

A phenetic and cladistic study of spermatozoal ultrastructure in the Oligochaeta (Annelida)

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Abstract

Spermatozoal ultrastructure of nine oligochaete families has been examined for congruence with phylogenetic and taxonomic systems for the Oligochaeta based on general morphology, particularly the holomorphological hennigian analysis of Jamieson (1978a, 1980, 1983). Estimation of congruence has been made following phenetic and cladistic (phylogenetic) analysis. Correspondence, in phenograms and phylograms, of sperm types with taxonomic and phylogenetic groupings previously recognized is generally good. Departure from this rule in the similarity of the phreodrilid sperm to that of the Lumbricina suggests a corresponding alteration of fertilization biology in the phreodrilids. The results indicate that the Haplotaxidae lie at the base of the opisthopores though they do not unequivocally contraindicate acceptance of a *Haplotaxis* like form as a stem form of the Haplotaxida (opisthopores and Haplotaxidae) and Tubificida. An even more basal position for prosopores, now represented by the Lumbriculida, cannot yet be dismissed.

Introduction

The subclass Oligochaeta was divided into three orders by Brinkhurst & Jamieson (1971): the Lumbricida, Moniligastrida and Haplotaxida. Jamieson (1977) showed that the Moniligastrida were in fact transitionally opisthoporous and should be placed in the Haplotaxida, a view with which Brinkhurst & Fulton (1981) concurred. In a detailed computer analysis of the opisthoporous families and the Haplotaxidae, employing the principles of Hennig (1966), Jamieson (1978a, 1980) concluded by extrapolation that the Tubificina, of which major families are the Tubificidae, Naididae, Phreodrilidae and Enchytraeidae, should be removed from the Haplotaxida to constitute the separate order Tubificida, thus giving three orders with the Lumbriculida and Haplotaxida.

Independently, Timm (1981) recognized a similarly constituted order Tubificida but as the sole order of a superorder Naidimorpha separate from

the superorder Lumbricomorpha (both superorders *sensu* Chekanovskaya, 1962). Brinkhurst (1982b, 1984) has come to accept a separate order for the Tubificida (despite adverse criticism of this step in another recent work, Brinkhurst, 1982a) but has further advanced the contention of Brinkhurst & Jamieson (1971) that the Haplotaxidae are representatives of very basal (plesiomorph) oligochaetes to the extent of deriving all oligochaetes from a haplotaxid-like stem form. He emphasizes the significance of the Haplotaxidae by restricting the order Haplotaxida to this family and consequently erects an order Lumbricida for the opisthoporous oligochaetes while recognizing also the orders Lumbriculida and Tubificida.

Derivation of Tubificida, modern Haplotaxidae and the opisthopores from an octogonadial, plesiomorphous haplotaxid-like form accords with the views of Brinkhurst & Jamieson (1971) and is not contrary to the phylogenetic suggestions of Jamieson (1978a, 1981a), but the author has differed from

Brinkhurst's current system in regarding the proso-porous, multigonadial condition, which is retained in the Lumbriculidae, as precursory to the octogonadial, plesio-porous haplotaxid condition.

The author (Jamieson, 1983) has examined, by intuitive means, congruence of spermatozoal ultrastructure with his earlier, holomorphological phylogeny (Jamieson, 1978a) and has found the two studies to be, on the whole, consistent although the position of the Lumbriculidae cannot be considered settled.

The present study was designed to investigate to what extent a computerized phenetic and cladistic classification of spermatozoal ultrastructure for all oligochaete families for which this is comprehensively known might illuminate these and other obscure areas in our understanding of oligochaete phylogeny and taxonomy. Most particularly, it is concerned with investigating congruence of sperm ultrastructure with the holomorphological phylogeny proposed by the author (Jamieson, 1978a, 1980).

Material and Methods

Electron micrographs of the sperm of species listed in Table 1, from the sources indicated, were

Table 1. Species and sources from which spermatozoal data were obtained.

1. *Bythonomus lemani*; Ferraguti & Lanzavecchia 1977 (Lumbriculidae). (Probably *Stylodrilus lemani* (Grube).
2. *Lumbricillus rivalis*; Webster & Richards 1977 (Enchytraeidae).
3. *Rhyacodrilus arthingtonae*; Jamieson, Daddow & Bennett 1978, and original (Tubificidae). (Now *Rhizodrilus arthingtonae*; Baker & Brinkhurst 1981).
4. *Limnodriloides winckelmanni*; Jamieson, Daddow & Bennett 1978; Jamieson & Daddow 1979 (Tubificidae). (Now *L. australis* Erséus, 1982).
5. *Phreodrilus* sp. Jamieson 1981b, and original (Phreodrilidae).
6. *Haplotaxis ornamentus*; Jamieson 1982 (Haplotaxidae).
7. *Sparganophilus tamesis*; Richards, Fleming & Jamieson 1981; Jamieson, Fleming & Richards 1982; and original (Sparganophilidae).
8. *Hormogaster redii*; Ferraguti & Jamieson 1984 (Hormogastridae).
9. *Lumbricus rubellus*; Jamieson, Richards, Fleming & Erséus 1983 (Lumbriculidae).
10. *Fletcherodrilus unicus*; Jamieson 1978b (Megascolecidae).
11. *Amyntas gracilis*, original (Megascolecidae).

