9 Blood-sucking lice (Anoplura) of small mammals: True parasites[1]

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1 Introductory remarks

The sucking lice (Anoplura) are true parasites of the eutherian mammals. True to their mode of parasitic life, the sucking lice are obligate, permanent parasites of specific mammalian hosts, inhabiting their hosts' fur habitats (except human body lice). They are equipped with unique piercing-sucking mouthparts with which these blood-sucking insects directly feed from small blood vessels of host mammals (Snodgrass 1944; Lavoipierre 1967). Their lives are completely dependent on the fate of their mammalian hosts and their close associations with specific taxa of mammals epitomize coevolution of the parasite-host lineages (Kim 1985a). All these factors together also make the sucking lice efficient vectors of the typhus and related bacterial pathogens: e.g., louse-borne/epidemic typhus (Harwood and James 1979). Accordingly, the sucking lice have been subjects of extensive research and they are often used as models for the ecology of ectoparasitic insects (e.g., Wenzel and Tipton 1966; Marshall 1981) and epidemiology of vector-borne diseases (e.g., Zinsser 1935; Busvine 1976).

In 2003, anthropologists determined the age of human clothing by the human louse, *Pediculus humanus*, which consist of two distinct taxa (currently considered as "subspecies"), *P. h. humanus* (body louse) and *P. h. capitis* (head louse) that inhabit and feed in the hair environment on the human scalp. Unlike all other sucking lice, however, the human body louse is adapted to inhabiting habitats of natural fibers used for human clothing. Using molecular clock techniques, Kittler et al. (2003) estimated that body lice diverged from ancestral head lice as early as 72000±42000 years ago. This information certainly stirred up interest in news media and thus scien-

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[1] Blair Hedges has kindly assisted in tracking the estimated age of several higher taxa of mammals in preparation of this chapter

tific, cultural and religious circles (Lorenzi 2003; Wade 2004; Berenbaum 2006). In a recent forensic investigation of an unusual rape case, the blood in the gut of a pubic louse (*Pthirus pubis*) collected from the victim was analyzed for human DNA to confirm the suspect (Goff 2000). These are some of many examples which draw scientific and societal interests in the sucking lice which are known rather negatively as "vermin."

The sucking lice certainly are interesting insects to study, as they took over 30 years of my scientific career. In recent years many articles on human lice and their applications have been published in various scientific and technical journals which were also carried by news media worldwide. By being obligate, permanent parasites and largely host-species specific, the sucking lice not only are unique models for studying the biology and evolution of parasites but also offer diverse applications to scientific research and even in forensic investigations. Since a synthesis of taxonomic studies on sucking lice of the world by Ferris (1951), much of which were his own contributions, considerable advances were made on the biodiversity and classification of Anoplura by dedicated scientists like P.T. Johnson (USA), D.I. Blagoveshtechensky (Russia), K.C. Kim (USA), K. Kaneko (Japan), H.W. Ludwig (Germany), H.-J. Kuhn (Germany), T.-H. Chin (China), L.A. Durden (USA), and D.C. Castro (Durden and Musser 1994). Recently, anopluran research has focused on phylogenetic analysis by molecular taxonomy, all the different aspects of human lice, chemical control, and epidemiology of louse-borne diseases.

In this chapter I review the state of Anoplura biodiversity and the association of sucking lice with diverse small mammals, and discuss the dynamics of disruption in distribution and association of sucking lice in diverse lineages of mammals, adaptation in life history strategies in Anoplura, and future perspectives.

2 The sucking lice, true parasites

The sucking lice (Anoplura) are dorsoventrally flattened, wingless insects with elaborate piercing-sucking mouthparts that are similarly developed in all species of diverse lineages and with highly modified legs and claws adapted for grasping host hairs. As obligate, permanent parasites, most of the sucking lice are closely associated with the fur environment of the mammalian hosts in which temperature is relatively constant and optimal, although skin and fur temperatures vary among different areas of the body surface of a host animal (e.g., Marshal 1981; Piotrowski 1992).

In general, the relationship between the sucking lice and mammalian hosts is relatively stable and the impact of sucking lice infestation is hardly lethal to host animals and host populations. This relationship makes the sucking lice "good parasites" and they may even be considered as ecological and evolutionary partners rather than "vermin," coevolving along the parallel phylogenetic processes.

