Insect Systematics and Diversity, 2025, **9(5)**, ixaf034
DOI: https://doi.org/10.1093/isd/ixaf034
Review

Phthiraptera systematics: past, present, and future

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Subject Editor: Dr. Hojun Song

Abstract

Parasitic lice (Psocodea: Phthiraptera) are small, wingless parasites of birds and mammals that have been at the forefront of coevolutionary studies since the 1990s, and at the forefront of human–insect interactions since the dawn of humankind. Despite this, an unfortunate overreliance on a co-radiation model of evolution between lice and their hosts ("Fahrenholz's Rule") has left a muddled legacy in their classification and taxonomy. In recent decades, the classifications of lice at the order, suborder, family, genus, and species levels have all been examined by a mixture of morphological, genetic, and genomic data, which have challenged many traditional taxon limits and relationships. Here, we discuss the traditional classification of parasitic lice, the data that challenged it, and our current understanding of the group. We give an overview of the morphological characters that identify the major radiations of lice, and point out a number of areas that need further work.

Keywords: phthiraptera, systematics, chewing lice, sucking lice

Introduction to Louse Biology

The word "louse" conjures up unpleasant childhood memories and perhaps the study of lice is revolting to outsiders. In fact, Henry Denny, one of the earliest researchers of parasitic lice, mentioned that while writing his monograph (Denny 1842) he was often asked "Why not take up some more interesting or popular department of Entomology?" Denny countered that "to render any service to science, [we] must not consult popular taste or ephemeral fashion, but [we] must take a page from that great Book of Nature, less generally read, and consequently, less understood and appreciated by the world at large." These are sentiments to which we, living 180 years later, can add little.

Parasitic lice (order Psocodea, infraorder Phthiraptera) constitute a relatively small group of small, wingless insects parasitic on either mammals or birds. Phthiraptera has historically been divided into 2 groups based on mouthparts used for feeding: chewing lice (biting mouthparts) and sucking lice (piercing mouthparts). Although these groups are no longer recognized formally, these terms are still used informally, with sucking lice consisting of the parvorder Anoplura and chewing lice represented by the parvorders Amblycera, Ischnocera, Rhynchophthirina, and Trichodectera.

Parasitic lice derive virtually all their nutrition from their hosts. There are 2 main food types utilized by parasitic lice, blood or epidermal associated materials such as skin cells, feathers, and glandular secretions. Sucking lice (Anoplura) and some chewing lice (Amblycera and Rhynchophthirina) have specialized mouthparts that allow them to pierce or chew the host's skin and drink blood. In contrast, the remaining chewing lice (Amblycera, Ischnocera, and Trichodectera) use their mouthparts to feed primarily on skin and feathers or fur. Occasional reports of mite pieces in louse guts (Oniki and Butler 1989) suggest lice may have some degree of feeding flexibility,

Received: 9 September 2024. **Revised:** 20 April 2025. **Accepted:** 14 August 2025

but the commonality of this behavior is unknown. These lice typically obtain water from water vapor (Rudolph 1983), although some lice are known to drink liquids from the host's eyes (Mey 2013).

The gross morphology of lice varies among groups, but in general lice have reduced morphology compared to free-living insects. Antennae never have more than 5 segments, the number of distinct mouthparts is reduced, and eyes are very small or absent. The number of thoracic and abdominal segments differs between (and sometimes within) parvorders through fusion of segments. The external male genitalia are often rather simple, and all female lice lack true ovipositors. The legs of lice are also simple, and distal segments may be much reduced in some groups, but are highly modified in Anoplura (see below).

Without exception, lice lack free-living stages. Mating and egg-laying occur on the host, and all lice go through 3 nymphal stages before reaching adulthood. The generation time of lice is generally 1–1.5 months, and each female typically lays around 10 eggs during its lifetime. Mating may be very fast, but time spans from 10–15 s to 10–40 h have been recorded (Schmutz 1951, Agarwal 1967); the longer time spans probably include long periods of mate guarding (Villa et al. 2019). Movements of lice between hosts are generally limited to instances where 2 hosts come into direct contact, although exceptions to this are known (eg. Bartlow et al. 2016). For many groups of lice, limited transmission has, over time, resulted in high levels of host specificity, often correlated with patterns of co-speciation.

Interactions With Hosts

Lice may harm their host in several ways. Feather-feeding lice consume the fluffy portion of the abdominal contour feathers reducing their insulative properties. Heavily infested birds experience thermoregulatory stress (Booth et al. 1993), which leads to reduced mating success (Clayton 1990, David and Heeb 2009) and reduced survival (Clayton et al. 1999). Blood feeding lice take small meals but heavy infestations of lice can cause irritation, weight loss, and severe anemia (Marshall 1981, Wikel 1996, Durden 2001, Clayton et al. 2008, Light et al. 2010). In addition, blood feeding lice can vector harmful parasites and pathogens (Durden 2001, 2005, Clayton et al. 2008) and some lice vector heartworm nematodes (eg. Herzog et al. 2024). Most notoriously, human body lice (Anoplura: *Pediculus humanus*) vector bacteria that cause trench fever, relapsing fever, and epidemic typhus (Raoult and Roux 1999). During and after World War I, epidemic typhus infected 25 million people in eastern Europe and Russia, killing as many as 3 million people in some estimates (Bechah et al. 2008). Furthermore, human body lice may have contributed significantly to the spread of plague throughout human history (Barbieri et al. 2020).

Anti-parasite behaviors are the first defenses that birds and mammals deploy against lice. Initially, the selection of parasite-free mates or avoidance of other infected individuals may prevent infestation (Hillgarth 1996, Darolova et al. 2001, Beltran-Bech and Richard 2014). Once infested, grooming is the primary defense against these ectoparasites. Although grooming takes a considerable amount of time and energy (Hart et al. 1992, Mooring et al. 2004, Bush and Clayton 2023), grooming is incredibly effective, allowing most individuals to keep their louse loads to low, chronic, levels. Birds groom themselves by preening with the bill and scratching with the feet (Bush and Clayton 2018, Goodman et al. 2020; Fig. 1A). Most birds have a small overhang at the tip of their bill that is used to crush and remove lice from the plumage; if this overhang is removed or damaged on a host, its louse populations increase dramatically (Clayton et al. 2005). Mammals groom their pelage with their teeth and tongue or groom with their feet and hands (Hart 1994). Many hosts engage in other behaviors such as allogrooming, sunning, dusting, and anting, which may help

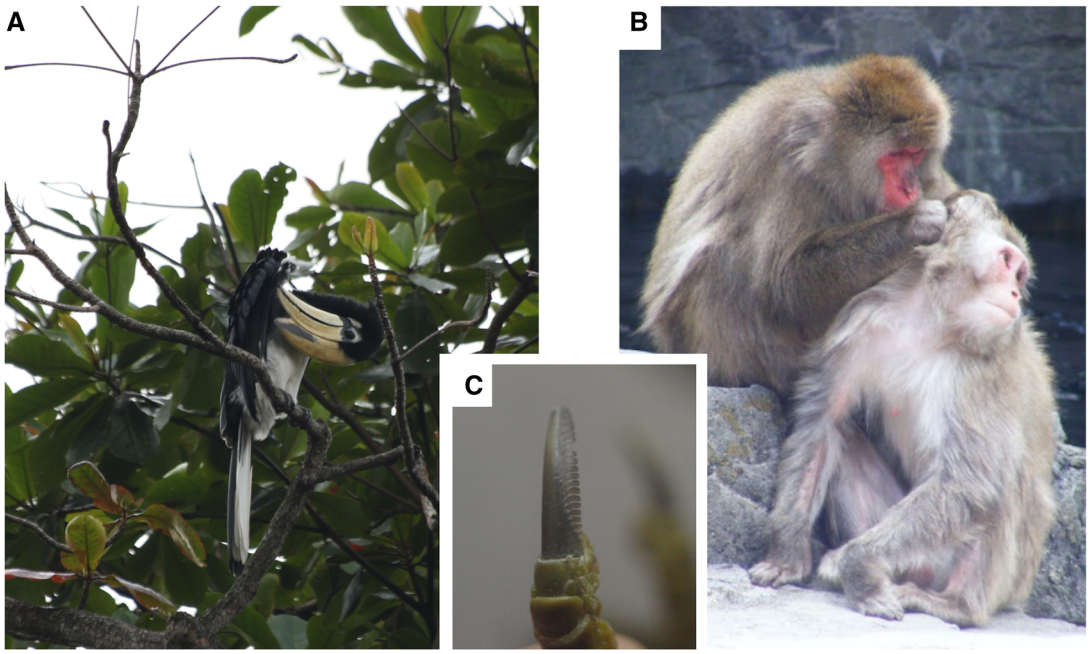

Fig. 1. Anti-parasite behaviors of hosts. A) Asian pied hornbill preening, photo by DRG. B) Japanese macaques allogrooming, photo by Mamorita (CC BY-SA 2.0). C) Pectinate claw of black-crowned night-heron, photo by DRG.

control ectoparasites such as lice (Zamma 2002, Bush and Clayton 2018; Fig. 1B). In addition, some birds scratch with comb-like claws, although it is not known if these "pectinate" claws aid in the removal of ectoparasites (Waller et al. 2024; Fig. 1C).

Birds and mammals also have immunological defenses that combat blood feeding lice (Wikel 1996, Lehane 2005, Møller and Rózsa, 2005, Owen et al. 2010). Immunological defenses may result in tradeoffs between physiological processes such as parasite defense and reproduction (Manjerovic and Waterman 2012). Behavioral and immunological defenses are not entirely independent; blood feeding parasites often cause itching, which triggers grooming behaviors directed at body regions infested by parasites (Durden 2001, Waite et al. 2014, Duboscq et al. 2016). In turn, grooming behaviors such as scratching can cause upregulation of immune responses (Mack and Kim, 2018).

Community Ecology

Hosts are home to communities of ectoparasites. Birds and mammals are often co-infested with several species of lice, as well as other ectoparasites such as fleas, flies, mites, and ticks. The host infested by the most species of lice is the little tinamou (*Crypturellus soui*); 20 species of lice (including Ischnoceran and Amblyceran) are known to parasitize this host species (Price et al. 2003), and 9 species were found co-infesting a single individual (Ward 1957)!

