



Can we infer heteronemertean phylogeny from available morphological data?

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Abstract

This study uses morphological data from the primary literature to make a first pass at a cladistic analysis of the order Heteronemertea, which includes about one-third of the accepted species of the phylum Nemertea. This produced numerous trees and almost completely unresolved consensus trees. We conclude that this stems from imprecise and inadequate taxonomic descriptions of species and their morphological features, resulting in a limited number of characters and extensive homoplasy. The analyses neither support previously proposed *ad hoc* hypotheses of internal grouping nor do they propose robust new hypotheses. Rather, the analyses indicate that morphology-based cladistic studies of heteronemerteans will require very extensive, critical comparative study of heteronemertean morphological features. Re-examination of type material and common species appears to be the most fruitful approach to developing a clade-based classification of heteronemerteans.

Introduction

The phylum Nemertea contains approximately 1200 accepted species (Gibson, 1995), known mostly from intertidal habitats, but also from all major marine biotopes as well as fresh-water and terrestrial habitats. However, this phylum remains largely unknown to biologists. Their relative anonymity results mostly from difficulty in identifying species. Surveys of biodiversity that include nemerteans usually list them uninformatively as 'Nemertea sp.' when they list them at all. This has deterred biologists from attempting to use them in their research and relegated the entire phylum to widespread obscurity in scientific discourse. The problem of identifying nemerteans to genus or species is partly inherent; the nemertean fauna includes many undescribed species in most parts of the world, and most collected material requires histological study for identification.

The order Heteronemertea contains one-third of the known nemertean species, with approximately 87 genera (Gibson 1995; Cantell, 1996, 1998; Morretto, 1998; Wern, 1998), of which 58 are monotypic,

while most of the remaining genera have from two to four species. *Cerebratulus* Renier, 1804, *Lineus* (Gunnerus, 1770), and *Micrura* Ehrenberg, 1831, together contain approximately 240 species, over 61% of the described species in the order. These three 'mega-genera' lack definitive diagnoses and have become dumping grounds for new heteronemertean species. Monotypic genera are erected for new species not fitting into one of these three genera, and cause additional taxonomic confusion.

The diagnoses of the 'mega-genera' use character combinations that are wide-spread among heteronemerteans; e.g. the number of proboscis muscle crosses and arrangement of proboscis wall strata. These characters have overlapping states for all three genera and, therefore, are not phylogenetically informative, because they are not mutually exclusive synapomorphies for the species in those genera. The presence or absence of a caudal cirrus and of neurochord cells, routinely are the only two characters used to discriminate membership in one or another of these three genera. Both characters are prone to misinterpretation; the caudal cirrus often is lost during collection, and

neurochord cells are at present without clear definition of cell type and precise location in heteronemerteans. Examples of these problems are common in the literature. W.R. Coe, an astute nemerteanologist, originally placed the lineiform heteronemertean, *Micrura wilsoni* (Coe, 1904), in the genus *Lineus* based on its lack of a caudal cirrus (Coe, 1904). Later, after re-collecting specimens with a caudal cirrus, he revised the taxonomy to reflect that fact (Coe, 1940). Neurochord cells are often cited as simply present or absent in descriptions. These cells have also been identified in hoplonemerteans (Riser, 1998), where misinterpretation is a clear problem (Crandall, pers. comm.; Norenburg, unpubl. obs.). Not surprising, recent molecular studies have demonstrated paraphyly of *Lineus* and *Micrura* (Sundberg & Saur, 1998).

