

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

Tomáš Scholz^{1,2}, Rodney A. Bray³, Roman Kuchta^{1,2}, Radmila Řepová¹

¹Institute of Parasitology, Academy of Sciences of the Czech Republic and ²Faculty of Biological Sciences, University of South Bohemia, Branišovská 31, 370 05 České Budějovice, Czech Republic;

³Department of Zoology, The Natural History Museum, Cromwell Road, London SW7 5BD, UK

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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: *Amirthingamia* Bray, 1974 (1 species), *Ascodilepis* Guildal, 1960 (1), *Cyclusteria* Fuhrmann, 1901 (4), *Dendrouterina* Fuhrmann, 1912 (1), *Glossocercus* Chandler, 1935 (3), *Neogryporhynchus* Baer et Bona, 1960 (1), *Paradilepis* Hsü, 1935 (5), *Parvitaenia* Burt, 1940 (2), and *Valipora* Linton, 1927 (3). However, most published records concern only three species, namely *Neogryporhynchus cheilancristrotus* (Wedl, 1855) from the intestinal lumen, *Paradilepis scolecina* (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 *Cyclusteria 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 cheilancristrotus* (Wedl, 1855), *Paradilepis scolecina* (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. cheilancristrotus* and *V. campylancristrota*.

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, Dubinina 1962, 1971, 1987, Molnár 1970, Kozicka 1971, Kennedy 1974, Bona 1975, Ergens et al. 1975, Chubb 1980, Kachcheva-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 cheilancristrotus*, reported as two valid species by some authors, especially in Russia (e.g., Dubinina 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. campylancristrota*) 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. cheilancristrotus* and *V. campylancristrota* (Jarecka 1970a, b) and *Mesocyclops oithonoides* Sars, 1863 was a suitable intermediate host of *N. cheilancristrotus*. Jarecka (1970a) also infected carp fry, which probably serve as the second intermediate host, with larvae of *V. campylancristrota* 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. campylancristrota*. Copepods such as *Arctodiaptomus salinus* (Daday, 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 cheilancristrotus* (as *Gryporhynchus* sp.) in Ukraine (Ivasik 1953), *Paradilepis scolecina* (as *Cysticercus dilepidis*) also in Ukraine (Komarova 1957), *Valipora campylancristrota* (as *Cysticercus dilepidis campylancristrotae* and *Dilepis unilateralis*) in Poland (Jara and Olech

1964a) and Ukraine (Sapozhnikov 1975), respectively, and undetermined species of Dilepididae in Ontario, Canada (Cone and Anderson 1977). More recent data are also very scarce (e.g., Moravec 1983, 1985, 1986, Pietrock and Scholz 2000).

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, Ivasik (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

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 (1964b) reported a marked congestion and mechanical damage to the blood vessels of carp infected with *V. campylancristrota* but they did not find that this had a negative influence on the condition and weight-gain of parasitized fish.

Körting (1984) reported focal haemorrhages, necrosis and clinical signs of enteritis in the intestines of farmed carp and tench fry infected with gryporhynchid larvae, most probably those of *Neogryporhynchus cheilancristrotus*, which penetrated deeply into the sub-epithelial layers of the gut.

Suvorov (1981), Studnicka et al. (1984), Nikulina (1985) and Skvortsova et al. (1985) tested treatment of fish infected with metacestodes of *V. campylancristrota* and Nikulina (1985) observed the haematological parameters of carp infected with this cestode.

SURVEY OF SPECIES RECORDED

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 vouchers of gryporhynchid cestodes deposited in helminthological 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 simoni* Rausch, 1949 – four specimens from the liver of *Oncorhynchus nerka* (Walbaum) (HWML 38672 and 38673), *Oncorhynchus mykiss* (Walbaum) (HWML 38674) and *Prosopium williamsoni* (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 *Amirthalinghamia macracantha* (Joyeux et Baer, 1935) from *Tilapia zillii* (Gervais), Naivasha Lake, Kenya (IPCAS C-292); 5 specimens of *Cycluster 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 cyprinodontis* 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 caeruleus* (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 langsdorffii* 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* (Cantor), 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 present authors, including those from previous studies on gryporhynchids (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).

Amirthingamia macracantha (Joyeux et Baer, 1935) Bray, 1974 Fig. 1A

Synonyms: *Dilepis delachauxi* Joyeux et Baer, 1930, *nec* Fuhrmann, 1909; *Paradilepis macracantha* Joyeux et Baer, 1935.

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

Site of infection: Liver and intestinal wall.

Distribution: Africa: Kenya*, Sudan*.

References: Bray (1974), Aloo (2002 – as *Amirthingamia* sp.), present study.

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 *Phalacrocorax 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 *Amirthingamia* sp., are conspecific with those of *A. macracantha*, as indicated by their morphology, 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

Fig. 4A

Synonyms: *Taenia transfuga* Krabbe, 1869; *Dilepis transfuga* (Krabbe, 1869) Fuhrmann, 1908; *Cysticercoides menidia* Chandler, 1935.

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

Site of infection: Intestinal wall, mesenteries.

Distribution: North America: USA* (Texas).

References: Chandler (1935), Scholz (2001).

Remarks. Metacestodes were originally reported under the name *Cysticercoides menidia* 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).

Cyclustera capito (Rudolphi, 1819) Fuhrmann, 1901

Fig. 2A

Synonym: *Taenia capito* Rudolphi, 1819.

Fish host: *Floridichthys polyommus** (Cyprinodontiformes: Cyprinodontidae).

Site of infection: Mesenteries.

Distribution: North America: Mexico* (Yucatán).

Reference: Scholz and Salgado-Maldonado (2001).

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).

Cyclustera ibisae (Schmidt et Bush, 1972) Bona, 1975

Fig. 2B

Synonyms: *Parvitaenia ibisae* Schmidt et Bush, 1972; *P. eudocimi* Rysavy et Macko, 1973.

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

Site of infection: Mesenteries.

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

Reference: Scholz et al. (2002b).

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*, *Phalacrocorax 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.

Cyclustera magna (Baer, 1959) Bona, 1975

Fig. 2C

Synonym: *Parvitaenia magna* Baer, 1959.

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

Site of infection: Intestinal wall.

Distribution: Africa: Kenya*.

Reference: Aloo (2002 – as *Cyclustera* sp.), present study.

Remarks. Metacestodes collected by Aloo (2002) from the gut wall of *Tilapia zillii* from Kenya, tentatively identified as *Cyclustera* 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 rostellum 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 *Amirthingamia 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*.

