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Review

Origin and evolution of feather mites (Astigmata)

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Abstract. Feather mites are highly specialized plumage and skin ectoparasites that are variously adapted for inhabiting certain microhabitats on a bird's body. Different feather mite taxa of higher (familial) rank adapted to the same microhabitats display similar main morphological adaptations even if they are rather distantly related to one another. Hypotheses on the evolution of general adaptations in morphology of feather mites during colonization and establishment in different microhabitats are presented. According to recent data, feather mites are a paraphyletic group consisting of three superfamilies: Analgoidea, Pterolichoidea and Freyanoidea. We present our view on the general feather mite phylogeny course at the familial rank for the Analgoidea by means of cladistic analysis. Co-speciation of parasites with their hosts is postulated as a main factor driving feather mite evolution. Examples are given of non-coevolutionary events, for example recolonization from one host species onto another, extinction and multiple speciation.

Key words: Feather mites, morphological adaptations, phylogeny, coevolution, co-speciation, birds, ectoparasites.

Introduction

Feather mites are obligatory permanent ectoparasites or paraphages living exclusively on birds. They occur on various parts of the plumage, mainly on flight feathers and large coverts of the wings, sometimes in the down layer and on the skin. Almost all recent orders of birds, excluding penguins (Sphenisciformes) and cassowaries and emus (Casuariiformes), have their own specific feather mite fauna. About 2000 species of 444 genera and 33 families have been described, and the assumed total number of species is probably about 10 000 (Gaud and Atyeo, 1996) or even much more (Atyeo and Gaud, 1979; personal observation).

In this paper we will present general information about feather mites' morphological adaptations, evolutionary strategies and phylogenetic relationships between main lineages. We also show examples of host–parasite co-speciation and some non-coevolutionary events affecting feather mites' evolution.

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General Morphological Adaptation to Microhabitats

Feather mites belong to three superfamilies of the suborder Astigmata: Analgoidea, Pterolichoidea and Freyanoidea (Gaud and Atyeo, 1977). (OConnor (1982) synonymized the superfamily Freyanoidea with the Pterolichoidea.) Generally they have a typical astigmatic appearance, but due to their parasitic life style, feather mites may have several specific body modifications.

Dubinin (1951, 1953) first noted that certain morphological structures of feather mites may have a functional relation to the location of these mites in feathers. The formal comparative description of feather mite morphotypes was given by Mironov (1987). Feather mites occupy four main types of microhabitats on the body of birds: (1) plumulaceous down feathers; (2) vane surfaces of contour feathers; (3) the interior of the quills of flight and tail feathers; and (4) the surface of the skin. For each of these four microhabitats, we can identify basic evolutionary trends and corresponding morphotypes of feather mites. The specific adaptations to particular microhabitats originated partly convergently and independently in many feather mite taxa.

Down mites (Fig. 1A)

Mites living among soft downy feathers do not need strong sclerotization. Air-flow is minimal here. Correlated with this, the idiosomal setae tend to be as long as in ancestral free-living mites. These setae help feather mites to orient themselves in the three-dimensional down layer. Down mites move slowly in the thicket of downy feathers; their movement resembles brachiation of gibbons or swimming. Most often, specific apophyses are present on the first or second pair of legs (*Analges*, *Megninia*, *Leptosphyra*). Sometimes whole podomeres of the first leg (*Dogielacarus*) are modified into special clasping structures. Ambulacra, especially on the posterior legs, are poorly developed. The pretarsi of the first pairs of legs are retractable which probably protects these structures during crawling in the down layer. Since female tritonymphs and adult females are attached to males during precopulatory guarding or copulating, male adanal discs are supported by the hypertrophied third or fourth pair of legs.

Vane mites (Fig. 1B)

This morphotype is the most varied in shape and the most common among feather mites. Mites occupying this habitat possess adaptations to surviving in conditions of strong air-flow and incessant movement caused by reciprocal friction of feathers during flight. All mites from vanes are strongly dorsoventrally flattened. Sometimes the body margin is enlarged by various types of lateral membranes or flattened setae to make the body shape more streamlined. Frequently, especially in males, the idiosomal terminus is divided into two flattened opisthosomal lobes which may bear well-developed lamellae. Dorsal setae are usually very short or sometimes completely reduced. Terminal setae are usually shaped as macrochaetae and often

