Is the Turbellaria polyphyletic?

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Abstract

Within the last two decades, syntheses of both light-microscopic and ultrastructural characters have shown that there are three well-defined monophyletic groups within the Platyhelminthes: 1) the Catenulidale, 2) the Nemertodermatida-Acoela, and 3) the Haplopharyngida-Macrostomida-Polycladida-Neoophora (+ parasitic platyhelminth classes). However, the relationships among these three groups are problematic. The possible apomorphies that would unite them are either not true homologues (i.e. frontal organ), are mutually conflicting (i.e. 9+1 axoneme in spermatozoa vs. biflagellate spermatozoa, epidermal ciliary rootlet structure, and protonephridia), or are unrooted with any outgroup and hence untestable or uncertain as apomorphies (protonephridia, mode of epidermal replacement, absence of accessory centrioles on cilia). The chief obstacle to deciphering the relationships of these groups is the lack of information on them; presently available information is insufficient to test potential synapomorphies and insufficient also to allow agreement upon a narrowly defined outgroup for the Turbellaria.

A view consistent with the present evidence (and admittedly an unsatisfactory view) is to regard the Turbellaria (and hence the Platyhelminthes) as polyphyletic, consisting of three separate and unrelatable groups.

Introduction

If one compares the various phylogenetic schemes that have been proposed for turbellarian taxa [Karling, 1940, 1974; Ehlers, 1984 (with references to earlier schemes), 1985a, 1985b], it is evident that there is considerable agreement on relationships of most of the higher taxa but that there is uncertainty and dispute concerning especially relationships of more primitive groups. As more characters have been discovered, particularly with the use of electron microscopy (see Rieger, 1981), more higher-level relationships – that is, those traditionally recognized as inter-order relationships – have been revealed. It is clear now that the neoophoran orders Proseriata, Tricladida, Rhabdocoela, and Temnocephalida share a common ancestor with the more primitive (traditionally 'archoophoran') orders Haplopharyngida, Macrostomida, and Polycladida (Tyler, 1976; Smith *et al.*, 1982; Rieger, 1981), and also with the parasitic platyhelminth classes. Relationships of the remaining orders are unclear, however. The Lecithoepitheliata and Prolecithophora are thought (at least by general agreement) to share on ancestor with other neoophoran orders (Karling, 1974; Ehlers, 1977, 1984); the Nemertodermatida and Acoela undoubtedly share a common ancestor (Karling, 1940, 1974; Tyler & Rieger, 1977), but how they are related to other turbellarians is subject to debate; and the Catenulida is particularly problematic, showing no unequivocal relationship with any other orders (Sterrer & Rieger, 1974; Rieger, 1978).

The common denominator of all recently pro-

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posed phylogenetic schemes for the platyhelminths is recognition of three clearly monophyletic groups: one containing the Acoela and Nemertodermatida ('Acoelomorpha' of Ehlers, 1984, 1985a), one the Catenulida, and the third all other turbellarian orders together with the parasitic classes ('Rhabditophora' of Ehlers, 1984, 1985a).

The question remains, however, as to how these three groups are related (see also Hendelberg, 1977, 1983). Because we cannot find evidence for a close phylogenetic relationship among them, it is possible to argue that they are not directly related, that the Turbellaria (and thus the Platyhelminthes) is actually polyphyletic. It is already established that the Turbellaria is a paraphyletic class since the parasitic platyhelminth classes have ancestors that would be classified as rhabdocoel turbellarians (Karling, 1974). Whether the Turbellaria, and hence the Platyhelminthes, may also be polyphyletic, has not been addressed before.

Methodology of phylogenetic reconstruction

To some extent the matters of dispute between phylogenetic hypotheses arise because of differences in methodology for formulating those hypotheses. The methodology we use is an iterative, two-step process. First, homologous characters (homologues) among the taxa under consideration are identified (see Rieger & Tyler, 1979) to produce a grouping of the taxa (as would be done, essentially, for making a Venn diagram); second, we hypothesize which states of the homologous are primitive or advanced. The 'rules' by which character states can be ordered were discussed by Hennig (1950) and Remane (1956) (see also Wiley, 1981, for summary).

