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DIGENEA, PLAGIORCHIIDA

XIPHIDIATA

Allocreadiidae Looss, 1902 (Family)

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- Phylum Platyhelminthes
  - Class Trematoda
    - Subclass Digenea
      - Order Plagiorchiida
        - Family Allocreadiidae

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Chapter 43

Allocreadiidae Looss, 1902 (Family)

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Introduction

Allocreadiids are digeneans mainly found as parasites of the digestive tracts of freshwater fishes. The taxonomy and classification system of the family Allocreadiidae has been controversial. The detailed taxonomic history of the family within the Digenea was revised in great detail by Caira and Bogéa (2005). Due to work by helminthologists interested in top-down systematics of these trematodes, species composition, the validity of the genera, and the taxonomic arrangement within subfamilies have fluctuated over time. Some species included in the genera *Bunodera, Bunoderella, Crepidostomum, Megalogonia, Creptotrema, Creptotrematina*, and *Auriculostoma* possess muscular papillae associated with the oral sucker, which led Sewell Hopkins (1934) to coin the term "papillose allocreadiids." This concept, of synapomorphies in the group was developed by Hopkins (without him knowing the term synapomorphy) was modified much later by Caira (1989) who referred only to the North American forms and did not consider other allocreadiids such as species of *Creptotrema* and *Creptotrematina* occurring mainly in South American freshwater fishes, which also possess these structures. It is not known if these muscular papillae, more correctly called oral lobes, are homologous in all allocreadiids, since oral lobes are also found in other unrelated genera of digeneans; for example, in species of the lepocreadiid genus *Enenterum*. Furthermore, it is now widely accepted that species of the Allocreadiidae comprise forms with and without these muscular oral lobes which may show up with scanning electron microscopy (Figures 1 and 2). The currently accepted classification of the family does not consider subfamilies as a taxonomic category based on the presence or absence of these traits because they do not represent natural groups (Gibson, 1996; Caira, 1989).

Members of the Allocreadiidae include digeneans commonly found, as adults, in the digestive tract of freshwater fishes, and only 2 species (allocated in monotypic genera: *Caudouterina rhyacotritoni* and *Bunoderella metteri*) are found, respectively, in salamanders or frogs in the United States (Schell, 1964; Martin, 1966). After their description in the 1960s, these 2 species have not been reported again. The main morphological traits of allocreadiids are well described in the diagnoses of Yamaguti (1971) and Caira and Bogéa (2005), although the species and groups differ between these 2 taxonomic treatments. The reader must refer to these 2 references for a detailed taxonomic description of the family. Following is a brief morphological characterization of the Allocreadiidae.

Main Morphological Characteristics

Allocreadiids are digeneans with an elongate or oval body, lacking spines on the tegument. Eye spots, fully developed or as remnants, might be observed on the ventral surface of some species. Muscular oral lobes, variable in number and shape are present in some species (Figure 2).

Most species of allocreadiids possess long cecae extending to the level of the posterior testis, or to the posterior end of body; they possess 2 testes, smooth, slightly, or deeply lobated, situated in tandem, oblique, or symmetrical. The well-developed cirrus sac contains an internal seminal vesicle; they lack an external seminal vesicle. The genital pore is located anterior to the ventral sucker, immediately posterior to or at level of, intestinal bifurcation, occasionally pre-bifurcal, between the intestinal bifurcation and the pharynx. The ovary is smooth, round to pyriform, and pre-testicular. The uterus is entirely pre-testicular in most species of allocreadiids (Figure 3), but in some species, uterine coils can extend to the posterior extremity of the body. The eggs are variable in size and number, and they lack spines or filaments. The vitelline follicles are located in the lateral fields of the body, and their