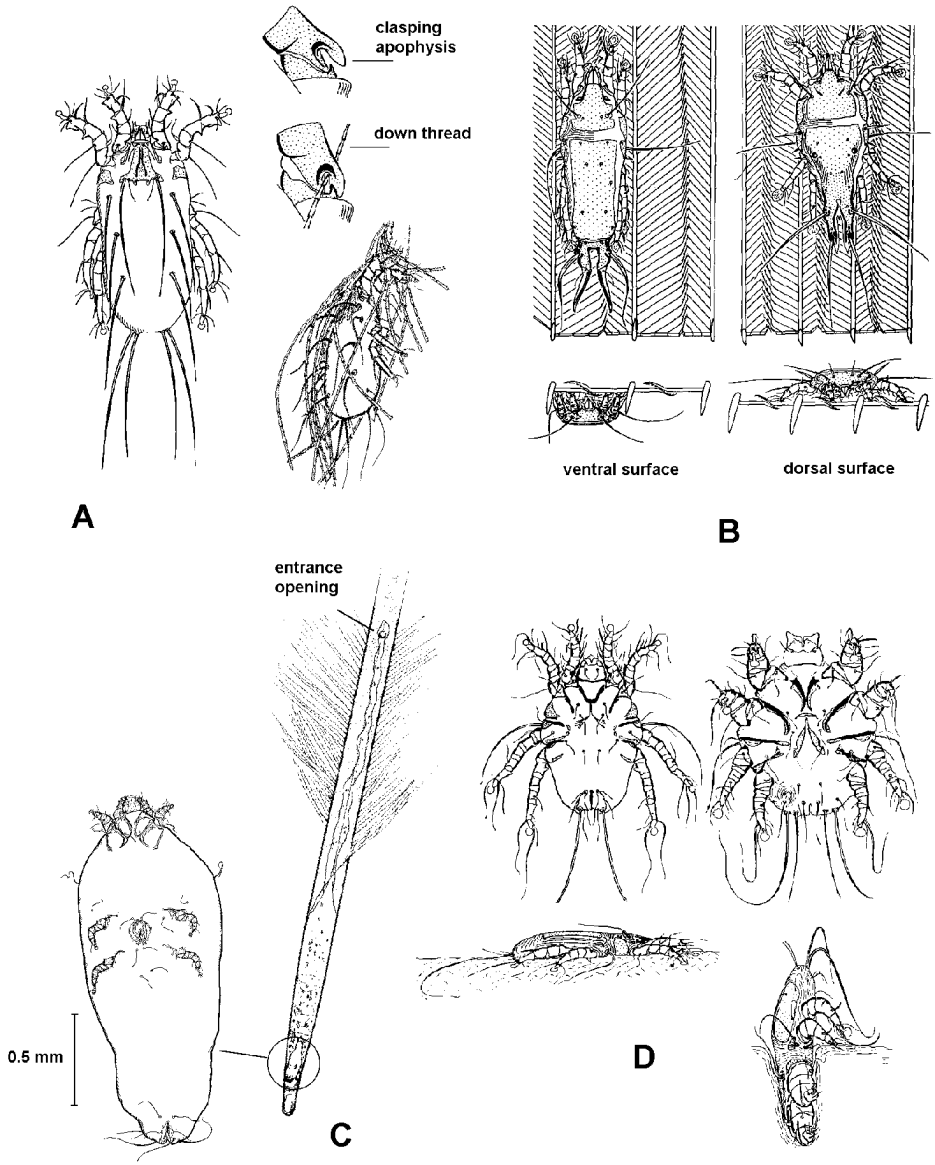

Figure 1. Main microhabitats inhabited by feather mites, and corresponding morphotypes: (A) down layer; (B) vane surface of contour feather; (C) quills of flight feathers; (D) surface of the skin and subepidermal layer.

flattened. In extreme cases, all the marginal setae are leaf-like (*Opisthocomacarus*). Legs of feather mites crawling on the vanes are mostly short and inserted laterally. All legs have well developed ambulacra which serve as hold-fast organs and prevent the mites from being blown away. Apophyses are seldom found on the legs. The

dorsal surface is usually covered by broad, highly sclerotized shields. Moreover, epimeres may be fused into a strong coxisternal network on the ventral surface. The coxisternum can fuse with additional shields into a uniform armature. The strong sclerotization apparently protects mites from injury when feathers rub together. It is also possible that the thick cuticle prevents mites from drying out in the highly ventilated microhabitat. Some vane mites are asymmetrical (i.e. *Dinalloptes*).

Quill mites (Fig. 1C)

A specialized group of feather mites inhabits the quills and the inside of the shaft of flight and tail feathers and the large coverts. In this microhabitat they are fully protected from air-flow and friction between feathers. Mites find their way into the quill lumen through the *superior umbilicus*, a small opening near the vane base or through an opening gnawed out by themselves. Quill mites were probably derived primarily from vane inhabitants; some may have migrated here from down feathers. This shifting took place several times during the feather mites' evolutionary history. The most recent invaders are practically non-modified vane mites. The ultimate quill morphotype is either an elongated, cylindrical or a sack-like mite. Some of these forms achieve the greatest sizes among feather mites and stay here for their entire life as adults. In these cases, the larva is the dispersal stage. Lateral and terminal idiosomal setae may be long, especially in smaller forms. Setae are erected and pointed in all directions, making a hemispherical tactile zone around the mites (Dubinin, 1956). Sclerotization is weak, especially in the hysterosomal region. Some quill mites which feed on the spongy medula of the shaft, possess a highly sclerotized propodosoma and massive chelicerae (Ascouracaridae, nymphs of *Plutarchusia*). Males often possess highly hypertrophied posterior pairs of legs provided with variously shaped apophyses.

Skin mites (Fig. 1D)

A small group of feather mites, comprising the families Epidermoptidae, Dermationidae and Knemidocoptidae, is adapted to living on or sometimes under the epidermis of birds. They differ in appearance from all other feather mites and more closely resemble species of the Psoroptidae or Sarcoptidae which live on and under the skin of mammals. Mites which live on the skin surface have a round and flat idiosoma (Epidermoptidae, Dermationidae). Tissue parasites (Knemidocoptidae) tend to be spherical. Sclerotization of the body is relatively weak. Short, telescoping legs often possess hook-like apophyses to attach to skin.

Phylogeny of Feather Mites

Although the taxonomy of feather mites has been investigated for a long time, phylogenetic investigations are in their infancy. Rigorous analyses using cladistic or

phenetic tools are recent and still rare (Moss *et al*., 1977; Mironov, 1991a; Dabert and Ehrnsberger, 1995, 1998).

There is no direct evidence on the phylogenetic history of feather mites because of the lack of fossil data. Extremely strong morphological and biological specialization and the great number of species living on almost all recent bird taxa point to a very long period of adaptation. It is assumed that the first feather mites originated from ancestors which inhabited bird nests in the Cretaceous period, 130–65 million years ago (Atyeo and Gaud, 1979). The first modern bird groups originated at this time, i.e. the greatest part of aquatic and, probably, terrestrial non-Passeriformes. Atyeo and Gaud (1979) suppose that feather mites originated from two different ancestor groups of astigmatic mites. The Pterolichoidea and Freyanoidea superfamilies arose from the mites which probably resembled an acaroid ancestor, yet the Analgoidea originated from preglycyphagid mites. The main indication for such an interpretation is the tarsal chaetotaxy and the structure of the pretarsus. These authors conclude that Analgoidea and the mammal parasite superfamily Psoroptoidea are more closely related to each other than they are to the Freyanoidea or Pterolichoidea (Atyeo and Gaud, 1979; Gaud and Atyeo, 1996).

It is not clear if all superfamilies of feather mites arose simultaneously or not. Until now the only existing hypothesis was the one formulated by Atyeo and Gaud (1979). The starting-point for their considerations was the assumption on a high degree of coevolutionary congruence between parasites and hosts. According to this hypothesis, Pterolichoidea and Freyanoidea originated in the late Cretaceous period during the radiation of non-passeriform birds. The second invasion took place when the Passeriformes originated in the Eocene, 55–40 million years ago. For unknown reasons, the Pterolichoidea and Freyanoidea did not invade new hosts. The passeriform birds were occupied by diverse nidicolous preglycyphagid groups, among which the ancestor of recent Analgoidea was presumably present. This hypothesis implies the invasion of analgoid mites on non-passeriform birds and partial extinction of the native acarofauna. Today the Analgoidea constitute about 50% of the feather mite acarofauna on non-passeriform birds, whereas on passeriform birds, their supremacy is practically absolute.

