

# On the Anatomy and Affinities of the Turbellarian Orders

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The phylogeny of the turbellarian orders will be discussed on the basis of a diagram influenced by the sister-group principles of Hennig (1966).<sup>1</sup> A revision of the turbellarian system is outside my actual approach and entanglement in theoretical discussions on the affinities of the Turbellaria to other Metazoa is avoided.

Today, as earlier, comparative anatomy must be the basis for the turbellarian system; information of systematic bearing from other fields of

<sup>1</sup>I thank my friend Dr. Lars Brundin for valuable discussions on systematic principles.

turbellarian research is sparse. Another question is to what degree this basis is reliable. The turbellarian orders are kept together by similarities based on characters of highly different evolutionary age, and opinions diverge as to what is primitive and what is derived. Moreover, it is not easy to state what is homology and what is analogy. These difficulties are pronounced in animal taxa with a low degree of differentiation in general, such as the turbellarians.

The principal idea in Hennig's approach is the absolute demand for monophyly of every group (cf. also Brundin, 1967). A monophyletic group is constituted by the species—all the species—with an ancestral species in common, which is not at the same time the ancestral species of species outside the group. Two groups originating from the same ancestral species are *sister groups*. One of two sister groups is more conservative, *plesiomorph*; the other is more derived, *apomorph*. The attributes plesiomorph and apomorph are also used to indicate primitive and derived conditions respectively. A special homology characterizing a group (or species) is one of its *autoapomorphies*. For the taxa of a monophyletic group it can be at the same time an exclusive *synapomorphy*. These taxa have further nonexclusive homologies in common with species of other groups, *symplesiomorphies*. The systematic value of the common homologies thus diminishes with the further hierarchic ramifications: a synapomorphy for a larger taxon, e.g., an order, is a plesiomorphy for every one of its suborders. Thus, the application of these ideas depends upon recognition of what is apomorph and what is plesiomorph in a series of transformation.

### THE TURBELLARIAN ARCHETYPE

By a comparative analysis of all the turbellarian orders, an analysis impossible to review here as a whole, I have arrived at an archetype which I place at the base of the hierarchic diagram of the Turbellaria (Fig. 1). The attributes of this archetype, listed below, are at the same time the basic plesiomorphies for every order. Progress in the field of turbellarian research during the last decades has forced me to revise the pictures of the turbellarian archetype and the turbellarian phylogeny which I outlined in the year 1940. A third archetype was presented by Peter Ax in his excellent review on turbellarian anatomy and phylogeny at the Asilomar Symposium in 1960 (published 1963).

1 Epidermis one-layered, entirely ciliated, cellular, with rhabdites and intracellular nuclei. Basement membrane lacking or weakly developed. Subepidermal musculature with an outer layer of circular fibers and an inner layer of longitudinal fibers. This organization of the body wall is the original in all orders except the Nemertodermatida. EM studies on rhabdites can con-

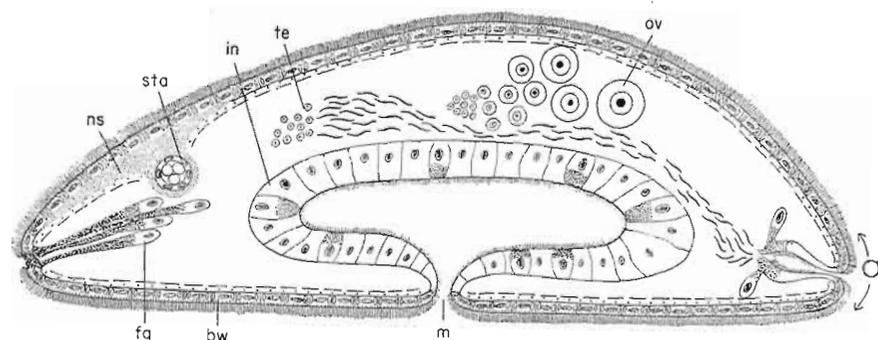


Figure 1 Sagittal scheme of the turbellarian archetype according to the author. (Original.) For abbreviations see Fig. 2.

