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Review Article

Life cycles of species of *Proteocephalus*, parasites of fishes in the Palearctic Region: a review

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Abstract

The life cycles of species of *Proteocephalus* Weinland, 1858 (Cestoda: Proteocephalidea) parasitizing fishes in the Palearctic Region are reviewed on the basis of literary data and personal experimental observations, with special attention being paid to the development within the intermediate and definitive hosts. Planktonic crustaceans, diaptomid or cyclopid copepods (Copepoda), serve as the only intermediate hosts of all *Proteocephalus* species considered. A metacestode, or procercoid, develops in the body cavity of these planktonic crustaceans and the definitive host, a fish, becomes infected directly after consuming them. No previous reports of the parenteral location of metacestodes within the second intermediate host as it is in the Nearctic species *P. ambloplitis* have been recorded. Thus, the life cycles of *Proteocephalus* tapeworms resemble in their general patterns those of some pseudophyllidean cestodes such as *Eubothrium* or *Bothriocephalus*, differing from the latter in the presence of a floating eggs instead of possessing an operculate egg from which a ciliated, freely swimming larva, a coracidium, is liberated. The scolex of *Proteocephalus* is already formed at the stage of the procercoid within the copepod intermediate host; in this feature, proteocephalideans resemble caryophyllidean rather than pseudophyllidean cestodes. The morphology of procercoids of individual species is described with respect to the possibility of their differentiation and data on the spectrum of intermediate hosts are summarized. Procercoids of most taxa have a cercomer, which does not contain embryonic hooks in contrast to most pseudophyllidean cestodes. The role of invertebrates (alder-fly larvae – Megaloptera) and small prey fishes feeding upon plankton in the transmission of *Proteocephalus* tapeworms still remains unclear but these hosts are likely to occur in the life cycle. Data on the establishment of procercoids in definitive hosts, morphogenesis of tapeworms within fish hosts, and the length of the prepatent period are still scarce and new observations are needed. Whereas extensive information exists on the development of *P. longicollis* (syns. *P. exiguus* and *P. neglectus*), almost no data are available on the ontogeny of other taxa, in particular those occurring in brackish waters (*P. gobiorum*, *P. tetrastomus*). The morphology of *P. cernuae* and *P. osculatus* procercoids from experimentally infected intermediate hosts is described for the first time.

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Introduction

Tapeworms of the genus *Proteocephalus* Weinland, 1858 are parasites of fishes, amphibians and reptiles (Freze, 1965a; Schmidt, 1986; Rego, 1994). The systematics of this genus has not been sufficiently clarified and there are difficulties in the identification of individual taxa (Freze, 1965a; Priemer, 1982; Chubb *et al*., 1987; Dubinina, 1987; Scholz, 1989a; Šnábel *et al*., 1994; Hanzelová *et al*., 1995a,b; Scholz *et al*., 1998a).

It has been found that Palearctic species of *Proteocephalus* parasitic in fishes are highly uniform in their overall morphology (Scholz & Hanzelová, 1998). On the contrary, several taxa are polymorphic (Anikieva, 1992a,b, 1993, 1995; Hanzelová & Špakulová, 1992; Šnábel *et al*., 1996; Scholz & Hanzelová, 1998). This results in a shortage of morphological or biometrical features potentially suitable for species identification. Studies on the life cycles, mainly those on the morphogenesis of larval stages, might provide data helpful for this purpose (Freeman, 1973; Scholz, 1991a, 1993a; Scholz *et al*., 1997; Rego *et al*., 1998).

To date, the developmental cycles of only a few *Proteocephalus* tapeworms have been studied and, compared with other cestode groups such as the Pseudophyllidea and Cyclophyllidea, the biology of proteocephalidean tapeworms is much less well known (Smyth & McManus, 1989; Mariaux, 1996; Rego *et al*., 1998). Moreover, existing data are scattered in numerous papers, many published in Russian, and these are not readily available.

Consequently, the life cycles of *Proteocephalus* species occurring in fishes in the Palearctic Region are reviewed with emphasis on the morphology of larval stages and development of parasites within the intermediate and definitive hosts. Gaps in the present knowledge of biology of *Proteocephalus* tapeworms are discussed and some areas for future research are proposed. Besides the literary data, unpublished results of experimental studies on the development of *P. cernuae* (Gmelin, 1790) and *P. osculatus* (Goeze, 1782) are presented.

Literary data

Up to the present, the data on the life cycles of the following *Proteocephalus* species occurring in the Palearctic Region have been provided: *P. ambiguus* (Dujardin, 1845) – Willemse (1968), Sysoev (1985, 1987a – as *P. filicollis*), Sysoev *et al*. (1992, 1994); *P. cernuae* (Gmelin, 1790) – Willemse (1969), present study; *P. filicollis* (Rudolphi, 1802) – Meggitt (1914), Kuczkowski (1925 – as *P. percae*), Hopkins (1959), Willemse (1968); *P. longicollis* (Zeder, 1800) (syns. *P. exiguus* La Rue, 1911 and *P. neglectus* La Rue, 1911 – see Hanzelová *et al*., 1995a, and Scholz & Hanzelová, 1998) – Jarecka (1956), Willemse (1969), Albetova (1975, 1976), Anikieva & Malakhova (1975), Prouza (1978), Priemer (1980, 1987), Anikieva (1982), Anikieva *et al*. (1983), Priemer & Goltz (1986), Rusinek (1987a,b), Hanzelová *et al*. (1988, 1989, 1990), Rusinek & Pronin (1991), Scholz (1991a), Hanzelová (1992), Sysoev *et al*. (1992, 1994); *P. macrocephalus* (Creplin, 1825) – Doby & Jarecka (1966), Willemse (1969), Scholz *et al*. (1997); *P. percae* (Müller, 1780) – Wierzbicka (1956), Jarecka (1960), Wootten (1974), Sysoev (1987a,b), Sysoev *et al*. (1992, 1994); *P. plecoglossi* Yamaguti, 1934 – Kataoka & Momma (1935 – as *P. neglectus*); *P. thymalli* (Annenkova-Chlopina, 1923) – Rusinek (1989), Rusinek & Pronin (1991), Rusinek *et al*. (1996); *P. torulosus* (Batsch, 1786) – Gruber (1878), Mrázek (1891, 1917), Wagner (1917), Dubinina (1952), Kennedy & Hine (1969), Sysoev (1983, 1987a), Sysoev *et al*. (1992, 1994), Scholz (1993a), Moravec *et al*. (1997); *Proteocephalus* sp. (most probably *P. longicollis*) – Doby & Jarecka (1964), Jarecka & Doby (1965), Morandi & Ponton (1989).

Data on seasonal patterns in the occurrence and maturation of *Proteocephalus* tapeworms published until the beginning of the 1980s were reviewed by Chubb (1982). More recently, life histories and population biology of species of *Proteocephalus* have been studied by Yakushev & Chizhov (1982), Sysoev (1983, 1985), Yakushev (1984, 1985), Scholz (1986, 1989b), Rusinek (1987b), Hanzelová *et al*. (1988, 1989, 1990, 1996), Rintamäki & Valtonen (1988), Morandi & Ponton (1989), Valtonen & Rintamäki (1989), Andersen & Valtonen (1990), Nie & Kennedy (1991), Rusinek & Pronin (1991), Hanzelová (1992), Scholz & Moravec (1994), Sysoev *et al*. (1994), and Balling & Pfeiffer (1997).

Basic stages in life cycle

As in other tapeworms, the basic sequence of *Proteocephalus* development consists of an adult, which produces an egg, containing an oncosphere, i.e. a six-hooked (hexacanth) larva, which migrates to a parenteral site (body cavity) of the intermediate host, where it metamorphoses and grows as a metacestode, and a sexually reproducing adult (Freeman, 1973).

Egg

The egg results from oogenesis, fertilization of the oocyte and subsequent embryogenesis. This process, including the formation of sperm, i.e. spermatogenesis, will be briefly reviewed, with emphasis on the morphology of formed eggs.

Spermatogenesis

The male reproductive plan of *Proteocephalus* species is typical of parasitic platyhelminths (Neodermata) (Smyth & McManus, 1989). Despite the fact that the first study on the ultrastructure of cestode sperm flagellum was that by Gresson (1962) in *P. pollanicola* (syn. of *P. longicollis* – Scholz *et al*., 1998b), there is limited information about spermatogenesis and sperm ultrastructure of *Proteocephalus* species (Justine, 1998). It has been found that *P. longicollis* has a spermatozoon and spermiogenesis with the following chief features: (i) a long thread-like body; (ii) an elongated nucleus; (iii) cortical microtubules underlying the plasma membrane; (iv) the absence of mitochondria; and (v) the absence of a typical acrosome (Gresson, 1962; Rybicka, 1966; Swiderski & Eklu-Natey, 1978; Euzet *et al*., 1981; Ubelaker, 1983; Swiderski, 1985, 1996; Smyth & McManus, 1989). Because of the presence of two axonemes, *Proteocephalus* seems to belong to the ‘two-axoneme’ type of cestodes, found typically in the Pseudophyllidea and reported also in the Trypanorhyncha and Tetraphyllidea (Ubelaker, 1983; Euzet *et al*., 1981; Smyth & McManus, 1989). This type is considered primitive (plesiomorphic) because it is present in free-living platyhelminths (Smyth & McManus, 1989; Justine, 1998).

Oogenesis and insemination

There are few studies on oogenesis and insemination in cestodes, which is valid also for proteocephalideans (Rybicka, 1966; Smyth & McManus, 1989). Although no data exist, it can be assumed that the chemical composition and ultrastructure of oocytes of *Proteocephalus* species resemble those of other cestode groups (see Smyth & McManus, 1989).

