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Synopsis of the life cycles of Digenea (Platyhelminthes) from lagoons of the northern coast of the western Mediterranean

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Synopsis of the life cycles of Digenea (Platyhelminthes) from lagoons of the northern coast of the western Mediterranean

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Abstract

The present document reports on the large amount of data relating to digenean parasites recorded from or known to be present in various hosts in lagoons of the northern coast of the western Mediterranean, which has been compiled from the literature of more than a century. In these lagoons, at least 72 nominal species of digeneans have been recorded. This total corresponds to approximately 12% of the 584 “marine” digenean species reported for Europe. Data are provided on the life cycles of 56 digenean species. The life cycle has been totally elucidated for 44 species (25 from fish, 19 from birds), and partly for the other 12 species (seven from fish, five from birds). This means that the life cycle is known for 61.1% of the recorded fauna (44/72) and partly for 16.7%, but remains unknown for 22.2%, making it, in this respect, one of the best understood digenean marine faunas in the world. In addition, a checklist is provided dealing with the cercarial and metacercarial forms recorded from lagoons of the northern coast of the western Mediterranean, which have been described only on the basis of characters of these larval stages and which remain without demonstrated links to a corresponding sexual adult stage in a vertebrate.

Keywords: *Birds, Digenea, lagoons, life cycles, Platyhelminthes, teleosts, Western Mediterranean*

Introduction

Throughout the world, the number of nominal species of the Subclass Digenea has been estimated at 25,000–26,000 (Gibson and Bray 1994; Esch et al. 2002), while our current reckoning for the number of known valid species is about 18,000. In Europe, according to the *Fauna Europea* (Gibson 2004), there are 1567 terrestrial and freshwater digenean species, whereas marine species number only 584 according to the *European Register of Marine Species* (Gibson 2001). In the case of marine digenean species, most studies are related to the sexual adult stage in the definitive host, while only few are devoted to “larval” forms. Surprisingly, concurrent studies on both adults and larvae of the marine digeneans

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are generally rare, resulting in a very poor understanding of the life cycles of these parasites. Among the marine digenean species, the number of the fully elucidated life cycles is much higher for species from the lagoon ecosystem than for those from open-sea ecosystems. This situation is undoubtedly related to the greater accessibility of lagoons, since such studies are scarce in other ecosystems where local digenean species have been investigated. By contrast, for more than 100 years, the lagoons of the northern coast of the Western Mediterranean have been the subjects of numerous studies conducted on the ecology of digenean life cycles, resulting in a detailed knowledge of the ecological relationships of these parasites. The present report provides a synopsis of the life histories of 56 digenean species from the lagoons along the northern coast of the western Mediterranean based on information scattered in an abundant literature.

The Mediterranean lagoons

Lagoons are numerous all along the northern coast of the western Mediterranean, in particular along the French Mediterranean coast. Because normal tides are absent in the Mediterranean, variations in water level in the lagoons are caused only by infrequent, small barometric tides.

Two types of environmental condition, which grade into one another, are observed in these lagoons: (1) the first is restricted to shallow waters adjacent to the coast, with a muddy substrate, where the renewal of water is restricted and where environmental factors are severe and variable (temperature, salinity, dryness); only specialized species are well adapted to such drastic conditions, resulting in a poor biodiversity but with a high abundance of individual species; and (2) the second environment is located in between the previous one and the open sea; in such areas, ecological features are more homogeneous and the water is renewed more often, resulting in a higher biodiversity but with a lower abundance of individual species (Pères and Picard 1964).

Digeneans in general

Organisms living in lagoons are susceptible to parasitism by numerous species belonging to various groups (Haplosporidia, Microsporidia, Monogenea, Digenea, Cestoda, Nematoda, Acanthocephala, Crustacea, etc.). However, in the present study, we are including only data on trematodes of the subclass Digenea.

The digenean life cycle

Digeneans are normally endoparasitic flukes with a heteroxenic life cycle. During the course of their life, most are successively parasites of two or, more usually, three different hosts, all of them being more or less specific. The cycle usually includes three generations, two parthenogenetic and one sexual (Gibson 1987). In virtually all cases, the first host is a mollusc. Depending on the digenean species, the second one, when present, can be either an invertebrate or a vertebrate, while the final (definitive) host is almost always a vertebrate. Transmission strategies selected by various digeneans to complete a successful life cycle have been described by Combes et al. (2002).