However, we are not sure whether the preacaridid and preglycyphagid invasions were as distant in time as several million years and if there were two independent invasions at all. If analgoid mites originated on passeriform birds and from there secondarily invaded non-passeriform birds, the mites from this last host group should be more recent in evolutionary time than those of passerifom birds. In fact the situation is the reverse. The more evolutionarily advanced birds, for example Passeriformes, have younger and more progressive acarofaunas of analgoid mites, for example Trouessartiidae or Proctophyllodidae, than older bird orders, for example Charadriiformes with Avenzoariidae. This pattern can be observed at all taxonomic levels of both birds and mites.

The second reason for our doubts is the assumption that analgoid mites had invaded birds already occupied by well-adapted pterolichoid or freyanoid acarofaunas and had partly replaced the native mites. Observations on recent feather mites show that the contamination by foreign mites or acarofauna replacement is actually

very rare and apparently has a very limited evolutionary significance (Dubinin, 1951; Gaud and Atyeo, 1979). On the contrary, there are numerous examples of close fit of the particular acarofaunas to their host. The feather mites of birds of prey are a perfect example. These falconiform birds have the largest possibility of natural accidental contamination by feather mites coming from various species of their prey birds. However, falconiform birds have their stable, specific acarofauna composed of species, genera and even families (Cheylabididae) which are typical for them and different from the mites on their potential prey. Although it is relatively common to find some individuals of mite species from other birds, mostly from Passeriformes, these mites never survive on falconiform birds. One more example is the acarofauna of cuckoos (Cuculiformes). These birds (both brood parasites and non-parasitic species) have their own specific mites which are transmitted during copulation and they never possess mites from adoptive parents.[1]

Our hypothesis regarding the ways of successive occupation of various microhabitats on the bird's body surface is presented in Fig. 2. Microhabitats differ in temperature and humidity fluctuations, aeration or the mechanical influence of reciprocal movements of feathers. It is likely that the first non-specialized feather mites must have invaded the least harsh microhabitats (Mironov, 1987). Early feather mites probably occupied the skin surface and the outer surface of feather shafts. In these microhabitats there are mild and stable temperature conditions and the influence of aeration is non-existent. Among the recent feather mites the genus *Strelkoviacarus* (Analgidae) presents such a primitive way of living. From these microhabitats the further conquest of niches probably proceeded in two directions. One group of feather mites adapted to down feathers (Analgidae, Xolalgidae, Psoroptoididae), the second entered the subcutaneous layer (Epidermoptidae and especially Knemidocoptidae). The next, more recent invasion took place on the feather vane surface where most severe conditions are present and which requires several strong morphological and biological adaptations. This microhabitat is a rich food resource for feather mites, because of a thin layer of oil gland secretion. Therefore the greatest proportion of the recent feather mites inhabits this microhabitat. The last microhabitat to be occupied was the quill. This protected microhabitat was invaded several times either from the down feathers (for example Dermoglyphidae) or from the vane surface (for example Syringobiidae, some Proctophyllodidae).

Analgoid mites are the only group of feather mites which inhabit all the above-mentioned microhabitats. In our opinion analgoid mites were the first feather mites which invaded the birds. It is also possible that all feather mite ancestors made it simultaneously but then the analgoids adapted fastest to the new niches. It is clear that the early invaders stemmed from the nidicolous mites and first occupied the least harsh microhabitats. Subsequently they became adapted to these places and became serious competitors for any invader to come. The 'late' Pterolichoidea and Freyanoidea

[1] Recently, Lindholm *et al*. (1998) presented the first record of persistence of passerine ectoparasites on a cuckoo (*Chrysococcyx caprius*).

probably never occupied the skin and the down layer and were forced to compete with Analgoidea on the vane surface. In this microhabitat with harsh conditions all feather mites had the same chance of survival. Therefore, analgoid mites form half of the acarofauna on non-passeriform birds while pterolichoid and freyanoid mites together make the second half of the acarofauna on these birds. Analgoid mites were better preadapted to new niches when the new big host group, Passeriformes, originated. These mites are simply smaller and more mobile than pterolichoid and freyanoid mites. That could give the analgoid mites an advantage for invading these generally smaller birds.

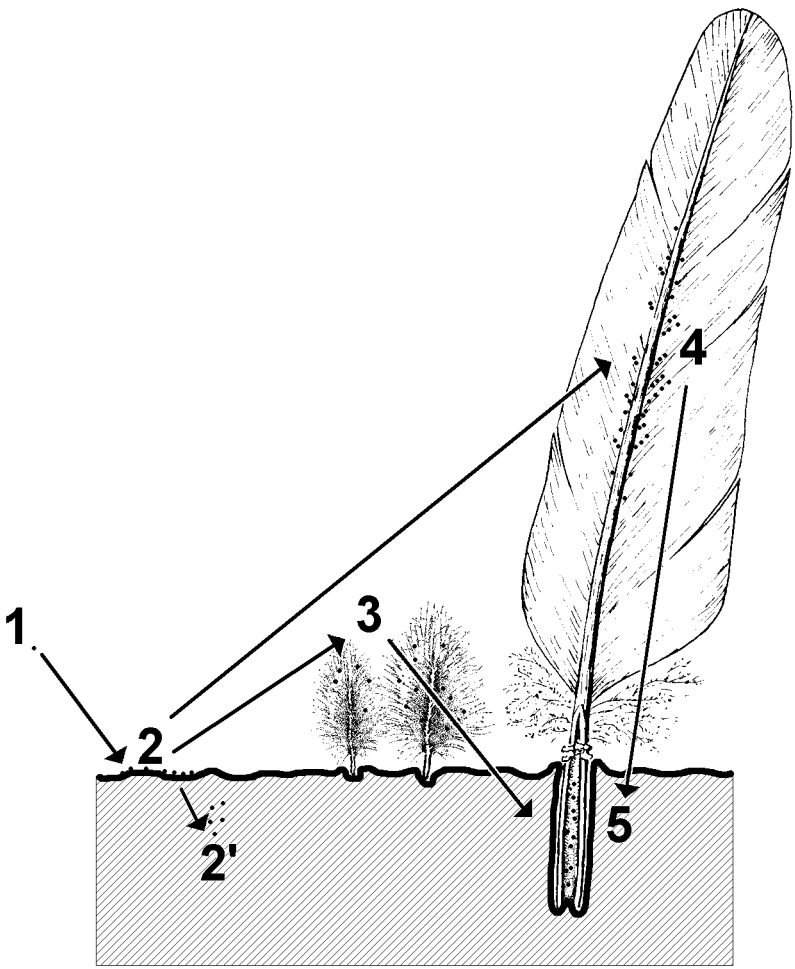

Figure 2. Hypothetical sequence of successive capturing of various microhabitats on bird body surface by feather mites.

