

PHYLOGENETIC AND PHENETIC SYSTEMATICS OF THE
OPISTHOPOROUS OLIGOCHAETA (ANNELIDA: CLITELLATA)

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ABSTRACT: The methods of Hennig for deducing phylogeny have been adapted for computer and a phylogram has been constructed together with a stereophylogram utilizing principle coordinates, for all families of opisthoporous oligochaetes, that is, the Oligochaeta with the exception of the Lumbriculida and Tubificina. A phenogram based on the same attributes compares unfavourably with the phylograms in establishing an acceptable classification. Hennig's principle that sister-groups be given equal rank has not been followed for every group to avoid elevation of the more plesiomorph, basal clades to inacceptably high ranks, the Oligochaeta being retained as a Subclass of the class Clitellata. Three orders are recognized: the Lumbriculida and Tubificida, which were not computed and the affinities of which require further investigation, and the Haplotaxida, computed. The Order Haplotaxida corresponds precisely with the Suborder Opisthopora of Michaelsen or the Sectio Diplotesticulata of Yamaguchi. Four suborders of the Haplotaxida are recognized, the Haplotaxina, Alluroidina, Moniligastrina and Lumbricina. The Haplotaxina and Moniligastrina retain each a single superfamily and family. The Alluroidina contains the superfamily Alluroidoidea with the families Alluroididae and Syngenodrilidae. The Lumbricina consists of five superfamilies. Of these the Biwadriloidea and Sparganophiloidea superfam. nov. contain each a single genus and family. The Almoidea superfam. nov. contains the families Almidae and Criodrilidae and, provisionally, the Lutodrilidae. The Lumbricoidea is constituted by the Lumbricidae (redefined to include the Diporodrilidae as a subfamily), Komarekionidae, Kynotidae, Glossoscolecidae s. strict., Microchaetidae and Hormogastridae (redefined to include the Ailoscolecidae as a subfamily, with the Hormogastrinae and Vignysinae formerly included). The Megascolecoidea, as previously, contains the Megascolecidae, Eudrilidae and Ocnerodrilidae, although the phylogram indicates that the Ocnerodrilidae should be placed in a separate and primitive superfamily of the Lumbricina.

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Introduction

A higher, suprafamilial, classification of the Oligochaeta has been attempted by Benham (1890), Beddard (1895, 1901), Michaelsen (1921, 1928, 1929, 1930), Meyer (1929) and Yamaguchi (1953) and Brinkhurst and Jamieson (1971). Of these, those of Michaelsen (1930), of Yamaguchi and of the latter two authors are the most pertinent to a contemporary discussion of the phylogeny of the earthworms. A study of the phylogeny of earthworms cannot be divorced from consideration of that of the Haplotaxidae and the Alluroididae, the total complex comprising the Opisthopora of Michaelsen, (1930), the Subsectio Diplotesticulata of Yamaguchi (1953), or the order Moniligastrida and the order Haplotaxida, ignoring the suborder Tubificina, in the system of Brinkhurst and Jamieson. Jamieson (1976) has reduced the orders of the Oligochaeta to two, the Lumbriculida

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and the Haplotaxida, by inclusion of the Moniligastridae as a suborder Moniligastrina in the Haplotaxida following reinterpretation of the nature of the moniligastrid testis-sac and construction of a phylogeny of the Moniligastridae according to the principles of Hennig.

Gates (e.g. 1972) recognized no categories between the order Oligochaeta and the familial ranks, and therefore attempted no groupings (other than an alphabetic listing) of the families Acanthodrilidae, Alluroididae, Criodrilidae, Eudrilidae, Glossoscolecidae (s.strict.) Haplotaxidae, Hormogastridae, Lumbricidae, Megascolecidae, Microchaetidae, s. Gates, Moniligastridae, Ocnerodrilidae, Octochaetidae and Sparganophilidae. In 1976, however, Gates recognized a suprafamilial grouping, the Lumbricoidea, more restricted in constitution than that of Brinkhurst and Jamieson, to include those families known or supposed to have ovaries with a single egg string, the Lumbricidae, Biwadrilidae, Komarekionidae, Lutodrilidae, Sparganophilidae, Hormogastridae, Ailoscolecidae and Diporodrilidae, all holarctic groups. Inclusion of the Biwadrilidae went contrary to a statement of Nagase and Nomura (1937:348) for the type-species that the ovary "becomes divided into lobes" and the author is unable to trace the evidence for regarding the ovaries of the Ailoscolecidae and Diporodrilidae as single-stringed. The remaining families, with the possible exception of the Hormogastridae, are well known to possess single-stringed ovaries, however. The only monothetic character of the Lumbricoidea s. Gates is the ovariañ one and the present study attempts to elucidate the significance of this shared character.

One of the major differences between the systems proposed by Jamieson (1971d, 1976a) and the classification, albeit solely at a familial level, of Gates lies in his treatment of those familial or subfamilial taxa typified by *Glossoscolex*, *Microchaetus*, and *Alma*. Jamieson (1971d) has argued that *Alma* and other genera grouped with it should be removed from the Microchaetidae, in which, on the basis largely of posttesticular spermathecae, they were placed by Michaelsen and Gates, and that the African genera *Microchaetus* and *Tritogenia* have their closest relatives in the S. American Glossoscolecidae such as *Glossoscolex* and *Pontoscolex*. The S. American genera *Drilocrius* and *Glyphidrilocrius* are regarded as belonging with *Alma* in the Alminae (Jamieson, 1971d) or Almidae (Jamieson, 1976a). *Criodrilus* is grouped with *Alma*, though as a separate tribe or subfamily but a special affinity between *Criodrilus* and the Lumbricidae is recognized (Jamieson, 1971d). Omodeo (1956) anticipated the author in recognizing that *Alma* and *Drilocrius* were widely separate from *Microchaetus* and from the Glossoscolecoid earthworms, although the group to which they belonged was not named. The family Microchaetidae was reconstituted to contain *Callidrilus* and *Glyphidrilus*, which the author considers closely related to *Alma* and *Drilocrius*, in addition to *Microchaetus* and *Tritogenia*. *Kynotus* was also included in the Microchaetidae in which *Hormogaster* formed a subfamily, the Hormogastrinae. *Lumbricus* was considered by Omodeo to be descended from a form similar to *Criodrilus*, as supported by Jamieson (1971d).

A further major area of debate has been the classification of the Family Megascolecidae in sensu lato of Stephenson (1930). The alternative classifications of Stephenson (1930), Michaelsen (1933), Pickford (1937), Omodeo (1958), Lee (1959), Gates, (1959) and Sims (1966, 1967) have been extensively reviewed by Sims (1966) and Jamieson (1971b) and it will suffice here to note the chief areas of disagreement in the proposals of Gates (1959), Sims (1967) and Jamieson (1971a). Gates (1959) recognized four distinct families for the Megascolecidae s. Stephenson: the Megascolecidae (racemose prostates), the Acanthodrilidae (with tubular prostates and meronephridia) and the Ocnerodrilidae (prostates and nephridia as the

Table 1

Species Computed

- Species are the types of their genera except where asterisked.
- 1.* *Haplotaeniæ violaceus* (Beddard, 1891); Brinkhurst, 1971: 294 New Zealand
 2. *Alluroidea pondagei* Beddard, 1894; Jamieson, 1971d: 713-714 E. Africa
 3. *Brinkhurstia americana* Jamieson, 1968b: 80-81. S. America
 4. *Standeria transvaalensis* Jamieson, 1968b: 82-84 S. Africa
 5. *Syngonodrilus lamensis* Smith & Green, 1919; Jamieson, 1971d: 718-719 E. Africa
 - 6.* *Montigaster troyi* Jamieson, 1977a: 111-113 India
 7. *Besmogaster dorica* Rosa, 1890; Gates, 1972: 242 Burma
 8. *Biwadriulus bathybatēs* (Stephenson, 1917); Jamieson, 1971d: 809-810 Japan
 9. *Sparganophilus tamesis* Benham, 1892; Jamieson, 1971d: 812-815 N. America & England
 10. *Alma nilotica* Grube, 1855; Jamieson, 1971d: 786-788 E. Africa
 11. *Glyphidrilus weberi* Horst, 1889; Jamieson, 1971d: 766-768 Java
 12. *Driiloerius alfari* (Cognetti, 1904); Jamieson, 1971d: 795-796 S. America
 - 13.* *Driiloerius hummelincki* Michaelsen, 1933; Jamieson, 1971d: 799-800 S. America
 14. *Glyphidrilus ehrhardti* (Michaelsen, 1926); Jamieson, 1971d: 802-803 S. America
 15. *Callidrilus scrobifer* Michaelsen, 1890; Jamieson, 1971d: 744-745 Central Africa
 - 16.* *Callidrilus ugandaensis* (Jamieson, 1968a); Jamieson, 1971d: 745-746 E. Africa
 - 17.* *Microchaetus benhami* Rosa, 1891; Pickford, 1975: 24-31 S. Africa
 - 18.* *Glossocoelax paulistus* Michaelsen, 1926; Righi, 1971: 48-49; 1972: 1-97 S. America
 - 19.* *Pontocoelax corethrusus* (Muller, 1856). Gates, 1972: 54-58; Righi, 1972: 155-178; Jamieson m.s. S. America
 20. *Kyotus darwini* (C. Keller, 1887); syn. *K. madagascariensis* Michaelsen, 1891: 3-8; Kynotinae; Jamieson, 1971d: 740 Madagascar
 21. *Hormogaster redii* Rosa, 1887; Omodeo, 1948: 6-10. Bouché, 1970: 247; 1972: 200-201. Hormogastrinae Stephenson, 1930: 903; Jamieson, 1971d: 728; Hormogastridae Gates, 1972: 60-61 Italy
 22. *Vignysa popi* Bouché, 1970: 249-250; 1972: 210-212 France
 23. *Hemigastrodriulus monticae* Bouché, 1970: 248-249; 1972: 208-209 France
 24. *Diporodrilus pilosus* Bouché, 1970; 1972: 463-465 France
 25. *Atlosoelax lacteospinosus* Bouché, 1969: 525-531; 1972: 197-199 France
 26. *Komamekiona eatoni* Gates, 1974: 2-12 U.S.A.
 27. *Lutodrilus multivesiculatus* McMahan, 1976: 6-8 U.S.A.
 28. *Criodrilus lacuum* Hoffmeister, 1845; Jamieson, 1971d: 804-806 Germany
 29. *Limbriicus terrestris* Linnaeus, 1758; Sims, 1972: 27-33; Gates 1972: 118-123 Europe
 30. *Eiseniella tetraedra* (Savigny, 1826); Jamieson, 1967: 70-74; Gates, 1972: 108-113 Europe
 31. *Oenerodrilus occidentalis* Eisen, 1878; Gates, 1972: 273-275 California and circumundane
 32. *Eukerria garmani argentinae* Jamieson, 1970: 143-144 S. America
 33. *Eudrilus eugeniae* (Kinberg, 1867); Gates, 1942: 137-143; 1972: 51-53
 34. *Nemertodrilus griseus* Michaelsen, 1890; Jamieson, m.s. British Museum Registration Number 1904. 10.5.959-61. Mozambique
 35. *Microcoelax (Notiodrilus) georgianus* (Michaelsen, 1889); Jamieson, 1974c: 61-64 S. Georgia
 36. *Diploptrema fragilis* Spencer, 1900; Jamieson m.s. National Museum Victoria G31 Australia
 - 37.* *Diploptrema* sp. (meronephric species); Dyne m.s. Australia
 38. *Octochaetus multiporus* (Beddard, 1885); Beddard, 1895: 351, Lee, 1959: 115-116; Jamieson, m.s. New Zealand
 39. *Perronyx excavatus* Perrier, 1872; Gates, 1972: 141-143 Saigon and circumundane
 40. *Heteropodrilus tryoni* (Fletcher, 1889); Jamieson, 1970a: 125-129 Australia
 41. *Diporochaeta intermedia* (Beddard, 1889); Jamieson, 1976: 37-44
 42. *Cryptodrilus rusticus* Fletcher, 1887; Jamieson, 1972: 156-159 Australia
 - 43.* *Dichogaster bolawi* (Michaelsen, 1891); Jamieson, m.s. Queensland; Gates, 1972: 279 Hamburg and circumundane
 - 44.* *Dichogaster oraeivivis* (Cognetti, 1904); Jamieson, 1974: 80-82 Costa Rica
 - 45.* *Dichogaster bradburyi* Jamieson, 1970: 35-40; 1975: 275-276 Australia
 46. *Megascolides australis* Spencer, 1888; Jamieson, m.s. Australia
 - 47.* *Spenceriella penolaensis* Jamieson, 1974: 105-106 Australia
 - 48.* *Lampito sylvicola* Michaelsen, 1907; Jamieson, 1977b: 498-501 India.
 - 49.* *Celerrella bursata* Jamieson, 1977b; 487-489 India
 50. *Pheretima montana* Kinberg, 1867; Sims & Easton, 1972: 219-221; Gates, 1972: 148-149 Tahiti (Indonesia or Malaysia?)

