17

Family Anoplocephalidae Cholodkovsky, 1902

I. BEVERIDGE

Veterinary Clinical Centre, School of Veterinary Science, University of Melbourne, Princes Highway, Werribee, Victoria 3030, Australia.

Introduction

Traditionally, the cyclophyllidean family Anoplocephalidae has been characterized by the lack of a rostellum and any form of scolex armature. The implication is that this condition is plesiomorphic or primitive when compared with related families in which an armed rostellum is present, such as the Davaineidae, Dilepididae and Hymenolepididae. However, the rostellum and/or its armature can be lost as a secondary phenomenon and there are numerous species or genera within the latter three families which have secondarily lost their rostellum and/or their rostellar armature. Thus, because of the obvious limitations of the principal character defining the family, the four subfamilies of the Anoplocephalidae could conceivably be a polyphyletic assemblage of taxa, and there is considerable morphological evidence to indicate that this is indeed the case (see Voge, 1969). Four types of uterine development have been described within the family, and these form the basis of the division into the subfamilies Anoplocephalinae, Linstowiinae, Inermicapsiferinae and Thysanosomatinae. In the Anoplocephalinae, the uterus is tubular or reticular but persists in gravid proglottids; in the Linstowiinae, eggs are embedded singly in the parenchyma in so-called 'uterine' capsules; in the Inermicapsiferinae eggs are enclosed in groups in 'fibrous' parenchymatous capsules, while in the Thysanosomatinae, eggs are enclosed in paruterine organs which develop as appendages of the uterus.

Lopez-Neyra (1954, 1955) and Joyeux & Baer (1961) drew attention to the remarkable similarity in uterine structure between the various subfamilies of the Anoplocephalidae, Dilepididae and Davaineidae. In each family, there are subfamilies with tubular uteri, with parenchymatous egg capsules, with paruterine organs, or with eggs embedded singly in the parenchyma. Lopez-Neyra (1954, 1955) attempted to translate this observation into a taxonomic system based on uterine structure rather than rostellar armature by transferring many davaineid genera to the Anoplocephalidae, while Joyeux & Baer (1961) transferred a number of linstowiid genera to the Davaineinae. The latter authors hesitated to follow this course to its conclusion because of the immensity of the taxonomic upheavals involved.

Considerable confusion surrounds the relationships of the Inermicapsiferinae. The Inermicapsiferinae resembles very closely those genera of the Davaineinae with several eggs per egg capsule, not only in uterine structure but also in features of the mature proglottid, differing solely in lacking rostellar and sucker armature. Species of the davaineid genus *Baerfainia* Yamaguti, 1955 are known which have a vestigial rostellum (Baer & Fain, 1955), providing an obvious link between the Inermicapsiferinae and the Davaineidae. So close is the morphological resemblance between these two taxa, that Baer & Fain (1955) transferred most of the genera of the Linstowiinae (which at that time included the Inermicapsiferinae) to the Davaineidae.

There are also important biological differences between the anoplocephalid subfamilies supporting the morphological differences, and these have been summarized by Stunkard (1961, 1969). The anoplocephaline members have oribatid mites as intermediate hosts, the linstowiine members have coleopterans as intermediate hosts and the thysanosomatine members have psocopterous insect intermediate hosts. The life-cycles of the inermicapsiferines have not been adequately documented.

More recently, Freeman (1973) proposed a phylogeny of the Cyclophyllidea based on the characters of the metacestode, placing the Anoplocephalinae close to the Hymenolepididae, Davaineidae and Dipylidiinae in possessing a cysticercoid and cercomer, while the Linstowiinae was aligned with the Taeniidae, Amabiliidae and some Dilepidinae, all of which possess an acaudate metacestode. In his view, the Anoplocephalidae is clearly a polyphyletic assemblage, with the Linstowiinae quite distinct from the Anoplocephalinae. He did not consider the two other subfamilies.

In spite of these recent advances in our understanding of cestode phylogeny, it seems unlikely that the time is yet ripe for the taxonomic upheaval foreseen by Joyeux & Baer (1961) or for a classification based on phylogeny. While the phylogenetic relationships of several representative genera from the various anoplocephalid subfamilies are now much clearer, the positions of many others still remain obscure, and it seems reasonable to insist on the clarification of the relationships of these genera before major dislocations occur. In particular (discussed below), *Taufikia* Woodland, 1928, traditionally placed in the Anoplocephalinae, is probably a genus of unarmed dilepidids which has been included in the Anoplocephalidae for convenience. Similarly, the 'rostellar sac' of *Sudarikovina* Spasskii, 1951 (see Hunkeler, 1974) could well represent a vestigial rostellum, and this genus may properly belong in a taxon other than the Anoplocephalinae, probably the Dilepididae or Hymenolepididae. Because of these constraints, the traditional structure of the Anoplocephalidae has been utilized in this key, since the presence of an unarmed rostellum is a useful character in identification, if not in elucidating the phylogeny of cestodes. Hopefully, in the not too distant future, it will be possible to construct a key which more closely reflects the phylogeny of the anoplocephalid cestodes.

The following key to genera of the family Anoplocephalidae has been based, wherever possible on an examination of specimens, preferably types, rather than on the literature. In several instances, the whereabouts of types are unknown and the extant descriptions are too poor to allow the validity of a genus to be assessed. In such cases, there has been no option other than to exclude the genera from consideration. Genera omitted and regarded as *genera inquirenda* are: *Coelodela*, described by Shipley (1900), *Neoaporina* erected by Saxena & Baugh (1973) for *Aporina borealis* Linstow, 1905 and *Spasskofuhrmina* erected by Palladwar & Kalyankar (1989). Specimens were not available for examination of the following genera, but they have been well or adequately described in the literature: *Diuterinotaenia* Gvozdev, 1961, *Witenbergitaenia* Wertheim, Schmidt & Greenberg, 1986, *Thysanotaenia* Beddard, 1911 and *Eranuides* Semenova, 1972.

Generally, a conservative approach has been taken to the genera of each subfamily. Where the generic characters appeared poor or in any way dubious, the genus has not been allowed to stand, although several exceptions were made. Additional work is required in a number of areas to establish the validity or otherwise of particular genera, and these are indicated below in the text.

Illustrations provided are diagrammatic only and are intended to show the principal features of the mature and gravid proglottids. The dorsoventral relationships of various organs have frequently been sacrificed for the sake of clarity, particularly with respect to the position of the uterus, which provides a series of useful taxonomic characters.

Anoplocephalinae

The subfamily Anoplocephalinae is characterized by a persistent uterus which is initially either tubular or reticular, but which finally becomes saccate. Three principal modes of uterine development have been recognized (Spasskii, 1951; Rausch, 1976). In the commonest form of development, the uterine anlage is first visible as a cord-like aggregation of cells extending transversely across the proglottid. With further development, the uterus becomes a well-defined tube of uniform diameter with a clearly detectable lumen. The diameter of the tube increases as eggs appear in its lumen (Figs 17.23, 17.24), and diverticula may appear along its anterior and posterior margins (Fig. 17.26). As the eggs develop, the uterus fills the entire proglottid (Rausch, 1976). A modification of this form of development occurs in species such as *Anoplocephaloides wimerosa*. In this species, the uterine anlage extends to the poral excretory vessels, but only two-thirds of the way across the proglottid to the aporal canals (Fig. 17.15). As the uterus fills, it extends aporally to reach the aporal canals. A more extreme situation occurs in *Crossotaenia baeri* in which the uterine anlage commences as a circular sac anterior to the ovary, and as it fills, extends laterally across the proglottid medulla (Mahon, 1954) (Figs 17.4, 17.5).

In the second form of development, the uterine anlage is first visible as a cord of cells crossing the proglottid. The lateral extremities of the uterus subsequently increase in width and become fenestrated, assuming a reticulate structure, followed by the central part of the uterus. The central part of the uterus subsequently develops anterior and posterior diverticula (Fig. 17.53), and the entire uterus eventually fills the proglottid. This type of development occurs in *Paranoplocephala omphalodes* (see Rausch, 1976).

In a third form of development, the uterine anlage appears as a broad cellular band anterior to the ovary and spreads to cover the ventral surface of the medulla. The uterus subsequently becomes reticulate, forming a uniform, complex reticulum across the entire ventral aspect of the proglottid. As eggs fill the uterus, the reticulate appearance is lost and the uterus appears saccate. Such development occurs in the genera *Diandrya* (Fig. 17.58) and *Moniezia* (Fig. 17.59).

These types of uterine development form a continuum from a simple tubular uterus to a complex reticulated type, but in each case the uterus is persistent in gravid proglottids, immediately distinguishing them from the Linstowiinae, Thysanosomatinae and Inermicapsiferinae.

While the various types of uterine development appear to be distinctive and the subdivision of the Anoplocephalidae (*sensu* Spasskii, 1951) into the Anoplocephalinae with a tubular uterus and the Monieziinae with a reticular uterus appears as a perfectly logical consequence, the distinction of the two modes of uterine development in practice remains difficult. Rausch (1976) showed that the uterine development in the genera *Andrya* and *Paranoplocephala* from rodents had been completely misunderstood by numerous earlier workers, and that while some species of *Paranoplocephala* had a slightly reticulated uterus, other species included in the genus had a simple tubular uterus. He resurrected the genus *Anoplocephaloides* Baer, 1923 for the species with a simple tubular uterus, but (Rausch, 1976) remained uncertain as to whether there were any major differences between the genera *Andrya* and *Paranoplocephala* in terms of pattern of uterine development. However, Tenora, Murai & Vaucher (1984, 1986) have subsequently reported that early uterine development differs in the two genera. Further detailed study is required to resolve these and other uncertainties, but for the present it has been decided not to utilize the Monieziinae at any level, following Schmidt (1986), until detailed studies on the uterine development of a number of other genera have been made. Particular problems remain with genera such as *Lentiella* and *Perutaenia* which have been described from extremely poor specimens, and in which the detail of the development of the uterus cannot be determined from the only existing specimens.

Uterine development in *Taufikia* Woodland, 1928 (syns *Gidhaia* Johri, 1934, *Neophronia* Saxena, 1967) is not typical of the Anoplocephalinae. In this genus, the uterus develops as an outgrowth of the uterine duct, with three main branches (Fig. 17.6), gradually branching laterally and anteriorly throughout the proglottid (Fig. 17.7). The mature uterus is branched but not reticulated and resembles representatives of the Dilepididae (see Bona, 1975) rather than the Anoplocephalinae. This genus may in fact belong to the Dilepididae, but without life-cycle studies, no definitive decision can be made.

The pyriform apparatus surrounding the embryophore figures prominently in definitions of the Anoplocephalinae. Typically characterized by two elongate horns (Spasskii, 1951), more recent studies have revealed a much greater diversity in its structure (Freeman, 1952; Rausch & Maser, 1977; Beveridge, 1976, 1985). From a taxonomic point of view, its presence may be difficult to establish, since in certain species, the pyriform apparatus only develops after eggs have been voided (Beveridge, 1976). Nevertheless, the pyriform apparatus is present in virtually all genera of Anoplocephalinae occurring in mammals, but is absent from most of the genera present in birds except for *Stringopotaenia* and possibly *Paronia* in which it is described as 'vestigial' by Burt (1939b). A detailed study of unfixed material would be needed to see if these differences, apparent from the literature, are real or not.

A major problem associated with the taxonomy of anoplocephalid cestodes is genera of which the scolex is unknown and, therefore, the lack of armature is not certain. *Aporina* Fuhrmann, 1902 has been included in spite of the lack of description of a scolex, primarily because of the unique structure of the uterus. However, the genus has been restricted to the type species. *Crossotaenia* Mahon, 1954 was initially described in the absence of a scolex, but new specimens examined in the Natural History Museum collections (BMNH 1984.6.4.4) indicate that the scolex is indeed unarmed and the genus belongs to the Anoplocephalinae. Other genera in which the scolex has been described subsequent to the erection of the taxon are *Pulluterina* Smithers, 1954 (see Weekes, 1981) and *Triuterina* Fuhrmann, 1921 (see Joyeux, Gendre & Baer, 1928; Jones, 1982). *Killigrewia* Meggitt, 1927, described without a scolex and from an unknown host is also retained for reasons discussed below. Other genera such as *Francolina* Capoor, Sawada, Bhalya & Rastogi, 1987 have been erroneously assigned to the Anoplocephalidae in spite of possessing an unarmed rostellum and obviously belong to another family, probably the Paruterinidae. By contrast, *Himalaya* Malhotra, Sawada & Capoor, 1983, described as having an unarmed rostellum, is clearly *Mosgovoyia pectinata*.

Several genera admitted as valid by Schmidt (1986) have been reduced to synonymy following examination of type or other specimens. *Perutaenia* Parra, 1953 is synonymized with *Monoecocestus* Beddard, 1914 since the vagina opens to the genital atrium anterior to the cirrus-sac. The type and only specimens are extremely macerated and few internal features can be seen clearly, particularly the uterus. Thus, new specimens are required to confirm the relationships of this species, but the position of the vagina anterior to the cirrus-sac (Parra, 1953) and the posterior distribution of the testes suggest that this species belongs within *Monoecocestus*.

Lentiella is also a synonym of *Monoecocestus*. The testes lie in the posterior part of the medulla and the vagina, which is only clearly visible in two proglottids, opens to the genital atrium anterior to the cirrus-sac, in contradistinction to Rego's (1964) description. The uterus is prominently lobed and appears to be slightly reticulated; however, in the only specimen available, from the collections of the Instituto Oswaldo Cruz (IOC 29.779), the proglottids in which the critical stages of uterine development occur are damaged. More material is required for a detailed study of uterine development, and pending this, the genus is made a synonym of *Monoecocestus*.

Eranuides Semenova, 1972 was described without a scolex and placed in the Anoplocephalinae because it had paired 'sac-like' uteri. The drawings associated with the description (Semenova, 1972, Fig. 5) in fact show a reticulated uterus and the genus is, therefore, a synonym of *Moniezia*.

Fuhrmannella Baer, 1925 was synonymized with *Moniezia* by Baylis (1935) and the decision is upheld here following a study of relevant specimens. *Flabelloskrjabinia* was erected by Spasskii (1951) for *Anoplocephala tapirus* Chin, 1938 found in a tapir from the Philippines (Chin, 1938). Chin (1938) stated that the testes were mainly in the aporal region of the proglottid and this is shown in his Fig. 2. His Fig. 3, however, shows a large number of testes in the poral region. The whereabouts of Chin's specimens are unknown; however, examination of new material from the same host species in the collections of the International Institute of Parasitology, St Albans, UK (IIP 1700) indicate that Chin's description rather than his illustration is correct and that virtually all the testes are aporal. Thus, *A. tapirus* is allied to *Anoplocephaloides* rather than *Anoplocephala* as suggested by Spasskii (1951). In addition, Sawada & Tongchai (1966) described a new cestode, *Paranoplocephala indicata*, from the Malaysian tapir, *Tapirus indicus* which, because the testes were aporal, they assigned to *Paranoplocephala*. Following Rausch's (1976) resurrection of *Anoplocephaloides*, *P. indicus* would appear to belong here. Rausch (1976) considered *Flabelloskrjabinia* distinct from *Anoplocephaloides* because of the distribution of testes shown in Chin's Fig. 3. If Chin's Fig. 3 is incorrect, *Flabelloskrjabinia* would fall as a synonym of *Anoplocephaloides*. Through the kindness of Dr Sawada, a paratype of *P. indicata* was also examined and conforms closely with the IIP material. There is probably only one species of cestode in tapirs at present and its name is *Anoplocephaloides tapirus* (syn. *P. indicata*). Thus, *Anoplocephaloides* would contain two species from perissodactyls, *A. mamillana* and *A. tapirus*. As indicated by Rausch (1976) and Genov & Georgiev (1988), *Anoplocephaloides* currently contains several groups of species, each of which may eventually warrant generic rank. If so, the generic name *Flabelloskrjabinia* would have priority as a name for the taxa parasitic in perissodactyls. Pending further study, *Flabelloskrjabinia* is here retained, provisionally, as a synonym of *Anoplocephaloides*.

Species of *Anoplocephaloides* parasitizing lagomorphs have recently been removed to a new genus *Leporidotaenia* Genov, Murai, Georgiev & Harris, 1990 based on the presence of a large, armed cirrus with a retractor muscle, a 'spinose' tegument, a protrusible genital atrium and the vagina posterior to the cirrus-sac (Genov *et al.*, 1990). Their arrangement of species differs from that utilized by Rausch (1976) and can be criticized from the point of view that most of the characters selected are relative and gradations are possible. Baer (1927) utilized the degree of development of the cirrus-sac and its associated structures in separating *Prototaenia* from *Bertiella*, a separation which has not stood the test of time. *Leporidotaenia* may, therefore, prove to be a valid taxon along with the other species groups defined by Genov & Georgiev (1988), but pending corroborating evidence it is maintained provisionally as a synonym of *Anoplocephaloides*.

In contrast to Schmidt (1986), *Gallegoides* is retained as a valid genus based on the descriptions by Tenora & Mas-Coma (1978) and Feliu *et al.* (1984) as well as examination of type specimens. *Gallegoides* differs significantly from *Anoplocephaloides* in that the uterus terminates anterior to the cirrus sac, the testes lying posterior to the uterus. A similar difference exists between *Mosgovoyia* and *Cittotaenia* when compared with *Pseudocittotaenia*, all the latter genera having paired genitalia. Beveridge (1978) hypothesized that *Cittotaenia* was derived from species of *Anoplocephaloides* by doubling of the genitalia; *Gallegoides* would likewise be a suitable ancestor for *Pseudocittotaenia*.

A number of anoplocephaline genera occur in birds rather than mammals. Several genera occur in Psittaciformes, namely *Triuterina*, recently redescribed by Jones (1982), *Biporouterina*, erected by Burt (1973), *Hemiparonia*, recently redefined by Schmidt (1972), *Paronia*, studied extensively by Burt (1939b), *Pulluterina*, recently redescribed by Weekes (1981) and *Stringopotaenia*, described by Beveridge (1978). The taxonomy of the remaining anoplocephaline genera present in psittaciform and non-psittaciform birds has been the source of considerable controversy, particularly the genera *Aporina*, *Taufikia* and *Killigrewia*. *Aporina* was erected by Fuhrmann (1902a) for a cestode from a parrot from Brazil. The scolex was not described, but the uterus is characteristic, being single, arched anterior to the female genital complex, with two lateral branches extending anteriorly. Genital pores are absent. Although several species have been added to the genus subsequently (see Spasskii, 1951, Yamaguti, 1959, Schmidt, 1986), none has the characteristic uterus or lacks genital pores, and the genus is here considered to be restricted to the type species. Validation of its position must await a redescription based on specimens with scoleces.

The genus *Killigrewia* was established by Meggitt (1927b) for a cestode, *K. frivola*, without a scolex, taken from an unknown host in Egypt. Fuhrmann (1932) reduced the genus to synonymy with *Aporina*, but Johri (1934) reinstated *Killigrewia*, redescribing what he believed to be *K. frivola* from a pigeon in India, while Saxena & Baugh (1973) have also provided evidence that the two are not synonymous, since the structure of the uterus differs and a genital pore is absent in *Aporina* but present in *Killigrewia*. They transferred *Aporina delafondi* (Railliet, 1892) to *Killigrewia*, thus conserving an otherwise dubious genus. The type specimens of *K. frivola* (BMNH 1934.5.11.3–4) were re-examined and are re-illustrated below (Fig. 17.41). The label associated with the types gives the host as 'probably *Neophron percnopterus*'. *Killigrewia* appears to be a valid genus and Saxena & Baugh (1973) appear to have been correct in their decision to transfer *A. delafondi* to *Killigrewia*. *Nepalesia* Sharma, 1943, is treated as a synonym of *Killigrewia* following Schmidt (1986). *Columbia* Srivastava & Capoor, 1966 is also a synonym of *Killigrewia* according to Capoor & Srivastava (1967) who had mistaken a seminal receptacle for a paruterine organ in their original description of *Columbia*.

The second species of *Killigrewia* described by Meggitt (1927b), *K. pamelae*, possesses a scolex and was incompletely described by this author. Examination of the description indicated that the uterus is similar to *Taufikia* and it is, therefore, transferred to the latter genus as *T. pamelae* comb. nov.

Taufikia was described from a vulture by Woodland (1928). Spasskii (1951) implied (p. 197) that the genus belonged to the Dilepididae, and as mentioned above, examination of the development of the uterus strongly supports this view. However, lacking life-cycle data, it is impossible to make a definitive decision. It is here retained only provisionally within the Anoplocephalinae.

Gidhaia Johri, 1934 resembles *Taufikia* in uterine development, but the testes in *Taufikia* are mainly anterior to the female genitalia, while in *Gidhaia* many extend laterally to the female genitalia as well. *Neophronia* Saxena, 1967 is a synonym of *Gidhaia*. Dollfus (1963) employed a definition of *Taufikia*, with *Gidhaia* as its synonym, which clearly allowed for a lateral distribution of the testes. The two genera differ slightly in testis distribution, but the patterns merge, as they do with *Neophronia*. The differences in testis distribution noted by Saxena (1969) are valid at the species level, but their generic value has yet to be determined. Consequently, *Gidhaia* and *Neophronia* are synonymous with *Taufikia*.

