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PARASITOLOGICAL REVIEW

Caryophyllidea (Cestoidea): A Review

John S. Mackiewicz

Department of Biological Sciences, State University of New York at Albany,
Albany, New York 12222

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I. INTRODUCTION

In having a single set of reproductive organs within a nonsegmented body (Figs. 1–22) and utilizing aquatic oligochaetes (Annelida) as intermediate hosts caryophyllideans are unique among the true cestodes. Perhaps best known are *Archigetes,* a tapeworm that can complete its life-cycle in an invertebrate, and *Caryophyllaeus,* known since the 18th century. Despite their long history there has been no review of the group as a whole although there have been excellent ones dealing chiefly with systematics (Nybelin 1922; Hunter 1930), European species (Janiszewska 1954) or a genus, *e.g., Archigetes* (Wiśniewski 1930). The purpose of this paper is to briefly review the literature, morphology, ultrastructure, biology, host–parasite relationships, iconography, phylogeny, zoogeography, and classification of the Caryophyllidea for the period 1781–1971 (July). Appraisal of individual host records and an analysis of the systematics of each species are not considered; no new binomials are introduced. Complete binomials can be found in Table VIII. Additional detail is presented on morphology because of its importance in assessing the systematic and phylogenetic position of these cestodes and of the data, not yet available in translation, contained in papers from Poland and the Soviet Union.

II. LITERATURE REVIEW

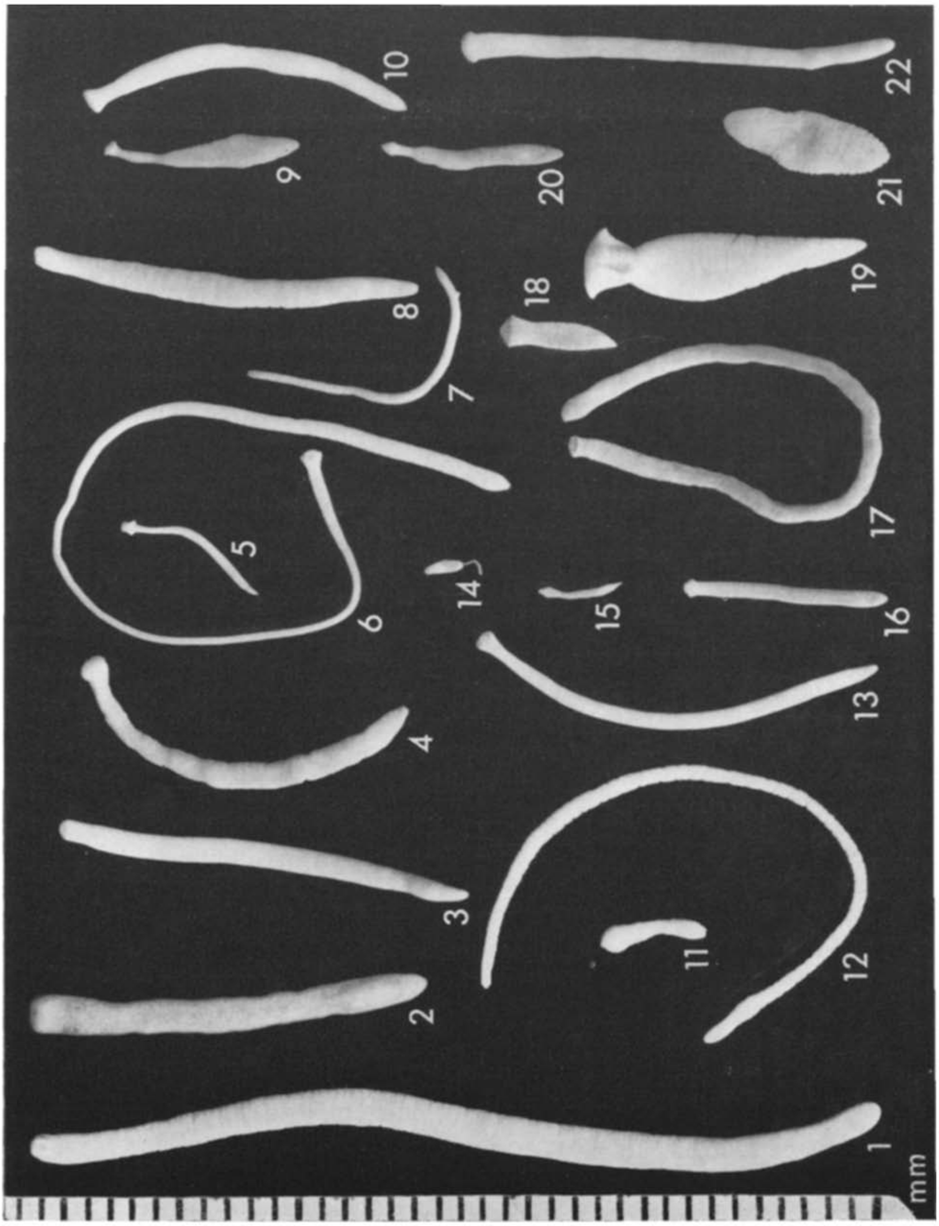
A. *1781–1877*

Beginning with the discovery of *C. laticeps* by Pallas (1781) there followed a long period characterized chiefly by observations on anatomy and morphology (Blanchard 1848; Moniez 1880a,b; Ratzel 1868; Schultz 1852; Stuedener 1877; and von Siebold 1837), general accounts with some attention to classification (Bremser 1819; van Beneden 1850, 1858, 1870; Goeze 1782; Herman 1783; and Zeder 1803) and the cataloguing of species, often with some descriptive material (Abildgaard 1790; Baird 1853; de Blainville 1828; Risso 1826; and Müller 1787). Descriptions of "new species" began to appear (Molin 1858, 1861; Schrank 1788; d'Udekem 1855; and Wagener 1854) as did illustrations of known species (Bremser 1824 and Carus 1857). Attempts at classification became more common (Carus 1863; Claus 1876; Diesing 1850, 1863; Gmelin 1790; von Nordmann 1840; and Rudolphi 1802, 1810, 1819).

Most significant were the papers by van Beneden, which summarized what was then known, and by Carus (1857) which provided the first detailed illustration of *C. laticeps.* The theory of spontaneous generation was still widely held during this period; it is, therefore, not surprising that as late as 1819 it was thought that the "Nelkenwurm" formed in the intestine of fish from strands of mucus that became covered by epidermis (Bremser 1819).

B. *1878–1921*

With the description of *Archigetes* by Leuckart (1878a) speculation on the origin and systematic value of neoteny and monozooty became more common (Claus 1889; Goette 1921; Lönnberg 1897; Monticelli



FIGS. 1–22. Representative caryophyllid cestodes; from the United States unless otherwise specified. 1. *Monobothrium ingens* from *Ictiobus niger*; Texas. 2. *Edlintonia ptychocheila* from *Ptychocheilus oregonense*; Idaho. 3. *Caryophyllaeus terebrans* from *Catostomus ardens*; Wyoming. 4. *Caryophyllaeus laticeps* from *Abramis brama*; France. 5. *Biacetabulum carpiodi* (lateral view) from *Carpiodes carpio*; Texas. 6. *B. infrequens* from *Hypentelium nigricans;* Tennessee, 7. *Promonobothrium minytremi* (lateral view, cirrus partially everted) from *Minytrema melanops*; Tennessee. 8. *Caryophyllaeides fennica* from *Scardinius erythophthalmus*; Switzerland. 9. *Isoglaridacris folius* from *Moxostoma erythrurum*; Oklahoma. 10. *I. hexacotyle* from *Catostomus insignis*; Arizona. 11. *Hunterella nodulosa* from *Catostomus commersoni;* Colorado. 12 *M. ulmeri* (lateral view) from *M. melanops;* Oklahoma. 13. *Glaridacris catostomi* from *C. commersoni;* New York. 14. *Archigetes sieboldi* from Tubificidae; Poland (courtesy of J. Janiszewska). 15. *G. confusus* from *I. bubalus*; Texas. 16. *G. laruei* from *C. commersoni*; New York. 17. *Spartoides wardi* from *Carpiodes carpio*; Texas. 18. *Balanotaenia bancrofti* from *Tandanus tandanus*; Australia (courtesy of M. Angel). 19. *Capingens singularis* from *I. cyprinellus;* Oklahoma. 20. *Atractolytocestus huronensis* from *Cyprinus carpio;* Oklahoma. 21. *Notolytocestus major* from *T. tandanus*; Australia (courtesy of M. Angel). 22. *Khawia iowensis* from *Cyprinus carpio*; Tennessee.

1892; Rosen 1918; and Spengel 1905). Schemes of classification (Ariola 1899; Braun 1894; Lühe 1902, 1910; and Odhner 1912) often reflected the views of the preceding workers or of the new information on anatomy (Fraipont 1880; Mrázek 1898; Pintner 1881; Saint-Remy 1890; and Will 1893). There was the beginning of work on eggshell formation (Mueller 1914) and glycogen distribution (Ortner-Schönbach 1913). New species began to accumulate at a rapid rate (Annenkova-Khlopina 1919; Cholodkowsky 1915; Cohn 1908; Cooper 1920; Lamont 1921; Linton 1893; Monticelli 1892; Mrázek 1908; Schneider 1902; and Skrjabin 1913). The relationship between *Archigetes* and larval *Caryophyllaeus*, the subject of much controversy, became further clarified (Mrázek 1901).

The most significant papers of this period were by Braun (1894) who reviewed the literature; Lühe (1910) who placed caryophyllideans in the Pseudophyllidea thus influencing many subsequent workers; and Will (1893) and Mrázek (1898) whose work on *C. laticeps* and *Archigetes*, respectively, became the basic anatomical studies.

C. *1922–1929*

A thorough reappraisal of the systematic position of caryophyllideans by Nybelin (1922), based chiefly on morphological characteristics and including a review of the European species, marks the beginning of this third short period that is largely characterized by descriptions of new species by Baylis (1928), Bovien (1926), Fuhrmann and Baer (1925), Hunter (1927, 1929a), Johnston (1924), Kulmatycki (1924), Moghe (1925), Motomura (1927), Popoff (1924), Wiśniewski (1928), and Woodland (1923, 1924). There were also further attempts at classification by Mola (1929) and Poche (1926) often with sharply differing views (Fuhrmann and Baer 1925; Woodland 1926). The only detailed study of the embryology of any species was done at this time by Motomura (1929).

D. *1930–1971* (*July*)

The extensive monographs of Wiśniewski (1930) on the anatomy, histology and histogenesis, biology and systematics of *Archigetes* and of Hunter (1930) on caryophyllidean systematics, with some attention to their growth, pathological effects, and host distribution, laid a firm foundation for future studies. So numerous have they been that only the most significant ones are mentioned here.

These studies have been largely dominated by descriptions of new species scattered in over 40 papers. Most prominent among the systematic studies have been those of Calentine (1962), Calentine and Ulmer (1961), Calentine and Mackiewicz (1966), Fischthal (1951, 1953, 1954), Janiszewska (1950a, 1953, 1954), Kennedy (1965b), Kulakovskaya (1961, 1962c), Kulakovskaya and Akhmerov (1965), Mackiewicz (1963a,b, 1965a, 1968c, 1969, 1970a), Mackiewicz and Beverly-Burton (1967), Mackiewicz and McCrae (1962, 1965), Szidat (1937b, 1938, 1942) and Woodland (1923, 1937a,b). Although largely confined to the systematics of European species, Janiszewska's paper (1954) also considered a historical sketch of the group, general morphology and histogenesis, development and biology, and geographical distribution (in Europe) and phylogeny. Several general treatments of the systematics of these cestodes appeared (Fuhrmann 1931; Joyeux and Baer 1961; Wardle and McLeod 1952; and Yamaguti 1959).

But it is in the subjects of life cycles and host–parasite relationships that the greatest strides were made. Particularly noteworthy because of their experimental approach have been the series of Calentine (1963, 1964, 1967), Calentine and DeLong (1966), Calentine and Williams (1967) and Calentine *et al.* (1970), dealing with infections in tubificid annelids; of Kennedy (1965a) and Kulakovskaya (1962b) on the biology of larval stages in the annelid; and of Sekutowicz (1934) on general biology. Population biology and/or immune responses of the adult stages have been discussed by Kennedy (1968, 1969b) and Kennedy and Walker (1969). Others dealing with various aspects of host–parasite relationships have been those by Kulakovskaya (1962a, 1964a), Kulakovskaya *et al.* (1965), and Wunder (1939). Pathology of caryophyllid infections has been studied by Kanaev (1956a,b).

More recently there has been some attention to ultrastructure (Béguin 1966a,b), cytology (Jones and Mackiewicz 1969; Mackiewicz and Jones 1969), and vitellogenesis and eggshell formation (Mackiewicz 1968a).

The most significant papers of this period were those of Wiśniewski (1930) because of the exhaustive treatment of the biology of *Archigetes*; of Hunter (1930), because it laid the foundations for future work on the systematics of the group; and of Calentine, Kennedy and Kulakovskaya because of the experimental and ecological studies of the larval stages.

Reference to unpublished theses (M.S. and Ph.D. dissertations from universities in the United States) dealing chiefly with caryophyllid biology can be found in Mackiewicz (1968b) and Williams and Ulmer (1971); other theses include those of Hunter (1924) and Lawrence (1969).

Most common names used throughout the literature have referred to *C. laticeps*; for example "Der breitköpfige Bandwürm" (Pallas 1781; Batsch 1786), "Nelkenwurm" (Bloch 1782; Goeze 1782; Müller 1787; Schrank 1788; Zeder 1803; Bremser 1819), "bladworm" (= leafworm; Abildgaard 1790) "Géroflé des poissons" (Nordman 1840), "Caryophyllé changeant" (Blanchard 1848) and "clove worm" (van Duijn 1967). Most recently, *E. ptychocheila* was named "Schell's caryophyllid" by Mackiewicz (1970a). From the Russian гвоздичников the whole group has been translated as "clove" or "gillyflower" worms (Dubinina 1962).

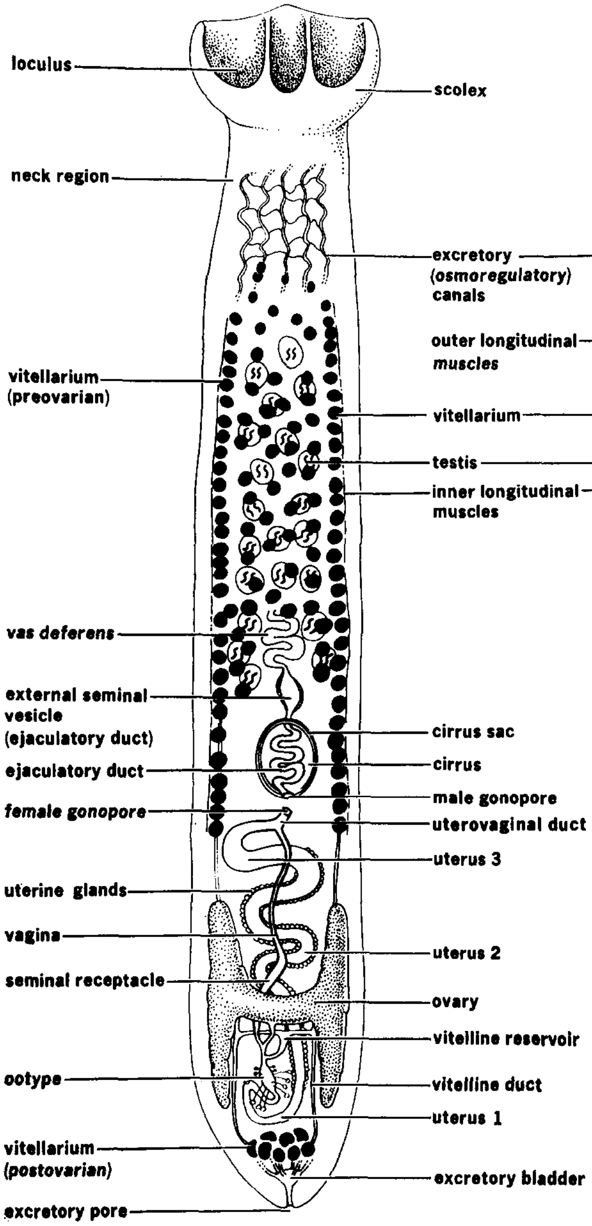
III. Morphology and Anatomy

A. *Size, Shape, Color*

The features of a generalized, hypothetical caryophyllidean are shown in Fig. 23. A synopsis of caryophyllidean morphology was recently presented in abstract form by Mackiewicz (1970b).

Caryophyllideans are characteristically long and narrow tapeworms (Figs. 1–22) bearing no trace of internal or external segmentation at any stage of their development (Figs. 41–63). Gravid stages may range in length from 0.9 (*P. oklensis*) to 95 mm (*K. sinensis*); there is much inter- and intraspecific variation. Since living worms often stretch two to three times their normal length, the data of Fig. 26 are only approximate. Many of the variations in shape can be seen in Figs. 1–22. Some species show little differentiation of the body region (Figs. 49, 53, and 63) or more often, are tapered toward the anterior end (Figs. 44 and 57). A distinct neck, best observed in contracted specimens, is often present (Figs. 51 and 61). Despite the great variation found in many species, some, such as *C. singularis* (Figs. 19 and 52) or *I. folius* (Figs. 9 and 44), have distinct shapes characteristic of the species. Rarely, however, is there a specific body feature, such as the swollen neck of *P. minytremi*, that helps to identify a species.

Cestodes are normally opaque white in color. I have observed, however, a distinct pinkish hue in a single live gravid *B. infrequens* from *M. erythrurum* (Houlston River, TE, May 1968) examined in tap water and three live gravid *G. laruei* from *C. commersoni* (Mohawk River, NY, October 1969) examined in 0.7% saline. In both



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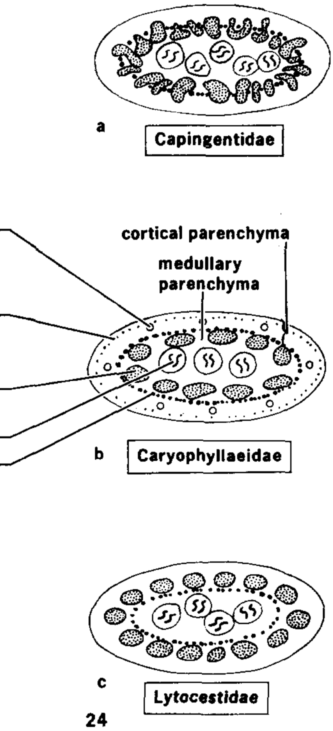

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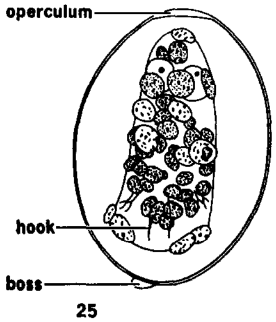

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FIGS. 23–25. Caryophyllidean morphology and anatomy. 23. Hypothetical species illustrating principal features. 24A–C. Cross sections through body illustrating how the distribution of the inner longitudinal muscles differs among the families. 25. Egg (approx. 62 μ long) of *Archigetes* sp. showing oncosphere; two "vesicular nuclei" are visible in the posterior part of the larva and six "micronuclei" lie in the "mantel" (after Motomura, 1929: Fig. 29).

cases the cestodes were the only ones from the host. The pinkish color apparently developed after the worms had been removed to the respective solutions and appeared to be in the parenchyma surrounding the vitellaria and ovary. After 10 min in Carnoy's fixative, the color disappeared. Other individuals of the same or different species (*G.*

catostomi) observed at the same time under identical conditions exhibited no color.

B. *Scolex*

The scolex is highly variable with no single type being characteristic of caryophyllideans (Figs. 27–40). It is necessary to study live material in order to observe the great variations possible even from those forms having an apparently unspecialized scolex. Few genera, however, exhibit the remarkable change in shape shown by *Bothrioscolex* (Fig. 40). Some of the modifications of the scolex include acetabula (*Biacetabulum*, Fig. 31a), loculi (*Spartoides*, Fig. 30; *Isoglaridacris*, Fig. 44; *Glaridacris*, Fig. 49), bothria (*Archigetes*, Fig. 83; *Capingens* Fig. 36), terminal introvert (*Monobothrium*, Fig. 27b,c), folds (*Caryophyllaeus*, Fig. 39) fimbriae (*Khawia*, Fig. 34), frills (*Balanotaenia*, Fig. 35), or entirely lack special attachment organs (*Hunterella*, Fig. 45; *Caryophyllaeides* Fig. 33; *Notolytocestus*, Fig. 60). More than one type of specialization may occur within the same genus (*e.g.*, *Biacetabulum*, *Glaridacris*). Neither rostellum nor hooks are present; there is often a distinct neck (*Djombangia*, Fig. 61). What appears to be a terminal sucker of *Djombangia* is, as Fuhrmann (1931; Fig. 323) has shown and I have verified, primarily a glandular structure. More than one type of modification can occur on a single scolex; thus loculi may occur in conjunction with the acetabula of *Biacetabulum* (Fig. 31) or bothria of *Archigetes*, *Penarchigetes* (Fig. 25), or *G. confusus* (Fig. 38); or bothria with a terminal introvert as in *M. ingens* (Fig. 27b). One can only speculate as to whether this enormous variety is a consequence of adaptive radiation from a single basic form or indicative of a polyphyletic origin with radiation from several stem forms.

C. *Reproductive Systems*

Female

This system consists of ovary, uterus, vagina, vitellaria and associated ducts.

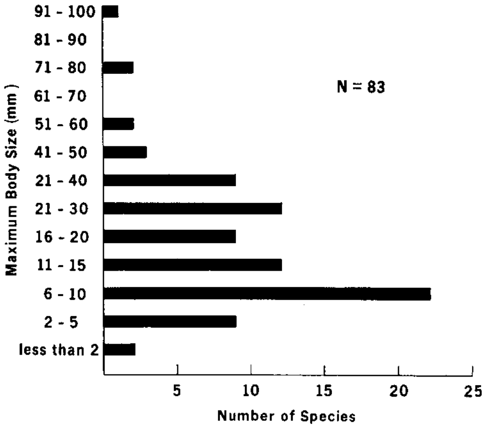
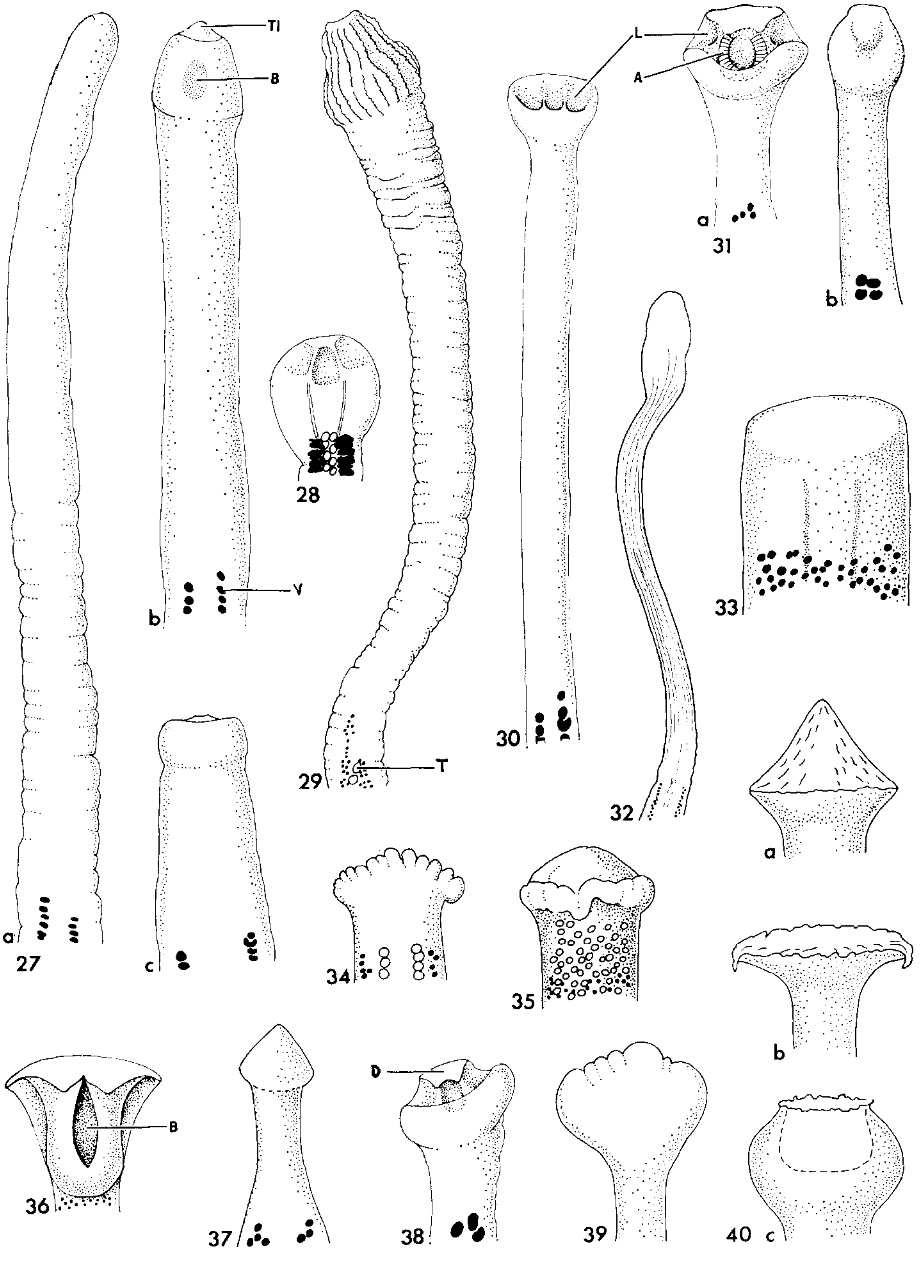
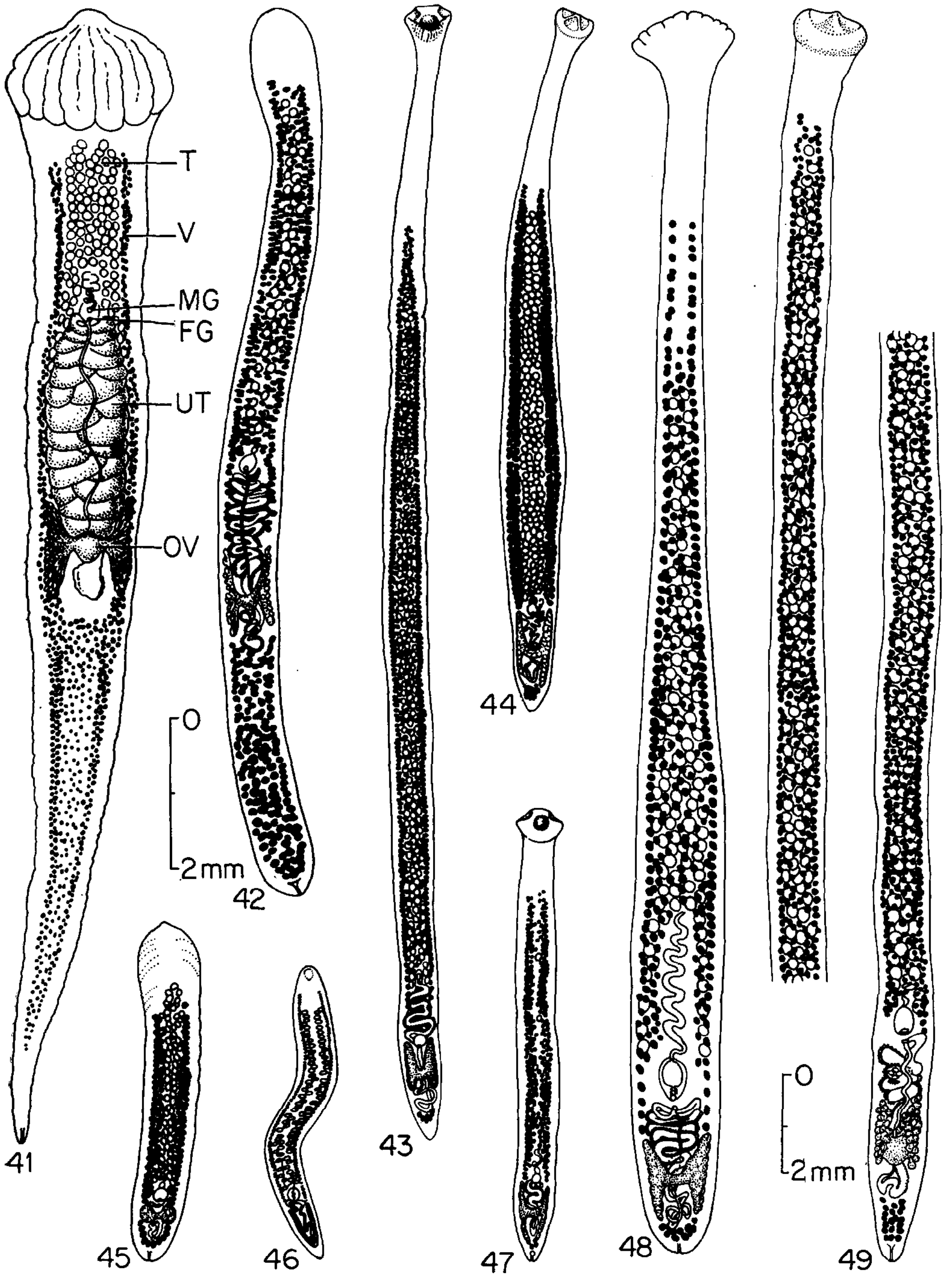


FIG. 26. Distribution of species with respect to maximum body size.

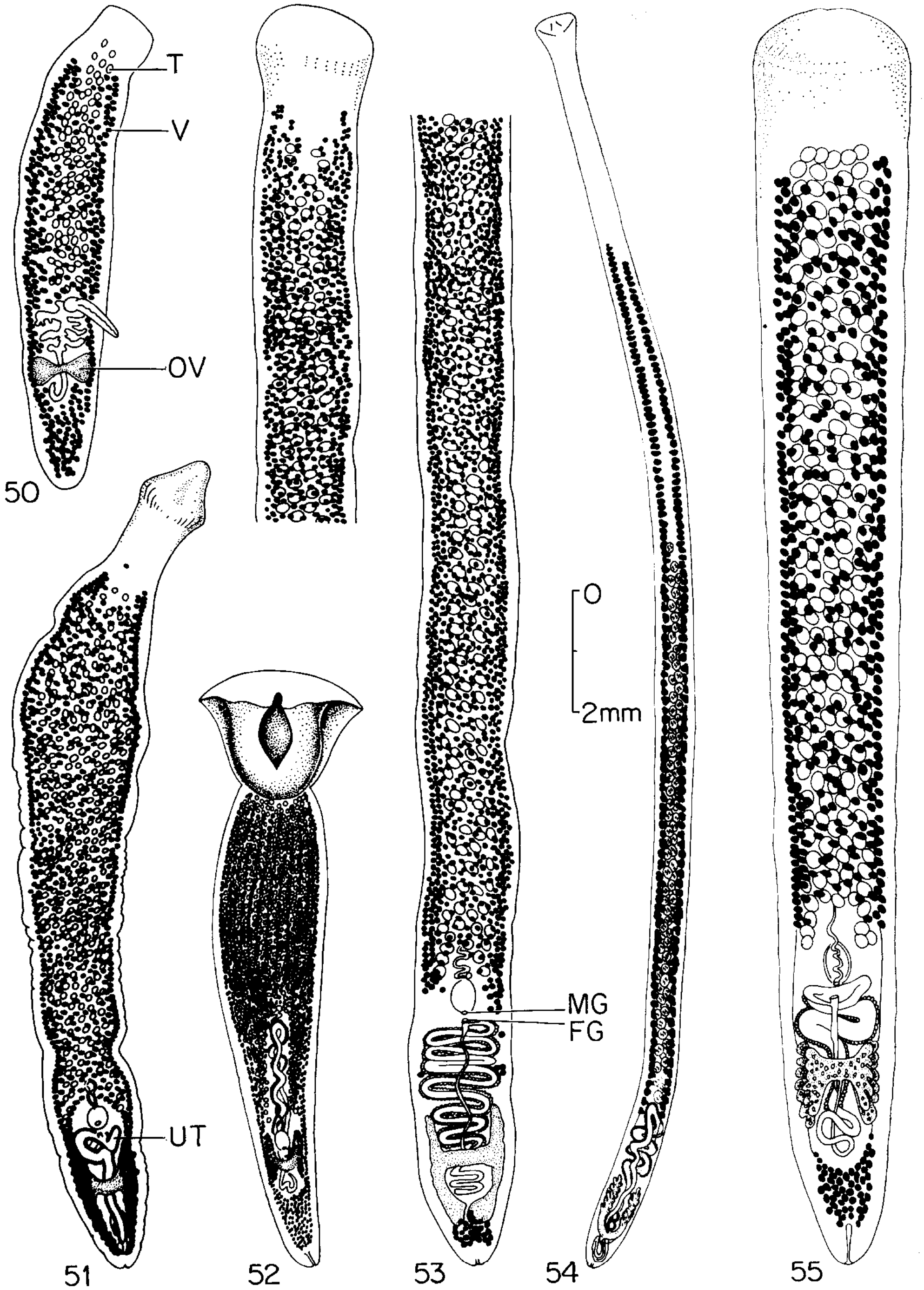
The ovary consists of two large lobes, wings or clusters of follicles that are connected by a ventrally arched commissure. Except in the genera *Pliovitellaria* and *Wenyonia*, which have the ovary near the middle of the body (Figs. 41 and 42), it is clearly posterior. It has been described as having the shape of a "dumbbell" (*Archigetes*, *Hunterella*, Figs. 45 and 83), "butterfly (*Breviscolex*, Fig. 50), or the letters "U" (*Spartoides*, Fig. 54), "V" (*Bialovarium*, Fig. 46), inverted "A" (*Caryophyllaeides*, Fig. 63) or as is most often the case, some variation of "H" (*Pseudolytocestus*, Fig. 51, and many other genera). Rarely do two different forms occur in the same genus; an exception is *Isoglaridacris* which has both the inverted "A" and normal "H" morphology (Mackiewicz, 1965a, 1968b). A distinctly follicular ovary occurs in some genera (*Monobothrioides*, Fig. 59) but the compact nonfollicular types are most common. Some of these latter types, particularly that of *Caryophyllaeides* consist of thick interconnected strands and numerous lacunae; these lacunae are also present in the ovary of *Edlintonia* (Fig. 55) although no strands are present. Between the distinctly follicular and compact types many intermediate conditions exist. From the posterior margin of this commissure, usually



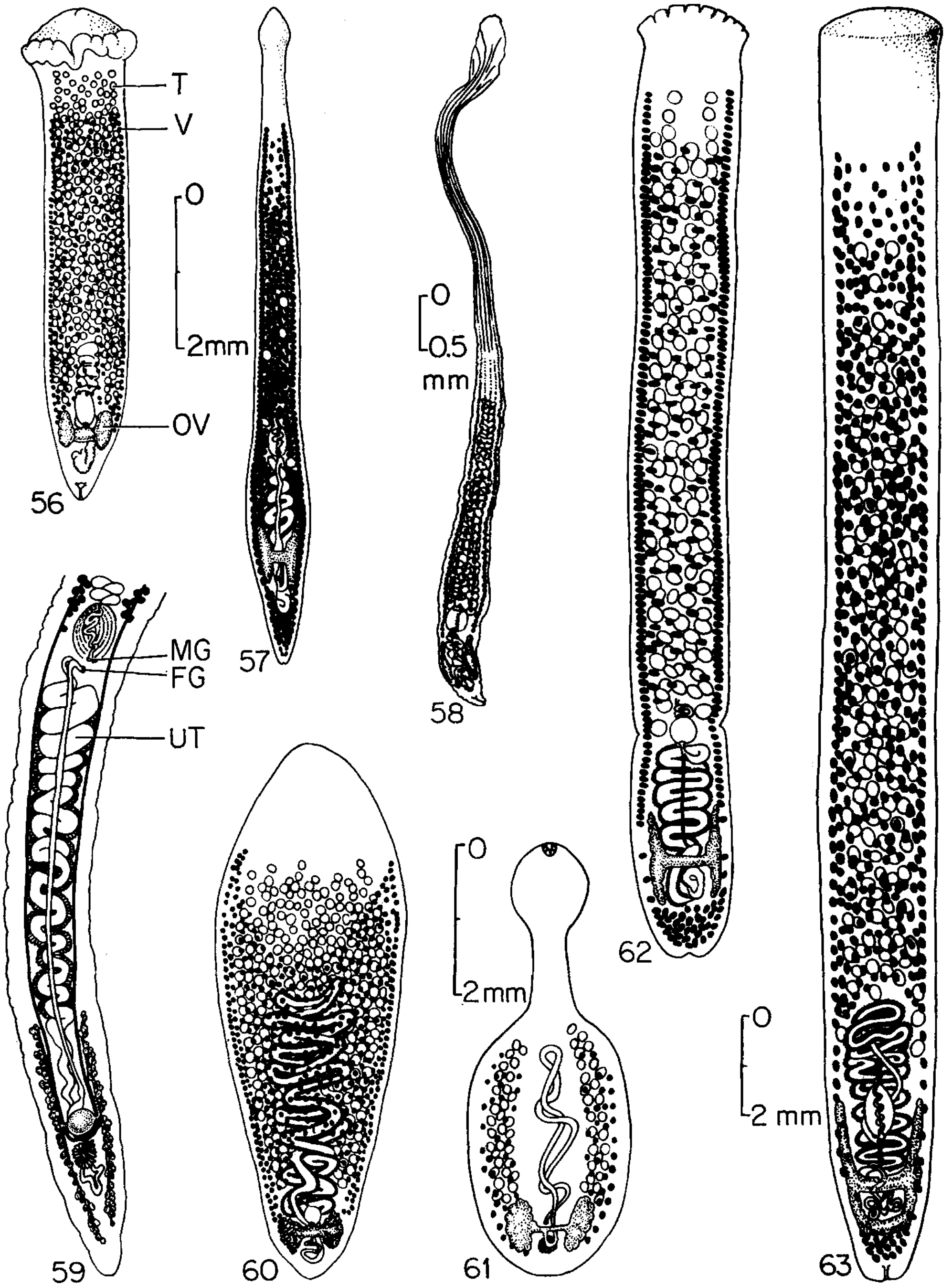
FIGS. 27–40. Scolexes of Caryophyllidea; not to scale. 27a. *Monobothrium ulmeri*, b. *M. ingens*, c. *M. hunteri*. 28. *Penarchigetes oklensis* (after Mackiewicz, 1969: Fig. 4). 29. *Monobothrioides cunningtoni*. 30. *Spartoides wardi*. 31a. *Biacetabulum carpiodi*, b. *B. biloculoides*. 32. *Lytocestus parvulus* (after Furtado, 1963: Fig. 2). 33. *Caryophyllaeides fennica*. 34. *Khawia iowensis*. 35. *Balanotaenia bancrofti*. 36. *Capingens singularis*. 37. *Atractolytocestus huronensis*. 38. *Glaridacris confusus*. 39. *Caryophyllaeus laticeps*. 40a-c. *Bothrioscolex rossitensis*, sequence of movements (after Szidat, 1937a: Fig. 7). Abbreviations: A, acetabulum; B, bothrium; D, disc; L, loculus; T, testis; TI, terminal introvert; and V, vitellarium.