used to assemble the data for attributes listed in Table 2. Phenograms of spermatozoal similarity were prepared by group-average and nearest neighbour sorting from similarity matrices computed with the Gower metric from one of which an ordination was prepared by the principal coordinates procedure. A divisive classification was also constructed. Ordered values were coded as cumulative binary states and disordered multistate characters as binary states; a hierarchy was then produced using a binary divisive technique based on an information statistic (DMIS). Computations and dendrograms were prepared on the CSIRONET system of the Commonwealth Scientific and Industrial Research Organization.

Results

The analyses are based on data for the attributes shown in Table 2 obtained from the micrographs of sperm listed in Table 1. The cladistic study has required recognition of plesiomorph states detailed in Jamieson (1983). Phenetic and cladistic nearest neighbours for each species are listed in Table 3.

Phenetic analyses

The attributes used for computing affinities, whether phenetic or cladistic, and in the latter case their deduced polarity with plesiomorph and apomorph states, are listed in Table 2.

Phenetic dendrograms (Figs. 1–5) and the ordination (Fig. 10) show close congruence whether resulting from group-average (Figs. 1–3) or nearest neighbour sorting (Figs. 4 and 5) and show good agreement with relationships and taxonomic groupings proposed from general morphology by Jamieson (1978a, 1980, 1981a, 1983) (Fig. 11). Thus *Haplotaxis* and *Sparganophilus* lie at the base of the opisthoporous oligochaetes; ignoring *Phreodrilus*, *Hormogaster* links with *Lumbricus* and these lumbricoids link with the Megascolecidae (Megascolecoida) represented by *Fletcherodrilus* and *Metaphire*. Furthermore, as proposed in the previous work, the Tubificida, represented by the tubificids *Limnodriloides* and *Rhyacodrilus* and by the enchytraeid *Lumbricillus*, form the nearest-affinity group of the Haplotaxida (Haplotaxidae and families Sparganophilidae through Megascolecidae).

Table 2. Sperm attributes computed. Q1–4, qualitative (binary); D1–3, disordered multistate; N1–19, numeric attributes; 1–78 binary equivalents of these used only for the divisive analysis.

		Attribute	Plesiomorph state	Apomorph state
Q1	1	Connectives	Absent	Present
Q2	2	Connectives	Anterior	Posterior
Q3	3	Nuclear tip	Domed	Flat
Q4	4	Nuclear pad	Without	With central boss
D1	5–6	Secondary tube	Straight	(1) divergent (2) nodelike
D2	7–10	Limen	Absent	(1) conjoined (2) pointed (3) bulbous (4) flat
D3	11–12	Nucleus	Simple	(1) spiral (2) spirally flanged
N1	13–15	Acrosome length	Short	Long (3 states)
N2	16–18	Acrosome tube length	Short	Long (4 states)
N3	19–22	PAV emergence:length	Large	Small (4 states)
N4	23–25	PAV withdrawal:tube l	Small	Large (3 states)
N5	26–29	Axial rod projection:tube length	Large	Small (4 states)
N6	30–32	Axial rod projection:rod length	Large	Small (3 states)
N7	33–36	Distance axial rod to nucleus:tube length	Large	Small (4 states)
N8	37–41	Axial rod length:tube length	Large	Small (5 states)
N9	42–43	Capitulum	Absent	(1) rudiment, (2) full
N10	44–46	Axial rod width:tube width	Large	Small (3 states)
N11	47–52	Axial rod width:length	Large	Small (6 states)
N12	53–58	Axial rod fraction post PAV	Large	Small (6 states)
N13	59–61	Sec. invagination:acrosome length	Small	Large (3 states)
N14	62–65	Sec. invagination:PAV length	Large	Small (4 states)
N15*	66–68	Sec. acrosome tube:acrosome tube length	Large*	Small (3 states)
N16	–	Projection axial rod behind sec. tube:rod length	–	–
N17*	69–73	Midpiece length:width	Large*	Small (5 states)
N18	74–75	No. of mitochondria	4	(1) 6, (2) 8
N19*	76–78	No. of midpiece gyres	15*	(1) 6, (2) 3, (3) 0
or				
N19	–	Mitochondria (1) straight, (2) intermediate, (3) spiral		
N20	–	No. midpiece gyres if spiral		

*Polarity reversed for Fig. 8.

