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REVIEW ARTICLE

Some aspects of the taxonomy and biology of dracunculoid nematodes parasitic in fishes: a review

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Abstract. The nematode superfamily Dracunculoidea includes 166 recognized species, of which 150 (90%) are parasitic in about 300 species of freshwater, brackish-water and marine fishes. Fish dracunculoids are placed in 31 genera (86% of all dracunculoid genera) belonging to eight of the nine dracunculoid families: Anguillicolidae, Daniconematidae, Guyanemidae, Lucionematidae, Micropleuridae, Philometridae, Skrjabillanidae, and Tetanonematidae; the genus *Lockenloia* is considered *incertae sedis*. Because of difficulties in studying fish dracunculoids, associated with their morphological and biological peculiarities, most species of these largely histozoic parasites are poorly known and males of the majority of species and of eight genera have not yet been discovered. It is apparent that the present classification system of dracunculoids as a whole does not reflect phylogenetic relationships and a taxonomic revision of this nematode group, based on detailed morphological (including SEM and TEM), life history and molecular studies of individual species, is quite necessary. Data on the biology of fish dracunculoids is scarce. In known cases, their life cycles involve copepods, ostracods or branchiurids as intermediate hosts and, sometimes, fish paratenic hosts are known to occur in dracunculoid species parasitizing as adults piscivorous definitive hosts. However, nothing is known about the life cycles of representatives of 20 genera. Some species of dracunculoids, particularly of philometrids, are highly pathogenic and are known as agents of serious fish diseases. During recent years, especially the importance of *Philometra* spp. parasitizing the gonads of many species of marine fishes has increased due in particular to the rapid development of marine aquaculture, because they may significantly decrease fish reproduction or even cause full parasitic castration. Therefore, further detailed studies on fish dracunculoids are significant not only from the theoretical viewpoint, but they may also have practical implications.

Nematodes of the superfamily Dracunculoidea Stiles, 1907, which are characterized by certain morphological features and some biological peculiarities, represent a large, diverse group of parasites with a worldwide distribution. Members are noted for the presence of a simple oval or triangular mouth surrounded by a variable number of cephalic papillae usually arranged in two circles (Fig. 1). The buccal capsule, if present, is usually reduced (Fig. 2). The oesophagus is largely divided into muscular and glandular parts but may be entirely muscular (Fig. 3). Two spicules or a sclerotized copulatory plate may be present or absent (Fig. 4). Most forms are viviparous. After fertilisation, females grow markedly as first-stage larvae fill their uteri. In some groups the vulva and anus atrophy in fully gravid females and larvae are dispersed into the environment by bursting as they come in contact with water, whereas in others their larvae are released into the tissues. Many dracunculoids exhibit marked sexual dimorphism in which females are highly modified and considerably larger than the males. The body size of gravid females in different species ranges between 1 mm in *Lucionema balatonense* from European pikeperch to more than 1 m in *Philometra* sp. from wreckfish (pers. comm. of C.J. Fennesy, Virginia Institute of Marine Science, USA).

The hosts of the numerous species of these nematodes are members of all main classes of vertebrates (fishes, amphibians, reptiles, birds, mammals) including man, but their highest species and morphological diversity occurs in fishes. Some species parasitize a wide range of hosts, others exhibit a relatively narrow host specificity. The dracunculoids are mostly parasites of various tissues and organ cavities and different species attack, for example, the skin and subcutaneous tissue, body musculature, eyes, orbits, gills and the swimbladder (in fishes), kidneys, gonads and the circulatory system, or are found in the body cavity of the host (Ivashkin et al. 1971, Chabaud 1975, Moravec 1994).

The dracunculoid life cycles involve aquatic crustaceans (copepods, ostracods or branchiurids) as intermediate hosts and, consequently, the transmission and the occurrence of these parasites in vertebrate definitive hosts is always associated with the aquatic environment. Therefore, it is not surprising that the absolute majority of dracunculoids is found in fishes, both freshwater and marine. Of the nine dracunculoid families, eight (89%) include the forms from fishes, whereas the family Dracunculidae Stiles, 1907 contains a few species

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parasitic in amphibians (species of the monotypic genera *Kamegainema* Hasegawa, Doi, Araki et Miyata, 2000 and *Protenema* Petter et Planelles, 1986), birds (species of *Avioserpens* Wehr et Chitwood, 1934) and reptiles and mammals (members of *Dracunculus* Reichard, 1759); the Micropleuridae Baylis et Daubney, 1926 contains four species of *Micropleura* Linstow, 1906 from reptiles and two species of *Granulinema* Moravec et Little, 1988 from fish (sharks) (Muller 1971, Petter and Planelles 1986, Moravec and Little 1988, Moravec et al. 1998a, 2004, Hasegawa et al. 2000). Of a total number of 36 valid genera of dracunculoid nematodes with 166 recognized species, 31 (86%) genera with 150 (90%) species are found in fishes.

According to Moravec et al. (1998a), the following dracunculoid families include adult forms from fishes: Anguillicolidae Yamaguti, 1935 (1 genus, 5 species), Daniconematidae Moravec et Køie, 1987 (3 genera, 4 species), Guyanemidae Petter, 1975 (5 genera, 9 species), Lucionematidae Moravec, Molnár et Székely, 1998 (1 genus, 1 species), Micropleuridae Baylis et Daubney, 1926 (1 genus, 2 species), Philometridae Baylis et Daubney, 1926 (12 genera, 115 species), Skrjabillanidae Shigin et Shigina, 1958 (4 genera, 7 species), and Tetanonematidae Skryabin et Shikhobalova, 1948 (1 genus, 1 species); the monotypic dracunculoid genus *Lockenloia* Adamson et Caira, 1991 with *L. sanguinis* Adamson et Caira, 1991 from sharks has not been assigned to any family and is considered *incertae sedis*.