FIGS. 41–49. Representatives of the family Caryophyllaeidae (same scale for 41–47). 41. *Wenyonia virilis*. 42. *Pliovitellaria wisconsinensis* (courtesy of J. Fischthal). 43. *Biacetabulum infrequens*. 44. *Isoglaridacris folius*. 45. *Hunterella nodulosa*. 46. *Bialovarium nocomis* (after Fischthal, 1954: Fig. 1). 47. *Glaridacris oligorchis*. 48. *Caryophyllaeus laticeps*. 49. *G. catostomi*. Abbreviations: FG, female gonopore; MG, male gonopore; OV, ovary; UT, uterus; T, testis; and V, vitellarium.



Figs. 50–55. Representatives of the family Capingentidae. 50. *Breviscolex orientalis* (modified from Kulakovskaya 1962c: Fig. 1). 51. *Pseudolytocestus differtus* (after Mackiewicz 1970a: Fig. 9). 52. *Capingens singularis* (*ibid*: Fig. 8). 53. *Adenoscolex oreini* (Paratype; courtesy of D. Fotedar). 54. *Spartoides wardi* (*ibid:* Fig. 10). 55. *Edlintonia ptychocheila* (*ibid*: Fig. 1). Abbreviations: as for Figs. 41–49.



FIGS. 56–63. Representatives of the family Lytocestidae. 56. *Balanotaenia bancrofti*. 57. *Atractolytocestus huronensis*. 58. *Lytocestus parvulus* (modified from Furtado, 1963: Fig. 2). 59. *Monobotrioides cunningtoni*, posterior end, no scale (after Fuhrmann and Baer, 1925: Fig. 3). 60. *Notolytocestus major* (slightly flattened). 61. *Djombangia penetrans* (after Bovien, 1926: Fig. 4). 62. *Khawia iowensis* (after Calentine and Ulmer, 1961: Fig. 1). 63. *Caryophyllaeides fennica*. Abbreviations: as for Figs. 41–49.

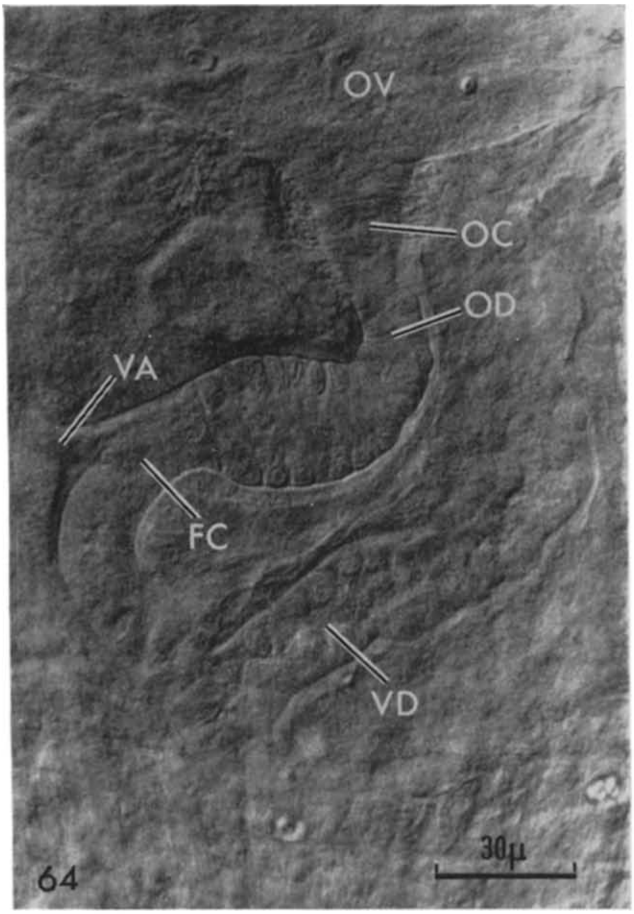
along the midline, the oviduct takes its origin.

Details of the histology and morphology of the oviduct and uterus are found in many descriptions; those of Hunter (1930), Löser (1965), Will (1893), and Wiśniewski (1930) are particularly helpful in this regard. Briefly, a sphincter or oöcapt (Fig. 64; ovicapt of Löser 1965) surrounds the oviduct which leaves the posterior margin of the ovarian commissure and passes posteriorly, forming a small fertilization chamber as the spermioduct from the vagina or seminal receptacle is received on one side (Figs. 64 and 65). Further along, usually on the other side, the vitelline duct joins the oviduct which now becomes the ovovitelloduct before expanding into the specialized oötype that is surrounded by serous and mucous glands. According to Löser (1965), the serous glands are smaller, confined to the proximal part of the oötype and are less numerous than the larger more widely dispersed mucous glands (Fig. 65). In *C. laticeps* there are 48 serous glands and 850 mucous glands while in *K. iowensis* there are 23 and 240 glands, respectively. Both types communicate via individual ducts into the lumen of the oötype. Mucous glands are PAS positive (Löser 1965; Mackiewicz 1968a). There seems little doubt that both of these glands are associated with eggshell formation yet the specific biochemical nature of the secretions, and their role in eggshell formation is not known. Adjacent to the oöcapt, distal vitelloduct, and proximal portion of the uterine duct of *K. iowensis* is an x-cell, absent from comparable locations in *C. laticeps* (Löser 1965; Fig. 65). Thought to be nerve cells, they may serve in coordinating the complex process of ova release, fertilization, and eggshell formation (Löser 1965). The lack of x-cells in *C. laticeps* may have reflected a stage when these cells were not readily demonstrable rather than their complete absence. A short, wide uterine duct connects the oötype with the uterus proper.

The portion of the uterus distal to the oötype has been divided into various regions by different authors. Though not the first to do so, Will (1893) recognized three distinct parts (Figs. 23 and 66): "Anfangsteil" (ut_1) that begins near the oötype, is nonglandular and twists ventrally, gradually becoming the "eigentliche Uterus" (ut_2) that is long, glandular, and constitutes the uterus proper and the "Endabschnitt" portion (ut_3) that is short, nonglandular, and joins the vagina. Working with *Wenyonia*, Kulmatycki (1924) recognized an "Anfangsteil" but divided the "eigentlichen Uterus" into a wide uterus (ut_2 of Will) and a narrow uterus (ut_3 of Will), with the uterovaginal canal constituting the third part of the uterus. Yamaguti (1934), Hunter (1930), and Janiszewska (1953, 1954), however, have followed Will's scheme; according to the latter author, these three parts are found in all European species. Will's scheme has utilitarian value and perhaps should be utilized more often.

Uterine glands, sometimes designated radial cells (Furtado, 1963) after the "Radialzellen" of Will (1893), are characteristic of caryophyllids (Fig. 66). In some instances, however, they have been reported absent, *e.g., W. minuta, W. acuminata,* and *W. virilis* (Woodland 1926). Because Kulmatycki (1924: Fig. 10) clearly pictures a glandular uterus in *C. niloticus* (= *W. virilis*) it is quite possible that additional study of the other two species might reveal uterine glands; *W. minuta* was described from a whole mount of a single gravid individual, it should be noted. A nonglandular uterus was also reported in *A. sieboldi* (Wiśniewski 1930; Calentine 1962) yet subsequent descriptions state that they are present (Calentine and Delong 1966; Janiszewska 1954) or present or absent (Kennedy 1965b). Clarification of the status of these glands in the above-mentioned species is obviously needed.

Normally these glands are conspicuous and more easily observed on sections (Fig.



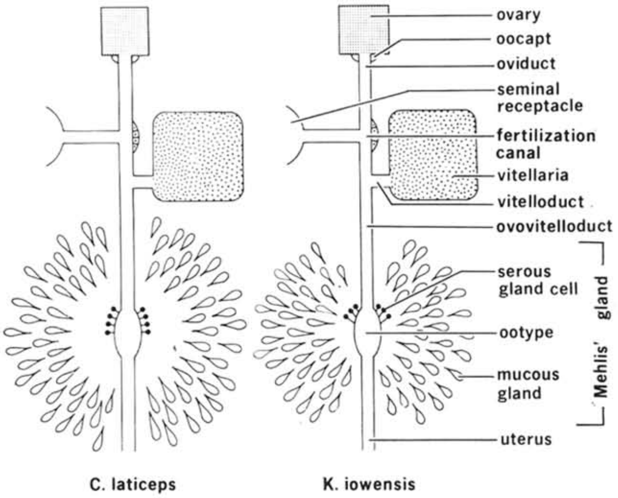


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FIG. 64-65. 64. Oviduct complex of living larval *Glaridacris catostomi* (Nomarski Differential Interference Contrast Optics: photo by C. Izzard). Abbreviations: FC, fertilization canal; OC oöcapt; OD, oviduct; OV, ovary; VA, vagina; and VD, vitelloduct. 65. Diagrammatic representation of the oviduct and Mehlis' gland complex of *Caryophyllaeus laticeps* and *Khawia iowensis*; see text for location of X-cells in K. *iowensis* (adapted from Löser 1965: Figs. 22b,c).

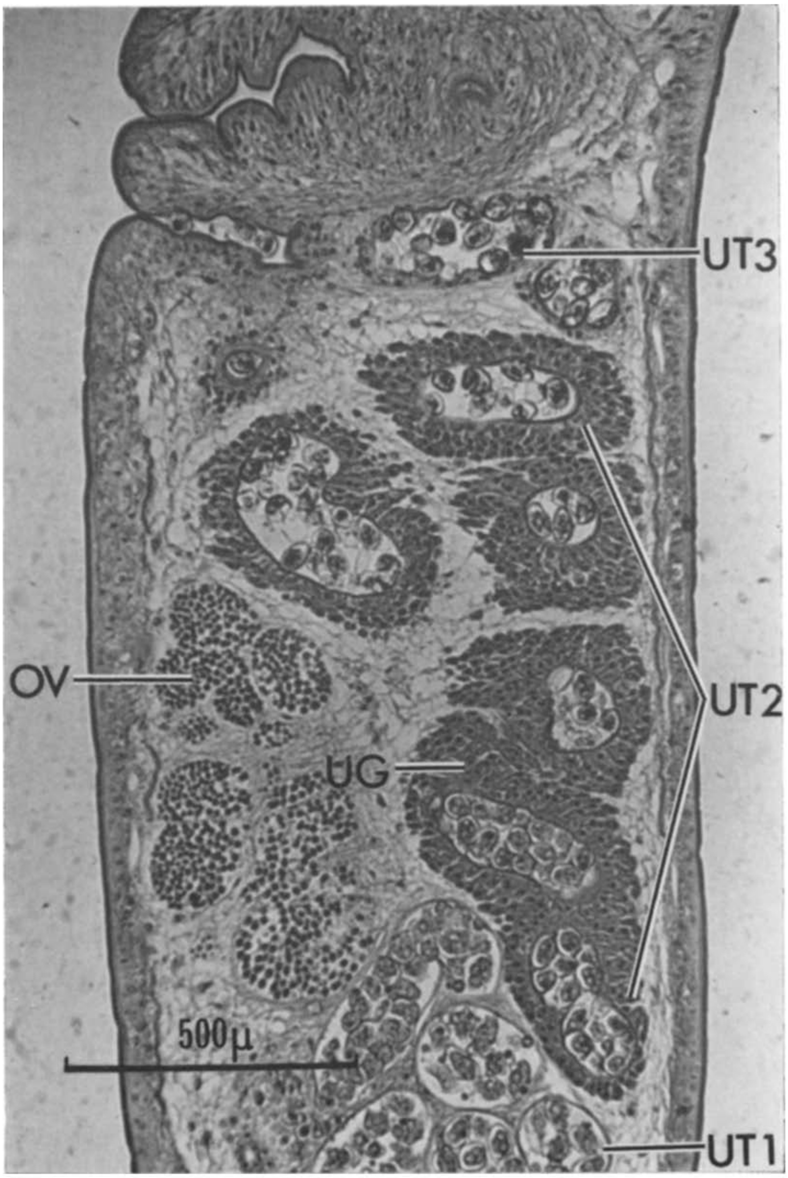


FIG. 66. Midsagittal section of the female reproductive complex of *Glaridacris catostomi*. Abbreviations: OV, ovary; UG, uterine glands; UT1–3, regions of uterus (see text for details).

66) than on whole mounts. They are absent from the distal and proximal parts of the uterus, reaching their greatest development on the longer, twisting middle portion. In some cases (*B. meridianum* and *B. infrequens*) the differences in their distribution has been used to separate species (Hunter, 1930). Similar glands are present in *Cyathocephalus*, *Bothrimonus*, and *Diplocotyle* (Pseudophyllidea) but they are weakly developed in members of the Dibothriocephalidae and Ptychobothriidae (Nybelin 1922; Fuhrmann 1931): they are, however, absent from pseudophyllideans having marginal genital pores (Fuhrmann 1931).

Little is known of the histology and function of these glands. That they are unicellular and club or pyriform shaped was shown by several workers (St. Remy 1890; Hunter 1930; Yamaguti 1934; Löser 1965), as was their basophilic staining characteristic (Hunter 1930; Yamaguti 1934). Löser (1965) found that the uterine gland cells of *K. iowensis* had vacuoles, usually near the nucleus, and that each cell tapered to a fine duct that opened into the uterus. Although Hunter (1930) and Fuhrmann (1931) knew of no function ascribed to these cells, an early observation of Bovien (1926) suggests that they might be involved in eggshell formation. Bovien noted that the eggs of *Djombangia* became spinous only after they had entered the glandular portion of the uterus and not before. Indeed, Yamaguti (1934) later observed secretory granules associated with these cells of *K. japonensis*. These observations have been further corroborated by Löser (1965) who, on the basis of similarities of staining reaction with azan and anilin blue, concluded that the secretion of the uterine glands is analogous to the mucous secretion of Mehlis' gland and that it forms the fine spines on ova of *K. iowensis*. These data, however, do not explain their function with respect to nonspinous eggs, which include most caryophyllidean eggs. Yet they are nonetheless interesting in the light of recent work on the trematode *Syncoelium spathulatum* Coil and Kuntz in which the glandular uterine epithelium was found to secrete the proteins and phenols that contribute to the finished eggshell (Coil and Kuntz 1963).

A vagina communicates between the oviduct and the ventral surface (Fig. 67). At its proximal end it may join the uterus to form the uterovaginal duct (as in *C. laticeps* or *P. differtus*) opening posterior to the male gonopore (Fig. 67a); or it may form the uterovaginal duct that also receives the ejaculatory duct thus forming a short distinct canal, here designated as the hermaphroditic duct (Fig. 67c), that terminates at a small, common gonopore (as in *Caryophyllaeides, Isoglaridacris* and *Biacetabulum*). Nybelin (1922: Fig. 56) considered this duct the *ductus uterovaginalis* while Hunter (1930), in part, the common atrium or genital atrium. Because these latter three terms apply to essentially different structures and some, *e.g.*, genital atrium, have been used in different ways, it seems advisable to use the term "hermaphroditic duct" (new usage) to avoid further confusion. A third condition (as in *Atractolytocestus*) occurs when the ejaculatory duct and uterovaginal duct open together at or very close to the surface thus forming a

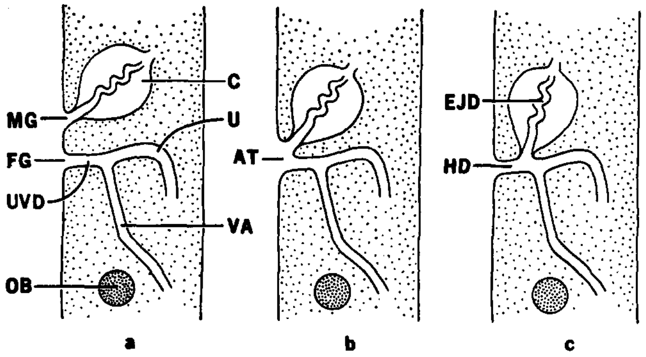


FIG. 67. Gonopore types as shown in midsagittal sections (diagrammatic). Abbreviations: AT, atrium; C, cirrus; EJD, ejaculatory duct; FG, female gonopore; HD, hermaphroditic duct; MG, male gonopore; OB, ovarian bridge or commissure; U, uterus; UVD, uterovaginal duct; and VA, vagina.

shallow atrium with a single large gonopore through which one can see the male and female gonopores (Fig. 67b). Because the relationship of the gonopores to each other changes with the contraction or eversion of the cirrus one must study median sagittal sections of different individuals in order to establish which type is present. Additional comparative studies are needed to determine if indeed these three gonopore types are distinct from each other or whether they form part of a continuous series.

In some species (*e.g., C. laticeps,* Fig. 48) a large well-developed seminal receptacle is present; however, in most species the vagina is only slightly specialized for sperm storage, if at all, before joining the oviduct as the narrow spermioduct.

Vitellaria are represented by a well-developed system of oval, round, or lobate follicles. They are usually smaller than the testes, sometimes conspicuously so, *e.g., N. major* (Fig. 60), *B. bancrofti* (Fig. 56), or *W. virilis* (Fig. 41). Like the testes they may vary in size with the smallest occurring toward the neck region. Follicles occur in any of three groupings: preovarian (Fig. 54), preovarian with a separate postovarian cluster (Fig. 53), or one continuous pre- and postovarian arrangement (Fig. 50). Preovarian vitelline follicles may be arranged in two lateral rows (Fig. 41), intermingled with testes (Fig. 43), or annularly distributed about the testicular region (Figs. 24 and 49). In only a few instances (*L. parvulus, C. singularis*) are they arranged in dorsal and ventral longitudinal rows (Figs. 52 and 58). Usually they extend more anteriorly than the testes (Fig. 43). Depending upon the family, the preovarian follicles may occur in the cortical parenchyma (Caryophyllaeidae, Figs. 24b and 68), medullary parenchyma (Lytocestidae, Figs. 24c and 70), or portions of both (Capingentidae, Figs. 24a and 69). In some instances, however, the preovarian follicles may be in the cortical parenchyma while some of the postovarian ones are in the medullary parenchyma (*e.g., K. sinensis, K. japonensis*). Small vitelline ducts interconnect the follicles, eventually forming two large ducts that form a larger transverse duct in the vicinity of the ovarian commissure (Fig. 23). From this transverse duct, that functions as a vitelline reservoir, a vitelloduct connects the vitelline gland system with the oviduct (Fig. 64).

Male

This system consists of testes, vas efferens, vas deferens, ejaculatory duct and its modifications, and cirrus.

Testes are a conspicuous part of caryophyllid anatomy. They occur in a broad area between the cirrus and neck, occasionally in distinct dorsal–ventral and lateral rows (*I. folius, G. confusus*) but most often without specific arrangement. Occasionally they extend further anteriorly than the vitellaria (Figs. 45 and 55). In *G. catostomi* (Fig. 49) the size of the testes change gradually, with the smallest near the neck, largest near the cirrus (Mackiewicz, 1965b). This size relationship is also true for a large number of other species and must be borne in mind when sampling for variation.

Data on testes number is available for approximately 42 species, but specific information on the range in testes number per species is present for only 35. Great overlap in range distribution makes it difficult to establish frequency classes or special patterns of species arrangement based on testes number. Some species show little variation (*G. confusus,* 25–35 testes; Hunter, 1930), while others show a much greater range (*G. catostomi,* 171–463; Mackiewicz 1965b). The fewest number of testes occur in *G. oligorchis* (1–8; Fig. 47) and *A. huronensis* (6–22; Fig. 57); the maximum in *K. iowensis* 328–490; Fig. 57), *M. ulmeri* (355–643) and *P. differtus* (725–775; Fig. 51). Haderlie (1953) reported no testes in some gravid *G. oligorchis*. The range for maximum numbers of testes is 8 to 775 ($\bar{X}$ = 189), minimum numbers, 1–725 ($\bar{X}$ = 137). There are

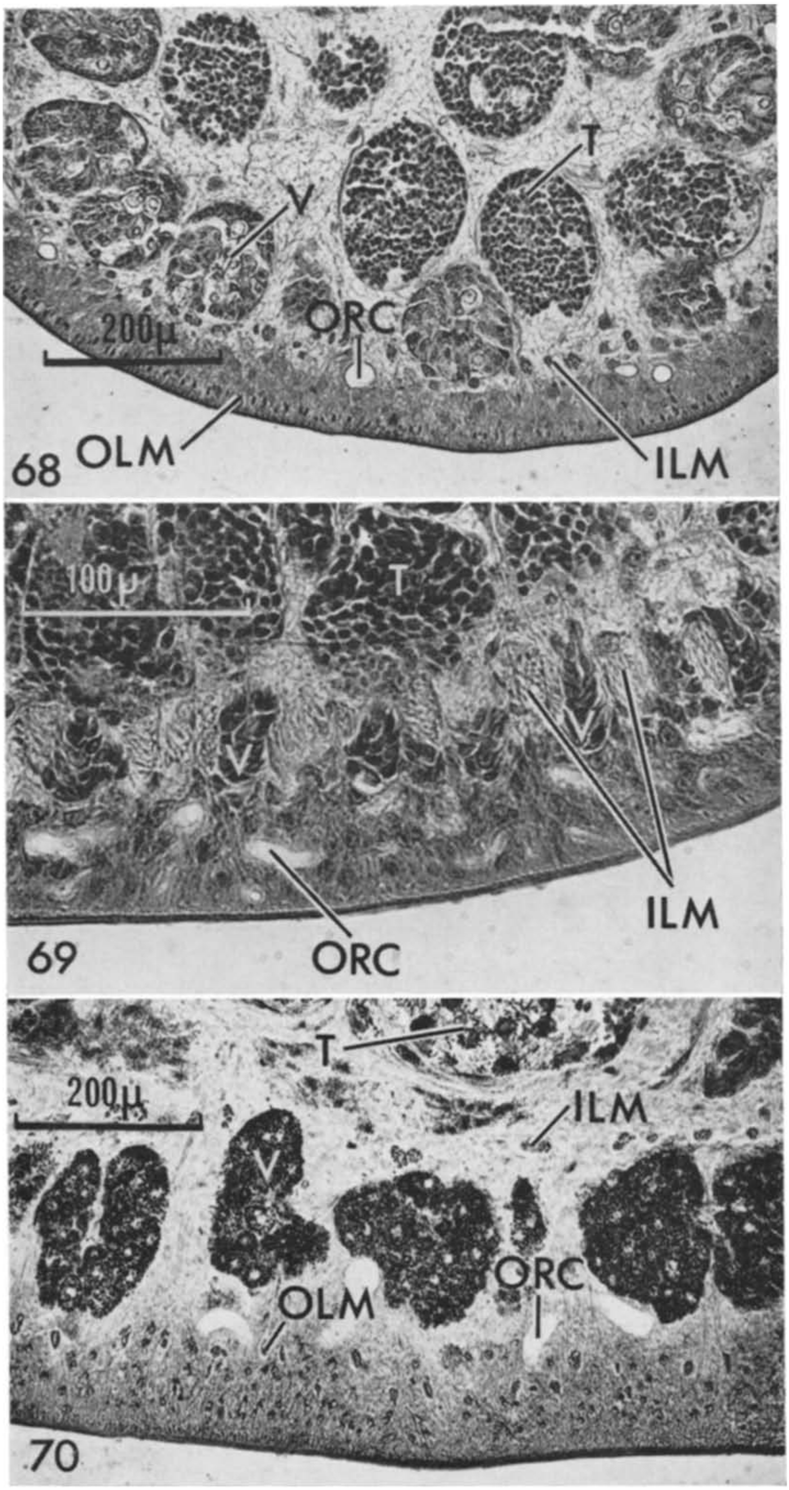


FIG. 68–70. Cross sections illustrating family characteristics based on the placement of inner longitudinal muscles. 68. Caryophyllaeidae, *Glaridacris catostomi*. 69. Capingentidae, *Capingens singularis*. 70. Lytocestidae, *Caryophyllaeides fennica*. Abbreviations: ILM, inner longitudinal muscles; OLM, outer longitudinal muscles; ORC, osmoregulatory canal; T, testis; and V, vitellarium.

no critical morphometric studies that have examined testes number in worms from different hosts or from different geographical regions.

From each testis, vas efferens communicate with each other to form the larger, convoluted vas deferens anterior to the cirrus sac. Specific details of organization and histology of the former ducts are found in Will (1893) and Janiszewska (1954) and the histogenesis, in Wiśniewski (1930). Before entering the cirrus sac, the thin-walled, nonmuscular vas deferens may either enter the sac directly (*Caryophyllaeus, Wenyonia,* palearctic *Monobothrium* and a few other genera) or may form an ejaculatory duct that is specialized as a muscular external seminal vesicle before joining the cirrus sac (*Archigetes, Biacetabulum,* nearctic *Monobothrium,* and many other genera). In the first instance a portion of the ejaculatory duct may function as an internal seminal vesicle (*C. laticeps*); in most cases, however, it is a narrow convoluted duct within the cirrus sac. When an external seminal vesicle is absent there is a question of whether or not a spermiducal vesicle assumes the same function.

The cirrus sac varies greatly in size, less so in structure. Rarely does it occupy the whole width of the medullary parenchyma as in *I. bulbocirrus*; generally it is from one-fifth to one-half that width. While obviously strongly muscular in most genera, in others such as *Wenyonia* (Fig. 41) and *Penarchigetes,* it is weakly so. There are no prostate glands. Internally, the cirrus is usually muscular and rarely, as in *Monobothrium,* may consist of a bulbous proximal portion and a less well-defined distal portion that represents the genital papilla (Nybelin 1922; Hunter 1930; Mackiewicz 1963b). The cirrus is usually eversible and contrary to Yamaguti (1959) and Gupta (1961) has no spines.

D. *Musculature*

The most detailed descriptions of the musculature of caryophyllids have been by Hunter (1930) on various North American species, Will (1893) on *C. laticeps* and Wiśniewski (1930) on *Archigetes* spp. Following the treatment of Janiszewska (1954) the muscles of the body can be divided into three groups: external cuticular, parenchymal, and special.

The external cuticular group includes the circular cuticular (CCM) just beneath the tegument, and internally the longitudinal cuticular muscles (LCM), the "Stäbchenschicht" of Will (1893). Both of these groups consist of small fascicles or strands. According to Furtado (1963), there are "subdermal" muscles consisting of neuromuscular cells internal to the LCM.

Parenchymal muscles are the most prominent, their organization with respect to the vitellaria forming the basis for family classification (Figs. 24 and 68–70). They consist of small fascicles of the outer longitudinal muscles (OLM: subcuticular longitudinal and cortical muscles of Woodland, 1926) that separate the subcuticular from the cortical parenchyma, and larger fascicles of inner longitudinal muscles (ILM) that separate the cortical from the medullary parenchyma. The OLM usually consist of small fascicles or may be absent altogether as in *H. nodulosa, H. paratarius, A. sieboldi,* and *A. iowensis.* In sharp contrast are the ILM (epimedullary longitudinal muscles of Woodland 1926 and Furtado 1963) which usually consist of a ring of larger fascicles (*e.g., B. giganteum, C. singularis*) or a band of smaller ones (*e.g., H. nodulosa, L. filiformis*). In *Wenyonia* spp. the parenchymal longitudinal muscles are scattered throughout the cortical region. In the neck and scolex the ILM often come together and form a small number of large bundles, whose number may be characteristic of the species (*e.g., G. confusus*). Other, but less prominent parenchymal muscles include: the dorsal–ventral series [radial(?) of Furtado 1963; sagittal of Hunter 1930], transverse (frontal of Hunter 1930) at right angles to the previous series and sometimes in close association with the ILM, and diagonal (Wiśniewski 1930) or oblique strands (Hunter 1930). Except for the apparent absence of the last two types and the OLM, body musculature of caryophyllids is much like that of the plerocercoid of *Diphyllobothrium dendriticum* Nitzch, 1824 (Kuhlow 1953; Fig. 4).

Special musculature includes that of the scolex, bladder, and the associated ducts of the reproductive system, *e.g.*, external seminal vesicle, cirrus, and vagina.

While Wiśnienski (1930) has discussed the histogenesis of muscle cells in *Archigetes* and Janiszewska (1954: Figs. 2 and 5) has illustrated the myoblasts, and Will (1893: Fig. 14) the muscle cells, of *C. laticeps,* similar information is not available for other species. Yet to be studied is the location of all sphincters and the muscular organization of the scolex of such genera as *Capingens, Biacetabulum* and *Wenyonia.*

E. *Nervous System*

Principal studies of the nervous system have been those on *C. mutabilis* (Will 1893), *A. appendiculatus* (Mrázek 1898) and *A. sieboldi* (Wiśniewski 1930). Without illustrating the whole system Will (1893) described 10 longitudinal nerve cords interconnected by approximately 20 transverse strands. Anteriorly, 12 nerve cords branch from a nerve ring in the neck, again joining in the center of the scolex at a second nerve ring. Sensory cells (Will 1893: Fig. 8 (NZ_3 cells) were more common in the scolex than in other parts of the body where ganglion cells were found (Will 1893: Fig. 15, NZ_2 cells). Will considered the nervous system of *C. mutabilis* to be most like that of trematodes. This view was soundly criticized by Lühe (1902) who correctly pointed out that the arrangement of the 10 longitudinal cords was indeed no different from that of other cestodes.

Mrázek (1898: Fig. 2), on the other hand illustrated a single large scolex nerve ring and a pair each of short dorsal and ventral cords and two longer lateral ones with 16 nodes. Wiśniewski, however, (1930: Fig. U) illustrated a neck and scolex nerve ring, similar to those in *C. mutabilis* (Will, 1893).

Other accounts of the nervous system are minor parts of species descriptions. Cooper (1920), among others, could find two lateral cords but no dorsal or ventral ones as described by Will (1893); he did, however, find two ganglia in the scolex. The location of these ganglia in *G. confusus* and *B. infrequens* is illustrated in Hunter (1930: Figs. 12 and 22) but described only for *M. ingens* and *H. paratarius.*

Our knowledge of the nervous system of caryophyllids is, therefore, fragmentary. That there are at least two main lateral nerve cords is well established; but the number of anterior nerve rings, of dorsal and ventral cords, and the fine detail of sensory structures, as well as the relationship of transverse and longitudinal cords to each other, and whether or not the lateral cords are joined posteriorly, are points that need further elaboration. Nothing is known of tegumentary sensory organs. Indeed, the use of current histochemical techniques on whole mounts, such as those used by Hart (1967) or tetrathyridia of *Mesocestoides* or by Wilson and Schiller (1969) on the strobila of *Hymenolepis diminuta* and *H. nana,* would help to clarify many of these points.

F. *Osmoregulatory System*

Original observations on the excretory or osmoregulatory system date from the middle 19th century and are largely confined to *C. mutabilis* and *Archigetes* spp. Working

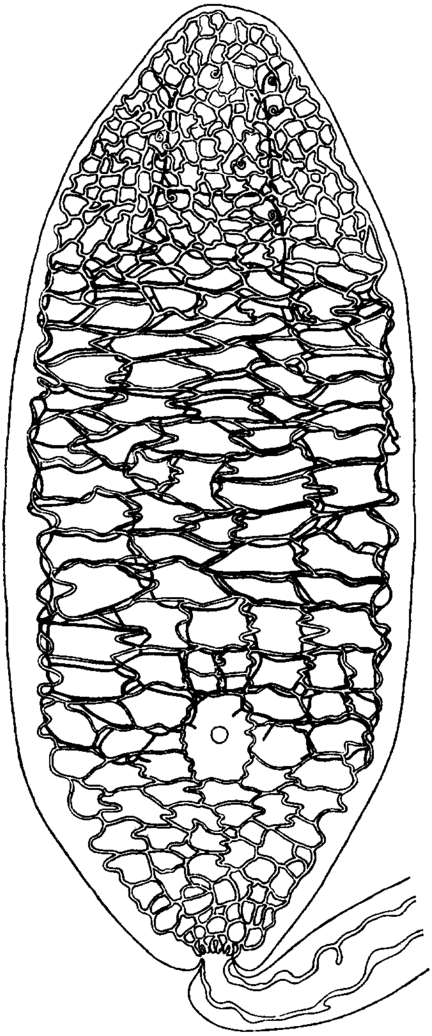


FIG. 71. Osmoregulatory canal system of *Archigetes sieboldi;* ascending system, solid canals (after Mrázek 1898: Fig. 18).

with *C. mutabilis,* Blanchard (1848) was one of the first to picture the characteristic net-like arrangement of canals, while Schultze (1852) reported flame cells ("Wimperläppchen") and a terminal contractile bladder into which eight longitudinal canals emptied. That there were two net-like systems, one of 8–10 internal large canals terminating in a pulsating vesicle, and the other consisting of an external net of smaller canals was described and figured by van Beneden (1858). A terminal pulsating bladder was observed by Steudener (1877) but not finding flame cells, he concluded that fluids in the canals moved by pressure or muscular contractions. While adding new details, none of the preceding studies viewed the excretory system as a whole.

Such an approach was presented by Fraipont (1880) who described and illustrated the principal elements of the osmoregulatory system of *C. mutabilis.* Working with live material Pintner (1881) reported that the deeper-lying large canals (Hauptstämme: "canaux descendents" of Fraipont) and superficial network ("Gefässnets") were interconnected in the body as well as in the scolex and that the flame cells did not communicate with any lymphatic spaces and were connected to both canal systems. While a contractile bladder is mentioned by Pintner, the terms "descending" or "ascending" are not used to designate specific canal systems. It remained for Will (1893), however, to finally establish that both canal systems in *C. mutabilis* were in the cortical parenchyma in the body but that in the neck the two pairs of ascending canals passed into the medullary parenchyma, fusing to form two single canals in the scolex before they joined the anastomosing canals of the descending system. Basing his views on the extent of musculature development Will concluded that the excretory bladder was contractile; he did not find flame cells ("flame bulbs" of Hyman 1951).

