# Evolution in the Annelida

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The aquatic Oligochaeta as well as the earthworms can be derived from ancestors closely resembling living Haplotaxidae. Four of the five required intermediate forms are represented by living haplotaxid species. The polychaetes are also thought to be derived from simple earthworm-like forms. These concepts are in accord with recent locomotor theory separating the evolution of the coelom and segmentation as a two-step process related to sustained burrowing activity, as opposed to the earlier complex of theories involving the simultaneous evolution of coelom and segmentation. Unsegmented coelomates are seen as representatives of an intermediate condition between acoelomates and segmented coelomates instead of problem phyla derived by degeneration of segmented ancestors.

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Les oligochètes aquatiques, comme les vers de terre, peuvent être dérivés de formes ancestrales qui ressemblent de très près aux Haplotaxidae actuelles. Quatre des cinq formes intermédiaires requises sont représentées par des espèces vivantes d'Haplotaxidae. Les polychètes semblent eux aussi dérivés de formes simples semblables à des vers de terre. Ces concepts sont en accord avec la théorie locomotrice récente qui considère l'évolution du coelome et la segmentation comme un processus en deux temps relié à l'activité fouisseuse plutôt qu'avec les théories précédentes qui supposent la simultanéité de l'évolution du coelome et de la segmentation. Les coelomates non segmentés sont considérés comme des représentants d'une condition intermédiaire entre les acoelomates et les coelomates segmentés plutôt que des phylums problèmes issus, par dégénérescence, d'ancêtres segmentés.

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## Introduction

Theories of the evolution of the Annelida have traditionally been based on the proposition that the marine polychaetes gave rise to the freshwater and terrestrial oligochaetes. Textbooks commonly cite the fact that the setae of earthworms are found in two pairs on each side of every segment as evidence of their derivation from biramous parapodia rather than as a feature of adaptive significance in relation to burrowing. Some very simple polychaetes were termed Archiannelida in the belief that they provided antecendents for both the more complex polychaetes and the freshwater oligochaetes. The latter were said to have retained some of the complex setae of their ancestors while developing reproductive organs capable of sheltering the gametes from the rigours of the hostile freshwater environment. The freshwater oligochaetes then supposedly gave rise to the Haplotaxidae, a family of simple earthworm-like forms with reduced setae and rudimentary male ducts. All oligochaete biologists agree that the Haplotaxidae provided the ancestors of the earthworms, and this last step in the evolutionary sequence has recently been supported by Jamieson (1978) in a phylogenetic and phenetic study.

The classical interpretation of annelid phylogeny outlined above has most recently been restated by Timm (1981) and is the dominant theme in the publications of most early oligochaete biologists, including Michaelsen (1921). This line of thought was modified by Michaelsen (1930) who concluded that two alternative systems were equally possible. In the first system, the Haplotaxidae, a family without complex setae, was thought to be ancestral to both terrestrial and aquatic lines of oligochaete descent. The alternative was to suppose that the oligochaetes were polyphyletic, with different ancestors for the terrestrial and freshwater forms. Although Michaelsen suggested that there was insufficient evidence to permit a choice between these alternatives at the time, he proceeded to classify the Haplotaxidae with the earthworms despite the fact that they share more anatomical characteristics with the aquatic species than with the terrestrial ones, and so from that date on they have been omitted from consideration as aquatic oligochaetes. The two most important subsequent phylogenetic accounts of the oligochaetes (Stephenson 1930; Yamaguchi 1953; reviewed and supported by Clark (1969)) also identified an ancestor to the aquatic forms that had four sets of paired setae per segment, but the Haplotaxidae were excluded from both schemes, presumably because of Michaelsen's classification.

Brinkhurst and Jamieson (1971) concluded that the Haplotaxidae could be regarded as the modern descendents of the stem forms of all of the oligochaetes and that these and the polychaetes both arose from a very simple earthworm-like annelid lacking discrete gonads. Their view was supported independently by Fauchald (1974)

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in reference to a possible polychaete ancestor. Jamieson (1978, 1981*a*) has modified his earlier views to allow for the separate evolution of the main aquatic line of descent from that of the earthworms. Some of the other evidence presented by Brinkhurst and Jamieson a decade ago needs to be reexamined, especially as some highly significant new haplotaxid species have been described. In addition, the nature and distribution of the setae of aquatic oligochaetes was not adequately dealt with in the earlier account and it seems appropriate to correct this omission here, in view of the publication by Timm (1981).

The phylogeny advanced here is heavily influenced by the publications of Clark (1964, 1969, 1978) who provides functional rather than architectural hypotheses for the derivation of metazoans in an orderly sequence of increasing complexity from diploblasts to triploblasts, acoelomates to coelomates, unsegmented to segmented forms. This contrasts with the awkward necessity of regarding unsegmented coelomates, such as sipunculids, as being degenerate annelids, or even worse, the Platyhelminthes as being similarly derived. It is only fair to point out that this critical work was, until recently, not available to Dr. T. Timm (personal communication).

Some of the growing volume of ultrastructural work on selected metazoans does not seem to be influenced by the views of R. B. Clark, as evidenced by the inclusion of the unsegmented acoelomate Lobatocerebridae in the Oligochaeta by Rieger (1980). These worms are more obviously allied to the Platyhelminthes if one makes no evolutionary assumptions in classifying them. The ultrastructural work on oligochaetes has been reviewed by Jamieson (1981*b*) and will not be discussed here. This is partly due to the author's unfamiliarity with the field, but mainly because it is based on work with only a relatively few species. In the following account all of the characteristics used are fully described for all known species, and no extrapolation from examples is necessary.

The phenetic approach employed by Jamieson (1978) is also avoided here for similar reasons. The strength of Jamieson's effort with the earthworms is that many anatomical characteristics could be included, but as few aquatic species have been described in such detail, it would be necessary to generalize from a few specific accounts in adopting this approach. This difficulty is accepted in phenetic studies because it would be impossible to include every taxon in such a complex analysis, but the weakness of the approach is also rooted here. For example, Jamieson (1978) chose a single *Haplotaxis* species to represent the family, but the phylogenetic approach used here enables me to refer to highly significant variations in certain anatomical characters in the family as a whole.

The account will begin with an introduction to the taxonomy, anatomy, and distribution patterns of the oligochaetes for the sake of the nonspecialist. The reproductive system will then be considered, and a phylogeny erected based only on the available facts in so far as preconceptions can be identified and avoided. The setae will then be considered, and an independent phylogeny erected. These will be compared, and the resulting single phylogeny will be tested against previous phylogenies on the basis of parsimony. This approach is an attempt to follow the suggestion outlined by Orrhage (1973) in his critique of "single character" phylogenies.

## Anatomy, taxonomy, and distribution of oligochaete families

In this brief account I intend to present only the most relevant information on the reproductive system, setae, and distribution with very little reference to other characteristics used in more formal familial definitions.

Two major groupings of oligochaetes can be recognized, the microdriles and megadriles. The microdriles have large yolky eggs, a clitellum only one cell thick in the region of the gonopore, a thickened roof to the pharynx that is everted during feeding, and lateral lines, but no typhlosole, gizzard, or digestive glands (other than septal glands) anteriorly, no subneural blood vessel, and a reduction in number of anterior nephridia. The megadriles, primarily the Lumbricina (see below) are characterized by the opposite of these features (i.e., small eggs, multicellular clitellum, with typhlosole, etc.).

Each gonadal segment in an oligochaete contains a pair of gonads and a pair of ciliated funnels through which mature gametes reach the gonoducts and then the exterior. All of the living oligochaetes can be derived from an octogonadal form (Fig. 1), the few multigonadal species having all been recognized as parthenogenic forms in which there is considerable intraspecific variability in both the number and disposition of gonads. The different families exhibit varying degrees of gonad reduction. A complex terminology employing prefixes holo, pro, and meta associated with the roots "androus" or "gynous" is traditionally used in referring to the resulting patterns, but I will refer to the testicular segments as GI and GII, the ovarian segments as GIII and GIV, and the septa separating them as S1 to S4 (the respective use of roman and arabic numerals being standard practice).