It is important to keep in mind that these two steps are separable but complementary. The first, identification of homologues, is an inductive process and can be performed without consideration of evolutionary theory; it springs directly from the recognition of patterns of similarity in nature. The second step, identifying given states of homologous characters as being more or less primitive, is a deductive process that posits evolution as the cause of the ordering. It is essential that once the second step has been performed, the first is rechecked to ensure that the primitive and derived states of each character linked by the postulate of evolution are actually homologous; the second step would then be repeated itself to order character states in any further homologues that may emerge.

A phylogenetic system is the most efficient means for expressing relationships. The formalized approach of phylogenetic systematics as it is now practiced, however, seems to us to fall short in one important aspect, namely that its adherents too often neglect rigorous homology analysis and commence their phylogenetic reconstruction with the ordering of character states for which homology is questionable. The important matter of distinguishing homologue from analogue similarity is often done solely by means of the 'parsimony principle' which is hardly reliable by itself as a criterion of homology. Evolutionary history, like social history, is better regarded as a series of accidents than as a series of events obeying one simple rule of parsimony, and so reliance on parsimonious distribution of characters among taxa as being the primary criterion of their homology is simplistic.

Autapomorphies for the Phylum Platyhelminthes

If the Platyhelminthes is a monophyletic group, then it must have one or more autapomorphies that defines it (synapomorphies among groups Catenulida, Acoelomorpha, and Rhabditophora – Fig. 1, solid circles). Older systems are rather vague about the definition of the phylum probably because even though it is intuitively obvious what a turbellarian is, a listing of characters that strictly distiguish the Turbellaria from other groups is difficult to construct. Recently, Ehlers (1984, 1985a, b; see also Ax,

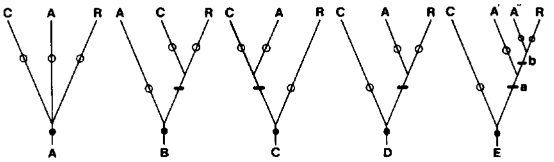


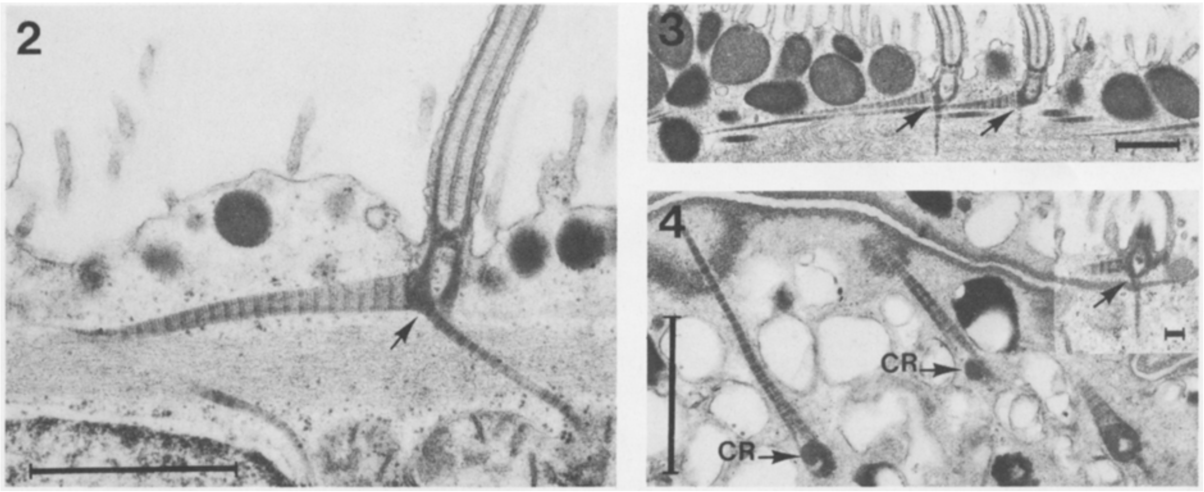
Fig. 1. Four possible cladograms relating the three most probable monophyletic groups of platyhelminth evolution, and a fifth, assuming monophyly of the Catenulida and Rhabditophora and paraphyly of the Acoelomorpha. Open circles are apomorphies for each line (see Ehlers, 1985a, b). Closed circle represents autapomorphies for the Phylum Platyhelminthes. Black bar represents synapomorphy necessary to produce groupings B–E. A = Acoelomorpha, A′ = Nemertodermatida, A″ = Acoela, C = Catenulida, R = Rhabditophora.

