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Caryophyllidea (Cestoidea): perspectives

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INTRODUCTION

Caryophyllids are widely distributed cestodes of the fresh water siluriform and cypriniform fishes of the world. There are about 126 species and 45 genera and they constitute approximately 25 % of the cestode fauna of fresh water fish (Mackiewicz, 1972). Benthic-feeding fish become infected by eating tubificid worms (Annelida; Oligochaeta) that harbour the cercomer-bearing, infective stage; the tubificids, in turn, are infected by eating the operculated eggs in mud. Such a brief synopsis belies the fact that these well-known tapeworms are at the very heart of important questions concerning the evolution of Cestoidea. One has but to read Bazitov (1976), Freeman (1973), Kulakovskaya & Demshin (1978), Mameav (1975), Malmberg (1974) and Mackiewicz (1981) to appreciate that great differences still exist as to how caryophyllids evolved and what role they may have played in the evolution of the more numerous strobilate tapeworms.

The past and current controversy regarding the evolution and phylogenetic position of Caryophyllidea can in large measure be traced to an inordinate emphasis on morphological features and a lack of perspective of the group as a whole. My purpose in this paper is to try to provide some of that perspective concerning the monozoic body plan, progenesis, life-cycles, zoogeographical distribution, terminology and systematics; some recommendations for future research conclude the paper. Two new terms are introduced (monopleroid; polypleroid); there are no nomenclatorial changes.

SYNOPSIS

Caryophyllids are remarkable cestodes. Except for the hexacanth embryo they are surprisingly different from all other tapeworms: they are monozoic (Fig. 1 A), have tubificid annelids as intermediate hosts, and some forms (for example, *Archigetes*) may complete their cycle in tubificids, which is the only known instance of a tapeworm utilizing an invertebrate as a definitive host. Histologically, the nucleus of the vitelline cells become vacuolated and serve as a glycogen storage structure in the egg. Conversion of the nucleus from a regulatory to storage function is rare in the animal kingdom, in fact caryophyllids appear to be the only animals having this phenomenon as a normal process of cell maturation. Cytologically, their chromosomes are large (up to 12 μm long); chromosome numbers have the greatest range (6–30) for any group of cestodes; polyploidy, not yet found in other cestodes, is recorded from 5 species (Grey, 1979); and parthenogenesis, also apparently confined to caryophyllids, is known for 4 species.

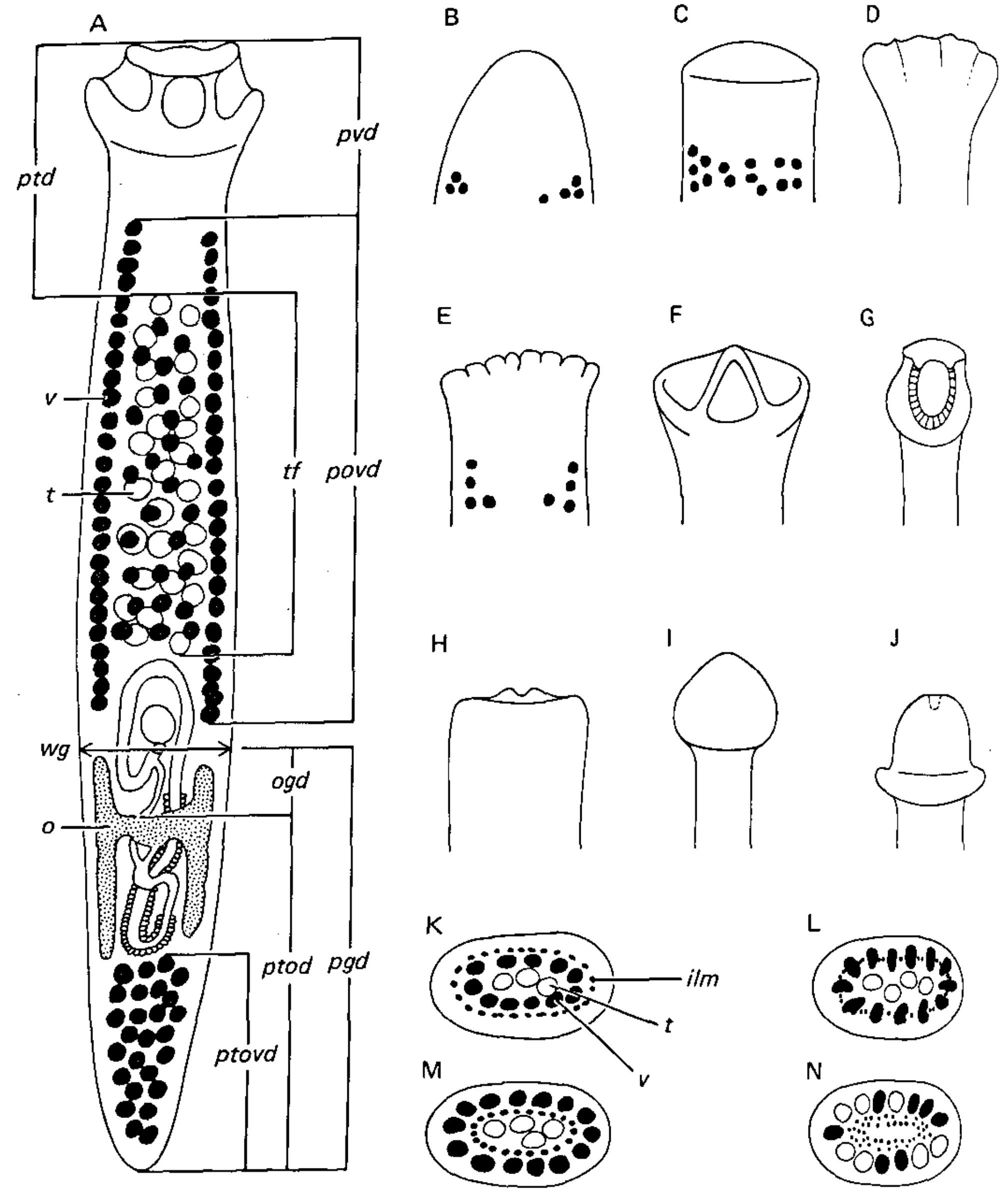

Fig. 1. Morphology and anatomy of caryophyllideans.

A. Hypothetical species, with bothrioloculodiscate scolex, indicating regions: previtellaria distance (*pvd*), pre-testes distance (*ptd*), pre-ovarian vitellaria field (*povd*), testes field (*tf*), post-gonopore distance (*pgd*), width at gonopore (*wg*), ovary–gonopore distance (*ogd*), post-ovarian distance (*ptod*), post-ovarian vitellaria distance (*ptovd*) and structures: ovary (*o*), testes (*t*) and vitellaria (*v*).

B–J. Some scolex types and example genera: Tholate (B, *Hunterella*, *Tholophyllaeus*), Cuneiform (C, *Caryophyllaeides*, *Edlintonia*), Cuneicrispitate or Flabellate (D, *Caryophyllaeus*), Cuneifimbriate (E, *Khawia*), Cuneiloculate (F, *Glaridacris*, *Spartoides*), Biacetabulate (G, *Biacetabulum*, *Rogersus*), Monobothriate (H, *Monobothrium*), Bulbate (I, *Atractolytocestus*), Choanocampanulate (J. *Caryoaustralus*).