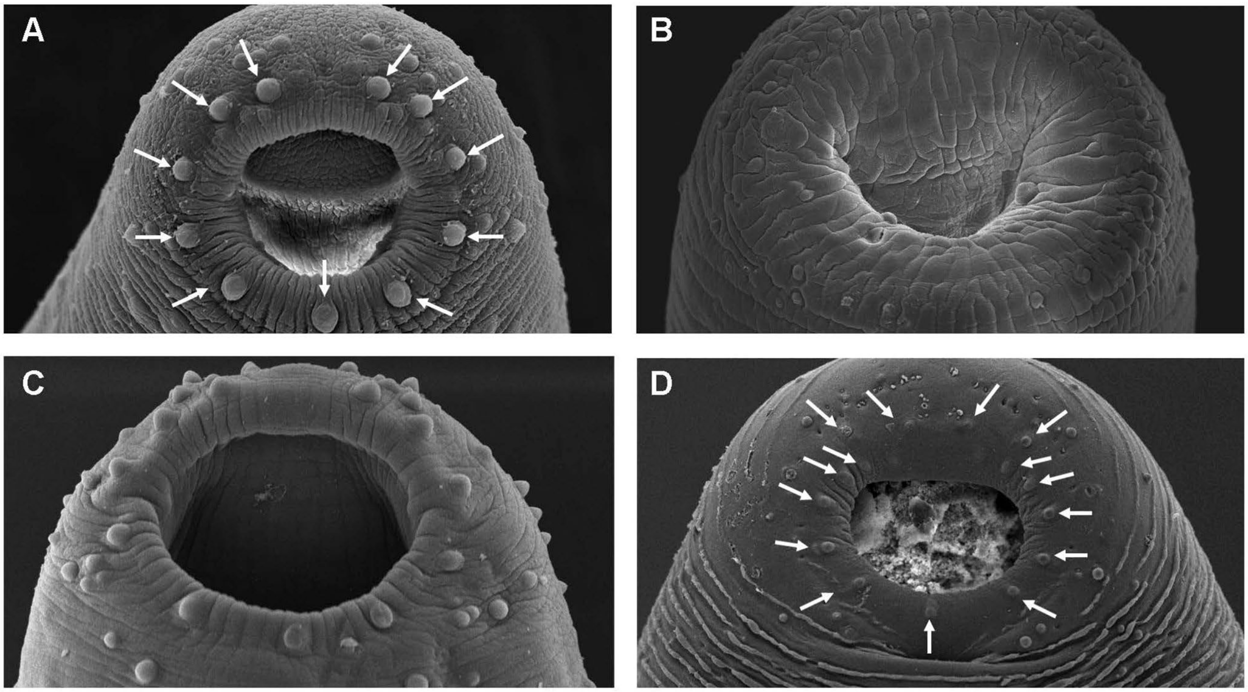


Figure 1. Scanning electron microscopy microphotographs of 4 species of allocreadiids lacking muscular oral lobes on the oral sucker. A) *Margotrema resolanae* from *Xenotaenia resolanae*. Note the arrows pointing to 15 dome-like papillae; B) *Wallinia mexicana* from *Astyanax mexicanus*; C) *Pseudoparacreptotrema macroacetabulata*; D) *Allocreadium isoporum* from *Capoeta* sp. Note the arrows pointing to 11 well-developed dome-like papillae. Sources: A) Adapted from Aydogdu et al., 2018. B) G. Pérez-Ponce de León, D. I. Hernández-Mena, and B. Solórzano-García. C) Adapted from Pérez-Ponce de León et al., 2016. D) Adapted from Pérez-Ponce de León et al., 2013. License for all: CC BY-NC-SA 4.0.

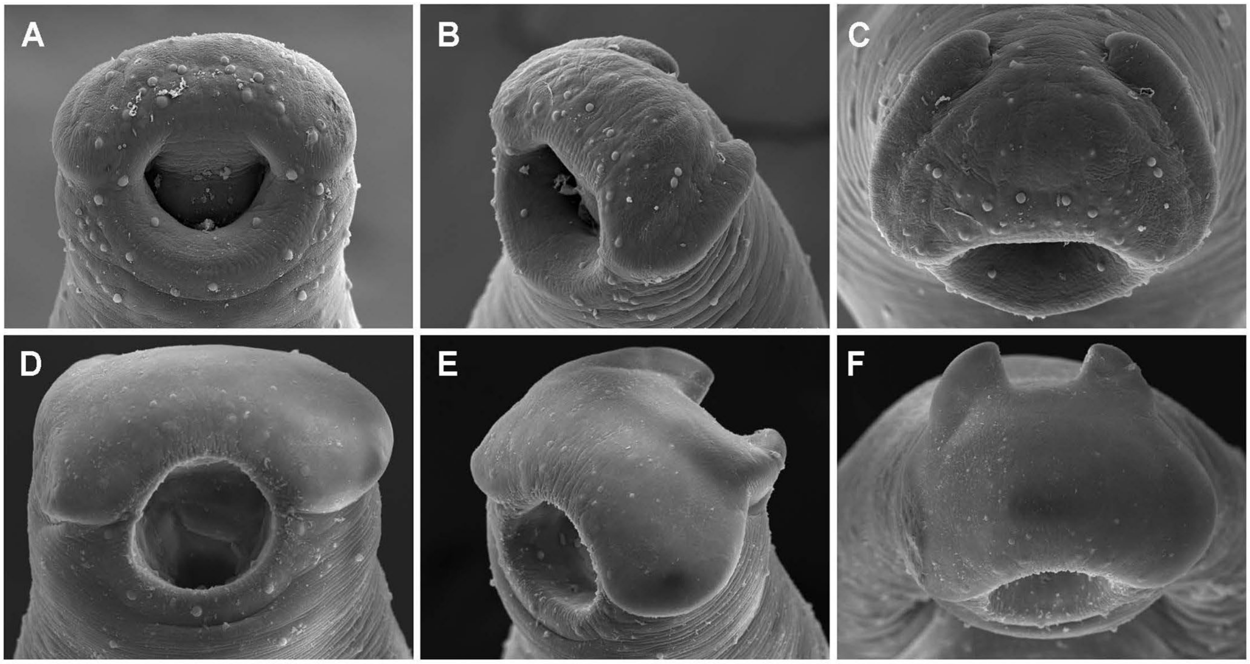


Figure 2. Scanning electron microscopy microphotographs of 2 species of allocreadiids possessing muscular oral lobes on the oral sucker (frontal, lateral, and anterior views); A–C) *Auriculostoma totonacapenensis* from *Astyanax mexicanus*; D–F) *A. lobata* from *Brycon guatemalensis*. Sources: A–C) Adapted from Razo-Mendivil et al., 2014; D–F) Adapted from Hernández-Mena et al., 2014. License for all: CC BY-NC-SA 4.0.

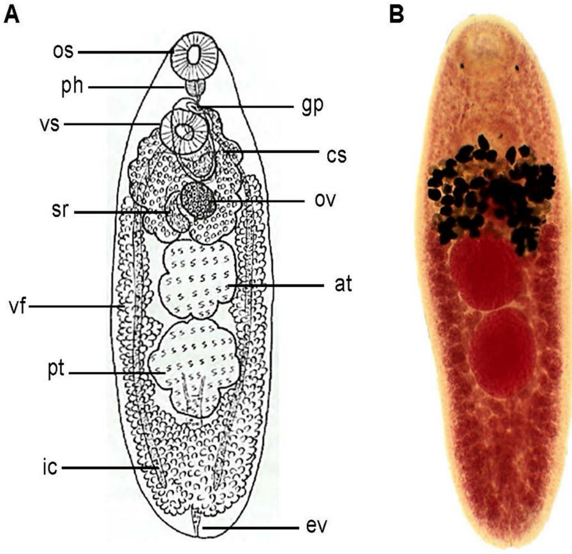


Figure 3. *Allocreadium lobatum*, ventral view. A). Line drawing; B) Microphotograph of a stained specimen from *Semotilus atromaculatus*. Note the pretesticular position of the uterus (eggs hydrated), and the eye spots on the posterior border of the oral sucker. Sources: A) Adapted from Hoffman, 1999; B) A. Choudhury. License: CC BY-NC-SA 4.0.

distribution is variable, sometimes extending the full length of the body, or sometimes being restricted anteriorly by the ventral sucker or posteriorly by the testes. The excretory vesicle is I-shaped. The type genus of the family is *Allocreadium*, with around 70 species described worldwide associated mainly with cyprinid fishes.

