central sclerite.

The Fusacaridae and Hyadesiidae (not figured) appear to lack even remnants of the condylophores regardless of the size of the claw, i.e., small in Fusacarus and small to large Hyadesiidae, depending on the leg.

Rosensteiniiidae


The Rosensteiniiidae, associated with bats, bat guano and guano-living cockroaches, has been assigned to either the Canestrinioidea or Acaroidae. On the basis of the number of setae (2) on tibia I, the lack of a deutonymphal stage, and the type of pretarsus, I believe that these mites should not be assigned to either of the superfamilies. In ancillary studies on the chaetotaxy of the legs, it was noted that in the Anoetoidea, Ewingioidea, most Rosensteiniiidae and most Acaroidae there are two setae on tibia I in addition to the solenidion; in the Canestrinioidea there are no setae on this segment and in other superfamilies there is one seta (gT). Deutonymphs are known for most families of the Acaroidae (a notable exception being Hyadesiidae), but it is unlikely that this life stage exists in the Rosensteiniiidae as it has never been discovered, even with considerable collecting from bats and bat caves.

The pretarsi of the Rosensteiniiidae are different from the typical Acaroidae and Ewingioidea as the ambulacra are greatly expanded. In toto they are distinct even from the external parasites of insects, the Canestriniidae, which they superficially resemble.

In the Rosensteiniiidae, the large claw is exposed for most of its length and the distal portion of the ambulacral membrane is afforded limited rigidity by a series of fanlike thickenings in the dorsal surface of the ambulacral envelope; these characteristics are similar to the Canestri-
Canestrinioida


The development of the pretarsus of the Canestriniidae has been discussed and figured (Figs. 3-6); in each of the species, there is a large and well-developed pretarsus. The opposite extreme to the well-developed and varied ambulacra of the Canestriniidae is the reduced, bell-shaped ambulacra of Hemisarcoptes. In the single species studied, the only recognizable structures are the stalk and the small condylophores which have anastomosed for most of their lengths. It appears that the distal ends of the condylophores are thin and expanded over the dorsal surface of the bell to maintain the shape of the ambulacral stalk and ambulacral remnants (if present).

Ewingioidea

Material. Ewingiidae: Ewingia coenobitae Pearse, 1929.

Inexplicably, condylophores can not be observed in these mites. Using the least sclerotized form, a larva, the posterior pair of legs has the empodial claw very enlarged, but rather than articulating through a pair of condylophores, the articulating surfaces appear to be the tarsus proper and the dorsal surface of the claw (Fig. 24). The depressor tendon is very visible in all stages, but the levator tendon is indistinct.

Legs I-II have the empodial claws of the same type but smaller; again there are apparently no condylophores and the claw seemingly moves against apophyses at the apex of the heavily sclerotized tarsal cylinder.
ANALGOIDEA (s.l.)

All members of the three superfamilies of feather mites recently established by Gaud and Atyeo (1978a, b) are ectoparasites on or in the feathers of birds or on the skin (Epidermoptidae). The family Turbinoptidae, occurring in the external nares, has been placed in the Analgoidea (Krantz, 1978), but the discussion of this family will be after the Psoroptidae as the pretarsi of these two families have marked similarities. Lastly, another family, the Pyroglyphidae, currently assigned to the Psoroptoidea, has genera restricted to bird feathers (see Psoroptoidea for discussion).

In the Analgoidea (s.l.), there are study specimens for almost 250 named and 100 new genera; representatives of these taxa have been examined during this investigation. However, it is not my intention to detail the ambulacra of feather mites, rather, I will briefly point out similarities and common modifications. Suffice to say that the ambulacra of these mites can often be used to recognize and define higher taxa, usually at the subfamilial levels. Finally, the Materials sections will be summarized for the Analgoidea (s.s.), Freyanoidea and Pterolichoidea to avoid nomenclatural problems and to reduce the lengths of these sections.