Despite the scope of Will's study it was not until the work of Mrázek (1898) and Wiśniewski (1930) on *Archigetes* that the whole osmoregulatory system of any caryophyllid was accurately described and pictured. Perhaps because it was written in Czechoslovakian, Mrázek's detailed and well-illustrated study of the anatomy of *A. appendiculatus* Ratz. (= *A. sieboldi*) has largely been ignored by subsequent workers. Mrázek was the first, however, to establish that the smaller ascending and larger descending canals were usually paired in the cortical parenchyma and that the descending system terminated in a series of small vesicles rather than one large one, as in *Caryophyllaeus*, while the ascending system originated near the ovary (Fig. 71). Wiśniewski (1930) corroborated most of Mrázek's observations. Because the flame cell capillaries joined both the small (ascending) and large (descending) canals Wiśniewski preferred to use the terms "inneren Netze" and "aussern Netzes" [= "canaux ascendants" and "canaux descendants" of Fraipont (1880); "oberflächliche Gefässnetz" and "Hauptstämme" of Pintner (1881), respectively] (note that the position of these two systems was reversed by the latter two authors). He found that young *Archigetes* had five to six descending canals while mature ones had 8–10. In only one case, which was regarded as an exception, did he find any excretory canal in the cercomere (Mrázek 1898: Fig. 18); a kind of contractile vacuole was said to be the normal excretory apparatus of the cercomere. Wiśniewski concluded that except for the absence of a single terminal bladder in *Archigetes*, the excretory system of *Archigetes* and *Caryophyllaeus* was essentially similar. His paper presents the only account of the histogenesis of flame cells (*Archigetes*) and excretory canals (*Archigetes* and *C. laticeps*).

Other accounts of the osmoregulatory system are in species descriptions. Especially notable are the papers of Cooper (1920) and particularly of Hunter (1927, 1929a, 1930) whose comprehensive monograph contains many details on the systems of 13 species. In his description of *G. catostomi*, later shown to be based on a mixed infection of *G. catostomi*, *G. laruei* and *H. nodulosa* (Mackiewicz 1965b). Cooper (1920) described and figured an amoeboid cell suspended by pseudopodia in a vesicle as the functional part of the excretory system. He suggested that perhaps Will (1893) had mistaken some of these amoeboid cells for certain nerve cells. Will (1893: Fig. 15, NZ_2 cells) did indeed describe a "Ganglienzellen" that had a nucleus surrounded by a clear area, as did Cooper's excretory cell, but in other respects they were similar to nerve cells in staining reaction and histological structure; none were associated with canals. Because Cooper's description was based on a mixture of three species it is difficult to determine precisely which one contained these amoeboid cells. Describing them as "renal corpuscles," Hunter (1930) reported them again from *G. catostomi*, and for the first time, from *C. singularis* (Hunter 1927, 1930). Yet his redescription too is also based in part on *H. nodulosa*; however, supporting details (e.g., citing fewer canals than in *H. nodulosa*) indicates that *G. catostomi* contains the renal corpuscles. The osmoregulatory system of this species is already well developed in the procercoid (Calentine 1967).

Thus, in the cortical parenchyma of the body there is an ascending system of small interconnected longitudinal canals and a similar system of larger descending canals; both canals are often paired and, according to Pintner (1881), may be joined to each other. The ascending system is joined by smaller tubules that terminate in flame cells. Anteriorly in the neck region these ascending ducts pass into the medullary parenchyma, fuse, and usually form a pair of large tubules that enter the scolex, eventually joining the descending system. This latter system is wholly cortical, usually forming an anastomosing net in the scolex, a specific number of interconnected longitudinal canals in the body, and terminating posteriorly at the excretory bladder. Of 37 species having sufficient details of the excretory system, 28 have between 8 and 12 descending canals, four have six, two have between 14 and 18, and three have no definite number in the body region. Longitudinal orientation of ducts is lacking in some species, *e.g.*, *H. nodulosa* (Calentine 1967). As the number of canals varies with position in the cestode, the least variable count might be the number that directly empties into the excretory bladder. A generally similar system, but lacking collecting stems and apparently composed of a single system of longitudinal canals was described for *Nippotaenia chaenogskii* by Yamaguti (1939) and Wardle and McLeod (1952).

How the tegument-lined bladder functions to discharge its contents is not known; earlier authors (d'Udekem 1855; Steudener 1877; Pintner 1881; Leuckart 1886) indicate that it is a pulsating organ, later ones (Cooper 1920; Hunter 1930), that it is nonpulsating. Further observations on living material and more careful study of the musculature of the bladder, with attention to the possible presence of a sphincter near the excretory pore, would help to resolve this dispute.

It seems probable that the protonephridial system of caryophyllids functions in the same manner as in other flatworms. Hunter (1930), however, has suggested that the tubules also might aid in producing scolex movements. His suggestion is based on the fact that he found no tubules in the relatively immobile scolex of *C. singularis,* while many were found in the motile scolexes of other species. An alternate explanation for Hunter's interesting observation could be that the number of tubules is directly correlated with the level of metabolic activity, being more numerous in a motile scolex. On the other hand, I have observed the descending canals in the body of *G. laruei* to abruptly contract, thus suggesting an active rather than passive role, one that does not exclude influencing body and scolex movements. According to Wardle and McLeod (1952) body movements tend to fill and empty the canals.

Flame cells are known from *C. laticeps* (Schultz 1852; Pintner 1881), *C. brachycollis* (Janiszewska 1953), *L. parvulus* (Furtado 1963), *M. ingens* (Hunter 1930), *A. sieboldi* (Mrázek 1898; Wiśniewski 1930), *A. iowensis* (Calentine 1962), and *G. catostomi* (personal observation) while "renal corpuscles" are known from *G. catostomi* (Cooper 1920; Hunter 1930) and *C. singularis* (Hunter 1930). Nothing is known of these "renal corpuscles" which bear a striking resemblance to the myoblasts of Janiszewska (1954: Fig. 4). Whether both types of cells can occur in the same individual, what the pattern of distribution is for each type, and what their relationship is to the ascending and descending systems are points that need further elaboration.

G. *Parenchyma and Calcareous Corpuscles*

The only detailed descriptions of the parenchyma are those for *Archigetes* spp. by Wiśniewski (1930) and *C. laticeps* by Will (1893).

Calcareous corpuscles are a conspicuous element of the larval and adult stages of most cestodes (von Brand 1966). Nevertheless, their status in the Caryophyllidea is difficult to appraise because they are seldom mentioned in descriptions. They are recorded as absent in *Archigetes, Caryophyllaeus* (Leuckart 1878a), *G. catostomi* (Cooper 1920), *B. bancrofti* (Johnston 1924) and from the caryophyllideans as a group (Woodland 1923; Subramaniam 1939); but present in *C. mutabilis* (= *C. laticeps*) (Zschokke 1884; Schneider 1884). This reviewer is unable to find any mention of them in the detailed anatomical and histological studies of Will (1893) on *C. laticeps,* of Wiśniewski (1930) on *Archigetes* spp., or in the developmental studies on *Archigetes* and other genera by Calentine (1962, 1964, 1965, 1967), Calentine *et al.,* (1961, 1967), Kennedy (1965a,b), and Kulakovskaya (1962a,b). I have never observed them in any species, yet Mr. R. Mankes, working in our laboratory, has found inclusions in gravid *G. laruei* that appear to be calcareous corpuscles because they stain with alizarin red and sodium rhodizonate. Use of these stains on larval and mature stages of other caryophyllideans should do much to clarify the status of these corpuscles. One should note that they have been described for *Spathebothrium* (Yamaguti 1934) and *Cyathocephalus* (Wiśniewski 1932). Although Schneider (1884) reported them from the cestodarians *Gyrocotyle* and *Amphilina,* von Brand *et al.* (1969) were unable to find any.

H. *Anomalies*

Anomalies in the Caryophllidea are rare (Janiszewska 1954). Some that have been recorded are: postovarian vitellaria in the cercomere of *A. brachyurus* (Mrázek 1908); absence of postovarian vitellaria in *C. laticeps* (Janiszewska 1954) and *G. laruei* (Mackiewicz 1965a); postovarian vitellaria in *M. hunteri* (Mackiewicz 1963b); testis posterior to the ovary in *A. huronensis* (Jones and Mackiewicz 1969); fusion of posterior lobes of ovary in *G. laruei* (Mackiewicz 1965a); shortened posterior ovarian lobe in *I. hexacotyle* (Mackiewicz 1968b) and isolated vitelline follicles in the neck of *G. catostomi* (Mackiewicz 1965b). Others, whose status is unclear, include absence of postovarian vitellaria in *Biacetabulum* sp. and their presence in a *Monobothrium* sp. (personal observations). In the latter two instances, the samples are so small that it is not known if the "anomalies" are, in fact, just part of the normal morphology of undescribed species. Of interest is the fact that no anomalies involving the scolex or duplication of reproductive organs (ovary or cirrus, for example) have been reported. The practice of describing new species on small samples and the lack of critical morphometric studies on large samples from various hosts may account for our lack of data on anomalies. But having observed many thousands of specimens representing many species, I have been struck by the apparent lack of anomalies, a condition that may reflect a high degree of genetic stability in the group.

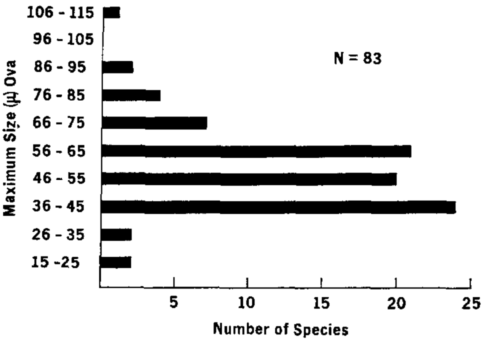


FIG. 72. Distribution of species with respect to the maximum size of eggs.

I. *Egg*

The egg is most like that of *D. latum* and other pseudophyllean cestodes, *i.e.,* thin-shelled and operculate (Figs. 25 and 74–76). There is great variation in size with a range of 17 × 11 μ (*L. fossilisi:* Gupta 1961) to "about" 111 × 80 μ (*L. tanganyikae:* Baylis 1928): most eggs, however, are between 35 and 65 μ long (Fig. 72). In addition, considerable intraspecific variation in egg size has been shown for some species; for example, 335 eggs from *G. catostomi* from five widely scattered areas in the United States had a range in length of 57–90 μ (Mackiewicz 1965b). There are, however, no critical studies that have attempted to correlate egg size with host, worm length, or geographical distribution. Within the egg is a single ovum and several vitelline cells that number from 3 to 5 (*B. macrocephalum;* McCrae 1962) to 8–11 (*H. nodulosa;* Mackiewicz and McCrae 1962).

There is much confusion regarding the presence of an operculum (Figs 25 and 76). Early illustrations of van Beneden (1858, 1870) do not picture one, nor is an operculum mentioned by von Siebold (1837). Some more recent descriptions explicitly state that one is absent from the eggs of *C.*

terebrans, *G. laruei*, and *H. paratarius* (Hunter 1930) and *C. batrachii*, *P. indica*, and *P. clariae* (Gupta 1961). Joyeux and Baer (1961) indicate incorrectly that the eggs of *Caryophyllaeus* and *Archigetes* are nonoperculate. On the other hand, an operculum is described for the eggs of *A. brachyurus* (Mrázek 1908), *Archigetes* sp. (Motomura 1928; Wiśniewski 1930), *C. laticeps* (Nybelin 1922; Sekutowich 1934; Kulakovskaya 1962b), *B. bancrofti* (Johnston 1924), to mention only a few. Unfortunately, many descriptions omit any reference to an operculum, yet as early as 1910, Lühe characterized the family Caryophyllaeidae as having operculate eggs.

Part of this confusion stems from the practice of describing and measuring eggs *in utero*. Regardless of species, I have found it very difficult to detect an operculum on eggs *in utero*. Indeed, even with the best optical equipment it is difficult to see because of its inconspicuous nature and small size, that varies as follows: 10 μ, *Archigetes* sp. (Motomura 1928); 9–11 μ. *G. laruei* (personal observation); 12 μ, *H. nodulosa*, *M. hunteri* (Mackiewicz and McCrae 1962; Mackiewicz 1963b); and 14–16 μ, *E. ptychocheila* (Mackiewicz 1970a) and *G. catostomi* (Mackiewicz 1965b). Good illustrations of operculate eggs include those of Kulmatycki (1924), Wiśniewski (1930), Sekutowicz (1934), Calentine (1964), and Mackiewicz (1968b). There is often a small boss at the anopercular end (Fig. 25). Though usually smooth, the shell may be pitted (*B. macrocephalum:* Calentine 1965a), rough (*I. hexacotyle:* Mackiewicz 1968b), or with small spines or processes (*B. bancrofti:* Johnston 1924; *W. accuminata:* Woodland 1923: *D. penetrans:* Bovien 1926; and *K. iowensis:* Calentine and Ulmer 1961). According to Gupta (1961) the nonoperculate eggs of *L. fossilisi* have a polar filament; this observation needs corroboration. In the instance of *K. iowensis* the spines may be 3 μ in length (Calentine and Ulmer 1961) and, according to Löser (1965), are formed from secretions in the uterine glands, being attached to the eggs as they pass distally down the uterus.

Methods of collecting and culturing eggs and infecting oligochaetes can be found in Calentine and Ulmer (1961). Nothing is known of the weight or volume of eggs of different species nor the number produced by a single worm in a given time period.

IV. Vitellogenesis and Eggshell Formation

Vitellogenesis was initially described in *Archigetes* spp. by Wiśniewski (1930) who noted the progressive appearance of refractile globules (eggshell precursors) in the cytoplasm and the vacuolation of the nucleus. This vacuolation (Figs. 74 and 84A) had earlier been noted by Mrázek (1898) in *Archigetes* and in *C. laticeps* by Ortner-Schönbach (1913) and Mueller (1914), and later in the same species and *K. iowensis* by Löser (1965). More recently Mackiewicz (1969a) demonstrated by histochemical means that vitellogenesis in *C. laticeps* and *C. fennica* is characterized by an increase in cell size, vacuolation of the nucleus with displacement of the nucleolus, and synthesis of protein globules in the cytoplasm of the cell. He further noted that there was an apparent decrease in the DNA in the nucleus and an increase in RNA in the cytoplasm as protein synthesis is initiated, and that the nuclear vacuole is strongly PAS positive before but not after saliva digestion. It would appear that the contents of the nuclear vacuole, presumably glycogen, serve as an energy source for the developing embryo. Vitelline cells having vacuolated nuclei (Fig. 74) are known for 18 genera and 37 species of caryophyllids, thus suggesting that it may be characteristic for the whole group (Mackiewicz 1968a). Such nuclei have not been described from any other cestodes.

Eggshell formation in caryophyllids was first studied in *C. laticeps* by Mueller (1914) who correctly identified the globules of the vitelline cells as precursors of the eggshell. This association was further corroborated by Wiśniewski (1930) in his work with *Archigetes* spp. Without giving any details Kennedy (1965c) stated in an abstract that the shell of *A. limnodrili* was a quinone-tanned protein. More recently Mackiewicz (1968a) demonstrated that eggshell formation in *C. laticeps* and *C. fennica* was basically similar to that reported by Smyth (1951, 1956) for *D. latum* and *Schistocephalus,* namely, that shell precursors in the form of phenolic compounds (vitelline globules) are synthesized in the vitelline follicles and, in the presence of polyphenol oxidase, are oxidized to a quinone which becomes tanned to form the sclerotin of the eggshell.

V. Cytology and Gametogenesis

Cytological information is available for three species: *Archigetes* sp., *H. nodulosa,* and *A. huronensis.* Working with "*A. appendiculatus* Ratzel" from oligochaetes collected near Tokyo, Motomura (1929) observed a diploid number of 18 in the embryo, the chromosomes being less than 4 μ in length and of unequal size. While there are serious doubts concerning the species of tapeworm Motomura used (Mackiewicz and Jones 1969), its progenetic nature clearly indicated *Archigetes* was involved. In a more detailed study Mackiewicz and Jones (1969) found that *H. nodulosa* (Figs. 11 and 45) from *C. commersoni* in Virginia and Tennessee had a diploid number of 14 in vitelline and spermatogonial cells, with three pairs of metacentrics ("V's," two long and one short pair), three pairs of short acrocentrics ("rods"), and one pair of long submetacentrics ("J's"). At mitotic metaphase the largest chromosomes were 6–8 μ, the shortest 2.5–3 μ, long. Studying *A. huronensis* from *C. carpio* in Tennessee, Jones and Mackiewicz (1969) discovered that this species was a triploid with 24 chromosomes, each set containing one large and three small metacentrics, two large and one small acrocentric, and one "minute." Analysis of meiosis in spermatogenesis clearly showed that only a few functional sperm were produced thus indicating that *A. huronesis* reproduced parthenogenetically. According to Coil (1970) the dioecious tapeworm *Gyrocoelia* (Cyclophllidea) also reproduces parthenogenetically. Possible origins of this unusual condition and their evolutionary significance in caryophyllideans are discussed in some detail by Jones and Mackiewicz (1969).

Little is known of gametogenesis in caryophyllidean cestodes; the few reports concern spermatogenesis primarily (Jones and Mackiewicz 1969; Mackiewicz and Jones 1969; Motomura 1929). The most detailed study of spermatogenesis is that of Jones and Mackiewicz (1969) on the parthenogenetic species *A. huronensis* (Figs. 20 and 57). Two meiotic divisions, both abnormal, were observed. In the first, 16 meiotic first metaphases were observed rather frequently in a follicle; the absence of many metaphase II, anaphase II, or telophase II indicated that the second division was rapid. Results of both divisions produced only pycnotic, malformed, and scanty spermatozoa; fully formed "normal" sperm were almost absent from testes ducts. No sperm were found in 530 eggs of *A. huronensis* stained by the Feulgen method. Less is known about gametogenesis in *H. nodulosa* in which Mackiewicz and Jones (1969) found that spermatogenesis resulted in normal sperm being formed after two meiotic divisions. Nothing is known of sperm morphology.

The only reference to oögenesis appears to be that of Motomura (1929) who found in *Archigetes* sp. that (p. 113) "... the oöcyte shows an ordinary type of maturation division and receives only one spermatozoan, the sperm nucleus from which remains nearly unchanged till the formation of the female pronucleus." Only two polar bodies were accounted for by Motomura (1929).

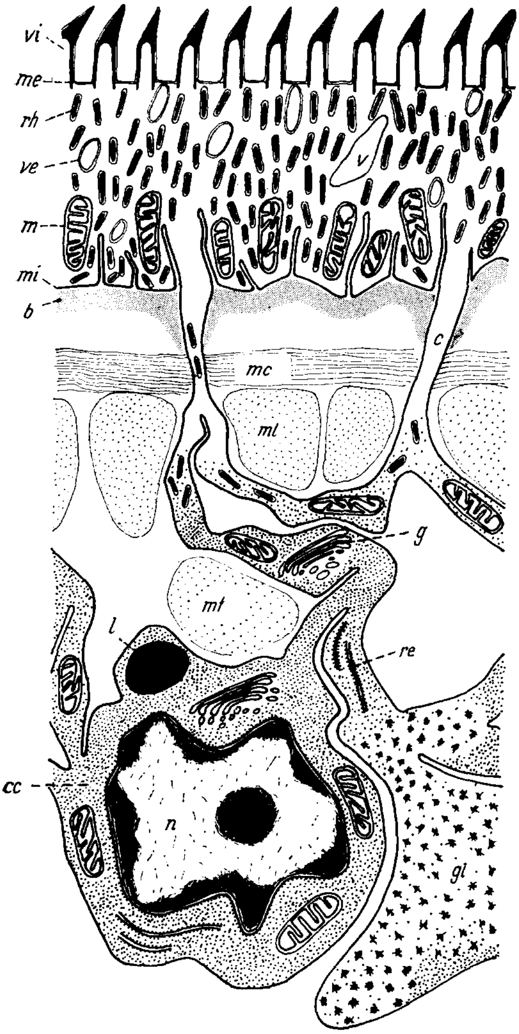


FIG. 73. Ultrastructure of the tegument and associated structures of *Caryophyllaeus laticeps*. Abbreviations: b, basal membrane; c, connection canal; cc, cellular body of subcuticular cell; g, golgi zone; gl, glycogen zone; l, lipid inclusion; m, mitochrondrion; mc, circular muscles; me, external plasma membrane; mi, internal plasma membrane; ml, longitudinal muscles; n, nucleus; rh, rhabdiform organelle; v, vacuole; ve, vesicle; and vi, microvillae (after Béguin 1966: Fig. 10; by permission of author and publisher).

VI. Histochemistry

Histochemical observations, except for those mentioned under vitellogenesis and eggshell formation, are confined chiefly to glycogen, and less so to lipid, distribution. The presence of glycogen in the "Faserzellenstränge" of *C. laticeps* was first noted by Ortner-Schönbach (1913) and later confirmed in the same species and in *C. fennica* by Mackiewicz (1968a). Ginetsinskaya and Uspenskaya (1965) found that glycogen was primarily concentrated in the medullary parenchyma of *C. laticeps* (from *A. brama*) with the highest concentration in the posterior part of the body surrounding the sex glands, which lacked glycogen. Compared with *Triaenophorus nodulosus* (from *Esox lucius*) *C. laticeps* had less glycogen and almost a complete absence of "excreted fat," conditions they attributed to a greater use of aerobic metabolic processes. The greater availability of oxygen to *C. laticeps* than to *T. nodulosus* was associated with the air-swallowing capacities of the host and the anterior placement of the parasite where free atmospheric oxygen was said to be available. Unfortunately, these conclusions are chiefly theoretical with no support from actual oxygen tension measurements near the parasites or considerations of the role of parasite activity and host diet to carbohydrate metabolism.

VII. Ultrastructure

Ultrastructure studies have been confined to the cuticle (tegument) of *C. laticeps* (Fig. 73) and *Caryophyllaeides fennica* (Béguin 1966a,b); no significant differences were found between these two species. Short microvilli (microtriches), having a pointed electron-dense apex, cover the surface of the cuticle; there are 16 microvilli per sq. micron in *C. laticeps*, 25 in *C. fennica*. Three organelles are found in the cuticle of *Caryophyllaeus;* (a) mitochondria, chiefly in the basal portion and perpendicular to the basal membrane, (b) rhabdomorphous organites, numerous and throughout the cuticle but generally oriented perpendicularly to the surface and, (c) vesicles of various sizes, thought to represent pinocytotic vesicles. Vacuoles occur infrequently. Beneath the basal membrane are subcutaneous cells differentiated into a basophilic portion that communicates with the cuticle via a "canal de connection" which, according to Béguin (1966a), contains rhabdomorphous organites. A comparative analysis of the structure and analogous function of the cuticle of *Caryophyllaeus* and *Anomotaenia* (Cyclophyllidea) to the intestinal epithelium of the mouse and *Ascaris* is included in Béguin's work. The tegument of caryophyllids is, therefore, basically similar to that of other cestodes.

VIII. EARLY DEVELOPMENT

A. *Embryology*

The only detailed study of cleavage and early development of any caryophyllid is that of Motomura (1929). Utilizing *Archigetes* sp., in which the eggs embryonated *in utero,* he found that the first cleavage yielded two almost equal blastomeres but that the later divisions are unequal and asynchronous. Because the blastomeres became indistinguishable from each other by the six-cell stage and he could no longer recognize cell boundaries, Motomura distinguished the blastomeres on the basis of size and staining characteristics of their nuclei. He thus designated cells (micromeres) containing a "micronucleus" as forming (Fig. 25) the nonciliated "mantel" (terminology of Schauinsland 1885; "embryophore" of Rybicka 1966, and others) while those (macromeres) containing a "macronucleus" formed the body of the oncosphere. At the seven- and eight-cell stage, a single micromere (the smallest), indistinguishable from polar bodies, was transformed from the nucleus of a micromere. According to Rybicka (1966), who regards the other micromeres as mesomeres, this smallest micromere is in fact a true micromere that arose from further unequal division of a macromere. Subsequent histogenesis was not followed in detail hence little is known about onchoblast and myoblast activity. Wiśniewski (1930) was able to distinguish two types of cells that formed the body proper of the larva of *Archigetes* sp.; other cells that were not part of the body but whose origin was not clarified were associated with the nonciliated "Embryonalhüllen." The six hooks appear by Day 5 to 13 in *K. iowensis* (Calentine and Ulmer 1961), Day 7 to 10 in *C. laticeps* (Sekutowicz 1934) and by Day 11 in *I. folius* (Fredrickson and Ulmer 1967).

That embryonation time varies with species and external conditions is readily apparent from Table I. Some interesting variations include the eggs of *K. sinensis* that can embryonate and complete development after ingestion by the tubificid (Kulakovskaya 1964a) and those of *A. sieboldi* whose development is said to be little influenced by differences in temperature, being about 40 days under winter and summer conditions (Wiśniewski 1930). Except for *Archigetes* in which embryonation is usually completed *in utero,* or at least begun *in utero* and finished after they are released (Wiśniewski 1930; Kennedy 1965a), the eggs of most other caryophyllids are unembryonated when shed. Some exceptions are *Djombangia* (Bovien 1926) and *Wenyonia* spp. (Woodland 1923) in which embryonated eggs have been found in the uterus. I have observed developing onchospheres in the uterine eggs of *Hunterella* and *Biacetabulum* sp., thus suggesting that there is a greater variation when embryonation starts than hitherto suspected.

B. *Oncosphere*

Oncospheres vary in size with respect to species (Table I). They are characterized by a nonciliated membrane, six hooks, and a pair of granular cells beneath the median pair (largest) hooks, and correspond to the "infective egg" type of oncosphere of Ja-

TABLE I

Embryonation Time and Oncosphere Size of Caryophyllideans

Species	Time in days (temperature, C)	Size (μ)	References
A. iowensis	14, *in utero* ("room temp")	14–21 × 32–42	Calentine 1964
A. limnodrili	20 (ca. 14)		Kennedy 1965a
A. sieboldi	ca. 40[a]		Wiśniewski 1930
	ca. 16 (18–24)		Calentine and Delong 1966
Archigetes sp.		62, smallest	Motomura 1929
A. huronensis	7–10	ca. 32 (from illustration)	Anthony 1958
B. infrequens	14-15 (18–22)	18–21 × 35–46	Calentine 1965
B. macrocephalum	14 (18–22)	18–21 × 35–42	Calentine 1965
C. laticeps	14	40–65	Sekutowicz 1934
G. confusus	ca. 15 (18–24)	14–18 × 25–32	Calentine and Williams 1967
G. catostomi	19 (18–22)	21–25 × 35–49	Calentine 1967; Calentine and Fredrickson 1965
H. nodulosa	14 (18–22)		Calentine 1967
I. folius	"month"	ca. 23 (from illustration)	Fredrickson and Ulmer 1967
I. longus	21 ("room temp")	ca. 37 (from illustration)	Fredrickson and Ulmer 1967
K. iowensis	15 ("room temp")	24 × 42	Calentine and Ulmer 1961
K. sinensis	30–32		Kulakovskaya 1962b
M. ingens	22–25 (18–22)		Calentine 1967
M. hunteri	18 (18–22)	21–14 × 42–49	Calentine 1967
M. ulmeri	ca. 22 (18–22)	18–25 × 42–49	Calentine and Mackiewicz 1966
W. longicauda		14.6 × 25.6	Woodland 1937

[a] Summer and winter conditions.

recka (1970). Cilia have never been reported on any caryophyllid oncosphere (Figs. 76 and 77) although on theoretical grounds a free-swimming larva might be expected from an operculate egg. A study of the ultrastructure of the oncosphere membrane would do much to establish whether cilia are indeed absent or occur as vestiges. That six hooks are present in the oncospheres of *Archigetes* or *Caryophyllaeus* had been known from the early reports of Leuckart (1878b, 1886), Braun (1894), and Lankester (1901); still earlier Ratzel (1868) had observed six hooks in the cercomere of *C. laticeps*. The central pair are longer, 11 μ in *Archigetes* sp. (Wiśniewski 1930), 12 μ in *K. iowensis* (Calentine and Ulmer 1961), and 13 μ in *Archigetes* sp. (Motomura 1929) than the two lateral pairs, 8 μ in *Archigetes* sp. (Motomura 1929) and 9 μ in *K. iowensis* (Calentine and Ulmer 1961). Two large granular cells are shown near the median hooks of *Archigetes* sp. (Wiśniewski 1930: Fig. 5, Mzh; copied by Olsen 1967), *C. laticeps* (Sekutowicz 1934: Fig. 5), *C. fimbriceps* (Kulakovskaya 1962b: Fig. 1), *K. iowensis* (Calentine and Ulmer 1961: Fig. 14), and *A. iowensis* (Calentine 1964: Fig. 4). In the oncosphere of *I. longus* and *I. folius* only a single one has been figured by Fredrickson and Ulmer (1967: Figs. 3 and 13). Within the egg the larva of *Archigetes* sp. shows an "active" motion (Motomura 1929), that of *C. laticeps* is slow and difficult to observe (Sekutowicz 1934), while *K. iowensis* moves slowly but shows some rapid elongation and contraction movements (Calentine and

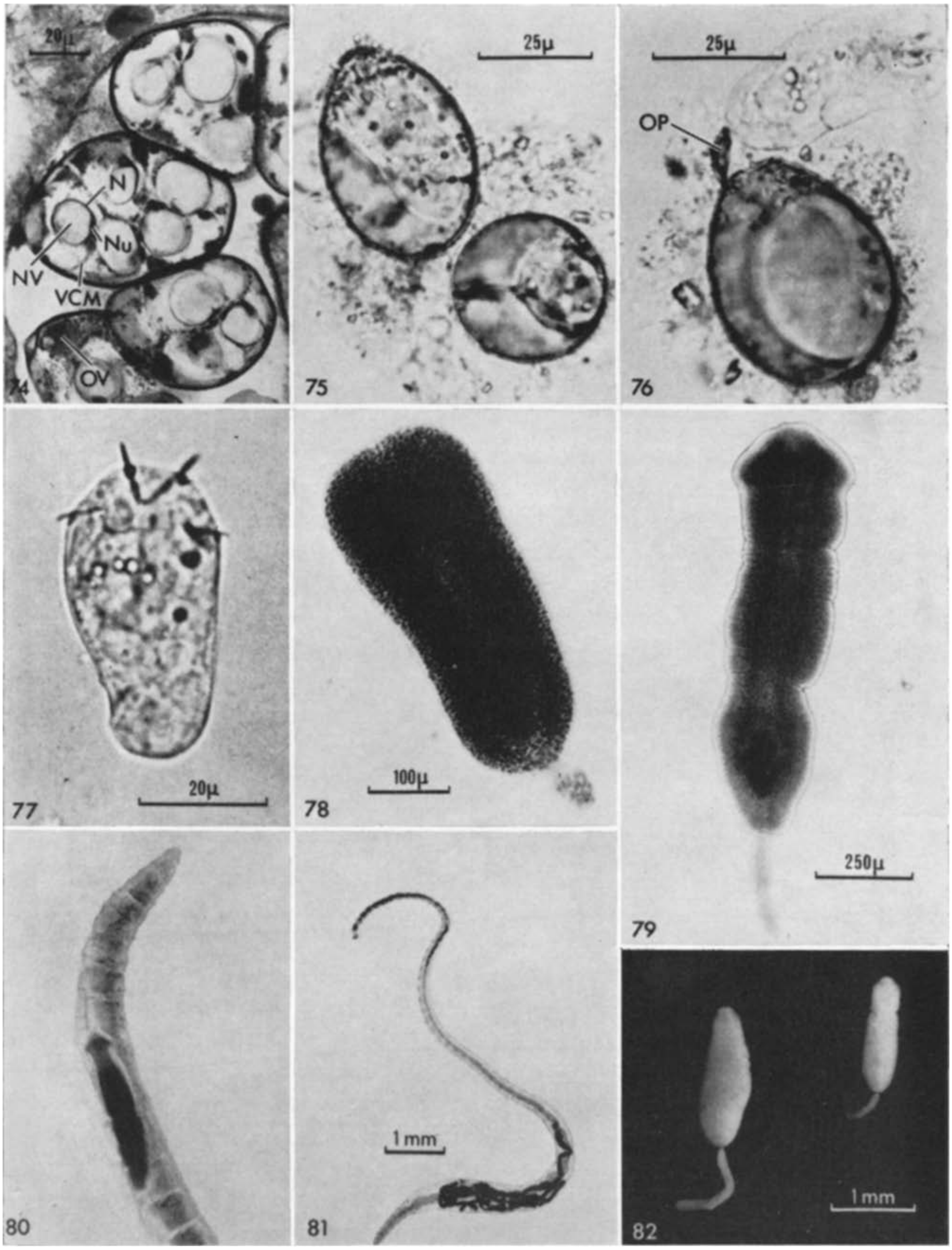


FIG. 74–82. Caryophyllid development. 74. Eggs of *G. catostomi*, *in situ* (methacrylate section); N, nucleus; Nu, nucleolus; NV, nuclear vacuole; OV, ovum; and VCM, vitelline cell membrane. 75. Eggs of *B. infrequens*, each containing an oncosphere. 76. Oncosphere of *B. infrequens*, released by slight pressure on egg, OP, operculum. 77. Newly hatched oncosphere of *B. infrequens*; note absence of cilia. 78. Larva of *B. macrocephalum* from experimental infection of *T. templetoni*, 45 days old (carmine stain). 79. Procercoid of B. *biloculoides*, from seminal vesicle of experimental infection of *L. hoffmeisteri*; fully developed; note vagina, uterus, and ovary anlagen (carmine stain). 80. *A. huronensis in situ* in *L. hoffmeisteri* (carmine stain). 81. *B. macrocephalum* in experimental infection of T. *templetoni* (carmine stain). 82. *A. sieboldi* from coelom of tubificid; note the disc on the scolex; cercomere has been damaged on smaller specimen (courtesy of J. Janiszewska and C. Kennedy) Figs. 75–77, 80 enlarged from Kodachrome pictures taken by R. Calentine; Figs. 78, 79, 81 from slides prepared by R. Calentine).

Ulmer 1961). Out of the egg, however, it is capable of strong stretching and contracting movements (Wiśniewski 1930). There appears to be no information regarding the presence of flame cells or calcareous corpuscles.

Viability also varies with species. At 5–10 C oncospheres of *G. catostomi* are still viable at 217 days (Calentine 1967), of *M. ulmeri* for 120 days but not 206 (Calentine and Mackiewicz 1966), of *B. infrequens* for at least 215 days and *B. macrocephalum* for 230 days but not 300 (Calentine 1965). At room temperature or under other conditions (unspecified) oncospheres of *A. iowensis* live for 80 days (Calentine 1964), of *A. limnodrili* for 2 months (Kennedy 1965a), of *K. sinensis* for 3 months (Kulakovskaya 1962b), and of *C. laticeps* for 3 months (Sekutowicz 1934).

C. *Hatching*

Eggs hatch only in the intestine of oligochaetes. After subjecting embryonated eggs of *A. limnodrili* to different conditions of light, pH, osmotic pressure, and to a variety of enzyme solutions (proteinases, lipases, amylase, and hyaluronidase) Kennedy (1965c:18P) concluded that hatching is "...not brought about by activity of the oncosphere, increased hydrostatic pressure within the egg or simple enzymatic digestion of the opercular seal. It appears to be a result of mechanical pressure probably aided by enzymic digestion."

IX. Life Cycles

There have been numerous attempts to elucidate the life cycle of caryophyllid tapeworms (Table II), but the only ones that have succeeded in going from one egg stage through to another have been with *Archigetes*. From the experimental work of Wiśniewski (1930), Calentine (1964), or Kennedy (1965a) there is absolutely no doubt that species of *Archigetes* can complete their cycle in oligochaete annelids and that on occasion can also infect fish. Repeated attempts to infect fish with *Archigetes*, however, have failed although Kulakovskaya (1962a) appears to have succeeded in doing so; regrettably there are no details of her experiments. The fact that *A. sieboldi* was recovered up to 12 but not 24 hr later in fish (Table II) prompted Nybelin (1962) to regard fish as an accidental host, thus refuting Szidat's (1937a) claim that *Archigetes* was the annelid stage, *Biacetabulum* the vertebrate stage. There seems little doubt, however, that fish can indeed enter into the cycle of some *Archigetes* cycles, *e.g.*, *A. iowensis* (Calentine 1964; Fig. 83), *A. sieboldi* (Calentine and DeLong 1966) and *A. limnodrili* (Yamaguti 1934). There is some experimental evidence indicating that the vertebrate and oligochaete cycles of at least one *Archigetes* sp. (*A. iowensis*) represent two separate physiological strains. After finding that 80% of procercoids in fish were gravid as compared to 3.2% in oligochaetes and conducting numerous feeding experiments Calentine concluded (1964: 457), "Experimental results suggest that perhaps only those procercoids derived from eggs of progenetic larvae are capable of producing eggs within the intermediate host." The general failure to infect fish with *Archigetes* species may thus be in part because procercoids representing physiological strains from oligochaete cycles were used rather than those from oligochaete-fish cycles. The relationship of the progenetic, coelom-dwelling stages of *Archigetes* in oligochaetes to the intestinal stages in fish has yet to be clarified despite the careful experiments on *Archigetes* life cycles by Calentine (1962, 1965), Kennedy (1965b), and Nybelin (1962).

