44

DIGENEA, PLAGIORCHIIDA

XIPHIDIATA

Haematoloechidae Odening, 1964 (Family)

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Phylum Platyhelminthes
  Class Trematoda
    Subclass Digenea
      Order Plagiorchiida
        Family Haematoloechidae

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Chapter 44

Haematoloechidae Odening, 1964 (Family)

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Introduction

Members of the family Haematoloechidae are parasites of the lungs of amphibians and they are found on every continent except Antarctica. Their life cycle includes a snail and an aquatic arthropod as first and second intermediate hosts, respectively, and a frog or salamander as the definitive host.

Main Characters

Their body is elongate, the forebody is usually tapered, and the posterior body is oval; the tegument may be spined or not, but spines are easily lost. The oral sucker is well developed and is located near the anterior end of the body. The pharynx is well developed, the esophagus is short, and the digestive ceca extend to near the posterior extremity (Figure 1). The ventral sucker is located anterior to the midbody; in most species it is well developed, but in a few of them it is reduced and difficult to observe (Figure 2). The male reproductive system is composed of 2 oval or lobed testes in the posterior part of the body that are usually diagonally arranged (rarely symmetrical or in tandem); they are intracecal, with the exception of 1 species, *Haematoloechus exoterorchis,* in which they are extraceacally arranged (Figure 3). Species in this family have a cirrus sac that is cylindrical, narrow, and long, winding between the 2 suckers. The genital pore is ventral, median, and located at the level of the pharynx or esophagus. The female reproductive system comprises the ovary, which is located between the ventral sucker and the testes, and can be oval or lobed. The seminal receptacle is a large structure located laterally and dorsal to the ovary. Mehlis' gland is dorsal to the seminal receptacle and ovary. The vitelline follicles are arranged in clusters, sometimes overlapping each other; they are distributed laterally along the ceca for most of their length; in some species they are distributed only in the pretesticular region. The uterine loops fill the entire hindbody, passing

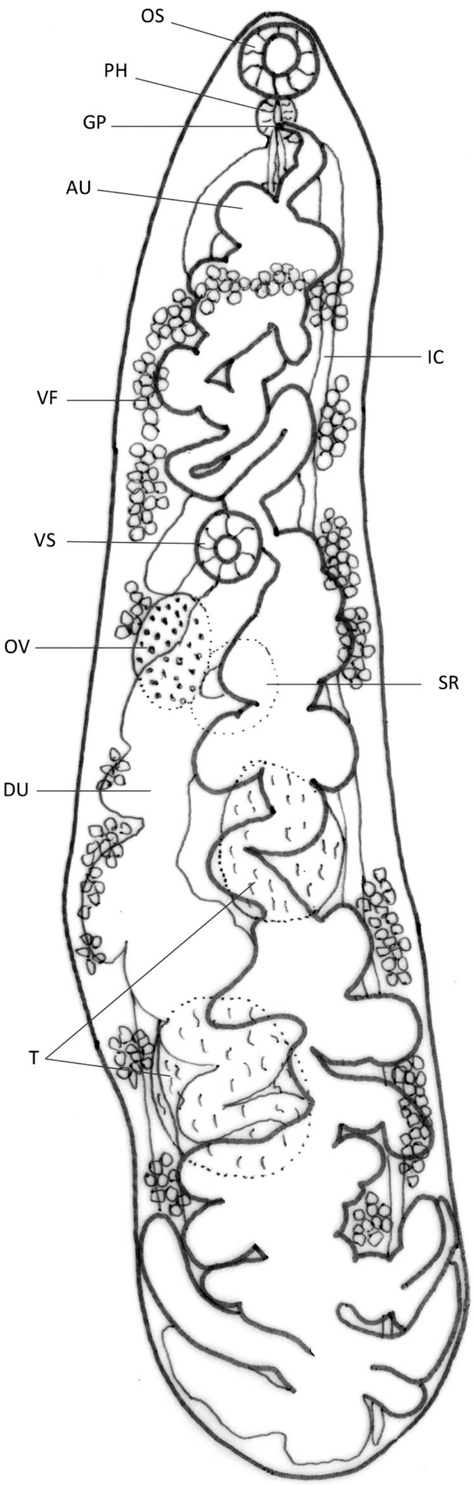

Figure 1. *Haematoloechus caballeroi*. AU: Ascending uterus; DU: Descending uterus; GP: Genital pore; IC: Intestinal ceca; OS: Oral sucker; OV: Ovary; PH: Pharynx; SR: Seminal receptacle; T: Testes; VF: Vitelline follicles; VS: Ventral sucker. Source: V. León-Règagnon. License: CC BY-NC-SA 4.0.