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Acanthodrilidae but hearts confined to X-XI, intestinal origin in or usually anterior to XIV, calciferous tissue in IX-X). Sims (1966), approved Gates classification as a result of a taxonomic investigation but later (1967), while retaining the same groupings and the criteria for these, suggested a special affinity with each other of three of the groups which became the subfamilies Ocnerodrilinae, Acanthodrilinae and Octochaetinae within the family Acanthodrilidae, the Megascolecidae remaining as a distinct family. In a series of papers Jamieson (1970a, 1971a, b, c, e, 1972a, b, 1974a) and Jamieson and Nash (1976) have refuted division on the basis of prostatic morphology and of holonephry versus meronephry, as proposed by Gates, on the grounds that this would split homogeneous groups even at the generic level. Division of the Megascolecidae into three subfamilies was proposed: the Ocnerodrilinae, Acanthodrilinae and the Megascolecinae. While the constitution of the Ocnerodrilinae did not differ from Gates' Ocnerodrilidae, the author (Jamieson, 1971b) presents evidence in agreement with Gates' view that ocnerodriles are very distinct from other megascolecoids and (1971d) questions the belief that Eudrilidae (also placed in the Megascolecoidae) are descended from ocnerodriles. The constitution and definition of the Acanthodrilinae and Megascolecinae s. Jamieson is radically different from that of Gates and of Sims. Full definition of these subfamilies and their tribes is given in Jamieson (1971a-c) but the following may be noted in relation to the phylogeny discussed below. The Megascolecinae consists of three tribes, the Perionychini, the Dichogastrini and the Megascolecini. The Perionychini have tubular to racemose prostates, are partly or wholly holonephric and have the male and prostatic pores on segment XVIII, the megascolecic arrangement of pores. The Dichogastrini are meronephric with, caudally, a stomate nephridium median to astomate micromeronephridia; prostates are tubular to racemose; and the male pores are acanthodrilin or megascolecic. The author has since formed the opinion that the Dichogastrini may be at least diphyletic. This is suspected because all African dichogastrins have acanthodrilin male pores and the Acanthodrilinae are well represented in Africa while perionychins (with the megascolecic arrangement) are absent, while Australian dichogastrins have megascolecic (perionychin) pores and perionychins are very numerous in Australia. The third megascolecic group, the Megascolecini, typically has megascolecic male pores, racemose or tubular prostates and is exclusively meronephric with very diverse nephridial conditions, often including multiple nephrostomes per segment; any median stomate nephridium is (always?) enteronephric. The Acanthodrilinae are heterogeneous with regard to the male pores and nephridia, but the pores are usually acanthodrilin (prostate pores paired in XVII and XIX, male pores in XVIII) and never show the megascolecic arrangement and the nephridia are usually holonephric, though partial or total meronephry has supervened in some; prostates are tubular or rarely racemose.

The choice of species for the phylogenetic analysis will allow detailed investigation of the validity in terms of phylogenetic systematics of former classifications of the lumbricoid, especially almid, genera but less profound evaluation of the affinities of the megascolecoid genera (Table 1).

Methodology

The methods here employed are (1) a modification of the phylogenetic systematics of Hennig (1966) and (2) a phenetic method derived from principles reviewed by Sokal and Sneath (1963) and Sneath and Sokal (1973), here using the set of attributes selected for the phylogenetic analysis.

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(1) Phylogenetic

Methods for deducing branching sequences representative of the evolution (phylogeny) of animal groups require decisions as to the direction of change which has occurred in attributes which exist in more than one state. In terms of numerical, phenetic taxonomy these attributes may be binary (e.g. dorsal pores absent or present), ordered multistate (e.g. male pores in segment 12, 13, 14.. n) or disordered multistate (e.g. caudal nephrostomes per side one, or more, or none). Sneath and Sokal (1973:10) who insist that evolutionary branching sequences must be inferred largely from phenetic relationships among existing organisms nevertheless indulge in such decisions as to direction of change and, indeed, Sokal has contributed a valid and precise method (Camin and Sokal, 1965) for deducing the most parsimonious phylogeny for organisms with a given set of characters. Their methodology provides a mechanism for dealing with ordered multistate characters, that is "transformation series" from the primitive (plesiomorph) to a sequence of advanced states (apomorphies) in the terminology of Hennig (1966). Such alternative apomorphies cannot be satisfactorily treated in Hennig's method even when regarded (e.g. Ball, 1973) as non-congruent apomorphies. This problem is especially evident when dealing with translocation of organs in evolution through successive metameres in metamerically segmented animals and is further discussed, with an attempt at solution, below. We are initially, however, concerned with the argumentation for deducing direction of change in all characters, whether binary or multistate.

Several authors have proposed sets of criteria which they consider to allow deduction as to the direction of change, which state of an attribute is primitive (plesiomorph) and which advanced (apomorph). While the criteria proposed are in some cases unacceptable, often on the grounds of circularity, it is important to note that decisions of a phylogenetic nature are not necessarily less valid than deductions in other areas of science where inferences are drawn from observed phenomena. The criticism that they are untestable and therefore are not to be regarded as part of deductive logic seems inappropriate when it is considered that, where the aim is merely the most parsimonious phylogeny, the efficacy of methods such as that of Camin and Sokal in retrieving a hypothetical phylogeny can readily be demonstrated and that the accuracy of inference as to direction of change can also be shown to be high on the basis of "invented" phylogenies for hypothetical animals (e.g. Camin's imaginary animals Sokal, 1966). The difficulty of convincingly proposing criteria for diagnosing plesiomorphy and apomorphy appears greater than that of intuitively recognizing these states for a group which is well known to the worker concerned. The "unreconstructed logic" (*sensu* Hull, 1970) of intuitive decisions may be retrievable for each character in turn but the erection of criteria for the set of characters may be elusive.

Selection of characters

The characters selected were those features of the general anatomy of the oligochaetes concerned, embracing as many organ systems as possible, which presented characters resolvable into more than one state. This approach appears to differ from that of Hennig (1966) and Brundin (1965, 1966) who commence by a "search for the sister-group" and for the internal apomorphies which define groups.

Table 2
Attributes Employed

Two State

- 1 Prostomium attached to peristomium (p) or separate (a)
- 2 Lateral lines present (p) or absent (a)
- 3 Dorsal pores absent (p) or present (a)
- 4 Caudal cross section not quadrangular (p) or quadrangular (a)
- 5 Anus terminal (p) or dorsal (a)
- 6 Copulatory alae absent (p) or present (a)
- 7 Claspers bearing male pores absent (p) or present (a)
- 8 Genital lobes or claspers lateral to male pores absent (p) or present (a)
- 9 Longitudinal tubercula pubertatis absent (p) or present (a)
- 10 Somatic setae in 4 bundles (p) or perichaetine (a)
- 11 Penial setae distinct from any other genital setae absent (p) or present (a)
- 12 Longitudinally grooved genital setae absent (p) or present (a)
- 13 Prostate-like setal glands absent (p) or present (a)
- 14 Clitellum unilayered (p) or multilayered (a)
- 15 Dorsal vessel continued onto the pharynx (p) or not (a)
- 16 Subneural vessel absent (p) or present (a)
- 17 Muscular thickening of intestine absent (p) or present (a)
- 18 Intestinal caeca absent (p) or present (a)
- 19 Intestinal typhlosole absent (p) or present (a)
- 20 Paired enterosegmental organs absent (p) or present (a)
- 21 Holonephric (p) or meronephric (a)
- 22 Nephridial bladder absent (p) or present (a)
- 23 Nephridial caeca absent (p) or present (a)
- 24 Caudal nephridia exonephric (p) or enteronephric (a)
- 25 Testes in 10 (p) or absent from 10 (a)
- 26 Testes in 11 (p) or absent from 11 (a)
- 27 Male pores per side, two (p) or one, by fusion (a)
- 28 Purely muscular male bursa absent (p) or present (a)
- 29 Glandular male bursa absent (p) or present (a)
- 30 Ovaries in 12 (p) or absent from 12 (a)
- 31 Ovaries in 13 (p) or absent from 13 (a)
- 32 Ovaries multistringed (p) or single-stringed (a)
- 33 Ovaries free (p) or in septal chambers (a)
- 34 Spermathecae present (p) or absent (a)
- 35 Spermathecae a pair or median per segment (p) or multiple (a)
- 36 Spermathecae discrete (p) or communicating with the oviducts (a)

OM Ordered Multistate

- 1 Supra-oesophageal vessel absent (p), oesophageal only (a1) or oesophageo-pharyngeal (a2)
- 2 Commissurals throughout (p) or discrete hearts to 11, 12 or 13 (a1-3)
- 3 Number of segments with oesophageal gizzard o (p) 1, 2, 3-12 (a1-12)
- 4 Segment of first oesophageal gizzard (*), 5-13 (a1-9)
- 5 First intestinal segment 9 (p), 10-38 (a1-29)
- 6 Last male pores posterior to 11 or equivalent by 1 (p) 2-16 segments (a1-15)

DM Disordered Multistate

- 1 Setal interval $cd = ab$ (p) or $> ab$ (a1) or $< ab$ (a2)
- 2 Caudal nephrostomes per side one (p) or more (a1) or none (a2)
- 3 Testis-sacs absent (p) or segmental (a1) or "intra-septal" (a2) or capping the testes (a3)
- 4 Seminal vesicles extensive (p) or short (a1) or absent (a2)
- 5 Male pores anteriorly on the clitellum (p) or anterior to it (a1) or on posterior region or behind it (a2)
- 6 Prostates absent (p) or tubular (a1) or tubuloracemose-racemose (a2) or capsular (a3) or euprostatic (a4)
- 7 Last spermathecae pretesticular (p) or testicular (a1) or post-testicular (a2)
- 8 Spermathecae adiverticulate (p) or with seminal diverticulum (a1) or with non-seminal diverticulum (a2)
- 9 Prostates absent or arrangement acanthodrilin (a1) or microscolecin (a2) or megascolecin (a3)

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The phylogenetic procedure adopted here agrees with that of Hennig and Brundin in recognizing phylogenetic affinity only on the basis of shared advanced characters (synapomorphies) and, unlike Camin and Sokal, ignoring symplesiomorphies though the methodology of the latter workers appears no less valid.

Hennig's mode of constructing phylogenies on the basis of synapomorphies is duplicated by computer means by summing shared character states of each species (OTU) against each of the other species so as to give a matrix of scores equivalent to a matrix of coefficients of resemblance (here computed as distance). Only "positive matches" (synapomorphies) are counted and the absolute sum of the matches between two OTU's is used as the coefficient of similarity without recourse to division by the number of characters. A special procedure, and metric has been adopted for any character for which different states are differences in metameric location only. An example is character OM 6 in Table 2, last male pores posterior to segment 11 (or moniligastrid equivalent) by 1 (plesiomorph state) 2-16 segments (15 apomorph states). This character may be regarded as having 15 sequential apomorph states, beyond the plesiomorph state, believed to represent an actual posteriad segment by segment migration of the pores in evolution. To allow each of these segmental positions the value of a full character would have grossly overweighted position of the male pores relative to other characters. A single character only is therefore used. Two species sharing the same terminal state, whether at 1 or 15, or intermediate, score a similarity of 1 for the character. Where their states differ the similarity is computed by dividing the smaller by the larger; in this way the score for the character cannot exceed 1. In practice the same metric can be used for all characters, including the two-state characters.

Computation was made using a modification of the "Clustr" program of the University of Queensland Department of Computer Science (Andrews, 1976). The program was modified to ensure that for disordered multistate characters only identical apomorph states received a score (unity), shared plesiomorph or non-congruent apomorph states scoring zero.

The similarities in the matrix were clustered by the nearest neighbour (highest single linkage) method (Fig. 1). Those critical of this clustering method will recognize that only it reproduces Hennig's method of establishing affinities from synapomorphies. (A corollary of this is that if Hennig's method does validly retrieve at least parsimonious phylogenies, rejection of nearest neighbour clustering in numerical taxonomy on the grounds that it tends to produce chaining may be unwarranted). An ordination was also prepared from the similarity matrix by the method of principal coordinates. It was considered of value to relate the first phylogram to the first and second axes of the ordination, giving the three dimensional reproduction shown in Fig. 1. The first phylogram is alternatively called a hennigram, in deference to Hennig, while the three dimensional representation is termed a stereophylogram.

Determination of direction of change

The criteria for recognizing plesiomorphy or apomorphy of a character suggested by Hennig (1966) have been reviewed and criticized by Colless (1967) and Sneath and Sokal (1973). Sporne (1948), Marx and Rabb (1970), Crowson (1970), Ross (1974), Harper (1976) and Liem (1970);

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the latter following the work of Inger) have also suggested criteria. The criteria of Marx and Rabb (1970) have been paraphrased and modified by Ball (1974). Although Ball's decisions as to direction of change are not questioned, the criteria cannot be considered wholly satisfactory. For example, the first criterion is that of uniqueness of a character. A decision concerning the phylogenetic relationships of the families of Paludicola having been made, a character state unique to a derived family is thereby inferred to be apomorph. There is, perhaps, more circularity in this criterion than is desirable.

Criteria for determining direction of evolutionary change

In the present study, the following criteria for diagnosing plesiomorphy or apomorphy are recognized and the characters employed are listed under the criteria most pertinent to determination of direction of change in each character. In keeping with previous remarks, it is considered that while the criteria may have unsatisfactory aspects, experienced oligochaetologists will not dispute the direction of change inferred for each character. Construction of the most parsimonious phylogeny is central to each criterion.

1. Relative abundance

a. The greater the number of annelid groups (e.g. archiannelids, polychaetes, oligochaetes, leeches, branchiobdellids etc.) possessing a character state (including absence), the greater is the likelihood that the character state is plesiomorph.

The crux of this criterion is that it is more parsimonious to consider that a character state widespread in diverse groups has been carried over from ancestral forms than to postulate independent origin of the character state in each group. Like most phylogenetic criteria it necessitates *a priori* recognition of groupings which must be either intuitive or phenetic.

Characters: TS1,3-13,15?,17-21,24,29,32?,33; DM3,6,9.

b. A character which is limited to yet widespread in oligochaetes (i.e. which occurs in diverse morphologically defined groups of the Oligochaeta) is likely to be plesiomorph for the Oligochaeta. The presence of spermathecae (TS34) is an example of such plesiomorphy. An exception is the widespread occurrence of the multilayered condition of the clitellum which, if leeches are taken into account, also transgresses criterion 1a. Application of the set of criteria here proposed to the totality of characters selected suggests that the multilayered condition of the clitellum is derived, as is generally accepted by oligochaetologists though it is not beyond question. While this exception shows that a derived condition may be more common than a primitive condition within a group, lack of universality of this criterion is partly attributable to the difficulty of defining what is meant by "widespread". It clearly refers to occurrence in a large proportion of divergent subgroups rather than numbers of species but recognition of such subgroups *a priori* to a phylogenetic analysis creates circularity unless initial (e.g. phenetic) classification of the group be permitted. Such *a priori* classification seems unavoidable and is evident in all phylogenetic analyses of other workers which the author has studied. Where an apomorph character evolved very early in the history of a group, as presumably was the case with the development of the multilayered clitellum,

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it may nevertheless be widespread in the sense defined and such commonness will not reflect plesiomorphy for the group as a whole.

