

PRELIMINARY PHYLOGENETIC SYSTEMATIC ANALYSIS OF THE MAJOR LINEAGES OF THE EUCESTODA (PLATYHELMINTHES: CERCOMERIA)

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Abstract.—Phylogenetic systematic analysis of the major groups of eucestodes, based on a suite of morphological characters, supports the hypothesis that pseudophyllideans are the sister-group of all other eucestodes, and nipotaeniideans are the sister-group of the lecanicephalideans, tetraphyllideans, and proteocephalideans, which occur in an unresolved trichotomy. Character data support inclusion of the Caryophyllidea within the Pseudophyllidea, as secondarily monozoic species related to cyathocephalids and spathebothriids, inclusion of the trypanorhynch and tetrabothriideans within the Tetraphyllidea, and inclusion of the Cyclophyllidea within the Proteocephalidea. The Cyclophyllidea as a whole appears to be a monophyletic group but, with the exception of the taeniates, the relationships among its included members are highly ambiguous. The hypothesis that tapeworm phylogeny mirrors host phylogeny at the highest levels is not supported. Elasmobranchs appear to have been colonized secondarily at least once, but that colonization may have occurred so long ago that the eucestodes of extant elasmobranchs still show strong phylogenetic associations with their hosts.

One of the most fascinating and enigmatic products of evolution is the group of parasitic platyhelminths called the Eucestoda, or true tapeworms. The Eucestoda represents one of the major groups of parasitic platyhelminths, and its monophyly is supported by at least 12 anatomical and ultrastructural synapomorphies (Brooks 1989a, 1989b). A recent encyclopedic compilation of the known diversity of tapeworms (Schmidt 1986) listed more than 3800 species inhabiting vertebrates of all classes except the Agnatha. This substantial diversity in a wide range of hosts makes tapeworms excellent models for studying major patterns of evolution and coevolution. Such studies are hampered by a lack of rigorously documented phylogenetic hypotheses. Those few phylogenetic systematic reconstructions that have been attempted (Brooks 1978a, 1978b; Brooks et al. 1981; Brooks & Rasmussen 1985; Hoberg 1986,

1989; Moore & Brooks 1987; Brooks & Deardorff 1988; Weekes, in prep.) either concern restricted groups or are highly ambiguous due to poor understanding of appropriate outgroups.

It is our purpose in this study to provide a concise picture of the state of the evidence supporting the current higher-level relationships among eucestodes, point out potential problem areas, and encourage new studies in eucestode phylogenetics. We have based our study on traits used by previous workers to support their classifications, and checked by our own studies, so the database for our study is comparable to those used by previous workers. Consequently, we believe that this study is a worthwhile first step towards producing a solid phylogenetic classification of tapeworms. We think it is important to state, at the beginning, that the results of this analysis differ markedly from those presented previously for other major

groups of parasitic platyhelminths (Brooks et al. 1985a, 1985b, 1989; Bandoni & Brooks 1987a, 1987b). First, we have found relatively few characters useful for supporting relationships among groups. Second, we have found a great deal of unresolved ambiguity in the characterization of some key character complexes. Third, the eucestodes appear to be fascinating evolutionarily because they contain a number of "red herring" groups, whose placement in any phylogenetic scheme takes us boldly where no one has gone before. And fourth, the phylogenetic tree that results from this study supports some groupings that are highly inconsistent with widely used classifications of the tapeworms.

Methods

Determination of outgroups.—Phylogenetic systematic analysis requires evidence that the study group, or ingroup, is monophyletic, and one or more suitable outgroups, one of which is preferably the putative sister-group of the ingroup, and characters that serve to distinguish groups within the ingroup, based on outgroup comparisons (Wiley 1981, Wiley et al. 1991, Brooks & McLennan 1991). Extensive phylogenetic analysis has produced a highly-corroborated phylogenetic tree of the major groups of parasitic platyhelminths, which comprise the sub-phylum Cercomeria (see Brooks 1989b for a summary). Within that framework, the tapeworms comprise one of two sub-cohorts of the cohort Cestoidea (the other being the Amphilinidea). The sister-group of the Cestoidea is the cohort Gyrocotylidea, and the two cohorts form the infraclass Cestodaria. The monophyly of each group and the sister-group relationships of the gyrocotylideans, amphilinideans, and eucestodes are supported by the synapomorphies in the cladistic diagnoses listed below (an asterisk [*] indicates a character that is homoplasious within the Cercomeria).

Infraclass Cestodaria

Diagnosis: Osmoregulatory system becomes reticulate in late ontogeny; intestine lacking; posterior body invagination; copulatory stylet lost*; cercomer paedomorphic, reduced in size and at least partially invaginated; male genital pore not proximate to uterine opening; oral sucker/pharynx complex vestigial; ovary follicular; ovary bilobed; testes multiple, in two lateral bands; ten equal-sized hooks on cercomer in larvae; larval epidermis syncytial; viteloducts syncytial; neodermis does not protrude to surface between epidermal cells; no desmosomes in the passage of the first excretory canal cells; no evidence of endoderm in embryos*; vitellogenic cells with only one kind of electron-dense vesiculated inclusions*.

Cohort Gyrocotylidea

Diagnosis: Rosette at posterior end of body; funnel connecting with rosette short; funnel narrow; antero-lateral genital notch present; body margins crenulate; body spines small over most of body, large at pharyngeal level; large body spines long and narrow; testes extending posteriorly only to level of metraterm; vitellaria encircling entire body, extending along entire body length; no nuclei in larval epidermis; no multiciliary nervous receptors; no extensions of neodermis into intercellular space between epidermis and basal lamina.

Cohort Cestoidea

Diagnosis: Male genital pore and vagina proximate; cercomer totally invaginated during ontogeny; excretory system opens posteriorly in later ontogeny; hooks on larval cercomer in two size classes (6 large and 4 small); protonephridial ducts lined with microvilli; subepidermal ciliary receptors with true photoreceptor functions lacking in larvae; protonephridia in larvae in posterior end of body; inner longitudinal muscle layer

well-developed [new character, see discussion below].

Sub-Cohort Amphilinidea

Diagnosis: Uterine pore and genital pores not proximate; male pore at posterior end; vaginal pore at posterior end; tegument of adults with irregular ridges and depressions; uterus "N"-shaped; uterine pore proximal to vestigial pharynx; inner longitudinal muscle layer weakly-developed [new character, see discussion below].

Sub-Cohort Eucestoda

Diagnosis: Body of adults polyzoic; cercomer lost during ontogeny; six hooks on larval cercomer; excretory system reticulate in early ontogeny; medullary portion of proglottids restricted; hexacanth embryo hatches from egg, is ingested in water; second larval stage a proceroid; third larval stage a plerocercoid; protein embeddings in epidermis of hexacanth; tegument covered with microtriches; sperm lacking mitochondria; cerebral development paedomorphic, none seen in larvae.

