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0020-7519(94)00109-XADAPTATION, SPECIFICITY AND HOST-PARASITE COEVOLUTION
IN MITES (ACARI)

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Abstract—Fain A. 1994. Adaptation, specificity and host-parasite coevolution in mites (Acari). *International Journal for Parasitology* 24: 1273-1283. Parasitism by mites is widespread and involves all the classes of vertebrates, from fishes to mammals. Owing to their small size and their great plasticity, mites are able to adapt to a wide range of habitats. Most of the species are ectoparasites but endoparasitism, especially in the respiratory tract, is common in birds and mammals. The morphological modifications appearing during the process adaptation to parasitic life, especially in Myobiidae, are analysed. Two kinds of characters are particularly important: the constructive specialized characters, consisting of the production of new structures, especially attachment organs allowing the mite to attach to the skin and the hair of the host, and regressive characters. Regression of the external structures is the most important phenomenon appearing in the process of evolution of parasitic mites. The importance of the regression in the parasite is correlated with the degree of evolution of the host. Host and parasite have a parallel evolution, but they go in opposite directions. The author surmises that the regressive evolution is related to the immunological reactions of the host that tend to reject the parasite. To escape from this rejection the parasite tends to select the less antigenic and therefore the most regressed phenotype. Specificity is generally strict in permanent parasites. Coevolution of host and parasite is studied in the family Myobiidae which parasitizes marsupials, insectivores, bats and rodents. The concordance between the radiations of the mites and that of their hosts is very high.

INDEX KEY WORDS: adaptation; specificity; coevolution; mites (Acari); mammals.

INTRODUCTION

I would like to deal here with some aspects of parasitic life in mites (Acari). Parasitic mites, chiefly those from higher vertebrates, have been extensively collected and researched during these last 3 decades and these studies have contributed substantially to a better knowledge of these parasites, specially in regard to their classification, geographic distributions, specificity and host-parasite coevolution.

CLASSIFICATION

Mites and ticks form the subclass Acari, in the class Arachnida. They are divided into 7 orders, of which only 4 include parasitic forms, i.e. the Metastigmata, also called ticks, and the Mesostigmata, Prostigmata and Astigmata, forming the group of mites (Evans, Sheals & Macfarlane, 1961). Ticks are generally distinctly larger than mites and they are all obligate parasites of vertebrates. The 3 orders of mites include both free-living forms and parasites. In this paper I will deal only with mites.

PARASITIC NICHES

Ectoparasitism

Mites are very plastic creatures, capable of adapting to very different conditions of life. Their small size enables them to occupy a very wide range of habitats. Usually their body length ranges from 0.5 to 1mm, but in the smallest species this length does not exceed 0.1 mm. Most of the species are free living but there are also numerous parasitic forms living on plants or on animals, both invertebrates and vertebrates. Among the invertebrates only 2 phyla, i.e. the molluscs and the arthropods, especially insects, are parasitized by mites, whilst in the phylum Chordata (= Vertebrates), all the classes, from fishes to mammals, have been found to be infected by them. Parasitism by mites is particularly frequent in birds and mammals. A large number of species are ectoparasitic and live on the skin or in the superficial layers of the skin, where they feed on the corneous material of the skin or on the blood or the lymph that they suck by means of specialized piercing mouth pieces. The feathers of birds are colonized by about 2000 species. These mites are generally highly specialized and they feed on the corneous

material desquamating from the feathers (Gaud & Atyeo, 1982). Fur mites of mammals also form a large group. The most important are the Listrophoroidea (Astigmata) (about 1000 species) and the Myobiidae (Prostigmata) (more than 400 species).

Endoparasitism

Endoparasitism by mites is widely distributed in vertebrates and it affects especially birds. Most of the species live in the respiratory tract of their hosts, from the nasal cavities to the air-sacs. Until now more than 500 species have been described in birds from this habitat; they belong to 3 orders and 5 families of mites. Three of these families (Turbinoptidae, Cytoditidae and Rhinonyssidae) are completely restricted to this habitat (Fain, 1957, 1965b). In the nasal cavities of birds the various species are not distributed randomly but they occupy distinct sites according to the family to which they belong. The Turbinoptidae (Astigmata) are confined to the superficial cutaneous parts of the nasal cavities and they never invade the deeper cavities. These species have strong chelicerae and feed on the corneous layers of the skin. A second family, Rhinonyssidae (Mesostigmata), includes only blood sucking species living on the mucosa of the turbinates. Among this family 1 species, *Sternostoma tracheacolum*, lives in the trachea and the bronchi and may cause pneumonia. A third family, Cytoditidae (Astigmata) includes a few very small mites living in the deeper parts of the nasal cavities including the nasal sinuses. One of these species, *Cytodites nudus* infects the air-sacs where it feeds on exudate (Fain, 1960). The species of the fourth family, Ereyetidae (Prostigmata), do not have a defined niche but run freely through the entire nasal cavity and they are covered by a whitish, water-repellant substance which prevents these mites from being caught by the mucus covering the turbinates. The last family, Ascidae (Mesostigmata), includes about 40 species parasitizing the nasal cavities of hummingbirds (Trochilidae). These mites, actually, are not true parasites as they feed upon the nectar of flowers (Bromeliaceae, Heliconiaceae, Ericaceae, etc.) and they are phoretically transported from flower to flower by these birds (Colwell, 1973; Fain, 1992). Besides the respiratory passages, several other endoparasitic niches are known in birds, e.g. feather follicles, in the shaft of the feathers, under the skin or in the deeper cellular tissues enveloping the viscera.

