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Order Caryophyllidea van Beneden in Carus, 1863

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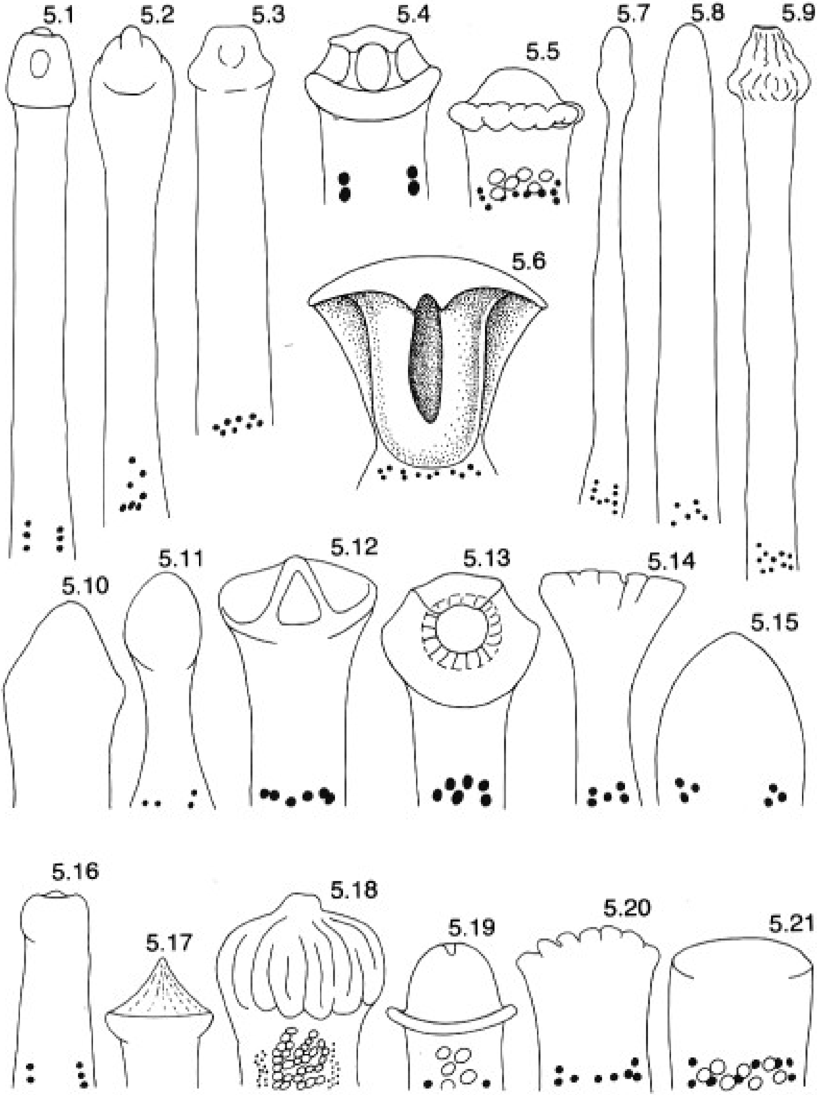
Introduction

Caryophyllid cestodes are unique among the Cestoidea in having a monopleuroid body plan, i.e. without internal or external proglottidization and with a single set of reproductive organs. They thus superficially resemble cestodarians. In fact, Yamaguti (1959) considered them an order under the subclass Cestodaria Monticelli, 1892. Even *Hunteroides* Johri, 1959 (= *Gephyrolina* Poche, 1926), a true cestodarian, was mistakenly identified as a caryophyllidean cestode. Unlike the Cestodaria that have a 10-hooked lycophora, the caryophyllideans have a 6-hooked oncosphere, characteristic of the true cestodes or Cestoidea Rudolphi, 1808. However, the monopleuroid body plan has prompted some workers to view them as distinct from and of coequal systematic rank with the more dominant strobilate cestodes (Bazitov, 1976; Kulakovskaya & Demshin, 1978; and Ehlers, 1986). I support this view.

There are about 42 genera and 137 species in four families. They are widely distributed intestinal parasites of benthic-feeding siluriform and cypriniform freshwater fishes. Polyploidy is known for several species. One genus, *Archigetes* Leuckart, 1878, is commonly progenetic in tubificid annelids, the intermediate host for this well defined group of cestodes.

Classification at the family level has either had a single family with multiple subfamilies, or as followed here, the subfamilies have been raised to family rank. The primary family criterion is the arrangement of the longitudinal musculature (Figs 5.26–5.29) because it is a fundamental non-adaptive and conservative character, not significantly influenced by other anatomical features (Mackiewicz, 1982). There are many different scolex types (Figs 5.1–5.21).

Classification at the genus level reflects an ancient group where host and parasite isolation has played a major role in cestode evolution. As a consequence of this isolation, about 50% of genera are monotypic. Only four genera have 10 or more species and most of these, viz. *Lytocestus* Cohn, 1908, *Biacetabulum*



Figs 5.1-5.21 Scolex shapes and sample genera (original or after Mackiewicz, 1972, 1982, unless otherwise stated. 5.1. Loculomonobothriate, *Monobothrium*. 5.2. Loculopapillate, *Diefluvium* (after Williams, 1978). 5.3. Loculotruncate, *Promonobothrium* (after Mackiewicz, 1968). 5.4. Bothrioloculodiscate, *Archigetes*. 5.5. Coronulate, *Balanotaenia*. 5.6. Fixomegabothriate, *Capingens*. 5.7. Spatulate, *Lytocestus*. 5.8. Digitiform, *Crescentovitus*. 5.9. Rugomonobothriate, *Monobothrioides*. 5.10. Hastate, (adapted from Hunter, 1930), *Pseudolytocestus*. 5.11. Bulbate, bulboacuminate, *Atractolytocestus*. 5.12. Cuneiloculate, *Glaridacris*. 5.13. Biacetabulate, *Biacetabulum*. 5.14. Cuneicrispitate, flabellate, *Caryophyllaeus*. 5.15. Tholate, *Hunterella*. 5.16. Monobothriate, *Monobothrium*. 5.17. Montanate, *Khawia* (= *Bothrioscolex*). 5.18. Rugomontanate, *Wenyonia*. 5.19. Choanocampanulate, *Caryoaustralus* (after Mackiewicz & Blair, 1980). 5.20. Cuneifimbriate, *Khawia*. 5.21. Cuneiform, *Caryophyllaeides*.

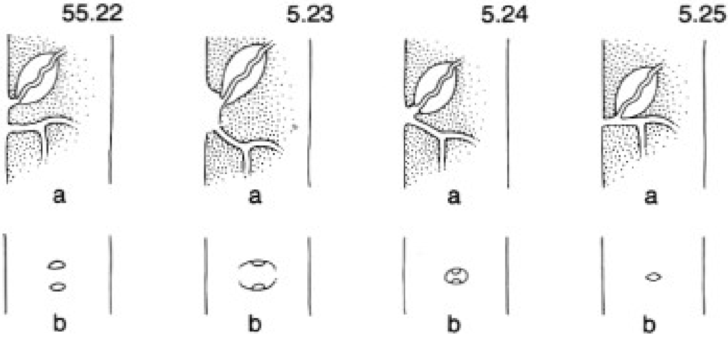
Hunter, 1927 and *Isoglaridacris* Mackiewicz, 1965 may reflect generic complexes. Our concept of the genus is far from stabilized. Perhaps introduction of the subgenus, not yet used in this group, may be helpful in partitioning some larger genera.

Many of the differences in systematic treatments of genera can be traced to various sources. Some are intrinsic to the organism and include variation associated with different states of maturity, different hosts and universal intraspecific variation. On the other hand, a factor such as small sample size may give a very limited view of a species but by far the two most important practices that have had a profound influence on and greatly hindered a genuine understanding of the systematics of caryophyllaeid cestodes have been (a) descriptions of new genera (or species) from specimens that have been dead in a host for a long period and may even be partially decomposed, and (b) the all too prevalent practice of compressing specimens between two glass slides prior to fixation. Consequently, natural characters are obliterated and, often, new fictitious ones created. While it is not always possible to collect adequate samples of specimens or even to observe them alive, new taxa should not be described from specimens that have been flattened or have come from hosts in which the gut has begun to decompose. Phantom genera born from such practices create subtle havoc and endless confusion whose legacy is a classification that is more illusion than reality.

Generic diagnoses in the present treatment contain the fewest number of pertinent characters (Mackiewicz, 1982) and thus should be considered as differential diagnoses. All species currently described in a genus may not fit within a diagnosis, hence reflecting systematic uncertainty. On the other hand, it is clear to me that some genera, as defined here, should be divided into one or more new genera. No new genera are proposed here; however, they will be erected elsewhere.

The following characters have been used in the keys to separate genera: scolex, vitelline follicle arrangement, ovarian morphology, gonopore condition and position, presence of external seminal vesicle, anterior extent of uterus and presence of postovarian vitelline follicles. The seminal receptacle is not used because its status in many genera is not known. Furthermore, it appears to be a transient structure visible only when full of sperm. The general topic of generic characters has been discussed by Mackiewicz (1969, 1982).