2.1 Life history strategy

Being obligate, permanent parasites, the sucking lice, once established on the host animal, live, feed, reproduce, and die in the fur environment from generation to generation until the host animal's life is ended. They go through a predictable life cycle: egg, three instars of larval stage, and adult, consecutively for most species. The eggs are glued to the hair near the skin in the fur environment. The adult female of the human head louse *P. h. capitis*, for example, lays an average of 57 eggs with 7.5 eggs per day. From oviposition by adult females, the egg requires about 8.5 days of incubation at 30°C and after hatching the larva (=nymph) goes through three relatively simple larval stages and the mature 3rd instar moults to become an adult, the development taking on average 9.7 (from 8.5 to 12.2) days. The female adult life lasts on average 13.3 (from 9 to 22) days. Thus, the human lice complete the entire life cycle in about 18 days. The sucking lice have literally ready-made food resources which are available for feeding at any time, usually twice a day for human lice (Busvine 1976). An exception to the general biology of sucking lice is the human body louse (*P. h. humanus*) which inhabits a highly specialized microhabitat - human clothing rather than animal hair and fur. Females lay eggs on man-made fibers, and the longevity of a female is much longer (20-21 days) than that of the head louse.

2.2 Lice and external environment

The sucking lice of aquatic mammals such as seals and sea lions and river otters are highly adapted to cold and wet environments. Species of Echinophthriidae, such as *Antarctophthirus callorhini* of the Northern fur seal (*Callorhinus ursinus*), *A. ogmorhini* of the Weddell seal (*Leptonychotes weddellii*), *Lepidophthirus macrorhini* of the Southern elephant seal (*Mirounga leonine*), are usually resilient and can survive for many days at low temperature, for many hours in submergence, and for many days of starvation (Busvine 1976; Murray 1976). For example, starving human head lice can survive 55 hours at 23°C, whereas starving *A. ogmorhini* can

survive 12 days at 6°C and *L. macrorhini* – 6-8 weeks at 5-10°C. *A. ogmorhini* can even survive supercooling by an exposure to -20°C for 36 hours (Murray et al. 1965).

Life history of the sucking lice of marine carnivores becomes opportunistic due to the life cycle and beaching behaviour of the host mammals and is also limited to the period of the host breeding season out of water (e.g., Murray and Nichols 1965; Kim 1971). The life history of the sucking lice parasitic on *C. ursinus* takes place in two different habitats: *Proechinophthirus fluctus* inhabiting the fur and *A. callorhini* inhabiting the skin at the base of flippers, anal and genital orifice, eyelids and nostrils. They are not only opportunistic but their life cycle is also precarious because the hosts breed on the beach areas in the Pribilof Islands of the Bering Sea but by the end of summer they migrate to the south as far south as Baja California. On land, the adults of these lice on the pregnant female migrate to newborn pups during parturition and almost immediately mate and start the new life cycle on the pups. These species go through 2-3 generations on the growing pups as well as older seals (Kim 1971). The louse populations established on juvenile or adult hosts begin a long, slow life cycle on the migrating seals for many months and then they become mature adults when their host animals return to the breeding ground next spring. At this point the sucking lice again begin the new generation of louse populations on the seals, particularly on newborn pups on land (Kim 1989).

3 Anoplura biodiversity

Ever since the Linnean taxonomy was established and consistently applied in biology, world taxonomists have recorded about 1.75 million species (Heywood and Watson 1995) which barely represents 18% of the extant global biodiversity (if the figure of 10 million species as an average estimate of global biodiversity is accepted). As this labour took approximately 250 years, it will be an enormous task to explore and describe the remainder of global biodiversity, approximately 8.25 million species. We must come to grips very soon with how extant global biodiversity is to be explored and documented, particularly for the backyard biodiversity that is the essence of ecosystem function and the source of sustainable development at the grassroots. Considering the rapidly increasing human population that already passed 6.4 billion, biodiversity and biological resources must be studied and conserved for the sustainable economic development which all of us stride for, requiring ecosystem management for our backyards, whether in rich or poor countries, or for cities or the countryside.

Considering the state of global biodiversity, the Anoplura biodiversity is relatively better known because of the dedicated efforts of taxonomic specialists during the productive period from the late 1800s through the 20th century. Global Anoplura biodiversity is commonly estimated to be around 1500 species (Kim and Ludwig 1978; Kim 1985a, b; Kim et al. 1990), of which 532 species were listed as valid in "The Sucking Lice of the World" by Durden and Musser (1994). Considering the mammalian biodiversity that is far better known than that of most other animal taxa (perhaps 95% or more described), about 64% of the living mammals, equivalent approximately to 2671 species, are suspected to harbour sucking lice, of which the known species of sucking lice were recorded from only about 31% of potential mammalian host species. In other words, there still are over 828 species of living mammals, which could yield new species of sucking lice if they are closely examined for ectoparasites (Kim et al. 1990).

