

## Phylogenetics of some Enchytraeidae (Annelida: Oligochaeta): A preliminary investigation of relationships to the Haplotaxidae

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### Abstract

In phylogenetic considerations of the Oligochaeta and the family Enchytraeidae, *Propappus* has been considered the ancestral or even the archetypal enchytraeid genus. Three nominal species are presently included in *Propappus* Michaelsen, 1905, *P. volki* Michaelsen, 1916, *P. arhyncotus* Sokolskaja, 1972, and the type species of the genus, *P. glandulosus* Michaelsen, 1905. Examination of type material of *P. glandulosus* and *P. volki*, as well as other material of the latter, showed that these species have a single pair of testes in segment XI and a single pair of ovaries in segment XIII. According to current classifications of the Oligochaeta, these species of *Propappus* cannot be retained in the Enchytraeidae. A phylogenetic analysis including two species of *Propappus* and 29 species of Haplotaxidae suggest a sister group relationship between *Propappus* and some Enchytraeidae and Haplotaxidae.

### Introduction

The “primitive” enchytraeid genus *Propappus* Michaelsen, 1905 has occupied a pivotal position in both early and recent evaluations of the relationships of enchytraeids to other oligochaetes (Michaelsen, 1916; Stephenson, 1930; Cernovitov, 1937; Timm, 1981; Kasprzak, 1982, 1984; Brinkhurst and Jamieson, 1971).

In describing *Propappus glandulosus*, type species of the genus, Michaelsen (1905) noted that all the setae were distinctly double-pointed, a unique characteristic relative to other Enchytraeidae then known. This characteristic is no longer unique as *Barbidrilus* Loden and Locy, 1980, another enchytraeid genus, has setae of similar description. Michaelsen’s (1905) detailed species description also included other character states anomalous for Enchytraeidae. These included 1) the presence of a large, glandular organ associated with each setal bundle, 2) the absence of a glandular, preseptal

sperm funnel, and 3) the location of the ovaries on septum 12/13, in the segment posterior to that bearing the male pores. *Propappus glandulosus*, as described by Michaelsen (1905), was plesiopore like all other enchytraeids. Unlike others in this family it had a sterile segment between the testicular and ovarian segments. In this it resembled many earthworms as well as some Haplotaxidae and Lumbriculidae.

In the original description of *Propappus volki* Michaelsen (1916) recognized further that the spermathecae of species of *Propappus* originated in segment IV rather than V as in other enchytraeids. Michaelsen (1923) later indicated that the single pair of ovaries in *P. volki* was located in XII, suspended on the posterior of septum 11/12. Michaelsen’s (1923) diagnosis of *Propappus* and description of *P. volki* are still accepted. Nielsen and Christensen (1959) “rather doubtfully” placed *Propappus* in the Enchytraeidae but did not give the reasons for their doubts.

Coates (1986) in a re-examination of type material of *Propappus glandulosus* and *P. volki*, found testes in XI and ovaries in XIII in both species. According to recent classifications (Kasprzak, 1982; Jamieson, 1978; Timm, 1981; Brinkhurst, 1982) *Propappus* would thereby be excluded from the Enchytraeidae. Coates (1986) established the new family Propappidae for *P. glandulosus* (type species of the type genus, by monotypy), *P. volki* and *P. arhyncotus* Sokol-skaja, 1972 incertae sedis.

The primary objectives of this study were to investigate the phylogenetic relationship of *Propappus* to the Enchytraeidae and to other plesiopore oligochaetes, and to utilize computerized phylogenetic methods to gain an evolutionary understanding of this entire group of related oligochaetes.

## Materials and methods

Specimens of *Propappus volki* examined here included cotypes from the British Museum (Natural History) (BMNH) (see Coates, 1986) as well as new material from southwestern England and the Massif Central region of France. Both whole-mounted and sectioned specimens were examined. Four additional, partially mature, specimens of *Propappus* from Lake Baikal, assigned to this species, were studied.

Cotypes of *Propappus glandulosus* from the BMNH, including sectioned and whole-mounted material, were examined.

Computerized phylogenetic analyses were made on a data matrix of 36 species (Table 1) examined for 70 binary characters (Table 2), including both two-state characters and multistate characters recoded by the method of additive binary recoding. Outgroup polarization and intuition, for multistate characters, were employed. Included were 29 nominal species of Haplotaxidae (excluding the very recently described *Metataxis eliae* Righi, 1985), two species of *Propappus*, one tubificid and one enchytraeid, as well as an outgroup consisting of three megadriles of the families Moniligastridae and Syngenodrilidae. The tubificid and enchytraeid were *Tubifex tubifex* and *Enchytraeus albidus*, respectively, both type species

of the type genera of their respective families. This does not necessarily mean that they are in most or even many ways "average" members of those families but they should possess synapomorphies diagnostic for the families. The outgroup species are related to but removed, at familial rank, from the groups of primary interest – in this instance the Haplotaxidae and *Propappus*.

As many as possible of the characters considered by Jamieson (1978) in his numerical analysis of the earthworms, and by Brinkhurst (1982) in his consideration of the phylogenetics of the Oligochaeta, were included. The major limitation to character inclusion was the underived condition of all Haplotaxidae for many characters.

Character data regarding the Haplotaxidae were extracted from the literature. Not all recently suggested synonymies (Brinkhurst, 1966; Brinkhurst and Jamieson, 1971) were incorporated. Both specimens and literature were used as sources of character state data on the microdriles. For the megadriles, these states were determined largely from Jamieson's (1978) data matrix.

Information on all characters could not be obtained for all species. For such incomplete character sets, inclusion in the analysis allows some predictions of what further examination of specimens might reveal.

The computerized Wagner tree algorithm, WAGNER, of the PHYSYS software package (Mickevich and Farris, 1982) was used for phylogenetic analysis of the resulting 36 × 70 data set (Table 3). This algorithm allows missing character data. LFIT and DIAGNOSE programs were used to generate standard tree statistics, lengths, consistency index (CI), and F-ratio (Mickevich and Farris, 1982), and character diagnostics. ADAMS was used to generate a consensus tree (Adams, 1972) of the set of "shortest" Wagner trees.

