

*Ursicoptes americanus* Fain and Johnston

## Chapter 12

# Evolution of Astigmatid Mites on Mammals

*Alex Fain and Kerwin E. Hyland, Jr.*

Introduction	641
Parasitism in the Astigmata	642
Morphological Adaptation to Parasitism	642
Regressive Evolution in the Parasitic Mites	642
Biological Adaptations of Mites to Parasitism	643
Parasitic Astigmatic Mites	643
Family Listrophoridae	643
Family Chirodiscidae	645
Family Myocoptidae	646
Family Atopomelidae	646
Family Psoroptidae	646
Family Sarcoptidae	648
Family Teinocoptidae	648
Family Lemurnyssidae	648
Family Rhyncoptidae	651
Family Audycoptidae	651
Family Gastronyssidae	651
Families Acaridae and Glycyphagidae	651
Family Pyroglyphidae	652
Conclusions and Summary	653
References	656

## INTRODUCTION

During the Fifth International Congress of Acarology a symposium was held which dealt with the specificity, adaptation, and parallel evolution of hosts and their parasitic acarines. It was shown that in some families of

mites, such as the Myobiidae, specificity and parallel evolution are well marked and can be used to evaluate the degree of primitiveness of the hosts as well as the relationships existing between certain hosts or groups of hosts (Fain 1979b).

The study of evolution of both host and parasite has revealed that some groups of parasitic mites are almost as old as their hosts (Fain 1976a, 1977a). Specificity is more marked in permanent parasites than in temporary ones. The pilicolous specialization has produced a particularly strong specificity not only in mites (e.g., Myobiidae and Listrophoroidea) but also in some insects such as the lice.

It seems probable that many parasitic mites have been derived from species living in the nests of birds or mammals. This appears particularly true for some parasitic Astigmata such as the Psoroptoidea which live on mammals and the Analgoidea on birds, both of whose ancestors were probably the nidicolous Pyroglyphidae living in contact with these animals. As a matter of fact, members of this family of mites are morphologically closer to these parasitic groups of acarines than to the free-living Astigmata of the family Acaridae. In the Pyroglyphidae the regressive evolution seems to have preceded the infestation of the host. We have called this phenomenon *preadaptation* (Fain 1979b).

## PARASITISM IN THE ASTIGMATA

### Morphological Adaptation to Parasitism

In the adaptation to parasitism two different kinds of phenomena are involved which are independent of each other: one is constructive, the other is regressive (Fain 1969). The constructive adaptations involve the hypertrophy of existing organs and are adaptations toward particular conditions of the parasitic way of life. They occur more frequently in ectoparasites than in endoparasites and are especially important in mites that attach themselves to the hair or the skin. These phenomena are secondary adaptations or specializations and not directly related to the phylogeny of the animal.

In contrast, regressive phenomena are characterized by the progressive disappearance of external structures such as tarsal claws, sclerotized plates, and setae. The regression is particularly well marked in the endoparasites, and as a rule it is more important in parasites living on more highly evolved hosts than in those parasitizing more primitive animals. This kind of evolution is directly related to the phylogeny of the parasite.

### Regressive Evolution in the Parasitic Mites

It is well known that the general trend in the evolution of animals is toward complication or complexity of structures. In the parasitic mites, however,

this rule is not respected, and their evolution is fundamentally of the regressive type. Generally 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.

Fain (1979b) surmised that regressive evolution is related to the immunological reactions of that part of the host that tends to kill and reject the parasite. To escape from this rejection the mite always tends to select the less antigenic and therefore the most regressed phenotype.

### Biological Adaptations of Mites to Parasitism

Parasitic life usually produces an acceleration of the postembryonic development. Generally the free-living and the ectoparasitic mites are oviparous. In the true endoparasites ovoviviparity or viviparity is the rule. The remainder of the developmental cycle is also accelerated. Some or all of the nymphal stages may disappear in the endoparasitic forms. It is to be noted, however, that acceleration of the cycle may also be observed in some highly adapted ectoparasites such as the larval Trombiculidae or the nidicolous Hypoderidae, whose deutonymphs are tissue parasites of birds or mammals.

