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ARTHROPODA

Phthiraptera (Order): Lice

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Phylum Arthropoda

    Class Insecta

        Order Phthiraptera

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Chapter 64

Phthiraptera (Order): Lice

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Introduction

Parasitic lice (superorder Psocodea, order Phthiraptera; also known as true lice, or lice, singular: louse) constitute the largest insect taxon (with about 5,000 known species) of permanent and obligate parasites. The taxon is subdivided into 4 suborders: Amblycera, Ischnocera, Rhynchophthirina, and Anoplura (Johnson and Clayton, 2003).

Morphology

Lice are secondarily wingless (this means that their ancestors had wings, but the current forms of lice have no wings) ectoparasites having a dorsoventrally flattened head and (to a lesser extent) flattened body. They possess reduced compound eyes (or may be eyeless), have no ocelli, and their mouthparts are either mandibulate (with mandibles for chewing) or modified for piercing the host skin and sucking blood (with stylets). The labial palps are reduced and the antennae have 3–5 segments and are either recessed into the head (as in Amblycera), filiform (as in Ischnocera), or short (as in Anoplura). The first thoracic segment is usually free, while the second and third segments may be partially fused. Their legs are relatively short and stout, the tarsi have 1 or 2 segments, and are equipped with a single or paired pretarsal claws. The tibio-tarsal claws of Anoplura are adpated for grasping host hairs. The abdomen comprises 8–11 visible segments with no cerci. The coloration of lice may vary, including shades of black, gray, brown, yellow, or white, often more-or-less matching the host's pelage or plumage (Bush et al., 2010).

Lice are small-bodied insects (adults 0.35–11 mm-long) with their body size covarying with the host's body size in at least 2 ways (Harnos et al., 2017). First, species of hosts with larger body sizes tend to harbor species of lice that also have larger body sizes (Harrison, 1915) and, second, hosts with larger body sizes also tend to harbor species of lice with more variable body sizes (Poulin, 2007). Practically, this means that only small lice can parasitize small hosts, while both small and large lice (thus, on average larger) species may occur on large-bodied host species. The optimal body size of a species of louse is a compromise between 2 opposing selection pressures; host defenses may select for smaller body size, and fertility selects for larger body size (Villa et al., 2018b). If invading markedly different-sized hosts, these selection pressures can result in different-sized louse populations with reproductive isolation emerging between them due to size incompatibility during copulation which can be considered a pre-mating isolating mechanism (Villa et al., 2018a). It is worth noting that practically all body size data on lice refer to slide-mounted individuals flattened essentially into 2-dimensions by force (Palma, 1978) so any morphometric evaluations need to take this into consideration.

Feeding

Amblyceran lice mostly consume dead fragments or living tissues of the host skin, and also partially feed on blood and other excretions. In contrast, ischnoceran lice mostly feed on non-living tissues, such as skin fragments and the fluffy microstructures of feathers (Johnson and Clayton, 2003). To a lesser extent, both of these taxa may also predate on ectoparasitic mites (Oniki and Butler, 1989; Valim, 2006) and other lice, including cannibalizing members of their own species (Nelson, 1971). Living in a relatively dry environment (such as the host's plumage or pelage), they possess sclerites between the mouthparts specialized for water vapor uptake from the air (Rudolph, 1982). Some amblycerans even drink the eye fluids of the host (Mey et al., 2006). Members of Rhynchophthirina and Anoplura lice feed exclusively on mammal blood (Durden, 2019).

In species that feed on non-living tissues like feathers, endosymbiotic bacteria belonging to the phylum Proteobacteria help digest the keratin and supply vitamins and other trace nutrients to the host. These symbionts are maternally transmitted through the oocytes and inhabit specialized cells, called bacteriocytes in the body cavity of lice (Fukatsu et al., 2007). Further, the diverse microbial community of *Acinetobacter* and *Staphylococcus* species may often accompany them (Reed and Hafner, 2002). Blood-sucking lice also carry mutualistic *Rickettsia*-like bacteria that supply lice with vitamin B and cofactor biosynthesis (Perotti et al., 2009; Rio et al., 2016).

Host Range

Most louse species are known to parasitize only 1 or very few closely related host species. Although the known range of host species may often be underestimated due to sampling bias (more sampling in countries with higher income, etc.) (Poulin, 1992), lice seem to have a more narrow host-range relative to other major taxa of ectoparasitic arthropods. A few species (or morphospecies, like *Menacanthus eurysternus*) appear to be more generalists, parasitizing several host taxa. These species may involve morphologically similar but genetically distinct species that are sometimes called cryptic species in light of the fact that they appear morphologically similar but are genetically divergent.

Host Distribution

Practically all avian families host several genera of lice (up to 20 in the family Tinamidae). Only a very few species-poor bird families (including the families Balaenicipitidae, Rhynochetidae, Picathartidae, and Todidae) are not yet known to host any lice (Price et al., 2003), probably due to inadequate research intensity. Contrarily, their occurrence is much less diverse and less prevalent on mammals. Some major taxa of mammals, such as the monotremes, pangolins (order Pholidota), bats (order Chiroptera), sea cows or sirenians (order Sirenia), tapirs (family Tapiridae), rhinoceroses (family Rhinocerotidae), and the clade Whippomorpha (which includes whales, dolphins, and hippopotamuses) are free of lice (Durden and Musser, 1994).

Lice always inhabit the integumentary structures of the outer surface of their hosts, the plumage of birds or the pelage of mammals. Only a very few taxa may slightly shift toward endoparasitism, such as *Piagetiella peralis*, which occurs inside the pouch of pelicans, or *Somaphantus lusius* and *Rediella mirabilis*, that may live within the quill (calamus) of feathers.

Life Cycle

The vast majority of lice species reproduce sexually, very few are parthenogenetic. They exhibit a hemimetabolous life cycle with all developmental phases completed on the host body surface. Their eggs, often called nits, are glued firmly to the hairs or feathers. After hatching, the nymphs develop through 3 nymphal stages to reach the adult stage (note that, being hemimetabolous insects, lice do not include a larval stage; their immature stages are called nymphs). The morphology of the nymphs resembles that of the adults, although it is much simplified, especially in chaetotaxy (that is, the arrangement of the bristles).

Sex-ratios are often female-biased in lice, or close to equal, and are rarely male-biased. Male bias may occur in host individuals with high intensity infestations (Rózsa, 1997a) or in host populations that carry highly prevalent infestations (Rózsa et al., 1996; Pap et al., 2012), where multiple infestations are more likely to occur. In contrast, female-biased sex-ratios characterize scarce infestations, for example, on the peripheries of the geographic distribution (Rózsa et al., 2015) where multiple infestations are rare and thus inbreeding may be strong.

Macroecology

From a macroecological point of view, the distribution, abundance, and richness of lice is very much determined by the host characteristics. The most prominent effect is traditionally called Eichler's rule, a hypothesis that predicts a positive covariation between host diversity and parasite diversity (Eichler, 1942; Vas et al., 2012). Past bottlenecks in host population size often result in long-lasting reductions of louse species richness; this is why birds introduced from Europe to New Zealand harbor fewer species than the same species in Europe (Paterson et al., 1999; MacLeod et al., 2010). In comparisons across species, large-bodied hosts tend to harbor more individuals than smaller ones (Rózsa, 1997b). Colonial host species, living a more social life, do not harbor more lice but the same number of parasites are distributed in a less aggregated (less biased) way than in territorial breeders (Rózsa et al., 1996; Rékási et al., 1997). Bird and mammal species that dive under water to feed tend to host species-poor communities of lice as compared to sister clades (Felső and Rózsa, 2006; 2007).

