63

Arthropoda

Siphonaptera (Order): Fleas

Marcela Lareschi

Phylum Arthropoda

   Class Insecta

      Order Siphonaptera

Chapter 63

Siphonaptera (Order): Fleas

Marcela Lareschi

Centro de Estudios Parasitológicos y de Vectores
(CEPAVE), Consejo Nacional de Investigaciones
Científicas y Técnicas (CONICET), Universidad Nacional
de La Plata, La Plata, Argentina
mlareschi@cepave.edu.ar

Introduction

Adult fleas (order Siphonaptera) are highly specialized holometabolous arthropods adapted to parasitic life and are morphologically very different from other insects. Fleas are parasites of birds and mammals, but their greatest specific richness is associated with rodents. There are nearly 3,000 species and subspecies placed in 19 families that are currently known worldwide (Lewis, 1998; Whiting et al., 2008).

Both male and female fleas feed exclusively on host blood. Larvae benefit from the host blood indirectly since they ingest the adult fleas' feces after the adults digest the blood (Marshall, 1981; Linardi and Guimarães, 2000; Medvedev and Krasnov, 2006).

External Morphology of the Imago (Figures 1 and 2)

Adult fleas (the **imago** is the adult or reproductive stage of the flea (Maggenti et al., 2005)) are laterally compressed, wingless insects, and are usually brownish-yellow in color. The flea body averages 4–5 mm in length, while a few giant flea species measure up to 1 cm in length and, in these species, female-biased sexual size dimorphism occurs. The body generally is covered with **bristles** angled backward that permit easy movement through the hairs or feathers of their hosts. The body is resistant, able to withstand great pressure, probably an adaptation to survive attempts of elimination by crushing or scratching by the host. The **head** is usually small, narrow, and cuneiform, and is sometimes helmet-shaped. **Eyes** may be present, vestigial, or absent. The **antennae** are short and serve as chemoreceptors. When not in use they retract back into furrows on the sides of the head. The **mouthparts** are specialized for piercing and sucking. In some species, the mouthparts are adapted to attach to the epidermal tissue of the host. Some fleas have **ctenidia**, or combs, which are rows of spines, similar to strong teeth, directed backwards and which are located on the head (frontal and genal) and in the **thorax** (pronotal and mesonotal). The ctenidia are species specific and can be used for flea identification (Figure 2). The thorax has 3 pairs of **legs** with **tarsi** with bristles, plantar spines, and a pair of long claws to cling to the host (Figures 1 and 2). The **abdomen** has 10 segments, 8 each with a pair of **spiracles**, and includes the **pygidium**, or **sensilium** (sensory organ), at the posterior end. The last segments are modified variously, for copulation in males and egg laying in females.
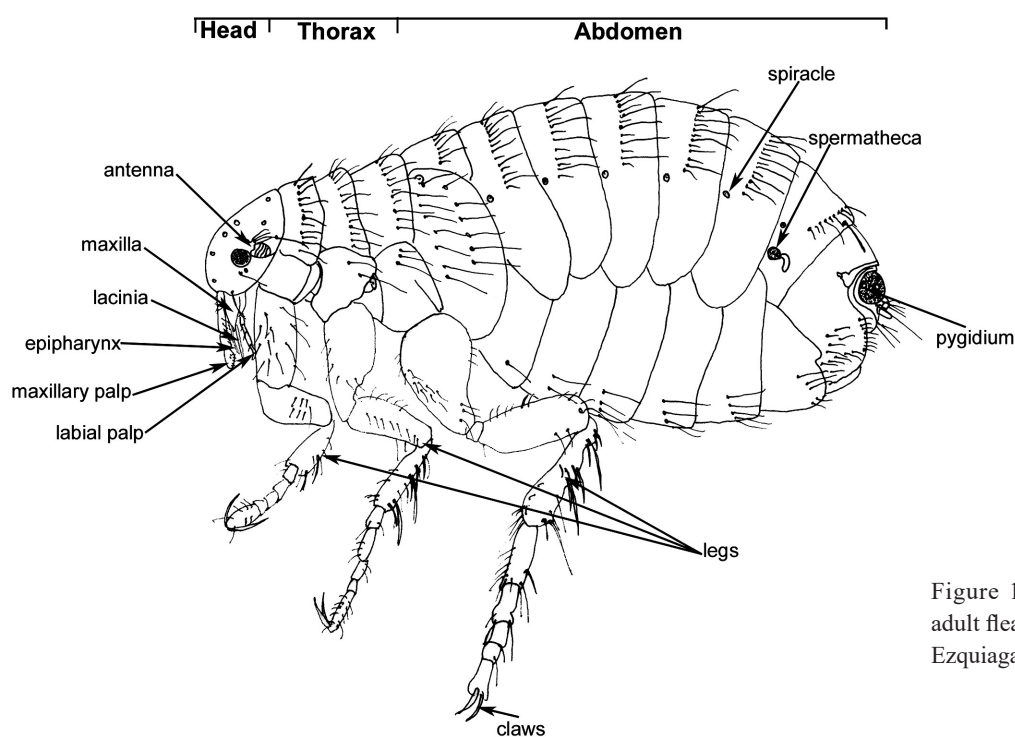

Figure 1. External morphology of an adult flea (*Pulex irritans*). Source: M. C. Ezquiaga. License: CC BY-NC-SA 4.0.

Figure 2. Details of the cteniodia (*Craneopsylla minerva*). Source: J. Sánchez, M. Urdapilleta, and L. Giambelluca. License: CC BY-NC-SA 4.0.
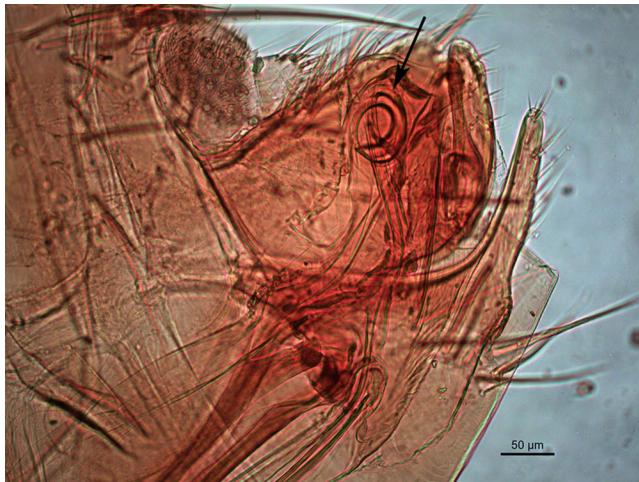

Figure 4. *Hectopsylla* sp. Source: J. Sánchez, M. Urdapilleta, and L. Giambelluca. License: CC BY-NC-SA 4.0.

