

The Acanthocolpidae (Digenea) of fishes from the north-east Atlantic: the status of *Neophasis* Stafford, 1904 (Digenea) and a study of North Atlantic forms

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Abstract

The genus *Neophasis* is defined. The taxonomic status of the genus is discussed in the light of its life-cycle, hosts and cercarial and adult morphology. It is considered to be closest to the family Acanthocolpidae due to the utilisation of a fish second intermediate host, the form of the cercarial excretory system and, in the adult, the presence of a uterine seminal receptacle and the absence of an external seminal vesicle. The taxonomic value of morphological features are discussed and a key to the north Atlantic species given. The following species are described: *Neophasis oculatus* (Levinsen) from *Myoxocephalus scorpius* off West Greenland (type-material), Norway and Denmark, *Lycodes esmarkii* off NW Scotland and the Faroes, and *L. vahli* off Newfoundland; *N. burti* n. sp. (distinguished from *N. oculatus* by sucker-ratio and testicular configuration) from *Myoxocephalus octodecemspinosus* off Nova Scotia (type-locality) and New Brunswick, also ? immature in *Gadus morhua* from the Gulf of St. Lawrence; *N. anarrhichae* (Nicoll) from *Anarrhichas lupus* in the North Sea and off the Faroes; and *N. pusilla* Stafford from *A. lupus* off 'eastern Canada' (type-material) and Nova Scotia. The only other species in the genus is *N. symmetrorchis* Machida from the NW Pacific Ocean.

Introduction

The genus *Neophasis* Stafford, 1904 includes about five species which are restricted to northern temperate and cold seas. The status of the genus has been unclear since its erection and, therefore, this paper includes an attempt to clarify its relationship with the two families, the Acanthocolpidae and the Lepocreadiidae, with which it has generally been associated. In addition, the species found in the north Atlantic Ocean are redescribed and discussed.

Materials and methods

Specimens collected by the authors were fixed in glacial acetic acid or Berland's fluid. They were stained in Mayer's paracarmin and mounted in Canada balsam. Serial sections were stained in Mayer's haemalum and eosin. Other material was fixed and processed in various ways. The measurements are given in micrometres throughout.

The distribution information is fitted into the framework of the FAO's "Major Fishing Areas" map.

Registration numbers refer to specimens from the following collections:

BM(NH) – The Natural History Museum, London.

USNM – United States National Parasite Collection, Beltsville, Maryland.

NMCP – National Museum of Natural Sciences, Ottawa.

Acanthocolpidae Lühe, 1906

Acanthopsolinae Ward, 1938

Synonym: Neophasiinae Dollfus, 1953

***Neophasis* Stafford, 1904**

Synonym: *Acanthopsolus* Odhner, 1905

Definition

Body small, fusiform to lanceolate. Tegument spinose. Eye-spots normally present. Oral sucker with wide aperture. Prepharynx distinct. Pharynx large. Oesophagus short. Caeca terminate blindly [?], close to posterior extremity. Excretory pore terminal; vesicle I-shaped, saccular, reaches to testes. Testes two; usually oblique but occasionally tandem or symmetrical; large; adjacent. Cirrus-sac large, claviform. Seminal vesicle internal; oval to bipartite. Pars prostatica long; lined with filaments and blebs. Ejaculatory duct short. Male duct projects into genital atrium as small permanent papilla. Genital pore median; adjacent to anterior margin of ventral sucker. Ovary suboval; dextral; anterior to and usually contiguous with posterior testis; antero-lateral to anterior testis. Mehlis' gland dorsal to uterus. Laurer's canal present. Seminal receptacle uterine. Uterus between gonads and ventral sucker. Metraterm muscular, wide; ensheathed in gland-cells; lined with irregular filaments. Eggs large; tanned; operculate; without spines or filaments. Vitelline follicles large; closely packed; fields reach from posterior extremity into posterior forebody. Parthenitae in prosobranch gastropods. Cercariae develop in rediae. Cercariae oculate; tail straight. Second intermediate host not always present; where present usually teleost, occasionally bivalves. Definitive hosts marine teleosts.

Type-species. *Neophasis pusilla* Stafford, 1904 (by original designation).

Discussion

The life-cycle, hosts and cercarial and adult morphology are discussed in relation to these features in the families Acanthocolpidae and Lepocreadiidae.

Life-cycle and hosts

Two species of *Neophasis* have known life-cycles and some information is available on unidentified species. *N. oculatus* (Levinsen, 1881) is considered to have the more primitive type of life-cycle, from which the life-cycle of *N. anarrhichae* (Nicoll, 1909) has been derived (Køie, 1985a; Bray, 1987). *N. oculatus* utilises the prosobranch gastropod *Cryptonatica* [or *Tectonatica*] *clausa* as a first intermediate host in which rediae develop. These give rise to tailed cercariae which become free-living and encyst in bivalve molluscs (Chubrik, 1966) and in teleost fishes (Levinsen, 1881; Polyansky, 1955; Zhukov, 1963). The definitive teleost host presumably gains the parasite by ingestion of these hosts, often apparently involving cannibalism. Levinsen (1881) observed that the metacercariae were encysted in the skin of small *Myoxocephalus scorpius*, the same host species as harboured the adult. Unidentified *Neophasis* rediae and cercariae were reported by Marasaev (1984) from *Neptunea* spp. and *C. clausa* from the White Sea. Appy & Burt (1982) found encysted metacercariae of an un-named *Neophasis* in a fish preyed on by cod. The derived life-cycle of *N. anarrhichae*, on the other hand, involves invasion of the whelk *Buccinum undatum*, in the digestive gland and gonad of which rediae develop. Caudate cercariae develop within the rediae, but 'the tail is . . . shed during the stay inside the redia. The fully developed tailless cercaria may be considered as a metacercaria although it does not encyst' (Køie, 1973a). When the redia is full of mature, tail-less cercariae or metacercariae, it stops growing and the (meta)cercariae, which are no longer being produced, remain within it. Zelikman (1966) thought that *Cercaria neptuni* Lebour,

1911 [*sic*, presumably *C. neptuneae*] from *Buccinum groenlandicum* in the White Sea was very similar to the cercaria of *N. anarrichae*, but Wolfgang (1955) was of the opinion that it most closely resembled *Stephanostomum baccatum*. These conflicting views mean that *C. neptuneae* can give little useful information for this discussion. The final hosts, carnivorous teleosts of the genus *Anarrichas*, commonly prey on *Buccinum* in parts of their range (Bray, 1987), and gain their parasites directly by ingestion of the joint first and second intermediate host. Other fish, such as plaice *Pleuronectes platessa* and dab *Limanda limanda* preying on *Buccinum undatum*, acquire this parasite, but it does not mature and is lost in a few days (Køie, 1983).

Several acanthocolpid life-cycles are known, all of members of the genus *Stephanostomum* and summarised by Yamaguti (1975) and Køie (1978), although a little information is available on the second intermediate hosts of *Acanthocolpus* Lühe, 1906 and *Stephanostomoides* Mamaev & Oshmarin, 1966 (Mamaev & Oshmarin, 1966). The first intermediate hosts are prosobranch gastropods in which rediae develop. The caudate cercariae are shed and penetrate a large number of teleost species, where they encyst in the flesh. The definitive hosts are piscivorous teleosts which acquire the worms by ingestion of the second intermediate hosts.

The lepopocreadiid life-cycle was summarised by Bray (1988). They develop as rediae in gastropods, the cercariae encyst in polychaetes, gastropods, bivalves and echinoids, and unencysted metacercariae occur in cnidarians, ctenophores, gastropods, bivalves and possibly fishes. The final hosts are teleosts.

The primitive life-cycle of *Neophasis* is rather similar to that of both the Lepopocreadiidae and the Acanthocolpidae, but is more similar to the latter in that in *Neophasis* the second intermediate host is usually a fish. Encysted metacercariae in fish occur in the enenterids *Stegodexamene* Macfarlane, 1951 and *Tetracerasta* Watson, 1984, thought by many to be lepopocreadiids, and without doubt closely related to that family. Unencysted immature forms of the lepopocreadiid *Opechona bacillaris*

(Molin, 1859) occur in the gut of larval and adult teleosts (Bray & Gibson, 1990), but it is debatable whether these are metacercariae and whether they are an obligatory part of the life-cycle.

Cercariae

There are discrepancies in the descriptions of the cercarial morphology in all the groups under discussion.

The primitive *Neophasis* cercaria is oculate with a straight, undivided tail. No stylet is present and the excretory vesicle is subglobular in the cercarial body. The excretory duct in the tail reaches towards the posterior end of the tail in *N. oculatus*, according to Chubrik's (1966) figure. In *Neophasis* sp., according to Marasaev (1984), the excretory duct reaches about one third of the length of the tail and divides to give two lateral genital pores about one third of the distance along the tail from the body. The vesicle is saccular oval in the body, and is apparently fed by a mesostomate excretory system (see figures in Chubrik, 1966; Marasaev, 1984). In *N. anarrichae* the excretory vesicle in the body is bilobed, according to Lebour (1910). *N. oculatus* has penetration glands, which are lacking in *N. anarrichae*, along with other features associated with transmission through a second intermediate host, such as anterior sensory structures and cystogenous glands (Køie, 1973a).

Lepopocreadiid cercariae are usually trichocercous, occasionally microcercous (Køie, 1985b) and usually oculate, but lack a stylet. The excretory system is I-shaped to saccular in the cercarial body, but the system, which is usually described as stenostomate, does not enter the tail (Peters, 1961).

Four life-cycles of the acanthocolpid genus *Stephanostomum* have been reported in detail, and although the cycles revealed are uniform (see above) the morphology of the cercariae as described by these authors shows several conflicting features. Martin (1939) on *Stephanostomum tenue* (Linton, 1898) [Peters, 1961, reported in detail on the excretory system of what is probably this worm], Wolfgang (1955) on *S. baccatum* (Nicoll, 1907), Stunkard (1961) on *S. dentatum* (Linton, 1900) and Køie (1978) on *S. caducum* (Looss,

1901) [probably a synonym of *S. pristis* (Deslongchamps, 1824) according to Kjøie, 1984] are the authors involved. Stunkard (1961) noted that the differences reported were 'far greater than ordinarily encountered between species of a single genus', and he doubted that Wolfgang's cercaria was correctly designated. He made a detailed critique of Wolfgang's results, but MacKenzie & Liversidge (1975) confirmed the results as far as the life-cycle pattern is concerned. They did not, however, verify the questionable morphological information.

Two authors (Martin and Kjøie) reported a stylet, two (Wolfgang and Stunkard) failed to find one. All authors reported the cercaria to be oculate with a straight tail, usually unornamented, but Stunkard described the tail as lophocercous, having lateral fins 'the crests of which simulate setae', and postero-median ventral and dorsal fins. The mature cercariae usually have enlarged circum-oral spines as are found in the adult, but Wolfgang did not find them. The excretory system is particularly difficult to pin down. According to Kjøie, the excretory system does not enter the tail, which is hollow. Martin does not mention the excretory system in the tail, but Peters described the development of paired excretory ducts in the anterior part of the tail which fuse in the median line, but retain separate lateral pores. Wolfgang described an excretory duct which opens at a pore on the terminal tip of the tail, a feature which was doubted by Stunkard (1961) and Yamaguti (1975). Stunkard described the excretory duct in the young cercariae as passing along about a quarter of the tail where it divides and forms two lateral pores. Later the ducts regress and open only at pores at the junction of the body and the tail. The only real agreement as to the caudal excretory system is, therefore, between Peters and Stunkard, who report lateral pores on the tail, although this feature is apparently lost as the cercaria develops. Even the excretory system within the body is confused. Martin described and figured a Y-shaped vesicle and Wolfgang described the excretory vesicle as 'large, globular, and heavy walled'. Stunkard described the excretory vesicle as V-shaped when filled, Y-shaped when empty and

figured a rather angular saccular vesicle. Kjøie described the vesicle as 'slightly heart-shaped'. Martin, Stunkard, Peters and Kjøie all showed the excretory system to be stenostomate, but Wolfgang illustrated it as mesostomate in the cercaria, and, as pointed out by Stunkard (1961), stenostomate in the metacercaria.

Because of the discrepancies between the descriptions of the cercariae, it is not straightforward to assess the relationships of *Neophasis* cercariae to those of the two families in question. The entry of the excretory vesicle into the tail, and the report of paired lateral excretory pores (by Marasaev, 1984), suggests a relationship with the Acanthocolpidae. The mesostomate excretory system is unlike either of the families, if Stunkard is right about doubting Wolfgang's report on the cercaria. The lack of a stylet is not significant, and neither is the saccular excretory vesicle. We must await more work on the cercariae of *Neophasis* and the Acanthocolpidae before we can make much more than vague suggestions of similarities.