While the sequence of gonads is constant, the basic segmental position of them in X–XIII may vary quite widely, usually by a forward shift of the series. I do not think this to be of any phylogenetic significance as the segmental position of the gonadal segments varies within some otherwise recognizable families. Such shifts can be induced by regeneration following damage

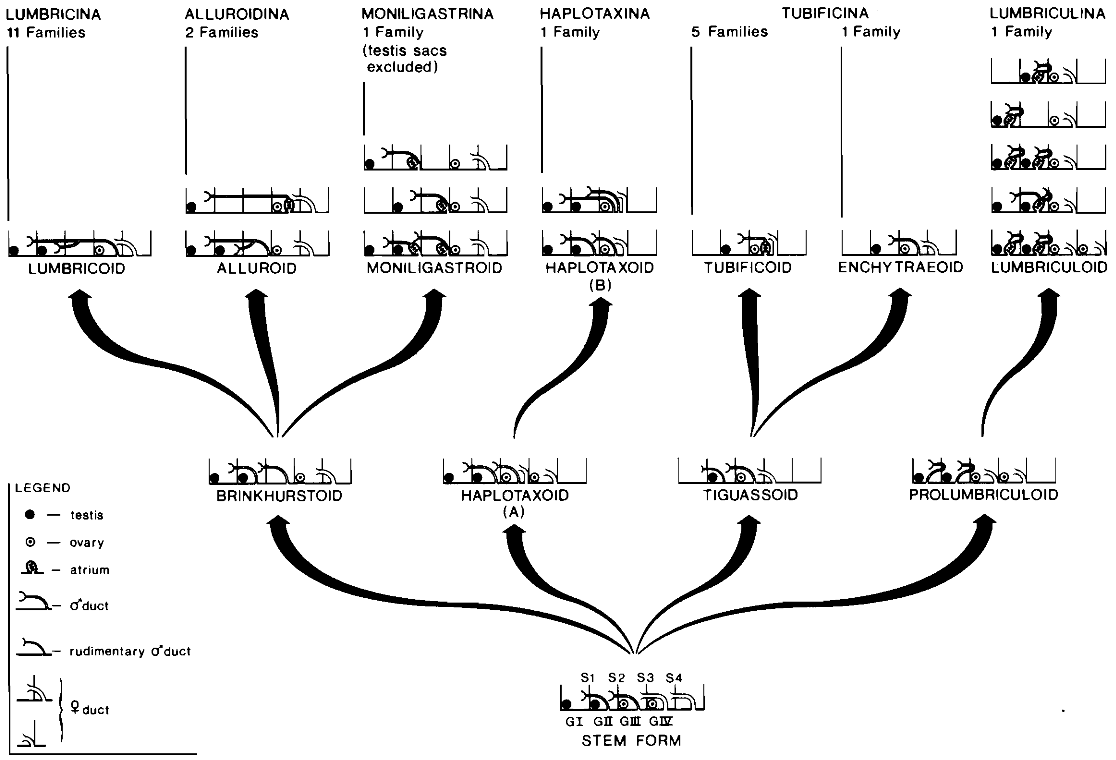

FIG. 1. Evolutionary scheme in oligochaetes based on reproductive system, displayed as sagital section of one side, anterior to left. GI–GIV are usually segments X–XIII but position depends on family. Moniligastrid testis sacs omitted for clarity.

or asexual reproduction or by reduction in the number of anterior segments demarcated during ontogeny. According to the alternative multigonadal ancestry concept, the modern families retain different gonadal segments of an original long series, which means that some segments would have been changed from testicular to ovarian. The gonoducts are composed of two elements: (*a*) the ciliated funnel that collects sperm from the coelom leading to a vas deferens that grows back from its septum to the body wall, and (*b*) a terminal part derived from an inversion of the body wall (Brinkhurst and Jamieson 1971). In most microdriles the latter is, in the male gonoduct, enlarged to form a storage organ, termed the atrium. The atrial lining (originally the ectodermal element of the body wall) is usually modified by the migration of the cell bodies through the muscle layers into the coelom, creating more space within the atrium for sperm storage and freedom for growth of the prostate gland so formed (Fig. 1). The male ducts may terminate in a variety of penial structures.

In the megadriles, the male ducts may be associated with similar inversions of the body wall, referred to as prostate glands (rather than atria and prostates), but they do not usually open into them. The degree of homology of megadrile prostates and microdrile atria has not been established, but as both are derived from body wall inversions, the issue may not be resolvable.

In many microdrile families, the male pore lies in the segment behind that containing the testis and funnel it serves, which is termed the plesiopore condition (Fig. 2). In the megadriles, the vas deferens penetrates two septa, at least, before reaching the male pore in the opisthopore condition. The prosopore condition is found only in the male ducts of one family.

Female gonoducts are much simpler than those of the males and are usually clearly plesiopore, but in some instances they approach the prosopore condition as they open in the intersegmental furrow immediately behind the ovarian segment. Little, if any, functional significance can be attributed to these shifts in the relative positions of funnels and gonads. Even in the prosopore condition, the funnels are supported by the posterior septum of the appropriate segment.

The number of paired spermathecae may match the number of male pores or may exceed them. They may be located in front of, behind, or actually in the gonadal segments, but no phylogenetic significance can be attached to differences in their number and location.

The arrangement of setae observed in ordinary earthworms is referred to as the lumbricine condition, in

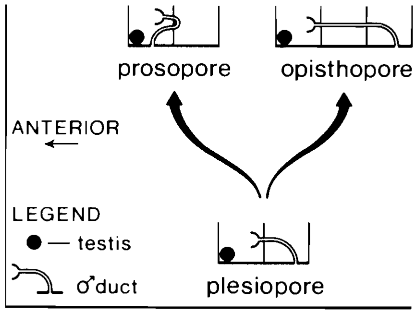

FIG. 2. Derivation of prosopore and opisthopore male ducts from plesiopore ancestor.

contrast to the more numerous and complex setae of freshwater forms. The addition of simple-pointed setae around the circumference of some earthworms is referred to as the perichaetine condition.

Some of the major characteristics of the various families will now be listed. For further details see Brinkhurst and Jamieson (1971) and Jamieson (1978).

*Microdriles*

*Haplotaxidae*

Formerly classed as Opisthopora because of their supposed ancestry to the earthworms, these moderately sized worms are in fact microdrile plesiopores with lumbricine setae. Both male and female ducts may be quite similar, and 11 of the 18 species are octogonadal. Gonad reduction often occurs by the loss of GIV but in two important species the reduction involves GIII and GI plus GIV, respectively. The family is discontinuously distributed, often in ground water, in ancient lakes or glacial refugia. Several occur in the Antipodes.

*Lumbriculidae*

A large family of prosopore microdriles with atria on the male ducts. All are holarctic apart from two peregrine forms known from the Antipodes, half of the species being restricted to Lake Baical. The setae are lumbricine, sometimes bifid. The gonads are sometimes all present, but the GIV pair are often missing; other reductions are observed as well as replication in parthenogenic forms.

*Tubificina*

Six families of microdrile plesiopores with only GII and GIII present (Figs. 1, 3), nearly all aquatic, with terrestrial forms in the Enchytraeidae. Atria are present on the male ducts except for the Enchytraeidae, in which the male ducts lead to ectal penial bulbs or masses. Setae are lumbricine (Dorydrilidae, some Enchytraeidae) or multiple per bundle, often complex. The Tubificidae and Naididae are large cosmopolitan families, the Opistocystidae is a small obscure family (Harman and Loden 1978). The Phreodrilidae, with a mostly southern hemisphere circumpolar distribution, have paired ventral setae but the dorsal setae are complex; the male ducts enter very simple atria basally. The families are separated on the basis of the segments occupied by the gonads and the spermathecae in addition to the characteristics already mentioned.

*Mixed Megadrile–Microdrile*

*Moniligastridae*

A family in which the testes are suspended in unique sacs that include the sperm funnels. Originally plesiopore, the male pores now lie at the bases of S2 and S3, GIII are lost and either pair of testes may be lost in addition. There are five genera, some with many species, limited to southeast and east Asia apart from some peregrine forms. While large earthworms with lumbricine setae, they are also largely microdrile in anatomy, with yolky eggs, thin clitella, anterior male ducts, and with male ducts opening jointly with the prostates (or atria), but gizzards and a subneural blood vessel are present (Jamieson 1977).

*Alluroidina*

Two very small families, Syngenodrilidae and Alluroididae (Jamieson 1978), the former monotypic, the latter with five species; four are African and two alluroidids are from Argentina. The setae are lumbricine but the other characteristics are microdrile. GIII are missing and so are GII in the Syngenodrilidae.

*Megadriles*

*Lumbricina*

The number of families in this suborder may vary from 4 to as many as 14 according to the latest count (Jamieson 1978) owing to differences in the rank accorded the groups of genera included, rather than to differences between authors concerning inclusions in the group. These are the true opisthopore megadriles with lumbricine setae and with only GIII missing in most of them. This group will be treated as a single unit throughout this discussion, as it has been long conceded that they are all derived from a haplotaxoid ancestor. The families Lumbricidae, Megascolecidae, and Eudrilidae will be more familiar than some of those created by the breakup of the Glossoscolecidae, in particular.

