24 Family Davaineidae Braun, 1900

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Introduction

The family Davaineidae Braun, 1900* has often been divided into subfamilies based on the nature of the uterus: Davaineinae with parenchymatous uterine capsules each containing one or several eggs; Ophryocotylinae with a persistent saccular uterus and the eggs not in capsules (except when small portions of the periphery of the uterus are pinched off by parenchyma); and Idiogeninae with a large paruterine organ surrounding the uterus with its main bulk placed anteriorly to the uterus, which is saccular or an inverted U-shape with no egg-capsules.

The relationship between the davaineids and the anoplocephalids is clearly close, as indicated by the parallel development of the uterus and related structures. We have adopted a pragmatic approach in our treatment of the Davaineidae, with the intention of producing a key for identification rather than to reflect phylogenetic relationships which are currently not well understood. As treated here, the davaineids remain a polyphyletic assemblage. This key does not take account of the likelihood that some davaineid genera are probably more closely related to the anoplocephalids than to most davaineids, or of the premise that anoplocephalids are essentially unarmed davaineids. It is also probable that some idiogenine genera are very closely related to some unarmed paruterinids. These relationships are suggested by the nature of the uterus and its derivatives, which clearly needs much more attention in cestode systematics. It is becoming clear that the paruterine organ in the Cyclophyllidea has polyphyletic origins (Georgiev & Kornyushin, this volume).

The nature and origin of the egg-capsule is not clear in such genera as *Davainea, Skrjabinia, Cotugnia* and *Ophryocotyle*. The situation may parallel that of the anoplocephalid subfamily Linstowiinae (see Conn, 1985; Beveridge, this volume) where in some cases the eggs are said to be embedded in the parenchyma in uterine capsules. Conn (1985) described the eggs of *Oochoristica* from

*According to *ICZN* Art. 50(c), the author of this taxon should be Braun, 1900.

transmission electron microscope observations but, as far as we are aware, there are no equivalent observations on davaineids. Light microscope observations of *Skrjabinia* (by Reid, Ackert & Case, 1938) and Cotugnia (by Singh & Baugh, 1984) give conflicting information. Reid *et al.* (1938) described the two outer membranes around the oncosphere as being connected by smaller membranes which are probably the remains of the uterine wall, but they did not state whether they considered the outer membranes as remains of the uterus and did not discuss a 'uterine capsule'. Singh & Baugh (1984) described various concentric layers around the oncosphere as three membranes and three envelopes and contested the presence of parenchymatous capsules in *Cotugnia*. Their observations were based only on the use of light microscopy and are, therefore, limited in value. We are not convinced that the situation in the subfamilies Davaineinae and Ophryocotylinae is well enough understood to separate them confidently. As this key is for ease of identification, we have departed from the traditional recognition of three subfamilies in the Davaineidae and have not recognized the Davaineinae and Ophryocotylinae as distinct (cf. Spasskii & Spasskaya, 1976).

The family characteristically has small, numerous hammer-shaped rostellar hooks. This is the one feature totally diagnostic of the Davaineidae, and the position of taxa which lack it has often been, and still remains, controversial.

Some characters previously used to separate genera are not recognized at that level here. The scolex characters significant at generic level are: presence or absence of the rostellum; shape and continuity or discontinuity of the rostellar crown; hook shape and size; number of rows of rostellar hooks and the presence (or rarely absence) and shape of the suckers. Accessory rostellar spines and sucker armature are of only specific significance. Significant strobilar characters include: the number of proglottids and of osmoregulatory canals; single or paired genitalia; and modifications of the genital atrium and terminal genital ducts. The number of testes is significant only when consistently very low, e.g. two. Their distribution is significant only when distinctly and consistently poral and is generally used in conjunction with other characters. The position of the ovary when distinctly poral is regarded as generically significant but its shape is not. Unilaterality or alternation of the genital pores is significant at generic level. In gravid proglottids, the presence of a paruterine organ is significant at subfamily level. Where egg capsules are present, they either have thick fibrous walls and enclose several eggs or have thin delicate walls and enclose a single egg. The number of eggs per capsule (i.e. one or several) is of generic significance. Only in one instance does a species have one or several eggs per capsule: *Calostaurus mundayi* Beveridge, 1975 has one to three eggs per capsule according to Beveridge's (1975) original description, confirmed by examination of the type specimens (BMNH 1976.1.6. 29–30). The capsule walls are, however, thin and delicate like those of taxa with monovular capsules and are quite unlike the fibrous-walled capsules in most taxa with several eggs per capsule. Other species of *Calostaurus* have a single egg enclosed in a thin-walled capsule. *C. mundayi* is regarded here as exceptional. The number of capsules per proglottid is generically significant only if consistently very low. Capsules containing a single egg are invariably numerous.

Davaineinae

The davaineids with paired genitalia form an easily recognizable group which has been elevated to subfamily rank by Movsesyan (1969) but the Cotugniinae was not recognized by Schmidt (1986) and is not recognized here because the character is of generic rather than subfamily significance. It has not been used to distinguish subfamilies in the anoplocephalids or the dilepidids (see this volume). Six nominal genera have consistently paired genitalia: *Cotugnia* Diamare, 1893, *Abuladzugnia* Spasskii, 1973, *Erschovitugnia* Spasskii, 1973, *Rostelugnia* Spasskii, 1984, *Pavugnia* Spasskii, 1984 and *Multicotugnia* López-Neyra, 1943. Of these, Movsesyan (1987, 1989) recognized only *Cotugnia* and *Multicotugnia*. Schmidt (1986) accepted *Abuladzugnia* but synonymized *Erschovitugnia* and *Multicotugnia* with *Cotugnia*; the remaining two genera were published too late to be available for his key.

Abuladzugnia is recognized here as valid.

Multicotugnia was erected by López-Neyra (1943a) for *Cotugnia brotogerys* Meggitt, 1915 because each egg capsule contained several eggs, a character regarded here as significant at the generic level. Meggitt (1915) stated clearly twice in his description of the species that the capsules contain several eggs but his illustration suggests that each capsule contains only one. The genus is provisionally retained. Descriptions of *C. brotogerys* by Southwell (1930b) and Mudaliar (1939) confirm the presence of several eggs per capsule, but our attempts to obtain specimens for examination proved unsuccessful.

The major feature of *Erschovitugnia* is the size of its rostellar hooks (70–90 μm). This is large for the group but is regarded here as of specific rather than generic significance; the synonymy of *Erschovitugnia* with *Cotugnia* is upheld, following Schmidt (1986) and Movsesyan (1987). Although large, the hooks are of the typical davaineid hammer shape.

Manitaurus Spasskaya & Spasskii, 1971 is considered valid following examination of the type specimens of *M. rahmi* (Baer & Fain, 1955) (BMNH 1960.7.12. 8–14), which confirmed that the gravid proglottids each have two to three large egg capsules each containing several eggs. This precludes synonymy with *Diorchiraillietina contorta* (Zschokke, 1895) Yamaguti, 1959 which has 30–40 egg capsules per proglottid, each with one egg (confirmed from specimens at the BMNH). Schmidt's (1986) synonymy of *M. rahmi* with *D. contorta* and hence of *Manitaurus* with *Diorchiraillietina* cannot be supported. Movsesyan (1987) regarded *Manitaurus* as an inermicapsiferine anoplocephalid on the grounds that the scolex was unarmed. This view is not shared here. Probably, as stated in Baer & Fain's (1955) original description, the type specimens have a rostellum from which the hooks have been lost. Specimens examined by us lacked scoleces.

Movsesyan (1987, 1989) transferred *Baerfainia* from the Davaineidae to the Hymenolepididae but the type species has a few large fibrous egg capsules each containing several eggs rather than a persistent uterus, which seems to preclude this. We have retained it in the Davaineidae because of its otherwise close resemblance to other genera in this family. Movsesyan (1987) quoted Spasskaya & Spasskii's (1971) opinion that *Baerfainia*, *Manitaurus* and *Metadavainea* Baer & Fain, 1955 were inermicapsiferines and that this subfamily belonged in the

Anoplocephalidae. The position of the two former genera will remain rather equivocal until the nature of the scolex in both can be elucidated by the examination of new specimens. A transfer to the Inermicapsiferinae might become appropriate for *Baerfainia* if the absence of a rostellum in *B. anoplocephaloides* were confirmed, but would be inappropriate for *Metadavainea* which has a rostellum armed with large, robust hooks. These hooks are not typically davaineid in shape or number but other morphological characters are consistent with the Davaineidae and the genus has been retained in this family, a course also taken by Movsesyan (1987, 1989). Schmidt (1986) appears inadvertently to have omitted the genus from his keys.

Delamuretta Spasskii, 1977 (syn. *Delamurella* Spasskii & Spasskaya, 1976 preoccupied, also spelled *Dalamurella*) was erected for *Davainea polycalceola* Janicki, 1902 and characterized by possession of six longitudinal osmoregulatory canals. Schmidt (1986) listed *D. polycalceola* as a species of *Davaineoides* Fuhrmann, 1920, the type-species of which, *D. vigintivasus* (Skryabin, 1914) Fuhrmann, 1920, has 20 osmoregulatory canals. He followed Fuhrmann (1920a) and Yamaguti (1959) in defining *Davaineoides* as possessing 6–20 osmoregulatory canals but inappropriately listed *Delamurella* [sic] and *Delmuretta* [sic] as synonyms of *Raillietina* (*Skrjabinia*), not of *Davaineoides*. The *Raillietina* group *sensu lato* has a maximum of four osmoregulatory canals. *Delamurella* was listed as a synonym of *Davaineoides* by Movsesyan (1987, 1989) without mention of the later name *Delamuretta*. The genus has been retained pending further evaluation.

The large *Raillietina* group has traditionally been treated as one genus, *Raillietina* Fuhrmann, 1920, with four subgenera *R. (Raillietina)* Fuhrmann, 1920, *R. (Fuhrmannetta)* Stiles & Orleman, 1926, *R. (Skrjabinia)* Fuhrmann, 1920 and *R. (Paroniella)* Fuhrmann, 1920. Although many authors have followed this system (e.g. Fuhrmann, 1920a; Stiles & Orleman, 1926; López-Neyra, 1931; Artyukh, 1966; Schmidt, 1986), the subgenera were elevated to generic rank by Movsesyan (1966). Following recognition of the generic significance of the number of eggs per capsule plus genital pores unilateral or irregularly alternating, the generic status of *Raillietina, Fuhrmannetta, Skrjabinia* and *Paroniella* is recognized here. Their further subdivision into subgenera by Movsesyan (1966) based on the presence or absence of sucker armature is not accepted because this character is of specific significance only. Accordingly, the subgenus *Armacetabulum* Movsesyan, 1966 is a synonym of *Skrjabinia*. The subgenus *Nonarmiella* erected by Movsesyan (1966) in the genus *Paroniella* was based on a species described as new by Purvis (1932), *Raillietina (Paroniella) acanthovagina*. Purvis later (1940) accepted an opinion by Baylis that his specimens were misidentified specimens of *R. (R.) volzi*. There is some confusion in Purvis's text, because at one point he stated that *R. (P.) southwelli*, also described as new in his first paper, was synonymous with *R. (R.) volzi* but this is presumably an error because he subsequently accepted the synonymy, also proposed by Baylis, of *R. (P.) southwelli* with *R. (P.) rangoonica*. Examination of Purvis's specimens (BMNH 1977.11.11.79) suggests that the eggs are encapsulated in groups, whereas in *Paroniella* the eggs are encapsulated singly. *Nonarmiella* is therefore based on a misidentified taxon and must be synonymous with *Raillietina* as its type-species is a synonym of a *Raillietina* species.

Corvinella Spasskaya & Spasskii, 1971 was characterized primarily by the arrangement of the testes in two lateral groups, a character of only specific significance; it is synonymized with *Paroniella*. The name is preoccupied by *Corvinella* Lesson, 1830 (Aves).

Tetraonetta Spasskaya & Spasskii, 1971 has, according to its original generic diagnosis, genital pores which alternate irregularly or are unilateral (Spasskaya & Spasskii, 1971) but a later key by Spasskii & Spasskaya (1976) states that the pores are unilateral. López-Neyra (1931) established that specimens described by various authors under the name of the type-species, *Davainea urogalli* (Modeer, 1790) Blanchard, 1891, which he discussed under the name *Meggittia urogalli*, belonged to more than one species. He stated that the genital pores are unilateral. Consequently, *Tetraonetta* has nothing to distinguish it from *Paroniella*.

Metaparonia Spasskii & Spasskaya, 1976 was erected in a key, without a formal generic diagnosis, with *R. (P.) bovieni* Baer & Fain, 1955 as type-species. From Spasskii & Spasskaya's (1976) key and from the original description of the type-species by Baer & Fain (1955), its distinguishing character is a long cirrus-sac figured as intersecting the osmoregulatory canals but not approaching the midline. We do not consider this sufficient to separate it from *Paroniella*.

Numidella Spasskaya & Spasskii, 1971 has been retained *pro tem* because it has an unusually large cirrus-sac which crosses the mid-line of the proglottid, a cirrus armed with large spines, and a distal inflation of the vagina conspicuously armed in several species allocated to the genus. Examination of specimens of *N. numida* (Fuhrmann, 1912) has confirmed these characters. The terminal genital ducts of *Davainea* are similar but the strobila in this genus consists of only a few proglottids.

Gvosdevinia Spasskii, 1973 is recognized as valid because of its combination of a distinctly poral ovary and the restriction of the testes to a poral, postovarian field.

Daovantienia Spasskii & Spasskaya, 1976, erected for *Raillietina (Skrjabinia) centropi* Southwell, 1922, was distinguished by the possession of a bilobed ovary and of testes surrounding the female organs and extending laterally beyond the osmoregulatory canals. Examination of the type (BMNH 1977.11.1.27) and other specimens (BMNH 1983.6.15.13–15; 1983.6.20.15; 1983.7.12.7–10; 1983.6.16.11) has confirmed these characters but they are of specific rather than generic significance and the genus is synonymized with *Skrjabinia*, following Movsesyan (1987, 1989) and Schmidt (1986) (as *R. (Skrjabinia)*).

Markewitchella Spasski & Spasskaya, 1976, based on *Raillietina (Skrjabinia) bonini* (Megnin, 1899) Fuhrmann, 1932, does not differ significantly from *Skrjabinia*, and their synonymy is recognized here, following Schmidt (1986) and Movsesyan (1987, 1989).