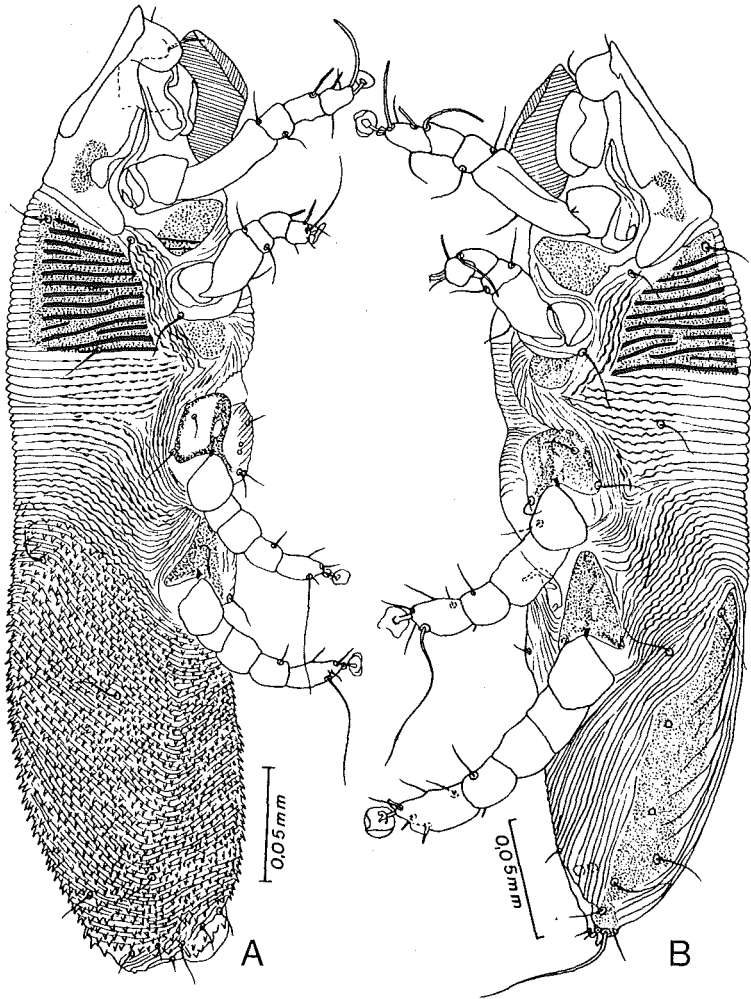
The ectoparasitic Astigmata are generally oviparous. Their life cycles may be summarized as follows: egg, prelarva, protonymph, tritonymph, and adult. The prelarva is only represented by an ecdysial organ composed of two small sclerotized conical structures situated on a transparent membrane (Fain 1977b). This organ is also present in the free-living Astigmata: Acaridae, Glycyphagidae, and Pyroglyphidae (Fain and Herin 1979). In the endoparasitic Astigmata the prelarva is absent and viviparity is the rule. This is the case in the Gastronyssidae living in the respiratory tract or in the stomach of bats. In *Sarcoptes scabiei* (Linnaeus), which is not a true endoparasite because it lives in the external noncellular layer of the epidermis, the prelarva is absent.

### PARASITIC ASTIGMATIC MITES

We wish to consider here the more important families of Astigmata parasitic on mammals.

#### Family Listrophoridae

Listrophorids are fur mites that are permanently attached to the bases of hairs during all stages of their development. The organ of attachment consists of two striated chitinous membranes situated in the anterior region of the sternum (Fig. 12.1). These mites probably feed on fatty substances produced by the hair follicles. Their life cycle consists of egg, protonymph, tritonymph, and adults (Fain 1971, 1973; Fain and Hyland 1974).



**Figure 12.1** *Listrophorus phenacomys* Fain and Hyland (lateral view). (A) Female, (B) male. (From Fain and Hyland 1974. *Bull. Inst. R. Sci. Nat. Belg.* 50:1–69. By permission of the Royal Institute of Natural Sciences of Belgium.)

The host specificity at the species level is generally strict. The same genus may be present in two or three families of the same order of hosts or more rarely in two different orders of hosts.

In the genus *Afrolistrophorus* the dorsum bears a large postscapular median shield which indicates that this genus is primitive. It consists of twelve species on Afrotropical rodents, eight species on Oriental rodents, one species on a European rodent, one species on *Mus musculus*, one species on a rodent of Patagonia, and one species on the marsupial, *Lesloros inca*.

The genus *Geomylichus* is also primitive but more specialized than *Af-*

*rolistrophorus*. It contains 13 species all confined to the New World of which eight live on Geomyoidea, four on Cricetidae (Hesperomyinae), and one on the rabbit, but this was probably accidental (Fain et al. 1978).

The genus *Prolistrophorus* has a postscapular shield which has partially disappeared. It is therefore more regressed and thus more evolved than the preceding genera. It contains 12 species living on American Cricetidae or on Echymyidae.

In the genus *Listrophorus* the postscapular shield is divided into two dorsolateral shields, which indicates that it is more regressed and more evolved than *Prolistrophorus*. The genus *Listrophorus* contains 13 species in North America which live mostly on Microtidae. In Europe it is represented by nine species four of which are also represented in North America. All these species live on Microtidae. This taxon is absent in the Afrotropical and Oriental regions as well as in Madagascar and Australia. Six other genera are found in the rodent families Aplodontidae, Cricetidae, Spalacidae, and Sciuridae.

The Insectivora are parasitized by 11 species belonging to four genera (*Asiochirus*, *Olistrophorus*, *Dubininetta*, and *Echinosorella*). All of these species are endemic on Insectivora except one which lives on a rodent. In the Lagomorpha (family Leporidae) there is only one endemic genus, *Leporacarus*, which has three species. In the Carnivora there are four genera represented by 10 species. In three of these genera (*Lynxacarus*, *Lutracarus*, and *Hemigalichus*) the postscapular shield is well developed, which suggests a primitive condition.

*Lynxacarus* contains five species living on Carnivora and four species living on other mammals (one on a rodent, and three on *Tupaia* spp.). *Lutracarus* is monotypic and is specialized for *Lutra canadensis* (Schreber). It is more evolved than *Lynxacarus*. *Hemigalichus* is also monotypic and lives on an Asiatic carnivore of the genus *Hemigalus*.

