KEYS TO THE TREMATODA

Volume 3

Edited by
Rodney A. Bray,
David I. Gibson and
Arlene Jones

NATURAL HISTORY MUSEUM

cabi
www.cabi.org

21 Family Troglotrematidae Odhner, 1914

D. Blair,[1] V.V. Tkach[2] & D.P. Barton[1,3]

[1]*School of Marine and Tropical Biology, James Cook University, Townsville, Queensland 4811, Australia;* [2]*Department of Biology, University of North Dakota, Grand Forks, ND 58202, USA;* [3]*Present address: Parasitology Section, South Australia Museum, North Terrace, Adelaide, South Australia 5001, Australia*

Introduction

Troglotrematids are small to medium-sized gorgoderoids found in the lumen of the intestine, cavities of the upper respiratory tract, kidneys or liver of mammals and seabirds. Distinctive morphological features uniting all genera in the family are few, perhaps indicating that the family is not a natural taxon. All members have oral and ventral suckers, a pair of symmetrical testes and caeca that are not markedly sinuous. The uterus is mostly or entirely in the hindbody, the seminal vesicle is commonly bipartite and the genital pore is typically just posterior to the ventral sucker. Included in the family are the important genera *Nanophyetus* Chapin, 1927 (vector of a rickettsial disease of dogs in North America and common parasites of humans in East Siberia) and *Troglotrema* Odhner, 1914 (associated with skull lesions in mustelids).

The Troglotrematidae Odhner, 1914, Nanophyetidae Wallace, 1935 and Paragonimidae Dollfus, 1939 have a complicated, shared history. At times, a single family, the Troglotrematidae, has been accepted, often subdivided in various ways. Recently, the three nominal families have been generally regarded as distinct entities. Here, we do not recognize the Nanophyetidae as distinct and place its genera within the Troglotrematidae.

Odhner (1914) proposed the Troglotrematidae (as Troglotremidae) to contain five genera: *Pholeter* Odhner, 1914, *Collyriclum* Kossack, 1911, *Troglotrema, Paragonimus* Braun, 1899 and *Renicola* Cohn, 1904 (the last added in an addendum). They all live in cysts in tissues or in cavities in the body other than the lumen of the digestive tract.

Odhner figured and described the type-species, *T. acutum* (Leuckart, 1842), as possessing a caudal projection or cone. Baer (1931a) stated such a projection to be absent from numerous specimens he examined and implied that it might have been a fixation artefact in Odhner's specimen. Other authors have generally not remarked on its presence. Andreiko (1973) stated it to be present in *T. srebarni* Genov, 1964, although Genov (1964) apparently did not mention it. Unfortunately, Odhner's drawing of a presumably atypical specimen of *T. acutum* has been reproduced frequently (e.g. Fuhrmann, 1928; Yamaguti, 1971).

Baer (1931b) added to the Troglotrematidae the new subfamily Nephrotrematinae Baer, 1931 to house *Nephrotrema* Baer, 1931 from the kidneys of mammals. Wallace (1935) added the intestinal parasites *Nanophyetus* Chapin, 1927 and his new genus *Sellacotyle* Wallace, 1935 in a new subfamily, the Nanophyetinae Wallace, 1935.

Dollfus (1939) considered the Troglotrematidae, as then constituted, to be an unnatural group and proposed that its genera, listed above, could be distributed among six families: Paragonimidae; Collyriclidae Ward, 1917; Pholeteridae Dollfus, 1939; Renicolidae Dollfus, 1939; Nanophyetidae (presumably containing only *Nanophyetus* and *Sellacotyle*); and Troglotrematidae (containing only *Troglotrema* and *Nephrotrema*). Dollfus' arrangement offered a simple means of distinguishing between the nominal families Troglotrematidae and Nanophyetidae. Genera included by him in the former family have a Y-shaped excretory vesicle and live in sites distant from the intestine; those in the latter have a more-or-less saccate excretory vesicle and occur in the intestine. This convenient distinction has become less clear as additional genera have been added to the families. Some genera with a bifurcate excretory vesicle live in the intestine (e.g. *Macroorchis* Ando, 1919 (first placed tentatively in a family, the Troglotrematidae, by Witenberg, 1932); *Paragono* Pearse, 1930 (placed by its author in the Troglotrematidae); and *Xiphidiotrema* Senger, 1953 (placed by its author in the Troglotrematidae)). Further evidence that these two nominal families are not distinct from one another comes from cercarial morphology and from molecular sequences (see below).

Cercariae are known for one or more species of *Nephrotrema, Troglotrema, Skrjabinophyetus* Dimitrova & Genov, 1967, *Nanophyetus* and *Sellacotyle*. In each case, the cercaria has a cluster of gland-cells arranged radially around a ventral opening near the posterior end of the body (discussed and figured by Vogel & Voelker, 1978). This is a unique feature uniting this group and distinguishing it from *Paragonimus*, the sole genus in the Paragonimidae (see Blair, Chapter 19, this volume). Furthermore, Bayssade-Dufour & Jourdane (1976) noted similarities in cercarial chaetotaxy between *Nephrotrema* (Troglotrematidae *sensu* Dollfus) and *Skrjabinophyetus* (Nanophyetidae *sensu* Dollfus) consistent with them belonging to the same family.

We also have molecular evidence favouring synonymy of the Troglotrematidae and Nanophyetidae. Relevant sequences are from the nuclear 28S rRNA gene of *Nephrotrema truncatum* (Leuckart, 1842), *S. neomydis* Dimitrova & Genov, 1967, *Nanophyetus salmincola* (Chapin, 1926) and three species of *Paragonimus*. All other available sequences from members of the Gorgoderoidea (see fig. 6 in Olson *et al.*, 2003) were included in the analysis. In the phylogenetic tree (Fig. 21.1, details of methods in caption), *Nephrotrema truncatum* (Troglotrematidae) and *S. neomydis* (Nanophyetidae) appear as sisters with *Nanophyetus salmincola* (Nanophyetidae), sister to these two in turn. The three species of *Paragonimus* form a sister clade to this. Branch lengths between all genera, including *Paragonimus*, are no greater than between genera of several well-established families on the tree (e.g. Dicrocoeliidae Looss, 1899) and less than among, for example, genera of the Gorgoderidae Looss, 1899. This shows that the troglotrematids and nanophyetids are scarcely diverged enough to merit separate family status. We shall retain *Paragonimus* in a separate, but sister, family, the Paragonimidae, in this volume (see Blair, Chapter 19, this volume). Despite the blurred line separating the Troglotrematidae and the Nanophyetidae, many authors have retained both as distinct families (e.g. Baer & Joyeux 1961; Yamaguti, 1971).