There are many holes in our understanding of heteronemertean morphology that need to be addressed before phylogeny and taxonomy can usefully enter the 21st century. Cladistic analysis provides a useful context for guiding this process as well as a testable hypothesis of relationships. Cladistics requires that statements of homology (the characters and their states) are explicit and can be tested in a rigorous manner, following which these statements may be refined. This is a valuable exercise, requiring that characters and their states are defined as precisely as possible. Although Gibson (1985) summarized heteronemertean morphological data to diagnose families of heteronemerteans, only one study (Norenburg, 1993) has attempted to evaluate critically the implied homologies of some of the characters most widely used in heteronemertean classification. The present study is the first attempt to examine heteronemertean implied homologies empirically, i.e. with cladistics, by coding characters directly from the primary nemertean literature. In the process, we propose an initial set of explicitly defined characters and states. We also test the hypotheses of relationship implied in the traditional taxonomy of heteronemerteans and the recent, more explicit, *ad hoc* hypotheses proposed by Gibson (1985) and Norenburg (1993).

Materials and methods

Descriptions and supplemental information of type species were used to code characters (Table 1). Most of the terminal taxa effectively represent individual species, because 58 of 87 included genera are monotypic, while those with few species are monomorphic

for all or most characters. As this is an exploratory study, we coded the type species for *Lineus* and *Micrura* and their genera as separate taxa. We could not do so for *Cerebratulus* because the original description of its type species, *Cerebratulus marginatus* (Renier, 1804), is based solely on external characters and subsequent observations from putative *C. marginatus* material were not made from specimens collected at or near the type locality in the Adriatic. To capture the range of variation within *Cerebratulus*, *Lineus* and *Micrura*, polymorphisms were coded to account for the overlapping nature of some key taxonomic characters, such as proboscis muscle layers and number of muscle crosses (Appendix 1).

All characters were equally weighted and non-additive. Characters used in generic diagnoses, such as body wall muscle strata and position, were not included in the analysis because they turned out to be uninformative despite exploration of several different coding methods (i.e. binary and multistate). Nona 2.0 (Goloboff, 1998) was used with the heuristic search method as implemented through Winclada 0.9.9 (Nixon, 1999). The abundance of missing data for some characters and taxa may cause cladistic software, e.g. Hennig86 and PAUP*, to choose a most parsimonious optimization in which missing data determines the placement of taxa in trees (Strong & Lipscomb, 1999). Nona (Goloboff, 1998) treats missing data in a semi-strict manner, not allowing placement of taxa to be determined by missing data. Taxa with more than 10% missing data, an arbitrary cut-off chosen to allow specific terminals to remain within the analysis, were removed to reduce ambiguity in the analysis, leaving 27 taxa and 36 parsimony informative characters. *Cerebratulus*, *Lineus* and *Micrura* were left in the analysis because of the large number of species they represent and their importance to understanding heteronemertean phylogeny, despite having more than 10% of their character states as ambiguous or missing data. However, subsequent removal of these terminals individually and collectively did not affect the topology of the consensus tree. *Hubrechtella dubia* Bergendal, 1902, a putative member of the order Paleonemertea, was selected as an outgroup based upon recent morphological cladistic study of the phylum and supported by molecular data (Norenburg, unpub. obs.).

Table 1. Morphological characters used for parsimony analysis. Characters are taken directly as described in the literature. Abbreviations: BV – blood vessel, CM – circular muscle, CNS – central nervous system, DLM – dermal longitudinal muscle, ICM – inner circular muscle, ILM – inner longitudinal muscle, LM – longitudinal muscle, NP – neural plexus, OCM – outer circular muscle, and OLM – outer longitudinal muscle. Consistency index is listed for each character for tree in Figure 1.