Figure 3. Details of the aedeagus (*Polygenis platensis*). Source: J. Sánchez, M. Urdapilleta, and L. Giambelluca. License: CC BY-NC-SA 4.0.

Figure 5. Male *Malacopsylla grossiventris* (family Malacopsyllidae). Source: M. C. Ezquiaga and E. Soibelzon, 2021. License: CC BY-NC-SA 4.0.

Sexual dimorphism is pronounced, with females larger than males; the posterior part of females is rounded, while that of males is upturned, to accommodate the copulatory apparatus in the last segments; the males have an internal structure that is projected during copulation, called the **aedeagus** (Figure 3). The sperm receptacle in the female is called the **spermatheca** (Figures 1 and 2). Genitalia and the associated modified segments have diagnostic value at the species level (Hopkins and Rothschild, 1953; Johnson, 1957; Beaucournu and Launay, 1990; Linardi and Guimarães, 2000; Medvedev and Krasnov, 2006; Linardi, 2017).

Some fleas, most of them belonging to the genus *Tunga* (family Tungidae), are particular in that the females are the ones that penetrate the hosts' skin. The abdomen of a gravid female of these species increases up to 20 times its original size, which is referred to as **neosomy**. Neosomy is an external transformation of shape involving the formation of new cuticle during a larval stadium. The best species known is *Tunga penetrans* in which the second stage larvae do not feed, but the adult females penetrate into the toes of humans and produce eggs. Neosomy also occurs in species other than *T. penetrans*, such as those of the genus *Hectopsylla* (Figure 4) and in the family Malacopsyllidae (Figure 5). These fleas attach to the outside of the host by remarkably well-developed mouthparts (Audy et al., 1972; Marshall, 1981).

Morphological Adaptation to Parasitism

Morphological adaptation to parasitism in fleas includes the mouthparts and their jumping mechanism. Flea mouthparts (Figure 1) are adapted to obtain blood from the host. The suctorial mouthpart of fleas includes the **maxilla**, **maxillary palp**, **labial palp**, the **epipharynx**, and two **laciniae** of the maxillae, which together enclose a food channel for inbound blood. The laciniae form a smaller salivary channel for outbound saliva. These structures have an elongated stylet-like form, and each outer side of the laciniae has 2 rows of backward-pointed **teeth** which cut or saw the skin of the host and anchor the mouthparts. The length of the mouthparts and the number and development of the teeth vary among flea species (Hopkins and Rothschild, 1953; Linardi and Guimarães, 2000; Medvedev and Krasnov, 2006).

The best known locomotory characteristic of the fleas is their ability to jump, which allows these wingless insects to parasitize their hosts successfully. The legs are adapted for jumping, with the hind leg longer than the 2 prior legs. This mechanism has been studied by various authors (see the literature cited in Medvedev and Krasnov, 2006) where differences in the jumping ability between the sexes and among species is reported. For example, it has been found that male fleas jump shorter distances than female fleas and jump length varies among species (Rothschild et al., 1975; Medvedev and Krasnov, 2006).

Morphology of the Larvae and Pupae

Whereas the morphology of adult fleas is well known, the morphology of flea larvae and eggs has not been investigated so intensively. The larvae (Figure 6) of the fleas are of a grayish transparent appearance, and many segments may be covered with very fine **setae**, which may obscure their honeycomb appearance. Larvae are eyeless but possess dermal light receptors and are generally negatively phototropic. The larvae are vermiform and legless, with chewing **mouthparts**. The larvae are characterized by the presence of **anal lobes**, which play a major role in locomotion. The anal lobes possess slightly divergent fingerlike expansions on segment X providing the larva with support points on the substrate and this enables the larva to move. Three stages of larvae are recognized, with the exception of the species of Tungidae, which present only 2. The first stage is recognized by the presence of a front tooth that aids in hatching, while the remaining 2 are differentiated only by being larger than the other one. Although flea larvae are highly active, they generally remain buried in organic debris in the host's environment, and it is within this that they pupate. Prior to pupation, they empty their alimentary canal and spin a silken cocoon around them which may adhere to the substrate, and in which they come
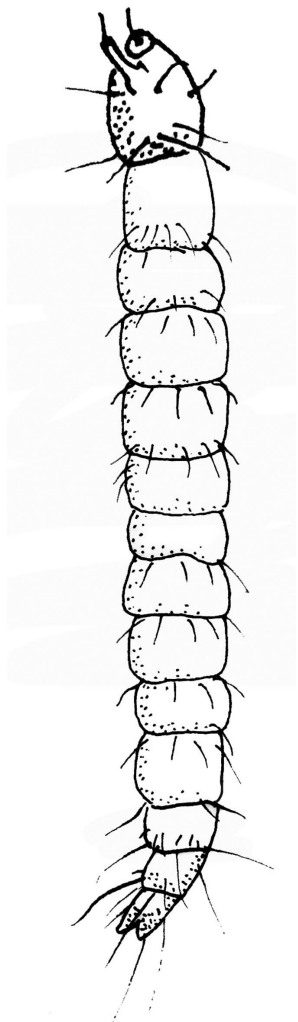

Figure 6. External morphology of the larva. Source: J. Sánchez, M. Urdapilleta, and L. Giambelluca. License: CC BY-NC-SA 4.0.

to lie in a U-shaped position prior the first pupal molt (Cotton, 1963; Marshall, 1981; Beaucournu and Launay, 1990; Pilgrim, 1992; Linardi and Guimarães, 2000; Pilgrim and Galloway, 2000; Linardi, 2017).

Morphology of the Eggs

Flea species can be identified based on the external morphological characters of their **eggs**. The posterior end of the egg has holes termed **micropyles** and the anterior end of the egg has holes termed **aeropyles**. The characters that help aid in the identification of the eggs include various distributions and combinations of reticulation on the surface, micropyles, anterior aeropyles, lateral aeropyles, and the egg's size.

A scanning electron microscope (SEM) is used to examine the flea egg **exochorion** (Figure 7). The eggs of Malacopsyllidae are large, as is the case for other large-sized fleas, such as *Sphinctopsylla ares*, and species of Hystrichopsylla. Species with relatively very large eggs never have more than 2 eggs within the **oviduct** at any one time, but in contrast with these species, malacopsyllids present neosomy and it is possible

Figure 7. External morphology of the egg of *Malacopsylla grossiventris* (scanning electron microscope image). Source: J. Sánchez, M. Urdapilleta, and L. Giambelluca. License: CC BY-NC-SA 4.0.

