A taxonomic analysis of the Haplotaxidae (Annelida, Oligochaeta)

R. O. Brinkhurst

Ocean Ecology Laboratory, Institute of Ocean Sciences, P.O. Box 6000, Victoria, B.C., Canada V8L 4B2

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A combination of classical and computer-aided methods suggests that the Haplotaxidae can now be divided into several genera. *Alphadrilus* nov.gen. is monotypic for *Alphadrilus smithii* n.comb. *Delaya* nov.gen. contains *D. bureschi, D. leruthi, D. corbarensis, D. cantabronensis,* and *D. navarrensis,* all n.comb. *Adenodrilus* is retained for *A. denticulatus, Heterochaetella* for *H. glandularis,* and *Villiersia* for *V. guanivora.* The new genus *Hologynus* nov.gen. is erected for *H. ornamentus* and *H. hologynus* and its probable synonyms. *Haplotaxis* is retained for the *gordioides*-like species with specialized pharynx and chaetae associated with a predaceous habit. *Pelodrilus* is retained for *P. violaceus* and perhaps *P. ignatovi* and *P. africanus* (incertae sedis) and its probable synonyms. *Tiguassu* is elevated to the status of the type of a new family, **Tiguassidae.** *Metataxis* sensu Omodeo is placed incertae sedis in the order Lumbricina.

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La combinaison de méthodes classiques et d'analyses à l'aide d'un ordinateur permet de croire que les Haplotaxidae peuvent être séparés en plusieurs genres. *Alphadrilus* nov.gen. ne contient qu'une espèce, *Alphadrilus smithii* n.comb. *Delaya* nov.gen. contient *D. bureschi, D. leruthi, D. corbarensis, D. cantabronensis,* and *D. navarrensis. Adenodrilus* contient *A. denticulatus, Heterochaetella* contient *H. glandularis,* et *Villiersia* contient *V. guanivora.* Un nouveau genre, *Hologynus* nov.gen., est créé pour regrouper *H. ornamentus* et *H. hologynus* et ses synonymes probables. *Haplotaxis* est retenu pour désigner les espèces apparentées à *gordioides* qui possèdent un pharynx spécialisé et des soies associées à une habitude prédatrice. *Pelodrilus* est retenu et contient *P. violaceus* et peut-être aussi *P. ignatovi, P. africanus* (incertae sedis) et ses synonymes probables. *Tiguassu* devient le type d'une nouvelle famille, celle des **Tiguassidae.** *Metataxis* sensu Omodeo est placé sous toutes réserves dans l'ordre des Lumbricina et son statut demeure incertain.

[Traduit par la revue]

Introduction

In a revision of the Haplotaxidae, Brinkhurst (1966) merged the existing species into the single genus *Haplotaxis* Hoffmeister because of an apparent overlap in the characteristics of this and the three other genera (*Pelodrilus* Beddard, 1891, *Heterochaetella* Yamaguchi, 1953, and *Adenodrilus* Cekanovskaya, 1959). Three *Pelodrilus* species were considered to have been included in the family on the basis of insufficient evidence, and two taxa referred to by Omodeo (1958) were listed as nomina nuda. Since that time, a number of species and some further genera (*Tiguassu* Righi, Ayres, and Bittencourt, 1978, *Metataxis* Righi, 1985, *Villiersia* Omodeo, 1987) have been described, as have the earlier nomina nuda. Careful retranslation of some original descriptions, reevaluations of characters such as the ornamentation of the chaetae, and the development of objective hypothesis-testing methods (the selection of methods used here being justified by Nemec and Brinkhurst, 1987) now make possible a new analysis of this interesting group. The family has been identified as containing descendants of the earliest line of oligochaetes, according to one possible scenario (Brinkhurst 1982, 1984, 1989; Brinkhurst and Nemec 1987). The analysis of primitive groups proves difficult, even by recent techniques, because of a lack of synapomorphic characters, and for this reason the monophyletic status of the haplotaxids has not always been accepted (for example, Jamieson 1978). This contribution is designed to test the monophyletic status of the group, and to review possible generic groupings within the identified monophyly where possible.

Material and methods

Anatomical work has been restricted to the examination of a number of *Haplotaxis* s.str. specimens, including the description of a new species reported elsewhere (Brinkhurst and Marchese 1987). These were unstained whole mounts for the most part. The type specimen (fragments) of *Haplotaxis vermivorus* (Michaelsen, 1932) was borrowed from the Institute of Taxonomic Zoology—Zoological Museum, Amsterdam (ZMUA 318) and examined in alcohol. Only a posterior fragment remains, the slides prepared by W. Michaelsen having been destroyed in Hamburg together with the rest of the pre-1940 oligochaete slide material. Most of the character states used in the analyses were derived from the original fragmentary literature on this poorly known group, much of the material available having been examined previously (Brinkhurst 1966).

Two computerized analytical methods were employed. The first is a hybrid method, described by Nemec and Brinkhurst (1987), which uses a Jaccard similarity index with average linkage. As the Jaccard index virtually ignores zero matches, the user may elect to polarize character states and accord the apomorphic state a 1 or + value to emphasize synapomorphies. It should be noted that absence of a feature, such as chaetae, say, may be taken to be apomorphic and scored " + "; there is no compunction to score absence as " − " or zero. This technique allows a rapid examination of groupings based on shared advanced characters. The use of average linkage prohibits the identification of the points along the tree where characters change, but in a future development using complete linkage this should be possible. Our data contain few apomorphic character states. Inclusion or exclusion of either some taxa or characters entered made very little difference and the resulting tree is very stable. This method is used to obtain a rapid first estimate of groupings, and to provide a basis for an independent comparison with the results of the second method. Although a phenogram and a dendrogram cannot be compared directly, prepared classifications of the taxa derived from them can be. Examination of the differences in groupings often leads to a better appreciation of the way characters are used by the second technique. Congruence is taken to indicate independent support for the groupings identified.

The second method is a parsimony analysis, the IBM/PC version of PAUP 2.4.1 distributed by D. L. Swofford (Illinois Natural History Survey). The final runs of the analyses used the following options: addseq = closest, Farris, Mulpars, swap = global, hold = 10, maxtree = 10, weights added (character 3 × 2, 19 × 1/3), multistates unordered, root as outgroup or ancestor.