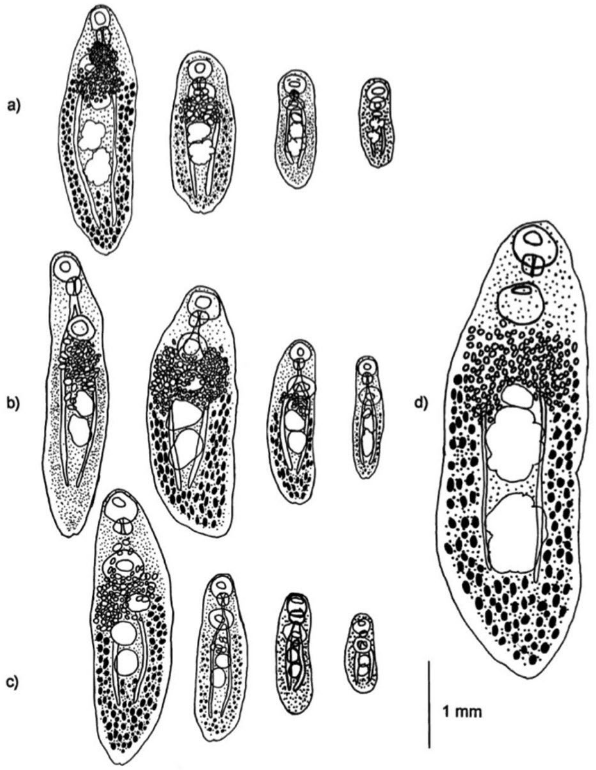


Figure 4. Morphological types in descending size classes of *Allocreadium lobatum*: a) lobate; b) asymmetrical; c) round; and d) syntype. Sources: Willis, 2002: a) Left to right, HWML slides 35119 (37-5), 35119 (37-4), 35117 (24-3), 35120 (53-8); b) Left to right, slides 35126 (79-2), 35114 (1-10), 35127 (84-2), 35139 (139-3); c) Left to right, slides 35117 (20-1), 35139 (140-1), 35117 (21-13), 35139 (151-7); d) slide 35114 (1-5). License: CC BY-NC-SA 4.0.

Morphological Variability

Some species of allocreadiids exhibit a wide geographical and host range, and some are endemic to certain localities and/or host species. This has led to the recognition of polymorphic species in this group. For example, one of the North American species, *Allocreadium lobatum*, was originally described by Wallin (1909) as a parasite of the fallfish *Semotilus corporalis* (Cyprinidae) at Sebago Lake, Maine, United States. In the original description, the presence of lobed testes was the diagnostic character that differentiated it from the European species, *A. isoporum* (the type species of the genus, commonly found in cyprinids). Willis (2002) studied 636 individuals of *A. lobatum* from the creek chub, *S. atromaculatus* collected in Nebraska, United States, and demonstrated that the shape of the testes in this digenean lies in a continuum from round to lobate and represents intraspecific morphological variation (Figure 4). Not only did Willis (2002) demonstrate the intraspecific variability of this morphological trait, he also discussed 3 possible reasons for this morphological variation in the testes including: Differences in mounting technique, species polymorphism, and the possible existence of new species. Because of this polymorphism, it is important to note that when workers identify specimens of *Allocreadium* from North America, the presence of lobated testes may or may not be diagnostic to the level of the species. Thus far, only 2 species are considered valid as parasites of freshwater fishes (Choudhury et al., 2016). *Allocreadium lobatum* is widely distributed throughout at least 12 states of the United States, and in 3 provinces of Canada (McDonald and Margolis, 1995; Hoffman, 1999; McAllister et al., 2014). The other species, *A. lucyae*, has only been recorded from cyprinids in Alabama, United States (Williams and Dyer, 1992; Hoffman, 1999).

Life Cycle

The life cycles of several species of allocreadiids included in the genera *Allocreadium, Crepidostomum, Bunoderella*, and *Bunodera* have been elucidated either by looking at the

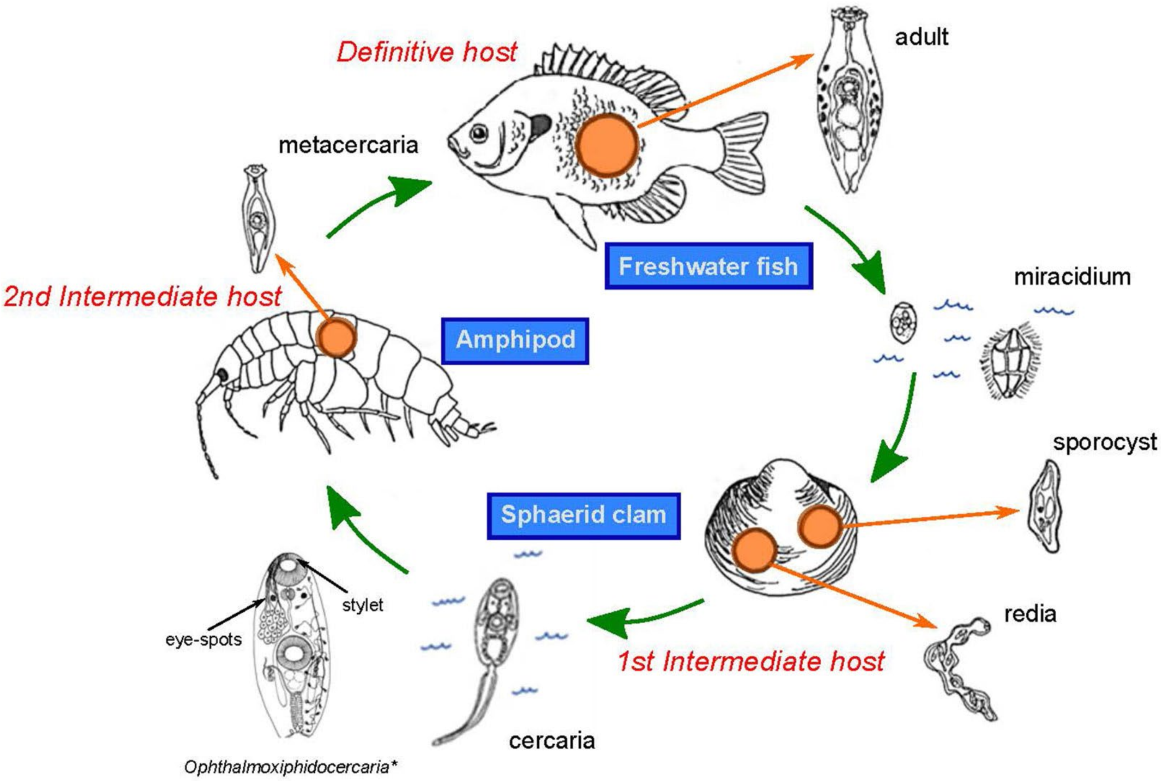


Figure 5. Generalized 3-host life cycle of an allocreadiid trematode. Sources: Adapted from Caira, 1989; Niewiadomska and Valtonen, 2007. License: CC BY-NC-SA 4.0.

