Part V

ECTOPARASITES

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PLATYHELMINTHES

Monogenea (Class)

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Phylum Platyhelminthes

Class Monogenea

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Chapter 60

Monogenea (Class)

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Introduction

The phylum Platyhelminthes, known as flatworms, includes the class Monogenea, mainly ectoparasites of the skin, fins, gills, and urinary bladder of fishes, amphibians, and some reptiles (Kearn, 2014). However, there is one species that is a parasite of mammals, *Oculotrema hippopotami* Stunkard, 1924, from the eye of the African hippopotamus *Hippotamus amphibius* (see Stunkard, 1924; Yamaguti, 1963). There also are a few species of monogeneans that infect cephalopods (Rohde, 2011). *Isancistrum loliginis* has been reported from squids, (*Loligo* spp.) and *Polystoma loliginum* has been reported and collected from other cephalopods (Overstreet and Hoschberg, 1975). Sometimes, instead of living as ectoparasites as is usual, a few monogeneans may be found living within the stomodeum, proctodeum, bladder, or diverticula of a host (Roberts and Janovy, 2008).

Classification: Historical Review

Entobdella hippoglossi was the first species of Monogenea described. Müller described it as *Epibdella hippoglossi*, a parasite from the skin of the Atlantic halibut *Hippoglossus hippoglossus*. In the original descriptions of this monogenean, it was mistaken for a leech and the author named it *Hirudo hippoglossi* (see Kearn, 2014).

There is controversy about whether the name that refers to this group of Platyhelminthes should be "Monogenea" or "Monogenoidea." The Latin term Monogenea derives from van Beneden's (1858) use of the French term "monogénèses" in French (cited in Carus, 1863) and is now the generally-used term for this group (Carus, 1863; Wheeler and Chisholm, 1995). Monogenoidea sensu Bychowsky (1937) is not the correct name because its use predates use of the term Monogenea. In addition, the ending of -oidea in animal taxonomy always refers to superfamily designations. Some have argued for the use of Monogenoidea as the valid name of the class; however, this is based on erroneous assumptions of authorship, priority, and rank as defined in the International Code of Zoological Nomenclature (ICZN, 2012). The resolutions adopted at the Fourth International Congress of Parasitology (ICOPA IV) in Warsaw, Poland in 1978 during the Round Table "Monogenea: Problems of Systematics, Biology, and Ecology" resulted in an agreement supported by all participants to adopt Monogenea as the name of the class rather than Monogenoidea. For more information on this process, see Wheeler and Chisholm (1995).

The Monogenea have been divided into 2 major subgroups: **Polyopisthocotylea** (which means, in adults, possession of a more complex opisthaptor) and **Monopisthocotylea** (which means possession of a single opisthaptor). The morphology of the adult's attachment organs is what distinguishes these subgroups. The morphology of the attachment organ in the larval forms is what distinguishes the **Oligonchoinea** (**oligo** = few; Greek) and **Polyonchoinea** (**poly** = many; Greek) (Justine, 1998). The groups do not overlap because of the position of the polystomatids and sphyranurids.

A phylogenetic analysis using morphological data, the ultrastructure of spermiogenesis, and spermatozoa of the taxon Rhabdocoela (Platyhelminthes) produces a hypothesis that Monogenea is a monophyletic group that is more closely related to tapeworms than other platyhelminths (Justine, 1991; Zamparo et al., 2001); however, analyses of molecular data (18S or 28S rDNA sequences) do not support the monophyly of the Monogenea (Mollaret et al., 1997). The analyses conducted by Mollaret and colleagues (1997) suggest that Monogenea is a paraphyletic group, although the monophyly of Monopisthocotylea and Polyopisthocotylea were suggested (Mollaret et al., 2000). The molecular data agree with studies of the ultrastructure of spermiogenesis of Polyopisthocotylea, all of which share the synapomorphy of having lateral microtubules present in the principal region of the spermatozoon. In the monopisthocotyleans, dorsal and ventral microtubules are absent from the principal region of the spermatozoon (Justine, 1991). However, an analysis with both the morphological and molecular data of 18S rDNA analyses supports the monophyly of the group as Monogenea (Mollaret et al., 2000).

Current Classification

The current classification of Monogenea divides the class into 3 subclasses: **Polyonchoinea**, **Oligonchoinea**, and **Polystomatoinea** (Boeger and Kritsky, 1993). The monophyly of Monogenea as a class is supported by the following morphological synapomorphic (shared derived) characteristics: Adult and oncomiracidium possessing 2 pairs of eyespots, 16 marginal hooks in the haptor, a haptor with a single ventral pair of hamuli (= anchors; Boeger and Kritsky, 1993), and an oncomiracidium with 3 rows of ciliary epidermal bands present (Brooks, 1989; Boeger and Kritsky, 1993).

The monophyly of Polyonchoinea is supported by the mouth being on the ventral surface, the reduced numbers of subsurface sperm microtubules, the oncomiracidium, and adults having 14 marginal hooks and 2 central hooks in the haptor (Boeger and Kritsky, 1993). The monophyly of Oligonchoinea is supported by having a crochet en fléau present that is hook-like (the crochet en fléau is the form of the termination of the central part of the clamp of the haptoral sclerite), and the presence of a single pair of lateral sclerites, 4 pairs of haptoral suckers, and diverticula in the walls of the intestine (Boeger and Kritsky, 1993).

The monophyly of subfamily Polystomatoinea is supported by the absence of egg filaments (Boeger and Kritsky, 1993). Polystomatoinea is the sister group of Oligonchoinea. The relationship is supported by 6 shared synapomorphies, namely: Having more than 2 testes; the presence of a gastrointestinal canal; the presence of haptoral suckers in the adults; the presence of hooks in the adults' haptoral sucker; that there are 3 parts of the haptoral suckers; and the presence of 2 lateral vaginal ducts (Boeger and Kritsky, 1993). The clade formed by Oligonchoinea + Polystomatoinea is the sister group of Polyonchoinea (see Figure 1) (Boeger and Kritsky, 1993).

Brabec et al. (2023) show 2 different arrangements of the phylogenetic relationships of the flatworms. They elevated the Monopisthocotylea and Polyopisthocotylea to the level of class. For additional clarification see the modified trees given in the introduction to the Platyhelminthes in this book as well the paper by Brabec and colleagues (2023).

Body Wall

The monogeneans, like the digeneans (trematodes/flukes) and cestodes (tapeworms), possess an external layer called a tegument. The surface of this is a syncytial stratum laden with vesicles and mitochondria. This layer is enclosed externally by a plasma membrane and glycocalyx and internally by a membrane and basal lamina. This stratum is the distal cytoplasm and it is connected by trabeculae (internuncial processes) to the cell bodies, or cytons (perikarya), located inside a layer of superficial muscle. Often, the outer surface of the tegument has scattered short microvilli. In some species the microvilli are absent and in their place shallow pits occur (Roberts and Janovy, 2008).

The tegument is the site of the exchange by diffusion of gases and nitrogenous waste between the body and the environment. Some nutrients in the form of amino acids are taken in by pinocytosis or the cellular mechanism of taking liquids through the cellular membrane and forming a vesicle (Brusca and Brusca, 2003).

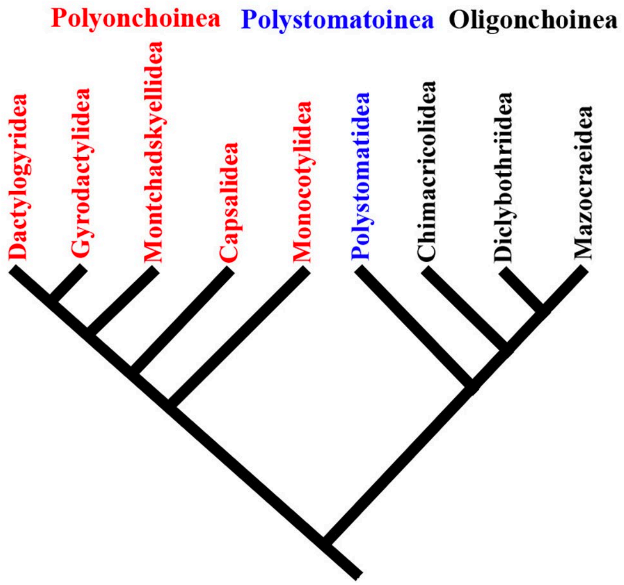

Figure 1. Relationships of the orders of Monogenea; synapomorphies of each other. Source: Adapted from morphologies in Boeger and Kristky, 1993. License: CC BY-NC-SA 4.0.

Life Cycles of Monogeneans

All monogeneans have a direct life cycle, which means that they do not have an intermediate host. They have tiny, free-swimming ciliated larvae called oncomiracidia (singular: miracidium) that hatch directly from an egg. Some life cycles have been studied, particularly those of *Dactylogyrus*, *Polystoma, Diplozoon*, *Benedenia*, and *Microcotyle* (see Bychowsky, 1957). For example, *Polystoma nearcticum*, a parasite of North American hylid frogs, lives in the urinary bladder of adult frogs and tadpoles of *Hyla versicolor* (= urinary bladder generation) and on the gills of their tadpoles (= branchial generation) (Bentz et al., 2006). In the urinary bladder of toads, the adults of the bladder generation release embryonated eggs into the urinary bladder and are voided with urine. The development of the eggs begins in the water and fully developed larvae enter the gill chambers of the tadpoles, thereby ending the urinary bladder generation and initiating the branchial (gill) generation. These larvae attach to gills of tadpoles and mature in about 22 days (see Figure 2) (Olsen, 1962).

The life cycle of monogeneans has been shown to be influenced by water temperature. For example, in *Neobenedenia girellae* infections, parasite growth, egg production, and emerging second generations stay on the same host. Infection levels and growth change on the skin corresponding with

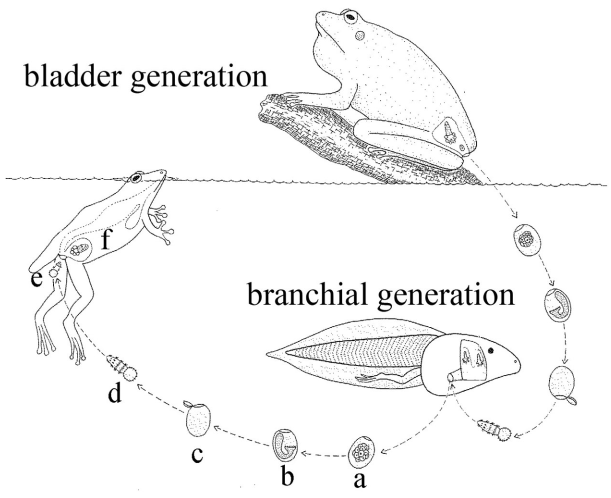

Figure 2. Life cycle of *Polystoma nearcticum* showing 2 generations. Note: a) unembryonated eggs laid on gills of tadpoles are washed into the water; b) fully developed larva, identical to those from the bladder generation; c) empty egg shell; d) the larva free in the water; e) the larva enters the cloaca of the metamorphosing toad eventually ending up in the urinary bladder; f) developing monogeneans enter the bladder and initiate the urinary bladder generation, reaching sexual maturity simultaneously with the toad. Source: Adapted from Olsen, 1962. License: CC BY-NC-SA 4.0.

differences in water temperatures. At 30 °C, the body length of worms is significantly greater than worms from fish reared at 20 °C or 25 °C. In the same manner, the number of eggs produced by adults is greater at 30° C than 20 °C or 25 °C (Hirazawa et al., 2010).

In most species of monogeneans, new hosts are infected directly by the oncomiracidia, the tiny, free-swimming ciliated larva (the adults are oviparous). The exceptions to this involve members of the Gyrodactylidae, most of which are viviparous; that is, small, unciliated larval individuals, similar to the parent, are produced within the body of the parent. After they have developed sufficiently, these young worms spread to new hosts by contagion. They use the substrate of the water body as a staging post where feeding fish may pick up the parasites. In some species the young worms float in the water until they come in contact with fish. When an infected fish dies, its parasites will infect a new host that comes close to the dead fish. Adult members of *Gyrodactylus* have several generations of embryos (young worms) within them, and each embryo has another embryo inside, even before it is released from the adult. In this manner, each adult worm produces fully developed offspring that may attach to either the same or a different host. This produces exponential population growth, which proves to be particularly problematic in freshwater fish farms (see Figure 3) (Cable and Harris, 2002).

Body Form

Monogeneans are flatworms, more or less dorsoventrally flattened, with bilateral symmetry and small sizes. The majority of them are tiny, but some species have larger bodies. In general, size range of the body is from 0.2 mm to 10.0 mm, but sometimes can be even larger. Usually, they are lanceolate, elliptical, or discoid in outline shape. The body may be clear to whitish or gray, depending upon the species, and the **eggs** generally are yellowish. The body is subdivided into

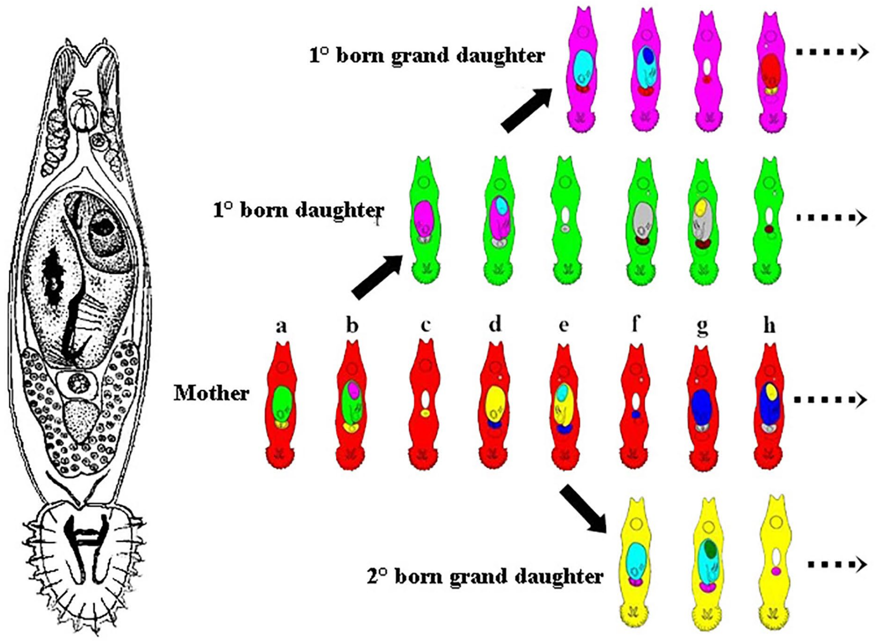

Figure 3. Life cycle of *Gyrodactylus* sp. Source: Adapted from Cable and Harris, 2002. License: CC BY-NC-SA 4.0.

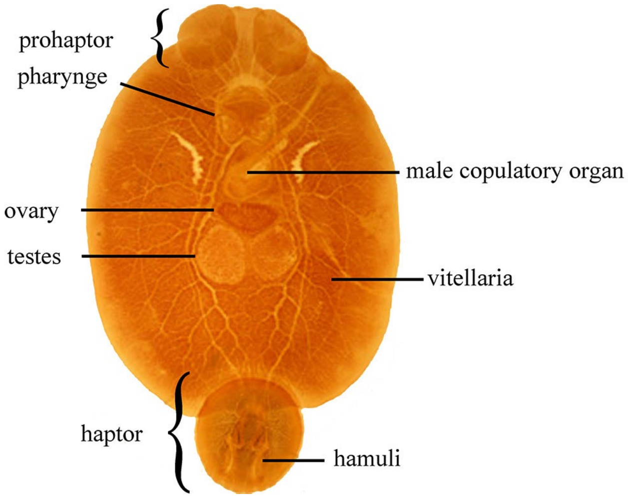

Figure 4. Subclass Polyopisthocotylea *Protomicrocotyle manteri* Bravo-Hollis, 1966, parasite of the Crevalle jack *Caranx hippos* from Campeche, Mexico. Source: G. Pulido-Flores. License: CC BY-NC-SA 4.0.

3 regions: The **cephalic region** (anterior to the **pharynx**), the **trunk** (body proper), and the **haptor** (sometimes called the **opisthaptor**; the organ used to attach to the host).

Cephalic Region

The anterior end of the body, usually called the **prohaptor**, includes the feeding and adhesive organs. Sometimes the prohaptor structures are called **head lappets**, **cephalic glands**, **head organs**, and/or **pre-oral suckers**. For example, in *Protomicrocotyle manteri* and *Benedeniella posterocolpa*, the prohaptor is formed by 2 large suckers (Figures 4 and 5), and in *Polystomoidella oblongum*, the prohaptor has an oral sucker (Figure 6).

Haptor

The haptor of monogeneans is the posterior attachment organ. In the past, the majority of the papers referred to the attachment organ as an opisthaptor (meaning posterior haptor). Malmberg (1990) called the attachment organ of the oncomiracidium a haptor and he referred to the organ in adults as an opisthaptor. In most of the recent literature, the authors refer to the attachment organ as a haptor without regard to the developmental state.

The haptor of adults may be a single unit forming a simple muscular disc or a muscular sucker with 1 or 2 pairs of **hamuli** (Figure 5) and may have 1 or 2 transverse bars. Or they may have a complex attachment organ consisting of 2 or more muscular **suckers** or **clamps**. In some taxa, the haptor also has a **haptoral appendix** and the suckers are armed with **sclerites** (Figures 4 and 6) (Yamaguti, 1963;

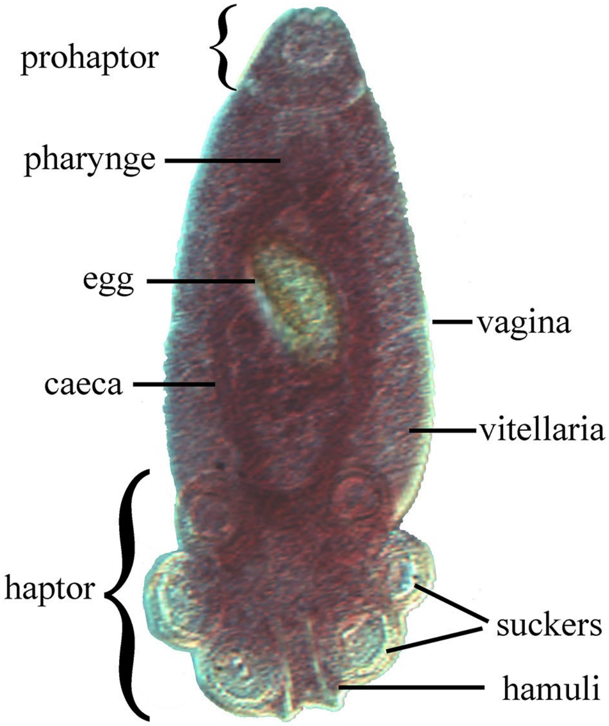

Figure 5. *Benedeniella posterocolpa* (Hargis, 1955) Yamaguti, 1963 (subclass Polyonchoinea), parasite of *Rhinoptera bonasus* from Ciudad del Carmen, Campeche, Mexico. Source: G. Pulido-Flores. License: CC BY-NC-SA 4.0.

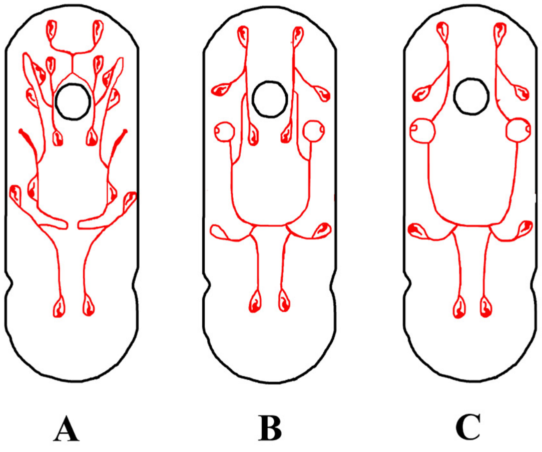

Figure 6. *Polystomoidella oblongum* (Wright, 1879) (subclass Polystomatoinea), parasite of *Kinosternon hirtipes* from Tezontepec de Aldama, Hidalgo, Mexico. Source: G. Pulido-Flores. License: CC BY-NC-SA 4.0.

Schell, 1970; Malmberg, 1990). For example, *Denarycotyle gardneri* has a haptor with a central loculus, an additional loculus on either side of the central loculus, and 10 peripheral loculi. There are 2 accessory structures (for which the function is unknown) on the dorsal surface of the haptor and on each hamulus is a sclerotized accessory piece. The margin of the haptor has 14 hooklets (for a visual depiction, see Figure 1A from Pulido-Flores et al., 2015). *Neonchocotyle violantei* has an asymmetrical haptor with 3 paired sucker-sclerite complexes with the longitudinal axis of the haptor forming an angle of approximately 45° from the midline of the body and a dorsal haptoral appendix with pairs of microhooks (for a visual depiction, see Figures 1 and 4 from Quiterio-Rendon et al., 2018).

For all monogeneans, the haptor is the principal attachment organ. Even a larva has a tiny haptor when it hatches from an egg. It might be armed with sclerotized unhinged or hinged marginal hooks or spines that give it a strong capacity for attachment. This structure is retained in adults in the majority of the species and, as it grows, it expands into the characteristic haptor of the adult.

The total number of marginal hooks on the haptor differs among species. Some species have unhinged marginal hooks that number 10, 14, 16, or 18. They present in a symmetrical manner, such as, in species with 10 hooks, they are arranged with 5 hooks on each side of the hamuli; that is, 5 lateral + 5 lateral = 10 total hooks. In species with hinged marginal hooks, the number is either 10 or 16. The details of how these patterns of hooks were defined can be seen in Malmberg (1990). Generally, the unhinged and hinged marginal hooks retain their shape during ontogeny, but certain marginal hooks can move from their original position or sometimes even disappear (for more information, see Malmberg, 1990). The various patterns of marginal hooks are consistent among each different group of monogeneans.

Osmoregulatory System

The osmoregulatory system in monogeneans is similar to that of other Platyhelminthes and composed of **flame cells** interconnected by tubular **ducts**. Malmberg (1990) described 3 types in monogeneans and related them to 3 groups characterized by the different patterns of marginal **hooks**. Members of group A have 10 marginal hooks and a type of **spermatozoa** that is in taxa more basal in the cladogram of Monogenea. Members of group B (called the intermediate type) also have 10 marginal hooks but the spermatozoa is more derived than those of group A. Members of group C, called the Dactylogyrid type, are those with other patterns of marginal hooks (not 5 + 5 = 10) (see detailed characterizations in Malmberg, 1990).

Group A has the most simple type of osmoregulatory system, consisting of an anterior and a posterior protonephridial arrangement in the body of the oncomiracidium that has few flame bulbs, both arrangements opened laterally, either separately or by a common bladder. Members of group B, the intermediate type (also with 5 + 5 = 10 haptoral hooks), has an osmoregulatory system consisting of an anterior protonephridial arrangement (which extends through one half of the body) that opens into the posterior arrangement. The members of group C, the Dactylogyrid type, have an osmoregulatory system consisting of propulsive flame cells in the anterior and the posterior main canals (see the figure in Malmberg, 1990).

It is interesting to reflect on how the patterns of haptoral hooks and the patterns of the osmoregulatory systems are consistent with each other. Of course, that is the type of evolutionary pattern that one should expect—groups of characteristics/features that show patterns of evolution that are the same. This subject cannot be dealt with here, but it is sufficient to note that this type of similar pattern of characters (character evolution) is the basis of modern hypotheses of the phylogenetic relationships of the taxa (natural groups) of organisms. For those interested in the evolution of species and the methodology used to discover patterns of character evolution, see Brooks and McLennan (1991; 1993; 2002), as well as the studies cited within those, and those who have cited these works.

Digestive System

In general, in most species of monogeneans the digestive system is incomplete (they do not have an anus). Often, the **mouth** is surrounded by an **oral sucker** that opens in a short **prepharynx**, which connects to the muscular, glandular **pharynx**. In turn, the pharynx connects to the **esophagus**, which leads to the **intestine**. The intestine is divided into 2 **cecae** in most species; however, some species have an intestine composed of only a single cecum. Species of the genera *Tetraonchus* and *Udonella* are examples of those with only a single cecum (Schell, 1970). The cecae may be branched or unbranched, and they may end blindly or they may anastomose (connect) posteriorly.

Nervous System

The nervous system in monogeneans is ganglionic; that is, it is formed by 2 **cerebral ganglia** located in the anterior region of the body that are united by a transverse commissure. From each node arise 2 **nerves**: 1 dorsolateral and 1 ventrolateral, that run toward the posterior end of the body. From these, numerous secondary branches lead from the lateral nerves then anastomose with each other, forming a complex, ladder-like network. Also, some anterior nerves run out from the cerebral ganglia, in particular, those associated with the **sense organs**, such as ocelli, which are located in the anterior region. Many larval or juvenile forms have **ocelli** (**eyespots**) that provide orientation using light. The adults of some taxonomic groups retain the larval ocelli and others lose them, sometimes leaving fragments of retinal pigment where they were.

Male Reproductive System

Monogeneans are hermaphroditic, but cross-fertilize. In general, the male and female **gonopores** are located some distance from each other, making self-fertilization difficult to impossible, although in some taxa they are located close together. The male reproductive system consists of 1 to several **testes**, which are located anterior or posterior to the single **ovary**. A **vas efferent duct** (**vas efferens**) runs out from each testis, if there is more than one; the vasa efferentia join together to form a single duct, the **vas deferens** that connects to the **seminal vesicle**. That in turn is connected to the male copulatory organ. Sometimes the **genital atrium** (that is, the area where the male and female gonopores can be found) may be present or absent. The **male copulatory organ** (called a **cirrus**) can be armed or unarmed, is sometimes sclerotized, and extends out of the common genital pore, which usually opens ventrally. Sometimes **prostatic glands** are present. For example, *Denarycotyle gardneri* has 1 testis with the vas deferens arising from the left side of the testis. The vas deferens is enlarged to form a spherical reservoir to hold sperm, and it leads to a smaller reservoir that is curved toward the left side of the body. The vas deferens is a loosely coiled, narrow duct that ascends dorsally, posterior to the genital pore, to connect to a seminal vesicle, then to the ejaculatory bulb and the male copulatory organ. In this species, the male copulatory organ is a short, sclerotized tube (for a visual depiction, see Figure 1B from Pulido-Flores et al., 2015). *Neonchocotyle violantei* has 8 testes. Its seminal vesicle is elongate, extending anteriorly to the proximal male copulatory organ, which is located within a pouch that is longer than the male copulatory organ (for a visual depiction, see Figure 1A from Quiterio-Rendon et al., 2018).

Female Reproductive System

The female reproductive system consists of 1 **ovary** of variable shape and position among the different species. The **oviduct** connects the ovary with the **ootype** and the **vitelline duct**, and the **vagino**- and **genitointestinal ducts** also open out. Associated with these structures is the **Mehlis' gland**, a duct that runs from the ootype and ends in the **genital pore**. Monogeneans usually have 1 **vagina**, but some groups have 2 vaginas that usually are connected to the **seminal receptacle**.

Denarycotyle gardneri has an ovary that is elongate, V-shaped, with the lateral arm of the "V" encircling the right intestinal cecum dorsoventrally, and then it narrows to form the oviduct. The oviduct, the seminal receptacle, and the common vitelline duct all join at the ootype. In this species, the vagina is muscular, unsclerotized, and sac-like. The seminal receptacle is present and the vitellaria (yolk-producing glands) extend from the level of the posterior portion of the pharynx to the posterior of the body proper (for a visual depiction, see Figure 1B from Pulido-Flores et al., 2015).

Neonchocotyle violantei has 2 vaginae that run parallel in the proximal portion and non-parallel in the distal portion. The proximal region, connected to the vitelline reservoir, is glandular and the muscular distal region connects to the vaginal pore (female gonopore). The vaginal pores open ventrally. The ovary of this species is tubular, with deep lobes and ascending and descending branches that reach to the region of the oviduct. The descending branch is coiled and connects posteriorly to the ootype. The ootype is dorsal to the ovary, but ventral to the vas deferens, and it leads to the uterus and the seminal receptacle (for a visual depiction, see Figures 1A and 2, and the detailed description in Quiterio-Rendon et al., 2018).

In *Neonchocotyle violantei*, the vitellaria are abundant, follicular, and they are arranged laterally along the entire body, and sometimes into the haptor. An efferent duct extends from the vitellaria and fuses to form the vitelline duct in close proximity to the oviduct. Near this point, they form a vitelline reservoir. In this species, the transverse vitelline ducts are dorsal, forming a Y-shaped reservoir; the proximal region of the vaginae are connected to the anterior branches of the reservoir and the posterior region of the reservoir is joined to the oviduct (for a visual depiction, see Figures 1A and 2 from Quiterio-Rendon et al., 2018).

Fertilization of the ova occurs in the ootype. Fully developed eggs are operculated and they have 2 polar filaments (some species have a single filament, others have none). The number of eggs is variable among the species; these are released to the outside through the genital pore.

The structural details of the various species of Monogenea are complex and sometimes difficult to envision. Studying the descriptions of several different species will provide a better understanding of this complexity.

Taxonomic Classification

The taxonomic classification of the Class Monogenea follows the phylogenetic analysis of Boeger and Kritsky (1993).

Class Monogenea van Beneden, 1858
- Subclass Polyonchoinea Bychowsky, 1937
  - Order Monocotylidea Lebedev, 1988
    - Family Monocotylidae Taschenberg, 1879
    - Family Loimoidae Price, 1936

Order Capsalidea Lebedev, 1988
Family Acanthocotylidae Price, 1936
Family Capsalidae Baird, 1853
Family Dionchidae Johsnton & Tiegs, 1922
Order Montchadskyellidea Lebedev, 1988
Family Montchadskyellidae Bychowsky, Korotajeva & Gusev, 1970
Order Gyrodactylidea Bychowsky, 1937
Family Gyrodactylidae Van Beneden & Hesse, 1863
Family Anoplodiscidae Tagliani, 1912
Family Bothitrematidae Price, 1936
Family Tetraonchoididae Bychowsky, 1951
Order Dactylogyridea Bychowsky, 1937
Suborder Calceostomatinea Gusev, 1977
Family Calceostomatidae Parona & Perugia, 1890
Suborder Neodactylodiscidae Kamegai, 1972
Family Neodactylodiscidae Kamegai, 1972
Suborder Amphibdellatinea Boeger & Kritsky, 1993
Family Amphibdellatidae Carus, 1885
Suborder Tetraonchinea Bychowsky, 1937
Family Tetraonchidae Monticelli, 1903
Family Neotetraonchidae Bravo-Hollis, 1968
Suborder Dactylogyrinea Bychowsky, 1937
Family Dactylogyridae Bychowsky, 1933
Family Pseudomurraytrematidae Krtisky, Mizelle, & Bilqees, 1978
Family Diplectanidae Monticelli, 1903
Subclass Polystomatoinea Lebedev, 1986
Order Polystomatidea Lebedev, 1988
Family Polystomatidae Gamble, 1896
Family Sphyranuridae Poche, 1926
Subclass Oligonchoinea Bychowsky, 1937
Order Chimaericolidea Bychowsky, 1957
Family Chimaeridolidae Brinkmann, 1942
Order Diclybothriidea Bychowsky, 1957
Family Diclybothriidae Price, 1936
Family Hexabothriidae Price, 1942
Order Mazocraeidea Bychowsky, 1957
Suborder Mazocraeinea Bychowsky, 1957
Family Plectanocotylidae Monticelli, 1903
Family Mazoplectidae Mamaev & Splipchenki, 1975
Family Mazocraeidae Price, 1936
Suborder Gastrocotylinea Lebedev, 1972 sedis mutabilis
Infraorder Anthocotylina Boeger & Kritsky, 1993
FamilyAnthocotylidae Price, 1936
Infraorder Gastrocotylina Lebedev, 1972
Family Pseudodiclidophoridae Yamaguti, 1965 incertae sedis
Superfamily Protocomicrocotyloidea Johnston & Tiegs, 1922 sedis mutabilis
Family Protomicrocotylidae Johnston & Tiegs, 1922
Family Allodiscocotylidae Tripathi, 1959
Family Pseudomazocraeidae Lebedev, 1972
Family Chauhaneidae Euzet & Trilles, 1960
Superfamily Gastrocotyloidea Price, 1943 sedis mutabilis
Family Bychowskycotylidae Lebedev, 1969
Family Gastrocotylidae Price, 1943
Family Neothoracocotylidae Lebedev, 1969
Family Gotocotylidae Yamaguti, 1963
Suborder Discocotylinea Bychowsky, 1957 sedis mutabilis
Family Discocotylidae Price, 1936
Family Diplozoidae Tripathi, 1959
Family Octomacridae Yamaguti, 1963
Suborder Hexostomatinea Boeger & Kritsky, 1993
Family Hexostomatidae Price, 1936
Suborder Microcotylinea Lebedev, 1972
Superfamily Microcotyloidea Taschenber, 1879
Family Axinidae Monticelli, 1903
Family Diplasiocotylidae Hargis & Dillon, 1965, sedis mutabilis
Family Heteraxinidae Unnithan, 1957, sedis mutabilis
Family Microcotylidae Taschenberg, 1879, sedis mutabilis
Superfamily Diclidophoroidea Cerfontaine, 1895, sedis mutabilis
Family Diclidophoridae Cerfontaine, 1895
Family Pyragraphoroidea Yamaguti, 1963, sedis mutabilis
Family Pterinotrematidae Caballero y Caballero & Bravo-Hollis, 1955
Family Rhinecotylidae Lebedev, 1979, sedis mutabilis
Family Pyragraphoridae Yamaguit, 1963, sedis mutalibis
Family Heteromicrocotylidae Unnithan, 1961, sedis mutabilis

Taxa incertae sedis*:* Sudanonchidae Malmberg, 1990 [Polyonchoinea]; Iagotrematidae Mañé-Garzón & Gil, 1962 [Polyonchoinea]; Microbothriidae Price, 1936 [Monogenea].

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61

PLATYHELMINTHES

Transversotrematidae (Family): Ectoparasitic Trematodes

Scott C. Cutmore and Thomas H. Cribb

Phylum Platyhelminthes
  Class Trematoda
    Subclass Digenea
      Order Plagiorchiida
        Suborder Transversotremata
          Superfamily Transversotrematoidea Witenberg, 1944
            Family Transversotrematidae

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2024. *In* S. L. Gardner and S. A. Gardner, eds. Concepts in Animal Parasitology. Zea Books, Lincoln, Nebraska, United States.

Chapter 61

Transversotrematidae (Family): Ectoparasitic Trematodes

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Introduction

The suborder Transversotremata is a small but biologically significant group of plagiorchiid digenean trematodes. There are just 1 superfamily, 1 family (family Transversotrematidae), 4 genera, and about 30 species known at present. It seems likely that the family Transversotrematidae is far richer than presently realized given that only a few workers have looked for them actively. All species are known from marine fishes of the Indo-West Pacific region or from freshwater fishes from the surrounding land masses. They are of particular interest because of the site of infection of the sexually adult worms. Species of this family live under the trailing edge of the scales of a wide range of marine and freshwater bony fishes. They are described as ectoparasites in the title to this chapter, but it is true that, when removed from the fish, they survive better in physiological saline than in either fresh or sea water; thus, they are evidently well sealed off from the external environment. No other trematodes are known to occupy this niche.

