BOLETIM

MUSEU DE HISTÓRIA NATURAL DO FUNCHAL

Vol. LXVII (2017), Art. 348: 25-45

ISSN 2183-279X (online edition) | | Available online at: http://boletim.cm-funchal.pt

A checklist of digenean parasites (Platyhelminthes: Digenea) infecting molluscs and fishes in Portuguese waters (Northeast Atlantic)

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With 1 figure and 1 table

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ABSTRACT: The present work is a compilation of the digenean parasites infecting molluscs (gastropods and bivalves), crabs and fishes of the Atlantic coast of Portugal and the Archipelagos of Azores and Madeira, based on literature sources, including research conducted by the present authors. A total of 65 digenea taxa were found, belonging to 24 families, infecting gastropods, bivalves, shore crabs and fishes. The most representative families of digeneans were the Hemiuridae (11 taxa), followed by the Bucephalidae (5 taxa), Opecoelidae (5 taxa) and the Zoogonidae (5 taxa). Hosts, site of infection, sampling locality and life cycle strategy are given when available. Further fields of research on the digenean parasites are suggested.

Keywords: digeneans, gastropods, bivalves, fishes, faunal survey, Portugal, Madeira, Azores, North Atlantic.

RESUMO: A presente revisão pretende compilar os registos publicados de digenéticos parasitas de moluscos (gastrópodes e bivalves), caranguejos e peixes da costa continental Portuguesa, e dos arquipélagos dos Açores e Madeira. Estes registos foram obtidos através de extensa consulta bibliográfica, sendo alguns destes registos resultado de investigação dos presentes autores. Um total de 65 taxa, de digenéticos, organizados por 24 famílias, parasitam diversos organismos marinhos da costa portuguesa. A família mais representativa é a Hemiuridae (11 taxa), seguida de 3 famílias cada uma representada por 5 taxa de digenéticos (Bucephalidae, Opecoelidae, Zoogonidae). Os hospedeiros, o local de amostragem, local de infestação, e ciclo de vida do parasita são indicados sempre que possível. Sugerem-se alguns campos de investigação na temática dos digenéticos parasitas de organismos marinhos.

Palavras-chave: digenéticos, gastrópodes, bivalves, peixes, estudo faunístico, Portugal, Madeira, Açores, Atlântico Norte.

Received: 01 August 2017; Available online: 13 November 2017; Published: 31 December 2017

INTRODUCTION

Taxonomic inventories of marine parasite species are important to determine patterns of geographic distribution, according to depth and to latitudinal gradients (Rohde, 1993) as well as to inform about the fish hosts migratory routes and the species richness of the ecosystem (Poulin & Morand, 2000; Poulin *et al*., 2016). Marine digenean parasites are particularly interesting to elucidate about the species richness of a given ecosystem as they develop through complex life cycles involving two and more hosts with fishes or birds as definitive hosts (Marcogliese, 2002; Zander & Reimer, 2002). Portugal has an extensive marine economic exclusive zone (EEZ) in the North-east Atlantic Ocean, encompassing the coastal waters of mainland at the Iberian Peninsula and the Archipelagos of Azores and Madeira. The total coastline of mainland Portugal extends to 943 km, the Madeiran one to 250 km and the Azores coastline to 667 km (Carneiro *et al*., 2014). A number of rocky shore areas and river estuaries in mainland Portugal, sustain a rich diversity of molluscs and fishes, many of which are commercially exploited (Instituto Nacional de Estatística, 2015). Molluscs, both gastropods and bivalves, are common intermediate hosts of digenean parasites, with definitive hosts being either fish or marine birds (Cribb, 2001; Poulin & Cribb, 2002). In insular regions, such as in Madeira and Azores Archipelagos, representing oceanic habitats, it is expected that the life cycles of digeneans parasites of marine fishes, include mainly members of the zooplankton as intermediate hosts (Køie, 1991, 1992) due to the coastal characteristics, with only a few sandy shores, mostly pebbles in the shore areas, and abrupt depth slopes. The island archipelagos of Madeira and Azores are part of the Macaronesian biogeographic region, which includes also the Canary and Cape Vert archipelagos. They have a strong influence of ocean currents from the Mediterranean and the Gulf of Mexico, with some parasite species suggesting these links with those marine regions (Gibson & Costa, 1997; Costa *et al*., 2013). Furthermore, Madeira lies on the border between temperate and tropical regions (see Rohde, 1993). Here, it is to expect a mixture of digeneans common to sub-tropical and temperate waters as well as species typical of the Mediterranean (Gibson & Costa, 1997). On the other hand, the parasites of the coastal rocky shores and estuaries of mainland Portugal show similarities with parasites found in other European Atlantic coastal habitats and the Mediterranean habitats (Santos & Eiras, 1995; Russell-Pinto *et al*., 2006; Costa *et al*., 2016). Nevertheless, changes in faunal diversity can be expected, due to the distribution of intermediate and definitive hosts and climate change (see Mouritsen & Poulin, 2002; Thieltges *et al*., 2008; Lafferty, 2009; Reid & Beaugrand, 2012). In particular, due to this last factor, climatic changes, which propitiates invasion of species from tropical areas further north (Palm, 2011; Poulin *et al*., 2011) it is important to elaborate up to date checklists of parasites and hosts. Earlier studies of digenean parasites in Portugal were those of Tendeiro (1955) on a description of a new species *Dolichoenterum manteri* (Bucephalidae) from the intestine of conger eels, *Conger conger*. After a lapse of about 40 years, increased research on the occurrence of digeneans in fish and molluscs started (Russell-Pinto, 1990, 1993), with some new species of digeneans described, as well as the elucidation of their life cycles strategies. In the last 20 years, a number of papers have been published with studies of the occurrence, infection dynamics and life cycles of digeneans in Portugal, based on both morphological and molecular approaches (Russell-Pinto *et al*., 2006; Pina *et al*., 2007, 2009, 2011a, b; Francisco *et al*., 2010a, b, 2011), increasing substantially our knowledge about species diversity and life cycle strategies of these parasites. The aim of the present work was to compile the available data of species of digeneans, their life cycle strategies, and the geographical range from mainland Portugal and archipelagos of Azores and Madeira, with a view of providing current research findings on the diversity of this group of parasites, and identify future areas of research to complement our present knowledge on this group.

MATERIALS AND METHODS

Records of digenean parasites of marine organisms (molluscs and fishes mainly and some crabs) were obtained from published scientific literature between 1950 and 2016, our own results and literature records appearing in Web of Science database. The taxonomy of the digenean species is in accordance with Gibson *et al*. (2002), Jones *et al*. (2005) and accepted taxa in WoRMS (World Register of Marine Species). Fish families and taxa are in accordance with the database FishBase (Froese & Pauly, 2016). Digenea families are in alphabetical order, with the digenean taxa described in each family in Portuguese waters, their sampling locality, intermediate and definitive hosts (when known) cercarian group, habitat, and life cycle strategy (obtained by experimental study or inferred

from literature). Figure 1 shows the sampling localities, along the mainland Portuguese Atlantic coast and the Archipelagos of Azores and Madeira, of the molluscs and fishes examined for the presence of digenean parasites. Table 1 gives the geographic coordinates of the sampling localities refered in this work.

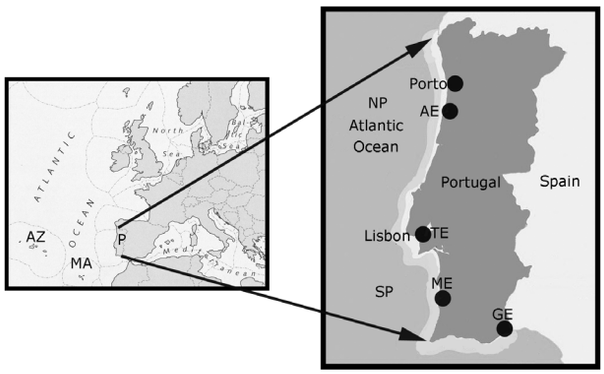

Fig. 1 – Location of the sampling localities along the mainland Portuguese Atlantic coast (P) and the archipelagos of Azores (AZ) and Madeira (MA). (AE) = Aveiro estuary; (TE) = Tagus estuary; (ME) = Mira estuary; (GE) = Guadiana estuary; (NP) = Northern Portuguese coastal waters; (SP) = Southern Portuguese coastal waters.