Figure 8. *Polygenis* sp. (family Rhpalopsyllidae). Source: J. Sánchez, M. Urdapilleta, and L. Giambelluca. License: CC BY-NC-SA 4.0.

that there may be more than 2 clutches of eggs (Rothschild et al., 1986; Chen and Wang, 1993; Lynley et al., 1994; Krasnov, 2008; Ezquiaga and Lareschi, 2012).

Phylogeny, Systematics, and Taxonomy

The combination of morphological with molecular data provides compelling evidence for a sister group relationship between the winged mecopteran family Boreidae and the Siphonaptera (Rothschild, 1975; Whiting, 2002; Whiting et al., 2008). The ancestor of fleas, with detritus-feeding larvae and adults feeding upon plant material or live arthropods, was probably afirst associated with the nests of mammals. Fleas remain primarily mammal parasites, but some have secondarily moved to birds, such host-switches or ecological fitting occurring at least 16 times in the evolution of the order. Many bird fleas have arisen from the fleas of tree-climbing rodents, whereas others have moved from burrow-dwelling mammals to burrow-dwelling birds (Holland, 1964; Marshall, 1981; Whiting et al., 2008).

Hopkins and Rothschild published a 5-volume series on flea systematics based on the extensive Rothschild Flea Collection deposited at the Natural History Museum in London, United Kingdom (Hopkins and Rothschild, 1953; 1956; 1962; 1966; 1971). Subsequently, 3 additional volumes were published for the families Pygiopsyllidae (Mardon, 1981), Ceratophyllidae (Traub et al., 1983), and Malacopsyllidae and Rhopalopsyllidae (Smit, 1987).

Currently, the most accepted higher classification for Siphonaptera is based on morphological characteristics, provided by Medvedev (1998) and Lewis (1998), and which

have been modified by Whiting and colleagues (2008), by analyzing flea relationships based on molecular data. Whiting and colleagues (2008) present the first formal analysis of flea relationships based on a molecular matrix. Almost 3,000 species and subspecies are known, from 238 genera and 19 families in the order Siphonaptera.

The family **Tungidae** is the most basal flea lineage, a sister group to the remainder of the extant fleas. Tungidae includes a group of fleas that have an unusual morphology, with a characteristic compression of the 3 thoracic segments, having mouthparts that are always enlarged and modified for firm attachment to the host, an eye that is reduced or absent, and no ctenidia. As noted above, they live a neosomic lifestyle. Tungidae is placed at the base of the phylogeny, as sister to the remaining flea taxa, and includes species allocated to the genera *Tunga* and *Hectopsylla* (Figure 4). Of all the fleas, females of the species *Tunga* are the only ones known to live within the host's cutaneous tissues.

The majority of the natural mammalian hosts of the genus *Tunga* are sloths and armadillos, and secondarily seem to have switched hosts via ecological fitting and diversified extensively on various species of rodents. Although humans and domestic animals are the principal hosts for *T. penetrans*, from an evolutionary standpoint, these are certainly secondary associations. *Hectopsylla* prefers caviomorph rodents, birds, and bats. The geographical distribution of its members covers the Neotropics (*Tunga* and *Hectopsylla*), Africa (*Tunga*), and East Asia (*Tunga*) (Hopkins and Rothschild, 1953; Johnson, 1957; Hastriter and Méndez, 2000; Linardi and Guimarães, 2001; Whiting et al., 2008).
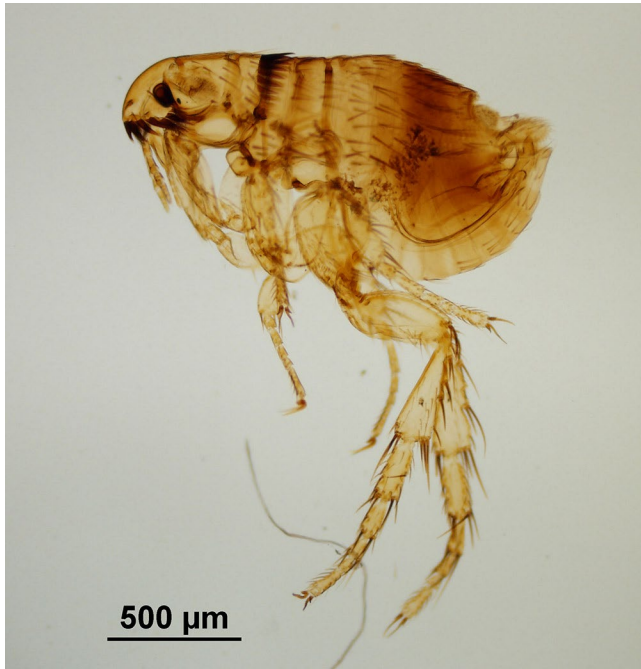
Figure 9. *Adoratopsylla intermedia intermedia* (family Ctenophthalmidae). Source: J. Sánchez, M. Urdapilleta, and L. Giambelluca. License: CC BY-NC-SA 4.0.

Figure 10. *Ctenocephalides* sp. (family Pulicidae). Source: J. Sánchez, M. Urdapilleta, and L. Giambelluca. License: CC BY-NC-SA 4.0.

Species included in the **Lycopsyllidae**, **Pygiopsyllidae**, and **Stivaliidae** families are classified in the suborder Pygiopsyllomorpha, with a sister group relationship between the latter 2 families. These 3 families each have general biogeographic differences with a few exceptions of sympatry where they have been shown to occur in the same region. Lycopsyllidae is restricted to Australia including Tasmania. The distribution of Pygiopsyllidae is far broader and includes Australia and East Asia, with 1 genus, *Ctenidiosomus*, represented in South America. Stivaliidae is mainly distributed in New Guinea. Species of the family Pygiopsyllidae usually lack genal and pronotal ctenidia, but present several abdominal terga with well-developed combs, and have an eye, though it is reduced. Pygiopsyllidae contains more than 30 genera, that are associated with metatherians in Australia and South America and with callosciurine squirrels and tree squirrels (Tupaiidae) in the Indo-Malayan subregion. Species in the genus *Ctenidiosomus* are found in cricetid rodents. In addition, some species are associated with birds in Australia (Johnson, 1957; Mardon and Dunnet, 1972; Whiting et al., 2008; Hastriter, 2012).