K–N. Cross-sections with inner longitudinal muscle (*ilm*) arrangement for various families: Caryophyllaeidae (K), Capingentidae (L), Lytocestidae (M), Balanotaeniidae (N).

Natural selection, of course, has profoundly affected the presence of these characteristics, yet it is difficult to understand how each may have contributed to the survival of the group as a whole. Central to any consideration of selection and evolution in the Caryophyllidea are the biological consequences of monozoism and progenesis.

PARADOX

Caryophyllid cestodes are an evolutionary paradox – they have become successful tapeworms despite the fact that they lack the adaptation that is the hallmark of other cestodes – high reproductive potential. Among the polyzoic cestodes, this high reproductive potential is facilitated by a body plan consisting of a long chain of proglottids, each bearing at least one set of reproductive organs. By continuously producing new proglottids in the neck region there is insured a continuous production of eggs. Indeed, this production may proceed for years, up to 14 as Read (1967) demonstrated for *Hymenolepis diminuta,* a common cestode of rats. Without selection for proglottids to provide the great number of eggs needed to compensate for the risks of completing a cycle, it is doubtful that cestodes would have become successful parasites. In some minute cestodes such as *Staphylocystis pistillum* of shrews (*Sorex* spp.) or *Echinococcus granulosus* of humans, that have few proglottids, the metacestode stage may reproduce asexually (e.g. staphlocyst, hydatid) thus further increasing the biotic potential of the species. In other larger forms such as *Multiceps* or *Mesocestoides,* asexually reproducing metacestode stages (e.g. coenurus, tetrathyridium) may also be found. However, asexual reproduction of the metacestode stage does not supplement the often prodigious proglottid and egg production (e.g. *Diphyllobothrium*) in many other cestodes.

On the other hand, caryophyllid cestodes with their monozoic body plan, generally small size (from less than 1 mm to about 100 mm, with the majority less than 30 mm long), short life-span (1–3 months) and lack of asexually reproducing stages, are also successful cestodes. How does one explain this apparent paradox? The answer may lie in part with the evolutionary consequences of a monozoic body plan.

MONOZOIC BODY PLAN

A monozoic body plan in cestodes (i.e. with a single set of reproductive organs) carries with it 3 important consequences – (1) reduced reproductive capacity, (2) less morphological and developmental complexity and (3) tendency for small size. In the absence of data on the biotic potential of any caryophyllid, it does not seem unreasonable to theorize that a cestode with a continually growing chain of proglottids would have a higher egg output than one with only one set of reproductive organs, assuming that all other factors are equal. If this supposition is correct then one can expect that fecundity has become less of an evolutionary necessity and that other aspects of parasite biology assume more important roles in species survival. Just as the comparative biology and ecology of digenetic and monogenetic trematodes are greatly influenced by profound differences in basic reproductive biology (high egg output and asexual reproduction in molluscs versus low egg output and no asexual reproduction, respectively), caryophyllid biology and evolution too have been influenced by a lowered reproductive capacity.

Unlike the polyzoic cestodes with a proliferative region in the neck giving rise to proglottids, such a zone is absent in caryophyllids (Mackiewicz, 1972) and, with only one set of reproductive organs, only one level of development is ever present at a time. Reduced complexity is also evident in the number of stages (metacestode) present in the cycle (see below). In fact, in *Archigetes* spp. there can be direct development to the ovigerous stage in the intermediate tubificid host.

One consequence of this comparative simplicity in form and development may be a shortened life-span. Without the capability to replace spent reproductive units, and there is no evidence that regeneration of any sort takes place, a worm does not live long after egg production ceases. Another may be related to a possible reduced genetic complexity augmented by obligatory self-fertilization, giving rise to populations with rather fixed genotypes. As discussed by Price (1980) the probability of evolution and speciation is much higher in a population of such individuals than in one where there is random outbreeding because selection has a chance to act on all genes in each generation. The net effect is to permit rapid differentiation or speciation once genetic changes appear in the population.

Small size is not unique to caryophyllids. Several genera of the Cyclophyllidea (for example, *Mathevolepis*, *Protogynella*, *Staphylocystis*), parasitic in Insectivora, have strobilae less than 1 mm long; in many of the other orders there are species less than 40 mm long. Except for *Cyathocephalus truncatus* (Pseudophyllidea), none of the others, as far as we know, is either small enough or capable of maturing in the invertebrate intermediate host. With *Archigetes*, however, its small size (less than 3 mm) is intimately related to the evolution of progenesis in the Caryophyllidea. In no other group of cestodes has progenesis been such a dominant feature in their evolution. There can be little doubt that the monozoic body plan has had a profound influence on the evolution of the Caryophyllidea, particularly as it relates to progenesis and the life-cycle.

The fact that only the Caryophyllidea has evolved with the monozoic body plan is strong evidence that such a morphology lacks the high survival value of the more common strobilate type. In my opinion, monozoism in the Cestoidea is an evolutionary dead-end that has been carried to its fullest potential in the Caryophyllidea.

PROGENESIS

(a) *Caryophyllid stages*

Progenesis, or the precocious sexual maturation of an organism while it is morphologically in a juvenile stage, has been a dominant feature in the evolution of caryophyllids. Neoteny, a term often confused with progenesis, is the retention of juvenile characters in the sexually mature *adult* stage of an organism. These terms are often used interchangeably in referring to caryophyllids since the end result is a sexually mature individual with juvenile characteristics. It is, however, important to distinguish between them (see Gould (1977) and Mackiewicz (1981) for a more complete discussion) because the evolutionary implications are quite different for each one. If caryophyllids (vertebrate stage) are considered progenetic then there must have been another adult stage, now lost, sometime in the cycle; if neotenic, then all parts of the original cycle, including adult, are present. Clearly one must define 'adult' in order to decide which phenomenon prevails. And there's the rub.

It is a simple task to define 'adult' with a tapeworm such as *Diphyllobothrium*, with a well-defined procercoid–plerocercoid–strobila sequence, or *Hymenolepis* with the cysticercoid–strobila stages, where the strobila is obviously the adult stage. Not so obvious is what to call the egg-bearing stage of caryophyllids in vertebrates because there is no strobila. If one defines the strobila of tapeworms as the adult stage then caryophyllids are either exceptions to that rule or they lack an 'adult' stage. If an exception, then it is quite possible that they are, in fact, examples of a second type of tapeworm, one with no strobila stage. Such a view would alter our concept of tapeworms and would necessarily elevate caryophyllids to co-equal rank with strobilate tapeworms, dividing the class Cestoidea into 2 sub-classes based on the strobilate and non-strobilate condition. This interpretation was taken long ago when caryophyllids were incorporated into the Cestodaria (see Mackiewicz (1972) for taxonomic history). More recently, Bazitov (1976) and Kulakovskaya & Demshin (1978) have recommended that caryophyllids be elevated to separate status based on broad morphological, histological and biological criteria. *Gyrocotyle* and *Amphilina*, true cestodarians with a lycophoran larva and having a morphology and biology very different from caryophyllids, tend to be given separate status from each other and other tapeworms. However, see Wardle, McLeod & Radinovsky (1974) for still another view.

