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Phylogenetic study of pelagic nemerteans (Pelagica, Polystilifera)

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Abstract

Pelagic polystiliferous nemerteans, often referred to as Pelagica, represent one of the most enigmatic groups of nemerteans. The group includes 98 valid species assorted into 41 genera and 3–11 families, depending on the classification. Pelagica inhabit the water column of the world oceans, occupying depths from several hundred to several thousand meters. As is the case with most meso- or bathypelagic soft-bodied animals, specimens are few and numerous difficulties are associated with obtaining and preserving them, resulting in incomplete descriptions and, therefore, an obscure classification. Most genera and families of pelagic nemerteans are based upon unique combinations of two or three characters. Here, we present results of the first cladistic analysis of pelagic nemertean phylogeny. The analysis is based on morphological character data available from the primary literature and personal observations. A large percentage of missing entries in the data (21.5%), due to incompleteness of descriptions, results in a large number of maximum parsimonious cladograms, which translates into a drastic lack of resolution on the strict consensus tree. Traditional families supported by the cladistic analysis are Armaueriidae Brinkmann, 1917 and Pelagonemertidae (*sensu* Korotkevitsch, 1955). We propose a new diagnosis for Armaueriidae and discuss morphological characters traditionally used in pelagic nemertean classification. A few potentially informative characters are suggested for greater attention in future studies of specimens.

Introduction

Pelagic nemerteans referred to as Pelagica (Polystilifera, Hoplonemertea) are delicate, gelatinous creatures inhabiting the water column of the world oceans. Pelagica are commonly found between a few hundred and several thousand meters depth, and are most abundant at 625–2500 m (Roe & Norenburg, 1999). Pelagica has been designated in the literature either as a 'tribus' (Stiasny-Wijnhoff, 1936) or an order (Sundberg, 1991; Crandall, 1993). We use it as a group name of unspecified rank that includes all pelagic polystiliferan nemerteans. Throughout 'pelagic nemerteans' refers only to polystiliferous nemerteans inhabiting the water column.

The key mystery of the evolution of pelagic nemerteans is in their relative morphological simplicity as compared to benthic hoplonemerteans. They lack ocelli, the paired neuroglandular sensory organs (so-called 'cerebral organs') and a nephridial system, while other features show varying degrees of structural simplicity. Therein lies a fundamental problem for phylogenetic studies; that is, distinguishing primary absence from 'adaptive' loss, when a large portion of the data is missing.

Although different taxonomic rankings have been proposed from time to time, the group mostly has been treated as a derived monophyletic taxon (e.g. Brinkmann, 1917a; Coe, 1926; Gibson, 1988; Crandall, 1993), except for Bürger (1895) and Korotkevitsch (1955), who postulated more than one monostiliferan ancestor. These views contrast sharply with Stiasny-Wijnhoff's (1923) assertion, that the pelagic nemerteans are the most 'primitive' nemerteans and ancestral to benthic hoplonemerteans. Stricker (1985) argued for the primitiveness of the polystiliferous stylet apparatus on the basis of an hypothesis of functional progression in evolution of the proboscis armature. Recent cladistic analyses of hoplonemertean phylogeny by Sundberg (1990) and Norenburg (unpubl.

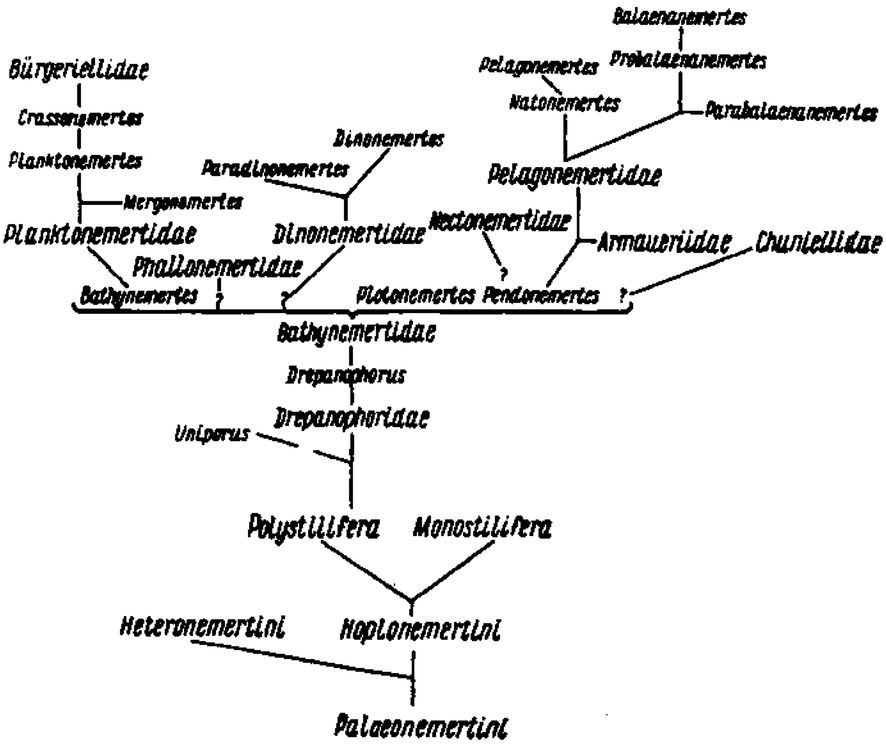

Figure 1. Classification of the pelagic nemerteans after Brinkmann (1917a).

obs.), based on morphological characters, provided some evidence for (1) Pelagica being a sister group to a clade including monostiliferans and benthic polystiliferans (Reptantia); (2) Monostilifera being a derived member of Reptantia. Although Sundberg's analysis, which includes a representative of every pelagic family, points to monophyly of the Pelagica, only a few, not well defined, synapomorphies support this hypothesis (see 'Discussion'). Norenburg's phylum-level analysis includes only a single pelagic representative and does not address, but assumes monophyly of the group.

Pelagica currently includes 98 species assorted into 41 genera, 19 of which are monotypic (Gibson, 1995) (Table 1). These include *Bathynemertes alcocki* Laidlaw, 1906. Although Gibson (1995) referred to the latter as *nomen dubium*, we have seen easily identifiable examples in collections of the U. S. National Museum of Natural History. The currently used classification (Table 1) follows Brinkmann (1917a) and Coe (1926, 1954). It comprises eleven families (Armaueriidae, Balaenanemertidae, Buergeriellidae, Chuniellidae, Dinonemertidae, Nectonemertidae, Pachynemertidae, Pelagonemertidae, Phallonemertidae, Planktonemertidae and Protopelagonemertidae). Brinkmann (1917a) recognized 9 families. Coe (1926) changed the name Bathynemertidae Brinkmann, 1917 to Protopelagonemertidae and established families Balaenanemertidae Coe, 1945 and Pachynemertidae Coe, 1954. Korotkevitsch (1955, 1977) argued that Brinkmann's system did not reflect the historical relationships among the taxa and was overloaded with a large number of poorly defined monotypic and oligotypic families and genera. She synonymized most of the genera and families, leaving three families (Armaueriidae, Nectonemertidae and Pelagonemertidae) and eight genera. However, her system has not been adopted in subsequent non-russian literature.

Attempts to reconstruct the phylogeny of the Pelagica were undertaken in the 20th century by Brinkmann (1917a) (Fig. 1) and later Korotkevitsch (1955) (Fig. 2). Although these systems differ in the number of genera and families considered and the view on origin of the Pelagica, they both are similar in being essentially non-phylogenetic, representing the evolution of the taxa as a *scala naturae* rather than the divergence of lineages (Härlin, 1998). The former approach is subjective, based on a few characters considered to be phylogenetically important by the

Table 1. List of valid species of pelagic nemerteans (after Gibson, 1995). Type species of each genus indicated with an asterisk (*).

Species		Authority	Comments
ARMAUERIIDAE Brinkmann, 1917			
Armaueria	*rubra**	(Brinkmann, 1917)	3 males,1 female; North Atlantic
Neoarmaueria	*angusta*	(Korotkevitsch, 1955)	2 females (see Appendix 2 for details); Bering Sea
	crassa	(Korotkevitsch, 1955)	single female (second specimen was collected later); Bering Sea
	divaricata	(Korotkevitsch, 1955)	single female, in a very poor shape; Sea of Okhotsk
	laticeps	(Korotkevitsch, 1955)	1 female, 1 male (second female was referred to this species later); North Pacific, Sea of Okhotsk
	*tenuicauda**	(Korotkevitsch, 1955)	1 female, 1 immature male; Bering Sea
Proarmaueria	*korotkevitschae*	(Chernyshev, 1992)	2 males (see Appendix 2 for details); Sea of Okhotsk
	*pellucida**	(Coe, 1926)	2 hermaphroditic specimens; Sea of Okhotsk. Multiple specimens preliminary identified as *P. pellucida* were recently collected off the coast of California (Roe & Norenburg, 1999)
Proarmaueriella	*caudata**	(Korotkevitsch, 1955)	single hermaphroditic specimen; Sea of Okhotsk
Xenarmaueria	*acoeca**	(Korotkevitsch, 1955)	single specimen, possibly hermaphroditic; Bering Sea
Zinarmaueria	*platonovae**	(Chernyshev, 1992)	single female (see Appendix 2 for details); Sea of Okhotsk
BALAENANEMERTIDAE Coe, 1945			
Balaenanemertes	*chavesi*	(Joubin, 1906)	single male, superficially studied; North Atlantic
	*chuni**	(Bürger, 1909)	asingle male; Indian Ocean
	grandis	(Brinkmann, 1917)	2 males; North Atlantic
	hjorti	(Brinkmann, 1917)	single male; North Atlantic
	lata	(Brinkmann, 1917)	single male; North Atlantic
	lobata	(Joubin, 1906)	single male originally described, 7 females reported later (Brinkmann, 1917a); North Atlantic
	minor	(Coe, 1936)	single female; Atlantic (Bermuda)
	musculocaudata	(Brinkmann, 1917)	5 males; North Atlantic
BUERGERIELLIDAE Brinkmann, 1917			
Buergeriella	*notabilis**	(Brinkmann, 1917)	single male described originally, second specimen reported by Van Der Spoel (1985); North Atlantic
Alexandronemertes	*ductor*	(Chernyshev, 1992)	2 females, 1 male; North Pacific
	*mollis**	(Coe, 1926)	single female originally described from Equatorial Pacific, a few specimens, supposedly belonging to this species (Chernyshev, 1992b) reported later from North Atlantic (Van der Spoel, 1985)
CHUNIELLIDAE Brinkmann, 1917			
Chunianna	*opaca**	(Coe, 1954)	single female; North Pacific
	pacifica	(Coe, 1954	3 females, 1 male; North Pacific
Chuniella	*agassizii*	(Bürger, 1909)	single immature female; Atlantic (west of Sierra Leone)
	elongata	(Joubin, 1906)	single immature specimen, superficially studied; North Atlantic
	*lanceolata**	(Brinkmann, 1917)	single immature male described originally, second male collected later; North Atlantic
	pelagica	(Bürger 1909)	single female; Southern Indian Ocean
	tenella	(Coe, 1954)	3 females, 1 male; North Pacific
DINONEMERTIDAE Brinkmann, 1917			
Dinonemertes	*alberti*	(Joubin, 1906)	1 male originally described; 3 females referred to the species later (Brinkmann, 1917a); Arctic Ocean (between Iceland and Norway)

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Table 1. contd.