The present author does not consider useful to provide a key to the families and genera of Dracunculoidea or to list valid dracunculoid species in this paper, because important taxonomic changes are expected soon, as indicated by contemporary studies. The Dracunculoidea will be dealt with in detail in the author's monograph intended to be published within two next years.

Dracunculoid nematodes are widely distributed among freshwater, brackish-water and marine fishes, being reported from at least 300 fish species, belonging to 84 fish families and 25 orders. Some of them are highly pathogenic and are known to be agents of serious diseases of fish with economic importance, where they may cause mass mortalities, in stocks of both free-living and cultured fish (e.g., anguillicolosis of eels, philometroidosis of carps, philonemosis of salmonids); the frequent destruction of gonads caused by *Philometra* spp. in cultured marine perciform fishes may decrease considerably the reproduction of these fishes and may even cause full parasitic castration (Ramachandra 1975, Sakaguchi et al. 1987, Moravec et al. 2002a, 2003). A fish philometrid was also recorded as facultative human parasite (Deardorff et al. 1986).

In addition to adult forms, fishes may harbour larval dracunculoids, serving thus as paratenic hosts for some species of *Anguillicola*, *Philometra*, *Avioserpens* and *Dracunculus* and an additional source of infection for the definitive host (e.g., Ivashkin et al. 1971, Molnár 1976, Moravec and Dyková 1978, Thomas and Ollevier 1992, Székely 1994).

Besides the practical importance of fish dracunculoids as pathogens, this nematode group represents a significant experimental group for testing theoretical questions concerning the host – parasite relationships, morphological adaptations to parasitism, biology, ecology, zoogeography and phylogeny of these parasites and their fish hosts, as also some questions of general biology.

In view of their unusual location in the host's body and some morphological, physiological and biological peculiarities, the majority of dracunculoids remains poorly known and the classification within this parasite group is, besides trichinelloids, one of the most difficult and unsatisfactory in the Nematoda (Anderson 2000).

TAXONOMY AND CLASSIFICATION

The first fish dracunculoid was described by Zeder (1803) as *Filaria ovata* (= *Philometra ovata*) from European cyprinids. During the 19th and especially 20th century, the number of nominal philometrid species rapidly increased, but the identification of many of them remained questionable (Ivashkin et al. 1971). Most species descriptions were based solely on large-sized females, whereas conspecific males remained unknown because they often are very small, have a rare or temporary occurrence in the host, and usually locate in different host tissue than the gravid female.

In the past, the majority of philometrids were assigned to the generally recognized genus *Philometra* Costa, 1845. In 1963, Rasheed carried out a detailed revision of members of this genus and, in attempt to make species identification easier, she created a taxonomic system of Philometridae based principally on the female morphology. Taking into account certain genera established by previous authors (*Philonema* Kuitunen-Ekbaum, 1933, *Ichthyofilaria* Yamaguti, 1935, *Philometroides* Yamaguti, 1935, *Nilonema* Khalil, 1960, *Rumai* Travassos, 1960), she proposed two more new genera, *Buckleyella* and *Thwaitia*, and a few new subgenera.

The system of Rasheed (1963) is based essentially on the number, arrangement and character of female cephalic papillae and the structure of various cuticular ornamentations on the body are considered to be the main taxonomic features. In spite of progress, the system proposed by Rasheed (1963) is still not a natural system, the genera are often heterogenous, including morphologically different and obviously unrelated species. This system was followed e.g. in the monographs by Ivashkin et al. (1971) and Chabaud (1975), but its practical use is often problematic for the generic identification of nematodes, because the study of cephalic papillae in females with the aid of the light microscope is sometimes difficult (see Rasheed 1963) and may lead to wrong conclusions. In the following years, a number of additional new philometrid species and a few genera were established.

