Larvae of gryporhynchid cestodes (Cyclophyllidea) from fish: a review

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Abstract. Larvae (metacestodes) of tapeworms of the cyclophyllidean family Gryporhynchidae (previously included in the Dilepididae) occur in different internal organs of fresh- and brackish water fish (110 fish species of 27 families in 12 orders reported), which serve as the second intermediate hosts. The species composition, spectrum of fish hosts, sites of infection, and geographical distribution of gryporhynchids recorded from fish are reviewed here on the basis of literary data and examination of extensive material from helminthological collections. Metacestodes of the following genera have been found in fish: Amirthalingamia Bray, 1974 (1 species), Ascodilepis Guildal, 1960 (1), Cyclustera Fuhrmann, 1901 (4), Dendrouterina Fuhrmann, 1912 (1), Glossocercus Chandler, 1935 (3), Neogryporhynchus Baer et Bona, 1960 (1), Paradilepis Hsiü, 1935 (5), Parvitaeenia Burt, 1940 (2), and Valipora Linton, 1927 (3). However, most published records concern only three species, namely Neogryporhynchus chialancristrotus (Wedl, 1855) from the intestinal lumen, Paradilepis sceleolina (Rudolphi, 1819) from the liver and mesenteries, and Valipora campylancristrota (Wedl, 1855) from the gall bladder of cyprinids and other fish in the Palaearctic Region. Data on other species as well as reports from other regions are very scarce and almost no information is available from Australia, tropical Asia and South America. A recent study of gryporhynchid metacestodes from Mexico (Scholz and Salgado-Maldonado 2001), which reported 13 species, suggested that they may be more common than indicated by records in the literature. Although only a few cases of pathogenic influence of larvae on fish hosts have been reported, the veterinary importance of gryporhynchids remains to be assessed on the basis of more detailed studies. The data available indicate a strict host and site specificity of some species whereas others occur in a wide spectrum of fish hosts and are not strictly site-specific. Evaluation of Paradilepis larvae from the liver of salmonid fish from British Columbia, Canada, identified as P. simoni Rausch, 1949 by Ching (1982), has shown that they probably belong to two species, P. simoni and P. rugovaginosus Freeman, 1954. Metacestodes of the latter species and those of Cyclustera magna (Baer, 1959) from the intestinal wall of Tilapia zillii (Gervais) from Kenya are reported from fish for the first time.

INTRODUCTION

Larval stages (metacestodes) of cestodes previously placed in the Dilepididae (Cyclophyllidea) are parasites of fresh- and brackish water fish (Bona 1975, Chubb 1980, Dubinina 1987). Spassky and Spasskaya (1973) proposed the subfamily Gryporhynchinae to accommodate those species of dilepidids that mature in fish-eating birds and have larvae (metacestodes) which occur in fish; Spassky (1995) raised it to family level. Recent phylogenetic studies have confirmed its validity and its distinctness from the Dilepididae sensu stricto (Mariaux 1998, Hoberg et al. 1999, 2001). Therefore, the species previously reported as dilepidids by parasitologists, including the present authors (e.g., Scholz 2001, Scholz and Salgado-Maldonado 2001, Scholz et al. 2002a, b), are considered here to belong to the Gryporhynchidae.

Gryporhynchid metacestodes have been known since the 19th century (see Baer and Bona 1960, and Bona 1975 for a historical overview). However, most data concern only three taxa, namely Neogryporhynchus chialancristrotus (Wedl, 1855), Paradilepis sceleolina (Rudolphi, 1819) and Valipora campylancristrota (Wedl, 1855). In addition, most papers reported only the occurrence of larvae and data on the taxonomy, life cycles, ecology and pathogenic influence of larvae on their fish hosts are scarce.

The shortage of data may be partly related to the fact that gryporhynchid larvae are often overlooked due to their site of infection (mesenteries, liver, etc.). A high number of misidentifications and persistent nomenclatural problems (see Bona 1975) are apparently influenced by the poor quality of available material or its absence in numerous cases. The morphology (number and arrangement, shape and size) of the rostellar hooks represents the basis of species identification (Bona 1975, Scholz and Salgado-Maldonado 2001) but they are often

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difficult to observe and measure because of inappropriate processing.

Several methods have been proposed to make good-quality preparations to enable adequate morphological and biometrical evaluation, e.g., squashing the scolex, clearing in Berlese’s fluid or flattening the worms and their subsequent fixation with glycerin-ammonium picrate according to Malmberg (1957) and Ergens (1969).

In the present paper, a survey of metacestodes of the Gryporhynchidae reported from fish is provided together with data on their fish hosts, sites of infection and geographical distribution. The information is primarily focused on the data published between 1975 and 2003 because Bona (1975) presented a comprehensive overview of records of dilepidid (= gryporhynchid) genera found as larvae in fish. However, some papers published before 1975, especially those from neglected geographical regions, are also included because Bona (1975) reported larvae of only two species, *N. cheilancristotus* and *V. campylancristota*.

**HOST SPECTRUM**

Fish of numerous families of the following orders (Appendix 1) serve as the second intermediate hosts of gryporhynchids: Acipenseriformes, Atheriniformes, Characiformes, Clupeiformes, Cypriniformes, Cyprinodontiformes, Esociformes, Gasterosteiformes, Perciformes, Salmoniformes, Scorpaeniformes, Siluriformes. Cyprinid fish (Cypriniformes: Cyprinidae) represent the most frequent fish intermediate hosts of metacestodes (45 fish species) but perciform fish, in particular cichlids, harbour the highest number of gryporhynchid species (Appendix 1).

**GEOGRAPHICAL DISTRIBUTION**

Most data on gryporhynchid larvae have been accumulated from Europe and countries of the former USSR. However, only three species have been recorded there despite long-term research on fish parasites in this region (e.g., Baer and Bona 1960, Dubinin 1962, 1971, 1987, Molnár 1970, Kozicka 1971, Kennedy 1974, Bona 1975, Ergens et al. 1975, Chubb 1980, Kakacheva-Avramova 1983, Chubb et al. 1987, Priemer and Scholz 1989, Scholz 1989a, Baccarani et al. 1998, Pietrock and Scholz 2000, Moravec 2001). Larvae identified as *Gryporhynchus pusillus* von Nordmann, 1832 and *Neogryporhynchus cheilancristotus*, as two valid species by some authors, especially in Russia (e.g., Dubinin 1987), are considered, in accordance with Baer and Bona (1960) and Bona (1975), to be conspecific.

In Canada and USA, the number of records is considerably lower, many of them not being identified to species level, misidentified or unpublished (see Hoffman 1999 for a survey of unpublished findings). Recently, as many as 13 species of gryporhynchid metacestodes have been found in freshwater and brackish water fish in Mexico (Scholz et al. 1996, Scholz and Salgado-Maldonado 2001). This suggests that gryporhynchid larvae may be much more widely distributed in individual regions and continents than indicated by records in the literature. In total, 16 species of gryporhynchid metacestodes have been reported from North America whereas only one (*V. campylancristota*) is known from South America.

Gryporhynchid metacestodes have also been reported from freshwater fish, especially tilapias, from Africa, but most have not been identified to species level except for two species (see Taxa of uncertain taxonomic status, doubtful records and synonyms). On the other hand, no species of gryporhynchids has been found in fish from Australia.

**LIFE CYCLES**

Data on the biology of gryporhynchids are limited (Beveridge 2001). Jarecka (1970a, b) demonstrated experimentally that the planktonic copepod *Eudiaptomus graciloides* (Lilljeborg, 1880) served as the first intermediate host of *N. cheilancristotus* and *V. campylancristota* (Jarecka 1970a, b) and *Mesocyclops oithonoides* Sars, 1863 was a suitable intermediate host of *N. cheilancristotus*. Jarecka (1970a) also infected carp fry, which probably serve as the second intermediate host, with larvae of *V. campylancristota* from copepods; the larvae (named plerocercus – see Chervy 2002) were located in the gall bladder of carp three days after their experimental infection.

