Caryophyllidea (Cestoidea): Evolution and Classification

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I. INTRODUCTION

Since the discovery of *Caryophyllaeus* in 1781, there has been more speculation on the evolution of caryophyllid cestodes than on any other—and with good reason. With a monozoic body plan, a life cycle involving annelids, and boasting the only tapeworm (*Archigetes*) that can complete a life cycle in an invertebrate (tubificid annelid), caryophyllideans stand in sharp contrast to the far more numerous strobilate tapeworms that generally utilize arthropod intermediate hosts and lack examples with invertebrate definitive hosts. There is little speculation that cestodes arose from free-living flatworms, more on the identity of the specific ancestral flatworm and most on the phylogenetic relationships of caryophyllid cestodes to all others. Before these areas of speculation can be clarified, we must have answers to such questions as (a) what is the evolutionary significance of the monozoic body plan, (b) how do caryophyllids differ from strobilate cestodes, and (c) are caryophyllid cestodes ancestral to or secondarily evolved from strobilate cestodes? A consideration of these key questions forms the basis of this analytical review.

Much of the early literature on the biology, morphology and evolution of caryophyllid cestodes has been reviewed earlier (Mackiewicz, 1972). Since then there has been a number of significant papers dealing with cestode evolution, some of them breaking with traditional views. These recent papers (1971–1979) are reviewed after a consideration of the evolutionary significance of various aspects of caryophyllid biology and morphology. No new taxa nor nomenclatorial changes are proposed in this paper.

A. DEFINITIONS

Lack of uniform definitions can produce confusion in dealing with certain important concepts. Both Spengel (1905) and Rosen (1918) have used the term "monozootie" and "polyzootie" in describing whether a strobilate tapeworm is a single *individual* (monozootie) or a colony or collection of individuals (polyzootie). This same concept, with the terms "monozootic" and "polyzootic", has been used by Wardle and McLeod (1952) and Wardle *et al.* (1974) in separating the classes Cotyloda and Eucestoda. "Monozootie" or "monozootic" should not be confused with the very similar term "monozoic", which is used to refer to a tapeworm with a single set of reproductive organs. This meaning is unambiguous and, except for the above exceptions, has been used consistently and accurately throughout the literature on caryophyllid morphology. This is not true, however, for "progenesis" or "progenetic" and "neoteny" whose precise meaning is so crucial to an understanding of past and current interpretation of caryophyllid evolution. A summary of the problems associated with the definition of these terms was presented by Mackiewicz (1972).

For the purposes of this paper, I am utilizing the definitions from Gould (1977) who has not changed the original meaning of each word. *Progenesis* is (p. 485): "Paedomorphosis (retention of formerly juvenile characters by adult descendants) produced by precocious sexual maturation of an organism still in a morphologically juvenile stage". *Neoteny* is (p. 483): "Paedomorphosis (retention of formerly juvenile characters by adult descendants) produced by retardation of somatic development". The essential difference between the two is that there is an *acceleration* of maturation in progenesis; in neoteny, there is a *retardation* of somatic development. Both produce a mature individual with larval or juvenile features, but the mechanism for doing so is quite different. This differs from the definition of Smyth (1976) in which there is a continuum from progenesis, or the *advanced* development of genitalia in the larval or immature stage, to neoteny, the actual *sexual maturity* of a larval stage. Clearly it is difficult to distinguish between the two phenomena with this latter definition. In fact, one can argue that progenesis is incipient neoteny and the two are, or can be, the same phenomenon except for the time factor. The reader is here referred to Gould (1977) for an extensive analysis of the history and meaning of these often confused terms. I agree with Gould that it is the *process* rather than the *result* that is important in separating the two. In progenesis, it is the *immature* stage that is sexually mature; in neoteny, it is the *adult* stage that is sexually mature but juvenile characteristics have not kept the same pace and are retained in the true adult stage.

In my opinion, characters of parasites need not be purely morphological to qualify as "adult" or "juvenile", they can refer also to parts of the cycle. As Freeman (1973) points out, a characteristic of the adult stage of cestodes is their enteral habit, whereas the metacestode stage ("Juvenile stage") is parenteral. Hence, in *Archigetes* the coelom habitat as well as morphological features can be used to establish the developmental state of the individual.

B. CESTODARIA

From time-to-time, caryophyllideans have been grouped with *Amphilina* and *Gyrocotyle* (Figs. 1a and 1b) in the subclass Cestodaria Monticelli, 1892. Variations on this theme continue to the present, despite the fact that the only basic similarity between caryophyllids and the two genera above is the monozoic body form. Features of life cycle, development and morphology of amphilinids and gyrocotylids are so different from caryophyllideans that to include all three groups together in one class, as recently proposed by Wardle *et al.* (1974), is to imply a close evolutionary relationship that has not been supported by any new evidence. On the contrary, workers who have recently studied evolutionary relationships of all monozoic cestodes (Freeman, 1973; Dubinina, 1974a, b; Malmberg, 1974; Stunkard, 1975) conclude that caryophyllideans are along different evolutionary lines from any of the other monozoic cestodes. Indeed, Dubinina (1974a) has erected the new class Amphilinoidea, considering it closer to the monogenetic trematodes than to the cestodes. All the data from earlier work and that since 1972 convince me that caryophyllids have evolved separately from amphilinids and gyrocotylids and therefore the latter two groups will be outside further discussions in this paper.

Also outside the coverage, are some other so-called monozoic forms. Because their morphology is quite unlike either *Amphilina* or *Gyrocotyle*, there seems no question whatsoever that the genus *Biporophyllaeus* Subramanian, 1939, is based on a detached proglottid. According to Joyeux and Baer (1961), it may be a Tetraphyllidean proglottid, whereas Yamaguti (1959) indicates that this genus, as well as *Anteropora* Subhapradha (1957), may be detached proglottids or hyperapolytic ones of Tetraphyllidean or Trypanorhynchidean cestodes. To these examples of isolated proglottids mistaken for cestodarians should be added the genus *Mastocembellophyllaeus* recently described by Shinde and Chincholikar (1977). Until the complete strobilae from which the detached proglottids came are described, it is pointless to make extensive systematic judgments, including synonomies, of any of these genera.

C. BIOLOGY OF CARYOPHYLLIDEANS

1. *General*

Caryophyllidea are monozic tapeworms parasitic in the intestine of freshwater fish, primarily of the orders Cypriniformes and Siluriformes. There are approximately 111 described species in 42 genera scattered in all zoogeographical regions with the largest number (46) in the nearctic and the smallest (1) in the neotropical region. There is a high degree of endemism with only two species, *Archigetes sieboldi* and *Glaridacris catostomi* being reported from more than one zoogeographical region. Fish become infected by eating tubificid worms (Oligochaeta) that harbor the metacestode stage. Aquatic oligocheates eat the operculate eggs that liberate a non-ciliated, six-hooked oncosphere which metamorphoses to the procercoid stage in the coelom or seminal vesicles of the tubificid worm. Except for some species of *Archigetes*, which may also mature in oligochaetes, the procercoid stage loses the cercomer on ingestion by the fish host and develops directly *in situ* into the plerocercoid-like adult stage. For more specific details of the life cycle, zoogeography and host–parasite relationships, see Mackiewicz (1972).

Caryophyllideans are not the only monozoic or unsegmented cestodes; nor are they the only ones that can mature in an invertebrate. In the small (less than six species) order Aporidea, species of the genera *Nematoparataenia* and *Apora* from duck and swans are monozoic, but share no other features with caryophyllids. *Gastrotaenia*, also of the order Aporidea, is not monozoic but lacks segments and like *Apora* is also found embedded in tissue (Willers and Olsen, 1969). According to Ginetsinskaya (1944), the lack of gonopores, characteristic of the order, and the subcutaneous habit can be considered aberrant characteristics indicative of neotenic forms.

The more common cestodes lacking external segmentation are the monotypic genera *Cyathocephalus* (Fig. 11b), *Spathebothrium* (Fig. 11c) and *Bothrimonus* (Fig. 11d; see Burt and Sandeman, 1969, for review of this genus) of the Spathebothridea, and the pseudophyllidean *Anantrum* Overstreet, 1968 (=*Acompsocephalum* Rees, 1969); *Cyathocephalus* is from salmonid and coregonid freshwater fishes, the others are from marine hosts. In *Anantrum*, the uterine pore and genital atrium are on opposite surfaces, and in *Bothrimonus* they are usually together and occasionally on alternate surfaces; in the other genera, the genital pores are also together but are normally on alternate surfaces. All have conspicuous internal proglottization and are thus unlike caryophyllids. The phylogenetic and systematic significance of the lack of segmentation and placement of genital pores has been discussed by Rees (1969).

Cyathocephalus, like *Archigetes*, is one of the few other cestodes that can mature in an invertebrate. On the basis of an extensive study of the development of *C. truncatus*, Wiśniewski (1932) concluded that this species was a neotenic plerocercoid. However, sexually mature forms were not found in the intermediate host, an amphipod crustacean *Gammarus*. More recently, Amin (1978) found 10 gravid procercoids of *C. truncatus* in the haemocoel of the large amphipod *Pontoporeia affinis*. Eggs were found in the haemocoel, but it was not clear whether they had come from a broken cuticular pouch (as in *Archigetes*) or from functional genital pores. Nevertheless, the fact that the procercoid stage was gravid is a clear indication of progenesis. In my opinion, the vertebrate phase of *Cyathocephalus* may also be a progenetic stage rather than an adult phase because it so closely resembles a plerocercoid with primary segmentation. Whether such progenetic procercoids can complete their cycle without a fish host is not known. In my opinion, it is quite possible that eggs liberated from a decaying *Pontoporeia* could be eaten by others to complete a one-host cycle; the success of such a cycle would depend on dispersion of eggs and the population density of the crustaceans. It appears to me, however, that the factors for success of a one-host cycle for *Cyathocephalus* are not as favourable as they have been for *Archigetes*.

2. *Classification*

The long and tortuous history of the classification of the monozoic tapeworms is one of the most complex of all the cestodes. As reviewed earlier (Mackiewicz, 1972), modern classification (since 1900) has regarded caryophyllids either as cestodarians, a family of the Pseudophyllidea, or as an independent order. Most helminthologists have abandoned the cestodarian status (but see Wardle *et al.*, 1974) because of the absence of a 10-hooked, lycophora larva so characteristic of *Gyrocotyle* and *Amphilina* as well as morphological features such as the placement of the genital pores (Figs 1a and 1b). The Pseudophyllidean status, too, has lost considerable adherents for various reasons, among them the monozoic condition and realization that caryophyllids constitute a large group (over 100 species) that have oligochaetes as intermediate hosts. Since 1972 the separate ordinal status of the Caryophyllidea has been acknowledged by helminthologists who have had experience with the broad aspects of cestode classification (Freeman, 1973; Dubinina, 1974a; Wardle *et al.*, 1974; Schmidt and Roberts, 1977) and is accepted here (see the discussion in Section VD).

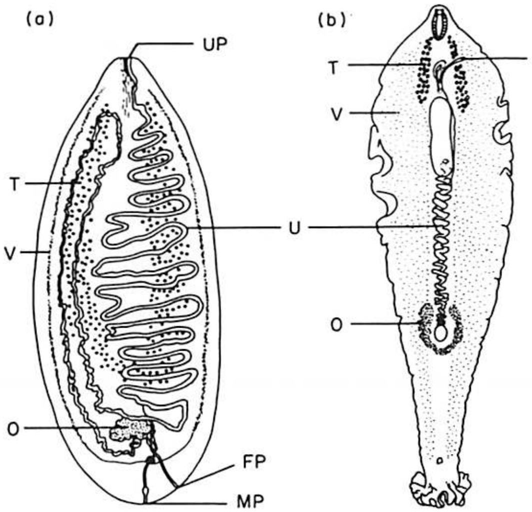

FIG. 1. (a) *Amphilina foliacea* (Rud.). (Adapted from Dubinina, 1974a.) Note position of uterine pore (UP), much removed from the female gonopore (FP) (compare with Fig. 11a). (b) *Gyrocotyle urna* (Grube and Wagener) Dorsal aspect. Male gonopore on venteral side (compare with Fig. 14). (Adapted from Lynch, 1945.)

3. *Intermediate hosts*

All evidence indicates that caryophyllids use only tubificid annelids as intermediate hosts (Table 1); in *Archigetes*, tubificids may also serve as definitive hosts. A list of the cestodes found in tubificid species may be found in Mackiewicz (1972) and Demshin (1975); additional records, primarily from the USSR, are in Grigelis (1972) and Dremkova (1974). With the studies on the life cycle of *Khawia sinensis* by Demshin (1977), *K. japonensis* by Demshin (1978), *Glaridacris vogei* by Williams (1978) and *Isoglaridacris wisconsinensis* by Williams (1980) the total number of caryophyllids experimentally infected in tubificids is now eleven. These data, in concert with the great number of records of naturally occurring infections, establish beyond doubt that caryophyllids do not need additional invertebrates, such as copepods or amphipods, to complete their development to the procercoid stage. Whether or not copepods or amphipods can be experimentally infected is not known, however.

All known life cycles of caryophyllideans involve aquatic oligochaetes of the families Naididae and Tubificidae. Among the 20 species recorded as intermediate hosts (Table 1) a number have a cosmopolitan distribution, and one, *L. hoffmeisteri*, is the most common and wide-spread tubificid known (Brinkhurst and Jamieson, 1971). An account of the biology of this species may be found in Kennedy (1966), and Brinkhurst and Jamieson (1971) have reviewed the aquatic oligochaetes of the world.

TABLE 1

Aquatic oligochaete hosts of caryophyllid cestodes

(Compiled from Demshin (1975), Dremkova (1974) and Grigelis (1972).)

Oligochaete	Number of cestode species
Class Oligochaeta	
Order Naidomorpha	
Family Naididae	
Stylaria lacustris (L.)	2
Dero digitata (Müller)	1
D. limosa Leidy	1
Unicinais unicnata (Oersted)	2
Ophidonais serpentina (Müller)	1
Family Tubificidae	
Euilyodrilus hammoniensis (Michaelsen)	3
Psamoryctes albicola (Michaelsen)	1
P. barbatus (Grube)	3
Peloscolex multisetosus (Smith)	2
Limnodrilus aurostriatus (Southern)	2
L. udekemianus Claparède	6
L. hoffmeisteri Claparède	14
L. claparedeanus Ratzel	5
L. cervix (Brinkhurst)	1
L. goti Hatai	1
L. willeyi Nomura	1
Tubifex tubifex (Müller)	8
T. templetoni Southern	4
T. barbatus Grube	1
T. hattai Nomura	1

In general, most species live in fresh water where they are a conspicuous part of the benthos, living in mud and sediment from which they extract organic matter (Stephenson, 1930). In addition to being an important but much underestimated source of food of fish (Kennedy, 1969), there are several important characteristics of tubificids that have a direct bearing on their role in the evolution of caryophyllids. Among these are (a) tolerance of low oxygen levels, (b) possessing a large coelom, and (c) having a relatively long life cycle.

The tolerance of tubificids to low oxygen tensions is well known. According to Palmer (1968), *T. tubifex* is a respiratory regulator down to a critical level of about 1·0 to 1·5% oxygen, below which its oxygen consumption drops off sharply. It is doubtful, however, that tubificids can respire anerobically for any length of time; it is possible, however, that they can be facultative anerobes (Brinkhurst and Jamieson, 1971). By being able to survive, in fact thrive, in an environment generally hostile to most other aquatic metazoans, tubificids remained as new, unexploited hosts (or intermediate hosts) for any newly evolving parasitic organism with stages that could also survive such environmental conditions.

The coelom is a large cavity that extends the length of the tubificid body, providing ample space for parasite (procercoid) development. For example, the length of the body for the three commonest intermediate hosts of caryophyllids is: *Limnodrilus hoffmeisteri*, 20–35 mm; *L. udekemianus*, 20–90 mm; and *Tubifex tubifex*, 20–200 mm. Of 83 species of caryophyllids, over 51% are less than 15 mm long as adults, with about 12 species less than 5 mm in length (Mackiewicz, 1972). Unlike the restricted space in the coelom of copepods or amphipods, that of tubificids can theoretically allow for growth beyond the normal metacestode stage, and in small species such as *Archigetes* this additional space, as well as a relatively long life span, may have been another of the factors leading to the evolution of progenesis in that genus. With the elimination of the definitive host and a shortening of the cycle, selection would favour such a progenetic form and eventually lead to the evolution of a progenetic species. Since tubificids had been established by the Permian period (Stephenson, 1930) more than 200 million years ago, there has been sufficient time for such associations to evolve.

According to Kennedy (1966), *L. hoffmeisteri* may take from one to two years to mature. Once infected with a caryophyllid, such a long life span greatly increases the period of infectivity thus compensating for a lowered egg output by the parasite (as compared with a polyzoic cestode). Any life cycle characteristic that increases the probability of parasite contact with the host would seem to have selective value.

By living in a habitat where oxygen often becomes a limiting factor, by feeding on mud and thereby allowing easy access within the oligochaete, by having a spacious coelom of the same shape and length as the worm itself and by living for more than a few months—these features collectively offered an extraordinary opportunity for exploitation by a newly evolving parasite. The wonder is that there have not been many other parasites as successful as the caryophyllids in evolving adaptations for cycles with the very common aquatic tubificid oligochaetes.

4. *Definitive hosts*

Vertebrate hosts of caryophyllids are exclusively freshwater fish although there are some scattered records, regarded here as accidental, from estuarine fishes such as *Pleuronectes* (Pleuronectidae), *Gobius* (Gobiidae) and *Zoarces* (Zoarcidae). Other rare and probably accidental hosts ingest infected tubificids while feeding on benthic organisms. Such host families as Clupeidae, Salmonidae and Percidae are of this type and serve to illustrate that a wide variety of hosts are exposed to and ingest infected tubificids, thus exerting selective pressure on cestode survival.

However, the dominant hosts are, by far, ostariophysan fishes (Table 2) with about 75% of the hosts from the cyprinoid families Cyprinidae (minnows) and Catostomidae (suckers). Next in importance are six siluriform families (catfish), which contain collectively about 17% of the hosts. These two orders contain over 90% of caryophyllid hosts, a figure that strongly suggests a definite relationship (coevolution?) between host and parasite.

According to Greenwood *et al.* (1966), ostariophysan fish (a) consist of from 5000 to 6000 known species and thus constitute the major group of freshwater fish, (b) have some marine members (i.e. in the Plotosidae; see Table 2) and (c) are relatively primitive teleosts being placed near the base of a dendrogram showing evolutionary relationships of Division III (distinctively teleostean level ancestry) teleosts (Greenwood *et al.*, 1966, Fig. 1, p. 349). They are known from the Tertiary period. The Cyprinidae, the dominant hosts for caryophyllids, is the dominant family of freshwater fish in the world, with some 2000 known species and distributed on all continents except Australia and South America (Darlington, 1957). Catostomids, with less than 100 species, are found almost exclusively in North America with two species in Asia; the siluriform families are widely distributed in the Ethiopian and Oriental zoogeographical regions, with one (Plotosidae) from Australia.

TABLE 2

Zoogeographical distribution and principal families of freshwater fish hosts of caryophyllid cestodes

Hosts	Genera	Species	Zoogeographical region[1] (number of hosts)
Superorder Osteoglossomorpha			
Order Mormyriformes			
1. Mormyridae	1	1	E
Superorder Ostariophysi			
Order Cypriniformes			
Suborder Characoidei			
2. Characidae	1	1	E
Suborder Cyprinoidei			
3. Cyprinidae	40	51	P(37), N(10), O(3), E(1)
4. Catostomidae	9	25	N(25), P(1)
5. Cobitidae	3	4	P
Order Siluriformes			
6. Bagridae	3	3	E(2), O(1)
7. Clariidae	1	5	E(3), O(2)
8. Heteropneustidae	1	1	O
9. Mochokidae	1	4	E
10. Plotosidae	1	3	A
11. Schilbeidae	1	1	O
TOTALS	62	99	P(42), N(35), E(12), O(7), A(3)

[1] A, australian; E, ethiopian; N, nearctic; O, oriental; P, palearctic.