Table 1 – Geographic coordinates of the sampling localities of digenean hosts.

Sampling locality	Coordinates
Aveiro estuary (AE)	40º 00′ N, 8º 50′ W
Azores Archipelago (AZ)	36º 55′ N-39º 45′ N, 25º W-31º 15′ W
Guadiana estuary (GE)	37º 12′ N, 7º 25′ W
Madeira Archipelago (MA)	32º 22′ N-33º 8′ N, 16º 16′ W-17º 16′ W
Mira estuary (ME)	37º 43′ N, 8º 46′ W
Tagus estuary (TE)	39º 30′ N, 8º 00′ W
Porto, North Portugal (NP)	41º 18′ N, 8º 68′ W

RESULTS

A total of 65 different taxa of digeneans, from 24 different families, were identified infecting molluscs, crabs and fishes from Portuguese marine waters. Adult digeneans were found in the digestive tract of commercial important fishes belonging to pelagic-neritic and pelagic-oceanic, demersal, benthic and bathypelagic environments. Cercariae were found in gastropods and bivalves, metacercariae in bivalves and in shore crabs mainly. Most studies were conducted in the Aveiro estuary (AE) and in sandy beaches and rocky shores in Porto (North Portugal, NP), some in river estuaries to the south of Portugal (Tagus, TE; Mira, ME; and Guadiana, GE) and in the coast of Algarve, in the south of Portugal (SP) (Fig. 1). In these near shore habitats it was possible to elucidate the life cycle strategies in many occasions. Nevertheless many life cycles were not studied locally, and they were suggested from literature data obtained elsewhere. A few studies were done in the archipelagos of Madeira (MA) and Azores (AZ), which represent oceanic habitats. In these cases, elucidation of the life cycle strategies of digeneans were based on previous literature published data.

PARASITE HOST LIST

PHYLUM PLATYHELMINTHES Gegenbaur, 1859
SUBPHYLUM NEODERMATA (Ehlers, 1995)
CLASS TREMATODA Rudolphi, 1808
SUBCLASS DIGENEA Carus, 1863

FAMILY ACANTHOCOLPIDAE **Lühe, 1906**

Stephanostomum pristis (Deslongchamps, 1824) Looss, 1899
Host: *Trisopterus luscus* (Gadidae)
Cercarian group: ophthalmoxiphidiocercariae
Habitat: benthopelagic
Sampling locality: unknown since fish were obtained at Lisbon fish market
Site of infection: intestine
Life cycle strategy: gastropods act as first intermediate hosts, metacercariae are found in bivalves and fish muscles, definitive hosts are piscivorous teleosts (Køie, 1978; Bray *et al*., 2005).
References: Rodrigues *et al*., 1972.

FAMILY ACCACOELIIDAE **Odhner, 1911**

Accacladocoelium petasiporum Odhner, 1928
Host: *Pagellus bogaraveo* (Sparidae)
Cercarian group: unknown
Habitat: oceanic, benthopelagic
Sampling locality: Azores Archipelago (AZ)
Site of infection: stomach
Life cycle strategy: The first intermediate host is unknown, metacercariae are common in gelatinous zooplankton (cnidarians and ctenophores), and adults in fish, most typically sunfishes, *Mola mola* (Gibson *et al*., 2002).

References: Hermida *et al*., 2013, 2014.
Odhnerium sp. Yamaguti, 1934
Host: *Helicolenus dactylopterus* (Sebastidae)
Cercarian group: not known
Habitat: oceanic, benthopelagic
Sampling locality: Azores Archipelago (AZ)
Site of infection: mesenteries
Life cycle strategy: Like other accacoelids intermediate hosts are planktonic organisms, and the usual definitive hosts are sunfishes, where the parasite occurs in the intestine.
References: Sequeira *et al*., 2010.

Paraccacladium Bray & Gibson, 1977 (juveniles)
Host: *Trachurus picturatus* (Carangidae)
Cercarian group: not known
Habitat: oceanic, pelagic
Sampling locatity: Azores Archipelago (AZ)
Site of infection: digestive tract
Life cycle strategy: Ctenophores and jellyfishes act as intermediate hosts. The adults are typical of deep-water Macrouridae. Its presence on *T. picturatus* was considered accidental.
References: Gaevskaya & Kovaleva, 1985.

Tetrochetus coryphaenae Yamaguti, 1934
Host: *Trachurus picturatus*
Cercarian group: not known
Habitat: oceanic, pelagic
Sampling locality: Azores Archipelago (AZ)
Site of infection: digestive tract
Life cycle strategy: metacercariae are found in planktonic invertebrates such as chaetognaths and ctenophores, and pelagic fish are paratenic hosts. The final host are fishes of the genus *Coryphaena* and *Coryphaenoides*.
References: Gaevskaya & Kovaleva, 1985; Bray & Gibson, 1977.

FAMILY APOCREADIIDAE **Skrjabin, 1942**

Homalometron galaicus (= *Apocreadium galaicus*) SanMartin, Alvarez, Quintero & Paniagua, 1995
Host: *Dicologlossa cuneata*, *Microchirus azevia*, *M. variegatus*, *Solea senegalensis* (Soleidae)
Cercarian group: not known
Habitat: coastal waters, benthic
Sampling locality: Atlantic coast of Portugal (NP to SP)
Site of infection: digestive tract
Life cycle strategy: adults in the intestine of marine fishes (Jones *et al*., 2005). No data about other aspects of the life cycle are referred in the literature.
References: Marques *et al*., 2006, 2009, 2011.

FAMILY AZYGIIDAE **Lühe, 1909**

Otodistomum veliporum (Creplin, 1837) Stafford, 1894
Host: *Torpedo torpedo* (Torpedinidae)
Cercarian group: furcocystophorous
Habitat: benthic
Sampling locality: Coast of Algarve (SP)
Site of infection: stomach
Life cycle strategy: this digenean species was first described from the stomach of the deep-water shark, *Hexanchus griseus*. It occurs also in other shark species and in rays. The life cycle includes a gastropod as first intermediate host, fishes can act as paratenic hosts, and elasmobranchs are the final hosts. Metacercariae of *Otodistomum* sp., were recently found in the digestive tract of sole, *Solea solea* and visceral cavity of *Solea kleinii* (Marques *et al*., 2011).
References: Tendeiro & Valdez, 1955.

FAMILY BUCEPHALIDAE **Poche, 1907**

Bucephallus baeri Maillard & Saad-Fares, 1981
Host: *Dicentrarchus labrax* (Moronidae)
Cercarian group: gasterostome
Habitat: coastal sandy shores
Sampling locality: Aveiro estuary (AE)
Site of infection: intestine
Life cycle strategy: the life cycle of this digenean should follow the pattern known for other *Bucephallus* sp. which includes bivalves as first intermediate hosts and benthic or benthopelagic fishes as final hosts (Pina *et al*., 2009b).
References: Santos, 1996.

Bucephallus minimus Stossich, 1887
Host: *Dicentrarchus labrax*
Type of cercaria: gasterostome
Habitat: coastal sandy bottoms
Sampling locality: Aveiro estuary (AE), Douro estuary (Porto, NP)
Site of infection: heart, liver, spleen
Life cycle strategy: cercariae are found in bivalves, metacercariae in fish, such as *Mugil cephalus* (Mugilidae), *Pomatoschistus microps* (Gobiidae), *Sparus aurata* (Sparidae), adults in seabass, *D. labrax* (see Faliex & Morand, 1994).
References: Russell-Pinto, 1993; Russell-Pinto *et al*., 2006; Pina *et al*., 2009b.