The problem with the Haplotaxidae in terms of the requirements for

TABLE 1. The taxa considered in the analyses

Principal taxon	Significant generic attributions	Associate taxa
gordioides Hartman, 1821*	*Haplotaxis*	*ascaridoides* Michaelsen, 1905 *dubius* Hrabĕ, 1931 (*ichthyophagus* Gates, 1971, *forbesi* Smith, 1918, *villiersi* Omodeo, 1988 not analyzed)
vermivorus Michaelsen, 1932	*Haplotaxis*	
heterogyne Behham, 1904	*Haplotaxis*	
aedeochaeta Brinkhurst and Marchese, 1987	*Haplotaxis*	
gastrochaetus Yamaguchi, 1953	*Haplotaxis*	
smithii Beddard, 1888	*Haplotaxis*	
ornamentus Brinkhurst and Fulton, 1980	*Haplotaxis*	
bureschi Michaelsen, 1924	*Pelodrilus*	*leruthi* Hrabĕ, 1958 and (as *Haplotaxis*) *corbarensis* Delay, 1972 *cantabronensis* Delay, 1973 *navarrensis* Delay, 1973
ignatovi Michaelsen, 1903	*Pelodrilus*	
violaceus Beddard, 1891*	*Pelodrilus*	
africanus Michaelsen, 1908	*Pelodrilus*	*monticola* Michaelsen, 1908 *darlingensis* Michaelsen, 1907 *tuberculatus* Benham, 1909
hologynus Michaelsen, 1907	*Pelodrilus*	*bipapillatus* Michaelsen, 1924 *aucklandicus* Benham, 1909
denticulatus Cekanovskaya, 1959*	*Adenodrilus*	
glandularis Yamaguchi, 1953*	*Heterochaetella*	
guanivorus Omodeo, 1987*	*Villiersia*	(syn. of *Haplolumbriculus insectivorus* Omodeo n.n.)
kraepelini Michaelsen, 1914	*Villiersia* and *Pelodrilus*	
americanus Cernosvitov, 1939	*Pelodrilus* and *Metataxis*	
brinkhursti Cook, 1975	*Haplotaxis* and *Metataxis*	
carnivorus Omodeo, 1987	*Pelodrilus* and *Metataxis*	(*falcifer* Omodeo, 1958 not analyzed)
eliae Righi, 1985*	*Metataxis*	
reginae Righi et al., 1978*	*Tiguassu*	

*Type species of the genus.

this method is that there is no clear sister group and no obvious plesiomorphic outgroup available if the evolutionary position of the family is, in fact, basal to all other oligochaetes. Analyses were run in two ways, with a hypothetical ancestor as the root or alternatively with representation of the two more apomorphic families Enchytraeidae and Propappidae as outgroup. These are referred to as ROOT 1 and ROOT 2 in the results. A special feature of the PAUP analysis was used to answer the initial question "is the Haplotaxidae a monophyletic group?" If one attempts to root the analysis using the outgroup when the ingroup is not a monophyly, PAUP will print the message "Rooting such that specified ingroup is monophyletic not possible. Tree will be rooted using midpoint method." The first runs of the matrix produced this result, as anticipated, and so suspect taxa were deleted one at a time until the largest single monophyly could be identified. Then the analyses were rerun with ROOT 1 (ancestor). This process resulted in trees showing the outgroup as the most apomorphic members of the ingroup (all oligochaetes) and, as anticipated, it reversed the polarization of four characters (4, 8, 9, 19) that separated major nodes on the tree.

The emphasis here is primarily on the identification of possible genera within the monophyletic group discovered by the method described above, using as objective a method as possible. Recovering the correct evolutionary relationships of such old, poorly known taxa is an ideal that may not be achievable even if the constituent species

were all properly described, which is not true of this set. The final classification, then, is likely to be a compromise proposal based on the best evidence from all methods.

The taxa

The taxa included in this study are listed in Table 1. Many have never been redescribed since their original discovery. The so-called associate taxa consist of those routinely associated with the principal taxa in all initial analyses. In the final analyses whole groups were represented by the principal taxa for the sake of economy. In most instances the associate taxa were classed as synonyms of their principal taxa by Brinkhurst (1966).

The outgroup taxa used in the ROOT 2 analyses were *Enchytraeus albidus* Henle and *Propappus volki* Michaelsen. These were shown to belong to different families by Coates (1986). The antecedents of these taxa are thought to be evolutionarily more recent than the antecedents of the modern haplotaxids according to the version of annelid phylogeny espoused by Brinkhurst (1982, 1984, 1989). Several species proved to be unrelated to *Haplotaxis* and were omitted from the final analyses. The final ROOT 1 (ancestor) analyses were run with these species excluded.

For Jaccard analyses, the outgroup taxa were also excluded because these tests were used to test relationships within the ingroup identified by PAUP. The ancestor was also excluded because of its close

TABLE 2. Character states for various taxa

	Characters																					
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22
ANCESTOR	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Propappus volki	1	0	1	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	3	1	0	0
Enchytraeus albidus	1	0	0	1	0	0	0	1	1	1	1	1	1	0	0	0	0	0	3	0	0	0
gordioides	0	0	0	0	0	0	0	1	1	0	0	0	0	1	0	0	0	1	1	0	1	0
vermivorus	0	0	0	1	0	0	0	(1)	(1)	0	0	0	0	1	0	0	0	0	9	0	1	(0)
heterogyne	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	2	0	1	0
aedeochaeta	1	0	0	1	0	0	0	(1)	1	0	0	0	0	1	0	0	0	2	1	0	1	0
gastrochaetus	0	0	0	1	0	0	0	(1)	(1)	0	0	0	0	1	0	0	1	0	2	0	1	0
smithii	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0
ornamentus	0	0	0	0	0	1	0	1	1	0	0	0	0	0	0	0	0	0	2	0	0	0
bureschi	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0
ignatovi	0	0	0	1	0	0	0	1	1	0	0	0	0	0	0	0	0	0	2	0	0	0
violaceus	0	0	0	1	0	0	1	1	1	0	0	0	0	0	0	0	0	0	3	0	0	0
africanus	0	0	0	1	0	0	0	1	1	0	0	0	0	0	0	0	0	0	3	0	0	0
hologynus	0	0	0	0	0	1	0	1	1	0	0	0	0	0	0	0	0	0	3	0	0	0
denticulatus	0	0	0	0	1	0	0	1	1	0	0	0	0	0	0	1	0	0	3	0	0	0
glandularis	0	0	0	0	0	0	0	(1)	(1)	0	0	0	0	0	1	0	0	0	0	0	0	0
guanivorus	1	0	0	0	1	0	0	1	(1)	0	0	0	0	0	0	0	0	1	2	0	0	0
kraepelini	1	0	0	1	1	0	0	(1)	(1)	0	0	0	0	0	0	0	0	1	9	0	0	(0)
americanus	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
carnivorus	1	0	1	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	1	0	0	1
eliae	0	0	1	0	0	0	0	1	1	0	0	0	0	0	0	0	0	1	2	0	0	0
brinkhursti	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	2	0	0	0
reginae	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	1	0	0

NOTE: Characters are identified in the text. In PAUP, characters enclosed in parentheses were coded 9. In Jaccard, 19 and ANCESTOR were omitted. Character 2 was omitted from these analyses as it is consistent throughout. Character 22 was omitted once *carnivorus* was dropped.

similarity to *H. smithii* in the data matrix, and also because an assumed common apomorphic character would have had to be added o each taxon, since the computerized version of the Jaccard analysis available to us when those tests were run could not accept all-zero data rows.