Cyclustera cf. ralli (Underwood et Dronen, 1986) Bona, 1994

Fig. 2D

Fish hosts: *Cyprinus carpio**, *Notropis salleri** (Cypriniformes: Cyprinidae); *Allophorus robustus**, *Girardinich-*

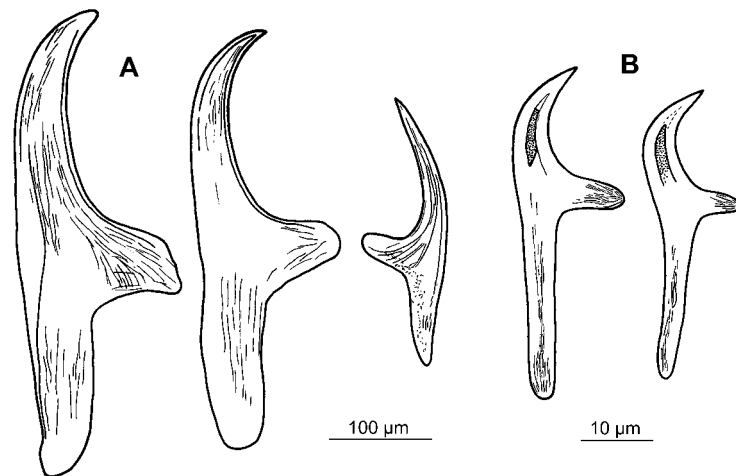


Fig. 1. Rostellar hooks of metacestodes from fish. **A** – *Amirthalingamia macracantha* from the intestinal wall of *Tilapia zillii*, Kenya (IPCAS C-292). **B** – *Dendrouterina pilherodiae* from the gall bladder of *Rhamdia guatemalensis*, Yucatán, Mexico (IPCAS C-241).

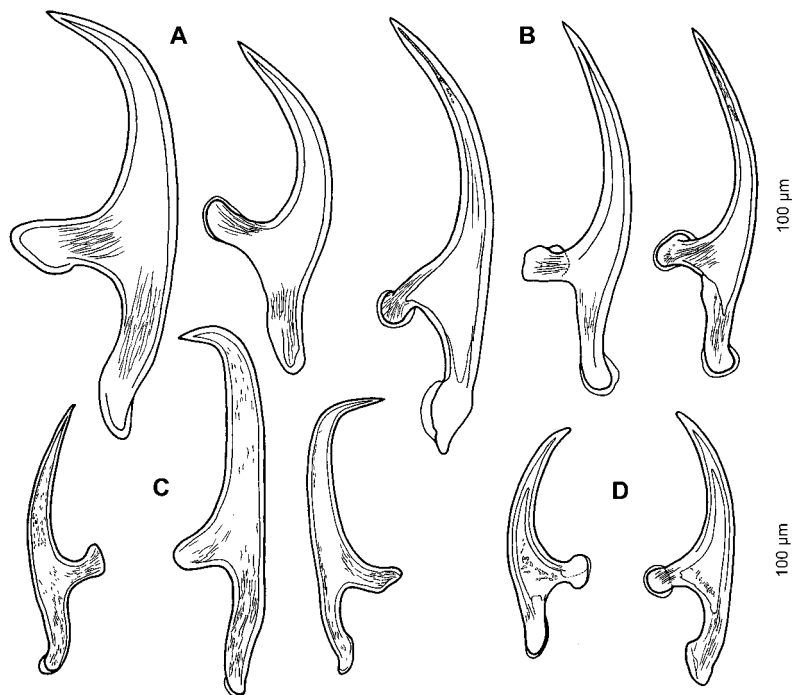


Fig. 2. Rostellar hooks of species of *Cycluster*. **A** – *C. capito* from the mesenteries of *Floridichthys polyommus*, Yucatán, Mexico (IPCAS C-279). **B** – *C. ibisae* from *Fundulus heteroclitus*, South Carolina, USA (left and right hooks; IPCAS C-337) and from the intestine of *Phalacrocorax olivaceus*, 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).

*thys multiradiatus**, *Xenotoca variata** (Cyprinodontiformes: Goodeidae).

Site of infection: Mesenteries.

Distribution: North America: Mexico* (Guanajuato, State of México and Michoacán).

Reference: Scholz and Salgado-Maldonado (2001).

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 *Cycluster ralli* (syn. *Neocycluster ralli*

Underwood et Dronen, 1986, according to Bona 1994). However, the shape of the hooks of the *C. ralli* paratype (USNPC 78464) and those of metacestodes from Mexico are somewhat different (see Scholz and Salgado-Maldonado 2001). Therefore, the identification of Mexican specimens as *Cyclustera* cf. *ralli* is only tentative. It cannot be ruled out that the larvae from Mexican fish belong to a new species of *Cyclustera*, the adults of which are still unknown.

The type and the only known definitive host of *C. ralli*, which has been reported only from Texas, USA, is the clapper rail *Rallus longirostris* (see Underwood and Dronen 1986).

Dendrouterina pilherodiae Mahon, 1956 Fig. 1B

Fish host: *Rhamdia guatemalensis** (Siluriformes: Heptapteridae).

Site of infection: Gall bladder.

Distribution: North America: Mexico* (Yucatán).

Reference: Scholz et al. (1996).

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

Glossocercus cyprinodontis Chandler, 1935 Fig. 3A

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

Site of infection: Body cavity.

Distribution: North America: USA* (Texas).

Reference: Chandler (1935).

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, 1819) Bona, 1994

Fig. 3B

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

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

Site of infection: Liver, mesenteries, intestinal wall.

Distribution: North America: Mexico* (Guerrero, Hidalgo, Oaxaca, Veracruz).

References: Salgado-Maldonado et al. (2001), Scholz and Salgado-Maldonado (2001).

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 Fig. 3C

Synonyms: *Parvitaenia caribaensis* Rysavy et Macko, 1973; *P. heardi* Schmidt et Courtney, 1973.

Fish hosts: *Fundulus grandissimus**, *F. heteroclitus**, *F. majalis**, *F. persimilis** (Cyprinodontiformes: Fundulidae); *Cichlasoma urophthalmus** (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 urophthalmus*, which may live also in brackish water (Vidal-Martínez 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 cheilancristrotus (Wedl, 1855) Baer et Bona, 1960 Fig. 7A

Synonyms: *Taenia cheilancristrota* Wedl, 1855; ? *Gryporhynchus pusillus* von Nordmann, 1832; *G. cheilancristrotus* (Wedl, 1855) Fuhrmann, 1907; *G. tetrorchis* Hill, 1941; *Gryporhynchus* sp. Kozicka, 1959; *Cysticercus gryporhynchus-pusillae* Joyeux et Baer, 1936; *C. gryporhynchus-cheilancristroti* 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*, *Aspiolucius esocinus*, *Aspius aspius*, *Barbus brachycephalus*, *B. capito*, *Blicca bjoerkna**, *Capoeta capoeta*, *Capoetobrama kuschakewitschi*, *Carassius auratus**, *C. carassius**, *Chalcalburnus chalcoides*, *Ctenopharyngodon idella*, *Cyprinus carpio**, *Gnathopogon caeruleus**, *Hemiculter eigenmanni*, *Leucaspis delineatus*, *Leuciscus cephalus**, *L. idus*, *L. lehmanni*, *Pelecus cultratus*, *Rhodeus sericeus*, *Rutilus rutilus**, *Scardinius erythrophthalmus*, *Schizothorax intermedius*, *Tinca tinca**, *Zacco platypus** (Cypriniformes: Cyprinidae); *Cobitis taenia*, *Misgurnus anguillicaudatus**, *M. fossilis** (Cypriniformes: Cobitidae). Other fish may also serve as second intermediate hosts, e.g., *Pseudoscaphirhynchus kaufmanni* (Acipenseriformes: Acipenseridae); *Alosa kessleri* (Clupeiformes: Clupeidae); *Esox lucius* (Esociformes: Esocidae); *Gymnocephalus cernuus*, *Perca fluviatilis*, *P. schrenkii*, *Zingel streber* (Perciformes: Percidae); *Channa argus** (Perciformes: Channidae); *Liza abu* (Perciformes: Mugilidae); *Silurus asotus*, *S. glanis* (Siluriformes: Siluridae).