Bauer et al. (1981) presented data of Sysolyatina-Andakulova (1979), who also studied the life cycle of *V. campylancristota*. Copepods such as *Arctodiaptomus salinus* (Dayad, 1885) served as the first intermediate hosts, in the body cavity of which metacestodes (“cercoscolex”) became infective after two weeks at 17–25°C (20–22 days at 13–19°C). After ingestion by the second intermediate host, the metacestode migrated from the intestinal lumen to the gall bladder, where it lay free within its cavity. In the bird definitive host, the parasite matured after 12–15 days, when the first eggs were released. The longevity of the cestode in the definitive host was estimated to be about 9 months (Sysolyatina-Andakulova 1979).

**ECOLOGY**

The data on the ecology of gryporhynchid metacestodes from fish are fairly limited. Those on seasonal patterns in the occurrence of gryporhynchid larvae in freshwater fish by 1980 were reviewed by Chubb (1980). The author reported only a few studies on seasonality in the occurrence of gryporhynchid metacestodes, namely that of *Neogryporhynchus cheilancristotus* (as *Gryporhynchus* sp.) in Ukraine (Ivasik 1953), *Paradilepis scolecina* (as *Cysticercus dilepidis*) also in Ukraine (Komarova 1957), *Valipora campylancristota* (as *Cysticercus dilepidis campylancristotae* and *Dilepis unilateralis*) in Poland (Jara and Olech...
IMPORTANCE

SURVEY OF SPECIES RECORDED
PATHOGENICITY AND VETERINARY IMPORTANCE

Almost all published data on the pathogenic influence of gryporhynchid larvae concern metacestodes of Valipora campylancristrota from the gall bladder of carp (Cyprinus carpio) and other cyprinids from the former USSR and Poland. The disease, valiporosis, has been considered of veterinary importance in heavily infected fish (Bauer et al. 1981). Pathological changes in the gall bladder and other internal organs appeared only when the worm burden exceeded tens to hundreds of larvae; heavily infected fish were retarded in growth and weight compared with uninfected fish or hosts with low infections (Bauer et al. 1981).

Jara and Olech (1964a) found that carp fry can be infected with metacestodes of V. campylancristrota in the first months of their life, as evidenced by the presence of small larvae in their gall bladder. Similarly, Bauer et al. (1981) stated that even 5–7 days old carp were infected with metacestodes. On the other hand, Ivaski (1953) for N. cheilancristrotus and Sapozhnikov (1975) for V. campylancristrota reported the infection rate (prevalence and intensity of infection) of small fry to be generally low. Niemczuk and Chorbinski (1996) studied the localisation and activity of some hydrolases in metacestodes of N. cheilancristrotus from the intestine of Cyprinus carpio L.

PATHOGENICITY AND VETERINARY IMPORTANCE

To summarise existing data, a list of species of the Gryporhynchidae found as metacestodes in fish is presented here. The list of references provided below is not complete as the most pertinent papers, particularly those summarising previous studies (checklists, monographs), are preferentially cited. Reports from poorly studied areas are also cited, using as a main source the Host-Parasite Data Base from The Natural History Museum, London. Taxa of uncertain taxonomic status and doubtful records are omitted here; they are briefly discussed in the following section.

Besides the review of literary data, available voucher specimens of gryporhynchid cestodes deposited in herminto logical collections have been examined because of the existence of numerous doubtful records and apparent misidentifications. The following specimens have been studied (for a survey of additional extensive material of gryporhynchids from Eurasia and North America previously studied by the present authors see Scholz et al. 1996, 2002a, b, Scholz 2001, Scholz and Salgado-Maldonado 2001):

Harold W. Manter Laboratory of Parasitology, University of Nebraska, Lincoln, USA: Paradilepis simonti Rausch, 1949 – four specimens from the liver of Oncorhynchus nerka (Walbaum) (HWML 38672 and 38673), Oncorhynchus mykiss (Walbaum) (HWML 38674) and Prosopium williamsonii (Girard) (HWML 38676) from British Columbia, Canada.

Institute of Parasitology, Academy of Sciences of the Czech Republic, České Budějovice, Czech Republic (IPCAS): one specimen of Amirthalingamia macracanthha (Joyeux et Baer, 1935) from Tilapia zillii (Gervais), Naivasha Lake, Kenya (IPCAS C-292); 5 specimens of Cyclostera magna (Baer, 1959) from the same host and locality (IPCAS C-293), all collected by P.A. Aloo.

U.S. National Parasite Collection, Beltsville, USA: Dendrouterina papillifera (Fuhrmann, 1908) (in fact Valipora minuta (Coil, 1950) – see Scholz and Salgado-Maldonado 2001) – one specimen from the liver of Poecilia sphenops Valenciennes, Mexico (USNPC 88228); Glossocercus cypriodontis Chandler, 1935 – paratype (USNPC 39528) and 4 vouchers (USNPC 80403) from the body cavity of Cyprinodon variegatus Lacepède, Texas, USA; Paradilepis simoni – paratype (squash of the scolex of an adult cestode) from Pandion haliaetus (L.), Wyoming, USA (USNPC 46403).

In addition, the following specimens of Neogryporhynchus cheilancristrotus from freshwater fish in Japan, collected by Takeshi Shimazu, were studied: (i) from the liver of Gnathopogon caerulescens (Sauvage), Lake Biwa at Moriyama, Shiga Prefecture, 2 May 1992; (ii) from the outer layer (tunica serosa) of the intestine of Zacco platypus (Temminck et Schlegel), Lake Suwa at Suwa, Nagano Prefecture, 21 July 1994; (iii) from the inner layer (mucosa) of the intestine of Carassius auratus langsдорfii Valenciennes in Cuvier et Valenciennes, Hiroi River at Kotobuki, Iiyama, Nagano Prefecture, 12 June 1999; (iv) from the inner layer (mucosa) of the intestine of Misgurnus anguillicaudatus (Cantar), Hiroi River at Kotobuki, Iiyama, Nagano Prefecture, 20 May 2000.

In the lists of fish hosts of individual gryporhynchid species and their geographical distribution (countries),
records confirmed by the authors, including those from previous studies on gyrocysticulates (see References), are marked with an asterisk. The nomenclature of fish hosts follows that of Froese and Pauly (2003). Scientific names of fish-eating birds are according to del Hoyo et al. (1992).

**Amirthalingamia macracantha** (Joyeux et Baer, 1935) Bray, 1974


**Fish hosts:** Oreochromis niloticus*, Tilapia zillii* (Perciformes: Cichlidae).

**Site of infection:** Liver and intestinal wall.

**Distribution:** Africa: Kenya*, Sudan*.

**Remarks.** The most characteristic feature of the species (and the monotypic genus as well) is the presence of 20 massive hooks of three sizes (up to 480 µm in length), arranged in two rows in a bilaterally symmetrical pattern (Bray 1974). Adults have been found in *Phalacroncorax africanus* (type host) and *P. carbo* in Africa (Mali, Sudan) (Joyeux and Baer 1935, Bray 1974).

Metacestodes found by Aloo (2002) in the intestinal wall of *T. zillii*, designated as *Amirthalingamia sp.*, are conspecific with those of *A. macracantha*, as indicated by their morphological similarity, including the arrangement, shape and size (458, 408 and 260 µm, respectively) of the rostellar hooks (Fig. 1) (see Bray 1974).

**Ascodilepis transfuga** (Krabbe, 1869) Guildal, 1960

**Fish host:** *Menidia menidia* (Atheriniformes: Atherinidae).

**Site of infection:** Intestinal wall, mesenteries.

**Distribution:** North America: USA* (Texas).

**Remarks.** Metacestodes originally reported under the name *Cysticercoides menidiae* by Chandler (1935) but a study of the holotype revealed its conspecificity with *Ascodilepis transfuga* (see Scholz 2001). Adults of *A. transfuga* have been found in the spoonbill (*Platalea ajaja*) in Brazil and Venezuela (Díaz-Ungria 1968, Bona 1975).

**Cyclusteria capito** (Rudolphi, 1819) Fuhrmann, 1901

**Synonym:** *Taenia capito* Rudolphi, 1819.

**Fish host:** *Fundulus heteroclitus* (Perciformes: Fundulidae).

**Site of infection:** Mesenteries.

**Distribution:** North America: USA* (South Carolina).

**Remarks.** Adults have been found in spoonbills and other fish-eating birds, such as ibises (*Platalea ajaja, Eudocimus albus, Mycteria ibis, Plegadis falcinellus, P. leucorodia*) from South and North America (Brazil, Mexico, Cuba, southeastern USA), Africa (Egypt), and ex-USSR (Coil 1955a, Rysavy and Macko 1973, Bona 1975, Sepúlveda et al. 1994, Scholz et al. 2002a).

