



Review of the parasitic nematodes of marine fishes from off the American continent

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Review Article

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Cite this article: Pereira FB, González-Solís D (2022). Review of the parasitic nematodes of marine fishes from off the American continent. *Parasitology* **149**, 1928–1941. <https://doi.org/10.1017/S0031182022001287>

Received: 1 August 2022
Revised: 29 August 2022
Accepted: 31 August 2022
First published online: 9 September 2022

Key words:

America; Chondrichthyes; marine ecoregions; Nematoda; Osteichthyes; parasites; parasitological survey; systematics; taxonomy

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Abstract

The ichthyofauna of the Atlantic and Pacific coasts off the American continent is very rich. Consequently, a high biodiversity of nematodes parasitizing these vertebrates is also expected. Currently, data on nematode parasites of marine fish off the Americas are fragmented. A review of all adult nematode species reported parasitizing marine fish from off the American continent is herein presented, as well as comments on their patterns of diversity, life cycles and advances in the taxonomic and phylogenetic knowledge. A total of 209 valid species, 19 *species inquirendae* and 6 dubious records have been recorded, the majority from the fish taxa Eupercaria and Perciformes. The families Sciaenidae, Serranidae and Lutjanidae, as well as the tropical and temperate Atlantic waters, exhibited the highest records of parasitic nematodes. The Cucullanidae, Philometridae and Cystidicolidae were the most speciose families of nematodes, which may be related to technological advances and relatively recent efforts of taxonomists, resulting in description of new taxa and the resolution of taxonomic problems. Numerous taxonomic questions still need resolution and, even though genetic data have been important for this process, the database is very scarce. This is the first review on all currently known nematode species parasitizing marine fish off the Americas and may serve as an important basis of reference for future approaches on these organisms.

Introduction

The Nematoda is a diverse phylum of worm-like, free-living or parasitic animals that plays an important role in the decomposition process and recycling of nutrients in the aquatic environment (free-living forms) to the extent that it may influence host population dynamics (parasitic forms). This is considered the fifth most diverse phylum of metazoans, behind the Arthropoda, Mollusca, Craniata and Platyhelminthes (Hodda, 2022a, 2022b). Currently, almost 30 000 species of nematodes have been recognized as valid, but, according to the minimum estimate, the real number of species is around 500 000, half of which are represented by parasites (Hodda, 2022a, 2022b). This overwhelming diversity has represented a real challenge for better understanding these parasites, especially regarding their taxonomy and systematics that represent the basis for investigation of more complex questions related, for example, to life cycles, pathology and other host–parasite interactions (Moravec, 1998; Padiál *et al.*, 2010).

In aquatic environments, parasitic nematodes can be found within several different trophic levels, representing foodweb links (Anderson, 2000; Lafferty *et al.*, 2008; Lafferty, 2013). In this sense, fish can act as paratenic, intermediate or definitive hosts for nematodes (Anderson, 2000), in which certain taxa of parasites, especially from marine environment, are important as zoonotic agents or causative of serious fish diseases resulting in considerable losses and problems for the seafood, fishing and fishery industries (Moravec and de Buron, 2013; Shamsi and Suthar, 2016; Mattiucci *et al.*, 2018). This reinforces the importance of these organisms by their ecological, economic and health implications in addition to their high biodiversity potential.

Since the first mention of nematode parasites of fish from American waters by Rudolphi (1819), it is possible to visualize 2 clear scenarios: firstly, these are still neglected organisms (Scholz and Choudhury, 2014; Luque *et al.*, 2017), and secondly, there are imbalances on the study efforts carried out on freshwater compared with marine environments, depending on the geographic area. For example, in South America, the number of studies including nematode parasites of freshwater fish is much higher than those marine (Luque *et al.*, 2017). An opposite situation is observed in Canada, where studies on nematodes from marine fish are more numerous (Arai and Smith, 2016).

One of the best sources of assistance for estimating biodiversity patterns of a group are checklists with accurate taxonomic data and, in case of parasites, information on host and geographic occurrence. Currently, such checklists dealing with the parasitic nematodes of fish in the American continent are scattered, geographically limited to a local scale and mixed with other metazoan groups (see McDonald and Margolis, 1995; Garrido-Olvera *et al.*, 2006; Luque *et al.*, 2011, 2016; Arai and Smith, 2016; Santos *et al.*, 2016; Lehun *et al.*, 2020; Santos-Reis *et al.*, 2021; Ramallo and Ailán-Choke, 2022). This scenario along with taxonomic problems (e.g. inadequate description and dubious diagnosis of species) hampers the understanding of

the real and general biodiversity patterns associated with nematode parasites of marine fish from the Americas, and its configurations within host and geographic gradients.

With the technological advances of genetic studies in the last 20 years, the systematics of Nematoda has changed significantly (see Blaxter *et al.*, 1998; De Ley and Blaxter, 2002, 2004; Meldal *et al.*, 2007; Anderson *et al.*, 2009). In fact, genetic approaches have been crucial for the advancement of knowledge pertaining to nematodes reported parasitizing marine fish in the American continent, such as supporting species validity, improving identification of larval forms and clarifying phylogenetic relationships (see e.g. Mejía-Madrid and Aguirre-Macedo, 2011a, 2011b; Sardella *et al.*, 2017; Roca-Geronès *et al.*, 2018; Aguilar-Aguilar *et al.*, 2019; Barton *et al.*, 2022). However, the related genetic databases still remain very scarce proportionally to the biodiversity of the group.

Based on the importance of the nematode parasites of marine fish from off the American continent previously highlighted, a review on the aspects of the diversity of these organisms is herein shown, associating it with host taxa and geographic distribution, as well as aspects of their current taxonomy, systematics and knowledge on life cycles, genetics and phylogeny.

Survey of species recorded and related data

A review of the parasitic nematodes in marine fish from off the Americas (including the Caribbean Islands and Hawaii) is presented herein. Only reports of adult specimens identified to species level and occurring in hosts from marine or brackish environments were included. There are some reports of nematodes in anadromous and catadromous fishes which were excluded from the present survey, since they are nematode genera or species of freshwater origin, such as *Camallanus*, *Salmonema*, *Salvelinema* and *Truttaedacnitis*. The taxonomic classification of Hodda (2022a) was followed, although some taxonomic authorities were changed. The review was based on an extensive literary search gathered from different databases, i.e. Google Scholar, Web of Science and Biological Abstracts, and also supplemented by data from the Host-Parasite Database of the Natural History Museum, London, UK (Gibson *et al.*, 2005), the World Register of Marine Species (WoRMS Editorial Board, 2022) and personal libraries. Data from the so-called 'grey literature' (theses) were excluded, since they represent unverified and/or unpublished information. GenBank was used as a source for searching of genetic data of the nematode species.

Patterns of nematode diversity associated with host taxa

Species richness was used as the indicator for evaluating diversity of the nematodes parasitizing marine fish from off the American continent. As previously stated, only those reports of nematodes identified to species were considered; consequently, most reports of larval forms were not accounted, except when molecular identification was used. For the association of nematode diversity with host taxa orders, including those recently proposed *incertae sedis*, and families of bony and cartilaginous fish were considered, according to Froese and Pauly (2022).

A total of 209 nematode species were accounted in 504 marine fish from 46 orders and 114 families. Chondrichthyan hosts were much less numerous than Osteichthyes, represented by 62 (12% of the total) species from 10 (22%) orders and 17 (15%) families. The highly diverse order Perciformes was by far the most representative with 27 (24%) families and the second was the *incertae sedis* taxon Eupercaria that included 11 families (10%), most of which were previously allocated in Perciformes (see Betancur-R *et al.*, 2017). In addition to Carcharhiniformes and

Centrarchiformes that were represented by 5 (4%) and 4 (3%) families, respectively, the remaining orders of bony and cartilaginous fish were represented by less than 3 families, most of which included only 2 or 1.