First host. Eggs produced through a sexual reproduction of the adult stage in the definitive host are usually passed to the environment within the faeces. Infection of the mollusc host occurs through the ingestion of egg and/or the penetration of a larva (miracidium) which hatches from the egg. The miracidium enters the tissues of the mollusc and transforms into a sac-like mother sporocyst, which gives rise asexually to one, or occasionally more, generations of asexual adults (parthenitae) called daughter sporocysts or rediae, depending on their morphology. Within the mollusc, these asexual generations invade either the digestive gland and/or gonad. Later, they give rise to numerous cercariae, which are usually emitted in the environment as a motile, free-living, larval transmission stage, the cercaria. Nevertheless, in some cases, cercariae are retained inside the first host and encyst as metacercariae, often inside the parthenita. In the latter case, as a second host is not utilized, the life cycle is telescoped.

Second host. The numerous cercariae shed from the mollusc into the environment search for or are fed upon by a suitable second host, or in some cases they encyst (as metacercariae) upon vegetation or other items which might form part of the diet of the definitive host. In some other cases, cercariae swim actively towards their target host; others move or are brightly coloured in order to attract the second (or occasionally definitive) host. When contact occurs, cercariae enter or are eaten by the host and normally encyst as metacercariae, usually in a specific organ or cavity.

Definitive host. The specific definitive host (or group of hosts) is infected when eating the second host or other items (e.g. vegetation) containing the metacercariae. The definitive host harbours the sexual adult, most often in its alimentary canal or associated organs, but many parts of the body can be infected by specialized digeneans.

Identification of digenean species

The identification of digenean species is currently based on the sexual adult stage, due to the numerous useful anatomical criteria which are available. Knowledge of the life cycle is also useful for identification. Most species which have been well described on the basis of their sexual adult stage can be identified; nevertheless, several species complexes have been demonstrated, often resulting in a confused situation.

By contrast, many of the anatomical characters of the larval stages and parthenitae are not very useful for systematics, because they are often not known or are unspecific. Despite these handicaps, numerous larval digeneans have been described as new species, although known only from these stages. Those based on cercariae, either from the first host or free-living, are usually given the suprageneric name of "*Cercaria*"; less often metacercariae from the second host are described with the suprageneric names of "*Metacercaria*", "*Diplostomulum*", "*Tetracotyle*", etc. Quite often the species with a suprageneric nomenclature are given "invalid" specific names containing numerals in order to avoid nomenclatural confusion. Many of these "larval" species have been described without demonstrated links to corresponding sexual adults. Fortunately, the links for some of the larval forms have been elucidated thanks to experimental infections or to molecular tools. However, the situation is still unclear for some species allocated to *Cercaria* or *Metacercaria*, which must remain *species inquirendae*.

Digeneans from lagoons

Lagoon or marine status of digeneans

In lagoons, the definitive hosts of digeneans are either teleosts or birds (mammals are absent in such areas). Most of these vertebrates change their habitat, either occasionally or frequently (from the lagoon to the open sea, or vice versa). Consequently, for a given adult digenean species found in one of these erratic definitive hosts, it is not possible to postulate whether or not it is a marine or a lagoon species. Such a decision has to be based on the known or supposed life cycle of the species. In this respect, information on the first host is critical, since molluscs are more sedentary. Consequently, the habitat of the first host underscores the ecological designation of its digenean species. If the life cycle of a digenean species is not known, then it is not possible to speculate on its lagoon or marine status.

Life cycles of digeneans in lagoons from the northern coast of the western Mediterranean

During the last century, numerous studies were conducted on the digenean parasites of the fauna of the lagoons all along the northern coast of the western Mediterranean. Data from published reports are compiled below.

Due to the confused situation described above, the present synopsis takes into account only: (1) the readily recognized digenean species with a valid binomial nomenclature; and (2) the digenean species with a "lagoon" status, excluding those from the open sea. Within these limits, we provide information on the life cycles of 56 species, which are fully elucidated for 44 species and partly so for the 12 other species. In addition, we provide a checklist of 16 nominal species (some with invalid names) described from their larval stages, usually the cercaria, from hosts in the lagoons. As a result, the present report indicates that at least 72 nominal digenean species have been reported from lagoons of the northern coast of the western Mediterranean. Almost all the cited references relate to ecological studies on life cycles rather than to systematics. Some important references from other areas of the Mediterranean are cited (marked with an asterisk), especially in cases where forms known to occur in the lagoons have not been reported in the literature.

Elucidated life cycles

Digenea from fishes

1. *Bucephalus minimus* (Stossich, 1887). Bucephalidae Poche, 1907.

First host: *Cerastoderma glauca* Poiret, Bivalvia.

Second hosts: *Atherina boyeri* Risso, Atherinidae. *Pomatoschistus microps* Kröyer, Gobiidae. *Chelon labrosus* (Risso), *Liza ramada* (Risso), Mugilidae. *Sparus auratus* L., Sparidae.