Egg formation

Most studies on cestode egg formation have dealt with pseudophyllidean and cyclophyllidean tapeworms and practically nothing is known about the process of formation of egg envelopes of species of *Proteocephalus* (see Rybicka, 1966; Swiderski *et al*., 1978; Smyth & McManus, 1989). Four main types of egg-forming systems are recognized in cestodes and proteocephalidean tapeworms are considered to belong to the 'pseudophyllidean-type' (Smyth & McManus, 1989). Cestodes with life cycles associated with water are placed in this group. Many of them, in particular pseudophyllideans, have a thick, sclerotin capsule, produced by cestodes with well-developed vitellaria (Ubelaker, 1983; Smyth & McManus, 1989). In this feature, proteocephalideans distinctly differ from these groups in possessing a thin-walled, transparent outer envelope. On the basis of this feature, Ubelaker (1983) placed them, together with the Tetraphyllidea, to a distinct subgroup among these tapeworms. Jarecka (1975) named the eggs of proteocephalideans as 'egg-like oncospheres' to distinguish them from coracidia of pseudophyllideans.

In pregravid proglottides of *Proteocephalus* species, all eggs contain an unformed oncosphere, i.e. there are no embryonic hooks. The hooks appear simultaneously in most eggs in more developed proglottides, which are named gravid. The number of pregravid proglottides is highly variable in *Proteocephalus* species, ranging from a few to numerous.

Egg morphology

Eggs of *Proteocephalus* species are similar in their overall appearance and are composed of an oncosphere covered by membranes (fig. 1). The oncosphere (hexacanth), already formed within the uterus of gravid worms (fig. 2), contains three pairs of embryonic hooks with a straight, long and fine base, a short, slightly curved blade and a short, anteriorly directed guard (fig. 3). Hooks of the median pair are longer than those of lateral pairs (Ieshko, 1980; Rusinek, 1986; Morandi & Ponton, 1989; Scholz, 1993a). Two dark areas considered to be penetration glands (Fischer, 1968; Befus & Freeman, 1973a; Wootten, 1974), are situated on the opposite side of the oncosphere to the embryonic hooks (Freeman, 1973).

Ieshko (1980) and Rusinek (1986) studied the morphology of the embryonic hooks of *P. exiguus* (= *P. longicollis*), *P. percae* and *P. thymalli* from Russia. They found significant differences in the size of the hooks of individual taxa studied. However, differences were also found between different populations of the same species (Ieshko, 1980; Rusinek, 1986). The differing lengths of embryonic hooks were also used for distinguishing procercoids of *P. macrocephalus* and *Proteocephalus* sp. (most probably *P. longicollis*) in naturally infected copepods (Jarecka & Doby, 1965). It is recommended that further investigations are performed in order to confirm the suitability of embryonic hooks for species differentiation, as in oncospheres of pseudophyllidean tapeworms of the genus *Diphyllobothrium* (Hilliard, 1960).

Proteocephalus oncospheres probably have no flame cells (Freeman, 1964), but these are present in oncospheres of some tapeworms, e.g. in *Diphyllobothrium* (Freeman, 1973). A formed oncosphere of *Proteocephalus* tapeworms is enclosed in layers, the number and names of which have been subject to controversy by individual workers. Smyth & McManus (1989) distinguish three basic embryonic envelopes: (i) capsule (= egg shell); (ii) outer envelope; and (iii) inner envelope, which is a syncytial layer showing much variation and giving rise to the oncospheral membrane.

In papers dealing with proteocephalideans, however, a somewhat different terminology has been used: (i) 'outer thin pliable membrane' (Freeman, 1964); 'enveloppe la plus externe' (Doby & Jarecka, 1966); 'hyaline swimming envelope' (Priemer, 1987) or 'external membrane' (de Chambrier & Rego, 1995); this membrane apparently corresponds to the 'capsule' after Rybicka (1966) and is thin and transparent; (ii) 'enveloppe médiane' (Doby & Jarecka, 1966); 'outer envelope' (Rybicka, 1966); or 'embryophore' (de Chambrier & Vaucher, 1994; Smyth, 1994); this membrane covers a thick granular layer (fig. 1); (iii) 'membrane interne' (Doby & Jarecka, 1966); 'internal envelope' (Rybicka, 1966; Smyth, 1994); this membrane is transparent, thin and it is closely applied to the inner border of the granular layer; normally it is not seen in intact eggs (Freeman, 1964).

It seems to be appropriate to follow the terminology proposed by Rybicka (1966) and Smyth & McManus (1989), i.e. to name envelopes as a 'capsule', 'outer envelope', covering a thick granular layer, and an 'internal envelope' (fig. 1).

Egg size

The size of eggs has been used as an important feature in differentiating species of *Proteocephalus* (see, e.g. La Rue, 1914; Freze, 1965a). However, data taken from eggs in permanent preparations are of limited value because the eggs are generally deformed due to staining and dehydration; the capsule is collapsed so that most measurements provided in the literature seem to relate to the outer envelope. It has been suggested (Rego *et al*., 1998) that only measurements of eggs expelled from the uterus into the water should be measured. However, only ripe eggs, i.e. those containing fully formed and motile oncospheres with embryonic hooks, should be considered. In table 1, measurements of ripe eggs of *Proteocephalus* species are compared with literary data. It

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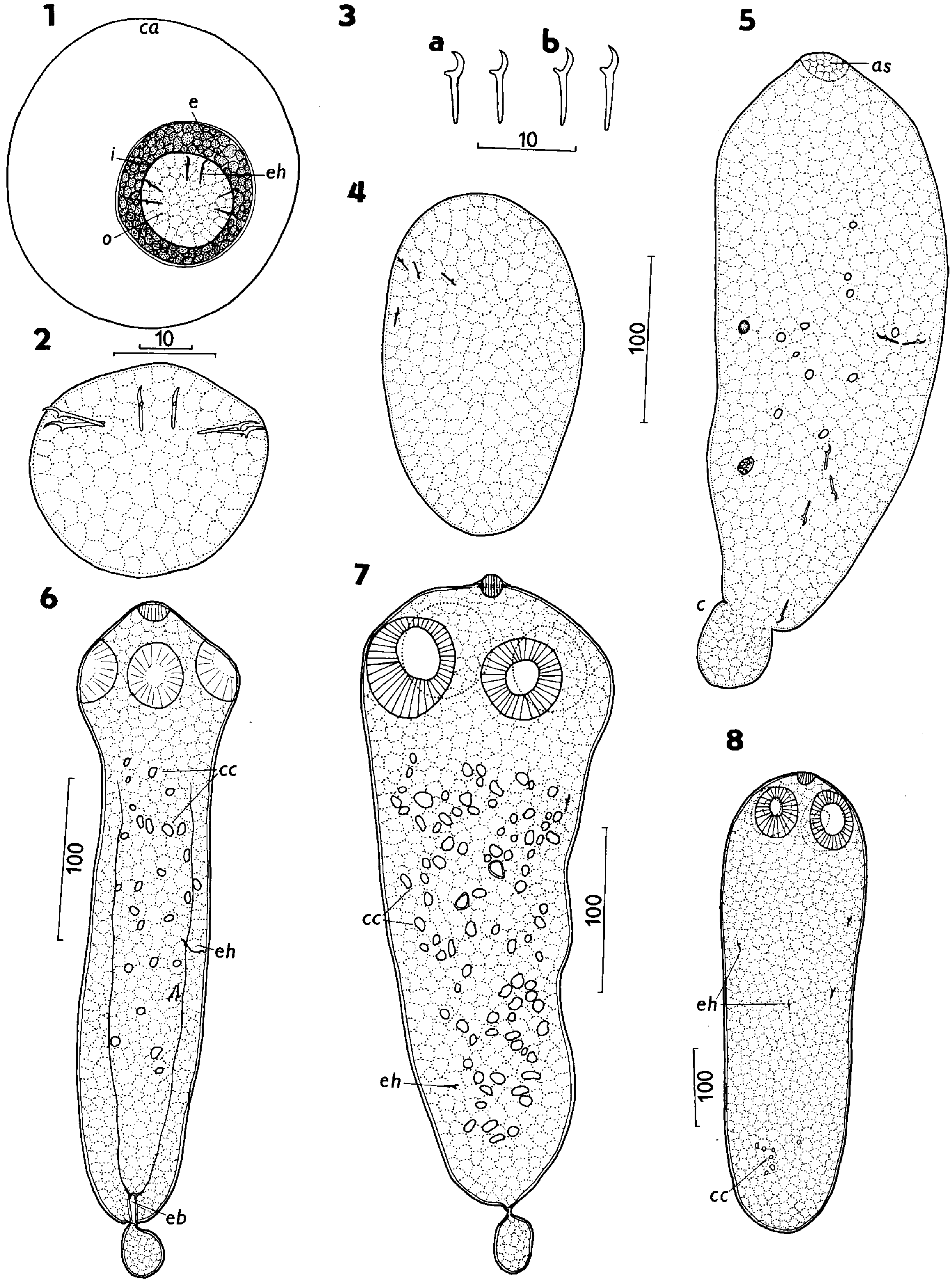