Maturation times to the gravid stage of different species of *Archigetes* in *L. hoffmeisteri* are: *A. iowensis*: 70 and 100 days at room temperature (Calentine 1964); *A. limnodrili*: 140 days at approximately 14 C (Kennedy 1965a); and *A. sieboldi*: 60–70

TABLE II

Experimental Caryophyllid Life Cycles Involving Fish Hosts

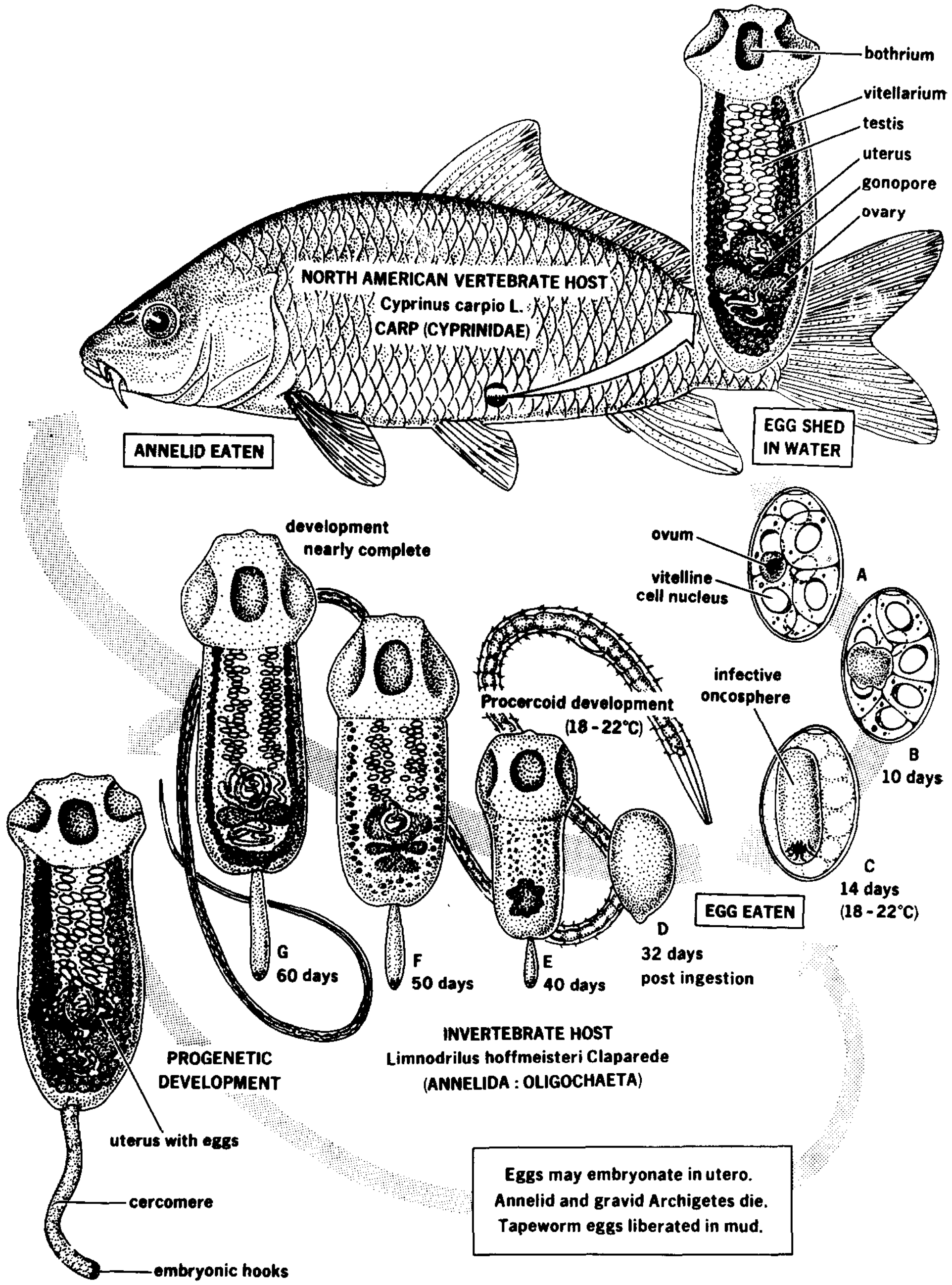
Cestode	Oligochaete	Fish	Results	References
A. appendiculatus	*T. tubifex*[a]	*T. tinca*	Infected 10 days later	Kulakovskaya 1962a
A. iowensis	*L. hoffmeisteri*[a]	*C. commersoni*, *C. carpio*, *C. auratus*, *P. promelas*, *P. notatus*	All negative 24 hr later	Calentine 1964
	L. hoffmeisteri[b] (119 days old)	*C. carpio*	Negative 24 hr later	
A. sieboldi	*L. hoffmeisteri*[a]	*C. carassius*	Negative	Wiśniewski 1930
	Limnodrilus sp.[a]	13 *P. phoxinus*	Two had cestodes 3 and 6 hr later; others negative 12–24 hr later	Nybelin 1962
		C. carpio	Negative 24 hr later	
		I. idus	Negative 24 hr later	
		T. tinca	Three worms present 12 hr later	
		T. tinca	Negative 24 hr later	
		A. brama	Negative 24 hr later	
	L. hoffmeisteri[a]	*C. carpio*	Dead cestode after 24 hr	Calentine and DeLong 1966
B. macrocephalum	*T. templetoni*[b] (62 days old)	*C. commersoni*	Attached to gut 20 hr later	Calentine 1965
C. laticeps	*P. barbatus*[a]	*L. leuciscus*	Infected 4–16 days later	Kennedy and Walker 1969
G. catostomi	*L. hoffmeisteri*[b]	*C. commersoni*	Not successful (no details given)	McCrae 1961
G. oligorchis	*L. hoffmeisteri*	*C. commersoni*	Not successful (no details given)	McCrae 1961
H. nodulosa	*L. hoffmeisteri*	*C. commersoni*	Not successful (no details given)	McCrea 1961

[a] Naturally infected.

[b] Experimentally infected.

days under summer conditions and 160–170 days under winter conditions (Wiśniewski 1930), and 120 days at 18–24 C (Calentine and Delong 1966). Progenetic species appear to produce two generations per year (Kulakovskaya 1964a). This is certainly true for *A. sieboldi* (Wiśniewski 1930) and possibly for *A. limnodrili*, judging from Kennedy's (1965a) data.

Although it is generally accepted that fish become infected by eating oligochaetes harboring procercoids, no one has experimentally infected laboratory-reared fish and recovered gravid worms with fertile eggs. So abundant and overwhelming is the circumstantial evidence for such a cycle (see Akhmetova 1966; Ivasik 1952; Kennedy 1969b; Sekutowicz 1934 and others) that it is difficult not to accept such a cycle as the true one. Where there has been limited success, that is, recovery of cestodes after experimental feeding (Table II) it was not made clear whether the cestodes were growing or merely being maintained in the fish. The presence of cestodes after experimental feeding does not in itself prove that fish are



Eggs may embryonate in utero.
Annelid and gravid Archigetes die.
Tapeworm eggs liberated in mud.

FIG. 83. Life cycle of *Archigetes iowensis*; based on data from Calentine (1964). Cestode stages from Calentine (1964; used by permission of author and publisher) except for A and B which have been modified from the same paper.

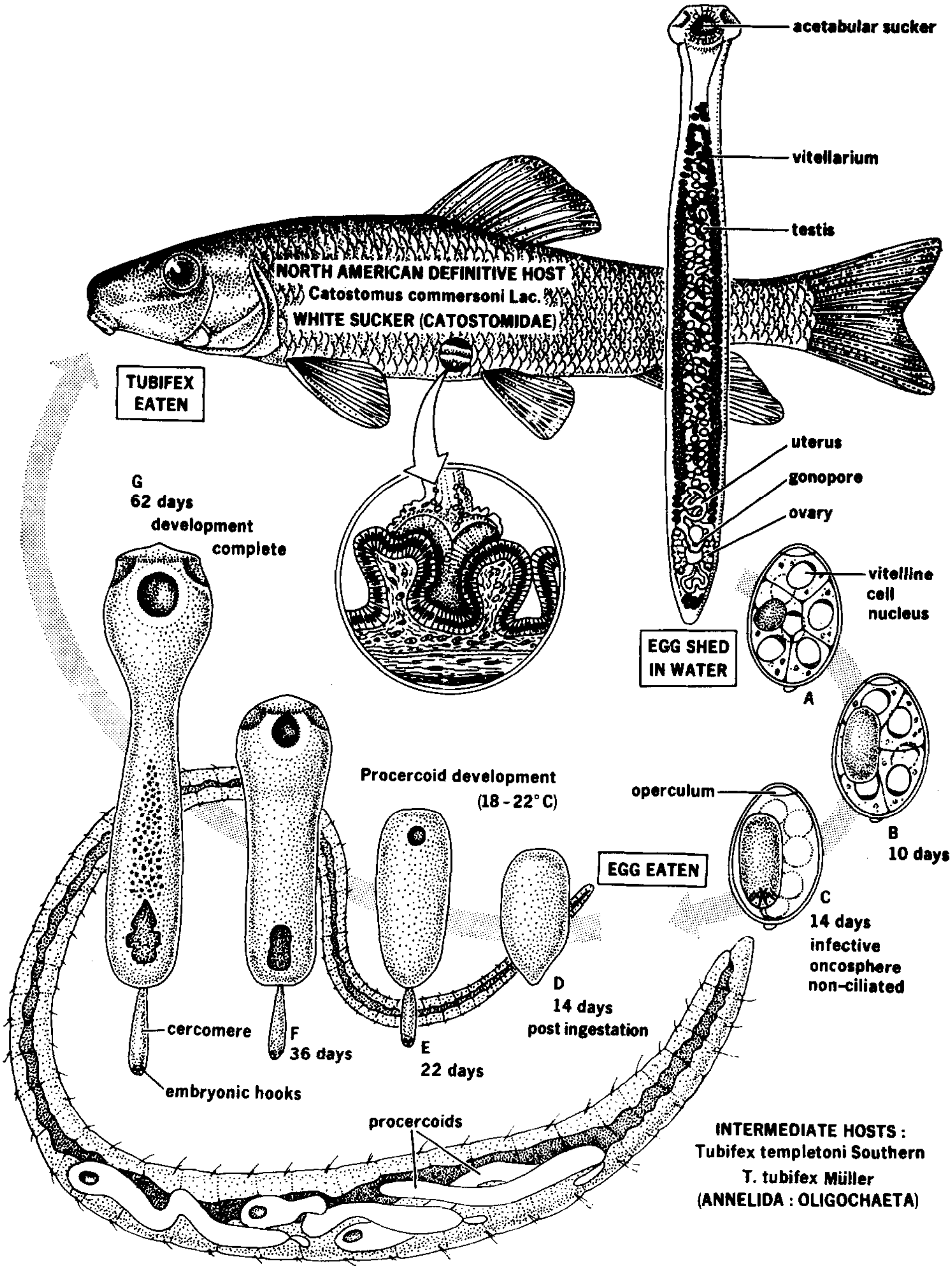


FIG. 84. Life cycle of *Biacetabulum macrocephalum*; based on data from Calentine (1965). Cestode stages, and infected annelid, from Calentine (1965; used by permission of author and publisher) except for scolex insert and A and B which have been modified from same paper; mature cestode is a composite drawing with scolex from McCrae (1962: Fig. 1) and body from type slide, USNM No. 39440. *T. templetoni* has recently been transferred to the genus *Illyodrilus*.

suitable or even normal hosts as Nybelin (1962) revealed in his experiments with *A. sieboldi*. Furthermore, all fish used in experiments apparently came from ponds or streams and hence could have been previously infected. Although Calentine and Delong (1966) found gravid *A. sieboldi* in tubificids and fish (carp), experimental feeding of infected tubificids to fish were unsuccessful. Hence, the published illustrations of cycles involving fish hosts (Kulakovskaya 1964a; Olsen 1967; and the present paper, Figs. 83 and 84) are largely based on circumstantial evidence. Unequivocal experimental proof for such cycles still appears to be lacking.

There seems little doubt, however, that oligochaetes are the primary intermediate hosts for caryophyllids because their procercoids have not been found in any other organisms. Long ago Hunter (1930) suggested that perhaps copepods might be part of the cycle but in the absence of controlled feeding experiments there is no evidence to support this view. More recently Musselius *et al.* (1963) suggested that other benthos or plankton can also serve as intermediate hosts (none was specified) when it was found that fish became infected in ponds that had few oligochaetes. After unsuccessful attempts to infect tubificids with oncospheres of *I. longus*, Fredrickson and Ulmer (1967) suggested that perhaps another intermediate host, other than a tubificid, might be involved in that cycle. But in one of the few studies in which a large number of different invertebrates were examined for larval stages of helminths, caryophyllid procercoids were found only in oligochaetes (Wiśniewski 1958). It has recently been suggested that possibly a paratenic host may be involved in the cycle of *E. ptychocheila* whose host is primarily carnivorous, apparently feeding little on tubificids (Mackiewicz 1970a). Until there is evidence to the contrary, oligochaetes appear to be the only invertebrate involved in caryophyllid life cycles.

While Mrázek (1916) thought that a ciliated larva was present and that it could possibly penetrate the oligochaete all current evidence indicates that the egg bearing the nonciliated oncosphere must be eaten to be infective.

In summary, three broad types of cycles can be recognized (Kulakovskaya 1962b). The first (progenetic type) is exemplified by *Archigetes* spp. in which the procercoid may become progenetic in the annelid without a vertebrate (fish) entering the cycle (Fig. 83). Examples include: *A. sieboldi* (Poland: Wiśniewski 1930; Iowa, USA: Calentine and DeLong 1966), *A. limnodrili* (Great Britain: Kennedy 1965a) and *A. iowensis* (Iowa, USA: Calentine 1962). *A. sieboldi* and *A. iowensis* (in Iowa) may mature in fish. That these forms are indeed neotenic larvae is evidenced by the presence of a cuticular covering over the common gonopore (Fig. 97) and of a cercomere, important characters absent from all caryophyllids found in fish (Calentine 1962).

A second (interrupted type) is that exemplified by *Caryophyllaeus* spp. in which the larva may grow to a large size and achieve considerable morphological development but still require a vertebrate in order to attain sexual maturity.

The third type of cycle (complete type), exemplified by *K. sinensis* and many other forms, is that in which the procercoid develops only to the infective stage corresponding to stage one of the interrupted type and requires a vertebrate for continued growth and eventual sexual maturity (Fig. 84). Regardless of the developmental type, the pattern of initial development is essentially the same, namely, oncospheres hatch in the intestine of the annelid, enter the coelom through the intestinal wall, and grow to the procercoid stage either in the coelom (Fig. 98) or seminal vesicle, occasionally in both regions. The period spent in the annelid, number of generations per year, role of fish host in the cycle, and maturation time in fish host as well as other aspects of the biology of life cycles are all highly variable depending upon the type of cycle involved. Hence, if *Archigetes* is eaten by a fish before becoming progenetic, it may lose its cercomere and mature in a fish, thus assuming an interrupted-type cycle (Fig. 83); or *C. laticeps* may be eaten as a young procercoid thus completing its development in the fish and assuming a complete-type cycle. It is, therefore, difficult to make generalizations regarding procercoid development.

X. Biology in Annelid Host

A. *Annelid Hosts*

All known natural or experimental intermediate hosts, or definitive hosts in the case of progenetic *Archigetes* spp., are oligochaete annelids (Table III). Some other tubificids that Kennedy (1965a) reported as not infected with caryophyllids are: *Aulodrilus pluriseta* (Piquet), *Euilyodrilus bavaricus* (Oschmann), *Rhyacodrilus coccineus* (Vejdovsky), and *Tubifex ignotus* (Stolc).

B. *Procercoid Development and Morphology*

Most information on larval development in the annelid comes from the series of excellent studies, chiefly experimental, of Calentine (1964, 1965, 1967), Calentine and Mackiewicz (1966), Calentine and Ulmer (1961), Calentine and Williams (1967), Calentine *et al.* (1970), Kennedy (1965a, 1969b), Kulakovskaya (1962a, b, 1964a), Sekutowicz (1934), and Wiśniewski (1930), dealing with the genera *Archigetes, Biacetabulum, Glaridacris, Hunterella, Khawia,* and *Monobothrium.*

Development

According to Sekutowicz (1934) procercoid development of *C. laticeps* can be divided into two stages: the first from oncosphere to an infective stage of 1.5–2 mm having a scolex, cercomere, and the rudiments of reproductive organs; the second (only if the larval cestode is not ingested by a fish) where the larva remains infective but growth continues to as much as 20 mm (including cercomere) with the female system becoming well developed. The first stage may take 6 months, the second 2 years, based on growth estimates. This alternate two-stage type of development, deduced from naturally infected tubificids, appears to be characteristic for only *Caryophyllaeus*, not being found either in any other palearctic genus (Kulakovskaya 1962b), or in any nearctic one, judging from the aforementioned experimental studies of Calentine. There is circumstantial evidence, however, that a two-stage type of development may occur in the cycle of the nearctic species *G. laruei.*

A more specific analysis of developmental stages has been made by Kennedy (1965a). He recognized five stages of development of *A. limnodrili:* Stage I, absence of a cercomere; Stage II, presence of cercomere and genital rudiments; Stage III, presence of bothria and full complement of reproductive organs; Stage IV, (adult) commencement of egg production; and Stage V, eggs occupying the greater part of the body. Despite the fact that there is much overlap in the size ranges for each stage, the Kennedy Stage System has great utility in evaluating development of progenetic species as well as prospective *in vitro* culture results. Perhaps modifications would be necessary when considering nonprogenetic species, such as *Caryophyllaeus*, in which stage one of Sekutowicz corresponds to Kennedy Stage I and II, and stage two to part of Kennedy Stage III. In any event the Kennedy System is an important step in the systematic evaluation of growth, so necessary if one is to make comprehensive and comparative *in vivo* and *in vitro* studies of caryophyllideans. Progress along these lines has already been made for some other cestodes (see Smyth 1969, Chapters 9 and 10).

Developmental time usually varies with temperature and annelid species (Table

TABLE III

Oligochaete Hosts[a] *(Annelida) of the Caryophyllidea*

Oligochaete and cestode(s)	Region	Type of infection[b]	References
Aulodrilus piqueti Kowalevski			
G. catostomi	USA	E	Calentine *et al.* 1970
M. ingens	USA	E, U	Calentine *et al.* 1970
Branchiura sowerbyi Beddard			
B. biloculoides	USA	E, U	Calentine et al. 1970
B. infrequens	USA	E[c]	Calentine et al. 1970
G. catostomi	USA	E, U	Calentine and Frederickson 1965
G. confusa	USA	E[c]	Calentine *et al.* 1970
K. iowensis	USA	E, U	Calentine 1967
M. hunteri	USA	E, U	Calentine *et al.* 1970
M. ingens	USA	E[c]	Calentine *et al.* 1970
M. ulmeri	USA	E, U	Calentine *et al.* 1970
Dero digitata (Müller)			
B. infrequens	USA	E, U	Calentine *et al.* 1970
G. catostomi	USA	E, U	
G. confusa	USA	E	Calentine and Williams 1967; Calentine *et al.* 1970
Dero limosa Leidy			
G. catostomi	USA	E, U	Calentine and Fredrickson 1965
K. iowensis	USA	E, U	Calentine 1967
S. wardi	USA	E, U	Calentine 1967
Euilyodrilus hammoniensis (Michaelson)			
A. limnodrili	Britain	E, U	Kennedy 1965a
Euilyodrilus moldaviensis (Vejdovsky and Mrázek)			
A. limnodrili	Britain	E, U	Kennedy 1965a
Ilyodrilus hammoniensis (Michaelsen)			
Caryophyllaeus sp.	Demnark	N	Berg 1948
K. sinensis	Ukraine	N	Kulakovskaya 1962b; Kulakovskaya *et al.* 1965
Limnodrilus sp.			
A. brachyurus	Czechoslovakia, USSR and Britain	N	Kennedy 1965b
A. cryptobothrius	Poland Denmark	N	Kennedy 1965b
A. limnodrili	Germany, USSR, Britain and Japan		Kennedy 1965b
A. sieboldi	Germany, France, Italy, Poland, Czechoslovakia, Denmark, Sweden, Finland, Britain, Ireland, USSR, USA, Brazil and South Africa	N	Kennedy 1965b
G. catostomi	USA	E	Calentine and Fredrickson 1965
G. limnodrili	Japan	N	Yamaguti 1934
S. wardi	USA	E, U	Calentine 1967

TABLE III—*Continued*

Oligochaete and cestode(s)	Region	Type of infection[b]	References
Limnodrilus aurostriatus (Southern)			
A. cryptobothrius	Denmark	N	Berg 1948
A. sieboldi	Denmark	N	Berg 1948; Kennedy and Chubb 1963
Limnodrilus cervix (Brinkhurst)			
A. limnodrili	Britain	N, E	Kennedy 1965a
Limnodrilus claparedeanus Ratzel			
A. appendiculatus Ratzel	Czechoslovakia	N	Mrázek 1898
A. appendiculatus (Mrázek) Janiszewska	USSR	N	Kulakovskaya 1961
A. limnodrili	Britain	N, E	Kennedy 1965a
B. appendiculatum (Szidat) Janiszewska	Ukraine	N	Kulakovskaya 1962a
G. brachyurus	Ukraine	N	Kulakovskaya 1962a
Limnodrilus goti Hatai			
A. appendiculatus (Ratzel)	Japan	N	Motomura 1928, 1929
Limnodrilus hoffmeisteri (Claparède)			
A. appendiculatus Mrázek	Britain	N	Brinkhurst *et al.* 1962
A. brachyurus	Czechoslovakia	N	Mrázek 1908
A. cryptobothrius	Poland	N	Wiśniewski 1928, 1930
A. iowensis	USA	N, E	Calentine 1962, 1964
A. limnodrili	Britain	N, E	Kennedy 1965a
Limnodrilus hoffmeisteri Claparède			
A. sieboldi	Poland	N, E	Wiśniewski 1930
	Brazil	N	Marcus 1948
	Poland	N	Janiszewska 1958
	USSR, Lithuania	N	Kulakovskaya 1961b
	Sweden	N	Nybelin 1962
	Britain	N	Brinkhurst *et al.* 1962
	USA	N, E	Calentine and DeLong 1966
B. biloculoides	USA	E	Calentine *et al.* 1970
B. infrequens	USA	E	Calentine *et al.* 1970
	USA	E, U	Calentine 1965
B. macrocephalum	USA	E, U	Calentine 1965; Calentine and Fredrickson 1965
C. brachycollis	Ukraine	N	Kulakovskaya 1962b
G. brachyurus	Ukraine	N	Kulakovskaya 1962a, b
G. catostomi	USA	E	Calentine *et al.* 1970; Calentine and Fredrickson 1965; Calentine 1967
G. confusa	USA	E, U	Calentine and Williams 1967; Calentine *et al.* 1970
H. nodulosa	USA	E	Calentine 1967; Calentine and Fredrickson 1965
K. sinensis	Ukraine	N	Kulakovskaya 1962b Kulakovskaya *et al.* 1965
K. iowensis	USA	E, U	Calentine 1967
M. hunteri	USA	E	Calentine 1967; Calentine and Fredrickson 1965; Calentine *et al.* 1970
M. ingens	USA	E	Calentine 1967; Calentine *et al.* 1970

TABLE III—*Continued*

Oligochaete and cestode(s)	Region	Type of infection[b]	References
M. ulmeri	USA	E	Calentine and Mackiewicz 1966; Calentine *et al.* 1970
S. wardi	USA	E, U	Calentine 1967
Undescribed species (= *B. biloculoides*)	USA	E	Calentine and Fredrickson 1965
Limnodrilus udekemianus Claparède			
A. limnodrili	Britain	N, E	Kennedy 1965a
A. sieboldi	Brazil	N	Marcus 1948
C. brachycollis	Poland	N	Janiszewska 1953
G. catostomi	USA	E[d]	Calentine 1967
	USA	N, E	McCrae 1961
G. oligorchis	USA	N, E	McCrae 1961
H. nodulosa	USA	N, E	McCrae 1961
K. sinensis	Ukraine	N	Kulakovskaya 1962b Kulakovskaya *et al.* 1965
Limnodrilus willeyi Nomura			
A. appendiculatus (Ratzel)	Japan	N	Motomura 1928, 1929
Nais communis Piquet			
B. infrequens	USA	E, U	Calentine *et al.* 1970
G. catostomi	USA	E, U	Calentine *et al.* 1970
G. confusa	USA	E[e]	Calentine and Williams 1967; Calentine *et al.* 1970
Nais proboscideae Müller			
Scolex[f]	Belgium(?)	N	d'Udekum 1855
Ophidonais serpentina (Muller)			
B. infrequens	USA	E, U	Calentine *et al.* 1970
Psammoryctes albicola (Michaelsen)			
C. fimbriceps	Ukraine	N, E	Kulakovskaya 1962b; Kulakovskaya *et al.* 1965
Psammoryctes barbatus (Grube)			
A. limnodrili	Britain	E, U	Kennedy 1965a
C. laticeps	Britain	N	Kennedy 1969a, b; Kennedy and Walker 1969
K. sinensis	Ukraine	N	Kulakovskaya *et al.* 1965
Peloscolex multisetosus (Smith)			
B. infrequens	USA	E	Calentine *et al.* 1970
G. catostomi	USA	E	Calentine *et al.* 1970
Saenuris rivulorum			
A. sieboldi	Germany	N	Leuckart 1878a; Gruber 1881
Stylaria lacustris (L.)			
G. catostomi	USA	E, U	Calentine *et al.* 1970
G. confusa	USA	E[e]	Calentine and Williams 1967; Calentine *et al.* 1970
Tubifex sp.			
C. mutabilis	Czechoslovakia	N	Mrázek 1901
Tubifex barbatus Grube			
C. laticeps	Poland	N	Sekutowicz 1934
Tubifex hattai Nomura			
A. appendiculatus (Ratzel)	Japan	N	Motomura 1928, 1929
Tubifex rivulorum Lam.			
Caryophyllaeus larva	Britain (?)	N	McIntosh 1872
C. appendiculatus Ratzel	Germany	N	Ratzel 1868
Scolex[g]	Belgium (?)	N	d'Udekem 1855

TABLE III—*Continued*

Oligochaete and cestode(s)	Region	Type of infection[b]	References
Tubifex templetoni Southern (= *Ilyodrilus*)			
B. infrequens	USA	E	Calentine 1965; Calentine *et al.* 1970
B. macrocephalum	USA	E	Calentine 1965; Calentine and Fredrickson 1965; Buchwald and Ulmer 1964
B. biloculoides	USA	E, U	Calentine *et al.* 1970
G. catostomi	USA	E	Calentine and Fredrickson 1965; Calentine *et al.* 1970; Calentine 1970
G. confusa	USA	E	Calentine and Williams 1967; Calentine *et al.* 1970
H. nodulosa	USA	E, U	Calentine 1967; Calentine and Fredrickson 1965
K. iowensis	USA	E, U	Calentine 1967
M. hunteri	USA	E, U	Calentine 1967; Calentine and Fredrickson 1965; Calentine *et al.* 1970
M. ulmeri	USA	E, U	Calentine *et al.* 1970
M. ingens	USA	E, U	Calentine 1967
		E	Calentine *et al.* 1970
S. wardi	USA	E, U	Calentine 1967
Undescribed species (= *B. biloculoides*)	USA	E, U	Calentine and Fredrickson 1965
Tubifex tubifex Müller			
A. appendiculatus Ratzel	Czechoslovakia	N	Mrázek 1898
A. sieboldi	Poland	N	Wiśniewski 1930; Janiszewska 1958
B. appendiculatum (Szidat) Janiszewska	Ukraine	N	Kulakovskaya 1962a
B. biloculoides	USA	E, U	Calentine *et al.* 1970
B. infrequens	USA	E	Calentine 1965; Calentine *et al.* 1970
B. macrocephalum	USA	E	Calentine 1965; Calentine and Fredrickson 1965
C. brachycollis	Ukraine	N	Kulakovskaya 1962b
C. fimbriceps	Ukraine	N	Kulakovskaya 1961b; Kulakovskaya *et al.* 1965
C. laticeps	Poland	N	Sekutowicz 1934
	Ukraine	N	Kulakovskaya 1962b
G. catostomi	USA	E	Calentine 1967; Calentine and Fredrickson 1965; Calentine *et al.* 1970
G. confusa	USA	E	Calentine *et al.* 1970
K. sinensis	Ukraine	N, E	Kulakovskaya 1962b; Kulakovskaya *et al.* 1965
M. hunteri	USA	E, U	Calentine *et al.* 1970
M. ingens	USA	E	Calentine *et al.* 1970
M. ulmeri	USA	E	Calentine *et al.* 1970

TABLE III—*Continued*

Oligochaete and cestode(s)	Region	Type of infection[b]	References
Uncinais uncinata Ørsted			
B. biloculoides	USA	E, U	Calentine *et al.* 1970
B. infrequens	USA	E, U	Calentine *et al.* 1970
G. catostomi	USA	E	Calentine *et al.* 1970
G. confusa	USA	E	Calentine and Williams 1967; Calentine *et al.* 1970
M. ingens	USA	E, U	Calentine *et al.* 1970
M. ulmeri	USA	E, U	Calentine *et al.* 1970

[a] See Brinkhurst and Jamieson (1971) for synonyms.
[b] Natural (N); Experimental-Successful (E); Experimental-Unsuccessful (E, U).
[c] Procercoid died before development was complete.
[d] Probably this host.
[e] Killed oligochaete.
[f] Probably *C. fennica* according to Nybelin (1922).
[g] *Caryophyllaeus* larva.

TABLE IV

Size of Infective Nonprogenetic Procercoids. Development is at 18–22 C Unless Otherwise Specified

Cestode	Annelid	Age (days)	*N*	Size (mm)		References
				Body	Cercomere	
B. macrocephalum	*Tubifex templetoni*	62	9	1–1.3	0.1–0.3	Calentine 1965
B. infrequens	*T. templetoni*	51	22	0.9–1.6	0.09–0.18	Calentine 1965
C. laticeps[a]	*Tubifex* sp.	ca. 180 ca. 730		1.5–2 18		Sekutowicz 1934
G. catostomi	*T. templetoni* or *Limnodrilus hoffmeisteri*	58–70		1–1.7	0.1–0.4	Calentine 1967
G. confusus	*T. templetoni* (?)	15–25	15	0.5–0.7	0.07–0.16	Calentine and Williams 1967
H. nodulosa	*L. hoffmeisteri*	46	20	0.7–1.2	0.5–1	Calentine 1967
K. sinensis[a]	*Limnodrilus* sp. *T. tubifex* *Iliodrilus hammoniensis*			1–1.5		Kulakovskaya 1962b
M. ingens	*L. hoffmeisteri*	45	8	1.7–2.5	0.1–0.3	Calentine 1967
M. hunteri	*L. hoffmeisteri*	50		0.7–1	0.8–1.2	Calentine 1967

[a] No temperature data.

IV). According to Wiśniewski (1930) *A. sieboldi* matures in 60–70 days in summer but requires 160–170 days in winter. Buchwall and Ulmer (1964) found that experimentally produced procercoids of *B. macrocephalum* in *T. templetoni* were small and did not attain full development even after 110 days at 6 C while at 22 C they were larger, had a cercomere, and scolex and reproductive fundaments after 24 days; at 33 C the larvae were small and showed neither cercomere nor scolex development at 35 days, when they died. On the other hand, the growth of neither *C. laticeps* nor its oligochaete host, *P. barbatus* bore any close relationship to temperature changes (Kennedy 1969b). Most European species overwinter in oligochaetes (Kulakovskaya 1964a).

Morphology

The infective procercoid (Fig. 93) is characterized by a cercomere containing the six hooks of the oncosphere, a scolex that does not invaginate and shows a high degree of differentiation that is characteristic of the particular genus and, except for an increase in size, is retained through to the sexually mature stage, and the rudiments of a single set of reproductive organs (Figs. 85–97). Considering descriptions and illustrations of the pseudophyllidean procercoids of *Diphyllobothrium* (Rosen 1918; Vogel 1930) *Triaenophorus, Abothrium,* (Rosen 1918), *Ligula* (Rosen 1919), *Cyathocephalus* (Wiśniewski 1932), and *Spirometra* (Mueller 1966) it is clear that they differ significantly from that of caryophyllids, sharing only the cercomere, a structure also found in other types of cestode larvae, *i.e.,* cysticercoid. Indeed, one wonders if the term "procercoid" ("Urcestoden" type larva of Goette, 1921) is applicable to such a caryophyllid larva if one accepts the definition of Freeman (1970) or of Wardle and McLeod (1952: 58), "The procercoid may be described as a solid-bodied larva in which the oncospheric hooks are retained and in which the future holdfast has not yet differentiated." To be sure, the procercoid of *Cyathocephalus* has a differentiated scolex but it also has primordia of multiple sets of reproductive organs. The preceding example as well as that of procercoids of caryophyllids dramatically illustrates what Voge (1969) has so eloquently presented as one of the primary difficulties in cestode taxonomy, namely, the lack of precise definitions for terms describing larvae and the indiscriminate use of the terms in current usage. Attempts to analyze this problem have recently been made by Jarecka (1970) and Freeman (1970). Until these difficulties are resolved, the term "procercoid" is herein used in its nonspecific, general sense.

The cercomere, whose histogenesis is discussed by Wiśniewski (1930) and Janiszewska (1954), begins as a small protuberance (Fig. 78) containing the hooks, enlarges, and eventually attaches to the body by a narrow stem that passes through the future excretory pore into the region of the excretory bladder (see Fig. 7, Mrázek 1897; Text Fig. O, Wiśniewski 1930; and text Fig. 1b, Markowski 1938). Illustrations of cercomere development of a number of species have been presented by Calentine (1964, 1965, 1967). Occasionally vitellaria are found in the cercomere (Mrázek 1908). In rare instances it can be found on the vertebrate phase of the cycle but then only in a degenerating condition (Markowski 1938). Not only is there no basis of fact for the opinion, attributed to Goette (1921) by Motomura (1929), that the cercomere of *Archiegetes* represents the asexual generation and the trunk the sexual one, but I am unable to verify that Goette ever expressed such an opinion.