The nematode diversity followed that observed for host taxa, in which a total of 96 (45%) and 66 (31%) species were reported parasitizing the most diverse host groups, Perciformes and Eupercaria, respectively (Fig. 1A). The highest numbers of nematode species were also observed in families belonging to Eupercaria (Sciaenidae and Lutjanidae) and Perciformes (Serranidae) (Fig. 1B). Parasite diversity usually is proportional to that of their hosts (Hechinger and Lafferty, 2005; Poulin, 2014), which may be a result of numerous pathways for speciation processes. Moreover, combined with the high diversity, many species of sciaenid, lutjanid and serranid fish have commercial importance (Polovina and Ralston, 1987; Chiappone *et al.*, 2000; Claro *et al.*, 2001; Ramcharitar *et al.*, 2006), attracting interest for parasitological studies on such hosts. In this sense, other fish families including species with remarkable economic value, i.e. Carangidae, Paralichthyidae and Scombridae (Honebrink, 2000; Astarloa, 2002; Juan-Jordá *et al.*, 2016), showed nematode richness that stands out in relation to most of the others (Fig. 1B). Only 2 or 1 nematode species have been reported in the orders Chimeariformes, Hexanchiformes, Squatiniformes and Torpediniformes (all Chondrichthyes) and Acanthuriformes, Albuliformes, Cichliformes, Lampriformes, Mugiliformes, Myliobatiformes, Osmeriformes, Ovalentaria (*incertae sedis*), Syngnathiformes and Zeriformes (all Osteichthyes), as well as in several families of Perciformes (see Supplementary Material 1). These numbers do not necessarily mean that the nematode richness is indeed low in these host taxa, but most likely indicates that some of these fish can harbour larval stages and not adults considered in the present review or that parasitological studies are incipient for most of them, especially those focused on nematode taxonomy.

Currently, specific studies estimating only nematode diversity in marine fish from the American continent are inexistent. Studies that include diversity estimations normally analyse parasite community structures rather than be focused on specific parasite taxa. Moreover, there is no approach specifically relating nematode diversity with that of fish taxa in the referred region, which complicates a general and conclusive discussion regarding the subject. Almost all studies that deal with parasite diversity, including nematodes, and its relations with marine fish populations in off the Americas are restricted to 1 or few host species within a limited geographic area. The study by Luque and Poulin (2008) represents one of the few exceptions, in which authors performed a large-scale investigation on factors influencing parasite diversity in Neotropical marine fish. These authors concluded that host traits were weakly correlated with parasite species richness; however, habitat exploitation, diet and behaviour intrinsic to fish species were important for taxonomic diversity of parasites. Recently, Silva *et al.* (2022) observed similar results on parasites of clupeiform fish in South Atlantic, indicating that fish species is a strong determinant for parasite diversity, especially their diet composition and infection by endoparasites as nematodes, which are mostly transmitted by food chain links in marine environments (Lafferty, 2013). It should be highlighted that several approaches including parasite diversity estimations use parasites as biological tags for discriminating host populations from the South Atlantic and Pacific Oceans, where nematodes always show representative richness in the parasite communities (Timi, 2003; Timi *et al.*, 2005, 2010; Braicovich and Timi, 2010; Canel *et al.*, 2019; Espinola-Novelo and Oliva, 2021).

Based on the present survey, patterns of nematode diversity in marine waters of the American continent are proportional to that of their host taxa, in which Perciformes and Eupercaria that allocate highly diverse fish families support the richest nematofauna.

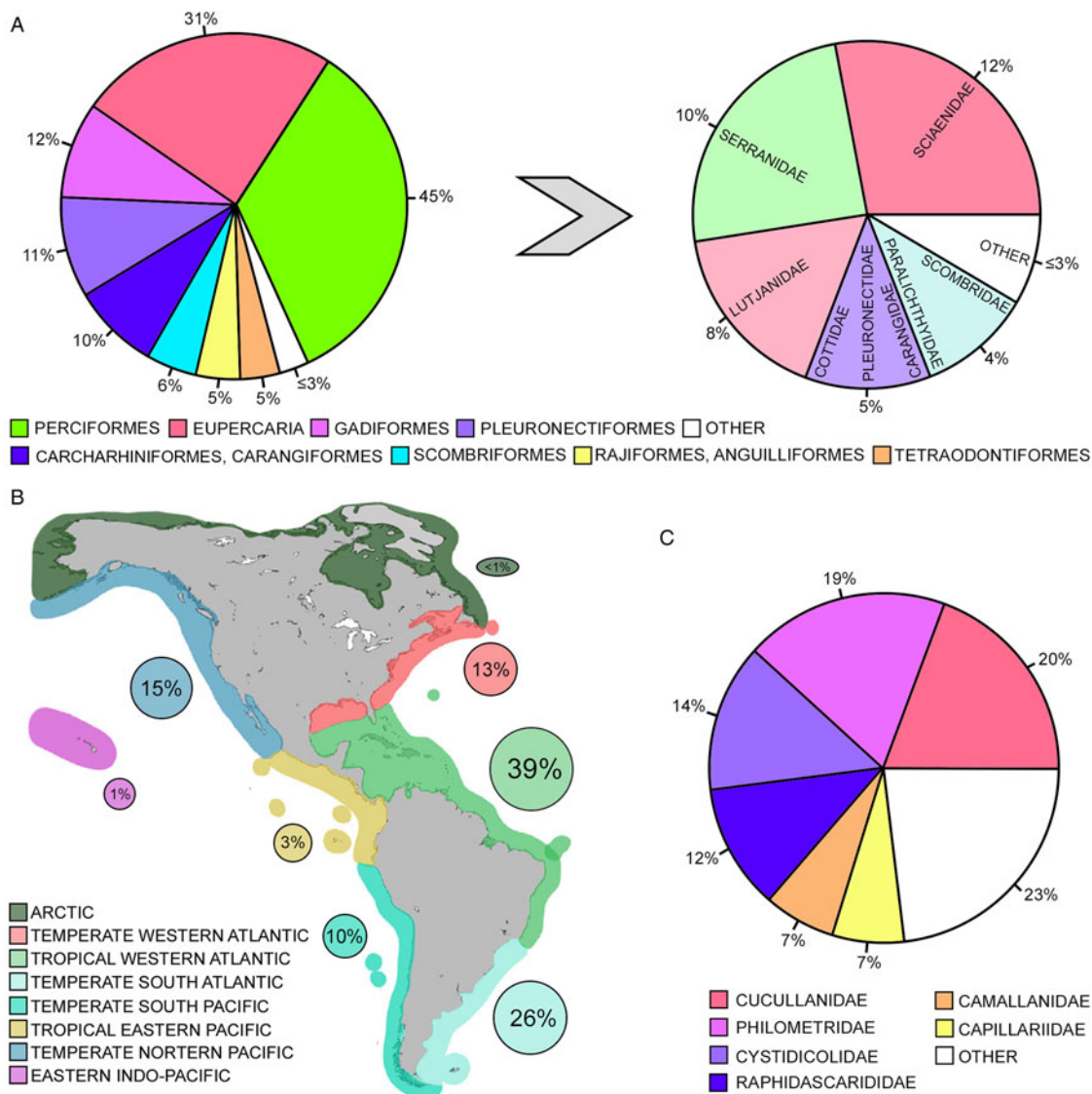


Fig. 1. Graphic representations (percentage, %) of the fish orders and families (A), marine regions (B) and nematode families (C) related to the 209 nematode parasites in marine fish of the Americas. More details regarding number of nematode species by host taxa, geographic distribution and parasite taxa are shown in Supplementary Materials 1 and 2.