The fourth genus, *Carnilistrophorus*, is completely devoid of a postscapular shield and is therefore the most evolved of the entire family. It contains five species, of which three live on Afrotropical Carnivora, one on Macroscelididae, and one on the genus *Myospalax*.

The family Sciuridae is host to four genera (*Sciurochirus*, *Metalistrophorus*, *Pteromychirus*, and *Aeromychirus*) made up of 10 species. All of these species are highly specialized and are restricted to these rodents.

## Family Chirodiscidae

The family Chirodiscidae is divided into four subfamilies of which the most important is the subfamily Labidocarpinae. It contains 19 genera and 147 species. Sixteen of these genera (with 128 species) are found on bats; the others are specialized for other mammals [e.g., *Soricilichus*, *Schizocarpus*, and *Lutrilichus* (see list of genera in Appendix A)].

All of these species are compressed laterally and attach to the hair of

their hosts by means of legs I and II which are strongly modified and bear large striated chitinous membranes.

The postembryonic development in the Labidocarpinae from bats is very peculiar. There are two morphologically distinct lines: one for the female and one for the male. The larva, protonymph, and tritonymph of the female line are modified in that they bear copulatory lobes. In the male line all the stages are normal and lack the copulatory lobes (Fain 1971).

### Family Myocoptidae

The family Myocoptidae consists of 50 species grouped in six genera, of which four are endemic for rodents, one for insectivores, and one for marsupials (Fain 1970; Fain et al. 1970). These mites attach to the hair of their hosts by means of their posterior legs (legs III and IV in female and leg III in male) which are strongly modified into clasper organs. Development is the same as for the Listrophoridae. This family is generally cosmopolitan, but so far it has not been recorded from Madagascar or Australia.

### Family Atopomelidae

The Atopomelidae is a large family made up of 45 genera and 351 species. The great majority of these species are found only in tropical or subtropical regions. Most of the genera are endemic to a particular family of hosts. Among them, 24 are endemic to marsupials (six genera on American and 18 on Australian marsupials). The Australian marsupials contain genera and species different from those found on American marsupials. However, the genus *Didelphoecius* is widespread in American Didelphidae and is very close to *Dasyurochirus* living in Australian Dasyuridae, suggesting that the hosts are also close to each other.

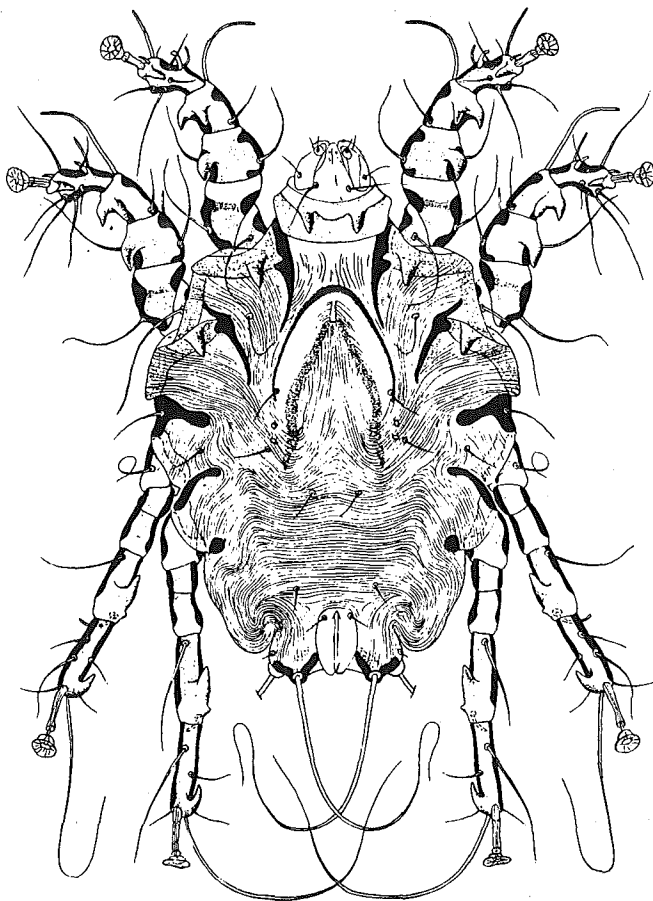
These mites also infest certain primitive Neotropical mammals of the families Caviidae, Echimyidae, Capromyidae, and Solenodontidae. They are also found on Old World mammals such as Talpidae, Soricidae, Erinaceidae, and Tenrecidae; as well as on rodents such as Nesomyidae and Bathyergidae, or on primates like Lemuridae (Fain 1972, 1976).

The postembryonic development has been described for *Chirodiscoides caviae* Hirst. It resembles that of the Labidocarpinae, with two morphologically different lines of immatures, a male and a female line (Fain 1979a). Host specificity is generally well marked, but less so than in the Myobiidae.

### Family Psoroptidae

The family Psoroptidae is economically very important because it contains several species producing mange in various domestic animals, especially in cattle. It is divided into nine subfamilies (see Appendix A).

