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REVIEW ARTICLE

A synthesis of our current knowledge of philometrid nematodes, a group of increasingly important fish parasites

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Abstract: Members of the Philometridae represent the most important group of dracunculoid nematodes parasitizing fishes. In his monograph treating the Dracunculoidea, Moravec (2006) reported a total of 11 genera and 105 species of philometrids parasitizing freshwater, brackish-water and marine fishes. However, during the last six years (2007–2012), an additional 42 new species of Philometridae have been described, representing a 40% increase of the number of nominal species. Most of these species (30) belong to *Philometra* Costa, 1845, mainly represented by parasites of marine fishes, a few others (8) to *Philometroides* Yamaguti, 1935, and a single one to each of the following genera: *Caranginema* Moravec, Montoya-Mendoza et Salgado-Maldonado, 2008, *Dentiphilometra* Moravec et Wang, 2002, *Dentirumai* Quiazon et Moravec, 2013* and *Spirophilometra* Parukhin, 1971. Moreover, three new genera, *Afrophilometra* Moravec, Charo-Karisa et Jirků, 2009, *Caranginema* and *Dentirumai*, were erected. Representatives of seven genera, *Afrophilometra*, *Buckleyella* Rasheed, 1963, *Caranginema*, *Dentiphilometra*, *Dentirumai*, *Paraphilometroides* Moravec et Shaharom-Harrison, 1989 and *Rumai* Travassos, 1960, were studied using scanning electron microscopy (SEM) for the first time. Thirteen known but poorly described philometrid species were redescribed and, in some species of *Caranginema* and *Philometra*, previously unknown conspecific males were discovered and described. The male surface ultrastructure studied by SEM provided new taxonomically important features for species distinction. Gene sequencing was used in several recent studies and advanced our understanding of phylogenetic interrelationships among representatives of seven genera (*Afrophilometra*, *Alinema* Rasheed, 1963, *Caranginema*, *Nilonema* Khalil, 1960, *Philometra*, *Philometroides* and *Rumai*) and of the extent of the biodiversity of philometrids. New data were obtained on the biology and pathogenicity of several species of *Nilonema*, *Philometra*, *Philometroides* and *Rumai*. The need to carry out surveys in order to find males and to use SEM and gene sequencing to identify philometrids is emphasized. Appropriate quantitative methods to determine the impact of philometrids in ovarian tissue on host fecundity are recommended. Further detailed studies on philometrids would be significant not only from the theoretical viewpoint, but also because of their practical implications. A list of philometrid nematode species by continents is provided.

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*The respective paper of Quiazon and Moravec appeared online in 2012, but its printed version only in 2013.

Keywords: Nematoda, Philometridae, parasites, fish, taxonomy, morphology, biology, pathology

Species of the family Philometridae Baylis et Daubney, 1926 represent the largest and most important group of dracunculoid nematodes (Dracunculoidea Stiles, 1907) parasitizing teleost fishes. Philometrids are a diverse group of parasites with a worldwide distribution that is characterized, like other dracunculoids, by specific morphological features and some biological peculiarities that have been outlined in Moravec (2006). Herein, we first provide an overview of the group's taxonomy, ecology and pathology, and an update of our knowledge of this group based on studies published over the past six years (2007–2012).

GENERAL CHARACTERIZATION

All philometrids are ovoviviparous and after fertilization, females grow markedly as first-stage larvae (L_1) fill their uteri. In fully gravid females the vulva and anus atrophy (except for *Alinema* Rasheed, 1963) and L_1 are dispersed into the environment when females burst as they come in contact with water. Philometrids exhibit a marked sexual dimorphism in which females are highly modified and considerably larger than the males. Whereas the males are most frequently 2–4 mm long, the conspecific gravid females may be several tens of centimetres long and even

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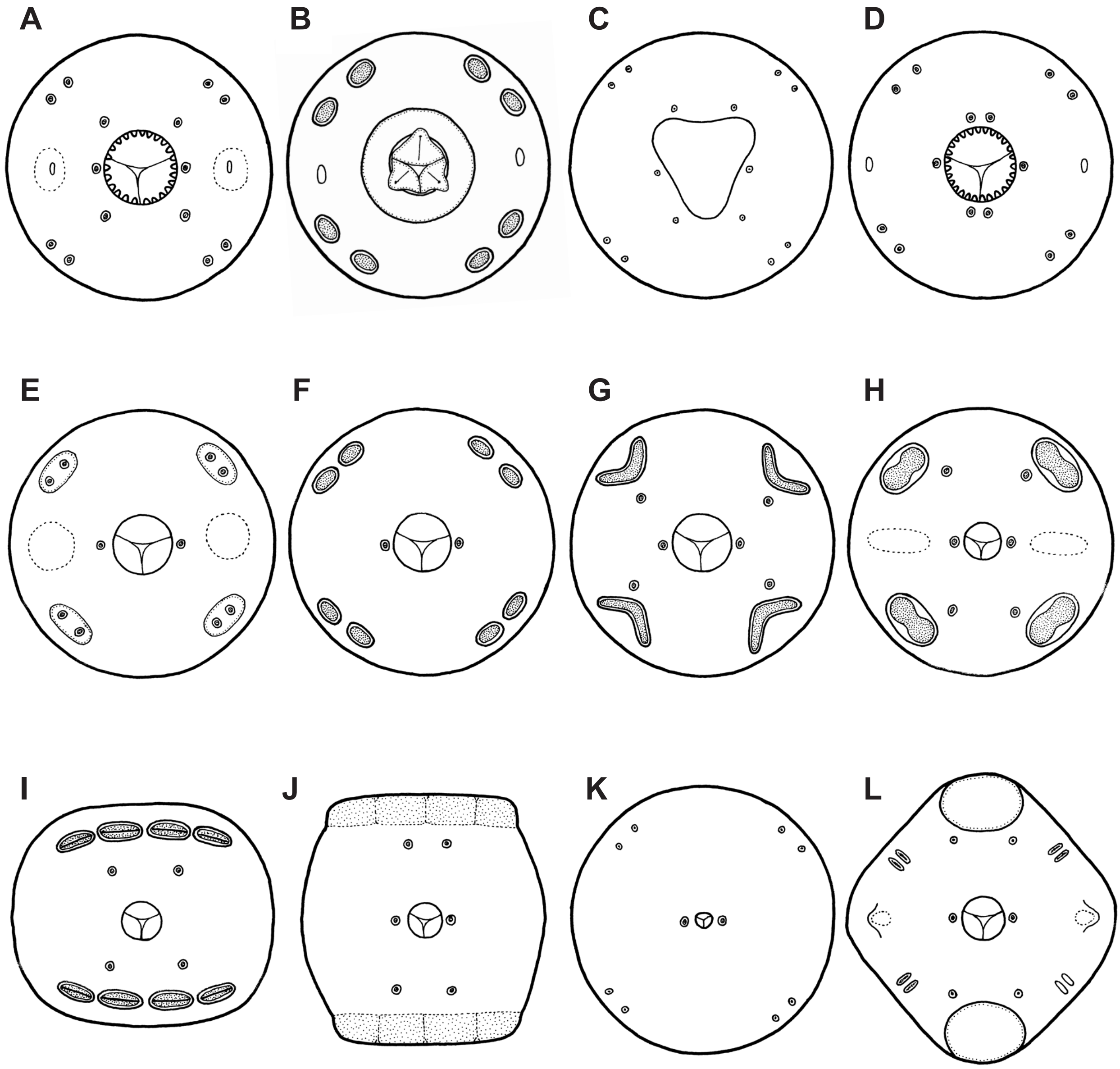

Fig. 1. Variations in the structure of the cephalic extremity of gravid female philometrid nematodes (apical views, diagrammatic). **A** – *Alinema amazonicum*; **B** – *Buckleyella buckleyi*; **C** – *Clavinema mariae*; **D** – *Dentiphilometra lutjani*; **E** – *Philometra ovata*; **F** – *P. salgadoi*; **G** – *P. ocularis*; **H** – *P. bagri*; **I** – *P. beninensis*; **J** – *Paraphilometroides nemipteri*; **K** – *Nilonema senticosum*; **L** – *Rumai rumai*.

more than 1 m in one unidentified species of *Philometra* Costa, 1845 from the abdominal cavity of the wreckfish *Polyprion americanus* (Polyprionidae) (pers. comm. of C.J. Fennesy, Virginia Institute of Marine Science, USA).

Philometrid females are noted for the presence of a simple circular to oval or roughly triangular mouth (Fig. 1), which is sometimes armed with numerous minute circumoral sclerotized formations (denticles) that support the peribuccal rim internally (Figs. 1A,D, 2A). A buccal capsule is absent in all known philometrids, although a reduced capsule is present in *Neophilometroides* Moravec, Salgado-Maldonado et Aguilar-Aguilar, 2002.

The cephalic papillae are generally numerous and most often arranged in two circles (Fig. 1). The papillae of the outer circle are submedian and may be single (two dorsolateral and two ventrolateral) but are more frequently in pairs (Fig. 1A–F,I–L), and sometimes the papillae of each pair are fused together (Fig. 1G,H). Each submedian pair of papillae may be situated on a somewhat elevated lobe or may form a marked, fleshy protrusion (Fig. 2J). Sometimes, fleshy external papillae (still four) are close one another and may form dorsal and ventral rows (Fig. 1I) or they may fuse together to form a dorsal and a ventral transverse cephalic mound-like shape (Fig. 1J).

Papillae of the internal circle are usually formed by four single submedian and two lateral papillae, but their number may be considerably reduced (Fig. 1E,F,I,K). However, these inner papillae may also be completely

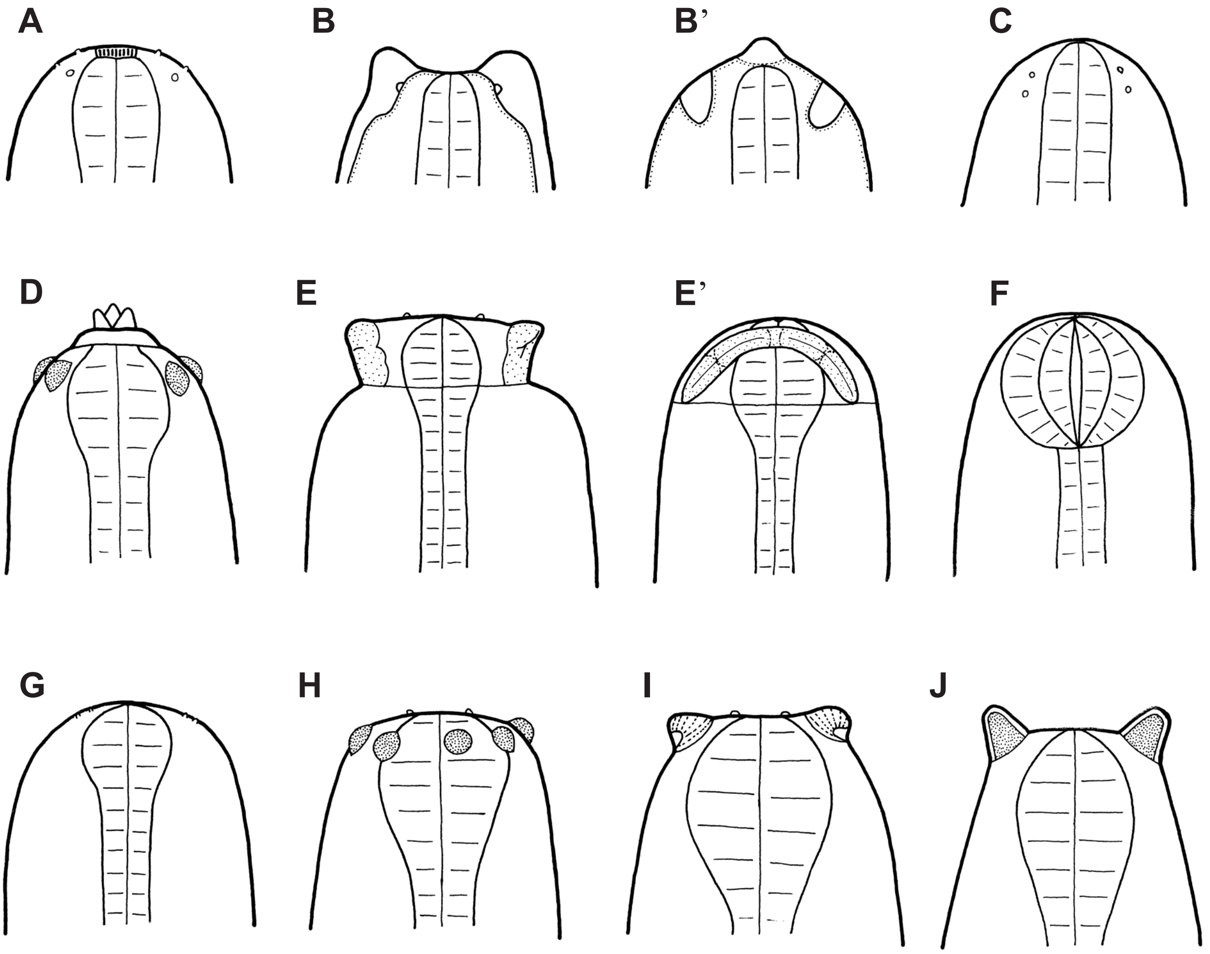

Fig. 2. Variations in the shape and structure of the cephalic extremity of gravid female philometrid nematodes (lateral views, except for B' and E'; diagrammatic). **A** – *Alinema amazonicum*; **B** – *Rumai rumai* (**B'** – dorsoventral view); **C** – *Nilonema senticosum*; **D** – *Buckleyella buckleyi*; **E** – *Paraphilometroides nemipteri* (**E'** – dorsoventral view); **F** – *Clavinema mariae*; **G** – *Philometra ovata*; **H** – *P. salgadoi*; **I** – *P. ocularis*; **J** – *P. rischta*.