*Other familes*

Two families, the Aeolosomatidae and Potamodrilidae, were regarded as a single family by Brinkhurst and Jamieson (1971) but were excluded from the Oligochaeta, as they share only the basic annelidan features of setae and segmentation with them. Every other anatomical characteristic was shown to differ from the equivalent in the oligochaetes. Timm (1981) has confirmed this opinion and erected the subclass Aphanoneura, order Aeolosomatida, for these families. Both exhibit similarities to the Archiannelida, which may be

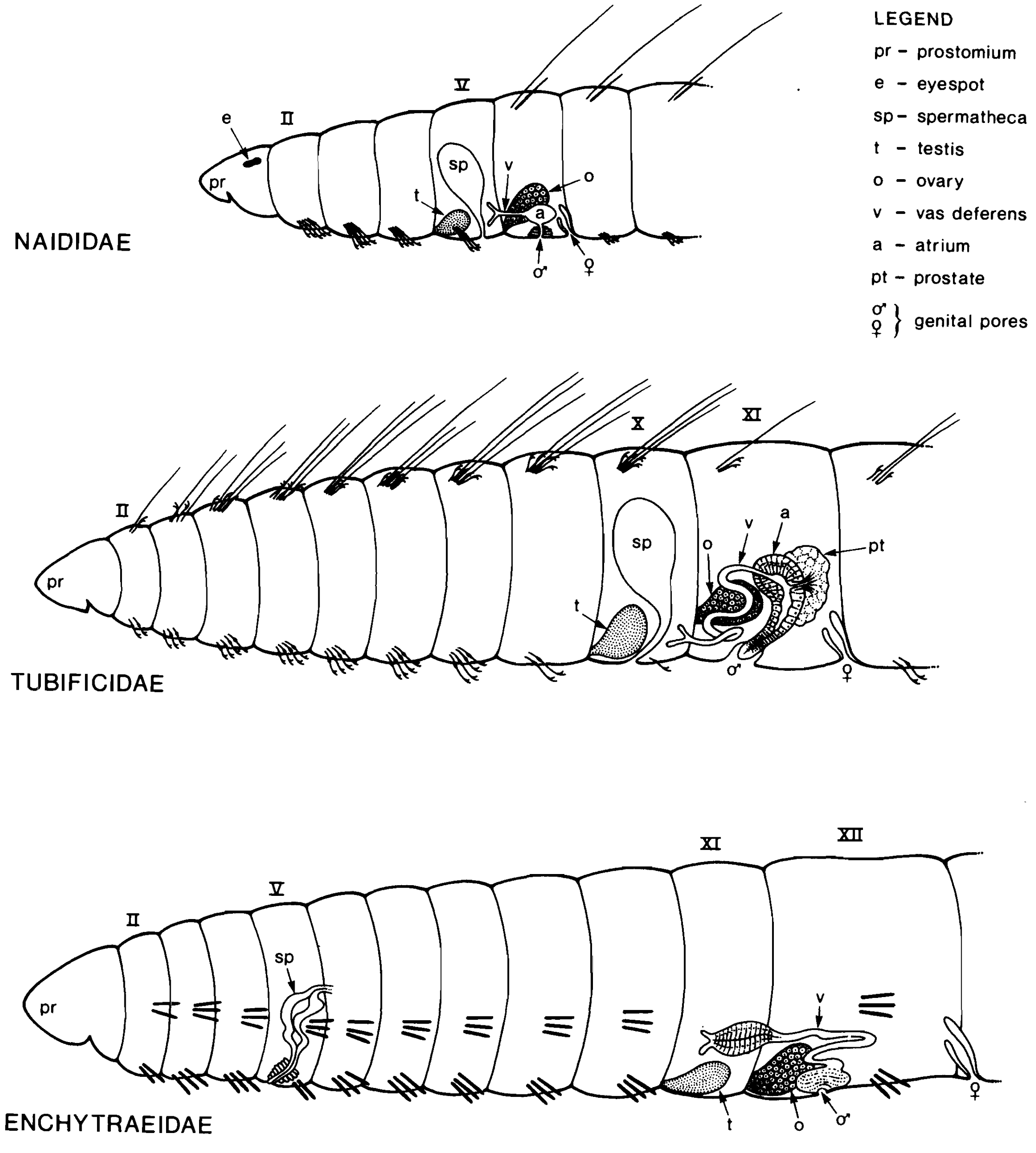

FIG. 3. Some characteristics of three families of the Tubificina.

due to convergence. They will only be referred to in the following discussion in terms of previous phylogenies in which they occupied a key position.

### Phylogeny based on the reproductive system

All of the living Oligochaeta can be derived from an octogonadal ancestral form, assuming that the parthenogenic multigonadal forms are excluded and attention is focused on sequence rather than segmental position occupied by the gonads. In the stem form indicated in Fig. 1, the male and female ducts are plesiopore and quite similar. This condition is found in *Haplotaxis smithii* (Beddard), *H. bureschi* (Michaelsen), and to some extent in *H. heterogyne* (Benham), although this species is missing the gonads in GIV. Eleven of the 18 haplotaxid species are octogonadal, whereas this condition is otherwise limited to two glossoscolecids, except as a transient, nonfunctional, developmental phase that reveals an octogonadal ancestry in those forms in which gonad reduction has taken place (Brinkhurst 1966).

In the Alluroidina, Moniligastrina, and Lumbricina, the ovaries of GIII are missing in the basic forms; loss of one or other pair of testes is observed in some members of the first two suborders, but not the Lumbricina. The intermediate between the stem form and these three suborders, referred to as the Brinkhurstoid form in Fig. 1, is represented by the living *Haplotaxis brinkhursti* (described by Cook 1975). It should be noted that living species are not here considered to be ancestral to other living forms, a fault that may be identified in some of the early monographs on the group. The living forms are presumed to be conservative descendants of such intermediate forms. The derivation of all of these three suborders from a haplotaxoid ancestor is generally accepted in oligochaete phylogenies (Jamieson 1977, 1978), and the detailed arguments in favour of this position need not be repeated here. It should be noted that the male ducts of the Moniligastridae reach the exterior through the bases of the prostates just as they do in some of the less advanced Tubificina, and that the male pores are not quite opisthopore. In the Alluroidina the prostates either discharge separately, or in conjunction with the male pores, or the male ducts enter them entally, as in *Alluroides* itself, in which case they are termed atria with prostates. Many of the aquatic stem forms of the Lumbricina have glandular masses around the male pores, or have prostates lacking the muscular ectal duct (the presumed equivalent of the atria of the microdriles). Glandular structures are associated with the male pores of several haplotaxids. In the Megascolecoidea of the Lumbricina, the prostates usually have muscular walls to the glandular section, and the vasa deferentia may open within this portion, rather than the more usual ectal position. Such structures, termed euprostates, are rarely found in the Lumbricoidea, in which the male pores exit via glandular or muscular bursae, still inversions of the body wall but presumably of a plesiomorphic form.

While the male pores of the Lumbricina are illustrated as opening in GIV in Fig. 1, in many instances they actually open many segments behind that position (i.e., in XV or beyond rather than in XIII). As this situation is quite clearly derived from the simplest opisthopore condition, further consideration of this modification is irrelevant here. It is, however, foreshadowed in the most advanced development along the haplotaxoid line of descent. Eight or nine living haplotaxoid species exhibit the condition of the haplotaxoid A form in Fig. 1, which is octogonadal, but with female ducts not obviously plesiopore. This condition persists in the two or three living species with plesiopore male ducts, but no gonad in GIV. These are termed the haplotaxoid B condition in Fig. 1. Above these in the illustration is the single species *Haplotaxis violaceus* (Beddard), in which the male ducts from GI exit via male pores in GIII, along with those draining GII, anticipating the opisthopore state of the megadriles, although this development must be convergent, as reduction in ovaries has occurred in different segments in the two lines (Brinkhurst 1966).

The important monotypic haplotaxid genus *Tiguassu*, described by Righi et al. (1978), provides a living representative of the necessary Tiguassoid intermediate between the haplotaxids and the Tubificina. The gonads of GI and GIV are lost, but rudimentary male funnels and ducts are still associated with GI. The female pores are plesiopore, as they are in the family Enchytraeidae, which appears to be an early offshoot of the Tubificina, as indicated in Fig. 1. There are no atria in *Tiguassu*, but in the Enchytraeidae there are glandular structures associated with the male pores, termed penial bulbs. Only in the very divergent enchytraeid *Propappus* are their atrial structures similar to those of the other tubificines. In the Phreodrilidae, another family of the Tubificina, the atria are usually elongate tubes with thin external muscle layers, and the vasa deferentia open into them ectally (Fig. 4). There is no significant atrial lumen until the epithelial cells discharge their secretions and shrink at late stages of maturation (as interpreted from individuals at various stages in development, rather than following the progress of individuals in culture). In the Tubificidae the prostate cells have penetrated the muscular layers of the atria to lie free in the coelom in a variety of different ways. The vasa deferentia open into the ectal part of the atria proper in the subfamily Rhyacodrilinae, which have the simplest form of the prostate glands and arrangement of sperm in the spermathecae and which are thought to be plesiomorph in regard to these characteristics. The vasa deferentia do sometimes reach the ental end of the atria by running through the muscle layers up to the summit (Fig. 4), but in many other tubificids and some of the family Naididae, they open directly into the tops of the atria. In many other naidids, the supposed vasa deferentia bear prostate cells, but as these arise from the lining layers of the atria, the narrow canals bearing these prostate cells may in fact be part of the atria. The male ducts of the small family Opistocystidae resemble those of the Naididae, those of the Dorydrilidae have muscular walls but no prostate cells. The female ducts of these microdrile families terminate in pores in the intersegmental furrows of the ovarian segment like those of some haplotaxids, but not the genus *Tiguassu*.