Species	Authority		Comments
	arctica	(Korotkevitsch, 1977)	?; Arctic Ocean
Dinonemertes	*grimaldii*	(Joubin, 1906)	2 females, superficially studied; North Atlantic
	*investigatoris**	(Laidlaw, 1906)	type specimen (female) from Indian Ocean; 3 females and a male reported later from North Atlantic (Brinkmann, 1917a; Van der Spoel 1985); a single specimen reported from North Pacific (Roe & Norenburg, 1999)
Tubonemertes	*aureola*	(Coe, 1954)	4 females; North and South Pacific
	*wheeleri**	(Coe, 1936)	6 specimens described originally from Atlantic (Bermuda), two reported later from North Pacific (Coe, 1954) and one from North Atlantic (Van der Spoel, 1985)
Planonemertes	*labiata*	(Coe, 1936)	1 male and 1 female; Atlantic (Bermuda)
	*lobata**	(Coe, 1926)	single male; Equatorial Pacific
Plionemertes	*constricta*	(Coe, 1954)	single immature male originally described from Pacific (northwest of Galapagos Islands); two specimens recently collected in North Pacific (Roe, pers. comm.)
	*plana**	(Coe, 1926)	single female; Equatorial Pacific
Paradinonemertes	*drygalskii**	(Brinkmann, 1915–16)	2 young males; Tropical Atlantic
	macrostomum	(Coe, 1954)	5 females, 3 males; North and Equatorial Pacific
NECTONEMERTIDAE (Verrill) Brinkmann, 1917			
Nectonemertes	*acanthocephala*	(Korotkevitsch, 1955)	single immature male; Bering Sea
	acutilobata	(Korotkevitsch, 1964)	single female; South Pacific
	compacta	(Korotkevitsch, 1964)	single immature male; South Pacific
	japonica	(Foshay, 1912)	6 males, poorly described; Japan (off the coast of Misaki)
	major	(Korotkevitsch, 1955)	11 specimens; Bering Sea, Sea of Okhotsk, Pacific (east of Cape Lopatka)
	minima	(Brinkmann, 1915–16)	8 specimens; North, Tropical and South Atlantic
	*mirabilis**	(Verrill, 1892)	multiple specimens; Atlantic, Bering Sea and North Pacific
	pelagica	(Cravens & Heath, 1906	5 males and 2 females described originally, multiple specimens recently collected off California (Roe, pers. comm.), North and South Pacific
	primitiva	(Brinkmann, 1917)	2 males and 1 female originally described from North Atlantic, multiple specimens from North Atlantic (Van der Spoel, 1985) and Equatorial and North Pacific reported later (Coe, 1926; Roe, pers. comm.)
	tenuis	(Korotkevitsch, 1964)	single immature male; South Pacific
PACHYNEMERTIDAE Coe, 1954			
Pachynemertes	*obesa**	(Coe, 1936)	single female; Atlantic (Bermuda)
PELAGONEMERTIDAE (Moseley) Brinkmann, 1917			
Pelagonemertes	*brinkmanni*	(Coe, 1926)	multiple specimens; North Pacific, Bering Sea, Sea of Okhotsk
	excisa	(Korotkevitsch, 1955)	single male; Bering Sea
	joubini	(Coe, 1926)	a single female originally described from South Pacific, several specimens reported later from North and South Pacific (Coe, 1954) and Atlantic (Friedrich, 1969; Van der Spoel, 1985)

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Table 1. contd.

Species	Authority		Comments
	korotkevitschae	(Friedrich, 1969)	single female; Tropical Atlantic
	laticauda	(Korotkevitsch, 1955)	single female; Bering Sea
	moseleyi	(Bürger, 1895)	single specimen described originally from Pacific (near Japan), several other specimens reported later (Kato & Tanaka, 1938; Friedrich, 1969; Van der Spoel, 1985) from Pacific and Atlantic
	oviparus	(Korotkevitsch, 1955)	single female; Bering Sea
	parvula	(Korotkevitsch, 1964)	single male; South Pacific
	robusta	(Korotkevitsch, 1955)	single female; North Pacific
	*rollestoni**	(Moseley, 1875)	multiple specimens; Atlantic, Pacific, Indian Ocean
Loranemertes	*nana**	(Korotkevitsch, 1964)	single immature female; South Pacific
Nemertobus	*maximovi**	(Korotkevitsch, 1960)	3 males, 2 females; South Pacific, Indian Ocean
Obnemertes	*latilobata**	(Korotkevitsch, 1960)	1 male, 1 female; Indian Ocean
	ramosa	(Korotkevitsch, 1960)	single damaged specimen; Indian Ocean
	solida	(Korotkevitsch, 1960)	single immature female; Indian Ocean
Cuneonemertes	*elongata*	(Coe, 1954)	single female originally described, several specimens recently reported by Roe & Norenburg (1999); North Pacific
	*gracilis**	(Coe, 1926)	single female; Equatorial Pacific
	nigra	(Coe, 1945)	a single male originally described from Atlantic (Bermuda), several specimens reported from North Pacific (Coe, 1954; Roe, pers. comm.)
	obesa	(Coe, 1954)	2 males, 6 females; North Pacific
Natonemertes	*acutocaudata**	(Brinkmann, 1917)	2 males; North Atlantic
Parabalaenanemertes	*fusca**	(Brinkmann, 1917)	2 females, 1 male; North Atlantic
	zonata	(Joubin, 1906)	2 specimens superficially studied; North Atlantic
Probalaenanemertes	*irenae*	(Wheeler, 1934)	2 females; South Atlantic (west of the Cape of Good Hope)
	*wijnhoffae**	(Brinkmann, 1917)	single female; North Atlantic
Gelanemertes	*richardi**	(Joubin, 1906)	single male, superficially studied; North Atlantic
PHALLONEMERTIDAE Brinkmann, 1917			
Phallonemertes	*murrayi**	(Brinkmann, 1912)	multiple specimens; originally described from North Atlantic, recently collected specimens from Pacific (off the coast of California)
PLANKTONEMERTIDAE Brinkmann, 1917			
Planktonemertes	*agassizii**	(Woodworth, 1899)	5 females; Tropical Pacific
	curvicephala.	(Korotkevitsch, 1964)	single immature male; South Pacific
	vanhoeffeni	(Brinkmann, 1915–16)	single female described originally from South Atlantic, second specimen reported from North Atlantic (Van der Spoel, 1985)
Mergonemertes	*woodworthii**	(Bürger, 1909)	single female; Tropical Indian Ocean (southwest of Java)
Crassonemertes	*robusta**	(Brinkmann, 1917)	single female described originally from North Atlantic; later several specimens reported from Equatorial Atlantic and Equatorial and North Pacific (Coe, 1954; Roe & Norenburg, 1998a, 1999)
	rhomboidalis	(Joubin, 1906)	single female, superficially studied; North Atlantic (Sargasso Sea)
Monanemertes	*sargassicola**	(Joubin, 1906)	single specimen, superficially studied; North Atlantic (Sargasso Sea)
	scarlata	(Coe, 1945)	single male; Atlantic (Bermuda)
Tononemertes	*pellucida**	(Coe, 1954)	2 females; North and Tropical Pacific
Plenanemertes	*rubella**	(Coe, 1954)	single female; North Pacific (near Japan)
Neuronemertes	*aurantiaca**	(Coe, 1926)	single male originally described from Equatorial Pacific, another specimen reported from North Atlantic (Van der Spoel, 1985)

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Table 1. contd.

Species	Authority		Comments
PROTOPELAGONEMERTIDAE Coe, 1926			
Calonemertes	*hardyi**	(Wheeler, 1934)	single female originally described from South Atlantic (west of Cape of Good Hope); second specimen reported from North Atlantic (Van der Spoel, 1985)
Pendonemertes	*levinseni**	(Brinkmann, 1917)	3 females described originally, several specimens reported later by Van der Spoel (1985); North Atlantic
Plotonemertes	*adhaerens**	(Brinkmann, 1917)	multiple specimens; North Atlantic, North and South Pacific
	aurantiaca	(Coe, 1936)	single female; Atlantic (Bermuda)
Protopelagonemertes	*beebei*	(Coe, 1936)	single female; Atlantic (Bermuda)
Protopelagonemertes	*hubrechti**	(Brinkmann, 1917)	3 (4?) females originally described from Bermuda; several specimens reported later from North and South Atlantic and North Pacific (Coe, 1954; Roe, pers. comm.)
	joculatori	(Van der Spoel, 1988)	single female; Banda Sea
Species of uncertain taxonomic position			
Nannonemertes	*indica**	(Wheeler, 1937)	single female; Indian Ocean
Bathynemertes	*alcocki**	(Laidlaw, 1906)	*nomen dubium* (Gibson, 1995); type specimen from Indian Ocean, several specimens reported from Atlantic and Pacific (Roe, pers. comm.)