The data set was slightly modified after the first computerized phylogenetic analyses. Some initially missing character data were obtained and six additional binary characters were included (Table 4). In consideration of the results of the first analysis and of the added data some intuitive transformations were modified and some binary characters reversed. A phylogenetic tree utilizing 22 of the two-state

Table 1. Species list with abbreviations used to identify taxa in Figures 3 through 6.

	Abbreviations
Syngenorilidae	A
<i>Syngenorilus lamuensis</i> Smith and Green, 1919	Syn
Moniligastridae	B
<i>Desmogaster doriae</i> Rosa, 1890	Des
<i>Moniligaster troyi</i> Jamieson, 1977	Mon
Haplotaxidae	
<i>Haplotaxis aucklandicus</i> (Benham, 1909)	auc
<i>Haplotaxis bipapillatus</i> (Michaelsen, 1924)	bip
<i>Haplotaxis hologynus</i> (Michaelsen, 1907)	hol
<i>Haplotaxis bureschi</i> (Michaelsen, 1924)	bur
<i>Haplotaxis cantabronensis</i> Delay, 1973	can
<i>Haplotaxis corbarensis</i> Delay, 1972	cor
<i>Haplotaxis glandularis</i> (Yamaguchi, 1953)	gla
<i>Haplotaxis leruthi</i> (Hrabe, 1958)	ler
<i>Haplotaxis navarrensensis</i> Delay, 1973	nav
<i>Haplotaxis ornamentus</i> Brinkhurst and Fulton, 1980	orn
<i>Haplotaxis smithii</i> (Beddard, 1888)	smi
<i>Haplotaxis africanus</i> (Michaelsen, 1908)	afr
<i>Haplotaxis darlingensis</i> (Michaelsen, 1907)	dar
<i>Haplotaxis ignatovi</i> (Michaelsen, 1903)	ign
<i>Haplotaxis monticola</i> (Michaelsen, 1908)	mon
<i>Haplotaxis tuberculatus</i> (Benham, 1909)	tub
<i>Haplotaxis violaceus</i> (Beddard, 1891)	vio
<i>Haplotaxis gastrochaetus</i> Yamaguchi, 1953	gas
<i>Haplotaxis ascaridoides</i> Michaelsen, 1905	asc
<i>Haplotaxis dubius</i> (Hrabe, 1931)	dub
<i>Haplotaxis gordioides</i> (Hartmann, 1821)	gor
<i>Haplotaxis heterogyne</i> Benham, 1904	het
<i>Haplotaxis vermivorus</i> (Michaelsen, 1932)	ver
<i>Metataxis americanus</i> (Cernovsytov, 1939)	Met ame
<i>Metataxis brinkhursti</i> (Cook, 1975)	Met bri
<i>Metataxis falcifer</i> (Omodeo, 1958)	Met fal
<i>Haplotaxis kraepelini</i> (Michaelsen, 1914)	kra
<i>Haplotaxis denticulatus</i> (Cekanovskaja, 1959)	den
<i>Tiguassu reginae</i> Righi, Ayres and Bittencourt, 1978	Tig reg
Enchytraeidae	C
<i>Enchytraeus albidus</i> Henle, 1837	Enc
Propappidae	
<i>Propappus volki</i> Michaelsen, 1916	Pro vol
<i>Propappus glandulosus</i> Michaelsen, 1905	Pro gla
Tubificidae	D
<i>Tubifex tubifex</i> (Muller, 1774)	Tub

characters (Table 5) from the modified data set was constructed manually (Brooks, *et al.*, 1984). Two-state characters with individual CI's greater than 33.3 in the full data analysis and with little missing information were selected. A few cluster analyses of the full, modified data set (Russel and Rao, and Jac-

card's coefficients with average and/or single linkage clustering), and a minimum spanning network using average taxonomic distances, were generated using the numerical analysis software package NTSYS (Rohlf, Kispough, and Kirk, 1982).

Table 2. Character list (plesiomorph, ..., apomorph state).

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1.	testes in IX (absent, present)
2.	testes in X (present, absent)
3.	testes in XI (present, absent)
4.	ovaries in XI (absent, present)
5. – 7.	ovaries in XII (present with oviducts 100, absent with oviducts 110, absent no oviducts 111)
8.	ovaries in XIII (present, absent)
9.	pairs of male pores per segment (one, two)
10.	male gonoduct in XI (present, absent)
11.	male and female gonoducts (dissimilar, similar)
12.	female pore position relative to septum (in septal line, posterior)
13.	sperm “funnel” development (none, glandular)
14. – 18.	number of setae per bundle (two 10000, two and one 11000, three 10100, many 10110, one 11001)
19. – 21.	similarity of setae within bundles (similar 100, dissimilar ventrally 110, dissimilar ventrally and dorsally 111)
22. – 24.	dorsal setae (all present 100, some absent 110, all absent 111)
25. – 28.	similarity ventral to dorsal setae (similar 1000, sickleshaped ventrals 1100, sizes different 1010, pectinates and hairs dorsally 1001)
29. – 31.	setal tips (simple-pointed 100, bifid 110, pectinate 111)
32.	setal tips (not keeled, keeled)
33.	setal tips (not pitted, pitted)
34.	genital setae (not modified, modified)
35. – 37.	position of “cd” setal bundles (dorso-lateral 100, midlateral 110, ventro-lateral 111)
38.	setal nodulus (present, absent)
39.	prostomial proboscis (absent, present)
40.	muscular gizzard (present, absent)
41.	glandular pharynx (absent, present)
42.	pharyngeal glands (diffuse, discrete)
43.	head pore (absent, present)
44.	length of clitellum (long, short)
45.	nephridia in anterior segments (present, absent)
46.	gut diverticula in XIII – XIV (absent, present)
47.	oesophageal peptonephridia (absent, present)
48. – 50.	prostatelike setal glands (absent 100, present ventrally only or dorsally and ventrally 110, present dorsally only 101)
51.	midventral epidermal glands (absent, present)
52.	copulatory cushion around male pores (absent, present)
53.	spermathecae in IV (absent, present)
54.	spermathecae in V (absent, present)
55.	spermathecae in VI (present, absent)
56.	spermathecae in VII (present, absent)
57.	spermathecae in VIII (present, absent)
58.	spermathecae in IX (present, absent)
59.	spermathecae in X (absent, present)
60.	location of spermathecal pore relative to septum (intrasegmental, at septal line)
61.	spermathecal structure (simple, duct and ampulla distinct)
62.	spermathecae in a segment (paired, unpaired)
63.	spermathecal association with gut (none, connected)
64.	spermathecal glands (absent, present)
65.	spermathecal extent (about one segment, elongate)
66.	sperm sacs (present, absent)
67.	number of testes associated with a male pore (one, two)
68.	prostomium (attached, not attached)
69.	male pore (plesiopore, opisthopore)
70.	male pore modifications (none, atrialike or glandular or muscular)

