THE LIFE-CYCLE AND BIOLOGY OF *HEMIURUS COMMUNIS* ODHNER, 1905 (DIGENEA, HEMIURIDAE)

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Summary :
Previously undescribed cystophorous cercariae which develop in sporocyst germinal sacs in the opisthobranch snail *Retusa truncatula* (Bruguière) are shown to be the cercariae of *Hemiurus communis* Odhner, 1905 (Hemiuridae), a common stomach parasite of non-clupeid fishes off the north-western coasts of Europe. The free-swimming cercaria is ingested by calanoid copepods. The cercarial body is injected into the copepod haemocoel via the delivery tube. The cystophorous cercaria and life-cycle of *H. communis* are compared with those of other hemiurids from the North-East Atlantic, and the known biology of this species is reviewed.

KEY WORDS : Digenea. Trematoda. Hemiuridae. cercaria. life-cycle. *Hemiurus*. *Retusa*. copepod. fish.

Résumé : CYCLE ET BIOLOGIE D'*HEMIURIS COMMUNIS* ODHNER, 1905 (DIGENEA, HEMIURIDAE)
Il est démontré que des cercaires cystophores non encore décrites qui se développent dans les sacs germinaux du Mollusque opistobranche Retusa truncaluta *(Bruguière) sont celles de* Hemiurus communis *Odhner, 1905 (Hemiuridae), parasite stomacal de Poissons des côtes nord-occidentales d'Europe. La cercaire nageante est ingérée par des Copépodes calanoïdes. Le corps cercarien est injecté dans l'hémocoele du Copépode par le tube inoculateur. La cercaire cystophore et le cycle biologique de* H. communis *sont comparés avec ceux des autres Hémiurides de l'Atlantique nord-oriental et la biologie des espèces connues est passée en revue.*

MOTS CLES : *Digenea. Trématode. Hemiuride. cercaire. cycle de vie.* Hemiurus. Retusa. *poisson. copépode.*

INTRODUCTION

Hemiurus communis Odhner, 1905 (Digenea, Hemiuridae) is a common stomach parasite of non-clupeid fishes in the boreal region of the North-East Atlantic. Its molluscan host has hitherto been unknown. Since the larval stages of the hemiurids *Hemiurus luehei* Odhner, 1905, *Lecithocladium excisum* (Rudolphi, 1819) Lühe, 1901 and *Brachyphallus crenatus* (Rudolphi, 1802) Odhner, 1905 were found in bullomorph opisthobranch gastropods (*Philine denticulata*, *P. aperta* and *Retusa obtusa*, respectively) (Køie 1990c, 1991, 1992), it was expected that the larval stages of *H. communis* would also be found in this group of opisthobranchs. In this paper it is shown that a previously undescribed cystophorous cercaria found in *Retusa truncatula* from the Øresund and the Isefjord, Zealand, Denmark, is the cercaria of *H. communis*.

The taxonomy, morphology and distribution of the species of the North-East Atlantic Hemiuridae, including *H. communis*, were reviewed by Gibson & Bray (1986). The taxonomy of the hemiuroid digeneans was reviewed by Gibson & Bray (1979), who restricted the Hemiuridae to ecsomate forms : this classification is followed in the present paper.

MATERIALS AND METHODS

Specimens of *Retusa truncatula* (Bruguière) (Gastropoda, Opisthobranchia, Bullomorpha, Retusidae) were dredged in the Øresund (January and February 1992) and the Isefjord (March, May, June and August 1992, and May 1993) at a depth of 6-15 m. In the laboratory the snails were observed for the release of cercariae. Within two days of dredging all the snails were dissected to reveal any immature infections. Free-swimming cercariae from crushed snails and laboratory-reared *Acartia tonsa* Dana (copepodids and adults) were placed together in 250 ml blue-cap bottles, which were immediately attached to a rotating wheel. The exposed copepods were kept at 15°C and treated as described by Køie (1991). Specimens of the three-spined stickleback, *Gasterosteus aculeatus* L., previously kept in aquaria for one year and fed on frozen food only, were used as experimental final hosts and controls. Metacercariae and adult specimens were fixed in Berland's fluid (glacial acetic acid : 40% formaldehyde, 19:1), cleared in lactic acid and mounted in glycerine-jelly.

