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Character-matrix based descriptions of two new nemertean (Nemertea) species

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Ribbon worms (phylum Nemertea) have traditionally been described and classified based on a combination of internal and external morphological characters. The extent, and wealth of details, of these descriptions vary both over time and amongst authors. In addition, definitions of characters and character states are in many cases vague, causing problems both for identification and in phylogenetic analyses. Here, we suggest a system of describing nemerteans based on a list of characters and their states with the actual description in the form of a vector of character state symbols. We argue that this system makes it easier for other systematists to extract the necessary characters/character states for comparative and phylogenetic analyses. The proposed list of characters can also act as a checklist for nemertean description, whereby hopefully ambiguities (such as does the nonmentioning of a character actually mean 'missing' or just not looked for) can be avoided in the future. We describe two new species and one new genus ***Carinina ochracea* sp. nov.** and ***Raygibsonia bergi* gen.** et **sp. nov.** using this concept in combination with molecular analyses based on 18S and cytochrome oxidase I (COI) DNA sequences.

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ADDITIONAL KEYWORDS: Hoplonemertea – molecular systematics – morphology – Palaeonemertea.

INTRODUCTION

Nemerteans (phylum Nemertea), a group of worm-like mainly marine animals, have few obvious external characters and the morphology-based classification and systematization is essentially based on internal characters. Clearly, the extent and wealth of details of these characters have increased over time as a result of improved technical resources and techniques and because of an increasing awareness of the variation and need for further details to distinguish species. For example, Abildgaard (1806) described *Planaria dorsalis* (now *Oerstedia dorsalis*) in fewer than 30 words (in Latin) – which probably was considered valid and enough at that time considering the knowledge of the taxon in those days. The same species was later redescribed by Stiasny-Wijnhoff (1930) in one of the first more comprehensive anatomical descriptions of a nemertean species. Later, Gibson (e.g. 1973, 1974), alone and in collaboration with other taxonomists (e.g. Gibson, Moore & Crandall, 1982; Gibson *et al.*, 1986; Moore & Gibson, 1993) described nemerteans in a way that more or less became a standard for detailed morphological descriptions. An example of a contemporary follower of this tradition is Kajihara (2006) – the typical description goes through the organ systems in turn and the text is accompanied with sketches or photomicrographs.

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The systematic discussions leading to decisions of new species/new taxa also follow the lines drawn up by Gibson. The author(s) compare the morphology at hand, comparing it with presumably closely related species, or candidate names. One looks for differences, and combinations of characters, not found in other species. Sundberg (1993) has already criticized this practice and we will not reiterate the arguments against this procedure from a systematic/phylogenetic point of view. Instead, in this paper we focus on two other aspects of this tradition.

The first is information retrieval and what is sought from a description. Essentially, it is a matter of finding particular characteristics to be compared with a specimen at hand for identification, or taxonomic/systematic, purposes. To extract this information from a running text can be time-consuming and inexact, especially when descriptions are written as prose instead of an information-dense telegraphic style. The second aspect concerns clarity and unambiguousness. It is not always clear what an author exactly means with a particular character/character state. See, for example, the detailed critique by Moore & Gibson (1993) of two cladistic studies of terrestrial nemerteans by Sundberg (1989a, b). To take another example; Moore & Gibson (1981: table 1) list the character state 'cerebral organs elaborated' as present in *Pantinonemertes winsori* and the two *Geonemertes* species *pelaensis* and *rodericana*. However, when the cladistic analysis in Sundberg (1989a) established this character as a uniting synapomorphy for these species, the conclusion was dismissed by Moore & Gibson because 'the cerebral organs are elaborated in completely different ways' (Moore & Gibson, 1993: 94). There are more examples in Moore & Gibson (1993) clearly showing the need for a standardized approach to morphological descriptions in the systematics of nemerteans.

Here, we suggest and exemplify an approach to nemertean species description which we think has two major advantages over current practice. First, the information is standardized and easily retrieved in a way that facilitates comparisons with other species/taxa and phylogenetic analyses. Especially when several descriptions appear in this format, or are transferred to this format, we will have a good database for adequate phylogenetic analyses – something urgently needed when it comes to current nemertean systematics, which does not reflect evolutionary relationships and where many higher taxa are nonmonophyletic (see discussions in e.g. Sundberg, 1993; Sundberg, Turbeville & Lindh, 2001; Thollesson & Norenburg, 2003). Second, it works like a checklist of what to look for, and to tick, when describing a nemertean. We hope that this study will inspire other taxonomists interested in the group to add/extend characters and refine definitions, and to help in developing a standardized approach to nemertean taxonomy. This idea was also suggested by, for example, Gibson (1985) and Hylbom (1993). Admittedly, our character lists are not complete, and will obviously need amendments with increasing knowledge but we regard this more as a starting point.

The lack of good and consistent species descriptions has also hampered phylogenetic analyses within the phylum, especially when the only option was to base these on morphological characters. Although the number of nucleotide sequences from nemerteans is rapidly increasing, there have been only a few studies explicitly aiming to test the monophyletic status of taxa above the species level (e.g. Strand & Sundberg, 2005). So far, nothing has been published on the monophyletic status of the families in the phylum based on molecular information, although several studies indicate that families such as *Lineidae*, *Amphiporus*, and *Cerebratulus* are nonmonophyletic. In the current situation, it may be advisable to take some care when placing new species and new genera in existing higher taxa, and also to include molecular information when making systematic conclusions. Here we describe two new species, one hoplo- and one palaeonemertean, using the proposed checklist of characters. Systematic conclusions are established on morphological evidence combined with phylogenetic analyses based on 18S rRNA and COI mtDNA gene sequences.

MATERIAL AND METHODS

Samples

Worms were collected from the Swedish west coast by dredging from depths between 4 and 40 m. Specimens of *Raygibsonia bergi* were collected around Kristineberg Marine Research Station in November 2002 and June 2006 by dredging, and specimens of *Carinina ochracea* from around Tjärnö Marine Biological Laboratory in August 2006, both located on the Swedish west coast. Specimens were observed alive, and those for histological examination were fixed in 4% paraformaldehyde in filtered seawater or Bouin's fluid, sectioned at 6 μm and stained by the Mallory trichrome technique for histological examination. Other specimens were preserved in 70–80% ethanol and stored for subsequent DNA extraction using DNeasy (QIAgen, Inc.) following the protocol recommended by the manufacturer.

The phylogenetic analyses below are based on a combination of sequences new for this study, and sequences from GenBank. Table 1 lists species and accession numbers for the analysis based on the 18S

Table 1. List of nemertean species included in the phylogenetic analysis based on 18S rDNA sequences, with accession numbers. Sequences new for this study are marked with asterisk*

Species	Accession number
Amphiporus allucens Bürger, 1895	AY928343
Amphiporus hastatus McIntosh, 1873	AY928344
Antiponemertes novaezealandiae Dendy, 1895	AY928345
Argonemertes australiensis Dendy, 1892	AY928346
Balionemertes australiensis Sundberg *et al.*, 2003	AY238988
Callinera sp.†	EU495305*
***Carinina ochracea* sp.nov.**	EU495306*
Carinina plecta Kajihara, 2006	EU495307*
Carinoma tremaphoros Thompson, 1900	AY039675
Cephalothrix queenslandica Sundberg *et al.*, 2002	AY238989
Cephalothrix rufifrons Johnston, 1837	AY039677
Cerebratulus lacteus Leidy, 1851	AY145368
Emplectonema gracile Johnston, 1837	AY928347
Emplectonema neesii Örsted, 1843	AY928348
Hubrechtella dubia Bergendal, 1902	AY039674
Hubrechtella kimuraorum Kajihara, 2006	EU495308*
Lineus bilineatus Renier, 1804	DQ279932
Lineus ruber Müller, 1774	AY039672
Malacobdella grossa Müller, 1776	AY039670
Nipponnemertes pulchra Johnston, 1837	AY928352
Oerstedia dorsalis Abildgaard, 1806	AY928353
Prostoma graecense Böhmig, 1892	AY039666
Prostoma eilhardi Montgomery, 1894	U29494
***Raygibsonia bergi* gen. et sp. nov.**	AY928351
Tetraneuronemertes lovgreni Sundberg *et al.*, 2007	AY928350
Tetrastemma robertianae McIntosh, 1873–1874	AY928372
Tetrastemma stimpsoni Chernyshev, 1992	AY928376
Tetrastemma vermiculum Quatrefages, 1846	AY928377
Tubulanidae sp‡	EU495309*
Tubulanus annulatus Montagu, 1804	AY210452
Vulcanonemertes rangitotoensis Gibson & Strand, 2002	AY928379
Zygeupolia rubens Coe, 1895	AY039671
Zygonemertes virescens Verrill, 1879	AY928381
Outgroup	
Phoronis australis Haswell, 1883	AF119079
Phoronis hippocrepia Wright, 1856	U08325
Phoronis vancouverensis Pixell, 1912	AY210450

†An undescribed species from Peter the Great Bay, Russia.
‡An undescribed species from Peter the Great Bay, Russia.