Adult morphology

The general adult morphology is similar in all of the forms under discussion. The two testes, pregonadal uterus, follicular vitellarium and well-developed cirrus-sac are shared along with many other features. Also shared is the tegumentary spination. Members of the type-genus of the family Acanthocolpidae, *Acanthocolpus* Lühe, 1906, are often described as unarmed (e.g. Lühe, 1906; Yamaguti, 1971), but enough records of tegumentary spines occur (e.g. Srivastava, 1939; Fernandes & Souza, 1973; S.P. Gupta & R.C. Gupta, 1980; V. Gupta & Ahmad, 1981) to strongly suggest that they occur as a rule and their apparent absence is due to poor fixation. Madhavi (1976) found that spines, including enlarged circum-oral spines were sometimes present in *A. orientalis* Srivastava, 1939, and transferred the species to *Stephanostomum*, and similar considerations caused Hafeezullah (1978) to transfer the species *A. tenuis* Manter, 1963 to *Stephanostomoides*. A suspicion arises that all *Acanthocolpus* species may really belong in *Stephanostomum* or some

other genus with enlarged circum-oral spines. The circum-oral spines of so many acanthocolpids suggest one differentiating feature between *Neophasis* and this family, but some genera of acanthocolpids apparently lack them (e.g. *Acanthocolpus* (but see above) and *Tormopsolus* Poche, 1926), and they are possessed by some lepocreadiid genera (e.g. *Cephalolepidapedon* Yamaguti, 1970, *Acanthogalea* Gibson, 1976 and *Clavogalea* Bray, 1985).

The excretory vesicle in the Lepocreadiidae is I-shaped, tubular or saccular, as it is in *Neophasis*. The excretory vesicle in the Acanthocolpidae is usually described as Y-shaped, but it is very difficult to find this feature well illustrated. It may be that some authors have followed early workers and have not studied their worms in section. Dollfus (1973), although he had earlier reckoned the excretory vesicle of *Stephanostomum* to be Y-shaped, stated that he now knew this to be wrong, and the vesicle was 'simple, sacciforme ou tubulaire, comme chez les Neophasiinae'. The branches of the 'Y' may be the distended laterally directed collecting *tubules*. These tubules were described by Wolfgang (1955), who did not mention that they were distended. Our own study of the excretory vesicle of *Stephanostomum baccatum* in sections shows an I-shaped vesicle reaching just posterior to the ovary. The anterior extremity is rounded and two narrow muscular tubules feed into the antero-lateral margins of the vesicle. In this species the tubules are not distended at all.

The seminal receptacle is uterine in the Acanthocolpidae, but canalicular in the Lepocreadiidae. Contrary to some reports, in *Neophasis* the seminal receptacle is uterine.

All groups under discussion have a well-developed cirrus-sac, and the contents are so variable in the Lepocreadiidae that little useful comparison can be made. The external seminal vesicle, which is a diagnostic feature of the Lepocreadiidae, according to Gibson & Bray (1982), does not occur in the Acanthocolpidae or in *Neophasis*. The value of this comparative character is open to question, however, as some enenterid forms which are clearly close to the Lepocreadiidae, and considered to belong in that family by

many, e.g. *Stegodexamene* and *Tetracerasta*, lack an external seminal vesicle.

The genital atrium is often very deep in the Acanthocolpidae, although in certain functional conditions it may be reduced. In the Lepocreadiidae and *Neophasis* the genital atrium is small.

The status of Neophasis

Neophasis was not placed in a family by its original author, Stafford (1904), but its synonym *Acanthopsolus* was placed in the Allocreadiidae near *Stephanochasmus* Looss, 1900 by its original author, Odhner (1905). Nicoll (1909) considered it allied to, but not in, the Lepocreadiinae. Most subsequent authors have placed the genus in the Acanthocolpidae (or its synonyms): these authors include Poche (1926), Issaitschikov (1928), Ivanov & Murygin (1937), Ward (1938), Cable & Hunninen (1942), Shulman-Albova (1952), Yamaguti (1953), Skrjabin (1954), Zhukov (1963), Chubrik (1966), Marasaev (1984) and Kjøie (1985a). Some authors have, however, considered *Neophasis* a lepocreadiid: these include Miller (1941), Zhukov (1960), Yamaguti (1971), Machida *et al.* (1972), Machida (1984) and Shimazu (1984). Yamaguti (1958) and Brinkmann (1975) placed *Neophasis* in the Allocreadiidae. Gibson & Bray (1982) placed the genus in the Enenteridae, a family which, in their conception was a 'convenient phenetic rather than a phyletic assemblage'. The life-cycle of the type-genus, *Enenterum* Linton, 1910, is unfortunately not known, but our knowledge of some of the genera placed in the family, in particular *Stegodexamene* and *Tetracerasta* suggest that the group may not be robust. The evidence we have marshalled above suggests to us that *Neophasis* can be seen as an aberrant acanthocolpid, and, we provisionally recognise Ward's (1938) subfamily Acanthopsolinae, awaiting a full modern revision of the Acanthocolpidae. The features used as evidence for this can be summarised as the fish second intermediate host, the divided excretory ducts in the cercarial tail, the lack of an external seminal vesicle and the uterine seminal receptacle. We would also like to suggest that the families Acanthocolpidae and Lepocreadiidae are not distantly related. We prefer the placement of the families

together in the same higher taxon (e.g. in the same superfamily by La Rue, 1956) to Brooks *et al.*'s (1985) erection of the new suborder the Acanthocolpata *sedis mutabilis* in the order Plagiiorchiiformes. The suborder originally had as its diagnosis: 'Plagiiorchiiforms with spinose terminal oral sucker'. Brooks *et al.* (1985) defined the Acanthocolpidae as, *inter alia*, using oligochaete and polychaete worms as hosts. In fact *Deropristis* is the only genus that uses annelids as second intermediate hosts which has been considered an acanthocolpid by some authors, but Brooks *et al.* (1985) placed it in the family Deropristidae of their new order Lepocreadiiformes, so their statement is without foundation. Later, Brooks *et al.* (1989) introduced four additional characters to the diagnosis of the Acanthocolpata, of which only one, '(5) subterminal to terminal oral sucker', is exhibited by *Neophasis*. We do not feel that the Lepocreadiidae and the Acanthocolpidae are dissimilar enough to belong in different orders, although we are aware that this type of argument does not convince strict cladists.

The taxonomic value of some morphological characters

Various morphological features have been used to substantiate species. We have studied these features, in particular those tabulated by Brinkmann (1975), in the specimens we have available. Our conclusions are as follows, and are based on ovigerous specimens only. We have usually referred to the two forms from *Anarrhichas lupus* by their specific names (i.e. *N. pusilla* and *N. anarrhichae*), but in the case of the various forms of *N. oculatus* and *N. burti* n. sp., they are referred to by the name of their host.

Length of body. Brinkmann (1975) showed that the length of *N. oculatus* is distinctly greater than that of *N. pusilla* and *N. anarrhichae*. Our observations (Table I) support this, but in general body-length is of little value in digenean taxonomy, as it is known that it can increase in length several-fold during their life-span and may vary in different hosts.

Tegumental spines or scales. Brinkmann (1975) suggested that they are lacking in the posterior fifth of the body of *N. pusilla*, but cover the whole worm in the case of the other two species. Our observations suggest that this is not a useful character, as in most well-fixed specimens the spines cover the whole body surface. They may be lost by fixation or freezing, etc, and may also appear to be absent over varying amounts of the posterior part of the body. The spines often are embedded and do not reach above the surface of the tegument in the hinder parts of the body. The following observations of *Neophasis* from various hosts show that the feature is of no taxonomic value:

Lycodes esmarkii – present all over (4 of 7), missing due to freezing (3 of 7).

Lycodes vahli – present all over (10 of 10).

Myoxocephalus scorpius – present all over (5 of 5).

M. octodecemspinus – present all over (24 of 27), missing in posterior region (3 of 27).

Anarrhichas lupus (NW Atlantic) – present all over (70 of 76), posterior end naked (5 of 76), few spines in forebody (1 of 76).

A. lupus (NE Atlantic) – present all over (19 of 26), forebody only (2 of 26), missing due to freezing (5 of 26).

Eye-spots. The pigment material is sometimes gathered together in a discrete body, or the granules may be scattered in the parenchyma at the prepharynx/pharynx level. The degree of dispersion varies. According to Brinkmann (1975) the pigment is discrete in *N. pusilla* and *N. oculatus* but scattered in *N. anarrhichae*. Our results (Table I) do not substantiate this view. *N. anarrhichae* has a mixture of dispersed, discrete and absent. In several cases specimens have a discrete eye-spot on one side of the body and dispersed eye-spot material on the other.

Position of ventral sucker. Brinkmann (1975) considered that it was in the middle of the body in *N. pusilla* and in the anterior half in the other species. We have measured the forebody and calculated it as a proportion (percentage) of the

Table 1. Summary of taxonomic characters of *Neophasis* spp.

Host	Locality	Body-length	Eye-spot pigment		
1. <i>Lycodes esmarkii</i>	NE Atlantic	1,035–1,620 (1,411) (n = 7)	Discrete – 1.5 Dispersed – 5.5 (n=7)		
2. <i>Lycodes vahli</i>	NW Atlantic	880–1,070 (945) (n = 10)	Discrete – 1 Dispersed – 9 (n = 10)		
3. <i>Myoxocephalus scorpius</i>	NE Atlantic	500–505 (n = 2)	Dispersed – 2 (n = 2)		
4. <i>Myoxocephalus scorpius</i>	NW Atlantic	860–1,145 (1,035) (n = 3)	Discrete – 1 Absent – 3 (n = 4)		
5. <i>Myoxocephalus octodecemspinosus</i>	NW Atlantic	740–1,420 (1,056) (n = 26)	Dispersed – 26 (n = 26)		
6. <i>Anarhichas lupus (pusilla)</i>	NW Atlantic	465–730 (630) (n = 58)	Discrete – 44 Absent – 38 (n = 82)		
7. <i>Anarhichas lupus (anarrhichae)</i>	NE Atlantic	383–615 (460) (n = 25)	Discrete – 7 Dispersed – 11, mixed – 5 Absent – 5 (n = 28)		
Sucker-ratio	Testes overlap	Lateral testes overlap	Egg-size	Forebody % of body length	Post-testicular region % of body-length
(1)					
1:1.20–1.69 (1.41) (n = 7)	38–89 (61%) (n = 7)	8–62 (33%) (n = 7)	104–130 × 51–76 (115 × 62) (n = 13)	34–51 (40%) (n = 7)	8–14(11)% (n = 7)
(2)					
1:1.09–1.43 (1.29) (n = 10)	45–91 (66%) (n = 10)	0–55 (29%) (n = 8)	104–123 × 54–72 (114 × 59) (n = 8)	35–43 (39%) (n = 10)	9–18 (14)% (n = 9)
(3)					
1:1.30 (n = 1)	100% (n = 1)	–	101–111 × 57–54 (108 × 55) (n = 3)	27–28% (n = 2)	21% (n = 1)
(4)					
1:1.0–1.16 (1.075) (n = 4)	47–62 (53%) (n = 3)	26% (n = 1)	92–115 × 45–63 (97 × 54) (n = 15)	33–36 (35%) (n = 3)	14–17 (15)% (n = 3)
(5)					
1:0.78–1.19 (0.96) (n = 23)	8–91 (38%) (n = 27)	44–97 (69%) (n = 25)	90–110 × 45–59 (98 × 52) (n = 19)	23–35 (30%) (n = 25)	10–25 (18)% (n = 25)
(6)					
1:0.73–1.12 (0.94) (n = 48)	0–100 (61%) (n = 55)	0–38 (16%) (n = 20)	87–104 × 38–55 (92 × 47) (n = 33)	31–44 (37%) (n = 61)	5–19 (13)% (n = 50)
(7)					
1:1.00–1.32 (1.14) (n = 12)	22–100 (69%) (n = 20)	0–42 (25%) (n = 6)	76–95 × 36–57 (84 × 48) (n = 41)	35–44 (40%) (n = 25)	6–18 (13)% (n = 23)

body-length. We did not find the relationship given by Brinkmann (Table I).

Sucker ratio. Brinkmann (1975) found the oral-sucker smaller than the ventral in *N. pusilla* and *N. anarrhichae*, but the suckers equal in *N. oculatus*. In contrast, we have found the sucker-ratio means in *N. pusilla* and *M. octodecemspinosus* to be 1:<1, and other forms have sucker-ratio means distinctly 1:>1 (Table I). The specimens from *Lycodes* spp. have generally relatively larger ventral suckers.