Dolichoenterum manteri Tendeiro, 1955
Host: *Conger conger* (Congridae)
Cercarian group: not known
Habitat: coastal sandy shores
Sampling locality: Coast of Algarve (Southern Portugal) (SP)
Site of infection: intestine
Life cycle strategy: no data on the life cycle of this digenean is available in the literature. It was only reported once infecting the intestine of conger eels from coastal waters at the south of Portugal.
References: Tendeiro, 1955.

Prosorhynchus aculeatus Odhner, 1905
Host: *Mytilus galloprovincialis* (Bivalvia, Mytilidae); *Conger conger*
Cercarian group: gasterostome
Habitat: coastal sandy and rocky shores
Sampling locality: Aveiro estuary (AE), Tagus estuary (TE)
Site of infection: stomach, rectum (in fish), branchial arches, muscles (in mussels)
Life cycle strategy: mussels are the first intermediate hosts, metacercariae are found in several fishes (*e.g*. *Solea solea*) and adults in Conger eels, *Conger conger*.
References: Santos & Gibson, 2002; Marques *et al*., 2006, 2009; Durieux *et al*., 2007b; Francisco *et al*., 2010a, b, 2012.

P. crucibulum (Rudolphi, 1819) Odhner, 1905
Host: *Mytilus galloprovincialis* (and other *Mytilus* spp.)
Cercarian group: gasterostome
Habitat: sandy and rocky shores
Sampling locality: Aveiro estuary (AE), Tagus estuary (TE)
Site of infection: kidney, stomach, muscles, digestive tract (of fishes) branchial arches (in mussels)
Life cycle strategy: bivalves (*Mytilus* spp.) are the first intermediate hosts, metacercariae are found in rock shore fishes and flatfishes (*Dicologlossa cuneata*, *Solea kleinii*, *S. lascaris*, *S. senegalensis*, *S. solea*), associated with sandy bottoms, and definitive host is conger eel, *C. conger*, although adults of this digenea were additionally found in *Dicentrarchus labrax*. Furthermore metacercariae of *Prosorhynchus* sp. were found in the common goby, *Pomatoschistus microps* (Freitas *et al*., 2009; Costa JL *et al*., 2012).
References: Santos, 1996; Santos & Gibson, 2002; Durieux *et al*., 2007b; Marques *et al*., 2006, 2009; Francisco *et al*., 2010a, b, 2012.

FAMILY CRYPTOGONIMIDAE **Ward, 1917**

Acanthostomum Looss, 1899
Host: *Pomatoschistus microps* (Gobiidae)
Cercarian group: biocellate, parapleurolophocercous
Habitat: sandy and rocky shores
Sampling locality: Tagus estuary (TE)
Site of infection: digestive tract
Life cycle strategy: since species of the genus *Timoniella* (previously named *Acanthostomum*) have been found in the same locations, it is possible that the present taxon is a *Timoniella* species (see Durieux *et al*., 2007a, b). The present record refers to the occurrence of metacercariae.
References: Costa JL *et al*., 2012.

Timoniella imbutiforme (= *Acanthostomum imbutiforme*) (Molin, 1859) Brooks, 1980
Host: *Solea solea*
Cercarian group: unknown
Habitat: coastal sandy and rocky shores
Sampling locality: Tagus estuary (TE)
Site of infection: muscles
Life cycle strategy: gastropods of the genus *Hydrobia* are the first intermediate hosts, metacercariae are found in muscles of benthic fishes (*Dicentrarchus labrax*, *Solea solea*) and adults in the intestine of conger eels (Durieux *et al*., 2007a).
References: Durieux *et al*., 2007b.

T. prateterita (Looss, 1901) Maillard, 1974
Host: *Dicentrarchus labrax*, *Solea solea*
Cercarian group: biocellate, pleurolophocercous
Habitat: coastal sandy shores
Sampling locality: Aveiro estuary (AE), Tagus estuary (TE)
Site of infection: muscles, intestine
Life cycle strategy: metacercariae found in benthic and benthopelagic fishes such as *Solea solea* and *Dicentrarchus labrax*, adults are parasites of Conger eels, *C. conger*. Nevertheless, Santos (1996) and Maillard (1976) refer to the occurrence of adults in *D. labrax*.
Reference: Santos, 1996; Durieux *et al*., 2007b.

FAMILY DEROGENIDAE **Nicoll, 1910**

Derogenes varicus (Müller 1784) Looss, 1901
Host: *Dicentrarchus labrax*, *Dicologlossa cuneata*, *Microchirus azevia*, *M. variegatus*, *Solea kleinii*, *S. lascaris*, *S. senegalensis*, *Pagellus bogaraveo* (Sparidae) *Platichthys flesus* (Pleuronectidae) *Scophthalmus rombus* (Scophthalmidae)
Cercarian group: cystophorous
Habitat: pelagic, benthopelagic
Sampling locality: Azores Archipelago (AZ), Atlantic coast of North Portugal (NP)

Site of infection: digestive tract, gills
Life cycle strategy: gastropods are first intermediate hosts, calanoid and harpacticoid copepods ingest free-swimming cercariae, small fishes (gobids) and flatfishes harbour immature stages and adults develop in benthopelagic or demersal fishes (Køie, 1979). This digenean was first known from gastropods as *Cercaria appendiculata*.
References: Carvalho-Varela & Cunha-Ferreira, 1987; Santos, 1996; Marques *et al*., 2006, 2009, 2010, 2011; Hermida *et al*., 2013, 2014.

FAMILY DIPLOSTOMIDAE **Poirier, 1886**

Diplostomum sp. von Nordmann, 1832
Host: *Platichthys flesus*
Cercarian group: furcocercous
Habitat: coastal sandy shores
Sampling locality: Atlantic coast of North Portugal (NP)
Site of infection: eyes
Life cycle strategy: metacercariae are found in several fish species. Final hosts are marine birds. There are several species of *Diplostomum*, with *D. paracaudum* being the most similar to the present specimens, based on 18S + ITS1 + 5.8S region of the rDNA (see Cavaleiro *et al*., 2012).
References: Cavaleiro *et al*., 2012.

FAMILY FELLODISTOMIDAE **Nicoll, 1909**

Lomasoma stephanskii Dollfus, 1960
Host: *Microchirus variegatus*
Cercarian group: furcocercous
Habitat: coastal sandy shores
Sampling locality: Atlantic coast of Portugal (NP)
Site of infection: digestive tract
Life cycle strategy: the life cycle of this digenean is unknown to date (see Alvarez *et al*., 2002). As a fellostomid it is assumed that cercariae are furcocercous.
Reference: Marques *et al*., 2006, 2009, 2011.

Monascus filiformis (Rudolphi, 1819) Looss, 1907
Host: *Trachurus picturatus*
Cercarian group: furcocercous
Habitat: oceanic, benthopelagic and epi-pelagic
Sampling locality: Atlantic coast of Portugal (NP)
Site of infection: intestine
Life cycle strategy: bivalves are first intermediate hosts, small fishes can act as paratenic hosts and several fish species act as definitive hosts. Transmission in coastal habitats appears to be from bivalves to fish, whereas in off shore habitat requires a fish as transport host. Final hosts are mainly carangids (Køie, 1979; Bray & Gibson, 1980; Martorelli & Cremonte, 1998).
References: Hermida *et al*., 2015.