absent (Fig. 1B). Although the number and arrangement of cephalic papillae are some of the most important taxonomic features in philometrids, in most species these papillae are difficult to observe using light microscopy (LM) and, therefore, the use of scanning electron microscopy (SEM) is necessary for their study.

The identification of philometrid species is best made using males but is often limited to female specimens, which are most frequently collected because they are larger and easier to find. However, it is important to have gravid (larvigerous) females, which typically have more taxonomic features than do subgravid (ovigerous) and nongravid females.

The cephalic end of gravid female philometrids is mostly rounded in lateral view and lacks any lips or lip-like formations (Fig. 2A,C,F–H). However, large cephalic papillae of the external circle in some species of *Philometra* and in *Caranginema* Moravec, Montoya-Mendoza et Salgado-Maldonado, 2008 (Fig. 2D,H–J) or the dorsal and ventral cephalic protrusions in *Rumai* Travassos, 1960 (Fig. 2B) are distinct.

In some species conspicuous anteriorly protruding oesophageal teeth are visible (Fig. 2D). The cephalic end of *Paraphilometroides* Moravec et Shaharom-Harrison, 1989 is rounded in lateral view (Fig. 2E') but almost rectangular from a dorsoventral perspective (Fig. 2E). The caudal end of gravid females is usually rounded (Fig. 3), with or without a pair of caudal, mostly papilla-like protrusions (Fig. 3D–H,J). This end may also sometimes have one (Fig. 3K) or two cuticular lobes (Fig. 3L). Rarely is the caudal end of gravid females forked (Fig. 3I) or pointed (*Nilonema* Khalil, 1960) (Fig. 3A).

The body of female philometrids is most often long, filiform and covered with a relatively thin cuticle that often appears smooth using LM but which is usually finely transversely striated when seen under the SEM. The surface of the cuticle may exhibit various ornamentations, such as cuticular cones or bosses in species of *Nilonema* and *Philometroides* Yamaguti, 1935 (Fig. 4A,B), transverse or longitudinal cuticular mounds in some species of *Philometroides* (Fig. 4C,D), oval inflations bearing transverse rod-like formations in species of *Buckleyella*

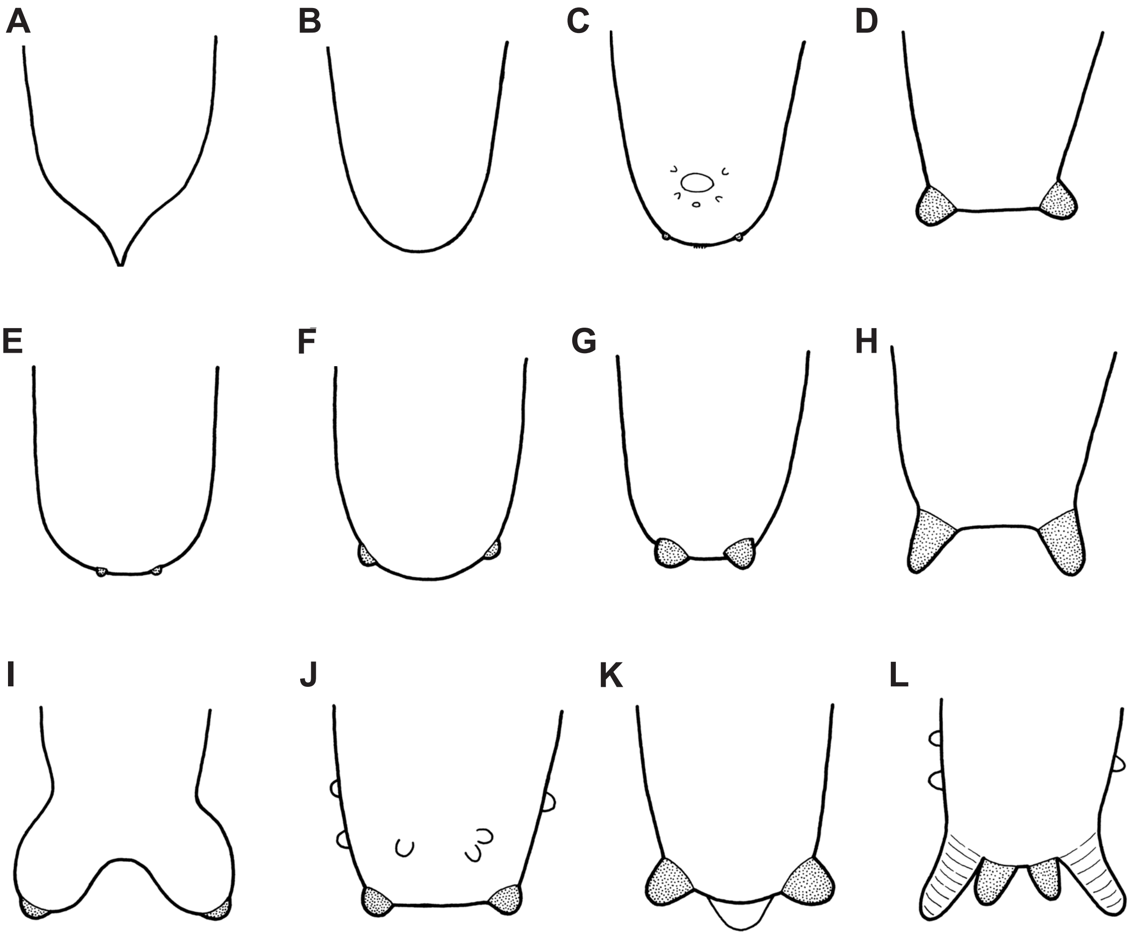

Fig. 3. Variations in the shape and structure of the tail of gravid female philometrid nematodes (dorsoventral views, diagrammatic). **A** – *Nilonema senticosum*; **B** – *Clavinema mariae*; **C** – *Alinema amazonicum*; **D** – *Dentiphilometra monopteri*; **E** – *Philometra lethrini*; **F** – *P. cyprinirutili*; **G** – *P. parasiluri*; **H** – *P. rischta*; **I** – *P. bagri*; **J** – *Philometroides aphanonaris*; **K** – *P. cyprini*; **L** – *P. barbi*.

Rasheed, 1963 (Fig. 4E), transverse semicircular bands of inflated cuticle separated by smooth lateral fields in species of *Afrophilometra* Moravec, Charo-Karisa et Jirků, 2009 (Fig. 4F), minute spines in species of *Spirophilometra* Parukhin, 1971 (Fig. 4G) or two parallel cordons on either side extending along the body that demarcate narrow smooth lateral fields as in species of *Caranginema* (Fig. 4H).

Many philometrids are haematophagous and consequently the body colour of subgravid and gravid females is frequently pink, red or dark brown, whereas others are whitish or yellowish. It is not known what these latter philometrids feed on. Although Radhakrishnan et al. (2009) found sperm cells in the body of *Philometra cephalus* infecting testes of the long-arm mullet *Valamugil cunnesius*, these authors stated that the worms seemed to be sanguinivorous based on the presence of host blood cells inside their body.

The oesophagus of philometrids is relatively short and undivided or it may have a markedly large unicellular dorsal oesophageal gland with a large cell nucleus. The anterior end of the oesophagus is often bulbously inflated and a small ventriculus is usually present. The anus and vulva of gravid females are atrophied (except in *Alinema* spp.).

Although the morphology of males is very important in philometrid taxonomy, males of numerous species (and even some genera) remain unknown. As such, current taxonomic issues related to species described solely on the basis of females will likely be resolved once males are discovered. As for females, some details of the morphological structure of males can be observed only by SEM. The spicules and gubernaculum are usually well sclerotized in philometrids and, therefore, their shape, lengths, length ratio and the length ratio of spicules and the gubernaculum may be important specific features. Recent studies have shown that the structure of the gubernaculum may be an especially good specific feature because one or two distinct dorsal barbs may be present on its distal end in some *Philometra* species (Fig. 5B–J) and absent in others (Fig. 5A). Moreover, the distal end of the gubernaculum may also exhibit many transverse lamellae either laterally (Fig. 5N) or dorsally (Fig. 5K–M). Lastly, there

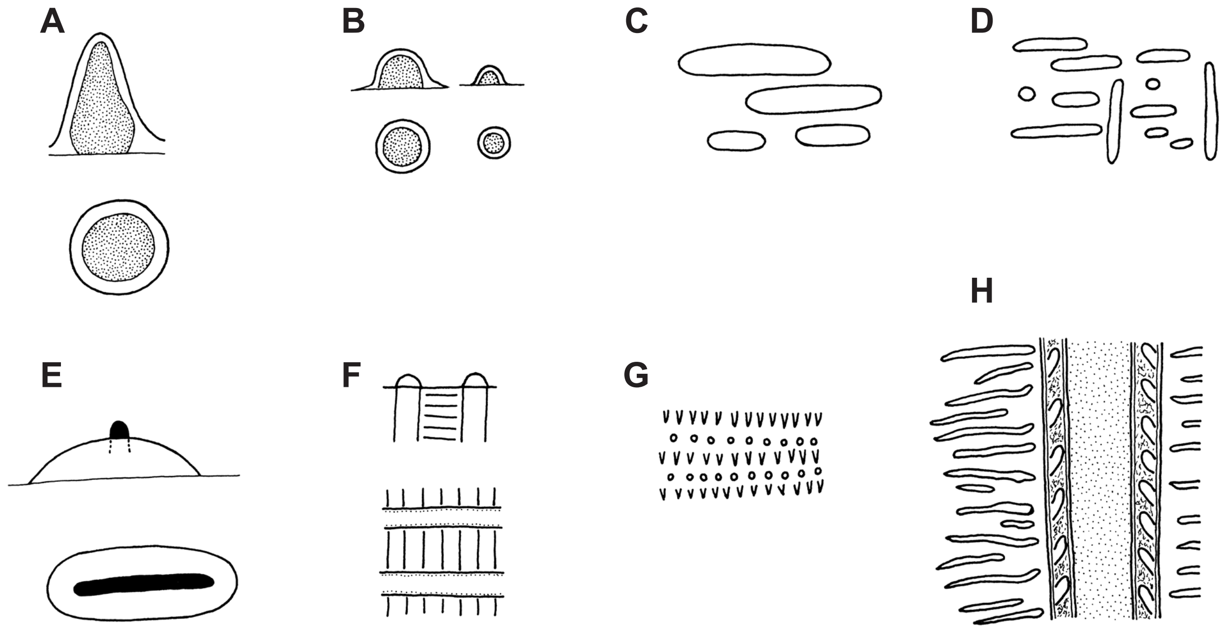

Fig. 4. Types of cuticular ornamentations on the body of gravid females in some philometrid nematodes. **A** – *Nilonema senticosum* (cone-shaped cuticular projection, lateral and apical views); **B** – *Philometroides aphanonaris* (bosses, lateral and apical views); **C** – *P. pseudaspii* (transversely oval cuticular inflations, apical view); **D** – *P. paralichthydis* (transversely oval, longitudinal and circular cuticular inflations, apical view); **E** – *Buckleyella buckleyi* (transversely oval cuticular inflation bearing sclerotized rod-like formation, lateral and apical views); **F** – *Afrophilometra hydrocyoni* (transverse bands of inflated cuticle, lateral and apical views); **G** – *Spirophilometra pacifica* (minute cuticular spines, apical view); **H** – *Caranginema americanum* (two parallel cordons and numerous transversely elongated cuticular moulds, apical view).

may be interspecific differences in the relative length of the dorsally oriented proximal part (shaft) of the gubernaculum in relation to its entire length. Very important interspecific differences are also found in the shape of the male caudal mound and the number and distribution of caudal papillae in *Philometra* spp. (Fig. 6).