Cirrus-spines. These are supposedly present in *N. anarrhichae* and *N. oculatus*, but absent from *N. pusilla*. Despite the detailed descriptions and figures of cirrus-spines (e.g. Levinsen, 1881; Odhner, 1905) we believe that they are absent in *Neophasis*. The filamentous lining of the pars prostatica can be confused with spines if viewed in whole-mounts, but in sectioned material it can be seen that this is an artifact.

Seminal vesicle. This is almost always seen to be bipartite, but may occasionally appear to be saccu-

lar. In all sectioned specimens a bipartite seminal vesicle is seen.

Seminal receptacle. This is said to be present in *N. pusilla* and *N. anarrhichae*, but absent in *N. oculatus*, according to Brinkmann (1975). By this he presumably meant that the seminal receptacle is canalicular in the first two species. Our observations show that in all forms sectioned the seminal receptacle is uterine, and that it is quite impossible to determine the nature of the seminal receptacle from whole-mount preparations. We found this condition in single sectioned specimens from *Lycodes esmarkii* and *Myoxocephalus octodecemspinosus*, two sets of serial sections from *L. vahli* and in three sets of sections from *Anarrhichas lupus* in the NW Atlantic (*N. pusilla*): in the fourth set of serial sections from this latter material no seminal storage organ was seen, in fact sperm were seen only in the testes. In the three specimens of *N. pusilla* with sperm in the uterus a few isolated sperm could also be seen in Laurer's canal, but not enough to distend the canal at all. Bray's (1979) report of a blind seminal receptacle in *N. pusilla* is in error.

Number of eggs. Brinkmann (1975) reckoned that in *N. pusilla* and *N. anarrhichae* there were fewer eggs (2–8) than in *N. oculatus* (10–40). Our observations suggest that, although egg numbers are an ontogenetic feature of limited taxonomic value, large numbers of eggs are never found in some forms. In four specimens from *Lycodes esmarkii* there were from about 20 to about 40 with an approximate mean of 30. From *L. vahli*, six worms had few (2–6) eggs, one had 10 and one about 30 (mean c.8). From *Myoxocephalus octodecemspinosus* egg number varied between 3 and c.14 (mean c.7, $n = 28$). In both mature specimens from *M. scorpius* from the NE Atlantic 6 eggs were seen, but from the NW Atlantic the figures were 8–15 (mean 11, $n = 4$). In *N. pusilla* there were 2–7 eggs (mean 4, $n = 77$) and in *N. anarrhichae*, 1–5 (mean 3, $n = 27$). It should be noted that it is increasingly difficult to accurately count the eggs as more are present, because the eggs tend to be collapsed, distorted and squashed

together. Any count over about 5 is likely to have an element of an estimate about it.

Testicular arrangement. Machida (1984) erected a new species *N. symmetrorchis*, a name which suggested that he recognized the value of relative testicular position. He noted that Zhukov (1960) thought that the testes varied from symmetrical to diagonal (oblique) during development, but did not find this in his species. We have attempted to quantify this feature by measuring the length of the anterior testis and the amount of overlap of the anterior testis over the posterior testis, giving a percentage figure such that 0% represents tandem testes and 100% symmetrical testes. Our results are given in Table I. Four forms have rather similar mean overlaps, but the form from *M. octodecemspinosus* has a distinctly lower mean and the form from *M. scorpius* has more or less symmetrical testes in the single mature specimen where this observation could be made. These findings may be significant. This parameter is not available from other descriptions, although it can be reconstructed from illustrations, but unfortunately this gives little idea of the variation which is known to occur in this character. Using illustrations of ovigerous specimens only the following figures are found:

N. pusilla – 89% (Miller, 1941), 50–87% (Brinkmann, 1975).

N. anarrhichae – 99% (Lebour, 1910), 12–42% (Brinkmann, 1975).

N. oculatus – 64% (Levinsen, 1881), 47% (Odhner, 1905), 29% (Zhukov, 1960), 53% (Brinkmann, 1975), 14% (Machida, 1984).

N. symmetrorchis – 74% (Machida, 1984).

Another way of looking at this is to take a lateral overlap figure which is the transverse overlap of the testes as a percentage of the anterior testes width, such that 0% represents symmetrical testes and 100% tandem testes. As with the figures given above (Table I) this feature distinguishes the worms from *Myoxocephalus octodecemspinosus* as a form with much more tandem testes than is usual in the other forms. Figures taken from illustrations in the literature are:

N. pusilla – 0% (Miller, 1941), 7% (Brinkmann, 1975).

N. anarrhichae – 0% (Lebour, 1910), 0–32% (Brinkmann, 1975).

N. oculatus – 4% (Levinsen, 1881), 32% (Odhner, 1905), 52% (Zhukov, 1960), 18% (Brinkmann, 1975), 73% (Machida, 1984).

N. symmetrorchis – 0% (Machida, 1984).

Egg-size. Brinkmann (1975) differentiated the species *N. pusilla* and *N. anarrhichae* with eggs 90 μm from *N. oculatus* with eggs 115 μm long. This agrees reasonably well with the other literature in that the latter species tends to have considerably larger eggs (lengths in μm):

N. pusilla – c.80 (Miller, 1941), 87–89 (Bray, 1979).

N. anarrhichae – 99 (Lebour, 1908), 80–100 (Lebour, 1910).

N. oculatus – 119 (Levinsen, 1881), 115–135 (Odhner, 1905), 83–117 (Zhukov, 1960), 106–116 (Machida, 1984).

Our results (Table I) also show how the egg-size of *N. oculatus* (*sensu lato*) is consistently larger than for the other forms. Untanned eggs can be enormous (we have measured them up to 130 μm), which may account for the upper limit given by Odhner (1905). It is important that the eggs measured are relatively undistorted, lying in a level plane, well tanned and preferably in the distal uterus.

Post-testicular region. The distance from the posterior edge of the posterior testis to the posterior extremity also appeared to be proportionately larger in specimens from *M. octodecemspinus*. This distance was calculated as a percentage of body-length (Table I), and although the impression is borne out by the figures, the differences are very slight and of doubtful taxonomic value.

Our observations indicate that four forms from the North Atlantic can be distinguished by use of the following key in conjunction with Table I.

Key to North Atlantic species of *Neophasis*

- 1 Length not exceeding 750 μm ; mean egg-length <95 μm ; in *Anarrhichas* spp. 2
 - Length up to 1,620 μm ; mean egg-length >95 μm ; mainly in cottids and zoarcids 3
- 2 Mean sucker ratio 1:<1; mean egg-length >90 μm ; in NW Atlantic
 - *Neophasis pusilla* Stafford, 1904
 - Mean sucker ratio 1:>1; mean egg-length <90 μm ; in NE Atlantic
 - *Neophasis anarrhichae* (Nicoll, 1909)
- 3 Mean sucker ratio 1:>1; mean testes overlap 50–100%; mean lateral testes overlap 26–32% *Neophasis oculatus* (Levinsen, 1881)
 - Mean sucker ratio 1:<1; mean testes overlap 38%; mean lateral testes overlap 69%
 - *Neophasis burti* n. sp.

These species may be distinguished with some difficulty. The differences are slight and may not stand up to further observations.

North Atlantic species

***Neophasis oculatus* (Levinsen, 1881) Miller, 1941**
(Figs 1–5)

Synonyms: *Distomum oculatum* Levinsen, 1881; *Acanthopsolus oculatus* (Levinsen, 1881) Odhner, 1905; *Acanthopsolus ocellatus* of Faust (1918) *lapsus*

Material studied

From the NE Atlantic Ocean

Lycodes esmarkii Collett [intestine] NNW of Rona, just east of Wyville-Thompson Ridge (60° N, 07° W, depth 790–820 m, April 1973), BM(NH) 1986.10.13.7; Foula (60° N, 06° W, depth 800 m, June 1974), BM(NH) 1986.10.13.8; Faroes (1988), Collector: M. Kjøie, Kjøie collection.

Myoxocephalus scorpius (L.) [intestine] Trondheim, Norway (1.7.1914), Collector: O. Nybelin, Zoological Museum, University of

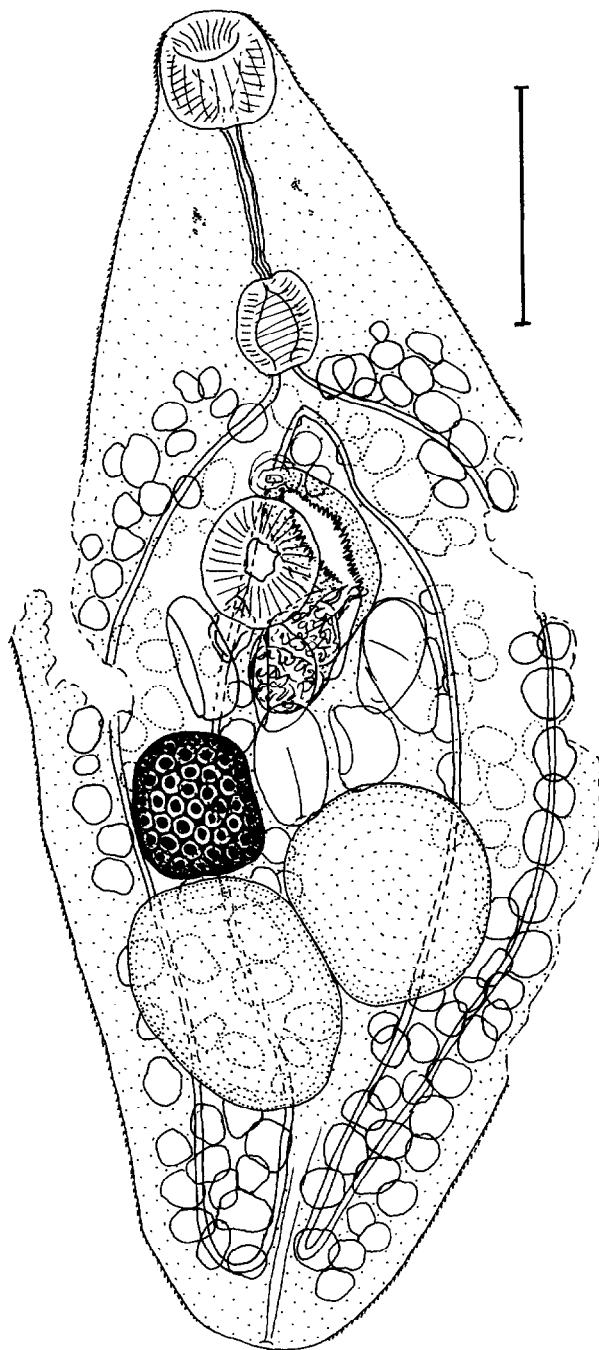


Fig. 1. *Neophasis oculatus* (Levinsen). Ventral view of type-specimen; margins damaged. Scale-bar: 200 μ m.

Bergen; Frederikshavn, Denmark (Aug. 1979),
Collector: M. Kjøie, Kjøie collection.

From elsewhere

Lycodes vahli Reinhardt [intestine] Grand Bank,

Newfoundland (47° N, 52° W, depth 172 m, and 46° N, 51° W, depth 80 m, July 1975), BM(NH) 1977.2.15.1–8 (see Bray, 1979).

Myoxocephalus scorpius (L.) [intestine] Egedesminde, W Greenland, types from Zoologisk Museum, Copenhagen.

Description

Based on 5 type whole-mounts (3 complete adults, one fragment of adult and one immature), 2 poorly fixed mature worms (Nybelin material) and 2 immature specimens (Kjøie material) from *M. scorpius*, 7 whole-mounts and one set of serial sections from *L. esmarkii*, and 7 whole-mounts and 2 sets of serial sections from *L. vahli*. Measurements are given on Tables I and III.

Body small, oval, fusiform or lanceolate (Figs 1–4). Body-surface covered with small spines in regular annular rows. Eye-spot pigment in discrete bodies or dispersed laterally to prepharynx and pharynx or absent; occasionally differ in single specimens. Oral sucker subglobular; aperture wide, subterminal. Ventral sucker rounded. Prepharynx long. Pharynx large; oval. Oesophagus short to very short. Intestinal bifurcation in posterior forebody. Caeca narrow to wide; reach adjacent to excretory vesicle near posterior extremity; distinct union to form uroproct not detected.

Excretory pore terminal; vesicle saccate, dorso-ventrally flattened; reaching to anterior testis.