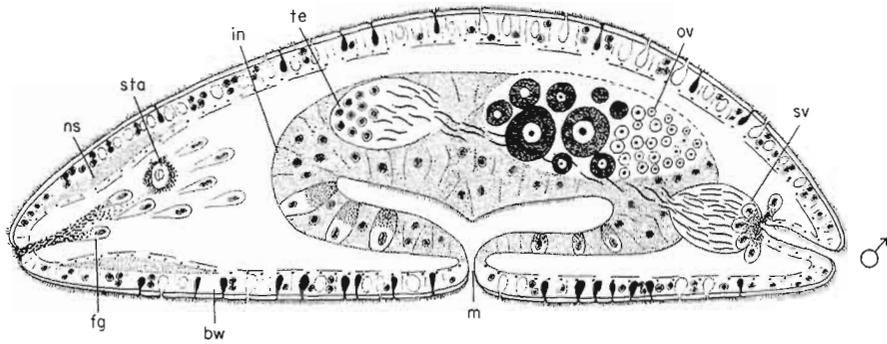
tribute to our understanding of the phylogeny in the Turbellaria; today only scattered observations are available (Reisinger, 1969, with references).

2 Nervous system epidermal-subepidermal. This type of nervous system has been found in many species of different acoel genera (Dörjes, 1968) and in the two nemertodermatid genera (*Nemertoderma*, Westblad, 1937; *Meara*, Westblad, 1949), i.e., in the taxa with the most primitive conditions. Most authors regard the epidermal location—even in the Turbellaria—as a primitive condition (Hyman, 1951), but Ax regards it as secondary, “a parallel persistence of juvenile characters” (1963, pp. 201–202). The acceptance of an epidermal nervous system as primitive in species of different genera in the Acoela requires that these species represent “direct descendants of a common stem type with an epidermal system and that they all belong together systematically (phylogenetically)” (loc. cit.). However, if we regard the epidermal condition as a basic plesiomorphy, the common stem type is the turbellarian archetype, the internal nervous system arising from trends in several evolutionary lines.

3 Eyes lacking or epidermal. The typical internal turbellarian pigment-cup eyes evolve from epidermal “pigment spots” evidently separately in different lines. Epidermal eyes occur in the primitive taxa Acoela and Microstomidae as well as in the genus *Gnosonesima* (basic plesiomorphic feature, Karling, 1968, with references). The eyes are secondarily lost in many taxa.

4 Weakly differentiated statocyst containing a variable number of statoliths. A statocyst belongs to the fundamental qualities in the Acoela, the Nemertodermatida, a part of the Catenulida, and in the Proseriata. It is sometimes secondarily lost in these taxa. I regard as primitive a statocyst with epithelial wall and a variable number of statoliths (cf. below, the taxa with statocyst).

5 Simple mouth pore or pharynx simplex. These conditions can be realized secondarily in some parasites. From a phylogenetic point of view



**Figure 2** Sagittal scheme of *Nemertoderma* sp. (Original after several figures in Westblad, 1937, and Karling, 1967.)

Abbreviations (applicable also to Figs. 4 and 5): ac, male accessory organ; br, brain; bw, body wall; fg, frontal glands; gi, genitointestinal communication; in, intestine; m, mouth; ns, nervous system; ov, ovary; ph, pharynx; pi, pigment; pr, prostatic vesicle; sb, sensory bristle; sta, statocyst; sty, stylet; sv, seminal vesicle; te, testis.

there is no reason to keep the simple mouth pore and the pharynx simplex apart, these conditions being variations on the same theme; i.e., the pharynx simplex can arise from trends in several lines.

**6** Sac-shaped intestine with ciliated epithelial wall, no anal pore. Some authors regard the lack of an anal pore in the Turbellaria as a secondary condition, an opinion lacking support in the turbellarian anatomy (Reisinger, 1961; Karling, 1965). Several species in different groups have a weakly differentiated, mostly temporary anal pore (Karling, 1966a). There is thus anatomical evidence that the turbellarians can give rise to taxa with a true digestive canal.

**7** Two alternatives must be considered: (a) no excretory organs; (b) some kind of primitive (diffuse) protonephridia. No methods have hitherto revealed any kinds of excretory organs in the Acoela, not even in the limnic species *Oligochoerus limnophilus* Ax and Dörjes, 1966. Opinions differ as to the primitiveness of this phenomenon (Westblad, 1948, p. 65: primitive; Ax, 1961, pp. 24–31, and Reisinger, 1968, p. 20: secondary). I accept preliminarily the assertion that an excretory system is lacking also in *Nemertoderma* and *Meara* (cf. above), but no EM studies have hitherto been carried out on these subjects. EM studies have revealed a complicated structure of the turbellarian flame bulbs, and further studies in this field will certainly contribute to our understanding of the affinities between the turbellarian taxa (Reisinger, 1970, with references).