Four taxa were excluded on the basis of inadequate information, but three are clearly related to the *gordioides* group (see Table 1). The position of *Metataxis falcifer* (Omodeo) is more conjectural.

Characters

Twenty-two characters are listed in their plesiomorphic states as follows[1]: 1, gonad 1 present; 2, gonad 2 present; 3, gonad 3 present; 4, gonad 4 present; 5, gonads not shifted from X to XIII; 6, male pores separate; 7, male pores one pair per segment; 8, oviducts plesiopore; 9, male and female gonoducts similar; 10, sperm funnels nonglandular; 11, head pore absent; 12, peptonephridia absent; 13, chaetae less than three per bundle; 14, chaetae not *gordioides*-like; 15, chaetae more or less similar in each bundle; 16, at least one if not both chaetae simple-pointed; 17, chaetae not abruptly enlarged from II through XX and then smaller; 18, genital chaetae absent, present and wide, or present and hairlike (multistate); 19, spermathecae in 4, 3, 2, or 1 segments (multistate); 20, proboscis absent; 21, eversible pharynx and septal glands present; 22, spermathecae paired.

Some explanantion may be required here. Character 6 reflects the fact that the male pores of two segments are closely associated in a glandular mass in *H. hologynus* (apomorphy: male pores close together). Character 14 refers to the apomorphic condition of the chaetae in *H. gordioides* and others on which the ventrals are single, large, and sickle-shaped, the dorsals small and usually missing from a variable number of segments.

Characters were weighted equally (apart from characters 3 ($\times$ 2)

'Characters 1−4 may be identified later by the symbols GI−GIV for gonad 1 − gonad IV, i.e., the complete set of 2 pairs of testes, 2 pairs of ovaries, or combinations thereof (e.g., GI−II, GIV).

and 19 ($\times$ 1/3)) and multistates were unordered. Character 19 (numbers of segments with spermathecae) showed the greatest number of reversions when it was used in early analyses, but weight reduction made no difference. Jaccard analyses and some experimental PAUP analyses were run without this character, and then the latter were run with it at equal weight to other characters. Character 2 was omitted when it was seen to be uniform, and character 22 was omitted once the taxon *carnivorus* was dropped. Unknown characters coded 9 in PAUP were estimated or omitted in the Jaccard analyses as shown in Table 2.

The resulting matrix (Table 2) was iater modified from this version, which assumes an ancestral oligochaete with four pairs of gonads in successive segments (as argued by Brinkhurst 1989 and earlier) and allows a character for "gonad shift," normally apparently forward. The revised matrices were run assuming a multigonadal ancestor (i.e., simply reporting the actual segments in which testes or ovaries appear, with presence as plesiomorphic) or in another arrangement in which the presence of testes in X and XI is considered plesiomorphic, whereas their presence in, say, VIII or IX is apomorphic. The resultant clusters and parsimony analyses differ from those resulting from the "gonad I − gonad IV plus shift" version (Brinkhurst 1989), even in these preliminary trees, marred as they are by the inclusion of taxa which turned out to be excluded from the haplotaxids later. The main groupings are still recognizable, of course, but there are quite a few detailed changes within the tree, as there should be if the methods are at all sensitive. The separation of gonad sequence from gonad shift is considered to be a complex question that involves the recognition of character sets with quite distinct bases for natural selection (Brinkhurst 1989). These results are not displayed here.

Results

Classical studies

The first significant result comes from the reexamination of *H. vermivorus*. The supposedly unusual carnivorous habit of
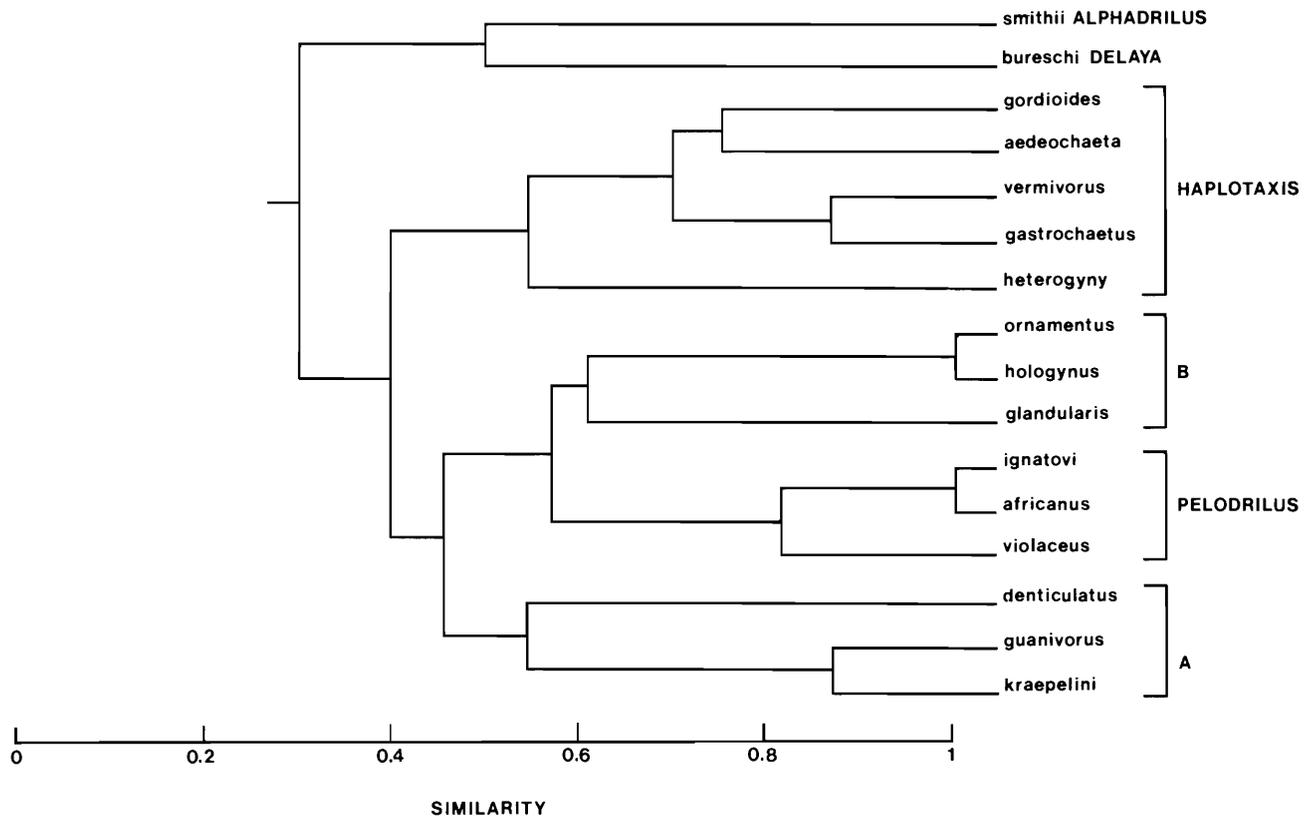
FIG. 1. Results of a Jaccard − average linkage cluster analysis of data from Table 2. Suggested generic groupings and the A and B groups shown on the right are discussed in the text.

