SPECIFICITY, ADAPTATION AND PARALLEL HOST-PARASITE EVOLUTION IN ACARINES, ESPECIALLY MYOBIIDAE, WITH A TENTATIVE EXPLANATION FOR THE REGRESSIVE EVOLUTION CAUSED BY THE IMMUNOLOGICAL REACTIONS OF THE HOST

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INTRODUCTION

I would like to discuss here some general phenomena as they relate to parasitic life, especially in the mites of the family Myobiidae.

My paper will be divided in three parts. The first part will deal with the general phenomena of adaptation to parasitism in mites. In a second part I will deal with the specificity and parallel-evolution of mites in the family Myobiidae. The third part is a tentative explanation for regressive evolution in parasites caused by the immunological reactions of the hosts.

GENERAL PHENOMENA IN RELATION WITH PARASITISM IN MITES

Antiquity of parasitic mites

Because of the lack of fossils we cannot prove with certainty that mites are ancient parasites but there are some indirect arguments which support this statement.

One of these arguments is the multiplicity of the hosts that harbor mites and also the great variety of parasitic niches which the mites can occupy on their hosts. Many of these mites have become highly modified through evolution, some being strongly regressed while others have acquired new specialized characters.

It is reasonable to believe that the colonization of such great numbers of

host species and of parasitic niches, as well as the important modifications observed in these mites, are the result of a long evolution. This suggests that the parasitism is a very old one.

Another argument of the antiquity of parasitic mites is the high specificity that many of them exhibit toward a particular groups of hosts. Specificity indicates that the mite and its host have lived in close relationship for a long time which in turn indicates that these mites are ancient parasites.

Finally, the study of evolution of both host and parasite has revealed that the parasites in some groups are almost as old as their hosts. This is particularly clear in the Sarcoptidae and Gastronyssidae living on bats (Fain, 1976, 1977). These two families parasitize both Mega- and Microchiroptera, however, the genera that infest the first group are more primitive than those living on the second group of bats. This suggests that the relationship started at a very early time, apparently before these hosts began to divide into Mega- and Microchiroptera. Similar observations have been made with the Mesostigmata living on bats. Rudnick (1960) has shown that the most primitive genera of Spinturnicidae live only on Megachiroptera, while the most evolved genera are found on Microchiroptera. According to Radovsky (1967) the Macronyssidae which parasitize Rhinolophidae, have been derived from the more primitive Laelapidae living on Pteropidae.

Specificity of the Parasitic Mites

There is a close correlation between permanency of a parasite and its specificity. The mites that remain on their host during all stages of their development are more specific than those that leave their hosts occasionally, e.g. for oviposition. In that respect the fur mites, such as the Myobiidae and the Listrophoroidea, are particularly specific. The pilicolous specialisation has produced a strong specificity not only in mites but also in some insects, as lice, which are both permanent and highly specific. On the contrary, in the semi-permanent parasites such as ticks and many ectoparasitic Mesostigmata, specificity is generally low.

Origin of the Parasitism in Mites:
Preadaptation to Parasitism in Pyroglyphidae.

It seems highly probable that parasitism has started in the nest and that it was first occasional and temporary. Later the parasite became more and more adapted to the parasitic life at a point where a free-living existence was no longer possible (Fain, 1963).

The mites of the family Pyroglyphidae provide a good example of such adaptation. This family contains at present 14 genera and 35 species. Most of these species live in nest of birds or mammals, a few species live in other habitats, mainly in house dust. These mites occupy an intermediate position between free-living and parasitic manner of life. Ecologically the

Pyroglyphidae are still free-living mites. However, from the morphological point of view they present all the characters of the parasitic Psoroptidia. The genital suckers are vestigial. The tarsal claws are vestigial or absent and are replaced by well-formed suckers. Further, the chaetotaxy is strongly reduced and they possess the same pattern on the body and legs, as do those in the genus *Psoroptes*. I have postulated (Fain, 1963, p. 47) that all the parasitic Psoroptidia of mammals and all the parasitic Analgoidea of birds, could have been derived from these nidicolous Pyroglyphidae. It seems that in this group of mites the regressive evolution toward parasitism has preceeded the invasion of the host as if there were a preadaptation. It has, probably, been induced by the repeated contacts between host and mite which have elicited the same reactions as true parasitism.

Morphological Adaptations to Parasitism

I have noted previously (Fain, 1969) that in the process of adapting to parasitism two different kinds of phenomena, completely independent of each other, are involved: one is constructive, the other regressive. The constructive adaptations consist of the hypertrophy of existing organs or acquisition of new structures. These specialized structures are secondary adaptations towards particular conditions of the parasitic manner of life. Constructive structures are much more frequent in ectoparasites than in endoparasites and they are particularly important in mites that attach themselves permanently to the host, especially to hairs or skin.