Characters: TS25,26,30?,31 (opisthopores only?); 34.

c. A character state, whether restricted to oligochaetes or not, is considered apomorph if it occurs in few oligochaete taxa and if these cannot be considered plesiomorph if a parsimonious phylogeny on the basis of all characters is to be produced. This approaches the uniqueness criterion of Ball but, by invoking parsimony, avoids the subjectivity of recognizing a derived subgroup prior to determination of direction of change. Mere restriction of a character state to few taxa is not considered a criterion of apomorphy but where, as is particularly well exemplified by the Moniligastridae, restricted character states occur in a group which could not be conceived as ancestral to groups lacking the characteristics (or, objectively, would not give a parsimonious phylogeny if so regarded) apomorphy is indicated.

Characters: TS1,4-8,9?,10,11?,12,13?,18,20,21,24,29?,32-36; DM3,6,7?,8,9.

2. Complexity

a. A character state which is restricted to or mainly found in oligochaetes with the most complex organization is likely to be apomorph. This also relates to Ball's uniqueness criterion but introduces the concept of complexity. Higher complexity is considered to be an indication of apomorphy of the total organism and to be more objectively assessable than whether a group is "derived". For instance, *Pheretima*, with several types of nephridia, with enteronephry and exonephry, intestinal caeca, perichaetine setae and testis-sacs, is clearly more complex than an alluroidid or a haplotaxid.

To some extent to recognize complexity is to postulate apomorphy for each of the characters or systems showing such complexity. There is also no distinct borderline between complexity and relative simplicity. The line between primitive and derived taxa is, however, equally arbitrary. This criterion is in some regards a restatement of criterion 2c, for a complex animal could not generally be regarded as basal in a parsimonious phylogeny. The list of characters which follows is restricted to animals with a high degree of complexity.

Characters: TS4-8,10,12,17,18,19?,33,35,36?; DM2.

b. A character state which is restricted to or mostly found in oligochaetes with the least complex organization is likely to be plesiomorph. The arguments given for 2a pertain to this criterion also.

Characters: TS2,14,27,30; OM2,6; DM1,4.

3. Ecological specialization

A character state which is significantly more abundant in oligochaetes with a particular ecological specialization is likely to be apomorph. This is the "ecological specialization" criterion of Marx and Rabb and of Ball. Some circularity is involved in determining which mode of life is specialized and which primitive. In this case a limnic mode of life in earthworm-like forms (almids, *Eiseniella*) appears secondary (i.e. specialized) and to correlate with a quadrangular cross section and dorsal anus. The haplotaxids, also limnic but plesiomorphic in most characters and therefore ecologically unspecialized do not share these character states.

Characters: TS4,5.

Table 3

O.T.U.	Phylogenetic nearest neighbour	R	Phenetic nearest neighbour	D
1. Haplotaxis	2. Alluroides	50.0	2. Alluroides	14.3
2. Alluroides	4. Standeria	46.3	4. Standeria	6.8
3. Brinkhurstia	4. Standeria	45.1	4. Standeria	6.4
4. Standeria	3. Brinkhurstia	45.1	3. Brinkhurstia	6.4
5. Syngenodrilus	19. Pontoscolex	43.5	2. Alluroides	14.8
6. Moniligaster	7. Desmogaster	37.5	7. Desmogaster	7.1
7. Desmogaster	6. Moniligaster	37.5	6. Moniligaster	7.1
8. Biwadrilus	17. Microchaetus	42.5	9. Sparganophilus	17.7
9. Sparganophilus	26. Komarekiona	42.3	26. Komarekiona	12.6
	27. Lutodrilus	42.3		
10. Alma	14. Glyphidrilocrius	37.2	14. Glyphidrilocrius	10.4
11. Glyphidrilus	12. Drilocrius a.	37.0	16. Callidrilus u.	13.7
	16. Callidrilus u.			
12. Drilocrius a.	13. Drilocrius h.	36.0	13. Drilocrius h.	9.8
13. Drilocrius h.	15. Callidrilus s.	35.0	14. Glyphidrilocrius	7.6
14. Glyphidrilocrius	13. Drilocrius h.	36.8	13. Drilocrius h.	7.6
15. Callidrilus s.	16. Callidrilus u.	34.1	16. Callidrilus u.	4.2
16. Callidrilus u.	15. Callidrilus s.	34.1	15. Callidrilus s.	4.2
17. Microchaetus	25. Ailoscolex	36.5	25. Ailoscolex	12.6
18. Glossoscolex	19. Pontoscolex	36.1	19. Pontoscolex	14.0
19. Pontoscolex	18. Glossoscolex	36.1	18. Glossoscolex	14.0
20. Kynotus	18. Glossoscolex	37.4	34. Nemertodrilus	18.9
21. Hormogaster	25. Ailoscolex	35.1	25. Ailoscolex	11.9
22. Vignysa	29. Lumbricus	38.0	23. Hemigastrodrilus	4.9
23. Hemigastrodrilus	21. Hormogaster	37.3	22. Vignysa	4.9
24. Diporodrilus	29. Lumbricus	36.1	30. Eiseniella	7.6
25. Ailoscolex	21. Hormogaster	35.1	21. Hormogaster	11.9
26. Komarekiona	17. Microchaetus	37.7	9. Sparganophilus	12.6
27. Lutodrilus	11. Glyphidrilus	38.0	15. Callidrilus s.	17.4
28. Criodrilus	13. Drilocrius h.	37.5	13. Drilocrius h.	17.3
29. Lumbricus	30. Eiseniella	34.7	30. Eiseniella	7.3
30. Eiseniella	29. Lumbricus	34.7	29. Lumbricus	7.3
31. Ocnerodrilus	32. Eukerria	41.2	32. Eukerria	12.8
32. Eukerria	35. Microscolex	40.1	31. Ocnerodrilus	12.8
33. Eudrilus	34. Nemertodrilus	35.1	34. Nemertodrilus	8.1
34. Nemertodrilus	33. Eudrilus	35.1	33. Eudrilus	8.1
35. Microscolex	36. Diplorema f.	34.5	36. Diplorema f.	4.9
36. Diplorema f.	37. Diplorema sp.	34.3	35. Microscolex	4.9
37. Diplorema sp.	43. Dichogaster b.	33.1	43. Dichogaster b.	8.1
38. Ochochaetus	43. Dichogaster b.	33.6	43. Dichogaster b.	7.1
39. Perionyx	50. Pheretima	34.3	40. Heteroporodrilus	10.5
40. Heteroporodrilus	42. Cryptodrilus	32.7	42. Cryptodrilus	5.2
41. Diporochoeta	49. Celeriella	35.8	35. Microscolex	8.1
42. Cryptodrilus	40. Heteroporodrilus	32.7	40. Heteroporodrilus	5.2
43. Dichogaster b.	37. Diplorema sp.	33.1	44. Dichogaster o.	4.8
44. Dichogaster o.	43. Dichogaster b.	33.4	43. Dichogaster b.	4.8
45. Digaster b.	42. Cryptodrilus	34.0	42. Cryptodrilus	7.8
46. Megascolides	47. Spenceriella	35.3	45. Digaster b.	8.7
	48. Lampito			
47. Spenceriella	50. Pheretima	30.9	48. Lampito	3.9
48. Lampito	47. Spenceriella	31.0	47. Spenceriella	3.9
49. Celeriella	47. Spenceriella	34.0	47. Spenceriella	7.8
50. Pheretima	47. Spenceriella	30.9	47. Spenceriella	7.6

R = Relationship expressed as dissimilarity by deducting total synapomorphies for two O.T.U's from total possible apomorphies (51).

D = Phenetic similarity expressed as dissimilarity by deducting from 100 the sum of positive and negative matches for two O.T.U's, divided by the number of actual comparisons, expressed as a percentage.

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The criteria of "morphological specialization" and "geographical restriction" of Marx et al, though appearing valid, cannot readily be applied to the oligochaetes in this study.

(2) Phenetic

The phenetic method employed in this study differed from conventional neo-Adansonian numerical taxonomy in that the attributes used were subjected to *a priori* selection, that is they were not a random sample of attributes though derived from as many organ systems as practicable. The basis for this selection was that the attributes were those used for the phylogenetic systematics, being attributes divisible into plesiomorph and apomorph states. The method was phenetic in that negative matches (shared plesiomorphies in Hennigian terms) contributed equally to the similarity coefficient in comparison with positive matches (shared apomorphies).

The program was adjusted so that only identical states of multistate attributes, whether positive or negative, were recorded as matches, no fractional scores being allowed. The similarity matrix was again computed with the 'Clustr' program and a nearest neighbour (highest single linkage) dendrogram (phenogram) was generated.

Results

The results of the phylogenetic analysis are shown in the hennigram (Fig. 1) and stereophylogram (Fig. 2) and those of the phenetic analysis in the phenogram (Fig. 3). Lack of space does not permit inclusion of the similarity matrices but the character states for all OTU's are reproduced in Fig. 1 which shows the synapomorphic relationships and Table 3 lists phylogenetic and phenetic nearest neighbours.

Discussion

The discussion will centre on the phylogenetic analysis using fractional scores (hennigram, Fig. 1 and stereophylogram, Fig. 2). Comparison will be made with the phenetic analysis (phenogram, Fig. 3).

Although Hennigian principles have been applied in developing the hennigram, a rigidly Hennigian interpretation of the Hennigian will not be made as the author has some reservations concerning the view of speciation and phylogenesis which lies behind Hennig's methodology. Hennig's methods have been used, with modification, chiefly for their value in facilitating treatment of large amounts of data (especially where computerized), for their relative objectivity, their repeatability and for the heuristic qualities of the resultant phylogram.

One of the chief reservations relates to the view expressed by Hennig and by his protagonist Brundin that evolution to sister species and thence higher groups proceeds by dichotomy of single species (both the dichotomy and origin from single species are questionable) and the belief that a grouping of forms which have evolved similar characteristics by parallelism is not taxonomically valid. The author has previously explained variability and apparent reversion to primitive characters in a group in terms of both intra- and inter-specific and morphogenetic lability

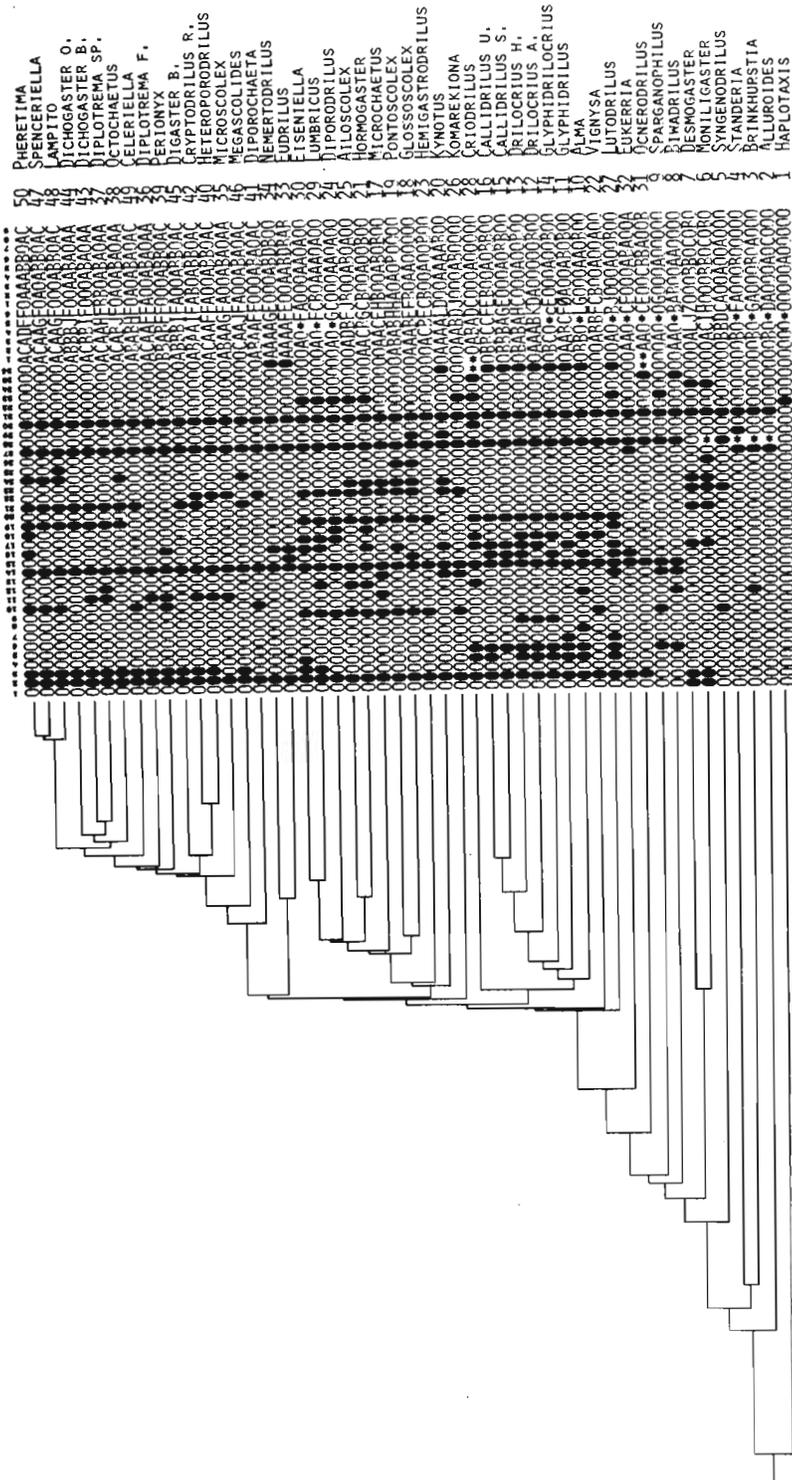


Fig. 1. Henniggram (phylogram) for all families of the opisthoporou oligochaetes constructed by nearest neighbour clustering, the nearest neighbour of an entity (OTU) being that entity sharing with it the greatest number of advanced (apomorph) character states. Plesiomorph states for all characters are indicated by blank ovals. For each of the 6 ordered multistate and 9 disordered multistate characters successive apomorph states, as given in Table 2, are indicated alphabetically by upper case letters. For ordered multistate character 5, in which there are more than 26 apomorph states, apomorph state 29 is indicated by a lower case "c". Asterisks denote missing or inadmissible data.