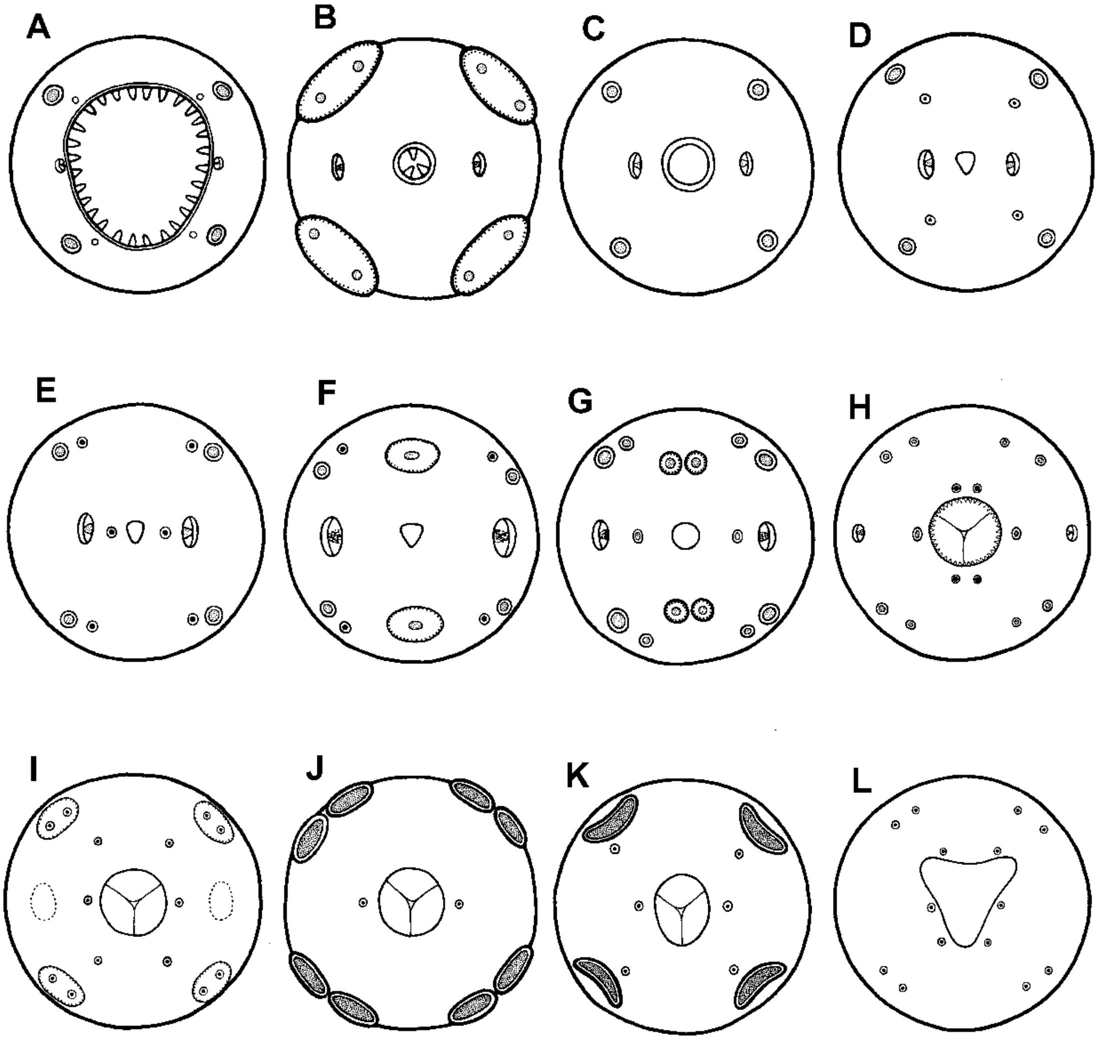

Fig. 1. Variations in the arrangement of cephalic papillae in fish dracunculoids (apical views, schematized). **A** – *Anguillicola*; **B** – *Molnaria*; **C** – *Skrjabillanus*; **D** – *Lucionema*; **E** – *Granulinema*; **F** – *Daniconema*; **G** – *Histodytes*; **H** – *Dentiphilometra*; **I** – *Philometra* (*P. ovata*); **J** – *Philometra* (*P. salgadoi*); **K** – *Philometra* (*P. ocularis*); **L** – *Clavinema*.

The recent use of scanning electron microscopy (SEM) provided not only new possibilities to obtain reliable data on the numbers and distribution patterns of cephalic papillae in these nematodes but, surprisingly, led to the discovery of new forms of philometrids with an armed oral aperture (genera *Neophilometroides* Moravec, Salgado-Maldonado et Aguilar-Aguilar, 2002, *Dentiphilometra* Moravec et Wang, 2002), showing thus their affinities to anguillicolids (Moravec et al. 2002b, Moravec and Wang 2002). Unfortunately, to date, SEM studies have infrequently been used to study just a few species of *Clavinema* Yamaguti, 1935, *Philometra* and *Philometroides* (see, e.g., Uhazy 1976, Obiekezie and Anders 1991, Vidal-Martínez et al. 1995, Moravec et al. 1998b, 2002a, Blaylock and Overstreet 1999, Moravec and Van As 2001).

In 1921, Steiner established a new genus *Phlyctainophora* to accommodate *P. lamnae* Steiner, 1921, a species described from females with an unusual shape of body, collected in sharks of the North Atlantic. Another congeneric species was established by Mudry and Dailey (1969) based on females from sharks of the Pacific Ocean. This genus has mostly been considered within the family Philometridae (e.g., Mudry and Dailey 1969, Chabaud 1975). However, Adamson et al. (1987), who first described the male of this genus, showed that certain characters of the male agree with those of members of the Philometridae, but others are, more or less, characteristic of the Guyanemidae and, consequently, they treated *Phlyctainophora* as a Dracunculoidea *incertae sedis*.

The first non-philometrid dracunculoid genus *Anguillicola* was established by Yamaguti (1935) for *A. globiceps* Yamaguti, 1935 from the swimbladder of Japanese eels in Japan, for which the author created the family Anguillicolidae. This monotypic family now includes five species of *Anguillicola* originally distributed in eels of East Asia, Australia, New Zealand and South Africa, of which the highly pathogenic species *A. crassus* Kuwahara, Niimi et Itagaki, 1974, originating from East Asia, has been introduced into other continents and is now widely distributed also in Europe, North Africa and North America (e.g., Moravec 1994, Fries et al. 1996, Barse et al. 2001, Rahhou et al. 2001). The taxonomic revision of *Anguillicola* spp. was carried out by Moravec and Taraschewski (1988), who separated the species into two subgenera, *Anguillicola* and *Anguillicoloides* Moravec et Taraschewski, 1988.

As to the recognition of fish dracunculoids and their taxonomy, probably the greatest discovery in this respect was the finding of a remarkable nematode *Skrjabillanus tincae* Shigin et Shigina, 1958, a very fine histozoic parasite of tench, *Tinca tinca* (L.), in Europe, representing a new family Skrjabillanidae Shigin et Shigina, 1958 (see Shigin and Shigina 1958, Moravec 1994). In the following years, there were discovered and described additional genera and species of these interesting nematodes, largely from cyprinids in Europe and palaearctic Asia (Molnár 1966a, Garkavi 1972, Tikhomirova and Rudometova 1975, Moravec 1977a, Molnár and Moravec 1997). Two related species, *Daniconema anguillae* Moravec et Køie, 1987 and *Lucionema balatonense* Moravec, Molnár et Székely, 1998, each representing a new family (Daniconematidae and Lucionematidae), were described from European eels and zanders, respectively (Moravec and Køie 1987, Moravec et al. 1998a).