The validity of *Nanophyetus, Sellacotyle, Pseudotroglotrema* Yamaguti, 1971 and *Skrjabinophyetus*, and their species, needs careful consideration. Chapin (1926) described *Nanophyes salmincola* Chapin, 1926 from the intestines of dogs. The generic name *Nanophyes* was subsequently found to be pre-occupied and was replaced by *Nanophyetus* in 1927 (Chapin, 1927). Chapin placed his genus in the Heterophyidae Leiper, 1909. Although some later authors (e.g. Skrjabin & Podjapolskaja, 1931) agreed with this placement, Witenberg (1932) pointed out the similarity between *Nanophyetus* and *Troglotrema* and regarded the former as a junior synonym of the latter.

Wallace (1933), in an abstract, coined the name *Troglotrema mustelae* Wallace, 1933 for a worm from the intestine of mustelids in the USA. He did not provide a description until 1935,

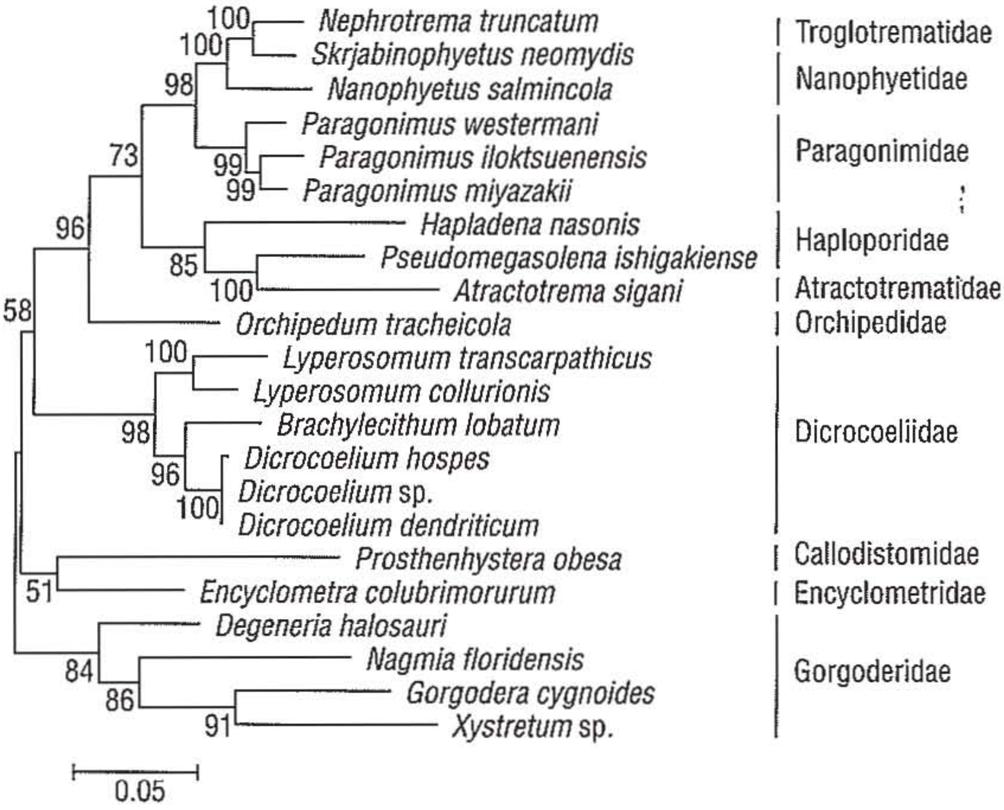


Fig. 21.1. Midpoint-rooted maximum-likelihood tree inferred from partial 28S ribosomal RNA sequences from all available members of the Gorgoderoidea (*sensu* Olson *et al.*, 2003). Sequences were aligned using ClustalW. All sites with gaps in any sequence were subsequently removed, leaving 1169 sites for analysis. Tree-Puzzle 5.2 (Schmidt *et al.*, 2002) was used to find the tree. This program estimates a number of parameters from the data as follows: number of constant sites 673 (= 57.6% of all sites); most appropriate model of substitution is HKY (Hasegawa *et al.*, 1985); transition/transversion parameter (estimated from data set) is 2.61 (SE 0.21). All sequences passed the test for similar base composition. Numbers on branches indicate the percentage of (1000) puzzling steps in which that bipartition was found.

at which time he (Wallace, 1935) erected *Sellacotyle* to contain it. A second species of *Sellacotyle, S. vitellosa* Sogandares-Bernal, 1961, was described from mustelids in Louisiana by Sogandares-Bernal (1961). *Sellacotyle* and *Nanophyetus* are very similar. Wallace (1935) separated them on the basis of body-size, the presence of a cirrus-sac in the latter (absent in the former, the bipartite seminal vesicle lying free in the parenchyma) and the length of the caeca (extending at most to the posterior edge of the ventral sucker in the former genus but posterior to this in the latter). Of these three features, the first and last seem hardly of generic significance, leaving only the presence or absence of a cirrus-sac to distinguish between the genera. Wallace (1935) had apparently overlooked the description of *N. schikhobalowi* Skrjabin & Podjapolskaja, 1931 by Skrjabin & Podjapolskaja (1931), which implied that a cirrus-sac was absent from this species. Witenberg (1932) considered Skrjabin & Podjapolskaja (1931) to have been in error in this regard. Later Russian authors (e.g. Filimonova, 1965) reported a cirrus-sac in *N. schikhobalowi.* It seems that the presence or absence of a cirrus-sac is a valid means of separating these genera.

Pseudotroglotrema Yamaguti, 1971 was erected for *P. asadai* Yamaguti, 1971, found in the intestine of a stray dog near Tokyo. Yamaguti (1971) implied that *Pseudotroglotrema* can be distinguished from *Nanophyetus* in that the base of the cirrus-sac of the latter is anterior to the genital pore. This does not always seem to be the situation (e.g. fig. 1 in Skrjabin & Podjapolskaja, 1931). Another feature used to distinguish between them was the length of the caeca, extending posterior to the testes in *Pseudotroglotrema*, whereas in *Nanophyetus* they do not reach the posterior margin of the testes. However, in *N. japonensis* Saito, Saito, Yamashita, Watanabe & Sekikawa, 1982 as redescribed by Saito (1985), the caeca extend almost to the posterior end of the body. The shape of the excretory vesicle is not known for *P. asadai*. From the published information, *P. asadai* can hardly be distinguished from *N. japonensis* except in body-size. We regard *Pseudotroglotrema* as a synonym of *Nanophyetus. P. asadai* was said to lack spines (Yamaguti, 1971), which is an unusual feature for a troglotrematid if correct: some species of *Paragono* also apparently lack spines.