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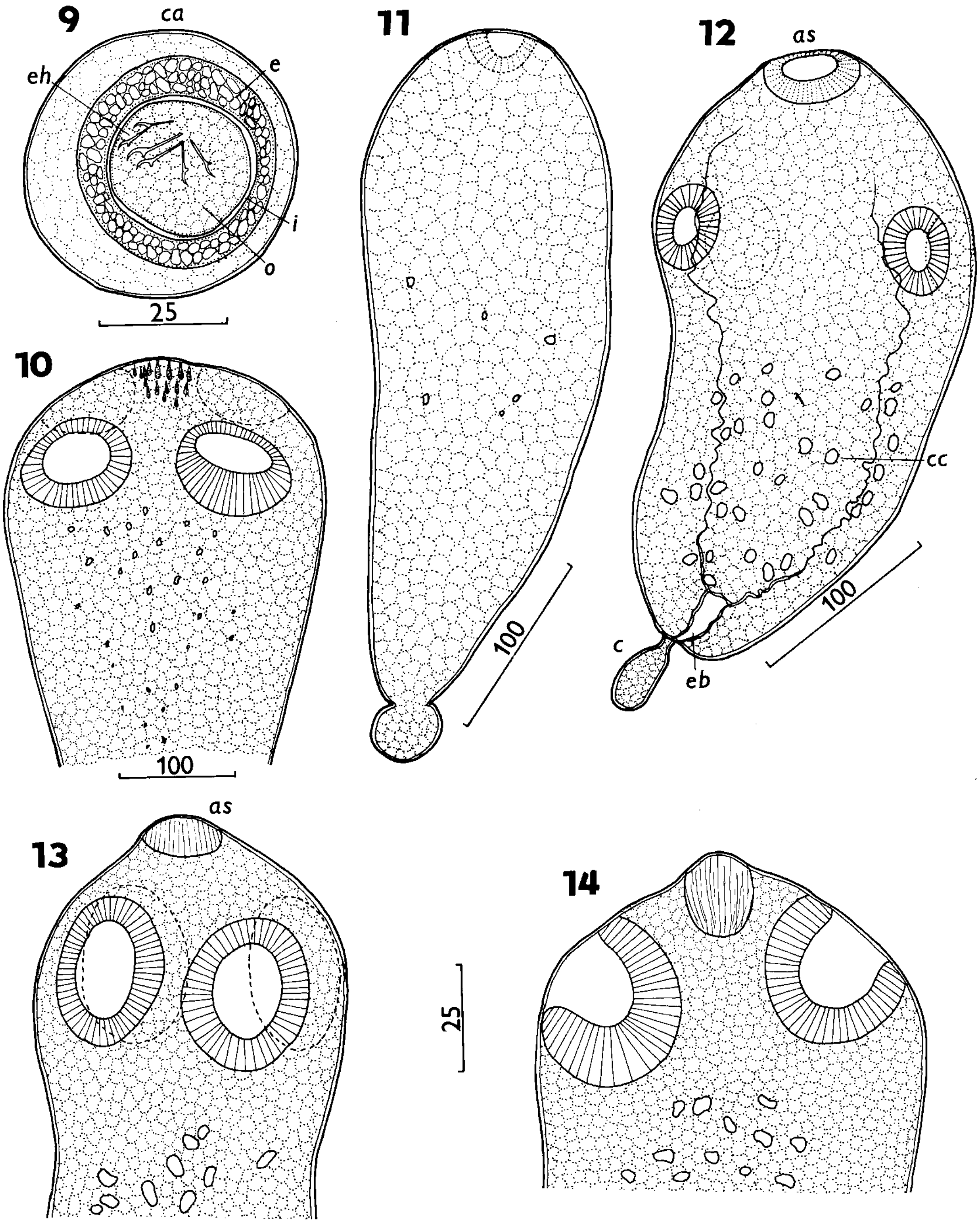

Fig. 1. Egg of *Proteocephalus cernuae* laid in water. Figs 2–7. Development of *P. cernuae* in copepod intermediate host (*Cyclops strenuus*) at 20–22°C; 2, oncosphere from body cavity; 3, embryonic hooks (a, lateral; b, median); 4, larva 5–6 days post infection (DPI); 5, larva 7–8 DPI (note forming cercomer, apical sucker and first calcareous corpuscles; embryonic hooks are located within the body); 6, procercoid 8–9 DPI (note presence of lateral suckers, apical sucker and excretory bladder); 7, fully formed (infective) procercoid 13–14 DPI. Fig. 8. Juvenile *P. cernuae* from the intestine of *Cichlasoma* sp. experimentally infected with *C. strenuus* containing procercoids, 8 DPI (note small number of calcareous corpuscles and presence of embryonic hooks within body). Fig. 9. Egg of *Proteocephalus torulosus*. Fig. 10. Scolex of *P. torulosus* procercoid (note absence of apical sucker replaced by numerous gland cells). Figs. 11–12. Procercoids of *P. osculatus* from *C. strenuus* kept at 20–22°C; 11, procercoid 12 DPI (from copepod infected with five larvae; note cercomer, first calcareous corpuscles and developing apical sucker); 12, fully formed procercoid 21 DPI (note thick-walled excretory bladder and large apical sucker with distinct cavity). Fig. 13. Scolex of *P. neglectus* (= *P. longicollis*) procercoid. Fig. 14. Scolex of *P. macrocephalus* procercoid (note elongate apical sucker). Scale bars in micrometres. Abbreviations: as, apical sucker; c, cercomer; ca, capsule; cc, calcareous corpuscles; e, outer membrane; eb, excretory bladder; eh, embryonic hooks; i, internal membrane; o, oncosphere.

should also be pointed out that the capsule of most *Proteocephalus* tapeworms inflates in water which makes it difficult to compare with measurements of eggs present at different times in water. Therefore, it seems reasonable to provide measurements of a more stable structure, i.e. those of the outer envelope covering the rigid, granular layer, and of the oncosphere.

Egg release

Ripe eggs, i.e. those containing oncospheres with embryonic hooks (hexacanth), are released through the uterine pores. In *Proteocephalus* species, the uterine pores are few (about 2–4), small, oval to spherical openings along the median line on the ventral side of gravid proglottides. To date, no data on the formation of uterine pores have been provided.

Eggs are spontaneously released after the tapeworms are placed in water (Freeman, 1964) and it seems that this release corresponds with the strategy of egg release under natural conditions. It has been observed (unpublished data) that eggs of some species, e.g. *P. osculatus* and *P. torulosus*, are released directly within the lumen of fishes. However, it is possible that this release is linked with the death of the host and it does not occur in nature. Eggs of *Proteocephalus* tapeworms have no tanned egg shells (Rybicka, 1966; Kearn, 1998), which are, on the other hand, present in pseudophyllideans. Their outer membrane is thin and apparently unable to prevent digestion by host enzymes in the anterior part of the intestine, the site of location of adult tapeworms. The eggs, protected against unfavourable conditions of the intestinal lumen within the uterus of the worm, can reach the external environment with more safety by expulsion of the whole egg-containing parasite or by expulsion of the detached part of the strobila (Kearn, 1998). Indeed, the body of gravid *Proteocephalus* is often fragmented within the intestinal lumen (unpublished observations). Another way of expelling eggs was reported by Meggitt (1914), who observed *P. filicollis* tapeworms partly protruded from the anus and expelling eggs through the uterine pores.

Stimuli of egg release have not been studied in detail but it is likely that the most important is direct contact of gravid worms with water. Eggs are released from proglottides quite rapidly and a large amount of eggs is expelled in a few minutes. However, no information exists on the fecundity of *Proteocephalus* tapeworms.

After the egg is laid in water, the external membrane quickly increases in size, becoming two or three times larger (Freeman, 1964; Priemer, 1980; Morandi & Ponton, 1989; Scholz, 1991a; this study, fig. 1). Although no experiments on the influence of fluids of different osmotic pressures to the swelling of the capsule have been carried out, it is presumed that this process is due to osmotic intake of water. It is also assumed that the swelling of the capsule helps in the floating of the egg because freshly laid eggs remained on the bottom whereas the eggs with inflated capsules may float in the water (Jarecka & Doby, 1965; unpublished observations). Since intermediate hosts are mostly pelagic copepods, this is an adaption to facilitate transmission by selective ingestion (Mackiewicz, 1988). Available information indicates that eggs of all but one *Proteocephalus* species from Palearctic fishes are closely similar in their morphology as described above.

Eggs of *P. torulosus* are relatively large (table 1) and they differ from those of congeners in possessing a somewhat thicker granular layer and a less inflated capsule (fig. 9; Scholz, 1993a, figs. 1A and 4). This is probably an adaptative character because *P. torulosus* is a riverine species, occurring even in rivers with strong current (Scholz & Moravec, 1994). In these localities, eggs which sink to the bottom are likely to survive for successful transmission to potential intermediate hosts, such as benthic copepods.

Survival and infectivity

It has been observed that not all eggs spontaneously laid in water are ripe. Some eggs are apparently smaller than others and contain either unformed oncospheres, i.e. without embryonic hooks, or undifferentiated, granular tissue. The proportion of ripe eggs of *P. exiguus* (= *P. longicollis*) was found to change during the year with the highest proportion in summer–autumn but only very few during the winter and spring (Anikieva *et al.*, 1983). However, more details have not been provided.

Infectivity, i.e. the ability of oncospheres to infect intermediate hosts, was tested by experimental infections of copepods with eggs preserved in water of different temperatures (Scholz, 1991a, 1993a). It has been demonstrated that eggs maintain their infectivity for a relatively long time (Willemse, 1969; Wootten, 1974; Priemer, 1980, 1987; Scholz, 1991a, 1993a) and that infectivity depends mainly on the temperature as documented by Scholz (1991a, 1993a). At least some oncospheres of *P. neglectus* (= *P. longicollis*) were able to infect *Cyclops strenuus* copepods in experiments after 25 days at 10°C, 20 days at 5°C and 10 days at 21–22°C; those of *P. torulosus* 35 days at 5–7°C, 12 days at 10–12°C and 8 days at 20–22°C (Scholz, 1991a, 1993a).

Dubinina's (1952) observations that only freshly released *P. torulosus* eggs are infective to copepods and that they lose their infectivy very quickly seem to be incorrect because they contradict successful experimental infections with *P. torulosus* eggs several days old (Scholz, 1993a). It is possible that Dubinina (1952) used a high proportion of unripe eggs, which might have led to negative results in her experiments. Scholz (1993a) also found the prevalence of copepod infection with *P. torulosus* eggs to be relatively low, i.e. 6–12% in *C. strenuus*.

