

The position of the Haplotaxidae in the evolution of oligochaete annelids

R. O. Brinkhurst

Institute of Ocean Sciences, P.O. Box 6000, Sidney, British Columbia, Canada V8L 4B2

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Abstract

The Haplotaxidae have all the characteristics to support the hypothesis that they are the living descendents of the stem forms from which all of the Oligochaeta Clitellata (Orders Lumbriculida, Haplotaxida, Lumbricida, Tubificida) can be derived. The Aphanoneura are distinct from the Clitellata and are raised to a separate Class. There is no evidence to support the view that the elaborate setae of many Tubificida are derived from a polychaete ancestry; both are held to be independent modifications to aquatic life derived from a simple burrowing protoannelid with lumbricine setae.

Introduction

After more than thirty years experience with systematics of the Oligochaeta, Michaelsen (1930) concluded that two alternative phylogenetic systems were equally credible, and that it was impossible to choose between them. According to one scheme, the family Haplotaxidae could be visualised as ancestral to both the terrestrial and aquatic lines of oligochaete evolution; the alternate hypothesis being that those aquatic forms which may have complex dorsal setae (the modern Tubificida; see Brinkhurst, 1982) were derived from polychaete ancestors other than those that gave rise to the haplotaxids and thence the Lumbricida (the earthworms of familiar terminology).

Prior to that date, a linear evolutionary sequence was visualised beginning with the archiannelids which supposedly provided the ancestors of first the Aeolosomatidae and from them the Naididae, Tubificidae, thence to the Lumbriculidae (with their bifid but paired instead of abundant setae) and from them to the haplotaxids and hence to the earthworms. This sequence has been thoroughly discredited at every step of the supposed sequence

(Brinkhurst, 1982 reviews the literature). Indeed, the later accounts attempted to reverse the sequence to read Lumbriculidae-Tubificidae-Naididae-Aeolosomatidae, which idea contains the most important but unrecognised premise that the complex dorsal setae of most Tubificida were derived from forms with lumbricine paired setae. Stephenson (1930) was in fact inconsistent in this respect in first claiming the polychaete ancestry of tubificid hair setae, but electing the lumbriculids as the ancestral group a few pages later. Yamaguchi (1953) also saw the lumbriculids as ancestral (because of the variability of the male reproductive system) but Clark (1978) was more aware of the problems inherent in this selection. These authors missed the alternative proposition that the Haplotaxidae might provide the stem forms for all of the Oligochaeta, later restated by Brinkhurst & Jamieson (1971). This was largely because Michaelsen chose to classify the haplotaxids with the opisthoporous megadriles despite the fact that they are plesioporous microdriles (see Brinkhurst, 1982 for definitions). Their position as ancestors of the terrestrial forms was recently confirmed by Jamieson (1977, 1978, 1981) who also concluded that the Tubificida could not be

interposed between the haplotaxids and their terrestrial descendents but could be independently derived from the haplotaxids but not the Lumbriculida. I concur with these findings with the exception that I now regard the prosopore condition of the lumbriculids to be derived from the plesiopore condition of the haplotaxids (see Brinkhurst, 1982).

The most recent phylogenetic account (Timm, 1981) seeks to return to the concept that hair setae in oligochaetes are derived from an ancestral polychaete and that the lumbricine setal state is derived from forms with more complex setae by a progressive simplification akin to the progressive specialisation of segmental organ systems seen throughout phyla such as the annelids, arthropods and chordates. I am indebted to Dr. Timm for the many exchanges of correspondence in regard to this and other issues, and trust I have quoted his views accurately in the following account.

Origin from proto-haplotaxids

Brinkhurst & Jamieson (1971) focused attention on the sequential arrangement of gonads in existing oligochaetes and demonstrated that all of the multi-gonadal forms were parthenogenetic, and that all oligochaetes can be derived from a worm with four pairs of gonads in successive segments with the testes in front of the ovaries (G.I-G.IV Fig. 1). The segmental position of the gonads varies but this is a secondary condition, not necessarily derived from a multigonadal ancestor. Eleven of the 18 living haplotaxid species have all eight gonads whereas this condition is only found in two relatively primitive species of the Lumbricida. The male and female gonoducts of the earliest oligochaete may be supposed to have been very similar, just as they are in the haplotaxids. In all other families the male ducts become larger and more elaborate than the female