Character analysis. — The above data provide evidence supporting the monophyly of the ingroup, and identifying, for use as outgroups, the sister-group of the ingroup and the sister-group of those two taxa. Relationships among various members of the ingroup are hypothesized on the basis of putative synapomorphies indicated by outgroup comparison of additional characters. As mentioned in the introduction, we based the study reported herein on traits used by previous workers to support their classifications, so the database for our study is comparable to those used by previous workers. The particular characters that we have chosen are those which we have confirmed to the best of our ability, based on our mutual experience with at least some members of all the major groups which we will discuss. The following are character argumen-

tations for the various characters used to support the phylogenetic hypothesis discussed herein.

1. Structure of the uterus I: The plesiomorphic condition, exhibited by the gyrocotylideans, amphilinideans, monogeneans, digeneans, aspidobothriideans, and udonellideans, is a sinuous, tubular uterus that opens to the surface through a permanent pore. This *plesiomorphic* condition is characteristic of pseudophyllideans. All other eucestodes, including the nippotaeniideans, possess bilateral saccate uteri lacking permanent pores. This *apomorphic* character places the nippotaeniideans in the same clade as the other non-pseudophyllidean eucestodes, and supports the placement of the Pseudophyllidea as the sister-group of the rest of the eucestodes. Among those groups of non-pseudophyllideans in which pores are recognized (e.g., tetraphyllideans and tetrabothriideans), the pores form by an invagination of the subtegument that eventually fuses with an evagination of the uterine wall (Baylis 1926, Wardle & McLeod 1952). These slitlike or porelike modifications of the tegument (a dehiscence) allow the release of eggs with the expansion of a gravid proglottid.

2. Structure of the uterus II: Within those tapeworms having bilateral saccate uteri, a number of types of uterine structures have been reported. Nippotaeniideans, lecanicephalideans (in our sense, and including cathetocephalideans for reasons discussed below), and tetraphyllideans (in our sense, and including trypanorhynch, tetrabothriideans, litobothriideans, and dioecotaeniideans, for reasons discussed below) possess relatively simple longitudinal saccate structures that occupy most of the middle of the proglottid. Proteocephalideans and taeniates possess a similar saccate structure with lateral diverticula. Other forms are found among cyclophyllidean taxa having retractable rostellums. The most widespread of these is a saccate structure that tends to fill

the proglottid (Matevosyan 1953). Two variants of this structure are recognizable, each of which may be derived independently (and we are assuming they are independent for the purposes of this preliminary analysis). These are the saccate uterus beginning to form and then breaking down into egg capsules and the saccate uterus becoming fibrotic and forming one or more paruterine organs. The structural homology of the remaining form of the uterus, a reticulum, is unclear although it may be derived from a saccate condition (Matevosyan 1953). Evaluation of the uterine structure has played a significant role in development of classifications for non-taeniate cyclophyllideans. Matevosyan (1953) suggested the necessity to elucidate fully patterns of uterine ontogeny in addition to providing definitions of structural relationships for the mature uterus in each group. Additionally, it is necessary to establish the homology for the origin of egg capsules (parenchymatous vs. uterine) (Bona 1955, 1975) and to clarify the relationships for the various forms of reticulate uteri that exist among a wide range of cyclophyllideans (e.g., among the Dilepididae: Kitner 1938; Bona 1957; Rybicka 1956, 1966; Spasskii 1966, 1968). We treat the condition found in nippotaeniideans, lecanicephalideans and tetraphyllideans as plesiomorphic to that found in proteocephalideans and taeniates; further, the condition found in proteocephalideans and taeniates is considered plesiomorphic to the expanded saccate condition found in non-taeniate cyclophyllideans; and finally, egg capsules and paruterine organs are considered independently derived from the expanded saccate condition.

3. Structure of the anterior holdfast in the adult: The plesiomorphic condition, exhibited by both the gyrocotylideans and amphilinideans, is a single apical suckerlike organ, which has been postulated to be a vestigial pharynx (Brooks et al. 1985a, Brooks 1989a). This structure is found in adult members of the Nippotaeniidea.

Members of the Pseudophyllidea have bilaterally symmetrical, bipartite scolices (the "difossate" condition), in which the modifications for attachment consist of leaflike longitudinal flaps (bothria) and their modifications. All other eucestodes have bilaterally symmetrical, quadripartite scolices (the "tetrafossate" condition), in which the modifications for attachment consist of four suckers or four flaplike structures called bothridia. If the nippotaeniideans belong in the same clade as the tetrafossate eucestodes, and with the pseudophyllideans as their sister-group, which is indicated by their uterine structure, then the difossate condition characteristic of the pseudophyllideans is an autapomorphy for the group, and is derived from an earlier ancestor than the common ancestor of the nippotaeniideans plus the tetrafossate eucestodes. This supports an interpretation that both the difossate and tetrafossate conditions are apomorphic characters derived independently from the plesiomorphic condition of a single apical sucker. Developmental support for this interpretation includes the presence of an apical invagination (which we interpret as apical sucker anlagen) in procercoids of all eucestodes, and the presence of apical suckers in plerocercoids of nippotaeniideans, lecanicephalideans, most tetraphyllideans, and many proteocephalidean eucestodes.

4. Major modifications of the anterior holdfast: We have considered three major apomorphic modifications of the apical sucker at this level of analysis. The plesiomorphic condition, as indicated in character 3, is a simple apical sucker. That structure may be atrophied, in the form of a glandular mass characteristic of many proteocephalideans. It may be greatly enlarged, in the form of a protrusible myzorhynchus, characteristic of members of the lecanicephalidean lineage. The structure of the myzorhynchus itself may be variable (including its apparent secondary loss in *Discobothrium arrhynchum*), and this trait has been

used in characterizing genera of lecanicephalideans. Finally, the apical sucker may be modified into a structure containing hooks, called a *rostellum*, characteristic of cyclophyllideans and a few proteocephalideans. The rostellum may be retractable or not, and the shape and number of the hooks are variable. In addition, the rostellum has apparently been secondarily lost in a number of cyclophyllidean groups.

5. Major modifications of the tetraforesate condition: Tetraforesate eucestodes appear, at first glance, to come in two distinct varieties; those with four suckers and those with four flaplike structures called bothridia. We cannot use outgroup comparisons directly to determine which of the two major modifications of the tetraforesate condition might have arisen first because the sister-groups of the tetraforesate eucestodes, the Nippotaeniidea and the Pseudophyllidea, are not tetraforesate. However, developmental data are strongly suggestive. The plerocercoids of members of both groups (excluding the trypanorhynchs) have four suckers, and bothridia appear to arise as modifications of the sucker margins of plerocercoids (e.g., adult structures of *Calyp-trobothrium* spp.; see Alexander 1963). On the basis of that evidence, we suggest that the plesiomorphic tetraforesate condition is one in which the scolex comprises four laterally-positioned suckers. Bothridia, arising as modifications of sucker margins, are apomorphic to suckers.

6. The structure of the margins of the bothridia: Among species of tetraforesate eucestodes having bothridia, members of the Trypanorhyncha, Onchobothriidae, and some of the Phyllobothriidae have relatively rigid bothridial margins. Other members of the Phyllobothriidae have rather flimsy bothridial margins. If the scolices of *Calyp-trobothrium* spp. and relatives are indicative of the plesiomorphic bothridial nature (see e.g., Alexander 1963), it would appear that having flimsy margins is plesiomorphic. Hence, all those species having bo-

thridia with rather rigid margins would form a monophyletic group within the tetraphyllideans, and those having flimsy margins would exhibit the plesiomorphic condition for the tetraphyllideans.