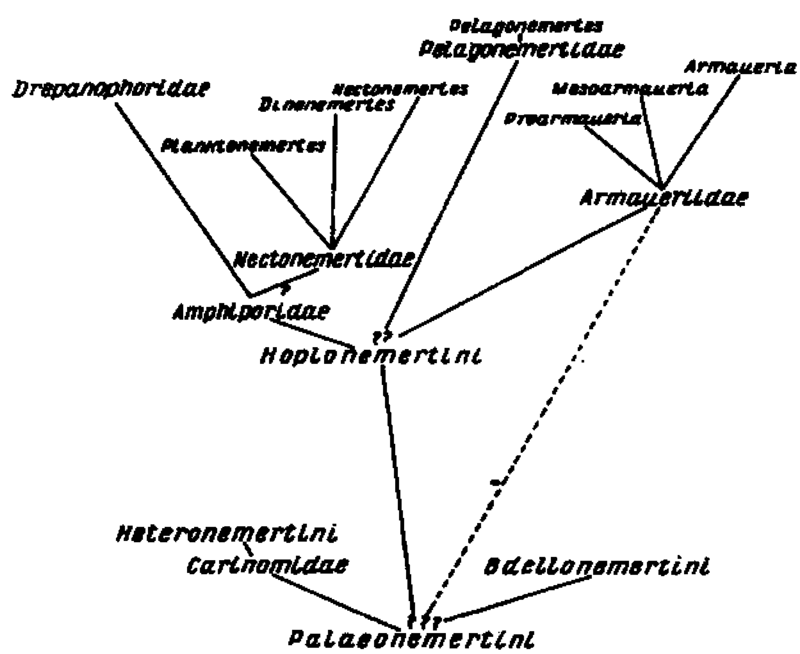

Figure 2. Classification of the pelagic nemerteans after Korotkevitsch (1955).

author. Often it is left unclear what characters and assumptions have been used. Thus, homology statements represent hypotheses that are not being tested by character congruence. Chernyshev (1992a) suggested some evolutionary considerations on the origin and relationships of the family Armaueriidae. However, some of his arguments are typical of non-phylogenetic systematists; e.g., he claims close relationship of the

Nectonemertidae and Armaueriidae on the basis of shared plesiomorphies.

It is necessary to mention that systematics of pelagic nemerteans is greatly hampered by the mutilated condition of most of the type and voucher material. As individuals are sparsely distributed in the ocean and difficult to collect, 51 out of 98 species descriptions are based upon single specimens. Only 17 species are represented by 5 or more specimens (Table 1). As is the case with most of the delicate meso- and bathypelagic organisms, pelagic nemerteans become badly disfigured and damaged during the trip to the surface in a trawl net packed with crustaceans and fish. The epidermis, containing a number of important characters (Roe & Norenburg, 2001), is often completely lost. Information on the external appearance of living or very well-preserved (in formalin) specimens is almost essential in taxonomy of these nemerteans, but it is unavailable for most of the described species. Most specimens studied by specialists were preserved at sea in bulk fixations of large unsorted collections. Appropriate handling and fixation of the specimens requires special attention and is optimally performed by a nemertean specialist on board of the research vessel (Roe & Norenburg, 1999).

A collection of specimens exceptional in diversity and good condition was recently obtained off the shores of Hawaii and California (Roe & Norenburg, 1999). As many as 76 putative species were collected, most of which are yet to be identified or described. This material enabled many important observations on the morphology, reproductive biology and distribution of pelagic nemerteans (Norenburg & Roe, 1998a, b; Roe & Norenburg, 1999, 2001) and provides new opportunities for insights into the phylogeny and classification of the group.

This study falls in a row of recent phylogenetic studies on various nemertean groups (Sundberg 1989a, b, 1990; Sundberg & Hylbom, 1994; Härlin & Sundberg, 1995; Sundberg & Saur, 1998) and represents a first and preliminary cladistic analysis of the relationships of genera and species in the Pelagica. The analysis is based on the morphological characters available from the primary literature and personal observations. We discuss characters previously used in systematics of pelagic nemerteans and propose a number of new potentially informative characters.

Materials and methods

Of the 98 valid species of pelagic nemerteans (Table 1) scored for the characters, 83 were included in the analysis. A data matrix was constructed in MacClade 3.08 (Maddison & Maddison, 1992) (Appendix 1). Because a large amount of missing entries would result in an overwhelmingly large number of maximum parsimonious trees (MPT) and, consequently, lack of resolution on the consensus tree, we excluded species that had more than 50% of missing entries. We also applied MacClade option "search for and merge potentially equivalent taxa," which eliminated taxa that can not be distinguished on the basis of scored characters. Potential differences hidden in the missing entries provides no additional resolution to the consensus tree, but increases the number of calculations. Fifteen species excluded from the analysis are: *Balaenanemertes lata* Brinkmann 1917, *Balaenanemertes chavesi* (Joubin, 1906), *Bathynemertes alcocki*, *Crassonemertes rhomboidalis* (Joubin, 1906), *Cuneonemertes obesa* Coe, 1954, *Dinonemertes arctica* Korotkevitsch, 1977, *Dinonemertes grimaldii* (Joubin, 1906), *Gelanemertes richardi* (Joubin, 1906), *Mononemertes sargassicola* (Joubin, 1906), *Nectonemertes japonica* Foshay, 1912, *Parabalaenanemertes zonata* (Joubin, 1906), *Planktonemertes vanhoeffeni* Brinkmann, 1915–16, *Probalaenanemertes irenae* Wheeler, 1934, *Chuniella elongata* (Joubin, 1906), and*Zinarmaueria platonovae* Chernyshev, 1992. Recent phylogenetic analysis of the phylum (Norenburg, unpubl. obs.) shows Pelagica as the most basal hoplonemertean group, with hoplonemerteans a likely sister to heteronemerteans. The former basal position of Pelagica is suspect because of the overall simple morphology. For outgroups we chose the heteronemertean *Baseodiscus* and the palaeonemertean *Carinoma*, both certain to be outside of the hoplonemertean clade. The ingroup was treated as monophyletic; the outgroup as a basal polytomy.

The analysis is based on 30 morphological characters (Table 2). Species data are mostly compiled from the primary literature. Type and voucher material was studied whenever available (Appendix 2). All characters were parsimony informative, unordered and equally weighted.

Heuristic parsimony search was performed in PAUP*4.0b3a (Swofford, 1993), using the TBR branch swapping algorithm with maximum number of trees to be saved set to 25 000, and random addition sequence (1000 replicates with 5 trees held at each step).

Table 2. Characters and character states as used in the analysis

Character	Character states	Coding
1. Body shape	rounded	0
	broad and flat	1
2. Body	translucent	0
	opaque	1
3. Tail fin	absent	0
	indistinct	1
	well developed	2
4. Tentacles	absent	0
	present in males	1
	present in both sexes	2
5. Mouth and proboscis opening	united	0
	separate	1
6. Lateral body wall muscles	rudimentary	0
	well developed	1
7. Position of the lateral nerve cords	close to the body wall	0
	deep in 'parenchyma'	1
8. Lateral nerve cord muscles	absent	0
	present	1
9. Dorsal blood vessel: length	ends blindly in the foregut region	0
	reaches posterior end of the body	1
10. Dorsal blood vessel	does not enter rhynchocoel	0
	enters rhynchocoel	1
11. Cephalic blood vessel	absent	0
	present	1
12. Rhynchocoel wall muscles	interwoven	0
	outer circular/inner longitudinal	1
	outer circular/longitudinal/inner circular	2
	outer longitudinal/inner circular	3
13. Rhynchocoel length	equal to body length or slightly shorter	0
	much shorter (equal or less than 2/3 of body length)	1
14. Caecal diverticula	none or 1–3 pairs	0
	more than 3 pairs, non-branched	1
	more than 3 pairs, profoundly branched	2
15. Number of pairs of intestinal diverticula	fewer or equal 20	0
	more than 20	1
16. Intestinal diverticula: density	densely packed	0
	widely separated by 'parenchyma'	1
17. Intestinal diverticula: branching	simple or only slightly lobed	0
	branched	1
18. Ventral branch of intestinal diverticula	absent	0
	rudimentary	1
	well developed	2
19. Dorsal intestinal diverticula	meet above rhynchocoel	0
	do not meet above rhynchocoel	1
20. Intestinal diverticula	extend laterally beyond nerve cords	0
	do not extend	1
21. Anterior intestinal diverticula	reach brain	0
	do not reach brain	1

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Table 2. contd.

Character	Character states	Coding
22. Arrangement of testes	rows of testes reach to posterior end	0
	rows or clusters of testes limited to the anterior part of the body	1
23. Testes, if anteriorly arranged	in dense clusters in front or besides the brain	0
	in more or less regular rows, reaching posterior to the brain	1
24. Nephridia	present	0
	absent	1
25. Sex	sexes separate	0
	hermaphroditic	1
26. Testes opening via	simple pores	0
	raised glandular papillae	1
	terminal pores on 'phalli'	2
27. Band-shaped organs	absent	0
	present	1
28. Modified lateral epithelium	absent	0
	present	1
29. Postero-lateral glandular organs	absent	0
	present	1
30. 'Rudimentary eyes'	absent	0
	present	1

Due to the large number of missing entries (21.5%) in the data matrix, the number of maximum parsimonious trees of length 186, found during the first replicate, exceeded 25 000 and the search was terminated. In order to obtain MPTs from different replicates, we conducted a new search (1000 replicates, 5 trees held at each step) with a limit of 1000 trees saved per each replicate limited to 1000. After 255 replicates of random addition, 12 000 MPTs were collected, at which point we terminated the search and computed Strict and Adams consensus in order to summarize the information. On the request of a referee we conducted another parsimony analysis with the genera and families of the current classification (Table 1) constrained to be monophyletic in order to compare the length of the resulting trees with maximum parsimonious trees. We use branch length as simple indicator of the clade support. Of all currently available sophisticated methods of estimating clade support, i.e. bootstrap, jack-knife and Bremer support (Bremer, 1994), the latter seems to be the least flawed and provides a useful general guide (Kitching et al., 1998). However, Bremer support only makes sense when all the MPTs are collected followed by the trees that are one step longer, two steps longer, etc. Calculating Bremer support is impractical with hundreds of thousands of MPTs, especially considering that the number of near parsimonious trees rapidly increases with length. In these conditions, it is very likely to overestimate support.