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or plasticity in ancestral populations for the characters concerned (Jamieson, 1971d).

These ancestral 'populations' may have been groups of closely related species evolving similar characters in common by virtue of similar responses, to selection, of gene pools which were basically similar because of relationship. An example is the parallel acquisition of mechanisms for internal fertilization in different lineages of the Eudrilidae argued for by Jamieson (1969). This view of evolution of a given group by parallelism from a stock of interrelated species is fundamentally at variance with the principles of Hennig and Brundin (cf. origin of marsupials and eutherians from a single species, Brundin, 1966). The view here presented is that evolution commonly, if not normally, proceeds by parallelism from closely related species.

Reappearance of the plesiomorph condition, two pairs of ovaries, in three of the known species of megadriles (*Enantiodrillus borellii*, *Diplocardia sandersi* and *Glyphidrillus kukenthali*) or of two pairs of male pores in the megascolecoid genus *Hoplochaetella* are probably examples of morphogenetic plasticity although they may more questionably be the result of persistence of these characters in some species of a common ancestral pool of species. Similarly, occurrence of alternative conditions of the male terminalia (for instance the acanthodrilin and megascolecoid conditions) may indicate (intraspecific?) variability in these characters in ancestral stocks rather than the occurrence of only one or the other in a single ancestral species.

The possibility of misclassification, that is spurious association or separation of clades in the hemigram, also has to be recognized and is suspected for the Ocnerodrilidae.

Two chief sources of misclassification would seem to exist in Hennigian methodology: (1) failure to use the totality of extant species of the group under consideration, or (2), more fundamental, the fact that determination of groupings is essentially probabilistic. Thus the smaller the number of symplesiomorphies, the smaller is the confidence that the consequent grouping is not the result of convergent acquisition of the shared apomorphies.

Megascolecidae and Eudrilidae

The Eudrilidae (represented by *Eudrilus* and *Nemertodrillus*, subfamilies Eudrilinae and Pareudrilinae respectively) appear as the plesiomorph sister-group of the Megascolecidae excluding the Ocnerodrilinae. Their relative plesiomorphy is striking in view of the unique and highly apomorph development of mechanisms for internal fertilization in both divisions of the Eudrilidae. The Eudrilid-Megascolecoid grouping is the superfamily Megascolecoidae of Brinkhurst and Jamieson and retains this status here but the Ocnerodrilinae were also included by us in the Megascolecoidae and will be discussed below. The sister-group of the megascolecoid grouping in the phylogram includes lumbricids and glossoscolecids *sensu lato* but notably excludes the aluids. This sister-group, here termed Lumbricoidea, is composed of *Lumbricus* and *Eiseniella* (Lumbricidae), and recently erected families Diporodrilidae and Ailoscolecidae (all four taxa being part of the Lumbricoidea in the narrow sense of Gates, 1976), and the core of the glossoscolecids *s. lat.* Brinkhurst and Jamieson,

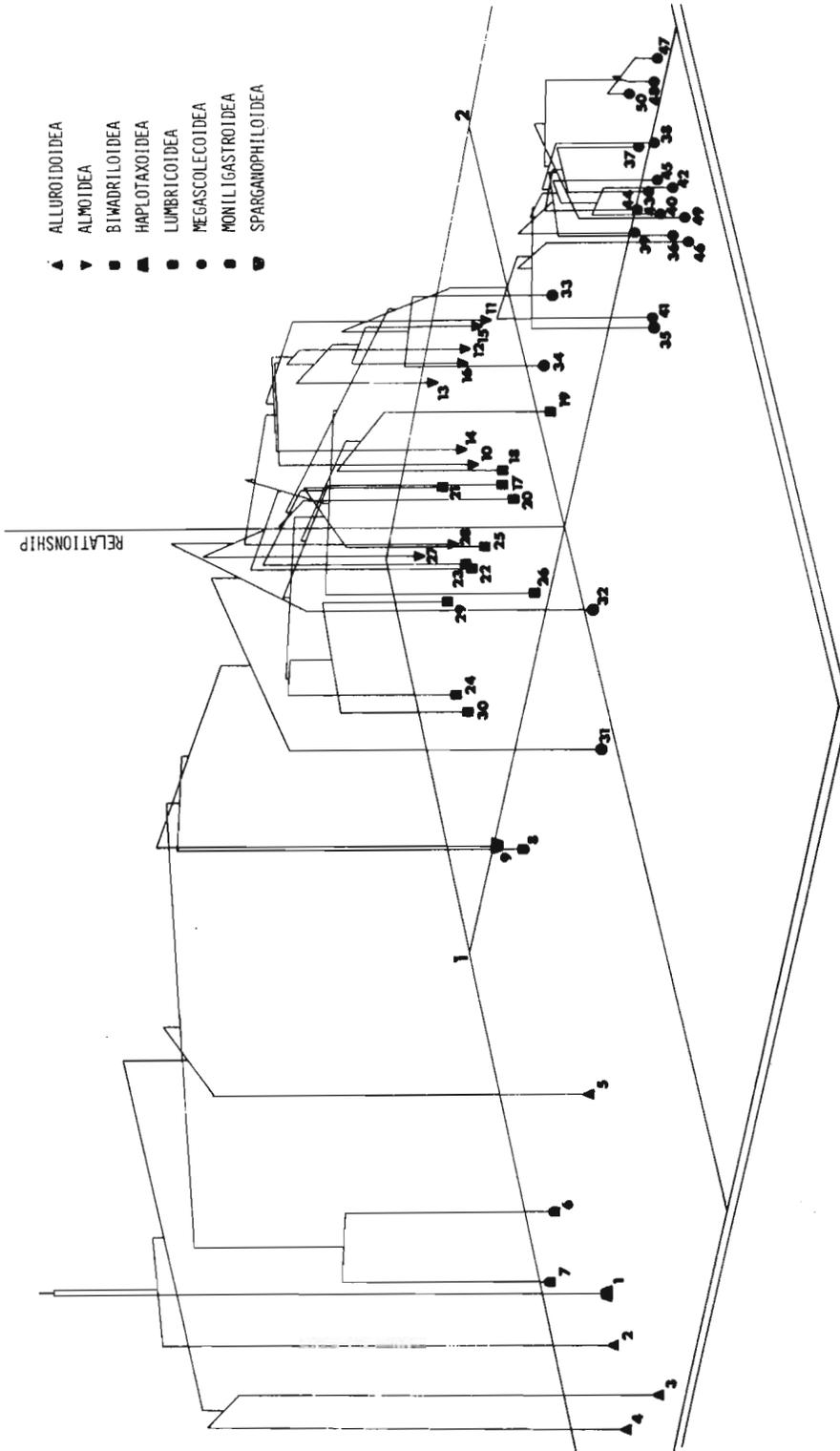


Fig. 2. Stereophylogram for all families of opisthoporou oligochaetes (*Haplotaxida*). This stereophylogram has been constructed by combining the hennigram shown in Fig. 1 with an ordination. The ordination, which is represented by its first and second axes, was obtained by principal coordinates analysis from the matrix of synapomorphy coefficients used to construct the hennigram. The superfamilial classification adopted is indicated by symbols which are explained in the key to the diagram.

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namely *Hormogaster*, *Microchaetus*, *Pontoscolex*, *Glossoscolex*, *Hemigastrodriilus* and *Kynotus*. This grouping represents a restriction of the Lumbricoidea s. Jamieson, 1971d, to exclude the almid, *Criodrilus*, *Sparaganophilus* and *Biwadriilus*.

The fact that the superfamily Megascolecoidea (excluding the ocnerodrilids) is the apomorph sister-group of the Lumbricoidea, with the latter intervening between them and the almid complex is of the greatest interest. It suggests the former existence of a common ancestor intermediate in form between the megascolecids and the lumbricoids. This ancestor, it is indicated, had no lateral lines, possessed a multilayered clitellum, with small yolked eggs, was holandric with 2 pairs of male pores united in segment 13, (unspecialized) ovaries (in XIII only?) long series of prostate-like setal glands, last hearts in XI, intestinal origin in XIV and adiverticulate pretesticular spermathecae. A special relationship between the Megascolecidae and non-almid "glossoscolecids" was anticipated by Jamieson (1974a) in a discussion of *Hickmaniella* which is almost unique in the Megascolecidae in having an intestinal gizzard. All the shared characters noted between megascolecids and glossoscolecids are now seen to be apomorphies in Hennig's terminology. Inclusion of the Glossoscolecidae and Lumbricidae in the superfamily Lumbricoidea and of the Megascolecidae and Eudrilidae in the superfamily Megascolecoidea was upheld and recognition of the suborder Lumbricina as a natural grouping was endorsed. The Alluroididae, included in the Lumbricina by Brinkhurst and Jamieson (1971), related the suborder to other haplotaxid suborders, especially the Haplotaxina but they are excluded from the Lumbricina in the present study.

Whereas the coverage of the Almidae in this investigation includes all known genera of that family, only a few genera of the Megascolecidae, representative of the Acanthodrilinae, the three tribes of the Megascolecinae sensu mihi, 1971a, and the Ocnerodrilinae, are included. The phylogram and phenogram for the Megascolecidae cannot therefore be regarded as more than heuristic. Interesting aspects of this portion of the phylogram are the distinctness of the Ocnerodrilinae, here recognized, as did Gates long ago, as a separate family, confirmation of the Eudrilidae as the plesiomorph sister-group of the Megascolecidae, and the very distinct, highly apomorphic status of the three representatives of the tribe Megascolecini Jamieson, 1971a, *Pheretima* (type-species from Tahiti but probably Indonesian or Malaysian), *Spenceriella* (Australia) and *Lampito* (India), the close grouping of which lends some support to recognition of this tribe. Another heuristic grouping is that of two species of *Dichogaster* (Africa and Asia; Megascolecinae, tribe Dichogastrini Jamieson, 1971a) with the meronephric *Diploctrema* sp. (Australia; Acanthodrilinae, tribe Acanthodrilini) and *Octochaetus* (New Zealand; tribe Octochaetini) as the plesiomorph sister-group of the Megascolecini. This grouping tends to confirm the author's suspicion that those Dichogastrini with acanthodrilin male pores (India and Africa) are descended from Acanthodrilinae and are distinct from dichogastrins with megascolecin male pores (Oriental and Australia). Such megascolecin dichogastrins are presumably descended from megascolecin holonephric forms (Megascolecinae, tribe Perionychini Jamieson, 1971a). The latter view is supported by the sister-group relationship between the megascolecin dichogastrin *Digaster*, on the one hand, and the perionychins *Heteropodrilus*

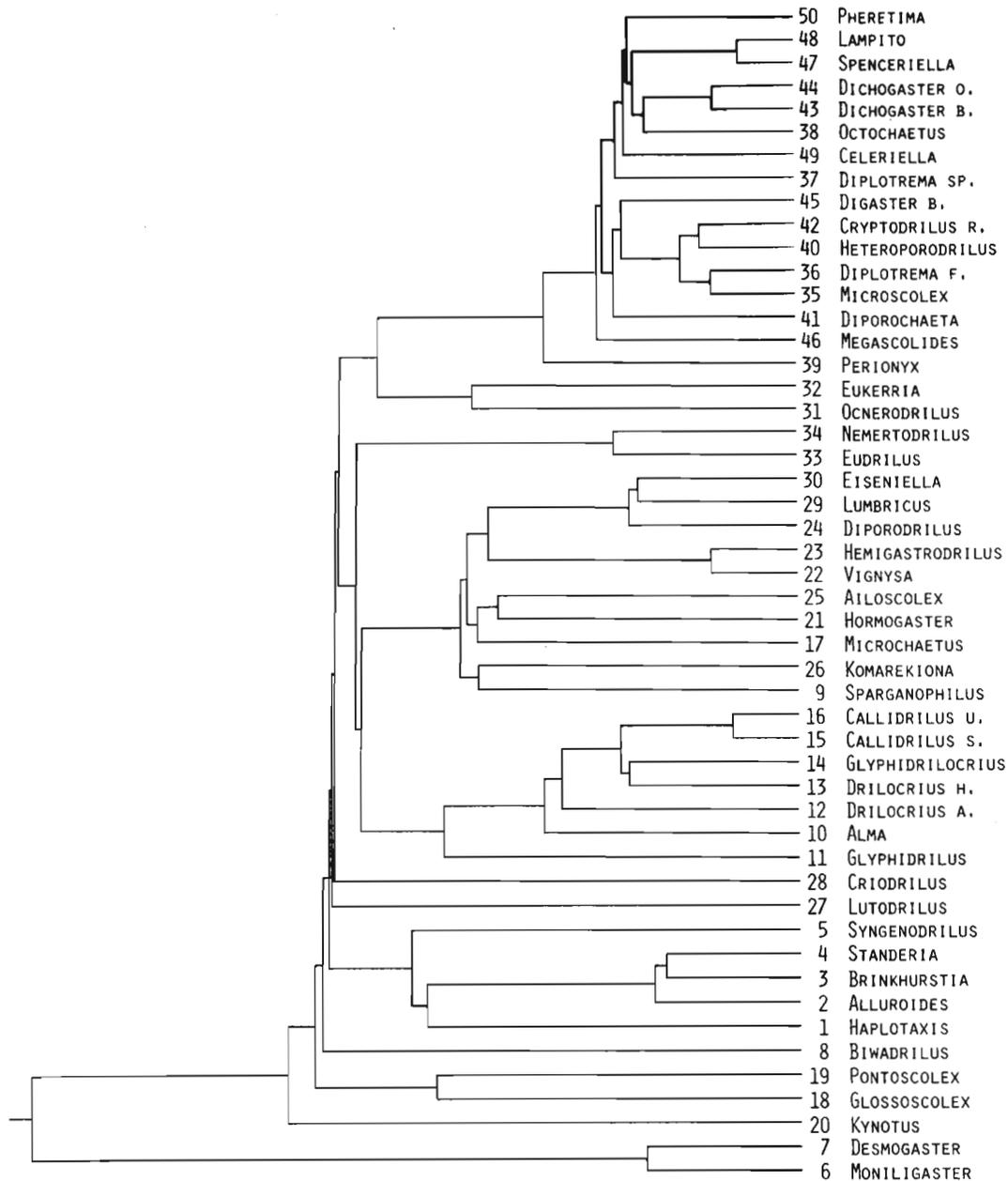


Fig. 3. Phenogram for all families of opisthoporous oligochaetes (*Haplotaxida*). The phenogram was constructed by nearest neighbour clustering of the similarities indicated in a matrix of coefficients of similarity. These coefficients were obtained by summing positive and negative matches for the characters employed in preparation of the hemnigram shown in Fig. 1. Positive matches were synapomorphies and negative matches were symplesiomorphies in Hennigian terms but in phenetic terms these were merely matching character-states requiring no consideration of evolutionary change. The phenogram differs from a neo-Adansonian dendrogram insofar as selection of characters was influenced by consideration of their utility for Hennigian analysis. For treatment of multistate characters see text.