The above analysis would seem to be sound except for the disturbing resemblance of caryophyllid cestodes (Fig. 1 A) to the plerocercoids of Pseudophyllidea. Given the high visual impact and powerful persuasive nature of a comparison between the procercoid–plerocercoid–strobila sequence found in *Diphyllobothrium* and procercoid–plerocercoid(?) stage in caryophyllids, is there any wonder that the two sequences are considered homologous to each other? Accepting such a homology means that the terminal, adult stage in the cycle is missing and that the stage in vertebrates is either progenetic or neotenic, but not 'adult' *sensu* strobilate tapeworms. We have then a truncated series, one in which the 'original' adult strobilate stage has dropped from the series, perhaps through extinction of former hosts, and has been replaced by the plerocercoid stage. Such a scenario is held by those espousing the view that caryophyllids are simply progenetic or neotenic (the latter term is used most often in the literature) plerocercoids.

On the other hand, and remembering that caryophyllids are one of the most successful groups of tapeworms, would it not be possible to regard the above interpetation as that of the evolutionary origin of caryophyllids *as a group* rather than the evolutionary mechanism for *each* contemporary species? Given such a large number of species, it seems unlikely that each one lost a strobilate stage, developed along similar morphological lines and with the characteristic tubificid cycle. The coherent nature of caryophyllid morphology and life-cycles is clear evidence of evolution from a single, or at most, few stem forms. Thus the egg-bearing stage (plerocercoid-like) in vertebrates could be regarded as a true, non-progenetic (or neotenic) adult form, that through progenesis initially evolved to a stage that underwent considerable radiation and evolution, giving rise to contemporary caryophyllids. Whether one regards the monozoic egg-bearing stage as progenetic (because of the plerocercoid-like morphology and absence of a former strobilate stage) or neotenic (because the adult has a juvenile, plerocercoid morphology) or simply as adults without reference to the cycles of any other group of cestodes, depends on how one views the evolutionary history of the group. To consider them as neotenic plerocercoids would appear to be a contradiction because how could the plerocercoid-like morphology be, on the one hand, 'adult', implying there was no succeeding stage and, on the other hand, juvenile, implying there was? Nor does it seem logical, in my judgement, to regard as progenetic any stage that may have evolved from a stem form that itself may have arisen through progenesis. Unless one can prove that each species had a strobilate stage, and no such proof appears evident, there seems little reason to consider the stage in vertebrates as progenetic plerocercoids. Like strobilate stages, the monozoic one should thus be considered as a terminal *adult* stage.

One can, however, consider *Archigetes* as a progenetic procercoid because the egg-bearing stage in tubificids has discrete juvenile characters, for example, non-functional gonopores and a cercomer. When *Archigetes* is eaten by a fish before progenesis is achieved, development continues to the characteristic caryophyllid adult stage lacking a cercomer and having functional gonopores. 'Progenetic' can be used properly in this case because juvenile characters are lost when a later (adult) stage is reached.

(*b*) *Evolution and biology*

What is the relationship of progenesis to caryophyllid evolution and biology? Far from being a phenomenon indicative of a relict stage (Stunkard, 1959) it has been shown in plagiorchid trematodes to have definite adaptive value (Grabda-Kazubska, 1976). Progenesis, or the tendency toward it in cestodes, appears to be chiefly in the Pseudophyllidea, particularly with *Schistocephalus*, *Ligula* and *Digramma* (Ligulidae) where there is advanced maturation (but not maturity) in the fish intermediate host (Dubinina, 1966). In *Cyathocephalus*, the procercoid may mature in the arthropod (amphipod) intermediate host. In each of these cases the net effect of progenesis is to shorten the cycle, theoretically allowing for more generations and hence a higher net reproductive capacity. But what of the caryophyllids?

In the caryophyllids, progenesis has truncated the *Archigetes* cycle such that maturity occurs at the earliest stage possible – the procercoid. Because the oncosphere does not have the level of organization necessary to produce eggs, progenesis has made the *Archigetes* cycle the shortest possible for any cestode. Obviously, *Archigetes* provided a combination of factors or conditions that allowed for the selection of such a truncated cycle. One of these factors may have been small size that allowed the procercoid to remain in the tubificid coelom. Selection could only be successful, however, if such a progenetic stage could complete its cycle in the tubificid, or with a fish. It is largely because tubificids are so common and often clumped that wide dissemination of eggs was not necessary, thus allowing for a cycle to evolve in a single host. In *Archigetes limnodrili* we have such a cycle with maturation only in tubificids; in *A. iowensis*, on the other hand, maturation takes place in either a fish *or* tubificid. This latter, facultative cycle illustrates perhaps the most efficient type of cestode cycle or strategy, one that has the fewest number of developmental stages (through progenesis) and survives with or without the definitive host. Apparently, few other cestodes have the combination of characteristics (such as size, abundant intermediate hosts and other adaptations) that allows for such a cycle to develop, a cycle that is so reduced in complexity that it has become an evolutionary dead-end. Once a caryophyllidean has achieved the *Archigetes*-type cycle there is nowhere else to go. For that reason it seems reasonable to consider *Archigetes* at the end of a long history of evolution and not the beginning as an archtype that gave rise to strobilate cestodes.

If we now take progenesis one step further, that is to the plerocercoid stage, it is possible to briefly speculate on the origin of the caryophyllids. Given a cycle comparable to *Diphyllobothrium* with a parenteral plerocercoid in a fish intermediate host, is it not possible that such a stage could have become progenetic *before* moving to a parenteral location? It is difficult to know just what factors could have been selected for in this case. Obviously the cycle would have been shortened and, along with other events involving tubificids, the shortened cycle may have had a greater chance of success and thus was selected for. As interesting as this speculation may be the important question is not: did progenesis occur? but rather, what stimulated the premature maturation?

We know that Dubinina (1966) was able to induce experimentally progenesis in *Digramma* in goldfish by elevating the temperature of an aquarium. The use of elevated temperatures to speed up development is well known, but it is most successful when the definitive host is a homeotherm. As far as we know, homeotherms were never part of a caryophyllid cycle.