Testes large; irregularly oval; contiguous; usually oblique to some degree, but occasionally tandem or symmetrical (Table I); often flattened on contiguous surfaces; in mid-hindbody; often less than one testis diameter from posterior extremity. Cirrus-sac long; claviform; arcuate; thin-walled; reaches into hindbody. Seminal vesicle internal; bipartite, with large sub-equal moities; mainly in hindbody; narrows distally; sphincter delimits pars prostatica (Fig. 5). Pars prostatica long; lumen wide; lined with filamentous or conical non-cellular projections (no spines seen); narrows distally to become narrow ejaculatory duct without distinct transition. Distinct layer of gland-cells surround pars prostatica and ejaculatory duct. Distal

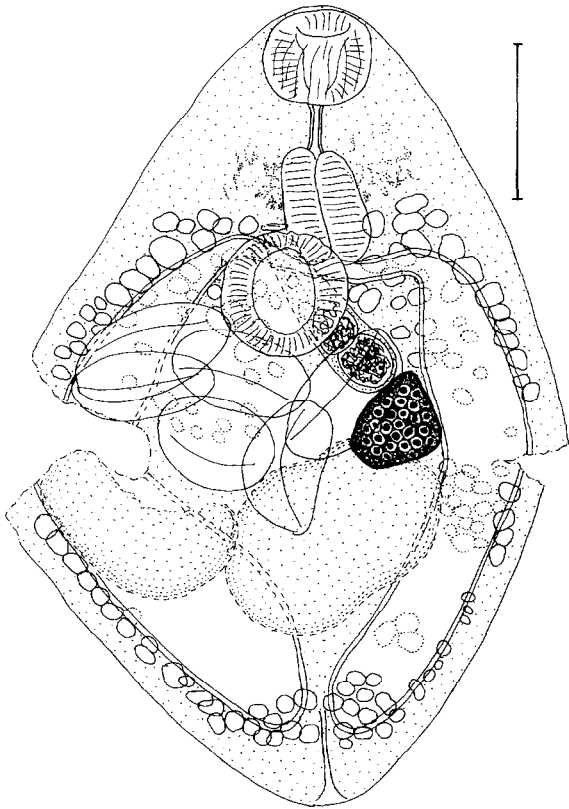


Fig. 2. *Neophasis oculatus* (Levinsen). Ventral view, specimen from *Myoxocephalus scorpius*, Trondheim; poor specimen, margins damaged. Scale bar: 100 μ m.

part of cirrus-sac protrudes into genital atrium as distinct papilla (? permanent cirrus). Genital atrium distinct; deep; narrow. Genital pore median, more or less immediately anterior to ventral sucker.

Ovary irregularly subglobular; immediately anterior to dextral (posterior) testis, antero-lateral or lateral to sinistral (anterior) testis or occasionally separated from testes by loops of uterus. Oviduct passes from sinistral side of ovary. Mehlis' gland dorsal to uterus. Laurer's canal opens dorsally to anterior testis. Seminal receptacle uterine. Uterus usually between ventral sucker and gonads; contains few eggs or may be greatly distended with eggs, deformed eggs or egg-shell material. Metraterm commences dorsally to ventral sucker; wide; muscular; with thick, glandular sheath; opens into genital atrium sinistrally to male duct. Eggs large; operculate. Vitellarium follicular; follicles large, closely packed; anterior extent from

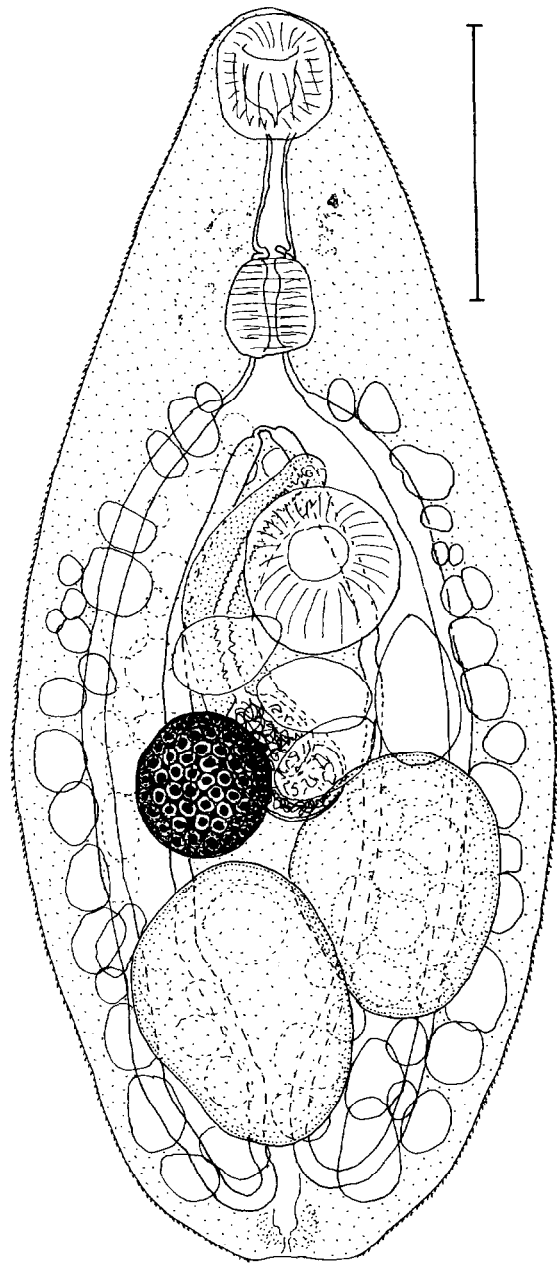


Fig. 3. *Neophasis oculatus* (Levinsen). Ventral view, specimen from *Lycodes vahli*. Scale-bar: 200 μ m.

about mid-pharynx to intestinal bifurcation; extends to posterior extremity; lateral fields continuous, contiguous or almost so, approaching each other ventrally anterior to genital pore, encroaching ventrally lateral to uterus, absent ventrally to gonads, confluent ventrally in post-testicular region; lateral fields contiguous dorsally from anterior extremity to anterior or mid-ventral

Table II. Dimensions of *Neophasis oculatus*.

Host	<i>Lycodes esmarkii</i>	<i>Lycodes vahli</i>	<i>Myoxocephalus scorpius</i> (NE Norway)	<i>Myoxocephalus scorpius</i> (W Greenland)
n	7	7	2	4
Length	1,035–1,620 (1,411)	880–1,070 (945)	500–505	860–1,145 (1,035)
Width	385–670 (594)	340–490 (401)	237–348	265–490 (378)
Oral sucker	75–155 × 90–175 (123 × 125)	88–102 × 85–103 (95 × 92)	54–59 × 63–73	66–105 × 68–100 (83 × 79)
Prepharynx	90–184 (134)	28–100 (72)	26–42	75–145 (107)
Pharynx	75–120 × 82–115 (100 × 94)	65–95 × 65–76 (78 × 70)	58–76 × 54	58–85 × 48–75 (68 × 58)
Oesophagus	32–115 (60)	5–50 (28)	0?	5–13 (10)
IB–VS	58–158 (109)	68–130 (60)	dorsal to VS	50–91 (68)
Vit–VS	135–223 (175)	84–168 (108)	16	91–125 (105)
Ventral sucker	120–195 × 128–130 (171 × 180)	111–134 × 98–130 (123 × 116)	92 × 95	76–115 × 75–105 (91 × 85)
Cirrus-sac	285–400 × 84–140 (343 × 112)	235–310 × 50–95 (262 × 76)	135 × 46	152–225 × 52–75 (192 × 63)
VS–Ovary	0–125 (31)	overlap to 55	10	85–105 (93)
Ovary	125–238 × 82–168 (183 × 137)	100–237 × 102–208 (112 × 93)	63 × 70	88–135 × 75–115 (109 × 97)
Testes:				
Anterior	202–405 × 175–290 (345 × 238)	190–237 × 102–208 (204 × 151)	111 × 108	145–195 × 110–185 (167 × 140)
Posterior	235–399 × 175–375 (355 × 260)	185–237 × 95–177 (211 × 149)	120 × 142	150–210 × 115–165 (178 × 142)
PTR	95–221 (153)	85–195 (137)	108	135–195 (160)
C–PE	32–87 (60)	38–60 (48)	51–54	45–75 (62)

IB–VS. Distance from intestinal bifurcation to anterior margin of ventral sucker.

Vit–VS. Distance from anterior-most extent of vitelline fields to anterior margin of ventral sucker.

VS–Ovary. Distance from posterior margin of ventral sucker to anterior margin of ovary.

PTR. Length of post-testicular region.

C–PE. Distance from posterior-most extent of the intestinal caeca to posterior extremity of worm.

sucker level, encroaching dorsally lateral to uterus and gonads, confluent dorsally in post-testicular region.

Type host and locality: *Myoxocephalus scorpius*, Egedesminde, W. Greenland.

Records: 1. Levinsen (1881); 2. Odhner (1905); 3. Issaitschikov (1928); 4. Dogiel & Rozova (1941); 5. Bauer (1948); 6. Shulman-Albova (1952); 7. Shulman & Shulman-Albova (1953); 8. Polyansky (1955); 9. Polyansky & Shulman (1956); 10. Strelkov (1960); 11. Zhukov (1960); 12. Skrjabina (1963); 13. Zhukov (1963); 14. Chubrik (1966); 15. Baeva (1968); 16. Korotaeva (1968); 17. Machida, Araki, Kamiya & Ohbayashi (1972); 18. Brinkmann (1975); 19. Bray (1979); 20. Machida (1984); 21. Shimazu (1984); 22. Present study.

Descriptions: 1, 2, 3, 11, 18, 20, 22.

Definitive hosts: Cottidae: *Alcichthys elongatus*

(11), *Blepsias bilobus* (13), *Enophrys diceraeus* (13, 16), *E. diceraeus namiyei* (11), *Gymnancanthus galeatus* (16), *G. herzensteini* (11), *Hemilepidonus gilberti* (11, 16), *Hemitripterus villosus* (11), *Melletes papilio* (13), *Myoxocephalus axillaris* (13), *M. brandti* (11, 16), *M.* [= *Ainocottus*] *ensiger* (17), *M. jaok* (10, 12, 16), *M. platycephalus* (13), *M. polyacanthocephalus* (13), *M. quadricornis* (3, 4, 5), *M.* [= *Acanthocottus*] *scorpius* (1, 2, 3, 6, 7, 8, 9, 18, 22), *M. stelleri* (21), *M. verrucosus* (13); Cyclopteridae: *Careproctus* sp. (10), *Careproctus trachysoma* (20), *Liparis gibbus* (13), *Liparis* sp. (11); Hexagrammidae: *Hexagrammos lagocephalus* (11, 17), *H. octogrammus* (11), *H. stelleri* (13), *Pleurogrammus azonus* (11, 15); Zoarcidae: *Lycodes esmarkii* (22), *L. pallidus* (2), *Lycodes polaris* [= *agnostus*] (3), *L. vahli* (19, 22); Pleuronectidae: *Platessa quadrituberculata* (10), *Pleuronectes stellatus* (13); Stichaeidae: *Lumpenella mackayi* (11), *Stichaeus grigor-*

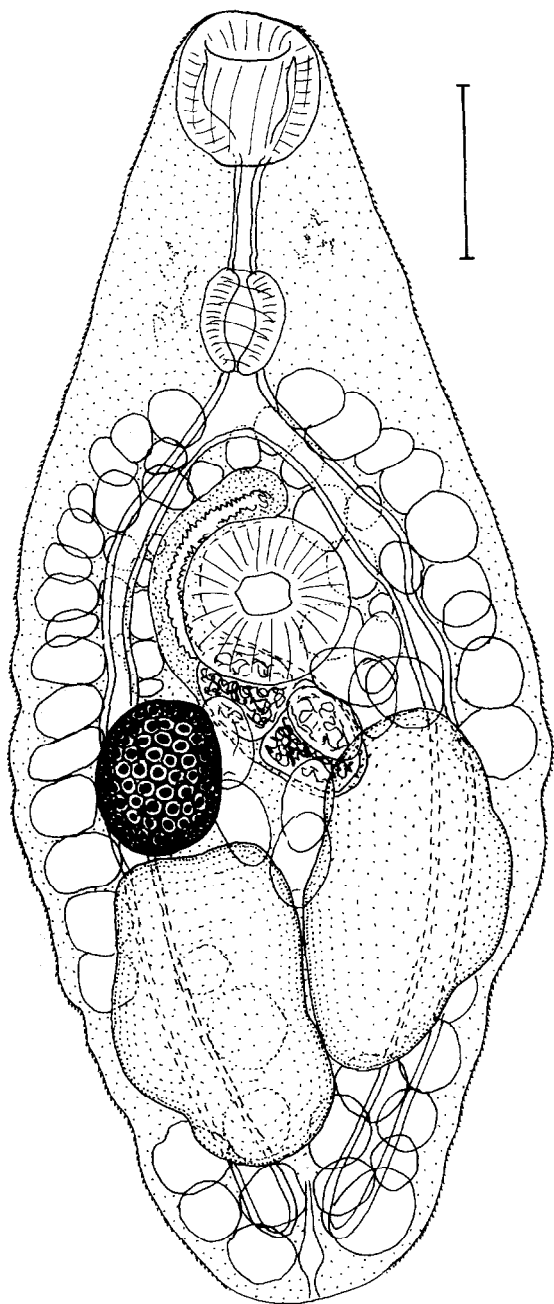


Fig. 4. *Neophasis oculus* (Levinsen). Ventral view, specimen from *Lycodes esmarkii*. BM(NH) 1986.10.13.7. Scale-bar: 200 μ m.

jewi (11); Agonidae: *Podothecus acipenserinus* (13); Gadidae: *Eleginus gracilis* (13); Icelidae: *Icelus spiniger* (16); Salmonidae: *Salvelinus malma* (13); Scorpaenidae: *Sebastes trivittatus* (11).