There is no known living equivalent to the Prolumbriculoid form shown in Fig. 1, but the posterior male ducts of *H. smithii* (Beddard), *H. hologynous* (Mich.), and *H. ornamentus* Br. are short and open close to the anterior margin of GIII and are very close to being prosopore. Further evolutionary patterns within the Lumbriculidae were described by Dr. D. G. Cook in Brinkhurst and Jamieson (1971) and need not be repeated here. The female pores in this family are situated in the intersegmental furrows behind the ovarian segments as in the Tubificina above the Enchyt-

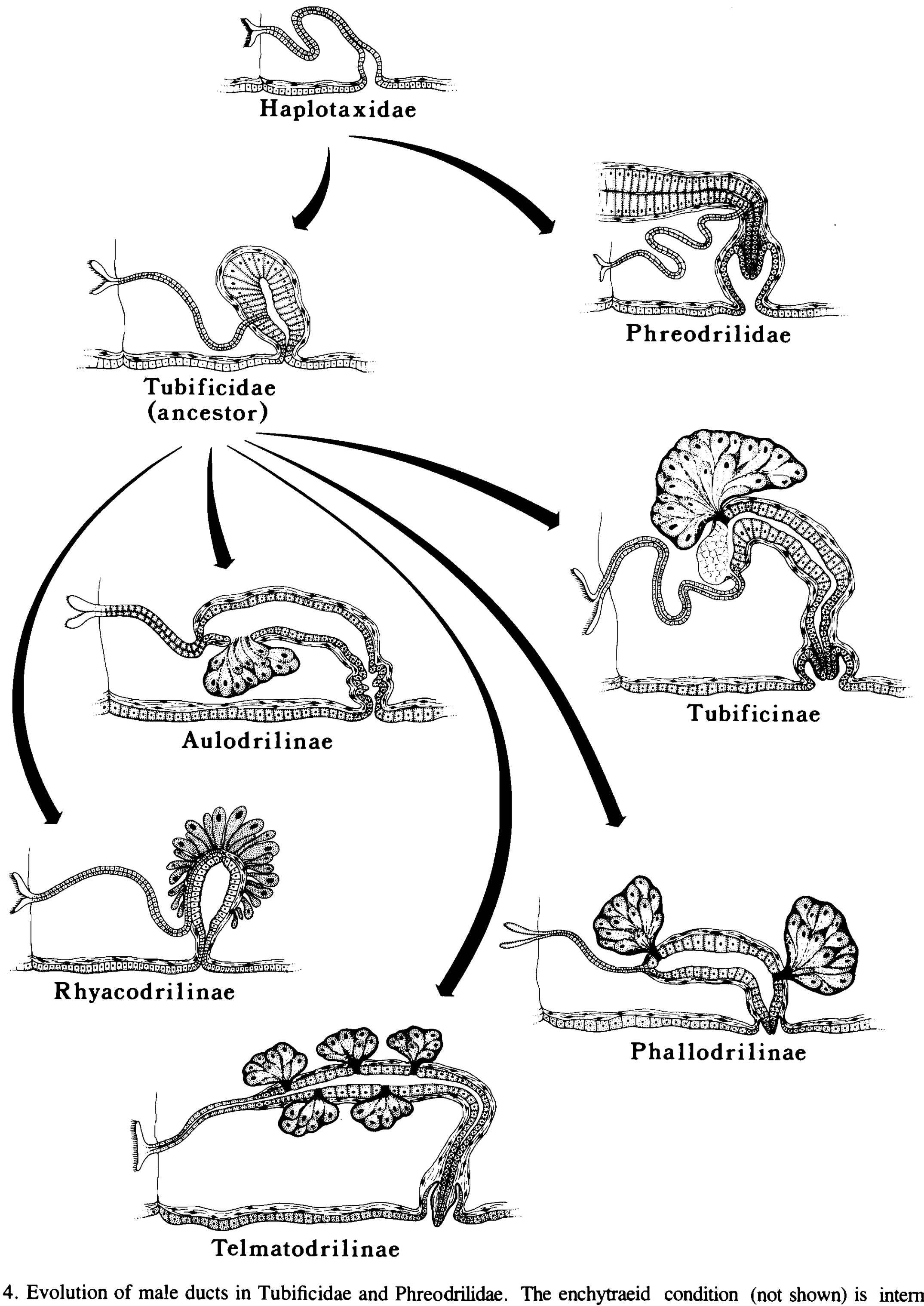

FIG. 4. Evolution of male ducts in Tubificidae and Phreodrilidae. The enchytraeid condition (not shown) is intermediate between the Haplotaxidae and the rest (reprinted from Baker and Brinkhurst 1981).

raeidae, and the atria and prostates resemble those of the Tubificidae in particular. In some genera the vasa deferentia open into the atria basally, but in most instances they then run inside the muscle layers towards, or even to, the summits of the atria. Various forms of penes are developed, again resembling those of the Tubificidae. These are also present in the Phreodrilidae, which otherwise have simple atria. True penes with elaborate cuticular sheaths are limited to two subfamilies within the Tubificidae, but other forms of penes (eversible, protrusible, and naked true penes (see Baker and Brinkhurst 1981)) have arisen independently in many genera of these three families. As penes are formed from invaginations of the body wall in the same way as the atria of microdriles and the prostates of megadriles, their independent evolution may be an indication that atria and atrium-like prostates may also have been independently evolved several times, as implied in Fig. 1.

Two major points emerge from this review. There is a great deal of evidence to support the contention that the Tubificina arose from haplotaxid ancestors rather than from a prolumbriculid or from an archiannelid polychaete. The reverse line of descent is difficult to argue because of the apomorphic condition of the gonads, gonoducts, atria, and penes in the Tubificidae in particular.

Evidence of the origin of the Tubificina from the Lumbriculidae revolves around the interpretation of the reproductive system of the family Dorydrilidae. This small family was erected by Cook in Brinkhurst and Jamieson (1971) for the single genus *Dorydrilus* which has only three European species. The badly known genus *Lycodrilus* was tentatively assigned to this family by the same author, pending redescription of material from Lake Baical. The setae of the genus *Dorydrilus* strongly resemble those of certain members of the family Lumbriculidae in that they retain the lumbricine arrangement and they are thin and sharply simple pointed. The reproductive organs of *Dorydrilus* are, however, completely tubificine in form, with the atria lying in the ovarian segment, the gonads having been reduced to a single pair of testes and a single pair of ovaries. The male ducts of the family Lumbriculidae are prosopore, the male pores lying in the testicular segments. While it can be argued that the male ducts in the Lumbriculidae penetrate the septa behind the testes only to return to the testicular segment in many genera, and that this is evidence for the origin of the prosopore condition from the plesiopore condition exhibited by the haplotaxids and tubificines, it is not, in itself, sufficient to warrant the derivation of the family Lumbriculidae from the Dorydrilidae. Many members of the Lumbriculidae retain the testes in GI and in GII, even though in some of them the male ducts from GI enter atria in GII, along with the ducts of that particular segment. The traces of rudimentary atria in GI provide evidence of the rearward movement of the anterior vasa deferentia.

The Dorydrilidae and the Lumbriculidae must, therefore, have been derived from a common ancestor which was presumably plesioporous. The Dorydrilidae may be regarded as quite primitive tubificines in that they retain the lumbricine setae and lack external prostates on the atria just as in the family Phreodrilidae. The vasa deferentia do enter near the summit of the atria in the Dorydrilidae however, which is here considered to be an apomorph characteristic.

## Oligochaete setal types

Eight setae arranged in four pairs per segment are found in the microdrile Haplotaxidae, the Lumbriculidae, Dorydrilidae, many enchytraeids, and the two ventral bundles of the Phreodrilidae (Fig. 5). The same setal arrangement is found throughout the Moniligastrina, Alluroidina, and the bulk of the Lumbricina. The setal number is increased by loss of the paired state in the perichaetine forms in the latter. In nearly all of these families the setae are all simple pointed, somewhat sigmoid in shape, and bear a more or less median nodulus. The setae may be minutely ornamented with pits, frills, or similar elaborations (Brinkhurst and Jamieson 1971). The high frequency of occurrence of this lumbricine condition is taken to indicate it is a plesiomorphic characteristic.

It is possible that the simplest arrangement of setae in a burrowing organism would be one in which the setal pairs were arranged at equal distances around the circumference of each segment. In living oligochaetes, the distance between the two dorsolateral pairs is usually greater than the distances separating the others, and this dorsoventral differentiation becomes more pronounced in families with more complex setal patterns.

The number of setae is greater than two per bundle in a number of species of Enchytraeidae. In this family the setae may be straight, may lack a nodulus, and may be of two distinct sizes in a single bundle. The setae may be even more ventrally displaced than in naidids or tubificids. Only in the recently described genus *Barbidrilus* Loden and Locy and in *Propappus* Mich. are the setae bifid. In the former, the straight anodular setae with two very small round teeth at the distal end are restricted to II and III. In *Propappus* there are two species with two or three sigmoid bifid setae per bundle, but these species differ from other enchytraeids sufficiently to cause some doubt about their inclusion in that family (Nielsen and Christensen 1959).

Bifid setae may replace the simple-pointed form in the Lumbriculidae, in one or both setae of the ventral pairs of the Phreodrilidae (Fig. 6*k*) and in one or two species in the Lumbricina.