Proctoeces maculatus (Looss, 1901) Odhner, 1911
Host: *Platichthys flesus*
Cercarian group: furcocercous
Habitat: coastal sandy shores
Sampling locality: Aveiro estuary (AE)
Site of infection: digestive tract
Life cycle strategy: bivalves, such as *Mytilus galloprovincialis* (Mytilidae) as first intermediate hosts, harbouring the cercariae, polychaetes as second hosts and labrids and sparids usually as definitive hosts (Antar & Gargouri, 2016). However, progenetic metacercariae, and adults, were found in gastropods (see Dollfus, 1965; Lauckner, 1980) and bivalves (*Mytilus edulis*) (Stunkard & Uzmann, 1959).
References: Dias & Serrano, 1972; Marques *et al*., 2009, 2010, 2011.

Tergestia sp. Stossich, 1899
Host: *Trachurus picturatus*
Cercarian group: furcocercous
Habitat: oceanic, epi-pelagic
Sampling locality: Atlantic coast of Portugal (NP)
Site of infection: intestine
Life cycle strategy: cercariae occur in planktonic organisms, pelagic fishes as definitive hosts. *Tergestia laticollis* (Rudolphi, 1819) Stossich 1899 was described from *Trachurus trachurus* (see Bray & Gibson, 1980). It is possible that present taxon corresponds to *T. laticollis*.
References: Hermida *et al*., 2015.

FAMILY GYMNOPHALLIDAE **Odhner, 1905**

Parvatrema minutum (= *Meiogymnophallus minutus*) Cobbold, 1859
Host: *Cerastoderma edule* (Bivalvia, Cardiidae)
Cercarian group: furcocercous
Habitat: coastal sandy and rocky shores
Sampling locality: Aveiro estuary (AE)
Site of infection: mantle margin
Life cycle strategy: the cercaria are found in gills of cockles, such as *Scrobicularia plana*, metacercaria in mantle margin of cockles, such as *Cerastoderma edule* and adults in the intestine of marine birds, oystercatchers.
References: Russell-Pinto, 1990; Russell-Pinto & Bartoli, 1992; Russell-Pinto *et al*., 1996.

Parvatrema fossarum (= *Meiogymnophallus fossarum*) Bartoli, 1965
Host: *Cerastoderma edule*
Cercarian group: furcocercous
Habitat: coastal sandy and rocky shores
Sampling locality: Aveiro estuary (AE)
Site of infection: mantle margin
Life cycle strategy: this digenean should include a gastropod as first intermediate host, and bivalves as second hosts, with adults in the intestine of oystercatchers. Nevertheless the life cycle is still unknown.
References: Russell-Pinto & Bartoli, 1992.

Gymnophallus choledochus Odhner, 1900
Host: *Cerastoderma edule*
Cercarian group: furcocercous
Habitat: coastal sandy and rocky shores
Sampling locality: Aveiro estuary (AE)
Site of infection: mantle of the bivalves
Life cycle strategy: bivalves, as *C. edule*, harbour the cercaria and metacercaria. Polychaetes such as *Nereis* spp. can also be infected with metacercaria. The definitive hosts are ducks, *Tadorna tadorna*. Recently Rangel & Santos (2009) found a polychaete, *Diopatra neapolitana*, as second intermediate host of this digenean.
References: Russell-Pinto, 1993.

Parvatrema rebecqui (= *Gymnophallus rebecqui*) Bartoli, 1983
Host: *Cerastoderma edule*, *C. glaucum*
Cercarian group: furcocercous
Habitat: coastal and sandy rocky shores
Sampling locality: Aveiro estuary (AE)
Site of infection: mantle
Life cycle strategy: bivalves harbour metacercariae and birds, like the common duck are the definitive hosts. The first intermediate host is still unknown however it is assumed that cercariae belong to the furcocercous type.
References: Russell-Pinto, 1993.

FAMILY HETEROPHYIDAE **Braun, 1901**

Cryptocotyle lingua Creplin, 1825
Host: *Pomatochistus microps*
Cercarian group: lophocercous
Habitat: coastal and sandy coastal shores
Sampling locality: In the Aveiro estuary (AE), and other estuaries in central and southern Portugal
Site of infection: digestive tract
Life cycle strategy: cercariae develop in gastropods of the genus *Littorina*, metacercaria are found in several fishes (*e.g*. *Pomatoschistus microps*, *Pleuronectes platessa*, *Solea solea*) and marine fish eating birds are the definitive hosts (James, 1968; Lauckner, 1980).
Reference: Carvalho Varela *et al*., 1981; Freitas *et al*., 2009; Costa JL *et al*., 2012.

FAMILY HAPLOSPLANCHNIDAE **Poche, 1926**

Schikhobalotrema longivesiculatum Orecchia & Paggi, 1975
Host: *Parablennius parvicornis* (Bleniidae)
Cercarian group: biocellate, distomatous cercariae
Habitat: rocky shores
Sampling locality: Madeira Archipelago (MA)
Site of infection: intestine
Life cycle strategy: the life cycle is currently unknown. It is possible that gastropods are first intermediate hosts and several marine fishes are definitive hosts. An interesting feature of the life cycle of these haplosplanchnids is that the metacercariae encyst on vegetation and herbivorous fishes are the final hosts. The species was first described from *Blennius sanguinolentus* (see Orecchia & Paggi, 1975).
References: Gibson & Costa, 1997.

FAMILY HAPLOPORIDAE **Nicoll, 1914**

Haploporus benedeni Stossich, 1887
Host: *Mugil cephalus* (Mugilidae)
Cercarian group: gymnocephalous
Habitat: coastal sandy shores, estuarine
Sampling locality: coastal waters of Portugal
Site of infection: digestive tract
Life cycle strategy: the life cycle of this digenean includes gastropods of the superfamily Rissooidea, and the definitive hosts are estuarine and freshwater herbivorous fishes (Overstreet & Curran, 2005).
Reference: Carvalho Varela *et al*., 1981.

FAMILY HEMIURIDAE **Looss, 1899**

Ectenurus lepidus Looss, 1907
Host: *Solea solea*, *Trachurus picturatus*, *T. trachurus*
Cercarian group: cystophorous
Habitat: oceanic, pelagic, sandy shores
Sampling locality: Atlantic coast of Portugal (NP), Azores Archipelago (AZ)
Site of infection: stomach
Life cycle strategy: gastropods as first intermediate hosts,

second intermediate hosts planktonic organisms such as copepods and chaetognaths (metacercariae) and fishes as definitive hosts (Gibson & Bray, 1986).
Reference: Gaevskaya & Kovaleva, 1985; Carvalho Varela & Cunha-Ferreira, 1987; Mackenzie *et al*., 2008; Hermida *et al*., 2015.

Ectenurus virgulus Linton, 1910
Host: *Trachurus picturatus*
Cercarian group: cystophorous
Habitat: oceanic, pelagic
Sampling locality: Azores Archipelago (AZ)
Site of infection: stomach
Life cycle strategy: gastropods as first intermediate hosts, second intermediate hosts planktonic organisms such as copepods and chaetognaths (metacercariae) and fishes as definitive hosts (Gibson & Bray, 1986).
Reference: Gaevskaya & Kovaleva, 1985.

Glomericirrus macrouri (Gaevskaya, 1975) Gaevskaya, 1979
Host: *Pagellus bogaraveo*
Cercarian group: cystophorous
Habitat: benthopelagic
Sampling locality: Northern Portuguese Atlantic coast (NP)
Site of infection: stomach
Life cycle strategy: although the life cycle is not known it is suggested it follows the pattern of other hemiurids, having as first intermediate hosts planktonic invertebrates and benthopelagic fishes as definitive hosts (see Gibson & Bray, 1986).
Reference: Hermida *et al*., 2013, 2014.