Endoparasitism is also widespread in mammals and, as in birds, the respiratory tract is heavily

infected. Three families of mites are completely restricted to this habitat: i.e. Halarachnidae (Mesostigmata), Pneumocoptidae (Astigmata) and Lemurnyssidae (Astigmata). The Halarachnidae, represented by 6 genera and 34 species, parasitize 15 families of mammals (Furman, 1979). This family is homologous to the Rhinonyssidae living in birds. Both groups probably derive from the ectoparasitic Mesostigmata (Macronyssidae) living on these hosts (Radovsky, 1985). The Pneumocoptidae are represented by 1 genus and 3 species living in the lung of North American and European rodents (Baker, 1951), and the family Lemurnyssidae, 2 genera and 4 species, occupying the nasal cavities of the African *Galago* and of Neotropical monkeys (Fain, 1964b). Another family, Gastronyssidae (Astigmata) represented by 3 subfamilies, is endoparasitic in bats and rodents: Gastronyssinae, Rodhainyssinae and Yunkeracarinae. The Gastronyssinae, with 1 genus and species, *Gastronyssus bakeri*, is a common parasite of the stomach of the African Megachiroptera. The Rodhainyssinae, with 4 genera and 18 species are confined to the nasal cavities and the conjunctival sac of bats, both Mega and Microchiroptera. The third subfamily, Yunkeracarinae, with 2 genera and 5 species is restricted to the nasal cavities of rodents (Fain, 1964a, 1967).

Besides the respiratory passages, mites have also been found under the skin or in the deeper cellular tissues around the muscles, e.g. Epimyodicinae in *Talpa europaea* and rats (Fain, Lukoschus & Rosmalen, 1982) and in the hair follicles, e.g. Demodicidae (Nutting, 1985), Rhyncoptidae (Lawrence, 1956; Fain, 1965a) and Audycoptidae (Lavoipierre, 1964; Fain & Johnston, 1970). Endoparasitism by mites is not restricted to higher vertebrates but is also frequent in lower vertebrates such as snakes: e.g. lung mites of the family Entonyssidae, specific for these hosts (Fain, 1961), turtles: Cloacaridae, parasitizing the cloaca and the muscles of their hosts (Camin, Moss, Oliver & Singer, 1967; Fain, 1968b), frogs and toads: Ereyetidae parasitizing the nasal cavities (Fain, 1962), and fishes: Histiostomatidae living in the swim-bladder of an aquarium fish (Fain & Lambrechts, 1985). As a rule endoparasitic mites are highly specific for both their hosts and the niche that they occupy.

The multiplicity of habitats occupied by mites demonstrates their ability to adapt to various conditions of life. No other group of parasites is capable of occupying such a wide range of parasitic niches. The chances of finding complete phylogenetic lineages, including both ectoparasites and endopara-

sites and often their nidicolous ancestors, is therefore much greater in mites than in any other group of parasites. In insects (fleas, lice, mallophaga, flies), ectoparasitism is almost the only form of parasitism, whilst in helminths endoparasitism is the rule, except for a small group of ectoparasitic Monogenea. Mites appear, therefore, as probably the most suitable group of parasites in the study of host-parasite coevolution.

MULTIPLE SPECIATION

Multiple speciation is relatively frequent in the fur mites of the superfamily Listrophoroidea. In Australia, the potoroo, *Potorous tridactylus*, harbours 21 endemic species of the genus *Cytostethum* (Atopomelidae) for a total of 15 potoroos examined (Fain & Domrow, 1974).

Multiple speciation is particularly marked in the beavers *Castor fiber* and *C. canadensis*. In U.S.S.R. Dubinina (1964) examined 22 beavers, *Castor fiber*, from the Voronesh Reservation, and found 12 endemic species of the genus *Schizocarpus* (Chirodiscidae) and among them 11 were new. These investigations were continued by Fain & Lukoschus (1985) who collected from 4 beavers (*C. fiber*) caught in the river Elbe, Germany. They found 25 species of *Schizocarpus*, of which 21 were new, raising the number of species living on this beaver up to 31. The North American beaver, *Castor canadensis*, is parasitized by 17 species of *Schizocarpus*, all restricted to this host and clearly distinct from the species found in the European beavers. In both species of beavers most of the mites occupied specific microhabitats on the body and the head of the beavers (Fain & Whitaker, 1988). Such extreme speciation is probably unique in parasitology. The cause of this phenomenon is not known but Fain & Lukoschus (1985) supposed that it might result from the combination of 2 different mechanisms. The first process is the isolation of the various populations of beavers in separate areas. The second mechanism is the microisolation resulting from the existence on the beavers of different microhabitats differing from each other by the texture and the thickness of the hairs, the differences in the skin secretions, etc.