Skrjabinophyetus Dimitrova & Genov, 1967 was erected for a small worm, *S. neomydis*, from the intestine of soricids in Bulgaria. The species was subsequently described from southern France (Euzet & Jourdane, 1970) and Germany (Brendow, 1970). Brendow (1970) questioned the name of the type-species, preferring *S. repens* (Bregenzer, 1916). He based this on the similarity between *Cercaria repens* Bregenzer, 1916 and the cercaria he demonstrated to be that of a *Skrjabinophyetus* species. Subsequent workers have not followed this suggestion, and we shall not do so here. Jourdane (1977) pointed out that Brendow (1970) included features of cercariae of both *S. neomydis* and *Nephrotrema truncatum* in his description. A striking feature of *S. neomydis* is the large oral sucker, the diameter of which is about three times that of the ventral sucker. Jourdane (1973a) described a second species, *S. soricis* Jourdane, 1973, from southern France. This species differs markedly from the type-species in being much smaller, in having ventral and oral suckers of near-equal size and in the anterior extent of the vitelline follicles, which occur up to the level of the oral sucker. We consider that *S. soricis* can hardly be distinguished from members of *Nanophyetus* and refer it to that genus as *N. soricis* n. comb. Jourdane (1977) described the cercariae of both nominal species of *Skrjabinophyetus*. These differ from each other, and from those of *Nanophyetus* and *Sellacotyle* species, in details of numbers of penetration gland-cells and in flame-cell formulae. The taxonomic significance of these differences is hard to evaluate. Bayssade-Dufour & Jourdane (1976) and Jourdane (1977) relied on cercarial chaetotaxy (based on the distribution of sensory endings on the tegument) for evidence that the two nominal *Skrjabinophyetus* species were congeners. However, they only had comparative data for one other troglotrematid, *Nephrotrema truncatum*, making a definitive statement on relationships impossible.

Three genera included here were first noted as metacercariae in freshwater crustaceans from eastern Asia. In each case, rudiments of the gonads and associated organs were sufficiently developed to indicate adult morphology clearly, and in two cases adults were raised in experimentally infected mammals. *Macroorchis* Ando, 1919 was erected by Ando (1919 – in a published abstract from the ninth meeting of the Japanese Pathology Society) based on specimens developing experimentally in the intestines of various mammals fed metacercariae from freshwater crabs. Yamaguti (1958b) placed *Macroorchis* in his new nanophyetid subfamily, Macroorchiinae Yamaguti, 1958. The early Japanese literature on this genus was summarized by Dollfus (1925).

Nakagawa (1917) briefly described and figured, from crabs in Taiwan, various developmental stages of metacercariae he regarded as belonging to *Paragonimus westermani* (Kerbert, 1878). Subsequently, he (Nakagawa, 1918) named a new genus and species for these, *Stephanolecithus parvus* Nakagawa, 1918. A brief mention in English is given in Nakagawa (1919). Adults were obtained from the liver and gall-bladder of experimentally infected mammals. A fuller description, including a figure, was given by Nakagawa (1958, details in English from Yamaguti, 1975). In the title of this paper, he appeared to ascribe authorship of the genus and species names to

Goto. However, this was apparently because he had sought advice from Goto as to an appropriate name: Nakagawa remains the appropriate author. Nakagawa (1958) compared his genus with *Prosthogonimus* Lühe, 1899 (Prosthogonimidae Lühe, 1909) but regarded it as very distinct. Yamaguti (1958b), at that time unaware of Nakagawa's (1958) paper, placed the genus in the Opisthorchiidae Looss, 1899, subfamily Stephanolecithinae Yamaguti, 1958. Subsequently, Yamaguti (1971) transferred *Stephanolecithus* Nakagawa, 1918 and the Stephanolecithinae to the Troglotrematidae. Lee (1965), also apparently unaware of Nakagawa's work, described two species of his new genus *Beaveria* Lee, 1965 from the liver and small intestine of Malaysian rats and assigned the genus to the Troglotrematidae in his new subfamily Beaveriinae Lee, 1965. Yamaguti (1971) pointed out that *Beaveria* is clearly a synonym of *Stephanolecithus*. Betterton & Lim (1975) questioned the troglotrematid affinities of *Stephanolecithus* (as *Beaveria*) and also suggested, independently of Nakagawa (1958), that it might belong close to *Prosthogonimus*.

Pearse (1930) described *Paragono kelloggi* Pearse, 1930 based on encysted metacercariae with a Y-shaped excretory vesicle from estuarine crabs in China. Pearse placed it in the Troglotrematidae. Yamaguti (1971) erected for it the subfamily Paragoninae Yamaguti, 1971 and suggested that the definitive host for *Paragono* might be crab-eating mammals. However, adults of two species clearly belonging to *Paragono* were described by Zhang *et al.* (1984) from the intestine of seabirds in China. *Paragono* is the only troglotrematid genus to occur in birds.

Type-species of all remaining genera were based on adult specimens. *Xiphidiotrema lockerae* Senger, 1953 was described by Senger (1953) from adult worms in the intestine of shrews in the USA. Senger noted the similarity of his new genus with *Nephrotrema*. However, because in size and habitat it more closely resembled *Sellacotyle* and *Nanophyetus*, he placed it closer to the other two genera (in the Nanophyetinae). Yamaguti (1958b, 1971) preferred to ally it with *Nephrotrema*, presumably on the basis of its bifurcate excretory vesicle. Chin & Gu (1980) agreed, and went one step further, proposing that the Nephrotrematinae be raised to family rank to contain *Nephrotrema* and *Xiphidiotrema*.

Soricitrema baeri Bykhovskaya-Pavlovskaya, Vysotzkaya & Kulakova, 1970 was described from the kidneys of shrews in Russia (Bykhovskaya-Pavlovskaya *et al.*, 1970). Jourdane (1971) pointed out that the reported differences between this nominal species and *N. truncatum* were not sufficient even to recognize it as a separate species, let alone merit the erection of a new genus. *Soricitrema* is therefore regarded as a synonym of *Nephrotrema*.