Soninotaurus Spasskii, 1973 is accepted as valid. The type-species, *S. rhynchota* (Ransom, 1909), is distinguished by an undulating crown of rostellar hooks which forms eight lobes. The undulating crown separates it from all other davaineine genera (*sensu stricto*) except *Calostaurus* and *Abuladzugnia*. *Calostaurus* species parasitize Australasian marsupials and the rostellar crown forms four or six lobes or a Maltese cross. *Abuladzugnia* has a laterally interrupted rostellar crown and paired genitalia. *S. rhynchota*, a parasite of North American

Piciformes, has a continuous crown and single genitalia. Its characters have been confirmed by examination of type and other specimens (USNM 7235).

Paspalia is recognized as the only *Raillietina*-like form with hooks of this large size or relatively small number. Schmidt (1986) and Movsesyan (1987) consider it a synonym of *Raillietina*, but we have examined type specimens and found that, contrary to the original description by Paspalewa & Woidowa (1969), egg capsules containing several eggs are not present. Hook number and shape are not typical of the davaineids and the genus probably has affinities with the dilepidids. The uterus is not clear in the available material, nor is the presence of single-egg capsules. The material is not in good condition and some features of the mature proglottid, e.g. the testes distribution and number, can be interpreted differently from Paspalewa & Woidowa (1969).

Idiogenoides is retained as valid as it shows an unusual combination of an *Idiogenes*-like mature proglottid and parenchymatous egg-capsules enclosing several eggs (Kotlan, 1921). The genus was erected by López-Neyra (1929) and, as well as the type-species, included *I. oligorchida* (Fuhrmann, 1911) and *I. birmanica* (Meggitt, 1926). Spasskaya & Spasskii (1971) added a further five species, all from parrots, to the genus. It is not entirely clear what features unite these species; Spasskii & Spasskaya (1976) in their key stress the two groups of testes, the few testes (<20), well-developed cirrus-sac and the thick and powerfully armed cirrus. On the other hand, we provisionally recognize the genus based on the large size of the cirrus-sac, which in the type-species, *I. allagea*, reaches close to the mid-line of the proglottid and on this basis we recognize only the type-species as belonging to the genus. Unfortunately the type-species has only been described once (Kotlan, 1921).

The following synonyms of *Raillietina* were differentiated from *Raillietina* on minor features, not considered significant by us. The only relevant distinguishing feature of *Kotlanotaurus* as keyed by Spasskii & Spasskaya (1976) is the penetration of the egg-capsules into the cortical parenchyma. We do not consider that this feature, which may be ontogenetic, has generic importance. The subgenus *Nonarmina* Movsesyan, 1966 has unarmed suckers, a feature which we do not consider of generic importance as it is so often a fixation artifact. *Roytmania* was distinguished in Spasskii & Spasskaya's (1976) key by minor features of the testicular distribution which are, in fact, not exhibited by the type-species *R. weissi* (Joyeux, 1923). *Skrjabinotaurus* was distinguished by its incomplete ring of sucker spines, the size of its rostellum relative to the suckers and the relatively few (*ca.* 4–9) testes. The first two characters are not of generic importance. The number of testes is significant when consistently low, e.g. *Diorchiraillietina*, but not when variable.

Spasskii (1973) stated that *Vadifresia* and *Raillietina* are the only genera and subgenera of davaineids with a single row of rostellar hooks but the type of *Raillietina, R. tetragona*, often has two rows of rostellar hooks, as do most species in the genus. We examined specimens of the type-species of *Vadifresia, V. baeri* (Meggitt & Subramanian, 1927), and confirm that only a single row of rostellar hooks is present. The hooks in the row are not all entirely aligned, but show no regular alternation of rows as found in related genera. This suggests that the single row of rostellar hooks is a consistent feature, but other authors have different

views. Baer (1959) described *Raillietina baeri* with two rows of hooks. Quentin (1964) described 'les crochets sont disposés en une seule couronne, ou bien en une double couronne' and illustrated a single row. Hunkeler (1974) described a single row, but thought more study was needed to evaluate the validity of this character, pointing out that Chandler (1942b) described *R. bakeri* with 'double crown . . . appearing as single row, alternate hooks being set only about 2 μm out of line'. The hooks in *V. baeri* cannot be said to alternate in this way. The genus is provisionally retained, consistent with our recognition elsewhere of the number of rows of rostellar hooks as a generic character.

Demidovella is provisionally recognized here. It was erected by Spasskii & Spasskaya (1976) based on the description of *Davainea leptotrachela* by Hungerbühler (1910) from *Pterocles namaqua*. The genus *Gvosdevinia* Spasskii, 1973 is from similar hosts and has a similar mature proglottid morphology, but unlike *Demidovella* does not have an egg-capsule enclosing several eggs. Schmidt (1986) considered *Demidovella* a synonym of *Raillietina (Fuhrmannetta)* and Movsesyan (1987) of *Fuhrmannetta*.

Mathevossianetta Movsesyan, 1966 and *Fuhrmannetta* Stiles & Orleman, 1926 differ in the reported absence or presence, respectively, of hooks on the suckers. This is not a generic criterion and *Mathevossianetta* is synonymized here with *Fuhrmannetta*. Movsesyan (1977) considered these taxa to be congeneric subgenera.

Dollfusoquenta Spasskii, 1973, erected for *Dilepis dollfusi* Quentin, 1964, a parasite of African rodents, has been retained in the Davaineidae as a pragmatic measure. It was originally placed in the Dilepididae by Quentin (1964) who described the uterus as persistent, a feature recognized in Spasskii's (1973) generic diagnosis. Despite this, Schmidt (1986) placed it in the Davaineinae although he recognized the uterus as a persistent irregular sac and inclusion in the Ophryocotylinae would have been more appropriate. Movsesyan (1987, 1989) did not include it in his lists of davaineid genera.

Daveneolepis Spasskii, 1979 is a genus of uncertain affinities which Spasskii (1979) appeared to regard as a dilepidid, although based on *Raillietina campanulata* (Fuhrmann, 1909) (syn. *Davainea campanulata*), previously in the Davaineidae. It was excluded from the davaineids by Movsesyan (1987, 1989) but synonymized with *R. (Skrjabinia)* by Schmidt (1986). The hooks of the type-species are atypical of the Davaineidae and the nature of the gravid proglottids is uncertain (Fuhrmann, 1909c; López-Neyra, 1931; Artyukh, 1966). The position and validity of the genus are unclear, as it is based on an inadequately described species. It is treated here as a *genus incertae sedis*.

Spasskii & Kornyushin (1977) considered the Ophryocotylidae to contain only *Ophryocotyle* and *Burtiella*. *Burtiella*, erected by Spasskii & Kornyushin (1977) for *Ophryocotyle zeylanica* (Linstow, 1906), apparently differs from *Ophryocotyle* in having the genital ducts passing between the osmoregulatory canals rather than dorsal to them (Burt, 1962). We have reservations as to the value of this character. We have examined several *Ophryocotyle* species and can confirm that usually the genital ducts pass dorsally to the osmoregulatory vessels, but in transverse sections of *O. zeylanica* we have not confirmed Burt's (1962) observation. In fact, we can detect only the large ventral osmoregulatory vessel and no sign of the dorsal vessel.

The cirrus-sac of *O. zeylanica* has an internal seminal vesicle, not detected by us in other *Ophryocotyle* species but the figure of *O. proteus* in Spasskii & Kornyushin (1977) suggests that it may occur in this species and the character is not, therefore, considered by us to validate *Burtiella*.

Ophryocotylus was described, but not figured, by Srivastava & Capoor (1977) with the type-species *O. dinopilium*. Although no illustrations were given, the description was detailed enough and the status of the taxon was discussed in enough detail to make the names available. The form was described again, as new, by Srivastav [*sic*] & Capoor (1982) with the type-species spelled *O. dinopii*. The genus is distinguished from related forms by its single row of rostellar hooks. Despite the somewhat perfunctory nature of the description and figures, the genus is provisionally recognized here as the authors emphasize the number of hook rows seen. We stress, however, that we are not totally convinced of its validity.

Ophryocotyloides is poorly known. The type-species, *O. uniuterina*, is known only from its original description by Fuhrmann (1909c). The type-material in the Naturhistorisches Museum, Vienna (No. V.2799), consists of two fragments, a piece of pre-mature strobila and a piece of gravid strobila. No scolex or mature proglottids are present. The unilaterality of the genital pores is confirmed. The uterus develops as a distended sac, becomes very lobate as the eggs develop and then in the later gravid proglottids the septa of the lobations disappear and the uterus fills the whole proglottid up to the margins of the body, overlapping the longitudinal osmoregulatory canals. No indication of egg-capsules was seen. The characters of the genus are taken from this material and Fuhrmann's (1909c) description, and not from later descriptions of species supposedly in the genus (e.g. Singh, 1960) as Spasskii & Kornyushin (1977) stated that the systematic position of the genus is unclear and it contains representatives of several (at least four) other genera. We follow Schmidt in recognizing *Ophryocotyloides*, but only provisionally and pending a careful redescription of the type-species.

Fernandezia is, according to Spasskii & Kornyushin (1977), close to the davaineine genus *Skrjabinia*, which is said to have single eggs in uterine capsules. Binder (1971) described the uterus of *F. spinosissima* (von Linstow, 1894) as saccular, with deeply lobate margins which can simulate capsules.

Dasyurotaenia Beddard, 1912 has been included by Schmidt (1986) in the Davaineidae, subfamily Ophryocotylinae. Other authors (e.g. Baer, 1925b; Sandars, 1957; Yamaguti, 1959; Abuladze, 1964) placed it in the Taeniidae but Rausch (1981, this volume) rejected this on phylogenetic and morphological grounds. However, the morphology of the scolex and proglottids, but not the eggs, of *Dasyurotaenia*, as described by Beveridge (1984), is more similar to the taeniids than the davaineids. Beveridge (1984) speculated that the genus might be derived from the linstowiids of marsupials, but the absence of information on the life-cycle renders allocation to a family difficult. At present, we see no reason to include this genus in the Davaineidae and regard it as a *genus incertae sedis*.

The genus *Barbusa* Capoor & Srivastava, 1975, and the tribe Barbuseini, erected in the Davaineinae by Capoor & Srivastava (1975) are based on poorly-described specimens. It is not clear from the description that these are definitely davaineids. *Barbusa* is treated here as a *genus inquirendum*. The shape and

arrangement of the rostellar hooks are unknown for the Davaineidae and require confirmation.

Idiogeninae

The type-species of the type-genus, *Idiogenes otidis*, was described by Krabbe (1868) from the bustard, *Otis tarda*, from a zoological collection in Jutland, Denmark. The bustard is not, and probably never has been, a regular breeding bird in Denmark (Dr Niels Otto Preuss, pers. comm.). Krabbe did not describe a scolex and we can confirm that no scoleces were present in the dried-out type material in the Zoological Museum, Copenhagen. Some authors have considered that the strongly craspedote proglottids can attach as pseudoscoleces. Several authors have subsequently described scoleces for species they considered *I. otidis*. Yeh (1957) and Gómez (1981) have reported on worms from *O. tarda* in Spain: both described four rows of rostellar hooks, and Gómez described a patch of small accessory spines proximally to the rostellar hooks. Our observations of specimens from *O. tarda* from London Zoo (IIP 1246) confirm the presence of four rows of hooks (could be interpreted as three or five in parts of the circle) and the accessory spines (Fig. 24.84). Joyeux, Gendre & Baer (1928) described two rows of rostellar hooks for *I. otidis* from *Eupodotis* [as *Trachelotis*] *senegalensis* from Guinea, West Africa. Mahon (1954) renamed this form *I. pseudotidis*. Borgarenko (1981) figured a scolex of *I. otidis* with, apparently, one row of rostellar hooks and listed the hosts *O. tarda* and, mainly, *O. undulata* in Tadzhikistan. This evidence suggests to us that *I. otidis* is characterized by four rows of rostellar hooks and the patch of accessory spines, and this calls into question the validity of *Ersinogenes* Spasskaya, 1961 and *Paraidiogenes* Movsesyan, 1971. *Ersinogenes* is said to differ from *Idiogenes* in having five rows of rostellar hooks, and also possesses accessory spines. The type-species, *E. spinatum* Spasskaya, 1961 was described from *Otis tarda* in Tuva, USSR. As it is possible to interpret the number of rows in the specimens of *I. otidis* we have seen, as from three to five, we do not consider this a useful differentiating character. In every other way this genus resembles *Idiogenes*. Because of this, and because of its host, we consider *Ersinogenes* a synonym of *Idiogenes*. *Paraidiogenes* is supposedly differentiated from *Idiogenes* by having three rows of rostellar hooks and accessory spines are described. The type-species of *Paraidiogenes, P. mongolica* (Danzan in Spasskaya & Spasskii, 1971) was originally described as *Idiogenes kori* Ortlepp, 1938 by Spasskaya (1961b) from *Otis tarda* in Mongolia and renamed *Idiogenes mongolica* by Danzan in a thesis in 1964. The first published use of the name was by Spasskaya & Spasskii (1971). Movsesyan (1970) mentioned the name *Paraidiogenes* in a list and key, but no constituent species were mentioned and he formally erected the genus in 1971. We believe there are no grounds for considering this genus distinct from *Idiogenes*. Our own observations on several species make it clear, however, that many of the species currently considered to belong to *Idiogenes* have only two rows of rostellar hooks. We have, therefore, defined *Idiogenes* sensu stricto as having three to five rows of rostellar hooks and with accessory spines present, based on the type-species *I. otidis*.

Movsesyan (1970) created *Pseudidiogenes* as a subgenus of *Idiogenes*, but no

constituent species were mentioned and, therefore, this name is not valid from this date (*ICZN* Art. 13(b)). The name was erected legally by the same author in 1971, with the type-species *I. (P.) flagellum*, and in both papers the new subgenus was differentiated from *Idiogenes (I.)* by having armed suckers. Kornyushin (1989) raised *Pseudidiogenes* to generic rank, based on the same criteria as Movsesyan, i.e. whether the suckers were armed or not. The *Idiogenes* forms with two rows of rostellar hooks should, we believe, be considered generically distinct from those with three to five rostellar hook rows, and we consider that the genus *Pseudidiogenes* can be redefined to accommodate them.