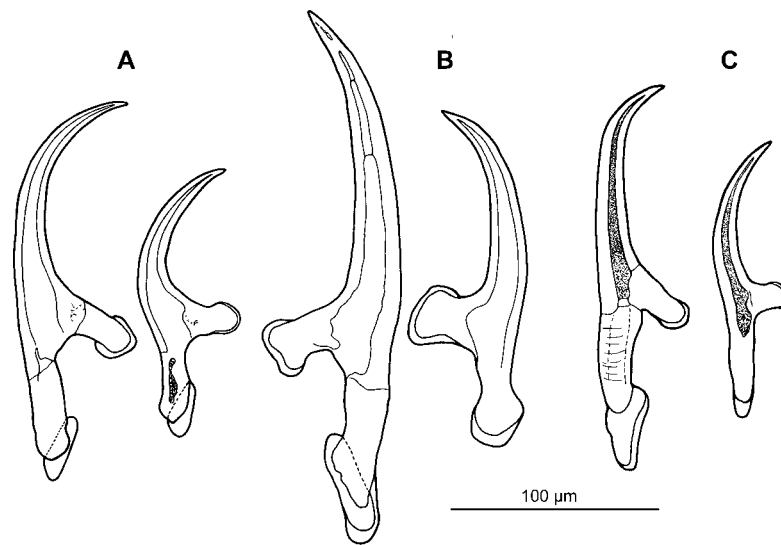


Fig. 3. Rostellar hooks of metacestodes of *Glossocercus*. **A** – *G. cyprinodontis* from the body cavity of *Cyprinodon variegatus*, Texas, USA (USNPC 80403). **B** – *G. auritus* from the mesenteries of *Poecilia catemaconis* (large hook) and *Poeciliopsis gracilis* (small hook), Veracruz and Guerrero, Mexico (IPCAS C-281). **C** – *G. caribaensis* from *Fundulus heteroclitus*, South Carolina, USA (IPCAS C-282).

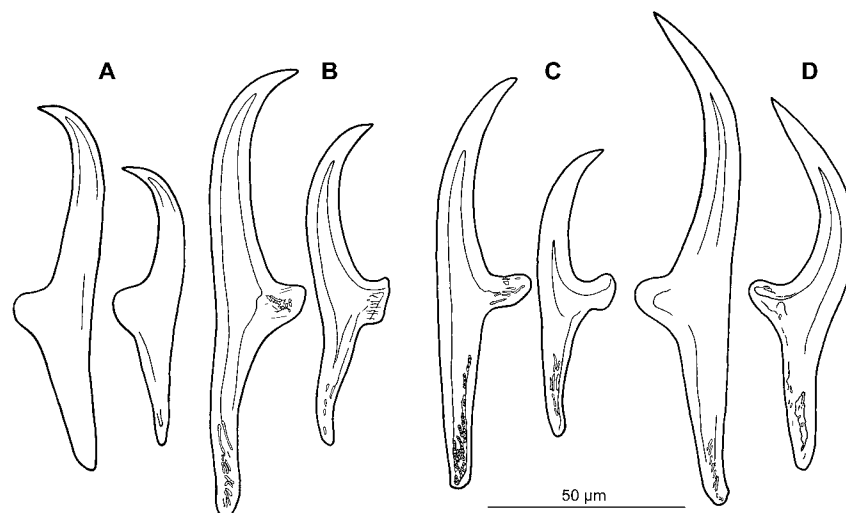


Fig. 4. Rostellar hooks of metacestodes of *Ascodilepis* and *Paradilepis*. **A** – *A. transfuga* from the intestinal wall and mesenteries of *Menidia menidia* from Texas, USA (USNPC 39530). **B** – *P. caballeroi* from the liver of *Chirostoma jordani*, Guanajuato, Mexico (IPCAS C-313). **C** – *P. 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: Azerbaidzhan, Georgia, Iraq, Japan*, Kazakhstan, Tadjikistan, Turkmenia, Uzbekistan.

References: Baer and Bona (1960), Kozicka (1971), Bona (1975), Ergens et al. (1975), Pastuszko et al. (1984), Ali et al. (1987a), Dubinina (1987), Grabda-Kazubska et al. (1987), Scholz (1989a), Pojmańska (1991), Baccarani et al. (1998), Hanzelová and Ryšavý (1999), Pietrock and Scholz (2000), Kirin (2001), Moravec (2001), Popiolek (2002),

present study (specimens from Japan). As *Gryporhynchus cheilancristrotus* – Bogdanova (1961), Esinenko-Marits (1965), Kulakovskaya (1969), Dubinina (1971), Osmanov (1971), Astachova and Stepanova (1972), Kulakovskaya and Koval (1973), Skryabina (1974), Margaritov (1976), Izyumova (1977), Andakoulova (1978), Adamczyk (1979), Kurashvili et al. (1980), Kakacheva-Avramova (1983), Rautskis (1988), Gavrilova and Karimov (1989), Naimova and Roitman (1989), Margaritov (1992); as *Gryporhynchus pusillus* – Iskov (1965), Kulakovskaya (1969), Osmanov (1971), Skryabina (1974), Kurashvili et al. (1980), Dubinina (1987), Ibragimov (1988), Gavrilova and Karimov

(1989), Razmashkin (1990), Ermolenko and Butorina (1998), Boutorina and Ermolenko (2001); as *Gryporhynchus* sp. – Molnár (1970); as Dilepididae gen. sp. 2 – Shimazu et al. (2000).

Remarks. The complicated taxonomic history of this species was reviewed in detail by Baer and Bona (1960) and Bona (1975). The former authors proposed a new genus, *Neogryporhynchus*, to accommodate Wedl's species *Taenia cheilancristrota* because of impossibility to identify *Gryporhynchus pusillus* von Nordmann, 1832.

In this study, metacestodes of *N. cheilancristrotus* are reported from Japan for the first time. However, conspecific larvae, which had been reported as Dilepididae gen. sp. 2 (see below) by Shimazu et al. (2000), have also been found to belong to this species.

Jarecka (1970b) proved experimentally that the copepod *Mesocyclops oithonoides* served as the first intermediate host. Adults of *N. cheilancristrotus* are intestinal parasites of herons, such as *Ardea cinerea*, *A. herodias*, *A. purpurea*, *Botaurus stellaris* (type host), and *Nycticorax nycticorax* (Bona 1975).

Paradilepis caballeroi Rysavy et Macko, 1973 Fig. 4B

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

Site of infection: Mesenteries and liver.

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

Reference: Scholz and Salgado-Maldonado (2001).