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and *Cryptodrilus* on the other, all three from Australia. The diphyletic nature of the Dichogastrini, and origin of African members from acanthodrilids, is further indicated by the absence of perionychins from Africa.

While the diphyletic origin of the Dichogastrini emerges clearly, the interrelationship of acanthodrilids and perionychins suggested are perplexing. The classical view of origin of the perionychin arrangement of male pores (a pair of male and prostatic pores on XVIII) from the acanthodrilin condition (male pores on XVIII, prostatic pores two pairs, on XVII and XIX), a view questioned by Jamieson, (1963), is not supported. This is not to deny the probability of origin of the microscolecin, balantini, or some megascolecin conditions from the acanthodrilin condition. The phylogram is not inconsistent with the revolutionary view that the acanthodrilin condition may have originated by replication of prostates from the perionychin condition. In view of the occurrence of sexprostatic forms (e.g. *Dichogaster damonis* and *Pickfordia*) in the Dichogastrini and Acanthodrilinae and of forms with six or more prostates in the Ocnerodrilidae, a multiprostatic origin of the Megascolecidae, giving the acanthodrilin and perionychin conditions independently seems more likely, however. The alternative, origin of perionychins from acanthodrilids with homeotic displacement of the anterior prostates to segment XVIII (a displacement common in New Caledonia which harbours the most primitive known perionychin genus) will be discussed in a later work.

Separation of *Diplostroma fragilis*, the type of this Australian genus, from the meronephric *Diplostroma* sp. when morphological studies indicate that the two are very closely related is not easily explained; nor is the interpolation of the Indian *Celeriella* (tribe Megascolecini) between it and the acanthodrilin group. Nevertheless, the *Diplostroma* sp. remains the phylogenetic nearest neighbour of *Diplostroma fragilis*, and *Spenceriella* is the phenetic and phylogenetic nearest neighbour of *Celeriella*. The position of *Microscolex* (*Notiodrilus*) *georgianus*, (S. Georgia) the type-species of the Acanthodrilinae, separated from other acanthodrilids by the three Australian Megascolecinae is also difficult to interpret. It is noteworthy that the phyletic and phenetic nearest neighbour of *M. (N.) georgianus* is *Diplostroma fragilis*, *Diplostroma* being placed in *Microscolex* as a subgenus by Jamieson (1974c).

The relatively isolated position of *Megascolides australis* is consistent with the author's view that this species has acquired longitudinal ureters (placing it in the Megascolecini) independently of the true Megascolecini as is apparently the case in similarly characterized (but not computed) species of *Cryptodrilus* (see Jamieson, 1974a).

It will be noted that the phylogram calls into question division of the Megascolecidae into the subfamilies Acanthodrilinae and Megascolecinae. The subfamilies are retained for the present pending a thorough analysis of the family. It may be possible taxonomically to retain them by including those dichogastrins with acanthodrilin male pores in the *Acanthodrilinae*.

The lack of cohesion of the Perionychini (computed for *Perionyx* (India), *Diporochoaeta* (New Zealand), *Heteroporodrilus* and *Cryptodrilus* (Australia)) may reflect the fact that this tribe is based on the symplesiomorphy holonephridia, though in combination with the relatively apomorphic but not unique character male and prostatic pores on XVIII.

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However, the special relationship between *Cryptodrilus* and *Heteropordrilus* suggested by Jamieson (1972a) is borne out by both nearest neighbour relationships. Those Dichogastrini with male pores on XVIII would remain a valid group within the Megascolecinae though removal from this tribe of the, mainly African, acanthodrilin members (including the type-species of *Dichogaster*) would require the megascolecina portion to be renamed. The tribe Megascolecini would appear valid for forms with male and prostatic pores in XVIII lacking the dichogastrin or perionychin conditions of the nephridia, though some members which have convergently acquired a megascolecina excretory system may have to be excluded. Meronephric, non-dichogastrin members of the genus *Cryptodrilus* possessing ureters have already been excluded (Jamieson, 1974a).

Lumbricidae

Within the Lumbricoidea the Diporodrilidae are cladistically, in phylogenetic and phenetic nearest neighbour relationships and in the phenogram, closest to the Lumbricidae, of which they form the plesiomorph sister-group. Significant diporodrilid synapomorphies with the Lumbricidae are: presence of tubercula pubertatis; location of male pores on XV, well anterior to the clitellum; presence of an intestinal gizzard preceded by a crop; the intestinal typhlosole; possibly single-stringed ovaries; adiverticulate spermathecae in the testicular segments and the presence of adiverticulate nephridial bladders. The symplesiomorphy absence of an oesophageal gizzard also seems worthy of mention. It is here considered that the single genus, *Diporodrilus*, must only be assigned to a subfamily, the Diporodrilinae, within the Lumbricidae. Presence of a longitudinal ureter interconnecting the postclitellar nephridia is no obstacle to inclusion in the Lumbricidae as a similar duct occurs in *Allolobophora antipae*. The unique autapomorphy of the Diporodrilidae is the paired coelomic pores contrasting with the median unpaired pores of the Lumbricidae. They may have evolved from median dorsal pores or may represent an independent development from an ancestral imperforate condition. The prior groups in the phylogeny (Haplotaxidae through Almidae) lack dorsal pores. Bouche (1970) considered that the Diporodrilidae could be derived from either the Lumbricidae or the Hormogastridae but later (1972) decided that origin was from the Hormogastridae.

Ailoscolecidae and Hormogastridae

Linkage of *Ailoscolex* with *Hormogaster* is heuristic. *Ailoscolex* agrees with the Hormogastridae s. Bouché (1972; including *Hormogaster*, *Hemigastrodrilus* and *Vignysa*) in significant respects: setal intervals, presence of longitudinally grooved genital setae (personal observation), presence of nephridial caeca, probably in having a single egg-string to the ovary (uncertain in *Ailoscolex* in which the ovary is certainly not fan-shaped, personal observation), location of last hearts in XI, in possessing two oesophageal gizzards (as in *Vignysa*; *Hormogaster* and *Hemigastrodrilus* have three) and in location of the first gizzard in VI; but the male pores are far posterior in *Ailoscolex* (1/3 XXII) compared with *Hormogaster*, *Hemigastrodrilus* and *Vignysa* (XV). Because

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Hormogaster links with, and is the nearest neighbour of, *Ailoscolex* both phyletically and phenetically, it is here proposed to include it in a family Hormogastridae with the three other genera mentioned, regarding it as apomorph in being the only hormogastrid in which male pores have migrated posteriorly of segment XV but plesiomorph in having spermathecae in, but not behind, the testis-segments. Subfamilies recognized are the Hormogastridae (*Hormogaster*, *Hemigastrodrilus*), Vignysinae (*Vignysa*), both included by Bouche, 1970, and Ailoscolecinae (*Ailoscolex*) proposed as a separate family by Bouche, 1969.

Microchaetidae

Microchaetus appears to be the plesiomorph sister-group of the families Lumbricidae s. lat. and Hormogastridae (represented by *Hormogaster* and *Ailoscolex*). Somewhat unexpectedly its phyletic and phenetic nearest neighbour is *Ailoscolex*. The view that it is the sister-group of the Glossoscolecini s. Jamieson, 1971d, is not confirmed. It is here proposed to recognize the family Microchaetidae for *Microchaetus* and (not computed) *Tritogenia*, differing fundamentally from the Microchaetidae s. Gates in exclusion of the almidids.

Kynotidae

The Malaysian *Kynotus* was shown as the sister-group of the hormogastrins, microchaetins and glossoscolecins in the "intuitive" phylogeny of Jamieson (1971d). It maintains this position in the present phylogenetic study.

Hennig's view that affinities should be determined only on the basis of shared apomorphies is nowhere more clearly supported than in the phenetic relationships of *Kynotus* for, when negative (plesiomorph) matches are included, this genus is far displaced from hormogastrids and microchaetids in the phenogram and has as its nearest neighbour (Table 3) the eudrilid *Nemertodrilus*, affinities which seem unacceptable. *Kynotus* is here assigned to the monotypic family Kynotidae and, as formerly, lies within the Lumbricoidea.

Glossoscolecidae

Glossoscolex and *Pontoscolex*, representing the S. American glossoscolecids, here given familial rank as the Glossoscolecidae s. strict. in accordance with the views of Gates (1972), are phenetic and phyletic nearest neighbours. The Glossoscolecidae s. lat. is a large and heterogeneous group, with, for instance, spermathecal locations varying from pre- to post-testicular, and may be found on further analysis to require subdivision into subfamilies or even further families.

Komarekionidae

The plesiomorph sister-group of the superfamilies Megascolecoida and Lumbricoidea in the phylogram is the nearctic Komarekionidae of Gates, 1974, but *Komarekiona* has *Microchaetus* as its phylogenetic and *Sparganophilus* as its phenetic nearest neighbour. It is here included in the

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Lumbricoidea as a distinct family. Bouché (personal communication) considers *Komarekiona* to be an "Ailoscolecoid" and there are, indeed, striking similarities including location of the male pores on XXII, but *Komarekiona* has only a single oesophageal gizzard, in VI, (2 in VI-IX in *Ailoscolex*) and intestinal origin in XIII, not XV; lacks nephridial caeca and intestinal typhlosole and has pretesticular, not testicular, spermathecae. The spermathecal difference seems significant though the other differences are known to occur within good genera in, for instance, the Megascolecidae. *Ailoscolex* lacks the two pairs of lateroparietal vessels of *Komarekiona* (personal observation for *A. lacteospinosus*) and, coupled with the spermathecal difference, this suggests that the Komarekionidae should be retained.

Almidae and Criodrilidae

The phylogram gives strong support for recognition of a grouping the Almidae (Jamieson, 1971d) or Almidae (Ljungstrom, 1974; Jamieson, 1976). At least familial rank is justifiable for this assemblage. Indeed, if Hennig's view that sister-groups must be given co-ordinate rank be accepted, the almid group must be regarded as at least coordinate with and perhaps of higher rank than the combined megascolecoid and lumbricoid superfamilies. Thus the almid and their plesiomorph sister group *Criodrilus* may be regarded as comprising the families Almidae and Criodrilidae of a single superfamily, the Almoidea. The sole genera of the Almidae, all represented in this study, are *Callidrilus*, *Drilocrius*, *Glyphidrilocrius*, *Alma* and *Glyphidrilus* as noted by Jamieson (1971d, 1976). Origin of the Lumbricidae from the Criodrilidae, (vide Jamieson, 1971d) is not supported.

Lutodrilidae

The genus *Lutodrilus*, unique in the earthworms in having ten pairs of testes, in XII-XXI, and a lumbricoid s. Gates, is a sister-group of the almid lumbricoid-megascolecoid clade (ignoring the questionably placed *Vignysa*). According to Hennig's principles it therefore warrants a rank higher than superfamily. Its phylogenetic nearest neighbour is, however, *Glyphidrilus* and its phenetic nearest neighbour is *Callidrilus*, both almid. While the author accepts the evidence of McMahan (1976) that presence of testes in XII-XXI is normal for the single known species, the affinities of the genus have been computed as though it had the normal megadrile arrangement of testes in X and XI. *Lutodrilus* has clearly interpolated ten segments, the last eight of them testicular, anterior to this normal location but to have recognized this for computational purposes would have made other organ systems consequentially non-congruent with other megadriles. If the ten additional segments are deducted, comparison with *Glyphidrilus* and *Callidrilus* is facilitated. Apomorphies which *Lutodrilus* shares with these genera which are of particular note are: (a) the quadrangular posterior cross section; (b) dorsal anus; (c) copulatory alae (with *Glyphidrilus* only); (d) presence of a subneural vessel, (e) an intestinal typhlosole, (f) multiple posttesticular spermathecae and (g) last hearts in XI. It is here proposed, *a posteriori*, to weigh the almid apomorphies (a-c,f) which are rare or unique within

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the Oligochaeta, to the extent of including *Lutodrilus* as a third family in the Almoidea. This family stands apart from other almooids in having single-stringed ovaries.