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	H. communis	*H. luebei*	*B. crenatus*	*L. excisum*
Cercarial body immediately prior to withdrawal into caudal cyst	90 × 40	100 × 40	100 × 40	85 × 30
Caudal cyst (with withdrawn cercarial body)	85 × 45	85 × 55	80 × 60	55 × 40
Excretory appendage, length	180	190	170	110
Distance: excretory appendage to cyst aperture	45	55	25	20
Everted delivery tube, length	280	295	290	140
Extension(s) on delivery tube	1 small, hemispherical	2 small, hemispherical, tandem, or partly overlapping	1 large, triangular	1 very small, pointed
Reference	Present study	Køie (1990c)	Køie (1992)	Køie (1991)

Table I. – Cercariae of *Hemiurus communis, H. luebei, Brachyphallus crenatus* and *Lecithocladium excisum*. Measurements in micrometres of slightly flattened live specimens.

Species	Subfam.	Molluscan host	Reference
Lecithocladium excisum	Elytrophallinae	*Philine aperta*	Køie (1991)
Hemiurus luebei	Hemiurinae	*P. denticulata*	Køie (1990c)
H. communis	"	*Retusa truncatula*	present study
Brachyphallus crenatus	Lecithochiriinae	*R. obtusa*	Køie (1992)
Lecithochirium rufoviride	"	*Gibbula cineraria*	Køie (1990b)
L. furcolabiatum	"	*G. umbilicalis*	Matthews (1981)
L. fusiforme	"	*G. varia*	Chabaud & Campana-Rouget (1959)

Table II. – Known hemiurid cercariae from the North-East Atlantic and their molluscan hosts.

RESULTS

Natural infection of the molluscan host

A total of 23 (10%) of the 234 specimens of *Retusa truncatula* examined were infected. Infected snails were found in all samples, apart from August. Due to the small number of snails examined any seasonal variation in prevalence can not be determined. During January and February only germinal sacs containing germinal balls were found in the snails. In March a few snails contained apparently fully-developed infective cercariae, and in May and June all, apart from one, of the 10 infected snails harboured infective cercariae. In January the snail shells measured 1.5-2.0 mm in length, in March they were 2.5-4.0 mm and in May and June 3.0-4.5 mm. In August only small (< 1.0 mm long) and empty shells of the parent generation were found.

Cercariae

The cercariae develop in sporocyst-like germinal sacs of up to 1.5 mm in length. No gut caecum or pharynx were seen. The cercariae leave the germinal sac through the terminal birth pore. The exact position of the germinal sacs in the snails was not determined.

Various developmental stages of the cercariae are shown in Fig. 1. Fig. 3 shows the cercaria of *H. communis* beside the three other hemiurid cercariae found in opisthobranch snails in Danish waters (see table II). The measurements of fully-developed cercariae of *H. communis* are presented in table I, where they are compared with those of the three related cercariae from opisthobranchs.

The presumptive cercarial body is spherical in the earliest stages (Fig. 1 A-C). The tail is provided with two projections, the primordium of the delivery tube and the motile excretory appendage (Fig. 1 B-D). In the fully-developed intra-sporocyst cercaria (Figs. 1 E, 3 A,a) the delivery tube is withdrawn into the caudal cyst. Here it is coiled and attached to the internal surface of the pointed end of the almost pyriform caudal cyst. Cercariae at this developmental stage squeeze through the birth canal of the germinal sac. Shortly after emergence from the snail, the cercarial body retracts, via the cyst aperture, into the caudal cyst (Fig. 1 F). The oral and ventral suckers are approximately identical in size. No other details were seen in the cercarial body. In the free-swimming infective cercaria the cercarial body occurs coiled within the caudal cyst (Figs. 1 G, 3 A,b). The motile excretory appendage is attached externally on the caudal cyst,

