7 Mesostigmatid mites as parasites of small mammals: Systematics, ecology, and the evolution of parasitic associations

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1 Introductory remarks

The Acari represent the most diverse assemblage within the Arachnida and are currently subdivided into three major lineages: Acariformes, Opilioacariformes, and Parasitiformes. This chapter focuses on the Mesostigmata, a morphologically and ecologically diverse group of parasitiform mites, many of which are parasitic on small mammals.

The majority of mesostigmatid species are found as free-living predators of other arthropods and nematodes in a wide variety of habitats. Only a small proportion of total species diversity is parasitic and all confirmed vertebrates parasites are currently placed within the cohort Dermanyssina. More specifically, most of the parasite diversity is found in the superfamily Dermanyssoidea, which will be the primary focus of this chapter. The diversity of ecological strategies found in the Dermanyssoidea is great and includes everything from predatory to endoparasitic mites. This chapter aims to introduce the reader to the systematics, biology, and ecological strategies of dermanyssines associated with small mammals and will examine the evolution of parasitism within this amazingly diverse group of mites.

2 Taxonomy, phylogeny, and distribution

Over the past few decades, mesostigmatid classification has been fairly stable. For a summary of mesostigmatid classification see Krantz (1978; note that Krantz uses the term Gamasida in place of Mesostigmata). The Mesostigmata is a suborder within the Parasitiformes, one of three currently recognized acarine orders. Within the Mesostigmata almost all vertebrate parasites are found in the superfamily Dermanyssoidea with a couple exceptions.

Unlike Mesostigmata, the taxonomy of the Dermanyssoidea has been in a perpetual state of flux since the late 19th century. Many classification schemes (Berlese 1892, 1913; Vitzthum 1943; Zumpt and Patterson 1951; Baker and Wharton 1952; Evans and Till 1966, 1979; Radovsky 1967; Karg 1971; Krantz 1978; Johnston 1982), often contradictory, have been proposed by different researchers, typically based more upon ecology and host associations than any character evidence. Because dermanyssoids exhibit such wide ecological amplitude and display high levels of morphological variability, it has been difficult to determine phylogeny based upon morphological characters alone. The remaining discussion follows the classification scheme of Johnston (1982) with modifications based on Radovsky (1985) and recent molecular evidence by Dowling (2005).

Most classifications have placed all parasitic mesostigmatid groups in the Dermanyssoidea, primarily based on their parasitic lifestyles, which has often led to highly modified morphological features. Until recently, no modern phylogenetic methods had been used to test the monophyly of the Dermanyssoidea or the phylogenetic relationships within the entire subfamily. Systematics of the group has been based entirely on morphological characteristics and ecological associations. Casanueva (1993) and Strong (1995) conducted phylogenetic studies, but both focused on arthropod associated Laelapidae, effectively ignoring the evolution of vertebrate parasitism. Morphology presents a problem to phylogenetic reconstruction because of the amount of convergence due to multiple independent evolutions of a parasitic lifestyle. Dowling (2005) was the first to use molecular sequence data to test dermanyssoid relationships across the superfamily and within the Dermanyssina. Results suggest that the two obligate bat parasite families, Spinturnicidae and Spelaeorhynchidae, do not belong within the Dermanyssoidea, but do remain within the Dermanyssina. Further discussions of dermanyssoid systematics and evolution will exclude these two families, but parasitic adaptations in each family will be discussed later as they are both important bat parasites. The families Laelapidae, Haemogamasidae, Hirstionyssidae, Macronyssidae, Dermanyssidae, Halarachnidae, Dasyponyssidae, Manitherionyssidae, and Hystrichonyssidae all contain species that are parasitic on small mammals. Specific adaptations to parasitism in each group will be discussed later.