Sites: Intestine, pyloric caeca.

Life-cycle:

First intermediate host: Gastropoda: *Cryptonatica* [= *Tectonatica*] *clausa* (14).

Second intermediate hosts: Bivalvia: *Astarte crenata* (9), *Cerastoderma ciliatum* (9); Cottidae: *Gymnacanthus tricuspis* (fins) (8), *Melletes papilio* (gills) (13), *Myoxocephalus axillaris* (gills, fins) (13), *M. platycephalus* (gills, fins) (13), *M. polyacanthocephalus* (gills, fins) (13), *M. scorpius* (skin, fins) (1, 8), *M. verrucosus* (gills, fins) (13); Cyclopteridae: *Liparis gibbus* (gills) (13); Gadidae: *Gadus macrocephalus* (gills) (13); Hexagrammidae: *Hexagrammos stelleri* (fins) (13); Agonidae: *Podothecus acipenserinus* (gills) (13).

Distribution: 18 Arctic Sea [Kara Sea (3), N. Siberia (4, 5)], 21 Atlantic, NW [W. Greenland (1, 18), Newfoundland (19, 22)] 27 Atlantic, NE [E Greenland (2), Faroes (22), Norway (22), Denmark (22), Sweden (2), Barents Sea (8, 9, 14), White Sea (4, 6, 7, 9), off NW Scotland (22)], 61 Pacific, NW [Japan (17, 21), E. Kamchatka (10, 12), Putjatin (11), Shikotan (11), Bering Sea (13), Chukotsk Peninsula (13), Sea of Japan (15, 20)].

Discussion

The type-material of this species shows metrical features (egg-size, testes overlap and sucker-ratio) that are somewhat intermediate between, on the one hand, the specimens from *Lycodes* spp. and the type-host, *Myoxocephalus scorpius* at Trondheim, and, on the other, *N. burti*. It is difficult to be certain how to interpret this. It might be thought to suggest that there is a cline with extremes in the NE Atlantic and in the NW Atlantic (the latter represented by *N. burti*). The evidence that this is not so is furnished by the specimens from *Lycodes vahli* in the NW Atlantic. We believe that the form we designate *N. burti* can be separated from *N. oculus* by mean testes overlap and sucker-ratio.

N. oculus is a widespread species, from the North Atlantic, North Pacific and the Arctic Ocean. Its major hosts are members of the family Cottidae with 59% of records and members of the genus *Myoxocephalus* with 40%. Eighty-one percent of all records are from Scorpaeniformes.

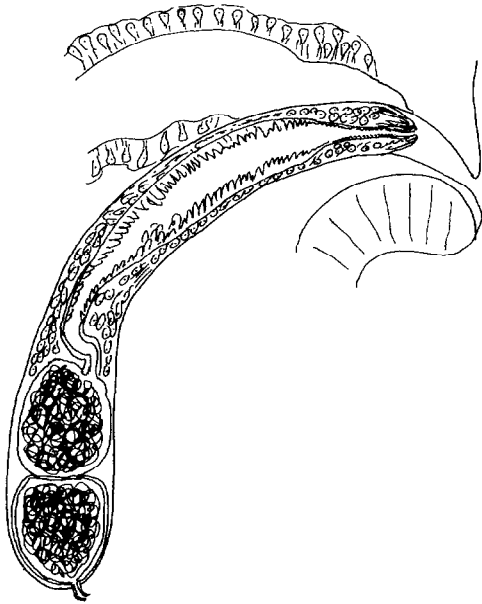


Fig. 5. *Neophasis oculus* (Levinsen). Ventral view, terminal genitalia reconstructed from sections of specimen from *Lycodes esmarkii*. BM(NH) 1986.10.13.8.

Other more commonly reported hosts are Hexagrammidae (10%), Zoarcidae (9%) and Cyclopteridae (7%). It has been recorded from 11 families, 22 genera and 39 species of teleost fish. Its highest reported prevalences include *Myoxocephalus brandti* (86.6%, int. 3–220) and *Liparis* sp. (81.8%, int. 4–173) at Putjatin (Zhukov, 1960), where it is also quite high (about 26%) in several other cottid species. From the Bering Sea, Zhukov (1963) reported high prevalence and intensity of both adults and metacercariae (e.g. 85.1%, 2–309 of adult in *M. verrucosus*, and 90.4%, 1–62 of metacercariae in *M. axillaris*). Prevalence is twice as great, and intensity higher, in *M. scorpius* in summer (May–Oct., 28.7%, 1–46) than in winter (Nov.–April, 12.3%, 1–9) in the Barents Sea (Polyansky, 1955). Shulman & Shulman-Albova (1953) reported the species in *M. scorpius* in the White Sea with a prevalence of 50% and an intensity of 1–40 (13%). In contrast, we have not been successful in finding this worm in more than 30 specimens of *M. scorpius* in the western North Sea off Scotland. Skrjabina (1963) reported an intensity of up to 1,000 in *M. jaok* from eastern Kamchatka. The species is reported to invade

young (0+) *M. scorpius* at a prevalence of 8.3% and intensity of 1.2.

von Linstow (1889) reported '*Distomum oculatum* Rud.' from the herring *Clupea harengus* with no locality information. Arthur & Arai (1984) listed this under *Neophasis oculata*, but it appears to us that von Linstow's citation is an error, and he is in fact referring to *D. ocreatum* (Rudolphi, 1802), now considered a synonym of *Hemiurus luehei* Odhner, 1905 (see Gibson & Bray, 1986), a common parasite of herring. von Linstow cross-referenced this record to three others, all of which refer to records of larval '*D. ocreatum* Rud.'

Neophasis burti n. sp. (Fig. 6)

Synonyms. *Neophasis oculatus* of Bray (1979) in part; (?) *Neophasis* sp. of Appy & Burt (1982)

Material studied

Myoxocephalus octodecemspinosus (Mitchill) [anterior intestine], type-material, Sable Island Bank, Nova Scotia (43° N, 61° W, depth 72 m, July 1975), BM(NH) holotype 1977.2.15.9, paratypes 1977.2.15.10–26 (see Bray, 1979); Passamaquoddy Bay, New Brunswick (Aug. 1982), BM(NH) paratypes 1982.9.28.86–87.

(?) *Gadus morhua* [intestine] Gulf of St Lawrence (47°10' N, 62°01' W, Sept. 1975), Collector: R.G. Appy (see Appy & Burt, 1982), NMCP 1982–0015.

Description

Based on 10 whole-mounts and one set of serial sections from type-host. Measurements are given on Tables I and III.

Body small, oval, fusiform or lanceolate (Fig. 6). Body-surface covered with small spines in regular annular rows. Eye-spot pigment in discrete bodies or dispersed laterally to prepharynx and pharynx. Oral sucker subglobular; aperture wide, subterminal. Ventral sucker rounded. Prepharynx distinct. Pharynx large; oval. Oesophagus short to very short. Intestinal bifurcation in posterior forebody. Caeca narrow to wide; reach adjacent to excretory vesicle near posterior extremity; distinct union to form uroproct not detected.

Table III. Dimensions of *Neophasis* spp.

Species	<i>N. burti</i>	<i>N. anarrhichae</i>	<i>N. pusilla</i>
Host	<i>Myoxocephalus octodecemspinosus</i>	<i>Anarrhichus lupus</i>	<i>Anarrhichus lupus</i>
n	10	12 + fragments	10
Length	920–1,260 (1,104)	383–615 (489)	555–695 (636)
Width	227–322 (274)	101–335 (220)	199–300 (251)
Oral sucker	90–133 × 100–133 (115 × 120)	48–94 × 47–95 (69 × 67)	82–100 × 82–101 (92 × 91)
Prepharynx	17–88 (66)	8–73 (40)	17–73 (41)
Pharynx	65–80 × 48–72 (73 × 59)	47–80 × 46–70 (62 × 55)	67–78 × 54–68 (72 × 60)
Oesophagus	20–42 (29)	21–38	4–35 (17)
IB–VS	34–91 (63)	12–23	4–41 (22)
Vit–VS	66–134 (99)	4–48 (27)	47–75 (59)
Ventral sucker	105–130 × 97–133 (117 × 112)	51–105 × 61–98 (70 × 76)	73–100 × 73–108 (89 × 91)
Cirrus-sac	193–250 × 55–76 (217 × 64)	155–170 × 35–38	133–211 × 30–57 (186 × 44)
VS–ovary	55–80 (70)	overlap–32	0–73 (36)
Ovary	88–158 × 64–126 (119 × 91)	45–88 × 38–68 (64 × 49)	73–123 × 68–80 (91 × 74)
Testes:			
Anterior	133–193 × 110–183 (160 × 143)	48–139 × 37–80 (82 × 66)	80–133 × 64–90 (97 × 74)
Posterior	152–230 × 111–170 (187 × 136)	54–92 × 35–85 (69 × 66)	82–133 × 66–105 (106 × 81)
PTR	105–265 (200)	23–102 (60)	32–100 (68)
C–PE	38–60 (44)	12–30 (22)	26–76 (46)

IB–VS. Distance from intestinal bifurcation to anterior margin of ventral sucker.

Vit–Vs. Distance from anterior-most extent of the vitelline fields to anterior margin of ventral sucker.

VS–Ovary. Distance from posterior margin of ventral sucker to anterior margin of ovary.

PTR. Length of post-testicular region.

C–PE. Distance from the posterior-most extent of intestinal caeca to posterior extremity of worm.

Excretory pore terminal; vesicle dorso-ventrally flattened sac reaching to anterior testis.

Testes large; irregularly oval; contiguous; oblique to varying degree (Table I); often flattened on contiguous surfaces; in mid-hindbody; often less than testis diameter from posterior-extremity. Cirrus-sac long; claviform; arcuate; thin-walled; reaches into hindbody. Seminal vesicle internal; bipartite, with large, sub-equal moities, mainly in hindbody; narrows distally; sphincter delimits pars prostatica. Pars prostatica long; lumen wide; lined with filamentous or conical non-cellular projections (no spines seen); narrows distally to become narrow ejaculatory duct without distinct transition. Distinct layer of gland-cells around pars prostatica and ejaculatory duct. Distal part of cirrus-sac protrudes into genital atrium as distinct papilla (? permanent cirrus). Genital atrium distinct;

deep; narrow. Genital pore median, more or less immediately anterior to ventral sucker.

