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Some aspects of the taxonomy, biology, possible evolution and biogeography of nematodes of the spirurine genus *Rhabdochona* Railliet, 1916 (Rhabdochonidae, Thelazioidea)

František Moravec*

Institute of Parasitology, Biology Centre of the Academy of Sciences of the Czech Republic, Branišovská 31,
370 05 České Budějovice, Czech Republic

Abstract

At present the nematode genus *Rhabdochona* Railliet, 1916 (Rhabdochonidae) comprises 92 possibly valid species, mostly intestinal parasites of freshwater fishes in all zoogeographical regions. Because of the absence of any phylogenetic studies using molecular methods in this nematode group, an attempt to evaluate affinities among these parasites and their zoogeography on the basis of morphological features and host-parasite relationships has been carried out. Only true definitive hosts should be considered for such evaluation. It appears that, during the evolution of *Rhabdochona* spp., there occur an increase in the number of anterior prostomal teeth, loss of lateral alae, the right spicule attains a boat-like shape and a dorsal barb develops on its distal tip, and the distal tip of the left spicule attains gradually a more complex structure; the eggs with a smooth surface are considered to be more primitive. Nematodes of this genus most probably originated in the region of present southern Asia at the beginning of Tertiary. Closest to the initial type appear to be members of the subgenus *Globochona* Moravec, 1972, from which lineages leading to the subgenera *Globochonoides* Moravec, 1975, *Rhabdochona* Railliet, 1916 and *Sinonema* Moravec, 1975 can be derived. The morphology of *Rhabdochona* spp. indicate a close relationship between the Palaearctic fauna of these nematodes with the Nearctic species, and the Oriental fauna with the Ethiopian fauna. The Neotropical species can be derived from Nearctic members of the subgenus *Rhabdochona*; the latter probably penetrated, along with leuciscine hosts into North America from Palaearctic Eurasia at the end of Tertiary. The distribution of Palaearctic species of *Rhabdochona* corresponds to faunistical complexes in the conception of ichthyologists.

Keywords

Parasitic nematode, *Rhabdochona*, taxonomy, biology, evolution, zoogeography, fish

Introduction

The genus *Rhabdochona* Railliet, 1916 (Rhabdochonidae, Thelazioidea) includes a large number of species representing an interesting group of spirurine nematodes parasitic in the digestive tract of fishes (Moravec 2007a); one species (*R. edentati* Paul et Majumdar, 1994) was described from a frog in India and another (*R. puylaerti* Moravec, 1983) from a snake in Africa (Moravec 1983, Paul and Majumdar 1994), but these hosts evidently acquired a secondary infection while feeding on the true fish definitive hosts of these parasites. Moravec *et al*. (2008) considered 92 species of this genus to be possibly valid, but an additional 9 recently described species were not included: *R. bifidum* Kakar et Bilqees, 2007, *R. bolani* Kakar, Bilqees et Ahmad, 2008, *R. cephalodiverticula* Kakar, Bilqees et Ahmad, 2008, *R. hingoli* Kakar et Bilqees, 2007, *R. milesi* Kakar, Bilqees et Nawaz, 2008, *R. nushkiai* Kakar et Bilqees, 2007, *R. uvaginus* Kakar et Bilqees, 2007, *R. varmai* (Gupta et Masoodi, 1990) Moravec, Lorber et Konečný, 2007 and *R. watsoniai* Kakar et Bilqees, 2007 (see Kakar and Bilqees 2007a, b, c; Kakar *et al*. 2008a, b; Moravec *et al*. 2007); however, due to poor descriptions, all these additional species should be considered *species inquirendae*.

Species of *Rhabdochona* are exclusively freshwater parasites (sometimes they may be brought into brackish or sea water by their migratory hosts), occurring largely in rheophilous fish species; *Rhabdochona* spp. have been infrequently described from marine fishes (e.g., Yamaguti 1935, Johnston and Mawson 1945, Holloway and Klewer 1969, Bilqees 1979, Lakshmi and Sudha 1999) or crabs (Pearse 1932, Poinar and Kannangara 1972). Later on these species were either transferred to other genera or have been considered *species in-*

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*Corresponding author: moravec@paru.cas.cz

quirendae (Campana-Rouget 1955; Moravec 1972a, 1975; Moravec *et al*. 2007).

Rhabdochona species are distributed in all zoogeographical regions. Earlier they were considered to be absent from the Australian Region (Moravec 1972a, 2007a; Mejía-Madrid *et al*. 2007a), but Moravec *et al*. (2008) have recently recorded a representative of this genus from a freshwater fish in Papua New Guinea. Some species are limited in distribution to tropical or subtropical environments, whereas others occur in temperate zones, often reaching cold northern parts in Eurasia. Although most species occur largely in lowland and submontane streams, some others step up on high to the mountains [e.g., *R. hellichi* (Šrámek, 1901) was found in Afghanistan at an altitude of about 4000 m (Moravec, unpublished) and it was also recorded from the Lhasa River in Tibet, China (Li *et al*. 2008)]. One species (*R. longleyi* Moravec et Huffman, 1988) occurs only in endemic blind catfishes in subterranean waters in Texas (Moravec and Huffman 1988), whereas another one [*R. kidderi* (Pearse, 1933)] is known to parasitize cave and cenote (= sinkhole) fishes in Yucatan, Mexico (Moravec 1998). To date, there are considerable gaps in the knowledge of the biology, ecology and distribution of these parasites.

Taxonomy and classification

In the past, the taxonomy of nematodes belonging to this genus was dealt with by many authors (e.g., Choquette 1951, Saidov 1953, Roytman and Trofimenko 1964), but the identification of these parasites became problematic mainly due to inadequate or erroneous descriptions of many species. Moreover, frequent misidentifications of the species also resulted from considerable intraspecific variation in the morphology of these nematodes as also their possible occurrence in phylogenetically distant groups of hosts, etc. In the sixties, species of *Rhabdochona* represented one of the most perplexing groups of nematode parasites of fishes (Rasheed 1965).

In the seventies, Moravec and Arai (1971) and Moravec (1972a, b; 1975) made a taxonomic revision of these nematodes, where, for the first time in helminthology, the method of an extensive global revision based on a re-study of all then available materials of *Rhabdochona* from many scientific institutions of the world was used. The number of valid species was considerably reduced and the genus was subdivided into five subgenera principally based on the numbers of prostomal teeth and the structure of the female tail tip (Moravec 1975). The presence of egg filaments or swellings was taken for a good specific feature, but no greater taxonomic value was assigned to it. This system is widely used till now. In the meanwhile, many new species of *Rhabdochona* have been described mainly from previously little-explored regions of the Americas, Africa and Asia, so that the number of nominal species has approximately been doubled (Moravec 2007a). However, even though some recently described species have also been studied by SEM (Sánchez-Alvarez *et al*. 1998; Caspeta-Mandujano and Moravec 2000; Caspeta-Mandujano *et al*. 2001, 2002, 2005; Cremonte *et al*. 2002; Mejía-Madrid and Pérez-Ponce de León 2003; Ramallo 2005; Moravec and Muzzal 2007; Moravec *et al*. 2008, 2009), descriptions of the majority of these nematodes (see e.g., Ghazi *et al*. 2003; Kakar *et al*. 2006, 2008a, b; Kakar and Bilqees 2007a, b, c) became again inadequate, not corresponding to the requirements of current nematode taxonomy.

Mejía-Madrid *et al*. (2007a) have recently published an interesting paper reporting results of the phylogenetic analysis of 40 *Rhabdochona* spp., including all 21 at that time considered valid in the Americas, based on the cladistic analysis of 51 morphological characters. However, some of the evaluated characters seem to be rather problematic, particularly those relating to the structures and shapes of the spicules, which, on the contrary, the authors consider to be more important for phylogenetic analyses than any other morphological features. Of the evaluated characters, 17 relate to the form of the distal tip of the left spicule, where the authors distinguish five spicule types (pointed, lanceolate thin, lanceolate wide, lanceolate bifurcate and lanceolate blunt). However, their distinction as given by the authors is not clear-cut and there often exist interstages in different species of *Rhabdochona* and certain intraspecific variability in this feature. The left spicule of *R. milleri* Choquette, 1951 was illustrated by Mejía-Madrid *et al*. (2007a) as "blunt", but it was found as widely bifurcated in the type specimen by Moravec and Arai (1971). Moreover, the form of the tip of the left spicule may be an unreliable taxonomic feature, because it may have a different appearance when observed in different positions (the same concerns the shape of the right spicule). While evaluating the numbers of anterior prostomal teeth in adult *Rhabdochona* spp., no attention was paid to evident association of this character with morphological changes during the ontogenetic development, which may be of phylogenetic importance (Moravec 1972c, 1975).

Moreover, three North American species of *Rhabdochona* described by Maggenti *et al*. (1992), *R. californiensis*, *R. paxmani* and *R. salmonis*, which were considered by Mejía-Madrid *et al*. (2007a) to be valid, have recently been synonymized with previously described species *R. cascadilla* Wigdor, 1918 or *R. kisutchi* Margolis, Moravec et McDonald, 1975 (see Moravec and Muzzall 2007). It is worth mentioning that these synonymized species were placed in other clades in the above mentioned analysis than those with which they were synonymized. On the contrary, in this way, some evidently unrelated species of *Rhabdochona* appeared in the same clade, for example, *R. cascadilla* and *R. milleri*, or *R. fortunatowi* Dinnik, 1933, *R. gnedini* Skryabin, 1948 and *R. lichtenfelsi* Sánchez-Alvarez, García-Prieto et Pérez-Ponce de León, 1998.

Since the above mentioned taxonomic revisions by Moravec and Arai (1971) and Moravec (1972a, b; 1975), many new species of *Rhabdochona* were described and some new data on the life cycles of these nematode parasites were published (e.g., Moravec 1977, 1989, 1995, 2007b; Byrne 1992; Barger and Janovy 1994; Shimazu 1996; Moravec *et al*. 1997; Moravec and Huffman 2001; Saraiva *et al*. 2002 a, b; Hirasawa and

Urabe 2003; Hirasawa and Yuma 2003). These studies substantially contributed to the knowledge of the morphology, morphological diversity, geographical distribution, range of hosts and ecology of these nematodes, enabling also considerations about their possible evolution and ways of dispersal. There exists no direct evidence in the form of fossil remnants and, to date, only three *Rhabdochona* species have been examined using molecular methods (Wijová *et al*. 2006; Mejía-Madrid *et al*. 2007; Černotíková, unpublished). Nadler *et al.* (2007) have recently provided a thorough account of the molecular phylogeny of clade III nematodes (after Blaxter *et al.* 1998) parasitic in vertebrates, including spirurines, but it only indicates that *Rhabdochona denudata* (Dujardin, 1845) and a few representatives of Cystidicolidae are monophyletic. In this situation, it is possible to judge the origin and evolution of *Rhabdochona* spp. only on the basis of the morphology and distribution of present species, their relationships, and according to the types of the obligatory hosts and their phylogeny.

Definive hosts

All representatives of the genus *Rhabdochona* are exclusively parasites of fishes (even though some of them were accidentally recorded from other vertebrates). Some species have been reported from great numbers of host species often belonging to phylogenetically distant families. As already pointed out by Moravec (1972a, 1975, 1976), the hosts of these nematodes can be roughly divided into two groups: (1) primary, obligatory true definitive hosts as defined by Odening (1976), in which a major part of the population of a certain nematode species develops and which are quite necessary to secure the parasite's reproduction in a given locality; (2) subsidiary, atypical facultative hosts often belonging to phylogenetically distant groups of fishes, or conceivably even to other vertebrates, in which adult nematodes or their larvae can only survive for a certain period. The latter host group includes on the one hand predatory fishes acquiring infection by the ingestion of obligatory definitive hosts (fishes) (so called postcyclic hosts) and on the other hand various other fishes become infected by the parasite while feeding on infected intermediate hosts (aquatic insects) (i.e., paratenic hosts). Of them, only the primary, obligate definitive hosts are important for the evaluation of relationships among individual species of *Rhabdochona*.

All the hitherto known obligatory hosts of *Rhabdochona* belong exclusively to the fish division Teleostei in the conception of Nelson (2006), namely to the freshwater representatives of the orders Cypriniformes (53 species), Siluriformes (15 species), Characiformes (7 species), Perciformes (7 species), Cyprinodontiformes (5 species), Salmoniformes (2 species), Anguilliformes (1 species), Atheriniformes (1 species), Beryciformes (1 species), and Scorpaeniformes (1 species). Representatives of other fish orders serve only as facultative postcyclic, paratenic, paradefinitive or accidental hosts of *Rhabdochona* spp. (Moravec 1994).