Character with	Character states	Coding
1. Circular cephalic furrow 0.50	Absent	0
	Present	1
<i>Comments:</i> This feature is also known as an annular cephalic furrow, usually anterior to the mouth with the cerebral organs opening into the furrow in some species (Norenburg, 1993). Often this is a subtle feature and it is doubtful that it has been recognized in all described species possessing it.		
2. Caudal cirrus 0.11	Absent	0
	Present	1
<i>Comments:</i> Caudal cirri may be mis-scored because they are easily lost during collection.		
3. Dermal connective tissue 0.14	Absent	0
	Above DLM	1
	Below DLM	2
4. Dermal glands 0.33	Absent	0
	Above DLM	1
	In DLM	2
	Below DLM	3
	Above and through DLM	4
	Below connective tissue	5
5. Medial longitudinal muscle plate 0.10	Absent	0
	Present	1
	Surrounds rhynchocoel	2
6. Body wall muscle cross 0.50	Absent	0
	Present	1
7. Proboscis wall strata 0.18	LM-NP-CM-LM	0
	NP-CM-LM	1
	NP-LM	2
	LM-NP-LM	3
	CM-LM-NP-LM	4
<i>Comments:</i> Possible homology statements for several strata have been explored only once (Norenburg, 1993). We prefer this coding because it is informative for this paper. Alternative coding methods, such as binary coding of each layer, result in multiple uninformative characters. This coding assumes that the neural plexus is a stationary landmark (Norenburg, 1993).		
8. Proboscis rhynchothelium circular muscle 0.25	Absent	0
	Present	1
9. Proboscis muscle crosses 0.18	Absent	0
	One	1
	Two	2

Continued on p. 168

Table 1. Continued

Character with	Character states	Coding
10. Proboscis nerves 0.25	One or pair	0
	Two pair	1
	Multiple	2
	Plexus	3
11. Proboscis symmetry 0.22	Radial	0
	Asymmetric	1
	Glandular ridge	2
12. Proboscis regions 0.50	Uniform	0
	Gradual	1
	Discrete-Armed	2
	Alternate branching	3
	Dichotomous branching	4
	Spiral branching	5
<i>Comments:</i> This character implicitly tests the homology of the branched condition. Gradual versus uniform refer to terminology in the literature.		
13. Dorsal ganglion 0.25	Not bifurcated	0
	Bifurcated posterior	1
	Bifurcated anterior and posterior	2
14. Neurochords 0.12	Absent	0
	Present	1
<i>Comments:</i> Neurochords have been identified in many heteronemertean. Descriptions of this character, such as cell features and their placement, are lacking sufficient detail to assess the homology of this character. Further examination of this feature is required before it can be reliably used as phylogenetic character.		
15. Rhynchocoel dorsal nerve 0.25	Absent	0
	Present	1
16. Subepidermal nervous sheath 0.50	Absent	0
	Present	1
17. Cerebral organ opening 1.00	Pit anterior to cerebral ganglion	0
	Pit next to cerebral ganglion	1
	Pit posterior to cerebral ganglion	2
18. Cerebral organ furrow 0.33	Vertical groove	0
	Pit	1
	Lateral longitudinal furrow	2
	Shallow lateral furrow	3
	Ventral longitudinal furrow	4
19. Cephalic fissures 0.33	Absent	0
	Present	1
20. Cerebral organ depth 1.00	With CNS	0
	With BV or below ILM	1

Continued on p. 169

Table 1. Continued

Character with	Character states	Coding
21. Cerebral organ and brain relative position 1.00	Anterior to brain	0
	Next to brain	1
	Posterior to brain	2
	Tightly fused	3
22. Adult ocelli 0.20	Absent	0
	Present	1
23. Apical sense organ 0.57	Absent	0
	Single	1
	Three	2
	Three plus central	3
	Two	4
<i>Comments:</i> We are skeptical that states 3 and 4 exist, but have not had the opportunity test that hypothesis.		
24. Cephalic gland 0.20	Absent	0
	Present	1
25. Cephalic gland opening 0.42	Absent	0
	To apical organs	1
	To frontal pore	2
	To integument	3
	To anterior pores and integument	4
	Present	5
<i>Comments:</i> While state five is redundant, it is often the case that there is no information other than the presence/absence of the character in taxonomic descriptions. Coding as simply present/absent leaves this character uninformative, while coding in this manner allows us to retain information in our matrix for future refinement. This character does not affect the topology of the tree in the current analysis.		
26. Salivary glands 0.14	Absent	0
	Present	1
27. Foregut subepidermal glands 0.09	Absent	0
	Present	1
28. Splanchnic muscle 0.27	Absent	0
	Circular	1
	Longitudinal	2
	Circular + longitudinal	3
	Spiral	4
29. Foregut vasculature 0.25	Two lateral vessels	0
	Vascular plexus	1
30. Foregut blood vessels 0.20	Paired vessels	0
	Plexus	1