Although the hosts of the Caryophyllidea are a diverse group they have one common characteristic—similar feeding habits. For example, such species as *Mormyrus cashive* (Mormyridae), *Cyprinus carpio* (Cyprinidae), *Catostomus commersoni* (Catostomidae), *Clarias batrachus* (Clariidae), *Tandanus tandanus* (Plotosidae), *Synodontis schall* (Mochokidae) and *Heteropneustes fossilis* (Heteropneustidae) generally have benthic feeding habits. There can be little doubt that the feeding habits of the host have played a key role in the initial stages of the evolution of these cestodes by bringing tubificids and fish together, thus enabling a cycle to evolve. In my opinion, feeding habits are more important than the phylogenetic relationships of hosts *per se* when considering the evolutionary relationships of hosts to their parasites. *Esox* (pike, Esocidae), *Perca* (perch, Percidae) and *Micropterus* (bass, Centrarchidae) have not evolved as hosts of caryophyllids because they are primarily non-benthic feeders and not because they are phylogenetically more (or less) advanced than the cypriniformes, or even that they are non-ostariophysan. Whether caryophyllids are now physiologically incompatible with such hosts is problematical. However, judging from the extensive host list (Mackiewicz, 1972, Table V), which includes more than 104 species in six superorders, it is apparent that these tapeworms have a potentially wider host spectrum, limited to a great extent by the feeding habits of the host.

II. PERSPECTIVE

A. PROGENESIS

The essence of evolution involves the action of natural selection on the adaptations of organisms to their environment. These adaptations may involve morphology, physiology, development, behaviour, or the life cycle itself; in truth evolution is an interrelationship of all of these. But this fact does not mean that all adaptations have had an equal influence on the evolutionary direction of a group. So it is with the Caryophyllidea that progenetic development, much more widely spread in the Trematoda (Grabda-Kazubska, 1976), has been a key feature in their evolution.

Perhaps the best current treatment of progenesis and evolution is that of Gould (1977). The statement of Løvtrup (1978) notwithstanding, I believe the sections dealing with progenesis and life-history strategies provide a valid framework for viewing caryophyllid evolution. Those ideas or conclusions in Gould (1977) that have particular significance in understanding caryophyllid evolution are as follows.

1. *A primary variable in setting life-history strategy is the timing of maturation*

Progenesis is one important consequence of altering maturation time and thus itself becomes the object of natural selection. Rather than just a phenomenon that affects maturation only, it must be viewed in the context of the whole cycle in order to understand its role in the evolution of an organism. Features of a progenetic stage, such as morphology, site selection, or size, may in fact have no adaptive significance but be the normal consequence of progenetic development. Only by understanding the relationship between how progenesis affects survival and the developmental consequences of progenesis can one study the evolution of the Caryophyllidea. Without progenesis it is possible there would be no Caryophyllidea.

2. *Some adult features will accompany progenesis as a result of precocious maturation*

Maturation is an integration of complex physiological and developmental processes throughout a whole organism. One system does not complete its development without concommitant effects or changes in other systems. As a result of these interrelationships, a progenetic organism can be a mixture of "adult" and "juvenile" characters. Just as precocious maturation leads to the production of eggs, an adult developmental character, so too it may accelerate changes in other adult characters which may be more closely related to morphology. Viewed in this light, the presence of an adult morphological character (well-developed scolex, for example) becomes the *result* of progenesis and therefore is not evidence that the character is an adaptation *for* the progenetic stage.

3. *Progenesis plays a role in the rapid origin of higher taxa*

The conclusion is based on the answer to the following questions. What are the genetic consequences of progenesis? Or, what is the fate of the genes of the adult stage when that stage is not fully expressed in progenesis? Since evolution is basically a cytogenetic process (White, 1973) the fate of these "left over" genes may have a potentially profound effect on the evolution of an organism. By a process analogous to gene duplication that yields "extra" genetic material, Gould (1977) believes that the "unemployed" genes (he uses DeBeer's term) are transformable genes that are now available for experimental change. Progenesis is thus a mechanism that gives an organism unusual capacity to evolve rapidly in a new direction with very little genetic input. In theory, this mechanism allows for rapid evolution of new taxa because, though the gene transformations may be rare, few are needed to cause great changes. In speaking about origins of the Ctenophora, Gould (1977, p. 341) comments "Only one creative progenesis is required for the entire phylum". Surely the evolution of a monozoic tapeworm from a polyzoic one (or the reverse) is a relatively small and plausible step or series of steps when viewed against the enormous genetic potential and the millions of years of geological time available for experimentation and selection.

4. *Components of life-history strategies are adaptations selected by, and not merely consequences of, evolutionary process*

Timing of reproduction, fecundity, or other aspects of theoretical population ecology are integral aspects of the evolutionary process. Among other things, survival of a parasite depends ultimately on how well the whole cycle, *as a cycle*, has been selected for and adapted to the environment (or environments) in which it lives. Past studies on caryophyllid evolution have relied almost exclusively on classical evolutionary theory in which adaptations have been defined in terms of morphology or behaviour. Results, not process, have been elaborated. By not relating life cycle strategies to selective pressures, any scheme on the evolution of caryophyllids is lacking in justification and is little more than an exercise in speculation.

B. REPRODUCTIVE FITNESS

The monozoic body plan *per se* carries with it several important implications for the reproductive biology and evolution of caryophyllids. Consider for a moment that, by not having the capacity to strobilate, monozoic tapeworms are deprived of that feature which is characteristic of most helminth parasites—enhanced reproductive capacity. There can be little doubt that there is a net loss in reproductive capacity in monozoic forms compared with polyzoic cestodes actively producing proglottids. Furthermore, this net loss is not compensated for by asexually reproducing stages in an intermediate host (as in the Digenea, also monozoic) or by asexual reproduction in some metacestodes (i.e. *Echinococcus*). Thus, fitness in caryophyllids may be less dependent on the absolute reproductive capacity of the adult stages and more so on the interrelationships of their other aspects of biology; reproductive capacity, of course, remains an important aspect of that fitness. In my opinion, one of these aspects is the life cycle itself, especially the ecological relationships of the intermediate host, aquatic oligochaetes. Viewed in this perspective, one of the central themes directing the evolution of caryophyllids has been the natural selection of adaptations and loss of genetic capacity in the cyle that increases fitness in the absence of greatly enhanced reproductive potential.

In the final analysis, the factors that have contributed to the evolutionary success of caryophyllids should be related to reproductive fitness and to increasing the probability of completing a cycle. According to Fairbairn (1970), the major contributions to reproductive fitness are adaptations and loss of genetic capacity; adaptations are goal directed, the loss of genetic capacity is not. The difference between these two concepts is not always clear because, according to Fairbairn, the identification of an adaptation may be basically independent of the evolutionary history of a species, whereas the identification of the loss of genetic capacity always assumes that in the past such information was present. But to make this assumption, one must have a good understanding of phylogeny and evolution of the organism; unfortunately this is not true for caryophyllids. In the absence of a knowledge of the evolutionary history of caryophyllids and the functions or adaptive significance of characteristics, it is very difficult to assess accurately their relationship to reproductive fitness. Despite these severe constraints, the evolution of caryophyllids will not be fully elucidated unless each characteristic or life cycle feature is viewed in the total perspective of adaptations, loss of genetic capacity and reproductive fitness.

III. CHARACTERISTICS AND POSSIBLE EVOLUTIONARY SIGNIFICANCE

A. EXPERIMENTAL MONOZOIC FORMS

Caryophyllids are the only naturally occurring monozoic tapeworms with a hexacanth embryo (see Section IC1). Anomalies with a second set of reproductive organs on a lateral branch have been reported from *G. catostomi* by Mackiewicz (1978) and Williams (1979) and from *Penarchigetes* sp. (=*P. fessus*) by Mackiewicz (1978). As in *Cyathocephalus*, the dorsal and ventral surfaces of these individuals are not fixed; a reversal of the dorsoventral axis also appears to be the condition in *Taenia pisiformis* but not in *T. saginata*, *T. solium* or *D. latum* (Mueller, 1953). There is no evidence that any caryophyllid can produce multiple sets of reproductive organs other than by branching. There is some evidence that the reverse is true, namely that a monozoic condition can be derived from a polyzoic one.

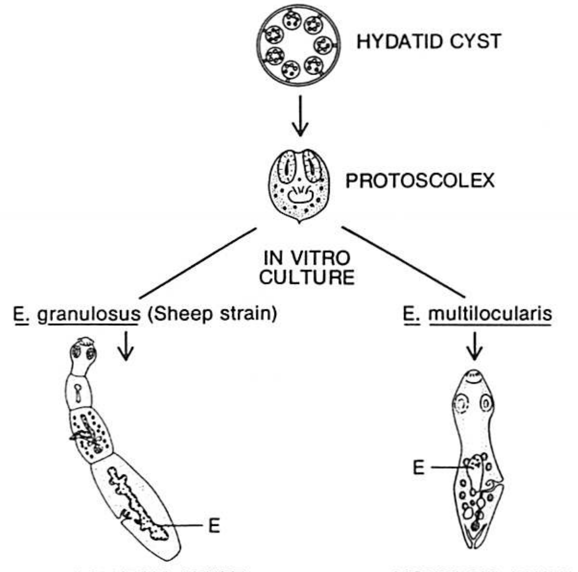

FIG. 2. Experimental production of monozoic adults of *Echinococcus multilocularis*. "Horse" and "cattle" strains of *E. granulosus* do not grow in culture. Monozoic adults appeared to have a full complement of reproductive organs but eggs (E) are unfertilized and do not embryonate. (Modified from Smyth and Davies (1975) and Smyth (1979).)

The experimental (*in vitro*) cultivation of sexually mature but sterile monozoic adults of *Echinococcus multilocularis*, less often *E. granulosus*, by Smyth and Davies (1975) and Smyth (1975) is the only direct experimental evidence that monozoic forms can be secondarily derived from a normally polyzoic species (Fig. 2). By using various media, these authors were able to produce easily and consistently up to 70% monozoic forms (*E. multilocularis*) in culture, thus indicating that such production was not a rare, isolated event. Monozoic adults had a full complement of male and female reproductive organs but unlike polyzoic forms insemination had not taken place and eggs remained unfertilized and did not embryonate. Many questions regarding the process of strobilization, onset of sexuality in cestodes, and induction of monozoic differentiation in *E. multilocularis* are discussed by the authors. However, they state no conclusions regarding the evolutionary significance of this important discovery. It would appear that the production of monozoic forms would greatly strengthen the view that monozoic cestodes are secondarily derived from polyzoic ones. Until we are able to compare the cytodifferentiation in the neck of *Echinococcus* with that of any caryophyllid, such a conclusion is premature in my opinion.

A basic developmental difference between monozoic and polyzoic cestodes is that monozoic ones apparently lack the germinative region in the neck (Wiśniewski, 1930), so characteristic of polyzoic worms. It is proglottid production (or strobilization) and not segmentation that separates the two body forms. In *Cyathocephalus* (see Fig. 11b) and *Spathebothrium* (see Fig. 11c), for example, we have proglottidization but not segmentation. Because either polyzoic or monozoic forms can be produced, depending on the medium, it would appear that the germinal region in the neck of *Echinococcus* has been suppressed, rather than being absent. In my opinion, any cestode that is genetically polyzoic, regardless of the morphology, is basically a polyzoic tapeworm. The ultimate test that a cestode is basically monozoic or polyzoic must be decided at the genetic and cytodifferential level—not only from the morphology of the adult stage. It is quite clear from the outstanding work on *Echinococcus*, that through suitable manipulation in culture, a polyzoic worm may be genotypically polyzoic but phenotypically polyzoic or monozoic. True monozoic cestodes, as far as we know, are genotypically and phenotypically monozoic.

This is not to minimize the evolutionary importance of the experimentally produced forms. If segmentation can be suppressed *in vitro* surely it is possible that other basic developmental processes of polyzoic cestodes may have been altered through a long history of genetic experimentation and selection in the immensity of geological time. Whether similar alterations can be induced in metacestode or immature stages remains to be seen. It is important to bear in mind, however, that caryophyllids may not be *adult* polyzoic cestodes that have become monozoic through suppression of strobilization but that they are sexually precocious *immature* cestodes. Neither the procercoid nor plerocercoid stages are normally characterized by segmentation, hence their maturation by progenesis does not involve suppression but rather a truncation of ontogeny. Segmentation may occur in some plerocercoids in advanced stages of development, such as in the large plerocoids of *Ligula* or those of some *Diphyllobothrium* spp. whose plerocercoids form a primary strobila once ingested by a vertebrate (Freeman, 1973). Although a plerocercoid may not be segmented under the proper conditions, it may indeed form segments indicating that the capacity to segment is present. Progenesis may so truncate ontogeny that this capacity to segment is not expressed for lack of time rather than a true suppression of a capability that would ordinarily be expressed. Biologically and developmentally the monozoic *Echinococcus* can, therefore, be quite different from a caryophyllid though they both share the same morphological body plan.

Perhaps most important from an evolutionary point of view in the context of polyzoic *vs* monozoic, is that a cestode, as a biological entity or species, is composed of *all* life-cycle stages and not only the adult one. A change in only one stage cannot be interpreted as representing a basic change in the cestode as a life form. Without information on comparative cytodifferentiation between monozoic *Echinococcus* and caryophyllids, or whether or not the monozoic culture forms give rise to stages lacking asexual reproduction, a basic feature of the life cycle of caryophyllids, the monozoic *Echinococcus* should be regarded as aberrant or anomalous polyzoic tapeworms, comparable to polyradiate cestodes, and not monozoic cestodes at the same developmental or biological level as caryophyllids.

B. CALCAREOUS CORPUSCLE DISTRIBUTION

Calcareous corpuscles are a common characteristic of most cestodes (von Brand, 1973). They are a conspicuous element primarily of immature stages, being numerous and generally scattered randomly throughout the body. That there is indeed no discrete pattern to corpuscle distribution in the procercoid or plerocercoid stages can be verified by examining some representative illustrations of the following few species. Pseudophyllidea: *D. latum* (Rosen, 1918, Plate I, Fig. 2; Wardle and McLeod, 1952, Figs. 32F and 35), *D. norvegicum* (Vik, 1957, Plate I, Figs. 3 and 4), *Schistocephalus pungitti* (Dubinina, 1966, Figs. 82, 83), *Triaenophorus nodulosus* (Rosen, 1918, Plate II, Fig. 5), *Eubothrium salvelini* (Boyce, 1974, Figs. 10–12); Proteocephalidea: *Proteocephalus percae*, *P. macrocephalus* (Jarecka, 1960, Table I, Figs. 2 and 3; Table II, Fig. 5), *P. filicollis* (Freze, 1965, Figs. 39, 8–10); Cyclophyllidea: *Paruterina candelabraria* (Freeman, 1957, Plate I, Fig. 10); *Valipora campylancristrota*, *Neogryporhynchus cheilancristrotus*, *Paradilepis scolecina* (Kozicka, 1971, Figs. 1, 2 and 3) and *Ophiotaenia filaroides* (Mead and Olsen, 1971, Figs. 3 and 5).

Recently, Mackiewicz and Ehrenpris (1980) found that the distribution of calcareous corpuscles in some caryophyllids is unlike that in any other tapeworm. Briefly, they found that in *Glaridacris laruei* and *G. catostomi* the corpuscles are in discrete clusters that form a serially repeating pattern in two lateral dorsal and ventral rows (Figs. 3 and 4); there is little change in the number and distribution of clusters between small immature worms and much larger, mature ones; and clusters are lost in the posterior part of gravid worms but few in the organ-free neck region (Fig. 4d). Despite the basically different morphology of the two species, there was a mean of 22·4 cluster pairs (corresponding lateral clusters are considered a pair) with a range of 17–28 in 129 *G. laruei*; in 17 *G. catostomi* there was a mean of 23 with a range of 17–33 cluster pairs. These, as well as other data, indicated that morphology

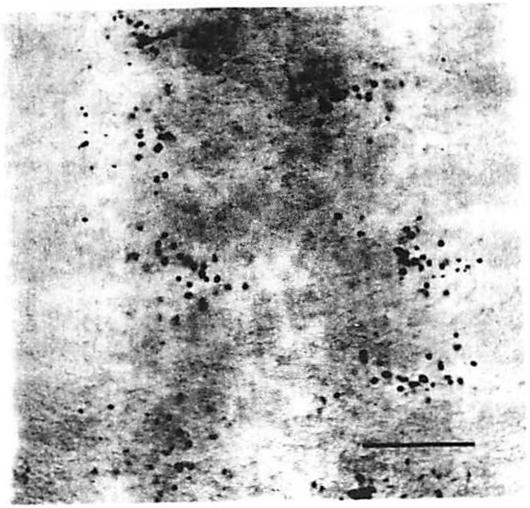

FIG. 3. Portion of *Glaridacris catostomi* illustrating the distribution of calcareous corpuscles that is strongly suggestive of cryptic segmentation. Approximately 33 lateral pairs of corpuscle clusters were present on the immature worm, 6 mm long. Note that each cluster does not always have a corresponding one on the opposite side. Corpuscles stained with silver nitrate; scale equals 0.1 mm. (From Mackiewicz and Ehrenpris, 1980; with permission of the editor of the *Proc. Helminthol. Soc. Wash.*)

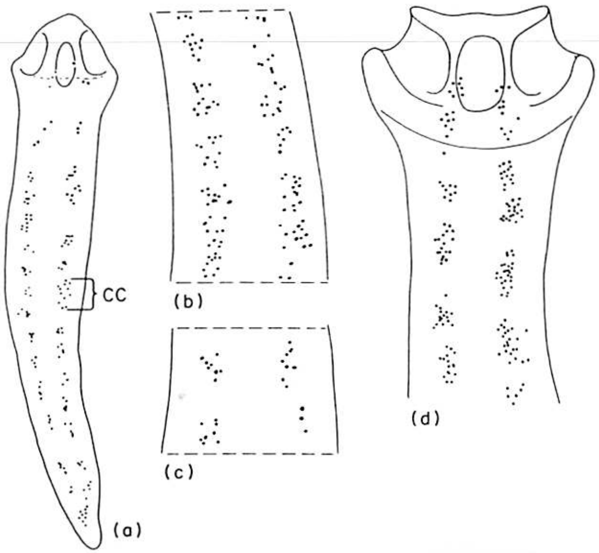

FIG. 4. Drawings of calcareous corpuscle distribution in *Glaridacris;* one side shown. (a) Immature *G. laruei*, corpuscle cluster (CC). (b) Immature *G. catostomi.* (c) Immature *G. laruei* showing four cluster pairs in neck region. (d) Scolex and neck of gravid *G. laruei.* (Adapted from Mackiewicz and Ehrenpris, 1980.)

per se is not the sole determinant of corpuscle distribution. They concluded that the loss of corpuscles in gravid worms was probably correlated with increased calcium utilization rather than an alteration of the basic pattern that appears to be a characteristic morphological feature of each species. No such pattern, however, was found in *Hunterella nodulosa* and *Monobothrium hunteri* where corpuscles occurred either in scattered clusters in the scolex or were randomly, but not homogeneously, distributed throughout the body of the worm.