**Cyclusteria ibisae** (Schmidt et Bush, 1972) Bona, 1975


**Fish hosts:** *Fundulus heteroclitus*, *F. majalis* (Percinodontiformes: Fundulidae).

**Site of infection:** Mesenteries.

**Distribution:** North America: USA* (South Carolina).

**Remarks.** The species was described from the white ibis (*Eudocimus albus*) from Florida by Schmidt and Bush (1972). At almost the same time, Rysavy and Macko (1973), apparently unaware of the paper by the former authors, described conspecific cestodes from the same host and other piscivorous birds (*Casmerodius albus, Pelecanus occidentalis, Phalacroncorax auritus, and P. mexicanus*) from Cuba (see Bona 1975). Adults of *C. ibisae* have been found in numerous groups of fish-eating birds, but existing records are restricted to southeastern USA (Florida, Georgia), Cuba and southeastern Mexico (Yucatán) – see Scholz et al. (2002b) and references herein.

**Cyclusteria magna** (Baer, 1959) Bona, 1975

**Synonym:** Parvitaenia magna Baer, 1959.

**Fish host:** *Tilapia zillii* (Perciformes: Cichlidae).

**Site of infection:** Intestinal wall.

**Distribution:** Africa: Kenya*.

**Remarks.** Metacestodes collected by Aloo (2002) from the gullet wall of *Tilapia zillii* from Kenya, tentatively identified as *Cyclusteria sp.*, are apparently conspecific with adults of *C. magna*. This cestode was described (as *Parvitaenia magna*) on the basis of one adult cestode from the intestine of *Mycteria ibis* from Zaire by Baer (1959). According to Bona (1975), who examined the holotype, the rostellar hooks of *C. magna* measure 159–182 µm (larger hooks) and 131–134 µm (smaller hooks) in length. Since the original description, the adult of *C. magna* has not been found (Bona 1975).

Metacestodes from Kenya are 904–1,480 µm long by 496–740 µm wide (n = 5); the rostellar has 28 massive hooks in two circles of 14 hooks each; the outer (anterior) circle is composed of two types of hooks of similar shape but different size, 4 hooks being apparently larger (length 179–198 µm) than the 10 remaining ones (154–163 µm). The small hooks have almost straight and narrow blade and are 138–147 µm long. In the presence of two kinds of large hooks, the metacestodes of *C. magna* resemble those of *Amirthalingamia macracantha* (see above). However, the latter has 10 hooks (4 and 6) in the outer circle instead of 14 (4 and 10) in *C. magna*.

**Cyclusteria cf. pulli** (Underwood et Dronen, 1986) Bona, 1994

**Fish hosts:** *Cyprinus carpio*, *Notropis sallei* (Cyprinodontiformes: Cyprinidae); *Alloophorus robustus*, *Girardinich-
Fig. 1. Rostellar hooks of metacestodes from fish. A – *Amirthalingamia macracantha* from the intestinal wall of *Tilapia zillii*, Kenya (IPCAS C-292). B – *Dendrouterina pilherodiae* from the gall bladder of *Rhamdia guatemalensis*, Yucatán, Mexico (IPCAS C-241).

Fig. 2. Rostellar hooks of species of *Cyclustera*. A – *C. capito* from the mesenteries of *Floridichthys polyommus*, Yucatán, Mexico (IPCAS C-279). B – *C. ibisae* from *Fundulus heteroclitus*, South Carolina, USA (left and right hooks; IPCAS C-337) and from the intestine of *Phalacrocara olivacea*, Yucatán, Mexico (hook in the middle; IPCAS C-280). C – *C. magna* from the intestinal wall of *Tilapia zillii*, Kenya (IPCAS C-293) (note the presence of larger hooks of different shape and size). D – *C. cf. ralli* from mesenteries of *Cyprinus carpio*, State of México, Mexico (IPCAS C-312).

**Remarks.** Metacestodes found in the mesenteries of several species of small cyprinid and goodeid fish from central Mexico resembled in the shape and size of their rostellar hooks those of *Cyclustera ralli* (syn. *Neocyclustera ralli*).
Site of infection: Liver, mesenteries, intestinal wall.

Fig. 3B

Fish host: Cyprinodon variegatus (Siluriformes: Cyprinodontidae).

Site of infection: Gall bladder.


Remarks. The definitive hosts of D. pilherodiae are herons, namely Pilherodius pleatvs (syn. Nycticorax pleatvs) (type host), Egretta alba and Casmerodius albus. Adults have been found in South America (Brazil, Argentina) and southeastern USA (Florida) (Mahn 1956, Bona 1983a, b, Sepúlveda et al. 1999).

Glossocercus cyprinodontis Chandler, 1935

Fish host: Cyprinodon variegatus* (Cyprinodontiformes: Cyprinodontidae).

Site of infection: Body cavity.


Remarks. The type species of Glossocercus Chandler, 1935 is known only as a larval form and its adult form remains unknown (Bona 1994, Pichelin et al. 1998). Metacestodes have never been found since the original description by Chandler (1935).

Glossocercus auritus (Rudolphi, 1808) Bona, 1994

Synonyms: Taenia aurita Rudolphi, 1819; Parvitaenia aurita (Rudolphi, 1819) Bona et Bona, 1960; Anomotaenia aurita (Rudolphi, 1819) Fuhrmann, 1908.

Fish hosts: Astyanax fasciatus (Characiformes: Characidae); Poecilia catenata* (Poeciliidae); Poecilia mexicana*, P. sphenops*, Poecilia sp.*, Poeciliopsis gracilis* (Cyprinodontiformes: Poeciliidae).

Site of infection: Liver, mesenteries, intestinal wall.


Remarks. This cestode seems to be a specific parasite of herons of the genera Egretta and Casmerodius and has been found only in Brazil, Cuba, Nicaragua and Neotropical Mexico (Veracruz) (Schmidt and Neiland 1971, Rysavy and Macko 1973, Bona 1975, Scholz et al. 2002a).

Glossocercus caribaensis (Rysavy et Macko, 1973) Bona, 1994


Fish hosts: Fundulus grandissimus*, F. heteroclitus*, F. majalis*, F. persimilis* (Cyprinodontiformes: Fundulidae); Cichlasoma urchinatum* (Perciformes: Cichlidae).

Site of infection: Mesenteries and liver.

Distribution: North America: Mexico (Yucatán), USA (South Carolina, Texas). References: Chandler (1935) (as Glossocercus cyprinodontis – see remarks), Scholz and Salgado-Maldonado (2001), Scholz et al. (2002b).

Remarks. The cestode was originally described from the intestine of the herons Ardea herodias and Casmerodius albus in Cuba and then found also in southeastern USA (Florida, South Carolina) (Rysavy and Macko 1973, Schmidt and Courtney 1973 – as Parvitaenia heardi, Sepúlveda et al. 1999). Chandler (1935) misidentified one specimen of G. caribaensis from the mesenteries of Fundulus heteroclitus (USNPC 80404) as Glossocercus cyprinodontis (see Scholz and Salgado-Maldonado 2001).

With the exception of two specimens found (? accidentally) in the cichlid Cichlasoma urchinatum, which may live also in brackish water (Vidal-Martinez et al. 2001), fish of the genus Fundulus are exclusive second intermediate hosts of the parasite. Metacestodes of G. caribaensis have not been found in other cyprinodontid fish (Cyprinodon, Floridichthys) living sympatrically in brackish waters in southeastern USA and Mexico.

Neogryporhynchus cheilancristroten (Wedl, 1855) Baer et Bona, 1960

Synonyms: Taenia cheilancristroten Wedl, 1855; ? Gryporhynchus pusillus von Nordmann, 1832; G. cheilancristroten (Wedl, 1855) Fuhrmann, 1907; G. tetrochis Hill, 1941; Gryporhynchus sp. Kozicka, 1959; Cysticercus gryporhynchis-pusillae Joyeux et Baer, 1936; C. gryporhynchis-cheilancristroten Joyeux et Baer, 1936 (for complete list of synonyms, see Baer and Bona 1960, and Bona 1975).