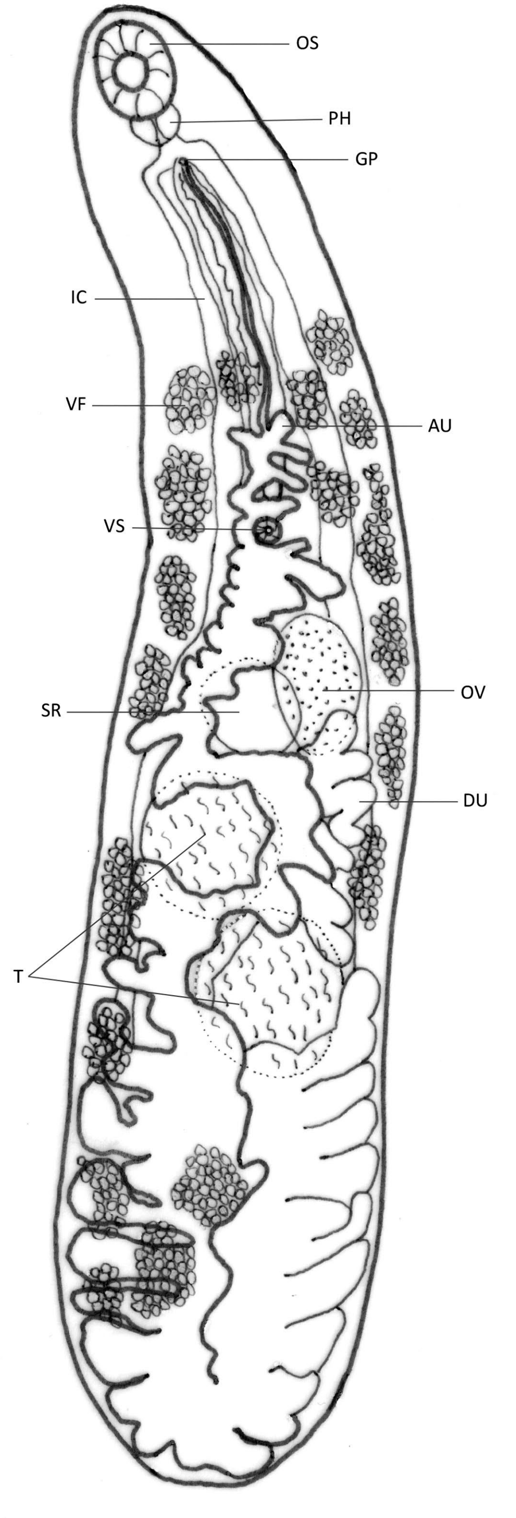

Figure 2. *Haematoloechus meridionalis*. AU: Ascending uterus; DU: Descending uterus; GP: Genital pore; IC: Intestinal ceca; OS: Oral sucker; OV: Ovary; PH: Pharynx; SR: Seminal receptacle; T: Testes; VF: Vitelline follicles; VS: Ventral sucker. Source: V. León-Règagnon. License: CC BY-NC-SA 4.0.