Ovary regularly or irregularly oval; antero-lateral or lateral to sinistral (anterior) testis or occasionally separated from testes by uterus. Oviduct passes from sinistral side of ovary. Mehlis' gland dorsal to uterus. Laurer's canal opens dorsally to anterior testis. Seminal receptacle uterine. Uterus usually between ventral sucker and gonads; contains few (3–c.14) eggs. Eggs large; operculate. Metraterm commences dorsally to ventral sucker; wide; muscular; with thick, glandular sheath; enters genital atrium sinistrally to cirrus-sac. Vitellarium follicular; follicles closely packed; anterior extent to about mid-pharynx to intestinal bifurcation; posterior extent to posterior extremity; lateral fields continuous, contiguous or approaching ventrally anterior to geni-

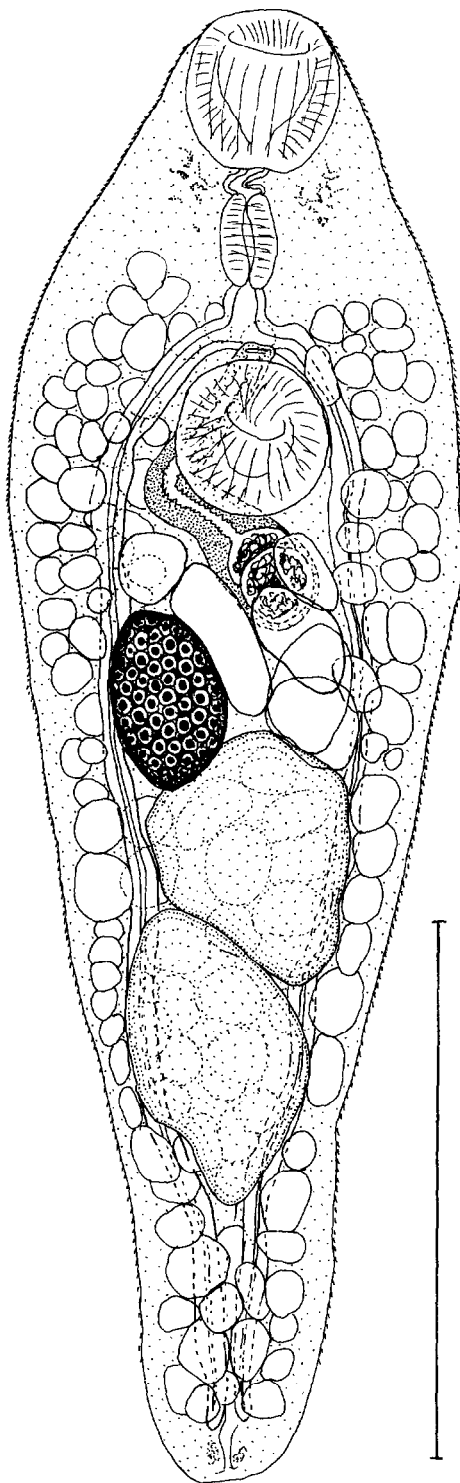


Fig. 6. *Neophasis burti* n. sp. Ventral view of holotype. Scale-bar: 500 μ m.

tal pore, encroaching ventrally lateral to uterus, not ventral to gonads, confluent ventrally in post-testicular region; lateral fields contiguous dorsally from anterior extremity to anterior or mid-ventral sucker level, encroaching dorsally lateral to uterus and gonads, confluent dorsally in post-testicular region.

A single, immature specimen from *Gadus morhua*, as mentioned by Appy & Burt (1982), appears to belong to this species. Its dimensions are: 750 long, 340 wide, forebody 41% of body-length, oral sucker 82 \times 88, ventral sucker 90 \times 95, sucker-ratio 1:1.08, prepharynx 70, pharynx 80 \times 45, ovary 50 diameter, anterior testis 115 diameter, posterior testis 120 diameter, testes overlap 35%, post-testicular region 255 (35% of body length). Its tegument is spinous throughout and its eye-spots are entire. In terms of its sucker ratio and testis overlap it fits into *M. burti*. Appy & Burt (1982) also reported the 'same type' of immature worm from the mesenteries of *Hippoglossoides platessoides* in the cod's gut.

Type-host and locality: *Myoxocephalus octodecemspinosus*, Sable Island Bank, Nova Scotia, off eastern Canada.

Records: 1. Bray (1979); 2. Appy & Burt (1982); 3. Present study.

Description: 3.

Definitive hosts: Cottidae: *Myoxocephalus octodecemspinosus* (1, 3); Gadidae: ? *Gadus morhua* (2, 3).

Site: Intestine.

Life-cycle: Immature worms: Pleuronectidae: ? *Hippoglossoides platessoides* (2).

Distribution: 21 Atlantic, NW [Nova Scotia (1, 3), Gulf of St Lawrence (2, 3), Passamaquoddy Bay (3)].

Discussion

The features differentiating this form from *N. ocellatus* are discussed above and summarised in the key. Both specimens of *M. octodecemspinosus* examined in 1975 harboured this worm at intensities of 12 and 14. Of the three specimens of this fish examined in 1982, one was infected with 6 worms.

Neophasis anarrichae (Nicoll, 1909) Bray, 1987
(Figs 7–8)

Synonyms: 'sporocyst and cercaria from liver of *Buccinum undatum*' of Lebour (1905); *Distomum* sp. of Lebour (1908); '(*Acanthopsolus*)' *anarrichae* Nicoll, 1909; *Acanthopsolus lageniformis* Lebour, 1910; *Neophasis lageniformis* (Lebour, 1910) Miller, 1941

Material studied

From NE Atlantic Ocean

Anarrichas lupus L. [intestine] Cullercoats, Northumberland, England (1910), Collector: M.V. Lebour, USNM 49971; Northern North Sea (59° N, 01° E, depth 107–117 m, Dec. 1979), BM(NH) 1985.7.22.5; Forty Mile Ground (60° N, 00°30' E, depth 124 m, May 1984), BM(NH) 1986.2.6.31–32; Faroes (19.10.1981), Collector M. Kjøie, Kjøie collection; Halibut Bank, Shetlands (61° N, 00°30' E, depth 146 m, May, 1990), BM(NH) 1990.7.9.1–11.

Description

Based on 3 damaged whole-mounts plus some fragments of Lebour's material, and 21 whole-mounts (including 4 from frozen hosts) of recently collected material. Measurements are given in Tables I and III.

Body small; oval, fusiform or lanceolate (Figs 7,8). Body-surface covered throughout or in part with small spines in regular annular rows (lost in frozen specimens). Eye-spot pigment in discrete bodies or dispersed laterally to prepharynx and pharynx or absent; may have both discrete and dispersed in same worm. Oral sucker subglobular; aperture subterminal. Prepharynx distinct. Pharynx large; oval. Oesophagus short to very short. Intestinal bifurcation in posterior forebody. Caeca narrow to wide; reach to point adjacent to excretory vesicle near posterior extremity. Ventral sucker rounded; in mid-body.

Excretory pore terminal; vesicle extent not seen.

Testes large; irregularly oval; contiguous; oblique to almost tandem (Table I); often flattened

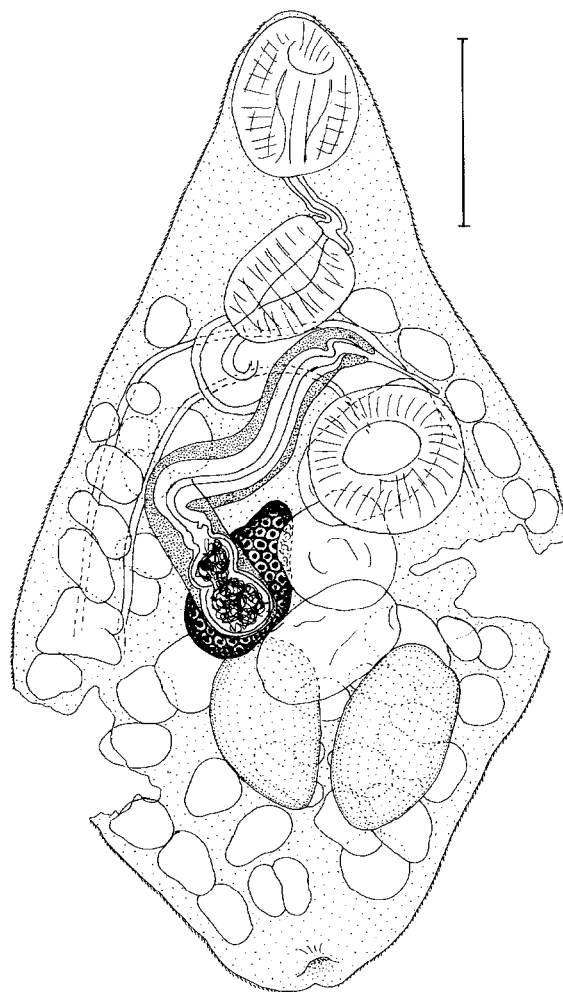


Fig. 7. *Neophasis anarrichae* (Nicoll). Ventral view of specimens of *Acanthopsolus lageniformis* from Lebour's collection, margins damaged, posterior part of caeca not visible. USNM 49971(a). Scale-bar: 200 μ m.

on contiguous surfaces; in posterior hindbody; often less than one testis diameter from posterior extremity. Cirrus-sac long, claviform, undulating; thin-walled; reaching to testes. Seminal vesicle internal; bipartite, with large sub-equal moities; in hindbody. Pars prostatica long; lumen wide; lined with filamentous or conical non-cellular projections (no spines seen); narrows distally to become narrow ejaculatory duct without distinct transition. Distinct layer of gland-cells around pars prostatica and ejaculatory duct. Distal part of cirrus-sac protrudes into genital atrium as distinct papilla (? permanent cirrus). Genital atrium distinct; deep; narrow. Genital pore median, more or less immediately anterior to ventral sucker.

Ovary irregularly subglobular; immediately anterior to dextral (posterior) testis, antero-lateral or lateral to sinistral (anterior) testis or occasionally separated from testes by uterus. Uterus usually between ventral sucker and gonads; contains few eggs or may be distended with deformed eggs or egg-shell material. Eggs large; operculate. Metraterm commences dorsally to ventral sucker; wide; muscular; with thick glandular sheath; enters genital atrium sinistrally to cirrus-sac. Vitellarium follicular; follicles large, closely packed; anterior extent from about mid-pharynx to intestinal bifurcation; posterior extent to posterior extremity; lateral fields encroaching to approaching in forebody; confluent ventrally in post-testicular region; lateral fields confluent dorsally in post-testicular region.

Type-host and locality: *Anarhichas lupus*, Northumberland coast, England.

Records: 1. Lebour (1905); 2. Lebour (1908); 3. Nicoll (1909); 4. Lebour (1910); 5. Lebour (1912); 6. Shulman-Albova (1952); 7. Shulman & Shulman-Albova (1953); 8. Polyansky (1955); 9. Chubrik (1966); 10. K ie (1968); 11. K ie (1969); 12. K ie (1971); 13. K ie (1973a); 14. K ie (1973b); 15. K ie (1974); 16. Brinkmann (1975); 17. Zubchenko (1980); 18. K ie (1983); 19. Bray (1987); 20. Present study.

Descriptions: 2,4,16,20.

Definitive hosts: Anarhichadidae: *Anarhichas* [= *Lycichthys*] *denticulatus* (8), *A. lupus* (2,3,4,6,7,8,13,?17,19,20), *A. minor* (8,?16,?17).

Sites: Intestine (upper, anterior), stomach (immature).

Life-cycle:

First intermediate host: *Buccinum undatum* (1,2,4,5,9,10,11,12,13,14,15,18).

Immature worms: Pleuronectidae: *Limanda limanda* (18), *Pleuronectes platessa* (18).

Distribution: 21 Atlantic, NW [W. Greenland (?16), NE Newfoundland to Baffin Land (?17)], 27 Atlantic, NE [North Sea (18), North Sea-England (1,2,4,5,20), North Sea-Scotland (3,20), Shetlands (4,20), Faroes (18,20), Moray Firth (19),  resund (10,11,12,13,18), Barents Sea (8,9), White Sea (6,7)].

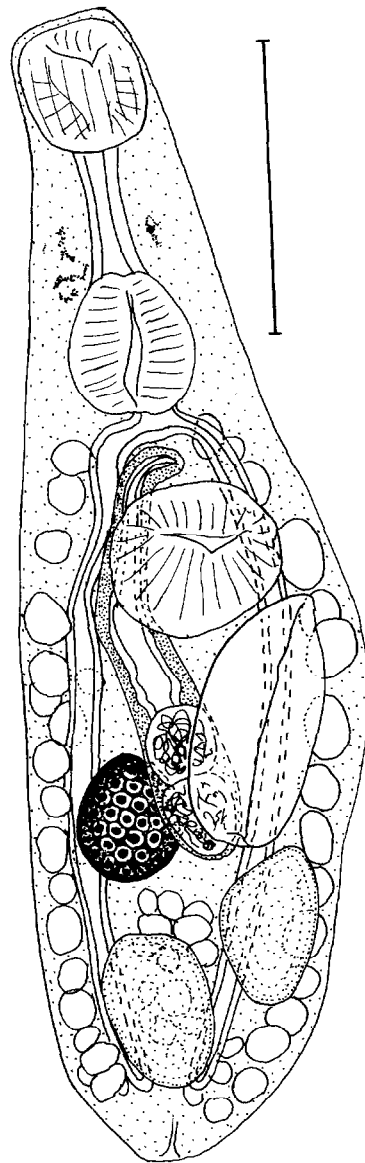


Fig. 8. *Neophasis anarrichae* (Nicoll). Ventral view of specimens lent by M. K ie. Scale-bar: 100 μ m.

Discussion

Lebour's material from the United States National Collection may be types of *A. lageniformis*, but this is not stated in that Collection's archives. The species, as differentiated in this paper, is a NE Atlantic form, and some doubt must be expressed as to the status of reports from the NW Atlantic (Brinkmann, 1975; Zubchenko, 1980) which may represent *N. pusilla*.