Fish hosts: primarily cypriniform fish, such as Abramis brama, A. ballerus*, A. sapa, Alburnoides taeniatus, Alburnus alburnus, Aspiolus ascius, Aspius aspius, Barbos brachycephalus, B. capito, Blicca hjoerkna*, Capoeta capoeta, Capoetobrama kuschakewitschi, Carassius auratus*, C. carassius*, Chalcalburnus chalcoides, Ctenopharyngodon idella, Cyprinus carpio, Gnathopogon caerulescentes*, Hemiculter Please*, Leuciscus delta, Leuciscus cecalus*, L. idus, L. lehmanni, Peloculis cultratus, Rhodeus sericeus, Rutulus rutilus*, Scardinius erythrophthalmus, Schizothorax intermedius*, Tanca tenca*, Zacco platypus* (Cypriniformes: Cyprinidae); Cobitis taenia, Misgurnus anguillicaudatus*, M. fossilis* (Cypriniformes: Cobitidae). Other fish may also serve as second intermediate hosts e.g., Pseudoscaphirhynchus kauffmanni (Acipenseriformes: Acipenseridae); Alosa kessleri (Clupeiformes: Clupeidae); Esox lucius (Esociformes: Esocidae); Gymnocephalus cernuus, Perca fluviatilis, P. schrenkii, Zungel streber (Perciformes: Percidae); Channa argus* (Perciformes: Channidae); Liza Abu (Perciformes: Mugilidae); Silurus asotus, S. glanis (Siluriformes: Siluridae).
Fig. 3. Rostellar hooks of metacestodes of *Glossocercus*. A – *G. cyprinodontis* from the body cavity of *Cyprinodon variegatus*, Texas, USA (USNPC 80403). B – *G. auritus* from the mesenteries of *Poecilia catemaconis* (large hook) and *Poeciliopsis gracilis* (small hook), Veracruz and Guerrero, Mexico (IPCAS C-281). C – *G. caribaensis* from *Fundulus heteroclitus*, South Carolina, USA (IPCAS C-282).

Fig. 4. Rostellar hooks of metacestodes of *Ascodilepis* and *Paradilepis*. A – *A. transfuga* from the intestinal wall and mesenteries of *Menidia menidia* from Texas, USA (USNPC 39530). B – *P. caballeroi* from the liver of *Chirostoma jordani*, Guanajuato, Mexico (IPCAS C-313). C – *P. scolecina* from mesenteries of *Rutilus rutilus*, Czech Republic (IPCAS C-127). D – *P. cf. urceus* from the liver of *Chirostoma jordani*, Guanajuato, Mexico (IPCAS C-315).

**Site of infection:** Intestine (lumen).

**Distribution:** Europe: Belorussia, Bulgaria, Czech Republic*, Germany*, Hungary, Italy, Lithuania, Moldavia, Poland, Romania, Russia, Slovakia*, Ukraine; Asia: Azerbaijan, Georgia, Iraq, Japan*, Kazakhstan, Tadjikistan, Turkmenia, Uzbekistan.

Site of infection: Mesenteries and liver.

Species which differs from


Remarks. Although adults are frequent and widely distributed parasites of coromnants in Europe, Asia, Africa and Australia (Matevosyan 1963, Ryzhikov et al. 1985, Schmidt 1986), metacestodes in fish are known from Eurasia only. The pathological effect of adults of P. scoleciona on its definitive host, the white-necked coromrant (Phalacrocorax carbo), was studied by Karstad et al. (1982). The copepod Eulaitopomus graciloides is the first intermediate host under experimental conditions (Jarecka 1970b).

Paradilepis caballeroi Rysavy et Maack, 1973 Fig. 4B

Fish hosts: Chirostoma jordani* (Atheriniformes: Atherinidae); Cichlasoma callolepis* (Percoformes: Cichlidae).

Site of infection: Mesenteries and liver.

Distribution: North America: Mexico* (Campeche, Guanajauto).


Remarks. Adults are specific parasites of corornants (Phalacrocorax auritus, P. brasilianus and P. olivaceus) found only in Cuba, Neotropical Mexico (Veracruz) and USA (Rysavy and Maack 1973, Fedynich et al. 1997, Scholz et al. 2002a). Scholz et al. (2002a) discussed the validity of the species which differs from P. scoleciona (Rudolphi, 1819), a common parasite of coromnants in Eurasia, Africa and Australiia (Ryzhikov et al. 1985), only in the higher number of rostellar hooks (12 in one row, i.e. 24 in total, versus 10 + 10 = 20 in P. scoleciona).

Paradilepis scoleciona (Rudolphi, 1819) Synonyms: Taenia scoleciona Rudolphi; Dilepis scoleciona (Rudolphi, 1819) Fuhrmann, 1908; Cystercercus dilepidis Digiel et Bychowsky, 1934; Paradilepis daboisi Hsü, 1935; P. brevis Burt, 1940.

Fish hosts: The most common hosts are cyprinds, e.g. Abramis brama, A. sapa, Alburnus albidus, A. alburnus, Aristichthys nobilis*, Aspius aspius, Barbus brachycephalus, B. capito, Blicca bjoerkna, Capoeta capoeta, Carassius auratus, C. carassius*, Chalcalburnus cladozoides, Chondrostoma cyri, C. nasus, Culter alburnus, Cyprinus carpio*, Gephyrogenius elongatus, Hemiculter leucisculus, Leuciscus idus, Oreoleuciscus humilis*, O. potanini, Pelleculustratus, Rhodeus sericeus, Rutulus rutulus*, Scardinius erythrophthalmus*, Schizopygopsis stoliczkae, Tinca tinca, Tribolodon hakonensis*, Varicorhinus sp. (Cypriniformes: Cyprinidae); Acipenser nuidiventris, Pseudacathiphrynus kauffmanni (Acipenseriformes: Acipenseridae); Esox lucius (Esociformes: Esocidae); Gasterosteus aculeatus, Pungitius pungitius, P. platygaster (Gasterosteiformes: Gasterosteidae); Gymnocephalus cernuus, Perca fluviatilis (Percoformes: Percidae); Neogobius melanostomus (Percoformes: Gobiidae); Silurus glanis (Siluriformes: Siluridae).

Site of infection: Mesenteries and liver.

Distribution: Europe: Bosnia and Hercegovina, Bulgaria, Czech Republic*, Germany*, Greece, Hungary, Italy, Lithuania, Poland*, Romania, Russia, Ukraine, Yugoslavia (Monte Negro); Asia: Azerbaidzhahn, Georgia, Japan*, Kazakhstan, Mongolia*, Tajikistan, Uzbekistan.

Fig. 5. Rostellar hooks of *Paradilepis simoni* adult (paratype) from the intestine of *Pandion haliaetus*, Wyoming, USA (USNPC 46403). Note presence of 28 hooks (14 + 14).

Fig. 6. Large (capital letters) and small (lowercase letters) rostellar hooks of species of *Paradilepis*. A, B – *P. simoni*. A – adult (paratype) from the intestine of *Pandion haliaetus*, Wyoming, USA (USNPC 46403); B – metacestode from the liver of *Oncorhynchus nerka*, British Columbia, Canada (HWML 38673). C–E – Metacestodes of *P. rugovaginosus* from the liver of *Oncorhynchus nerka* (C) (HWML 38672), *O. mykiss* (D) (HWML 38674) and *Prosopium williamsoni* (E) (HWML 38676), British Columbia, Canada. F – *Paradilepis* sp. from the liver of *Chirostoma jordani*, Guanajuato, Mexico (IPCAS C-314).

(HWML 38673) are also slightly more robust, in particular larger ones (Fig. 6B).

The different number of hooks and slight difference in their shape indicate that the larvae found by Ching (1982) belong to two different species of *Paradilepis* Hsi, 1935, most probably *P. simoni* (larva from *O. nerka* with 28 hooks – HWML 38673) and *P. rugovaginosus* Freeman, 1954 (metacestodes with 32 hooks – HWML 38672, 38674, 38676).

Species identification of metacestodes from *Pychochelus coregonensis* and *Cottus asper* could not be confirmed because voucher specimens were not available.