1984) has admirably made a concerted effort to identify autapomorphies for a phylogenetic system of the Platyhelminthes and has proposed that characters of protonephridia, of cilia in epidermal cells, and of the mode of epidermal cell replacement are autapomorphic for the phylum. As for any characters identified as autapomorphies, it must be established that these are homologous (i.e. are valid synapomorphies). Our research on ultrastructure of epidermal cells has provided and abundance of evidence that is relevant to establishing probability of homology for two of the proposed autapomorphies: 1) epidermal cells multiciliated and 2) absence of mitosis in epidermal cells and other somatic cells.

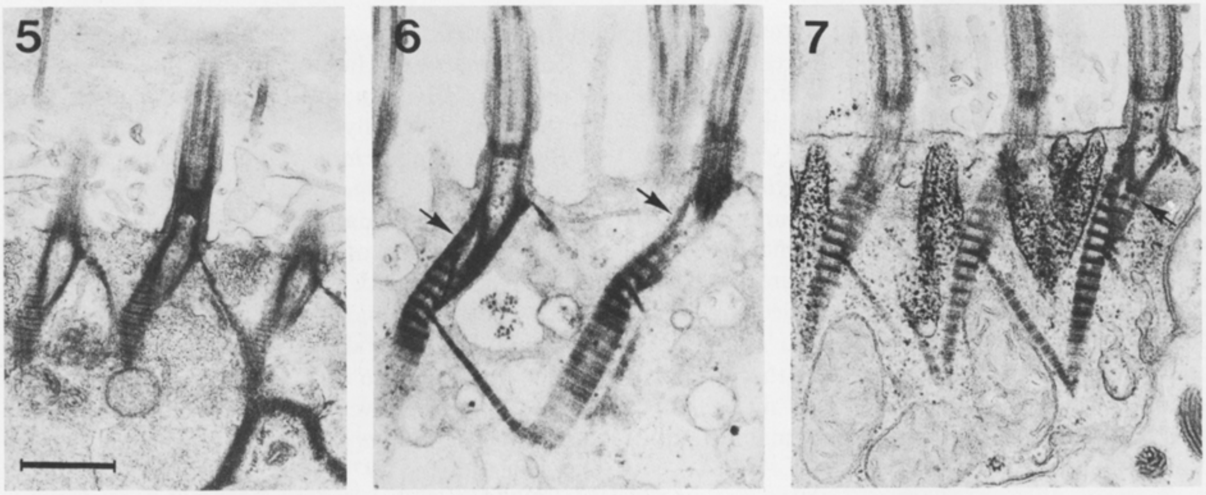
Epidermal multiciliation

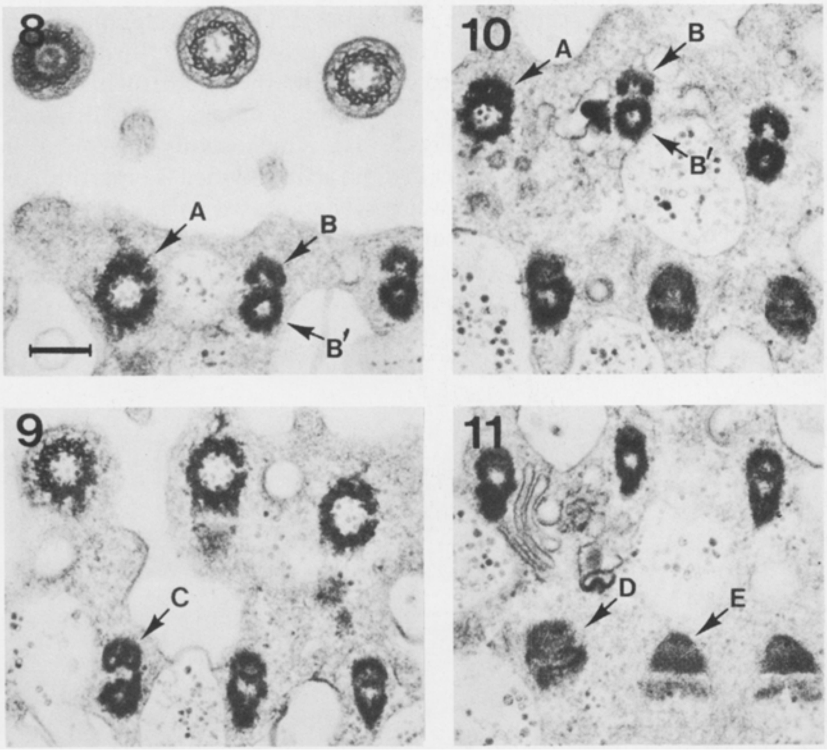
The multiciliated nature of epidermal cells appears to be a homologous feature in the Rhabditophora and Catenulida especially because the ciliary structures in these cells are probably homologous. Rieger (1976) first pointed out that ciliary rootlet systems in the Catenulida and Macrostomida (in particular the genus *Myozona*) appeared to be homologous because both possess a rostral-caudal rootlet system without accessory centrioles. We have further evidence for homology of rootlets in two other macrostomids and *Haplopharynx* (Haplopharyngida). The caudally directed caudal rootlet of *Psammomacrostomum* and the vertically directed caudal rootlet of *Bradynectes* and *Haplopharynx* originate at the anterior proximal edge of the basal body, as apparently does the caudal rootlet in the monociliated epidermal cells of gnathostomulids (Figs. 2–4, compare