The sucking lice have evolved closely with eutherian mammals through their parallel lineages through a long evolutionary process. As stated earlier, their intimate biological relationships resulted in a high level of monoxeny with some species still being oligoxenous or polyxenous, perhaps since as early as the late Cretaceous (Kim and Ludwig 1982). The associations of Anoplura and Mammalia show that 29 genera of sucking lice are associated with a single mammalian family, six genera with two mammalian families, three genera with three mammalian families, and four genera with four to six mammalian families (Ludwig 1968). Recent studies based on molecular data in relation to fossil records show that the geological timing of placental mammal diversification is closely aligned with Anoplura phylogeny, thus forming close parasite-host associations (e.g., Kim 1982, 1985b; Springer et al. 2003).

Viewed from the perspective of placental mammalian cladogenesis, the emergence of mammalian splits and new clades closely mirrors the phylogeny and distribution pattern of parallel lineages of sucking lice and eutherian mammals (Kim 1982, 1985b; Springer et al. 2003). These phylogenetic patterns strongly suggest that sucking lice and their mammalian hosts had a high level of early associations and coevolution between them which led to close phylogenetic parallelism (Tables 1 and 2). Today's sucking lice are found on the species of diverse eutherian mammals: Artiodactyla, Carnivora, Pinnipedia, Dermoptera, Hyracoidea, Insectivora, Lagomorpha, Macroscelidae, Perissodactyla, Primates, Rodentia, Scandentia, and Tubulidentata (Table 1) (Kim 1985a; Kim et al. 1990; Durden and Musser 1994).

Strangely, some taxa within those orders that harbour large numbers of anopluran lineages are completely devoid of sucking lice and exclusively

infested with other ectoparasites such as ischnocerans (Trichodectidae) on pocket gophers (Geomyidae, Rodentia), whereas some mammalian lineages such as Monotremata, Marsupialia, Xenarthra, Pholidota, Chiroptera, Cetacea, Proboscidea, and Sirenia, are not associated with sucking lice but with other parasitic arthropods such as Hemiptera, Diptera, and Acarina (Kim 1985a; Kim et al. 1990).

Table 1. Mammalian hosts and their sucking lice (Kim 1988)

Host mammals	Sucking lice
Artiodactyla	Linognathidae
	Haematopinidae (*Haematopinus*)
Camelidae	Microthoraciidae (*Microthoracius*)
Tayassuidae	Pecaroecidae (*Pecaroecus*)
Perissodactyla	Linognathidae
	Haematopinidae (*Haematopinus*)
Suidae	Ratemiidae (*Ratemia*)
Carnivora	
Fissipedia	Echinophthiriidae (*Latagophthirus*)
Pinnipedia	Echinophthiriidae
Macroscelidea	Neolinognathidae (*Neolinognathus*)
Insectivora	Hoplopleuridae (*Ancistroplax*, *Haematopinoides*)
Rodentia	Hoplopleuridae
	Polyplacidae
Sciuridae	Enderleinellidae
Lagomorpha	Polyplacidae (*Haemodipsus*)
Dermoptera	Hamophthiriidae (*Hamophthius*)
Scandentia	Polyplacidae (*Docophthirus, Sathrax*)
Primates	Polyplacidae
Cercopithecidae	Pedicinidae
Anthropoidea	Pthiridae, Pediculidae
Hyracoidea	Linognathidae (*Prolinognathus*)
Tubulidentata	Hybophthiridae (*Hybophthirus*)

In the cladistic analysis, no direct concordance exists between the family cladograms of Anoplura and their mammalian hosts. When close resolutions were made for specific family clades, however, highly closely parallel phylogeny emerged between anopluran and mammalian lineages (Kim 1988). The Anoplura cladogram recognized three primary lineages, Polyplacoid, Microthracoid, and Pediculoid groups (Table 2). It is interesting to note that a recent analysis of the placental mammal diversification related to the Cretaceous-Tertiary (K-T) boundary shows that Dermoptera and Scandentia are sister taxa that split before the K-T boundary, more than 80 million years ago (Springer et al. 2003), as was the case with *Hamophthirius* and *Sathrax-Docophthirus* of the Polyplacoid lineage of

Anoplura (Table 1 and 2). A closer examination of the cladistic disconcordance reveals that there are considerable similarities between cladistic patterns between the sucking lice and eutherian mammals. It suggests that the initial colonization and primary infestations of diverse mammals by the sucking lice must have taken place erratically at different times and regions before the cladogenesis of mammalian hosts was undertaken. Then, these sucking lice closely co-evolved with the host mammals with sporadic host shifts that established new host associations, in the end resulting in parallel lineages between them throughout the entire history of their associations (Kim 1985b, 1988).