7. Paedomorphic development of the scolex: Within the group of tetraphyllideans having rather rigid bothridial margins are two groups (the Onchobothriidae and the Tetrabothriidae) which exhibit apparent paedomorphic development of the scolex. In those species, the adult form does not emerge until the plerocercoid is established in the definitive host (Hamilton & Byram 1974, Cake 1976, Hoberg 1987). In other eucestodes, the fully functional adult scolex morphology is expressed in the larval or juvenile stages found in intermediate hosts (Wardle & McLeod 1952, Riser 1956, Jarreca 1975, Avdeeva & Avdeev 1980, Jarreca & Burt 1984). Hoberg (1987, 1989) has suggested, on the basis of developmental sequences in the plerocercoid and young adults, that the tetrabothriideans have true bothridia with relatively rigid margins (see also Andersen and Lysfjord 1982) and exhibit paedomorphic scolex development (Baer 1954, Temirova & Skrjabin 1978).

8. Scolex tentacles: The Trypanorhyncha has been considered a member of the Tetraphyllidea by some, because of the uniform possession of bothridia in all species, and as a member of the Pseudophyllidea by others, because of the presence of four tentacles in both *Haplobothrium* and in the Trypanorhyncha, and because some trypanorhynchs have been described as being difossate and having pseudophyllidean-like eggs. However, those trypanorhynchs described as being difossate actually have two pairs of fused bothridia. Trypanorhynchs show X-shaped ovaries in cross section, and have bothridia with rather rigid margins. However, they do not exhibit paedomorphic scolex development. In addition, the tentacles of *Haplobothrium* do not usually persist in the adult scolex and are non-retractable; hence, we do not consider them

homologous with the tentacles of the trypanorhynchs. Therefore, we suggest that the tentacles of trypanorhynchs represent an autapomorphy for the group, rather than a synapomorphy linking them with *Haplobothrium*.

9. Scolex hooks: The members of the Onchobothriidae possess 1–2 pairs of hooks at the apical end of each bothridium. We do not have any reason to believe that they are in any way homologous with the tentacles of trypanorhynchs, the bothrial hooks of the pseudophyllidean genus *Triaenophorus*, or the rostellar hooks of certain cyclophyllideans and proteocephalideans. Consequently, we consider this trait synapomorphic for the Onchobothriidae.

10. Apical armature: Members of the genera *Silurotaenia* and *Electrotaenia* are characterized by having rows of prominent spines encircling the apical sucker. Members of the genera *Vermaia* and *Gangesia* have rows of hooks encircling the apical sucker, which functions as a non-retractable rostellum. We interpret the hooks as modified tegumental spines, and believe that these taxa represent the sister-groups of the cyclophyllideans. Within the cyclophyllideans, the taeniates have non-retractable rostella with *Gangesia*-like hooks surrounding them. All others, including the enigmatic *Dasyurotaenia*, have retractable rostella, suggesting that this genus be excluded from the Taeniidae (Beveridge 1984). We consider the structural relationships of the rostellum in *Gangesia* and the taeniates to be evidence that the latter are the sister-group of all other cyclophyllideans.

11. Development of the internal longitudinal muscle layer in proglottids: Pseudophyllideans are characterized by having extensive, but relatively poorly-organized, inner longitudinal muscle systems. Consequently, the extent or organization of the cortex is limited in each proglottid. This condition is similar to that found among gyrocotylideans and amphilinideans, and is hence considered plesiomorphic for euce-

todes. Among other eucestodes (i.e., proteocephalideans and cyclophyllideans) there are highly distinct medullary and cortical regions of the parenchyma, the latter being relatively extensive, that are defined by the longitudinal musculature (Wardle & McLeod 1952). We consider this latter character apomorphic for the proteocephalidean plus cyclophyllidean assemblage provisionally, as it appears to occur convergently in members of other groups (e.g., in *Nippo-taenia chaenogobii*), and because its condition in lecanicephalideans and tetraphyllideans is not well-documented.

As an aside, we note that gyrocotylideans and eucestodes tend to be highly muscular, as indicated by difficulties in relaxing and flattening the worms for fixation, when compared with amphilinideans. Consequently, we consider a high degree of muscularity to be plesiomorphic for eucestodes and gyrocotylideans, and the condition found in amphilinideans to be a synapomorphy for that group (see diagnoses for gyrocotylideans, amphilinideans, and eucestodes, above).

12. Development of the egg and embryophore: Pseudophyllideans and trypanorhynchs, like amphilinideans and gyrocotylideans (and most other cercomerians), have "polylecithal" eggs [a large component of vitelline material forming a true shell that is quinone tanned; one embryonic membrane formed by the embryo (with the consequent lack of an embryophore); and "oviparous" development in which the embryo matures in the external (non-host) environment]. These forms additionally have operculate shells, and the hexacanth is a ciliated coracidium, with a unicellular protonephridium (except among the Trypanorhyncha) (Rybicka 1966, Freeman 1973, Burt 1987, Sakanari & Moser 1989). The remaining eucestodes possess "oligolecithal" eggs (a minimal vitelline component, and a shell formed by the embryo; two embryonic membranes; and "ovoviviparous" development in which the hexacanth matures in utero) (Jarecka 1975, Euzet &

Mokhtar-Maamouri 1976, Burt 1987). Among oligolecithal forms, ciliated coracidia and onchospherical flame cells are absent. The polylecithal condition is considered plesiomorphic, based on outgroup comparisons. However, based on other apomorphic characters linking trypanorhynch with tetraphyllideans (particularly the form of the scolex and ovary) (see discussion), polylecithal eggs in trypanorhynch would seem to be non-homologous with those in pseudophyllideans. This hypothesis is corroborated by the fact that trypanorhynch embryos lack the unicellular protonephridium of pseudophyllidean embryos.

13. Embryophore: Among most tetrafoosate eucestodes the embryophore is nucleated and not hardened, structurally resembling a non-ciliated coracidium. In cyclophyllideans the embryophore is rigid, being formed from the inner envelope (Rybicka 1966). The rigid embryophore in all taeniate cyclophyllideans is striated, a trait unique for the group. Additionally, some non-taeniate cyclophyllideans have a cytoplasmic layer surrounding the embryophore (*Paricterotaenia*, *Diorchis*, *Hymenolepis*, *Moniezia*) whereas in others it is absent (*Dipylidium*, *Mesocetoides*, *Catenotaenia*). Beyond supporting the monophyly of the taeniates, the phylogenetic significance of the structure of the embryophore requires additional assessment; it may provide important information in resolving the relationships among the proteocephalideans and cyclophyllideans (Freeman 1973, Burt 1987).