It cannot be discarded that several parasitological studies including nematode parasites of marine fish in the Americas are driven by economic importance of host species (Luque *et al.*, 2017; see also the following examples Cantatore and Timi, 2015; George-Nascimento and Oliva, 2015). In this sense, a significant part of these studies is focused on larval forms of Anisakidae and Raphidascarididae due to their zoonotic potential (Siendermann, 1961; Kuhn *et al.*, 2016; Alves *et al.*, 2020; Ferreira *et al.*, 2020; Diniz *et al.*, 2022). The nematode larval forms were excluded for diversity estimations, since their identification is mostly not to species level reducing the precision of the results or making them biased. Despite the current scenario of nematode diversity among the taxa of marine fish herein observed indicates interesting trends, it is still superficial since several fish species remain unstudied for parasites and the parasite fauna of hosts from several orders and families are poorly known.

Regional patterns of nematode diversity

For analysing regional patterns of nematode diversity along the coast of the American continent, species richness was accounted by marine ecoregions according to the classification of Poore

and Bruce (2012). About 78% of the nematode species in the present survey was reported in the coast of the Atlantic Ocean vs only 29% in the Pacific. The highest percentage of species (39%) was observed in the tropical part of the Atlantic, followed by that observed in the temperate southern region of the same ocean (26%) (Fig. 1B). These Atlantic ecoregions were by far the most representative in terms of nematode species richness. The tropical and southern temperate regions of the Pacific Ocean accounted only by 3 and 10% of the nematode species, respectively (Fig. 1B). The percentages of nematode species reported in northern temperate zones of the Atlantic and Pacific were 13 and 15%, respectively (Fig. 1B). The less representative regions regarding nematode species were the Arctic and Indo-Pacific, in which 1% or less of the total richness was observed (Fig. 1B).

It has been documented that local characteristics of marine environments may be strongly related to the parasite community structure of fish, including patterns of species richness (Luque and Poulin, 2008; Merckx *et al.*, 2009; Timi *et al.*, 2010). In large scale as within latitudinal diversity gradient (LGD), the relationships between endoparasites of fish and diversity are unclear (Poulin, 1995; Rohde and Heap, 1998; Rohde, 1999; Preisser, 2019). However, for both bony and cartilaginous fish, LGD is

clear in that species richness reaches its maximum in low latitudes (i.e. intertropical zone) and decreases in high latitudes (i.e. temperate and polar zones) (Miloslavich *et al.*, 2011; Carrillo-Briceño *et al.*, 2018; Manel *et al.*, 2020). Moreover, fish diversity is higher in the Atlantic than in the Pacific coast of America (Miloslavich *et al.*, 2011; Carrillo-Briceño *et al.*, 2018; Manel *et al.*, 2020). This uneven diversity of hosts, according to oceans and marine ecoregions, most likely is the main factor responsible for the regional patterns of nematode diversity observed here, since parasite diversity tends to be accompanied by that of hosts as previously discussed (Hechinger and Lafferty, 2005; Poulin, 2014). An interesting observation is that the diversity of possible intermediate hosts for nematode parasites of marine fish, such as crustaceans and molluscs (Anderson, 2000; Lafferty, 2013), is more or less similar between the Atlantic and Pacific Oceans (Miloslavich *et al.*, 2011), reinforcing that differences on fish diversity may be important for the regional patterns of nematode diversity observed here.

Another important fact is that the most prolific research groups on parasites of marine fish in the Americas, including nematode taxonomists, are based near the Atlantic coast and, consequently, most of their studies are developed along this region, boosting the knowledge about nematode diversity. It should be highlighted that the number of nematode species described, infecting marine fish in the Atlantic coast, has been increasing considerably in the last 20 years as a result of the work of research groups mainly from Argentina (e.g. Timi and Sardella, 2002; Timi and Lanfranchi, 2006; Timi *et al.*, 2006, 2007, 2009; Rossin and Timi, 2009; Rossin *et al.*, 2012), Brazil (e.g. Santos *et al.*, 2004; Pereira *et al.*, 2012, 2013, 2014a, 2014b, 2014c; Paschoal *et al.*, 2014; Vieira *et al.*, 2015) and Mexico (e.g. González-Solis *et al.*, 2002a, 2002b, 2007a, 2007b; Gopar-Merino *et al.*, 2005; Mejía-Madrid and Pérez-Ponce de León, 2007; López-Caballero *et al.*, 2009; Mejía-Madrid and Guillén-Hernández, 2011), as well as from USA in collaboration with the renowned Czech taxonomist of nematode parasites of fish Dr František Moravec (e.g. Moravec *et al.*, 2005, 2006, 2008a, 2010, 2013, 2014, 2016, 2020, 2021). Such increase on species descriptions as a result of actuation of these research groups (see also Moravec *et al.*, 2007, 2008b, 2018) is strongly related to the results observed in Fig. 1B.

As a conclusion, regional patterns of nematode diversity in marine fish off the American continent are related to 2 main factors: the stronger activity of research groups and the higher host diversity along the Atlantic coast in comparison to that of Pacific, as well as fish LGD. It should be highlighted that research groups actuating in ecoregions from the Pacific Ocean, for example, from Chile (e.g. Muñoz and George-Nascimento, 2007; Muñoz, 2010; Cerna *et al.*, 2019) have been also describing nematode species in the last 2 decades. However, the number of studies is considerably less numerous in comparison with those in the Atlantic, and most of the species were described from 1950 to 1990 (see Olsen, 1952; Mudry and Dailey, 1969; Mateo, 1972a, 1972b; Caballero-Rodríguez, 1974; Moravec and McDonald, 1981; Moravec *et al.*, 1981; Moravec, 1987). Therefore, evidence indicated that Pacific ecoregions of the American continent, including the Hawaiian Indo-Pacific coast, remain understudied for nematode parasites of fish.

Life cycles and biological considerations

The most comprehensive compilation of life cycle information pertaining to nematode parasites of vertebrates was provided by Anderson (2000). However, proportionally to the biodiversity of nematode parasites in marine fish, our knowledge regarding their biology and development is rather limited. A common

characteristic shared by almost all taxa of parasitic nematodes in marine fish is the indirect transmission (heteroxeny), mediated by trophic relationships, in which both invertebrates and vertebrates are used as intermediate or paratenic hosts (Anderson, 2000; Lafferty *et al.*, 2008; Lafferty, 2013).

Most literature dealing with the life cycles of nematode parasites in marine fish is focused on the species with foodborne zoonotic potential, mainly those of the family Anisakidae (Anderson, 2000). However, those zoonotic anisakids (e.g. *Anisakis*, *Pseudoterranova*) only occur as larval stages in fish, which are used as intermediate or paratenic hosts (Anderson, 2000). The general life cycle aspects of the most representative nematode families, reported in the present study, are presented briefly below.