Table 2. Associations between the sucking lice and mammalian hosts (Kim 1988)

Anoplura clades	Major host groups
Polyplacoid group	
Hamophthridae	Dermoptera
Neolinognathidae	Macroscelidea
Hoplopleuridae	Rodentia, Insectivora
Enderleinellidae	Rodentia (Sciuridae)
Polyplacidae	Rodentia, Primates, etc.
Linognathidae	Artiodactyla, Perissodactyla, Hyracoidea
Microthoracoid group	
Ratemidiidae	Perissodactyla (Suidae)
Microthoraciidae	Artiodactyla (Camelidae)
Echinophthiriidae	Carnivora
Pediculoid group	
Hybophthiriidae	Tubulidentata
Haematopinidae	Artiodactyla, Perisodactyla
Pecaroecidae	Artiodactyla (Taayassuidae)
Pedicinidae	Primates (Cercopithecidae)
Pthiridae	Primates (Anthropoidea)
Pediculidae	Primates (Anthropoidea)

4 The sucking lice and eutherian mammals: Coevolutionary partnership

Host associations in the Anoplura and Mammalia system are related to ecological and physiological interactions between parasites and hosts in a short time frame and genetics and coevolution over geological time. Therefore, a scientific approach to determine the origin and age of lineages or understand the phylogenetic processes of coevolutionary relationships of the parasite-host systems demands a synthesis based on multivariate data

from comparative studies of morphological, genetic, ecological and geo-logical parameters, where necessary.

The sucking lice have endured well with host mammals, the latter pro-viding rather constant and steady fur environments within each specific mammalian lineage, unless fur habitats were threatened with abrupt envi-ronmental changes by host shift that could change habitats or habitat envi-ronment. In general, infraspecific genetic variation in Anoplura is rela-tively small (e.g., Kim et al. 1963) and their genetic variation within a genus-taxon is also relatively small, often with interspecific variation pri-marily limited to the genital structures. However, there are distinct differ-ences in morphological configuration between specific lineages, such as Hoplopleuridae and Polyplacidae of rodents and Antarctophthriidae of pinnipeds.

Considering information on the biology and behaviour of sucking lice so far available, the sucking lice like many other "pest" species can readily adapt to specific environmental changes. In a laboratory setting, human body lice became resistant to insecticides like DDT within ten generations. For example, the sucking lice associated with the arctoid-fissiped ancestors of modern pinnipeds must have developed behavioural and morphological adaptations to stay on the host and survive in changing environments, as their mammalian hosts frequent the water environment. There are a num-ber of morphological adaptations linked to aquatic habitats such as flatten-ing of body setae to scales and enlargement and elaborate modification of tibia-tarsal segments of mid- and hind legs in the generalist genus, *Antarc-tophtirus* (Kim 1971, 1975, 1988; Kim et al. 1975).

All species in a given lineage of sucking lice are exclusively parasitic on the specific taxon of their specific parallel lineage of eutherian mammals; e.g., Enderleinellidae associated with Sciuridae; Pediculidae versus Pri-mates; Microthoracidae versus Camelidae. The sucking lice are highly host-specific and over 63% of all known species of Anoplura are monox-enous (one species of parasite on one host species), whereas 24% of spe-cies are hetero- or oligoxenous (specific to two or three host species). In other words, most species of sucking lice (87% or more) are associated with one or 2-3 host species. The sucking lice parasitic on rodents show 62% host specificity of which 66% of total known species of the Ender-leinellidae are specific to single host species, 62% for Hoplopleuridae, and 58% for Polyplacidiae, while ungulate-infesting taxa (or clades) like Haematopinidae and Linognathidae demonstrate 95% host specificity (Kim 1985b, Kim et al. 1990).

Considering their broad and mostly consistent distribution throughout the diverse lineages of today's global mammal biodiversity, the sucking lice are resilient and persistent parasites, evolved closely along the evolu-

tion and radiation of specific mammalian host lineage. It is reasonable to hypothesize that once ancestral sucking lice successfully established on a specific ancestral mammalian species to begin a parasite-host lineage, they must have evolved rapidly along the evolution of their hosts in specific mammalian lineage, as their hosts continued to radiate and evolve along the evolutionary history of mammals (Kim 1985a; Kim 1993). Conversely, anthropogenic stresses that cause today's mass extinction also directly affect the delicate parasite-host relationship, causing the loss of coevolutionary partners, host species and their associated sucking lice.