Ocnerodrilidae

A noteworthy feature of the remainder of the phylogram is exclusion of the two ocnerodriles, *Ocnerodrilus* and *Eukermia*, from the Megascolecidae by intervention of the Almoidea and Lumbricoidea. The ocnerodriles are, however, linked with the Megascolecidae in the phenogram (Fig. 3) in which the two are mutual nearest neighbours whereas the phylogenetic nearest neighbour of *Eukermia* is the megascolecid *Microscolex georgianus*. If credence is to be attached to this portion of the phylogram it would have to be accepted that the Ocnerodrilinae arose from early megadriles which, like present day ocnerodriles, and *Sparganophilus*, which they are cladistically near, had the last hearts in XI and (*Sparganophilus*) a very short oesophagus and metamERICALLY repeated prostate-like glands. These glands persist, supernumerary to true prostates, in several ocnerodrilid genera.

In the phylogram the ocnerodriles are the plesiomorph sister group of the megascolecid-lumbricoid-amoid complex. A close cladistic affinity of ocnerodriles with the almooid-lumbricoid complex has rarely been proposed but it has been noted (Jamieson, 1965) that the ocnerodriles *Nematogenia lacuum* and *N. panamaensis* resemble glossoscolecids in having the male pores anterior to the middle of a long clitellum, unlike megascolecoids.

If the ocnerodriles were accepted as cladistically very distinct from the Megascolecidae and from the sister-group of the latter, the Eudrilidae, the supposed origin of eudrilids from ocnerodriles could not be upheld. Ocnerodriles can no longer be categorically associated with the Megascolecidae and Eudrilidae and separate familial status, as the family Ocnerodrilidae, advocated by Gates (e.g. 1959) and by Sims (1966, 1967), though these authors did not suggest almooid-lumbricoid affinities, appears justified. If ocnerodriles were accepted as being cladistically distinct from the Megascolecidae, the development of tubular prostates and in some ocnerodriles (e.g. *Eukermia*) of the acanthodrilin condition of the male terminalia (prostate pores in XVII and XIX, male pores in XVIII) would have to be regarded as remarkable anticipations or convergent development of prostates in megascolecids and of the acanthodrilin arrangement of these in acanthodrilin and Afro-Oriental dichogastrin Megascolecidae. It would also necessitate acceptance that prostate-like glands ("setal glands") capable of giving rise to prostates secreting into the spermathecae of the concopulant were persistent through successive ancestral forms which gave rise respectively to the Sparganophilidae (and earlier groups such as the Biwadrilidae), Ocnerodrilidae, Almoidea, Lumbricoidea and Megascolecidae. Prostates or prostate-like glands are seen in some or most members of all of these groups.

In the light of the present phylogram we may envisage ancestral forms of the Megascolecidae and Eudrilidae with long series of setal glands (precursors of true prostates which latter are here termed metaprostates) and with a facultative tendency to modify the ectal ends of the sperm ducts (precursors of euprostates). From such ancestors it

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could be surmised that megascolecids originated by emphasis on development of metaprostates from the setal glands, though not always to the exclusion of modification of the vasa, whereas eudrilids developed by adopting the euprostate, losing the setal glands, and foregoing the development of the prostate. These conclusions still leave the question whether ocnerodriles are as distinct from megascolecids as the phylogram and phenogram indicate, at least for the small sample taken. If they are distinct, convergent development of metaprostates and of the microscolecin and acanthodrilin conditions in ocnerodriles and megascolecids would have to be accepted.

Before such convergence, or parallelism is dismissed as inconceivable it must be recognized that some such convergences have to be accepted whether ocnerodriles are considered to derive from (1) an immediate ancestor of the Megascolecidae-Eudrilidae or (2) a common ancestor of the megascolecoid-lumbricoid-almoid assemblage. Thus if ancestor (1) were a proto-ocnerodrile (with or without the auto-apomorphy of extant ocnerodriles, presence of calciferous-tissue or glands in IX) it would have to be accepted that it gave rise to forms in the Megascolecidae-Eudrilidae with a wide variety of arrangements of the male terminalia (acanthodrilin, as in the ocnerodrile *Eukerria*; microscolecin, the common ocnerodrile and eudrilid condition; megascolecin and balantin, to name the chief variants) and that either the acanthodrilin or the microscolecin conditions of ocnerodriles of which the former is infrequent and the latter usual, developed as a convergence in relation to the megascolecids. Parallel development of these arrangements, which appear from their frequency to have been highly successful, is not more surprising than the evolution of the wide diversity of arrangements (which seem to have had limited success) exemplified by *Gordiodrilus*, *Nannodrilus*, *Thatonia*, *Deccania* and other ocnerodriles which have neither the acanthodrilin nor the megascolecin arrangement.

If the ocnerodriles were divorced further from the Megascolecidae-Eudrilidae (condition 2) as in the phylogram, and the proto-ocnerodrile were at the root of the megascolecoid-lumbricoid-almoid assemblage, it would have to be postulated either that the proto-ocnerodrile which gave rise to the Ocnerodrilidae on the one hand and the assemblage on the other had setal glands unmodified as prostates or that it had already modified at least some of these as metaprostates. In the former case the prostates and shared arrangements of ocnerodriles and megascolecoids would be examples of convergence. In the latter case it would be inferred that prostates had been lost in almids and lumbricoids lacking them while setal glands were not infrequently retained. Origin of prostates and their arrangements in ocnerodriles independently from that in megascolecoids cannot be categorically rejected. Alluroidids, especially *Brinkhurstia*, (vide Jamieson, 1968b) demonstrate origin of simple tubular prostates in a lineage which now appears to be remote from the Ocnerodrilidae despite similarities cited by Jamieson (1968b) and Ljungstrom (1974). In *Brinkhurstia* each prostate opens with the corresponding vas deferens, into an atrial chamber much as in the ocnerodrile genus *Nannodrilus*. Alluroidids could thus be taken as evidence either for independent origin of metaprostates or for the existence of prostates in early ancestral worms which gave rise to modern alluroidids, to moniligastrids and to the Lumbricina, including ocnerodriles.

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Returning to the possibility of direct ocnerodrilid-megascolecoid affinities, a common ancestor of the Megascolecidae and Eudrilidae may be assigned plesiomorph features of either or both families, e.g. short oesophagus with intestine commencing in XII, absence of spermathecal diverticula, and location of last hearts in XI. Only calciferous modification of the oesophagus in IX (or IX and X) would be necessary to produce an ocnerodrilid. Although these plesiomorphies would also be attributable to ancestors of the megascolecoid-lumbricoid-almoid ancestors, the latter ancestors would have had male pores on XV (or even XIII) as in lumbricids, hormogastrids and *Criodrilus*. It is on this point, position of the male pores, that convergence rather than monophyly, of ocnerodrilids and megascolecids with regard to male terminalia is difficult to accept. Although it must be accepted that some megascolecoid-ocnerodrilid arrangements of the terminalia have evolved more than once, the location of the pores of the vasa deferentia on XVII and/or XVIII (though also seen in some lumbricoids and almoids) taken in conjunction with unique similarities of the prostate arrangements (albeit by parallelism) in the two families inclines the author to consider ocnerodrilids as monophyletic with the Megascolecidae-Eudrilidae and as little changed representatives of the ancestors of the latter couplet.

Sparganophilidae

Jamieson (1971d) placed *Sparganophilus* as a monotypic subfamily in the Glossoscolecidae s. lat. on the grounds that glossoscolecoid affinities were indicated by the intraparietal sperm ducts (a condition shown by Pickford, 1976, not to be universal in the glossoscolecids, however) and a group of characters which individually were not restricted to or even general in the family, viz. the extensive clitellum, and the histology of this, the intraclitellar male pores with longitudinal tubercula pubertatis; the transversely cicatriced setae; the tendency to transverse multiplication of the adiverticulate spermathecae; the posterior dorsal groove and the dorsal anus, seen in the Almidae which were then included in the Glossoscolecidae. These character-states, with the possible exception of the intraclitellar location of the male pores, and presence of prostate-like glands, are apomorphic, a fact further supporting recognition of glossoscolecoid (i.e. lumbricoid-almoid) affinities of *Sparganophilus*. Possession of prostate-like glands, shared with *Kynotus* but also with *Biwadrilus* (then placed in the Glossoscolecidae) was a further similarity.

It has been pointed out (Jamieson, 1971d) that in *Sparganophilus* the tendency to backward movement of the male pores is well developed and that the brain has moved back to segment III but that evidence of the primitive origins of the genus relative to many "glossoscolecids" were seen in the exceptionally short, unspecialized oesophagus, in absence of a subneural vessel, and retention of precardiac commissural vessels. *Sparganophilus* was shown to resemble the Lumbricidae in having a single-stringed ovary, intraclitellar tubercula pubertatis, a saddle-shaped clitellum and no oesophageal gizzard. It was considered that *Sparganophilus* was a little modified representative of the ancestral Glossoscolecidae s. lat. and, accepting a glossoscolecoid origin of the

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Lumbricidae, it was thought probable that the lumbricid-like features of *Sparganophilus* were an example of parallelism in related forms rather than convergence of unrelated forms.

Omodeo (1956) saw *Sparganophilus* as representative of the ancestral stock of the Microchaetidae; *Hormogaster* (which he placed in a subfamily of the Microchaetidae); the Lumbricidae; and *Criodrilus*, *Alma* and *Drillocrius*, which he considered might be placed in the Lumbricidae or in a separate family. The Glossoscolecidae s. strict. were shown as the sister-group of *Sparganophilus* and its above-mentioned supposed descendants. *Kynotus* was assigned to the subfamily Microchaetinae. Removal of *Alma* and *Drillocrius* from the Microchaetidae is endorsed in the present account though the other affinities recognized differ significantly from those deduced by Omodeo. Yamaguchi (1953) ascribed a relatively advanced position to *Sparganophilus*.

In the phylogram origin of *Sparganophilus* from the basal stock of the Glossoscolecidae s. lat. (Lumbricoidea, Almoidea and *Biwadrilus*) is confirmed if the intervention of the Ocnerodrilidae, questioned above, be ignored. It now seems acceptable that *Sparganophilus* is descended from the root of the almid-lumbricoid (megascolecoid) complex as supported by its nearest neighbour relationships which are phylogenetically with *Komarekiona* and *Lutodrilus*, (fringe members respectively of the Lumbricoidea and Almoidea) and phenetically with *Komarekiona*.

It is particularly noteworthy that longitudinal tubercula pubertatis seen in *Sparganophilus* but very rare elsewhere in the Oligochaeta, occur in all the lumbricoids computed with the exception of *Kynotus* (*Eiseniella*, *Lumbricus*, *Diporodrilus*, *Ailoscolex*, *Hormogaster*, *Microchaetus*, *Pontoscolex*, *Glossoscolex*, *Hemigastrodrilus* and *Komarekiona*) and that tuberculum-like structures occur in the almid *Callidrilus*. The longitudinal alae of the almid *Glyphidrilus* are probably homologues of tubercula pubertatis.

In summary, *Sparganophilus* is here envisaged as being descended from a precursor of the almid-lumbricoid assemblage, with intraclitellar tubercula pubertatis, male pores on the multilayered clitellum, in XIII, prostate-like setal glands in many segments though lacking prostates, last hearts in XI, intestinal origin in IX, lacking a typhlosole and probably agiceriate; holonephric but perhaps lacking preclitellar nephrida (or is this absence merely a derived character of haplotaxids, alroids and *Sparganophilus* in response to an amphibious existence, as in the megascolecoid *Pontodrilus*?); holandric; and metagynous. Whether the ovaries were single-stringed, or webbed, or as in *Criodrilus* lacking linear strings, is less certain. All the lumbricoids computed with the apparent exceptions of *Microchaetus*, *Pontoscolex*, *Glossoscolex* and *Kynotus*, have single-stringed ovaries. This may be a device for facilitating placement of the eggs in the ovisacs (Gates, 1976) and parallel development of this feature has probably been a strong trend throughout the Lumbricoidea s. mihi presumably starting from an unspecialized criodrilid condition. Gates considered the single-stringed ovary diagnostic of his restricted Lumbricoidea.

In Hennigian terms *Sparganophilus* must be accorded a rank higher than superfamily but it is here placed in the new superfamily Sparganophiloidea.

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Biwadrilidae

The monotypic Japanese family Biwadrilidae (Biwadrilinae s. Jamieson, 1971d) appears in the phylogram to form a monophyletic grouping with the sparganophiloid through megascolecoid complex. Its sole species, *Biwadrilus bathybates*, was removed from the genus *Criodrilus* by Jamieson (1971d) and assigned to a subfamily Biwadrilinae of the Glossoscolecidae s. lat. Features warranting placing it in the Glossoscolecidae but now considered to be of suprafamilial significance are: the extensive, multilayered clitellum; the location of male pores near the posterior limit of the latter; the presence of setal glands resembling those of *Microchaetus*; and the intraparietal sperm ducts. Affinity with *Sparganophilus* was considered to be indicated by presence of two pairs of lateroparietal vessels, their origin in segment XIV, and the absence of a subneural vessel. This relationship is underlined by the fact that *Sparganophilus* is its phenetic nearest neighbour though its phylogenetic nearest neighbour is *Microchaetus*.

Reported presence of lateral lines, absence of spermathecae, the anterior location of the brain (in segments I and II) and other peculiarities necessitated placing it in a separate and apparently very primitive subfamily of the Glossoscolecidae. As it now appears as the plesiomorph sister-group of the sparganophiloid-almoid-lumbricoid-megascolecoid complex, it deserves, if Hennigian principles are strictly followed, a status above that of superfamily. It is proposed here to give it the status of a monotypic family within its own superfamily in the suborder Lumbricina.