N. anarrhichae is stenoxenic to fishes of the perciform genus *Anarrhichas*, the most frequently reported host being *A. lupus* with 71% of records. This may well reflect the more frequent examination of this common species. It apparently occurs rather locally, and was not often found by Bray (1987) in British waters, and we have found it only once recently despite several attempts. Elsewhere it can be found at high prevalence and intensity. Shulman & Shulman-Albova (1953) reported a prevalence of 73.3% in *A. lupus* from the White Sea, and Polyansky (1955) and Zubchenko (1980) reported a 50% prevalence in *A. minor* in the Barents Sea and the NW Atlantic, respectively. The only report from *A. denticulatus* is of a prevalence of 33% in the Barents Sea (Polyansky, 1955). Intensities may be high, up to 3,000 (mean 1,000) in *A. lupus* according to Shulman & Shulman-Albova (1953) and Polyansky (1955) found 'several 1,000' per fish. Kjøie (1983) reported hundreds of immature worms in *Pleuronectes platessa* and *Limanda limanda*. According to Kjøie (1968), 6.8% of the gastropod *Buccinum undatum* are infected with rediae in the Øresund.

***Neophasis pusilla* Stafford, 1904 (Fig. 9)**

Material studied

Anarrhichas lupus L. [urinary bladder] Eastern Canada – type-material, NMCP 1900–1820.

Anarrhichas lupus L. [intestine] Banquereau, Nova Scotia (44° N, 57° W, depth 76 m, July, 1975), BM(NH) 1977.2.14.2–6 (see Bray, 1979).

Description

The type-slide bears 6 specimens, only one of which is mature and is mounted laterally. These specimens were redescribed by Miller (1941).

Important measurements of the only mature specimen are: length 625, forebody 43% of body-length, oral sucker 95 long, ventral sucker 80 long, sucker-length ratio 1:0.89, prepharynx 65 long, pharynx 70 long, ovary 80 long, anterior testis 85 long, posterior testis 105 long, testis overlap 73%, post-testicular region 87 (14% of body length),

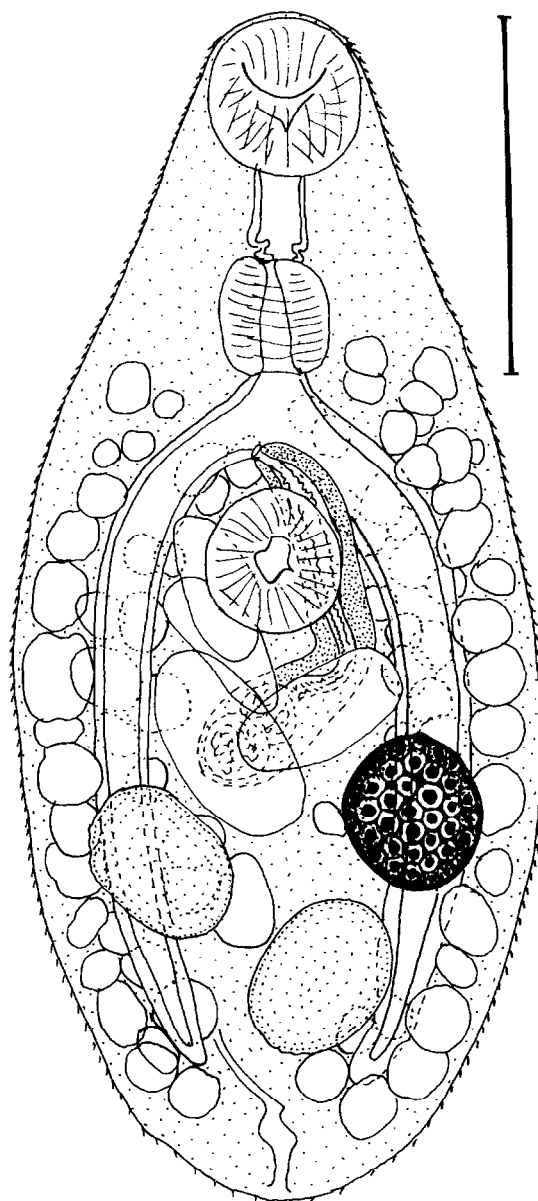


Fig. 9. *Neophasis pusilla* Stafford. Ventral view. BM(NH) 1977.2.14.2–6. Scale-bar: 200 μ m.

3 eggs at about 80×63 . Tegumental spination complete. Eye-spots discrete.

The 5 immature specimens are 490–560 long, with a sucker-width ratio of 1:0.96–1.04. The worms bear spines all over or practically so and in all but one worm 2 discrete eye-spots were seen. The odd specimen has only one discrete eye-spot.

In addition 99 whole-mounts and 4 sets of serial sections were studied from Banquereau. This spe-

cies is so similar to *N. anarrhichae* that a full description is not necessary. The points differentiating this species from *N. anarrhichae* are mentioned elsewhere and in Table I. Full measurements of 10 whole-mounts are given in Table III.

Type-host and locality: *Anarrhichas lupus*, Eastern Canada.

Records: 1. Stafford (1904), 2. Miller (1941), 3. Brinkmann (1975), 4. Bray (1979), 5. Present study.

Descriptions: 1,2,3,4,5.

Definitive hosts: Anarrhichadidae: *Anarrhichas lupus* (1,2,4,5), *A. minor* (3).

Sites: Urinary bladder (1,2,5), gall-bladder (3), intestine (4,5).

Distribution: 21 Atlantic, NW [E. Canada (1,2,5), Nova Scotia (4,5)], W. Greenland (3)]

Discussion

This species may be synonymous with *N. anarrhichae*, in which case its name would take priority. It is reported from various sites in the host. Bray (1979) reported it in one of eight specimens of *A. lupus* examined. It is possible that records of *N. anarrhichae* (or its synonyms) from the NW Atlantic represent this species. Zubchenko (1980) reported *N. anarrhichae* in *A. lupus* and *A. minor* with prevalences of 46.7% and 50%, respectively. The intensity was high, with a range of 4–1,364 (mean 180.5) in *A. lupus* and 3–764 (mean 88.4) in *A. minor*.

Other species

Neophasis symmetrorchis Machida, 1984

Type-host and locality: *Careproctus trachysoma*, off Yamagata, Sea of Japan.

Record, Description: Machida (1984).

Definitive host: Cyclopteridae: *Careproctus trachysoma*.

Site: Intestine.

Distribution: 61 Pacific, NW [Sea of Japan].

Comment: Machida (1984) used the position of the ventral sucker, testes and ovary plus the extent

of the cirrus-sac to distinguish this species. The ovary is dextral to the ventral sucker, a condition unique in the genus, and the cirrus-sac is recurved and does not reach into the hindbody. These features look as if they should be related to flattening at fixation, but other specimens from the same host described by Machida (1984) as *N. oculatus* and presumably fixed in the same way show more or less normal *N. oculatus* features, but with almost tandem testes. Machida (1984) based his study on 12 specimens of *N. oculatus* and 23 of *N. symmetrorchis*, so some credence must be given to his results and the latter species be retained on the basis of ovary and cirrus-sac position, although the testes arrangement is similar to that of other forms of *N. oculatus*.

Neophasis spp. **innom.**

Records: 1. Marasaev (1984), 2. Galaktionov & Marasaev (1986).

Life-cycle:

First intermediate hosts: Gastropoda: *Cryptonatica clausa* (1,2), *Neptunea borealis* (1,2), *N. despecta* (1).

Distribution: 27 Atlantic, NE [Murmansk Region (1), Barents Sea (1,2)].

Neophasis ochotensis Gubanov, 1954 **nomen nudum**

Record: Gubanov (1954).

Description: None.

Definitive host: Hexagrammidae: *Hexagrammos octogrammus*.

Site: Intestine.

Distribution: 61 Pacific NW [Sea of Okhotsk].

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References

- Appy, R.G. & Burt, M.D.B. (1982) Metazoan parasites of cod, *Gadus morhua* L., in Canadian Atlantic waters. *Canadian Journal of Zoology*, **60**, 1,573–1,579
- Arthur, J.R. & Arai, H.P. (1984) Annotated checklist and bibliography of parasites of herring (*Clupea harengus* L.). *Canadian Special Publication of Fisheries and Aquatic Sciences*, **70**, 26 pp.
- Baeva, O.M. (1968) [Helminth fauna of *Pleurogrammus azonus* in the Sea of Japan.] In: Skrjabin, K.I. & Mamaev, Y.L. (Eds) [*Helminths of animals of the Pacific Ocean.*] Moscow: Izdatel'stvo Nauka, pp. 80–88 (In Russian).
- Bauer, O.N. (1948) [Parasites of fish in the Lena River.] *Izvestiya Vsesoyuznogo Nauchno-Issledovatel'skogo Instituta Ozer'nogo i Rechnogo Rybnogo Khozyaistva*, **27**, 157–174 (In Russian).
- Bray, R.A. (1979) Digenea in marine fishes from the eastern seaboard of Canada. *Journal of Natural History*, **13**, 399–431.
- Bray, R.A. (1987) A study of the helminth parasites of *Anarhichas lupus* (Perciformes: Anarhichadidae) in the North Atlantic. *Journal of Fish Biology*, **31**, 237–264.
- Bray, R.A. (1988) A discussion of the status of the subfamily Baccigerinae Yamaguti, 1958 (Digenea) and the constitution of the family Fellodistomidae Nicoll, 1909. *Systematic Parasitology*, **11**, 97–112.
- Bray, R.A. & Gibson, D.I. (1990) The Lepocreadiidae (Digenea) of fishes of the north-east Atlantic: review of the genera *Opechona* Looss, 1907 and *Prodistomum* Linton, 1910. *Systematic Parasitology*, **15**, 159–202.
- Brinkmann, A. Jr. (1975) Trematodes from Greenland. *Meddelelser om Grønland*, **205**, 2–88.
- Brooks, D.R., Bandoni, S.M., Macdonald, C.A. & O'Grady, R.T. (1989) Aspects of the phylogeny of the Trematoda Rudolphi, 1808 (Platyhelminthes: Cercomeria). *Canadian Journal of Zoology*, **67**, 2,609–2,624.
- Brooks, D.R., O'Grady, R.T. & Glen, D.R. (1985) Phylogenetic analysis of the Digenea (Platyhelminthes: Cercomeria) with comments on their adaptive radiation. *Canadian Journal of Zoology*, **63**, 411–443.
- Cable, R.M. & Hunninen, A.V. (1942) Studies on *Deropristis inflata* (Molin), its life history and affinities to trematodes of the family Acanthocolpidae. *Biological Bulletin. Marine Biological Laboratory, Woods Hole. Massachusetts*, **82**, 292–312.
- Chubrik, G.K. (1966) [Fauna and ecology of trematode larvae from molluscs in the Barents and White Seas.] *Trudy Murmanskii Biologicheskii Institut*, **10**(14), 78–166 (In Russian).
- Dogiel, V.A. & Rozova, A. (1941) Die Parasiten des *Myoxocephalus quadricornis* in verschiedenen Gebieten seiner verbreitung. *Uchenye Zapiski Leningradskogo Gosudarstvennogo Universiteta, Leningrad*, (74), Seriya Biologicheskikh Nauk, (18), 4–19 (In Russian).
- Dollfus, R.P. (1973) Parasitologia mauritanica. Digénétiques de Téléostéens. 1^{re} note. Du genre *Stephanochasmus* A. Looss, 1900 (Trematoda Digenea). *Bulletin de l'Institut Fondamental d'Afrique Noire*, **34**, 809–827.
- Faust, E.C. (1918) Eye-spots in Digenea. *Biological Bulletin. Marine Biological Laboratory, Woods Hole, Massachusetts*, **35**, 117–127.
- Fernandes, B.M.M. & Souza, S.V. de (1973) Sobre uma nova espécie do gênero *Acanthocolpus* Lühe, 1906. *Memorias do Instituto Oswaldo Cruz*, **71**, 241–245.
- Galaktionov, K.V. & Marasaev, S.F. (1986) Ecological analysis of trematode fauna of benthic molluscs in the southeast region of the Barents Sea. *Parazitologiya*, **20**, 455–460 (In Russian).
- Gibson, D.I. & Bray, R.A. (1982) A study and reorganization of *Plagioporus* Stafford, 1904 (Digenea: Opecoelidae) and related genera, with special reference to forms from European Atlantic waters. *Journal of Natural History*, **16**, 529–559.
- Gibson, D.I. & Bray, R.A. (1986) The Hemiuroidae (Digenea) of fishes from the north-east Atlantic. *Bulletin of the British Museum (Natural History)* (Zoology series), **51**, 1–125.
- Gubanov, N.M. (1954) [Helminths of some animals of commercial importance of the Sea of Okhotsk and the Pacific Ocean.] *Trudy Gel'mintologicheskoi Laboratorii*, **7**, 380–381 (In Russian).
- Gupta, S.P. & Gupta, R.C. (1980) Three new trematodes of the family Acanthocolpidae Luhe, 1909 from marine fishes of Puri, Orissa. *Indian Journal of Helminthology*, **32**, 61–71.
- Gupta, V. & Ahmad, J. (1981) Digenetic trematodes of marine fishes. On three trematodes of the genus *Acanthocolpus* Lühe, 1906 from marine fishes of Bay of Bengal, at Puri coast, Orissa. *Rivista di Parassitologia*, **42**, 61–66.
- Hafeezullah, M. (1978) Acanthocolpid trematodes of marine fishes of India, with considerations on synonymies in the group. *Bulletin of the Zoological Survey of India*, **1**, 29–36.
- Issaitschikov, I.M. (1928) Contributions to parasitic worms of some groups of vertebrates from Russian Arctic. *Trudy Morskogo Nauchnogo Instituta*, **3**(2), 1–79 (In Russian).
- Ivanov, A.S. & Murygin, S.I. (1937) To the knowledge of the helminthofauna of fishes of the Volga-river. In: Schulz, R.-E.S. & Gnyedina, M.P. (Eds) *Papers on helminthology published in commemoration of the 30 year jubileum of the scientific, educational and social activities of the honoured worker of science K.I. Skrjabin, M. Ac. Sci. and of fifteenth anniversary of the All-Union Institute of Helminthology*. Moscow: All-Union Lenin Academy of Agricultural Sciences, 253–268 (In Russian).
- Køie, M. (1968) *Buccinum undatum*'s larvale trematoder, deres indflydelse på vaertens fertilitet og udvikling af sekundære køns karakterer. *Information, Åbo Akademi*, **9**, 21–22.
- Køie, M. (1969) On the endoparasites of *Buccinum undatum* L. with special reference to the trematodes. *Ophelia*, **6**, 251–279.
- Køie, M. (1971) On the histochemistry and ultrastructure of the redia of *Neophasis lageniformis* (Lebour, 1910) (Trematoda, Acanthocolpidae). *Ophelia*, **9**, 113–143.
- Køie, M. (1973a) The host-parasite interface and associated