Perhaps because of the unusual site of infection, transversotrematids were recognized relatively late. The first described species, *Transversotrema patialense* (Soparkar, 1924), was actually first described as a cercaria. It was not until 1944 that the first sexual adult, *Transversotrema haasi* Witenberg, 1944, was reported and, even then, the host and site of infection was not really known as the specimens were found in basin of preserved fishes. Crusz and his colleagues (Crusz and Sathananthan, 1960; Crusz et al., 1964) first realized that the distinctive cercarial type of *Cercaria patialense* matched with adult worms from the skin of freshwater fishes.

Identifying Transversotrematids

Transversotrematids can perhaps be first suspected as such by the site that they infect. Work in our laboratory suggests that they are most easily detected by simply soaking the body of the dead (potential host) fish in 0.85% saline solution for 30–60 minutes. The worms emerge from under the scales and fall to the bottom of the container where they can be easily collected by inspecting the sediment with a stereo microscope.

All transversotrematids are at least partly transversely elongate (from which the type-genus name is derived) and exceptionally flat and thin, consistent with their subscale niche (Figure 1). The largest known species, *Transversotrema gigantica* Hunter et al., 2010, has been reported as reaching just over 8 mm in width (always greater than length) but most species are closer to 2 mm-wide. Most species lack an oral sucker, but the 2 known species of *Prototransversotrema* Angel, 1969 possess what might be either a true **oral sucker** or an analogous structure (Figure 1C). All species have a **ventral sucker**, a **pharynx**, and a **cyclocoel gut**. The **gonads** (2 **testes** and an **ovary**) are enclosed by the cyclocoel. **Vitelline follicles** are usually extensive but in the single described species of *Crusziella* Cribb, Bray & Barker, 1992 (Figure 1B) they are highly reduced and, in apparent association, the **eggs** embryonate in utero and will hatch to active **miracidia** as soon as they are laid. Importantly, members of the specious genus *Transversotrema* Witenberg, 1944 (Figure 1A) are now considered to be largely morphologically cryptic; although some species of *Transversotrema* are morphologically distinct, most have overlapping metric features and can only be definitively distinguished using genetic data.

Life Cycles and Host Range

The life cycle of transversotrematids is highly distinctive and specialized (Figure 2). Notably, although far more marine than freshwater species are known, all knowledge of the life cycle relates to freshwater species; nothing at all is known with respect to marine life cycles. However, it can be predicted that the life cycle does not vary greatly except perhaps with respect to the gastropod intermediate hosts infected.

Eggs embryonate and hatch as unremarkable miracidia. These actively seek and penetrate gastropod intermediate hosts (families Tateidae and Thiaridae known at present), in which the miracidium develops to a mother sporocyst. This has been described only once (Cribb, 1988) and in that case the sporocyst appears to produce only a single redia which in turn produces another generation of rediae, which then

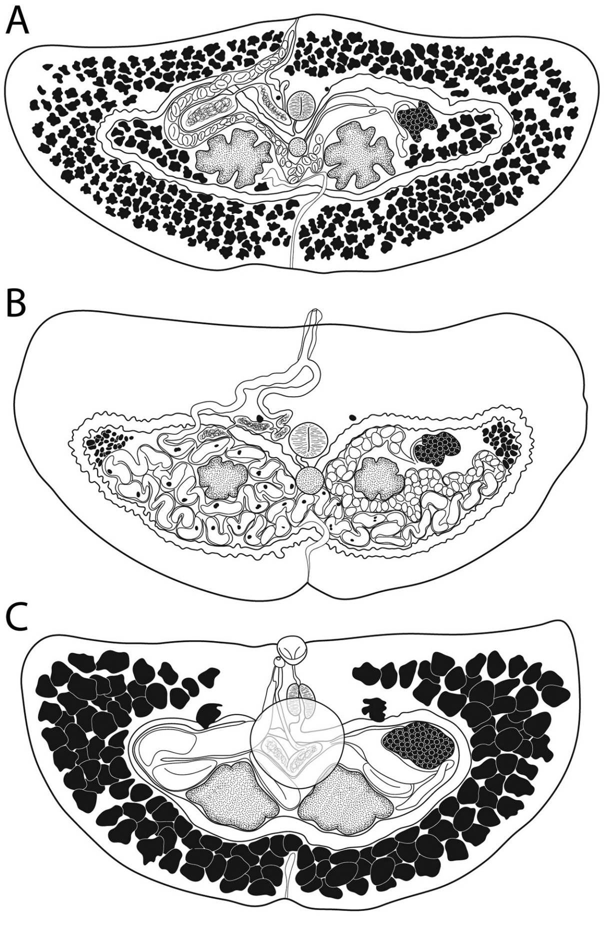

Figure 1. Transversotrematid morphology, showing cross-sections of:. A) *Transversotrema* sp.; B) *Crusziella* sp.; C) *Prototransversotrema* sp. Source: S. C. Cutmore and T. H. Cribb. License: CC BY-NC-SA 4.0.

produce cercariae. The cercaria is relatively enormous. The cercarial body is up to 0.5 mm wide, there is a pair of large eyespots, and the gonads and gut are essentially fully developed. The reproductive system may be so well developed that there is sperm in the seminal vesicle. The cercarial tail is unique among the Digenea. It is large and forked and has arm processes arising from the base of the tail. On their ends these arm processes have distinctive pads which have been shown to be concentrations of sensilla and are critical in host recognition (Whitfield et al., 1975).

Transversotrematid cercariae are highly active although relatively short-lived swimmers. They swim tail-first with the cercarial body wrapped around the tail-stem (Whitfield et al., 1975). When the cercaria bumps into a suitable fish it will recognize it as such with the pads on the arm processes, the cercarial body immediately slips under a scale and the tail detaches and swims away. Development to egg-producing adults is very quick, taking as few as 4 days (Cribb, 1988).

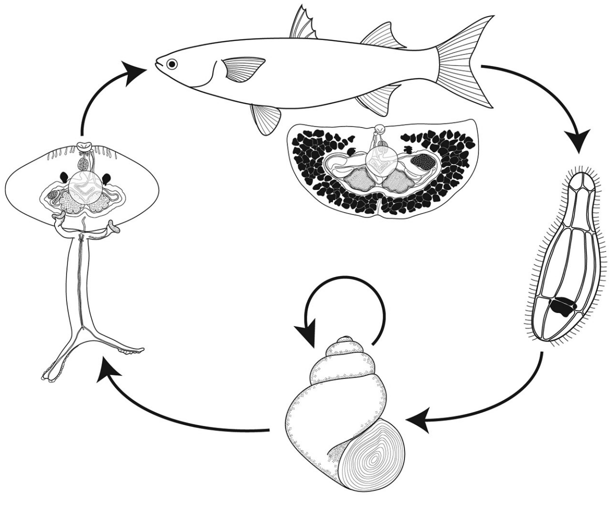

Figure 2. The generalized life cycle of transversotrematids. Source: S. C. Cutmore and T. H. Cribb. License: CC BY-NC-SA 4.0.

Interestingly, members of the Transversotrematidae exhibit a range of host specificities. Although a few species have been found to be **oioxenous** (infecting a single fish species), the overwhelming trend is for **stenoxenous** (infecting more than 1 species of a single fish family) and **euryxenous** (infecting more than 1 fish family) specificity (Hunter and Cribb, 2012; Cribb et al., 2014). Notably, *Transversotrema licinum* Manter, 1970 has been shown, using molecular data, to infect fishes of at least 8 families and 3 orders (Cutmore et al., 2016). It is likely that more extensive host sampling will show that all species of this group are either stenoxenous or euryxenous.

Significance of the Tranversotrematids

The main significance of the Transversotrematidae is in the combination of their evolutionary position and their biology. In the phylogeny of Olson and colleagues (2003), the Transversotrematidae fell unambiguously in the Plagiorchiida, sister to all other taxa except for the Bivesiculidae, the most basal taxon in the Plagiorchiida. In this context, the life cycle of the Transversotrematidae is highly intriguing. Apart from being relatively simple as a 2-host life cycle, there is little apparent connection with the life cycle of the Bivesiculidae in which the cercaria is eaten. Brooks and colleagues (1985) interpreted the ectoparasitic position of the Transversotrematidae as having occurred as the result of a secondary shift and Brooks and colleagues (1989) argued that the life cycle was secondarily reduced from a 3-host life cycle (so that perhaps the present sexual adult was once a metacercaria and the adult has been lost). These interpretations were made prior to what it now understood about the phylogenetic position of the Transversotrematidae. Cribb and collagues (2003) suggested that, if the 2-host life cycle of transversotrematids is not a secondary condition, it might be consistent with multiple adoptions of vertebrate parasitism by the Digenea. These matters cannot yet be considered resolved, and thus the Transversotremata is a small group that should not be overlooked in the overall understanding of the evolution of the Trematoda.

The Special Case of *Transervotrema patialense*

An interesting aspect of transversotrematid biology is that 1 species, *Transervotrema patialense*, appears to be invasive. It has been reported from several countries outside its apparent native range (see Womble et al., 2015). It is transmitted by several thiarid gastropods, but especially by *Melanoides tuberculata*, which is itself a seriously invasive species. There is no evidence that *T. patialense* poses any real threat to native fish species outside of its natural range. Rather, these reports are testament to the simplicity of the life cycle.

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62

HIRUDINIA

Hirudinia (Class): Parasitic Leeches

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Phylum Annelida

  Class Hirudinia

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Chapter 62

Hirudinia (Class): Parasitic Leeches

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Leeches as Parasites

Some of the most charismatic and well-known leeches are blood-feeding species that rely on vertebrates, yet some species feed on the hemolymph of invertebrates, while others are strictly predatory, while scavengers in the leech world are rare (Siddall et al., 2011). In this section, only the leeches that feed on vertebrate blood will be covered (for other species, see Govedich and Moser, 2015).

Leeches are considered temporary, mostly ectoparasites of vertebrates, feeding only for short periods of time, from a few minutes or hours as in the case of *Hirudo medicinalis* or species of *Haementeria,* to days or weeks in the case of species of family Praobdellidae (*Limnobdella, Tyrannobdella, Praobdella*, or *Limnatis*) that feed from the nasal passages of mammals, including humans (Sawyer, 1986; Phillips et al., 2010). Some leeches, such as those of the genus *Placobdella* are semi-permanent parasites mainly of freshwater turtles, but some species feed on salamanders or birds (Bolek and Janovy, 2005; McCallum et al., 2011; Oceguera-Figueroa et al., 2010). Species of the genus *Theromyzon* are also semi-permanent parasites of the nasal passages of aquatic birds, such as waterfowl. One of the most extreme cases of parasitism in leeches is represented by species of the genus *Ozobranchus*, which are permanent parasites of both marine and freshwater turtles, spending their whole life attached to their host and even lay their eggs onto the body surface of their hosts (Sawyer, 1986; Nakano et al., 2017). Notably, *Placobdelloides jaegerskioeldi* is only known from the rectal tissues of African hippopotamuses (Oosthuizen and Davies, 2011). Most blood-feeding leeches are generalists in terms of the number of species of hosts that can be parasitized, and many instances of blood-feeding species supplementing their diet with fish or amphibian eggs have been documented (Light et al., 2005; Romano and Di Cerbo, 2007).

General Morphology

Several morphological characteristics distinguish Hirudinida from other annelids, including their possession of a fixed number of 34 **somites** superficially subdivided into **annuli**, a reduced or fully absent coelom, the absence of chaeta in adult stages, and the presence of 2 **suckers**, 1 at the most anterior part of the body with the mouth laying inside (**oral** or **anterior sucker**) and 1 at the most posterior part of the body (**anal** or **posterior sucker**) (Govedich and Moser, 2015; Sawyer, 1986).

Leeches are, in general, elongated with parallel body sides, without regionalized body parts, and are slightly dorsoventrally flattened (that is, *Hirudo* and *Macrobdella* species); however, this general pattern is somewhat variable (see Figures 1–3). Some fish parasites (such as those in the family Piscicolidae) are circular in cross-section and may have distinct body regions such as the slender anterior **trachelosome** and the posterior, wider **urosome**. Species of Glossiphoniformes are, in general, foliaceous and dorsoventrally flattened. At least 2 groups of parasitic leeches, *Branchellion* and *Ozobranchus,* have developed lateral projections of the body walls forming membranous branchiae (Sawyer, 1986; also see Figure 4).

The most conspicuous morphological characteristic of leeches, in addition to the annulated body, is the presence of suckers located at the anterior and posterior ends of the body. Suckers are rather large and muscularized organs mainly used for locomotion and attachment to their host and prey (Sawyer, 1986). In general, the posterior sucker is larger than the anterior and, in some species, like the members of the family Praobdellidae, the former can be considerably wider than the width of the main body (Phillips et al., 2010). In general, 2 main types of feeding apparatuses are recognizable for blood-feeding leeches: The **proboscis** and **jaws**. The proboscis is an eversible muscular organ used to penetrate the skin of the leech prey, whereas the jaw is armed with sclerotized denticles that pierce the skin.

Reproduction

Leeches are hermaphroditic worms that perform cross-fertilization during copulation; some species have developed complex reproductive systems with a penis and vagina, such as the species of *Hirudo* and *Macrobdella*, whereas others have a simpler reproductive system with testisacs and ovisacs

Figure 1. Dorsal view of *Macrobdella decora* (family Macrobdellidae; collected from Buckingham, Gatineau, British Columbia, Canada) representing the morphological variation within the subclass Hirudinea. Source: C. Grenier, 2015. License: CC0.

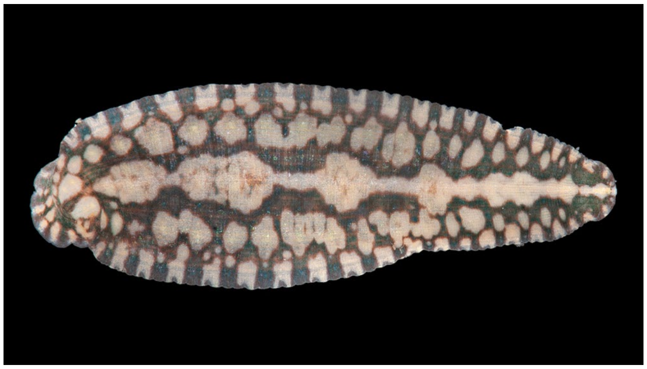

Figure 2. Dorsal view of *Placobdella parasitica* (family Glossiphoniidae; collected from Ingleside, Maryland, United States) representing the morphological variation within the subclass Hirudinea. Source: SERC Fisheries Conservation Laboratory, 2022. License: CC BY-NC.

Figure 3. Dorsal view of *Haementeria officinalis* (family Glossiphoniidae) representing the morphological variation within the subclass Hirudinea. Source: E. Caballero y Caballero and C. Loyola. License: CC BY-NC-SA 4.0.

connecting to their respective gonopores through relatively simple tubes, such as the species *Placobdella* and *Haementeria*. Fertilization is internal. In species with complex reproductive systems, the penis is inserted into the vagina to discharge the spermatozoids. In species with simple reproductive systems, the sperm transfer occurs through the implantation of spermatophores on the epidermis of the recipient leech (Salas-Montiel et al., 2017). Eggs are produced and enveloped by a proteinaceous membrane secreted by the clitellum (glandular area of the reproductive somites). In most of the species, this membrane hardens and forms a protective cocoon or case where the eggs develop; all the members of Glossiphoniformes keep the eggs within a thin and flexible membrane attached to the ventral surface where the eggs develop into young leeches that remain attached to their parent, representing an uncommon case of parental care within the Annelida (Sawyer, 1986). Their ontogeny is direct, without larval stages (Sket and Trontelj, 2008).

Leeches as Vectors and Hosts

Leeches, like many blood-feeding invertebrates, may transmit bacteria or other microorganisms between hosts during the feeding process. PCR-based (Polymerase Chain Reaction-based) techniques have been used to detect bacterial communities in the digestive tract of leeches with relevant findings of *Bartonella* spp. in *Haemadipsa rjukjuana* from Korea, representing a human health concern (Kang et al., 2016). Recently, an unidentified blood-feeding leech has been implicated in the transmission of *Rickettsia* to humans (Slesak et al., 2015); however, the detailed mechanisms of the transmission patterns and frequencies need to be investigated in more detail. Leeches are occasionally vectors of *Trypanosoma* spp. and hemogregarines, particularly among fish, frogs, and turtles (Siddall and Desser, 1991; 1992).

Marine leeches of the genus *Ozobranchus*, which are permanent parasites of marine turtles, have been discussed as possible vectors of the chelonid fibropapilloma-associated herpesvirus (CCFPHV) due to the presence of relatively large loads of this virus in their body (Greenblatt et al., 2014). However, more experiments are needed to finally determine the role of leeches as vectors in these systems.

Leeches have also been recorded as intermediate hosts of cestodes (Regel, 2010), digeneans (McCarthy, 1990), and nematodes (Riggs and Ulmer, 1983). Macrophagous and blood-feeding leeches, such as *Haemopis* spp. and *Macrob-*

della spp., respectively, are definitive hosts for digeneans of the genus *Alloglossidium* that reach their adult stage in the leech intestine (Schmidt and Chaloupka, 1969; Beckerdite et al., 1974).

Recently, blood-feeding leeches (*Haemadipsa* spp.) have been successfully used to screen mammal diversity in Vietnam and southern Asia (Bangladesh, Cambodia, and China). PCR-amplification of the DNA (ingested DNA or iDNA) stored in the blood meal inside the crop of the leeches collected in the field revealed the presence of a wide diversity of mammal blood, such that a broad scope of host preference can be inferred for the leeches. In total, mammals of 6 orders (Artiodactyla, Carnivora, Chiroptera, Lagomorpha, Primates, and Scandentia) and 4 species of Aves were detected using this method. Amplifiable mitochondrial DNA was recovered from the gut content up to 140 days after blood ingestion; making leeches a promising candidate to uncover hidden vertebrate diversity (Schell et al., 2012; 2015; Tessler et al., 2018b).

Proboscis-bearing leeches that feed exclusively on vertebrate blood, such as species of *Placobdella*, *Placobdelloides*, and *Haementeria,* as well as species of Oceanobdelliformes (of the genera *Ozobranchus*, *Piscicola*, *Pontobdella*, *Branchellion*, and *Myzobdella,* among others) have established extreme symbiotic associations with bacteria, mainly Proteobacteria. Leeches of these groups house bacteria in specialized cells (bacteriocytes) that form specialized organs (bacteriomes) connected to the digestive system. It has been suggested that bacteria might complement the diet of these monophagous blood-feeding leeches, given the lack of, or low proportion of, vitamin B in vertebrate blood (Perkins et al., 2005: Kvist et al., 2011; Manzano et al., 2015). Associations between nutrient-supplying bacteria and their diet-restricted eukaryotic hosts have been heavily studied in various insect groups but poorly studied outside Arthropoda (see, for example, Aksoy, 1995; Douglas, 1998). Through genomic analyses of symbiotic bacteria, it has been demonstrated that the symbiont of the leech *Haementeria officinalis* has a much-reduced genome in terms of size, with high A + T content, and a reduced set of metabolic capabilities, all of which are a common characteristics of ancient obligate endosymbionts of arthropods. The genome of the *H. officinalis*-symbiotic bacterium*, Providencia siddalli*, has retained many pathways related to the biosynthesis of vitamin B, pointing towards a role in supplementing the blood-restricted diet of its host (Manzano-Marín et al., 2015).

Zoogeography

Most leeches inhabit freshwater habitat, but there are marine, brackish, and terrestrial species, too. They are distributed worldwide, and their patterns of distribution broadly correspond with the biogeographic regions described based on other zoological groups, with some recognizable transitional zones and areas of endemism (Ringuelet, 1985, Sawyer 1986; Sket and Trontelj, 2008). Each biogeographic region is characterized by species flocks or genera; in the Nearctic, parasitic leeches are represented by the genera *Macrobdella*, *Philobdella*, and *Placobdella,* whereas in the Neotropics, parasitic leeches include *Mesobdella gemmata*, *Haementeria*, and *Oxyptychus*. In the transitional zone between these 2 areas (Mesoamerica), leeches from both areas co-occur, including *Macrobdella*, *Placobdella*, *Haementeria*, and endemics, such as *Limnobdella* and *Pintobdella* (Moser et al., 2016; Ringuelet, 1985; Oceguera-Figueroa and León-Règagnon, 2014). Palearctic parasitic leech fauna is characterized by species of *Hirudo*; however, other blood-feeding leeches are distributed in the region, such as those of the genus *Limnatis* and a single species of the otherwise Nearctic genus

Figure 4. General view of a leech, *Ozobranchus branchiatus* (family Ozobranchidae), displaying lateral branchiae. Source: Adapted from Lagunas-Calvo et al., 2021. License: CC BY-NC-SA 4.0.

Placobdella [*Placobdella costata* (Müller, 1846)] (Trontelj and Utevsky, 2005; Siddall et al., 2005). The leech fauna in the Afro-Tropical region is characterized by *Parapraobdella, Placobdelloides, Aliolimnatis*, and *Oosthuizobdella* (Sawyer, 1986; Phillips et al., 2011). The leech fauna of the Indian region is characterized by species in the genera *Haemadipsa*, *Hirudinaria*, and *Poecilobdella* (Sawyer, 1986), whereas the leech fauna in the East Asia region (Sino-Japanese region) is characterized by species of *Batracobdella, Hirudinaria, Hirudo nipponia, Poecilobdella*, and *Dinobdella* (Lai and Chen, 2010; Sawyer, 1986). Australia and New Zealand have a characteristic leech fauna, mainly represented by species of the genus *Chtonobdella* (Tessler et al., 2016), and other enigmatic leeches, such as *Ornithobdella edentula* found on nests of the New Zealand penguins *Eudyptes robustus* or the leech *Euranophila central,* a parasite of the frog *Litoria gilleni* from central Australia (Sawyer, 1986).

Some species display wide geographic distributions. For example, *Theromyzon* is a cosmopolitan genus (excluding Antarctica). This unusually broad distribution is probably related to the biology of their waterfowl hosts. Marine leeches such as those in the genera *Ozobranchus*, *Pontobdella*, and *Branchellion* display a broad geographic distribution attributable to the dispersal abilities of their hosts across the oceanic basins (Sawyer, 1986).

Introduction to Hirudinea Classification

Jean Baptiste Lamarck coined the term Hirudinea in 1818 and the taxon was originally conceived of as a class within Annelida, or segmented worms, along with Polychaeta and Oligochaeta (Govedich and Moser, 2014). After 200 years of investigation, including the discovery of numerous species and groups, as well as the development of methods to better infer the phylogenetic relationships within this taxon, several changes have been proposed. These investigations have helped to reconcile taxonomic names and classification with the phylogenetics (Figure 5). It is now fully accepted that Oligochaeta is paraphyletic due to the inclusion of Hirudinea and, together, Oligochaeta, Hirudinea, and 2 small groups of leech-like worms (Branchiobdellida and Acanthobdellida) form the class Clitellata. Furthermore, phylogenetic studies have recovered Polychaeta as paraphyletic due the inclusion of Clitellata (Zrzavý et al., 2009; Struck et al., 2011; Kvist and Siddall, 2013; Weigert et al., 2014; Aguado et al., 2014). In further complicating the current conception of Annelida, Sipuncula (peanut worms), Siboglinidae, including pogonophores and vestimentiferans (deep-sea beard worms), and Myzostomida (which are parasitic on echinoderms) are now also considered to be annelids, although their morphological characteristics depart from the most common conditions of typical annelids and, interestingly, their phylogenetic position within the phylum is still unsettled (Aguado et al., 2014).

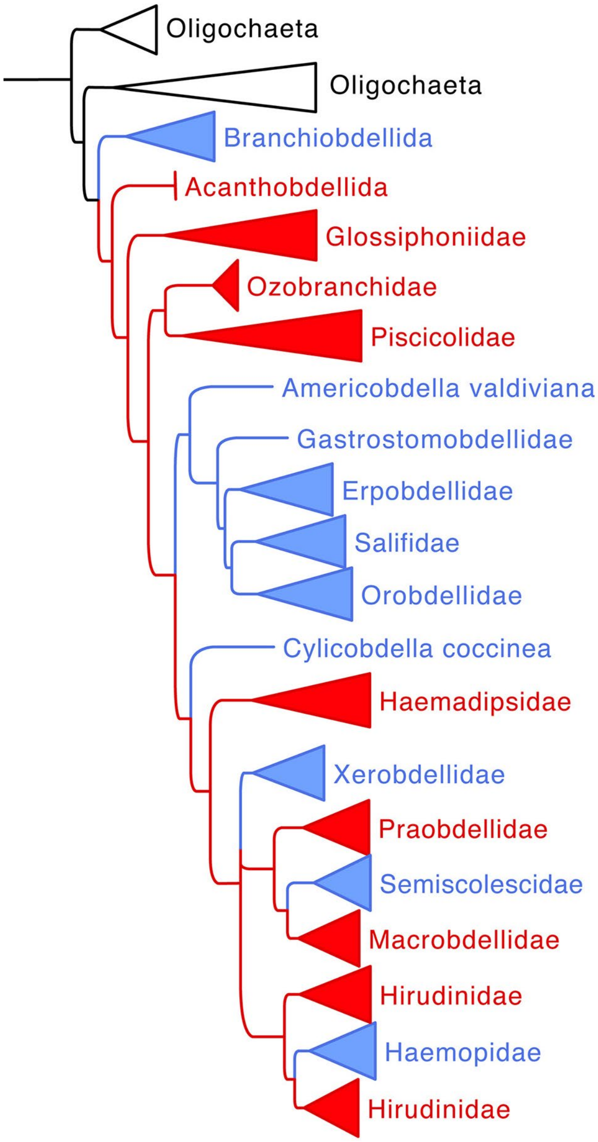

Figure 5. Composite phylogenetic diagram of the subclass Hirudinea summarizing the current knowledge of the relationships of major groups. Blood-feeding lineages are shown in red, non-blood-feeding lineages in blue. Source: A. Oceguera-Figueroa and S. Kvist. License: CC BY-NC-SA 4.0.

Order Acanthobdellida (salmonid parasites) and order Branchiobdellida (crayfish worms) were considered leech-like organisms that were thought to have developed suckers independently as an adaptation to their parasitic lifestyle. However, recent phylogenetic studies based mainly on molecular data clearly support their affinities with subclass Hirudinida (Siddall et al., 2001; Tessler et al., 2018). Both groups, Acanthobdellida and Branchiobdellida, are less speciose in comparison to Hirudinida, with only 2 species (*Acanthodella* *peledina* and *Paracanthobdella livanowi*) and approximately 140 species, respectively (Gelder, 2009; Sawyer, 1986).

The number of species included in this group is still growing, with more than 680 species distributed worldwide (Sket and Trontelj, 2008).

Classification and Phylogeny

Historical classification of subclass Hirudinida recognized 2 orders, separated on the basis of the presence or absence of an eversible proboscis: Rhynchobdellida was used for proboscis-bearing leeches and Arhynchobdellida was used for species that lack such a structure (Sawyer, 1986). Recent phylogenetic studies based on molecular data failed to recover Rhynchobdellida as a monophyletic group (Apakupakul et al., 1999; Trontelj et al., 1999) and, consequently, Tessler and colleagues (2018) suppressed Rhynchobdellida and recognized 5 groups at the ordinal rank for all leeches: **Oceanobdelliformes**, including the families **Piscicolidae** (fish leeches; marine, brackish and freshwater species) and **Ozobranchidae** (turtle leeches; mainly marine, few species freshwater and brackish); **Glossiphoniformes** (blood and hemolymph feeders, freshwater species), **Americobdelliformes** (macrophagous, semi-terrestrial), **Erpobdelliformes** (macrophagous, freshwater), and **Hirudiniformes** (hematophagous and macrophagous, freshwater species).

Based on phylogenetic hypotheses and the mapping of feeding preferences onto the tree, as well as on the evidence provided by the analyses of the peptides of the saliva of some leeches (Siddall et al., 2011; Kvist et al., 2016), it has been suggested that the last common ancestor of all leeches was a blood-feeder (that is, adapted to feed on the vertebrate blood) and this feeding preference switched to macrophagy (feeding on small invertebrates and dead animals) and to liquidosomatophagy (feeding on hemolymph) on at least 6 or 7 independent occasions.

Leech Therapy: History of Medical Applications

The so-called medicinal leeches are without doubt the most charismatic and infamous members of the group. Medicinal leeches have been used for centuries ostensibly to correct imbalances of the traditionally recognized 4 humors, namely, blood, phlegm, black bile, and yellow bile (Singh, 2010; Whitaker et al., 2004), as well as a variety of other ailments including mental disorders, whooping cough, gout, tumors, epilepsy, headaches, arthritis, and obesity (Weinfeld et al., 2000; Porshinsky et al., 2011). Leeching, or hirudotherapy, became the most popular mode of bloodletting in the Old World during the 18th and 19th centuries, in particular through the application of the renowned European medicinal leech *Hirudo medicinalis*. In order to fulfill the heavy demand on the medicinal leech, local leech populations were over-harvested to the point of local extinction; as a consequence, in 1823, restrictions were implemented to manage the number of leeches being exported through Hannover, Germany and collecting seasons were instituted in Russia (Wells and Combes, 1987; Whitaker et al., 2004; Elliott and Kutschera, 2011).

Currently, surgeons use leeches to aid in the salvage of venous-congested extremities that result from an imbalance between arterial inflow and venous outflow following surgery; this includes digits (Brody et al., 1989), nipples (Güneren et al., 2000), ears (Cho and Ahn, 1999), lips (Walton et al., 1998), nasal tips (Mortenson et al., 1998), and penis (Pantuck et al., 1996). Medicinal leech therapy has enormous utility in removing stagnant blood and allowing veins to recover (Singh, 2010; Porshinsky et al, 2011) and *Hirudo medicinalis* was approved as a medical device by the United States Food and Drug Administration (US FDA) in 2004 (Rados, 2004).

Recent phylogenetic analyses have clearly demonstrated that medicinal leeches do not form a monophyletic group. Instead, and with a broad definition of the term medicinal leech, 6 different groups include species that have been used for medicinal purposes around the world: *Haementeria* spp. in South America and Mexico; *Limnobdella* spp. in Mexico; *Macrobdella*, *Philobdella*, and *Oxyptychus* in the New World; *Hirudo* spp. in the Palearctic; *Haemadipsa* spp. and *Hirudinaria* in Southeast Asia, *Chtonobdella* spp. in Australia; and *Aliolimnatis* spp. in Africa (Oceguera-Figueroa, 2012; Phillips and Siddall, 2005; 2009; Phillips et al., 2010; Tessler et al., 2018).

Preparation of Specimens

Proper fixation of leeches for morphological and molecular studies is important and necessary to understand biodiversity. To avoid morphological distortion of the specimen, it is important to narcotize or relax specimens before fixation. The main method consists of gradually adding drops of 95–100% ethanol to the water-filled container until the leeches' movements and reactions to touching stop. This process can take up to 30 minutes, depending on the specimen's size and, subsequently, the mucus produced during this operation should be removed with paper towels. Once relaxed, leeches must be straightened and placed in a container between paper towels and covered with 95–100% ethanol for 24 hours or more, depending on the size of the specimens. For molecular analyses, tissues (commonly parts of the posterior suckers, in order to avoid contaminations by potential blood meals), should be placed directly in 96% ethanol and kept at 4 °C, or colder conditions, if possible. For permanent slide preparations, in particular for small leeches, specimens should be flattened between 2 glass slides immediately after narcotization. Staining should be carried out with a mixture of Mayer's paracarmine and Ehrlich's haematoxylin and mounted on slides with Canada balsam. For histological preparations, the use of 4% paraformaldehyde, 2.5% glutaraldehyde, or instead, Fleming's or Bouin's fixatives is recommended.

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63

ARTHROPODA

Siphonaptera (Order): Fleas

Marcela Lareschi

Phylum Arthropoda

Class Insecta

Order Siphonaptera

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Chapter 63

Siphonaptera (Order): Fleas

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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.

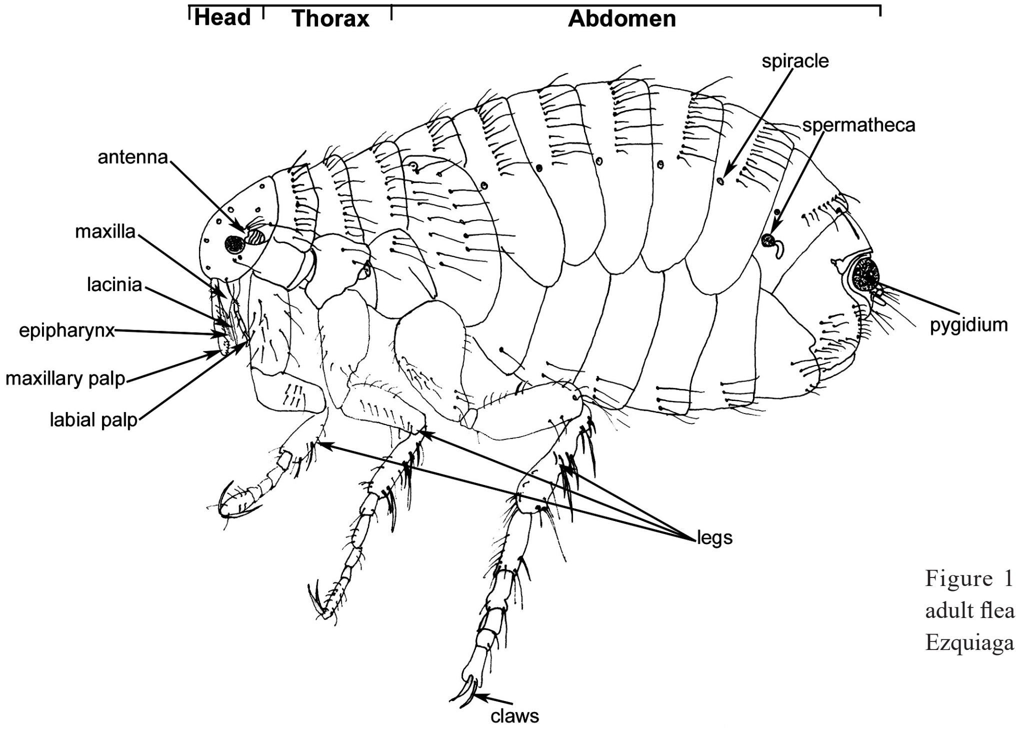

Figure 1. External morphology of an adult flea (*Pulex irritans*). Source: M. C. Ezquiaga. License: CC BY-NC-SA 4.0.

Figure 2. Details of the ctenidia (*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.