The biology of trichinelloids in general and, especially regarding those species parasitic in marine fish, remains little known (Worsham *et al.*, 2016), similar to the scenario observed for the less common taxa reported below (e.g. Gnathostomatoidea, Habronematoidea, Oxyuroidea). Eggs of trichinelloids are generally thick-walled, barrel-shaped and provided with polar plug-like structures or filaments, which are laid unembryonated or fully larvated and released to the external environment with host's urine or feces (Moravec, 2001). It is still controversial if hosts became infected by the first-, second- or third-stage larvae, although Worsham *et al.* (2016) found the second-stage larva to be infective to the definitive host. The most recent experimental life cycle known of a parasitic nematode related to the marine environment was that of *Huffmanella huffmanii* (Trichinelloidea, Trichosomoididae) (Worsham *et al.*, 2016), thus representing the first elucidated cycle in this genus. This nematode species was found in a freshwater locality (upper San Marcos River, Texas) and seems to be restricted to that area, so it is believed that *H. huffmanii* is a marine-relict, since all other congeners infect marine fish (see Huffman and Moravec, 1988). Species of *Huffmanella* uses aquatic invertebrates (e.g. amphipods) as intermediate hosts, which ingest nematode eggs; first-stage larvae hatch from the eggs and develop in the invertebrate haemocoel into a second stage is infective to the definitive host; such features are commonly observed in trichinelloid nematodes (Anderson, 2000; Worsham *et al.*, 2016).

Members of the Camallanoidea are frequently found in the digestive tract of marine fishes. The life cycle of a number of camallanid species has been investigated (see Anderson, 2000). These parasites are haematophagous and ovoviviparous, as the first-stage larvae hatch *in utero* and are passed into water, where they are ingested by copepods that act as intermediate hosts (Anderson, 2000). Infective third-stage larvae in the copepod haemocoel will persist if ingested by planktivorous fish, but do not develop beyond the fourth stage in these paratenic hosts. The development will be completed only when larvae are ingested by piscivorous fish through the food chain (Anderson, 2000).

The biology of the Thelazioidea is highly diverse among their families, and rhabdochonids are not the exception, since they are found in the digestive tract and pancreatic ducts of their fish hosts. The life cycle of most species occurring in marine fishes is unknown but like those parasitizing freshwater forms have smooth-shelled eggs with or without floats and filaments, use insects or crustaceans as intermediate hosts and sometimes teleosts may act as intermediate or paratenic hosts (McVicar and Gibson, 1975; Anderson, 2000).

The Habronematoidea is another highly biologically diverse superfamily of nematodes and includes economically important groups of tetramerids of the proventriculus of birds and habronematids in horses and certain ruminants (Anderson, 2000). The family Cystidicolidae is the best represented with 27 genera (Moravec, 2007; Moravec and Justine, 2010; Moravec and Sobecka, 2012), among which several species infect the digestive

tract of marine fish. Given the high biodiversity of cystidicolid nematodes, their life cycles are almost unknown; only 9 species of more than 140 have been investigated (Moravec, 2007; Appy and Butterworth, 2011). The main intermediate hosts of cystidicolids in marine environments are crustaceans of different types, where nematode larvae attain the infective third-stage prior to ingestion by the fish definitive host (Moravec, 2007). Interestingly, in some cases these larvae can develop early into adulthood and become gravid, thus representing a source of environmental contamination *via* egg production, as well as being infective to the definitive host (Moravec, 2007). Some small fish are also reported as paratenic hosts (Moravec, 2007), but their role in the transmission of these parasites appears not to be as important as observed for anisakids and raphidascaridids.

The Dracunculoidea is characterized by having large females filled with huge number of first-stage larvae that must be dispersed into the environment and be available to copepod intermediate hosts. One important family is Philometridae, which is highly speciose in marine and freshwater environments and exclusive to fish (Anderson, 2000; Moravec and de Buron, 2013). However, life cycles of these parasites have received attention only recently (Perez *et al.*, 2009; Chávez and Oliva, 2011; de Buron *et al.*, 2011; Séguin *et al.*, 2011; Williams *et al.*, 2012). Philometrids are tissue-dwelling parasites commonly haematophagous, which may negatively impact their hosts, causing economic losses in economically important fish (Moravec, 2006; Moravec and de Buron, 2013). Females of philometrids are ovoviparous giving birth to first-stage larvae, through bursting their bodies when in contact with water (except *Alinema*) (Anderson, 2000; Moravec and de Buron, 2013). Evidence indicates that the development of philometrids can be seasonal, and that the copepod component of the zooplankton and some prey fish may act as intermediate and paratenic hosts, respectively, for these parasites (see Molnár and Fernando, 1975; Perez *et al.*, 2009; Chávez and Oliva, 2011; de Buron *et al.*, 2011; Séguin *et al.*, 2011; Williams *et al.*, 2012).

The biology of most members of Gnathostomatoidea have not been studied extensively, except the species of the genera *Gnathostoma* due to their significance to human and animal health (Anderson, 2000). The genus *Echinocephalus* is the only one represented in marine fishes and uses probably marine crustaceans (copepods) as intermediate hosts, and molluscs, echinoderms and other marine organisms as paratenic or second intermediate hosts in which growth occurs (Anderson, 2000).

The Oxyuroidea is also a highly diverse superfamily, with families parasitizing herbivorous lower vertebrates, mammals and reptiles (Anderson, 2000). The only genus occurring in marine fishes is *Echinocephalus*, whose life cycle is unknown, but as other pharyngodonid genera the transmission seems to be direct, without any intermediate hosts (Moravec, 1998).

The Ascaridoidea mostly includes nematode families parasitizing aquatic mammals and fishes. The most remarkable are Anisakidae and Raphidascarididae, the former for including species with zoonotic potential. Anisakids have mostly mammals as definitive hosts and use fish as intermediate and/or paratenic hosts, while raphidascaridids use invertebrates as intermediate hosts (e.g. mysids, copepods, isopods) and fish as paratenic and/or definitive hosts (Anderson, 2000). It is known that the transmission of the most studied raphidascaridid genera (i.e. *Goezia*, *Hysterothylacium* and *Raphidascaris*) involves small aquatic invertebrates (mainly arthropods), fry or other smaller foraging fish as paratenic or intermediate hosts, in which the biological strategy depends upon the parasite species (see Anderson, 2000; Klimpel and Rückert, 2005). Life cycles of some anisakid (e.g. genera *Anisakis* and *Contracaecum*) and raphidascaridid (e.g. genera *Hysterothylacium*) nematodes are known

(Anderson, 2000), although all for other genera within these families are still scarce or absent.

The Seuratoidea represents a diparate group of genera, whose transmission and development are very limited for most of the species. Cucullanidae is one of the most common families of parasitic nematodes occurring in fish. However, our knowledge relating to the life cycle of these species is still imperfect (Anderson, 2000). These intestinal parasites are primarily heteroxenous using vertebrates (e.g. prey fish) or invertebrates (e.g. polychaetes) as intermediate hosts, but there is also evidence that, in some species, the intermediate host was replaced by a histotropic phase in the definitive host (see Anderson, 2000; Koie, 2000, 2001; Pronkina *et al.*, 2017).

Advances in the taxonomic and phylogenetic knowledge

Even though several taxa of nematode parasites in marine fishes from off the Americas require taxonomic revision (see the following section), relatively recent technological advances have been very important for improving our knowledge concerning these organisms. Scanning electron microscopy (SEM) and genetic characterization appear to be the most important new tools in this process.