In contrast to constructive adaptations, one observes degenerative or regressive phenomena. These are characterized by the progressive disappearance of most of the external structures such as the shields, the claws, the chaetotaxy etc. . . . Some organs may completely disappear during this process of regression. This type of regression is particularly evident and important in the endoparasites.

The cause or mechanism for this regressive evolution in parasites is unknown. I have suggested that the immunological reactions on the part of the host probably play an important role in this type of evolution (Fain, 1977).

Correlation Between Evolution of Host and Parasite

The hypothesis that evolution of host and parasite occurs in a parallel direction was formulatd for the first time by Fahrenholz (1913).

Parallel-evolution can happen only when the association between host and parasite has lasted for a long time, which means in ancient parasites. A consequence of this rule is that the primitive hosts harbor more primitive parasites than evolved hosts (Szidat's rule, 1956).

The study of many parasitic groups has substantiated this hypothesis.

SPECIFICITY AND PARALLEL-EVOLUTION
HOST-PARASITE IN THE MYOBIIDAE

This family is specially interesting in the study of specificity and parallel-evolution of the host and its parasites. It is composed of about 300 species which parasitize Marsupials, Insectivores, Bats and Rodents.

Specificity Of Myobiidae

The Myobiidae are fur-mites and permanent parasites. They exhibit a high degree of specificity. Except in a few cases each genus of myobid parasitizes only one family and in some cases one subfamily of hosts. The specificity is also very strict at the species level. In most instances each species of Myobiidae is confined to a single host genus.

Correlation Between The Evolution Of The Myobiidae And Of Their Hosts

The Myobiidae are not only very specific but some arguments tend to prove that they are very old parasites. One may therefore infer that hosts and parasites have evolved along parallel lines over a long period. A careful study of all the group has shown that parallel-evolution is generally well marked in all the host orders except in some families or subfamilies of Insectivora or Bats. For example the Myobiidae living on Tenrecidae and Macroscelididae are distinctly more evolved than all the genera (except *Blarinobia*) living on Soricidae and Talpidae. A similar situation exists in the Chiroptera where it is not the Megachiroptera which harbor the most primitive genera of Myobiidae (e.g. *Acanthrophthirius*) but some fo the Microchiroptera, particularly the Vespertilionidae. Similar observations have been made with other families of fur-mites parasitic on bats such the Chirodiscidae (Astigmata) (Fain, 1976). These exceptions indicate that at least some families living on bats have arisen from the Microchiroptera, and from there have passed to the Megachiroptera.

It must be emphasized that the reverse situation, e.g. the presence of a primitive myobiid on an evolved host, has never been observed. This tends to confirm the concept that a primitive parasite is less capable of adapting to a new host, especially an evolved host, than is an evolved parasite.

As we have noted above, in other groups of bat parasites, such as the Sarcoptidae, Gastronyssidae, Laelapidae and Spinturnicidae, these discrepancies are not observed and in these groups the most primitive genera are living on Megachiroptera.

Evaluation Of The Primitivity In The Myobiidae

It is very difficult to decide which are the most reliable characters in the evaluation of primitivity or evolution in parasitic mites. These characters vary according to the group of parasites.

In the Myobiidae the best character for that purpose is the structure of leg I. This organ is very important in these mites for it is utilized for the attachment to the hosts. Using this character it is possible to distinguish 3 main groups in the Myobiidae. In the first group, the least evolved, leg I is well developed with all the segments distinct and bearing one pair of claws. This group includes all the genera and species known from the Marsupials and the most primitive genus known in the Insectivores. In the second group, the apical segments of leg I are reduced and tarsus and tibia I are more or less completely fused. The apical claws may be present or not. This group is more evolved than the preceeding one. It includes all the genera and species living on Insectivora, except one genus which belongs to group I, and all the genera and species living on Chiroptera. In the third group leg I is strongly reduced and the 3 apical segments are fused. The claws are always lacking. This group is specialized for Rodentia (Fain, 1975).

Within these 3 main groups of Myobiidae one can distinguish secondary groups according to the degree of reduction of the claws or of the chaetotaxy (Fain, 1974; Fain and Lukoschus, 1977).

REGRESSIVE EVOLUTION OF METAZOAN PARASITES EXPLAINED BY THE IMMUNOLOGICAL REACTIONS OF THEIR HOSTS

Complication of structures is a general trend in the evolution of animals. In the parasitic acarines, and this is also true for other parasitic arthropods and worms, this rule is not represented, and evolution at least of the external structures, is always of the regressive type. Constructive structures in parasites, when they exist, are confined to the production of some specialized characters required for adaptation to a particular function, essentially attachment to the host (e.g. the philicolous insects (lice) or the fur-mites (listrophoroids and myobiids) (Fain, 1969). They are nothing else than adaptive characters without phylogenetic significance.

I have observed that in the same evolutionary line, the endoparasitic mites are always more regressed than the ectoparasitic species, their probable ancestors, and that the latter in turn are more regressed than the free-living ones (Fain, 1969).