Intermediate host

Range of intermediate hosts

Planktonic crustaceans of the order Copepoda (families Diaptomidae and Cyclopidae) serve as intermediate hosts for *Proteocephalus* tapeworms in the Palearctic Region (table 2). An exception to this rule is the calanoid *Epischura baicalensis* (Temoridae), which is an intermediate host of *Proteocephalus* species in Baikal Lake, Russia (Rusinek *et al.*, 1996). The finding of *Proteocephalus* larvae in cladocerans (*Bosmina coregoni*, *Bythotrephes cederstroemi*, *Daphnia* spp.) should be considered as accidental or even doubtful (Anikieva, 1982; Anikieva

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Table 1. Comparison of measurements of eggs and oncospheres of *Proteocephalus* species. A, present data (diameter of granular layer; expressed as range; mean ± SD in parentheses when available); B, literary data ('egg size' after Freze, 1965a).

Species	Egg			Oncosphere		
	A		B	A		B
P. cernuae	27–36	(33 ± 2)	19–24	19–22		13–17
P. longicollis	41–52		31–46	23–32		18–35
P. macrocephalus	25–31	(27 ± 1)	23–31	16–20	(18 ± 1)	16–21
P. osculatus	23–26	(25 ± 1)	18–21	14–18	(16 ± 1)	12–15
P. torulosus	45–53		22–36	21–25		20–25

et al., 1983) because experimental infections have always failed (Freeman, 1964; unpublished data). Rusinek (1989) observed that the eggs ingested by cladocerans survived within the intestine for a short time (maximum 48 h) but oncospheres were unable to penetrate through the intestinal wall and quickly died (Rusinek, 1989).

The suitability of individual copepod species as intermediate hosts of *Proteocephalus* species differs and is dependent upon the species and developmental stages of copepods as well as particular ecological conditions such as locality and season (Freeman, 1964; Doby & Jarecka, 1966; Sysoev, 1983, 1985, 1987a,b; Yakushev, 1984; Sysoev *et al.*, 1988, 1994; Hanzelová *et al.*, 1989, 1990; Hanzelová, 1992). There are also considerable differences in the susceptibility of copepods to infection between experimental and natural conditions, e.g. *C. strenuus*, serving as a suitable experimental host (Scholz, 1991a, 1993a), can play an insignificant role in the transmission under natural conditions (Sysoev, 1987a; Sysoev *et al.*, 1988; Hanzelová *et al.*, 1989; Hanzelová, 1992).

Some copepods tend to be more susceptible to *Proteocephalus* infection than others (Wagner, 1954; Jarecka & Doby, 1965; Doby & Jarecka, 1966; Morandi & Ponton, 1989; Scholz, 1991a, 1993a), but data which would explain these differences are not available. The different developmental stages of copepods have also distinct susceptibilities to infection with *Proteocephalus* oncospheres. Priemer (1987) found nauplii of *C. strenuus* to be more heavily infected with *P. exiguus* (= *P. longicollis*) procercoids in experiments (prevalence 96%) than other developmental stages (copepodites and adult copepods) (prevalence 64%). He explained this difference by the presence of a thinner gut wall in nauplii compared to that in adult copepods (Priemer, 1987). However, other authors reported higher prevalence values in adult copepods than in copepodites (Freeman, 1964; Markevich & Kuperman, 1982; Hanzelová *et al.*, 1989; Hanzelová, 1992; Scholz, 1993a; Rusinek *et al.*, 1996).

Infection of the intermediate host

Willemse (1968) stated that copepods are attracted by floating eggs and ingest them quickly but other authors (Essex, 1927; Hopkins, 1959) suggest that copepods reject oncospheres and the consumption of eggs is occasional and accidental. The results of experimental infections, indicating high prevalences in infected copepods, support the assumption of Willemse (1968) rather than accidental ingestion of proteocephalidean eggs.

It can be assumed that eggs of *Proteocephalus* species, because of their size, are accessible to most planktonic copepods because they are found in young developmental stages such as the nauplii and copepodites (Priemer, 1987). After ingestion, oncospheres are liberated

Table 2. Survey of natural (N) and experimental (E) intermediate hosts of *Proteocephalus* species. With the exception of *Epischura baicalensis* (Calanoida), all intermediate hosts belong to the families Diaptomidae and Cyclopidae (Copepoda).

Species	Intermediate host
P. ambiguus	*Eudiaptomus gracilis* (N), *Cyclops strenuus* – Willemse (1968), Sysoev *et al.* (1994)
P. cernuae	*Cyclops strenuus* (E) – Willemse (1967), present data
P. filicollis	*E. gracilis* (N), *C. strenuus* (E), *Eucyclops serrulatus* (E), *Mesocyclops oithonoides* (N,E) – Kuczkowski (1925)
P. longicollis[1]	*E. gracilis* (N,E), *E. graciloides* (N), *E. zachariasi* (N), *Cyclops furcifer* (E), *C. kolensis* (N,E), *C. lacustris* (N), *C. strenuus* (N,E), *C. vicinus* (N,E), *C. scutifer* (N,E), *Eucylops serrulatus* (E), *Macrocyclops albidus* (N), *Mesocyclops oithonoides* (N) – Kuczkowski (1925), Freze (1965a,b), Prouza (1978), Priemer (1980, 1987), Anikieva (1982), Anikieva *et al.* (1983), Scholz (1991a)
P. macrocephalus	*Acanthocyclops vernalis* (E), *Cyclops abyssorum* (E), *C. strenuus* (E) – Doby & Jarecka (1966), Willemse (1966–1967), Scholz *et al.* (1997)
P. osculatus	*C. strenuus* (present data)
P. percae	*Eudiaptomus graciloides* (N), *Cyclops agilis* (E), *C. kolensis* (N), *C. vicinus* (N), *Megacyclops gigas* (N), *M. viridis* (E), *Mesocyclops leuckarti* (E) – Wierzbicka (1956), Jarecka (1970), Wootten (1974), Sysoev *et al.* (1994)
P. thymalli	*Epischura baicalensis* (N,E), *Cyclops kolensis* (E), *C. vicinus* (E) – Rusinek (1989), Rusinek & Pronin (1991), Rusinek *et al.* (1996).
P. torulosus	*Diaptomus castor* (E), *E. gracilis* (N), *Heterocope appendiculata* (N), *C. strenuus* (N,E), *Cyclops* sp., *Eucyclops serrulatus* (N,E), *M. oithonoides* – Gruber (1878), Mrázek (1891, 1917), Wagner (1917), Scholz (1993a)
Proteocephalus sp. (probably *P. longicollis*)	*Cyclops abyssorum* (N,E), *C. strenuus* (?N,E), *C. vicinus* (E), *Epischura baicalensis* – Doby & Jarecka (1964), Jarecka & Doby (1965), Morandi & Ponton (1989), Rusinek *et al.* (1996)

[1]Data originally provided for *P. neglectus* and *P. exiguus* (synonyms of *P. longicollis* – Scholz & Hanzelová, 1998) are included.

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from surrounding membranes in the gut of copepod (Wootten, 1974), and presumably the release of the larvae in the intestine is stimulated by the environment of the intestinal lumen. The process of liberation is rather rapid and oncospheres appear to be free of the egg membranes as early as 5 min after contact with the copepods (Wootten, 1974). This liberation of the oncosphere has also been observed in eggs in water (Jarecka & Doby, 1965; Priemer, 1980, 1987; figs 2, 3, 5 and 7 in Scholz, 1991a) and it can be stimulated by applying slight pressure on the coverslip (Morandi & Ponton, 1989). However, those oncospheres which are liberated directly into water do not survive.

The success of oncosphere establishment within copepods and the proportion of intermediate hosts becoming infected are influenced by many factors, including physiological compatibility, ecological conditions and the geographic origin of the host and parasite, the time of contact of copepods with eggs, the density of copepods, and water temperature (Morandi & Ponton, 1989; Rusinek, 1989; Rusinek & Pronin, 1991; Scholz, 1991a, 1993a).

Following ingestion, oncospheres are liberated from egg membranes and, if in a suitable host, actively penetrate the gut of the copepod into the body cavity. Some authors (Wootten, 1974; Smyth, 1994) suggested that the penetration of oncospheres though the gut wall is assisted by the mechanical action of embryonic hooks. However, Freeman (1973) assumes that '... these hooks may be used more for attachment to the gut wall, and that secretions facilitate a more passive less disruptive penetration than that resulting from 'clawing'... ' A few existing studies in other cestode groups (Scholz, 1997) support this opinion. The secretion of penetration glands, with presumably histolytic secretions, may play a crucial role in the process of penetration (Freeman, 1964; Befus & Freeman, 1973a; Wootten, 1974; Smyth & McManus, 1989). The time of penetration of the gut wall is short, lasting 5–30 min (Wootten, 1974; Rusinek, 1989; Rusinek & Pronin, 1991). Within the body cavity, the oncosphere develops into a metacestode (Freeman, 1973).

A number of terms have been used to describe *Proteocephalus* metacestodes in the intermediate host. These include: plerocercoid (Willemse, 1968), plerocercoid I (Befus & Freeman, 1973b; Freeman, 1973), cercoscolex (Jarecka, 1975; Anikieva *et al.*, 1983; Scholz, 1991a; Gulyaev, 1997) or procercoid (Wardle & McLeod, 1952; Hopkins, 1959; Freze, 1965a; Markevich & Kuperman, 1982; Kennedy *et al.*, 1992; Sysoev *et al.*, 1992, 1994; Marcogliese, 1995; Rusinek *et al.*, 1996). Although the aim of this review is not to extensively discuss the terminology of metacestodes, some comments on this topic are provided and the term 'procercoid' is used here.

Freeman (1973) reviewed extensively the life cycle patterns of tapeworms and presented a new classification of metacestodes, based on descriptive terminology, which reflects the morphogenesis and morphology of metacestodes. Freeman (1973) considers primitive metacestodes, which develop neither a primary cavity nor a scolex recognizably similar to that of the adult, as procercoids as originally proposed by Janicki & Rosen (1917). He concludes that 'If procercoid is the appropriate term for a metacestode which does not develop a scolex identifiable with that of the adult in the first site of development, then obviously a metacestode that does develop such a scolex requires another name'. For these metacestodes, the term 'plerocercoid' was proposed by Freeman (1973). However, the term 'plerocercoid' has usually been restricted to pseudophyllidean metacestodes from the second intermediate host (Jarecka, 1975; Smyth, 1994).