Perhaps more to the point is the illuminating suggestion by Szidat (1959) that host hypophyseal and thyroid hormones may have been responsible for the neotenic (his term) development in caryophyllids in much the same way that hormones regulate the occurrence of neotenic generations and maturity of *Polystomum integerrimum* in tadpoles and frogs. Increased hormonal activity in fish such as *Gasterosteus* and *Salmo*, as evidenced by the presence of hormone in the intestine, may be correlated with migrations from marine to fresh water, according to Szidat (1959). His speculation that neoteny in cestodes and trematodes may be correlated with hormonal changes accompanying migrations to and from different environments is not without considerable merit in my opinion. It is no coincidence that both of the above hosts have pseudophyllidean cestodes (*Schistocephalus*, *Diphyllobothrium*, *Cyathocephalus*) with procercoid and plerocercoid stages. Given hosts with migratory behaviour and normal repeated hormonal changes, we have ideal conditions for the repeated exposure of developing cestode stages to highly active biological molecules. Far from being a chance event, the precocious development of a juvenile cestode stage could have occurred many times on a predicted, regular schedule until a 'strain' or 'race' was selected for. In time, a portion of the parasite cycle would become adapted to a fresh water, not marine, environment. It is then a short step to the evolution of a 'new' form, given the scale of geological time. Although the principal hosts (ostariophysan fish) are considered primary fresh water fishes (Greenwood, Rosen, Weitzman & Meyers, 1966), dating from the Tertiary age, all evidence is that they are much older and are a group of relatively primitive teleosts, a fact consistent with possessing primitive cestodes, i.e. caryophyllids. While there are no true marine hosts many of the principal ones in North America (such as catostomid fish) have pronounced migratory habits. We may never know how progenesis or neoteny arose but the Szidat hormone theory provides a testable hypothesis: do host hormones influence cestode development? Perhaps the ancestral hosts of the stock that gave birth to the caryophyllideans may have been a migratory marine fish, not a fresh water one, as generally believed.

LIFE-CYCLE

How did the life-cycle of caryophyllids evolve? Because it is possible to theorize several plausible scenarios in which tubificids, definitive hosts, predators and other hosts, some extinct, are arranged in various ways, this question defies an absolute answer. Without methods of testing critical parts of any scheme it is doubtful that there will ever be a consensus among helminthologists as to which series of events comes closest to reality – such is the great weakness of this somewhat simplistic approach. On the other hand, one can achieve the same end by asking: what are the adaptations and selective pressures that enabled such a cycle to evolve? By placing emphasis on survival value and viewing evolution in an ecological-population context it may be possible to appreciate the reasons for certain structures or events or most important, to understand how adaptations or events may have influenced the direction of life-cycle evolution. It would be very helpful, for example, if we knew what was the adaptive significance and survival value of: nuclear storage vacuoles in vitelline cells, small size of *Archigetes*, operculate eggs that do not release a swimming embryo, high vitamin B_{12} storage, or, the monozoic body plan itself. Unfortunately, we do not have the answers to all of these questions, but some recent discoveries and new ideas have brought a better understanding of the relationship of caryophyllids to the rest of the Cestoidea (see Mackiewicz (1981) for a more extensive review).

(*a*) *Intermediate host*

A key feature of the life-cycle is an aquatic oligochaete intermediate host. (families: Tubificidae and Naididae), in sharp contrast to an arthropod that is so common in other cestode cycles with an aquatic phase (for example, *Diphyllobothrium*, *Ligula*, *Eubothrium*, *Triaenophorus* or some *Proteocephalus* spp.). In fact, the only other cestodes with tubificid intermediate hosts, according to Demshin (1975), are a single species each of the bird cyclophyllideans *Hymenolepis*, *Paricterotaenia*, *Haploparaxis*, *Sacciuterina* and 2 of *Apolparakis*. Other helminths include 3 nematodes and 1 trematode, thus making a total of 10 worms, a small number compared to all the species in the Caryophyllidea. Clearly, tubificids provided such a rich combination of ecological and physiological 'benefits' that monozoism was able to evolve and radiate into a whole new group of cestodes.

Among the 'benefits' could be a long narrow body cavity and longevity that allowed for *more* growth and a *longer* growth period, the latter of possible importance in the origin of progenesis in trematodes (Grabda-Kazubska, 1976).

These may not have been possible in the coelom of zooplankton such as *Cyclops* or *Diaptomus*. In small tubificids, however, too much growth causes rupture of the body wall with the result that selection for progenesis must be confined to small forms like *Archigetes*. With periods of from 60 to 170 days for *Archigetes* maturation, a life-span of over a year for tubificids offered conditions favourable for progenesis to emerge as a life-cycle strategy.

Other 'benefits' could be less competition for the resources of the coelom as well as for the tubificids themselves, a common and widespread but little exploited inhabitant of the benthos. An indirect but significant benefit was that tubificids were also part of the trophic level of a different group of hosts – benthic feeders. Thus new hosts became available for exploitation, ones that until then probably had not been incorporated into many cestode life-cycles. Indeed, even today, the great majority of cestodes of catostomid fish, predominantly benthic feeders, are caryophyllids. Even *Cyprinus carpio*, the most widely distributed cyprinid fish, and largely a benthic feeder, has more caryophyllids than strobilate tapeworms.

That caryophyllids are almost exclusively parasites of fresh water fish may be attributed in large measure to the distribûtion of the intermediate host–benthos of fresh water habitats. However, various genera such as *Tubifex* and *Peloscolex* have species in estuarine and marine habitats (Brinkhurst & Jamieson, 1971), thus accounting for infections in the marine fish *Gobius*, *Pleuronectes* and *Zoarces*. Records of such infections, although rate and consisting of immature stages, provide evidence that some marine fish are indeed exposed to infected tubificids. In the short run such encounters between marine fish and tubificids are transitory events of little evolutionary or biological significance; but in the long run of geological time, with repeated exposure and possible selection of a cycle adapted to estuarine conditions and hosts, new species may slowly evolve in far different hosts and habitats than known today.

(*b*) *Definitive hosts*

Without exception, and here we must excuse *Archigetes* in tubificids as a species complex utilizing the strategy of progenesis for survival, hosts are fresh water fish, marine ones being rare and generally considered accidental. Other accidental hosts are fresh water fish in the families Centrarchidae, Salmonidae and Percidae. Of the approximately 100 other host species the great majority (90 %) are ostariophysan fishes with the Cyprinidae (minnows) predominating and Catostomidae (suckers) close behind; the remainder consist of 6 families of siluriformes or catfish. All of these share benthic-feeding habits, a necessary pre-requisite for ingesting tubificid annelids.

A vivid illustration of how benthic-feeding habits have determined hosts is illustrated by the occasional occurrence of *Khawia armeniaca* in *Salmo ischchan*, sevan trout of Lake Sevan, Armenia. Young *S. ischchan* feed on the benthos, a habit facilitated by its inferior mouth, a characteristic absent in other salmonids. Clearly, such determinants as feeding habits have played a dominant role in the selection of oestariophysan hosts.

Host specificity, as evidenced by a preponderance of catostomid, cyprinid and silurid hosts appears to be maintained by host feeding habits rather than physiological differences. When there is a disruption in the normal feeding habits of non-benthic feeders host range increases. Evidence of this is provided by the rare records of caryophyllids (immature stages) from largely carnivorous or insectivorous fish as *Esox* (pike: Esocidae), *Perca* (perch: Percidae) and *Lepomis* (sunfish: Centrarchidae). Evidently, large numbers of fish may include tubificids in their diet since the host list includes fish from some 8 orders, 18 families and 66 genera. Fish are not the only possible hosts. There is one record of *Glaridacris catostomi* in the salamander *Necturus maculosus* (Amphibia: Proteidae). In transfaunation experiments in our laboratory we found that *Glaridacris laruei* from donor *Catostomus commersoni* lived longer in a frog (Ranidae), *Rana pipiens* than in 3 different fish species. It is doubtful that under normal conditions an adult *R. pipiens* would ever eat tubificids, yet this simple experiment illustrates just how plastic host specificity may be. To be sure, maintenance for 72 h is hardly evidence that maturation would take place, yet it is surprising that the tapeworms were not immediately digested. Perhaps additional feeding experiments with amphibians (*Rana*, *Bufo*, etc.) and reptiles such as water snakes (*Natrix*) and aquatic turtles (*Chrysemys*, *Chelydra*) would establish the limits of survival in poikilotherms other than fish.