ANALGOIDEA (s.s.)

MATERIALS. Representatives of 180 genera. Only in the Epidermoptidae is there limited material. Epidermoptinae: Myialges (Promyialges) sp.; Myialges (Metamicrilichus), 2 spp.; Microlichus avus (Trouessart, 1887). Dermationinae: Apodicoptes sp.; Pelecanoptes onocrotali (Fain and Atyeo, 1975); Passeroptes (P.) dermicola (Trouessart, 1886) + 1 sp.; P. (Paddacoptes) paddae (Fain, 1964) + 1 sp.

The key characteristics of the Analgoidea (s.s.) would be the presence of flexible and lengthened condylophores, retainer ligaments and a condylophore guide. Most, if not all, species, appear to have the capability of completely retracting the pretarsus into the tarsal stalk (Figs. 25-27).

A primitive ambulacrum of this superfamily might be similar to the hypothetical pretarsus illustrated in figures 7-10, which in turn is similar to the pretarsal configuration of the Pteronyssidae (Figs. 28, 29) and the Proctophyllodidae. From the “primitive” condition, there may be elaboration of the folding and supporting structures and/or reduction of the sclerites, particularly the condylophore guide. In the larger families it is not uncommon to find different trends in different subfamilies. For example, in the Analgidae there may be extensive ancillary structures which in aggregation would appear as in figure 30, a reduction in the condylophore guide (Fig. 31), and finally, a condition known only for one species, the complete loss of all pretarsal structures (the condylophores and ambulacral stalk have formed a “clawed” condition) (Fig. 32). Also illustrated in the Analgidae are the varied conditions of the pretarsal apex which can be rounded (Fig. 31), convex (Fig. 30) or pointed as an ace-of-spades.

The Alloptidae illustrate the reduction of the central sclerite from a triangular or oval to a rectangular structure (Figs. 33-35) as well as a reduction in the size of the condylophore guide. The last trends to be mentioned are the fusion of the condylophore guide to the unguiform sclerites (Fig. 36) and the loss of the condylophore guide through reduction; these trends are most common in the Xolalgidae.

The Epidermoptidae, skin parasites of birds, need additional explanation because of the heteromorphic tritonymph of one species. In general, the Epidermoptidae are similar to the
Alloptidae: *Echinacarus* sp. (33), *Ceraturoptellus* sp. with base of retainer ligament (34), *Alloptoides* sp. (35). 
Xolalgidae: n. g. near *Xolalges* (36). Scales: A : 32 ; B : 31, 33-36 ; C : 30.
Analgidae and Xolalgidae, having small pretarsi with reduced sclerites. The difference between the subfamilies Epidermoptinae and Dermationinae are minimal and concerns the condylophore guide — present and fused to the unguiform sclerites in the former subfamily and almost invisible or absent in the latter subfamily. The phenomenal species is *Microlichus avus* (Trouessart, 1887) in which the pretarsi of all stages except the tritonymph are normal. In the tritonymph the tarsi are shorted and bear many heavy retrorse hooks and the ambulacra are huge (Fig. 37). The condylophores are not long and flexible, but very short and heavy while the condylophore guide, if present, can not be seen due to the tremendous interference of the tarsal apices.

**Figs. 37-44.** Pretarsi of Epidermoptidae: *Microlichus avus* tritonymph (37), *Myialges (Metamicrolichus)* sp. (38). Freyanoidea: *Oustaletia* sp. (39), *Calaobia* sp. (40), *Freyana* sp. protonymph (41). Condylophores of *Michaelichus* sp. (42), *Cornyella* (43), *Vexillaria* (44). Scales: A : 39 ; B : 37, 40 ; C : 41 ; D : 38.