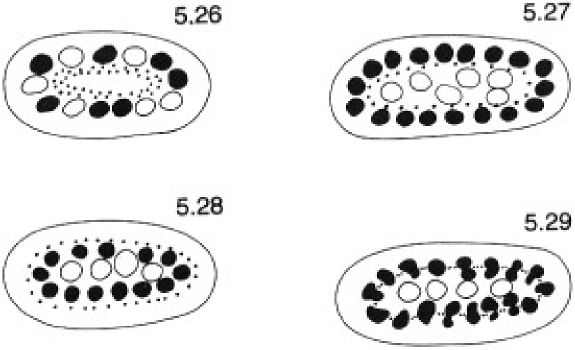
The following should be borne in mind when using these keys. Except for the massive, fixed scolex of *Capingens* (Fig. 5.6), the scolex of many other genera is highly mobile and capable of forming diverse shapes. Determination of gonopore condition can be difficult and is best done on well preserved, non-contracted specimens; unless the gonopore status is obvious, it is usually necessary to section specimens to clarify duct relationships. A single gonopore is formed when the cirrus (ejaculatory duct) joins the uterovaginal canal forming a hermaphroditic duct to the surface (Fig. 5.25) or when a deep, well defined genital atrium is formed. Gonopores are separate when (a) the cirrus and uterovaginal canal clearly open separately on the surface (Fig. 5.22), (b) when they open together into a shallow genital atrium as in some *Glaridacris* (Fig. 5.23) or when there is a distinct genital atrium (Fig. 5.24) as in *Khawia*. Although one can usually see both gonopores when a distinct genital atrium is present, the genital



Figs 5.22–5.25 Gonopore status, (a) mid-sagittal and (b) surface view. 5.22. Separate. 5.23. Separate, shallow genital atrium. 5.24. Separate, distinct genital atrium. 5.25. Single, no genital atrium.

atrium itself may appear as a single, large gonopore if the specimen is even slightly contracted. If the maximum anterior extent of the uterus in mature worms is at the level of or only anterior to the cirrus-sac by the width of the uterus, then it is not considered to **loop** anterior to the cirrus-sac (Fig. 5.49). Preovarian vitelline follicles are designated as lateral and median when they are intermingled with or surround the testes (Figs 5.38, 5.47, 5.56, 5.60). In the diagnoses, 'lateral and median' means that the vitellarium is annular or the follicles are intermingled with testes because the two states can merge with each other (Figs 5.26–5.29). If the ovary is strongly follicular, the follicles of the posterior arms can easily be mistaken for postovarian vitelline follicles (Figs 5.40, 5.41). While the posterior ovarian follicles characteristically form a lateral cluster on each side above the excretory bladder (Fig. 5.40), postovarian vitelline follicles form a single median cluster (Figs 5.52, 5.65). If the ovary is strongly follicular and the posterior follicles form a single median cluster, special care must be taken to separate ovarian from vitelline follicles to determine if the ovary is shaped like an inverted letter A. In sections, or under high magnification, ovarian follicles lack the vacuolated nuclei of mature vitelline cells. Histochemically, ovarian follicles are negative for polyphenol oxidase, vitelline follicles are positive.

Terminology continues to cause confusion in this group of cestodes. Loculus and bothrium, for example, have been used interchangeably. To avoid further confusion in this key, a loculus is regarded as any shallow cavity that can appear or disappear, depending on scolex mobility. A species may have from one to three pairs of loculi (Figs 5.3, 5.4, 5.12). When a medial cavity is deeper, well developed and assumes a permanent form it becomes a bothrium (Figs 5.4, 5.6). As in the difossate scolex of the Pseudophyllidea, the bothria of caryophyllideans always occur as a single medial pair (Fig. 5.6) with or without accessory loculi (Fig. 5.4). It may be argued, and correctly so, that when there is only one pair of medial cavities or depressions they should be regarded as bothria, regardless of their state of development. While this may be technically correct, i.e. that medial loculi are just weakly developed bothria, it becomes difficult to apply this interpretation to *Isoglaridacris* or other genera with a wedge-shaped or cuneiform



Figs 5.26–5.29 Placement of inner longitudinal muscles (vitelline follicles solid, testes open circles). 5.26. Balanotaeniidae. 5.27. Lytocestidae. 5.28. Caryophyllaeidae. 5.29. Capingentidae.

scolex bearing three pairs of shallow cavities or depressions (Fig. 5.12). All of these depressions appear similar in fixed material and thus are here regarded as loculi. To be consistent, all other shallow medial depressions on any other scolex are considered loculi.

Previously published regional keys include: USSR (Kulakovskaya, 1961), North America (Hoffman, 1967), Wisconsin, USA (Williams, 1977) and Iowa, USA (Williams, 1978). Keys to species of caryophyllidean genera include: *Khawia* by Calentine & Ulmer (1961); *Archigetes* by Kennedy (1965) and Calentine (1962); *Glaridacris* by Mackiewicz (1976); *Wenyonia* by Ukoli (1972); *Isoglaridacris* by Mackiewicz (1974); and *Monobothrium* by Calentine & Mackiewicz (1966).

Unless otherwise indicated, all figures are of the type of the genus or its character states. Partial figures of the posterior portion are of larger species (over 10 mm) and are diagrammatic, standardized, and not drawn to scale in order to emphasize generic characters. Smaller species, usually less than 10 mm, are pictured whole and with a scale. Since ovarian **shape** rather than **structure** is the primary focus, no attempt has been made to picture the compact ovarian follicles of many genera (Figs 5.51, 5.55). On the other hand, the loosely follicular ovary of other genera (Figs 5.39–5.41) is figured because it is so prominent as to be confused with vitelline follicles. Uterine glands have been omitted from all drawings in the interests of simplicity.

ORDER CARYOPHYLLIDEA VAN BENEDEN IN CARUS, 1863

Diagnosis: Elongate body without internal or external proglottization, with a single set of reproductive organs. Scolex unspecialized or with loculi, bothria, acetabula or a terminal introvert or disc; hooks absent. Genital pores ventral, median; uterovaginal pore opens posterior to or together with male gonopore. Testes preovarian. Vitelline follicles preovarian, with or without a postovarian cluster. Eggs operculate. Primarily intestinal parasites of cypriniform and siluriform freshwater fishes. Some genera with progenetic cycles and development in the coelom of intermediate host, aquatic Annelida.

Key to families

1a. Testes and vitellarium in same plane in cortical parenchyma, neither internal to inner longitudinal muscles (Fig. 5.26) .... Balanotaeniidae Mackiewicz & Blair, 1978.
Diagnosis: Scolex aloculate. Testes in medullary parenchyma. Vitellarium in cortical parenchyma, external to inner longitudinal muscles. Type-genus *Balanotaenia* Johnston, 1924.

1b. Testes, vitellarium or both internal to inner longitudinal muscles .... 2.

2a. Vitellarium completely in cortical parenchyma. Inner longitudinal muscles separate medullary testes from cortical vitellarium (Fig. 5.27) .... Lytocestidae Hunter, 1927.
Diagnosis: Scolex aloculate. Testes in medullary parenchyma. Vitellarium in cortical parenchyma, external to inner longitudinal muscles. Type-genus *Lytocestus* Cohn, 1908.

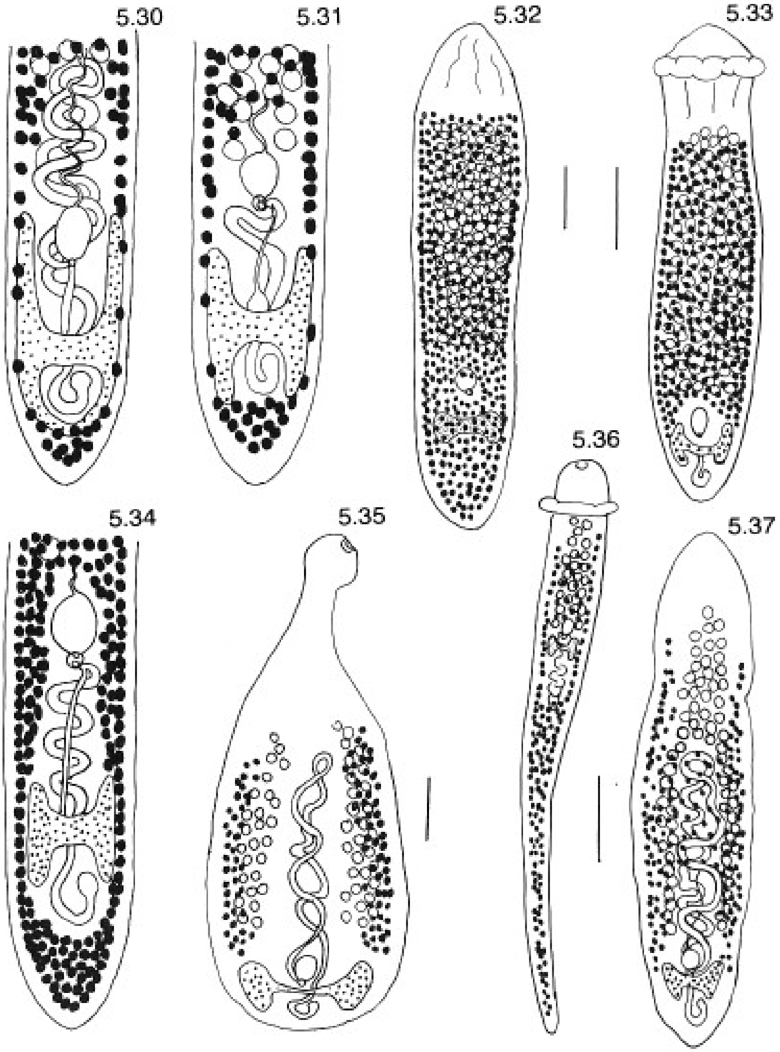
2b. Vitellarium either completely in medullary parenchyma or partially in medullary and cortical parenchyma .... 3.