As in other parasites, *Rhabdochona* spp. with large areas of distribution may also have different preferred hosts in different regions; this has always two grounds, an adaptation to environmental conditions and a genetic predisposition (Mayr 1963). An example may be *R. hellichi* (Šrámek, 1901): whereas its obligatory hosts in Europe are fishes of the genus *Barbus* Cuvier et Cloquet, in Central Asia this parasite occurs largely in species of *Schizothorax* Heckel and only rarely in those of *Barbus* (see Moravec 1975). According to Mayr (1963), the shift from one host to another makes an increased selective pressure, which later results in a genetic change of the parasite's population and gradually leads to the rise of a new species. Consequently, host specificity is an ideal prerequisite for rapid speciation (Mayr 1963). Therefore, if the host specificity has a genetic base (even when it is governed by ecological conditions), then also the types of the obligatory hosts may, to a certain degree, reflect relationships of the parasites. The degree of host specificity in species of *Rhabdochona* is not the same, being mostly at the level of fish families, subfamilies or genera. It can be deduced from it that the evolution of these nematodes, provided that it follows that of their hosts, does not depend on the evolution of host species but higher taxonomic units (genera, subfamilies, families); it means that the evolution of these parasites lags behind that of the hosts. This fact has already been pointed out by Stunkard (1970) in digeneans, who explains it as follows: "New opportunities for diversification and dispersal may become available by alternation in either internal or external conditions. The environment of the parasite is, overall, less variable and more constant than that of the host; consequently evolutionary changes tend to be slower and of less magnitude in the parasite than in the host species." Consequently, it may be deduced that the present species of *Rhabdochona* are mostly phylogenetically older than species of the host fishes, even though their evolution need not always follow the evolution of hosts (Inglis 1968).

Long-term observations on the seasonal cycles of the occurrence and maturation of *Rhabdochona* spp. in their fish definitive hosts have so far been carried out in *R. anguillae* Spaul, 1927, *R. denudata*, *R. gnedini*, *R. hellichi* and *R. phoxini* in Europe (Czech Republic, Spain, Portugal) (Moravec 1977, 1989; Pereira-Bueno 1978; Moravec and Scholz 1995; Saraiva *et al*. 2002a, b), *R. zacconis* Yamaguti, 1935 in Asia (Japan) (Moravec *et al*. 1998), and *R. canadensis*, *R. cascadilla* (reported as *R. rotundicaudatum*) and *R. kidderi* Pearse, 1936 in North America (Canada, Mexico) (Byrne 1992, Caspeta-Mandujano *et al*. 2000, Moravec *et al*. 2002, Caspeta-Mandujano and Mejía-Mojica 2004). These studies show that, depending on local ecological conditions, these parasites can produce eggs throughout the year or only during a certain period, mostly in the spring and summer in the temperate zone. These maturation cycle patterns are important adaptations of *Rhabdochona* spp. to the ecology and ethology of the intermediate and definitive hosts in the respective locality, ensuring thus their transmission.

Intermediate hosts

Weller's (1938) data on the experimental infection of crustaceans with the eggs of *Rhabdochona ovifilamenta* Weller, 1938 and those of Janiszewska (1960) on the finding of the larvae of *Rhabdochonoides barbi* (= *Rhabdochona hellichi*) in freshwater oligochaetes are evidently faulty (Moravec and Arai 1971, Moravec 1972a). Gustafson (1939, 1942) was the first to successfully infect experimentally several species of mayfly nymphs in North America with the eggs of *Rhabdochona* spp. In his later taxonomic paper (Gustafson 1949), he mentioned various mayflies as intermediate hosts of the North American species *Rhabdochona cascadilla*, *R. decaturensis* Gustafson, 1949 and *R. cotti* Gustafson, 1949; for the latter species also stonefly nymphs.

Later, the life cycle has been experimentally studied in the European species *Rhabdochona denudata*, *R. ergensi* Moravec, 1968 and *R. phoxini* Moravec, 1968 and in the North American species *R. canadensis* Moravec et Arai, 1971 and *R. kidderi texensis* Moravec et Huffman, 1988 (see Moravec 1972c, 1976, 2007b; Barger and Janovy 1994; Moravec and Huffman 2001).

Infective larvae or juvenile adults of the following eight species of *Rhabdochona* have so far been recorded from naturally infected intermediate hosts (aquatic insects): *R. denudata* and *R. phoxini* in ephemeropterans (*Caenis* Stephens, *Ecdyonurus* Eaton, *Ephemera* Linnaeus, *Ephemerella* Walsh, *Heptagenia* Walsh) and *R. hellichi* and *R.* (?) *gnedini* Skryabin, 1948 in trichopterans (*Hydropsyche* Pictet) in Europe (Shtein 1959; Vojtková 1971; Moravec 1977, 1989, 1995, 2004; Moravec *et al.*1997; Saraiva *et al.* 2002b), *R. coronacauda* Belous, 1965, *R. denudata honshuensis* Moravec et Nagasawa, 1989, and *R. oncorhynchi* (Fujita, 1921) in ephemeropterans (*Chloroterpes* Eaton, *Ephemera*, *Ephemerella*, *Potamanthus* Pictet, *Siphlonurus* Eaton) in Japan (Shimazu 1996, Hirasawa and Urabe 2003, Hirasawa and Yuma 2003), and *R. cascadilla* (syn. *R. rotundicaudatum*) and *R. kidderi texensis* Moravec et Huffman, 1988 in ephemeropterans (*Ephemera*, *Tricorythodes* Ulmer) in North America (Byrne 1992, Moravec and Huffman 2001). To date, no data on intermediate hosts of *Rhabdochona* spp. are available from South America, Africa and the Australian Region (New Guinea).

Although, generally, the life cycles of *Rhabdochona* spp. have little been studied, the hitherto data indicate that the main intermediate hosts of these parasites are mayflies (Ephemeroptera) and less often some other aquatic insects such as caddisflies (Trichoptera) or stoneflies (Plecoptera) (Gustafson 1939, 1942; Moravec 1995). Since these intermediate hosts are restricted to fresh waters, it explains the reason why species of *Rhabdochona* occur exclusively in fresh waters. Due to their antiquity, mayflies are presently distributed practically everywhere (absent from the Hawaiian archipelago) (Obenberger 1958). Species of some genera (*Ecdyonurus*, *Ephemera*, *Ephemerella*, *Heptagenia*, *Leptophlebia* Westwood) have almost a worldwide distribution and representatives of these genera are among the most frequent intermediate hosts of nematodes of the genus *Rhabdochona*. A low degree of host specificity of individual *Rhabdochona* species to ephemeropteran intermediate hosts suggests that there is either no or very little influence of intermediate hosts on the evolution of these parasites.

As observed, e.g., by Gustafson (1942), Shtein (1959), Vojtková (1971), Moravec (1972c, 1976, 1989, 1995) and Byrne (1992), larvae of *Rhabdochona*, after attaining the infective third stage, can continue to develop further inside the body of the intermediate host and may even become mature (a precocious development – see Anderson 1988). Precocity markedly reduces the time for the parasite to produce gametes and fertilized eggs in the definitive host and may be an important phenomenon for transmission because of the ecology and ethology of the respective definitive host, as observed by Byrne (1992) in *R. cascadilla* (syn. *R. rotundicaudatum*) parasitic in the common shinner *Luxilus cornutus* (Mitchill) in a stream in Ontario, Canada. Chabaud (1971) took this mode of development for "a condensed cycle in the parasites well adapted to the intermediate host, which occurs in some primitive aquatic Spiruroidea". As is suggested by the systematic relationships of the nematodes in which precocity occurs, this tendency of development seems to be phylogenetically fixed and may represent, from the evolutionary viewpoint, a transitional stage in the evolution from diheteroxeny to secondary homoxeny (Moravec 1994).

The phenomenon of precocity in *Rhabdochona* spp. is also important for understanding why adults and fourth-stage larvae of these parasites are often found in fish hosts which are phylogenetically distant from their true definitive hosts. Such facultative hosts acquire the infection either by feeding on the insect intermediate hosts harbouring *Rhabdochona* fourth-stage larvae or young adults, or by eating the infected true fish definitive hosts; the former then act as paratenic or paradefinitive hosts, whereas the latter as postcyclic hosts. The presence of *Rhabdochona* infective larvae in the body does not prevent the mayfly nymph from completing its metamorphosis and, subsequently, the source of infection for fish hosts is not only the infected mayfly nymphs but mainly their winged imagoes, as demonstrated by Hirasawa and Yuma (2003) in *R. denudata honshuensis* parasitic in the dark chub *Nipponocypris temmincki* (Temminck et Schlegel) in Japan. Apparently, infected winged aquatic insects was the source of infection with two types of *Rhabdochona* spp. fourth-stage larvae, found in the intestine of two species of bats in Afghanistan (Baruš and Tenora 1970).

Possible evolution of morphological characters in **Rhabdochona**

As reported by Mayr (1963), all features of the phenotype is a result of selection, but the development of individual organs is not even; because of it, each evolutionary type is a mosaic of primitive and progressive, general and specialized characters. Therefore, also the features found in nematodes of this

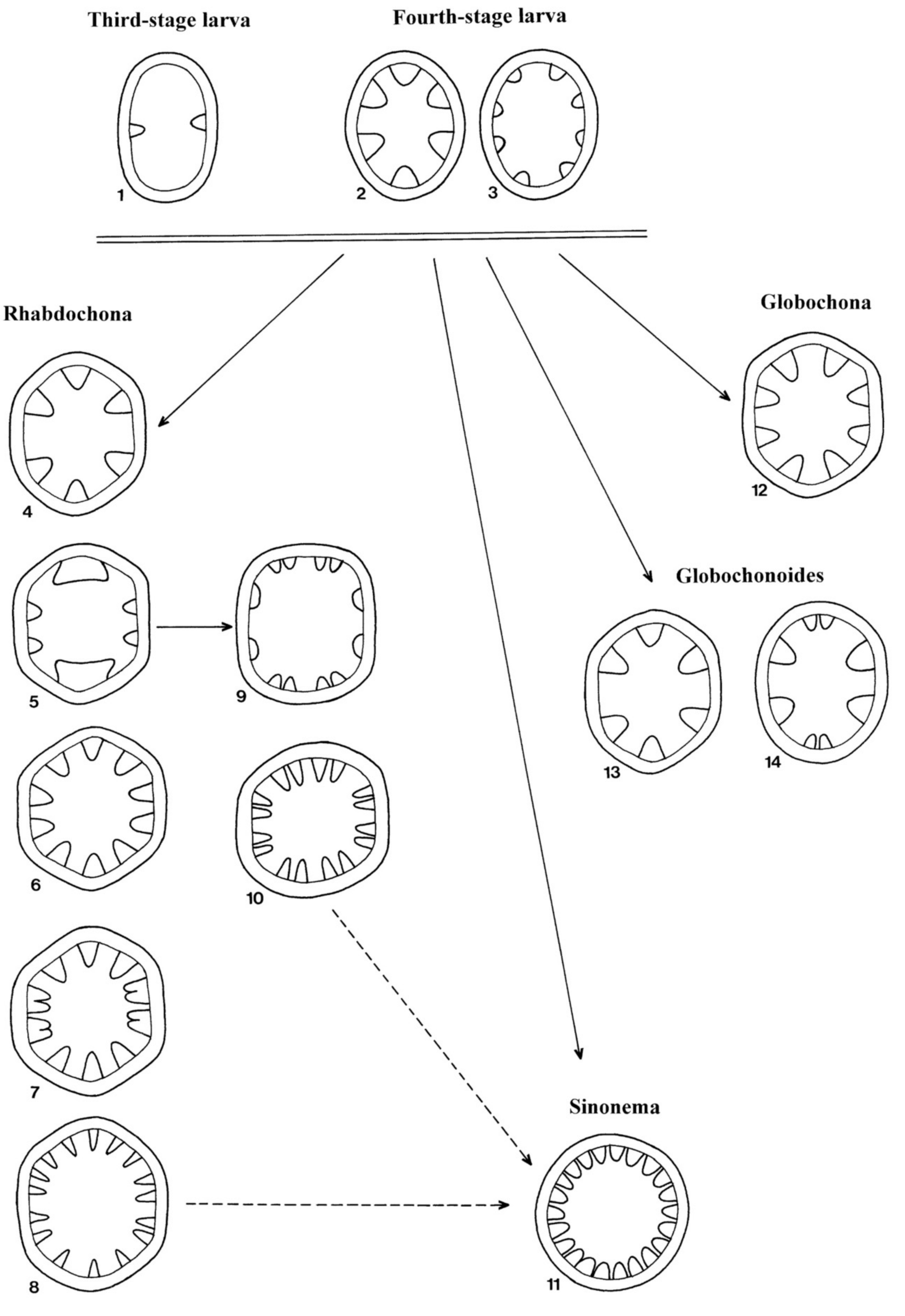

Fig. 1. Possible evolution of anterior prostomal teeth in adults of *Rhabdochona*: **1 –** *R. phoxini*, **2** – *R. phoxini*, **3** – *R. moraveci*, **4** – *R. longleyi*, **5** – *R. xiphophorasi*, **6** – *R. oncorhynchi*, **7** – *R. phoxini*, **8** – *R. denudata*, **9** – *R. guerroensis*, **10** – *R. fabianae*, **11** – *R. euchiloglanis*, **12** – *R. chodukini*, **13** – *R. squaliobarbi*, **14** – *R. coronacauda*

genus should be evaluated in this way. However, it is fairly difficult to determine which feature is primitive and which is derived. In the case of *Rhabdochona* spp., we are essentially dependent on the method used, for example, by Petter (1974), issuing from a correlation of the development of morphological features and the old age of hosts and, in part, from the larval morphogenesis during the ontogenetic development. Even though these phyletic hypotheses are not based on so-called modern phylogenetic systematics methods (see, e.g., Brooks and McLennan 1991, 1993) used by some present authors, they propose scenarios of the possible evolution of some morphological features in *Rhabdochona*. The following main features of adult *Rhabdochona* spp. can be taken into account:

Number of anterior prostomal teeth (Fig. 1). It is generally considered (see, e.g., Trofimenko 1967, Chabaud 1975b) that the mouth structures of nematodes develop very slowly and, consequently, may serve as an important taxonomic feature. The analysis of hosts of *Rhabdochona* spp. suggests that an increase in the number of anterior prostomal teeth takes place during the evolution of these nematodes. The subgenera *Globochona* and *Globochonoides* are characterized by the presence of only 6 or 8 (perhaps also 12) teeth and their species are parasites of the primitive Cyprinidae (*Barilius* Hamilton, *Barbus*, *Opsariichthys* Bleeker) and Siluroidei; the genesis of catfishes is not sufficiently known, but they are noted for many primitive features indicating the antiquity of this group. An increase in the number of anterior prostomal teeth also occurs during the ontogenesis of members of *Rhabdochona*. Whereas adult forms of *R. acuminata* (Molin, 1860), *R. ergensi*, *R. hellichi*, *R. humili* Roytman et Trofimenko, 1964, *R. phoxini*, and *R. moraveci* Puylaert, 1973 have 14 teeth, the fourth-stage larvae of the first five species have only 6 teeth (Moravec 1972c, 1976, 1995; Cremonte *et al*. 2002) and those of the last-named species 8 teeth (Puylaert 1973); 8 teeth were also found in the fourth-stage larvae of *Rhabdochona* (*Globochona*) sp. reported from fishes in Iraq by Moravec *et al*. (2009). The number of teeth (20–22) in *Sinonema* may be considered a derived feature, even though other characters (e.g., the presence of cervical alae) indicate the antiquity of these nematodes.

Lateral alae. These are present only in three species, *R. coronacauda* Belous, 1965, *R. squaliobarbi* Moravec et Sey, 1988 and *R. euchiloglanis* Wu, 1949. The first species is typical of Cultrinae, some genera of which (*Opsariichthys*) are sometimes considered to be closest to the initial type of the Cyprinidae, whereas the two last-named species are known from Cyprinidae (*Squaliobarbus* Günther) and Sisoridae (*Euchiloglanis* Regan), respectively. Consequently, the presence of lateral alae appears to be a primitive feature preserved perhaps from some cosmocercoid ancestors.

Shape of deirids (Fig. 2). The bifurcated shape of deirids seems to be more primitive and occurs in fourth-stage larvae (Moravec 1972c, 1976), including those species where adult forms possess simple, non-bifurcated deirids. At present the bifurcated deirids are preserved in the majority of species of the subgenus *Rhabdochona*; in some members of this subgenus (*R. cubensis* Moravec et Coy Otero, 1987, *R. fortuna-*

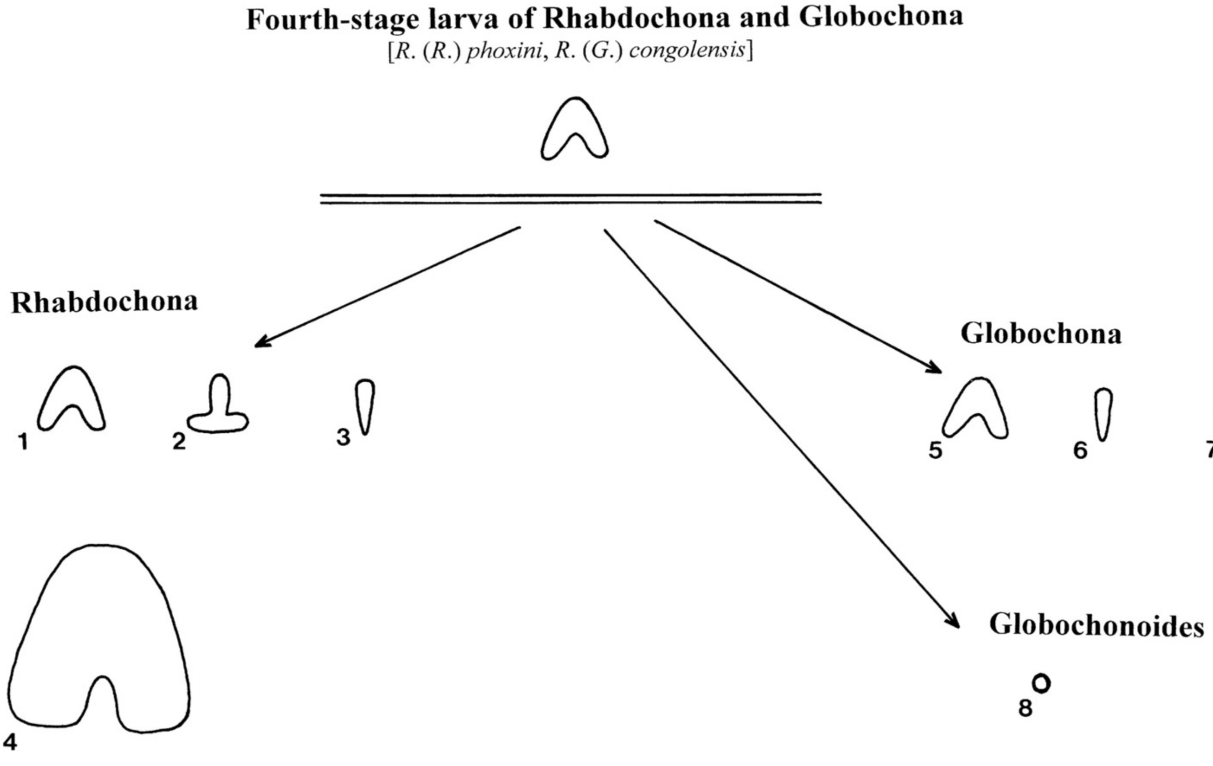

Fig. 2. Possible evolution of deirids in adults of *Rhabdochona*: **1** – *R. hellichi*, **2** – *R. papuanensis*, **3** – *R. moraveci*, **4** – *R. fortunatowi*, **5** – *R. garuai*, **6** – *R. congolensis*, **7** – *R. gambiana*, **8 –** *R. coronacauda*

towi Dinnik, 1933, *R. macrostoma* Moravec et Mikailov, 1970, *R. tigridis* Rahemo, 1978), a marked increase in size of deirids occurs. Within the subgenus *Globochona*, bifurcated deirids are preserved only in the Indian species *R. garuai* Agrawal, 1965 and *R. mazeedi* Prasad et Sahay, 1965, whereas in other recent representatives of this subgenus and of *Globochonoides* the deirids are simple, often strongly reduced.

Spicules (Fig. 3). It can be deduced that closest to the initial type is the shape of spicules occurring in some recent species of the subgenus *Globochona* (i.e., spicules are simple, mutually little distinguished by shape). This type remains essentially preserved in all representatives of the subgenera *Globochona* and *Sinonema*, as well as in the derived genera *Johnstonmawsonia* Campana-Rouget, 1955, *Heptochona* Rasheed, 1965, *Hepatinema* Rasheed, 1964 and *Trichospirura* Smith et Chitwood, 1967. In representatives of the subgenus *Rhabdochona*, the right spicule increasingly substitutes the function of a gubernaculum, becomes boat-shaped, and a dorsal barb develops on its distal tip. The distal tip of the left spicule has a more complex structure. An interstage between *Globochona* and *Rhabdochona* is the subgenus *Globochonoides*; although the shapes and the mutual length ratio of spicules are retained in this subgenus, the short (right) spicule of its two representatives is provided with a dorsal barb.

Female tail (Fig. 4). The shape and structure of the female tail is a good specific character in *Rhabdochona* (see Moravec 1972a). In various species its shape may be conical, with a sharp terminal cuticular spike or with a rounded tip, or the whole tail may be bluntly rounded. Various modifications such as small

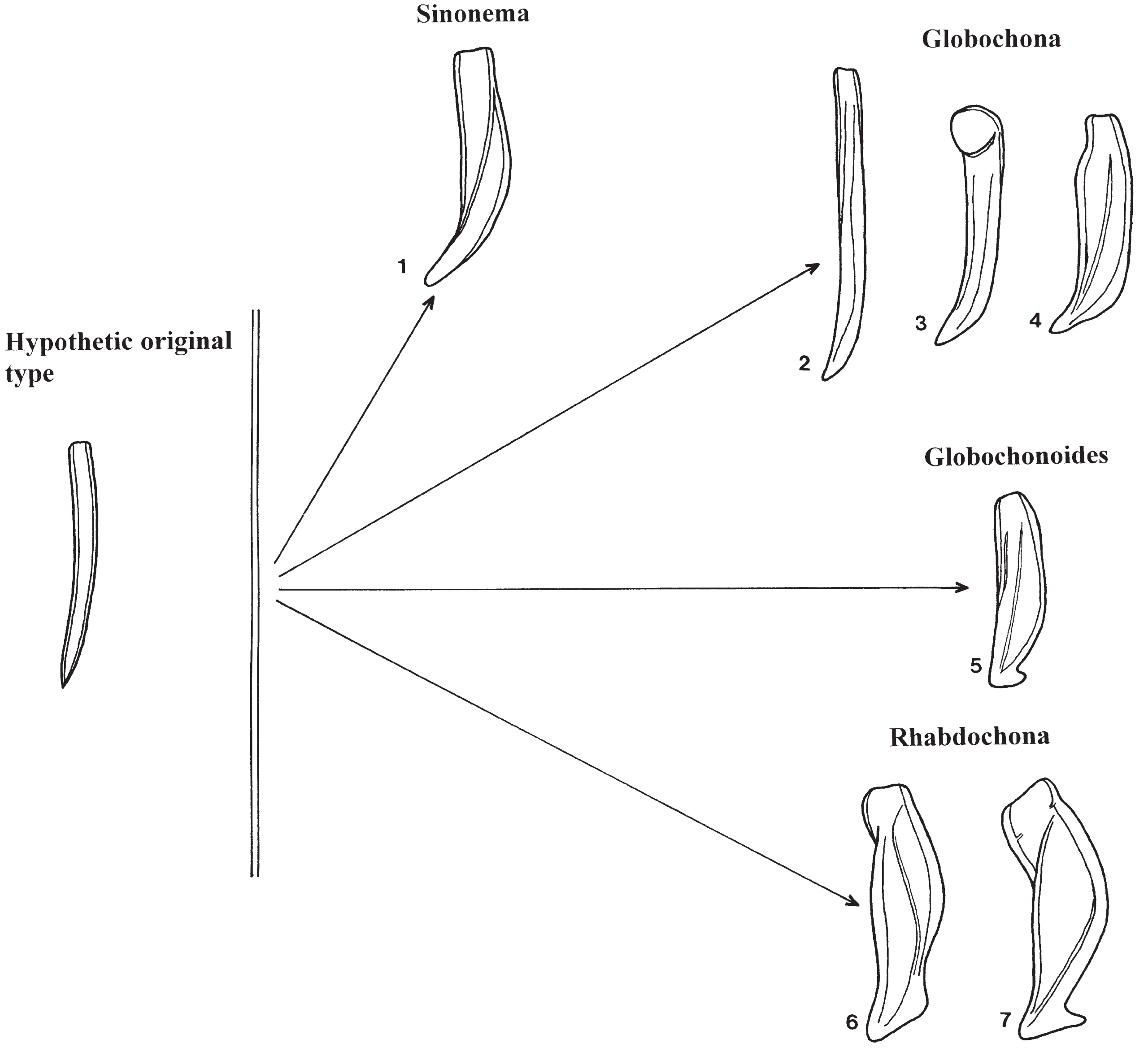

Fig. 3. Possible evolution of left spicule in *Rhabdochona*: **1** – *R. euchiloglanis*, **2** – *R. garuai*, **3** – *R. chodukini*, **4** – *R. barusi*, **5** – *R. coronacauda*, **6** – *R. longispicula*, **7** – *R. hellichi*

mucronate points, spikes etc. are present on the tail tips of the females of some species, whereas such ornamentations are absent from the tail tip of the conspecific male; the only exception is *R. equispiculata* Moravec et Scholz, 1991 parasitizing the cyprinids *Hampala* Kuhl et van Hasselt in van Hasselt spp. in Laos, where both females and males possess a few spikes on the tail tip (Moravec and Scholz 1991). Except for *Sinonema*, such ornamentations occur on the tail tip of some representatives of all remaining subgenera. A hypothetic founder type is the simple conical tail with a sharply pointed tip.