VARIABILITY

Individual variations, i.e. variations of morphological characters within a population, are not rare in parasitic mites. It is an important question, for certain "new" species have been based on such variable characters. In this respect I would like to recall here briefly the interesting history of *Sarcoptes scabiei*, a common parasite causing mange in man

and in domestic mammals (e.g. cats, dogs, horse, cattle, pig, sheep, etc). This species is very rare in wild animals living in their natural habitat but it becomes frequent when these animals are sheltered in zoos. More than 30 species and 15 varieties have been described in the genus *Sarcoptes*. From 1962 to 1968 I had the opportunity to examine, not only single specimens, but also good series of these described species. This study has shown that all these "species" were based on variable characters without taxonomic value and that there is only one valid but variable species in the genus *Sarcoptes*. The wide variability of *S. scabiei* suggests that this species is not completely adapted to any of the present hosts but remains in a continuous process of adaptation. The variability is probably related to the great number of hosts that this species is capable of parasitizing. The mite causes scabies in 40 different hosts belonging to 17 families and 7 orders of mammals. I have surmised that the frequent interbreeding of the mite in zoologically remote, mostly domestic mammals, has prevented speciation and at the same time provided new genetic characters which have enhanced the adaptability of the mite to infect new hosts. The variability of *S. scabiei* is probably the result of continuous interbreeding in these strains (Fain, 1968a, 1978a).

Another highly variable species is *Sternostoma tracheacolum* (Rhinyonyssidae) living in the respiratory tract (nasal cavities, trachea and lungs) of birds and causing pneumonia in the canary. This species has been found from 24 species, belonging to 11 families, of birds, mostly Passeriformes (Fain & Hyland, 1962).

SPECIFICITY AND COEVOLUTION

Host specificity in parasites of vertebrates has been extensively treated in two international symposia. The first was organized by J. Baer in Neuchâtel, Switzerland, in 1957. No paper on mites was presented. The second was held in Paris, in 1981 (proceedings published in 1982). The organizer was A. Chabaud. Among the 40 papers presented at this symposium 4 dealt with parasitic mites, of which 2 were on ticks (Hoogstraal & Aeschlimann, Morel), 1 on feather-mites (Gaud & Atyeo) and 1 on Myobiidae (Fain). Most recently, Kim (1985) published a significant amount of data concerning host-specificity and coevolution of parasitic arthropods and mammals. Four chapters of this book dealt with Acari. All the groups of mites are not equally suitable for the study of specificity and coevolution, but the permanent parasites, i.e. those that remain on their host during all their stages of development,

can be used for this purpose. In the case of mites that leave their host periodically, such as ticks and many ectoparasitic mesostigmates, specificity is low and coevolution poorly marked. Pilicolous specialization has induced a strong specificity, not only in mites (especially Listrophoroidea and Myobiidae) but also in some insects, such as lice which are both permanent and highly specific. In these groups the attachment to the hairs of their hosts has induced the production of highly specialized clasping organs which prevent the parasite from attaching to other hosts. As a rule, host-specificity is marked in permanent parasites but exceptions are common (Fain, 1975, 1977). In animals kept for long periods in zoos, parasites may be transferred from their normal host to atypical hosts living in close association with them. I have reported (Fain, Mignolet & Beresnay, 1958) a case of infection by lung mites in an Asiatic macaque in the zoo of Antwerp. This animal was infected by 3 species of *Pneumonyssus* (Halarachnidae) normally restricted to African cercopithecids and never reported from Asia. The macaque had probably been contaminated by the heavily infected African cercopithecids living in association with it.

Low host-specificity has also been reported in *Rhinonyssus rhinoletrum* (Rhinonyssidae), a common nasal mite parasitic in Anseriformes, specially in ducks. This species has been recovered from 40 species of Anatidae belonging to 20 genera (Fain, 1965b). According to Strandtmann (1958) the lack of specificity in this mite might be explained by the gregariousness of the aquatic birds creating favourable conditions for the transfer of the mites. Gaud & Atyeo (1982) observed that the feather mites living on aquatic birds are less specific than those from terrestrial birds, probably for the same reason. Two other examples of low specificity in permanent parasitic mites are those of *Sarcoptes scabiei* and *Sternostoma tacheacolum*.