Table 2. List of nemertean species included in the phylogenetic analysis of ***Carinina ochracea* sp. nov.** based on COI mtDNA sequences, with accession numbers. Sequences new for this study are marked with asterisks*

Species	Accession number
Callinera grandis Bergendal, 1903	EU489491*
***Carinina ochracea* sp. nov.**	EU489492*
Carinina plecta Kajihara, 2006	EU489493*
Carinoma mutabilis Griffin, 1898	AJ436942
Carinoma tremaphoros Thompson, 1900	AJ436943
Cephalothrix rufifrons Johnston, 1837	EU489494*
Hubrechtella dubia Bergendal, 1902	EU489495*
Cephalothrix filiformis Johnston, 1828	EU489496*
Cephalothrix filiformis Johnston, 1828	AJ436944
Cephalohtrix simulus Iwata, 1952	AJ436945
Cephalothrix spiralis Coe, 1930	AJ436946
Tubulanus annulatus Montagu, 1804	EU489497*
Tubulanus lutescens Cantell, 2001	EU489498*
Tubulanus punctatus Takakura, 1898	AJ436947
Tubulanus rhabdotus Corrêa, 1954	AJ436948
Tubulanus sexlineatus Griffin, 1898	AJ436949
Tubulanidae sp.†	EU489499*
Outgroup	
Emplectonema neesii Örsted, 1843	EU489487*

†An undescribed species from Peter the Great Bay, Russia.

rDNA gene, Table 2 for the palaeonemerteans based on the COI mtDNA gene, and Table 3 for the hoplonemerteans using the same gene.

Amplification and sequencing

Amplification of the 18S rRNA gene was carried out by PCR using a thermal cycler (MJ Research Inc. PTC-100 Programmable Thermal Controller) and eukaryotic specific primers (Medlin *et al.*, 1988; Turbeville, Field & Raff, 1992; Nygren & Sundberg, 2003). The gene was either amplified in one region of approximately 1850 base pairs or in two shorter regions of approximately 1000 base pairs each. PCR was performed with PuRe taq Ready-To-Go pcr beds (GE Healthcare). Thermal cycling was initiated with 1–2 min of denaturation at 94–95 °C followed by 35–60 cycles of 30 s at 94 °C, 1 min at 44–50 °C, and 2 min at 72 °C. After cycling the reaction was ended with an extension phase at 72 °C for 7 min. PCR products were purified with EZNA Cycle-Pure Kit PCR Clean-up (VWR International).

The COI mtDNA gene was amplified using the LCO 1490/HCO 2198 (Folmer *et al.*, 1994) primer combination and the standard recommendations of illustra™ PuReTaq Ready-To-Go PCR Beads kit from GE Healthcare. PCR reactions were run initially at 95 °C

Table 3. List of nemertean species included in the phylogenetic analysis of ***Raygibsonia bergi* gen**. et **sp. nov.** based on COI mtDNA sequences, with accession numbers. Sequences new for this study are marked with asterisks*

Species	Accession number
Amphiporus angulatus Müller, 1774	AJ436896
Amphiporus formidabilis Griffin, 1898	AJ436897
Amphiporus imparispinosus Griffin, 1898	AJ436898
Amphiporus lactifloreus Johnston, 1828	AJ436899
Carcinonemertes sp414	AJ436901
Emplectonema buergeri Coe, 1901	AJ436902
Emplectonema gracile Johnston, 1837	AJ436903
Emplectonema neesii Örsted, 1843	EU489487*
Malacobdella grossa Müller, 1776	AJ436905
Nemertellina yamaokai Kajihara *et al.* 2000	AJ436907
Nemertopsis bivittata Delle Chiaje, 1841	AJ436908
Nipponnemertes punctatula Coe, 1905	AJ436910
Oerstedia sp.†	EU489488*
Ototyphlonemertes sp21	AJ436913
***Raygibsonia bergi* gen. et sp. nov.**	EU489489*
Prostoma graecense Böhmig, 1892	EU489490*
Tetrastemma wilsoni Coe, 1943	AJ436921
Zygonemertes simonae Corrêa, 1961	AJ436922
Zygonemertes virescens Verrill, 1879	AJ436923
Outgroup	
Reptant nemertean sp 500	AJ436930

†A *Oerstedia dorsalis* looking species from Faial, the Azores; genetic analysis (P. Sundberg pers. observ.), however, indicates an undescribed species.

for 5 min, then cycled 40 times with the following programme: 95 °C for 40 s, 45 °C for 45 s, and 72 °C for 1 min, with a final step at 72 °C for 8 min. Completed PCR-reactions were purified with a Qiagen™ Qiaquick Kit.

For both 18S and COI, sequencing was performed by the genetic service facilities of Macrogen (Korea) with the same primer pairs as in the initial PCR procedure for each gene. The primer concentration was in all cases increased to 5 µM during the sequencing procedure.

Alignment

Sequences of the 18S rDNA gene were edited with LASERGENE (DNASTAR Inc.) and aligned in MegAlign using the CLUSTAL W algorithm with the slow and accurate option using default values. Regions that could not be unambiguously aligned were excluded in MacClade 4.0 (Maddison & Maddison, 2001). The alignment can be obtained upon request from the corresponding author.

Sequences of the COI mtDNA gene were edited with LASERGENE (DNASTAR Inc.) and aligned by using the amino acid triplets. End trimming of the complete dataset was necessary because of sequencing difficulties in some of the samples. However, complete sequences from most specimens are deposited at GenBank.

Phylogenetic analyses

18S analysis

Phylogenetic analyses were carried out using Bayesian inference performed with MrBayes v. 3.1.2 (Huelsenbeck & Ronquist, 2001). We used the default values of one cold and three heated Markov chains with the model GTR + I + G [according to MrModeltest v. 2.2 (Nylander, 2004)], allowing sites to vary independently. Parameters were altered in the proposal mechanism to acquire a span within 20–60%, this for the acceptance rates for the moves in the 'cold' chain of each run. Three separate analyses were run to ensure congruence. In each analysis the Monte Carlo Markov chain (MCMC) length was 1 000 000 generations with sampling of every 100th generation chain. Log-likelihood values for sampled trees stabilized after approximately 100 000 generations and burnin was set to 2000 leaving the last 8000 sampled trees for estimating posterior probabilities (Bayesian support values).

Three phoronid species (*Phoronis vancouverensis*, *Phoronis australis*, and *Phoronis hippocrepia*) were used as the outgroup in the 18S rDNA analysis. The phylogenetic position of phylum Nemertea amongst the metazoans is uncertain, and several sister taxa (including Phoronida) have been suggested. The 18S gene is difficult to align, and this choice of outgroup turned out to be the most easily aligned of several other alternatives.

COI analyses

Phylogenetic analysis using Bayesian inference was performed with MrBayes v. 3.1.2 (Huelsenbeck & Ronquist, 2001) using default values of four (three hot, one cold) Markov chains, with site-specific rates and gamma distribution, lset nst = 6 (model GTR, General Time Reversible). Parameters were altered in the proposal mechanism to acquire a span within 20–60%, this for the acceptance rates for the moves in the 'cold' chain of each run. The Monte Carlo Markov chain (MCMC) length was 1 000 000 generations with sampling of every 100th generation chain. Burnin was set to 50% leaving the last 5000 sampled trees for estimating posterior probabilities (Bayesian support values). Four separate analyses were run starting from random trees to ensure congruence.

In the restricted COI analysis of palaeonemerteans (including *Carinina ochracea* sp. nov.), a hoplonemertean, *Emplectonema neesii*, was used as the outgroup. Several studies (e.g. Sundberg *et al.*, 2001; Thollesson & Norenburg, 2003) have indicated that Palaeo- and Heteronemertea are nonmonophyletic, and it is not clear which taxon amongst these groups to choose as an outgroup. We thus used a hoplonemertean as the outgroup species.

In the restricted COI analysis of hoplonemerteans (including *Raygibsonia bergi* gen. et sp. nov.), a species from the group Polystilifera, a reptant species, was chosen, according to the analysis in Thollesson & Norenburg (2003), in which the polystiliferans form a sister group to the monostiliferans.