The families **Macropsyllidae** and **Coptopsyllidae** are sister groups. Macropsyllidae is a small family comprising 2 genera: *Macropsylla* (2 species) and the monotypic genus *Stephanopsylla*. These occur in Australia and are found on murid rodents. Morphologically, Macropsyllidae is very similar to Stephanocircidae, but differs in the single, continuous comb on the head of macropsyllids compared with 2 separate cones in Stephanocircidae. Additionally, Macropsyllidae present an abdomen with combs of long spines, and females have 2 spermathecae of unequal size (Hopkins and Rothschild, 1956; Whiting et al., 2008). Coptopsyllidae fleas are completely combless and vestigial abdominal combs or pseudosetae are absent, with antepygidial bristles. Females possess 2 spermathecae. Coptopsyllidae is also a small group (1 genus, 19 spp.) with Palearctic distribution (Hopkins and Rothschild, 1956; Whiting et al., 2008).

The family **Stephanocircidae** (Figure 2), or helmeted fleas, are unique among fleas because of the division of the forward portion of the head that forms a sort of helmet, which presents more-or-less vertical combs along the posterior margin. A second vertical comb is present along the genal margin. The helmet serves in a manner similar to that of the prow of a boat as it separates hairs as the flea moves through the pelage of its host. The family includes 2 subfamilies, Stephanocircinae, which is restricted to metatherians in the Australian region, and Craneopsyllinae, which is more speciose than Stephanocircinae and is restricted to metatherian and rodent hosts in the Neotropical region (Hopkins and Rothschild, 1956; Traub, 1980; Schramn and Lewis, 1988; Sánchez et al., 2015).
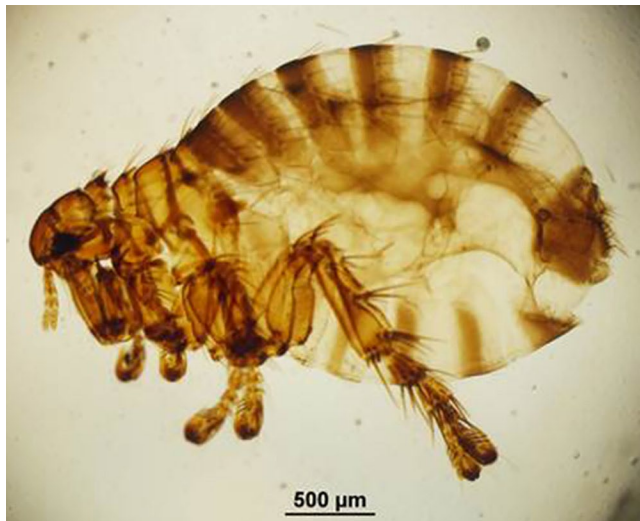
Figure 11. *Dasypsyllus* sp. (family Ceratophyllidae). Source: J. Sánchez, M. Urdapilleta, and L. Giambelluca. License: CC BY-NC-SA 4.0.

Figure 12. Life cycle of the fleas. Source: M. C. Ezquiaga. License: CC BY-NC-SA 4.0.

Vermipsyllidae is a small family comprising 3 genera and 42 species, characterized by lacking a ctenium, the absence of an anal stylet in females, the presence of a frontal tubercle, lacking antepygidial bristles, having very large spiracles, possessing reduced tergites and sternites, especially in females, and having 1 spermatheca. Vermipsyllids are found on carnivores, mustelids (Chaetopsylla), and ungulates (Hopkins and Rothschild, 1956; Whiting et al., 2008).

The family **Rhopalopsyllidae** (Figure 8) is characterized by the absence of true ctenidia, the presence of a lower haft of fronds with a well-developed large or very large somewhat trapezoid-shaped tubercle situated in a groove, a large and sinuate eye, terga with 1 or 2 (or sometimes 3) rows of setae, a complete or incomplete mesocoxal oblique break (this has importance for taxonomic purposes), a symmetrical or asymmetrical antennal club with sexual dimorphism, 4 lateral plantar bristles on the fifth segment of all tarsi, 2 heavy ventral subapical bristles, a solitary long, antepygidial bristle in both sexes, and females with 1 spermatheca. Two very speciose subfamilies are recognized, Rhopalopsyllinae, represented mainly in the Neotropical region of South America, and Parapsyllinae, which is more abundant in the Andean Patagonia region. Although Rhopalopsyllidae is almost exclusively Neotropical, it extends into the southern part of the Nearctic region while 1 genus, associated with birds, is widespread on many islands in the seas surrounding Antarctica and has radiated into the Australian region. Most of the species infest cricetid rodents but a few species have host-switched to birds (Smit, 1987; Linardi and Guimarães, 2000; Beaucournu et al., 2014; Lareschi et al., 2016).
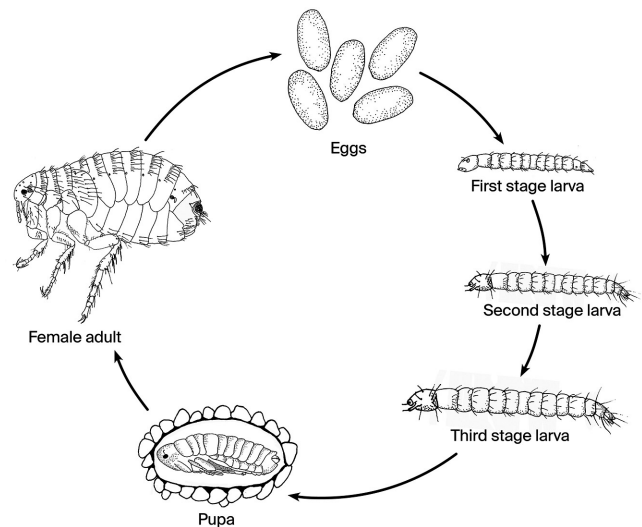
Hystrichopsyllidae, a paraphyletic family, present horizontal, oblique, or vertical genal ctenidia, but these are sometimes very reduced. If a vertical ctenidium is present, it extends far dorsally and has some spines drawn out into long, thin points. A fifth tarsal segment is present with 5 pairs of lateral plantar bristles, and females possess 2 spermathecae. Hystrichopsyllinae is composed of the tribes Ctenopariini with 1 Neotropical genus, and Hystrichopsyllini with 2 Nearctic genera and 1 Palearctic genus (Johnson, 1957; Hopkins and Rothschild, 1962; Whiting et al., 2008).