Unlike the procercoids of *Diphyllobothrium, Ligula, Abothrium,* and *Eubothrium,* that have a conspicuous anterior funnel-like structure richly supplied by frontal glands, caryophyllid procercoids usually have a large scolex characteristic of a particular genus (Figs. 85–97; compare Figs. 37, 57, and 80). It is only in the plerocercoid and vertebrate-dwelling stage of the pseudophyllid genera mentioned above that the scolex of the adult appears. This developmental sequence is in marked constrast to that of the caryophyllid scolex which is formed while the metacestode is still in the invertebrate host; it thus does not require a vertebrate to initiate its formation. On occasion, however, it may form in the vertebrate host, particularly if the larva is in-

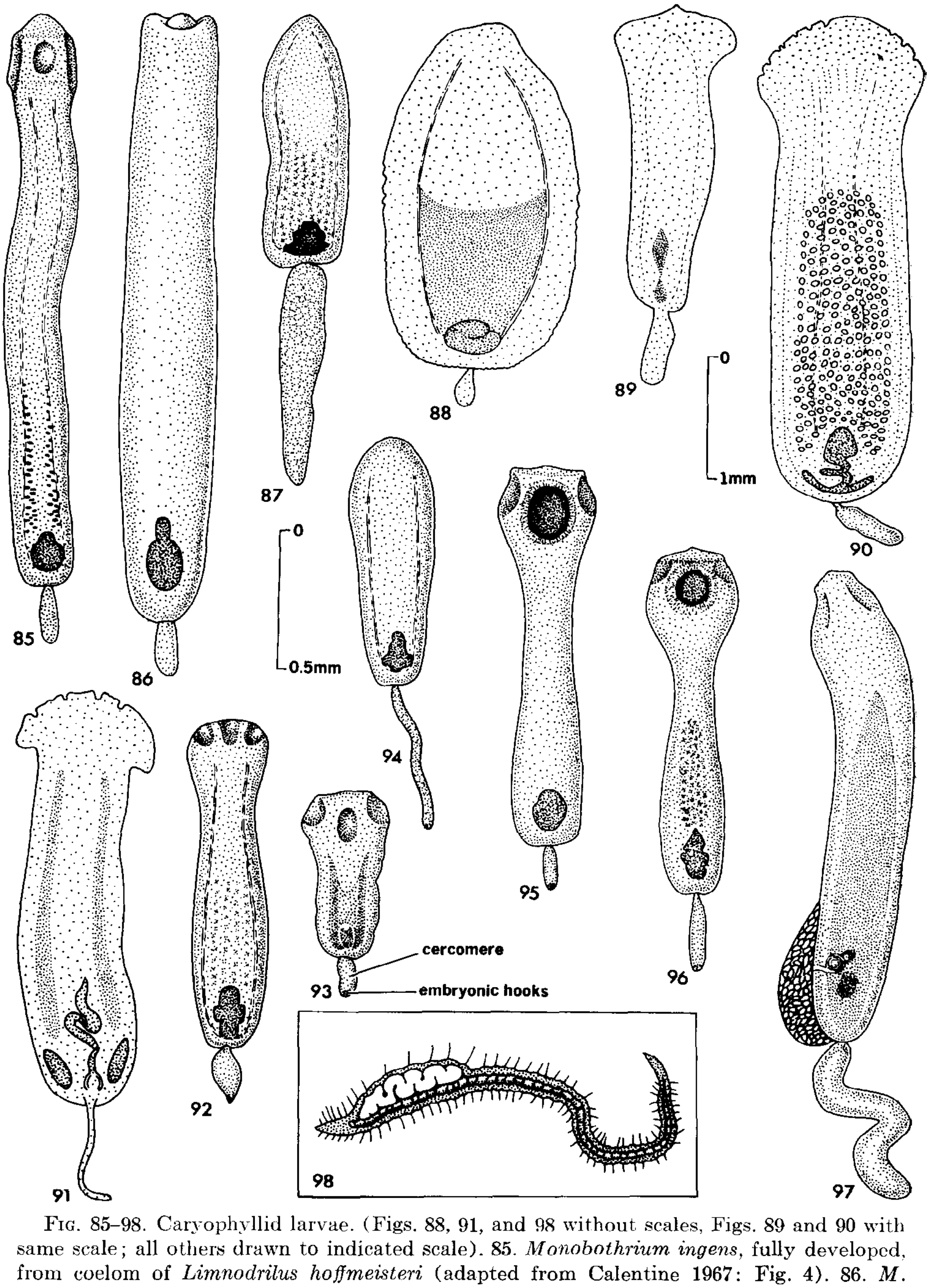


FIG. 85–98. Caryophyllid larvae. (Figs. 88, 91, and 98 without scales, Figs. 89 and 90 with same scale; all others drawn to indicated scale). 85. *Monobothrium ingens*, fully developed, from coelom of *Limnodrilus hoffmeisteri* (adapted from Calentine 1967: Fig. 4). 86. *M. ulmeri*, fully developed, 70 days, coelom of *L. hoffmeisteri* (after Calentine and Mackiewicz 1966: Fig. 6). 87. *M. hunteri*, fully developed, 50 days, coelom of *L. hoffmeisteri* (after Calentine 1967: Fig. 3). 88. *M. wageneri*, contracted, from *L. hammoniensis*. 89. *Caryophyllaeus brachycollis*, coelom of *L. udekemianus* (after Janiszewska 1953: Fig. 6). 90. *C. laticeps*, from *L. hoffmeisteri*. 91. *C. fimbriceps*, from Tubificidae (after Kulakovskaya 1962b: Fig. 4). 92. *Glaridacris catostomi* fully developed, coelom of Tubificidae (after Calentine 1967: Fig. 6). 93. *G. confusus*, 25 days, coelom of *Tubifex templetoni* (after Calentine and Williams 1967: Fig. 1). 94. *Hunterella nodulosa*, about 46 days old, from *L. hoffmeisteri* (after Calentine 1967: Fig. 5). 95. *Biacetabulum infrequens*, fully developed, 51 days, coelom of *T. templetoni* (after Calentine 1965: Fig. 11). 96. *B. macrocephalum*, fully developed, 62 days, coelom of *T. templetoni* (after Calentine 1965: Fig. 8). 97. *Archigetes sieboldi*, side view, seminal vesicle of *L. hoffmeisteri* (after Calentine and DeLong 1966: Fig. 8). 98. *Khawia sinensis in situ* in *T. tubifex* (after Kulakovskaya, 1962b: Fig. 3).

gested before the scolex normally has a chance to develop, as often is the case with *K. sinensis* (Kulakovskaya 1962b). This scolex is, therefore, not a transient, larval structure, but one that will function as the holdfast of the adult worm. Because of this relationship, one is usually able to ascertain some caryophyllid genera at a very early stage of development. Not only is there no basic change from the procercoid scolex to that from a sexually mature worm but there is also no basic change in body structure, except the loss of the cercomere. There is no evidence that any other part of the body (except the cercomere) is replaced or lost once the vertebrate host is attained, as is the case in the plerocercoid of *Spirometra* for example (Berntzen and Mueller 1964). Thus, once the cercomere is lost, development to the sexually mature stage is direct.

Associated with the scolex and body of procercoids are glands whose disposition, function, and even existence in many species is far from clear. Because they first become visible in the young larva they are discussed in this section. These glands have been described under various terms: "Frontaldrüsen" (Mrázek 1901; Wiśniewski 1930; Sekutowicz 1934), "Faserzellen" (Mrázek 1901), "Halszellen" (Wiśniewski 1930), "head glands" and "neck glands" (Janiszewska 1954), "gland cells" (Fotedar 1958), and "Faserzellenstränge" (Will 1893; Sekutowicz 1934). Two types have been described: frontal glands (Frontaldrüsen) that usually have ducts and occur only in the scolex, and neck cells or Faserzellenstränge that apparently lack ducts and extend from the neck down into the testicular field, often as far as the cirrus. Although detailed histological descriptions of the first type are given by Wiśniewski (1930) and of the second by Wiśniewski (1930) and Will (1893), the distinction between them is not clear.

Frontaldrüsen form a conspicuous part of the procercoids of pseudophyllidean cestodes (see plate I, Fig. 1 of Rosen 1918); they are less prominent in caryophyllid larvae. In *A. brachyurus* they appear as two groups whose ducts open to the center of the scolex disc (Mrázek, 1901: Fig. 4). Individual or fused ducts have been reported for *A. sieboldi* (Wiśniewski 1930) but in *C. brachyurus* it is not clear if a common duct is present (Janiszewska 1953). In some species frontal glands are weakly developed (*A. iowensis;* Calentine 1962) or absent (*W. virilis:* Kulmatycki 1924). Both Wiśniewski (1930) and Sekutowicz (1934) noted that they were more developed in the young *Caryophyllaeus* and less so or absent in older individuals.

Their function is postulated on the assumption that the frontal glands are homologous to those of pseudophyllidean procercoids or *Amphilina,* which probably secrete lytic enzymes enabling the organism to penetrate the gut wall and pass into the body cavity (Wiśniewski 1930). But since there is no evidence that caryophyllids pass through the intestinal wall, although *Djombangia* will perforate the serosa (Bovien 1926), nor is there any histochemical evidence for such a function, perhaps frontal glands may serve to assist in attachment (Hunter 1930; Szidat 1937b). I have found that they are less numerous in species having well-developed attachment organs (*Biacetabulum*) than those without (*Hunterella, Monobothrium*).

More is known of the histology and general nature of the Faserzellenstränge ("Halszellen" of Wiśniewski 1930; "gland cells," Fotedar 1958; Hunter 1930) because of their extensive development and widespread occurrence in many species. As Fig. 99 illustrates, they can easily be observed in the scolex of gravid *C. laticeps.* Originally described by Will (1893) from the scolex and body of *C. laticeps* they have been reported for most species although they have not been found in *A. cryptobothrius* (Wiśniewski 1930), *M. wageneri* (Janiszewska 1954), *M. chalmersius* (Woodland 1924), and *W. virilus* (Woodland 1923). According to Wiśniewski (1930) Faserzel-

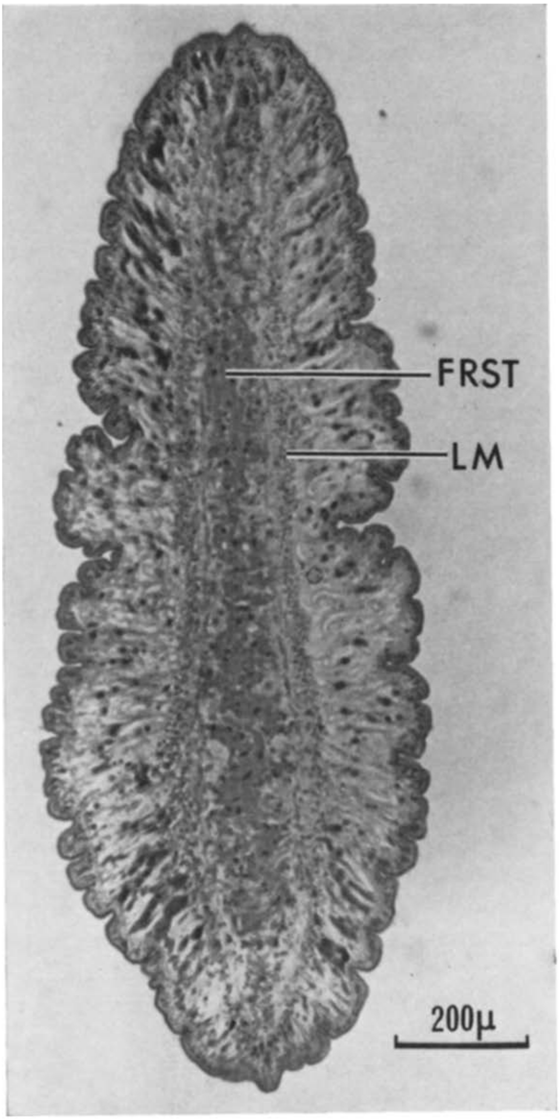


FIG. 99. Cross section of scolex of gravid *C. laticeps* illustrating the extent and position of the "Fraserzellenstränge," FRST and longitudinal muscles, LM (hematoxylin and eosin).

lenstränge are absent when the Frontaldrüsen are well developed, as in *A. cryptobothrius;* the same relationship also appears to be true with *W. virilis*. Unlike the frontal glands that are composed of individual cells in a dense mass, the Faserzellenstränge are fibrous or spindle-shaped with a granular and vacuolized cytoplasm (Wiśniewski 1930). In *C. brachyurus* they consist of two lateral and one median medullary band that runs the entire testicular field; in structure and staining reaction they resemble the uterine glands (Janiszewska 1954). Very fine glycogen granules have been found in the "Faserzellen" by Ortner-Schönback (1913), who used the Best's carmine technique, while Mackiewicz (1968a) reported that these cells and the frontal glands of *C. laticeps* and *C. fennica* were PAS positive after saliva digestion, as was Mehlis' gland. Further histochemical studies are obviously needed to clarify these conflicting results.

Theories concerning the origin and function of Faserzellenstränge are varied. Mrázek (1901) and Rosen (1918) both believed that they were remnants of a digestive system, an idea that has gained little support. Yamaguti (1934:6) considered them "...nothing but the complex of the longitudinal muscle fibers and the particularly condensed parenchymatous tissue of the medulla." But the most prevalent view appears to be that of Pintner (1906), namely, that these cells are homologous to the frontal glands; in fact, Wiśnewski (1930) considered them modified frontal glands. One can not deny the striking resemblance in distribution between the Frontaldrüsen of the scolex and body of plerocercoids of *Diphyllobothrium* spp. to that of caryophyllid Faserzellenstränge (Fig. 99; compare with Figs. 5 and 9 of Kuhlow, 1953). Nevertheless, Sekutowicz (1934) noted that the frontal glands were present in the larva of *C. laticeps* but that Faserzellenstränge appeared in the mature stages; he was unable to determine if the latter came from the former or were newly formed structures. If, indeed, the two structures are homologous, then does it follow that they would have similar functions? The distinctly different histological nature of the cells in question, the absence of any proof that the Faserzellenstränge are secretory in nature or that they are continuous with and functionally part of the frontal gland complex, as well as great differences in size, distribution, and occurrence of each gland strongly suggest that the respective functions of each structure could be quite different.

As far as is known only one set of reproductive organs occurs in caryophyllids, even in the larval stage. There are, however, some interesting variations as to the extent of their development in the procercoid that has a pronounced influence on subsequent protandric or protogynous development when in the vertebrate host. For example, if the procercoid of *C. laticeps* is eaten by a fish just when the gonad primordia are beginning to form, protandry results; on the other hand, if the procercoid has developed to a later stage and the gonad primordia are well developed, protogyny results (Sekutowicz 1934). But, considering that Sekutowicz was working with cestodes from *C. carpio* and *A. brama*, it is possible, as he was aware, that two cestode species (and hence two types of development) were involved, a fact that would raise serious questions concerning the validity of his conclusions. In support of them, Janiszewska (1954) found protandric and protogynous *C. laticeps* in *A. brama*, as well as those with both male and female systems at the same stage of development. And I have found *G. laruei* with distinct protogyny, although protandry appears to be the rule. If, indeed, the sequence of gonadial development is dependent on the stage reached when the larva is ingested, then this would be one other factor, crowding and age in host being possibly two others, that would influence size and maturation time in the vertebrate host. Surely this difficult question of protandrous and protogynous development in the same species must remain as one of the most obvious problems whose solution may depend on the experimental approach.

Other but less conspicuous structures are the ducts of the osmoregulatory system. Apparently their arrangement and number are established early as shown for example in *B. macrocephalum* (Calentine 1965), *G. catostomi* and *H. nodulosa* (Calentine 1967), and *A. sieboldi* (Calentine and DeLong 1966). Calcareous corpuscles, so conspicuous in the larvae of many tapeworms and often a prominent feature of the procercoids of *Diphyllobothrium*, *Abothrium*, *Ligula*, and *Eubothrium* (Rosen 1918, 1919), have not been reported from caryophyllid procercoids.

C. *Annelid–Procercoid Relationships*

Incidence and intensity data are available for both natural and experimental infections (Calentine 1964, 1965, 1967; Kennedy 1965a, 1969b; Kulakovskaya 1962b, 1964b). In natural habitats the incidence is invariably low, usually less than 3% and rarely above 15%; but under fish-farming conditions it may go as high as 50% (Kulakovskaya *et al.* 1965). According to Kulakovskaya (1962b) incidence is higher in ponds than in streams. Intensity is usually less than 10 larvae per host, occasionally as high as 20. Experimental infections have yielded higher incidence and intensity rates dependent on the species of cestode, annelid, and exposure time. For example, after 48 hr exposure to eggs of *G. catostomi* 38 of 50 *T. templetoni* became infected but only 25 of 50 *L. hoffmeisteri* did so (Calentine 1967); with *B. infrequens*, 34 of 50 *T. templetoni* became infected after only 24-hr exposure (Calentine 1965). Infections with as many as 55 *B. macrocephalum*, 25 *B. infrequens* (Calentine 1965), and 29 *K. sinensis* (Kulakovskaya 1962b) have been produced under experimental conditions; such heavily infected oligochaetes do not live long, however.

Other factors appear to influence incidence. At least with *G. catostomi* and *A. limnodrili* young annelids acquired infections more readily than did older, larger ones (Calentine 1967; Kennedy 1965a). That annelids do not develop immunity to subsequent infections is illustrated by the fact that *T. tubifex* already infected with *G. catostomi* became reinfected by the same species (Calentine 1967). Kennedy (1965a) and Sekutowicz (1934) both found tubificids with larvae in various stages of development thus suggesting that reinfection can also occur under natural conditions

Larvae occupy different locations in the annelid. Some, such as *G. catostomi, M. hunteri, M. ingens* (Calentine 1967), *C. laticeps, K. sinensis* (Kulakowskaya 1962b), occur in the coelom (Figs. 81 and 98); others, *A. iowensis* (Calentine 1964), *A. sieboldi* (Calentine 1966), *B. infrequens* (Calentine 1965), and *A. limnodrili* (Kennedy 1965a) occur in the seminal vesicle or testes sac; while still others, *B. macrocephalum* (Calentine 1965) and *H. nodulosa* (Calentine 1967), may occur in both regions, especially in heavy infections. In most species there is a migration from the site of oncosphere penetration to the seminal vesicles, coelom near the genital segments, or coelom between segments 9 and 37.

Annelid size also influences cestode development. Calentine (1967) found that, whereas procercoids of *G. catostomi* from four different species of annelids were indistinguishable, those in *L. hoffmeisteri* (largest host) averaged 1.2 mm in length by 46 days while those from *T. templetoni* (smallest host) averaged 0.9 mm at 63 days under the same experimental conditions. There was thus an inverse relationship between the development time and annelid size.

The effect of larvae on their annelid host is highly variable. Sterilization of the host may occur with *G. catostomi* (Calentine 1967), *B. infrequens* (Calentine 1965), *K. sinensis* (Kulakovskaya 1962b), and *C. laticeps* (Sekutowicz 1934) while *C. laticeps* merely depresses the growth rate and delays the breeding period of infected *P. barbatus* (Kennedy 1969b). In heavy infections, 5–10 larvae, host mortality is usually high (Kulakovskaya 1962b). But some species, such as *A. limnodrili* or *H. nodulosa*, cause little harm to the host (Kennedy 1965a; Calentine 1967); in the latter species host reproduction is not altered while in the former, the annelid body ruptured when the cestode became gravid. McCrae (1961) observed that *G. catostomi* and *H. nodulosa* caused loss of the posterior segments of *L. hoffmeisteri*. At the population level uninfected oligochaetes lived longer than infected ones (Calentine *et al.* 1970).

Quantitative data on the seasonal aspects of larval development and incidence in oligochaetes are available for *Archigetes* spp. (chiefly *A. sieboldi*) in Poland (Wiśniewski 1930) and for *C. laticeps* in Great Britain (Kennedy 1969b). A general treatment of the seasonal cycles of the larvae of *Archigetes, Caryophyllaeus,* and *Khawia* in western Ukraine is given by Kulakovskaya (1964a). Larval periodicity of five species in *Limnodrilus* in Iowa (USA) is presented by Calentine and Fredrickson (1965). Wiśniewski (1930) found that there was no seasonal cycle of *A. sieboldi* in *Limnodrilus* but that a steep peak of mature forms, almost 70%, occurred in July. *A. limnodrili* and *A. iowensis* also occur throughout the year in *Limnodrilus* (Kennedy 1965a; Calentine 1962); in the former species there is no seasonal maturation cycle (Kennedy 1965a). Kulakovskaya (1964a) noted that two generations of *A. appendiculatum* occurs within the annelid, June to October and December to May. She also found that *Caryophyllaeus* is present in the annelid from July to March and in the vertebrate from March to June while *Khawia* has the annelid cycle from August to March, the vertebrate cycle from November or March to August. In the most detailed study (Kennedy 1969b) the general incidence and intensity of larval *C. laticeps* infections was constant throughout the year in the River Avon, England. There was, however, a seasonal cycle in size structure within the population with the largest larvae occurring from January to June; in July a second generation was initiated, yet infective larvae (3 mm long) were present at all months except August. Kennedy (1969b) furthermore found that no particular size group of tubificids appeared particularly prone or immune to infection and that the annual cycle did not differ from place to place.

Host specificity of nonprogenetic annelid-parasite systems from the nearctic have recently been summarized by Calentine *et al.* (1970). After experimental infections with seven species of Caryophyllaeidae in six species of Tubificidae and five of Naididae, they concluded (p. 346), "Assuming that the taxonomic relationships of the cestodes studied are correct, there is little correlation between a tapeworm's generic status and the kinds of annelids which serve as its intermediate hosts." *Monobothrium* and *Biacetabulum*, whose interspecific relationships are far from clear (Mackiewicz 1963b, 1969), are two genera used to support this conclusion. In fact, these data on annelid infections provide life-cycle evidence that accentuates and supports the morphological differences between the nearctic *Monobothrium* spp. having loculi (Fig. 27b) and those without (Fig. 27c) and *Biacetabulum* spp. having a well-developed acetabular sucker (Fig. 31a) from those having only loculi (Fig. 31b). That there can indeed be host specificity in some species is shown by the fact that *A. limnodrili* is specific for a genus (*Limnodrilus*) but not for a particular species in the genus (Kennedy 1965a). In the Lytocestidae *K. sinensis* has a wider annelid host spectrum than does *C. fimbriceps* (Caryophyllaeidae; Kulakovskaya 1964b; Kulakovskaya *et al.* 1965). It would thus appear that host specificity in the annelid does occur, at least at the generic level, but that it is highly variable among the tapeworm species.

As Calentine *et al.* (1970) have found there are three factors that determine host specificity in the annelid. The major factor is whether or not cestode eggs hatch in the annelid's intestine; eggs did not hatch in 21 of 28 instances where annelids proved refractory to infection. A second factor was host intracoelomic reactions involving both cellular (phagocytic cells) and chemical responses. A third was related to the size of the annelid. In small oligochaetes of the family Naididae, procercoid growth of a number of caryophyllids usually ruptured the host's body causing death of the host. The small size of *Archigetes*, as compared to the large one of *Caryophyllaeus*, therefore, favors progenetic development in the annelid (Janiszewska 1954; Kulakovskaya 1964a); all progenetic species are usually less than 2 mm long and have bothria.

Once established the larva may live up to two years in the annelid, *e.g.*, *C. laticeps* (Sekutowicz 1934) and *A. iowensis* (Calentine 1964). Because it is difficult to maintain tubificids over an extended period of time experiments have usually been terminated after a few months. As a consequence actual survival times are not known for most species studied; however, periods of over 100 days are not uncommon, *e.g.*, 303 days for *G. catostomi*, 323 for *M. ingens*, 344 for *M. ulmeri* (Calentine *et al.* 1970), and 466 for *H. nodulosa* (Calentine 1967). Additional data on other species in various tubificid hosts can be found in the same paper. Calentine *et al.* (1970) found that (p. 349), "Termination of infection by host death was three times more common than was termination by death of the parasites within the annelid." Longevity in the intermediate host, unlike that in the vertebrate host, is thus a function of annelid life span.

Maturation of the metacestode from the procercoid to the plerocercoid-like stage requires, in all cases, some unknown stimulus in the fish. Although a variety of species have been reared experimentally in different oligochaetes for varying periods of time, procercoids have always retained the cercomere, even in the progenetic species.

XI. Biology in the Vertebrate Host

A. *Vertebrate Hosts*

Studies involving vertebrate hosts are usually limited to local or regional records or host–parasite checklists. Some of the more conspicuous examples are: Africa (Ogamba-Ongoma and Canaris 1967), Europe (Janiszewska 1954), France (Joyeux and Baer 1936), Germany (Lühe 1910), North America (Hoffman 1967; Mackiewicz 1961, 1970a), Switzerland (Fuhrmann 1926), USSR (Dubinina 1962; Kulakovskaya 1961), and the World (Hunter 1930; Mackiewicz 1959). A discussion of the phylogenetic relationships of the different groups of fishes and their caryophyllid cestodes is also presented by Janiszewska (1954); Mackiewicz (1970a) summarizes only the cyprinid hosts of the Capingentidae. Additional host records can be found in the Parasite–Subject catalogues of the Index-Catalogue of Medical and Veterinary Zoology (U.S. Department of Agriculture, 1966–1969).

Except for the Wisconsin (USA) record (Pearse 1924) of *G. catostomi* from the "mud puppy," *Necturus maculosus* Raf. (Amphibia: Proteidae), all others from vertebrates involve fish (Table V). Assuming the determination was accurate, then this unusual record may represent an accidental infection because the diet of *Necturus* includes aquatic oligochaetes and fish (Bishop 1941). Of historical interest is Rudolphi's (1819) report of von Olfer's account of *Caryophyllaeus* from the proventriculus of *"Mergi merganseris"* (= *Mergus merganser* L. Aves: Anatidae). Rudolphi did not accept this record, preferring to call it *"Vermes paradoxicum."*

Evaluation of the validity of many host records solely on the basis of literature reports is an impossible task. So numerous have been the changes in nomenclature and systematic treatment, that it is often difficult to determine accurately the identity of the original host. Furthermore, and most important, one cannot assume that the original cestode determinations are correct. While these considerations pertain especially to most pre-1930 records, they also apply to more recent ones. Indeed, as a result of reexamining many of the caryophyllids that formed the basis for North American literature records prior to 1960, I found that a high proportion of the published determinations were clearly in error. While it is beyond the scope of this review to reappraise critically all of the North American records, attempts to correct some of them have been already made (Hoffman 1967; Mackiewicz and McCrae 1962, 1965; Mackiewicz 1961, 1965b, 1969, 1970a). Because the problems discussed above are not unique to the evaluation of North American literature, a host–parasite checklist is not included in this review; instead, there is a list of hosts compiled from the literature (Table V). Though surely incomplete and possibly containing erroneous records, this list nevertheless serves to illustrate the broad, general host-spectrum of these cestodes.

The following important facts emerge from the data of Table V: 50% of the families, 87% of the orders, and 90% of the species are ostaryophysan, primary division freshwater fishes that probably lack a marine ancestry; 22% of all the families, 74% of the genera and species are Cypriniformes while 28% of families, 11% of genera, and 12% of species are Siluriformes; and 57% of all the genera and 50% of all the species are in the minnow family Cyprinidae, the largest family of freshwater fishes, while 13% of all the genera and 22% of the species are in the sucker family Catostomidae. Some of the more common hosts are shown in Figs. 100–106. That the Ostaryophysi are primitive teleosts is a well-accepted fact although some workers consider them at the very beginning of teleostean phylogeny (Hoedeman 1960) while others such as

TABLE V

Fish Hosts of the Caryophyllidea

Class Osteichthyes
Subclass Actinopterygii
Infraclass Teleostei

Division I[a]

Superorder Clupeomorpha
Order Clupeiformes
Suborder Clupeiodei
Family Clupeidae
Dorsoma cepedianum (LeSueur),[b] N[c]

Division II

Superorder Osteoglossomorpha
Order Moryiformes
Family Mormyridae
Mormyrus cashive L., E

Division III

Superorder Protacanthopterygii
Order Salmoniformes
Suborder Salmonoidei
Family Salmonidae
Salmo irideus Gibbons,[b] P.; *S. ischchan* Kessler,?[b] P
Suborder Esocoidei
Family Esocidae
Esox lucius L.,[b] P
Superorder Ostariophysi
Order Cypriniformes
Suborder Characoidei
Family Characidae
Alestes nurse (Rüppell), E
Suborder Cyprinoidei
Family Cyprinidae (Palearctic, except as indicated)
Abramis ballerus (L.), *A. brama* (L.), *A. sapa* (Pallas); *Acrocheilus alutaceus* Agassiz and Pickering, N; *Alburnus alburnus* (L.); *Alburnoides bipunctatus* (Bloch); *Aspius aspius* (Kessler); *Barbus barbus* (L.); *B. brachycephalus* Kessler; *B. ksibi* Boulenger; *B. longiceps* Cuvier and Valenciennes; *B. meridionalis* Risso; *B. setivimensis* Cuvier and Valenciennes; *B. tropidolepsi* Boulenger, E. *Blicca bjoerkina* (L.); *Carassis auratus* (L.); *C. carassius* (L.); *Chilogobio czerskii* Berg; *Chondrostoma nasus* (L.); *Ctenopharyngodon idella* (Valenciennes): *Cyprinus carpio* L., N; *Elopichthys bambusa* (Richardson); *Gilia atraria* (Girard), N; *Gobio gobio* (L.): *Hemibarbus maculatus* Bleeker; *Hybopsis biguttatus* (Kirtland), N; *Leuciscus cephalus* (L.) *L. idus* (L.), *L. leucisus* (L.); *Leucaspicus delineatus* (Heckel); *Mylocheilus caurinus* (Richardson), N; *Mylopharyngodon piceus* (Richardson): *Notropis bifranitus* (Cope), N. *N. deliciosus* (Cope), N. *N. rubellus* (Agassiz), N; *Notemigonus crysoleucus* (Raf.), N; *Oreinus sinatus* (Heckel), O; *Pelecus cultratus* (L.); *Phoxinus phoxinus* (L.); *Pimphaels notatus* (Raf.), N. *P. promelas* Raf., N; *Pseudaspius leptocephalus* (Pallas); *Pseudogobio esocinus* (Temminick and Schegel); *Ptychocheilus oregonense* (Richardson), N; *Rhodeus sericeus* (Bloch); *Richardsonius balteatus* (Cope), N; *Rutilus rutilus* (L.); *Scardinius erythrophthalmus* (L.); *Schizothorax intermedius* McClelland, O; *S. micropogon* Heckel, P; *Tinca tinca* (L.); *Varicorhinus capoeta* (Filippi); and *Vimba vimba* (L.)

TABLE V—*Continued*

Family Catostomidae (Nearctic)

Carpiodes carpio (Raf.), *C. cyprinus* (LeSueur), *C. velifer* (Raf.); *Catostomus ardens* Jordan and Gilbert, *C. catostomus* (Forster), *C. columbianus* (Eigenmann and Eigenmann), *C. commersoni* (Lacépède), *C. insignis* Baird and Girard, *C. macrocheilus* Girard, *C. occidentalis* Ayres, *C. tahoensis* Gill and Jordan. *Erimyzon oblongus* (LeSueur), *E. sucetta* (Lacépède): *Hypentelium nigricans* (LeSueur); *Ictiobus bubalus* (Raf.) *I. cyprinellus* (Valenciennes), *I. niger* (Raf.); *Minytrema melanops* (Raf.): *Moxostoma anisurum* (Raf.), *M. erythrurum* (Raf.), *M. macrolepidotum* (LeSueur); and *Pantosteus clarki* (Baird and Girard).

Family Cobitidae (Palearctic)

Cobitis taenia L. and *Misgurnus anguillicaudatus* (Cantor)

Order Siluriformes

Family Bagridae

Auchenoglanis occidentalis (Cuvier and Valenciennes), E; *Chrysichthys auratus* (Geoffrey), E; and *Macrones nigriceps* Cuvier and Valenciennes, O

Family Clariidae

Clarias anguillaris (L.), E; *C. batrachus* (L.), O; *C. fuscus* Cuvier, O; *C. lazera* Cuvier and Valenciennes, E and *C. mellandi* Boulenger, E

Family Heteropneustidae

Heteropneustes fossilis (Bloch), O

Family Mochokidae (Ethiopian)

Synodontis batensoda Rüppell, *S. clarias* (L.), *S. gambienses* Gunther, *S. membranaceus* (Geoffrey) and *S. schall* (Bloch-Schneider).

Family Plotosidae

Tandanus tandanus Mitchell, A

Superorder Paracanthopterygii

Order Gadiformes

Suborder Zoarcoidei

Family Zoarcidae

Zoarces viviparus L.[b], P, Marine

Superorder Acanthopterygii

Order Perciformes

Suborder Percoidei

Family Percidae

Acerina schraetser (L.),[?b] P and

Perca fluviatilus L.,[?b] P

Family Cichlidae

Parectodus sp., E

Suborder Gobioidei

Family Gobiidae

Gobius minutus Pallas,[b] P, Marine

Order Pleuronectiformes

Family Pleuronectidae

Pleuronectes flesus L.,[b] P, Marine

Summary: Superorders, 6; Orders, 8; Families, 18; Genera, 66; and Species, 104

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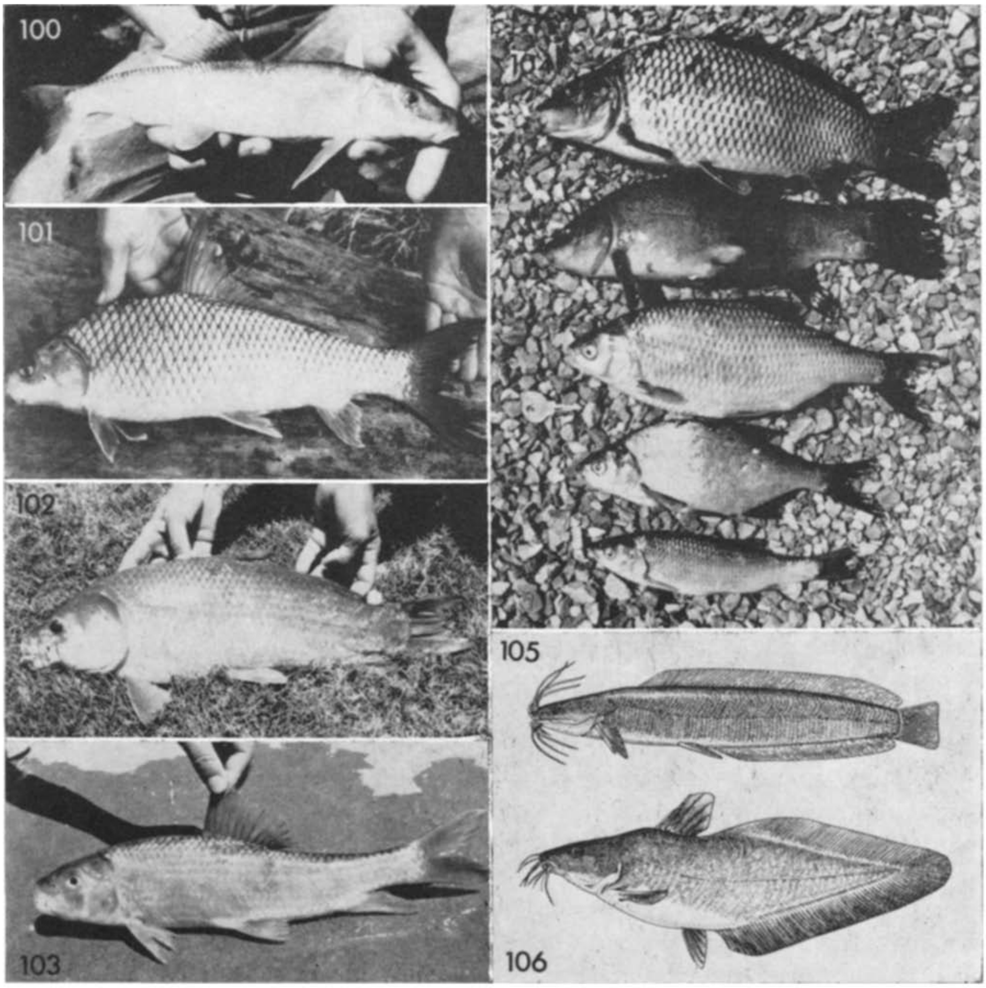
[a] Classification after Greenwood *et al.* (1966).

[b] Accidental hosts.

[c] Zoogeographical region: A, Australian; E, Ethiopian; N, Nearctic; O, Oriental; P, Palearctic. There are no published records from neotropical fishes.

Greenwood *et al.* (1966) regard them as "relatively" primitive teleosts. If one accepts the co-evolution of hosts and parasites, and there is ample evidence from our knowledge of other host–parasite systems to do so, then the preponderance of ostaryophysan hosts assumes considerable phylogenetic significance for their caryophylli-



FIGS. 100–106. Some representative fish hosts of caryophyllids. 100. *Catostomus ardens,* Wyoming. 101. *Carpiodes carpio,* Tennessee. 102. *Ictiobus cyprinellus,* Oklahoma. 103. *Moxostoma erythrurum,* Oklahoma. 104. Top to *bottom*: *Cyprinus carpio, Tinca tinca, Abramis brama, Scardinius erythrophthalmus* and *Rutilus rutilus,* France. 105. *Clarias batrachus,* from photograph of specimen introduced into Florida. 106. *Tandanus tandanus,* Australia, from photograph in Whitley (1957: p.8).

dean cestodes. This significance is further emphasized by the presence of the still more primitive Mormyriformes.

Within the Cyprinidae most records are from *Abramis, Cyprinus, Leuciscus, Rutilus,* and *Tinca* (Fig. 104), the Catostomidae: *Catostomus* (Fig. 100) and *Ictiobus* (Fig. 102); and Siluriformes: *Clarias* (Fig. 105) of the Clariidae. All of these fish, as well as many others, have feeding habits that include, to varying degrees, benthic organisms.

The only records from marine fish (here considered as accidental hosts) are from the coastal brackish waters of the Baltic (Janiszewska 1939; Markowski 1935, 1938) and include immature *Caryophyllaeus.*

Other hosts classed as accidental by virtue of the isolated record or their planktonic, insectivorous, or piscivorous feeding habits are: *Dorosoma* (Hunter 1929b); *S. irideus* (= *S. gairdneri* Richardson: Brandes 1958); *Esox* (Pearse 1924; Pucilowska 1969); and *Acerina, Perca* (Kašták

1957) and "log-perch" (*Percina* sp., not in Table V; Pearse 1924). Although Popov (1926) found three of 105 endemic *S. ischchan* infected with a single small worm each of *K. armeniaca*, Platonova (1963) failed to find it in the same host in her extensive survey of Lake Sevan (Armenia) parasites. This latter point plus the fact that *S. ischchan* feeds mainly on amphipods (Nikolsky 1963) strongly suggest an accidental infection. Another (MacPhee 1961; not in Table V), of *Glaridacris* sp. from 12 of 20 *Lepomis gibbosus* (L.) (Centrachidae), could not be verified and may also represent an accidental infection. Dr. W. Rogers of Auburn, Alabama (USA) has recently sent me an immature caryophyllid (identification uncertain) from the pyloric caeca of another centrarchid, *L. cyanellus* Raf., thus indicating that sunfishes may indeed rarely become infected with caryophyllids.