Rieger & Mainitz, 1977: Fig. 1). At the very least, the epidermal ciliary rootlet system of *Haplopharynx* (and, we would predict, that of other members of the Rhabditophora; see also Ehlers, 1984) can be derived from the more primitive condition seen in *Psammomacrostomum* and *Myozona* (see Rieger, 1976, 1985).

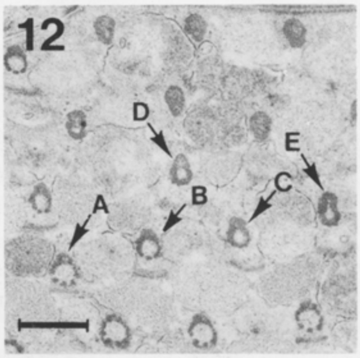
Ciliary rootlets in the multiciliated epidermal cells of the Acoelomorpha are quite complex (Hendelberg & Hedlund, 1974; Tyler & Rieger, 1977), and detailed analysis of their substructure shows them to be even more complex than originally thought (Figs 5–11). The rostrally directed principal rootlet in most acoels studied is bipartite, consisting of two closely appressed portions: a posterior, cone-shaped rootlet arising proximally from the basal body and an anterior rootlet arising like a strap from the anterior face of the basal body and continuing as a trough until joining the posterior rootlet just above the knee-like bend (Figs 8–11).



Figs. 2–4. Epidermal ciliary rootlet systems in Rhabditophora. All scales 1 µm unless noted otherwise. (2) *Psammomacrostomum* (O. Macrostomida), longitudinal section; (3) *Bradynectes* (O. Macrostomida), longitudinal section, scale = 0.5 µm; (4) *Haplopharynx* (O. Haplopharyngida), tangential section parallel to epidermal surface; inset: longitudinal section, scale ≈ 200 nm. Note origin of caudally-directed (*Psammomacrostomum*) or vertically-directed (*Bradynectes, Haplopharynx*) caudal rootlet (CR) from the anterior proximal margin of the basal body in each case (arrows). Anterior is to the left in Figs. 2 & 3, to the upper left in Fig. 4.