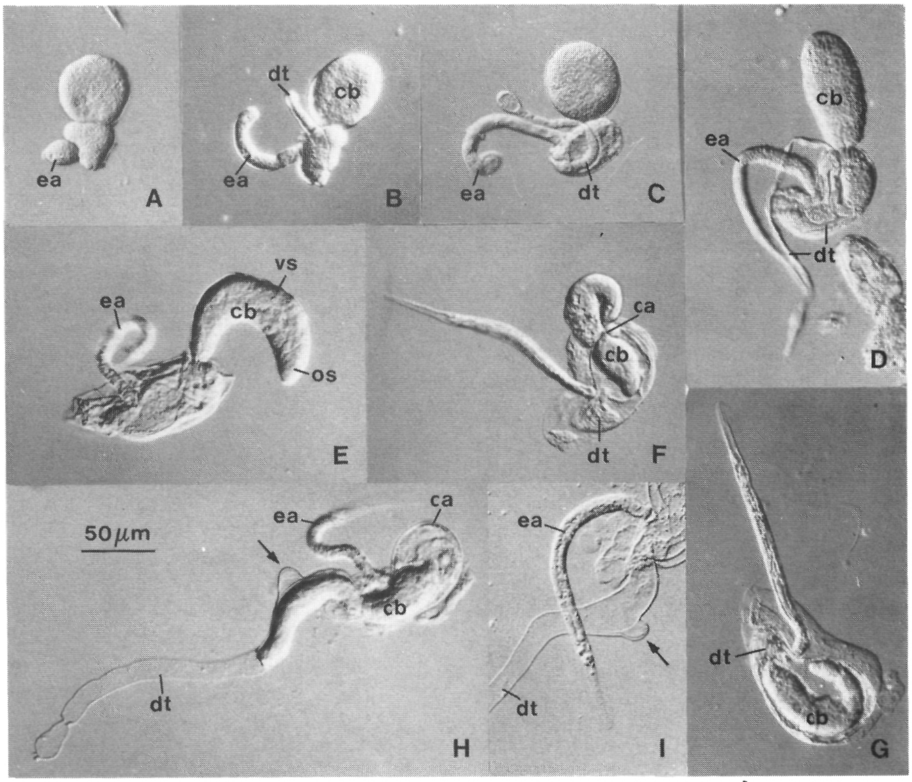

Fig. 1. – Different developmental stages of the cercaria of *Hemiurus communis*. Interference contrast micrographs, all to same scale. A-D. Undeveloped cercariae from germinal sacs. E. Recently released cercaria. The delivery tube is withdrawn into the caudal cyst. F. Cercaria shortly after emergence from the snail host. The cercarial body is partly withdrawn into the caudal cyst. G. Infective, free-swimming cercaria. Both the delivery tube and the cercarial body are withdrawn into the caudal cyst. H. *In vitro* delivery tube eversal. Half of the cercarial body has entered the everted delivery tube. Arrow shows extension on delivery tube. I. Base of delivery tube after passage of the cercarial body showing the extension (arrow). Abbreviation: ca, cyst aperture, the aperture through which the cercarial body has withdrawn; cb, cercarial body; dt, delivery tube; ea, excretory (motile) appendage; os, oral sucker; vs, ventral sucker.