Results

Analysis resulted in 12 000 MPTs ($L = 186$; CI = 0.20; RI = 0.74; RC = 0.15). Strict ($L = 468$, CI = 0.08, RI = 0.03; RC = 0.02) and Adams ($L = 238$, CI = 0.16, RI = 0.65, RC = 0.10) consensus of these cladograms are presented in Figures 3 and 4, respectively. Sixteen clades are retained on the strict consensus cladogram. However, only two correspond to traditional groupings: Pelagica and Armaueriidae (Fig. 3). The rest of the retained clades do not correspond to any traditionally or recently hypothesized groupings, which is why we leave them out of discussion until more studies can be done. Constrained analysis of the current classification (Table 1) resulted in 25 000 equally parsimonious trees at which point we terminated the search. Resulting trees were 48 steps longer ($L = 234$)

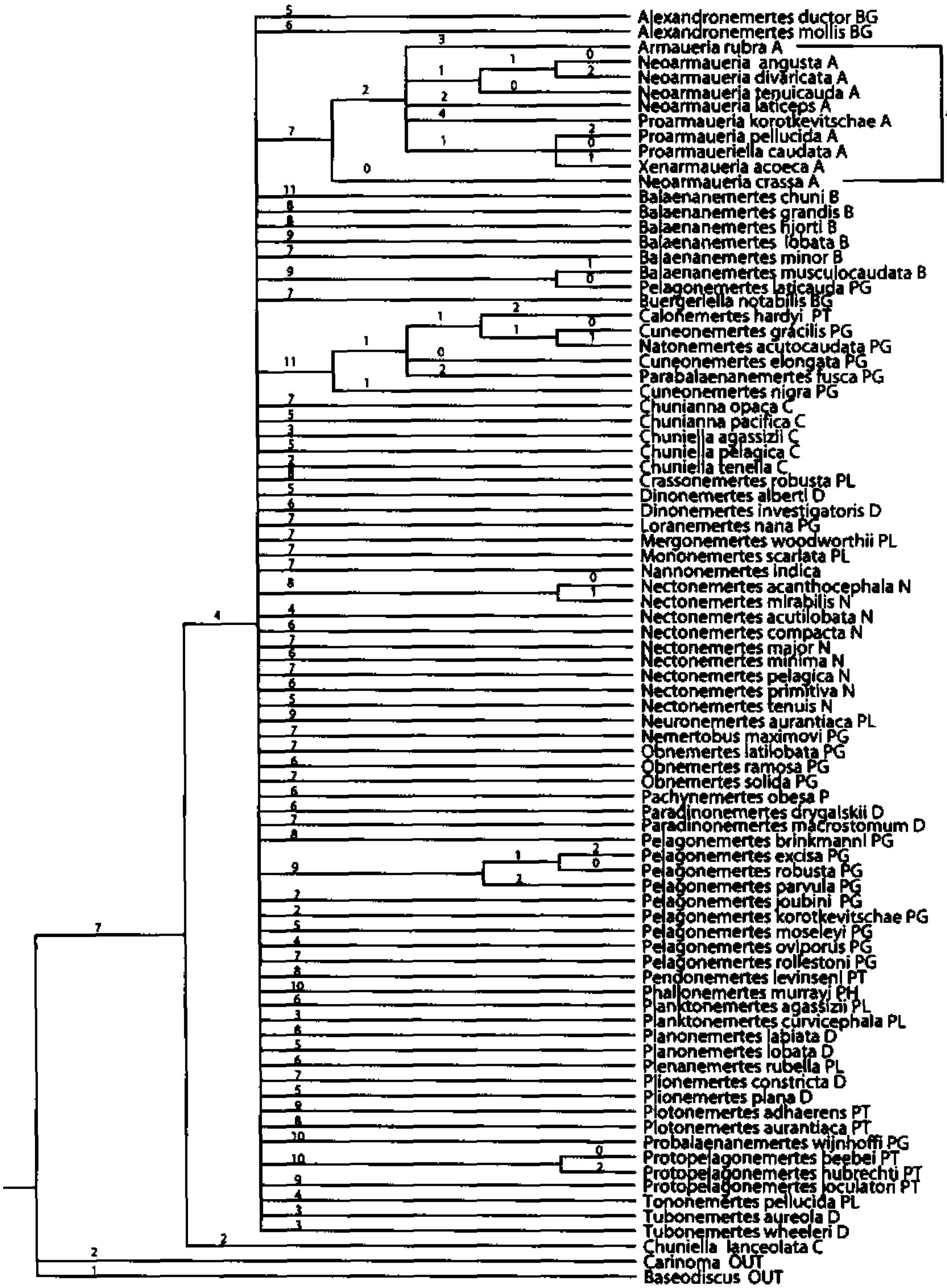

Figure 3. Strict consensus of 12 000 MPTs. L = 468, CI = 0.08, RI = 0.03; RC = 0.02. Branch length values above the branches. A – Armaueriidae, B – Balaenanemertidae, BG – Buergeriellidae, C – Chuniellidae, D – Dinonemertidae, P – Pachynemertidae, PG – Pelagonemertidae, PH – Phallonemertidae, PL – Planktonemertidae, PT – Protopelagonemertidae.

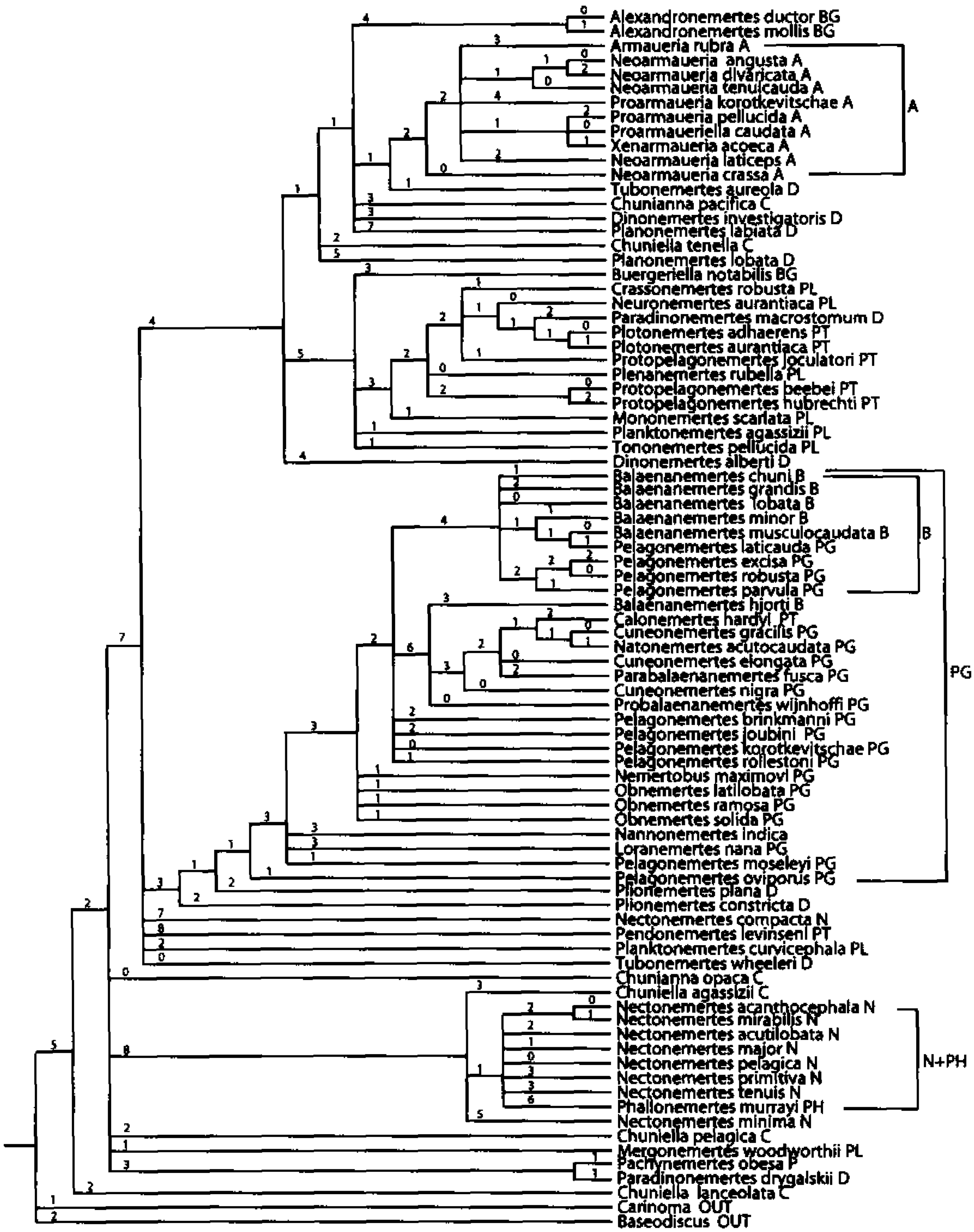

Figure 4. Adams consensus of 12 000 MPTs. L = 238, CI = 0.16, RI = 0.65, RC = 0.10. Branch length values above the branches. A – Armaueriidae, B – Balaenanemertidae, BG – Buergeriellidae, C – Chuniellidae, D – Dinonemertidae, P – Pachynemertidae, PG – Pelagonemertidae, PH – Phallonemertidae, PL – Planktonemertidae, PT – Protopelagonemertidae.

than maximum parsimonious trees resulting from the unconstrained analysis.

Discussion

Pelagica

Two major clades that remain in the strict consensus and correspond to the traditional groupings are Pelagica and Armaueriidae (Fig. 3). Only one prior study employed cladistic analysis to address monophyly of Pelagica (Sundberg, 1990). That analysis included one representative from each family and was based on 34 morphological and 1 ecological characters. Seven of those characters represent autapomorphies and, therefore, are parsimony uninformative. Although Pelagica comes out as a monophyletic group on the strict consensus tree, there are only four synapomorphies for this clade: (1) pelagic habitat; (2) alimentary canal: 'other' (i.e., not 'simple,' not with 'dolliiform foregut,' and not with 'oesophagus, stomach, pylorus, and intestinal region'); (3) gonads 'not in the intestinal region;' and (4) testes close, or in front of brain even when female gonads are in intestinal region. However, characters (3) and (4) refer to the same feature, while it is unclear what exactly is the uniting feature of character (2).