Figs. 5–7. Epidermal ciliary rootlet systems in Acoelomorpha. (5) *Flagellophora cf. apelti* (O. Nemertodermatida); (6) *Diopisthoporus* 'gymnopharyngeus' (O. Acoela); (7) *Convoluta* 'pulchra' (O. Acoela). Anterior is to the left in all figures. Scale = 500 nm.

Figs. 8–11. Serial sections, nearly parallel to epidermal surface, showing details of ciliary rootlet structure in *D.* 'gymnopharyngeus'; scale = 200 nm; see Fig. 8. Anterior is to the top of the figures, the view is from inside the animal (along cilia from base to tip). Note curved anterior portion of rootlet (Figs. 8, 10 A–B), which joins hollow rootlet arising from basal body (Figs 8, 10 B'), thickens (Fig. 9 C), and continues as principal rootlets (Fig. 11 D, E). Gap between two parts is visible in Figs. 6, 7 (arrows).

Fig. 12. Tangential section of ciliary rootlet system in *Flagellophora cf. apelti*: anterior is toward the top of the figure. Note rostral portion of rootlet that arises on the anterior face of basal body (arrows A–C), continues along it (arrow D) and fuses with it (arrow E). Scale = 400 nm.

Fig. 13. Pulsatile body, posterior epidermis of *Convoluta* 'pulchra.' Note free axonemes in cytoplasm (arrowheads) and fully formed ciliary tips (arrow). Scale = 1 μm.