natural infections of intermediate and definitive hosts or through experiments (see Yamaguti, 1975; Caira, 1989 and references therein). The general life cycle pattern for allocreadiids involves 3 hosts (Figure 5). The first intermediate host is usually a clam of the family Sphaeridae where the free-living miracidium penetrates to form either a sporocyst or a redia, or in some cases both. In some species, lymnaeid gastropods are the first intermediate host, as in *Crepidostomum metoecus* (see Awachie, 1968). Cercariae are characterized by having eye spots and a stylet, and because of that they are known as ophthalmoxiphidocercariae. They are released into the mantle cavity of the clams. Free-swimming cercariae exit the clam, search for, and penetrate the second intermediate hosts, usually an aquatic arthropod, where the cercariae loses their tails, encyst, and develop into a metacercariae. The definitive hosts, which are freshwater fishes, and in a few cases amphibians, are infected when they feed on infected arthropods; the metacercariae excyst in the digestive tract of the definitive host and the adult forms develop in the intestine. In some cases, the life cycle is truncated and the metacercariae reach maturity in the second intermediate hosts through a process known as progenesis. This phenomenon has been documented at least in 4 species of allocreadiids (Bray et al., 2012), 3 of *Allocreadium*, and 1 of *Crepidostomum* in which progenesis occurs in either crustaceans (decapods or amphipods) or in insects (coleopterans or ephemeropterans) (Lefebvre and Poulin, 2005).

The life cycles of 3 species of *Allocreadium* are relatively well-known, including that of the type species of the genus, *A. isoporum*, and also for those of both *A. lobatum* and *A. alloneotenicum* (see Yamaguti, 1975; Bray et al., 2012). In case of the type species, the mollusc acts as both the first and second intermediate host. The rediae develop in clams (*Sphaerium rivicola*), as the first intermediate host. Cercariae are released from the clam and encyst on the same clam where they develop into metacercariae. Cyprinids are infected when they feed on clams, and the adults develop in the intestine. In the life cycle of *A. lobatum*, commonly found in cyprinids in the United States and Canada, species of clams in the genus *Pisidium* act as the first intermediate host; in this case, cercariae are released from the clam into the water (DeGiusti, 1962). The second intermediate hosts are amphipods and isopods (see McAllister et al., 2014 and references therein). Fish are infected when they feed on these crustaceans (Yamaguti, 1975). The adults of *A. lobatum* also may develop progenetically in the haemocoel of amphipods (*Gammarus pseudolimneus* and *Crangonyx gracilis*).

Population Biology

The ecology of some species of allocreadiids has been studied to a certain extent in freshwater systems of the United States and Europe, particularly those of *Allocreadium* and *Crepidostomum*. For example, in Europe, the population dynamics of *A. isoporum* was studied by Moravec (1992), and more recently by Koyun and colleagues (2016) and Aydogdu and colleagues (2018). In the Danube River basin, the most important definitive host is the chub, *Leuciscus cephalus*, where *A. isoporum* exhibits a seasonal cycle of maturation characterized by quantitative changes in the abundance of young to mature worms having eggs in the uterus throughout the year (Moravec, 1992). This pattern is determined by ecological factors such as the temperature fluctuations in the locality. Aydogdu and colleagues (2018) discovered a seasonal dynamic throughout the year, when looking at the presence of *A. isoporum* in several species of cyprinids (*Capoeta* spp.) in Turkey, and found that the prevalence of infection varied with respect to host size and sex; prevalence was higher in males than females. In this case, changes in food composition and different biological characteristics between the sex of the hosts explains the difference (Koyun et al., 2016). In North America, the population dynamics of *A. lobatum* in the creek chub, *Semotilus atromaculatus,* was studied by several authors, for example, Camp (1989) and Willis (2001). In these studies, seasonal changes in the prevalence and/or mean intensity were reported in association with changes in parasite maturity. However, Willis (2001) reported seasonal changes in prevalence but not mean intensity of *A. lobatum*; the opposite pattern was found by Camp (1992). Also, an increase of mean intensity of *A. lobatum* as a function of host size was described. These studies demonstrate the complexity and diverse patterns in the population biology of allocreadiids, not only among species of the same genus, but also among populations within species. The population dynamics of some species of *Crepidostomum* have also been studied in Europe and North America, for example, *C. metoecus* and *C. farionis* in salmonids of north Wales (Awachie, 1968), *C. cooperi* in their second intermediate hosts, the burrowing mayfly, *Hexegenia limbata* in Michigan, United States (Esch et al., 1986), and *Crepidostomum* spp. in *Hexagenia* spp. in the Great Lakes in the United States and Canada (Scholoesser, 2005).