Of considerable interest are two unidentified gravid specimens from *Lermichthys multiradiatus* (Meek) (Goodeidae) from Mexico sent to me by Dr. Rafael Lamothe-Argumedo. Not only does this represent the first record of these cestodes from Mexico but also it extends the host spectrum to the Cyprinodontoidei, an important group that is well represented in Central America. More extensive parasite surveys of small fishes, particularly those with known benthic feeding habits or with a ventral mouth, of this region as well as in other parts of the world, may well reveal that caryophyllids are not as restricted in their hosts as previously thought.

A certain level of host specificity, suggested by the dominance of ostaryophysan hosts, is borne out by a review of host records. In Europe and the USSR the usual host for *M. wageneri* is *Tinca* and of *C. fimbriceps, C. carpio;* in Australia only *T. tandanus* (Fig. 106) has been found infected; in Africa *W. virilis* has only been found in *Synodontis;* in India most species are from *C. batrachus* (Fig. 105), and in North America *A. iowensis* and *A. huronensis* appear restricted to *C. carpio*, *H. nodulosus* to *Catostomus* spp., *G. laruei* to *C. commersoni*, and *S. wardi* and *B. carpiodi* to *Carpiodes* spp. These relationships do not just reflect limited sampling because in many cases large numbers of different hosts from various regions had been examined. Szidat (1942) felt that, at least for the European species, there was strong specificity for one host species; on the other hand, Janiszewska (1954) noted that several species had two, three, or four different hosts. There are, however, other examples reporting caryophyllid infections in one species but not in other, closely related fish in the same habitat, presumably sharing similar feeding habits (Akhmetova 1966; Calentine and Mackiewicz 1966; Kennedy 1969b; Mackiewicz 1965a,b, 1968c, 1969a; Mackiewicz and McCrae 1965; McCrae 1961).

There appears little doubt that host specificity exists to varying degrees depending on the cestode species. Whether it has a physiological basis gained through a long period of association and selection, or an ecological one primarily associated with benthic feeding habits, is something that must be answered for each species; in all probability it is a combination of the two. There appear to be no studies that have attempted to feed adult worms to different fish nor to infect or transplant them to amphibian, avian, mammalian, or reptilian hosts.

B. *Location and Worm Burden*

Almost without exception nonprogenetic caryophyllids are found in the intestine of the vertebrate host. *C. biloculus* was initially reported from the coelom of *Heteropneustis fossilis* Bloch (Murhar 1963) but all subsequent collections have been from the intestine of the same host (Murhar, personal communication). It would thus appear that the initial record may have been based on worms accidentally translocated during autopsy procedures. A single live and active *I. hexacotyle* was found in the gallbladder of a heavily infected *C. insignis* thus suggesting to Amin (1969b) that this cestode has a wide tolerance to different chemical environments, possibly reflecting a more primitive pattern in site choice than that shown by *G. laruei*, normally found in the posterior part of the intestine, or *H. nodulosa*, usually confined to the intestinal swelling. All others of the 2126 *I. hexacotyle* from the same host were found in the upper part of the small intestine (Amin 1969b).

Distribution along the intestine varies although specific information for most species is lacking. The most common region appears to be the first and second loop of the anterior part of the intestine, posterior to the intestinal swelling ("stomach"). Some examples are: *G. catostomi* (Lawrence 1969), *K. sinensis* (Musselius *et al.* 1963), *I. bulbocirrus* (Amin 1969b; Lawrence 1969), and *C. fimbriceps* (Shcherban 1965). More rarely they may attach to the posterior part of the intestine as in the case of *G. laruei* (Lawrence 1969). In the carp, which lacks an intestinal swelling, *K. iowensis* and *A. iowensis* are found throughout the gut (Calentine and Ulmer 1961; Calentine 1962) although gravid *K. iowensis* generally occur in the first third of the intestine. *C. singularis* appears to be one of the few species restricted to the intestinal swelling of *Carpiodes* spp. (Fig. 101) and *Ictiobus* spp. (Fig. 102). Other species also found in the intestinal swelling are *E. ptychocheila*, *B. carpiodi*, *B. biloculoides*, and *H. nodulosa;* the last three may also occur in the anterior intestine, particularly in heavy infections. In these heavy infections such species as *I. bulbocirrus* and *B. infrequens*, that normally occur in the anterior intestine, may also occupy the intestinal swelling (Amin 1969b; personal observations). There is, however, sufficient evidence to indicate that niche stratification occurs in the intestine particularly in instances of mixed infections. However, the ecology of caryophyllids within the gut remains a relatively unexplored subject; for example, nothing is known of possible diurnal migrations in the gut.

Because intensity of infection varies greatly with respect to cestode and host species, host size and feeding habits, season and locality, it is not surprising that there is much variation in worm burden. From a review of a large number of records it is apparent that most infections involve fewer than 50 worms. Some examples of higher populations include the following from carp: 3000 *C. fimbriceps* (Kulakovskaya *et al.* 1965), 1523 *A. iowensis* (Calentine 1964), 624 *K. iowensis* (Calentine and Ulmer 1961), 497 *C. laticeps* (Wunder 1939), and 900–1000 *B. infrequens* from *H. nigricans* (personal observation) and 836 *G. confusus* from *I. bubalus* (Calentine and Williams 1967). These higher rates reflect the great number of oligochaetes that must be consumed and suggest, in some cases at least, that premunition or other immunological mechanisms may not be important factors in determining population size. While the history of past infections for each host is not known, it is doubtful that all heavy infections represent initial ones because the fish were generally large and presumably exposed earlier to infection. Some of the complex factors related to assessing worm burden and ingestion of oligochaetes are discussed by Kennedy (1969a).

C. *Growth, Maturation, Longevity*

Growth in the vertebrate phase of caryophyllidean life cycles is confined to the studies of Hunter (1930) on 26 *H. paratarius* and 196 *G. confusus* and of Amin (1969b) on 182 *I. hexacotyle*. Both workers plotted and compared the change in length of the region from the tip of the scolex to the most anterior vitellarium (previtelline region of Amin 1969b) to that from the

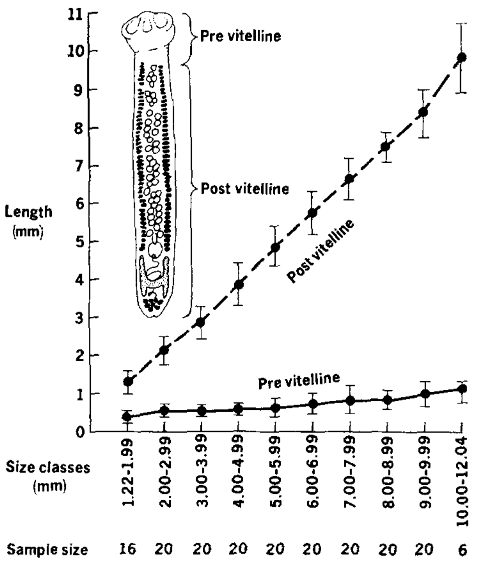


FIG. 107. Graph of growth of different regions of *Isoglaridacris hexacotyle*. Vertical lines represent range; illustration and graph adapted from Amin (1969b).

most anterior vitellarium to the posterior tip of the worm (postvitelline region of Amin 1969b). In all cases it was found that the length of the scolex neck region (previtelline) changed less than that of the rest of the body which gradually increased as the worms got longer (Fig. 107). This relationship was less pronounced with *H. parmatarius*. From these data Hunter (1930: 143) concluded, "The region of growth lies, to all intents and purposes, in the neck, for it is this region and the portion of the body just posterior to it, which shows the greatest changes," and therefore, "It is evident that the neck region in the Cestodaria (*sic*) as in the cestodes is the region of growth." Unfortunately, there is no histological evidence to support this conclusion; neither Wiśniewski (1930) nor Will (1893) could identify any zone of proliferation in the neck. It is, therefore, not surprising that other workers consider growth as diffuse (Nybelin 1922; Janiszewska 1954).

Growth as a whole was observed to be opposite that of the procercoid (Janiszewska 1954), in which the anterior end shows greater increase in size and differentiation than the posterior one. In a penetrating analysis of the growth characteristics of pseudophyllidean tapeworms Nybelin (1922) concluded that those with an anapolytic strobila (*i.e.*, *Cyathocephalus*, *Caryophyllaeus*) had a diffuse type of growth and lacked any histologically marked proliferation zone or "Keimzone." This view and its bearing on the whole question of the origin of proglottisation, segmentation and neoteny are discussed by Wardle and McLeod (1952: 10–11). How a caryophyllidean grows is thus very much an open question whose answer may lie with more detailed histological studies or those utilizing ^{3}H-thymidine labeling or colchicine techniques, similar to those of Wikgren and Gustafsson (1967) and Wikgren (1964) on *Diphyllobothrium* spp. plerocercoids.

Further morphometric studies on *I. hexacotyle* by Amin (1969b) showed that there was a gradual increase in the width of the scolex, neck, cirrus, and body at the gonopore through the length class 7.00–7.99 mm after which there was a slight decrease thought to be due to a smaller sample size.

Maturation of the plerocercoid-like stage to the point of egg-laying also requires, except for some progenetic species of *Archigetes*, some unknown stimulus provided by the fish host. In *Archigetes* the oligochaete also provides the stimulus although it acts on the procercoid stage, thus producing a neotenic larva. Should an immature *Archigetes* be ingested by a fish it quickly matures and has a short life span. Szidat (1937a) compared this short-term development to that of a coelom-dwelling tapeworm (no doubt referring to *Ligula*) in its definitive host (bird), the implication being that similar mechanisms might also serve to stimulate egg-laying in *Archigetes*. But as is now known a simple rise in termperature (provided by the bird host) is enough to stimulate egg production in *Ligula* (Smyth

1969), while temperature does not appear to be such a factor in *Archigetes,* contrary to the assertions of Schwabe and Kilejian (1968). The egg-laying stimulus of the fish–bird system of *Ligula* is, therefore, quite different from the oligochete-fish system of *Archigetes* spp. where there is little temperature differential between the two hosts (Nybelin 1962). But temperature does appear to play a role, though not as directly as Borgström and Halvorsen (1968) suggest after finding that gravid *C. fennica* were present only from June to August. This role appears to be an indirect one on the host by influencing hormone levels and thus initiating spawning. According to Kennedy (1969b), egg production in *C. laticeps* (from *L. leuciscus*) appears to be governed by this change in host hormone level; the same relationship also appears to be true for *A. iowensis* which were found in carp only while the host was spawning (Calentine 1962). Earlier, Szidat (1959) had proposed that the neotenous condition of the Caryophyllidea arose because of the effect on larval stages of increased concentrations of hypophysis and thyroid hormone, eliminated through the intestine and stimulated by the gradual evolution of the then marine host as it became migratory and adapted to fresh water. There are no studies, however, that have critically measured hormone levels in the intestinal lumen and assayed their effect on the maturation of caryophyllids. The technical and experimental difficulties of obtaining such data *in vivo* are so formidable that an alternate method may have to be devised utilizing *in vitro* culture techniques. At present (July, 1971) there are no *in vitro* cultivation studies of caryophyllid tapeworms.

An alternate explanation for the precocious development of *Archigetes* may be, as Clegg and Smyth (1968) suggested for *A. iowensis,* the failure of an inhibitory neurosecretory control to function properly. The merit of such a system is that its function does not necessarily depend upon development to a new stage (plerocercoid-like) nor a new environment (fish) in order to operate; hence it can function while the larva is still a procercoid and in the invertebrate host. Once initiated in the procercoid stage, maturation would, theoretically, continue regardless of the habitat. If, indeed, the control of egg production in *Archigetes* has a neurosecretory basis, and there is no evidence for or against this interesting proposal, then the trigger for its regulation can not be as specific as for other caryophyllids which mature only in the fish.

Estimates of total life span or for only the vertebrate phase are based in part on natural infections and hence will vary depending upon what stage the procercoid had attained when eaten. Thus, a procercoid having well-developed gonadial primordia will require less time to mature in the fish than one not having primordia formed (Kulakovskaya 1962b). Considering that *C. laticeps* is infective from 6 months to 2 years with a procercoid that may vary in development and size (1.5–18 mm; Sekutowicz 1934), longevity figures for this species, and probably many others are relative.

Few figures on life span have been published; most concern palearctic species. In the USSR *Caryophyllaeus* lives for 1–1.5 months in carp (Bauer 1959; Kulakovskaya 1964a). But on the basis of extensive studies on the seasonal incidence of *C. laticeps* in *L. leuciscus* from Great Britain, Kennedy (1969b) concluded that no more than 3 months are spent in the fish and that the total life span is probably no more than a year, the same life span as its intermediate host, *P. barbatus.* Yet, in Poland, the procercoid of *C. laticeps* may live twice as long as the whole life span of the species in England because of the longer life span of the intermediate host (*Tubifex*). *Caryophyllaeus* dies shortly after the single egg-laying period (Ivasik 1952; Kulakovskaya 1964a). Assuming that *C. laticeps* eggs embryonate in 14 days (Table I), that it requires 4–6 months to become an infective procercoid of 1.5–2 mm, and, at the same rate of growth, would take 2 years to become a procercoid of 18 mm and still be infective, and that the life span in the vertebrate host varies from 1 to 3 months, then the total life span can vary from 7.5 to 25.5 months.

A. sieboldi can complete its cycle in the oligochaete from infective egg to infective egg in 100–110 days in summer and 200–210 days in winter (Wiśniewski 1930). *A. appendiculatum* lives in the fish from April to the beginning of June (Kulakovskaya 1962a) as does *A. iowensis* (Calentine 1964). The European progenetic species have a 6-month cycle (Kulakovskaya 1964a).

Representatives of the Lytocestidae (*Khawia* and *Caryophyllaeides*) remain in the oligochaete for 2–3 months, and, at least for *Khawia*, 5–6 months in carp (Kulakovskaya 1962b). Assuming an embryonation time of 32 days (Table I), then the total life span is 8–10 months. According to Kulakovskaya (1964a), both of the above genera have a life cycle of exactly 1 year. Except for *C. laticeps* and other species having an extended infective period in the oligochaete it would appear from data on embryonation and procercoid development (Tables I and IV), that many caryophyllids probably have a total life span of less than a year. Of course this period can be extended considerably if one considers that embryonated eggs are viable (and presumably infective) for long periods, up to 217 days for *G. catostomi*, for example, and that some procercoids (in addition to *C. laticeps*) can live for long periods of time, 344 days for *M. ulmeri* (Calentine *et al.* 1970) and 466 days for *H. nodulosa* (Calentine 1967). On theoretical grounds it may thus be possible to have a total life span of 2½–3 years. Approximate as these figures are, they assume considerable value when considering immunity, intra- and interspecific competition and dispersal by intermediate hosts and migratory fishes.

Evidence of senescence, though scant, has been found in natural infections. Dubinina (1949) found that *C. laticeps* (from *A. brama*) were in a state of degeneration during the winter, appearing like a transparent ribbon with testes and cirrus sac visible but with eggs reabsorbed and genital glands degenerated. Gonads were also degenerating in gravid *A. iowensis* having large numbers of eggs in the uterus even though the cestodes were still in the oligochaete (Calentine 1962). Mackiewicz (1970a) recently found that senescence in *E. ptychocheila* begins in the posterior part of the testicular field followed by degeneration of the pre- and postovarian vitelline follicles and ovary. It would be desirable to know if a similar pattern prevails with other species. It is remarkable that a worm lacking a major part of the reproductive system would still be present in the host for I have found apparently "normal" cestodes (*C. laticeps*) spontaneously expelled from captive fish (*A. brama*). Though hardly a normal situation, caryophyllids may also be expelled from fish that have been placed into 10% formalin (personal observation), an important consideration when utilizing preserved fish for incidence or distributional studies.

D. *Seasonal Incidence*

The most important studies dealing with the quantitative aspects of seasonal incidence in the vertebrate host are by Calentine and Fredrickson (1965), Kanaev (1956b), Kennedy (1968, 1969b), Kulakovskaya (1962d, 1964a,b), Lawrence (1970), and Wunder (1939). Those by Kennedy are clearly the most comprehensive with particular attention given to an analysis of seasonal fluctuations in terms of host and oligochaete ecology and population dynamics of *C. laticeps* in *L. leuciscus* and its intermediate host, *P. barbatus*. That by Lawrence is particularly noteworthy for its rigorous statistical analysis. Graphs of seasonal fluctuations for various species are presented by Kulakovskaya (1964a,b). Numerous other papers, such as those by Akhmetova (1966), Bauer (1959), Borgström and Halvorsen (1968), Calentine (1964), Calentine and Ulmer (1961), Dubinina (1949), Fredrickson and Ulmer (1967), Kennedy (1969a), Kozicka (1959), Kulakovskaya *et al.* (1965), Mackiewicz (1965b), and Williams and Ulmer (1971), to mention a few, present additional data on seasonal incidence.

That there is indeed a distinct seasonal incidence cycle in caryophyllids is brought out by many studies. Specific examples include: *C. laticeps* in carp (Poland) only during April through August (Wunder 1939), in *A. brama* (USSR) only in the Spring (Dubinina 1949), and in *L. leuciscus* (Great Britain) only from December through July (Kennedy 1969b); *A. iowensis* in carp (USA) only from April through June, no samples from December to February (Calentine 1964); *M. hunteri* in *C. commersoni* (USA) only during May through July, and *B. macrocephalum*, June through August, no December sample (Calentine and Fredrickson 1965); *C. fennica* in *R. rutilus* (Norway) only from May through November, no December sample (Borgström and Halvorsen 1968); *C. fimbriceps* in carp (Ukraine) with a peak infection in June with gradual decline and loss in following May (Kanaev 1956b) or present only in spring (USSR) in another region (Dubinina 1949); and of *K. sinensis* in carp (Ukraine) in May and June (Kulakovskaya *et al.* 1965). Less dramatic fluctuations were shown for *G. catostomi*, *G. laruei*, and *I. bulbocirrus* in *C. commersoni* (USA), each showing a significantly higher incidence from January through April, than from May through August or September through November (Lawrence 1970). A remarkably similar seasonal fluctuation for *G. catostomi* in the same host was also reported by Calentine and Fredrickson (1965). Most of these studies indicate that the period of highest incidence is in late winter, or more commonly, early spring, and that the highest incidence of gravid stages is also in the spring when water temperature rises and fish are spawning.

There are exceptions however. For example, *S. wardi*, from *Carpiodes* spp. (chiefly from Iowa and Nebraska), showed no seasonal periodicity (Williams and Ulmer 1971); nor did *H. nodulosa* exhibit any seasonal fluctuations in New York or Colorado (Mackiewicz and McCrae 1962), with gravid individuals being found throughout the year in Iowa (USA) by Calentine and Fredrickson (1965). This latter species differs from all the others mentioned above in its pit-dwelling habit, a condition that may favor longer association with the host.

Several different factors have been used to explain incidence of caryophyllids. Kulakovskaya *et al.* (1965) found that, under fish-farming conditions, the degree of infection of *C. fimbriceps* in carp was related to the species composition and number of tubificids, degree of their infection with larval tapeworms and how much they were utilized for food. Temperature as it affects feeding habits or the physiology of the host has been cited as another factor by several authors. Perhaps best known is Ivasik's (1952) observation of an epizootic in young carp that resulted when fish that were normally feeding on plankton became massively infected when they abruptly began feeding on the benthos (chiefly tubificids) because of a sudden drop in temperature. Reduced feeding because of the seasonal drop in temperature was considered by Scheuring (1929) to be the principal factor in regulating the seasonal incidence of *Caryophyllaeus*. Support for this indirect temperature effect is provided by Bauer (1959) who cites Reĭnsone's (1955) report of heavy winter infections of *C. laticeps* in *A. brama* in Lake Kals (Latvian, SSR) that is warmed by hot springs thus enabling fish to feed throughout the winter. Normally carp and many other cyprinids, particularly in lakes in northern regions (USSR), overwinter in a state of reduced activity with complete cessation or sharp reduction of food consumption (Nikolsky 1963). Similar overwintering behavior is less common in river and stream fish (Nikolsky 1963) yet in *C. commersoni* in a stream in eastern Canada (Ontario) there was an acceleration of feeding as water temperature rose in spring (Keast 1968).

A somewhat different effect of temperature was proposed by Kennedy (1969b) and later expressed in model form (Kennedy 1970). As a result of earlier work in which the ability to resist *C. laticeps* (from *L. leuciscus*) was found to be temperature dependent (Kennedy and Walker 1969), Kennedy (1969b: 792) explained the seasonal cycle in this way: recruitment was restricted to the coldest months (when the ability to respond was lowest) but with the spring rise in temperature and with the increased worm burden the "... response increased in strength thus simultaneously preventing the establishment of new infections and eliminating existing ones. Temperature thus bears a direct causal relationship to the seasonal cycle of *C. laticeps* and its population changes in dace. It does not, however, act directly on the parasite but indirectly by altering the physiological condition of its host. The temperature-dependent response of dace is therefore acting as a control system determining the rate of flow of parasites through the host-parasite system. The system is an open one, and whilst the feeding behavior of dace may influence input, the state of dynamic equilibrium that exists at any one time between the gain and loss of parasites is determined primarily by the temperature control system." Many years earlier Wunder (1939) had suggested that the decline in summer *C. laticeps* infections in carp was due to a host "Gegengiften"; he did not, however, implicate temperature.

The role that host sex may have in determining incidence is difficult to assess. Lawrence (1970), for example, found that while incidence of *G. catostomi* and *I. bulbocirrus* between male and female *C. commersoni* was not statistically significant, it was slightly so for *G. laruei;* he offered no explanation for this latter difference. On the other hand, Borgström and Halvorsen (1968) considered the physiological differences between male and female *R. rutilus* enough to account for the absence of *C. fennica* in 25 males, and its presence in 12 of 118 females. Sexual differences in fish are accentuated during the spawning season and, as is well known, may be reflected in the feeding habits (Nikolsky 1963).

Interaction of cestode species may be still another factor affecting incidence. For example, Calentine and Fredrickson (1965) found that both *M. hunteri* and *B. macrocephalum* tended to be absent from *C. commersoni* when *Glaridacris* was present. On the other hand, *I. bulbocirrus* and *G. catostomi* were found together in the same host to a greater extent than could be attributed to chance (Lawrence 1969). In the Ukraine the introduced *K. sinensis* has successfully competed with *C. fimbriceps,* the indigenous species, replacing it in carp from certain regions (Kulakovskaya 1964b). This success may be partially explained by the wider intermediate host spectrum of *K. sinensis* and its ability to overwinter in fish (Kulakovskaya 1964b); on the other hand, there may also be important but subtle interspecific interactions within the intermediate host or fish intestine. Because multiple infections with caryophyllids are common more information on niche width for each species as well as on the inter- and intraspecific interactions in the vertebrate host is needed before the dynamics of incidence and maturation cycles can be fully understood.

It would thus appear that incidence is the result of the interactions of such complex factors as availability and kind of infected intermediate hosts, variations in host feeding habits, environmental changes (*e.g.*, temperature), physiological changes in host resistance, host sex, and the interspecific interaction (competition?) of the parasites themselves. While the population dynamics within the vertebrate host appear to be governed by host reactions (immunity) stimulated by temperature, the general incidence picture appears to be more a function of feeding habits, as influenced by temperature, than any other factor.

E. *Immunity and Age Resistance*

Proven cases of immune responses by fish to their helminth parasites, regardless of the type, are rare (for recent reviews see Arme and Walkey 1970; Williams 1967; Snieszko 1969, 1970), or absent (Kennedy 1970). Recently McVicar and Fletcher (1970) demonstrated an immune response of *Raja radiata* Donovan (Rajidae) to the tetraphyllid *Acanthobothrium quadripartitum* Williams while Harris (1970) found a precipitin reaction of *Leuciscus cephalus* to saline extracts of the acanthocephalan *Pomphorynchus laevis* Müller. That fish may possibly exhibit immunity to caryophyllid infections through prior exposure or because of an age factor, however, is suggested by the work of some authors. The fact that populations of *C. laticeps* in carp showed a progressive decline and subsequent loss from May to August suggested to Wunder (1939: 712), "Die grösste Wahrscheinlichkeit besteht, dass der Wirtskörper durch Absonderung von Gegengiften die Begrenzung der Parasitenzahl bewirkt." And in *I. bulbocirrus* in *C. commersoni* over one-half of the infections were in fish under 125 mm although many large fish, up to 381 mm, were examined (Mackiewicz 1965a). Similarly, Rakova (1953) found that the incidence of *C. laticeps* decreased with age in *L. idus* from 27.2% in 1-year-old fish to 6.2% in 7-year-old fish, a decrease attributed, however, to the nonbenthic feeding habits of older fish.

Kanaev (1956b) found that both the incidence and intensity (worm burden) of *C. fimbriceps* decreased in carp ranging in age from 1 to 4 years, and that this trend extended to those more than 10 years old in which infections were extremely rare. Kanaev attributed this reduced incidence and intensity, as well as a reduction in size of parasites and shortening of their period in the older fish, to a relative immunity correlated with host age. Support for an immunity mechanism was further illustrated by the fact that 2-year-old carp, previously infected in their first year, had six to eight times fewer *C. fimbriceps* than fish first infected in their second year. Furthermore, Kanaev found that both the incidence and intensity of the second infection in 2-year-old fish was inversely proportional to the incidence and intensity of the initial, first-year infection. These data provide only circumstantial evidence for a possible immunological reaction, evidence that needs experimental verification (Bauer 1959) and comparative serological studies on immune and nonimmune carp before they can be fully accepted (Kanaev 1956b).

While some studies tend to corroborate Kanaev's observations, others do not. For example, Bauer (1961) reported that *C. fimbriceps* usually affects older rather than younger carp. Fredrickson and Ulmer (1967) found that *I. longus* was least common in *M. macrolepidotum* under 200 mm and over 400 mm, a difference attributed to either different food habits or age immunity. Kennedy (1968) found that large and small *L. leuciscus* had a similar incidence and intensity with *C. laticeps*. Finally, Lawrence (1970) very recently showed that the degree of infection for both *I. bulbocirrus* and *G. catostomi* in *C. commersoni* showed a positive correlation with age, *i.e.*, as age increased, the degree of infection tended to increase; no significance was noted for *G. laruei* although the intensity was highest in 5+ fish. Amin (1969a) noted that *G. confusus* was more frequent in larger *Ictiobus* than smaller ones, a fact he attributed to increased food volume and the cumulative effect of repeated infections in larger fish. Without supporting data on antibody levels it is difficult to reconcile the results of the aforementioned studies.

An experimental and serological approach to this complex problem of immunity and caryophyllosis was attempted by Kennedy and Walker (1969). They fed tubificids (*P. barbatus*), naturally infected by *C. laticeps*, to *Leuciscus* collected from the River Avon, and subsequently tested for the presence of circulating antibodies by the Ouchterlony technique of immunodiffusion in agar and by passive cutaneous anaphylaxis by intradermal inoculation of serum followed by antigen in guinea pigs. All tests for circulating antibodies from control and experimentally infected fish were negative. Despite these results the experiments "... show quite clearly that dace can respond to the presence of *C. laticeps* by rejecting them and that this response depends upon temperature" (Kennedy and Walker 1969: 581). The failure to detect circulating antibodies was thus attributed in part to unsuitable techniques or possibly too low temperature (8 C) rather than evidence that an immune reaction was not involved. In later work on the seasonal dynamics of *C. laticeps* infections in dace this temperature-dependent resistance response, enabling the tapeworm to better establish and persist for larger periods at low temperatures than high ones, was considered very similar to the self-cure reaction of mammals to nematode infections (Kennedy 1969b).

F. *Helminth Associations*

In studies on the mutual influence of helminths to each other, Reichenback-Klinke (1966) found that while in *A. sapa* the acanthocephalan *Pomphorhynchus laevis* (Müller) was absent or occurred in small numbers when 8–30 *C. laticeps* were present, in *B. barbus* and *I. idus* no cestodes of any species were found when 31–250 *P. laevis* were present. This apparent antagonism, which was not complete in *A. sapa,* was thought to have a chemical basis related to the effects of the metabolic secretions of the helminths on each other. On the other hand no significant interspecific antagonisms were found between *G. catostomi* or *I. bulbocirrus* and *Pomphorhynchus bulbocolli* Linkins in *C. commersoni* (Lawrence 1969). He did find, however, that there was a significant positive association between *P. bulbocolli* and *G. laruei,* species that live in the posterior part of the digestive tract. Another significant degree of association has also been found between the cestode *Proteocephalus torulosus* (Batsch) and *C. laticeps* in *L. leuciscus* (Kennedy and Hine 1969). In this case simultaneous feeding on both planktonic copepods, the intermediate host of *P. torulosus,* and benthic oligochaetes appeared to be the most logical reason for this positive association according to these authors. However, heavy infections of one were never found together with heavy infections of the other. Simultaneous or exclusive feeding on both or one intermediate host may also be the explanation for the positive *P. bulbocolli–G. laruei* association or the apparent antagonism of *P. laevis* and other helminths.

From these data it would thus appear that, at least in some cases, there is competitive antagonism whose interpretation depends on a fuller understanding of not only the niche width, nutritional requirements, movements within the intestine, and mutual effect of metabolic products of caryophyllids and their helminth associates, but also of the food habits of each host.

G. *Hyperparasites*

There are no literature reports of parasites from the Caryophyllidea. Recently, however, Dr. A. W. Jones and I found many *G. confusus* from a single *I. bubalus* (in Tennessee) heavily infected by microsporidia. Determined as *Nosema* sp. by Dr. V. Sprague, this protozoan occurred throughout the tissues of the cestode being especially abundant in the testes where it disrupted spermatogenesis almost to the point of failure. Microsporidia, as yet unidentified and in less severe infestations, were also found in *H. nodulosa, K. iowensis* and *I. folius* from Tennessee hosts.

H. *Pathology, Treatment, and Control*

Pathology

Studies of the effect of caryophyllids on the vertebrate host are confined almost exclusively to Europe, particularly the USSR, where fish-farming with carp, an important host of these cestodes, is an important enterprise. Some of the more important references to the pathogenic effect of *C. laticeps* on *C. carpio* include: Amlacher (1961), Dyk (1961), Hofer (1904), Plehn (1924), Schaperclaus (1954), and Sekutowicz (1934); *C. laticeps* on *A. brama:* Amlacher (1961), and Schaperclaus (1954); *C. fimbriceps* on *C. carpio*: Bauer (1958, 1959), Bauer *et al.* (1969), Dogiel and Bauer (1955), Ivasik (1952), Kanaev [1956a,b; according to Bauer (1959), Kanaev's species should be *C. fimbriceps* instead of *C. laticeps*], and Shcherban (1965); *K. sinensis* on *C. carpio* or its hybrids: Akhmetova (1966), Bauer *et al.* (1969), Musselius *et al.* (1963), and Shcherban (1965); *K. iowensis* on *C. carpio*: Calentine and Ulmer (1961); *M. wageneri* on *T. tinca*: Sonsino (1891), Janiszewska (1954); *M. hunteri* on *C. commersoni;* Mackiewicz (1963b); *H. nodulosa* on *C. commersoni*; Mackiewicz and McCrae (1962); *D. penetrans* on *C. batrachus*: Bovien (1926) and Fuhrmann (1931); *L. javanicus* on *C. batrachus*: Bovien (1926); *A. iowensis* on *C. carpio*: Calentine (1962); *B. rossitensis* on *C. carassius,* Szidat (1937b); and of *B. biloculoides* on *C. commersoni*: Mackiewicz and McCrae (1965). Illustrations of cestodes *in situ* or of sections of the scolex attached to the mucosa are included in the works of Bovien (1926), Calentine (1962), Calentine and Ulmer (1961), Cooper (1920), Fuhrmann (1931), Janiszewska (1954), Joyeux and Baer (1961), Kanaev (1956a), Mackiewicz (1963b, 1968c), Mackiewicz and McCrae (1962, 1965), Sekutowicz (1934), Wesenberg-Lund (1939) and Wunder (1939). While a general review of pathological effects is lacking, considerable detail can be found in Kanaev (1956b) and Shcherban (1965) although only *C. fimbriceps* and *K. sinensis* are considered. See Williams (1967) for a recent review of helminth diseases of fish.

Diseases caused by these tapeworms have been designated by Russian authors (Akhmetova 1966; Bauer *et al.* 1969; Musselius *et al.* 1963; and Shcherban 1965) as caryophyllosis when caused by *Caryophyllaeus* spp. and khawiosis when caused by *K. sinensis*.

Caryophyllids affect their host in several ways: by mechanical obstruction of intestinal tract, production of lesions or other pathological conditions of the intestinal tract, and by causing a general physiological imbalance in the host.

Mechanical obstruction appears rare although Ivasik (1952) reported that 20 to 40 *C. fimbriceps* killed very young *C. carpio* by preventing them from utilizing food. According to Shcherban (1965) *K. sinensis* can also kill fish by completely obstructing the intestinal canal. On the other hand, I found an adult *H. nigricans* with a massive infection of 900–1000 immature and mature *B. infrequens* that effectively blocked the "stomach" and whole gut and, while there was no trace of food in the gut, the fish appeared "normal."

The production of lesions or inflammation appears to be a more widespread condition. With *M. hunteri* the lesion may be small, having little proliferation of tissue but with the scolex resting in the *lamina propria* with resulting destruction of epithelial cells

(Mackiewicz 1963b). With others it may be more extensive, for example, *M. wageneri* produces a raised plaque-like formation surrounding the firmly embedded scolex (Janiszewska 1954; Sonsino 1891); *M. ingens* occurs in deep pits that show considerable proliferation of tissue into the intestinal lumen (Hunter 1930), *M. ulmeri* may also occur in pits but with less proliferation of tissue (Mackiewicz 1968c); *H. nodulosa* produces conspicuous deep pits of fibrous tissue easily seen as nodules on the serosal surface (Linton 1893; Cooper 1920; Mackiewicz and McGrae 1962); *B. biloculoides* produces a small nodule with extensive proliferation of the *lamina propria* and circular muscles (Mackiewicz and McCrae 1965); and *D. penetrans* will actually perforate the intestinal wall, much like the proboscis of some acanthocephala (Bovien 1926). *K. sinensis* first causes irritation to the mucous membrane followed by deep lesions that are accompanied by inflammations that often cause rupture of the intestinal wall (Musselius *et al.* 1963). Inflammation is also caused by *C. fimbriceps* (Ivasik 1952). Lesions by *Caryophyllaeus* may predispose carp to red disease (Kocyłowski 1952). Most species, however, appear to cause little pathology.

Gross pathology may also result when species that normally cause little mechanical damage occur in large numbers; this is especially true with small fish. In an infection of over 200 *C. laticeps* the infected part of the intestine was clearly thinner thus rendering the parasites visible through the normally opaque intestinal wall (Sekutowicz 1934). With a similar number of *G. catostomi* the normal pattern of mucosal folds was disrupted by numerous small superficial mucosal pits (Mackiewicz 1965b).

A more serious effect is that which causes mortality. That heavy *Caryophyllaeus* or *K. sinensis* infections can indeed cause death occasionally in carp, usually under fish-farming conditions, is well documented by Bauer (1958), Bauer *et al.* (1969), Ivasik (1952), Kanaev (1956b), Kulakovskaya *et al.* (1965), Kulwieciowna (1930), Musselius *et al.* (1963), Plehn (1924), and Shcherban (1965). After studying two epizootics Ivasik (1952) concluded that 70–100 *C. fimbriceps* were sufficient to cause death of year-old carp (18–19 cm long) in April and that 20–40 could kill carp fry (average length 4.1 cm) in June. In an epizootic in August involving *K. sinensis* in 3-year-old carp Musselius *et al.* (1963) found 35–45 worms, varying in size from 80 to 170 mm, in dead and dying carp; 18 of 124 fish died. From three to five *K. sinensis* were sufficient to cause death of first summer (very young) carp; from 25 to 350 of *C. fimbriceps* caused death in 2-year-old carp (Kulakovskaya *et al.* 1965). That fish may become infected when they are very young was also demonstrated by Kurochkin (1964) who found *R. rutilus* and *C. carpio,* 10.5–15 mm long, infected with *C. laticeps* and *C. fimbriceps,* respectively.