Co-infested hosts provide opportunities for parasites to interact with each other. Some of these interactions benefit the lice; for example, co-infestation of lice and hippoboscid flies provide opportunities for lice to hitchhike and disperse phoretically to new hosts (Bartlow et al. 2016; Fig. 2). Lice may also avoid each other by partitioning the microhabitat on the host (eg. pocket gopher trichodecteran lice belonging to the genera *Geomydoecus* and *Thomomydoecus*; Fig. 3). However, ectoparasites can also have negative effects on each other. For instance, in rock pigeons (*Columba livia*) co-infested with the ischnoceran body louse *Campanulotes compar* and the ischnoceran wing louse *Columbicola columbae*, *C. compar* is the superior competitor, inhibiting the size of *C. columbae* populations and influencing the distribution of *Columbicola* on the bird's body (Bush and Malenke 2008); however, the nature of this interaction is mediated by host defense. Lice also compete with other ectoparasites; for example, the amblyceran *Menacanthus stramineus* can competitively exclude northern fowl mites (*Ornithonyssus sylviarum*); competition between these parasites is also mediated by host defense (Chen et al. 2011).

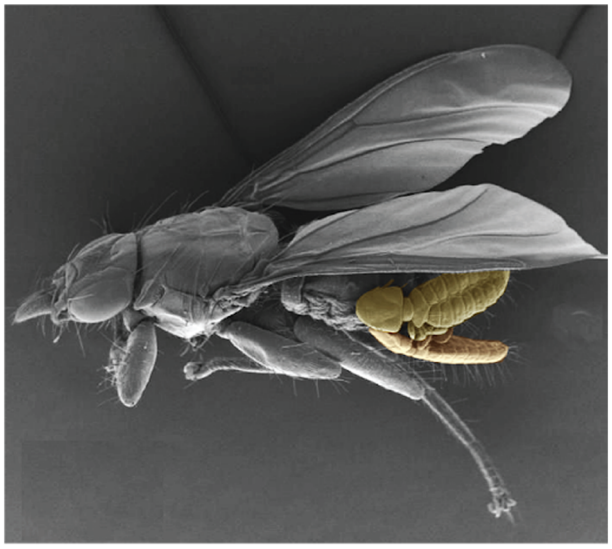

Fig. 2. Phoretic *Brueelia* sp. (colored) hitching a ride on a hippoboscid fly. Fly collected from a blackbird, *Turdus merula*. Photo by V. S. Smith; Specimen Image Database.

Competition has likely been an important factor in the adaptive radiation of lice. In many ways, lice appear to follow a pattern similar to that of Caribbean anoles (*Anolis* spp.). Over macroevolutionary time, anoles diversified across the Caribbean as they evolved in isolation on different islands, and subsequent colonization of islands with resident anoles led to competition and character displacement between species (Losos et al. 1998). This pattern of repeated colonization and character displacement led to the convergent evolution of similar forms, or "ecomorphs" on the different islands (Losos 2011). Likewise, lice have colonized and re-colonized hosts, and most ischnoceran lice appear to be distinct "ecomorphs" that are associated with particular microhabitat niches (Fig. 3). Although many ischnoceran genera do not fall clearly into any ecomorph, these ecomorphs have evolved convergently multiple times (Johnson et al. 2012), and closely related louse genera may often include representatives of several ecomorphs. Competition with resident species, in addition to evolution to avoid host defense may help to explain the repeated evolution of distinct louse ecomorphs (Johnson et al. 2012, Clayton et al, 2016; Fig. 3). For instance, "wing lice" are long and slender, fitting into the interbarb-space on flight feathers, "head lice" of birds have broad, typically triangular, heads and strong jaw muscles likely aiding them in remaining attached when the host scratches (Kolencik et al. 2024a). The distinct morphology of typical "body lice" of birds, with rounded heads and bodies, is not as obviously associated with a defense mechanism, yet this form appears repeatedly among distantky related louse genera. More research is needed to elucidate the adaptive function of this louse ecomorph.

Biogeographic Patterns

To a large extent, the geographical distribution of a louse species mirrors that of its host(s). However, not all louse species associated with a host species are found on all host populations (Fig. 4). Partially, this is due to historical sorting events (Boyd 1951, Paterson et al. 1999, Jarayseh et al. 2023; Fig. 4B). For example, insular hosts often have less speciose louse faunas than mainland populations of the same host (Literák et al. 2015, Oslejskova et al. 2020), and this pattern may also apply to fragmented habitat patches on the mainland (Bush et al. 2013; Fig. 4C). It is also rare for a host species to be examined for lice across its entire geographic distribution. Therefore, for many louse species, the extent of their geographic distributions may be greater or smaller than that of their hosts.

The external environment may also affect the geographic distribution of louse communities. For instance, hosts with wide ranges may harbor different louse communities in drier versus more humid parts of their range (Bush et al. 2009, Malenke et al. 2011, Gustafsson and Zou 2020; Fig. 4D). Some louse genera appear to be better adapted to humid or dry areas, and may occur on hosts in such regions regardless of the phylogenetic relationships of the hosts (Gustafsson and Bush 2019,

Fig. 3. (Left) Pocket gophers are commonly infested with different species of chewing lice (eg. *Geomydoecus* sp. and *Thomomydoecus* sp.) which are morphologically similar, yet exhibit dorso-ventral microhabitat partitioning consistent with interspecific competition (Reed et al. 2000, Clayton et al. 2016). (Right) Ischnoceran louse ecomorphs have evolved convergently: "head lice" have oval bodies with large, triangular heads; "wing lice" have long slender bodies, and long legs; "body lice" have oval bodies and round heads (Johnson et al. 2012). Niche overlap between lice of different ecomorphs varies between host systems. (Photos: Botta's pocket gopher by V.J. Anderson and Major Mitchell's Cockatoo by J.J. Harrison, CC BY-SA 4.0).

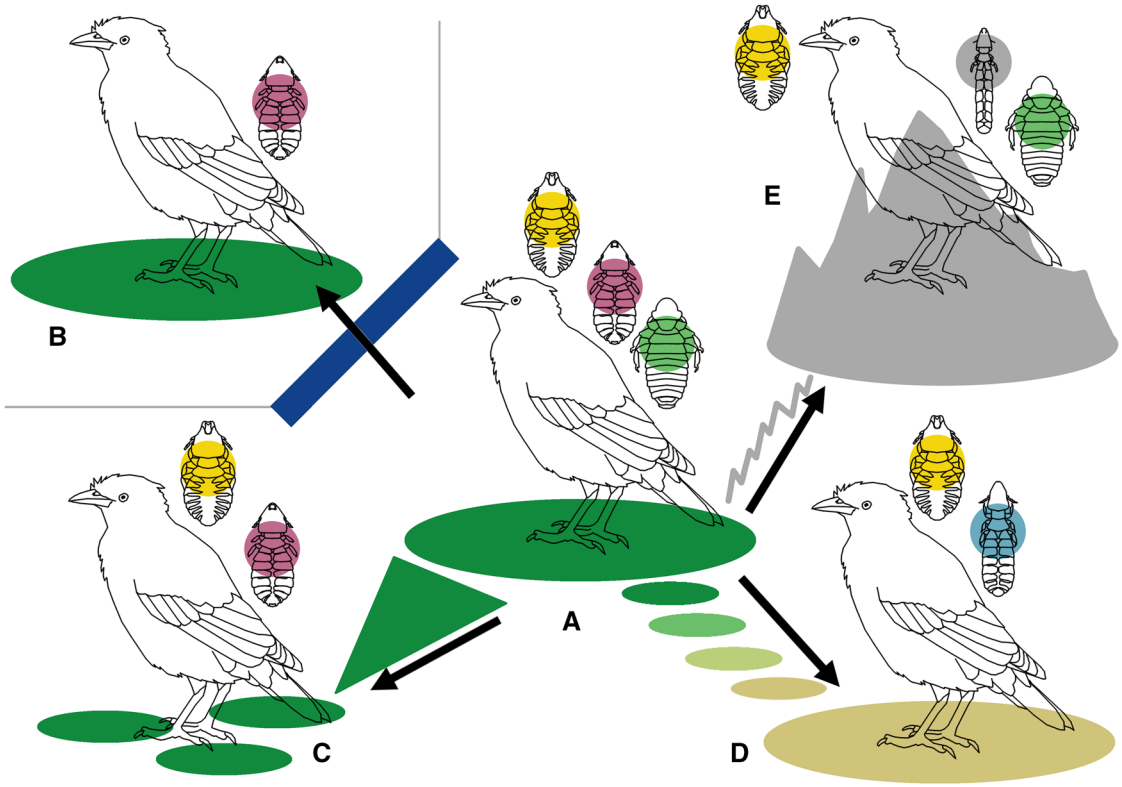

Fig. 4. Schematic overview of processes that affect louse biogeography. In A) a bird species living in a humid lowland environment is parasitized by 3 louse species. In B) a bird has dispersed across a biogeographic barrier to a new region, and in the process lost 2 of its associated louse species (yellow, green). In C) the available habitat for the bird has fragmented, leading to a diminished louse community (losing green). The same bird species living in more arid areas in D) has lost 2 humidity-adapted lice (red, green) but gained an aridity-adapted louse (blue). Similarly, the same bird species living at higher altitudes of E) has gained a louse common at high altitudes (gray), but lost one louse that is more common at lower altitudes (red).

Takano et al. 2019). Similarly, some louse genera appear to be associated with higher elevantions, which may be driven by correlated changes in humidity, temperature, or oxygen levels (Gustafsson et al. 2022, 2024a; Fig. 4E). Such broad-scale patterns are poorly studied for almost all groups of lice, and may be complicated by the presence of unrecognized cryptic diversity in many widely distributed louse groups (eg. Light and Hafner 2007a; Escalante et al 2016).