3a. Vitellarium and testes in medullary parenchyma. Inner longitudinal muscles external to vitellarium (Fig. 5.28) ... Caryophyllaeidae Leuckart, 1878.
Diagnosis: Scolex variable. Testes and vitellarium in medullary parenchyma, internal to inner longitudinal muscles. Type-genus *Caryophyllaeus* Gmelin, 1790.

3b. Vitellarium partially in medullary and cortical parenchyma. Inner longitudinal muscles between adjacent vitelline follicles (Fig. 5.29) .... Capingentidae Hunter, 1930.
Diagnosis: Scolex variable. Testes and vitellarium partially in medullary and cortical parenchyma, neither completely external nor internal to inner longitudinal muscles. Type-genus *Capingens* Hunter, 1927.

Family Balanotaeniidae Mackiewicz & Blair, 1978

This small family has testes and vitellarium in the cortical parenchyma (Fig. 5.26), illustrating that testes need not be confined to the medullary parenchyma as in the other three families. Such an unusual arrangement allows for mingling of testes and vitelline follicles and theoretically would seem to preclude having vitelline follicles in two lateral rows, a common arrangement in the other families. Perhaps most interesting is that the cortical position allows for more testes per



Figs 5.30–5.32, 5.34–5.37 Lytocestidae. **5.33**. Balanotaeniidae. 5.30. *Caryophyllaeides fennica*. 5.31. *Khawia sinensis*. 5.32. *Lytocestoides tanganyikae* (adapted from Baylis, 1928). 5.33. *Balanotaenia bancrofti*. 5.34. *Atractolytocestus*. 5.35. *Djombangia* (adapted from Satpute & Agarwal, 1974). 5.36. *Caryoaustralus sprenti*. 5.37. *Notolytocestus minor* Johnston & Muirhead, 1950. Figs 5.33, 5.36, 5.37 adapted from Mackiewicz & Blair (1980). Scales = 1 mm.

worm diameter, a fact that may be related to the very small size (less than 1 mm) of *Balanotaenia newguinensis* Mackiewicz & Blair, 1978, one of the smallest tapeworms known. This family contains the single genus *Balanotaenia* Johnston, 1924 with two species, both in the Australian zoogeographical region.

Genus *Balanotaenia* Johnston, 1924 (Figs 5.5, 5.33)

Diagnosis: Scolex coronulate. Gonopores separate, in definite genital atrium. External seminal vesicle absent. Ovary H- to dumbbell-shaped. Uterus does not loop anterior to cirrus-sac. Vitelline follicles and testes in same plane, annularly distributed around medullary parenchyma. Postovarian vitelline follicles absent. In Plotosidae. Australia, New Guinea. Type-species *B. bancrofti* Johnston, 1924.

Family Lytocestidae Hunter, 1927

(Syns Lytocestinae Hunter, 1927; Bovieninae Fuhrmann, 1931; Lallidae Johri, 1959)

This family is characterized by having the inner longitudinal muscles separate the cortical vitellarium from the medullary testes (Fig. 5.27). As a result of this configuration, the testes generally appear in wholemounts as a narrow central core with lateral or annular vitelline follicles arranged close to the tegument. By being in different planes, the testes and vitellarium usually do not mix with each other and thus the vitelline follicles can surround and often obscure the testes. If the follicles appear close to the tegument in wholemounts one should suspect the Lytocestidae, a suspicion that should be checked through sections.

The family Lytocestidae now consists of 16 genera, six in the Oriental region and others scattered in all but the Neotropical. There are about 47 described species; *Lytocestus* Cohn, 1908 is by far the largest genus with approximately 13 species; *Khawia* Hsu, 1935 is next with seven. There are five monotypic genera. Except for *Stocksia* Woodland, 1937 (Fig. 5.42) described from a single specimen, descriptions of other genera are from two or more.

Unlike the Caryophyllaeidae, this family lacks a diversity of scolex types by not having any with loculi, bothria or acetabula. In addition, all genera appear to lack an external seminal vesicle; preovarian vitelline follicles in the annular or lateral and median positions predominate.

Generic synonymies are more frequent in this family than any other, largely because descriptions have been based on poorly preserved material, have been incomplete or there has been misinterpretation of anatomical structure. *Bothrioscolex* Szidat, 1937 is an exception, however. Opinion has been divided as to whether the massive, eversible terminal cavity, described only by Szidat (1937), is alone sufficient to separate this genus from *Khawia* Hsu, 1935. General opinion is that it is not (Yamaguti, 1959; Kulakovskaya, 1961; Dubinina, 1962; Schmidt, 1986). Recent observation of this terminal cavity in live *Khawia* by Calentine & Ulmer (1961) appears to be convincing evidence that the two genera are the same. *Tsengia* Li, 1964, from *Cyprinus carpio* in Mongolia, differs from *Khawia* only in having an ovary in the shape of an inverted letter A. Williams & Sutherland (1981), unaware of the description by Li (1964), referred similar specimens from the same host in North America to *Khawia*, a conclusion accepted here because the fusion of ovarian arms is a common variation in other genera.

Re-examination of the type specimens reveals that ovarian follicles of *Lucknowia* Gupta, 1961 have been mistaken for postovarian vitelline follicles (Mackiewicz, 1981b). Consequently, this genus is synonymized with *Lytocestus*, here regarded as a complex because of the diverse forms, wide distribution and broad host spectrum, the widest of any 'genus' in the order. From Fig. 1C of Satpute & Agarwal (1980), it is apparent that ovarian follicles of *Introvertus* also have been mistaken for postovarian vitelline follicles. In addition, the swollen vas deferens has been misinterpreted as the external seminal vesicle and the apical elongation of the scolex as an introvert; *Introvertus* Satpute & Agarwal, 1980 is here synonymized with *Bovienia* Fuhrmann, 1931.

Comparison of the descriptions, illustration and examples of *Atractolytocestus* Anthony, 1958 and *Markevitschia* Kulakovskaya & Akhmerov, 1965 (one specimen) from *Cyprinus carpio* reveal that, except for testes number, there are no other major differences between the two (Jones & Mackiewicz, 1969). *Markevitschia* is, therefore, synonymized with *Atractolytocestus* (Fig. 5.34) even though the latter is a triploid.

The genera *Neolytocestus* and *Moravekia* reported briefly (1976a,b) by S.N. Sahay & U. Sahay in abstracts of the First National Convention of Indian Helminthologists, Bhubaneswar, India are lacking in sufficient detail to allow for critical comparison with other genera and thus are considered *genera inquirenda*.

Key to genera

1a. Uterus loops anterior to cirrus-sac .... 2.
1b. Uterus does not loop anterior to cirrus-sac .... 4.

2a. Postovarian vitelline follicles present. Ovary in shape of inverted letter A .... *Caryophyllaeides* Nybelin, 1922. (Figs 5.21, 5.30)

Diagnosis: Scolex cuneiform. Gonopore single. External seminal vesicle absent. Uterus loops anterior to cirrus-sac. Vitelline follicles lateral and median. In Cyprinidae. Scandinavia, Germany, Russia. Type-species *C. fennica* (Schneider, 1902) Nybelin, 1922.

2b. Postovarian vitelline follicles absent. Ovary H-shaped .... 3.

3a. Scolex tholate. Some testes and vitelline follicles anterior to uterus .... *Notolytocestus* Johnston & Muirhead, 1950. (Fig. 5.37)

Diagnosis: Gonopore single. External seminal vesicle absent. Ovary H-shaped. Uterus primarily anterior to cirrus-sac. Testes anterior and lateral to uterus. Vitelline follicles surround uterus and posterior testes. Postovarian vitelline follicles absent. In Plotosidae. Australia. Type-species *N. major* Johnston & Muirhead, 1950.