Eggs (Fig. 5). Although the importance of the type of eggs was frequently overestimated in *Rhabdochona*, it is impossible to deny a certain significance of this highly adaptable feature when evaluating mutual relationships among individual species. It appears that the original type within this genus is an egg with a smooth surface, which is found in representatives of all four subgenera. Apparently, from this type evolved, on the one hand, those eggs provided with lateral swellings (floats), which are found in some species of *Globochona*, and on the other hand, those eggs whose surface is covered with an undefinable fine gelatinous coating, polar caps or filaments (subgenus *Rhabdochona*).

Recent geographical distribution and relationships amongst nematodes of the genus Rhabdochona

Until recently, species of the genus *Rhabdochona* were considered to be widespread in all zoogeographical regions except for the Australian one (Moravec 1975, Mejía-Madrid *et al*. 2007a); however, Moravec *et al*. (2008) have recently described *Rhabdochona papuanensis* Moravec, Říha et Kuchta, 2008 parasitizing a native freshwater fish in Papua New Guinea, belonging to the latter region. The highest diversity and the variability of types is found in Eurasia, particularly in its southern and southeastern parts, where species of all four subgenera (*Rhabdochona*, *Globochona*, *Globochonoides* and *Sinonema*) are present (Moravec 1975). In Africa, representatives of two subgenera (*Rhabdochona* and *Globochona*) occur (Moravec 1972b, Mashego 1990, Boomker and Petter 1993), whereas only species of the subgenus *Rhabdochona* are

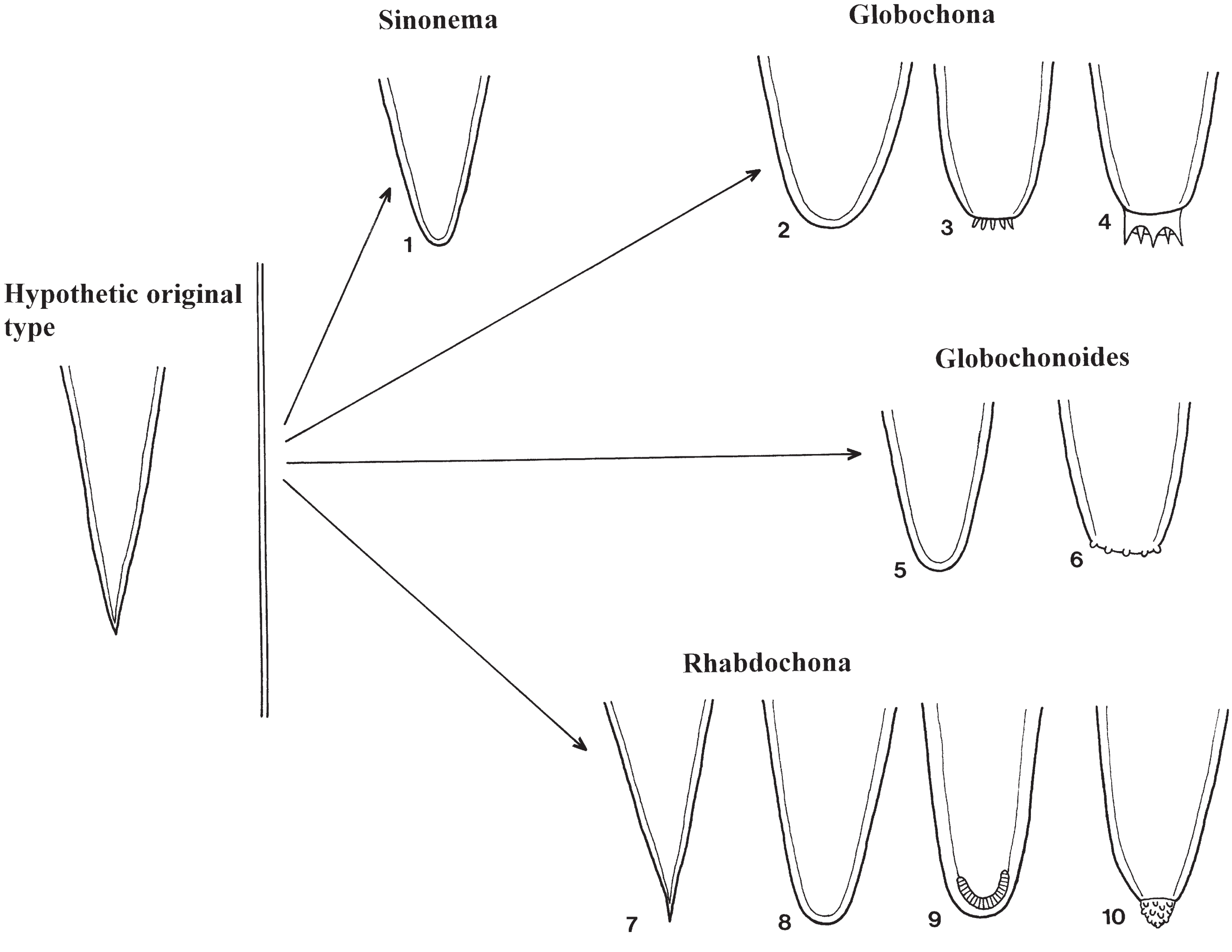

Fig. 4. Possible evolution of female tail tip in *Rhabdochona*: **1** – *R. euchiloglanis*, **2** – *R. garuai*, **3** – *R. congolensis*, **4** – *R. barusi*, **5** – *R. squaliobarbi*, **6** – *R. coronacauda*, **7** – *R. canadensis*, **8** – *R. ergensi*, **9** – *R. longicauda*, **10** – *R. salgadoi*

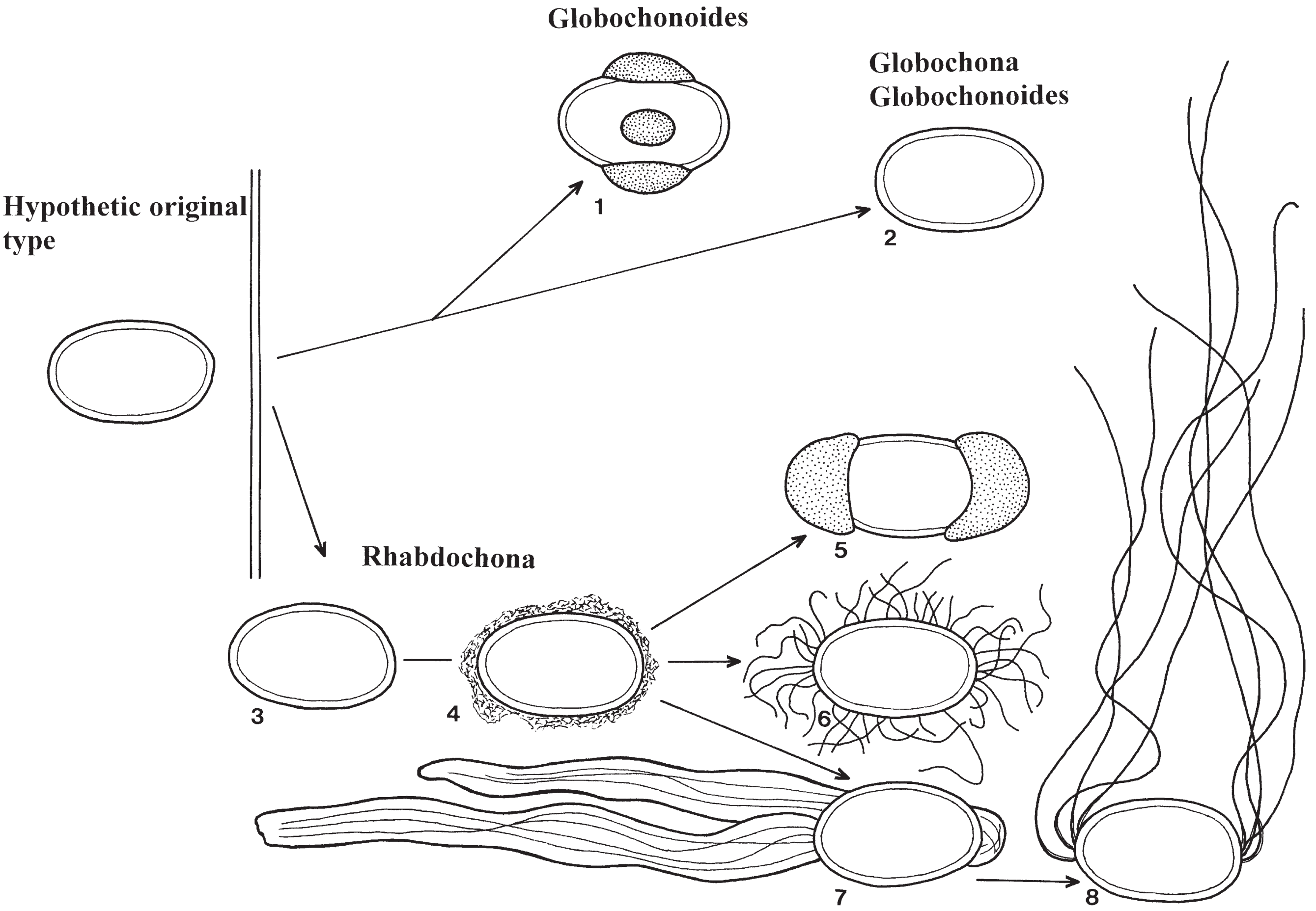

Fig. 5. Possible evolution of superficial formations on eggs in *Rhabdochona*: **1** – *R. barusi*, **2** – *R. paski*, *R. coronacauda*, **3** – *R. cascadilla*, **4** – *R. denudata*, **5** – *R. kisutchi*, **6** – *R. ovifilamenta*, **7** – *R. gnedini*, **8** – *R. ergensi*

known from North and South America and the West Indies (Moravec and Arai 1971; Moravec 1972a; Moravec and Coy Otero 1987; Sánchez-Alvarez *et al.* 1998; Caspeta-Mandujano and Moravec 2000; Caspeta-Mandujano *et al.* 2001, 2002; Mejía-Madrid and Pérez-Ponce de León 2003; Ramallo 2005; Mejía-Madrid *et al.* 2007b; Moravec and Muzzall 2007), as well as in New Guinea (Moravec *et al.* 2008).

At present, a total of 61 *Rhabdochona* species is known from fishes of Eurasia. Their analysis shows that there are considerable differences between the faunas of the Palaearctic and Oriental species of these nematodes. The Palaearctic species indicate their close affinities to the Nearctic fauna. Even though almost no species are known to be common for both regions (except for *R. zacconis* Yamaguti, 1935 reported from East Asia and western Canada), there are a few couples of morphologically very similar species, moreover occurring in related hosts (Table I). Thus, for example, an analogy of the Palaearctic species *R. denudata* and *R. phoxini* is a Nearctic species *R. cascadilla*, while all the three are parasitic in Leuciscinae; the Asian species *R. humili* is closely related to *R. canadensis* Moravec et Arai, 1971 from western Canada (both parasitic in Leuciscinae), the Palaearctic species *R. oncorhynchi* (Fujita, 1921) and *R. kisutchi* Margolis, Moravec et McDonald, 1975 from the western coast of North America (both from Salmonidae) differ only in the type of eggs, etc. However, the Palaearctic fauna of *Rhabdochona* spp. is not uniform, but corresponds essentially to several faunistic complexes in the conception of ichthyologists (Shul'man 1958). Thus the species *R. gnedini* Skryabin, 1948, *R. fortunatowi*, and *R. macrostoma* are characteristic of the Asiatic Minor complex, of which the first two also occur in the Upland-Asian complex; typical species of the latter complex are *R. longicauda* Dzhalilov, 1964 and *R. chodukini* Osmanov, 1957. The last-named species, as well as the nematode *Procamallanus siluri* Osmanov, 1964 (see Dzhalilov and Gavrilova 1967), can be considered in this region as relicts of the former Indian fauna. The Transitory Amur Region is characterized by the species *R. longispicula* and *R. coronacauda*, of which the latter (occurring also in Japan) is undoubtedly an element of the Indian freshwater fauna, which, at the turn of Paleogene and Neogene was shifted to the north (Gusev 1969).