The definitive hosts of philometrid nematodes are freshwater, brackish-water and marine fishes. Many of these nematodes are histozoic, infecting various tissues, whereas others are found in body cavities. Depending on the species, philometrids may infect, for example, the skin and subcutaneous tissues, body musculature, eyes, orbits, swimbladder, gonads, circulatory system or body cavity of their fish host.

Many philometrids are highly pathogenic to their hosts and some are known to be agents of serious fish diseases, such as, for example, philometroidosis in pond-reared common carp (*Cyprinus carpio*) in Europe (caused by *Philometroides cyprini*), or philometroidosis in crucian and Prussian carps (*Carassius carassius* and *C. gibelio*) traditionally cultured in Russia and some Asian countries (e.g. Japan, China, Korea) (caused by *Philometroides sanguineus*). These parasites represent serious problems for fish farms and may be the cause of considerable economic losses (Vismanis and Nikulina 1968, Vasilkov 1983). Ivashkin et al. (1971) mentioned that *P. cyprini* may cause the mortality of infected young common carp, and a mass mortality of the pond-cultured crucian carp due to *P. sanguineus* was observed in the Altai Region in Asian Russia in May of 1966 (Vismanis and Nikulina 1968).

Of the many species of philometrids that parasitize marine fishes the most pathogenic are probably the *Philometra* species that are found inside host gonads (mostly ovaries). Female *Philometra* spp. may be very long: over 360 mm for *Philometra* sp. (misidentified as *P. lateolabracis*) in the westralian jewfish, *Glaucosoma hebraicum*, in Australia (Hesp et al. 2002); 530 mm for an unidentified *Philometra* species in the tigertooth croaker *Otolithes ruber* (syn. *O. argentatus*) in India (Annigeri 1960); and over 900 mm in *P. floridensis* from the sciaenid *Sciaenops ocellatus* in the USA (Moravec et al. 2010a). Heavy infections by these worms are frequently recorded in species of wild and cultured fishes of economic importance (Hine and Anderson 1981, Clarke et al. 2005, Perez et al. 2009).

These parasites are often reported, although not always (Oliva et al. 1992, Hesp et al. 2002), to cause serious damage to the fish's gonads by inducing various degrees of inflammation, haemorrhage, oedemas and granuloma formation (Ramachandran 1975, Hine and Anderson 1981, Clarke et al. 2005). Such infections are reported from both male and female fishes, although they most often affect only one gender for any given species. In the instances where infection occurs in both sexes of the same fish species, worm prevalence seems to always differ significantly between the two genders (Ramachandran 1975, Hine and Anderson 1981, Oliva et al. 1996, Radhakrishnan et al. 2010).

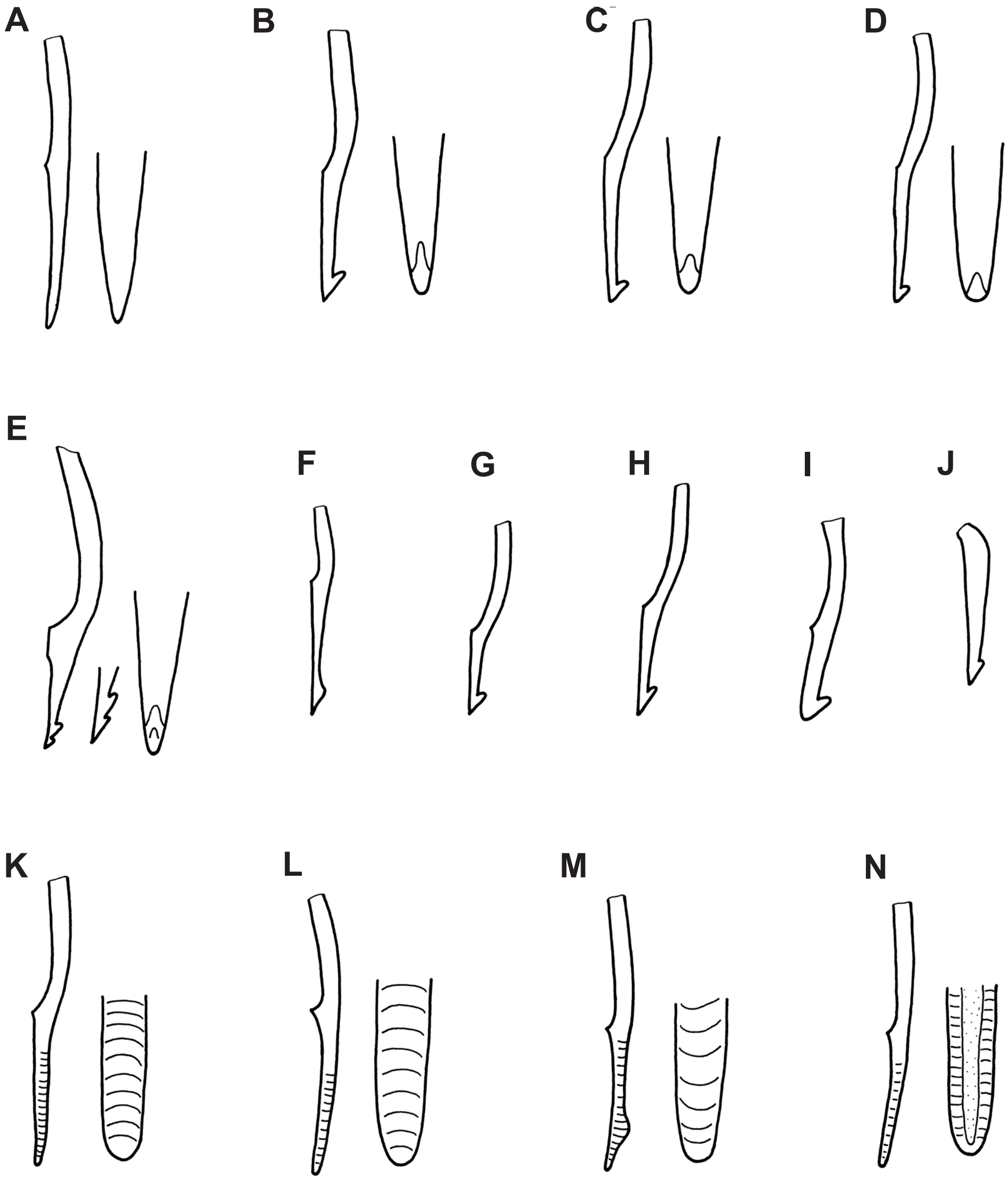

Fig. 5. Variations in the shape and structure of the gubernaculum in some philometrid nematodes (gubernaculum in lateral view and its distal end in dorsal view, except F–J). **A** – *Philometra lethrini*; **B** – *P. cyprinirutili*; **C** – *P. floridensis*; **D** – *P. carolinensis*; **E** – *P. rischta*; **F** – *P. tenuicauda*; **G** – *Philometroides sanguineus*; **H** – *P. moraveci*; **I** – *Clavinema parasiluri*; **J** – *Neophilometroides caudatus*; **K** – *Philometra charlestonensis*; **L** – *P. saltatrix*; **M** – *P. priacanthi*; **N** – *P. brevicollis*. (E – after Sokolov and Kazakov 2007, I – after Wu and Yu 1987).

In several fish species, the presence of philometrids in host ovaries seems to occur in fish that have reached maturity (Hesp et al. 2002, Perez et al. 2009, Radhakrishnan et al. 2010, Chávez and Oliva 2011), and it has been suggested that immature fish are not susceptible to infection (Chávez and Oliva 2011) or that there might be a synchrony between host and parasite maturation (Perez et al. 2009). The presence of philometrids in host gonads has been suggested by numerous authors to negatively affect the reproduction of some species of marine fishes (Hine and Anderson 1981, Sakaguchi et al. 1987, Moravec and Salgado-Maldonado 2007, Moravec et al. 2007a) and recent studies (see below) generally support this contention. Philometrids found in extra-gonadal organs may also be pathogenic (e.g. Vasilkov 1967, Benz and Pohley 1980, Vidal-Martínez et al. 1995). Fish philometrids have also very occasionally been recorded as accidental human parasites (Deardorff et al. 1986, Kuroda et al. 1991), indicating a risk for people handling or eating uncooked fish infected with philometrids.

As in the case of other dracunculoids, data on the life cycles of philometrids are scarce and only reported for a few species of *Philometra* and *Philometroides* (see Moravec 2004 and update below). Based upon what is known so

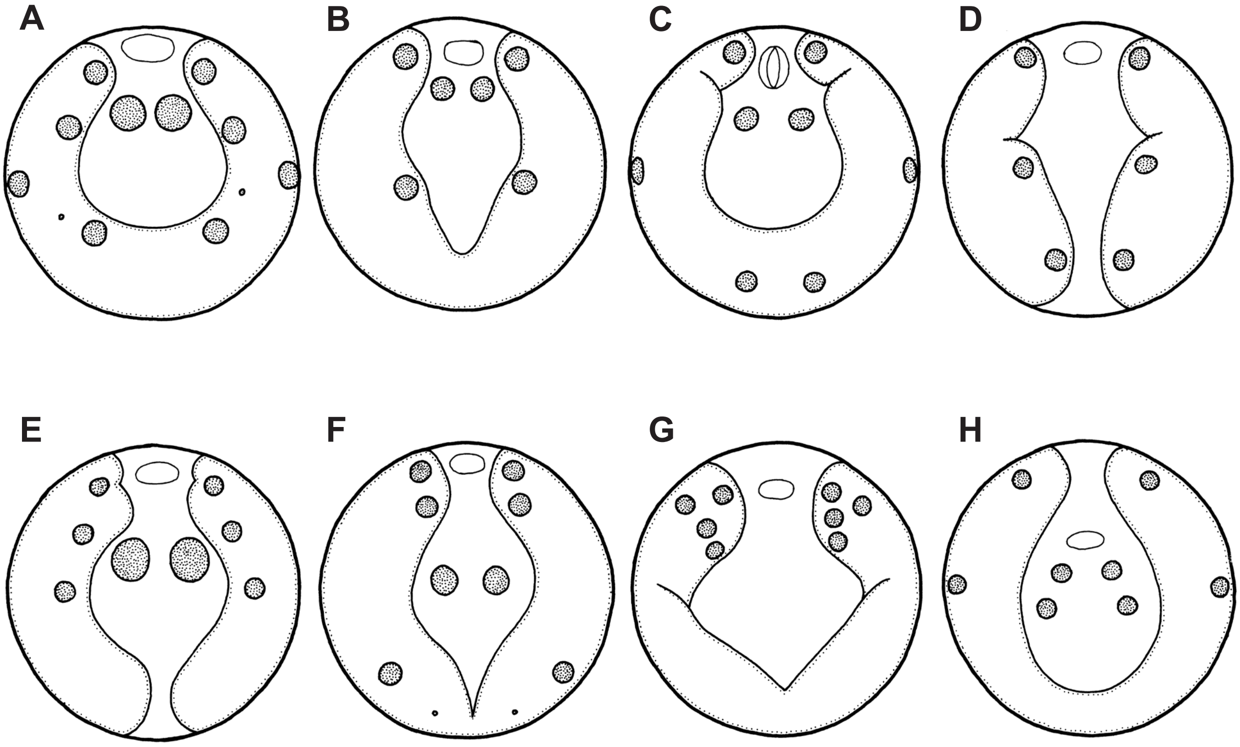

Fig. 6. Variations in the structure of male tail (note different numbers and distribution of papillae and the shape of caudal mound) in some species of *Philometra* (apical views, diagrammatic). **A** – *Philometra diplectri*; **B** – *P. dentigubernaculata*; **C** – *P. carolinensis*; **D** – *P. lethrini*; **E** – *P. charlestonensis*; **F** – *P. saltatrix*; **G** – *P. terapontis*; **H** – *P. rischta* (H – after Sokolov and Kazakov 2007).

far, the intermediate hosts of philometrids are copepods, which become infected after ingesting the free-living L_1 larva released into the water by gravid female worms. Of note, however, and reported only once and in an unpublished thesis (Wellborn 1970), an ostracod has also been reported to be a suitable experimental intermediate host (*Cypridopsis* sp. for *Philometroides wellborni* [reported as *Philometra intraoculus*], a parasite of *Lepomis* spp. in the USA). Philometrid larvae moult twice in the intermediate host's haemocoel to attain the third stage (L_3), which is then infective to the fish host. Some philometrids are known to utilize fish paratenic hosts as the main source of infection (Molnár 1976, 1980, Moravec and Dyková 1978) and others are also suspected to do so based upon their population dynamics (de Buron et al. 2011).