The names *Otiditaenia* and *Schistometra* were both coined in publications in 1912. They are generally considered synonymous, but different authors recognize different priority. Beddard (1912) was 'published, March 1912' whereas Cholodkowsky (1912) has no date other than the year and, therefore, according to the *ICZN* should be dated as 31 December 1912. We believe that Baer (1955a) is correct in arguing for the priority of *Otiditaenia*.

We have examined 'co-types' of the type-species of *Paraschistometra*, i.e. *P. macqueeni* Woodland, 1930 (BM(NH) 1965.2.19.1–23) and agree with Baer (1955a) that it is synonymous with *Otiditaenia*.

Capsodavainea is an objective synonym of *Chapmania* as it is based on the same type-species. Our observations on *Chapmania* are based mainly on Kornyushin (1989).

We have recognized *Satyanarayana* Khan, 1984 although it is similar to *Chapmania* Monticelli, 1893. The type-species of the former genus, *S. satyanarayani* was described by Khan (1984) from the **lungs** of the heron *Ardea cinerea* in India. In many respects the species appears close to *Chapmania*, but the ovary is poral with all the testes aporal to it. In *Chapmania*, the ovary is median or just porally submedian (see Baer, 1955a; Hörchner, 1962; Movsesyan, 1977; Kornyushin, 1989) with the testes passing poral to the ovary. We consider this character to be of generic importance, but it should be noted that the site of *S. satyanarayani* is very unusual and that Khan (1984) had to tease the worms from the lung tissue with the help of needles.

Most text illustrations are original; others have been modified and redrawn from the sources named in the figure legends.

Family Davaineidae Braun, 1900

Diagnosis: Rostellum usually present, rarely rudimentary, varies from small to enormous, armed with hooks in usually two rows but occasionally in one, three, five or 10–12 rows. Hook crown round, oval or undulating, interrupted or not. Hooks characteristically numerous, small and hammer-shaped, rarely otherwise. Rostellar spines present or absent. Suckers present, rarely absent, unarmed or armed with rows of minute spines. Strobila small to large, rarely tiny. Proglottids usually numerous, rarely few. Osmoregulatory canals four (dorsal and ventral pairs), two (ventral pair only), or rarely six or twenty. Genitalia single or double; when single, genital pores unilateral or alternate irregularly. Cirrus-sac small to large, variable in extent relative to osmoregulatory canals. Testes few to numerous,

distribution variable. Ovary commonly median, exceptionally poral, lobed, occasionally distinctly bilobed. Vitellarium postovarian. Uterus persistent or replaced by paruterine organ or by egg capsules containing one or several eggs. In birds and mammals. Type-genus *Davainea* Blanchard, 1891.

Key to subfamilies

1a. Paruterine organ absent ..... **Davaineinae Braun, 1900.** (Syn. Ophryocotylinae Fuhrmann, 1907.)

Diagnosis: Davaineidae. Uterus persistent or replaced by egg capsules, either numerous thin-walled capsules containing a single egg or few to numerous fibrous capsules containing several eggs.

1b. Paruterine organ present ..... **Idiogeninae Fuhrmann, 1907.**

Diagnosis: Davaineidae. Paruterine organ present.

Subfamily Davaineinae Braun, 1900

Key to genera

1a. Egg capsules present, each containing several eggs ..... **2.**

1b. Not as above ..... **11.**

2a. Genital organs double per proglottid .... ***Multicotugnia*** **López-Neyra, 1943.** (Not illustrated; this genus resembles *Cotugnia* (Figs 24.30–24.32) except for having several eggs per capsule.)

Diagnosis: Rostellum armed with double row of small hammer-shaped hooks. Suckers unarmed. Proglottids numerous, craspedote. Paired dorsal and ventral osmoregulatory canals present. Genital pores bilateral. Cirrus-sac small, extravascular. Testes numerous, confluent behind female organs, extending laterally beyond osmoregulatory canals. Ovaries lateral, strongly lobed. Vitelline glands postovarian. Egg capsules numerous, each containing several eggs. In Psittaciformes. Brazil. Type-species *M. brotogerys* (Meggitt, 1915).

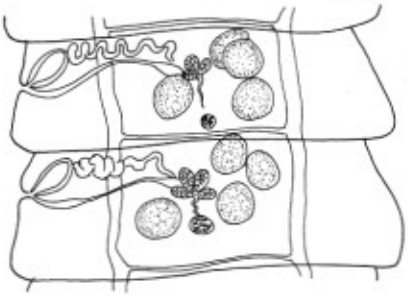
2b. Genital organs single per proglottid ..... **3.**

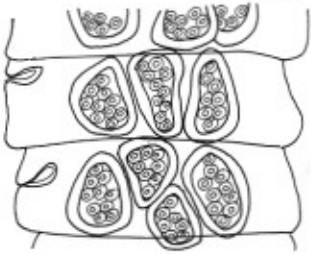
3a. Egg capsules few (<5) per proglottid. Testes few (<5). Parasites of Pholidota ..... **4.**

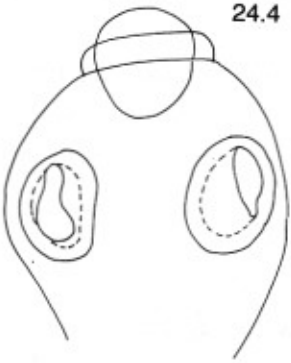
3b. Egg capsules more than 5 per proglottid. Testes few or numerous . **5.**

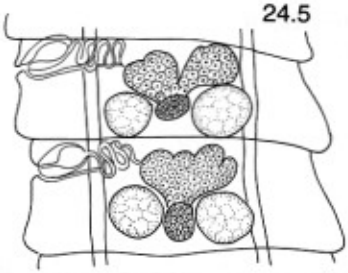
4a. Rostellum rudimentary, unarmed .... ***Baerfainia*** **Yamaguti, 1959. (Figs 24.1–24.3)**

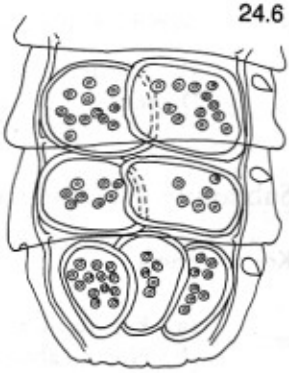
Diagnosis: Suckers armed. Proglottids numerous, craspedote. Only ventral osmoregulatory canals present. Genitalia single. Genital pores unilateral. Cirrus-sac small, extravascular. Testes few (three to four), one poral, remainder aporal.

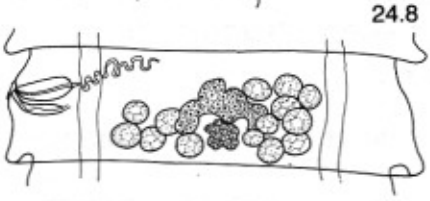


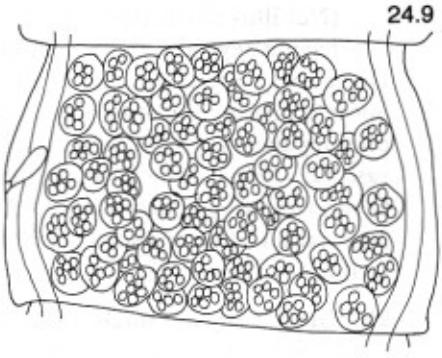












Figs 24.1-24.3 *Baerfainia anoplocephaloides* (Baer & Fain, 1955). (After Baer & Fain, 1955.) 24.1. Scolex. 24.2. Mature proglottids. 24.3. Gravid proglottids.
Figs 24.4-24.6 *Manitaurus rahmi* (Baer & Fain, 1955). (Figs 24.4, 24.5 after Baer & Fain, 1955.) 24.4. Scolex. 24.5. Mature proglottids. 24.6. Gravid proglottids.
Figs 24.7-24.9 *Pentocoronaria rusannae* Matevosyan & Movsesyan, 1966. (After Matevosyan & Movsesyan, 1966.) 24.7. Scolex. 24.8. Mature proglottid. 24.9. Gravid proglottid.

Ovary median, lobed. Vitellarium postovarian. Egg capsules very large, few (three to four), each containing numerous eggs. In Pholidota. Africa. Type-species *B. anoplocephaloides* (Baer & Fain, 1955).

4b. Rostellum present, well-developed ..... ***Manitaurus* Spasskaya & Spasskii, 1971. (Figs 24.4– 24.6)**

Diagnosis: Hooks unknown. Suckers unarmed. Proglottids numerous, craspedote. Genitalia single. Genital pores unilateral. Cirrus-sac reaching osmoregulatory canals. Testes two, one either side of ovary. Ovary median, lobed. Vitellarium postovarian. Egg capsules few (two to three), large, containing numerous eggs. In Pholidota. Africa. Type-species *M. rahmi* (Baer & Fain, 1955).

5a. Rostellar hooks in five circles ..... ***Pentocoronaria* Matevosyan & Movsesyan, 1966. (Figs 24.7–24.9)**

Diagnosis: Rostellum armed with small hammer-shaped hooks. Suckers armed. Proglottids numerous, craspedote. Only ventral paired osmoregulatory canals present. Genitalia single. Genital pores unilateral. Cirrus-sac pyriform, muscular, extravascular in mature proglottids. Testes relatively few, lateral and posterior to ovary. Ovary median, slightly lobed. Vitellarium postovarian. Egg capsules numerous, each containing several eggs. In Columbiformes. USSR. Type-species *P. rusannae* Matevosyan & Movsesyan, 1966.

5b. Rostellar hooks in two rows ..... **6.**

5c. Rostellar hooks in one row ..... ***Vadifresia* Spasskii, 1973. (Figs 24.10, 24.11)**

Diagnosis: Suckers armed. Proglottids craspedote. Reproductive organs single. Genital pores unilateral. Cirrus-sac small. Testes numerous. Ovary median. In rodents and lagomorphs; Ethiopian, Nearctic. Type-species *V. baeri* (Meggitt & Subramanian, 1927).

6a. Rostellar hooks 24 or less ..... ***Metadavainea* Baer & Fain, 1955. (Figs 24.12–24.15)**

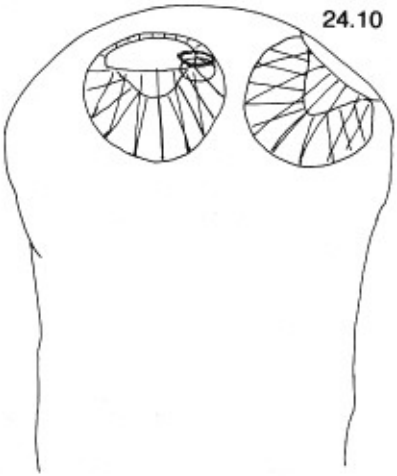
Diagnosis: Rostellum armed with double row of relatively few large robust hooks with well-developed blades, thick guards and reduced handles. Suckers armed. Accessory rostellar spines present. Proglottids numerous, craspedote. Pair of dorsal and of ventral osmoregulatory canals present. Genitalia single. Genital pores unilateral. Cirrus-sac extravascular. Testes numerous, lateral and anterior to ovary. Ovary median, slightly lobed. Vitellarium postovarian. Egg capsules relatively few (8–15), each containing several eggs. In Pholidota. Africa, Asia. Type-species *M. aelleni* Baer & Fain, 1955.

6b. Rostellar hooks numerous ..... **7.**

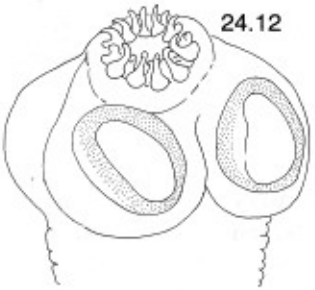
7a. Ovary poral ..... **8.**

7b. Ovary median ..... **9.**

8a. Genital pores unilateral. Testes in poral and aporal fields. In Struthioniformes and Rheiformes .....


24.10


24.11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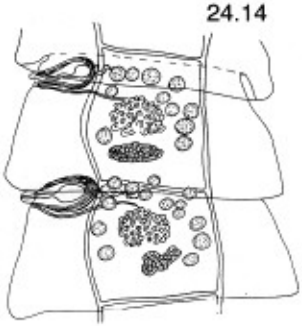
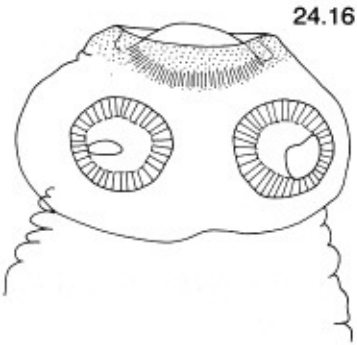

24.14


24.15


24.13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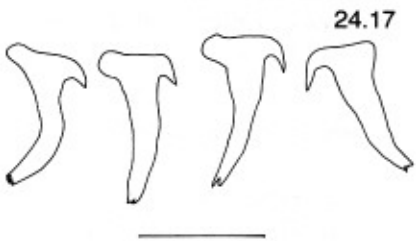
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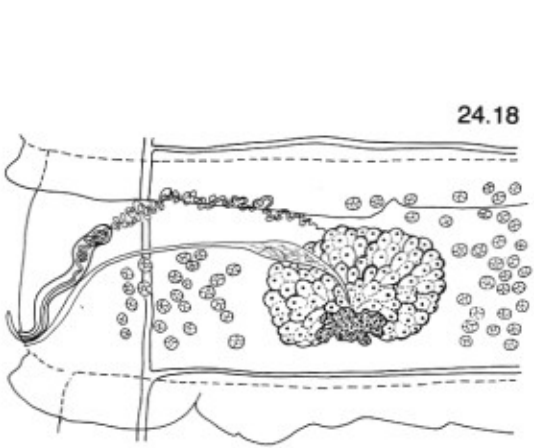
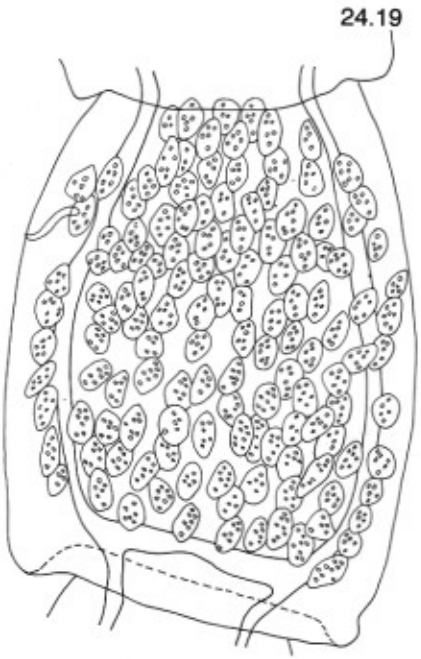