SYSTEMATICS

Phylogenetic studies have confirmed earlier statements (e.g. Sundberg, 1993) that supraspecific taxa in the phylum Nemertea are based on previous principles and practices that do not lead to monophyletic taxa. Sundberg & Hylbom (1994); Sundberg *et al.* (2001), and Thollesson & Norenburg (2003) all clearly show that many genera are paraphyletic assemblages and that the 'family' category amongst nemerteans in many (most?) cases is meaningless from a phylogenetic point of view. The higher classification of phylum Nemertea traditionally recognizes the most inclusive taxa Enopla and Anopla; species belonging to Hoplonemertea have been classified into the Enopla, and Heteronemertea and Palaeonemertea species into the Anopla. Sundberg *et al.* (2001) and Thollesson & Norenburg (2003) corroborate the monophyly of Enopla, but the situation in Anopla is more problematic. Without going into details, it is clear that the monophyletic status of both Heteronemertea and Palaeonemertea as currently circumscribed is questionable. In view of this, we have decided not to place the two new species described below in any higher taxonomic category – the genus placement is required by present nomenclatural rules.

Type specimens are deposited in the Göteborg Natural History Museum (GNHM).

RAYGIBSONIA GEN. NOV.

Diagnosis: The genus is diagnosed by the following morphological characters: presence of large cerebral organs lying alongside/close to anterior part of the brain and opening laterally in the cerebral region, the ciliated cerebral canals opening from pores rather than from cephalic furrows; cephalic glands encircling the foregut in the brain region; four groups of anterior eyes and isolated pair of posterior eyes.

Etymology: The new genus is named in honour of Professor emeritus Ray Gibson as a tribute to his accomplishments and significance in nemertean taxonomy.

Type species: Raygibsonia bergi.

Systematic discussion: The phylogenetic analysis based on the 18S rRNA gene shows that the type species belongs in the taxon Hoplonemertea with 100% support (Fig. 1). A more detailed analysis of a selected number of hoplonemerteans based on the COI gene analysis (Fig. 2) places *R. bergi* in the same clade as *Zygonemertes virescens*. However, we have chosen not to place the new species in the taxon *Zygonemertes* for two reasons. First, the taxon sampling was limited in this analysis, and with only one *Zygonemertes* species available the result can only be indicative. Second, Chernyshev (2005) placed the three genera *Zygonemertes*, *Quequenia*, and *Pheroneonemertes* in the same taxon based on the synapomorphy 'postcerebral eyes along longitudinal nerve cords'. This character is absent in *Raygibsonia*, and although this does not *per se* contradict a close relationship, we interpret this as an indication of two different taxa. *Raygibsonia bergi* furthermore differs from all species of 'Zygonemertidae'-group by the absence of postcerebral eyes and the lack of sickle-shaped bodies.

RAYGIBSONIA BERGI GEN. ET SP. NOV.

(FIGS 3, 4; TABLE 4)

Hoplonemertean sp. 3 Strand & Sundberg (2005).

Holotype: Sexually immature, series of transverse sections (GNHM Nemertini 84). Mud, 20 m depth, south of Flatholmen (58°14′48″N, 11°22′54″E according to the WGS 84), 18.xi.2002. 18S rDNA sequence of the species has been deposited with GenBank (accession number AY928351) together with sequences of the mtDNA COI gene (accession number EU489489).

Paratype: Sexually immature, series of transverse sections (GNHM Nemertini 85) from mud with boulders, fauna dominated by *Mycale lingua*, 92–106 m depth, Väderöarna (58°19′16″N, 10°57′52″E), 25.iv.2006.

Further material: Amongst shell gravel, 30 m depth, Humlesäcksrännan (58°16′08″N, 11°24′85″E), 10.v.2006.

External characters (Fig. 3): The largest specimen was about 15 mm long and 1–1.5 mm wide. The body is of more or less uniform width slightly nar-

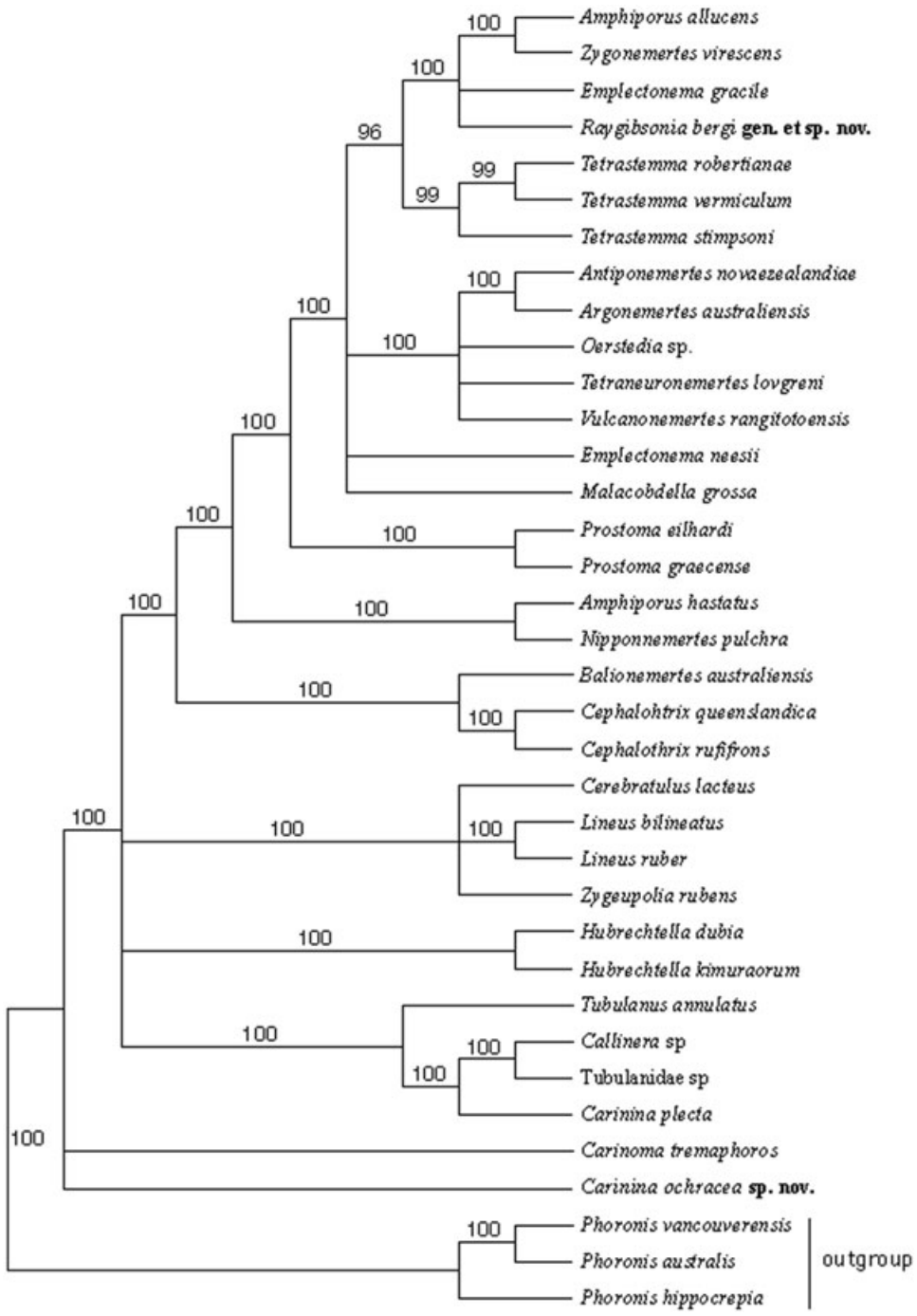

Figure 1. Phylogeny of a selected number of nemertean taxa to show the position of the two new species described here (in bold). Majority rule consensus tree from a Bayesian analysis based on 18S rDNA sequences. Numbers above branches refer to a posteriori probabilities (only values > 95% reported). Three phoronid species were used as outgroup: *Phoronis vancouverensis, Phoronis australis, Phoronis hippocrepia.*

rowing close to the rounded posterior tip. The primary body colour is light brown, the head is pinkish red with the cerebral ganglia visible as a red lobe in front of the cephalic furrows. Lateral margins translucent to whitish. The head, which is somewhat wider than the body, possesses a lower lip-like projection and two groups of eyes and a single pair of distinct eyes on each side. The foremost group is situated on the lower lip-like projection and a bit further back, above the lower lip-like