These surprising findings were possible only due to the use of better methods of fish dissection (including thorough examinations of the abdominal cavity and the serosa of the swimbladder), because these very fine nematodes pass unnoticed during routine examinations of fish. It is apparently the main reason why these parasites were not recorded by previous authors and, with a few exceptions, have not been reported from the countries of western and southern Europe. Most of these species were discovered accidentally while searching for the very small males of philometrids with the same localisation in the host (Moravec 1994). Even though *Daniconema anguillae* has already been recorded from eels in Canada (Marcogliese and Cone 1993), it is highly probable that also skrjabillanids and lucionematids will be discovered in freshwater fishes in the USA and Canada; this is suggested by the recent finding of dracunculoid larvae in the haemocoel of *Argulus americanus* Wilson, 1904 (Branchiura) collected on the bowfish, *Amia calva* L., in Illinois, USA (pers. comm. of W.J. Poly, California Academy of Sciences, USA).

A taxonomically important new family Guyanemidae was erected by Petter (1974); two genera, *Guyanema* Petter, 1974 and *Travassosnema* Costa, Moreira et Oliveira, 1991, include several species parasitic in South American freshwater characiform fishes and two other monotypic genera, *Pseudodelphis* and *Histodytes*, comprising the parasites of marine fishes, have been established and assigned to this family by Adamson and Roth (1990) and Aragort et al. (2002), respectively.

In contrast to philometrids, which are markedly modified by their adaptation to life within tissues, all the above mentioned non-philometrid dracunculoids show relatively little specialisation and their morphology is close to that in the Camallanoidea (Chabaud 1975).

In 1988, Moravec and Little erected the genus *Granulinema* to accommodate two new species, *G. carcharhini* and *G. simile*, from the bull shark in Louisiana, USA; the genus was provisionally assigned to the family Micropleuridae.

During recent years, two genera, *Mexiconema* Moravec, Vidal et Salgado-Maldonado, 1992 and *Syngnathinema* Moravec, Spangenberg et Frasca, 2001, have been established within the Daniconematidae: the former includes two species, *M. cichlasomae* Moravec, Vidal et Salgado-Maldonado, 1992 from cichlids and the poeciliid *Xiphophorus helleri* Heckel in Mexico and *M. liobagri* Moravec et Nagasawa, 1998 from the endemic amblycipitid catfish in Japan (Moravec et al. 1992, Moravec and Nagasawa 1998). Recently, Ribu and Lester (2004) have established a new genus *Moravecia*, listed in the Guyanemidae, to accommodate the species *M. australiensis* Ribu et Lester, 2004 from gills of the marine tetraodontiform fish *Tragulichthys jaculifer* (Cuvier) in Australia.

However, it is necessary to remark that the present assignment of some genera (e.g., *Syngnathinema* or *Tetanonema*) where the male is unknown to the respective family is uncertain and subsequent studies may show that they are members of other families. The male morphology remains unknown for 7 genera (21% of all dracunculoid genera and 24% of those containing species from fish): *Buckleyella*, *Lockenloia*, *Nilonema*, *Paraphilometroides*, *Rumai*, *Syngnathinema*, and *Tetanonema*). But due to frequent difficulties to obtain conspecific males, these remain unknown also for the great majority of species of *Philometra* and *Philometroides* and some of *Clavinema*, *Guyanema* and *Philonema*.

The species identification of fish dracunculoids, in particular the philometrids, is usually difficult, because the existing descriptions of most species, often based only on females, are inadequate. This is usually associated with the fact that gravid females are very sensitive to osmotic pressure and, therefore, only considerably damaged specimens or their body fragments are often available to study. Moreover, their morphology is rather uniform, not providing many features for distinguishing the species. The cephalic papillae of gravid philometrids

