

## PROPOSAL OF A NEW SYSTEMATIC ARRANGEMENT OF NEMATODES OF THE FAMILY CAPILLARIIDAE

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*Dedicated to Prof. V. Dyk D.Sc. on the occasion of his 70th birthday*

**Abstract.** A new delimitation of genera within the nematode family Capillariidae is proposed on the basis of reevaluation of the features used in the taxonomy of these nematodes. The following genera are recognized as valid: *Schulmanella* Ivashkin, 1964 (subgenera *Schulmanella* Ivashkin, 1964, *Piscicapillaria* subgen. n. and *Amphibiocapillaria* subgen. n.), *Paracapillaria* Mendonça, 1963, *Capillostrongyloides* Freitas et Lent, 1935, *Pseudocapillaria* Freitas, 1959 (subgenera *Pseudocapillaria* Freitas, 1959 and *Ichthyocapillaria* subgen. n.), *Freitascapillaria* gen. n., *Baruscapillaria* gen. n., *Liniscus* Dujardin, 1845, *Pearsonema* Freitas et Mendonça, 1960, *Capillaria* Zeder, 1800, *Echinocoleus* López-Neyra, 1947, *Eucoleus* Dujardin, 1845, *Pterothominx* Freitas, 1959, *Aonchotheca* López-Neyra, 1947 and *Calodium* Dujardin, 1845; previously established genera are newly defined. The systematic status of the genera *Gessyella* Freitas, 1959 and *Skrjabinocapillaria* Skarbilovich, 1946 has not been so far elucidated. The author newly synonymizes the genera *Ritaklossia* Freitas, 1959 (= *Eucoleus*), *Armocapillaria* Gagarin et Nazarova, 1966 (= *Pterothominx*) and *Hepaticola* Hall, 1916 (= *Calodium*) and the species *Hepaticola bakeri* Mueller et Van Cleave, 1932 (= *Pseudocapillaria catostomi* (Pearse, 1924)) and *Pseudocapillaria nuda* Mendonça, 1963 (= *Freitascapillaria maxillosa* (Vaz et Pereira, 1934)); many new combinations of specific names are given. A key to the genera and subgenera of the family Capillariidae is provided.

From the viewpoint of taxonomy and systematics, nematodes of the family Capillariidae represent at present one of the most difficult groups of helminths. It results mainly from inadequate knowledge of the morphology of individual species whose descriptions are often poor. Moreover, the situation is complicated considerably by substantial differences in the opinions of various authors as to the taxonomic value of various characters in these nematodes and, accordingly, the number of genera in the family Capillariidae.

Although there have been several attempts to make up a system of these nematodes, the most important of which being the papers by Dujardin (1845), Travassos (1915), Yorke and Maplestone (1926), López-Neyra (1947), Skryabin et al. (1957) and Freitas (1959), the situation in capillariid classification remains very confused. Until now, a total of 19 nominal genera have been established in this family: *Capillaria* Zeder, 1800 (= *Trichosoma* Rudolphi, 1819), *Trichosomum* Creplin, 1829, *Liniscus* Dujardin, 1845, *Thominx* Dujardin, 1845, *Calodium* Dujardin, 1845, *Eucoleus* Dujardin, 1845, *Hepaticola* Hall, 1916, *Capillostrongyloides* Freitas et Lent, 1935, *Skrjabinocapillaria* Skarbilovich, 1946, *Aonchotheca* López-Neyra, 1947, *Gessyella* Freitas, 1959, *Pterothominx* Freitas, 1959, *Pseudocapillaria* Freitas, 1959, *Ritaklossia* Freitas, 1959, *Pearsonema* Freitas et Mendonça, 1960, *Orthothominx* Freitas et Silva, 1960, *Paracapillaria* Mendonça, 1963, *Schulmanella* Ivashkin, 1964 and *Armocapillaria* Gagarin et Nazarova, 1966. Many of these genera were, however, based on inconvenient morphological features (length ratios of oesophagus and body, number of eggs in uterus, etc.) or inaccurate observations (alleged absence of spicule), or contingently only on the basis

of different location in the host. Consequently, most of them are not generally recognized and many recent authors (e.g. Yamaguti 1961, Inglis and Coles 1963, Kutzer and Otte 1966, Caballero 1971, Huffman and Bullock 1973, Bell and Beverley-Burton 1981, Butterworth and Beverley-Burton 1980) even share the opinion of Baylis (1931) that the entire group of capillariids is represented by a single genus *Capillaria* s.l.

During the last years, the present author could get acquainted with the morphology of a number of capillariids parasitizing cold-blooded vertebrates, mainly fishes. During these studies there were often found such interspecific differences, mainly in the structure of the male caudal end, which in other nematode groups are usually taken for the differences amongst genera or even subfamilies. Owing to the chaotic situation in the system of the nematode family Capillariidae, all these species were, however, assigned provisionally to the genus *Capillaria* Zeder, 1800 with a remark that their true generic appurtenance would be determined only after a new delimitation of genera within this family (see Moravec 1980a, Moravec and McDonald 1981, Moravec et al. 1981, Moravec and Lomakin 1982). Our studies supported the views of Skryabin et al. (1957), Freitas (1959) and some other authors that the morphological features of various capillariid species, their different location and also the heterogeneity of their definitive hosts give evidence for the existence of several genera in the family Capillariidae.

In 1959 Freitas drew attention to the necessity of dividing this nematode group into genera with the use of new generic criteria and creating a new system based on morphological features and phylogeny. The author suggested division of capillariids into 10 genera of which the earlier established ones, mostly considered synonyms of *Capillaria* — *Capillaria*, *Thominox*, *Hepaticola*, *Capillostrongyloides*, *Skrjabinocapillaria* and *Aonchotheca* are newly defined and are supplemented by newly established genera *Gessyella*, *Pterothominox*, *Pseudocapillaria* and *Ritaklossia*. In the following years, additional genera, *Orthothominox*, *Pearsonema* and *Paracapillaria* were created by Brazilian helminthologists (Freitas and Silva 1960, Freitas and Mendonça 1960, Mendonça 1963) and two genera, *Schulmanella* and *Armocapillaria*, were added by Soviet authors (Ivashkin 1964, Gagarin and Nazarova 1966). Unfortunately, also the above-mentioned genera were often based on inconvenient features, some of them being apparent synonyms of the genera described earlier. When considering the validity of separate genera it is necessary to keep consistently to the principle of type species.

