ORIGINAL PAPER

Heliconema longissimum (Ortlepp, 1923) (Nematoda: Physalopteridae) from *Pisodonophis boro* (Teleostei: Ophichthidae) in Thailand, with remarks on the taxonomy of the Proleptinae Schulz, 1927

František Moravec · Horst Taraschewski · Malinee Thairungroj Anantaphruti · Wanna Maipanich · Thitiporn Laoprasert

Received: 19 January 2006/Accepted: 11 April 2006/Published online: 29 November 2006 © Springer Science+Business Media B.V. 2006

Abstract Physalopterid nematodes identified as *Heliconema longissimum* (Ortlepp, 1923) were collected from the stomach of rice-paddy eels *Pisodonophis boro* (Hamilton) (Anguilliformes: Ophichthidae) from two brackish-water localities (mangroves) in Thailand: one in Phan-Nga Province, southwestern Thailand, northeast of Phuket Island, and one in Ranong Province, near the border with Myanmar. Study of the morphology of this hitherto insufficiently known nematode species, including its first SEM examination, enabled a detailed redescription of *H. longissimum*. Present taxonomic problems in the subfamily Proleptinae Schulz, 1927 are

Abteilung Ökologie und Parasitologie, Zoologisches Institut der Universität Karlsruhe (TH), Kaiserstrasse 12, 76128 Karlsruhe, Germany

M. T. Anantaphruti · W. Maipanich Department of Helminthology, Faculty of Tropical Medicine, Mahidol University, 420/6 Ratchawithi Road, Ratchadewee, Bangkok 10400, Thailand

T. Laoprasert

Department of Fisheries, Aquatic Animal Health Research Institute, Paholyothin Road, Chatuchak, Bangkok 10900, Thailand discussed, where a new delimitation of *Proleptus* Dujardin, 1845, *Heliconema* Travassos, 1919 and *Paraleptus* Wu, 1927 is proposed based on the cephalic dentation. *H. minnanensis* [sic] Damin & Heqing, 2001 is transferred to *Paraleptus* Wu, 1927 as *P. minnanensis* (Damin & Heqing, 2001) n. comb. and *Paraleptus chiloscyllii* Yin & Zhang, 1983 transferred by Damin & Heqing (2001) to *Heliconema*, is retained in *Paraleptus. H. ahiri* Karve, 1941 is considered a junior synonym of *H. longissimum* (Ortlepp, 1923). The present finding of *H. longissimum* in *Pisodonophis boro* represents the first host record and the first record of this nematode from Thailand.

Introduction

To date, there are generally few data on the helminth parasites of freshwater, brackish-water and marine fishes in Thailand (Sirikanchana, 1982; Sood, 1989) and no anguilliform fish of this region has so far been examined for parasites. During recent years, studies on the parasites of anguilliforms in different regions of the world have been of special interest to fish parasitologists, particularly in the connection with questions of the origin and distribution of the highly pathogenic swimbladder nematodes of the genus *Anguillicola* Yamaguti, 1935.

F. Moravec (⊠)

Institute of Parasitology, Biological Centre, Academy of Sciences of the Czech Republic, Branišovská 31, 370 05 České Budějovice, Czech Republic e-mail: moravec@paru.cas.cz

H. Taraschewski

In March 2001, a collection of the metazoan parasites of four species of anguilliform fishes (eels), *Anguilla bicolor* McClelland, *A. japonica* Temminck & Schlegel, *A. marmorata* Quoy & Gaimard and *Pisonodophis boro* (Hamilton) was made during a short stay by one of us (H.T.) in Thailand. Results of the systematic evaluation of nematode material from *Anguilla bicolor* have been published by Moravec et al. (2006), whereas those concerning nematodes found in *P. boro* are presented herein.

Materials and methods

Eels were caught in fish traps by local fishermen. After their capture they were examined for parasites within 24 h. All eels infected with physalopterids were the rice-paddy eel *Pisodonophis boro* (Hamilton), 15 specimens of which were examined (total body length 70–92 cm): 10 from mangroves (brackish water) in Phan-Nga Province, southwestern Thailand, northeast of Phuket Island, and five from mangroves in Ranong Province, near the border with Myanmar.