Is there any evolutionary significance to the serial distribution of calcareous corpuscles in some caryophyllids? From a review of the diverse functions of corpuscles in invertebrates (Simkiss, 1976), trematodes (Erasmus and Davies, 1979) and cestodes (Chowdhury and DeRycke, 1977; Befus and Podesta, 1976) it does not seem unreasonable to assume that such ubiquitous structures have essentially similar functions in polyzoic and monozoic cestodes. If this assumption is correct, then it is probable that the unusual corpuscle *distribution* may be more related to some developmental or morphological feature *characteristic of the monozoic body plan*, than to a generalized physiological *function*.

After failing to correlate cluster distribution with any developmental or morphological feature, although correlation with the ganglia nodes on the lateral nerve cords of *G. laruei* was inconclusive, Mackiewicz and Ehrenpris (1980) concluded that the serially arranged clusters (1) "... are a form of cryptic segmentation that reflects differing physiological states in adjacent groups of cells", and (2) "... reflect a type of 'physiological segmentation' that preceded somatic segmentation and the formation of a strobila". In the first instance, there is no other corroborating evidence that supports this view; in the second, it assumes that caryophyllids had a strobila that was subsequently lost through the evolution of a progenetic cestode as Wiśniewski (1930) and Janicki (1930) proposed long ago. Yet one can also argue that such "physiological segmentation" had to precede somatic segmentation that has yet to evolve. As attractive as this alternative may be, it would suggest that caryophyllids were preadapted to be segmented. At present I see no genetic, physiological, or morphological basis for accepting this alternative view because there are no adaptive or selective pressures that would appear to have influenced the *expression* of this clustering characteristic *before* the appearance of the related strobilar morphology.

An alternative new interpretation related to strobilization is (3) that the corpuscle distribution is a vestige of the pattern in an ancestral *segmented* worm. In this case, we must assume that the genes for corpuscle distribution and function are linked. So vital are corpuscles for the life of a cestode that the genes for them (and their distribution) would be retained in the genome regardless of how many life cycle stages are dropped or added. Because the procercoid, plerocercoid and strobilate stages are in different hosts or different sites in the same host, thus being exposed to different physiological conditions, it is possible that there are separate genes regulating corpuscle distribution for each stage. The fact that there is no discernible pattern to corpuscle distribution in the immature stages of the cestodes mentioned above, would support this view because the genes regulating strobilization, and hence the segmental pattern of corpuscle distribution, have not been turned on. With progenesis, however, the genes for the sequential production of corpuscles (but not strobilization with which it was formerly related) in the *adult stage* are turned on and expressed, even though the strobilate stage no longer exists. Of possible significance in this regard is the fact that the segmental pattern is best developed in the neck region of *Glaridacris*; in polyzoic cestodes strobilization begins in the neck. If this analysis of events is accurate, then corpuscle distribution in some caryophyllids may be a true vestige of an *adult* character of polyzoic cestodes. The prospect that this may be the first visible indication of a masked gene related to segmentation in an ancestral polyzoic stage in the early evolution of caryophyllids is an exciting one.

C. INTRANUCLEAR GLYCOGEN VACUOLE IN VITELLINE CELLS

1. *General*

Electron microscope study of vitellogenesis of *Glaridacris catostomi* by Swiderski and Mackiewicz (1976a) has confirmed an earlier report (Mackiewicz, 1968) that the nuclei of mature vitelline cells have a single, large glycogen vacuole which serves as one of the food reserves in the egg. First appearing as beta glycogen particles, larger aggregates of alpha glycogen are soon formed, eventually fusing together to produce a very large, non-membrane-bound vacuole that displaces the nucleus to one side (Fig. 5a). Such a nuclear vacuole appears to be unique among cestodes, not being found in the vitelline cells of the proteocephalidean *Proteocephalus longicollis* by Swiderski *et al.* (1978), cyclophyllideans *Catenotaenia pusilla*, *Inermicapsifer madagascariensis* and *Hymenolepis diminuta* by Swiderski *et al.* (1970), tetraphyllid *Echeneibothrium beauchampi* by Mokhtar-Maamouri and Swiderski (1976a) and pseudophyllideans *Diphyllobothrium latum* by Schauinsland (1885, Plate 7, Fig. 2), *Cyathocephalus truncatus* by Wiśniewski (1932, Plate 13, Fig. 1), *Schistocephalus solidus* by Smyth (1956, Fig. 3), and *Bothriocephalus clavibothrium* by Swiderski and Mokhtar (1974). Vitelline cells of the proteocephalideans and tetraphyllids have glycogen and "yolk" or lipid as energy reserves whereas the caryophyllids and cyclophyllids have glycogen only (Mokhtar-Maamouri and Swiderski, 1976a). The presence of the nuclear vacuole is therefore not correlated with the absence of lipid in the vitelline cells; of greater importance is whether there are lipid reserves in the egg. Eggs of caryophyllideans and pseudophyllideans are quite similar to each other (Mackiewicz, 1968) each having an ovum surrounded by numerous vitelline cells and enclosed in a rigid capsule; however, caryophyllidean eggs have only glycogen as a reserve whereas those of the pseudophyllids have glycogen and lipid (Fig. 5b). The presence of both glycogen and fat in the eggs of pseudophyllideans is corroborated by the studies of Ginetsinskya *et al.* (1971) on *D. latum*. Her studies showed also that the eggs of the pseudophyllideans *Ligula columbi* and *Triaenophorus nodulosus* lacked glycogen but had lipid. In my opinion, this difference in energy reserve in the egg is correlated with the intranuclear glycogen vacuole, and may be of major consequence in the evolution of caryophyllid cestodes.

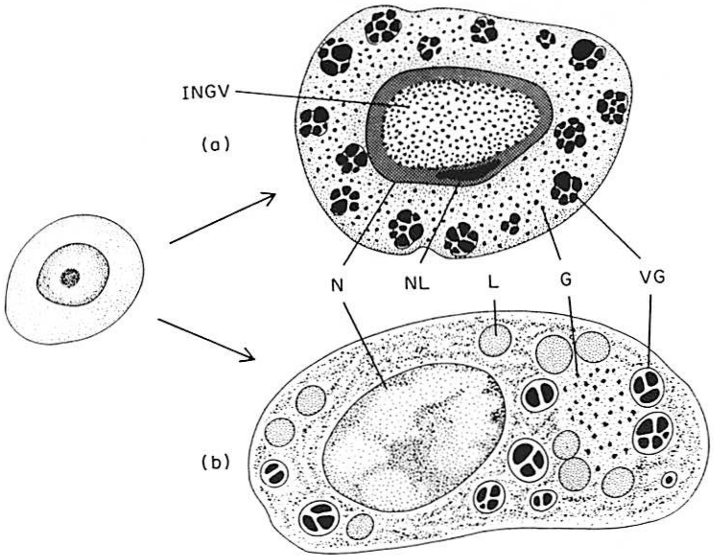

FIG. 5. Mature vitelline cells from electron microscope studies. (a) Caryophyllidea, *Glaridacris catostomi*; showing prominent intranuclear glycogen vacuole (INGV), glycogen in cytoplasm (G), and vitelline globules (VG). Note how the nucleolus (NL) is displaced to one side. (Adapted from Swiderski and Mackiewicz, 1976a.) (b) Pseudophyllidea, *Bothriocephalus clavibothrium*; Note absence of vacuole in nucleus (N) but presence of lipid (L) in cytoplasm. (Adapted from Swiderski and Mokhtar, 1974.) Both cells develop from a common type of gonial cell with a large nucleus and relatively little cytoplasm.

The presence of nuclei that synthesize and store glycogen as a *normal* cell function appears to be a unique phenomenon possibly confined to caryophyllideans. They have not been found in the vitelline cells of three polyopisthocotylean and one monopisthocotylean monogenea, nor in the digeneans *Fasciola hepatica* and *Schistosoma mansoni* (Halton *et al.*, 1974). No intranuclear vacuoles occur during vitellogenesis in the free-living triclad *Dugesia lugubris* according to Domenici and Gremigni (1974); nor are they known from any other turbellarian (J. B. Jennings, personal communication). I am unable to find any reference to such intranuclear glycogen vacuoles in any other invertebrate, although they have been described from vertebrate cells.

Among vertebrates, on the other hand, intranuclear glycogen has long been associated with pathological conditions particularly in the liver (Himes and Pollister, 1962). More recently, there has been considerable interest in studying the synthesis of intranuclear glycogen in tissue cultures of Ehrlich ascites cells (Zimmerman *et al.*, 1976). Tadpole liver cells appear to be one of the few places where intranuclear glycogen synthesis appears normally; however, in this case the occurrence is a sporadic phenomenon (usually less than 10% of the cells) and glycogen vacuoles disappear with metamorphosis of the tadpole (Himes and Pollister, 1962). Clearly, the formation of intranuclear glycogen vacuoles as a normal part of vitellogenesis in caryophyllid tapeworms is apparently a rare phenomenon in the animal kingdom.

2. *Significance*

What is the adaptive significance and possible selective value of the intranuclear glycogen vacuoles in the vitelline cells of these tapeworms? There are four attractive possibilities. The first is that, with an increase in glycogen, without a concommitant increase in the number of vitelline cells per egg or in egg size, the period of infectivity would be prolonged; such a characteristic would be selected for (Mackiewicz, 1968). An adaptation for prolonged periods of survival cannot be the entire picture because on an energy/weight ratio lipid would be a more favourable energy source than glycogen. If survival with respect to time were the only factor, then why would not lipid be a more favourable energy source than glycogen? The second is that, by having intranuclear *and* cytoplasmic glycogen, the energy reserves are partitioned and could be available at different times (Swiderski and Mackiewicz 1976a), much as in starving tadpoles, where the nuclear glycogen is utilized after cytoplasmic glycogen has been depleted (Himes and Pollister, 1962). Whether such partitioning takes place in normal embryogenesis or as a special adaptive feature to insure egg survival under adverse environmental conditions remains to be determined.

Regardless of the specific function, partitioning would allow for more efficient use of energy reserves, a characteristic that also would have selective value. The third possibility is that, since vitelline cells, and hence eggs, lack "yolk" or lipid energy reserves, the increase in glycogen per cell may help to compensate (balance?) this energy loss without increasing the number of cells per egg. Unfortunately, there are no comparative data on the calorific values of caryophyllid and other comparable eggs, but with lipid. If we assume that the calorific values were somewhat equal then the increased glycogen would enable the species to survive in the absence of the more common lipid–glycogen reserve.

Before going further, it is important to examine some of the glycogen–lipid energy relationships in cestodes. As Calow and Jennings (1974) have found, free-living platyhelminths generally have an energy source rich in lipids whereas entosymbionts generally are rich in glycogen. Reasons for this difference are related to the stable food source in the gut, which removes the need for long-term storage, and the energetics of high fecundity. More recently, Jennings and Calow (1975) elaborated on their hypothesis stating that the large quantities of glycogen are an adaptation for the high fecundity which is an "automatic consequence" of the nutrient-rich gut. Formerly, it was believed, however, that the high glycogen content of parasitic worms was primarily an adaptation, or pre-adaptation (Jennings, 1973), to the low or variable oxygen tensions of the gut. Regardless of whether or not the high glycogen is an adaptation for, or a consequence of, the nutrient-rich gut, the low oxygen tensions necessitate that glycogen and not lipid be used as an energy source. In caryophyllid biology, I believe that this same glycogen–low oxygen relationship may not apply directly to the fecundity question (because no proglottids are formed) but to the ecology of the eggs. Considering that glycogen is heavier than lipid and that unlike lipid it can be utilized under anerobic conditions, these two characteristics are consistent with a life cycle that has a benthic intermediate host (see Section IC3).

As a result of these characteristics, there is a fourth possibility, the most important one for the adaptive significance of intranuclear glycogen. As a consequence of having additional glycogen in the egg to compensate (balance?) for the lack of lipid, the caryophyllid egg is better adapted *to sink* and *to survive* in a habitat (mud) with little or variable oxygen tension and as a esult the organism is able to make an evolutionary "breakthrough"—*that of enabling viable eggs to be exposed to, and exploited by, a new potential intermediate host, tubificid annelids*. As so elegantly demonstrated by Jarecka (1961), the eggs of tapeworms with aquatic cycles are adapted in various ways that greatly enhance the probability of their being eaten by intermediate hosts such as Copepoda, Ostracoda, Cladocera, Amphipoda and Oligochaeta. Without doubt, the caryophyllids have been the most successful helminths in exploiting these annelid hosts, who live in a physiologically hostile environment. According to Demshin (1975, pp. 158–161) the only other cestodes that have oligochaetes as intermediate hosts are *Hymenolepis moghensis*, *Paricterotaenia* (=*Sacciuterina*) *stellifera*, *Haploparaxis* (=*Monocholepis*) *dujardini*, *Aploparakis filum* and *A. furcigera*, all cyclophyllideans of birds. The eggs of *A. furcigera* also sink, being large and in small, relatively heavy packets (Jarecka, 1961). Nematodes have been less successful, with only two species recorded (Demshin, 1975). Even the marine polychaeta, other benthic annelids, rarely serve as intermediate hosts of cestodes (Margolis, 1971). From the very beginning, the absence of much competition for tubificid intermediate hosts allowed caryophyllids successfully to incorporate them into a cycle that also involved benthic feeding fish, thus establishing the basic caryophyllid cycle.

If the preceding analysis of the adaptive significance of intranuclear glycogen vacuoles is correct, it is not surprising that other cestodes have not been able to exploit tubificids because of the limited occurrence of such vacuoles. Furthermore, if the nuclear vacuoles are primarily an adaptation for egg survival and development, and not for some physiological functions of the mature worm, there is little reason to search for them in free-living or symbiotic turbellarians as possible clues to ancestral stock. The apparent absence of intranuclear vacuoles in the turbellaria is, therefore, of little evolutionary significance.

D. CYTOLOGY

Since 1972, our knowledge of the chromosome numbers of the Caryophyllidea has increased considerably (Table 3), largely because the chromosomes are common in testes squashes and they can be readily stained with leucobasic

TABLE 3

Chromosome numbers of caryophyllid cestodes

Species	2n	References
Caryophyllaeidae		
Archigetes sp.	18	Motomura (1929)
Hunterella nodulosa Mackiewicz and McCrae	14	Mackiewicz and Jones, (1969), Grey (1979)
Glaridacris laruei (Lamont)	16	Grey and Mackiewicz (1974)
	16, 18; 24–27 (3n)	Grey (1979)
G. confusus Hunter	16	Grey (1979)
G. catostomi Cooper	20; 30 (3n)	Grey and Mackiewicz (1980)
G. vogei Mackiewicz	20	Grey (1979)
Monobothrium hunteri Mackiewicz	20	Grey (1979)
Biacetabulum biloculoides Mackiewicz and McCrae	20	Grey (1979)
Isoglaridacris folius Fredrickson and Ulmer	18	Grey (1979)
I. jonesi Mackiewicz	18	Grey (1979)
I. bulbocirrus Mackiewicz	18; 27 (3n)	Grey (1979)
Caryophyllaeus laticeps (Pallas)	30 (3n)?	Grey (1979)
Lytocestidae		
Atractolytocestus huronensis Anthony	24 (3n)	Jones and Mackiewicz (1969), Grey (1979)
Lytocestus indicus (Moghe)	16	Vijayaraghavan and Subramanyam (1977)
Khawia iowensis Calentine and Ulmer	16	Grey (1979)
K. rossittensis Szidat	16	Grey (1979)
Notolytocestus minor Johnson and Muirhead	12	Grey (1979)
Caryoaustralus sprenti Mackiewicz and Blair[1]	6	Grey (1979)
Capingentidae		
Capingens singularis Hunter	14	Grey (1979)
Balanotaeniidae		
Balanotaenia bancrofti Johnson	14	Grey (1979)

[1] Listed as "gen. et sp.n. from Australia", recently described by Mackiewicz and Blair (1980).

fuchsin. Unlike chromosomes from other cestodes those of caryophyllids are quite large; for example, the largest (in μm) for several species are: *Hunterella nodulosa*, 6–8; *Glaridacris laruei* (diploid), 7–12; and *G. catostomi* (triploid) 6–8. For the first time it is now possible to make accurate idiograms and comparative studies of cestode karyotypes, techniques commonly used in contemporary systematic studies of other organisms. With refined techniques such as banding, it may be possible also to get precise information on translocations, inversions, deletions and duplication on chromosomes and

thus learn something of the cytogenetics involved in cestode speciation. With this combination of desirable cytological characteristics, it is little wonder that caryophyllids have been designated the *Drosophila* of tapeworms (Mackiewicz, 1976).

Although only 18 species have been studied cytologically (Table 3) there are some patterns emerging that may aid in understanding the evolution and systematics of this group of cestodes. For example, there is a greater range in chromosome numbers (6 to 20) than has been found in any other order. The Lytocestidae have the lowest number; the genus *Glaridacris* has more than one number but *Isoglaridacris* has only one; and some species, such as *Glaridacris laruei*, have at least two cytologically distinct diploid populations. Unlike the Pseudophyllidea where $2n=18$ for four species of *Diphyllobothrium*, the wide range in chromosome numbers for caryophyllids suggests that the evolution of the Caryophyllidea was accompanied by various changes in chromosome number and other structural rearrangements of the karyotype. Clearly, the Caryophyllidea provide a rare opportunity to study the cytotaxonomical relationship within a cestode group. Cytological studies are needed to better understand the systematic relationships of genera to each other and to intepret the difficult questions dealing with intra- and interspecific variation.

However, the greatest discovery by far is that of polyploidy (triploidy), to date not described from any other cestode. Chromosome numbers are known for approximately 53 species of strobilate tapeworms. Polyploidy in *Atractolytocestus huronensis* and *Glaridacris catostomi* has been described in detail by Jones and Mackiewicz (1969) and Grey and Mackiewicz (1980); further examples (Grey, 1979) will be described in subsequent publications. In both cases of triploidy, spermatogenesis was abnormal to the point of complete failure and parthenogenesis was presumed to occur because eggs remained unfertilized. This cytological evidence, as well as the lack of any for hybridization, indicates that these triploids are autoploids. Except for *A. huronensis*, which may have *Markevischia sagittata* (chromosome number unknown) from the Amur carp in North Asia as the diploid parent or biotype (Jones and Mackiewicz, 1969), diploid and triploid forms have been demonstrated in the other three species, a fact that has an important bearing on the evolution and speciation of caryophyllids.

The role of polyploidy in evolution and speciation in animals has been studied much less than in plants; for reviews see Mayr (1963), White (1973, 1978) and Jackson (1976). As in caryophyllids, most cases of polyploidy in animals are associated with parthenogenesis because of the adverse effects of ploidy on meiosis. It appears, however, that polyploidy, despite its incompatibility with sexual reproduction, has selective advantages. According to Jackson (1976), polyploids have a greater ecological amplitude that allows them to better exploit new environments, even though they have the identical genes of a diploid. In many organisms, where survival of widely dispersed progeny is a key factor in species survival, the ability to survive in new environments would clearly have adaptive value. However, in obligate parasites with complex life cycles involving more than one host, increased (physiological) amplitude must involve all stages in the cycle in order to maintain the complex host–parasite interrelationships in the cycle. Unless this is done, the cycle would fail and, with it, the species. In such highly specialized parasites as cestodes, survival depends not so much on being able to radiate into new hosts but in evolving ways of consistently reaching the same or narrow group of hosts. The hallmark of cestodes is specificity, not adaptability. An increase in the number of eggs or reproductive potential has a much greater adaptive and selective value than has the increased ecological amplitude of adults. Indeed, one of the chief diagnostic features of cestodes is the chain of proglottids which provides such large numbers of eggs. Perhaps polyploidy is so rare (absent?) in strobilate tapeworms because an increase in the ecological amplitude of any stage would so disrupt the cycle that such stages would be selected against. On the other hand, the ability to survive in diverse ecological situations may have played an important role in the early evolution of parasite species. How such a possible increase in ecological amplitude resulting from polyploidy might be applied to *A. huronensis* in the carp, *Cyprinus carpio*, was discussed at some length by Jones and Mackiewicz (1969).