this species is now considered to be an attribute of all the *gordioides* group of taxa with a modified pharynx and chaetae (the *gordioides* group of Table 1 plus *heterogyne, vermivorus, aedeochaeta*, and *gastrochaetus*, but not *smithii* even though it was originally described as a *Haplotaxis* rather than a *Pelodrilus* species). Similar large sickle-shaped chaetae in a recently described lumbriculid are used to assist in the capture and ingestion of live prey (McKey-Fender and Fender 1988). The remains of tubificids have been observed in the digestive tracts of other *gordioides*-like specimens (unpublished observations). A careful translation of the original description by Michaelsen (1932) of *H. vermivorus* indicates that too much was made of Michaelsen's comment about the existence of an enchytraeid-like dorsal pharyngeal pad, because he goes on to say that a gizzard occupies IV and part of V, and that the anterior part of this organ is thickly muscular whereas the rest is thinner. Brinkhurst and Marchese (1987) have shown this to be true of taxa in the *gordioides* complex, though the segments involved appear to vary. This variation may be related to the degree of contraction of the pharynx. The chaetae are clarly those of the *gordioides* group, as observed on the holotype. This discovery removes the lynch pin from the argument for the unification of the original genera *Haplotaxis* and *Pelodrilus*, as the former group possesses the modified chaetal arrangement and the specialized gizzard apparently associated with a carnivorous diet. *Haplotaxis smithii* is an exception and will now be excluded from the genus (see below).

A second recent shift in character evaluation was begun by Omodeo (1987) who recognized a set of small depressions on the chaetae of *H. gordioides* of the form originally associated with the chaetae of the *Pelodrilus bureschi* group (Table 1). This group of five species is distributed between France and Spain to Jugoslavia, Bulgaria, and Roumania, in caves. Another species, *H. ornamentus*, was described for Tasmania by Brinkhurst and Fulton (1980) and it, too, has ornamented chaetae. The species shares a number of supposedly plesiomorphic character states with the European forms but no shared apomorphy apart from the ornamentation. Following the discovery of ornamentation on the chaetae of *H. gordioides*, confirmed by examination of material of both *H. gordioides* and *H. vermivorus* (Brinkhurst and Marchese 1987), *ornamentus* has been removed from the *bureschi* group, which now has a coherent geographic distribution. The character "ornamented chaetae" has been excluded from recent analyses as it is now unknown for a large proportion of the included taxa. Rechecking the description of *ornamentus* shows that it shares an apomorphy of character 6 (male pores close together) with the *hologynus* group, which creates a group with a more rational zoogeographic distribution.

Jaccard analysis

The final run of the Jaccard analysis with the *Metataxis* species excluded produced the result illustrated in Fig. 1. As the hypothetical ancestor and *smithii* were identical once character 19 was dropped, *smithii* now represents the ancestral condition. The *bureschi* group clusters close to this. The *Haplotaxis* s.str. group recognized by classical considerations is clearly recognizable. The taxa *ornamentus* and *hologynus* are associated with *glandularis* at a low level of similarity (B group), and these are then associated with *violaceus, ignatovi*, and *africanus*. The final group of three taxa (group A) are associated with each other and with the other groups at a similarity level of less than 0.6.