As a mass extinction by anthropogenic stresses continues, it is likely that as many mammalian species that harbour specific sucking lice become extinct, their parasitic partners will also be lost at the same time (co-extinction). Although we have no specific way to detect and measure this, it is not far-fetched to predict that there are good numbers of host-specific sucking lice already lost by recent extinction of host mammals (Stork and Lyal 1993). Today's anopluran biodiversity is the descent of interactive parasite-host relationships between the sucking lice and their host mammals. In the co-evolutionary process, once established as a clade in a specific parasite-host lineage, the sucking lice appear to have successfully established a phylogenetic base on the host species and its subsequent lineage. In many lineages sucking lice successfully modified their life history strategy to survive in heterogeneous environments; for example, sucking lice on marine carnivores (Murray 1965; Murray and Nicholls 1965; Murray et al. 1965; Kim 1985a).

5 Anoplura biodiversity and micromammals

Micromammals (= small mammals) as defined in this volume include Chiroptera, Insectivora, Rodentia, and Lagomorpha, of which Chiroptera as a specialized taxon are not of concern here because sucking lice are not associated with them at all. The discussion here is limited to the sucking lice of Insectivora, Rodentia and Lagomorpha. The latter order is associated with two anopluran genera: *Haemodipsus* is parasitic on Leporidae and *Hoplopleura ochotonae* is a characteristic louse species of Ochotonidae (pikas). Additional small mammals, used to be considered closely related to Insectivora, harboring polyplacoid sucking lice are Tupaiidae (Scandentia) with *Sathrax* and *Docophthirus* and Macroscelididae (Macroscelidea) with *Neolinognathus*.

5.1 Sucking lice of Insectivora and related mammals

The "Insectivora" used to include all small insectivoran mammals including Monotyphlan families, Macroscelididae and Tupaiidae (their phylogenetic relationships are yet unclear). Today's Insectivora is a monophyletic group that includes six recent Lipotyphlan families: Erinaceidae, Talpidae, Solenodontidae, Tenrectidae, Chrysochloridae, and Soricidae. Their associations with the sucking lice are summarized in Table 3.

Table 3. Anopluran genera parasitic on lipotyphlan and monotyphlan mammals. In parentheses – number of species

Insectivoran families	Anoplura partners
LIPOTYPHLANS	
Talpidae	*Haematopinoides* (1)
Soricidae	*Ancistroplex* (5), *Polyplax* (3)
MONOTYPHLANS	
Macroscelididae (order Macroscelidea)	*Neolinognathus* (2)
Tupaiidae (order Scandentia)	*Sathrax* (1), *Docophthirus* (1)

Among six lipophylan families, only two (Talpidae and Soricidae) are recorded to harbour sucking lice. Of 31 talpid species, only two species, *Parascalopus breweri* and *Scalopus aquaticus*, have lice, with both harbouring a single species of Hoplopleuridae, *Haematopinoides squamosus*. On the other hand, Soricidae, distributed throughout the world except the Polar regions, Australian region, and central and southern South America, are parasitized by specialized *Ancistroplax* (Hoplopleuridae) of which five species are so far recorded from *Soriculus*, *Crocidura*, and *Suncus* (Anderson and Jones 1984). Considering that the sucking lice of Hoplopleuridae are primarily rodent parasites, *Ancistroplax* and *Haematopinoides* must have shifted host from rodents early in the evolution of the Hoplopleuridae lineage and solidly established and evolved along the Insectivore lineage.

The elephant shrews (Macroscelidea) and tree shrews (Scandentia) are two distinct taxa of the menotyphlan insectivores. They are parasitized mainly by two genera of sucking lice, representing two separate phylogenetic lines, *Neolinognathus* and *Sathrax*, respectively.

5.2 Associations of sucking lice and rodents

The species diversity of Anoplura is closely related to the diversity of mammalian hosts within a specific lineage. About 70% of anopluran spe-

cies are associated with rodents (Kim 1988), which are hosts to three families of sucking lice, namely Enderleinellidae, Polyplacidae, and Hoplopleuridae. Oddly enough, certain mammalian lineages, such as Geomyidae (pocket gophers) are completely devoid of sucking lice, although the Geomyidae is a clade within Rodentia, highly infested by sucking lice. Other rodent clades that are completely devoid of sucking lice include Hystricidae, Aplodontidae, Anomaluridae, Spalacidae as well as several other sciurognath and hystrichognath families (Kim 1985b). The distribution of the genera of the sucking lice among rodents is summarized in Table 4.