Major Louse Taxonomists

Louse taxonomists may be said to belong to 1 of 2 "lineages," defined by mutual collaborations (research visits, specimen loans, co-authorships) and general outlook on louse classification and taxonomy. Here, we discuss these lineages as the "German" and "Anglo-American" lineages, but neither group is really that narrowly defined, nor are these lineages mutually

exclusive. Most louse taxonomists have been at least loosely associated with one of these 2 main lineages, but research on lice was also started independently by researchers in other regions of the world: for example, Japan by S. Uchida (1884–1975), Russia by D.I. Blagoveshtchensky (1901–1995) and E.F. Sosnina (1911–after 1994), Brazil by F.L. Werneck (1894–1961) and L.R. Guimarães (1908–1998), China by T.H. Chin (dates unknown), Argentina by A.C. Cicchino (1951–present) and D. del Carmen Castro (1947–present), and in New Zealand by R. L. C. Pilgrim (1921–2010) and R.L. Palma (1948–present).

The "German Lineage"

von Linnaeus (1758) was the first to formally describe species of parasitic lice, with a total of 24 species included in his *Systema Naturae* (Clay and Hopkins 1950), including 2 of the 3 currently recognized taxa that parasitize humans. However, louse taxonomy really started with C.L. Nitzsch (1782–1837), who first separated lice into groups roughly corresponding to major divisions used today. Nitzsch was the first researcher since pre-Linnaean times to make lice his special field of interest, but unfortunately, however, he died before his monograph could be published. His collection and unpublished manuscripts were later published by K.H.K. Burmeister (1807–1891) and C.G.A. Giebel (1820–1881), who provided names and descriptions for the majority of known lice at the time. Nitzsch's louse collection, located in Halle, Germany, was largely destroyed in World War II, but parts of it remain, and were later studied by for example, S. von Kéler (1897–1967).

In the early 20th century, G. Enderlein (1872–1968) and H. Fahrenholz (1883–1945) were, together with von Kéler among the most important louse researchers in Germany. However, after World War II, louse research in Germany was divided in 2 parts, with louse research in Eastern Germany and much of the Warsaw Pact countries dominated by W. Eichler (1912–1994). Eichler championed parasitology and louse research through an almost unbelievable diversity of publications aimed at all parts of society, particularly in the journal Angewandte Parasitologie, which he founded in 1960. His passion for all aspects of louse biology shines through strongly in his work, and helped to inspire numerous researchers in Eastern Europe, above all his student, J. Złotorzycka (1926–2002). In contrast, several West German louse researchers such as G.A.F. Timmermann (1908–1979) and H. Klockenhoff (1937–1984) worked more closely with researchers in the United Kingdom and the United States.

The "Anglo-American Lineage"

The Anglo-American lineage originated with H. Denny (1803–1871), whose collection was deposited in London, where it eventually merged with one of the largest collections of the 19th century, that of E. Piaget (1817–1910), containing lice from around the world. Simultaneously, large and important early collections, now largely stored in the United States, were amassed by V.L. Kellogg (1867–1937) and M.A. Carriker (1879–1965), including extensive collections from North and South America. Other early researchers in this lineage include B.F. Cummings (1889–1919), G.B. Thompson (1911–1979), and J. Waterston (1879–1930) in London, as well as the Australian L. Harrison (1880–1928), who published the first significant global checklist of lice (Harrison 1916), attempting to summarize the knowledge to that point.

The London part of this lineage really took off when T. Clay (1911–1995) started publishing on lice, initially with G.H.E. Hopkins (1898–1973). The importance of Clay for our current understanding of the taxonomy, classification, and morphology of lice cannot be overstated. Above all, her patient work in identifying and redescribing lice named by early researchers, clarifying morphological terminology, and together with Hopkins writing the first critical checklist of chewing lice (Hopkins and Clay 1952), has been foundational to modern louse classification. Hopkins (1949) also provided the first world checklist of host associations for lice parasitizing mammals. Moreover, Clay extensively supported the development of louse taxonomy in parts of the British Commonwealth, not least in India. For instance, M.A.R. Ansari (1911–1979), one of the most important early Indian louse researchers, worked closely with Clay at the Natural History Museum, and Clay provided specimens for publications by B.K. Tandan (1921–2004) and his collaborators on Asian lice. Both J.L. de S. Tendeiro (1916–1991) and J.A. Ledger (1942–present), whose main focuses were on African lice, also collaborated extensively with Clay. The collection in London paved the way for the research of C.H.C. Lyal (1952–present) and many others.

In the United States, louse taxonomy became the focus of several prolific researchers, including H.E. Ewing (1883–1951), G.F. Ferris (1893–1958), P.T. Johnson (1926–present), and K.C. Kim (1934–present), all of whom worked primarily with sucking lice. Of these, Ferris was the most prolific sucking louse taxonomist having described 8 new genera and 93 new species (Ferris 1951, Durden and Musser 1994a). From the 1950s onwards, R.E. Elbel (1925–2005), K.C. Emerson (1918–1993), and R.D. Price (1929–2024) often collaborated to describe lice from all parts of the world. In particular, Price was important in his tireless work to revise almost all large amblyceran genera, and several ischnoceran genera, over a period of over 55 years, giving him the distinction of being the person who has described the most species of lice to date (583 valid species and subspecies). Many of the most prominent chewing louse researchers today, including several of the authors of this manuscript, started out working with Price.

Current Classification

In the 1800s, parasitic lice were placed in 2 separate insect orders based on the morphology of their mouthparts: Anoplura Leach, 1815 (sucking lice) and Mallophaga Nitzsch, 1818 (chewing lice). This classification persisted into the 1980s, but Hopkins (1949) and others recognized that these 2 groups of lice were morphologically similar and proposed combining Anoplura and Mallophaga into a single order, Phthiraptera Haeckel, 1896. Gradually, this single order of parasitic lice with 4 separate suborders (Anoplura and 3 chewing louse suborders, Amblycera Kellogg, 1896; Ischnocera Kellogg, 1896; and Rhynchophthirina Ferris, 1931) was accepted by most authors.

The close relationship between parasitic lice and nonparasitic book lice (Psocoptera) has been recognized for decades. The most recent classifications have further modified the taxonomic status of parasitic lice by placing them within the order Psocodea. Based on phylogenomic analyses, de Moya et al. (2021) recognized 3 suborders within the Psocodea, including the suborder Troctomorpha, within which are 4 book louse infraorders and the infraorder Phthiraptera, which includes 5

parvorders of parasitic lice (Amblycera, Anoplura, Ischnocera, Rhynchophthirina, Trichodectera; Song et al. 2019; Table 1). This classification recognizes parasitic insect lice as being monophyletic and places the 3 groups of lice that solely parasitize mammals phylogenetically close to each other.

Amblycera Kellogg, 1896

Amblyceran lice parasitize birds and mammals. The most thorough definition and discussion of Amblycera was published by Clay (1970), who listed over 10 morphological characters defining Amblycera, although many of these are internal or variable among subgroups. The only universal synapomorphies that can readily be seen without dissection are: (1) antennae with 4–5 segments, including a pedunculate third segment (flagellomere I), are not visible from the dorsal surface because they are situated in lateral grooves of head; and (2) long and filiform maxillary palp present, often projecting beyond head margin. Examples of 2 amblyceran lice are in Fig. 5.

Table 1. Current classification and number of species of the 5 parvorders of Phthiraptera

Parvorder	Family	#Species
Amblycera Kellogg, 1896	Boopiidae Mjöberg, 1910	55
	Gyropidae Kellogg, 1896	96
	Laemobothriidae Mjöberg, 1910	20
	Menoponidae Mjöberg, 1910	1264
	Ricinidae Neumann, 1890	118
	Trimenoponidae Harrison, 1915	18
Anoplura Leach, 1815	Echinophthiriidae Enderlein, 1904	13
	Enderleinellidae Ewing, 1929	56
	Haematopinidae Enderlein, 1904	21
	Hamophthiriidae Johnson, 1969	1
	Hoplopleuridae Ewing, 1929	200
	Hybophthiridae Ewing, 1929	1
	Linognathidae Webb, 1946	71
	Microthoraciidae Kim and Ludwig, 1978	4
	Mirophthiridae Chin, 1980	1
	Neolinognathidae Fahrenholz, 1936	2
	Pecaroecidae von Kéler, 1963	1
	Pedicinidae Enderlein, 1904	20
	Pediculidae Leach, 1817	2–4[a]
	Polyplacidae Fahrenholz, 1912	202
	Pthiridae Ewing, 1929	2
	Ratemiidae Kim and Ludwig, 1978	3
Ischnocera Kellogg, 1896	Goniodidae Mjöberg, 1910	305
	Heptapsogasteridae Carriker, 1936	194
	Philopteridae Nitzsch, 1818	2579
Rhynchophthirina Ferris, 1931	Haematomyzidae Enderlein, 1904	3
Trichodectera Song et al. 2019	Trichodectidae Kellogg, 1896	382

Data for the Amblycera, Ischnocera, Rhynchophthirina, and Trichodectera are derived from Price et al. (2003), but updated with species described 2003–2023 (Gustafsson et al., in prep.). Data for Anoplura are derived from Durden and Musser (1994a) with updated families, genera, and species since 1994.
[a]The species status of some species differs among authorities.

Clay (1970) recognized 6 families within Amblycera: Boopiidae Mjöberg, 1910, Gyropidae Kellogg, 1896, and Trimenoponidae Harrison, 1915, mainly on mammalian hosts, and Laemobothriidae Mjöberg, 1910, Menoponidae Mjöberg, 1910, Ricinidae Neumann, 1890 on avian hosts. This classification is generally accepted today (Price et al. 2003), although genomic data analyzed by Najer et al. (2024) places Trimenoponidae inside Gyropidae; this placement may also have morphological support (Clay 1970). Almost 75% of all amblyceran species and genera are placed in Menoponidae (Price et al. 2003). The characters that Clay (1970) used to define the different families have a mosaic distribution, and none are both universal within Menoponidae and exclusive to that family. The combination of the following characters separates the Menoponidae from other families: (1) pro-, meso-, and metanota separate, and metanotum separate from abdominal tergopleurite I; (2) labial palp with 5 distal setae; (3) subocular comb row present; (4) "anal corona" present in females (but secondarily lost in some species).