Hemiurus appendiculatus (Rudolphi, 1802) Looss, 1899
Host: *Alosa alosa*, *A. falax* (Clupeidae) *Pomatoschistus microps*
Cercarian group: cystophorous
Habitat: estuarine, coastal sandy bottoms
Sampling locality: Atlantic coast of Portugal, and adjacent the river estuaries
Site of infection: stomach
Life cycle strategy: as other hemiurids should include gastropods as first intermediate hosts, metacercariae in planktonic invertebrates and fishes as definitive hosts (Gibson & Bray, 1986).
Reference: Tendeiro & Valdez, 1955; Rodrigues *et al*., 1972; Costa JL *et al*., 2012.

Hemiurus communis Odhner, 1905
Host: *Dicentrarchus labrax*, *Pagellus bogaraveo*, *Solea solea*
Cercarian group: cystophorous
Habitat: coastal sandy bottoms
Sampling locality: Northern Portuguese Atlantic coast (NP)
Site of infection: stomach
Life cycle strategy: gastropods are first intermediate hosts, free swimming cercariae invade second intermediate hosts, calanoid copepods, and benthic demersal fishes are the definitive hosts.
Reference: Carvalho Varela & Cunha-Ferreira, 1987; Santos, 1996; Hermida *et al*., 2013, 2014.

Hypohepaticola Yamaguti, 1934
Host: *Helicolenus dactylopterus* (Sebastidae)
Cercarian group: unknown
Habitat: coastal waters, benthopelagic
Sampling locality: Atlantic coast of Portugal
Site of infection: digestive tract
Life cycle strategy: although the life cycle is unknown, the diet of *Helicolenus dactylopterus*, a benthic deep-water fish, is based on crustaceans and fishes, which suggests that intermediate hosts could be benthic crustaceans.
Reference: Sequeira *et al*., 2010.

Lecithochirium furcolabiatum (Jones, 1933) Dawes, 1947
Host: *Gibbula umbilicalis* (Gastropoda, Trochidae), *Conger conger*, *Lipophrys pholis* (Blenniidae).
Cercarian group: cystocercous
Habitat: coastal sandy and rocky shores, oceanic
Sampling locality: Northern Portuguese Atlantic coast (NP) Madeira Archipelago (MA)
Site of infection: gonads (cercariae), mesenteries (metacercariae), stomach (adult)
Life cycle strategy: cercariae in hepatopancreas and gonads of gastropods, in copepods (2nd intermediate hosts), metacercariae in rock pool fishes (*Lipophrys pholis*, *Pomatoschistus microps*), adults in conger eels, *C. conger* and other fishes.
References: Santos & Eiras, 1995; Costa *et al*., 2009, 2016.

L. grandiporum (= *L. fusiforme* Lühe, 1901) (Rudolphi, 1819) Lühe, 1901
Host: *Conger conger*
Cercarian group: cystophorous
Habitat: benthic rocky shores
Location: Madeira Archipelago
Site of infection: stomach
Life cycle strategy: *Lecithochirium grandiporum* was revised by Bartoli & Gibson (2007) in moray eel, *Muraena helena* (Muraenidae). It was concluded that previously described

species *L. fusiforme* from conger eels was a junior synonym of *L. grandiporum*. This taxon thus occurs in conger eels and moray eels.
References: Tendeiro & Valdez, 1955; Costa *et al*., 2009.

L. musculus (Looss, 1907) Nasir & Diaz, 1971
Host: *Aphanopus carbo* (Trichiuridae), *Dicentrarchus labrax*, *Conger conger*
Cercarian group: cystophorous
Habitat: oceanic, bathypelagic, benthic rocky shores
Sampling locality: Azores Archipelago (AZ), Madeira Archipelago (MA), Aveiro estuary (AE)
Site of infection: digestive tract, stomach, intestine
Life cycle strategy: although the life cycle is unknown, it is suggested that gastropods act as first intermediate hosts, while free swimming cercariae infect planktonic copepods, which transmit the parasite to gobiids such as *Pomatoschistus microps* (metacercariae) and to the definite hosts. Its occurrence in a deep-water fish (*A. carbo*) could be an accidental infection since this digenean has been described from benthic fishes.
References: Santos, 1996; Freitas *et al*., 2009; Costa *et al*., 2009; Santos *et al*., 2009; Costa JL *et al*., 2012.

L. rufoviridae (Rudolphi, 1819) Lühe, 1901
Host: *Arnoglossus laterna* (Bothidae), *Citharus linguatula* (Citharidae), *Conger conger*, *Dicologlossa cuneata*, *Lepidorhombus boscii* (Scophthalmidae), *Microchirus azevia*, *Platichthys flesus*, *Scophthalmus maximus*, *S. rombus* (Scophthalmidae)
Cercarian group: cystophorous
Habitat: benthic coastal waters, rocky shores
Sampling locality: Northern Portuguese Atlantic coast (NP)
Site of infection: digestive tract
Life cycle strategy: this digenean is a parasite characteristic of eels and conger eels, although it occurred also in different flatfish species. The low prevalence of this digenean in the examined flatfishes suggests that they are not the usual definitive hosts (see Gibson & Bray, 1986).
References: Tendeiro & Valdez, 1955; Marques *et al*., 2006, 2009, 2010, 2011.

Lecithocladium excisum (Rudolphi, 1819) Lühe, 1901
Host: *Pagellus bogaraveo*, *Scomber scombrus*, *S. colias* (Scombridae), *Trachurus picturatus*
Cercarian group: cystophorous
Habitat: oceanic, epi-pelagic and benthopelagic
Sampling locality: Azores Archipelago (AZ), Atlantic coast of Portugal (NP and SP)
Site of infection: stomach
Life cycle strategy: cercariae in benthic invertebrates such as harpacticoid copepods as first intermediated hosts, polychaetes and ctenophores act as second intermediate hosts, harbouring the metacercariae, pelagic fishes as definitive hosts (Køie, 1991).
References: Gaevskaya & Kovaleva, 1985; Rego *et al*., 1985; Shukhgalter, 2004; Hermida *et al*., 2013, 2014.

FAMILY HIMASTHLIDAE **Odhner, 1910**

Himasthla quissetensis (Miller and Northup, 1926) Stunkard, 1938
Host: *Tritia reticulata* (= *N. reticulatus*) (Gastropoda, Nassariidae), *Cerastoderma edule* (Bivalvia, Cardiidae)
Cercarian group: leptocercous
Habitat: coastal sandy shores
Sampling locality: Aveiro estuary (AE)
Site of infection: mantle of *C. edule*
Life cycle strategy: the life cycle was studied by Stunkard (1938) from molluscs and birds of Woods Hole (USA). The cercariae found in the gastropod *Nassa obsoleta*, metacercariae are found in gills, mantle and foot of several bivalves and adults in herring gull, *Larus argentatus*.
Reference: Russell-Pinto, 1993; Russell-Pinto *et al*., 2006; Rato *et al*., 2009.

Himasthla elongata (Mehlis, 1831) Dietz, 1909
Host: *C. edule*
Cercarian group: leptocercous
Habitat: sandy and rocky shores
Sampling locality: Aveiro estuary (AE)
Site of infection: foot of *C. edule*
Life cycle strategy: metacercariae were found encysted in the foot of the second host, *C. edule*. Probably the first intermediate host is a gastropod and the definitive host a coastal marine bird.
References: Russell-Pinto *et al*., 2006.

Himasthla interrupta Loos-Frank, 1967
Host: *C. edule*
Cercarian group: leptocercous
Habitat: coastal sandy and rocky shores
Sampling locality: Aveiro estuary (AE)
Site of infection: mantle and foot
Life cycle strategy: metacercariae were found encysted in the mantle and foot of the second host, *C. edule*. The definitive hosts are birds from the family Laridae.
References: Russell-Pinto *et al*., 2006.