14. Cysticeroid stage: A number of proteocephalideans, including coralbothriids and proteocephalids, have a cysticeroid stage intercalated between the proceroid and plerocercoid stages (Freeman 1973, Jarreca 1975). The majority of cyclophyllideans (non-taeniates) have the cysticeroid stage and no recognizable plerocercoid stage. We believe that the presence of a cysticeroid stage distinguishes a large group of sucatoriates, possibly leaving only some species

of *Proteocephalus* (those having an apical sucker and no cysticeroid stage) as a basal group. We are assuming that the cysticeroid stage in proteocephalideans is homologous with the cysticeroid stage in cyclophyllideans. Documenting the distribution of this trait among other sub-groups of proteocephalideans is important in resolving the basal relationships within this clade.

15. Cysticercus stage: All members of the taeniates have cysticerci or modifications thereof. We consider this to be a modification of the cysticeroid stage, based on the assumption (above) that all cysticercoids are homologous.

16. Primary lacuna: The absence of a primary lacuna appears to be plesiomorphic for eucestodes (Freeman 1973), and its presence apomorphic. However, as we will discuss later, either the presence or absence of a primary lacuna may be plesiomorphic for the cyclophyllideans (Freeman 1973) (and perhaps for nippotaeniideans; Yamaguti 1951, Demshin 1985).

17. Shape of ovary in cross section: The great majority of species of the Tetraphyllidea, including members of the Litobothriidea and Trypanorhyncha, have distinctive "X-shaped" ovaries when viewed in cross section. We consider this condition apomorphic, as it does not occur among the outgroups, or indeed among any other cercomerians, to our knowledge. It is true that not all tetraphyllideans possess X-shaped ovaries, and we will discuss the implications of that observation later.

18. Relative position of the vitellaria: Proteocephalideans (except for the Monticelliidae), most lecanicephalideans, and most tetraphyllideans have medullary vitellaria. A few pseudophyllideans have medullary vitellaria (including all of the caryophyllideans), and all eucestodes with compact vitellaria, including the Cyclophyllidea, have medullary vitellaria. The cortical condition is found in the outgroups and extensively among pseudophyllideans (it also occurs among some tetraphyllid-

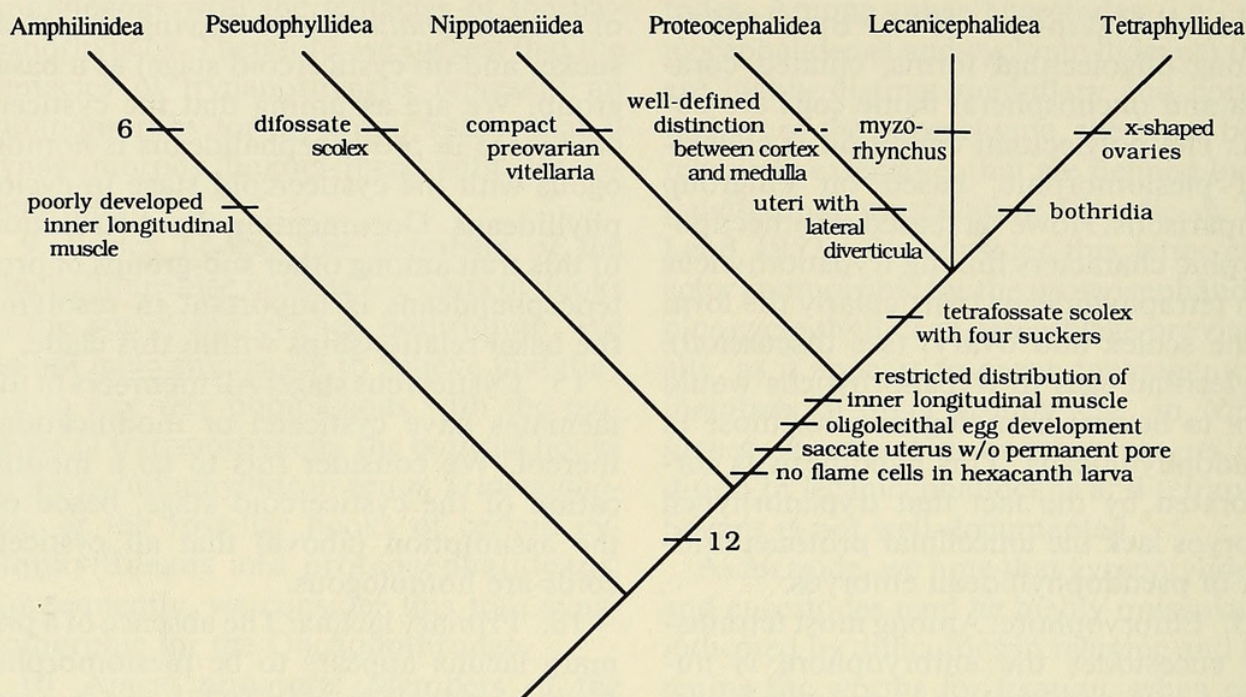


Fig. 1. Phylogenetic tree depicting five major groups of eucestodes based on the synapomorphic traits listed next to each slash mark on the tree. Numbers next to slash marks on the Amphilinidea line (sister-group) and the line uniting all eucestodes indicate number of synapomorphic traits supporting the monophyly of the groups.

eans, lecanicephalideans, and all or most of the trypanorhynchs). We consider cortical vitellaria plesiomorphic and medullary vitellaria apomorphic.

19. Distribution and structure of vitellaria: The plesiomorphic condition, exhibited by amphilinideans, some pseudophyllideans, and some tetrafossate eucestodes, is vitellaria in two cortical lateral longitudinal rows of follicles. There are several variations in vitelline structure and distribution. Most pseudophyllideans and trypanorhynchs, along with some tetraphyllideans and lecanicephalideans, exhibit circum-cortical vitellaria. Most proteocephalideans possess vitellaria in two medullary lateral longitudinal rows of follicles. The nippotaeniideans and most tetrabothriideans have single compact *preovarian* vitellaria. The members of the Cyclophylleida have compact *postovarian* vitellaria, as do members of *Philobythos* and *Philobythoides*, which are pseudophyllideans (Campbell 1977, 1979). We consider circum-cortical vitellaria, lateral medullary vitellaria, and some instances of compact

vitellaria (in the nippotaeniideans, pseudophyllideans, and tetrabothriideans) to be derived independently from lateral cortical vitellaria. The compact vitellaria of cyclophyllideans we consider derived from a lateral medullary condition, based on the relationship between proteocephalideans and cyclophyllideans, discussed below. We consider the compact vitellaria of some pseudophyllideans, the nippotaeniideans, tetrabothriideans, and cyclophyllideans all to be independently derived conditions. We also consider the circum-cortical vitellaria found in some tetrafossate eucestodes to be derived independently from the similar condition found in many pseudophyllideans.