There are approximately 1,600 described species of amblyceran lice. By far the most speciose genus of amblyceran lice is the menoponid genus *Myrsidea*, which currently comprises around 400 species (Kolencik et al. 2024b); however, there are estimates that the diversity of this genus may be more than twice as high in Brazil alone (Valim and Weckstein 2013), and the global diversity of this genus likely numbers in the thousands. Gustafsson et al. (2025) estimated that the global diversity of Amblycera may be around 16,000 species.

Anoplura Leach, 1815

All members of Anoplura parasitize mammals. Anopluran synapomorphies include a head narrower than the thorax and sucking mouthparts that retract into the head when not being used for blood feeding. Antennae are short, 3–5 segmented, and protrude laterally from the head. Legs in all developmental stages terminate in unique, highly specialized, tibio-tarsal claws, with opposable elements that securely grasp the hairs of their host. The gap formed inside the closed tibio-tarsal claws often correlates with the host hair diameter for host-specific sucking lice. Almost all sucking lice have a prominent thoracic sternal plate and adults can have an array of sclerotized sternal, tergal, and/or paratergal plates. Examples of 2 anopluran lice are shown in Fig. 6.

Based mostly on morphology, 16 families, 51 genera, and 597 species of sucking lice are currently recognized. Fifteen anopluran families were recognized by Kim and Ludwig (1978) and Durden and Musser (1994a), but Chin (1998) recognized a 16th family, the monotypic, and morphologically aberrant, Mirophthiridae. Kim and Ludwig (1978) recognized 42 anopluran genera, Durden and Musser (1994a) recognized 49 genera and another 2 genera have been described since then (Durden and Webb, 1999, Durden et al. 2024). The family Polyplacidae, as currently recognized, includes ~20 genera, and family placement of some of these genera may require revision.

By far the 2 most speciose groups of sucking lice are the hoplopleurid genus *Hoplopleura* (177 species) and the polyplacid genus *Polyplax* (81 species) although the enderleinellid genus *Enderleinellus* (46 species), the linognathid genus *Linognathus* (53 species), and the polyplacid genus *Neohaematopinus* (31 species) are also diverse.

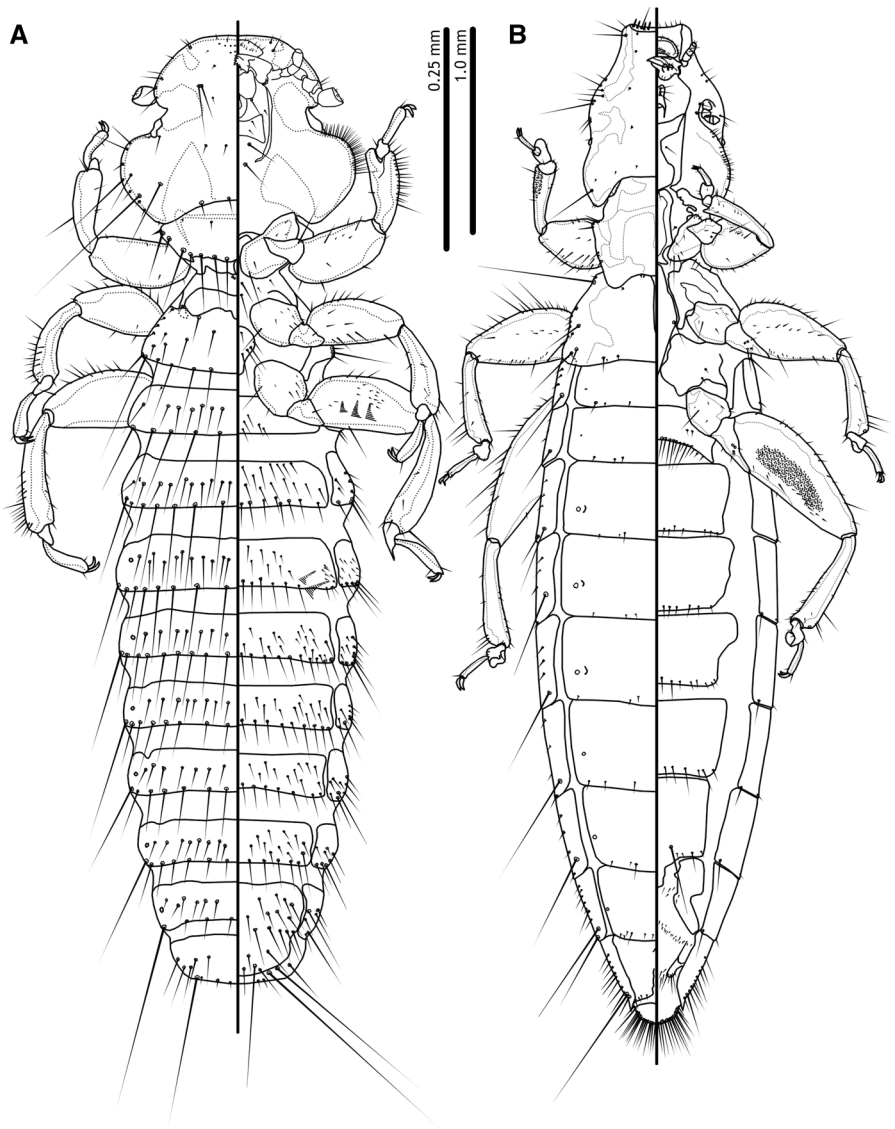

Fig. 5. Examples of Amblycera. A) *Colpocephalum zebra* (Burmeister 1838), male habitus, dorsal and ventral views (Menoponidae). B) *Laemobothrion atrium* (Nitzsch, 1818), female habitus, dorsal and ventral views (Laemobothriidae). Both modified after Gustafsson et al. (2019a).

Ischnocera Kellogg, 1896

The Ischnocera have traditionally included the Trichodectera, but phylogenetic analyses of genetic data by Song et al. (2019) indicate that these groups are distantly related. With the removal of Trichodectera, all Ischnocera parasitize birds except for one, *Trichophilopterus babakotophilus*, which parasitizes Malagasy lemurs. The Ischnocera are circumscribed by the following synapomorphies: (1) abdominal segment I entirely absent; (2) antennae 5-segmented and situated on or near the lateral margin of the head; (3) spiracular openings present on abdominal segments III–VIII; (4) tarsi with 2 claws; and (5) meso- and metathorax always fused into pterothorax. Examples of 2 ischnoceran lice are in Fig. 7.

Ischnocera contains substantial morphological variation, but relationships between genera are often obscured by convergent evolution of ecomorphs (Johnson et al. 2012; see above). The taxonomy is further muddied by an inordinate fondness of some authors to delimit taxa based on host associations. As a result, most researchers have used a system of dividing the group into complexes, rather than families, and many authors have accepted only one family, Philopteridae Nitzsch, 1818. The families Goniodidae Mjöberg, 1910 and Heptapsogastridae Carriker, 1936 are also sometimes accepted as valid, each of which contain <10% of the known ischnoceran diversity. Members of the Goniodidae have a central tergal plate on abdominal segment IX+X in males, and the Heptapsogastridae have tergopleurite II fused to the pteronotum, or much reduced and flanked at least partially by antero-lateral extensions of tergopleurite III on either side; neither of these characters are found in Philopteridae. A revision of the family-level taxonomy of the Ischnocera is much overdue.

Over 3,100 species of Ischnocera are described. However, ongoing morphological and genetic revisions of ischnoceran genera have revealed that most speciose genera are polytypic or paraphyletic. Among those genera recently revised with the advantage of genetic information, and thus likely to remain validly circumscribed, *Brueelia* currently contains ~200 species, *Philopterus* ~170 species, and *Guimaraesiella* ~100 species. In

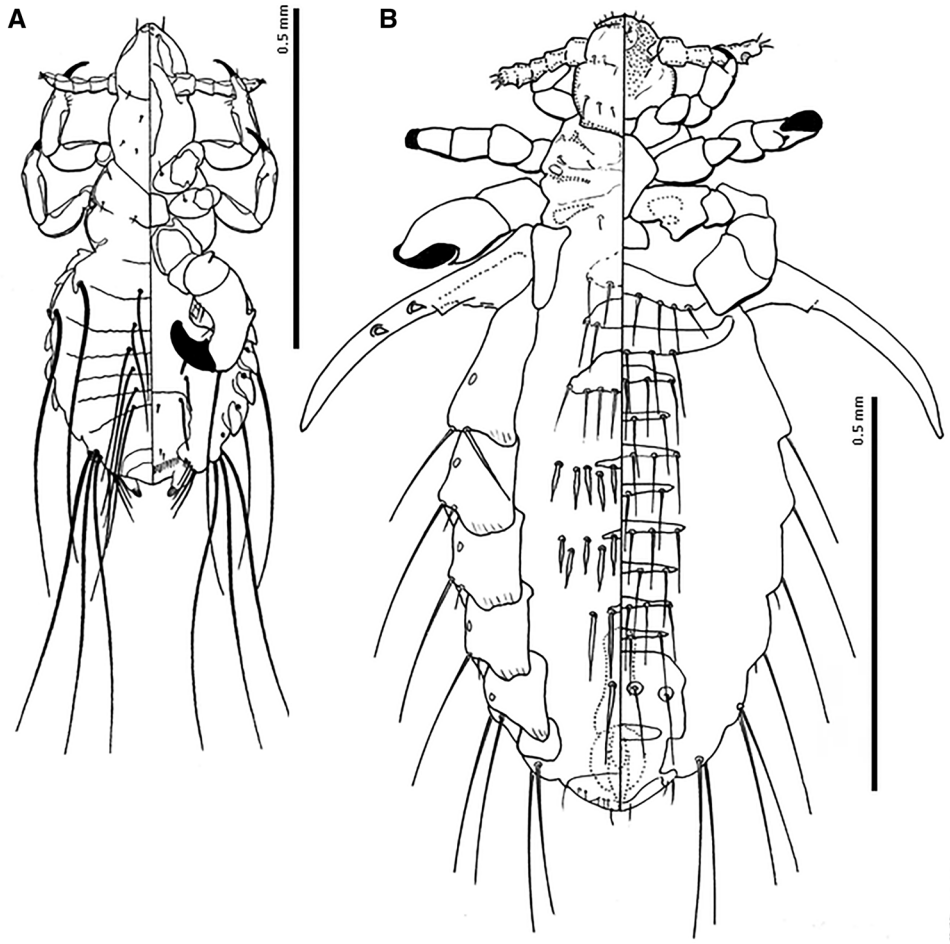

Fig. 6. Examples of Anoplura, A) *Enderleinellus euxeri* Ferris, 1920, female habitus, dorsal and ventral views (Enderleinellidae). Redrawn from Ferris (1920). B) *Pterophthirus splendida* Johnson, 1972, male habitus, dorsal and ventral views (Hoplopleuridae). Redrawn from Johnson (1972).

all cases, it is likely that only a fraction of the real diversity has been described; Gustafsson et al. (2025) estimated that the true diversity of Ischnocera may exceed 25,000 species.