Table 4. Anopluran genera parasitic on rodents (Anderson and Jones 1984; Kim 1985b). In parentheses – number of species

Rodent families	Anoplura partners		
	Enderleinellidae	Polyplacidae	Hoplopleuridae
Sciuridae	*Enderleinellus* (45), *Microphthirus* (1), *Werneckia* (5), *Phthirunculus* (1), *Atopophthirus* (2)	*Neohaematopinus* (22), *Johnsonpthirus* (5), *Linognathoides* (11), *Polyplax* (1)	*Hoplopleura* (10), *Paradoxophthirus* (1)
Heteromyidae		*Fahrenholzia* (12)	
Dipodidae		*Eulinognathus* (16)	*Schizophthirus* (3)
Muridae		*Eulinognathus* (2), *Fahrenholzia* (1), *Neohaematopinus* (2), *Polyplax* (77), *Proenderleinellus* (1), *Mirophthirus* (1), *Typhlomyophthirus* (1)	*Hoplopleura* (122)
Pedetidae		*Eulinognathus* (1)	
Myoxidae			*Schizophthirus* (6)
Bathyergidae		*Eulinognathus* (2)	
Petromuridae		*Scipio* (1)	
Thryonomyidae		*Scipio* (2)	
Chinchillidae		*Cuyana* (1), *Eulinognathus* (1), *Lagidiophthirus* (1)	
Caviidae		*Galeophthirus* (1)	*Trimenopon* (1)
Ctenomyidae		*Eulinognathus* (5)	
Octodontidae			*Hoplopleura* (2)
Abrocomidae		*Polyplax* (1)	
Echimyidae		*Ctenophthirus* (1), *Fahrenholzia* (1)	*Hoplopleura* (3), *Pterophthirus* (3)

Large rodent families are usually infested by relatively large number of louse species. For example, the speciose Sciuridae are colonized by 11 genera and about 100 species of sucking lice, whereas a smaller taxon like the Dipodidae harbours only two genera and 19 species (Kim 1985b; Durden and Musser 1994). The sucking lice of Enderleinellidae are exclusive ectoparasites of Sciuridae which also are infested with four polyplacid and two hoplopleurid genera. Both polyplacid and hoplopleurid lice infest also Muridae, Dipodidae, Echimyidae, and Caviidae. In addition, Polyplacidae are found on Heteromyidae, Pedetidae, Bathyergidae, Petromuridae, Thryonomyidae, Chinchillidae, Ctenomyidae, and Abrocomidae, whereas Hoplopleuridae are found on Octodontidae and Myoxidae. The highest diversity of both polyplacids and hoplopleurids is associated with murid hosts.

6 Coevolution of squirrels and their lice: Unfinished speciation

Squirrels (Sciuridae) constitute one of the largest families of rodents that contain an abundant and diverse group of species well known in many biological and cultural perspectives. They also are primary hosts to the sucking lice of Enderleinellidae at large and polyplacids (*Neohaematopinus* genus-group including *Neohaematopinus*, *Linognathoides*, *Johnsonphthirus*), and straggler species of *Polyplax*. As mentioned above, Enderleinellidae are exclusive parasites of squirrels and their fate and evolution have been closely linked to the evolutionary success of the Sciuridae. There are five genera of Enderleinellidae, namely *Enderleinellus*, *Microphthirus*, *Werneckia*, *Phthirunculus*, and *Atopophthirus*, of which *Enderleinellus* is most diverse (Kim 1966, 1977, 1985b, 1988; Kim and Ludwig 1978; Kim and Adler 1982) (Table 5).

Enderleinellus is a generalist genus which exploits various host species from most tribes within Sciuridae (Table 6). Looking at the host associations of the sucking lice in Sciuridae, it has been observed that the known species of *Enderleinellus* from tree squirrels (*Sciurus*) are monoxenous, one species of lice being associated with a single host species, whereas the species complexes from ground squirrels (*Spermophilus*) are oligoxenous or polyxenous, meaning that one species of parasite is associated with a number of closely related species of ground squirrels (Kim et al. 1963; Kim 1966, 1985c, d; 1988; Kim and Ludwig 1978).

Considering the current state of parasite-host association in Enderleinellidae and Sciuridae (Table 5), most taxa at species and generic level of Enderleinellidae are closely associated with their respective host taxa at simi-

lar taxonomic levels. Most sciurids are parasitized by one species of Enderleinellidae except *Spermophilus*. *Atopophthirus, Microphthrius*, and *Phthirunculus* are parasites of flying squirrels (Pteromyinae) and species of both *Atopophthirus* and *Phthirunculus* are parasitic on *Petaurista*. Species of *Enderleinellus* are broadly associated with diverse species of Sciurinae, primarily on tree squirrels (Sciurini, Callosciurini, Protoxerini, Xerini, and Funambulini) and marmots (Marmotini), whereas species of *Werneckia* are parasitic on species of the Funambulini in Africa. Although some of the recorded host associations need to be re-examined and verified for species identity and taxonomic status, most species of *Enderleinellus* are associated with single species of tree squirrels in the New World and of other squirrels in tropical Asia (Calloschiurini, Funambulini) and Africa (Protoxerini, Xerini).