Clinical symptoms of caryophyllosis in carp include anemia (Pheln 1924) and pronounced emaciation (Shcherban 1965); of khawiosis, general weakening, reduced activity, loss of weight and an anemic condition of fins and skin (Shcherban 1965). Part of this clinical picture is said to be due to the release of toxins (Dogiel and Bauer 1955; Ivasik 1952; Kanaev 1956b); proof that caryophyllids produce toxins is lacking however. By dividing 2-year-old carp into a lightly infected group (having only immature worms) and a strongly infected one (having established clusters of mature worms with 6–12 times the volume of those in the other group) Kanaev (1956b) was able to compare the blood picture, coefficient of fatness, growth, and index of filling of the intestine of the two groups with each other and, in some cases, with uninfected fish. The incidence normally varied from 80 to 100% with intensities of 1–263 parasites per fish; his study included the peak peri-

TABLE VI

Blood Pictures, in Percentage, of Two-Year-Old Carp Infected with Caryophyllaeus fimbriceps[a]

Leukocyte types	Normal (%)[b]		Weakly infected		Strongly infected	
	June	Sept.-Oct.	June	Sept.-Oct.	June	Sept.-Oct.
Lymphocytes	97.75	98.25	49.2	81.3	72.5	63.95
Monocytes	1.85	1.05	38.7	18.1	23.1	34.25
Polymorphonuclear leukocytes	0.35	0.65	1.4	0.4	1.8	1.2
Neutrophils	0.05	0.05	9.8	0.2	2.6	0.6
Eosinophils	None	None	0.9	None	None	None

[a] Adapted from Kanaev 1956b.
[b] According to Antipova (1954).

ods (June) through the low periods of infection (October).

Hemoglobin levels in strongly infected fish in June were 11.9 units of fat (*sic*) lower than weakly infected fish and 11.3 units lower than "healthy" carp; sedimentation rate in strongly infected fish was 2.1 times higher than that of weakly infected ones. These hemoglobin changes were also reflected in the August, September, and October samples. Changes in the leukocyte picture are summarized in Table VI. According to Kanaev the appearance of eosinophiles during the initial phase of infection (weakly infected group) was tied to toxins secreted by the parasites while the high monocyte level was apparently associated with "alternate infection" (inflammation?) of the intestinal walls. It is interesting to note that in *G. gobio* infected with *Ligula* sp. lymphocytes increased from 65.5 to 84.8% and neutrophils from 0.5 to 0.8% while monocytes dropped from 16.5 to 10.4% and polymorphonuclear leukocytes from 17.5 to 4.0% (Sadkovskaya 1953).

The coefficient of fatness of heavily infected fish in June was 0.31 lower than that of lightly infected ones and 0.34 and 0.15 lower in August and October, respectively. In younger fish at the end of the wintering period (March) the drop in the coefficient of infected fish was almost two times that in healthy fish. This drop was thought to weaken the fish and lower their cold-resistance during the wintering period, a view also expressed by Petrushevski and Kogteva (1954). With such a drop in both young and 2-year-old carp it is not surprising that the growth rate of heavily infected fish was adversely affected; according to Kanaev, heavily infected fish weighed 14.8% less than lightly infected ones.

Related to the above coefficient of fatness was "index of fullness of the intestine." In 2-year-old carp with an average of 32.6 parasites weighing 10 mg, the index was almost two times lower than in fish that had an average of 7.3 worms, weighing 4.7 mg. Thus, the index of fullness was associated with a lower degree of feeding and hence a lower coefficient of fatness and reduced growth rate, according to Kanaev (1956b). But whether these observations reflect absolute differences in the amount of food eaten or a differential absorption of nutrients by the cestodes is not known and should be further explored by rigidly controlled feeding experiments.

Treatment and Control

Control and treatment of caryophyllid infections on fish farms has been reviewed by Bauer *et al.* (1969), Kanaev (1956a) and Shcherban (1965), among others. Control consists primarily of periodic (*i.e.*, once every 4 or 5 years), thorough draining, plowing, and treatment of the soil of holding ponds with quick lime in order to kill all tubificids. Only noninfected fish should then be used for restocking. The introduction of chironomid larvae (Diptera: Chironomidae) as an additional natural food for carp has a beneficial effect in ponds with infected 2-year-old carp (Shcherban 1965). As a treatment for khawiosis, kamala, a preparation from *Mallotus philippinensis* Muell. (Euphorbiaceae), is added to the food to equal a dose of 0.1 g per fry or 1-year-old fish and 0.3–0.4 g per 2-year-old fish; individual large fish can be administered a dose of 0.8–1.0 g per kg of fish by catheter and syringe. The same dosage applies for caryophyllosis (Bauer *et al.* 1969). Other antihelminthics include phenothiazin mixed with food to give a dose of 80 mg per year-old fish (Shcherban 1965), 0.16 g powdered rhizomes and underground leaves of the spinulose shield fern, *Dryopteris spinulosa* (Müll.) (Polypodiaceae) per gram of fish, or a mixture of kamala and the shield fern preparation (Kanaev 1956a). The last two drugs are mixed with the food, sunflower, and flax oilcakes.

XII. ICONOGRAPHY

Poorly executed, improperly labeled, or inaccurate drawings have led to errors in interpretation of the systematics or morphology of caryophyllid species. So great has been the tendency to recopy illustrations or rely on them for identification that some notable examples and their role in the study of caryophyllids are briefly noted here (Table VII).

One such example is that of *C. fuhrmanni,* described by Szidat (1937b) solely on the basis of Fuhrmann's illustration of *C. laticeps* (Fuhrmann 1931: Figs. 355a,b) from which the median vitellaria had been omitted (see Mackiewicz, 1962b for a more complete discussion). Another more subtle example, is Yamaguti's (1959) diagnosis of the genus *Bovienia* in which he states that a spined cirrus is present. Since neither Bovien (1926) nor Fuhrmann (1931) mention such an obvious characteristic, it would appear that it was based on Fuhrmann's illustration (Fuhrmann 1931: Fig. 340). This fictitious character was incorporated in a key by Yamaguti (1959), subsequently repeated in keys by Gupta (1961) and Murhar (1963) and, though corrected by Mackiewicz (1963a), has again appeared in the literature (Schmidt 1970).

Of the other less dramatic examples listed in Table VII the most common inaccuracy is that of drawing the uterus or vagina, or both, ventral to the ovarian commissure. This apparently minor error (both structures are always dorsal to the commissure) has the effect of reversing the position of the ovary, thus suggesting the possibility that gonopores (which, like the commissure, are ventral) may appear on alternating surfaces, a condition normally found on some Pseudophyllidea (*e.g., Bothrimonus* and *Cyathocephalus*).

Sources of some of the artifacts or inaccuracies may be traced to carelessness, the utilization of parasites that have died in the host and are partially decomposed, or to flattening specimens. In this last category belong, in my view, Fig. 8 (*A. appendiculatus* Ratz.) of Mrázek (1898), since recopied by Fuhrmann (1931: Fig. 356, cercomere added), Sprehn (1960: Fig. 16, cercomere added), Joyeux and Baer (1936: Fig. 540), Janiszewska (1954: Fig. 26), Kulakovskaya (1961: plate 4, Fig. 3) and Joyeux and Baer (1961: Fig. 429); and Fig. 4 (*A. cryptobothrius*) of Wiśniewski (1930), copied by Janiszewska (1954: Fig. 33). As anyone familiar with the confused systematics of the genus *Archigetes* knows, much of the problem stems from comparisons based on poorly executed illustrations (see Janiszewska 1950b; Kennedy 1965b). Unfortunately, the example of *Archigetes* is not an isolated one. The absence of accurate illustrations of many species remains as an important obstacle in analyzing the system-

TABLE VII

Annotated List of Selected Figures of Caryophyllid Cestodes that have Errors because of Inaccuracies, Misidentification, or Artifacts

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Inaccuracies

Bauer (1958) Fig. 31a, *C. fimbriceps*. Median vitellaria omitted (see Mackiewicz, 1962)

Benham (1901) Fig. 11, *C. mutabilis*. Median vitellaria absent, preovarian vitellaria continuous with postovarian vitellaria

Carus (1857) Plate 7, Fig. 11, *C. mutabilis* (by Prof. M. Schultze). Diagrammatic, lacking postovarian vitellaria, uterus, and vagina ventral to ovarian commissure. Perhaps the most widely copied illustration of *C. laticeps;* with various modifications, recopied as *C. mutabilis* or *C. laticeps* by: Hatschek (1891, Fig. 333), Shipley (1893, Fig. 69D), Hofer (1904, Fig. 151), Lühe (1910, Fig. 4b), Plehn (1924, Fig. 84), Kulwieciowna (1930, Fig. 1), Wesenberg-Lund (1939, Fig. 220), Schäperclaus (1954, Fig. 128), Amlacher (1961, Fig. 150), and van Duijn (1967, Fig. 7.9)

Dubinina (1962) Fig. 867, *G. brachyurus;* Fig. 879, *K. armeniaca*. Uterus and/or vagina ventral to ovarian commissure

Cooper (1920) Fig. 6, *G. catostomi*. Uterus ventral to ovarian commissure

Fuhrmann (1926) Fig. 17a,b, *C. laticeps*. Median vitellaria omitted (see Mackiewicz, 1962); copied by Fuhrmann (1931, Figs. 355a,b), Caullery (1952, Figs. 52a,b), Yamaguti (1959, Figs. 166a,b), Joyeux and Baer (1961, Figs. 317, 349), Dubinina (1962, Fig. 848). Szidat (1937b, Fig. 2) used Fuhrmann's Fig. 17a as a basis for his new species *C. fuhrmanni,* copied by Janiszewska (1954, Fig. 14)

Fuhrmann (1931) Fig. 340, *B. serialis*. Incomplete worm, scolex missing (see Mackiewicz, 1963a); copied by Yamaguti (1959, Fig. 83)

Gupta (1961) Fig. 9, *P. indica;* Fig. 13, *C. batrachii*. Median vitellaria omitted; vagina ventral to ovarian commissure. Fig. 9 copied by Schmidt (1970, Fig. 63)

Hoffman (1967) Fig. 179, *A. huronensis*. Faithfully copied from Fig. 1 of Anthony (1958) but lacks notation that vitellaria are omitted

Janiszewska (1950a) Fig. 1, *P. silesiacus*. Postovarian vitellaria not drawn in (see Mackiewicz, 1965a), vagina ventral to ovarian commissure. Copied by Janiszewska (1954, Fig. 19), Yamaguti (1959, Fig. 140) and Schmidt (1970, Fig. 54)

Janiszewska (1954) Fig. 16, *M. wageneri*. Uterus ventral to ovarian commissre but not so in original from Nybelin (1922, Fig. 45)

Kulakovskaya (1961) Plate 2, Fig. 2, *K. baltica* and Fig. 5 *K. armeniaca*. Uterus and/or vagina ventral to ovarian commissure

Kulakovskaya (1962c) Fig. 1, *B. orientalis*. Uterus ventral to ovarian commissure; copied by Schmidt (1970, Fig. 59)

Linton (1893) Fig. 15, *C. terebrans*. Composite species, *H. nodulosa* and *C. terebrans*

Moghe (1925) Fig. 2, *C. indicus;* "p. ov. vit." and "vit. s." mistaken for ovary, "vit. d." mistaken for oviduct. "ov." = ? (see Woodland, 1926; Moghe, 1931)

Voge (1969) Fig. 1, Caryophyllaeidea. Apex of median loculus should be terminal

Woodland (1923) Fig. 25, *C. filiformis*. Median vitellaria omitted (see Woodland, 1925: 531); uterus and vagina ventral to ovarian commissure

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TABLE VII—*Continued*

Yamaguti (1934) Fig. 15, *G. limnodrili*. Uterus and vagina ventral to ovarian commissure

Zmeev (1936) Fig. 4, *C. parvus*. Median vitellaria omitted (see Mackiewicz, 1962)

Misidentifications

Cooper (1920) *G. catostomi*, Figs. 1, 2 and 5 = *G. laruei;* Fig. 7 = *H. nodulosa*. (see Mackiewicz and McCrae, 1962)

Johri (1959) Figs. 1 to 4, *Hunteroides mysteri*. Cestodaria (see Joyeux and Baer, 1962: 346)

Meyer (1958) Figs. 26 and 31, *G. catostomi* = *B. biloculoides* (see Mackiewicz and McCrae, 1965); Figs. 28 and 33, *G. confusus* = *G. laruei;* Figs. 29, 30 and 34, *B. infrequens* = ? *B. macrocephalum*

Van Cleave and Mueller (1932) Plate 33, Fig. 1, *G. catostomi* = *B. biloculoides* (see Mackiewicz and McCrae, 1965); Fig. 2, *G. confusus* = *G. laruei;* Fig. 3, *M. ingens* = *M. hunteri;* Fig. 4, *B. infrequens* = *Biacetabulum* sp., copied by Hoffman (1967, Fig. 167)

Artifacts

Gupta (1961) Fig. 2, *L. fossilisi*. Decomposed scolex?

Woodland (1923) Figs. 26c and 26b, *C. filiformis*. Decomposed scolex (see Woodland, 1924: 531); Fig. 25, "LD," postmortem artifact

atics and comparative morphology of the Caryophyllidea.

XIII. ZOOGEOGRAPHY

In the absence of a comprehensive analysis of the zoogeographical distribution of caryophyllid cestodes one must rely on host–parasite checklists for general distributional data. Regions for which there is some inforamtion include Africa (Khalil 1969, 1971), France (Joyeux and Baer 1936), Great Britain and Ireland (Chappel and Owen 1969), Israel (Paperna 1964), North America (Hoffman 1967), Switzerland (Fuhrmann 1926), and the USSR (Dubinina 1962). Some papers devoted specifically to caryophyllid distribution include those of Hunter (1930), who presented a general discussion of distribution and listed all of the hosts and localities by countries; Janiszewska (1954), who mapped the distribution of seven species in Europe and the eastern part of the USSR; Shulman (1958), who specifically listed the regions, subregions, provinces, and districts for 10 species in the USSR; Kulakovskaya (1961), who dealt with the distribution of 18 species in the USSR; Mackiewicz (1966), who presented a brief synopsis of caryophyllid zoogeography; and Bauer and Gusev (1969) who considered 16 genera in their comparison of the parasitofauna of fish from the palearctic and nearctic. From these and other studies it is apparent that caryophyllids form almost one-fourth of the cestode fauna of the freshwater fishes of North America and Russia (Fig. 109).

At the generic and specific levels there appears to be little inter- and transcontinental dissemination of caryophyllids (Hoffman 1970) despite the extensive worldwide introduction of one of their principal hosts—carp. To be sure *K. sinensis* has become successfully established in western USSR through the introduction of carp from China (Kulakovskaya and Krotas 1961) but it is surprising that there are no other carefully documented cases of this sort. Consider for example that the introduced carp in North America harbors *A. iowensis, A. huronensis* and *K. iowensis,* cestodes that are apparently absent from the palearctic and, paradoxically, are not normally found in native nearctic fishes

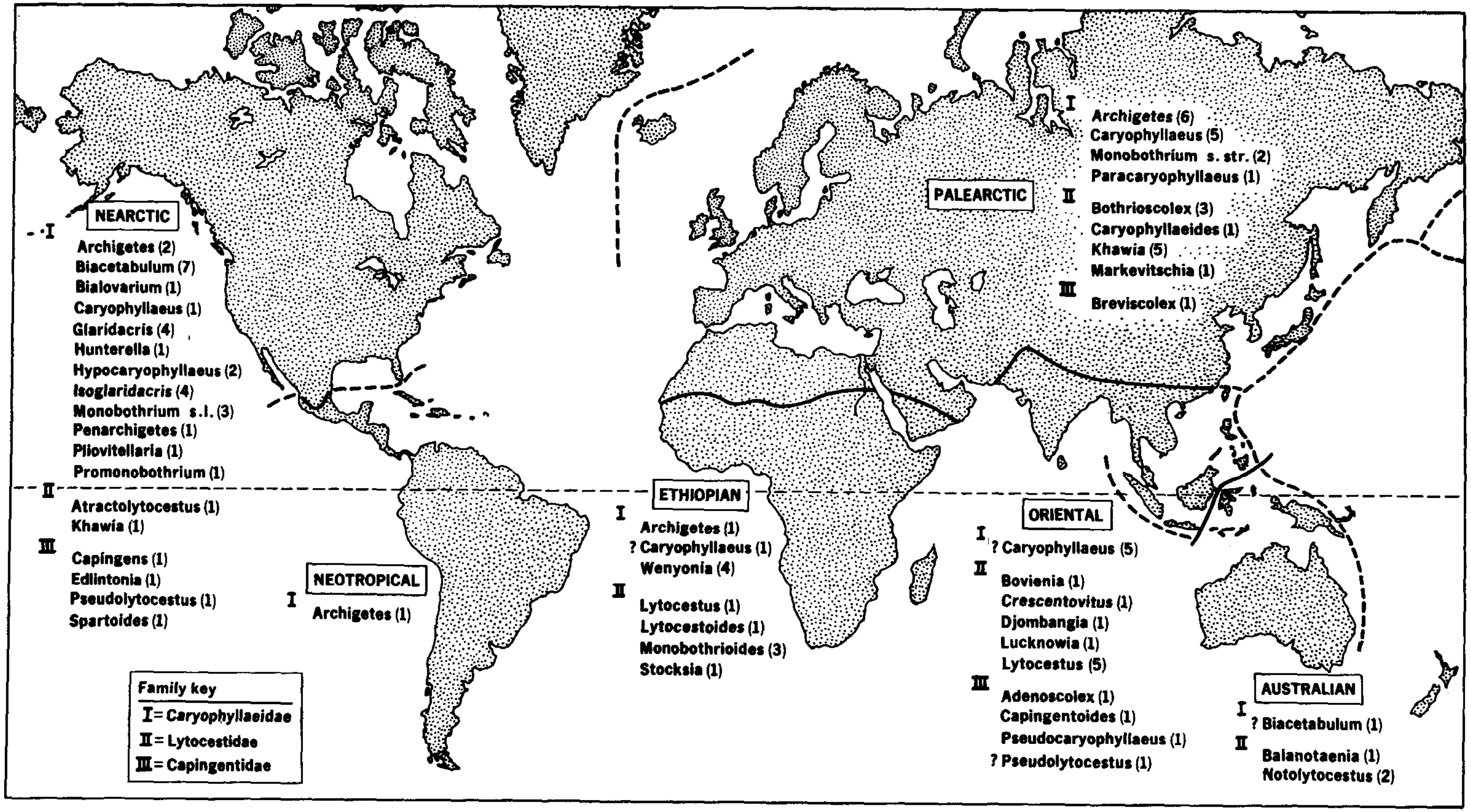

FIG. 108. Zoogeographical distribution of caryophyllid genera. The numbers of species are in parentheses.

(Mackiewicz 1970a). As more is learned of the fish parasites of nearctic fish it will be interesting to see if any palearctic or oriental caryophyllids have been introduced into the nearactic with *Clarias, Tinca* and *Scardinius.* At present the only species common to the nearctic and palearctic is *A. sieboldi,* which also occurs in a tubificid. *Khawia, Caryophyllaeus* and *Monobothrium* have also been recorded from both regions (Fig. 108), but until the systematics of the latter two is better understood the zoogeographical significance of their distribution must remain obscure (Mackiewicz 1965b). According to Bauer and Gusev (1969), *Caryophyllaeus, Monobothrium, Glaridacris, Biacetabulum,* and, possibly, *Khawia,* introduced into North America in carp from West Germany, are common to the palearctic and nearctic. As has been discussed elsewhere (Mackiewicz 1963b, 1965b, 1968b, 1969a) the systematics and zoogeography of the first four genera are far from resolved. Other genera whose systematics are too poorly understood to serve as a basis for critical zoogeographical studies are *Lytocestus* and *Pseudolytocestus* of the oriental region.

From Fig. 108 it is clear that caryophyllids are widely distributed. For the sake of clarity the classification and number of genera and species reflects the present scheme as compiled from the literature. Obviously it will vary with different interpretations as shown in Table VIII. Despite limitations, Fig. 108 shows some general trends, namely, that with few exceptions the caryophyllid fauna of each faunal region appears to be distinct with an apparent high degree of endemism reflected in 23 of 37 genera being monotypic. Furthermore, there are no cosmopolitan species and indeed few genera that are found in more than one region. Their general absence from the neotropical region may reflect our lack of knowledge of the parasites of the freshwater fishes of that region; on the other hand caryophyllids may have not yet radiated to South America in the absence of cyprinid (except the introduced *C. carpio*) and catostomid hosts (Darlington 1957; Lagler *et al.* 1962).

XIV. SYSTEMATICS

The foundations of caryophyllid systematics were laid down by Hunter (1930) who described five genera, erected two of the three currently recognized families, and established many of the family and generic criteria still accepted today. A comprehensive review of earlier systematic treatments can be found in his monograph. Prior to Hunter's work Nybelin (1922) had helped to clarify the status of *Monobothrium* and *Caryophyllaeus* while Woodland (1923, 1926) had attempted (unsuccessfully) to better define the generic concept within the group. Some of the principal workers who have been active in caryophyllid systematics since Hunter's monograph have been: Calentine, Fischthal, Ulmer, Mackiewicz (North America); Kennedy (England); Janiszewska (Poland); Szidat (Germany); Kulakovskaya (Russia); Gupta (India). The greatest systematic activity has been between 1920 and 1940 and in the past 10 years. This activity has revealed caryophyllids to be one of the principal cestode groups in freshwater fishes (Fig. 109); there are 37 genera and 89 species.

While most papers are descriptions of new species, some have also attempted to deal with basic problems in systematics, *e.g.,* family, generic, and specific criteria or relationships of genera to each other; such papers are those of Calentine (1965a), Janiszewska (1953, 1954, 1964), Johri (1959), Kennedy (1965b), Mackiewicz (1963a,b; 1968b; 1969a) and Szidat (1942). Subfamily criteria as they apply to the status of Wenyoninae (Hunter 1930), Bovieninae (Fuhrmann 1931) and family Lallidae (Johri 1959) are discussed by Mackiewicz (1963a).

Genera or species that have been erroneously assigned to the Caryophyllidea include: *Caryophyllaeus truncatus* Sieb. (in Baird 1853), *C. trisignatus* Molin, 1858, and *C. punctulatus* Molin, 1858, which were shown to be *Cyathocephalus* or larvae of Tetraphyllidea by Monticelli (1892) and *Hunteroides mysteri* Johri, 1959, considered to be a true cestodarian by Joyeux and Baer (1961). As *nomina nuda* there are: *Stocksia lazera* Woodland, 1937 (Woodland 1937c) see Yamaguti 1959); *Cryptobothrius* (Olsen 1967: 264); *Archigetes hepatica* Kennedy (1965c); and *H. lintoni* Mackiewicz, 1960 (Amin 1969b).

There are numerous systematic problems at all levels. The variation in the placement of longitudinal muscles had led some investigators (Szidat 1942; Janiszewska 1954; Mackiewicz and McCrae 1962) to question their prominent use as diagnostic characteristics at the family level. Among the numerous problems at the generic level are the diagnoses of *Caryophyllaeus, Monobothrium, Glaridacris,* and *Biacetabulum* where the differences among some species are greater than that among some genera. As generic criteria become better defined there is little doubt that these genera, as well as several others, will have to be critically revised. Such revisions should carefully consider the use of the subgeneric concept as initially proposed for *Paraglaridacris* by Janiszewska (1964). Until such revisions are made it is folly to attempt an analysis of generic relationships based on presently recognized forms. At the species level, the absence of thorough descriptions (Table VIII) has relegated numerous species to the status of *incertae sedis.* Many species should be redescribed with particular attention to intraspecific variation. With many more species yet to be described one can expect significant changes, at all levels, in the current primitive state of the systematics of caryophyllids.

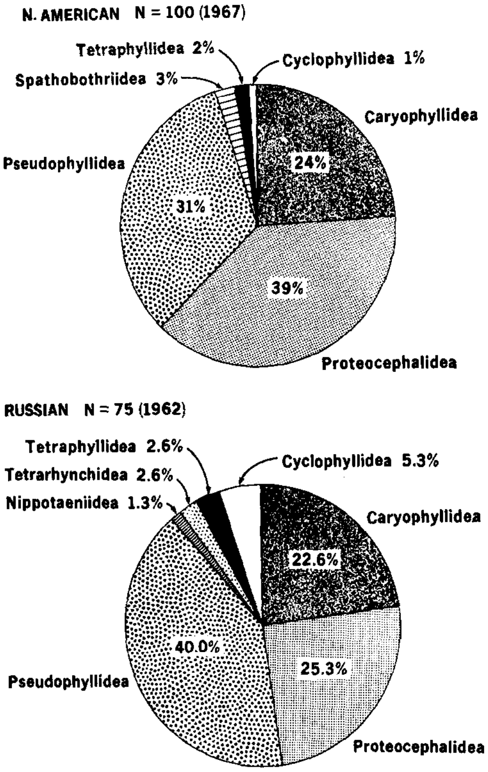

FIG. 109. Pie diagrams indicating the percentage of cestodes from indicated orders occurring in freshwater fish of North America (top) and Russia (bottom). Compiled from Hoffman (1967) and Dubinina (1962).

Keys

Keys to the various taxa of caryophyllids are available. The following lump in one key all genera for the indicated region: World (Hunter 1930), Russia (Kulakovskaya 1961; Dubinina 1962), and of North America (Hoffman 1967). Keys to the genera of Caryophyllaeinae (or Caryophyllaeidae) include those of Fischthal (1951), Wardle and McLeod (1952), Yamaguti (1959), and Schmidt (1970); of Lytocestinae (or Lytocestidae), Wardle and McLeod (1952), Yamaguti (1959), Gupta (1961), Murhar (1963), and Schmidt (1970); and of the Capingentinae (or Capingentidae), Wardle and McLeod (1952), Yamaguti (1959), Schmidt (1970), and

TABLE VIII

Tentative List of Families, Genera, and Species of the Order Caryophyllidea

- Class: Cestoidea Rudolphi, 1808
  - Subclass: Cestoda Carus, 1863
    - Order: Caryophyllidea Van Beneden (in Carus, 1863)
      - Family: Caryophyllaeidae Leuckart (in Lühe, 1910) (= Caryophyllaeinae Nybelin, 1922; Caryophyllaeinae Hunter, 1927) [includes Wenyoninae Hunter, 1927 and Wenyonidae Wardle and McLeod, 1952 *fide* Yamaguti, (1959), Mackiewicz (1963a)].
        - *Caryophyllaeus* Gmelin, 1790[a]
          - *C. laticeps* (Pallas, 1781) Lühe, 1910[a] [= *C. mutabilis* Rudolphi, 1802 *fide* Lühe (1910). *A. appendiculatus* Ratzel, 1868, *nec* Mrázek, 1897 *fide* Nybelin (1922)]
          - *C. terebrans* (Linton, 1893) Woodland, 1923
          - *C. syrdarjensis* Skrjabin, 1913
          - *C. fimbriceps* Annenkova-Khlopina, 1919
          - *C. brachycollis* Janiszewska, 1953
          - *C. kashmirensis* Mehra, 1930, *species inquirenda.*
        - *Monobothrium* Diesing, 1863 *s.l.* [= *Caryophyllaeus p.p.* according to Woodland (1923)].
          - *M. wageneri* Nybelin, 1922 [= *M. tuba* (v. Siebold, 1853) Diesing, 1863 *fide* Nybelin (1922)].
          - *M. ingens* Hunter, 1927
          - *M. auriculatum* Kulakovskaya, 1961
          - *M. hunteri* Mackiewicz, 1963
          - *M. ulmeri* Calentine and Mackiewicz, 1966
        - *Archigetes* Leuckart, 1878 [= *Brachyurus* Szidat, 1938 and *Paraglaridacris* Janiszewska, 1950 *fide* Kennedy (1965b); *Szidatinus* McCrae, 1961].
          - *A. sieboldi* Leuckart 1878 (*sensu* Wiśniewski, 1930) [= *Biacetabulum sieboldi* Szidat, 1937; *B. appendiculatum* (Szidat, 1937) Janiszewska, 1950 *fide* Kennedy (1965b)].
          - *A. appendiculatus* Mrázek, 1897 *nec* Ratzel, 1868. [= *A. sieboldi* Leuckart, 1878 according to Kennedy (1965b)].
          - *A. brachyurus* Mrázek, 1908 [= *Brachyurus brachyurus* Szidat, 1938; *Paraglaridacris silesiacus* Janiszewska, 1950; and *Glaridacris brachyurus* Yamaguti, 1959 *fide* Kennedy (1965b)].
          - *A. cryptobothrius* Wiśniewski, 1928
          - *A. limnodrili* (Yamaguti, 1934) Kennedy, 1965 [= *Glaridacris limnodrili* Yamaguti, 1934; *Brachyurus gobii* Szidat, 1938 and *G. gobii* Yamaguti, 1959 *fide* Kennedy, (1965b); *A. gobii* (Yamaguti, 1959) Kennedy, 1964].
          - *A. iowensis* Calentine, 1962
          - *A. hepatica* Kennedy, 1965 *nomen nudum.*
        - *Glaridacris* Cooper, 1920 [= *Caryophyllaeus p.p.* according to Woodland (1923); *Brachyrus* Szidat, 1938 according to Wardle and McLeod (1952) and Yamaguti (1959)].
          - *G. catostomi* Cooper, 1920
          - *G. laruei* (Lamont, 1921) Hunter, 1927 [= *G. intermedius* Lyster, 1940 *fide* Mackiewicz, (1965a)].
          - *G. confusus* Hunter, 1929
          - *G. oligorchis* Haderlie, 1953
        - *Wenyonia* Woodland, 1923
          - *W. acuminata* Woodland, 1923
          - *W. virilis* Woodland, 1923 [= *Caryophyllaeus niloticus* Kulmatycki, 1924 *fide* Woodland (1926), Hunter (1930). *W. niloticus* (Kulmatycki, 1924) Yamaguti (1959)].
          - *W. longicauda* Woodland, 1937
        - *Biacetabulum* Hunter, 1927 [= *Archigetes* according to Szidat (1937a)].
          - *B. infrequens* Hunter, 1927
          - *B. giganteum* Hunter, 1929
          - *B. meridianum* Hunter, 1929
          - *B. macrocephalum* McCrae, 1962
          - *B. biloculoides* Mackiewicz and McCrae, 1965

TABLE VIII—*Continued*

- *B. banghami* Mackiewicz, 1968
- *B. carpiodi* Mackiewicz, 1969
- *Hypocaryophyllaeus* Hunter, 1927
  - *H. paratarius* Hunter, 1927
  - *H. gilae* Fischthal, 1953
- *Pliovitellaria* Fischthal, 1951
  - *P. wisconsinensis* Fischthal, 1951
- *Bialovarium* Fischthal, 1953
  - *B. nocomis* Fischthal, 1953[b]
- *Paracaryophyllaeus* Kulakovskaya, 1961
- *Hunterella* Mackiewicz and McCrae, 1962
  - *H. nodulosa* Mackiewicz and McCrae, 1962
- *Isoglaridacris* Mackiewicz, 1965
  - *I. hexacotyle* (Linton, 1897) Mackiewicz, 1968
  - *I. bulbocirrus* Mackiewicz, 1965
  - *I. folius* Fredrickson and Ulmer, 1967
  - *I. longus* Fredrickson and Ulmer, 1967
- *Promonobothrium* Mackiewicz, 1968
  - *P. minytremi* Mackiewicz, 1968
- *Penarchigetes* Mackiewicz, 1969
  - *P. oklensis* Mackiewicz, 1969

Family: Lytocestidae Wardle and McLeod, 1952 (= Lytocestinae Hunter, 1927) [Includes Bovieninae Fuhrmann, 1931 and Lallidae Johri, 1959 *fide* Mackiewicz (1963a)].

- *Lytocestus* Cohn 1908
  - *L. adhaerens* Cohn, 1908
  - *L. filiformis* (Woodland, 1923) Fuhrmann and Baer, 1925 [= *Monobothrioides filiformis* (Woodland, 1923) Woodland, 1937; *L. alestesi* Lynsdale, 1956[b] *fide* Mackiewicz (1962)].
  - *L. indicus* (Moghe, 1925) Woodland, 1926 [= *Monobothrioides indicus* (Moghe, 1925) according to Woodland (1937)].
  - *L. javanicus* (Bovien, 1926) Furtado, 1963 [= *Caryocestus javanicus* (Bovien, 1926) Anthony, 1952].
  - *L. birmanicus* Lynsdale, 1956 [= *L. alestesi* Lynsdale, 1956 according to Johri (1959)].
  - *L. parvulus* Furtado, 1963
- *Caryophyllaeides* Nybelin, 1922 [= *Caryophyllaeus p.p.* according to Woodland (1923)].
  - *C. fennica* (Schneider, 1902) Nybelin, 1922 [= *Caryophyllaeus skrjabini* Popoff, 1924 *fide* Kulakovskaya (1961)].
- *Balanotaenia* Johnston, 1924
  - *B. bancrofti* Johnston 1924
- *Monobothrioides* Fuhrmann and Baer, 1925
  - *M. cunningtoni* Fuhrmann and Baer, 1925
  - *M. chalmersius* (Woodland, 1924) Woodland, 1937
  - *M. woodlandi* Mackiewicz and Beverley-Burton, 1967
- *Djombangia* Bovien, 1926
  - *D. penetrans* Bovien, 1926
- *Lytocestoides* Baylis, 1928
  - *L. tanganyikae* Baylis, 1928
- *Bovienia* Fuhrmann, 1931
  - *B. serialis* (Bovien, 1926) Fuhrmann, 1931
- *Stocksia* Woodland, 1937
  - *S. pujehuni* Woodland, 1937[b]
- *Khawia* Hsü, 1935
  - *K. armeniaca* (Cholodkowski, 1915) ? Shulman, 1958
  - *K. sinensis* Hsü, 1935

TABLE VIII—*Continued*

K. japonensis (Yamaguti, 1934) Hsü, 1935 [= *Bothrioscolex japonensis* (Yamaguti, 1934) according to Szidat (1935)].
K. iowensis Calentine and Ulmer, 1961
Notolytocestus Johnston and Muirhead, 1950
N. major Johnston and Muirhead, 1950
N. minor Johnston and Muirhead, 1950[b]
Atractolytocestus Anthony, 1958 [= *Khawia* Hsü, 1935 according to Yamaguti (1959)].
A. huronensis Anthony, 1958
Lucknowia Gupta, 1961
L. fossilisi Gupta, 1961
Crecentovitus Murhar, 1963
C. biloculus Murhar, 1963
Markevitschia Kulakovskaya, 1965
M. sagittata Kulakovskaya, 1965
Family: Capingentidae Wardle and McLeod, 1952 (= Pseudolytocestinae Hunter, 1929; Capingentinae Hunter, 1930).
Capingens Hunter 1927
C. singularis Hunter, 1927
Pseudolytocestus Hunter, 1929
P. differtus Hunter, 1929
Spartoides Hunter, 1929
S. wardi Hunter, 1929
Adenoscolex Fotedar, 1958
A. oreini Fotedar, 1958
Pseudocaryophyllaeus Gupta, 1961
P. indica Gupta, 1961
Capingentoides Gupta, 1961
C. batrachii Gupta, 1961
Breviscolex Kulakovskaya, 1962
B. orientalis Kulakovskaya, 1962
Edlintonia Mackiewicz, 1970
E. ptychocheila Mackiewicz, 1970
Incertae sedis (Information lacking on the disposition of the longitudinal muscles.)
Wenyonia minuta Woodland, 1923[b]
Caryophyllaeus oxycephalus Bovien, 1926[b]
C. tenuicollis Bovien, 1926
C. microcephalus Bovien, 1926
C. acutus Bovien, 1926
C. gotoi Motomura, 1927
Lytocestoides tanganyikae Baylis, 1928
Khawia parvus (Zmeev, 1936) Kulakovskaya, 1961
Bothrioscolex prussicus Szidat, 1937[b]
B. dubius Szidat, 1937
Biacetabulum tandani Johnston and Muirhead, 1950[b]
Pseudolytocestus clariae Gupta, 1961[b]
Paracaryophyllaeus dubininae Kulakovskaya, 1961

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[a] See Stiles and Hassall (1912) for complete synonomy.
[b] Described from a single specimen.

Mackiewicz (1970a). Keys to species of various genera include: *Archigetes,* Joyeux and Baer (1936), Calentine (1962), and Kennedy (1965b); *Biacetabulum,* McCrae (1962); *Caryophyllaeus,* Popov (1926), Motomura (1927), Dubinina (1962), and Markevich (1951); *Khawia,* Calentine and Ulmer (1961) and Dubinina (1962); *Mono-*

bothrium, Calentine and Mackiewicz (1966) and Dubinina (1962).