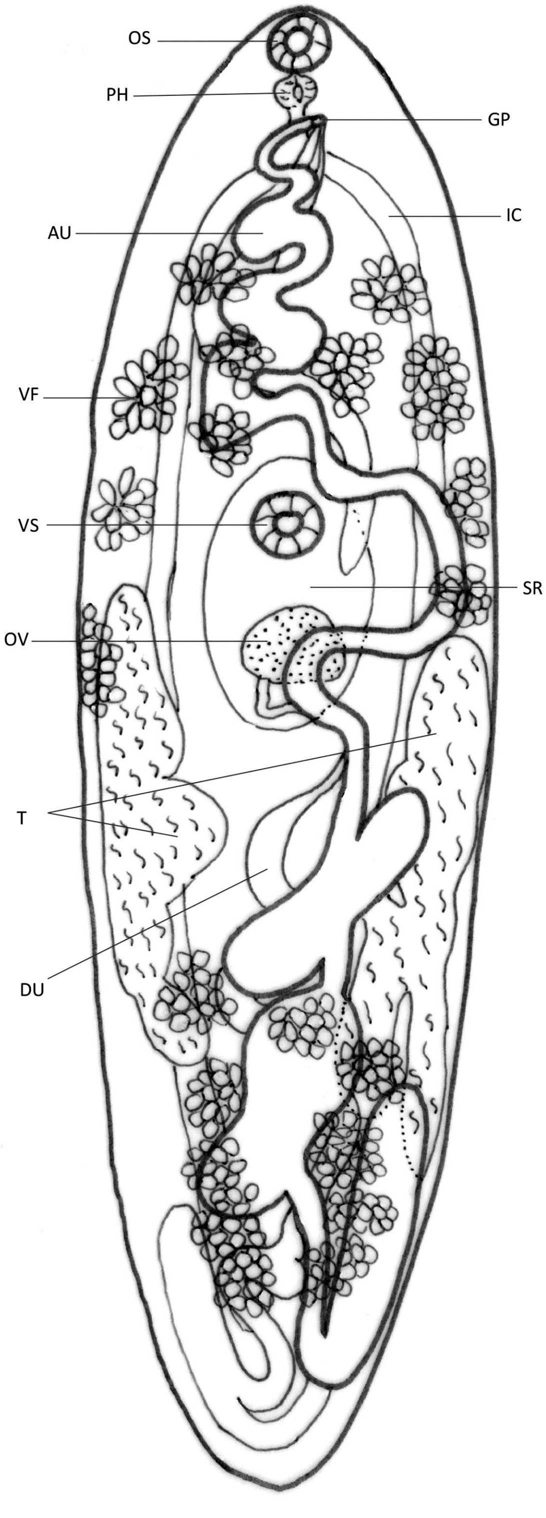

Figure 3. *Haematoloechus exoterorchis*. AU: Ascending uterus; DU: Descending uterus; GP: Genital pore; IC: Intestinal ceca; OS: Oral sucker; OV: Ovary; PH: Pharynx; SR: Seminal receptacle; T: Testes; VF: Vitelline follicles; VS: Ventral sucker. Source: V. León-Règagnon. License: CC BY-NC-SA 4.0.

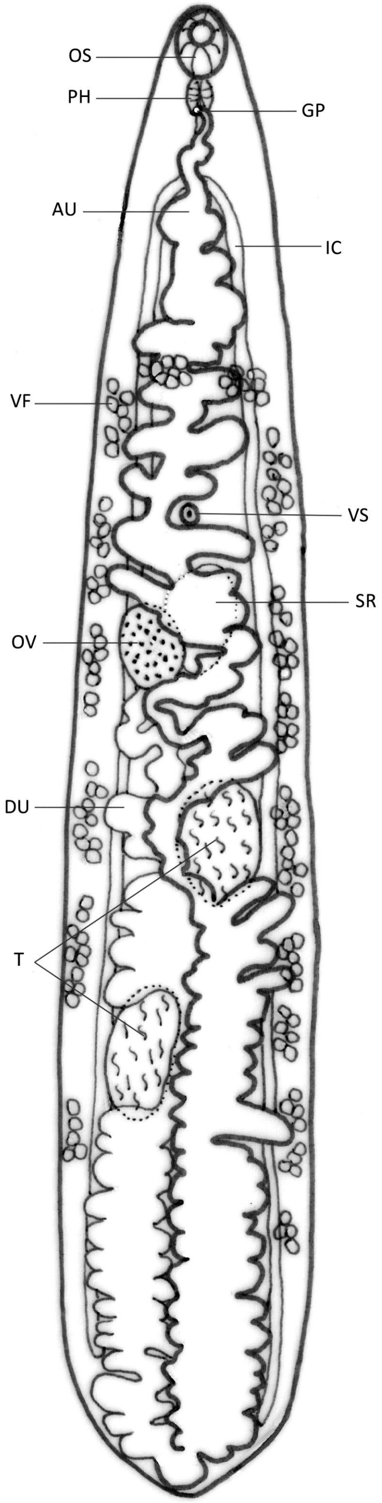

Figure 4. *Haematoloechus caballeroi*. AU: Ascending uterus; DU: Descending uterus; GP: Genital pore; IC: Intestinal ceca; OS: Oral sucker; OV: Ovary; PH: Pharynx; SR: Seminal receptacle; T: Testes; VF: Vitelline follicles; VS: Ventral sucker. Source: V. León-Règagnon. License: CC BY-NC-SA 4.0.

Figure 5. *Haematoloechus medioplexus*. AU: Ascending uterus; DU: Descending uterus; GP: Genital pore; IC: Intestinal ceca; OS: Oral sucker; OV: Ovary; PH: Pharynx; SR: Seminal receptacle; T: Testes; VF: Vitelline follicles; VS: Ventral sucker. Source: V. León-Règagnon. License: CC BY-NC-SA 4.0.

among the testes, sometimes forming extracecal loops that can extend forward at different levels; the ascending uterus forms several loops in the forebody. The eggs are tiny and numerous; in the distal uterus they are heavily pigmented and can obscure other structures (Figure 4).

Taxonomy and Phylogenetics

The taxonomic history of this family has been complicated. The first member of this family was formally described in the early 19th century. That species was originally named *Distomum variegatum* Rudolphi, 1819, and later was transferred to the newly erected genus *Haematoloechus* by Looss (1899). A few years later, the type genus of this family was renamed as *Pneumonoeces* Looss, 1902 because a hemipteran genus had previously been named *Haematoloecha* Stal (Looss, 1902). Although Harwood (1932) and Ingles (1932) independently reinstated *Haematoloechus* based on the existing International Code of Zoological Nomenclature (ICZN, 1895), some other authors continued to use *Pneumonoeces* (Mehra, 1937; Skrjabin and Antipin, 1962).