Philometrids, in particular those of freshwater fishes in temperate zones, often show a pronounced seasonal maturation cycle, with gravid females occurring only during a short period in spring and summer (see review in Moravec 2004). This information, however, is limited to a very few species of philometrids; more studies, including species in the marine environment, for which almost no information is available, need to be carried out before such seasonality can be confirmed as a group-wide phenomenon.

Despite the practical importance of philometrids as pathogenic parasites, most are poorly known and the classification within this group is, besides that of the trichinelloids, one of the most difficult and unsatisfactory in the Nematoda (Anderson 2000). The identification of philometrids is difficult mainly because of the following reasons: (1) inadequate species descriptions, frequently based solely on females or female body fragments; (2) males of most species, and even some genera, remain unknown (mainly because of their small size and because they are often not in the same location as females in the host); (3) large females are sensitive to osmotic pressure and their body easily bursts in water, formalin or alcohol, leading to inadequate specimen preparation; (4) female morphology in most philometrids is rather uniform; (5) female cephalic papillae of numerous species are very small and hardly visible by LM, so the only reliable method of observation is the use of SEM; (6) the male morphology of philometrids can be properly studied only with the use of SEM; and (7) the availability of males and gravid females of numerous philometrid species may be limited in time because of pronounced seasonal maturation cycles of the worms.

Classification of philometrids

In the past, the majority of philometrids were assigned to the generally recognized genus *Philometra*. However, Rasheed (1963), in attempt to make species identification easier, carried out a detailed revision of members of this genus and created a taxonomic system for the Philometridae that was based principally on female morphology. Taking into account certain genera established by previous authors, she proposed two new genera, two new subgenera within *Philometra*, synonymized *Clavinema* Yamaguti, 1935 with *Philometra*, described several new species, and proposed several new combinations and synonymies. Even though some of Rasheed's conclusions later proved not to be well-founded, her revision at the time was important for subsequent studies on philometrids. For instance, her classification system (Rasheed 1963) was followed in the monographs by Ivashkin et al. (1971) and Chabaud (1975).

In the years following Rasheed's revision, several additional philometrid species and genera were established. However, the practical use of Rasheed's revision was often problematic for the generic identification of these nematodes because it was based on the study of cephalic papillae in females using LM, which is difficult and could lead to wrong conclusions (see reviews by Moravec 2004, 2006 for more details about the history of studies on philometrids).

Moravec (2006) published the first book monograph treating all dracunculoid nematodes known at that time and created a new classification system based on morphological, biological and, when available, molecular data. Within this system three genera previously listed in the Philometridae were transferred to other dracunculoid families, i.e. *Ichthyofilaria* Yamaguti, 1935 to the Guyanemidae Petter, 1974, and *Philonema* Kuitunen-Ekbaum, 1933 and *Phlyctainophora* Steiner, 1921 to the Micropleuridae Baylis et Daubney, 1926. In accord with this classification, the family Philometridae included three subfamilies, the Alineminae Moravec, 2006 (monotypic), Neophilometroidinae Moravec, Salgado-Maldonado et Aguilar-Aguilar, 2002 (monotypic) and Philometrinae Baylis et Daubney, 1926. Moravec (2006) recognised 11 philometrid genera (*Alinema*, *Buckleyella*, *Clavinema*, *Dentiphilometra* Moravec et Wang, 2002, *Neophilometroides*, *Nilonema*, *Paraphilometroides*, *Philometra*, *Philometroides* Yamaguti, 1935, *Rumai* and *Spirophilometra*) and a total of 105 species. The subgenus *Ranjhinema* Rasheed, 1963 of *Philometra* was not recognised. One species, *Philometra neolateolabracis*, poorly described from the ovary of the sciaenid fish *Pennahia argentata* (Houttuyn) off India (Rajyalakshmi et al. 1985), was omitted in the monograph and later designated a *species inquirenda* by Moravec et al. (2011a).

The above mentioned monograph (Moravec 2006) provided keys to species and higher taxa, adapted descriptions and illustrations of all valid species of known philometrids and, for each species, available information on host(s), site(s) of infection, distribution, pathogenicity, life cycle and biology. A plethora of studies on philometrids during the past six years (2007–2012) has resulted in numerous achievements of important advances, particularly regarding the morphology, taxonomy, biology, ecology, geographical distribution, pathogenicity, and phylogenetic relationships of these parasites. The most important results obtained during this period are outlined below.

NEWLY DESCRIBED TAXA, MORPHOLOGY, GEOGRAPHICAL DISTRIBUTION

During the 2007–2012 period, 42 new species belonging to Philometridae were described worldwide, which represents a 40% increase in the number of nominal philometrid species reported in 2006. These are as follows:

Caranginema (1 species): *C. americanum* (see Moravec et al. 2008a).

Dentiphilometra (1): *D. lutjani* (see González-Solís et al. 2007).

Dentirumai Quiazon et Moravec, 2013 (1): *D. philippinensis* (see Quiazon and Moravec 2013).

Philometra (30): *P. brevispicula*, *P. charlestonensis*, *P. cyanopodi*, *P. dentigubernaculata*, *P. diplectri*, *P. fasciati*, *P. floridensis*, *P. genipteri*, *P. gymnosardae*, *P. gymnothoracis*, *P. isaki*, *P. javaensis*, *P. lagocephali*, *P. lati*, *P. lethrini*, *P. lobotidis*, *P. madai*, *P. mexicana*, *P. morii*, *P. nattereri*, *P. obladae*, *P. orbitalensis*, *P. poblana*, *P. priacanthi*, *P. psettoditis*, *P. sawara*, *P. spicarae*, *P. spiriformis*, *P. tenuicauda* and *P. terapontis* (see Moravec and Salgado-Maldonado, 2007, Moravec et al. 2007b, 2008b, c, f, 2009a, 2010a,b,c, 2011a,b, 2012c, Moravec and Justine 2008, 2009, 2011, Quiazon et al. 2008a,b, Caspeta-Mandujano et al. 2009, Moravec and de Buron 2009a, Moravec and Bakenhaster 2010a,b, Cárdenas et al. 2012).

Philometroides (8): *P. acanthopagri*, *P. aphanonaris*, *P. branchiostegi*, *P. grandipapillatus*, *P. indonesiensis*, *P. marinus*, *P. trichiuri* and *P. wellborni* (see Moravec et al. 2008f, 2012a,b,c, Moravec and de Buron 2009a, Moravec and Bakenhaster 2010a).

Spirophilometra (1): *S. pacifica* (see Moravec et al. 2007c).

Whereas 34 of these newly described species (*Caranginema* 1, *Dentiphilometra* 1, *Philometra* 25, *Philometroides* 6, *Spirophilometra* 1) are parasites of marine fishes, eight species (*Dentirumai* 1, *Philometra* 5, *Philometroides* 2) infect freshwater fishes. These recent studies on philometrids not only enabled the discovery of many new species, but also extended our knowledge of the morphological and genetic diversity of these nematodes (see below). The unusual increase in newly discovered philometrid species within a relatively short period of six years likely reflects an interest in this group by parasitologists. However, it documents not only the vast void in our knowledge of the global diversity of this parasite group, especially in the marine environment, which remains neglected, but many other species can be expected to be discovered if sought for.

Three new and so far monotypic philometrid genera, *Afrophilometra* (type species *A. hydrocyoni*), *Caranginema* (type species *C. americanum*) and *Dentirumai* (type species *D. philippinensis*), were erected based only on female morphological features (Moravec et al. 2008a, 2009a, Quiazon and Moravec 2013). However, previously unknown males have been described for *Caranginema* (*C. americanum*) (Moravec and Bakenhaster 2012) and for three species of *Philometra* (*P. filiformis*, *P. lateolabracis* and *P. nemipteri*) (Quiazon et al. 2008a,b, Gaglio et al. 2009), which parasitize marine fishes.

Sixteen poorly known species of *Afrophilometra* (*A. hydrocyoni*), *Buckleyella* (*B. buckleyi*), *Paraphilometroides* (*P. nemipteri*), *Philometra* (*P. bagri*, *P. cryptocentri*, *P. filiformis*, *P. hyderabadensis*, *P. lateolabracis*, *P. nemipteri*, *P. parasiluri*, *P. rischta*, *P. rubra*, *P. saltatrix*, *P. sciaenae*), *Philometroides* (*P. seriolae*) and *Rumai* (*R. rumai*) were redescribed based on newly collected specimens (Sokolov and Kazakov 2007, Moravec et al. 2008b,c,d,e, 2009a,b, 2012b, Moravec and de Buron 2009b, Quiazon et al. 2008a,b, 2010, Gaglio et al. 2009, Santos and Moravec 2009, Moravec 2010, Moravec and Harris 2010, Moravec and Chavan 2012). For the first time, representatives of seven philometrid genera, *Afrophilometra*, *Buckleyella*, *Caranginema*, *Dentirumai*, *Paraphilometroides*, *Rumai* and *Spirophilometra* were studied using SEM (see below).

PHILOMETRIDS FROM FRESHWATER FISHES

Three new species of philometrids were described from centrarchid freshwater fishes in the USA (Alabama, Georgia and South Carolina – Moravec et al. 2008f): *Philometra orbitalensis* and *Philometroides wellborni* from the oculo-orbits of *Micropterus salmoides* and *Lepomis* spp., respectively, and *Philometroides aphanonaris* from the subcutaneous tissues of the head of *M. salmoides*. One other North American philometrid, *Philometra rubra*, a parasite of the abdominal cavity of *Morone* spp. (Moronidae) in fresh waters, was redescribed by Moravec et al. (2009b) based on subgravid females collected from its type host, *M. saxatilis* in South Carolina, USA. The original description of *P. rubra* by Leidy (1856) is inadequate and, although this species was subsequently recorded in the USA on several occasions (e.g. Paperna and Zwerner 1976, Hoffman 1999), most of its taxonomically important features remained unknown. The above-mentioned redescription of *P. rubra* has shown that its cephalic papillae of the external circle differ from those in other congeners in that the dorsolateral and ventrolateral papillae are large and dome-shaped, whereas the dorsodorsal and ventroventral papillae are small. However, further studies on *P. rubra* are needed, as gravid females and males remain undescribed.