3b. Scolex bulbate with apical glandular structure. Testes and vitelline follicles lateral to uterus .... *Djombangia* Bovien, 1926. (Fig. 5.35)

Diagnosis: Gonopore single, genital atrium present. Cirrus-sac weakly developed. External seminal vesicle absent. Ovary bilobed. Uterus loops far anterior to cirrus-sac. Postovarian vitelline follicles absent. In Clariidae, Heteropneustidae. India, Java. Type-species *D. penetrans* Bovien, 1926.

4a. Postovarian vitelline follicles present .... 5.
4b. Postovarian vitelline follicles absent .... 8.

5a. Gonopore single in anterior half of body .... *Caryoaustralus* Mackiewicz & Blair, 1980. (Figs 5.19, 5.36)

Diagnosis: Scolex choanocampanulate. External seminal vesicle absent. Ovary H-shaped. Uterus does not loop anterior to cirrus-sac, primarily postovarian. Vitelline follicles lateral and median, confluent with extensive postovarian follicles. In Plotosidae. Australia. Type-species *C. sprenti* Mackiewicz & Blair, 1980.

5b. Gonopore(s) single or double, in posterior quarter of body .... 6.

6a. Scolex tholate. Neck absent. Single gonopore with deep genital atrium .... *Lytocestoides* Baylis, 1928. (Fig. 5.32)

Diagnosis: (External seminal vesicle status unknown.) Ovary bilobed. Uterus does not loop anterior to cirrus-sac. Pre- and postovarian vitelline follicles form extensive layer covering all organs except for cirrus-sac. In Characidae. Africa. Type-species *L. tanganyikae* Baylis, 1928.

6b. Scolex not tholate. Neck present. Two gonopores in deep atrium ... 7.

7a. Scolex cuneifimbriate or montanate, may form terminal eversible cavity. Neck short .... *Khawia* Hsu, 1935. (Figs 5.17, 5.20, 5.31)

(Syns *Bothrioscolex* Szidat, 1937; *Tsengia* Li, 1964.)

Diagnosis: Gonopores separate but close together in distinct genital atrium. External seminal vesicle absent. Ovary H-shaped, less often like an inverted letter A. Vitelline follicles lateral and median, postovarian follicles present. In Cyprinidae. North America, Europe, Russia, China. Type-species *K. sinensis* Hsu, 1935.

7b. Scolex bulbate to bulboacuminate. Distinct neck present .... *Atractolytocestus* Anthony, 1958. (Figs 5.11, 5.34)

(Syn. *Markevitschia* Kulakovskaya & Akhmerov, 1965.)

Diagnosis: Gonopores separate in genital atrium. External seminal vesicle absent. Ovary H-shaped or bilobed. Uterus does not loop anterior to cirrus-sac. Vitelline follicles lateral and medial, confluent with postovarian follicles. In Cyprinidae. North America, Russia. Type-species *A. huronensis* Anthony, 1958.

8a. With one gonopore .... 9.
8b. With two gonopores, may be in genital atrium .... 10.

9a. Scolex tholate. Vitellarium annular .... *Tholophyllaeus* Mackiewicz & Blair, 1980. (Fig. 5.38)

Diagnosis: Gonopore single. External seminal vesicle absent. Ovary H-shaped. Uterus does not loop anterior to cirrus-sac. Vitelline follicles lateral and median, postovarian follicles absent. In Plotosidae. Australia. Type-species *T. johnstoni* Mackiewicz & Blair, 1980.

9b. Scolex not tholate. Vitelline follicles predominantly in lateral rows .... *Stocksia* Woodland, 1937. (Fig. 5.42)

Diagnosis: (Scolex shape undetermined; slightly expanded, possibly with grooves.) Gonopore single. Ovary H-shaped. Uterus does not loop anterior to cirrus-sac. Vitelline follicles crescentic to testes in cross section. Postovarian follicles absent. In Clariidae. Africa. Type-species *S. pujehuni* Woodland, 1937.

10a. Vitelline follicles in narrow lateral rows, no median follicles. Ovary generally H-shaped, rarely like inverted letter A .... *Bovienia* Fuhrmann, 1931. (Fig. 5.40)

(Syn. *Introvertus* Satpute & Agarwal, 1980.)

Diagnosis: Scolex digitiform to pyriform, may have protrusible apex. Gonopores separate. External seminal vesicle absent. Uterus does not loop anterior to cirrus-sac. Postovarian vitelline follicles absent. In Clariidae. Java, India. Type-species *B. serialis* (Bovien, 1926) Fuhrmann, 1931.

10b. Vitellarium annular or lateral and median .... 11.

11a. Scolex rugomonobothriate .... *Monobothrioides* Fuhrmann & Baer, 1925. (Fig. 5.9)

Diagnosis: Gonopores separate. External seminal vesicle absent. Ovary H-shaped. Uterus does not loop anterior to cirrus-sac. Vitelline follicles lateral and median, postovarian follicles absent. In Bagridae and Clariidae. Africa. Type-species *M. cunningtoni* Fuhrmann & Baer, 1925.

11b. Scolex digitiform unspecialized or spatulate .... 12.

12a. Ovary H-shaped, loosely follicular. Gonopores separate, far apart, genital atrium inconspicuous .... (Complex) *Lytocestus* Cohn, 1908. (Figs 5.7, 5.39)

(Syn. *Lucknowia* Gupta, 1961.)

Diagnosis: Scolex variable, from unspecialized to spatulate, pyriform; neck present. External seminal vesicle absent. Uterus does not loop anterior to cirrus-sac. Vitelline follicles lateral and median, postovarian follicles absent. In Mormyridae, Heteropneustidae, Clariidae, Characidae. Africa, India, Singapore, Hong Kong. Type-species *L. adhaerens* Cohn, 1908.

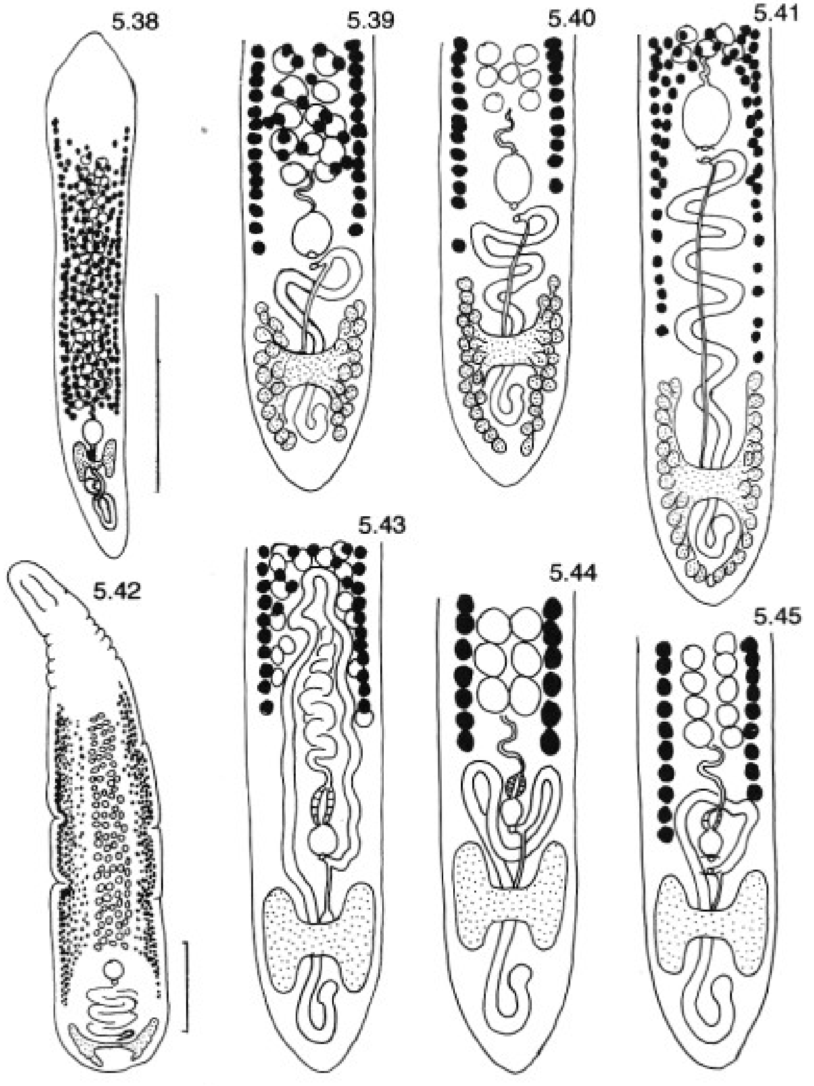
12b. Ovary loosely follicular shaped like inverted letter A, rarely H-shaped. Gonopores separate but in conspicuous genital atrium .... *Crescentovitus* Murhar, 1963. (Figs 5.8, 5.41)

Diagnosis: Scolex digitiform. Neck absent. Gonopores separate, close together in genital atrium. External seminal vesicle absent. Uterus does not loop anterior to cirrus-sac. Vitelline follicles lateral and median, postovarian follicles absent. In Heteropneustidae. India. Type-species *C. biloculus* Murhar, 1964.