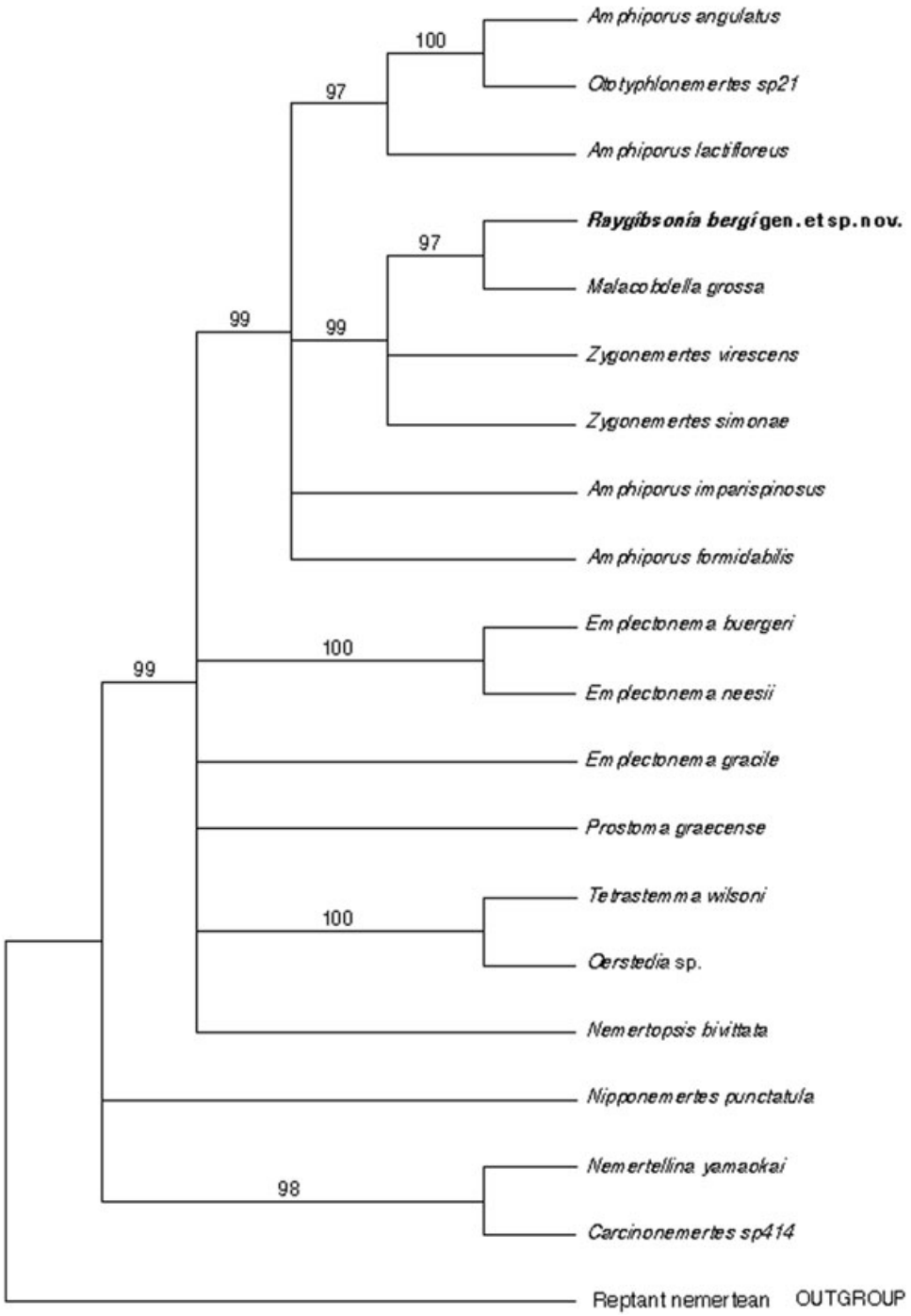

Figure 2. Phylogeny of a selected number of hoplonemertean taxa to show the position of the new hoplonemertean species described here (in bold). Majority rule consensus tree from a Bayesian analysis based on COI mtDNA sequences. Numbers above branches refer to a posteriori probabilities (only values > 95% reported). Outgroup species is Reptant nemertean sp500 (from Thollesson & Norenburg, 2003).

projection, the second group. Each group contains two to five eyes, probably depending on age. The single pair of posterior eyes lies in front of the cerebral ganglion and is visible from the ventral side of the body. The head is demarcated from the rest of the body by a pair of dorsal cephalic furrows. Moreover, another pair of cephalic furrows are present ventrally, they arch their way from the terminal

Figure 3. ***Raygibsonia bergi*** **gen.** et **sp. nov.** Drawing by Helena Samuelsson, The Encyclopedia of the Swedish Flora and Fauna.

proboscis pore to the lateral margins on each side of the head. The body possesses a brown middorsal longitudinal band that ends close to the posterior tip. Under higher magnification this band is composed of densely packed pigment spots. Dorsolaterally on each side of the body surface, faint and sometimes abruptly ending longitudinal bands of sparsely packed pigment spots are present (Fig. 3).

Internal characters: Figure 4, Table 4, and Appendix.

Systematic discussion: As for the genus.

Etymology: The species is named in honour of Dr Gunnar Berg (1937–2006) for his contribution to nemertean taxonomy and systematics.

CARININA OCHRACEA **SP. NOV.** (FIGS 5, 6; TABLE 4)

Holotype: Sexually immature, series of transverse sections GNHM Nemertini 83. Type locality 58°53′124″N, 11°07′275″E. The 18S rDNA sequence of the species has been deposited with GenBank (accession number EU495306) together with sequences of the mtDNA COI gene (accession number EU489492).

Further material: Mud and soft bottom, depth from 5 m and down to 40 m. All in the Koster area.

External characters (Fig. 5): The specimen was 13–15 mm long and about 1 mm wide. The body is of more or less uniform width slightly narrowing towards the bluntly rounded posterior tip. The head, which is bluntly rounded, is not wider than the rest of body but sometimes demarcated by a small neck. Posterior half of body yellowish orange with a pronounced transition to orange of anterior half. Lateral margins thin and with same colour as body. Head orange as the anterior part but with reddish touch on margins. Dorsally, the head possesses shallow longitudinal furrows that might be broken, eyes are absent. Proboscis pore subterminal and lies in a small triangular pit on the foremost ventral tip of the head. The mouth, situated further back, is surrounded by wrinkled lips. Individual specimens are slow moving and when mechanically disturbed they first back up and when touched several times they coil in a spiral moving head back and forth. When specimens were fixed they contracted strongly.

Internal characters: Figure 6, Table 4, and Appendix.

Systematic discussion: We have chosen to place this new species in the genus *Carinina* based on the two synapomorphies: (1) brain and lateral nerve cords situated in epidermis; (2) longitudinal muscle plate