Two new *Philometra* spp., *P. poblana* and *P. nattereri*, have recently been described from the fins of *Cichlasoma istlanum* (Cichlidae) in southern Mexico (Caspeta-Mandujano et al. 2009) and from the oculo-orbits and nasal cavity of *Pygocentrus nattereri* (Characidae) in Amazonia, Brazil (Cárdenas et al. 2012), respectively. Despite the addition of these two species, the fauna of dracunculoid nematodes parasitizing Neotropical freshwater fishes remains little known (see Moravec 2006) and it can be expected that more new species of philometrids will be discovered and described from South and Central Americas and from southern Mexico.

Based on many newly collected specimens (unfortunately, only females) from the head tissues of *Arapaima gigas* (Arapaimidae) in Amazonia, Brazil, Santos and Moravec (2009) made a detailed redescription of the poorly known species *Rumai rumai*, originally inadequately described from a single female specimen by Travassos (1960). Using confocal laser microscopy and SEM, it was possible to study, for the first time in detail, the unique structure of the cephalic end of this remarkable, highly pathogenic species (see below).

Regarding philometrids from the freshwater fishes of Africa, Moravec et al. (2009a) reported four species (females only) from Lake Turkana, Kenya. Two of these species were new *Philometra* species from the same host, *Lates niloticus* (Latidae): *P. lati* from the abdominal cavity and *P. spiriformis* from capsules on the inner surface of the gill opercula. A marked characteristic feature of the latter species is a spirally coiled body in both fixed and live gravid females, by which it differs from all other congeners. Such a spirally coiled body has previously been described only in the gravid female of *Spirophilometra eichleri*, a parasite of the spleen of the marine perciform fish *Lethrinus nebulosus* (Lethrinidae) in the Indian Ocean (Parukhin 1971). In addition, and also from Lake Turkana, two known species were recorded from their type hosts, i.e. *Philometra bagri* and *Philometroides hydrocyoni*, originally described from the Sudan and Egypt, respectively. Based on SEM examinations, both species were redescribed and, because of the presence of unique cuticular ornamentations, the latter was transferred to the newly erected genus *Afrophilometra*.

New data on four species of philometrids parasitizing freshwater fishes have come from Asia, the most important addition being the recent description of a new genus and species, *Dentirumai philippinensis*, from the body cavity and subcutaneous tissues of the goby *Rhyacichthys aspro* (Gobiidae) in the Bianuan River, Philippine Archipelago, by Quiazon and Moravec (2013). The general female morphology of this nematode is very similar to that of *Rumai rumai* mentioned from *Arapaima gigas* in South America, but it differs from it substantially in possessing circumoral sclerotized denticles.

LM and new SEM examinations of specimens of two previously inadequately described Asian species, *Philometra hyderabadensis* and *P. parasiluri*, newly collected from their type hosts (freshwater catfishes) *Wallago attu* in India and *Silurus asotus* in Japan (both Siluridae), respectively, made possible their detailed redescriptions and comparison with other congeners (Moravec et al. 2008d, Moravec and Chavan 2012). These studies represented the first record of these species since their original descriptions several decades ago. Although both species are somewhat similar morphologically and occur in hosts belonging to the same family, they differ distinctly from each other in the number, size and distribution of cephalic papillae, in the absence/presence of oesophageal teeth, their location in the host (body cavity *vs* oculo-orbits), their host species, and in their geographical distribution (India *vs* Japan). Based on new data on *P. hyderabadensis,* it was possible to synonymize *P. suraiyae* Kalyankar, 1971 from *Ompok bimaculatus* (Siluridae) in India with this species (Moravec and Chavan 2012). *Philometra rischta* was first recorded from the Caspian Sea coast off Iran (Tajbakhsh et al. 2010). Recently, Sokolov (2013), based on newly collected specimens, provided new data (including the first observations by SEM – see below) on the Asian species *Philometroides moraveci*, a parasite of the subcutaneous tissues of *Perccottus glenii* (Odontobutidae) in the Russian Far East.

Philometroides moraveci (as *P. parasiluri*) was erroneously reported in Europe from the introduced Chinese sleeper (*Perccottus glenii*) in the River Danube in Serbia (Nikolic et al. 2007). The philometrids reported in the latter study were in fact larvae of the nematode genus *Eustrongylides* Jägerskiöld, 1909 (Dioctophymatidae) (Moravec 2008b).

In Europe, Pegg et al. (2011) and Williams et al. (2012) published new data on the biology and pathogenicity of *Philometroides sanguineus* in wild crucian carp, *Carassius carassius* (Cyprinidae), in England, where this nematode was introduced and recorded for the first time (see below).

PHILOMETRIDS FROM MARINE FISHES

During the period 2007–2012, the large majority of new species of philometrids described were from marine fishes from various oceans and seas. Interestingly many of these species were gonad-infecting *Philometra* spp. Prior to the work of Quiazon et al. (2008a), most gonad-infecting philometrids were erroneously identified as *Philometra lateolabracis*, even though they occurred in various fish species belonging to different families and orders. *Philometra lateolabracis* was an inadequately described species from females infecting three species of perciform fishes off Japan (Yamaguti 1935). Quiazon et al. (2008a) made a detailed redescription of *P. lateolabracis* based on both male and female specimens newly collected from the type host in Japanese waters and questioned previous records of *P. lateolabracis* from other fish hosts.

These authors also drew attention to the importance of male caudal papillae and the detailed structure of the gubernaculum as taxonomic features of philometrids, which later made possible the distinction of otherwise morphologically similar species when based solely on the description of females. From marine fishes off Japan, Quiazon et al. (2008a,b) also established three new gonad-infecting species, *P. isaki*, *P. madai* and *P. sawara*, and redescribed *P. nemipteri* and *P. sciaenae*. Later, Quiazon et al. (2010) redescribed females of the type species of *Philometroides*, *P. seriolae*.

Nagasawa (2008) published a list of dracunculoid (including philometrid) and anguillicoloid nematodes recorded in fishes and amphibians in Japan during the period 1916–2008. Just recently, still off Japan, another new philometrid, *Philometroides branchiostegi*, was described by Moravec et al. (2012b), who also redescribed *Philometra cryptocentri* based on newly collected specimens from three species of gobies (Gobiidae) more than 50 years after its original description.

Much has been discovered in the South Pacific over the past six years, especially off New Caledonia. Here, Moravec and Justine (2008, 2009, 2011) described a total of nine new species of *Philometra* (*P. brevicollis*, *P. cyanopodi*, *P. dentigubernaculata*, *P. fasciati*, *P. lagocephali*, *P. lethrini*, *P. mira*, *P. priacanthi* and *P. tenuicauda*), primarily from the gonads of coral reef fishes belonging to six families (Belonidae, Lethrinidae, Lutjanidae, Priacanthidae, Serranidae and Tetraodontidae). These authors also recorded *P. ocularis*, a parasite previously described from off Japan, from the oculo-orbits of *Epinephelus* spp. (see also Justine et al. 2010a,b). This array of newly described species indicates a rich fauna of philometrids in this region of the world, which still remains largely unstudied, given the great diversity and species richness of its fish fauna and the narrow host specificity of philometrids.

From the eastern Pacific, a new gonad-infecting species of *Philometra*, *P. genypteri*, was described from *Genypterus chilensis* (Ophidiidae) off the Chilean coast by Moravec et al. (2011b), whereas based upon female specimens taken off the Pacific coast of Mexico (Chiapas), Moravec et al. (2007c) described *Spirophilometra pacifica*, a new species infecting the oral cavity of *Centropomus robalito* (Centropomidae); the latter included the first SEM study of specimens of *Spirophilometra*. These authors also transferred *Philometra centropomi,* a parasite of *Centropomus undecimalis* (Centropomidae) from the Atlantic coast of Mexico (Gulf of Mexico), to *Spirophilometra*. The only other known species of this genus is *S. eichleri*, which was reported from *Lethrinus nebulosus* (Lethrinidae) in the Gulf of Saukara, Indian Ocean (Parukhin 1971).

From the northern Indian Ocean, three new species of philometrids have been described: *Philometra gymnosardae* based on a male and gravid females collected from the body cavity of the dogtooth tuna *Gymnosarda unicolor* (Scombridae) off the Maldive Islands (Moravec et al. 2007b), *P. terapontis* from the gonads of *Terapon jarbua* (Terapontidae) in the Bay of Bengal, India (Moravec et al. 2011a), and *Philometroides acanthopagri* from the musculature of *Acanthopagrus latus* (Sparidae) in the Persian Gulf off Iraq (Moravec et al. 2012a). *Philometra cephalus*, a gonad-infecting parasite of mullets (Mugilidae), was recorded 37 years after its original description from an estuary in India (Deepthi et al. 2007, Radhakrishnan et al. 2009, 2010). Moravec et al. (2011a, 2012a) provided keys to gonad-infecting species of *Philometra* and to *Philometroides* spp. parasitizing marine and brackish-water fishes, respectively.

From the southern Indian Ocean, five new species of philometrids, *Philometra javaensis*, *P. lobotidis*, *P. psettoditis*, *Philometroides indonesiensis* and *P. trichiuri*, have recently been described from the abdominal cavity, musculature or fins of several fishes of different families (Belonidae, Lobotidae, Psettotidae, Tetraodontidae, Trichiuridae) off the southern coast of Java, Indonesia (Moravec et al. 2012c). *Philometra ocularis* has also been recorded from the oculo-orbit of *Epinephelus fuscoguttatus* in Lampung Bay off Sumatra, Indonesia by Rückert et al. (2010). Many other species of philometrids can be expected to be found in this region, which is also vastly understudied.

Numerous new philometrid species have also been described from fishes in different regions of the North Atlantic. In the Gulf of Mexico, six new species of *Philometra* (*P. atlantica*, *P. brevispicula*, *P. diplectri*, *P. floridensis*, *P. mexicana*, *P. morii*), one of *Philometroides* (*P. grandipapillatus*) and one of *Caranginema* (*C. americanum*) have been described (Moravec and Salgado-Maldonado 2007, Moravec et al. 2008a, 2010a,c, 2013a, Moravec and Bakenhaster 2012). Three additional new species of *Philometra* (*P. carolinensis*, *P. charlestonensis* and *P. gymnothoracis*) and one of *Philometroides* (*P. marinus*) were described from marine and estuarine fishes (Sciaenidae, Muraenidae, Rachycentridae) along the Atlantic coast of South Carolina, USA (Moravec et al. 2008b, Moravec and de Buron 2009a). Also in this area, *Philometra saltatrix* Ramachandran, 1973 was redescribed from the bluefish *Pomatomus saltatrix*, its type host and type locality, and *P. floridensis* was recorded from its type host *Sciaenops ocellatus* (see Moravec and de Buron 2009b). In addition, *Philometra charlestonensis* has been recorded from its type host, *Mycteroperca phenax*, in the Gulf of Mexico (Moravec and Bakenhaster 2012) and *P. atlantica* was described from specimens collected from the Atlantic Spanish mackerel *Scomberomorus maculatus* in both the Gulf of Mexico and off the South Carolina coast (Moravec et al. 2013a).

From the western Atlantic region off the Caribbean coast of southern Mexico (Quintana Roo), González-Solís et al. (2007) described a new philometrid species, *Dentiphilometra lutjani*, based on females collected from the musculature of *Lutjanus griseus* (Lutjanidae). This finding was remarkable in that the only other species of this genus, *Dentiphilometra monopteri*, is parasitic in the abdominal cavity and mesentery of the freshwater swamp eel, *Monopterus albus* (Synbranchidae), in central China. The species *Philometra katsuwoni*, a gonad-infecting parasite of the skipjack tuna *Katsuwonus pelamis* (Scombridae), was redescribed by Cárdenas et al. (2009) from off the Atlantic coast of Rio de Janeiro State, Brazil, where it was recorded for the first time. Included in the description were new data from large females. Since this species was originally described from the Gulf of Guinea, this is an important finding which may indicate the migration of this fish from one side of the Atlantic to the other. Such a transatlantic migration is currently only a hypothesis (Foucher 1996), but the use of this parasite as a biological indicator could provide evidence for such an occurrence.