Remarks. Adults are specific parasites of cormorants (*Phalacrocorax auritus*, *P. brasilianus* and *P. olivaceus*) found only in Cuba, Neotropical Mexico (Veracruz) and USA (Rysavy and Macko 1973, Fedynich et al. 1997, Scholz et al. 2002a). Scholz et al. (2002a) discussed the validity of the species which differs from *P. scolecina* (Rudolphi, 1819), a common parasite of cormorants in Eurasia, Africa and Australia (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. scolecina*).

Paradilepis scolecina (Rudolphi, 1819) Fig. 4C

Synonyms: *Taenia scolecina* Rudolphi; *Dilepis scolecina* (Rudolphi, 1819) Fuhrmann, 1908; *Cysticercus dilepidis* Dogiel et Bychowsky, 1934; *Paradilepis duboisi* Hsü, 1935; *P. brevis* Burt, 1940.

Fish hosts: The most common hosts are cyprinids, 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 chalcoides*, *Chondrostoma cyri*, *C. nasus*, *Culter alburnus*, *Cyprinus carpio**, *Gnathopogon elongatus*, *Hemiculter leucisculus*, *Leuciscus idus*, *Oreoleuciscus humilis**, *O. potanini**, *Pelecus cultratus*, *Rhodeus sericeus*, *Rutilus rutilus**, *Scardinius erythrophthalmus**, *Schizopygopsis stoliczkae*, *Tinca tinca*, *Tribolodon hakonensis**, *Varicorhinus* sp. (Cypriniformes: Cyprinidae); *Acipenser nudiventris*, *Pseudoscaphirhynchus kaufmanni* (Acipenseriformes: Acipenseridae); *Esox lucius* (Esociformes: Esocidae); *Gasterosteus aculeatus*, *Pungitius pungitius*, *P. platygaster* (Gasterosteiformes: Gasterosteidae); *Gymnocephalus cernuus*, *Perca fluviatilis* (Perciformes: Percidae); *Neogobius*

melanostomus (Perciformes: 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: Azerbaidzhan, Georgia, Japan*, Kazakhstan, Mongolia*, Tadjikistan, Uzbekistan.

References: Yamaguti (1940), Dubinin (1952), Dubinina (1962, 1971, 1987), Kulakovskaya (1965, 1969), Kažić (1970), Molnár (1970), Kozicka (1971), Osmanov (1971), Kulakovskaya and Koval (1973), Skryabina (1974), Mikailov (1975), Margaritov (1976), Izyumova (1977), Knezević et al. (1978), Kurashvili et al. (1980), Mikailov and Ibragimov (1980), Kazieva (1981), Kiskaroly et al. (1981), Kakacheva-Avramova (1983), Dzhililov (1985), Ryzhikov et al. (1985), Grabda-Kazubska et al. (1987), Dupont and Crivelli (1988), Rautskis (1988), Priemer and Scholz (1989), Scholz (1989b), Kazieva and Mikailov (1990), Scholz and Ergens (1990), Pojmańska (1991), Margaritov (1992), Molnár and Székely (1996), Murai et al. (1997), Baccarani et al. (1998), Grupcheva and Nedeva (1999), Rolbiecki et al. (1999), Boutorina and Ermolenko (2001), Kalbe et al. (2002), present study (specimens from the Czech Republic and Japan).

Remarks. Although adults are frequent and widely distributed parasites of cormorants 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. scolecina* on its definitive host, the white-necked cormorant (*Phalacrocorax carbo*), was studied by Karstad et al. (1982). The copepod *Eudiaptomus graciloides* is the first intermediate host under experimental conditions (Jarecka 1970b).

Paradilepis simoni Rausch, 1949 Figs. 5, 6A, B

Fish hosts: *Oncorhynchus nerka* (Salmoniformes: Salmonidae) (voucher HWML 38673); ? *Ptychocheilus oregonensis* (Cypriniformes: Cyprinidae); ? *Cottus asper* (Scorpaeniformes: Cottidae) (see Remarks).

Site of infection: Liver.

Distribution: North America: Canada (British Columbia).

Reference: Ching (1982).

Remarks. Ching (1982) identified metacestodes found in salmonids from British Columbia, Canada, as *P. simoni* on the basis of the number of rostellar hooks (30–36 according to her observations) and their shape (proportion of the handle and blade). *Paradilepis simoni* was described from the intestine of *Haliaeetus carolinensis* in the USA (Rausch 1949) and then redescribed by McLaughlin (1974). In the original description, a total of about 36 hooks was reported (Rausch 1949) but the paratype (squash of the scolex; USNPC 46403) has only 28 hooks in two rows of 14 hooks each (Figs. 5, 6A).

A study of Ching's specimens has revealed that one larva from *Oncorhynchus nerka* (HWML 38673) possesses only 28 hooks (14 larger hooks 103–104 µm long and 14 smaller hooks 70–76 µm – Fig. 6B) whereas another larva from the same fish host (HWML 38672 – Fig. 6C) as well as those from *O. mykiss* (HWML 38674 – Fig. 6D) and *Prosopium williamsoni* (HWML 38676 – Fig. 6E) have 32 hooks arranged in two circles of 16 each. The hooks of the former metacestode

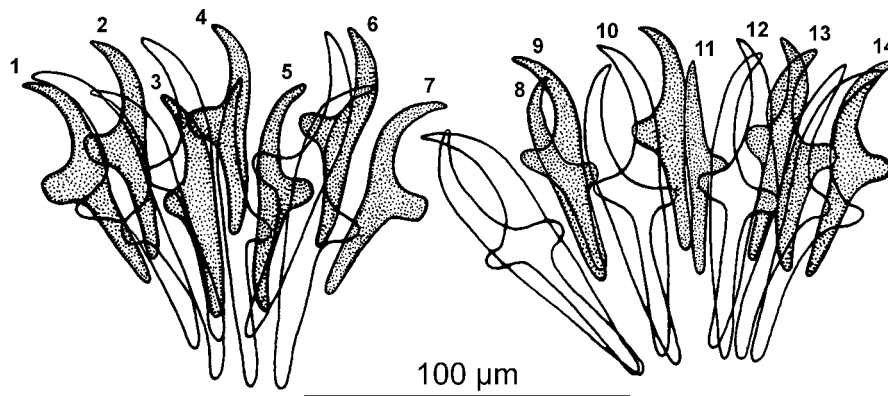


Fig. 5. Rostellar hooks of *Paradilepis simoni* adult (paratype) from the intestine of *Pandion haliaetus*, Wyoming, USA (USNPC 46403). Note presence of 28 hooks (14 + 14).