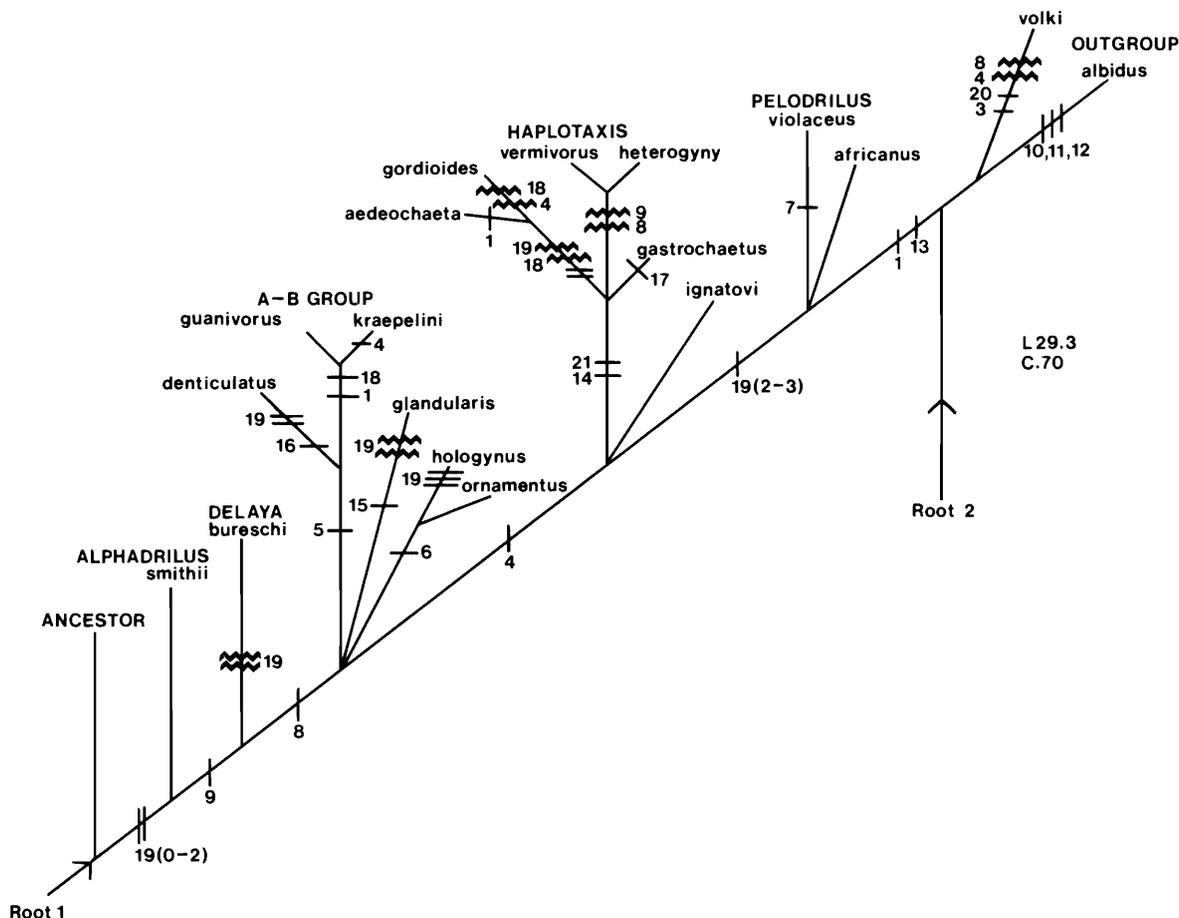This arrangement has remained quite stable despite explora-

FIG. 2. PAUP analysis results of data from Table 2. Two different root positions are shown. Characters 4, 8, 9, and 19 reverse polarity depending on the root selected. Straight lines represent character changes from 0 to 1 (one line) or 1 to 2 (two lines), etc.; wavy lines represent equivalent reversals. L, tree length; C, consistency index.

tory changes in both taxa and characters included, with the exception of runs assuming a multigonadal ancestor involving the first five characters of the list used here. These placed the *gordioides* group between *violaceus* and *denticulatus*.

The generic names shown on the right of Fig. 1 are those proposed later in this study.

Parsimony analyses

The taxa that were excluded from the Haplotaxidae by using the device of rooting by the outgroup with character 3 given a weight of 2 were those identified as *Metataxis* by Righi (1985) and Omodeo (1987), confirming earlier results reported elsewhere (Brinkhurst 1989).

The parsimony analysis results are illustrated by the final tree shown in Fig. 2, which differs from earlier versions only in terms of rotations in the positions of some unresolved taxa. These are identified by calling for TREEOUT = 1, a print showing the lengths of branches proportional to the number of changes on those branches.

The first obvious grouping of species on the tree is labelled *Haplotaxis*, which is defined by apomorphies on 14 and 21, the characters of the pharnyx and chaetae associated with the predatory habit. This group contains the same species as those identified by the cluster technique.

The second major node consists of three unresolved lines, the A and B groups of the cluster analysis. The taxon *glandularis* is placed here only because characters 8 and 9 are

assumed to be coded 1 rather than unknown (9) as seems reasonable. Visual inspection of Fig. 2 shows that if these characters were coded 0, PAUP would place it beside the ancestor.

The A group is defined by the apomorphy of 5, the forward shift of the gonads, which is a rather weak character (see below). Both *glandularis* and the *hologynus* group are defined by unique apomorphies (characters 15 and 6, respectively).

The type species of *Pelodrilus*, *P. violaceus*, is defined by the apomorphy of 7, but this does not apply to its original congeners, the *africanus* group and *ignatovi*. These three cluster together as *Pelodrilus* in Fig. 1. The separation of *ignatovi* from the others by PAUP is entirely due to the coding of character 19, which is extremely variable for *ignatovi*. Hrabě (1974) provided one of the very few redescriptions of a haplotaxid species in which he showed that *ignatovi* could have a single pair of spermathecae in VIII and other variations, and so the cluster grouping is more representative of the true situation than PAUP, because of my coding of character 19.

The only former *Pelodrilus* species not so far accounted for are those belonging to the *bureschi* group (the others being *kraepelini* in the A group, *hologynus* and associate taxa in B, and two members of *Metataxis*; see Table 1). The five *bureschi* group species can only be distinguished from the rest of the family by the synapomorphy of 9 but the plesiopore state of 4 and 8. The group is similarly isolated in the clusters.

Five former *Haplotaxis* species have been removed from that

genus; *H. navarrensis, H. cantabronensis*, and *H. corbarensis* are placed in the *bureschi* group. They were placed in *Haplotaxis* only after my 1966 revision reduced the family to a single genus. *Haplotaxis ornamentus* has been recognized as part of the *hologynus* group as noted above. The last *Haplotaxis* species to be considered, *H. smithii*, is not identified by any autapomorphy at this point. Indeed, *smithii* has only a change in the number of spermathecae separating it from the hypothetical ancestor in the PAUP analysis. As character 19 was omitted from the Jaccard analysis, *smithii* and the ancestor are identical in that data matrix and so the hypothetical ancestor was dropped.

The only major difference between the results of the two analyses, therefore, is the intervention of *Haplotaxis* between the lowermost groups and *Pelodrilus* in PAUP, whereas the cluster results emphasize the separation of *Haplotaxis* from those groups with the more usual body form, chaetae and pharynx. Again, this is solely related to coding for character 19, but the pattern persists even when 19 is downgraded from a weight of 1 to one third the value of other characters. I have not identified any synapomorphy from the "non-*Haplotaxis*" group.

Zoogeography

Zoogeographic evidence supports the separation of the *bureschi* group from the other taxa, especially *ornamentus*, which was erroneously associated with it until recently. The latter sits between the localities for the three members of the *hologynus* group (Figs. 3A, 3B). The taxa *Tiguassu, denticulatus, glandularis*, and the *guanivora* − *kraepelini* pair are all widely separated, which tends to support the concept of retaining separate genera for each, but the suggested *Pelodrilus, Metataxis*, and *Haplotaxis* (Figs. 3C, 3D) are just as widely dispersed. There are records of *gordioides*-like forms from all the continents, but their specific status is unclear in most instances.