Continued on p. 170

Table 1. Continued

Character with	Character states	Coding
31. Cephalic blood vessel 0.23	Single dorsal	0
	Single ventral	1
	Two lateral	2
	Three	3
32. Rhynchocoel and blood vessel interface 0.50	No connection	0
	Elongate villus	1
	Plug	2
33. Nephridial units 0.33	Absent	0
	Pair	1
	2-10	2
	> 10	3
34. Excretory pore 0.66	In dorsal body wall	0
	In ventral body wall	1
	In gut	2
35. Dermal muscle 0.75	Absent	0
	OCM + ILM	1
	Mixed	2
	CM only	3
	LM only	4
	OLM+ICM in head, OCM+ILM posterior	5
36. Dermal connective tissue structure 0.66	Absent	0
	Present	1
	Lamellar	2

Comments: This character may be significantly influenced by fixation variables. On account of this, the character may have been overlooked in many descriptions, but appears to be phylogenetically informative.

Results and discussion

An analysis of the complete data set including 87 genera and 67 characters results in an almost completely unresolved consensus tree. A reduced data set of 27 taxa and 36 characters results in marginally more informative trees, with length of 152, CI=0.40, and RI=0.50. The strict consensus tree of 695 resulting trees, however, shows very little grouping information (Fig. 1). Although these trees are not useful estimates of phylogenetic relationships among the Heteronemertea, they do, however, provide the first and only empirical demonstration of the current state of heteronemertean systematics.

The consensus tree shows the main branch leading to a massive polytomy (Fig. 1) supported by several synapomorphies that have in the past been important to heteronemertean taxonomy. These include the presence of lateral cephalic slits (Friedrich, 1960), and the presence of proboscis muscle crosses (Böhmig, 1929; Gibson, 1985). Other synapomorphies include easily recognizable features of heteronemerteans such as the apical sense organ and cephalic gland openings. *Riserius* is sister to rest of the heteronemerteans by absence of rhynchothelial circular muscle, undifferentiated proboscis epithelium and the cerebral organ opening to a pit posterior to the cerebral ganglion. The placement of *Riserius* outside the main branch is not surprising (Norenburg, 1993). However, the consensus