3 Morphology and development

The primitive dermanyssoid varies little from the typical Mesostigmata form. These mites are predatory in nature and found in a wide range of habitats, primarily soil and decomposing leaf litter. They are typically 0.2-2.0 mm in length with long legs for active locomotion. The first pair of legs is usually elongated, slender, and used as sensory structures and all four tarsi contain paired claws and an ambulacral sucker. The gnathosoma contains a mouth, palps, and chelicerae. The palps are paired leg-like structures used primarily as sensory apparatus and sometimes to manipulate food items. The chelicerae are a pair of retractable structures equipped with an anterior claw comprised of a fixed dorsal chela and a moveable ventral chela. Both chelae are often equipped with one or more teeth and the chelicerae are used for capturing, tearing, and puncturing prey. Like most arachnids, mesostigmatid mites are typically fluid feeders and the chelicerae macerate the food item in preparation for feeding. The gnathosoma and legs are attached to the opithosoma, which is unsegmented and contains a number of sclerotized shields for protection and as rigid points for muscle attachment. The remainder of the opithosoma is typically comprised of soft, expandable cuticle. Genital openings in adults are positioned ventrally, in a mid to anterior position and the anus is positioned ventral and posterior. Respiration occurs through a pair of spiracular openings (stigmata) located ventrally, and usually between coxae III and IV, hence the group name Mesostigmata.

Development in the Mesostigmata includes an egg, larva, protonymph, deutonymph, and adult. The larva is hexapod, lacking the fourth pair of legs, while the nymphal and adult stages are all octopod. Each stage has distinct setal and idiosomal shielding patterns. The larva typically is non-feeding and possesses very little, if any shielding, and reduced setation. Each successive molt increases both shielding and setation until the full complement of each is reached at the adult stage.

Morphological features and development are fairly uniform among the free-living predatory Mesostigmata and primitive Dermanyssoidea, but a high degree of variability in many features is found in taxa with parasitic and commensal associations formed with vertebrates and arthropods. Evans (1963) noted extreme variability in palpal chaetotaxy among species that have developed close associations with other animals. The chelicerae have undergone amazing modifications across the parasitic groups. Multiple groups have independently converged on slender, edentate chelicerae that function similar to stylets of blood-sucking insects. Paedomorphosis also seems to be a common occurrence among parasitic dermanyssoids, especially the endoparasitic lineages, as reflected by reductions in setal count, sclerotization, and dorsal shield shape and size. Variations in the life cycle also exist among the parasitic groups. While all stages are present, many may be suppressed and completed inside the female or passed inside the ecdysed cuticle of the preceding stage. The Macronyssidae and Halarachnidae are two groups with independent modifications to the life cycle. The Macronyssidae have a highly suppressed, non-feeding deutonymph and halarachnids are characterized by suppression of both nymphal stages. This variability in morphology and development among vertebrate associates has been one of the main confounding factors in attempts to accurately classify the Dermanyssoidea.

4 Evolution of parasitism

The ecological amplitude of dermanyssoid mites is phenomenal, and life-histories across the superfamily include free-living, soil dwelling predators, arthropod predators in vertebrate and invertebrate nests or colonies, facultative and obligatory vertebrate parasites, and respiratory and auditory endoparasites of birds, mammals, and lepidosaurs. The Dermanyssoidea provide a unique opportunity to study the evolution of parasitism because of the many intermediate forms between predators and parasites represented among extant lineages. The full range of ecological associations is even represented within single genera such as *Androlaelaps* and *Haemogamasus*, which will be discussed later. The remainder of this chapter will focus on the evolutionary transition to parasitism and the adaptations that have evolved in each of the parasitic dermanyssine families.

4.1 Transitions to parasitism: Pre-adaptation or opportunistic exposure

Two competing hypotheses prevail in describing the evolutionary transition from a predatory to parasitic lifestyle. These have been described as type A and type F routes or pathways to parasitism by Waage (1979). In Type A routes, associations with hosts preceded adaptations for parasitic feeding. It is widely agreed on that the diversity of feather mites followed this pathway, where they went from feeding on bird debris in the nest to permanently inhabiting the body of the bird (Proctor 2003). For example, Fain and Hyland (1985) suggested that parasitic psoroptoids and analgids in the acariform acarine lineage Astigmata probably arose from nidicolous Pyroglyphidae. Type F routes involved adaptations to feeding on a host that preceded the actual association, such as the stylet mouthparts of nectar feeding mosquitoes and plant feeding Hemiptera that were easily adaptable to blood-feeding (Radovsky 1985). The evolution of parasitism in dermanyssoid mites was likely a combination of the two pathways.