Phylogenetic Relationships

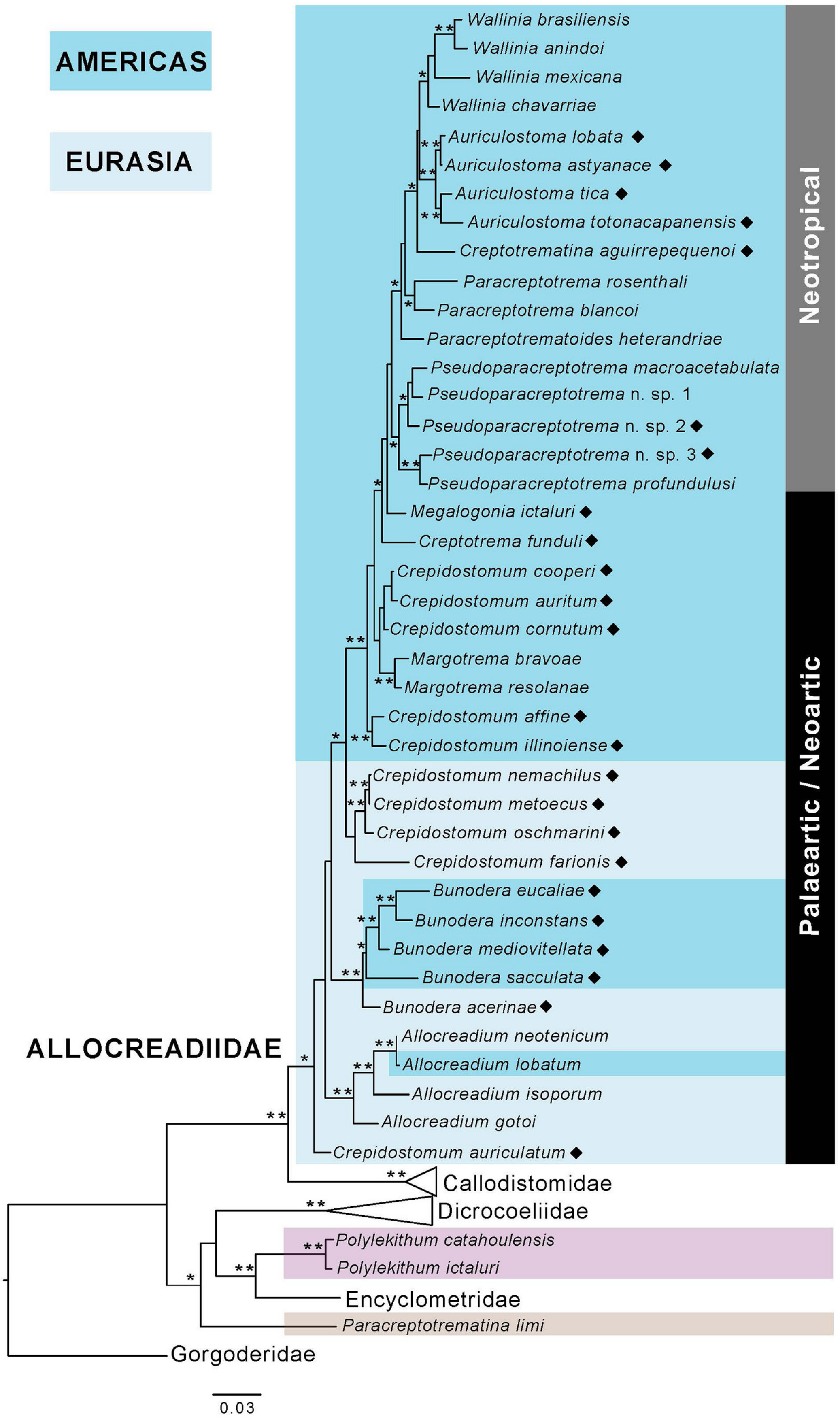
A taxonomic assessment of the family Allocreadiidae was conducted by Caira and Bogéa (2005). A cladistics analysis using morphological characters was conducted earlier by Caira (1989) and Caira and Bogéa (2005). Morphology was not very useful to assess the interrelationships among members of the family, since unresolved polytomies were recovered after the parsimony analyses. Significant progress has been made on the evolutionary history, classification, and historical biogeography of this group of digeneans. Molecular tools and scanning electron microscopy have provided useful information to expand the knowledge about the family. For the purposes of contributing data to this chapter of the textbook, the authors conducted a new molecular phylogenetic analysis of the Allocreadiidae based on 28S rDNA sequences; 1 representative sequence of each allocreadiid species allocated in 12 of the 14 genera was used. The genetic library for this molecular marker in allocreadiids has increased steadily in the last decade, a tendency observed for all digeneans (Pérez-Ponce de León and Hernández-Mena, 2019). Nevertheless, no sequence data have been produced for 2 allocreadiids, *Caudouterina rhyacothritoni*, and *Bunoderella metteri*; actually, no records of these species have been published after the original descriptions were made. The new phylogenetic analysis is based on Maximum Likelihood (ML) (Figure 6). The complete alignment consists of 1,409 base pairs. ML analyses were run in RAxML version 7.0.4 (Stamatakis, 2006). The reliability of clade support was estimated through a bootstrap with 1,000 replicates.

According to the currently accepted classification scheme of the Digenea using 28S rDNA sequences (Pérez-Ponce de León and Hernández-Mena, 2019), the family Allocreadiidae belongs to the superfamily Gorgoderoidea, within the suborder Xiphidiata, in the order Plagiorchiida. Figure 6 depicts the interrelationships among allocreadiids and other members of the Xiphidiata, some of them used as outgroups for rooting the tree. The Allocreadiidae is a monophyletic group, with high bootstrap support values (blue shadow in Figure 6). The sister group of allocreadiids is represented by the callodistomids, that is, the genus *Prosthenhystera*. Two groups of digeneans considered in the past to be allocreadiids, specifically, *Polylekithum* spp. and *Paracreptotrematina limi* (see Caira and Bogéa, 2005; Platta and Choudhury, 2006) are not members of the family (purple and brown shadows in Figure 6, respectively). Molecular evidence has demonstrated that both species are sister taxa to other groups of xiphidiatans (Choudhury et al., 2007; Curran et al., 2011).

Three additional facts are also evident in Figure 6 regarding the evolutionary and biogeographical history of allocreadiids.

1) A clear pattern of geographical association among members of Allocreadiidae is not observed, probably other than the clade composed by species of the genera *Wallinia, Auriculostoma, Creptotrematina, Paracreptotrema, Paracreptotrematoides*, and *Pseudoparacreptotrema*, which is distributed in

Figure 6. Phylogenetic tree of 28S rDNA sequences of members of Allocreadiidae based on Maximum Likelihood analysis. Blue shadow denotes monophyly of Allocreadiiidae. Diamond marks indicate species possessing muscular oral lobes. One asterisk refers to bootstrap support values from 70 to 90; 2 asterisks refer to bootstrap values from 90 to 100. Source: G. Pérez-Ponce de León, D. I. Hernández-Mena, and B. Solórzano-García. License: CC BY-NC-SA 4.0.



the Neotropical biogeographical region. The other species are distributed in the Nearctic or Palaearctic biogeographical regions. Species labeled with an intense blue shadow are found in the Americas and those labeled with a light blue shadow occur in Eurasia. There is no question that a former continuity occurred between North America and Eurasia, in a landmass known as Laurasia. The American parasitologist Harold W. Manter pointed out that the trematodes of fishes of these continents were related and he used the allocreadiid genus *Crepidostomum* as one of the examples of such connection (Manter, 1963). *Crepidostomum farionis* occurs widely in both North America and Eurasia. This is the result of an ancient connection and the breakup of Pangaea into northern and southern landmasses, namely Laurasia and Gondwana. North America separated from Europe and later became closer to northeast Asia (see Choudhury et al., 2016 and references therein).