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Table 3. Data set for 70 binary characters and 36 species (see Fig. 5).

auc	000010000000010001001000100000100001100100010001001011011000100000
bip	0000100000000100001001001000100000110001100901010001001101091000000000
hol	0000100000000100001001001000100000100001100100010001001011010000100000
bur	000010000001010000100100100010000101110011000100110000000001011000000000
can	000010000000010000100100100010000101000011000000011000000001090000000000
cor	00001000000001000010010010101000010100001100011000100110000000010100000000
gla	0000100000100100001111001000110000100001110900010100000000019000000000
ler	0000100000000100001001001000110100111001100010011000000001010000000000
nav	0000100000000100001001001000100001011100110001001100000000109000000000
orn	0000100000000100001010001010100001010000110001001000000100101100000000
smi	00001000001001000010010010101000010000110001001000000000100000000000
afr	0000100100000100001001001000100000000000000000000000000000000000000000
dar	000010010000010000100100100010000010000110900010000000101011000000000
ign	0000100100000110001001001010100000100001100900010010001011011000000000
mon	0000100100000100001001001000100000110001900190010010001101010000000000
tab	000010010000010000100100101010000010000110100010010001101010000000000
vio	000010011000010000100100100010000010000110100010010001101010000000000
gas	00001001909991100111011110101000001001000000000000000000000000000000
asc	0000100000001011001110110110010000010000000000000101000000001000000000
dub	0000100000000110011101101100100001999000000000001010001000011000000000
gor	00001000000001001110110110010000010000000000001010001000010000000000
bet	00001001000101100011010001100100000000000000000000000000000000000000
ovr	00001001999991100111011110101000001000011009100100000000000000000000
Metame	00001110001101000010010010001000001000011011001000000000000000000000
Metbri	0000111000010100001001001010100000100001100190011000001100001000000000
Metfal	010011000110010000110100110010000000000100910010000011111010100000000
Progla	01001110010901010010010010001000010000110010001100010111011000100000
Provol	01001110010101010000000000000000000000000000000000000000000000000000
kra	0011111100000100001001001010100001100001100900011000010000100000000000
Tigreg	010010010011010000100100100010000010001010000010000001101010000000000
Enc	01001001001010101010010010001000001001011110011000101111011011000001
den	1011100100000100001001001001111000100001100900011000101101001000010000
Mon	01001110010901000010010010001000001000000000000000000000000000000000
Des	00001110000001000010010010001000001000000000000000000000000000000000
Syn	00001110100901000010010010001000001000000000000000000000000000000000
Tab	0011111100000101011110010001110011000011001000100000011100000000000001

**Taxonomic results**

Diagnosis of *Propappus* Michaelsen, 1905 (Fig. 1) (after Coates, 1986): Setae in four bundles per seg-

ment, including male pore segment. Setae usually three, rarely two, per bundle; sigmoid, bifid, nodulate. Setal gland opening through body wall immediately posterior to each setal bundle. Head and other dorsal pores absent. Clitellum single-layered, usually extending over XII-XIV. Spermathecal pores anterior-lateral on IV. Male pores anterior to ventral setal bundles of XII, simple. Female pore ventral, in or just posterior to septal groove at 13/14. Brain deeply cleft posteriorly, divided into almost separate lobes. Dorsal pharyngeal pad poorly developed, protrusible. Bodies of glandular cells of pharyngeal pad not organized into compact or discrete glands on septa. Gut without appendages or diverticula. Nephridia with small preseptal parts, including funnel only; postseptal part lobed, with little interstitial tissue. Spermathecae paired, originating in IV, not communicating with gut. Ectal duct of spermatheca thick-walled, aglandular. Ampulla of spermatheca abruptly expanded, thin-walled, extending posteriad through a few segments. One pair of testes ventro-lateral on posterior of 10/11. Seminal vesicle unpaired, extending as far anteriad as VI. Sperm fun-

Table 4. Modifications to first data set (plesiomorph, ..., apomorph).

11.	reversed
12.	reversed
19. – 21.	changed to 19. – 22., coding modified (all similar 1000, dissimilar in ventral bundles 1100, dissimilar in dorsal and ventral bundles 1111, dissimilar in dorsal bundles 1011)
22. – 24.	changed to 23. – 25.
25. – 28.	changed to 26. – 29., coding modified (similar 1000, ventrals larger 1100, ventrals different shape (sickles) 1010, dorsals larger 1001)
29. – 40.	changed to 30. – 41.
41.	changed to 42. – 44., recognized states modified (no glandular pharynx 100, thin glandular pharynx 110, well-developed glandular pharynx 111)
42. – 47.	changed to 45. – 50.
48. – 50.	changed to 51. – 54., states modified (no prostatelike glands 1000, ventral only, 1100, dorsal and ventral 1110, dorsal only 1111)
51. – 54.	changed to 55. – 58.
55.	changed to 59., reversed
56.	changed to 60., reversed
57. – 70.	changed to 61. – 74.
Additions:	
75.	male pore position in segment (posterior, both midsegmental)
76.	position of posterior male pore in segment (posterior or mid, anterior)
Modifications made for manual analysis	
75.	reversed

Table 5. List of characters used in manual Hennigian analysis of 36 species and 22 binary characters: +, present; -, absent.