The most important feature distinguishing the genera of capillariids seems to be the structure of the posterior end of male (presence or absence and character of caudal papillae, lobes, dorsal cuticular membrane, caudal lateral alae, etc.). The significance of these structures have already been emphasized by e.g. López-Neyra (1947), Freitas (1959), Butterworth and Beverley-Burton (1980), Baruš et al. (1981) and others. Unfortunately, in many species the structure of the male caudal end is inadequately described, preventing thus their correct generic listing; the use of scanning electron microscopy may play an important role in this respect. Additional significant features distinguishing the genera of capillariids are, in my opinion, the character of the spicular sheath (spiny or nonspiny), presence or absence of the spicule and probably also the structure of stichosome, number and arrangement of bacillary bands and presence or absence of the vulvar appendage in gravid females. Other features as the length of body, length ratio of oesophagus and body, situation of vulva, length of vagina, character and length of spicule, structure of eggs and position of anal opening in females may serve at most for the separation of species.

A prerequisite for creation of a new system of capillariid nematodes, respecting true phylogenetic relationships, is a detailed revision of the entire group. However, due to an

enormous number (some 300) of nominal species of capillariids parasitic in all main groups of vertebrates (fishes, amphibians, reptiles, birds, mammals), the accomplishment of such a revision is very problematic and there is no doubt that to gain detailed knowledge on the morphology of most species is the matter of many years. In this situation the author of this paper consider it reasonable to separate capillariids into several genera according to the present state of knowledge, considering that the system of these nematodes will be further elucidated and made more precise gradually with newly obtained knowledge on the morphology, biology, and phylogeny of these parasites.

The author suggests to divide capillariids into the following 16 genera; however, he is aware of the fact that the assignment of many species to certain genera is due to their inadequate descriptions only provisional and some species, sometimes even recently described, cannot be listed in genera at all at the present time. By assigning the species to separate genera the author pursued only the objective documentation of content and extent of generic diagnoses but not a revision of species within the genera; owing to frequently dissimilar opinions of different authors as to the synonymy of some species, also some specific names considered by some authors as junior synonyms are listed; moreover, the list of species is incomplete, because some species inadequately described or exceptionally those whose original descriptions were not available to the present author have not been included. A revision of the species composition of the separate genera will have to be the subject of future studies. Fig. 1 indicates a hypothetical evolution of capillariids.

#### 1. genus *Schulmanella* Ivashkin, 1964

Diagnosis: Caudal lateral alae in male absent; posterior end of male with small membranous bursa supported by pair of dorsolateral digital projections (rays), bent along margin of bursa to dorsal side; dorsal caudal projection present or absent; pair of large round adanal papillae present; spicule medium-sized, well sclerotized, often with superficial transverse grooves at its middle part; spicular sheath spiny; vulvar appendage in females present or absent; parasites of intestine and liver of fishes and amphibians. Type species: *S. petruschewskii* (Shulman, 1948) Ivashkin, 1964

##### i) subgenus *Schulmanella* (*Schulmanella*) Ivashkin, 1964

Diagnosis: Stichosome consisting of three longitudinal rows of stichocytes; bursa of male without dorsal caudal projection; parasites of liver of fishes. Type species: *S. (S.) petruschewskii* (Shulman, 1948) Ivashkin, 1964

Other species: ? *S. (S.) cyprinodonticola* (Huffman et Bullock, 1973) comb. n.

##### ii) subgenus *Schulmanella* (*Piscicapillaria*) subgen. n.

Diagnosis: Stichosome consisting of single row of stichocytes; bursa of male with dorsal caudal projection; intestinal parasites of fishes. Type species: *S. (P.) freemani* (Moravec, Margolis et McDonald, 1981) comb. n.

Other species: *S. (P.) tuberculata* (Linstow, 1914) comb. n.

##### iii) subgenus *Schulmanella* (*Amphibiocapillaria*) subgen. n.

Diagnosis: Stichosome consisting of single row of stichocytes, only some of stichocytes of its posterior end may be doubled; bursa of male without dorsal caudal projection; parasites of intestine and liver of amphibians.

Type species: *S. (A.) tritonispunctati* (Diesing, 1851) comb. n.