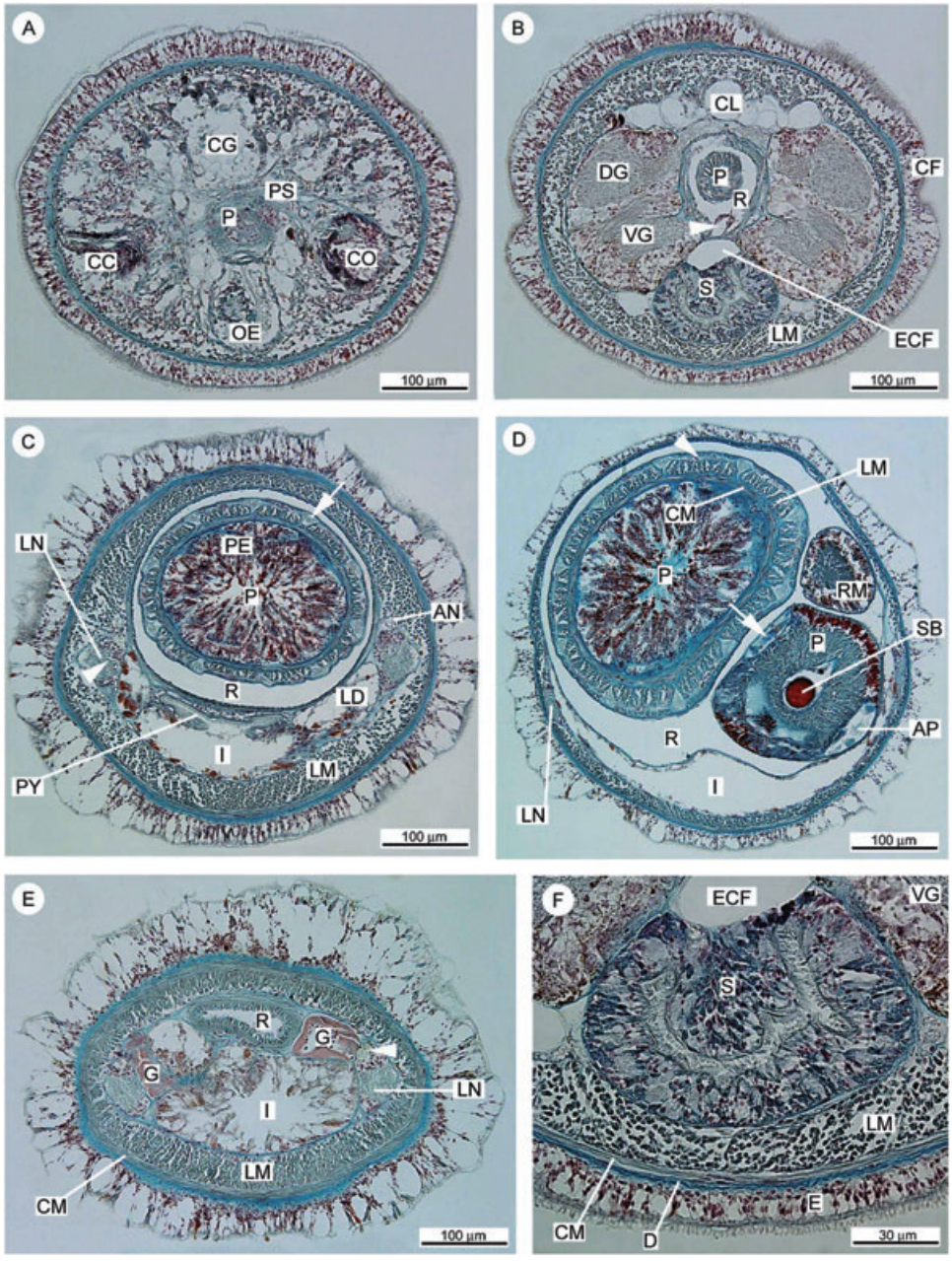

Figure 4. A–F, ***Raygibsonia bergi* gen.** et **sp. nov**. A, section through anterior-most part of body showing cephalic glands, cerebral organs, oesophagus, and the poorly developed precerebral septum. B, section through cephalic region showing cephalic blood supply, stomach, and cerebral ganglia. Note the vascular plug (arrowhead). C, section through pyloric region showing the connection between pylorus and intestine. Note the myofibrillae in the lateral nerve cord (arrowhead) and the nerves of the proboscis (arrow). D, section through proboscis armature region of body showing the stylet apparatus. Note the accessory stylet (arrow) and the peripheral neural sheath (arrowhead) that connect the proboscis nerves. E, section through gonad region of body showing immature gonads (probably sac-like). Note the accessory lateral nerve (arrowhead). F, section through stomach region of body, showing distribution of gland cells. Abbreviations: AP, accessory stylet pouch; AN, accessory lateral nerve; CB, cerebral ganglion; CC, cerebral canal; CF, cephalic furrow; CG, cephalic glands; CL, dorsal lobules of cephalic glands; CM, circular muscle layer; CO, cerebral organ; D, dermis; DC, dorsal commissure; DG, dorsal ganglion; E, epidermis; ECF, cephalic gland encircling the foregut; G, gonad; I, intestine; IC, intestinal caecum; LD, lateral diverticula; LM, longitudinal muscle layer; LN, lateral nerve cord; LV, lateral blood vessel; MDV, mid-dorsal vessel; OE, oesophagus; P, proboscis; PE, proboscis epithelium; PN, proboscis nerve; PS, precerebral septum; PY, pylorus; R, rhynchocoel; RM, retractor muscle; S, stomach; SB, stylet basis; VG, ventral ganglion.

Table 4. Descriptions of the two species ***Carinina ochracea* sp. nov**. and ***Raygibsonia bergi* gen**. et **sp. nov**. Character numbers refer to the Appendix

Character	*Carinina ochracea*	*Raygibsonia bergi*	Figure
1	0	0	
2	0	0	
3	2	2	
4	N/A	N/A	
5	0	0 & 2	
6	2	Not observed	
7	0[1]	2	
8	N/A	0	
9	N/A	0	
10	N/A	0	3
11	0	1	3
12	N/A	2	3
13	1	0	3
14	2	1	3
15	2	1	3
16	0	9	3, 5
17	N/A	0	3
18	N/A	1	3
19	N/A	1	
20	N/A	0	3
21	N/A	3	3
22	6	5	3, 5
23	0	2	
24	1	1	
25	0	0	3
26	0	2	
27	2	Not seen	
28	1	N/A	6A
29	1	N/A	
30	0	0	4, 5
31	0	3	4, 5
32	0	N/A	
33	2	0	4, 5
34	1	N/A	
35	N/A	0	
36	N/A	3	4A
37	2	N/A	
38	0	0	4, 6
39	1	N/A	6A
40	1	0	8
41	0	1	8, 4A
42	1	1	
43	1	2	6B, 4C
44	0	N/A	
45	1	2	
46	1	0	6C
47	0	1	4D
48	0	0	
49	2	2	
50	Not seen	1	4C, D
51	1	3	
52	0	1	4D
53	N/A	0	
54	0	2	4D
55	N/A	0	
56	N/A	1	
57	N/A	0	8
58	N/A	0	8
59	N/A	1	8
60	N/A	1	8
61	0	0	
62	2	0	
63	0	1	4A
64	N/A	2	4A
65	1?	0	
66	N/A	1	4C
67	N/A	2	
68	0	1	
69	N/A	2	
70	N/A	1	
71	3	1?	
72	3	0	6A
73	N/A	1	4B
74	2	N/A	6B
75	1	N/A	6B–D
76	0	1	
77	N/A	1	
78	0	0	
79	N/A	0	
80	1	N/A	
81	0	N/A	6A
82	1	1	4B
83	0	1	4B
84	0	0	
85	0	0	
86	N/A	1	4C
87	N/A	2	
88	0	N/A	
89	0	N/A	
90	Not seen	Not observed	
91	0	0	
92	0?	0	
93	0?	1	4C
94	N/A	0	
95	0	0	
96	1	1	
97	0	0	
98	0	N/A	
99	1	N/A	6D
100	N/A	Not seen	
101	0	Not seen	
102	0	Not seen	
103	2	Not seen	
104	0	0?	6E, 4E
105	0	0	
106	N/A	N/A	
107	N/A	N/A?	
108	Not observed	Not observed	
109	1	2	6E
110	0	Not seen	
111	0	1	
112	0	2	4A
113	N/A	2	4A
114	N/A	0	
115	2	2	4A
116	0	2	4A
117	0	1	4A
118	N/A	0	
119	0?	N/A	
120	0	N/A	

present between rhynchocoel and alimentary canal. The phylogenetic analyses in Figures 1 and 7 do not contradict this conclusion. The genus *Carinina* is currently placed in the taxon Palaeonemertea, but as mentioned above the monophyletic status of the name is unsettled.

The organization of the blood system in this new species is unusual because of the presence of a precerebral unpaired cephalic blood lacuna situated dorsal and lateral to rhynchodaeum; it is randomly pierced by dorsoventral muscle bundles. Just in front of the brain the cephalic lacuna is divided into a pair

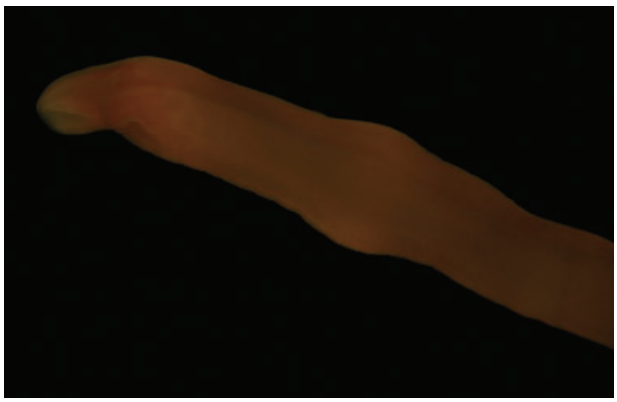

Figure 5. ***Carinina ochracea*** **sp. nov.** (living specimen).

of lateral cephalic lacunae, and two to three anastomosed ventral lacunae. In the mouth region two ventral lacunae form the vascular plexus, which surrounds foregut and anastomoses with two lateral vessels (lacunae). In the posterior part of the foregut region the vascular plexus disappears. In the foregut region the lateral vessels repeatedly send out branches that penetrate the rhynchocoel wall to form vascular plugs (about ten plugs on left side and about 12 plugs on right side). The only other *Carinina* species with numerous vascular plugs is *Carinina plecta* Kajihara (2006).