On the taxonomic level below superfamily the evolutionary pathway is analysed only for the Analgoidea.[2] The reconstruction of analgoid phylogeny was based on cladistic analysis of 32 morphological characters (data matrix with character states in the Appendix). Plesiomorph states are designated as '0'. Characters coded as having multiple states should be interpreted as polymorph. All binary characters were treated as ordered; multistate characters were treated as unordered. An equal weight 1 was given to all characters. Trees were rooted using a method with outgroups treated as being paraphyletic.

We obtained nine shortest trees with one highly polytomous consensus tree shown in Fig. 3. We doubt whether the position of the Apionacaridae in the presented phylogram is proper. These quill-inhabiting mites possess many apomorphic characters that are mostly reductions of various structures. Possibly, these apomorphies are homologous to many reductions in other advanced analgoid families, for example Knemidocoptidae. There is no doubt that many of these character states are homoplasies caused by entirely different factors. In the highly evolved knemidocoptid mites the reduction of dorsal idiosomal and leg setae is probably an adaptation to living in the subcutaneous layer of birds. In the case of apionacarid mites we have to do with reduction of several structures, including the chaetome which is probably a specific adaptation to living in the quill and caused by neoteny (Gaud and Atyeo, 1975; Atyeo *et al*., 1984). Apart from Apionacaridae, several other feather mite taxa, for example the pterolichoid family Ascouracaridae, show similar body morphology. Adults of these mites have a very large sac-like or cylindrical body with weak idiosomal sclerotization and reduced body and leg setae. These mites never leave the quill and long tactile setae are unnecessary.

After deleting the family Apionacaridae from the analysis we have obtained only one shortest tree (Fig. 4). At present we cannot find any good synapomorphic characters for the grouping of the main clades of the Analgoidea. We hope that the DNA sequence analysis we are starting now will solve this question. On the other hand this polytomy points probably at an explosive radiation that took place shortly after the analgoid origin.

Cluster 1 (Fig. 5) probably originated from the ancestor living in the down feathers. The more ancestral families Analgidae and Psoroptoididae remain in this microhabitat, while the more advanced Dermoglyphidae went into the quills. To cluster 2 belong the most advanced analgoid families inhabiting vane surface. Some of these mites can survive on the most severe external surface of the vane (for example some Alloptidae, Trouessartiidae). Cluster 3 contains the typical vane mites

[2] Knemidocoptidae were included in the feather mites by Dubinin (1953). This family is also treated as belonging to Analgoidea by OConnor (1982). Pyroglyphidae, Turbinoptidae and Laminosioptidae are not included in the analysis. The first two families have similar structures to psoroptid parasites of mammals, but not to 'true' Analgoidea. Two subfamilies of Laminosioptidae, Laminosioptinae and Fainocoptinae, perhaps should be considered as separate families sharing no common ancestry. Also, both subfamilies differ in occupying different microhabitats; the members of the first live in skin of birds, while members of the second are called quill-wall mites. OConnor (1982) included them to the Analgoidea. We agree with his opinion, but suggest the performance of a systematic revision of the laminosioptid mites prior the considerations about its position within Analgoidea. *Gaudoglyphus* (Gaudoglyphidae) is included into Dermoglyphidae (OConnor, 1982).

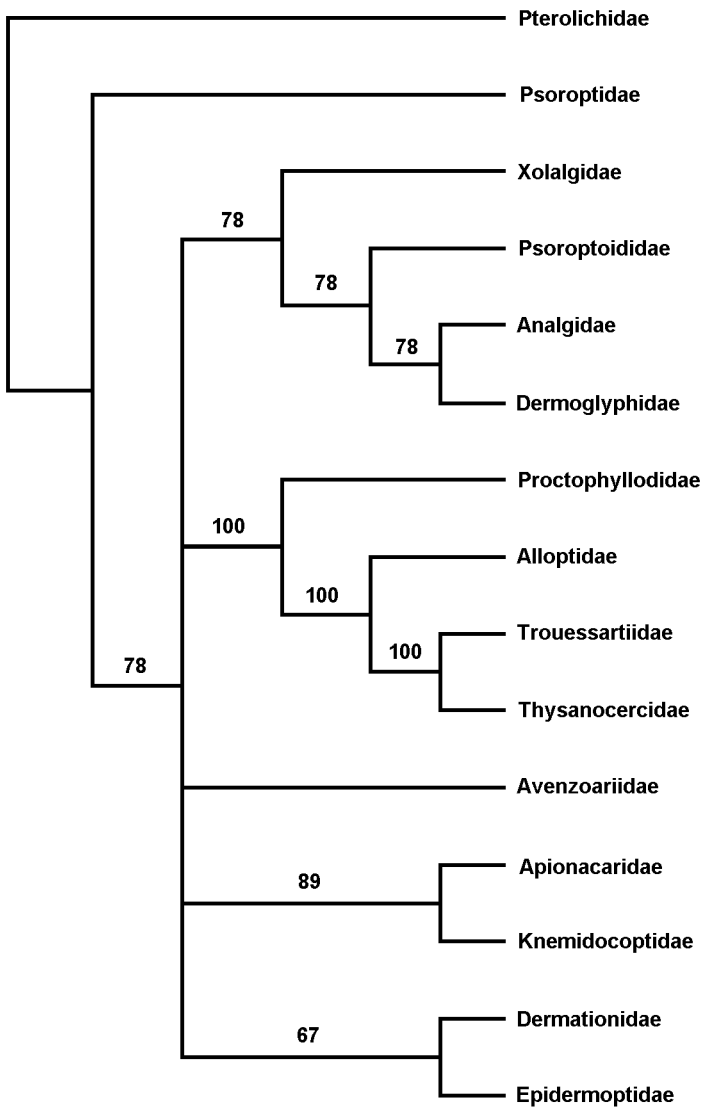

Figure 3. Fifty per cent majority-rule consensus tree of nine shortest trees obtained after including the family Apionacaridae: 53 steps, CI = 0.755 (excluding uninformative characters: 0.690), RC = 0.594, 32 characters. Numbers indicate the percentage of shortest trees having the resolution shown.