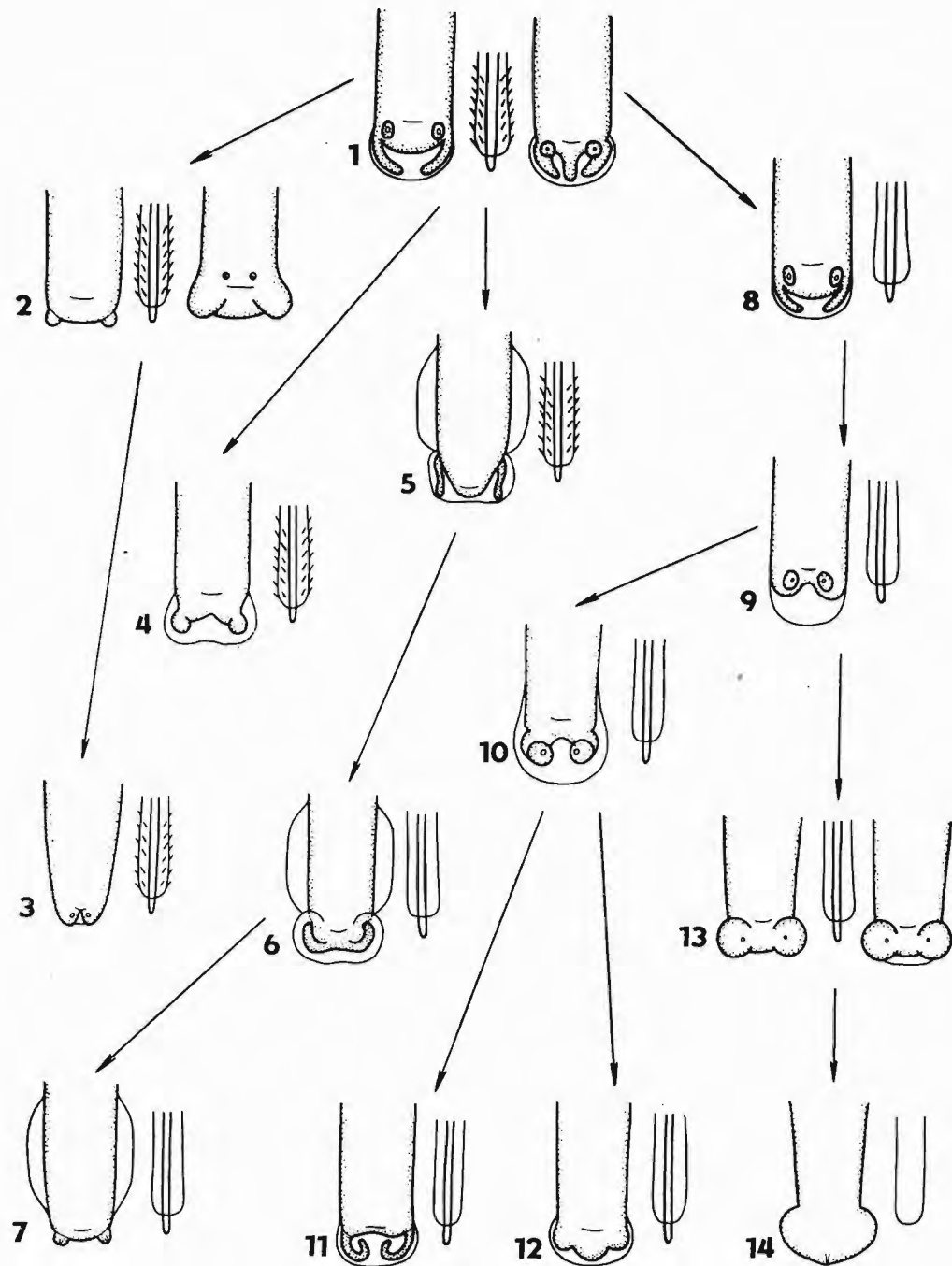


Fig. 1. A hypothetical evolution of capillariids as indicated by structure of the male caudal end and spicule sheath of recent forms. Genera: 1 — *Schulmanella*; 2 — *Capillaria*; 3 — *Eucoleus*; 4 — *Echinocoleus*; 5 — *Pterothomina*; 6 — *Aonchotheca*; 7 — *Calodium*; 8 — *Paracapillaria*; 9 — *Capillostrongyloides*; 10 — *Baruscapillaria*; 11 — *Pearsonema*; 12 — *Liniscus*; 13 — *Pseudocapillaria*; 14 — *Freitascapillaria*.

Other species: *S. (A.) brevicollis* (Walton, 1935) comb. n.; *S. (A.) costacruzi* (Travassos, 1932) comb. n.; *S. (A.) inequalis* (Walton, 1935) comb. n.; *S. (A.) tenua* (Mueller, 1932) comb. n.; *S. (A.) tritoniscristati* (Diesing, 1861) comb. n.

Comments: The genus *Schulmanella* was established by Ivashkin (1964) on the basis of an inadequate original description of the type species, *S. petruschewskii*; later Ivashkin and Shmytova (1969) synonymized it with the genus *Hepaticola* Hall, 1916 (= *Calodium* Dujardin, 1845). However, in contrast to *Schulmanella*, the latter genus is characterized by presence of caudal lateral alae and by absence of a dorsal membrane on the male tail and by a nonspiny spicular sheath.

## 2. genus *Paracapillaria* Mendonça, 1963

Diagnosis: Caudal lateral alae in male absent; membraneous bursa well developed, supported by two dorsolateral digital projections (rays), bent along margin of bursa to dorsal side; one pair of large sessile adanal or postanal papillae present; spicule medium-sized, well sclerotized; spicular sheath nonspiny; vulvar appendage absent; parasites of digestive tract of fishes, amphibians and reptiles.

Type species: *P. piscicola* (Travassos, Artigas et Pereira, 1928) Mendonça, 1963

Other species: *P. bufonis* (Morishita, 1926) comb. n.; *P. colubra* (Pence, 1970) comb. n.; *P. helenae* (Layman, 1930) Mendonça, 1963; *P. longispicula* (Sonsino, 1889) comb. n.; *P. madagascariensis* (Ghadirian, 1968) comb. n.; *P. mingazzini* (Rizzo, 1902) comb. n.; *P. parophrysi* (Moravec, Margolis et McDonald, 1981) comb. n.; *P. sonsinoi* (Parona, 1897) Mendonça, 1963; *P. teixeirafreitas* (Caballero, 1971) comb. n.

## 3. genus *Capillostrongyloides* Freitas et Lent, 1935

Diagnosis: Caudal lateral alae in male absent; membraneous bursa well developed, considerably exceeding posterior end of body, supported by two short, wide, rounded subventral lobes located below cloacal opening; spicule moderately sclerotized, relatively short; spicular sheath nonspiny; vulvar appendage absent; parasites of stomach of freshwater fishes.

Type species: *C. zederi* Freitas et Lent, 1935

Other species: *C. früschi* (Travassos, 1914) comb. n.; *C. minima* (Travassos, Artigas et Pereira 1928) Freitas et Lent, 1935; *C. sentinosa* (Travassos, 1927) comb. n.

Comments: Freitas and Lent (1935) erected this genus to accommodate the species *C. zederi* and *C. minima* and they characterized it by the generally small measurements of the body and a small number of eggs in the uterus of females; however, the given characters cannot be taken for generic criteria.

## 4. genus *Pseudocapillaria* Freitas, 1959

Diagnosis: Caudal lateral alae in male absent; posterior end of male rounded, provided with two large round subventral lobes located below cloacal opening; dorsal, cuticular membrane absent or reduced to narrow band practically not exceeding posteriorly both subventral caudal lobes; spicule medium-sized, well sclerotized; spicular sheath nonspiny; vulvar appendage absent; parasites of intestine and stomach of fishes, reptiles, birds and mammals.

Type species: *P. (P.) catostomi* (Pearse, 1924) comb. n.

### i) subgenus *Pseudocapillaria (Pseudocapillaria)* Freitas, 1959

Diagnosis: Dorsal cuticular membrane on male tail absent.

Type species: *P. (P.) catostomi* (Pearse, 1924) comb. n.

Other species: *P. (P.) amarali* (Freitas et Lent, 1934) comb. n.; *P. (P.) americana* (Read, 1949) comb. n.; *P. (P.) brevispicula* (Linstow, 1873) comb. n.; *P. (P.) carangi* (Parukhin, 1971) comb. n.; *P. (P.) cesarpinui* (Freitas et Lent, 1934) comb. n.; *P. (P.) cooperi* (Johnston et Mawson, 1945) comb. n.; *P. (P.) echenei* (Parukhin, 1967) comb. n.; *P. (P.) falconis* (Goeze, 1782) comb. n.; *P. (P.) gobionina* (Lomakin, 1971) comb. n.; *P. (P.) mergi* (Madsen, 1945) comb. n.; *P. (P.) microspicula* (Mamaev, Parukhin et Baeva, 1963) comb. n.; *P. (P.) picorum* (Rudolphi, 1819) comb. n.; *P. (P.) pusilla* (Travassos, 1914) comb. n.; *P. (P.) sphyraeni* (Parukhin, 1971) comb. n.; *P. (P.) zochimilcensis* (Caballero et Caballero, 1943) comb. n.