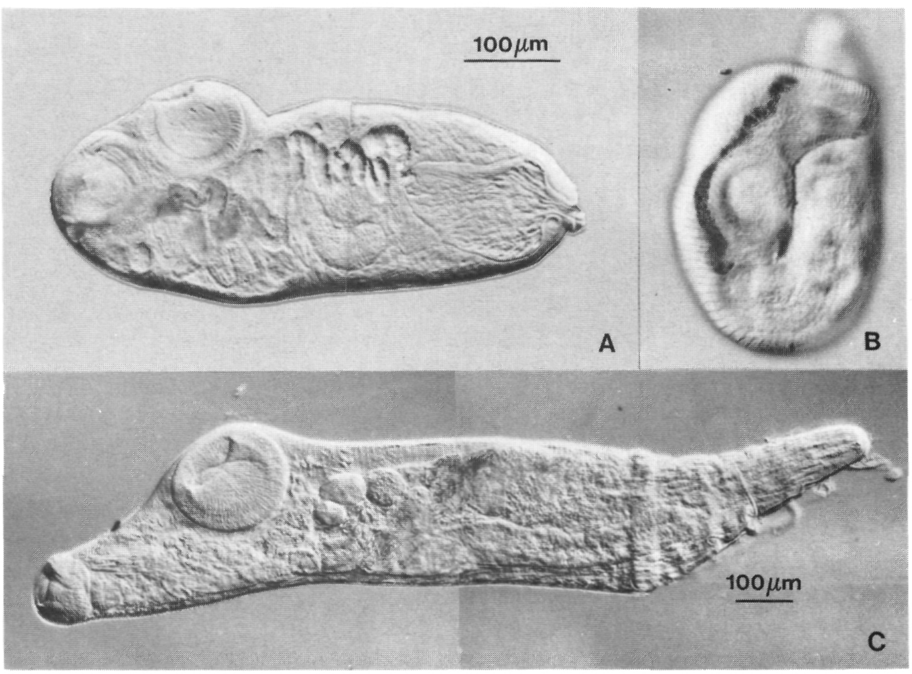

Fig. 2. – A, B. Metacercariae of *Hemiurus communis*, max. of 14 days old, from experimentally infected *Acartia tonsa*. Interference contrast micrographs of live specimens, to same scale. C. Adult specimen of *H. communis*, 4 weeks old, from experimentally infected sticklebacks. Interference contrast micrograph of fixed specimen.