An exception to this correspondence with previous phylogenetic taxonomy based on non-spermatological data, is the close similarity of the sperm of *Phreodrilus* (also Tubificida) to those of *Hormogaster* and *Lumbricus*, a similarity already noted from intuitive considerations (Jamieson, 1982).

Insufficient data are available for lumbriculid (*Bythonomus*) sperm to allow satisfactory determination of their similarities. The significance of Figs. 2 and 3 in which the *Bythonomus* sperm groups within the Tubificida, a position not supporting the very distinct and basal position of the Lumbriculidae previously proposed (Brinkhurst & Jamieson,

1971; Jamieson, 1978a, 1981a) is therefore uncertain. *Bythonomus* was eliminated from later analyses because of the inadequacy of its data set.

Cladistic analyses

From a survey of the ultrastructure of the spermatozoa of eight oligochaete families (those for which we have an extensive knowledge for one or more species) and from a comparison with related groups (leeches and Branchiobdellida), Jamieson (1983) recognized plesiomorph states which were attributed to a hypothetical sperm type in the ances-

Table 3. Nearest neighbours of the 10 genera from matrices of sperm similarity. Phenetic data correspond with Figs. 4 and 5*. Phylogenetic data correspond with Fig. 7* and 8**.

Similarity values shown (for Figs. 4 and 7) are on an arbitrary scale but serve to show degree of resemblance, lowest values being highest similarities.

Genus	Phenetic nearest neighbour		Phylogenetic nearest neighbour*	
1. <i>Bythonomus</i>	—		—	
2. <i>Lumbricillus</i>	<i>Rhyacodrilus</i>	.24	<i>Rhyacodrilus</i>	.37
3. <i>Rhyacodrilus</i>	<i>Limnodriloides</i>	.19	<i>Limnodriloides</i>	.18
4. <i>Limnodriloides</i>	<i>Rhyacodrilus</i>	.19	<i>Rhyacodrilus</i>	.18
5. <i>Phreodrilus</i>	<i>Hormogaster</i>	.20	<i>Hormogaster</i>	.23
6. <i>Haplotaxis</i>	<i>Sparganophilus</i>	.24	<i>Sparganophilus</i>	.295
7. <i>Sparganophilus</i>	<i>Haplotaxis</i>	.24	<i>Metaphire</i>	.28
<i>Sparganophilus</i>			** <i>Haplotaxis</i>	
8. <i>Hormogaster</i>	<i>Lumbricus</i>	.20	<i>Phreodrilus</i>	.23
<i>Hormogaster</i>	* <i>Phreodrilus</i>		<i>Phreodrilus</i>	
9. <i>Lumbricus</i>	<i>Hormogaster</i>	.20	<i>Metaphire</i>	.21
10. <i>Fletcherodrilus</i>	<i>Metaphire</i>	.13	<i>Metaphire</i>	.197
11. <i>Metaphire</i>	<i>Fletcherodrilus</i>	.13	<i>Fletcherodrilus</i>	.197

* Numeric 16 eliminated.

** N15 reversed: short secondary acrosome tube plesiomorph.

** N17 & N19 reversed: short, uncoiled midpiece plesiomorph.

tral stock of the Oligochaeta. The attributes, with their plesiomorph states and apomorphic transformation series are listed in Table 2.