IMPORTANCE OF REGRESSION IN THE EVOLUTION OF MYOBIID MITES

Fahrenholz (1909) during his researches on Anoplura and Mallophaga noted the narrow relationships between hosts and their parasites. In 1913, he concluded that in hosts of different species, the parasites diverge from one another to the same degree as their hosts are related (in Eichler, 1942, cited by Klassen, 1992). Szidat, 1940 (in Eichler, 1942, cited by Klassen, 1992) postulated that primitive hosts harbour primitive parasites. This author explained the close relationship between host and parasite lineages by orthogenesis (= progressive evolution). These authors did not explain by which

morphological characters they recognized a primitive form from an evolved parasite and they did not make reference to the regressive characters appearing in the parasites during their evolution. Several authors, Jameson (1955), Dusbabek (1969a,b), Uchikawa & Harada (1981) and Uchikawa (1986, 1987), have given numerous examples of specificity and host-parasite coevolution in mites of the family Myobiidae, especially in the species parasitizing bats, confirming the observations of the preceding authors about the relationship between hosts and their parasites, but again they did not mention the role of regression in the evolution of the parasites.

Mites of the family Myobiidae parasitize 4 orders of mammals of particular interest in evolutionary studies, marsupials, insectivores, bats and rodents. Up to now 413 species and 37 subspecies, belonging to 49 genera and 23 subgenera have been described in the Myobiidae. Fain (1969, 1974, 1977, 1982, 1988) studying a large collection of myobiids from various hosts and countries concluded that the most important phenomenon appearing during the process of evolution of parasitic mites is the regression of the external structures. These observations are summarized below.

Complication of structures is a general trend in the evolution of animals. In parasitic mites, and that is also true for many other parasites, evolution, at least that which concerns the external structures, is of the regressive type. That means that myobiids living on evolved hosts show more regressive characters than those living on primitive hosts. The host and the parasite follow a parallel course of evolution, although they go in opposite directions. Moreover in the same evolutionary line, the endoparasitic mites always show more regressive features than their ectoparasites, their probable ancestors (Fain, 1969, 1974). Regression in parasites probably involves only external structures, and there is no apparent reason that the internal organs should not follow the general trend of complication. An argument in favour of this view is the fact that primitive myobiids have never been found on evolved hosts, while the reverse, e.g. the occasional presence of an evolved species on a primitive host, is not rare. Evolved (regressed) parasites are probably capable of adapting to both primitive and evolved hosts, whilst primitive parasites seem to be unable to colonize evolved hosts.

The mechanism of regression of the external structures of the parasites is not known. I have proposed the hypothesis that regression is a result of the immunological reactions of the host which tends to reject the parasite in the same way that it rejects any

other foreign antigen. To escape from the rejection the mite tends to select less antigenic and therefore the most regressed phenotype (Fain, 1979).

There is generally a good correlation between the degree of regression in the parasite and the degree of evolution of the host. Moreover, the regression of the structures is gradual and quantifiable so that it is possible, to some extent, to evaluate indirectly the respective degree of evolution of their related hosts (Fain, 1974, 1977). The progressive regression of the parasite appears to be directly related to the efficiency of the immunological system and accordingly to the degree of evolution of the host. It is therefore in concordance with the phylogeny of the latter. The fact that the same organ is always more regressed in parasites living on evolved hosts than in those from primitive hosts proves that the regression does not result simply from a lack of use of this organ by the parasite.

Some structures are more susceptible to regression than others and they are therefore more reliable in the estimation of the degree of evolution. These characters vary according to the group of parasites. In Myobiidae the best character for that purpose is the structure of the leg I (Figs 1–8). Using this character it is possible to distinguish three main groups in the Myobiidae. In the first group, the most primitive, all the segments of leg I are free and well developed and they end in a pair of small claws. This group includes the 5 genera living on marsupials and the 2 most primitive genera from insectivores (*Nectogalobia* and *Protomyobia*). The second group, more regressed than the first, includes the 14 other genera living on insectivores and all the genera found from bats. In this group, the 2 apical segments of leg I are fused and the apical claws are lacking except in 3 genera from bats (*Acanthophthirus*, *Pteracarus* and *Hipposiderobia* and 1 from insectivores (*Eadiea*) in which tarsus I is free but very short and the apical claws inconstant. These 3 genera from bats appear to be the most primitive of all the genera from these hosts. In the third group, the most regressed, hence the most evolved, the third apical segments of leg I are completely fused forming a single segment oriented transversely and devoid of claws. This leg resembles superficially that of *Hipposiderobia* living on bats but in this genus the third apical segments are free. This third group includes 7 genera, entirely restricted to rodents.