Table 5. Diversity and associations of Enderleinellidae and Sciuridae (Durden and Musser 1994)

Enderleinellidae	Sciuridae
Atopophthirus (2)	Pteromyinae
emersoni	*Petaurista* (Malasia)
setosus	*Petaurista* (Malasia)
Microphthirus (1)	Pteromyinae
uncinatus	*Glaucomys* (Canada, USA.)
Phthirunculus (1)	Pteromyinae
sumatranus	*Petaurista* (Indonesia: Sumatra)
Enderleinellus (45)	Sciurinae
	Tribe Sciurini
arizonensis	*Sciurus alleni, S. arisonensis*(USA: Arizona)
brasiliensis	*Sciurus aestuans* –species complex (Brazil)
deppei	*Sciurus aureogaster, S. granatensis, S. deppei* (Mexico)
extremus	*Sciurus aureogaster, S. deppei* (Guatemala, Mexico)
hondurensis	*Sciurus yucatanensis, S. variegatoides* (Columbia, Honduras, Mexico)
insularis	*Sciurus granatensis* (Venezuela)
kaibabensis	*Sciurus alberti* (USA: Arizona)
kelloggi	*Sciurus giseus*(USA: California)
krochinae	*Sciurus anomalus* (Azerbajian)
longiceps	*Sciurus carolinensis, S. niger* (USA)
mexicanus	*Sciurus aureogastger* (Mexico)
nayaritensis	*Sciurus nayaritensis* (Mexico)
nitzschi	*Sciurus vulgaris* (Eurasia)
oculatus	*Sciurus alleni* (Mexico)
paralongiceps	*Sciurus aberti* (USA)
pratti	*Sciurus colliaei* (Mexico)
urosciuri	*Sciurus igniventris* (Brazil)

venezuelae	*Sciurus granatensis* (Venezuela)
	Tribe Callosciurini
kumadai	*Callosciurus* (Japan)
malaysianus	*Callosciurus* (Borneo, Mayanmar, Malaysia, Thailand)
puvensis	*Callosciurus* (China)
dremomydis	*Dremomys* (China: Sichuan, Thailand)
corrugatus	*Tamiops*, *Callosciurus* (Thailand)
	Tribe Protoxerini
gambiani	*Heliosciurus* (Liberia)
heliosciuri	*Heliosciurus* (Liberia)
	Tribe Xerini
heliosciuri	*Epixerus* (Angola, Kenya, Liberia)
	Tribe Funambulini
nishimarui	*Funambulus* (India)
platyspicatus	*Funambulus* (Ceylon)
euxeri	*Xerus* (Kenya, Dahomey, Liberia, Sudan, Nigeria)
zonatus	*Paraxerus* (Kenya)
larisci	*Lariscus* (Borneo)
menetensis	*Menetes* (Thailand)
nannosciuri	*Nannosciurus* (Indonesia: Java)
	Tribe Marmotini
blagoveshchenskyi	*Marmota* (Kyrgyzstan)
dolichocephalus	*Marmota* (Russia: Yakutia-Sakha)
marmotae	*Marmota* (USA)
tamiasis	*Tamias* (Korea)
disparillus	*Spermophilus* (Russia: Amur)
ferrisi	*Spermophilus* (Bulgaria)
osborni	*Spermophilus* (USA)
propinquus	*Spermophilus* (Kazakhstan, Poland, Romania)
suturalis	*Ammospermophilus*, *Cynomys*, *Spermophilus* (USA)
	Tribe Microsciuini
microsciuri	*Microsciurus* (Columbia, Panama)
	Pteromyinae
replicatus	*Pteromys* (Russia: Tatarstan)
Werneckia (5)	Sciurinae
	Tribe Funambulini
funisciuri	*Funisciurus* (Nigeria)
nigiriensis	*Funisciurus* (Nigeria)
africana	*Funisciurus* (Nigeria)
paraxeri	*Paraxerus* (Kenya)
minuta	*Paraxerus* (Kenya)

Most *Sciurus* species harbour one species of *Enderleinellus*. However, four species (*S. aberti, S. alleni, S. augeogaster,* and *S. granatensis*) are associated with two species of sucking lice (Table 6). In addition, five

Holarctic species of *Enderleinellus* are associated with many species of ground squirrels (*Spermophilus*) (Table 7).