## ii) subgenus *Pseudocapillaria* (*Ichthyocapillaria*) subgen. n.

Diagnosis: Dorsal cuticular membrane connecting subventral lobes of male tail present.

Type species: *P. (I.) salvelini* (Polyansky, 1952) comb. n.

Other species: *P. (I.) adriatica* (Nikolaeva et Naidenova, 1964) comb. n.; *P. (I.) delamurei* (Zablotskiy, 1971) comb. n.; *P. (I.) freitasi* (Read, 1949) comb. n.; *P. (I.) magalhaesi* (Lent et Freitas, 1937) comb. n.; *P. (I.) murinae* (Travassos, 1914) comb. n.; *P. (I.) pearsei* (Baylis, 1928) comb. n.

Comments: Freitas (1959) established this genus for the species described under the name *Hepaticola bakeri* Mueller et Van Cleave, 1932 from the intestine of several species of North American freshwater fishes. Although the original description and drawings of this species are very incomplete and evidently erroneous in some respects, it is obvious that this species is identical with the species described as *Capillaria cato-stomi* Pearse, 1924, which has recently been redescribed by Bell and Beverley-Burton (1981) and Moravec (1980b); hence, this species is a type species of *Pseudocapillaria* and it is, therefore, characterized by presence of the spicule in the male. For the other species described in the genus *Pseudocapillaria*, *P. nuda* Mendonça, 1963, a new genus *Freitascapillaria* gen. n. is now proposed; the latter is characterized by absence of the spicule.

It is probable that subsequent studies on the species parasitic in reptiles, birds and mammals, now being tentatively assigned to *Pseudocapillaria*, will prove appurtenance of these species to other genera.

## 5. genus *Freitascapillaria* gen. n.

Diagnosis: Caudal lateral alae in male absent; posterior end of male rounded, distinctly laterally expanded, with terminal cloacal opening; spicule absent; spicular sheath nonspiny; vulvar appendage present on anterior vulvar lip; parasites of stomach and pyloric caeca of freshwater fishes.

Type and the only species: *F. maxillosa* (Vaz et Pereira, 1934) comb. n.

Comments: Mendonça (1963) described under the name *Pseudocapillaria nuda* a new species of capillariids from the pyloric caeca of the Brazilian fish *Salminus maxillosus*. This species is evidently identical with the species described from the stomach of the same fish in Brazil as *Capillaria maxillosa* (Vaz et Pereira, 1934), that is the type of the genus *Freitascapillaria*; accordingly, *P. nuda* Mendonça, 1963 becomes a junior synonym of *F. maxillosa* (Vaz et Pereira, 1934).

## 6. genus *Baruscapillaria* gen. n.

Diagnosis: Caudal lateral alae in male absent; membranous bursa well developed, lobular or nonlobular, supported on either side by mostly one or sometimes two small rounded lobes, often narrowed at base; each lobe provided with minute projection,

usually bent ventrally; spicule well sclerotized, relatively long; spicular sheath nonspiny; vulvar appendage present or absent; parasites of intestine and stomach of birds and mammals.

Type species: *B. obsignata* (Madsen, 1945) comb. n.

Other species: *B. appendiculata* (Freitas, 1933) comb. n.; *B. belopolaskaiae* (Jogis, 1968) comb. n.; *B. caerulea* (Sood, 1972) comb. n.; *B. calliopsis* (Yamaguti, 1941) comb. n.; *B. carbonis* (Rudolphi, 1819) comb. n.; *B. emberizae* (Yamaguti, 1941) comb. n.; *B. herodiae* (Boyd, 1966) comb. n.; *B. inflexa* (Rudolphi, 1819) comb. n.; *B. jaenschi* (Johnston et Mawson, 1945) comb. n.; *B. kutori* (Rukhlyadeva, 1946) comb. n.; *B. montevidensis* (Calzada, 1937) comb. n.; *B. multilocularis* (Yamaguti, 1941) comb. n.; *B. ovopunctata* (Linstow, 1873) comb. n.; *B. pachykeramota* (Wedl, 1856) comb. n.; *B. phalacrocoraxi* (Borgarenko, 1975) comb. n.; *B. pitti* (Wakelin, Schmidt et Kuntz, 1971) comb. n.; *B. podicipitis* (Yamaguti, 1941) comb. n.; *B. prashadi* (Maplestone et Bhaduri, 1942) comb. n.; *B. quisicali* (Read, 1949) comb. n.; *B. ransomia* (Barker et Noyes, 1915) comb. n.; *B. ryjikovi* (Borgarenko et Daiya, 1972) comb. n.; *B. spiculata* (Freitas, 1933) comb. n.; *B. traverae* (Ash, 1962) comb. n.

Comments: The newly erected genus *Baruscapillaria* includes principally the parasites of birds; the species from mammals and also some from birds are assigned to this genus only provisionally. This genus is named in honour of the distinguished Czechoslovak helminthologist Academician V. Baruš, D.Sc., who contributed greatly to the knowledge of a number of capillariid species.

## 7. genus *Liniscus* Dujardin, 1845

Diagnosis: Caudal lateral alae in male absent; small membranous bursa present, being supported by two short, simple round dorsolateral projections; spicule thin, long; spicular sheath nonspiny; vulvar appendage present or absent; parasites of urinary bladder and kidneys of small mammals (insectivores, rodents).

Type species: *L. incrassatus* Diesing, 1851

Other species: *L. capillaris* (Linstow, 1882) comb. n.; *L. himizu* (Ohbayashi, Masegi et Kubota, 1972) comb. n.; *L. maseri* (Rausch et Rausch, 1973) comb. n.; *L. papillosus* (Polonio, 1860) comb. n.; *L. reni* (Shaldybin, 1968) comb. n.; *L. sunci* (Chen, 1937) comb. n.; *L. urinicola* (Soltys, 1952) comb. n.

Comments: Regarding inadequate descriptions of the species listed in this genus, particularly as to the structure of the male caudal end, in future, when new data are available, it will be necessary to define the genus *Liniscus* more precisely.

## 8. genus *Pearsonema* Freitas et Mendonça, 1960

Diagnosis: Caudal lateral alae absent; small membranous bursa present; posterior end of male provided with two minute dorsolateral lobes or rounded; two narrow, fairly long digital projections present, originating dorsolaterally and bent ventrally and to median line, supporting thus margin of membranous bursa; spicule thin, very long; spicular sheath nonspiny; vulvar appendage absent or present; parasites of urinary bladder of mammals (carnivores).