The nematodes found were washed in physiological saline and then fixed in either boiling or cold 70% ethanol and preserved in 70% ethanol. For light microscopical examination the nematodes were cleared with glycerine. Drawings were made with the aid of a Zeiss microscope drawing attachment. Specimens used for scanning electron microscopy (SEM) were post-fixed in 1% osmium tetroxide, dehydrated through a graded alcohol series, critical point dried and sputter-coated with gold; they were examined using a JSM-6300 scanning electron microscope at an accelerating voltage of 15 kV. All measurements are in micrometres unless otherwise stated. The scientific names of fishes are according to Froese and Pauly (2005).

Family Physalopteridae Railliet, 1893 Subfamily Proleptinae Schulz, 1927

Heliconema longissimum (Ortlepp, 1923)

Syns Physaloptera longissima Ortlepp, 1923; Heliconema anguillae Yamaguti, 1935; H. ahiri Fig. 1 Heliconema longissimum (Ortlepp, 1923) from Pisodonophis boro. A,B, anterior end of body, lateral and dorsoventral views; C, cephalic end, apical view (reconstructed from SEM micrograph); D, small (right) spicule, lateral view; E, distal end of large (left) spicule, lateral view; F, cephalic end of male, lateral view; G, cephalic end of female, dorsoventral view; H, deirid, lateral view; I, mature egg; J, region of vulva, lateral view; K, tail tip of male, subventral view; L, caudal end of gravid female, lateral view; M,N, posterior end of male, lateral and ventral views. Scale-bars in mm

Karve, 1941; Notopteroides alatae Majumdar, 1965; Paraleptus komiyai Sood, 1970

Host: Rice-paddy eel Pisodonophis boro (Hamilton) (Anguilliformes: Ophichthidae). Site of infection: Stomach.

Localities: Mangroves (brackish water) in Phan-Nga Province, southwestern Thailand, northeast of Phuket Island, and mangroves from Ranong Province, near the border with Myanmar.

Infection: Phan-Nga: prevalence 60% (6 of 10 eels examined); intensity 2–33 (mean 19). Ranong: prevalence: in 2 of 5 eels examined; intensity 1 and 7.

Voucher material: Institute of Parasitology, ASCR, in České Budějovice (cat. no. N–862).

Description (Figs. 1, 2)

General. Body medium-sized, whitish, with thick transversely striated cuticle. Cephalic end rounded. Cuticle in cephalic region inflated to form cephalic vesicle extending posteriorly to level of deirids. Oral aperture dorsoventrally elongate, oval, rather large, surrounded by 2 massive, rounded lateral pseudolabia; pseudolabium roughly rectangular in apical view (Fig. 2A), bearing 2 large submedian (dorsolateral and ventrolateral) cephalic papillae and oval lateroterminal depression; small lateral amphid situated at base of pseudolabium. Inner surface of each pseudolabium with elongate lateral mound bearing marked triangular terminal lateral tooth (internolateral tooth) and simple flat tooth at each dorsoventral extremity; surface of each pseudolabium forming 2 distinct small, narrow submedian areas demarcated by grooves between pseudolabium proper and inner lateral mould, in apical view being broadest near lateral tooth and





Fig. 2 Heliconema longissimum (Ortlepp, 1923) from Pisodonophis boro, SEM micrographs. A, cephalic end, apical view; B, precloacal region of male, ventral view; C, posterior end of male, lateral view; D, tail of male, ventral view

gradually narrowing towards each dorsoventral extremity (Fig. 2A); any series of denticles absent. Buccal cavity short. Oesophagus divided into short, narrow anterior muscular portion and much longer, wide glandular portion. Nerve-ring encircles muscular oesophagus posterior to its middle. Small simple deirids situated at level of nerve-ring. Excretory pore slightly posterior to anterior end of glandular oesophagus. Tail of both sexes with rounded tip. *Male* (5 specimens). Length of body 23.50–27.00 mm, maximum width 530–612. Pseudolabia 12–18 long. Cephalic vesicle 354–422 long, 218–258 wide. Entire oesophagus 3.73–4.03 mm long, representing 14–17% of body length; muscular oesophagus 476–571 long, 68–95 wide; glandular oesophagus 3.16–3.50 mm long, 177–218 wide; length ratio of parts of oesophagus 1:5.53–6.89. Nerve-ring, deirids and excretory pore 340–408, 313–422 and 422–503, respectively, from anterior extremity. Caudal end spirally coiled, provided