The first time this taxonomic group received a formal name was as the subfamily Pneumonoecinae (Mehra, 1937), then renamed Haematoloechinae (Freitas and Lent, 1939) within the Plagiorchiidae. It was not until 1964 that this group was recognized as an independent family within the Plagiorchioidea, the Haematoloechidae (Odening, 1960), for which the monophyly is currently supported by phylogenetic analyses based on ribosomal and mitochondrial DNA sequences (Tkach et al., 2000; 2001; León-Règagnon and Topan, 2018).

Several genera have been proposed to include species of haematoloechids based on the varying arrangement of the uterine loops or the distribution of the vitelline follicles. *Ostiolum* Pratt, 1903 was proposed for species lacking extracecal longitudinal uterine loops (Pratt, 1903) as in *Haematoloechus medioplexus* Stafford, 1902 (Figure 5) or *H. complexus* Seely, 1906. *Pneumobites* Ward, 1917, was proposed for those with longitudinal uterine loops extending to the pre-acetabular region of the body, with *H. longiplexus* as its type species (Ward, 1917) (Figure 6). *Skrjabinoeces* Sudarikov, 1950 was proposed for species with vitelline follicles in clusters limited to the pre-testicular region, with *H. similis* as its type species (Sudarikov, 1950) (Figure 7). Odening (1958) recognized the genera *Ostiolum* and *Haematoloechus,* this later with 3 subgenera based on the arrangement of the vitelline follicles: *Skrjabinoeces* (as described above), *Anomolecithus* (vitelline follicles not in clusters, extending to the post-testicular region, like in *H. asper* (Figure 8)) and *Haematoloechus* (vitelline follicles in clusters, extending to the post-testicular region, as in *H. longiplexus* (Figure 6) and most other members of Haematoloechidae). The genus *Neohaematoloechus* Odening, 1960 was erected for those species described as lacking a ventral sucker, with *H. neivai* (Travassos and Artigas, 1927) as its type species (Odening, 1960) (Figure 9).

The genus *Ostioloides* Odening, 1960 was proposed to include *Haematoloechus rappiae,* which was first described as *Haplometroides rappiae* Szidat 1932, then transferred to *Haematoloechus* by Yamaguti (1958), and finally used as the type species to erect *Ostioloides* by Odening (1960). The intestinal ceca extending only two-thirds of the body and the post-bifurcal position of the genital pore in *O. rappiae* supports the validity of the genus *Ostioloides* and indicates that it does not belong to the family Haematoloechidae, but to the Plagiorchiidae (Tkach, 2008).

In his extensive revision of the Trematoda, Yamaguti (1971) recognized the genera *Haematoloechus, Neohaematoloechus*, *Ostioloides*, and erected a new genus, *Metahaematoloechus* Yamaguti, 1971*,* for species with extracecal testes, with *H. exoterorchis* Rees, 1964 as the type species.

More recent research, using molecular data, has aided the identification of morphological characters that are useful for the differentiation of species, and revealed that most genera previously included in Haematoloechidae are not monophyletic (León-Règagnon et al., 1999; 2001; Snyder and Tkach, 2001; León-Règagnon and Paredes-Calderón, 2002; León-Règagnon and Brooks, 2003; León-Règagnon, 2010; Zamparo et al., 2011; León-Règagnon and Topan, 2018). Characters such as the ratio of the suckers, the oral sucker/pharynx ratio, the shape of the ovary and testes, the arrangement of the uterine loops, and the distribution of the vitellaria are valuable characters to differentiate species. Nevertheless, none of them appears to reflect the evolutionary history of the group (see León-Règagnon and Topan, 2018). Mapping the morphological traits that led to previous taxonomic arrangements into their phylogenetic tree, these authors found that they do not support the monophyly of previously proposed groups, consequently synonymizing *Ostiolum, Pneumobites, Anomolecithus, Neohaematoloechus*, and *Metahaematoloechus* with *Haematoloechus* (León-Règagnon and Topan, 2018). There is no molecular evidence for species previously assigned to the subgenus *Skrjabinoeces*; it is necessary to include these species in a phylogenetic framework to test the validity of this genus. Tkach (2008) considered it to be valid based on the morphology of the cercariae. According to León-Règagnon and Topan (2018), the only valid genus in the family is *Haematoloechus,* containing 70 valid species.