While the Palaearctic fauna is largely related to the Nearctic fauna, the representatives of the Oriental (Indo-Malayan) Region have their closest relatives mainly in tropical

Table I. Some Eurasian species of the genus *Rhabdochona* and their possible affinities

A. *Rhabdochona* with African affinities:	
Subgenus *Rhabdochona*:	
R. hospeti Thapar, 1950	(*R. gendrei* Campana-Rouget, 1961)
Subgenus *Globochona*:	
R. barusi Majumdar et De, 1971	(*R. gambiana* Gendre, 1921)
R. minima Moravec et Daniel, 1976	(*R. gambiana* Gendre, 1921)
R. singhi Ali, 1956	(*R. gambiana* Gendre, 1921)
R. mazeedi Prasad et Sahay, 1965	(*R. paski* Baylis, 1923)
B. *Rhabdochona* with North American affinities:	
Subgenus *Rhabdochona*:	
R. denudata (Dujardin, 1845)	(*R. cascadilla* Wigdor, 1918)
R. phoxini Moravec, 1968	(*R. cascadilla* Wigdor, 1918)
R. humili Roytman et Trofimenko, 1964	(*R. canadensis* Moravec et Arai, 1971)
R. zacconis Yamaguti, 1935	(*R. canadensis* Moravec et Arai, 1971)
R. oncorhynchi (Fujita, 1921)	(*R. kisutchi* Margolis, Moravec et McDonald, 1975)

Africa. In spite of inadequate descriptions of some species from South and East Asia and from Africa, where comparisons are so far impossible, there are some pairs of related species there, mostly in the subgenus *Globochona*, indicating a considerable genetic affinity of both faunas (Table I). An analogy of the Indian species *R. mazeedi* Prasad et Sahay, 1965 is, for instance, the African species *R. paski* Baylis, 1923 and *R. congolensis* Campana-Rouget, 1961 (all parasites of siluroid fishes), the Indian species *R. barusi* Majumdar et De, 1971 is markedly similar to the African *R. gambiana* Gendre, 1921, while both are parasitic in cyprinids of the genus *Barilius*, etc.

The African fauna of *Rhabdochona* is not too varied. To date, only 7 species are known from this continent; a part of them shows apparent affinities with the Oriental species, whereas in others it is difficult to establish any affinity.

The Nearctic fauna of *Rhabdochona* includes a total of 10 species, indicating distinct affinities to the Palaearctic fauna, as mentioned above. In this region, only representatives of the subgenus *Rhabdochona* occur. Even though there are no sufficient data to date on the distribution of individual species, it appears that the species *R. canadensis* and *R. kisutchi* are spread only in western parts of Canada and the USA. The territory of Mexico is very interesting from the zoogeographical point of view, where the Nearctic and Neotropical faunas come into contact and where a high degree of endemism occurs. Whereas one species of *Rhabdochona* (*R. acuminata*) from southern Mexico is identical to that in South America, other Mexican species either show affinities to Nearctic species (e.g., *R. kidderi* Pearse, 1936, *R. canadensis bifilamentosa* Moravec et Huffman, 1988) or are endemic to this region (*R. ahuehuellensis* Mejía-Madrid et Pérez-Ponce de León, 2003, *R. guerreroensis* Caspeta-Mandujano, Aguilar-Aguilar et Salgado-Maldonado, 2002, *R. lichtenfelsi* Sánchez-Alvarez, García-Prieto et Pérez-Ponce de León, 1998, *R. mexicana* Caspeta-Mandujano, Moravec et Salgado-Maldonado, 2000, *R. salgadoi* Caspeta-Mandujano et Moravec, 2000, *R. xiphophori* Caspeta-Mandujano, Moravec et Salgado-Maldonado, 2001). The only species described from West Indies is *R. cubensis* Moravec et Coy Otero, 1987 from *Gambusia punctata* Poey from Cuba, which belongs to the subgenus *Rhabdochona*; its affinities are uncertain.

At present, the Neotropical fauna of *Rhabdochona* spp. in South America appears to be poor in species and, to date, only 3 valid, mutually related species of the subgenus *Rhabdochona* parasitizing mostly characids are known (Cremonte *et al*. 2002, Ramallo 2005). It is interesting that despite the large number of various species of siluroids in this region, no *Rhabdochona* species adapted to these hosts have been recorded. Also, none of the South-American species of *Rhabdochona* parasitizing characid fishes resembles morphologically congeneric species parasitic in characids in Africa.

Three species of *Rhabdochona*, *R. jaenschi* Johnston et Mawson, 1940, *R. coelorhynchi* Johnston et Mawson, 1945 and *R. beatriceinsleyae* Holloway et Klewer, 1969 were described from marine fishes from Australia and Antarctica, but these were subsequently transferred to the genera *Ascarophis* van Beneden, 1871, *Johnstonmawsonia* Campana-Rouget, 1955 and *Comephoronema* Layman, 1933, respectively (Campana-Rouget 1955, Rasheed 1965, Moravec and Klimpel 2007). Therefore, until recently, *Rhabdochona* spp. were considered to be completely absent from the Australian Region (Moravec 1972a, 2007a; Mejía-Madrid *et al*. 2007a; Moravec and Muzzal 2007). However, Moravec *et al*. (2008) have recently described *Rhabdochona papuanensis* from the freshwater fish *Melanotaenia affinis* (Weber) (Melanotaeniidae, Atheriniformes) in Papua New Guinea, which belongs to the same zoogeographical region. Fish species of *Melanotaenia* Gill are distributed in New Guinea and Australia (Nelson 2006). Surprisingly, most morphological features of *R. papuanensis* (e.g., the number of anterior prostomal teeth, the presence of a dorsal barb on the right spicule, the shape of the female tail) are also typical of the majority of *Rhabdochona* spp. in other zoogeographical regions. A unique feature of this species is only the possession of hammer-shaped deirids; this type of deirids does not occur neither in other congeners nor in rhabdochonids generally, being recorded only in one (*Comephoronema macrochiri* Moravec et Klimpel, 2007) of many species of the related family Cystidicolidae (Moravec and Klimpel 2007).

Hypothetic evolution and spreading of nematodes of the genus **Rhabdochona**

The structure of the vestibule (= stoma or buccal capsule) in third-stage larvae of some recent species of *Rhabdochona* suggests a certain relationship of these nematodes with those of the Cystidicolidae, supporting thus the opinions of Trofimenko (1967), Skryabin *et al*. (1967) or Puylaert (1973) about mutual affinities of these nematode groups. On the contrary, Chabaud and Krishnasamy (1975) considered Rhabdochonidae and Cystidicolidae to be distant. In the present author's opinion, it is possible to be inclined towards the view of McVicar and Gibson (1975) that some cystidicolid genera (e.g., *Cystidicola* Fischer, 1798, *Ascarophis*-like genera) show affinities with rhabdochonids. Consequently, it can be presumed that both these parasite groups evolved from a common ancestor. It can be justifiably deduced that the aforementioned freshwater nematodes of the genus *Rhabdochona* originated from marine ancestors at the Early Cretaceous; during the Cretaceous, borders between sea and dry land unceasingly changed, new river-beds arose, and this resulted in a quick speciation of both host fishes and their parasites.

Comparison of the numbers of *Rhabdochona* species parasitizing hosts in individual fish orders (see p. 146) show that these parasites are by far most frequently present in Cypriniformes, where they exhibit considerable species diversification and, in these species, the most primitive morphological features are found. Accordingly, it can be deduced that the origin of this nematode group is closely connected with that of Cypriniformes. According to Nelson (2006), Cypriniformes belong, along with Characiformes, Siluriformes and Gymnotiformes, to the series Otophysi, superfamily Ostariophysi, being the primitive sister taxa to the remaining three groups.

The nematode group represented by the present genus *Rhabdochona* appears to be very ancient. It can be judged from the relationships of representatives of this genus, as can be deduced by the types of obligatory hosts, their geographical distribution, and phylogeny, that the origin and the main geographic expansion of *Rhabdochona* species is closely connected to the origin of fishes of the family Cyprinidae, whose fossil representatives are known from the Eocene from Asia and from the Oligocene in Europe and North America (Nelson 2006). It is believed that cyprinids were absent from North America in the Eocene, a time when other otophysans were present, because major extinctions occurred about 40 and 38 million years ago (Eocene) in the North American forms when a marked global cooling occurred (Cavender 1991). Their centre of their origin is usually considered the dry-land extending in present southern Asia and India, and formerly connected to Africa (Darlington 1957); this land was separated from northern Asia by the Tethys Sea. Hence, apparently here originated, probably from a marine ancestor, the nematode species of the genus *Rhabdochona*. This hypothesis is supported by the fact that, at present, representatives of all four subgenera of *Rhabdochona* occur solely in the region of southern and southeastern Asia. Even though the main expansion of nematodes of this genus is evidently connected with that of the Cyprinidae, it may well be that their original hosts are also Siluriformes (catfishes), which occurred in this region at the beginning of Tertiary. In spite of the fact that the genesis of catfishes remains insufficiently known, these fishes are noted by many primitive characters indicating the antiquity of the group, which probably arose as early as in the middle of the Cretaceous (Nikolskiy 1971, Nelson 2006). It is remarkable that, for example, the recent fauna of digeneans of Indian catfishes still shows a strong sea influence (Manter 1967). The transition of the initial forms of *Rhabdochona* to life in fresh waters also involved their adaptation to new intermediate hosts, i.e., from marine crustaceans to aquatic insects, mainly ephemeropterans (mayflies); mayfly fossils are already known from Jurassic (Obenberger 1958).

Present *Rhabdochona* species parasitizing salmonids (Salmonidae) as obligatory hosts (*R. kisutchi*, *R. oncorhynchi*) are morphologically very close to congeneric species (*R. denudata*, *R. phoxini*) parasitic in cyprinids (Moravec 1975, Margolis *et al*. 1975). Although Garstang (1931) brought salmonids and cyprinids nearer to each other, at present Salmoniformes (represented only by Salmonidae) are considered to belong to a different superorder Protacanthopterygii (see Nelson 2006). Therefore, the explanation of the above phenomenon may be that a group of species parasitizing salmonids originated by a divergence of *Rhabdochona* spp. from Leuciscinae; the latter occupied free niches arising by the progress of salmonids since the second half of the Tertiary and adapted to the salmonids living permanently or partly in fresh waters.

It is possible to consider species of the subgenus *Globochona* as closest to the initial type of *Rhabdochona*. They are characterized by many primitive morphological features (e.g., the number of prostomal teeth or the type of spicules) and representatives of this subgenus occur mostly in siluroid fishes and ancient Cypriniformes, such as Barbinae (*Barbus*) and Rasborinae (*Barilius*, *Opsariichthys*). Very early, probably in consequence of an adaptation to Cyprinidae manifesting a considerable expansion in the Palaeogene, these nematodes diverged and an independent evolutionary lineage leading to recent representatives of the subgenus *Rhabdochona* turned out. The split of the latter line had to occur in time when southern Asia was connected with Africa, because now representatives of both subgenera, *Globochona* and *Rhabdochona*, occur in the Ethiopian Region. Today's African species of *Rhabdochona* (mainly those of the subgenus *Globochona*) exhibit so far a considerable similarity to species from southern Asia (see p.153) and also their hosts are mutually related, often belonging to the same fish genus. New morphological types have not yet developed in Africa.

Probably at the same time when a subgeneric separation into *Globochona* and *Rhabdochona* occurred or somewhat later, two additional lines, represented by the present subgenera *Globochonoides* and *Sinonema*, arose; the latter appears to be younger and derived from the former. The ancientness of *Globochonoides* is indicated not only by morphology (e.g., the presence of lateral alae), but also by the type of the definitive (obligatory) hosts; of them, *Opsariichthys* was considered by some ichthyologists (Nikolskiy 1971) to be closest to the initial type of the Cyprinidae, of which the lines Barbinae and Leuciscinae were formed. Apparently, nematodes of the genus *Rhabdochona* penetrated into Europe and Siberia along with cyprinids as early as in the Eocene age and later, during the elevation of the bottom of the Tethys Sea, when they, as well as their hosts, spread to the north (Gusev 1969). The northern latitudes were first reached by Leuciscinae, only later by Barbinae. All present subfamilies of cyprinids were formed at the turn of the Palaeogene and Neogene, whereas all present genera were already present in the Oligocene; during the Miocene, formation of all main faunistical complexes took place, which also have their reflection regarding the representatives of *Rhabdochona*.