In the genus *Proteocephalus*, all metacestodes from intermediate hosts as well as juvenile worms from the definitive host were regarded as plerocercoids by Freeman (1973) and descriptive prefixes characterizing individual types of metacestodes were added. For example, the metacestode of *P. filicollis* from a copepod intermediate host is named 'caudate culcitacetabuloplerocercoid I' and that of *P. ambloplitis* 'acaudate invaginated glandacetabuloplerocercoid I' (Freeman, 1973). However, this terminology is very complicated and it has not received general acceptance among helminthologists.

Jarecka (1975) proposed a simple terminology for the larval stages of tapeworms but she only dealt with three cestode orders, namely Pseudophyllidea (including the caryophyllideans), Proteocephalidea and Cyclophyllidea. She divided cestodes into 'oviparous', i.e. those possessing a coracidium (Pseudophyllidea) and 'viviparous'. Four basic metacestode types were recognized: a procercoid in oviparous pseudophyllideans, and a cercoscolex, cysticercoid and cysticercus in viviparous groups. As a procercoid, gymnosomic (acystic) larvae with a bothriate type of the scolex are considered, whereas gymnosomic (acystic) metacestodes with an acetabulate type of the scolex, i.e. those of proteocephalideans and some cyclophyllideans, were described as cercoscoleces (Jarecka, 1975).

The terminology proposed by Jarecka (1975) seems to be reasonable and easy to apply in *Proteocephalus* metacestodes. However, if Jarecka's definition of a cercoscolex is strictly applied, then metacestodes of caryophyllidean tapeworms, which have no bothriate type of the scolex and possess a fully formed scolex morphologically similar to that of adult worms (Scholz, 1991b, 1993b), should be cercoscoleces as well and not procercoids as suggested by Jarecka (1975; see Wardle & McLeod, 1952; Mackiewicz, 1972; Scholz, 1991b, 1993b). In addition, metacestodes of some proteocephalidean tapeworms, including some *Proteocephalus* taxa (Wagner, 1917; Hunter, 1928, 1929; Freeman, 1973; Scholz, 1993a), do not possess a cercomer, i.e. they are acaudate. For these larvae, the term 'cercoscolex' therefore is inappropriate.

In the present review, the term 'procercoid' is used because it has been most widely accepted in the literature whereas the newly proposed terminology has not. Although there are distinct differences between the morphology of metacestodes in different orders from planktonic copepods, as stressed by Freeman (1973), it appears to be appropriate to regard an acystic metacestode from the first intermediate host as a 'procercoid' rather than a 'plerocercoid' or 'cercoscolex'. Marcogliese (1995) stated that 'the procercoid stage is typically associated with zooplankton' but Jarecka (1975) also considered procercoids as caryophyllidean metacestodes developing in tubificids (Oligochaeta); this terminology has also been followed by Scholz (1991b, 1993b).

Morphogenesis of procercoids

Procercoid morphogenesis within the intermediate host is similar in all species hitherto studied (Wagner, 1917; Kuczkowski, 1925; Wootten, 1974; Priemer, 1980, 1987; Anikieva *et al*., 1983; Morandi & Ponton, 1989; Scholz, 1991a, 1993a; Scholz *et al*., 1997). The development of *P. cernuae* within *Cyclops strenuus* at 20–22°C is briefly described (figs 2–7), with remarks on other species.

Within the body cavity, i.e. in the parenteral site, the oncosphere quickly grows due to cellular proliferation (Freeman, 1973) and it metamorphoses into the developing metacestode. However, no precise data exist on the process of metamorphosis of the oncosphere into the metacestode, i.e. when resorption of oncospheral structure, if it occurs, is completed (Freeman, 1973). The metacestode becomes elongate 4–6 days post infection (DPI, fig. 4), with one end more actively moving. On the opposite side, a small protuberance, ultimately becoming detached from the body and representing the primordium of a cercomer, appears 5–8 DPI (fig. 5). The cercomer is formed 7–9 DPI (fig. 6) as a small spherical appendix connected to the body by a narrow stem. The cercomer detaches from the body after 1–3 days (Wootten, 1974; Rusinek, 1989; Scholz *et al*., 1997) or persists for three weeks (Priemer, 1980). A detached cercomer can remain viable within the body cavity of a copepod for as long as 60 days (Jarecka & Doby, 1965).

A cercomer has not been observed in *P. filicollis* and *P. torulosus* metacestodes (Meggitt, 1914; Wagner, 1917; Scholz, 1993a) and in North American species *P. ambloplitis* (Leidy, 1887) and *P. pinguis* La Rue, 1911 (Hunter, 1928, 1929). As discussed by Scholz (1993a), the absence of a cercomer in the above mentioned taxa should be confirmed because it can persist for only a limited time of the development within the copepod intermediate host. The presence/absence of the cercomer has important phylogenetic consequences according to Freeman (1973), because he proposed that two main lineages of proteocephalideans and cyclophyllideans evolved from primitive proteocephalideans. Members of one stem (with taeniids as the most derived group) have acaudate metacestodes, those of the second stem, leading to hymenolepidids and anoplocephalids (Freeman, 1973, fig. 11), have caudate metacestodes, i.e. with a cercomer.

The cercomer of *P. exiguus* and *P. neglectus* metacestodes (both taxa considered synonyms of *P. longicollis* by Scholz & Hanzelová, 1998) was described as containing embryonic hooks (Priemer, 1980, 1987). However, embryonic hooks are normally located within the body, most often near its lateral margins in procercoids of the same species (Prouza, 1978; Scholz, 1991a) and those of other *Proteocephalus* taxa (Kuczkowski, 1925; Jarecka & Doby, 1965; Doby & Jarecka, 1966; Wootten, 1974; Scholz *et al*., 1997; figs 5–7). The location of hooks within the cercomer is apparently exceptional (Doby & Jarecka, 1966). In this extracercomeral location of embryonic hooks, the procercoids of *Proteocephalus* species differ from those of most pseudophyllidean tapeworms, in that the cercomer of which contains embryonic hooks (see, e.g. Wardle & McLeod, 1952; Kuperman, 1973; Dubinina, 1980). However, the extracercomeral position of embryonic hooks in *Proteocephalus* metacestodes is not unique among cestodes (Freeman, 1973). Notwithstanding the final position of embryonic hooks in a metacestode, it is suggested that they have no further role in the subsequent development of the cestode (Freeman, 1973).

In some cestodes, a distinct cavity, the 'primitive lacuna', develops whereas other metacestodes grow as a compact mass of cells (Freeman, 1973). Although Kuczkowski (1925) reported the presence of a cavity or 'lacuna primitiva', it seems that in *Proteocephalus* a cavity normally does not develop and metacestodes are acystic and gymnosomic (Freeman, 1973; Jarecka, 1975).

Within 7–8 days, the primordium of an apical sucker appears in *P. cernuae* procercoid slightly before or simultaneously with the primordium of the lateral suckers (fig 5). A similar phenomenon has been observed in *P. macrocephalus* and *P. exiguus* (= *P. longicollis*), and in other proteocephalideans (Befus & Freeman, 1973b; Scholz, 1991a; Scholz *et al*., 1997). Although the development of the scolex may vary considerably, the appearance of a single structure at the extreme tip is often the first sign of scolex differentiation during the exogenous development of acystic metacestodes (Freeman, 1973). Suckers develop quickly in *Proteocephalus* procercoids, being well formed 9–10 DPI in *P. cernuae*. As a rule in metacestodes of other tapeworm groups, the cercomer is recognizable before scolex differentiation (Freeman, 1973).

Calcareous corpuscles of irregular shape and various size first appear 7–8 DPI; their number increases rapidly reaching up to 150–200 in infective procercoids (fig. 7). Although calcareous corpuscles are typical features of metacestodes and may persist in juvenile tapeworms in the definitive host, their function is still unknown (Smyth & McManus, 1989). It is assumed that they play an important role in the metabolism of early developing intestinal worms and they buffer anaerobically produced acids and gastric hydrochloric acid (Smyth & McManus, 1989). The excretory system is established by 8–9 DPI and fully developed *P. cernuae* procercoids are formed at 12 DPI at 20–22°C (fig. 7). Regarding the longevity of procercoids within the intermediate host, some larvae are able to survive until the death of copepods, at least 2–2.5 months at 17–20°C (Jarecka & Doby, 1965; Priemer, 1987).

Morphology of procercoids

Fully formed (infective) procercoids are elongate and highly mobile. The shape and size of procercoids vary considerably due to their high motility and there is also much individual variation in size (Scholz, 1991a). The size of procercoids is influenced by the species and stage of intermediate host and the intensity of infection (Anikieva *et al*., 1983; Morandi & Ponton, 1989; Sysoev *et al*., 1994). High individual and intraspecific variability exists in the size of fully developed procercoids of *Proteocephalus* species, with the length ranging from 140 to 730 μm and maximum width between 50 and 150 μm (see references in table 2). However, metrical differences between

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individual species should be confirmed in larger material. In addition, some procercoids studied by Sysoev *et al.* (1994), e.g. those of *P. neglectus* (= *P. longicollis*) are apparently contracted, probably due to fixation with cold fixative (Scholz *et al.*, 1998a), which casts doubts upon the reliability of species-specific distinguishing characters.