Definitive host: *Dicentrarchus labrax* (L.), Moronidae.

References: Carrère (1937); Rebecq (1964); Maillard (1975, 1976); Faliex (1991); Overstreet and Curran (2002, p 75).

2. *Bucephalus labracis* Paggi and Orecchia, 1965. Bucephalidae.

First host: *Tapes decussata* (L.), Bivalvia.

Second host: *Atherina boyeri*, Atherinidae.

Definitive host: *Dicentrarchus labrax*, Moronidae.

References: Paggi and Orecchia (1965)*; Maillard (1976); Gargouri-Ben Abdallah and Maamouri (2005)*.

3. *Bucephalus baeri* Maillard, 1976. Bucephalidae.

First host: *Paphia aurea* (Gmelin), Bivalvia.

Second host: *Pomatoschistus microps*, Gobiidae.

Definitive host: *Dicentrarchus labrax*, Moronidae.

References: Palombi (1934)*; Maillard (1976).

4. *Bucephalus anguillae* Spakulova, Macko, Berrilli, and Dezfuli, 2002. Bucephalidae.

First host: *Abra tenuis* (Montagu), Bivalvia.

Second host: *Aphanius fasciatus* (Valenciennes), Cyprinodontidae.

Definitive host: *Anguilla anguilla* (L.), Anguillidae.

References: Spakulova et al. (2002)*; Gargouri-Ben Abdallah and Maamouri (2002)*.

5. *Monorchis parvus* Looss, 1902. Monorchidae Odhner, 1911.

First and second host: *Cerastoderma glauca*, Bivalvia.

Definitive hosts: *Diplopus annularis* (L.), *D. vulgaris* (Geoffroy Saint-Hilaire), Sparidae.

Reference: Bartoli et al. (2000).

6. *Paratimonia gobii* Prévot and Bartoli, 1967. Monorchidae.

First host: *Abra tenuis*, Bivalvia.

Second hosts: *Abra tenuis*, *Cerastoderma glauca*, Bivalvia.

Definitive host: *Pomatoschistus microps*, Gobiidae.

Reference: Maillard (1976).

7. *Bacciger bacciger* (Rudolphi, 1819). Faustulidae Poche, 1926.

First hosts: *Paphia aurea*, *Tapes decussata*, Bivalvia.

Second hosts: Corophiidae spp., Amphipoda.

Definitive hosts: *Atherina boyeri*, *A. hepsetus* L., *A. presbyter* Cuvier, Atherinidae.

References: Palombi (1932, 1933, 1934, 1940)*; Carrère (1938); Maillard (1976).

8. *Aphalloides coelomicola* Dollfus, Chabaud, and Golvan, 1957. Cryptogonimidae Ward, 1917.

First host: *Hydrobia ventrosa* (Montagu), Gastropoda.

Second and definitive host: *Pomatoschistus microps*, Gobiidae.

References: Maillard (1973a, 1976); Deblock (1980).

9. *Deropristis inflata* (Molin, 1858). Acanthocolpidae Lühe, 1909.

First hosts: *Hydrobia ventrosa*, *Bittium reticulatum* (da Costa), Gastropoda.

Second host: *Nereis diversicolor* (Müller), Polychaeta.

Definitive host: *Anguilla anguilla*, Anguillidae.

References: Carrère (1938); Bayssade-Dufour and Maillard (1974); Maillard (1976); Deblock (1980).

10. *Timoniella imbutiforme* (Molin, 1859). Acanthostomidae Poche, 1926.

First hosts: *Hydrobia ventrosa*, *H. acuta* (Draparnaud), Gastropoda.

Second hosts: *Pomatoschistus microps*, Gobiidae. *Atherina* spp., Atherinidae.

Definitive host: *Dicentrarchus labrax*, Moronidae.

References: Maillard (1973b, 1976); Deblock (1980).

11. *Timoniella praeterita* (Looss, 1901). Acanthostomidae.

First hosts: *Hydrobia ventrosa*, *H. acuta*, Gastropoda.

Second hosts: *Pomatoschistus microps*, Gobiidae. *Atherina* spp., Atherinidae.

Definitive host: *Dicentrarchus labrax*, Moronidae.

References: Maillard (1974a, 1976); Deblock (1980).

12. *Centroderma spinosissima* Stosich, 1883. Mesometridae Poche, 1926.

First hosts: *Rissoa ventricosa* Desmaret, *R. auriscalpium* (L.), *R. similis* Scacchi, Gastropoda.

Second host: encystment on sea grass.

Definitive host: *Sarpa salpa* (L.), Sparidae.