Can we assume that caryophyllid host specificity is a function only of host feeding habits? No. Although the Siluriformes (catfishes) are dominant hosts in the ethiopian and oriental zoogeographical regions, I am aware of only one record (unpublished) of a caryophyllid (immature) from any catfish in North America. In South America, where the catfishes are a dominant part of the fish fauna with over 450 species in the Amazon (Darlington, 1957), there are no records of caryophyllids. In the latter instance we have too few data to know if indeed caryophyllids other than *Archigetes* even exist in South America. This is not true for the Nearctic region, however. Perhaps the apparent lack of infections in catfishes in North America may be related to bile acid differences of cyprinid, catostomid and siluriform hosts. We know, for example, that the dominant component is a bile acid in *Carpiodes carpio* (Catostomidae) and is allocholic, while that in several siluriform fish is cholic acid (Brigg & Bussjaeger, 1972; Anderson & Halsewood, 1962). In some Cypriniformes on the other hand, a bile alcohol either 5α-cyprinol (from *Cyrinus carpio*) or 5α-chimaeral (from *Catostomus commersoni*) was the dominant component (Anderson & Haslewood, 1970). Whether or not bile component differences may influence host specificity in caryophyllids, as it has with some cyclophyllidean tapeworms, is not known. It would be of interest to learn what effect different bile components have on the viability of caryophyllids and if such effects are correlated with the general distribution and evolution of the more primitive bile salts in ostariophysan fish.

ZOOGEOGRAPHY

If one arranges the genera according to zoogeographical regions (Table 1) some important facts emerge. Except for the neotropical region, caryophyllids are commonly found in all the other regions. *Archigetes* has been reported from tubificids in South America but there are no records from fish. However, data are lacking for many suitable hosts. Catostomids range to the northern part of the neotropical region (Guatemala) and hence may offer the best host possibilities. In

Table 1. *Zoogeographical distribution of the* Caryophyllidea

Families ...	Number of species in regions					
Genera	Nearctic	Neotropical	Palearctic	Ethiopian	Oriental	Australian
Caryophyllaeidae						
Archigetes (6)*	2	1	5	1	—	—
Biacetabulum (10)	9	—	—	—	—	?‡
Bialovarium (1)	1	—	—	—	—	—
Calentinella (1)	1	—	—	—	—	—
Caryophyllaeus (8)	—†	—	4	?	4?	—
Diefluvium (1)	1	—	—	—	—	—
Glaridacris (6)	6	—	1	—	—	—
Hunterella (1)	1	—	—	—	—	—
Hypocaryophyllaeus (2)	2	—	—	—	—	—
Isoglaridacris (11)	11	—	—	—	—	—
Janiszewskella (1)	1	—	—	—	—	—
Monobothrium (7)	5	—	2	—	—	—
Paracaryophyllaeus (1)	—	—	1	—	—	—
Penarchigetes (2)	2	—	—	—	—	—
Pliovitellaria (1)	1	—	—	—	—	—
Promonobothrium (1)	1	—	—	—	—	—
Rogersus (1)	1	—	—	—	—	—
Rowardleus (1)	1	—	—	—	—	—
Wenyonia (8)	—	—	—	8	—	—
Lytocestidae						
Atractolytocestus (1)	1	—	—	—	—	—
Bothrioscolex (4)	—	—	4	—	—	—
Bovienia (2)	—	—	—	—	2	—
Caryoaustralus (1)	—	—	—	—	—	1
Caryophyllaeides (1)	—	—	1	—	—	—
Crescentovitus (1)	—	—	—	—	1	—
Djombangia (3)	—	—	—	—	3	—
Khawia (5)	1	—	4	—	—	—
Lytocestoides (3)	—	—	—	1	2	—
Lytocestus (11)	—	—	—	3	8	—
Lucknowia (1)	—	—	—	—	1	—
Markevitschia (1)	—	—	1	—	—	—
Monobothrioides (4)	—	—	—	4	—	—
Notolytocestus (2)	—	—	—	—	—	2
Stocksia (1)	—	—	—	1	—	—
Tholophyllaeus (1)	—	—	—	—	—	1
Capingentidae						
Adenoscolex (1)	—	—	—	—	1	—
Breviscolex (1)	—	—	1	—	—	—
Capingens (1)	1	—	—	—	—	—
Capingentoides (3)	—	—	—	—	3	—
Edlintonia (1)	1	—	—	—	—	—
Pseudocapingentoides (1)	—	—	—	—	1	—
Pseudocaryophyllaeus (1)	—	—	—	—	1	—
Pseudolytocestus (2)	1	—	—	—	?	—
Spartoides (1)	1	—	—	—	—	—
Balanotaeniidae						
Balanotaenia (2)	—	—	—	—	—	2

* Number of species.
† Not present.
‡ Questionable occurrence.

the absence of cypriniforms, so common in other regions, it is possible that caryophyllids have not been able to radiate very far into South America.

Another important fact is that certain families tend to predominate in a particular region; in the nearctic it is the Caryophyllaeidae; palearctic, the Caryophyllaeidae and Lytocestidae; Ethiopean, the Lytocestidae; oriental, the Lytocestidae and Capingentidae; and in the Australian the Lytocestidae. Deviations from this pattern can often be explained by imported hosts, as in the nearctic where the only species (2) in the Lytocestidae are from carp (*Cyprinus carpio*), an introduced host. In other cases, such as '*Biacetabulum*' in the Australian region and '*Caryophyllaeus*' in the oriental region, there is insufficient information (namely, data on muscle disposition) to allow placing the species in any family.

Perhaps the most important fact to emerge from a summary of the distribution is the high degree of endemism exhibited at the generic level. There are only 7 of the 45 genera reported for more than one region: *Archigetes*, *Caryophyllaeus*, *Glaridacris*, *Monobothrium*, *Khawia*, *Lytocestus*, *Lytocestoides* and *Pseudolytocestus*. Of these, only *Archigetes*, *Glaridacris* and *Khawia* appear to be true cases of a disjunct distribution. As noted above, *Khawia* occurs in carp, a widely introduced fish; and *Archigetes*, the most widely distributed genus, is primarily a parasite of invertebrates (tubificid annelids), while *Glaridacris* is from *Catostomus catostomus*, native to the palearctic and nearactic. *Lytocestus* and *Lytocestoides* are from the Clariidae, a family common to both regions. However, there is reason to seriously question these records, like those of *Monobothrium*, because the genera are not sufficiently well defined. In the case of *Caryophyllaeus* and *Pseudolytocestus* the records (Oriental region) are highly questionable because of insufficient data. This high degree of endemism is in large measure a reflection of the fish fauna of each region. It would appear that to the extent the fish fauna of each region differs, so too do the caryophyllids. This relationship is especially evident with the catostomid fish of the nearactic, none of whose caryophyllids, save *Archigetes*, occurs also in a non-catostomid host. *Archigetes* is an exceptional case because of its progenetic status in an invertebrate whose distribution is not as restricted as that of the vertebrate hosts.