**Freyanoidea**

**Material.** Specimens of 25 genera.

The Freyanoidea is the smallest of the feather mite superfamilies with 30 genera. The freyanids, associated with shore and sea birds, usually have the empodial claw rather distinct and supported by a broad U-shaped and expanded basilar plate (Fig. 41); in addition, each ambulacrum is directed away from the central axis of the leg (also observed in a few Pteroli-
choidea). The vexillariids, restricted to the Bucerotidae, have two types of pretarsi, one (Fig. 39) distinct to one subfamily, the other (Fig. 40) similar to many of the Pterolichoidea.

The character uniting the families into the superfamily Freyanoidea is the odd modification of the condylophores. In each, the mesal articulation appears to be ventral rather than dorsal, each is almost straight and incapable of flexion, and in relation to the ambulacral diameter, each is very short and broad (Figs. 42-44).

**Pterolichoidea**

**Material.** Specimens from over 135 genera.

The members of the Pterolichoidea are almost exclusively non-passeriform birds. When the revisionary investigations are completed, there will be ten or eleven families included in the superfamily with about 150 genera. The largest family will be the Pterolichidae with over 60 genera.


With a few notable exceptions, mites of the Pterolichoidea have ambulacra each with a broad central sclerite and broad, vaculated lateral and unguiform sclerites; they lack a condylophore guide. The condylophores are basically L-shaped and non-flexible; the resulting movement of the ambulacra should be limited. I have never seen any indication of the complete
retraction of the apical segment into the ambulacral stalk as in the Analgoidea and I have never seen retainer ligaments. Apically, the ambulacral envelope can have various configurations from dentate (Fig. 45), pebbled (Figs. 47, 48), concave (Figs. 46, 49), rarely pointed (Fig. 50) and smooth (not figured).

**Cytoditoidea**


Reduction or loss of the pretarsus are the prevalent conditions for this group of internal parasites. The most complex pretarsus is the Cytoditidae in which there is a central sclerite and elongated condylophores. In one female of Cytodites nudus, the muscles and tendons are in evidence although the insertions are obscured; the levator and depressor muscles both arise in the tibia (Figs. 51-53). The levator tendon is directed between the Y-shaped arms of the condylophores, these being fused for most of their lengths. Even though the pretarsus can be fully retracted into the stalk, there is no indication that retainer ligaments are present.

The ambulacra of the Pneumocoptidae are simple and bell-shaped and the condylophores are thin and divergent (Figs. 54-55). With the evident loss of the empodial claws and pretarsal sclerites, practically the only remaining structures are slightly modified ambulacral stalks.

The Gastronyssidae usually lack pretarsi and stalks. In the material examined many tarsal setae are modified as claws and the tarsal apices are usually rounded (Fig. 56). FAIN (1959) illustrates a pneumocoptid type of ambulacrum on legs III and IV of a female gastronyssid, Mycteronyssus polli Fain, 1959. The condition of the male pretarsus is unknown as the species is based on two females.

**Rhyncopoidea**

**Material.** Rhyncopoidea: Rhyncoptes anastosi (Fain, 1962).

FAIN (1971) suggests that the Audycoptidae and Rhyncopoidea be combined in the superfamily Rhyncopoidea. Both families have modifications apparently for clinging to the hair, the hair follicle, and/or in the skin. Little can be said about the pretarsi of this superfamily from direct examination as the single slide available of Rhyncoptes anastosi has only one intact ambulacrum and even this had to be reconstructed for the illustration (Fig. 57). I think the long ambulacral stalk is surmounted by a small circular ambulacrum with weak central and unguiform sclerites. Except for the condylophores, other connections between the tarsus and pretarsus are not evident.