**8** Female gonads homocellular (ovaries), sometimes with nutritive cells, eggs entolecithal. This type of female gonad characterizes the grade (formerly order; cf. below, Nemertodermatida, etc.) Archoophora. Reduction

of the vitelline parts in heterocellular gonads can in some cases give rise to homocellular gonads (Karling, 1967).

**9** With male genital pore in a variable position (primitive copulatory organ, internal fertilization), no female pore (common oviduct). We do not know any turbellarian without male genital pore and with external fertilization. A female pore is lacking in the Acoela, the Nemertodermatida, and the Catenulida, the primitive mode of copulation being injection (impregnation) and the primitive mode of egg laying being rupture of body wall or gut wall. The oviduct is secondarily lost in some higher taxa, e.g., *Bresslauilla* (Ax, 1963, p. 205).

The archetype presented by Ax (1963) principally differs from that presented here in the following respects:

**1** Pharynx simplex. As shown above (point 5), this difference can be disregarded.

**2** "Internal nervous system with a brain, several pairs of longitudinal cords and transverse commissures (orthogon)," cf. above, point 2.

**3** "Single statocyst with one statolith." Ax believes that "in the few instances with two or three statoliths . . . a secondary multiplication has taken place" (op. cit., p. 202). I think the evolution starts with a low grade of stability and leads to more fixed conditions, such as in the Acoela and the Proseriata.

**4** A pair of protonephridia. My alternative *b* presupposes protonephridia in the archetype, but I find it easier to derive the unpaired system of the Catenulida (as well as the paired condition in most other taxa) from a diffuse system of emunctories (Ax, op. cit., pp. 203–204).

**5** Separate male and female gonopores, oviducts, a simple bursa, and a vagina. This high level of organization is based on Ax's assumption that the turbellarians are highly reduced Spiralia (op. cit., pp. 211–215). Like most other specialists, he holds to the theory, first presented by Meixner (1926), that the first female pore was a vagina and that "the atrium femininum and the vagina of the Macrostomida are respectively homologous with the bursa and the vagina of the Acoela" (op. cit., p. 204). Regarding the Acoela as extremely reduced, he reverses the evolutionary direction Acoela → Macrostomida accepted by most authors. However, the real basis for this vagina-oviduct theory is rather weak (Karling, 1940, p. 210). In most turbellarians the female apparatus opens behind the male apparatus, separately or into a common atrium. In the Prolecithophora, evidently the most primitive Neophora, the common oviduct always opens from behind into a common atrium (also in *Protomonotresis centrophora* Reisinger, 1923, originally described as lacking female gonoducts; Reisinger, *in litt.*) and that seems to be the primary condition also in the Proseriata, Tricladida, and Rhabdocoela, and perhaps also in the Polycladida, though in this order the female pore is mostly removed from the

male one. Also in the Lecithoepitheliata the female apparatus is situated as a whole behind the male organs. The bursal organs arise independently of the common duct (Prolecithophora, many Proseriata and Rhabdozoa) or as a derivative of that duct. A bursal organ separated from the common duct seems to have a positive selective value, and a trend toward a separation of these structures appears in many lines. Also in the two families of the Macrostromida (Macrostromidae, Microstromidae) this trend is realized, a separate vagina being differentiated in some genera and species (Papi, 1950; Westblad, 1953). Further, we can regard the female ducts from another point of view: are they all homologous? If the common oviduct arises from a vagina in the Macrostromida, this mode of evolution is not in any way necessary in other lines (cf. below).

### ON THE ANATOMY AND AFFINITIES OF THE TURBELLARIAN ORDERS

As seen in the diagram (Fig. 3), I have here abandoned the division of the Turbellaria into two groups, the Archoophora and the Neophora. The main common attribute of the Archoophora, the homocellular female gonads (the ovaries), is a primitive attribute of the Turbellaria, a *symplesiomorphy*, the group Archoophora being thus a paraphyletic grade (*Stadiengruppe*), not a monophyletic taxon. The turbellarian orders with heterocellular female gonads, i.e., with germaria and yolk glands, constitute the group Neophora, a group appearing monophyletic from the diagram. I shall later return to this question. I thus regard the Nemertodermatida, Acoela, Catenulida, Macrostromida and Haplopharyngida, earlier brought together in the Archoophora, as orders. The Polycladida too have sometimes been regarded as Archoophora.