Another closely related "benefit" of polyploidy (also based on data from free-living organisms) is the ability of polyploids to regulate some sets of genes whereas others are expressed totally. The net effect is to give certain types of polyploids, "exceptional genetically based amplitude with which they should be able to move into new habitats with requirements beyond their progenitors capabilities" (Jackson, 1976, p. 223). Since the functional aspects of this "benefit" would serve also to increase the ecological amplitude of the species, it would probably not be adaptive for cestodes for the reasons discussed above. Furthermore, the triploid caryophyllids are not found in a wider variety of hosts, a fact that tends to support the view that polyploidy has not led to a wider host spectrum. Regrettably, there are no data on the comparative distribution of polyploids and triploids in the intestine. Nor do we know if polyploids in single-species infections have larger populations because of an increased capability to extend beyond their normal sites in the intestine; or if polyploids have a competitive advantage for available sites in multiple infections (two to four species), which may be as high as 29% in some regions (Mackiewicz *et al.*, 1972).

A final effect of polyploidy is to increase the size of the organism. In the only species studied in detail, diploid and triploid individuals of *Glaridacris catostomi* were very similar in size (Grey and Mackiewicz, 1980). However, though not significantly different in size, ten mature triploids had a mean size of 23·2 mm (range, 10–47 mm) whereas ten diploids had a mean size of 17·5 mm (range, 11·5–24 mm) (A. J. Grey, personal communication). It is not unreasonable to assume that a larger parasite would have a greater capacity to store eggs but whether there would be an absolute increase in egg production is not known. If there is an increase in egg production (see Section IIIE) correlated with increased worm size, then even though the increase in body size between diploid and triploids is not statistically significant, at the population level this difference might result in enough eggs being liberated by the polyploids to have them selected for over the diploid ones. In the Bozenkill river, only triploid *G. catostomi* were found, indicating that the polyploids had indeed been selected for but the exact reason for this dominance has yet to be explained (Grey and Mackiewicz, 1980).

Without more information on reproductive potential, site preference and population biology of diploids and polyploids in the same species, it is difficult to assess the evolutionary significance of polyploidy in the caryophyllids. Of course the most immediate effect of triploidy has been to alter the reproductive biology of the individual from sexual to asexual reproduction (parthenogenesis). The net effect of this change is to have the potential for establishing populations, as in the Bozenkill river, with virtually no gene flow and essentially little further evolution. Combined with the consequences of parthenogenesis, discussed in the next section, possible increased egg production (correlated with increased body size) may serve to give polyploids selective advantage over their diploid parent species. If this assumption is true, then it is not unreasonable to expect polyploidy to occur with increasing frequency in caryophyllideans.

E. PARTHENOGENESIS

Parthenogenetic reproduction among tapeworms is rare (Cable, 1971). *Ilisha parthenogenetica* (of unknown systematic status), known only from plerocercoids in the mesentery and liver of the Indian shad *Hilsa ilisha*, was originally thought to be a parthenogenetic adult (Southwell and Prashad, 1918) but later Southwell and Prashad (1923) thought it was reproduction by a plerocercoid in a manner similar to the production of germ balls by trematodes. According to Wardle and McLeod (1952), however, *Ilisha* reproduced by endogenous budding. A report (Coil, 1970) that the dioecious cyclophyllidean *Gyrocoelia* is parthenogenetic was subsequently corrected (Coil, 1972).

Parthenogenesis in the Cestoidea would appear then to be confined to the Caryophyllidea. First described from the triploid *Atractolytocestus huronensis* by Jones and Mackiewicz (1969) it has since been found in three other species. Study of spermatogenesis of the triploid "race" of *Glaridacris catostomi* reveals that functional sperm are not produced and parthenogenesis is presumed to occur (Grey and Mackiewicz, 1980). Similar conditions appear to be true (Grey, 1979) in two other cases of polyploidy (Table 3), *G. laruei* and *Isoglaridacris bulbocirrus*. Since the effect of parthenogenesis is to produce cestodes that are essentially functional females one could use the term "thelytoky" rather than parthenogenesis. It is clear that without parthenogenesis none of the sterile polyploids would survive. Except for *A. huronensis*, which apparently has no diploid forms in North America, the other three species have such diploid forms, a condition that raises important problems regarding the systematic status of diploids and triploids of the same species. Some of these problems have been addressed by Enghoff (1976) and White (1978).

No less important are the evolutionary implications with populations of parthenogenetically produced clones. The evolutionary significance of parthenogenesis has been discussed at length by many workers, among them Suomalainen (1962), Suomalainen *et al.* (1976), Mayr (1963), Tomlinson (1966), White (1973, 1978) and Maynard Smith (1978). Except for Price (1977), who has an illuminating discussion of parthenogenesis and parasite evolution, the other treatments generally deal with biparental, non-parasitic species. The type of parthenogenesis may determine its evolutionary significance. Oogenesis has not been studied in any of the triploid caryophyllids hence it is not known whether the parthenogenesis is of the automictic or apomictic type, the latter being most common (Suomalainen *et al.*, 1976). If apomictic, there are no new gene combinations, except by mutation, and there is a greater chance of giving rise to a stable parthenogenetic form; the offspring retain the genetic make up of the parent worm. In ecologically diverse environments, the lack of genetic diversity resulting from this genetic stability would have an adverse effect on the evolution of a species. However, the disadvantage of having genetically uniform progeny is lowered for an intestinal parasite because of a highly stable and predictable environment provided by the homoeostasis of the host (Price, 1977). Such genetic stability (resulting from parthenogenesis) may, in fact, be selected for if particularly adaptive gene combinations are fixed in homozygous individuals, especially, according to Price (1977), those gene combinations that may be essential in the coevolutionary tracking of the host system. Because of their hermaphrodism, strobilate structure, isolation in hosts and ease of self-fertilization, tapeworms are considered largely homozygous (Jones, 1967; Logachev, 1970). If the maintenance of genetic stability is an adaptive feature for some intestinal parasites such as cestodes, why then should parthenogenesis, one way of preserving genetic stability (another would be selfing, undoubtedly a common phenomenon in strobilate tapeworms), be much more common in (restricted to?) the Caryophyllidea than in other cestodes?

A possible answer may be related to the monozoic body plan. It is obvious that strobilization greatly increases the reproductive potential of polyzoic cestodes; without such an increase it is doubtful that polyzoic cestodes would have been successful parasites. Caryophyllids, however, lack the reproductive advantage associated with strobilization yet are also successful parasites. How does one resolve this apparent contradiction? Unlike trematodes, also monozoic, and small tapeworms with few proglottids (e.g., *Echinococcus*) where the limited reproductive capacities in their adult stages have been greatly supplemented by a much increased asexual reproductive capacity in other stages, caryophyllids lack all traces of asexual reproduction in any part of their cycle and have the basic reproductive formula: 1 egg = 1 adult. Clearly, any adaptation or change in the reproductive biology that would increase egg production or egg survival would have obvious selective value. Unfortunately, we do not have any data on either of these two important aspects of caryophyllid biology, but on theoretical grounds it is possible that through parthenogenesis, the energy normally devoted to sperm and egg production could all be used for egg production, thus effectively increasing the reproductive potential. Through parthenogenesis, such individuals would have greater fitness under non-stress conditions and also when the density of tubificids or fish is low. By having sexually and parthenogenetically reproducing individuals in the same species, and thus having the benefits of both modes of reproduction, the species would have a greater fitness than could be achieved with only one form of reproduction. Whether this reproductive polymorphism is wide-spread (we know of it in three species so far) remains to be seen. In my opinion, however, parthenogenesis, so wide-spread in parasitic and non-parasitic arthropods (Price, 1977) and found in numerous other animals including vertebrates, is an important, and perhaps even common, adaptation preventing sterility (resulting from polyploidy) and at the same time may increase the reproductive potential of caryophyllids.

F. SPERM MORPHOLOGY

Fine structure of sperm is known for only one species—*Glaridacris catostomi*. The spermatozoon is a very elongate, filiform structures about 260 μm long consisting of a body portion and a single axoneme (flagellum) with a 9+1 structure (Swiderski and Mackiewicz, 1976b). As in other cestode sperm, an acrosome and mitochondria are absent. Paradoxically, the presence of a single axoneme places the Caryophyllidea together with the Cyclophyllidea, anoplocephalids and some tetraphyllids (Table 4; Figs 6a–g) with which they share few other characteristics, and not the Pseudophyllidea, that have two axonemes, with which they are most often associated. Although sperm morphology has been used to assess phylogenetic and taxonomical

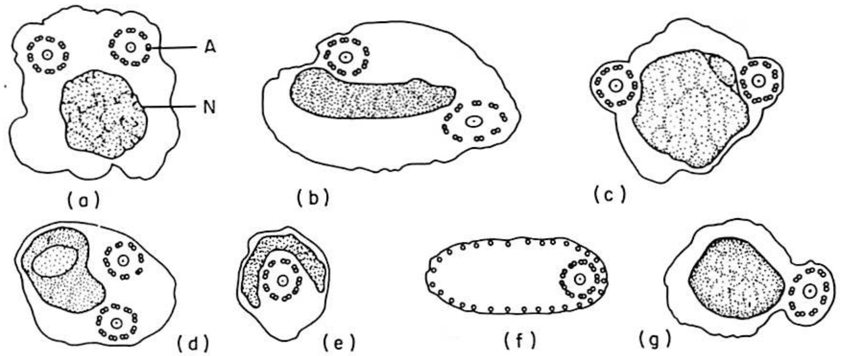

FIG. 6. Diagrammatic drawings from electron micrographs of cestode spermatozoa. (a) Trypanorhyncha: *Lacistorhynchus tenuis* (from Swiderski, 1976), axoneme (A), nucleus (N). (b) Proteocephalidea: *Proteocephalus longiocollis* (from Swiderski and Eklu-Natey, 1978). (c) Pseudophyllidea: *Diphyllobothrium latum* (from von Bonsdorff and Telkka, 1965). (d) Tetraphyllidea: *Acanthobothrium filicolle* (from Mokhtar-Maamouri and Swiderski, 1975). (e) *Echeneibothrium beauchampi* (from Mokhtar-Maamouri and Swiderski, 1976b). (f) Cyclophyllidea: *Hymenolepis diminuta* (from Sun, 1972). (g) Caryophyllidea: *Glaridacris catostomi* (from Swiderski and Mackiewicz, 1976b).

TABLE 4

Axoneme number in cestode and some turbellarian spermatozoa

Organism	Reference
ONE AXONEME (9+1)	
CESTOIDEA	
Caryophillidea	
Glaridacris catostomi	Swiderski and Mackiewicz (1976b)
Cyclophyllidea	
Hymenolepis nana	Rosario (1964)
Echinococcus granulosus	Morseth (1969)
H. diminuta	Rosario (1964), Lumsden (1965), Sun (1972)
H. microstoma	Swiderski (1970)
Catenataenia pusilla	Swiderski (1970)
Inermicapsifer madagascariensis	Swiderski (1970)
Taenia hydatigena	Featherston (1971)
Anoplocephalidea	
Monieza expansa	Swiderski (1968)
Tetraphyllidea	
Echeneibothrium beauchampi	Mokhtar-Maamouri and Swiderski (1976b)
TWO AXONEMES (9+1), SINGLE AXIAL FILAMENT	
CESTOIDEA	
Pseudophyllidea	
Diphyllobothrium latum	von Bonsdorff and Telkka (1965)
Tetraphyllidea	
Acanthobothrium filicolle	Mokhtar-Maamouri and Swiderski (1975)
Onchobothrium uncinatum	Mokhtar-Maamouri and Swiderski (1975)
Trypanorhyncha	
Lacistorhynchus tenuis	Swiderski (1976)
TURBELLARIA	
Rhabdocoela	
Kalyptorhynchia	Hendelberg (1969, 1974, 1977)
Acoela	Hendelberg (1969, 1974, 1977)
TWO AXONEMES (9+1), TWO AXIAL FILAMENTS	
CESTOIDEA	
Proteocephalidea	
Proteocephalus longicollis	Swiderski and Eklu-Natey (1978)
TURBELLARIA	
Rhabdocoela	
Dalyellioida	Hendelberg (1969, 1977)
Typhloplanoida	Hendelberg (1969, 1977)
ONE AXONEME (9+2)	
TURBELLARIA	
Nemertodermatida	Tyler and Rieger (1975), Hendelberg (1977)
Rhabdocoela	
Kalyptorhynchia (?)	Hendelberg (1977)

relationships in the turbellaria by Hendelberg (1974, 1977), it is clear that great caution should be exercised when using sperm morphology as an indicator of phylogenetic relationships within the cestoidea. Yet when one considers that the primitive metazoan sperm has a single axoneme (Franzen, 1956) like that of the Nemertodermatida, which have been separated from the Acoela and are placed near the base of the phylogenetic tree of platyhelminth relationships by Hendelberg (1977), then the occurrence of a single axoneme in some cestodes (i.e., caryophyllids) may not be due to reduction, as suggested by Hendelberg (1970), but rather evidence of a close relationship to primitive turbellarians. If this is the case, how does one reconcile the presence of one axoneme (Fig. 6g) in the sperm of acknowledged primitive cestodes (Caryophyllidea) as well (Fig. 6f) as highly advanced ones (Cyclophyllidea)? Without some knowledge of the fertilization biology of concerned groups and the factors that influence sperm motility it will be difficult to answer this question.

G. VITAMIN B_{12}

The presence of high concentrations of vitamin B_{12} (cyanocobalamin) in *D. latum* and its relationship to pernicious anaemia in humans is well known (Tötterman, 1976). High concentrations have also been recorded from other pseudophyllidean cestodes such as the plerocercoids of *Ligula* sp. and *Spirometra mansonoides*, where the values have been, respectively, between 200–600 and 100–600 μg B_{12} per 100 g dry weight (Weinstein and Mueller, 1970). Rausch *et al.* (1967) reported a value of 2·6 μg B_{12} per g dry weight for adults of *Schistocephalus solidus*. In contrast to the high concentrations in pseudophyllidean cestodes, no detectable amounts of vitamin B_{12} have been found in cyclophyllidean cestodes, namely *H. diminuta* and *Taenia taeniaeformis*, using microbiological assays (Weinstein and Mueller, 1970; Tkachuck *et al.*, 1976).

Since first reporting a pink colour for some specimens of *Biacetabulum infrequens* and *Glaridacris laruei* (Mackiewicz, 1972), assays for vitamin B_{12} have been done on two species. Radioisotope assay of adult *Hunterella nodulosa* and *Glaridacris laruei* from *Catostomus commersoni* yielded values of vitamin B_{12} per 100 g dry weight of 248·9 and 1228·8 μg respectively. Although these results are preliminary, they establish that caryophyllidean cestodes, like pseudophyllideans studied thus far, have high concentrations of vitamin B_{12}. Apparently cestodes with vitamin B_{12} are able to form propionate from succinate, whereas those without cyanocobalamin cannot. The implications for energy metabolism for these pathways in cestodes have been discussed by Tkachuck *et al.* (1977).

Can one attribute any selective advantage to cestodes with the capacity to accumulate large amounts of vitamin B_{12}? It is already known that cestodes that accumulate vitamin B_{12} also have propionate as a product of anerobic energy metabolism (Tkachuck *et al.*, 1977). According to Tkachuck *et al.* (1977) vitamin B_{12} is converted into a coenzyme (methylmalonyl-CoA mutase) which is used in the reverse pathway reaction of succinate to propionate. In the process, ATP is also formed as one of the products of this reaction. The authors conclude that organisms with high concentrations of vitamin B_{12}, which accumulate propionate rather than succinate as a product of anerobic energy metabolism, may have the advantage of an increased energy yield (ATP) from their substrates. Apparently, all known helminths that form propionate as a major product of fermentation, rather than primarily succinate, lactate or products unrelated to propionate, contain high concentrations of vitamin B_{12}; species without vitamin B_{12} do not form propionate. It may be inferred from these observations that caryophyllids form propionate. However, nothing is known of the major metabolic end products of any caryophyllid, although there is some information on the enzymes of the glycolytic sequence and the tricarboxylic acid cycle in *Khawia sinensis* (Körting, 1976). If propionate is an end product in the energy metabolism of caryophyllids, accumulations of vitamin B_{12} could function to increase the energy *available for egg production*. If applied to egg production, the *increase* in egg production would help compensate for a lowered reproductive potential resulting from the monozoic body plan and the lack of asexual reproduction. Any physiological process that would increase fecundity would, of course, have adaptive and selective value.

H. C-TYPE VIRUS PARTICLES

First described from the excretory tubules of a pseudophyllid *Sparganum proliferum*, by Mueller and Strano (1974) possible C-type virus particles have subsequently been described from the following species and stages in the same order: *Spirometra mansonoides*, coracidia, procercoid, plerocercoid and adult; *Diphyllobothrium ditremum*, *D. sebago* and *Ligula intestinalis*, plerocercoids (Dougherty *et al.*, 1975). Different, nodular-like particles, some branched but not showing internal structures were also found lining the excretory ducts of an unknown proteocephalid plerocercoid, and adults of cyclophyllids *Taenia taeniaformis*, *Dipylidium caninum* and *Hymenolepis diminuta*. Earlier workers, beginning with Race *et al.* (1966), had also found nodular-like projections or processes in the excretory canals of various other cyclophyllids. Although there is some doubt that the particles from *S. mansonoides* are in fact viruses, because of the apparent absence of nucleic acids, the presence of entities lining the excretory ducts of such diverse cestodes as cyclophyllids and pseudophyllids suggests that they may be characteristic of the excretory systems of all cestodes. Recent studies by Edwards and Mueller (1978) clearly indicate that this supposition is not true because they found that C-type virus particles were not present in the following nine caryophyllid cestodes from three families: Caryophyllaeidae, *Glaridacris laruei*, *G. terebrans*, *Monobothrium ulmeri*, *Isoglaridacris folius*, *I. calentinei* and *Hunterella nodulosa;* Lytocestidae, *Atractolytocestus huronensis* and *Caryophyllaeides fennica;* Capingentidae, *Capingens singularis*. If these data are true, then one may wonder if the absence of these structures, whether viruses or simple modified microvilli, from the excretory ducts of caryophyllids is evidence of functional differences between the excretory systems of these cestodes and others or whether they reflect *a basic difference between the excretory system of monozoic and polyzoic tapeworms*. Clearly, more specific information on the origin, development and function of these C-type virus particles, or microvilli, is needed before their evolutionary significance and possible selective value can be assessed.

IV. *Archigetes* EVOLUTION

A. GENERAL

As the only cestode that has a complete, one-host life cycle in an invertebrate (see Section IC1, *Cyathocephalus*), *Archigetes* occupies a singular position in any discussion of cestode evolution. As its name indicates, *Archigetes* has been regarded either as a primitive ancient tapeworm, and for some as an ancestral cestode (Baer, 1952), modified form with a precestode cycle (Freeman, 1973; Demshin, 1971), relict of the most primitive one-host cycle (Jarecka, 1975), or an example of a cercomeromorphaean progenitor (Malmberg, 1974). Despite its long history, there are still questions regarding the evolutionary significance of *Archigetes* and there is little agreement whether or not it can be regarded as a procestode, an adult cestode, or as evidence that cestodes were originally parasites of invertebrates.