As previously stated, literature review has generally been fruitless in the pretarsal study; the Rhyncopoidea is a case in point. The Audycoptidae, which have ambulacra only on tarsi I-II has been differently or incompletely illustrated. Saimirioptes paradoxus Fain, 1968 has, according to the illustration, a long stalk and a small disc-like ambulacrum with possibly a small, indistinct central sclerite; condylophores are not indicated. The audycoptid from the black bear, Ursicoptes americanus Fain and Johnston, 1970, is illustrated as having long annulated stalks (similar to Psoroptes) and bell-shaped ambulacra (as in some Knemidocoptes); sclerites and condylophores are not shown.
Figs. 51-61. Cytodites nudus, lateral aspect of distal leg segments to demonstrate muscles (51), lateral (52) and dorsal (53) aspects of leg apex. Pretarsi of Pneumocoptidae: Pneumocoptes penrosei (54), P. jelli-seni (55). Gastronyssidae: Osponyssus brutsaerti, female leg I (56). Rhyncoptidae: Rhyncoptes ana-stosi female leg I (57). Sarcoptoidae: Sarcoptes scabei (58), Notoedres muris (59), Batheroptes cynopteri (60), Knemidocoptes pilae (61). Scales: A: 51; B: 52, 59, 60; C: 53-58, 61.
Sarcoptoida


In all groups the tarsi are shortened, have clawlike spines and/or setae and long stalks without annulations. The condylophores and discs are weakly developed; the only visible ambulacral sclerite is the reduced central sclerite. Ancillary supporting structures are present in a few species, namely, bifurcated condylophores and rays along the mesal disc margins.

In the Notoedrinae (Fig. 59) and Teinoctidae (Fig. 60), ambulacral development is similar; the size of the component parts are correlated with disc diameter. In both, the condylophores are distally bifurcated with the lateral branch almost paralleling the disc margin and the internal branch apparently connecting with the reduced central sclerite. Supporting rays of the mesal disc may appear as one or more units.

Sarcoptes scabei (Fig. 58) and Knemidocopes pilae (Fig. 61) lack the ancillary supporting structures. The two species differ in that S. scabei has a small subapical spine on each ambulacral stalk and the disc is apically rounded; K. pilae may have a small spine at the junction of the stalk and disc and the distal margin is strongly concave (as in some Epidermoptidae).

Listrophoroidea


Three families have similar pretarsi, Atopomelidae, Listrophoridae and Myocoptidae. In each, the condylophore guide is usually present and the distal portion of the disc is enlarged and has supporting rays (Figs. 62-64). Listrophorus americanus is the simplest form, lacking branched condylophores and with a rectangular central sclerite (Fig. 63). Leporacarus gibbus is similar to Myocoptes musculinus; each has branched condylophores independent of the distal rays and each has a triangular central sclerite. Koalachirus perkinsi is also similar to M. musculinus but the rays cannot be seen. The most ornate species in this series is L. bakeri in which the lateral branches of the condylophores are incorporated into a fan-like arrangement with the distal rays (Fig. 64).

The chirodiscid species (Fig. 65) is the simplest of the Listrophoroidea. The ambulacra lack condylophore guides, mesal or distal rays, and the claw and basilar piece are distinct. Whether the absence of the condylophore guide is a plesiomorphic or apomorphic condition is not known.

Chirorhynchobia urodermae (Fig. 66) demonstrates another trend, the enlargement of the mesal disc margins with many radiating thickenings for support. Distinct unguiform sclerites and condylophore guides are absent, but it is possible that one or more of these structures are incorporated in the strengthening modifications. The junction of the stalk and the dorsal surface of the disc is marked by a heavily sclerotized ring on the dorsal disc surface (not figured). This type of thickening is often seen in astigmatic mites, but it is usually not as conspicuous.
Psoroptoidea


The simplest pretarsus is encountered in the Yunkeracaridae (Fig. 67) and the Lemunyssidae. This pretarsus is a simple corolla with the condylophores extending almost to the dorsal apex of the corolla; presumably this type is not retractible. Within the Astigmata this same type of pretarsus occurs in the Pneumocoptidae (Cytoditoidea) and probably other Gastronyssidae (Fain, 1959); all have adaptations for internal parasitism with strong claws or claw-like setae at the apices of the tarsi.