Number	Description (plesiomorph, apomorph state)	
2*	testes in X	(+, -)
3	testes in XI	(+, -)
8*	ovaries in XIII	(+, -)
10*	male ducts in XI	(+, -)
33*	keel on setae	(-, +)
34*	pits on setal tips	(-, +)
35	modified genital setae	(-, +)
39	setal nodulus	(+, -)
40	proboscis	(-, +)
41*	muscular 'gizzard'	(+, -)
56*	copulatory cushion at male pores	(-, +)
57*	spermatheca in IV	(-, +)
58	spermatheca in V	(-, +)
59*	spermatheca in VI	(-, +)
60*	spermatheca in VII	(-, +)
61*	spermatheca in VIII	(+, -)
62*	spermatheca in IX	(+, -)
69*	spermathecal ampulla	(short, elongate)
72*	prostomium	(not fused, fused)
73	male pore	(plesiopore, opisthopore)
75	male pore position	(midsegmental, posterior)
76	posterior male pore position	(midsegmental or posterior, anterior)

\* = nonterminal (synapomorphic) in computerized analysis.

nels simple, on 11/12. Vasa deferentia confined to XII; walls thickened (glandular?). Atria, prostates and other copulatory glands lacking. One pair of ovaries ventro-lateral on posterior of 12/13. Female ducts simple, on 13/14.

In sand or gravel of lake bottoms, or running waters with moderate to strong currents. Known only from Europe and the USSR (Fig. 2).

The contrast between many of these characteristics and those of Enchytraeidae are indicated in Table 6.

## Systematic analyses

### Cluster analyses

The minimum distance spanning network indicated species neighbourhoods and was used here as confirmatory evidence for monophyly of the ingroup relative to the outgroup.

The dendrogram resulting from Jaccard's coefficient of community with UPGMA (average linkage) clustering (Fig. 3) on the modified data set (Table 4), resulted in the best one-dimensional representation of a set of multidimensional similarity relationships for the 36 species. The cophenetic correlation coefficient (Sneath and Sokal, 1973) for this analysis was 0.86, compared to 0.80 and 0.74 for Jaccard's with single linkage and for the Russel and Rao coefficient with single linkage, respectively. According to Sokal and Sneath (1973) the cophenetic correlation coefficient "seems a satisfactory measure of the agreement of a phenogram with a similarity matrix, and gross differences... are generally meaningful" (pp. 279–280).

Using an arbitrary similarity value about 0.6 (Fig. 3), four groups of Haplotaxidae can be recognized (Table 7), in the UPGMA clustering on Jaccard's coefficient. A similarity value slightly greater than 0.5 would distinguish Propappidae and all the traditional families (A, B, C, D) in the analysis excepting



Fig. 1. *Propappus volki*, drawing from a whole-mounted specimen; scale bar equals 0.50 mm.

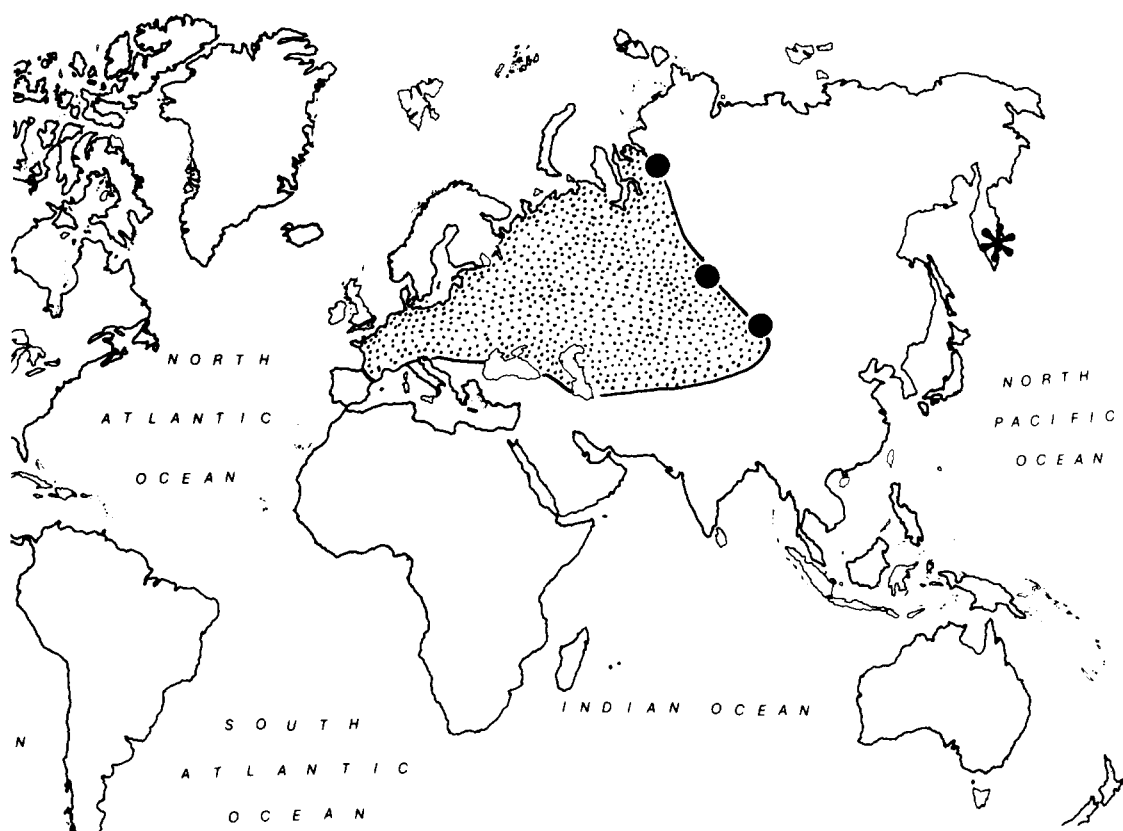


Fig. 2. Distribution of *Propappus* species; ● — *P. glandulosus* \* — *P. arhyncotus*, ⊛ *P. volki*.

the Haplotaxidae. The Haplotaxidae would still be recognized as two very distinct clusters, group 1 and groups 2+3+4. Of the four species excluded at the higher cut off level (Table 7), *Haplotaxis denticulatus*, *Metataxis falcifer*, and *Tiguassu reginae* would

Table 6. Comparison of taxonomic characteristics of *Propappus* and Enchytraeidae.