The study of leg I in the Myobiidae reveals a clear concordance between the degree of regression of the parasites and that of the evolution of the hosts. This feature of leg I seems to have evolved very slowly

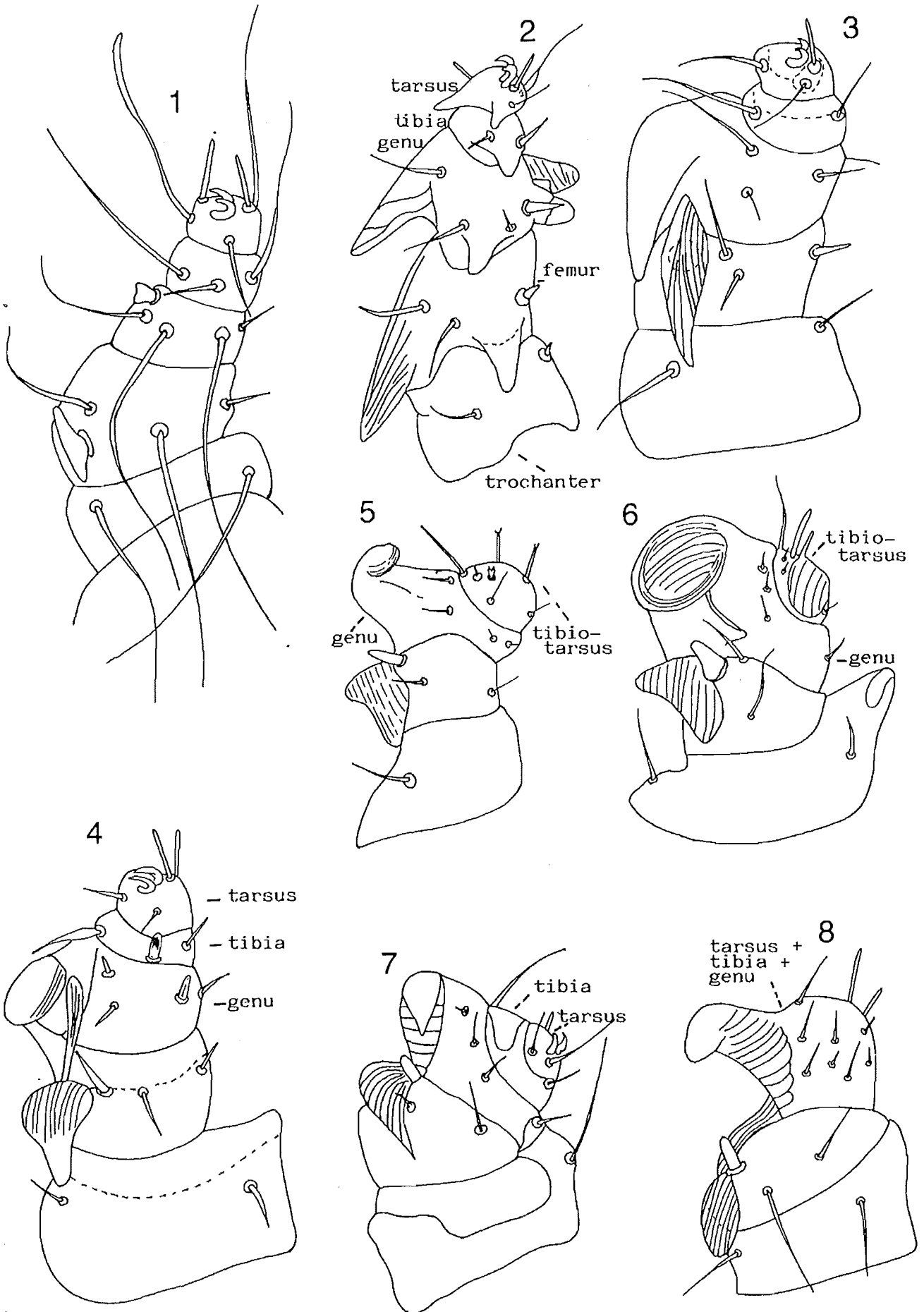
and it dates probably from the time of emergence of the order hosts.

This character of leg I allows the recognition of 3 main groups in the Myobiidae but it does not provide valuable information concerning the degree of evolution of the different genera of each group. Two other characters may, accordingly, be used for this purpose: the first is the number and the degree of regression of the claws on legs II–IV, the second is the number and the shape of setae on the legs and the body. These characters, however, are less stable, but more sensitive, than the shape of leg I. They can be used for comparing the degree of evolution in the genera within the main groups of mites.