Rhynchophthirina Ferris, 1931

The Rhynchophthirina comprises only 3 species in one genus (Price et al. 2003). The group can easily be identified based on the much elongated rostrum with mandibles located at the tip. Rhynchophthirina species parasitize elephants, warthogs, and red river hogs with *Haematomyzus elephantis* parasitizing both African savanna elephants (*Loxodonta africana*) and Asian elephants (*Elephas maximus*). However, recent research indicates cryptic species within *H. elephantis*, with African and Asian elephants parasitized by genetically distinct Rhynchophthirina species (Kelly et al. 2024). An example of a rhynchophthirinan louse is in Fig. 8A.

Trichodectera Song et al. 2019

The Trichodectera consists of one family, Trichodectidae, comprising chewing lice that exclusively parasitize mammals (Lyal 1985a; Price et al. 2003). Twenty genera and about 400 species are described. In addition to having chewing mandibles, members of Trichodectera have antennae that project from the lateral margins of the head. They are distinguished from ischnoceran lice in having one simple claw at the end of each tarsus. An example of a trichodecteran louse is in Fig. 8B.

The most speciose groups are the genera *Damalinia* (34 species), *Felicola* (56 species), and *Geomydoecus* (88 species). Taxonomic work on *Geomydoecus* and *Thomomydoecus* lice and their associations with different species and subspecies of Nearctic pocket gophers has been extensive (Hellenthal and Price 1991) and serve as a model system for host-parasite coevolutionary studies. Trichodectid lice parasitize mammals from all across the mammalian tree (Fig. 9). With the exception of the pocket-gopher louse assemblage and trichodectid lice parasitizing mammals important in agriculture, little is known about these lice, their host associations, and evolutionary history.

Evolutionary History

Origin

Parasites often have simplified morphologies owing to their parasitic lifestyle; lice are no exception. This simplification has made reconstructing the evolutionary tree for lice based on morphology alone particularly challenging, although some major morphological datasets have been developed (Lyal 1985b, Smith 2001, Marshall 2003). Even molecular datasets have been problematic because of the high rates of DNA substitution in lice compared to other insects (Johnson et al. 2003, 2014) and changes in DNA base composition compared to other psocodeans (Yoshizawa and Johnson 2013, Grant et al. 2024). Notwithstanding these challenges, extensive new

Fig. 7. Examples of Ischnocera. A) *Campanulotes heteroceros* (Tendeiro 1969), male habitus, dorsal and ventral views (Goniodidae). B) *Quadraceps legatus* (Timmermann 1952), female habitus, dorsal and ventral views (Philopteridae). Redrawn after Gustafsson et al. (2024b).

insights regarding the phylogeny of lice at many timescales have been gained by integrating molecular based datasets with morphological information. In addition, new techniques in whole genome sequencing have made thousands of genes available for phylogenomic studies, greatly improving confidence and stability in the results (Johnson 2019, 2022).

From morphological data alone, there is strong evidence that lice are descended from within free-living bark lice ("Psocoptera"), making Psocoptera paraphyletic (Lyal 1985b). Lyal's study, together with many subsequent studies based on molecular datasets (Johnson et al. 2018a, 2018b, 2022, de Moya et al. 2021), also provided strong evidence that chewing lice ("Mallophaga") are paraphyletic with respect to sucking lice (Anoplura). Early analyses of molecular data, particularly the nuclear 18S ribosomal RNA gene suggested that parasitic lice may be paraphyletic (Johnson et al. 2004). However, more recent molecular datasets based on over 2,000 genes from transcriptomes (Johnson et al. 2018a) and integration of transcriptomes with data from whole genomes (de Moya et al. 2021) have now refuted this result, providing strong evidence that parasitic lice form a monophyletic group, sister to the bark louse family Liposcelidae. Based on agreement between these morphological and molecular datasets, bark lice and parasitic lice are currently classified together into one insect order, Psocodea.

Given this strong evidence that parasitism only evolved once in Psocodea, dating the emergence of parasitism within this order becomes feasible. The presence of lice on all groups of birds raises the question: did lice parasitize nonavian dinosaurs before their extinction at the Cretaceous-Paleogene (K-Pg) boundary? Several studies have addressed this question (Smith et al. 2011). The fossil evidence of lice is scant, but 2 major fossil finds shed light on the timing of the origin of parasitic lice. The first definitive fossil of a parasitic louse was dated to around 44 mya (millions of years ago), well after nonavian dinosaurs went extinct (Wappler et al. 2004), and represented a louse of the family Menoponidae. The second major fossil find was a parasitic louse from amber (Zhang et al. 2024) dating to the mid-Cretaceous (99 mya). This louse, which is preserved among feather material, appears to be a stem lineage of Amblycera. There are similar fossils in amber from the same deposits for the bark louse family Liposcelididae (Grimaldi and Engel 2006).

Further evidence for the timing of the origin of parasitic lice comes from combining this and other fossil information with molecular phylogenetic studies of lice and knowledge about the timing of well-studied codivergence events between lice and their vertebrate hosts. Time of divergence of lice from its common ancestor within bark lice has been estimated in several studies (Smith et al. 2011, Johnson et al. 2018a, 2018b, de Moya et al. 2021), and these are all in general agreement that the origin of, and earliest divergences within, parasitic lice substantially predate the K-Pg mass extinction event. The occurrence of parasitic lice on nonavian dinosaurs is therefore plausible.

Diversification

Although molecular dating studies have pointed to the earliest divergences within parasitic lice occurring before the K-Pg boundary, much of the diversification among the major lineages of lice appears to have occurred around this time or slightly after it (Johnson et al. 2018b). This coincided with a burst of diversification among major host lineages of birds and mammals (O'Leary et al. 2013, Renne et al. 2013, Jarvis et al. 2014, Prum et al. 2015). This coincidence of timing suggests the early radiation of birds and mammals may have facilitated similar radiations in lice, including all parvorders (Light et al. 2010, Johnson et al. 2018b, de Moya et al. 2021).

Phylogenomic studies have also shed new light on the possible ancestral host group for parasitic lice and major host-switching events between birds and mammals. The recognition that Trichodectidae, exclusively parasitizing mammals, is more closely related to Anoplura and Rhynchophthirina than to Ischnocera (Johnson et al. 2018b, 2022, Song et al. 2019, de Moya et al. 2021; Fig. 9) has reduced the number of inferred transitions between bird and mammal hosts by at least one (Johnson et al. 2018b). However, such switches must have happened, given that the 2 most diverse lineages of lice (Ischnocera and Amblycera) contain a mix of avian and mammalian lice. This makes reconstruction of the ancestral host somewhat challenging, but evidence from several studies points to birds being the ancestral host lineage (Smith et al. 2011, Johnson et al. 2022). Most recently, in a densely sampled phylogenetic study, 4 switches from birds to mammals were inferred: 2 within Amblycera, one within Ischnocera, and the final switch giving rise to the origin of the major mammal louse clade (Trichodectera + Rhynchophthirina + Anoplura) (Johnson et al. 2022; Fig. 9). Furthermore, phylogenetic relationships within the Trichodectera + Rhynchophthirina + Anoplura