The whole family is discontinuously distributed, with a maximum focus in Australasia (nine species) and with more in the Old World (seven in Europe, six in Asia, five in Africa) than the New World (one species in each of North America and South America, unless the *gordioides*-like forms are shown by detailed work to be distinct species).

Discussion
Classical approaches

The retranslation of the description of *H. vermivorus* leads automatically to a reexamination of the earlier decision (Brinkhurst 1966) to unite *Haplotaxis* and *Pelodrilus*. If we concentrate on synapomorphies it is apparent that *Haplotaxis* s.str. should include those species with characteristically modified chaetae and pharynx associated with a predaceous habit. The only member of the pre-1966 assemblage that does not share this character is *H. smithii*, and so it is now seen to require a new generic placement on classical grounds alone. Several species were assigned to *Haplotaxis* after 1966 by authors following the decision to recognize a single genus. Of these, *H. aedeochaeta* belongs to the true *Haplotaxis* group as noted in the original description (Brinkhurst and Marchese 1987).

A second decision that can be made on classical evidence is that the ornamentation of the chaetae is apparently widespread, and so there is no longer any need to relate *H. ornamentus* to the *bureschi* group which was thought to be defined by this

character as a unique apomorphy. The zoogeographic evidence did not support that relationship in the first place. The character was omitted from the present analysis as its status in most taxa outside the *bureschi* group was thrown into doubt following the work of Omodeo (1987).

As indicated above, *ignatovi* varies in regard to character 19 and can be considered in relation to *violaceus* and the *africanus* group on classical grounds.

Supraspecific groups

All three lines of evidence support the separation of *Haplotaxis* s.str. from all other species. The definition and list of included taxa are presented in Table 3. The material in Table 3 leads to the suggestion that the other branches identified in Fig. 2 be considered potential genera. The familial level ranking will be discussed later.

The type species of *Pelodrilus*, the second of the original genera, is *P. violaceus*. While *P. violaceus* can be related to the *africanus* group and also to *ignatovi* (as documented above) there is no obvious synapomorphy for the group so formed. The nature of the copulatory glands in this and other taxa (*bureschi* and *hologynus* groups, *heterogyne, guanivora*, and *denticulatus*) might be the basis for synapomorphies if homologies could be established by a comparative study of new material, but the original descriptions lack sufficient detail. The best resolution for now seems to be to accept *Pelodrilus violaceus* as a monotypic genus based on the shift of the anterior male pores rearward (character 7) and to place *ignatovi* and the *africanus* groups here incertae sedis. In this way they retain their original generic name for reference purposes. Other previous *Pelodrilus* species cannot be placed here with any confidence.

We may now consider the position of other type species of older genera, in date order. *Heterochaetella* is a monotypic genus for *H. glandularis* defined here on the basis of character 15, the presence of a simple and a bifid chaeta in each bundle. Only *denticulatus*, the type and only species of *Adenodrilus*, has bifid chaetae, but here both are bifid or even pectinate. As noted above, characters 8 and 9 are unknown for *glandularis* but when coded 1 (as in Jaccard) rather than 0 (as translated from 9 by PAUP), these two taxa appear together in the unresolved A − B group. It seems best to retain *Heterochaetella* as a convenient taxon. *Adenodorilus* would seem to be part of a monophyly including *Villiersia* (*V. guanivora* and the poorly known *V. kraepelini*) but this speculation is only based on the shifting of the gonad sequence forward (character 5), which has been shown elsewhere to be a quite trivial issue (Brinkhurst 1989). *Villiersia* shares with only *H. aedeochaeta* the loss of the anterior testes, but it does have the spermathecae opening in the median dorsal line and genital chaetae (again also found in *H. aedeochaeta*, but of very different form, more similar ones being seen in *H. dubius*). All of these genera should, perhaps, be retained until new evidence is developed to test the relationships suggested by these analyses. The other existing genera, *Metataxis* and *Tiguassu*, have now been shown to belong outside the Haplotaxidae, and will be discussed after the remaining ingroup members have been placed.

Haplotaxis smithii is clearly not a member of *Haplotaxis* as now defined. As it has all the characters of the hypothetical ancestor, apart from a supposed reduction in the number of spermathecae, it will be treated as a monotypic genus as suggested by Wiley (1981), convention 8. It has no defining apomorphy. The *bureschi* group still separates out from *Pelo-*
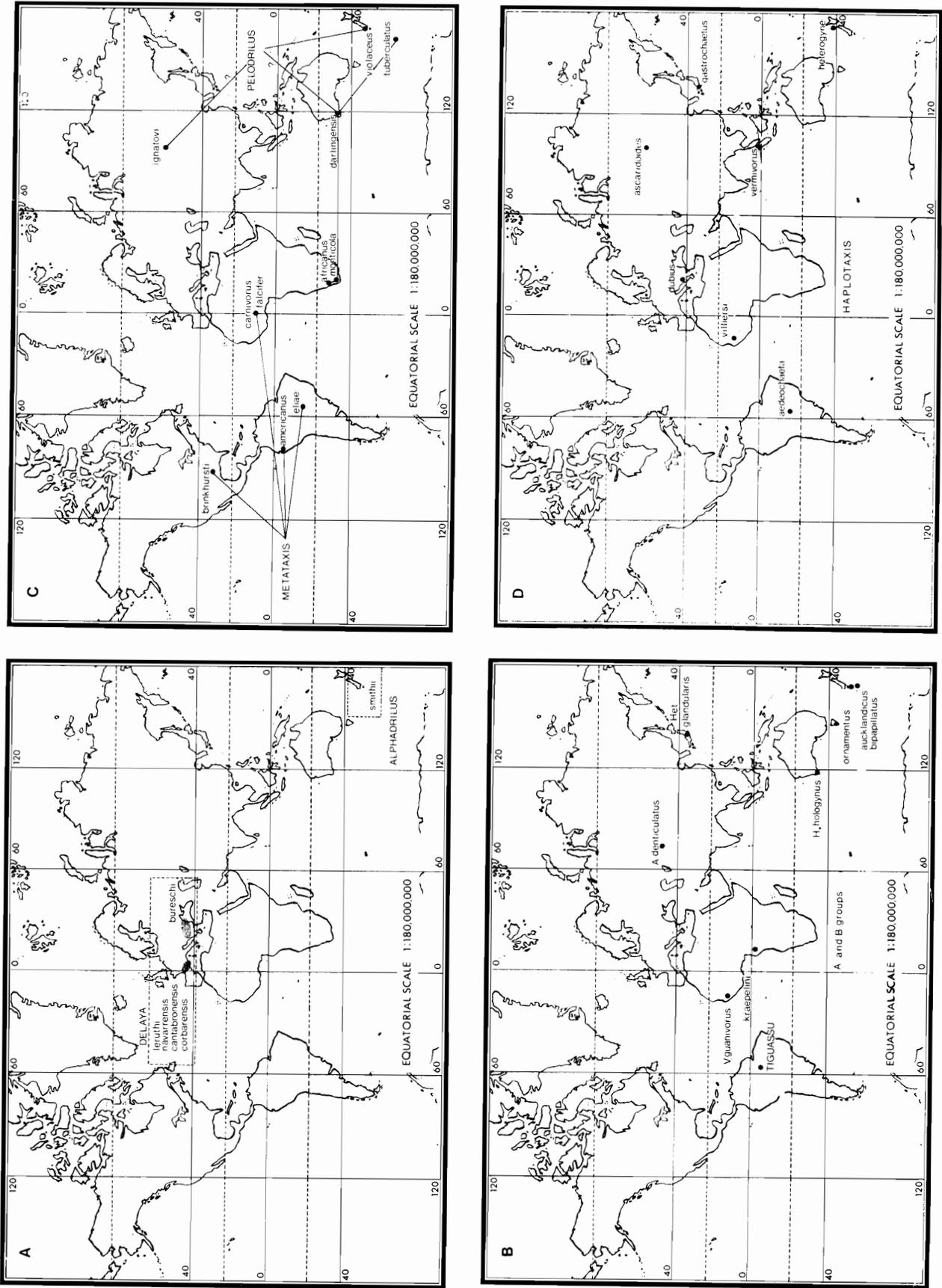
Fig. 3. Zoogeographic distributions of various taxa discussed in the text.