The two genera that fit least well into the Troglotrematidae are *Paragono* and *Stephanolecithus*. Both are included here provisionally. *Paragono* is atypical in having the genital pore anterior to the ventral sucker and a branched or dendritic ovary. *Stephanolecithus* has the genital pore near the anterior end of the body and a more extensive uterus than is usually seen in troglotrematids.

Of the seven different subfamilies among which Yamaguti (1971) distributed the genera discussed here, only two contained more than one genus. We remain uncertain about the relationships between the genera, even those, such as *Nephrotrema* and *Xiphidiotrema*, placed in the same subfamily by Yamaguti (1971). Consequently, we prefer not to recognize any subfamilies.

Family Troglotrematidae Odhner, 1914

(Syns Troglotremidae [*sic*] Odhner, 1914; Nephrotrematinae Baer, 1931; Nanophyetinae Wallace, 1935; Stephanolecithinae Yamaguti, 1958; Macroorchiinae Yamaguti, 1958; Sellacotylinae Yamaguti, 1958; Beaveriinae Lee, 1965; Paragoninae Yamaguti, 1971)

Diagnosis: Body small to medium-sized, pyriform, fusiform or flattened, may be attenuated or rounded at either end. Tegument almost always armed. Oral sucker subterminal. Ventral sucker equatorial or pre-equatorial, usually similar in size to oral sucker. Prepharynx very short or absent. Pharynx present. Oesophagus short or long, or not apparent. Intestinal bifurcation at various levels between oral sucker and about one-third of body-length. Caeca two, simple, variable in length, sometimes not extending beyond ventral sucker. Testes two, often large and longer than wide, symmetrical or subsymmetrical, anterior or posterior (usually) to ventral sucker, often overlap it, rarely at posterior end of body, usually entire. Cirrus-sac present or absent; if absent, bipartite seminal vesicle free in parenchyma; if present, cirrus-sac may contain bipartite seminal vesicle. Genital pore usually in middle third of body immediately posterior to ventral sucker, exceptionally just anterior to ventral sucker or at anterior of body. Ovary median or submedian in middle third of body (rarely anterior to this), pre-, inter- or post-testicular, usually entire, rarely lobed. Laurer's canal usually present. Seminal receptacle often present, in form of expansion of oviduct, blind diverticulum from oviduct, canalicular or uterine. Uterus variable in extent, usually rather short and intercaecal or postcaecal and posterior to genital pore. Eggs small to large, numerous or few. Vitelline follicles variably distributed, typically extensive but sometimes very restricted. Excretory vesicle Y-, V- or I-shaped, or saccate; pore terminal. In tissue, body sinus or digestive tract of mammals and birds; cosmopolitan. Type-genus *Troglotrema* Odhner, 1914.

Key to genera

1a. Genital pore anterior or lateral to ventral sucker; posterior median indentation of body often present .... 2.

1b. Genital pore posterior to ventral sucker; posterior median indentation of body absent .... 3.

2a. Testes at posterior extremity; genital pore just anterior or anterolateral to ventral sucker .... *Paragono* Pearse, 1931. (Fig. 21.2)

Diagnosis: Body small, flattened, tapered anteriorly, rounded posteriorly, often with median indentation at posterior end. Tegument spined or not. Oral sucker small, subterminal. Ventral sucker equal to or larger than oral sucker, equatorial or slightly anterior to this. Oesophagus long, narrow. Intestinal bifurcation about midway between suckers. Caeca simple, narrow, terminate laterally close to anterior edges of testes. Testes large, symmetrical, lateral at posterior end, irregularly lobed. Cirrus-sac present, transverse, curved around anterior edge of, or dorsal to, ventral sucker, apparently contains bipartite seminal vesicle. Genital pore at, or just anterior to, left margin of ventral sucker. Ovary irregularly and deeply lobed, median, just posterior or posterodorsal to ventral sucker. Mehlis' gland posterior to ovary. Laurer's canal and seminal receptacle not known. Uterus extensive in postovarian region with loops passing to posterior end of body between testes. Eggs small, probably numerous. Vitelline follicles in lateral extracaecal fields anterior to testes in second and third quarters of body. Excretory vesicle apparently Y-shaped; pore terminal, opens into posterior median indentation if present. In intestine of seabirds (Charadriiformes); coastal China. Type-species *P. kelloggi* Pearse, 1930.

2b. Testes in mid-body, separated from posterior end by ends of caeca and vitelline follicles; genital pore beside oral sucker or pharynx .... *Stephanolecithus* Nakagawa, 1918. (Fig. 21.3)
(Syn. *Beaveria* Lee, 1965)

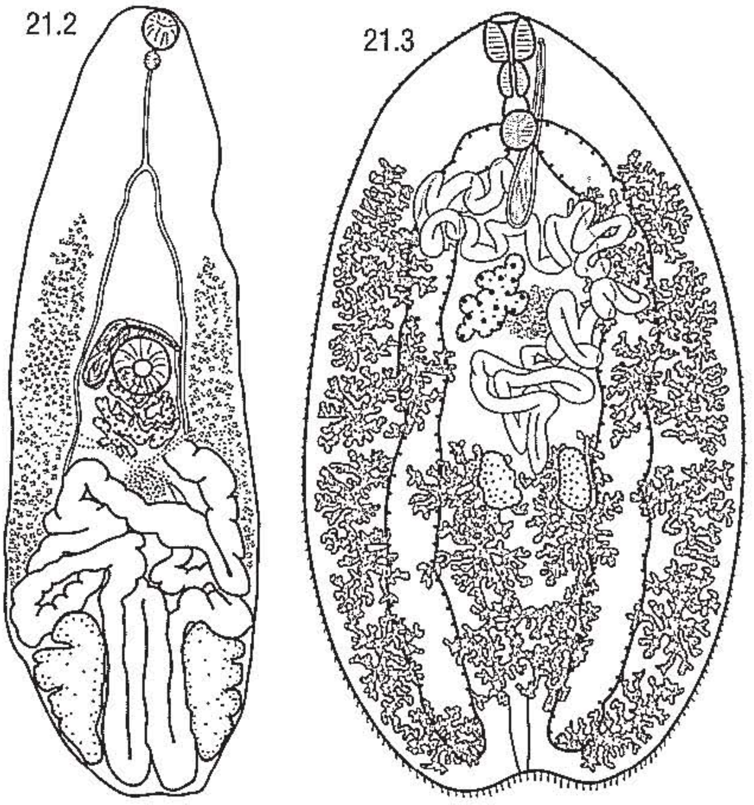


Fig. 21.2. *Paragono numenii* Zhang, Qiu & Li, 1984. Ventral view. After Zhang *et al.* (1984).
Fig. 21.3. *Stephanolecithus* as *Beaveria beaveri* Lee, 1965. Ventral view. After Lee (1965).