Mesostigmatid mites in general are very well pre-adapted to parasitism. The chelicerae, even in the most primitive free-living predatory forms, can effectively feed on secretions, scales, scabs, and even tear into the skin of young vertebrates to reach a blood meal. The chelicerae of many free-living dermanyssoids are more generalized than those of other predatory mesostigmatids, which may have provided the necessary advantage to invade the nidicolous niche. In fact, the morphological change from the general dermanyssoid type in some parasites is so subtle that without the context of a host, it would be difficult to tell that the mite was an obligate parasite (Evans 1955; Radovsky 1985). Even though this generalized cheliceral form is suitable for parasitism, slender edentate chelae specialized for piercing skin are widely found throughout the Dermanyssoidea.

A second key feature that helped lead to the radiation of parasitic types within Dermanyssoidea and not in the other mesostigmatid groups may be the utilization of an exceptional number of niches by primitive *Hypoaspis* types (Radovsky 1985). Members of the *Hypoaspis*-complex are found in soil, litter, decaying substrates, the nests of social insects, burrows and galleries of beetles, and in the nests and on the bodies of mammals and birds. Most *Hypoaspis* species studied are predators (Karg 1961; Nelzina et al. 1967) and have not been shown to have any predilection to feeding on the host, but the association as a predator in vertebrate nests has been hypothesized to be the origin of vertebrate parasitism in dermanyssoid mites (Radovsky 1969). While most Mesostigmata have characteristics suitable for parasitism, it may be that hypoaspidines were the first predators to colonize and utilize vertebrate nests and they competitively limited other predatory mites. Mesostigmatid groups, such as the Parasitidae and Ologamasidae, contain species that are obligate nest predators, but the Laelapidae are typically the most abundant and commonly encountered. Constant exposure to a potential host while occupying the nest niche may have possibly opened the door for dermanyssoid radiation into a parasitic lifestyle.

4.1.1 Androlaelaps and Haemogamasus

The transition from predator to obligate parasite is most readily observed within two genera, *Androlaelaps* and *Haemogamasus*. The laelapine lineage from *Hypoaspis* is thought to have begun with *Androlaelaps*, due to many shared morphological characters between the two genera (Radovsky 1969). *Androlaelaps* are found worldwide and exhibit varying degrees of dependence on a diversity of vertebrate hosts. Reytblat (1965) compared the feeding behavior of four species of *Androlaelaps, A. fahrenholzi, A. longipes*, *A. casalis,* and *A. semidesertus*. The degree of adaptation for parasitism was based upon reproductive success of laboratory-reared mites fed on a blood diet versus an arthropod diet as well as their ability to feed from a host. *A. longipes* and *A. casalis* had comparable numbers of offspring on blood or arthropods, but both had highest reproductive output when fed a mixed diet. *A. fahrenholzi* and *A. semidesertus* were unable to reproduce on a diet of arthropods alone, showing dependence on a host. All four possess typical *Hypoaspis*-type chelate-dentate chelicerae and readily inflicted wounds to start blood flow from suckling mice. *A. fahrenholzi* frequently feeds from preexisting wounds, dried blood, scabs, as well as on other small arthropods (Reytblat 1965; Radovsky 1985).

The genus *Haemogamasus* exhibits a range of feeding ecologies as well, from non-parasitic predators to polyphagous and facultative nidicoles to obligatory hematophages (Radovsky 1985). *Haemogamasus pontiger* is the only *Haemogamasus* often found free-living and is common in detritus on warehouse floors (Hughes 1961) and in granaries (Evans and Till 1966). Furman (1959a) found that 63% of *H. pontiger* in laboratory studies would feed from flowing blood on mice hosts, but unlike *A. fahrenholzi*, none would feed on dried blood. Hughes (1961) found that *H. pontiger* can complete its lifecycle if only supplied with wheat germ as food indicating that *H. pontiger* is a predator and saprophage with zero dependence on a host.