For example, in the Cystidicolidae that allocates 26 genera with complicated taxonomy and the generic diagnosis is mainly based on minute cephalic structures, SEM observations have proven to be crucial for the resolution of taxonomic problems and the improvement of morphological knowledge (Moravec, 2007; Moravec and Justine, 2010). Similarly, in the Philometridae, which includes commonly very small male specimens and minute cephalic structures, the use of SEM has been very important (Moravec and de Buron, 2013) especially for those parasites of marine fish off the American continent, which have been studied intensively during the last decade (see Moravec and de Buron, 2013; Moravec *et al.*, 2014, 2016, 2020, 2021). The application of SEM is not restricted to few taxa of nematode parasitizing marine fish in the Americas; it has been practically mandatory for taxonomic studies regarding these parasites during the last 20 years, proving to be very important for the description of new species (e.g. Vieira *et al.*, 2015; Irigoitia *et al.*, 2017; Aguilar-Aguilar *et al.*, 2019; Moravec *et al.*, 2020, 2021), as well as for improving the knowledge of poorly known taxa and resolution of taxonomic issues (e.g. Mejía-Madrid and Aguirre-Macedo, 2011a; Pereira *et al.*, 2015; Moravec *et al.*, 2017; Sardella *et al.*, 2017). Even though the use of SEM has been increased exponentially in studies pertaining to nematodes parasitizing marine fish in the American continent, certain species from different families still remain poorly known regarding their morphology, and/or have never been observed using SEM, especially those that are reported less frequently, such as *Caballeronema wardlei* (Smedley, 1934), *Spinitectus beaveri* Overstreet, 1970, *S. cristatus* Railliet et Henry, 1915 (all Cystidicolidae), *Cucullanus longipapillatus* Olsen, 1952 and *C. elongatus* Smedley, 1933 (both Cucullanidae), *Dollfusnema piscicola* Caballero-Rodríguez, 1974 (Spiruridae), *Echinocephalus pseudouncinatus* Millemann, 1951 (Gnathostomatidae), *Heliconema heliconema* Travassos, 1919 (Physalopteridae), *Lappetascaris lutjani* Rasheed, 1965 (Raphidascarididae), *Laurotravassosyuris travassosi* Viguera, 1938 (Pharyngodonidae), *Oncophora melanocephala* (Rudolphi, 1819) (Rhabdochonidae) and *Phlyctainophora squali* Mudry et Dailey, 1969 (Micropleuridae).

Genetic characterization of nematodes infecting marine fish from the Americas is a more recent tool that has also been very valuable for the better comprehension of different aspects related to these parasites. However, genetic database is rather scarce, since only about 18% (38/209) of the species have genetic sequences available in GenBank. Most genetic markers used are nuclear, in which 18S rDNA sequences are

the most common type. Sequences of *cox1* mtDNA are the second most common, followed by the nuclear 28S rDNA and ITS1-5.8S-ITS2. *Cox2* and 12S mtDNA sequences are also available, but they are very rare. According to the database, only representatives of the following nematode families have been genetically characterized: Anisakidae (3 species), Camallanidae (3), Capillariidae (1), Cucullanidae (6), Cystidicolidae (2), Daniconematidae (1), Gnathostomatidae (2), Philometridae (11), Physalopteridae (1) and Raphidascarididae (8). Genetic markers used for raphidascaridids are the most diverse, followed by those used for cucullanids and anisakids (see Supplementary Material 2 for details). Raphidascaridid and anisakid larval forms are commonly found in marine fish and, in addition to their zoonotic potential (Mattiucci *et al.*, 2014; Macchioni *et al.*, 2021), specific diagnosis based upon larval morphology is almost impossible (Moravec, 1994, 1998), facts that can boost the genetic characterization of these parasites and, increasingly, the search for new markers. Cucullanids and philometrids currently are the most speciose taxa of nematode parasites in marine fish from the Americas (see Fig. 1C). Consequently, it is expected that genetic studies focused on these groups will also stand out.

In addition to the fragmentary genetic database, a great part of genetic sequences in GenBank comes from direct submissions, i.e. in the absence of a supporting scientific publication. Such submissions limit checks on the accuracy of taxonomic identifications, and some likely misidentifications have been noted by some authors (see Černotíková *et al.*, 2011; Ailán-Choke *et al.*, 2019, 2020). However, despite the limited and sometimes inaccurate data, the genetic characterization of nematodes reported herein has been crucial for supporting species validity and the evaluation of their phylogenetic positions (Mejía-Madrid and Aguirre-Macedo, 2011a, 2011b; Sardella *et al.*, 2017; Aguilar-Aguilar *et al.*, 2019; Sokolov and Gordeev, 2021), genetic variability (Li *et al.*, 2014), broad phylogenetic studies of higher taxa (Nadler and Hudspeth, 1998, 2000; Nadler *et al.*, 2007; Li *et al.*, 2018; Barton *et al.*, 2022), specific identification of larval forms (Palesse *et al.*, 2011; Haarder *et al.*, 2013; Roca-Geronès *et al.*, 2018) and even the elucidation of life cycles (May-Tec *et al.*, 2018). It should be mentioned that some of these works were not specifically carried out in marine waters off the American continent (Nadler and Hudspeth, 1998, 2000; Nadler *et al.*, 2007; Haarder *et al.*, 2013; Li *et al.*, 2014, 2018; Roca-Geronès *et al.*, 2018), but included nematode species that have been reported in this region.

As previously commented, phylogenetic relationships within the Nematoda have changed considerably with the use of genetic analyses (see the reviews by Mitreva *et al.*, 2005; Blaxter, 2011; Blaxter and Koutsovoulos, 2015). Broad and pioneer phylogenetic works on nematode parasites included very few representatives that infect marine fish and have been reported in the American continent (Nadler and Hudspeth, 1998, 2000). Wjová *et al.* (2006) published the first phylogenetic work including a representative number of samples from nematode parasites of fish; the study emphasized on the superfamily Dracunculoidea. However, it included only 1 parasite of marine fish from the American continent, namely *Dentiphilometra* sp. from Mexico. Posteriorly, Černotíková *et al.* (2011) investigated the phylogenetic relationships within Spirurina specifically in regards to parasites of fish including and providing sequences for several nematode species from the tropical and temperate zones of the western Atlantic. Subsequent studies including nematode species herein listed have been focused on phylogenetic and systematic aspects of the most speciose families Cucullanidae (Choudhury and Nadler, 2018) and Philometridae (Negreiros *et al.*, 2019; Barton *et al.*, 2022), as well as Raphidascarididae and Anisakidae (Pereira and Luque, 2017a), Camallanidae (Ailán-Choke and Pereira, 2021) or a combination of these families (Holterman

et al., 2019). The approaches used in the remaining phylogenetic studies are narrower and focused on reduced taxonomic groups (i.e. genus or restricted to some species) (see Mejía-Madrid and Aguirre-Macedo, 2011a, 2011b; Sardella *et al.*, 2017; Roca-Geronès *et al.*, 2018; Aguilar-Aguilar *et al.*, 2019).

Even though the knowledge on the phylogeny of nematode parasitic in marine fish from the American continent remains superficial, since only few representatives have been genetically characterized and included in broad phylogenetic studies, evidence supports the following conclusions. The monophyly of the families Camallanidae, Cucullanidae, Philometridae and Raphidascarididae is strongly supported (Černotíková *et al.*, 2011; Pereira and Luque, 2017a, 2017b; Choudhury and Nadler, 2018; Negreiros *et al.*, 2019; Ailán-Choke and Pereira, 2021; Barton *et al.*, 2022), whereas in Anisakidae and Cystidicolidae, evidence showed lack of monophyly and, consequently, suggests their artificiality (Pereira *et al.*, 2018). Moreover, monophyly is not supported for the genera *Procamallanus* and *Spirocamallanus* (Camallanidae) (*sensu* Ailán-Choke and Pereira, 2021), *Cucullanus* and *Dichelyne* (Cucullanidae), *Philometra* and *Philometroides* (Philometridae), *Hysterothylacium* (Raphidascarididae), *Contracaecum* (Anisakidae) and *Ascarophis* (Cystidicolidae) (Černotíková *et al.*, 2011; Pereira and Luque, 2017a, 2017b; Choudhury and Nadler, 2018; Pereira *et al.*, 2018; Negreiros *et al.*, 2019; Mata *et al.*, 2020a, 2020b; Ailán-Choke and Pereira, 2021; Barton *et al.*, 2022). Thus, it is pertinent that the classification system of the previously mentioned taxa, which includes the most representative ones, should be revised in the future with the improvement of both genetic and morphological databases. Extra efforts in the genetic characterization of most of the species listed herein are sorely needed.