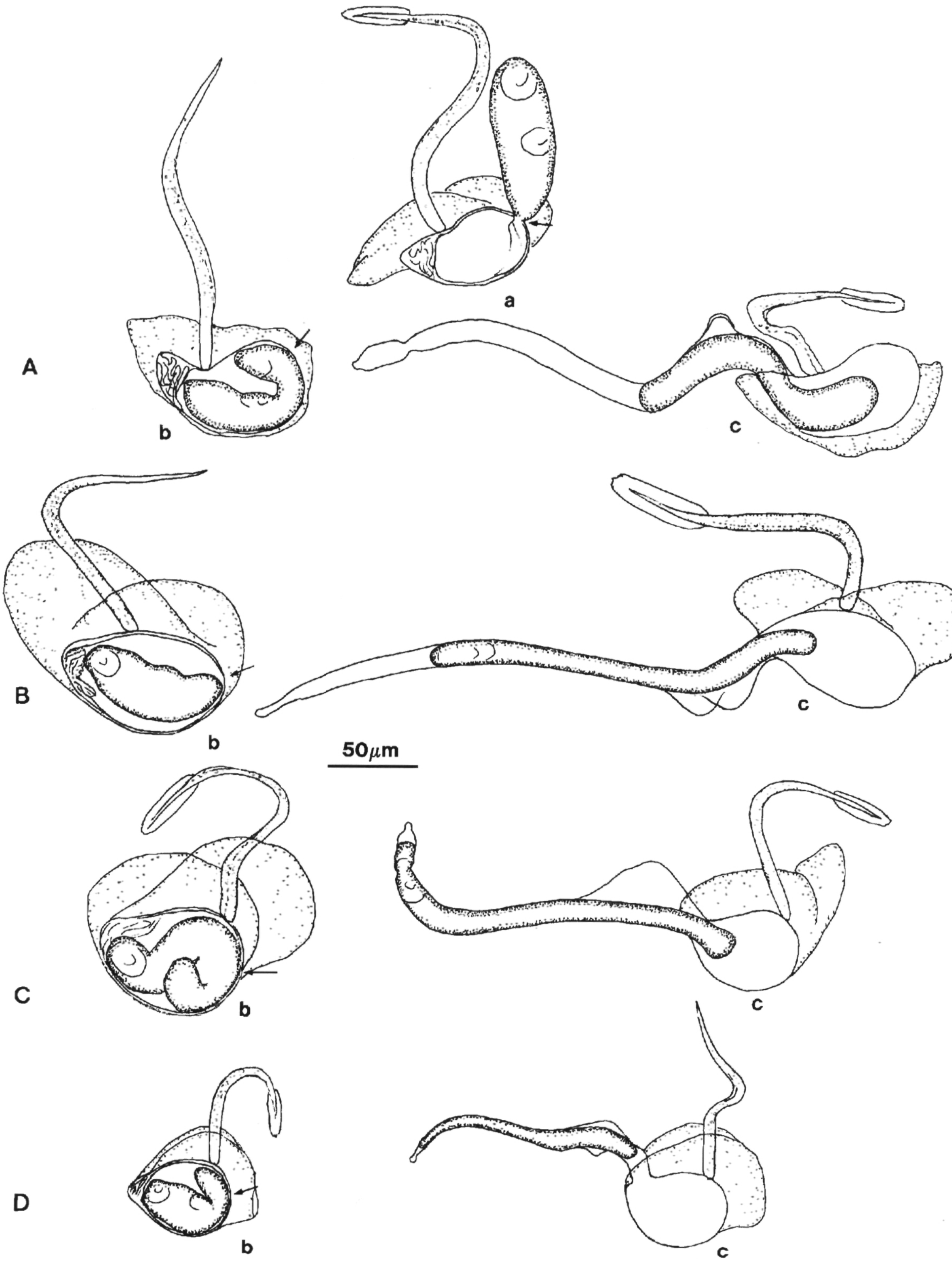

Fig. 3. – Cercariae of four hemiurids which develop in *Retusa* spp. (A, C) and *Philine* spp. (B, D). A. *Hemiurus communis*. B. *Hemiurus luehei*. C. *Brachyphallus crenatus*. D. *Lecithocladium excisum*. a, cercaria immediately after emergence from the snail host. b, free-swimming infective cercaria. c, cercaria with cercarial body in everted delivery tube. Arrows indicate position of cyst aperture.

which is provided with membranous folds or outgrowths. The excretory appendage is flattened, has a median longitudinal furrow on each side and possesses a finely annulated surface. Apart from the apical oar-shaped fin-fold, the appendage is rich in small, highly refractile droplets.

Coverslip pressure induced delivery tube eversion and the extrusion of the cercarial body through the thin membraneous tube (Figs. 1 H, I, 3 A,c). The forcibly everted delivery tube has an apical endpiece and one small hemispherical extension, which appears split apically, close to the tube base. The cercarial body becomes extremely elongate during the expulsion, which usually occurs simultaneously with the eversion of the delivery tube. Shortly after the extrusion, the cercarial body attains its normal shape. Less than 100 infective cercariae, i.e. free-swimming cercariae with a withdrawn cercarial body, were available after dissection of the sporocysts released from each crushed snail.

EXPERIMENTAL AND NATURAL INFECTION OF THE CRUSTACEAN HOST

Acartia tonsa readily became infected when exposed to free-swimming cercariae. No attempts were made to infect other copepod species. Natural infections of metacercariae of *H. communis* have been found in *Acartia* sp., *Sagitta* sp. and *Pleurobrachia pileus* from western Kattegat, the Øresund and the Isefjord, Zealand (Køie, 1983).