with broad lateral alae supported by 4 twin pairs of subventral pedunculate pre-anal papillae and 6 single pairs of subventral postanal papillae, of which papillae of first 4 pairs are rather large and pedunculate, and those of last 2 pairs are very small and sessile; additional pair of rather small postanal sessile papillae situated ventrally at level of first subventral postanal pair. Each caudal papilla surrounded by ring consisting of numerous small cuticular, papilla-like protuberances (Fig. 2 B,D). Pair of minute phasmids present just posterior to last pair of postanal papillae. Cloacal lips somewhat elevated. Ventral pre-cloacal surface with about 17 longitudinal tesselated ridges (area rugosa). Spicules unequal and dissimilar; left spicule 520-734 long, with sharply pointed distal tip and distal half (approximately) alate except for conical tip; right spicule broader, boat-shaped, 232-286 long, tapered towards distal tip. Length ratio of spicules 1:1.82-3.16. Length of tail 381-422.

Female (5 gravid specimens). Length of body 28.19-39.07 mm, maximum width 578-762. Pseudolabia 12-18 long. Cephalic vesicle 422-435 long, 231-340 wide. Entire oesophagus 4.38-5.00 mm long, 13-16% of body length; muscular oesophagus 530-680 long, 82-122 wide; glandular oesophagus 3.85–4.38 mm long, 218-340 wide; length ratio of parts of oesophagus 1:5.66-7.26. Nerve-ring, deirids and excretory pore 367-422, 408-435 and 544-585, respectively, from anterior extremity. Rectum a hyaline tube. Vulva situated 10.92-25.64 mm from anterior end of body, at 39-66% of body length. Vagina narrow, muscular, initially directed anteriorly from vulva and then oriented posteriorly. Uteri containing numerous oval, thick-shelled, embryonated (larvated) eggs; eggs $75-81 \times 42-48$, with wall 5 thick. Tail short, 136-313 long, with rounded tip; pair of small lateral phasmids present near tail tip.

Discussion

The general morphology of nematode specimens of the present material shows that they belong to the physalopterid subfamily Proleptinae of the family Physalopteridae following the conception of Chabaud (1975). However, mainly because of the many inadequate species descriptions of proleptines from fishes and occasionally the use of unsuitable generic criteria, the taxonomy of this group, and especially regarding the delimitation of the genera, remains somewhat confused.

Within the Proleptinae, Chabaud (1975) recognised four genera, *Proleptus* Dujardin, 1845, *Heliconema* Travassos, 1919, *Paraleptus* Wu, 1927 and *Bulbocephalus* Rasheed, 1966, whereas the morphologically similar *Pseudoproleptus* Khera, 1955, originally assigned to the Physalopteridae, was listed in the habronematoid family Cystidicolidae Skryabin, 1946, as previoulsy suggested by Chabaud (1965).

Unfortunately, in the key to genera of Proleptinae given by Chabaud (1975), differential features, such as the position of the vulva and the length ratio of the spicules, are used, which, in our opinion, are only of specific significance. For example, in different species of the cystidicolid genus Spinitectus Fourment, 1883, the situation of the vulva is highly variable and may be near the anus (S. allaeri Campana-Rouget, 1961), at about the middle of the body (S. multipapillatus Petter, 1987) or in the first third of the body length (S. agonostomi Moravec & Baruš, 1971). As pointed out by Threlfall and Carvajal (1984) in Heliconema psammobatidus Threlfall and Carvajal, 1984, and as observed in the present material, the vulva may be somewhat pre-equatorial or postequatorial within the same species. Regarding the length ratio of spicules, this may be very variable within a genus, as previously mentioned by Sood (1970); for example, between different species of Rhabdochona Railliet, 1916, where the spicules may be equally long (R. equispiculata Moravec & Scholz, 1991) or very unequal (1:18-23 in R. kidderi texensis Moravec & Huffman, 1988); and a similar situation occurs within the camallanid genus Procamallanus Baylis, 1923.

In our opinion, the delimitation of genera within the Proleptinae, which are objectively determined by their type species, should be based on the cephalic features. It has already been suggested by Chitwood and Wehr (1934) that the morphological structure of the cephalic region should be used as an important character in the classification of spiruroid nematodes. In physalopterids, Chabaud (1975) regarded the cephalic dentation, which corresponds to a great extent with a distribution in one or another group of hosts, to be a valuable character.