Systematics and species list of nematodes

A total of 209 valid species, 19 *species inquirenda* and 6 dubious records of nematodes were reported parasitizing 504 marine fishes off the Americas. The most represented suborder was the Ascaridina (37%, 78/209), followed by the Spirurina (27%, 56/209), Dracunculina (24%, 51/209), Trichinellina (10%, 21/209), Gnathostomatina (1%, 2/209) and Oxyurina (0.5%, 1/209). The Cucullanidae was the family with the highest number of species (20%, 42/209), followed by the Philometridae and Cystidicolidae (19%, 40/209 and 12%, 25/209, respectively). More information can be found in Supplementary Material 2 and Fig. 1C.

Phylum Nematoda Cobb, 1932
 Class Dorylaimea Hodda, 2007
 Order Trichocephalida Spasski, 1954
 Suborder Trichinellina Hodda, 2007
 Superfamily Trichinelloidea Ward, 1907

This superfamily forms part of the order Trichocephalida Spasski, 1954, the latter frequently phylogenetically grouped in a strongly supported cluster formed by Dorylaimida, Mermithida and Mononchida (see Dorris *et al.*, 1999). The superfamily is apparently derived from ancestors that were initially tissue parasites of freshwater fishes (Anderson and Bain, 1982) and characterized by having members with the anterior part of the body narrowed and the posterior part considerably expanded; oesophagus divided into a shorter anterior muscular part and a longer posterior glandular part (stichosome). Trichinelloids are parasites of the digestive tract of vertebrates (amphibians, birds, fishes, mammals, reptiles) in both terrestrial and aquatic (freshwater and marine) environments; those species parasitizing fishes utilize aquatic oligochaetes as intermediate hosts. Three families are included in this superfamily: Capillariidae Railliet, 1915 (with 6 genera, 6 subgenera, 13 species), Trichosomoididae Hall, 1916 (1 genus, 7

species) and Trichuridae Ransom, 1911 (1 genus, 1 species). All these 21 species are valid, although *P. (P.) hathawayi* was originally described based only in females and provisionally assigned to *Piscicapillaria* Moravec, 1982 (see Moravec, 1987). Since trichineloids are host-specific, the finding of *C. (P.) gracilis* in hosts of different fish orders and geographical localities requires re-confirmation. *Capillaria (H.) cyprinodonticola* Huffman et Bullock, 1973 was reported in fishes inhabiting marine, brackish and freshwater habitats, although its origin does not seem to be purely marine. *Capillostrongyloides congiopodi* Cantatore, Rossin, Lanfranchi et Timi, 2009 was listed as a part of Trichuridae by Hodda (2022a) instead of Capillariidae where it was first classified.

Class Chromadorea Inglis, 1983

Order Spirurida Chitwood, 1933

Suborder Spirurina Railliet et Henry, 1915

Superfamily Camallanoidea Railliet et Henry, 1915

The order Spirurida Railliet, 1915 includes the superfamilies Camallanoidea, Thelazioidea and Habronematoidea and formed a phylogenetic clade along with the zooparasitic orders Ascaridida, Oxyurida and Rhigonematida (Blaxter *et al.*, 1998; Dorris *et al.*, 1999). The Camallanoidea is monophyletic, forms a sister group to Dracunculoidea (Černotíková *et al.*, 2011) and is represented by spirurid nematodes occurring in the digestive tract of fishes, amphibians and reptiles all over the world. These nematodes have an oral opening with rudimentary or without lips, pseudolabia absent, oesophagus divided into muscular and glandular sections and the body size of females is rarely double the size of males. Camallanoids use copepods as intermediate hosts, small fish as paratenic hosts and larger fish as definitive hosts. Paratenesis and precocity during transmission may help to explain the wide host distribution of many camallanoids (Anderson, 1988). The superfamily includes 2 families: Camallanidae Railliet et Henry, 1915 (2 genera, 1 subgenus and 15 species) and Physalopteridae Railliet, 1893 (3 genera and 9 species); of these, *Procamallanus (Spirocamallanus)* is valid and the fourth most speciose in marine fishes off America (14 species). All these taxa are valid, although some records of *O. melanocephala* (Rudolphi, 1819) Baudin-Laurencin, 1971, *Mooleptus rabuka* (Machida, Ogawa et Okiyama, 1982) Özdikmen, 2010 and *Proleptus obtusus* Dujardin, 1845 should be confirmed, since they are from very distant geographical areas and hosts. *Procamallanus (Spirocamallanus) cruzi* (Guimarães, Cristofaro et Rodrigues, 1976) Moravec et Sey, 1988 and *Proleptus elegans* (Örley, 1885) were not included because they are *species inquirendae* (see Sardella *et al.*, 2017). *Procamallanus (Spirocamallanus) pereirai* (Annereaux, 1946) Olsen, 1952 was commonly reported in different regions off the Americas, but according to Sardella *et al.* (2017), all specimens reported in the South Atlantic belong to *P. (S.) macaensis*. Bashirullah and Williams (1980) poorly described *P. (S.) garnotus* (Bashirullah et Williams, 1980) Moravec et Sey, 1988, *P. (S.) papillicaudatus* (Bashirullah et Williams, 1980) Moravec et Sey, 1988, *P. (S.) partitus* (Bashirullah et Williams, 1980) Moravec et Sey, 1988, *P. (S.) plumierus* (Bashirullah et Williams, 1980) Moravec et Sey, 1988 and *P. (S.) spinicaudatus* (Bashirullah et Williams, 1980) Moravec et Sey, 1988, from Puerto Rico and Venezuela, which are morphologically similar and a deep revision of the type material is required. *Proleptus carvajali* Fernández et Villalba, 1985 was reported in *Anisotremus scapularis* (Tschudi), *Isacia conceptionis* (Cuvier) (both Haemulidae), *Cilus gilberti* (Abbott) (Sciaenidae), *Labrisomus philippii* (Steindachner) (Labrisomidae) (all Eupercaria) from Perú (see Chero *et al.*, 2014a, 2014b; Cruces *et al.*, 2015; Iannacone *et al.*, 2015), but they could be misidentifications. Whereas Torres *et al.* (2018) and Chero *et al.* (2019)

reported larval nematodes such as *P. carvajali* in *Emerita analoga* (Decapoda) and *Cheilodactylus variegatus* (Cheilodactylidae), respectively, from Perú, but the identity of the nematode should be verified.