	<i>Propappus</i>	Enchytraeidae
setae	bifid	simple-pointed*
setal gland	present	absent
head pore	absent	present
spermathecae	in IV	in V
pharyngeal gland	not discrete	discrete
sperm funnels	simple	preseptal glandular
testes	in XI	in XI
ovaries	in XIII	in XII
male ducts	plesiopore	plesiopore

\* = except *Barbidrilus*.

still be excluded from haplotaxid clusters. In this analysis, species of *Propappus* show the greatest average similarity to *M. falcifer*, and then link to the enchytraeid.

The same four groups of Haplotaxidae can be more or less distinguished in the dendrogram resulting from the single linkage clustering of the Jaccard's similarity matrix. However, groups 1+3+4 (Table 7) form a cluster before linking with the three group 2 species, *Haplotaxis kraepelini*, *Metataxis brinkhursti*, and *M. americanus*. With average linkage group 1 species formed the most dissimilar cluster. All of the haplotaxids, excluding as previously *Tiguassu reginae*, *H. denticulatus* and *M. falcifer*, constitute a discrete cluster relative to the enchytraeid, the tubificid, *Propappus*, and megadriles. The species of *Propappus* are linked at an equal similarity to *M. falcifer*, and to the tubificid plus haplotaxids.

The dendrogram resulting from single linkage





Table 7. Haplotaxid species groups resolved by Jaccard's + UPGMA (Fig. 3).

Haplo 1 ●	Haplo 2 ◻	Haplo 3 ▲	Haplo 4 ○
vermivorus	kraepelini	ornamentus	ignatovi
gordioides	brinkhursti (Metataxis)	smithii	darlingensis
dubius	americanus (Metataxis)	corbarensis	violaceus
ascaridooides		cantabronensis	tuberculatus
heterogyne		navarrensensis	monticola
gastrochaetus		leruthi	africanus
		buresschi	bipapillatus
			hologynus
			aucklandicus

other species: denticulatus, glandularis, Tiguassu reginae, Metataxis falcifer

### Phylogenetic analysis

The manual Hennigian analysis (Fig. 4) considered characters of the male and female reproductive systems, setae, gut, and prostomium (Table 5). Only one "shortest" tree, of length = 50 and CI = 44, has been shown here; however, it would not be surprising to find other equally short trees especially as there is considerable homoplasy. This set of characters was not adequate for resolving many of the phylogenetic relationships within the phenetic haplotaxid groups 3 and 4 (Table 7), but did partially resolve the haplotaxids into two clades above the outgroup, one also including the tubificid.

These two clades can be diagnosed as clade 1) lacking spermathecae in IX (62), lacking muscular gizzards (41), possessing spermathecae in VII (60); and clade 2) lacking spermathecae in IX (62), lacking muscular gizzards (41), lacking ovaries in XIII (8). Clade 1 includes all of the species of phenetic haplotaxid group 3, and *H. bipapillatus*, *H. hologynus*, *H. aucklandicus*, and *H. glandularis*. Clade 2 includes six of the species of group 4, and *H. vermivorus*, *H. kraepelini*, *H. denticulatus*, and the tubificid. Haplotaxid group 3 is very robust, recurring intact in all the analyses discussed. The phylogenetic analyses did not consistently reconstruct Jaccard + UPGMA general (adansonian) similarity relationships of values less than about 0.7.

The manual analysis indicates that there may be some problem with the original assumption that the ingroup was monophyletic. Six ingroup taxa,

*Haplotaxis gordiooides*, *H. dubius* and *H. ascaridooides* (which may be conspecific according to Brinkhurst, 1966), *H. heterogyne*, *H. gastrochaetus* and *Tiguassu reginae* are not resolved from the outgroup. The former three taxa are diagnosed by the presence of spermathecae in VII (60) and the latter three by the absence of ovaries in XIII (8), character states otherwise occurring only in ingroup taxa. Five of these six species are members of the phenetic haplotaxid group 1, which was not closely clustered with the other haplotaxid species by Jaccard's coefficient with UPGMA.

The *Propappus* species exhibit a sister relationship to the enchytraeid plus *Metataxis falcifer*. Basally, this clade is not resolved. It is diagnosed by the absence of spermathecae in IX (62), absence of muscular gizzards (41), absence of spermathecae in VIII (61), absence of male ducts from XI (10), and absence of testes in X (2). *Propappus* is diagnosed by the presence of spermathecae in IV (57) and elongate spermathecal ampullae (69). *Enchytraeus albidus* plus *Metataxis falcifer* is diagnosed by the presence of spermathecae in V (58).

The Wagner parsimony analysis using PHYSYS produced a set of 9 "shortest" trees. According to LFIT statistics, each tree required 160 character state changes, and had a CI of 37.8. The maximum consensus tree (ADAMS tree) that could be resolved by this analysis is shown in Fig. 5. All nonconflicting parts of the 9 "shortest" trees are allowed in the Adams consensus tree. A "shortest" set containing a large number of trees, such as 9, com-