In the eastern Atlantic, two new species of *Philometra* were described from the Mediterranean region: *P. obladae* from the body cavity of *Oblada melanura* (Sparidae) in the Tyrrhenian Sea off Sicily, Italy (Moravec et al. 2008c) and *P. spicarae* from the body cavity of *Spicara smaris* (Centracanthidae) in the Ionian Sea off Sicily, Italy (Moravec et al. 2010b). In addition, the gonad-infecting species *P. jordanoi*, a parasite of *Epinephelus marginatus* (Serranidae) in the Mediterranean Sea and previously considered a synonym of *P. lateolabracis*, was revalidated by Moravec (2008a) with respect to the redescription of *P. lateolabracis* by Quiazon et al. (2008a). Moravec (2008a) also suggested designating nematodes from *Mycteroperca rubra* (Serranidae) and *Seriola dumerili* (Carangidae), originally identified as *P. lateolabracis*, as *Philometra* sp., until further material is available. The poorly known species *P. filiformis*, a gonad-infecting parasite of *Pagellus erythrinus* (Sparidae), has been redescribed (including the first description of the male) from specimens collected from the type host in the Tyrrhenian Sea off Sicily, Italy (Moravec et al. 2008c, Gaglio et al. 2009). *Philometra saltatrix*, a specific gonad-infecting parasite of the bluefish, *Pomatomus saltatrix* (Pomatomidae), was also redescribed from European waters (Tuscan Sea, off Italy) by Moravec et al. (2008e). Previously, this species was known only from off the Atlantic coast of North America (see above), and these authors provided a detailed redescription of this species based on both LM and SEM studies.

Innominate philometrids, usually reported as *Philometra* sp., from, for example, the gonads of *Argyrosomus regius* (Sciaenidae) off the Atlantic coast of Portugal, were recorded. Such records from *Micropogonias undulatus* (Sciaenidae) off the Atlantic coast of the USA, from *Strongylura marina* (Belonidae) and *Acanthocybium solandri* (Scombridae) in the northern Gulf of Mexico and from *Lutjanus synagris* (Lutjanidae) from off Brazil (Moravec et al. 2007a, 2008b, Jenkins and McBride 2009, Cavalcanti et al. 2010, Moravec and Bakenhaster 2012) show that more collection and studies are needed to expand our knowledge of philometrids from this area, and that there are still numerous undescribed philometrid species parasitizing marine fishes around the world.

NEW STUDIES BY SEM

As previously noted by Moravec (2004), many morphological structures of taxonomic importance in philometrids are difficult or almost impossible to observe by LM and, consequently, the use of SEM is necessary to identify species of philometrids. This need for high resolution concerns, in particular, the cephalic structures in gravid females (i.e. the number and distribution of cephalic papillae, the shape and size of the oral aperture, the presence/absence of cephalic projections or oesophageal teeth), the ornamentation on bodies, the caudal structures in males (the shape of the caudal mound and the number and distribution of caudal papillae), and the structure of the distal portion of the gubernaculum.

The fact that most philometrid descriptions over the past six years have been based on both LM and SEM examinations has been a great advancement. In addition, SEM was used for the first time to describe representatives of the genera *Afrophilometra*, *Buckleyella*, *Caranginema*, *Dentirumai*, *Paraphilometroides*, *Rumai* and *Spirophilometra* (see Moravec et al. 2007c, 2008a, 2009a, Santos and Moravec 2009, Moravec 2010, Moravec and Harris 2010, Quiazon and Moravec 2013).

SEM studies of *Afrophilometra hydrocyoni*, *Buckleyella buckleyi*, *Caranginema americanum* and *Spirophilometra pacifica* in particular (see Moravec et al. 2007c, Moravec et al. 2008a, Moravec et al. 2009a, Moravec and Harris 2010), have revealed differences in the structure of cuticular ornamentations on the body of gravid females of these genera (Fig. 4E–H) and such ornamentations represent important taxonomic characters of these nematodes. The presence of two distinct cuticular cordons extending along either side of the body in *C. americanum* is a unique feature for a philometrid. In *Dentirumai philippinensis* and *Rumai rumai,* the SEM examinations by Santos and Moravec (2009) and Quiazon and Moravec (2013) revealed the presence of peribuccal denticles in the the former species and made possible the detailed study in both species of unusual structures on the head of the female (Figs. 1L, 2B,B'). SEM also enabled confirmation of a unique structure on the head of female *Paraphilometroides nemipteri* (see Moravec 2010), where the flattened external papillae are fused to form single dorsal and ventral curved cephalic alae (Figs. 1J, 2E,E') (Moravec 2010). Large, flat external papillae unusually arranged into dorsal and ventral rows were also observed in gravid females of *Philometroides grandipapillatus* (see Moravec and Bakenhaster 2010a).

Using SEM, Sokolov (2013) observed that the anterior oesophageal lobes in the mouth of gravid females of *Philometroides moraveci* bear many small sclerotized denticles arranged into a pattern forming a structure not previously seen. Subsequently, females of *Philometra javaensis*, a parasite of the abdominal cavity of *Arothron immaculatus* (Tetraodontidae) off Indonesia, were shown to bear the same structures (Moravec et al. 2012c) and the presence/absence of such oesophageal denticles in gravid females may prove to be a taxonomic feature useful for the identification of philometrid species in the future (Moravec et al. 2012c).

SEM has also enabled the identification of characters of primary importance in male philometrids. Based on LM, it has long been known that some philometrids (species of *Clavinema*, *Neophilometroides*, *Philometra* and *Philometroides*), mainly those parasitizing freshwater fishes including *Philometra cyprinirutili*, *P. kobuleji*, *P. kotlani*, *P. ovata* and *P. percalates*, possess a gubernaculum whose distal end displays a reflexed dorsal barb (Fig. 5B,G–J) (see Moravec 2006). However, SEM showed the recognition that this feature was also found in brackish-water/marine species. These include *Philometra carolinensis* and *P. floridensis*, both gonad-infecting parasites from North-American estuarine perciforms (Fig. 5C,D) (Moravec and de Buron 2009b, Moravec et al. 2010a) and *P. dentigubernaculata* from the oculo-orbits of the needlefish *Tylosurus crocodilus* (Belonidae) off New Caledonia (Moravec and Justine 2009).

Furthermore, Sokolov and Kazakov (2007) pointed out that the distal end of the gubernaculum of *Philometra rischta*, a common parasite of subcutaneous tissues of Palaearctic cyprinids, is provided with two (one being larger than the other) dorsal barbs (Fig. 5E). In their subsequent paper, which provides SEM micrographs of this feature, Sokolov and Kazakov (2008) also reported two barbs on the gubernaculum of *Philometroides cyprini* (reported as *P. lusii*), a parasite of the subcutaneous tissues of the common carp *Cyprinus carpio* in Europe and East Asia. More recently, two barbs on the gubernaculum have also been found to occur in the gonad-infecting species *Philometra atlantica*, a parasite of the Atlantic Spanish mackerel *Scomberomorus maculatus* off the Atlantic coast of the USA (Moravec et al. 2013a).

Similarly, the use of SEM allowed Quiazon et al. (2008a,b) to report that the distal portion of the gubernaculum of some gonad-infecting species of *Philometra* parasitizing marine fishes off Japan bears numerous dorsal transverse lamella-like formations and, in some species, a dorsal protuberance. Such dorsal lamella-like formations on the gubernaculum have also been observed in other gonad-infected species of *Philometra* from marine fishes, e.g. in *P. charlestonensis, P. cyanopodi*, *P. genypteri*, *P. priacanthi*, *P. saltatrix* and *P. terapontis* from off the Atlantic coasts of North America, the Mediterranean region, the Pacific coast of South America, and off the coasts of New Caledonia and India (Fig. 5K–M) (Moravec and Justine 2008, 2009, Moravec et al. 2008b,e, 2011a,b). In *Philometra brevicollis*, a gonad-infecting parasite of *Lutjanus vitta* off New Caledonia, Moravec and Justine (2011) made the unique observation that the distal portion of the gubernaculum bears lamella-like formations only on the sides, its dorsal surface being smooth (Fig. 5N). These recent observations indicate the taxonomic importance of these structures on the gubernaculum of gonad-infecting philometrids and the need for using SEM in order to identify and describe species because these structures are not visible using LM.

The use of SEM is also necessary for the observation of the male tail, which exhibits considerable interspecific variability, in particular the shape of the caudal mound and the number and distribution of genital papillae (Fig. 6). As indicated in, for example, the papers of Sokolov and Kazakov (2007, 2008), Moravec and Justine (2008, 2009, 2011), Moravec et al. (2008b,e, 2010a, 2011a,b, 2013a), Quiazon et al. (2008a,b), Moravec and de Buron (2009b) and Moravec and Bakenhaster (2010b) for *Philometra atlantica*, *P. brevicollis*, *P. carolinensis*, *P. charlestonensis*, *P. chilensis*, *P. cyanopodi*, *P. dentigubernaculata*, *P. diplectri*, *P. floridensis*, *P. isaki*, *P. lateolabracis*, *P. lethrini*, *P. mira*, *P. priacanthi*, *P. rischta*, *P. saltatrix*, *P. sawara* and *P. terapontis*, and also for *Philometroides cyprini*, these features may be very important for the species identification of philometrids. Although SEM observations of the male cephalic end may also be of some use, this region appears to be much less important than the posterior end and gubernaculum for philometrid taxonomy.

New molecular data

Although still understudied, philometrids have been the object of a growing interest in recent years with respect to the use of molecular techniques to decipher their taxonomy. Since the pioneer work of Wijová et al. (2006), who first provided a phylogenetic analysis focused on dracunculoid nematodes, the increasing recognition that the confusing and probably inacurrate classification based largely on inadequate morpho-anatomical characters has led to several useful studies that included a range of nematode parasites of vertebrates (Nadler et al. 2007, van Megen et al. 2009, Černotíková et al. 2011).

These studies were based on small subunit rRNA (SSU rRNA) gene sequences that were obtained entirely or partly from GenBank. The studies by Nadler et al. (2007) and van Megen et al. (2009) included sequences of species of *Dentiphilometra, Margolisianum* Blaylock et Overstreet, 1999 [*genus inquirendum*] and *Philometra*, whereas those of van Megen et al. (2009) also included sequences of species of *Alinema* and *Nilonema*. Černotíková et al. (2011) evaluated 32 sequenced philometrid species belonging to eight genera (*Afrophilometra*, *Alinema*, *Caranginema*, *Dentiphilometra*, *Nilonema*, *Philometra*, *Philometroides* and *Rumai*), nearly half of which (15) were used for the first time in a molecular study, including some representatives of the previously uncharacterized genera *Afrophilometra*, *Caranginema* and *Rumai*.

Whereas both Nadler et al. (2007) and van Megen et al. (2009) considered *Philonema* Kuitunen-Ekbaum, 1933 to be a member of the Philometridae based on morphological features, Moravec (2006) had removed *Philonema* from the Philometridae and transferred it to the Micropleuridae. The separation of *Philonema* from the philometrids was supported by the molecular analyses of Wijová et al. (2006) and (Černotíková et al. 2011) and, although molecular data also showed that *Micropleura* and *Philonema* likely belong to two separate families, they confirmed that the Philometridae is paraphyletic.

Furthermore, Wijová et al. (2006) and Černotíková et al. (2011) also showed that, contrary to other philometrids, the genera *Philometra* and *Philometroides* as currently conceived, are paraphyletic, suggesting that this division may not reflect a true phylogenetic relationship and may not be valid. Supporting this idea are the findings of Quiazon et al. (2008b) and de Buron et al. (2011), whose analyses grouped into the same clades various species of *Philometroides* and *Philometra*. Although Quiazon et al. (2008b) used the internal transcribed spacer (ITS2) region of the ribosomal DNA and de Buron et al. (2011) partly sequenced the cytochrome oxidase I (COI) mitochondrial gene to perform their respective analysis, these authors found in common that some of the species of *Philometra* they studied were more closely related to species of *Philometroides* than to other *Philometra* species.