The subfamily Psoroptinae contains all of the species parasitic on domestic animals. The life cycles of both *Psoroptes* and *Chorioptes* have been



**Figure 12.2** *Gaudalgies caparti* Fain; female (ventral view). (From Fain 1963, *Bull. Inst. R. Sci. Nat. Belg.* 39:1–125. By permission of the Royal Institute of Natural Sciences of Belgium.)

elucidated and found to be similar to those of the Labidocarpinae and the Atopomelidae (Fain 1975). There are two different lines of development, one female, the other male. The protonymph and tritonymph of the female line have copulatory lobes, whereas the nymphs in the male line are devoid of these lobes (Sweetman 1958; Fain 1964b).

The Psoroptidae are skin mites. They are characterized by the presence of an apical recurved, conical process on the anterior legs and sometimes on the posterior legs as well (Fig. 12.2). Their bodies are flattened dorso-ventrally, and in the most primitive genera the idiosoma and the legs bear retrose processes serving to attach them to the host skin. These processes for attachment are lacking in the Psoroptinae. In most of the genera, legs IV and sometimes also legs III are reduced, sometimes very strongly so. The Psoroptinae live on the surface of the skin, generally at the base of thick crusts produced by the host. They parasitize four orders of hosts. All

the other subfamilies are peculiar to one order of host except for the Psoralginae which are found on Edentata and on Australian Marsupialia (Vombatidae) (Fain 1963, 1965b) (see list of genera in Appendix A).

### Family Sarcoptidae

The family Sarcoptidae contains several genera carrying important agents of scabies which affect both man and animals. The family has been divided into four subfamilies, the most important being the subfamily Sarcoptinae which contains six genera: *Sarcoptes*, *Prosarcoptes*, *Cosarcoptes*, *Pithesarcoptes*, *Trixacarus*, and *Tychosarcoptes*.

It has been suggested that the genus *Sarcoptes* contains only one species, *S. scabiei*, and that all of the 30 other species described in this genus are synonymous with the latter. All of these "species" are based on variable morphological characters without any taxonomic value. *Sarcoptes scabiei* is a very variable species, and it possesses a mixture of both stable and variable morphological characters (Fig. 12.3).

The great variability seen in *S. scabiei* (Linnaeus) suggests that this species is not completely adapted to any of the present hosts but remains in a continuous process of adaptation in different hosts. The cause of this instability is probably related to the large number and variety of hosts that the mite infests. This mite produces scabies in more than 40 different hosts belonging to seven orders of mammals. The variability of this species is probably the result of the continuous interbreeding of the strains living on man and animals (Fain 1968, 1978). The development of *S. scabiei* comprises the following stages: egg, larva, protonymph, tritonymph, and adults.

The family Sarcoptidae is distinguished from the Psoroptidae by the absence of an apical process on the tarsi. This process is replaced by several short spines (Fig. 12.4) which allow the mite to form a tunnel in the corneous layers of the skin of the hosts. They produce deeper lesions than the Psoroptidae and are often more difficult to find.

Other genera of Sarcoptidae, such as *Notoedres* and *Trixacarus*, contain species that cause mange in domestic animals.