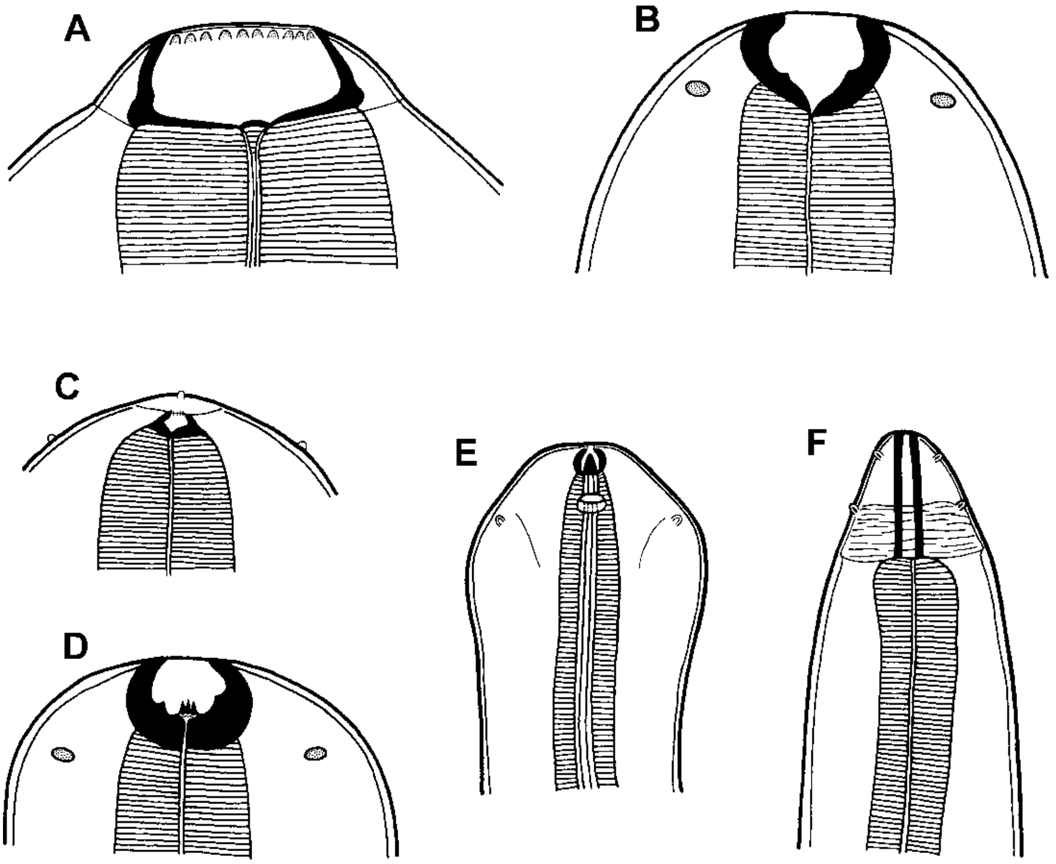

Fig. 2. Types of the buccal capsule in some fish dracunculoids. **A** – *Anguillicola crassus*; **B** – *Skrjabillanus tincae*; **C** – *Neophilometroides caudatus*; **D** – *Skrjabillanus scardinii*; **E** – *Skrjabillanus cyprini*; **F** – *Esocinema bohemicum*.

are usually difficult to observe due to a various degree of their reduction and atrophy, and the same concerns the very flat male caudal papillae.

Although the cephalic papillae of females may be an important taxonomic feature in philometrids, their possible utilisation as a generic character necessitates the comparative studies based on their exact establishment by SEM in a number of species. However, to date the cephalic papillae have been studied in the type species for only 5 of the 13 presently recognized philometrid genera.

Like in other groups of nematodes, the structure and shape of the oesophagus and the degree of the development of oesophageal glands are apparently most important for the taxonomy of philometrids. Undoubtedly, some differences in the structure of their oesophagus are of generic significance and they can be considered much more important than, for example, the superficial ornamentations on the body cuticle that were used by Rasheed (1963) for the distinction among some genera. However, a detailed oesophageal structure is not known so far for the majority of species. The shape and structure of the female posterior end can also be taken for very important features.

Although molecular studies provide new possibilities for the solution of many problems of the taxonomy and phylogeny of these remarkable nematodes, to date they have been applied quite exceptionally in dracunculoids. In fact, only two papers have been published: Adamson et al. (1992) compared restriction fragment length differences (RFLD) in highly repetitive DNA in *Philonema* spp. parasitizing *Oncorhynchus nerka* (Walbaum) and *O. mykiss* (Walbaum) from various localities in British Columbia, Canada, and found that *Philonema* spp. represent two distinct species corresponding to their different hosts. Hirose et al. (1998) sequenced the 18S rRNA gene of two congeneric swimbladder nematodes of eels, *Anguillicola crassus* and *A. globiceps*, and showed 98.8% similarity in their nucleotide sequences and lesser homology values with other nematodes.

It is clear that the taxonomy and classification of dracunculoids requires a fundamental re-evaluation based on detailed studies of individual species, including the use of new methods such as SEM and molecular studies. The new delimitation of genera will have to be based on a combination of morphological features, mainly the structure of the oesophagus, morphology of the male and female caudal ends, structure of the cephalic end, and possibly the cuticular ornamentations on the body of gravid females; also the site of infection in the host and host types should be considered. The delimitation of genera should be strictly based on the principle of type species.

Of course, such a global taxonomic revision will require a broad international collaboration and a multidisciplinary approach to the recognition of this nematode group. The solution of the present unsatisfactory situation in the taxonomy of dracunculoids is very urgent, because it can be expected that many new species and new morphological types of these parasites will be discovered mainly from hitherto little-studied geographical regions and from marine fishes, where a negligible number of fish species has so far been examined for parasites.

LIFE CYCLES

Generally, data on the life cycles of fish dracunculoids is scarce. Linstow (1874) was probably the first to attempt to clarify the development of "*Ichthyonema sanguineum*" (= ? *Philometra ovata*); under the influence of the works of Mecznikow (1866) and Fedchenko (1870) dealing with *Dracunculus medinensis* and *Camallanus lacustris*, he judged that the larvae of philometrids require to undergo a part of their development in the intermediate host (copepod) before they are able to infect the fish. This was confirmed by Strassen (1907), who succeeded in experimental infection of copepods (*Cyclops*, *Diaptomus*) with larvae of "*Ichthyonema sanguineum*" (= ? *Philometra ovata*). Various members of Copepoda were later found to be the only intermediate hosts in several species of *Philometra* and some related genera.

Within the Philometridae, the life cycle has been experimentally studied in 7 species of *Philometra* (5 in Europe, 1 in Asia, 1 in North America): *P. abdominalis* (= a synonym of *P. ovata* – see Moravec 2004) (Molnár 1967, Moravec 1977b), *P. cylindracea* (Molnár and Fernando 1975), *P. cyprinirutili* (reported as *P. ovata* – see Moravec 2004) (Molnár 1966b, Moravec 1980), *P. fujimotoi* (Furuyama 1934), *P. kotlani* (Molnár 1969), *P. obturans* (Molnár 1976, Moravec 1978, Moravec and Dyková 1978), and *P. rischta* (Molnár 1966b).

Life cycles in the related genus *Philometroides* were experimentally elucidated in 6 species (1 in Europe, 2 in Asia, 2 in North America, and 1 both in Europe and Asia): *P. cyprini* (e.g., Vismanis 1964, 1970, Ivasik et al. 1967, Vasilkov 1968, Borisova 1981), *P. fulvidraconi* (Yu et al. 1993), *P. huronensis* (Uhazy 1977a), *P. moraveci* (Ermolenko 1984), *P. nodulosus* (Thomas 1929), and *P. sanguineus* (Wierzbicki 1960, Yashchuk and Vasilkov 1970, Ouk and Chun 1973, Nakajima and Egusa 1977).