Reference: Jousson and Bartoli (1999).

13. *Lepocreadium album* (Stossich, 1890). Lepocreadiidae (Odhner, 1905).

First hosts: *Nassarius mutabilis* (L.), *Conus mediterraneus* Hwass, Gastropoda.

Second hosts: *Aplysia punctata* (Cuvier), Gastropoda; *Tapes decussata*, *Paphia aurea*, Bivalvia.

Definitive hosts: *Spondyliosoma cantharus* (L.), *Oblada melanura* (L.), Sparidae.

References: Palombi (1931, 1934, 1937)*; Bayssade-Dufour and Maillard (1974).

Remark: note that there has been confusion between *Lepocreadium album* and *L. pegorchis*.

14. *Lepocreadium pegorchis* (Stossich, 1904). Lepocreadiidae.

First hosts: *Nassarius corniculum* (Olivi), *N. mutabilis*, Gastropoda.

Second hosts: *Cerastoderma glauca*, *Paphia aurea*, *Parvicardium ovale* (Sowerby), *Venus verrucosa* L., Bivalvia.

Definitive hosts: *Diplodus annularis*, *Lithognathus mormyrus*, *Pagellus erythrinus* (L.), *Sarpa salpa*, *Sparus auratus*, Sparidae.

References: Bartoli (1966, 1967, 1983a).

15. *Saccocoelium tensum* Looss, 1902. Haploporidae Nicoll, 1914.

First hosts: *Hydrobia acuta*, *H. ventrosa*, Gastropoda.

Second host: absent; encystment on surface meniscus of lagoon.

Definitive hosts: *Chelon labrosus* (Risso), *Liza aurata* (Risso), *L. ramada* (Risso), *L. saliens* (Risso), *Mugil cephalus* L., Mugilidae.

References: Fares and Maillard (1974); Deblock (1980).

16. *Saccocoelium obesum* Looss, 1902. Haploporidae.

First hosts: *Rissoa* spp., Gastropoda.

Second host: absent; encystment on surface meniscus of lagoon.

Definitive hosts: *Chelon labrosus*, *Liza aurata*, *L. ramada*, *L. saliens*, *Mugil cephalus*, Mugilidae.

References: Fares and Maillard (1974).

17. *Haploporus benedeni* (Stossich, 1887). Haploporidae.

First hosts: *Hydrobia acuta*, *H. ventrosa*, Gastropoda.

Second host: absent; encystment on surface meniscus of lagoon.

Definitive hosts: *Chelon labrosus*, *Liza aurata*, *L. ramada*, *L. saliens*, *Mugil cephalus*, Mugilidae.

References: Fares and Maillard (1974); Deblock (1980).

18. *Dicrogaster perpusilla* Looss, 1902. Haploporidae.

First hosts: *Hydrobia acuta*, *H. ventrosa*, Gastropoda.

Second host: absent; encystment on surface meniscus of lagoon.

Definitive hosts: *Chelon labrosus*, *Liza aurata*, *L. ramada*, *L. saliens*, *Mugil cephalus*, Mugilidae.

References: Fares and Maillard (1974); Deblock (1980); Sarabeev and Balbuena (2003)*.

Remark: records of this species are under *D. contracta* Looss, 1902, recently shown by Sarabeev and Balbuena (2003) to be a synonym of *D. perpusilla*.

19. *Haplospilachnus pachysomus* (Eysenhardt, 1829). Haplospilachnidae Poche, 1926.

First hosts: *Hydrobia acuta*, *H. ventrosa*, Gastropoda.

Second host: absent; encystment on surface meniscus of lagoon.

Definitive hosts: *Chelon labrosus*, *Liza aurata*, *L. ramada*, *L. saliens*, *Mugil cephalus*, Mugilidae.

References: Carrère (1938); Fares (1974); Saad-Fares (1985); Deblock (1980).

20. *Cainocephalus labracis* (Dujardin, 1845). Opaeoelidae Ozaki, 1925.

First host: *Gibbula adansonii* (Payrodeau), Gastropoda.

Second hosts: *Gobius niger* L., *Pomatoschistus microps*, Gobiidae.

Definitive host: *Dicentrarchus labrax*, Moronidae.

References: Maillard (1974b, 1976).

21. *Helicometra fasciata* (Rudolphi, 1819). Opaeoelidae.

First hosts: *Gibbula adansonii*, *G. umbilicaris* (L.), *Fujubinus striatus* (L.), Gastropoda.

Second host: *Hippolyte inermis* Leach, Decapoda.

Definitive hosts: *Anguilla anguilla*, Anguillidae. *Gobius niger*, *Zosterisessor ophiocephalus* (Pallas), Gobiidae.