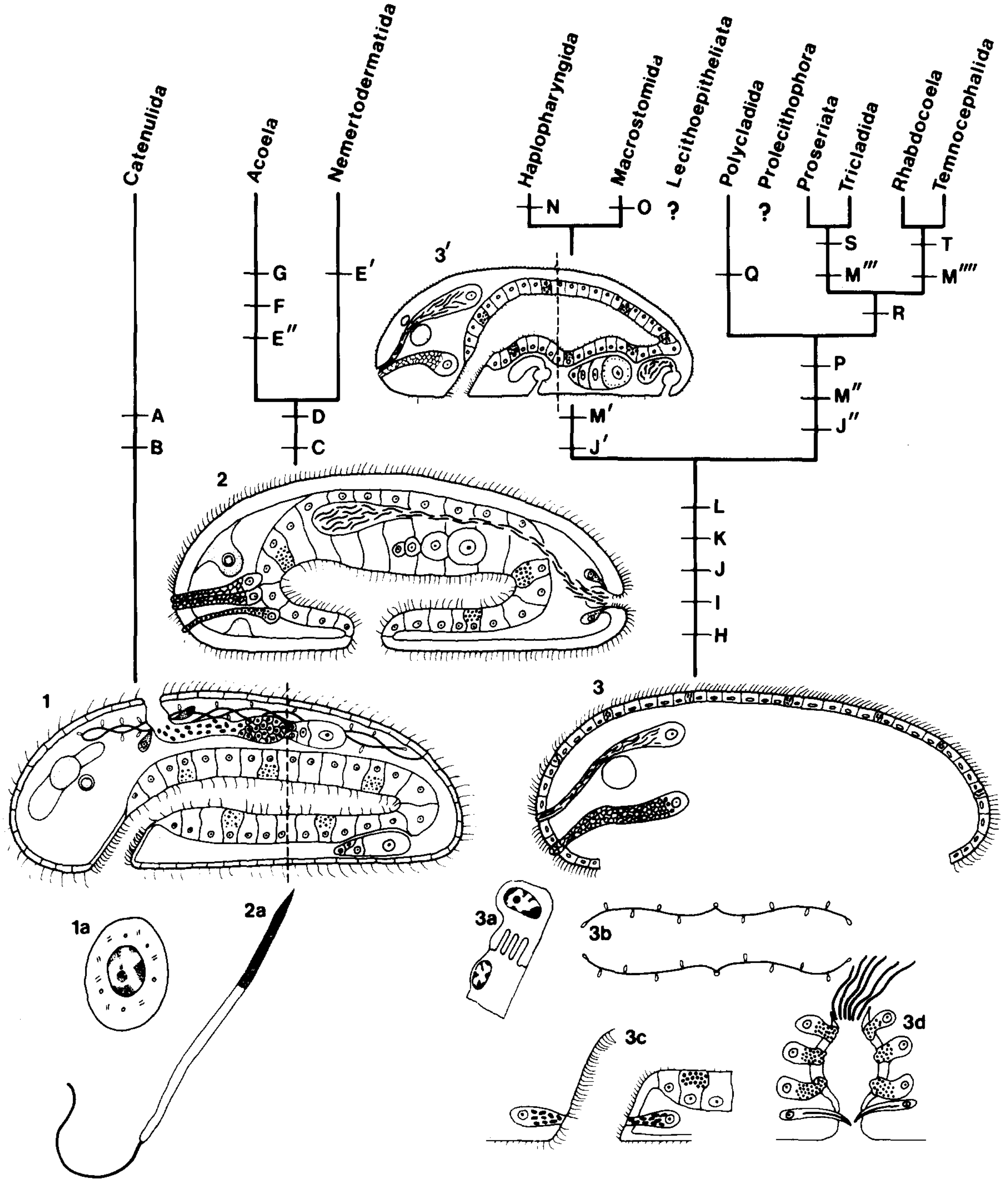


Fig. 14. Summary of turbellarian phylogenetic relationships based on present data. There are three monophyletic groups: Catenulida (1), 'Acoelomorpha' (2), and 'Rhabditophora' (3). Reconstruction (2) modified after Karling; others original. Additional potentially-plesiomorphic characters of each lineage are shown: sperm of Catenulida (1a) and Nemertodermatida (2a), and protonephridial system (3a, b), pharynx simplex (3c) and male organ (3d) of 'Rhabditophora'.

Homologues of both these parts can be identified in nemertodermatids (Fig. 12; Smith ms. in prep.) and thus the already strong probability of homology in the epidermal ciliation of the Acoela and Nemertodermatida (Tyler & Rieger, 1977) is further strengthened. It is possible even to identify some trends in rootlet evolution within the Acoelomorpha – for instance, the reduction of the laterally compressed, blade-shaped tip of the principal rootlet in Nemertodermatida to a pointed tip in some acoels follows a reading sequence (Figs 5–7) that agrees with data on the parenchyma (cf. Smith & Tyler, 1985a). Despite the abundance of characters that can be discerned in these rootlet there is still no homology that can be identified between those of the acoelomorphs and those of other turbellarians (except perhaps one comparing basal feet with posterior fiber bundles). It is still entirely possible that the multiciliated nature of these cells is homologous even if the rootlets are not. Such a possibility depends on whether the outgroup for the Turbellaria has monociliated epidermal cells, and that outgroup has not been identified unequivocally.

Epidermal replacement

A second character presumed to be apomorphic for the Platyhelminthes is the absence of mitosis in epidermal and other somatic cells (Ehlers, 1984). While epidermal cell division has been reported for catenulid turbellarians it is likely that what was actually observed was division of epidermal stem cells lying at the base of the epidermis (see also Ehlers, 1984: 22–23). Because mitosis of dedifferentiated epidermal cells is known for the Cnidaria (Martin & Thomas, 1981) but has not been (adequately) documented for any bilaterian phyla, it appears that the lack of mitosis in epidermal cells is a plesiomorphy at the level of the Platyhelminthes and apomorphic for the bilaterian stem (we believe the platyhelminth and bilaterian stems are not equivalent – see Smith & Tyler, 1985a).