Superfamily Thelazioidea Sobolev, 1949

This superfamily is paraphyletic and was grouped with the taxa of Acuarioidea, Diplotrienoidea, Filaroidea, Habronematoidea, Physalopteroidea and Spiruroidea (see Černotíková *et al.*, 2011; Choudhury and Nadler, 2018). Members of this superfamily have an oral opening round or hexagonal (not compressed laterally), stoma variable in size and are viviparous. Thelazioids are represented by 2 families: Rhabdochonidae Travassos, Artigas, et Pereira, 1928 (3 genera, 3 species) and Thelaziidae Railliet, 1910 (1 genus, 1 species), which are all valid, although the rhabdochonid genus *Megachona* Mejía-Madrid et Pérez-Ponce de León, 2007 was not listed by Hodda (2022a), but no reason to be invalid. Most of rhabdochonid genera (e.g. *Heptochocha* Rasheed, 1965; *Rhabdochocha* Railliet, 1916) are of freshwater origin, although there are others, such as *Johnstonmawsonia* Campana-Rouget, 1955, *Megachona* Mejía-Madrid et Pérez-Ponce de León, 2007, *Pancreatonema* McVicar et Gibson, 1975 and *Vasorhabdochocha* Martin et Zam, 1967, that were found in marine or freshwater fish. Superfamily Habronematoidea Chitwood et Wehr, 1932

This superfamily along with Thelazioidea are not natural groups (paraphyletic) as stated by Černotíková *et al.* (2011) and Choudhury and Nadler (2018). Habronematoids bear pseudolabia, with or without cephalic cuticular ornamentation, caudal alae in male and include 3 families: Cystidicolidae Skryabin, 1946 (9 genera, 25 species), Habronematidae Chitwood et Wehr, 1932 (1 genus, 1 species) and Hedruridae Petter, 1971 (1 genus, 2 species). All these are valid, although *Similascarophis* is considered as genus by Hodda (2022a) and not a subgenus of *Ascarophis* as proposed by Moravec and Justine (2007). Despite the high number of genera, they are monotypical and restricted to certain regions of the continent, such as *Caballeronema* Margolis, 1977 in Canada and *Comephoronema* Layman, 1933 in Brazil. On the other hand, the genus *Ascarophis* van Beneden, 1871 (Cystidicolidae) has the higher number of species within this superfamily (10 species), of which some show narrow geographical distribution (*A. brasiliensis* Pinto, Vicente et Noronha, 1984 in Brazil, *A. carvajali* Muñoz et George-Nascimento, 2007 and *A. draconis* Muñoz et George-Nascimento, 2007 in Chile, *A. cestus* Chitwood, 1934 in Puerto Rico, *A. extalicola* Appy, 1981 in Canada and *A. morronei* Aguilar-Aguilar, Ruiz-Campos, Martorelli, Montes et Martínez-Aquino, 2019 in Mexico). Meanwhile, *A. arctica* Polyanskiy, 1952, *A. filiformis* Polyanskiy, 1952, *A. morrhuae* van Beneden, 1871 and *A. Sebastodis* Olsen, 1952 were reported in fishes of different families and orders, as well as from distant localities, thus the identity of the specimens from each host and geographical region should be corroborated. *Ascarophis helix* Cobb, 1928 was not included since Dollfus and Campana-Rouget (1956) considered it as a *species inquirenda*. Suborder Dracunculina Stiles, 1907

Superfamily Dracunculoidea Stiles, 1907

This superfamily is monophyletic, with Camallanoidea as sister group, thus showing some remote affinities between them (see Černotíková *et al.*, 2011). Its members are parasites of a variety of host tissues and cavities in both cold- and warm-blooded vertebrates (Anderson, 2000), including freshwater, brackishwater and marine fishes. Dracunculoid nematodes are represented by 5 families: Daniconematidae Moravec et Køie, 1987 (1 genus, 1 species), Guyanemidae Petter, 1974 (2 genera, 5 species), Micropleuridae Baylis et Daubney, 1926 (2 genera, 3 species), Philometridae Baylis et Daubney, 1926 (8 genera, 40 species) and Skrjabilianidae Shigin et Shigina, 1958 (1 genus, 2 species). All these taxa are valid, although *Caranginema* Moravec,

Montoya-Mendoza et Salgado-Maldonado, 2008, which was not listed by Hodda (2022a) but no reason to be considered invalid. Moreover, family Dracunculidae Stiles, 1907 is not herein listed because the genus *Lockenloia* Adamson et Caira, 1991, represented in marine fishes off America, is considered as *incertae sedis* within Dracunculoidea (see Moravec, 2004). The genus *Margolisianum* Blaylock et Overstreet, 1999 and the species *Philometra fariaslimai* Fortes, 1981 were not included because the former is considered as a *genus inquirendum* (see Moravec and de Buron, 2006) and the latter as a *species inquirenda* (see Moravec, 2006). *Clavinema mariae* (Layman, 1930) Margolis et Moravec, 1987 probably represents a complex of related species with almost identical female morphology (see Moravec et al., 2019); whereas *Philometra chilensis* Moravec, Chávez et Oliva, 2011 reported by Chávez and Oliva (2011) represents a *nomen nudum* and refers to *P. genypteri* Moravec, Chávez et Oliva, 2011. The philometrid genus *Philometra* Costa, 1845 is the most speciose in the whole continent (40 species), while other genera are represented by much less species, such as *Caranginema*, *Clavinema* Yamaguti, 1935, *Dentiphilometra* Moravec et Wang, 2002, *Digitiphilometroides* Moravec et Barton, 2018, *Mexiconema* Moravec, Vidal et Salgado-Maldonado, 1992, *Moravecchia* Ribu et Lester, 2004, *Phlyctainophora* Steiner, 1921, *Barracudia* Moravec et Shamsi, 2017 (1 each) and *Granulinema* Moravec et Little, 1988 (2 species). *Philometra globiceps* (Rudolphi, 1819) Railliet, 1916 and *Philometra lateolabracis* Yamaguti, 1935 only parasitize *Uranoscopus scaber* Linnaeus (see Moravec and Tedesco, 2015) and *Lateolabrax japonicus* (Cuvier), respectively (see Quiazon et al., 2008), which do not occur in American waters, thus both nematode species are absent from the Americas.

Suborder Gnathostomatina Skryabin et Ivashkin, 1973
Superfamily Gnathostomatoidea Railliet, 1895

This superfamily, along with Anguilliculoidea, formed a well-supported sister group with the clade III composed by the orders Ascaridida, Oxyurida and Rhigonematida (see Černotiková et al., 2011). Gnathostomatoids have a large, trilobed pseudolabia, 4–6 large unicellular lemniscus-like cephalic glands, and are parasites of fishes, amphibians, reptiles and mammals. Most of its genera (e.g. *Gnathostoma* Owen, 1836, *Spiroxys* Schneider, 1866) use fishes as intermediate hosts, while adults are represented by the family Gnathostomatidae Railliet, 1895 and genus *Echinocephalus* Molin, 1858 (2 species). This is one of the less represented taxa in marine fishes off the Americas.

Suborder Oxyurina Railliet, 1916
Superfamily Oxyuroidea Cobbold, 1864

This superfamily is monophyletic (see Sata and Nakano, 2020) and represented by small parasitic nematodes of all classes of vertebrates and invertebrates. They are also called ‘pinworms’ and characterized by the presence of a bulb in the posterior end of the oesophagus and a prolonged caudal extremity of the female. It is represented in marine fishes off America by the family Pharyngodonidae Travassos, 1919 and genus *Laurotravassosoxyuris* Vigueras, 1938 (1 species). Like the latter superfamily, this is also one of the less represented taxa.