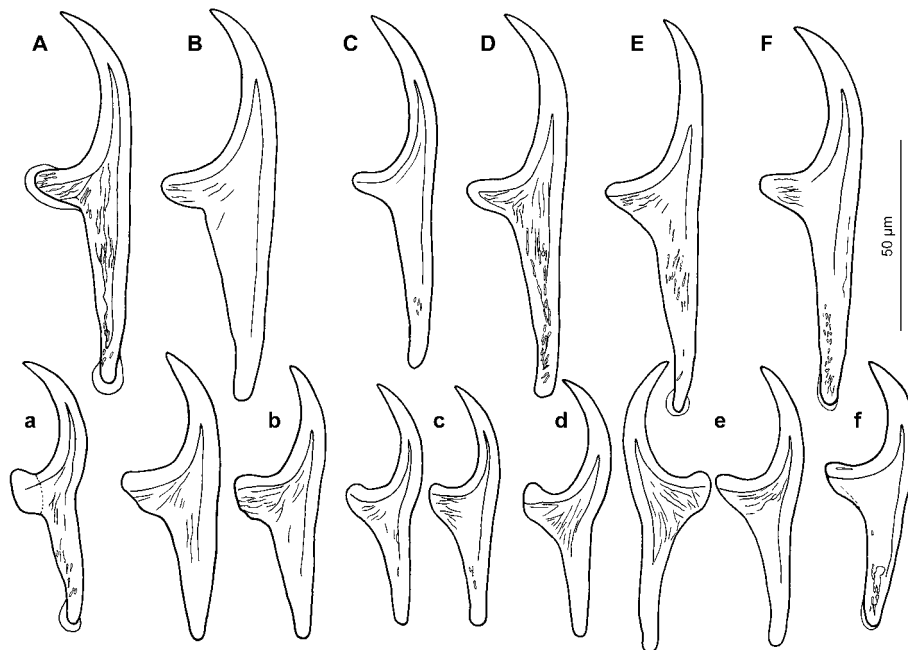


Fig. 6. Large (capital letters) and small (lowercase letters) rostellar hooks of species of *Paradilepis*. **A, B** – *P. simoni*. **A** – adult (paratype) from the intestine of *Pandion haliaetus*, Wyoming, USA (USNPC 46403); **B** – metacystode from the liver of *Oncorhynchus nerka*, British Columbia, Canada (HWML 38673). **C–E** – Metacystodes 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* Hsü, 1935, most probably *P. simoni* (larva from *O. nerka* with 28 hooks – HWML 38673) and *P. rugovaginosus* Freeman, 1954 (metacystodes with 32 hooks – HWML 38672, 38674, 38676).

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

***Paradilepis rugovaginosus* Freeman, 1954** Fig. 5C–E

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. Metacystodes 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 cf. urceus (Wedl, 1855) Joyeux et Baer, 1950
Fig. 4D

Synonym: *Taenia urceus* Wedl, 1855

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

Site of infection: Liver.

Distribution: North America: Mexico* (Guanajuato).

Reference: Scholz and Salgado-Maldonado (2001).

Remarks. Metacestodes from the liver of an atherinid fish in Mexico closely resembled in their hook morphology the adults of *P. urceus*, a parasite of *Plegadis 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
Fig. 7B

Fish hosts: *Atherinella crystallina** (Atheriniformes: Atherinidae); *Poeciliopsis gracilis** (Cyprinodontiformes: Poeciliidae); *Dormitator latifrons**, *Gobiomorus maculatus** (Perciformes: Eleotridae); *Agonostomus monticola** (Perciformes: Mugilidae).

Site of infection: Liver.

Distribution: North America: Mexico* (Guerrero, Jalisco, Nayarit).

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 (Wedl, 1855) Baer et Bona, 1960
Fig. 7C

Synonyms: *Taenia macropeos* Wedl, 1855; *Anomotaenia macropeos* (Wedl, 1855) Fuhrmann, 1908; *Parvitaenia echinata* Metrick, 1967; *Gryporynchus pusillus 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 *Nycticorax nycticorax* 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 (Wedl, 1855) Baer et Bona, 1960
Fig. 7D, E

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

Fish hosts: primarily cyprinid fish (Cypriniformes: Cyprinidae), such as *Abramis brama*, *Alburnoides taeniatatus*, *Alburnus alburnus*, *Aristichthys nobilis*, *Aspius aspius*, *Barbus brachycephalus*, *B. capito*, *Carassius auratus**, *C. carassius**, *Chalcarburnus chalcoides*, *Ctenopharyngodon idella**, *Cyprinus carpio**, *Hemiculter eigenmanni*, *Hypophthalmichthys molitrix*, *Leuciscus cephalus*, *Leucaspis 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 nudiventris*, *A. stellatus*, *Pseudoscaphirhynchus kaufmanni* (Acipenseriformes: Acipenseridae); *Chirostoma humboldtianum**, *C. jordani**, *C. riojai** (Atheriniformes: Atherinidae); *Prochilodus lineatus* (Characiformes: Prochilodontidae); *Alosa caspia* (Clupeiformes: Clupeidae); *Girardinichthys multiradiatus** (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 guatemalensis** (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 (Monte Negro); Asia: Iraq, Japan, Kazakhstan, Mongolia*, Tajikistan, Uzbekistan; North America: Canada, Mexico*; South America: Brazil.

References: Jarecka (1970a), Kozicka (1971), Skvortsova (1979), Bauer et al. (1981), Razmashkin (1984), Studnicka et al. (1984), Ryzhikov et al. (1985), Ali et al. (1987b, 1988), Dubinina (1987), Scholz (1989a), Priemer and Scholz (1989), Razmashkin (1990), Scholz and Ergens (1990), Pojmańska (1991), Takemoto et al. (1994), Mhaisen and Khamees (1995), Kirichenko (1996), Baccarani et al. (1998), Ermolenko and Butorina (1998), Hanzelová and Ryšavý (1999), Rego et al. (1999), Moravec (2001), Scholz and Salgado-Maldonado (2001), Kalbe et al. (2002). As *Cysticercus dilepidis* – Agapova (1960); as *Dilepididae* gen. sp. 1 – Shimazu et al. (2000); as *Dilepis campylancristrota* – Jara and Olech (1964a, b); as *Dilepis unilateralis* – Golikova (1960), Esinenko-Marits (1965), Molnár (1970), Osmanov (1971), Molnár et al. (1974), Skryabina (1974), Izumova (1977), Adamczyk (1979), Grabda-Kazubska et al. (1987), Chernova et al. (1988), GavriloVA and Karimov (1989); as *Ophiovalipora unilateralis* – Kulakovskaya (1969), Kulakovskaya and Koval (1973); as *Valipora unilateralis* – Rautskis (1988).