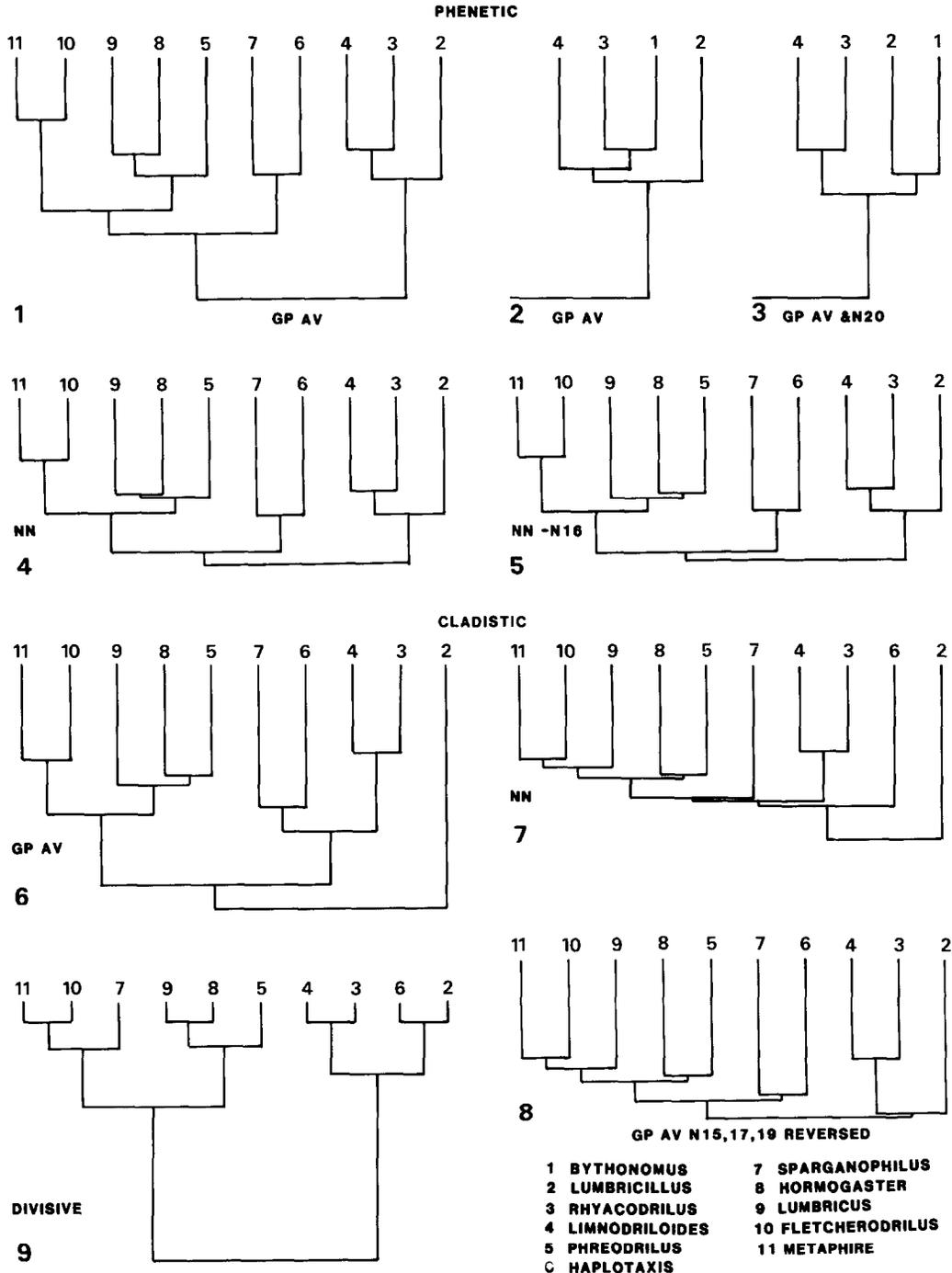
Deduced plesiomorph features not used in the computer analysis are the condition, constant in clitellates but rare among other taxonomic groups, of failure of the axoneme to penetrate the midpiece mitochondria (the sole, distal centriole or basal body lying behind the mitochondria) and a 9 + 2 axoneme differing from that of leeches and branchiobdellids in lacking a sheath around the pair of central microtubules (a notable synapomorphy of those two groups). The axoneme differs from the classical condition, however, in the addition of two supernumerary fibrils in a plane at right angles to that of the two singlets to give a tetragon configuration, as shown for many oligochaetes (see Jamieson, 1981c). *Pheretima s. lat.* (pers. observ. of *Amyntas gracilis* and *Metaphire californica*) is exceptional in having a 9 + 1 axoneme with a central core lacking evidence of singlets, though two free singlets have been demonstrated distal to the glycogen region in *A. gracilis*.

Construction of phylograms. Although the phenograms (Figs. 1–5 and the ordination, Fig. 10) validly represent overall similarity of the spermatozoa of the constituent taxa according to the similarity

measure and sorting strategies used, and although, despite frequent assertions to the contrary, phylogenetic interpretation of phenograms is not unreasonable, the objection may be levelled at them from the view-point of hennigian phylogenetic systematics that association of taxa is partly based on what is considered an invalid matching of plesiomorph states (symplesiomorphies). To obviate this problem, in the cladistic analyses, the deduced plesiomorph states have been suppressed in preparation of the matrix of coefficients of resemblance while using the same (Gower) similarity measure and the same (group-average and nearest neighbour) sorting strategies.

Comparison of phylogenies. Suppression of plesiomorphies with group-average sorting (Fig. 6) gave very similar results to the phenetic analysis (Fig. 5) with no suppression, including continued linkage of *Haplotaxis* and *Sparganophilus*, but these linked with the tubificids and the enchytraeid occupied an even more isolated position.

Suppression of plesiomorphies with nearest neighbour sorting, which is the strict hennigian approach, gave a phylogram (Fig. 7) closely resembling the phenograms and the group average phylogram in many respects but with some major differences despite a general agreement of sperm



Figs. 1-9. Phenetic and phylogenetic dendrograms of sperm ultrastructure all except 9 based on similarity matrices computed with the Gower metric, 9 being divisive. Numeric attributes 19 and 20 separate in Fig. 3, fused in all others (see Table 2). 1-3. Phenetic, group-average sorting: (1) for 10 species with numeric attributes 19 and 20 fused; (2-3) identical groupings obtained but with addition of the lumbriculid, numerics 19 and 20 fused and separate respectively. 4-5. Phenetic with nearest neighbour sorting, (4) with, (5) without, numeric 16. 6-8. Cladistic, with plesiomorphic states and numeric 16 suppressed: (6) group-average; (7) nearest neighbour sorting; (8) as 7 but with short, uncoiled midpiece and short secondary tube regarded as plesiomorph. 9. Divisive, with numeric 16 suppressed and plesiomorphic states contributing but coded as zero in cumulative scoring.