In the first alternative here presented I regard the lack of excretory organs as primitive, the Acoela and Nemertodermatida thus constituting the plesiomorph sister group, all the other orders the apomorph group with excretory organs as synapomorphy. The systematic relationship of the orders Nemertodermatida and Acoela, and thus the position of these orders in the phylogenetic diagram, cannot be definitely fixed today owing to our deficient knowledge on some points and also owing to divergent opinions about the primitiveness of some structures. The two genera of the Nemertodermatida, *Nemertoderma* and *Meara*, evidently stand closest to the turbellarian archetype, but their organizations diverge at some important points and I am not convinced that they belong together.

The statocyst of the Acoela consists of a thin wall with two matrix nuclei in dorsal position. The single statolith is about plane-convex with one single matrix nucleus on its dorsal side (*Convoluta* type, Luther, 1912; Westblad, 1940; Ax and Dörjes, 1966). The nuclei are difficult to see on squeezed material owing to their dorsal position. Two statoliths are sometimes seen in

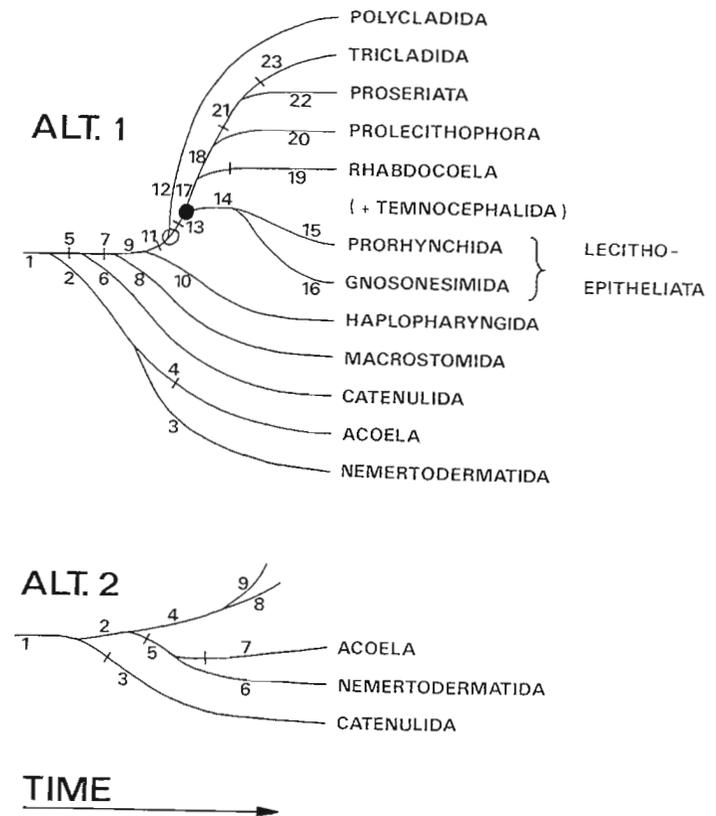


Figure 3 Phylogenetic diagram of the turbellarian orders (and the suborders Prorhynchida and Gnosonesimida). A short bar indicates the comparatively apomorph sister group; a ring indicates the common ancestral species of the taxa with complex pharynx; a black dot indicates the common ancestral species of the taxa with heterocellular ovaries. Other explanations in the text.

species of the Hofsteniidae (Steinböck, 1966, pp. 75–76). The Nemertodermatida mostly have two statoliths, but Riedl has seen three statoliths in *Nemertoderma* (1960). The wall of the statocyst is epithelial with a variable number of cellular nuclei, concentrated to a vertical girdle between the statoliths in *Meara* (Westblad, 1937, 1949; my own observations).

The parenchymal condition of the digestive tract in the Acoela is one of the most-discussed features in turbellarian anatomy. *Nemertoderma* and *Meara* have a true intestine, which in *Nemertoderma* is in part ciliated (Fig. 2) (Karling, 1967, pp. 5–8). In the Acoela a central lumen is often found in

the digestive tract. According to my own observations *Archiproporus minimus* An der Lan, 1936 has a distinct gastroderm, and in many other species there is a tendency toward a similar construction (Antonius, 1968; Dörjes has informed me that the genus name *Archiproporus* is valid). These observations support the opinion of Hyman (1959) that absence of a lumen in the acoels is not of any importance. The existence or nonexistence of an epithelial gut wall has a greater phylogenetic bearing but has often been exaggerated. In any case the parenchymal condition of the digestive tract remains—besides the *Convoluta*-type statocyst—the principal diagnostic character of the Acoela. I regard these two characters as synapomorphies of the Acoela. The nemertine-like epidermis and the two statoliths are synapomorphies of the Nemertodermatida.