The procercoid possesses a well-developed anterior part (scolex) with four muscular suckers. Although the scolex does not reach the ultimate size of that of the adult worm, its morphology generally does not differ from that of tapeworms from the definitive host. The procercoid of *P. osculatus* has a well-developed, functional apical sucker with a deep cavity (fig. 12). In other species (*P. cernuae*, *P. filicollis*, *P. longicollis*, *P. macrocephalus*, *P. percae*, *P. thymalli*, *Proteocephalus* sp. from *Coregonus*), the procercoid possesses just a vestigial, but distinct apical sucker, with its morphology similar to that in the adult (Kuczkowski, 1925; Wagner, 1953, Doby & Jarecka, 1966; Wootten, 1974; Priemer, 1980, 1987; Rusinek, 1989; Scholz, 1991a; Scholz *et al.*, 1997, 1998a; Scholz & Hanzelová, 1998; figs 12–14). The procercoids of *P. torulosus*, similar to adult worms of this species (Scholz *et al.*, 1998a; Scholz & Hanzelová, 1998), possess no apical sucker but numerous glandular cells concentrated in the apical part of the scolex (Wagner, 1917; Scholz, 1993a; fig. 10). *Proteocephalus* metacestodes resemble those of the order Caryophyllidea in possessing a scolex already developed within the intermediate host, but differ from the Pseudophyllidea, the scolex of which is incomplete within the copepod intermediate host but develops further either in the second intermediate host if present or in the definitive host (Freeman, 1973).

The procercoid body is covered with well-developed microtriches (Freeman, 1964; Priemer & Goltz, 1986; Priemer, 1987; Scholz, 1991a, 1993a; Sysoev *et al.*, 1994; Scholz *et al.*, 1997). Sysoev *et al.* (1994) found slight differences in the density of microtriches between procercoids of four taxa studied. The excretory system of *Proteocephalus* metacestodes, first described by Wagner (1917), consists of flame cells, secondary canals and two pairs of main collecting ducts united posteriorly and opening by ventral ducts into an elongate, thick-walled excretory bladder (Wagner, 1917; Freeman, 1964, 1973; figs 6, 12). In the anterior part of the body, the main ducts divide into secondary canals forming a dense network mainly around the lateral suckers (Wagner, 1917; Jarecka & Doby, 1965; Doby & Jarecka, 1966; Priemer, 1980, 1987) corresponding in its appearance to that present in adult worms (Scholz *et al.*, 1998a).

The procercoid body contains numerous calcareous corpuscles of variable shape, measuring 4–14 μm in length (Wagner, 1917; Kuczkowski, 1925; Jarecka & Doby, 1965; Scholz *et al.*, 1997); the corpuscles persist in the body of juvenile tapeworms within the definitive hosts but their number rapidly decreases (Doby & Jarecka, 1966; Scholz, 1991a).

A uniform morphology of *Proteocephalus* procercoids makes it difficult to identify them specifically (Anikieva *et al.*, 1983; Rusinek & Pronin, 1991; Kennedy *et al.*, 1992). However, Sysoev *et al.* (1994) found differences between the procercoids of four *Proteocephalus* species, i.e. *P. ambiguus*, *P. exiguus*, *P. percae* and *P. torulosus*, in the shape of the body and scolex, in the body size and relative position of suckers. The morphology of the excretory system, size of embryonic hooks and the motion of larvae liberated from hosts into water can also be used to identify procercoids from naturally infected copepods (Doby & Jarecka, 1966; A. Sysoev, personal communication).

As mentioned above, scoleces of procercoids are identical in their overall appearance to those in adults (Andersen, 1979; Scholz *et al.*, 1998a), which makes it possible to specifically identify metacestodes of some taxa such as *P. osculatus* or *P. torulosus*.

No primary cavity develops within the body of *Proteocephalus* procercoids during their formation. Therefore, this type of development is primitive according to the classification of Freeman (1973) and corresponds to that typical of other 'lower' cestode orders, such as the caryophyllideans and pseudophyllideans.

Rate of development

The rate of development of procercoids can be influenced by many factors, including the species of copepods, their developmental stages, intensity of infection and species of parasite (Wootten, 1974; Rusinek & Pronin, 1991). However, the crucial factor controlling the rate of development is water temperature and the higher the temperature the faster the development of procercoids (Hunter, 1928; Wagner, 1954; Jarecka, 1960; Freeman, 1964; Fischer, 1968; Willemse, 1968; Priemer, 1980, 1987; Anikieva, 1982; Anikieva *et al.*, 1983; Scholz, 1991a). The rate of the development of *P. neglectus* (= *P. longicollis*) in *Cyclops strenuus* is clearly temperature dependent, as fully developed procercoids were observed 59–65 DPI at 6°C, 24–28 DPI at 10°C, 18–21 DPI at 15°C, and 8 DPI at 20–22°C (Scholz, 1991a).

A temperature of about 20°C is optimal for the development of *P. cernuae*, *P. longicollis*, *P. macrocephalus*, *P. osculatus* and *P. torulosus* (Albetova, 1975; Anikieva, 1982; Anikieva *et al.*, 1983; Scholz, 1991a, 1993a; Scholz *et al.*, 1997; present data). At higher temperatures, a further acceleration of development does not occur, but it is unclear whether this is due to high copepod mortality, inability of larvae to grow and develop at this temperature or other factors. A temperature range of 26–28°C appears to be the maximum for complete development of *P. longicollis* (syns *P. exiguus* and *P. neglectus*), a parasite of salmonoid fishes (Albetova, 1975; Anikieva, 1982; Anikieva *et al.*, 1983). On the contrary, development is prolonged with decreasing temperature and inhibited at 4–6°C (Wootten, 1974; Scholz, 1991a). In contrast to other species, the procercoids of *P. percae* develop only in copepods kept at 14°C whereas larvae do not complete their development in copepods maintained at 20°C (Wootten, 1974). Since perch, the definitive host of *P. percae*, are less likely to prefer cold water than salmonid fish, the biological significance of this low-temperature related development is difficult to explain. Further work is needed, therefore, to confirm the observations of Wootten (1974). However, Freeman (1964) reported optimal growth of metacestodes of *P. parallacticus* MacLulich, 1943, a parasite of cold-water salmonid fish, *Salvelinus namaycush*, at 16°C, suggesting that rate of

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development is also influenced by the geographical origin of the parasite.

Localization of larvae

Larvae are freely moving within the body cavity of copepods but they are located most frequently in the first segments of the cephalothorax. At the beginning of development, larvae can also be located in the antennulae (Prouza, 1978; Priemer, 1980; Scholz, 1993a) followed by exclusive development within the cephalothoracic or abdominal segments, apparently due to space limitation in the antennulae. Prouza (1978) reported the migration of larvae from the antenulae to the body cavity after 3 days of development but Priemer (1980) found *P. neglectus* (= *P. longicollis*) metacestodes in the antennulae of *C. strenuus* as late as 13 days after infection at 9°C. Only insignificant changes in the site preference of *P. neglectus* metacestodes within the body cavity of copepods were observed during their development (Scholz, 1991a).

Occurrence in intermediate hosts

The infection level of procercoids in naturally and experimentally infected intermediate hosts differs considerably, with values of prevalence and intensity of infection being much higher in experimental infections. As many as 32 developing larvae were observed in experimentally infected copepods (Wootten, 1974; Rusinek, 1989) although it is exceptional to find more than one *Proteocephalus* larva in a naturally infected intermediate host (Hopkins, 1959; Hanzelová *et al*., 1989, 1990).

Values of prevalence reach up to 100% in experimentally infected copepods but in natural populations of conspecific copepods the prevalence values are considerably lower. Generally, the prevalence of infection of zooplankton with *Proteocephalus* procercoids (and other metacestodes) is extremely low, ranging between 0.001 and 1% (Doby & Jarecka, 1966; Markevich & Kuperman, 1982; Sysoev, 1983, 1985; Hanzelová *et al*., 1990; Marcogliese, 1995). Although the prevalence values of copepod infection under natural conditions are very low, parasites can accumulate within fish hosts due to an intensive consumption of zooplankton by fishes (Marcogliese, 1995). The absolute number of *Proteocephalus* procercoids in naturally infected copepods can reach 853–1193 specimens per m^3 with mean values 3–178 specimens per m^3 (Sysoev, 1987b; Hanzelová *et al*., 1989; Rusinek *et al*., 1996).

The prevalence of infection markedly fluctuates under natural conditions, being dependent on factors such as the species of copepod infected and their developmental stages, seasonality and locality (Anikieva, 1982; Markevich & Kuperman, 1982; Anikieva *et al*., 1983; Rusinek & Pronin, 1991; Rusinek *et al*., 1996). However, only limited data exist on the spatial and temporary distribution of copepod infections. Seasonal patterns in the occurrence of *Proteocephalus* metacestodes in naturally infected copepods depend on the time of egg release, which is controlled mainly by water temperature (see below). It has been observed that intermediate hosts are infected almost exclusively in the summer or early autumn (Hanzelová *et al*., 1990), with maximum prevalence values of *P. ambiguus* and *P. neglectus* (= *P. longicollis*) infections, respectively, being observed in the middle of summer (Sysoev, 1985, 1987a; Hanzelová *et al*., 1989, 1990; Hanzelová, 1992; Sysoev *et al*., 1992). It is also assumed that *Proteocephalus* procercoids survive diapause in the copepods (Morandi & Ponton, 1989).

The role of individual copepod species changes during the year with a gradual substitution of copepod species more susceptible to infection by less susceptible ones (Sysoev *et al*., 1988; Hanzelová, 1992). This appears to be related to seasonal changes in the occurrence of potential intermediate hosts and their availability: more susceptible copepods may be absent when cestode eggs are released into water and thus less susceptible species of copepods may play an important role as intermediate hosts.

Definitive host

Range of definitive hosts

Host specificity of most *Proteocephalus* species from fishes has been considered to be quite narrow but there are marked differences in the range of fish hosts infected by individual species (see Freze, 1965a; Priemer, 1982; Chubb *et al*., 1987; Dubinina, 1987; Scholz & Hanzelová, 1998). Some species are specific to one host genus or one species of definitive host, e.g. *P. ambiguus* to the nine-spined stickleback (*Pungitius pungitius*), *P. filicollis* to the three-spined stickleback (*Gasterosteus aculeatus*), *P. macrocephalus* to eels (*Anguilla* spp.), *P. osculatus* to wels (*Silurus glanis*), and *P. thymalli* to graylings (*Thymallus* spp.). Other taxa, however, occur in a variety of fish species of one or more families: *P. gobiorum* in gobiids (Gobiidae), *P. longicollis* in salmonid fishes (Coregonidae, Salmonidae), *P. percae* in percids (Percidae), *P. tetrastomus* in smelt (Osmeridae), and *P. torulosus* in cypriniform fishes (Cyprinidae and Cobitidae) (Scholz & Hanzelová, 1998).