Wu et al. (2005), based on a molecular study using the SSU rRNA gene showing similar results, had already questioned the validity of *Philometroides*, which they suggested should be split into several genera. Whereas Quiazon et al. (2008b) concluded that the genetic divergence observed between species of the same genera could be explained by host evolution (some fish being marine, others freshwater), this explanation did not hold for the cryptic species studied by de Buron et al. (2011), since all infected the same host species. Despite the divergent opinions of these authors, a common conclusion remains that the genera *Philometra* and *Philometroides* should be re-evaluated and that the importance of using molecular tools in parallel with morphological identification cannot be over emphasized for this group of nematodes.

New studies of impact of infection by philometrids on their hosts

As mentioned in the introduction, some species of philometrids seem not to affect their hosts, while others are known to cause serious damage to various organs of their fish hosts, particularly if the worms are present in large number. Over the past six years, new data were obtained on the pathogenicity of philometrids. In particular, it seems that increasing attention has been paid to species parasitizing fish gonads, which in some instances are known to cause heavy infections in numerous marine (mainly perciform) wild or cultured fishes of economic importance (Moravec 2006).

The impact of the parasites on their fish host's fecundity ranged from being not significant (Jenkins and McBride 2009) to full blown parasitic castration (see below). In some cases, fibrosis of the gonad was initiated by dead parasites (Mohamed et al. 2010). However, it is important to note that these effects were evaluated by various authors who used different assessment tools (and rarely according to acceptable ichthyological methods). Heavy infections were recently reported in the gonads of *Epinephelus adscensionis* infected by *Philometra mexicana* in the southern Gulf of Mexico (Moravec and Salgado-Maldonado 2007), *E. cyanopodus* infected by *P. cyanopodi* off New Caledonia (Moravec and Justine 2008), *Mycteroperca phenax* infected by *P. charlestonensis* and *Sciaenops ocellatus* infected by *P. floridensis* off the Atlantic coast of South Carolina, USA (Moravec and de Buron 2009b), *Valamugil cunnesius* infected by *P. cephalus* in the Ashtamudy Estuary, Kerala, India (Radhakrishnan et al. 2009), and *Terapon jarbua* infected by *P. terapontis* off the coast of India (Moravec et al. 2011a).

Although intensity is not always possible to determine since worms may be so long that they break into pieces, Chávez and Oliva (2011) reported a high number of 99 individuals of *P. genypteri* (erroneously reported as *P. chilensis*) in the ovary of the red cusk-eel *Genypterus chilensis* in Chilean waters. These authors, as well as Moravec and Salgado-Maldonado (2007) in the case of *E. adscensionis* infected by *P. mexicana*, reported the fact that the gonads of the fish were filled with worms resulting in parasitic castration. Although Perez et al. (2009) observed little overall host reaction in *Cynoscion nebulosus* infected by *P. charlestonensis*, they suggested a negative impact of the infection on the host based on localized damaged ovarian lamellae when in contact with the worms. Similarly, Radhakrishnan et al. (2010) observed host tissue destruction upon contact with the worms.

These authors also showed that, despite a low impact on the host health (as indicated by condition factor and both hepatosomatic and gonadosomatic indices) and no significant host reactions, *P. cephalus* likely had an adverse effect on the host population, *V. cunnesius*, by significantly reducing female fish fecundity (using an acceptable ichthyological method). Furthermore, Deepthi et al. (2007) showed that infection by *P. cephalus* elicited a molecular stress response in the infected ovaries (but not the testes) of *V. cunnesius*. SDS-PAGE electrophoresis used in this latter study indicated that five proteins (of which two were High Molecular Stress Proteins) were newly elicited, that three others had increased synthesis, and that about ten proteins (of which one Low- and one Very Low Molecular Weight Stress Proteins) were suppressed. These authors concluded that male *V. cunnesius* appeared to tolerate infection better than females and that analysis of the host stress response could help in interpreting fish host-philometrid parasite relationships.

Heavy infections with philometrids parasitizing other fish organs were also recorded in recent studies. For example, *Dentiphilometra lutjani* was found in the musculature of *Lutjanus griseus* off the southern coast of Quintana Roo, Mexico (prevalence 40%, intensity of females up to 11) (González-Solís et al. 2007), whereas *Caranginema americanum* was found in the subcutaneous tissue of *Caranx hippos* in the southern Gulf of Mexico (prevalence 100%, intensity of females 11–27) (Moravec et al. 2008a). Three freshwater species from the West Point Reservoir, Alabama-Georgia, USA, *Philometra orbitalensis* (prevalence 17–71%, intensity up to 14) and *Philometroides aphanonaris* (prevalence 26–71%, intensity up to 15) parasitic in oculo-orbits and in the subcutaneous tissue, respectively, of *Micropterus salmoides*, and *P. wellborni* (prevalence 31–66%, intensity up to 12) in oculo-orbits of *Lepomis macrochirus* also exhibited high infections (Moravec et al. 2008a).

Only a few studies describe the pathological changes associated with philometrids in extra-gonadal organs. Saraiva et al. (2008) reported that gudgeon *Gobio lozanoi* infected with *Philometra ovata* in their abdominal cavity were heavier because of the parasite load and displayed a reduced swimming ability. Infected fish exhibited a swollen abdomen but only mild chronic inflammation, and some necrotic tissues were observed histologically. De Buron and Roumillat (2010) carried out a histological study of *P. overstreeti* and *Philometroides paralichthydis*, which both infect the southern flounder *Paralichthys lethostigma*. Results indicated significant intraspecific variation in pathology relative to the host-parasite interface according to the site of the worms. Individuals of *P. overstreeti* associated with fish teeth induced a degradation of the enameloid epithelium and some tissue congestion but elicited minimal host reaction, whereas those located in the branchial arches induced an intense inflammatory response. Individuals of *P. paralichthydis* associated with bones of the fish buccal cavity were contained in a thick collagenous capsule, whereas those associated with the muscles controlling the dorsal and anal fins elicited no host reaction, but induced damage of the inclinator muscle. Such effects were shown in a subsequented study (Umberger et al. 2013) to the impede swimming performance of small flounders and, thus, infection by *P. paralichthydis* likely impacts the population structure of this important fish species.

Williams et al. (2012) described pathological changes associated with *Philometroides sanguineus*, an invasive parasite of the wild crucian carp *Carassius carassius* in England. The severity of the damage caused by this parasite was strongly influenced by host size (fish < 60 mm in length being the most affected), and increased inflammation was associated with the seasonal migration of female worms within host tissues. Whereas male and unfertilized female nematodes (located on the swimbladder wall) and fertilized female worms (dormant between migratory periods) caused only minor and localized changes, the emergence of gravid females to release larvae was shown to induce a suite of tissue reactions (hyperplasia, acute inflammation, necrosis) and gross pathology (fin distortion, swelling of dorsal and caudal fin tissues, scale displacement). These authors concluded that the pathology induced by *P. sanguineus* on fry may be serious enough for this parasite to be considered an added pressure on a fish population already at risk (Pegg et al. 2011).

Regarding captive fishes, the known vulnerability of young fish to infection was further addressed by Santos and Moravec (2009), who studied tank-reared arapaimas *Arapaima gigas* off Mexiana Island in the Amazon River delta, Brazil and by Seguin et al. (2011), who reported mortalities of captive striped bass *Morone saxatilis* reared in captivity for restocking and restoration purposes in Canada. In the former case, the philometrids *Nilonema senticosum* (swimbladder parasites) and *Rumai rumai* (found in mouth, tongue, operculum and head tissues of the host) were, along with the anisakid *Goezia spinulosa* (Diesing, 1839), suggested to be most pathogenic parasites for young arapaimas because of their blood feeding behaviour, which resulted in the adopted practice of cooking plankton served as food to reared fish.

In the latter study, a high mortality episode of wild-hatched fingerlings of *M. saxatilis* reared in captivity was associated with an extensive pathology caused by *Philometra* sp. (subsequently identified as *P. rubra* by Moravec et al. 2013b) in the body cavity of the fish. Although infection was acquired in the wild, the higher water temperatures in the captive conditions were thought to explain the premature development of worms (normally gravid in spring/summer during spawning) and the subsequent death of host fish that were not physiologically ready to allow the larvae to be released (not spawning). These authors concluded that, since this parasite is likely to not occur in captive conditions, a captive breeding programme would likely be best in such restoration projects.

Given these results, the increasing practice of fish farming, and their potential impact on fisheries management practices throughout the globe, further studies on the pathogenicity of philometrids are greatly needed.

STUDIES ON PHILOMETRID LIFE CYCLES

As mentioned above, philometrid life histories often exhibit patterns that have been associated with various factors, such as season, fish length, gender and spawning activity. New data concerning these patterns are mentioned above (Perez et al. 2009, de Buron et al. 2011, Chávez and Oliva 2011, Seguin et al. 2011, Williams et al. 2012). However, despite the fact that life history data are lacking for the great majority of philometrid species, too little attention (only three papers) has been paid to the life cycles of these nematode parasites in the recent years and few studies have been initiated to address this problem.

Bryan at al. (2008) experimentally studied the development of *Philometra overstreeti* and *Philometroides paralichthydis*, both parasites of the brackish-water southern flounder *Paralichthys lethostigma* in the estuaries of the southern USA. Of five common local copepods exposed to the L_1 of both philometrid species, only the cyclopoid *Oithona colcarva* was found to be a suitable experimental host for both philometrid species. Larval development in the haemocoel of copepods was studied using both LM and TEM, and both larval moults were found to occur within seven days post-infection at 23 °C, with the L_3 remaining within the second moult. This was the first reported intermediate host of philometrids parasitizing non-freshwater fish hosts, which indicates that copepods probably serve as intermediate hosts for all philometrids.

Also, and for the first time, cyclopoid copepods, subsequently identified as *Mesocyclops brasilianus* and *Thermocyclops decipiens* (Santos, unpublished), were succesfully infected with the L_1 of *Nilonema senticosum* and *Rumai rumai*, both pathogenic philometrid parasites of *Arapaima gigas* in South America (Santos and Moravec 2009).

Most recently, Palesse et al. (2011) have used molecular tools (polymerase chain reaction with restriction fragment length polymorphism [PCR-RFLP] and the sequencing of the COI gene) to identify philometrid larvae found in small fishes. *Ctenogobius shufeldti* (Gobiidae) was found to serve as a paratenic host for *Philometra carolinensis* and *P. overstreeti*, parasites of *Cynoscion nebulosus* and *Paralichthys lethostigma*, respectively, and *Fundulus heteroclitus* (Fundulidae) proved to be a paratenic host for *P. overstreeti*. Although this study, when combined with that of Bryan et al. (2008), can be considered to have shed some light on the life cycle of *P. overstreeti*, the finding of RFLP-PCR profiles and COI sequences that could not be matched to the control species demonstrated an unexpected higher diversity of philometrids than was previously known in these estuaries. This conclusion is likely applicable throughout the world and further emphasizes the need for the additional prospecting for philometrids across the globe.

CONCLUSIONS AND PROSPECTS

Despite the progress made in recent years, and even with the completion of more detailed morphological studies using SEM and the use of molecular tools, philometrids still remain poorly known. Nevertheless, the achievements of more recent investigations can be used as a stepping stone for future studies as outlined below.

As is the case for members of the suborder Spirurina in general, the present classification of philometrids remains unsatisfactory. A new classification system of these nematodes needs to be created that includes a delimitation of the genera which is concordant with their phylogenetic relationships. A prerequisite for this is a taxonomic revision of the entire group based on the detailed and comprehensive study of individual species, including their morpho-anatomy, life history and genetics. However, because it can be assumed that we currently know only a very small number of the extant philometrid species, the pursuit of prospective surveys, in particular of freshwater fishes in the little explored Neotropical, Ethiopian, Oriental and Australian Regions, and of marine fishes in general, should be prioritized.

The need for using the recommended fixative (hot buffered 4% formaldehyde solution is preferred for morphological studies) and the need to find the minute males of each species (particularly in the case of the otherwise very similar gonad-infecting species of *Philometra*) cannot be emphasized enough. Also, a few conspecific specimens should always be collected using recommended techniques for DNA analysis. Species descriptions should be as detailed as possible and include SEM observations, and barcoding should be associated with each description whenever possible. Specimens, especially the type specimens, but also some fixed in 95% ethanol for molecular studies, should be deposited in internationally recognized helminthological collections where they will be accessible to other researchers.