Type species: *P. pearsoni* Freitas et Mendonça, 1960

Other species: *P. cameroni* (Gupta, Pande et Kala, 1963) comb. n.; *P. feliscati* (Diesing, 1851) Freitas et Mendonça, 1960; *P. linsi* (Freitas et Lent, 1935) Freitas et Mendonça, 1960; *P. mucronata* (Molin, 1858) comb. n.; *P. plica* (Rudolphi, 1819) comb. n.

Comments: Freitas and Mendonça (1960) assigned to *Pearsonema* two additional species, viz. *P. inflexa* and *P. ransomia*, which are now considered members of the genus *Baruscapillaria*.

## 9. genus *Echinocoleus* López-Neyra, 1947

Diagnosis: Caudal lateral alae in male absent; posterior end of male provided with small membranous bursa, often two-lobed, supported on either side by one short, round or more elongate lobular dorsolateral projection; dorsal caudal projection absent; spicule well sclerotized, medium-sized; spicular sheath spiny; vulvar appendage absent or present; intestinal parasites of birds and mammals.

Type species: *E. cyanopicae* López-Neyra, 1947

Other species: *E. auritae* (Travassos, 1914) López-Neyra, 1947; *E. confusus* (Freitas et Almeida, 1935) López-Neyra, 1947; *E. ellisi* (Johnston et Mawson, 1945) comb. n.; *E. euryercus* (Oshmarin et Parukhin, 1963) comb. n.; *E. hydrochoeri* (Travassos, 1916) comb. n.

## 10. genus *Capillaria* Zeder, 1800

(Syn.: *Trichosoma* Rudolphi, 1819, partim; *Trichosomum* Creplin, 1829; *Thominx* Dujardin, 1845; *Orthothominx* Freitas et Silva, 1960)

Diagnosis: Caudal lateral alae in male absent; posterior end of male rounded, provided with two lateral, ventrolateral or dorsolateral lobes; membranous bursa absent; two minute preanal sessile papillae often present; spicule well sclerotized; spicular sheath spiny; vulvar appendage absent or present; intestinal parasites of fishes, amphibians, reptiles, birds and mammals.

Type species: *C. anatis* (Schrank, 1790) Travassos, 1915

Other species: *C. aramidesi* Freitas et Lent, 1933; *C. brasiliiana* Freitas, 1933; *C. carioca* Freitas et Lent, 1935; *C. catenata* Van Cleave et Mueller, 1932; *C. collaris* (Linstow, 1873) Skryabin et Shikhobalova, 1954; *C. gracilis* (Bellingham, 1844) Travassos, 1915; *C. hirundinis* (Rudolphi, 1819) Travassos, 1915; *C. indica* Subramanian, 1969; *C. javanensis* Wakelin, Schmidt et Kuntz, 1971; *C. kabatai* Inglis et Coles, 1963; *C. longistriata* Walton, 1924; *C. madseni* Wakelin, Schmidt et Kuntz, 1970; *C. manica* (Dujardin, 1845) Travassos, 1915; *C. margolisi* Moravec et McDonald, 1981; *C. nyrocinarum* Madsen, 1945; *C. orectolobi* Johnston et Mawson, 1951; *C. parusi* Wakelin, Schmidt et Kuntz, 1970; *C. phasianina* Kotlan, 1940; *C. pterophylli* Heinze, 1933; *C. recondita* Freitas et Lent, 1942; *C. recurvirostrae* Mawson, 1968; *C. rigidula* (Dujardin, 1845) Travassos, 1915; *C. serpentina* Harwood, 1932; *C. skerjabini* (Lubinova, 1947) comb. n.; *C. spinulosa* (Linstow, 1890) Travassos, 1915; *C. tenuissima* (Rudolphi, 1809) Yamaguti, 1941; *C. totani* (Linstow, 1875) Skryabin et Shikhobalova, 1954; *C. tridens* (Dujardin, 1845) Travassos, 1915; *C. uruguayensis* Calzada, 1937; *C. vazi* Freitas, 1933; *C. venusta* Freitas et Mendonça, 1958; *C. wickinsi* Ogden, 1965.

Comments: Skryabin et al. (1954, 1957) determined a new type species for the genus *Capillaria*, *C. obsignata* (Madsen, 1945), instead of *C. anatis* (Schrank, 1790); this proceeding was, however, in contradiction with the international rules (ICZN) (see Moravec 1981). The species listed now in this genus represent a considerably heterogeneous group, this being reflected also by a wide range of their hosts. Future studies will apparently result in breaking up this group into additional independent genera.

## 11. genus *Eucoleus* Dujardin, 1845

(Syn.: *Ritaklossia* Freitas, 1959)

Diagnosis: Caudal lateral alae in male absent; posterior end of male narrowed, with rudimentary pseudobursa formed by two minute, rounded, posteriorly directed lateral lobes connected between each other by reduced dorsal cuticular membrane; spicule slender, moderately sclerotized and, accordingly, little distinct (sometimes indistinct); spicular sheath long, densely covered by cuticular spines; vulva not elevated; parasites of respiratory system and mucous cover of oesophagus, oral cavity and stomach of birds and mammals.

Type species: *E. aerophilus* (Creplin, 1839) Dujardin, 1845

Other species: *E. annulatus* (Molin, 1858) López-Neyra, 1947; *E. bacillatus* (Eberth, 1863) López-Neyra, 1947; *E. baskakowi* Schulz, 1929; *E. boekmi* (Supperer, 1953) comb. n.; *E. cairinae* (Freitas et Almeida, 1935) López-Neyra, 1947; *E. contortus* (Creplin, 1839) Gagarin, 1951; *E. didelphis* (Butterworth et Beverley-Burton, 1977) comb. n.; *E. dispar* (Dujardin, 1845) López-Neyra, 1947; *E. dubius* (Travassos, 1917) López-Neyra, 1947; *E. eberthi* (Freitas et Lent, 1935) López-Neyra, 1947; *E. fluminensis* (Freitas, 1946) López-Neyra, 1947; *E. frugilegi* (Czapliński, 1962) comb. n.; *E. gastricus* (Baylis, 1926) López-Neyra, 1947; *E. garfai* (Gallego et Mas-Coma, 1975) comb. n.; *E. lemni* (Retzius, 1841) Skryabin, Shikhobalova et Orlov, 1957; *E. lophortygis* (Baylis, 1934) López-Neyra, 1947; *E. marii* (Rukhlyadev, 1946) comb. n.; *E. medjerdae* (Bernard, 1964) comb. n.; *E. oesophagicola* (Soltys, 1952) Skryabin et Shikhobalova, 1954; *E. penidoi* (Freitas et Almeida, 1935) López-Neyra, 1947; *E. perforans* (Kotlan et Orosz, 1931) López-Neyra, 1946; *E. procyonis* (Pence, 1975) comb. n.; *E. raillieti* López-Neyra, 1946; *E. rickardi* (Beveridge et Barker, 1975) comb. n.; *E. schvalovoj* Kontrimavichus, 1963; *E. spiralis* (Molin, 1858) comb. n.; *E. suppereri* Kutzer, Frey et Kotremba, 1980; *E. thomascameroni* (Mawson, 1969) comb. n.; *E. trilobus* (Linstow, 1875) López-Neyra, 1946; *E. urotrichi* (Ohbayashi, Masegi et Kubota, 1972) comb. n.; *E. vanelli* (Rudolphi, 1819) López-Neyra, 1947.