References: Palombi (1929); Reversat et al. (1989, 1991); Reversat (1990); Reversat and Silan (1991); Jousson et al. (1999); Jousson (2001).

22. *Helicometra gobii* (Stossich, 1883). Opaeoelidae.

First host: *Fujubinus striatus*, Gastropoda.

Second hosts: *Gammarus insensibilis* Stock, Amphipoda. *Palaemon serratus* (Pennant), Decapoda.

Definitive hosts: *Anguilla anguilla*, Anguillidae. *Gobius niger*, Zosterisessor ophiocephalus, Gobiidae. *Symphodus cinereus* (Bonnaterre), Labridae.

References: Palombi (1929); Reversat et al. (1989, 1991); Reversat (1990); Reversat and Silan (1991).

23. *Podocotyle scorpaenae* (Rudolphi, 1819). Opecoelidae.

First host: *Clanculus jussieu* (Payraudeau). Gastropoda.

Second host: *Octopus vulgaris* Cuvier. Cephalopoda.

Definitive host: *Scorpaena porcus* L., Scorpaenidae.

References: Jousson (2001); Bartoli and Jousson (2003).

24. *Bunocotyle meridionalis* Chabaud and Buttner, 1959. Bunocotylidae Dollfus, 1950.

First hosts: *Hydrobia acuta*, *H. ventrosa*, Gastropoda.

Second host: *Popella guermi* Richard, Copepoda, with progenetic metacercariae.

References: Chabaud and Biguet (1954); Chabaud and Buttner (1959); Rebecq and Augesse (1960).

25. *Diptherostomum brusinae* (Stossich, 1889). Zoogonidae Odhner, 1911.

First hosts: *Nassarius mutabilis* (L.), *N. pygmaeus* (Lamarck), Gastropoda.

Second hosts: absent; metacercariae encyst in sporocysts inside the infected first host.

Definitive hosts: *Diplodus annularis*, *D. vulgaris*, *D. sargus*, *Oblada melanura* (L.), *Sparus auratus*, *Lithognathus mormyrus*, Sparidae. *Labrus merula* L., *Symphodus roissali* (Risso), Labridae. *Blennius ocellaris* L., *Parablennius gattorugine* (L.), Blenniidae.

References: Palombi (1930, 1934)*; Bartoli et al. (2005).

Digenea from birds

26. *Gymnophallus nereicola* Rebecq and Prévot, 1962. Gymnophallidae Morozov, 1955

First host: *Abra tenuis*, Bivalvia.

Second hosts: *Nereis diversicolor*, *Perinereis cultrifera* (Grube), Polychaeta.

Definitive hosts: *Haematopus ostralegus*, *Charadrius alexandrinus* L., *C. hiaticula* L., *Pluvialis squatarola* (L.), *Erolia (Calidris) minuta* (Leisl.), *E. alpina* (L.), Charadriidae. *Larus ridibundus* L., Laridae.

References: Bartoli (1972, 1974a).

27. *Gymnophallus fossarum* Bartoli, 1965. Gymnophallidae.

First host: *Scrobicularia plana* (Da Costa), Bivalvia.

Second hosts: *Cerastoderma glauca*, *Paphia aurea*, *Tapes decussata*, *Solen marginatus* Pulteney, Bivalvia.

Definitive hosts: *Haematopus ostralegus* L., Charadriidae; *Larus cachinnans michaelis* Naumann, Laridae.

References: Bartoli (1972, 1974a).

28. *Gymnophallus rebecqui* Bartoli, 1983. Gymnophallidae.

First host: *Abra tenuis*, Bivalvia.

Second hosts: *Abra tenuis*, *Cerastoderma glauca*, Bivalvia.

Definitive hosts: *Aythia ferina* (L.), *A. fuligula* (L.), *Anas clypeata* L., *Tadorna tadorna* (L.), Anatidae.

References: Bartoli (1974a, 1983b); Campbell (1985)*.

29. *Gymnophallus choledochus* Odhner, 1900. Gymnophallidae.

First host: *Cerastoderma glauca*, Bivalvia.

Second host: *Nereis diversicolor*, Polychaeta.

Definitive host: *Larus cachinnans michaelis*, Laridae.

References: Loos-Frank (1969)*; Bartoli (1974a, 1974b).

30. *Gymnophallus rostratus* Bartoli, 1982. Gymnophallidae.

First host: *Loripes lacteus* (L.), Bivalvia.