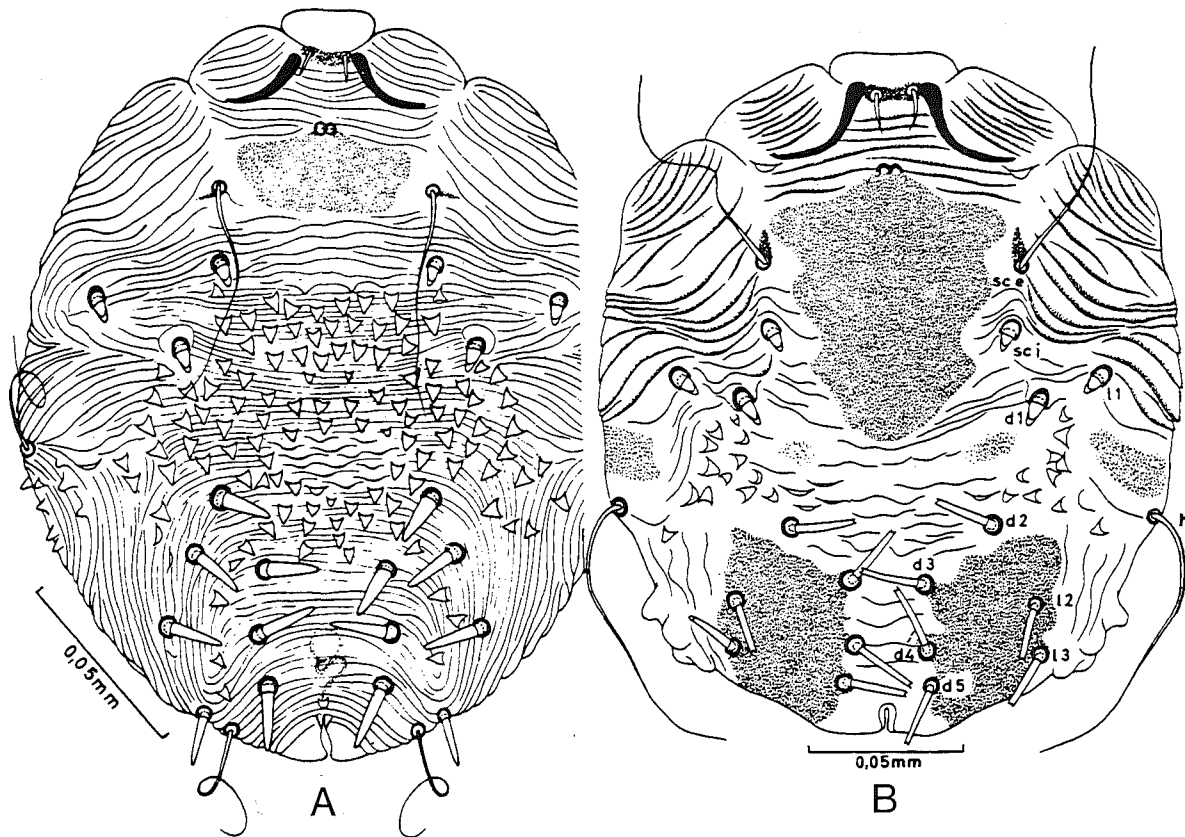
### Family Teinocoptidae

This family contains two genera and 17 species, all parasitic on bats. They are regressed, and in the females leg IV is either strongly reduced (*Teinocoptes*) or absent (*Chirobia*) (Fain 1959).

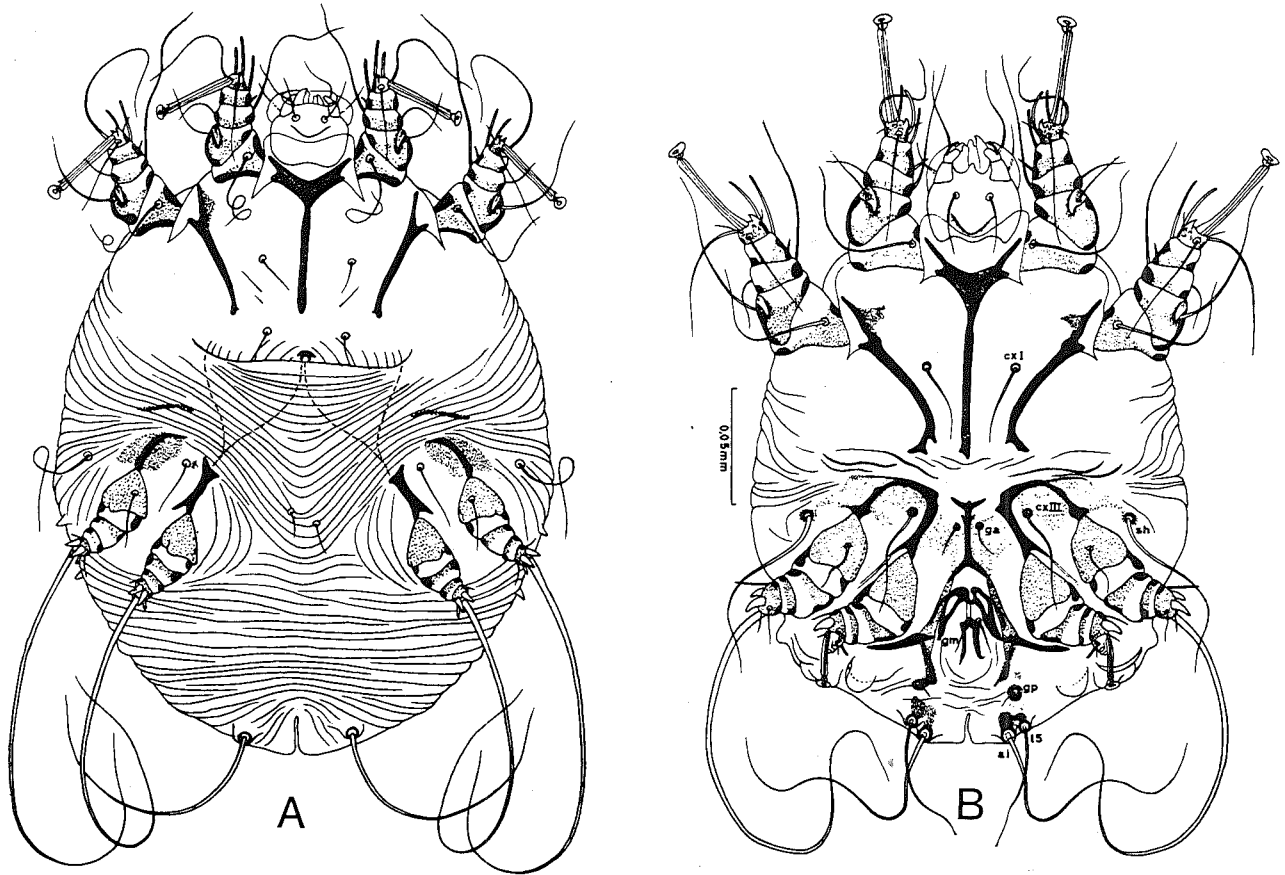
### Family Lemurnyssidae

The family consists of two genera. The monotypic genus *Lemurnyssus* lives in the nasal cavity of *Galago senegalensis* (Galagidae) in Africa; the genus *Mortelmansia*, which has three species, lives in the same habitat in South





**Figure 12.3** *Sarcoptes scabiei* (Linnaeus) (dorsal view). (A) Female, (B) male. (From Fain 1968. *Acta Zool. Pathol. Antverpiensia* 47:1-96. By permission of the Konink. Maats. v. Dierk. v. Antwerp.)