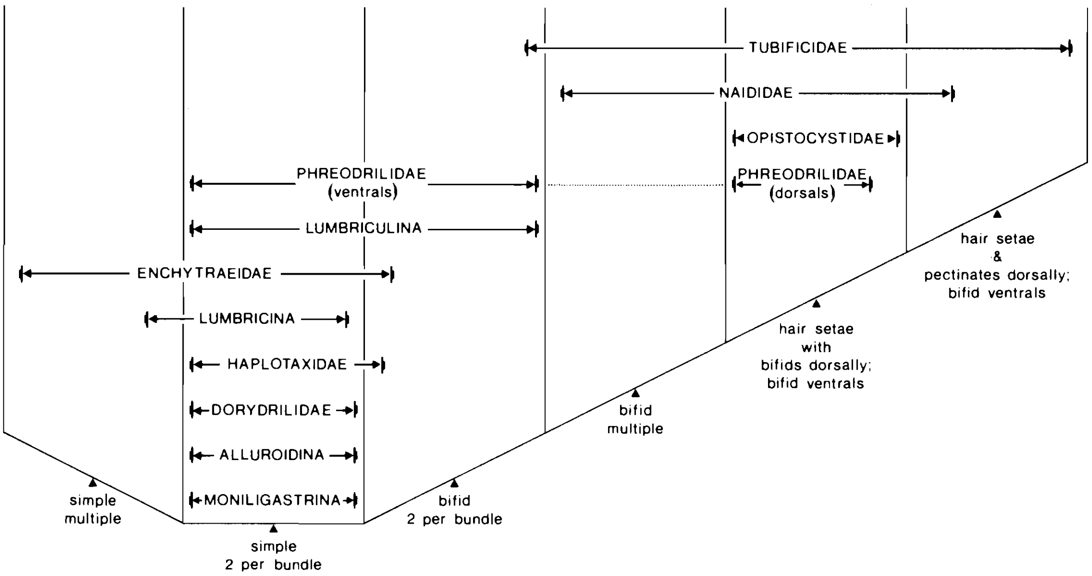

FIG. 5. Diversity in setal pattern in oligochaetes. Slight extension of range into a category (enchytraeids into bifid seta for example) indicates rarity of condition.

While the number of setae per bundle remains small in some of the Tubificina, notably the marine tubificid subfamily Phallodrilinae, they usually possess more than two setae per bundle, up to a maximum of 20 or more (the tubificids *Branchiura sowerbyi* Beddard, *Quistadrilus multisetosus* (Smith), *Antipodrilus multiseta* Br. and Fulton, *Telmatodrilus* Eisen; the naidid *Arcteonais* Piguet; the doubtful enchytraeid *Pelmatodrilus* Moore). All of the setae may be bifid (as in the tubificid genus *Limnodrilus* Clap., and certain species of other well-defined genera such as *Potamothrix* Vejd. and Mr. and the naidid *Paranais* Czern.), but the adaptive significance of bifid rather than simple-pointed setae remains obscure. A typical bifid setae is illustrated in Fig. 6*p*.

The dorsal setae often become more elaborate. In the Phreodrilidae the dorsal setal bundles consist of from one to many elongate hair setae, accompanied by short paired rods that do not extend beyond the setal sacs, and which may in fact be part of them. Only one species from Tasmania (to be described, R. O. Brinkhurst, in preparation) lacks hair setae. The hair setae may sometimes be modified by the presence of minute lateral hairs (Fig. 6*o*) and these may become elaborate where the main shaft is shortened and the lateral hairs expanded into one of the most complex setal types found among the oligochaetes (*Phreodrilus plumaseta* Br. and Fulton Fig. 6*j*).

Hair setae are usually accompanied by needle setae in those members of the Naididae and Opistocystidae in which hairs are found. Needles differ from the bifid ventral setae; they are often thin, straight, and simple pointed, or they bear minutely bifid tips, and the nodulus may be reduced or absent (Figs. 6*m*, 6*n*). In most tubificids with hair setae, the other dorsal setae closely resemble the ventrals in size and shape, but they are usually more elaborate in that pectinations are present (Fig. 6*r*). These may range from the very fine intermediate teeth found in *B. sowerbyi* that were overlooked in early descriptions, to the more obvious intermediate teeth of *Tubifex tubifex* (Müller). Pectinate setae are rare in the Naididae, although they may be present in *Dero* Oken, for example, where they may even become palmate, as they are in the tubificid species *Tubifex costatus* (Clap.) and *Psammoryctides barbatus* (Grube) (Fig. 6*q*).

The most complex setal arrangement in the oligochaetes, then, is that of the several naidids and many tubificids that possess multiple bifid setae in each ventral bundle, accompanied by many hair and pectinate setae in each dorsal bundle. This arrangement reaches its maximum development in number and size of setae in a few preclitellar bundles, and is usually reduced in complexity in and behind the reproductive segments.

## Modified oligochaete setae

Many oligochaetes exhibit what are clearly apomorphic setal patterns, but as no systematic review of setal types is available and many erroneous statements about oligochaete setae appear in textbook accounts, a brief review of this is presented. The most extreme setal modification observed in oligochaetes is the total loss of all setae in the enchytraeids *Achaeta* Vejd. and two *Marionina* Mich. species. Dorsal setae are absent in *Chaetogaster* von Baer (Naididae) and two *Haplotaxis*. Setae are reduced in size in some dorsal bundles, absent in many, in *Grania* Southern (Enchytraeidae) and two other *Haplotaxis* species in which the ventrals are reduced to single large setae on each side of each segment. Giant ventral setae may be found in a few anterior bundles of *Limnodrilus grandisetosus* Nomura (Tubificidae), *Vejdovskyella* Mich., *Nais* Müller, *Pristina* Ehr. (Naididae), *Haplotaxis gastrochaetus* (Yam.) (Haplotaxidae), and *Phreodrilus magnaseta* (Br. and Fulton) (Phreodrilidae) (Fig. 6*l*). No genital function has been ascribed to these giant ventral setae in contrast to the specialized setae on those segments bearing male or spermathecal pores, or sometimes the immediately pregenital segments. Spermathecal setae are often solitary, large, with the two teeth of a normal bifid seta lengthened and apparently fused to form something approaching the shape of an apple-coring tool. Glands are often associated with the setal sacs of these structures. Penial setae may be of the same form, or may be simpler (in many phallodriline tubificids, for example). They may be multiple, with long straight proximal ends, and short curved distal ends which lie close together, each terminating in the usual bifid tip which may be inflated. The two sets of setae point towards the midline, often associated with a median depression of the body wall in which the paired or single, fused male pores open (rhyacodriline tubificids for example). In some phallodriline tubificids the penial setae may be of two sizes, the larger being very elongate. In other phallodrilines, the body wall is modified to provide anchorage points for the penial setae of a concopulant, but in all other instances their function remains conjectural as copulation has never been observed.

In some instances, the bifid setae may be replaced by simple-pointed setae, especially in the posterior segments of the marine genus *Tubificoides* Last. In *Telmatodrilus* Eisen (Tubificidae) the bifid setae have very small upper teeth which may be absent from anterior bundles, but all postclitellar setae are unique in being pectinate, such modifications usually being most pronounced anteriorly. The dorsal setae of *Ophidonais* Gervais (Naididae) are single, thick, and rod-like. In the tubificid *Aulodrilus* Bretscher lateral wings or vertical paddle-shaped tips to the setae are developed.