Remarks. Herons, e.g., *Ardea cinerea* (type host), serve as the definitive hosts of the cestode, the adults of which have

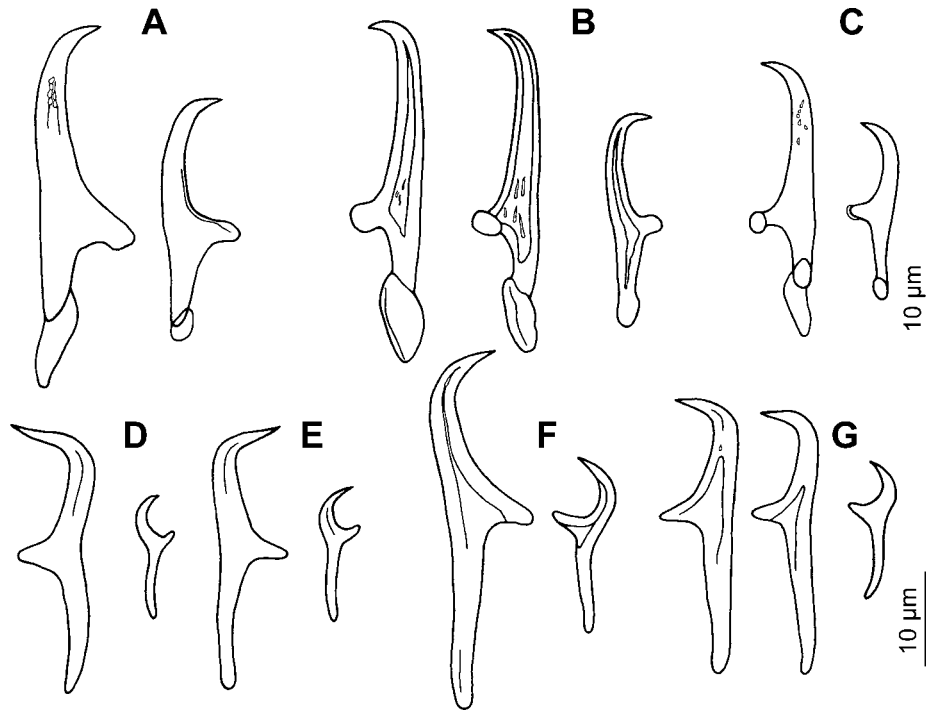


Fig. 7. Rostellar hooks of metacestodes of *Neogryporhynchus* from the intestinal lumen, *Parvitaenia* from the liver and *Valipora* from the gall bladder. **A** – *N. cheilancristrotus* from *Channa argus*, Japan (IPCAS C-39). **B** – *P. cochlearii* from *Gobiomorus maculatus*, Jalisco, Mexico (IPCAS C-254). **C** – *P. macropeos* from *Cichlasoma istlanum*, 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 (left 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 Solyatina-Andakulova (1979).

Valipora minuta (Coil, 1950) Baer et Bona, 1960 Fig. 7F

Synonym: *Ophiovalipora minuta* Coil, 1950

Fish hosts: *Poecilia sphenops** (Cyprinodontiformes: Poeciliidae); *Rhamdia guatemalensis** (Siluriformes: Heptapteridae); *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).

References: Davis and Huffman (1975 – as *Ophiovalipora minuta*), Scholz et al. (1996 – as *Dendrouterina*

papillifera), W. Evans (unpublished data – see Hoffman 1999), Scholz and Salgado-Maldonado (2001).

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

Valipora mutabilis Linton, 1927

Fig. 7B

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

Fish hosts: *Rhamdia guatemalensis* (Siluriformes: Heptapteridae); *Ameiurus melas* (= *Ictalurus melas*) (Siluriformes: Ictaluridae); *Cichlasoma beani*, *C. geddesi*, *Thorichthys 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 nycticorax*) 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.

Species	Number	Large hooks				Small hooks				Source
		Length	Blade	Handle	B/H ratio	Length	Blade	Handle	B/H ratio	
<i>Amirthalingamia macracantha</i>	(4 + 6) + 10	448–480 390–450	272–296 140–280	240–296 224–256	1.00–1.16 1.00–1.18	240–290	157–184	144–160	0.98–1.11	1, PD
<i>Ascodilepis transfuga</i>	10 + 10	57–60	28.5–32	30.5	0.93–1.15	42–46	21	24–25.5	0.81–0.87	2
<i>Cyclustera capito</i>	14 + 14	221–234	112–122	118–125	0.94–0.97	173–182	90–93	99–105	0.85–0.93	3
<i>Cyclustera ibisae</i>	10 + 10	221–240	141–160	74–86	1.73–2.09	173–194	112–128	70–80	1.45–1.82	4
<i>Cyclustera magna</i>	(4 + 6) + 10	179–198 154–163	109–141 93–109	67–96 64–70	1.14–1.96 1.43–1.70	138–147	90–102	61–70	1.33–1.67	PD
<i>Cyclustera cf. ralli</i>	10 + 10	125–141	75–83	59–66	1.20–1.35	111–123	63–70	57–66	1.09–1.24	3
<i>Dendrouterina pilherodiae</i>	10 + 10	48–49	19–20	31–33	0.59–0.63	40–45	14.5–16	26–32	0.45–0.62	5
<i>Glossocercus auritus</i>	10 + 10	242–267	141–165	102–114	1.56–1.89	189–202	93–115	83–96	1.10–1.39	3
<i>Glossocercus caribaensis</i>	10 + 10	189–211	106–126	72–88	1.20–1.73	124–146	66–83	56–75	0.97–1.29	3, 4
<i>Glossocercus cyprinodontis</i>	10 + 10	180–195	122–128	86–93	1.30–1.49	129–141	79–86	62–74	1.08–1.27	3, 6, PD
<i>Neogryporhynchus cheilancristrotus</i>	10 + 10	49–57	31–36	18–23	1.40–1.66	34–40	20–23.5	15–18.6	0.94–1.43	7–9, PD
<i>Paradilepis caballeroi</i>	12 + 12	110–121	55–59	53–62	0.90–1.09	83–88	39–41	43–49	0.80–0.97	3
<i>Paradilepis scolecina</i>	10 + 10	101–115	55–60	50–55	1.12–1.23	74–81	38–41	36–39	0.91–1.13	8, 10, 11
<i>Paradilepis simoni</i> (No. 46403)**	14 + 14	99–102	44–49	58–61	0.72–0.83	72–75	31–34	44–45	0.71–0.78	PD
(No. 38673)	14 + 14	103–104	51–53	62–63	0.82–0.85	70–75	39–40	44–49	0.82–0.89	PD
<i>Paradilepis rugovaginosus</i>	16 + 16	93–108	41–53	53–65	0.65–0.91	67–76	35–41	40–49	0.80–0.98	PD
<i>Paradilepis cf. urceus</i>	10 + 10	125–138	72–83	55–62	1.06–1.33	91–96	47–54	46.5–50	1.00–1.11	3
<i>Parvitaenia cochlearii</i>	10 + 10	49–56.5	26.5–33	23–26.5	1.09–1.36	32–37	16.5–20	17–18.5	0.96–1.36	3
<i>Parvitaenia macropeos</i>	10 + 10	43–46	24.5–27	18.5–22	1.15–1.45	26–30	12–15	15–17	0.71–0.89	3
<i>Valipora campylancristrota</i>	10 + 10	23–30.5	9–14.5	14–18.5	0.60–0.91	10–16.5	3.5–6	8–12	0.34–0.56	3, 7, 8
<i>Valipora minuta</i>	10 + 10	36–40	15.5–19	21–24.5	0.60–0.88	18–21.5	5.5–8.5	12–15.5	0.46–0.59	3
<i>Valipora mutabilis</i>	10 + 10	28–30	11–13	16.5–18	0.60–0.76	13.5–15.5	4–5	9–11.5	0.41–0.56	3

*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 – Pietroock 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 *Cyclustera* sp. of Aloo (2002)

Aloo (2002) reported metacestodes identified as *Amirthalingamia* sp. from the intestine of *Tilapia zillii* and those of the genus *Cyclustera* 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; IPCAS C-292 and C-293) has shown their conspecificity with *A. macracantha* and *C. magna*, respectively (see Survey of species).