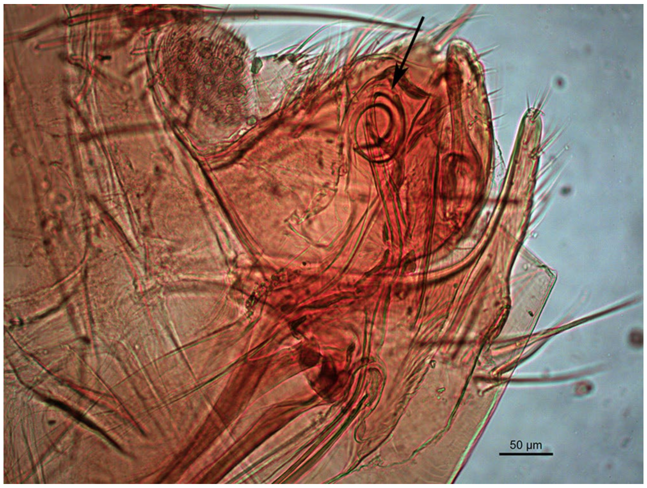

Figure 3. Details of the aedeagus (*Polygenis platensis*). Source: J. Sánchez, M. Urdapilleta, and L. Giambelluca. License: CC BY-NC-SA 4.0.

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 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).

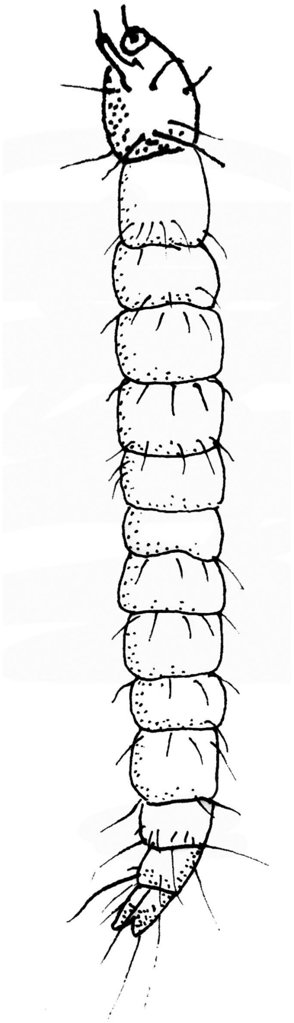

Figure 6. External morphology of the larva. Source: J. Sánchez, M. Urdapilleta, and L. Giambelluca. License: CC BY-NC-SA 4.0.

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.

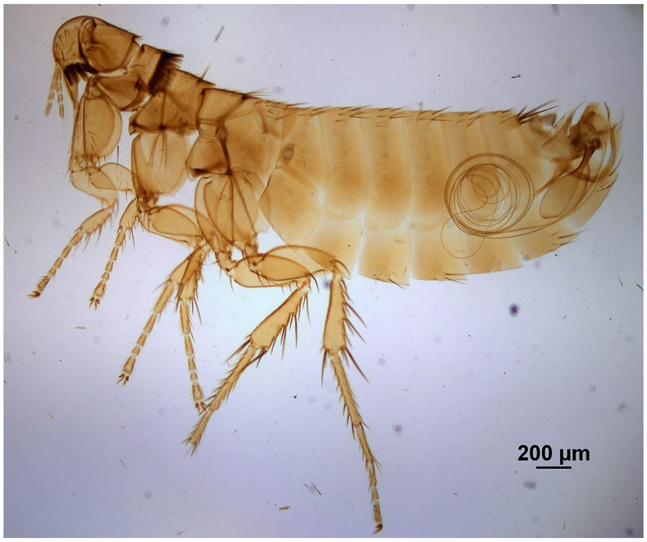

Figure 8. *Polygenis* sp. (family Rhpalopsyllidae). Source: J. Sánchez, M. Urdapilleta, and L. Giambelluca. License: CC BY-NC-SA 4.0.

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).

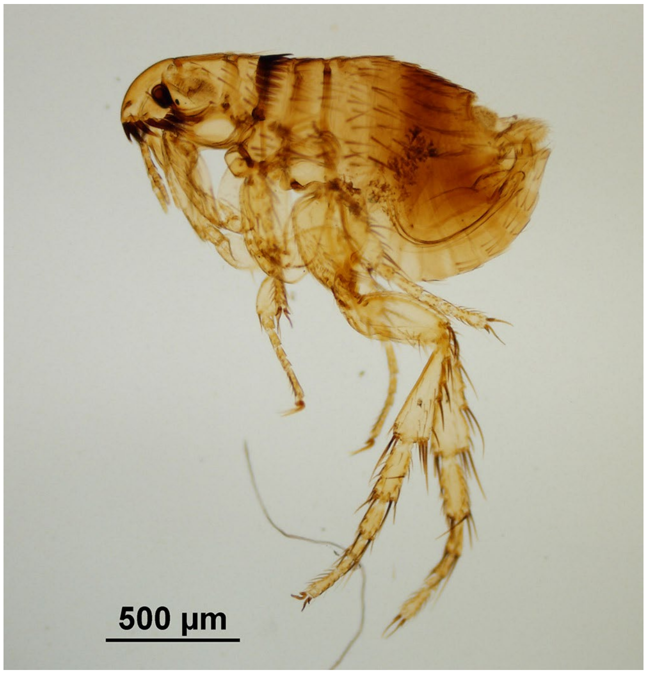

Figure 9. *Adoratopsylla intermedia intermedia* (family Ctenophthalmidae). Source: J. Sánchez, M. Urdapilleta, and L. Giambelluca. License: CC BY-NC-SA 4.0.

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.

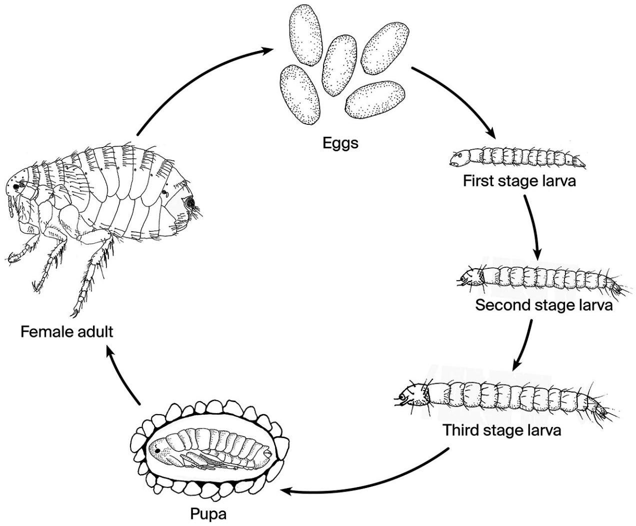

Figure 12. Life cycle of the fleas. Source: M. C. Ezquiaga. License: CC BY-NC-SA 4.0.

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 Neartic 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 Paleartic 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 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).

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.

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).

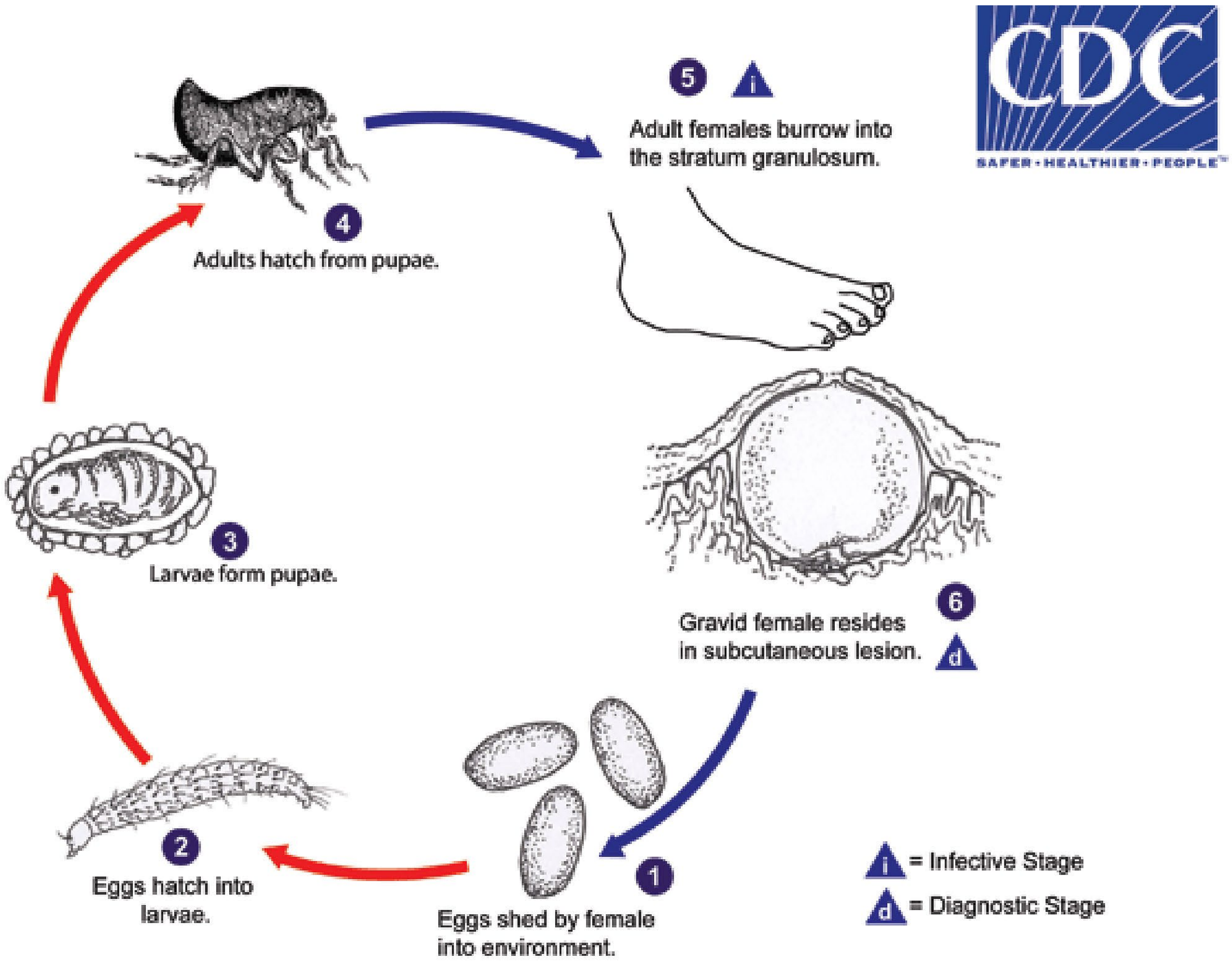

Figure 14. Tungaiasis life cycle. *Tunga penetrans* eggs are shed by the gravid female into the environment (1). Eggs hatch into larvae (2) in about 3–4 days and feed on organic debris in the environment. There are 2 larval stages before forming pupae (3). The pupae are in cocoons that are often covered 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 armadillos. 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 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).

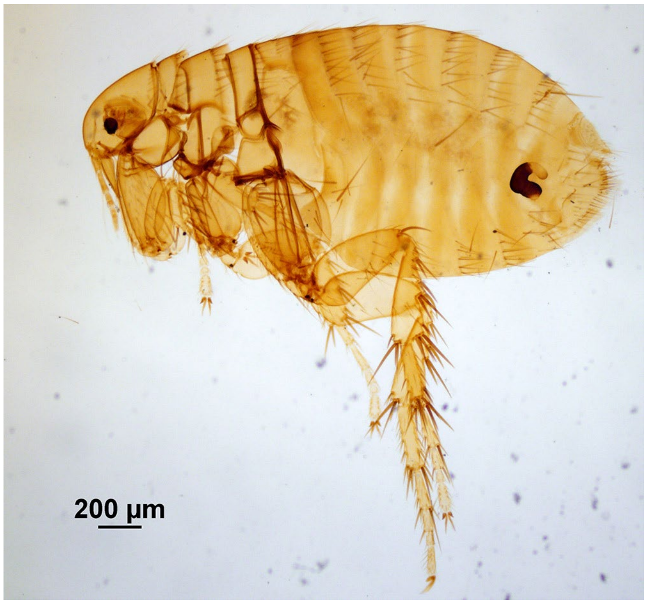

Figure 15. *Xenopsylla cheopis*. Source: J. Sánchez, M. Urdapilleta, and L. Giambelluca. License: CC BY-NC-SA 4.0.

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

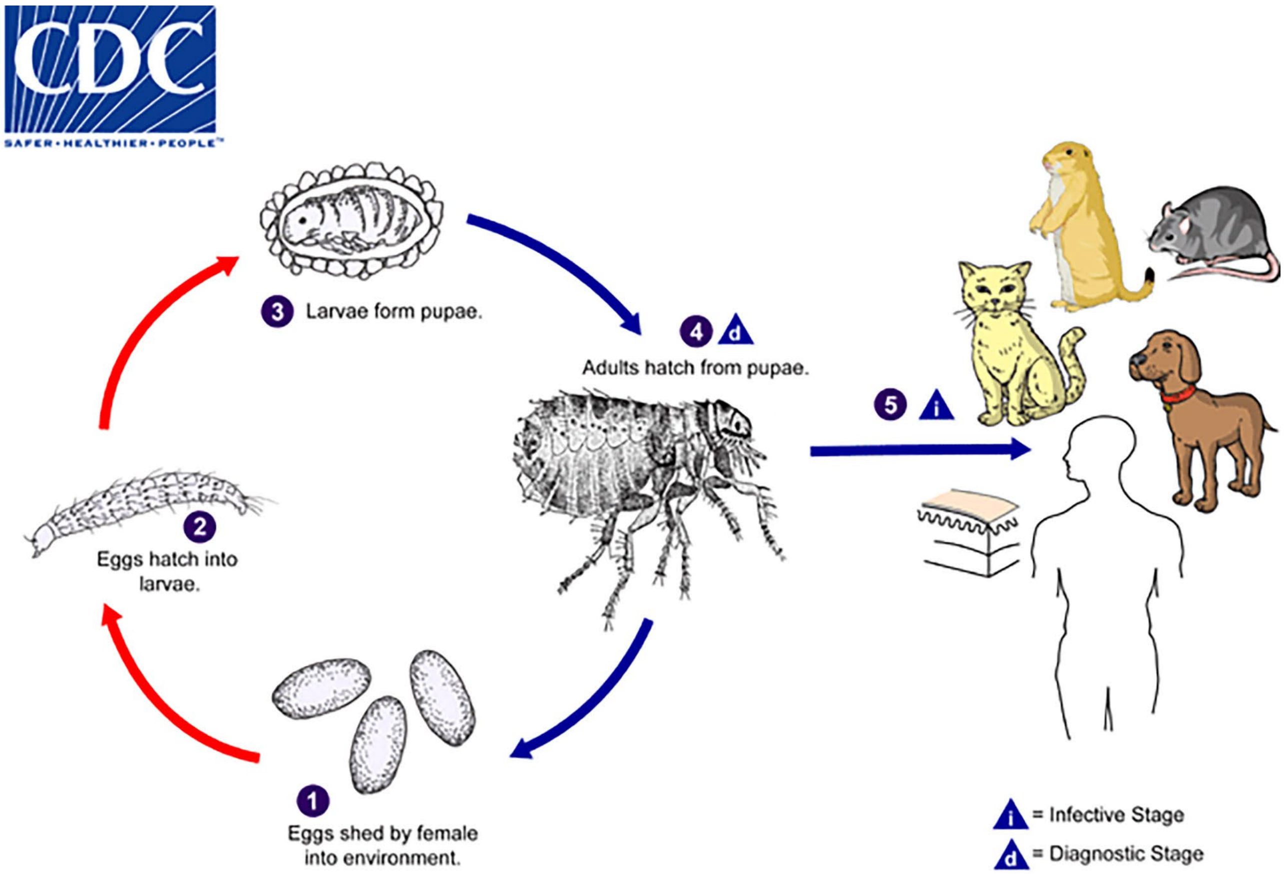

Figure 16. General flea life cycle. Fleas, like other holometabolous insects, have a 4-part life cycle consisting of eggs, larvae, pupae, and adults. Eggs are shed by the female in the enviroment (1). Eggs hatch into larvae (2) in about 3–4 days and feed on organic debris in the environment. The number 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 *Tung*a 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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ARTHROPODA

Phthiraptera (Order): Lice

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Phylum Arthropoda
    Class Insecta
        Order Phthiraptera

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Chapter 64

Phthiraptera (Order): Lice

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Introduction

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

Morphology

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

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

Feeding

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

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

Host Range

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

Host Distribution

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

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

Life Cycle

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

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

Macroecology

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

Transmission

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

Effects on Hosts and Role as Vectors

Although most infestations are symptomless, lice may

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

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

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

Host Defenses

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

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

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

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

Conservation

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

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

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

Origins

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

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

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

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

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

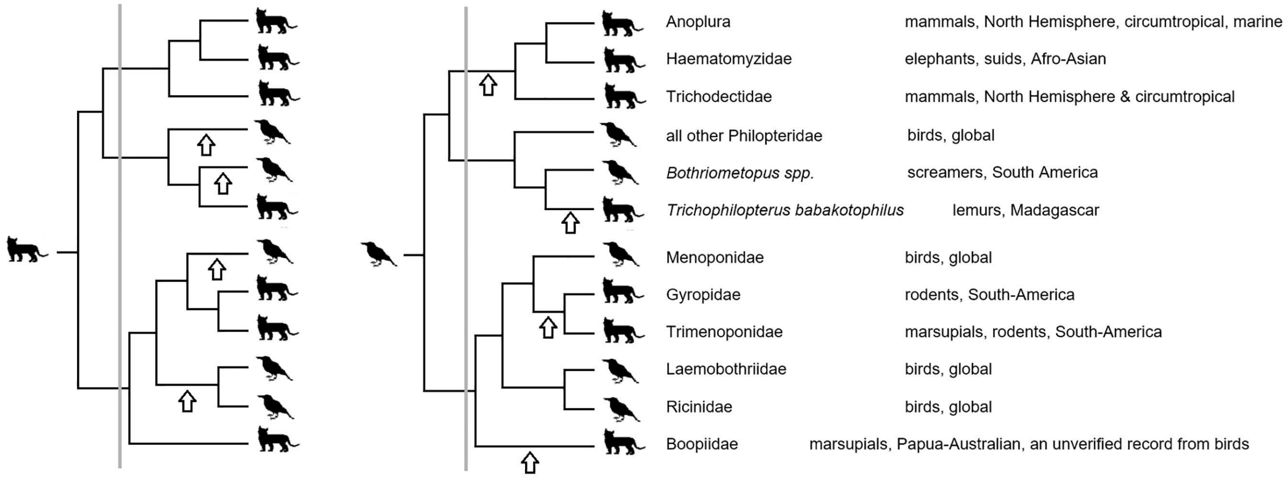

Figure 2. The most parsimonious scenarios for the major host-switches between mammals and birds illustrated along a dendogram represnting a simplified phylogeny of lice. The minimally required major switches are indicated by arrows. The left scenario is based on the presumption that lice originate from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

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

Phylogeny

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

Lice Nuclear Genome

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

Taxonomic Classification

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

Suborder Amblycera

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

Family Boopiidae

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

Family Ricinidae

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

Family Laemobothriidae

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

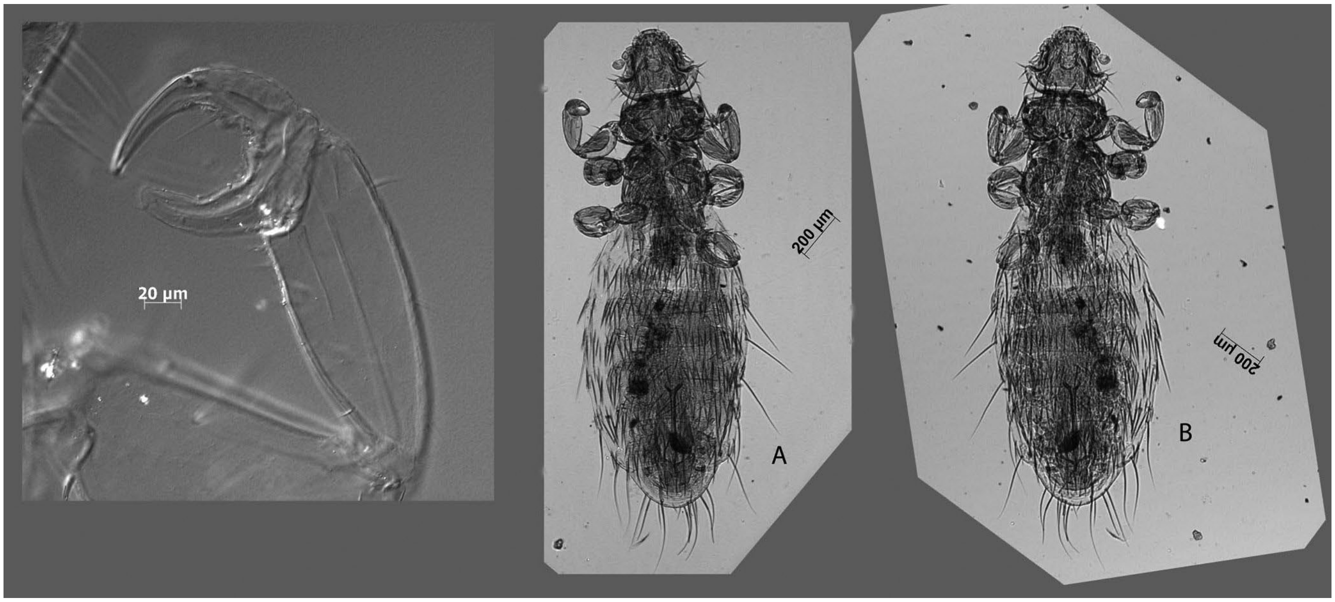

Figure 3. Chewing lice, genus *Phtheiropoios* from rodents of the genus *Ctenomys* collected in Bolivia in the 1980s. Source: S. L. Gardner, HWML. License: CC BY.

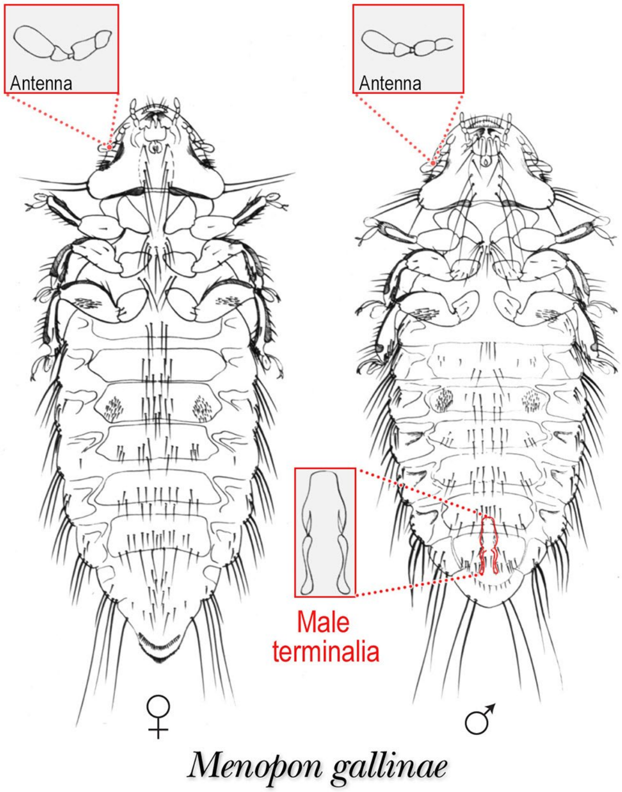

Figure 4. A female and a male *Menopon gallinae* lice revealing the insect's ventral morphology. Source: United States Centers for Disease Control and Prevention, 1975, available at the Public Health Image Library, image 5496. Public domain.

Family Trimenoponidae

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

Family Gyropidae

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

Family Menoponidae

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

Suborder Ischnocera

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

Family Philopteridae

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

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

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

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

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

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

Family Trichodectidae

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

Suborder Rhyncophthirina (Elephant and Suid Lice)

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

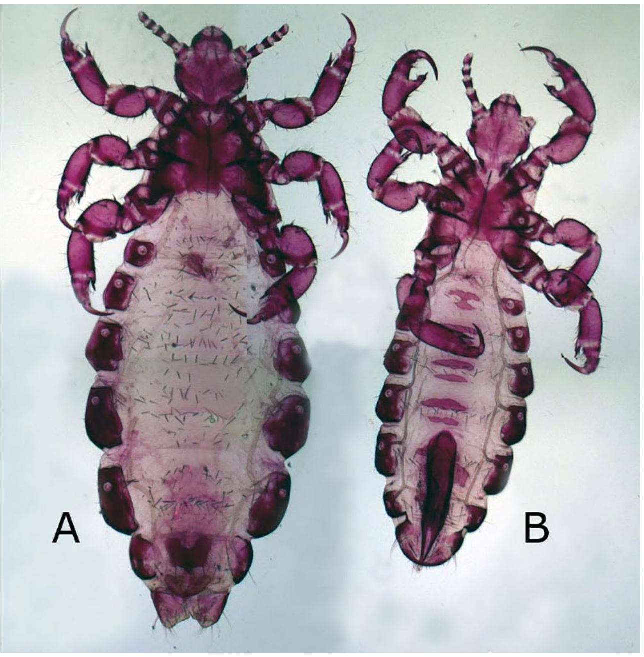

Figure 5. Sucking lice *Pediculus humanus* showing a female (A) and male (B) taken from a human host, preserved in 70% ethanol and stained in Semichon's acetic carmine and mounted in gum Damar. Source: G. Racz, HWML, 2016. License: CC BY.

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

Suborder Anoplura: Sucking Lice

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

Morphology

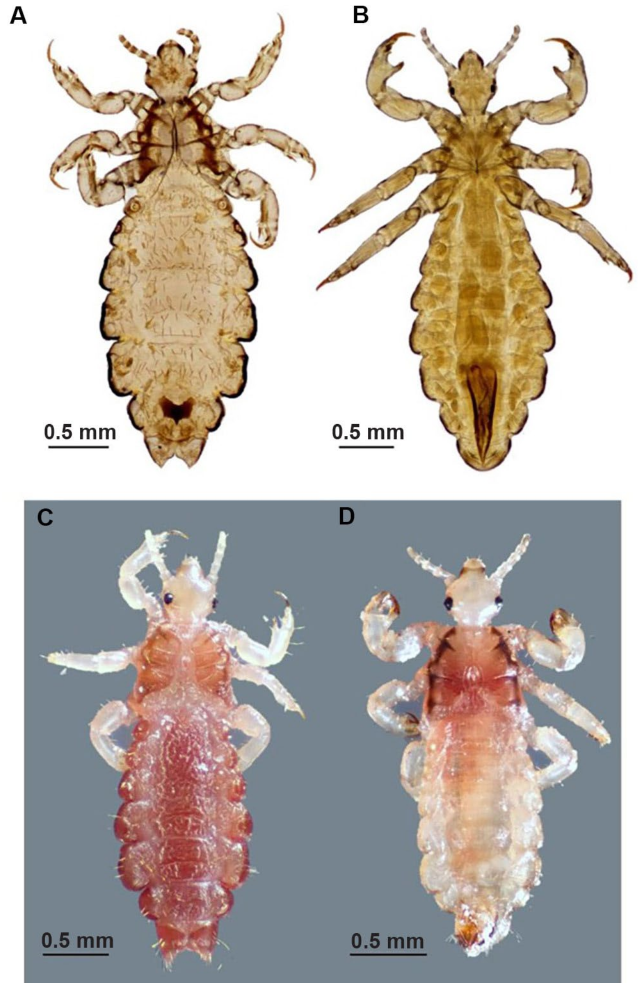

Figure 6. Adult body louse and head lice. A) Ventral view of slide-mounted female head louse; B) ventral view of slide-mounted male body louse; C) dorsal view of ethanol-preserved female head louse; D) dorsal view of ethanol-preserved male head louse. All photographs were taken using a Visionary Digital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

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

Mode of feeding

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

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

Pediculus humanus

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

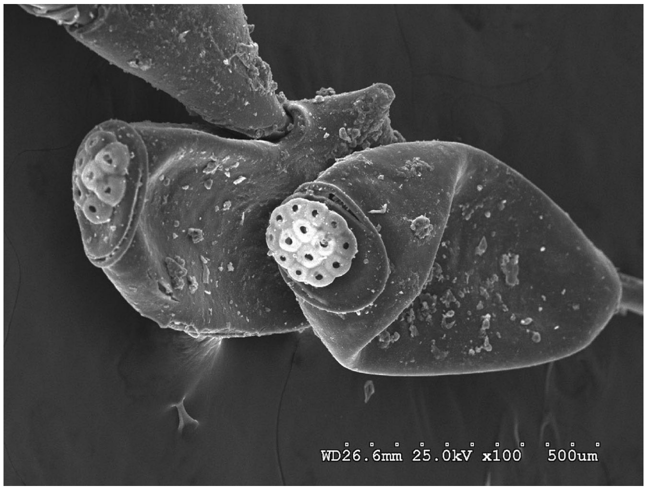

Figure 7. Sucking lice nits (lice eggs) from a mummy. High magnification view of head louse eggs from a South American mummy, 900–1200 CE. Opercula are intact and the pores can be seen. Source: N. Searcey, UNL. License: CC BY.

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

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

Phthirus pubis

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

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

Sucking lice as vectors of human disease

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

Epidemic, or louse-borne, typhus.

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

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

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

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

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

Brill-Zinsser diease.

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

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

Relapsing fever.

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

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

Control of Lice

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

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

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

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

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

Acknowledgements

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65

ARTHROPODA

Triatominae (Subfamily): Kissing Bugs

Sue Ann Gardner, compiler

Phylum Arthropoda
  Class Insecta
    Order Hemiptera
      Suborder Heteroptera
        Family Reduviidae
          Subfamily Triatominae

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Chapter 65

Triatominae (Subfamily): Kissing Bugs

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Introduction

Triatomines are insects belonging to the order Hemiptera, suborder Heteroptera, family Reduviidae, and subfamily Triatominae. All members of this subfamily are hematophagous, which is considered to be a recently derived characteristic in evolutionary terms. In relation to the taxonomy and phylogenesis of triatomines, it is interesting that the Hemiptera order has dispersed representatives throughout tropical and temperate regions. In this order more than 80,000 species are known. Traditionally, Hemiptera is divided into two suborders, Homoptera and Heteroptera. Some Homoptera and most Heteroptera are adapted to feeding on plant sap. Some insects of the Heteroptera suborder are predators on insects and on other invertebrates, sucking their hemolymph, while other Heteroptera have become hematophagous, for instance, the Triatominae subfamily (Schofield and Dolling, 1993).

Triatomine Hematophage Biology (Excerpted and adapted from Schofield, 2000a)

Relative to digestion, a whole series of physiological adaptations is required for an obligate hematophage (see Lehane, 1991). Blood is a nutritionally rich resource, but it is highly alkaline, and much of the protein is locked in the blood cells. Consequently, the Triatominae require both a hemolysin to open the blood cells and a system to acidify the blood meal before it can be digested. Species of Reduviidae are derived from plant-sucking Hemiptera which have lost the ability to secrete trypsin, the usual digestive protease, because plant sap has virtually no protein, and plant seeds have potent antitrypsins (Schofield, 1996). Thus, the Reduviidae, including Triatominae, must make use of secreted cathepsins as proteases, which are generally active only at acid pH. Blood is also generally deficient in certain vitamins, particularly folate and B vitamins, so that all obligate bloodsuckers require symbionts to assist in producing these compounds. These symbionts are so important that all other obligate blood-suckers carefully conserve them either intracellularly or in a special organ known as the mycetome. But in Triatominae these symbionts are free in the gut lumen, which is taken as additional evidence that the blood-sucking habit is a relatively recent adaptation (Schofield and Dolling, 1993).

Morphology of a Representative Species, *Triatoma sanguisuga* (Extracted verbatim from Byron and Capinera, 2019)

Eggs

The eggs of *Triatoma sanguisuga* are pearly-white, oval, and approximately 1.5 mm-long. Eggs are indiscriminately deposited individually on the substrate. Once a blood meal is taken, females begin oviposition after 4–6 days, depositing 1–5 eggs per day (Grundemann, 1947). In a study by Hays (1965), female nymphs collected in the field that developed into adults under laboratory conditions each laid an average of 711 eggs in their lifetime. However, the range of eggs laid per female was large (from 312 to 1,166) indicating a need for more research in this area.

Nymphs

According to Grundemann (1947), *Triatoma sanguisuga* goes through 8 instars, determined by measuring the head capsule (because of the swelling associated with blood-feeding, body size is an inaccurate measurement). In a laboratory setting, each instar lasted approximately 41 days. Each molt requires blood-feeding. Development time is directly linked to temperature and host availability.

Adults

Triatoma sanguisuga adults are approximately 19 mm-long, with dark brown to black, flattened bodies and elongate, cone-shaped heads (Griffith, 1947). Antennae are elbowed, with six segments. The head bears a slender beak-like structure used to administer the notorious kiss, or bite. The abdomen is wide, with sides sticking out past the wing margins, displaying 6 reddish-orange spots on each side (Drees and Jackman, 2018) (Figure 2).

History of the Subfamily Triatominae (Extracted from Tartarotti et al.., 2006)

Triatomines probably evolved from Reduviidae predator groups. The Reduviidae early on in their evolution possibly fed on soft forms of invertebrate animals that inhabited vertebrate nests, such as caterpillars, larvae, and spiders. Later they began to attempt perforating the skin of small vertebrates. It is possible that, in the first phase, hematophagy was optional, and, since the saliva of these insects had no anesthetic properties, the triatomines would have been driven to feed on newly born vertebrates, which would be attacked in a special form of predation. Later in this phase, starting with adaptations for hemolysis, the hematophagous process would have begun (Carcavallo et al., 1999).

To avoid the predatory vertebrates in the nests and burrows, it was necessary to make adaptations, such as cryptic behavior and inverse activity pattern, for feeding while the vertebrate is asleep. In predators, the saliva has a proteolytic effect, a characteristic that was lost by most of the hematophagous insects to make it possible to ingest blood by a painless bite. Hematophagy also requires a rapid compensation of the enormous amount of blood that triatomines ingest. The insect therefore excretes great amounts of water and salts immediately to reduce its weight. Another adaptation to hematophagy is the erythrocytic rupture and hemolytic process at the beginning of digestion (Carcavallo et al., 1999). Triatomines are little different from Reduviidae predators, in habitat and forms, which also corroborates the argument that this group is a recent one.

Gorla and colleagues (1997) consider that triatomines are polyphyletic in origin and they believe that hematophagy have appeared recently, associated with the evolution of vertebrate nests. The polyphyletic hypothesis suggests that the adaptative steps from free life predators to hematophagous feeding might have occurred several times, not only among different groups of Reduviidae, but also among other Hemiptera groups. Deep phylogenetic analysis should resolve this question of polyphyly.

This hypothesis may explain the close relationship between genera and species of triatomines associated with certain vertebrates. For instance, *Psammolestes* associated with bird's nests, *Dendrocolaptidae*, *Cavernicola pilosa barber* with Chiroptera, *Microtriatoma* with the biocenosis of the great Bromeliads, *Panstrongylus geniculatus* associated with the *Edentates* (see Figure 1), and some species of the *Triatoma protracta* complex associated with the *Neotoma genus*. The polyphyletic hypothesis also helps to explain most of the anatomical differences found between some tribes and their notable similarity with taxa of other Reduviidae subfamilies. For example, species of *Alberproseniini* possesses morphological characteristics of the Cetherinae and species of *Psammolestes* possesses anatomical characteristics present in the Physoderinae subfamily. Among the most convincing studies, it has been discovered that there are fundamental differences in salivary components between species of Rhodniini and Triatomini, as well as differences in sensorial patterns, suggesting different origins for these two tribes. Therefore, the Triatominae subfamily should be assumed, more correctly, to be a utilitarian group, defined on the basis of their hematophagous habits and adaptations associated to this diet, and not a phylogenetic group of individuals sharing a common ancestry (Carcavallo et al., 1999).