Results and Discussion

Phylogenetic hypothesis. — Figures 1–4 depict the phylogenetic hypothesis best supported by the data described above. We recognize five major putatively monophyletic lineages within the eucestodes, based on those characters and their polarities (Fig. 1). They are characterized as follows: (1) the

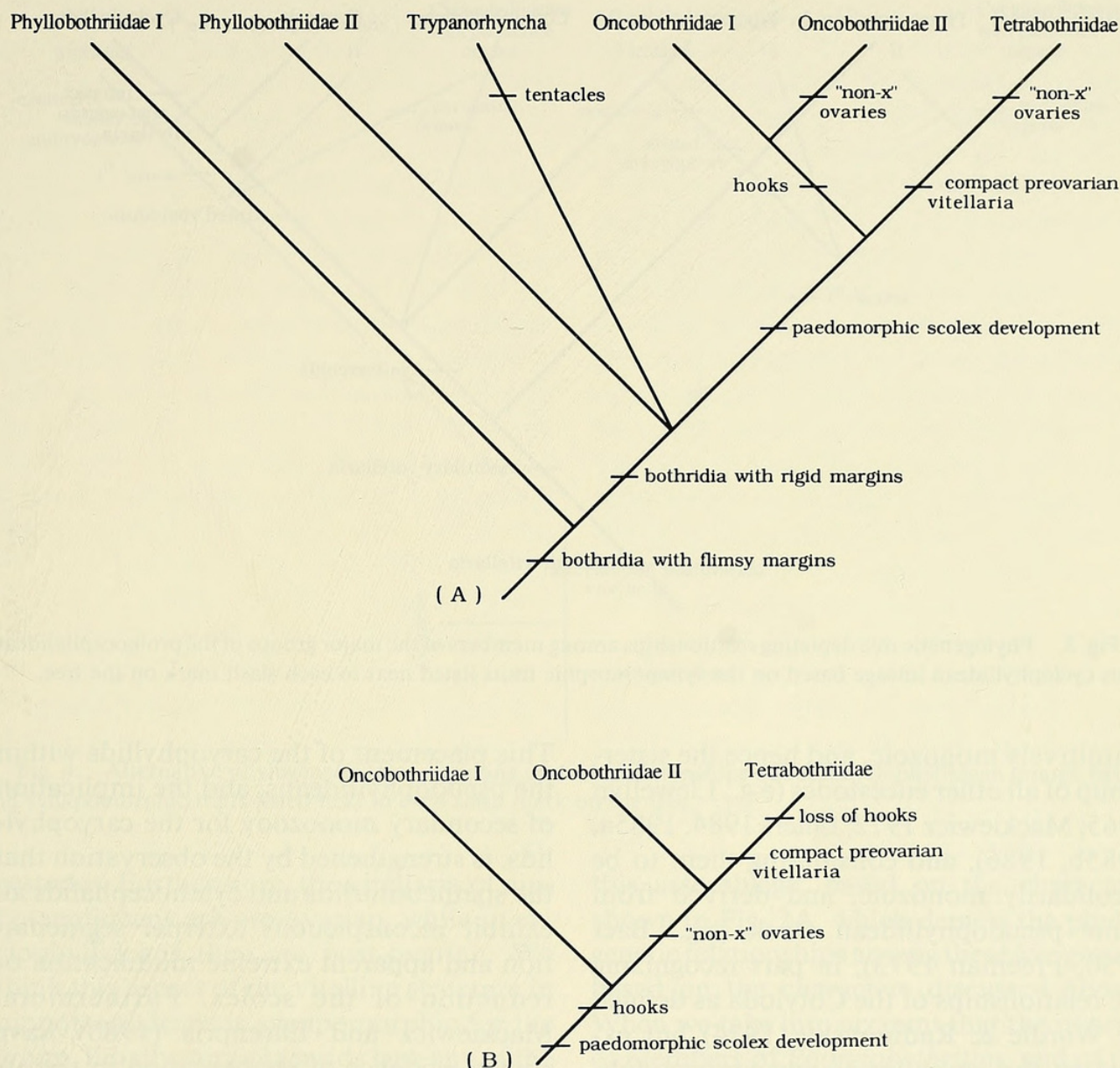


Fig. 2. (A) Phylogenetic tree depicting possible relationships among major groups of tetraphyllidean eucestodes based on the synapomorphic traits listed next to each slash mark on the tree. (B) Equally parsimonious alternative arrangement for the onchobothriids and tetrabothriideans.

Pseudophyllidea (difossate lineage), which is the sister-group of all other eucestodes; (2) the Nippotaeniidea, which is the sister-group of all other non-pseudophyllidean eucestodes; (3) the Tetraphyllidea (bothridiate lineage); (4) the Lecanicephalidea (myzorrhynchoid lineage); and (5) the Proteocephalidea (proteocephalidean plus cyclophyllidean lineage). Lineages 3–5 are coordinate sister-groups and represent the tetrafossate eucestodes. The groupings depicted in Fig. 1 comprise the basic framework of eucestode relationships. Within each of these lin-

eages are groupings of particular relevance to hypotheses of phylogenetic relationships and to evaluation of current classifications of eucestodes. Next, we will discuss some aspects of the relationships among members of each of these major groupings.

Caryophyllidea

All members of the Caryophyllidea are monozoic, and their scolex morphology is unique among eucestodes. Opinion has fluctuated between considering them to be

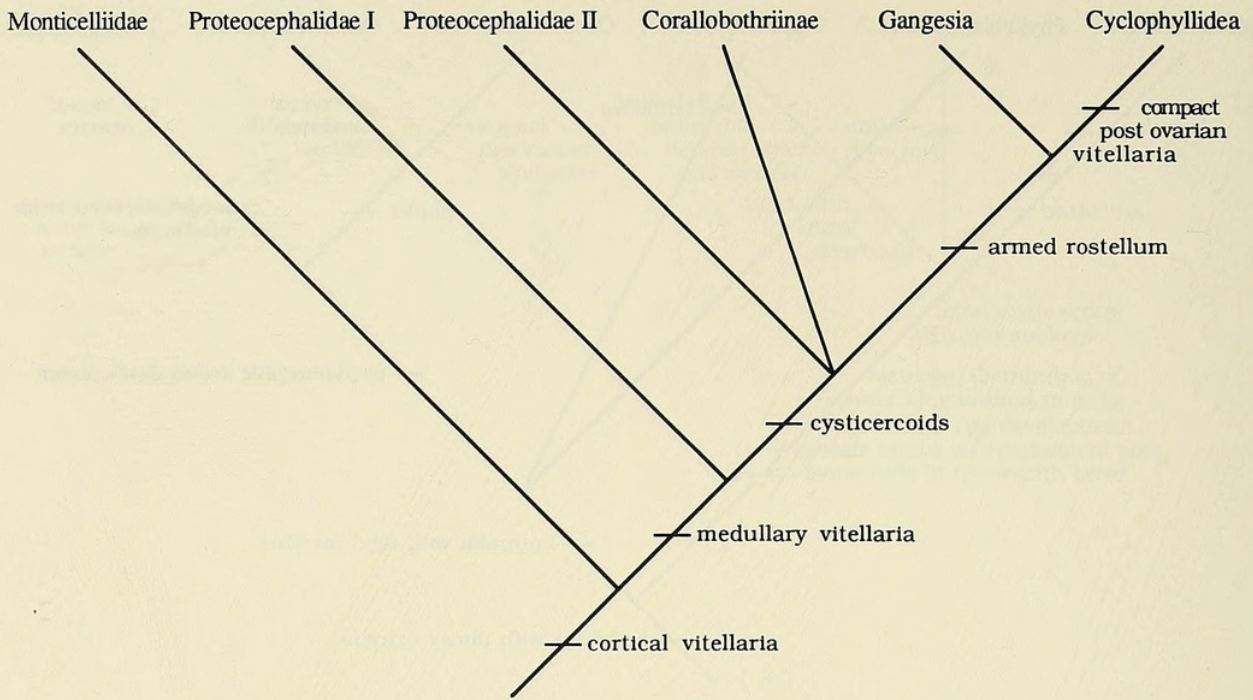


Fig. 3. Phylogenetic tree depicting relationships among members of the major groups of the proteocephalidean plus cyclophyllidean lineage based on the synapomorphic traits listed next to each slash mark on the tree.