The development of *Clavinema mariae* was experimentally studied by Sakaguchi and Fukuhara (1975) in Japan, whereas that of *Philonema* spp. from North American salmonids by Vik (1964), Platzer and Adams (1967) and Ko and Adams (1969). Adams (1969) demonstrated experimentally that after the copepod intermediate host is ingested by small salmon, the infective third-stage larvae of *Philonema oncorhynchi* penetrate through the wall of the digestive tract of this fish host to its abdominal cavity.

All these studies have confirmed that the life cycles of philometrids are similar to that of *Dracunculus medinensis*, i.e., that always a copepod intermediate host is involved, in which the nematode larvae moult twice to attain the third stage; the latter is infective to the fish host. However, Molnár (1976, 1980) and Moravec and Dyková (1978) determined for *Philometra obturans* that the philometrids with a piscivorous definitive host may utilize fish paratenic hosts as the main source of infection.

An important part of life history studies of fish nematodes are observations on their seasonal cycles in maturation. This has so far been studied in a few species of *Philometra* and *Philometroides*; the species parasitic in freshwater fishes in the temperate zone were mostly found to have a pronounced seasonal cycle in maturation (e.g., *Philometra cyprinirutili*, *P. ovata*, *Philometroides cyprini*, *P. sanguineus* – e.g., Wierzbicki 1960, Molnár 1966b, 1967, Vasilkov 1968, Vismanis 1970, Moravec 1977c, Uhazy 1977b), with gravid females occurring only within a short period in spring and summer, whereas some others, such as *Philometra obturans*, have not (Moravec and Dyková 1978). A remarkable case documenting the influence of the host's sexual hormones as a causal factor on the parasite's maturation was described in *Philonema oncorhynchi* by Platzer and Adams (1967) and Bashirullah and Adams (1983).

Within the Anguillicolidae, the most intensively studied life cycle has been that of *Anguillicola crassus*, a widespread swimbladder parasite of eels (e.g., Hirose et al. 1976, Egusa 1979, Petter et al. 1989, Moravec et al. 1994a). In contrast to viviparous philometrids, the gravid female of *Anguillicola* lays thin-walled eggs containing second-stage larvae. These are eaten by intermediate hosts, in which the infective third-stage larva develops; not only copepods (like in philometrids) but ostracods (Ostracoda) also serve as suitable intermediate hosts. Many species of fishes, amphibians and invertebrates (aquatic snails and insects) were recorded as paratenic hosts (e.g., Székely 1994, Moravec 1996, Moravec and Škoríková 1998). Similar life-cycle patterns have been found in other three congeneric species,