Biporouterina Burt, 1973, with its single species, *B. psittaculae*, was distinguished from the related genera *Hemiparonia* and *Pulluterina* by the spur-like anterior extension of the uterus in mature proglottids, a character it shared with *Triuterina*. The presence of so-called 'uterine pores', from which the generic name is derived, is not considered significant. Baylis (1927) thought that uterine pores were a significant diagnostic feature in *Bertiella anapolytica* from rodents but more recent studies (Beveridge, 1985) have not supported this notion. Burt (1973) distinguished *Biporouterina* from *Triuterina* by the presence of polar processes on the eggs of *Biporouterina* and unspecified differences in the osmoregulatory systems. Neither character seems to be of generic significance and the two taxa have, therefore, been merged.

Burt (1939b) also described a species of *Paronia*, *P. calcaruterina*, from the red-vented bulbul, *Molpastes haemorrhous*, which differed from congeners in the presence of a spur on the anteromedian aspect of the uterus, from whence the specific name was derived. A new genus, *Bulbultaenia*, is, therefore, proposed to accommodate *P. calcaruterina*. *P. calcaruterina* and *B. psittaculae* differ only in having paired rather than single genitalia, thus resembling the morphological similarities seen between the genera *Hemiparonia* – *Paronia* and *Pulluterina* – *Stringopotaenia*, all from Psittaciformes, the first of each pair having single genitalia, and the second having paired genitalia.

Moniezoides rouxi Fuhrmann, 1918 was placed in an independent genus because of morphological peculiarities of the suckers and the presence of four glands on the scolex. The uterus has been described and illustrated as being single. However, examination of the type specimens, which are in poor condition, showed apparently paired uteri. Until new material is available, it is impossible to resolve this apparent dichotomy and reliance has been placed on the characters of the scolex in the interim.

The genus *Progamotaenia* Nybelin, 1917 *sensu* Beveridge, 1976 was subdivided into four genera by Schmidt (1986). *Progamotaenia* and *Adelataenia* Beveridge, 1976 had testes in two lateral groups, with either paired uteri or a single uterus while *Fuhrmannodes* Strand, 1942 and *Wallabicestus* Schmidt, 1975, each had a single band of testes but with two uteri and a single uterus, respectively. The division of testes into one or two groups is unreliable as a specific character in several species of *Progamotaenia* (see Beveridge, 1976) and a generic division on this basis is, therefore, not advisable. *Adelataenia* Beveridge, 1976 is a *lapsus* in Schmidt (1986), and should have been *Adelataenia* gen. nov. The division of the genus into those species with a single uterus and those with paired uteri is straightforward at first sight, but genetic evidence on speciation within this taxon (Baverstock *et al.*, 1985b) suggests that the presence of a single uterus in *P. effigia* Beveridge, 1976 is a secondary reversion to a plesiomorphic character state. This being the case, a more conservative approach has been adopted here and the various genera mentioned have been included as synonyms of *Progamotaenia*. Schmidt's (1986) analysis may prove to be correct, but more evidence is needed.

Neoctenotaenia Tenora, 1976 differs from *Mosgovoyia* Spasskii, 1951 in the structure of the osmoregulatory system, which Tenora (1976) believed was a conservative taxonomic character warranting generic rank. By contrast, the species of *Mosgovoyia* and *Neoctenotaenia* share a number of characters in the distribution of the testes and the anatomy of the genital ducts (Beveridge, 1978) and are here considered congeneric.

As defined here, the genus *Moniezia* consists of a diverse collection of cestodes. Apart from the well-known representatives from ruminants and suids, there is a single species (*M. bequarti*) in rodents, as well as one (*M. rhea*) in ratite birds and one (*M. rugosa*) in primates. *M. rhea* differs from congeners in that Mehlis' gland is poorly developed (Beveridge, 1978), though this does not appear to be a useful generic character. The genus clearly warrants a detailed revision, but its subdivision at present would be premature.

Palaia Shipley, 1900 is unrecognizable and is treated as a *nomen nudum*.

Shindeia Gaikwad & Shinde, 1985 is unrecognizable and is almost certainly not an anoplocephalid. It is treated here as a *genus incertae sedis*.

Linstowiinae

In members of the Linstowiinae, the uterus is ephemeral, either persisting briefly or not being detectable at any stage in developing proglottids. The uterine epithelium forms a thin outer envelope around individual eggs (Conn, 1985) which are embedded singly in the parenchyma of the proglottid.

The genera within the Linstowiinae have been in a constant state of flux since Spasskii (1951) attempted to subdivide the large genus *Oochoristica* Lühe, 1898. His approach was rejected entirely by Della Santa (1956), while both Dollfus (1957) and Stunkard (1961) have pointed out that some genera erected by Spasskii (1951) could have been usefully retained.

In this key, where reliable morphological criteria for distinguishing genera, such as the distribution of testes, presence of lappets on the suckers and the presence of a velum on proglottids exist, then the genera have been maintained as valid. Genera or subgenera based on dubious criteria have been eliminated.

Spasskii (1987a,b, 1988a,b) erected a series of new linstowiid genera (*Peramelinia, Pseudolinstowia, Sharpilia, Timorenia, Hickmania, Priodontia, Linstoparonia, Mangustella, Vasoramia*) which again appear to be based on host distribution rather than reliable morphological characteristics. None is accepted in this review.

One major source of disagreement has been over the validity of the genus *Mathevotaenia* Akhumyan, 1946 which was described as having craspedote proglottids, rather than acraspedote ones as in *Oochoristica* and being parasitic in mammals rather than reptiles. Spasskii (1951) was criticized for basing his taxonomy on the hosts rather than on the morphology of the cestodes themselves

(Dollfus, 1954). Some species of *Oochoristica* have been described which are acraspedote but occur in mammals (see Beveridge, 1977). As well, the monotypic genus *Sinaiotaenia*, parasitic in gerbillid rodents, has acraspedote proglottids. In this key, the presence of craspedote or acraspedote proglottids has been accepted as a valid morphological criterion, and the genus *Mathevotaenia* has been allowed to stand. However, using this criterion, *Oochoristica* contains cestodes from both mammals and reptiles. The presence or absence of a seminal receptacle is not considered an important generic character, in contradistinction to Spasskii (1951), and has not been used as a diagnostic character.

Oschmarenia Spasskii, 1951 was erected to contain *Thysanotaenia incognita* Meggitt, 1927 described from a wallaby in a zoo in Rangoon, Burma. The type specimens were re-examined by Beveridge (1976) who noted that they appeared to be specimens of the davaineid cestode genus *Calostaurus* which had lost their rostellar hooks, a common phenomenon with poorly preserved specimens of this genus. Consequently, *Oschmarenia* and its nominal subgenus, *Oschmarenia*, are excluded from the Anoplocephalidae and are considered *genera inquirenda*. Spasskii (1951) erected two additional subgenera within *Oschmarenia*, namely *Inversia* and *Morosovella*. The type specimens of the relevant species in the United States National Museum Helminth Collection (USNMHC) have been examined and both *O. (I.) oklahomensis* (Peery, 1939) (USNMHC 93306) and *O. (M.) mephitis* (Skinker, 1935) (USNMHC 39861) have slightly craspedote proglottids, although this character is not mentioned in any published descriptions. Consequently, both subgenera become synonyms of *Mathevotaenia*.

The genus *Atriotaenia* Sandground, 1926 has been retained. It is based on the presence of extremely well-developed radial musculature surrounding a prominent genital atrium and the entry of the genital ducts through the posterior wall of the atrium. Joyeux (1945) believed that the presence of muscles around the genital atrium was not a reliable character. However, when taken in conjunction with the site at which the ducts enter an enlarged atrium (posterior), it appears to be a useful secondary character. Members of the subgenus *Ershovia* Spasskii, 1951 also possess a well developed genital atrium and associated musculature (see Chandler, 1942c, Joyeux & Baer, 1936b). Consequently the subgenus, with its two species *A. procyonis* (Chandler, 1942) and *A. incisa* (Railliet, 1899), becomes a synonym of *Atriotaenia*.

Atriotaenia baltazardi, described more recently by Quentin (1967) has the genital ducts opening directly into the genital atrium and is made a synonym of *Quentinotaenia mesovitellinica* Rego, 1967 (see Quentin, this volume). Spasskii (1969b), in a conference proceedings, erected a new genus, *Quentinia*, within the Anoplocephalidae for *A. baltazardi*. This genus now becomes a member of the Catenotaeniidae.

Opossumia Spasskii, 1951 was removed as a subgenus of *Linstowia* by Beveridge (1983) and is here included as a synonym of *Mathevotaenia*.

Schizorchodes Bienek & Grundmann, 1973, from rodents, was established as a new genus within the Anoplocephalinae. Examination of a paratype specimen indicates, however, that the genus belongs to the Linstowiinae since the uterus is ephemeral and the eggs are embedded singly within the parenchyma. The genus was illustrated as having the testes distributed in two separate groups posterior to the female genitalia. In the material studied, the testes were arranged either in two groups or a single group, both arrangements occurring within a single strobila. Because of this, *Schizorchodes* is treated as a synonym of *Mathevotaenia*. *Witenbergitaenia* Wertheim, Schmidt & Greenberg, 1986 was also erected for a cestode from gerbillid rodents and was characterized by having the testes distributed in two lateral groups posterior to the female genitalia. Since the new genus was established for a single specimen, the reliability of the generic characteristic needs to be established from a greater range of material given the variability seen in *Schizorchodes*. *Witenbergitaenia* is here treated provisionally as a valid genus pending the availability of additional material.

There is some confusion in the literature over the relative positions of the genital ducts in *Panceriella*. Southwell (1926) showed the vagina entering the genital atrium anterior to the cirrus-sac, while Baer (1927) showed the reverse orientation. The material upon which both workers based their descriptions has been re-examined. Baer's specimens are poorly stained, while those of Southwell clearly show the vagina anterior to the cirrus-sac. This character thus becomes an important means of distinguishing *Panceriella*.

Cleberia was described as an anoplocephalid, in spite of the fact that the scolex was lacking (Rego, 1967a), and was placed in the Linstowiinae. Through the kindness of Dr Rego, a specimen was made available for examination. The eggs develop in capsules, but no fully gravid proglottids are present and it is not clear whether the numerous cells in each capsule will form a single egg or several eggs. If they form several eggs, then the genus belongs to the Dilepididae rather than the Anoplocephalidae. As a scolex is lacking, the genus is considered *inquirendum*.

Doublesetina Srivastava & Srivastav, 1989 is treated here as a *genus inquirendum*. It is poorly described (see Srivastava & Srivastav, 1989) and cannot be confidently allocated to a family.

Multicapsiferina Fuhrmann, 1922 is a genus of uncertain family and subfamily status, treated here as a *genus incertae sedis*. *Zschokkea* Fuhrmann, 1902 and *Zschokkeella* Ransom, 1909, both preoccupied, are synonyms of *Multicapsiferina*.

Thysanosomatinae

Genera of the subfamily are characterized by the development of paruterine organs adjacent to or attached to the uterus and the movement of eggs from the uterus into the paruterine organs. The development of paruterine organs in the subfamily has been described in considerable detail by Spasskii (1951). Eggs first enter a tubular uterus. In *Thysaniezia*, *Wyominia* and *Thysanosoma*, numerous paruterine organs with fibrous walls develop as exvaginations of the uterus. Several eggs pass into each paruterine organ and the paruterine organs remain attached by one pole to the uterus. In *Stilesia*, the paruterine bodies commence as solid structures adjacent to the uterus. They then become hollow. The uterus disappears as eggs pass into the two paruterine organs present in each proglottid.

In *Avitellina*, a single paruterine organ is present, but it contains paruterine capsules, each with several eggs.

The family Avitellinidae was erected by Skryabin (1926) for all anoplocephalid genera possessing paruterine organs but Stunkard (1961) pointed out that the rules of nomenclature had not been followed in the selection of the name and that Thysanosomatinae was the correct name. Stunkard's (1961) usage is followed here.

Most genera of the family are well characterized. *Wyominia* is an exception in that it was poorly described by Scott (1941). Baer (1954b) re-examined Scott's specimens and provided a more detailed description, which was utilized by Schmidt (1986) in his key to genera. However, the type and only species *W. tetoni* still warrants redescription as the redescription by Baer (1954b) is inadequate by contemporary standards.

Inermicapsiferinae

In the Inermicapsiferinae, the uterus is again ephemeral, but the eggs are finally enclosed within fibrous or parenchymatous capsules, each containing several eggs, indicating a close similarity with the Davaineinae. The structure differs clearly from that seen in the Linstowiinae, within which subfamily these genera at times have been included. Their placement in the separate subfamily, the Inermicapsiferinae, is fully justified on the grounds of uterine development. Spasskii (1951) recognized four genera, *Inermicapsifer, Pericapsifer, Metacapsifer* and *Thysanotaenia*. However, Deblock & Diaouré (1962) suggested that *Thysanotaenia* may be a synonym of *Inermicapsifer*. It has been allowed to stand for the time being.

Metacapsifer was erected by Spasskii (1951) for *I. aberratus* Baer, 1925 which Baer (1925c) considered to be an aberrant species of *Inermicapsifer*. It is the only species of the subfamily with the testes exclusively aporal. The type and only specimens consist of poorly oriented serial sections. As a consequence, a detailed redescription is impossible, and Spasskii's genus is accepted provisionally, pending a redescription of the species. Baer's (1925c) figure is reproduced.

'Cotype' specimens of *Megacapsula leiperi* Wahid, 1961 (in IIP, C1225–1226) were examined and the genus is transferred to synonymy with *Oochoristica*.

Phylogeny

The phylogeny of the anoplocephalid cestodes has been considered in detail by a number of authors (Baer, 1927; Spasskii, 1951; Tenora, 1976) leading to the proposal of several different schemes for their evolution. Genera in the Australasian region have been investigated by Beveridge (1976, 1985) and in North America and Europe by Rausch (1976, 1982) and Beveridge (1978). The origin of the Anoplocephalinae from the Linstowiinae (Baer, 1927) is no longer tenable following Freeman's (1973) analysis based on morphogenesis of the metacestodes; however, the derivation suggested by Freeman (1973) of the Linstowiinae from the Proteocephalidae in aquatic reptiles, amphibians and fish is consistent with host distribution, since most Linstowiinae occur in reptiles, with relatively few genera in insectivorous mammals. Thus a transition is apparent in the hosts, from aquatic vertebrates to terrestrial reptiles where a major radiation has occurred, and finally a few genera have invaded mammals. The Inermicapsiferinae are evidently derived from the Davaineidae by the loss of a rostellum and sucker armature. The Anoplocephalinae, as suggested by the present morphological analysis, consists of two major groups, one parasitic in birds and the other parasitic in mammals. The evolution of the genera in birds apparently centres on the Psittaciformes, with a few genera only occurring in Passeriformes. The genus *Taufikia* probably does not belong within the Anoplocephalidae and has not been considered from a phylogenetic point of view. *Moniezia rhea* presents a phylogenetic anomaly which cannot at present be resolved, as does the occurrence of one species of *Monoecocestus* in a rheiform bird. Whether or not the principal avian lineage of anoplocephalids predates the mammalian lineage is not clear. The hypothesis of an avian origin of the subfamily is attractive in view of Freeman's (1973) demonstration of a close association between the Anoplocephalinae, Davaineidae and Dilepidinae, all of which occur principally in birds, an idea also suggested by Joyeux & Baer (1961). However, the genus *Anoplocephala*, the origin of the mammalian anoplocephalids, occurs in a wide range of mammals, namely perissodactyls, primates, elephants and hyraxes, possibly suggesting a long association between hosts and parasites. Lacking a detailed analysis of the genus, the hypothesis can only be considered tentative, since the antiquity of the hosts is not necessarily related to the length of association with their parasites. Tenora (1976) considered that the most primitive genera of anoplocephalids were those in marsupials, since the hosts demonstrate a range of primitive characteristics. By contrast, Beveridge (1985) has provided evidence to suggest that the anoplocephalids in fact are relatively recent parasites of Australasian diprotodont marsupials and are derived from precursors in rodents which invaded the Australian continent 5–10 million years ago. Whatever their origin, the most important radiation of the Anoplocephalinae has been with the rodents and lagomorphs, based on the number of genera present in these hosts. Transfer from rodents has apparently occurred to primates, dermopterans and marsupials involving the genera *Bertiella* and *Progamotaenia* (see Beveridge, 1985) while *Andrya* and *Diandrya* in rodents have given rise to *Moniezia* in rodents and in ruminants (Beveridge, 1978; Rausch, 1982). *Anoplocephala* appears to have a number of ancestral characteristics, but which, if any, of the current hosts of the genus were the original ones is not clear. Other examples of transfer to perissodactyls and primates within the Anoplocephalinae are known, and a detailed analysis of species of *Anoplocephala* is required to determine the origins of the genus. The importance of the duplication of genitalia as an evolutionary mechanism in the Anoplocephalidae was emphasized by Baer (1955b). Currently two pairs of such genera are recognized in the Linstowiinae (*Linstowia–Echidnotaenia*, *Oochoristica–Panceriella*), while in the Anoplocephalinae, a series of such pairs exist, *Paronia–Hemiparonia*, *Pulluterina–Stringopotaenia*, *Biporouterina–Bulbultaenia* among the avian genera (Baer, 1955b; Beveridge, 1978) and *Bertiella–Progamotaenia* in marsupials, *Schizorchis–Mosgovoyia* in lagomorphs and *Anoplocephaloides–Ctenotaenia*, *Andrya–Diandrya* and *Gallegoides–*

Pseudocittotaenia in rodents. Duplication of genitalia thus occurs invariably within the same host group and is clearly a common phenomenon within the Anoplocephalidae.

Paramoniezia represents an anomaly in any attempt to provide a phylogenetic analysis of the Anoplocephalinae (Beveridge, 1976). The principal characteristics of the genus (e.g. distribution of testes) are plesiomorphic, and this provides little or no information about its phylogenetic position. Consequently, it has been omitted from consideration. Although a common parasite of vombatid marsupials, its possible occurrence in feral ungulates in Australia (Beveridge, 1976) and the presence of a species in suids from Africa (Baylis, 1927; Graber *et al.*, 1980) have to be resolved before definitive comments can be made about its relationships.

The position of the Thysanosomatinae is also uncertain. All constituent genera are characterized by a paruterine organ and are parasitic in ruminants. Mahon (1954) suggested that *Crossotaenia* was intermediate between the Anoplocephalinae and the Thysanosomatinae since it and several genera of the Thysanosomatinae possess a poorly developed Mehlis' gland. Her suggestion is adopted here. Paruterine organs also occur in genera of the Nematotaeniidae, Paruterinidae and Idiogeninae; however, Jones (1988) concluded that the extent of morphological differences between the so-called paruterine organs in the different families indicated parallel rather than related evolutionary developments.

Thus, the evolution of the anoplocephalids is poorly understood. Clearly some general hypotheses can be advanced, but a rigorous, detailed examination of anoplocephalid phylogeny is warranted. A speculative phylogeny based on the schemes of various authors and on currently available information is presented in Fig. 17.89. Much of the phylogeny has clearly been derived intuitively but is presented here in a cladistic framework. A cladistic approach does present some difficulties, such as with *Triplotaenia*, a genus apparently derived from *Progamotaenia*, but so modified that many of the characteristics used in breaking up the subfamily are inappropriate. It and *Phascolotaenia* have been inserted following the relationships suggested by Beveridge (1976). *Triplotaenia* is so bizarre morphologically that it was placed in a separate family by Yamaguti (1959) and a separate subfamily by Beveridge (1976). Viewed from a cladistic view point, these taxa are inappropriate and neither has been used in the preparation of the key.

Family Anoplocephalidae Cholodkovsky, 1902

Diagnosis: Cestodes of small to large size; scolex without rostellum; suckers unarmed; proglottids craspedote or acraspedote; reproductive organs single or double; testes numerous; genital pores marginal, alternating regularly or irregularly. Uterus either saccate or reticulate, persisting in gravid proglottids, or ephemeral and breaking down into egg capsules or developing paruterine organs; egg frequently with pyriform apparatus. In mammals, birds and reptiles. Cosmopolitan. Type-genus *Anoplocephala* Blanchard, 1848.

Key to subfamilies

1a. Uterus tubular (Figs 17.23, 17.24), reticular (Figs 17.47, 17.53) or saccate (Fig. 17.5) in mature proglottids, persistent in gravid proglottids .... Anoplocephalinae Blanchard, 1891.

Diagnosis: Anoplocephalidae; uterus saccate or reticular, persisting in gravid proglottids. In mammals and birds. Cosmopolitan.

1b. Uterus ephemeral, breaking down into capsules. Eggs scattered through parenchyma singly, with a thin outer membrane termed the uterine capsule .... Linstowiinae Fuhrmann, 1907.

Diagnosis: Anoplocephalidae; uterus ephemeral, breaking down into simple egg capsules. Eggs lodged singly in parenchyma. In mammals and reptiles. Cosmopolitan.