Moniligastriidae

Of the three orders of the Oligochaeta recognized by Brinkhurst and Jamieson (1971d), the Moniligastriida and Haplotaxida are represented in the present study and it is seen (Figs. 1 & 2) that separate ordinal status for the Moniligastriidae (Oriental) is not justified. This reduction in rank has already been advocated by Jamieson (1977a) on demonstration that moniligastriid testis-sacs are not intraseptal proliferations. On the other hand the phenetic analysis (Fig. 3) depicts the moniligastriids as a highly distinct group as shown in a previous phenetic study (Jamieson, 1968b). Their distinctness is also indicated by the fact that they are phylogenetically and phenetically nearest neighbours and do not constitute the nearest neighbours of any other OTUs in the study. The reinterpretation of the nature of the moniligastriid testis-sac reveals that each of the one or two pairs of male pores opens at the posterior border of the segment behind the corresponding testes. This initial opisthopore condition and the extremely plesiomorph retention, in *Desmogaster*, of two pairs of male pores in separate segments are limited elsewhere in the Haplotaxida to the Haplotaxidae. Moniligastriids are therefore extraordinarily primitive in these respects, as in the possession of a unilayered clitellum (queried by Gates, 1972, but here confirmed for *Moniligaster troyi*) and the correlated large-yolked eggs. However, as Gates (1972) has stressed, they have an unusually large complement of unique characters which in Hennigian terms are to be regarded as apomorph.

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These include suspension of the testis-sacs on septa, the presence of enterosegmental organs, the ovarian sacs (see also some eudrilids), the multiple postoesophageal gizzards, the absence of peristomial attachment of the prostomium and (not computed because of lack of knowledge in other groups) union of hearts before communication with the dorsal blood vessel. These auto-apomorphies, while unifying the Moniligastridae, by virtue of their uniqueness do not determine the position of the family relative to other OTUs in the phylogram. It is the apomorphies shared with various other groups which do this.

The Moniligastridae are seen as the plesiomorph sister-group of the complex *Biwadrilus* through Megascolecidae (the Lumbricina). The Moniligastridae will therefore constitute the suborder Moniligastrina. The chief evolutionary step at this dichotomy is fusion of the two vasa deferentia of a side in the Lumbricina. In *Desmogaster* the two vasa remain separate, giving two pairs of male pores, while in *Moniligaster* there is only one pair of male pores, not because of fusion but because loss of the anterior pair of testes has occurred.

Syngenodrilidae

Syngenodrilus, imperfectly known from a single Ethiopian specimen, was placed in the Moniligastridae by Stephenson (1930) as a monotypic subfamily but was later transferred to the Alluroididae (Pickford, 1945; Gates, 1945; Jamieson, 1968b, 1971d). Association with alluroidids may have been unduly influenced by the symplesiomorphy single-layered clitellum and the relatively primitive location of the male pores, on XIII. Its nearest neighbour phyletically is *Pontoscolex* (Table 3) and phenetically is *Alluroides* (Table 3 and Fig. 3). Notable apomorphies of *Syngenodrilus* distinguishing it from haplotaxids and alluroidids are the presence of intraclitellar tubercula pubertatis, of three pairs of prostate glands (in XI, XII and XIII) of gizzards, in VIII and IX, of nephridial bladders and apparently the loss of lateral lines. It is possible that fusion of the male pores indicates that it is a survivor of the earliest stock of the Lumbricina, alone retaining the single-layered clitellum and large yolked eggs. It is here proposed to retain it as a monotypic family in the Alluroidoidea notwithstanding the paraphyletic nature of the superfamily so constituted in strict Hennigian terms.

Alluroidinae

The alluroidids *Standeria* and *Brinkhurstia* form the plesiomorph sister-group of *Syngenodrilus* through the Moniligastrina and Lumbricina. It is unlikely that the *Desmogaster* condition of two pairs of male pores is a reversion and it is therefore inferred that the ancestor which gave rise to the Alluroididae and Moniligastridae similarly had 2 pairs of pores with fusion occurring in *Syngenodrilus* independently of the Lumbricina. The interesting conclusion therefore emerges that the Alluroididae, characterized by a single pair of male pores, on XIII, and a single pair of testes, in X, (the proandric condition) have never fused the vasa deferentia and it may reasonably be supposed that the ancestor of the Alluroidoidea had two pairs of male pores, in XI and XII, as in *Desmogaster* and some Haplotaxidae, and that loss of the posterior testes probably occurred before movement of the remaining male pores from

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segment XI to XIII.

The affinities of the three alluroidid genera here computed have been discussed by Jamieson (1968b, 1971d). The phylogram supports the view there stated that the S. African *Standeria* and S. American *Brinkhurstia* are related to each other more closely than either is to the Ethiopian *Alluroides*, as is also indicated by the phyletic nearest neighbour relationships. A notable synapomorphy of *Standeria* and *Brinkhurstia*, with the fourth genus of the Alluroididae, the monotypic *Barriejamiesonia* Ljungstrom, 1971, (not computed) is the opening of the atrial prostates into the terminal chamber of the male deferent apparatus separately from the vasa deferentia whereas in *Alluroides* the vasa deferentia discharge into the ental region of the tubular or bulbous atria. It has been suggested (Jamieson, 1968b) that *Standeria* and *Brinkhurstia* may be descended from a form with *Alluroides*-type male terminalia. The phylogram is not inconsistent with this view but suggests that *Alluroides* is paraphyletic relative to the other two computed genera. At present, however, no useful purpose would be served by splitting the Alluroididae into two taxa of suprafamilial or higher rank; it is probable that autoapomorphies will be found to unify the group.

According to Hennigian principles the Alluroidoidea merit a rank coordinate with the combined Lumbricina and Moniligastrina, that is superior to subordinal status. They are here, however, referred to a new suborder, the Alluroidina.

Haplotaxidae

The Haplotaxidae form the plesiomorph sister-group of the combined suborders Alluroidina, Moniligastrina and Lumbricina but are here referred to as the suborder Haplotaxina, a taxon proposed by Brinkhurst and Jamieson (1971). It is remarkable that the only apomorphies of the haplotaxid computed (*H. violaceus*) are short seminal vesicles, egress of both pairs of vasa deferentia in a single segment and absence of ovaries from XIII. *H. gordioides*, the type-species (not computed) lacks even these apomorphies and is plesiomorph for all attributes employed in this study. This means that unless some internal synapomorphy (autoapomorphy) be found for the Haplotaxidae it will have to be considered a paraphyletic grouping falsely constructed on symplesiomorphy of which the diagnostic one is location of the male pores one segment behind the corresponding testes. In this regard it is noteworthy that Gates (1972), for a different reason, recognized the possibility that the family is polyphyletic when he stated "what now needs to be determined is whether and how much of the simplicity in haplotaxid somatic structure is secondary and perhaps independently acquired in various areas separated from each other by wide oceanic distances". It is here considered that characters such as the unilayered clitellum, large yolked eggs, the lateral lines (the apparent homologues of these lines occurring in some polychaetes, Jamieson, 1968b) and octogonadial condition are unlikely to have been secondarily acquired and are indication that many other features are genuinely plesiomorph. Erection of a separate family for progynous forms, including *H. violaceus*, as opposed to the type-species on the grounds that the absence of shared apomorphies indicates paraphyly would be of dubious value taxonomically. The remarkable metagynous *H. brinkhursti* recently discovered by Cook

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(1975) lacks synapomorphic links with *H. gordioides* and *H. violaceus* but similarly, is better included in the Haplotaxidae for the present. Brinkhurst and Jamieson (1971) have shown loss of the posterior pair of ovaries to be a haplotaxid trend but the discovery of a universal autapomorphy of the Haplotaxidae has yet to be made.

Other families.

The remaining groups of the Oligochaeta are the families which were placed in a suborder Tubificina within the order of Haplotaxida by Brinkhurst and Jamieson (1971). These are the aquatic microdrile families typified by the Tubificidae and the very distinct family Enchytraeidae. The additional oligochaete family, the Lumbriculidae, was placed in the monotypic order Lumbriculida. With the reinterpretation of the moniligastrid testis-sacs and the relationship of them to the male ducts, the Lumbriculidae became the only family with the prosopore condition (male pores opening in the same segment as the corresponding testes) and in view of their very few apomorphies it appears that if computed they would have formed the plesiomorph sister-group of the remainder of the Oligochaeta. It seems reasonable, therefore, to retain the Order Lumbriculida.

The position of the Tubificina is uncertain. It now appears most unlikely that if computed they would have intervened between the Haplotaxidae and any of the remaining computed forms. Yamaguchi's concept of a monotesticulate group for tubificids, naids, enchytraeids and similarly characterized microdriles seems to have considerable substance. Nevertheless, the tubificid arrangement of gonads and male terminalia (one pair of testes and of funnels in the segment preceding that containing male pores, ovaries and oviducal funnels) is not derivable from a lumbriculid arrangement but, as suggested by Brinkhurst and Jamieson (1971), is derivable from an octogonadial, protohaplotaxid condition. It appears that the Tubificidae, with the other monotesticulate groups, comprise the sister-group of the opisthoporous oligochaetes (Haplotaxida) and an order Tubificida is here recognized for all monotesticulate forms, the former Tubificina. Lumbriculids as the sister-group of the group Haplotaxida+Tubificida strictly merit supra-ordinal rank but are retained as an order. If, as Michaelsen (1928) and Yamaguchi (1953) consider, the parasitic Branchiobdellidae and acanthobdellid leeches are derived from protolumbriculids a strict application of Hennigian principles would demand that a monophyletic grouping including these and forms currently regarded as oligochaetes were recognized.

Whether the term Oligochaeta could strictly be retained for this grouping would be questionable. If other leeches were considered to derive from a proto-acanthobdellid it would be necessary to include them in the monophyletic grouping and the term Clitellata would remain available for this group.

As the present application of Hennig's principles to oligochaete systematics has proved of considerable value it is to be hoped that a similar study may be conducted on what may be termed the thecophorate (spermatheca bearing) annelids, including the Clitellata and the enigmatic Aeolosomatidae, and what may be called the trochophorate annelids (Archannelida and Polychaeta).

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Summary of the new classification

Full definitions are given only for new groupings.

Order Lumbriculida

At least one pair of male pores in the same segment as the corresponding male funnels.

Family Lumbriculidae (As defined by Cook, 1971)

Order Tubificida

Male pores 1 pair, in the segment behind the single pair of testes and seminal funnels. Ovaries 1 pair, in the segment behind the testes. Suborders Tubificina and Enchytraeina

Suborder Tubificina

Spermathecal pores in segments immediately in front of or behind those bearing the male pores, rarely in the same segment.

Superfamily Tubificoidea (As for the suborder)

Families: Tubificidae, Dorydrilidae, Naididae, Opistocystidae, and Phreodrilidae (As in Brinkhurst and Jamieson, 1971).

Suborder Enchytraeina

Spermathecae anterior to the segment bearing the reproductive organs, separated by a gap of five segments.

Superfamily Enchytraeoidea (As for the suborder)

Family Enchytraeidae (As in Brinkhurst and Jamieson, 1971)

Order Haplotaxida

Male pores 1 or 2 pairs in 2 successive segments or a single segment, at least one segment behind the posterior testes and seminal funnels. With two pairs of testes and two pairs or more commonly one pair of ovaries. If testes reduced to one pair these are separated from the ovaries by one or two segments.

Suborders Haplotaxina, Alluroidina, Moniligastrina and Lumbricina

Suborder Haplotaxina

Male pores 1 or 2 pairs in 2 successive segments or a single segment, the last pair only one segment behind the posterior of the two pairs of testes and funnels. With two pairs of ovaries or only the anterior pair or (*H. brinkhursti*) only the posterior pair. Clitellum one cell thick.

Superfamily Haplotaxoidea (As for the suborder)

Family Haplotaxidae

As in Brinkhurst (1971) but including deletion of the anterior ovaries and retention of those in XIII in *Haplotaxis brinkhursti*.

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Suborder Alluroidina

Male pores 1 pair, in XIII; testes in X or X and XI; ovaries in XIII. Clitellum one cell thick.

Superfamily Alluroidoidea (As for the suborder)

Family Alluroididae (As for the Alluroidinae in Jamieson, 1971d)

Family Syngenodrilidae (As for the Syngenodrilinae in Jamieson, 1971d)

Suborder Moniligastrina

Testes 1 or 2 pairs in testis-sacs each of which is suspended in the posterior septum of its segment and is detached from the anterior septum; male pores 1 or 2 pairs, each pair at the posterior border of the segment behind the corresponding testis-sac. Clitellum one cell thick.

Superfamily Moniligastroidea (As for the suborder)

Family Moniligastridae (As for the suborder)

Suborder Lumbricina

Testes 1 or 2 pairs, in X and XI or their homeotic equivalent; male pores 1 pair or (*Hoplochaetella*) 2 pairs, 2 or more segments behind the posterior testes. Where there are 2 pairs of testes the 2 vasa deferentia of a side uniting at the male pores (exceptionally, *Hoplochaetella*, remaining separate); ovaries a pair in XIII or its homeotic equivalent, rarely with a second pair in the preceding segment. Clitellum multi-layered.

Superfamilies: Lumbricoidea, Biwadriloidea, Sparganophiloidea, Almoidea and Megascolecoidea.

Superfamily Biwadriloidea

Lateral lines present between the ventral and dorsal setal couples. Body grooved dorsally but cross section not quadrangular. Anus dorsal, subterminal. Dorsal pores absent. Testes two pairs, in X and XI. Ovaries lobulated, in XIII. Calciferous glands, typhlosoles and gizzard-like thickening of the alimentary musculature absent; intestinal origin indefinite, in the region of XI-XIII. Supra-oesophageal blood vessel present. Subneural vessel absent. Lateroparietal vessels 2 on each side, one originating from the dorsal, the other from the suboesophageal vessel. Last hearts in XI. Male pores 1 pair, in XIII, immediately preclitellar. Vasa deferentia embedded in the bodywall. Lobular masses of prostatic glands discharging near the male pores together with a pair of prostate-like setal glands. Nephridia holonephridia; absent from the forebody; lacking terminal bladder, caecum or sphincter; all exonephric. Spermathecae absent. Clitellum extensive, multilayered, annular.