Of the four above-mentioned genera of the Proleptinae, *Bulbocephalus* is easily distinguished by the unusual structure of its cephalic end (presence of protrusible oesophageal lobes, reduced pseudolabia, absence of cephalic collarette). The characters of the remaining three genera are rather similar and, in fact, there are frequent confusions in assigning different species to these genera. In our opinion, there is a need to re-diagnose them on the basis of a detailed study of the cephalic structures of their type-species, all of which are inadequately described in this respect. Until a relevant revision is made, we suggest distinguishing these three genera on the basis of their cephalic dentation:

Proleptus: Each pseudolabium with a single internolateral tooth; outer rim of buccal cavity wall with a circumoral row of minute denticles (serrations). [These denticles were found in all three *Proleptus* spp. studied by SEM and are apparently a generic feature – see Specian, Ubelaker, & Dailey, 1975; Moravec, Van As, & Dyková, 2002.]. Mainly parasites of elasmobranchs.

Heliconema: Internal border of each pseudolabium with an internolateral tooth only and usually with a simple tooth at each dorsoventral extremity. Mostly parasites of teleosts, particularly anguilliforms.

Paraleptus: Internal border of each pseudolabium with a series of larger denticles in addition to the internolateral tooth. Mainly parasites of elasmobranchs.

In having many denticles in the buccal cavity, *Proleptus* and *Paraleptus* appear to be more closely related to each other than to *Heliconema*, as reflected by their common principle hosts (elasmobranchs). However, it is necessary to note that the cephalic structures of most proleptine species have not yet been studied in detail (preferably by SEM) and, accordingly, their present generic allocations may not be correct. With respect to the above delimitation of the genera, the recently described *Heliconema* *minnanensis* [sic] Damin & Heqing, 2001 should be transferred to *Paraleptus* as *P. minnanensis* (Damin & Heqing, 2001) n. comb.; and *P. chiloscyllii* Yin & Zhang, 1983, transferred by Damin and Heqing (2001) to *Heliconema*, should be retained in *Paraleptus*.

The morphology of the present material from Pisodonophis boro shows that they belong to a species of Heliconema, which is supported by their eel host. At present this genus includes the following 13 species, which are listed chronologically: H. heliconema Travassos, 1919 (type-species); H. longissimum (Ortlepp, 1923); H. brevispiculum Baylis, 1934; H. ahiri Karve, 1941; H. urolophi (Johnston & Mawson, 1951); H. baylisi Ogden, 1969; H. hamiltonii Bilgees & Khanum, 1970; H. serpens Fusco & Palmieri, 1980; H. izecksohni Fabio, 1982; H. psammobatidus Threlfall & Carvajal, 1984; H. kherai Gupta & Duggal, 1989; H. brooksi Crites & Overstreet, 1991; and H. savala Akram, 1996. Of these, H. hamiltonii, H. izecksohni and H. urolophi should be considered species inquirendae (Crites and Overstreet 1991; Moravec 1998).

The taxonomy of Heliconema spp. is complicated by the fact that some morphological structures are difficult to observe under the light microscope and, therefore, some species are evidently inadequately described. Moreover, Fusco and Palmieri (1980) started to use the numbers of ventral precloacal tesselated longitudinal ridges (area rugosa) as the principle differentiating feature between the species, which was followed by some subsequent authors. However, in our opinion, this feature is quite unreliable, because the number of such ridges is rather variable within a species and depends partly on the body size and age of the worm, as has been observed in some other spirurine nematodes (e.g. Rhabdochona spp.), where these may even be absent in younger specimens (Moravec, 1972).

The present specimens can easily be distinguished by the length ratio of their spicules (1:1.8– 3.2) from *H. heliconema* (1:12.7–20.0), *H. brooksi* (average 1:10.6), *H. psammobatidus* (1:4.1–4.3) and *H. baylisi* (1:1.1–1.4), whereas *H. brevispiculum* differs in possessing conspicuously large papillae in the last two postanal pairs. *H. serpens*, described from a snake in Malaysia, allegedly has only four pairs of postanal papillae and a spicule ratio averaging 1:1.7.

The general morphology, including the length ratio of the spicules, of the present specimens corresponds, more or less, to the existing descriptions of *H. longissimum* (see Ortlepp, 1923; Yamaguti, 1935; Ogden, 1969; Sood, 1970; De et al., 1978; De, 1988), except for some details in the structure of mouth and the number and arrangement of the postanal papillae. However, this species was not previously studied by SEM, and some details are hardly visible under the light microscope.