Ctenophthalmidae (Figure 9) is a paraphyletic family and is sometimes considered a subfamily within Hystrichopsillidae. It is distinguished from the Hystrichopsillidae by the presence of the fifth tarsal segment with 4 pairs of lateral plantar bristles (at times with 1 anterior plantar pair on the ventral surface) and the female possessing only 1 spermatheca (Johnson, 1957; Hopkins and Rothschild, 1966; Whiting et al., 2008).

Pulicidae (Figures 1 and 10) and **Chimaeropsyllidae** are sister groups. Both families share the following characters: A pygidium with 14 pits per side, the inner side of the hind coxa having spiniform setae, having generally 1 row of setae per tergite, and having setae that are usually fine and rather sparse. In addition, Pulicidae is characterized by well-developed eyes without an internal sinus and the female having an anal stylet. In Pulcidae, a genal and pronotal ctenidium may be present or absent in the female, and both sexes usually possess an antepigypdial seta on each side. Species of Chimaeropsyllidae are found exclusively in the Ethiopian region, in xeric environmental conditions, associated with elephant

shrews (Macroscelidae) and small rodents. Pulicidae present cosmopolitan distribution because some of its species have experienced secondary dispersal by their hosts, which are synanthropic rodents, domestic animals, and humans; therefore, some species of Pulicidae are of medical and/or veterinary importance (Linardi and Guimarães, 2000; Whiting et al., 2008).

Leptopsyllidae, **Ischnopsyllidae**, and **Ceratophyllidae** are included in Ceratophyllomorpha. The family Leptopsyllidae is characterized by the presence of a vertical, or subvertical, genal ctenidia (sometimes with at least 3 teeth oriented in a vertical position), the presence or absence of a pronotal ctenidium, and a reduced eye. Leptopsyllidae currently consists of 2 subfamilies, Amphipsyllinae and Leptopsyllinae, mostly Paleartic, with some cosmopolitan species (for example, *Leptopsylla segnis*) associated with cricetid and synanthropic rodents (Johnson, 1957; Hopkins and Rothschild, 1956; 1971).

Species included in the family **Ischnopsyllidae** are known as the bat fleas since they occur exclusively on bats. They are distinguished by the preoral placement of the genal ctenidium at the extreme anterior end of the ventral margin of the head. This ctenidium is typically composed of 2 broad, flattened spines, present in most of the species within the family. Ischnopsyllidae comprises 2 subfamilies distributed on every continent with the exception of Antarctica; with the species being highly host-specific, since the distribution of genera follow that of their hosts on which they have evidently cospeciated (Hopkins and Rothschild, 1956; Johnson, 1957; Linardi and Guimarães, 2000; Withing et al., 2008).

All species of **Ceratophyllidae** (Figure 11) are characterized by the absence of a genal ctenidium and the possession of vestigial eyes. Ceratophyllidae comprises 2 subfamilies, Ceratophyllinae and Dactylopsyllinae, mostly Paleartic, with some cosmopolitan species (for example, *Nosopsyllus fasciatus*) associated predominantly with sylvatic and synanthropic rodents, with some species parasitizing birds (Johnson, 1957; Smit, 1983: Traub et al., 1983; Withing et al., 2008).

Species allocated to the families **Xiphiopsyllidae**, **Ancistropsyllidae**, and **Malacopsyllidae** were not included in the molecular analyses by Whiting and colleagues (2008). Xiphiopsyllidae is an Ethiopian flea, without combs in the head region, with a pronotal ctenidum present, an abdomen with spinelets, and a metanotum without either spinelets or pseudosetae (Hopkins and Rothschild, 1956). Malacopsyllidae (Figure 5) are big fleas; they do not present true ctenidia, their frontal tubercle may be absent or deciduous, and they possess a main row of long setae on the pronotum shifted forward to a sub-basal position, and a hind tarsus

Figure 13. Tungiasis: The leg of a dog infested with *Tunga penetrans*. Source: J. Sánchez, M. Urdapilleta, and L. Giambelluca. License: CC BY-NC-SA 4.0.

with the fifth tarsal segment of all legs enlarged with strong claws and plantar bristles. Finally, species of Malacopsyllidae include only 2 monotypic genera, *Malacopsylla* and *Phthiropsylla*, which occur only in Argentina in association with armadillos and carnivores with carnivores probably as secondary hosts (Johnson, 1957; Smit, 1987; Lareschi et al., 2016).