Family Caryophyllaeidae Leuckart, 1878

(Syns Caryophyllaeinae Nybelin, 1922; Wenyoninae Hunter, 1927)

The distribution of both vitellarium and testes internal to the inner longitudinal muscles characterizes this family (Fig. 5.28). Two consequences follow from this



Figs 5.38–5.42 Lytocestidae. **5.43–5.45**. Caryophyllaeidae. 5.38. *Tholophyllaeus johnstoni* (adapted from Mackiewicz & Blair, 1980). 5.39. *Lytocestus birmanicus* Lynsdale, 1956. 5.40. *Bovienia serialis*. 5.41. *Crescentovitus biloculus*. 5.42. *Stocksia pujehuni* (adapted from Woodland, 1937). 5.43. *Diefluvium unipapillatum*. 5.44. *Rowardleus pennensis*. 5.45. *Hypocaryophyllaeus paratarius*. Scales = 1 mm.

organization that may aid in family allocation from wholemounts. One is that the testes and vitelline follicles can mingle, often imparting a mosaic effect; or, if the follicles are very numerous, they may surround and obscure the testes. A second is that the thickness of the cortical parenchyma is generally greater than in the Lytocestidae. As noted in the key, this family has an astonishing array of diverse scolex types, greater than in any other family.

The family Caryophyllaeidae consists of 20 genera with 17 in the Nearctic; nine are monotypic. *Isoglaridacris* Mackiewicz, 1968 is the largest genus with 12 species, *Biacetabulum* Hunter, 1927 is next with 10. Except for *Paracaryophyllaeus* Kulakovskaya, 1961, data on the disposition of the longitudinal muscles are known for all other genera. This genus is placed here on the basis of the provisional allocation of Kulakovskaya (1961). *Bialovarium* Fischthal, 1951 was described from a single individual, all other generic descriptions involved multiple specimens. The family includes about 73 described species, predominantly from catostomid fish with a few from cyprinid, cobitid and silurid freshwater fishes.

Generic synonymies are most evident with *Archigetes* Leuckart, 1878 which occurs progenetically in tubificid annelids and as an adult in fish. These synonymies reflect over 100 years of controversy revolving around whether *Archigetes* represents a valid genus with a number of species (Kennedy, 1965) or is the progenetic stage of other genera such as *Glaridacris* Cooper, 1920, *Biacetabulum* Hunter, 1927 and *Brachyurus* Szidat, 1938 (see Janiszweska, 1954; Kulakovskaya, 1962). The origin of this controversy is both the progenesis phenomenon involving tubificid annelids and the intraspecific variation or changing states with maturation that have led to a single species being placed into two separate genera. Unlike Kennedy (1965), I see no logical, biologically based reason to regard progenesis as a character restricted to only one genus, i.e., *Archigetes*; it is a universal, physiological and developmental phenomenon that can occur in various genera, as it does in the Trematoda. In support of this view is the unusually wide array of characters ascribed to *Archigetes* by Kennedy (1965). Based on a review of the literature and study of examples of most species involved in this controversy, I tend to concur with Janiszweska (1954) and Kulakovskaya (1962) in principle, i.e. that some *Archigetes* species are larval forms of other genera. On the other hand, I also concur with Calentine (1962) that *Archigetes* is a valid genus name. I, therefore, recognize *Archigetes* and *Brachyurus* as separate genera, a conclusion reinforced by my discovery (Mackiewicz, 1965) that the type specimen of *Paraglaridacris* has postovarian vitelline follicles and that the vitelline follicles of *A. iowensis* Calentine, 1962 (identified by the describer) are lateral and median, contrary to the original description. *Szidatinus* was proposed by McCrae (1961), in an abstract, for *Brachyurus* Szidat, 1938, that was preoccupied. Resolution of the *Archigetes* question, one of the most perplexing in all of cestodology, requires additional comparative studies and more extensive discussion of various genera and species, not appropriate in this publication. Because the name *Brachyurus* is preoccupied by *Brachyurus* Fischer-Waldheim, 1913 (rodent), *Paraglaridacris* Janiszewska, 1950 is here used in the key as the next available name.

Because of the great diversity of characters, several genera occur more than once in the key; these include: *Glaridacris* Cooper, 1920, *Biacetabulum* Hunter, 1927, *Monobothrium* Diesing, 1863 and *Isoglaridacris* Mackiewicz, 1965. Whether this phenomenon reflects hidden complexes of multiple genera or possibly subgenera remains to be determined after a thorough analysis of all genera in the family. They are each designated as a complex to reflect this systematic uncertainty.

General diagnoses are faithful to previous ones except that of *Hypocaryophyllaeus* Hunter, 1927, emended from 'postovarian vitellaria present' to 'postovarian vitellaria absent', based on the observations of Mackiewicz & Deutsch (1976) and Williams (1978).

Biacetabuloides Mackiewicz, 1960 and *Hunterium* Mackiewicz, 1960 are regarded as *nomina nuda* because they were initially proposed in a thesis, never formally proposed in publication, and thus do not satisfy Article 9 of the *International Code of Zoological Nomenclature* (XX General Assembly of the International Union of Biological Sciences).

Except for *Wenyonia* Woodland, 1923 all other genera appear to represent a distinct group united by the disposition of longitudinal musculature and over-all morphology. *Wenyonia* is the only one with gonopores clearly in the anterior half of the body (Fig. 5.61), a character that led Hunter (1927, 1930) to erect a separate subfamily, Wenyoninae. Although this character is consistent among the eight species (Ukoli, 1972), gonopore placement is not used to characterize the other families. Furthermore, its position depends to some degree on variation in length of the postovarian region as shown by *Pliovitellaria* Fischthal, 1951 (Fig. 5.60) and *Caryoaustralus* Mackiewicz & Blair, 1980 (Fig. 5.36) in the Lytocestidae. Family criteria must be more fundamental than one that is so closely linked with another morphological feature. More important, testes and vitellarium are in the medullary parenchyma, a diagnostic feature of the Caryophyllaeidae. The systematic value of the diffuse longitudinal musculature in the cortical parenchyma of *Wenyonia* remains to be seen.

Key to genera

1a. Uterus obviously loops anterior to cirrus-sac by more than width of uterus .... 2.
1b. Uterus does not loop anterior to cirrus-sac .... 7.

2a. Preovarian vitelline follicles in distinct lateral rows .... 3.
2b. Preovarian vitelline follicles annular or lateral and median .... 4.

3a. With two gonopores. Scolex cuneiloculate (Fig. 5.12) .... *Hypocaryophyllaeus* Hunter, 1927. (Fig. 5.45)
Diagnosis: Genital atrium present. External seminal vesicle present. Ovary H-shaped. Uterus loops anterior to cirrus-sac. Vitelline follicles in lateral rows, postovarian follicles absent. In Catostomidae. North America. Type-species *H. paratarius* Hunter, 1927.

3b. With one gonopore. Scolex cuneiloculate (Fig. 5.12) .... *Rowardleus* Mackiewicz & Deutsch, 1976. (Fig. 5.44)
Diagnosis: External seminal vesicle present. Ovary H-shaped. Uterus loops anterior to cirrus-sac. Vitelline follicles in lateral rows, postovarian follicles absent. In Catostomidae. North America. Type-species *R. pennensis* Mackiewicz & Deutsch, 1976.

4a. Postovarian vitelline follicles absent. Scolex loculopapillate .... *Diefluvium* Williams, 1978. (Figs 5.2, 5.43)

Diagnosis: Gonopore single. External seminal vesicle present. Ovary H-shaped. Uterus loops anterior to cirrus-sac. Vitelline follicles lateral and median. In Catostomidae. North America. Type-species *D. unipapillatum* Williams, 1978.

4b. Postovarian vitelline follicles present. Scolex not loculopapillate ..... 5.

5a. Scolex unspecialized, expanded and flattened. Ovary H-shaped .... *Paracaryophyllaeus* Kulakovskaya, 1961. (Fig. 5.46)

Diagnosis: Gonopore apparently single. External seminal vesicle absent. Seminal receptacle large. Uterus loops anterior to cirrus-sac. Vitelline follicles lateral and median, postovarian follicles present. In Cobitidae. Russia, Japan. Type-species *P. gotoi* (Motomura, 1927) Dubinina, 1971.

5b. Scolex specialized: biacetabulate, bulboloculate or bothrioloculodiscate .... 6.

6a. Scolex bothrioloculodiscate. Defined neck absent. Ovary in shape of dumb-bell or band. Small forms, generally less than 3 mm .... (Complex) *Archigetes* Leuckart, 1878. (Fig. 5.47)

Diagnosis: ADULT. Small size, generally less than 3 mm. Cercomer absent. Gonopore single, functional. External seminal vesicle present. Uterus loops slightly anterior to cirrus-sac, more so in gravid individuals. Vitelline follicles lateral and median, postovarian follicles present, may be continuous with preovarian follicles. In intestine of Cyprinidae and Cobitidae. North America, Britain, Europe, Russia. Type-species *A. sieboldi* Leuckart, 1878. PROGENETIC STAGE. Cercomer present. Gonopore nonfunctional, covered by tegument. Eggs deposited in cuticular pouch. Other characters like those of adult. In coelom of tubificid annelids. North and South America, Europe, Russia.