Allocreadium is by far the most speciose genus of allocreadiids. Their species are distributed worldwide except Australia and the species distribution pattern might also be the result of the breakup of Pangaea, following the diversification and dispersal of their main host group, represented by cyprinids. Also, according to Manter, species of *Allocreadium* are predominately parasites of cyprinids but adaptable to several other species of hosts, and he hypothesized that the genus may have followed cyprinids from an Asiatic origin to Europe, North America, and a few into Africa; however, no phylogenetic evidence is currently available to test such a hypothesis, mainly because very few representative species of the genus *Allocreadium* have been sequenced thus far (Figure 6).

2) As seen in Figure 6, even though allocreadiids tend to be very host specific and many of them are part of the biogeographical core fauna of their hosts (see Pérez-Ponce de León and Choudhury, 2005), an overall host association pattern is not evident. Most of the Neotropical species are found either in characiforms or siluriforms, with some species infecting cyprinodontiforms. These groups are highly diverse components of the Neotropical freshwater fish fauna.

3) From the data presented in Figure 6 relative to the presence or absence of muscular lobes on the oral sucker, the molecular phylogenetic tree of allocreadiids corroborates the fact that the species possessing these structures do not form a monophyletic group, and the presence of oral lobes arose several times during the evolutionary history of the family (see the diamond-shaped symbols in Figure 6). A formal test of this hypothesis is required through a comprehensive analysis of xiphidiatan digeneans to determine if the lack of oral lobes is the plesiomorphic condition.

Species Diversity among the Allocreadiidae

Caira and Bogéa (2005) recognized 15 valid genera within the family and presented an identification key to recognize them. Later on, of the 15 genera, 3 were synonymized with *Bunodera*, that is, *Bunoderina* (as *Bunodera eucaliae*), *Allobunodera* (as *Bunodera mediovitellata*), and *Culeatrema* (as *Bunodera inconstans*). Furthermore, the genus *Pseudoallocreadium* was synonymized with *Allocreadium*, as *A. neotenicum* and *A. alloneotenicum*. Finally, molecular evidence demonstrated that 2 genera, *Paracreptotrematina* and *Polylekithum,* do not belong to Allocreadiidae (see Curran et al., 2006; 2011; Platta and Choudhury, 2006; Choudhury et al., 2007).

The current classification of the Allocreadiidae includes 14 genera and approximately 130 species. Twelve of these genera for which 28S rDNA sequences have been generated are depicted in Figure 6. No sequences are available for *Caudouterina* and *Bunoderella*, both amphibian allocreadiids. *Allocreadium* is the richest genus, with approximately 71 species. The other genera include between 1 and about 24 species, and 3 genera are monotypic. An account of the species richness and geographical location of species of Allocreadiiidae is presented below in alphabetical order. Representative species of some of the genera are shown in Figure 7(A–F).

***Allocreadium* Looss, 1900**

***Allocreadium isoporum* (Looss, 1894) Looss, 1900; type host; Cyprinidae; Europe**

Species of this genus are mainly found in cyprinids around the world, with isolated records in other fish families. The list of congeneric species validated in the synopsis of Yamaguti (1971) includes 25 species. At least 21 species were described after that; however, according to Decock and colleagues (2020), the genus contains over 70 described species, although that list does not include several additional species, including, *Allocreadium alloneotenicum* from trichopterans in the United States and Canada, *A. lucyae* from cyprinids in the United States, and *A. mexicanum* from atherinopsids and goodeids in central Mexico (although the authors have gathered molecular evidence showing that this species does not belong in *Allocreadium*); and 4 species from cyprinids in Japan: *A. aburahaya*, *A. brevitellatum A. tosai*, and *A. tribolodontis* (see Margolis and Arthur, 1979; McDonald and Margolis, 1995; Hoffman, 1999; Shimazu et al., 2016a; Ostrowski de Nuñez et al., 2017; Kudlai et al., 2018, among others). Another congeneric species is *A. danjiangensis*, described from 5 species of cyprinid fishes in China (Gao, 2018).

The species composition in the genus is clearly in need of revision. The list of species of *Allocreadium* includes those