which have invaded this microhabitat as the first in the whole superfamily. It is possible that clusters 2 and 3 could be a monophyletic clade which originated from the ancestor living on the vane surface. Cluster 4 is built of three families which are probably ecologically similar to the first analgoid skin inhabitants but now they represent a highly evolved group of epidermal parasites. The most primitive Dermationidae

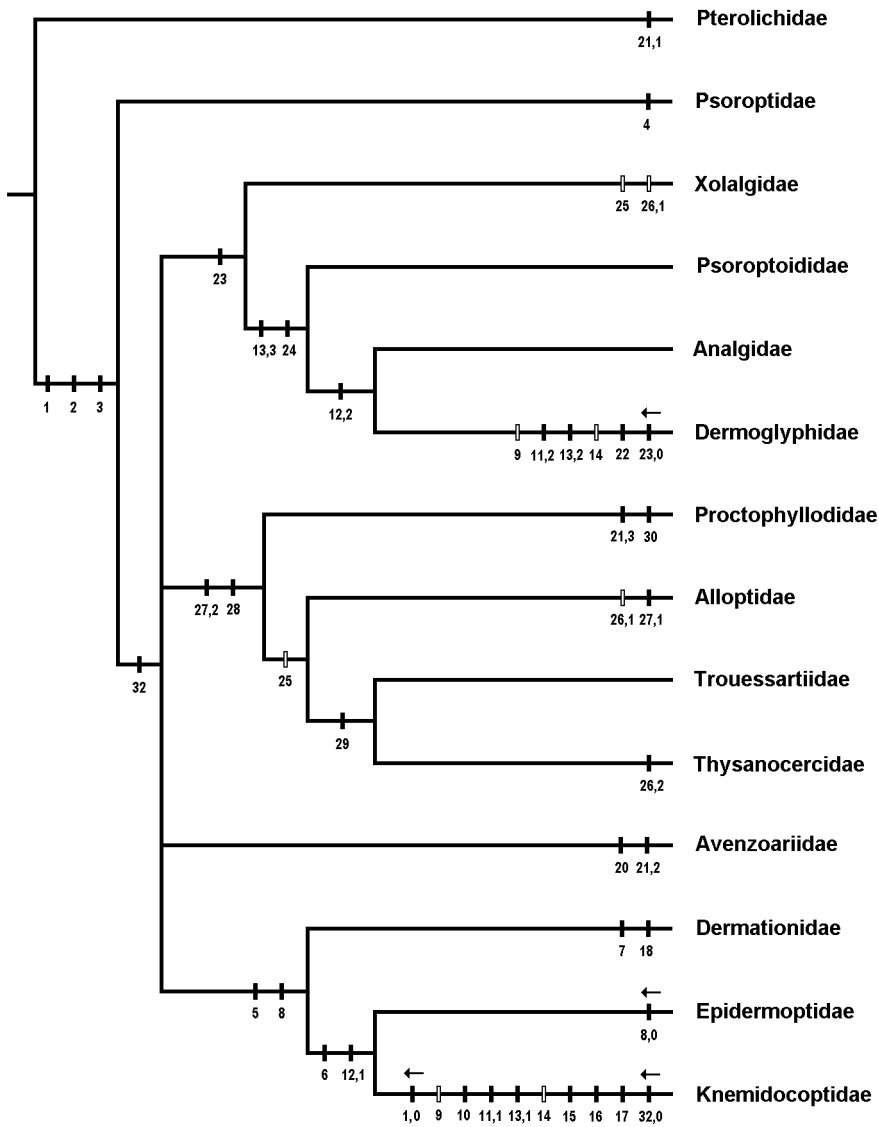

Figure 4. Reconstruction of Analgoidea phylogeny after removing the family Apionacaridae. One shortest tree: 45 steps, CI = 0.822 (excluding uninformative characters: 0.724), RC = 0.692, 32 characters. Filled boxes: aut- and synapomorphies, open boxes; homoplasies, arrows: reversals.

which live on the skin surface are probably most similar to the ancestor of the cluster or even to the ancestor of the Analgoidea. More evolved Epidermoptidae live on skin and often plunge into the epidermis to suck the lymph (Dubinin, 1953; S.V. Mironov,

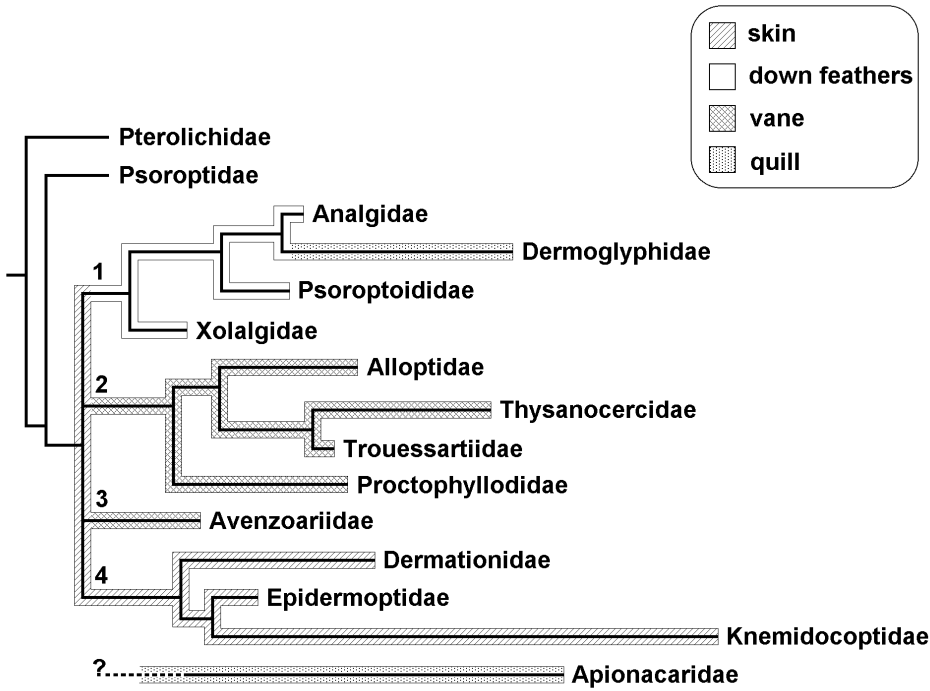

Figure 5. Phylogram of the superfamily Analgoidea compared with the microhabitats occupied by mites from particular families.

personal observation). The most advanced Knemidocoptidae are real skin parasites living under scales of bird legs (some in feather follicles or quills).