Family Biwadrilidae (Definition as for the Biwadrilinae Jamieson 1971d)

Superfamily Sparganophiloidea

Lateral lines absent. Anus dorsal but body not quadrangular. Dorsal pores absent or sporadically present intraspecifically. Setae sigmoid, simple pointed, 8 per segment. Testes two pairs, in X and XI. Ovaries 1 pair, single-stringed, in XIII. Calciferous glands, gizzards typhlosole and muscular thickening of the intestine absent. Intestine commencing in IX. Supra-oesophageal and subneural vessels absent. Lateroparietal vessels 2 on each side, originating from the dorsal and ventral

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vessels. Last hearts in XI. Male pores intraclitellar anteriorly in XIX. Prostates absent but prostate-like glands may be present in a few to many segments. Vasa deferentia deeply embedded in the body wall. Spermathecae intracoelomic, pretesticular, paired or multiple.

Family Sparganophilidae (As for the Sparganophilinae Jamieson, 1971d).
Superfamily Almoidea

Lateral lines absent. Body quadrangular in cross section; dorsal groove (always?) present; anus dorsal or dorsoterminal; dorsal pores absent. Setae sigmoid, simple pointed, 8 per segment. Testes 2 pairs or (*Lutodrilus*) 10 pairs in XII-XXI by interpolation of 10 segments, of which the last 8 are testicular, anterior to the normal 2 pairs of X and XI. Ovaries 1 pair, with many egg-strings, or (*Criodrilus*) not forming egg-strings, in XIII or (1 species) persisting in XII also. Digestive system not usually possessing oesophageal gizzard(s) but thickening of the anterior intestinal musculature usual. Intestine commencing in or far behind XV (to XXXVIII) or (Lutodrilidae) dilating gradually in posterior gonadal segments; dorsal typhlosole present; calciferous glands absent. Vascular system with dorsal, ventral and often supra-oesophageal and subneural vessels. If a supra-oesophageal is present, some hearts (always?) latero-oesophageal. Last hearts in XI or less commonly XII or XIII or (*Lutodrilus*) in XI-XXI. Male pores 1 pair, in or behind XV, intra- or ante-clitellar. Longitudinal tubercula pubertatis absent or indistinctly developed or represented by aliform ridges. Prostate glands or prostate-like glands rarely present; prostate glands if present lacking ectal muscular duct. Vasa deferentia deeply embedded in the body wall, sometimes discharging through glandular bursae. Spermathecae adiverticulate, post-testicular, rarely extending into or anterior to the testis segments; largely intraparietal; never with clearly differentiated intracoelomic duct; usually multiple in each intersegment occupied; rarely absent. Nephridia absent from 10 or more anterior segments; all exonephric holonephridia, sometimes vesiculate but never with diverticulum; terminal sphincter absent. Clitellum multilayered; annular. Cocoon elongate, fusiform, with several to many embryos.

Families: Almidae, Criodrilidae (Definitions as for the Alminae and Criodrilinae; Jamieson, 1971d) and Lutodrilidae McMahan, 1976.

Superfamily Lumbricoidea. Emend.

Lateral lines absent. Body approximately circular in cross section with posterior terminal anus; exceptionally (*Eiseniella*) quadrangular with dorsoterminal anus. Dorsal pores present or absent. Setae sigmoid, simple pointed (exceptionally bifid?), 8 or (*Periscollex*) numerous per segment. Testes two pairs, in X and XI (or one pair in one of these). Ovaries 1 pair, fan shaped or single-stringed, in XIII or (1 species) persisting in XII also. Digestive system usually with oesophageal gizzard(s) (pre-gizzards) less frequently with thickening of the anterior intestinal gizzard (post gizzard) or with pre- and post-gizzards. Intestine usually commencing in XV. Vascular system with dorsal, ventral and often with supra-oesophageal and subneural vessels. If a supra-oesophageal is present, some hearts (always?) latero-oesophageal. Last hearts usually in XI, sometimes more posterior. Male pores 1 pair, rarely 2 pairs, in XV to many segments more posteriorly; almost always anterior to the mid-clitellum, often preclitellar, exceptionally (*Opistodrilus*) postclitellar, opening directly or from glandular or muscular bursae but prostate glands

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rarely present and never (?) with ectal muscular ducts; euprostates unknown. Vasa deferentia frequently deeply embedded in the body wall. Spermathecae adiverticulate, very variable in number and location, pre- or post-testicular, paired or multiple; or absent. Excretory system holonephric or (*Tritogenia*) nephridia duplicated; sometimes with anterior enteronephry, vesiculate or avesiculate. Clitellum multilayered, usually saddle-shaped, often associated with longitudinal tubercula pubertatis.

Families: Lumbricidae, Hormogastridae, (both redefined below), Microchaetidae, (Definition as for the Microchaetini Jamieson, 1971d), Kynotidae (Definition as for the Kynotinae Jamieson, 1971d), Glossoscolecidae (Definition as for the Glossoscolecini Jamieson, 1971d) and Komarekionidae Gates, 1974. Family Lumbricidae Claus 1876. Emend.

Prostomium prolobous to tanylobous, never? zyglobous. Form cylindrical or rarely posteriorly quadrangular or trapezoidal in cross section. Pigment present or absent. Setae in 8 longitudinal rows commencing on II, sigmoid, simple pointed, often cicatriced distally, closely or widely paired or unpaired. Some ventral setae often on genital tumescences and modified as genital setae each of which (always?) bears 4 longitudinal grooves. Nephropores on each side in a single series or alternating. Clitellum usually saddle-shaped, beginning between the 17th and 52nd segments and occupying 4 to 32 segments. Tubercula pubertatis situated in the clitellar region and shorter than to longer than the clitellum, forming a pair of continuous strips or ridges; or series of pairs of isolated papillae or sucker-like tubercles. Male pores intrasegmental, anteclitellar, almost always on XV, sometimes on XIII, rarely on XI or XII, often in slits in glandular tumescences each of which may correspond internally with a short glandular atrium projecting into the coelom but prostates with muscular ducts absent. Female pores on XIV. Spermathecal pores usually in front of the ovaries, never on the clitellum; 2-8 pairs in intersegments 5/6-19/20, varying in position from setal lines *a* to the middorsal line but usually in 9/10 and 10/11 in *cd* lines; sometimes multiple in each segment occupied; sometimes absent. Dorsal pores present in median single file or bilateral pores present in line with the dorsal setal couples.

Oesophagus lacking gizzards but with calciferous glands in X, XI-XIII, XIV, XV (always?) comprising longitudinal chambers that open at their anterior ends into the oesophageal lumen which may or may not form extramural pouches or diverticula. The intestine beginning in XV or (*Diporodrilus*) XIV or XVI with a "crop" followed by a gizzard. The gizzard occupying 1 to 3 segments, usually in XVII and XVIII, never behind XX. Typhlosole (always?) present. Intestinal caeca and supra-intestinal glands absent. Dorsal, ventral and subneural blood vessels well developed; the subneural adherent to the nerve cord. Hearts 5-7 pairs, of which the last pair is in XI or (*D. octaedra*) 3 or 4 pairs with the last in IX or X. Supra-oesophageal vessel absent. Latero-oesophageal vessels median to the hearts and passing to the dorsal vessel in the region of X-XI. Lateroparietals absent. Nephridia holonephridia, vesiculate, the bladder sometimes with diverticulum. Nephridia sometimes discharging into longitudinal ureters. Testes in X and XI or, rarely, in only one of these, free or in suboesophageal or peri-oesophageal testis-sacs (the latter type of sac enclosing the hearts and seminal vesicles of X and XI). Sperm ducts apparently never concealed

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in the body wall musculature; sometimes expanded or coiled behind the sperm funnels to form epididymes. Seminal vesicles 4 pairs, in IX-XII: 3 pairs, in IX, XI and XII, or 2 pairs, in XI and XII. Ovaries in XIII, always (?) with a single terminal string of oocytes. Oocytes maturing in ovisacs which project into XIV from its anterior wall. Spermathecae adiverticulate though sometimes appearing diverticulate owing to constriction by septa; sessile or pedunculate but lacking distinct duct. Subfamilies: Lumbricinae and Diporodrilinae

Subfamily Lumbricinae

Definition as for the family with dorsal pores in median single file, lacking paired, bilateral coelomic pores.

Subfamily Diporodrilinae

Differing from the Lumbricinae in lacking dorsal pores and possessing bilateral coelomic pores. Prostomium epilobous. Form cylindrical. Lacking cutaneous pigmentation. Sculpturing of somatic and genital setae not recorded. Nephropores on each side in a straight line. Clitellum in the region XXI-XXXIII. Tubercula pubertatis shorter than the clitellum. Male pores on XV. Spermathecal pores in the region 8/9-11/12. Hearts in VI, VII-XI but vascular system otherwise undescribed. Crop within the region of XIV-XVII; gizzard in two of segments XVII-XX. Posterior nephridia retaining segmental pores but interconnected on each side by a longitudinal ureter. Holandric; testis-sacs absent. Seminal vesicles in XI and XII. Spermathecae intraparietal or intracoelomic, sessile.

Family Hormogastridae Michaelsen, 1928. Emend.

Setae 8 per segment, closely paired; genital setae longitudinally grooved. Dorsal pores absent. Male pores intraclitellar, anteriorly or posteriorly on the clitellum, varying from $\frac{1}{2}$ XV to 15/16 or (Ailoscolecinae) at $\frac{1}{4}$ XXII; on or anterior to tubercula pubertatis if these are present; such tubercula groove-like. Female pores between $\frac{1}{2}$ XIV and 14/15, varying from ventral to *a* to the region of *c* lines. Last hearts in XI. Oesophageal gizzards (progizzards) well developed. Intestinal gizzards (postgizzards) rudimentary or absent. Calciferous glands present or absent. Holonephric; nephridia vesiculate and (always?) with diverticulum. Holandric; testis-sacs absent; two pairs of short seminal vesicles, in XI and XII. Prostates absent or (Ailoscolecinae) sessile prostate-like glandular masses associated with the tubercula pubertatis in the vicinity of the male pores. Metagynous; ovaries single-stringed(?). Spermathecae adiverticulate, paired or multiple, always with some in the genital segments but sometimes extending anterior to them. Subfamilies Hormogastrinae, Vignysinae and Ailoscolecinae

Hormogastrinae Bouché, 1970

Hormogastridae with 3 distinct gizzards, in VI, VII and VIII. Rudimentary intestinal gizzards present or absent. No blood vesicles on the ventroparietal vessels. Body wall not especially thickened. With or without calciferous glands. Female pores in the region of *b* lines. Male pores varying from $\frac{1}{2}$ XV to 15/16, on or anterior to the tubercula pubertatis if these are present. Spermathecal pores paired or multiple.

Vignysinae Bouché, 1970

Hormogastridae with 2 unequal gizzards in VI and 6/7 and with subparietal blood vesicles. Intestinal gizzard present. Calciferous glands

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absent. Male pores posterior in XV, well anterior to the tubercula pubertatis which are groove like. Female pores ventral to *a* lines. Spermathecal pores paired.

Ailoscolecinae Bouché, 1969

Male pores intraclitellar, discharging on tubercula pubertatis at $\frac{1}{4}$ XXII; tubercula groove like. Spermathecal pores immediately anterior to the testes. Two progizzards, in VI-VII and VIII-IX. Intestinal gizzard absent. Calciferous glands present. Prostate glands associated with the tubercula pubertatis in the vicinity of the male pores. Female pores shortly above *b* lines. Spermathecal pores paired.

Superfamily Megascolecoidea

Lateral lines absent. Body approximately circular in cross section with posterior terminal anus or if not circular not quadrangular and not with dorsoterminal anus. Dorsal pores usually present. Setae sigmoid, simple-pointed, 8 per segment or perichaetine. Testes two pairs, in X and XI (or their homeotic equivalent) or one pair in one of these. Ovaries 1 pair with several to many egg strings in XIII or (1 species) persisting in XII also. Digestive system often with oesophageal gizzard(s), rarely with thickening of the anterior intestinal musculature. Intestine beginning in XII or XIII or, usually, more posteriorly. Vascular system with dorsal, ventral and often with supra-oesophageal and subneural vessels. If a supra-oesophageal is present, some hearts (always?) latero-oesophageal. Last hearts in or, usually, behind XI. Male pores 1 pair or rarely (*Hoplochaetella* part) two pairs, in XVII-XX, commonly XVII but predominantly XVIII, shortly behind or anterior to the posterior end of the clitellum, rarely anterior to the midclitellum. Usually with prostates, at or in the vicinity of the male pores, the glandular part of which may have muscular walls and receives the vasa deferentia entally (euprostates) or with insignificant muscularization of the glandular part but usually with muscular ectal duct and with the vasa deferentia entering the duct ectal to, or rarely within, the glandular portion (metaprostates). Metaprostates tubular, with simple internal duct, or tubuloracemose, with laterally branched or diverticulate lumen, or racemose, with ramifying internal ducts. Vasa deferentia not deeply embedded in the body wall. Spermatheca(e) paired, sometimes unpaired or multiple, diverticulate or less commonly adiverticulate, rarely absent, the diverticula usually sperm-storing; predominantly with spermathecae pretesticular but (Eudrilidae) showing a tendency to become post-testiculate or even posterior to the male pores; if post-testicular frequently communicating with the oviducal apparatus. Excretory system holonephric and/or meronephric, exonephric and/or enteronephric, sometimes vesiculate. Clitellum multilayered; annular rarely saddle-shaped; longitudinal tubercula pubertatis rare.

Families: Megascolecidae, Eudrilidae and Ocnerodrilidae

Family Megascolecidae (As in Jamieson, 1971a, but excluding the Ocnerodrilinae).

Subfamily Megascolecinae (As in Jamieson, 1971c).

Subfamily Acanthodrilinae (As in Jamieson, 1971b).

Family Eudrilidae (As in Gates, 1972).

Subfamilies Eudrilinae and Pareudrilinae (As in Gates, 1972).

Family Ocnerodrilidae (As for the Ocnerodrilinae in Jamieson, 1971b).

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Subfamily Ocnerodrilinae (As for the tribe Ocnerodrilini in Jamieson, 1971b).

Subfamily Malabarinae (As for the tribe Malabarini in Jamieson, 1971b).

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