1c. Uterus ephemeral, breaking down into 'fibrous', parenchymatous capsules. Eggs in groups in parenchymatous capsules (Fig. 17.87) .... Inermicapsiferinae López-Neyra, 1943.

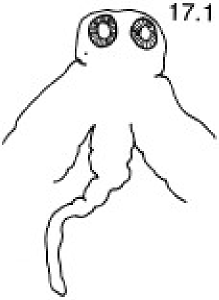
Diagnosis: Anoplocephalidae; uterus ephemeral, breaking down into thick, fibrous capsules enclosing eggs; several eggs per capsule. In mammals. Africa, Asia.

1d. Uterus developing paruterine organs into which eggs pass (Figs 17.74–17.77, 17.80). Distinct ovary and vitellarium often absent, replaced by germovitellarium .... Thysanosomatinae Skryabin, 1933.

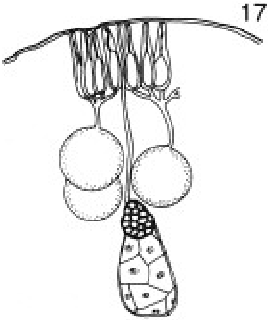
Diagnosis: Anoplocephalidae; uterus with one or several paruterine organs. In ruminants. Cosmopolitan.

Key to genera of the Anoplocephalinae

1a. Two strobilae per scolex (Figs 17.1, 17.2) .... *Triplotaenia* Boas, 1902. (Figs 17.1–17.3)


17.1


17.2


17.3

Figs 17.1, 17.2 *Triplotaenia undosa* Beveridge, 1976. Scoleces with paired strobilae originating from them. Redrawn from Beveridge (1976).

Fig. 17.3 *Triplotaenia undosa* Beveridge, 1976. Genital system. Modified from Beveridge (1976).

Diagnosis: Strobilae elongate, undulate or spirally coiled; external segmentation lacking; genital pores on external margin; internal margin irregularly fringed. Each testis supplies several cirrus-sacs (Fig. 17.3). Uterus saccate, persistent. Pyriform apparatus present. In macropodid marsupials. Australia. Type-species *T. mirabilis* Boas, 1902.

1b. Single strobila per scolex .... 2.

2a. Uterus initially spherical or trilobed, anterior to ovary, extending to fill proglottid .... 3.
2b. Uterus initially tubular or reticulate .... 4.

3a. Uterus initially spherical (Fig. 17.4), extending laterally (Fig. 17.5) to fill proglottid. Testes posterior to ovary .... ***Crossotaenia* Mahon, 1954. (Figs 17.4, 17.5.)**
Diagnosis: Strobila small; proglottids prominently craspedote, wider than long. Genitalia single. Genital pores regularly alternating. Genital ducts pass between canals. Seminal vesicles absent. Testes in single band across medulla posterior to female genitalia. Ovary poral. Vagina posterior to cirrus-sac. Seminal receptacle present. Uterus anterior to female genitalia. Pyriform apparatus absent. In bileducts of ruminants. Africa. Type-species *C. baeri* Mahon, 1954.

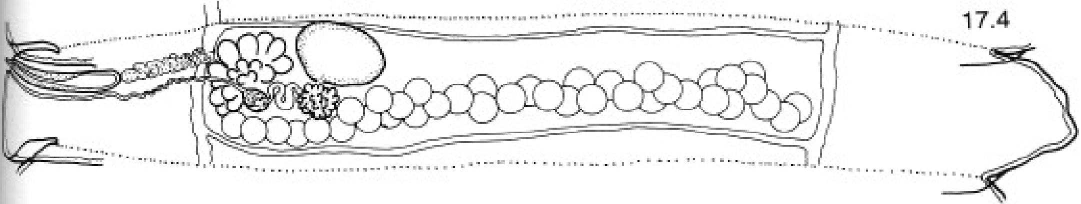
3b. Uterus initially trilobed (Fig. 17.6), elongating and branching laterally and anteriorly to fill proglottid (Fig. 17.7) .... ***Taufikia* Woodland, 1928. (Figs 17.6, 17.7)**
(Syns *Gidhaia* Johri, 1934; *Neophronia* Saxena, 1967.)
Diagnosis: Strobila slender. Proglottids ascraspedote, wider than long. Genitalia single. Genital pores alternate irregularly. Genital ducts cross ventral osmoregulatory canals dorsally. Internal seminal vesicle present. Testes pre-ovarian or scattered. Ovary central. Vagina posterior to cirrus-sac. Seminal receptacle present. Pyriform apparatus absent. In accipitriform birds (vultures). Africa, India, Asia. Type-species *T. edmondi* Woodland, 1928.

4a. Uterus tubular initially, becoming saccate, developing diverticula, never reticulate .... 5.
4b. Uterus reticulate during part of its development (Figs 17.46–17.48) .... 27.

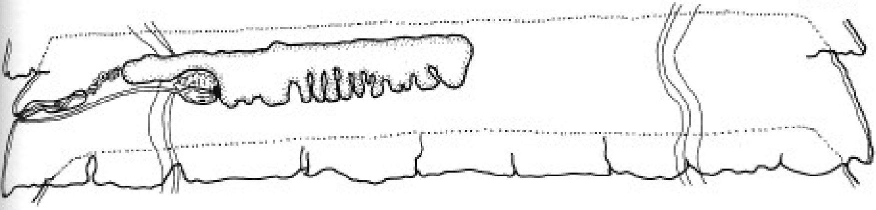
5a. Uterus a straight transverse or longitudinal tube (Figs 17.8, 17.12) .... 6.
5b. Uterus arched anterior to female genitalia, or with paired posterior diverticula on either side of vitellarium (Figs 17.36, 17.41, 17.43) .... 19.

6a. Testes originate anterior to uterus (Figs 17.8, 17.10); (occasionally becoming displaced posteriorly in *Progamotaenia ewersi*) .... 7.
6b. Testes not entirely anterior to uterus .... 8.

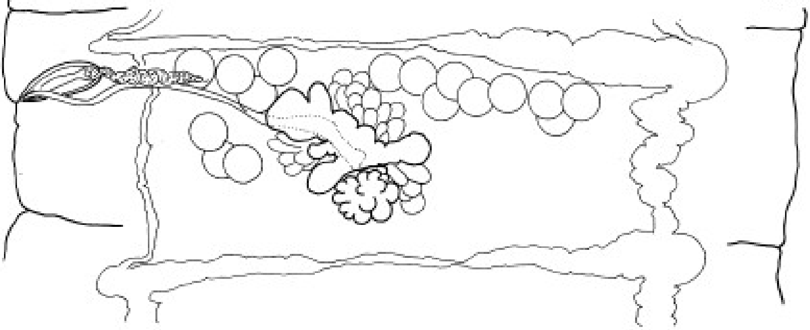
17.4



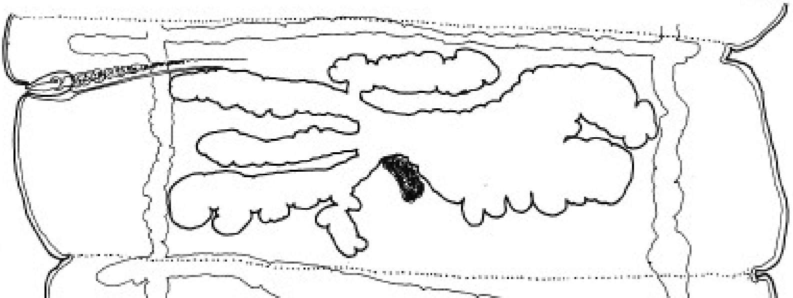
17.5



17.6



17.7



Figs 17.4, 17.5 *Crossotaenia baeri* Mahon, 1954. 17.4. Mature proglottid. Original. 17.5. Developing uterus. Redrawn from Mahon (1954).

Fig. 17.6 *Taufikia edmondi* Woodland, 1928. 'Cotype', mature proglottid. Original.

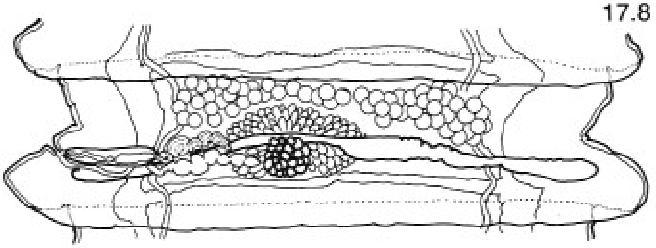
Fig. 17.7 *Taufikia edmondi* Woodland, 1928. 'Cotype', developing uterus. Original.

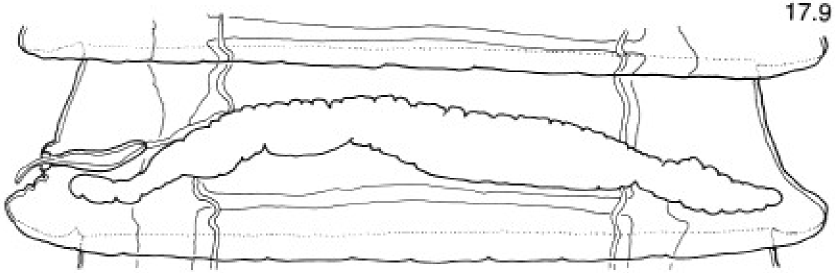
7a. Genitalia single ...... ***Bertiella*** **Stiles & Hassall, 1902. (Figs 17.8, 17.9)**
(Syns *Bertia* Blanchard, 1891; *Parabertiella* Nybelin, 1917; *Indotaenia* Singh, 1962; *Prototaenia* Baer, 1927; *Beveridgia* Spasskii, 1988.)

Diagnosis: Strobilae of various sizes. Proglottids craspedote, wider than long. Genital pores unilateral or irregularly alternate. Genital ducts cross canals dorsally. Internal seminal vesicle present. Testes in single band or two groups, entirely anterior to uterus. Ovary poral, central or aporal. Vagina posterior to cirrus-sac. Seminal receptacle present or absent. Uterus single, transverse, tubular (Fig. 17.9). Pyriform apparatus present. In primates (including man), rodents, dermopterans and Australasian marsupials. Cosmopolitan. Type-species *B. studeri* (Blanchard, 1891).

7b. Genitalia paired .... ***Progamotaenia*** **Nybelin, 1917. (Figs 17.10, 17.11)**
(Syns *Hepatotaenia* Nybelin, 1917; *Baeriella* Fuhrmann, 1932; *Fuhrmannodes* Strand, 1942; *Adelataenia* Beveridge, 1976 *lapsus calami* in Schmidt, 1986; *Wallabicestus* Schmidt, 1975.)

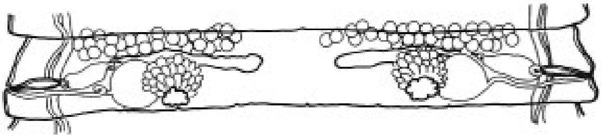
Diagnosis: Strobilae of variable size. Proglottids craspedote often fringed, wider than long. Genital ducts cross canals dorsally; internal and external seminal vesicles present. Testes originate anterior to uterus in single band or two groups, sometimes become displaced posteriorly in *P. ewersi*. Ovaries poral. Vagina posterior to cirrus-sac. Seminal receptacle present. Uterus single or paired, transverse, tubular (Fig. 17.11). Pyriform apparatus present. In bile-ducts or intestines of macropodid marsupials. Australia. Type-species *P. bancrofti* (Johnston, 1912).



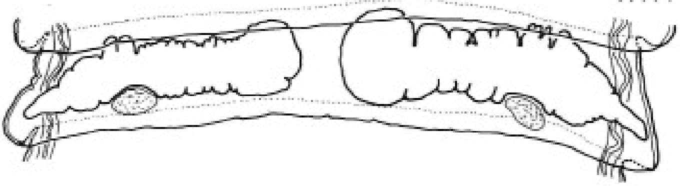


Figs 17.8, 17.9 *Bertiella phalangeris* Beveridge, 1985. 17.8. Mature proglottid. 17.9. Gravid proglottid. Redrawn from Beveridge (1985).

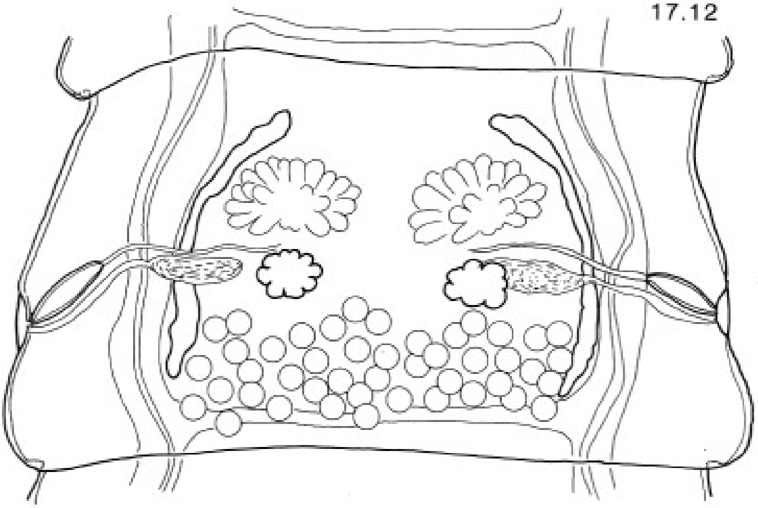
17.10



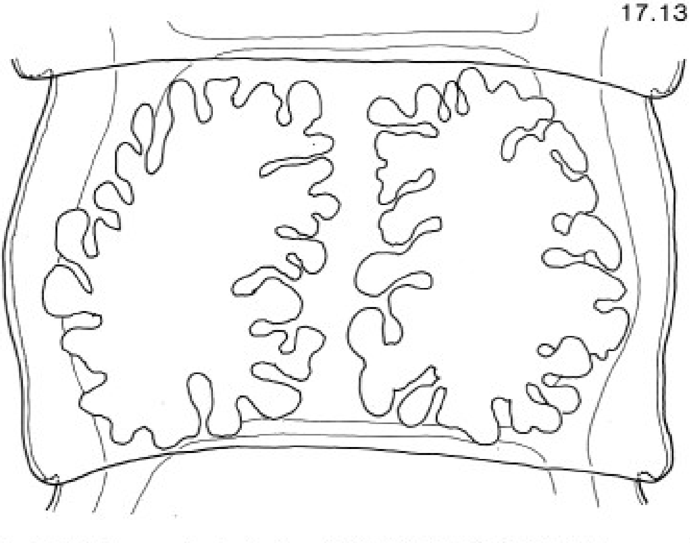
17.11



17.12



17.13



Figs 17.10, 17.11 *Progamotaenia festiva* (Rudolphi, 1819). 17.10. Mature proglottid. 17.11. Gravid proglottid. Redrawn from Beveridge (1976).

Figs 17.12, 17.13 *Diuterinotaenia spasskii* Gvozdev, 1961. 17.12. Mature proglottid. 17.13. Gravid proglottid. Redrawn from Gvozdev (1961a).

8a. Testes exclusively posterior to uterus or in posterior half of proglottid (Figs 17.12, 17.14, 17.15) .... 9.
8b. Testes not exclusively posterior to uterus .... 15.

9a. Uteri paired, longitudinal (Figs 17.12, 17.13) ....
.... *Diuterinotaenia* Gvozdev, 1961. (Figs 17.12, 17.13)
Diagnosis: Strobila small, slender. Proglottids craspedote; wider than long. Genitalia paired. Seminal vesicles absent. Genital ducts cross osmoregulatory canals dorsally. Testes in single band posterior to female genitalia. Ovaries poral. Vagina posterior to cirrus-sac. Seminal receptacle present. Uteri tubular. Pyriform apparatus absent. In ochotonid lagomorphs. Asia. Type-species *D. spasskii* Gvozdev, 1961.

9b. Uterus single or double, transverse .... 10.

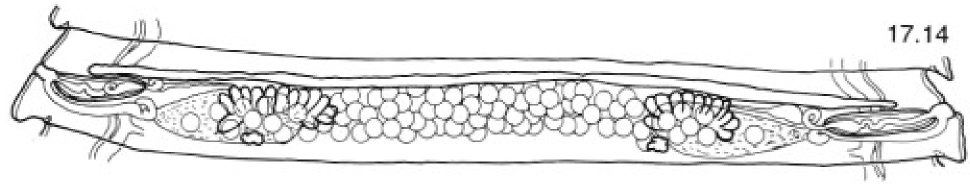
10a. Lateral terminations of uteri anterior to cirrus-sac and vagina (Figs 17.14, 17.17) .... 11.
10b. Lateral termination of uteri posterior to cirrus-sac and vagina (Figs 17.19, 17.21) .... 13.

11a. Genitalia single .... 12.
11b. Genitalia paired .... *Pseudocittotaenia* Tenora, 1976. (Fig. 17.14)
Diagnosis: Strobilae small. Proglottids craspedote, wider than long. Genital ducts cross osmoregulatory canals dorsally. Internal seminal vesicle present. Testes posterior to uterus (Fig. 17.14). Ovaries poral. Vagina posterior to cirrus-sac; seminal receptacle present. Uterus single, transverse, tubular, extending ventrally beyond osmoregulatory canals, terminating anterior to cirrus-sac. Pyriform apparatus present. In geomyid rodents. North America. Type-species *P. praecoquis* (Stiles, 1895).

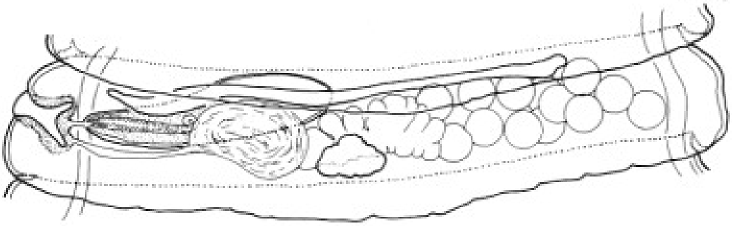
12a. Testes aporal to ovary (Fig. 17.15) ....
.... *Anoplocephaloides* Baer, 1923 (in part). (Figs 17.15, 17.16)
(Syn. *Leporidotaenia* Genov, Murai, Georgiev & Harris, 1990.)
Diagnosis: Strobila small to medium sized. Proglottids craspedote, wider than long. Genitalia single. Genital pores usually unilateral. Genital ducts cross osmoregulatory canals dorsally; internal and external seminal vesicles present. Ovary poral. Vagina posterior to cirrus-sac. Uterus transverse, tubular (Fig. 17.16). Pyriform apparatus present. In rodents, lagomorphs, perissodactyls. North and Central America, Africa, Europe, Asia. Type-species *A. infrequens* (Douthitt, 1915).

12b. Testes poral and aporal to ovary (Fig. 17.17) ....
.... *Gallegoides* Tenora & Mas-Coma, 1978. (Fig. 17.17)
Diagnosis: Strobila small. Proglottids craspedote, wider than long. Genitalia single. Genital ducts cross osmoregulatory canals dorsally. Internal and external seminal vesicles present. Testes in band posterior to uterus. Ovary slightly poral. Vagina posterior to cirrus-sac. Seminal receptacle present. Uterus single, tubular, transverse, extending beyond osmoregulatory canals, terminating anterior to

17.14



17.15



17.16

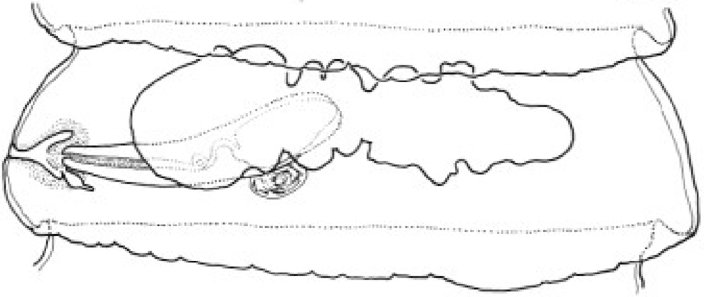


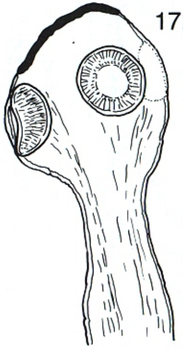
Fig. 17.14 *Pseudocittotaenia praecoquis* (Stiles, 1895). Mature proglottid. Redrawn from Beveridge (1978).
Figs 17.15, 17.16 *Anoplocephaloides wimerosa* (Moniez, 1880). 17.15. Mature proglottid. 17.16. Gravid proglottid. Original.

cirrus-sac. Pyriform apparatus present. In arvicoline rodents. Asia, Europe. Type-species *G. arfaai* (Mobedi & Ghadirian, 1977).