Before any of these questions can be answered, the status of *Archigetes* with respect to other caryophyllids should be clarified. The systematics and biology of *Archigetes* have been reviewed by Kennedy (1965a, b), Calentine (1962) and Kulakovskaya (1962b) and need not be repeated in detail here. It is quite possible, judging from the extensive synonomy of the genus that includes *Brachyurus*, *Paraglaridacris*, and in part *Glaridacris* and *Biacetabulum*, that *Archigetes* is in fact a collection of species from various genera. For the present, however, it is the biology and development of *Archigetes* and not the systematics that is relevant here. Except for *A. cryptobothrius*, found only in tubificids, the other five species apparently mature in both tubificids and fish. Since the stage in fish is no different from any other caryophyllid, it is the stage in the tubificid that concerns us here.

B. EGG DISPERSAL

Stages of *Archigetes* in the coelom of tubificids have two basic and unmistakable characteristics of immature (procercoid-like) stages: a cercomer and a non-functional genital pore. Both of these characteristics are absent from stages found in fish. The cercomer, a common feature on the immature stages of cestodes of various orders (Freeman, 1973), is indeed a recognized and genuine feature of "larval" cestodes and needs no elaboration. The genital pore, the second characteristic, is rendered non-functional by a covering cuticular layer (Calentine, 1964). As eggs are produced they may either accumulate in a greatly distended uterus that may occupy most of the whole worm (Fig. 7b) or they may fill a cuticular pouch formed by a splitting of the outer and inner cuticular layer (Figs 7a, 7ci and 7cii), according to Calentine (1964). Sometimes both types of egg retention take place in the same species (i.e., *A. sieboldi*). Regardless of which type occurs, eggs can be liberated only by rupturing the cuticular layers of the worm itself, processes which kill the cestode. Such mechanisms of egg deposition are surely abnormal, even aberrant. The chief way that cestode eggs can leave the infected tubificid is by rupture of the body wall and release of the cestode into the substrate where it subsequently dies, liberating the eggs. Effective egg dissemination is thus accomplished by the death of both host and parasite, clearly

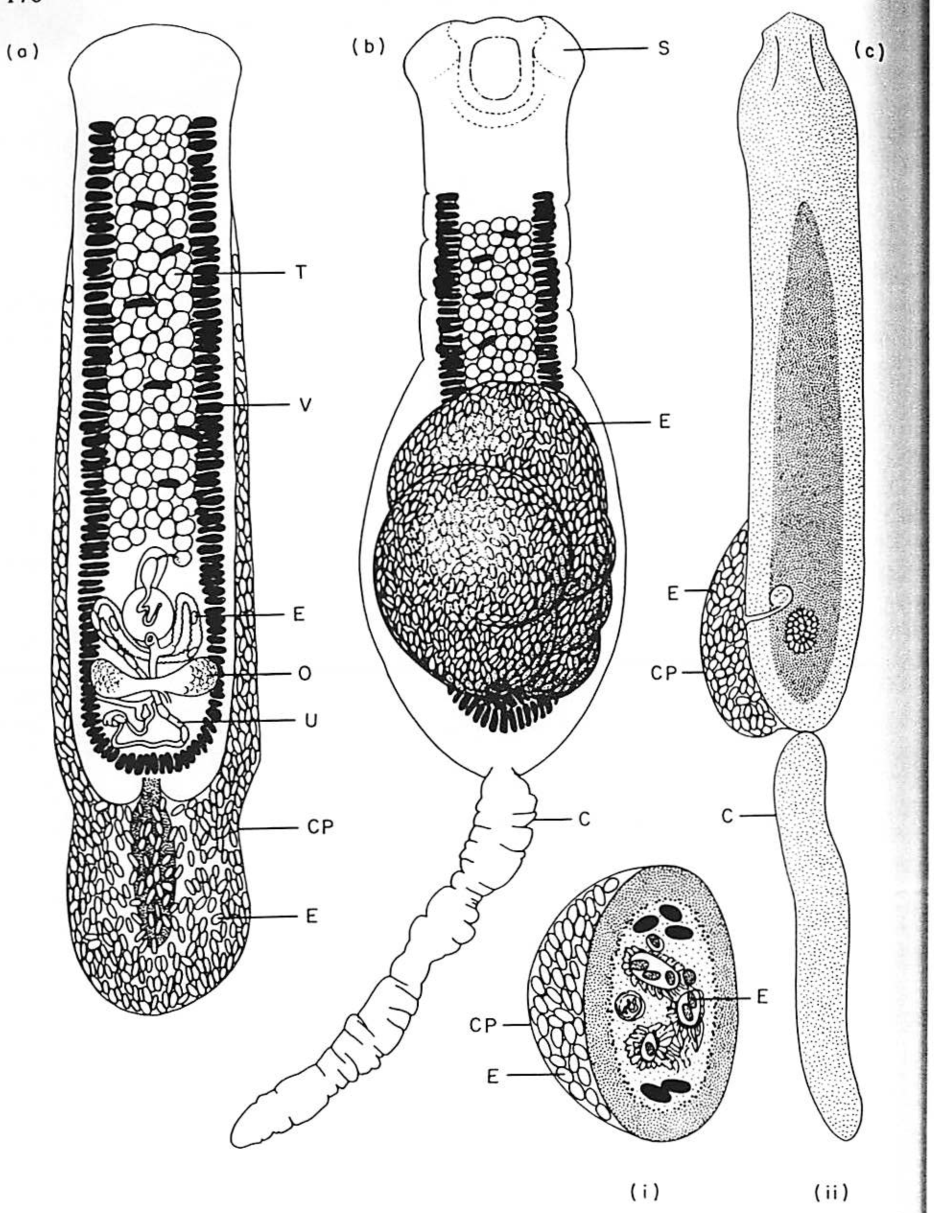

FIG. 7. (a) *Archigetes cryptobothrius* with cuticular pouch (CP) filled with eggs (E). Testes (T), vitellaria (V), ovary (O), and uterus (U) are clearly visible. (Adapted from Wiśniewski, 1930). (b) *Archigetes sieboldi* with greatly swollen uterus filled with eggs (E); well developed scolex (S) and cercomer (C) are evident. (Adapted from Wiśniewski, 1930.) (c) *Archigetes sieboldi*. (i) Cross-section through posterior portion of cercomer bearing individual illustrating cuticular pouch (CP) filled with eggs (E), also visible in the uterus. (ii) Lateral view with cuticular pouch (CP) distended with eggs (E) but not involving the cercomer (C). (Adapted from Calentine and DeLong, 1966.)

an abnormal, perhaps aberrant, mode of completing the reproductive cycle. In view of this mode of egg dissemination, the presence of a cercomer, the coelom or seminal vesicle habitat, and normally reproducing adults in fish, the conclusion is inescapable that the egg-producing stage in the tubificid is a progenetic cestode, secondarily derived from an intestinal stage in fish. Some species such as *A. limnodrili* and *A. sieboldi* appear to be able to complete and sustain a cycle in tubificids (Kennedy, 1965b; Calentine and DeLong, 1966, Nybelin, 1962), others such as *A. iowensis* can occasionally mature in tubificids but are more common in fish (Calentine, 1964); strain differences may explain why there have been conflicting data on whether a fish can be in the cycle. Additional work is necessary to determine if any species of *Archigetes* is facultatively progenetic.

C. PROGENESIS

Comparing the development of progenetic *Archigetes* with that of other caryophyllids, one finds one basic difference between the two: maturation in *Archigetes* occurs before the cercomer is lost, in the other, after. There is one immediate consequence of this acceleration: maturation is in the coelom of the tubificid, in other caryophyllids it is in the intestine of the vertebrate host. The developmental difference between the coelom stage and intestinal one can be very slight. The intestinal stage of *Archigetes* is identical to the coelom stage except that it lacks a cercomer and has a functional genital pore. Furthermore, there is a pronounced tendency toward progenesis in many caryophyllids, for example, in such genera as *Caryophyllaeus* (Sekutowicz, 1934), Kulakovskaya, 1962a; Mackiewicz, 1972; *Hunterella, Monobothrium, Glaridacris, Biacetabulum* (Calentine, 1965, 1967) and *Khawia* (Demshin, 1978) reproductive organs reach various degrees of development (but not maturity) in the cercomer-bearing stage in the tubificid coelom. We therefore have a continuum with *Archigetes* at one end and various other examples approaching complete progenesis. But what factors may have selected for complete progenesis in *Archigetes*?

A possible answer may be related to small size. If small size is the primary object of selection for progenesis, as Gould (1977) suggested for a number of free-living organisms where space is a limiting factor, then progenesis may be a passive consequence and not itself the product of selection. Space limitations within the tubificid coelom or seminal vesicle may exert a selective influence for small size. If space (and therefore some resources) is one of the limiting factors, it is therefore not surprising that progenesis is most common in small forms, such as *Archigetes*, that are generally less than 3 mm long. Should this be the case, then on theoretical grounds one can expect progenetic stages in other small forms as *Penarchigetes* (1·7 mm) and *Balanotaenia newguinensis* (0·85 mm). In my view, it is quite possible that progenesis may not be restricted to *Archigetes*, a fact also suggested by the *Biacetabulum*–*Archigetes* controversy (see Calentine, 1964, for review) as well as synonomies with other genera (see above).

According to Gould (1977), who accepts the classical view of *Archigetes*, progenesis in *Archigetes* has been ecologically determined by parasitism. Just how parasitism acts as a selective mechanism, however, is not explained. The question remains: what are the biological or ecological factors that select for progenesis whose consequence is a simplification of the life cycle? Among the possibilities, is that progenesis leads to increased fecundity, a principal attribute of parasites. Unfortunately, we do not have any data on comparative egg production for progenetic *Archigetes* and those in the two-host cycle. We know that development to the gravid stage in tubificids is very slow, 140 days for *A. limnodrili* (Kennedy, 1965a), 120 for *A. sieboldi* (Calentine and DeLong, 1966) and 100 days for *A. iowensis* (Calentine, 1964). Presumably development would be faster in the nutrient-rich intestine of a fish. If the shortest two-host cycle is less than the shortest for a one-host cycle, then there would appear to be no selective advantage for the progenetic cycle in terms of fecundity. On the other hand, it would appear that a shorter one-host cycle could produce more generations with a resultant net gain in fecundity. As Lewontin (1965) and MacArthur and Wilson (1967) have concluded, a speeding up of maturity can be more effective in the long run than increasing the fecundity or fertility per individual. These conclusions, however, are based on organisms that prolong the reproductive period by starting earlier, of obvious selective value in colonizers. In *Archigetes*, however, eggs are shed all at once because the genital pore is *non-functional* and eggs are retained until the cestode ruptures the body wall of the tubificid and dies outside the host. Unless progenesis so shortens the generation time in a one-host cycle to allow for more generations than the two-host cycle (3 to 4 months can hardly be considered short), it is difficult to see how selection is for fecundity. Even if the generation time was shortened, oligochaetes seldom have more than six parasites and thus the overall increase in egg production is not large —certainly not compared with worms in fish where there may be over 1000 individuals (Calentine, 1964). It would appear that progenesis does not greatly increase fecundity over that from a population in fish; there must, therefore, be some other basis for selection.

D. SELECTION

That basis may be related to the fact that on theoretical grounds (no actual information is available) fewer eggs are probably needed to sustain a population of *Archigetes* in a population of tubificids than in a fish population. Liberated eggs from a decaying cestode in mud can be ingested readily by other tubificids, an event of high probability because of the clumping habits of some tubificids (Brinkhurst and Jamieson, 1971) or the general abundance of oligochaetes in the benthos. Selection would favour populations of progenetic *Archigetes* because there probably would be a greater probability of their eggs being eaten by another tubificid over an egg expelled from an intestinal dwelling (fish) *Archigetes*. In my view, progenesis may so increase the probability of infection by another tubificid that the genome for this precocious development would be selected for. In this way, selection would be for limited dispersal in contrast to the wide dispersal found in the two-host cycle.

Depending on the degree of isolation and selection pressure for the progenetic trait, it is possible to get a series of *Archigetes* species showing various degrees of selection for one- and two-host cycles. With *A. iowensis*, Calentine's (1964) data suggested that only eggs from progenetic individuals would produce other progenetic cestodes; only 3·2% of 567 naturally infected tubificids were progenetic, yet 80% of the worms in carp had eggs. Clearly fish maintained the tubificid infection in nature but there was evidently a small population of cestodes with a one-host cycle. It would appear that we have here a one-host (progenetic) and two-host (non-progenetic) cycle in the same species. In *A. sieboldi*, on the other hand, the fish host appears to play a minor role in maintaining the cycle because Calentine and DeLong (1966) found that 56% of 472 procercoids were gravid in *Limnodrilus* whereas 19 *Cyprinus carpio* harboured only five gravid cestodes. Nybelin (1962) considered fish to be accidental hosts of *A. sieboldi*. In *A. limnodrili*, at the end of the series, it appears that only progenetic development takes place (Kennedy, 1965a). Its patchy distribution in *Limnodrilus*, a result of limited egg dispersal, is consistent with the hypothesis that fish are not necessary where a progenetic population (or species) has evolved. Progenesis, then, favours the one-host cycle, not because it increases fecundity, but more likely because it increases the probability of tubificid to tubificid infection.

How does one now relate the one-host and two-host cycles to the evolution and biology of *Archigetes*? Clearly, both cycles have responded to different selective pressures and in so doing have greatly increased the probability of survival for the species. The two-host cycle, normal for caryophyllids and in my view the original cycle, has a fish as the primary agent of dispersal. The risk of widely dispersed eggs not being ingested by tubificids is partially compensated for by the increased egg production from the population of intestinal cestodes; for example Calentine (1964) found up to 1523 *A. iowensis* in one carp. Success of such a cycle depends on many factors, among them the number of fish; if high, the two-host cycle can be completed more easily than when there are few fish. It is when the fish population is low, or fish are absent, that the one-host cycle has a greater selective value. Under conditions of low oxygen or high water temperatures, or any other that would limit or kill off the fish population, *Archigetes* would be able to survive without the definitive host. Should the definitive host (vertebrate) *never* return the species is still able to survive. Perhaps some species (*A. sieboldi*, *A. limnodrili* and others) have become facultative progenetic cestodes with alternate cycles in response to adverse environmental conditions or fluctuating fish populations. By being able to switch from one cycle to another, or have the potential to do so, *Archigetes* is able to survive under a greater range of stress conditions than any other caryophyllid. In terms of r–K strategies, it would appear that the two-host cycle is toward r-selection, whereas the one-host cycle is toward the K side of the r–K continuum. Whatever the genetic mechanism, production of two types of eggs or development of physiological strains, we have in *Archigetes* a remarkable cestode, one that survives by a mixture of one- and two-host cycles, rather than a cestode by-passed by evolution and surviving as an ancestral form or relict of some prehistoric tapeworm.

E. CONCLUSIONS

In the light of the developmental status of a progenetic organism and the role of natural selection in determining ecological and host–parasite relationships, what are the answers to some basic questions regarding the evolutionary position of *Archigetes* in the one-host cycle?

1. *Is Archigetes an adult cestode?* If by "adult" is meant a final reproducing stage possessing only adult morphological characteristics then the stage in the intestine of fish is an adult. The gravid stage in the tubificid is not an adult in the same sense because of the presence of *bona fide* "larval" characteristics, i.e., cercomer and non-functional genital pores. An organism cannot be both progenetic and an adult. Of course, if one regards any reproducing stage of a caryophyllid as an adult, regardless of morphological features, then *Archigetes* is an adult.

2. *Is Archigetes an ancestral cestode?* If one is convinced that *Archigetes* is an adult stage that has evolved as a parasite of tubificids, its original and only host, and is now evolving or has evolved a two-host cycle by adding a vertebrate host—the answer is yes. In my view, the evidence that (a) *Archigetes* is secondarily derived from a vertebrate dwelling stage, and (b) tubificids are intermediate hosts, is persuasive if not conclusive. Accordingly, the *Archigetes* one-host cycle must have evolved after (not before, and possibly concurrent with) the two-host cycle; the one-host cycle is thus a simplificaiton of a pre-existing two-host cycle. The one-host cycle can be adequately derived from a two-host cycle by the application of ecological theory, an elaboration of the dynamics of natural selection. Deriving a two-host cycle *from* an ancestral one-host cycle, on the other hand, requires numerous assumptions and a chain of events that become difficult to justify using ecological theory and natural selection. Viewed in this perspective, *Archigetes* is not an ancestral cestode (or precestode, procestode, relict cestode, Urcestode, or cercomeromorphean progenitor) but a form that has diverged from a two-host cycle stock through selection of progenesis as an ecological strategy. Just as progenetic digenea or monogenea are not regarded as ancestral forms, nor should *Archigetes* be.

3. *Is Archigetes more primitive than other caryophyllids?* No, if by primitive one means original, earliest, primary, ancestral or ancient; a secondarily derived form cannot be, by definition, more primitive than its ancestors. Yes, if one can provide proof that *Archigetes* is ancestral to other forms.

4. *Was the original host of Archigetes an invertebrate or vertebrate?* The answer to this question, pondered for centuries, is the same for *Archigetes* as it is for polyzoic cestodes. It is beyond the scope of this paper to review all the theories on the first hosts of cestodes.

Rosen (1918) felt that *Archigetes* is a species "*sui generis*" and is a primitive cestode of invertebrates whose relationship to other cestodes is expressed in the statement: *Fecampia–Archigetes; Archigetes–Procercoide.* He clearly felt that the parental habit of *Archigetes* was not evidence of regression in the cycle, citing the symbiotic rhabdocoel, *Fecampia* as an example of another flatworm with similar habits. Furthermore, he regarded the well-developed scolex, as he did the oncosphere, as an adaptation for parasitism and not proof that *Archigetes* was once an intestinal parasite. These views have proved to be the strongest in favour of the invertebrate origin of cestodes through an *Archigetes*-like ancestor. However, in the light of subsequent information on the morphology (i.e., cuticular pouch) and life cycle, these views should be critically reevaluated. In my opinion, it is not warranted to use *Archigetes* to support the thesis that invertebrates were the original hosts because there is no conclusive proof that the vertebrate stage followed the invertebrate one. On the contrary, the opposite appears to be true. If invertebrates were the original hosts, even in some cases, why are there no examples living today? To say they are extinct begs the question, as does indicating that evolution selected for the more complex two-host cycle.

V. EVOLUTIONARY SCHEMES (1971–1979)

A. GENERAL: ENTODERM QUESTION

There has been a long history of speculation regarding the role played by caryophyllids in cestode evolution; much of this history was reviewed by Mackiewicz (1972). Hypotheses concerning the primary or secondary nature of the monozoic condition and whether or not invertebrates or vertebrates were the original hosts form the basis of most of the speculation. With few exceptions (Cameron, 1956, 1964, for example) past hypotheses have assumed that cestodes arose through a rhabdocoel line allied to the Dalyellioida turbellarians and through the parasitic habit gradually lost all traces of a digestive system. These assumptions, together with additional arguments linking the cestoda with the monogenea (Bychowsky, 1957; Llewellyn, 1965) have formed the foundations of perhaps the most widely known recent hypothesis of cestode origin. As some of the basic assumptions of this hypothesis have been challenged, new theories of cestode origins and especially the role of caryophyllids in cestode evolution have developed.