TABLE 3. Supraspecific groupings of the species

Family Haplotaxidae
    Type genus *Haplotaxis* Hoffmeister, 1843
        The family cannot be defined by unique apomorphies. It may be characterized as microdrile oligochaetes with two pairs of testes, one or two pairs of ovaries with the second pair rather than the first being lost where reduction has occurred. The dorsal and ventral blood vessels are connected by long comissural vessels, often in each segment. The chaetae are single or paired, usually simple-pointed, rarely bifid or pectinate. The spermathecae lie in front of the gonadal segments. The gonoducts are simple but there may be glands around the pores.

    Alphadrilus nov.gen. Type species by monotypy *Phreoryctes smithii* Beddard, 1988
        This taxon is close to the hypothetical ancestor, deviating from that as conceived here by the loss of at least one pair of spermathecae (which occur on VII and VIII and sometimes in VI). It is created on the basis of convention 8 of Wiley (1981).
        ETYMOLOGY: A potentially ancestral form.

    Delaya nov.gen. Type species by priority *Pelodrilus bureschi* Michaelsen, 1925
        This taxon shares the apomorphy of dissimilar male and female gonoducts with all taxa above *Alphadrilus*, but the female ducts retain the supposedly plesiosmorphic plesioporous condition. There are usually three, sometimes four, pairs of spermathecae. There is, as yet, no autapomorphy.
        ETYMOLOGY: Named for B. Delay, who described most of the species.
        INCLUDED SPECIES: *Delaya leruthi, Delaya corbarensis, Delaya cantabronensis, Delaya navarrensis*, all n.comb.

    Haplotaxis Hoffmeister, 1843. Type species by priority *Lumbricus gordioides* Hartman, 1821
    =*Phreorcyctes* Hoffmeister, 1845
        This taxon is defined by the apomorphies associated with a predatory habit: replacement of eversible pharnx and septal glands by a massive muscular pharynx, ventral chaetae large, single, sickle-shaped, dorsals small, straight, single, often lost in many or all segments.
        INCLUDED SPECIES: *H. aedeochaeta, H. vermivorus, H. villiersi, H. gastrochaetus, H. heterogyne, H. dubius, H. ascaridoides.*
        SPECIES DUBIA: *H. emissarius, H. forbesi, H. ichthyophagus*, all seen as potential synonyms of *H. gordioides* but based on immature material. Other taxa, such as *H. heterogyne* and *H. ascaridoides* are also very similar to *gordioides*. Material is too scarce and fragmentary to allow a proper revision of these species.

    Pelodrilus Beddard, 1891. Type species by priority *Pelodrilus violaceus* Beddard, 1891
        The apomorphy for the type species above is the rearward shift of the anterior male pores to a position ahead of the posterior pores on XII. The other taxa are placed here incertae sedis as there is no shared apomorphy.
        SPECIES INCERTAE SEDIS: *P. ignatovi, P. africanus, P. darlingensis, P. monticola, P. tuberculatus*, and an unnamed specimen from Queensland, Australia (Brinkhurst and Jamieson 1971, p. 295). The four species other than *ignatovi* are at least closely related, and were synonymized by Brinkhurst (1966).

    All of the following taxa are considered as incertae sedis in familia, their generic ranks being conserved because of a lack of resolution in the analyses to date.

    Adenodrilus Cekanovskaya, 1959. Type species by monotypy *Adenodrilus denticulatus* Cekanovskaya, 1959
        Apomorphies include copulatory glands in X − XIII that appear different from other such structures, and the possession of bifid or pectinate chaetae. Neither of these characters was used in the analyses. All four pairs of gonads are retained.

    Heterochaetella Yamaguchi, 1953. Type species by monotypy *Heterochaetella glandularis* Yamaguchi, 1953
        Apomorphies include chaetal bundles comprising one bifid and one simple-pointed chaeta, and the thin, transparent body wall with gland cells. All four pairs of gonads are retained.

    Villiersia Omodeo, 1987. Type species by designation *Villiersia guanivora* Omodeo, 1987
        Apomorphies include loss of the anterior pair of testes, forward shift of the gonad sequence (shared with *Adenodrilus*), and presence of genital chaetae (like those of *H. dubius*), spermathecal pores opening near the mid dorsal line.