Diagnosis: Body small to medium-sized, flat, oval in ventral view, rounded posteriorly, where usually with conspicuous median indentation. Tegument spined. Oral sucker small, subterminal. Ventral sucker slightly smaller or larger than oral sucker, in anterior quarter of body. Oesophagus short. Caeca simple, sometimes follow slightly sinuous course, terminate close to posterior end. Testes symmetrical, intercaecal, entire or lobed, in mid-body. Cirrus-sac elongate, close to median line, with base dorsal or posterior to ventral sucker, tapers towards genital pore at left side of oral sucker or pharynx, contains elongate seminal vesicle, pars prostatica and ejaculatory duct from which cirrus may form. Ovary lobed or not, just dextrally submedian, between testes and ventral sucker. Mehlis' gland median to ovary. Laurer's canal present. Seminal receptacle present or absent, when present apparently a blind diverticulum from oviduct. Uterine loops mostly intercaecal between testes and ventral sucker, intrude into intertesticular region and may extend lateral to caeca. Metraterm short, dorsal to cirrus-sac. Eggs of medium size, numerous. Vitelline follicles extensive laterally and dorsolaterally, overlap caeca, may not extend anterior to ventral sucker and always absent from immediate vicinity of oral sucker and pharynx, often approach or reach median line posterior to testes. Excretory vesicle Y-shaped, with long stem bifurcating between testes; pore opens into terminal indentation if present. In small intestine and liver (probably gall-bladder and bile-ducts) of mammals (Rodentia), also in cats and dogs experimentally; China, Taiwan, Malaysia, Indonesia. Type-species *S. parvus* Nakagawa, 1918.

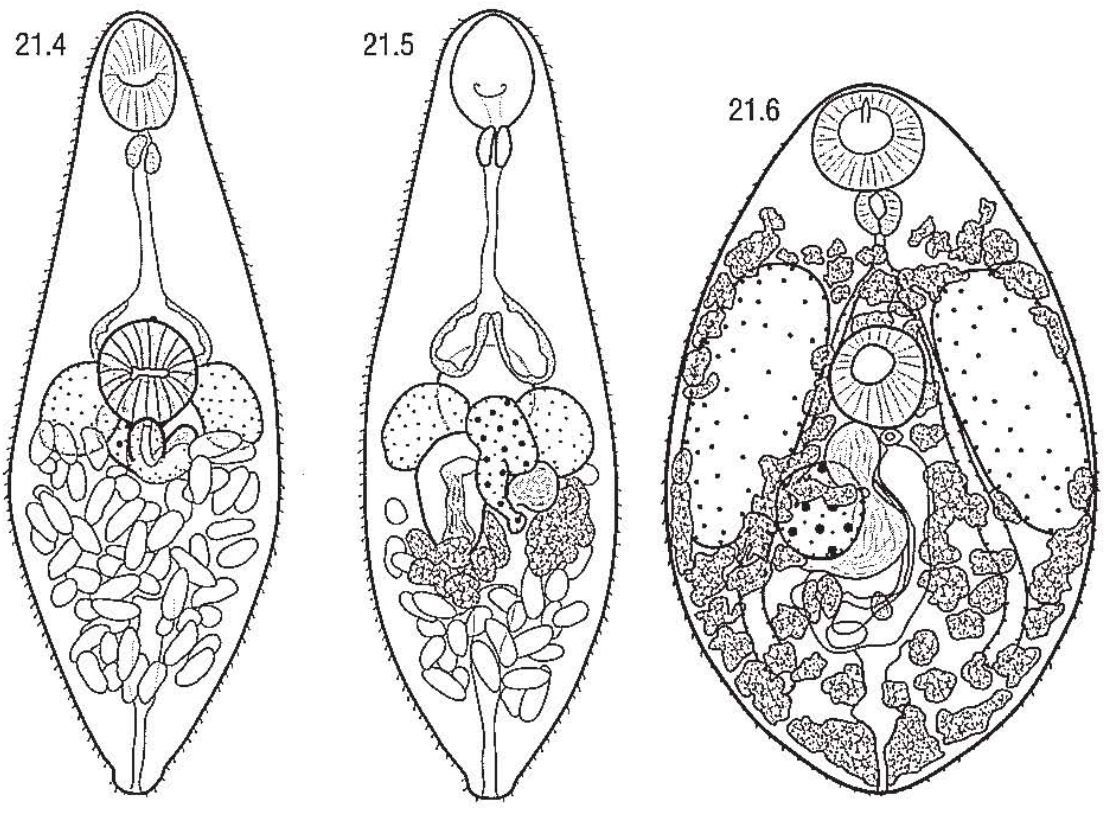
3a. Oesophagus much longer than caeca; caeca very short, not extending posterior to ventral sucker .... *Baiohelmins* Cribb & Pearson, 1988. (Figs 21.4, 21.5)

Diagnosis: Body minute, fusiform. Tegument spined. Oral sucker aperture just subterminal. Ventral sucker at about equator, similar in size to oral sucker. Oesophagus long. Intestinal bifurcation close to ventral sucker. Caeca very short and broad, not extending posterior to ventral sucker. Testes entire, symmetrical, posterolateral to ventral sucker, abut ends of caeca. Cirrus-sac S-shaped in lateral view, posterior to ventral sucker, contains internal seminal vesicle, pars prostatica and ejaculatory duct, from which cirrus may form. Genital pore median, immediately posterior to ventral sucker. Ovary entire, median, between and dorsal to testes, overlaps ventral sucker. Laurer's canal and saccate seminal receptacle present. Uterus occupies most of hindbody. Eggs small, moderately numerous. Vitelline follicles in two small dorsolateral groups posterior to testes, ovary and cirrus-sac. Excretory vesicle tubular, I-shaped or, if contracted, saccate; pore terminal. In intestine of mammals (Rodentia); Australia. Type-species *B. elegans* Cribb & Pearson, 1988.