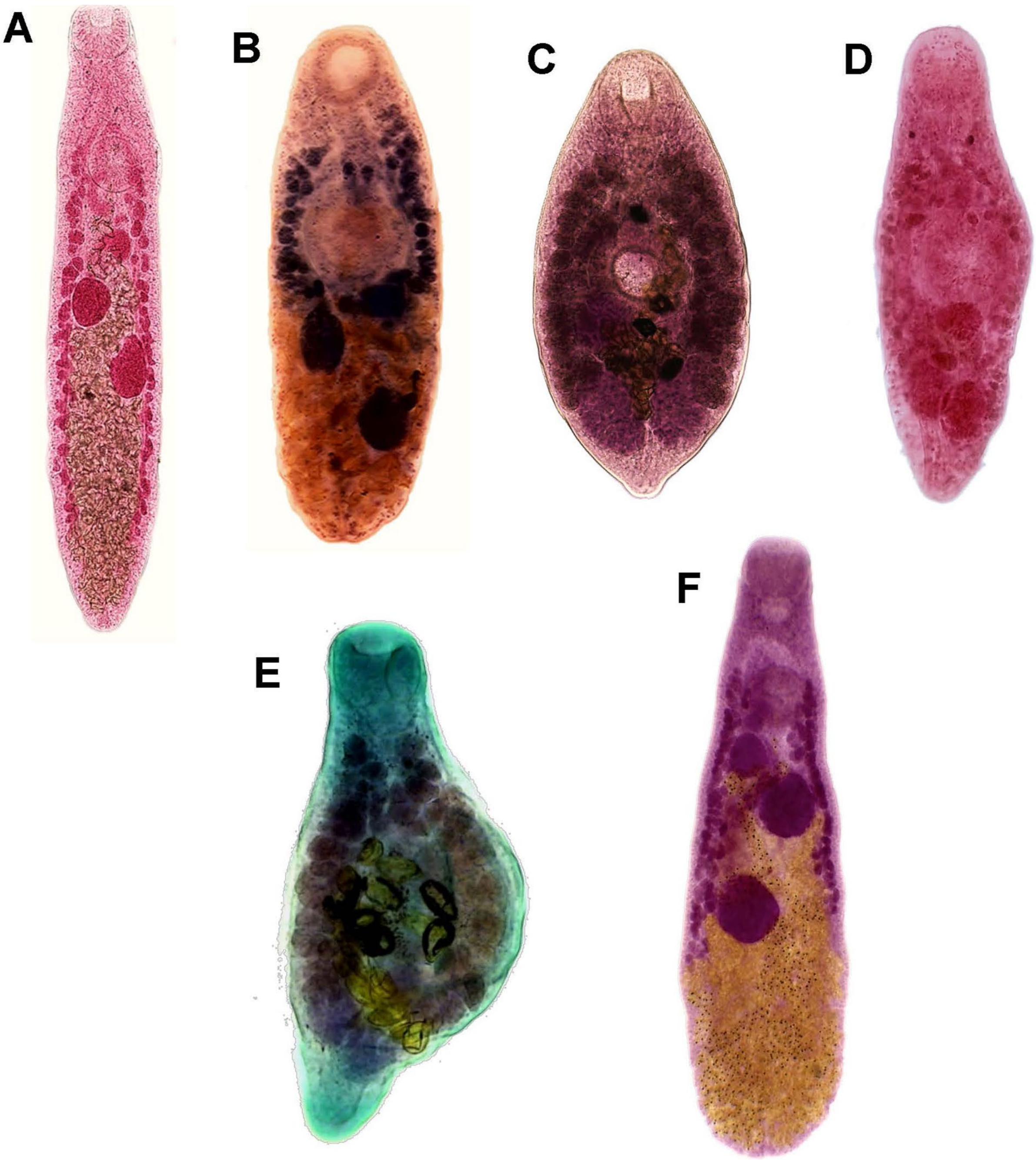


Figure 7. Microphotographs of stained specimens of allocreadiids representing some of the genera in the family. A) *Creptotrematina aguirrepequenoi,* B) *Margotrema resolanae,* C) *Paracreptotrema blancoi,* D) *Paracreptotrematoides heterandriae,* E) *Pseudoparacreptotrema magacetabulata,* F) *Wallinia anindoi*. Source: G. Pérez-Ponce de León, D. I. Hernández-Mena, and B. Solórzano-García. License: CC BY-NC-SA 4.0.

from North America, South America, Europe, Russia, China, Japan, and Africa. Even though the genus is recognized as Palearctic, 2 species have been reported from South America in non-cyprinid hosts (Ostrowski de Nuñez et al., 2017), and 7 from Africa, with most records in cyprinids and some in characiforms and siluriforms (Kudlai et al., 2018).

***Auriculostoma* Scholz et al., 2004**

***Auriculostoma astyanace* Scholz et al., 2004; type host; Characidae (*Astyanax* sp.); Nicaragua**

The genus contains 9 species; 5 of these are found in South America, including *Auriculostoma macrorchis* from perciforms and siluriforms in Argentina, *A. platense* from siluriforms and gymnotiforms in Argentina and Brazil, *A. stenopteri* from Characidae in Uruguay, *A. diagonale* and *A. foliaceum* from Characidae in Peru, *A. astyanace* from Characidae in Nicaragua, *A. totonacapanensis* and *A. lobata* from Characidae in Mexico, and *A. tica* from Gymnotidae in Costa Rica (Scholz et al., 2004; Kohn et al., 2007; Curran et al., 2011; Razo-Mendivil et al., 2014; Hernández-Mena et al., 2016; 2019; Ostrowski de Nuñez et al., 2017).

***Bunodera* Railliet, 1896**

***Bunodera luciopercae* (Müller, 1776) Lühe, 1909; type host; Percidae; Holarctic**

Seven species comprise the genus *Bunodera*: *B. acerinae* in percids in Russia, *B. eucaliae* and *B. inconstans* in freshwater sticklebacks in the United States and Canada, *B. luciopercae* in percids in the Holarctic, *B. mediovitellata* in the three-spine stickleback and *Gasterosteus aculeatus* in the Holarctic, *B. sacculata*, an endemic North American species found in percids, and *B. vytautasi* in gasterosteids (*Pungitius pungitius*) in northeast Asia (McDonald and Margolis, 1995; Hoffman, 1999; Petkevičiūtė et al., 2010; Atopkin et al., 2018).

***Bunoderella* Schell, 1964**

***Bunoderella metteri* (Schell, 1964); type species; tailed frog *Ascaphus truei*; United States**

The genus is monotypic. The only known species is *Bunoderella metteri*, from tailed frogs in Idaho and Washington, United States. The species is characterized by having 2 anterodorsal and 2 ventrolateral muscular oral lobes. No additional records have been published after the original description.

***Caudouterina* Martin, 1966**

***Caudouterina rhyacotritoni* Martin, 1966; type species; Olympic salamander *Rhyacotriton olympicus*; United States**

The genus is monotypic. The only described species is *Caudouterina rhyacotritoni* from the Olympic salamander in Oregon, United States. The species lacks muscular oral lobes and possesses a uterus that reaches the posterior end of the body. No additional records have been published after the original description.