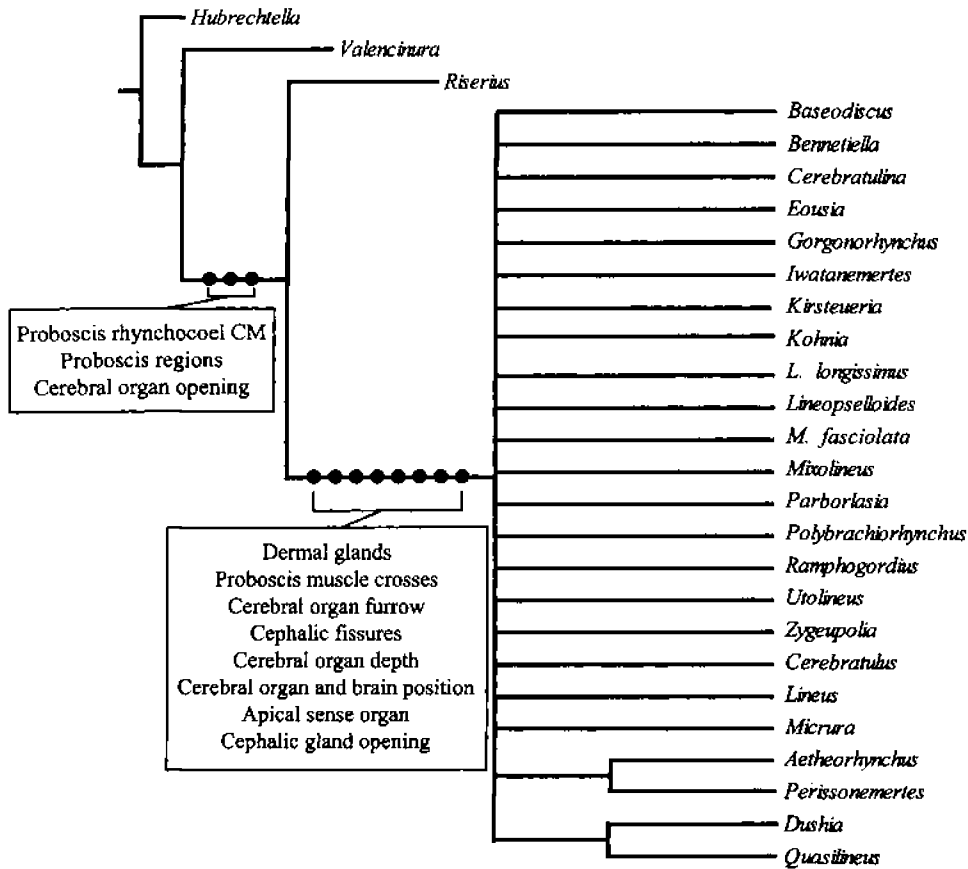


Figure 1. Strict consensus tree of 695. Synapomorphies are marked by black circles.

does not include a Lineiformes clade sensu Norenburg (1993), which anticipated cephalic slits to be a synapomorphy for a group excluding most species that lack slits, such as the Baseodiscidae. Placement of *Valencinura* is caused by numerous absent characters and is also unsurprising.

Resolution of the cladogram is greatly affected by the large amount of missing data in the matrix. There are several explanations for so much missing data. Many early descriptions are limited to external features such as color or head shape. As we now understand, most species require histological serial sectioning for adequate identification. Additionally, many species were described from specimens that are contracted to various extents, causing fixation artifacts and obscuring key features, such as the presence or absence of a muscle layer, or the composition of a structural feature, such as cephalic gland opening (Table 1, Character 25). Contraction can lead to misinterpretation or inconsistent interpretation of

morphological features. Fixation artifacts can be informative when they are consistent; this, for example, is the premise of histological staining. However, interpretation of unique features from single, poorly preserved specimens cannot inspire confidence. Uncontrolled variables in the fixation process can cause variable extraction of water, resulting in substantial differences in the form and appearance of extracellular matrix, such as the dermis. For example, connective tissue in the dermis is occasionally described as having a lamellar appearance. These and other so-called connective tissue laminae are likely caused by collapse of the extracellular matrix as water is extracted during the fixation process, with fibrous elements and cellular debris being compacted. The extent to which such artifacts are consistent, and therefore informative, cannot be judged from single specimens. Relaxing agents have alleviated some of these problems and permit more detailed and careful analysis, but even this remains an imprecise enterprise. Thorough comparative

studies are essential to achieving confidence in basic observations.

Homoplasy is a substantial problem in this data set. We are at a stage of nemertean systematics where refining homology statements is most of the work. For example, neurochord cells are a discriminating feature between *Cerebratulus* and *Micrura*. These are supposed to be present in *Cerebratulus* and *Lineus*; yet, it is unknown whether they are homologous in all cases, because important features resolvable by light microscopy, such as position, number, and cell characteristics are rarely noted in the literature. In some cases among hoplonemerteans, it is evident that authors have mistaken other neural cells for neurochord cells (Crandall, pers. comm.; Norenburg, unpubl. obs.). Unfortunately, numerous nemertean morphological characters provide easy opportunities for inexperience, lack of information, and lack of comparative study to lead to erroneous conclusions about homology or character state.

It may be that homoplasy is rampant in the nemerteans as alleged by Moore & Gibson (1993); however, this will not be known without further cladistic analyses using additional character data with homology statements that are more refined than is possible now from the literature. Some characters do show promise of providing useful grouping information, and we may be able to eliminate some homoplasy by more carefully defining characters and their states. For instance, the position and arrangement of gland cells in the epidermis and the nature of foregut musculature are in need of reexamination in this regard. They have been considered phylogenetically informative by other authors (Riser, 1993) and their consistency index is high in other analyses (pers. obs.).