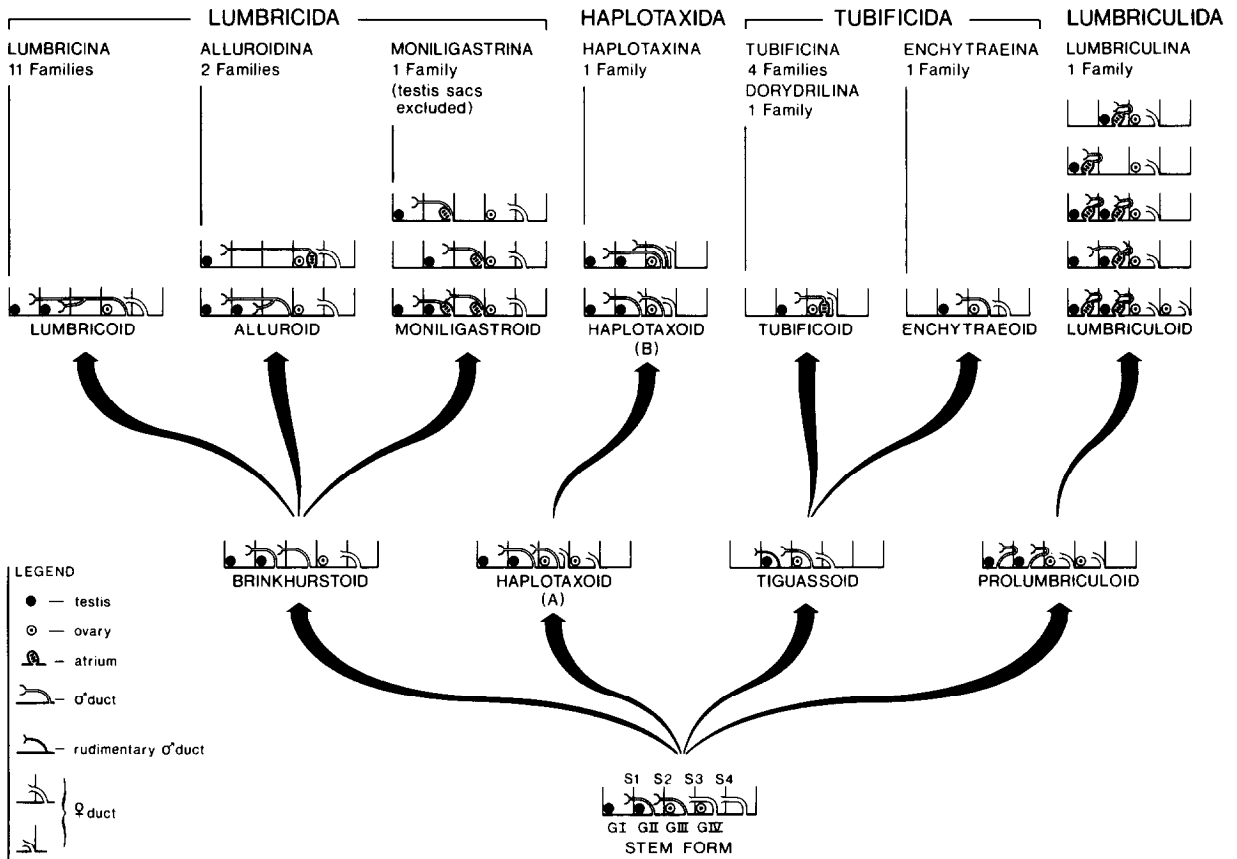


Fig. 1. Phylogeny of the Oligochaeta based on gonad sequence, form of gonoducts and presence of atria (from Brinkhurst, 1982). Dorydrilidae should be shown as equivalent to Tubificoid and Enchytraeoid stems (but see Fig. 2 and Brinkhurst, 1984).

ducts. The latter tend towards the prosopore condition but interestingly retain the plesiopore condition in many supposedly ancient families, including the Enchytraeidae. The male ducts develop some form of sperm storage and feeding organs, which are termed atria (with or without prostates) in microdriles and prostates in the megadriles. The haplotaxids are the only group that totally lacks such structures, the male ducts opening to the exterior via very short ectodermal invaginations that are the precursors of the atria/prostates.

The opisthoporous state of the megadrile male ducts is quite clearly secondary and I now believe that this is true of the prosopore state of the Lumbriculidae (Brinkhurst, 1982). Modern representatives of earlier, less specialized, intermediate forms between the octogonadal haplotaxids and two of the three other Orders (which show various patterns of gonad reduction) are to be seen in *Haplotaxis brinkhursti* and *Tiguassu*. It is not surprising to find that such living forms show advanced characteristics as well as traces of their ancestry. The latter for example has a proboscis and a simple gizzard but still has the eversible pharyngeal roof of all aquatic oligochaetes. It reveals its ancestry by retaining non-functional male funnels in G.I. with ducts in G.II, but there are no testes in G.I. Similar rudimentary organs are found in many Lumbriculidae in which the presence of non-functional atria in G.I. assures us that the two pairs of male ducts associated with atria in G.II must have been derived from the prosopore condition. It is for this reason that the Dorydrilidae can never have been derived from the lumbriculids, as their atria lie in G.III in the plesiopore condition only found in the Tubificida (Fig. 2). All other superficial similarities to the Lumbriculidae are of necessity convergent (Brinkhurst, 1984).

The rearward extension of the anterior pair of male ducts in *Haplotaxis violaceus*, resulting in both pair of male pores opening in G.III, is evidence that at least one living haplotaxid shows some signs of the development of the opisthopore condition. The direct ancestor of the opisthopores would have had a different gonadal reduction sequence though as the ovary of *H. violaceus* is in G.III not G.IV as it is in the Lumbricida. Traces of a prosopore state can be seen in haplotaxids like *H. smithii*, *H. hologynous*, and *H. ornamentus* in which the second pair of male ducts open close to the anterior border of G.II if not in G.I.

While many college texts refer to the similarity of oligochaete and polychaete setae, there has been very little careful comparison of them. Brinkhurst (1982) reviewed setal form and function and revealed, among other things, that most of the Enchytraeidae, as well as all of the Lumbricida and Lumbriculida, have the lumbricine setal condition (Fig. 3). These are usually simple-pointed, but they may be bifid with simple upper teeth in many lumbriculids. Other aquatic families usually adopt fully bifid rather than simple-pointed setae and more complex setae are found in the dorsal bundles of many species. This suggests a substrate crawling antecedent with long dorsal setae for protection from predators. The multiple simple-pointed setal condition is found in few Tubificina (the ancient *Telmatodrilus* shows such a tendency) and in the recent perichaetine earthworms. There is no sign of it in forms I consider to be ancestral by virtue of other anatomical and zoogeographic features, whereas Timm (pers. corresp.) sees the ancestral annelid as essentially perichaetine.

The wide taxonomic distribution of the lumbricine state indicates it is the basic pattern which conforms with the theories of Clark concerning fundamental annelid form. The most useful disposition of a few setae in an ancestral active burrower might well be at the 'corners'; a further modification to allow for slight dorso-ventral specialization would permit surface crawling through loose particles. So widespread a phenomenon as this setal positioning cannot be seriously attributed solely to the last pale shadow of the former glory of parapodia without reference to selective advantage to maintain it. Polychaete setae are not in fact similar to oligochaete setae in form, number or disposition (Brinkhurst, 1982).