A relatively narrow host specificity of *Proteocephalus* species has also been demonstrated experimentally by cross infections (Doby & Jarecka, 1966; Willemse, 1967, 1968, 1969; Priemer, 1980; Anikieva *et al*., 1983; Rusinek, 1987a). It appears that some species are able to adapt to unsuitable host species under particular ecological conditions. Such a shift by the definitive host has been documented in *P. neglectus* and *P. exiguus* (both species synonymized with *P. longicollis* by Scholz & Hanzelová, 1998), originally occurring in brown and rainbow trout (*Salmo trutta* m. *fario* and *Oncorhynchus mykiss*) in small lakes in Latvia and Slovakia, respectively, but currently using unusual fish hosts, such as *Cobitis taenia* and perch (*Perca fluviatilis*), respectively (Shulman, 1954; Hanzelová *et al*., 1996).

Infection of the definitive host

Definitive hosts become infected after ingestion of copepods harbouring procercoids. Anikieva *et al*. (1983) assumed, without providing any detailed data to support it, that the larvae continue to develop within the digestive tract of the fish host, with subsequent formation of attachment organs, nervous and excretory systems and musculature. The growth of these organs occurs within the definitive host but considerable changes in scolex morphology or structure of the osmoregulatory

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system do not occur (figs 6, 10, 12–14). As previously mentioned, the morphology of the scolex of procercoids closely resembles that in the adult worms (Scholz, 1991a, 1993a; Scholz *et al.*, 1997, 1998a) and its morphology plays a crucial role in the process of establishment of tapeworms within the definitive host (Smyth & McManus, 1989).

Anikieva *et al.* (1983) observed that the scolex of living *Proteocephalus* larvae becomes invaginated immediately after ingestion by the definitive host and this is related to the parasite being protected against unfavourable conditions such as the high acidity within the stomach of the fish definitive host. Procercoids become more active and the scolex evaginates in alkaline conditions (Willemse, 1969), so the role of chemical stimuli in the process of evagination requires further investigation.

The invagination of the scolex has also been observed in procercoids in experimentally infected copepods and in larvae artificially isolated from the body cavity of intermediate hosts and maintained in water or saline (Freman, 1964; Jarecka & Doby, 1965; Prouza, 1978; Priemer, 1980; Sysoev *et al.*, 1994). Metacestodes are readily affected by changes in the osmotic pressure of the medium but they remain mobile within the copepod haemocoel. Freeman (1964) occasionally observed invagination of the scolex of metacestodes in saline or methylene blue in saline but never *in situ*, and thus experimental studies of this phenomenon are needed.

Only a very small proportion of juvenile tapeworms is able to establish within the gut of the definitive host (Meggitt, 1914; Jarecka & Doby, 1965; Doby & Jarecka, 1966; Willemse, 1968, 1969; Malakhova & Anikieva, 1976; Prouza, 1978; Priemer, 1980; Rintamäki & Valtonen, 1988; Morandi & Ponton, 1989; Hanzelová *et al.*, 1990; Scholz, 1991a, 1993a; Kennedy *et al.*, 1992). Anikieva *et al.* (1983) suggested that some time ('physiological maturation') after complete formation of internal organs is necessary for procercoids to become fully infective. Intraspecific competition between young worms within the pyloric caeca or in the intestine of infected fish is likely to occur but the very low establishment rate requires additional studies.

Dynamics of infection

Very little is known about the dynamics of infection of fish hosts with *Proteocephalus* procercoids via zooplankton (Marcogliese, 1995). Hanzelová *et al.* (1989) estimated 67% of *P. neglectus* (= *P. longicollis*) metacestodes to be transmitted to the definitive host but other information is lacking.

Development in the definitive host

Some proteocephalideans show extensive periods of growth before proglottidation begins (Freeman, 1964, 1973; Doby & Jarecka, 1966; Befus & Freeman, 1973b; Prouza, 1978; Priemer 1980, 1987; Scholz, 1991a) but only limited information is available on the development of *Proteocephalus* species in the definitive host. In addition, different rates of development and length of prepatent period have been reported. A short developmental time was reported by Albetova (1975) who found 'mature' *P. exiguus* (syn. of *P. longicollis*) cestodes in experimentally infected fry of *Coregonus peled*, maintained at 12–21°C, as early as after 1.5–2 months. However, Albetova (1975) did not clearly state what her term 'mature' means, i.e. whether the worms were mature, without eggs but with sperms in sperm ducts, subgravid, i.e. with unripe eggs not containing hooked oncospheres, or gravid, i.e. with ripe eggs containing formed hexacanths. Therefore, the time reported by Albetova (1975) does not necessarily represent the complete prepatent period if only mature or subgravid worms were found.

Rusinek (1989) found juvenile, unsegmented *P. thymalli* in experimentally infected grayling fry 30 DPI and immature, segmented worms 50 DPI. Out of 39 tapeworms found in fish 74 DPI, only four were mature ('with formed genital complexes'); others were immature or even unsegmented (Rusinek, 1989). As in the case of Albetova (1975), the description of maturity by Rusinek (1989) was unclear.

On the basis of field observations, Hanzelová *et al.* (1990) estimated the prepatent period of *P. exiguus* (= *P. longicollis*) from rainbow trout to last only a few weeks. Pronina & Pronin (1988) recovered gravid *P. exiguus* (= *P. longicollis*) tapeworms in fry of *Coregonus autumnalis* and *C. lavaretus* 2–2.5 months after feeding them with small gobiid fish, harbouring juvenile *Proteocephalus* cestodes about 1 mm long and thus representing paratenic hosts of the tapeworm (see Rusinek, 1987b; Rusinek & Pronin, 1991); the experiments were performed at 10–12°C.

Results of other authors indicate longer prepatent times. Malakhova & Anikieva (1976) reported 4 months to be the prepatent period of *P. exiguus* (= *P. longicollis*) in the vendace, *Coregonus albula*, under natural conditions in Karelia, Russia. A similar prepatent time was reported by Wagner (1954), who found gravid tapeworms of *P. tumidocollis* Wagner, 1953 (syn. of *P. longicollis* – Hanzelová & Scholz, 1993; Scholz & Hanzelová, 1998) 3.5 months post-infection (106 DPI) at 18°C, and Fischer (1968), who recovered gravid tapeworms of *P. fluviatilis* Bangham, 1934 four months (118 DPI) after challenging experimental fish. Very slow growth and development of *P. exiguus* and *P. neglectus* (syns of *P. longicollis*) in experimentally infected rainbow trout and *P. macrocephalus* in eel have also been described by other authors (Doby & Jarecka, 1966; Prouza, 1978; Priemer, 1980, 1987; Scholz, 1991a).

Maturation dynamics

As in the case of the development of procercoids in copepods, the growth and maturation of tapeworms in the fish definitive host are controlled mainly by water temperature. The influence of host hormones, as observed in some pseudophyllideans, such as *Triaenophorus* spp. (Smyth & McManus, 1989), may also play some role but no data are available.

Although it is possible that one cycle may be completed in 1.5–2 months at water temperatures of 15–20°C, field

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data suggest that species of *Proteocephalus* have a one-year life span (i.e. the life cycle in total, including all developmental stages) with a pronounced seasonality in their maturation (Chubb, 1982). The recruitment of new cestode generations takes place mainly in the summer or autumn. The tapeworms overwinter in fish and they start to grow rapidly and mature after the water temperature increases in the spring. Eggs are laid in late spring and summer. Such seasonal patterns in occurrence and maturation have been observed in several taxa of *Proteocephalus*, e.g. *P. cernuae*, *P. exiguus* (= *P. longicollis*), *P. filicollis*, *P. osculatus*, *P. percae*, *P. torulosus* (Chubb, 1982; Scholz, 1986, 1989b; Scholz & Moravec, 1994).

It should, however, be emphasized that this general pattern is modified in each species, being dependent on its geographical position and particular ecological conditions, as the same species of cestode may show different patterns of maturation in distinct latitudes (see, e.g. Hopkins, 1959; Willemse, 1968; Chubb, 1982; Scholz, 1986, 1989b; Morandi & Ponton, 1989; Nie & Kennedy, 1991; Rusinek & Pronin, 1991; Scholz & Moravec, 1994).

Hopkins (1959) studied the maturation dynamics of *P. filicollis* from the three-spined stickleback (*Gasterosteus aculeatus*). On the basis of values of intensity of infection, he estimated that only about 0.5% of tapeworms which establish within the definitive host become gravid.

With regard to the recruitment of new generations and the occurrence of procercoids in intermediate hosts, it has been shown that there are neither temporal nor quantitative correlations between the number of cestode larvae in the water body and the abundance of juvenile tapeworms in fish (Sysoev *et al.*, 1992).

Localization within the definitive host

As a rule, adult *Proteocephalus* tapeworms are located in the anterior part of the intestine (Hopkins, 1959; Willemse, 1968; Chubb, 1982; Anikieva *et al.*, 1983; Priemer & Goltz, 1986; Scholz, 1986; 1989b, 1991a; Priemer, 1987; Pronina & Pronin, 1988; Scholz & Moravec, 1994). In fishes possessing pyloric appendages, adult tapeworms are attached by their scoleces to the epithelium of these appendages with the strobilae lying within the intestinal lumen.