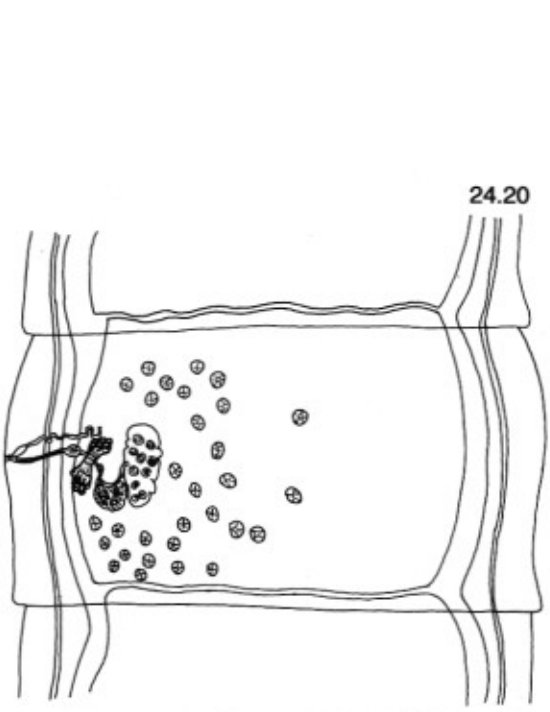


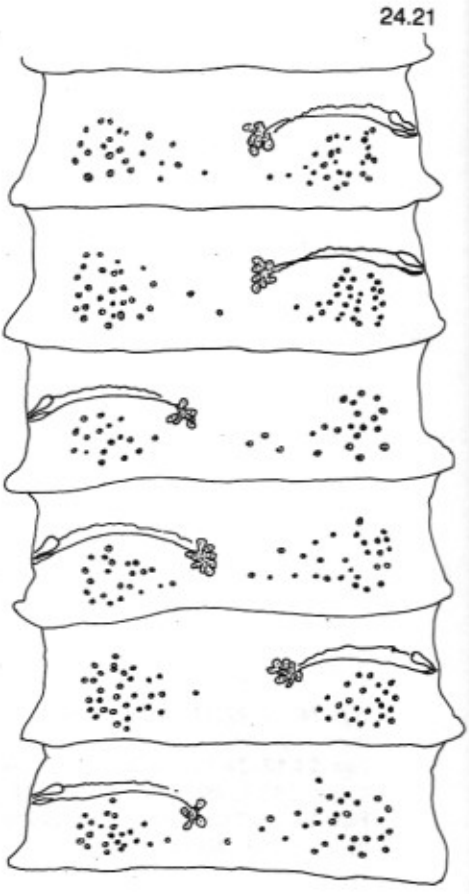
Figs 24.10, 24.11 *Vadifresia baeri* (Meggitt & Subramanian, 1927). 24.10. Hook. ring. 24.11. Hook ring and rostellum (detail).
Figs 24.12-24.15 *Metadavainea aelleni* Baer & Fain, 1955. 24.12. Scolex. 24.13. Rostellar hooks. 24.14. Mature proglottids. 24.15. Gravid proglottids.
Figs 24.16-24.19 *Houttuynia struthionis* (Houttuyn, 1772). 24.16. Scolex. 24.17. Rostellar hooks. 24.18. Mature proglottid, poral region. 24.19. Gravid proglottid.

..... ***Houttuynia*** **Fuhrmann, 1920. (Figs 24.16–24.19)**
Diagnosis: Rostellum wide, armed with double row of large hammer-shaped hooks. Rostellar spines present. Suckers unarmed. Strobila large. Proglottids numerous, craspedote. Paired ventral osmoregulatory canals present. Genitalia single. Genital pores unilateral. Cirrus-sac elongate, not crossing osmoregulatory canal. Testes numerous, in poral and aporal fields lateral to ovary, extend lateral to osmoregulatory canals. Ovary slightly poral, lobed, fan-shaped. Vitellarium postovarian. Egg capsules numerous, contain several eggs. In Struthioniformes and Rheiformes. Africa, South America. Type-species *H. struthionis* (Houttuyn, 1772).

8b. Genital pores alternate irregularly. Testes restricted to poral field. In Pteroclidae ..... *Demidovella* Spasskii & Spasskaya, 1976. (Fig. 24.20)
Diagnosis: Rostellar hooks in two circular rows. Suckers armed. Proglottids craspedote. Reproductive organs single. Three to four eggs per capsule. In sandgrouse. Ethiopia. Type-species *D. leptotrachela* (Hungerbühler, 1910).

9a. Genital pores unilateral ..... 10.
9b. Genital pores alternate irregularly .....





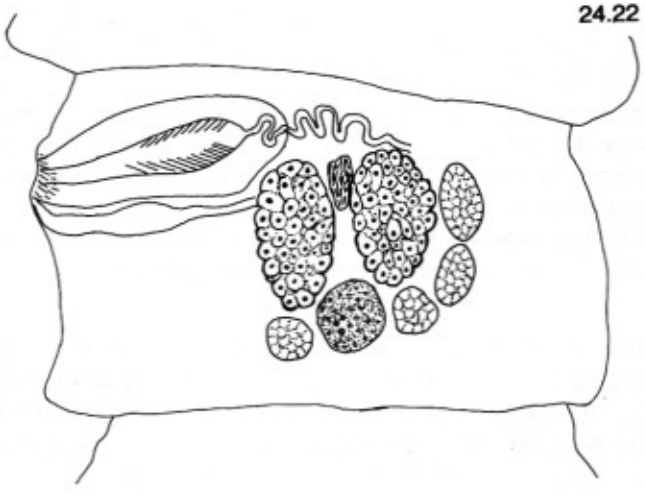


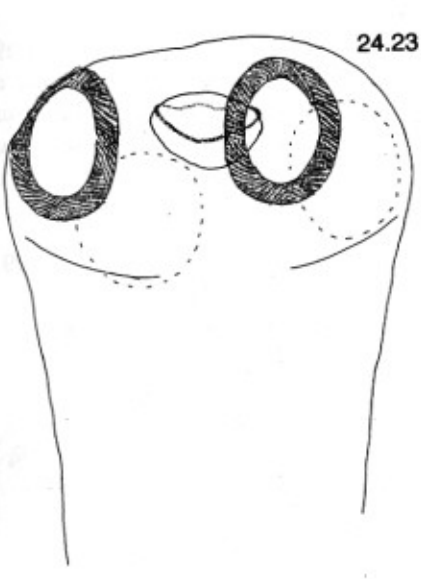
Fig. 24.20 *Demidovella leptotrachela* (Hungerbühler, 1910). (After Hungerbühler, 1910.)
Fig. 24.21 *Fuhrmannetta crassula* (Rudolphi, 1819). Mature proglottids.
Fig. 24.22 *Idiogenoides allagea* (Kotlan, 1921). Mature proglottid. (After Kotlan, 1921.)

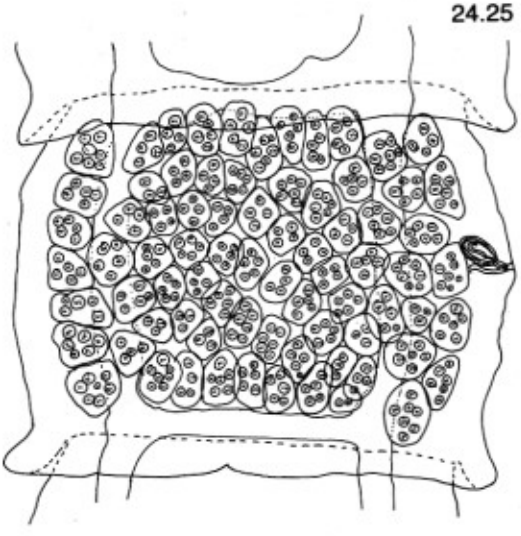
..... ***Fuhrmannetta*** **Stiles & Orleman, 1926. (Fig. 24.21)**
(Syns *Johnstonia* Fuhrmann, 1921 preoccupied; *Mathevossianetta* Movsesyan, 1966.)

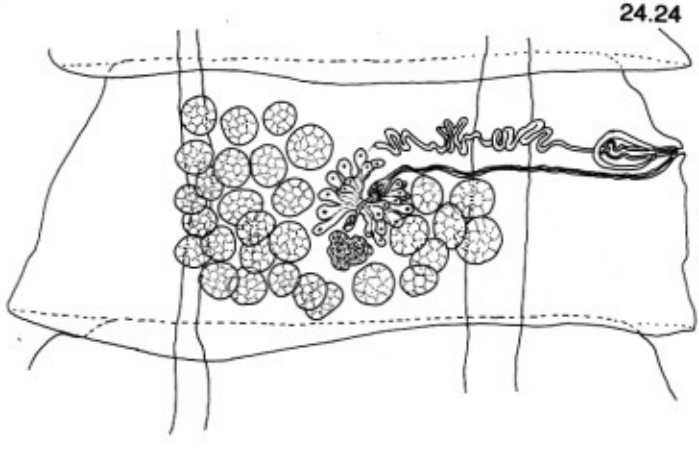
Diagnosis: Rostellar hooks in two circular rows. Suckers armed or not. Proglottids wider than long. Reproductive organs single. Testes numerous. Ovary median. Three to five eggs per capsule. In birds and mammals. Cosmopolitan. Type-species *F. crassula* (Rudolphi, 1819).

10a. Cirrus-sac large, closely approaching mid-line .....
..... ***Idiogenoides*** **López-Neyra, 1929. (Fig. 24.22)**

Diagnosis: Rostellar hooks in two circular rows. Suckers armed. Proglottids craspedote. Reproductive organs single. Genital pores unilateral. Testes few (four







Figs 24.23-24.25 *Raillietina* Fuhrmann, 1920. 24.23. *R. echinobothrida* (Megnin, 1880). Scolex. 24.24. *R. tetragona* (Molin, 1858). Mature proglottid. 24.25. *R. tetragona*. Gravid proglottid.

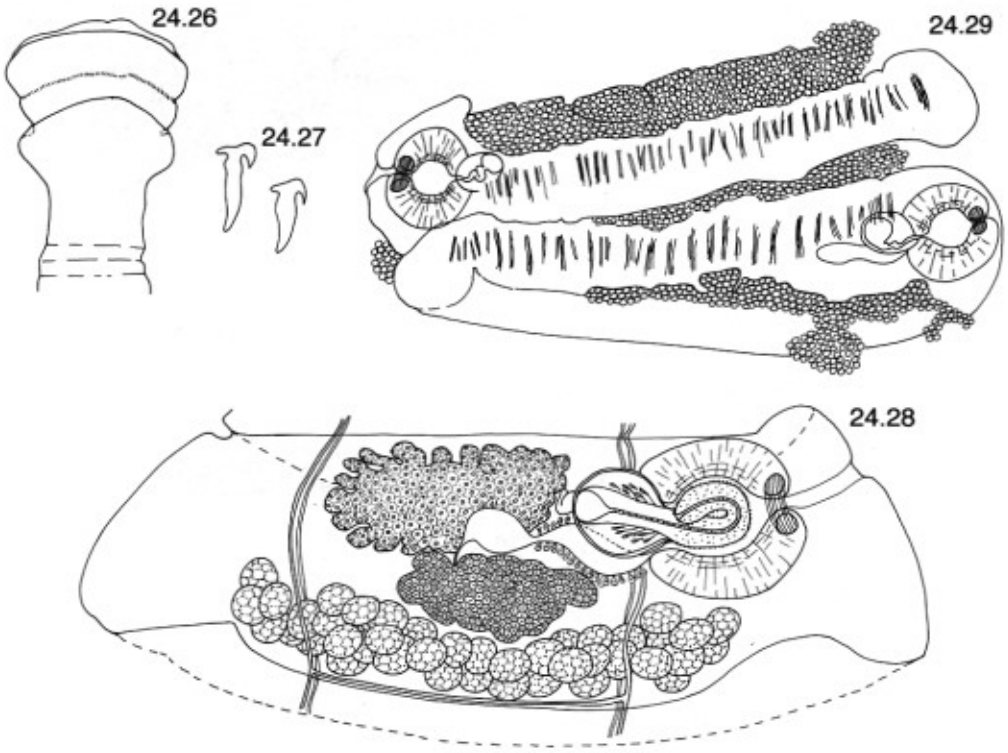
to six). Ovary median. Six to seven eggs per capsule. In parrot. New Guinea. Type-species *I. allagea* (Kotlan, 1921).

10b. Cirrus-sac small, not reaching or just crossing the osmoregulatory canals ..... ***Raillietina*** **Fuhrmann, 1920. (Figs 24.23–24.25)**
(Syns *Kotlania* López-Neyra, 1929; *Kotlanotaurus* Spasskii, 1973; *Nonarmiella* Movsesyan, 1966; *Nonarmina* Movsesyan, 1966; *Oschmarinetta* Spasskii, 1984; *Ransomia* Fuhrmann, 1921; *Roytmania* Spasskii, 1973; *Skrjabinotaurus* Spasskii & Yurpalova, 1973.)

Diagnosis: Rostellar hooks in circular row. Suckers armed, partly armed or unarmed. Proglottids craspedote. Reproductive organs single. Genital pores unilateral. Testes numerous. Ovary median. Two to eight eggs per capsule. In birds and mammals. Cosmopolitan. Type-species *R. tetragona* (Molin, 1858).

11a. Suckers absent ..... ***Pluviantaenia*** **Jones, Khalil & Bray, 1992. (Figs 24.26–24.29)**

Diagnosis: Rostellum inflated, enormous, armed proximally with double row of many small hammer-shaped hooks. Proglottids numerous, craspedote. Two pairs of osmoregulatory canals present. Genital pores generally alternate regularly but



Figs 24.26–24.29 *Pluviantaenia kassalensis* Jones, Khalil & Bray, 1992. (After Jones *et al.*, 1992.) 24.26. Scolex. 24.27. Rostellar hooks. 24.28. Mature proglottid. 24.29. Gravid proglottid.