The order Catenulida is rather specialized, most of its taxa being limnic, mainly with a sexual propagation. The statocyst is often difficult to see, owing to its extremely thin wall. The number of statoliths varies. I have seen two to four statoliths in *Rhynchoscolex* species (cf. also Rixen, 1961). Sterrer reports one to six statoliths in a marine catenulid (1966). The internal structure of the catenulid statocyst is not sufficiently known. Marcus has found a variable number of cells in its matrix (1945).

I derive the unpaired excretory system of the Catenulida from a diffuse system of emunctories, others deriving it from the paired system of most other groups (cf. above, the archetype of Ax). I regard the dorsally situated male copulatory apparatus of the Catenulida as homologous with that of other turbellarians, but this opinion can be criticized and I myself have earlier regarded this apparatus as independently evolved (1940). Recent studies on a *Stenostomum* species (Borkott, 1970) have revealed a highly aberrant structure of the male apparatus.

Synapomorphies of the Catenulida are the unpaired excretory system and the dorsostroral position of the male copulatory organ. Group 7 (Fig. 3, alternative 1) is the apomorph sister group compared with the Catenulida with the synapomorphies common oviduct and paired excretory system.

The orders hitherto discussed can be arranged in another way, here presented as a second alternative, if we provide the archetype with some kind of excretory system, perhaps irregularly arranged emunctories. The synapomorphy of group 5 (Fig. 3, alternative 2), the Acoela and the Nemertodermatida, would then be the loss of the excretory organs. It is difficult to find out true synapomorphies for group 2, i.e., all turbellarians except the Catenulida. The synapomorphies of the Catenulida are the same as in the first alternative.

I have earlier regarded it necessary from a practical point of view to include the family Haplopharyngidae in the order Macrostomida (1965), but this measure is incompatible with the ideas of plesiomorphy and apomorphy, the Macrostomida s. lat. lacking true synapomorphies. The Haplo-

pharyngida have the caudal position of the female apparatus (common oviduct, female genital canal, indeed the existence of this canal is not granted) in common with most higher taxa. However, I would not like to say whether this condition or the opposite position of the outleading genital apertures is the primitive one, and consequently none of the actual lines has been indicated as apomorph compared with its sister group (cf. above, Ax's archetype, point 5). The Macrostomida s. str. have the synapomorphy of common oviduct in front of the male apparatus, but this character is sometimes indistinct in taxa with common atrium. The synapomorphy of group 9 (Fig. 3) is the position of the common oviduct behind the male atrial apparatus, but this condition can also here be indistinct or secondarily altered. The differentiation of a proboscis is the most pronounced autoapomorphy of the Haplopharyngida. The synapomorphy of the apomorph sister group 11 (Fig. 3) is the complex pharynx, characteristic of all the higher turbellarian orders. The first stage in the transformation of this pharynx type is the plicate pharynx. However, the homology of all kinds of complex pharynges is not warranted.

The order Lecithoepitheliata contains the isolated suborders Prorhynchida *mihi* and Gnosonesimida *mihi* with the lecithoepitheliate type of female gonads as synapomorphy, i.e., with a common layer for ovocytes and vitellocytes and the growing ovocytes enclosed by vitellocytes (Figs. 4 and 5). Prorhynchida is only a new name for Typhlocoela Steinböck (1923) [abandoned in favor of Lecithoepitheliata (Reisinger, 1924; Steinböck, 1925)] with the families Prorhynchidae and Hofsteniidae. The family Gnosonesimidae was later (Reisinger, 1926) included in the Lecithoepitheliata. Steinböck (1966) accepted the opinion that the Hofsteniidae belonged to the Acoela.