- structures of the cercaria and adult *Neophasis lageniformis* (Lebour, 1910). *Ophelia*, **12**, 205–219.
- Køie, M. (1973b) The ultrastructure of the caecal epithelium of the intraredial cercaria of *Neophasis lageniformis* (Lebour, 1910) (Trematoda, Acanthocolpidae). *Zeitschrift für Zellforschung und Mikroskopische Anatomie*, **139**, 405–416.
- Køie, M. (1974) The fine-structure of rediae and daughter sporocysts in relation to their effect on the host tissue. *Proceedings. Third International Congress of Parasitology* (Munich), **1**, 417–418.
- Køie, M. (1978) On the morphology and life-history of *Stephanostomum caducum* (Looss 1901) Manter 1934 (Trematoda, Acanthocolpidae). *Ophelia*, **17**, 121–133.
- Køie, M. (1983) Digenetic trematodes from *Limanda limanda* (L.) (Osteichthyes, Pleuronectidae) from Danish and adjacent waters, with special reference to their life-histories. *Ophelia*, **22**, 201–228.
- Køie, M. (1984) Digenetic trematodes from *Gadus morhua* L. (Osteichthyes, Gadidae) from Danish and adjacent waters, with special reference to their life-histories. *Ophelia*, **23**, 195–222.
- Køie, M. (1985a) *The surface topography and life-cycles of digenetic trematodes in Limanda limanda (L.) and Gadus morhua L.* (Summary of doctoral thesis, University of Copenhagen). Helsingør: Marine Biological Laboratory, 20 pp.
- Køie, M. (1985b) On the morphology and life-history of *Lepidapedon elongatum* (Lebour, 1908) Nicoll, 1910 (Trematoda, Lepocreadiidae). *Ophelia*, **24**, 135–153.
- Korotaeva, V.D. (1968) [Helminth fauna of Cottidae.] In: Skrjabin, K.I. & Mamaev, Y.L. (Eds) [*Helminths of animals of the Pacific Ocean.*] Moscow: Izdatel'stvo Nauka, 89–96 (In Russian).
- La Rue, G.R. (1956) The classification of digenetic Trematoda: a review and a new system. *Experimental Parasitology*, **6**, 306–349.
- Lebour, M.V. (1905) Notes on Northumbrian trematodes. *Northumberland Sea Fisheries Committee. Report on the Scientific Investigations for the year 1905*, 100–105.
- Lebour, M.V. (1908) Fish trematodes of the Northumberland coast. *Northumberland Sea Fisheries Committee. Report on the Scientific Investigations for the year 1907*, 23–67.
- Lebour, M.V. (1910) *Acanthopsolus lageniformis*, n. sp., a trematode in the catfish. *Northumberland Sea Fisheries Committee. Report on the Scientific Investigations for the year 1909, and to June 15th, 1910*, 29–35.
- Lebour, M.V. (1912) A review of British marine cercariae. *Parasitology*, **4**, 416–456.
- Levinsen, G.M.R. (1881) Bidrag til Kundskab om Grønlands Trematodfauna. *Oversigt over det Kongelige Danske Videnskabernes Selskabs Forhandlinger*, **23**(1), 52–84.
- Linstow, O. von (1889) *Compendium der Helminthology. Nachtrag. Die Literatur der Jahre 1878–1889*. Hannover: Hahn'sche Buchhandlung, 151 pp.
- Lühe, M. (1906) Report on the trematode parasites from the marine fishes of Ceylon. *Royal Society's Report on the Pearl Oyster*, **5**, 97–108.
- Machida, M. (1984) Trematodes of marine fishes from depth of 200–400 m off Yamagata, the Japan Sea. *Memoirs of the National Science Museum. Tokyo*, **17**, 101–110.
- Machida, M., Araki, J., Kamiya, H. & Ohbayashi, M. (1972) Trematodes collected from sea fishes of the Hidaka District, Hokkaido. *Memoirs of the National Science Museum, Tokyo*, **5**, 1–9 (In Japanese).
- MacKenzie, K. & Liversidge, J.M. (1975) Some aspects of the biology of the cercaria and metacercaria of *Stephanostomum baccatum* (Nicoll, 1907) Manter, 1934 (Digena: Acanthocolpidae). *Journal of Fish Biology*, **7**, 247–256.
- Madhavi, R. (1976) Digenetic trematodes from marine fishes of Waltair coast, Bay of Bengal. Family Acanthocolpidae. *Rivista di Parasitologia*, **37**, 115–128.
- Mamaev, Y.L. & Oshmarin, P.G. (1966) Trematodes of the family Acanthocolpidae Lühe, 1901 in herrings of North-Vietnam Bay. *Helminthologia*, **7**, 155–164 (In Russian).
- Marasaev, S.F. (1984) Three types of cercariae from benthic molluscs of the central and south-east parts of the Barents Sea. In: Polyansky, Y.I., Galaktionov, K.V. & Dobrovolsky, A.A. (Eds). *Ecological-parasitological investigations of northern seas*. Apatity: Kola Branch of Academy of Sciences of the USSR, Murmansk Biological Institute, 51–59 (In Russian).
- Martin, W.E. (1939) Studies on the trematodes of Woods Hole. II. The life cycle of *Stephanostomum tenue* (Linton). *Biological Bulletin. Marine Biological Laboratory, Woods Hole, Massachusetts*, **77**, 65–73.
- Miller, M.J. (1941) A critical study of Stafford's report on "Trematodes of Canadian fishes" based on his trematode collection. *Canadian Journal of Research*, **19D**, 28–52.
- Nicoll, W. (1909) A contribution towards a knowledge of the entozoa of British marine fishes. Part II. *Annals and Magazine of Natural History, (Series 8)*, **4**, 1–25.
- Odhner, T. (1905) Die Trematoden des arktischen Gebietes. *Fauna Arctica*, **4**, 289–374.
- Peters, L.E. (1961) The allocreadioid problem with reference to the excretory system in four types of cercariae. *Proceedings of the Helminthological Society of Washington*, **28**, 102–108.
- Poche, F. (1926) Das System der Platyzoaria. *Archiv für Naturgeschichte, (Abteilung A)*, **91**, 1–458.
- Polyansky, Y.I. (1955) Studies on the parasitology of the fish in the northern seas of the USSR. Parasites of fish of the Barents Sea. *Trudy Zoologicheskogo Instituta*, **19**, 5–170 (In Russian: English translation (1966) Israel Program for Scientific Translations, Cat. No. 1655, 158 pp.)
- Polyansky, Y.I. & Shulman, S.S. (1956) [Changes in the parasite fauna of fishes with age.] *Trudy Karelo-Finskogo Filiala Akademii Nauk SSSR*, **4**, 3–26 (In Russian).
- Shimazu, T. (1984) *Proctoeces maculatus* from Wakkanai, North Hokkaido, Japan, with comments on the validity of some other species in the genus *Proctoeces* (Trematoda: Fellodistomidae). *Proceedings of the Japanese Society of Systematic Zoology*, **29**, 1–15.
- Shulman, S.S. & Shulman-Albova, R.E. (1953) [*Parasites of fishes of the White Sea.*] Moscow, Leningrad: Izdatel'stvo Akademii Nauk SSSR, 198 pp. (In Russian).
- Shulman-Albova, R.E. (1952) [Fish parasites of the White Sea around the village of Gridina. Part I. Monogenetic and digenetic trematodes.] *Uchenye Zapiski Karelo-Finskogo Gosudarstvennogo Universiteta*, **4**(3), 78–97 (In Russian).
- Skrjabin, K.I. (1954) [Family Acanthocolpidae Lühe, 1909.] *Trematody Zhivotnykh i Cheloveka. Osnovy Trematodologii*, **9**, 45–224 (In Russian).
- Skrjabin, E.S. (1963) On the helminths of marine fishes in Kamchatka. *Trudy Gel'mintologicheskoi Laboratorii*, **13**, 313–329 (In Russian).
- Srivastava, H.D. (1939) Three new parasites of the genus *Acanthocolpus* Lühe, 1906 (Family – Acanthocolpidae). *In-*

- dian *Journal of Veterinary Science and Animal Husbandry*, **9**, 213–216.
- Stafford, J. (1904) Trematodes from Canadian fishes. *Zoologischer Anzeiger*, **27**, 481–495.
- Strelkov, J.A. (1960) Endoparasitic worms of marine fishes of East Kamchatka. *Trudy Zoologicheskogo Instituta, Leningrad*, **28**, 147–196 (In Russian).
- Stunkard, H.W. (1961) *Cercaria dipteroerca* Miller and Northup, 1926 and *Stephanostomum dentatum* (Linton, 1900) Manter, 1931. *Biological Bulletin. Marine Biological Laboratory, Woods Hole, Massachusetts*, **120**, 221–237.
- Ward, H.B. (1938) On the genus *Deropristsis* and the Acanthocolpidae (Trematoda). In: *Livro Jubilar do Professor Lauro Travassos*. Rio de Janeiro: Typographia do Instituto Oswaldo Cruz, 509–522.
- Wolfgang, R.W. (1955) Studies on the trematode *Stephanostomum bacatum* (Nicoll, 1907). III. Its life cycle. *Canadian Journal of Zoology*, **33**, 113–128.
- Yamaguti, S. (1953) *Systema helminthum. Part I. Digenetic trematodes of fishes*. Tokyo: S. Yamaguti, 405 pp.
- Yamaguti, S. (1958) *Systema helminthum. Volume I. Digenetic trematodes*. New York: Interscience Publishers Inc., 1,575 pp.
- Yamaguti, S. (1971) *Synopsis of digenetic trematodes of vertebrates*. Tokyo: Keigaku Publishing Co., Vol. 1, 1,074 pp., Vol. 2, 349 pls.
- Yamaguti, S. (1975) *A synoptical review of the life histories of digenetic trematodes of vertebrates, with special reference to the morphology of their larval forms*. Tokyo: Keigaku Publishing Co., 575 pp., 219 pls.
- Zelikman, E.A. (1966) [Ecology of some parasites associated with parts of the northern shores of Kandalak Bay.] *Trudy Murmanskii Biologicheskii Institut*, **10**(14), 7–76 (In Russian).
- Zhukov, E.V. (1960) Endoparasitic worms of the fishes in the Sea of Japan and South-Kuril shallow-waters. *Trudy Zoologicheskogo Instituta, Leningrad*, **28**, 3–146 (In Russian).
- Zhukov, E.V. (1963) On the fauna of parasites of fishes of the Chukotsk Peninsula and adjoining seas. II. Endoparasitic worms of marine and freshwater fishes. *Parazitologicheskii Sbornik*, **21**, 96–139 (In Russian).
- Zubchenko, A.V. (1980) Parasitic fauna of Anarhichadidae and Pleuronectidae families of fish in the Northwest Atlantic. *International Commission for the Northwest Atlantic Fisheries. Selected Papers*, **6**, 41–46.