The Pyroglyphidae are characterised by the apical positions of the solenidia on tarsi I and simple ambulacral discs. In all material examined (except Paramealia and Paralgopsis), the only sclerotized structures in the pretarsi are long, triangular claws, small unguiform sclerites and narrow lateral sclerites; the condylophore guides are not visible (Fig. 68). In Paramealia and Paralgopsis the aforementioned structures are comparatively larger and the condylophore guides are visible (Fig. 69). It is probable that in the Pyroglyphidae these two ambulacral conditions are monophyletic, that the condylophore guides in the former group are absent through reduction; a similar regression is seen in the Xolalguida (Analgoidea). It is possible that the tarsal stalk could be weakly annulated in Onychalges as illustrated in Fig. 68.

In the Psoroptidae studied there are three types of pretarsi. The simplest is found in Psoroptes species which have long annulated stalks and a simple central sclerite (Figs. 70-72) (similar to Congocoptes phoeniculi, Turbinotidae). The second type is similar to some Freyanoidea as there is a large central sclerite, branched condylophores, connected unguiform sclerites and distinct lateral sclerites (Fig. 73); this type is seen in Caparinia tripliis, Choriopites bovis and Otodectes cynotis. The last type, typical of the Analgoidea (s.s.), is found in Fonsecalges saimirii and Psoralges libertus. In these, the lateral, basilateral, unguiform and central sclerites are distinct as is the condylophore guide. The essential difference between the two species is the lengths of the tarsal stalks, long in Psoralges (Fig. 74) and short in Fonsecalges (Fig. 75).

Turbinotidae

Material. Congocoptes phoeniculi Fain, 1956; Mycteroptes basilewskyi Fain, 1956; Passer-rhinocoptes sp.; Rhamphocoptes capitonidis Fain, 1956; Rhinoptes ptternistis Fain, 1956; Schutedenocoptes dartevellei Fain, 1956; S. aquilae Fain, 1956 + 1 sp.; Turbinoptes congolensis Fain, 1956.

Although the turbinoptids are currently classified in the Analgoidea (s.s.) I have chosen to discuss them here as many of the pretarsal adaptations parallel those found in the Psoroptidae. The Turbinotidae occur in the dry passages of the nares and the various mechanisms for holding the host, although analogous, are certainly not homologous.
The development of a holding structure at the end of the tarsi may take the form of tarsal spines or claw-like setae; the same type may be on all of the tarsi or in some species, one type on legs I-II, another type on legs III-IV, or rarely, legs III-IV are without such modifications. Examples of these differences include *Mycteroptes* with tarsal claws on all legs, *Turbinoptes* and *Congocoptes* with enlargement of dorsal or dorsolateral setae, and *Passerrhinoptes* with enlargement of the ventral setae.

Ambulacral stalks are varied; they may be short to long (e.g., *Mycteroptes* vs. *Turbinoptes*) and may be smooth or annulated (*Turbinoptes* vs. *Congocoptes*). The stalk in *Congocoptes* is indistinguishable from *Psoroptes* species.

There are three major types of ambulacral configurations, two similar to other superfamilies, one that is distinct to the Turbinoptidae. The ambulacral discs of the simplest type are similar to those of *Psoroptes*, that is, each with only a long, triangular central sclerite and long tarsal stalk and condylophores. The difference between the two species with this type of ambulacral disc is in the development of the stalk, smooth in *Turbinoptes congoensis* (Fig. 76) and annulated in *Congocoptes phoeniculi* (Fig. 77) and *Rhamphocoptes captioniis*. The second disc is similar to *Otodectes cynotis* (Psoroptidae) except that the lateral sclerites are absent. This relatively simple ambulacrum has the basilar piece larger than the *Congocoptes* type, has the unguiform sclerites broadly joined beneath the stalk in *Mycteroptes basilewskyi* (Fig. 78), or narrowly joined in *Rhinoptes pternistis* (this last interpretation may be incorrect as the slide material is in poor condition).