The results of the present study indicate to us that elucidating phylogenetic relationships of a particular species will, in most cases, require re-collecting and re-examining it and a number of potentially relevant species. Overall, it is our belief that the most effective way to proceed is setting a new baseline for heteronemertean taxonomy by comparative study of common species, mostly already named species, rather than uncritical addition of new monotypic genera based on single specimens. Recent molecular studies (Sundberg & Saur, 1998; unpubl. obs.) provide more data and already have shown promising results. Molecular systematics coupled with better taxonomic descriptions and additional data from morphological features will significantly alter heteronemertean systematics,

providing useful and new insights into evolution of nemertean relationships of and within the phylum.

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Appendix I. Matrix used for parsimony analysis A=0/1 B=0/2 C=2/3 D=1/2 E=0/1/2/3 ?=Missing data.

Genus	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22
<i>Hubrechtella</i>	0	0	0	0	?	0	1	1	0	0	0	1	0	0	1	1	1	1	0	0	2	0
<i>Aetheorhynchus</i>	0	?	0	1	1	0	1	1	1	3	2	0	1	0	0	0	2	2	1	1	3	1
<i>Baseodiscus</i>	0	0	1	1	0	0	2	1	0	C	0	0	?	0	?	?	0	1	0	1	3	1
<i>Bennetiella</i>	?	1	1	1	0	0	0	0	2	3	2	0	1	0	0	0	2	2	1	1	3	0
<i>Cerebratulina</i>	?	0	1	1	1	0	0	0	2	3	2	0	1	0	1	?	2	2	1	1	3	0
<i>Dushia</i>	0	0	0	1	1	0	0	0	2	3	0	0	1	1	0	0	2	2	1	1	3	0
<i>Eousia</i>	?	1	0	2	1	0	1	0	2	3	1	0	1	1	0	?	2	2	1	1	3	1
<i>Gorgonorhynchus</i>	0	1	1	1	0	0	0	0	2	3	0	4	1	1	0	0	2	2	1	1	3	0
<i>Iwatanemeries</i>	?	0	0	1	0	0	0	0	1	0	2	0	1	0	0	?	2	2	1	1	3	0
<i>Kirsteueria</i>	?	0	0	1	1	0	1	0	1	0	2	0	0	0	?	?	2	2	1	1	3	0
<i>Kohnia</i>	0	0	0	2	1	0	1	0	1	0	0	0	1	0	0	1	2	2	1	1	3	0
<i>L. longissimus</i>	0	0	1	1	?	0	1	0	2	3	2	0	1	0	1	0	2	2	1	1	3	1
<i>Lineopselloides</i>	?	0	0	1	0	0	1	0	0	0	0	0	1	0	0	?	2	2	1	1	3	0
<i>M. fasciolata</i>	0	1	0	4	1	1	1	0	2	3	0	0	?	1	?	0	2	2	1	1	3	0
<i>Mixolineus</i>	1	0	0	2	0	1	1	0	0	?	0	1	?	0	0	0	2	2	1	1	3	0
<i>Parborlasia</i>	0	0	1	1	0	0	0	0	2	1	0	0	1	0	?	0	2	2	1	1	3	0
<i>Perissonemertes</i>	?	1	0	1	1	0	0	0	1	3	2	2	1	0	0	?	2	2	1	1	3	1
<i>Polybrachiorhynchus</i>	0	1	1	1	1	0	0	0	2	3	0	3	0	1	0	0	2	2	1	1	3	0
<i>Quasilineus</i>	0	0	0	1	0	0	0	0	0	3	0	2	1	0	0	0	2	2	1	1	3	0
<i>Ramphogordius</i>	0	0	0	2	0	0	1	0	0	3	?	0	?	0	0	0	2	2	1	1	3	1
<i>Riserius</i>	1	0	0	0	0	0	2	0	0	0	0	0	0	0	0	?	2	1	0	0	2	0
<i>Utolineus</i>	?	0	0	2	1	0	1	0	0	0	0	1	1	1	0	?	2	2	1	1	3	?
<i>Valencinura</i>	0	1	0	2	0	0	0	1	0	3	1	1	1	0	0	0	1	1	0	0	2	0
<i>Zygenpolia</i>	0	1	0	2	1	0	1	1	2	3	2	1	1	1	1	0	2	1	0	1	3	0
<i>Cerebrandus</i>	0	1	A	?	?	0	A	0	B	?	?	?	?	1	?	?	2	2	1	1	?	A
<i>Lineus</i>	0	0	A	?	?	0	A	0	B	?	?	?	?	0	?	?	2	2	1	1	?	?
<i>Micrura</i>	0	A	A	1	0	0	A	0	B	?	?	?	1	0	?	?	2	2	1	1	3	?