Transmission

Lice almost exclusively transfer from host to host through bodily contacts between conspecific hosts. Parent-offspring contacts that enable vertical transmission of lice are particularly important for many species. In birds, the evolutionary transitions to brood parasitism caused the loss of this transmission route and, consequently, all brood parasitic clades (for example, cuckoos) host poorer louse communities than their sister clades (Vas et al., 2013). Horizontal transmission often relies on sexual contacts (Hillgarth, 1996), aggression, or other bodily contacts between conspecifics. Some ischnoceran lice often attach to hippoboscid flies for transmission, a phenomenon called phoresy (Keirans, 1975). This is a secondary route of transmission, more often exhibited when the host is diseased or dying, and it likely plays a prominent role in creating non-specific infestations that may accidentally result in host-switches (Harbison et al., 2009).

Effects on Hosts and Role as Vectors

Although most infestations are symptomless, lice may

Figure 1. A lateral view of a female body louse *Pediculus humanus* var. *capitis* as it was obtaining a blood-meal from a human volunteer, who in this case, happened to be the photographer (J. Gathany). Note its elongated abdominal region without any processes and 3 pairs of legs, which are all equal in length and width, features displayed by *Pediculus* members. Source: J. Gathany and F. Collins, 2006. Public domain.

reduce host life expectancy in severe infestations (Brown et al., 1995), reduce avian thermoregulation (Booth et al., 1993), and decrease the sexual attractiveness of their hosts (Clayton, 1990). Lice also play a vector role for several other infections, including *Pediculus humanus humanus* (see Figure 1), transmitting at least 3 potentially lethal human bacterial infections (Raoult and Roux, 1999). Amblyceran and ischnoceran lice may also play a vector role in domestic and wild animals (Clayton et al., 2008), such as the species *Trinoton anserinum* that transmits filarioid juveniles of the heartworm of geese and swans (*Sarconema eurycerca*) (Seegar et al., 1976).

Severe infestations of chewing lice may cause irritation, resulting in restlessness and a loss of sleep. In case of extreme infestations, skin lesions may arise that become the site of secondary infections (Durden, 2019). This is not at all typical in the wild, where most infestations are practically symptomless. In domestic animals, however, such effects may incur losses of millions of US dollars (Kunz et al., 1991) to the poultry, dairy, and leather industries through the decline of egg, milk, meat, and leather production (Durden, 2019).

Host Defenses

Birds and mammals exhibit a variety of immunological, physiological, or behavioral defenses against lice (Clayton et al., 2010; Bush and Clayton, 2018). Grooming behavior, such as preening by the bill and scratching by the legs in birds, as well as scratching by the legs and oral grooming (the alternate use of both teeth and tongue) in mammals, plays a predominant role in defense against lice. Experimentally, impaired grooming not only triggers a dramatic increase in louse populations, but also increases their body size–indicating that preening exerts a strong selection pressure for small body sizes (Murray, 1987; Clayton et al., 1999). Lice exhibit morphological adaptations to resist grooming such as the tibio-tarsal claws of anoplurans and the mandibles of ischnocerans enabling a strong attachment to the hair or feather of hosts. Since birds rely on the visual detection of lice during preening, lice can evolve a camouflage coloration in response to host-imposed selection (Bush et al., 2010). On the other hand, hosts evolve adaptations to improve the efficacy of grooming. Thus the minor bill overhang on the upper mandible of several birds (Clayton et al., 2005), the pectinate claws of barn owls (Bush et al., 2012), the grooming claws (or toilet-claws) of prosimians (Soligo and Müller 1999), or the laterally mobile lower incisors (acting like tweezers) of house mice (Murray, 1987), all exemplify morphological adaptations of hosts.

Blood-sucking insects inject saliva into the wound created by their piercing mouthparts, which contains proteins that manipulate capillary blood flow and suppress host defensive responses. Such proteins provoke immune responses against anopluran lice (Mumcuoglu et al., 1997; Lehane, 2005; Rózsa and Apari, 2012) and apparently also against amblycerans (Møller and Rózsa, 2005) that feed on blood, at least partially.

Birds possess uropygial glands on the rump that secrete a sort of preening oil, and they spread this secretion throughout the plumage during preening. Experimental studies could not unambiguously verify the antiparasitic effect of preen oils in rock pigeons (Moyer et al., 2003); however, comparative studies have shown that the relative size of avian uropygial glands coevolve with the richness of amblyceran lice (Møller et al., 2010).

Contrary to conventional wisdom (see, for example, Post and Enders, 1970), molting does not reduce louse burdens in avian hosts (Moyer et al., 2002), most likely because feather lice (just like feather mites; Pap et al., 2006) avoid adjacent feathers.

Conservation

The human-induced size decline and fragmentation of several host populations necessarily drives many parasite species to extinction due to random population fluctuations (Rózsa, 1992). In spite of this, conservation biologists rarely consider issues about conserving parasite biodiversity (but see Whiteman and Parker, 2005; Tydecks et al., 2018), and this extinction crisis is mostly undocumented (Koh et al., 2004).

At least 6 species of lice (Table 2) are classified as coextinct, that is, they were specific exclusively to hosts that already went extinct and an additional 40–41 species are known to be critically co-endangered, parasitizing critically endangered hosts exclusively. More surprisingly, 4 louse species apparently have gone extinct due to purposeful conservation efforts, specifically, due to the administration of veterinary antiparasitic treatments during captive-breeding and translocation efforts to save endangered hosts (Table 2) (Rózsa and Vas, 2015).

Conversely, some apparently "extinct lice" anecdotes that are widespread in the conservation literature have never been verified. Thus, *Columbicola extinctus* did not go extinct with *Ectopistes migratorius* (the passenger pigeon), because it was also parasitizing *Patagioenas fasciata* (band-tailed pigeon), a bird that is still extant (Clayton and Price, 1999). *Campanulotes defectus* also did not go extinct with passenger pigeons (Price et al., 2000) as was formerly concluded from an erroneous host record. Similarly, the black-footed ferret (*Mustela nigripes*) did not host a separate species of trichodectid louse (Emerson, 1964); thus, it was not extirpated by conservationists, as had been suggested (Gompper and Williams, 1998).

Origins

Lice are phylogenetically embedded within bark lice (superorder Psocodea, order Psocoptera, suborder Troctomorpha, family Liposcelididae (or Liposcelidae)) (Lyal, 1985; Yoshizawa and Johnson, 2003; 2010; Johnson et al., 2004). Free-living bark lice are small-bodied, often wingless insects feeding on fungi, algae, and organic debris. They are not parasitic, although several species inhabit the nests of birds or mammals, including human habitations. They also feed on materials shed from mammals or birds, such as dead skin, loose hair, or feathers, and may even accidentally end up on the pelage or plumage of these animals. This nest-dwelling commensal way of life likely served as a pre-adaptation to the evolutionary shift to ectoparasitism, an event considered as a key innovation that gave rise to the original parasitic lice. Accordingly, from a taxonomic point of view, the order of bark lice is a paraphyletic taxon with respect to parasitic lice.