Through Beringia, forming a bridge between Asia and America up to Pliocene, representatives of the subgenus *Rhabdochona* got to North America, where, similarly as Leuciscinae, they radially spread and gave rise to new species. Then the representatives of this subgenus penetrated from North America to Central and South America (including West Indies). This hypothesis is supported by the fact that in the Americas there occur only representatives of the subgenus *Rhabdochona* and South and Central American species are morphologically close to North American species. Consequently, all American species can be derived from members of the subgenus *Rhabdochona*, which penetrated in here along with Leuciscinae from Asia and adapted as well to other fish groups. Nowadays, North American Leuciscinae are parasitized by the species (*R. canadensis*, *R. cascadilla*) morphologically very similar to Palaearctic species (see p. 152). From this morphological group, the species parasitizing both the Catostomidae (*R. milleri* Choquette, 1951, *R. ovifilamenta* Weller, 1938) and Salmonidae (*R. kisutchi*) and Cottidae (*R. cotti* Gustafson, 1949) can be derived. Also the North American species from catfishes (*R. decaturiensis* Gustafson, 1949, *R. kidderi*), noted for the conspicuously long left spicule, can be derived from species from Leuciscinae; in contrast to representatives of the subgenus *Rhabdochona* parasitizing catfishes in Eurasia, these are characterized by a pointed tail tip and non-filamented eggs. In contrast to other North American species of *Rhabdochona*, *R. longleyi* Moravec et Huffman, 1988, a parasite of the endemic blind catfishes *Trogloglanis pattersoni* Eigenmann and *Satan eurystomus* Hubbs et Bayley (both Ictaluridae) from subterranean waters in Texas, possesses only 6 prostomal teeth, resembling thus *R. cubensis* from *Gambusia punctata* from Cuba; both these otherwise unrelated species were also assigned to the subgenus *Rhabdochona* by Moravec and Coy Otero (1987) and Moravec and Huffman (1988).

Even though catfishes are very numerous in the ichthyofauna of South America and this region is usually considered a centre of their origin, there seem to be no obligatory hosts of *Rhabdochona* there. The three species of these nematodes (*R. acuminata*, *R. fabianae* Ramallo, 2005, *R. uruyeni* Díaz-Ungría, 1968), morphologically similar to North American species, are known mainly from the Characidae. Members of Cyprinidae do not occur in South America (Nelson 2006) and according to Eigenmann (1905) all of the South American forms of catfishes can be derived from the marine Tachysuridae (= Ariidae); according to some authors (Szidat 1954, Manter 1963), also the recent trematode fauna of South American freshwater fishes shows strong marine affinities. Consequently, the only explanation comes on offer, that representatives of *Rhabdochona* migrated here since Pliocene times with characiforms or other hosts from North America through the Panama Isthmus, as many other vertebrates (Manter 1963). Since the cyprinids and, consequently, also the *Rhabdochona* nematodes penetrated into the Americas only in the Late Tertiary, they were unable to develop here new morphological types during this relatively short period.

The penetration of Eurasian members of *Rhabdochona* to the north probably took place in several waves and not only along with Leuciscinae, but later also with Barbinae, or contingently with Balitoridae. This is indicated, for instance, by the present occurrence of the species *R. ergensi* and *R. hellichi* in Europe (conspecific nematodes or closely related species are known from the former Soviet Central Asia and from the Oriental Region) (Moravec 1975, Moravec and Amin 1978). The present Palaearctic Region comprises almost exclusively species belonging to the subgenus *Rhabdochona*. In Leuciscinae, there are two morphological groups of species: the first of them, probably older, is noted for the presence of eggs with a smooth surface (or provided with a fine, undefinable gelatinous coating) (*R. denudata*, *R. phoxini*), whereas the second one includes species with long polar filaments (*R. humili*, *R. zacconis*). From the first group, whose representatives spread over the whole territory of the present Palaearctic Region and in the Pleistocene penetrated into the Amur Transitory Region, it is possible to derive also *R. oncorhynchi* occurring in Salmonidae in East Asia and, perhaps, *R. longispicula* Belous, 1965 from Cultrinae of the same region. The second group is tied up with fishes of the genus *Oreoleuciscus* Warpachowski in the region of the West-Mongolian Lakes and some other leuciscine hosts (*Leuciscus* Cuvier, *Tribolodon* Sauvage, *Zacco* Jorda et Evermann) of the Far East. Eurasian species of the subgenus *Rhabdochona* from Barbinae are noted for the presence of ribbon-like polar filaments of a fibrous structure; in the middle of the Tertiary, these probably penetrated from southern Asia to the north to the plains at the site of present high-mountainous Central Asia along with barbels; due to a later elevation of the Himalayas, the barbels remained isolated there and the present *Schizothorax*-like forms evolved from them. An evidence for a close genetic relationship of the latter fishes to barbels is given, for example, by the fact that representatives of both *Schizothorax* and *Barbus* still have a common species of these nematodes, *R. hellichi*; this species spread up to Europe with fishes of the genus *Barbus*. In fishes of the genera *Capoeta* Valenciennes in Cuvier et Valenciennes and *Varicorhinus* Rüppell, which evolved from the ancient Barbinae, there are *Rhabdochona* species (*R. fortunatowi*, *R. macrostoma*, *R. tigridis*) whose morphology strongly reminds that of the representatives parasitizing *Barbus* spp.; however, their deirids became conspicuously large and the lateral preanal papillae of the male became more numerous. At present, these species are known from Transcaucasia, Central Asia and Middle East.

Eurasian representatives of the subgenus *Rhabdochona* from catfishes are very similar to the species *R. ergensi* from Balitoridae (*Barbatula* Linck, *Triplophysa* Rendahl), which indicates their close relationship. This nematode group is noted for the presence of a rounded tail tip and tufts of thin polar filaments on the eggs. It appears that the original parasites of catfishes are members of *Globochona*, whereas those of the subgenus *Rhabdochona* passed to these hosts secondarily from Cyprinidae (probably from Barbinae), probably before the migration of barbels to the north. At present, species of the subgenus *Globochona* are, in addition to Africa, distributed in southern and southeastern Asia, from where they spread most northwardly into the Amu-Darya River basin in Central Asia. A single species of *Sinonema* is known from southeastern Asia (China) and those of *Globochonoides* from southeastern and eastern Asia (Russian Far East, Japan, Vietnam).

As already pointed out by Chabaud (1975a, b) and Chabaud and Krishnasamy (1975), in the course of evolution, the *Rhabdochona* line adapted to hosts including marine fishes, amphibians, reptiles and mammals, in which it diverged into several genera (*Beaninema* Caspeta-Mandujano, Moravec et Salgado-Maldonado, 2001, *Fellicola* Petter et Køie, 1993, *Hepatinema*, *Heptochona*, *Johnstonmawsonia*, *Megachona* Mejía-Madrid et Pérez-Ponce de León, 2007, *Pancreatonema* McVicar et Gibson, 1975, *Prosungulonema* Roytman, 1963, *Trichospirura*, *Vasorhabdochona* Martin et Zam, 1967) (see Moravec 2007a). During this evolution, especially as a result of passing from the host's intestinal lumen into its tissues, a prolongation of the body and especially of the vestibule (stoma), an atrophy of prostomal teeth, a reduction of the number of male caudal papillae, a backwards shift of the nerve ring and of the vulva, and a reduction of one of the two uteri can be observed.

Conclusions

An analysis of the final hosts of *Rhabdochona* spp. and the circulation of these parasites in nature show that only obligatory or primary fish hosts (true definitive hosts) should be considered for the evaluation of relationships in these nematodes; the significance of facultative (paratenic, paradefinitive and postcyclic) hosts and intermediate hosts is negligible for this purpose.

It appears that, during the evolution of *Rhabdochona* species, there occur an increase in the number of anterior prostomal teeth and the loss of lateral alae; the right spicule, substituted the gubernaculum, attained a boat-like shape and a dorsal barb developed on its distal tip; the distal tip of the left spicule attained gradually a more complex structure; the eggs with a smooth surface (without lateral swellings or polar caps or filaments) are considered to be more primitive.

The morphology of *Rhabdochona* species indicates a close relation of the Palaearctic fauna of these nematodes with the Nearctic species, and the Oriental (Indo-Malayan) fauna with the Ethiopian (African) fauna.

Nematodes of this genus most probably originated in the region of present southern Asia at the beginning of Tertiary. Closest to the initial archetype appear to be members of the subgenus *Globochona*, from which lineages leading to the subgenera *Globochonoides*, *Sinonema* and *Rhabdochona* can be derived; the expansion of the members of the latter subgenus was apparently associated with a rapid progress of Cyprinidae since the Oligocene.

The present distribution of representatives of the genus *Rhabdochona* suggests that the Neotropical (Central and South American) species of these nematodes were derived from Nearctic (North American) members of the subgenus *Rhabdochona*; the latter penetrated, along with leuciscine hosts into North America from Palaearctic Eurasia at the end of Tertiary. The distribution of Palaearctic species of *Rhabdochona* corresponds to faunistical complexes in the conception of ichthyologists.

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References

Anderson R.C. 1988. Nematode transmission patterns. *Journal of Parasitology*, 74, 30–45. DOI: 10.2307/3282477.

Barger M.A., Janovy J., Jr. 1994. Host specificity of *Rhabdochona canadensis* (Nematoda: Rhabdochonidae) in Nebraska. *Journal of Parasitology*, 80, 1032–1035. DOI: 10.2307/3283455.

Baruš V., Tenora F. 1970. Further discoveries of nematodes in the bats of Afghanistan. *Acta Universitatis Agriculturae Brno*, *A*, 18, 133–141.

Bilqees F.M. 1979. *Rhabdochona parastromatei* sp. n. (Nematoda, Rhabdochonidae) from the fish *Parastromateus niger* (Bleeker) of the Karachi coast. *Zoologica Scripta*, 88, 107–110. DOI: 10.1111/j.1463-6409.1979.tb00622.x.

Blaxter M.L., De Ley P., Garey J.R., Liu L.X., Scheldeman P., Vierstraete A., Vanfleteren J.R., Mackey L.Y., Dorris M., Frisse

L.M., Vida J.T., Thomas W.K. 1998. A molecular evolutionary framework for the phylum Nematoda. *Nature*, *London*, 392, 71–75. DOI: 10.1038/32160.

Boomker J., Petter A.J. 1993. Parasites of South African freshwater fish. III. *Rhabdochona* (*Rhabdochona*) *versterae* n. sp. (Nematoda: Rhabdochonidae) from the spot-tailed robber, *Alestes imberi* Peters 1852. *Onderstepoort Journal of Veterinary Research*, 60, 23–27.

Brooks D.R., McLennan D.A. 1991. Phylogeny, ecology and behavior. University of Chicago Press, Chicago, 434 pp.

Brooks D.R., McLennan D.A. 1993. Parascript. Smithsonian, Institution University Press, Washington, D.C., 429 pp.

Byrne P.J. 1992. On the biology of *Rhabdochona rotundicaudatum* and *R. cascadilla* (Nematoda: Thelazioidea) in stream fishes from southern Ontario. *Canadian Journal of Zoology*, 70, 485–493. DOI: 10.1139/z92-073.

Campana-Rouget Y. 1955. Sur deux nouveaux genres de spirurides parasites de poissons; discussion systématiques des genres voisins. *Annales de Parasitologie Humaine et Comparée*, 30, 346–362.

Caspeta-Mandujano J.M., Aguilar-Aguilar R., Salgado-Maldonado G. 2002. *Rhabdochona guerreroensis* n. sp. (Nematoda: Rhabdochonidae) from the intestine of the gobiid *Sicydium multipunctatum* from fresh waters in Mexico. *Journal of Parasitology*, 88, 746–749, DOI: 10.1645/0022-3395(2002)088 [0746:RGNSNR]2.).CO;2.

Caspeta-Mandujano J.M., Cabañas-Carranza G., Salgado-Maldonado G., Gosztonyi A.E., Cremonte F. 2005. Nematode parasites of the characid freshwater fish *Brycon guatemalensis* in the Usumacinta River, Chiapas, Mexico. *Helminthologia*, 42, 41–44.

Caspeta-Mandujano J.M., Mejía-Mojica H. 2004. Seasonal dynamics of the occurrence and maturation of *Rhabdochona canadensis* in its definitive host, *Notropis boucardi*, of the Chalma River, State of Morelos, Mexico. *Helminthologia*, 41, 121–123.

Caspeta-Mandujano J.M., Moravec F. 2000. Two new intestinal nematodes of *Profundulus labialis* (Pisces, Cyprinodontidae) from fresh waters in Mexico. *Acta Parasitologica*, 45, 332–339.