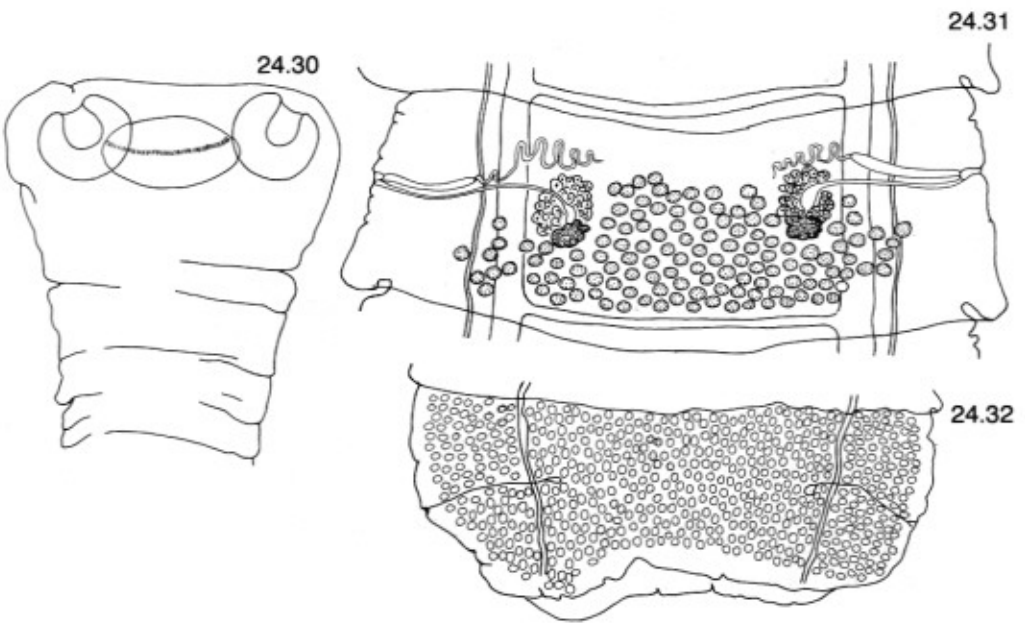
may alternate irregularly or be bilateral. Genital atrium enormous, sucker-like with massive sphincter distally; atrial region protrusible. Duplication of genital atria and cirrus-sacs may occur. Cirrus-sac thin-walled. Cirrus large, armed. Testes numerous, along posterior margin of proglottid. Vagina sigmoid, inflated and glandular distally. Ovary median. Vitellarium postovarian. Uterus persistent. In Glareolidae. Sudan. Type-species *P. kassalensis* Jones, Khalil & Bray, 1992.

11b. Suckers present ..... **12.**

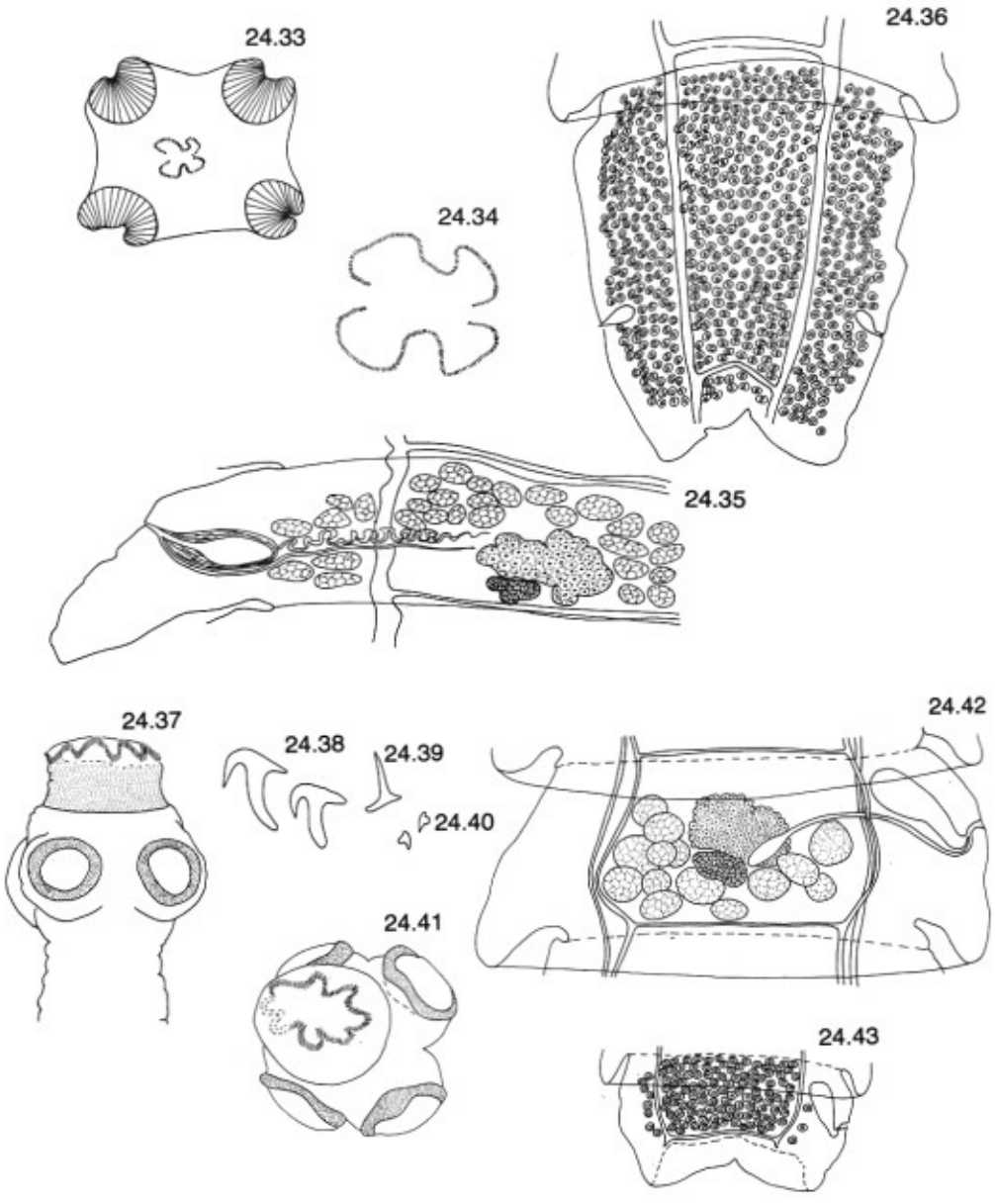
12a. Rostellar hook crown round or oval ..... **13.**
12b. Rostellar hook crown undulating or lobed ..... **14.**

13a. Genital organs consistently double per proglottid .....
..... ***Cotugnia* Diamare, 1893. (Figs 24.30–24.32)**
(Syns *Erschovitugnia* Spasskii, 1973; *Pavugnia* Spasskii, 1984; *Rostelugnia* Spasskii, 1984.)

Diagnosis: Rostellum broad, armed with a double row of small (rarely large) hammer-shaped hooks. Suckers usually unarmed, rarely armed. Proglottids numerous, craspedote. Dorsal pair of osmoregulatory canals present or absent, ventral pair present. Genital pores bilateral. Cirrus-sac small, extravascular. Testes numerous, in one or two fields. Ovaries lateral, lobed. Vitelline glands postovarian. Egg capsules numerous, each containing single egg. In birds. Cosmopolitan. Type-species *C. digonopora* (Pasquale, 1890).



Figs 24.30–24.32 *Cotugnia digonopora* (Pasquale, 1890). 24.30. Scolex. 24.31. Mature proglottid. 24.32. Gravid proglottid.



Figs 24.33-24.36 *Abuladzugnia gutterae* (Ortlepp, 1938). 24.33. Apex of scolex. 24.34. Rostellar crown. 24.35. Mature proglottid (one side). 24.36. Gravid proglottid.
Figs 24.37-24.43 *Soninotaurus rhynchota* (Ransom, 1909). 24.37. Scolex. 24.38. Rostellar hooks. 24.39. Sucker spine. 24.40. Rostellar spines. 24.41. Scolex, apical view. 24.42. Mature proglottid. 24.43. Gravid proglottid.

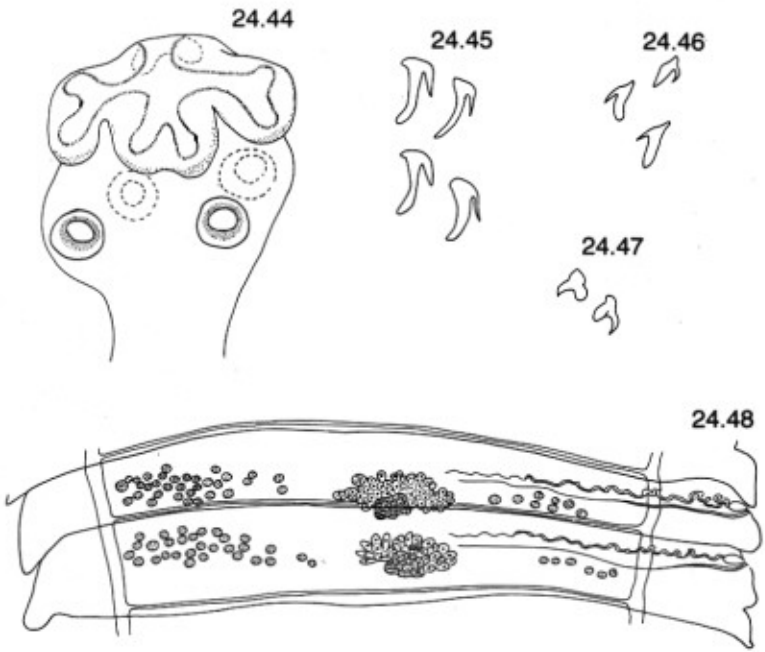
13b. Genital organs single per proglottid ..... **18.**

14a. Genital organs double per proglottid. Rostellar crown four-lobed, discontinuous laterally ..... ***Abuladzugnia*** **Spasskii, 1973. (Figs 24.33–24.36)**
Diagnosis: Rostellum large, armed with a double row of small hammer-shaped hooks. Suckers unarmed. Proglottids numerous, craspedote. Only ventral osmoregulatory canals present. Genital pores bilateral. Cirrus-sac small, extravascular. Testes numerous, internal and external to osmoregulatory canals. Ovaries lateral, lobed. Vitelline glands postovarian. Numerous egg capsules, each containing single egg. In Galliformes. Africa. Type-species *A. gutterae* (Ortlepp, 1938).

14b. Genital organs single. Rostellar crown uninterrupted ..... **15.**

15a. Rostellar crown lobed. Uterus replaced by egg capsules containing a single egg ..... **16.**
15b. Rostellar crown undulating or in flattened rows. Uterus persistent .... **17.**

16a. Rostellar crown forms eight lobes. Parasites of North American Piciformes ..... ***Soninotaurus*** **Spasskii, 1973. (Figs 24.37–24.43)**
Diagnosis: Rostellum armed with double row of small, hammer-shaped hooks. Accessory spines present. Suckers armed. Proglottids numerous, craspedote. Dorsal and ventral pairs of osmoregulatory canals present. Genitalia single. Genital



Figs 24.44–24.48 *Calostaurus macropus* (Ortlepp, 1922). 24.44. Scolex. 24.45. Rostellar hooks. 24.46. Rostellar spines. 24.47. Sucker spines. 24.48. Mature proglottids.

pores unilateral. Cirrus-sac small, extravascular. Testes numerous, lateral and posterior to female organs. Ovary median, lobed. Vitellarium postovarian. Egg capsules numerous, containing single egg. In Piciformes. North America. Type-species *S. rhynchota* (Ransom, 1909).

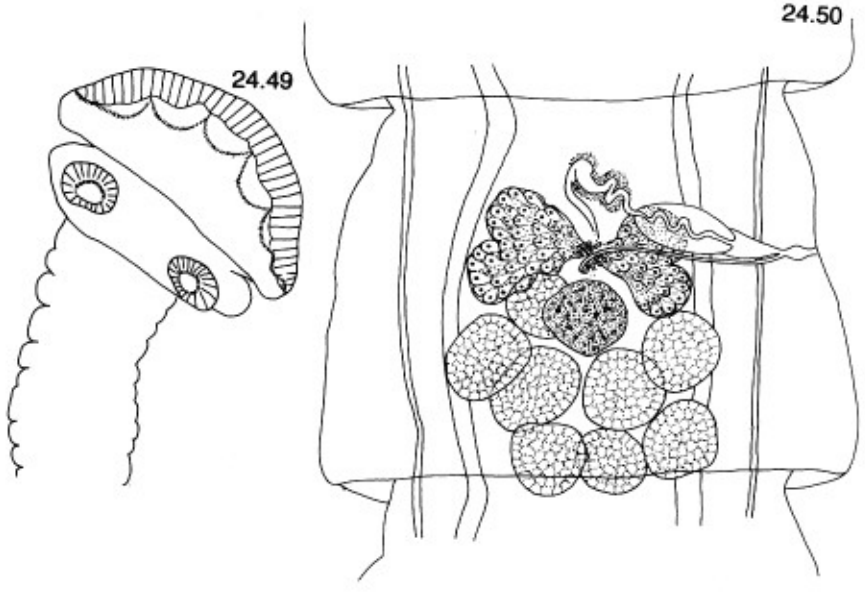
16b. Rostellar crown forms four or six lobes or a Maltese cross. In Australian marsupials ..... ***Calostaurus*** **Sandars, 1957. (Figs 24.44–24.48)**

Diagnosis: Rostellum enormous, armed with double row of small hammer-shaped hooks. Accessory spines present. Suckers armed. Proglottids numerous, craspedote or not. Paired dorsal and ventral osmoregulatory canals present. Genitalia single. Genital pores unilateral. Cirrus-sac small, extravascular. Testes numerous, usually in two lateral fields but occasionally confluent behind female organs. Ovary median, lobed, often distinctly bilobed. Vitellarium compact, postovarian. Egg capsules numerous, containing one egg (exceptionally up to three). In marsupials. Australia, Papua New Guinea. Type-species *C. macropus* (Ortlepp, 1922).