primitively monozoic, and hence the sister-group of all other eucestodes (e.g., Llewellyn 1965; Mackiewicz 1972; Ehlers 1984, 1985a, 1985b, 1986), and considering them to be secondarily monozoic, and derived from some pseudophyllidean stock (e.g., Baer 1950, Freeman 1973), in part recognizing the relationships of the Cotyloda as defined by Wardle & Radinovsky (1974) but excluding the amphilinids and gyrocotylids, as advocated by Mackiewicz (1981). Although a full-scale phylogenetic analysis of the pseudophyllideans is beyond the scope of this study, there are clear implications about the placement of the caryophyllideans. Members of this group have non-ciliated embryos and genital pores separated by the uterine pore, two traits that appear to be apomorphic among pseudophyllideans and that place the caryophyllideans with the group of pseudophyllideans including the Spathebothriidae and Cyathocephalidae (Freeman 1973). In addition, *Cyathocephalus* and all caryophyllids share a unique feature, the utero-vaginal atrium, a common depression receiving the uterine and vaginal pores (Hart & Guberlet 1936).

This placement of the caryophyllids within the pseudophyllideans, and the implication of secondary monozooy for the caryophyllids, is strengthened by the observation that the spathebothriids and cyathocephalids all exhibit inconspicuous external segmentation and apparent extreme modification or reduction of the scolex. Furthermore, Mackiewicz and Ehrenpreis (1980) have shown evidence of segmentation in the arrangement of calcareous corpuscles in caryophyllids. The medullary position of the vitellaria is regarded as a secondarily derived condition in this group.

Nippotaeniidea

Most authors have recognized the primitive nature of the scolex of nippotaeniideans, but have continued to link them with the relatively highly-derived Cyclophyllidea because they possess compact vitellaria (Yamaguti 1940, Hine 1977, Schmidt 1986). However, as discussed above, various members of the Pseudophyllidea and Tetraphyllidea also possess compact vitellaria, so this trait appears to be plastic among eu-

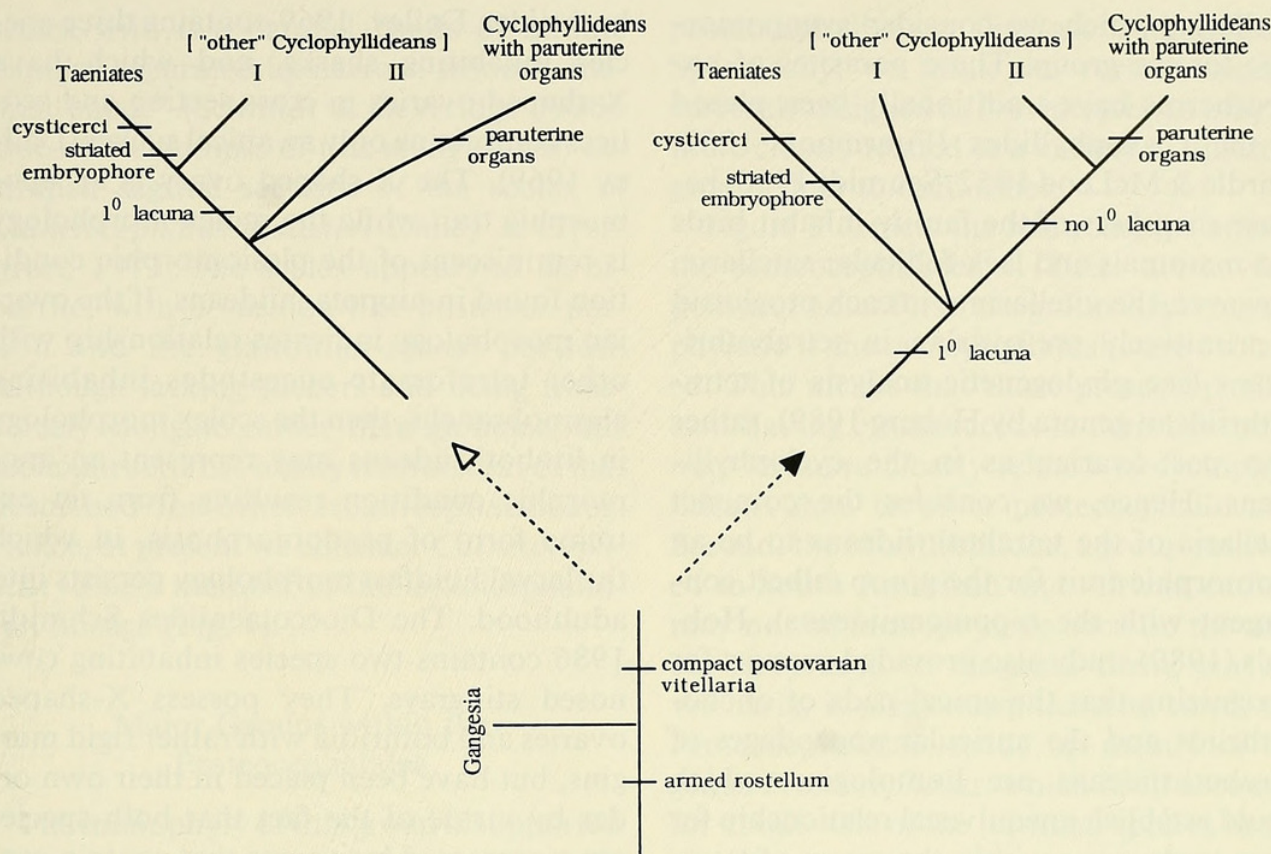


Fig. 4. Alternative phylogenetic trees depicting possible relationships of basal cyclophyllidean groups based on synapomorphic traits listed next to each slash mark on the tree.

cestodes. Furthermore, the vitellaria of nippotaeniideans are pre-ovarian, while in cyclophyllideans they are post-ovarian. We think this aspect of the vitelline structure in nippotaeniideans is synapomorphic for the group. Finally, nippotaeniids lack any of the other presumed apomorphic traits exhibited by cyclophyllideans. Consequently, the phylogenetic analysis places them in a relatively plesiomorphic position (Freeman 1973).

Majors Groups within the Tetraphyllidea

Traditionally, two major groups have been recognized within this assemblage, those having hooks on the scolex and those lacking such hooks. We believe that the first group, the Phyllobothriidae, is paraphyletic, based on differences in bothridial morphology (character 6, above and Fig. 2) and that two additional groups also belong in

this assemblage, based on the characters shown in Fig. 2A, which depicts the phylogenetic relationships among these five groups based on the characters discussed above. When we take into account that the ovaries of members of *Phoreiobothrium*, and of the Tetrabothriideans, are digitiform and not X-shaped in cross section, the set of relationships shown in Fig. 2B becomes possible. If this second arrangement is consistent with the phylogenetic relationships among these tapeworms, it would imply that the ancestor of the tetrabothriideans secondarily lost its bothridial hooks. At present, we have no evidence that this might be the case, although we do have evidence among the cyclophyllideans that rostellar hooks have been lost on more than one occasion.