Comments: The morphology of the type species of *Ritaklossia*, *R. penidoi* (Freitas et Almeida, 1935), indicates its appartenance to the genus *Eucoleus* and, consequently, *Ritaklossia* Freitas, 1959 becomes a synonym of the genus *Eucoleus* Dujardin, 1845.

## 12. genus *Pterothominx* Freitas, 1959

(Syn.: *Armocapillaria* Gagarin et Nazarova, 1966)

Diagnosis: Caudal lateral alae in male present, well developed; posterior end of male provided with fairly large membranous bursa supported on either side by one or two narrow lateral projections; spicule well sclerotized; spicular sheath covered by minute spines or sclerotized protuberances; vulvar appendage present or absent; parasites of intestine and stomach of birds and mammals.

Type species: *P. meleagrisgallopavo* (Barile, 1912) Freitas, 1959

Other species: *P. angrensis* (Freitas, 1934) comb. n.; *P. erinacei* (Andreiko, 1969) comb. n.; *P. jamaicanensis* (Webster, 1971) comb. n.; *P. moschiferi* (Gagarin et Nazarova, 1966) comb. n.; *P. neopulchra* (Babos, 1954) comb. n.; *P. pulchra* (Freitas, 1934) comb. n.; *P. sadovskoi* (Morosov, 1956) comb. n.; *P. wavilovoi* (Skryabin, Shikhobalova et Orlov, 1957) comb. n.

Comments: This genus seems to include clean-cut morphological groups of species associated with the types of their hosts; accordingly, subsequent studies might lead to separation of the genus *Armocapillaria* Gagarin et Nazarova, 1966, now considered a synonym of *Pterothominx*, or, contingently, to erection of one or more additional genera.

## 13. genus *Aonchotheca* López-Neyra, 1947

Diagnosis: Caudal lateral alae in male present, well developed; posterior end of male provided with membranous bursa supported by one or more pairs of narrow, elongate, often ventrally bent lateral projections; spicule present, sometimes indistinct due to insufficient sclerotization; spicular sheath nonspiny; vulvar appendage absent or present; parasites of digestive tract of mammals, less frequently birds and amphibians.

Type species: *A. putorii* (Rudolphi, 1819) López-Neyra, 1947

Other species: *A. annulosa* (Dujardin, 1845) López-Neyra, 1947; *A. armeniaca* (Kirschenblatt, 1939) comb. n.; *A. baylisi* (Quentin, 1966) comb. n.; *A. bilobata* (Bhalerao, 1933) comb. n.; *A. bovis* (Schnyder, 1906) comb. n.; *A. brevipes* (Ransom, 1911) comb. n.; *A. buccalis* (Yamaguti, 1943) comb. n.; *A. bursata* (Freitas et Almeida, 1934) comb. n.; *A. caprae* (Sathianesan et Peter, 1972) comb. n.; *A. caudinflata* (Molin, 1858) comb. n.; *A. corneti* (Baer, 1959) comb. n.; *A. cubana* (Freitas et Lent, 1937) comb. n.; *A. erinacei* (Rudolphi, 1819) López-Neyra, 1947; *A. euryali* (Ricci, 1949) comb. n.; *A. exilis* (Dujardin, 1845) comb. n.; *A. fidelii* (Rutkowska, 1980) comb. n.; *A. gastrovici* (Pigolkin, 1965) comb. n.; *A. italica* (Ricci, 1949) comb. n.; *A. martinezi* (Caballero, 1942) comb. n.;

*A. megrelica* (Rodonaya, 1947) comb. n.; *A. minuta* (Chen, 1937) comb. n.; *A. myoxinitelae* (Diesing, 1851) comb. n.; *A. murissylvatici* (Diesing, 1851) López-Neyra, 1947; *A. mustelorum* (Cameron et Parnell, 1933) comb. n.; *A. nycticeiysi* (Agrawal, 1965) comb. n.; *A. okapi* (Leiper, 1935) comb. n.; *A. palmata* (Chandler, 1938) López-Neyra, 1947; *A. papuensis* (Copland, 1975) comb. n.; *A. paranalis* (Forstner et Geisel, 1980) comb. n.; *A. pereirai* (Freitas et Lent, 1935) comb. n.; *A. petrovi* (Rukhlyadeva, 1946) comb. n.; *A. philippinensis* (Chitwood, Valesquez et Salazar, 1968) comb. n.; *A. phyllo-nycteris* (Barus et Valle, 1967) comb. n.; *A. plathyspicula* (Pigolkin, 1965) comb. n.; *A. pintoii* (Freitas, 1934) comb. n.; *A. rara* (Ricci, 1949) comb. n.; *A. rhinolophi* (Mészáros, 1973) comb. n.; *A. riukiensis* (Shoho et Machida, 1979) comb. n.; *A. rivarolai* (Lent, Freitas et Proenca, 1946) comb. n.; *A. romana* (Ricci, 1949) comb. n.; *A. speciosa* (Beneden, 1873) comb. n.; *A. tamiastriati* (Read, 1949) comb. n.; *A. viguerasi* (Freitas et Lent, 1937) comb. n.; *A. vietnamensis* (Mészáros, 1973) comb. n.; *A. wioletti* (Rukhlyadeva, 1950) comb. n.

Comments: The genus *Aonchotheca* represents a very heterogeneous group of species, consisting of rather distinct morphological groups according to the type of their hosts (bats, carnivores, birds, amphibians, etc.); in future some of them may prove to be justified independent genera.

#### 14. genus *Calodium* Dujardin, 1845

(Syn.: *Hepaticola* Hall, 1916)

Diagnosis: Caudal lateral alae in male present, well developed; posterior end of male rounded, provided with two small lobular lateral papillae; dorsal cuticular membrane absent; spicule medium-sized, spherical in transverse section, sometimes little sclerotized; spicular sheath nonspiny; vulvar appendage present or absent; tissue parasites (spleen, liver) of mammals.