**Paradilepis rugovaginosus** Freeman, 1954

**Fish hosts:** *Oncorhynchus mykiss*, *O. nerka*, *Prosopium williamsoni* (Salmoniformes: Salmonidae).

**Site of infection:** Liver.

**Distribution:** North America: Canada (British Columbia).

**Reference:** Ching (1982 – as *P. simoni*), present study.

**Remarks:** Metacestodes from *Oncorhynchus nerka* (HWML 38672), *O. mykiss* (HWML 38674) and *Prosopium williamsoni* (HWML 38676), all possessing 32 hooks arranged...
in two circles of 16 each, are considered to be conspecific with *P. rugovaginosus* described by Freeman (1954) from the osprey, *Pandion haliaetus*, from Ontario, Canada. Freeman (1954) reported adult tapeworms to possess 32 rostellar hooks 99–103 µm (larger hooks) and 70–72 µm (smaller hooks) long, respectively. This corresponds well with measurements of the hooks of metacestodes (93–108 µm and 67–76 µm; present data, Table 1), which further supports the assumption that these larvae are conspecific with *Paradilepis rugovaginosus*.

**Paradilepis cl. urceus** (Wedell, 1855) Joyeux et Baer, 1950

**Synonym:** *Taenia urceus* Wedell, 1855

**Fish host:** *Chirostoma jordani* (Atheriniformes: Atherinidae).

**Site of infection:** Liver.

**Distribution:** North America: Mexico* (Guadalajara).  
**References:** Scholz and Salgado-Maldonado (2001).

**Remarks:** Metacestodes from the liver of an atherine fish in Mexico closely resembled in their hook morphology the adults of *P. urceus*, a parasite of *P. falcinellus*, *Platalea leucorodia*, and *Milvus migrans* recorded from Europe, Africa (Egypt) and Asia (India) (Bona 1975). However, there was a marked difference in the position of the guard in the large hooks, i.e. in the blade/handle ratio: 1.06–1.33 in metacestodes (Scholz and Salgado-Maldonado 2001) versus 1.50 in adults (Bona 1975).

**Parvitaenia cochlearii** Coil, 1955

**Fish hosts:** *Atherinella crystallina* (Atheriniformes: Atherinidae); *Poeciliopsis gracilis* (Cyprinodontiformes: Poeciliidae); *Dorobutia latifrons*; *Gobiomorus macula* tus* (*Perciformes: Electridae); *Agonostomus monticola* (Perciformes: Mugilidae).

**Site of infection:** Liver.

**Distribution:** North America: Mexico* (Guadalajara).  
**Reference:** Scholz and Salgado-Maldonado (2001).

**Remarks:** The spectrum of fish hosts of *P. cochlearii* is fairly wide and includes members of four families. This contrasts with the fact that adult cestodes have been found only once in the boat-billed heron *Cochlearius cochlearius* from Mexico (Coil 1955b).

**Parvitaenia macropeos** (Wedell, 1855) Baer et Bona, 1960

**Synonyms:** *Taenia macropeos* Wedell, 1855; *Anomoataenia macropeos* (Wedell, 1855) Fuhrmann, 1908; *Parvitaenia echinatia* Metrick, 1967; *Grypohynchus pasillus auctorum* (see Baer and Bona 1960, p. 92), nec von Nordmann, 1832.  
**Fish host:** *Cichlasoma istlanum* (Perciformes: Cichlidae).

**Site of infection:** Liver.  
**Distribution:** North America: Mexico (Guerrero).  
**References:** Scholz and Salgado-Maldonado (2001).

**Remarks:** The cestode is a specific parasite of *Necticorax nortonocorax* occurring in Europe (Hungary, Italy), Asia (Japan, Java, Sri Lanka, Taiwan) and Africa (Zambia) (Bona 1975, Jensen et al. 1983). Metacestodes are known only from central Mexico (Scholz and Salgado-Maldonado 2001).

**Valipora campylancristrota** (Wedell, 1855) Baer et Bona, 1960

**Synonyms:** *Taenia campylancristrota* Wedell, 1855; *Grypohynchus pasillus* Aubert, 1857; *Dilepis unilateralis* Clerc, 1906 nec Rudolphi, 1819; *D. campylancristrota* (Wedell, 1855) Fuhrmann, 1908; *Cysticercus dilepis-campylancristrotae* Joyeux et Baer, 1936.

**Fish hosts:** primarily cyprinid fish (Cypriniformes: Cyprinidae), such as *Abramis brama*, *Alburnoides taeniatus*, *Alburnus alburnus*, *Arichthys nubiclis*, *Aspius aspius*, *Barbus brachycephalus*, *B. capito*, *Carassius auratus*, *C. carassius*, *Chalcobarius chalcoides*, *Chenoparyngodon idella*, *Cyprinus carpio*, *Hemiculter eigenmannii*, *Hypophtalmichthys miliaris*, *Leuciscus cephalus*, *Leuciscus delineatus*, *Pelecus cultratus*, *Rhodeus sericeus*, *Rutilus rutilus*, *Scardinius erythrophthalmus*, *Schizothorax intermedius*, *Tinca tinca* (most common host).

Numerous fish of other families have also been reported as second intermediate hosts, e.g., *Acipenser nivaliventris*, *A. stellatus*, *Pseudoscapaphirynchus kauflmanni* (Acipenseridae); *Chirostoma humboldtianum*, *C. jordani*, *C. riojai* (Atheriniformes: Atherinidae); *Procilodus lineatus* (Characiformes: Prochilodontidae); *Alosa caspia* (Clupeiformes: Clupeidae); *Girardinichthys multi- radiatus* (Cyprinodontiformes: Goodeidae); *Esox lucius* (Esociformes: Esocidae); *Gasterosteus aculeatus* (Gasterosteiformes: Gasterosteidae); *Perca fluviatilis*, *Sander lucioperca* (Perciformes: Percidae); *Salaria fluviatilis* (Perciformes: Blenniidae); *Silurus glanis* (Siluriformes: Siluridae); *Mystus halepensis* (*Mystus pelusius*) (Siluriformes: Bagridae); *Rhamdia guatemalenesis* (Siluriformes: Heptapteridae).

**Site of infection:** Gall bladder (records from the intestine are considered to be doubtful).

**Distribution:** Europe: Czech Republic*, Germany*, Hungary, Italy, Latvia, Lithuania, Moldavia, Poland, Romania, Russia, Slovakia*, Ukraine, Yugoslavia (Montenegro); Asia: Iraq, Japan, Kazakhstan, Mongolia*, Tadjikistan, Uzbekistan; North America: Canada, Mexico*, South America: Brazil.


**Remarks:** Herons, e.g., *Ardea cinerea* (type host), serve as the definitive hosts of the cestode, the adults of which have
Fig. 7. Rostellar hooks of metacestodes of *Neogryporhynchus* from the intestinal lumen, *Parvitaenia* from the liver and *Valipora* from the gall bladder. **A** – *N. cheilancristrotus* from *Channa argus*, Japan (IPCAS C-39). **B** – *P. cochlearii* from *Gobionorus maculatus*, Jalisco, Mexico (IPCAS C-254). **C** – *P. macropoeos* from *Cichlasoma izlanum*, Guerrero, Mexico (IPCAS C-283). **D** – *V. campylancristrota* from *Cyprinus carpio*, Czech Republic (IPCAS C-27). **E** – *V. campylancristrota* from *Rhamdia guatemalensis*, Yucatán, Mexico (large hook) and *Chirostoma jordani*, State of México, Mexico (small hook). **F** – *V. minuta* from *Rhamdia guatemalensis*, Yucatán, Mexico (large hook) and *Poeciliopsis gracilis*, Guerrero, Mexico (small hook) (IPCAS C-240). **G** – *V. mutabilis* from *Cichlasoma beani*, Nayarit, Mexico (large hook and small hook) and *C. meeki*, Campeche, Mexico (right large hook) (IPCAS C-302).

been found only in Europe (Hungary, Italy, Moldavia and Russia – Ural) (Baer and Bona 1960, Spasskaya et al. 1974, Ryzhikov et al. 1985), which contrasts with wide distribution of metacestodes reported from Europe, Asia and North and South America.

Jarecka (1970a) demonstrated experimentally that the copepod *Eudiaptomus graciloides* is a suitable first intermediate host for *V. campylancristrota*. Data on development in the copepod *Arctodiaptomus salinus*, were also provided by Sy-solyatina-Andakulova (1979).