The *Passerrhinoptes* and *Schoutedenoptes* species are different from all other material studied. First, the apparent junction between the ambulacral disc and stalk is mesal to the disc proper as indicated by an infolding of the stalk. The area of the central sclerites is so modified that the condylophores each connect to small claw-like remnants of the basilar piece (possibly derived from separate basilar pieces and claws as in the Canestriniidae). Mesal to the minute “claws” are radiating thickenings which in the *Schoutedenoptes* species are differentiated into two types, thick and thin rays; the thickened rays occur in the region usually occupied by the condylophore guides and might represent fused unguiform sclerites and guides; the thinner rays are lateral and mesal.

**Discussion**

The great surprise in this study was the many instances in which both bird and mammal parasites had the same basic type of ambulacrum; this was especially true when the habitats were similar (e.g., dermal, internal), regardless of the major taxon of the host. Conversely, it can be stated that within one family or superfamily (as currently classified), there may be different types of ambulacra which may be similar to ambulacra of other major Astigmata categories. Are the lack of correlations within a family or superfamily due to our historical division of higher acarine taxa by host group or are these multiple cases of convergent evolution?

In figures 82-95 I have attempted to show two series of pretarsi to illustrate reductions in the ambulacral sclerites without consideration of the various modifications of the condylophores. There is no attempt to discuss these as evolutionary pathways, only to portray possibilities in the simplest fashion using stylized structures; there is no effort to include the many variations in size and shape of the parts. With the exception of figure 82, basi- and paralateral sclerites and the many devices for strengthening the ambulacral envelope (except Figs. 94-5) have been omitted.
FIGS. 82-95. Diagrammatic series illustrating reduction in pretarsal elements of condylophore guide bearing groups (82-91) and condylophore guide lacking groups (92-95). Except for fig. 82 (based on hypothetical pretarsus) and Figs. 94, 95, para- and basilateral sclerites and ancillary strengthening devices are not shown.

The most extensive series is given in Figs. 82-91; it includes taxa with pretarsi similar to the hypothetical pretarsus to taxa lacking pretarsi. Although not indicated, there is a definite correlation between the diameters of the pretarsi and the size (and usually number) of the various sclerites; in general, the series from Figs 82-89 would be from the greatest diameter to the smallest.

To summarize, the groups of mites having similarly modified pretarsi will be listed by figure number. When comparing these simplistic illustrations, with the previous detailed illustrations, it will be obvious that some assignments are arbitrary. For the feather mite superfamilies Analgoidea (s.s.) and Pterolichoidea only representative families are listed.

Most groups included under each type of ambulacrum are obvious. The first series (Figs. 82-91) include those which have, or probably have had, a condylophore guide. The second series (Figs. 92-95) are considered as never having had guides, but included are two types with extensive mesal rays; these rays may have incorporated into them a condylophore guide (Figs. 94-95).
Fig. 82
Hypothetical pretarsus
Analgoidea
Avenzoariidae

Fig. 83
Analgoidea
Alloptidae
Analgidae
Psoroptoidea
Psoroptidae
Fensecalges
Psoralges

Fig. 84
Analgoidea
Alloptidae
Analgidae
Epidermoptidae
Epidermoptinae
Xolalgidae
Psoroptoidea
Pyroglyphidae
Paramesitia
Paraloposis

Fig. 85
Analgoidea
Epidermoptidae
Dermationinae

Fig. 86
Analgoidea
Xolalgidae
Listrophoroidea
Listrophoridae
Koalachirus
Leporacarus
Listrophorus
Myocoptidae
Myocoptes

Fig. 87
Listrophoroidea
Chirodiscidae
Psoroptoidea
Psoroptidae (?)
Caparinia
Choriopites
Otodectes
Pyroglyphidae
Bontiella
Dermatophagoides
Faimoglyphus
Hirstia
Hullia
Onychalges
Sturnophagoides