Continued on p. 174

Appendix 1. Continued

Genus	23	24	25	26	27	28	29	30	31	32	33	34	35	36
<i>Hubrechtella</i>	0	0	0	0	?	3	7	0	2	0	0	-	0	0
<i>Aetheorhynchus</i>	2	1	5	0	0	1	1	1	2	1	1	0	1	0
<i>Buseodiscus</i>	1	1	5	A	1	1	1	1	2	1	2	2	1	2
<i>Bennetiella</i>	2	1	2	0	0	1	1	1	0	1	1	0	1	?
<i>Cerebratulina</i>	2	1	5	1	0	1	1	1	3	1	2	0	1	?
<i>Dushia</i>	0	0	0	?	0	1	0	0	3	0	2	0	1	0
<i>Eousia</i>	2	1	5	0	1	2	1	1	0	1	1	0	1	0
<i>Gorgonorhynchus</i>	2	1	5	1	0	0	1	1	2	1	1	0	1	1
<i>Iwatanemertes</i>	2	1	5	0	0	1	1	1	3	1	2	1	1	0
<i>Kirsteueria</i>	0	0	0	0	0	0	1	1	2	1	1	0	4	0
<i>Kohnia</i>	2	1	5	1	0	1	0	0	0	1	1	0	1	0
<i>L. longissimus</i>	2	?	?	0	1	3	1	1	0	1	1	0	1	?
<i>Lineopselloides</i>	2	1	5	0	1	1	1	1	0	1	1	0	1	0
<i>M. fusciolata</i>	2	1	5	0	1	2	1	1	2	1	1	0	1	0
<i>Mixolineus</i>	4	1	5	?	0	0	1	1	1	1	1	0	1	0
<i>Parborlasia</i>	2	1	5	1	1	3	1	1	B	1	1	0	1	2
<i>Perissonemertes</i>	3	1	5	0	0	1	1	1	2	1	1	0	1	0
<i>Polybrachiorhynchus</i>	2	1	1	1	1	1	1	1	2	1	1	0	1	?
<i>Quasilineus</i>	2	1	5	0	0	1	0	0	3	1	3	1	1	0
<i>Ramphogordius</i>	2	0	0	0	1	2	0	0	0	1	2	0	1	0
<i>Riserius</i>	0	0	0	1	0	0	0	0	0	1	1	0	3	0
<i>Utolineus</i>	2	1	5	0	1	1	1	1	0	1	1	0	1	0
<i>Valencinura</i>	0	1	2	?	0	3	1	1	0	1	2	0	1	0
<i>Zygeupolia</i>	0	?	?	1	1	1	1	1	2	1	1	0	0	0
<i>Cerebratulus</i>	2	1	5	?	0	2	1	1	2	1	2	0	1	A
<i>Lineus</i>	?	?	?	?	1	D	A	A	B	?	?	?	?	A
<i>Micrura</i>	?	?	?	?	0	E	1	1	0	?	?	?	1	A