If we compare the host–parasite associations among the analgoid mites, we notice that all four clusters are distributed in a wide range of bird orders. Generally, in all clades more primitive (= older) families are associated with more primitive bird groups and the advanced mite taxa inhabit more evolved hosts. This observation suggests co-speciation between feather mites and their hosts.

Co-speciation with Birds and Non-coevolutionary Events

It is widely accepted that the main evolutionary history of feather mites involves co-speciation with their hosts (Gaud and Atyeo, 1979; Mironov, 1991b). A simple analysis of host–parasite associations points to the general rule that almost all main bird lineages have their own, characteristic feather mite faunas (Černý, 1971; Peterson, 1975; Gaud and Atyeo, 1982; Mironov, 1982). This phenomenon can be seen at all taxonomic levels. Even individual bird species have on average two or three typical mite species (Peterson, 1975). To answer the question whether feather mites co-speciated with their hosts, we have to know the phylogenies of both mites

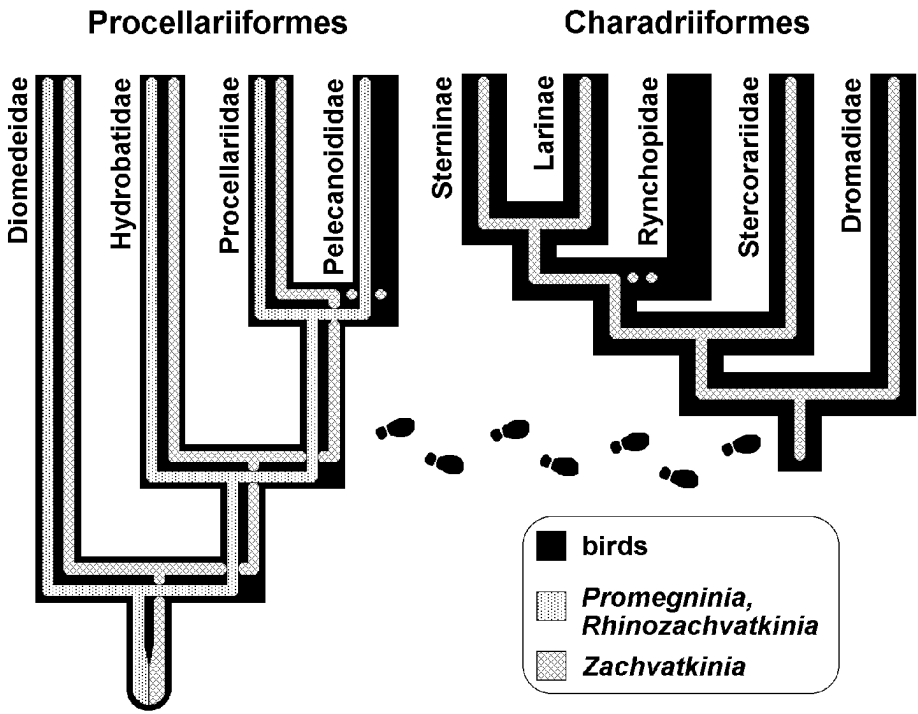

Figure 6. Evolution of feather mite genus *Zachvatkinia* (subgenera *Zachvatkinia* s.s. *Promegninia* and *Rhinozachvatkinia*). Multiple speciation and co-speciation with birds took place on the primary host group (Procellariiformes). Secondary co-speciation happened after shifting to the new host group (Charadriiformes).

and birds. The phylogenetic studies of feather mites are in a very preliminary stage and we have only a few partial phylogenetic reconstructions at our disposal. Literature data are insufficient for more detailed analyses. Surprisingly, the phylogenetic studies of birds are also far from satisfactory. This group of animals has been studied for over a hundred years. There are many phylogenetic hypotheses for birds which are based on various methodologies. Unfortunately, they are mostly mutually inconsistent, and it is difficult to choose a proper scheme for comparisons.

We present a general scheme of relationships (Fig. 6) between the evolution of some water birds and the avenzoariid mites of closely related genera *Zachvatkinia*, *Promegninia* and *Rhinozachvatkinia* (Mironov, 1991b). About 20 species of the genus *Zachvatkinia* exclusively inhabit water birds from two orders – Procellariiformes and Charadriiformes. These three genera constitute two distinct and different evolutionary lineages. The genus *Zachvatkinia* belongs to the first group comprising large, strongly sclerotized and morphologically uniform mites. Genera *Promegninia* and *Rhinozachvatkinia* from the second group are small, weakly sclerotized and highly specialized mites. Both mite groups coexist even on one individual procellariiform bird. The origin of this division is an example of sympatric speciation. The term

'sympatric' is used here in a special meaning. It covers speciation events on one bird species due to the isolation of the ancestral mite population in two different and separated parts of plumage or even within a feather. Large mites from the first group (*Zachvatkinia*) inhabit the vanes of large flight feathers. Small mites from the second group (*Promegninia* and *Rhinozachvatkinia*) can be found exclusively on smaller coverts of the wing. After the splitting, both groups evolved independently but parallel with their hosts. The rate of evolution was different for both mite groups. Mites of the first group evolved more slowly and formed only specific groups of species on birds from particular procellariiform families. The ancestors of the second group evolved quickly and now it forms well-defined genera: more primitive *Promegninia* on albatrosses (Diomedeidae) and more advanced *Rhinozachvatkinia*, divided into well-defined species groups inhabiting storm petrels (Hydrobatidae), diving petrels (Pelecanoididae), fulmars and allied birds (Procellariidae).

If we compare the scheme of phylogenetic relationships between these birds (Kuroda, 1954; Cracraft, 1981) with the analogous scheme for *Zachvatkinia*-like genera, we can observe a very close coevolutionary tracking of bird phylogeny by the mites. An interesting exception is the situation in the diving petrels. Only the most evolutionary advanced, *Rhinozachvatkinia pelecanoidi*, lives in the plumage of these birds. There is no representative of the genus *Zachvatkinia*. We suppose that large *Zachvatkinia* species were eliminated from diving petrels. All the species of large mites from the flight feathers which live on all diving birds using wings for swimming in the water, as diving petrels also do, were subject to extreme conditions and probably became extinct. Only small mites protected in deeper layers of plumage had a chance to survive. We can observe an analogous situation in auks (Alci), loons (Gaviiformes) and grebes (Podicipediformes).