Figure 1. Subfamily Triatominae Jeannel, 1919. Species: *Panstrongylus geniculatus*. Locality: Montebello, Amalfi Municipality, Departmento de Antioquia, Colombia (6°55’58’’N; 75°05’30’’ W, 18-24 °C). Source: F. Otálora Luna, 2006. License: CC BY-SA 3.0.

Some authors, including Usinger and colleagues (1966) believe, however, that the triatomines represent a monophyletic group and that their hematophagy have appeared only once. Gaunt and Miles (2000) also postulate that the triatomines are of monophyletic origin, based on the appearance of a salivary protein (anti-thrombin).

The monophyletic hypothesis is not only difficult to support, but it also causes problems in the understanding of the insects' distribution, association with animals, source of feeding and adaptation to different habitats. The comparison between population and behavioral parameters, association with vertebrates and habitat, as well as their biogeographical characteristics support the hypothesis that triatomines probably appeared several times within the Reduviidae and that they represent species of polyphyletic origin, based on their apomorphic character with relation to hematophagy (Schofield, 1988; Lyman et al., 1999; Bargues et al., 2000, Marcilla et al., 2001).

Figure 2. Adult *Triatoma sanguisuga*, eastern blood-sucking cone-nose. Locality: Pryor, Mayes County, Oklahoma, United States. Source: R. Webster, 2012. License: CC BY-SA 4.0.

Biogeographic History (Extracted from Tartarotti et al.., 2006)

The New World is clearly the center of triatomine origin and diversity. Of the approximately 137 triatomine species (Galvão et al., 2003), 105 occur in this area. Of the 14 genera, 12 are found exclusively in America: *Alberprosenia*, *Belminus*, *Bolbodera*, *Cavernicola*, *Dipetalogaster*, *Eratyrus*, *Microtriatoma*, *Panstrongylus*, *Parabelmintos*, *Paratriatoma*, *Psammolestes,* and *Rhodnius*. Only 2 genera, *Linshcosteus* and *Triatoma*, occur in the Old World, and the *Triatoma* is also found in the New World. The *Linshcosteus genus*, with 5 species, is confined to the Indian subcontinent, 7 species of *Triatoma* are present in Southeast Asia, and 1 species, *T. rubrofasciata*, is cosmopolitan in the tropics. Its wide distribution can be explained by marine transport from the 17th century to the early 20th century. This species is also present in the Brazilian northeast (Schofield and Dolling, 1993). *T. rubrofasciata* is considered to be an ancestor of the other 7 *Triatoma* species in Southeast Asia (*T. amicitiae*, *T. bouvieri*, *T. cavernicola*, *T. leopoldi*, *T. migrans*, *T. pugasi*, *T. sinica*) because they share morphological characteristics and are all included in the Rubrofasciata group. Another interesting characteristic that confirms the hypothesis that *T. rubrofasciata* is an older species is related to its painful bite, considered a primitive characteristic (Schofield, 1988).

The almost total absence of triatomines in Africa, except *Triatoma rubrofasciata*, probably brought to African ports by ships, suggests that the hematophagous evolution of Reduviidae in Africa was inhibited by the evolution of the hematophagous Anthocorideos, now known as Cimicidae, which had already occupied the available niches. The high degree of morphological specialization of Cimicidae suggests that they arose prior to the triatomines and that the latter evolved independently in America after the separation of the continents. This hypothesis is better than the view that triatomines may have appeared in Africa and, subsequently, were locally extinguished (Schofield, 2000a).

The dispersion of triatomines by vertebrates was studied on *Rhodnius prolixus* in Central America. It is believed that these insects migrated from South America to Central America, transported by birds. Enzymatic and RAPD (Random Amplification of Polymorphic DNA) analyses corroborated this view, the limited genetic variability denoting the recent origin of populations from South America (Dujardin et al., 1998).

Similarly, the presence of *Rhodnius prolixus* in Mexico is associated with the migration of vertebrates. The expansion and distribution of *T. infestans*, for example, is closely related to human activity (Schofield, 1988). The species is endemic in Bolivia and has been dispersed by human action, their domiciliary invasion obeying an opportunist mechanism provided by the stimulus of shelter and feeding (Forattini, 1980).

Triotamine Phylogeny

In the triatomine group, the Rhodniini, Cavernicolini, Bolboderini, Alberproseniini, and Linshcosteini tribes appear to be monophyletic groups, that is, each tribe possesses an ancester in common, while the Triatomini tribe is considered to be polyphyletic (Lent and Wygodzinsky, 1979; Galvão et al., 2003). The recognition of Rhodiniini as a monophyletic tribe takes into account characteristics of the *Rhodnius* genus not shared with other triatomines, such as, apical antenna insertion, body forms, post-ocular callosities, male genital characteristics, egg surface architecture, and nitroforine presence in the salivary glands. Besides these characteristics, the species of both *Rhodnius* and *Psammolestes* are primarily arboreal in contrast with the terrestrial habits of most of the other triatomines (Schofield and Dujardin, 1999). In addition, studies of sequence of ribosomic RNA mitocondrial and cytochrome B genes cluster *Psammolestes coreodes* with the species *Rhodnius prolixus*, *R. robustus*, and *R. neglectus* (Lyman et al., 1999).

Currently the most widely accepted hypothesis is that triatomines are a polyphyletic group, based on their convergent apomorphic hematophagy characters which have appeared independently several times in Reduviidae. These insects are highly adaptable to different habitats created by the constant expansion by humans and other animals. The hypothesis of a polyphyletic assemblage is corroborated by several studies on the Rhodiniini and Triatomini tribes. Analyses of sequences of mitochondrial (Stothard et al., 1998; Lyman et al., 1999) and ribosomal DNA (Bargues et al., 2000; Marcilla et al., 2002) and analysis of polymorphism length of intergenic transcribed rDNA (Tartarotti and Ceron, 2005), enzymatic studies, morphological analyses and taxonomic (Carcavallo et al., 1999), ecological studies (Schofield, 1988) show the non-monophyletic nature of this group.

Life Cycle: Triatomines as Vector for *Trypanosoma cruzi* (Extracted verbatim from DPDx, 2023)

An infected triatomine insect vector (or kissing bug) takes a blood meal and releases trypomastigotes in its feces near the site of the bite wound (see Figure 3, including life cycle phases numbered in the text). Trypomastigotes enter the host through the wound or through intact mucosal membranes, such as the conjunctiva (1). Common triatomine vector species for trypanosomiasis belong to the genera *Triatoma*, *Rhodnius*, and *Panstrongylus*. Inside the host, the trypomastigotes invade cells near the site of inoculation, where they differentiate into intracellular amastigotes (2). The amastigotes multiply by binary fission (3) and differentiate into trypomastigotes, and then are released into the circulation as bloodstream trypomastigotes (4). Trypomastigotes infect cells from a variety of tissues and transform into intracellular amastigotes in new infection sites. Clinical manifestations can result from this infective cycle. The bloodstream trypomastigotes do not replicate (different from the African trypanosomes). Replication resumes only when the parasites enter another cell or are ingested by another vector. The kissing bug becomes infected by feeding on human or animal blood that contains circulating parasites (5). The ingested trypomastigotes transform into epimastigotes in the vector's midgut (6). The parasites multiply and differentiate in the midgut (7) and differentiate into infective metacyclic trypomastigotes in the hindgut (8).

Triatomine Behavior (Extracted verbatim from Tartarotti et al., 2006)

Primitive predatory behavior still occurs in many triatomine species, including *Triatoma rubrofasciata*, which feeds on caterpillars, *T. rubrovaria* which can feed on spiders and silkworm, and *T. circummaculata*, which feeds on vertebrates' blood and cockroach hemolymph. Young nymphs of *Eratyrus mucronatus* preferentially feed on invertebrate animals, while nymphs in more advanced stages and adults feed on vertebrates' blood. Cannibalistic behavior can be a transitional stage between predation and hematophagy. There are reports of nymphs sucking blood from other nymphs in laboratory colonies. Such cleptohematophagous behavior occurs in *Belminus herreri* which obtains blood from species of recently fed *Rhodnius*. In short, all of these observations suggest that hematophagy is a recent characteristic in triatomines and that adaptations to this habit are still occurring (Schofield, 2000b).

For mammals, the bite from Reduviidae predators tends to be very painful and can cause death, especially by anaphylactic shock in small animals. The same happens in the case of certain triatomines. For instance, the bite of *Panstrongylus geniculatus* in pigs and humans in the Amazon leaves painful lesions and, in the case of *Triatoma rubrofasciata*, there has been at least 1 report of human death (Schofield, 2000b).

Medical Importance (Excerpted and adapted from Barreto Vieira et al., 2018)

Triatominae bugs are the vectors of Chagas disease, a major concern to public health especially in Latin America, where vector-borne Chagas disease has undergone resurgence due mainly to diminished triatomine control in many endemic municipalities. Although the majority of Triatominae species occurs in the Americas, species belonging to the genus *Linshcosteus* occur in India, and species belonging to the *Triatoma rubrofasciata* complex have been also identified in Africa, the Middle East, Southeast Asia, and the Western Pacific. Not all Triatominae species have been found to be infected with *Trypanosoma cruzi*, but the possibility of establishing vector transmission to areas where Chagas disease was previously non-endemic has increased with global population mobility. Additionally, the worldwide distribution of triatomines is concerning as they are able to enter into contact and harbor other pathogens, leading to concern that they could have competence and capacity to transmit them to humans during the bite or after successful blood feeding, spreading other infectious diseases. There are reports suggesting that triatomines may be competent vectors for pathogens such as *Serratia marcescens*, *Bartonella*, and *Mycobacterium leprae*, and that triatomine infection with other microrganisms may interfere with triatomine-*T. cruzi* interactions, altering their competence and possibly their capacity to transmit Chagas disease.

The transmission of Chagas disease by species of Triatominae is very well reported in the literature. Infection with vector-borne *T. cruzi* begins when metacyclic trypomastigotes, which are motile forms of the parasite, penetrate into the vertebrate host through the triatomine feces and urine. Once in the vertebrate host, these forms, which have evolved to survive inside host cells, infect nucleated cells. Within the cell, they differentiate into amastigotes in a phagosomal compartment known as the parasitophorous vacuole, escape to the cytoplasm, and replicate asexually

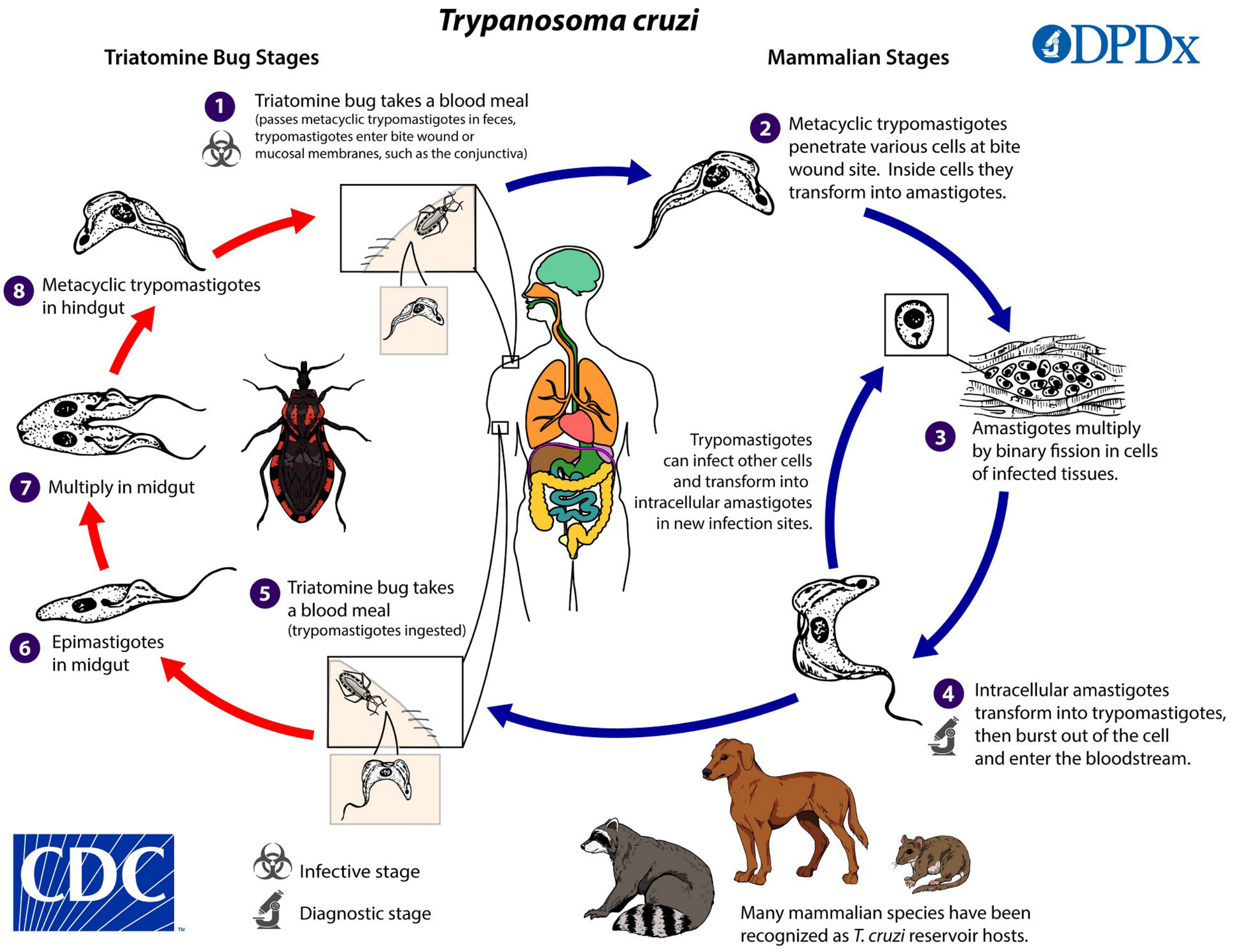

Figure 3. Life cycle of the protozoan parasite, *Trypanosoma cruzi*, the cause of Chagas disease, a zoonotic disease that can be transmitted to humans by blood-sucking triatomine bugs. Source: DPDx, 2023. Public domain.

through longitudinal binary division to form several amastigotes. As the cell becomes full of amastigotes, these convert into trypomastigotes and breach it, invading adjacent tissues and spreading to distant sites through bloodstream and lymphatics. The parasite population expands due to repeated cycles of cell invasion and replication, which lead to immune responses and can give rise to Chagas-associated pathologies (Tyler and Engman, 2001).

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Arthropoda

Acari (Order): Ticks

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and Filipe Dantas-Torres

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Chapter 66

Acari (Order): Ticks

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Tick Biology and Life Cycles

Ticks (order Ixodida Leach, 1815) are blood-feeding ectoparasites of vertebrates representing important vectors of pathogens that cause diseases in humans and other animals (see Figure 1). They are obligate parasites at 1 or more developmental stages and may parasitize different classes of terrestrial vertebrates including mammals, birds, reptiles, and amphibians. All species of ticks have 4 stages in their life cycle, including the **embryonated egg** and 3 active stages: **Larva**, **nymph** (one or more instars), and **adult** (male and female). The tick life cycle may have many variations depending on the family and species. Depending on the number of hosts on which they feed, the tick may have a 1-host, 2-host, 3-host, or multi-host life cycle. During their off-host development phases, they can persist for long periods in the environment without feeding, particularly ticks in the family Argasidae (the soft ticks; see Sonenshine, 1991).

Ixodid ticks (family Ixodidae, the hard ticks) have a single nymphal instar and of them are **non-nidicolous**, meaning living in open and exposed habitats. In some species, only females result from the nymphal stage. These females reproduce **parthenogenetically**, that is, they do not need to mate to produce eggs (Sonenshine, 1991). Larvae and nymphs take a blood meal before molting to the next stage. Females lay several hundreds or thousands of eggs after engorging. Larvae, nymphs, and females may feed for several days, whereas males are usually intermittent feeders, taking small blood meals at each feeding and may remain on the host for long periods of time (Oliver, 1989; Sonenshine, 1991; 2013). Ixodid females have a single **gonotrophic cycle**. After completing feeding, they detach from the host to initiate oviposition in a secluded place, such as under vegetation, at the base of tree trunks, animal burrows, or even in cracks and crevices on the walls of human houses and animal sheds. Once oviposition is complete, the female dies. Males of Metastriata may stay on the hosts for long periods, mating with several females. These males usually mate on the host and need a blood meal to produce viable sperm. Males of the genus *Ixodes* (Prostriata) typically mate off the host, which is typical of nidocolous tick species. Most ixodids have a 3-host life cycle, where each stage falls to the ground after feeding. Engorged larvae detach from a host to molt in the environment, the same occurring with resulting nymphs that seek another host to feed and detach as engorged nymphs to molt into males or females, which in turn will complete the parasitic life cycle onto another host (Oliver, 1989; Sonenshine, 1991).

Other species of ixodids have a 2-host tick life cycle, characterized by larvae that feed and molt on the same host, whereas the nymphs feed and detach after engorgement. Nymphs molt in the environment and the resulting males or females attach to another host to complete the parasitic life cycle. There are a few species, including some of economic importance, that have a 1-host life cycle. They molt on the host (from larva to nymph and then to adult) and detach from the host as engorged females (Oliver, 1989; Sonenshine, 1991).

Almost all argasid species (family Argasidae, the soft ticks) are **nidicolous**, meaning living in the protected habitat of a nest of a bird or mammal, and usually have more than 1 nymphal instar in their life cycle. Many species have a multi-host life cycle, with the exception of some species, such as

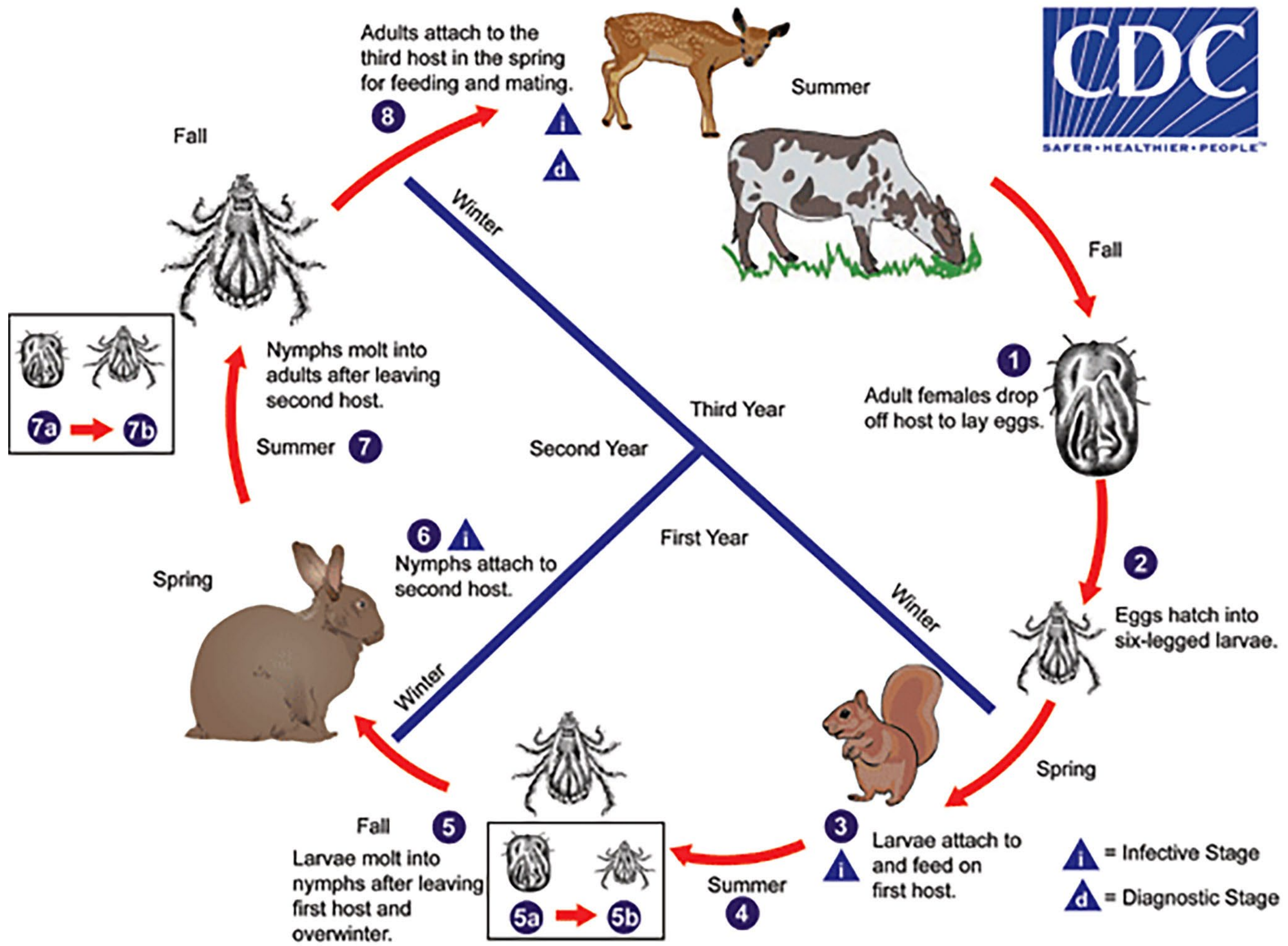

Figure 1. Life cycle of 3-host ixodid (hard) ticks. The adult is considered the diagnostic stage, as identification to the species level is best achieved with adults. Most ticks of public health importance follow this pattern, including members of the genera *Ixodes* (Lyme borreliosis, babesiosis, human granulocytic ehrlichiosis), *Amblyomma* (tularemia, ehrlichiosis, and Rocky Mountain spotted fever), *Dermacentor* (Rocky Mountain spotted fever, Colorado tick fever, tularemia, tick paralysis), and *Rhipicephalus* (Rocky Mountain spotted fever, boutonneuse fever). — Three-host ixodid ticks have a life cycle that usually spans 3 years, although some species can complete the cycle in only 2 years. Adult females drop off the third host to lay eggs after feeding (1), usually in the fall. Eggs hatch into 6-legged larvae (2) and overwinter in the larval stage. In the spring, the larvae seek out and attach to the first host, usually a small rodent (3). Later in the summer, engorged larvae leave the first host (4) and molt into nymphs (5), usually in the fall. The ticks overwinter in this stage. During the following spring, the nymphs seek out and attach to the second host (6), usually another rodent or lagomorph. The nymphs feed on the second host and drop off later in the summer (7). Nymphs molt into adults (7a–7b) off the host in the late summer or fall and overwinter in this stage. The next spring, adults seek out and attach to a third host, which is usually a larger herbivore (including cervids and bovids), carnivore, or human (8). The adults feed and mate on the third host during the summer. Females drop off the host in the fall to continue the cycle. Females may reattach and feed multiple times. The 3 hosts do not necessarily have to be different species, or even different individuals. Also, humans may serve as first, second, or third hosts. Source: United States Centers for Disease Control and Prevention, Division of Parasitic Diseases and Malaria, 2017. Public domain.

Ornithodoros lahorensis Neumann, 1908 that has a 2-host life cycle, and *O. megnini* that is a 1-host tick. In most argasid species, nymphs and adults are rapid feeders (generally taking around 30 to 40 minutes to complete a meal), but larvae usually remain feeding on a host for several days (Oliver, 1989; Sonenshine, 1991; 2013). Each immature stage feeds before molting to the next stage, but in some species of the genus *Ornithodoros*, such as *O. brasiliensis* Aragão, 1923, larvae molt to nymphs without feeding (Ramirez et al., 2016).

Some species of *Argas* and *Ornithodoros* may reproduce by **autogeny** (for example, *A. persicus* (Oken, 1818), *O. lahorensis*, *O. tholozani* (Laboulbène and Mégnin, 1882), *O. tartakovskyi* Olenev, 1931, and *O. parkeri* Cooley, 1936) (see Feldman-Muhsam, 1973; Oliver, 1989), and nymphs of some species (for example, *O. fonsecai* (Labruna and Venzal, 2009) and *Nothoaspis amazoniensis*) molt from the first to the second instar without feeding (Nava et al., 2010). Facultative autogeny may occur in the absence of a host. Females present multiple gonotrophic cycles and can feed many times, usually before mating and oviposition (Sonenshine, 1991). But for some species, the feeding behavior remains unknown.

Mating takes place off-host, and the female can lay a few hundred eggs after each meal, in each gonotrophic cycle. This is a survival mechanism, especially for nest dwelling species that depend on the presence, not always frequent, of their hosts. Exceptions may occur, for example, in adults of *Antricola* and *Otobius* that have vestigial mouthparts and a female may even lay eggs without feeding (this is called obligate autogeny) (Oliver, 1989; Sonenshine, 1991; 2013).

The biological life cycle involving multiple hosts is typical of argasids, which inhabit restricted environments and feed on the same individual host several times or in several hosts (of the same species or not) during their lifetime. Their habitat is intimately associated with that of their hosts. However, they can be found in remote locations far from human habitations such as loose soil, tree bark, animal burrows, caves, and in nests of wild and marine birds. Those that inhabit animal nests live in relatively stable microhabitats, feeding and reproducing continuously throughout the year. In this group, as in ixodids that inhabit nests, the development can be adapted seasonally, and a generation can take a year or more to develop in temperate climates (Oliver, 1989; Sonenshine, 1991; 2013).

The life cycle of the only species of family Nuttalliellidae is still unknown and the main hosts for each stage are uncertain. As an ixodid tick, *Nuttalliella namaqua* has a single nymphal instar and recently it has been shown that *N. namaqua* females may feed multiple times, like argasid females (Latif et al., 2012; Mans et al., 2012). Potential hosts already described for *N. namaqua* include mammals, reptiles, and birds (Mans et al., 2014). Larvae have been found parasitizing different species of rodents (Horak et al., 2012), and adults have been found in nests of birds (Keirans et al., 1976). Results of DNA analysis of the gut meals of females indicated that the ticks had fed on lizards of different species. Nymphs and adult females, therefore, have been shown to successfully feed on lizards in an experimental setting (Mans et al., 2011; 2014). Nymphs and adult females have been found in a variety of microhabitats in different regions of Africa (Mans et al., 2014). Although larvae may generally feed on rodents, the nymphal and adult stages seem to prefer reptiles, it is still premature to conclude that natural hosts of immature individuals or adults may feed exclusively on either mammals or reptiles. All these data may suggest a wider geographic distribution as well as host preference for *N. namaqua.*

Host Range

Ticks have variable degrees of specificity for their hosts, with some species parasitizing very different groups of animals. Some species of ticks only feed on a narrow range of host groups or on a specific host species (host-specific = narrow host range), whereas others are less selective (generalists), using a wide range (broad host range) of vertebrates as hosts (Sonenshine, 2013). Mammals serve as hosts for more tick species than birds, reptiles, and amphibians. Among mammals, rodents are one of the most common host groups, particularly for immature stages of hard ticks.

In general, immature stages of species that have a 2- or 3-host life cycle feed on small animals (for example, rodents), whereas adults prefer medium- and large-sized animals. In ticks that use more than 1 host, as happens with most species of the genus *Amblyomma*, immature stages are less specific than the adults, and may parasitize a greater diversity of hosts (Sonenshine, 2013). Host specificity is influenced by several factors, including host defense mechanisms against tick infestations, such as physical barriers in the body, self-cleaning behavior, and immunological responses.

Both passive and active questing methods are used by ticks to find their hosts. Passive species, such as most nidicolous ticks, remain in their habitat (for example, grassy fields, brushy areas, animal burrows, nests) and depend upon contact with vertebrate animals that invade their space incidentally. Most non-nidicolous ticks are hunters; they use ambush behavior (called questing), referring to ticks living in grass or brush-covered habitats typically climbing to the tips of stems or branches of vegetation where they wait for passing hosts to brush against them (Sonenshine, 2013). The success of a tick in finding a host depends on several factors, including the height of the vegetation on which ticks of different stages are waiting for a host, as well as the response of ticks to specific stimuli, such as body odor, body heat, and carbon dioxide (CO_2), which are emitted from the host. Also, the type of environment has a direct influence on the qualitative and quantitative availability of hosts for the ticks.

The seasonal variation in the biological cycles and development of a species of tick is determined by the host and by abiotic factors, such as temperature, photoperiod, and relative humidity. Temperature plays an important role in determining the duration of each off-host development phase such as: For example, oviposition, egg incubation, larvae hatching, and ecdysis (molting from one stage to another). The photoperiod has a direct influence in the induction of diapause, mainly in nonequatorial regions, modulating the cycles in seasonal rhythms that assure the ticks the synchronization of their activities with the appropriate climatic conditions (Oliver, 1989; Sonenshine, 2013).

Two types of diapause are known: Behavioral (suppression of host-seeking activity or delay of engorgement) and morphogenetic or developmental (delay during embryogenesis) in the ecdysis of immature stages or in the oviposition (egg laying) of females (Sonenshine, 2013). This is an important strategy in the biology of both nidicolous and non-nidicolous ticks, such as *Amblyomma sculptum*, that use both larval and behavioral diapause (Labruna et al., 2002; 2003).

Taxonomic History

Millions of years ago, during the Paleozoic Era, ticks diverged from other Acari Leach, 1817, probably as parasites of the ancestors of modern vertebrates such as reptiles and amphibians (Dantas-Torres, 2018). Therefore, ticks disappeared when their conquering continental hosts went extinct. Fossil evidence indicates that modern tick lineages originated and diverged during the Mesozoic Era (Mans et al., 2016).

There are 2 fossil species in the family Argasidae Koch, 1844 (soft ticks), both of which are in the genus *Ornithodoros* Koch, 1844, namely, *O. antiquus* Poinar, 1995 and *O. jerseyi* (Klompen and Grimaldi, 2001). The third argasid fossil with an adequate morphological description corresponds to a male of *Ornithodoros* sp. found in Dominican amber from about 25 Ma (= million years ago) (Estrada-Peña and De La Fuente, 2018). These authors suggested that many of the lineage splits were produced when the landmasses were still forming the supercontinent Pangea, or Laurasia and Gondwanaland. Fossil species in the family Ixodidae Koch, 1844 (hard ticks) include *Amblyomma birmitum* Chitimia-Dobler, Araujo, Ruthensteiner, Pfeffer and Araujo, 2017, *Cornupalpatum burmanicum* Poinar and Brown, 2003, *Compluriscutula vetulum* Poinar and Buckley, 2008, *Ixodes succineus* Weidner, 1964, and *Haemaphysalis cretacea* Chitimia-Dobler, Pfeffer and Dunlop, 2018. The only fossil of the genus *Haemaphysalis* Koch, 1844 may actually belong to another genus (Guglielmone et al., 2016; see also Dantas-Torres, 2018). Recently, a fossil species, namely *Deinocroton draculi* Peñalver, Arillo, Anderson and De la Fuente, 2017, was described in a recently proposed fossil family Deinocrotonidae Peñalver, Arillo, Anderson and Pérez-de la Fuente, 2017. This species resembles *Nuttalliella namaqua* Bedford, 1931, which represents a basal lineage within the order Ixodida.

Current Taxonomic Position of Tick Genera

The Ixodida is currently represented by 956 species (948 extant and 8 fossil species) (see the supplementary material for more about this), which we now consider to be distributed into 4 families: **Argasidae** (215 species), **Ixodidae** (733 species), **Nuttalliellidae** Bedford, 1931 (monospecific), and **Deinocrotonidae** (monospecific) (Dantas-Torres, 2018; Du et al., 2018; Kwak, 2018; Barker, 2019; Tomlinson and Apanaskevich, 2019).

Excluding the monospecific families, the genus-level classification of ticks has been a long issue of debate and changes are constantly proposed, particularly in the family Argasidae.

Following are detailed descriptions of some groups of ticks.

Family Argasidae: The Soft Ticks

The family Argasidae, or the soft ticks, includes 215 extant and 2 fossil species (Dantas-Torres, 2018), many of which have not been yet adequately described. Estrada-Peña and colleagues (2010) suggest that there is still a long way to go to achieve an accurate view of the main evolutionary lines of the family. The soft ticks are so-named because they have no hard plate on their back (called the scutum in hard ticks; see below). They also commented that there is no consensus about the relevant morphological features for the determination of argasid species nor there is consensus on the appropriate genus for many species. According to Venzal and colleagues (2008), only larval morphological features have been adequately defined for a specific determination, mainly in the absence of DNA sequence data.

In this chapter, the genus-level classification adopted by the last lists of ticks of the world is used (Guglielmone et al., 2010; Dantas-Torres, 2018). Also included are 2 recent genera proposed by Barker and Burger (2018) and new species described in 2019 (Barker, 2019; Martins et al., 2019; Tomlinson and Apanaskevich, 2019; Sun et al., 2019). However, the genus-level classification of argasids is still controversial, with some subgenera perhaps deserving to be elevated to the rank of genera (Burger et al., 2014; Mans et al., 2019). Based on 4 classification schemes for the argasid genera (the Soviet, American, French, and Cladistic schools), the subfamily Argasinae (Trouessart, 1892, pro parte) Pospelova-Shtrom, 1946 (ectoparasites of chickens and wild birds) is well supported by molecular data (Burger et al., 2014). However, this is not true for the subfamily Ornithodorinae Pospelova-Shtrom, 1946. After sequencing the mitochondrial genomes of 12 species, Burger and colleagues (2014) concluded that there is a clade of Neotropical species within the Ornithodorinae that includes the genera *Antricola* Cooley and Kohls, 1942 and *Nothoaspis* Keirans and Clifford, 1975, and the subgenera *Alectorobius* Pocock, 1907, *Parantricola* Cerny, 1966, and *Subparmatus* Clifford, Kohls and Sonenshine, 1964. On the other hand, the genera and subgenera of the Neotropical Ornithodorinae clade were placed in the genus *Carios* Latreille, 1796, as previously proposed by Klompen and Oliver (1993). Probably, the generic classification of argasids adopted here (Guglielmone et al., 2010) will change in the future, considering that new genomic data are becoming available, shedding new light onto this issue. For instance, Mans and colleagues (2019) generated a total of 83 whole mitochondrial genomes, 18S rRNA and 28S rRNA genes and proposed a revised genus-level classification for the family Argasidae. The new classification corresponds broadly with the morphological cladistic analysis of Klompen and Oliver (1993), however, with the erection of different subgenera to the genus level.