Second hosts: *Abra tenuis*, *Chamelea gallina* (L.), *Donax semistriatus* Poli, *D. trunculus* L., *Loripes lacteus*, *Macra stultorum* (L.), *Paphia aurea*, *Solen marginatus*, *Spisula subtruncata* (Da Costa), *Tapes decussata*, Bivalvia.

Definitive host: *Aythia ferina*.

References: Bartoli (1974a, 1982).

31. *Renicola lari* Timon-David, 1933. Renicolidae Dollfus, 1939.

First hosts: *Cerithium rupestre* Risso, *C. vulgatum* Bruguière, Gastropoda.

Second hosts: *Atherina boyeri*, *A. hepsetus*, Atherinidae.

Definitive hosts: *Larus cachinnans michaelis*, *L. ridibundus*, Laridae.

Reference: Prévot and Bartoli (1978).

32. *Maritrema misenensis* (Palombi, 1940). Microphallidae (Ward, 1961).

First hosts: *Cerithium rupestre*, *C. vulgatum*, Gastropoda.

Second hosts: *Orchestia mediterranea* Costa, *O. montagui* Audouin, Amphipoda.

Definitive hosts: *Charadrius alexandrinus*, Charadriidae. *Larus cachinnans michaelis*, Laridae.

References: Prévot et al. (1976); Bartoli and Prévot (1978).

33. *Maritrema subdolum* Jägerskiöld, 1909. Microphallidae.

First hosts: *Hydrobia acuta*, *H. ventrosa*, Gastropoda.

Second hosts: *Sphaeroma serratum* (Fabricius), Isopoda. *Orchestia gammarellus* (Pallas), Amphipoda. *Carcinus maenas* (L.), Decapoda.

Definitive hosts: Charadriidae and Laridae.

References: Deblock et al. (1961); Rebecq (1964); Deblock (1980).

34. *Microphallus claviformis* (Brandes, 1888). Microphallidae.

First hosts: *Hydrobia acuta*, *H. ventrosa*, Gastropoda.

Second hosts: *Orchestia mediterranea*, *Gammarus* spp., Amphipoda. *Idotea balthica* (Pallas), *Sphaeroma* spp., Isopoda.

Definitive hosts: *Charadrius alexandrinus*, Charadriidae. *Larus cachinnans michaelis*, Laridae.

References: Rebecq (1964); Prévot and Bartoli (1977); Deblock (1980).

35. *Microphallus papillorobustus* (Rankin, 1940). Microphallidae.

First hosts: *Hydrobia acuta*, *H. ventrosa*, Gastropoda.

Second hosts: *Gammarus aequicauda* (Martyinov), *G. insensibilis* Stock, Amphipoda.

Definitive host: *Larus cachinnans michaelis*, Laridae.

References: Rebecq (1961, 1964); Deblock (1980); Helluy (1981, 1983).

36. *Microphallus pirum* (Lebour, 1907). Microphallidae.

First and second host: *Hydrobia ventrosa* (same individual), Gastropoda.

Definitive hosts: various species of Anseriformes.

Reference: Deblock (1980).

37. *Microphallus bittii* Prévot, 1972. Microphallidae.

First host: *Bittium reticulatum*, Gastropoda.

Second host: *Carcinus maenas*, Decapoda.

Definitive hosts: *Larus cachinnans michaelis*, *L. ridibundus*, Laridae.

References: Prévot (1972b, 1974).

38. *Megalophallus carcini* Prévot and Deblock, 1970. Microphallidae.

First host: *Cerithium vulgatum*, Gastropoda.

Second host: *Carcinus maenas*, Decapoda.

Definitive host: *Larus cachinnans michaelis*, Laridae.

References: Prévot (1972a, 1974).

39. *Gynaecotyla longiintestinata* Leonov, 1938. Microphallidae.

First host: *Cyclope neritea* (L.), Gastropoda.

Second host: *Carcinus maenas*, Decapoda.

Definitive host: *Larus cachinnans michaelis*, Laridae.

Reference: Prévot (1974).

40. *Galactosomum timondavidi* Pearson and Prévot, 1971. Heterophyidae (Leiper, 1909).

First host: *Cerithium vulgatum*, Gastropoda.

Second hosts: *Anguilla anguilla*, Anguillidae. *Diplodus annularis*, Sparidae. *Mugil auratus*, Mugilidae. *Pomatoschistus microps*, Gobiidae. *Syngnathus abaster* Risso, Syngnathidae.

Definitive host: *Larus cachinnans michaelis*, Laridae.

Reference: Prévot (1973).

41. *Himasthla militaris* (Rudolphi, 1802). Echinostomidae Looss, 1899.

First host: *Hydrobia acuta*, Gastropoda.

Second host: *Nereis diversicolor*, Polychaeta.