Recent descriptions of new genera as well as generic revisions have rendered most of the above keys obsolete. They serve, nevertheless, to illustrate the diverse array of characters used to separate genera and to a lesser extent, species. At the generic level the following characters are used most often: scolex type, uterus extension with respect to the cirrus, presence or absence of external seminal vesicle and postovarian vitellaria, ovary shape, distribution of preovarian vitellaria (*i.e.*, in lateral rows or surrounding testes), and number of gonopores. At the specific level: size and morphology relationships of various organs or structures, *e.g.*, cirrus, ovary, eggs, scolex; testes number, and proportional relationships of neck length and vitellaria distribution. Regrettably there are no studies which have critically evaluated the systematic value of any of these characters.

Because it is the most recent and extensive key (35 genera), that by Schmidt (1970) is perhaps the most useful at the generic level. But having been constructed chiefly from descriptions or illustrations, many of which contain errors, it must be used with caution.

XV. Evolution and Classification

A. *Introduction*

The interrelated topics of evolution and classification are the most complex aspects of caryophyllid biology. By being linked to the difficult question of whether a strobilate stage ever occurred in the group, the complexity is compounded. Far more than an academic question its answer will determine whether these cestodes should be regarded as originally (or primarily) monozoic or secondarily so and thus progenetic or neotenic. Naturally the classification proposed and evolutionary pathway used to express their relationship to strobilate eucestodes will differ greatly, depending upon which alternative is accepted.

Before reviewing opposing views three points should be noted. First, since the morphological and developmental relationships of *Archigetes* to *Caryophyllaeus*-like forms are now well established (Calentine 1964; Kennedy 1965b) the cercomere-bearing stage (procercoid) of *Archigetes* should be considered separately from *Caryophyllaeus,* particularly on the question of progenesis. In the case of *Caryophyllaeus* and the non-cercomere-bearing stage of *Archigetes,* "progenetic" or "neotenic" (*i.e.*, sexually mature larva) implies that at one time a strobilate stage, characteristic of mature cestodes, was part of the cycle. With *Archigetes* (*i.e.*, without cercomere) or *Caryophyllaeus* on the other hand, the above implication does not necessarily follow for the plerocercoid-like stage may have always been the final stage. Thus, while "progenetic" may properly be used with the procercoid of *Archigetes,* its use with the plerocercoid-like stage of *Caryophyllaeus* is debatable. Second, there is the definition of the term "progenetic." As originally used by Giard (1887), it referred to sexual maturity in animals which had not yet attained adult condition. It is in this sense that progenetic or progenesis has had its widest application by referring to the precocious development of certain trematode metacercaria. Smyth (1962: 247), however, considered progenesis as, "Advanced development of genitalia in a larva (without actual maturation) . . ." which in its advanced stage becomes neoteny. He, therefore, considers the procercoid stage of *Archigetes and Caryophyllaeus* as progenetic as well as the plerocercoids of *Ligula* and *Schistocephalus.* Dubinina (1964) and Kulakovskaya (1964a) have used the same concept. But Dogiel (1962: 218) defined progenesis as the condition in a parasite, ". . . which begins sexual reproduction and the production of eggs while still in the intermediate host, before the usual stage for these processes in the life cycle, *i.e.*, before reaching the final host." *Archigetes* and *Caryophyllaeus* are thus considered progenetic because they mature in their respective intermediate hosts, an oligochaete or fish. There are subtle implications in the last two definitions, ones that could greatly influence the interpretation of caryophyllid evolution. As used in this review, progenesis (or neoteny) is the precocious sexual maturity of a larval or juvenile stage (Giard 1887; Hyman 1951). A somewhat simplified but similar definition has been used by Joyeux and Baer (1961), Szidat (1937a) and the majority of workers in describing the developmental status of caryophyllids. Third, most of the speculation regarding evolution occurred before many species had been described and the patterns of host specificity had emerged.

B. *Progenetic Question*

Overwhelming opinion is that the procercoid of *Archigetes* is a sexually mature larva. Some authors, however, have referred to *Archigetes* as "possibly neotenic" (Stunkard 1937) or "possibly neotenic procercoids" (Wardle and McLeod 1952). Rosen (1918) appears to be alone in regarding *Archigetes* as a primitive, nonlarval cestode. Calentine (1964), however, has established unequivocally that some species of *Archigetes* (*i.e.*, *A. iowensis*) lose their cercomere and become infective to fish (carp); the same may be true for *A. sieboldi* (Kennedy 1965b). Furthermore, Mrázek (1898), Wiśniewski (1930), and Calentine (1962) found that the oligochaete-dwelling stage lacks a functional gonopore, *i.e.*, the eggs of *Archigetes* are trapped beneath an integumental cover (Fig. 97). In fish *A. iowensis* loses its cercomere and the gonopore becomes functional. Because the cercomere and integumental covering over the gonopore are *bona fide* larval characteristics that are subsequently lost (Calentine 1962), there is, therefore, little question that the gravid coelom-dwelling procercoid of *A. iowensis*, and probably other species in the genus, are indeed progenetic (neotenic) caryophyllids.

In her analysis of the developmental status of *Apora* and *Nematoparataenia* (Cyclophyllidea) Ginetskinskaya (1944) considered the lack of segmentation on a cylindrical body, an excretory system of the type found in plerocercoids, follicular structure of genital glands, lack of genital orifices, and the divergence of scolex structure and internal organization as five of the seven characteristics of neoteny. All of these could well apply to the cercomere-bearing stage of *Archigetes*; the other two—subcutaneous habit and lack of efferent genital ducts—do not.

Caryophyllaeus and other similar forms have also traditionally been considered as sexually mature larvae. Among those who have characterized them as progenetic or neotenic larvae or plerocercoids have been Janicki (1918, 1930), Nybelin (1918), Wiśniewski (1930), Fuhrmann (1931), Szidat (1938), Hyman (1951), Janiszewska (1954), Joyeux and Baer (1961), Stunkard 1962), and Dogiel (1962). It was not until Janicki and Rosen (1917) had completed the life cycle of *D. latum* that the obvious resemblance between the cercomere-bearing and gravid stages of *Caryophyllaeus* to the procercoid and plerocercoid stages of bothriocephalids became dramatically apparent. This resemblance, more than any other, has given rise to the popular theory that *Caryophyllaeus* is a sexually mature larva.

Not all workers have agreed with this theory, however. Lönnberg (1897), Woodland (1926), and Llewellyn (1965) felt that *Caryophyllaeus* was not a larval form but either primarily monozoic or a primitive cestode. Even Baer (1952) and Stunkard (1962) have conceded that it might not be a larval stage. Indeed Stunkard (1967) has suggested that plerocercoids (which would include *Caryophyllaeus*) may be relics of an earlier period before a vertebrate was incorporated into the cycle. Others, such as Lühe (1902) and Hunter (1930) preferred not to pass judgment on the basis of insufficient information. In any case the progenetic question cannot be satisfactorily answered until the monozoic question is resolved.

C. *Monozoic Question*

With evidence strongly indicating that *Archigetes* (with cercomere) is a larval form (see above), the monozoic question must be confined to *Caryophyllaeus*-like forms. There is no agreement as to whether caryophyllids are primarily monozoic (*i.e.*, never had a strobilate stage) or secondarily so (*i.e.*, derived, with a strobilate stage present at one time). The second alternative is most favored judging by the large number of workers who accept their inclusion within the Pseudophyllidea (see below) and regard them as progenetic larvae for the reasons stated above. Other reasons included those of Spengel (1905), who considered that by definition cestodes are segmented and, therefore, *Caryophyllaeus* was secondarily modified, and Nybelin (1922), who concluded that on the basis of morphology and biology caryophyllids were closely allied to and secondarily derived from cyathocephalids. Poche (1926) accepted this latter interpretation.

Arguments for a primary monozoic condition vary. Long ago it was postulated that proglottid formation was a secondary development in cestodes and that the unsegmented condition of *Caryophyllaeus* was the original one (Claus 1889; Hatschek 1891). While expressing some doubt Lönnberg (1897) was inclined to believe that on the basis of the reproductive system and scolex, *Caryophyllaeus* was primarily monozoic but that *Archigetes* was not, referring to its neotenic state. Woodland (1926) felt that *Caryophyllaeus* was a primitive cestode, basing his views on a comparison of caryophyllids to *Gyrocotyle* and *Amphilina*. His paper is one of the most extensive on this monozoic question. It is perhaps significant that the eminent helminthologists Fuhrmann (1931), Baer (1952), and Stunkard (1962) have mentioned the possibility that caryophyllids are primarily monozoic, ancestral tapeworms or that they represent an earlier phylogenetic stage. Most recently Llewellyn (1965) has returned to the views of Claus (1889) and Woodland (1926) (see Evolution section). Unfortunately there appears to be no definitive answer to the monozoic question based on morphological criteria alone; perhaps using an evolutionary approach would be more fruitful.

D. *Evolution*

Depending upon the weight given the monozoic condition there are two basic schemes of evolution envisaged for caryophyllids.

The first and most generally accepted one is that of Wiśniewski (1930). Applying principally to *Archigetes,* it states that neoteny arose through the dying out of the second intermediate host (fish) or even the definitive host (not specified) in which the strobilate stage lived. This hypothesis was based wholly upon the assumed homologies of caryophyllid life cycle stages to those of bothriocephalids; the presence of *Caryophyllaeus* in fish helped reinforce his hypothesis. Many years earlier, the view that *Archigetes* was a neotenic form led Lönnberg (1897) to place it on the Pseudophyllidean branch of his phylogenetic tree, just below *Bothriocephalus; Caryophyllaeus* was not dealt with, however. A theory somewhat similar to Wiśniewski's, and proposed at the same time (independently?), was presented by Janicki (1930) to explain the evolution of *Amphilina* (Cestodaria). He proposed that the definitive hosts for the dropped strobilate stage were the now extinct mesozoic "Wasserreptilien." Janicki felt, moreover, that *Archigetes* and *Caryophyllaeus* were examples of convergence with neoteny being reached independently of the cestodaria. That there is a tendency toward neoteny in the Pseudophyllidea was said to be shown by the series: *Archigetes* — *Biacetabulum* — *Caryophyllaeus* — *Ligula*—*Schistocephalus* (Hyman 1951; Dubinina 1962a; Smyth 1962). It is this series, based partly on Szidat's erroneous assumption that *Biacetabulum* was the adult of *Archigetes* (Szidat 1937a), that led Hyman to conclude (Hyman 1951: 421) that "In general, no phylogenetic importance can be attributed to the monozoic condition." However, both Mayer (1963) and Hoar (1966) acknowledged that new phylogenetic lines can arise through neoteny; in the case of cestodes the lines could be monozoic. One could, therefore, theorize that the immediate ancestor of caryophyllideans arose through neoteny but that this neotenic form (or forms) gave rise to a whole new phyletic line that, except for the ancestral species, never had a strobilate stage. The fact that there has been speciation in some genera (*e.g.*, *Biacetabulum*) would tend to favor this argument. If, on the other hand, one assumes a polyphyletic scheme, with neoteny occurring as many times as there are species, then one would expect to find a high degree of monotypy or some trace of at least one strobilate stage that has survived extinction. And indeed there is a high degree of monotypy (23 of 37 genera), however there are no other strobilate tapeworms with scolexes similar to those found on caryophyllids. To be sure, *Eubothrium* has one suggestive of *G. laruei* but this could be convergence.

A second theory, in its most elementary state, is that of Claus (1889). It stated that the monozoic condition as exemplified by *Caryophyllaeus*, was the original (ancestral) one for cestodes and that strobilization evolved secondarily as a result of more favorable nutrition in the host (vertebrate) intestine.

Variations that include the basic idea of this second theory have been proposed by Joyeux and Baer (1961) and Baer (1952), the foremost student of cestode evolution. According to Baer (1952) a turbellarian-like ancestor is accidentally eaten by a fish, burrows through the gut wall and matures with eggs escaping through the abdominal pore of the host. These eggs are then eaten by an invertebrate scavenger, hatch in the gut with the larva entering the body cavity of the invertebrate (oligochaete or crustacean), which is eaten by a fish in whose intestine the unsegmented larva matures and becomes adult. By not being able to mature in the first fish but in a second, predatory one or another vertebrate, the characteristic pseudophyllidean cycle, with a strobilate stage, evolved. In his phylogenetic tree of cestodarian and cestode relationships caryophyllids are placed by Baer (1952) on a separate, dead-end branch arising from a primitive pseudophyllidean (Fig. 110).

A slightly different theory was recently proposed by Stunkard (1967), the difference being that the most primitive cestodes were thought to have originally been parasites of arthropods. Whether *Archigetes* and *Caryophyllaeus* were originally parasites of invertebrates (oligochaetes) is problematical; see Baer (1952) and Stunkard (1967) for opposing views. That they are, however, primitive cestodes has been acknowledged by Janicki (1918), Rosen (1918), Goette (1921), Nybelin (1922), and Will (1893), among others. With pseudophyllidean species the arthropod, with its parasitic procercoid, was eaten by a fish with the succeeding stages developing in other, larger fishes. The absence of a swimming larva and presence of an annelid host, in my view, would tend to disfavor a similar evolutionary history for caryophyllids. Dubinina (1966) also favors a nonpseudophyllidean line of evolution for caryophyllids, citing as evidence the nonswimming larva and monozoic structure. On the other hand, Stunkard (1967: 676) has stated that, "The plerocercoid may be relics of an earlier period, when their progenitors became mature as parasites of fishes, but with the advent of more

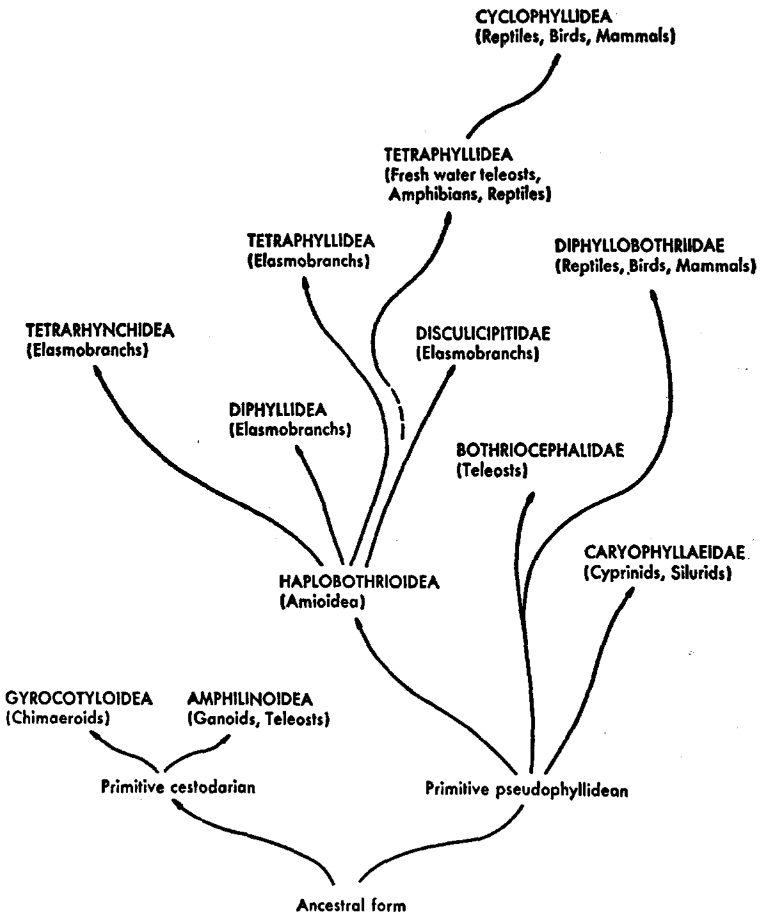

FIG. 110. Phylogenetic tree of cestodarian and cestode worms as deduced from their host relationships (from Baer, 1952; by permission of the publisher).

recent homeothermal vertebrates, birds, and mammals, a further link was added to the food chain and sexual maturity was deferred to the last hosts." In my opinion it is quite possible that caryophyllids could be such relics which, as Baer (1952) and Janiszewska (1954) have emphasized, is borne out by their persistence in primitive teleost fishes. One factor that may have determined the course of their evolution in both Baer's and Stunkard's theories may have been the type of invertebrate host utilized, with the strobilate pseudophyllideans arising from platyhelminths having crustacean hosts and nonstrobilate caryophyllids from those having annelids.

A third theory incorporating Claus's basic thesis is that of Llewellyn (1965), who derived the strobilate cestodes from a caryophyllidean ancestor which evolved along a monogenean–gyrocotylean line (Fig. 111). Briefly, he theorizes that cestodes evolved from monogeneans which became adapted to life in the gut, gave rise to a protogyrocotylidean that on one hand led to gyrocotylideans and on the other protocaryophyllideans which in turn led to caryophyllideans and to strobilate cestodes, with the incorporation of a "carrier" (intermediate host). Consult the original paper for a thorough discussion of the assumptions necessary to develop this theory, role of such characteristics as quinone-tanned eggs and an analysis of other views of plat-

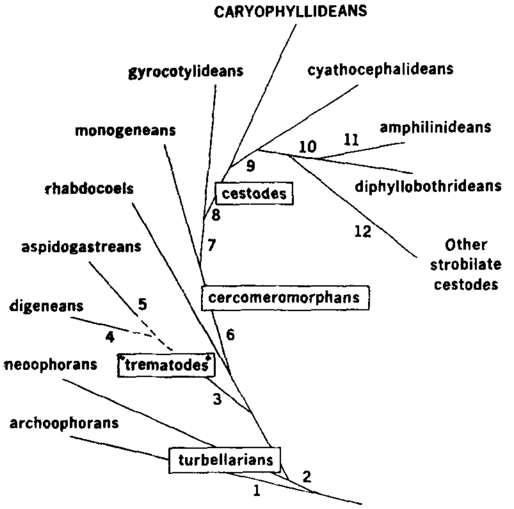

FIG. 111. Llewellyn's scheme for the evolution of parasitic platyhelminths. Events, stages, or changes indicated by the following numbers. 1. Spiral cleavage, undivided ovary, flame cells. 2. Irregular cleavage, germarium-vitellarium, flame cells present. 3. Endoparasitism in molluscs. 4. Polyembryonic larval multiplication in mollusc; preadult actively leaves mollusc and parasitizes vertebrates. 5 No polyembryony; adults do not actively leave mollusc host. 6. Ectoparasitism on vertebrates. 7. Endoparasitism in intestine of vertebrates. 8. Two-host life-cycle; six-hooked larva. 9. Strobilization. 10. Incorporation of a second intermediate host into life-cycle. 11. Progenetic development in second intermediate host, loss of definitive host, four supplementary larval hooks. 12. Loss tanning, closure of uterus, apolysis (adapted from Llewellyn 1965).

yhelminth evolution. While it is possible to raise many questions on specific aspects of this scheme, the essential feature for this review is that strobilization is believed to have developed after and not before caryophyllideans diverged from the protocaryophyllean stock. Once again, the nature of the invertebrate host, *i.e.*, annelid or arthropod, may have influenced this divergence. With the recent description of *Anatrum tortum* (Linton, 1905) Overstreet, 1968 (= *Acompsocephalum* Rees, 1969), a nonsegmented cestode from the marine fish *Synodus intermedius* (Agassiz), Rees (1969) has elaborated on the cestode aspects of Llewellyn's theory, retaining the protocaryophyllidean ancestor as the stock from which strobilate cestodes evolved. Thus, Woodland (1926) may have been correct in maintaining that gyrocotylids and caryophyllids should be regarded as procestodes. Much earlier, *Caryophyllaeus* had been regarded as a cestode prototype by Burmeister (1856).

Speculation as to when this early evolution occurred has been made by Janiszewska (1954), who, assuming parallel evolution of host and parasite, discussed the evolution of caryophyllids in terms of cyprinid speciation in Europe, which took place in the Tertiary with many cyprinid species already present in the Pliocene. The relationships of *C. laticeps* and *C. brachycollis* in *L. idus*, and *B. prussicus* and *B. rossitensis* in *C. carassius* are mentioned as examples of species that speciated separately but, with the loss of barriers, now occur together in the same host. According to Iwasik and Swircpo (1967) *C. fimbriceps* diverged from *C. japonensis* (= *K. japonensis*) at the beginning of the Miocene when the ancestor of *C. carpio* spread from Asia to Europe.

All of these theories are subject to criticism but the fact that caryophyllids have: a nonciliated, non-free-swimming larva; an annelid intermediate host; a single set of reproductive organs in a nonsegmented body, which zoological opinion generally accepts as a condition preceding strobilization; a large number of species which have scolexes generally unlike any found in strobilate tapeworms, with the possible exception of *Eubothrium*; exhibited extensive radiation of morphological types; a worldwide distribution; and occur predominantly in primitive, teleost freshwater fishes, argues forcefully in my opinion, for their being regarded as nonneotenic cestodes, distinct from but closely related to the Pseudophyllidea.

If the above analysis is correct then it would appear proper to regard the cercomere-bearing stage of *Archigetes* as a neotenic or progenetic caryophyllid and all others (plerocercoid-like) as genuine non-progenetic adult stages.

E. *Classification*

Historically the classification of cestodes has been based primarily on gross external characteristics. See Wardle and McLeod (1952) for a discussion of this subject and of the early schemes of cestode classification. It is, therefore, not surprising that *Caryophyllaeus* and *Archigetes* were often accorded separate rank among other tapeworms. In some instances *Caryophyllaeus* was even placed with trematodes (Goeze 1782; Risso 1826); indeed as late as 1891, Lang considered *Caryophyllaeus* to be an intenstineless trematode or a nonsegmented cestode. Others placed them in now obsolete categories such as Proboscephala (Blainville 1828), Heteromorphes (Nordman 1840), or Aplogonei (Blanchard 1848). Still others (Molin 1858; Diesing 1850, 1863; Pintner 1906; Poche 1926; Janicki 1918) utilized ranks such as sections, tribes or subtribes or designated families and orders (Carus 1863; Claus 1876; Shipley 1893; Olsson 1893) in an entirely different sense from present-day usage. For these reasons it is impossible to compare one system of classification with another.

It is possible, however, to distinguish three general ways in which caryophyllids have been classified: as cestodarians, as a family of the order Pseudophyllidea, or as a separate order, Caryophyllidea.

As Cestodaria

Attaching great significance to the monozoic condition, numerous workers have placed caryophyllids within the subclass Cestodaria or its equivalent (van Beneden 1858; Lang 1891; Monticelli 1892: Braun 1894; Ariola 1899; Benham 1901; Skrjabin 1913; Janicki 1918; Woodland 1923; Mola 1929; Southwell 1930; Subramaniam 1939; Caullery 1952; Yamaguti 1959 and Stunkard 1962). By separating the cestodes into two groups, Monogénèses (*Caryophyllaeus*) and Digénsès (all other cestodes) van Beneden (1858) anticipated the establishment of the Cestodaria, erected by Monticelli (1892) to contain *Gyrocotyle, Amphilina, Caryophyllaeus*, and *Archigetes.* Subsequent workers have either followed Monticelli without change or modified his system. Ariola (1899), for example, placed *Caryophyllaeus* and *Archigetes* each in a separate order. Janicki (1918), believing that the monozoic structure was strictly a larval characteristic, rejected Monicelli's scheme and divided all cestodes into two suborders: Bothriifera, with the five tribes: Larvoidea, Bothriocephaloidea, Tetraphyllidea, Diphyllidea, and Tetrarhynchoidea; and Acetabulifera, with the single tribe Cyclophyllidea. The Larvoidea was equivalent to Monticelli's Cestodaria.

The most detailed argument in favor of the cestodarian classification was that of Woodland (1923). In his scheme, seldom adopted by anyone else, the cestodaria were divided into two orders, Paralinidea (with the families Caryophyllaeidae and Gyrocotylidae) and the Amphinidea, with the single family Amphilinidae. According to Woodland (1923), the following similarities warranted placing the Caryophyllaeidae and Gyrocotylidae in a single order: number and position of gonopores, position of testes, uterus, and vagina relationships, shape of ovary, absence of calcareous corpuscles, type of excretory system, and embryos. Shortly thereafter Poche (1926) discussed Woodland's reasons point by point, clearly showing that most similarities did not apply to both families. Fuhrmann and Baer (1925) also rejected Woodland's scheme pointing out that only monozooty was common to both families. In a long counter argument to Fuhrmann and Baer, Woodland (1926) defended his initial views, adding still another similarity—the nervous system. While no one appears to have been persuaded by Woodland's arguments, those pertaining to the primary or secondary nature of monozooty (he thought it was primary) have considerable merit, in my opinion.

Arguments for a cestodarian status lost considerable impetus when Motomura (1929) and Wiśniewski (1930) conclusively proved that *Archigetes* had a six-hooked oncosphere, similar to that of all other cestodes, in contrast to the 10-hooked lycophora of *Gyrocotyle* and *Amphilina.* This fundamental larval difference is so acknowledged by Yamaguti (1959) who, after first placing the caryophyllids in the subclass Eucestoda (p. 7), proceeds to follow Southwell (1930) by placing all monozoic tapeworms (including caryophyllids), in the Cestodaria (p. 451). His treatment is thus like that of Benham (1901).

In North America caryophyllids have been often erroneously referred to as cestodarians by Ward (1911), Cooper (1920), Van Cleave and Mueller (1932), Hunter and Hunter (1932), Bangham and Hunter (1939), Hunter (1942), Bangham and Venard (1942), Bangham (1951), Griffith (1953), and Bangham (1955). Except for the record of Griffith (1953) which concerns *Cyathocephalus,* all of the others most certainly pertain to caryophyllids as host data (ostariophysan fishes) and other data (*e.g.,* illustrations or descriptions) clearly indicate.

As Pseudophyllidea

Caryophyllids have been placed within the order Pseudophyllidea, or its equivalent, by a large number of investigators, among them: Diesing (1850), Leuckart (1878a,b; 1886), Lühe (1902, 1910), Spengel (1905), Nybelin (1918, 1922), Meggitt (1924), Poche (1926), Baylis (1928), Wiśniewski (1930), Hunter (1930), Fuhrmann (1931), Stunkard (1937), Southwell and Lake (1939), Wesenberg-Lund (1939), Dogiel and Volkova (1946), Markevich (1951), Hyman (1951), Janiszewska (1954), Cameron (1956), Spasski (1958), Szidat (1959), Sprehn (1960), Joyeux and Baer (1961), Dollfus (1961), Kulakovskaya (1961), Smyth (1962), Noble and Noble (1971), Kaestner (1965), Kennedy 1965a), Burt and Sandeman (1969), and Rees (1969). Only some of the most significant contributions leading to their inclusion in the Pseudophyllidea can be considered here.

Basing his classification largely upon scolex morphology Diesing (1850) placed *Caryophyllaeus* and *Archigetes* in the "tribus" Bothriocephaliden (= Pseudophyllidea in part) in company with *Ligula, Schistocephalus,* and *Dibothrium* (= *Diphyllobothrium*). Leuckart (1878a) suggested that the life cycle of bothriocephalids might involve a tubificid and have a larval stage like that of a young caryophyllid. Later, on broader morphological grounds, Leuckart (1886) placed caryophyllids in the Bothriocephalidae. The monozoic nature of *Caryophyllaeus* led Claus (1889) to put it close to the ligulids (*Ligula*), a group later placed in the Pseudophyllidea. After his detailed morphological study of *C. mutabilis* Will (1893) concluded that the reproductive system was most like that of bothriocephalids while the nervous system was distinctly trematode-like. Lönnberg (1897) felt that *Archigetes* was related to bothriocephalids because of the similarities in type of bothria, excretory canals, and eggs; he further noted, as did Nybelin (1918), that both groups lived in freshwater hosts.

The most cogent arguments for a relationship with the Pseudophyllidea, however, came from Lühe (1902). In comparing *Archigetes* and *Caryophyllaeus* with the pseudophyllidean subfamilies Dibothriocephalinae, Lingulinae, and Cyathocephalinae, he cited the following seven important similarities: (1) cirrus, vagina and uterine openings on the ventral surface, (2) cirrus opening anterior to uterine pore, (3) vagina and uterus open into a genital atrium, (4) presence of seminal receptacle, and (5) external seminal vesicle, (6) vitelline follicles annularly arranged and external to the testes, and (7) operculate eggs with similar embryological development. Contrary to Will's conclusion regarding the nervous system Lühe (1902) felt that it was essentially similar to that of other cestodes. Spengel (1905) agreed with Lühe's analysis but added that since tapeworms were, by definition, segmented, *Caryophyllaeus* was, therefore, a secondarily derived form.

The family Caryophyllaeidae was formally placed in the order Pseudophyllidea by Lühe (1910). Nybelin (1918) added to Lühe's treatment by calling attention to the cercomere in *Archigetes* and bothriocephalid larvae and similar procercoid and plerocercoid stages of *Caryophyllaeus* to the same larva. He thus concluded that *Archigetes* was a sexually mature procercoid and *Caryophyllaeus* a sexually mature plerocercoid. This last conclusion, though not new (see above) has been generally accepted by many zoologists and, regardless of its validity, appears to be the strongest argument for relating caryophyllids to the Pseudophyllidea. Further elaboration of his views appeared in a later paper (Nybelin 1922). Morphological arrangement of the musculature and especially the scolex of *Capingens* and *Biacetabulum* led Hunter (1930: 26) to conclude that the Caryophyllaeidae were, "... undoubtedly closely allied to the bothriocephalid tapeworms."

With Wiśniewski's study (1930), the neotenic nature and pseudophyllidean affinities of *Archigetes* became well established. Since 1930 there have been few new facts or arguments in favor of the pseudophyllidean nature of caryophyllids with many helminthologists accepting the views of Lühe, Nybelin, and Wiśniewski.

There is little agreement regarding the classification of caryophyllids within the order Pseudophyllidea. Suggestions by Zschokke (1884) that they were related to *Cyathocephalus* or to *Ligula* by Claus (1889) were not supported by evidence other than the obvious similarities of monozooty. This same characteristic led Lühe (1910) to place the two species of *Archigetes* and one of *Caryophyllaeus* in a separate family, Caryophyllaeidae Leuck. But Nybelin (1918), greatly influenced by Odhner's interpretation that *Caryophyllaeus* and *Archigetes* were part of a developmental series showing a relationship to *Cyathocephalus,* placed them in Lühe's (1899) subfamily Cyathocephalinae. Odhner's views, given in lecture at Uppsala in 1911 (Nybelin 1918), apparently were not published although he did later compare the number and location of genital openings of the "Cyathocephalinen" and "Caryophyllaeiden" (Odhner 1912). According to Nybelin (1918), Odhner considered these two groups related because of the similar organization of the excretory ducts and sexual apparatus. Nybelin further added that the larval development of *Cyathocephalus* and *Caryophyllaeus* was much the same, *i.e.,* that both forms had a procercoid and plerocercoid stage, and that both genera could be considered neotenic forms. Later, with his erection of a new family, Cyathocephalidae, Nybelin (1922) created a new subfamily, Caryophyllaeinae, to contain *Caryophyllaeus* and *Archigetes*; his new scheme is supported by a detailed analysis of the morphology of the subfamilies, Cyathocephalinae and Caryophyllaeinae.

In this analysis Nybelin (1922) attempted to show that the genera *Monobothrium, Caryophyllaeus, Caryophyllaeides,* and *Archigetes* (all Caryophyllaeinae) formed one end of a continuous series starting with *Diplocotyle* Krabbe, *Bothrimonus* Duvernoy, and *Cyathocephalus* Kessler (all Cyathocephalinae). While Nybelin recognized that there were discontinuities in characters used, similarities were thought to outweigh them. These similarities were: uterus–vagina relationships, musculature and position of the cirrus sac with respect to the female gonopore, distribution of vitellaria, presence of operculum and egg size, uterine gland distribution, number of ovaries and the organization of genital system, form of scolex, and postembryonic development. Caryophyllids were considered the most primitive in the series and, therefore, primitive with respect to other cestodes. The single genital complex and postembryonic development of *Caryophyllaeus* and related genera was assumed to be evidence of secondary simplification, closely related to and probably derived from the Cyathocephalinae, also neotenic but with several reproductive units.

Despite the extensive analysis of Nybelin (1922) few workers have fully accepted his scheme, preferring to retain caryophyllids as a distinct and separate family of the Pseudophyllidea (Baylis 1928; Hunter 1930; Fuhrmann 1931; Janiszewska 1954; Szidat 1959 and Joyeux and Baer 1961). Hunter's (1930) classification, that of a single family with subfamilies (but not in the sense of Nybelin), is probably the most widely used system.

Order Caryophyllidea

From the time of their initial discovery these tapeworms have been placed in a separate, nonpseudophyllidean, noncestodarian group by Pallas (1781), Bloch (1782), Rudolphi (1810), Blainville (1828), Nordmann (1840), Blanchard (1848), Baird (1853), Molin (1858), Diesing (1863), Steudener (1877), Zschokke (1884) and Pintner (1906). With the emergence of a more stable classification caryophyllids were often regarded as a separate "family" of cestodes, a rank more or less equivalent to the present-day order (Carus 1863; Claus 1876; Shipley 1893; and Olsson 1893). A slightly different approach was taken by Braun (1883) who placed the Caryophyllaeidae and Archigetidae at the same level as Tetraphyllidae, Diphyllidae, Tetrarhynchidae, Bothriocephalidae, Ligulidae, and Amphilinidae.

Some of the more recent workers who have adopted the separate ordinal interpretation, and using the ordinal designation and spelling, Caryophyllidea, are: Wardle and McLeod (1952), Johri (1959), Mackiewicz (1959), Chandler and Read (1961), McCrae (1961), Rothschild (1961), Dubinina (1962), Blackwelder (1963), Calentine (1963), Cheng (1964), Olsen (1967), Jones (1967), and Schmidt (1970). Voge (1969) and Shults and Gvozdev (1970) accepted the ordinal status but used a slightly modified spelling—Caryophyllaeidea. In his tightly argued paper on the evolution of parasitic platyhelminths Llewellyn (1965) removes the caryophyllideans from the Cestodaria and Pseudophyllidea but failed to indicate their taxonomic rank.

Most of the above treatments simply follow the classification of Wardle and McLeod (1952) who justify their scheme by citing (p. 541) the following five features as being characteristic of the Caryophyllidea: "(1) monozooty, (2) lack of external segmentation, (3) presence of genital apertures on the same flat surface (ventral) as the uterine aperture, (4) occurrence of the uterine aperture between the male and female apertures and (5) the tendency of the uterus and vagina to open at the bottom of a uterovaginal depression." They admitted, however (p. 541), "... that only the first characteristic really separates these forms from Cyathocephalidae."; the monozootic condition, they felt, was sufficiently fundamental to justify the erection of a new order, Caryophyllidea. In reality the same classification had been established 89 years earlier by Carus (1863) when he listed the "family" Caryophyllidea van Ben. as one of five "families" of cestodes.

To my knowledge no one has proposed that caryophyllids be elevated to subclass status or to that of superorder under the subclass Eucestoda with all polyzoic tapeworms in another superorder.

XVI. CONCLUSION

Although investigators have touched upon many facets of caryophyllid biology, certain areas have yet to be explored. Some for which there are no data include: chemical composition; carbohydrate, lipid, and protein metabolism; respiration; mechanism of growth; differentiation and organogeny of nonprogenetic species; ultrastructure of internal organs and the oncosphere; histochemistry of the scolex, neck, and uterine glands; and localization of neurosecretory cells. Conspicuously absent is *in vitro* culture whose evaluation may be dependent on some of the above-mentioned studies. It would seem that *Archigetes* would be a logical candidate for such research. Absent, too, is a convenient laboratory host–parasite system that could serve as a basis for a physiological approach to caryophyllid biology. There has been some success with the *Archigetes*–tubificid system but it still is not refined to the point of being amenable to routine laboratory culture. Neither is there a cestode–tubificid–fish laboratory cycle; perhaps a *Khawia–Limnodrilus–Carassius* (goldfish) system could be developed to provide a source for large cestodes.

In addition to the many questions raised in this review some others that may serve as the basis for future studies include: How widespread is polyploidy? How is the variation of morphological characters related to different hosts and geographical regions? To what extent is the apparent host specificity physiologically or ecologically determined? To what degree has the architecture of the gut epithelium determined the niche width of a species? What is the function of the "Faserzellenstränge," frontal glands, and uterine glands? What is the mechanism of egg hatching? In what ways are the caryophyllid faunas of the different parts of the world similar to or different from each other? Because caryophyllideans constitute one of the principal cestode groups in freshwater fishes of the world, the answers to these as well as many other questions should do much to advance our knowledge of the biology and evolution of the Cestoidea as a whole.

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