An early molecular phylogenetic study suggested 2 parallel switches to parasitism and thus the polyphyly of the order of parasitic lice (Johnson et al., 2004). However, more detailed subsequent analyses failed to unambiguously support this hypothesis (Yoshizawa and Johnson, 2010) and later transcriptome data reject the double origin hypothesis in favor of a single origin (Johnson et al., 2018a). The single shift to parasitism might have occurred in relation to mammal, bird, or possibly some reptile hosts (like feathered theropod dinosaurs or haired pterosaurs). The earliest known fossil representing this order is an avian louse (*Megamenopon rasnitsyni*) that dates back to only 44 Ma (= million years ago) (Wappler et al., 2004). Since parasites fossilize poorly (Leung, 2017), the actual switch to parasitism might have occurred much earlier. The major louse suborders radiated before the Cretaceous–Paleogene (K–Pg) boundary 66–65 Ma (Smith et al., 2011) and they further diversified after this boundary (Johnson et al., 2018a; 2018b).

Studies dating the origin and earliest divergences within lice have varied extensively. Using molecular data of a few mitochondrial and nuclear genes, Light and colleagues (2010) estimated the origin of the suborder Anoplura to 75 Ma, with a 95% certainty ("highest posterior density") interval 96–58 Ma.

Table 1: Anopluran lice of main veterinary importance. Adapted from Durden, 2019.

Common name	**Scientific name**	**Host**
Horse louse	*Haematopinus asini*	Equids
Short-nosed louse	*Haematopinus eurysternus*	Cattle
Cattle tail louse	*Haematopinus uadripertusus*	Cattle
Hog louse	*Haematopinus suis*	Swine
Buffalo louse	*Haematopinus uberculatus*	Asiatic buffalo, cattle
	Hoplopleura capitosa	House mice
Tropical rat louse	*Hoplopleura pacifica*	Domestic rats
African blue louse	*Linognathus africanus*	Deer, sheep, goats
Sheep face louse	*Linognathus ovillus*	Sheep
Sheep foot louse	*Linognathus pedalis*	Sheep
Dog sucking louse	*Linognathus setosus*	Canids
Goat sucking louse	*Linognathus stenopsis*	Goats
Long-nosed louse	*Linognathus vituli*	Cattle
Little blue cattle louse	*Solenopotes capillatus*	Cattle

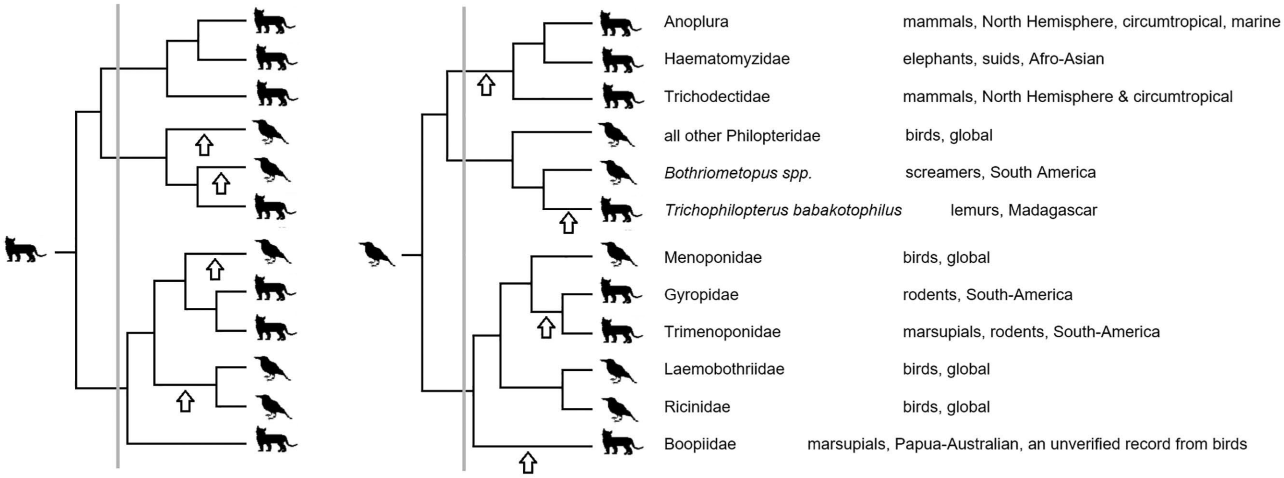

Figure 2. The most parsimonious scenarios for the major host-switches between mammals and birds illustrated along a dendogram represnting a simplified phylogeny of lice. The minimally required major switches are indicated by arrows. The left scenario is based on the presumption that lice originate from a mammal host archetype, the right one is presuming that lice originate from a bird archetype. The vertical gray lines represent the Cretaceous/Paleogene (K–Pg) boundary, but otherwise the graph is not drawn to scale. Source: Adapted from Johnson et al., 2018. License: CC BY-NC-SA 4.0.

More recently, Misof and colleagues (2014) based a phylogenomic analysis on a much greater gene sampling and concluded that parasitic lice began diverging about 53 Ma, well after the emergence of their bird and mammal hosts. However, a similar analysis with many additional taxa (Johnson et al., 2018b) put this date at 171 Ma, while an analysis of genomes (Johnson et al., 2018a) places it at 93 Ma. It is worth noting that the 95% confidence intervals of many of these estimates overlap. In general, it can be reasonably assumed that liposcelid ancestors most probably switched to a parasitic way of life and thus gave rise to the order of parasitic lice sometime during the middle or late Cretaceous, possibly well after the rise of mammals or birds.

Phylogeny

Presuming that their present-day host-range also holds for ancestral lineages, it is expected that the phylogeny of lice should mirror the host phylogeny due to co-speciation events (Fahrenholz, 1913; Hafner and Nadler, 1988). However, the similarity between the 2 trees more often does not exceed the level of similarity expected by chance (see, for example, Weckstein, 2004). This is because other evolutionary events, like parasite extinction or host switching, often eliminate similarity between the 2 trees. Ecological fitting (also known as host switching) is relatively common between closely related and morphologically similar potential host species. In contrast, host switches between taxonomically distant and anatomically dissimilar hosts are very unlikely. However, the likely monophyletic origin and present host-distribution of parasitic lice necessitates at least a few relatively major switches that must have occurred between birds and mammals (Johnson et al., 2018b). Figure 2 illustrates the most parsimonious scenarios of these major switches.

Lice Nuclear Genome

The nuclear genome of lice is the smallest known in any insects, suggesting that the parasitic way of life greatly reduced the size of its genome (Pittendrigh et al., 2006; Kirkness et al., 2010); this could be tested by looking at the genome of the closest relatives of the parasitic lice. The mitochondrial genome structure is extremely variable and complex due to RNA and protein coding gene rearrangements and, particularly in mammal lice, due to subdivision into multiple minichromosomes, and the splits and mergers of these minichromosomes (Cameron et al., 2011; Shao et al., 2017; Yoshizawa et al., 2018; Song et al., 2019). Further, the human head and body louse (*Pediculus humanus*) exhibits an unusual form of meiotic drive, in which the males transmit preferentially or exclusively only their maternally-derived chromosomes (de la Filia et al., 2018). Yoshizawa and Johnson (2013) concluded that selection is more relaxed on phthirapterans and a closely related clade of free-living bark lice than on other comparable bark lice taxa, yielding a more random base composition for both the mitochondrial and nuclear genes. Overall, the inheritance characteristics of louse genomes exhibits a set of unusual and surprising molecular evolutionary processes that often confounds molecular phylogenetic analysis.