**Figure 12.4** *Sarcoptes scabiei* (Linnaeus) (ventral view). (A) Female, (B) male. (From Fain 1968. *Acta Zool. Pathol. Antverpiensia* 47:1-96. By permission of the Konink. Maats. v. Dierk. v. Antwerp.)

American monkeys. The presence of very closely related mites in both Afrotropical galagids and Neotropical monkeys suggests the existence of some relationship between these primates (Fain 1964a).

### Family Rhyncoptidae

The family Rhyncoptidae strongly modified and specialized. They are fixed in the hair follicles of their hosts by the anterior half of the body while the posterior part is free and outside the follicle. This family comprises one genus, *Rhyncoptes*, containing four species of which one lives on a rodent of the family Hystricidae in South Africa, two other species on Neotropical monkeys, and one species on an Afrotropical monkey of the genus *Cercoptes* (Fain 1965a).

### Family Audycoptidae

Mites of the family Audycoptidae are morphologically closely related to the Rhyncoptidae, but their anterior legs are considerably less well developed, and the mites are completely embedded in the hair follicle. Three genera, *Audycoptes*, *Uriscopes*, and *Saimirioptes*, have been described so far with five species distributed among the host families Cebidae, Ursidae, and Procyonidae.

### Family Gastronyssidae

The gastronyssids are divided into two subfamilies: Gastronyssinae, endemic to bats, and Yunkeracarinae, endemic to rodents (Fain 1964c, 1967a). The Gastronyssinae contains five genera (*Gastronyssus*, *Rodhainyssus*, *Opsonyssus*, *Eidolonyssus*, and *Mycteronyssus*) and 20 species. *Gastronyssus bakeri* Fain lives attached to the gastric mucosa of a fruit bat in Africa. The species of the other genera live either attached to the cornea of the eye or in the nasal cavities of bats.

The subfamily Yunkeracarinae with two genera and three species parasitizes the nasal cavities of rodents.

### Families Acaridae and Glycyphagidae

The Acaridae and Glycyphagidae are not true parasites, however, some species, mainly those of the family Acaridae, may cause contact dermatitis in man. Some species of the family Glycyphagidae produce hypopi which may attach to the hair or invade the hair follicles of their hosts, primarily rodents. Their presence may result in a pathological condition.

Most of these species feed on fungi that develop in decaying organic material. They infest the nest of insects, birds, or rodents. They are also

found in stored food (grain, cheese, dried fruit, etc.), especially when this food has been stored under poor conditions (high level of moisture) and has become moldy (Hughes 1976).

Persons who have repeated contact with foodstuff infested with these mites may develop a skin allergy known as contact dermatitis. The most important species are *Tyrophagus putrescentiae* (Shrank), which causes copra itch; *Acarus siro* Linnaeus, the agent of baker's itch and of cheese mite dermatitis; *Carpoglyphus lactis* (Linnaeus), which produces dried fruit mite dermatitis, and *Glycyphagus domesticus* (De Geer), which causes grocer's itch (Baker et al. 1956).

Some Glycyphagidae produce heteromorphic deutonymphs or hypopi which attach to the hair of mammals, mainly rodents. These hypopi are phoretic nymphs which serve for both the dispersal of the species and for its survival under adverse conditions. In some species such as *Aplodontopus sciuricola* Hyland and Fain these hypopi invade the hair follicle or the subcutaneous tissues of their hosts (mainly rodents) and may cause skin lesions (Tadkowski and Hyland 1979).