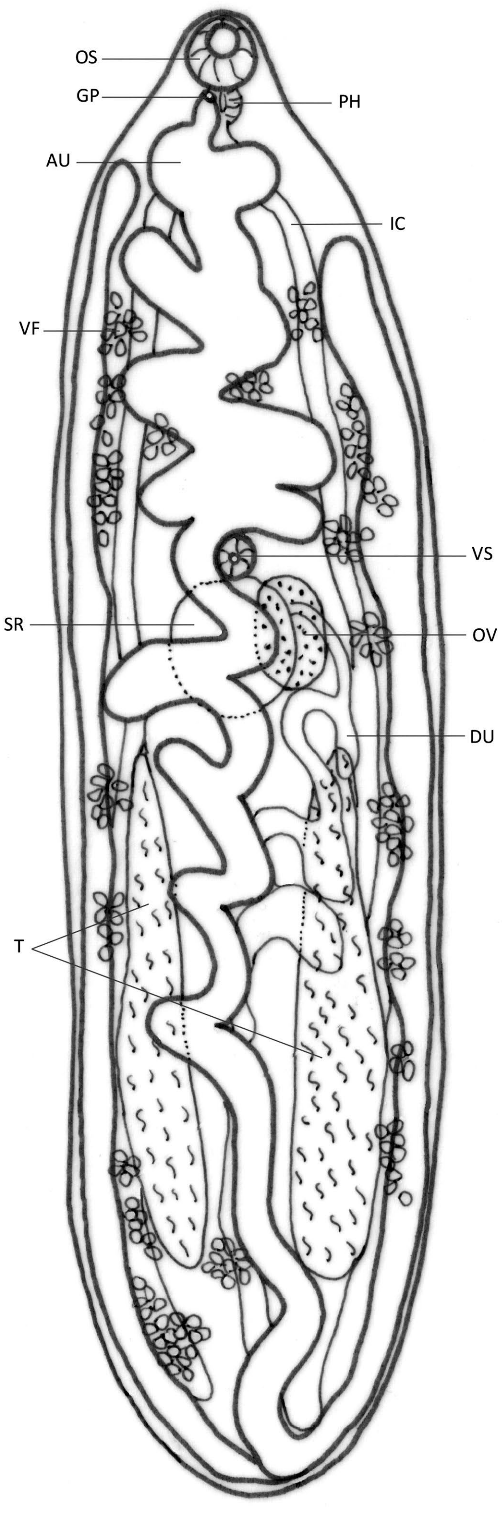

Figure 6. *Haematoloechus longiplexus*. AU: Ascending uterus; DU: Descending uterus; GP: Genital pore; IC: Intestinal ceca; OS: Oral sucker; OV: Ovary; PH: Pharynx; SR: Seminal receptacle; T: Testes; VF: Vitelline follicles; VS: Ventral sucker. Source: V. León-Règagnon. License: CC BY-NC-SA 4.0.

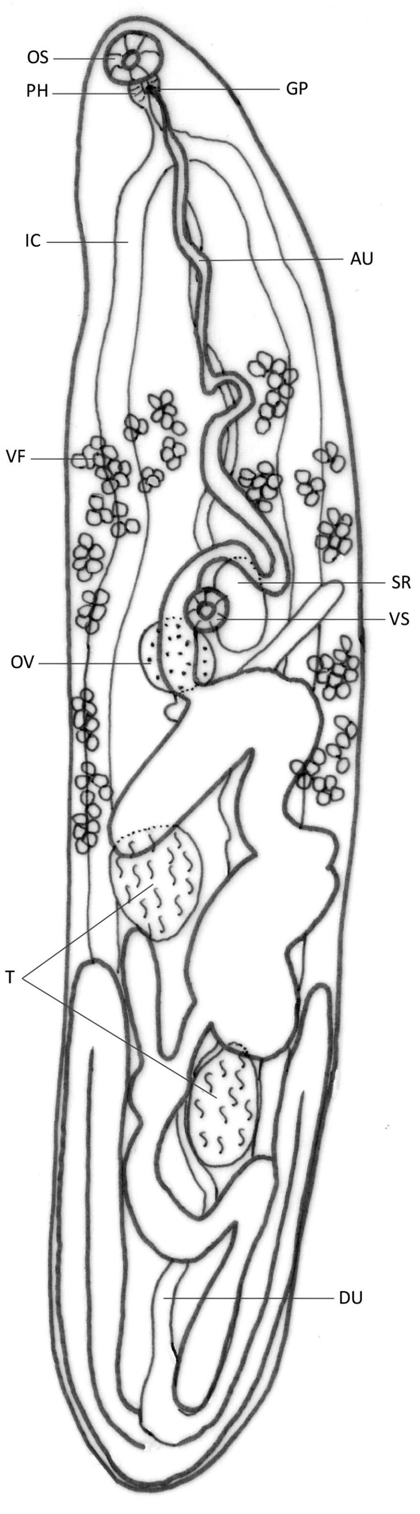

Figure 7. *Haematoloechus similis*. AU: Ascending uterus; DU: Descending uterus; GP: Genital pore; IC: Intestinal ceca; OS: Oral sucker; OV: Ovary; PH: Pharynx; SR: Seminal receptacle; T: Testes; VF: Vitelline follicles; VS: Ventral sucker. Source: V. León-Règagnon. License: CC BY-NC-SA 4.0.