3b. Oesophagus much shorter than caeca; caeca terminate at various levels between ventral sucker and posterior end of body .... 4.

4a. Ovary posterior or largely posterior to testes .... 5.
4b. Ovary anterior to testes .... 7.

5a. Cirrus-sac absent .... *Macroorchis* Ando, 1919. (Fig. 21.6)
Diagnosis: Body small to medium in size, oval, pyriform, rarely elongate and attenuated posteriorly. Tegument spined. Oral sucker subterminal, may contain stylet. Ventral sucker usually slightly pre-equatorial, sometimes much closer to anterior end, similar in size to oral sucker. Oesophagus short to medium length. Caeca simple, narrow, terminate in posterior quarter or



Figs 21.4, 21.5. *Baiohelmins elegans* Cribb & Pearson, 1988. 21.4. Ventral view. 21.5. Dorsal view. After Cribb & Pearson (1988).
Fig. 21.6. *Macroorchis spinulosus* Ando, 1919. After Chai *et al.* (1996).

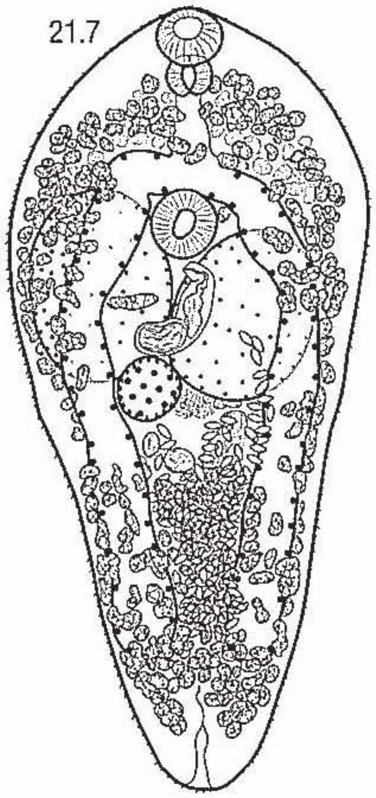
third of body. Testes large to very large, entire, much longer than broad, symmetrical, extracaecal, at level of ventral sucker or slightly posterior to this. Cirrus-sac absent. Seminal vesicle large, bipartite, free in parenchyma posterior to ventral sucker, opens via possible short prostatic region and ejaculatory duct at median genital pore immediately posterior to ventral sucker. Ovary usually rounded, median or slightly submedian to either side, between posterior ends of testes or slightly posterior to this. Laurer's canal present. Uterine seminal vesicle present. Uterus intercaecal, initially runs posteriorly, often reaches anterior edge of excretory vesicle and may extend beyond ends of caeca. Metraterm apparently not differentiated. Eggs of medium size, few to numerous. Vitelline follicles from level of intestinal bifurcation to posterior end, most abundant laterally but may reach median line, especially posterior to ventral sucker. Excretory vesicle somewhat elongate, broadest between ends of caeca and variously described as Y- or V-shaped; pore terminal. In intestine of mammals (Insectivora, Rodentia, Carnivora); Japan, Korea. Type-species *M. spinulosus* Ando, 1919.

5b. Cirrus-sac present .... 6.

6a. Vitelline follicles in fore- and hindbody .... *Nephrotrema* Baer, 1931. (Fig. 21.7)
(Syn. *Soricitrema* Bykhovskaya-Pavlovskaya, Vysotzkaya & Kulakova, 1970)
Diagnosis: Body of medium size, plump, pyriform, widest at level of ventral sucker and attenuated posteriorly. Tegument armed with spines. Oral sucker subterminal. Ventral sucker at about one-third from anterior end, similar in size to oral sucker. Oesophagus short. Caeca moderately broad, reach close to posterior extremity. Testes large to very large, longer than wide, entire, symmetrical or somewhat diagonal, sometimes contiguous medially, at level of ventral sucker or anterior or posterior to this, intercaecal and/or dorsal to caeca. Cirrus-sac elongate, close to ventral sucker and sometimes dorsal or lateral to it, contains small, usually bipartite seminal vesicle, well-differentiated pars prostatica and short ejaculatory duct. Genital pore median, slightly posterior to ventral sucker. Ovary entire, submedian, posterior or posterodorsal to right testis. Laurer's canal present. Seminal receptacle possibly present. Uterus posterior to ventral sucker, largely in second third or third quarter of body, intercaecal. Metraterm short. Eggs large, moderately numerous. Vitelline follicles distributed along entire length of body, most abundant laterally but may reach median line, especially posterior to ventral sucker. Excretory vesicle Y-shaped; main stem bifurcates posterior to uterus; pore terminal. In kidney of mammals (Insectivora); Europe. Type-species *N. truncatum* (Leuckart, 1842) Baer, 1931.

6b. Vitelline follicles in hindbody only .... *Xiphidiotrema* Senger, 1953. (Fig. 21.8)
Diagnosis: Body small, pyriform or fusiform, rounded anteriorly and pointed posteriorly. Tegument spinous. Oral sucker large, subterminal; small stylet sometimes present in dorsal wall. Ventral sucker equatorial or slightly anterior to this, smaller than, or equal to, oral sucker. Oesophagus short. Caeca simple, terminate close to posterior end of body or somewhat anterior to this. Testes large, symmetrical, sometimes much longer than wide, immediately anterolateral to ventral sucker, ventral to caeca or extracaecal. Cirrus-sac elongate-pyriform, posterolateral to ventral sucker, contains seminal vesicle, pars prostatica and ejaculatory duct, from which short cirrus may form. Genital pore median, slightly posterior to ventral sucker. Ovary just posterior to ventral sucker, dextrally submedian. Seminal receptacle and Laurer's canal not reported. Uterus intercaecal posterior to ventral sucker, with few moderately large eggs. Vitelline follicles entirely posterior to ventral sucker, extensive but sometimes absent from midline in region of ovary and cirrus-sac. Excretory vesicle V- or Y-shaped; pore terminal. In intestine of mammals (Insectivora); USA, China. Type-species *X. lockerae* Senger, 1953.