Analgoidea
Turbinoptidae (?)
Mycteropites
Rhinoptes
Rhyncoptidae
Rhyncoptidae
Rhyncoptes

Fig. 88
Analgoidea
Turbinoptidae
Congocoptes
Rhamphocoptes
Turbinoptes

Cytoditoidea
Cytoditidae
Cytodites

Psoroptoidea
Psoroptidae
Psoroptes
Sarcoptoidea
Knemidocoptidae
Knemidocoptes
Sarcoptidae
Sarcoptes

Fig. 89
Canestriinioidae
Hemisarcoptidae
Hemisarcoptes
Cytoditoidea
Gastronyssidae
Mysteronyssus
Pneumocoptidae
Pneumocoptes
Psoroptoidea
Yunkeracaridae
Yunkeracarus
Lemurnyssidae
Mortelmansia
A major problem with current classification is that both the Turbinoptidae and Psoroptoidea appear to be heterogenous groups based primarily on host preferences (see discussion, p. 265). One group from each of these taxa have been given for Fig. 87 and Fig. 93 — two genera of Turbinoptidae (*Mycterocoptes*, *Rhinoptes*) and three genera of the Psoroptidae (*Caparinia*, *Chorioptes*, *Otodectes*). All have relatively large ambulacra and well-developed central and unguiform sclerites, which would usually indicate that the taxa should be in the non-condylophore series (Fig. 93), but the related genera of both groups are considered as being condylophore-bearers.

The Cytoditoidea is another heterogenous group. *Cytodites* has a fully retractible pretarsus, a trait shared only with the Analgoidea (s.s.); the remaining families in the Cytoditoidea are from non-avian hosts and either lack the ambulacra and ambulacral stalks (Fig. 93) or have bell-shaped stalks with diverging condylophores. It would appear that non-*Cytodites* species should be separated from the internal avian parasites and that at least *Cytodites* would be more appropriately grouped with the Analgoidea.

Each of two suprageneric taxa are assigned to different superfamilies by various authors. One, the Yunkeracarinae, is included in the family Gastronyssidae (Cytoditoidea) by FAIN (1964) and is elevated to familial status and placed in the Psoroptoidea by KRANTZ (1970). I would agree that the Yunkeracarinae should be afforded familial rank, but question the relationship with the Psoroptoidea. The second group, the Knemidocoptidae, is placed in the Sarcoptoidea by KRANTZ (1970) while FAIN and ELSEN (1967) suggest that the family should be grouped with the Analgoidea (s.l.) with other skin parasites of birds, the Epidermoptidae. Pretarsal modifications of the knemidocoptids are quite distinct from the Epidermoptidae, but with the obscure origins of the family, placement in any superfamily as currently defined could only be regarded as tentative.
This study is certainly not a definitive work, but it does indicate that certain historical divisions of the acarine taxa based on host groups are tenuous. At this point, an investigation of the pretarsal modifications and other features of the many, many superspecific taxa of mites parasitic on non-avian hosts is needed.

LITERATURE CITED


GAUD (J.) and ATYEO (W. T.), 1978a. — « The superfamilies of feather mites ». — In, KRANTZ (G. W.), see below.

GAUD (J.) and ATYEO (W. T.), 1978b. — Nouvelles superfamilles pour les Acariens astigmates parasites d'oiseaux. — Acarologia, 19 : 678-685.


Errata.

Since submission, it has been discovered that the study material identified as *Hemisarcoptes* sp. should be *Nanacarus* sp., probably *N. minutus* Oudemans, 1902. References to *Hemisarcoptes* in the Canestrinioidea section, Fig. 23 and the explanation for Fig. 89 should be corrected.

KRANTZ (1978) re-assigns Yunkeracaridae from the Psoropditoidea to the Cytoditoidea and considers it a subfamily as originally proposed by FAIN (1964).