Geographic Distribution

Fleas are distributed all around the world, present in a range of habitats from equatorial deserts, distributed from the Arctic to Antarctica, through tropical rainforests to the tundra. Sometimes the distribution of fleas is a consequence of their introduction by humans and their pets and livestock. The flea fauna of the Palaearctic region has the most diverse world distribution, while the number of species in the Nearctic, Afro-Tropical, and Neotropical regions is fewer, and that in the East Asian and Australian regions is considerably less. Malacopsyllidae, Rhopalopsyllidae, and Craneopsyllinae are dominant in South America, Xiphiopsyllidae and Chimaeropsyllidae are present in Africa, and Macropsyllidae, Lycopsyllidae, and Stephanocircinae are present in Australia. In contrast, more speciose and paraphyletic flea families, such as, Hystrichopsyllidae, Ceratophyllidae, and Leptopsyllidae, inhabit the Northern Hemisphere (Medvedev and Krasnov, 2006; Whiting et al., 2008).
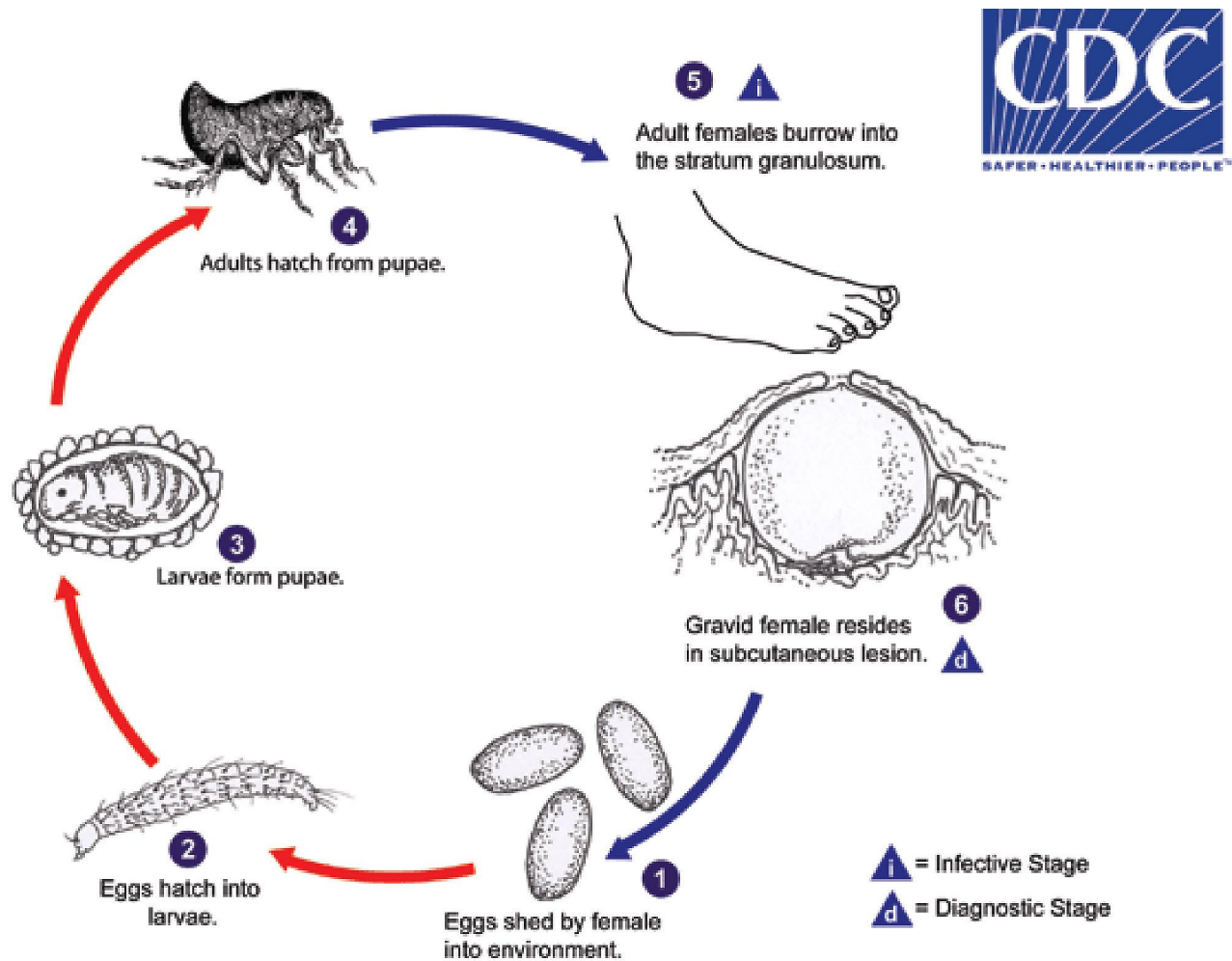
Figure 14. Tungaiasis life cycle. *Tunga penetrans* eggs are shed by the gravid female into the environment (1). Eggs hatch into larvae (2) in about 3–4 days and feed on organic debris in the environment. There are 2 larval stages before forming pupae (3). The pupae are in cocoons that are often covered with debris from the environment (sand, pebbles, etc). The larval and pupal stages take about 3–4 weeks to complete. Afterwards, adults hatch from pupae (4) and seek out a warm-blooded host for blood meals. Both males and females feed intermittently on their host, but only mated females burrow into the skin (epidermis) of the host, where they cause a nodular swelling (5). Females do not have any specialized burrowing organs, and simply claw into the epidermis after attaching with their mouthparts. After penetrating the stratum corneum, they burrow into the stratum granulosum, with only their posterior ends exposed to the environment (6). The female fleas continue to feed and their abdomens extend up to about 1 cm. Females shed about 100 eggs over a 2-week period, after which they die and are sloughed by the host's skin. Secondary bacterial infections are not uncommon with tungiasis. Source: Division of Parasitic Diseases and Malaria, United States Centers for Disease Control and Prevention, 2017. Public domain.

Host Associations

Throughout their history, fleas associated very early with mammals with 4 evidently independent shifts to birds. The majority of flea species are associated with mammal hosts, with about 74% of described species recorded from rodents. In addition, rodents comprise 82% of all specific and/or principal hosts for fleas. Primary association of fleas with rodents is observed in all parts of the world except Australia, where fleas are harbored mainly by marsupials (Marshall, 1981; Krasnov and Medvedev, 2006; Whiting et al., 2008).

Fleas vary greatly in the degree of their host specificity ranging from having a very narrow host-range (highly host specific) to being highly host-opportunistic with a wide host-range. Although Siphonaptera are rarely monoxenous at the host species level, there are clades of fleas associated with a particular host group at higher ordinal levels. For example, species of *Parapsyllus* (family Rhopalopsyllidae, subfamily Parapsyllinae) are exclusively associated with birds, fleas of the family Ischnopsyllidae are associated with bats, and fleas of the family Malacopsyllidae are associated mostly with ar-

madillos. Besides, mammals that generally have vast home ranges and do not inhabit dens for rearing their young almost always lack fleas of their own, whereas mammals or birds with dens or nests reused seasonally exhibit a more specific flea fauna (Marshall, 1981; Krasnov and Medvedev, 2006; Whiting et al., 2008; Beaucournu et al., 2014; Lareschi et al., 2016).

Biology and Reproduction

The life cycle of fleas (Figures 12 and 13), like other holometabolous insects, consists of eggs, larvae, pupae, and adults. Female fleas of some species oviposit on the host and the eggs drop off into the nest or burrow, while other species mate and oviposit both on-host and off-host (for example, *Xenopsylla cheopis*). Each female may lay 300–800 eggs per day in the soil or on the host body. Eggs then fall off the host and, depending on the species, temperature, and humidity, they hatch into first-stage larvae in about 3–4 days and feed on organic debris in the environment. Three stages of larvae are recognized (with the exception of species of *Tunga*, which presents only 2 stages). The larvae do not suck blood; they feed on feces of adult fleas that contain digested host blood, skin flakes, or the plumage of hosts, and other organic substances. The 3/2 larval stages last between 14 and 21 days. Then they stop feeding and molt to pupae, which live in cocoons that are often covered with debris from the environment (such as, sand, pebbles, etc.). The larval and pupal stages take about 3 to 4 weeks to complete. Afterwards, adults hatch from pupae and seek out a warm-blooded host for blood meals, but when the temperature is very low or in the absence of a host, the pupae remain quiescent in their cocoons for several months. The completely hematophagous adults must parasitize a host to feed themselves; if possible, they do so more than once a day and there is only development of eggs in females if they ingest blood. The cycle comprises a total of 3 to 6 weeks in optimal conditions, but often lasts several months, depending on the environmental conditions and the species. Fleas can withstand prolonged periods of desiccation (6 months or more) when the proper host is not present (Marshall, 1981; Linardi and Guimarães, 2000; Medvedev and Krasnov, 2006).