SPECIFICITY AND COEVOLUTION OF MYOBIIDAE AND MAMMALS

In marsupials

The Myobiidae have been divided into 3 subfamilies. Among them 2 Archemyobiinae and Xenomyobiinae, are restricted to American marsupials, the third, Myobiinae, is heterogenous and divided into 2 tribes: the Australomyobiini, restricted to Australian marsupials and the Myobiini including all the genera and species living on placental mammals. The Archemyobiinae include 2 genera, *Archemyobia*, with 2 subgenera and 7 species living on Didelphidae, and *Dromicimyobia*, with a single species parasitic on *Dromiciops* (Didelphidae, Microbiotheriinae). *Archemyobia* presents an unique character, i.e. the presence of the internal surface of both legs I of 2 chitinous striated projections serving to clasp the hair of the host. The Xenomyobiinae are represented by a single genus and species, *Xenomyobia hirsuta*, living on *Lestoros inca* (Caenolestidae). This genus differs from all the other genera in the Myobiidae by the absence of clasping organs on the legs I. The mite is fixed to the host by means of the strong and very thick and striated claws of the legs III and IV. This mite presents a mixture of primitive (no clasping organs on leg I but with clasping claws on legs III and IV) and specialized characters (hypertrichy and scaly aspect of the ventral surface of the body) (Fain & Lukoschus, 1976b). In the features of the legs *Xenomyobia* resembles *Nectogalobia*, a very primitive genus living on the insectivore *Nectogale elegans* (Soricidae) from China. In this genus the clasping organs of leg I are poorly developed and the claws III and IV are very thick and apparently serve for attaching to the hairs of the host (Fain & Lukoschus, 1976a). The Australomyobiini include 2 Australian genera, i.e. *Australomyobia*, with 3 species restricted to Dasyuridae, and *Acrobatobia*, monotypic and



Figs 1-8: Leg I of the female ventral view, in some genera of the family Myobiidae: 1. *Xenomyobia*; 2. *Archemyobia*; 3. *Australomyobia*; 4. *Nectogalobia*; 5. *Elephantulobia*; 6. *Binuncus*; 7. *Pteracarus*; 8. *Radfordia*.

specialized for *Acrobates pygmaeus* (Burrmyidae). In these genera, leg I possesses a normal clasping organ as in the Myobiinae and legs III and IV are thin and not adapted for clasping the hairs of the host (Fain & Lukoschus, 1979b).

These observations may be summarized as follows: the American marsupials of the families Didelphidae and Caenolestidae are parasitized each by a different subfamily of Myobiidae, Archemyobiinae and Xenomyobiinae, respectively. The genus *Dromiciops* (Didelphidae: Microbiotheriinae) is parasitized by a distinct genus in the Archemyobiinae. The Myobiidae from Australia, *Australomyobia* and *Acrobatobia*, living on Dasyuridae and Burrmyidae, respectively, are more evolved than those from South American Didelphidae suggesting that a derivation Didelphidae-Dasyuridae is possible. According to Hoffstetter (in Fain, 1982) the concordance between the radiations of the Myobiidae and that of their hosts is remarkable.

In insectivores

The 16 genera and 67 species of Myobiidae described from the insectivores all belong to the subfamily Myobiinae. Specificity is very strict, each genus is endemic for a subfamily of insectivores, except for *Eadiea* represented by 6 species, all parasitic on Talpidae but from 4 different subfamilies: 2 species from Scalopininae, two from Desmaninae, one from Talpinae and one from Condylurinae (Fain & Luckoschus, 1976a). Myobiidae have not been found from Chrysochloridae, Erinaceidae, Solenodontidae and Tupaiidae. The Tupaiidae were included in the insectivores before Corbert & Hill (1980) created the new order Scandentia for them.

The Soricidae are parasitized by 8 genera and 36 species of Myobiidae. The Talpidae harbour 2 genera and 9 species: *Eadiea* whose 6 species are represented in the four subfamilies of Talpidae (see above), and *Eutalpacarus* with 3 species, each of them being restricted to a different genus of Scalopininae. The Tenrecidae include 5 genera and 15 species. The 2 different species of the genus *Afromyobia* infect the genera *Potamogale*, and *Micropotamogale*, respectively. The 4 other genera, with 13 species, are restricted to the Oryzoryctinae of Madagascar, each of them being specialized for 1 host genus. *Microgalobia* harbour nine species of which 6 are living on the host-genus *Microgale*, two on *Nesogale* and one on *Geogale*. The three other genera are monotypic: *Limnogalobia* infects *Limnogale* and *Oryzoryctobia* parasites *Oryzoryctes*. The third genus *Madamyobia* contains 2 species, 1

parasitizes 5 species of *Microgale*, the other lives on *Limnogale*. The Macroscelididae are parasitized by a single genus, *Elephantulobia*, with three species, each of them living on a different species of *Elephantulus*.

We can summarize these observations as follows: The two most primitive genera of Myobiidae from insectivores are *Nectogalobia* with one species living on *Nectogale sinensis* (Blarinini) and *Protomyobia* with eight species living on Soricini and Blarinini. All these primitive species are confined to the Holarctic Region, as are their hosts. A third genus *Eadiea*, more evolved, is encountered on Talpidae, as holarctic. All the other genera are more evolved than *Eadiea*. The 6 genera from Madagascar or Central Africa parasitizing the Tenrecidae and the Macroscelididae form a rather homogenous group distinctly more evolved than the other genera. Paradoxically, *Blarinobia* with 2 species restricted to the North American Blarinini, is the most evolved of the group.