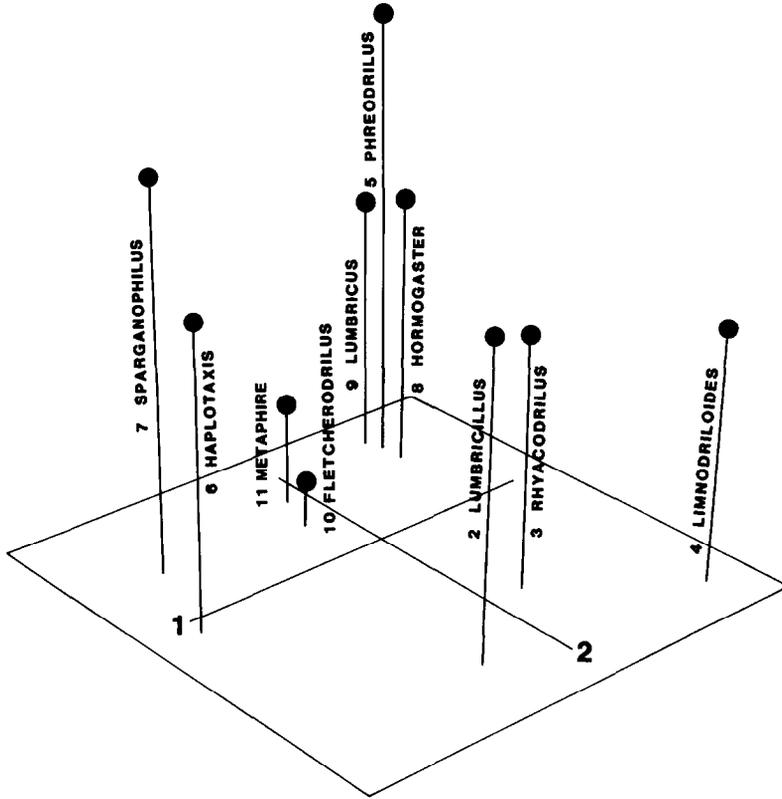


Fig. 10. Principal coordinates diagram of spermatozoal similarities, from same matrix as Fig. 4, showing vectors 1 to 3.

ultrastructure with taxonomic groupings. As acceptable phylogenies both phylograms, like the phenograms, are distorted by association of *Phreodrilus* not with the Tubificidae, with which it is conventionally placed in the Tubificida, but with one or both lumbricoids (Figs. 6 and 7). From general somatic and genital anatomy, there seems no question that *Phreodrilus* is a member of the Tubificida with sperm morphology convergent with that of megadriles rather than the opposite.

The only important divergence of the nearest neighbour phylogram from the phenograms lies in the position of *Haplotaxis*, a key genus, not least as the type-genus of the order Haplotaxida. In the phylogram (Fig. 7) it intervenes between the Tubificidae and the Enchytraeidae. This divergence disappears in the phylogram shown in Fig. 8: when the polarities of N17 and N19 are reversed and a short, uncoiled midpiece is regarded as plesiomorph and if, in addition, N15 is reversed so that a short secondary tube is considered plesiomorph, phylograms

result in which groupings are identical with the phenogram shown in Fig. 1 with the exception that *Lumbricus* (9) links first with *Fletcherodrilus* + *Metaphire* (10 and 11) (Fig. 8). In these phylograms *Haplotaxis* once more lies at the base of the opisthophores and is not associated with the Tubificida.

For the divisive analysis (Fig. 9) the polarity recognized for each attribute in the basic Gower analysis is retained but each attribute, including numerics, is represented by a shorter series of numbered states (Table 2), split into a series of binary states, in place of the raw data. The method differs notably from a strict hennigian analysis in utilizing plesiomorph states (coded as zero) but is hennigian in weighting synapomorphies. These are scored cumulatively for each attribute shared between two taxa. The method produces a dendrogram of monothetically defined groups.

The divisive analysis (Fig. 9) corresponds in many respects with the hennigian analyses using the Gower metric (Figs. 6 and 7) and detailed compari-

son is unnecessary. *Sparganophilus* and *Phreodrilus* remain linked with the higher opisthopores, as in the phenograms, but *Sparganophilus* is linked with the megascolecids, not an acceptable placing

phylogenetically (see Jamieson, 1978a). *Haplotaxis* shows a still closer association with the Tubificida as it constitutes the sister-group of the enchytraeid.