Fleas of the genus *Tunga* (Tungidae) are particular in having females that penetrate and embed in the skin of the host, while males move over the body of the host. No gravid females dig in the epidermis of the host, instead they penetrate mainly in the subungual, periungual, interdigital, and plantar areas, and once introduced, plunge their head toward the deepest part of the integument and, with their abdomen sticking out of the host's body, are fertilized by males from the outside. After embedding, the abdomen of the female
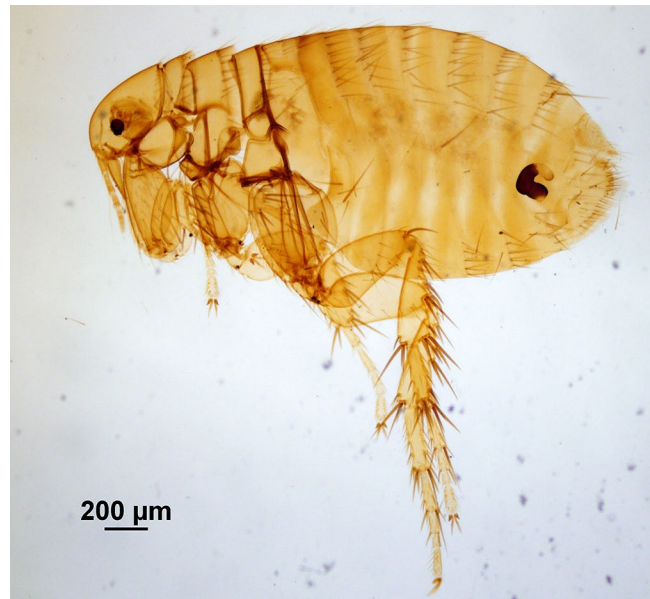

Figure 15. *Xenopsylla cheopis*. Source: J. Sánchez, M. Urdapilleta, and L. Giambelluca. License: CC BY-NC-SA 4.0.

begins to relax and the head and legs become less visible, depending on the species. This is termed neosomy. The last 2 or 3 abdominal segments are exposed on the surface and have spiracles for breathing, as well as the genital opening and the anus. The eggs mature in a week and are expelled, falling to the ground, where the 2 larval stages develop and in 10 to 14 days they change to pupae. After 1 week, the adult emerges and the female goes in search of a new host, and in this way the cycle is restarted, with a total duration of 17 to 21 days (Marshall, 1981; Linardi and Guimarães, 2000).

Although the laciniae are not heavily serrated, females of *Malacopsylla grossiventris* (Figure 5) fix their mouthparts to the skin of the venter of their armadillo hosts, clinging very firmly to the coarse hairs of these hosts. These fleas present enlarged tarsal claws, apparently modified for grasping, and copulate on the venter of their hosts (Johnson, 1957; Smit, 1987; Ezquiaga and Lareschi, 2012).

Medical and Veterinary Importance

From an epidemiological point of view, fleas are important as parasites, intermediate hosts, and vectors. Many species of fleas cause serious medical and economic problems, since flea bites on people and domestic animals are insidious, causing severe irritation and discomfort due to the formation of papules and urticarias, and they affect blood loss. The sites of bites are mainly the legs and the waist, and in allergic people the injuries can be more severe, including formation of lacerations and alopecias, and scratching can produce bacterial superinfection. Another pathology is tungiasis (Figure 14), caused by
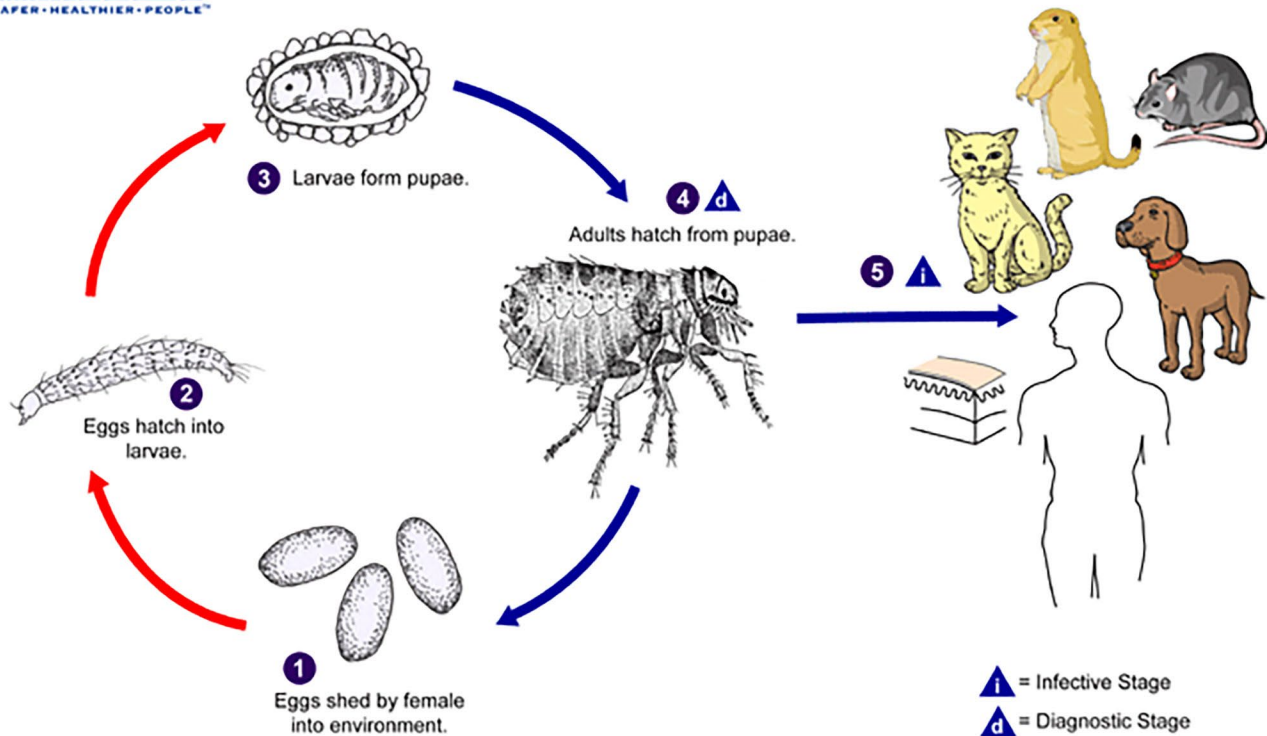
Figure 16. General flea life cycle. Fleas, like other holometabolous insects, have a 4-part life cycle consisting of eggs, larvae, pupae, and adults. Eggs are shed by the female in the enviroment (1). Eggs hatch into larvae (2) in about 3–4 days and feed on organic debris in the environment. The number of larval instars varies among the species. Larvae eventually form pupae (3), which are in cocoons that are often covered with debris from the environment (sand, pebbles, etc.). The larval and pupal stages take about 3–4 weeks to complete. Afterwards, adults hatch from pupae (4) and seek out a warm-blooded host for blood meals. The primary hosts for *Ctenocephalides felis* and *C. canis* are cats and dogs, respectively, although other mammals, including humans, may be fed upon. The primary hosts for *Xenopsylla cheopis* are rodents, especially rats. In North America, plague (*Yersinia pestis*) is cycled between *X. cheopis* and prairie dogs. Humans are the primary host for *Pulex irritans.* The chigoe flea (*Tunga penetrans*) has a different life cycle and is discussed above. Source: Division of Parasitic Diseases and Malaria, United States Centers for Disease Control and Prevention, 2017. Public domain.