Taxonomic Classification

In traditional classifications created for the lice by systematists, these parasites were typically divided into 2 orders according to their different mouthparts, that is, the old names: chewing lice (Mallophaga) and sucking lice (Anoplura). This was practical from a veterinary point of view, but did not reflect their true phylogenetic relationships. In fact, anopluran lice are phylogenetically embedded within a group of chewing lice, the suborder Ischnocera. The numbers of known species given below are only approximate; inconsistencies may arise due to the different species concepts applied by different authors (Mey, 2003).

Suborder Amblycera

Most amblycerans possess heavily sclerotized chewing mandibles forming relatively unspecialized mouthparts, although some taxa partially feed on host blood. Their body size is variable, with adult body length ranging from 1.0 to 11.0 mm.

Family Boopiidae

The 55 extant species of boopiid lice parasitize Australian and New Guinean marsupials. There is an unverified record of a single species, *Therodoxus oweni*, possibly parasitizing a bird species, the New Guinean southern cassowary (*Casuarius casuarius*) (Clay, 1971). *Heterodoxus spiniger*, the louse of the agile wallaby (*Macropus agilis*) in North Australia has secondarily switched to the domestic dog probably in historical times, and achieved a circumtropical distribution mostly on canids and, to a lesser extent, also on other carnivores.

Family Ricinidae

Approximately 110 species of ricinid lice parasitize hummingbirds (family Trochilidae) and small-bodied passerines (order Passeriformes), occurring more scarcely on some medium-sized passerines (perching birds) like thrushes (*Turdus* spp.) and Old World orioles (*Oriolus* spp.). Their adult body size is about 1.6–5.4 mm, relatively large for the small-sized hosts. Prevalence and infestation intensity is typically lower than in menoponid and philopterid lice. Chewing mouthparts are more-or-less modified for piercing the host's skin to enable feeding from a pool of blood caused by tissue laceration (Clay, 1949).

Family Laemobothriidae

This is a small family (20 species) of very large lice, with adult body length ranging between 5.7 and 11.0 mm. Like members of family Ricinidae, *Laemobothrion* spp. lice are also telmophagous (meaning, blood pool feeders). Their host range is more broad compared to other species of lice classified in other families. *Laemobothrion tinnunculi* is widespread on falcons (*Falco* spp.), *L. maximum* on several diurnal raptors (*Accipiter* spp., *Aquila* spp., *Buteo* spp., and *Circus* spp.), and *L. vulturis* on Old World vultures (*Aegypius* spp., *Gyps* spp., etc.) and eagles (*Aquila* spp.). A few more species, forming a separate clade, parasitize mostly moorhens (rails) and coots (order Gruiformes: family Rallidae).

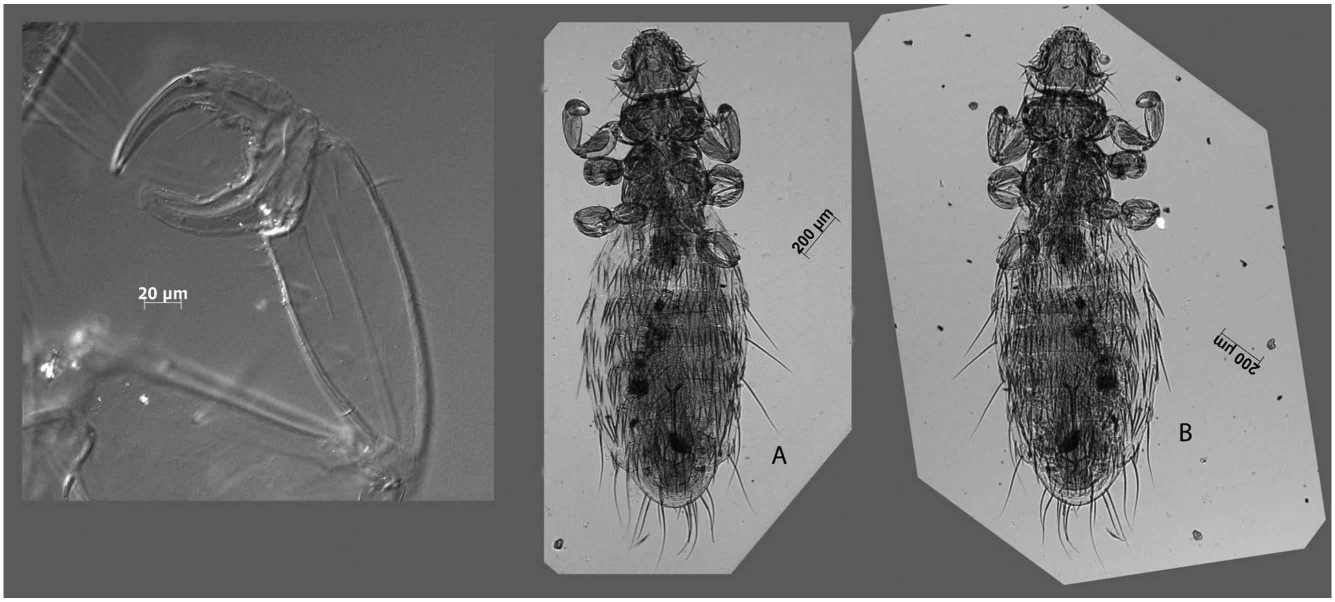

Figure 3. Chewing lice, genus *Phtheiropoios* from rodents of the genus *Ctenomys* collected in Bolivia in the 1980s. Source: S. L. Gardner, HWML. License: CC BY.

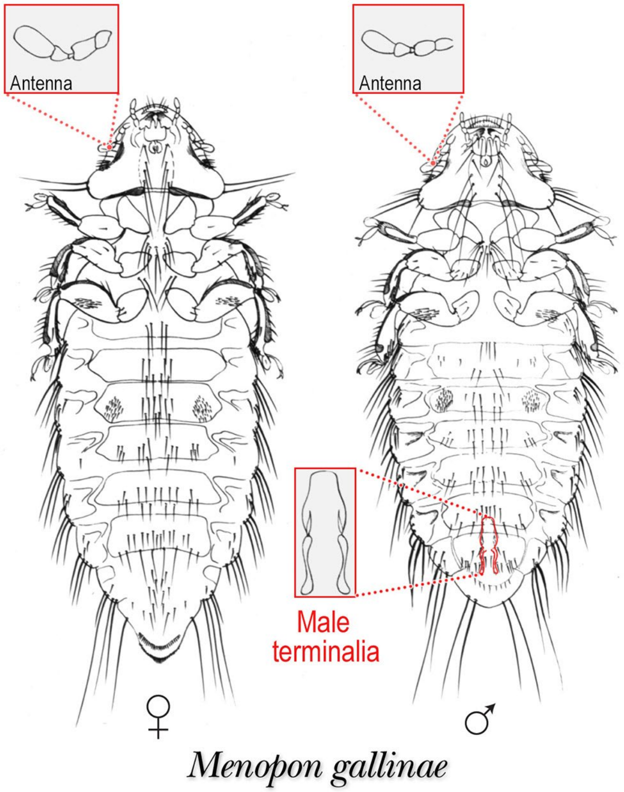

Figure 4. A female and a male *Menopon gallinae* lice revealing the insect's ventral morphology. Source: United States Centers for Disease Control and Prevention, 1975, available at the Public Health Image Library, image 5496. Public domain.