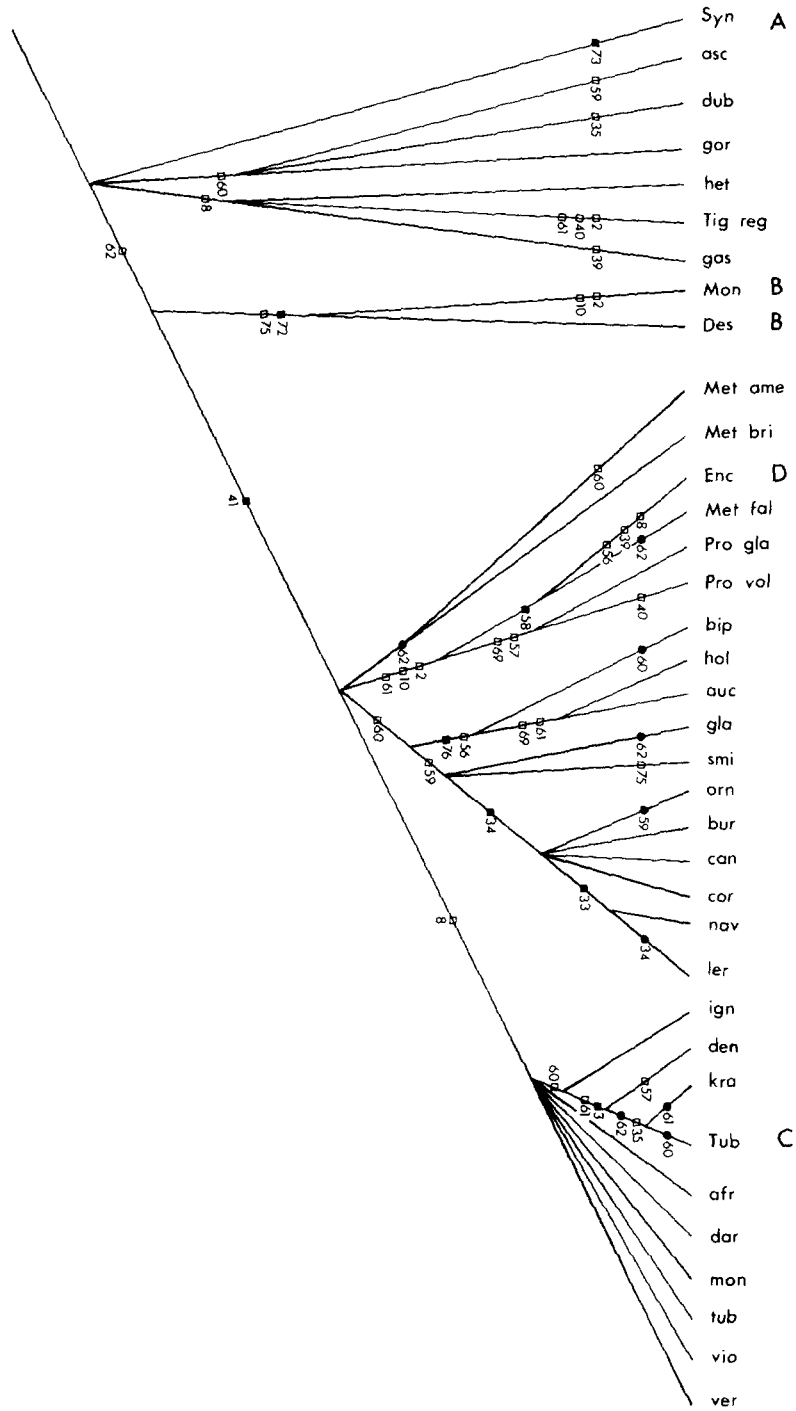


Fig. 4. One "shortest" manually constructed cladogram of 36 species  $\times$  22 two-state characters (Table 5); length = 50 and CI = 44; character state changes: ■, unique 0►1; □, 0►1; ●, 1►0. Character numbers (Table 4) are indicated adjacent to corresponding state change.