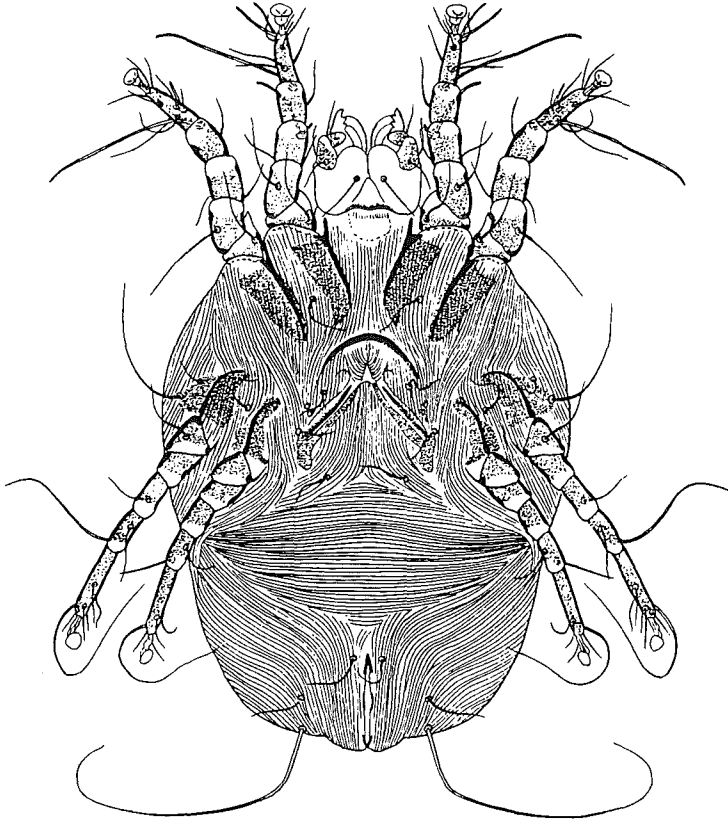
### Family Pyroglyphidae

Most of the Pyroglyphidae are free-living. They infest birds' nests and are devoid of pathological action. A few species live on the skin of birds and are true parasites. There is also a series of species that lives in house dust and is responsible for respiratory allergies, mainly bronchial asthma (Voorhorst et al. 1964; Spieksma 1967; Oshima 1967). These house-dust mites constitute a serious health problem in all countries of the world (Wharton 1976).

Thus far the Pyroglyphidae comprises 14 genera and 35 species. Most of these species live in birds' nests, one species has been found in the nest of a rodent, and 10 species are found mostly or exclusively in house dust.

The most important species in relation to house-dust asthma is *Dermatophagoides pteronyssinus* Trouessart (Figs. 12.5–12.7). It is present throughout the world, and its true habitat is the house (Fain 1966, 1967b). This mite is present in dust on the floor especially in living rooms and bedrooms. Recent studies have demonstrated that mattresses are the primary breeding grounds for this mite. It is especially abundant in wet maritime climates such as the coastal areas of England, Belgium, and the Netherlands.

Another species, frequently associated with *D. pteronyssinus* is *D. farinae* Hughes. In certain drier climates (central parts of the United States and Europe) *D. farinae* may become more abundant than *D. pteronyssinus*. Two other species also found frequently in house dust are *Euroglyphus maynei* (Cooreman) and *Hirstia domicola* Fain, Oshima, and Van Bronswyck, both of which have a more local distribution than the two preceding ones.

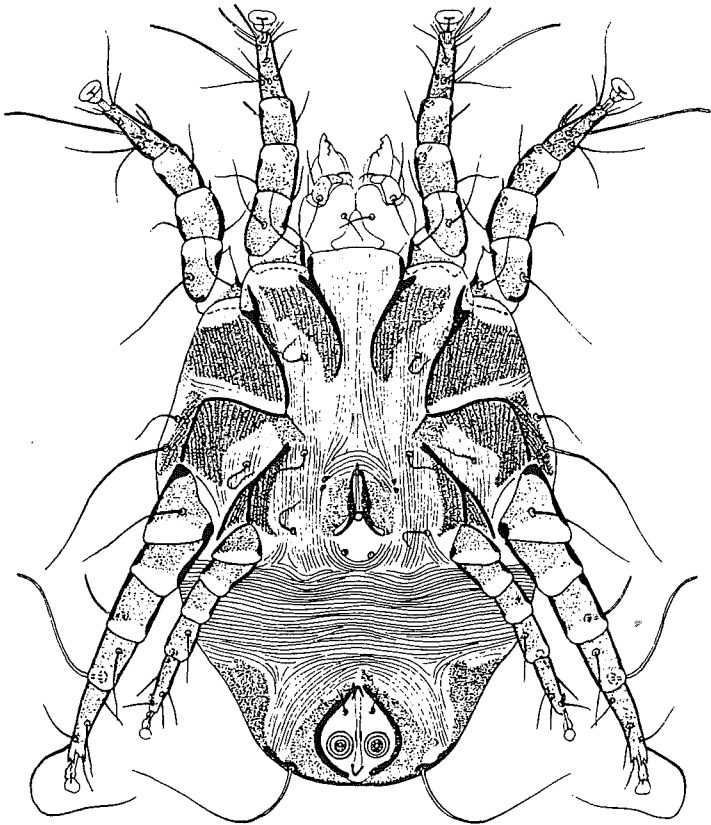


**Figure 12.5** *Dermatophagoides pteronyssinus* (Trouessart); female (ventral view). (From Fain 1966. *Acarologia* 8:302-327. By permission of the Centre National de la Recherche Scientifique.)

## CONCLUSIONS AND SUMMARY

The parallel evolution of host and parasite is well marked in many parasitic mites, especially in permanent parasites that spend their entire lives associated with the host. Specificity is closely related to the degree of permanency of the parasitism and is particularly strict in the pilicolous mites (e.g., *Myobiidae* and *Listrophoroidea*). Specificity and parallel evolution can be used to evaluate the degree of evolution of the host and the relationships existing among certain hosts.