The genus *Antricola* is represented by 17 species distributed in the Neotropical region, most of them being restricted to Cuba. Besides Cuba, some species have been described from Mexico, Puerto Rico, Brazil, and Venezuela (Jones et al., 1972; De La Cruz, 1973; 1976; 1978; De La Cruz and Estrada-Peña, 1995; Camicas et al., 1998; Estrada-Peña et al., 2004; Guglielmone et al., 2010). The main contributions to the taxonomy of this genus were produced by De La Cruz, during the 1970s (De La Cruz, 1973; 1976; 1978). The number of species described from 1910 to 2004 is shown in Figure 2A. A key for the currently known species of *Antricola* is available in Estrada-Peña and colleagues (2004).

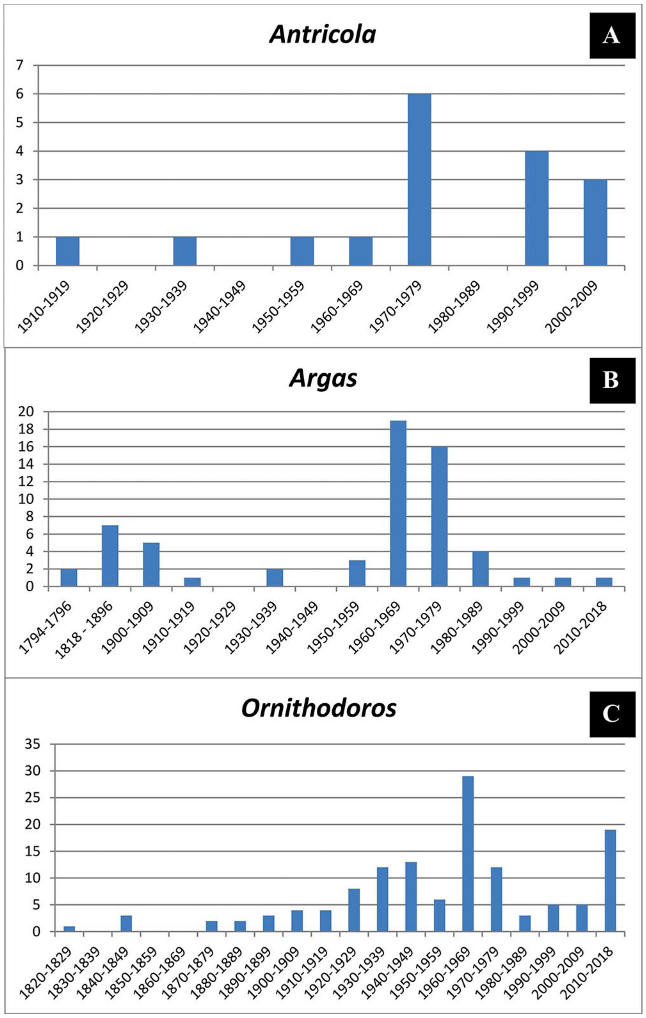

Figure 2. Argasidae genera. A) Number of *Antricola* species chronologically described from 1910 to 2004; B) number of *Argas* species chronologically described from 1795 to 2012; C) number of *Ornithodoros* species chronologically described from 1820 to 2019. Source: D. Moraes Barros-Battesti, V. Castilho Onofrio, and F. Dantas-Torres. License: CC BY.

The genus *Argas* Latreille, 1795 is currently represented by 62 species, distributed in the Afrotropical, Australasian, Neotropical, and Oriental regions (Camicas et al., 1998). The number of species described from 1795 to 2012 is shown in Figure 2B. Most of the species have been described in the last century, and half of them from 1960 to 1980 (35 species). The main contributions were those of Kohls and Hoogstraal (1961), Kohls and colleagues (1970), and Keirans and colleagues (1979). According to Muñoz-Leal (2018), the morphology of nymphs and adults of *Argas* are less informative taxonomically, but some integumental dorsal features may be useful for a specific identification.

The genus *Nothoaspis* is composed of 3 species (*N. reddelli* Keirans and Clifford, 1975 in Mexico; *N. amazoniensis* Nava, Venzal and Labruna, 2010 in Brazil; and *N. setosus* (Kohls, Clifford & Jones, 1969) n. comb. (Muñoz-Leal et al., 2019). The last species was previously assigned to the genus *Ornithodoros*, but the morphological and molecular analysis of *O. setosus* larvae recently collected of the local type of this species showed that it belongs to the genus *Nothoaspis.* This genus is restricted to the Neotropical region (Keirans and

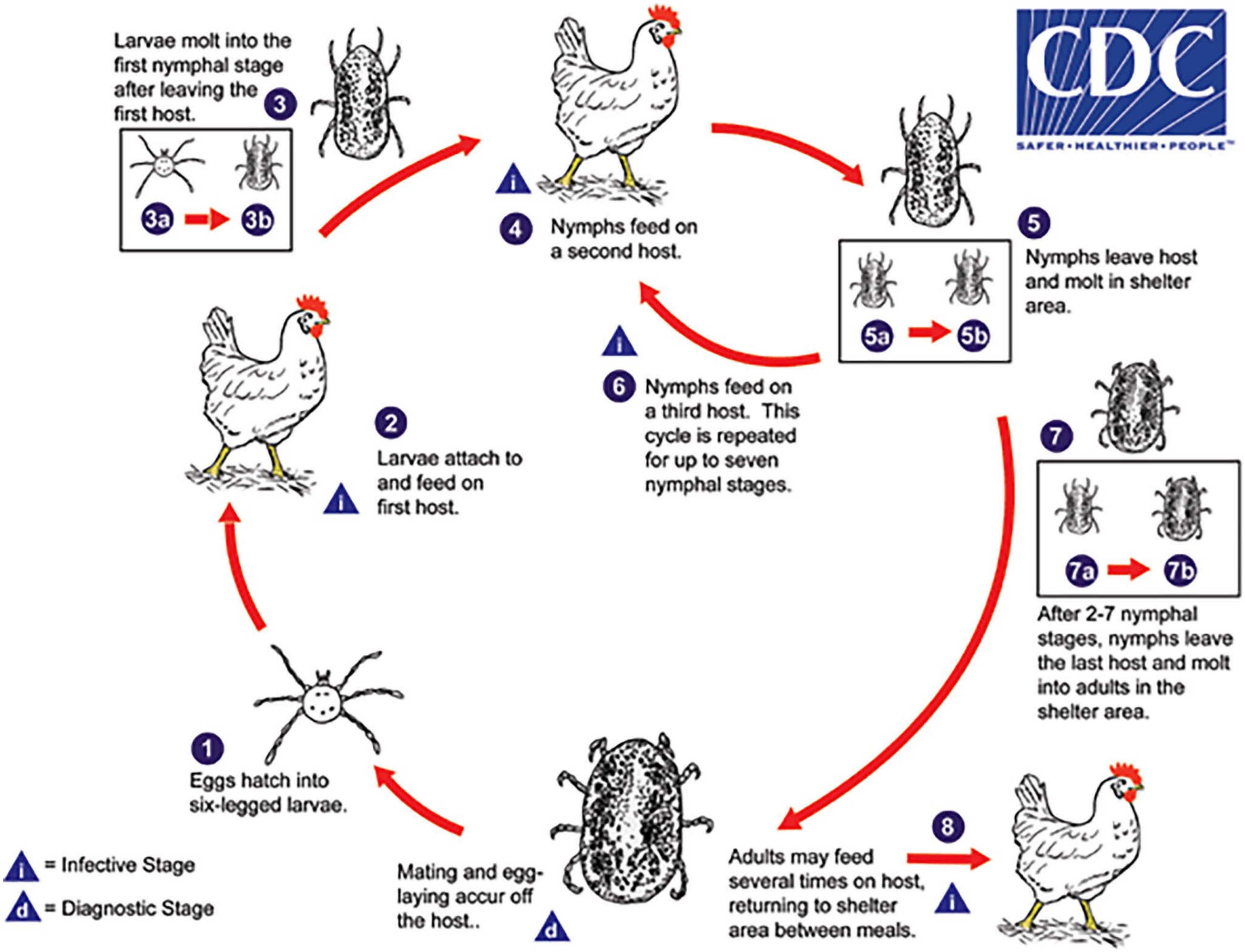

Figure 3. Multihost life cycle for argasid (soft) ticks. Unlike the Ixodidae, members of the family Argasidae have 2 or more nymphal stages, each of which requires a blood meal. This pattern is referred to as the multihost life cycle. Two species of public health concern in the United States, *Ornithodoros hermsi* and *O. turicata*, are vectors of tick-borne relapsing fever (TBRF) spirochetes. In Africa and Asia, *O. moubata* is a vector of TBRF spirochetes. Members of the genus *Carios* are vectors of TBRF spirochetes in Central America and South America. — Mating usually occurs, and egg-laying always occurs, off the host in a sheltered area (usually an animal nest). Eggs hatch into 6-legged larvae (1) in the parents' sheltered area. They quest for a host in the vicinity of the sheltered area. Once a suitable host is found, they feed for anywhere from 1 hour to several days, depending on the species (2). After feeding, the larvae leave the host and molt into the first nymphal instars in the sheltered area (3a–3b). The nymphs quest for, and feed on, the second host (4) rapidly (usually about an hour). The second host is usually the same species, and often the same individual, as the first host. The first nymphal instars leave the host and molt into the next nymphal instars in the sheltered area (5a–5b). This cycle can continue to accommodate up to 7 nymphal instars (6), depending on the species. After the last nymphal instar has fed, it leaves the host and molts into an adult (7a–7b) in the sheltered area. Adults may continue to feed on the host (8), feeding rapidly and detaching after each blood meal. Females of some species lay egg batches after each meal. Humans are usually only incidental hosts for argasid ticks and may be fed upon by any of the stages. Source: United States Centers for Disease Control and Prevention, Division of Parasitic Diseases and Malaria, 2017. Public domain.

Clifford, 1975; Nava et al., 2010; Muñoz-Leal et al., 2019). Note that *N. setosus* is referred to as *O. setosus* in the supplementary list for this chapter.

The genus *Ornithodoros* is the most speciose in the family Argasidae and comprises 131 extant and 2 fossil species (note that the fossil species are not included in the supplementary list for this chapter). They are distributed in the Afrotropical, Australasian, Oriental, Nearctic, Neotropical, and Palearctic regions (Camicas et al., 1998). The number of species described from 1820 to 2019 is shown in Figure 2C. As for *Argas*, most of them were described from 1960–1969 (29 species), and the main contributions are those of Clifford and colleagues (1964), Kohls and Clifford (1964), Kohls and colleagues (1965; 1969a), followed by those described from 2010–2019 (20 species) (Dantas-Torres et al., 2012a; Trape et al., 2013; Venzal et al., 2012; 2013; 2015; Barros-Battesti et al., 2015; Labruna et al., 2016; Muñoz-Leal et al, 2016; 2017; Bakkes et al., 2018; Sun et al., 2019).

The nymphs and adults of *Ornithodoros* are very similar and no reliable keys are currently available for their identification. On the other hand, larvae can be reliably separated by chaetotaxy of dorsum and venter, morphology of hypostome and, if present, dorsal plate.

The genus *Otobius* (Banks, 1912) includes 2 species, namely *O. megnini* (Dugès, 1883) and *O. lagophilus* Cooley and Kohls, 1940. The species *O. megnini* is thought to have had its original center of distribution in the arid lands of southwestern North America (Keirans and Pound, 2003). It was probably introduced into Central America and South America on both cattle and horses, and it was imported into South Africa in the ears of horses from South America or, perhaps, Mexico (Keirans and Pound, 2003). Currently, it is distributed worldwide, occurring in Afrotropical, Nearctic, Neotropical and Oriental regions (Camicas et al., 1998; Flores and Solís, 2018; Hosseini-Chegeni et al., 2018). The species *O. lagophilus* is restricted to the Nearctic region, parasitizing wild rabbits, occurring in Canada and the United States (Herrin and Beck, 1965).

Family Ixodidae: The Hard Ticks

The family Ixodidae currently comprises 733 extant and 5 fossil species. This family is divided into 2 lineages (that is, Prostriata and Metastriata) found in all zoogeographic regions of the world (Guglielmone et al., 2014). The ixodids are called hard ticks because they have a big plate on their back called the scutum. The Prostriata (anal groove curves anterior to anus) contains only 1 genus, whereas the Metastriata (when present, anal groove curves posterior to anus) contains 14 genera (Burger et al., 2012; Barker and Burger, 2018). In contrast to what occurs with the family Argasidae, the genus-level classification of Ixodidae is more stable and consensual (Barker and Murrell, 2002; Guglielmone et al., 2014; Dantas-Torres, 2018). Nonetheless, some systematic issues (for example, paraphyly of the genus *Amblyomma* Koch, 1844) are still under debate (Barker and Burger, 2018), but the 2 genera proposed by these authors are here included with the new combinations.

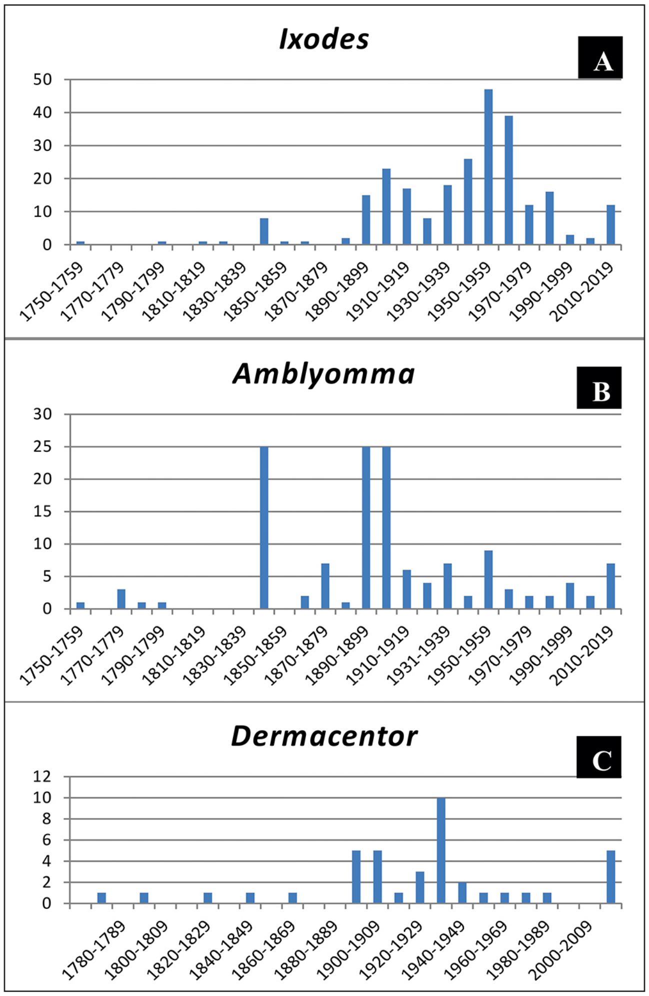

Figure 4. Ixodidae genera. A) Number of *Ixodes* species chronologically described from 1758 to 2019; B) number of *Amblyomma* species chronologically described from 1758 to 2019; C) number of *Dermacentor* species chronologically described from 1776 to 2016. Source: D. Moraes Barros-Battesti, V. Castilho Onofrio, and F. Dantas-Torres. License: CC BY.

The genus *Ixodes* Latreille, 1795 comprises 255 extant species and 1 fossil species. They are distributed in the Afrotropical, Australasian, Nearctic, Neotropical, Oriental, and Palearctic regions, and combinations of these regions including remote islands, and the polar area (circumpolar)

(Guglielmone et al., 2014; Estrada-Peña et al., 2014; Hornok et al., 2014, 2016; Ash et al., 2017; Apanaskevich and Bermúdez, 2017; Guo et al., 2017; Heath and Palma, 2017; Kwak et al., 2018; Barker, 2019). This is the largest tick genus, and most of the species originated on Gondwanaland (the southern continental landmass that began to break up in the early Jurassic around 184 million years BCE) (Guglielmone et al., 2014). The number of species described from 1758 to 2019 is shown in Figure 4A. The highest number of species were described during the 1950s and 1960s, with 47 and 39 species, respectively, mainly due to the contributions of Arthur (1956; 1960a), Kohls (1953; 1956a; 1956b; 1957; 1969), Kohls and Clifford (1962; 1966; 1967), and Kohls and colleagues (1969b).

The genus *Archaeocroton* Barker and Burger, 2018 was proposed for *Amblyomma sphenodonti* (Dumbleton, 1943), the tuatara tick of New Zealand. This new combination was mainly because this species in *Amblyomma* leaves this genus polyphyletic, and indeed, taxonomically unstable (Barker and Burger, 2018). The species was named *Archaeocroton sphenodonti* (Dumbleton, 1943).

The genus *Amblyomma* is 1 of the largest genera and comprises 137 extant and 1 fossil species, distributed in the Afrotropical, Australasian, Nearctic, Neotropical, and Oriental regions. Some species are found in more than 1 region, presenting Afrotropical-Neotropical, Afrotropical-Oriental, Afrotropical-Palearctic, Australasian-Oriental, Nearctic-Neotropical, Oriental-Palearctic, Afrotropical-Australasian-Oriental, or Australasian-Oriental-Palearctic distributions (Guglielmone et al., 2014; Nava et al., 2014a; 2014b; Krawczak et al., 2015; Apaneskevich and Apaneskevich, 2018). Chitimia-Dobler et al. (2017) commented that the genus *Amblyomma* was split in Gondwanaland, with a concurrent spread into what are now known as Africa, Australia, Asia, and South America. No species occurs exclusively in the Palearctic region (Guglielmone et al., 2014). The Neotropical region is home to the largest number of species within this genus, followed by the Afrotropical region. The number of species described from 1758–2019 is shown in Figure 4B. The highest number of species was described from 1840–1849 and 1890–1899, with 25 taxa each of those decades. The greatest contributions were those of Koch (1844) and Neumann (1899), who described 20 and 21 species of *Amblyomma*, respectively, during those years. In the first 10 years of the last century, Neumann (1901; 1904; 1905; 1906; 1907; 1911) described 16 species belonging to this genus.

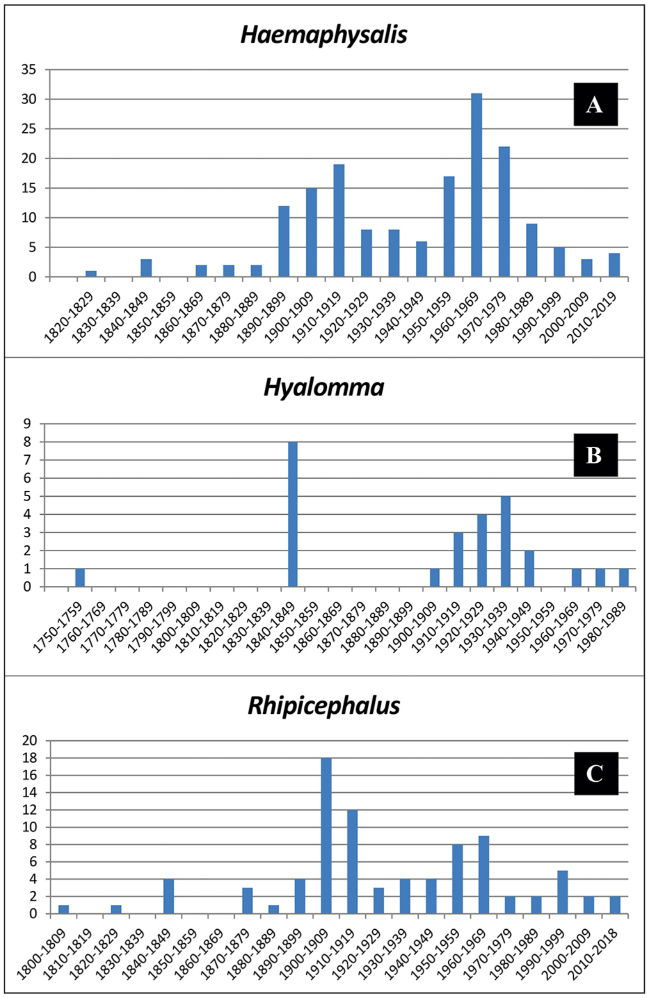

Figure 5. Ixodidae genera. A) Number of *Haemaphysalis* species chronologically described from 1826 to 2019; B) number of *Hyalomma* species chronologically described from 1758 to 1982; C) number of *Rhipicephalus* species chronologically described from 1806 to 2013. Source: D. Moraes Barros-Battesti, V. Castilho Onofrio, and F. Dantas-Torres. License: CC BY.

The genus *Anomalohimalaya* Hoogstraal, Kaiser and Mitchel, 1970 is represented by 3 species, namely *A. lamai* Hoogstraal, Kaiser and Mitchell, 1970 from Nepal, *A.lotozkyi* Filippova and Panova, 1978 from Tajikistan, and *A. cricetuli* Teng and Huang, 1981 from China. They are exclusive to the Palearctic region and found in lands that once constituted Laurasia (Hoogstraal et al., 1970; Filippova and Panova, 1978; Filippova and Bardzimashvily, 1992; Guglielmone et al., 2014).

The genus *Bothriocroton* Keirans, King and Sharrad, 1994 includes 7 species: *B. undatum* (Fabricius, 1775), *B. hydrosauri* (Denny, 1843), *B. concolor* (Neumann, 1899), *B. oudemansi* (Neumann, 1910), *B. auruginans* (Schulze, 1936), *B. tachyglossi* (Roberts, 1953), and *B. glebopalma* (Keirans, King and Sharrad, 1994). They are found exclusively in the

Australasian region (Klompen et al., 2002; Beati et al., 2008; Burger et al., 2012; Barker and Walker, 2014).

The monospecific genus *Cosmiomma* Schulze, 1919 is found in the Afrotropical region and it is represented only by *C. hippopotamensis* (Denny, 1843) (Arthur, 1960b).

The genus *Dermacentor* Koch, 1844 is represented by 40 species, which are of Afrotropical, Nearctic, Neotropical, Oriental, Palearctic, Australasian-Oriental, Nearctic-Neotropical, and Nearctic-Palearctic distribution (Guglielmone et al., 2014; Rubel et al., 2016; Vongphayloth et al., 2018). According to Nava and colleagues (2017), the species are more prevalent in lands of Laurasian origin than in Gondwanan lands. The number of species described from 1776–2016 is shown in Figure 4C. Most species were described during the 1930s, with 10 taxa described during that decade. The main contributions to this genus were those of Schulze (1933; 1935; 1937; 1939). In the last 5 years, 1 species was described in Central America (Apanaskevich and Bermúdez, 2013a) and 4 taxa were described to in the Oriental region (Apanaskevich and Apanaskevich, 2015a; 2015b; 2015c; 2016).

The genus *Haemaphysalis* comprises 169 extant species and 1 fossil species, distributed in the Afrotropical, Australasian, Nearctic, Neotropical, Oriental, and Palearctic regions, and combinations of these regions: Afrotropical-Neotropical, Afrotropical-Palearctic, Australasian-Oriental, Nearctic-Neotropical, Oriental-Palearctic, Afrotropical-Oriental-Palearctic, and Australasian-Oriental-Palearctic (Guglielmone et al., 2014). This genus is poorly represented in the Nearctic and Neotropical regions, with the majority of species occurring exclusively in the Oriental region. The inclusion of the fossil species *H. cretacea* in this genus (Chitimia-Dobler et al., 2018) has been questioned (Dantas-Torres, 2018). The number of species described from 1826–2019 is shown in Figure 5A. The greatest numbers of species were described during the 1960s with 31 taxa, followed by the 1970s with 22 species. The greatest contributions were those of Hoogstraal and colleagues (1965; 1969), Hoogstraal and Trapido (1966), and Hoogstraal and Kim (1985). In the last decade, 6 species were described (Tomlinson and Apanaskevich, 2019).

The genus *Hyalomma* Koch, 1844 is represented by 27 species, distributed in the Afrotropical, Oriental, Palearctic, Afrotropical-Palearctic, Oriental-Palearctic, and Afrotropical-Oriental-Palearctic regions (Guglielmone et al., 2014). The greatest number of species is found in the Afrotropical, followed by the Palearctic regions. According to these authors, the genus is absent in the Australasian, Nearctic, and Neotropical regions. The highest numbers of species were described during the 1840s with 8 taxa described, and the main contributions were those of Koch (1844) who described 7 species during that decade. The number of species described from 1758–1982 is shown in Figure 5B.

The genus *Margaropus* Karsch, 1879 is represented by 3 species, namely *M. reidi* Hoogstraal, 1956, *M. wileyi* Walker and Laurence, 1973, and *M. winthemi* Karsch, 1879, which occur only in the Afrotropical region (Arthur, 1960b; Walker and Laurence, 1973; Guglielmone et al., 2014).

The genus *Nosomma* Schulze, 1919 is represented only by 2 species, namely *N. monstrosum* (Nuttall and Warburton, 1908) and *N. keralensis* Prakasan and Ramani, 2007. Both species are exclusively from the Oriental region (Guglielmone et al., 2014).

The genus *Rhipicentor* Nuttall and Warburton, 1908 is represented by 2 species, namely *R. bicornis* Nuttall and Warburton, 1908 and *R. nuttalli* Cooper and Robinson, 1908, both of which are exclusively found in the Afrotropical region (Guglielmone et al., 2014).

The genus *Rhipicephalus* Koch, 1844 includes 85 species. According to Guglielmone and colleagues (2014), 63 species are exclusively found in the Afrotropical region, 7 species occur exclusively in the Palearctic region, and 3 are found only in the Oriental region. The remaining species are distributed in the Australasian, Nearctic, and Neotropical regions, but they are not exclusively from these regions. The number of species described from 1806–2013 is shown in Figure 5C. The highest numbers of species described were from 1900–1910 with 18 taxa, followed by the 1910s with 12 species. The greatest contributions were those of Neumann (1899; 1901; 1904; 1905; 1906; 1907; 1911; 1913). The 2 latest species described in this genus were in 2013 (Apanaskevich et al., 2013b; Horak et al., 2013).

The genus *Robertsicus* Barker and Burger, 2018 was proposed for *Amblyomma elaphensis* (Price, 1959), from the Chihuahuan Desert of Mexico and the southeastern United States. This new combination was meant to solve for the polyphyly of the genus *Amblyomma* that is in the same situation (Barker and Burger, 2018). These authors named the species *Robertsicus elaphensis* (Price, 1959).

Family Nuttalliellidae

Nuttalliellidae is a monospecific family, which presently is restricted to the Afrotropical region (Bedford, 1931; Keirans et al., 1976; Camicas et al., 1998; Mans et al., 2011; 2016). Based on analysis of mitochondrial genome and nuclear ribosomal RNA (18S and 28S) sequence data, Mans and colleagues (2011; 2019) suggested that the Nuttalliellidae is basal to other tick families, representing the closest extant lineage to the last common ancestral tick lineage.

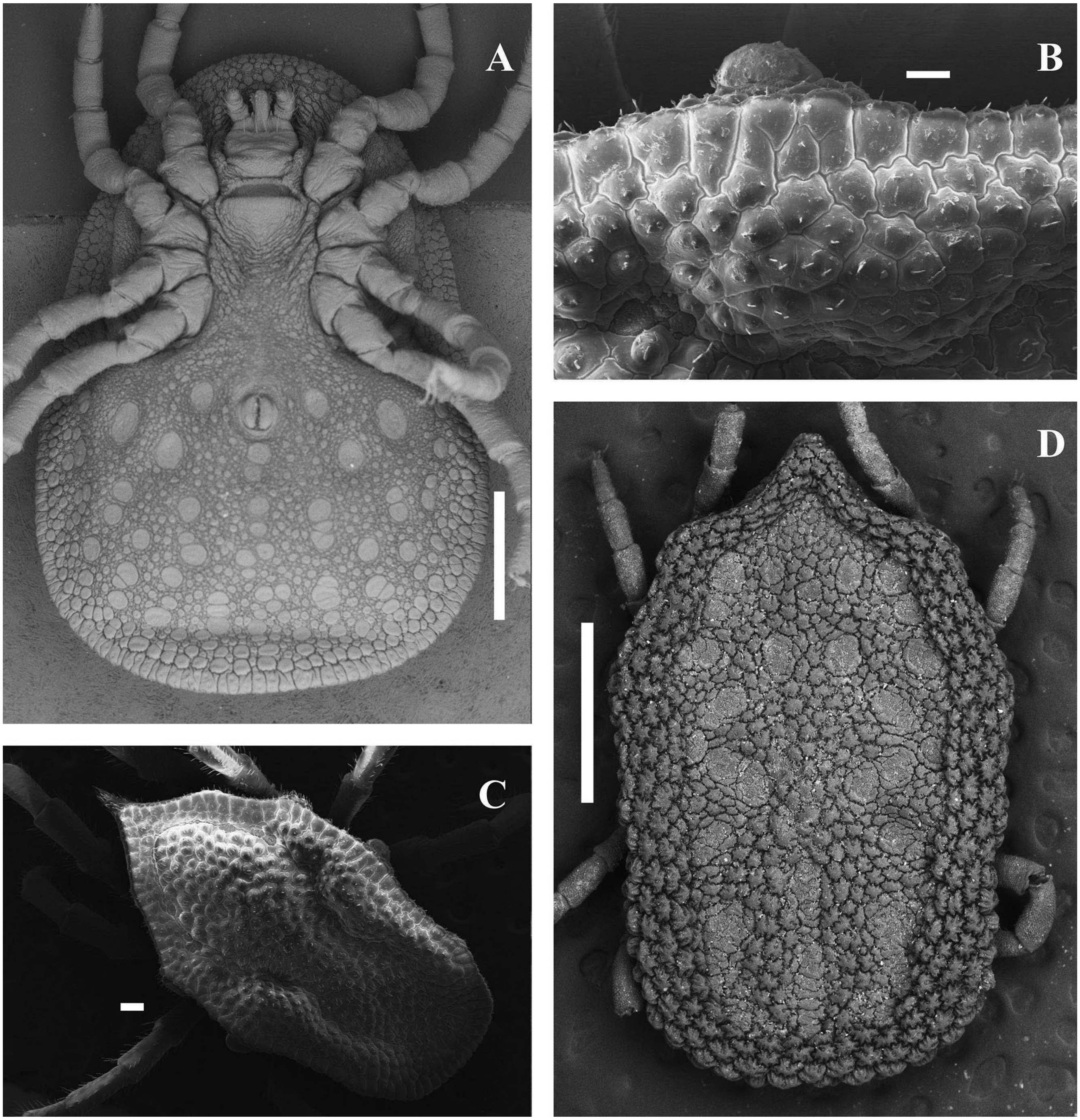

Figure 6. Adults of Argasidae genera. A) *Argas miniatus* female, ventral view; B, C) *Antricola guglielmonei*, spiracular plate and dorsal view; D) *Ornithodoros* sp., dorsal view. Scale bars: A, D = 1,000 µm; B = 100 µm; C = 200 µm. Source: D. Moraes Barros-Battesti, V. Castilho Onofrio, and F. Dantas-Torres. License: CC BY-NC-SA 4.0.

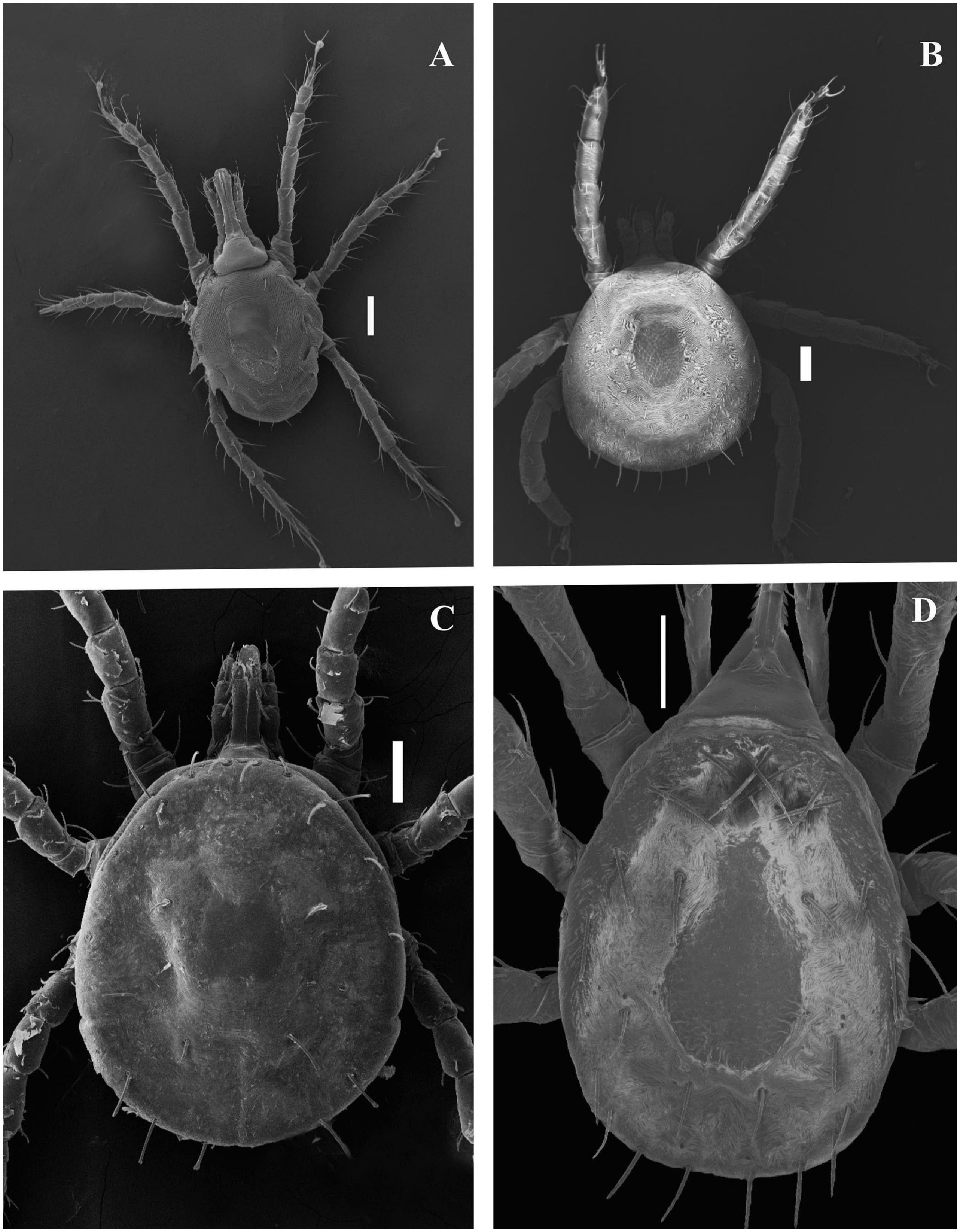

Figure 7. Larvae of Argasidae genera. A) *Otobius megnini*, dorsal view; B) *Argas miniatus*, dorsal view; C) *Ornithodoros brasiliensis*, dorsal view; D) *Or. fonsecai*, dorsal view. Scale bars: A–C = 100 µm; D = 120 µm. Source: D. Moraes Barros-Battesti, V. Castilho Onofrio, and F. Dantas-Torres. License: CC BY-NC-SA 4.0.

According to these authors, nuttalliellids almost became extinct during the great end-Permian mass extinction event, leaving *Nuttalliellia namaqua* as the closest living relative to the ancestral tick lineage.