Anomotaenia sp.

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

Cyclustera sp.

Heard (1970) found adult *Cyclustera* 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 *Cyclustera ibisae* and that those from clapper rails represented a different genus. It is, therefore, possible that larvae were in fact conspecific with *C. ibisae* or with a species of *Glossocercus* reported from cyprinodontiform fish, namely *G. caribaensis* and *G. cyprinodontis* (see Survey of species).

Cysticercoides menidia Chandler, 1935

Metacestodes from *Menidia menidia* described as *Cysticercoides menidia* by Chandler (1935) belong in fact to *Ascodilepis transfuga* (Krabbe, 1869) – see Scholz (2001).

Cysticercus gen. sp. of Dogiel and Bykhovskii (1938)

Russian authors reported metacestodes ("cysticeri") from the gall bladder of *Atherina boyeri* (Atheriniformes: Atherinidae) and, more rarely, *Caspialosa 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).

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

Scholz et al. (1996) misidentified larvae of *Valipora minuta* (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 langsdorfii* from Kami-dokanbori, Tokyo, Japan are considered to be conspecific with those of *Valipora campylancristrota* because of their morphology, in particular the shape and size of the rostellar hooks (about 28 µm and 13 µm, respec-

tively, 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 langsdorfii* in the Imperial Palace in Tokyo are apparently conspecific with *Neogryporhynchus cheilancristrotus* 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* Hsü, 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* (Perciformes: Centrarchidae) from Ontario, Canada (Cone and Anderson 1977, Dechtiar and Christie 1988, Dechtiar et al. 1989);

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

(iv) intestinal wall of *Notemigonus crysoleucas* (Cypriniformes: 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);

(vi) *Catostomum commersoni* (Cypriniformes: Catostomidae) and *Fundulus diaphanus* (Atheriniformes: Cyprinodontidae), Canada (Wiles 1975, M. Wiles – unpublished data in 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*, *Hemiculter leucisculus*, *Mylopharyngodon piceus*, *Parabramis liaohoensis* (= *P. pekinensis*), and *Rhinogobius giurinus* from the Hupei Province, China. These larvae may be conspecific with *Neogryporhynchus cheilancristrotus* but voucher specimens were not available to confirm this assumption.

Chen (1984) listed larvae of *Gryporhynchus* (possibly *Neogryporhynchus cheilancristrotus*) from *Ophiocephalus argus* (= *Channa argus*), *Misgurnus fossilis* and *Squaliobarbus curriculus*.

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 neogaeus* from Ontario, Canada. Comparative material of neither authors was available.

Scholz and Salgado-Maldonado (2001) reported an unidentified 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 *Phalacrocorax 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*) (Perciformes: 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

Petrushevskii et al. (1948) found metacestodes designated as *Cysticercus paradilepidis* in *Leuciscus idus* and *Tinca tinca* from the Ob and Irtysh rivers in Russia. The larvae most probably belonged to *Paradilepis scolecina*, 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) Joyeux et Baer, 1935, thus being probably conspecific with those reported as *Anomotaenia* sp. (cysticercus) from *O. niloticus* from Nigeria (Aderounmu 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 provided any information about their morphology, Batra (1984) stated they resembled metacestodes reported as “dilepidid larvae” (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*, *Dendro-uterina pilherodiae*, *Glossocercus 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 scolecina* and *Valipora campylancristrota*), but also *Glossocercus 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 *Glossocercus* 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*, *Glossocercus 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 para-

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).

Acipenseriformes: Acipenseridae (3 fish species infected with 3 gryporhynchid species)

Acipenser nudiventris – *Paradilepis scolecina*, *Valipora campylancristrota*

Acipenser stellatus – *Valipora campylancristrota*

Pseudoscaphirhynchus kaufmanni – *Neogryporhynchus cheilancristrotus*, *Paradilepis scolecina*, *Valipora campylancristrota*

Atheriniformes: Atherinidae (5/5)

Atherinella crystallina – *Parvitaenia cochlearii*

Chirostoma humboldtianum – *Valipora campylancristrota*

Chirostoma jordani – *Paradilepis caballeroi*, *Paradilepis cf. urceus*, *Valipora campylancristrota*

Chirostoma riojai – *Valipora campylancristrota*

Menidia menidia – *Ascodilepis transfuga*

Characiformes: Characidae (1/1)

Astyanax fasciatus – *Glossocercus auritus*

Characiformes: Prochilodontidae (1/1)

Prochilodus lineatus – *Valipora campylancristrota*

Clupeiformes: Clupeidae (2/2)

Alosa caspia – *Valipora campylancristrota*

Alosa kessleri – *Neogryporhynchus cheilancristrotus*

Cypriniformes: Cobitidae (3/1)

Cobitis taenia – *Neogryporhynchus cheilancristrotus*

Misgurnus anguillicaudatus – *Neogryporhynchus cheilancristrotus*

Misgurnus fossilis – *Neogryporhynchus cheilancristrotus*

Cypriniformes: Cyprinidae (45/5)

Abramis ballerus – *Neogryporhynchus cheilancristrotus*

Abramis bjoerkna – *Neogryporhynchus cheilancristrotus*, *Paradilepis scolecina*

Abramis brama – *Neogryporhynchus cheilancristrotus*, *Paradilepis scolecina*, *Valipora campylancristrota*

Abramis sapa – *Neogryporhynchus cheilancristrotus*

Alburnoides taeniatus – *Neogryporhynchus cheilancristrotus*, *Valipora campylancristrota*

Alburnus albidus – *Paradilepis scolecina*

Alburnus alburnus – *Neogryporhynchus cheilancristrotus*, *Paradilepis scolecina*, *Valipora campylancristrota*

Aristichthys nobilis – *Paradilepis scolecina*, *Valipora campylancristrota*

Aspiolucius esocinus – *Neogryporhynchus cheilancristrotus*

Aspius aspius – *Neogryporhynchus cheilancristrotus*, *Paradilepis scolecina*, *Valipora campylancristrota*

Barbus brachycephalus – *Neogryporhynchus cheilancristrotus*, *Paradilepis scolecina*, *Valipora campylancristrota*

Barbus capito – *Neogryporhynchus cheilancristrotus*, *Paradilepis scolecina*, *Valipora campylancristrota*

Capoeta capoeta – *Neogryporhynchus cheilancristrotus*, *Paradilepis scolecina*

Capoetobrama kuschakewitschi – *Neogryporhynchus cheilancristrotus*

Carassius auratus – *Neogryporhynchus cheilancristrotus*, *Paradilepis scolecina*, *Valipora campylancristrota*

Carassius carassius – *Neogryporhynchus cheilancristrotus*, *Paradilepis scolecina*, *Valipora campylancristrota*

Chalcalburnus chalcoides – *Neogryporhynchus cheilancristrotus*, *Paradilepis scolecina*, *Valipora campylancristrota*