Definitive hosts: Charadriidae.

References: Timon-David and Rebecq (1958); Rebecq (1961); Deblock (1980).

42. *Himasthla quissetensis* Miller and Northup, 1926. Echinostomidae.

First host: *Cyclope neritea*, Gastropoda.

Second hosts: *Cerastoderma glauca*, *Tapes decussata*, *Paphia aurea*, *Scrobicularia plana*, *Donax trunculus*, *D. semistriatus*, *Mactra stultorum*, *Spisula subtruncata*, *Chamelea gallina*, *Solen marginatus*, *Loripes lacteus*, *Lentidium mediterraneum*, *Dosinia lupinus*, Bivalvia.

Definitive host: *Larus cachinnans michaelis*, Laridae.

References: Stunkard (1938a, 1938b)*; Prévot (1974).

43. *Cardiocephalus longicollis* Szidat, 1926. Strigeidae Railliet, 1919.

First host: *Nassarius corniculum*, Gastropoda.

Second hosts: *Diplodus annularis*, *D. vulgaris*, *Sarpa salpa*, *Lithognathus mormyrus* (L.), Sparidae. *Belone belone* (L.), Belonidae.

Definitive host: *Larus cachinnans michaelis*, Laridae.

Reference: Prévot and Bartoli (1980).

44. *Psilochasmus aglyptorchis* Loos-Frank, 1968. Psilostomidae Looss, 1900.

First and second hosts: *Hydrobia ventrosa*, Gastropoda.

Definitive hosts: various Anseriformes.

Reference: Deblock (1980).

Partly elucidated life cycles

Definitive host(s) unknown

45. *Maritrema syntomocyclus* Deblock and Ky, 1966. Microphallidae.

First and second host: *Hydrobia ventrosa*, *H. acuta* (same individual), Gastropoda.

Definitive hosts: birds.

References: Deblock and Ky (1966); Deblock (1980).

46. *Microphallus scolectroma* Deblock and Ky, 1966. Microphallidae.

First and second host: *Hydrobia acuta* (same individual), Gastropoda.

Definitive hosts: birds.

References: Deblock and Ky (1966); Deblock (1980).

47. *Microphallus abortivus* Deblock, 1974. Microphallidae.

First and second host: *Hydrobia acuta* (same individual), Gastropoda.

Definitive hosts: birds.

References: Deblock (1974, 1980).

48. *Microphallus breviatus* Deblock and Maillard, 1975. Microphallidae.

First and second host: *Hydrobia ventrosa* (same individual), Gastropoda.

Definitive hosts: birds.

References: Deblock and Maillard (1975); Deblock (1980).

First host(s) unknown

49. *Lasiotocus longicystis* Bartoli, 1965. Monorchidae.

First host: Bivalvia.

Second hosts: *Tapes decussata*, *Paphia aurea*, Bivalvia.

Definitive host: *Anguilla anguilla*, Anguillidae.

References: Bartoli (1965); Altunel (1974).

50. *Macvicaria obovata* (Molin, 1859). Opecoelidae.

First host: Gastropoda.

Second host: *Tricolia speciosa* (Von Mühlfeldt), Gastropoda.

Definitive host: *Sparus auratus*, Sparidae.

References: Jousson et al. (1999); Jousson (2001).

51. *Macvicaria crassigula* (Linton, 1910). Opcoelidae.

First host: Gastropoda.

Second hosts: *Tricolia speciosa*, *Cantharus dorbignyi* (Payraudeau), *Haliotis tuberculata* L., Gastropoda.

Definitive hosts: *Diplodus sargus*, *D. vulgaris*, Sparidae.

References: Jousson et al. (1999); Jousson (2001).

52. *Genitocotyle mediterranea* Bartoli, Gibson, and Riutort, 1994. Opcoelidae.

First host: Gastropoda.

Second host: *Hippolyte inermis*, Decapoda.

Definitive host: *Pomatoschistus marmoratus* (Risso), Gobiidae. *Symphodus ocellatus*, Labridae.

References: Jousson et al. (1999); Jousson (2001).

53. *Cryptocotyle concava* (Creplin, 1925). Heterophyidae.

First hosts: probably *Hydrobia* spp.

Second host: *Atherina boyeri*, Atherinidae.

Definitive hosts: Anatidae and *Larus cachinnans michaelis*, Laridae.

Reference: Carrère (1938).

Second host(s) unknown

54. *Helicometra pulchella* (Rudolphi, 1819). Opcoelidae.

First host: *Tricolia tenuis* (Michaud), Gastropoda.

Definitive host: *Symphodus cinereus*, Labridae.