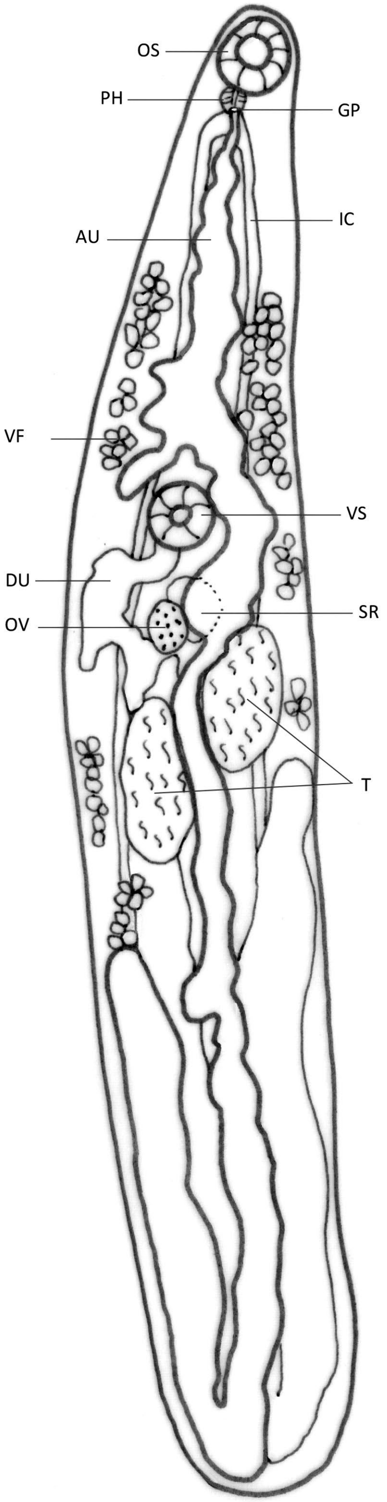

Figure 8. *Haematoloechus asper*. AU: Ascending uterus; DU: Descending uterus; GP: Genital pore; IC: Intestinal ceca; OS: Oral sucker; OV: Ovary; PH: Pharynx; SR: Seminal receptacle; T: Testes; VF: Vitelline follicles; VS: Ventral sucker. Source: V. León-Règagnon. License: CC BY-NC-SA 4.0.