Tunga penetrans (the life cycle of which is described above; see also Figure 15) that parasitizes humans, domestic animals, and wildlife in tropical areas. Tungiasis is a zoonosis which causes severe complications like deformation of digits, loss of toenails, tetanus, gangrene, and superficial lacerations prone to opportunistic infections. *Ctenocephalides canis* and *C. felis* (family Pulicidae) are intermediate hosts of helminths, such as *Dipylidium caninum* and *Hymenolepis diminuta*, respectively, parasites of carnivores and rats. The larvae of fleas ingest cestode eggs, and when the adult flea metamorphoses into an adult, the cestode cysticercoid transfers to the adult. These tapeworms can develop in humans if they inadvertently ingest an infected flea. In addition, fleas act as vectors for several disease-causing organisms, including bubonic plague (*Yersinia pestis*), murine typhus (*Rickettsia typhi*), among other species of pathogenic bacteria such as those from the genera *Bartonella* and *Rickettsia*, as well as viruses. In recent years, the flea-borne spotted fever agent *Rickettsia felis* has emerged and can be found throughout the world. Fleas have also been proven to harbor, and sometimes transmit, *Bartonella henselae*, the agent of cat-scratch disease. Flea-borne organisms are widely distributed throughout the world in endemic disease foci, where components of the enzootic cycle are present. However, flea-borne diseases may re-emerge in epidemic form because of changes in vector-host ecology due to environmental and human behavior modifications (Bitam et al., 2010; Tsai et al., 2011; Gutiérrez et al., 2015; Linardi, 2017; Abreu Yanes et al., 2018; Whiting et al., 2008).

Fleas of Medical Importance

Some species are notable for a variety of reasons. For instance, *Xenopsylla cheopis* (Figure 15) is perhaps the most notorious flea because it is the vector of the bacterium *Yersinia pestis* which causes both pneumonic and bubonic plague in humans. The plague produces an inflammation of the lymph nodes, in severe cases causing the rupture of these lymph nodes. It is fatal in almost 50% of untreated cases. Fleas contaminate by sucking infected blood from a rodent and the bacterium multiply to the point of clogging the proventriculus. When the flea returns to feed, the blood does not enter the digestive system and the contaminated blood is regurgitated at the point of the bite. *Xenopsylla cheopis* parasitizes not only rodents, but other vertebrates including humans and it is also a vector of murine typhus caused by *Rickettsia mooseri*. Transmission takes place due to the flea bite or by the contamination of wounds in the skin by the flea's feces. Primary pneumonia and primary septicemia may also ensue from interactions with infected fleas (Linardi and Guimarães, 2000; Krasnov, 2008; Linardi, 2017).

Pulex irritans (Pulicidae) (Figure 1), called the human flea since it was first described from a human, has been the most studied species within the genus *Pulex*. *Pulex irritans* has been confused with similar species for years, but recently characters of diagnostic importance to identify it have been reported. There is evidence of a long relationship between *P. irritans* and humans. Currently, *P. irritans* has cosmopolitan distribution, probably due to human transportation, but species in the genus *Pulex* appears to be Central American to South American in origin, where several congeners are known. Although this flea is presently relatively promiscuous, initial evolution is likely to have involved a single host, probably a peccary, closely associated with humans. Currently, a variety of mammals are known to serve as hosts of *P. irritans* and because of its close association with domestic mammals such as pigs and dogs, *P. irritans* can also bite humans, causing dermatitis. *Pulex irritans* is also well-able to transmit several zoonotic pathogens, includingthe flea-borne spotted-fever rickettsiosis, and it has been important in transmitting *Yersinia pestis* from human to human, and possibly from domestic animals to humans (Hopla, 1980; Marshall, 1981; Buckland and Sadler, 1989; Brouqui and Raoult, 2006; Lareschi et al., 2018).

Within the order Siphonaptera, species of the genus *Tunga* are particularly unique due to their biology and morphology. These fleas have the capacity to perforate the skin of their hosts by using their mouthparts and they all present neosomy. With the exception of *T. penetrans*, the remaining species are parasites of wild mammals, most of them rodents and armadillos (Linardi and Guimarães, 2000; Whiting et al., 2008; Pampiglione et al., 2009; De Avelar, 2012). Females of *T. perforans* are unique in perforating the osteoderms of their armadillo hosts and living inside the carapace. Osteoderms, or bony dermal scutes, are compact and are overlaid by epidermal horny scales which form a protective dorsal cover (carapace) of armadillos. Thus, these fleas have specialized mechanisms to perforate the thin skin between these plates (Ezquiaga et al., 2014). Additionally, osteoderms of piche armadillos (*Zaedyus pichiy*) with holes produced by *Tunga* were recovered at the archaeological shell midden called Las Hormigas, on the northern coast of the province of Santa Cruz in the Argentinean Patagonia (Hammond et al., 2014).

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