FAMILY HIRUDINELLIDAE **Dollfus, 1932**

Botulus microporus (Monticelli, 1889) n. comb.
Host: *Alepisaurus ferox* (Alepisauridae)
Cercarian group: unknown
Habitat: oceanic, epi-pelagic to bathypelagic
Sampling locality: Madeira Archipelago (MA)
Site of infection: intestine
Life cycle strategy: The life cycle is unknown. Adults are parasites in the stomach of *Alepisaurus* spp. It was first described from Madeira Archipelago but it occurs in other regions of the North Atlantic and the Pacific Ocean (see Gibson & Bray, 1977).
Reference: unpublished results of present authors.

Lampritrema miescheri (Zschokke, 1890) Margolis, 1962
Host: *Trachurus picturatus*
Cercarian group: unknown
Habitat: oceanic, epi- pelagic
Sampling locality: Azores Archipelago (AZ)
Site of infection: digestive tract, stomach, gills
Life cycle strategy: adults are parasites of the stomach of fishes, and sometimes of the gills. Immature specimens have been found in salmonids (Gibson & Bray, 1977).
References: Gaevskaya & Kovaleva, 1985.

FAMILY LEPOCREADIIDAE **Odhner, 1905**

Clavogalea trachinoti (Fischthal and Thomas, 1968) Bray & Gibson, 1990
Host: *Scomber colias*
Cercarian group: cystophorous
Habitat: oceanic, epipelagic
Sampling locality: Madeira Archipelago (MA)
Site of infection: stomach, digestive tract
Life cycle strategy: the life cycle was studied experimentally by Køie (1991). Cercariae collected from gastropods were infective to copepods and metacercariae were developed. Metacercariae were also found in naturally infected ctenophores and holoplanktonic polychaetes, *Tomopteris helgolandica*, invertebrates (ctenophores and chaetognaths), which agrees well with the diet of mackerels (Køie, 1975, 1991).
References: Costa *et al*., 2011.

Lepocreadium album Stossich, 1890
Host: *Pagellus bogaraveo*
Cercarian group: *Cercaria setifera*, tricocercous
Habitat: oceanic, benthopelagic and coastal sandy shores
Sampling locality: Azores Archipelago (AZ), Aveiro estuary (AE)
Site of infection: digestive tract
Life cycle strategy: the life cycle of lepocreadiids includes cercariae tricocercous (tailed with setae), which are parasites of molluscs, metacercariae infect polychaetes, gastropods and bivalves, also ctenophores. *Cercaria setifera* was found in the gastropod *Tritia reticulata* (= *Nassarius reticulatus*) in Aveiro estuary. Adults may infect benthic fishes (flatfishes) or benthopelagic fishes (*P. bogaraveo*) (see Hassanine, 2006; Soares, 2015).
Reference: Russell-Pinto *et al*., 2006; Hermida *et al*., 2013, 2014; Soares, 2015.

Opechona bacillaris (Molin, 1859) Dollfus, 1927
Host: *Scomber scombrus*, *Scomber colias*
Cercarian group: ophthalmotrichocercous
Habitat: oceanic, epi-pelagic
Sampling locality: Azores Archipelago (AZ); Atlantic coast of South Portugal (SP)
Site of infection: digestive tract, stomach, intestine
Life cycle strategy: gastropods of the genus *Tritia* (= *Nassarius*) are the first intermediate hosts. Metacercariae have been found in planktonic invertebrates such as ctenophores and chaetognaths. Adults are developed in a range of pelagic fishes (Køie, 1975; Bray & Gibson, 1990).
References: Rodrigues *et al*., 1972; Rego *et al*., 1985; Shukhgalter, 2004.

Prodistomum orientale (Layman, 1930) Bray & Gibson, 1990
Host: *Scomber colias*
Cercarian group: trichocercous
Habitat: oceanic, epi-pelagic
Sampling locality: Madeira Archipelago (MA)
Site of infection: digestive tract
Life cycle strategy: although the life cycle was not studied to date, it probably follows the pattern for other lepocreadids as described for *Opechona* (Bray & Gibson, 1990).
References: Costa *et al*., 2011.

FAMILY MICROPHALLIDAE **Travassos, 1920**

Gynaecotyla adunca (Linton 1905) Yamaguti 1934
Host: *Tritia reticulata*, *Carcinus maenas* (Decapoda, Carcinidae)
Cercarian group: leptocercous xiphidiocercaria
Habitat: coastal sandy and rocky shores
Sampling locality: Aveiro estuary (AE)
Site of infection: hepatopancreas of *T. reticulata*, antennal

glands of *C. maenas*
Life cycle strategy: gastropods of the genus *Tritia* harbor the cercariae and crabs are the second intermediate hosts, where the metacercariae develop. Birds are definitive hosts. This digenea was previously classified as "*Cercaria sevillana*". A new second host, the crab, *Polybius henslowii*, collected from Aveiro estuary, was found infected with metacercariae of this digenean in 2015 (Soares, 2015). This species was referred as *Gynaecotyla longiintestinata* Leonov, 1958 in Russell-Pinto & Bartoli (2002).
References: Russell-Pinto & Bartoli, 2002; Pina *et al*., 2007.

Maritrema portucalensis Pinto, Russell-Pinto & Rodrigues, 2011
Host: *Carcinus maenas*
Cercarian group: ophtalmoxiphidiocercous
Habitat: coastal sandy rocky shores
Sampling locality: Aveiro estuary (AE)
Site of infection: metacercariae in gills of crabs
Life cycle strategy: cercariae are found in gastropods, namely *Hydrobia ulvae*, metacercariae are parasites of crabs, namely *Carcinus maenas*, and adults developed in marine birds.
References: Pina *et al*., 2011a.

Microphallus primas Jägerskiöld, 1908
Host: *Carcinus maenas*
Cercarian group: ophthalmoxiphidiocercaria
Habitat: coastal sandy and rocky shores
Sampling locality: Aveiro estuary (AE)
Site of infection: hepatopancreas, gonads
Life cycle strategy: cercariae are found in gastropods, *Hydrobia ulvae*, metacercariae in crabs, *C. maenas* and adults develop in the intestine of marine birds, *Larus cachinnans* (Saville & Irwin, 2005; Sanmartin *et al*., 2005).
References: Pina *et al*., 2011b.

FAMILY MONORCHIIDAE **Odhner, 1911**

Monorchis parvus Looss, 1902
Host: *C. edule*
Cercarian group: unknown
Habitat: coastal sandy and rocky shores
Sampling locality: Aveiro estuary (AE)
Site of infection: Several tissues of the *C. edule* infected with cercariae and metacercariae
Life cycle strategy: the life cycle was developed experimentally by Bartoli *et al*. (2000). *Diplodus sargus* (Sparidae) was sucessfully infected with metacercariae collected from *C. edule* and adults were found in the intestine of this fish.
References: Russell-Pinto *et al*., 2006.

FAMILY OPECOELIDAE **Ozaki, 1925**

Cainocreadium labracis (Dujardin, 1845) Nicoll, 1909
Host: *Gibbula umbilicalis* (Gastropoda, Trochidae); *D. labrax*
Cercarian group: cotylocercous
Habitat: coastal sandy and rocky shores
Sampling locality: Atlantic coast of North Portugal (NP)
Site of infection: gonads and hepatopancreas of gastropod, intestine of fish.
Life cycle strategy: the life cycle includes the topshell *G. umbilicalis* and other topshells of this genus as first intermediate hosts, fishes of the families Gobiidae and Syngnathidae are infected with metacercariae on the fins and skin and the final host is *D. labrax* (Maillard, 1971; Born-Torrigos *et al*., 2012, 2014).
References: Santos, 1996; Costa *et al*., 2016.

Helicometra fasciata (Rudolphi, 1819) Odhner, 1902
Host: *Lepidorhombus boscii* (Scophthalmidae), *Lipophrys pholis* (Blenniidae)
Cercarian group: cotylocercous
Habitat: coastal sandy and rocky shores
Sampling locality: North Atlantic coast of Portugal (NP)
Site of infection: digestive tract, intestine
Life cycle strategy: cercariae develop in gastropods, metacercariae in shrimps, adults in several fish species.
References: Santos & Eiras, 1995; Marques *et al*., 2006, 2009, 2010, 2011.