### *Valipora minuta* (Coil, 1950) Baer et Bona, 1960

**Synonym:** *Ophiovalipora minuta* Coil, 1950

**Fish hosts:** *Poecilia sphenops* (Cyprinodontiformes: Poeciliidae); *Rhamdia guatemalensis* (Siluriformes: Haptapteridae); *Gambusia affinis* (Cyprinodontiformes: Poeciliidae); *Micropterus punctatus*, *M. salmoides* (Perciformes: Centrarchidae).

**Site of infection:** Gall bladder.

**Distribution:** North America: Mexico* (Guerrero, Quintana Roo, Yucatán), USA (Arkansas, Texas).


**Remarks.** Adults have been found in the intestine of *Buto-rides virescens* in the USA (Coil 1950).

### *Valipora mutabilis* Linton, 1927

**Synonyms:** *Ophiivalipora houdemeri* Hsi, 1935; *O. nycticoracis* (Olsen, 1937) Coil, 1950; *Dendrouterina lintoni* Olsen, 1937; *D. nycticoracis* Olsen, 1937.

**Fish hosts:** *Rhamdia guatemalensis* (Siluriformes: Haptapteridae); *Ameirus melas* (= *Ictalurus melas*) (Siluriformes: Ictaluridae); *Cichlasoma beani*, *C. geddesi*, *Thor-ichthys meeki* (Perciformes: Cichlidae).

**Site of infection:** Gall bladder.

**Distribution:** North America: Mexico (Campeche, Nayarit, Yucatán), USA

**Reference:** Olsen (1939 – as *Dendrouterina nycticoracis*), Scholz and Salgado-Maldonado (2001).

**Remarks.** Herons (*Butorides virescens*, *Nycticorax nycti-corax*) serve as the definitive hosts of *V. mutabilis* that has been found in North America (Cuba, Mexico, USA), Europe (Italy) and Asia (China) (Coil 1950, Rysavy and Macko 1973, Bona 1975, Scholz et al. 2002a). Metacestodes are known only from Mexico (Scholz and Salgado-Maldonado 2001).
Table 1. Measurements (in µm) of rostellar hooks of gryporhynchid metacestodes from fish.

<table>
<thead>
<tr>
<th>Species</th>
<th>Number</th>
<th>Large hooks</th>
<th></th>
<th>Small hooks</th>
<th>Source</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>Length</td>
<td>Blade</td>
<td>Handle</td>
<td>B/H ratio</td>
</tr>
<tr>
<td>Amirthalingia macracantha</td>
<td>(4 + 6) + 10</td>
<td>448–480</td>
<td>272–296</td>
<td>240–296</td>
<td>1.00–1.16</td>
</tr>
<tr>
<td>Ascodilepis transfuga</td>
<td>10 + 10</td>
<td>390–450</td>
<td>140–280</td>
<td>224–256</td>
<td>1.00–1.18</td>
</tr>
<tr>
<td>Cyclustria capito</td>
<td>14 + 14</td>
<td>221–234</td>
<td>112–122</td>
<td>118–125</td>
<td>0.94–0.97</td>
</tr>
<tr>
<td>Cyclustria ibisa</td>
<td>10 + 10</td>
<td>221–240</td>
<td>141–160</td>
<td>74–86</td>
<td>1.73–2.09</td>
</tr>
<tr>
<td>Cyclustria cf. ralli</td>
<td>10 + 10</td>
<td>154–163</td>
<td>93–109</td>
<td>64–70</td>
<td>1.43–1.70</td>
</tr>
<tr>
<td>Dendrouterina pilherodia</td>
<td>10 + 10</td>
<td>28.5–32</td>
<td>30.5</td>
<td>0.93–1.15</td>
<td>11–122</td>
</tr>
<tr>
<td>Glossocercus caribaensis</td>
<td>10 + 10</td>
<td>106–126</td>
<td>72–88</td>
<td>1.20–1.73</td>
<td>129–141</td>
</tr>
<tr>
<td>Glossocercus cyprinodontis</td>
<td>10 + 10</td>
<td>180–195</td>
<td>122–128</td>
<td>86–93</td>
<td>1.30–1.49</td>
</tr>
<tr>
<td>Neogryporhynchus cheilancristrota</td>
<td>10 + 10</td>
<td>49–57</td>
<td>31–36</td>
<td>18–23</td>
<td>1.40–1.66</td>
</tr>
<tr>
<td>Paradilepis caballeroi</td>
<td>12 + 12</td>
<td>110–121</td>
<td>55–59</td>
<td>53–62</td>
<td>0.90–1.09</td>
</tr>
<tr>
<td>Paradilepis scelecina</td>
<td>10 + 10</td>
<td>101–115</td>
<td>55–60</td>
<td>50–55</td>
<td>1.12–1.23</td>
</tr>
<tr>
<td>Paradilepis simoni (No. 46403)**</td>
<td>14 + 14</td>
<td>99–102</td>
<td>44–49</td>
<td>58–61</td>
<td>0.72–0.83</td>
</tr>
<tr>
<td>Paradilepis simoni (No. 38673)**</td>
<td>14 + 14</td>
<td>103–104</td>
<td>51–53</td>
<td>62–63</td>
<td>0.82–0.85</td>
</tr>
<tr>
<td>Paradilepis rugovaginosus</td>
<td>16 + 16</td>
<td>93–108</td>
<td>41–53</td>
<td>53–65</td>
<td>0.65–0.91</td>
</tr>
<tr>
<td>Paradilepis cf. arcus</td>
<td>10 + 10</td>
<td>125–138</td>
<td>72–83</td>
<td>55–62</td>
<td>1.06–1.33</td>
</tr>
<tr>
<td>Parvitaenia cochleari</td>
<td>10 + 10</td>
<td>49–56.5</td>
<td>26.5–33</td>
<td>23–26.5</td>
<td>1.09–1.36</td>
</tr>
<tr>
<td>Parvitaenia macropeae</td>
<td>10 + 10</td>
<td>49–56.5</td>
<td>26.5–33</td>
<td>23–26.5</td>
<td>1.09–1.36</td>
</tr>
<tr>
<td>Valipora campylancristota</td>
<td>10 + 10</td>
<td>32–37</td>
<td>16.5–20</td>
<td>17–18.5</td>
<td>0.96–1.36</td>
</tr>
<tr>
<td>Valipora minuta</td>
<td>10 + 10</td>
<td>32–37</td>
<td>16.5–20</td>
<td>17–18.5</td>
<td>0.96–1.36</td>
</tr>
<tr>
<td>Valipora mutabilis</td>
<td>10 + 10</td>
<td>32–37</td>
<td>16.5–20</td>
<td>17–18.5</td>
<td>0.96–1.36</td>
</tr>
</tbody>
</table>

References: 1 – Bray (1974); 2 – Scholz (2001); 3 – Scholz and Salgado-Maldonado (2001); 4 – Scholz et al. (2002b); 5 – Scholz et al. (1996); 6 – Chandler (1935); 7 – Scholz (1989a); 8 – Baccarani et al. (1998); 9 – Pietrock and Scholz (2000); 10 – Scholz (1989b); 11 – Priemer and Scholz (1989); PD – present data.

**Paratype (USNPC 46403) – adult worm from Pandion haliaetus.
Taxa of uncertain taxonomic status, doubtful records and synonyms

Amirthalingamia sp. and Cyclastera sp. of Aloo (2002)

Aloo (2002) reported metacestodes identified as Amirthalingamia sp. from the intestine of Tilapia zillii and those of the genus Cyclastera from the liver of Oreochromis leucostictus and T. zillii from Naivasha Lake in Kenya. Examination of voucher specimens from T. zillii provided by Aloo (2002; PCAS C-292 and C-293) has shown their conspecificity with A. macracantha and C. magna, respectively (see Survey of species).

Anomotaenia sp.

Aderoetu and Adeniyi (1972) described and figured a metacestode, designated as Anomotaenia sp., embedded in the upper intestinal wall of Henichromis fasciatus and Tilapia nilotica (= Oreochromis niloticus) from Nigeria. Rosellar hooks (10 only reported, unusual for this group) were 40 µm long but were not illustrated.

Cyclastera sp.