Family Deinocrotonidae (Fossil)

Deinocrotonidae is a fossil tick family recently described based on fossil material retrieved in 99-million-year-old Cretaceous amber from Myanmar (Peñalver et al., 2017). *Deinocroton draculi* was found in association with *Cornupalpatum burmanicum*, suggesting that both deinocrotonids and ixodids fed on blood from feathered dinosaurs (Peñalver et al., 2017). Morphologically, deinocrotonids resemble nuttalliellids, but no DNA sequences from the former are available to assess their phylogenetic relationship.

Descriptions of Selected Tick Genera

In this section, morphological descriptions are presented for the identification of several tick genera as used in scientific papers. The fossil family Deinocrotonidae and the fossil genera *Deinocroton*, *Cornupalpatum*, and *Compluriscutula* are not included.

ARGASID TICK GENERA

Genus *Argas*

The following morphological descriptions are based on Cooley and Kohls (1944) and Kohls and colleagues (1970).

Larva: Dorsal surface with around 25–30 pairs of setae, dorsal plate oval and elongated; ventral surface with less than 7 pairs of setae and 1 pair on valves; posteromedial seta present or absent; 2 pairs of short post-hypostomal setae; hypostome rounded at apex, dentition 2/2 at basis to 3/3 at apex. *Nymph*: Outline oval, discs present, distributed more or less symmetrically dorsally; idiosoma mamillated, flattened dorsoventrally, with suture and lateral margin demarcating the dorsal and ventral surfaces; Haller's organ with transversely slit-like aperture, placed slightly laterally. *Adults*: Idiosoma flattened, dorsal and ventral surface equal, margin distinct flattened, made up a radial striae or quadrangular plates; sutural line present; flattened margin not obliterated even when tick is fully fed; capitulum ventral; integument leathery, minutely wrinkled in folds, of many shapes often intermingled with small, rounded, buttons each with a pit on top and often bearing a hair in the pit; discs present on both dorsal and ventral surfaces and placed in more or less radial lines; eyes absent.

Genus *Antricola*

The following morphological descriptions are based on Cooley and Kohls (1944), Estrada-Peña and colleagues (2004), and Barros-Battesti and colleagues (2013).

Larva: Dorsal surface with 14 pairs of setae, typically 14 (11 dorsolateral, 3 central dorsal); dorsal plate, large and elongated with lateral margins parallel, narrowing anteriorly; eyes absent; ventral surface with 11 pairs of setae (3 sternal setae, 3 post-coxal setae, 4 circumanal + 1 on valves), and 1 posteromedial seta; 2 pairs of long post hypostomal setae, hypostome pointed, dentition 3/3 in anterior three-fourths, then 2/2 posteriorly to basis; palps with 18 setae, number of setae on palpal article 1–4, respectively 0, 4, 5 and 9; pulvilli large, claws absent (except in *A. marginatus*); dorsal hump absent; Haller's organ with a rounded capsule, open only in a small central portion. *Nymph*: Body outline suboval, pointed anteriorly, covered by tubercles, most of them bearing short setae, some single, others in groups; hypostome short, broad and rounded apically, with small denticles on anterior and lateral margins; cheeks absent; spiracular plates oval, relatively large, expanded and dorsally visible in some specimens, with numerous minute pores. *Adults*: Dorsal surface flattened and marginated; cuticle semi-translucent and smooth, shining, and with tubercles and tufts of setae; dorsomarginal grooves well defined; transverse post-anal groove present. Basis capituli slightly longer than wide, rounded laterally, hypostome small, slightly longer than wide, scoop-like, without denticles.

Genus *Ornithodoros*

The following morphological descriptions are based on Venzal and colleagues (2006) and Barros-Battesti and colleagues (2013).

Larva: Dorsal surface of idiosoma usually with 13–14 pairs of setae (with some exceptions); dorsal plate absent in few species, but present in the majority, varying in shape, from triangular to pyriform (bat-associated group) to elongated sub-rectangular with anterior extremity narrowed; venter with 7–8 pairs + 1 pair on anal valves, and 1 posteromedial seta (which may be absent). Basis capituli with lateral angles slightly rounded, lateral auriculae present or absent, hypostome with apex rounded or pointed, dental formula: 5/5 to 2/2 at apex, 4/4 to 2/2 in medial portion and 2/2 at basis; Haller's organ with capsule aperture transversely slit-like, large, occupying all of the dorsum with many small setae, or small occupying part of the dorsum. *Nymph*: Body outline oval, slightly pointed anteriorly, idiosoma covered by tile-like mammillae; presence of 4 pairs of bulging lateral structures resembling large mammillae on supracoxal

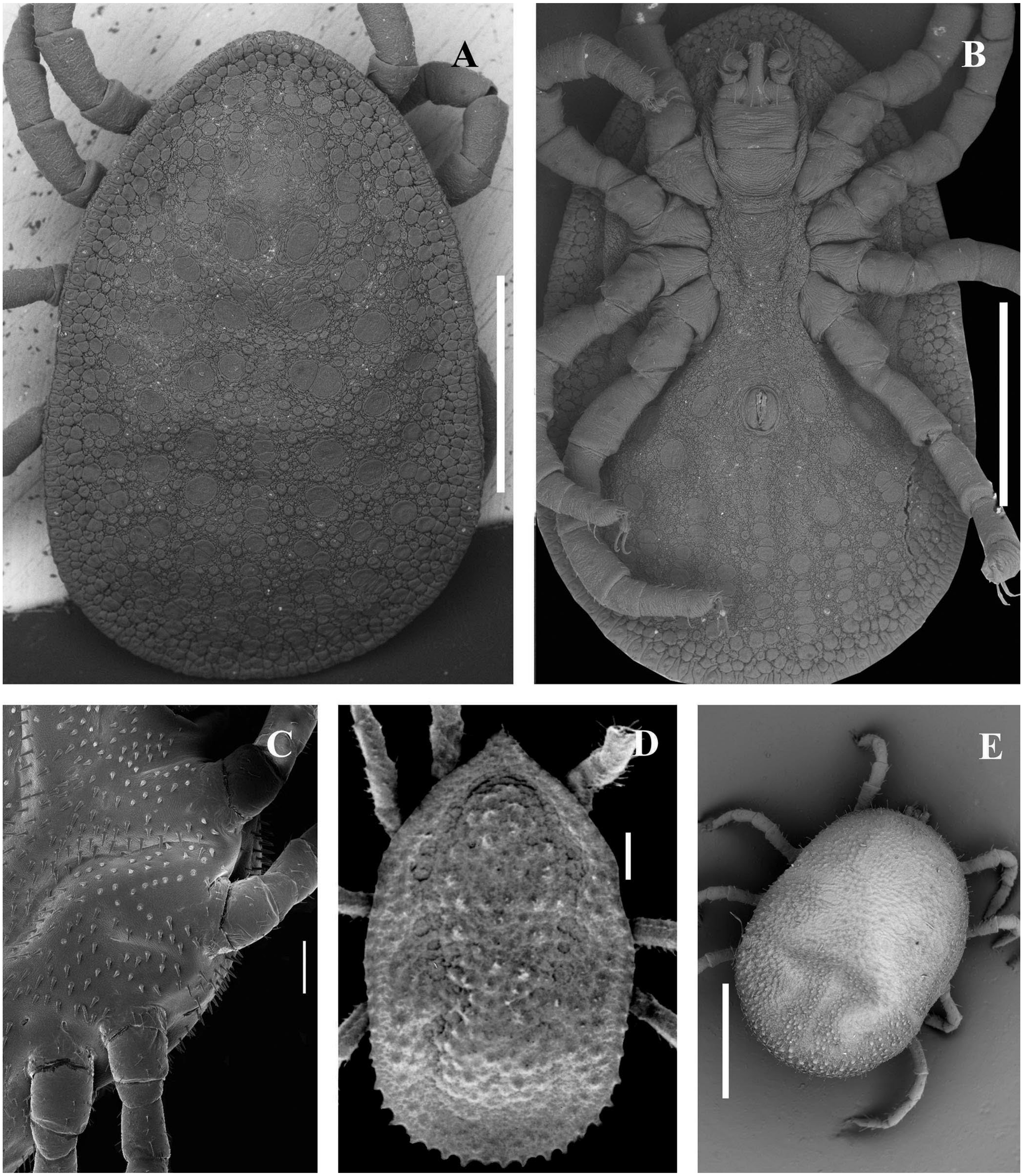

Figure 8. Nymphs of Argasidae genera. A, B) *Argas miniatus*, dorsal and ventral view, C) *Otobius megnini*, ventral view; D) *Antricola guglielmonei*, dorsal view; E) *Ornithodoros brasiliensis* dorsal view. Scale bars: A, B, E = 1,000 µm; C = 300 µm; D = 200 µm. Source: D. Moraes Barros-Battesti, V. Castilho Onofrio, and F. Dantas-Torres. License: CC BY-NC-SA 4.0.

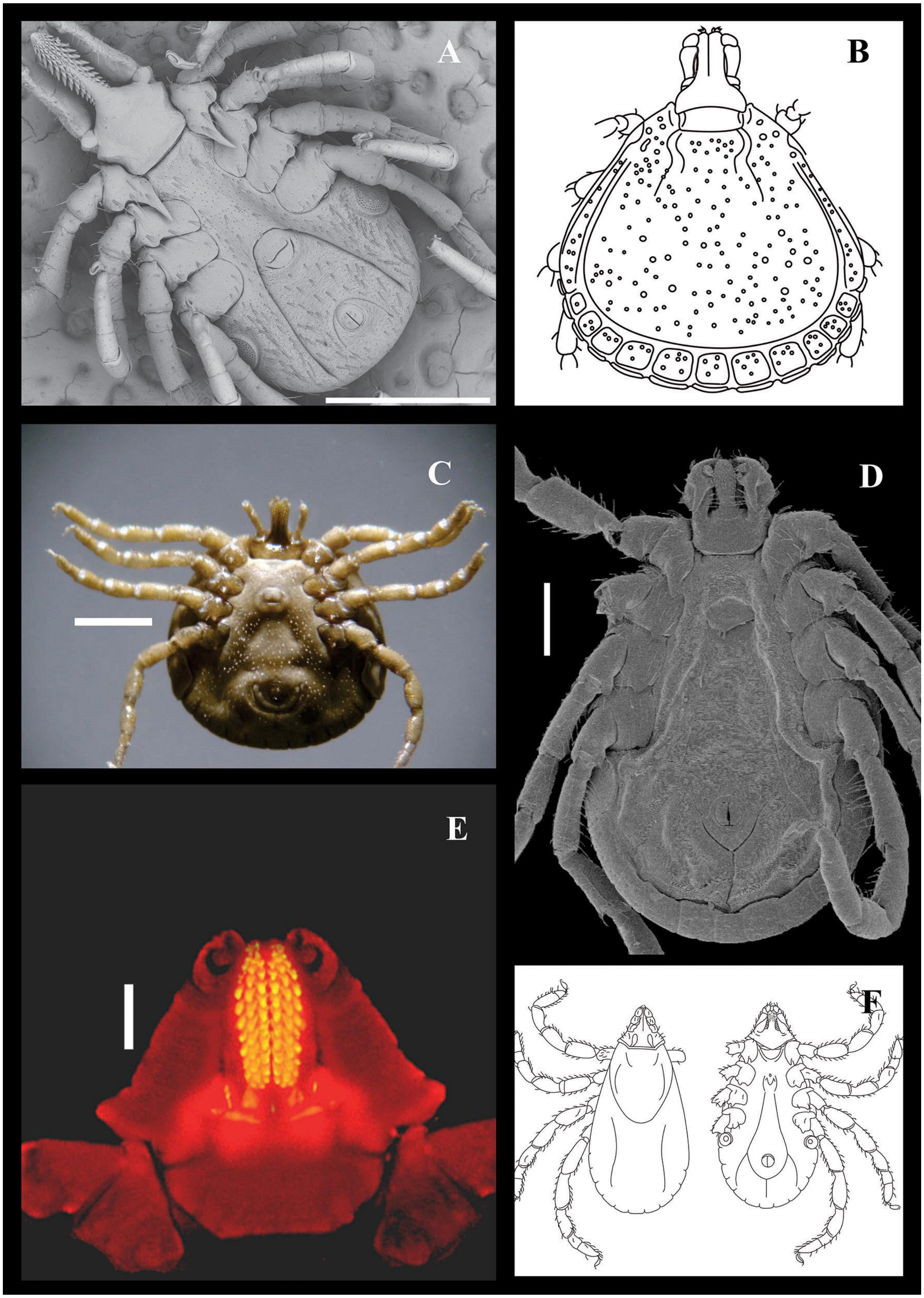

Figure 9. Adults of Ixodidae genera. A) *Ixodes aragaoi* female, ventral view; B) *Bothriocroton* male, dorsal view; C) *Amblyomma (Aponomma) quadricavum* female, ventral view; D) *Haemaphysalis juxtakochi* male, ventral view; E) *H. leporipalustris,* gnatosoma ventral view; F) *Anomalohimalaya* female, dorsal and ventral view. Scale bars: A = 500 µm; C = 1,000 µm; D = 300 µm; E = 100 µm. Sources: A, C–E) D. Moraes Barros-Battesti, V. Castilho Onofrio, and F. Dantas-Torres; B) adapted from Baker and Walker, 2004; F) adapted from Hoogstraal et al., 1970. License: CC BY-NC-SA 4.0.

folds between legs I–IV (soil-living group) or absent (bat-associated group), hypostome rounded on apex; humps present (only in the soil-living group) or absent (bat-associated group), Haller's organ similar to the larvae. *Adults*: Idiosoma suboval, with rounded margins, without marginal lateral sutures; well-developed hypostome with well-defined rows of denticles; hood present; sometimes cheeks present; eyes, when present are arranged anterolaterally to the supracoxaal folds; integument leathery, with tiny mammillated elevations, interspersed by discs on both the dorsal and ventral surfaces.

Genus *Otobius*

The following morphological descriptions are based on Cooley and Kohls (1940; 1944), Guglielmone and colleagues (2006), and Barros-Battesti and colleagues. (2013).

Larva: Integument striated, dorsal surface with 7–10 pairs of setae, dorsal plate large, elongate tapering slightly posteriorly; 2 pairs of eyes; ventral surface with 5 pairs of setae + 1 pair on valves; pulvilli present on all tarsi, not enlarged, claws present, Haller's organ with capsule aperture large and rounded, with posterior projections; hypostome long without corona, dental formula 2/2. *Nymph*: Camerostome and hood absent; hypostomal dentition 4/4; idiosoma panduriform, integument striated and spinous; spiracular plate cone-shaped; Haller's organ with capsule aperture transversely slit-like, elevated and large, bordered with prolonged pointed projections and with small setae internally. *Adult*: Integument granulated and with no change of pattern at the sides; small discs present; hood and eyes absent; hypostome vestigial, not functional to the hematophagy. The morphology is very similar between the 2 species, but the distance between the dorsal small discs in *Otobius megnini* is larger than in *O. lagophilus.*

Genus *Nothoaspis*

The following morphological descriptions are based on Nava and colleagues (2010) and Barros-Battesti and colleagues (2013) and Muñoz-Leal and colleagues (2019).

Larva: Dorsal plate with isosceles triangle shape occupying entire length of the dorsum of unfed specimens with a curvy-notched posterior margin; lateral margins of basis capitulum provided with a small bulge dorsal; surface with 12–13 pairs of setae; hypostome with apex pointed, dental formula 2/2 with 20 denticles in each row, corona absent. *Nymphs*: Idiosoma twice as longer as wide, anteriorly more abruptly narrowing than posteriorly; false shield covered by cells (irregular in shape and size) occupying the anterocentral area of dorsum, most of them at least with 1 seta; setae short, except for posterior margin of idiosoma, where setae are larger. Ventral surface with integument also covered by cells (irregular in shape and size), except for a narrow area located between coxae I and III; spiracular plate small; basis capituli subrectangular in outline, with 1 pair of post-hypostomal setae and at least 7 pairs of sublateral setae, bordered posteriorly by integumental fold; postpalpal setae absent; hood large, broadly rounded, not entirely covering capitulum, cheliceral blades, palpal articles II–IV visible dorsally; ventrally, article I forms elongate flaps protecting the pointed hypostome, dental formula 4/4 apically, 5/5 at base. *Adults*: Presence of false shield or nothoaspis (pseudoscutum), an anteriorly projecting hood covering the capitulum, a medial extension of palpal article I (flaps), genital plate extending from coxa I to IV, absence of 2 setae on the internal margin of the flaps, a small hypostome without denticles, presence of a central pore in the base of hypostome, and a reticulate surface pattern on the posterior half of the nothoaspis in males.

IXODID TICK GENERA

Genus *Ixodes*

The following morphological descriptions are based on Coley and Kohls (1945), Clifford and Anastos (1960), Clifford and colleagues. (1973), Nava and colleagues (2017), Apaneskevich and Lemon (2018), and Kwuat and colleagues (2018).

Larva: Anal groove anterior to anus; sensilla sagittiformia absent; with 2 pairs of post-hypostomal setae; eyes and festoons absent; 6 legs. *Nymph*: Anal groove anterior to anus; eyes and festoons absent; genital pore absent; spiracular plates circular ; 8 legs; nymphs are smaller than adults. *Adults*: An anal groove is present anterior to the anus, forming an arch; eyes and festoons are absent; an inornate scutum is present; spiracular plates are semicircular or oval; and there is a spur on the coxae. Sexual dimorphism is pronounced. The male venter is largely covered by 7 sclerotized plates. Males have ventral plates. Females have porose areas. The denticles of the female hypostome are well developed, while those of the male are usually few and small, often appearing only as mild crenulations.

Genus *Dermacentor*

The following morphological descriptions are based on Arthur (1960b), Yunker and colleagues (1986), Apanaskevich and Bermúdez (2013a), and Barker and Walker (2014).

Larva: Sensilla sagittiformia present; eyes present; a pair of posthypostomal setae; anal groove absent; 3 marginal dorsal setae anterior to the sensilla sagittiformia on dor-

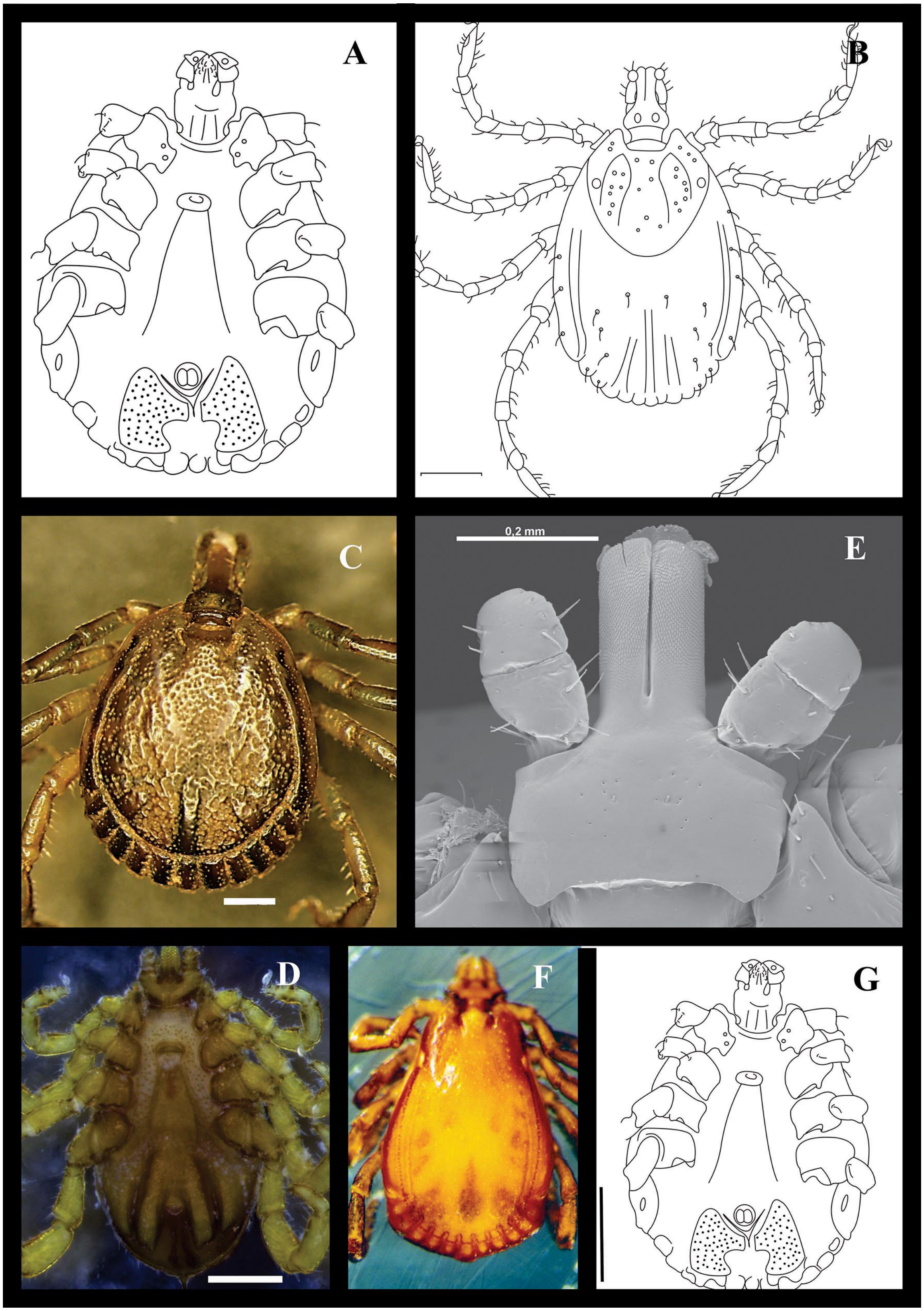

Figure 10. Adults of Ixodidae genera. A) *Nosomma* male, ventral view; B) *Hyalomma* female, dorsal view; C) *Amblyomma sculptum* male, dorsal view; D) *Rhipicephalus (Boophilus) microplus* male, ventral view; E) *Dermacentor* male, gnathosoma dorsal view; F) *Rhipicephalus sanguineus* s. l. male, dorsal view; G) *Rhipicentor* male, ventral view. Scale bars: C = 250 µm; D = 500 µm; E = 250 µm. Sources: A) Adapted from Prakasan and Ramani, 2007; B) adapted from Walker et al., 2003; C–F) D. Moraes Barros-Battesti, V. Castilho Onofrio, and F. Dantas-Torres; G)adapted from Nuttall and Warburton, 1908. License: CC BY-NC-SA 4.0.

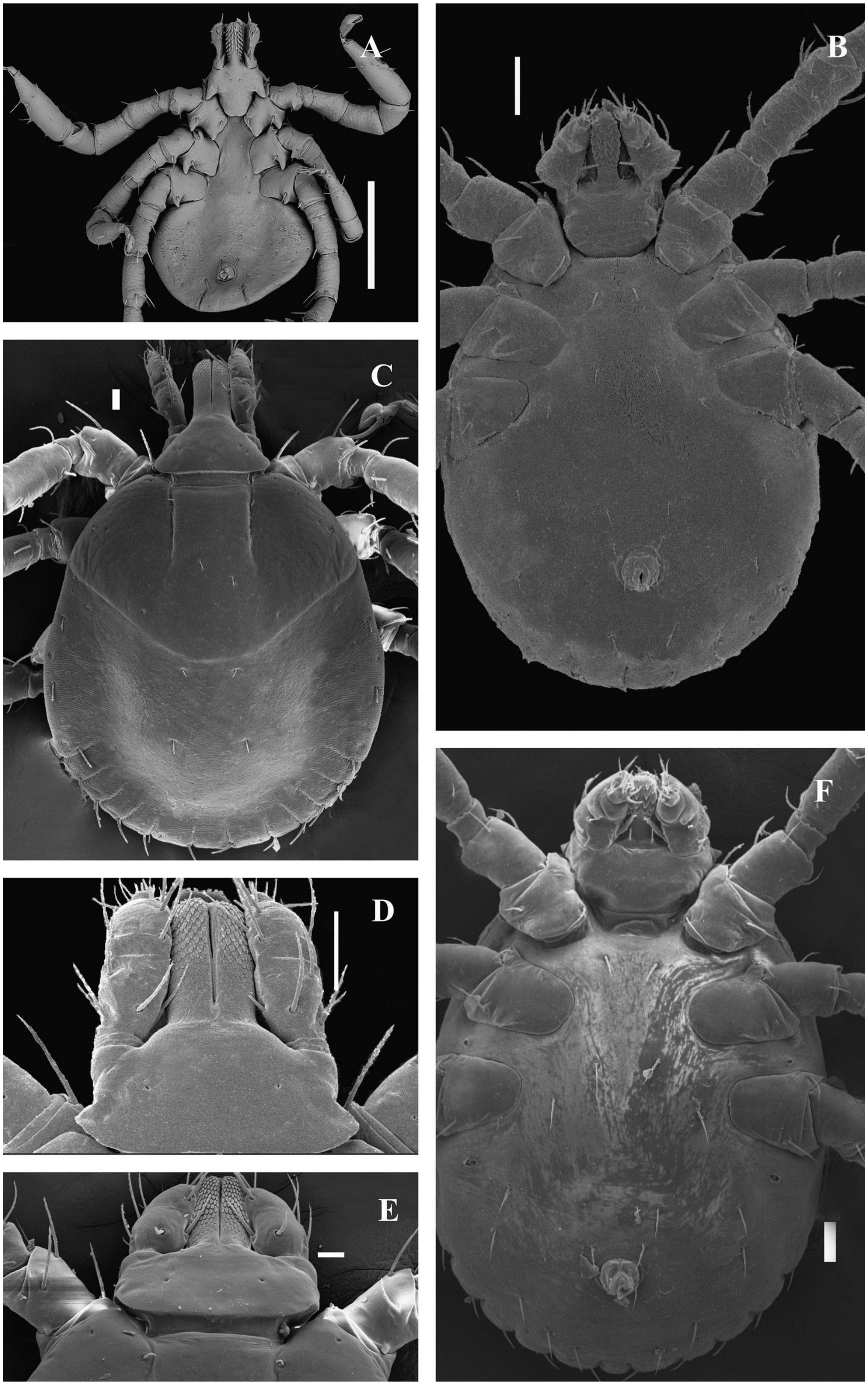

Figure 11. Larvae of Ixodidae genera. A) *Ixodes auritulus* group, ventral view; B) *Amblyomma romitii*, dorsal view; C) *Dermacentor nitens*, gnathosoma dorsal view; D) *Haemaphysalis juxtakochi*, ventral view; E) *Rhipicephalus microplus*, gnatosoma dorsal view; F) *Rhipicephalus sanguineus*, ventral view. Scale bars: A = 250 µm; B, F = 30 µm; C = 40 µm; D = 60 µm; E = 20 µm. Source: D. Moraes Barros-Battesti, V. Castilho Onofrio, and F. Dantas-Torres. License: CC BY-NC-SA 4.0.

sal surface; idiosoma with 9 festoons. *Nymphs*: Eyes present; anal groove absent; spiracular plate circular to suboval with few and large goblet cells. *Adults:* Scutum in females usually ornate (inornate in *Dermacentor nitens* Neumann, 1897); anal groove contouring the anus behind; spiracular plates subcircular to comma-shaped (subcircular in *D. nitens* with large goblet cells); basis capituli more broad than long, rectangular dorsally; eyes on the scutum usually present and distinct. *Males*: Scutum usually ornate (inornate in *D. nitens*); anal groove posterior to the anus; coxae I–IV increase progressively in size; dorsal and posterior margins with festoons.

Genus *Amblyomma*

The following morphological descriptions are based on Klompen and colleagues (1996), Barbieri and colleagues (2007), and Nava and colleagues (2017).

Larva: Anal groove absent, sometimes indistinct; sensilla sagittiformia present on idiosomal dorsal segment VIII and sometimes on segment V; hypostome with denticles arranged in rows; with 1 pair of posthypostomal setae; eyes and festoons present. *Nymph*: Anal groove posterior to the anus; eyes and festoons present; spiracular plates comma-shaped. *Adults*: Scutum ornate with rare exceptions; anal groove posterior to the anus; eyes and festoons present; spiracular plates in comma shape; spurs on coxae usually present; ventral plates absent in most males; porose areas present in females.

Genus *Hyalomma*

The following descriptions are based on Apanaskevich and colleagues (2008).

Larva: Eyes present; portion of scutum posterior to eyes 1/5 to 1/4 of scutal length; apex of spur on coxae I directed posteriorly or medially; narrower palps and hypostome; shorter legs. *Nymph*: posterior margin of scutum broadly rounded with moderate posterolateral depressions on either side of its extremity; spiracular plates with relatively large, wide, blunt dorsal prolongation. *Adults:* Deep cervical grooves; in females scutum with sparse large punctations, small punctations usually very sparse or absent; narrow V-shaped genital operculum; preatrial fold of genital operculum flat or very slightly convex; posteromedial spur of coxa I broad and with blunt apex; males with broadly oval shape of conscutum; deep and long cervical grooves; short marginal grooves; large punctations sparse; smaller punctations normally sparse or absent; adanal plates distinctly curved medially; subanal plates moderate in size; dorsal prolongation of spiracular plates long.

Genus *Rhipicentor*

The following morphological descriptions are based on Cooper and Robinson (1908) and Clifford and Anastos (1960).

Larva: Palps short with 3 articles (article 1 absent); 3 marginal dorsal setae anterior to the sensilla sagittiformia; eyes present; idiosomal with 9 festoons. *Adults:* females with scutum as long as broad, with few punctations, posterior border sinuous; eyes present slightly anterior to the lateral angles; cervical grooves parallel; spiracular plates short, comma-shaped; basis capituli protuberant laterally, small cornua present. Male of *Rhipicentor nuttalli* has idiosoma oval, narrow in front, slightly concave just behind level of eyes; scutum covers entire dorsum, glabrous, polished, punctations not numerous, coarse and showing a tendency to arrange linearly; numerous fine punctations at posterior end of body immediately anterior to festoons; cervical grooves short and deep, crescentic with convexity outwards; marginal grooves well-defined, commencing a little distance behind the eyes and terminating at the external festoon on either side; posteromedian and accessory grooves shallow and ill-defined; eyes large and pale. Venter yellowish-brown with few scattered pale hairs; genital grooves parallel anteriorly, divergent behind coxae and extending to festoons; spiracles comma-shaped. Capitulum short (length 1.1 mm), basis capituli large, with pronounced lateral angles, cornua strong, short and blunt; palps short and broad; articles 2 and 3 rounded laterally; slight ventral retrograde tooth on article 3; hypostome slightly spatulate, dentition 3/3. Legs strong, coxa I with 2 strong spurs placed close together, the internal pointed, the external blunt; coxae II and III with very stumpy blunt spurs; coxa IV very large, with 2 long almost equal spurs, widely separated and slightly divergent.

Genus *Rhipicephalus*

The following morphological descriptions are based on Neumann (1900; 1901; 1904; 1905; 1907; 1911), Apanaskevich and colleagues (2013b), Horak and colleagues (2013), and Nava and colleagues (2018).

Larva: Eyes present, with 4 pairs of marginal dorsal setae anterior to the sensilla sagittiformia; idiosomal with 9 festoons; lateral sides of basis capituli acute or slightly angular. *Nymph*: Eyes present; basis capituli hexagonal, hypostomal dentition 3/3, small auriculae present in *Rhipicephalus sanguineus* (Latreille, 1806) and related species that forms the *R. sanguineus* group; anal groove distinct or indistinct. *Female*: Scutum inornate; eyes present; basis capituli dorsally hexagonal; palps short and round apically, dental formula 3/3 to 4/4;

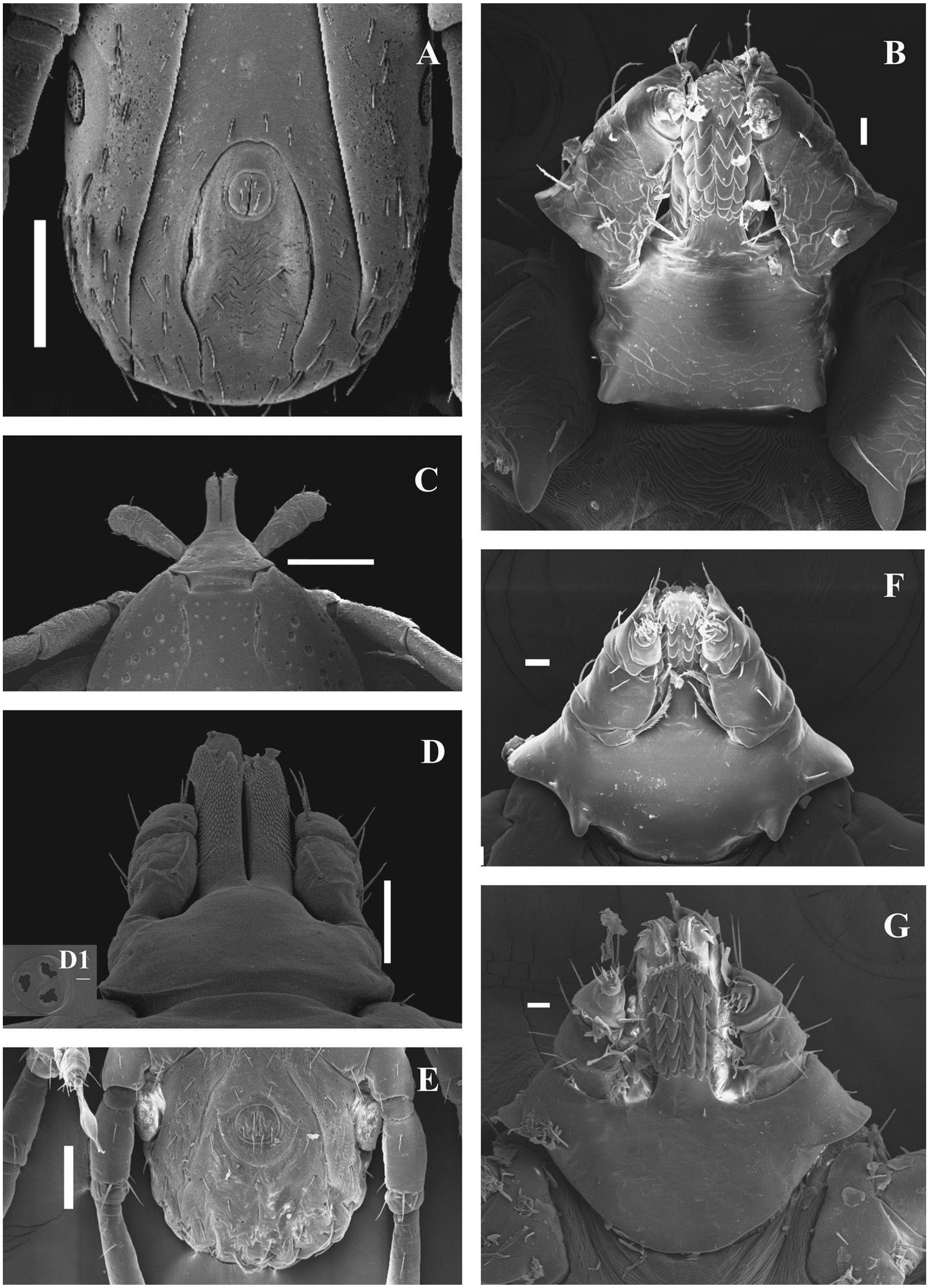

Figure 12. Nymphs of Ixodidae genera. A) *Ixodes luciae* anal groove, ventral view; B) *Haemaphysalis juxtakochi* gnathosoma, dorsal view; C) *Amblyomma longirostre*, dorsal view; D) *Dermacentor nitens* gnathosoma, dorsal view; d1) *Dermacentor nitens* spiracular plate; E) *Rhipicephalus sanguineus* s. l. anal groove, ventral view; F) *Rhipicephalus sanguineus* s. l. gnathosoma, ventral view; G) *Rhipicephalus microplus* gnathosoma, ventral view. Scale bars: A, E = 100 µm; B, G = 20 µm; C = 300 µm; D = 80 µm; d1 = 40 µm. Source: D. Moraes Barros-Battesti, V. Castilho Onofrio, and F. Dantas-Torres. License: CC BY-NC-SA 4.0.

anal groove distinct or indistinct; spiracular plates rounded to elongated. *Male*: Eyes present; basis capituli hexagonal dorsally; small cornua present or absent; palps short, palpal articles II and III with short, retrograde, internal process; dental formula 3/3 to 4/4; anal groove distinct or indistinct; spiracular plates round to elongated; adanal plates present, some species with caudal appendage.