The *Haemogamasus reidi* group (Williams et al. 1978) includes all *Haemogamasus* that do not possess special cheliceral adaptations for skin penetration as found in the *Haemogamasus liponyssoides* group, but are obligatory nidicoles, thus excluding *H. pontiger*. Members of this group are thought to typically feed from preexisting wounds, rather than puncturing the host's skin (Furman 1959a, b, 1968; Goncharova and Buyakova 1960). *H. reidi* can complete development and reproduce on a diet entirely of blood or arthropods (Furman 1959b). *Haemogamasus clitelli* had reduced rates of reproduction when restricted to either blood or arthropod meals, and if restricted entirely to blood showed an increasing tendency to cannibalize their young (Nelzina and Danilova 1956). *Haemogamasus nidi* was able to sustain reproduction on blood, but was not able to reproduce on an all-arthropod diet. Reproduction was highest on a mixed diet. Finally, *H. citelli*, associated with ground squirrels, was found to actively engorge on newborn gophers in the nest, potentially puncturing the skin, though more likely frequently feeding from preexisting wounds (Nelzina and Danilova 1956). Feeding from the adult ground squirrels was rarely witnessed, presumably due to the thicker and tougher skin of the adult host. The *H. reidi* group is very reminiscent of the *Androlaelaps* group previously discussed in its lack of modification specific to parasitism and the varying levels of blood feeding and dependence on a host found across species.

The *liponyssoides* group consists of several species of *Haemogamasus*, all of which are obligatory hematophages. The defining characteristic of the group is highly modified, slender and edentate chelicerae used to pierce the host skin rather than tear at it (Radovsky 1985). In laboratory conditions, *H. liponyssoides* would not feed on arthropods and only reluctantly and poorly on free-flowing blood (Radovsky 1960). *H. liponyssoides* frequently fed from both adults and suckling rodents by penetrating the skin to cause blood flow. Species in the *liponyssoides* group are also able to engorge (i.e. taking in more than their weight at a single meal) more so than other *Haemogamasus*, a trait commonly found in obligate blood-feeding parasites (Radovsky 1985).

The fact that two independent genera show such a graded transition from predator to obligate parasite among species is a strong indication that the transition began with opportunistic feeding in the vertebrate nest environment. The morphological components were available, as exhibited by active blood feeding in *Androlaelaps*, and the active predation of a *Hypoaspis*-like ancestor on microarthropods in vertebrate nests, provided the opportunity for host interaction. The ability to utilize a variety of nutrients for development and reproduction, as exhibited by species of *Androlaelaps* and *Haemogamasus*, also likely played a major role in the successful colonization of parasitic niches by dermanyssoid mites.

4.2 Host associations and specializations for parasitism

The remaining families of parasites are comprised of members that are entirely parasitic and in turn show many specialized adaptations to parasitism. The remainder of this chapter will focus on the unique modifications and diversity of host associations found in each group. A table summarizing the host associations of parasitic Mesostigmata will follow this section (Table 1).

4.2.1 Laelapidae, Haemogamasidae, and Hirstionyssidae

These three families are the most commonly found dermanyssoids associated with rodents and insectivores and the Laelapidae are the most speciose group. As discussed earlier, the Laelapidae and Haemogamasidae show a graded transition from predatory to parasitic mites. For most laelapids associated with mammals it is unknown whether they are nidicolous, facultative, or obligate parasites and one suspects that parasitism has arisen in the Laelapidae multiple times. The most common genera found are *Laelaps* and *Echinolaelaps*, both laelapids and restricted to muroid rodents. *Haemogamasus* is the most common haemogamasid genus and is found on various rodent groups and insectivores. Neither group exhibits extreme modifications to parasitism, but do posses a range of cheliceral changes towards the edentate type found in many other parasitic dermanyssoid groups. The hirstionyssids however, have slender edentate chelicerae designed for piercing and are clearly parasitic. The genus *Echinonyssus* is cosmopolitan and can be found on most small mammal groups except Chiroptera.