It is thus seen that various cladistic strategies

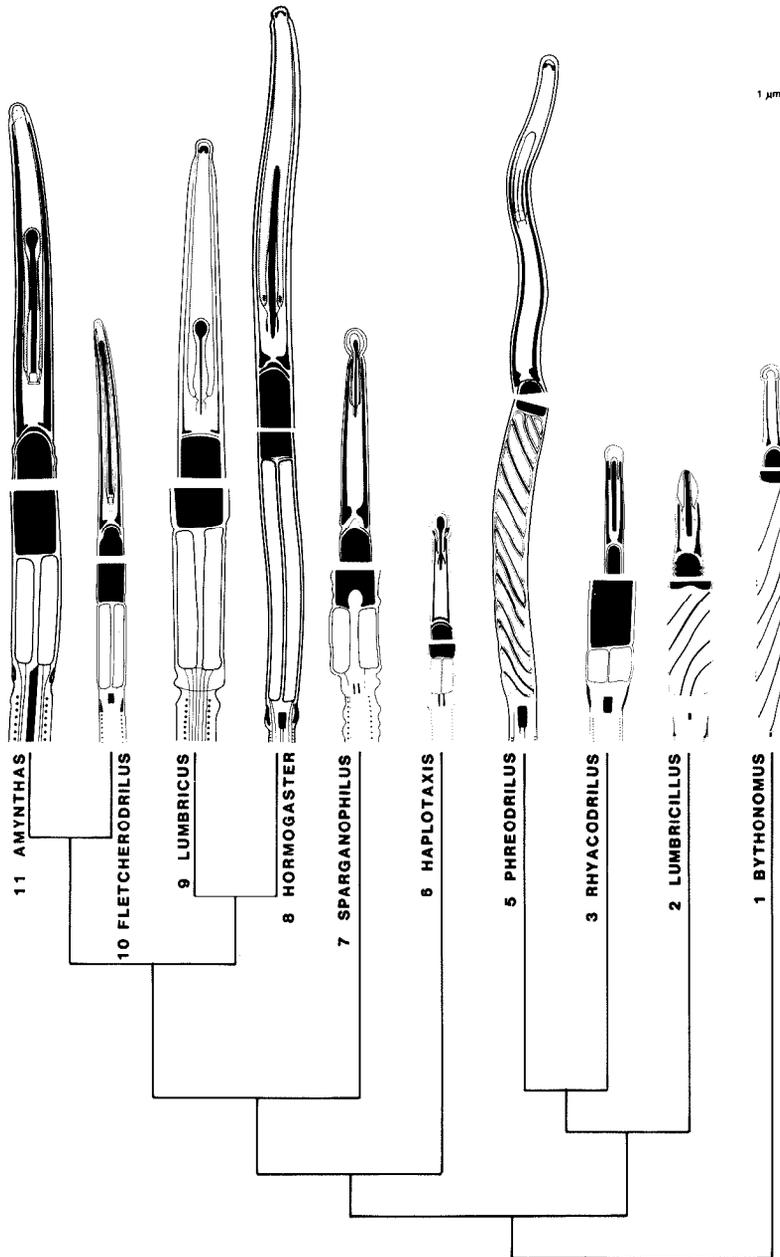


Fig. 11. Holomorphic phylogram (based on general, non-spermatzoal anatomy) for the families investigated in the present study, with sperm drawings (all to same scale) superimposed. *Pheretima s. lat.* is here represented by *Amynthus gracilis*, the sperm of which, though having a longer acrosome, closely resembles that of *Metaphire californica*. The portion from *Haplotaxis* to *Amynthus* is drawn from a Hennigian analysis of Jamieson (1978a), the remainder, for microdriles, is based on intuitive considerations (Jamieson, 1978a, 1981a). (From Jamieson, 1983).

produce phylograms with only limited mutual consistency although considerable similarity to conventional taxonomic groupings and to previously derived phylogenies based on holomorphological data is still demonstrated.

We may, alternatively to deriving phylograms from spermatozoal ultrastructure alone, examine congruence of this with the earlier non-spermatological holomorphological phylogeny and attempt to deduce the pathways which evolution of sperm structure has taken from the hypothetical plesiomorph sperm which was proposed above. This examination was made by Jamieson (1983) and is summarized in Fig. 11. The holomorphological phylogeny, originally for eighteen families, is represented in Fig. 11 for the five of these families for which sperm data are available. Added to the phylogram are tubificids, phreodrilids and enchytraeids in accordance with phylogenetic proposals by Jamieson (1978a, 1981a). It has many points of similarity with the phenograms. For a detailed discussion of origin of the spermatozoa of the various families from the plesiomorph precursor, see Jamieson (1983). The chief trends there deduced are summarized in the discussion below. These trends may be recognized independently of whether the holomorphological phylogram be accepted or not.

Discussion

The relationships in spermatozoal ultrastructure which have been demonstrated from phenetic and phylogenetic numerical analyses show close congruence in many respects with classification of the component oligochaete genera, representing their respective families, obtained by intuitive means or in holomorphological hennigian phylogenetic systematics (Jamieson, 1978a).