Genus *Archaeocroton*

The description presented below was that proposed by Dumbleton (1943) and by Kaufman (1972) for *Archaeocroton sphenodonti.*

Larva: Large elongate cervical grooves. *Nymph*: not available. *Adults*: Idiosoma suboval in both, scutum light brown, inornate, with small and very numerous punctations evenly distributed; eyes absent. Male with cervical and marginal grooves, cervical grooves short, slightly divergent; lateral grooves distinct, incomplete, extending half the distance between the first festoons and scapulae; basis capitulum subtriangular, cornuae distinct, blunt; palps elongate and somewhat thickened; hypostome spatulate, dentition 3/3 distally and 2/2 proximally, with large corona; 2 files with about 5–6 stout denticles and partial innerfile with 5 very fine denticles; all coxae with a single subtriangular spur; tarsi very elongate. Female with scutum subcordiform, broader than long, cervical groove present; cervical pits deep, slightly concave externally; cervical grooves short and slightly divergent; cornua extremely broad, very blunt; palps elongate, thickened, article (segment) 2 about twice as long as article (segment) 3; a pair of very large conical spurs on either side of the midline of the ventral basis capituli; hypostome spatulate, dentition 3/3 distally and 2/2 proximally, with large corona; 2 files with circa 5–6 stout denticles and partial innerfile with 5 very fine denticles; genital aperture opposite level of coxae II; genital groove divergent; spiracular plate subcircular, as wide as long; all coxae with a subtriangular spur that is as long as broad, and tarsi very slightly humped, noticeably elongate and without spurs.

Genus *Anomalohimalaya*

The following morphological descriptions are based on Hoogstraal and colleagues (1970) and Filippova and Bardzimashvily (1992).

Larva: Basis capituli dorsally 3.5 times as broad as long, the ventrally posteroexternal junctures are at an angle; dorsally with 2 small sensilla hastiformia, ventrally 1 pair post-hypostomal setae, palps 2 times as long as broad; scutum 1.7 times as broad as long; anterior emargination broad, shallow; scapulae slightly rounded; external margin gradually diverging to convex posterior margin; eyes are large, slightly convex, pale area in each posteroexternal juncture; festoons present. *Nymph*: The nymph of *Anomalohimalaya cricetuli* has a smooth nitidous scutum with closely moved lateral and cervical grooves, forming a narrow deep short furrow, whereas in 2 other species the scutum is dull, the furrow between the lateral and cervical grooves is short and nearly reaches posterolateral margins of the scutum. Shape and location of the lateral projections of the basis capituli corresponds to those of female. Anal valves equally get narrow forward and backward, whereas in *A. lotozkyi* they are narrower anteriorly; eyes absent in *A. lamai*. *Adults*: Basis capituli dorsally broadly quadrangular, externally converging to narrower, straight posterior margin; anteroventrally flanged; palps clavate, 2 times as long as broad, article I extended ventrointernally; eyes absent; scutum broadly pyriform, rugose, lacking lateral grooves, cervical grooves indistinct, punctations especially large and numerous. Basis capituli hexagonal in females; the dorsal scutum in *A. cricetuli*, is pointed posteriorly and the genital opening is U-shaped, whereas in 2 other species the scutum is rounded posteriorly and the genital opening is V-shaped. *Anomalohimalaya cricetuli* differs from *A. lotozkyi* in that it has less pointed and shorter lateral projections of the gnathosoma basis, apexes of which are moved forward from the posterior margin, and by concave laterally porous area. It differs from *A. lama* by the absence of the dorsal process on the spiracular plate, and a short tooth on coxae IV.

Genus *Bothriocroton*

The following morphological descriptions are based on Klompen and colleagues (2002), Barker and Walker (2014), and Beati and colleagues (2008).

Larva: Hypostomal dentition in the adults 2/2 or 3/3, internal row much smaller than other rows; 3 large wax glands lateral near setae s6 (= marginal dorsal setae Md3), and anterior to the first festoons; large wax glands on festoon 5 absent; eyes absent; idiosomal setation pattern generally as in other Metastriata; scutum more broad than long; leg and palpal chaetotaxy as in *Amblyomma* sensu lato *Nymph*: Scutum similar to the females, with conspicuous posterolateral indentations formed by confluence of larger punctations; eyes absent; anal groove posterior to the anus; spiracular plates extruding from lateral body margins in *Bothriocroton oudemansi*. *Adults*: Basis capituli subpentagonal in shape; eyes absent, but large punctations could be mistaken for an eye; hypostomal dentition 3/3 to 4/4; scutum of the males with partial or complete lateral grooves, with white ornamentation in some species; trochanters with a single subterminal ventral spur (absent in *B. glebopalma*); coxae I with anterior projection visible in some species; anal groove posterior to the anus; large spiracular plates anterior to first festoon, extruding from lateral body margin in male and female of *B. oudemansi.*

Genus *Cosmiomma*

The following morphological descriptions are based on adults (Arthur, 1960b); immature stages are unknown.

Adults: Basis capituli subtriangular dorsally; palpal article 2 appreciably narrower than article 3, and about twice as long; enamel pigmentation on the palps, basis capituli, scutum, and legs; eyes well developed; 11 festoons in the female more or less clearly defined, with large spiracular plate abutting against the margins of the anterior festoons; female with anal groove encircling the anus and produced behind in a median groove; male with 1 pair of adanal plates, accessory and subanal plates absent. Coxa I with long external spur and prominent internal spur, divergent.

Genus *Haemaphysalis*

The following descriptions are based on Apanaskevich and colleagues (2007).

Larva: Eyes absent; scutum inornate; 2 marginal dorsal setae anterior to the sensilla sagittiformia on each side; article II of palps laterally produced beyond the basis capituli; idiosoma with 11 festoons; anal groove posterior to the anus. *Nymphs*: Eyes absent; basis capituli rectangular dorsally; scutum inornate; article II of palps laterally produced; article III of palps with retrograde ventral spur; spiracular plate suboval; anal groove posterior to the anus. *Adults:* Article II of palps laterally produced; article III of palps with retrograde ventral spur; eyes absent; scutum inornate; article II of palps laterally produced; article III of palps with retrograde ventral spur; in females the scutum is 1.3 times as long as broad, cervical grooves narrow arcs extending 2/3 of total scutal length; posterior lip of genital aperture broadly U-shaped; spiracular plates varying in size, irregularly suboval or subcircular, dorsal projection short, broadly triangular; in males the spiracular plate is variable in size, usually slightly broader than long, suboval, dorsal projection triangular, submarginal row of perforations on spiracular plate complete; coxal pore absent. In male, the basis capituli rectangular dorsally; article II of palps laterally produced; article III of palps with retrograde ventral spur; marginal groove absent.

Genus *Margaropus*

The following morphological descriptions are based on Arthur (1960b), Clifford and Anastos (1960), Walker and Laurence (1973), and Walker and colleagues (2003).

Larva: 5 marginal dorsal setae, Md5, located anteriorly to the dorsal sensilla sagittiformia, all other larval morphology resembles those of the genera *Dermacentor* and *Rhipicephalus*. *Nymph*: Idiosoma with long setae; basis capituli 3 times as wide as long, with straight basal margin, rounded junctures, and divergent lateral margins; eyes present; palps 4 times as long as wide; segment I forming a slight pedicle; segments 2 and 3 of approximately equal length and subrectangular; apex more or less bluntly rounded; segment 3 ventrally with a short, wide spur not reaching basal margin of segment; hypostome similar with smaller corona and 3/3 dentition in files of 8 denticles; spiracular plates subcircular, with 6 large goblets in a circle. *Adults*: Festoons absent; in females the scutum is inornate, widest at midlength between the scapulae and the eyes, posterior margin bluntly pointed; eyes present which may be indistinct; porose areas vertically subtriangular; palpal articles 2 and 3 separated by a slight constriction; coxae conical, unarmed but for a small spur posteriorly on coxa I, tarsi elongate, narrow, tapering with a large apical hook-like projection; integument bears conspicuous hairs posteriorly; spiracular plate subcircular, 3 rows of large goblets around the ostium; males with expanded leg articles that are more or less deeply separated from each other; scutum with lateral margins convex, more strongly convergent anteriorly, bluntly rounded behind, about a third as long again as it is wide; spiracular plates similar to the females; a pair of adanal plates present; caudal appendage present in *Margaropus winthemi*, broad and has a hook on the ventral surface; hypostome about twice as long as broad, slightly notched in the mid-line distally, and behind a well-defined corona the dentition is 4/4. This species is distinguished from *Rhipicephalus* (*Boophilus*) by the thick legs that are very conspicuous in males.

Genus *Nosomma*

The following morphological descriptions are based on Arthur (1965), Singh (1968), and Prakasan and Ramani (2007).

Larva: Basis capituli triangular dorsally, posterior margin slightly convex, lateral margins slightly sinuous and meet posterior margin to form sharp lateral points; ventrally basis triangular with posterior margin bow shaped; palps long and slender, reaching to the apex of hypostome, hypostome slender, dentition 2/2; eyes flat; cervical grooves shallow, narrow anteriorly but broadening posteriorly to almost reach the hind margin of scutum; dorsally without marginal grooves but with 9 distinct festoons. *Nymph*: Basis capituli dorsally triangular; posterior margin almost straight; posterolateral angle sharp and pointed. Ventrally posterior margin bow shaped; palps long and slender, reaching to the tip of hypostome, article 2 twice as long as article 3, dentition 2/2; posterior margin of scutum broadly rounded; eyes flat and situated at posterolateral corners of scutum, cervical grooves subparallel anteriorly and diverging posteriorly reaching posterior margin; dorsal integument with faint marginal grooves and 11 well marked festoons; spiracular plates oval. *Adults: Nosomma* resembles *Dermacentor* in the shape of the capitulum and in having short palps; palpal articles 1, 2, and 3 of *Nosomma* are unlike those of known *Dermacentor* species in the possession of long, broad, strong sabre-like hairs on their infra-internal margin. Basis capituli of female is almost twice as broad as long; cornua prominent, basal breadth exceeding their length, broadly rounded; idiosomal with distinct median and paramedian grooves on the dorsal surface, posterior extremity of median groove continuous with depressions separating parma from adjacent festoons; 11 festoons present. Basis capituli of male is rectangular dorsally; palps conical lacking basolateral salience; median ridge like dorsal palpal spur; hypostome reaching apex of palps; hypostomal denticles formula 4/4; scutum outline elongated oval, brownish, whitish ornamentation present; cervical grooves short and deep; pseudoscutum well marked; eyes prominently colored; 11 festoons present, festoon 2 dorsally separated by well-marked sutures; palpal article III more broad than long with a stronger ventral process, hypostomal dentition 3/3; coxa I with 2 separated spurs; coxae II–IV with small spurs; tarsus IV with 2 ventral spurs, the distal one stronger than the proximal; ventral plates represented by adanal and accessory subadanal plates trilobed, middle lobes come close to each other behind the anal groove; anal groove posterior to the anus; spiracular plates comma-shaped.

Genus *Robertsicus*

Baker and Burger (2018) did not repeat the description for *Amblyomma elaphense* when the new combination for *Robertsicus elaphense* was proposed, but we present the one previously detailed by Keirans and Degenhardt (1985).

Larva: Outline suboval, widest at midlenght with 11 festoons; setae dorsally 13 pairs, all minute except for scutal central 1 (SC1); 2 central dorsal pairs; 8 marginal dorsal pairs, 2 of which are anterior to sensilla sagittiformia; supplementary setae absent; 3 scutal pairs; ventrally 15 pairs, 3 sternal pairs, 2 preanal pairs, 4–5 premarginal pairs, 5 marginal pairs, 1 pair on anal valves; palpal setae 10 on segment 4, 3 dorsally, 1 laterally, 2 ventrally on segment 3; 3 dorsally, 1 laterally, 2 ventrally on segment 2; 0 on segment 1; hypostome bluntly rounded apically with few minute hooklets, dental formula 2/2; scutum inornamented; eyes absent; cervical grooves and punctations absent; legs with small triangular external spur on coxae I–III, internal spurs absent; setae: coxa I with 3, coxae II and III with 2 setae each; Haller's organ with roof bifurcate; anterior pit setae: 1 porose, 2 fines, 1 fine or perhaps setiform. *Nymph*: Small, suboval, about as wide as long; scutum with scale-like markings over the surface, otherwise as in female; capitulum dorsally broadly triangular, corona absent; ventrally with hypostomal dentition 2/2, a small corona of minute denticles apically; legs each with a very small bluntly rounded spur on coxae I–IV; spiracular plate suboval, without dorsal prolongation. *Adults*: Inornate, light brown. Male with scutum smooth, without cervical or marginal grooves, setae and punctations minute, inapparent under binocular microscopy; capitulum dorsally subtriangular, lacking cornua; ventrally with hypostomal dentition 2/2 throughout, apically with a large corona of fine denticles; palps elongate; legs each with a single triangular spur on coxae I–IV; Haller's organ roof slit-like and slightly bifurcate medially, 5 anterior pit setae; spiracular plate suboval with a long narrow dorsal prolongation, globet cells minute. Female with scutum more broad than long, cordiform, smooth, without cervical grooves, setae and punctations minute; capitulum dorsally subtriangular, cornua absent; porose areas subcircular, shallow; ventrally with hypostomal dentition 2/2 (although the hypostome figured has a single supernumerary tooth between file 1 and 2 on the left side of the hypostome as viewed from above); legs with coxae as in male; genital aperture at level of coxae II; spiracular plate suboval with a short dorsal prolongation, goblet cells minute.

Genus *Nuttalliella*

The following morphological descriptions are based on Bedford (1931), Latif and colleagues (2012), and Mans and colleagues (2018).

Larva: Dorsum with a sclerotized scutum; cervical grooves and eyes absent; preanal groove present; anal plate with rows of denticles separated by the median post-anal groove; 5 posthypostomal setae present; apex of hypostome distinctly rounded, forming a ball-like structure, with 11 prominent denticles arranged in 2 rows. *Nymph*: Idiosoma circular; pseudoscutum with elevation between the cervical grooves; eyes absent; surface of alloscutum with dense-elevated and convoluted rosettes and setae in rosette pits; posthypostomal setae present; hypostomal denticles rudimentary; spiracular plates fenestrated and located posterior to coxa IV. *Female*: Idiosoma covered by leathery integument; scutum semi-sclerotized wider than long; preanal groove present; gnathosoma ventroapically, a pair of posthypostomal setae present; hypostomal denticles large and distinct arranged in 2 rows; palps 4-segmented; coxal organ absent; and spiracular plates fenestrated and located posterior to coxa IV. *Male*: Pseudoscutum present, covering most of the dorsum; chelicerae forming a unique rod-like structure similar to a spematodactyl in mites.

Medical and Veterinary Significance of Ticks

Ticks are obligate blood-sucking parasites with an almost worldwide distribution. As the second largest group of vectors of human disease agents (only trailing mosquitoes), ticks are among the most important vectors of pathogens causing disease in humans and other animals (Dantas-Torres et al., 2012). They are the most important ectoparasites of livestock in tropical and subtropical areas, and the diseases and direct damage caused by ticks are responsible for severe economic losses in livestock production (Jongejan and Uilenberg, 2004).

Human-tick interactions are extremely common, resulting in a great impact on human health. Due to saliva secretion during blood feeding, ticks transmit pathogens, such as viruses, bacteria, protozoa, and helminths, readily to hosts. Aside from mere irritation, their bite can also lead to allergy and even severe toxic conditions, such as paralysis and toxicosis in humans and other animals. Infection with multiple tick-transmitted pathogens can occur in an individual host after exposure to coinfected ticks or multiple ticks infected with different pathogens. The coinfection of individual ticks is a relatively frequent phenomenon and the same tick species may be a vector for different pathogens (Milutinovic et al., 2008; Nicholson et al., 2010), which may partially explain variations in clinical presentation, pathogenicity, and host response to therapy.

Pathogens ingested by a single larval tick may be passed through to subsequent developmental stages (that is, nymph and adult) through transstadial transmission from host to host (also called horizontal transmission) and, if a female is infected, may eventually be spread to her offspring through vertical or transovarial transmission. Female ticks are extremely fecund and may lay thousands of eggs, which enables effective dissemination of infectious agents.

Wildlife and ticks are the main reservoirs and vectors of tick-borne pathogens of medical and veterinary importance (Dantas-Torres et al., 2012b). Species of ticks that parasitize domestic animals are the most studied, while those that parasitize wildlife are still poorly understood as to their ability to transmit pathogens. Wild and domestic carnivores are considered the primary source of tick-borne zoonotic agents affecting humans (Otranto et al., 2015).

Ticks and tick-borne diseases have a zoogeographical range restricted by host movement and climatic factors. However, the increased mobility of humans and of domestic animals has resulted in a rapid extension of the zoogeographical ranges for many tick species and tick-transmitted pathogens. As such, the incidence of tick-borne diseases in humans and animals has increased in the 21st century (Estrada-Peña and Jongejan, 1999; Guglielmone et al., 2006). Additional factors associated with the emergence or re-emergence of vector-borne diseases include global warming (and resultant climate change), increased outdoor recreation, global travel, urbanization, encroachment of human development on natural environments, deforestation, and habitat fragmentation, which together promote greater contact between ticks, wildlife, humans, and domestic animals (Beugnet and Chalvet-Monfray, 2013; Dantas-Torres, 2015).

The major zoonoses whose causative agents are transmitted by ticks are rickettsioses, borrelioses, ehrlichiosis, and babesiosis. Rickettsioses are mainly associated with ticks of the genera *Amblyomma, Dermacentor, Ixodes*, and *Rhipicephalus*, borrelioses to *Ixodes* and *Ornithodoros*, and ehrlichiosis and babesiosis mostly to *Rhipicephalus* (Barros-Battesti et al., 2006). These diseases and other zoonotic tick-borne illnesses, such as those of viral origin, characterized by encephalitis and hemorrhagic fevers, are the major cause of host morbidity and mortality (Jongejan and Uilenberg, 2004; Dantas-Torres et al., 2012b). In the following sections, the main tick-borne diseases of humans and other animals are summarized.

Anaplasmosis

Anaplasmosis is a disease caused by gram-negative bacteria of the order Rickettsiales, family Anaplasmataceae, and genus *Anaplasma* (Dumler et al., 2001).

Bovine anaplasmosis occurs in tropical, subtropical, and temperate regions of the world, and is caused by the intraerythrocytic rickettsia *Anaplasma marginale*, a member of the ehrlichial genogroup II (Dumler et al., 2001); *A. marginale* is transmitted biologically by ixodid ticks, by hematophagous insects, and mechanically by needles contaminated with blood of infected animals.

After inoculation of a suitable bovine host, and after an incubation period of 20 to 40 days, there is an increase in rickettsemia, resulting in anemia, weight loss, abortion, and death (Richey, 1981). The disease can have serious consequences, especially when susceptible animals are introduced into endemic areas. In this case, mortality may exceed 50%, causing serious problems to genetic breeding programs, based on the importation of animals from disease-free areas (Machado, 1995).

Combining tick control and vaccination results in the most effective measure against this disease (Palmer, 1989). Immunized cattle may develop persistent field infections, acting as reservoirs of *Anaplasma marginale* helping to maintain the pathogen circulation in endemic areas.

The most important species in dogs is *Anaplasma platys*, which mainly infects platelets and causes infectious canine cyclic thrombocytopenia (Ferreira et al., 2007). It is generally found in coinfections with *Babesia* and *Ehrlichia*, and

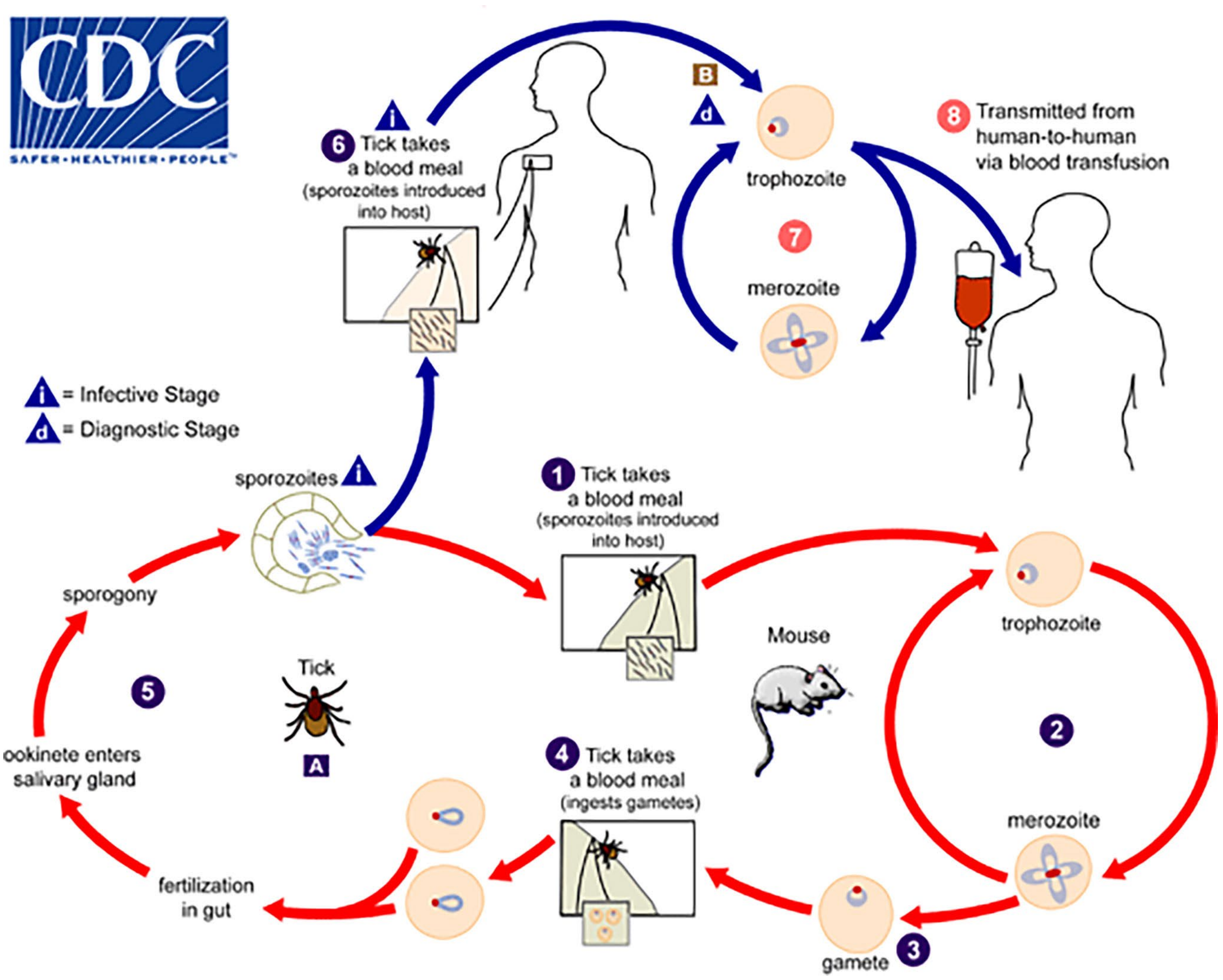

Figure 13. Babesiosis life cycle. Babesiosis is caused by apicomplexan parasites of the genus, *Babesia*. While more than 100 species have been reported, only a few have been identified as causing human infections, including *B. microti*, *B. divergens*, *B. duncani*, and a currently unnamed strain designated MO-1. — The *Babesia microti* life cycle involves 2 hosts, which includes a rodent, primarily the white-footed mouse, *Peromyscus leucopus*, and a tick in the genus *Ixodes*. During a blood meal, a *Babesia*-infected tick introduces sporozoites into the mouse host (1). Sporozoites enter erythrocytes and undergo asexual reproduction (budding) (2). In the blood, some parasites differentiate into male and female gametes although these cannot be distinguished at the light microscope level (3). The definitive host is the tick. Once ingested by an appropriate tick (4), gametes unite and undergo a sporogonic cycle resulting in sporozoites (5). Transovarial transmission (also known as vertical, or hereditary, transmission) has been documented for "large" *Babesia* spp. but not for the "small" babesiae, such as *B. microti* (A). — Humans enter the cycle when bitten by infected ticks. During a blood meal, a *Babesia*-infected tick introduces sporozoites into the human host (6). Sporozoites enter erythrocytes (B) and undergo asexual replication (budding) (7). Multiplication of the blood stage parasites is responsible for the clinical manifestations of the disease. Humans are, for all practical purposes, dead-end hosts and there is probably little, if any, subsequent transmission that occurs from ticks feeding on infected persons. However, human to human transmission is well recognized to occur through blood transfusions (8).

Rhipicephalus sanguineus sensu lato is suspected to be a vector, though its role remains unproven (Dantas-Torres, 2008; Ribeiro et al., 2017). This pathogen is widespread on several continents but has a predilection for tropical and subtropical regions (Ferreira et al., 2007).

Anaplasma phagocytophilum is incriminated as the causal agent of the human granulocytic anaplasmosis (HGA) in the Northern Hemisphere, tick-borne fever in cattle and sheep in Europe, and equine and canine granulocytic anaplasmosis in the United States (Woldehiwet, 2010; André, 2018).

Babesiosis

Babesiosis is caused by tick-transmitted intraerythrocytic protozoa of the order Piroplasmida, family Babesiidae, and genus *Babesia* (see Figure 13). *Babesia* protozoa are one of the most common blood parasites in the world and they have a wide host range, including mammals and bird species (Schnittger et al., 2012). Hard ticks are the known vectors of these protozoa, such as *Rhipicephalus sanguineus* sensu lato that transmits *B. vogeli* (Gray et al., 2010; René et al., 2012; Silva et al., 2012).

The disease can occur in subclinical, acute, hyperacute, or chronic forms, ranging from mild clinical signs to fatal disease. Severity of illness depends on many factors, such as *Babesia* species and immunocompetence of the patient (Schetters et al., 1997; Gray et al., 2010; Yabsley and Shock, 2013).

Bovine babesiosis (BB) is a tick-borne disease of cattle caused by protozoan parasites of the genus *Babesia* (phylum Apicomplexa, order Piroplasmida). The principal species of *Babesia* that cause BB are: *Babesia bovis, B. bigemina*, and *B. divergens.* Other species that can infect cattle include *B. major, B. ovata, B. occultans,* and *B. jakimovi. Rhipicephalus* tick species are most commonly involved in the transmission of this disease, generally in tropical and subtropical countries (WOAH, 2021).

Canine babesiosis may be caused by several species of *Babesia*, which are usually classified as small and large *Babesia*. Small *Babesia* species include *B. gibsoni*, *B. conradae*, and *B. microti*-like (also referred to *Theileria annae* and *B. vulpes*, but these are nomina nuda, meaning that the scientific names are used but without the necessary accompanying scientific description), whereas large *Babesia* species include *B. canis*, *B. vogeli*, *B. rossi*, and an unclassified species ("*Babesia* sp. Coco") found in dogs in North Carolina, United States (Citard et al., 1995; Schetters et al., 1997; Köster et al., 2015; Solano-Gallego et al., 2016). *Babesia gibsoni* is transmitted by *Haemaphysalis longicornis* Neumann, 1901 in Asia and possibly by blood exchange during dog fights. *Babesia canis* is transmitted by *Dermacentor reticulatus* in Europe, *B. vogeli* is transmitted by *R. sanguineus* sensu lato in tropical and subtropical regions, and *B. rossi* is transmitted by *H. elliptica* (Koch, 1844) in southern Africa (Uilenberg et al., 1989; Sasaki et al., 2007; Köster et al., 2015). The vectors of *B. conradae* and *B. microti*-like remain unknown.

Ehrlichiosis

Ehrlichiosis is a disease caused by several species of obligate intracellular gram-negative bacteria of the genus *Ehrlichia* that infect humans and other animals in different parts of the world (Dumler et al., 2001).

Human ehrlichiosis is caused by *Ehrlichia chaffeensis* (human monocytic ehrlichiosis), *E. ewingii* (human granulocytic ehrlichiosis), or *E. muris eauclairensis* (undetermined ehrlichiosis) (Dantas-Torres et al., 2012b; Pritt et al., 2017). *Ehrlichia chaffeensis* is the most common causative agent of human ehrlichiosis in the United States. It is maintained in a cycle that involves the white-tailed deer (*Odocoileus virginianus*) and the lone star tick *Amblyomma americanum* (Linnaeus, 1758), which play a role as primary reservoir and vector, respectively (Skotarczak, 2003; Yabsley, 2010). Even though white-tailed deer seem to be the main host for *E. chaffeensis*, serological and molecular evidence of infection by this agent has been reported in wild carnivores (André, 2018). *Amblyomma americanum* also transmits *E. ewingii*, while the vector of *E. muris eauclairensis* is *Ixodes scapularis* Say, 1821.

Canine monocytic ehrlichiosis (CME) is a life-threatening disease in dogs that requires rapid and accurate diagnosis in order to initiate appropriate therapy (Skotarczak, 2003). *Ehrlichia canis*, the agent of CME, infects monocytes and macrophages of domestic dogs and wild carnivores (Stich et al., 2008). *Rhipicephalus sanguineus* sensu lato and *Dermacentor variabilis* (Say, 1821) are the recognized vectors for *E. canis* (Johnson et al., 1998; Dantas-Torres, 2008). The disease is described around the world, but CME appears to be particularly prevalent in tropical regions where it is principally vectored by *R. sanguineus* sensu lato (Cicuttin et al., 2015). In South America, the occurrence of CME in tropical regions is related to the difference in vector competence. Populations of *R. sanguineus* sensu lato belonging to the tropical lineage are highly competent vectors of *E. canis*, while South American populations of *R. sanguineus* sensu stricto (= temperate lineage) are incompetent vectors of *E. canis*, which partly explains the scarcity or absence of CME in colder regions of South America (Nava et al., 2012; Moraes-Filho et al., 2015).

Lyme disease (or Lyme borreliosis)

Lyme borreliosis (LB) is the most frequent tick-borne disease in the Northern Hemisphere. The disease is caused by spirochetes of the *Borrelia burgdorferi* sensu lato complex, which are transmitted by several tick species of the genus *Ixodes* (Gray et al, 2002; Rauter and Hartung, 2005). LB is recognized as the most commonly reported arthropod-borne disease in North America and Europe, accounting for thousands of new cases yearly in both regions (Piesman and Eisen, 2008; Marques, 2010; CDC, 2017).

In most cases, the tick must be attached to its mammalian host for 36 to 48 hours or more before the bacteria can be transmitted. Typical symptoms include fever, headache, fatigue, and a characteristic skin rash called erythema migrans (CDC, 2017). The complications of untreated LB in humans can be severe and disabling (Dennis and Hayes, 2002).

Rickettsioses

Tick-borne rickettsioses are caused by intracellular bacteria belonging to the spotted fever group (SFG) of the genus *Rickettsia* and are among the oldest known vector-borne diseases of humans. The importance of the recognized rickettsial pathogens has increased in the past several years. Several species of tick-borne rickettsiae that were considered nonpathogenic for decades are now associated with human infections, such as *R. slovaca, R. aeschlimannii, R. massiliae, R. monacensis*, and *R. parkeri*. New species of *Rickettsia* of undetermined pathogenicity continue to be detected in or isolated from ticks around the world (Labruna et al., 2011; Parola et al., 2013).

Ticks can be reservoirs and vectors for most species of *Rickettsia*. Bacteria remain in tick populations by transovarial and transstadial transmission. However, some rickettsiae may also be deleterious to ticks, such as *R. rickettsii* (Labruna, 2009).

Vertical transmission of rickettsial agents in arthropods helps to maintain the infection in nature, but for some species of rickettsiae, a life cycle including infected arthropods and 1 or more amplifying hosts is required to guarantee survival of the bacteria (Davoust et al., 2010). Humans are only occasional hosts for ticks and, thus, play no role in maintaining these bacteria in nature (Socolovschi et al., 2009).

Rickettsia rickettsii is the most pathogenic *Rickettsia* species, and the disease caused by this agent is generally called Rocky Mountain spotted fever (RMSF), because it was first reported in the Rocky Mountain region of the United States (CDC, 2006). In Brazil, the disease is Brazilian spotted fever and has a high fatality rate (Oliveira et al., 2016). Despite the availability of accurate diagnostic tools and efficacious therapy, RMSF continues to be a life-threatening disease, with high lethality rate in several endemic geographic foci. The disease has been shown to have a complex ecology with participation of different vertebrate animals and tick species (CDC, 2006).

Several tick species have been implicated as vectors of *Rickettsia rickettsii* accordingly to different geographic areas. While *Dermacentor andersoni* Stiles, 1908 and *D. variablilis* are the main vectors in the United States, ticks of the *Amblyomma cajennense* (Fabricius, 1787) species complex, such as *A. cajennense* sensu stricto and *A. sculptum* (Berlese, 1888), have been implicated as the most important vectors in South America, mainly in Brazil (Labruna et al., 2017). Moreover, *R. sanguineus* sensu lato has been implicated as a vector in Mexico and the United States (Dantas-Torres, 2007).

Rickettsia parkeri is another SFG rickettsia recognized as a human pathogen, with several confirmed cases in the United States. The first confirmed human infection with *R. parkeri* was reported in the United States in 2004, more than 60 years after this bacterium was first isolated in that country, from the Gulf Coast tick *Amblyomma maculatum* Koch, 1844 (Paddock et al., 2004). *Rickettsia parkeri* rickettsiosis can be difficult to distinguish from RMSF and other spotted fevers, especially during the early stages. A retrospective study provided serological evidence that a number of cases previously diagnosed as RMSF in the United States were actually caused by *R. parkeri,* suggesting that both rickettsioses have been misidentified in that country. This disease is characteristically less severe than RMSF and almost always associated with an inoculation eschar (an ulcerated, necrotic lesion) at the site of tick attachment (Paddock et al., 2004).