Macvicaria soleae (Dujardin, 1845) Gibson & Bray, 1982
Host: *Dicoglossa cuneata*, *Microchirus azevia*, *M. variegatus*, *Platichthys flesus*, *Solea lascaris*, *S. senegalensis*, *S. solea*
Cercarian group: cotylocercous
Habitat: coastal sandy and rocky shores
Sampling locality: Atlantic coast of Portugal
Site of infection: digestive tract of fish hosts
Life cycle strategy: the life cycle starts with cercarial development in gastropods, which can also function as second intermediate hosts, as the cercariae have a sit- and wait behavior, and the final hosts are fishes (Born-Torrigos *et al*., 2014).
References: Durieux *et al*., 2007a, b; Marques *et al*., 2006, 2009, 2010, 2011.

Pachycreadium carnosum (Rudolphi, 1819)

Cortini & Ferretti, 1959
Host: *Pagellus bogaraveo*
Cercarian group: unknown
Habitat: oceanic, benthopelagic
Sampling locality: Azores Archipelago (AZ), Madeira Archipelago (MA)
Site of infection: pyloric caeca, intestine
Life cycle strategy: this digenean seems to be specific of Sparidae. Morato *et al*. (2001) identified only one species of gastropod in the diet of *P. bogaraveo* from the Azores Archipelago, *Diacria trispinosa*, occurring in 6.3% of examined stomachs. If this is a first intermediate host candidate, it could explain the low prevalence of this digenean in this fish host.
References: Hermida *et al*., 2013, 2014.

Pycnadenoides senegalensis Fischthal & Thomas, 1972
Host: *Pagellus bogaraveo*
Cercarian group: unknown
Habitat: oceanic, benthopelagic
Sampling locality: Azores Archipelago (AZ), Atlantic coast of Portugal
Site of infection: pyloric caeca, intestine
Life cycle strategy: no data is presently available about the life cycle of this digenean. Gastropods and fishes could act as first and second intermediate hosts. Since the prevalence is higher in coastal waters of Portugal, it appears that the abundance of intermediate hosts is higher here. Furthermore this parasite was found in the Western Mediterranean in sparid fishes (Bartoli *et al*., 1989), and mainland Portugal digenean species show strong connections with the western Mediterranean digenean fauna (Gibson & Costa, 1997; Marques *et al*., 2009).
Reference: Hermida *et al*., 2013, 2014.

FAMILY RENICOLIDAE **Dollfus, 1939**

Renicola roscovitus Stunkard, 1932
Host: *Cerastoderma edule*
Cercarian group: leptocercous
Habitat: coastal sandy and rocky shores
Sampling locality: Aveiro estuary (AE)
Site of infection: palps of *C. edule*
Life cycle strategy: this digenean infects gastropods of the genus *Littorina*, where cercaria develop, the second host are bivalves, (in the present study metacercariae were found in *C. edule*), and the definitive hosts are marine birds (Lauckner, 1980, 1983).
References: Russell-Pinto *et al*., 2006.

FAMILY STRIGEIDAE **Railliet, 1919**

Cardiocephaloides longicollis (Rudolphi, 1819) Dubois, 1982
Host: *Tritia reticulata*
Cercarian group: furcocercous
Habitat: coastal sandy and rocky shores
Sampling locality: Aveiro estuary (AE)
Site of infection: digestive gland
Life cycle strategy: gastropods such as *T. reticulata* are first intermediate hosts infected with cercariae, and birds are the definitive hosts. Sanmartin *et al*. (2005) found adults of this digenean in the marine bird, *Larus cachinnans*. In Russell-Pinto *et al*. (2006) this taxon was classified as "*Cardiocephallus longicollis*".
References: Russell-Pinto *et al*., 2006.

FAMILY SYNCOELIIDAE **Looss, 1899**

Copiatestes filiferus (= *Syncoelium filiferum*) (Leuckart in Sars, 1885) Gibson & Bray, 1977
Host: *Trachurus picturatus*
Cercarian group: unknown
Habitat: oceanic, epi-pelagic
Sampling locality: Azores Archipelago (AZ)
Site of infection: digestive tract
Life cycle strategy: this parasite occurs in several fish species. Metacercariae have been found in euphausid crustaceans, and in some occasions free floating metacercariae were found (see Gibson & Bray, 1977). The usual site of infection is the buccal cavity and gill-arch of fishes.
References: Gaevskaya & Kovaleva, 1985.

FAMILY ZOOGONIDAE **Odhner, 1902**

Brachyenteron helicoleni Bray & Kuchta, 2006
Host: *Pagellus bogaraveo*
Cercarian group: unknown
Habitat: oceanic, benthopelagic
Sampling locality: Atlantic coast of Portugal
Site of infection: intestine
Life cycle strategy: *Brachyenteron helicoleni* has been described as a deep-water parasite infecting *Helicolenus dactylopterus* (Bray & Kuchta, 2006). *P. bogaraveo* extends its depth range to 700 m deep, and consumes myctophids and other prey typical of deep-waters (Morato *et al*., 2001). It is therefore to expect that it would be infected by parasite species occurring in deep-waters.
References: Hermida *et al*., 2013, 2014.

Diphterostomum vividum (Nicoll, 1912) Bray & Gibson, 1986
Host: *Pagellus bogaraveo*
Cercarian group: unknown
Habitat: oceanic, benthopelagic
Sampling locality: Atlantic coast of Portugal (AP) and Madeira Archipelago (MA)
Site of infection: intestine
Life cycle strategy: apparently it is a rare species, described from the blackspot seabream only (see Bray & Gibson, 1986).
References: Hermida *et al*., 2013, 2014.

D. brusinae (Stossich, 1888) Stossich, 1903
Host: *Tritia reticulata*, *Cerastoderma edule*, *Mytilus galloprovinciallis*, *Diplodus sargus* (Sparidae)
Cercarian group: tailess xiphidiocercaria
Habitat: coastal sandy shores
Sampling locality: Aveiro estuary (AE)
Site of infection: digestive gland of gastropods, intestine of fishes
Life cycle strategy: gastropods are the first intermediate hosts, metacercariae can be found in bivalves, *Cerastoderma edule*, and in mussels, *Mytilus galloprovincialis*. Adults are parasites of the intestine of fishes. However in several occasions it was found that gastropods can be first and second intermediate hosts, and additionally cercariae can encyst in plants, hydroids and sponges. Sparidae is one of the families elected as definitive hosts, but other fish families are definitive hosts such as Labridae and Gobiidae (see Bray & Gibson, 1986).
References: Russell-Pinto, 1990; Russell-Pinto & Bowers, 1998; Russell-Pinto & Bartoli, 2002; Russell-Pinto *et al*., 2006; Pina *et al*., 2009a; Francisco *et al*., 2010, 2011.

Zoogonoides viviparus (Olsson, 1868) Odhner, 1902
Host: *Pomatoschistus microps*
Cercarian group: tailess xiphidiocercaria
Habitat: coastal sandy shores and estuaries
Sampling locality: Aveiro (AE), Tagus (TE), Mira (ME) and Guadiana (GE) estuaries.
Site of infection: digestive tract
Life cycle strategy: the first intermediate hosts are gastropods, metacercariae can be found in gastropods, bivalves, echinoderms, and polychaetes, and adults are parasites of the intestine of fishes from different families, all of them of benthic fishes (Bray & Gibson, 1986).
References: Costa JL *et al*., 2012.