Setae in the Haplotaxidae demonstrate that the family has within it the capability of forming all of the setal types of oligochaetes. While most species have lumbricine setae, there are paired, simple-pointed and bifid setae in *H. glandularis* (foreshadowing the situation of ventral setae in the Phreodrilidae) and bifid, if not pectinate, setae in *H. denticulatus*. The setae of the familiar *H. gordioides* and similar *H. heterogyne* are highly modified for life in coarse substrates (see also *Grania*, Enchytraeidae). A recently discovered South American haplotaxid has somatic setae like those of *H. gordioides*, but also has hair-like genital setae

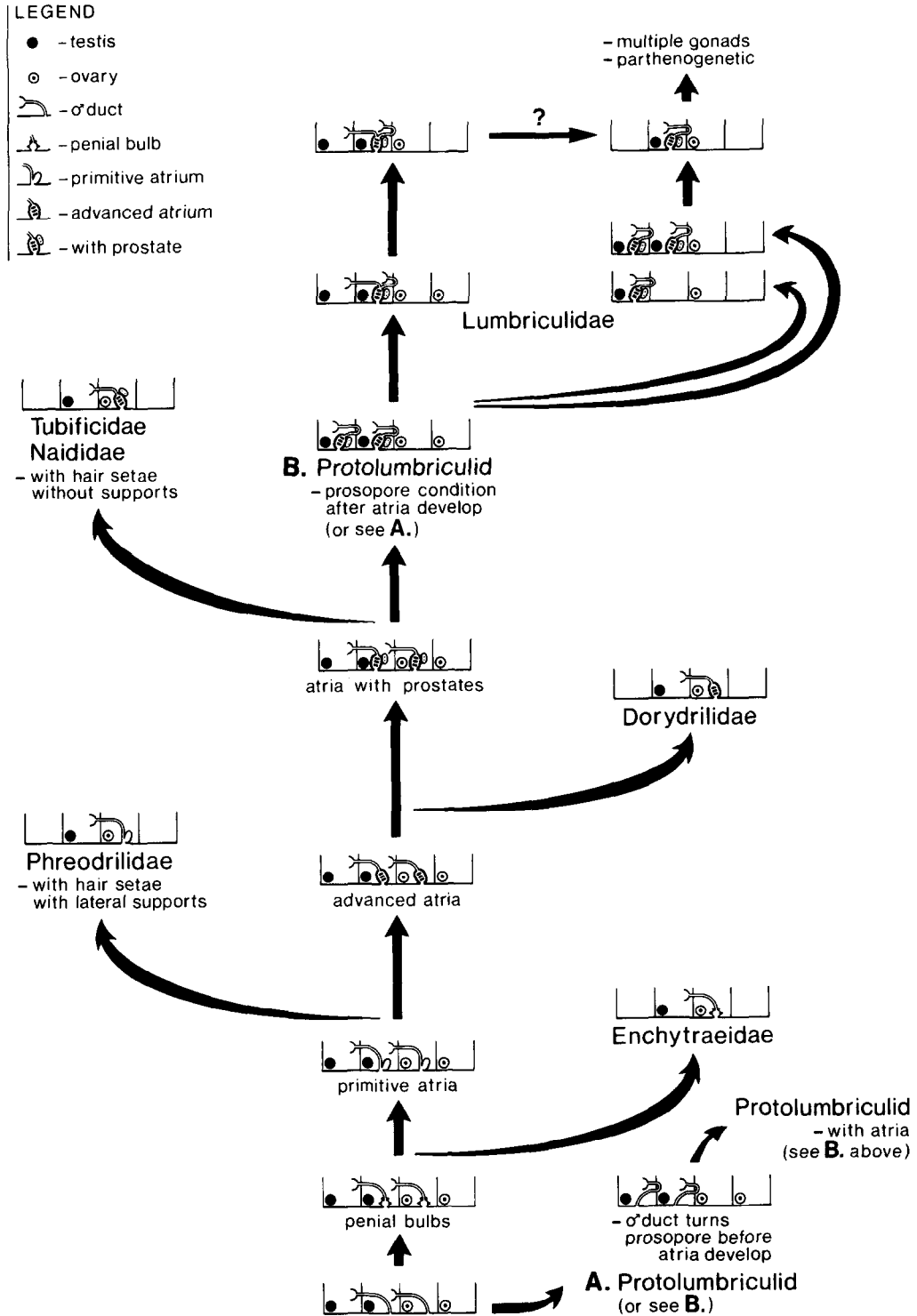


Fig. 2. Alternative origins of Lumbriculidae. If alternative A is adopted, all forms above the haplotaxids and lumbriculids should have gonads reduced to GII · GIII. If alternative B is adopted atria and prostates are evolved once, the main stem retains paired setae and, therefore, the hair setae of phreodrilids are derived independently from those of the naidids/tubificids, the lumbriculids can be derived from a theoretical proto-dorydrilid. (See also Brinkhurst, 1984 for modified version.)

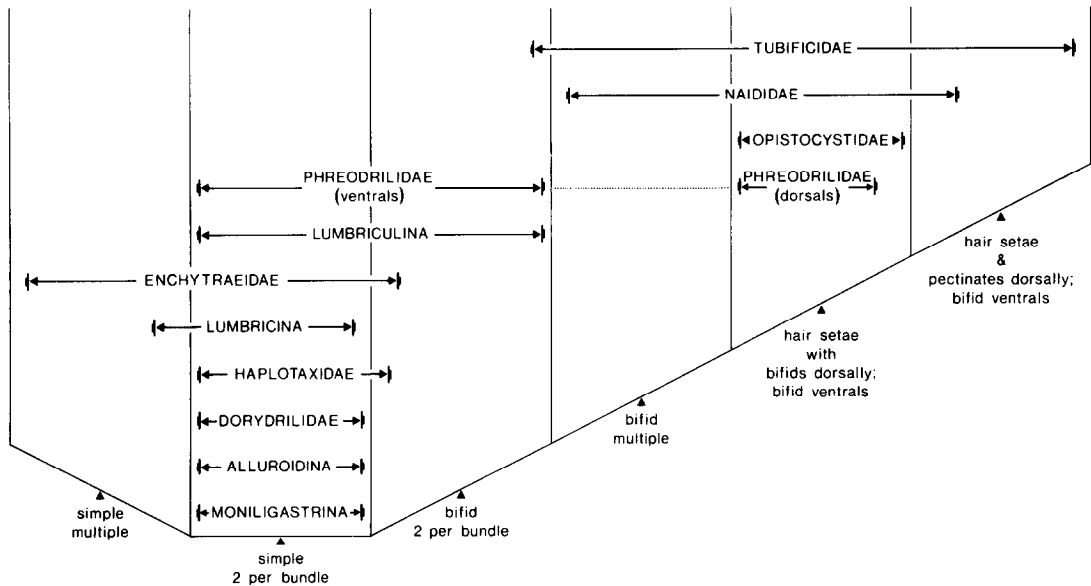


Fig. 3. Distribution of setal form and number in oligochaetes (from Brinkhurst, 1982).

which, while not ancestral to those of the Tubificida by any stretch of the imagination, demonstrate that the single cells that secrete setae can form a hair-like structure even within the haplotaxids (Brinkhurst, unpubl.). Hair setae with minute bifid tips in tubificids and naidids suggest there is no fundamental difference in form in any case.