    Hologynus nov. gen. Type species by priority *Pelodrilus hologynus* Michaelsen, 1907
        Apomorphy is the forward shift of the posterior male pores to the anterior border of XII, close to the anterior pair on XI, and (probably) the glandular mass associated with the pores.
        INCLUDED SPECIES: *Hologynus ornamentus, Hologynus auklandicus*, and *Hologynus bipapillatus*, all n.comb., with both the latter synonymized with *hologynus* by Brinkhurst (1966), and with *auklandicus* synonymized with *hologynus* by Michaelsen (see Brinkhurst and Jamieson 1971, p. 297).

Tiguassidae fam.nov. Type and only taxon *Tiguassu reginae* Righi, Ayres, and Bittencourt, 1978
    Apomorphy is the cylindrical gizzard in VI−VIII in a worm with an eversible pharynx and septal glands. The loss of posterior ovaries, reduction of anterior set of male organs, and presence of a proboscis are some of several microdile characters retained by this family. The decision to erect a family for this taxon was reached independently but simultaneously by B. G. M. Jamieson (St. Lucia, Australia; personal communication).

Superorder Megadrile, order Lumbricina
    Metataxis Righi, 1985 emm. Omodeo, 1987. Type species by designation *Metataxis eliae* Righi, 1985
        The genus shares the lumbricine arrangement of gonads, and shows relationships with the Syngenodrilidae and Alluroididae, both of which share the plesiomorphic condition of large yolky eggs and ample egg sacs, as well as the sparganophilid Neotropical *Areco*, according to Omodeo (1987). It seems better to recognize this relationship rather than to include the genus in the Haplotaxidae. It only required a slight weighting of character 3 (loss of GIII) to shift all of the included species to an outgroup status vis-à-vis the Haplotaxidae.
        INCLUDED SPECIES: *M. brinkhursti, M. carnivorus, M. falcifer, M. americanus* sp. dub.

drilus even though its original unifying apomorphy (possession of ornamented chaetae) has been destroyed. The generic rank suggested by the analytic results cannot be defined by means of a synapomorphy unless the reproductive glands prove to be different from those of other taxa. The *hologynus* group can be defined as a genus based on the unique forward shift of the rear male pores relative to other genera. Again, the genital glands may also prove unique.

The monotypic *Tiguassu* should be elevated to familial rank based on the presence of an eversible pharynx and small gizzard and the loss of the second pair of ovaries (GIV). The last character is only found in the Microdrili, which lack gizzards but are characterized by the eversible pharynx in all but predatory forms.

Metataxis shares the characteristic GI, II, IV arrangement of the Megadrili – Lumbricina, and will be regarded as incertae sedis in that taxon pending analyses of that group by others.

These decisions are formalized in Table 3.

Evolutionary concepts

The decisions resulting in the taxonomic rankings listed in Table 3 represent an attempt to apply the sequencing convention of Wiley (1981) to Fig. 2 using ROOT 1 rather than attributing names to each successive nested set in the hierarchy, as done by Ax and his associates (see Ax 1985, for example). I also follow the appeal for conservative classifications that retain as much as possible of the classical ranks as suggested by Wiley, which results in a provisional, noncladistic solution to the A – B group.

There is, of course, no need to see these nested sets as originating from a succession of single ancestors at each node, but the supposed difference between nested sets of characters and the recognition of ancestors discussed by Humphries and Parenti (1986) and many predecessors seems to become less significant if it is recognized that each node (or point at which branches diverge) of Fig. 2 may simply be taken to represent a telescoped (therefore hidden) set of branches. Quite possibly, no single ancestral species extant at one time had all the characters in the state postulated by the existence of each node or branching point in the tree, but the possible group of extinct species providing the common ancestry of the group as a whole certainly did. All species, after all, do arise from other species, and all monophyletic groups arise by definition from a single original taxon, or ancestor.

I have postulated a hypothetical ancestor with all of the character states polarized in a logical, consistent manner (and we should not forget that ''reasoning logic can be a more powerful tool than the speedy neutralism of the computer''; Bergstrom 1986). This logic is based on some assumptions, namely that the basis of metazoan evolution follows the general outline of that proposed most recently by Bergstrom on the basis of cytochrome c data and other classical and chemical information. Conflicting views of the original of the annelids exist, of course, as ably discussed by Mettam (1985), but it must be recognized that most originate with polychaete biologists who may well be as unfamiliar with oligochaetes as I am with their taxa, and who are surely more inclined to consider earthworms than microdriles in their models. The theories of R. B. Clark, debated by Bergstrom (1986) and Mettam (1985), seem to lead quite logically to the concept of a haplotaxid ancestor to the oligochaetes (Brinkhurst 1989). The adoption of any other concepts might well not do so.

If the haplotaxid ancestry is adopted as a starting point, then of course the PAUP analysis would recognize *Enchytraeus* and *Propappus* as ingroups if the analysis is rooted at the ancestor, because all of the oligochaetes would be ingroup by definition. As there is no satisfactory recognition of an ancestral polychaete, and as character states in polychaetes vary so widely in the group as to make no typical polychaete into a satisfactory outgroup for analytical purposes, I was forced to use a potential descendent of the ingroup as the outgroup for my analyses. This was expected to reverse the sequence of apparent evolution in the ingroup, as it did. Characters 4, 8, 9, and 19 reverse polarity depending on the rooting, and 1 and 13 are ambiguous in ROOT 2. The suggestion here is that the enchytraeid and all other higher microdriles evolved, not from some very early undifferentiated haplotaxid, but from a later, more developed group. While this seems eminently likely, in fact, the result is that we end up with the Haplotaxidae being paraphyletic.

In addition, what is clearly seen as a monophyletic assemblage when rooted at 2 becomes between five and seven groups of potentially equal rank to the outgroups when rooted at 1. The retention of the generic ranks in the ingroup is an appeal to common sense. Linear classifications and hierarchies do not match up perfectly in any case (or else there would be no need for conventions), and the proposed genera include few taxa, most of which are recognizable in classical terms as genera. While the enchytraeid outgroup represents a family with a very large number of species, *Propappus* represents a monogeneric family of only two or three species, so that small families do have a place in our system. However, to multiply the number of haplotaxoid families from one to five or six seems pointless. Surely the important point is to recognize the underlying relationships suggested by the analyses, which may be effectively supported or rejected if and when new material is analysed and significant new characters are included. This is highly unlikely to happen considering the scarcity of these species and their location in many areas where worm taxonomy is a trivial problem in relation to other human issues.

Alternatively, we could indicate some scepticism about our ability to reconstruct evolution in such a small group of poorly known species that may be very old. In that case the various lines of evidence may be said to converge on a reasonable classification.

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