Zoogonus rubellus (Olsson, 1868) Odhner, 1902
Host: *Dicologlossa cuneata*, *Platichthys flesus*, *Solea senegalensis*
Type of cercaria: tail-less xiphidiocercaria
Habitat: coastal sandy shores
Sampling locality: Southern Atlantic coast of Portugal (SP)
Site of infection: digestive tract
Life cycle strategy: gastropods are first intermediate hosts and annelids the second hosts. Limpets and echinorderms can also be second hosts. Pleuronectiformes and Perciformes seem to be the fish families, which most likely act as definitive hosts (Bray & Gibson, 1986).
References: Marques *et al*., 2006, 2009, 2010, 2011.

DISCUSSION

The present checklist compiles the presently known digenea taxa, found in molluscs, crabs and fishes from Portuguese marine zones. However, we are aware and hope, that more new taxa will be added to this checklist in the near future, due to the increased interest of investigations, in the field of marine parasitology. Some digeneans hereby referred are true parasites of their definitive hosts, others can be regarded as accidental infections. Such is the case of *Accacladocoelium* sp. which is a digenean taxon typical of sunfishes (Gaevskaya, 2002; Ahuir-Baraja *et al*., 2015) with gelatinous zooplankton acting as intermediate hosts (Bray & Gibson, 1977). The occurrence of *Accacladocoelium petasiporum* in *P. bogaraveo* from the Azores Archipelago appears to be an accidental infection (Hermida *et al*., 2014) and indicates that both the intermediate and final hosts are available in that region. *Glomericirrus macrouri* is a typical digenean of macrourid, which explains the very low prevalence in *P. bogaraveo*, a sparid (Bray & Gibson, 1986; Hermida *et al*., 2014). Many of the digeneans hereby reported occur in several fish species, they are generalists, some show family specificity, whereas others may be host specific. Perhaps this late case applies to the bucephalid, *Dolichoenterum manteri*, which was found only once in conger eels by Tendeiro (1955). Some digeneans were not identified to species level and thus require further study including molecular characterization. For example, *Tergestia* sp. found in *T. picturatus*, could be *T. laticollis* (Rudolphi, 1819) Stossich, 1899, which is a digenean occurring in the intestine of horse mackerels (Bray & Gibson, 1980). These authors referred to a *Cercaria kenti* that could represent the cercarial form of this digenean, and was found off the coast of Portugal. To link the cercarial type with the adult form it is necessary to collect fresh specimens and to use molecular approaches (Born-Torrigos *et al*., 2012).

Many digenean parasites share the first intermediate host, but show a diversification of their transmission pathways and final hosts. Such is the case of the gastropod *Tritia reticulata* (= *Nassarius reticulatus*) which is parasitized by cercariae of *Cardiocephaloides longicollis* (refered as *Cardiocephallus longicollis* by Russell-Pinto *et al*., 2006), *Diphtherostomum brusinae*, *Gynaecotyla adunca*, *Himasthla quissetensis*, and *Lepocreadium album* (Russell-Pinto *et al*., 2006; Rato *et al*., 2009; Soares, 2015), *Littorina litttorea* parasitized with at least 8 digenean taxa (James, 1968; Costa *et al*., 2016) and *Gibbula umbilicalis* with at least 2 digenean taxa (Born-Torrigos *et al*., 2012; Costa *et al*., 2016). Adults of these digenean species complete their development in different final hosts. This diversity of transmission pathways ensures success of survival of the parasite and shows adaptative strategies of the parasites to their environmental conditions (Bush *et al*., 2001; Esch *et al*., 2002; Marcogliese, 2002). High prevalences of microphallid digeneans in gastropods and benthic crustaceans, for example, suggested that seabirds were common in the food web (Zander *et al*., 2000; Mouritsen & Poulin, 2002). The digenean complex life cycles, presenting more than one intermediate host, and paratenic hosts, point to adaptations of the parasite, to a very dilute environment, such as an oceanic habitat, where the encounter of a parasite and its suitable host, requires more effort (Marcogliese, 2002). In some occasions, infection with digenean cercarial stages, leads to castration due to heavy infestation of gonads and replacement of reproductive tissue by parasites (Fredensborg *et al*., 2005; Hassine, 2006; Rato *et al*., 2009). This has been observed in *Littorina littorea* (Huxham *et al*., 1993; Mouritsen *et al*., 1999; Costa *et al*., 2016) and in *Tritia reticulata* (Rato *et al*., 2009). Behaviour changes can also occur due to parasites (Poulin, 1999; Davies & Knowles, 2001). The development of molecular approaches to the study of digenean parasites, has contributed to the linking and classification of previous unkown taxa such was the case of *Cercaria sevillana* (Russell-Pinto & Bartoli, 2002) now known as *Gynaecotyla adunca* (see Pina *et al*., 2007), and *Cercaria setifera* now known as *Lepocreadium album* (Russell-Pinto *et al*., 2006; Soares, 2015). Parasites can be indicators of population structure, which is particularly valuable for commercial exploited fish species, such as horse mackerel and mackerel, and digeneans do play a role in identifying fish populations and elucidating aspects of the fish host biology (Mackenzie *et al*., 2008; Oliva *et al*., 2008). They can also reveal trophic interactions, and in this respect, digeneans are particularly suitable, as they have complex life cycles involving different intermediate and definitive hosts (Marcogliese, 2002, 2005). Furthermore, to better understand food web dynamics and ecosystem health, the study of transmission patterns of digeneans is crucial (Mackenzie *et al*., 1995; Marcogliese, 2005). The digenean taxa found in sandy and near shore habitats are ideal candidates to understand the effects of environmental changes, and the health of the ecosystems, as well as to study the implications of parasitism in the behaviour of infected hosts. The pathological effect of digeneans in their hosts, was not yet studied in much detail, and could provide a further field of research. Finally, it is important to have a baseline of the occurrence of digeneans, in our changing world, in the light of recent reports on climate changes and biological invasive species (Palm, 2011; Poulin *et al*., 2011; Dunn & Hatcher, 2015; Goedknegt *et al*., 2015). The great diversity of digeneans in Portuguese marine waters, further characterizes its connectivity between the North Atlantic temperate waters (*e.g*. *Cryptocotyle lingua*, *Himasthla elongata*, *Hemiurus appendiculatus*, *Lecithochirium furcolabiatum*) the Mediterranean Sea (*Cainocreadium labracis*, *Schikhobalotrema longivesiculatum*, *Lepocreadium album*) and the South Atlantic (*Prodistomum orientale*). *Renicola roscovita*, *Monascus filiformis* and *Derogenes varicus* are species with broad distributional range in North and South Atlantic, whereas *Opechona bacillaris*, *Ectenurus virgulus*, and *Copiatestes filiferus*, are examples of cosmopolitan species occurring in the Atlantic and Pacific Oceans. Curiously the Monorchiidae, *Lasiotocus tropicus*, *L. typicum* and the Opecoelidae *Pseudopecoeloides chloroscombri*, which are parasites of the digestive tract of *Trachurus trachurus* and *T. picturatus* in the Western Mediterranean and the Bay of Biscay were not found in Portuguese Atlantic waters (Hermida *et al*., 2015), although these fish species are abundant in Portuguese waters and those digeneans occur within the biogeographic region where Portugal is included (Gaevskaya & Kovaleva, 1980, 1985; Bartoli *et al*., 2003; Bartoly & Bray, 2004; Mackenzie *et al*., 2008). Further parasitological surveys of these carangids along the Portuguese mainland coast, increasing the sampling effort, could reveal infection with more digenean parasites.

ACKNOWLEDGMENTS

The authors would like to thank the Director of the "Departamento de Imuno-Fisiologia e Farmacologia", and of the "Laboratório de Fisiologia" of the "Instituto de Ciências Biomédicas Abel Salazar (ICBAS)", for the laboratory facilities to conduct some of the research

in the scope of this paper. GC was financed by funds of ISOPlexis, Universidade da Madeira and both SS and FC were financed by funds of the "Departamento de Imuno-Fisiologia (ICBAS)".

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