The replacement of ciliated epidermal cells by cells arising and differentiating in the parenchyma is thought to occur in all platyhelminths (Lyons, 1977; Tyler, 1984; Ehlers, 1984, 1985a; Smith & Tyler, 1985a) and has been documented in rhabdocoels (Luther, 1904; Hein, 1928), in developing triclads (Skaer, 1965), and in larvae of non-turbellarian platyhelminths. Electron microscopy of presumed replacement cells in catenulids (Moraczewski, 1977, 1981, pers. commun.), haplopharyngids (Doe, 1981, Smith & Tyler unpublished observations), a microstomid (Reuter & Palmberg, 1983; Reuter personal communicattion), and triclads (Hori, 1978) shows they contain a bundle of centrioles, presumably centrioles differentiating into ciliary basal bodies. More important than the simple absence of mitosis in epidermal cells, therefore, is the process of epidermal replacement by kinetosome-containing cells that originate in the parenchyma; and we would prefer to consider this character an autapomorphy for the phylum. Certainly the prob-

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For summary references and background, see Karling (1974) and Ehlers (1984, 1985a). Some proposed autapomorphies of each group (with references to comparative studies) are:
A: Position and orientation of male system (Sterrer & Rieger, 1974). Special structure of spermatozoan (Rieger, 1978).
B: Unpaired, dorsally-located protonephridial system. Fine structure of flame bulb (Kümel, 1962; Rieger, 1981).
C: Special structure of basal body-rootlet system complex and of ciliary tips (Tyler & Rieger, 1977; Tyler, 1979).
D: Fine structure of frontal organ (Smith & Tyler, 1985b).
E′: Statocyst of Nemertoderma-type (Ehlers, 1985a).
E″: Statocyst of Convoluta-type (Ferrero, 1973; Ehlers, 1985a).
F: With digestive parenchyma (Mamkaev, 1979; Smith, 1981; Smith & Tyler, 1985a).
G: Biflagellate spermatozoan with 9+2, 9+0, or 9+1 axonemes (Hendelberg, 1977).
H: With true rhabdites (Smith *et al.*, 1982).
I: Paired protonephridia with flame bulb and canal cell interdigitating to form weir (Wilson & Webster, 1974; Ehlers, 1985a).
J: Duo-gland adhesive system with viscid and releasing gland cells (Tyler, 1976).
J′: Duo-gland adhesive system with viscid and releasing glands opening within a common collar of microvilli (Tyler, 1976).
J″: Duo-gland adhesive system with viscid and releasing glands opening separately through anchor cells (Tyler, 1976).
K: Frontal organ with acidophilic rhammites (Klauser *et al.*, 1985).
L: Epitheliosomes of basic protein (Tyler, 1984).
M′: Pharynx simplex coronatus (Doe, 1981).
M″: Pharynx plicatus or bulbosus (Karling, 1940; Ax, 1961).
M″′: Pharynx tubiformis (Steinböck, 1925; Ball, 1974).
M″″: Pharynx bulbosus rosulatus or doliformis (Karling, 1940; Ax, 1961).
N: Complex glandular, muscular proboscis, ventral to brain (Karling, 1965).
O: Details of pharynx cytology (Doe, 1981).
P: 9+1 axoneme in biflagellate spermatozoan (Hendelberg, 1977).
Q: Intestine with dendritic side branches.
R: Heterocellular female gonads (Karling, 1940; Westblad, 1948).
S: For characters, see Sopott-Ehlers (1985).
T: Unpaired gonopore with atrium commune (Karling, 1940).

ability of homology of centriole-containing epidermal replacement cells appears to be rather high between the Catenulida and Rhabditophora (see also Ehlers, 1984, 1985a).

Dorey (1965) suggests that acoels have a similar mode of epidermal replacement by immigration of cells from the parenchyma. These cells, called pulsatile bodies, have only been seen, however, as fully differentiated, cilia-bearing cells (Fig. 13; see also Dorey, 1965), even sometimes in the central syncytium apparently in the process of being digested (Smith & Tyler unpublished observations on acoels and *Nemertoderma* sp. B), and therefore are more likely to be epidermal cells being withdrawn from the epidermal surface than nascent epidermal cells. This possibility needs experimental verification, but until pulsatile bodies are convincingly demonstrated to be epidermal replacement cells, it seems to us that the probability of homology between the pulsatile bodies of the Acoelomorpha and the epidermal replacement cells of the Rhabditophora and Catenulida is low. So little is known about epidermal replacement in other metazoans that it is difficult to tell, in any case, whether any common features of epidermal replacement in Acoelomorpha and other turbellarians are apomorphic or plesiomorphic.