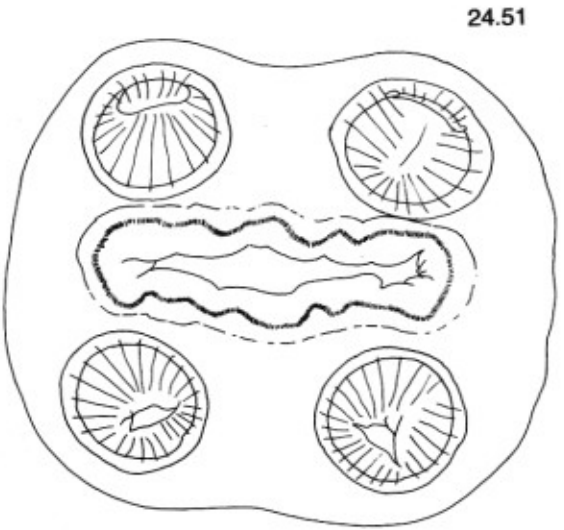
17a. Rostellar hooks in undulating rows ..... ***Ophryocotyle*** **Friis, 1870. (Figs 24.49, 24.50)**

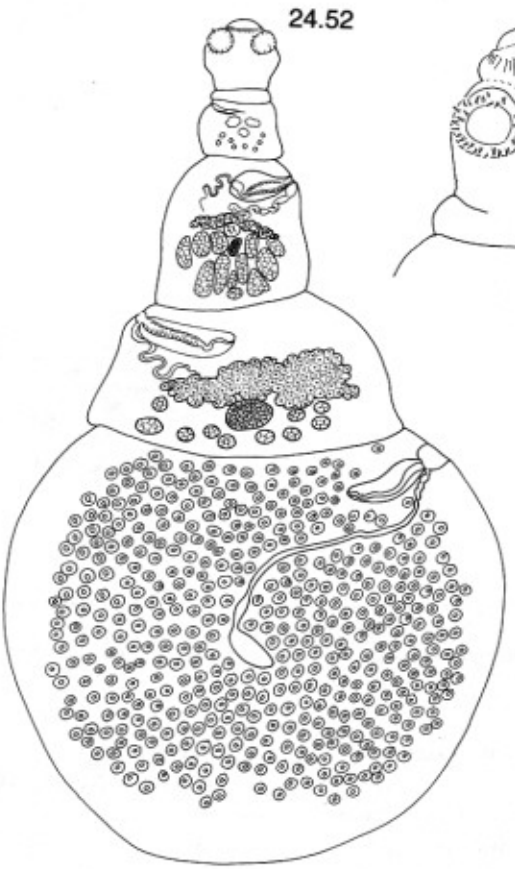
(Syn. *Burtiella* Spasskii & Kornyushin, 1977.)

Diagnosis: Rostellar hooks small, in two rows. Minute spines may be present on base of rostellum. Suckers armed. Proglottids craspedote. Reproductive organs single. Genital pores alternating regularly or irregularly. Cirrus-sac small. Ovary median to aporal. Uterus sac-like, lobed. In birds. Holarctic, Ethiopian, Neotropical, Oriental. Type-species *O. proteus* Friis, 1870.



Figs 24.49, 24.50 *Ophryocotyle proteus* Friis, 1870. 24.49. Scolex. 24.50. Mature proglottid.





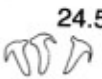
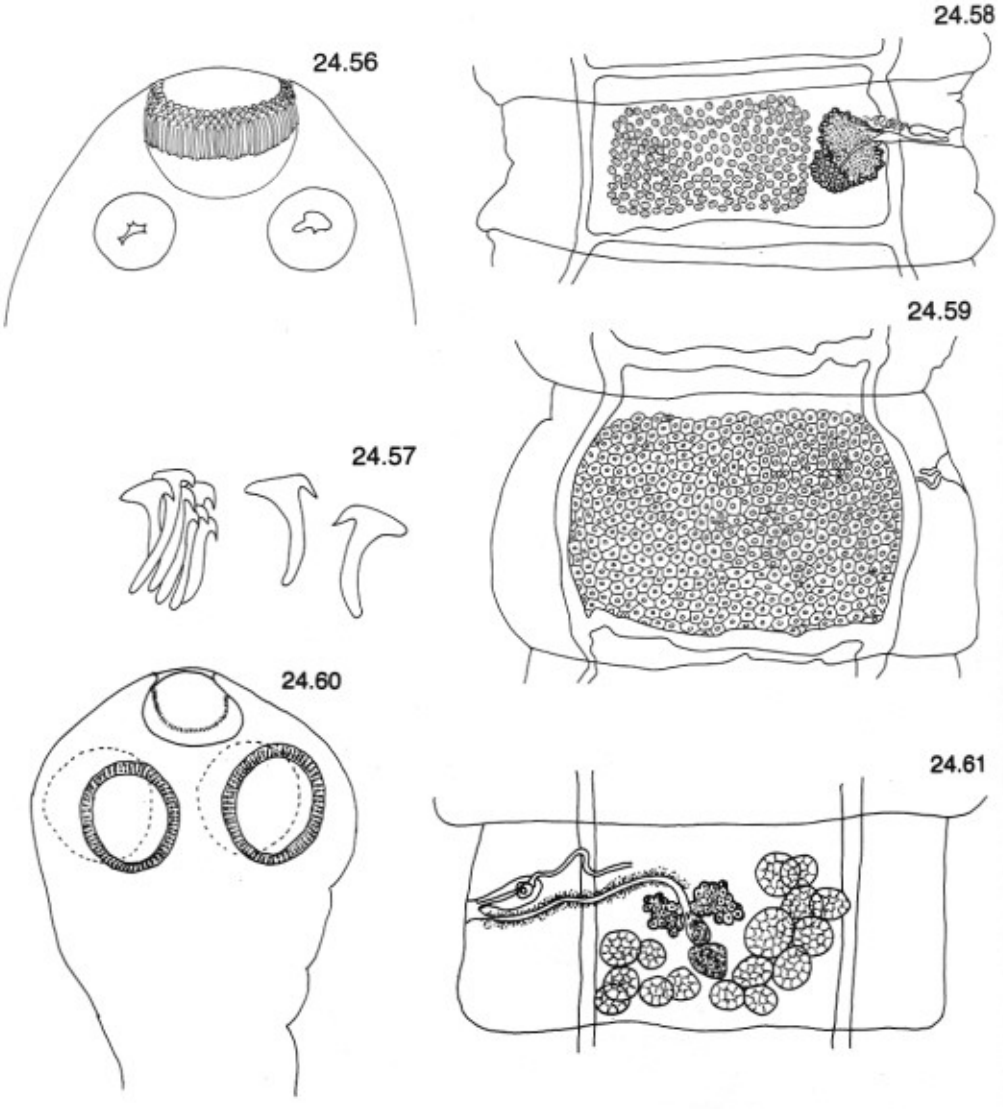


Fig. 24.51 *Fernandezia goizuetai* López-Neyra, 1936. Scolex, apical view.
Figs 24.52-24.55 *Davainea proglottina* (Davaine, 1860). 24.52. Entire worm. 24.53. Scolex. 24.54. Rostellar hooks. 24.55. Sucker spines.



Figs 24.56-24.59 *Porogynia paronai* (Moniez, 1892). 24.56. Scolex. 24.57. Rostellar hooks. *24.58.* Mature proglottid. *24.59.* Gravid proglottid.
Figs 24.60, 24.61 *Ophryocotylus dinopilium* Srivastava & Capoor, 1977. (After Srivastava & Capoor, 1982.) 24.60. Scolex. 24.61. Mature proglottid.

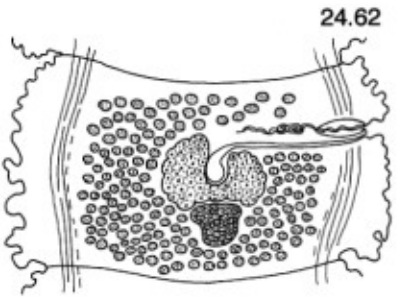
17b. Rostellar crown a flattened irregular oval .... ***Fernandezia*** **López-Neyra, 1936. (Fig. 24.51)**

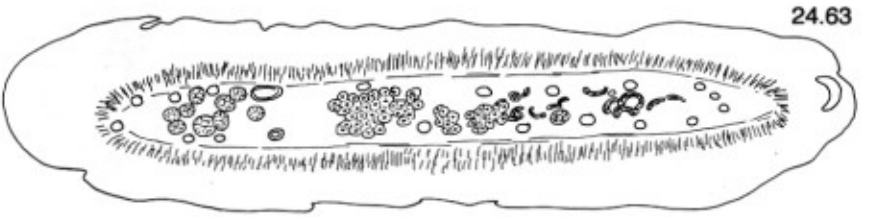
Diagnosis: Rostellar hooks small, in two rows. Suckers unarmed. Proglottids craspedote. Reproductive organs single. Genital pores irregularly alternating. Cirrus-sac small. Testes numerous. Ovary median. Uterus persistent, deeply lobate. In Passeriformes. Palaearctic, Ethiopian, Oriental. Type-species *F. goizuetai* López-Neyra, 1936.

18a. Proglottids few ..... ***Davainea*** **Blanchard, 1891. (Figs 24.52–24.55)**
Diagnosis: Rostellum armed with a double row of small hammer-shaped hooks. Suckers armed or not. Strobila small, proglottids very few. Genitalia single. Genital pores unilateral or alternating irregularly. Cirrus-sac large, crosses osmoregulatory canals and often crosses mid-line of proglottid. Cirrus conspicuously armed. Testes few, mainly postovarian. Vagina armed. Ovary median or slightly poral, lobed, often strongly bilobed. Vitellarium postovarian. Egg capsules numerous, each containing one egg. In birds. Cosmopolitan. Type-species *D. proglottina* (Davaine, 1860).

18b. Proglottids numerous ..... **19.**

19a. Rostellar hooks in three circles. Testes in a single aporal field. Ovary and vitellarium poral .... ***Porogynia*** **Railliet & Henry, 1909. (Figs 24.56–24.59)**
(Syn. *Polycoelia* Fuhrmann, 1907, preoccupied.)
Diagnosis: Rostellum armed with large hammer-shaped hooks. Suckers unarmed. Proglottids numerous, craspedote. Only ventral pair of osmoregulatory



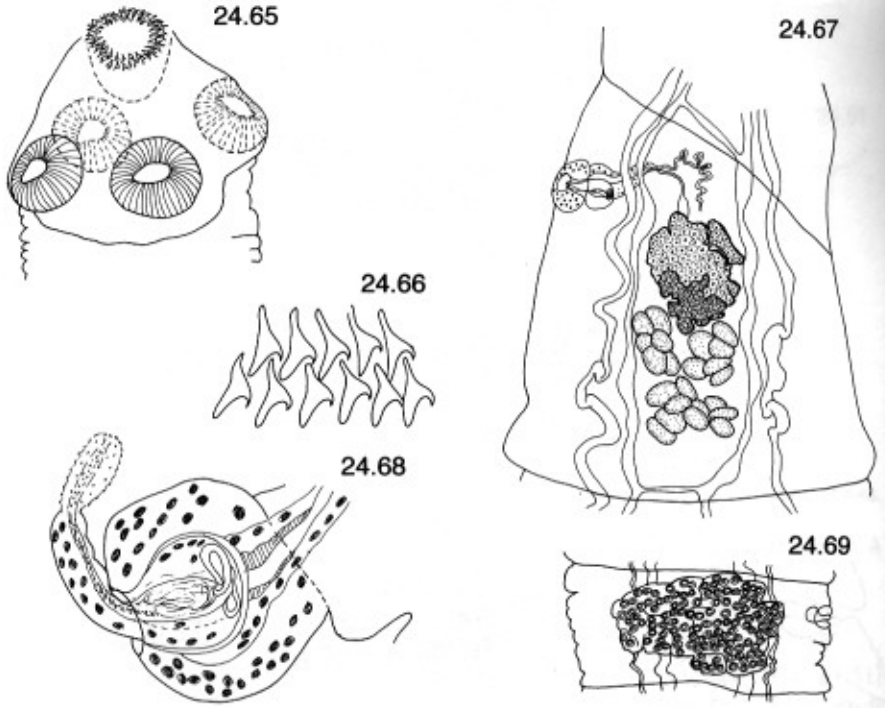


Figs 24.62, 24.63 *Davaineoides vigintivasus* (Skryabin, 1914). (Fig. 24.62 after Skryabin, 1914.) 24.62. Mature proglottid. 24.63. Same in transverse section.
Fig. 24.64 *Delamuretta polycalceola* (Janicki, 1902). (After Janicki, 1902.) Mature proglottid.

canals present. Genital pores unilateral. Cirrus-sac small, extravascular. Testes numerous. Ovary poral, fan-shaped. Vitellarium behind and slightly aporal to ovary. Egg capsules numerous, each containing single egg. In Galliformes and Hyracoidea. Europe, Africa. Type-species *P. paronai* (Moniez, 1892).

19b. Rostellar hooks in two circles ..... **20.**
19c. Rostellar hooks in one circle .....
..... ***Ophryocotylus*** **Srivastava & Capoor, 1977. (Figs 24.60, 24.61)**
Diagnosis: Rostellar hooks numerous, small. Suckers armed. Proglottids craspedote. Reproductive organs single. Genital pores unilateral. Cirrus-sac small. Testes numerous. Ovary median. Uterus sac-like, persistent. In Piciformes. India. Type-species *O. dinopilium* Srivastava & Capoor, 1977.

20a. Longitudinal osmoregulatory canals 20 .....
..... ***Davaineoides*** **Fuhrmann, 1920. (Figs 24.62, 24.63)**
Diagnosis: Scolex unknown. Proglottids numerous, wider than long. Osmoregulatory canals numerous, ten dorsal and ten ventral. Genitalia single. Genital pores alternate irregularly. Cirrus-sac small, reaching but not crossing poral osmoregulatory canals. Testes numerous, surrounding ovary. Ovary median,



Figs 24.65-24.69 *Dollfusoquenta dollfusi* (Quentin, 1964). (Figs 24.65, 24.68, 24.69 after Quentin, 1964.) 24.65. Scolex. 24.66. Rostellar hooks. 24.67. Mature proglottid. 24.68. Protruded atrial region. 24.69. Gravid proglottid.

bilobed. Vitellarium postovarian, compact. Egg capsules numerous, containing single egg. In Galliformes. Brazil. Type-species *D. vigintivasus* (Skryabin, 1914).