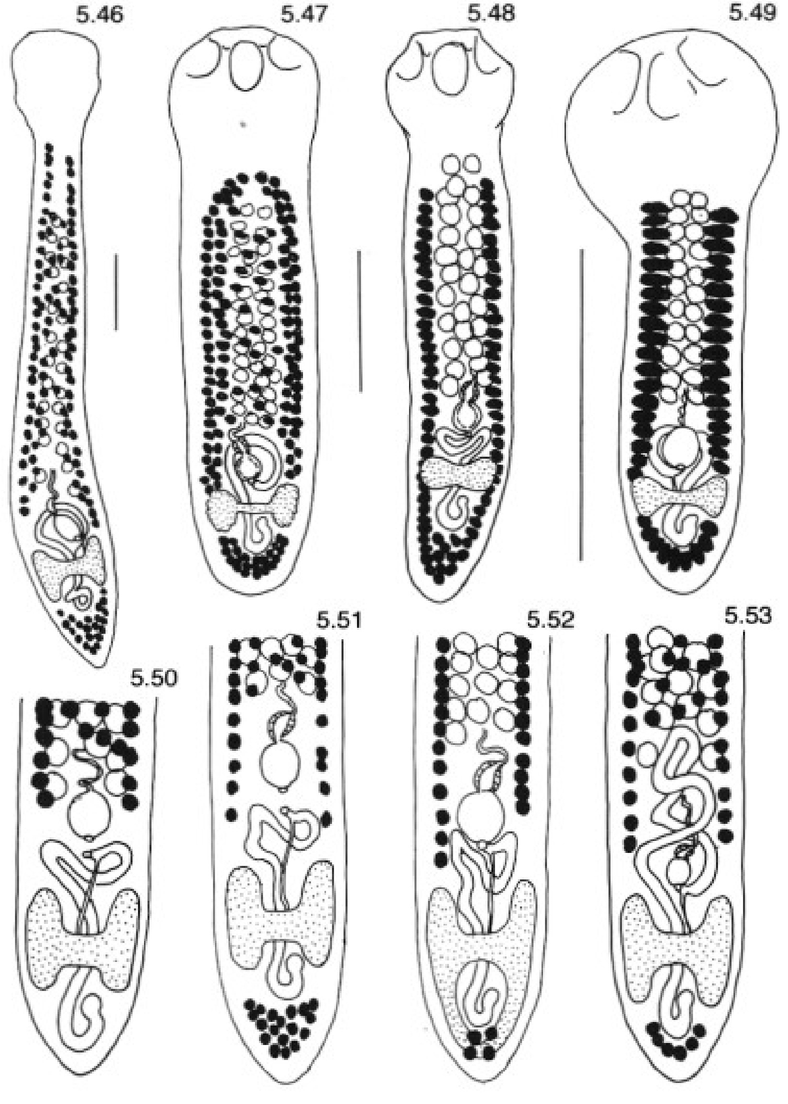
6b. Scolex biacetabulate, bulboloculate or bothrioloculodiscate (Fig. 5.4). Well defined neck present. Ovary generally H-shaped. Larger forms, 4 to 16 mm .... (Complex) *Biacetabulum* Hunter, 1927. (Figs 5.13, 5.53)

Diagnosis: Gonopore single. External seminal vesicle present. Uterus loops well anterior to cirrus-sac. Vitelline follicles lateral and median, postovarian follicles present. In Catostomidae. North America. Type-species *B. infrequens* Hunter, 1927.

7a. Scolex biacetabulate (Fig. 5.13). Postovarian vitelline follicles present or absent .... *Rogersus* Williams, 1980. (Fig. 5.50)

Diagnosis: Gonopores separate. External seminal vesicle absent. Ovary H-shaped. Uterus does not loop anterior to cirrus-sac. Vitelline follicles lateral and median. In Catostomidae. North America. Type-species *R. rogersi* Williams, 1980.

7b. Scolex not biacetabulate. Postovarian vitelline follicles present or absent .... 8.



Figs 5.46–5.53 Caryophyllaeidae. 5.46. *Paracaryophyllaeus gotoi* (adapted from Motomura, 1927). 5.47. *Archigetes sieboldi* (adapted from Calentine & DeLong, 1966; original figure with cercomer on specimen from *Limnodrilus*). 5.48. *Paraglaridacris limnodrili* (original). 5.49. *Penarchigetes oklensis* (adapted from Mackiewicz, 1969). 5.50. *Rogersus rogersi*. 5.51. *Glaridacris catostomi*. 5.52. *Isoglaridacris bulbocirrus*. 5.53. *Biacetabulum infrequens*. Scales = 0.5 mm.

8a. Preovarian vitelline follicles distinctly in lateral rows .... 9.
8b. Preovarian vitelline follicles annular or lateral and median .... 15.

9a. With two gonopores .... 10.
9b. With one gonopore .... 11.

10a. Gonopores separate, in anterior half of body .... *Wenyonia* Woodland, 1923. (Figs 5.18, 5.61)

Diagnosis: Scolex rugomontanate. External seminal vesicle absent. Ovary H-shaped. Uterus does not loop anterior to cirrus-sac. Vitelline follicles in lateral rows. Postovarian vitelline follicles present. In Bagridae, Mochokidae. Africa. Type-species *W. virilis* Woodland, 1923.

10b. Gonopores separate, in posterior quarter of body .... (Complex) *Glaridacris* Cooper, 1920. (Fig. 5.51)

Diagnosis: Scolex cuneiloculate (Fig. 5.12) or bothrioloculodiscate (Fig. 5.4). Genital atrium may be present. External seminal vesicle present. Ovary H-shaped. Uterus does not loop anterior to cirrus-sac. Vitelline follicles in lateral rows or lateral and median, postovarian vitelline follicles present. In Catostomidae. North America. Type-species *G. catostomi* Cooper, 1920.

11a. Ovary V-shaped. Scolex loculotholate ... *Bialovarium* Fischthal, 1953. (Fig. 5.63)

Diagnosis: Gonopore single. External seminal vesicle present. Uterus does not loop anterior to cirrus-sac, all pre-ovarian. Vitelline follicles in lateral rows. Postovarian region and vitelline follicles absent. In Cyprinidae. North America. Type-species *B. nocomis* Fischthal, 1953.

11b. Ovary H- or dumbbell-shaped or like inverted letter A. Scolex not tholate .... 12.

12a. External seminal vesicle present .... 13.

12b. External seminal vesicle absent .... *Penarchigetes* Mackiewicz, 1969. (Fig. 5.49)

Diagnosis: Scolex bothrioloculodiscate, expanded or not. Gonopore single. Ovary dumbbell-shaped. Uterus does not loop anterior to cirrus-sac. Vitelline follicles in lateral rows, sometimes continuous with postovarian follicles. In Catostomidae. North America. Type-species *P. oklensis* Mackiewicz, 1969.

13a. Scolex cuneiloculate (Fig. 5.12). Ovary in shape of inverted letter A or nearly so .... (Complex) *Isoglaridacris* Mackiewicz, 1965. (Fig. 5.52)

Diagnosis: Gonopore single. External seminal vesicle present. Uterus does not loop anterior to cirrus-sac. Vitelline follicles in lateral rows, sometimes with a third median row or a few median follicles. Postovarian follicles present or absent. In Catostomidae. North America. Type-species *I. bulbocirrus* Mackiewicz, 1965.

13b. Scolex bothrioloculodiscate. Ovary H-shaped or dumbbell-like .... 14.

14a. Pre- and postovarian vitelline fields continuous. Ovary in shape of dumbbell or band. Defined neck absent. Small forms, generally less than 3 mm .... *Paraglaridacris* Janiszewska, 1950. (Fig. 5.48)
(Syns *Brachyurus* Szidat, 1938 *nec* Fischer-Waldheim, 1913; *Szidatinus* McCrae, 1961).

Diagnosis: Gonopore apparently single. External seminal vesicle present. Uterus does not loop anterior to cirrus-sac. Vitelline follicles in lateral rows, continuous with postovarian follicles. Progenetic in tubificid annelids. In Cyprinidae, Cobitidae. Europe, Britain, Russia, Japan. Type-species *P. gobii* (Szidat, 1938), syn. of *P. limnodrili* n. comb. for *Glaridacris limnodrili* Yamaguti, 1934.

14b. Pre- and postovarian vitelline fields not continuous. Ovary H-shaped. Defined neck present. Larger forms, more than 4 mm .... *Janiszewskella* Mackiewicz & Deutsch, 1976. (Fig. 5.58)

Diagnosis: Gonopore single. External seminal vesicle present. Uterus does not loop anterior to cirrus-sac. Vitelline follicles in lateral rows, postovarian follicles present. In Catostomidae. North America. Type-species *J. fortobothria* Mackiewicz & Deutsch, 1976.

15a. With two gonopores .... 16.
15b. With one gonopore .... 21.