In bats

Since my paper on coevolution in Myobiidae (Fain, 1982) the number of described species from bats has increased from 179 to 230, and that of subspecies to 29; they are included in 21 genera and 7 subgenera.

The Megachiroptera are represented by a single family Pteropodidae divided into 4 subfamilies (Pteropodina, Nyctimeninae, Harpyionycterinae and Macroglossinae) and 44 genera. These hosts harbour 3 (? 2) genera and 1 subgenus of Myobiinae, i.e. *Binuncus*, with one subgenus *Probinuncus*, including 19 species, all restricted to Pteropodinae, except one living on Macroglossinae. The second genus *Pteropimyobia* includes 5 species of which 3 live on Macroglossinae and 2 on Nyctimeninae. The third genus, *Ugandobia* is represented by 9 species from Emballonuridae, 1 (*U. euthrix*) from Hipposideridae and 1 (*U. balionycteris*) from Pteropodinae. I think that this genus is restricted to the Emballonuridae and that the occurrence of 2 species on other hosts resulted from contamination in museum jars. Concerning *U. balionycteris*, this species has been recorded again, but as a new subspecies, from 3 species of *Emballonura*, which is probably the true host genus of this taxon (Fain, 1976a; Uchikawa, O'Connor & Klompen, 1991). The 19 species of *Binuncus* are all restricted to Pteropodinae, except for 1 species found on a Macroglossinae. Specificity is also very strict at the genus level of the host, each species being specialized for a single host genus, except for 1 species which was found on 2 closely related hosts (Fain, 1982). It is important to note

that *Binuncus* and *Pteropimyobia* living on Megachiroptera are more evolved than *Acanthophtirius* and *Pteracarus* from Microchiroptera. The subgenus *Probinuncus* is slightly more primitive and forms a link between the 2 groups.

From these observations it appears that the Myobiidae living on bats do not originate in Megachiroptera but in some primitive genera of Microchiroptera, especially Vespertilionidae, and from these have passed to Megachiroptera. Another argument that confirms this opinion is the fact that Megachiroptera harbour only a very small number of genera and species (2 genera and 24 species) compared to Microchiroptera (20 genera and 206 species of Myobiidae). The situation is peculiar to the Myobiidae for in other groups in mites such as the Mesostigmata and the Sarcoptidae the species living on Megachiroptera are more primitive than those from Microchiroptera (Fain, 1982). One might surmise that the Myobiidae originated on some primitive Vespertilionidae and that from there had transferred to the Megachiroptera.

Microchiroptera are parasitized by 207 species and 29 subspecies of Myobiidae. They belong to 19 genera and 6 subgenera. They have been found on 9 families of bats, and are specially abundant in the Vespertilionidae. Their specificity is generally very strict, the rare exceptions to this rule result probably from contamination in museum jars. Each genus of myobiid is generally restricted to a family and often to a subfamily of hosts and many species are specialized for one host genus. Microchiropteran families are not equally infected by myobiids. The Old World Emballonuridae harbour the genus *Ugandobia* with 9 species living on *Taphozous*, *Emballonura*, *Coleura* and *Saccolaimus*. The genus *Ugandobia* also contains 2 species described from Hipposideridae and Pteropodidae, respectively, but I surmise that they were due to contamination (see above). The New World Emballonuridae are parasitized by the genus *Expletobia* with 2 species living on *Saccolaimus* and *Rhynchiscus*, respectively. The Rhinolophidae are represented by the single genus *Rhinolophus*, which harbours 2 endemic genera of myobiids, the first is *Neomyobia*, with 13 species and 3 subspecies, the second *Rhinomyobia*, with one species. Radford (1952) described a new species, *Calcaromyobia rhinolophi*, from a *Rhinolophus* but, according to Uchikawa (1985), the true host of this species was probably *Miniopterus natalensis arenarius* (Vespertilionidae, Miniopterinae). One might consider therefore that *Neomyobia* and *Rhinomyobia* are restricted to the genus *Rhinolophus*. The Hipposideridae harbour 4 genera of myobiids