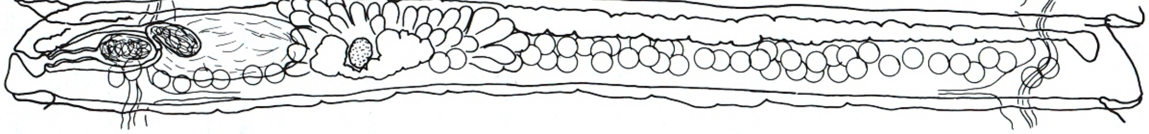
**13a. Neck greatly elongated, scolex covered with glands (Fig. 17.18) ....
.... *Ectopocephalium* Rausch & Ohbayashi, 1974. (Figs 17.18, 17,19)**
Diagnosis: Strobila small. Scolex with prominent apical glands. Genitalia paired. Genital ducts cross osmoregulatory canals dorsally; internal seminal vesicle present. Testes in band posterior to uterus (Fig. 17.19). Ovaries poral. Vagina posterior to cirrus-sac; distal vagina with gland cells. Seminal receptacle present. Uterus single, transverse, tubular, crossing osmoregulatory canals, terminating posterior to cirrus-sac. Pyriform apparatus present. In ochotonid lagomorphs. Nepal. Type-species *E. abei* Rausch & Ohbayashi, 1974.

13b. Neck not elongated, scolex without glands .... 14.

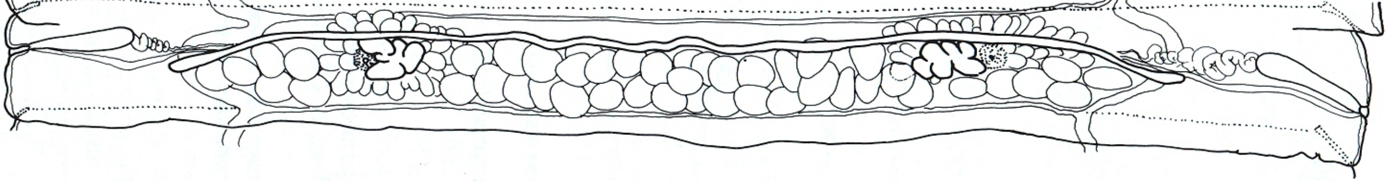
17.18



17.17



17.19



17.20

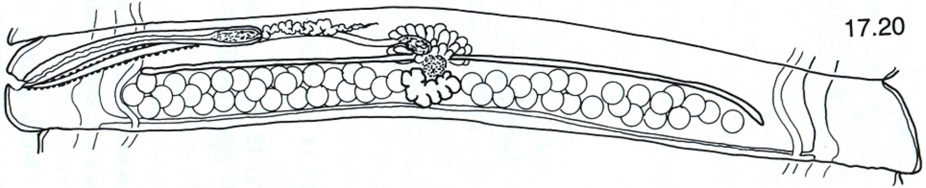


Fig. 17.17 *Gallegoides arfaai* (Mobedi & Ghadirian, 1977). Mature proglottid. Original. **Figs 17.18, 17.19.** *Ectopocephalium abei* Rausch & Ohbayashi, 1974. 17.18. Holotype, scolex; note scolex glands. 17.19. Mature proglottid. Original.
Fig. 17.20 *Schizorchis ryzhikovi* Rausch & Smirnova, 1984. Mature proglottid. Original.

14a. Genitalia single (Fig. 17.20) ... ***Schizorchis* Hansen, 1948. (Fig. 17.20)**
Diagnosis: Strobila small. Proglottids craspedote, wider than long. Genital pores alternate irregularly. Genital ducts cross osmoregulatory canals dorsally; internal and external seminal vesicles present. Testes posterior to uterus. Ovary central. Vagina posterior to cirrus-sac. Distal vagina with gland cells. Seminal receptacle present. Uterus single, transverse, tubular, restricted to medulla. Pyriform apparatus present. In ochotonid lagomorphs. North America, Asia. Type-species *S. ochotonae* Hansen, 1948.

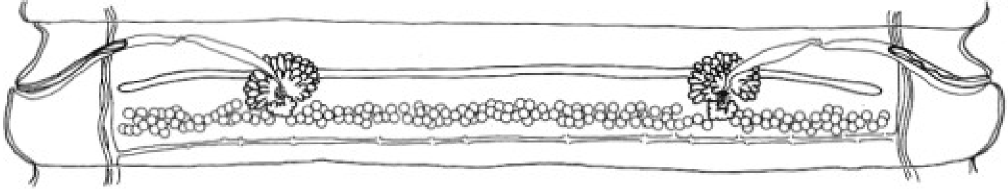
14b. Genitalia paired (Fig. 17.21) .... ***Mosgovoyia* Spasskii, 1951. (Fig. 17.21)**
(Syns *Neoctenotaenia* Tenora, 1976; *Himalaya* Malhotra, Sawada & Capoor, 1983.)
Diagnosis: Strobila large. Proglottids craspedote, wider than long. Genital ducts cross osmoregulatory canals dorsally; internal seminal vesicle present. Testes in single band or two groups posterior to uterus. Ovaries poral. Vagina posterior to cirrus-sac. Distal vagina with gland cells. Seminal receptacle present. Uterus single, transverse, tubular, restricted to medulla or crossing canals dorsally and terminating posterior to cirrus-sac. Pyriform apparatus present. In leporid lagomorphs, rarely in rodents. North and South America, Europe, Africa, Asia. Type-species *M. pectinata* (Goeze, 1782).

15a. Testes aporal to ovary, anterior and posterior to uterus (Fig. 17.22) .... **16.**
15b. Testes poral and aporal to ovary, anterior and posterior to uterus (Figs 17.23, 17.25) ....**17.**

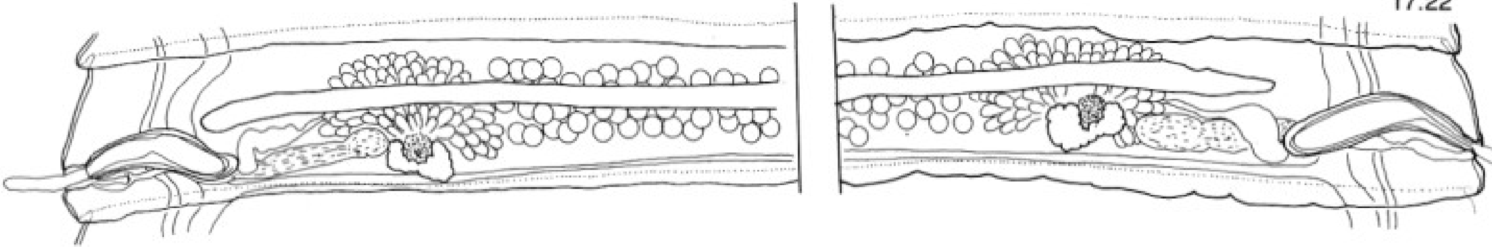
16a. Genitalia single .... ***Anoplocephaloides* Baer, 1923 (in part). (See 12a above.)**
(Syn. *Flabelloskrjabinia* Spasskii, 1951.)
16b. Genitalia paired .... ***Ctenotaenia* Railliet, 1893. (Fig. 17.22)**
Diagnosis: Strobila large. Proglottids craspedote, wider than long. Genital ducts cross osmoregulatory canals dorsally; internal and external seminal vesicles present. Testes in single band between ovaries, anterior and posterior to uterus. Vagina posterior to cirrus-sac. Seminal receptacle present. Uterus single, transverse, tubular, restricted to medulla (Fig. 17.22). Pyriform apparatus present. In sciurid rodents. Europe, Asia. Type-species *C. marmotae* (Froehlich, 1802).

17a. Genitalia single. Genital pores unilateral .... ***Anoplocephala* Blanchard, 1848. (Figs 17.23, 17.24)**
(Syn. *Plagiotaenia* Peters, 1871.)
Diagnosis: Strobila moderate to large. Proglottids craspedote, wider than long. Genital pores unilateral. Genital ducts cross canals dorsally. Internal and external seminal vesicles present. Testes scattered throughout medulla. Ovary poral. Vagina posterior to cirrus-sac. Seminal receptacle present. Uterus single, transverse, tubular, restricted to medulla (Figs 17.23, 17.24). Pyriform apparatus

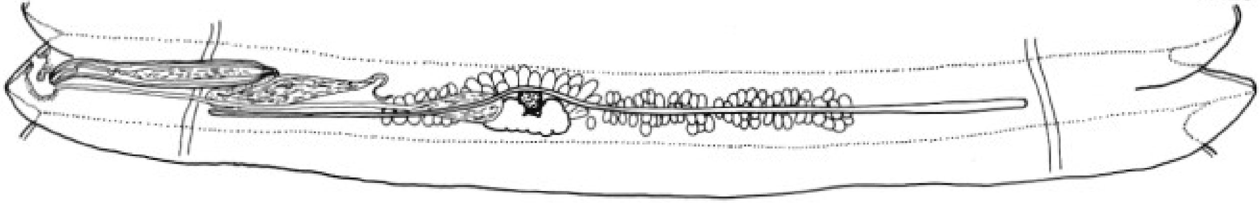
17.21



17.22



17.23



17.24

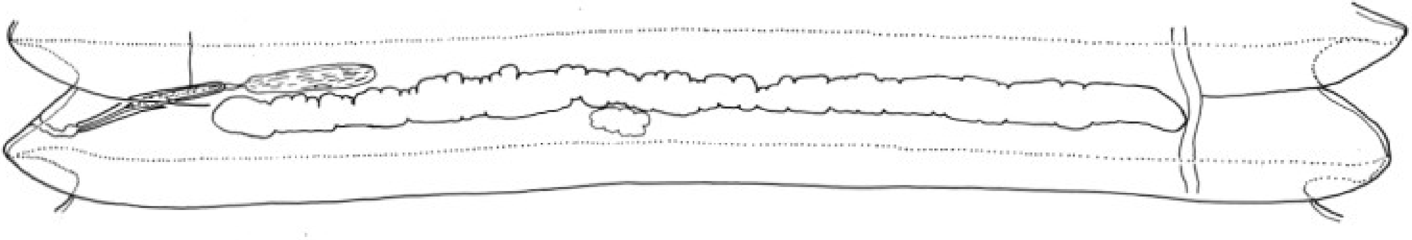


Fig. 17.21 *Mosgovoyia pectinata* (Goeze, 1782). Mature proglottid. Redrawn from Beveridge (1978). **Fig. 17.22.** *Ctenotaenia marmotae* (Froehlich, 1802). Mature proglottid. Redrawn from Beveridge (1978). **Figs 17.23, 17.24.** *Anoplocephala perfoliata* (Goeze, 1782). 17.23. Mature proglottid. 17.24. Gravid proglottid. Original.

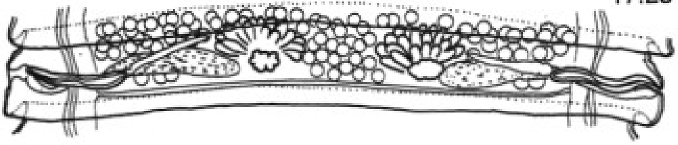
present. In hyracoids, perissodactyls, proboscoids, primates. Cosmopolitan. Type-species *A. perfoliata* (Goeze, 1782).

17b. Genitalia paired .... **18.**

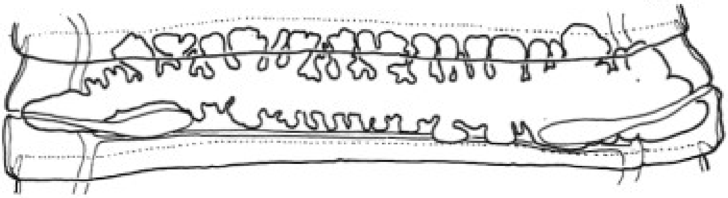
18a. Testes scattered through medulla (Fig. 17.25). Seminal receptacle elongate, merging into vagina (Fig. 17.26) ....
.... ***Paramoniezia*** **Maplestone & Southwell, 1923. (Figs 17.25, 17.26)**

Diagnosis: Strobila moderate. Proglottids craspedote, wider than long. Genitalia paired. Genital ducts cross osmoregulatory canals dorsally. Internal seminal vesicle present. Ovaries poral. Vagina posterior to cirrus-sac. Seminal receptacle present. Uterus single, transverse, tubular. Pyriform apparatus present. In vombatid marsupials and suids. Australia, Africa. Type-species *P. suis* Maplestone & Southwell, 1923.

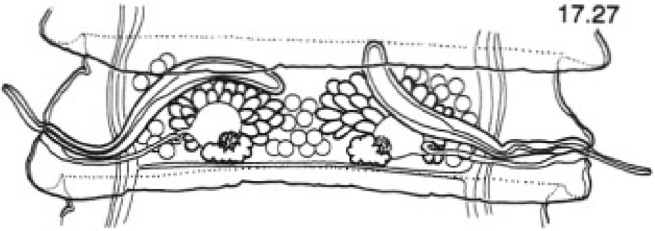
17.25



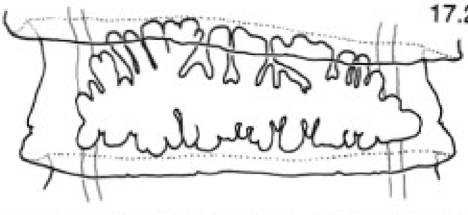
17.26



17.27



17.28



Figs 17.25, 17.26 *Paramoniezia johnstoni* Beveridge, 1976. 17.25. Mature proglottid. 17.26. Gravid proglottid. Redrawn from Beveridge (1976).

Figs 17.27, 17.28 *Phascolotaenia comani* Beveridge, 1976. 17.27. Mature proglottid. 17.28. Gravid proglottid. Redrawn from Beveridge (1976).

18b. Testes with central group posterior to uterus, two lateral groups anterior to uterus. Seminal receptacle circular, distinct from vagina (Fig. 17.27)
.... *Phascolotaenia* Beveridge, 1976. (Figs 17.27, 17.28)

Diagnosis: Strobila small. Proglottids craspedote, wider than long. Genitalia paired. Genital ducts cross canals dorsally. Cirrus-sacs cross canals, reaching mid-region of proglottid. Internal and external seminal vesicles present. Testes posterior to uterus between ovaries, anterior and posterior to uterus porally. Vagina posterior to cirrus-sac. Seminal receptacle present. Uterus single, transverse, tubular. Pyriform apparatus present. In vombatid marsupials. Australia. Type-species *P. comani* Beveridge, 1976.

19a. Genital pores absent. Uterus single, extends beyond osmoregulatory canals, with two anterior diverticula on each side of proglottid (Figs 17.29, 17.30)
.... *Aporina* Fuhrmann, 1902. (Figs 17.29, 17.30)

Diagnosis: Strobila moderate. Proglottids craspedote, wider than long. Genitalia single. Cirrus-sac and vagina alternate irregularly. Genital ducts cross canals dorsally. Cirrus-sac vestigial, non-functional. Seminal vesicles absent. Testes in two broad lateral bands, few extending posterior to ovary. Ovary central or slightly poral to mid-line. Vagina posterior to cirrus-sac. Seminal receptacle present. Uterus tubular, loops anteriorly around seminal receptacle with paired, extra-vascular, anteriorly-directed diverticula. Pyriform apparatus absent. In parrakeet. Brazil. Type-species *A. alba* Fuhrmann, 1902.

19b. Genital pores present. Uterus without paired, anterior diverticula
.. 20.

20a. Uterus with central anteriorly directed, spur-like diverticulum (Figs 17.31–17.33) .... 21.
20b. Uterus without central anteriorly directed, spur-like diverticulum 22.

21a. Genitalia single ...... *Triuterina* Fuhrmann, 1922. (Figs 17.31, 17.32)
(Syn. *Biporouterina* Burt, 1973.)

Diagnosis: Strobila moderate. Proglottids craspedote, wider than long. Genital pores alternate irregularly. Genital ducts cross canals (?) dorsally. Internal seminal

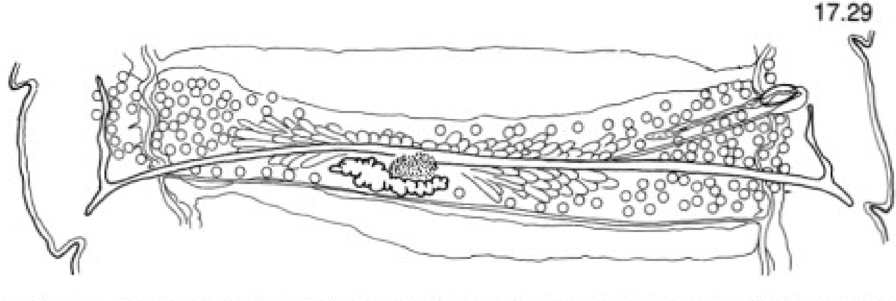
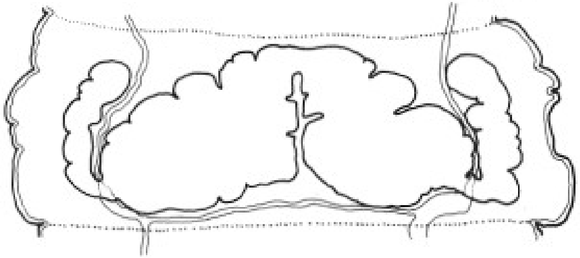


Fig. 17.29 *Aporina alba* Fuhrmann, 1902. Holotype; mature proglottid reconstructed from sections. Original.

17.30



17.32

17.31

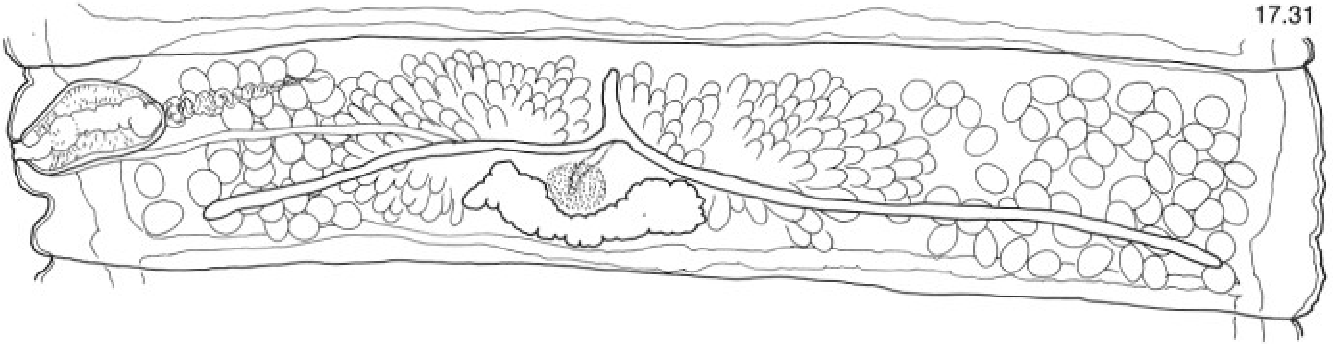


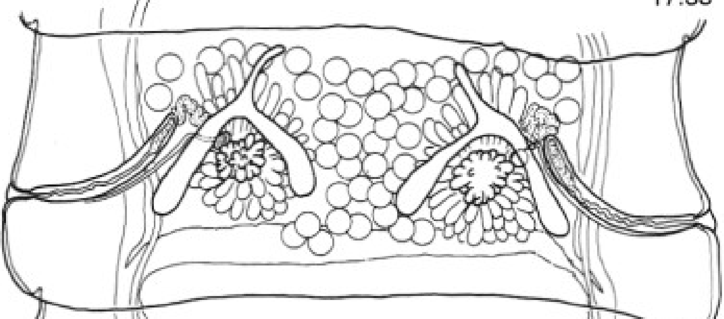
Fig. 17.30 *Aporina alba* Fuhrmann, 1902. Holotype; section of gravid proglottid. Original. **Figs 17.31, 17.32.** *Triuterina anoplocephaloides* (Fuhrmann, 1902). 17.31. Mature proglottid. 17.32. Gravid proglottid. Original.

vesicle present. Testes scattered throughout medulla. Ovary central. Vagina posterior to cirrus-sac. Seminal receptacle present. Uterus tubular, looped anteriorly around seminal receptacle, with anteriorly directed, median spur (Figs 17.31, 17.32). Pyriform apparatus absent. In psittaciform birds. Africa, Sri Lanka. Type-species *T. anoplocephaloides* Fuhrmann, 1902.

21b. Genitalia paired .... ***Bulbultaenia* n. g. (Figs 17.33, 17.34)**
Diagnosis: Strobila moderate. Proglottids craspedote, wider than long. Genital ducts cross canals dorsally. Internal seminal vesicles present. Testes scattered through medulla. Ovaries poral. Vagina posterior to cirrus-sac. Seminal receptacle present. Uteri paired, tubular, looped anteriorly around seminal receptacles, each with single, median, anteriorly directed spur. Pyriform apparatus absent. In red-vented bulbul, *Molpastes haemorrhous*. Sri Lanka. Type-species *B. calcaruterina* (Burt, 1939) n. comb. (Syn. *Paronia calcaruterina* Burt, 1939.)