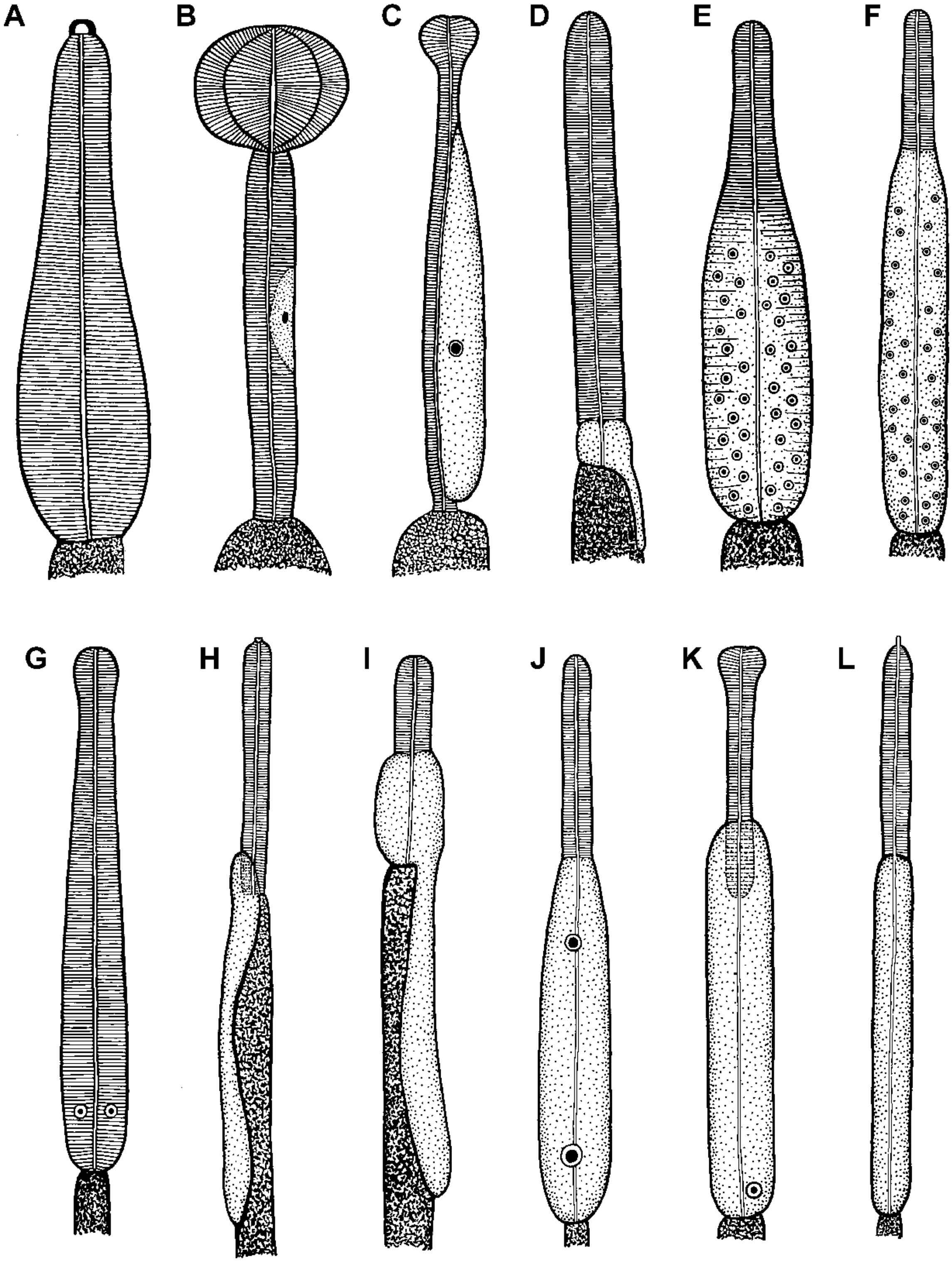

Fig. 3. Variability in the structure of oesophagus in fish dracunculoids (schematized). **A** – *Anguillicola*; **B** – *Clavinema*; **C** – *Philometra*; **D** – *Ichthyofilaria*; **E** – *Philonema*; **F** – *Histodytes*; **G** – *Lucionema*; **H** – *Skrjabillanus*; **I** – *Travassosnema*; **J** – *Mexiconema*; **K** – *Syngnathinema*; **L** – *Esocinema*.

A. globiceps, *A. novaezelandiae* and *A. papernai* (Wang and Zhao 1980, Moravec et al. 1994b, Taraschewski et al. 2004). The development of *A. australiensis* has not yet been studied.

Although the recognition of the life cycles of members of the Skrjabillanidae is highly interesting from a theoretical point of view and may have practical importance, Tikhomirova (1970, 1975) has so far been the only author who attempted to study experimentally the development of *Skrjabillanus scardinii* and *Molnaria intestinalis*, histozoic parasites of some European cyprinids. Tikhomirova (1980) mentions that she succeeded in studying a part of the development of *Skrjabillanus tincae* and that the third-stage larvae of this species were found in the proboscis of branchiurids (*Argulus*); without giving additional data, the author reports that the development of all skrjabillanids follows the same pattern in which one intermediate host, the branchiurid of the genus *Argulus*, is involved. Unlike members of the Philometridae and Anguillicolidae, gravid females of these skrjabillanids periodically release their first-stage larvae into the surrounding tissues of the fish host from where they migrate and concentrate themselves in the superficial layer of the skin. The intermediate hosts are ectoparasitic branchiurids (*Argulus* spp.) which acquire the infection while sucking blood from the host's skin. In the haemocoel of the intermediate host the larvae undergo two moults and the third-stage larvae are already infective for the fish. During the repeated sucking of infected branchiurids on the fish serving as a suitable definitive host, the nematode infective larvae penetrate through the mouth organs of the intermediate host into the skin of the fish. Consequently, there is no free-living stage in skrjabillanids.

Naturally infected *Argulus foliaceus* harbouring infective third-stage larvae of *Sinoichthyonema amuri* were found in Russia (Rudometova 1974, 1975) and those of *Skrjabillanus tincae* in the present Czech Republic (Moravec 1994). Molnár and Székely (1998) recorded different morphological types of skrjabillanid-like larvae commonly occurring in *A. foliaceus* in Hungary. Ecological aspects of some skrjabillanid species were also studied (Rudometova 1974, Tikhomirova 1975, Moravec 1985, 1986).

The morphological similarity of members of the Daniconematidae to skrjabillanid nematodes suggests that also the life-cycle patterns in both groups are similar (Moravec and Køie 1987). This was confirmed by the record of the larva of *Mexiconema cichlasomae*, a common parasite of cichlids in Mexico, in the branchiurid intermediate host *Argulus* sp. (Moravec et al. 1999). Third-stage larvae of *Daniconema anguillae* occurring in large numbers in fins and subcutaneous connective tissue of eels in Hungary were described by Molnár and Moravec (1994). However, to date no complete life cycle in the family Daniconematidae has been studied.

Unidentifiable dracunculoid larvae, usually considered to belong to the Philometridae, have several times been reported from different organs of sharks (e.g., Rosa-Molinar 1983, Benz et al. 1987).

Nothing is known so far about the life histories of members of the dracunculoid families Guyanemidae, Lucionematidae, Tetanonematidae and of the representatives of the Micropleuridae from fish.

However, even within the families in which life cycles have already been studied, the development of most species remains unknown. Of 150 presently known species of fish dracunculoids, the life cycle (or at least its portion) has been reported for 29, or 19%. Moreover, all available data in this respect concern only the species parasitic in freshwater fishes or, rarely, freshwater parasites of migratory fishes (salmon, eel), whereas absolutely nothing is known about the biology of the numerous dracunculoid species from marine fishes. The majority of life cycles of fish dracunculoids were studied in Europe, less often in East Asia and North America, but, to date, there is no information on the development of dracunculoids parasitizing fishes in South America, Africa, South Asia and Australia.

However, also in the species where the life cycle has already been studied, the existing data are often limited to the recognition of intermediate hosts in experimental conditions. There is usually a lack of detailed data for example on the time course of the development of larvae in the intermediate and definitive hosts, their morphogenesis, on the range of natural intermediate and paratenic hosts in different geographical regions and ecological conditions, factors determining the circulation of these parasites in the environment, seasonal occurrence and maturation in their fish hosts, etc. Particularly such data are important from the viewpoint of the prevention and control of dracunculoid infections in fish. Knowledge of the biology of fish dracunculoids is also significant from the viewpoint of a possible introduction of these often pathogenic parasites into new geographical regions or even continents. The introduction of the East-Asian species *Philometroides cyprini*, *Skrjabillanus schigini* and *Sinoichthyonema amuri* into Europe, and *Anguillicola crassus* into Europe, North Africa and North America, during recent decades are good examples.