20b. Longitudinal osmoregulatory canals six ..... ***Delamuretta* Spasskii, 1977. (Fig. 24.64)**

(Syn. *Delamurella* Spasskii & Spasskaya, 1976, preoccupied.)

Diagnosis: Rostellum armed with a double row of hammer-shaped hooks. Rostellar spines present. Suckers armed. Proglottids numerous. Genitalia single. Genital pores unilateral or alternate irregularly. Cirrus-sac small, extravascular. Testes numerous, in two fields lateral to ovary. Ovary median, bilobed. Vitellarium postovarian, compact. Egg capsules numerous, containing single egg. In murid rodents. Africa, India. Type-species *D. polycalceola* (Janicki, 1902).

20c. Longitudinal osmoregulatory canals two to four ..... **21.**

21a. Uterus persistent ..... **22.**

21b. Uterus replaced by egg capsules with a single egg ..... **23.**

22a. Rostellar hooks not typically davaineid. Genital atrium protrusible, encloses cirrus-sac and distal vagina. In African rodents ..... ***Dollfusoquenta* Spasskii, 1973. (Figs 24.65–24.69)**

Diagnosis: Scolex large in relation to strobila. Rostellum armed with double row of about 100 hooks with short blades and massive guards. Proglottids numerous. Paired dorsal and ventral osmoregulatory canals present. Genitalia single. Genital pores unilateral (occasionally alternating irregularly). Testes numerous, in single postovarian field. Ovary median, lobed. Vitellarium postero-dorsal to ovary, lobed. Uterus persistent, saccular. In rodents. Africa. Type-species *D. dollfusi* (Quentin, 1964).

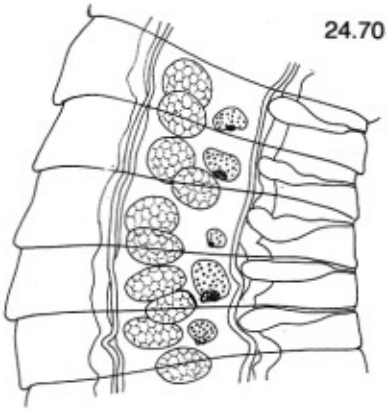
22b. Rostellar hooks typically davaineid. Genital atrium not as above. In birds, Ethiopian, Oriental, Neotropical ..... ***Ophryocotyloides* Fuhrmann, 1920. (Not illustrated.)**

Diagnosis: Rostellar hooks numerous, small. Suckers armed. Proglottids craspedote. Reproductive organs single. Genital pores unilateral. Cirrus-sac small. Testes numerous. Ovary median. Uterus persistent, lobate. In birds. Ethiopian, Oriental, Neotropical. Type-species *O. uniuterina* (Fuhrmann, 1908).

23a. Testes two. In Pholidota ..... ***Diorchiraillietina* Yamaguti, 1959. (Figs 24.70, 24.71)**

Diagnosis: Rostellum armed with a double row of small hammer-shaped hooks. Suckers armed. Proglottids numerous. Paired dorsal and ventral osmoregulatory canals present. Genitalia single. Genital pores unilateral. Cirrus-sac crosses osmoregulatory canals. Testes aporal to ovary. Ovary median, bilobed. Vitellarium postovarian. Egg capsules numerous, each containing single egg. In Pholidota. Sri Lanka, Java. Type-species *D. contorta* (Zschokke, 1895).

23b. Testes more than two ..... **24.**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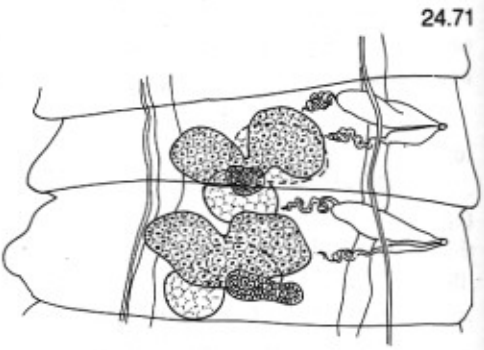
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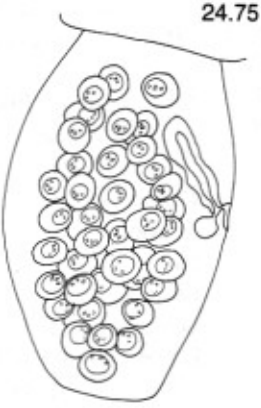
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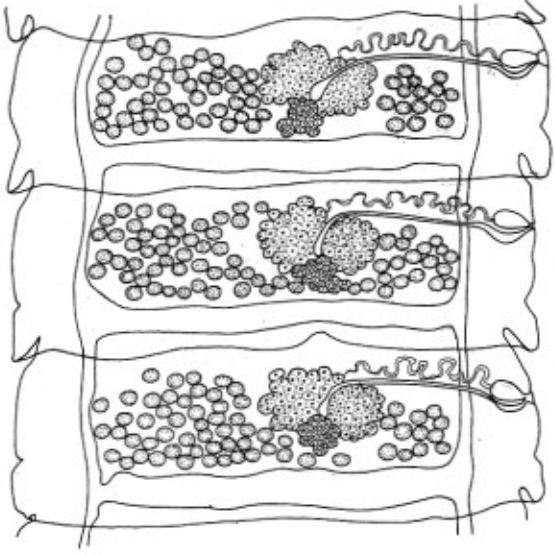
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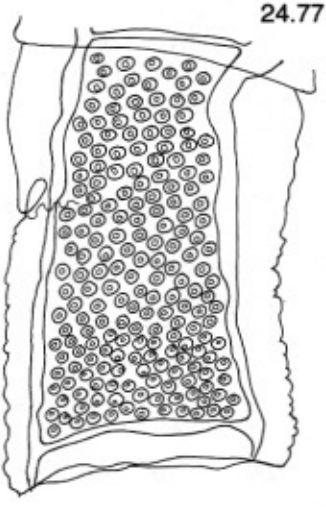

24.77

24a. Cirrus-sac crosses mid-line of proglottid. Cirrus armed with large spines. Vagina distally inflated, armed or not .... *Numidella* **Spasskaya & Spasskii, 1971. (Figs 24.72–24.75)**

Diagnosis: Rostellum armed with double row of small hammer-shaped hooks. Suckers armed. Proglottids numerous, craspedote. Genitalia single. Genital pores unilateral. Vagina usually armed distally. Testes relatively few, in semicircle around female organs. Ovary median to submedian, usually bilobed. Vitellarium postovarian. Egg capsules numerous, contain single egg. In Galliformes. Cosmopolitan. Type-species *N. numida* (Fuhrmann, 1912).

24b. Genital ducts not as above ..... **25.**

25a. Genital pores unilateral ..... **26.**
25b. Genital pores alternate irregularly ..... **27.**

26a. Rostellar hooks small, numerous .... *Paroniella* **Fuhrmann, 1920. (Figs 24.76, 24.77)**

(Syns *Corvinella* Spasskaya & Spasskii, 1971, preoccupied; *Meggittia* López-Neyra, 1929*; *Metaparonia* Spasskii & Spasskaya, 1976; *Raillietina* (*Paroniella*) Fuhrmann, 1920; *Tetraonetta* Spasskaya & Spasskii, 1971.)

Diagnosis: Rostellum armed with double row of small hammer-shaped hooks. Suckers armed or not. Proglottids numerous, usually craspedote. Genitalia single. Genital pores unilateral. Cirrus-sac usually small and extravascular but may be larger, crossing osmoregulatory canals. Testes usually numerous, variable in distribution. Ovary median or submedian. Vitellarium postovarian. Egg capsules numerous, each containing single egg. In birds and mammals. Cosmopolitan. Type-species *P. longispina* (Fuhrmann, 1909).

26b. Rostellar hooks few (26–32), large .... *Paspalia* **Spasskaya & Spasskii, 1971. (Figs 24.78, 24.79)**

Diagnosis: Large rostellar hooks in two circular rows. Suckers armed. Proglottids craspedote. Reproductive organs single. Genital pores unilateral. Cirrus-sac small, not crossing osmoregulatory canals. Testes numerous. Ovary median. Eggs single in capsules (?). In woodpecker. Palaearctic. Type-species *P. macracanthos* (Paspalewa & Woidowa, 1969).

27a. Ovary poral. Testes confined to poral postovarian field. In Pterocletiformes ..... *Gvosdevinia* **Spasskii, 1973. (Fig. 24.80)**

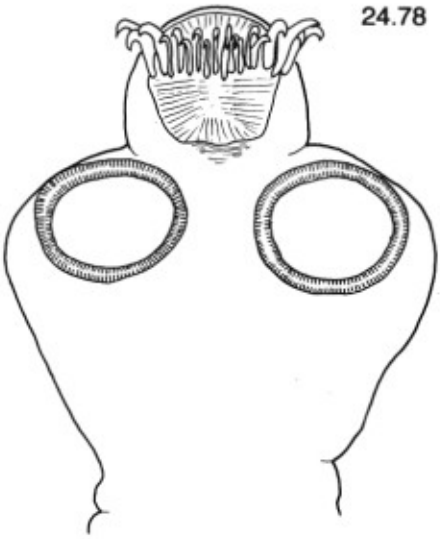
Diagnosis: Rostellum broad, armed with double row of small hammer-shaped hooks. Suckers unarmed. Proglottids numerous, wider than long. Pair of dorsal

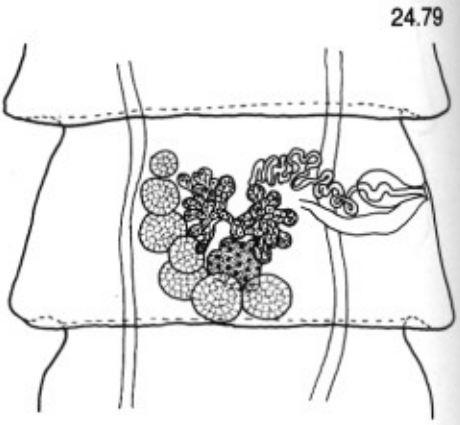
Figs 24.70, 24.71 *Diorchirailletina contorta* (Zschokke, 1895). 24.70. Early mature proglottid. 24.71. Mature proglottid.

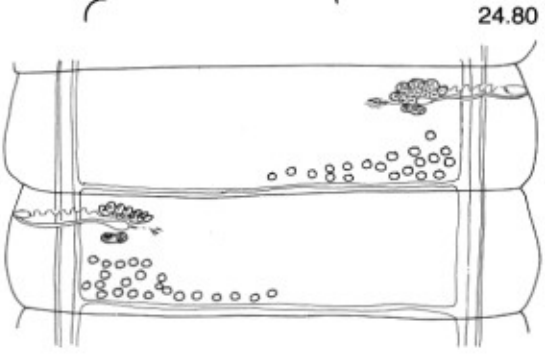
Figs 24.72–24.75 *Numidella numida* (Fuhrmann, 1912). 24.72. Scolex. 24.73. Mature proglottid. 24.74. Protruded cirrus. 24.75. Gravid proglottid.

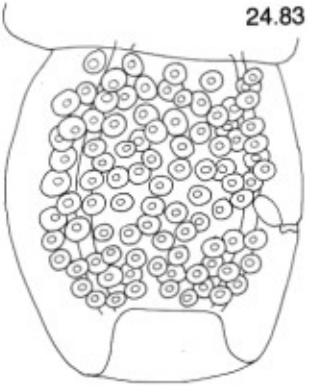
Figs 24.76, 24.77 *Paroniella urogalli* (Modeer, 1790). 24.76. Mature proglottid. 24.77. Gravid proglottid.

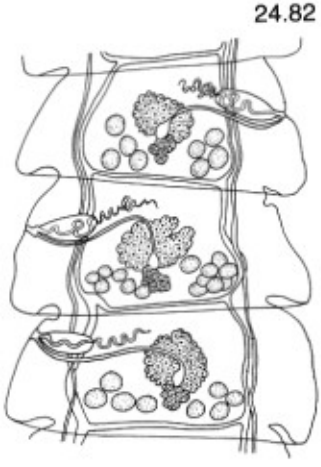
* See footnote p. 437.











Figs 24.78, 24.79 *Paspalia macracanthos* (Paspalewa & Woidowa, 1969). 24.78. Scolex. 24.79. Mature proglottid.

Fig. 24.80 *Gvosdevinia pterocleti* (Gvozdev, 1961). (After Gvozdev, 1961b.) Early mature proglottids.

Figs 24.81-24.83 *Skrjabinia cesticillus* (Molin, 1858). 24.81. Scolex. 24.82. Mature proglottids. 24.83. Gravid proglottid.

and of ventral osmoregulatory canals present, dorsal canals poral. Genitalia single. Genital pores alternate irregularly. Cirrus-sac extravascular. Testes numerous. Ovary fan-shaped. Vitellarium postovarian. Egg capsules numerous, containing single egg. In Pterocletiformes. Palaearctic. Type-species *G. pterocleti* (Gvozdev, 1961).

27b. Ovary median. Testes poral and aporal .... *Skrjabinia* Fuhrmann, 1920. (Figs 24.81–24.83)
(Syns *Armacetabulum* Movsesyan, 1966; *Brumptiella* López-Neyra, 1929*; *Daovantienia* Spasskii & Spasskaya, 1976; *Markewitchella* Spasskii & Spasskaya, 1972; *Raillietina (Skrjabinia)* Fuhrmann, 1920.)

Diagnosis: Rostellum armed with double row of small hammer-shaped hooks. Suckers armed or not. Proglottids numerous, craspedote. Genitalia single. Genital pores alternate irregularly. Cirrus-sac usually small and extravascular but may cross osmoregulatory canals. Testes usually numerous. Ovary median to submedian, lobed. Egg capsules numerous, each containing single egg. In birds and mammals. Cosmopolitan. Type-species *S. cesticillus* (Molin, 1858).

Subfamily Idiogeninae Fuhrmann, 1907

Key to genera

1a. Body robust. Uterus saccular. Cirrus-sac not reaching to mid-line of proglottid ..... 3.

1b. Body delicate. Uterus inverted U-shape. Cirrus-sac large, reaching to or beyond mid-line of proglottid ..... 2.