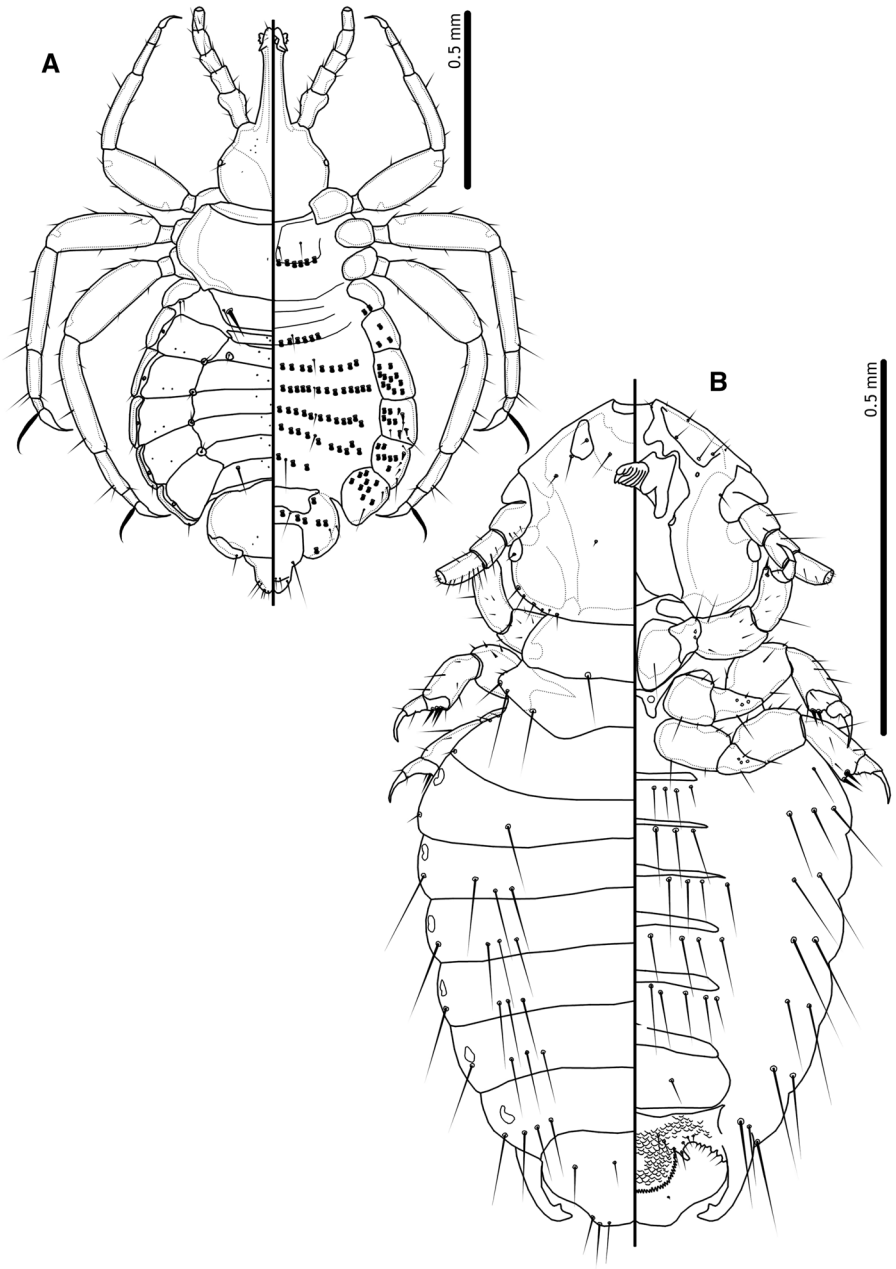

Fig. 8. Examples of Rhynchophthirina and Trichodectera. A) *Haematomyzus porci* Emerson and Price, 1988, male habitus, dorsal and ventral views [redrawn after Emerson and Price (1988)] (Rhynchophthirina). B) *Stachiella ermineae* (Hopkins 1941), female habitus, dorsal and ventral views [modified after Gustafsson et al. (2019a)] (Trichodectera).

mammal louse clade suggest that the common ancestor of Afrotheria may have been the host of the common ancestor of this clade of lice, with subsequent switches to other placental mammals (Johnson et al. 2022).

In addition to providing new insights into the diversification of mammalian lice, phylogenomic studies have provided resolution of the backbone of Ischnocera, identifying the relationships among major clades (Johnson et al. 2018b, de Moya et al. 2019). Given the instability in our understanding of the relationships among avian families and orders (eg. Jarvis et al. 2014 versus Prum et al. 2015), reconstruction of the ancestral host for Ischnocera presents challenges. However, the lice of palaeognaths are spread throughout the tree of Ischnocera in relatively derived positions. This result suggests that these lice did not originate on either palaeognaths or the common ancestor of all birds, but rather on neognaths, with several subsequent host-switching events to palaeognaths (de Moya et al. 2019).

Molecular and phylogenomic datasets are also being applied to studies within major groups to understand the relationships among genera and species of lice (Boyd et al. 2017, Virrueta Herrera et al. 2020, Johnson et al. 2021, San Juan et al. 2025). Together with continuing detailed examination of morphological features, these studies are providing reciprocal illumination regarding the relationships among lice, providing a basis for reassessing generic boundaries (eg. Bush et al. 2016, Gustafsson and Bush 2017) and identifying species groups (eg. Kolencik et al. 2022, 2024b).

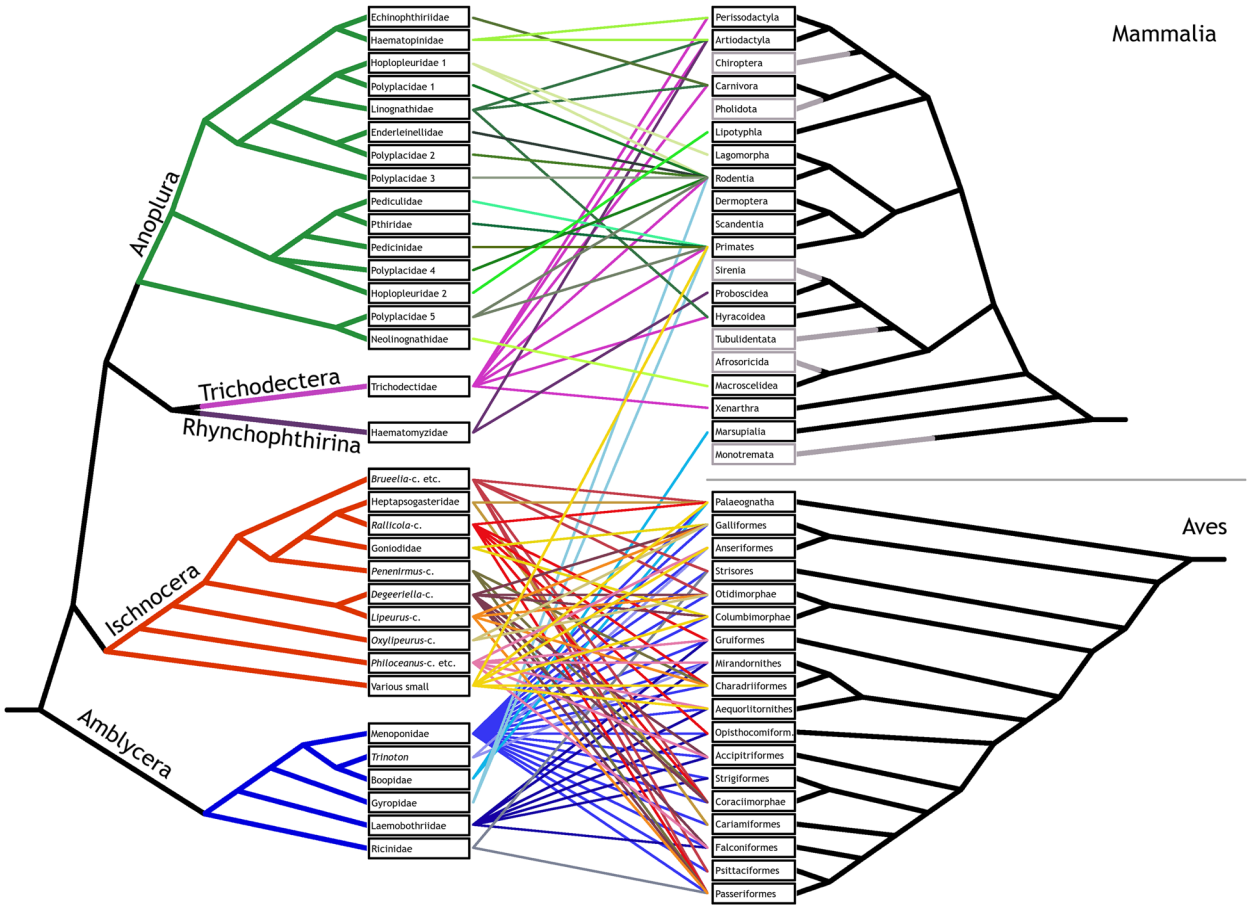

Fig. 9. Schematic overview of the classification of phthirapteran lice and their host associations. The louse tree is based on that of Johnson et al. (2022), but the Amblycera is based on Najer et al. (2024) and the Anoplura is an attempt to reconcile the trees of Johnson et al. (2022) and Light et al. (2010). Branches are not to scale, and only well supported clades are shown. Host trees are based on O'Leary et al. (2013) for mammals and Prum et al. (2015) for birds, except the Mirandornithes and Charadriiformes are shown separately from the rest of Aequorlitornithes for clarity. No lice are known from any members of mammal clades indicated in grey. Note that some families of Anoplura and complexes in Ischnocera were not included in the original trees. The ischnoceran group "Various small" includes several genera that are not commonly associated with a complex. Abbreviations used: c. = complex.

Cophylogenetic History With Hosts

Through their close associations, parasitic lice and their hosts share a common evolutionary history that make them ideal subjects for the study of the cophylogenetic patterns and mechanisms responsible for speciation and coadaptation. Lice vary in a range of life history characters, such as host specificity, ecomorphology, and feeding preferences, making them excellent models for understanding the ecological and evolutionary mechanisms (processes) that underlie cophylogenetic history (patterns). Parasitic lice have also been used as models for reconstructing the coevolutionary history between parasites and their hosts and have often been the subjects for the development of theory and testing of new host-parasite cophylogenetic methods (eg. Page 1991, 1993, Hafner and Page 1995, Page and Hafner 1996, Paterson and Banks 2001).

Although early cophylogenetic studies of lice and their hosts focused on cospeciation or codivergence (eg. Hafner and Nadler 1990, Johnson and Clayton 2003), these patterns are seldom perfect (Johnson et al. 2002). Many other macroevolutionary events, including host-switching, duplication, sorting, and cohesion events (see Clayton et al. 2016: Fig. 9.1) combine with codivergence to make more complex, discordant evolutionary histories than simple cospeciation (eg. Paterson et al. 2000). Cophylogenetic studies of lice and their hosts have been performed on many taxonomic levels (eg. Johnson and Clayton 2003, Weckstein 2004, Light and Hafner 2007b, 2008, Reed et al. 2007, Demastes et al. 2012, de Moya et al. 2019, Bell et al. 2021 Johnson et al. 2021). Early studies, including many foundational papers in the louse-host cophylogenetic literature, used phylogenies generated from Sanger DNA sequencing datasets, which are often weakly supported at basal nodes due to a limited number of sampled genes (Johnson 2022). Currently, cophylogenetic studies are being conducted with genomic scale datasets including thousands of genes that provide strong support for most branches (Johnson 2022).