According to Steinböck (1966) and Reisinger (1968) the prorhynchid bulbous pharynx has arisen from the simple pharynx of *Hofstenia* type without the intermediate plicate step. Such an evolution is perhaps not impossible, as we can see in the acoel species *Diopisthoporus brachypharyngeus* (Dörjes, 1968), but the construction of the pharynx in this species is far from that of all other known bulbous pharynx types; I would call it a bulbiform simple

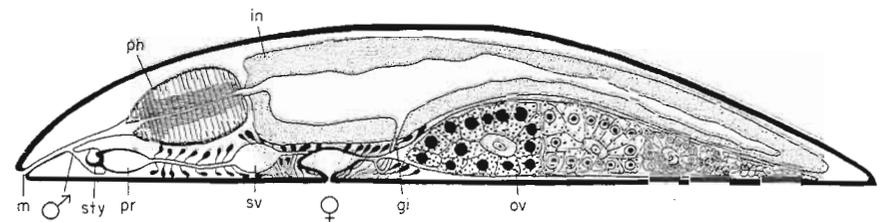


Figure 4 Sagittal scheme of *Geocentrophora sphyrocephala*. (From Steinböck, 1927.) For abbreviations see Fig. 2.

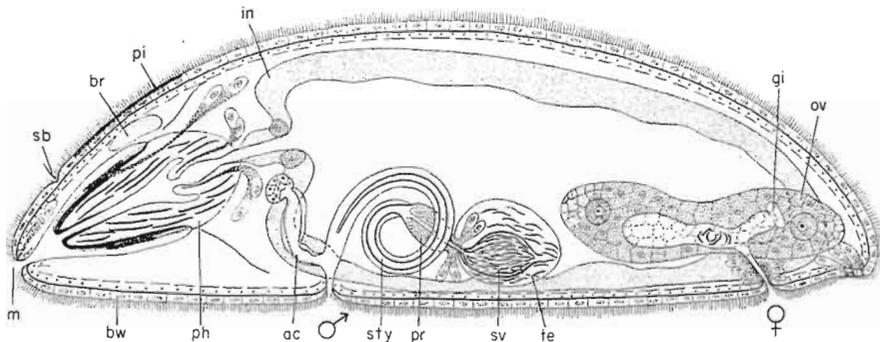


Figure 5 Sagittal scheme of *Gnosonesima brattstroemi*. (Original after Karling, 1968.) For abbreviations see Fig. 2.

pharynx. Anatomically the prorhynchid pharynx is nothing but a strongly muscular variable pharynx (Karling, 1940). The coniform pharynx, recently described by Karling (1968) in the genus *Gnosonesima* is a type of its own, evidently directly evolved from a plicate pharynx.

Reisinger and Steinböck base their derivation of the Lecithoepitheliata directly from acoel turbellarians mainly on the construction of the pharynx and the female gonads. Here I regard the complex pharynx, including the pharynges of Prorhynchida and *Gnosonesimida*, throughout as a homologous structure and moreover the female gonads of all the "Lecithophora" also as homologous, but I admit that a definite position in these questions is difficult to take. However, how can the highly differentiated excretory organs of the Prorhynchida be explained if we accept the evolution of this group directly from the Acoela? A more acceptable alternative could be to let the Lecithoepitheliata (or its two suborders separately, cf. Karling, 1968) branch off from the archoophoran stem in the vicinity of Haplopharyngida.

To indicate one of the two lecithoepitheliata suborders as the apomorph sister group would give a false impression of close phylogenetic affinity between the two taxa, a measure thus omitted here.

There is no doubt about the rather close affinity between the orders Prolecithophora, Proseriata, Tricladida, and Rhabdozoa (including the Temnocephalida), their heterocellular female gonads with different layers for ovocytes and yolk cells—the latter also producing shell substance—constituting a true synapomorphy for group 17 (Fig. 3) (Karling, 1940; Ax, 1963). The structure of the pharynx in different taxa of the first three orders plays an important part in fixing the origin of the Rhabdozoa. It is fundamentally of the plicate type, but there are trends toward a bulbous pharynx in many families of the Prolecithophora, and in the Proseriata there is at least one genus (*Ciliopharyngiella* Ax, 1952) with a bulbous pharynx. Here I have resolved the controversy about the origin of the Rhabdozoa (Ax, 1963)

by letting the rhabdozoan line branch off from the common stem of the other three orders.

The synapomorphies of the comparatively apomorph rhabdozoan sister group are the specific construction of the rosulate and doliiform pharynx types (diaphragm strongly developed, circular muscle layer next to the pharynx lumen. Karling, 1940, p. 172) and the compact gonads mostly provided with a tunica propria. In some species these gonads can be divided secondarily into follicles.