16a. Scolex loculate or monobothriate .... 17.
16b. Scolex aloculate .... 20.

17a. Postovarian vitelline follicles present .... 18.
17b. Postovarian vitelline follicles absent .... 19.

18a. Scolex bothrioloculodiscate (Fig. 5.4) or cuneiloculate. External seminal vesicle present (Figs 5.12, 5.51) .... (Complex) *Glaridacris* Cooper, 1920.
[See also 10b above]

18b. Scolex monobothriate. External seminal vesicle absent (Figs 5.16, 5.54) .... (Palaearctic) *Monobothrium* Diesing, 1863.

Diagnosis: Gonopores separate. External seminal vesicle present or absent. Ovary H-shaped. Uterus does not loop anterior to cirrus-sac. Vitelline follicles lateral and median, postovarian follicles present or absent. In Cyprinidae, Catostomidae. Europe, North America. Type-species *M. wageneri* Nybelin, 1922.

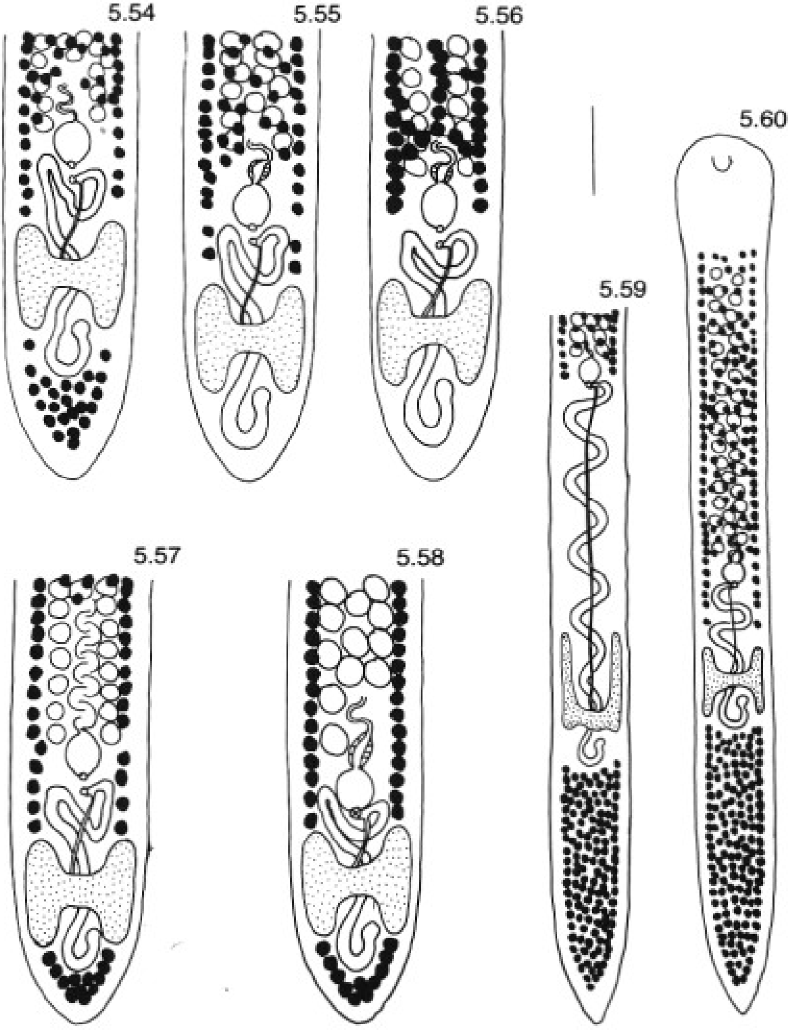
19a. Scolex monobothriate or loculomonobothriate. External seminal vesicle present .... (Nearctic) *Monobothrium* Diesing, 1863. (Figs 5.1, 5.16, 5.55)
[See also 18b above.]

19b. Scolex loculotruncate lacking terminal introvert. External seminal vesicle present .... *Promonobothrium* Mackiewicz, 1968. (Figs 5.3, 5.56)

Diagnosis: Gonopores separate. Ovary H-shaped. Uterus does not loop anterior to cirrus-sac. Vitelline follicles lateral and median, postovarian follicles absent. In Catostomidae. North America. Type-species *P. minytremi* Mackiewicz, 1968.

20a. Scolex flabellate or cuneicrispitate. External seminal vesicle absent .... *Caryophyllaeus* Gmelin, 1790. (Figs 5.14, 5.57)

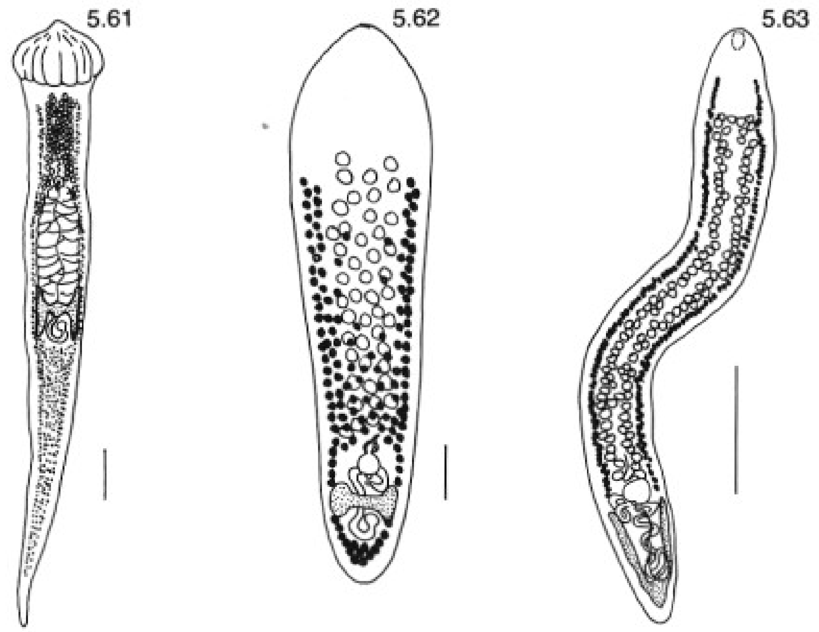
Diagnosis: Gonopores separate, atrium present. Ovary H-shaped. Uterus does not loop anterior to cirrus-sac. Vitelline follicles lateral and median, postovarian follicles present. In Cyprinidae. Europe, Russia, (?Africa, Asia). Type-species *C. laticeps* (Pallas, 1781).



Figs 5.54-5.60 Caryophyllaeidae. 5.54. *Monobothrium wageneri* (Palaearctic). 5.55. *Monobothrium hunteri*. 5.56. *Promonobothrium minytremi*. 5.57. *Caryophyllaeus laticeps*. 5.58. *Janiszewskella fortobothria*. 5.59. *Calentinella etnieri*. 5.60. *Pliovitellaria wisconsinensis*. Scales = 1 mm.

20b. Scolex tholate. External seminal vesicle present .... ***Hunterella*** **Mackiewicz & McCrae, 1962. (Figs 5.15, 5.62)**

Diagnosis: Scolex tholate. Gonopores separate. External seminal vesicle present. Ovary bilobed or dumbbell-shaped. Uterus does not loop anterior to cirrus-sac. Vitelline follicles lateral and median, postovarian follicles present. In Catostomidae. North America. Type-species *H. nodulosa* Mackiewicz & McCrae, 1962.



Figs 5.61-5.63 Caryophyllaeidae. 5.61. *Wenyonia virilis* (adapted from Mackiewicz, 1972). 5.62. *Hunterella nodulosa* (adapted from Mackiewicz & McCrae, 1962). 5.63. *Bialovarium nocomis* (adapted from Fischthal, 1954). Scales = 1 mm.

21a. External seminal vesicle present .... 22.
21b. External seminal vesicle absent ....
.... *Calentinella* Mackiewicz, 1974. (Fig. 5.59)

Diagnosis: Scolex cuneiform (Fig. 5.21). Gonopore single. Ovary U-shaped. Uterus does not loop anterior to cirrus-sac. Vitelline follicles lateral and median, postovarian follicles present. In Catostomidae. North America. Type-species *C. etnieri* Mackiewicz, 1974.

22a. Gonopore in anterior half or two-thirds of body. Scolex loculotholate
.. *Pliovitellaria* Fischthal, 1950. (Fig. 5.60)

Diagnosis: Gonopore single. External seminal vesicle present. Ovary H-shaped. Uterus does not loop anterior to cirrus-sac. Vitelline follicles lateral and median, postovarian follicles extensive, more than one half preovarian vitelline zone. In Cyprinidae. North America. Type-species *P. wisconsinensis* Fischthal, 1951.

22b. Gonopore in posterior one-sixth of body. Scolex cuneiloculate ....
.... (Complex) *Isoglaridacris* Mackiewicz, 1965.
[See also 13a above.]