PROSPECTS

Generally, fish dracunculoids remain poorly known, but opportunities for more detailed studies of these important parasites have greatly improved with the use of some new methods in helminthology, in particular SEM and DNA studies. The present classification system of dracunculoids is unsatisfactory and it will be necessary to create a new system of these nematodes with a new delimitation of genera, respecting phylogenetic relationships. A prerequisite for this is a taxo-

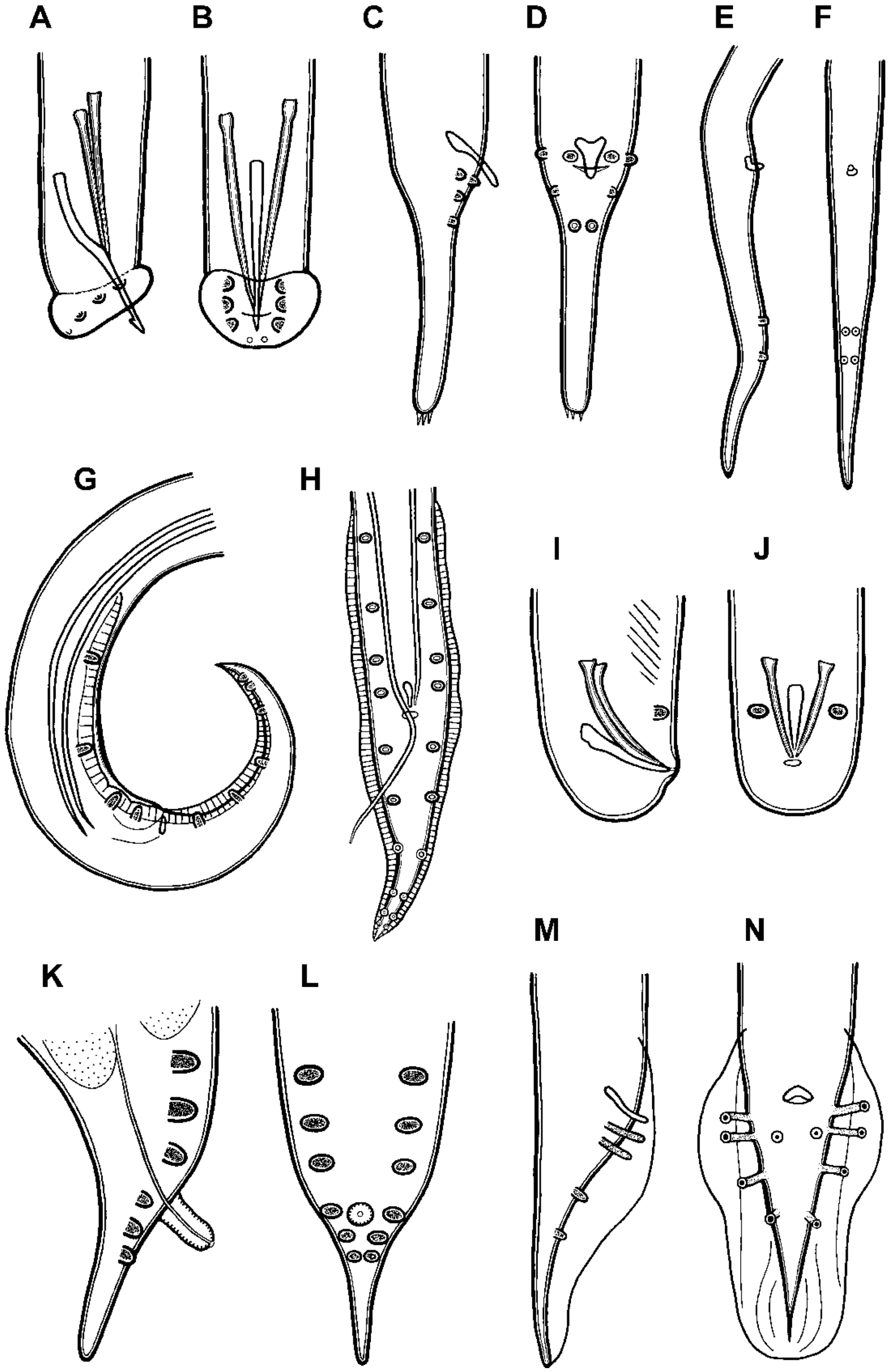

Fig. 4. Variations in the structure of the male caudal end in some fish dracunculoids (lateral and ventral views, schematized). **A**, **B** – *Philometra*; **C**, **D** – *Mexiconema*; **E**, **F** – *Lucionema*; **G**, **H** – *Guyanema*; **I**, **J** – *Neophilometroides*; **K**, **L** – *Anguillicola*; **M**, **N** – *Skrjabillanus*.

nomic revision of the entire group based on detailed studies of individual species, including mainly their morphology, biology and genetics. Very important in this group of tissue parasites is the necessity to pay more attention to the methods of collecting of these often very small and fine worms, which enables to detect also the mostly hitherto unknown males of philometrids and some related forms. The discovery of males may improve the possibility of species identification and a more correct assignment of the respective species to a family or a genus. The species descriptions should be detailed as much as possible, with a special attention to the type species of individual genera. Molecular methods may be very helpful particularly in distinguishing similar species (or where males are unknown) and for phylogenetic studies. More attention should be paid to fish dracunculoids parasitizing freshwater fishes in the hitherto little explored Neotropical, Ethiopian, Oriental and Australian Regions and those from marine fishes within a broad international collaboration of specialists in different countries.

Further progress should concern studies on various aspects of the biology, ecology and host-parasite relationships of these parasites. It will be necessary to recognize the life-cycle patterns of members of the families Guyanemidae, Lucionematidae, Micropleuridae and Tetanonematidae, where no data exist to date, but also of many species of other dracunculoid families, with a special attention to forms from marine fishes. These investigations should include broad laboratory and field studies, because the data on the biology of these parasites may have practical implications.

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