A unique setal arrangement is observed in *Telmato-*

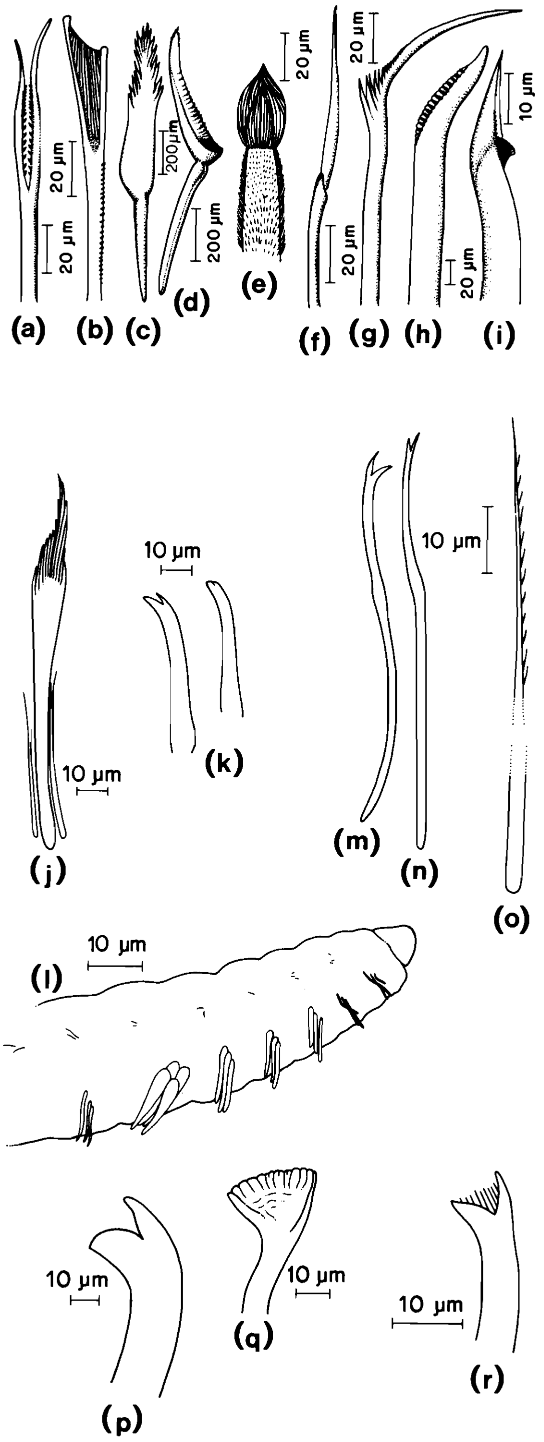

FIG. 6. Setae in polychaetes (*a-i*) and oligochaetes (*j-r*). (*a*) Pectinate *Aglaophamus*. (*b*) Pectinate *Nereis*. (*c*) Outer palea *Sabellaria*. (*d*) Inner palea *Sabellaria*. (*e*) Plumed *Disoma*. (*f*) Composite *Exogone*. (*g*) Simple *Fabricia*. (*h*) Hooded *Fabricia*. (*i*) Ridged *Fabricia* (all redrawn from originals by O. Hartman). (*j*) Dorsal *Phreodrilus plumaseta*. (*k*) Ventral *Phreodrilus plumaseta*. (*l*) *P. magnaseta*. (*m*) Ventral *Pristina rosea*. (*n*) Dorsal needle *Pristina rosea*. (*o*) Hair *P. longiseta*. (*p*) Ventral *Psammoryctides barbata*. (*q*) Dorsal *Psammoryctides barbata*. (*r*) Pectinate dorsal *Rhyacodrilus*. For other illustrations consult Brinkhurst and Jamieson 1971 and Fauchald 1977.

*drilus papillatus* Br. and Fulton, in which the shovel-tipped anterior setae of both dorsal and ventral bundles are gradually transformed into hair-like setae by the reduction of the teeth in progressive segments.

Three observations suggest environmental effects on setal development. In the naidids, Loden and Harman (1980) were able to change the setal form of some species by diluting the artificial pond water used in laboratory cultures or by adding salt. The changes observed were sufficient to cause the authors to synonymize species hitherto distinguished by differences within the range of envionmental effects observed.

In the presence of very high mercury levels the setae may become distorted according to Milbrink (1980).

In several tubificid genera there are sets of three species which appear to be identical apart from the dorsal setae. One form will have hair and pectinate setae, another nothing but bifid setae, and the rarer intermediate state has short hair setae with bifid setae in some anterior segments. The change is sometimes related to habitat, as in *Tubifex tubifex* (Müller) in which the *blanchardi* Vejd. form (sometimes accorded specific status) may be associated with estuaries or inland salt waters. The link between pectination of the bifid and the size and number of hair setae suggests that a gene or group of genes controls the amount of setal material secreted in response to quite simple environmental factors such as salinity.

Marine oligochaetes have such simple sets of bifid setae that they are of limited use in identifying species. One interesting development is the presence of accessory material running from the end of the lower tooth back to the shaft as if to act as a buttress (Erseus 1981). The same phenomenon is observed in the polychaete family Questidae (see Hobson 1970) although there the dorsal and ventral bundles of setae are similar and both contain hair setae (Fig. 7).

## Formation and microstructure

While little work has been done on oligochaete setae in regard to formation and microstructure, the recent literature concerning the fundamental uniformity of setae among Polychaeta, Brachiopoda, Pogonophora, Echiuroidea, Bryozoa, and Cephalopoda suggests that little useful information regarding phylogenetic relationships between oligochaetes and polychaetes can be derived from this approach (Orrhage 1979). The transitory larval bristles of sipunculids give no clues to intergroup phylogeny as they are dissimilar in formation to the setae of other groups in that they are secreted by a number of gland cells and may be readily softened or dissolved by most biological fixatives (Clark 1969). Their position in metameric rings is considered a result of functional requirements rather than a trace of metameric segmentation. The observation does suggest that annelid-type setae may have been advantageous in similar unsegmented eucoelomate annelid ancestors now extinct.

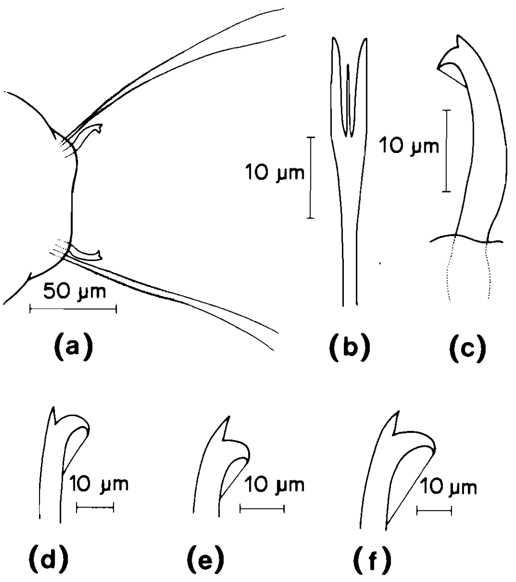

FIG. 7. Setae. (*a–c*) *Novaquesta* (Polychaeta, Questidae) Hair setae dorsal and ventral bundles, pectinates and bifids with support strut. (*d–f*) Setae of three *Phallodrilus* species (Oligochaeta, Tubificidae). No hair setae (but limited to dorsal bundles in some other tubificids), bifids with support struts unique in Oligochaeta.

## Comparison with polychaete setae

Owing to my own limited understanding of polychaete biology, a series of naive questions was presented to a number of colleagues (cited in the acknowledgements). From them and from a study of a large number of published accounts of polychaetes, the following statements can be made. (1) Compound setae and hooded setae are derived forms found in a restricted number of families. (2) The dorsoventral differentiation of setal groups is annelid-wide but hair (or capilliform) setae are not restricted to dorsal bundles as they are in oligochaetes. (3) Several families show a reduction or absence of parapodia, especially as an adaptation to burrowing. (4) Polychaete setae are not like oligochaete setae despite general statements as to their similarity in many standard reference texts (Figs. 6*a*–6*i*).

The setae of the two groups differ in number, form, and disposition. In the Capitellidae, for example, where parapodia are absent and the worms are readily mistaken for tubificids at first sight, the hair setae are found in anterior dorsal and ventral bundles, and are then replaced in posterior segments by hooded pectinate setae in all bundles from IX on. This is in complete contrast to the shape and form of setae in any oligochaete.

Hair setae may be restricted to dorsal bundles in some polychaetes (Oweniidae, Acrocirridae, Arenicolidae, Terebellidae, Spintheridae), but if so they are not accompanied by other setae more complex than those in the ventral bundles, as would be the case in naidids and tubificids. Polychaete setal types have been catalogued (by Fauchald (1977) for example) but the lists appear unnecessarily complex.

If a worm has only one of the following list of characteristics it is not an oligochaete: parapodia, compound setae, hooded setae, hair setae in ventral bundles, more than 25 setae per bundle. Many polychaetes exhibit more than one of these characteristics; all possess at least one.

## Phylogeny based on setae

Traditional belief in the plesiomorphic status of the complex setae of the Tubificina is based on the assumption that they closely resemble polychaete setae and are a reflection of the polychaetous ancestry of the group; however, the origin of complex setae is not considered by this school. As there is no a priori reason for this position, I will adopt the more parsimonious view that the lumbricine setal arrangement is the simplest starting point.

The presumption now is that the earliest coelomate forms became segmented as a response to sustained burrowing activity, and the possession of setae at roughly equidistant intervals around the circumference would clearly maximize the advantage accruing from their development. At a very early stage, no doubt, the dorsoventral differentiation caused by shifting the upper pair to the dorsolateral position occurred. This pattern can as easily be seen as the basis of the bifid nature of parapodia as it is a last vestige of it. The function of the divison of the parapodia in this manner is obscure, whereas the function of separated bundles of setae in lumbricine oligochaetes is not.

Within the oligochaetes the lumbricine form is dominant, so setal pattern contributes little to the discussion of evolution of the megadriles from the haplotaxids. The setal pattern of the haplotaxids is predominantly lumbricine, and they are therefore not excluded as stem forms in terms of this hypothesis.

Both Enchytraeidae and Phreodrilidae show traces of a lumbricine setal arrangement, with increase in setal number and development of hair setae in the latter, foreshadowing the complexity in setae of the Naididae and Tubificidae. Both of the latter have species not displaying the full range of complexity exhibited by the others. The complex dorsal setae and relatively simple ventral setae of these families suggest that evolution proceeded via a free-living habit retained by most naidids, but rejected by the tubificids in favour of the burrowing habit. The Naididae have several additional adaptations to life outside the sediment, including rudimentary eyespots and the ability to swim.

The complex dorsal setae of many of the Tubificina can be seen as protective devices, effectively enlarging the size of an organism crawling on the ventral surface which has appropriate locomoter setae. Return to a burrowing habit has not eliminated hair setae in the genus *Dero* or in the tubificids.