The shifting of these mites into a new group of hosts and secondary co-speciation are the next evolutionary events observed in the genus *Zachvatkinia* (Fig. 5). It is evident that the invaders must have belonged to the species group '*puffini*' from the *Zachvatkinia*. There are no representatives of the second generic group on charadriiform birds. These mites probably did not colonize charadriiform birds because of their closer adaptation to the particular host species and because they inhabit the more protected and inaccessible parts of the plumage. The process of *Zachvatkinia* migration probably took place after the differentiation of the ancestral charadriomorph birds into the primarily terrestrial plovers and allied birds (Charadrii) and more aquatic gulls and allied birds (Lari). The primary acarofauna of larids is represented now only by the very rare and relict genus *Laronyssus* associated with Larinae and the highly specialized genus *Hemifreyana* living on Rynchopidae (both of the Avenzoariidae). After the colonization, *Zachvatkinia* mites probably outcompeted the majority of the ancestral feather mites which could only survive in small numbers in suboptimal microhabitats, probably on the wing coverts. After the colonization took place, secondary co-speciation began on the new hosts. As mites from the genus *Zachvatkinia* evolved relatively slowly, the recent acarofauna of this genus from charadriiform birds differs only slightly from the initial fauna from the primary procellariiform host group. Mites from the ancestral species of the *puffini*-group now live on more archaic larid families, crab-plovers (Dromadidae) and skuas

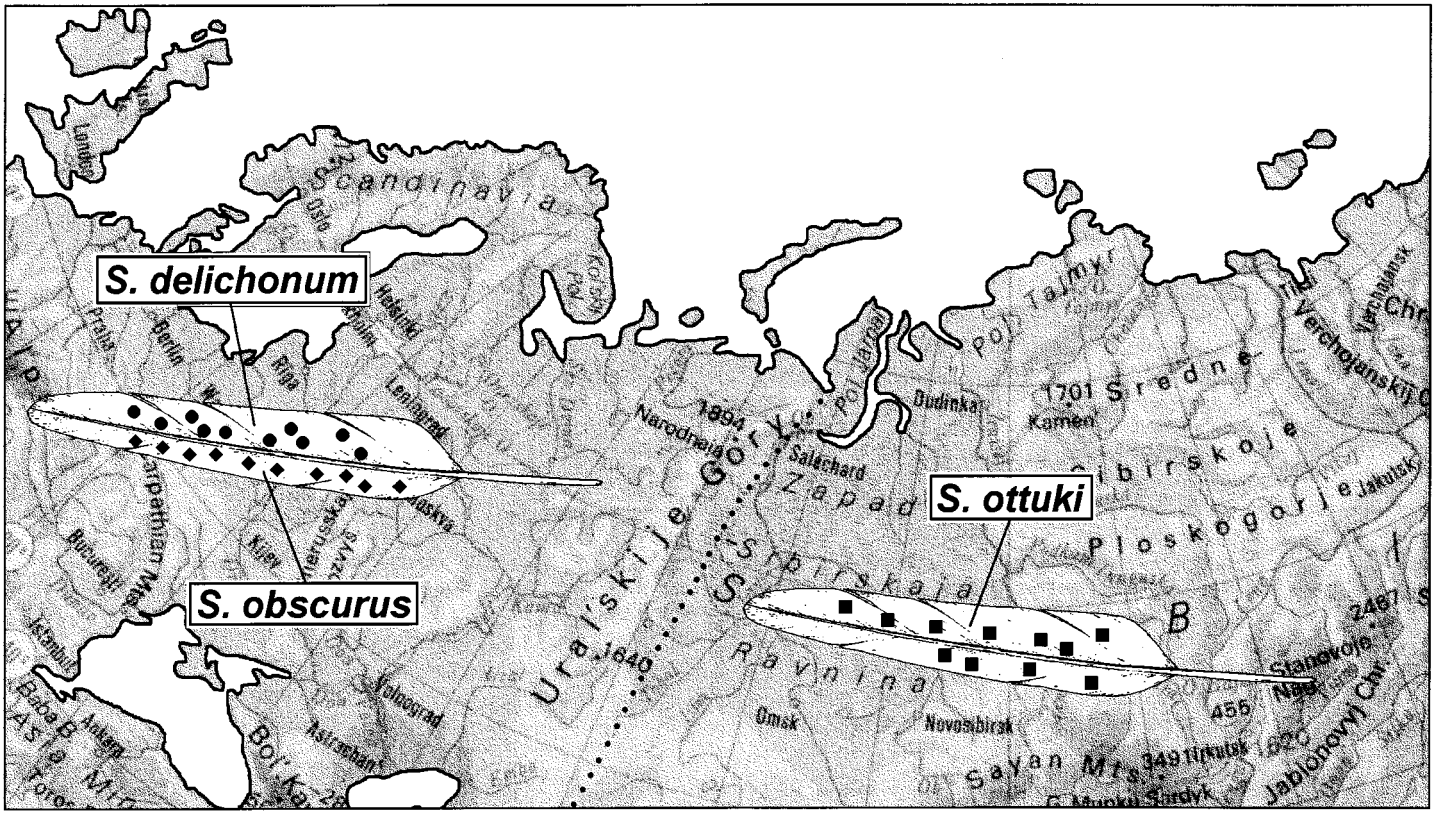

Figure 7. Geographical distribution of *Scutulanyssus* species on the House Martin, *Delichon urbica*. Dotted line: approximate border between ranges of European and Asiatic mite species.

and jaegers (Stercorariidae). Specific *Zachvatkinia* species belonging to the *sternae*-group have evolved on the more advanced gulls (Larinae) and terns (Sterninae). The absence of *Zachvatkinia* species on skimmers (Rynchopidae) is difficult to explain. The slowly evolving *Zachvatkinia* mites living on these highly specialized and unusual larids may have lost in competition with more expansive native mites of the genus *Hemifreyana* (Avenzoariidae). *Hemifreyana* is one of the most derived avenzoariid mites and is clearly very well adapted to the fast flying skimmers.