Suborder Ascaridina Inglis, 1983
Superfamily Ascaridoidea Railliet et Henry, 1915

This superfamily is monophyletic (see Nadler and Hudspeth, 1998) and its members are medium-sized to large nematodes with 3 lips (sometimes separated by interlabia) and inhabiting the stomach and intestine of all classes of vertebrates, including species that are of medical and economic importance. Out of the approximately 54 genera within Ascaridoidea, at least 11,

belonging to 3 families, are represented in marine fishes off America, namely Anisakidae Railliet et Henry, 1912 (5 genera, 12 species), Ascarididae Baird, 1853 (1 genus, 2 species) and Raphidascarididae Hatwich, 1954 (5 genera, 1 subgenus, 22 species). All are valid, although the genera *Euterranova* Moravec et Justine, 2020 and *Iheringascaris* Pereira, 1935 were not listed by Hodda (2022a), but there is no reason to consider them invalid. The genus *Terranova* Leiper et Atkinson, 1914 (and 3 species) was not included because it is considered as *genus inquirendum* (see Moravec and Justine, 2020). *Hysterothylacium* Ward et Magath, 1917 is the third most speciose genus represented in off the Americas (17 species), although also the most problematic because several species have been reported in various fish hosts and even distant locations. Similarly, the species *Acanthocheilus rotundatus* (Rudolphi, 1819) Hartwich, 1957, *Euterranova galeocerdonis* (Thwaite, 1927) Moravec et Justine, 2020 and *Pseudanisakis tricupola* Gibson, 1973 were reported in several elasmobranchs in different regions of the world, thus its identity should be corroborated in all of them. The systematic status of *Hysterothylacium deardorffoverstreetorum* Knoff, Felizardo, Iniguez, Maldonado Jr., Torres, Pinto et Gomes, 2012, *H. magnum* (Smedley, 1934) Deardorff et Overstreet, 1981, *H. melanogrammi* (Smedley, 1934) Deardorff et Overstreet, 1981 and *Raphidascaris (Raphidascaris) anchoviellae* (Chandler, 1935) Moravec et Nagasawa, 2002 is uncertain because they were poorly described or based on larval stages.

Superfamily Seuratoidea Chabaud, Campana-Rouget et Brygoo, 1960

The Seuratoidea was recognized as valid by Inglis (1967) and Chabaud et al. (1960), although phylogenetically it represents a non-natural group (see Skryabin and Ivashkin, 1968; Choudhury and Nadler, 2018) and more phylogenetic analyses with more extensive sampling of non-cucullanid taxa are required (see Choudhury and Nadler, 2018). Seuratoids are usually medium-sized nematodes with lips reduced or absent, a short oesophagus, precloacal sucker, and inhabit in all classes of vertebrates. The superfamily includes only 1 family: Cucullanidae Cobbold, 1864 (2 genera, 2 subgenera, 42 species). The genus *Cucullanus* Müller, 1777 is the second most speciose in the continent (26 species), while genus *Dichelyne* Jägerskiöld, 1902 subgenus *Cucullanellus* Törnquist, 1931 the fourth along with *Procamallanus (Spirocamallanus)* (14 species). Despite all 42 species are valid, *Dichelyne (Cucullanellus) travassosi* (Guimarães et Cristófar, 1974) Vicente, Magalhães et Aguilera, 1989 and *D. (C.) elongatus* (Törnquist, 1931) Petter, 1974 should be redescribed. Apparently, the latter only occurs in the Pacific coast of South America and all previous reports from the Atlantic coast (Argentina, Brazil, Venezuela) belong to *D. (C.) sciaenicicola* (see Timi et al., 2009). *Cucullanus hians* (Dujardin, 1845) Petter, 1974 was reported from a non-American marine fish (*C. conger*) collected from its southernmost distribution range in North America (65–70 fathoms off Gay Head, Massachusetts, USA) (see Linton, 1901), although most reports of this nematode are from the coasts of Europe and Africa, so its identity should be corroborated. There are several species that were not included because they are *species inquirendae* [*C. lopholatilus* (MacCallum, 1921) Petter, 1974, *C. rougetae* Vicente et Santos, 1974, *D. cylindricus* Chandler, 1935, *D. (C.) rodriguezi* (Pinto, Fábio et Noronha, 1970) Petter, 1974, *D. (D.) micropogonii* Pereira Jr. et Costa, 1996] or dubious records [*C. chrysophrydis* Gendre, 1927, *D. (C.) minutus* (Rudolphi, 1819) Törnquist, 1931, *D. (C.) tripapillatus* (Gendre, 1927) Törnquist, 1931].

There are records of *Ichthyostromylus thunni* Nikolaeva, 1969 (family Trichostrongylidae Leiper, 1908) from the USA and

Mexico (Nikolaeva, 1968, 1969), but Durette-Desset (1983) stated that they are insufficiently known to be classified.

Final considerations

It is assumed that parasite richness is proportional to that of the host communities (Hechinger and Lafferty, 2005; Poulin, 2014). In this sense, in the tropical western and temperate south Atlantic ecoregions, fish richness easily overcomes 2000 species (Froese and Pauly, 2022) and they showed the highest number of nematode species reported, thus supporting this assumption. However, the present compilation clearly shows that the biodiversity of nematode parasites in marine fish from off the Americas is underestimated, since the diversity of hosts in other ecoregions (e.g. tropical eastern Pacific) is also high (see Miloslavich *et al.*, 2011; Carrillo-Briceño *et al.*, 2018; Manel *et al.*, 2020) and there have been fewer reports of nematodes, thus indicating that more studies are needed.

Such panorama, combined with numerous taxonomic problems, represents a real challenge when dealing with the nematode parasites of marine fish from off the Americas. Therefore, the present review may provide useful data and a practical way to follow for researchers who desire to develop further studies on the subject.

Cucullanidae was the family with the highest richness of nematode species in the present survey. High diversity is commonly associated with cucullanids infecting fish in both marine and freshwater environments throughout the world (see Moravec *et al.*, 2005; Vieira *et al.*, 2015; Moravec and Justine, 2020), which is not different in the Americas. Philometridae was the second most species-rich family with numbers very close to those of Cucullanidae. Such representativeness of philometrids in terms of richness is related to the efforts of the taxonomists (especially Dr František Moravec) working on this group over the last 2 decades, resulting in the description of several species (see Supplementary Material 2 for all authorities and years). Cystidicolidae was also representative regarding its species richness and also showing high number of genera (Moravec, 2007; Moravec and Justine, 2010; Moravec and Sobocka, 2012). Nematodes of this family are assumed to be frequent in marine fish (Moravec and Justine, 2010). In the American continent, cystidicolids are particularly common in freshwater fish (especially from North America), in which the genus *Spinitectus* is the most frequently reported (Moravec, 1998; Luque *et al.*, 2011; Choudhury and Nadler, 2018). The present results reaffirm the high biodiversity potential of cystidicolid nematodes in marine environments of the Americas, and the real diversity of genera and species seem to be higher than in freshwater. Interestingly, the family Camallanidae, which is very speciose in freshwater fish of the Americas (especially in the Neotropical Region), appeared less diverse in marine waters (see Moravec, 1998; Luque *et al.*, 2011 for a general picture).

The present review indicates that nematode parasites of marine fish in the Americas are diverse, although a higher biodiversity is still unexplored. Moreover, the current taxonomy of these organisms still has numerous problems, in which certain taxa and reports require detailed reevaluation, as well as the life cycle aspects that are practically unknown. Advances on genetic and morphological analyses of these parasites have been producing more accurate data, helping the resolution of taxonomic issues, strengthening taxa validity, revealing evolutionary relationships, as well as suggesting and linking life cycle pathways of species. However, the current knowledge related to these nematodes is far from substantial, needing much additional efforts and having challenges to be overcome, especially with regard to genetic characterization. Steps are being taken towards a better understanding, but there is still a long way to go.

Author's contributions. F. B. P. and D. G. S. conceived and designed the study, as well as both wrote the article.

Financial support. This research received no specific grant from any funding agency, commercial or not-for-profit sectors.

Conflict of interest. None.

Ethical standards. Not applicable.

Supplementary material. The supplementary material for this article can be found at <https://doi.org/10.1017/S0031182022001287>.

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