4.2.2 Macronyssidae

Members of the Macronyssidae are obligate parasites of a wide range of hosts including bats, rodents, lizards, and birds and are cosmopolitan in distribution. Most members of this group still retain the dermanyssoid behavior of inhabiting the nest or roost and only making contact with the host when a blood meal is necessary. The Macronyssidae are characterized by an actively feeding protonymph, an inactive, non-feeding, and highly regressed deutonymph, and an actively feeding adult. This unique life-cycle modification is shared by all macronyssids and found nowhere else among the Mesostigmata, except in the Rhinonyssidae, a family of dermanyssoid avian endoparasites, clearly derived from the Macronyssidae (Dowling 2005).

Macronyssid mites are divided into two groups, the Macronyssinae and the Ornithonyssinae (Radovsky 1967, 1969), both of which have unique parasitic qualities. The Macronyssinae are primarily bat parasites, except for two genera, *Acanthonyssus* and *Argitis*, found on Neotropical rodents. Ornithonyssines have a much broader host range, including bats, rodents, lizards, snakes, and birds. Interestingly enough, although the widespread and apparent long standing association with bats, no macronyssids are found in association with any Megachiroptera.

Morphologically the two groups are easy to differentiate based upon characteristics associated with feeding. Ornithonyssines, unlike macronyssines, engorge heavily during prolonged feeding periods, resulting in bodies that are much less sclerotized and more able to greatly expand than macronyssines. Overall, dorsal and ventral shielding is reduced in ornithonyssines and although chelicerae in all macronyssids are edentate, ornithonyssine chelicerae are much further specialized for piercing skin than macronyssines.

4.2.3 Dermanyssidae

The family Dermanyssidae is primarily parasitic on birds, but contains a few species readily found on rodents. The group is recognizable by their highly specialized chelicerae. The second segment of each chelicera is elongated and the chela is small and edentate. The chelicerae apparently function as a stylet for piercing host tissue and sucking blood, much the way that blood sucking insects do (Radovsky 1969, 1985). Rodent associated dermanyssids are in the genus *Liponyssoides* and are nest inhabiting parasites that only contact the host when feeding.

4.2.4 Halarachnidae

Halarachnids are endoparasites of a wide range of mammal orders. The family can be divided into two subfamilies, the Halarachninae, which are respiratory endoparasites, and the Raillietiinae, which are auditory endoparasites. Both subfamilies share a unique developmental modification where the larva is an active, non-feeding stage responsible for transmission between hosts, followed by two suppressed, non-feeding nymphal stages. These nymphal stages are passed very quickly and oftentimes the deutonymph is passed inside the ecdysed protonymphal cuticle (Radovsky 1985). The adult is an actively feeding stage.

Only a few species of raillietines are known, all in the genus *Raillietia*, and infect the auditory passages of cattle, goats, antelope, and wombats. They are not known to typically damage the ear or negatively affect the host except in cases of very heavy infestations.

Halarachnines parasitize the respiratory tracts, mostly the nasal passages, of a wide range of mammals (Furman 1979) across a large geographic scale. The breadth of the host associations and distribution is suggestive of an ancient association with mammals and is worthy of a closer look. Based on host associations, four major groups of halarachnines exist. The first involves an infestation of pinnipeds, with the genus *Halarachne*, on phocid seals and *Orthohalarachne* on otariid seals and walruses. The second group includes two genera, *Pneumonyssus* and *Rhinophaga* that are primarily associated with Old World cercopithecid and pongid primates, but also parasitize African procaviids (Elephant shrews) and hystricids (porcupines). Domrow (1974) described *P. capricornii* from a New Guinea phalangerid that is very similar to *P. simicola* from Asian macaques, suggesting a host switch from primates to marsupials. The genus *Pneumonyssus* is the only halarachnid group found primarily in the lungs, all others typically reside in the nasal passages (except adults of *Orthohalarhne*, which are also found in the lungs of their hosts). The third group involves the genus *Zumptiella* parasitic in rodents, specifically Holarctic Sciuridae and African Pedetidae. One species has been found in an African mongoose, but whether or not it represents a natural association or a predator to prey transfer has not been determined (Furman 1979). The final genus, *Pneumonyssoides*, has a bizarre host range. Species are known only from African bush pigs and wart hogs, the domestic dog, and Neotropical primates in the family Cebidae.