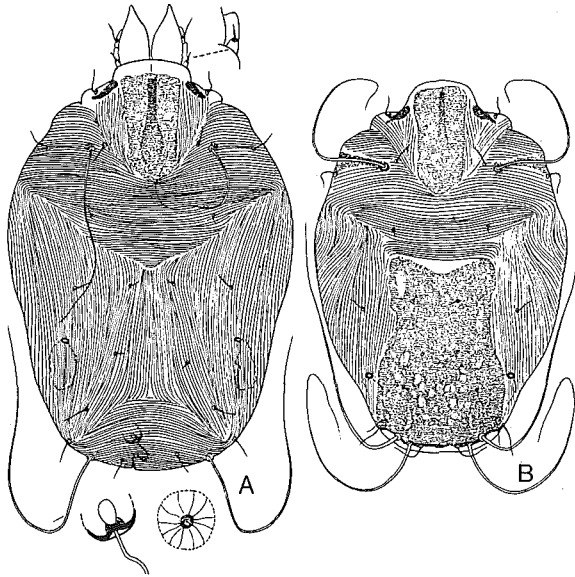
Some groups of parasitic mites are almost as old as their hosts. It appears that many groups of acarines, especially the Astigmata, originated from species living in the nests of mammals or birds. Free-living nidicolous species of the family *Pyroglyphidae* are probably the ancestors of most of the parasitic Astigmata living on both mammals and birds.



**Figure 12.6** *Dermatophagoides pteronyssinus* (Trouessart); male (ventral view). (From Fain 1966. *Acarologia* 8:302–327. By permission of the Centre National de la Recherche Scientifique.)

The adaptation of a free-living mite to a parasitic life is both morphological and biological. Two different kinds of phenomena, independent of each other, are involved in morphological adaptation: one is constructive, the other regressive. Constructive adaptation involves the hypertrophy and modification of existing organs favoring particular conditions of the parasitic life, especially the attachment to the hair or the skin of the host. This kind of adaptation represents secondary phenomena or specialization and is not directly related to the phylogeny of the parasite. Regressive adaptation is characterized by the progressive disappearance of external structures (e.g., claws, hairs, shields). Regression is particularly well marked in endoparasitic mites and as a rule is more important in parasites living on highly evolved hosts than in those living on more primitive animals. This kind of evolution is directly related to the phylogeny of the host.

The most prominent biological adaptation to parasitism is an accelera-



**Figure 12.7** *Dermatophagoides pteronyssinus* (Trouessart) (dorsal view). (A) Female, (B) male. (From Fain 1966. *Acarologia* 8:302–327. By permission of the Centre National de la Recherche Scientifique.)

tion of postembryonic development. In certain parasitic mites some or all of the nymphal stages may disappear completely. A rudimentary prelarva is present in the free-living and in most of the ectoparasitic Astigmata, but it is absent in the endoparasitic Astigmata.

Host–parasite parallel evolution is analyzed in the most important families of Astigmata parasitic on mammals. These mites belong to 15 families, 162 genera, and 849 species (through 1979).

In the Listrophoridae there is generally a good correlation between the degree of regression of the mite and the degree of evolution of the host. In the genus *Afrolistrophorus* the dorsum bears a large postscapular shield which indicates that the taxon is primitive. It contains 21 species, most of which are from Afrotropical rodents. The genus *Prolistrophorus* has a postscapular shield slightly eroded in its median part, which means it is more regressed, and hence more evolved, than *Afrolistrophorus*. It contains 12 species living on American Cricetidae or Echimyidae. In the genus *Listrophorus* the median part of the postscapular shield has completely disappeared, and there are only two lateral, but completely separated, postscapular shields. This genus, which contains 22 species living on Microtidae, is more regressed than *Prolistrophorus*. It appears from these observations that the most regressed, and hence the most evolved, genus of mites lives on the most evolved hosts (Microtidae).

Another family, Chirodiscidae, contains 147 species grouped into 19 genera. Most of these species live on bats. They are highly specialized fur

mites which have a laterally compressed body. Their postembryonic development is very unusual in that there are two morphologically different lines—one female and one male.

The largest group of fur mites (351 species and 45 genera) is the family Atopomelidae. This group is almost entirely tropical or subtropical. Most of the species infest rodents, but the family also infests marsupials, both Australian and American. All the genera found associated with marsupials are restricted to marsupials, however the genus *Didelphoecius*, which is widespread in American Didelphidae, is very close to the genus *Dasyurochirus* which lives on Australian Dasyuridae. This suggests that the hosts are also close to each other.

The Psoroptidae and Sarcoptidae are skin mites. The family Psoroptidae is large, divided into nine subfamilies each confined to one order of hosts, except the Psoralginae which is represented on American Edentata and on Australian Marsupialia. All of these mites live attached to the surface of the skin. The family Sarcoptidae contains numerous species producing mange in man and animals. It has been suggested that the genus *Sarcoptes* contains only one variable species, *S. scabiei*, which is able to parasitize man, numerous domestic mammals, and even wild mammals living in captivity.

In addition to these groups of parasitic Astigmata, there is a family of free-living mites, the Acaridae, which contains species causing contact dermatitis in man. Moreover, the deutonymphs of some Glycyphagidae may produce mange in rats. Another mite family, the Pyroglyphidae, lives in house dust and in the nests of birds and mammals. A few species are parasitic on birds, but most of them are free-living. *Dermatophagoides pteronyssinus*, a cosmopolitan species living in house dust, is the most important species of this family because it is frequently associated with allergic bronchial asthma in man.

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