1. *Did cestodes have a gut?*

One of the assumptions questioned recently is that cestodes have secondarily lost a gut. It has long been a zoological truth that cestodes have lost their gut through evolution in a nutrient-rich habitat, the intestine of vertebrates. There are no creditable studies, however, that present direct evidence that a gut or rudiments of one occur anywhere in the development of any cestode. By linking the cestodes with rhabdocoels or monogenea it is obvious that the gut *had* to be lost in order to make such a scheme reasonable. Inextricably tied to the question of a former gut is a related one dealing with basic cestode embryology: do cestodes have entoderm?

Both of these points have been challenged by Logacev (1968, 1970) whose influence is seen in some more recent treatments of cestode evolution. Summarizing his extensive studies on the embryology and development of cestodes, Logacev (1970) concludes that cestode cleavage is irregular and leads to a syncytial mass in which there is no entodermal layer; nowhere in cestode ontogeny is there any structure that is even remotely homologous to an intestine. Citing also the macrophagic mode of feeding through the tegument as the most primitive mode of feeding, Logacev (1970) concludes that cestodes are a phylogenetically independent branch of the intestineless Acoela. He cites the work of Severtov (1945) who concluded, with respect to the nutritional function of the tegument of endoparasites, that "the primary process depends on formation of new adaptations and not on reduction". According to Logacev, the lack of intestine, mode of feeding, absence of basal membrane and histological differentiation of inner and outer tissue link the Acoela and Cestoda together. The coracidium of the Pseudophyllidea is said to recapitulate the early turbellarian ancestor and the non-cellular character of the cestode embryo is considered a recapitulation of the phagocytoblastic or syncytial digestive parenchyma of the primitive intestineless turbellaria. His paper contains additional information on cestode histogenesis, strobilization, histology of proglottid separation, embryology, ecology and genetics which is brought to bear on his main thesis—that cestodes descended from a two-layered ancestor with no gut and are a dead-end branch evolved from ancient acoelous turbellarians.

It is well to remember that Logacev's hypothesis uses a different frame of reference, not that of classical germ-layer theory with the well-known ectoderm and mesoderm concepts, but that of the primary two-layer theory with kinetoblast and phagocytoblast. He is therefore quite correct in stating cestodes have no entodermal derivatives since the concept of entoderm is not incorporated in his basic theory of embryology for primitive metazoans. In the lower metazoa, which include the acoelous turbellarians, the kinetoblast forms the external layer and the phagocytoblast, the internal structures. Since the boundaries between these two layers are not always distinct, organs may have tissues partly derived from each layer. How the kinetoblast–phagocytoblast hypothesis applies to metazoan evolution is discussed at great length by Beklemishev (1969, Vol. 2; 194) who says of the Cestoda that there is a "complete reduction of the central phagocytoblast and of the entire internal digestive apparatus, as a result of their parasitism in the gut of vertebrates". He concludes that the absorptive function passes to the kinetoblast which forms the external epithelium (tegument) and that the low organization level of lower worms is why cestodes and acanthocephala lose the gut. Unlike Logacev, Beklemishev, using the same frame of reference, derives cestodes from the Dalyellioida rhabdocoels through reduction and loss of the gut.

Whether or not cestodes have entoderm may thus be more a question of definition rather than actual fact; however, since the term has been used so widely in the literature it will be retained here. According to Schauinsland (1885) and Vergeer (1936), who have done the most complete studies on pseudophyllidean embryology, the ciliated embryophore of *D. latum* is ectoderm and the inner part, mesoderm; Hyman (1951) designates the inner mass "mesentoderm". As pointed out by Burt (1963), such a view of an entodermally derived tegument would be consistent from a functional and morphological point of view. Cameron (1956) has even suggested that the adult cestode may be entirely entodermal, hence explaining the lack of a gut anywhere in cestode development; on the other hand, he also indicates that cestodes may be an entodermal sac whose lumen has been filled with mesoderm. Ogren (1956, p. 423), the foremost student of cestode embryology in the western hemisphere, concludes that "identification of germ layers is not possible with certainty at this time", after studying the embryology of *Mesocestoides corti*. He further states that the body covering of *M. corti* is not a digestive epithelium and therefore is not entodermal; there are no entodermal derivatives in *M. corti* according to Ogren (1956), who concludes (p. 423) "In the present state of our knowledge of tapeworm embryology, all that can be said is that the tapeworm strobila is predominantly 'mesodermal'". The concept of entoderm or any other germ layer is not used in the recent studies of cestode embryology by Euzet and Mokhtar-Maamouri (1976). It is perhaps significant that Rybicka (1966) does not use any germ-layer concept in her extensive review of embryogenesis in cestodes. When one tries in vain to reconcile cestode embryology with classical germ-layer theory it becomes clear why DeBeer (1958) considered the germ-layer theory of Haeckel as "fallacious".

From the above it is apparent that there is little question that cestodes lack a gut anywhere in their development, but how does the classical germ-layer theory relate to cestode embryology? Some attempt to resolve the issue has been made by Bazitov (1974) who studied the embryology of *Hymenolepis nana* in serial sections (5 µm, thick) prepared with a variety of stains including methyl green pyronine. Briefly, he found that a blastocoel is formed and that the two pale entodermal blastomeres protruding into the blastocoel gradually became lysed leaving an embryo with ectoderm and ectomesoderm, the latter eventually filling the blastocoel. Morphogenetic migrations and distinct layers are not evident because of the low level of complexity of the onchosphere; a two-layered gastrula, as generally understood, is not formed. In the opinion of Bazitov (1974), only the germ-layer theory can give a satisfactory explanation of the embryology of *H. nana*, even though there are some abnormalities in development such as the abortive character of gastrulation. In a subsequent paper on the embryology of the cyclophyllidean *Microsomacanthus paramicrosoma*, Bazitov and Lapkalo (1977) strengthen the evidence that entodermal blastomeres (micromeres), homologous to entomesodermal micromeres of other flatworms, abort at the coeloblastula stage (Figs. 8a–c). They report that in gastrulation of cestodes the vitelline-rich macromeres migrate to the surface of the embryo, whereas in the lower turbellaria they become part of the inner cell mass of entomesoderm. The macromeres form the vitelline envelope at the surface and function in the utilization of vitelline material and exogenous food. According to Bazitov and Lapkalo (1977, p. 110), "In connection with this the necessity for the formation of a gut disappeared. It is necessary to think that the reduction of the alimentary system in cestodes is tied not only to the changes in perspective significance of macromeres but also to the degeneration of

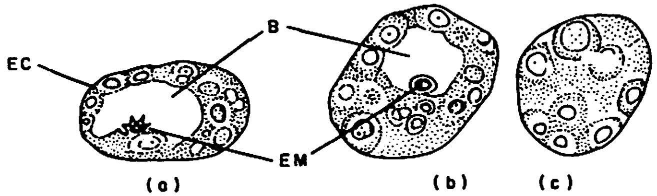

FIG. 8. Sections of embryos of *Microsomacanthus paramicrosoma* (a) Gastrula with blastocoel (B), ectoderm (EC), immigrated entomesodermal micromere (EM). (b) and (c) Consecutive serial sections at stage when blastocoel is being filled up. (Adapted from Bazitov and Lapkalo, 1977.)

micromeres that had immigrated". Except for terminology, these views are somewhat similar to those of Logachev (1970) regarding the trophic functions of the outer layer. They also conclude that the egg has features of duet and spiral fission characteristic of the lower groups of turbellaria, in contrast to Costello and Henley (1976) who do not mention cestodes but acknowledge that acoel turbellarians have a modified spiral cleavage.

Related to the entodermal question in cestodes, is a similar one in acoel turbellarians, the theoretical ancestral stock of cestodes according to Logacev (1970). The literature on this question is quite extensive and will not be reviewed here. As an example of how views differ, Boyer (1971) indicates that the endoderm and mesoderm of the Acoela are not clearly defined because of the absence of the 4d cell, yet Jennings (1974, p. 175) regards the intestine in Acoela as "... a syncytial undifferentiated mass of endoderm, containing numerous vacuoles in which digestion occurs". Costello and Henley (1976) appear to follow earlier workers and designate the non-ectodermal part of the early embryo as "internal parenchymal mass"; the question of entoderm or entomesoderm is not dealt with. From the above discussion, it is evident that there are no clear answers regarding the presence of entoderm in cestodes. The evidence appears in favour of some vestige of entodermal (or entomesodermal) cells which abort in early development with a change toward a trophic function for the outer layer of the embryo. Whether this interpretation can be used as evidence of a reduction of a gut remains to be seen as additional facts on cestode embryology emerge. On the basis of these studies, it appears to me that cestodes did not lose a gut by reduction but never had one, or if lost it was correlated with the parasitic habit and not necessarily an intestinal one. It is possible, however, with current data to make arguments for either an acoel ancestor or, as more generally believed, a rhabdocoel. A review of some of the more recent schemes of cestode and caryophyllid evolution will illustrate which arguments have had the greatest influence. So diverse are the views that the papers are taken in chronological order.

B. 1971–1975

Demshin (1971) is among the first to accept Logachev's (1970) views. The monogenea are not regarded as being in the cestode line of evolution for a number of reasons, among them characteristics of life cycle, morphology, ecology and, most important, a lack of explanation for one branch (cestodes) losing a germ layer and another (monogeans) keeping it. As a consequence, he believes that cestodes are an independent branch that evolved from an acoelous turbellarian ancestor and first became parasitic in the *body cavity of oligochaetes*. Oligochaetes were suitable hosts primarily because of their large size and also because of their population density, wide dispersal, and benthic habit, the latter allowing a greater exposure to eggs than by other invertebrates. Endoparasitic forms of acoels and rhabdocoels evolved in molluscs, starfish, sea urchins and decapod crustaceans, whereas *Archigetes* evolved in oligochaetes. Demshin (1971) thus regards *Archigetes* as originally parasitic in oligochaetes and unchanged until the present. As vertebrates evolved, the one-host cycle gradually developed into a two-host one with the obligate oligochaete phase as a permanent part of the cycle. *Archigetes* is thus considered a young cestode, basically organized as an adult but differing in size, state of development, and having fewer adaptive features. According to Demshin the procercoid is a young stage (juvenile?) and not a larval one because it does not have an embryonic character to its organization. He does not consider the coelom habit as a larval characteristic; nothing is said about the significance of the cercomer or of a non-functional genital pore. This latter characteristic of *Archigetes* is apparently overlooked, for he states that the cestode emerges from the ruptured tubificid and *deposits* eggs before perishing. Such a sequence overlooks the fact that *Archigetes* cannot deposit eggs at all but must rupture the tegument or cuticular pouch, either process killing the worm.

With the appearance of vertebrates that fed on oligochaetes, some *Archigetes*-like cestodes matured in the fish intestine and radiated into new forms, evolving cycles with oligochaetes as intermediate hosts. Other cestodes, however, did not mature in the gut but penetrated into the *body cavity* (how is not made clear by Demshin) where they matured. With the death of the vertebrate host the cestode eggs were liberated and became accessible to other invertebrates such as zooplankton. A series of adaptations, such as cilia on the oncosphere, coevolved with the development of a crustacean–fish cycle. In some cases, such as *Ligula*, strobilization began in the plerocercoid stage. Demshin (1971) further reasons that as in the cycle of *Ligula* the large plerocercoid rendered an infected fish more susceptible to predation thus adding a third, but warm-blooded host, to the cycle. In the final vertebrate, the strobilate stage completed development. In other cases, plerocercoids were liberated in the gut of predacious fish and matured to give strobilate forms. According to Demshin, the Pseudophyllidea were the first strobilate cestodes to evolve; with the rise of terrestrial vertebrates the cestodes radiated into different hosts and along different lines. His evolutionary scenario is thus: acoela ancestor to caryophyllid-oligochaete cycle (*Archigetes*) from which one branch evolves no further but the other incorporates zooplankton and eventually evolves to strobilate forms.

On the whole, this scheme is appealing because it starts with a supposedly primitive form (*Archigetes*) and derives the more complex cestodes. Unfortunately, he has completely overlooked the possibility of progenesis playing a part in caryophyllid evolution or even with *Ligula*, which has advanced development while still in the body cavity of fish. Furthermore, he does not deal effectively with the question of why oligochaetes are not more fully exploited by other cestodes since they were the original hosts of tapeworms. These and other important questions are dealt with in the paper by Mamaev (1975).

Czaplinski (1972) also accepts Logacev's (1970) basic thesis that cestodes lack entoderm. From a planula-like ancestor (acoelous prototurbellarian) he has two lines of evolution: one with entoderm that gives rise to a rhabdocoel ancestor from which the Trematoda, Rhabdocoela, Temnocephala, Unonelloidea and Monogenea arise and a second line, without entoderm, that gives rise to Acoela, Gyrocotyloidea, Cestodaria and Cestoda. The difossate cestodes diverge from the cestodaria stem but the tetrafossate ones branch off the ancestral line for all groups. Cestodes are said to have first parastized invertebrates and only radiated further with the appearance of vertebrates. His scheme makes no mention of the Caryophyllidea, unfortunately.

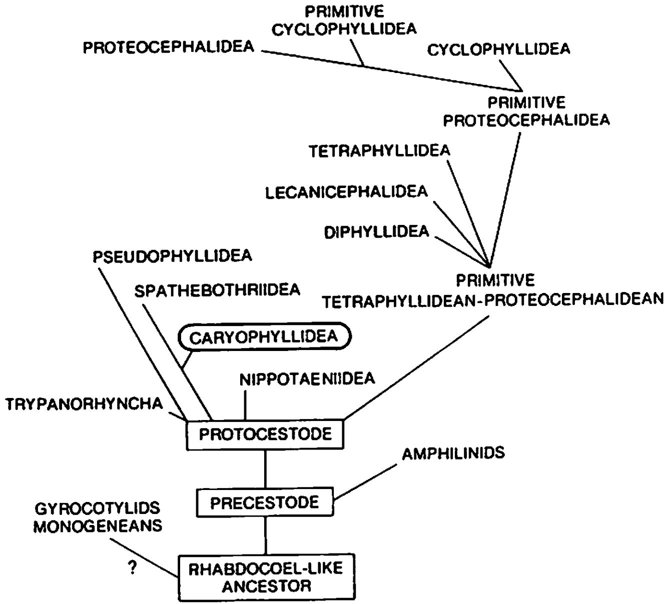

FIG. 9. Evolutionary scheme of cestodes according to Freeman (1973). The precestode stage had an adult that was single-suckered and free-living; the onchospere came from an anoperculate egg and developed parenterally in an invertebrate; the plerocercoid-preadult was tailed and free-swimming. The protocestode stage had an adult that was single-suckered and in the vertebrate gut; the oncosphere came from an anoperculate egg; and the plerocercoid had a metamorphosis (?) parenterally in an invertebrate. Nothing should be implied from the angle or length of connecting lines. (Adapted and simplified from Freeman, 1973.)

By far the most extensive, often brilliant, treatment of cestode evolution in recent times is that of Freeman (1973). Although he does not bring up the question of entoderm in cestodes or mention the possibility of an acoel ancestor, his arguments are generally well-presented and with fresh insights. His evolutionary scheme, somewhat simplified, is presented in Fig. 9. Clearly he regards cestodes as a polyphyletic group away from the monogenean line with caryophyllideans as a dead-end branch on the same line as the Spathebothriidea; the paper must be read to get the detailed rationale for such a scheme. Of particular interest for caryophyllid evolution, is the incorporation of a hypothetical precestode (in invertebrates) and protocestode (in vertebrates) stage between the rhabdocoel-like free-living ancestor and cestodes. It is the precestode cycle, consisting of a free-living, tailed pre-adult or adult that concerns us here. The fact that *Archigetes* is the only cestode that matures in a parenteral site suggested to Freeman (1973) that the precestode adult stage was free-living and the preadult stage was parasitic in invertebrates. A similar view is expressed by Stunkard (1975).

According to Freeman (1973), *Archigetes* is, as Rosen (1918) believed, a primitive adult cestode, or "caudate adult" in his new terminology. His interpretation of *Archigetes* is quite unlike that presented anywhere else. For example, he believes that *Archigetes* has a free-living stage, though brief, after it ruptures free of the tubificid and because of this is an example of the primitive precestode, the cercomer being a vestige of a former swimming organ. As far as I am aware, this is the first time that anyone has considered any stage of caryophyllids as free-living.

Unless one considers the brief period before death of a cestode expelled or ruptured free as free-living, there is no justification whatsoever for considering *Archigetes*, an obligate parasite, as having a free-living stage. Once free of the tubificid, *Archigetes* is doomed to decay; by no standard biological criterion can this period of slow death be called free-living. Unfortunately, other more important aspects of *Archigetes* morphology or biology are omitted. For example, there is no mention of the origin of the well-developed scolex, which is unlike the hypothetical single terminal sucker-like structure (unifossate) characteristic of precestodes (see Fig. 11a), or why *Archigetes* matures in a parenteral site, acknowledged to be the habitat of metacestodes. By failing to realize the significance of a non-functional genital pore and stretching the definition of free-living, Freeman (1973) has ascribed to *Archigetes* a far greater evolutionary role than is warranted; it has also prevented a consideration of progenesis as a possible explanation for the precocious maturity in the invertebrate host.

As for the evolution of other caryophyllideans, Freeman (1973) believes that they were primarily monozoic and evolved from a unifossate, monozoic ancestor in the protocestode stage. Little is said of the role of tubificids. The concept of progenesis receives little attention.

Without reference to Logachev (1970), Demshin (1971) or Freeman (1973), Malmberg (1974) develops a line of evolution for the Cercomeromorphae Bychowsky, 1937 (including the Caryophyllidea), utilizing the protonephridial system to show relationships. Some of the key points of his scheme that differ from an earlier one (Malmberg, 1971) are (a) the ancestor was a parasitic "acoelomatic creature", whose eggs were eaten by mud eaters, for example, gastropods and annelids (oligochaetes), (b) cestodes never had an intestine in any stage of their ontogeny, (c) a cercomer evolved *after* forms became parasitic, (d) caryophyllideans or monozoic cestodes are genuine non-progenetic or non-neotenic adults, and (e) strobilization evolved along a separate line with *intestinal* parasitism. Like Demshin (1971), Malmberg derives the cestodes from a caryophyllidean line through oligochaetes. Of the cercomeromorphean line he says (Malmberg, 1974, p. 77), "The body shape and the type of endoparasitism of these cercomeromorphean progenitors are best preserved in adult caryophyllideans with a retained cercomer, *i.e., Archigetes*". According to Malmberg, the incorporation of a vertebrate into the cycle allowed the procercoid stage to become a plerocercoid in a parenteral site; with the addition of a final predator, these plerocercoids developed a strobila and scolex under the influence of the intestinal habitat in the predator. This part of the hypothesis is very much like that of Freeman (1973) and others; however, there is no explanation why there is a well-developed scolex in the parenteral stages of caryophyllids, before the intestinal phase is reached. Malmberg believes that the caryophyllids evolved before other cestodes and that the monozoic and polyzoic body plans evolved along separate lines.

The preceding hypotheses of Demshin (1971) and Malmberg (1974) are discussed in detail by Mamaev (1975) who strongly disagrees with the basic thesis that *Archigetes* is a protocestode and that oligochaetes were the initial hosts of cestodes. Citing the non-functional genital pore, and references to *Archigetes* as a classical example of a progenetic procercoid (see Mackiewicz, 1972 for review), he rejects the view that *Archigetes* is an adult cestode and thus argues that it cannot be used as the stem form giving rise to other cestodes. On the other hand, he agrees with Demshin that the cercomer *per se* is not evidence of a larval condition; instead, it is an ancestral remnant still present on the larval stage. He places considerable emphasis on the role of progenesis in determining the evolution of caryophyllids and links *Archigetes* with those having a two-host cycle. He rejects the notion that oligochaetes were the first hosts of cestodes by asking a number of searching questions. Why are there no monogeneans on oligochaetes? Why are there no adult cestodes in oligochaetes? Why are there no primitive cestodes in terrestrial oligochaetes? Why are the closest relatives of caryophyllideans—*Cyathocephalus* and *Diplocotyle*—in salmonids with stages in amphipods rather than oligochaetes? Lack of satisfactory answers leads Mamaev (1975) to conclude that the primary host of cestodes were freshwater fishes, not invertebrates.