Type species: *C. splenaecum* (Dujardin, 1843) Dujardin, 1845

Other species: *C. cholidicola* (Soltys, 1952) comb. n.; *C. hepaticum* (Bancroft, 1893) comb. n.; *C. soricicola* (Yokogawa in Nischigori, 1924) comb. n.

#### 15. genus *Gessyella* Freitas, 1959

This genus was established by Freitas (1959) for *Capillaria latridopsis* Johnston et Mawson, 1945 from Australian fishes and it should differ from other genera mainly

Table 1. Distribution of genera of Capillariidae in various classes of the host vertebrates

Genus	Pisces	Amphibia	Reptilia	Aves	Mammalia
<i>Gessyella</i>	+	—	—	—	—
<i>Freitascapillaria</i>	+	—	—	—	—
<i>Capillostrongyloides</i>	+	—	—	—	—
<i>Schulmanella</i>	+	+	—	—	—
<i>Paracapillaria</i>	+	+	+	—	—
<i>Capillaria</i>	+	+	+	+	+
<i>Pseudocapillaria</i>	+	—	+	+	+
<i>Baruscapillaria</i>	—	—	—	+	+
<i>Echinocoleus</i>	—	—	—	+	+
<i>Eucoleus</i>	—	—	—	+	+
<i>Pterothominx</i>	—	—	—	+	+
<i>Aonchotheca</i>	—	+	—	+	+
<i>Liniscus</i>	—	—	—	—	+
<i>Pearsonema</i>	—	—	—	—	+
<i>Calodium</i>	—	—	—	—	+
<i>Skrjabinocapillaria</i>	—	—	—	—	+

in having caudal lateral alae in the male and eggs enclosed in special capsules. The description of *C. latridopsis* is, however, very poor and probably erroneous in some respects and, accordingly the existence of the genus *Gessyella* is considerably doubtful.

#### 16. genus *Skrjabinocapillaria* Skarbilovich, 1946

The genus *Skrjabinocapillaria* was established by Skarbilovich (1946) for the species *S. eubursata* Skarbilovich, 1946 from bats in the USSR; it is characterized mainly by the absence of a spicule, by nonspiny spicular sheath and by the presence of caudal lateral alae in the male. However, due to inadequate description of *S. eubursata*, which is probably erroneous in some respects (? absence of spicule), the systematic position of *Skrjabinocapillaria* remains hitherto unclear. Further studies may prove identity of this genus with *Aonchotheca*.

#### KEY TO GENERA AND SUBGENERA OF CAPILLARIIDAE

- 1 Eggs enclosed in special capsules . . . . . *Gessyella*
- Eggs without special capsules . . . . . 2
- 2 Lateral caudal alae in male present . . . . . 3
- Lateral caudal alae in male absent . . . . . 6
- 3 Posterior end of male provided with two lateral papillae; dorsal cuticular membrane absent; spicular sheath nonspiny; tissue parasites (spleen, liver) of mammals . . . . . *Calodium*
- Posterior end of male provided with membranous bursa supported by one or more pairs of elongate lobular projections; spicular sheath nonspiny or spiny; parasites of digestive tract of birds and mammals . . . . . 4
- 4 Spicular sheath covered by minute spines or sclerotized protuberances . . . . . *Pterothominx*
- Spicular sheath unequipped, smooth . . . . . 5
- 5 Spicule present . . . . . *Aonchotheca*
- Spicule absent . . . . . *Skrjabinocapillaria*
- 6 Spicule absent, spicular sheath nonspiny; posterior end of male laterally expanded, nude, without membranous bursa, papillae or lobes; parasites of digestive tract of fishes . . . . . *Freitascapillaria*
- Spicule present, spicular sheath nonspiny or spiny; posterior end of male provided with membranous bursa, papillae or lobes . . . . . 7
- 7 Posterior end of male rounded, provided with two lateral, dorsolateral or ventrolateral lobes; membranous bursa absent . . . . . 8
- Posterior end of male with membranous bursa, sometimes reduced to narrow membrane connecting dorsally two lateral lobes of posterior body end . . . . . 9
- 8 Spicular sheath spiny . . . . . *Capillaria*
- Spicular sheath nonspiny . . . . . *Pseudocapillaria* (*Pseudocapillaria*)
- 9 Spicular sheath nonspiny . . . . . 10
- Spicular sheath spiny . . . . . 15
- 10 Posterior end of male provided with small membranous bursa supported by either two small round dorsolateral projections or two slender digital dorsolateral projections bent to ventral side; parasites of urinary bladder and kidneys of mammals . . . . . 11
- Bursa of other type; parasites of digestive tract . . . . . 12
- 11 Bursa of male supported by two small round dorsolateral projections; parasites of small mammals . . . . . *Liniscus*
- Bursa of male supported by two slender digital dorsolateral projections bent to ventral side; parasites of carnivores . . . . . *Pearsonema*
- 12 Membranous bursa of male considerably reduced; posterior end of male provided with two large spherical ventrolateral lobes connected between each other by short cuticular membrane, not exceeding or only slightly exceeding posterior border of lobes . . . . . *Pseudocapillaria* (*Ichthyocapillaria*)
- Membranous bursa of male well developed, considerably exceeding posterior margin of body; posterior body end of male of other type . . . . . 13

- 13 Membraneous bursa of male supported by two dorsolateral rib-like projections, bent along posterior margin of bursa; two large sessile adanal or postanal papillae present; parasites of digestive tract of fishes, reptiles and apparently also amphibians . . . . . *Paracapillaria*  
— Membraneous bursa of male of other type, without dorsolateral rib-like projections . . . . . 14
- 14 Membraneous bursa of male unlobed, supported by two short, simple, wide round subventral projections situated below cloacal opening; stomach parasites of fishes . . . *Capillostrongyloides*  
— Membraneous bursa of male unlobed or lobed, supported on either side by one, more rarely two small round lobes, often narrowed at their base; each lobe provided with small projection, usually ventrally bent; parasites of intestine and stomach of birds and mammals . . . *Baruscapillaria*
- 15 Posterior end of male narrowed, with rudimentary bursa formed by two small, round, posteriorly directed lateral lobes connected between each other by short dorsal cuticular membrane; spicule very slender, little sclerotized and accordingly badly observable; parasites of respiratory system and mucous cover of oesophagus, mouth cavity and stomach of birds and mammals . . . *Eucoleus*  
— Cuticular membrane of male bursa well developed, bursa of other type; spicule well sclerotized; parasites of intestine, less often of oesophagus or liver . . . . . 16
- 16 Membraneous bursa of male supported on either side by short, round or more elongate lobular dorsolateral projection; dorsal caudal projection absent; intestinal parasites of birds and mammals . . . . . *Echinocoleus*  
— Membraneous bursa of male supported by pair of rib-like dorsolateral projections, bent along posterior margin of bursa; dorsal caudal projection present or absent; pair of large adanal sessile papillae present; parasites of intestine and liver of fishes and amphibians . . . . . 17  
. . . . . *Schulmanella*
- 17 Bursa of male with well developed dorsal caudal projection; stichosome consisting of single row of stichocytes; intestinal parasites of fishes . . . . . *Schulmanella (Piscicapillaria)*  
— Bursa of male without dorsal caudal projection; stichocytes arranged in three longitudinal rows; parasites of liver of fishes . . . . . *Schulmanella (Schulmanella)*  
— Bursa of male without dorsal caudal projection; stichocytes arranged in one longitudinal row (only some stichocytes of posterior stichosome end may be doubled); parasites of intestine and liver of amphibians . . . . . *Schulmanella (Amphibiocapillaria)*