Comparisons of higher level phylogenomic trees suggest that mammalian lice and their hosts exhibit more codiversification (57% of nodes) than avian hosts and their lice (17% of nodes), which on average exhibit more host-switching (de Moya et al. 2019, Johnson 2022). Perhaps this difference in the degree of codivergence versus host-switching is due to biological or ecological differences between mammalian and avian lice (Johnson 2022). For example, the high capacity for long distance dispersal among avian hosts might provide opportunities for louse host-switching (Boyd et al. 2022), whereas blood feeding mammalian lice directly interact with their hosts' immune systems

(Ratzlaff and Wikel 1990) and also have fewer opportunities for phoresy, potentially leading to the evolution of host-specificity and cospeciation (Johnson 2022). Notably, the high degree of host-switching events among bird lice has also been found at the species level (eg. Johnson et al. 2021). In ischnoceran *Columbicola* lice and their dove hosts, resident and newly colonizing doves in a region have exchanged lice with each other in both directions (Boyd et al. 2022), and switches between distantly related hosts have been recorded (Sychra et al. 2014).

Cophylogenomic studies of mammal lice are so far consistent with the idea that cospeciation plays a dominant role in louse/mammal coevolutionary history within host groups. For example, cospeciation is the principal driver of coevolutionary history among the anopluran Echinophthiriidae and their pinniped hosts (Leonardi et al. 2019). In anopluran lice on chipmunks (*Tamias*), are more varied, but recently diverged taxa may have cospeciated with their hosts, whereas others may have evolved via a history of host-switching (Bell et al. 2021). Given that louse-host systems have been models for studying cophylogenetic history for decades, future cophylogenomics studies of a diversity of louse-host groups will certainly be fruitful for understanding broad macroevolutionary histories, and the microevolutionary processes and life history traits driving these histories among these closely associated partners.

Taxonomic Databases

Printed Sources

There have been several efforts to develop checklists for lice, although few have covered all of louse diversity, as sucking and chewing lice have generally been treated separately. The earliest general checklists for the chewing lice were those of Kellogg (1908) and Harrison (1916), which included citations for species descriptions and their primary host. Although these lists are valuable for finding historical classifications of species, they were collated without critical analysis, and serve best as summaries of taxonomy and host associations.

In the 1930–1950s, new species and genera were described at an unprecedented rate, and the interruptions of communications during World War II meant that many taxa were described multiple times. Hopkins and Clay (1952) published "A check list of the genera and species of Mallophaga," which expanded and corrected the earlier works, and proposed numerous new synonymies and combinations. As Hopkins and Clay (1952) also had access to the type specimens of many older species (eg. those described by Denny, Piaget, and others), this checklist and associated publications also served as formal revision of many genera. After that, no comprehensive world checklist of chewing lice was published until Price et al. (2003), who also included illustrations of all louse genera, keys to louse genera arranged by host order associations, and checklists arranged by both louse species and host species. Although already somewhat dated, Price et al. (2003) is the most current published checklist for chewing lice.

For sucking lice, some of the earliest checklists and monographs date back to 1910–1920s, with earlier documents (eg. Kellogg and Ferris 1915, Ferris 1916a, 1916b) treating both sucking and chewing mammal louse diversity in the same publication. Many subsequent publications were regionally specific, and focused more specifically solely on Anoplura. The largest worldwide monographs in the 1920s were published by Ferris (1920, 1921). In 1951, Ferris (1951) published a checklist of 255 species; the number of described species has more than doubled since that time. Durden and Musser (1994a, 1994b) compiled a list of described Anoplura including type and principal host species, geographic regions, and synonyms. Durden and Musser (1994a, 1994b) are the most up-to-date checklists, but over 50 species have been described since then.

We note that there are regional checklists and guides for both sucking lice and chewing lice; for instance, Kim et al. (1986) is a useful, illustrated guide for North American sucking lice, including information on their biology. Similarly, Gustafsson et al. (2019a) provided a checklist to Swedish lice, with an identification key that can be used in much of Europe, and the recent checklist of Chinese Ischnocera (Gustafsson et al. 2024b) contains illustrations and descriptions of a wide range of Eurasian Ischnocera.

Online Sources

Online databases also are valuable resources for louse species descriptions, occurrences, and images. The most comprehensive and up-to-date online database at the species level is Phthiraptera.myspecies.info (Smith, Broom, and Dalgleish: http://phthiraptera.myspecies.info/). This database archives and provides access to literature, images, host associations, collections, and species checklists, and is regularly updated. This database also includes a list of contemporary louse researchers who can be contacted for their expertise. Psocodea Species File (Hopkins, Johnson, and Smith: https://psocodea.speciesfile.org/) is another online louse taxonomy resource, which is well-annotated and provides nomenclature references for louse species.

Beyond the online information pages and taxonomic databases, there are several other online resources for lice. Natural history collections often hold louse specimens either in an entomology collection (eg. the Natural History Museum in London) or in a parasite collection (eg. the Harold W. Manter Laboratory of Parasitology at University of Nebraska). In some cases, ectoparasites are held as associated data of their avian or mammalian hosts. While there have been tremendous efforts to digitize louse data in collections (eg. the Natural History Museum in London or the National Science Foundation-funded Terrestrial Parasite Tracker), many specimens are only cataloged at higher taxonomic levels due to lack of taxonomic expertise to identify to species. Through the work of digitization initiatives, many louse specimens are discoverable through database aggregators such as iDigBio (https://www.idigbio.org/portal/search) and Global Biodiversity Information Facility (GBIF, https://www.gbif.org/). Even if specimens are not identified, databases such as the Arctos platform (https://arctos.database.museum/) can be used to find louse specimens by searching for ectoparasite or louse occurrences by host species. Another option for finding louse records is through the Global Biotic Interactions database (GloBI, https://www.globalbioticinteractions.org/) which hosts datasets of known interactions, including point occurrences of louse-host records. In addition to documenting specimen data, digitization efforts have also scanned slides to make images of specimens available. The Natural History Museum has imaged its entire slide-mounted louse collection for a total of 70,000 images available (https://data.nhm.ac.uk/dataset/phthiraptera-collection).

Taxonomic Impediments and Understudied Areas

Legacy of Fahrenholz's Rule

The largest roadblock in louse systematics is the legacy of "Fahrenholz's Rule" (Fahrenholz 1913, Eichler 1942), which argues that lice are nearly perfectly host specific and thus should cospeciate with their hosts (Gustafsson and Najer 2022). This has led to the description of numerous louse species and genera based on host associations. Unfortunately, these are often accompanied by descriptions and illustrations that are vague or useless. This is especially the case for the ischnoceran family Philopteridae. For example, no useful descriptions or illustrations have ever been published for a long list of genera (eg. *Debeauxoecus, Paroncophorus*, and *Turnicola*). Additionally, there are several genera of lice where almost no species can be identified today (eg. *Anaticola* and *Penenirmus*), and other genera are not reliably separable morphologically (eg. *Capraiella* and *Degeeriella*).

This impediment is compounded by the lack of reliable identification keys for many genera, as well as a paucity of revisionary studies critically examining taxon limits and useful morphological characters, causing identifications to be based on host associations. In some cases, the most recent general revisions may be almost 100 years old (eg. Clay 1938). Moreover, most known species of lice were described prior to the development of modern polymerase chain-reactions (PCR) and sequencing methods. For these early descriptions, lice were cleared, stained, and mounted on slides. Often, these slide-mounted specimens were macerated in potassium hydroxide (KOH), and thus cannot be used for genetic studies. Direct comparisons with type specimens are therefore often required, but types are often missing (eg. Jałoszynski et al. 2014; Naz et al. 2020), requiring neotype designations of many taxa. Ischnocera may be worse off than the other parvorders, with genus-wide revisions likely needed for well over 50% of the genera in this group.

Megadiverse Genera

Identification and classification of many groups of lice is further complicated by the sheer number of species. For instance, Valim and Weckstein (2013) estimated that there may be almost 1,000 species of the amblyceran genus *Myrsidea* in Brazil alone, of which only ~10% are described. Similarly, Gustafsson et al. (2019b) estimated the diversity of the ischnoceran genus *Brueelia* in Africa to exceed 1,100 species, but <3% of these are known. Moreover, both of these genera are global in range and parasitize a wide diversity of host taxa, suggesting that the true diversity is much higher. Gustafsson et al. (2025) estimated the global diversity of these genera to be 4,273 and 3,520 species, respectively; they estimated that at least 8 other louse genera may contain >1,000 species each. Among lice parasitizing mammals, no genus is as speciose as described above for amblyceran or ischnoceran avian chewing lice. However, the anopluran genera *Hoplopleura* and *Polyplax* and the trichodecteran genus *Geomydoecus* are particularly diverse for mammal lice, with 177, 81, and over 80 described species, respectively.

Many of the megadiverse genera are morphologically rather homogeneous, and typically no thorough overviews of the morphological diversity in these groups have been published (but see Gustafsson and Bush 2017, Kolencik et al., 2024b). There are no complete overviews of species groups in ischnoceran genera such as *Brueelia, Quadraceps*, and *Philopterus*, and for simplicity new species of lice are often compared only to those known from related hosts (eg. Price and Hellenthal 1998, Gustafsson et al. 2022). Identification keys have generally only been published for small genera or distinct species groups in larger genera (eg. Gustafsson et al. 2018). Because the task of identifying and describing this diversity is so daunting, it is common for large louse collections at museums to contain vast numbers of undescribed species. Moreover, the number of active taxonomists working with lice is presently very low, particularly in comparison with the "Golden Era" [*sensu* Price et al. (2003): 1953–1972], slowing the transformation of results from phylogenetic and phylogenomic analyses into updated classifications.

Misidentification

Bush et al. (2021) suggested that louse research is presently in a "misidentification crisis." With increasing frequency, lice are incorrectly identified to genus, parvorder, or even subphylum level, with mites identified as lice (González-Acuña and Palma 2020). This crisis likely has many causes, among which are the lack of training in identification and taxonomy of lice, the unfortunate legacy of Fahrenholz's Rule, and the use of outdated or error-filled general veterinary textbooks for identification. In particular, Soulsby (1982) is often quoted as a basis for identifications, despite this book only treating the lice of selected domestic animals, and in many cases, even the information on these is incorrect.