Caspeta-Mandujano J.M., Moravec F., Delgado-Yoshino M.A., Salgado-Maldonado G. 2000. Seasonal variations in the occurrence and maturation of the nematode *Rhabdochona kidderi* in *Cichlasoma nigrofasciatum* of the Amacuzac River, Mexico. *Helminthologia*, 37, 29–33.

Caspeta-Mandujano J.M., Moravec F., Salgado-Maldonado G. 2001. Two new species of rhabdochonids (Nematoda: Rhabdochonidae) from freshwater fishes in Mexico, with a description of a new genus. *Journal of Parasitology*, 87, 139–143, DOI: 10.1645/0022-3395(2001)087[0139:TNSONR]2.0.CO;2

Cavender T.M. 1991. The fossil record of the Cyprinidae. In: (Eds. I.J. Winfield and J.S. Nelson) *Cyprinid fishes*: *systematics*, *biology and exploitation*. Stanford University Press, Stanford, California, 293–327 pp.

Chabaud A.G. 1971. Evolution of host-parasite adaptation in nematodes of vertebrates. *International Journal for Parasitology*, 1, 217–221. DOI: 10.1016/0020-7519(71)90024-5.

Chabaud A.G. 1975a. Camallanoidea, Dracunculoidea, Gnathostomatoidea, Physalopteroidea, Rictularioidea and Thelazioidea. Keys to genera of the order Spirurida, Part 1. In: (Eds. C.R. Anderson, A.G. Chabaud and S. Willmott) *CIH keys to the nematode parasites of vertebrates* 3. Commonwealth Agricultural Bureaux, Farnham Royal, Bucks (UK), 27 pp.

Chabaud A.G. 1975b. Spiruroidea, Habronematoidea and Acuarioidea. Keys to the genera of the order Spirurida, Part 2. In: (Eds. C.R. Anderson, A.G. Chabaud and S. Willmott) *CIH keys to the nematode parasites of vertebrates* 3. Commonwealth Agricultural Bureaux, Farnham Royal, Bucks (UK), 29–58.

Chabaud A.G., Krishnasamy M. 1975. Nouveaux nématodes du genre *Trichospirura* Smith et Chitwood, 1967, en Malaisie. Remarques sur l'évolution de la famille des Rhabdochonidae. *Annales de Parasitologie Humaine et Comparée*, 50, 813–820.

Choquette L.P.E. 1951. On the nematode genus *Rhabdochona* Railliet, 1916 (Nematoda: Spiruroidea). *Canadian Journal of Zoology*, 29, 1–16. DOI: 10.1139/z51-001.

Cremonte F., Navone G.T., Gosztonyi A.E., Kuba L. 2002. Redescription of *Rhabdochona* (*Rhabdochona*) *acuminata* (Nematoda: Rhabdochonidae) from freshwater fishes from Patagonia (Argentina), the geographical implications. *Journal of Parasitology*, 88, 934–941. DOI: 10.1645/0022-3395(2002) 088[0934:RORRAN]2.0.CO;2.

Darlington P.J., Jr. 1957. Zoogeography: The geographical distribution of animals. Wiley, New York, 675 pp.

Dzhalilov U.D., Gavrilova N.G. 1967. Zoogeographical analysis of fish parasites of the Turkestan Province of the Mediterranean Subregion. *Zoologicheskiy Zhurnal*, 46, 274–276 (In Russian).

Eigenmann C.H. 1905. The freshwater fishes of Patagonia and examination of the Archiplata-Archhelenis Theory. Reports of the Princeton University Expeditions to Patagonia 1896–1899, vol. 3, 2 (Ex Szidat 1954).

Garstang W. 1931. The phyletic classification of the Teleostei. *Proceedings of the Leeds Philosophical and Literary Society. Scientific Section*, 2, 240–261.

Ghazi R.R., Nisa N., Bilqees F.M. 2003. First report of the genus *Rhabdochona* (*Globochona*) *rahimi* sp. n. [sic] from a fresh water fish *Brilius* [sic] *pakistanicus* in Pakistan. *Acta Parasitologica Turcica*, 27, 217–221.

Gusev A.V. 1969. History of the fauna and attachment adaptations of the freshwater monogeneans of Eurasia and North America. *Parazitologicheskiy Sbornik Zoologicheskogo Instituta AN SSSR*, *Leningrad*, 24, 106–127 (In Russian).

Gustafson P.V. 1939. Life cycle studies on *Spinitectus gracilis* and *Rhabdochona* sp. (Nematoda: Thelaziidae). *Journal of Parasitology*, 25 (Suppl.), 12–13.

Gustafson P.V. 1942. A peculiar larval development of *Rhabdochona* spp. (Nematoda: Spiruroidea). *Journal of Parasitology*, 28 (Suppl.), 30.

Gustafson P.V. 1949. Description of some species of *Rhabdochona* (Nematoda: Thelaziidae). *Journal of Parasitology*, 35, 534–540. DOI: 10.2307/3273657.

Hirasawa R., Urabe M. 2003. *Ephemera strigata* (Insecta: Ephemeroptera: Ephemeridae) is the intermediate host of the nematodes *Rhabdochona denudata honshuensis* and *Rhabdochona coronacauda* in Japan. *Journal of Parasitology*, 89, 617–620. DOI: 10.1645/GE-3106RN.

Hirasawa R., Yuma M. 2003. *Ephemera strigata* imagoes are the likely source of a parasitic nematode infection of fish. *Folia Parasitologica*, 50, 313–314.

Holloway H.L., Klewer H.L. 1969. *Rhabdochona beatriceinsleyae* n. sp. (Nematoda: Spiruridea: Rhabdochonidae), from the Antarctic zoarcid, *Rhigophila dearborni*. *Transactions of the American Microscopical Society*, 88, 460–471. DOI: 10.2307/3224239.

Inglis W.G. 1968. Allopatric speciation in the nematode parasites of frogs in southern Western Australia. *Journal of Zoology*, *London*, 156, 405–413. DOI: 10.1111/j.1469-7998.1968.tv04362.x.

Janiszewska J. 1960. Studies on larval nematodes in Tubificidae (a hypothesis on the life-cycle of Rhabdochonidae). *Acta Parasitologica Polonica*, 8, 419–425.

Johnston T.H., Mawson R.M. 1945. Parasitic nematodes. *Reports of the B.A.N.Z. Antarctic Research Expedition 1929–1931*, 5 (Part 2), 73–159. DOI: 10.1016/0166-6851(96)02682-5.

Kakar A., Bilqees F.M. 2007a. *Rhabdochona uvaginus*, new species (Nematoda: Rhabdochonidae) from fish *Tor putitora* of river Bolan, Balochistan. *Pakistan Journal of Zoology*, 39, 51–55.

Kakar A., Bilqees F.M. 2007b. Two new species of *Rhabdochona* Railliet, 1916 (Nematoda: Rhabdochonidae) from the fishes of Hingol River and Bolan River of Balochistan. *Proceedings of Parasitology*, 44, 29–39.

Kakar A.U., Bilqees F.M. 2007c. Two new species of the genus *Rhabdochona* Railliet, 1916 (Nematoda: Rhabdochonidae) from the fishes *Cyprinion milesi* Day, 1880 and *C. watsoni* Day, 1872 of Nushki Balochistan, Pakistan. *Pakistan Journal of Nematology*, 25, 147–155.

Kakar A., Bilqees F.M., Kakar J.K. 2006. *Rhabdochona kharani* sp. n. (Nematoda: Rhabdochonidae) from the fish *Labeo gedrosicus* Zugmayer, 1912 from Garruk, District Kharan, Balochistan, Pakistan. *Acta Parasitologica Turcica*, 30, 63–68.

Kakar A.U., Bilqees F.M., Ahmad S. 2008a. Two new species of the genus *Rhabdochona* Railliet, 1916 (Nematoda: Rhabdochonidae) from the fish *Tor putitora* (Cyprinidae) from Bolan, Balochistan, Pakistan. *Pakistan Journal of Nematology*, 26, 21–28.

Kakar A., Bilqees F.M., Nawaz M. 2008b. A new species of *Rhabdochona* Railliet, 1916 (Nematoda: Rhabdochonidae) from a freshwater fish in Khaisar valley, Balochistan, Pakistan. *Proceedings of Parasitology*, 45, 53–66.

Lakshmi B.B., Sudha M. 1999. On a new species *Rhabdochona marina* (Nematoda: Rhabdochonidae) from the intestine of *Pempheris vanicolensis* (Cuvier) [sic] of Visakhapatnam. *Uttar Pradesh Journal of Zoology*, 19, 165–170.

Li W.X., Zhang L.Q., Gao Q., Nie P. 2008. Endohelminths and their community characteristics in fish of the Lhasa River in Tibet of China. *Chinese Journal of Zoology*, 43, 1–8.

Maggenti A.R., Abdel-Rahman F., Cid del Prado Vera I. 1992. New species of *Rhabdochona* Railliet, 1916 (Nematoda: Rhabdochonidae) from rainbow trout in California streams. *Journal of Nematology*, 24, 379–390.

McVicar A.H., Gibson D.I. 1975. *Pancreatonema torriensis* gen. nov., sp. nov. (Nematoda: Rhabdochonidae) from the pancreatic duct of *Raja naevus*. *International Journal for Parasitology*, 5, 529–535. DOI: 10.1016/0020-7519(75)90045-4.

Manter H.W. 1963. The zoogeographical affinities of trematodes of South American freshwater fishes. *Systematic Zoology*, 12, 45–70. DOI: 10.2307/2411621.

Manter H.W. 1967. Some aspects of the geographical distribution of parasites. *Journal of Parasitology*, 53, 1–9. DOI: 10.2307/3276610.

Margolis L., Moravec F., McDonald T.E. 1975. *Rhabdochona kisutchi* sp. nov. (Nematoda: Spiruroidea) from coho salmon, *Oncorhynchus kisutch* (Walbaum), of western Canada. *Canadian Journal of Zoology*, 53, 960–966. DOI: 10.1139/z75-111.

Mashego S.N. 1990. A new species of *Rhabdochona* Railliet, 1916 (Nematoda: Rhabdochonidae) from *Barbus* species in South Africa. *Annals of the Transvaal Museum*, 35, 147–149.

Mayr E. 1963. Animal species and evolution. The Belknap Press of Harward University Press, Cambridge, Massachusetts, 797 pp.

Mejía-Madrid H.H., Choudhury A., Pérez-Ponce de León G. 2007a. Phylogeny and biogeography of *Rhabdochona* Railliet, 1916 (Nematoda: Rhabdochonidae) species from the Americas. *Systematic Parasitology*, 67, 1–18. DOI: 10.1007/s11230-006-9065-3.

Mejía-Madrid H., Pérez-Ponce de León G. 2003. *Rhabdochona ahuehuellensis* n. sp. (Nematoda: Rhabdochonidae) from the Balsas goodeid, *Ilyodon whitei* (Osteichthyes: Gooedeidae [sic]), in Mexico. *Journal of Parasitology*, 89, 356–361. DOI: 10.1645/0022-3395(2003)089[0356:RANSNR]2.0.CO;2.

Mejía-Madrid H.H., Vázquez-Domínguez E., Pérez-Ponce de León G. 2007b. Phylogeography and freshwater basins in central Mexico: recent history as revealed by the fish parasite *Rhabdochona lichtenfelsi* (Nematoda). *Journal of Biogeography*, 34, 787–801. DOI: 10.1111/j.1365-2699.2006.01651.x.

Moravec F. 1972a. General characterization of the nematode genus *Rhabdochona* with a revision of the South American species. *Acta Societatis Zoologicae Bohemoslovacae*, 36, 29–46.

Moravec F. 1972b. A revision of African species of the nematode genus *Rhabdochona* Railliet, 1916. *Acta Societatis Zoologicae Bohemoslovacae*, 36, 196–208.

Moravec 1972c. Studies on the development of the nematode *Rhabdochona* (*Filochona*) *ergensi* Moravec, 1968. *Folia Parasitologica*, 19, 321–333.

Moravec F. 1975. Reconstruction of the nematode genus *Rhabdochona* Railliet, 1916 with a review of the species parasitic in fishes of Europe and Asia. Studie ČSAV No. 8. Academia, Prague, 104 pp.

Moravec F. 1976. Observations on the development of *Rhabdochona phoxini* Moravec, 1968 (Nematoda: Rhabdochonidae). *Folia Parasitologica*, 23, 309–320.

Moravec F. 1977. Life history of the nematode *Rhabdochona phoxini* Moravec, 1968 in the Rokytka Brook, Czechoslovakia. *Folia Parasitologica*, 24, 97–105.