Table 6. Associations between *Sciurus* and *Enderleinellus*

Sciurus	Enderleinellus
S. aberti	E. kaibabensis, E. paralongiceps
S. aestuans	E. brasiliensis
S. alleni	E. arizonensis, E. oculatus
S. anomalus	E. krochinae
S. arizonensis	?
S. aureogaster	E. extremus, E. mexicanus
S. carolinensis	E. longiceps
S. colliaei	E. pratti
S. deppei	E. deppei
S. flammifer	?
S. gilvigularis	?
S. granatensis	E. insularis, E. venezuelae
S. griseus	E. kelloggi
S. ignitus	E. urosciui
S. igniventris	?
S. lis	?
S. nayaritensis	E. nayaritensis
S. niger	E. oculatus
S. oculatus	E. oculatus
S. pucheranii	?
S. pyrrhinus	?
S. richmondi	?
S. sanborni	?
S. spadiceus	?
S. stramineus	?
S. variegatoides	E. hondurensis
S. vulgaris	E. nitschi
S. yucatanensis	E. hondurensis

Table 7. *Enderleinellus* and Sciurid hosts (Tribe Marmotini). * records needs verification of species identity

Sucking lice *(Enderleinellus)*	Squirrels *(*Tribe *Marmotini)*
Enderleinellus blagoveshtchenskyi	*Marmota baibacina*
E. dolichocephalus	*M. camchatica*
E. tamiasis	*Tamias stiatus*
	T. sibiricus
E. disparilis	*Spermophilus undulates*
E. ferrisi	*S. citellus*
E. osborni	*S. (Xerospermophilus)mohavensis*

	S. (X.) tereticaudus
	S. (Otiospermophilus) beecheyi
	S. (O.) variegatus
	S. (O.) atricapillus
	S. (Spermophilus) beldingi*
E. proqinquus	S. (Spermophilus) fulvus
	S. (S.) suslicus
	S. (S.) citellus
E. suturalis	Ammospermophilus harrisi
	A. nelsoni
	Cynomys gunnisoni
	C. leucurus
	Spermophilus (S.) beldingi
	S. franklinii
	S. lateralis
	S. mexicanus
	S. richardsonii
	S. spilosoma
	S. (X.) tereticaudus*
	S. townsendii
	S. tridecemlineatus

Eight species of *Enderleinellus* are parasitic on marmots, prairie dogs, and chipmunks and ground squirrels. Considering the host associations of polyxenous *E. osborni, E. proprinuus,* and *E. suturalis*, it is likely that other species such as *E. disparilis* and *E. ferrisi* are also similarly associated with many other host species beyond those originally recorded (Table 7). The populations of *E. suturalis* from three host species of ground squirrels, *S. tridecemlineatus*, *S. franklini,* and *A. harrisi*, were analyzed to determine if they can be discriminated by morphometric measurements (Kim et al. 1963). The populations of this species were determined to be distinct and could be separated by morphometric characters each of which could be treated as a taxon at the subspecies level. In other words *Enderleinellus* species associated with ground squirrels have not evolved far enough to be recognized as species like those associated with tree squirrels which have distinct characters separating them from other related species.

7 Concluding remarks

The sucking lice (Anoplura) are true parasites and provide an interesting model for speciation, phylogenetic studies, community ecology, and ecosystem function of parasite-host system. As with the global biodiversity of all other organisms, we are a long way from understanding the true extent

of Anoplura biodiversity. We should make a determined effort to explore and describe most species of sucking lice from those expected host species of extant mammals because anthropogenic extinction of mammals causes the loss of unknown species of sucking lice, their evolutionary and ecological partners.

Being well established obligate and permanent parasites, the sucking lice could provide better understanding of how parasites-hosts relationships are sustained in balance without serious threats to the survival of host species and how sucking lice evolve as host species split within a specific lineage such as Enderleinellidae and Sciuridae. The more empirical studies on biodiversity, host associations, distribution and community ecology of the sucking lice are pursued and new information established, the better understanding we achieve of parasite-host relationships and evolutionary dynamics of ecological partners. Better understanding of the community structure and the patterns of parasite distribution on host animals should help develop realistic models with sound assumptions and real-term parameters which could provide real-term predictions (e.g., Bittencourt and Rocha 2002; Choe and Kim 1987, 1988, 1989).

We can reach a better understanding of the intricate dynamics of ecosystems involving a community of parasite species interacting with host animals, if we approach the study of parasites-small mammalian host systems with morphological, ecological and molecular parameters. This could provide new means to control and manage parasite infestations of human systems. In the rapidly changing global environment, continued study of the life patterns and harmonious relationship of two ecosystem partners, parasites and host mammals, established through long coevolutionary processes, should offer a better understanding of the dynamics of parasite communities on host animals including humans.

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