The extreme anatomical simplicity of the other organ systems of the haplotaxids render them acceptable as ancestors of the other three orders. An independent study of nephridia for instance, led to the suggestion that the haplotaxids were the stem forms of oligochaetes (see Cekanovskaya, 1962). The haplotaxids have the discontinuous global distribution pattern of a very ancient group, and occupy refuge habitats in centers renowned for their relic faunas, such as Tasmania. Most other families clearly date from after the break up of continents and are northern or southern in origin. In order to emphasize the stem position of the haplotaxids my scheme differs from more recent classifications in erecting the Order Haplotaxida for the modern descendents of the stem group.

There is no impediment to the acceptance of the Haplotaxidae as modern descendents of the ancestors of the oligochaetes, not too far removed from the descendents of all annelids, which were themselves derived from unsegmented coelomate burrowing forms represented to-day by a few scattered

groups like the sipunculids. It should be emphasized that no modern living form is here seen as a direct antecedent to other modern living forms. In many early treatments there is an unfortunate tendency to expect the living forms to be derivable one from another with the only concessions to the possibility of extinction being to create theoretical intermediate types that could add or delete segments at will in order to pass from one form to another. No evidence for the existence of such intermediate forms was ever presented and the concept of the need for selective advantage of every new development was ignored. These problems also tainted the earlier views of simultaneous evolution of the coelom and segmentation, whereas such pitfalls were avoided by Clark (1946). His brilliant exposition of the independent origin of both leads us to the presumption of a simplified ancestor to both oligochaetes and polychaetes with earthworm-like anatomy apart from its reproductive system (Brinkhurst, 1982).

Evolution within the Tubificida

It is necessary to touch on one or two implications of this theory to the evolution of the various families within the Tubificida.

The Enchytraeidae are now seen to progress from

very simple forms with lumbricine setae and simple glandular precursors of the atria to the very advanced aquated *Propappus* with its bifid setae and well developed atria. *Propappus* has been claimed as derivative of an enchytraeid ancestor to fit the concept that the family must have been derived from the Tubificidae. While there is no intrinsic evidence yet available for reading the evolutionary sequence in one direction or the other, the common and widespread form of the enchytraeids should be regarded as basic rather than the rare and peculiar as expressed in *Propappus*. Recent evidence (K. Coates, pers. comm.) shows that *Propappus* can no longer be classified with the Enchytraeidae.

The Phreodrilidae/Opistocystidae seem to be (?earlier) southern hemisphere parallels to the originally northern Naididae/Tubificidae. The ventral setae of phreodrilids are primitive, as are their atria. These more nearly resemble megadrile prostates in that the male ducts do not open through them, and they lack externalized prostate cells. Elaborate penes have developed here as well as in the tubificids and the lumbriculids, evidence that such ectodermal invaginations as penes, atria and megadrile prostates have been evolved independently many times. The Opistocystidae are a very poorly known family.

The Dorydrilidae, formerly seen as the link between the Tubificidae and the lumbriculids en route to the haplotaxid-megadrile line, are clearly tubificine. Their atria lie in G.III which cannot be derived from nor lead to the lumbriculid condition, their gonad sequence is reduced. Other similarities are quite clearly convergent, but they were classified as a suborder along with the Enchytraeina and Tubificina (Tubificidae, Naididae, Phreodrilidae, Opistocystidae) by Brinkhurst (1982). The ancestral form interpolated between points of origin of the Phreodrilidae and Dorydrilidae (labelled 'advanced atria') must be classified as a dorydrilid and so the direct ancestors of that family might well lie along the main line of descent of lumbriculids from a proto-tubificine condition if we accept option B for the evolution of the lumbriculids (Fig. 4). This would then be in accord with the views of S. Hrabě as expressed elsewhere in this volume except that the various tubificine groups would have (independently) reduced the gonad series, as shown in Fig. 2. (Brinkhurst, 1984 elaborated this.)

The Naididae and Tubificidae are closely related,

with the former showing some advanced adaptations to aquatic life, such as locomotory methods, eyes and more forms of gill than in the other family, whereas all of the tubificids are obligate burrowers with more highly developed male ducts. If hair setae were a defensive adaptation in forms that gave rise to the four families in the Tubificida that still possess them, it is difficult to see the adaptive significance of the dorsal hair setae in those forms such as the tubificids and the naidid genus *Dero* that burrow. Some successful genera such as *Limnodrilus* totally lack hair setae, as do some species within genera that otherwise possess them (e.g. *Potamothrix*). We cannot assume that the tubificids are caught in the act of disposing of their hair setae as they have existed for far too long for this still to be an ongoing process. As species with and without hair setae successfully co-exist in large numbers, it is hard to see any adaptive significance to their possession. Those species which possess them may be represented by forms that lack them in certain biotopes, particularly those in which the water has a high conductivity (see *Tubifex* and *Ilyodrilus*). It is Timm's contention (1981) that burrowers lacking hair setae represent an important evolutionary step between the species with complex dorsal setae and the lumbricine types that are derived by further degeneration of the setal equipment. It is even suggested that this takes place by neoteny, a process commonly evoked in early phylogenetic speculations when no particular selective advantage could be identified. There is no evidence that immature stages of Tubificida possess earthworm-like setae and so Timm's suggestion is untenable. Secondary simplification clearly does take place, as evidence by the setae in *Clitellio* and the Phallo-drilinae.

The Aeolosomatidae and their allies (Class Aphanoneura) must be similarly derived from the ancestral annelid pool or perhaps not far from the archannelids, a specialised polychaete group with which they have much in common. This may again be regarded as convergence as they are anatomically totally distinct from the Oligochaeta, even to the point of lacking a clitellum, and they are no longer included within that Class. The ventral reproductive gland of the aeolosomatids is not a clitellum in any sense of the word, although it should not be referred to as a copulatory gland either (see Brinkhurst, 1982).