METACERCARIAE AND ADULTS FROM EXPERIMENTAL INFECTIONS

Due to the limited number of infective cercariae available, only a few metacercariae from experimentally infected *Acartia tonsa* were studied. Live two-week-old metacercariae (Fig. 2 A, B) were 600-800 µm long, the pharynx was 40 µm in diameter and the oral and ventral suckers were about 60 µm and 100 µm in diameter, respectively. Tegumental annular plications cover most of the surface.

Two-week-old metacercariae were infective when they, via infected copepods, were fed to sticklebacks. Small trematodes obtained from the stomach of experimentally infected sticklebacks a few days post-infection were identical with the infective metacercaria of *H. communis*. Fixed four-week-old adults of *H. communis* from sticklebacks (Fig. 2 C, D) measured 1.4 - 1.5 mm in length (1.2 mm with the ecsoma withdrawn). The pharynx was 60 µm in diameter and the oral and ventral suckers were 180-200 µm and 120-130 µm in diameter, respectively. Several hundred eggs occurred in the uterus and a few were found in the hermaphroditic duct. The stickleback controls were not infected with *H.communis*.

DISCUSSION

In Danish waters the snail host of *H. communis*, *Retusa truncatula*, has been recorded from the Isefjord, the Skagerrak, the western Kattegat and the western part of the Limfjord, the Little and Great Belts and also from the Øresund, where it is rare (reviewed by Rasmussen, 1944). It is present throughout the Isefjord, and often very numerous, particularly in the deeper muddy-sandy areas. It is also often taken from stony ground with algae (depth 8-10 m) and is abundant in the quite shallow sand and mud flats (Rasmussen, 1973). It occurs from the intertidal zone down to 50 m or more all around the British Isles, where it feeds upon foraminiferans and small molluscs (Thompson, 1988). Elsewhere, it has been reported from the western Baltic Sea, Norway (up even to Finnmark), Helgoland, the Dutch, Belgian, French and Portuguese coasts, the Canary Islands and from the Mediterranean Sea as far east as the Aegean and as deep as 200 m (Rasmussen, 1944; Thompson, 1988).

In the Isefjord the breeding of *R. truncatula* occurs from May (max. spawning) until July (Rasmussen, 1973). Maximum size is attained by May, and in August neither living snails nor egg masses were found (Rasmussen, 1944). In October the new generation had a shell length of 1-2 mm. The seasonal size dispersion indicates that *R. truncatula* in the Isefjord has an annual life history (Rasmussen, 1973).

These reports conform with my observations. It is not known at what size the snails of the new generation becomes infected with *H. communis*, but it is obvious that no cercariae are released after the time of the death of the spawning generation of snails and the appearance of infected specimens of the new generation, i.e. probably between late summer and early spring. The parasite survives this period as metacercariae in pelagic invertebrates and/or adults in fishes.

The distribution of *R. truncatula* does not exactly coincide with that of *H. communis* in fishes. Most records of *H. communis* are from the continental shelf between Trondheim in Norway and Brittany in France. It is common around the British Isles and extends eastwards into the Baltic. The distribution of *H. communis* is thus mainly boreal. Reported records from the Black Sea are very dubious (Gibson & Bray, 1986), and the lack of records from the Mediterranean Sea is noteworthy.

Hemiurus communis has been found in cod *Gadus morhua* from throughout Danish waters, except for the Baltic off Bornholm (Køie, 1984). It is less common in dab *Limanda limanda* and eel *Anguilla anguilla* (see Køie 1973, 1988). In the Danish waters *H. communis* and *Brachyphallus crenatus* usually occur sympatrically and often in the same fish host specimen (see Køie 1984, 1988). In the Isefjord the two species often occur concurrently in fishes such as stickleback, flounder and turbot (unpubl. obs.); but, while *H. communis* mostly occurs in shallow seas, *B. crenatus* extends into deeper water and further north (see Gibson & Bray, 1986; Køie, 1992). *H. communis* was found in a few specimens of saithe, *Pollachius virens*, caught near Tórshavn, the Faroes, but did not occur in local Faroese fishes (Køie, unpubl. obs.), indicating that the saithe must have acquired the parasite in another area, probably the coastal regions of Scotland or Norway.