Family Trimenoponidae

Only 18 species constitute this family that parasitize rodents in South America and Central America. *Trimenopon hispidum* is known in veterinary practices as a parasite of the domestic guinea pig (*Cavia porcellus*).

Family Gyropidae

Fewer than 100 species parasitize South American and Central American rodents, with the families of guinea pigs (Caviidae) and degus (Octodontidae) being the most preferred hosts (Figure 3). Only 1 species, *Macrogyropus dicotylis,* is hosted by peccaries (family Tayassuidae). *Gyropus ovalis* and *Gliricola porcelli* are both globally widespread on domestic guinea pigs.

Family Menoponidae

Menoponids occur exclusively on birds, constituting 1 of the 2 most species-rich (> 1,050 species), most prevalent, and abundant families of avian lice (the other being Philopteridae). Several genera are known to feed partially on blood and are capable of causing economic harm to the poultry industry (for example, *Menacanthus cornutus*, *Menopon gallinae* (Figure 4), and *Trinoton querquedulae*) (see, for example, Saxena et al., 1985; 2004; Sychra et al., 2008; Mullens et al., 2010; Kumar and Kumar, 2016; Kumar et al., 2017). The diversity of species in this group appears to be correlated with host defensive capabilities, like T-cell immune responses (Møller and Rózsa, 2005) and uropygial gland size (Møller et al., 2010).

Suborder Ischnocera

The majority of Ischnoceran lice inhabit avian plumage, and only a minority of them live in the mammalian pelage.

Family Philopteridae

Philopterids occur (almost) exclusively on birds. They constitute 1 of the 2 most species-rich (around 2,750 species), most prevalent, and abundant families of avian lice (the other being Menoponidae). However, one species, *Trichophilopterus babakotophilus*, parasitizes lemurs in Madagascar. Philopterids evidently feed on non-living tissues, and when on birds, they most often are found grazing like tiny cows, on the tiny barbs and barbules of plume feathers and on non-living skin fragments. There is little evidence of cospeciation in this group and studies have shown no correlation with speciation and host physiological defenses like a T-cell immune response (Møller and Rózsa, 2005) or uropygial gland size (Møller et al., 2010). On the contrary, they appear to be more strictly affected by mechanical defenses, and preening in particular. To evade preening pressure, it appears that philopterids have evolved morphological adaptations (shape, size, and color) to particular parts of the plumage, and even to major types of feathers.

The shape variability of philopterids is approximately described by applying the guild or ecomorph concepts of ecology. Accordingly, the so-termed body lice, generalist lice, head lice, and wing lice guilds are distinguished. These categories do not represent monophyletic groups but share distinct morphological and behavioral characteristics that have evolved repeatedly along parallel and independent lineages. As indicated by their names, they exhibit characteristically different specificities to particular areas of the host body surface (Johnson et al., 2012; Bush et al., 2016; Clayton et al., 2016). Overall, anatomical site specificity and site segregation appear to be even more pronounced in this group than in other taxa of lice. For example, head lice and wing lice often attach themselves firmly to feather surfaces using their strong mandibles.

The phylogeny of philopterids has not yet been studied in detail, and their systematics is somewhat controversial.

Table 2. Amblyceran and Ischnoceran lice of economical and veterinary importance. Adapted from Durden, 2019.

Vernacular name	Scientific name	Host
Dog louse	*Heterodoxus spiniger*	Dog, other carnivores
Chicken body louse	*Menacanthus stramineus*	Domestic fowl
Domestic fowl Shaft louse	*Menopon gallinae*	Domestic fowl
Goose body louse	*Trinoton anserinum*	Goose
Large duck louse	*T. querquedulae*	Duck
Slender goose louse	*Anaticola anseris*	Goose
Slender duck louse	*A. crassicornis*	Duck
Large turkey louse	*Chelopistes meleagridis*	Turkey
Chicken head louse	*Cuclotogaster heterographus*	Domestic fowl
Fluff louse	*Goniocotes gallinae*	Domestic fowl
Brown chicken louse	*Goniodes dissimilis*	Chicken
Large chicken louse	*Goniodes gigas*	Domestic fowl
Wing louse	*Lipeurus caponis*	Domestic fowl
Slender turkey louse	*Oxylipeurus polytrapezius*	Turkey
Cattle biting louse	*Bovicola bovis*	Cattle
Goat biting louse	*B. caprae, B. limbata*	Goat
Angora goat biting louse	*B. crassipes*	Goat
Horse biting louse	*B. equi*	Horse
Donkey biting louse	*B. ocellata*	Donkey
Sheep biting louse	*B. ovis*	Sheep
Cat biting louse	*Felicola subrostrata*	Cat
Dog biting louse	*Trichodectes canis*	Dog, other canids

Smith (2000) proposed family rank for Heptapsogasteridae and Goniodidae, two putatively basal clades of philopterids that are traditionally included in this family as subfamilies. Both parasitize relatively basal clades of birds. The former is hosted by tinamous (order Tinamiformes) a group of birds that live only in the Neotropical region (from South America, north to the Isthmus of Tehuantepec in Mexico), and the latter is globally widespread on galliform (order Galliformes) birds (such as, turkeys, guinea fowl, and quails) and columbiform (order Columbiformes) birds (such as, pigeons and doves). However, most molecular systematic studies suggest these 2 groups are well embedded within the order Philopteridae (Johnson et al., 2018). Further, the Madagascan lemur louse was also suggested (Cruickshank et al., 2001) to be a representative of a monotypic family ('Trichophilopteridae'), although more recent studies show that it is rather closely related to the genus *Bothriometopus* parasitizing birds, the South American screamers (Anhimidae) (Johnson et al., 2018).

Family Trichodectidae

This family includes around 380 species exhibiting a somewhat erratic distribution across some taxa of mammals. They possess large and heavy mandibles fitted to grasp a hair shaft so as to fix the louse firmly on it. A large proportion of them belong to the genera *Gemyodoecus* and *Thomomydoecus*, within a clade that has undergone an adaptive radiation on North American and Central American pocket gophers (family Geomyidae). This host-parasite system has been serving as a model for cospeciation and coadaptation studies (Hafner and Nadler, 1988; Hafner et al., 1994; Morand et al., 2000) although a recent re-analysis of the data shows that host parasite cospeciation accounts for less than half of the association and there are no data showing reciprocal evolution in these organisms (Brooks et al., 2015). While abundant and species-rich on this particular group of American rodents, they are absent from Old World rodents (Emerson and Price, 1985). Species of several genera parasitize carnivores, hyraxes, and ungulates; some of them (like *Bovicola*) harm domestic mammals, causing considerable economic damage to the dairy and meat industries (Table 2).