Other autapomorphies

Because the probability of homology of both epidermal replacement mode and ciliary ultrastructure between the Acoelomorpha and other turbellarians is so low, it is necessary that other proposed automorphies of the platyhelminths be thoroughly tested. Characters relating to protonephridial structure cannot link the Acoelomorpha to other platyhelminths because all known acoelomorphs lack protonephridia entirely. The one remaining proposed autapomorphy, namely lack of accessory centrioles on ciliary basal bodies, is a negative character that cannot stand alone as an autapomorphy.

In the final analysis, there are, at present, no synapomorphies common to the three monophyletic groups of the Platyhelminthes and thus no unequivocal autapomorphies for the phylum.

Relationships among platyhelminth taxa

Assuming, as most systematists of the Turbellaria do, that all turbellarians share a common ancestor, then the three clearly identifible monophyletic groups must be related in one of the four alternative ways depicted in Fig. 1 A–D. In the absence of synapomorphies common to all three groups (Fig. 1 A, filled circle) alternative A is ruled out; similarly, alternative C can be ruled out because no synapomorphies between Acoelomorpha and Catenulida are known. However, the anterior-dorsal position of the male reproductive system in a new genus of Nemertodermatida (pers. comm. N.W. Riser and own unpub. data), a feature unknown in other turbellarians except the Catenulida, is a potentially significant link worthy of further investigation.

Present evidence indicates strongly that the group Catenulida + Rhabditophora is monophyletic (Fig. 1B, black bar), but, as noted above, synapomorphies linking this group to the Acoelomorpha are not known (Fig. 1B, filled circle). The lack of this synapomorphy makes alternative B unlikely unless the Platyhelminthes is to be diphyletic.

The remaining alternative (Fig. 1D) circumvents the lack of synapomorphies between the Acoelomorpha and the other groups by considering that lack to be a case of reduction and linking the Acoelomorpha with the Rhabditophora (Fig. 1D, black bar). This is equivalent to 'alternative 2' of Karling (1974) and to Ehlers' (1984, 1985a, b) system and seems to be the one most systematists of the Turbellaria would support. With it, protonephridia, ciliary rootlet systems, and mode of epidermal cell replacement are considered homologous in the Catenulida and Rhabditophora. Lack of a synapomorphy for the Acoelomorpha + Rhabditophora (see Smith & Tyler 1985b, Klauser *et al.*, 1985) weakens this alternative, however. Moreover, it necessitates that the biflagellate nature of spermatozoa in members of the Acoela and Rhabditophora as well as the 9+1 axonemes in some members of both these groups are not homologous.

A variant on alternative D – one that considers the characters of the spermatozoa to be homologous – is that of Fig. 1E, in which the Acoelomorpha is depicted as being paraphyletic (logical consequence of arguments raised by Hendelberg, 1977).

There is at least one compelling reason for considering biflagellate spermatozoa among turbellarians to be homologous: the Plathyhelminthes is the only metazoan group to have spermatozoa with both a biflagellate morphology and an inverted orientation (flagellar basal body leads and nucleus trials in locomotion; see Hendelberg, 1985). While these conditions can be found in spermatozoa of other metazoan groups (inverted: Marchand & Mattei, 1976; biflagellate: see Baccetti & Afzelius, 1976), they are not known to occur together in the same sperm except among platyhelminths. If these characters are homologous among platyhelminths, then the characters of protonephridia, ciliary rootlet systems, and epidermal replacement mentioned above cannot be homologous in Catenulida and Rhabditophora.

Thus, for now, we prefer to leave open the construction of a phylogenetic system for the Platyhelminthes. Although we believe the phylum is monophyletic, we cannot demonstrate that monophyly; and so rather than forcing the three monophyletic groups together, it is preferable to treat each as independent (Fig. 14). Characters that may close the gap between these groups should come from study of catenulids and nemertodermatids, in particular. We need also to understand more fully the relationships of the phylum to other invertebrate groups, for its evolutionary origin remains one of the chief puzzles of metazoan phylogeny (Smith & Tyler, 1985a).

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