Moravec F. 1983. *Rhabdochona puylaerti* sp. n. (Nematoda: Rhabdochonidae) recorded from the African viper *Causus rhombeatus* (Lichtenstein). *Folia Parasitologica*, 30, 313–317.

Moravec F. 1989. Observations on the occurrence and maturation of the nematode *Rhabdochona denudata* (Dujardin, 1845) in chub, *Leuciscus cephalus* (L.), of the Rokytná River, Czechoslovakia. *Parassitologia*, 31, 25–35.

Moravec F. 1994. Nematodes of freshwater fishes of Europe. Academia and Kluwer Academic Publishers, Prague and Dordrecht, Boston, London, 472 pp.

Moravec F. 1995. Trichopteran larvae (Insecta) as the intermediate hosts of *Rhabdochona hellichi* (Nematoda: Rhabdochonidae), a parasite of *Barbus barbus* (Pisces). *Parasitology Research*, 81, 268–270. DOI: 10.1007/BF00937122.

Moravec F. 1998. Nematodes of freshwater fishes of the Neotropical Region. Academia, Prague, 464 pp.

Moravec F. 2004. Metazoan parasites of salmonid fishes of Europe. Academia, Prague, 510 pp.

Moravec F. 2007a. Some aspects of the taxonomy and biology of adult spirurine nematodes parasitic in fishes: a review. *Folia Parasitologica*, 54, 239–257.

Moravec F. 2007b. First experimental observations on the development of *Rhabdochona denudata* (Nematoda: Rhabdochonidae) in the intermediate host. *Folia Parasitologica*, 54, 236–238.

Moravec F., Amin A. 1978. Some helminth parasites, excluding Monogenea, from fishes of Afghanistan. *Acta Scientiarum Naturalium Academiae Scientiarum Bohemoslovacae*, *Brno*, 12, 1–45.

Moravec F., Arai H. 1971. The North and Central American species of *Rhabdochona* Railliet, 1916 (Nematoda: Rhabdochonidae) of fishes, including *Rhabdochona canadensis* sp. nov. *Journal of the Fisheries Research Board of Canada*, 28, 1645–1662.

Moravec F., Coy Otero A. 1987. *Rhabdochona cubensis* sp. n. (Nematoda: Rhabdochonidae) from the freshwater fish *Gambusia punctata* from Cuba. *Helminthologia*, 24, 103–110.

Moravec F., Huffman D.G. 1988. *Rhabdochona longleyi* sp. n. (Nematoda: Rhabdochonidae) from blind catfishes, *Trogloglanis pattersoni* and *Satan eurystomus* (Ictaluridae) from the subterranean waters of Texas. *Folia Parasitologica*, 35, 235–243.

Moravec F., Huffman D.G. 2001. Observations on the biology of *Rhabdochona kidderi texensis*, a parasite of North American cichlids. *Journal of Helminthology*, 75, 197–203.

Moravec F., Klimpel S. 2007. A new species of *Comephoronema* (Nematoda: Cystidicolidae) from the stomach of the abyssal halosaur *Halosauropsis macrochir* (Teleostei) from the Mid-Atlantic Ridge. *Journal of Parasitology*, 93, 901–906. DOI: 10.1645/GE-1065R.1.

Moravec F., Konečný R., Baska F., Rydlo M., Scholz T., Molnár K., Schiemer F. 1997. Endohelminth fauna of barbel, *Barbus barbus* (L.), under ecological conditions of the Danube basin in Central Europe. Studie ČSAV no. 3/1997. Academia, Prague, 96 pp.

Moravec F., Lorber J., Konečný R. 2007. Two new species of parasitic nematodes from the dogtooth tuna *Gymnosarda unicolor* (Pisces) off the Maldive Islands. *Journal of Parasitology*, 93, 171–178. DOI: 10.1645/GE-965R.1.

Moravec F., Mendoza-Franco E., Vivas-Rodríguez C., Vargas-Vázquez J., González-Solís D. 2002. Observations on seasonal changes in the occurrence and maturation of five helminth species in the pimelodid catfish, *Rhamdia guatemalensis*, in the cenote (= sinkhole) Ixin-há, Yucatán, Mexico. *Acta Societatis Zoologicae Bohemicae*, 66, 121–140.

Moravec F., Muzzall P. 2007. Redescription of *Rhabdochona cotti* (Nematoda, Rhabdochonidae) from *Cottus caeruleomentum* (Teleostei, Cottidae) in Maryland, USA, with remarks on the taxonomy of North American *Rhabdochona* spp. *Acta Parasitologica*, 52, 51–57. DOI: 10.2478/s11686-006-0049-x.

Moravec F., Nagasawa K., Urushibara Y. 1998. Observations on the seasonal maturation of the nematode *Rhabdochona zacconis* in Japanese dace, *Tribolodon hakonensis*, of the Okitsu River, Japan. *Acta Societatis Zoologicae Bohemicae*, 62, 45–60.

Moravec F., Říha M., Kuchta R. 2008. Two new nematode species, *Paragendria papuanensis* sp. n. (Seuratoidea) and *Rhabdochona papuanensis* sp. n. (Thelazioidea), from freshwater fishes in Papua New Guinea. *Folia Parasitologica*, 55, 127–135.

Moravec F., Saraiva A., Abdullah S.M.A., Bilal S.J., Rahemo Z.I.F. 2009. Two species of *Rhabdochona* Railliet, 1916 (Nematoda: Rhabdochonidae) parasitising cyprinid fishes in Iraq, with a redescription of *R. tigridis* Rahemo, 1978 (emend.). *Systematic Parasitology*, 74, 125–135. DOI: 10.1007/s11230-009-9196-4.

Moravec F., Scholz T. 1991. Observations on some nematodes parasitic in freshwater fishes in Laos. *Folia Parasitologica*, 38, 163–178.

Moravec F., Scholz T. 1995. Life history of the nematode *Rhabdochona hellichi*, a parasite of the barbel in the Jihlava River, Czech Republic. *Journal of Helminthology*, 69, 59–64. DOI: 10.1017/S0022149X00013845.

Nadler S.A., Carreno R.A., Mejía-Madrid H., Ullberg J., Pagan C., Houston R., Hugot J.-P. 2007. Molecular phylogeny of clade III nematodes reveals multiple origins of tissue parasitism. *Parasitology*, 134, 1421–1442. DOI: 10.1017/S003118200 7002880.

Nelson J.S. 2006. Fishes of the World. 4th edition. John Wiley & Sons, Inc., Hoboken, New Jersey, 601 pp.

Nikolskiy G.V. 1971. Special ichthyology. Vysshaya Shkola, Moscow, 471 pp. (In Russian).

Obenberger J. 1958. Entomologie IV. ČSAV, Praha, 614 pp. (In Czech).

Odening K. 1976. Conception and terminology of hosts in parasitology. *Advances in Parasitology*, 14, 1–93. DOI: 10.1016/ S0065-308X(08)60513-8.

Paul B., Majumdar G. 1994. Description of a new species of the genus *Rhabdochona* (Nematoda: Spiruridae). *Environment and Ecology*, *West Bengal*, 12, 854–856.

Pearse A.S. 1932. Observations on the ecology of certain fishes and crustaceans along the bank of the Malta River at Port Canning. *Records of the Indian Museum*, *Calcutta*, 34, 289–298.

Pereira-Bueno J.M. 1978. Seasonal occurrence of *Rhabdochona* spp. in cyprinid fishes of the rivers of León (NW Spain). *Proceedings of the IVth International Congress of Parasitology*, Warsaw, 19–26 August 1978, Sect. H, 45–46.

Petter A.J. 1974. Essai de classification de la famille des Cucullanidae. *Bulletin du Muséum National d'Histoire Naturelle*, *Sér*. 3, No. 255, Zoologie, 177, 1469–1490.

Poinar G.O., Kannangara D.W.W. 1972. *Rhabdochona praecox* sp. n. and *Proleptus* sp. (Spiruroidea: Nematoda) from fresh water crabs in Ceylon. *Annales de Parasitologie Humaine et Comparée*, 47, 121–129.

Puylaert F.A. 1973. Rhabdochonidae parasites de poissons africains d'eau douce et discussion sur la position systématique de ce groupe. *Revue de Zoologie et de Botanique Africaine*, 87, 647–665.

Ramallo G. 2005. Observations on two *Rhabdochona* species (Nematoda: Rhabdochonidae) from freshwater fishes in Argentina, including description of *Rhabdochona fabianae* n. sp. *Journal of Parasitology*, 91, 415–419. DOI: 10.1645/GE-3413.

Rasheed S. 1965. A preliminary review of the genus *Rhabdochona* Railliet, 1916 with description of a new and related genus. *Acta Parasitologica Polonica*, 13, 407–424.

Roytman V.A., Trofimenko V.Ya. 1964. Taxonomic significance of some morphological characters in rhabdochonids. *Helminthologia*, 5, 135–147 (In Russian).

Saidov Yu.S. 1953. Revision of the family Rhabdochonidae Skrjabin, 1946 and the subfamily Cyclozoninae Sobolev, 1949. Vol. "Raboty po gelmintologii" to 75 Anniversary of K.I. Skryabin, Moscow, 622–635 (In Russian).

Sánchez-Alvarez A., García-Prieto L., Pérez-Ponce de León G. 1998. A new species of *Rhabdochona* Railliet, 1916 (Nematoda: Rhabdochonidae) from endemic goodeids (Cyprinodontiformes) from two Mexican lakes. *Journal of Parasitology*, 84, 840–845. DOI: 10.2307/3284600.

Saraiva A.M., Felisberto P., Cruz C. 2002a. Occurrence and maturation of *Rhabdochona gnedini* (Nematoda: Rhabdochonidae) in the barbels of the Sousa River, Portugal. *Parasite*, 9, 81–84.

Saraiva A.M., Pereira A., Cruz C. 2002b. Observations on the occurrence and maturation of *Rhabdochona anguillae* (Nematoda: Rhabdochonidae) in the Sousa River, Portugal. *Helminthologia*, 39, 41–43.

Shimazu T. 1996. Mayfly larvae, *Ephemera japonica*, as natural intermediate hosts of salmonid nematodes, *Sterliadochona ephemeridarum* and *Rhabdochona oncorhynchi*, in Japan. *Japanese Journal of Parasitology*, 45, 167–172.

Shul'man S.S. 1958. Zoogeographic analysis of the parasites of freshwater fishes of the Soviet Union. In: (Eds. A.V. Dogel', G.K. Petrushevskiy and Yu.I. Polyanskiy) *Basic problems of the parasitology of fishes*. Publishing House of the University of Leningrad, Leningrad, 184–230 (In Russian).

Shtein G.A. 1959. On the questions of the life history and living conditions of the nematode *Rhabdochona denudata* (Dujardin, 1845). *Doklady Akademii Nauk of the USSR*, 127, 1320–1321 (In Russian).

Skryabin K.I., Sobolev A.A., Ivashkin V.M. 1967. Spirurata of animals and man and diseases caused by them. Part 4. Thelazioidea. Essentials of Nematology 16. Nauka, Moscow, 624 pp. (In Russian).

Stunkard H.W. 1970. Trematodes of insular and relict vertebrates. *Journal of Parasitology*, 56, 1041–1054. DOI: 10.2307/327 7544.

Szidat L. 1954. Trematodes nuevos de peces de agua dulce de la Republica Argentina y un intento para aclarar su caracter marino. *Revista de Instituciones Nacionales para Investigaciones en Ciencias Naturales*, *Buenos Aires*, 3, 1–85.

Trofimenko V.Ya. 1967. Reconstruction of the system of the family Rhabdochonidae Skryabin, 1946 based on the analysis of its phylogeny. *Sbornik Rabot po Gelmintologii Ryb i Ptic*. Moscow, 77–95 (In Russian).

Vojtková L. 1971. Beitrag zur Kenntnis der Helmintofauna der Wasserwirbellosen. III. Cestoda, Nematoda, Acanthocephala. *Acta Societatis Zoologicae Bohemoslovacae*, 35, 146–155.

Weller T.H. 1938. Description of *Rhabdochona ovifilamenta* n. sp. (Nematoda: Thelaziidae) with a note on the life history. *Journal of Parasitology*, 24, 403–408. DOI: 10.2307/3272116.

Wijová M., Moravec F., Horák A., Lukeš J. 2006. Evolutionary relationships of Spirurina (Nematoda: Chromadorea: Rhabditida) with special emphasis on dracunculoid nematodes inferred from SSU rRNA gene sequences. *International Journal for Parasitology*, 36, 1067–1075. DOI: 10.1016/j.ijpara.2006.04.005.

Yamaguti S. 1935. Studies of the helminth fauna of Japan. Part 9. Nematodes of fishes, 1. *Japanese Journal of Zoology*, 6, 337–386.

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