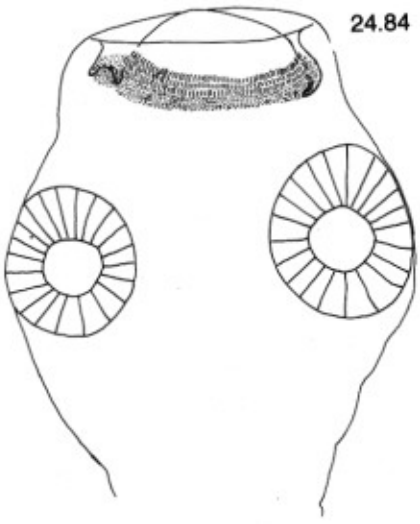
2a. Rostellum bearing three to five irregular rows of hooks .... *Idiogenes* Krabbe, 1868. (Figs 24.84, 24.85)
(Syns *Ersinogenes* Spasskaya, 1961; *Paraidiogenes* Movsesyan, 1971.)

Diagnosis: Pseudoscolex may develop. Rostellum with hammer-shaped hooks. Accessory spines in annular patch proximal to rostellar hooks (easily lost). Suckers unarmed (? or armed with hooks easily lost). Proglottids distinctly craspedote. Genital pores unilateral. Testes few to several. Ovary median. Uterus inverted U-shape. Paruterine organ large; extends anteriorly to uterus. In Gruiformes. Palaearctic. Type-species *I. otidis* Krabbe, 1867.

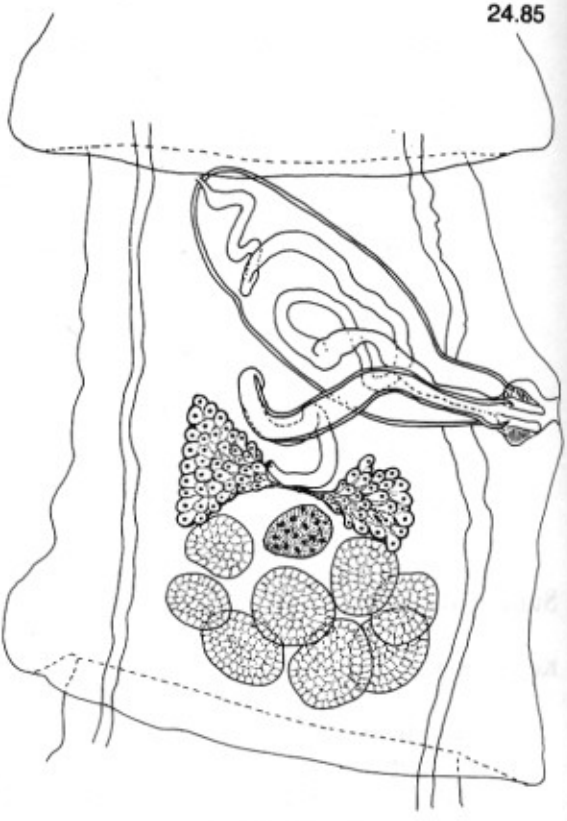
2b. Rostellum bearing two regularly alternating rows of hooks .... *Pseudidiogenes* Movsesyan, 1971. (Figs 24.86, 24.87)

Diagnosis: Accessory spines in annular patch proximal to rostellar hooks (easily lost). Suckers armed (hooks easily lost). Proglottids distinctly craspedote. Genital pores unilateral. Cirrus-sac large, reaches to or beyond mid-line of proglottid.

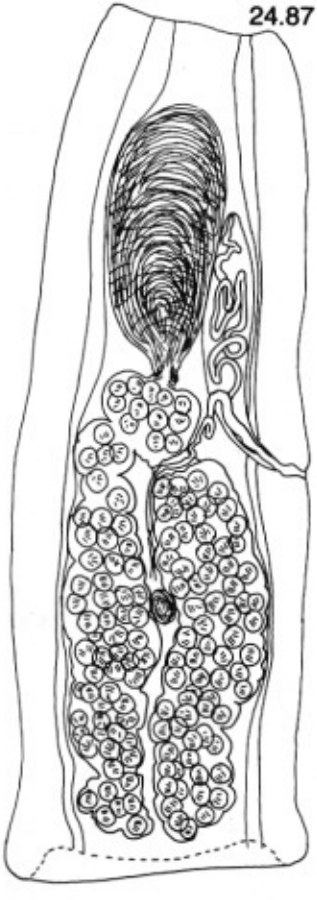
*NB. Schmidt's (1986) placement of *Brumptiella* and *Meggittia* as synonyms of two genera 'in part' is a confusion of nomenclature and systematics. *Brumptiella* shares the same type-species as *Skrjabinia* and must, therefore, fall as an objective synonym. The type of *Meggittia, M. bolivari* López-Neyra, 1929, has unilateral genital pores; therefore, the genus is a synonym of *Paroniella*. *Kotlania* López-Neyra, 1929, the type of which is *Raillietina echinobothrida* (Megnin, 1880) is a synonym of *Raillietina*. The genital pores of *R. echinobothrida* are normally unilateral and only exceptionally do they alternate in short series.



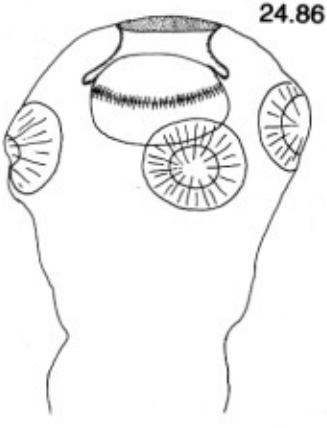
24.84



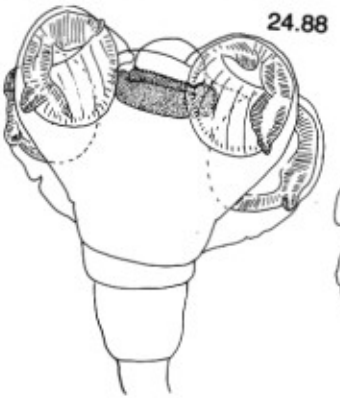
24.85

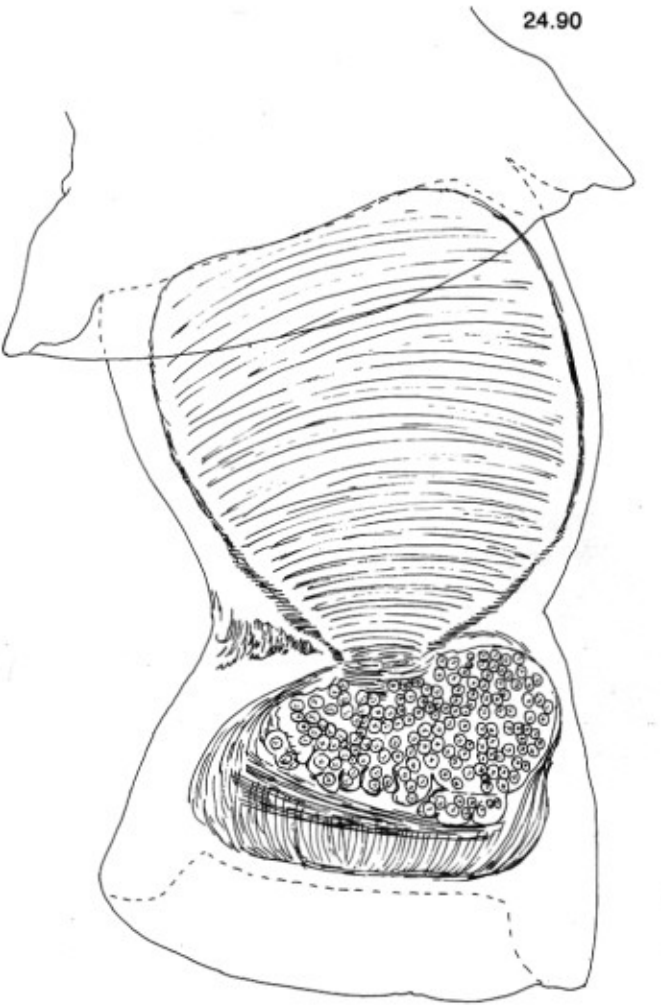


24.87



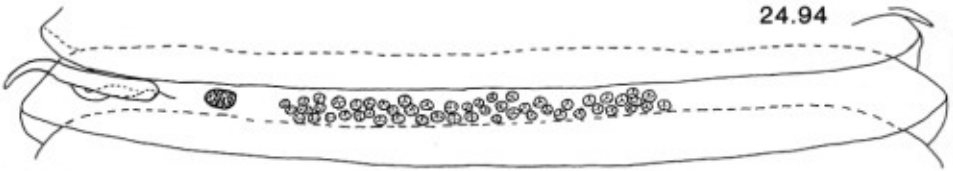
24.86

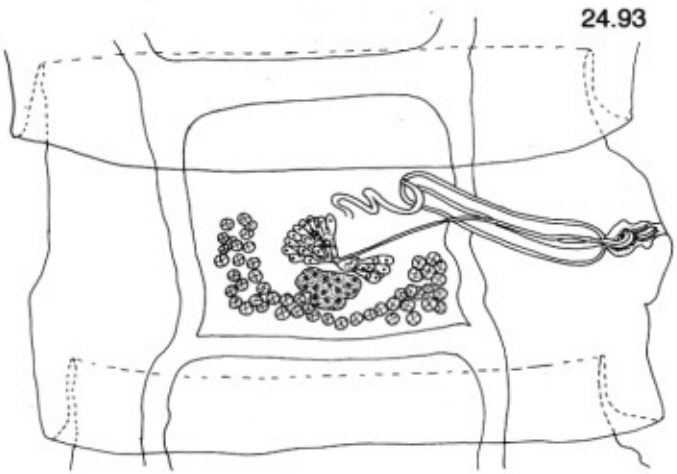




Figs 24.84, 24.85 *Idiogenes otidis* Krabbe, 1867. 24.84. Scolex. 24.85. Mature proglottid. **Figs 24.86, 24.87** *Pseudidiogenes flagellum* (Goeze, 1782). 24.86. Scolex. 24.87. Gravid proglottid.

Figs 24.88-24.90 *Otiditaenia* Beddard, 1912. 24.88. *O. macqueeni* (Woodland, 1930). Scolex. 24.89. *O. conoideis* (Bloch, 1782). Mature proglottid. 24.90. *O. conoideis*. Gravid proglottid. (Fig. 24.89 after Gomez, 1981.)





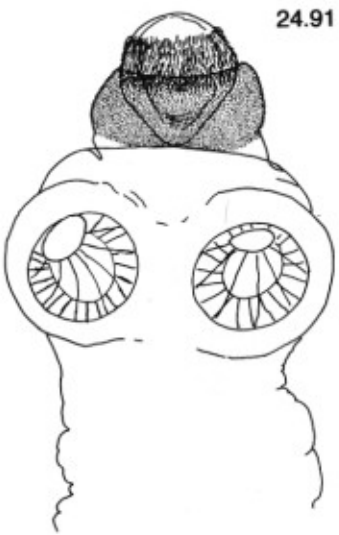


Fig. 24.91 *Sphyroncotaenia uncinata* Ransom, 1911. Scolex.
Figs 24.92, 24.93 *Chapmania tauricollis* (Chapman, 1876). 24.92. Scolex. 24.93. Mature proglottid.
Fig. 24.94 *Satyanarayana satyanarayani* Khan, 1984. (After Khan, 1984.) Mature proglottid.

Testes few to several. Ovary median. Uterus inverted U-shape. Paruterine organ large, extends anteriorly to uterus. In Gruiformes, Falconiformes, Passeriformes. Cosmopolitan. Type-species *P. flagellum* (Goeze, 1782).

3a. Suckers bearing lappets ..... ***Otiditaenia* Beddard, 1912. (Figs 24.88–24.90)**
(Syns *Schistometra* Cholodkowsky, 1912; *Paraschistometra* Woodland, 1930.)

Diagnosis: Rostellum with two rows of hooks; also bears accessory spines. Suckers unarmed. Proglottids craspedote. Reproductive system single. Genital pores unilateral or alternating irregularly. Cirrus-sac small. Testes numerous. Ovary poral. Uterus divided, saccular. Bulk of paruterine organ anterior to uterus. In Gruiformes. Palaearctic, Ethiopian. Type-species *O. eupodotis* Beddard, 1912 [now considered a synonym of *O. conoideis* (Bloch, 1782)].

3b. Suckers rounded ..... **4.**

4a. Two rows of small rostellar hooks ..... **5.**

4b. Twelve irregular rows of small hammer-shaped hooks ..... ***Sphyroncotaenia* Ransom, 1911. (Fig. 24.91)**

Diagnosis: Numerous accessory spines on rostellum proximal to hooks. Suckers rounded, unarmed. Proglottids craspedote. Osmoregulatory canals four reducing to two along strobila. Reproductive system single. Genital pores unilateral. Cirrus-sac small. Testes numerous. Ovary poral. Uterus sac-like. Paruterine organ mainly anterior to uterus. In Gruiformes. Ethiopian. Type-species *S. uncinata* Ransom, 1911.

5a. Ovary median or porally submedian. Testes numerous, poral and aporal to ovary ..... ***Chapmania* Monticelli, 1893. (Figs 24.92, 24.93)**
(Syn. *Capsodavainea* Fuhrmann, 1901.)

Diagnosis: Rostellum armed with two undulating rows of small, hammer-shaped hooks; accessory spines often present. Suckers rounded, no lappets but aperture closed by two or three semicircular valves. Proglottids craspedote. Osmoregulatory canals four, may reduce to two along strobila. Reproductive system single. Genital pores alternating irregularly. Cirrus-sac large, projecting into median field. Uterus ramifying when young; deeply lobed saccular later. Paruterine organ anterior to uterus. In Gruiformes, Rheiformes, Bucerotiformes. Palaearctic, Ethiopian, Neotropical, Oriental. Type-species *C. tauricollis* (Chapman, 1876).

5b. Ovary poral. Testes numerous, entirely aporal to ovary ..... ***Satyanarayana* Khan, 1984. (Fig. 24.94)**

Diagnosis: Rostellum armed with two rows of small hammer-shaped hooks. Suckers rounded, unarmed. Proglottids wider than long, craspedote. Osmoregulatory canals four. Genital organs single. Genital pores alternating irregularly. Cirrus-sac small. Uterus saccular. Paruterine organ anterior to uterus. In lungs of Ciconiiformes. India. Type-species *S. satyanarayani* Khan, 1984.