Seven characters support monophyly of Pelagica in our analysis (Fig. 3). Homoplastic characters include translucent body (2); rudimentary muscles of the lateral body wall (6) branched intestinal diverticula (17); presence of postero-lateral glands (29); and presence of modified lateral epithelium (28). The latter two are 'epithelial' characters, and cannot be scored for many taxa, because the epithelium is missing. Moreover, character 28 has been defined only recently (during this study) and is missing from descriptions, as people have not been looking for it, even where the material allowed its observation. Similarly, character 29 was known from only two species prior to the recent observations of Roe & Norenburg (2001) that suggest a much wider distribution. We hypothesized the presence of the postero-lateral glands in all the species of *Balaenanemertes*, *Pelagonemertes*, *Cuneonemertes* and *Probalaenanemertes* based on these observations. Characters 28 and 29 have only been scored for very few taxa (Appendix 1), which left question marks for the majority of the taxa and freedom for the cladistic algorithm to make assumptions. In existing cladistic programs, missing entries are assigned one or the other state, whichever minimizes the length of the tree. Thus, for our data it was most parsimonious to assign all the pelagic nemerteans with a state of 'present' for 'modified epithelium' and 'postero-lateral organs,' a solution that we think improbable. Anteriorly arranged testes (22) and absence of nephridia (24) are the two non-homoplastic characters supporting Pelagica. As we did not include any non-pelagic hoplonemerteans in the analysis, the question of monophyly of the group needs further investigation, although preliminary molecular data (unpubl. obs.) support monophyly.

Armaueriidae

The original diagnosis of the family, provided by Brinkmann (1917b), follows: "Forepart of the body broad, the posterior end tapered and ending in a feebly developed caudal fin. The intestinal diverticula without a ventral branch. The dorso-median blood vessel developed in its full length, but at no place being in connection with the proboscis sheath. Dorsal commissure of the vessels in the head lacking. Testicles arranged in two almost regular rows in the head, never united to groups." Korotkevitsch's diagnosis (Korotkevitsch, 1955) mostly agrees with the original one and includes additional characters: small stomach with slightly folded walls, number of intestinal diverticula pairs does not exceed 25; anterior 4–7 pairs without lobes, inflated distally; ovaries regularly alternate with intestinal diverticula; testes are in groups or rows in the brain area; body rarely exceeding 2 cm in length. Chernyshev (1992a) diagnosed the family in a different way: "Small pelagic nemerteans with broad body. Parenchyma well developed. Number of intestinal diverticula does not exceed 30 pairs. Rhynchocoel 1/3–2/3 of body length. Rhynchocoel wall comprised of 2–3 layers. Dorsal blood vessel does not enter rhynchocoel; cephalic blood vessel is missing. Brain commissures pass through the rhynchocoel wall. Lateral nerve cords with muscle fibers. Some species possess band-shaped organs. Testes are in longitudinal rows in the anterior third of the body" (trans. by SM). N.B.: "brain commissures passing through the rhynchocoel wall" also can be described as the radial muscle fibers that form the proboscis insertion overlapping the brain commissures on the way to the body wall. This is a characteristic of all hoplonemerteans but in pelagic forms it is especially evident that these radial muscles are continuous with the inner longitudinal musculature of the rhynchocoel (Norenburg & Roe, 1998b). Similarly, "ovaries regularly alternating with intestinal diverticula" (Korotkevitsch, 1955) is characteristic of most nemerteans. Degree of development of parenchyma is a continuous character that has not been separated into clearly defined states. We suggest that these characters are not diagnostics for the family.

Seven characters support monophyly of the family Armaueriidae (Fig. 3) in this analysis. The only non-homoplastic character is absence of contact between the dorsal blood vessel and rhynchocoel wall (10). This is a unique situation among Pelagica and exceptionally rare among other nemerteans. Most palaeonemerteans lack a dorsal blood vessel; hence, they lack the connection. Lack of this connection has also been reported for *Hubrechtia* (Bürger, 1895), *Paramicrura* (Gibson & Sundberg, 1992) and two species of *Hubrechtella* (Gibson, 1979). Six homoplastic characters support Armaueriidae: rhynchocoel wall comprised of inner circular, longitudinal and outer circular muscle layers (12); presence of nerve cord muscles (8); rhynchocoel equal or less than 2/3 of body length (13); non-branched intestinal diverticula (17); absence of cephalic blood vessel (11); and presence of band-shaped organs (27). The latter two have high character consistency indexes (ci = 0.5), implying that there is only one other origin or reversal elsewhere on the cladogram. Absence of the cephalic blood vessel also was reported for *Nannonemertes indica* Wheeler, 1937(Wheeler, 1937). However, the description is based on a single poorly preserved specimen, and the cephalic blood vessel could have been easily overlooked. Korotkevitsch (1955) mentions that she could not find the cephalic commissure in a few other species of pelagic nemerteans; e.g. *Nectonemertes acanthocephala* Korotkevitsch 1955, *Pelagonemertes robusta* Korotkevitsch, 1955 and *Pelagonemertes laticauda* Korotkevitsch 1955, each represented by a single poorly preserved specimen. We scored the cephalic blood vessel as present in each. In Armaueriidae, the cephalic blood vessel cannot be distinguished in any of the specimens – even on well-preserved and stained material, thus we consider this character a 'good' synapomorphy of Armaueriidae. Presence of so-called band-shaped organs is another striking characteristic of the family. Initially these organs were described only for the species of the genera *Neoarmaueria* and *Proarmaueriella* (Korotkevitsch, 1955; Chernyshev, 1992a). Our study revealed the presence of these organs in the type species of the family, *Armaueria rubra* Brinkmann, 1917, as well as all the other armaueriid species, except *Proarmaueria korotkevitschae* Chernyshev, 1992. Sections of a single specimen currently referred to the latter species are in very bad condition. We hypothesize presence of band-shaped organs in *P. korotkevitschae* and consider them a synapomorphy of the family. Our investigation of recently collected specimens of *Proarmaueria pellucida* Coe, 1926 showed presence of a pair of very small epithelial glandular organs, situated on ventral side of posterior part of the body and resembling those of Pelagonemertidae (Roe & Norenburg, 2001). Upon reinvestigating the type material of other armaueriid species, we found these organs in every specimen in which epidermis of the appropriate part of the body has remained intact. Armaueriid species in which we found postero-lateral glandular organs include *A. rubra*, *Neoarmaueria angusta* (Korotkevitsch, 1955) and *P. pellucida*. We hypothesize presence of these organs in all species of the Armaueriidae. To date, armaueriid genera were differentiated on the basis of rhynchocoel wall structure, presence or absence of the band-shaped organs and accessory nerve cord. Our reinvestigation of the type and voucher material showed that (1) band-shaped organs are present in all genera of Armaueriidae; (2) all armaueriid species have a uniform rhynchocoel wall comprised of ICM/LM/OCM and (3) presence of the accessory nerve cord is an unreliable character to differentiate genera, as it is subject to inter- and intraspecific variation (see 'Characters' section). This is supported by the cladistic analysis, which fails to show any genera to be monophyletic. Here we propose an emended diagnosis of the family Armaueriidae.

Diagnosis

Family of small pelagic nemerteans, with known maximum length of 24 mm, diagnosed by following synapomorphies: (1) dorsal blood vessel reaching to posterior end of the body without entering rhynchocoel wall; (2) lack of cephalic blood vessel (precerebral commissure); (3) presence of unique band-shaped organs; (4) rhynchocoel 1/3 to 2/3 of body length; (5) rhynchocoel wall comprised of ICM/LM/OCM; (6) presence of nerve-cord muscles; and (7) non-branched or slightly lobed intestinal diverticula. To distinguish armaueriid species from other pelagic nemerteans, these synapomorhpies can be combined with the following characters: body flattened and moderately transparent; proboscis pore terminally situated and well separated from the mouth; intestinal diverticula lacking ventral branches, never meet above rhynchocoel; number of intestinal diverticula normally not exceeding 25; caecum bears a few (1–3) pairs of lateral diverticula; a pair of very small epithelial glandular organs, resembling those of Pelagonemertidae, situated on ventral side of posterior part of the body; testes arranged in more or less irregular row on each side, starting at brain level and reaching esophagus region; sexes separate or hermaphrodites.

Pelagonemertidae

The Adams consensus tree (Fig. 4) allows some extra observations to be made. A 'traditional' group supported on the Adams consensus tree, in addition to Pelagica and Armaueriidae, is Pelagonemertidae *sensu lato* (Korotkevitsch, 1955) (Fig. 4). Korotkevitsch included family Balaenanemertidae in Pelagonemertidae arguing that the difference in presence/absence of the lateral tentacles and bilobed tail fin is not sufficient to separate the two families. She defined Pelagonemertidae by the following characters: dorsomedial blood vessel ends blindly after entering rhynchocoel in the foregut region; cephalic blood vessel present; so-called 'rudimentary eyes' present in precerebral area; band-shaped lateral organs absent. We use the name Pelagonemertidae *sensu* Korotkevitsch. Cladistic analysis shows that all pelagonemertid species form a monophyletic group (clade PG). The only non-pelagonemertid species included is *Calonemertes hardyi* (Wheeler, 1934) (Protopelagonemertidae). The non-homoplastic character supporting monophyly of the group is rudimentary dorsal blood vessel ending blindly in the foregut area (9), which corresponds to one of the characters traditionally used to define the family (Korotkevitsch, 1955). Rudimentary dorsal blood vessel is a unique situation among nemerteans. Presence of 'rudimentary eyes' appears as a synapomorphy of a subgroup of species within the family: from *Balaenanemertes chuni* Bürger, 1909 to *Pelagonemertes rollestoni* Moseley, 1875 (reading from the top to the bottom of Fig. 4). Presence of the cephalic blood vessel and absence of band-shaped lateral organs are plesiomorphic for the phylum, therefore, can not be used to diagnose a subgroup. Alternative states of these characters are synapomorphies of the family Armaueriidae. Although arrangement of the testes in a pair of dense clusters is not a synapomorphy of the family, it is a very characteristic feature of pelagonemertid species and can be used for rapid identification, as it is readily seen on non-sectioned material. This character appears as one of three synapomorphies of Pelagonemertidae and *Plionemertes* and arises independently only two other times: in *Alexandronemertes* and *Planonemertes labiata* Coe, 1936. An indirect evidence for monophyly of Pelagonemertidae is presence of the postero-lateral glands of similar structure in pelagonemertid genera *Balaenanemertes, Pelagonemertes, Parabalaenanemertes* and *Cuneonemertes*. They have been suggested to be a synapomorphy for an undefined group encompassing these taxa (Roe & Norenburg, 2001). The authors make no assertion about homology of the posterior glandular structures of the above taxa with respect to those of Armaueriidae and *Plotonemertes* but do imply that the three morphs are distinct (i.e. non-homologous) states. We coded only presence or absence of the postero-lateral glands without regard to differences in structure and position. Due to the large number of missing entries and a very few scored 'absences' (Appendix 1), the computer algorithm assumed the state 'present' for postero-lateral glands for most of the terminals, which resulted in presence of the postero-lateral glands being a synapomorphy of all pelagic nemerteans. An alternative analysis (unpubl. obs.), with the character split into four states (0 – absent, 1 – pelagonemertidae type, 2 – armaueriidae type, 3 – plotonemertes type) supports the hypothesis (Roe & Norenburg, 2001) that these states are distinct and independent. Again, due to the large amount of ambiguity in the data and most 'observed' taxa scored as possessing pelagonemertidae-type of postero-lateral organs, the latter appears as the inferred plesiomorphic state for pelagic nemerteans, from which armaueriidae-type and plotonemertes-type evolve. We believe that Pelagonemertidae is a monophyletic group; however, we prefer to leave it undiagnosed until more synapomorphies are recognized.