The family Rhinonyssidae (Mesostigmata) constitutes a good example of this rule. This group comprises several hundred species, all living in the respiratory tract of birds. In these mites most of the structures (shields, peritreme, chaetotaxy etc. . . .) are strongly reduced in comparison with those of the ectoparasitic Macronyssidae, their probable ancestors. A similar situation exists in another family of nasal mites of birds, the Turbinoptidae which is much more regressed than the ectoparasitic Epidermoptidae from which they probably derive.

It seems that endoparasitism creates special conditions which accelerate the

process of evolution. A comparable condition exists in some parasitic worms, especially nematodes. In this group the filariids living in intimate contact with the internal tissues are more regressed than the intestinal worms which are separated from the host by the intestinal barrier.

Another important feature in the evolution of parasitic mites, and specially for the Myobiidae, is the fact that regression is more marked in species that parasitize evolved hosts than in those (of the same mite genus) which live on more primitive hosts. Moreover there is generally a good correlation between the importance of the regression in the parasite and the degree of evolution of the host. The host and its parasite follow a parallel evolution, although they go in opposite directions. I have already given examples of such parallel-evolution when I have dealt with the myobiids that live on rodents (Fain, 1975; Fain and Lukoschus, 1977).

How can we explain that in species belonging to the same evolutionary line the endoparasites are more regressed than the ectoparasites, and that on the other hand the species living on evolved hosts are more regressed than those parasitizing more primitive hosts?

I think that this paradoxical situation is a result of the immunological reactions of the host against the parasite. The existence of such reactions has already been demonstrated for numerous parasites. In scabies produced by *Sarcotptes scabiei,* allergy not only produces pruritis and scratching whcih eliminates a number of mites but probably also destroys some of the parasites in the skin. That immunological factors play a role in the limitation of the *Sarcoptes* population is proved by the fact that under immunosuppressive therapy there is an unrestricted multiplication of the mites that leads to Norwegian scabies (Fain, 1978). Some helminths are able to elude the reaction of the host which tends to reject them. This is the case for *Schistosoma* spp. which can conceal themselves by coating their body with antigens of the host which are devoid of antigenic action for the latter.

We may surmize that the regression that we observe in the external organs of the parasitic mites is a response of the parasite to the immunological reactions of the part of the host which tends to reject it. When structures of the parasite are reduced, its contact with the host is lessened and so it becomes less antigenic and better tolerated. This reduction of the structures is, of course, not actively produced by the parasite but is a result of a strong selection pressure exerted on the parasite by the host.

The greater regression observed in endoparasites compared with the ectoparasites, could be explained by the fact that the former are in more intimate contact with the tissues of the host and are therefore more antigenic than the latter. On the other hand the higher degree of regression of the parasites living on evolved hosts is probably related to the greater complexity and effectiveness of the immunological system in the latter.

An argument in favor of this concept is the fact, already mentioned above, that some evolved species of myobiids are found on primitive hosts; but the opposite is not true, that means the primitive myobiids have never been en-

countered on evolved hosts. This suggests that an evolved parasite is better able to elude being rejected by the host than is a primitive parasite especially when the host is an evolved one.

SUMMARY

The general phenomenon in relation with the adaptation to parasitism are discussed. Several indirect arguments indicate that mites are ancient parasites. Specificity is more marked in permanent parasites especially pilicolous parasites such as Myobiidae. Parasitism probably started in the nests of mammals or birds. The existence of preadaptative characters in Pyroglyphidae supports the statement that these mites are the ancestors of parasitic Psoroptidia in mammals and Analgoidea in birds. Adaptation to parasitism in mites involves both constructive and regressive phemonena. Constructive characters are nothing else than specialization toward a special function especially the fixation to the host. Regressive characters are directly related to evolution.

Complication of structures is a general trend in evolution of animals. On the contrary, in parasites evolution is always of the regressive type. The author surmises that this paradoxical situation is related to the immunological reactions of the part of the host which tends to reject the parasite. The reduction of the structures in the parasite is a result of a selection pressure which tends to select always the less antigenic and therefore the most regressed phenotype.

Specificity and parallel-evolution is specially well marked in Myobiidae. The most reliable character for evaluating evolution in Myobiidae is the structure of leg I. According to this character one may distinguish three main groups. In the first group, the most primitive, the leg I is normally segmented, ending into two claws. It includes all genera and species living on Marsupials and the most primitive genus parasitizing Insectivores. In the second group, more evolved, the tarsus and tibia I are reduced, are partly or completely fused, and the claws are small or absent. This group includes all genera and species living on Insectivores except one genus belonging to group I, and all genera and species living on Chiropteres. In the third group, the most evolved, the leg I is strongly reduced, the three apical segments are fused and the claws are lacking. This group is specialized for Rodents. In each group of hosts except for a few cases, there is a significant correlation between the evolution of the host and that of the mite species.

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