The most commonly studied halarachnids are *Pneumonyssoides caninum*, found in the domestic dog, and species of *Pneumonyssus* (primarily *P. simicola*) because of their common presence in primates used for research. *Pneumonyssoides caninum* receives attention because of its presence in domesticated dogs, but rarely causes symptoms any more severe than extra mucous production (Yunker 1973) and antibody response to antigens (Gunnarsson and Zakrisson 2000). One case of *P. caninum* infection has been reported in a fox (*Vulpes vulpes*), but no other reports exist to suggest this is a typical association (Bredal et al 1997).

Unlike the rather asymptomatic *P. caninum*, the monkey lung mite, *Pneumonyssus simicola* (and other species) can cause severe pathogenecity and because the hosts are often laboratory research primates (Yunker 1973; Kim 1977, 1980; Leathers 1978), infestations garner great attention. Infestation, or pulmonary acariasis causes nodules or tubercules, each containing numerous adult mites, to form in the lungs of the host (Sundararaj et al. 1992; Hiraoka et al. 2001). Infestations can severely affect the health of the host, leading to death in the case of heavy infestations.

4.2.5 Spinturnicidae

Spinturnicid mites are more morphologically modified and adapted to an ectoparasitic lifestyle than any other mesostigmatid group. Spinturnicids are obligate blood-feeding ectoparasites of bats and are almost exclusively found on the wing and tail membranes. In some genera, such as *Periglischrus*, *Ancystropus*, and *Meristaspis*, adult females develop a greatly enlarged opithosoma and are found attached to the face, ears, and along the arm bones. Adult females of *Paraspinturnix* have only been found in the anal orifices of bats (Rudnick 1960), but all other stages of all these genera are typically found on the membranes. To facilitate a life on the wing membrane of bats, spinturnicids posses long, thick, and robust legs and large hooked tarsal claws on a comparatively small diamond shaped body. These mites can cling to the wings very effectively, but at the same time can release from the membrane and run rapidly across it. Spinturnicid mites are also nymphiparous, with the egg and larval stages passed intrauterine, which releases the most vulnerable stages (egg and larva) from pressures associated with living permanently on the wing membranes. Only the actively feeding stages are independently active on the host.

Spinturnicidae are found in association with all bat groups worldwide and Rudnick (1960) has produced the most extensive review of spinturnicid host associations and taxonomy. Based on the currently known geographic distributions and host groups, spinturnicids appear to have had a long coevolutionary history with the Chiroptera. Two genera, *Meristaspis* and *Ancystropus*, are exclusively found on Megachiroptera, while all other species are found only on Microchiroptera. Most genera are specific to the family of bats they parasitize. For example, *Eyndhovenia* and *Paraperiglischrus* are only associated with rhinolophid bats, *Periglischrus* only on phyllostomids, *Spinturnix* on natalids and vespertilionids, and *Paraspinturnix* only with vespertilionid bats.