Balaenanemertes, Nectonemertes and Phallonemertes

None of the other traditionally defined families of pelagic nemerteans appears as monophyletic (Fig. 4). Some 'support' is evident for the genera *Nectonemertes* and *Balaenanemertes*. Species of *Nectonemertes* (except for *N. minima* Brinkmann, 1915–16 and *N. compacta* Korotkevitsch, 1964) together with *Phallonemertes murrayi* (Brinkmann, 1912) form a monophyletic group (clade N + PH) supported by a single homoplastic character: presence of rudimentary ventral branch of intestinal diverticula (18). Monophyly of the group including clade N + PH, *N. minima* and *Chuniella agassizii* (Bürger, 1909) is supported by eight homoplastic characters: broad, flat and translucent body (1, 2), presence of well-developed tail fin (3), presence of lateral tentacles in males (4), rhynchocoel musculature consisting of OCM/ILM layers (12), more than two pairs of profoundly branched caecal diverticula (14), branched intestinal diverticula (17), testes opening via raised glandular papillae (26). The last character reverses to 'simple pores' in *Nectonemertes primitiva* Brinkmann, 1917 and develops into 'phalli' in *P. murrayi*. 'Openings on glandular papillae' arises independently from inferred plesiomorphic 'simple pores' three more times on the cladogram: *Parabalaenanemertes fusca* Brinkmann, 1917; *Planonemertes labiata*; and the 'balaenanemertid' clade (B), which includes *Pelagonemertes excisa* Korotkevitsch, 1955, *P. robusta*, *P. laticauda*, *P. parvula* Korotkevitsch, 1964 and all the species of *Balaenanemertes*, except *B. hjorti* Brinkmann, 1917. Four homoplastic characters support clade B (Fig. 4): testes open through glandular papillae (26), branching of intestinal diverticula (17), presence of tentacles in both sexes (4) and presence of well-developed tail fin (3).

Characters

Here we consider some characters that have not been discussed in the previous sections. The structure of the rhynchocoel wall (12) was of special interest to us. Although this character is always a part of the species description and often is given a lot of weight in the systematics of pelagic nemerteans (Brinkmann, 1917a; Coe, 1926; Korotkevitsch, 1955) our analysis shows it as highly homoplastic (Fig. 5) with each of the four states evolving two to many times within the group. Upon request of the referee, we conducted parsimony analysis constrained to make this character non-homoplasious in order to see how many additional steps it takes. Trees resulting from the constrained analysis were 22 steps (L=208) longer. We suggest several possible explanations for the observed high level of homoplasy: (1) true homoplasy, (2) misinterpretation of the state in the literature and (3) 'misplacement' of taxa due to the large number of ambiguities in the data matrix. While the structure of the rhynchocoel wall usually is relatively easy to interpret and score for other hoplonemerteans, there seems to be extensive variation among pelagics, with, apparently, all having some degree of interweaving. Interpretation and coding based on literature appears to be a major problem at this time, as was vividly demonstrated for Armaueriidae by Norenburg & Roe (1998b). Several additional characters, traditionally used in the systematics of pelagic nemerteans cause a great deal of confusion. For example, structure of the intestinal caecum, usually reconstructed from sections, might be interpreted in three different ways by three independent researchers (unpubl. obs.). In scoring quantitative continuous characters, it often is unclear how many and what character states should apply. This group of characters includes number of intestinal and caecal diverticula, body shape and length of the rhynchocoel. Presence of the accessory nerve cord was traditionally used in systematics of Pelagica. However, our study showed that this is a quantitative character, as is the case in several other hoplonemertean groups (unpubl. obs.). The accessory nerve cord might be well-developed in the anterior part of the body and completely disappear towards the posterior. Among presumed conspecific specimens some might have a distinct accessory nerve, while others lack it completely. Although we initially scored this character, we decided to exclude it from the analysis. A few characters used in the analysis could be somewhat refined or subdivided into several independent characters in the future; e.g., position of the lateral nerve cord muscles relative to the nerve cords can vary between taxa. However, lack of this information in the descriptions of most of the taxa does not allow to score it.

Finally, we would like to suggest a few characters that might be useful in the systematics of pelagic nemerteans. Some species of pelagic nemerteans are known to have nurse cells surrounding maturing oocytes, as was described by Norenburg & Roe (1998a). It is yet to be shown whether this is universal and how much variation occurs among the pelagic nemertean species. We suggest that number of nurse cells per oocyte and number of oocytes per ovary might also be useful, if these characters can be found to have clearly defined states. Study of recently collected, well-preserved and stained material provided several new 'epidermal' characters: presence/absence of postero-lateral glands, anterior epidermal gland specialization (Roe & Norenburg, 2001) and a glandular zone around the gonopores (Norenburg & Roe, 1998a). As morphological studies progress we should expect to discover various details of these structures that could help us to resolve the phylogeny of Pelagica.

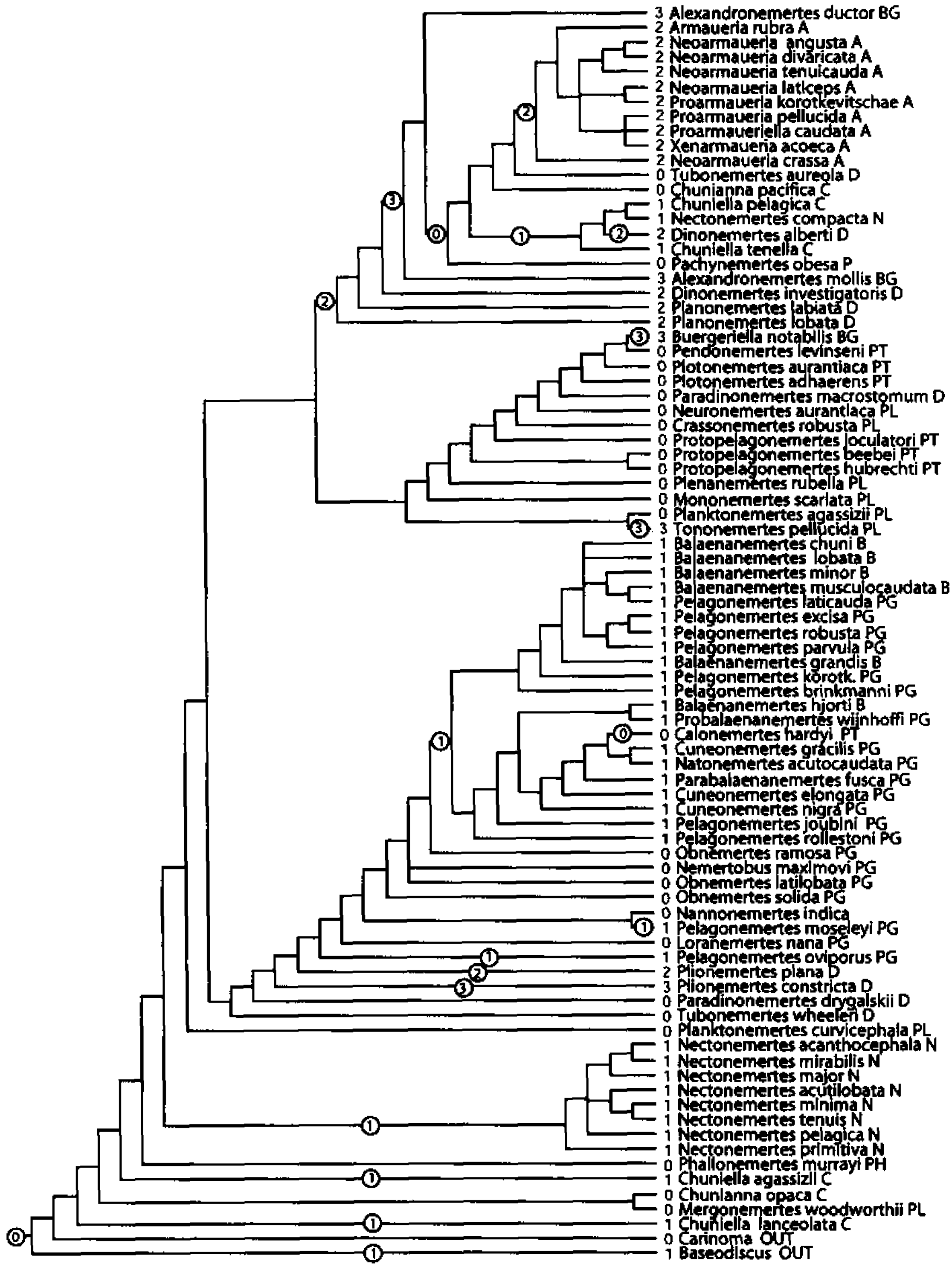

Figure 5. Changes of character 12 (rhynchocoel musculature) on one of 12 000 MPTs. 0 – interwoven, 1 – OCM/ILM, 2 – OCM/ILM/ICM, 3 – OLM/ICM. Inferred plesiomorphic state is 0.