Suborder Rhyncophthirina (Elephant and Suid Lice)

The preantennal region of the head bears a long rostrum armed with chewing mandibles, evidently adapted to enable the louse to pierce deeply into the thick skin of the host to feed on the blood pool (telmophagy). The elephant louse (*Haematomyzus elephantis*) is a relatively small-bodied (around 2 mm) parasite of at least 1 species of African elephant (*Loxodonta africana*, the savanna elephant) and also

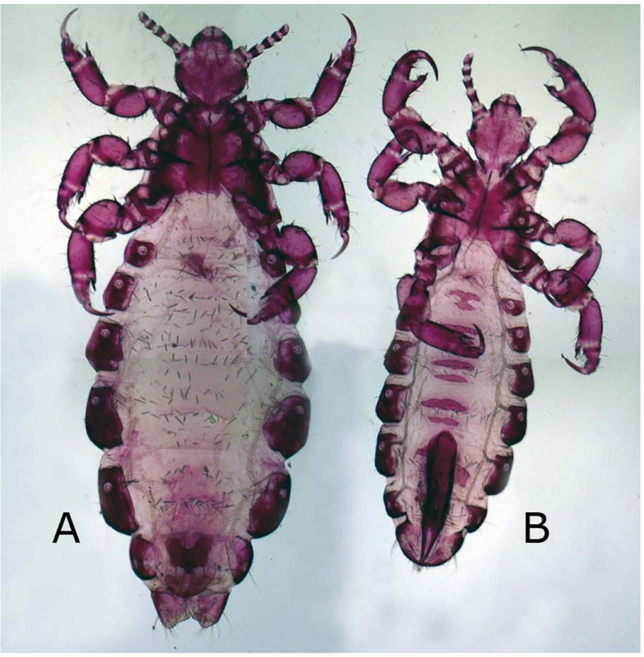

Figure 5. Sucking lice *Pediculus humanus* showing a female (A) and male (B) taken from a human host, preserved in 70% ethanol and stained in Semichon's acetic carmine and mounted in gum Damar. Source: G. Racz, HWML, 2016. License: CC BY.

occurs on *Elephas maximus*, the Asian elephant. It inhabits the hairy regions, and particularly the soft skin folds of the host body, such as the axilla, groin region, ears, neck, and the base of the tail (Sudan et al., 2015). Further, 2 species parasitize African suids (warthogs *Phacochoerus africanus* and *P. aethiopicus* and red river hogs *Potamochoerus porcus*).

Suborder Anoplura: Sucking Lice

Sucking lice occur only on mammals with around 500 known species and are much less diverse than chewing lice. They are more specialized than members of the other groups, but medically their importance and impact on human history are infinitely greater. Two species parasitize humans, *Pediculus humanus* and *Phthirus pubis*, of which *P. humanus* is the more important because it is a vector of rickettesia bacteria. The several species on domestic mammals are of considerable veterinary significance (Light et al., 2010; Kim and Ludwig, 1978).

Morphology

Sucking lice superficially resemble chewing lice, with their small, wingless, flattened bodies, but their heads are narrower than the prothorax. The sucking mouthparts are retracted into the head when the animal is not feeding. Each leg has a single tarsal segment with a large claw, an adaptation for clinging to host hairs. The first legs, with their terminal claws, are often smaller than the other legs, and the third legs and their claws are usually largest. Eyes, if present, are small, and there are no ocelli on the head. Antennae are short, clearly visible, and composed of a scape, a pedicel, and a flagellum that is divided into 3 subsegments. All 3 flagellar subsegments bear tactile hairs, and subsegments 2 and 3 bear chemoreceptors (see Figures 5 and 6) (Bonilla et al., 2013; Slifer and Sekhon, 1980).

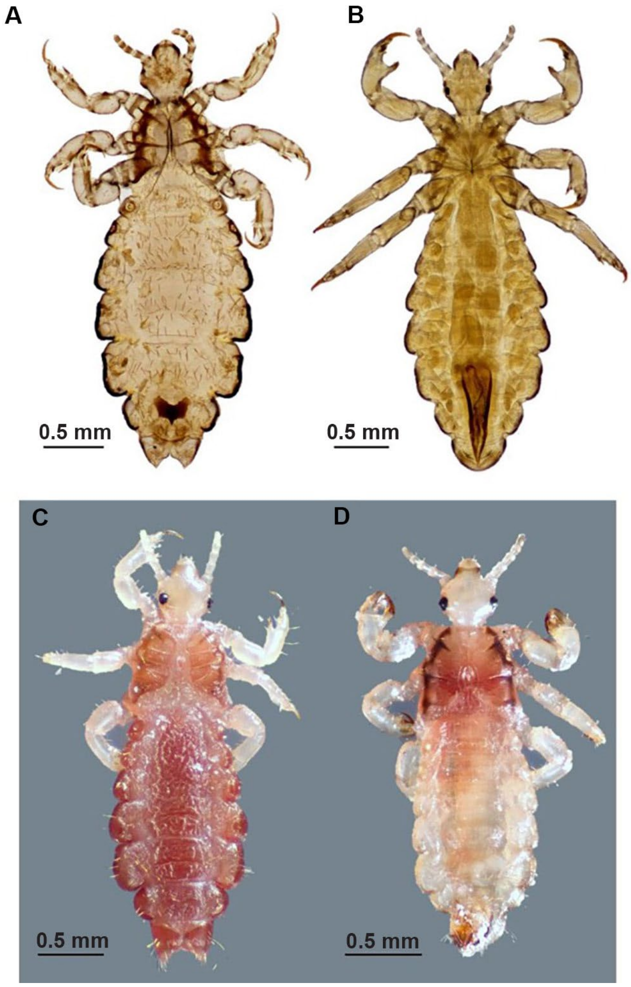

Figure 6. Adult body louse and head lice. A) Ventral view of slide-mounted female head louse; B) ventral view of slide-mounted male body louse; C) dorsal view of ethanol-preserved female head louse; D) dorsal view of ethanol-preserved male head louse. All photographs were taken using a Visionary Digital K2/SC long-distance microscope (from Infinity Photo-Optical Company, Boulder, Colorado, United States). Source: L. Beati, from Bonilla et al., 2013. Public domain.

Mode of feeding

Lavoipierre (1965) distinguished 2 distinct feeding methods used by bloodsucking arthropods. One of these he termed solenophagous (Greek for **pipe** + **eating**) for arthropods that introduce their mouthparts directly into a blood vessel to withdraw blood. The other he called telmophagous (Greek for **pool** + **eating**) for those whose mouthparts cut through the skin and blood vessels to produce and feed from a small pool of blood. Anoplurans are true solenophages (Lavoipierre, 1967). Their proboscis is formed from the maxillae, hypopharynx, and labium, which are produced into long, thin stylets.

The ability of lice (and fleas) to transmit prokaryotic pathogens such as louse-borne typhus caused by *Rickettsia prowazekii* may be due to the way in which they digest blood meals. In contrast to mosquitoes, lice hemolyze erythrocytes rapidly, their blood meals remain liquid, and they lack peritrophic membranes.