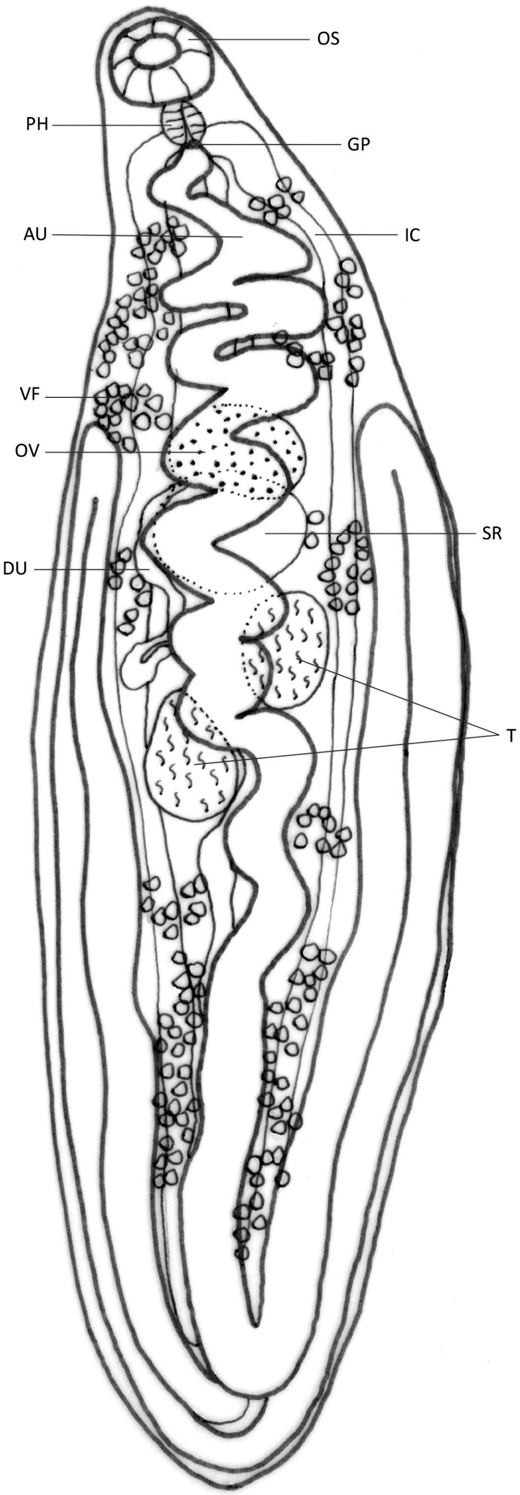

Figure 9. *Haematoloechus neivai*. AU: Ascending uterus; DU: Descending uterus; GP: Genital pore; IC: Intestinal ceca; OS: Oral sucker; OV: Ovary; PH: Pharynx; SR: Seminal receptacle; T: Testes; VF: Vitelline follicles. Source: V. León-Règagnon. License: CC BY-NC-SA 4.0.

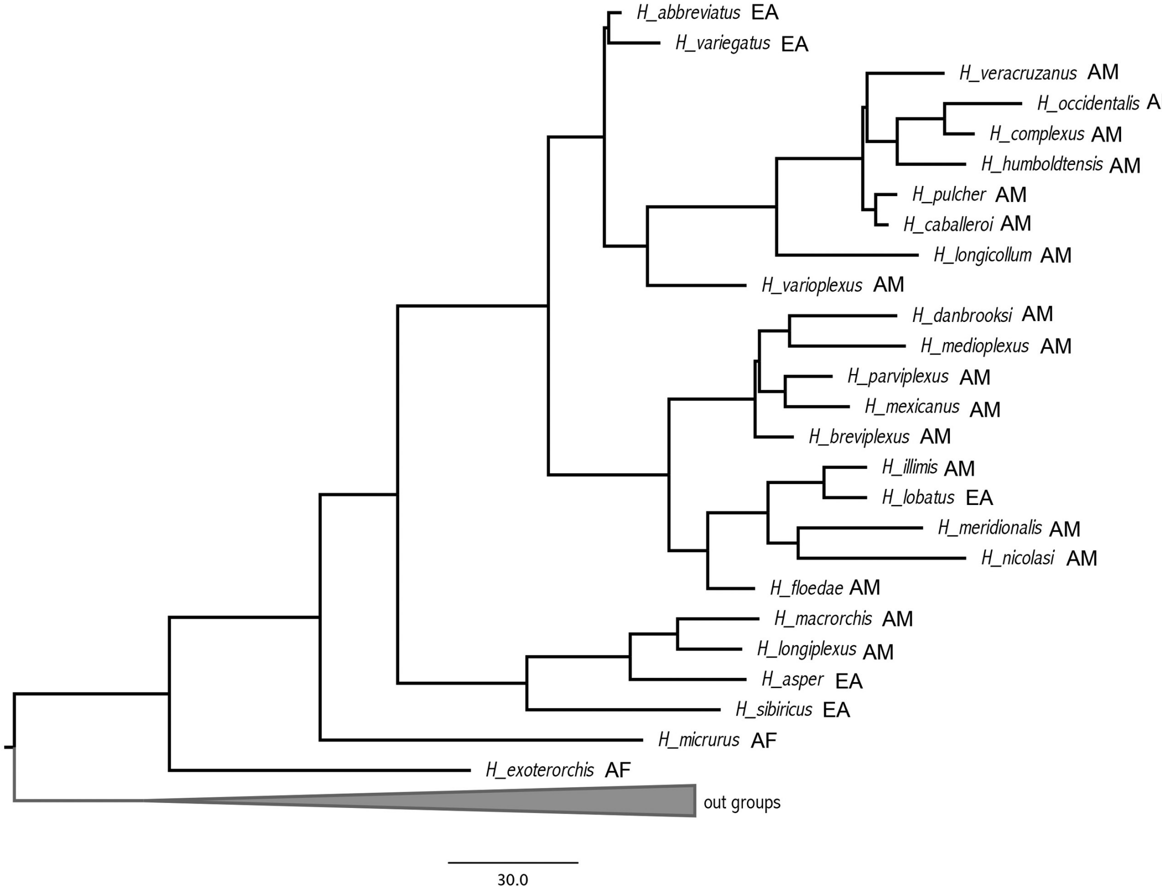

Figure 10. Phylogenetic hypothesis of *Haematoloechus* spp. based on mitochondrial and ribosomal DNA. AF: Africa, AM: America, EA: Eurasia, Out groups: *Brachycoelium salamandrae*, *Glypthelmins brownorumae*, *Opisthioglyphe ranae*, and *Plagiorchis koreanus*. Source: Adapted from León-Règagnon and Topan, 2018. License: CC BY-NC-SA 4.0.