Conclusions

The biggest problem encountered was a large amount of ambiguity in the data matrix due to incompleteness of descriptions. In many cases, type and voucher material need to be reinvestigated. Characters traditionally used in the literature are insufficient to resolve the relationships between pelagic nemerteans. Additional morphological and molecular studies are essential to uncovering new characters. Studies of recently obtained material (Norenburg & Roe, 1998a, b; Roe & Norenburg, 1999, 2001) provided a range of new potentially informative characters that are yet to be incorporated into analysis of the phylogeny of Pelagica. Monophyly of Pelagica, although supported in the preliminary analysis, needs further investigation. Two traditional families, supported by cladistic analysis are Armaueriidae Brinkmann, 1917 and Pelagonemertidae *sensu lato* (Korotkevitsch, 1955). Some support is evident for the genera *Nectonemertes* and *Balaenanemertes*. Future studies need to be focused on the morphology and relationships within these presumably monophyletic groups of pelagic nemerteans.

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Appendix 1. Data matrix used in the analysis. '?' missing data, '-' inapplicable character state. See Figure 3 for explanation of abbreviations.

											1	1	1	1	1	1	1	1	1	2	2	2	2	2	2	2	2	2	2	3
	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8	9	0
Alexandronemertes ductor BG	1	?	1	0	1	?	0	?	?	?	?	3	1	0	1	0	0	1	1	0	0	1	0	1	0	?	?	?	?	?
Alexandronemertes mollis BG	1	1	1	0	1	0	1	0	1	1	1	3	1	0	1	0	0	1	1	0	0	1	?	1	0	?	?	?	?	?
Armaueria rubra A	0	1	1	0	1	0	0	1	1	0	0	2	2	0	1	0	0	0	1	0	0	1	1	1	0	0	1	1	1	0
Balaenanemertes chuni B	1	0	2	2	1	0	0	1	0	-	1	1	1	0	0	1	0	0	1	0	0	1	0	1	0	1	?	?	1	1
Balaenanemertes grandis B	1	0	2	2	1	0	?	1	0	1	1	1	0	0	0	?	1	0	0	0	0	1	0	1	0	1	?	?	1	?
Balaenanemertes hjorti B	1	0	2	2	?	0	1	0	0	1	1	1	1	0	?	?	1	2	0	0	0	1	0	1	0	?	?	?	1	?
Balaenanemertes lobata B	1	0	2	2	1	0	0	1	0	1	1	1	0	0	0	1	0	0	1	0	0	1	0	1	0	1	?	?	1	?
Balaenanemertes minor B	1	0	2	2	1	0	0	1	0	1	1	1	2	0	0	0	0	0	?	0	0	1	?	1	0	?	?	?	1	?
Balaenanemertes musculocaudata B	1	0	2	2	1	0	0	1	0	1	?	1	0	0	0	0	?	1	1	0	0	1	0	1	0	1	?	?	1	1
Buergeriella notabilis BG	0	?	0	0	1	0	1	0	1	1	1	3	0	2	1	0	1	2	0	0	0	1	1	1	0	0	?	?	?	?
Calonemertes hardyi PT	0	1	0	0	1	1	1	?	?	1	?	0	0	?	?	?	1	1	1	0	0	1	?	1	0	?	?	?	?	?
Chuniania opaca C	0	1	0	0	1	0	0	0	1	1	1	0	0	1	1	0	0	0	0	0	?	1	?	1	0	?	?	?	?	?
Chuniania pacifica C	1	1	1	0	1	0	0	0	1	1	1	0	1	?	1	1	0	0	1	0	?	1	1	1	0	?	?	?	?	?
Chuniella agassizii C	0	0	0	0	1	0	0	0	1	1	1	1	0	2	1	0	1	0	?	0	0	1	1	1	0	?	?	?	?	?
Chuniella lanceolata C	0	?	0	0	1	0	0	0	1	1	1	1	0	1	1	0	1	0	0	1	1	1	1	1	0	0	?	?	?	?
Chuniella pelagica C	0	1	0	0	1	0	0	?	1	1	1	1	1	?	?	0	?	?	0	0	0	1	?	1	0	?	?	?	?	?
Chuniella tenella C	1	1	1	0	1	0	0	0	1	1	1	1	0	?	1	?	0	0	1	0	?	1	1	1	0	0	?	?	?	?
Crassonemertes robusta PL	0	?	1	0	1	1	1	0	1	1	1	0	0	2	1	0	1	2	0	0	1	1	1	1	0	0	?	?	?	?
Cuneonemertes elongata PG	0	?	0	0	1	1	1	1	0	1	1	1	0	0	0	?	1	2	0	0	0	1	?	1	0	0	?	?	1	?
Cuneonemertes gracilis PG	0	1	0	0	1	1	0	1	0	1	1	1	0	0	0	0	1	1	0	0	0	1	0	1	0	0	?	?	1	1
Cuneonemertes nigra PG	0	1	0	0	1	0	1	1	0	1	1	1	0	0	0	1	1	2	0	0	0	1	?	1	0	?	?	?	1	?
Dinonemertes alberti D	1	1	1	0	1	0	0	?	1	1	1	2	1	0	1	0	1	0	0	0	1	1	1	1	0	?	?	?	?	?
Dinonemertes investigatoris D	1	0	2	0	1	0	1	?	1	1	1	2	1	0	1	0	0	1	1	0	?	1	1	1	0	?	?	?	?	?
Loranemertes nana PG	1	0	0	0	1	0	0	?	0	1	1	0	0	0	0	1	0	0	1	0	1	1	?	1	0	?	0	?	?	0
Mergonemertes woodworthii PL	0	?	0	0	1	0	0	0	1	1	1	0	2	1	1	0	0	0	0	0	0	1	?	1	0	?	?	?	?	?
Mononemertes scarlata PL	1	1	1	0	0	0	1	0	1	1	1	0	0	2	1	0	0	2	1	0	0	1	1	1	0	0	?	?	?	?
Nannonemertes indica	0	?	1	?	1	0	1	0	0	?	0	0	0	?	?	?	1	0	1	1	1	1	?	1	0	?	?	?	?	?
Natonemertes acutocaudata PG	0	?	0	0	1	0	0	1	0	1	?	1	0	0	0	?	1	1	0	0	?	1	0	1	0	?	?	?	?	1
Nectonemertes acanthocephala N	0	1	2	?	1	?	?	?	1	1	?	1	0	?	1	0	?	?	?	?	?	1	1	1	0	?	0	?	?	0
Nectonemertes acutilobata N	1	1	2	?	1	0	0	0	1	1	1	1	0	2	1	0	1	0	0	0	?	1	?	1	0	?	0	?	?	0
Nectonemertes compacta N	0	1	1	0	1	0	0	0	1	1	1	1	1	0	1	0	0	0	0	1	?	1	1	1	0	?	0	?	?	0
Nectonemertes major N	0	0	2	1	1	0	0	?	1	1	1	1	0	2	1	0	1	1	0	0	?	1	1	1	0	1	0	?	?	0
Nectonemertes minima N	1	0	2	1	1	0	1	0	1	1	1	1	0	0	1	0	0	0	1	1	0	1	1	1	0	1	?	?	?	?
Nectonemertes mirabilis N	0	1	2	1	1	0	0	0	1	1	1	1	2	2	1	0	1	1	0	0	0	1	1	1	0	1	?	?	?	?
Nectonemertes pelagica N	1	0	2	1	1	0	0	0	1	1	1	1	0	2	1	0	1	1	0	0	0	1	1	1	0	1	0	1	0	0
Nectonemertes primitiva N	1	0	2	1	1	0	0	0	1	1	1	1	0	2	1	1	1	1	?	1	0	1	1	1	0	0	?	?	?	?
Nectonemertes tenuis N	1	0	2	1	1	0	0	0	1	1	1	1	0	1	1	0	0	0	0	0	?	1	1	1	0	?	0	?	?	0
Neoarmaueria angusta A	0	0	0	0	1	0	0	1	1	0	0	2	1	0	0	0	0	0	1	0	1	1	?	1	0	?	1	1	1	0
Neoarmaueria divaricata A	1	?	0	0	1	?	?	?	?	?	0	2	1	0	0	?	0	0	?	1	1	1	?	1	0	?	1	?	1	0
Neoarmaueria crassa A	1	0	1	0	1	0	0	1	1	0	0	2	1	0	1	0	0	0	1	0	0	1	?	1	0	?	1	1	1	0