Other hosts

Invertebrates

Information on the occurrence of *Proteocephalus* larvae in invertebrates other than planktonic crustaceans is limited and previous work includes the occurrence of *Proteocephalus* larvae in alder-fly larvae (Megaloptera) (Vojtková & Koubková, 1990; Kennedy *et al*., 1992; Scholz & Moravec, 1993). Vojtková & Koubková (1990) found unsegmented, actively moving tapeworms without an apical sucker (? *P. torulosus*) in the intestine of 14% of *Sialis* sp. larvae in Slovakia. Scholz & Moravec (1993) recovered *Proteocephalus* larvae (almost certainly conspecific with *P. torulosus*) in *S. lutaria* from South Moravia.

Kennedy *et al*. (1992) recorded juvenile *Proteocephalus* tapeworms (most probably belonging to *P. filicollis*) in *S. lutaria* larvae from a river in England. The juvenile *Proteocephalus* were unsegmented but relatively large with a mean length of 2.8 mm (range 0.5–3.7 mm). On the basis of the site of infection (mid-gut), the large size and common occurrence of these tapeworms, Kennedy *et al*. (1992) assumed that alder-fly larvae served neither as intermediate nor paratenic hosts but rather as additional, facultative invertebrate hosts. Since alder-fly larvae are predators, the ingestion of copepods infected with *Proteocephalus* procercoids is highly probable. Successful transmission of nematode larvae from the copepod intermediate host to *Sialis* larvae has been experimentally demonstrated (Moravec & Škoríková, 1998).

However, the actual role of alder-fly larvae and, possibly, of other invertebrates, in the transmission of *Proteocephalus* larvae is still unclear and requires further investigation.

Fish

In contrast to the North American species *P. ambloplitis*, with plerocercoids exhibiting the parenteral location (Cooper, 1915; Hunter, 1928; Hunter & Hunninen, 1934; Fischer & Freeman, 1969, 1973; Eure, 1976), all Palearctic species of the genus *Proteocephalus* have two-host life cycles (Wardle & McLeod, 1952; Freze, 1965a,b; Doby & Jarecka, 1966; Albetova, 1975; Malakhova & Anikieva, 1976; Pronina & Pronin, 1988). Small prey fishes may also play an important role in the transmission of *Proteocephalus* under natural conditions as in the case of *P. exiguus* (= *P. longicollis*) from Baikal Lake (Rusinek, 1987b). Small gobiids, such as *Cottocomephorus grewingki*, heavily infected with juvenile tapeworms, represent an important source of infection for the definitive host, *Coregonus autumnalis* (Rusinek, 1987b; Rusinek & Pronin, 1991).

The importance of small prey fishes as transport or paratenic hosts in the life cycle of *Proteocephalus* is also indicated by the relatively common occurrence of juvenile cestodes in these fishes (Jarecka & Doby, 1965; Willemse, 1969; Chubb, 1982; Anikieva *et al*., 1983; Chubb *et al*., 1987; Andersen & Valtonen, 1990). The *Proteocephalus* tapeworms are unable to grow or develop but they can survive some time in these hosts and thus represent a potential source of infection for predatory fishes and a reservoir of the parasite (Willemse, 1969; Molnár & Murai, 1978; Scholz, 1991a). In this study, an atypical host of South American origin, a *Cichlasoma* sp., was successfully infected with procercoids of *P. cernuae*, a species specific to ruff (*Gymnocephalus* spp. – Scholz & Hanzelová, 1998), after challenging it with infected copepods (fig. 8). The important role of zooplankton feeders, such as perch, in the transmission of pseudophyllidean tapeworms has also been documented (Dupont & Gabrion, 1986; Scholz, 1986, 1997).

The horizontal transmission of both juvenile and mature *Proteocephalus* by predation or cannibalism has been demonstrated experimentally (Willemse, 1967, 1969; Priemer, 1980, 1987). Numerous records of tapeworms in predatory fishes, such as pike (*Esox lucius*), pikeperch (*Stizostedion lucioperca*), coregonids (*Coregonus* spp.), graylings (*Thymallus* spp.), trout (*Salmo trutta* m. *fario*), turbot (*Lota lota*), and eel (*Anguilla anguilla*), apparently representing temporary hosts, indicate that

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this phenomenon is common under natural conditions (Molnár, 1968; Moravec, 1979; Chubb, 1982; Anikieva *et al.*, 1983; Chubb *et al.* 1987; Pronina & Pronin, 1988; Scholz & Hanzelová, 1998). These fishes serve as postcyclic, paradefinitive or accidental hosts only (Odening, 1976).

Phylogenetic considerations and transmission patterns

Palearctic *Proteocephalus* species have primarily two-host cycles (fig. 15, bold lines), with copepods serving as intermediate hosts. As in other aquatic cycles of tapeworms, there is the necessity to exploit the seasonal or periodic availability of aquatic intermediate hosts, with egg release synchronous with high abundance of zooplankton (Mackiewicz, 1988). However, existing data, although scarce, indicate the important role of some invertebrates and vertebrates (coarse fish) as additional, paratenic, hosts of *Proteocephalus* and this, in turn, increases the probability of successful transmission.

On the basis of the spectrum of definitive hosts, Freeman (1973) considered pseudophyllideans to be the best adapted for transferring to the final host, with proteocephalideans next best because they occur in fishes as well as amphibians and reptiles. He also claimed that all species of the Proteocephalidea require an aquatic first host, including species maturing in terrestrial vertebrates. In the latter group, a migratory plerocercoid occurs and its presence, together with some other adaptation(s), makes terrestrial life cycles possible (Freeman, 1973).

There are controversial opinions regarding cestode evolution and the life cycle patterns in precestode ancestors (Joyeux & Baer, 1961; Llewellyn, 1965; Stunkard, 1967; Freeman, 1973; Jarecka, 1975; Mackiewicz, 1988). Nevertheless, a two-host cycle with a direct alternation between parenteral and enteral sites, as in the case of aquatic cestodes, including *Proteocephalus*, is regarded as the most primitive life cycle pattern (Freze, 1965a,b; Freeman, 1973; Jarecka, 1975). With reference to the proteocephalideans, they are considered to be closely related to the Cyclophyllidea (Freeman, 1973; Hoberg *et al.*, 1997). Two main evolutionary stems are assumed to evolve from the primitive proteocephalids: one stem with metacestodes tending to eliminate a cercomer (acaudate metacestodes), the other where development of a cercomer is retained, i.e. the caudate metacestodes (Freeman, 1973). The latter author claimed that there is a correlation between the presence of a distinct cercomer and the subsequent development of a migratory acetabulo-plerocercoid. However, in *Proteocephalus* species considered in this review, both caudate and acaudate (*P. torulosus*) metacestodes are present, which would place them into two major stems, from which recent proteocephalidean and cyclophyllidean tapeworms have evolved. According to Freeman (1973), the genus *Proteocephalus* '... probably holds the key not only to understanding the Proteocephaloidea but to understanding the evolution of the Cyclophyllidea as well.' But, there still remain considerable gaps in our knowledge of metacestode morphogenesis as well as other aspects of the life cycles of these parasites.

Conclusions

The most detailed information exists on the biology of *P. longicollis* (syns. *P. exiguus* and *P. neglectus*), but also in this species many aspects of its life history remain to be studied. There are still gaps in our knowledge of biology of *Proteocephalus* tapeworms parasitizing fishes in the Palearctic Region and further investigations into the life cycles are needed. This is also valid for other proteocephalidean groups, because no data exist on the development of any member of the Monticellidae and most proteocephalid subfamilies, such as Acanthotaeniinae and Sandonellinae (Rego *et al.*, 1998).

It is difficult to list unsolved problems in the biology of *Proteocephalus* tapeworms, which should be addressed in future research, but the following deserve attention, namely the process of egg formation, including fertilization; ultrastructure of eggs and oncosphere, with special attention being paid to the penetration glands; comparative morphology of embryonic hooks; morphogenesis and ultrastructure of the procercoids, in particular those of *P. gobiorum* and *P. tetrastomus*; the dynamics of infection in intermediate and definitive hosts; spatial and temporal dynamics of procercoids in natural populations of copepods; factors influencing the establishment of juvenile tapeworms and their morphogenesis within the definitive host; the length of the prepatent period; the actual role of invertebrates and prey fishes in transmission; and factors resulting in the host specificity of some taxa in the definitive host.

Current phylogenetic analyses of cestode orders (Hoberg *et al.*, 1997; Justine, 1998; Mariaux, 1998) point out the necessity of comparing morphological and molecular data with those related to life cycles to further our understanding of the phylogeny of these parasitic worms (Mariaux, 1996; Hoberg *et al.*, 1997). Knowledge of tapeworm biology is still fairly limited despite the considerable progress being made in the past two to three decades (Freeman, 1973; Jarecka, 1975; Chubb, 1982; Mackiewicz, 1988; Smyth & McManus, 1989; Mariaux, 1996; Hoberg *et al.*, 1997).

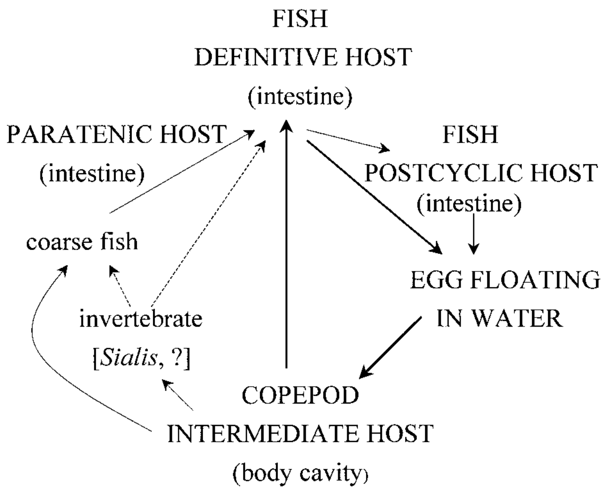

Fig. 15. Flow diagram of the life cycles of Palearctic *Proteocephalus* tapeworms. Dotted line indicates possible routes of transmission.

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