**Addendum.** Since this paper was submitted for publication, another new capillariid genus, *Pseudocapillarioides*, has been erected by Moravec and Cosgrove (Moravec F., Cosgrove G. E.: *Pseudocapillarioides xenopi* gen. et sp. nov. (Nematoda: Capillariidae) from the skin of the South African clawed frog, *Xenopus laevis* Daud. Rev. Zool. afr. 96: 129—137, 1982).

## ПРЕДЛОЖЕНИЕ НОВОГО СИСТЕМАТИЧЕСКОГО ПОСТРОЕНИЯ НЕМАТОД, ОТНОСЯЩИХСЯ К СЕМЕЙСТВУ CAPILLARIIDAE

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**Резюме.** Предлагается новое построение родов внутри семейства Capillariidae на основе переоценки применяемых в таксономии признаков. Следующие роды признаются валидными: *Schulmanella* Ivashkin, 1964 (подроды *Schulmanella* Ivashkin, 1964, *Piscicapillaria* subgen. n. и *Amphibiocapillaria* subgen. n.), *Paracapillaria* Mendonça, 1963, *Capillostrongyloides* Freitas et Lent, 1935, *Pseudocapillaria* Freitas, 1959 (подроды *Pseudocapillaria* Freitas, 1959 и *Ichthyocapillaria* subgen. n.), *Freitascapillaria* gen. n., *Baruscapillaria* gen. n., *Liniscus* Dujardin, 1845, *Pearsonema* Freitas et Mendonça, 1960, *Capillaria* Zeder, 1800, *Echinocoleus* López-Neyra, 1947, *Eucoleus* Dujardin, 1845, *Pterothominx* Freitas, 1959, *Aonchotheca* López-Neyra, 1947 и *Calodium* Dujardin, 1845. Дается новое определение раньше установленных родов. Систематическое положение родов *Gessyella* Freitas, 1959 и *Skrjabinocapillaria* Skarbilovich, 1946 пока не объяснено. Автор вновь свел в синонимы роды *Ritaklassia* Freitas, 1959 (= *Eucoleus*), *Armocapillaria* Gagarin et Nazarova, 1966 (= *Pterothominx*) и *Hepaticola* Hall, 1916 (= *Calodium*) и виды *Hepaticola bakeri* Mueller et Van Cleave, 1932 (= *Pseudocapillaria catostomi* (Pearse, 1924)) и *Pseudocapillaria nuda* Mendonça, 1963 (= *Freitascapillaria maxillosa* (Vaz et Pereira, 1934)); даны новые комбинации названий видов. Приведена таблица для определения родов и подродов семейства Capillariidae.

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**E. V. Gvozdev (Ed.): Parazity — komponenty vodnykh i nazemnykh biotsenozov Kazakhstana. (Parasites as components of water and ground biocenoses of Kazakhstan.)**  
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The volume edited by a group of editors, Panin, Belyakova and Sidorov, headed by Academician Gvozdev includes 16 original scientific papers written by 20 authors. There are the results of parasitological research of both purely theoretical and practical orientation. Only one paper deals with protozoans. Fedoseenko and Romanova found in *Rhombomys opimus* an interesting species of the genus *Sarcocystis* and though they did not give it a new name, obviously a new species is involved. A majority of papers (9) deal with the systematics, morphology and ecology of trematode species. Most of them are devoted to the complex of biocenological data from Kurgaldhim Lake system of Central Kazakhstan. Many years' investigations concern the following subjects: the ways of formation of metacercariae fauna of fishes (Sidorov), cercariae of lakes (Belyakova), dynamics of interrelation between the larvae of trematodes, mollusks and factors of the environment (Belyakova), leeches and their significance in the circulation of Strigeidae (Zhatkanbaeva, Akhmetova), biology and dynamics of the larval population of *Prosthogonimus cuneatus* in the water reservoirs (Kukashev, Belyakova), ecological characteristics and spreading of Lymnaeidae — intermediate hosts of *Orientobilharzia* (Uvalieva, Lavrov). Other papers on trematodes deal with ultrastructures of the intestine of *Corrigia* trematodes, comparative histology of sporocysts of *Leucochloridium paradoxum* and *L. problematicum* (Nacheva, Soboleva, Osipovskaya) and they concentrate their attention to the question of fine structure of the tegument of sporocyst and cercariae of *Dicrocoelium*

*lanceatum* (Nesterenko, Ždárská, Fedoseenko). The cestodes are dealt with in biocenological studies in the host-parasitic system "larvae of cestodes-crustacean" in biocenosis (Dobrokhotova), Hymenolepididae of snipes (Maksimova) and ecological aspects of interrelations among copepods, ostracods and hydrophytes in the water (Dobrokhotova). Of markedly practical orientation is the study "The apparatuses for determination of the viability of cestode eggs and infected crustaceans (Akaev). Two papers dealing with the systematics and taxonomy deserve particular attention. In the first one, "Principles of systematics and system of the family Dicrocoeliidae" by Panin, the family Dicrocoeliidae Looss, 1899 is newly divided into subfamilies Dicrocoeliinae Looss, 1899, Eutrematinae Panin, 1971, Proacetabulorchinae Odening, 1964 and Infidinae Travassos, 1944 and the generic composition of these taxons is amended. Of great value is the paper by Podgornova, Sokolova "Karyological researches of *Trichinella spiralis* and *T. nelsoni*" demonstrating that there are no differences between these two species and supporting thus recent results by Baruš et al. (Folia parasit. (Praha) 26: 97—101, 1979) obtained by scanning electron microscopy.

It may be concluded that the volume, which is a continuation of previous results achieved by the parasitological school in Kazakhstan, documents its further development and progress. It is to regret that foreign language abstracts are not attached to individual papers.

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