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Appendix I. contd.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30
Neoarmaueria laticeps A	1	0	1	0	1	0	0	1	1	0	0	2	1	0	0	1	0	0	1	0	0	1	?	1	0	?	1	1	1	0
Neoarmaueria tenuicauda A	0	?	0	0	1	0	0	1	1	0	0	2	1	0	0	?	0	0	1	0	0	1	1	1	0	0	1	1	1	0
Neuronemertes aurantiaca PL	0	1	1	0	1	1	1	0	1	1	1	0	1	2	1	0	1	2	0	0	0	1	1	1	0	0	?	?	?	?
Nemertobus maximovi PG	1	0	1	0	1	0	1	1	0	1	1	0	0	0	0	1	1	0	1	0	0	1	0	1	0	0	0	?	?	0
Obnemertes latilobata PG	1	0	1	0	1	0	0	1	0	1	1	0	0	0	0	1	1	1	1	0	0	1	0	1	0	0	0	?	?	0
Obnemertes ramosa PG	1	0	0	0	1	0	0	1	0	1	1	0	0	0	0	1	1	0	1	0	0	1	?	1	0	?	0	?	?	0
Obnemertes solida PG	1	0	1	0	1	0	0	1	0	1	1	0	0	0	0	1	1	0	1	0	1	1	0	1	0	0	0	?	?	0
Pachynemertes obesa P	0	1	1	0	1	0	0	0	1	1	1	0	1	?	1	?	0	1	?	?	?	1	?	1	0	?	?	?	?	?
Parabalaenanemertes fusca PG	0	?	1	0	1	1	1	1	0	1	1	1	0	0	0	?	1	2	?	0	0	1	0	1	0	1	?	?	?	?
Paradinonemertes drygalskii D	1	?	1	0	1	0	0	0	1	1	1	0	0	1	1	0	0	1	0	0	1	1	1	1	0	0	?	?	?	?
Paradinonemertes macrostomum D	1	1	2	0	1	1	1	0	1	1	1	0	1	?	1	0	1	1	?	0	0	1	1	1	0	0	?	?	?	?
Pelagonemertes brinkmanni PG	1	0	1	0	1	0	0	1	0	1	1	1	0	0	0	1	0	0	1	0	0	1	0	1	1	0	?	?	1	1
Pelagonemertes excisa PG	0	?	1	2	1	0	0	0	?	?	?	1	0	0	0	1	0	1	1	0	?	1	0	1	0	1	0	?	1	0
Pelagonemertes joubini PG	1	0	0	0	1	0	1	1	0	1	1	1	0	0	0	1	1	0	1	0	0	1	0	1	0	?	?	?	1	?
Pelagonemertes korotkevitschae PG	1	0	1	0	1	0	0	?	0	1	1	1	0	0	0	?	1	0	1	0	0	1	?	1	0	?	?	?	1	?
Pelagonemertes laticauda PG	1	0	2	0	1	0	0	?	0	1	?	1	0	0	0	0	0	1	1	0	0	1	?	1	0	?	0	?	1	1
Pelagonemertes moseleyi PG	1	0	1	0	1	0	1	?	0	1	1	1	0	0	0	1	1	0	1	0	1	1	?	1	0	?	?	?	1	?
Pelagonemertes oviporus PG	1	0	1	0	1	?	1	?	0	1	?	1	0	0	1	?	0	1	1	0	?	1	?	1	0	?	0	?	1	0
Pelagonemertes parvula PG	1	0	2	2	1	0	0	0	0	1	1	1	0	0	0	1	0	0	1	1	1	1	?	1	0	1	0	?	1	1
Pelagonemertes robusta PG	0	0	2	?	1	0	0	?	0	?	1	1	0	0	0	?	0	0	?	?	?	1	?	1	0	?	0	?	1	0
Pelagonemertes rollestoni PG	1	0	0	0	1	0	0	1	0	1	1	1	0	0	0	1	1	0	1	0	0	1	0	1	0	?	?	?	1	1
Pendonemertes levinseni PT	0	?	0	0	1	0	1	1	1	?	1	0	1	0	1	?	1	2	0	0	0	1	?	1	0	?	?	?	?	?
Phallonemertes murrayi PH	0	0	2	0	1	0	0	0	1	1	1	0	1	2	1	0	1	1	0	0	0	1	1	1	0	2	0	0	0	0
Planktonemertes agassizii PL	1	0	0	0	0	0	1	0	1	1	1	0	0	2	1	0	1	2	?	0	0	1	?	1	0	?	?	?	?	?
Planktonemertes curvicephala PL	1	0	1	0	1	0	0	0	1	1	1	0	0	2	1	0	1	1	1	0	?	1	1	1	0	?	0	?	?	0
Planonemertes labiata D	0	0	1	0	1	0	1	0	1	1	1	2	1	2	0	0	1	0	1	0	0	1	0	1	0	1	?	?	?	?
Planonemertes lobata D	1	0	1	0	1	0	1	0	1	1	1	2	0	2	1	1	1	1	1	0	0	1	1	1	0	0	?	?	?	?
Plenanemertes rubella PL	1	1	1	0	0	1	1	0	1	1	1	0	0	?	1	?	1	2	?	0	?	1	?	1	0	?	?	?	?	?
Plionemertes constricta D	1	0	1	0	1	0	1	0	1	1	1	3	0	1	1	0	0	1	1	0	1	1	0	1	0	?	?	?	?	?
Plionemertes plana D	1	0	1	0	?	0	0	0	1	1	?	2	0	?	1	1	0	1	1	0	1	?	?	1	0	?	?	?	?	?
Plotonemertes adhaerens PT	0	1	2	0	1	0	1	0	1	1	1	0	1	2	1	0	1	2	0	0	?	1	1	1	0	0	?	?	1	?
Plotonemertes aurantiaca PT	0	1	2	0	1	0	1	0	1	1	1	0	0	2	1	0	1	2	0	0	?	1	?	1	0	?	?	?	1	?
Proarmaueria korotkevitschae A	0	0	1	0	1	0	1	1	1	0	0	2	2	0	0	1	0	0	1	0	0	1	1	1	0	0	0	1	1	0
Proarmaueria pellucida A	0	0	1	0	1	0	0	?	1	0	0	2	1	0	0	0	1	0	0	0	0	1	1	1	1	0	?	?	1	?
Proarmaueriella caudata A	0	0	1	0	1	0	0	1	1	0	0	2	1	0	0	0	0	0	1	0	0	1	1	1	1	0	1	1	1	0
Probalaenanemertes wijnhoffi PG	0	?	2	0	1	0	1	1	0	1	1	1	1	0	0	?	1	2	0	0	?	1	?	1	0	?	?	?	1	1
Protopelagonemertes beebei PT	1	1	0	0	0	1	1	0	1	1	1	0	0	2	1	0	1	2	0	0	1	1	1	1	0	?	?	?	?	?
Protopelagonemertes hubrechti PT	0	1	0	0	0	1	1	0	1	1	1	0	0	2	1	0	1	2	0	0	1	1	?	1	1	?	?	?	?	?
Protopelagonemertes joculatori PT	0	1	1	0	0	1	1	?	1	1	?	0	0	2	1	0	1	2	0	0	0	1	?	1	0	?	?	?	?	?
Tononemertes pellucida PL	1	0	0	0	1	?	1	0	1	1	1	3	0	?	1	0	1	2	1	0	0	1	?	1	0	?	?	?	?	?
Tubonemertes aureola D	1	0	1	0	1	0	0	?	1	1	1	0	1	?	1	0	0	0	1	0	?	1	?	1	0	?	?	?	?	?
Tubonemertes wheeleri D	1	0	1	0	1	0	0	?	1	1	1	0	0	?	1	0	0	1	1	0	0	1	1	1	0	0	?	?	?	?
Xenarmaueria acoeca A	0	1	1	0	1	0	0	1	1	0	0	2	1	0	0	?	0	0	1	0	0	1	?	1	1	?	1	1	1	0
Baseodiscus OUT	0	1	0	0	1	1	0	0	1	1	1	1	1	-	1	0	0	0	1	1	1	0	-	0	0	0	0	0	0	0
Carinoma OUT	0	1	0	0	1	1	0	1	-	-	1	0	0	-	1	0	0	0	1	1	1	0	-	0	0	0	0	0	0	0

Appendix 2. Sectioned material examined

UBMZ Museum of Zoology of University of Bergen, Norway.
RASZ Zoological Institution of Russian Academy of Science, St.-Peterburg, Russia.
USNM National Museum of Natural History, Smithsonian Institution, Washington DC.

Armaueria rubra Brinkmann, 1917 – type series: 2 males (UBMZ 60100 XIV (11), 60100 XXII (4)) and a female (UBMZ 60100 XIX (12)).
Balaenanemertes sp. '753' – a male USNM.
Balaenanemertes sp. '36' – a male USNM.
Nectonemertes cf. *pelagica* – 15 recently collected specimens: 6 males and 10 females (USNM 174017, 18, 25–38).
N. angusta (Korotkevitsch, 1955) – a female RASZ 224 (lectotype). Since the holotype has not been designated originally and the original description was based on more than one specimen, the term 'holotype' as used by Chernyshev (1992a) is not applicable. We suggest that the specimen should be referred to as lectotype. Second female, mentioned in the original description (RASZ 230) was also used in a description of *M. pellucida* (Chernyshev, pers. com.) and subsequently referred to *Zinarmaueria platonovae* gen. nov. sp. nov. (Chernyshev, 1992a).
N. crassa (Korotkevitsch, 1955) – females: RASZ 233 (lectotype), RASZ 232. Same comment as above applies to the designation of the lectotype here. Korotkevitsch mentioned a single specimen in the original description; however, two specimens are found in her collection.
Neoarmaueria laticeps (Korotkevitsch, 1955) – females: RASZ 226 (lectotype), RASZ 227 and male RASZ 225. Chernyshev (1992a) referred #225 to a different species on the basis of presence of an accessory nerve cord. Although only two specimens (male and a female) were mentioned in the original, apparently, all three specimens contributed to the description. Some pictures in the original publication clearly depict slides of female #227 (Korotkevitsch, 1955, Fig. 46A), while others most likely refer to #226 (Korotkevitsch, 1955, Fig. 45A). Although Korotkevitsch had not published her designation of a type, she labeled #226 as a holotype and included its pictures in her dissertation (Chernyshev, pers. com.). Chernyshev (1992a) designated the latter specimen as a lectotype despite the fact that its caecum differs from that of nos. 225 and 227, and from the original description.
N. tenuicauda (Korotkevitsch, 1955) – a female RASZ 222 (lectotype, subsequently designated by Chernyshev, 1992a), and an immature male RASZ 223.
Phallonemertes murrayi – a male USNM 174021 and a female USNM 174019.
Proarmaueria korotkevitschae Chernyshev, 1992 – a male RASZ 229 (lectotype, subsequently designated by Chernyshev, 1992a). Second specimen from the type series (RASZ 230), labeled as a paratype by Korotkevitsch and mentioned in the original description has also contributed to the description of *M. angusta* Korotkevitsch, 1955 (Chernyshev, pers. com.), and subsequently referred to *Zinarmaueria platonovae* gen. nov. sp. nov. (Chernyshev, 1992a).

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Appendix 2. contd.

Proarmaueria cf. *pellucida* – 13 recently collected specimens: 7 females (USNM 174039, 174043–44, 174047–48, 174050–51), 3 males (USNM 174045–46, 174049) and 3 specimens in which both ovaries and testes were found (USNM 174040–42).

Proarmaueriella caudata (Korotkevitsch, 1955) – specimen RASZ 231, possibly hermaphroditic (holotype, by monotypy). Cells resembling immature oocytes are found in some of the testes; however, poor condition of the slides does not allow clear study.

Protopelagonemertes sp. – a female USNM 174058 .

Xenarmaueria acoeca (Korotkevitsch, 1955) – specimen RASZ 228, possibly hermaphroditic (holotype by monotypy). Cells resembling spermatocytes are found in some of the ovaries.

Zinarmaueria platonovae Chernyshev, 1992 – a female RASZ 230 (holotype by original designation). This specimens was labeled as a paratype of *M. pellucida* by Korotkevitsch and, at the same time, represented a second specimen of the type series of*M. angusta* (Chernyshev, pers. com). Chernyshev (1992a) proposed a new species and genus for this specimen, never mentioning the confusion. Instead, he indicated that the second specimen of *M. angusta* had been lost (Chernyshev, 1992a).