Chondrostoma cyri – *Paradilepis scolecina*

Chondrostoma nasus – *Paradilepis scolecina*

Ctenopharyngodon idella – *Neogryporhynchus cheilancristrotus*, *Valipora campylancristrota*

Culter alburnus – *Paradilepis scolecina*

Cyprinus carpio – *Cyclustera cf. ralli*, *Neogryporhynchus cheilancristrotus*, *Paradilepis scolecina*, *Valipora campylancristrota*

Gnathopogon caerulescens – *Neogryporhynchus cheilancristrotus*

Gnathopogon elongatus – *Paradilepis scolecina*

Hemiculter eigenmanni – *Valipora campylancristrota*

Hemiculter leucisculus – *Paradilepis scolecina*

Hypophthalmichthys molitrix – *Valipora campylancristrota*

Leuciscus cephalus – *Neogryporhynchus cheilancristrotus*, *Valipora campylancristrota*

Leuciscus idus – *Neogryporhynchus cheilancristrotus*, *Paradilepis scolecina*

Leuciscus lehmanni – *Neogryporhynchus cheilancristrotus*

Leucaspis delineatus – *Neogryporhynchus cheilancristrotus*, *Valipora campylancristrota*

Notropis sallei – *Cyclustera cf. ralli*

Oreoleuciscus humilis – *Paradilepis scolecina*

Oreoleuciscus potanini – *Paradilepis scolecina*

Pelecus cultratus – *Neogryporhynchus cheilancristrotus*, *Paradilepis scolecina*, *Valipora campylancristrota*

Ptychocheilus oregonensis – *Paradilepis simoni* (?)

Rhodeus sericeus – *Neogryporhynchus cheilancristrotus*, *Paradilepis scolecina*, *Valipora campylancristrota*

Rutilus rutilus – *Neogryporhynchus cheilancristrotus*, *Paradilepis scolecina*, *Valipora campylancristrota*

Scardinius erythrophthalmus – *Neogryporhynchus cheilancristrotus*, *Paradilepis scolecina*, *Valipora campylancristrota*

Schizopygopsis stoliczkae – *Paradilepis scolecina*

Schizothorax intermedius – *Neogryporhynchus cheilancristrotus*, *Valipora campylancristrota*

Tinca tinca – *Neogryporhynchus cheilancristrotus*, *Paradilepis scolecina*, *Valipora campylancristrota*

Tribolodon hakonensis – *Paradilepis scolecina*

Varicorhinus sp. – *Paradilepis scolecina*

Zacco platypus – *Neogryporhynchus cheilancristrotus*

Cyprinodontiformes: Cyprinodontidae (2/2)

Cyprinodon variegatus variegatus – *Glossocercus cyprinodontis*

Floridichthys polyommus – *Cyclustera capito*

Cyprinodontiformes: Goodeidae (3/2)

Allophorus robustus – *Cyclustera cf. ralli*

Girardinichthys multiradiatus – *Cyclustera cf. ralli*, *Valipora campylancristrota*

Xenotoca variata – *Cyclustera cf. ralli*

Cyprinodontiformes: Fundulidae (4/2)

Fundulus grandissimus – *Glossocercus caribaensis*

Fundulus heteroclitus – *Cyclustera ibisae*, *Glossocercus caribaensis*

Fundulus majalis – *Cyclustera ibisae*, *Glossocercus caribaensis*

Fundulus persimilis – *Glossocercus caribaensis*

Cyprinodontiformes: Poeciliidae (6/3)
Gambusia affinis – *Valipora minuta*
Poecilia catemaconis – *Glossocercus auritus*
Poecilia mexicana – *Glossocercus auritus*
Poecilia sphenops – *Glossocercus auritus*, *Valipora minuta*
Poecilia sp. – *Glossocercus auritus*
Poeciliopsis gracilis – *Glossocercus auritus*, *Parvitaenia cochlearii*

Esociformes: Esocidae (1/3)
Esox lucius – *Neogryporhynchus cheilancristrotus*,
Paradilepis scolecina, *Valipora campylancristrota*

Gasterosteiformes: Gasterosteidae (3/2)
Gasterosteus aculeatus – *Paradilepis scolecina*, *Valipora campylancristrota*
Pungitius platygaster – *Paradilepis scolecina*
Pungitius pungitius – *Paradilepis scolecina*

Perciformes: Blenniidae (1/1)
Salaria fluviatilis – *Valipora campylancristrota*

Perciformes: Centrarchidae (2/1)
Micropterus punctatus – *Valipora minuta*
Micropterus salmoides – *Valipora minuta*

Perciformes: Channidae (1/1)
Channa argus – *Neogryporhynchus cheilancristrotus*

Perciformes: Cichlidae (8/7)
Cichlasoma beani – *Valipora mutabilis*
Cichlasoma callolepis – *Paradilepis caballeroi*
Cichlasoma geddesi – *Valipora mutabilis*
Cichlasoma istlanum – *Parvitaenia macropeos*
Cichlasoma urophthalmus – *Glossocercus caribaensis*
Oreochromis niloticus – *Amirthalingamia macracantha*
Thorichthys meeki – *Valipora mutabilis*
Tilapia zillii – *Amirthalingamia macracantha*, *Cyclustera magna*

Perciformes: Eleotridae (2/1)
Dormitator latifrons – *Parvitaenia cochlearii*
Gobiomorus maculatus – *Parvitaenia cochlearii*

Perciformes: Gobiidae (1/1)
Neogobius melanostomus – *Paradilepis scolecina*

Perciformes: Mugilidae (2/2)
Agonostomus monticola – *Parvitaenia cochlearii*
Liza abu – *Neogryporhynchus cheilancristrotus*

Perciformes: Percidae (5/3)
Gymnocephalus cernuus – *Neogryporhynchus cheilancristrotus*, *Paradilepis scolecina*
Perca fluviatilis – *Neogryporhynchus cheilancristrotus*, *Paradilepis scolecina*, *Valipora campylancristrota*
Perca schrenki – *Neogryporhynchus cheilancristrotus*
Sander lucioperca – *Valipora campylancristrota*
Zingel streber – *Neogryporhynchus cheilancristrotus*

Salmoniformes: Salmonidae (3/2)
Oncorhynchus mykiss – *Paradilepis rugovaginosus*
Oncorhynchus nerka – *Paradilepis rugovaginosus*,
Paradilepis simoni
Prosopium williamsoni – *Paradilepis rugovaginosus*

Scorpaeniformes: Cottidae (1/1)
Cottus asper – *Paradilepis simoni* (?)

Siluriformes: Bagridae (1/1)
Mystus pelusius – *Valipora campylancristrota*

Siluriformes: Heptapteridae (1/4)
Rhamdia guatemalensis – *Dendroterina pilherodiae*,
Valipora campylancristrota, *Valipora minuta*, *Valipora mutabilis*

Siluriformes: Ictaluridae (1/1)
Ictalurus melas – *Valipora mutabilis*

Siluriformes: Siluridae (2/3)
Silurus glanis – *Neogryporhynchus cheilancristrotus*,
Paradilepis scolecina, *Valipora campylancristrota*
Silurus asotus – *Neogryporhynchus cheilancristrotus*