Comparison with the alternative hypothesis of Timm

The views of Timm (1981 and pers. commun.) are summarized in Figs. 4–6. Space does not permit a detailed consideration of this scheme beyond pointing out the salient criticisms of it in light of the haplotaxid origin theory. The diagrams will enable a detailed comparison to be made. Referring first to Fig. 4 I would suggest that there is little or no evidence of successful freshwater polychaetes that could provide an ancestor to the Tubificida. Apart from the reversed polarity of the evolution in the Enchytraeidae and the doubtful positioning of the Lycodrilidae* in terms of our ignorance of that family, the rest of the developments within the Tubificida do not require further comment. Both

* The Lycodrilidae are now seen to be attributable to other extant families (Brinkhurst, in press; Can. J. Zool., 1984).

schemes accept the Haplotaxidae as ancestors of the Lumbricida. The ancestor of the Lumbricomorpha postulated by Timm must be rather similar to my protohaplotaxid ancestor, which I also see as giving rise to the Lumbriculidae. The supposedly 'extraordinarily variable, shattered morphology of the genital system' of lumbriculids and moniligastrids referred to by Timm (1981) and earlier authors (e.g. Yamaguchi, 1953), depends upon undue focus on a few parthenogenetic species in the former and misunderstanding of the latter (see Brinkhurst, 1982; Jamieson, 1977). The Dorydrilidae, however, cannot be derived from the Lumbriculidae by any stretch of the imagination and the leeches are normally derived from the Lumbriculidae (see, e.g., Clark, 1969), in contrast to their position in Timm's scheme. They have recently been classified as Hirudinoidae (Richardson, 1970).

In Timm's theory the terrestrial species are all said to have lost the atria of the Tubificida, which

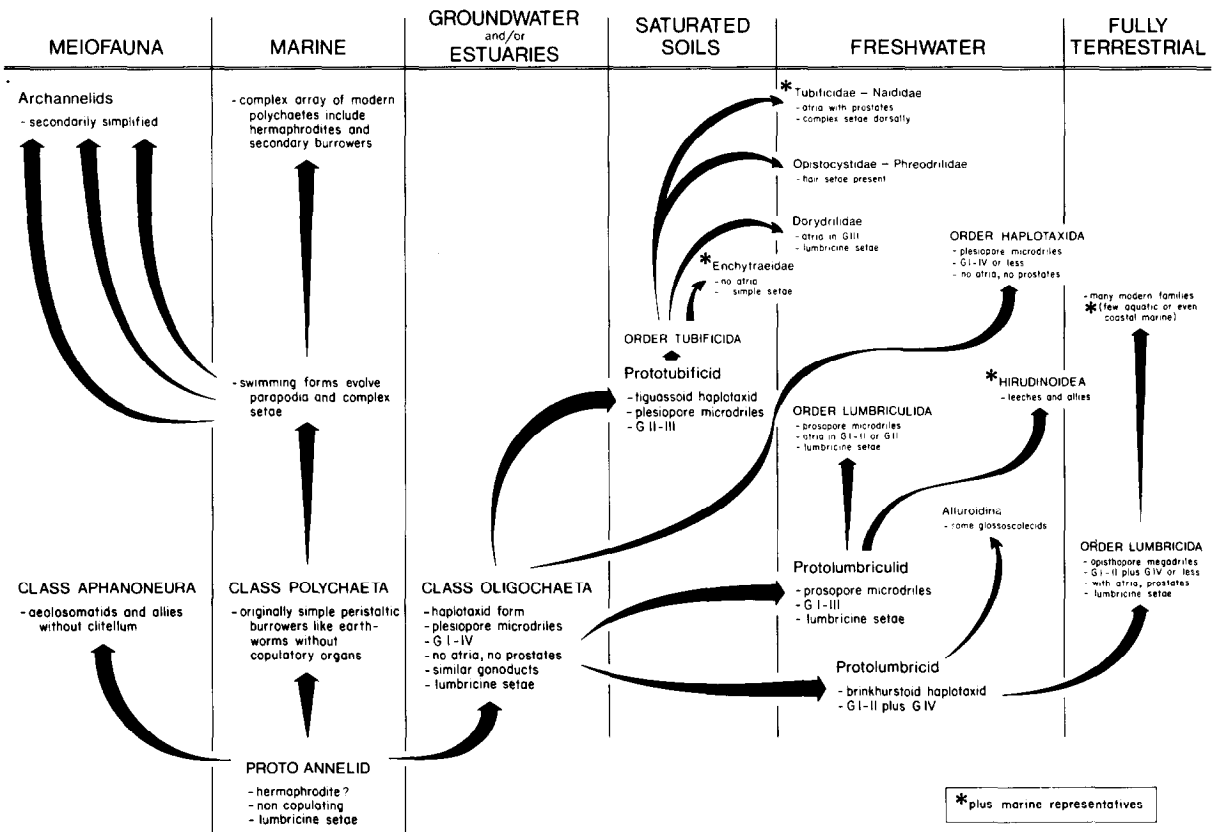


Fig. 4A. Oligochaeta phylogeny: Haplotaxid origin theory (some details such as marine enchytraeids and tubificids, freshwater polychaetes omitted where clearly secondary).