4.2.6 Spelaeorhynchidae

Spelaeorhynchids superficially resemble ticks with a soft expandable body and small dorsal and ventral plates, but the resemblance stops there. The dorsal and ventral plates on the body are small, but heavily sclerotized and form part of a strongly sclerotized gnathosomal ring. The chelicerae are chelate dentate (unlike ticks) and are short and stout with very large teeth. Spelaeorhynchids use their chelicerae for attachment to host tissue and often the leading edge of the gnathosomal ring and first pair of legs are embedded in the tissue. Because the anterior end of the adult female is typically embedded in the host, the location of the genital opening in spelaeorhynchids is uniquely positioned close to the anus, rather than in the more standard anterior position of most mesostigmatid mites. Like spinturnicids, they are also nymphiparous, passing the egg and larval stages in the female. Based on morphological features, it is impossible to suggest phylogenetic relationships to any specific group of Mesostigmata. Molecular evidence does suggest a relationship to the Spinturnicidae, which is circumstantially supported by the common host group and the intrauterine passing of egg and larva. Due to problems associated with long branch attraction in molecular systematics, and the fact that these two families represent the longest branches in current hypotheses, the suggested relationship is questioned.

Table 1. Summary of commonly found genera of Mesostigmata parasitic on mammals

Mite Family and Genera	Primary Host Associations
Laelapidae	
Laelaps, Echinolaelaps	Muridae
Andreacarus	Nesomyinae, Tenrecidae
Tur, Gigantolaelaps	New World Rodentia
Neolaelaps, Notolaelaps	Megachiroptera
Haemogamasidae	
Haemogamasus	Rodentia, Insectivora
Hirstionyssidae	
Echinonyssus	Rodentia, Insectivora, Carnivora
Dermanyssidae	
Liponyssoides	Muridae
Macronyssidae	
Macronyssus, Ichoronyssus	Vespertilionidae, Rhinolophoidea
Bewsiella, Megistonyssus	Rhinolophidae
Parichoronyssus	Phyllostomidae, Emballonuridae
Radfordiella, Macronyssoides	Phyllostomidae
Chiroptonyssus	Molossidae
Parasteatonyssus	Molossidae
Steatonyssus	Microchiroptera
Ornithonyssus, Acanthonyssus	Neotropical Rodentia
Argitis	Neotropical Rodentia
Halarachnidae	
Halarachne	Phocidae
Orthohalarachne	Otariidae, Odobenidae
Pneumonyssus, Rhinophaga	Cercopithecidae, Pongidae, Procaviidae, Hystricidae
Zumptiella	Sciuridae, Pedetidae
Pneumonyssoides	Suidae, Canidae, Cebidae
Dasyponyssidae	
Dasyponyssus, Xenarthronyssus	Dasypodidae
Manitherionyssidae	
Manitherionyssus	Manidae
Hystrichonyssidae	
Hystrichonyssus	Hystricidae
Spinturnicidae	
Meristaspis, Ancystropus	Pteropodidae
Eyndhovenia, Paraperiglischrus	Rhinolophidae
Periglischrus, Cameronieta	Phyllostomidae
Spinturnix, Paraspinturnix	Vespertilionidae
Spelaeorhynchidae	
Spelaeorhynchus	Phyllostomidae

4.2.7 Dasyponyssidae, Hystrichonyssidae, and Manitherionyssidae

The remaining three mesostigmatid mites parasitic on small mammals are all known from only one or two species. All are highly modified for an ectoparasitic lifestyle and their phylogenetic relationships to each other as well as to other dermanyssines is unknown. They are not presumed to be related to one another and are only treated together here because of the lack of overall knowledge regarding the families. The Dasyponyssidae are split into two monotypic genera (*Dasyponyssus* and *Xenarthronyssus*) and are restricted to armadillos in Central and South America. Manitherionyssidae and Hystrichonyssidae are both monotypic and restricted to the African pangolin and Asian porcupine, respectively. Characteristics in the legs, claws, and body of manitherionyssids are similar to that of dasyponyssids, but these similarities may simply be due to their evolution on scaled mammals. Hystrichonyssids are the most highly modified of the three families, with extremely thin, elongated chelicerae designed for piercing. The chelicerae resemble those of most Dermanyssidae, discussed earlier, except that hystrichonyssid chelicerae are elongated at the basal digit, rather than at the second digit.

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