DISCUSSION

Time for a change? Taxonomy, and the description of the world's biodiversity, is one of the biggest bioinformatic projects in science. Whereas sequence, genomic, and other molecular data have been organized in public databases within a few decades, the quantity of taxonomic information available on the internet is pitiful. Still, taxonomy is an information-rich subject and as such should be especially fit for the internet but the taxonomic community has not managed to create an internet-based taxonomy easily accessible to scientists and decision-makers. Good quality systematic revision and monographs take years to produce and should not need to be static documents published at extended periods (often longer than a taxonomist's career) given today's technology. The current codes of zoological and botanical nomenclature prevent original species description from being made purely on the internet but this will probably change in the future considering the rapid changes in publication in general. An internet-based taxonomy platform would imply new ways of describing organisms and ways of retrieving information for computerized comparisons amongst species, and for use in various systematic analyses. We think that a list of characters as proposed here could be helpful in developing an internet-based taxonomy of nemerteans (see Appendix). On the internet, it would also be easy to amend/correct the list and add illustrations and it would provide the space to explain characters and terms.

It has been argued that this kind of checklist will force taxonomists to think about a set of predefined characters/character states and therefore may obstruct rather than help. According to this way of reasoning, it may lead to careless descriptions where the practicing systematist would tick off the list without actually looking more carefully for additional details in the morphology. Without any lists, or 'rules', the argument is that the mind would be freer to find other/additional anatomical details. We see two problems with this line of thinking. First, we are all taught morphology as undergraduate students, and as such we already have a set of images of various organ systems in our minds. We have already learned what, for example, histologically defines a connective tissue layer and our minds are hence not blank slates when we start doing research. Second, species descriptions are about the communication of facts amongst people and amongst generations. It is like language – we learn what a chair is, and we can already use that word at an early age. It does not prevent us from, with growing experience, later distinguishing between, for example, an armchair and a stool. Later in life we may even start to associate different designers with different chairs. The point is that we still need a common basis (knowing what a chair is in this case) at the start to be able to communicate at all. We see this list as this starting point and emphasize that it is not the final word but instead a beginning for future discussions/amendments. Not only does it need to be refined in the way we define characters, but also with careful observations new characters/character states will hopefully be added. However, we still think it could act as guidance to anyone new to nemertean taxonomy and advise him/her as to which characters to look for. It will hopefully also be used as a guide to a standardized vocabulary to facilitate communication between nemertean morphologists and taxonomists. For us, science is an ongoing process which best takes place in public and we invite everybody to take part. Hence the publication of this list, and this suggestion, although we know that it is far from perfect or complete.

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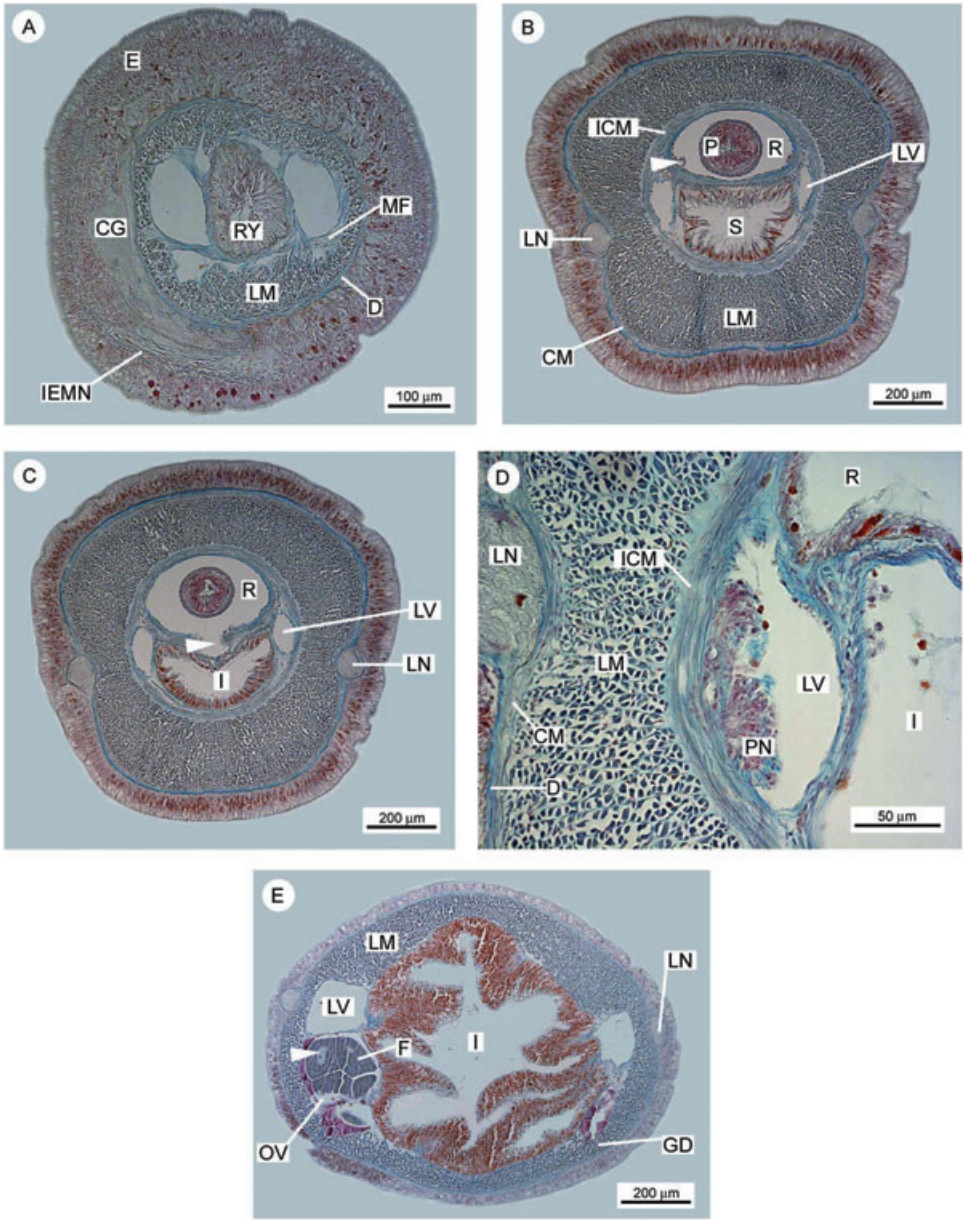

Figure 6. A–E. ***Carinina ochracea* sp. nov.** A, section through cephalic region showing cerebral ganglion and intra-epithelial muscle fibre network. B, section through stomach region showing proboscis and body wall muscle layers. Note the rhynchocoelic villus (arrowhead). C, section through intestinal region showing rhynchocoelic caecum (arrowhead). D, section through intestinal region showing the excretory system. E, section through gonad region of body showing intestine and ova with nucleus (arrowhead). Abbreviations: CG, cerebral ganglion; CM, outer circular muscle layer; D, dermis; E, epidermis; F, follicle; GD, gonoduct; I, intestine; ICM, inner circular muscle; IEMN, intra-epithelial muscle fibre network; LM, longitudinal muscles; LN, lateral nerve cord; LV, lateral blood vessel; MF, muscle fibre; OV, ovum; P, proboscis; PN, protonephridia; R, rhynchocoel; RY, rhynchodaeum; S, stomach.