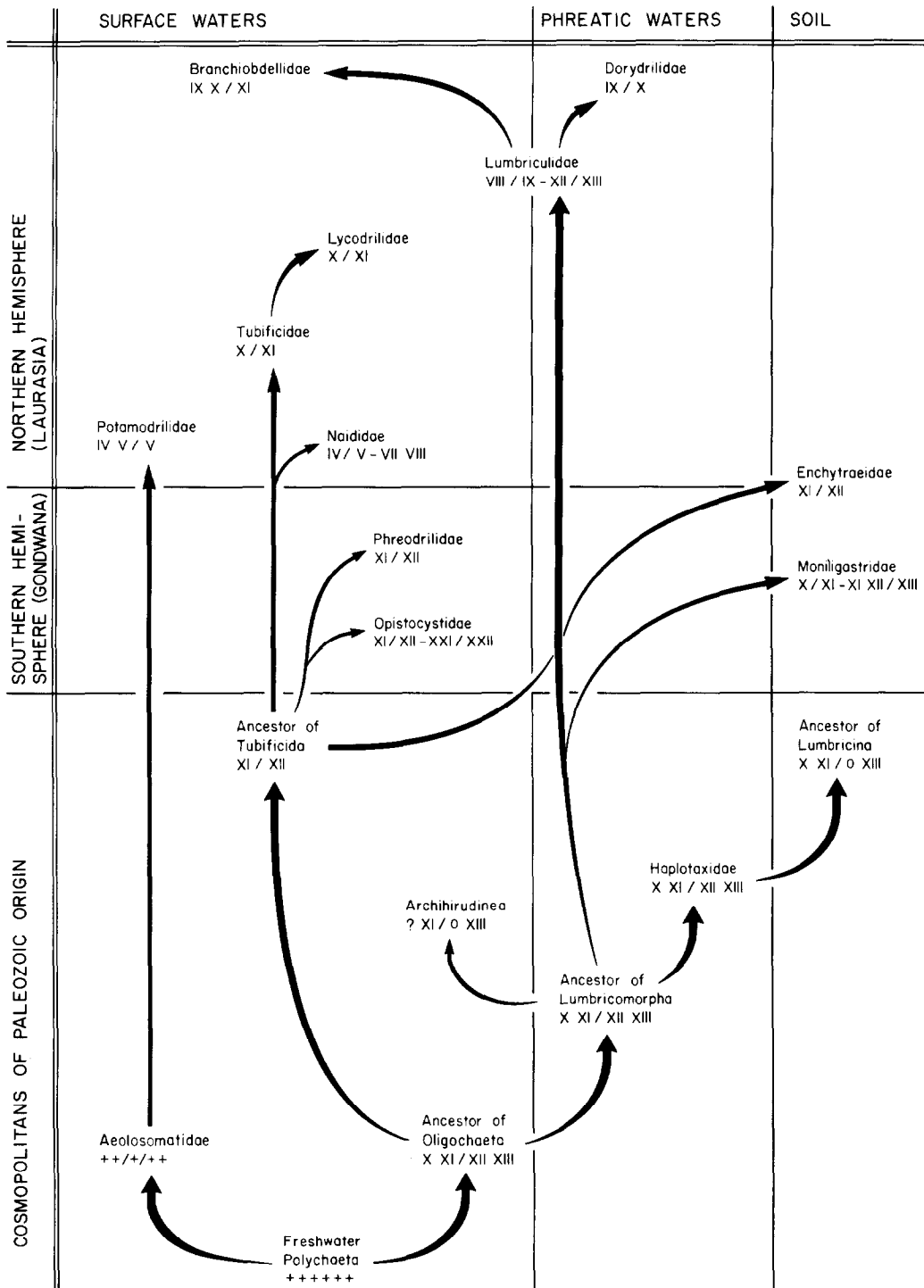


Fig. 4B. Oligochaete phylogeny: Theory from Timm (1981).

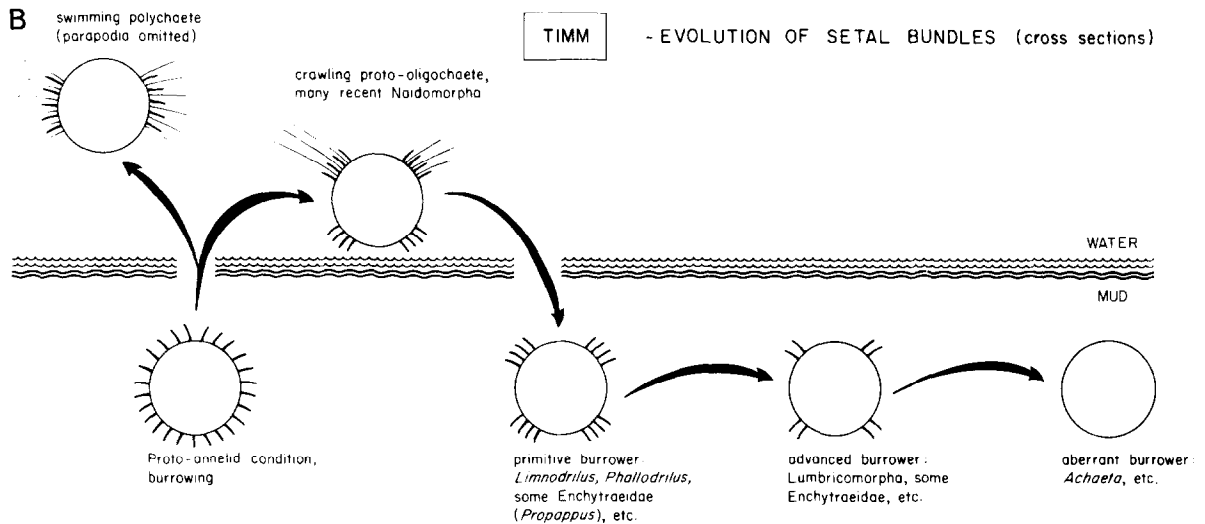
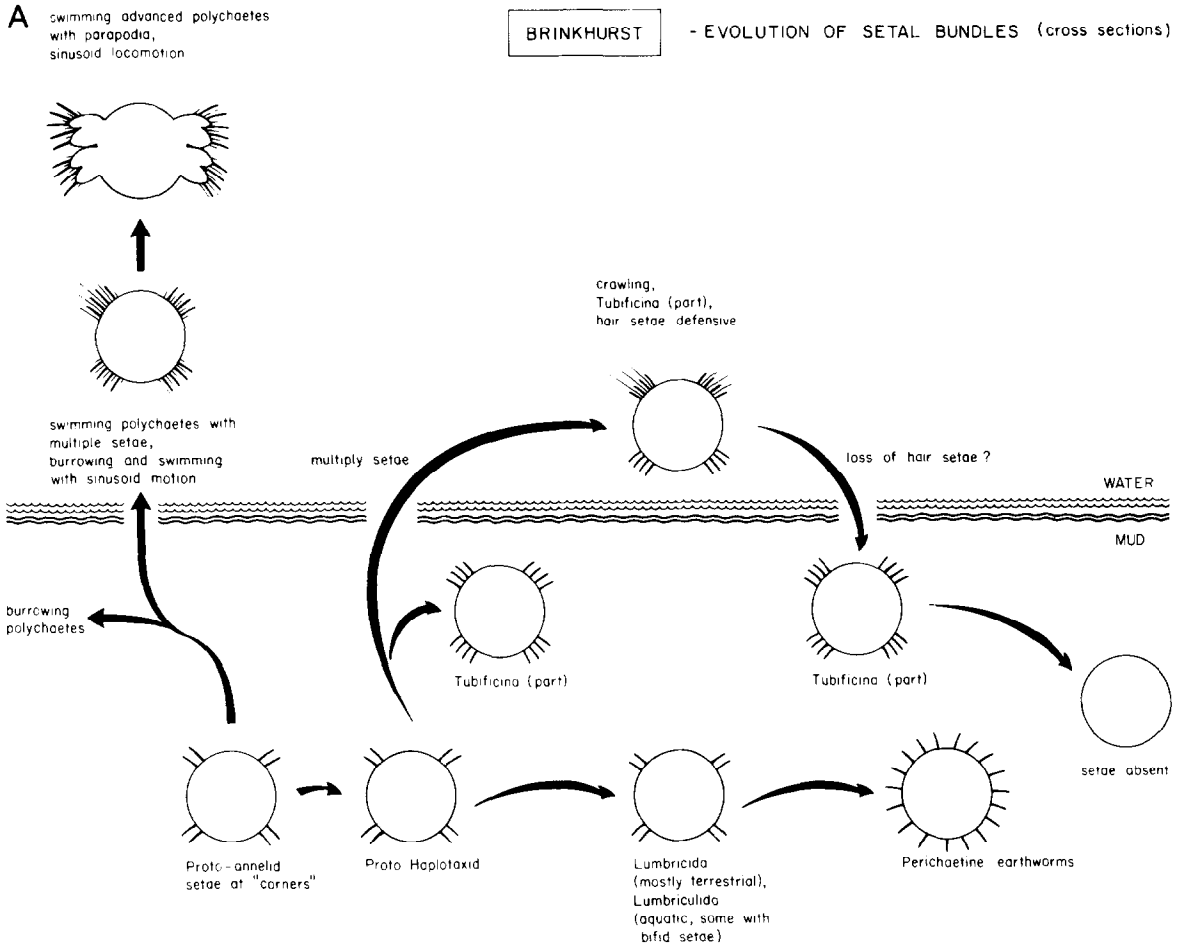