The order Prolecithophora can be characterized as neophoran turbellarians with fusiform or cylindrical shape, plicate to variable pharynx, sac-shaped intestine, and primary follicular to compact gonads, mostly without a tunica propria. For the specialist it appears as a very homogeneous group, but the characters here listed do not constitute good synapomorphies. This fact indicates that this group has been ranked on too high a level in the hierarchic diagram, but a more satisfactory position for the group in question could not yet be found. This situation also complicates the establishment of synapomorphies for the whole plesiomorph group 18 (compared with the apomorph sister group Rhabdozoa): testes and vitellaria diffuse—follicular, plicate pharynx with trends toward a bulbous type, penis fundamentally of the papilla type. Group 21 with the orders Proseriata and Tricladida is rather homogeneous, sometimes regarded as an order (Seriata, Metamerata), and the same is true for its two branches. Its synapomorphies are the fundamentally serial arrangement (i.e., in longitudinal rows) of the testes and yolk follicles, the backwards-directed tubiform pharynx and the elongate body shape. These features can be secondarily altered (one pair of testes, ruffled pharynx with vertical axis).

The synapomorphy of the Proseriata is the statocyst of *Monocelis* type (sometimes secondarily lost). This statocyst differs in some aspects from the acoel statocyst (*Convoluta* type). In its frontal wall a pair of nuclei are easily seen in live material, and often also another pair in a more caudal position. The single statolith within the statocyst is globular or frontally somewhat conical with two frontal groups of matrix cells, containing two to four nuclei each (Ax, 1956; Giesa, 1966; my own observations on representatives of all proseriate families). The isolated occurrence of a statocyst speaks in favor of an independent evolution of this structure in the Proseriata, just as in the rhabdozoan *Lurus evelinae* Marcus, 1950. Otherwise we must accept an independent loss of the statocyst in most turbellarian orders, which, however, is a theoretical possibility (Karling, 1966b).

The Tricladida constitute the apomorph sister group compared with the Proseriata. They have the synapomorphies: triclaid intestine, germaria anteriorly situated in the female gonads, and mostly a flattened body shape. This organization is sometimes secondarily changed.

From a purely anatomical viewpoint the order Polycladida belongs to

the grade Archoophora owing to their homocellular female gonads, but they are more highly differentiated than the other orders of this grade. I have repeatedly maintained the idea of a rather close relationship between the Polycladida and the complex around the Prolecithophora, but the diagram is made without attention to the hypothesis of a total reduction of the yolk glands in the Polycladida. A parallel evolution of the order Polycladida with the Prolecithophora complex has been indicated by the direction of the polycladid branch 12. The Polycladida and the Prolecithophora complex are both relatively conservative branches of the same stem, the two lines Rhabdocoela and Lecithoepitheliata being more advanced. Transferring the Lecithoepitheliata to a lower level would bring the Polycladida into a position closer to the Prolecithophora complex. The synapomorphies of the Polycladida are the polycladoid intestine and the (secondarily) follicular ovaries.

## DISCUSSION

Perhaps the diagram here presented, and consequently also its author, appear highly conservative. I have given all the species with complex pharynx a common ancestral species (here indicated with a ring) and in the same way all the species with heterocellular female gonads a common ancestral species (indicated with a dot), though there are facts indicating that the complex pharynx as well as the gonads in question can have arisen more than once. Thus, the monophyly of the Neophora is in no way warranted. There are many other subjects for criticism. The theoretical basis of the diagram, the search for sister groups, makes a fixed connection of all branches in the hierarchic tree necessary, a measure often avoided before. I have presented one partial alternative to the diagram and several more alternatives may have been desirable, but I have contented myself with pointing out the problems. The diagram may be regarded not as a demonstration of a fixed opinion but as an exponent of an unsatisfactory situation. Then also the question arises as to the correctness of the methodics, sharply criticized during the last years (Mayr, 1969). According to the definition of the concept "monophyly," the class Turbellaria in its whole is not monophyletic, its common ancestral species being at the same time the ancestral species for the classes Trematoda and Cestoda (derivatives of the Turbellaria Rhabdocoela). Here we find one of the points where ideas strongly diverge. Mayr rejects the "prospective postulate" of Hennig (that a monophyletic group must include all the species with an ancestral species in common). He says: "If a descendant group . . . evolves more rapidly than the other collateral lines, it not only can but must be ranked in a higher category than its sister groups. This does not violate the principle of monophyly, retrospectively defined" (loc. cit.). Thus, the question is how to define monophyly. According to Hennig the process of phylo-