Small fish species, such as stickleback and young specimens of the other above-mentioned species, acquire the parasite by ingesting infected copepods (and/or ctenophores or chaetognaths). Metacercariae probably occur in copepods between late March and late autumn, judging from the period of cercarial release (March to July) and the lifespan of a copepod (if copepods are ingested by ctenophores or chaetognaths, then the period of infection via pelagic invertebrates may be extended). Larger fishes as the above-mentioned species are believed usually to acquire the parasite by ingesting smaller infected fishes (Køie, 1984; Gibson & Bray, 1986). The findings of small parasite specimens in fishes might serve as an indicator of the seasonal occurrence of the parasite in the planktonic intermediate hosts. Apart from a possible accumulation of parasites in large piscivorous fishes in late autumn and winter, no apparent seasonal occurrence might be expected to occur in Danish and neighbouring waters. No obvious seasonal variation was found in the Øresund throughout a two-year study period (Køie, 1984). An accumulation similar to that found by Meskal (1967) in the largest specimens of cod at Bergen was not obvious in the Danish material.

Gibson & Bray (1986) found an increased prevalence in autumn of *H. communis* in flounder *Platichthys flesus* from an estuary on the east coast of Scotland. Möller (1975) found a slightly increased prevalence in late summer and autumn in cod from the Kieler Förde, the Baltic. Raymont (1952) found that the heaviest infections of *H. communis* (probably including some specimens of *B. crenatus*) in saithe in an enclosed loch in Argyll, Scotland, occurred during June-July, whereas from August to February very few parasites were encountered. Meskal (1967) observed that most young worms were found in November and that the maximum shedding of aged worms occurred in July. He suggested that the average lifespan of *H. communis* is eight months.

The cercaria of *Hemiurus communis* is morphologically very similar to the cercariae of *H. luehei*, *Brachyphallus crenatus* and *Lecithocladium excisum* (see Køie 1990c, 1992, 1991). Apart from their occurrence in different snail hosts, these cercariae are most easily separated by the distance between the excretory appendage and the cyst aperture and by the shape of the extension on the everted delivery tube (table I). These cercariae differ from other cystophorous cercariae by their motile, flattened excretory appendage with an apical oar-shaped structure and the small more or less pyriform caudal cyst provided with membranous folds.

The life-cycle of *H. communis* was discussed, *inter alia*, by Lebour (1923, 1935) and Dollfus (1923). Dollfus (1923) suggested that a cystophorous cercaria, *Cercaria calliostomae* Dollfus, 1923, found in the marine snail *Calliostoma ziziphinum* at Roscoff, France, might be the larval stage of a species of *Hemiurus*. The identity of this cercaria, which was redescribed by Matthews (1982), is still unknown. Metacercariae of *H. communis* (or those believed to be *H. communis*) were recorded in *Acartia clausi* by Lebour (1923, 1935) from off Plymouth and by Candeias (1957) from off the north coast of Portugal. Meek (1928) recorded the metacercaria from the body cavity of *Sagitta setosa*, and Yip (1988) found it in the stomach of *Pleurobrachia pileus*. Noble (1972) discussed the possibility of using parasites of marine plankton as biological indicators. He found that *Sagitta elegans* is host to the metacercaria of *Hemiurus levinseni*, while *S. setosa* harboured the metacercaria of *H. communis*.

The adult *H. communis* was redescribed by Dollfus (1960) and Gibson & Bray (1986). Gibson & Bray (1986) observed that well-fixed specimens could usually be split into two morphological groups separated by size, tegumental plication, the shape of the vitelline masses and the number of invaginations of the ecsoma. The present specimens from the experimental infected sticklebacks and from small natural infected fishes from the Isefjord belong to group B, being small, distinctly plicated, with lobed vitelline masses and a double invagination of the ecsoma. However, the latter authors suggest it most likely that form "B" is merely a younger condition of form "A". Kryvi (1972, 1973) studied the tegument and the muscles of the ventral sucker of *H. communis* using transmission electron microscopy, and Matthews & Matthews (1988) have compared the thick somal tegument with the ecsomal tegument of *H. communis* using ultrastructural, histochemical and autoradiographic techniques.