Published misidentifications, if not corrected, may impact our understanding of geographic distributions and host ranges of lice, and create error cascades that exacerbate the problems, as spurious data are used in downstream meta-analyses and models. Bush et al. (2021) made 5 suggestions to improve the accuracy of parasite identification in the literature (identify by morphology, not host associations; include images of lice; make morphological specimen comparisons explicit; make genetic data accessible and deposit voucher specimens in public collections; seek assistance from taxonomists when necessary), but above all recommended that louse researchers include information about how specimens were identified and incorporate photographs of specimens as identification vouchers.

Understudied Areas

In general, lice are better known from hosts breeding in Europe and North America while the lice of regions such as most of Sub-Saharan Africa and the Australo-Papuan area are largely unknown for many host groups. Even in understudied areas, lice are typically better known from larger hosts than smaller hosts. The undiscovered diversity of lice on smaller hosts such as songbirds or rodents may be enormous (see above). Lice occurring on hosts in alpine areas, in tree canopies, or generally geographic areas that are difficult to sample are generally worse known than those in more accessible habitats. Focused studies such as those on pocket gophers (eg. Hellenthal and Price 1991) or pigeons (eg. Adams et al. 2005, Bush et al. 2009) show that more complete coverage is possible, but often requires dedicated work over many decades, particularly as prevalence may be very low (<5%) for lice on many small-bodied hosts.

Future of Classification

Nano-CT Scans

Nano-computed tomography (nano-CT) uses X-ray imaging to reconstruct high resolution images of objects in 3D. This method is becoming more accessible for smaller-bodied organisms, and enables the visualization of lice in all 3 dimensions along with internal characters (Fig. 10). For example, the use of this method has confirmed that ischnoceran lice of the head louse ecomorph have proportionally larger chewing muscles than lice that reside on other parts of the body (Kolencik et al., 2024a).

AI Models

A recent study explored the possibility of harnessing artificial intelligence algorithms to identify lice (Rostami et al. in review). The study results were mixed: AI models were able to identify some lice but the models also misidentified many lice. The inability of AI to discriminate between different species of lice is largely driven by the small number of images available to train the models. This situation will likely improve as more photos of lice are taken and AI models improve predictions on smaller datasets. However, it is clear that the future of louse taxonomy will, for the many species and genera with few images, require humans to identify the specimens for the foreseeable future. To aid this process, introductory material needs to be published to guide beginning researchers in identification, and to help those with minimal access to specimens and other resources. In addition, revisionary work for many groups of lice infesting common or domestic hosts is desperately needed.

Traits and Genomes

With the advent of novel scanning methods and the corpus of genomes sequenced across lice, there are likely going to be many opportunities in the future for combining these datasets. For example, morphological traits can be associated with single nucleotide polymorphisms (SNPs) in genomes using genome wide association studies (GWAS). Patterns of selection can be examined across protein coding genes and associated with morphology or life history characteristics (eg. host associations). While the approach of combining trait and genomic data has great potential, there is a general lack of available assembled genomes across lice (eg. Pittendrigh et al. 2006, Baldwin-Brown et al. 2021, Sweet et al. 2023). However, due to the small genome size of lice (ca. 100–200 Mb), it is likely that more assemblies will become available for these kinds of studies.

Division of Ischnocera

Genetic data have revealed that many of the "species complexes" in Ischnocera are separated by long branches, indicating that they may have evolved independently for long time periods. For instance, at least 14 different groups of ischnoceran lice may have radiated in the Palaeogene (>25 mya; Johnson et al. 2018b). Morphological characters potentially useful for circumscribing families are known for some of these complexes (eg. Gustafsson and Bush 2017), whereas for other clades no such characters are known. Notably, the 2 smaller families often recognized within Ischnocera (Goniodidae, Heptapsogasteridae) are both nested inside Philopteridae (eg. Johnson et al. 2018b). Finding useful morphological characters that can circumscribe monophyletic groups within Ischnocera will be crucial not only for fine-tuning the classification of this group, but also to understand the evolution of the characters themselves.

Anoplura Waste-Basket Taxa

Based on phylogenetic data, Light et al. (2010) revealed that multiple taxonomic groups currently recognized within the Anoplura are not monophyletic, notably including the 2 most speciose families, Hoplopleuridae and Polyplacidae. In particular, Polyplacidae includes an array of morphologically diverse and widespread (both geographically and host associations) genera, some of which should be considered for re-classification. One polyplacid genus, *Eulinognathus*, has a disjunct geographical and host distribution (Durden and Musser 1994a), and should probably be split into 2 or more genera. It may also be appropriate to split Polyplacidae into multiple families that reflect evolutionary relationships. Phylogenomic and fine-scale morphological studies should help to resolve these and other taxonomic questions within Anoplura.

Family-Level Taxa in the Amblycera

Najer et al (2024) recently showed that the amblyceran family Menoponidae as currently circumscribed may be paraphyletic, with the genus *Trinoton* more closely related to the Boopiidae than to the rest of Menoponidae. However, even if *Trinoton* is

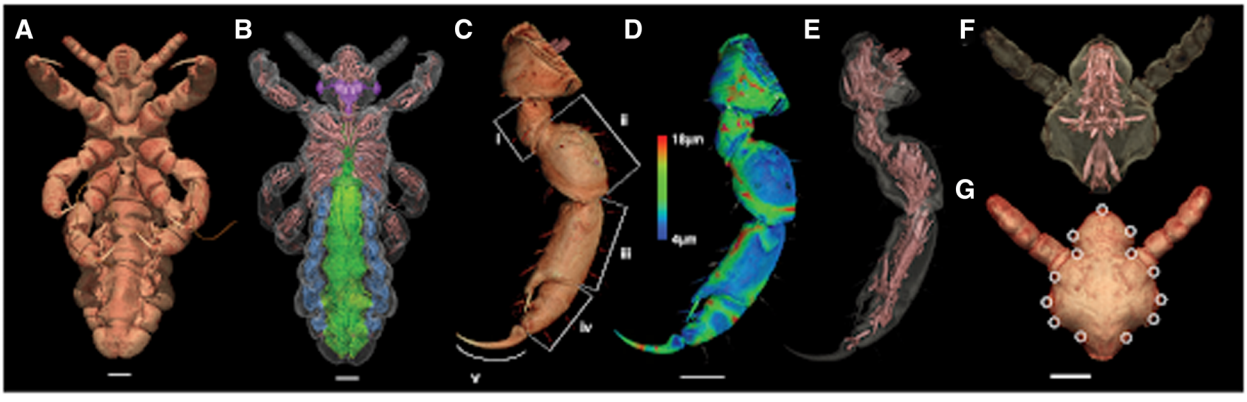

Fig. 10. Nano-CT scan of the anopluran human head louse, *Pediculus humanus*. A) full specimen in 3D, B) internal characteristics including muscles, C) isolated first limb showing linear measurements of segments and claw, D) thickness of external cuticle, E) first limb muscles, F) stylet eversion muscles, and G) external head with 3D landmarks. Photo credit to Edward Stanley, Florida Museum of Natural History.

separated to its own family (Trinotonidae Eichler 1941), the remainder of Menoponidae contains several large, diverse clades that are separated by long branches. In some cases, morphological characters support these clades, and several family-group names are available for resurrection for these groups (eg. Eichler 1963). A family-level revision of the Amblycera, taking both genetic and morphological data into account, is needed to assess whether Menoponidae should be divided into smaller groups.

Conclusions

The classification of parasitic lice is entering a new stage, in which long-held beliefs in the monophyly or relatedness of different taxa are challenged by genetic data and more detailed studies of previously neglected morphological characters. Moreover, studies on the patterns and processes underlying host specificity, host association patterns, and co-evolutionary trends are changing our understanding of how lice evolved and continue to evolve. The impacts of host-switching and the external environment on the evolutionary history of lice are being reevaluated, and experimental research on host transfer, preening, and phoresy are giving a clearer picture of what the world may look like from a louse perspective. Lice are emerging as far more dynamic and varied than the slowly evolving sluggards they were characterized as in the 20th century (eg. Hopkins 1939, Eichler 1963). Our classification of lice is still lagging behind the data, in part due to the shortage of active taxonomists, but the large buildup of data means future classifications will have a better grounding than those of the past. Given that lice are a model group for studying a variety of questions about the ecology and evolution of host-parasite interactions, researchers working on these topics will benefit from high quality taxonomic studies, phylogenetic studies, and revisions, because understanding the taxonomic limits and relationships of these parasites is critical to studying aspects of host-parasite associations, including coevolution.

Acknowledgements

We thank the great louse researchers of the past, on whose work our own rests, and the curators and collection managers worldwide keeping specimens and other research data safe and accessible.

Author Contributions

Daniel Gustafsson (Conceptualization [lead], Project administration [lead], Writing—original draft [equal], Writing—review & editing [equal]), Julie Allen (Visualization [equal], Writing—original draft [equal], Writing—review & editing [equal]), Kayce C. Bell (Writing—original draft [equal], Writing—review & editing [equal]), Sarah Bush (Visualization [equal], Writing—original draft [equal], Writing—review & editing [equal]), Lance Durden (Visualization [equal], Writing—original draft [equal], Writing—review & editing [equal]), Kevin P. Johnson (Writing—original draft [equal], Writing—review & editing [equal]), Jessica E. Light (Writing—original draft [equal], Writing—review & editing [equal]), and Jason D. Weckstein (Writing—original draft [equal], Writing—review & editing [equal])

Funding

This research was funded by the Introduction of Full-Time High-Level Talent Fund of the Institute of Zoology, Guangdong Academy of Sciences (grant GIABR-GJRC201701), the National Natural Science Foundation of China (grants 31961123003, 32001098), the Foreign Young Talent Plan (QN20200130012), the Pearl River Talent Recruitment Program of Guangdong Province (Grant 2019QN01N968), United States National Science Foundation Dimensions of Biodiversity Program (DEB-1926738), and United States National Science Foundation Systematic Biology Program (DEB-1855812, DEB-2206733, DEB-2206735). These agencies had no influence over the design and execution of this review.

Conflicts of interest

None declared.

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