21.7



21.8

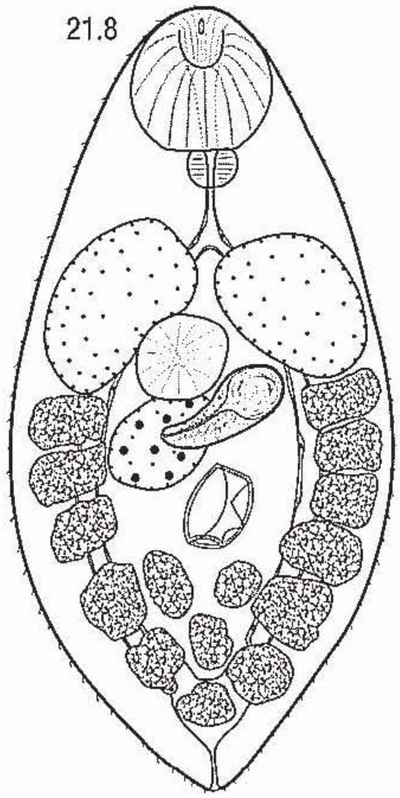


Fig. 21.7. *Nephrotrema truncatum* (Leuckart) as *Soricitrema baeri* Bykhovskaya-Pavlovskaya, Vysotzkaya & Kulova, 1970. Ventral view. After Bykhovskaya-Pavlovskaya *et al.* (1970).
Fig. 21.8. *Xiphidiotrema lockerae* Senger, 1953. Ventral view. After Senger (1953).

7a. Excretory vesicle small, saccate .... 8.
7b. Excretory vesicle Y-shaped with long stem .... *Troglotrema* Odhner, 1914. (Fig. 21.9)
Diagnosis: Body small to medium in size, rounded or pyriform, slightly attenuated posteriorly, where caudal projection sometimes reported. Tegument spinous. Oral sucker subterminal. Ventral sucker slightly pre-equatorial, similar in size to oral sucker. Oesophagus rather short, may be folded in sagittal plane. Caeca long, simple, may be slightly sinuous, sometimes locally dilate or constricted, terminate near posterior end. Testes large to very large, usually entire, almost symmetrical, usually posterior to level of ventral sucker but may overlap this level. Cirrus-sac quite large, median or submedian, largely posterior to ventral sucker or curled dorsally over sucker, contains bipartite seminal vesicle, prostatic complex and short unarmed cirrus. Genital pore median or just submedian, immediately posterior to ventral sucker. Ovary submedian, rounded to pyriform, anterior to or overlapping level of either testis, usually overlaps level of ventral sucker. Laurer's canal present. Seminal receptacle probably rudimentary. Uterus largely confined to region bounded by testes, cirrus-sac and ovary but may extend slightly posterior to testes. Eggs large and moderately numerous. Vitelline follicles extensive from level of oral sucker to posterior end of body, mostly close to caeca, approach median line dorsally and at each end of body. Excretory vesicle Y-shaped, dividing posterior to testes into two long arms extending anterior to ventral sucker; pore terminal. In frontal, ethmoidal and maxillary sinuses, gall-bladder and cysts attached to small intestine of mammals (Rodentia, Carnivora); Europe, southern Asia and probably Central Africa. Type-species *T. acutum* (Leuckart, 1842) Odhner, 1914.

8a. Diameter of oral sucker much less than twice that of ventral sucker .... 9.
8b. Diameter of oral sucker much greater than twice that of ventral sucker ....
.... *Skrjabinophyetus* Dimitrova & Genov, 1967. (Fig. 21.10)

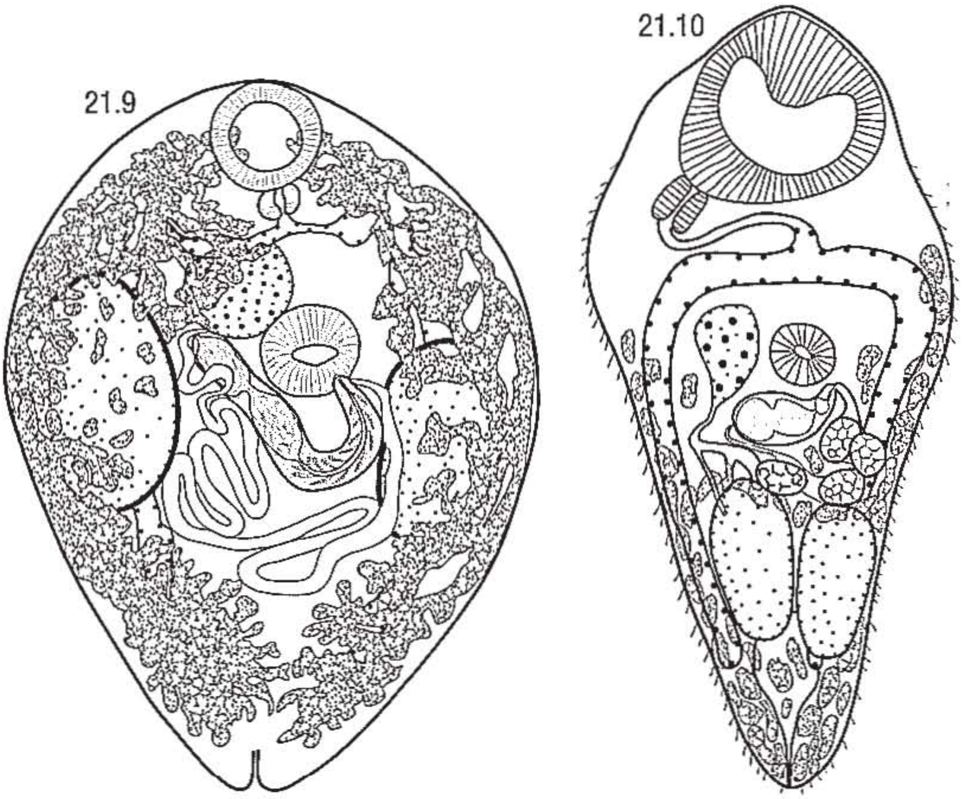


Fig. 21.9. *Troglotrema acutum* (Leuckart, 1842) Odhner, 1914. Ventral view. After Baer (1931a).
Fig. 21.10. *Skrjabinophyetus neomydis* Dimitrova & Genov, 1967. Ventral view. After Brendow (1970).