Unlike any other contemporary author who has recently addressed the evolution of caryophyllids in detail, Mamaev (1975) places considerable emphasis on the role of progenesis. It is his view that progenesis in pseudophyllidean cestodes ought to lead to (a) shortening the life-span of the adult stage in definitive hosts, (b) retarding growth of strobila and perhaps making it shorter, (c) multiplication of genital complexes as in *Ligula*, and (d) disturbing the process of strobilization. A complete loss of strobilization resulting in a monozoic body form might also be a consequence of progenesis, according to Mamaev. He believes, and I concur, that progenesis is of frequent occurrence in the caryophyllids and pseudophyllids because of their primitive structure and the fact that larger intermediate hosts allowed for greater development of larval stages. He is of the opinion that one cannot dismiss the idea that the vertebrate phase of caryophyllids are progenetic plerocercoids but that there is an alternative view that they may be adults which have become secondarily monozoic under the influence of progenesis. A somewhat similar proposal was expressed earlier by Mackiewicz (1972). Despite the fact that he theorizes that loss of strobilization of the adults could lead to a monozoic body plan through progenesis, Mamaev feels that caryophyllideans are primarily monozoic.

Not long after Freeman's (1973) fine contribution, there appeared another quite similar one by Jarecka (1975) who concentrated on the evolution of cestode cycles. Her paper also deals with larval terminology to a great measure yet does not cite Freeman's (1973) key paper nor those of Logachev (1970) or Demshin (1971). Some of her conclusions regarding monozoic cestodes are (a) the first-stage larva is the oncosphere, the second develops in tissues or body cavity of the first host, and the third stage is sexually mature and may be monozoic or polyzoic, (b) of the four basic second stages (proceroid, cercoscolex, cysticercoid and cysticercus) the procercoid of monozoic cestodes is the most primitive and is parasitic in the body cavity of oligochaetes, the most primitive of aquatic coelomates infected with cestode larvae, (c) there is a correlation between the host evolutionary level and that of larval morphology, and (d) the scolex adhesive organs in the second stage (procercoid) are a result of "interstadial acceleration" or preadaptation to the conditions for the third stage. Jarecka considers that monozoic cestodes represent the most primitive group of cestodes; among her reasons are: morphology, "neoteny", and being parasitic in oligochaetes, the most primitive coelomates as hosts of gymnosomic cercoides (acystic larvae). Her reference to "neoteny" is left without explanation.

Her speculations on the origins of the cestode life cycle are unlike those of other workers. Jarecka speculates that oligochaetes were the original and only hosts that *swallowed* a primitive flatworm that had a cercomer. Within the intestine the hooks of the cercomer are used to penetrate through the gut wall into the coelom where the primitive parasites reached sexual maturity, dispersing their eggs after the death of the host. *Archigetes limnodrili* is thought to be a relic of such a one-host cycle. Primitive vertebrates ate the infected coelomates and gradually became definitive hosts. With the addition of the vertebrate to the protocestode life cycle the third stage evolved in the vertebrate gut. Despite this evolutionary scenario for the two-host cycle of monozoic forms (i.e., *Caryophyllaeus*), Jarecka (1975) is frank to admit (p. 110) "It is difficult at present to try the question of polyzoic tapeworms derived from the monozoic ones or evolved independently from an ancestor characterized by alteration of sexual and asexual generations". Her scheme adds very little to those before it and even adds complexity by not accounting for the fate of the oncosphere in the one-host cycle. Like Demshin (1971), she gives a prominent role to oligochaetes as the first hosts of cestodes.

c. 1976–1979

Kulakovskaya (1976), the foremost authority on caryophyllids in the eastern hemisphere, regards them as the most primitive group of cestodes, diverging from the dalyellid ancestors (Fig. 10) at the beginning of the Paleozoic or even in the Proterozoic and becoming parasitic in oligochaetes; other cestodes evolved after the appearance of arthropods. The fact that caryophyllid eggs lacked floating adaptations allowed them to sink and come into contact with the intermediate hosts, oligochaetes (see Section IIIC).

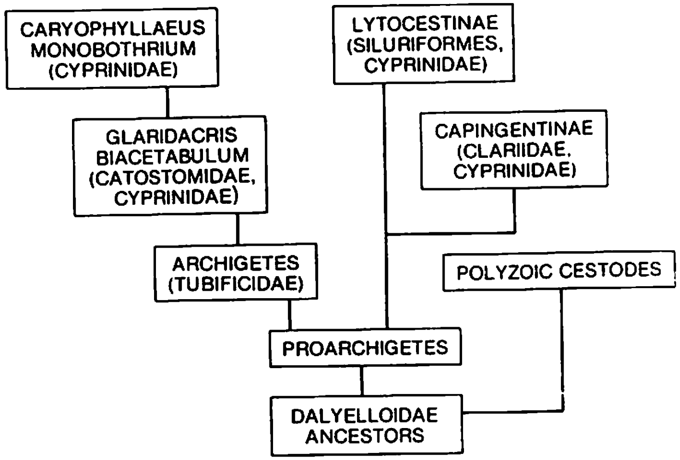

FIG. 10. A theoretical scheme of the phylogeny within the Caryophyllidea. The *Caryophyllaeus* branch and the subfamily designations used here correspond to the first three families on Table 3. (Adapted from Kulakovskaya, 1976.)

Because of their specificity for oligochaetes, Kulakovskaya believes that caryophyllids became fish parasites later than did other cestodes, certainly after cypriniformes had evolved, possibly in the middle Cretaceous. Another consequence of their long association with oligochaetes was that their evolution was retarded, thus explaining their monozoic form and low level of organization. Proof of their ancient mode of life, according to Kulakovskaya, is the maturation of some species in oligochaetes. Withing the group, the most primitive are the Caryophyllaeidae (Fig. 10) with medullary vitellaria, outer seminal vesicle and cercomer on sexually mature forms (i.e. *Archigetes*). Next are the Capingentidae with vitellaria partly cortical; and most advanced are the Lytocestidae, with cortical vitellaria, larger body size, inner seminal vesicle and "larval morphogenesis" in the intermediate host.

Of interest in this analysis by Kulakovskaya, is the reference to sinking eggs, a necessary prerequisite for tubificid infection. However, would one have not expected the eggs of the dalyellid ancestors (see Fig. 10) to have been already the sinking type since adults were free-living on the substratum? Her analysis places the caryophyllids as a polyphyletic group distinct from and along a separate evolutionary line from polyzoic cestodes. The inclusion of a proarchigetes stage is unlike that of other authors and appears to split the caryophyllids into two major lines whose primary difference would be the placement of the vitellaria with respect to the longitudinal muscles and presence of cercomer in mature forms. It seems doubtful that the former morphological feature should be accorded so much importance since it has been used only as a family or subfamily character. The cercomer is so clearly a transient structure common to all caryophyllids and should not be used to separate groups. Her paper has some interesting points, but she does not cite Demshin (1971), Freeman (1973), Malmberg (1974) or Mamaev (1975) and therefore does not deal with the question of a possible acoel ancestor, free-living stage, relationship to the monogenea, or the possible role that progenesis may have played.

The last two papers by Bazitov (1976) and Kulakovskaya and Demshin (1978) address themselves specifically to the phylogenetic relationships of the Caryophyllidea, but from different perspectives. Both are detailed treatments with bibliographies of 43 and 63 references respectively. However, neither paper seems aware of the work of Wardle *et al.* (1974) who place the Caryophyllidea, along with five other groups in a new class Cotyloda. Only the more significant observations or conclusions are reviewed here.

On the basis of a comparative study of cleavage, oncosphere morphology and histology of the parenchyma and subcuticula of caryophyllids with Cyclophyllidea and Pseudophyllidea, Bazitov (1976, p. 1785) concludes that, "Caryophyllids are a group distinct from cestodes and should be placed either in a subclass or in an independent *class* Caryophyllidea." (italics mine). No worker in modern times has made such a bold proposal elevating caryophyllids to the same level as the classes Trematoda, Monogenea, Turbellaria and Cestoidea. A subclass designation would presumably be comparable to subclass Cestodaria, and Cestoda or Eucestoda under the class Cestoidea as outlined by Noble and Noble (1971). Either position would elevate the caryophyllids to the status of a major platyhelminth group, a far cry from proposals that they are simply a family in the order Pseudophyllidea (Hyman, 1951; see Mackiewicz, 1972 for review of past schemes). Bazitov's proposal vividly illustrates how complex is the evidence upon which are made conclusions of the evolutionary and systematic position of these cestodes. What is the evidence used by Bazitov?

Cleavage pattern is one line of evidence. Using Motomura's (1929) study of the embryological development of *Archigetes appendiculatus* (it is the only one done on any caryophyllid), Bazitov regards the fact of indistinguishable macro- and micromeres by the 6-cell stage and an unequal second division as being a fundamental difference from strobilate cestodes in which there are two classes of blastomeres—micromeres and macromeres by the 4-cell stage.

Furthermore, there is no migration of blastomeres to the surface of the embryo nor is a cellular membrane formed. At the 4-cell stage of *Archigetes*, however, 2 macromeres and 2 micromeres *are* clearly distinguishable (Motomura, 1929; his Figs. 16 and 17). It is true that by the 6-cell stage the blastomeres become indistinguishable; however, based on nuclear characteristics (micronucleus=micromere; macronucleus=macromere) it is evident that at least two types of blastomeres can be distinguished through the oncosphere stage. It would appear to me that the alleged difference cited by Bazitov is not a functional one because macromeres and micromeres are indeed present although the size differential is small. Yet Motomura says little of cell migration and earlier he indicated that there is no blastocoel (Motomura, 1928), but the micromeres make the "mantel" or outer layer. Since there is no embryophore in caryophyllids, one cannot compare their development with that of the various pseudophyllids studied by Schauinsland (1885). It would appear that the embryology of caryophyllids, based on only one study, is different from that of pseudophyllids or other cestodes but it seems premature to regard such differences, which appear to be ones of degree rather than absolute, great enough to create a new class of flatworms.

Size of hooks of the oncosphere and morphogenesis of later stages are second lines of evidence. Again citing Motomura (1928), Bazitov attributes special significance to the fact that median hooks of *A. appendiculatus* are 13 µm and lateral ones 8 µm (in *K. sinensis* they are 12 µm and 9 µm respectively). This disparity in size is not typical of segmented cestodes according to Bazitov. I agree. Yet it is difficult to determine if such differences are indicative of separate class status. The absence of two membranes, present in pseudophyllidea, and presence of glands under the medial hooks as in cyclophyllids, are regarded as important because of the alleged similarities in the ecology of the oncospheres of caryophyllids and pseudophyllids. Such differences indicate that the two groups are indeed different from each other and not that caryophyllids should be removed from the cestoda.

Contrasting the morphogenesis of caryophyllids and segmented cestodes, Bazitov calls attention to the fact that metamorphosis in the former is associated with degeneration of the cercomer alone and involves no other larval structures. He does not feel that this difference, that is loss of cercomer only, can be explained by the neoteny hypothesis because (Bazitov, 1976, p. 1782); "... one would be forced to postulate secondary changes in the type of development, occurring with typical metamorphosis, in the ancestors of caryophyllids". He believes it is more reasonable to derive them from free-living turbellarians where there is a similar type of direct development. In my opinion, neoteny or progenesis need not be concerned with ancestors because either process could have occurred late in the evolution of the cestodes.

Final evidence is in the difference between the histological organization of the parenchyma between caryophyllids and segmented cestodes, differences Bazitov considers striking. His conclusions are based on a study of the histology of *Caryophyllaeus laticeps* and *Khawia sinensis*; Will's (1893) study of the former species is not cited. Perhaps the most outstanding difference is the presence of giant basophilic and oxyphilic cells, the former are compared with the neoblasts of planarians. Other differences are cited in the subcuticular layer. The "faserzellen", so prominent in the neck of caryophyllids, are designated as neoblast cells; these giant cells and other "specific cellular elements" are said to be absent from segmented cestodes. A final evidence of uniqueness is the extraordinary development of the uterine glands. According to Bazitov (1976, p. 1784), "The abundance of specific features, present in the parenchyma and tegument, is in direct contradiction with current views as to the place of caryophyllids in the systems of flatworms and as to their evolution". I agree that the histological structure and especially the size of cells of caryophyllids is striking and different from that of segmented cestodes. However, should one not expect such differences between primitive and advanced forms? One might also expect them in neotenic or progenetic forms.

According to Bazitov, the neotenic hypothesis should be supported by similarities in the cleavage pattern, morphology of oncosphere, and tissue organization between caryophyllids and segmented cestodes. I agree in the first case but not in the latter two because much would depend on the temporal relationship between the parent stock and the appearance of the progenetic stage. For example, because the progenetic (one-host) and adult (non-progenetic) stage of *Archigetes* often occur in the same species, it is doubtful that there is any difference in the cleavage pattern and other features between the two forms. Where there is no one-host cycle, as is the condition with the great majority of caryophyllids, then progenesis may have been a factor in the initial evolution of a monozoic condition from a polyzoic one. Once established, this monozoic form underwent evolution and radiated into diverse genera and species. Hence one would expect great differences between the present monozoic forms and the former polyzoic ancestors. If comparisons are to be made they should be between the most comparable stages, namely the monozoic caryophyllids and plerocercoids of pseudophyllids (assumed to have given rise to the monozoic forms) and not between monozoic and polyzoic stages which are at different developmental states. It would appear to me that the differences cited by Bazitov confirm that monozoic cestodes are basically different from polyzoic ones, but they do not disprove that one could have evolved from the other.

As a final line of evidence, Bazitov does not regard the similarities of the reproductive systems (vitellaria distribution) of caryophyllids and pseudophyllids as being evidence of relatedness but as examples of convergence. The similarities in the position of the genital pores is coincidental; since there is so much variation in the genital ducts of the pseudophyllidea it is a matter of chance that some of these variations would correspond to the condition in caryophyllids. He supports his argument with Dubinina's (1974b) view that the reproductive system is of secondary importance in defining large taxonomic units; more important are the attachment organs which are not discussed by Bazitov. Although he has some suggestions regarding the systematic position of caryophyllids, he is frank to admit (p. 1785) that ". . . . this problem remains open so far, it can be solved after a comparative study of all cercomeromorph groups of flatworms". In my view, Bazitov's approach to the complexities of caryophyllid phylogeny is sound for it deals not with speculation but with aspects of basic biological relationships.

The most extensive recent review of caryophyllid phylogeny is that of Kulakovskaya and Demshin (1978); both had written shorter reviews earlier (Demshin, 1971; Kulakovskaya, 1976). This joint paper is in part a reaffirmation of each other's views, plus a response to Mamaev's (1975) critique of Demshin's earlier paper: Bazitov's (1976) long paper is not mentioned, unfortunately. It does not add any new ideas but gives a comprehensive, but all too brief, review of past views. Some of their own ideas are expanded, for example, they believe that oligochaetes were the primary hosts of cestodes because of (a) narrow specificity of caryophyllideans in oligochaetes, (b) long period (4–6 months) of development in oligochaetes compared to short period in fish, (c) high degree of morphological differentiation in oligochaetes, and (d) wide range of infectivity, i.e. from moment of cercomer formation to almost mature stage in oligochaetes. Bothria evolved on *Archigetes* while it was a parasite in the *intestine* of oligochaetes and were retained when caryophyllids moved to the body cavity. What prompted this habitat change is not explained, nor is there any realization that the gut of tubificids is probably too small for *Archigetes* unless it was a much smaller parasite. Furthermore, the fact that there are no mature cestodes in the gut of any invertebrate, or that the oncosphere leaves the gut shortly after hatching, would argue against an intestinal habit in oligochaetes for *Archigetes*. Progenesis is rejected as an explanation for *Archigetes* because they admit to being unable to see the biological rationale for a parasite to move from the nutritionally rich environment of the intestine to the poorer one of the oligochaete body cavity (see Section IVC). Since they believe that oligochaetes were the original hosts, shortening the cycle by elimination of the most recently added vertebrate host does not appear reasonable. While the parasites of oligochaetes evolved to caryophyllideans, those of crustaceans gave rise to contemporary cestodes. The ancestors of rhabdocoela and acoela may also have given rise to the cestodes and monogeneans. They conclude by regarding the caryophyllideans as an ". . . independent group at the rank of superorder or subclass . . .". This is said to support the conclusions of Bazitov (1976) and Mackiewicz (1972); in the latter case the authors have clearly misinterpreted the paper.

D. COTYLODA CONCEPT

As a sequel to their influential earlier work (Wardle and McLeod, 1952), Wardle *et al.* (1974) attempt to summarize the advances in the zoology of tapeworms for the period 1950–1970. This work, like the first, contains a number of new taxa, nine new orders and one new class, and is destined to have a stimulating influence on the course of cestode classification. In their review of cestode phylogeny, they accept the hybrid scheme of Price (1967)

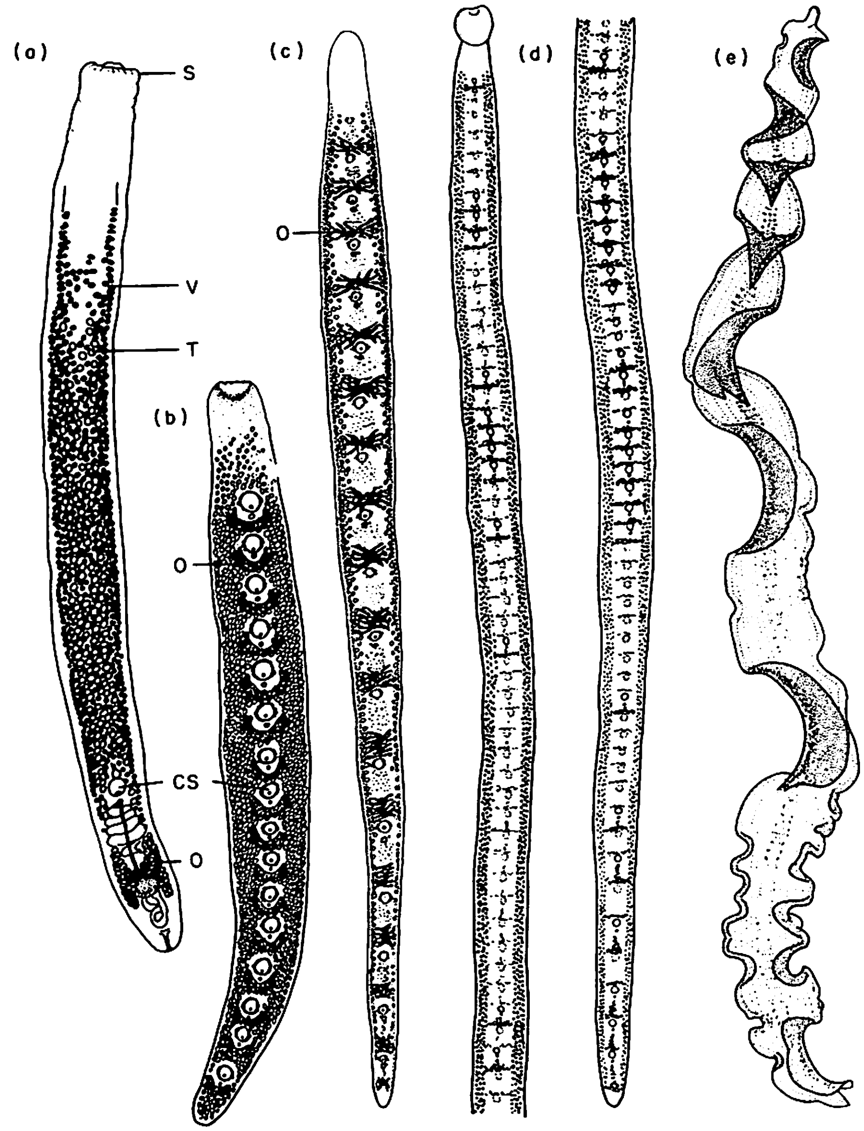

FIG. 11. (a) *Monobothrium hunteri*, (CS, cirrus sac; O, ovary; S, scolex; T, testis; vitellarium). (original). (b) *Cyathocephalus truncatus* (CS, cirrus sac; O, ovary) (original). (c) *Spathebothrium simplex* (O, ovary). (original). (d) *Bothrimonus* sp. (original). (e) *Anatrum tortum* (adapted from a photograph by Rees, 1969). Drawings are not to scale.

which is based primarily on the work of Bychowsky (1957) and Llewellyn (1965). In it, the cestodes are made an offshoot of the amphilinideans, which derive from gyrocotylideans that in turn branch from the monogeneans which evolved from the rhabodocoel turbellarians. The authors conclude that the primeval tapewor.ns were small, slender, without suckers, but with a sensory apical organ that was an invagination of the body surface that led into a loose mass of parenchyma which served as a gut. They also concluded that (p. 19) "Traces of a former alimentary tract and mouth perhaps occur in some tapeworm larval sta~es". They are no doubt referring to the terminal invagination and frontal gland complex of some procercoids, i.e., *Diphyllobothrium*. From such an ancestor, the pseudotapeworms (Cotyloda) and true tapeworms (Eucestoda) eventually evolved.