If this phenomenon of endemism is a true reflection of caryophyllid distribution then any genus (e.g. *Monobothrium*, *Biacetabulum*, *Pseudolytocestus*) occurring in diverse hosts in widely scattered zoogeographical regions should be carefully re-studied. Unless one is able to explain a disjunct distribution by tectonic events, host migration, or other means one may be forced to conclude that (*a*) the identification is in error, (*b*) the genus is poorly defined, or (*c*) a genus has evolved independently in two separate regions. This last alternative can be rejected as being contrary to evolutionary principles. In all probability a combination of the first two alternatives usually prevails. In my experience mis-identification often plays a major role in the origin of unusual distributional and host records.

TERMINOLOGY

(*a*) *Stages*

What is in a name? A great deal when considering caryophyllid stages. The problem of what to call the immature stage in tubificids can depend on one's view of the evolutionary history of the group. General consensus is that such an immature stage is a procercoid as evidenced by the cercomer, unless one is prepared to deny the obvious resemblance of this stage to the comparable one of *Diphyllobothrium*. This has been done by Freeman (1973) who has chosen to call the cercomer-bearing, immature stage a 'caudate postplerocercoid'. It is a 'postplerocercoid' because of the well-developed scolex, advanced development of gonads (for many) and site, i.e. parenteral. To use the term 'postplerocercoid' would seem to imply that 'plerocercoid' (*sensu* Freeman) could be used if advanced gonadial development was absent, as in some *Monobothrium* species. If this interpretation is correct, then caryophyllids would have the following series of stages: egg, oncosphere, caudate plerocercoid or caudate postplerocercoid and acaudate adult. The justification for this terminology rests with the assumption that there is no progenesis in the cycle and that the final, mature stage never was strobilate, even in past evolutionary history. Progenesis, a well-recognized and documented zoological phenomenon, should in my judgement be used to explain the procercoid morphology and developmental stage, because of the presence of the cercomer, non-functional gonopores, and, in the case of mature *Archigetes* in tubificids, cuticular pouch, all bonafide 'larval' characteristics. It would appear then that no new terminology is needed to described what clearly appears to be a progenetic procercoid with advanced development of scolex, genitalia (in some) and, in the case of *Archigetes*, egg production.

The problem of what to call the mature stage in the vertebrate also requires a decision regarding the evolutionary history of the group. Basically there are two choices concerning the acaudate adult. Extensive arguments for and against choice (1) can be found in the reports of Mackiewicz (1972, 1981) and Freeman (1973). In essence, use of that terminology assumes that each species has lost its strobilate stage, an assumption unsupported by any evidence. To assume that each of the 126 species independently lost their strobilate stage and evolved cycles in tubificids is to defy reason. Rather, we appear to have a group that once established with a tubificid cycle radiated to form the great number of genera we have today. It would appear to me that given the great number of species and evidence of radiation, the term 'progenetic' cannot be properly used to describe the mature stage in fish. If it is, then where is the proof that there exists or ever existed another following stage, conceivably strobilate, for each species?

To designate the vertebrate, mature stage of caryophyllids as an 'acaudate adult' is to indicate a state, not stage. 'Adult' is not a morphological designation since it can be used with a great variety of organisms; it simply means that the stage is mature. And 'acaudate' can obviously be applied to all stages lacking a cercomer, including all strobilate ones and many metacestodes. Clearly 'acaudate adult' is not a satisfactory term for the morphological type characteristic of the vertebrate phase of caryophyllids.

A new term, specific to this group of cestodes is needed to avoid making a judgement of the evolutionary history of the group, Perhaps a term like 'monopleroid' to signify the type of adult stage or type, characteristic of the mature, acaudate stage of caryophyllids would be desirable. Such a term would be purely descriptive and free from evolutionary implications, thus freeing it from the great controversy that has plagued the group through the centuries. Monopleroid could be defined as a: 'Mature stage of cestodes, lacking a cercomer, internal or external proglottidization, and with a single set of reproductive organs'. A monopleroid morphology or body type would be also characteristic of *Amphilina* and *Gyrocotyle*, if one regards them as cestodes *sensu strictu*. If more than one set of reproductive organs is present, in the absence of external segmentation (for example *Spathebothrium*, *Cyathocephalus*) then perhaps 'polypleroid' might be an appropriate designation.

(*b*) *Morphology*

It is unfortunate that anyone wishing to describe the morphology of caryophyllid cestodes, and to a large measure other cestodes, will find an appalling lack of appropriate, concise, descriptive terms. Absent too are names for, and identification of, particular parts of the body that can be useful in comparative studies on morphology and that all-important function of making keys. In the absence of an appropriate vocabulary or guide to basic morphological types and measurements, it is no wonder that there is so little standardization of descriptions and often chaotic confusion and misunderstanding of the few terms present. Some suggestions concerning kinds of body measurements and scolex terminology are presented below.

The body of caryophyllids lacks proglottids and thus one can identify specific reference points that may serve in establishing regions or making ratios. A number of these regions are shown on the hypothetical monogonoporate species in Fig. 1A; with digonoporate species the anterior or male gonopore may serve as a reference point. Principal reference points are the location of: gonopore(s), anterior-most testis and vitellarium, and anterior border of ovarian commissure. Of course, it is possible to select other points, such as the most anterior or posterior edges of the ovary but since there may be so much variation in arm length, the position of the ovarian commissure is a more representative and stable point. Furthermore, it may be quite difficult to clearly establish the limits of the ovary, particularly when it is follicular and continuous with the pre- and post-ovarian vitellaria (e.g. *Wenyonia*, *Lytocestus* spp.). Use of these points to identify body regions should facilitate the construction of keys, descriptions and in morphometric studies, differential growth patterns.

Perhaps the greatest need for new terminology in the Cestoidea as a whole is the development of a set of terms to describe overall scolex morphology. It is remarkable that after more than 100 years there has been no appreciable change in the way the scolex has been described. Specific structures such as acetabula, rostellum, bothridia, tentacles etc. have been identified, thus greatly simplifying descriptions, yet few scolexes are described in a systematic way utilizing a specific vocabulary so that descriptions are single words or a few at most. Some progress is being made to rectify the situation in the Caryophyllidea.

An early attempt to categorize scolex types of caryophyllideans was made by Hunter (1930) when he designated those of *Glaridacris laruei* and *Archigetes* as 'II type'. In this case the 'II' was meant to simulate the scolex shape, namely, central bothrium with lateral muscular ridges, topped with disc and supported on a scolex base (Fig. 1A). More recently I have begun to use a new terminology based largely on Greek and Latin descriptive terms. Some of this published terminology, and some new terms, are illustrated in Fig. 1B–J. The value of such terminology, though far from inclusive of all caryophyllid scolexes, is that it greatly simplifies characterization of each scolex, allowing for a broad classification of scolex types. Of even greater significance is that a systematized and standardized terminology of not only basic scolex types but all other aspects of cestode morphology, allows for a more precise identification of character states and subsequent analysis by cladistic techniques. If the ultimate goal of systematics is to elucidate the phylogenetic relationships of various taxa to each other then one must distinguish between general or primitive (plesiomorphic) character states and derived or apomorphic ones. Accurate, standardized descriptions of species is a major step in that direction.