Congruence of the phenetic systems mutually and with the hennigian analysis of general morphology includes delimitation of the opisthoporoid oligochaetes (*Sparganophilus*, *Hormogaster*, *Lumbricus*, *Fletcherodrilus* and *Metaphire*) as a distinct grouping; cohesion within these of the lumbricoids (*Hormogaster* and *Lumbricus*) as a group distinct from but the nearest affinity or sister-group of the well-defined megascolecoid grouping (*Metaphire* and *Fletcherodrilus*); linkage of *Sparganophilus* basally with the lumbricoid-megascolecoid assemblage; and

cohesion of the Tubificidae and linkage with these of the Enchytraeidae, represented by *Lumbricillus*, as the nearest-affinity (sister) group. In the phenetic analyses *Haplotaxis* forms a pair-group with *Sparganophilus* at the base of the opisthopores.

A notable exception to congruence with previous systems is seen in linkage of *Phreodrilus* with the lumbricoids, reflecting a remarkable divergence of its sperm structure from that of the Tubificida, to which it belongs, and convergence towards that of 'megadriles' or, more specifically, the lumbricoids. Phreodrilids evidently constitute an exception to the general rule that sperm structure and related fertilization biology correspond with taxonomic groupings erected on non-spermatological criteria. Phreodrilid fertilization biology is under investigation. From inadequate spermatozoal data, the prosoporoid *Bythonomus* (Lumbriculidae) groups with the enchytraeid or with the Tubificidae.

The cladistic procedures (Gower and divisive) produce variable phylograms, though these have major areas of agreement with the phenograms particularly with regard to placement of lumbricoids, megascolecids and *Phreodrilus*. The Gower metric is noteworthy in giving a very plesiomorph status to the Enchytraeidae; it and the divisive procedure link *Haplotaxis* more or less closely to the Tubificida. However, when a short, uncoiled midpiece and short secondary tube are regarded as plesiomorph, *Haplotaxis* retains its association with the opisthopores; enchytraeids, while again the most plesiomorph group, do not appear as distinctly basal as in the first Gower phylogeny, *Sparganophilus* has very equivocal affinities in the cladistic analyses, linking with the opisthopores or with *Haplotaxis* and hence the Tubificidae or (divisively) with the megascolecids. It must be stressed that the fact that *Haplotaxis* always has *Sparganophilus* as its nearest neighbour in phenetic and cladistic Gower spermatological analyses supports the conclusion that *Haplotaxis* is closer to the alluroidid through megascolecoid assemblage in the Haplotaxida *sensu* Jamieson (1978a) than to the Tubificida or Lumbriculida. To elevate the Haplotaxidae to ordinal rank, and create a separate order Lumbricida for the related assemblage, as Brinkhurst (1982b, 1984) has done would therefore necessitate elevation of the Tubificida to a rank above the level of order.

A hypothetical plesiomorph spermatozoon has been proposed by Jamieson (1983). The chief trends

from its plesiomorphies have been elongation of the acrosome and its tube; withdrawal of the PAV and the axial rod into the acrosome tube and development of a capitulum; development of connectives from the secondary tube to the axial rod (though there is some possibility that the reverse, absence of connectives, is apomorph); detorting and shortening of the midpiece (again, conceivably to be reversed) with an increase in numbers of mitochondria from the plesiomorph four to eight; modification of the base of the tube to form a limen of variable form; and, in one line (lumbricids) flattening of the tip of the nucleus and correspondingly of the limen.

The exceedingly plesiomorph condition of the enchytraeid sperm, with regard not only to the Lumbricina but also to their closest relatives, the Tubificina strengthens support for regarding the enchytraeids as the most plesiomorph oligochaetes with the possible exception of the Lumbriculidae the sperm of which is imperfectly known. Peculiar features of enchytraeids which are presumably autapomorphies are the double secondary tube and spirally flanged nucleus in the sperm (though requiring confirmation from further species) and, in the adult, the unique glandular postseptal region of the male funnels, and possibly the multiple batonsetae. Whether the frequent confluence of the spermathecae with the gut (also seen in some Tubificidae) is apomorph is debatable. The glandular funnels are here considered to support the view that absence of glands adding secretion to the seminal fluid is plesiomorph in the Oligochaeta and that development of such glands has proceeded in two distinct ways, specialization of the sperm funnels in enchytraeids or development of prostate glands, usually associated with atrial chambers of various forms, in other Tubificida and in some members of all groups of the Haplotaxida (with the notable exception of the Haplotaxidae).