totalling 26 species, i.e. *Hipposiderobia* whose 12 species live on 5 genera of Hipposideridae, each of them being restricted to 1 host genus, *Metabinuncus*, with 12 species parasitizing exclusively the genus *Hipposideros* and *Binunculoides* and *Triaenomyobia*, each with 1 species parasitizing *Hipposideros* and *Triaenops*, respectively. Two genera and 3 subgenera live on Molossidae: *Schizomyobia* with 1 species parasitizing *Tadarida* in the Old World and *Ewingana* with 2 subgenera *Doreyana* and *Mormomyobia*, totalling 17 species; among them 13 species were found on *Tadarida*, 2 on *Cheiromeles* and 2 on *Molossus*. In addition 2 species of *Ewingana* have been described from other hosts, 1 from a Nycteridae (probably a museum contamination) and another from the genus *Amorphochilus* (Furipteridae), a family close to the Molossidae. Among the species of *Ewingana*, 11 originated from the Old World and 8 from the New World. The New World families Phyllostomatidae, Desmodontidae and Mormoopidae harbour on the whole 32 species of Myobiidae belonging to 3 genera: *Eudusbabekia*, with a subgenus *Eudusbabekia* (*Synoecomomyobia*), *Phyllostomyobia* and *Ioanella*. All of these species, except 3, are restricted each to 1 host-genus. The Phyllostomatidae have been divided into 6 subfamilies. The presence of the genus *Dusbabekia* in all these families and subfamilies suggest that these higher taxa are closely related to one another. According to Uchikawa (1987) the 2 families Mormoopidae and Phyllostomatidae merely represented a single family. The genus *Phyllostomyobia* (= ? *Ioanella*), with 4 species known from Phyllostomatidae and Glossophaginae, is more primitive than *Eudusbabekia* (legs II-IV with 2 claws, instead of 1 claw in the latter). The family Vespertilionidae harbours 76 species of Myobiidae, belonging to 3 genera, i.e. *Acanthophtirius*, with 4 subgenera (*Acanthophtirius*, *Myotimyobia*, *Chiro-myobia*, *Mimetillobia*), *Pteracarus* and *Calcaromyobia*. *Acanthophtirius* and *Pteracarus* are the most primitive genera found on bats. Most of the species (47 for *Acanthophtirius* and 21 for *Pteracarus*) live on Vespertilioninae (Fain, 1982). The genus *Calcaromyobia* includes 18 species and 8 subspecies, all confined to the genus *Miniopterus* (Miniopterinae), except one species (*C. rhinolophi*) which had been described from a *Rhinolophus* but this host was very probably a contamination (see above). Finally I mention briefly 4 small families of Chiroptera, all represented by only their type genus, except one (Furipteridae) which includes 2 genera. The genus *Nycteris* (Nycteridae) harbours 1 species of the monotypic genus *Nycterimyobia*, parasitizing

several species of *Nycteris*. The genus *Mystacina*, in the Mystacinidae (= *Mystacops*, Mystacopidae) is parasitized by the monotypic and endemic genus *Mystacobia*. The genus *Amorphochilus* (Furipteridae) harbours 1 species of the genus *Ewingana*, specialized for Molossidae, which suggests close relationships between the 2 families of bats (Fain, 1982). The genus *Thyroptera* (Thyropteridae) is parasitized by 1 species of *Pteracarus*, specialized for Vespertilionidae, and 1 species of *Thyromyobia* a genus close to *Acanthophtirius*.

In rodents

Rodents are parasitized by 96 species and 7 subspecies of myobiids, included in 7 genera. Among these genera, 5 are restricted each to 1 family of rodents and 1 (*Radfordia*) has been divided into 11 subgenera (Fain & Lukoschus, 1977). More recently, 3 of these subgenera have been raised to the genus rank, i.e. *Cryptomyobia* living on Bathyergidae, *Lavoimyobia*, parasitizing Heteromyidae and *Austromyobia*, from Gerbillinae and Dendromurinae (Muridae) and Dipodidae. The 8 remaining subgenera live on Gliridae, Zapodidae and Muridae (Murinae, Cricetinae and Microtinae) (Fain, 1982). The 2 most primitive genera are *Proradfordia*, with 2 species living on Echimyidae (Neotropical Hystrichomorphes), and *Idiurobia*, more evolved and parasitic on *Idiurus* (Anomaluridae). The genus *Cryptomyobia*, living on *Cryptomys* (Bathyergidae), is monotypic and more evolved than *Idiurobia*. The genus *Austromyobia* includes 10 species, of which 6 live on Gerbillinae (Muridae), 2 on Dipodidae and 2 on the genus *Dendromus* (Muridae, Dendromurinae). The presence of *Austromyobia* on Gerbillinae and Dendromurinae suggests the existence of close affinities between these 2 subfamilies. The 10 species of *Austromyobia* form a rather homogenous group intermediate in evolution between *Cryptomyobia* and *Radfordia* s.str. The subgenus *Radfordia* (*Graphiurobia*) is represented in Gliridae by 4 species and in the Zapodidae by 2 species, which suggests the existence of affinities between these families. The hypothesis is confirmed by the discovery in both families of an astigmatic genus of mite, *Gliricoptes* (Myocoptidae) which is represented by 7 species in Gliridae and by 2 species in the Zapodidae (Fain, 1974, 1975). The most evolved genera of the family Myobiidae are *Radfordia* (*Radfordia*) and *Myobia*. They live on Muridae (Murinae).

One may conclude from these observations that the concordance between the radiations of the Myobiidae and that of their rodent hosts is remark-

able (Fain, 1976a,b; Fain & Lukoschus, 1977c, 1979c).

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