Fig. 5A. Comparison of theories of evolution of setal bundles: Haplotaxid origin.

Fig. 5B. Comparison of theories of evolution of setal bundles: Theory of Timm (pers. commun.).

process is seen 'in progress' in the enchytraeids. This ignores the evolution of the many forms of prostates in megadriles which are functional analogues of the atria in microdriles. The atria/prostates are even present in a simple form in the Lumbricidae and are only absent in haplotaxids. In fact, Timm makes relatively little use of the evidence based on reproductive organs as preference is given to the arguments based on the origin of oligochaete setae from those of polychaetes.

The two theories in regard to setal evolution are documented in Figs. 5 and 6. I would claim in support of my views that they are more parsimonious

than those of Timm, they accept the wide taxonomic distribution and hence antiquity of the lumbricine condition, they agree with the general notion that the perichaetine state is a rare experiment in extant megadriles and that tubificids do not have larvae with lumbricine setae as required by the concept of neoteny. The small upper tooth of the bifid setae of many species in the (unrelated) Tubificidae and Lumbriculidae may have much to do with the nature of the substrate the species inhabits but cannot seriously be viewed as representing a stage in the conversion of bifid to simple-pointed setae as Timm contends. Furthermore, there is little

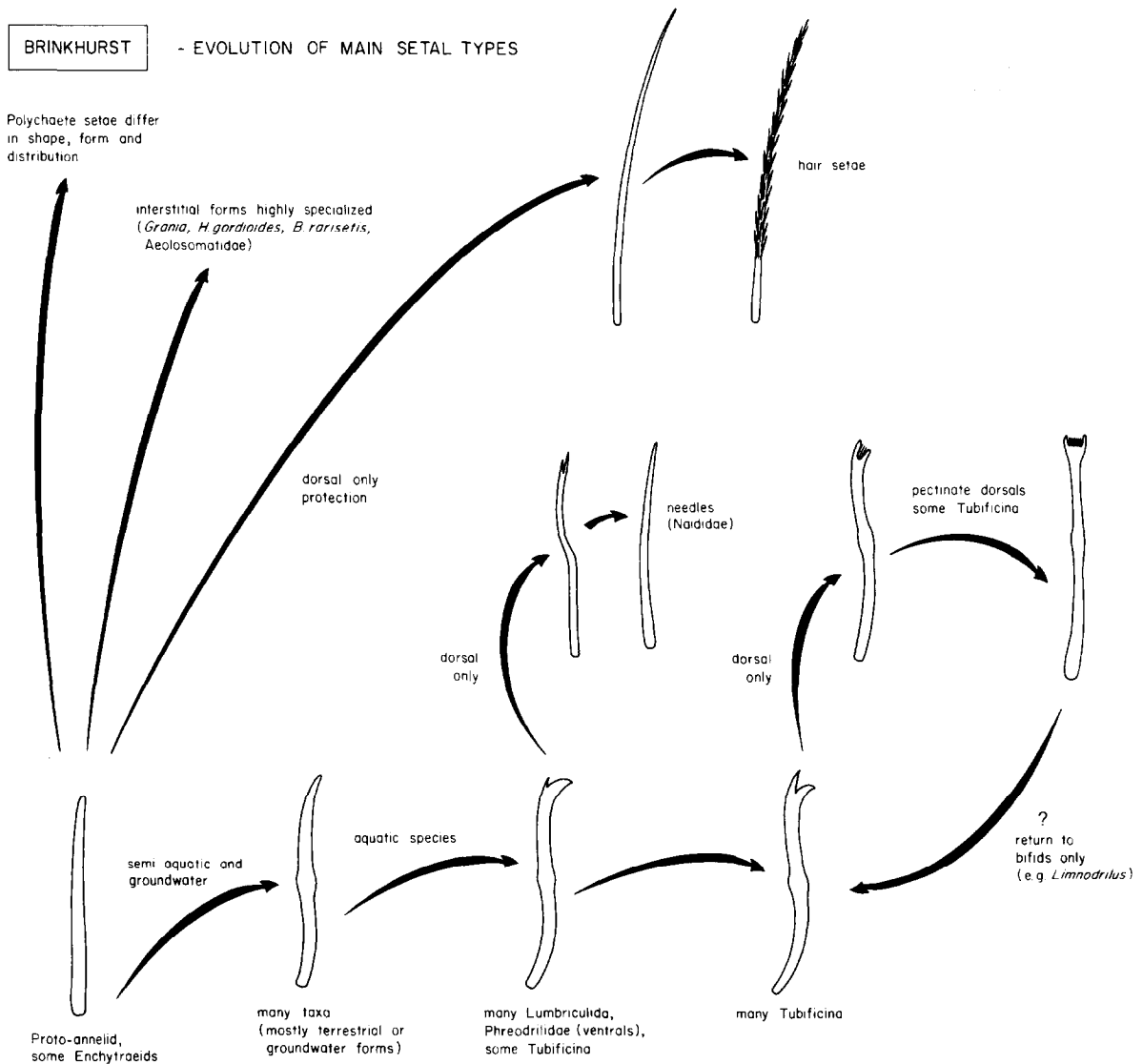


Fig. 6A. Comparison of theories of evolution of setal form: Haplotaxid origin.

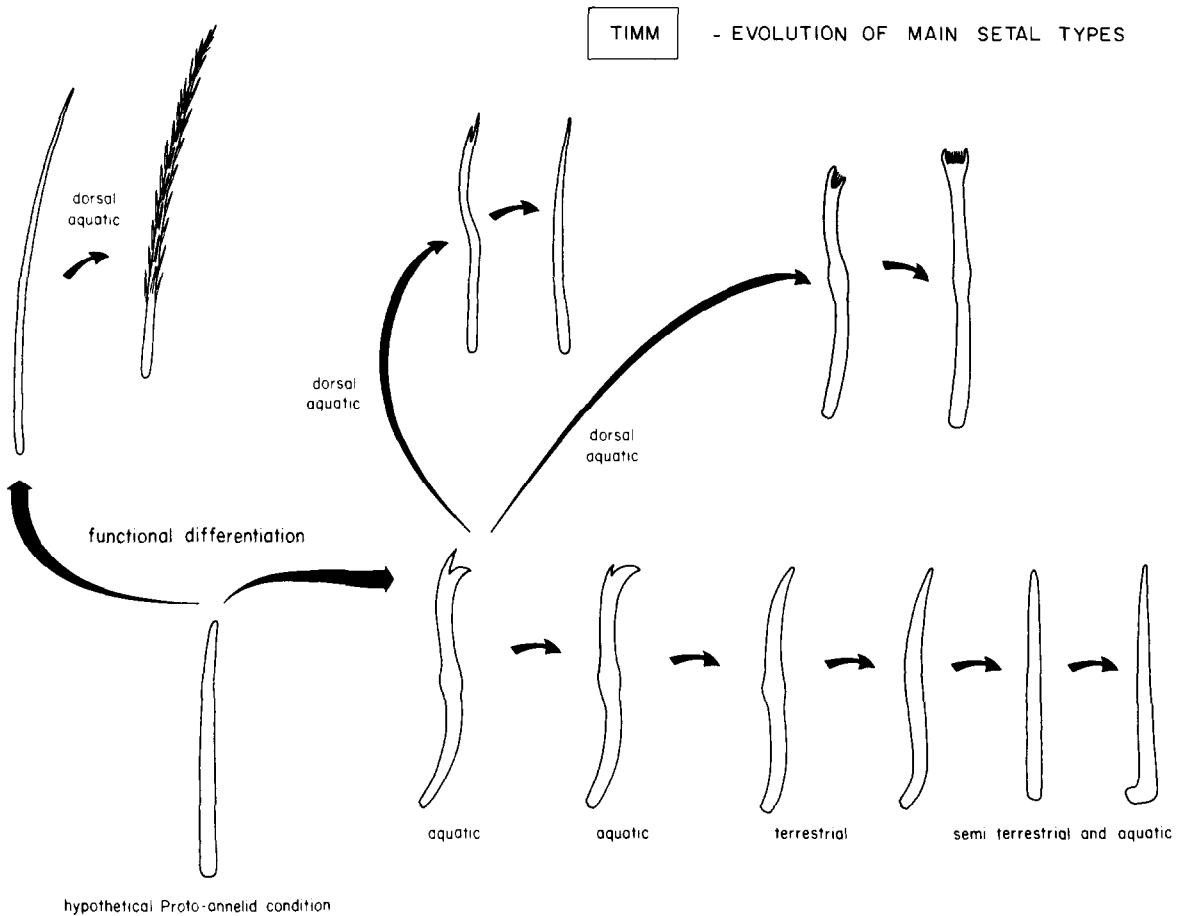


Fig. 6B. Comparison of theories of evolution of setal form: Theory of Timm (pers. commun.).

evidence of the octogonadal form with hair setae postulated by Timm, whereas there is evidence of the possible existence of the intermediate forms claimed by me. In fact, Timm's whole hypothesis is compromised from the outset by the assumption of a polychaete ancestry for hair setae, and that the paired lumbricine arrangement is an echo of the presence of parapodia. Clark has shown that parapodia interrupt the cylindrical body wall musculature and that they must be an adaptation for swimming in a form that is no longer dependent upon peristaltic burrowing. The oligochaetes retain the original intact cylindrical body wall, and I see the lumbricine setal placement as advantageous rather than accidental in an early annelid that became segmented in response to the burrowing habit that preceded all the later annelid life styles.

I would claim that the haplotaxid origin theory is not compromised by any unsupportable assumptions, that it fits all of the known facts, including

those fragments of evidence derived from traces of former reproductive structures among the lumbriculids and others and that it is based on the range of gonadal and setal plans found in the modern descendents of the original pool of haplotaxid ancestral forms. It is a more parsimonious theory than the alternative and, while it relies less on evidence of geological history than that proposed by Timm, it does not seem to be in conflict with that evidence.

Acknowledgements

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