Diagnosis: Body small, pyriform or fusiform, with shape and disposition of internal organs varying considerably according to method of preparation. Tegument spined. Oral sucker subterminal, very large, much greater than twice the size of ventral sucker. Ventral sucker equatorial or slightly anterior to this, much smaller than oral. Oesophagus short to long, sometimes not apparent. Caeca simple, almost reach posterior end. Testes symmetrical or almost so, large, entire, longer than wide; position highly variable but typically posterior to ventral sucker. Cirrus-sac transversely and/or dorsoventrally oriented just posterior to ventral sucker or curled around dorsal or lateral margins of sucker, contains bipartite seminal vesicle, pars prostatica and ejaculatory duct, from which cirrus may form. Genital pore median, just posterior to ventral sucker. Ovary entire, pyriform, ovoid or spherical, submedian, just anterior to either testis. Laurer's canal present. Seminal receptacle absent. Uterus short, forms loop between testes and may extend well posterior to these, may extend anteriorly as far as intestinal bifurcation. Eggs of medium size, not numerous. Vitelline follicles numerous, especially dorsally, occupy posterior two-thirds of body but rarely extend anteriorly as far as intestinal bifurcation. Excretory vesicle saccate; pore terminal. In intestine of mammals (Insectivora); Europe. Type-species *S. neomydis* Dimitrova & Genov, 1967.

9a. Cirrus-sac present .... *Nanophyetus* Chapin, 1927. (Fig. 21.11)
(Syns *Nanophyes* Chapin, 1926 *nec* Schoenherr 1838; *Pseudotroglotrema* Yamaguti, 1971)

Diagnosis: Body very small, variable in shape but typically oval to pyriform. Tegument spined. Oral sucker subterminal, moderately large. Ventral sucker equatorial or slightly anterior to this, generally slightly smaller than oral sucker. Oesophagus short, sometimes apparently absent. Caeca simple, usually terminate in middle third of body dorsal to anterior ends of testes but may almost reach posterior end of body. Testes large, oval, longer than wide, symmetrical, sometimes oblique, lateral at about middle of hindbody, may overlap level of ventral sucker. Cirrus-sac transverse or oblique, close to ventral sucker and generally opposite ovary, with base typically anterior to genital pore, contains bipartite seminal vesicle and pars prostatica; formation of cirrus from ejaculatory duct disputed. Genital pore midventral, slightly posterior to ventral sucker. Ovary spherical or oval, submedian, pretesticular, adjacent to ventral sucker. Laurer's canal present. Presence of seminal receptacle disputed; sperm reported in dilatation of oviduct between ovary and base of Laurer's canal (i.e. oviducal seminal receptacle). Uterus forms single or double loop in sagittal plane between testes; metraterm receives terminal male duct shortly before genital pore. Eggs large, few. Vitelline follicles occupy much of dorsal and lateral regions of body except anterior end. Excretory vesicle saccate, small; pore terminal. In intestine of mammals (Carnivora, Insectivora) including man, also many experimental hosts; North America, Europe, Asia. Type-species *N. salmincola* (Chapin, 1926) Chapin, 1927.

9b. Cirrus-sac absent .... *Sellacotyle* Wallace 1935. (Fig. 21.12)
Diagnosis: Body very small, pyriform. Tegument spinous. Oral sucker large, subterminal. Ventral sucker, in middle third of body, slightly larger than oral sucker. Oesophagus short. Caeca simple, terminate close to posterior edge of ventral sucker. Testes large, oval, longer than wide, symmetrical, lateral, occupy much of body posterior to ventral sucker. Seminal vesicle bipartite, free in parenchyma posterodorsal to ventral sucker or between this and right testis, continues into short pars prostatica. Cirrus-sac absent. Genital pore median, just posterior to ventral sucker. Ovary

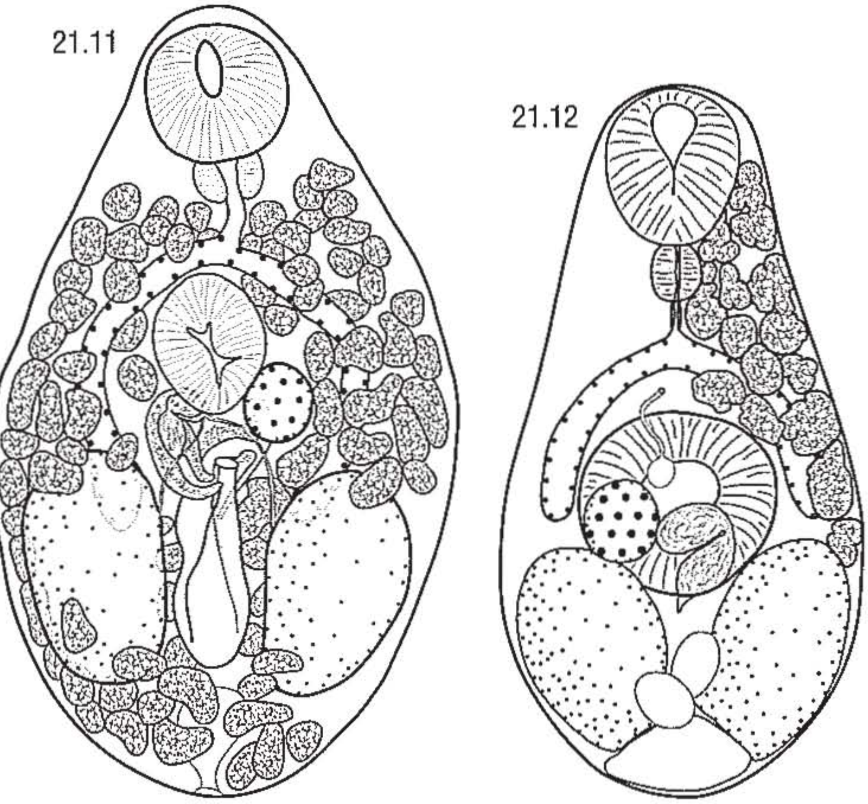


Fig. 21.11. *Nanophyetus salmincola* (Chapin, 1926). Ventral view. After Yamaguti (1971).
Fig. 21.12. *Sellacotyle mustelae* Wallace, 1935. Dorsal view with vitelline follicles omitted from left side. After Wallace (1935).

round, median or submedian, pretesticular or between anterior edges of testes, often partly dorsal to ventral sucker. Laurer's canal present. Seminal receptacle present. Uterus short, between testes; metraterm receives terminal male duct shortly before opening via genital pore. Eggs moderately large, few in number. Vitelline follicles lateral between levels of oral sucker and testes, sometimes reaching posterior end of body, occur towards midline dorsally in region of oesophagus and near posterior end. Excretory vesicle saccate; pore terminal. In intestine of mammals (Carnivora, Rodentia); North America. Type-species *S. mustelae* Wallace 1935.