Within the tubificids, rhyacodrilines have plesiomorphic male reproductive structures in comparison with the tubificines, but the setae may be equally complex in both groups. The setae of the other subfamilies are, in general, less complex than those of the two larger subfamilies. The very simple setae but most complex male ducts of the phallodrilines may be retained from early tubificid forms, but our knowledge of these marine forms is very recent. The presence of gutless specimens points to considerable advance in the marine stock. It is not possible to decide whether successful freshwater genera such as *Limnodrilus* Clap. have lost hair and pectinate setae or never developed them, but in those genera with species having complex setae, the simpler setal pattern can also be present. In examples like *Potamothrix* this cannot be attributed to faulty generic diagnosis, though efforts have been made to classify genera strictly by setal pattern. This is done in the naidids because of the rarity of mature specimens.

The Dorydrilidae have lumbricine setae, as do the Lumbriculidae, and both are seen as conservative in this regard, but the latter often have two bifid setae per bundle, which is rare elsewhere.

## Comparison with information derived from reproductive system

As so many families of oligochaetes have lumbricine setae, a test of the phylogeny based on reproductive systems with reference to a setal pattern-based phylogeny is limited, but there is at least no conflict between them. The family Haplotaxidae provides an appropriate model for the stem form by either approach. The Enchytraeidae and Phreodrilidae are placed at a level showing some apomorphic characteristics, and the Tubificidae and Naididae have the most apomorphic characteristics of the aquatic families. The Lumbriculidae constitute an independent line not only in respect to their prosopore male ducts but the frequency of paired but bifid setae.

## Discussion of oligochaete phylogeny

The phylogeny outlined above is consistent with views expressed earlier (Brinkhurst and Jamieson 1971) in most respects but differs in regard to the interpretation of the prosopore state of the Lumbriculidae and the position of the Enchytraeidae.

The prosopore state was believed to be that of the original coelomoduct, but Clark (1969) points out the misinterpretation of the work of Goodrich (1946) by those who do not notice that the coelomoduct must of necessity penetrate a septum if it drains a coelomic pouch. It could be argued that it might, in fact, have originally opened into the intersegmental furrow owing to the apposition of two coelomic pouches to form septa, but the rarity of the prosopore state is now considered sufficient evidence for its demotion. Additional evidence for the origin of the prosopore condition from a plesiopore condition is twofold. In the first instance, the male ducts of *Lamprodrilus* Mich., *Stylodrilus* Clap., and *Trichodrilus* Clap. penetrate the septum behind the gonosegment before reentering it. Secondly, in those species in which a single pair of atria serves both pairs of testes and male ducts, the rudimentary atria of GI in *Rhynchelmis* Hoff. for example, attest to the loss of an anterior (prosopore) system rather than the development of prosopore male ducts in GII by suppression of atria in GIII (of which no trace is found in any member of the family). The same reasoning is used to separate the Dorydrilidae from the Lumbriculidae (Brinkhurst and Jamieson 1971).

The female ducts, not used in the previous account, are seen to be plesiopore in a great many oligochaetes, though no longer obviously so in the Tubificina above the Enchytraeidae and many haplotaxids.

Previous adoption of the concept of the development of the Enchytraeidae by reduction from a tubificine state via a form such as *Propappus* with bifid setae was due to my unconscious retention of the pre-Stephenson phylogeny. Miss K. Coates (personal communication) challenged this position and showed me how much better placed the family is as an early offshoot of a line from a haplotaxoid–tiguassoid stem form to the Tubificina. The preponderance of species still have two, or at most three, simple setae per bundle and the male ducts well-defined atria. The aquatic *Propappus* becomes a derived form in this instance, foreshadowing developments in the Tubificina in bifid setae and better defined atria.

Adaptions to defence from predators may produce the convergent development of complex setae in polychaetes and aquatic oligochaetes, the separation into four bundles of setae (or biramous parapodia) being retained from an ancestor with one or two simple setae at four roughly equidistant points around the circumference of each segment. Weak cephalization is developed in both lines, with eyespots appearing in the naidids and the polychaetes. The archiannelids and aeolosomatids are specialized meiofaunal groups, convergent at least, but not related to stem forms of the annelids. The wider implications of these concepts are that very simple earthworm-like forms without complex copulatory reproductive ducts are the stem forms of the Annelida; they arose from unsegmented coelomates with groups of setae used to aid in burrowing and defence; unsegmented coelomates arose from acoelomate triploblast bilateria in the manner suggested by R. B. Clark in his penetrating analyses of functional evolution.

The function of hermaphrodite reproduction is not yet understood. Arguments about double reproductive output in animals that seldom meet (within sediment or deep in the bodies of hosts) ignore the abundance of many species and the possibility of enhanced fecundity as an alternative. Ghiselin (1969) has reviewed this widespread phenomenon, found in polychaetes as well as throughout oligochaetes. The hypothesis outlined here allow for a possible hermaphrodite annelid ancestor rather than its reappearance in the oligochaetes.

## The Hirudinea

Clark (1969) discussed the relationship between the leeches and oligochaetes and suggested that while the class Clitellata includes both, it may be more practical to separate the Hirudinea as a class too. The Lumbriculidae seem to provide models of the stem forms for leeches. *Agriodrilus* Michaelsen (seen as part of *Lamprodrilus* Mich. by Cook, in Brinkhurst and Jamieson (1971)) is a predatory worm with the coelom reduced by hypertrophy of the peritoneum in a manner resembling that of leeches, and with a sucking pharynx. The parasitic Acanthobdellidae and Branchiobdellidae are thought to provide intermediates between lumbriculids and leeches (Clark 1969), though the latter have the testes behind rather than before the ovaries, but the male pore retains its position ahead of the female pore, both being unpaired (a condition found in several lumbriculids and also a few tubificids). The multiplied testes in their sacs draining into paired vasa deferentia appear to be the outcome of the shrinkage of the coelom around the testis sacs of an original pair of anterior testes.

## Discussion of previous phylogenies

The classical oligochaete phylogenies, reviewed by Stephenson (1930) and Yamaguchi (1953) and typified by the last major expression of them by Michaelsen (1921), were based on an evolutionary sequence running from the Aeolosomatidae through the Naididae–Tubificidae–Lumbriculidae–Haplotaxidae to the megadriles. This argument was based on the belief, still widely quoted in textbooks, that the complex setae of the aquatic forms were derived from polychaetes, the ancestral annelids with a marine habit, separate sexes, and no complex reproductive system. The archiannelids were seen as the stem forms of both polychaetes and oligochaetes and these were derived from acoelomate flatworms with serially repeated organ systems that acquired coelom and segmentation simultaneously. The theories accounting for the origin of these major adaptations were reviewed by Clark (1964, 1969).

This pathway can be attacked from many viewpoints, summarized as follows. (1) The archiannelids are now regarded as specialized worms, probably even a polyphyletic assemblage of meiofaunal polychaetes (Hermans 1969; Orrhage 1974; Fauchald 1974). (2) The aeolosomatid families are not related to archiannelids according to the detailed account by Bunke (1967), though this opinion may be questioned (see below). (3) The aeolosomatid–naidid link is denied by my decision to exclude them from the oligochaetes entirely. It was also rejected by Sperber (1948) at the conclusion of her definitive study of the naidids, and by Timm (1981). (4) The tubificid–lumbriculid link is untenable as it involves going from a plesiopore male duct to a prosopore condition en route to the opisthopore state. The link has been supposed to be the genus *Dorydrilus*, but the tubificine nature of the male duct and atria cannot be derived from the prosopore state (Brinkhurst and Jamieson 1971). The lumbriculid–haplotaxid link can only work in the reverse direction according to my appraisal of the significance of the reproductive system.

The sequence was abandoned by Michaelsen (1929) who focused attention on the prosopore–plesiopore–opisthopore split of the families, but the Haplotaxidae were placed with their acknowledged descendents, the megadriles, in the opisthopore group. Hence the subsequent difficulty experienced by Stephenson (1930), Yamaguchi (1953), and Clark (1969) in finding a stem form for the plesioporous Tubificina. Their solution was to invert the earlier sequence to place the Lumbriculidae as the stem forms leading to the tubificids, then naidids essentially as before. Yamaguchi argued the case for the lumbriculids based on: (1) diversity in number and position of gonads, so each subsequent family could be derived with its gonads in the appropriate segments; (2) prosopore male ducts with all male pores in front of female pores, location of female pores in gonadal segments; (3) diversity in number and position of spermathecae allowing direct derivation of the pattern found in all other families; (4) clitellum on gonadal segments and including gonopores.