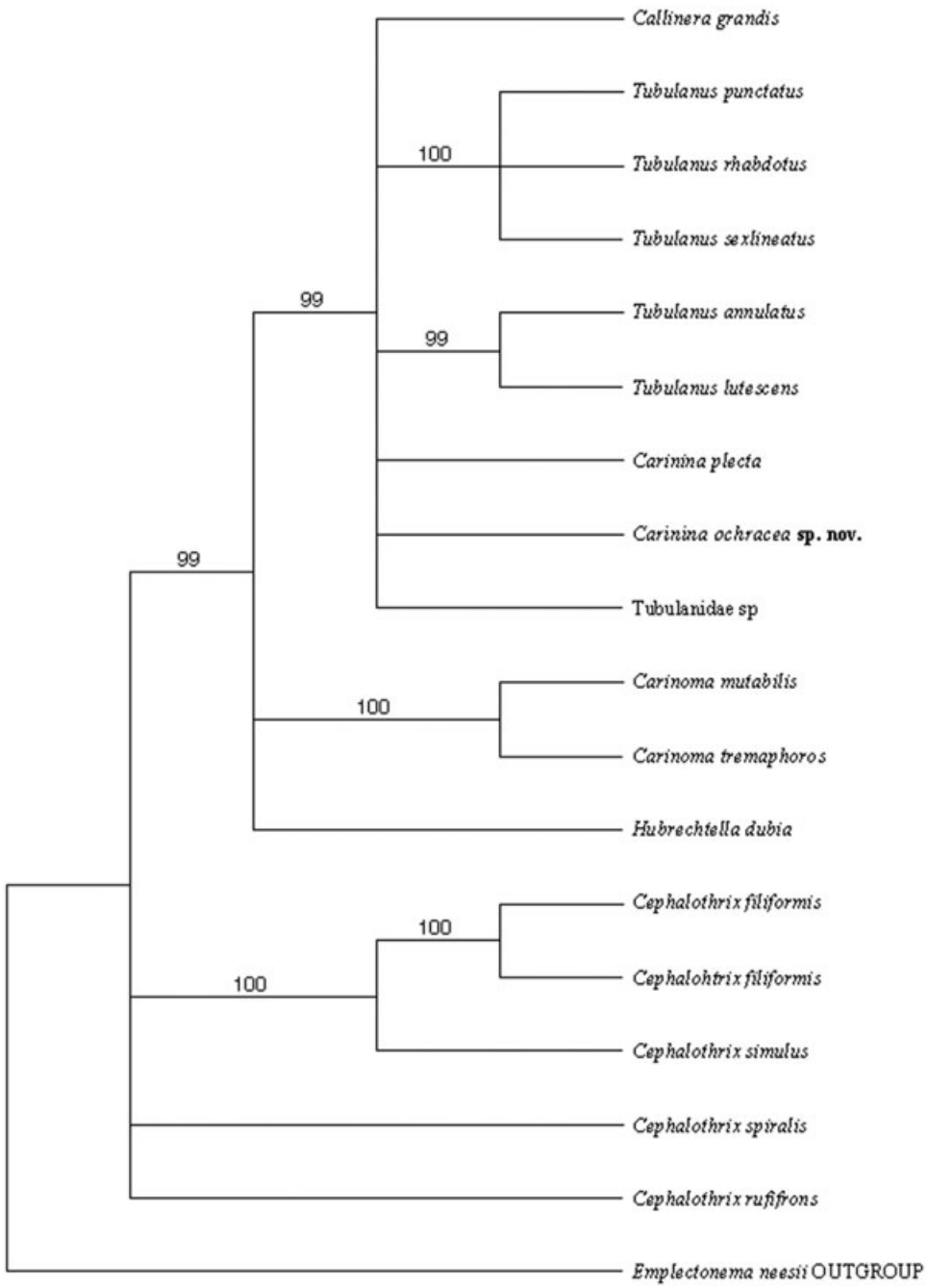

Figure 7. Phylogeny of a selected number of palaeonemertean taxa to show the position of the new species described here (in bold). Majority rule consensus tree from a Bayesian analysis based on COI mtDNA sequences. Numbers above branches refer to a posteriori probabilities (only values > 95% reported). Outgroup species is *Emplectonema neesii*.

comments from Jon Norenburg, which made us think about why to have a list of defined characters like this. The research was supported (for P. S.) by the Swedish Research Council and (for A. V. C.) by the Russian Foundation for Basic Researchers (grant N 07-04-00249).

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APPENDIX

List of morphological characters and character states used in the descriptions of the two new species named in this paper. (P) and (H) indicate characters or character states that are more common to palaeonemerteans and hoplonemerteans, respectively. All characters in this list apply to relaxed specimens. An electronic copy of this list of characters and their coding can be obtained from the corresponding author.

Character	Character state	Coding
1. Biology	Free-living	0
	Parasitic	1
	Commensal	2
2. Habitat	Marine	0
	Freshwater	1
	Terrestrial/Semi-terrestrial	2
	Estuarine	3
3. Benthic divisions (Nybakken & Bertness, 2004)	Supralittoral	0
	Littoral	1
	Sublittoral	2
	Bathyal	3
	Abyssal	4
4. Pelagic divisions (Nybakken & Bertness, 2004)	Epipelagic	0
	Mesopelagic	1
	Bathypelagic	2
	Abyssopelagic	3
5. Substrate	Mud	0
	Sand	1
	Gravel/shellgravel	2
	Rock/boulders	3
	Algae/algal holdfasts/sea grass	4
	Other	5
6. Behaviour when mechanically disturbed	Contracts without coiling into a spiral	0
	Contracts in a coiled spiral	1
	Contracts in a coiled spiral moving head back and forth	2
	Backs up	3
	Contracts into a knot	4
	Eversion of proboscis	5
	Production of mucus	6
	Fragmentation	7
External morphology		
7. Cephalic furrows (Figs 9, 10)	Absent	0
	One pair	1
	Two pairs	2
8. Distribution of anterior cephalic furrows	Ventral	0
	Dorsal	1
	Lateral	2
	Ventral and lateral	3
	Ventral and dorsal	4
9. Shape of anterior (dorsal) cephalic furrows (viewed with tip of head directing upwards) (H) (Figs 9, 10)	V-shaped or oblique	0
	V-shaped or oblique with secondary grooves	1
	Ventral transversal	2
	Lateral horizontal	3

APPENDIX *Continued*

External morphology		
10. Shape of posterior (dorsal) cephalic furrows (viewed with tip of head directing upwards) (H) (Figs 9, 10)	V/U-shaped or oblique	0
	Λ-shaped	1
11. Head demarcated from body	No	0
	Head wider than trunk	1
	Head not wider than trunk	2
12. Position of cephalic furrows (H)	If single pair behind brain lobes	0
	If single pair in front of brain lobes	1
	If two pairs, posterior pair behind brain lobes	2
	If two pairs, posterior pair in front of brain lobes	3
13. Shape of head/cephalic lobe (Fig. 9)	Rounded	0
	Bluntly rounded	1
	Pointed	2
	Bluntly pointed	3
	Oval	4
	Spatulate	5
	Truncated	6
	Tapered	7
	Diamond-shaped	8
	Lancet-shaped	9
	Shield-shaped	10
	Bilobed	11
14. Head viewed laterally	Without extensions	0
	Bilobed with ventral lobe further forward	1
	Flattened	2
	Flattened, 'duck bill'	3
15. Shape of posterior tip	Pointed	0
	Bluntly pointed	1
	Rounded	2
	Bluntly rounded	3
	With caudal fin	
	With caudal cirrus	4
	With caudal sucker	5
16. Eyes (Figs 3, 9)	Absent	0
	Two eyes near brain	1
	Two eyes on anterior tip of head	2
	Four eyes arranged at corners of square or rectangle (H)	3
	Six eyes arranged in row of three at each side of head (H)	4
	Three groups/rows of eyes on each side of head (H)	5
	Four groups of eyes (H)	6
	Eyes arranged in lateral rows or groups on each side of head	7
	Eyes irregularly distributed over head	8
	Two groups and one posterior eye on each side (cf. *Raygibsonia*)	9
17. Eye morphology*	Simple	0
	Double	1
18. Relative eye size (Fig. 9)	All eyes more or less of equal size	0
	Posterior pair/pairs more developed	1
	Anterior pair/pairs more developed	2
	Two or three pairs of more developed eyes and additional minute eyes	3
	Other	4

APPENDIX *Continued*

External morphology		
19. Eye distinctiveness	Eyes visible from ventral side	0
	No eyes visible from ventral side	1
20. Eye position relative to brain lobes	Confined entirely to precerebral cephalic region but may be located above brain	0
	Extending behind brain lobes but confined to lateral dorsal body margins	1
	Extending behind brain lobes along dorsal and lateral body margins	2
21. Colour pattern	Absent	0
	Confined to cephalic region	1
	Extending full body length on dorsal surface	2
	Restricted to post cephalic dorsal body surface	3
	On both dorsal and ventral body surfaces	4
22. Primary dorsal body colour	Red	0
	Green	1
	Yellow	2
	White	3
	Purple	4
	Brown	5
	Orange	6
	Pink	7
	Other	8
23. Body colour hue/tint	Without hue/tint	0
	Dark	1
	Light	2
24. Internal organs visible through dorsal epidermis	No	0
	Yes	1
25. Lateral margins	Appear paler than dorsal body surface	0
	No distinction in colour	1
26. Distribution of bristles/cirri	Not seen	0
	Only on head	1
	Only on tail	2
Internal morphology		
Body wall		
27. Epidermis non-cellular inclusions (H) (Fig. 11)	Absent	0
	Spicules	1
	Pigment granules	2
	Mineral granules	3
28. Epidermis of anterior body (P) (Fig. 6A)	Without intra-epithelial muscle fibre network	0
	With intra-epithelial muscle fibre network	1
29. Ratio thickness of epidermis/lateral body diameter in brain region (P)	< 0.1	0
	> 0.1	1
30. Dermis	Forming a distinct zone between epidermis and circular muscle layer	0
	Forming a distinct zone with a mesh like structure of inner layer (P)	1