***Crepidostomum* Braun, 1900**

***Crepidostomum metoecus* (Braun, 1900); type species; Salmonidae (brown trout) and occasionally in other fish families; Palearctic**

The genus *Crepidostomum* has a rather complex taxonomic history. According to Atopkin and Shedko (2014), the genus contains 40 nominal and 24 valid species. However, many species have been synonymized and there is not a current revision of the species composition in the genus (see Hoffman, 1999). Figure 6 corroborates that the genus is not monophyletic and requires detailed taxonomic revision based on phylogenetic analysis. In this chapter, 16 species are recognized, some of which have molecular data available, namely, *Crepidostomum affine* from the mooneye, *Hiodon tergisus* in the United States; *C. auritum* from the freshwater drum, *Aplodinotus grunniens* in the United States; *C. auriculatum* from sturgeons, *Accipenser schrenki* and *Huso dauricus* in the Holarctic; *C. bailcalense* from several fish families in Eurasia; *C. brevivitellatum* from *Anguilla rostrata* in Canada; *C. chaenogobii* from gobiids and cottids in Japan and the Russian Far East; *C. cooperi* from centrarchiids in North America; *C. cornutum* from centrarchiids in North America; *C. farionis* from various fish families in the Holarctic; *C. illinoiense* from hiodontids in the United States; *C. isostomum* from several fish families in the United States; *C. latum*, in several fish families in Europe; *C. metoecus* from salmonids in the Palearctic; *C. opeongoensis* from *Hiodon* spp. in Canada; *C. oshmarini* in Balitoridae and Cottidae in Europe; *C. percopsisi* from the trout perch, *Percopsis omiscomaycusi* in Canada; *C. wikgreni* in several fish families in Europe (Nelson et al., 1997; Hoffman, 1999; Choudhury and Nelson, 2000; Moravec, 2002; Tkach et al., 2013; Atopkin and Shedko, 2014; Shimazu, 2016b; Petkevičiūtė et al., 2018).

***Creptotrema* Travassos et al. 1928**

***Creptotrema creptotrema* Travassos et al. 1928; Characiformes and Siluriformes; Brazil, Argentina**

The genus contains 8 nominal species, 6 of them distributed in South American characiforms or siluriforms, that is, *Creptotrema creptotrema, C. lynchi, C. paranaensis, C. pati, C. sucumbiosa,* and *C. lamothei*; and in Central America, in mountain mullets, *C. agonostomi,* and 1 in fundulids of the United States, *C. funduli* (Kohn et al., 2007; Curran, 2008; Curran et al., 2012). Another species (yet undescribed) was recorded in pimelodid catfishes in Panama (Choudhury et al., 2017). Furthermore, another study demonstrates that the genus *Creptotrema*, as currently defined, is not monophyletic. *Creptotrema agonostomi,* and 3 genetic lineages corresponding to independent species, all from the Central American mountain mullets, *Dajaus monticola*, belong to the genus *Pseudoparacreptotrema* (see Figure 6). A new genus will be required to accommodate *C. funduli*.

***Creptotrematina* Yamaguti, 1954** (Figure 7A)

***Creptotrematina dissimilis* (Freitas, 1941) Yamaguti, 1954; type species; Characidae; Brazil, Argentina**

The species in this genus were originally placed in *Creptotrema*, but Yamaguti (1954) erected the genus *Creptotrematina.* It currently contains only 3 species: *C. dispar* and *C. dissimilis* in Characidae from Argentina and Brazil, and *C. aguirrepequenoi* from *Astyanax* spp. in Central America (Kohn et al., 2007; Curran et al., 2011; Razo-Mendivil et al., 2014; Ostrowski de Nuñez et al., 2017).

***Margotrema* Lamothe-Argumedo, 1970** (Figure 7B)

***Margotrema bravoae* Lamothe, 1970; type species; Goodeidae; central Mexico**

The genus belongs to Allocreadiidae (Pérez-Ponce de León et al., 2007), and contains only 2 species, the type species and *Margotrema resolanae* from the leopard splitfin, *Xenotaenia resolanae* (Goodeidae), in west-central Mexico (Pérez-Ponce de León et al., 2013).

***Paracreptotrema* Choudhury et al., 2006** (Figure 7C)

***Paracreptotrema mendezi* (Sogandares-Bernal, 1955) Choudhury et al., 2006; type species; Poeciliidae; Panama**

The genus *Paracreptotrema* includes 3 species, all of them found in Central American poeciliids: *P. blancoi* from *Priapichthys annectens* in Costa Rica, *Paracreptotrema mendezi* from *Brachyrhaphis episcopi* in Panama, and *P. rosenthali* from *Xiphophorus malinche* and *Pseudoxiphophorus jonesii* in Mexico (Choudhury et al., 2006; Bautista-Hernández et al., 2015; Pérez-Ponce de León et al., 2016).

***Paracreptotrematoides* Pérez-Ponce de León et al., 2016** (Figure 7D)

***Paracreptotrematoides heterandriae* (Salgado-Maldonado et al., 2012) Pérez-Ponce de León et al., 2016; type species; *Pseudoxiphophorus bimaculatus* (Poeciliidae); Mexico**

The genus is monotypic. The only species described in the genus is *Paracreptotrematoides heterandriae*, from the twospot livebearer *Pseudoxiphophorus maculatus* in Veracruz, Mexico. No additional records have been published after the original description.

***Pseudoparacreptotrema* Pérez-Ponce de León et al., 2016** (Figure 7E)

***Pseudoparacreptotrema profundulusi* (Salgado-Maldonado et al., 2012)**

The genus includes 2 nominal species, *Pseudoparacreptotrema macroacetabulata* from the killifish *Profundulus candalarius* in Chiapas, Mexico, and *Pseudoparacreptotrema profundulusi* from the killifish *Profundulus punctatus, Pr. balsanus*, and *Pr. oaxacae* from Oaxaca and Guerrero, Mexico (Pérez-Ponce de León et al., 2016). Newly gathered molecular data allowed the authors to determine that *"Creptotrema" agonostomi* from the mountain mullet, *Dajaus monticola* in Mexico actually belongs in *Pseudoparacreptotrema*. The same dataset led to the determination that 3 additional species of the genus had to be described as parasites of mountain mullets in localities of Central America (Pérez-Ponce de León et al., 2020).

***Wallinia* Pearse, 1920** (Figure 7F)

***Wallinia valenciae* Pearse, 1920; type species; *Geophyrocharax valenciae* (Characidae); Venezuela**

The genus *Wallinia* has 5 valid species: The type species from characids in Venezuela; *W. chavarriae* from *Bryconamericanus scleroparius* and *Astyanax aeneus* (Characidae) in Costa Rica, *W. mexicana* from *Astyanax mexicanus* in Mexico, *W. brasiliensis* from 2 species of *Astyanax* in Brazil, and *W. anindoi* from *A. aeneus* in Mexico (Choudhury et al., 2002; Pérez-Ponce de León et al., 2015; Dias et al., 2018; Hernández-Mena et al., 2019).

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Supplemental Reading

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