Several other SFG rickettsia (for example, *Rickettsia conorii*) are important human pathogens and may also infect and cause disease in animals, such as dogs, in Europe and elsewhere in the world. Comprehensive information about other rickettsiae infection humans can be found elsewhere (Dantas-Torres et al., 2012a; Parola et al., 2013; Portillo et al., 2015).

Epidemiological Tick Control and Preventative Measures

Human behavior (for example, sitting on logs, gathering wood, leaning against trees, and walking) might increase the risk of exposure to ticks (Lane et al., 2004). For instance, people visiting forested areas might be exposed to hard ticks whereas people entering tick-infested caves and encountering rodent burrows might be exposed to soft ticks.

Strategies to reduce populations of vector ticks through area-wide application of acaricides and control of tick habitats (for example, clearing leaf litter and brush) have been effective in small-scale trials. Community-based, integrated, tick-management strategies may prove to be an effective public health response to reduce the incidence of tick-borne infections. However, limiting exposure to ticks is currently the most effective method of prevention (Dantas-Torres, 2007; Pinter et al., 2011).

Whenever possible, areas that are likely to be infected with ticks should be avoided, particularly in the seasons in which larvae and nymphs feed and can be found in abundance. Ticks are commonly found in humid and shady environments, especially grassy or litter areas with low-lying vegetation.

From a practical perspective, it is unreasonable to assume that a person can eliminate all activities that may result in tick exposure. Therefore, measures should be aimed at personal protection (Dantas-Torres, 2007; Piesman and Eisen, 2008; CDC, 2006; 2017). The following measures are recommended:

- When walking through forested areas or with shrubby vegetation, avoid places potentially infested by ticks, and if possible, walk in the center of trails.
- Wear long-sleeved shirts and long trousers (not shorts) and tuck pant bottoms into tops of socks or boots. Wear light colored clothing which makes it easier to find crawling ticks.
- Check often for ticks especially after leaving forested areas. Common sites of attachment include the groin, the underarms, the nape of the neck, around the waist, and behind the knee.
- Examine children more often, paying special attention to the head, neck, and ears. Teach them to avoid tall grass and low brush.
- Do not let pets roam freely in these areas, and if they are allowed to go to these spots, check them daily, especially if allowed indoors. Free-roaming pets may carry ticks of all life stages and can be infected with tick-borne diseases. This is rather important for companion animals living in close contact with humans.
- To remove attached ticks, use fine-tipped tweezers or shield your fingers with a tissue, paper towel, or rubber gloves. Avoid removing ticks with bare hands.
- Grasp the tick with the tweezers as close as possible to the surface of the skin, turn it gently, and from time to time pull upward with steady, even pressure.
- Do not squeeze, crush, or puncture the body of the tick because its fluids (saliva, body fluids, gut contents) may contain infectious organisms.
- Save the tick for identification and potentially test for pathogens. This may help your doctor make an accurate diagnosis if you become sick.

Supplemental Materials

Supplemental documents are available online including keys for the identification of tick families and genera, and a list of extant species described chronologically from 1758 to October 2019.

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ARTHROPODA

Acari (Order): Mites

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Phylum Arthropoda

    Order Acari

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Chapter 67

Acari (Order): Mites

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Introduction

Mites (order Acari or order Acarina) are the most diverse and abundant of all arachnids, but because of their small size (usually less than a millimeter in length) they are rarely seen. Red velvet mites are among the giants of the Acari (up to 10 mm) and can often be seen hunting on the ground or on tree trunks. Water mites are rarely more than a few millimeters long, but their bright colors and rapid movement are eye-catching. At the smaller end of the mite size range are species like the human hair follicle mite *Demodex folliculorum* or the honeybee tracheal mite, small enough to raise a family within a human hair follicle or within a bee's respiratory tube, and too small (about 0.1 mm) to see without a microscope.

Mites are also among the oldest of all terrestrial animals, with fossils known from the early Devonian Era, nearly 400 Ma (= million years ago; Norton et al., 1988; Kethley et al., 1989). Three major lineages are currently recognized: superorders Opilioacariformes, Acariformes, and Parasitiformes (Krantz, 1978; Johnston, 1982; Evans, 1992). About 45,000 species of mites have been described; a small fraction (perhaps 5%) of the number of species estimated to be alive today.

Mites are truly ubiquitous. They have successfully colonized nearly every known terrestrial, marine, and freshwater habitat including polar and alpine extremes, tropical lowlands and desert barrens, surface and mineral soils to depths of >10 m, cold and thermal surface springs and subterranean waters with temperatures as high as 50 °C, all types of streams, ponds and lakes, and sea waters of continental shelves and deep-sea trenches to depths of 5,000 m. Some idea of mite abundance and diversity can be gained from analysis of 1 square m of mixed temperate hardwood or boreal coniferous litter, which may harbor upwards from 1 million mites representing 200 species in at least 50 families. Within this complex matrix of decomposing plant matter, mites help to regulate microbial processes directly by feeding on detritus and microbes, and indirectly by predation on other microfauna.

Many mites have complex symbiotic associations with the larger organisms on which they live. Plants, including crops and the canopies of tropical rainforests, are inhabited by myriads of mite species feeding on mosses, ferns, leaves, stems, flowers, fruit, lichens, microbes, other arthropods, and each other. Many mites found on agricultural crops are major economic pests (for example, spider mites) or useful biocontrol agents (for example, phytoseiid mites) of those pests. Mammals and birds are hosts to innumerable species of parasitic mites (for example, scabies and mange mites), as are many reptiles and some amphibians. Insects, especially those that build nests, live in semipermanent habitats like decaying wood, or use more ephemeral habitats like bracket fungi and dung, are hosts to a cornucopia of mite commensals, parasites, and mutualists. None of these mites exceed a cm in length, and the vast majority grow to less than a mm, yet they often have a major impact on their hosts.

Characteristics

The Acari can be defined by the following characteristics:

- Hexapod prelarva (lost in Parasitiformes and many derived Acariformes)
- Hexapod larval stage
- Three octopod nymphal stages (variously abbreviated in derived taxa)
- Gnathosoma delimited by a circumcapitular suture
- Palpcoxal endites fused medially forming a hypostome
- Hypostome with rutella or corniculi (lost in many derived Acariformes)
- Loss of external evidence of opisthosomal segmentation, that is, without tergites or sternites
- Ingestion of particulate food (lost in many derived taxa).

Figures 1–3 include images of morphological characters of mites.

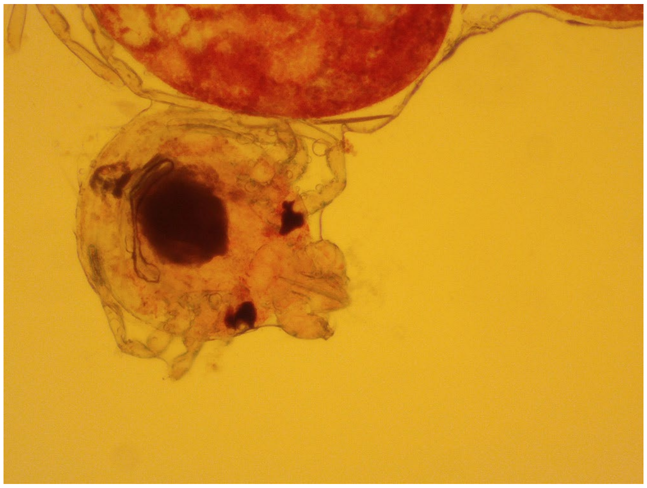

Figure 1. Larval mite of the genus *Hydrachna* that was removed from the wing of a backswimmer (genus *Notonecta*). The lateral dark spots are the eyes. Source: S. L. Gardner, HWML. License: CC BY.

Figure 2. *Ornithonyssys bacoti*, a mite (Acari: Mesostigmata: Macronyssidae) from the skin of a rodent (*Microtus ochrogaster*) collected at Cedar Point Biological Station, near Ogallala, Nebraska, United States, 2015. Source: S. L. Gardner, HWML. License: CC BY.

Scabies

Scabies is an infestation of the skin by the human itch mite (*Sarcoptes scabiei* var. *hominis*). The microscopic scabies mite burrows into the upper layer of the skin where it lives and lays its eggs. The most common symptoms of scabies are intense itching and a pimple-like skin rash. The scabies mite usually is spread by direct, prolonged skin-to-skin contact with a person who has scabies.

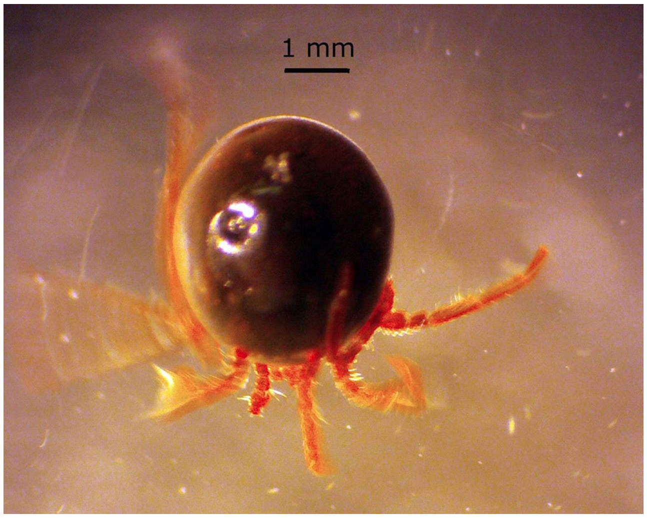

Figure 3. Aquatic mite, adult female collected from a cattle tank in the Sandhills of southwestern Nebraska, United States. The adults are free-living and the larvae are parasitic on backswimmers. Source: S. L. Gardner, HWML. License: CC BY.

Scabies is found worldwide and affects people of all races and social classes. Scabies can spread rapidly under crowded conditions where close body and skin contact is frequent. Institutions such as nursing homes, extended-care facilities, and prisons are often sites of scabies outbreaks. Child-care facilities also are a common site of scabies infestations.

Causal Agent of Scabies

Sarcoptes scabiei var. *hominis* is in the arthropod class Arachnida, order Acari, family Sarcoptidae. The mites burrow into the upper layer of the skin but never below the stratum corneum. The burrows appear as tiny raised serpentine lines that are grayish or skin-colored and can be a cm or more in length. Other races of scabies mites may cause infestations in other mammals, such as domestic cats, dogs, pigs, and horses. It should be noted that races of mites found on other animals may cause a self-limited infestation in humans with temporary itching due to dermatitis; however, they do not multiply on the human host.

Life Cycle of *Sarcoptes scabiei* var. *hominis* (Figure 4)

Sarcoptes scabiei undergoes 4 stages in its life cycle: Egg, larva, nymph, and adult. Females deposit 2–3 eggs per day as they burrow under the skin. Eggs are oval and 0.10 to 0.15 mm in length and hatch in 3 to 4 days. After the eggs hatch, the larvae migrate to the skin surface and burrow into the intact stratum corneum to construct almost invisible, short burrows called molting pouches. The larval stage, which emerges from the eggs, has only 3 pairs of legs and lasts about 3 to 4

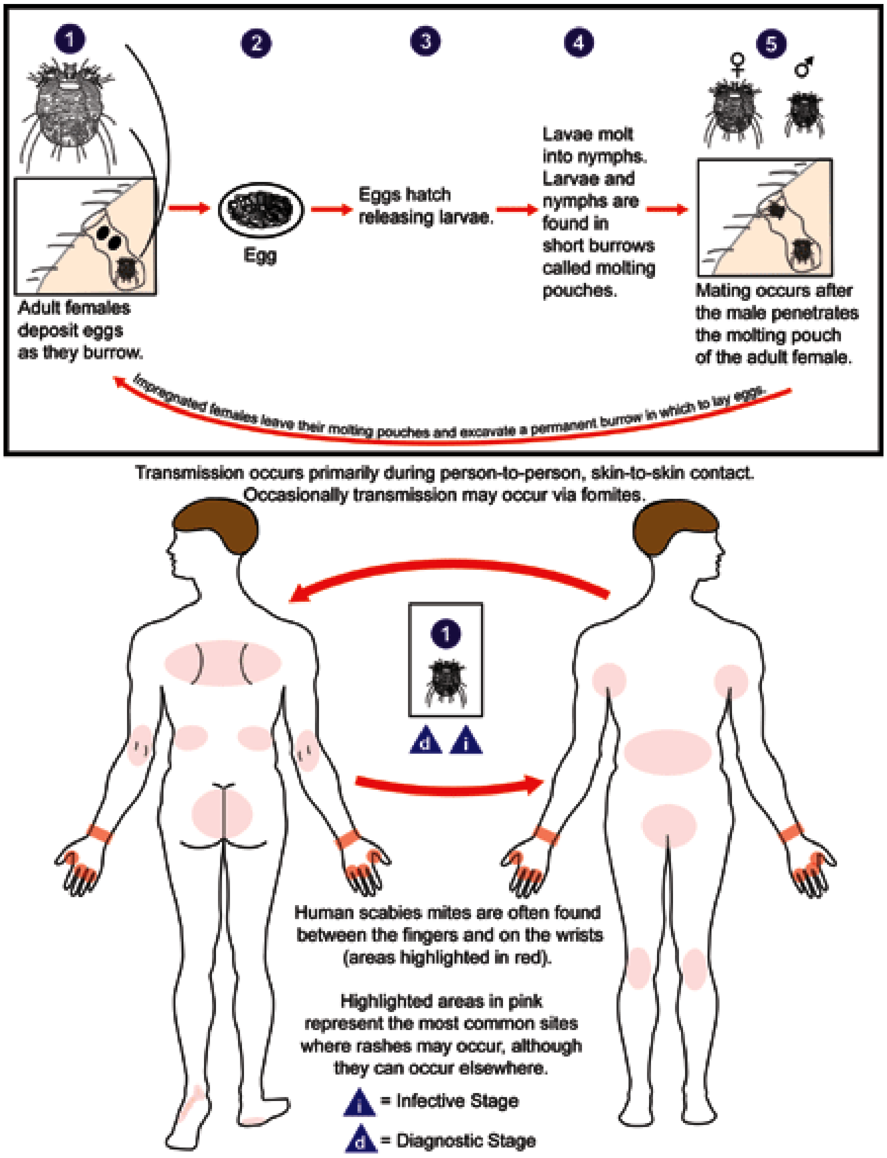

Figure 4. *Sarcoptes scabiei* life cycle. *Sarcoptes scabiei* undergoes 4 stages in its life cycle: Egg, larva, nymph, and adult. Females deposit 2–3 eggs per day as they burrow under the skin (1). Eggs are oval and 0.10 to 0.15 mm in length (2) and hatch in 3–4 days. After the eggs hatch, the larvae migrate to the skin surface and burrow into the intact stratum corneum to construct almost invisible, short burrows called molting pouches. The larval stage, which emerges from the eggs, has only 3 pairs of legs (3) and lasts about 3–4 days. After the larvae molt, the resulting nymphs have 4 pairs of legs (4). This form molts into slightly larger nymphs before molting into adults. Larvae and nymphs may often be found in molting pouches or in hair follicles and look similar to adults, only smaller. Adults are round, sac-like eyeless mites. Females are 0.30 to 0.45 mm-long and 0.25 to 0.35 mm-wide, and males are slightly more than half that size. Mating occurs after the active male penetrates the molting pouch of the adult female (5). Mating takes place only once and leaves the female fertile for the rest of her life. Impregnated females leave their molting pouches and wander on the surface of the skin until they find a suitable site for a permanent burrow. While on the skin's surface, mites hold onto the skin using sucker-like pulvilli attached to the 2 most anterior pairs of legs. When the impregnated female mite finds a suitable location, it begins to make its characteristic serpentine burrow, laying eggs in the process. After the impregnated female burrows into the skin, she remains there and continues to lengthen her burrow and lay eggs for the rest of her life (1–2 months). Under the most favorable of conditions, about 10% of her eggs eventually give rise to adult mites. Males are rarely seen; they make temporary shallow pits in the skin to feed until they locate a female's burrow and mate. Transmission occurs primarily by the transfer of the impregnated females during person-to-person, skin-to-skin contact. Occasionally transmission may occur via fomites (for example, bedding or clothing). Human scabies mites often are found between the fingers and on the wrists. Source: Division of Parasitic Diseases and Malaria, United States Centers for Disease Control and Prevention, 2017. Public domain.

days. After the larvae molt, the resulting nymphs have 4 pairs of legs. This form molts into slightly larger nymphs before molting into adults. Larvae and nymphs may often be found in molting pouches or in hair follicles and look similar to adults, only smaller. Adults are round, sac-like, eyeless mites. Females are 0.30 to 0.45 mm-long and 0.25 to 0.35 mm-wide, and males are slightly more than half that size.

Mating occurs after the active male penetrates the molting pouch of the adult female. Mating takes place only once and leaves the female fertile for the rest of her life. Impregnated females leave their molting pouches and wander on the surface of the host's skin until they find a suitable site for a permanent burrow. While on the surface of the host's skin, mites hold onto the skin using sucker-like pulvilli attached to the 2 most anterior pairs of legs. When the impregnated female mite finds a suitable location, it begins to make its characteristic serpentine burrow, laying eggs in the process. After the impregnated female burrows into the skin, she remains there and continues to lengthen her burrow and lay eggs for the rest of her life (1–2 months). Under the most favorable of conditions, about 10% of her eggs eventually give rise to adult mites. Males are rarely seen; they make temporary shallow pits in the skin to feed until they locate a female's burrow and mate.

Transmission occurs primarily by the transfer of the impregnated females during person-to-person, skin-to-skin contact. Occasionally transmission may occur via fomites (for example, bedding or clothing). Human scabies mites often are found between the fingers and on the wrists.

Some immunocompromised, elderly, disabled, or debilitated persons are at risk for a severe form of scabies called crusted, or Norwegian, scabies. Persons with crusted scabies have thick crusts of skin that contain large numbers of scabies mites and eggs. The mites in crusted scabies are not more virulent than in non-crusted scabies; however, they are much more numerous (up to 2 million per patient). Because they are infested with such large numbers of mites, people with crusted scabies are very contagious to other people. In addition to spreading scabies through brief direct skin-to-skin contact, persons with crusted scabies can transmit scabies indirectly by shedding mites that contaminate items such as their clothing, bedding, and furniture. Persons with crusted scabies should receive quick and aggressive medical treatment for their infestation to prevent outbreaks of scabies.

Phylogenetic Relationships (based on research through 1996)

Traditionally, the mites have been treated as a subclass of the Arachnida, and 3 major lineages have been recognized, though the names used to refer to these groups have varied considerably (Krantz, 1978; Johnston, 1982; Evans, 1992). Here the names are generally followed as used in Parker (1982), and consider 3 superorders (sensu Evans, 1992) of Acari that exist. The superorder Opilioacariformes consists of a single order and family (Opilioacarida, Opilioacaridae) with about 20 known species. The superorder Acariformes contains over 300 families and over 30,000 described species. Two major lineages are recognized, the Sarcoptiformes (Oribatida and Astigmata) and Trombidiformes (Prostigmata). Additionally, 8 families of very early derivative acariform mites are lumped into the Endeostigmata, usually considered a suborder of the Prostigmata, but clearly containing taxa that belong to both major acariform lineages. The superorder Parasitiformes consists of 3 orders: Ixodida, Holothyrida, and Mesostigmata. The Mesostigmata contains in excess of 65 families and 10,000 described species, the other 2 parasitiform orders each comprise 3 families. About 850 species of ticks are known, but only about 30 species of holothyrans have been recognized.

What then is a mite? Aside from being generally tiny chelicerate arthropods with hexapod larvae, a discrete gnathosoma, and a loss of primary segmentation, mites are difficult to characterize. Lindquist (1984) pointed out that many of the characters used to define mites were present in other chelicerate orders, especially in the Ricinulei. He proposed 11 apomorphic characteristics for the Acari (Lindquist, 1984, Table 8, p. 40), but several of these character states are not present in the Parasitiformes and presumably have been secondarily lost. It seems that mites often are most easily recognized by what they are not, other arachnids, rather than by a discrete set of acarine characters.

Among acarologists, arguments about monophyly or diphyly of the Acari have yet to be resolved, although currently the monophyleticists seem to be dominant (see Lindquist, 1984; Evans, 1992). The Parasitiformes and Opilioacariformes are thought to be sister groups, and in turn this taxon (the Anactinotrichida, so named because of the absence in their setae of optically active actinochitin) is considered the sister group of the Acariformes (also called the Actinotrichida). Outside of the acarological community, those interested in chelicerate phylogeny have tended to assume that the Acari were a monophyletic assemblage (for example, Weygoldt and Paulus, 1979; Shultz, 1990; Weygoldt, 1998).

Many acarologists have concluded that mites are closely related to the arachnid order Ricinulei (Lindquist, 1984; van der Hammen, 1989; Evans, 1992). Weygoldt and Paulus (1979) first proposed a sister group relationship between the Ricinulei and the Acari and named this taxon the Acarinomorpha. Schulz (1990) also supported this relationship, but like Weygoldt and Paulus, assumed that the Acari are monophyletic. Van der Hammen (1989) considered the Acari to be diphyletic, and the Acariformes and Parasitiformes to be at most only distantly related. According to van der Hammen, the Ricinulei and Anactinotrichida (Parasitiformes + Opilioacariformes) are sister groups and, within another lineage, the Actinotrichida (Acariformes) and the non-acarine Palpigradi also are sister groups. Lindquist (1984) presented four derived characters linking the Acari and Ricinulei (Lindquist, 1984, Table 9, p. 41) and concluded that, within the Acari proper, the Opilioacariformes and Parasitiformes form a sister group to the Acariformes.

Lindquist's (1984) hypothesis is followed here, which suggests that a monophyletic lineage includes the Ricinulei and the Acari. This hypothesis is based on the characters presented by Lindquist and is in agreement with that of Weygoldt and Paulus (1979) and Schulz (1990), but not with that proposed by Dunlop (1996).

Other Names for the Acari

Other names for the Acari include Acarina, Acaroides, Acaromorpha, Milben, acariens, acaros, Acarida, and mites.

Scope Note for This Textbook Section

This section was adapted by the textbook editors (S. A. Gardner and S. L. Gardner) from Walter and colleagues (1996), an open access contribution to the Tree of Life Web Project made available online under a CC BY-NC 3.0 license, and the public domain United States Centers for Disease Control and Prevention webpages on scabies (CDC, 2020). Since 1996, several other investigations into Acari systematics and genomics have been conducted, so other sources should be consulted to supplement this introduction to the topic.

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and
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Preface

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IMPETUS FOR PREPARING THIS BOOK

The United Nations (UN) has declared education as a basic human right. One of the UN's sustainable development goals is a call to ensure "inclusive and equitable quality education and promotion of lifelong learning opportunities for all" (United Nations, 2023; see also WOERC, 2012). Depending on the specifics of their implementation, financing, and dissemination models, open educational resources (OERs) have the potential to help in the effort to achieve equitable learning across the globe (Orr et al., 2015; Lee and Lee, 2021; see also Bali et al., 2020).

Open educational resources are "teaching, learning, and research materials in any medium that reside in the public domain or have been released under an open license that permits their free use and re-purposing by others" (Creative Commons, 2014). Wiley (2020) cites the Creative Commons' framing of OERs as providing explicit permission to "retain, re-use, revise, remix, and redistribute" openly-accessible educational material.

Aside from the obvious benefit of saving students money, OERs have been shown to promote equity among students. Their use has been shown to contribute to maintenance or improvement of student success, especially with respect to retention in school, course completion, grade point average, and subsequent educational attainment (Colvard et al., 2018; Griffiths et al., 2022; Fischer et al., 2015).

HOW TO USE THIS BOOK

Scope

This is a textbook covering concepts in animal parasitology. It is meant to be used by students, teachers, professors, researchers, and members of the public who are interested in learning about animal parasite biology, systematics, taxonomy, zoogeography, and ecology. The primary intended audience is upper-level undergraduate or graduate university students who have knowledge of basic biology and, particularly, basic animal biology.

Organization of the Book

This textbook was conceived to fill a gap in educational materials about parasitology. One of the main goals in both teaching and learning about parasites and parasitology is to understand the diversity of parasites and of parasitism as a way of life on Earth. With this in mind, the editors made a decision to treat the organization of the book as though led by the organisms themselves—a sort of bottom-up approach—and present the parasitic organisms as a parasitologist will first find them in nature, as in: Where they tend to exist in relation to their host, and more specifically, whether inside or outside the host animal. Therefore, the book includes sections covering a few taxonomic groups representing just some of the millions of extant endoparasite (Greek: **endo** = inside; **para** = beside; **sitos** = food) and ectoparasite (Greek: **ektos** = outside) species.

Examples of endoparasites are parasitic trematodes or nematodes that live inside the respiratory systems or gastrointestinal tracts of their hosts. Ectoparasites include lice and ticks, almost all fleas, many mites, a few platyhelminths that live on echinoderms, and even some chordates like the lamprey and vampire bat. Some groups of animals, such as monogeneans and mites, are not neatly categorized and may live part of their lives as endoparasites and part of their lives as ectoparasites or as free-living animals. Despite these myriad variations, the editors believe that the basic division between endo- and ecto- serves well enough to organize the chapters.

In approaching the organization in this way, the focus of the book is primarily at the level of species and other lower level taxonomy as opposed to higher-level groupings which are notoriously constantly in flux. The classification of parasites based on phylogenies is useful and necessary to understand the diversity, diversification, and evolution of parasites, but classification does not dictate the book's primary organization. Instead, the concept of biodiversity of parasites and their animal hosts is the main factor that motivates the research and teaching in the Harold W. Manter Laboratory of Parasitology (University of Nebraska State Museum, Lincoln, Nebraska, United States) where editor Scott L. Gardner conducts his work. It is this push toward understanding biological diversity of parasites that overarchingly informs the organization of this book.

Note about Bibliographical References

The citations in the book are formatted to promote finding usable copies, they are not meant to serve as an archival resource. As such, and to save space, only the first four authors are listed for each resource. A digital object identifier (doi) is included whenever one could be found; but the dois are not hot linked since these links would often take readers to paywalled versions. Readers are encouraged instead to attempt to locate free, legal versions of the resources included in the references whenever possible. For example, free-to-read versions (and sometimes also open access versions) of the papers may be available in institutional repositories, on authors' personal websites, or from academic social media sites.

Note about Images

When selecting images, the editors relied on the guidelines included in Egloff et al. (2017) regarding copyrightability of images that serve as biodiversity data. Beyond this broad framework to guide selection, the images in the book were chosen ultimately based on the following criteria: Conceptual applicability, quality, allowable copyright and permissions, and (for human subject images) an acceptable declaration of informed consent (see Roguljić and Wager, 2020). Due to the constraints of these criteria, there are several sections in the book that are lightly illustrated. Where images are sparse or lacking, instructors are encouraged to insert their own images or select images from other sources, including those used under applicable fair use/fair dealing or educational use guidelines.

Accompanying Glossary

A supplemental glossary is in the process of preparation. Until the glossary is completed, a work that may be used in its stead for many of the terms found in the book is the Dictionary of Invertebrate Zoology (Maggenti et al., 2017) available online for free: https://digitalcommons.unl.edu/zeabook/61/

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Disclaimers

Although students of pre-medical studies, medical studies, or veterinary studies may use this text to learn foundational concepts in animal parasitology, it is not a medical or veterinary text. Further, it is not meant for any medical- or veterinary-related purposes whatsoever. When medical or veterinary topics are touched upon in the text, this is for educational purposes for those studying or interested in the biological sciences generally. *No medical or veterinary advice of any kind is offered or implied anywhere in this textbook. No* medical or veterinary diagnoses, treatments, or conclusions of any kind may be construed using the knowledge offered herein.

For studies specifically related to medical parasitology, readers may consult any of a number of qualified texts in the subject, including Medical Parasitology: A Textbook (Mahmud et al., 2017), Medical Parasitology (Satoskar, 2009), and Modern Parasitology: A Textbook of Parasitology, 2nd edition, (Cox et al., 2009), among others. Numerous medical periodicals are also appropriate sources of knowledge about medical parasitology. For medical diagnoses, qualified practitioners of medicine may be consulted directly.

For studies specifically related to veterinary parasitology, readers may consult any of a number of qualified texts in the subject, including Veterinary Parasitology, 4th edition, (Taylor et al., 2015) and Georgis' Parasitology for Veterinarians, 11th edition, (Bowman, 2020), among others. Numerous veterinary parasitology periodicals are also appropriate sources of knowledge about veterinary parasitology. For veterinary diagnoses, qualified practitioners of veterinary medicine may be consulted directly.

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If any qualified readers would like to serve as a reviewer for any of the sections, you are invited to please contact one of the editors to discuss the possibility of being assigned the task of reviewing. You will be credited in revisions if you ultimately serve as a selected reviewer. In addition, if readers discover factual or typographical errors in the content, please contact one of the editors.

HOW THE BOOK WAS DEVELOPED

Origin of the Book

The concept for this book arose in 2018 around the time there was a concerted push to create open educational resources in universities (Austin, 2018; Sennott et al., 2015). This push seemed well-timed to the editors. In fact, the rising costs of textbooks has become a major problem for students to the point where it is basically untenable to expect students to pay for them anymore. The editors reasoned that it would be a good time to call on their esteemed and accomplished colleagues in academia to help create a new textbook in a massively collaborative endeavor, if they were willing to participate.

Also driving the idea of a new textbook, the seminal English-language parasitology textbook of our time, Gerald R. Schmidt and Larry S. Roberts' Foundations of Parasitology, 9th edition (Roberts et al., 2012), has recently gone out of print and there are no plans to update it. John J. Janovy, Jr., the lead author of the last several editions of the Schmidt and Roberts book, agreed that the creation of a new textbook was a good and timely idea.

Contributing to the decision to attempt the creation of a large-scale textbook project was the public access/open access platform available to the editors, namely, the Zea Books imprint of the University of Nebraska–Lincoln Libraries. In line with the OER ethos driving the creation of the content, this publishing imprint operates under a diamond open access model, such that neither the authors nor the readers have to pay to publish nor to read any work published as a Zea Book.

Development of the Book

At the time of the conception of the book idea, the edi-tors capitalized on the availability of visiting scholars in the Harold W. Manter Laboratory of Parasitology (Lincoln, Ne-braska, United States)—Griselda Pulido-Flores, Scott Monks, and Donald Gettinger, as well as local colleagues John J. Janovy, Jr. and Gabor Rácz, and student-colleagues Auggie Tsogtsaikhan Dursahinhan and Guin Drabik—and called to-gether a couple of meetings to discuss their idea with the group. They asked them to envision what they would like to see in a new textbook, one that would be available online for anyone with a computer connection to access for free. Among many other good ideas they shared, they suggested that the book could possibly include numerous links to other sources and interactive modules, and pointed out that the information may be kept more current than was possible with a printed volume. Colleagues Paul Royster, Linnea Fredrickson, Catherine Fraser Riehle, and Mary Bolin in the University of Nebraska–Lincoln Libraries (Lincoln, Nebraska, United States) also provided encouragement and expertise that helped the project on its way.

When preparing to solicit manuscripts for this project, based on the preliminary conversations with colleagues, the editors first prepared an outline of the concepts desired to have covered and then created streamlined style requirements (the instructions for authors and references style guide are available online here: https://digitalcommons.unl.edu/parasittext/). They then asked numerous colleagues—all experts in their subareas of parasitology—to contribute one or more sections based on the outline. So many of them agreed to write sections that it seemed that it really might be possible to create a high-quality work with the input of so many fine experts. Every one of them submitted manuscripts quickly.

The editors gave the authors quite a bit of latitude regarding how to approach their assignment to write sections. They provided an optional template to work from (available here), but use of this format was optional. They wanted the authors to be able to express themselves in the way they each felt was best to demonstrate knowledge of their respective areas of interest within the larger subject of animal parasitology. This liberal approach naturally resulted in some variation in presentation styles, which is perhaps a plus for the reader. It breaks up the tone and emphases from section to section, and the reader gets a sense of each author's different voice and approach. The editors have worked to retain much of each author's preferred style of presentation, but with normalizing of typography and other style elements to help the manuscript finally cohere as a unified whole.

Some of the sections were sent out for review. This review process was open, so the authors knew who was reviewing their work and the reviewers were aware that the authors knew they were reviewing. Reviewed sections are marked as such with the reviewer's name and affiliation. Whether reviewed or not, all of the sections were editor-reviewed by both editors: Sue Ann Gardner edited primarily for bibliographic details and style elements, and Scott L. Gardner edited primarily for content.

Delayed Publication

With best-laid plans, the editors started to review and edit the sections as soon as they were submitted. Then a great number of both quite-dire and less-dire issues arose that interfered with the ability to complete the editing and production in as timely a manner as intended (selected challenges include: The SARS-CoV-2 pandemic requiring remote teaching, a computer crash, a death in the family that then required weeks away from work and home, radical changes in administrations at the university, and other issues). With those issues finally receding in impact, five years after the project began, the book will be published at long last.

Demographic Data About the Authors

With editor Scott L. Gardner's large network of expert parasitologist colleagues, it was possible to seek out scholars who are experts in their field. While the first consideration when deciding who to invite to participate was expertise, the editors further worked toward the desired goal of equity and inclusion in the selection of authors. One result was a 1:2 ratio of women to men. While this does not represent parity, it is an improvement over days past when the majority of authors would likely have been men. Another result of efforts at equity and inclusion was the participation of many au-thors from outside the United States. Approximately 40% of authors are US-American and the remaining 60% are from one of 14 other countries (Argentina, Brazil, Australia, Japan, Mongolia, Bulgaria, Czechia, Germany, Hungary, Norway, Russia, Spain, Mexico, or Canada). Almost half of the authors (44%) do not have English as their first language.

Spanish-Language Version

In late 2018, the Office of the President at the University of Nebraska–Lincoln (Lincoln, Nebraska, United States) issued a call for proposals for Inclusive Excellence Development at the university. The editors were awarded funds to go toward translation of the textbook. With this, the editors partnered with a local professor of Spanish-language translation, Yoanna Esquivel Greenwood, who has created Spanish-language versions for numerous chapters in the book. Thanks to her work, and perhaps with the added input of some of the Spanish speakers among the authors, a comprehensive Spanish-language translation is forthcoming.

Acknowledgement of Authors' Contributions

From the Editors, Scott L. Gardner and Sue Ann Gardner

We sincerely thank all of the authors of this collaborative work. Your excellent contributions and dedication to the ad-vancement of knowledge of animal parasitology have the po-tential to positively change the lives of countless students and teachers worldwide.

While we were grappling with challenges and distractions that delayed the editing of the manuscript of this book, we lost a few of our esteemed author colleagues. We wish to posthumously acknowledge Bernie Fried, Akira Ito, and Robin M. Overstreet for what turned out to be some of their truly late-career contributions. We miss them, and we feel so fortunate to have benefitted from their long-acquired knowledge and their willingness to join in on this project.

Dedication

From the Editors, Scott L. Gardner and Sue Ann Gardner

This book is dedicated to **all** of our academic forebears and mentors who made this effort possible—some of whom are authors* of sections of the book! We can't list everyone, but we can provide a truncated list to commemorate some people especially.

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