22a. Uterus simple, U-shaped, surrounding vitellarium anteriorly (Figs 17.35–17.38) .... **23.**
22b. Uterus with prominent horizontal branches, small anterior U-shaped deviation anterior to vitellarium and paired posterior diverticula on either side of vitellarium (Figs 17.43, 17.45) .... **25.**

17.33



17.34

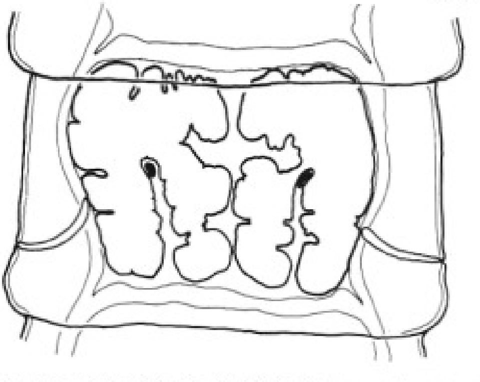
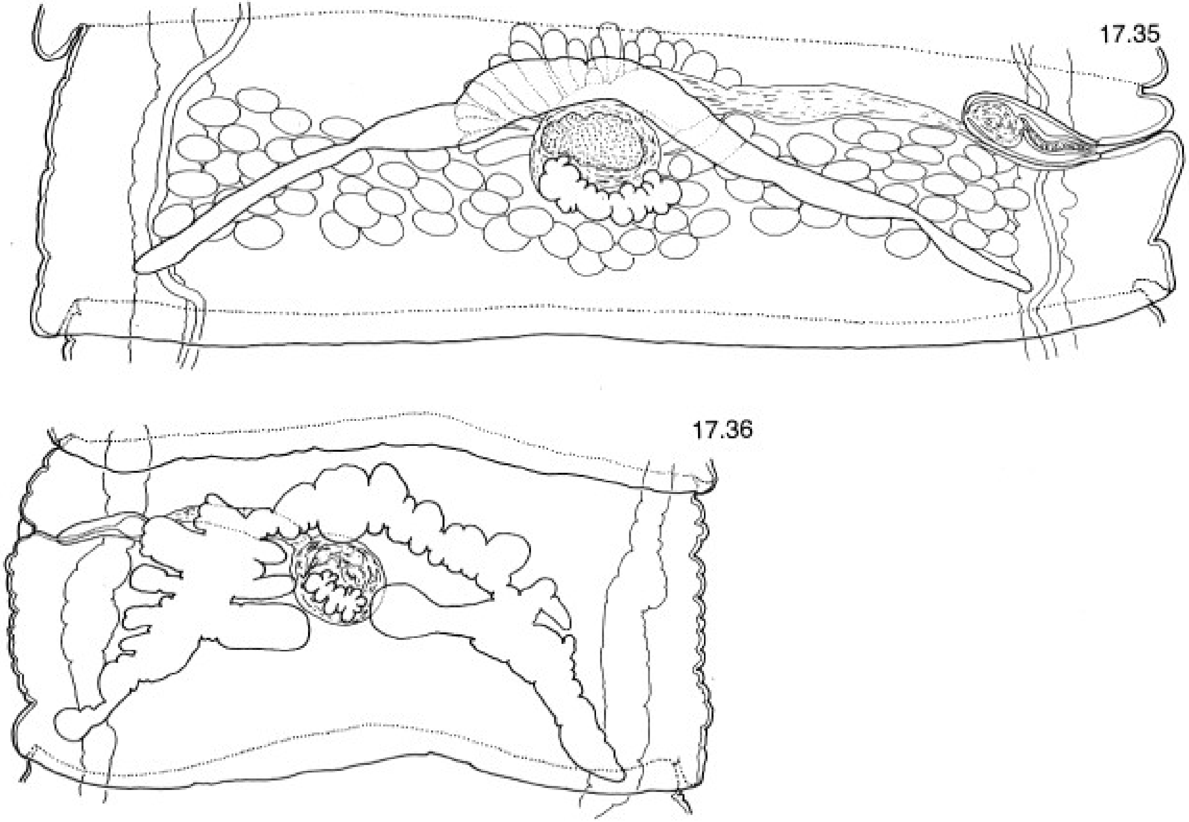


Fig. 17.33 *Bulbultaenia calcaruterina* (Burt, 1939). Holotype; mature proglottid. Original.
Fig. 17.34 *Bulbultaenia calcaruterina* (Burt, 1939). Holotype; gravid proglottid. Original.


17.35

17.36

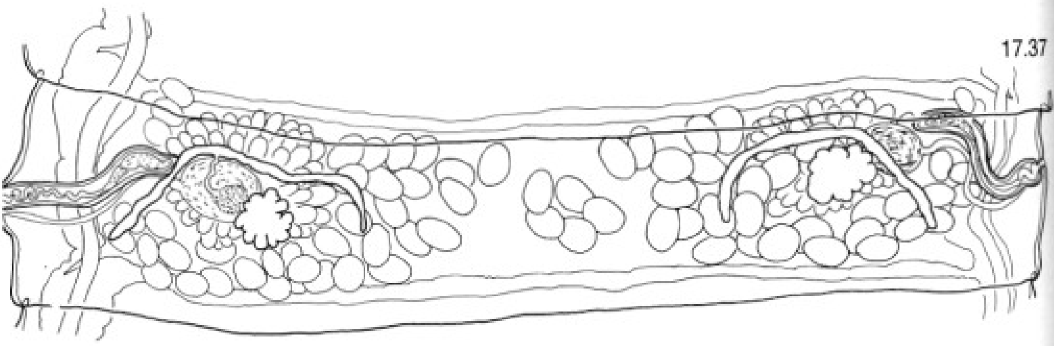
Figs 17.35, 17.36 *Hemiparonia bancrofti* (Johnston, 1912). 17.35. Mature proglottid. 17.36. Gravid proglottid. Original.

23a. Genitalia single .... ***Hemiparonia* Baer, 1925. (Figs 17.35, 17.36)**
Diagnosis: Strobila moderate. Proglottids craspedote, wider than long. Genital ducts cross canals dorsally. Seminal vesicles present. Testes in band posterior and lateral to ovary. Ovary central. Vagina posterior to cirrus-sac. Seminal receptacle present. Uterus single, tubular, looped anteriorly around seminal receptacle. Pyriform apparatus absent. In psittaciform birds. Australia. Type-species *H. cacatuae* (Maplestone, 1922).

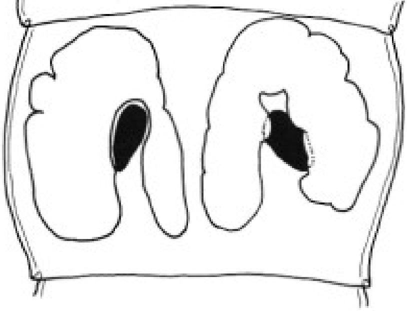
23b. Genitalia paired .... **24.**

24a. Uterus double, sometimes merging, scolex lacking glands anterior to suckers .... ***Paronia* Diamare, 1900. (Figs 17.37, 17.38)**
Diagnosis: Strobila moderate. Proglottids craspedote, wider than long. Genitalia paired. Genital ducts cross canals dorsally. Internal seminal vesicles present or absent; external vesicle absent. Testes scattered throughout medulla. Ovaries poral. Vagina posterior to cirrus-sac. Seminal receptacle present. Uteri tubular, looped anteriorly around seminal receptacles. Pyriform apparatus rudimentary or absent. In birds. Asia, Africa, South America, Australia. Type-species *P. trichoglossi* (Linstow, 1888).

17.37



17.38



17.39

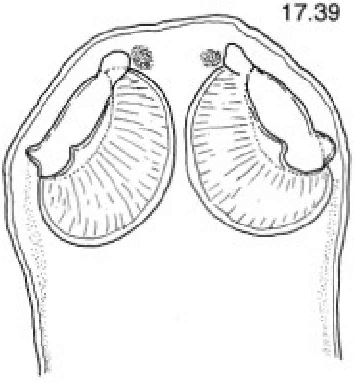


Fig. 17.37 *Paronia trichoglossi* (Linstow, 1888). Type; mature proglottid. Original.
Fig. 17.38 *Paronia trichoglossi* (Linstow, 1888). Gravid proglottid. Original.
Fig. 17.39 *Moniezoides rouxi* Fuhrmann, 1918. Type; scolex; note lappets on suckers and glands anterior to suckers. Original.

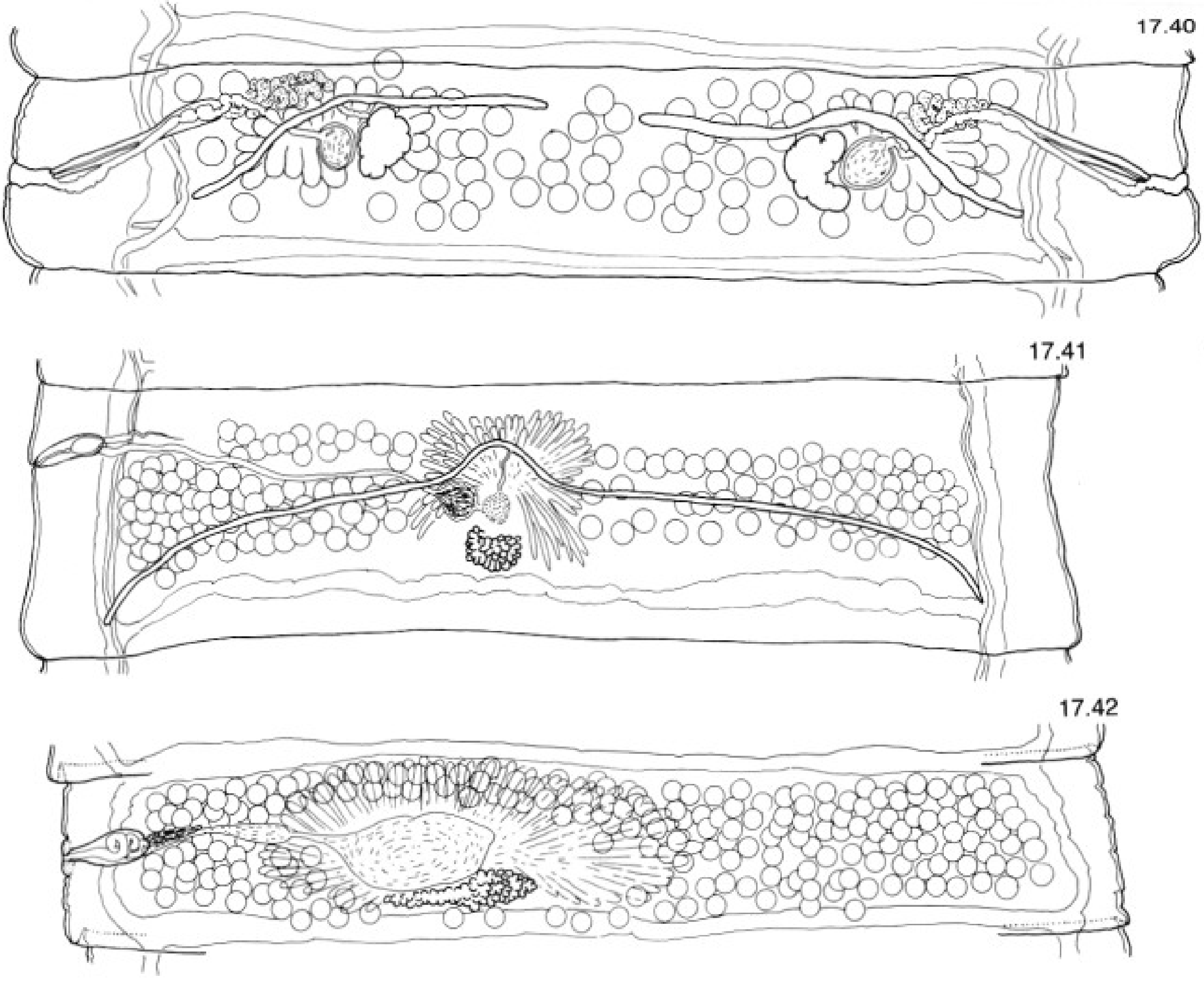


Fig. 17.40 *Moniezoides rouxi* Fuhrmann, 1918. Type; mature proglottid. Original. **Fig. 17.41.** *Killigrewia frivola* Meggitt, 1927. 'Cotype'; mature proglottid. Original. **Fig. 17.42.** *Pulluterina nestoris* Smithers, 1954. Mature proglottid. Original.

24b. Uterus (?) single (Fig. 17.40); glands present anterior to each sucker. Suckers with prominent lappets (Fig. 17.39) .... ***Moniezoides* Fuhrmann, 1918. (Figs 17.39, 17.40)**
Diagnosis: Strobila moderate. Scolex with four groups of glands anterior to suckers. Proglottids craspedote, wider than long. Genitalia double. Genital ducts cross canals dorsally. Internal and external seminal vesicles absent. Testes scattered throughout medulla. Vagina posterior to cirrus-sac. Seminal receptacle present. Uterus (?) single, tubular, looped anteriorly around both ovaries. Pyriform apparatus (?) absent. In psittaciform birds. South Pacific. Type-species *M. rouxi* Fuhrmann, 1918.

25a. Testes in two distinct, lateral groups (Fig. 17.41) .... ***Killigrewia* Meggitt, 1927. (Fig. 17.41)**
(Syns *Pseudoaporina* Saxena & Baugh, 1973; *Nepalesia* Sharma, 1943; *Columbia* Srivastava & Capoor, 1966.)
Diagnosis: Strobila small. Proglottids craspedote, wider than long. Genitalia single. Genital pores alternate irregularly. Genital ducts cross canals dorsally. Internal seminal vesicles present. Testes in two groups either side of ovary. Ovary slightly poral. Vagina posterior to cirrus-sac. Seminal receptacle present. Uterus single, tubular, looped broadly around seminal receptacle, terminating in posterolateral corners of medulla. Pyriform apparatus (?) absent. In birds. Africa, Asia, Europe, North and South America, Australia. Type-species *K. frivola* Meggitt, 1927.

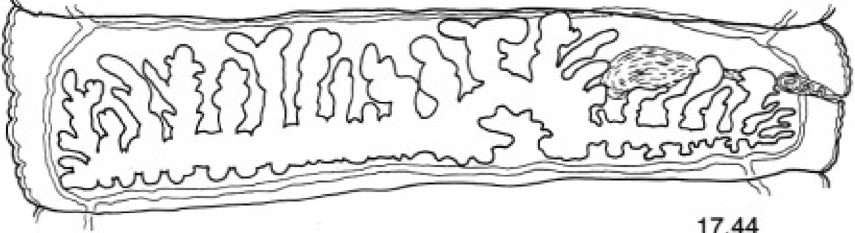
25b. Testes distributed across medulla .... **26.**

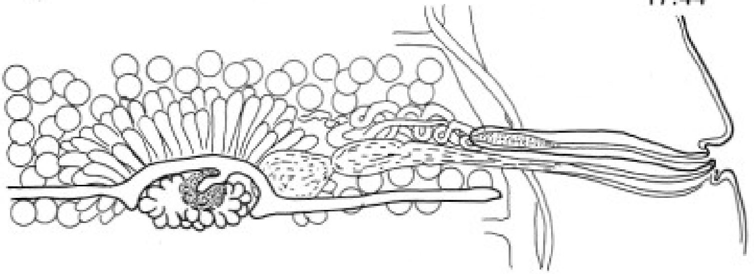
26a. Genitalia single .... ***Pulluterina* Smithers, 1954. (Figs 17.42, 17.43)**
Diagnosis: Strobila large. Proglottids craspedote, wider than long. Genital pores alternate irregularly. Genital ducts cross canals dorsally. Internal seminal vesicle present. Testes scattered throughout medulla. Ovary poral. Vagina posterior to cirrus-sac. Seminal receptacle present. Uterus single, tubular, looped anteriorly around seminal receptacle with pair of posterior diverticula on either side. Pyriform apparatus absent. In psittaciform birds. New Zealand. Type-species *P. nestoris* Smithers, 1954.

26b. Genitalia double .... ***Stringopotaenia* Beveridge, 1978. (Figs 17.44, 17.45)**
Diagnosis: Strobila moderate. Proglottids craspedote, wider than long. Genital ducts cross canals dorsally. Internal seminal vesicle present. Testes scattered throughout medulla. Ovaries poral. Vagina posterior to cirrus-sac. Seminal recep-

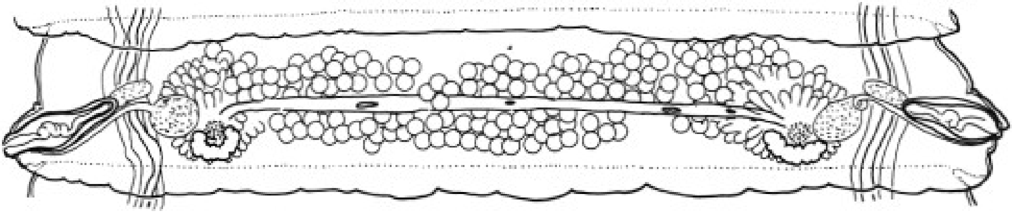
---

Fig. 17.43 *Pulluterina nestoris* Smithers, 1954. Gravid proglottid. Original.
Figs 17.44, 17.45 *Stringopotaenia psittacea* (Fuhrmann, 1904). 17.44. Holotype; part of mature proglottid. 17.45. Holotype; section through gravid proglottid. Redrawn from Beveridge (1978).
Figs 17.46–17.48 *Cittotaenia denticulata* (Rudolphi, 1804). 17.46. Mature proglottid. 17.47. Developing uterus showing reticulations. 17.48. Gravid uterus; note lack of reticulation. Redrawn from Beveridge (1978).

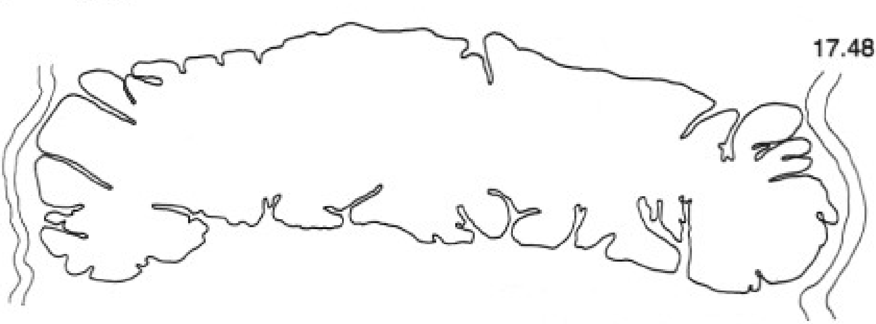

17.43


17.44


17.45


17.46


17.47


17.48

tacle present. Uterus single, tubular, transverse, looping anteriorly around each seminal receptacle, with paired, posteriorly directed diverticula on either side. Pyriform apparatus present. In psittaciform birds. New Zealand. Type-species *S. psittacea* (Fuhrmann, 1904).

27a. Uterus transverse, tubular, with few, simple reticulations (Figs 17.46, 17.47, 17.53) .... 28.

27b. Uterus develops as complex, finely reticulated net, finally becoming saccate when gravid (Figs 17.55, 17.57–17.59) .... 30.

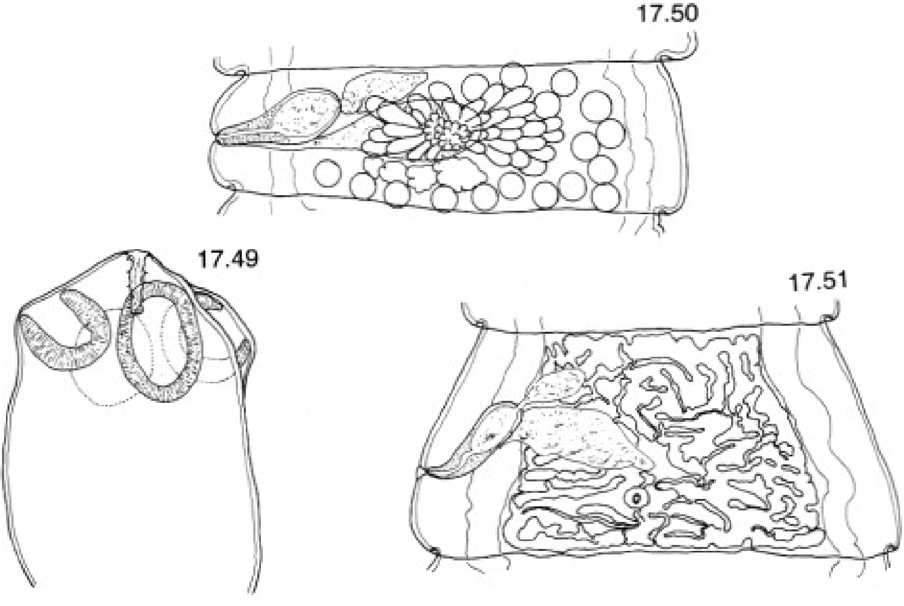
28a. Genitalia single .... 29.

28b. Genitalia paired .... *Cittotaenia* Riehm, 1881. (Figs 17.46–17.48)

Diagnosis: Strobila large. Proglottids craspedote, wider than long. Genital ducts cross canals dorsally. Cirrus-sac very powerfully developed. Internal and external seminal vesicle absent. Testes scattered throughout medulla or in two groups. Ovaries poral. Vagina posterior to cirrus-sac. Seminal receptacle present. Uterus single, transverse, slightly reticulate during development. Pyriform apparatus present. In leporid lagomorphs and chinchillid rodents. Europe, South America. Type-species *C. denticulata* (Rudolphi, 1804).