Pediculus humanus

Two distinct forms of *P. humanus* parasitize humans: Body lice *P. humanus humanus* and head lice *P. humanus capitis*. Body lice also have been called *P. humanus corporis* and *P. humanus vestimenti*. Common names include cooties, graybacks, and mechanized dandruff. The 2 subspecies are difficult to distinguish morphologically, although they have slight differences (see also Johnson, 2022). The subspecies will interbreed and are only slightly interfertile (Askew, 1971). It seems likely that body lice descended from ancestral head lice after humans began wearing clothes. Body lice are much more common in cooler than in warmer parts of the world; in tropical areas people who wear few clothes usually have only head lice (PAHO, 1973). This difference makes typhus a disease of cooler climates because only body lice are vectors. Curiously, however, head lice can serve as hosts for the typhus causing rickettsia and have a high potential for transmitting it (Murray and Torrey, 1975). Body lice are extremely unusual among Anoplura in that they spend most of their time in their host's clothing, visiting the host's body only during feeding. They nevertheless stay close to the body and are most commonly found in areas where clothing is in close contact. Eggs (nits) of body lice are cemented to fibers in clothes and have a cap at one end that admits air and facilitates hatching (Figure 7). Eggs hatch in about a week, and the combined 3 nymphal stages usually require 8–9 days to mature when they are close to a host's body. Lower temperature lengthens the time of a complete cycle; for example, if clothing is removed at night, the life cycle will require 2–4 weeks. If clothing is not worn for several days, the lice will die. A female can lay 9 or 10 eggs per day, up to a total of about 300 eggs in her life; therefore, she has a high reproductive potential. Fortunately, this potential is usually not realized. It is typical to find no more than 10 lice per host, although as many as a thousand have been removed from the clothes of one person (Pratt and Littig, 1973). Body lice normally do not leave their host voluntarily, but their temperature preferences are rather strict. They will depart when a host's body cools after death or if the person has a high fever. Nevertheless, they travel from one host to another fairly easily, and one can acquire them by contact with infested people in crowded locations such as buses, trains, and schools. Of course, they also may be acquired easily by donning infested clothing or occupying bedding recently vacated by a person with lice. Potential for transmission is highest when people are in crowded, institutionalized conditions, such as some prisons, where sanitation is bad and clothing cannot be changed often.

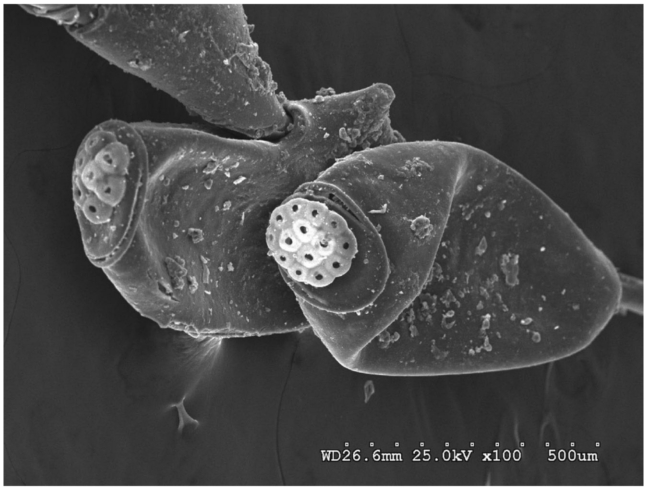

Figure 7. Sucking lice nits (lice eggs) from a mummy. High magnification view of head louse eggs from a South American mummy, 900–1200 CE. Opercula are intact and the pores can be seen. Source: N. Searcey, UNL. License: CC BY.

Head lice tend to be somewhat smaller than body lice: 1.0–1.5 mm for males and 1.8–2.0 mm for females, contrasted with 2–3 mm and 2–4 mm for male and female body lice, respectively (Pratt and Littig, 1973). Nits of both are about 0.8 mm × 0.3 mm. Head lice nits cement to hairs. Lice are usually most prevalent on the back of the neck and behind the ears and they do not infest eyebrows and eyelashes. They are easily transmitted by physical contact and stray hairs, even under good sanitary conditions. As in the case of body lice, however, the heaviest infestations are associated with crowded conditions and poor sanitation (Lindsey, 1993).

Infestation with lice (pediculosis) is not life threatening unless the lice carry a disease organism, but it can subject a host to considerable discomfort. The bites cause a red papule to develop that may exude lymph. Intense pruritis induces scratching, which frequently leads to dermatitis and secondary infection. Symptoms may persist for many days in sensitized people. Years of infestation lead to a darkened, thickened skin, a condition at times called vagabond's disease. In untreated cases of head lice the hair becomes matted together from exudate, a fungus grows, and the mass develops a fetid odor. This condition is occasionally known as plica polonica. Large numbers of lice are found under the mat of hair. *Pediculus humanus* carries symbiotic bacteria, including *Wolbachia* sp. (Covacin and Barker, 2007), some endosymbionts occur in mycetomes, and others have been used in coevolutionary studies of primates and their lice (Allen et al., 2007).

Phthirus pubis

Origin of the common name of this insect, crabs, is evident from its appearance. These lice are 1.5–2.0 mm-long and nearly as broad as long, and the grasping tarsi on the 2 larger pairs of their legs are reminiscent of crabs' pincers. *Phthirus pubis* dwells primarily in the pubic region but it may also be found in armpits, and, more rarely, in beards, mustaches, eyebrows, and eyelashes. *Phthirus pubis* is less active than *Pediculus* spp. and it may remain in the same position for some time with its mouthparts inserted in the skin. Bites can cause an intense pruritis but fortunately do not seem to transmit disease organisms.

Nits cement to hair and the complete life cycle requires less than a month. A female deposits only about 30 eggs during her life. Infestation can occur through contact with bedding or other objects especially in crowded situations, but transmission is characteristically venereal.

Sucking lice as vectors of human disease

Three important human diseases are transmitted by *Pediculus humanus humanus*: Epidemic, or louse-borne, typhus; trench fever; and relapsing fever.

Epidemic, or louse-borne, typhus.

Typhus is caused by *Rickettsia prowazekii*. Rickettsias are bacteria that usually are obligate intracellular parasites. Various species can infect vertebrate and/or invertebrate hosts with effects ranging from symptomless to severe. Epidemic typhus has had an enormous impact on human history, detailed in Zinsser's (1934) classic book Rats, Lice and History. Typhus epidemics tend to coincide with conditions favoring heavy and widely prevalent infestations of body lice, such as pre- and postwar situations, crowding, and mass migration. Mortality rates during epidemics may approach 100%. It is not certain which or how many of the great epidemics throughout human history were caused by typhus but in historical accounts of the decimation of the Christian and Moorish armies in Spain during 1489 and 1490, the role of typhus is clear. In 1528 typhus reduced the French army besieging Naples from 25,000 to 4,000, leading to its defeat, the crowning of Charles V of Spain as Holy Roman Emperor, and the dominance of Spain among European powers for more than a century. The Thirty Years' War can be divided epidemiologically into 2 periods: 1618–1630, when the chief scourge was typhus, and 1630–1648, when the major epidemic was plague. Zinsser contends that between 1917 and 1921, there "were no less and probably more than 25 million cases of typhus in the territories controlled by the Soviet Republic, with from 2.5 to 3 million deaths" (Zinsser, 1934).