Host Range

Most species of Haematoloechidae prefer amphibians of the family Ranidae (sensu Bossuyt et al., 2006) as their definitive hosts, although accidental infections (a few isolated records of species that are common in ranids) have been recorded in members of Bufonidae or Salamandridae, and some species have colonized members of other families, such as Ambystomatidae, Bombinatoridae, Leptodactylidae, Telmatobiidae, and others (León-Règagnon and Topan, 2018).

Snyder and Janovy (1994; 1996) examined the second intermediate host specificity of 4 North American species of *Haematoloechus*, including, *H. complexus, H. longiplexus, H. medioplexus,* and *H. varioplexus*. They found that cercariae of *H. complexus* act in a generalist way and are able to penetrate the intersegmental membranes of all 9 species of arthropods used in their experiments. *Haematoloechus longiplexus* penetrated only the base of the caudal gills of anisopteran (damselfly) and zygopteran (dragonfly) odonate naiads, while cercariae of *H. medioplexus* and *H. varioplexus* do not actively penetrate intermediate hosts, but are drawn into the branchial basket respiratory apparatus of the anisopteran naiads. They rarely attach to and never penetrate experimental hosts, suggesting that the evolution of disparate patterns of behavior among the cercariae of these 4 congeners directly affects subsequent patterns of transmission to the definitive host (Snyder and Janovy, 1994; 1996). Snyder and Tkach (2001) suggested that, based on the phylogenetic analysis of rDNA of 8 species of *Haematoloechus* and available data on life cycles of those species, intermediate host specificity reflected the evolutionary history of the group. However, this trait has been studied in only a few species of the genus and information in many more species is needed in order to corroborate this hypothesis.

Historically, host specificity (now referred to as host range) has been associated with the inability of the parasite to colonize a different host species, that is, the parasite has specialized in 1 (or a few) host species and is not capable of parasitizing other host species (for an extensive review, see Brooks and McLennan, 2002). Nevertheless, if the parasite has specialized in a resource, not in the host species, and if this resource is phylogenetically conserved among many host species, the parasite will be able to colonize other host species that carry that same resource if the opportunity presents itself. As noted elsewhere in this book, this phenomenon is called ecological fitting (Janzen, 1985). Even when host specificity is observed during a moment of time and in a particular space, it does not mean that host switching is not possible if the conditions change. For example, if new hosts are introduced in the area, or the original host is introduced in a new area, considering climate change and globalization can affect situations that are very common nowadays (Brooks and Hoberg, 2013; Brooks et al., 2014; 2019).

Haematoloechus floedae is a species native to the southeastern United States where it lives in the lungs of the bullfrog, *Lithobates catesbeianus*. When bullfrogs were introduced to the southwestern United States, the parasite went with them, and is now found in bullfrogs in that part of the country. Interestingly, the lung fluke was recently reported in other groups of frogs in the Yucatán Peninsula, Mexico (*L. brownorum*—leopard frog—and *L. vaillanti*—palmipes group) and in 2 leopard frogs, *Rana taylori* and *R.* cf. *forreri*, from the Área de Conservación Guanacaste, Costa Rica, where bullfrogs were introduced (León-Règagnon et al., 2005).

Haematoloechus floedae, despite having a supposedly complex, specialized life cycle, has become established in a number of endemic species in localities where bullfrogs were introduced, and even when in some of those localities bullfrogs have been extirpated, the parasite persists. These host switching events are clear examples of ecological fitting (Brooks et al., 2006).

Biogeography

According to León-Règagnon and Topan (2018), the association between *Haematoloechus* spp. and their hosts predates the ranid diversification in the Cretaceous Period (Bossuyt et al., 2006). Several African species of *Haematoloechus* (for example, *H. aubriae*, *H. combesi*, *H. darcheni*, *H. dollfusinum*, and *H. lobogonadus*) parasitize members of the Conrauinae, Ptychadeninae, and Pyxicephalinae groups that originated early in the radiation of the Ranidae in Africa (Bossuyt et al., 2006). When ancestral ranids colonized Europe (*Rana* and *Pelophylax*) and the New World (*Lithobates*) in the Oligocene or Miocene Period (Bossuyt et al. 2006), they must have been already associated with *Haematoloechus*, which is clearly reflected in the phylogenetic hypothesis presented by León-Règagnon and Topan (2018), as the African species *H. exoterorchis* and *H. micrurus* appear to have diverged early in the evolution of the group, and European and American species are present in the 3 larger clades of the tree (Figure 10).

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Supplemental Reading

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