We include two groups, the Tetrabothriidae and the Trypanorhyncha, within the Tetraphyllidea that have rarely been placed there previously. The vast majority of tetrabothriideans have compact preovarian

vitellaria, which we consider synapomorphic for the group. These parasites of homeotherms have traditionally been placed in the Cyclophyllidea (Fuhrmann 1932, Wardle & McLeod 1952, Schmidt 1986) because members of the family inhabit birds and mammals and lack follicular vitellaria. However, the vitellarium in each proglottid is primitively pre-ovarian in tetrabothriideans (see phylogenetic analysis of tetrabothriidean genera by Hoberg 1989), rather than post-ovarian as in the cyclophyllideans. Hence, we consider the compact vitellaria of the tetrabothriideans to be an apomorphic trait for the group (albeit convergent with the nippotaeniideans). Hoberg's (1989) study also provided support for recognizing that the apical pads of onchobothriids and the auricular appendages of tetrabothriideans are homologous which would establish unequivocal relationship for these tapeworms within the group of tetraphyllideans where they are placed in Fig. 2.

The Trypanorhyncha have been variously considered closely related to the Tetraphyllidea, because they inhabit elasmobranchs (e.g., Baer 1950), or to the Pseudophyllidea, because they have polylecithal eggs and ciliated embryos (e.g., Wardle & MacLeod 1952). Additional evidence supporting the former placement includes the presence of X-shaped ovaries, the tetrafossate condition of the scolex, the presence of 4 (sometimes 2 pairs of fused) bothridia with rigid margins, and the lack of a uninucleated protonephridium in the embryo. The widespread occurrence of circum-cortical vitellaria in trypanorhynchs could be used as evidence for their inclusion either in the Pseudophyllidea or the Tetraphyllidea. Consequently, we consider the current weight of evidence to support inclusion of the trypanorhynchs within the group of tetraphyllideans having bothridia with rigid margins.

We have also included two small groups within the Tetraphyllidea to which some have accorded ordinal status. The Lito-

bothriidea Dailey, 1969 contains three species inhabiting sharks, and which have X-shaped ovaries in cross section and scolices comprising only an apical sucker (Dailey 1969). The X-shaped ovary is an apomorphic trait while the scolex morphology is reminiscent of the plesiomorphic condition found in nippotaeniideans. If the ovarian morphology indicates relationship with other tetrafossate eucestodes inhabiting elasmobranchs, then the scolex morphology in litobothriideans may represent an apomorphic condition resulting from an extreme form of paedomorphosis, in which the larval holdfast morphology persists into adulthood. The Dioecotaeniidea Schmidt, 1986 contains two species inhabiting cow-nosed stingrays. They possess X-shaped ovaries and bothridia with rather rigid margins, but have been placed in their own order by virtue of the fact that both species are represented by worms that contain proglottids with only male or only female genitalia. While clearly a derived trait, having separate sexes is not unknown among eucestodes (e.g., the Dioecocestidae in the Cyclophyllidea) or among cercomerians (e.g., schistosomes among the Digenea). Furthermore, Brooks (1982) reported a detailed analysis of the scolex morphology of *Dioecotaenia*, and suggested close relationship with phyllobothriid genera including *Trilocularia*, *Pentaloculum* and *Zyxibothrium*.

The Lecanicephalidea

Schmidt & Beveridge (1990) recently proposed the order Cathetocephalidea to accommodate three species of tapeworms inhabiting primarily carcharhinid sharks, one in the Gulf of Mexico and two (one named) in Australian waters. The species exhibit ovaries that are bilobed rather than X-shaped in cross section and circum-cortical vitellaria. In addition, their scolices are described as "... lacking suckers, bothridia, or armature, transversely elongated perpendicular to the axis of the strobila. Apex of

scolex with two parallel bands of minute papillae separated by narrow, smooth, median band." (Schmidt & Beveridge 1990). One of the authors of this study (DRB) examined sagittal sections of the scolex of *Cathetocephalus thatcheri* Dailey & Overstreet, 1973. The scolex appears to be bipartite, with a cushion-like posterior portion and the glandular apical portion. Although lacking suckers and being transversely elongate rather than globular, this scolex structure is highly reminiscent of that described for other lecanicephalideans. Hence, at present we consider *Cathetocephalus* to be a member of the lecanicephalidean lineage (Fig. 1).

Major Groups within the Proteocephalidea

The monophyly of this group is supported by the presence of lateral branches and diverticula of the uterus. According to some authors, it is also supported by the well-developed distinction between the relatively large cortical and relatively restricted medullary regions of the proglottids (Wardle & McLeod 1952), which we include tentatively (see dashed line in Fig. 1) because the trait has not been documented extensively among tetraphyllidean and lecanicephalidean groups. This group includes those species assigned to both the Proteocephalidea and the Cyclophyllidea, excluding the nippotaeniideans and tetrabothriideans as already discussed.

Our assessment of the relationships among the members of this group is shown in Figs. 3–4. Freeman (1973) stated that the key to understanding cyclophyllidean evolution was understanding the proteocephalideans, especially *Proteocephalus*. We concur wholeheartedly! Our perspective differs from that of Freeman (1973) and Brooks (1978b), however. We do not think that the cyclophyllideans are paraphyletic or polyphyletic (once the tetrabothriideans have been removed). Rather, we think it is the

proteocephalideans that are paraphyletic. Specifically, we think the various species currently assigned to *Proteocephalus* may be more closely related to a variety of different groups than to each other.

Figure 3 depicts the relationships among the proteocephalideans. There are several points of note. First, the group is not monophyletic if the cyclophyllideans are excluded. This means that those proteocephalideans having cysticeroids in their life cycles may be more closely related to cyclophyllideans than to other proteocephalideans. Second, the Monticelliidae, a group restricted to South American and African catfish, may not be monophyletic because the trait currently used to diagnose them, cortical vitellaria, is plesiomorphic. And third, the Proteocephalidae, made up mostly of the genus *Proteocephalus*, which itself accounts for about 40% of the nominal species in the group, appears to be a composite group much like the Phyllobothriidae in the Tetraphyllidea (Fig. 2).

Two alternative arrangements for the cyclophyllideans are shown in Fig. 4. Based on outgroup comparisons, the presence of a primary lacuna is an apomorphic trait. Among the cyclophyllideans, however, there appears to be homoplasy associated with the secondary loss of the lacuna that could affect our hypotheses of relationships markedly. If species of *Gangesia* or *Vermaia* have primary lacunae (and this is not yet known), the presence of a primary lacuna is plesiomorphic for all cyclophyllideans, and has been secondarily lost in some groups. This would tend to support an interpretation in which taeniates would be considered basal members of the Cyclophyllidea, and those species lacking primary lacunae, including the species having paruterine organs, would be considered a highly derived group. If, on the other hand, the presence of a primary lacuna is synapomorphic for some cyclophyllideans only, the cyclophyllideans with paruterine organs would be the basal group. In both cases, the rest of the cyclophyllid-

eans would comprise at least two separate groups.