Typhus starts with a high fever (39.5 °C to 40.0 °C), which continues for about 2 weeks, and causes backache, intense headache, and often bronchitis and bronchopneumonia. There is malaise, vertigo, and loss of appetite, and the face becomes flushed. A petechial rash appears by the fifth or sixth day, first in the armpits and on the flanks and then extending to the chest, abdomen, back, and extremities. The palms, soles, and face are rarely affected (Olson, 2000). After about the second week, fever drops, and profuse sweating begins. At this point, stupor ends with clearing consciousness, which is followed either by convalescence or by an increased involvement of the central nervous system and death. The rash often remains after death, and subdermal hemorrhagic areas frequently appear.

The disease can be treated effectively with broad-spectrum antibiotics of the tetracycline group and chloramphenicol. Also, although prior vaccination with killed *Rickettsia prowazekii* does not result in complete protection, severity of disease is greatly ameliorated in vaccinated individuals.

Typhus also kills lice. When a louse contracts a rickettsial bacterium along with blood from a human host, the organisms invade the louse's gut epithelial cells and multiply so plentifully that cells become distended and rupture. After about 10 days so much damage has been done to the insect's gut that the louse dies. For several days before its demise, however, the louse's feces contain large numbers of rickettsiae. Scratching louse bites or crushing an infected louse inoculates the host human with typhus organisms from the louse's feces.

A louse's strong preference for normal body temperature causes it to leave a febrile patient and search for a new host, thus facilitating spread of the disease in epidemics. A person can also become infected with typhus by inhaling dried louse feces or getting them in the eye. *Rickettsia prowazekii* can remain viable in dried louse feces for as long as 60 days at room temperature (Harwood and James, 1979). Because infection is fatal to lice, transovarial transmission cannot occur, so humans are an important reservoir host.

Brill-Zinsser diease.

After surviving the acute phase of the disease, humans can be asymptomatic but capable of infecting lice for many years. The disease can recrudesce and produce a mild form known as Brill-Zinsser disease. Flying squirrels *Glaucomys volans* also can be a reservoir host with the infection transmitted by lice *Neohaematopinus sciuropteri* and fleas *Orchopeas howardii* (Sonenshine et al., 1978). Some cases in the United States were probably caused by contact with such animals (McDade et al., 1980). Human and possibly the animal reservoirs could provide the source for a new epidemic. As Harwood and James (1979) point out, "Current standards of living in well-developed countries have largely eliminated the disease there, but its cause lies smoldering, ready to erupt quickly and violently under conditions favorable to it."

Interesting facts: Howard Taylor Ricketts was a football player in college who went to medical school where he encountered an influential teacher, became fascinated with microbial disease transmission, and subsequently devoted his life to research. Tragically, both Ricketts and Stanislaus von Prowazek, the pioneers of typhus research, became infected with typhus and died in the course of their work (Roberts et al., 2012).

Relapsing fever.

The third important disease of humans transmitted by body lice is epidemic relapsing fever which is caused by a spirochete, *Borrelia recurrentis*. Mortality is usually low but the fatality rate can reach more than 50% in groups of undernourished people (Pratt and Littig, 1973). Lice pick up bacteria along with their blood meal, and spirochetes penetrate the insect's gut to reach the hemocoel. They multiply in hemolymph but do not invade salivary glands, gonads, or Malpighian tubules. Therefore, transmission is accomplished only when a louse is crushed by host scratching, which releases the spirochetes. Hence, infectious organisms gain entrance through abraded skin, but evidence also indicates that they can penetrate unbroken skin (Butler, 2000; Kahlig et al., 2021). Louse-borne relapsing fever apparently has disappeared from the United States, but scattered foci are in South America, Europe, Africa, and Asia (Harwood and James, 1979). Frequent epidemics occurred in Europe during the 18th and 19th centuries and major epidemics befell Russia, central Europe, and North Africa during and after World Wars I and II. During the war in Vietnam an epidemic occurred in the Democratic People's Republic of Vietnam (PAHO, 1973).

Clinically, louse-borne relapsing fever is indistinguishable from the tick-borne relapsing fevers that are caused by other species of *Borrelia*. After an incubation period of 2–10 days, the victim is struck rather suddenly by headache, dizziness, muscle pain, and a rapidly-developing fever. Transitory rash is common especially around the neck and shoulders and then extending to the chest and abdomen. The patient is severely ill for 4–5 days, when the temperature suddenly falls accompanied by profuse sweating. Considerable improvement is seen for 3–10 days, and then another acute attack occurs. The cycle may be repeated several times in untreated cases. Antibiotic treatment is effective but complicated in this disease by serious systemic reactions to the drugs. Humans are the only reservoirs and epidemics are associated with the same kind of conditions connected with louse-borne typhus epidemics. The diseases often occur together (Roberts et al., 2012).

Control of Lice

A variety of commercial preparations containing insecticides effective against lice are available. Insecticides (permethrin) may be incorporated into hair care products. In one study of 38,160 patients who used a permethrin rinse for 47,578 treatments, the delousing product proved both safe and effective (Andrews et al., 1992). But in a similar study in Israel 14 different antilouse shampoos varied in their ability to kill both lice and eggs (Mumcuoglu and Miller, 1991). An extensive literature review revealed 1% permethrin creme rinse to be the only chemical treatment virtually guaranteeing at least a 90% cure rate (Vander Stichele et al., 1995). However, permethrin resistance has been reported (Mumucuoglu et al., 1995).

Hot air also kills head lice and nits and in one study a single 30-minute treatment at temperatures slightly cooler than a standard hair dryer eradicated the parasites (Goates et al., 2006). Extensive combing and picking helps to reduce numbers of head lice. Ordinary laundering of garments, including dry cleaning of woolen and other fabrics, will help to control body lice. Devices for large-scale treatment of civilian populations, troops, and prisoners by blowing insecticide dust into clothing are effective and have controlled or prevented typhus epidemics.

Lice on pets and domestic animals can be controlled by insecticidal dusts and dips. Ear tags impregnated with cypermethrin (a synthetic pyrethroid) (James et al., 1990) and slow-release moxidectin injected subcutaneously (Webb et al., 1991) have both been used on livestock. However, acquired resistance to cypermethrin has been demonstrated in laboratory studies (Levot and Hughes, 1990). Several commercially available endectocides (primarily ivermectin, doramectin, and avermectin formulations) also are effective, depending on the dose and delivery method (Campbell et al., 2001).

Normal, healthy mammals and birds usually apply some natural louse control by grooming and preening themselves. Poorly nourished or sick animals that do not exhibit normal grooming behavior often are heavily infested with lice.

Many species of passerine birds show an interesting behavior known as anting that may represent another natural method of louse control. The bird settles on the ground near a colony of ants, allowing the ants to crawl into its plumage, or it picks up ants and applies them to the feathers. The bird uses only ant species whose workers exude or spray toxic substances in attack and defense but do not sting. Ants in 2 subfamilies of Formicidae either spray formic acid or exude droplets of a repugnant fluid from their anuses (Simmons, 1966). The worker ants liberally anoint the feathers with noxious fluids. Significant numbers of dead and dying lice have been found in the plumage of birds immediately after anting.

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