The apparent diversity of gonads in the lumbriculids is now related to parthenogenesis, the basic gonad plan being octogonadal not polygonadal. The Haplotaxidae and all the Tubificina share the fourth characteristic and the prosopore state is now seen to be apomorphic (see Discussion). The spermathecae are not generally considered to be of value in phylogenetic studies. In addition to this, the Lumbriculidae is fundamentally Holarctic with a large proportion of endemic species in Lake Baical, a less appropriate geographic distribution for a stem family than that of the Haplotaxidae. The family does possess atria on the male ducts, so that if the megadriles are derived from them via the Haplotaxidae the atria would have to be lost and then reevolved in the alluroidids, moniligastrids, and (as prostates) megadriles. Separate evolution of the various atrial structures from the simple haplotaxid condition is more acceptable. The acceptance of the lumbriculids as a stem family by these authors does signal their acceptance of the lumbricine setal condition as plesiomorphic, a fact that seems to be overlooked by those still wishing to see complex setae as a relic of a polychaete ancestry despite its abandonment for 50 years (i.e., Timm 1981). Clark (1969) was moved to reject the persistent claims for an archiannelidan ancestor in the strongest terms as "being grounded on a premise that no-one seriously entertains" and so they should be "totally discarded or justified on completely new grounds." His concepts of the evolution of unsegmented coelomates and then segmented coelomates, based on the functional advantages of a hydrostatic skeleton equipped with separate compartments for sustained burrowing, leads to the concept of a very simple earthworm lacking a complex reproductive system as the stem form of the annelids. Fauchald (1974) sees such a form as the basis of the polychaetes. It is naturally acceptable as the basis of the evolution of earthworms, and it is now claimed as the stem form for the Tubificina in place of the Lumbriculidae. The Haplotaxidae are the modern descendents of that stem form. They have an appropriate distribution pattern and anatomy, and living intermediate forms exist representing the type of organisation of the antecedents of the major groups apart from the Lumbriculidae.

Timm (1981) reviewed some early phylogenies but overlooked the work of Yamaguchi (1953) and of R. B. Clark. He provided a somewhat distorted representation of my earlier views by compressing them into a tree-like diagram with families shown at different levels rather than as contemporaries. For example, the leeches and allies are shown as preceding the lumbriculids rather than being derived from the ancestors of that family. The new phylogeny proposed by Timm is compromised by the assumption that tubificine setae must indicate direct kinship with the polychaete ancestor, but the question of origin of complex setae is not addressed. The Aeolosomatida and a protooligochaete are derived from a freshwater polychaete with multiple fertile segments of undetermined sex. The protooligochaete is an octogonadal version of a tubificine. From this are derived the Tubificina and the lumbricine ancestor of both the Haplotaxidae (with their megadrile descendents) and a separate moniligastrid–lumbriculid–dorydrilid line. None of the three supposed ancestors have living representatives, in contrast to the theory outlined above. The Dorydrilidae cannot be derived from the Lumbriculidae simply because of unspecified similarity because there is no basis for the shift of male pores from the testicular to the ovarian segment. The dorydrilids are more appropriate as early tubificines lacking prostates, as suggested here. Similarly, the enchytraeids are given their traditional position by Timm, as descendents of the aquatic *Propappus*, whereas they are seen here as early forms of the tubificine series with *Propappus* as a specialized form in accord with the opinions of recent specialists.

The views of Timm (1981) and myself would be largely coincident if his ancestor of the Tubificina were derived from the Haplotaxidae, omitting his three non-existing ancestors by allowing that polychaete and freshwater oligochaete setae are convergent. My scheme is the more parsimonious, and four of the five ancestral forms suggested are represented by living species of the Haplotaxidae. Reduction of complex setae to the lumbricine condition is said to be achieved by neoteny according to Timm; the origin of complex setae in annelids is not discussed. Timm does not account for the setal simplicity of the phallodriline marine tubificids which are being described at an accelerating rate. The tubificids are now a truly marine family.

## Classification

As a result of this study and the work of Jamieson (1977, 1978) and Timm (1981) I now propose the following classification. The species mentioned in the text will be inserted for reference.

| | |
|---|---|
| Phylum Annelida | |
| Class Oligochaeta | A common alternative is to regard the class Oligochaeta and the class Hirudinea as subclasses of the class Clitellata<br>The Aphanoneura will be regarded here as a class rather than a subclass (Timm 1981) as the ventral copulatory gland is not a clitellum, and all their other characteristics are unique. The Polychaeta are also a class |
| Order 1. Haplotaxida | Plesioporous microdriles. Octogonadal or lacking GIII, or GIV, or GI and GIV. Atria and prostates absent. Setae lumbricine or reduced. Distribution discontinuous, global, with many endemic species. |
| Family Haplotaxidae | Currently two genera (*Haplotaxis*, *Tiguassu*) but now in need of revision |
| Order 2. Lumbriculida | Prosopore microdriles. Octogonadal or with GIV lost, sometimes GI or GII also. Atria present, with external prostates. Setae lumbricine, sometimes bifid. Holarctic, with two peregrine species, half the order limited to Lake Baical. |
| Family Lumbriculidae | Includes *Agriodrilus*, *Lamprodrilus*, *Rhynchelmis*, *Stylodrilus*, and *Trichodrilus*, etc. |
| Order 3. Tubificida | Plesiopore microdriles. Gonads in GII and GIII. Atria usually present, with or without prostates. Setae from lumbricine to complex. Cosmopolitan |
| Suborder 1. Dorydrilina | New suborder. Plesioporous microdriles with testes in IX, ovaries in X. Atria without prostates. Spermathecae in X or XI or both. Setae lumbricine. Europe. ?Lake Baical |
| Family Dorydrilidae | Currently the single genus *Dorydrilus*. The genus *Lycodrilus* incertae sedis in the family, sometimes regarded as a family |
| Suborder 2. Enchytraeina | New suborder. Plesioporous microdriles with testes in XI, ovaries in XII, male ducts without atria, but with glandular penial bulbs. Spermathecae in V. Setae lumbricine or slightly more abundant, bifid in two genera, sometimes absent. Cosmopolitan |
| Family Enchytraeidae | Includes *Achaeta*, *Propappus*, *Barbidrilus*. *Marionina*, *Grania*, and ?*Pelmatodrilus*, etc. |
| Suborder 3, Tubificina | Plesioporous microdriles with gonads in variable position from IV–V to XXI–XXII. Atria present usually with prostates. Spermathecae in GII, GIII, or GIV. Setae usually numerous, hair setae may be present dorsally |
| Family Naididae | Includes *Arcteonais*, *Chaetogaster*, *Dero*, *Nais*, *Ophidonais*, *Paranais Pristina*, *Vejdovskyella* etc. |
| Family Tubificidae | Includes *Antipodrilus*, *Aulodrilus*, *Branchiura*, *Limnodrilus*, *Potamothrix*, *Psammoryctides*, *Quistadrilus*, *Telmatodrilus*, *Tubifex*, *Tubificoides*, subfamily Phallodrilinae, etc. |
| Family Opistocystidae | Five species in three genera only |
| Family Phreodrilidae | The single Gondwanaland genus *Phreodrilus* will eventually require division into genera |
| Order 4. Lumbricida | Opisthopore megadriles, or with microdrile characteristics in a few species. Gonads usually missing in GIII, very rarely in GI or GII as well. Prostates present or absent, atria with prostates very rare. Setae lumbricine or rarely perichaetine. Cosmopolitan |
| Suborder 1. Alluroidina | Opisthopore microdriles. Gonads lost in GIII or GII and GIII. Atria with prostates or separate prostates present. Spermathecae in one of VI or IX. Setae lumbricine. Africa, South America |

| | |
|---|---|
| Family Alluroididae | *Alluroides* mentioned in text |
| Family Syngenodrilidae | One species (in *Syngenodrilus*) from Kenya. |
| Suborder 2. Moniligastrina | Plesiopore–opisthopore with microdrile and megadrile characteristics. Gonads missing in GIII, sometimes also in GI or GII. Testes in specialized sacs. Spermathecae in VIII or IX or both. Setae lumbricine. Asia |
| Family Moniligastridae | Five small genera. |
| Suborder 3. Lumbricina | Opisthopore megadriles. GIII almost always lost, GI and GII usually present. No atria, with or without prostates. Spermathecae variable. Setae lumbricine. Cosmopolitan |
| Families as in Jamieson (1978) | |
| Class Aphanoneura | Ventral copulatory gland, no clitellum. Nerve cord double, in body wall. Cosmopolitan |
| Order Aeolosomatida | Segmentation reduced, locomotion by cilia. Testes in front of and behind ovaries. Hair setae in dorsal and ventral bundles or setae absent |

This classification is almost completely in accord with that proposed by Jamieson (1978) with the exception that the Haplotaxida is here limited to the single family Haplotaxidae. Three suborders of the much broader Haplotaxida of Jamieson, the Alluroidina, Moniligastrina, and Lumbricina, retain that rank here but are grouped in the order Lumbricida.

The statement by Jamieson (1978) to the effect that the Tubificina would be unlikely to have intervened between the Haplotaxidae and any of the remaining forms computed in his analysis (my Lumbricida), is upheld. As the Haplotaxidae also fulfill the requirements of descendents of the stem forms of the Tubificina, especially since the description of *Tiguassu*, the small but important family Haplotaxidae is now set apart. This action also recognises the status of the Haplotaxidae as microdrile plesiopores in contrast to the mostly opisthopore megadrile character of the Lumbricida.

As the prosopore condition is now thought to be derived from the plesiopore, the order Lumbriculida is thought to be similarly derived from an ancestral haplotaxid. Hence, the Tubificida are no longer considered to be part of a widely defined Haplotaxida in contrast to the prosopore Lumbriculida, both previously held to be derived from prosopore ancestors with multiple gonads (Brinkhurst and Jamieson 1971). All four orders identified here are thought to be derivable from an octogonadal, haplotaxoid microdrile with plesiopore gonoducts.

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