We suggest that a positive approach to sorting out this problematical group would begin with studies elucidating the patterns of distribution and the structural homologies (where unclear) for the following (see discussion above as well): uterine structure, embryophore structure, primary lacunae, cysticercoids (are they homologous in proteocephalideans and cyclophyllideans?), and tegumental "hairs" on developing metacestodes. As far as the latter is concerned, pleurocercoids of pseudophyllideans and trypanorhynch, tetrathyridia of *Mesocestoides* spp. (modified cysticercoids), and cysticercoi of taeniates all possess tegumental "hairs" during ontogeny. In contrast, the cysticercoids of at least some cyclophyllideans lack such hairs, having series of fibrous layers instead. The presence of such "hairs" on cysticercoi and tetrathyridia may be plesiomorphic or convergent, depending on the distribution of hairs and fibrous layers among cysticercoids of proteocephalideans. If proteocephalidean cysticercoids lack tegumental hairs, it is possible that the fibrous layers represent a synapomorphy uniting at least some proteocephalideans and some cyclophyllideans into a group separate from the group including the taeniates and *Mesocestoides*. In that case, the Cyclophyllidea might turn out to be polyphyletic (in addition to the Proteocephalidea being paraphyletic), thus supporting the contentions of Freeman (1973) and Brooks (1978b). At the moment, however, this does not seem to be the best supported interpretation based on the available evidence.

Comparison with previous estimates of eucestode phylogeny.—The primary criterion used to determine tapeworm phylogeny in the past has been the presumed phylogeny of the vertebrate hosts (Fuhrmann 1928, Baer 1950, Wardle & McLeod 1952, Wardle & Radinovsky 1974, Dubinina 1980, Burt & Jarecka 1982). The following statement by Wardle & McLeod (1952:147) is typical,

"On the basis of host distribution, the conclusion seems inescapable that tetrafoosate tapeworms are more primitive than difosate forms, and that the most primitive of present-day tapeworms are the tetraphyllidean forms and the collared proteocephalids, which appear to be the results of divergent evolution from a common ancestral tetraphyllidean proteocephalidean stock." In this study, we use the characteristics of the worms themselves as evidence for phylogenetic relationships. Despite this difference in approach, we would like to stress the following points of agreement between our findings and those of at least some workers in the past: pseudophyllideans are the sister-group of all other eucestodes (Fuhrmann 1928, Baer 1950); caryophyllideans are secondarily monozoic (Baer 1950, Freeman 1973); nippotaeniideans are relatively primitive (Freeman 1973); trypanorhynch are more closely related to some tetraphyllideans than to pseudophyllideans (Baer 1950); tetrabothriideans are most closely related to some tetraphyllideans [consider Baylis 1926: indeed many authors have (a) incorporated some tetrabothriideans with "tetraphyllideans" (Leiper & Atkinson 1915; see discussion in Wardle & McLeod 1952), (b) suggested possible affinities for these groups while referring them to different orders (Fuhrmann 1932, Baer 1954), or (c) provided classifications explicitly suggesting such relationships (Spasskii 1958, Temirova & Skrjabin 1978, Galkin 1987)]; tetraphyllideans, lecanicephalideans, and the proteocephalideans plus cyclophyllideans are coordinate groups (i.e., are related in a trichotomy [Freeman 1973]); proteocephalideans are the key to understanding cyclophyllideans (Freeman 1973; Brooks 1978a, 1978b); *Mesocestoides* might be relatively primitive (Perrier 1897, Voge 1967); and taeniates are a group (e.g., Ludwig 1886, Wardle & McLeod 1952, Freeman 1973, Wardle & Radinovsky 1974, Schmidt 1986).

Our findings diverge markedly from some of the conclusions drawn in the past, in par-

ticular with respect to the origin and evolution of tapeworms inhabiting elasmobranchs. Our phylogenetic tree identifies two lineages of eucestodes inhabiting primarily teleostean fishes, the Pseudophyllidea and the Nippotaeniidea, whose origins pre-date those of the Tetracophyllidea and Lecanicephalidea, which contain virtually all the tapeworm species inhabiting elasmobranchs. Consequently, we suggest that tapeworms inhabiting elasmobranchs originated from ancestors that inhabited bony fishes. If this is true, the high diversity of tapeworm species in elasmobranchs cannot be attributed solely to phylogenetic association. However, there is some evidence from phylogenetic studies that suggests a relatively long association between elasmobranchs and their tapeworms (Brooks et al. 1981, Brooks & Deardorff 1988). Hence, we would postulate, given the current database, that the colonization of elasmobranchs by tapeworms may have occurred very early in the evolution of vertebrates, so that the chondrichthyan species that were colonized were relatively basal members of that group.

There is additional phylogenetic evidence to support the idea that tapeworms arose after the divergence of chondrichthyans from the ancestor of the rest of the gnathostomous vertebrates. Brooks (1989b) noted that the basal members of the Aspidobothrea inhabit elasmobranchs, while none of the basal members of their sister-group, the Digenea, do so and suggested that this was evidence that the divergence of the stem aspidobothrean and stem digenean was coincident with the divergence of chondrichthyans from the stem of the rest of the gnathostomous vertebrates. We find a similar situation when we examine the members of the Cestodaria (sensu Brooks 1989b). The Gyrocotylidea are the sister-group of the Amphiliniidea plus Eucestoda. Gyrocotylideans inhabit chimaeroid fishes, chondrichthyans that are the sister-group of the elasmobranchs. Amphiliniideans inhabit bony fishes primitively (one derived species

inhabits turtles as a result of a host-switch, see Bandoni & Brooks 1987a), including members of some of the more basal groups, such as sturgeons, and the two basal groups of eucestodes, according to our analysis, also inhabit bony fishes, including members of basal groups not inhabited by Amphiliniideans. Consequently, the higher-level phylogeny of the cercomerians suggests that the evolutionary divergence between chondrichthyans and the rest of the gnathostomous vertebrates was associated with parasite divergence that pre-dated the origin of the true tapeworms.

One of the functions of phylogenetic systematic analysis is providing classifications that are indicative of current estimates of evolutionary history. At the same time, it is incumbent upon working systematists to maintain nomenclatorial stability, so that non-specialists will be able to use the classifications. In this regard, many phylogeneticists try to adopt classifications that conserve as many traditional names and taxonomic levels as possible within the context of consistency with phylogenetic relationships. In the case of this study, we have additional concern; our study is preliminary and deliberately cautious. Thus, we expect changes in the future, and phylogenetically based classifications may experience a period of relative instability for some time, although this does not seem to have been the case with the higher level classification of the cercomerians (compare Brooks et al. 1985a with Brooks 1989a, 1989b) or with the digeneans (compare Brooks et al. 1985b with Brooks et al. 1989). Therefore, we suggest that the phylogenetic hypothesis we present herein should be used as an index to the current state of phylogenetic systematic analysis of eucestodes, and not as a replacement for current classification.

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