genesis begins with the splitting up of an ancestral species into daughter species, these species giving rise to sister groups with true synapomorphies. Breaking out one of the groups of the turbellarian diagram, e.g., the Macrostomida, to a separate class leaves a heterogeneous rest—an artificial conglomerate—without the criteria of an exclusive organization (synapomorphies), its only features in common being nonexclusive (symplesiomorphies), inherited from the archetype, thus also in common with the Macrostomida. Replacing in this example the Macrostomida with the Trematoda leaves in the same way an artificial conglomerate, a heterogeneous turbellarian class, if the Trematoda and other derivatives of the Turbellaria are not degraded to turbellarian taxa. The phylum Platyhelminthes is evidently a monophyletic entity based on the turbellarian archetype. Its groups Turbellaria, Trematoda, and Cestoda are not sister groups or groups on the same hierarchic level and cannot consequently (according to Hennig) be of the same systematic rank, i.e., classes. Here we meet the same state of affairs as within the Turbellaria: taxa on different phylogenetic levels holding today the same absolute rank (orders, cf. introduction). The "cladistic" principles express without doubt the processes of phylogenesis in a clear and logical way, but their strict application leads to a breakdown of the classification of today. My intention is only to point out the controversy of the different systematic points of views in regard to the Turbellaria; I have no solution of the controversy at hand.

Focusing on the class Turbellaria only, we find that the search for sister groups throws a sharp light on our insufficient knowledge of the phylogenetic connections between the turbellarian taxa. In the future increasing information from EM studies, biochemistry, sperm morphology, etc., will elucidate many of these obscure points.

## SUMMARY

The structure and phylogeny of the turbellarian orders are discussed on the basis of a hierarchic diagram according to the sister-group schema of Hennig (1966).

A theoretical archetype is reconstructed at the root of the turbellarian stem with the following anatomical plesiomorphies (primitive characters) of all the Turbellaria: one-layered, cellular, entirely ciliated epidermis with rhabdites and intracellular nuclei; basement membrane lacking or thin; two-layered subepidermal musculature; epidermal-subepidermal nervous system; eyes lacking or epidermal; weakly differentiated statocyst with a variable number of statoliths; simple mouth pore; sac-shaped intestine with epithelial ciliated wall, no anal pore; no excretory organs (alternatively some kind of primitive protonephridia); homocellular female gonads, entolecithal eggs, no female pore; male genital pore, internal fertilization.

The turbellarian orders here considered are: Nemertodermatida, Acoela, Catenulida, Macrostomida *mihi*, Haplopharyngida *mihi*, Lecithoepitheliata (with the suborders Prorhynchida *mihi* and Gnosonesimida *mihi*), Rhabdocoela (with the Temnocephalida), Prolecithophora, Proseriata, Tricladida, Polycladida.

The sister-group principle demanding fixed connections of all the branches in the hierarchic diagram necessitates the controversial phylogenetic solutions that the complex pharynx and the heterocellular female gonads have arisen only once (ring and dot respectively in the diagram).

Also several other solutions are more or less controversial: the Nemertodermatida stand closest to the archetype; the unpaired excretory system of the Catenulida has arisen from a diffuse system of emunctories, not from a paired system; the origin of the oviduct from a vagina and thus the close relationship Macrostomidae-Convolutidae are called in question; the establishment of the complex Prolecithophora-Proseriata-Tricladida as sister group to the Rhabdocoela.

The direct connection of the Lecithoepitheliata with the Acoela is not accepted, although some conditions speak in favor of it. The close affinity between the two lecithoepitheliate suborders here nominated, Prorhynchida and Gnosonesimida, is questionable.

Consequent realization of Hennig's principle that sister groups must have the same absolute systematic rank is impossible without a thorough revision of the whole turbellarian system. The main obstacle for such a revision is our deficient knowledge of the series of transformation, i.e., of the true homologies in the Turbellaria.

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## Chapter 2

# History of the Study of Turbellaria in North America

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The first turbellarians of North America were described and named by Samuel S. Haldeman, a naturalist of manifold interests in geology, chemistry, entomology, conchology, archaeology, and even philology. These species were a freshwater triclad, *Planaria gracilis*, described in 1840, and an alloecoel, *Hydrolimax grisea*, published in 1843, both observed in eastern Pennsylvania. These findings were followed by studies of two of Haldeman's colleagues and friends, both associated with the important center of early faunistic study, the Academy of Natural Sciences of Philadelphia: Joseph Leidy, a very diligent collector and student of invertebrates who in his lifetime published over 800