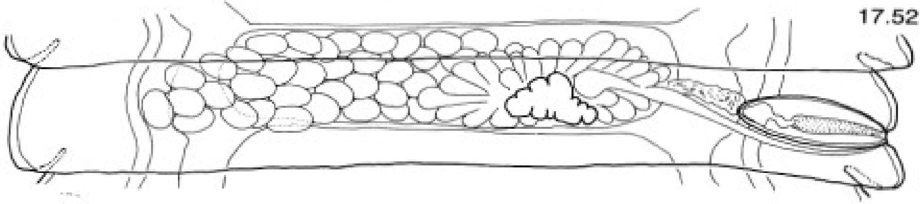
29a. Cavity present in apex of scolex (Fig. 17.49). Testes posterior and lateral to ovary (Fig. 17.50) ..... *Sudarikovina* Spasskii, 1951. (Figs 17.49–17.51)

Diagnosis: Strobila small. Proglottids craspedote, wider than long. Genitalia single. Genital pores unilateral. Genital ducts cross canals dorsally. Internal and

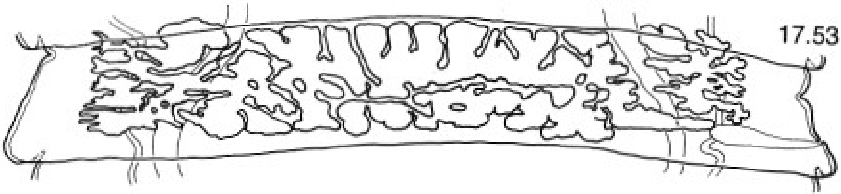


Figs 17.49–17.51 *Sudarikovina taterae* Hunkeler, 1972. 17.49. Scolex. 17.50. Mature proglottid 17.51. Gravid proglottid. Original.

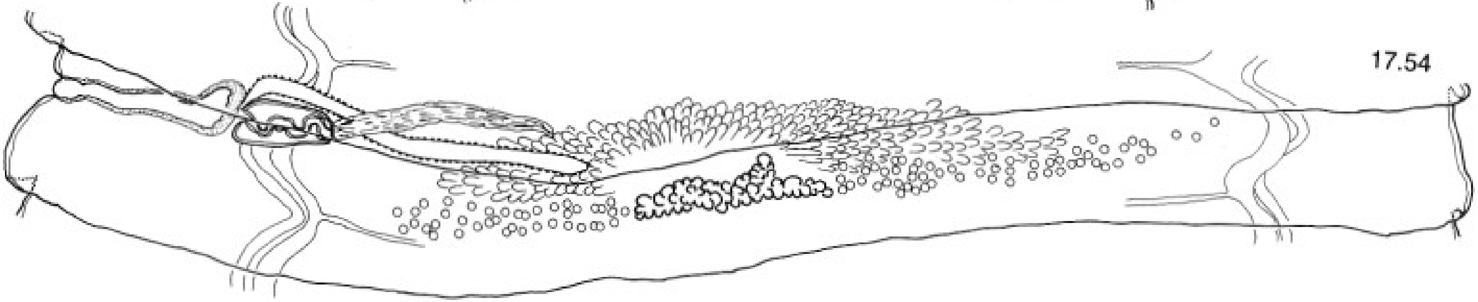
17.52



17.53



17.54



17.55

Figs 17.52-17.53 *Paranoplocephala omphalodes* (Hermann, 1783). 17.52. Mature proglottid. 17.53. Gravid proglottid. Original. **Figs 17.54, 17.55.** *Monoecocestus hagmani* (Janicki, 1904). 17.54. Mature proglottid. 17.55. Gravid proglottid. Original.

external seminal vesicles present. Ovary central. Vagina posterior to cirrus-sac. Seminal receptacle present. Uterus reticulate. Pyriform apparatus present or absent. In rodents. Africa. Type-species *S. monodi* (Joyeux & Baer, 1930).

29b. Cavity in scolex absent. Testes aporal to ovary .... *Paranoplocephala* Lühe, 1910. (Figs 17.52, 17.53)
(Syn. *Aprostatandrya* Kirschenblatt, 1932.)

Diagnosis: Strobila small to medium-sized. Proglottids craspedote, wider than long. Genitalia single. Genital pores unilateral or irregularly alternating. Genital ducts cross canals dorsally. Internal and external seminal vesicles present. Uterus single, at first rod-like, transverse, becoming reticulate with diverticula. Pyriform apparatus present. In rodents. Europe, Asia, North America. Type-species *P. omphalodes* (Hermann, 1783).

30a. Vagina opens to genital atrium anterior to cirrus-sac. Testes posterior to ovary (Fig. 17.54) .... *Monoecocestus* Beddard, 1914. (Figs 17.54, 17.55)
(Syns *Schizotaenia* Janicki, 1904 preoccupied; *Perutaenia* Parra, 1953; *Lentiella* Rego, 1964.)

Diagnosis: Strobila small to large. Proglottids craspedote, wider than long. Genitalia single. Genital pores alternate regularly. Genital ducts cross canals dorsally. Internal and external seminal vesicles present. Testes in band in posterior half of medulla. Ovary central or poral. Vagina anterior to cirrus-sac. Seminal receptacle present. Uterus reticulate. Pyriform apparatus present. In rodents, artiodactyls, rheiform birds. North and South America. Type-species *M. decrescens* (Diesing, 1856).

30b. Vagina opens to genital atrium posterior to cirrus-sac. Testes anterior and posterior to ovary .... 31.

31a. Genitalia single .... *Andrya* Railliet, 1893. (Figs 17.56, 17.57)

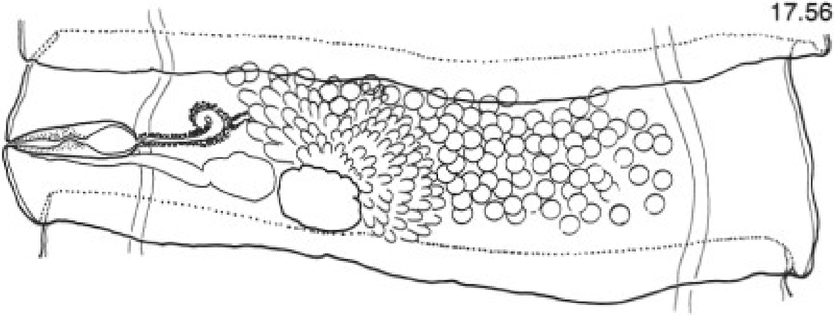
Diagnosis: Strobila moderate. Proglottids craspedote, wider than long. Genital pores alternate regularly. Genital ducts cross canals dorsally. Internal and external seminal vesicles present; external vesicle with prominent covering of 'glandular' cells. Testes scattered, mainly aporal. Ovary poral. Vagina posterior to cirrus-sac. Seminal receptacle present. Uterus finely reticulate when first develops. Pyriform apparatus present. In leporid lagomorphs. Europe, Africa, Asia. Type-species *A. rhopalocephala* (Riehm, 1881).

31b. Genitalia paired .... 32.

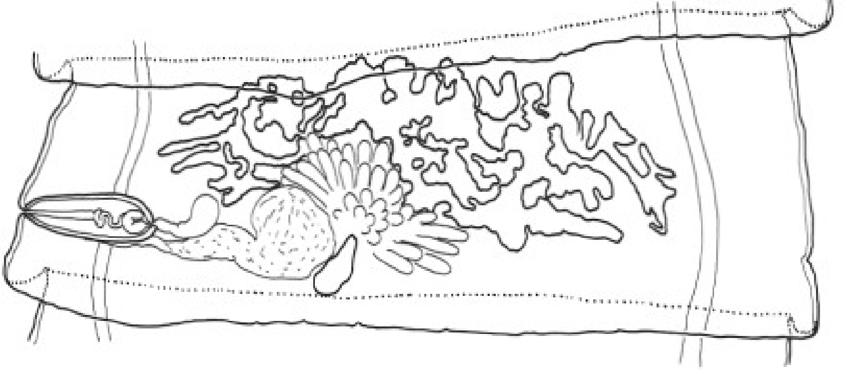
Figs 17.56, 17.57 *Andrya rhopalocephala* (Riehm, 1881). 17.56. Mature proglottid. Note thickened glandular covering of external seminal vesicle. 17.57. Developing reticulate uterus. Original.

Fig. 17.58 *Diandrya composita* Darrah, 1930. Lateral region of mature proglottid. Note thickened glandular covering of external seminal vesicle. Original.

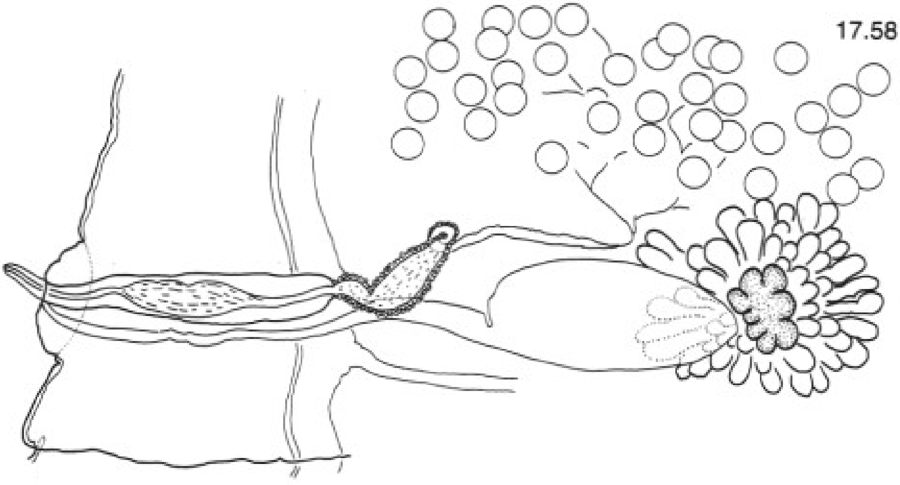
Fig. 17.59 *Moniezia expansa* (Rudolphi, 1810). Mature proglottid. Original.



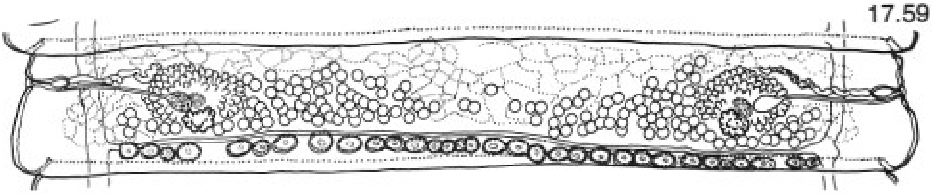
17.56



17.57



17.58



17.59

32a. External seminal vesicle covered with gland cells (Fig. 17.58) ....
.... ***Diandrya* Darrah, 1930. (Fig. 17.58)**

Diagnosis: Strobila large. Proglottids craspedote, wider than long. Genitalia paired. Genital ducts cross canals dorsally. Internal and external seminal vesicles present. Testes scattered throughout medulla. Ovaries poral. Vagina posterior to cirrus-sac. Seminal receptacle present. Uterus finely reticulate when first develops. Pyriform apparatus present. In sciurid rodents. North America. Type-species *D. composita* Darrah, 1930.

32b. External seminal vesicle absent ....
.... ***Moniezia* Blanchard, 1891. (Fig. 17.59)**
(Syns *Baeriezia* Skryabin & Schulz, 1937; *Blanchardiezia* Skryabin & Schulz, 1937; *Eranuides* Semenova, 1972; *Fuhrmannella* Baer, 1925.)

Diagnosis: Strobila large. Proglottids craspedote, wider than long. Genitalia paired. Genital ducts cross canals dorsally. Testes scattered throughout medulla. Ovaries poral. Vagina posterior to cirrus-sac. Seminal receptacle present. Uterus finely reticulate when first formed. Interproglottidal glands present or absent. Pyriform apparatus present. In ruminants, suids, rodents, primates, ratite birds. Cosmopolitan. Type-species *M. expansa* (Rudolphi, 1810).

Key to genera of the Linstowiinae

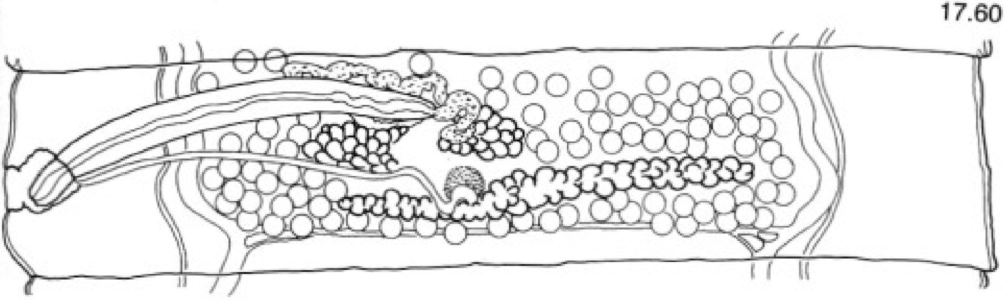
1a. Vitellarium compact, post-ovarian (Figs 17.65, 17.66, 17.68) .... **3.**
1b. Vitellarium transversely elongated, extending beyond ovary (Figs 17.60, 17.61) .... **2.**

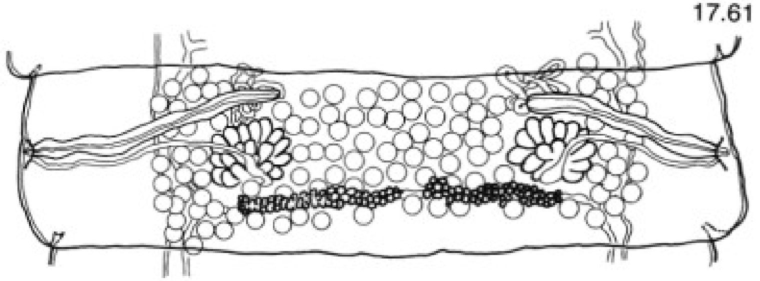
2a. Genitalia single .... ***Linstowia* Zschokke, 1899. (Fig. 17.60)**
(Syn. *Peramelinia* Spasskii, 1987.)

Diagnosis: Strobila large. Proglottids craspedote, wider than long. Genital pores alternate irregularly. Genital ducts cross canals ventrally. Internal and external seminal vesicles present. Testes scattered. Ovary poral. Vagina posterior to cirrus-sac. Seminal receptacle diminutive. Uterus ephemeral. Vitellarium transversely elongated. In monotremes and peramelid marsupials. Australia. Type-species *L. echidnae* (Thompson, 1893).

2b. Genitalia paired .... ***Echidnotaenia* Beveridge, 1980. (Fig. 17.61)**
Diagnosis: Strobila small. Proglottids craspedote, wider than long. Genital ducts cross canals ventrally. Internal and external seminal vesicles present. Testes scattered. Vagina posterior to cirrus-sac. Seminal receptacle present. Uterus ephemeral. Vitellarium transversely elongated. In monotremes. Australia. Type-species *E. tachyglossi* (Johnston, 1913).

3a. Genitalia single .... **4.**
3b. Genitalia paired .... ***Panceriella* Stunkard, 1969. (Fig. 17.62)**
(Syns *Panceria* Sonsino, 1895 preoccupied; *Pancerina* Fuhrmann, 1899 preoccupied)





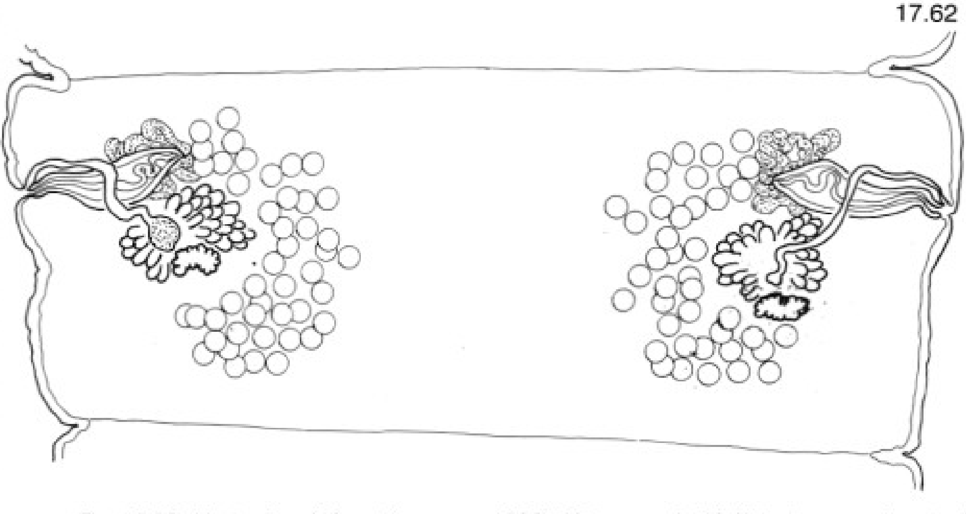


Fig. 17.60 *Linstowia echidnae* (Thompson, 1893). Mature proglottid. Note transversely extended vitellarium. Redrawn from Beveridge (1983).
Fig. 17.61 *Echidnotaenia tachyglossi* (Johnston, 1913). Mature proglottid. Note transversely extended vitellaria. Redrawn from Beveridge (1980).
Fig. 17.62 *Panceriella varani* (Stossich, 1895). Mature proglottid. Original.

Diagnosis: Strobila small. Proglottids acraspedote; mature proglottids wider than long. Genital ducts lie between canals. Seminal vesicles absent. Testes in two groups anterior, medial and posterior to female genitalia. Vagina opens to genital atrium anterior to cirrus-sac. Seminal receptacle present. Uterus ephemeral. Vitellarium compact. In varanid lizards. Africa. Middle East. Type-species *P. varani* (Stossich, 1895).

4a. Testes present anterior to ovary (Figs 17.63–17.66) .... 5.
4b. Testes posterior to ovary and/or on either side, not anterior (Figs 17.68–17.71) .... 8.

5a. Testes entirely anterior to ovary (Fig. 17.63) ....
.... *Sinaiotaenia* Wertheim & Greenberg, 1971. (Fig. 17.63)
Diagnosis: Strobila moderate. Proglottids acraspedote, longer than wide. Genitalia single. Genital pores alternate irregularly. Genital ducts lie between canals. Seminal vesicles absent. Testes scattered anterior and lateral to female genitalia. Ovary at posterior end of proglottid. Vagina posterior to cirrus-sac. Seminal receptacle present. Uterus ephemeral. In gerbillid rodents. Sinai. Type-species *S. witenbergi* Wertheim & Greenberg, 1971.

5b. Some testes posterior to ovary .... 6.

6a. Testes anterior to ovary in two distinct lateral groups (Fig. 17.64) ....
.... *Cycloskrjabinia* Spasskii, 1951. (Fig. 17.64)
Diagnosis: Strobila small. Proglottids acraspedote, longer than wide. Genitalia single. Genital pores alternate irregularly. Genital ducts cross canals ventrally. Internal and external seminal vesicles absent. Testes posterior to ovary and in two lateral bands extending to anterior end of proglottid. Ovary central. Vagina posterior to cirrus-sac. Seminal receptacle absent. Uterus ephemeral. Vitellarium compact. In Chiroptera. North America, Europe. Type-species *C. taborensis* (Loewen, 1934).

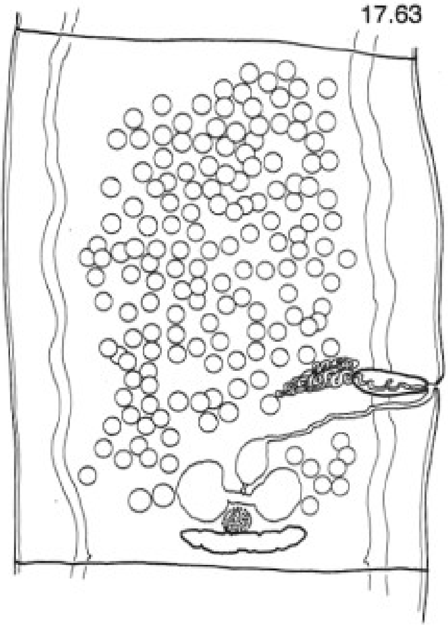
6b. Testes anterior to ovary not in two distinct lateral groups .... 7.

7a. Proglottids acraspedote (Fig. 17.65) ....
.... *Semenoviella* Spasskii, 1951. (Fig. 17.65)
Diagnosis: Strobila small. Genitalia single. Genital pores alternate irregularly. Genital ducts pass canals ventrally. Internal and external seminal vesicles absent. Testes surround female genital complex. Cirrus-sac large, crosses medulla. Ovary central. Vagina posterior to cirrus-sac. Uterus ephemeral. Vitellarium compact. In lizards. South America. Type-species *S. amphisbaenae* (Rudolphi, 1819).