The comparison of the phylograms of feather mites and their hosts can sometimes be useful for checking hypotheses concerning bird phylogeny. Such methods presume co-speciation. As an example, we tackle the problem by properly locating the above mentioned skimmers in the larid phylogenetic scheme. In some hypotheses, skimmers are treated as a sister group to Stercorariidae and separated from Laridae (McKitrick, 1991). More often they are placed near Laridae with Stercorariidae as more ancestral (for example Sibley and Alquist, 1990). There also exists the third possibility, that Stercorariidae are more closely related to the Laridae than to Rynchopidae (for example Hudson *et al*., 1969). Feather mites of the genus *Thecarthra* (Syringobiidae) live in the quills of these birds (excluding subfamily Larinae). Comparison of the phylogram prepared for these mites with three possible phylograms for birds strongly supports the notion that skimmers are more ancestral to stercorariids and larids, which are sister groups to each other (Dabert and Ehrnsberger, 1995).

Finally, we consider the geographical distribution of feather mites. Generally, feather mites have the same distribution as their hosts. It is true even for taxa living on cosmopolitan hosts. But there are some exceptions to this rule. Some representatives of the genus *Scutulanyssus* (Pteronyssinae) live on the House Martin, *Delichon urbica*, (Hirundinidae) among other feather mites. In the European range of the House Martin two species of *Scutulanyssus* occur: *S. delichonum* on the narrow part of the flight feather vane and *S. obscurus* on the broad part. In the Asiatic part of the House Martin range only one species occurs, *S. ottuki*. The border between the ranges of European and Asiatic mite species lies slightly to the west of the Ural Mountains (Fig. 7).

The second example is the distribution of *Falculifer* species (Falculiferidae) inhabiting plumage of pigeons (Gaud and Atyeo, 1976). Among several species of this genus, two species have the broadest range, namely *F. rostratus* and *F. lacertosus*. Both species inhabit several species in the genera *Columba* and *Streptopelia*. Some pigeon species can harbor both *Falculifer* species but never together on one host individual. *Falculifer rostratus* can be found in Eurasia, northern Africa, North and South America; *F. lacertosus* lives in central and southern Africa, India and the Far East. Two other feather mites from pigeon, *Pterophagus strictus* and *P. columbae* (Falculiferidae) have similar distributions.

Conclusions

We conclude that feather mites are highly specialized ectoparasites of birds' plumage and have accompanied their hosts from the beginning of their history. The key factor

of feather mite evolution is the evolutionary tracking of the host evolution. Due to their very long existence on birds, there were many opportunities for unforeseeable non-coevolutionary events such as host switching, acarofauna extinction and simple mite sorting without speciation. In some feather mite taxa we can observe specialization to particular microhabitats rather than to a particular bird host. All these phenomena make it more difficult to trace evolution of feather mites with that of their hosts.

Appendix

Data matrix for superfamily Analgoidea

	1234567891111111 0123456	1 7	112222222222333 890123456789012
Pterolichidae	0000000000000000	0	000100000000000
Psoroptidae	1111000000000000	0	000000000000000
Analgidae	1110000000023000	0	000001100000001
Psoroptoididae	1110000000003000	0	000001100000001
Dermoglyphidae	111000?010222100	0	000010100000001
Xolalgidae	1110000000000000	0	000001011000001
Alloptidae	1110000000000000	0	000000011110001
Thysanocercidae	1110000000000000	0	000000012211001
Trouessartiidae	1110000000000000	0	000000010211001
Proctophyllodidae	1110000000000000	0	000300000210101
Avenzoariidae	1110000000000000	0	001200000000001
Apionacaridae	1110000000100111	1	010110000000011
Dermationidae	1110101100000000	0	100000000000001
Epidermoptidae	1110110000010000	0	000000000000001
Knemidocoptidae	011011?111111111	(01)	000000000000000

Character argumentation:

1. Condylophore guide: 0 – absent, 1 – present.
2. Setae *p* and *q*: 0 – present, 1 – absent.
3. Setae *s* on tarsus IV: 0 – present, 1 – absent.
4. Solenidion *omega 1* on tarsus I: 0 – set in proximal half, 1 – set apically.
5. Solenidion *sigma* on genu III: 0 – present, 1 – absent.
6. Apical hook of tarsi I–IV: 0 – absent, 1 – present.
7. Epigynum: 0 – free, 1 – fused with epimeres I.
8. Setae *mg* II: 0 – present, 1 – absent.
9. Epigynum: 0 – present, 1 – reduced.
10. Ambulacrum: 0 – well developed, 1 – reduced (tendency).
11. Shape of idiosoma: 0 – ovoid and flattened, 1 – ovoid or spherical, 2 – spindle like.

12. Ambulacral stalk: 0 – short, cylindrical, 1 – thin, elongated, 2 – thick, enlarged.
13. Prodorsal crests: 0 – absent, 1 – thick lateral, 2 – narrow lateral, 3 – medial.
14. Adanal discs: 0 – present, 1 – absent.
15. Setae *d1*: 0 – present, 1 – absent.
16. Setae *e1*: 0 – present, 1 – absent.
17. Setae *h3*: 0 – present, 1 – absent.
18. Setae *f2*: 0 – present, 1 – absent.
19. Solenidion *phi* IV: 0 – present, 1 – absent.
20. Lateral sclerites of ambulacrum: 0 – small, 1 – enlarged.
21. Central sclerite: 0 – small, 1 – enlarged, trapezoid or rectangular, 2 – enlarged tridentate, 3 – rhomboid.
22. Position of legs III, IV: 0 – submarginal, 1 – ventral.
23. Ventral apophyses of tibiae I, II: 0 – absent, 1 – present.
24. Ventral apophyses of tarsi I, II: 0 – absent, 1 – present.
25. Fusion of femur and genu of legs III and IV: 0 – absent, 1 – present.
26. Fusion of femur and genu of legs I and II: 0 – absent, 1 – completed, 2 – with rudimental furrow.
27. Opisthosomal lobes in females: 0 – absent, 1 – present, nude, 2 – present, with various membranes or appendages.
28. Setae *c3* and *cp*: 0 – *c3* anteriorly to *cp*, 1 – *c3* posteriorly to *cp*.
29. Pronounced pattern on hysteronotal shield: 0 – absent, 1 – present.
30. Solenidion *sigma* on genu II: 0 – present, 1 – absent.
31. Setae *d*, *e*, *f* IV: 0 – present, 1 – absent.
32. Condylophores: 0 – thick, straight or angle-shaped, 1 – thin zigzag-like (flexible).

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