Family Capingentidae Hunter, 1930

(Syns Pseudolytocestinae Hunter, 1929; Capingentinae Hunter, 1930)

Because of the intermediate position of the inner longitudinal muscles that characterizes this family (Fig. 5.29) allocation to the Capingentidae can be a matter of judgement, more so than for any other family. Much depends on the extent of muscle development and on preovarian vitelline follicle size and shape. There is generally no problem when muscle fasciculi are numerous and arranged in a definite layer and where the vitelline follicles are large, lobed or irregular in shape so that most of them can be partially in both the cortical and medullary parenchyma. It is another matter, however, when muscles are small and irregularly spaced and vitelline follicles are small, round or large and not lobed. Unless the majority of vitelline follicles are lobed and protrude on either side of the muscle layer then allocation to the Capingentidae should be carefully reappraised.

Despite the fact that this is a small family of about 15 described species, it is the least well understood. Poor material, inadequate descriptions and misinterpretations of structures force one to recognize only six of the nine described genera with the remaining three relegated as *genera incertae sedis* or placed in synonymy. Of the six, five are monotypic and three are in the Nearctic. All original descriptions are based on multiple specimens and all except *Pseudocapingentoides* Verma, 1971 have data on the placement of longitudinal muscles.

Status of genera from India is uncertain (Mackiewicz, 1981b). Restudy of the type series of *Pseudocaryophyllaeus indica* Gupta, 1961 and *Capingentoides batrachii* Gupta, 1961 indicates that the musculature of both species appears to be that of the family Caryophyllaeidae and that the species may be conspecific. Furthermore, the *C. batrachii* series may consist of a mixed infection, a conclusion strengthened by the illustrations of Gupta (1961) that show annular vitelline follicles in cross sections but only lateral ones in whole mounts. Unfortunately, subsequent descriptions of *Pseudocaryophyllaeus mackiewiczi* Gupta & Parmar, 1982, *P. ritai* Gupta & Singh, 1983, *Capingentoides heteropneusti* Gupta & Sinha, 1969, *C. singhi* Verma, 1971, *C. moghei* Pandey, 1973 and *C. fotedari* Gupta & Parmar, 1985 do not include cross sections as well as consistently confusing the ovarian follicles as postovarian vitelline follicles. Until these two 'genera' can be critically restudied, *Capingentoides* is here considered a synonym of *Pseudocaryophyllaeus*. The latter is included in the key for this family pending clarification of the placement of the longitudinal musculature.

The descriptions and illustrations of *Pseudocapingentoides* Verma, 1971 lack sufficient detail to allow for family or generic allocation (Mackiewicz, 1981b). Schmidt (1986) placed this genus into synonymy with *Capingentoides* Gupta, 1961.

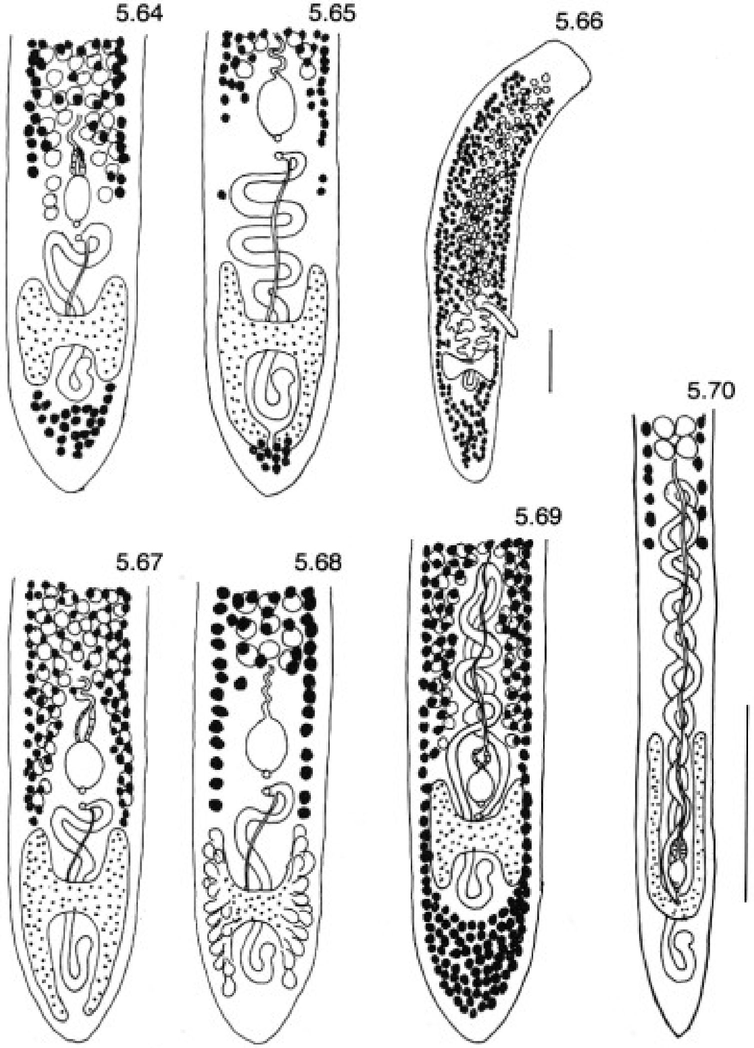
Key to genera

1a. Uterus loops anterior to cirrus-sac .... 2.
1b. Uterus does not loop anterior to cirrus-sac .... 3.

2a. Preovarian vitelline follicles in distinct lateral rows. Scolex cuneiloculate (Fig. 5.12) .... *Spartoides* Hunter, 1929. (Fig. 5.70)

Diagnosis: Gonopores separate. External seminal vesicle present. Ovary U-shaped. Postovarian vitelline follicles absent. In Catostomidae. North America. Type-species *S. wardi* Hunter, 1929.

2b. Preovarian vitelline follicles lateral and median or annular. Scolex massive, with pair of well developed bothria .... *Capingens* Hunter, 1927. (Figs 5.6, 5.69)



Figs 5.64–5.70 Capingentidae. 5.64. *Edlintonia ptychocheila.* 5.65. *Adenoscolex oreini.* 5.66. *Breviscolex orientalis* (adapted from Kulakovskaya, 1962). 5.67. *Pseudolytocestus differtus.* 5.68. *Pseudocaryophyllaeus indica* (adapted from Gupta, 1961). 5.69. *Capingens singularis.* 5.70. *Spartoides wardi.* Scales = 1 mm.

Diagnosis: Gonopores separate. External seminal vesicle present. Ovary H-shaped. Uterus loops anterior to cirrus-sac. Postovarian follicles present. In Catostomidae. North America. Type-species *C. singularis* Hunter, 1927.

3a. Postovarian vitelline follicles present .... **4.**
3b. Postovarian vitelline follicles absent .... **6.**

4a. Ovary in shape of inverted letter A .... ***Adenoscolex* Fotedar, 1958. (Fig. 5.65)**

Diagnosis: Scolex cuneiform (Fig. 5.21). Gonopores separate. External seminal vesicle absent. Uterus does not loop anterior to cirrus-sac. Vitelline follicles lateral and median, postovarian follicles present. In Cyprinidae. Kashmir. Type-species *A. oreini* Fotedar, 1958.

4b. Ovary not in shape of inverted letter A .... **5.**

5a. External seminal vesicle present. Pre-and postovarian vitelline fields not continuous .... ***Edlintonia* Mackiewicz, 1970. (Fig. 5.64)**

Diagnosis: Scolex cuneiform (Fig. 5.21). Gonopores separate. Ovary H-shaped. Uterus does not loop anterior to cirrus-sac. Vitelline fields lateral and median, postovarian follicles present. In Cyprinidae. North America. Type-species *E. ptychocheila* Mackiewicz, 1970.

5b. External seminal vesicle absent. Pre-and postovarian vitelline fields continuous .... ***Breviscolex* Kulakovskaya, 1962. (Fig. 5.66)**

Diagnosis: Scolex short, truncate, no neck. (Gonopore status unknown.) External seminal vesicle present. Ovary bilobed. Uterus does not loop anterior to cirrus-sac. Vitelline fields lateral and median, postovarian follicles present. In Cyprinidae. Russia. Type-species *B. orientalis* Kulakovskaya, 1962.

6a. External seminal vesicle present .... ***Pseudolytocestus* Hunter, 1929. (Figs 5.10, 5.67)**

Diagnosis: Scolex weakly hastate, aloculate. Gonopores separate. Ovary H-shaped. Uterus does not loop anterior to cirrus-sac. Vitelline follicles lateral and median, postovarian follicles absent. In Catostomidae, Clariidae. North America; India? Type-species *P. differtus* Hunter, 1929.

6b. External seminal vesicle absent .... ***Pseudocaryophyllaeus* Gupta, 1961. (Fig. 5.68)**

(Syns *Capingentoides* Gupta, 1961; *Pseudocapingentoides* Verma, 1971.)

Diagnosis: Scolex bulbate, apex truncate. Gonopores separate. External seminal vesicle absent. Uterus does not loop anterior to cirrus-sac. Vitelline fields lateral and median, postovarian follicles absent. In Clariidae. India. Type-species *P. indica* Gupta, 1961.