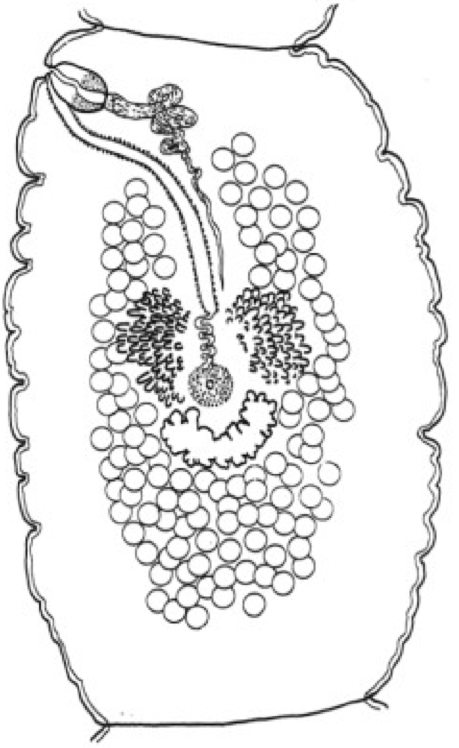
7b. Proglottids craspedote .... *Paralinstowia* Baer, 1927. (Fig. 17.66)
(Syn. *Pseudolinstowia* Spasskii, 1987.)
Diagnosis: Strobila small. Genitalia single. Genital pores unilateral or irregularly alternate. Genital ducts cross canals ventrally. Internal and external seminal vesicles absent. Testes scattered throughout medulla. Ovary central. Vagina posterior to cirrus-sac. Seminal receptacle present. Uterus ephemeral. Vitellarium compact. In didelphid, dasyurid and peramelid marsupials. South America, Australia. Type-species *P. iheringi* (Zschokke, 1904).

8a. Suckers with prominent, paired lappets (Fig. 17.67) ....
.... *Tupaiataenia* Schmidt & File, 1977. (Fig. 17.67)

17.63



17.64



17.65

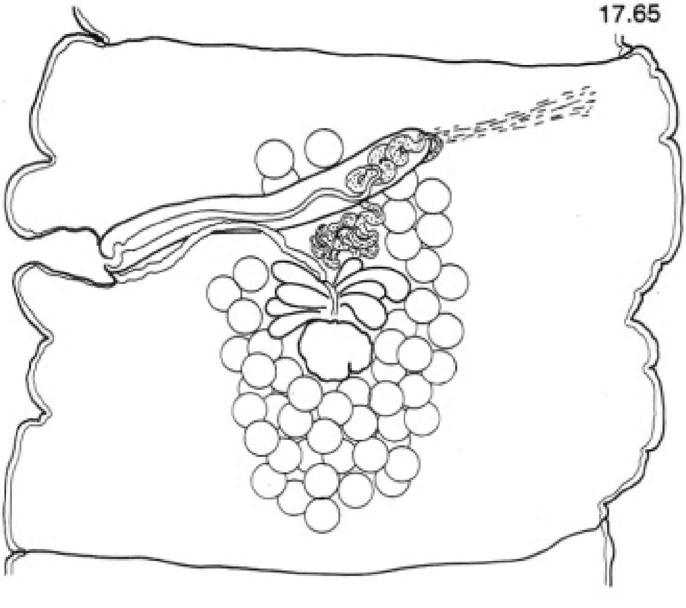
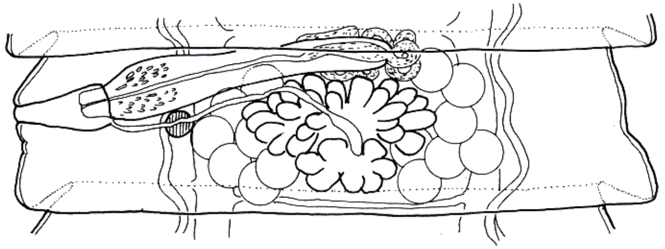
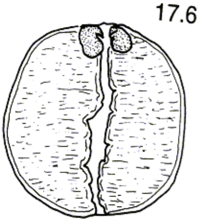


Fig. 17.63 *Sinaiotaenia witenbergi* Wertheim & Greenberg, 1971. Mature proglottid. Original.
Fig. 17.64 *Cycloskrjabinia taborensis* (Loewen, 1934). Mature proglottid. Original.
Fig. 17.65 *Semenoviella amphisbaenae* (Rudolphi, 1819). Mature proglottid. Original.

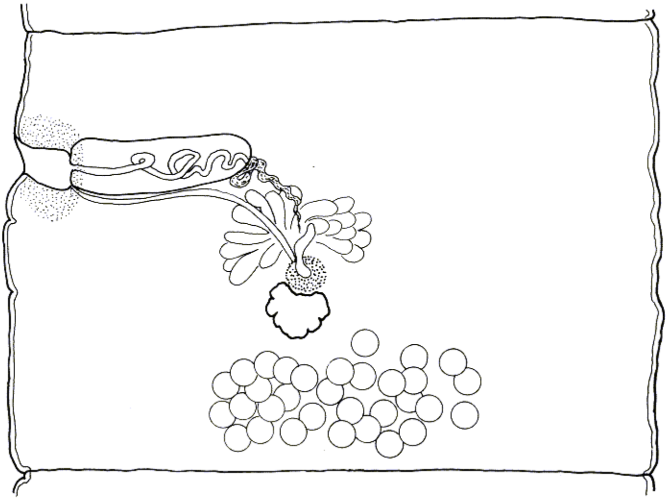
17.66



17.67



17.68



17.69

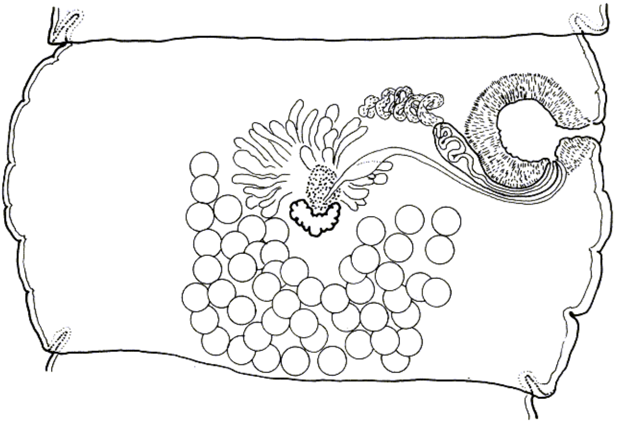


Fig. 17.66 *Paralinstowia semoni* (Zschokke, 1896). Mature proglottid. Redrawn from Beveridge (1983).
Fig. 17.67 *Tupaiataenia quentini* Schmidt & File, 1977. Sucker with anterior lappets. Original.
Fig. 17.68 *Oochoristica tuberculata* (Rudolphi, 1819). Mature proglottid. Original.
Fig. 17.69 *Atriotaenia sandgroundi* (Baer, 1935). Paratype; mature proglottid. Original.

Diagnosis: Strobila small. Proglottids craspedote, wider than long. Genitalia single. Genital pores alternate irregularly. Genital ducts cross canals dorsally. Internal seminal vesicle present; external vesicle absent. Testes posterior to vitellarium. Ovary central. Vagina posterior to cirrus-sac. Seminal receptacle present. Uterus ephemeral. Vitellarium compact. In tree-shrews. South-east Asia. Type-species *T. quentini* Schmidt & File, 1977.

8b. Suckers without lappets .... **9.**

9a. Proglottids acraspedote .... ***Oochoristica* Lühe, 1898. (Fig. 17.68)** (Syns *Diochetos* Harwood, 1932; *Skrjabinochora* Spasskii, 1948; *Megacapsula* Wahid, 1961; *Sharpilia* Spasskii, 1988; *Semenochetos* Palladwar & Kalyankar, 1989).

Diagnosis: Strobila small. Proglottids longer than wide. Genitalia single. Genital pores alternate irregularly. Genital ducts lie between canals. Internal and external seminal vesicles absent. Testes posterior to vitellarium. Ovary central. Vagina posterior to cirrus-sac. Seminal receptacle present or absent. Uterus ephemeral. Vitellarium compact. In reptiles, mammals. Cosmopolitan. Type-species *O. tuberculata* (Rudolphi, 1819).

9b. Proglottids craspedote .... **10.**

10a. Genital atrium prominent with well-developed radial musculature, genital ducts open into posterior part of atrium (Fig. 17.69) .... ***Atriotaenia* Sandground, 1926. (Fig. 17.69)** (Syn. *Ershovia* Spasskii, 1951.)

Diagnosis: Strobila small. Proglottids craspedote, wider than long. Genitalia single. Genital pores alternate irregularly. Genital ducts cross canals dorsally or lie between them. Cirrus-sac enters genital atrium posteriorly. Internal and external seminal vesicles absent. Testes posterior and lateral to female genital complex. Ovary central. Vagina posterior to cirrus-sac. Seminal receptacle present. Uterus ephemeral. Vitellarium compact. In mustelid and procyonid mammals. Europe, North and South America. Type-species *A. sandgroundi* (Baer, 1935).

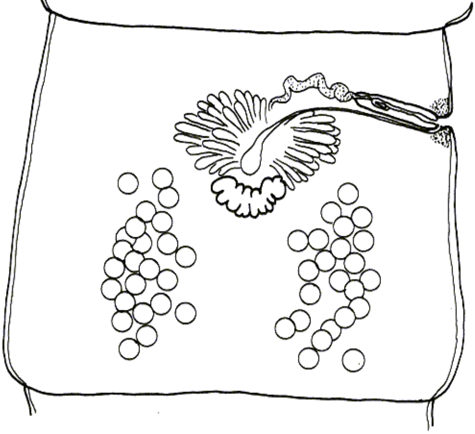
10b. Genital atrium without prominent muscular atrium. Genital ducts open into medial part of atrium .... **11.**

11a. Testes invariably divided into two lateral groups (Fig. 17.70) .... ***Witenbergitaenia* Wertheim, Schmidt & Greenberg, 1986. (Fig. 17.70)**

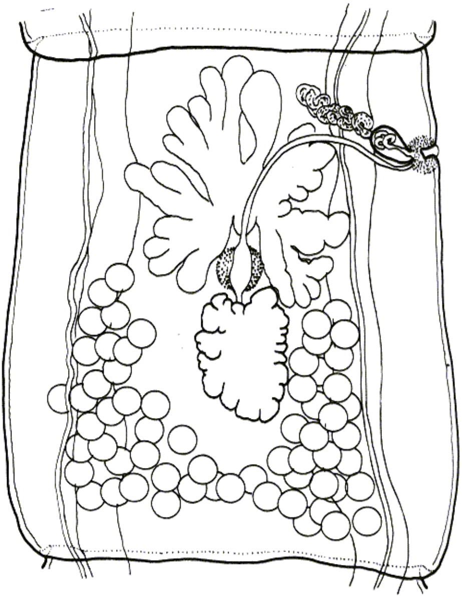
Diagnosis: Strobila small. Proglottids craspedote, as wide as long. Genitalia single. Genital pores alternate irregularly. Genital ducts cross canals dorsally. Internal and external seminal vesicles absent. Testes posterior to female genitalia. Ovary central. Vagina posterior to cirrus-sac. Seminal receptacle present. Uterus ephemeral. Vitellarium compact. In murid rodents. Israel. Type-species *W. sinaica* Wertheim, Schmidt & Greenberg, 1986.

11b. Testes in single group or some proglottids in strobila with testes in single group .... ***Mathevotaenia* Akhumyan, 1946. (Fig. 17.71)** (Syns *Opossumia* Spasskii, 1951; *Inversia* Spasskii, 1951; *Morosovella*

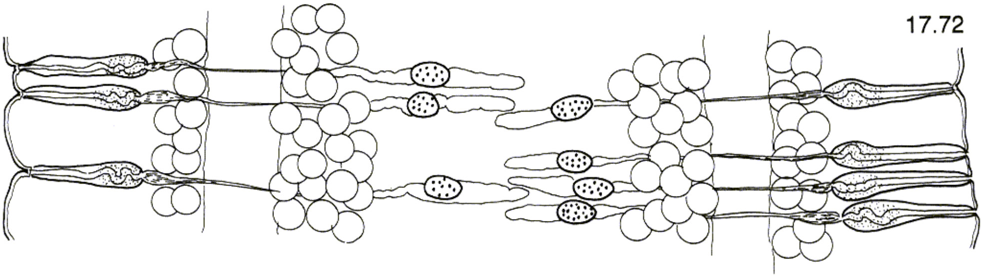
17.70



17.71



17.72



17.73

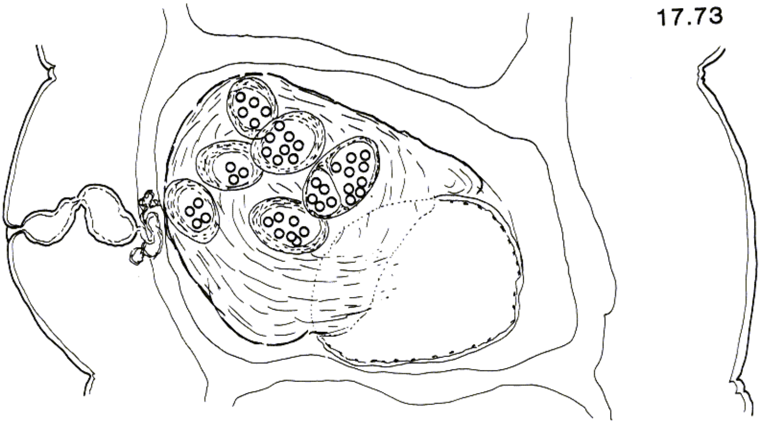


Fig. 17.70 *Witenbergitaenia sinaica* Wertheim, Schmidt & Greenberg, 1986. Mature proglottid. Redrawn from Wertheim *et al.* (1986).

Fig. 17.71 *Mathevotaenia symmetrica* (Baylis, 1927). Type; mature proglottid. Original.

Figs 17.72, 17.73 *Avitellina centripunctata* (Rivolta, 1874). 17.72. Mature proglottids; note lack of segmentation. 17.73. Gravid proglottid with single paruterine organ and eggs and paruterine capsules. Original.

Spasskii, 1951; *Paratriotaenia* Stunkard, 1965; *Markewitschitaenia* Sharpilo & Kornyushin, 1975; *Timorenia* Spasskii, 1987; *Hickmania* Spasskii, 1987, as *Hickmawia*; *Schizorchodes* Bienek & Grundman, 1973; *Priodontia* Spasskii, 1987; *Linstoparonia* Spasskii, 1987; *Mangustella* Spasskii, 1987; *Vasoramia* Spasskii, 1987.)

Diagnosis: Strobila small. Proglottids craspedote. Genitalia single. Genital pores alternate irregularly. Genital ducts cross canals dorsally or lie between them. Internal and external seminal vesicles absent. Testes posterior and lateral to female genitalia. Ovary central. Vagina posterior to cirrus-sac. Seminal receptacle present. Uterus ephemeral. Vitellarium compact. In mammals. Cosmopolitan. Type-species *M. symmetrica* (Baylis, 1927).

Key to genera of the Thysanosomatinae

1a. **One or two paruterine organs per proglottid (Figs 17.73, 17.77)** .... **2.**

1b. **Numerous small paruterine organs develop from each uterus (Figs 17.79, 17.80, 17.82)** .... **3.**

2a. **Single paruterine organ per proglottid (Fig. 17.73)** .... ***Avitellina* Gough, 1911. (Figs 17.72, 17.73)**

(Syns *Héxastichorchis* Blei, 1921; *Anootypus* Woodland, 1928; *Ascotaenia* Baer, 1927.)

Diagnosis: Strobila large. Proglottids poorly demarcated particularly in anterior region; wider than long. Genitalia single. Genital pores alternate irregularly. Genital ducts cross canals dorsally. Internal and external seminal vesicles absent. Testes in two lateral groups, each subdivided by osmoregulatory canal. Germovitellarium (combined ovary and vitellarium) present. Single paruterine organ with fibrous capsules each containing several eggs. In ruminants. Europe, Asia, Africa, North America. Type-species *A. centripunctata* (Rivolta, 1874).

2b. **Two paruterine organs per proglottid (Fig. 17.77)** .... ***Stilesia* Railliet, 1893. (Figs 17.74–17.77)**

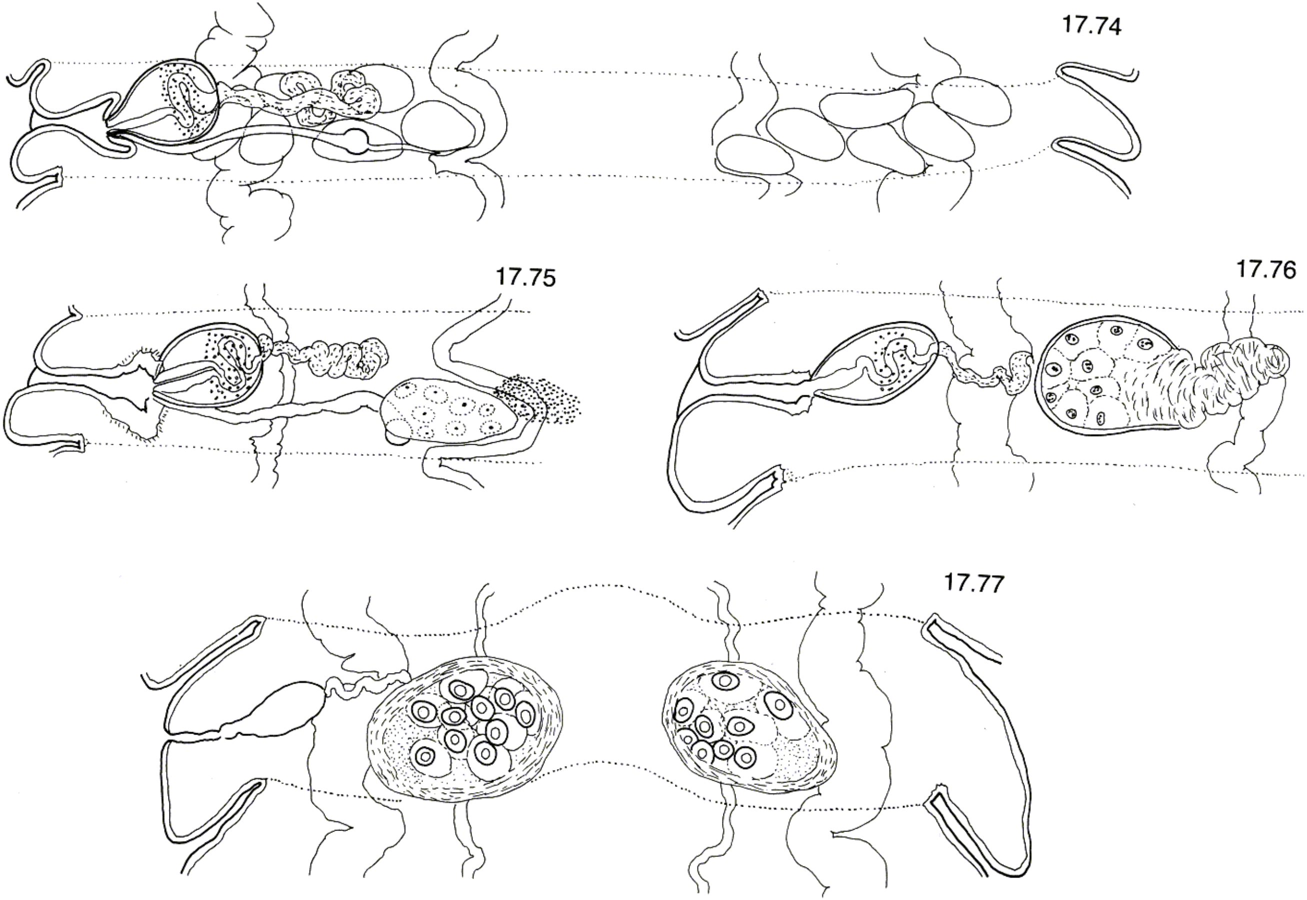
(Syn. *Aliezia* Shinde, 1969.)

Diagnosis: Strobila large. Proglottids craspedote, wider than long. Genitalia single. Genital pores alternate irregularly. Genital ducts lie between canals. Internal and external seminal vesicles absent. Testes in two lateral groups external to dorsal canals. Germovitellarium (combined ovary and vitellarium) present. Vagina posterior to cirrus-sac. Seminal receptacle absent. Uterus initially transverse tubular with enlarged ends; each extremity develops paruterine organ. In bile-ducts of ruminants. Asia, Africa. Europe. Type-species *S. globipunctata* (Rivolta, 1874).

3a. **Testes in two lateral, extravascular groups (Figs 17.78, 17.79), genitalia single** .... ***Thysaniezia* Skryabin, 1926. (Figs 17.78, 17.79)**

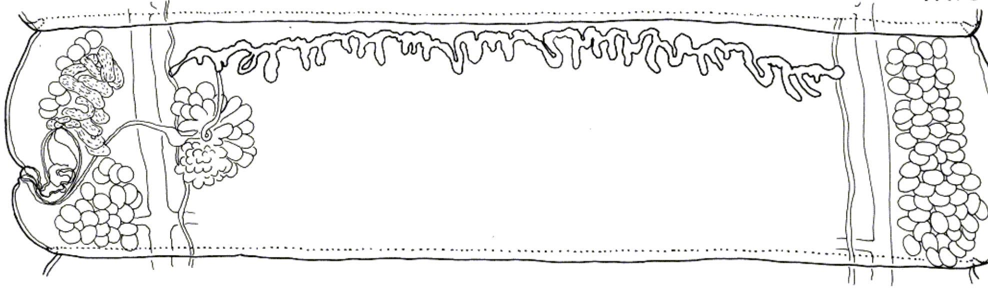
(Syn. *Helictometra* Baer, 1927.)