SYSTEMATICS

(*a*) *Classification*

The systematics of the Caryophyllidea is complex, with uncertainties at all levels. As one might expect with an organism having such a distinct morphology and life-cycle, there have been various schemes of classification. Briefly, caryophyllids have been classified as: cestodarians, a family of the Pseudophyllidea, or accorded separate ordinal status.

Of the three alternatives, affiliation with the cestodaria, that is, with *Gyrocotyle* and *Amphilina*, has gained little support in modern times (since 1930), so great are the morphological and life-cycle differences. This is not to say that everyone believes that they should be placed with the rest of the Cestoidea. More recently Bazitov (1976), and Kulakovskaya & Demshin (1978) have proposed that the caryophyllids should be given separate status of class, sub-class, or super-order to distinguish them from strobilate cestodes. These views, reviewed by Mackiewicz (1981), should not be discounted out of hand in my judgement. Kulakovskaya is the foremost authority of caryophyllids in the USSR; Bazitov's opinions are based on extensive histological and cytological evidence; and Demshin has had broad experience with tubificid–parasite relationships, as well as with the life-cycles of caryophyllids. Unless one assumes that all cestodes with a hexacanth larva should be united into a single class or sub-class, regardless of adult morphology, then separation into strobilate and non-strobilate groups can be supported by firm arguments, not the least of which is the obvious morphological difference in body form. This difference is of a high order of magnitude, much greater, in my judgement than any other used to separate cestode orders. Add to this the life-cycle characteristics (annelid intermediate hosts), histology (nuclear storage vacuoles in vitelline cells, for example) and a large number of inter-related species – all combine to form a natural group, distinct from the strobilate cestodes.

Similar proposals to separate caryophyllids from strobilate cestodes in the late 19th and early 20th centuries were not accepted largely because (*a*) caryophyllids were regarded as neotenic cestodes and (*b*) they could be closely associated with the Pseudophyllidea. Furthermore, they were often grouped together with the Cestodaria, an association that tended to confuse, rather than clarify relationships. As a result, the caryophyllids were regarded more as examples of aberrant, neotenic forms rather than members of one of the major groups of cestodes. The fact that *Archigetes* had been discovered in 1878 focused special attention on that genus and the progenetic aspect rather than on the group as a whole. In the absence of very many other species there was no way that early workers could realize that *Archigetes* was only 1 of some 45 genera and that progenesis similar to that of *Archigetes* was actually limited, being confined to a single small genus. In retrospect, a pre-occupation with *Archigetes*, excessive emphasis on progenesis, conclusions based on a small number of species (only 5 described before 1900), and the lumping with cestodarians have kept the singular nature of caryophyllids from being fully appreciated. With the Cotyloda concept of Wardle *et al.* (1974), but without the Cestodaria, there has been a move to reorganize the cestodes along monozoic–polyzoic lines.

There are equally strong arguments for not according caryophyllids separate status from all other cestodes. Chief among them is the resemblance of the procercoid and succeeding stage (monopleroid, see above) to the procercoid-plerocercoid series of the Pseudophyllidea. So great is this resemblance that it is difficult not to regard the stages as homologous ones. If one considers them homologous, and most zoological opinion takes this view, then at the very least the caryophyllids are cestodes, similar to strobilate ones, and related in some ways to pseudophyllidean tapeworms. The most common view is that caryophyllids are neotenic or progenetic plerocercoids and hence closely related to pseudophyllids. Whether this is an accurate interpretation is a complex question. Similarities of the reproductive system, non-tetrafossate scolex, basically aquatic cycle and prominent role of fish in the cycle, emphasize the relationships of the two groups to each other. Whereas it was once felt that all these characteristics merited Family status, it is not generally accepted that caryophyllids constitute a separate Order at the same level as the Pseudophyllidea to which they are related. The ordinal status, in my opinion, is certainly justified considering the nature of the criteria used to separate families in the various cestode orders. Monozoism, in itself, is so basic a characteristic that its use as a family character is untenable, in my judgement. In combination with other morphological and biological features it may assume even greater systematic significance.

(*b*) *Family*

At present there are two general schemes for arranging the hierarchical ranks between Order and Genus: Family or Sub-family. Both ranks utilize the arrangement of the longitudinal (parenchymal) muscles to determine the number of taxa (Fig. 1K–N): either 4 families or 1 family with 4 sub-families. Which scheme is followed depends on the weight given to muscle arrangement. It is a matter of taxonomic judgement that some may wish to rank as an art, others as a science. In either case it is still stark subjective judgement with arguments, rather than objective criteria, being used to support either view. The family–sub-family scheme was crystallized by Hunter (1930) in his classic monograph; the elevation of each sub-family to family status was done by Wardle & McLeod (1952). This latter interpretation enjoys the widest acceptance today; however, this does not mean that it is an accurate reflection of the natural order.

I have used and continue to use the family, rather than sub-family scheme because I believe that the arrangement of the longitudinal muscles through the mid-part of the body constitutes a fundamental, anatomical characteristic at a high level of organization. Of course there can be variation that makes it difficult to place certain genera, especially in the Capingentidae (Fig. 1 L). One must realize that no character is absolute. Even one dealing with so basic a feature as body musculature can be further refined. Unfortunately, exceptions will occur; as they accumulate it will be necessary to reassess criteria.

Evidence that the body musculature may be a basic anatomical feature is its conservative, apparently non-adaptive nature. With over 100 species, almost all (we lack data on numerous species) can be placed into 1 of the 4 families on the basis of internal musculature. This does not mean that only 4 families exist; indeed it is possible to arrange the longitudinal musculature (inner and outer parenchymal series) in a number of ways different from those now known. Perhaps these other arrangements will be discovered in the future. It is not inconceivable that other characters, alone or in combination with musculature, can be used to define families.

As one can see from Table 1, most of the families are large and with many genera; whether the genera under each family can be further divided into sub-families has yet to be determined. Until there are strong arguments to the contrary the sub-family concept in the caryophyllids should be used to explain the current 4 family organization in my judgement.

(c) *Genus*

An outstanding feature of caryophyllid systematics is the unusually high degree of monotypy in most of the families. Notice on Table 1 that 25 or 55 % of the genera have only 1 species! Even if this figure is reduced to one half or one quarter as new species come to light, there remains a high percentage. One may view such data as evidence of over-zealous taxonomists according undue significance to minor characters; or one may conclude that it is indicative of an ancient group that has undergone considerable evolution or is rapidly evolving. In my opinion the latter views are more valid because of the supporting evidence from cytological studies and the general consensus that caryophyllids are indeed an old group.