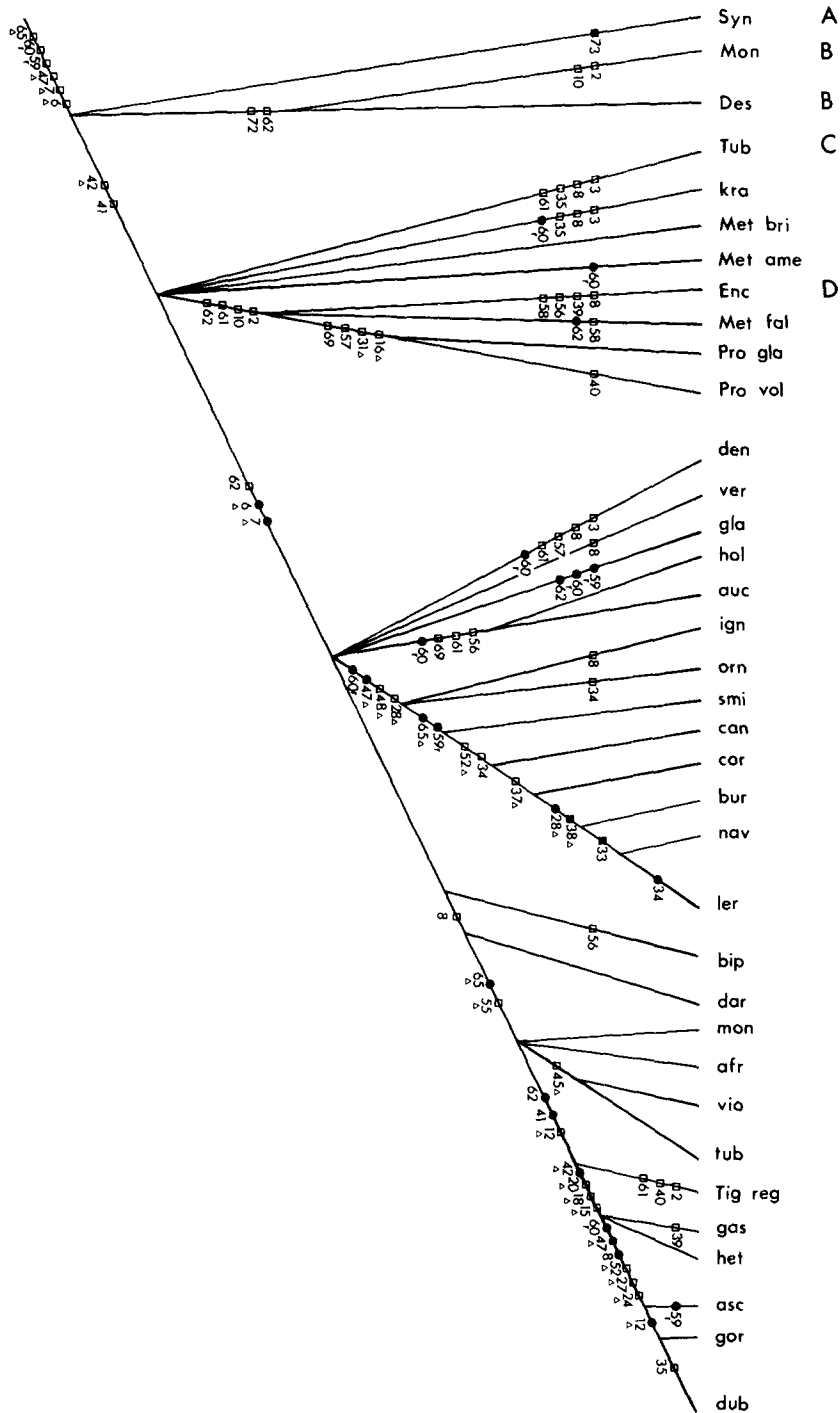


Fig. 5. Adams consensus tree of 9 WAGNER trees with length = 160 and CI = 37.8; based on 36 species × 70 binary character data set (Table 3); character state changes; ■, unique 0►1; □, 0►1; ●, 1►0. Character numbers (Table 4) are indicated adjacent to the corresponding state change. ◀, characters with reversed polarity relative to two-state analysis (Fig. 4). △, synapomorphic characters of this analysis, not included in the two-state analysis. All hypothesized transitions for characters used in both the two-state and the full data analyses are shown. Only additional, nonterminal transitions are shown.

bined with a low CI such as 38, is an indication that the available character data and/or its interpretation may not be as reliable as would be desirable. These conditions definitely indicate that much homoplasy must be hypothesized to account for the distribution of the character states included in the analysis (Table 2).

Of the 160 character state changes predicted by each of the Wagner trees, only 43 are non-terminal (synapomorphic) transitions supporting the resolution of the included species. There are more nonterminal changes (49) above the root on the Adams tree (Fig. 5) and it is longer than the Wagner trees. The nonterminal character state changes shown on the Adams tree represent several organ systems (Table 2), including female reproductive, male reproductive, gut, epidermal and setal. Fourteen of these characters were used for the manual analysis (Table 5). The polarities of the character states of both characters 59 and 60 (Table 4) are reversed in the computerized analysis relative to the manual analysis.

The ingroup (Fig. 5) is monophyletic according to the resolution made possible by the additional characters of the computerized analysis. The presence of spermathecae in IX (62) and presence of muscular gizzards (41) are, according to this analysis, homoplasious in *Tiguassu reginae*, *Haplotaxis gastrochaetus*, *H. heterogyne*, *H. ascaridoides*, *H. dubius*, and *H. gordioides*. The seven haplotaxid species of the phenetic group 3, plus *H. ignatovi*, are monophyletic.

The sister relationship, by consensus, of *Propappus* is unresolved between *Enchytraeus albidus* and *Metataxis falcifer*. The diagnosis of that four taxon clade is: muscular gizzards lacking (41), glandular pharyngeal pad present (42), spermathecae lacking from IX (62), spermathecae lacking from VIII (61), male ducts absent in XI (10), testes lacking from X (2). The diagnosis of *Propappus* within this is: spermathecae in IV (57), spermathecal ampulla elongate (69), setae three in a bundle (16), and setal tips bifid (31).

## Discussion

In these analyses, the haplotaxids and the other

microdriles included constitute a distinct overall similarity group or are monophyletic relative to the megadrile species used as the outgroup. One analysis, based on a small character set, failed to resolve six (of 29) haplotaxids from the outgroup (Fig. 4). Even phenetic analyses (Fig. 3) approximating those used by Jamieson (1978) do not indicate a cluster including these megadriles and haplotaxids, especially *Haplotaxis violaceus* (see Jamieson, 1978). Relationships are not yet well resolved within the microdrile-haplotaxid taxon.

The sister relationships of *Propappus* to *Metataxis falcifer* as well as to *Enchytraeus albidus* are indicated. As pointed out in the taxonomic section, the synapomorphies of the species of *Propappus* serve to distinguish them from the enchytraeids.

Very tentative phylogenetic listings that can be constructed from the two cladograms (Figs. 4 and 5) are indicated below. These are presented here only as "food for thought". In fact, many of the groups are at or beyond the resolution of the analyses. The ordering convention is used (Wiley, 1981).

### Phylogenetic groups from Hennigian analysis (Fig. 4):

	included taxa
Outgroup 1	<i>Syngenodrilus</i> , sedis mutabilis
Outgroup 2	<i>ascaridoides</i> , <i>dubius</i> , and <i>gordioides</i> , sedis mutabilis, incertae sedis
Outgroup 3	<i>heterogyne</i> , <i>gastrochaetus</i> , and <i>Tiguassu reginae</i> , sedis mutabilis, incertae sedis
Outgroup 4	<i>Moniligaster</i> and <i>Desmogaster</i>

### Phylogenetic groups

Level	1	<i>Metataxis americanus</i> and <i>M. brinkhursti</i> , sedis mutabilis, incertae sedis
	1	<i>Enchytraeus</i> , <i>Metataxis falcifer</i> , and <i>Propappus</i> , sedis mutabilis, incertae sedis
	1	<i>bipapillatus</i> to <i>leruthi</i> , sedis mutabilis, incertae sedis