Apart from the cercaria of *L. excisum* two other cystophorous cercariae have been found in *Philine aperta* (see Køie, 1991). It is likely that they also belong to the Hemiuridae. Candidates are *Hemiurus appendi-*

culatus (Rudolphi, 1802), *Ectenurus lepidus* Looss, 1907 and *Synaptobothrium caudiporum* (Rudolphi, 1819) which all have a Lusitanean/Mediterranean distribution (see Gibson & Bray, 1986) and have been recorded off the French coast where the infected snails were found.

Experiments have shown that the cercaria believed to be that of *Hemiurus levinseni* Odhner, 1905 (see Køie, 1990a) is the cercaria of an unidentified derogenid.

Apart from the larval stages in the four species of bullomorph opisthobranchs, members of the Hemiuridae in the North Atlantic have been found in unrelated prosobranchs, i.e. *Gibbula* spp. (Diotocardia (Archaegastropoda), Trochacea, Trochacae) and *Nassarius trivitattus* (Stenoglossa (Neogastropoda), Buccinacea, Nassariidae). Three species of *Gibbula* harbour each one species of *Lecithochirium* (table II) (see Køie, 1990b) and *N. trivitattus* is the snail host of the dinurine *Tubulovesicula pinguis* (Linton, 1940) (see Stunkard, 1980). It thus appears that related parasites occur in snails which are not systematically closely related. Within the subfamily Lecithochiriinae some species use prosobranchs of the genus *Gibbula*, whereas one species use the opisthobranch *Retusa obtusa* (table II). If the choice of snail hosts reflects the relationships of the parasites, then *Brachyphallus crenatus* should be more closely related to *H. communis* than to *Lecithochirium* spp. Gibson & Bray (1979) suggested that the subfamily Lecithochiriinae might be divided into two groups according to the shape and number of vitelline masses. This would separate the genera *Lecithochirium* and *Brachyphallus*. Unfortunately the snail hosts are known for only two of the nine genera of the Lecithochiriinae mentioned by Gibson & Bray (1979). An even more pronounced discrepancy between the taxonomy of the molluscan hosts and that of the parasite is found within the hemiuroid genus *Lecithaster* (Lecithasteridae). Here some cercariae apparently occur in species of the prosobranch genus *Thais* (*Lapillus*), while other cercariae occur in species of the opisthobranch genus *Odostomia* (see Køie, 1989).

Free-swimming cystophorous cercariae are apparently known for the Hemiuridae and Derogenidae (see Køie 1979, 1990a) only. Most cystophorous cercariae are unable to swim or have only a limited motility. Non-motile species which use free-swimming copepods may be almost spherical (see Ching, 1960) or have an inflated caudal cyst wall to improve buoyancy (see Køie, 1989). Cercariae which develop in snails living on algae may be non-swimming and are provided with appendages which enable the cercariae to become entangled in the algae so that they may be ingested by harpacticoid copepods (Køie, 1990b; Køie & Gibson, 1991).

A large number of marine cystophorous cercariae have been described from various kinds of molluscs, including scaphopods, bivalves, pteropods and heteropods (see, *inter alia*, Ching, 1960; Arvy, 1972; Wardle, 1975; Vande Vusse, 1980; Lester & Newman, 1986).

Some of the cystophorous cercariae from prosobranchs are larvae of the Didymozoidea (see Køie & Lester, 1985), and it is likely that (many or all) cystophorous cercariae from holoplanktonic snails, such as pteropods and heteropods, also belong to this group. No complete didymozoid life-cycle has yet been elucidated (see Køie & Lester, 1985).

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