Another, less dramatic feature of the genera is the small number of synonymies. For example, the number of genera with synonymies in each family is as follows: Caryophyllaeidae (5), Lytocestidae (2), Capingentidae (0), Balanotaeniidae (0). Most examples have come from early genera such as *Archigetes*, because of the confusion regarding the relationship between the caudate and acaudate stages in different hosts, and *Caryophyllaeus*, the first genus described and subsequently used broadly before generic patterns emerged. The low numbers of synonymies may suggest that the concept of the genus is well defined. One must not be mislead, however. Genera such as *Caryophyllaeus*, *Monobothrium*, *Glaridacris*, *Lytocestus*, *Biacetabulum*, or *Archigetes*, all with over 5 species, are in need of revision because of the great diversity in the species. It would appear that there are not very large genera comparable in size to *Taenia*, *Hymenolepis* or *Proteocephalus* that would dominate a family. Rather, the pattern appears to be a large number of genera each with a few species, a phenomenon consistent with a group of organisms in which isolation is a prominent feature of the environment, fresh water fish. If past experience is any guide, many more new genera remain to be found.

The concept of sub-genus has not been used in the caryophyllids and may offer promise in the treatment of some complex genera where various single character differences among members of the 'same' genus make division into new genera questionable.

A fundamental and complex question regarding the genus is what constitutes generic characters? In my opinion the following are potentially generic in nature because, except for the scolex, they represent some principal, largely non-adaptive structures: scolex (Fig. 1B–J), vitellaria arrangement (annular, lateral, etc.), ovarian morphology (H-shaped, inverted A, etc.), gonopore condition (mono or digonoporate), external seminal vesicle and seminal receptacle (present or not), anterior extent of uterus (to or beyond cirrus sac), post-ovarian vitellaria (present or not) and gonopore position. There may be others such as testes distribution that are more difficult to assess.

The relative merits of each of these characters is beyond the scope of this paper and perhaps is even irrelevant if one wishes to utilize the taxometric or the cladistic approach to systematics. On the other hand 'scolex type' raises the most provocative questions regarding the systematics and evolution at the generic level. Take for example, the following question. Can a caryophyllid genus contain species with more than one type of scolex – for example, cuneiloculate (Fig. 1F) and bothrioloculodiscate (Fig. 1A) on *Glaridacris*? The answer to this question will have a profound effect on the systematics of caryophyllids. Traditionally, the scolex has assumed an important role in cestode systematics, yet one must not forget that it is clearly an adaptive structure subject to the selective pressures of the gut mucosal architecture. Like the bill of Darwin's finches (*Geospiza*), could not there be selective pressures operating on the evolution of the scolex at the generic level?

(*d*) *Species*

There are a number of unusual characteristics at the species level. Firstly, the high degree of endemism has already been discussed in the section on zoogeography. Another, more fundamental, cytological feature is the presence of polyploidy, undescribed from any other cestodes. Thus far 5 polyploids are known with 3 also having the more normal diploid state. Except for one species for which data are incomplete, all the polyploids have incomplete spermatogenesis and are considered sterile, reproduction being achieved by parthenogenesis, not known for other cestodes. We thus have some species such as *Glaridacris catostomi* that have diploid *and* triploid populations (Grey & Mackiewicz, 1980) and others that are only triploids, for example, *Atractolytocestus huronensis*. Not only does the occurrence of polyploids with parthenogenetic reproduction influence speciation mechanisms but it raises important questions on the nature of the species itself. For example, should the polyploids be accorded separate species status from the diploids? Unless there is a marked morphological difference between the two forms separate species status seems unwarranted. Even with pronounced differences one may hesitate to designate two separate species because they share the same chromosomes. The polyploids of *G. catostomi* are larger and have more testes but not significantly so from diploids; in *G. laruei*, on the other hand, polyploidy may be responsible for the pronounced difference in testes number in different populations. Wherever few testes occur, as in *G. oligorchis*, the possibility that polyploidy is present should be carefully checked. In widely distributed species, such as *G. catostomi* and *G. laruei*, there appears little doubt that some of the variation observed in populations from different parts of the range may have a genetic basis related to polyploidy. *Caryophyllaeus laticeps*, a widely distributed species in the palearctic and one notorious for wide variation, also has a triploid form (Grey, 1979). Far from being a rare phenomenon, polyploidy in the caryophyllids may constitute an important mechanism in speciation and cause of intraspecific variation.

Sexual reproduction in normal diploid individuals appears to be the usual condition in most species. Diploid counts, with number of species in parentheses, are: 6(1), 12(1), 14(3), 16(5), 18(5), and 20(3). This range, combined with the triploids with a maximum of 30 chromosomes, is the greatest for any group of cestodes. Some species (e.g. *G. laruei*) not only has a triploid but 2 diploid ($2n = 16$, 18) populations. Clearly, some species of caryophyllids are genetically complex, a complexity that can only be elucidated by cytological studies. Descriptions of new species should be tempered with an appreciation that genetic variants may be involved. Because of this genetic complexity, reliance on the traditional comparative morphological studies to identify patterns of speciation and intraspecific variation is fraught with intrinsic limitations. One fact is clear, there are many more species yet to be described.

RECOMMENDATIONS

Research thrives on questions – the 'right' questions. Some that may yield other than trivial data in the perspective of cestode evolution and biology are as follows.

(1) *Life-cycle*

How does the reproductive potential of the progenetic (tubificid) stage of Archigetes compare with that of the same or similar genus in the vertebrate host?

The answer may shed some light on the selective advantage of progenesis and its role in the evolution of the Caryophyllidea.

(2) *Genetics*

To what extent do the chromosomal karyotypes vary in different populations of the 'same' species?

Unlike any other cestodes the chromosomes of caryophyllids can be studied with relative ease, thus offering an unusual opportunity to learn more of the extent of polyploidy and other aspects of the genetics of cestode speciation. *Caryophyllaeus*, *Khawia*, *Lytocestus*, *Glaridacris*, or any other genus occurring over a wide area would be the genera of choice.

(3) *Cytology*

Can banding be demonstrated on chromosomes of cestodes?

It is doubtful that this question can be answered using other than cells from caryophyllideans; the large size of their chromosomes and ease of study makes them the overwhelming choice for study. Successful demonstration of bands will provide a powerful technique for the elucidation of genetic relationships, particularly of closely related species. It may also shed some light on the general aspects of cestode speciation.

(4) *Systematics*

How does the scheme of relationships (cladogram) generated by cladistic analysis compare with that provided by other means?

Application of this important and powerful technique may reveal some surprising data and suggest new ways to view generic and family organization.

(5) *Culture*

Can cells from caryophyllids be cultured?

Because caryophyllids have carried the cestode cycle to its theoretical limit by eliminating the vertebrate host (i.e. *Archigetes*), is it possible that their cells have the capacity to go the next logical step – elimination of all hosts? Cells from the immature stage of any species, preferably small ones where progenesis is highly advanced, would offer the best promise. Little needs to be said of the value of a line of cestode cells in culture for study of cestode physiology at the molecular level.

CONCLUSIONS

No other group of cestodes provides the unusual array of characteristics relevant to the study of their morphology, biology, ecology and evolution as do the Caryophyllidea. Monozoism, single host cycles (*Archigetes*), annelid intermediate hosts, parthenogenetic species, polyploidy and storage nuclei combine to set these cestodes apart from all others. For this reason study of them may provide insight and perspective into the ecological evolutionary relationships within the whole of the Cestoidea.

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