Heard (1970) found adult Cyclastera cestodes in clapper rails, Rallus longirostris, from different states of the USA, and also in a red-breasted merganser and a glossy ibis from Georgia and North Carolina, respectively. According to the author, the conspecific larva occurs in the viscera of brackish water fishes Cyprinodon variegatus and Fundulus heteroclitus. However, Bona (1975), who revised Heard’s material, concluded that specimens from Mergus serrator were Cyclastera ibises and that those from clapper rails represented a different genus. It is, therefore, possible that larvae were in fact conspecific with C. ibises or with a species of Glossocercus (see Survey of species).

Cysticercoidea menidiae Chandler, 1935

Metacestodes from Menidia menidiae described as Cysticercoidea menidiae by Chandler (1935) belong in fact to Ascodilepis transjuga (Krabbe, 1869) – see Scholz (2001).

Cysticericus gen. sp. of Dogiel and Bykovskii (1938)

Russian authors reported metacestodes ("cysticerici") from the gall bladder of Atherina boyeri (Atheriniformes: Atherinidae) and, more rarely, Cispiaioska brashnikovi (= Alosa brashnikovi) (Clupeiformes: Clupeidae) and other fish from Caspian Sea. The size of the hooks (about 100 µm – larger hooks, and 70 µm – smaller hooks) and their shape (fig. 13) indicate the metacestodes belonged to a species of Paradilepis. However, the site of infection is not typical of larvae of this genus (see Scholz and Salgado-Maldonado 2001).

Dendroterina papillifera (Fuhrmann, 1908) of Scholz et al. (1996)

Scholz et al. (1996) misidentified larvae of Valipora minutula (Coil, 1950) as D. papillifera (see Scholz and Salgado-Maldonado 2001; USNPC 88228). Metacestodes of the latter species from fish have not been found.

Dilepididae gen. sp. 1 of Shimazu et al. (2000)

Metacestodes from the gall bladder of Carassius auratus langsdorffii from Kami-dokanburi, Tokyo, Japan, were conspecific with those of Valipora campylancristota because of their morphology, in particular the shape and size of the rostellar hooks (about 28 µm and 13 µm, respectively, as estimated from their photomicrograph – fig. 13 in Shimazu et al. 2000).

Dilepididae gen. sp. 2 of Shimazu et al. (2000)

The larvae found in the intestine of C. auratus langsdorffii in the Imperial Palace in Tokyo are apparently conspecific with Neogryporhynchus chelancristotus as indicated by their morphology, including shape (figs. 9 and 15 in Shimazu et al. 2000) and size (about 58 µm and 38 µm, respectively, as estimated from their photomicrographs). Conspecific larvae were found in the intestine of other freshwater fish from Japan (see Survey of species).

Dilepis sp.

Under this name, metacestodes apparently belonging to several gryporhynchid genera, most probably Paradilepis Hsu, 1935 and Valipora Linton, 1927, have been reported from North American freshwater fish (see Hoffman 1999):

(i) liver of Oncorhynchus nerka (Salmoniformes: Salmonidae) from northwestern Canada and USA (Bailey and Margolis 1987);

(ii) liver and mesenteries of Lepomis gibbosus (Percomor- phes: Centrarchidae) from Ontario, Canada (Cone and Anderson 1977, Dechtiar and Christie 1988, Dechtiar et al. 1989);

(iii) intestinal wall of Ctenopharyngodon idella (Cyprini- forms: Cyprinidae) and gall bladder of swordtail (aquarium fish) from the USA (Hoffman 1999);

(iv) intestinal wall of Notemigonus crysoleucas (Cyprini- forms: Cyprinidae) from the USA (unpubl. data of Riley and R. Walker – see Hoffman 1999);

(v) wall of gall bladder of Ictalurus melas (Siluriformes: Ictaluridae) from the USA (unpubl. data of J. Warren – see Hoffman 1999);


The above-listed metacestodes could not be identified because their morphology had not been described and voucher specimens are not available. Nevertheless, it is apparent that they do not belong to the genus Dilepis, the adults of which do not occur in fish-eating birds (Matevosyan 1963, Schmidt 1986).

Gryporhynchus sp.

Chen Chih-leu (1973) listed metacestodes designated as Gryporhynchus sp. from Aristichthys nobilis, Carassius auratus, Cyprinus carpio, Hemiculus leuciscus, Mylopharyngodon piceus, Parabramis liaoheensis (= P. pekinensis), and Rhinogobius guirinus from the Hupei Province, China. These larvae may be conspecific with Neogryporhynchus chelancristotus but voucher specimens were not available to confirm this assumption.

Chen (1984) listed larvae of Gryporhynchus (possibly Neogryporhynchus chelancristotus) from Ophiopcephalus argus (= Channa argus), Misgurnus fossilis and Squaliohab- bus curculius.

Paradilepis sp.

Prudhoe and Hussey (1977) illustrated the metacestodes identified as Paradilepis sp. by Bray (1974 – see below).

Dechtiar et al. (1989) reported metacestodes designated as Paradilepis sp. from Lepomis gibbosus and Phoxinus neo- gaeus from Ontario, Canada. Comparative material of neither authors was available.
Scholz and Salgado-Maldonado (2001) reported an unidentifed species of Paradilepis from the liver of Chirostoma jordani (Atheriniformes: Atherinidae) from central Mexico (Guanajuato) (Fig. 6F). The same authors (Scholz et al. 2002a) found a conspecific adult in Phalacrocirrus olivaceus from Veracruz (Mexico). This species is most probably new to science but the poor quality of the only adult specimen available did not enable them to describe this cestode formally as a new taxon.

Ezeri (2002) reported metacestodes of Paradilepis from cultured tilapia (Oreochromis niloticus) (Percoformes: Cichlidae) from Nigeria but voucher material has not been available.

Parvitaenia sp.

Wiles (1975) reported larvae of Parvitaenia sp. from the body cavity of Fundulus diaphanus (Atheriniformes: Cyprinodontidae) from Nova Scotia, Canada.

Other findings

Petrushesvki et al. (1948) found metacestodes designated as Cysticercus paradilepidis in Leuciscus idus and Tinca tinca from the Ob and Irtils rivers in Russia. The larvae most probably belonged to Paradilepis scoleceina, the only species of Paradilepis reported from freshwater fish in Russia (Dubinina 1962, 1987).

Bray (1974) reported two species of unidentified dilepidid (= gryporhynchid) metacestodes from Tilapia nilotica (= Oreochromis niloticus) from Sudan. The larva from the intestinal lumen may have been conspecific with Parvitaenia magna Baer, 1959 (= Cyclustera magna – see above), whereas those encysted in the intestinal wall appeared to belong to Paradilepis, possibly P. delachauxi (Fuhrmann, 1909) Joyce et Baer, 1935, thus being probably conspecific with those reported as Anomotaenia sp. (cysticercus) from O. niloticus from Nigeria (Adenunmu and Adeniyi 1972) and as dilepidid larvae from the intestinal wall of several species of tilapias (Haplochromis angustifrons, H. elegans, H. limax, H. nigripinnis, H. squamipinnus, H. wingattii, Pseudocrenilabrus multicolor, Oreochromis niloticus, T. zillii) from Uganda (Khalil and Thurston 1973).

Batra (1984) reported three metacestodes from the intestine of two tilapias (Oreochromis macrochir) from Zambia. Without having any information about their morphology, Batra (1984) stated they resembled metacestodes reported as “dilepidid larva” (possibly Paradilepis delachauxi) by Khalil and Thurston (1973) from fishes in Uganda (see above).

Bailey et al. (1988) and Groot et al. (1989) reported larvae of dilepidid cestodes from Oncorhynchus nerka in British Columbia, Canada. Species attribution of these metacestodes is not clear but they may well belong to Paradilepis as metacestodes which occur in the same host from British Columbia (see Ching 1982 and Survey of species).