Diagnosis: Strobila large. Proglottids craspedote, wider than long. Genital pores

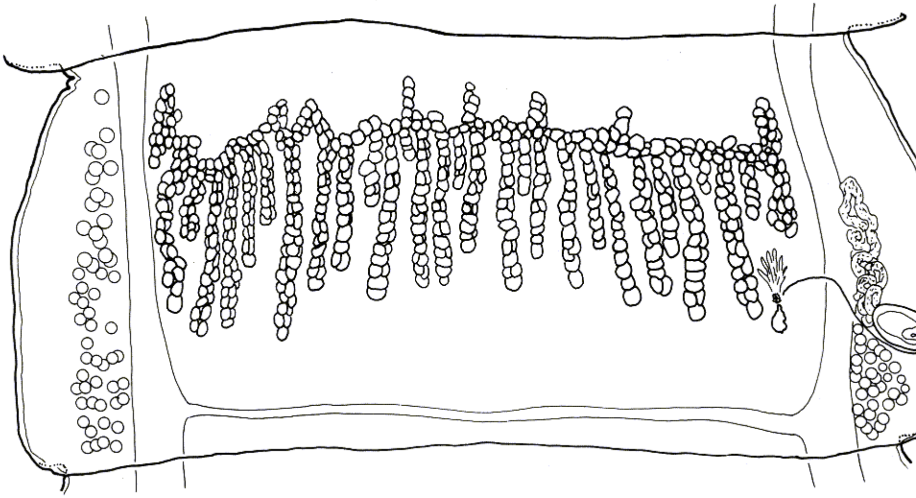


Figs 17.74-17.77 *Stilesia globipunctata* (Rivolta, 1874). 17.74. Mature proglottid. 17.75. Gravid proglottid, 17.76. Developing paruterine organ. 17.77. Gravid proglottid with two paruterine organs. Original.

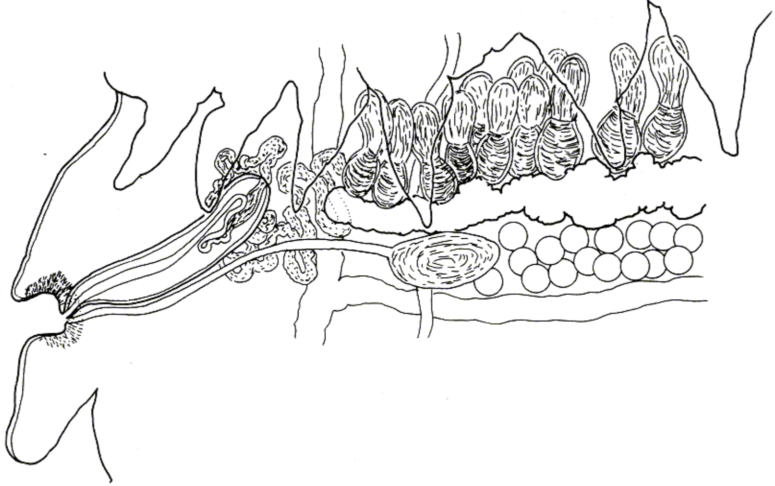
17.78



17.79



17.80



Figs 17.78, 17.79 *Thysaniezia ovilla* (Rivolta, 1878). 17.78. Mature proglottid. 17.79. Gravid proglottid. Original.

Fig. 17.80 *Thysanosoma actinioides* Diesing, 1835. Lateral region of mature proglottid showing fringed velum, uterus and paruterine organs. Original.

alternate irregularly. Genital ducts lie between canals. Internal seminal vesicles present. Ovary poral. Vitellarium post-ovarian. Vagina posterior to cirrus-sac. Seminal receptacle present. Uterus initially tubular, transverse, replaced by >300 paruterine capsules. In ruminants. Cosmopolitan. Type-species *T. ovilla* (Rivolta, 1878).

3b. Testes in single continuous band posterior to uterus (Figs 17.80, 17.81). Genitalia paired .... **4.**

4a. Proglottid prominently fringed (Fig. 17.80) .... ***Thysanosoma*** **Diesing, 1835. (Fig. 17.80)**

Diagnosis: Strobila large. Proglottids craspedote, wider than long. Genitalia paired. Genital ducts lie between canals. Seminal vesicles absent. Testes numerous, in band posterior to uterus. Germovitellarium present; posterior to level of cirrus-sac. Seminal receptacle present. Uterus single, transverse. Numerous (>250) small paruterine organs develop anteriorly from uterus. In bile-ducts of ruminants. North and South America. Type-species *T. actinioides* Diesing, 1835.

4b. Proglottid not prominently fringed (Figs 17.81, 17.82) .... ***Wyominia*** **Scott, 1941. (Figs 17.81, 17.82)**

Diagnosis: Strobila large. Proglottids craspedote, wider than long. Velum folded. Genitalia paired. Genital ducts lie between canals. Seminal vesicles absent. Testes numerous, in band posterior to uterus. Ovaries poral. Vitellarium post-ovarian. Vagina posterior to cirrus-sac. Seminal receptacle present. Uterus single, transverse, replaced by about 20 paruterine organs. In bile-ducts of ruminants. North America. Type-species *W. tetoni* Scott, 1941.

Key to genera of the Inermicapsiferinae

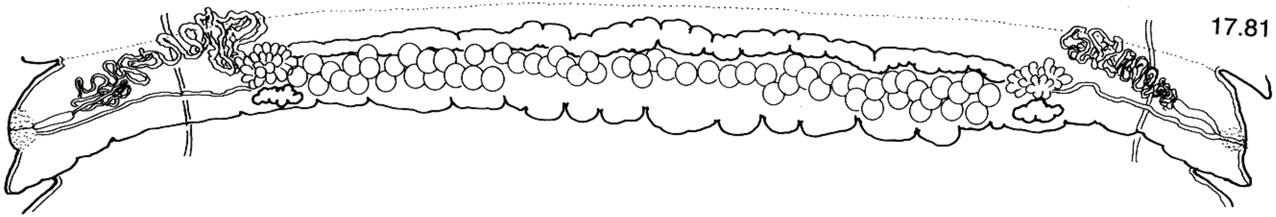
1a. Testes and egg capsules intervascular. Ovary central (Fig. 17.83) .... ***Thysanotaenia*** **Beddard, 1911. (Fig. 17.83)**

Diagnosis: Strobila large. Proglottids craspedote, wider than long. Genitalia single. Genital ducts cross canals dorsally. Seminal vesicles absent. Testes absent only from anterior, poral region of proglottid. Ovary subcentral. Vagina posterior to cirrus-sac. Seminal receptacle present. Uterus ephemeral; fibrous egg capsules intervascular. In lemurs. Malagasy Republic. Type-species *T. lemuris* Beddard, 1911.

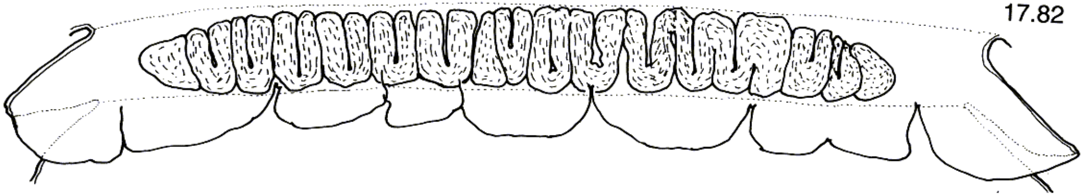
1b. Testes and egg capsules extending beyond osmoregulatory canals. Ovary poral (Figs 17.85, 17.86) .... **2.**

2a. Testes scattered uniformly throughout medulla (Fig. 17.84) .... ***Pericapsifer*** **Spasskii, 1951. (Fig. 17.84)**

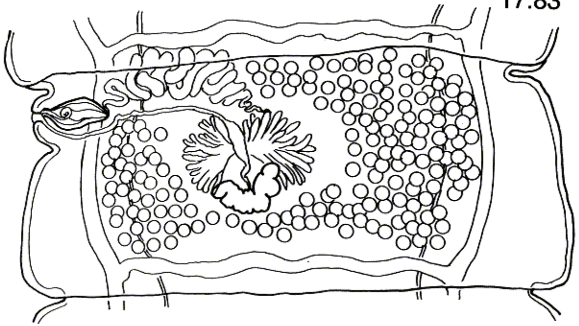
Diagnosis: Strobila small. Proglottids craspedote, wider than long. Genitalia single. Genital pores unilateral. Genital ducts cross canals dorsally. Seminal vesicles absent. Testes extending beyond canals. Ovary poral. Vagina posterior to



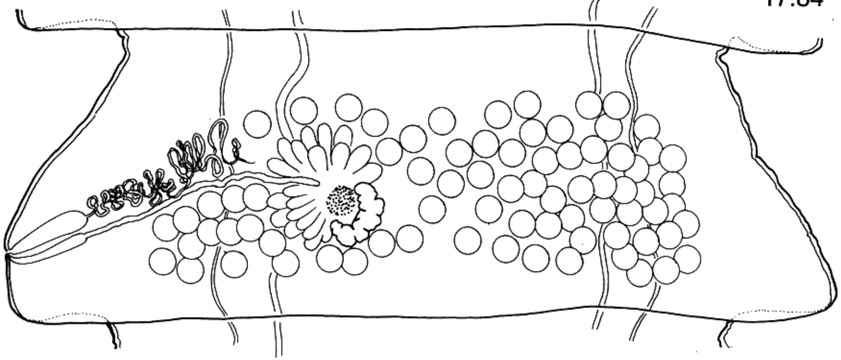
17.81



17.82

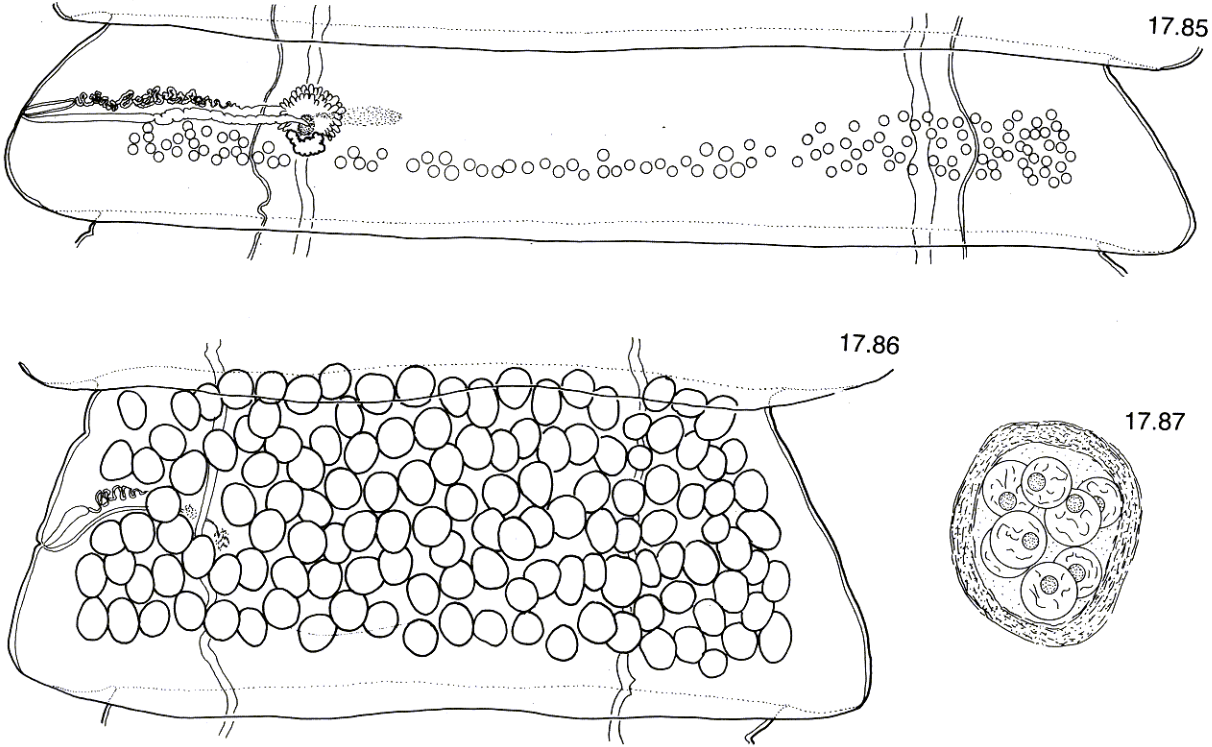


17.83



17.84

Figs 17.81, 17.82 *Wyominia tetoni* Scott, 1941. 17.81 Mature proglottid. 17.82. Gravid proglottid. Original.
Fig. 17.83 *Thysanotaenia lemuris* Beddard, 1911. Mature proglottid. Redrawn from Deblock & Diaouré (1962).
Fig. 17.84 *Pericapsifer pagenstecheri* (Setti, 1897). Mature proglottid. Original.



Figs 17.85-17.87 *Inermicapsifer hyracis* (Rudolphi, 1808). 17.85. Mature proglottid; note extent of testes beyond canals. 17.86. Gravid proglottid; note extravascular egg capsules. 17.87. Egg capsule. Original.

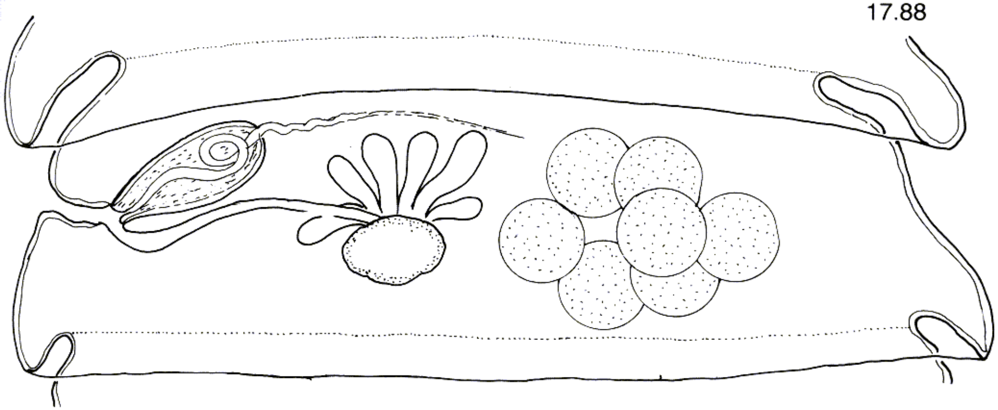


Fig. 17.88 *Metacapsifer aberratus* (Baer, 1925). Mature proglottid. Redrawn from Baer (1925c).

cirrus-sac. Seminal receptacle present. Uterus ephemeral; fibrous egg capsules extend laterally beyond canals. In hyracoids. Africa. Type-species *P. pagenstecheri* (Setti, 1897).

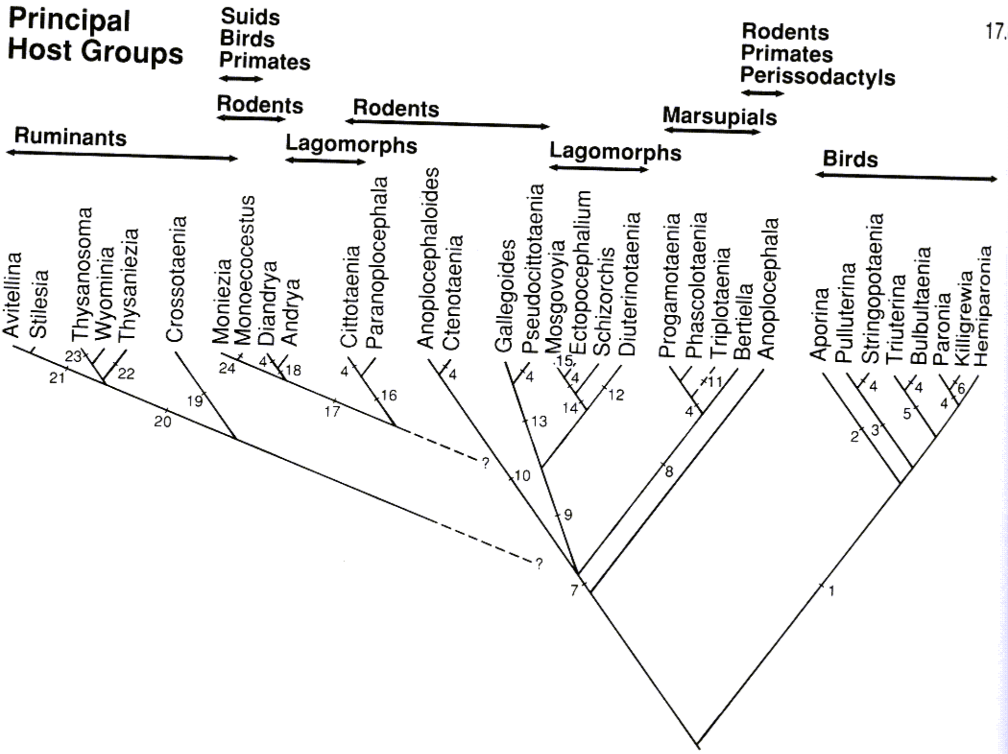
2b. Testes restricted in distribution .... **3.**

3a. Testes posterior to ovary or posterior and lateral or in two lateral groups (Fig. 17.85) .... ***Inermicapsifer* Janicki, 1910. (Figs 17.85–17.87)** (Syns *Arhynchotaenia* Pagenstecher, 1877 preoccupied; *Hyracotaenia* Beddard, 1912.)

Diagnosis: Strobila small to large. Proglottids craspedote, wider than long. Genitalia single. Genital pores unilateral. Genital ducts cross canals dorsally. Seminal vesicles absent. Testes in single band at posterior margin of proglottid, or posterior and lateral to ovary, or two lateral groups, extending beyond canals. Ovary poral. Vagina posterior to cirrus-sac. Seminal receptacle present. Uterus ephemeral; fibrous egg capsules extend laterally beyond canals. In hyracoids, rodents, lagomorphs. Africa, Asia. Type-species *I. hyracis* (Rudolphi, 1808).

3b. Testes restricted to aporal side of proglottid (Fig. 17.88) .... ***Metacapsifer* Spasskii, 1951. (Fig. 17.88)**

Diagnosis: Strobila small. Proglottids craspedote. Genitalia single. Genital pores unilateral. Seminal vesicles absent. Testes few. Ovary poral. Vagina posterior to cirrus-sac. Seminal receptacle present. Uterus ephemeral; fibrous egg capsules replace uterus. In rodents. Africa. Type-species *M. aberratus* (Baer, 1925).



17.89

Fig. 17.89 Speculative view of phylogenetic relationships within Anoplocephalinae and Thysanosomatinae. Figures on diagram represent the following character states which are considered to be derived or apomorphic; where relevant, the primitive or plesiomorphic state follows. 1. Uterus looped anteriorly around female genital complex with ends terminating at posterolateral corners of medulla (or beyond) - uterus a straight tube. 2. Uterus with paired anterolateral diverticula (Fig. 17.30) - without diverticula. 3. Uterus with pair of posterior diverticula on either side of seminal receptacle (Fig. 17.43) - diverticula absent. 4. Genitalia paired - single. 5. Uterus with anteriorly-directed spur (Fig. 17.33) - spur absent. 6. Testes in two lateral groups (Fig. 17.41) - testes uniformly distributed. 7. Testes distributed other than throughout medulla - distributed throughout medulla. 8. Testes entirely anterior to uterus (or seminal receptacle circular). 9. Testes entirely posterior to uterus. 10. Testes aporal to female genitalia. 11. Strobila subdivided (Figs 17.1, 17.2) - strobila entire. 12. Uteri longitudinal (Fig. 17.12) - uteri transverse. 13. Uterus crosses vessels ventrally, terminates anterior to cirrus-sac (Fig. 17.14) - uterus medullary. 14. Uterus crosses vessels dorsally, terminates posterior to cirrus-sac (Fig. 17.19) - uterus medullary. 15. Scolex elongate with glands (Fig. 17.18) - scolex not elongate, without glands. 16. Uterus slightly reticular (Fig. 17.47) - uterus tubular. 17. Uterus highly reticular - slightly reticular. 18. External seminal vesicle with glandular coat (Fig. 17.58) - gland cells absent. 19. Mehlis' gland reduced or paruterine organs present - gland not reduced, organs absent. 20. Paruterine organs present - absent. 21. Germovitellarium present - absent. 22. Testes extravascular - testes intravascular. 23. Velum fringed - not fringed. 24. Vagina anterior to cirrus-sac - vagina posterior to cirrus-sac.