The differences mainly concern the postanal papillae: while Ogden (1969) described six pairs of these papillae, De, Ghosh, and Majumdar (1978) illustrated seven pairs (including phasmids), and it is worth noting that a group formed by the two last pairs of minute papillae and a pair of phasmids is extremely difficult to observe. However, De et al. (1978) did not find the pair of small sessile ventral papillae just posterior to the cloaca at the level of the first pair of postanal pedunculate papillae. But such papillae were illustrated in this species (reported as Paraleptus komiyai Sood, 1970) by Sood (1970), who, conversely, failed to observe the last two pairs of minute papillae. The pair of sessile ventral papillae located just posterior to the cloaca, as confirmed by our SEM observations, has not yet been reported for any other Heliconema species. Because of this, the present material is considered to be *H. longissimum*.

De et al. (1978) and De (1988) synonymised two species, *Paraleptus komiyai* Sood, 1970 and *Notopteroides alatae* Majumdar, 1965, both described from *Mastacembelus armatus* (Lacépède) in India, with *H. longissimum*. But Sood (1989) had considered the former as probably belonging to *H. ahiri*, a species described by Karve (1941) from *Anguilla bengalensis* (Gray) in India, which allegedly differs from *H. longissimum* in having three pairs of minute papillae (apparently including phasmids) near the tail tip (the tail was observed only in lateral view). However, because such papillae are also present in *H. longissimum*, we consider *H. ahiri* a junior synonym of *H. longissimum*.

Heliconema longissimum (reported as Physaloptera longissima) was first recorded by Ortlepp (1923) from "snakes" in Australia, but, as mentioned by Ogden (1969) and some previous authors, the host (snakes) of the type-material is doubtful. Later, it was recorded from the eels Anguilla bengalensis, A. japonica Temminck & Schlegel, A. mossambica (Peters) and A. pekinensis (a probable synonym of A. japonica) (Anguilliformes: Anguillidae) and from the swampeel Mastacembelus armatus (Synbranchiformes: Synbranchidae) in China, Japan, India and South Africa (Li, 1934; Yamaguti, 1935; Karve, 1941; Ogden, 1969; Sood, 1970; De et al, 1978; De, 1988; Taraschewski, Boomker, Knopf, & Moravec, 2005). The present finding represents new host and geographical records.

Acknowledgements Thanks are due to the staff of the Department of Helminthology, Faculty of Tropical Medicine, Mahidol University, Bangkok, to Dr Somboon Laoprasert, Chief of the Ranong Coastal Aquaculture Station, Ratchakrut, Muang and to Dr Supranee Chinabut, Director of the Aquatic Animal Health Research Institute, Kasetsart University, Bangkok, for various forms of support, such as transport and/or accommodation. We also thank the staff of the Laboratory of Electron Microscopy at the Institute of Parasitology, ASCR, České Budějovice, for their technical assistance and Mrs Irena Husáková of the Department of Helminthology of the same Institute for her help with the preparation of the illustrations. The authors are very grateful to Dr David I. Gibson, Natural History Museum, London for revising the English and his help with the literature. This study was supported by grant no. 524/06/0170 from the Grant Agency of the Czech "Ichthyoparasitology" Republic, Research Centre (LC522) and a research project of the Institute of Parasitology, ASCR (no. Z60220518).

References

- Chabaud, A. G. (1965). Classe des nématodes. Sous-classe des Secernentea (=Phasmidia auct.). Ordre des Spirurida. In P.-P. Grassé (Ed.), *Traité de Zoologie*, *Tome 4, fasc. III. Némathelminthes (Nématodes, Gordiacés), Rotifères, Gastrotriches, Kinorhynques* (pp. 1025–1151, 1187–1200). Paris: Masson et Cie.
- Chabaud, A. G. (1975). Keys to genera of the order Spirurida. Part 1. Camallanoidea, Dracunculoidea, Gnathostomatoidea, Physalopteroidea, Rictularioidea and Thelazioidea. In R. C. Anderson, A. G. Chabaud, & S. Willmott (Eds.), *CIH keys to the nematode parasites of vertebrates*. No. 3(1) (pp. 27). Farnham Royal: Commonwealth Agricultural Bureaux.