The Cotyloda constitute a new class made up of the following six orders of pseudotapeworms: Gyrocotylidea and Amphilinidea (provisional members, Figs. 1a and 1b) and Caryophyllaeidea (Fig. 11a), Spathebothridea (Figs. 11b, 11c), Diphyllidea (Fig. 11d), and Pseudophyllidea (Fig. 11e); all the other tapeworms are relegated to the class Eucestoda. Among the characteristics of the Cotyloda are: difossate (dibothriate), segmentation weak or absent, segments (if present) produced by autotomy of an invading plerocercoid; true proglottization and apolysis lacking; life cycle with an operculated and embryonated egg, a procercoid (with cercomer) in an invertebrate, a plerocercoid (without cercomer) in a second invertebrate; and (p. 22) ". . . an adult worm in a vertebrate host, derived by instant autotomy of an invading plerocercoid representing a precociously sexual, long extinct pseudotapeworm". "We regard Cotyloda as monozootic and Eucestoda as polyzootic". Cotyloda is thus made up of essentially progenetic forms. Instead of "progenetic", the authors prefer to use "neotic" to describe difossate cestodes. Except for the Gyrocotylidea and Amphilinidea, commonly known as cestodarians and differing from the others in such basic features as a 10-hooked lycophora larva, the remaining orders were formerly subsumed as families in the order Pseudophyllidea. It is therefore not surprising that Wardle *et al.* (1974) have again united them but at the class level. There appears to be little acceptance of the Cotyloda in spite of the fact that Logacev (1970) has found that the connection between proglottids in the Pseudophyllidea was basically different from that in the Cyclophyllidea. Czaplinski (1972) earlier had used many of the ideas of Wardle and McLeod (1952) and derived the tetrafossate cestodes (Eucestoda) from Acoela and difossate ones from the Amphilinidea.

The evolution of the Caryophyllidea is similar to that of the difossate worms. According to Wardle and McLeod (1952) the difossate worms originated as endosymbionts of invertebrates from a protocestode stock that also gave rise to turbellarians. Such endosymbionts may have originated independently and many times. They lacked well-developed holdfasts and, most important, delayed autotomy (cross division of the body which produces primary segmentation) had not yet evolved. Instead, there is secondary segmentation imposed upon a plerocercoid-like form, as evident in *Ligula*. In some forms this segmentation became highly developed, e.g. *Diphyllobothrium*; however, the tapeworm remains basically monozootic because proglottids are not shed. Segmentation developed to various degrees and in caryophyllids, not at all. Thus they are, in the terminology of Wardle and McLeod (1952, p. 153) ". . . essentially neotenic forms". More recently, Wardle *et al.* (1974, p. 28) regard caryophyllids as ". . . actually sexually precocious juveniles of long-extinct protocestodes". I interpret the scheme of Wardle and McLeod (1952) and Wardle *et al.* (1974) to mean that caryophyllideans and other difossate forms are progenetic because the plerocercoid-like stage never developed true segmentation and apolysis characteristic of the tetrafossate line and thus remain basically a sexually mature juvenile tapeworm. In this scheme, caryophyllideans are primarily monozoic because they never developed instant autotomy.

In my view, the Cotyloda concept (without Gyrocotylidea and Amphilinidea, however) has considerable merit because it uses fundamental developmental patterns and scolex morphology to unite forms that share so many other characteristics. With such a scheme, various degrees of progenesis and segmentation can be explained easily for various cycles (*Ligula*, *Cyathocephalus*, etc.) because all share the same developmental potential. However, it does not explain why caryophyllids are not segmented although they live in the gut, the habitat that selected for segmentation. On the other hand, is it possible that the calcareous corpuscle distribution may also reflect a form of segmentation (see Section IIIB). In my view, another important value of the Cotyloda is conceptual because it breaks the cestodes into at least two new large groups and establishes a framework for re-examining cestode classification.

E. COMMENT

From the preceding 10 papers it is evident that there is remarkably little agreement as to the origin and evolutionary history of the caryophyllid cestodes. Differing interpretations, lack of data, lack of knowledge of earlier views, and the intrinsic complexities of dealing with hypothetical ancestral forms contribute to the confusion. Some believe caryophyllids evolved from acoels or acoelous ancestors (Demshin, 1971; Czaplinski, 1972; Malmberg, 1974) or rhabdocoels or rhabdocoel-like forms (Freeman, 1973; Wardle *et al.*, 1974; Kulakovskaya, 1976) or possibly both (Kulakovskaya and Demshin, 1978). Except for Mamaev (1975), who believes vertebrates were the first hosts, there appears to be general agreement that the first hosts were invertebrates; many believe that these invertebrates were oligochaetes (Demshin, 1971; Czaplinski, 1972; Malmberg, 1974; Jarecka, 1975; Kulakovskaya, 1976; Kulakovskaya and Demshin, 1978), and some derive all cestodes through a caryophyllid or caryophyllid-like line (Demshin, 1971; Freeman, 1973; Malmberg, 1974; Jarecka, 1975; Kulakovskaya, 1976; Kulakovskaya and Demshin, 1978). There appears to be unanimous agreement that caryophyllids are primarily monozoic even though progenesis may have played a role in their evolution (Wardle *et al.*, 1974; Mamaev, 1975). Finally, there are some who would elevate caryophyllids to the status of an independent Class or Subclass (Bazitov, 1976; Kulakovskaya and Demshin, 1978).

It is perhaps significant that so many workers now follow Llewellyn (1965) and derive the strobilate cestodes through a protocaryophyllidean or caryophyllidean line. Earlier, the origin through progenesis from a polyzoic line was widely held. Rees (1969), whose paper appears to have been overlooked by all authors cited above except Wardle *et al.* (1974), also develops the strobilate cestodes through a similar line. Like Llewellyn, she assumes that a protomonogenean invaded the gut of a vertebrate and evolved to the ancestral protocaryophyllidean, present today in the form of Caryophyllidea. From this monozoic ancestral stock evolved the strobilate cestodes through a series of morphological steps as follows (existing forms in parentheses): (1) genitalia repeated (Spathebothriidae, Fig. 11c) (2) elongation, better development of scolex with genital pores on one surface (Cyathocephalidae, Fig. 11b; Diplocotylidae, Fig. 11d) or uterine pore on ventral surface, cirro-vaginal pore on dorsal (*A. tortum*, Fig. 11e), (3) pseudopolysis, or shedding of exhausted posterior end as strobila gets too long to be secured in gut by unspecialized scolex (*A. tortum*), (4) scolex specialized (Pseudophyllidea), (5) dilation of uterine pore and temporary retention of eggs in uterus (Pseudophyllidea) and finally, (6) closure of uterine pore and retention of eggs in uterus, various types of apolysis (Cyclophyllidea and most other cestodes).

Because a gradually evolving series is formed, Rees (1969) concludes that it is difficult to divide it into orders and therefore (p. 536) "It might be advisable to accept Hyman's (1951) suggestion to include them all, in separate families, in the Pseudophyllidea". Such a conclusion is very much like that of Nybelin (1922), except that he also created a number of subfamilies, Caryophyllaeinae and the Cyathocephalinae. In judging the unified pseudophyllidea concept, it is important to remember that Nybelin (1922), Hyman (1951) and Rees (1969) have relied *exclusively* on morphological criteria, ignoring host-parasite relationships or life-cycle patterns. Hyman (1951, p. 421) went so far as to state that "In general, no phylogenetic importance can be attributed to the monozoic condition", after citing the series: *Archigetes–Biacetabulum–Caryophyllaeus–Ligula–Schistocephalus*. Because her basic assumption was that neotony led to the monozoic condition it is not difficult to understand why she reached that conclusion. Indeed, neotenic forms generally are not accorded any special phylogenetic position. It is precisely that point that convinces me that *Archigetes* should not be given special phylogenetic significance over that of other caryophyllids (see Section IVE) or that caryophyllideans as a group should not be regarded as stem forms although progenesis may have a role in the *early* evolution of the group. However, there is no *proof* that the monozoic condition is, as Hyman assumes, indeed a result of neoteny (her terminology). That there is a tendency for progenesis in the Pseudophyllidea is clearly evident in the reduction or absence of segmentation. But the hypothetical step from a polyzoic to a monozoic form is in no way a clear-cut example of neoteny (progenesis). If it were (there is still room for other interpretations), and such a change had a permanent genetic

basis (see Section II) and was accompanied by a completely new life cycle (with oligochaetes) or group of hosts (cypriniforme fishes), and had given rise to a large (over 100 species) widely distributed group (one of the major cestode groups in freshwater fishes)—then to designate such a group of monozoic forms simply a family of the Pseudophyllidea *because* neoteny (or progenesis) *may* have occurred somewhere in the past, is to ignore the evolutionary process of mechanisms for the formation of higher taxa (see Section II 3).

VI. Discussion

Absence of a fossil record and great adaptive changes in highly specialized forms through a long evolution as a parasite have greatly complicated the analysis of cestode evolution. Any evolutionary scheme is therefore clearly speculative and in truth it is possible to arrive at different conclusions utilizing the same facts. In the final analysis, the most reasonable evolutionary scheme and systematic positioning of caryophyllids will depend on the answers to certain key questions.

1. *Are caryophyllids primarily or secondarily monozoic?*

The majority of zoological opinion favours the primary origin. However, in my view, there are a number of possibilities. For example, it is possible that the early ancestral caryophyllideans were *secondarily* derived from progenetic plerocercoids of a pseudophyllidean stock and through a change in the role of the vitelline cell nucleus (Section III C) and an alteration of the segmentation process (Section III A), were able to move from arthropods to oligochaetes as intermediate hosts. Once in oligochaetes that line gave rise to the caryophyllideans. Having separated from a polyzoic ancestor, the newly evolving caryophyllidean is primarily monozoic with vestiges of the polyzoic potential for segmentation (Section III B) and has the procercoid stage of a polyzoic ancestor. Since no strobilate stage follows, or ever followed, the plerocercoid-like stage once the oligochaete became incorporated in the cycle, it seems logical to regard caryophyllids as primarily monozoic adult cestodes and not progenetic plerocercoids. If one accepts this scenario, then caryophyllids are best regarded as a dead-end branch off a polyzoic line, perhaps the Spathebothriidea or Pseudophyllidea.

In my opinion, this interpretation has considerable merit because (a) it is the most parsimonious when viewed in the total perspective of cestode evolution, (b) it involves only those cestodes (i.e. Pseudophyllidea or relatives) that share common morphological or biological features, (c) it is consistent with known evolutionary and ecological theory regarding parasitism and requires no hypothetical ancestors, and (d) it utilizes a biological phenomenon (progenesis, see Section II) that is common in the animal kingdom. The most important parts of this scheme are the changes in vitelline cell nuclear function, from a purely regulatory role to that of glycogen storage, and possible suppression and eventual loss of the capacity to segment. In the latter case, a monozoic cestode would evolve through the combination of progenesis, with its truncation of development, and a mutation that prevents the replication of reproductive systems. A mutation could of course also explain the appearance of the nuclear vacuole which, because it conferred greater fitness on the individuals, was selected for and became fixed in the genome of the stem form. Utilization of oligochaetes was initially a chance event that was selected for (see Section IV D) and thus became associated only with the caryophyllid cycle, whereas other cestodes continued to evolve with arthropods in their cycles.

A second alternative, the reverse of the first, is that the monozoic body plan is primary and that nowhere in the evolutionary history is there any polyzoic ancestor. In this view, caryophyllideans can be (a) ancestral to polyzoic cestodes or, (b) an independent group that diverged *before* proglottization evolved.

In the case of (a), it is assumed that some caryophyllideans did not evolve while others added a strobilate stage, at the same time changing the cycle from an oligochaete to an arthropod intermediate host. From this new strobilate form, there is radiation into different cestode groups. If one accepts this alternative, then it is necessary to explain why oligochaetes are not in the life cycles of many other cestodes, why procercoids and plerocercoids are not more widely distributed in cycles, why nuclear storage nuclei are absent from all other cestodes (as far as we know) and why some caryophyllideans strobilated and others did not, yet both lived in the gut. It is difficult for me to answer these and other equally puzzling questions without postulating numerous changes that are not supported by known facts or examples. Furthermore, by placing caryophyllids at the base of cestode evolution one wonders why no other cestodes have their principal characteristic—monozoic body plan. At the very least, a stem form would be expected to give rise to other forms, rather similar to it, yet caryophyllids remain so distinct from other cestodes.

In the case of (b), separate lines of evolution for monozoic and polyzoic cestodes from a common monozoic ancestor is fraught with problems of explaining morphological similarities of eggs, reproductive systems and procercoid or plerocercoid stages between caryophyllids and pseudophyllids. So profound are these problems that using convergence as an explanation seems to me to avoid the problems rather than solving them.

2. *Are tubificids the original host of caryophyllids?*

Archigetes, of course, is often used to support the affirmative opinion. But since it is possible to cast considerable doubt on the validity of such opinions (see Section IV), the support for an invertebrate original host is weakened considerably, if not completely lost. Further erosion of the affirmative view occurs when one considers that aquatic arthropods (copepods and amphipods) and annelids (oligochaetes) generally lack sufficient size, nutrient-rich habitats, and long enough life-span to allow a flatworm to become parasitic by providing enough space, food and time to evolve a reproductive potential high enough to sustain a parasitic mode of life. The almost total absence of one-host life cycles of cestodes with arthropods or annelids would tend to support this analysis. Unlike digenetic trematodes who have molluscs as a common thread in their biology, cestodes have a great variety of intermediate hosts that include invertebrates and vertebrates, suggesting that many were added to cycles as the original hosts, vertebrates, dispersed and exposed their evolving cestodes to various other organisms. Under some circumstances, however, where there are high invertebrate populations as well as desirable morphological features (e.g. size) and long life span, tubificids became hosts (Section I C 3) for sexually mature procercoids of small caryophyllids when progenesis truncated the normal two-host cycle. In this case, the original hosts were probably freshwater fish.

VII. CONCLUSIONS

(relevant Sections in parentheses)

The relationship of the evolutionary history of caryophyllid cestodes to strobilate forms is still poorly understood. Originally placed with Cestodaria (I B), there seems little question that they are true cestodes, allied to strobilate forms through a common oncosphere stage and basic similarities of morphology. Nevertheless, caryophyllid morphology and biology is remarkably different from that of any other group of cestodes (I C). Viewed in the perspective of progenesis (II) and current ecological theory, it is possible to develop an evolutionary scheme that offers explanations for the monozoic morphology and unique cycle with oligochaetes. Recent experimental evidence (III A) that the normally polyzoic *Echinococcus* can yield monozoic forms suggests that the developmental difference between the two body forms may not be too great. Conversely, studies on the distribution of calcareous corpuscles (III B) in *Glaridacris* indicate that some monozoic forms may have traces of cryptic segmentation.

A major consequence of the monozoic morphology is that caryophyllids lack the high reproductive potential so characteristic of the cestoda as a whole. Their evolution, survival and relationship to strobilate cestodes can be tied to adaptations that often may be related to this diminished reproductive capacity. Viewed in this perspective, a knowledge of various morphological features (III) may help to explain how they have contributed to the survival and evolution of such a unique group of cestodes. From cytological studies (III D), it is clear that caryophyllids have been actively evolving and show a tendency toward polyploidy. With ploidy has come parthenogenesis (III E), itself of possible selective value because more energy can be devoted to egg production. It would appear that the presence of a large glycogen vacuole in the nucleus of vitelline cells may have had considerable influence in directing the evolution of intermediate host selection from an arthropod to oligochaete. Another possible adaptation related to energy relationships may be the high levels of vitamin B_{12} (III G) which, like parthenogenesis, may allow a greater energy allocation for egg production than for male gametes.

However, not all features appear to have apparent adaptive significance, instead they may shed light on phylogenetic relationships. The apparent absence of C-type virus particles (III H) from caryophyllids and common occurrence in pseudophyllideans is difficult to assess. More difficult to reconcile, is the observation that caryophyllid sperm, with a single axoneme, are more similar to those of cyclophyllideans than pseudophyllideans (III F) whose sperm have two axonemes.

Of all cestodes, *Archigetes* has a singular position because it can have a one-host cycle. On the basis of an extensive analysis of *Archigetes* morphology, biology and ecology (IV), it would appear that it is not an adult or ancestral cestode, is no more primitive than other caryophyllids and was probably first parasitic in a fish and secondarily in oligochaetes.

Review of various evolutionary schemes since 1971 (V) shows that there is remarkably little agreement on the origin and evolutionary history of caryophyllids. Clearly, the question of the presence of entoderm (V A) in cestodes has influenced whether or not an acoel, rather than rhabdocoel, was the ancestral stock. Strong arguments can be made for both alternatives. Perhaps most interesting is the view, premature in my opinion, that caryophyllids should be placed with the pseudophyllidea, and a few other orders, in a new class of pseudotapeworms, Cotyloda (V B); or that they should be elevated to the status of an independent Class or Subclass (V C). Although few workers go this far, others take the equally extreme view, which I cannot support, that caryophyllids should be considered a family of the Pseudophyllidea (V D). In my opinion, there is ample justification for the order status.

The elusive nature of evolutionary process prevents dogmatic conclusions. With so complex a group as the caryophyllids, it is indeed possible to suggest various evolutionary pathways. In my opinion, a strong argument (VI) can be made for the view that the early ancestral caryophyllideans were secondarily derived from a progenetic plerocercoid but evolved quickly and very early to become primarily monozoic because the strobilate stage disappeared once oligochaetes became intermediate hosts. The original hosts were probably freshwater fish.

Whatever the interpretation of the evolution and phylogenetic position of caryophyllid cestodes, no one can deny that in them we have a remarkable group of cestodes from which we can learn much of the basic principles of parasite evolution.

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