**FINAL CONCLUSIONS AND PERSPECTIVES**

The present study has shown that the existing knowledge of the diversity, host spectrum and geographical distribution of metacestodes of gryporhynchid (dilepidid) tapeworms from fish is fragmentary and considerable differences exist in the amount of data accumulated in the Holarctic Region and other parts of the world. In most gryporhynchid genera, a low proportion of taxa have been reported both as adults from fish-eating birds and metacestodes from fish (see Scholz et al. 2002a for data from Mexico where the highest number of metacestodes was found). For example, out of 20 species of Paradilepis reported as adults by Schmidt (1986), metacestodes of only 4 taxa have been reported from fish, out of 15 species of Parvitaenia, only 2 taxa are known as larvae from fish, and out of 12 species of Valipora, metacestodes of only 3 taxa have been found in fish.

The existing data also indicate that there is not a unified pattern in the degree of specificity at the level of fish intermediate host as well as site preference. Some species, such as Cyclustera capito, C. magna, Dendrouterina ptheriodae, Glossococcus cyprinodontis and Paradilepis caballeroi, have been reported from only one species of fish host, thus being classified as stenoxenous parasites. Amirthalingamia macracantha and Cyclustera ibisae occur in members of closely related genera and correspond to the oioxenous type of host specificity. On the other hand, some species, especially those reported from Europe and the Holarctic part of Asia (Neogryporhynchus cheilancristrotus, Paradilepis scoleceina and Valipora campylancristrot), but also Glossococcus auritus, Parvitaenia cochlearii, Valipora minuta and V. mutabilis occur in a wide spectrum of fish hosts, thus exhibiting the euryxenous type of host specificity. However, further research may demonstrate that the host spectrum of most gryporhynchid metacestodes is actually wider and classification of individual species as to their host specificity will have to be changed.

Site of infection with gryporhynchid larvae differs among different genera, with most species occurring in only one microhabitat. Species of Cyclustera are confined to the mesenteries, whereas metacestodes of Glossococcus occur in the liver of fish hosts, similar to the larvae of Paradilepis. The specific site of infection with Neogryporhynchus cheilancristrotus larvae is the intestinal lumen, whereas that of metacestodes of Parvitaenia is the liver and of larvae of Valipora gall bladder.

Metacestodes of most gryporhynchid taxa have been found in freshwater fish but some, namely Ascodilepis transfuga, Cyclustera capito, C. ibisae, Glossococcus caribaensis and G. cyprinodontis, occur in brackish water fish, especially cyprinodontids from the Atlantic coast of North America (USA and Mexico), and may be limited in their occurrence to this water habitat.

The present review demonstrates that there are many missing data on the diversity, host specificity and distribution of metacestodes of gryporhynchids. It is obvious that future surveys on fish parasites should give more emphasis to searching for these larvae that may have been overlooked in previous ichthyoparasitological research. Appropriate fixation and processing of these larvae as well as their molecular characterisation seem to be necessary requirements for providing new, reliable information about this group of cestode par-
sites. Regarding the most neglected areas, the future research should focus on the occurrence of gryporhynchid larvae in tropical Asia, Australia, South America and Africa. The actual number of gryporhynchid species occurring in fish is undoubtedly much higher than that reported until now and it is probable that larvae of numerous taxa will be reported in the near future.

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Appendix 1. Host-Parasite List. Name of fish according to FishBase (Froese and Pauly 2003).

Aciapersteriformes: Aciapseridae (3 fish species infected with 3 gryporhynchid species)
Aciapser nudiventris – Paradilepis sceleca, Valipora campylancristrota
Aciapser stellatus – Valipora campylancristrota

Pseudoscaphirhynchus kaufmanni – Neogryporhynchus cheilancristrota, Paradilepis sceleca, Valipora campylancristrota

Atheriniformes: Atherinidae (5/5)
Atherinella crystallina – Parviaena cochlaria

Characiformes: Characidae (1/1)
Paradilepis scolecina

Cypriniformes: Cobitidae (3/1)
Cobitis taenia – Neogryporhynchus cheilancristrota

Misgurnus anguillaroaatus – Neogryporhynchus cheilancristrota
Misgurnus fossilis – Neogryporhynchus cheilancristrota

Cypriniformes: Cyprinidae (45/5)
Abramis ballerus – Neogryporhynchus cheilancristrota
Abramis bjorkna – Neogryporhynchus cheilancristrota, Paradilepis sceleca
Abramis braea – Neogryporhynchus cheilancristrota, Paradilepis sceleca, Valipora campylancristrota
Abramis sapa – Neogryporhynchus cheilancristrota
Alburnoides taeniatus – Neogryporhynchus cheilancristrota, Paradilepis sceleca, Valipora campylancristrota
Alburnus albidas – Paradilepis sceleca
Alburnus alburnus – Neogryporhynchus cheilancristrota, Paradilepis sceleca, Valipora campylancristrota
Aristichthys nobilis – Paradilepis sceleca, Valipora campylancristrota
Aspius aspinus – Neogryporhynchus cheilancristrota
Aspius aspinus – Neogryporhynchus cheilancristrota, Paradilepis sceleca, Valipora campylancristrota
Barbus brachicephalus – Neogryporhynchus cheilancristrota, Paradilepis sceleca, Valipora campylancristrota
Barbus capito – Neogryporhynchus cheilancristrota, Paradilepis sceleca, Valipora campylancristrota
Capeoeta capoeta – Neogryporhynchus cheilancristrota, Paradilepis sceleca
Capeotobrama kaschakeivitschi – Neogryporhynchus cheilancristrota
Carassius auratus – Neogryporhynchus cheilancristrota, Paradilepis sceleca, Valipora campylancristrota
Carassius carassius – Neogryporhynchus cheilancristrota, Paradilepis sceleca, Valipora campylancristrota
Chalcalburnius chaleoides – Neogryporhynchus cheilancristrota, Paradilepis sceleca, Valipora campylancristrota
Chondrostoma cyri – Paradilepis sceleca
Chondrostoma nasus – Paradilepis sceleca
Ctenopharyngodon idella – Neogryporhynchus cheilancristrota, Valipora campylancristrota
Culter alburnus – Paradilepis sceleca
Cyprinus carpio – Cyclusta cf. ralli, Neogryporhynchus cheilancristrota, Paradilepis sceleca, Valipora campylancristrota

Gnathopogon caeruleus – Neogryporhynchus cheilancristrota
Gnathopogon elongatus – Paradilepis sceleca
Hemiculter eugenei – Valipora campylancristrota
Hemiculter leuciscus – Paradilepis sceleca

Hypophthalmichthys molitrix – Valipora campylancristrota
Leuciscus cephalus – Neogryporhynchus cheilancristrota, Valipora campylancristrota
Leuciscus idas – Neogryporhynchus cheilancristrota, Paradilepis sceleca
Leuciscus lehmanni – Neogryporhynchus cheilancristrota
Leuciscus delineatus – Neogryporhynchus cheilancristrota, Valipora campylancristrota
Notropis salsee – Cyclusta cf. ralli
Oreoleuciscus humilis – Paradilepis sceleca

Oreoleuciscus picanii – Paradilepis sceleca
Pelaeus cultratus – Neogryporhynchus cheilancristrota, Paradilepis sceleca, Valipora campylancristrota
Ptychochilus oregonensis – Paradilepis simonsi (?)
Rhodeus sericeus – Neogryporhynchus cheilancristrota, Paradilepis sceleca, Valipora campylancristrota
Rutilus rutilus – Neogryporhynchus cheilancristrota, Paradilepis sceleca, Valipora campylancristrota
Scardinius erythrophthalmus – Neogryporhynchus cheilancristrota, Paradilepis sceleca, Valipora campylancristrota
Schizopygopsis stoliczkae – Paradilepis sceleca
Schizothorax intermedius – Neogryporhynchus cheilancristrota, Paradilepis sceleca, Valipora campylancristrota
Tinca tinca – Neogryporhynchus cheilancristrota, Paradilepis sceleca, Valipora campylancristrota
Tribolodon hakonensis – Paradilepis sceleca
Varicorhinus sp. – Paradilepis sceleca
Zacco platypus – Neogryporhynchus cheilancristrota

Cyprinodontiformes: Cyprinodontidae (2/2)
Cyprinodon variegatus variegatus – Glossocercus auritus

Cyprinodontiformes: Fundulidae (4/2)
Fundulus grandissimus – Glossocercus caribaensis
Fundulus heteroclitus – Cycluseta ibisae, Glossocercus caribaensis
Fundulus majalis – Cycluseta ibisae, Glossocercus caribaensis
Fundulus persimilis – Glossocercus caribaensis