- Chitwood, B. G., & Wehr, E. E. (1934). The value of cephalic structures as characters in nematode classification, with special reference to the superfamily Spiruroidea. Zeitschrift für Parasitenkunde, 7, 273–335.
- Crites, J. L., & Overstreet, R. M. (1991). Heliconema brooksi n. sp. (Nematoda: Physalopteridae) from the ophichthid eel Ophichthus gomesi in the Gulf of Mexico. Journal of Parasitology, 77, 42–50.
- Damin, L., & Heqing, H. (2001). *Heliconema minnanensis* n. sp. (Physalopteroidea: Physalopteridae) and *Raphidascaris trichiuri* (Yin et Zhang) n. comb. (Ascaridoidea: Anisakidae) in marine fishes. *Journal* of Parasitology, 87, 1090–1094.
- De, N. C. (1988). Remarks on the validity of the species Notopteroides alatae Majumdar, 1965. Folia Parasitologica, 35, 281–284.
- De, N. C., Ghosh, M., & Majumdar, G. (1978). Records of some little known nematodes from Indian fishes. *Folia Parasitologica*, 25, 317–322.
- Froese, R., & Pauly, D. (Eds.). (2005). FishBase. World Wide Web electronic publication. www.fishbase.org, version 12/2005.
- Fusco, A. C., & Palmieri, J. R. (1980). Heliconema serpens sp. n. (Nematoda: Physalopteridae) and Camallanides malayensis sp. n. (Nematoda: Camallanidae) from Cerberus rhynchops (Schneider) (Reptilia: Colubridae) in Malaysia. Proceedings of the Helminthological Society of Washington, 47, 72–79.
- Karve, J. N. (1941). Some parasitic nematodes of fishes. I. Journal of the University of Bombay, New Series, 10B, 9–42.
- Li, H. C. (1934). Report on a collection of parasitic nematodes, mainly from North China. Part 2. Spiruroidea. *Transactions of the American Microscopical Society*, 53, 174–195.
- Moravec, F. (1972). General characterization of the nematode genus *Rhabdochona* with a review of the South American species. *Acta Societatis Zoologicae Bohemoslovacae*, *36*, 29–46.
- Moravec, F. (1998). Nematodes of freshwater fishes of the Neotropical Region. Prague: Academia, 464 pp.
- Moravec, F., Taraschewski, H., Thairungroj Anantaphruti, M., Maipanich, W., & Laoprasert, T. (2006). Procam-

allanus (*Spirocamallanus*) *anguillae* sp. n. (Camallanidae) and some other nematodes from the Indonesian shortfin eel *Anguilla bicolor* in Thailand. *Parasitology Research*, in press

- Moravec, F., Van As, J. G., Dyková, I. (2002). Proleptus obtusus Dujardin, 1845 (Nematoda: Physalopteridae) from the puffadder shyshark Haploblepharus edwardsii (Sciliorhinidae) from off South Africa. Systematic Parasitology, 53, 169–173.
- Ogden, C. G. (1969). A revision of the genus *Heliconema* Travassos, 1919, Physalopteridae (Nematoda). *Journal of Natural History*, *3*, 423–431.
- Ortlepp, R. J. (1923). The nematode genus *Physaloptera* Rud. *Proceedings of the Zoological Society of London*, 999–1107.
- Sirikanchana, P. (1982). Check list of parasites of fishes in Thailand. Notes from Faculty of Fisheries, Kasetsart University, Bangkok, 10, 1–11.
- Sood, M. L. (1970). On Paraleptus komiyai n. sp. (Physalopteridae Leiper, 1908: Nematoda) from a fresh water fish, Mastacembelus armatus from Lucknow, India. Japanese Journal of Parasitology, 19, 437–439.
- Sood, M. L. (1989). *Fish nematodes*. New Delhi–Ludhiana: Kalyani Publishers, pp. 452–228.
- Specian, R. D., Ubelaker, J. E., & Dailey, M. D. (1975). Neoleptus gen. n. and a revision of the genus Proleptus Dujardin, 1845. Proceedings of the Helminthological Society of Washington, 42, 14–21.
- Taraschewski, H., Boomker, J., Knopf, K., & Moravec, F. (2005) Anguillicola papernai (Nematoda: Anguillicolidae) and other helminths parasitizing the African longfin eel Anguilla mossambica. Diseases of Aquatic Organisms, 63, 185–195.
- Threlfall, W., & Carvajal, J. (1984). Heliconema psammobatidus sp. n. (Nematoda: Physalopteridae) from a skate, Psammobatis lima (Chondrichthyes: Rajidae), taken in Chile. Proceedings of the Helminthological Society of Washington, 51, 208–211.
- Yamaguti, S. (1935) Studies on the helminth fauna of Japan. Part 9. I. Nematodes of fishes. *Japanese Journal* of Zoology, 6, 337–386.