It has been suggested previously (Michaelsen, 1928; Brinkhurst & Jamieson, 1971; Jamieson, 1980, 1981a) that the Lumbriculidae are the most plesiomorph living oligochaetes, the grounds for this being chiefly their prosoporous male genitalia. Unfortunately, sperm data have not been sufficient to aid a decision as to the validity of this view. On the few data available they show affinity with the Tubificida rather than basally with oligochaetes as a whole. Brinkhurst (1984), in a profound and sig-

nificant analysis, has abandoned our earlier view of the basal position of the Lumbriculida. He suggests that the prosoporous condition is derived from the plesioporous condition seen in Haplotaxidae. As foreshadowed in Brinkhurst & Jamieson (1971), he regards the frequently multigonadial condition of lumbriculids as an aberration due to parthenogenesis and not as evidence for a multigonadial origin of the Oligochaeta. Hrabě (1984), like several earlier workers, also argues strongly for regarding the prosoporous condition as a secondary derivation from a primitive, plesioporous condition.

The double penetration by the vasa deferentia of the septum bearing the prosoporous male funnels in lumbriculids is certainly enigmatic but there remain reasons for caution in considering this to be strong evidence for former plesiopory, as Brinkhurst and Hrabě do. (If this were accepted double penetration of a septum anterior to the male pores in moniligastrids might have to be taken as evidence for earlier prosopory of the Moniligastridae). The presence in the lumbriculid *Rhynchelmis* of vestigial atria, without male ducts, in a segment preceding that with functional atria which receive two pairs of vasa, one pair from the same segment and one pair from the preceding segment with its vestigial atria, has been used for (Brinkhurst, in Brinkhurst & Jamieson, 1971) and against (Hrabě, 1984) acceptance of a former prosopory. Possibly the prosoporous condition in acanthobdellid leeches, in which the single pair of testes (there in segment 10) is associated with a pair of male ducts discharging posteriorly in the same segment, represents the primitive condition for clitellates, though not in numbers of such genital segments. Branchiobdellids (with the *Rhynchelmis*-type plesio- and prosopory in a single segment), lumbriculids and acanthobdellids were placed in the Lumbriculida by Michaelsen (1928). Brinkhurst (1984) supports regarding the plesiopore condition as primitive on the grounds that this is also the condition for the female ducts. However, the female pores are 'prosoporous' in questid polychaetes and aeolosomatids, a further support for the present author's view that gonoducts, as modified coelomoducts, primitively discharged in the segment of their gonads. The female ducts are virtually prosoporous in lumbriculids and the Tubificida while in the Haplotaxida, including *Haplotaxis* and 'megadriles' they are plesioporous. Supposed transformation of plesioporous male

pores to the prosoporous condition in lumbriculids (Brinkhurst, 1983) is contrary to a well-defined and unequivocal trend for posterior migration of the pores in oligochaetes (with male pores in segments 12 and 13 in haplotaxids, 13 in alluroidids and some lumbriculids, 15 in most lumbriculids, 17 or 18 in many megascolecids and further posteriorly in other groups, including sparganophilids and lutodrilids, to cite some examples). There is no more reason to suppose that female pores have made the anteriorwards migration.

The view that plesioptory is the primitive condition of both male and female ducts probably stems from the common misconception that oligochaete gonoducts are modified nephridia. Thus Giere & Riser (1981) state, in their valuable paper on oligochaetoid polychaetes, that among the important synapomorphies characterizing the Clitellata is 'the gonoduct being derived from segmental organs', the latter, interestingly, an archaic term for nephridia. However, utilization of nephridia as gonoducts, though suspected in the Aeolosomatidae and seen in some polychaetes is not a basic annelid, or clitellate, condition. Some capitellid polychaetes have separate coelomoducts (as gonoducts) and nephridia in the same segment, many other polychaetes have combinations of the two (references in Schroeder & Hermans, 1975) and, more importantly, male and female funnels and their ducts coexist intrasegmentally in oligochaetes (e.g. Jamieson, 1970a, b; Reynolds, 1980). The fact that in most of these forms the coelomoducts are also 'plesioptorous' does not militate against regarding the plesiomorph coelomoduct to have opened to the exterior in the segment of its funnel as argued above. Certainly, the fiction that clitellate gonoducts are nephridia must be finally discarded.

With regard to number of gonads in ancestral oligochaetes, Brinkhurst's contention that opisthopores and the Tubificida are derivable from octogonadial forms is persuasive. However, it also seems reasonable to envisage that early annelids, including the first oligochaetes, had longer series of gonads, as in lumbriculids (see Jamieson, 1981a). In support of this is the multigonadial condition of many polychaetes (with no suggestion that polychaetes were ancestral to oligochaetes), of aeolosomatids (*Aphanoneura*) and leeches.

To conclude, the ultrastructure of spermatozoa unifies the oligochaetes and, while setting them

apart from the Branchiobdellida and the Hirudinea, indicates their closer relationship to these groups than to other annelids. The spermatozoal ultrastructure of many oligochaete families, of the Acanthobdellidae and the aeolosomatids awaits investigation, however.

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