Further studies on various aspects of the biology, ecology and pathogenicity of these fascinating worms would extend our understanding of the host-parasite relationships in this group, and research on the impact of ovarian philometrids on fish fecundity should especially be pursued. Importantly, more effort should be made to determine quantitatively the impact of these parasites using methods accepted by ichthyologists (Murua et al. 2003) in order for such studies to be taken into account in aquaculture programmes and fisheries management.

Studies on the life cycles of philometrids are highly neglected and should include not only the role of ostracods as potential intermediate hosts, but also fish paratenic hosts in the transmission of these worms. Special attention should be paid to philometrids parasitizing brackish water/marine fishes, where such data are practically nonexistent. As already mentioned by Moravec (2004), these investigations should include both laboratory and field studies, since biological data on these parasites may have practical implications.

ADDENDUM

Since this paper was submitted for publication, an additional seven new philometrid species have been described from marine fishes. Dewi and Palm (2013) established *Philometra epinepheli* and S*pirophilometra endangae* from opercula and fins, respectively, of *Epinephelus coioides* in the South Bali Sea, Indonesia, Moravec and Ali (2013) *Philometra johnii* from gonads of *Johnius dussumieri* in the Persian Gulf, Iraq and Moravec and Manoharan (2013) gonad-infecting *Philometra sphyraenae* from *Sphyraena jello*, *P. gerrei* from *Gerres filamentosus*, *P. otolithi* from *Otolithes ruber* and *Philometroides eleutheronemae* from *Eleutheronema tetradactylum* in the Bay of Bengal, India.

A list of presently known species of the Philometridae by continents is given in Table 1.

Table 1. List of valid species of philometrid nematodes (Philometridae) by continents.

EUROPE

From freshwater fishes:

Philometra cyprinirutili (Creplin, 1825)
Philometra kotlani (Molnár, 1969)
Philometra obturans (Prenant, 1886)
Philometra ovata (Zeder, 1803)
Philometra rischta Skryabin, 1923
Philometroides barbi Moravec, Šimková, Cakić, Špakulová et Hanzelová, 2006
Philometroides cyprini (Ishii, 1931)
Philometroides sanguineus (Rudolphi, 1819)

From marine fishes:

Philometra filiformis (Stossich, 1896)
Philometra fusca (Rudolphi, 1819)
Philometra globiceps (Rudolphi, 1819)
Philometra jordanoi (López-Neyra, 1951)
Philometra justinei Moravec, Ternengo et Levron, 2006
Philometra obladae Moravec, Gaglio, Panebianco et Giannetto, 2008
Philometra saltatrix Ramachandran, 1973
Philometra scomberesocis Nikolaeva et Naidenova, 1964
Philometra serranellicabrillae Janiszewska, 1949
Philometra spicarae Moravec, Gaglio, Giannetto et Marino, 2010
Philometra tauridica Ivashkin, Kovaleva et Khromova, 1971
Philometroides oveni Parukhin, 1975

ASIA

From freshwater fishes:

Clavinema fujimotoi (Furuyama, 1932)
Clavinema parasiluri Yamaguti, 1935
Dentiphilometra monopteri Moravec et Wang, 2002
Dentirumai philippinensis Quiazon et Moravec, 2012
Philometra biglobocerca Belous, 1965
Philometra clavaeceps Dogiel et Akhmerov, 1959
Philometra coreii Yu et Wang, 1997
Philometra gobioboti Yu et Wang, 1997
Philometra hyderabadensis Rasheed, 1963
Philometra karunensis Pazooki et Molnár, 1998
Philometra macronesi (Shendge et Deshmukh, 1977)
Philometra opsalichthydis Yamaguti, 1935
Philometra oreoleucisci Moravec et Ergens, 1970
Philometra parasiluri Yamaguti, 1935
Philometra rischta Skryabin, 1923
Philometra terapontis Moravec, Gopalakrishnan, Rajkumar, Saravanakumar et Kaliyamoorthy, 2011
Philometra thaiensis Moravec, Fiala et Dyková, 2004
Philometroides acanthopagri Moravec, Jassim et Al-Salim, 2012
Philometroides anguillae (Ishii, 1916)
Philometroides cyprini (Ishii, 1931)
Philometroides dogieli Vismanis et Yukhimenko, 1974
Philometroides fulvidraconi Yu, Wu et Wang, 1993
Philometroides masu (Fujita, 1940)
Philometroides moraveci Vismanis et Yunchis, 1994
Philometroides pseudaspii Moravec et Ergens, 1970
Philometroides pseudorasbori Wang, Yu et Wu, 1995
Philometroides sanguineus (Rudolphi, 1819)
Philometroides strelkovi Vismanis et Yunchis, 1994

From marine and brackish-water fishes:

Buckleyella buckleyi Rasheed, 1963
Clavinema mariae (Layman, 1930)
Paraphilometroides nemipteri Moravec et Shaharom-Harrison, 1989
Philometra balistii Rasheed, 1963
Philometra cephalus Ramachandran, 1975
Philometra cryptocentri Yamaguti, 1961
Philometra epinepheli Dewi et Palm, 2013
Philometra gerrei Moravec et Manoharan, 2013
Philometra gymnosardae Moravec, Lorber et Konečný, 2007

(continued)

Table 1. Continued.

Philometra inimici Yamaguti, 1941
Philometra isaki Quiazon, Yoshinaga et Ogawa, 2008
Philometra ivaschkini Parukhin, 1976
Philometra javaensis Moravec, Walter et Yuniar, 2012
Philometra johnii Moravec et Ali, 2013
Philometra lateolabracis (Yamaguti, 1935)
Philometra lobotidis Moravec, Walter et Yuniar, 2012
Philometra madai Quiazon, Yoshinaga et Ogawa, 2008
Philometra managatuwo Yamaguti, 1941
Philometra nemipteri Luo, 2001
Philometra neolateolabracis
Rajyalakshmi, Rao et Shyamasundari, 1985 [*species inquirenda*]
Philometra ocularis
Moravec, Ogawa, Suzuki, Miyazaki et Donai, 2002
Philometra otolithi Moravec et Manoharan, 2013
Philometra pellucida (Jägerskiöld, 1893)
Philometra pinnicola (Yamaguti, 1935)
Philometra plotosi Moravec et Nagasawa, 1989
Philometra polynemii Rasheed, 1963
Philometra psettoditis Moravec, Walter et Yuniar, 2012
Philometra rachycentri Parukhin, 1984
Philometra rasheedae Garg, 1983
Philometra robusta Moravec, Möller et Heeger, 1992
Philometra sawara Quiazon, Yoshinaga et Ogawa, 2008
Philometra sciaenae Yamaguti, 1941
Philometra scomberomori (Yamaguti, 1935)
Philometra sebastisci Yamaguti, 1941
Philometra sebastodis Yamaguti, 1941
Philometra spari Yamaguti, 1961
Philometra sphyraenae Moravec et Manoharan, 2013
Philometra strongylurae Moravec et Ali, 2005
Philometra tylosuri Moravec et Ali, 2005
Philometroides atropi (Parukhin, 1966)
Philometroides branchiostegi Moravec, Nagasawa et Nohara, 2012
Philometroides denticulatus Rasheed, 1965
Philometroides eleutheronemae Moravec et Manoharan, 2013
Philometroides indonesiensis Moravec, Walter et Yuniar, 2012
Philometroides seriolae (Ishii, 1931)
Philometroides trichiuri Moravec, Walter et Yuniar, 2012
Spirophilometra eichleri Parukhin, 1971
Spirophilometra endange Dewi et Palm, 2013

AFRICA

From freshwater fishes:

Afrophilometra hydrocyoni (Fahmy, Mandour et El-Naffar, 1976)
Nilonema gymnarchi Khalil, 1960
Philometra bagri (Khalil, 1965)
Philometra lati Moravec, Charo-Karisa et Jirků, 2009
Philometra spiriformis Moravec, Charo-Karisa et Jirků, 2009
Philometroides africanus Moravec et Van As, 2001

From marine fishes:

Philometra beninensis Obiekezie, 1986
Philometra katsuwoni Petter et Baudin-Laurencin, 1986
Philometra macroandri (Shchepkina, 1978)

NORTH AMERICA
(including Mexico)

From freshwater fishes:

Neophilometroides caudatus
(Moravec, Scholz et Vivas-Rodríguez, 1995)
Philometra cylindracea (Ward et Magath, 1917)
Philometra kobuleji Molnár et Fernando, 1975
Philometra ophisterni
Moravec, Salgado-Maldonado et Aguilar-Aguilar, 2002
Philometra orbitalensis
Moravec, Crosby, de Buron, González-Solís et Roumillat, 2008
Philometra poblana
Caspeta-Mandujano, Granados-Ramírez et Peralta-Rodríguez, 2009
Philometra rubra (Leidy, 1856)
Philometra translucida Walton, 1928
Philometroides aphanonaris
Moravec, Crosby, de Buron, González-Solís et Roumillat, 2008
Philometroides huronensis Uhazy, 1976
Philometroides nodulosus (Thomas, 1929)
Philometroides wellborni
Moravec, Crosby, de Buron, González-Solís et Roumillat, 2008

From marine and brackish-water fishes:

Caranginema americanum
Moravec, Montoya-Mendoza et Salgado-Maldonado, 2008
Clavinema mariae (Layman, 1930)
Philometra brevispicula Moravec et Bakenhaster, 2010
Philometra carolinensis Moravec, de Buron et Roumillat, 2006
Philometra charlestonensis
Moravec, de Buron, Baker et González-Solís, 2008
Philometra cheilopogoni Mordvinova, 1986
Philometra cynoscionis Moravec, de Buron et Roumillat, 2006
Philometra diplectri Moravec et Bakenhaster, 2010
Philometra floridensis Moravec, Fajer-Avila et Bakenhaster, 2010
Philometra gymnothoracis Moravec et de Buron, 2009
Philometra margolisi
Moravec, Vidal-Martínez et Aguirre-Macedo, 1995
Philometra mexicana Moravec et Salgado-Maldonado, 2007
Philometra morii Moravec, Bakenhaster et Fajer-Avila, 2010
Philometra overstreeti Moravec et de Buron, 2006
Philometra salgadoi
Vidal-Martínez, Aguirre-Macedo et Moravec, 1995
Philometra saltatrix Ramachandran, 1973
Philometroides grandipapillatus Moravec et Bakenhaster, 2010
Philometroides marinus Moravec et de Buron, 2009
Philometroides paralichthydis Moravec et de Buron, 2006
Spirophilometra centropomi (Caballero, 1974)
Spirophilometra pacifica
Moravec, Santana-Piñeros, González-Solís et Torres-Huerta, 2007

SOUTH AMERICA

From freshwater fishes:

Alinema amazonicum (Travassos, 1960)
Neophilometroides paraguayensis (Petter, 1995)
Nilonema senticosum (Baylis, 1927)
Philometra baylisi Vaz et Pereira, 1934
Philometra nattereri Cárdenas, Moravec, Fernandes et Morais, 2012
Philometroides maplestoni (Travassos, Artigas et Pereira, 1928)
Rumai rumai Travassos, 1960

From marine fishes:

Dentiphilometra lutjani González-Solís, Moravec et Tuz Paredez, 2007
Philometra genipteri Moravec, Chávez et Oliva, 2011
Philometra katsuwoni Petter et Baudin-Laurencin, 1986
Philometra neptomeni Mateo, 1972

AUSTRALIA AND OCEANIA

From freshwater fishes:

Philometra percalates Johnston et Mawson, 1940
Philometroides plectroplites (Johnston et Mawson, 1940)
Philometroides similis Moravec, 2006

From marine fishes:

Philometra cyanopodi Moravec et Justine, 2008
Philometra dentigubernaculata Moravec et Justine, 2009
Philometra fasciati Moravec et Justine, 2008
Philometra kohnae Moravec et Rohde, 1992
Philometra lagocephali Moravec et Justine, 2008
Philometra lethrini Moravec et Justine, 2008
Philometra lomi Moravec et Rohde, 1992
Philometra priacanthi Moravec et Justine, 2009
Philometra sydneyi Rasheed, 1963
Philometra tenuicauda Moravec et Justine, 2009

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