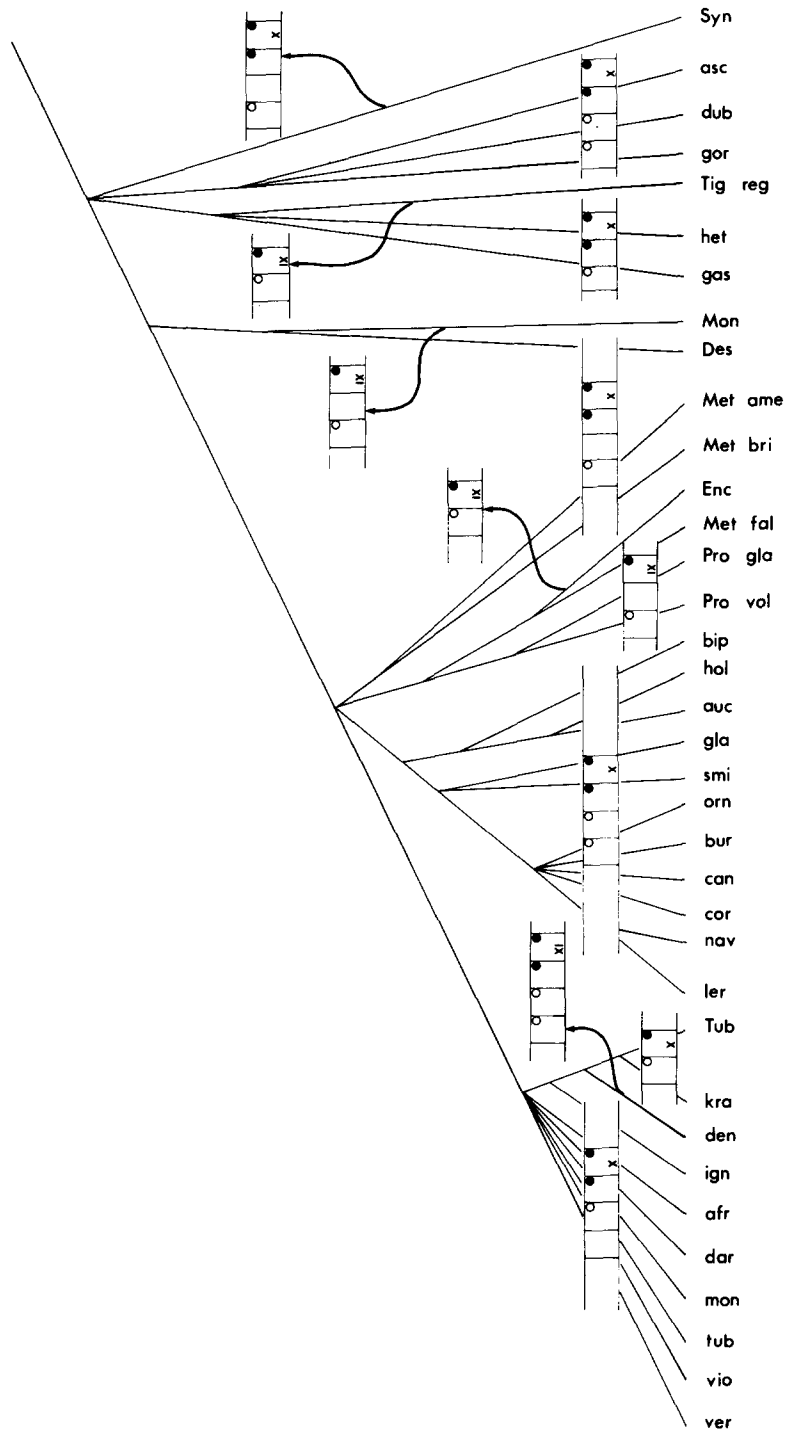


Fig. 6. Distribution of gonadal sequences on 36 species  $\times$  22 two-state character cladogram (Fig. 4); IX, X and XI, number of anterior fertile segment; ●, testis pair, ○, ovarial pair.

- Level 2 *Tubifex* and *ignatovi* to *vermivorus*, sedis mutabilis, incertae sedis
- 2.1 *Tubifex*, *ignatovi*, *denticulatus*, and *kraepelini*, sedis mutabilis, incertae sedis

Phylogenetic groups from Adams consensus (Fig. 5):

included taxa

Outgroup *Syngenodrilus*, and *Moniligaster* and *Desmogaster*

Phylogenetic groups

- Level 1 *Tubifex*, sedis mutabilis, incertae sedis
- 1 *kraepelini*, sedis mutabilis, incertae sedis
- 1 *Metataxis americanus*, sedis mutabilis, incertae sedis
- 1 *Metataxis brinkhursti*, sedis mutabilis, incertae sedis
- 1 *Enchytraeus*, *Metataxis falcifer*, and *Propappus*, sedis mutabilis, incertae sedis
- 1.1 Enchytraeidae, sedis mutabilis, incertae sedis
- 1.1 *Metataxis falcifer*, sedis mutabilis, incertae sedis
- 1.1 Propappidae, sedis mutabilis, incertae sedis
- Level 2 *denticulatus*, sedis mutabilis, incertae sedis
- 2 *vermivorus*, sedis mutabilis, incertae sedis
- 2 *glandularis*, sedis mutabilis, incertae sedis
- 2 *hologynus* and *aucklandicus*, sedis mutabilis, incertae sedis
- 2 *ignatovi* to *leruthi*, sedis mutabilis, incertae sedis
- Level 3 *bipapillatus* to *dubius* (including *Tiguassu reginae*), sedis mutabilis, incertae sedis

The species of *Propappus* would seem to be appropriately recognized at a familial rank if traditional families, including the Haplotaxidae, for the most part, are to be conserved.

Phylogenetic analyses, as well as cluster analyses, point out problems with current classifications of the Oligochaeta at ordinal, familial, and generic ranks. The erection of *Metataxis* and *Tiguassu* as genera of Haplotaxidae was not corroborated by the phylogenetic analyses. Examination of new, mature specimens of the haplotaxids and analysis of character distributions is essential for resolving these systematic problems.

As is shown in Fig. 6, some monophyletic groups of higher rank share a single segmental arrangement of testis and ovarial pairs but there is homoplasy in all these characters. Use of these as the basis of an evolutionary tree (Brinkhurst, 1982) might obscure phylogenetic relationships supported by other characters (for examples see Table 2) only superimposed a posteriori on the tree.

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