References: Palombi (1929)*; Reversat et al. (1989, 1991); Reversat (1990); Reversat and Silan (1991).

55. *Allopodocotyle pedicellata* (Stossich, 1887). Opcoelidae.

First host: *Tricolia speciosa*, Gastropoda.

Definitive host: *Sparus auratus*, Sparidae.

References: Jousson et al. (1999); Jousson (2001).

56. *Opcoeloides furcatus* (Bremser in Rudolphi, 1819). Opcoelidae.

First host: *Mitrella scripta* (L.), Gastropoda.

Definitive hosts: *Mullus barbatus*, *M. surmuletus*, Mullidae.

References: Jousson et al. (1999); Jousson (2001).

Checklist of digenean species from lagoons of the northern coast of the western Mediterranean described from their larval stages

Cercaria only known

1. *Cercaria lata* Lespès, 1857. Faustulidae Poche, 1926.

First host: *Tapes decussata*, Bivalvia.

Definitive hosts: fishes.

Reference: Lespès (1857).

2. *Cercaria plumosa* Sinitzin, 1911. Fellodistomidae Nicoll, 1913.

First host: *Abra tenuis*, Bivalvia.

Definitive hosts: fishes.

References: Sinitzin (1911)*; Bayssade-Dufour and Maillard (1975).

3. *Cercaria linearis* Palombi, 1938 (nec Lespès, 1857). Opecoelidae.

First host: *Tricolia speciosa*, Gastropoda.

Definitive hosts: fishes.

Reference: Palombi (1938)*.

4. *Cercaria ruvida* Palombi, 1938. Opecoelidae.

First hosts: *Calliostoma conulus* (L.), *Fujubinus striatus*, Gastropoda.

Definitive hosts: fishes.

Reference: Palombi (1938)*.

5. *Cercaria pisaniae* Palombi, 1938. Opecoelidae.

First hosts: *Pisania maculosa* Grube [= *striata* (Gmelin)?], Gastropoda.

Definitive hosts: fishes.

Reference: Palombi (1938)*.

6. *Cercaria sagittarius* Palombi, 1940 (nec Sinitzin, 1911). Hemiuridae Looss, 1899.

First hosts: *Cerithium rupestre*, *C. vulgatum*, Gastropoda.

Definitive hosts: fishes.

Reference: Palombi (1940)*.

7. *Cercaria rothschildi* Palombi, 1940. Hemiuridae.

First host: *Tricolia speciosa*, Gastropoda.

Definitive hosts: fishes.

Reference: Palombi (1940)*.

8. *Cercaire cystocerque* à panache sp. no. 2 of Deblock (1980). Hemiuridae.

First host: *Hydrobia acuta*, Gastropoda.

Definitive hosts: fishes.

Reference: Deblock (1980).

9. *Cercaria camarguensis* Rebecq, 1964. Microphallidae.

First host: *Hydrobia ventrosa*, Gastropoda.

Definitive hosts: birds.

References: Rebecq (1964); Deblock (1980).

10. *Cercaria* no. 15 of Deblock (1980). Microphallidae.

First host: *Hydrobia ventrosa*, Gastropoda.

Definitive hosts: birds.

Reference: Deblock (1980).

11. *Cercaria* no. 1 of Deblock (1980). Schistosomatidae Poche, 1907.

First hosts: *Hydrobia acuta*, *H. ventrosa*, Gastropoda.

Definitive hosts: birds.

Reference: Deblock (1980).

12. *Cercaria* sp. no. 11 of Deblock (1980). Notocotylidae Lühe, 1909.

First host: *Hydrobia ventrosa*, Gastropoda.

Second host: absent; encystment of metacercariae on plants.

Definitive hosts: birds.

Reference: Deblock (1980).

13. *Cercaria* no. 19 of Deblock (1980). Plagiorchiidae (Lühe, 1901).

First host: *Hydrobia acuta*, Gastropoda.

Definitive hosts: birds.

Reference: Deblock (1980).

14. *Cercaria* no. 20 of Deblock (1980). Heterophyidae.

First host: *Hydrobia ventrosa*, Gastropoda.

Definitive hosts: birds.

Reference: Deblock (1980).

15. *Cercaria tetralophocerca* Rebecq, 1964. Incertae sedis.

First host: *Hydrobia ventrosa*, Gastropoda.

References: Rebecq (1964); Deblock (1980).

Metacercaria only known

16. *Parvatrema* sp. 2 Rebecq, 1964. Gymnophallidae.

Second host: *Hydrobia ventrosa*, Gastropoda.

Definitive hosts: birds.

Reference: Rebecq (1964); Bartoli (1974a); Deblock (1980).

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