APPENDIX *Continued*

Internal morphology		
Body wall		
31. Thickness of dermis	Less than half epidermal height (P)	0
	More than half epidermal height (P)	1
	Much thicker than circular muscle layer (H)	2
	Approximately the same thickness as circular muscle layer (H)	3
32. Muscle processes from dermis into epidermis (P) (Fig. 11)	Absent	0
	Present	1
33. Muscle layers	Outer circular and inner longitudinal muscle layer	0
	Outer circular, middle diagonal and inner longitudinal muscle layer (H)	1
	Outer circular, middle longitudinal and inner circular muscle layer (P)	2
	With outer longitudinal, middle circular and inner longitudinal muscle layers + inner circular muscle layer in anterior part of body region (P)	3
	With outer circular, outer longitudinal, inner circular and inner longitudinal muscle layer	4
	Outer circular, diagonal, middle circular, longitudinal and inner circular muscle layer (P)	5
34. Muscle crosses between body wall circular muscle layers (P)	Absent	0
	Dorsal muscle cross/es only	1
	Both dorsal and ventral muscle crosses	2
35. Body wall longitudinal muscle layer just behind brain (H) (Fig. 12)	Not anteriorly divided	0
	Longitudinal muscle layer anteriorly divided by connective tissue	1
	Longitudinal muscle layer anteriorly divided by posterior extensions of cephalic glands	2
36. Precerebral septum (H) (Fig. 13)	Closed	0
	Split	1
	Mixed	2
	Open	3
37. Central (medial) muscle plate (P)	Absent	0
	Between foregut and rhynchocoel	1
	Surrounding rhynchocoel (cf. *Carinina*)	2
38. Parenchyma	Barely distinguishable other than as a membranes enclosing various body organ systems	0
	Moderately developed, particularly in intestinal regions of body	1
	Extensive	2
39. Muscle fibres in mouth/foregut region (P)	Absent	0
	Present	1
Proboscis apparatus		
40. Proboscis pore	Terminal	0
	Subterminal, ventral	1
41. Mouth and proboscis pore connection (H)	Open separately	0
	Open into atrium/rhynchodaeum	1
	Proboscis pore opens into foregut	2
42. Gland cells of rhynchodaeum	Absent	0
	Present	1

APPENDIX *Continued*

Proboscis apparatus		
43. Rhynchocoel musculature	Without distinct musculature, appearing as a simple membrane	0
	Circular muscles only	1
	Proximal circular and distal longitudinal muscle layer	2
	Proximal longitudinal and distal circular muscle layer	3
	Proximal circular, middle longitudinal and distal circular muscle layers	4
	Longitudinal and circular muscle fibres interwoven to form single layer of intermeshed fibres	5
44. Rhynchocoel musculature in posterior end (P)	Approximately as anterior part	0
	With circular muscle layer	1
	With extremely well developed circular muscle layer (muscle bulb)	2
45. Rhynchocoel length	Short, extending into stomach region of body or less	0
	Between one-third and two-thirds of body length	1
	Extending to or almost to posterior region of body	2
46. Rhynchocoelic caeca†	Absent	0
	Ventral (Fig. 6C)	1
	Dorsal	2
	Lateral (Fig. 11)	3
47. Size of posterior third of proboscis region	Small, less than 50% of body diameter in retracted position	0
	Large, more than 50% of body diameter in retracted position (Fig. 4D)	1
48. Musculature of proboscis (everted state)	Outer circular and inner longitudinal muscle layer	0
	Outer longitudinal and inner circular muscle layer	1
	Outer circular, middle longitudinal and inner circular muscle layer	2
	Outer longitudinal, inner circular and inner longitudinal muscle layer	3
49. Musculature of posterior proboscis region (everted state)	Longitudinal muscle layer only	0
	Circular muscle layer only	1
	Outer circular and inner longitudinal muscle layers	2
50. Epithelium of anterior proboscis region when everted	Not developed into papillae	0
	Developed into papillae (H)	1
	Developed into barbs/pseudocnids (secretory products of the epithelium) (P)	2
51. Number of proboscis nerves	Not distinguished	0
	2	1
	7–9	2
	10 (Fig. 4C, D)	3
	11–14	4
	15–20	5
	21–31	6
	> 31	7
52. Proboscis nerve arrangement	Peripheral neural sheath absent or indistinct	0
	Peripheral neural sheath distinct (Fig. 4D)	1
53. Secondary proboscis nerves (H) (Fig. 14)	Absent	0
	Present	1

APPENDIX *Continued*

Proboscis apparatus		
54. Proboscis armature	Absent	0
	As in *Callinera* (Kajihara, 2006)	1
	With central and accessory stylets (Fig. 4D)	2
	With central stylet only	3
55. Number of accessory stylet pouches (H)	Two	0
	More than two	1
	Absent	2
56. Number of stylets in each accessory stylet pouch (H)	One or two	0
	Three or four	1
	More than four	2
	Absent	3
57. Stylet : basis/stylet ratio (H)	1 : 1	0
	1.5 : 1	1
	3 : 1	2
	4 : 1	3
	1 : 1.5–2	4
58. Stylet shaft (H)	Smooth and straight	0
	Curved	1
	With helically arranged grooves	2
	With longitudinal grooves	3
59. Shape of stylet basis (H)	Oval (rounded)	0
	Pear-shaped	1
	Truncate	2
	Rod-shaped	3
	Cylindrical	4
	Falciform (Polystilifera)	5
60. Median waist of stylet basis (H)	Absent	0
	Present	1
61. Proboscis used for locomotion	Unknown	0
	Yes	1
Alimentary system		
62. Position of mouth	Under brain	0
	Far behind brain	1
	Just behind brain	2
63. Oesophagus	Absent	0
	Present	1
64. Oesophagus epithelium	Unciliated with glands	0
	Unciliated without glands	1
	Ciliated with glands	2
	Ciliated without glands	3
65. Stomach‡	Not regionally differentiated	0
	Regionally differentiated	1
66. Stomach connection with intestine (H)	Stomach opening directly into intestine, with no pyloric regions	0
	Posterior stomach developing into pyloric canal which opens into dorsal wall of intestine (Fig. 6C)	1
	Posterior stomach developing into pyloric canal which opens into ventral wall of intestine	2

APPENDIX *Continued*

Alimentary system		
67. Length of pyloric canal (H)	Indistinct or lacking	0
	Shorter than stomach	1
	As long as stomach	2
	Longer than stomach	3
68. Intestinal caecum (Fig. 11)	Absent	0
	Present ventral	1
	Present dorsal	2
69. Anterior pouches on intestinal caecum (H)	Absent	0
	Long, reach forwards to rear of brain lobes or alongside them	1
	Short, do not extend forward to reach brain lobes	2
70. Lateral diverticula on intestinal caecum (H)	Absent	0
	Shallow	1
	Deep	2
71. Intestinal diverticula (Fig. 15)	Absent	0
	Simple unbranched pouches	1
	Shallowly branched pouches	2
	Deeply branched pouches	3
Circulatory system		
72. Cephalic vasculature	Arranged as a simple cephalic loop	0
	Forming a cephalic loop but with extra vessels in cerebral region	1
	Developed into complex branched system of capillaries	2
	Forming a blood lacunae in front of cerebral ganglion (P)	3
	The cephalic loop is dorsoposteriorly re-curved	4
73. Vascular plugs (H) (Figs 4B, 11)	Absent	0
	One	1
	Two	2
74. Rhynchocoelic villus (P) (Fig. 6B)	Absent	0
	Present, one pair	1
	Present, numerous (cf. *Carinina ochracea*)	2
75. Position of lateral blood vessels (P)	First inside then outside inner circular body wall muscle layer	0
	Inside inner circular body wall muscle layer	1
	Outside inner circular body wall muscle layer	2
76. Mid-dorsal blood vessel	Absent	0
	Does not divide in brain region	1
	Divides in brain region to form two vessels (H)	2
77. Length of mid-dorsal blood vessel	Extends to posterior end of body	0
	Does not extend to posterior end of body	1
78. Extra vascular pouches/valves (Fig. 11)	Absent	0
	Present	1
79. Pseudometameric transverse connectives linking mid-dorsal and lateral blood vessels in intestinal region (H)	Absent	0
	Present	1
80. Vascular plexus in foregut region (P)	Absent	0
	Present	1

APPENDIX *Continued*

Nervous system		
81. Location of cerebral ganglia and lateral nerve cords (P)	In epidermis	0
	Cerebral ganglia and lateral nerve cords situated between epidermal basement membrane and outer circular body wall muscle layer	1
	Fibrous core of cerebral ganglia and lateral nerve cords situated between epidermal basement membrane and outer circular body wall muscle layer, cellular part of brain in epidermis	2
	Cerebral ganglia and anterior parts of lateral nerve cords external to body wall outer circular muscles, posterior parts of lateral nerve cords amongst inner longitudinal muscle fibres	3
	In longitudinal muscle layer	4
	First in epidermis then between basement membrane and outer circular body wall muscle layer	5
	Cerebral ganglia situated internal to body wall muscle layers, lateral nerve cords and extraganglionic tissue within body wall longitudinal muscle layer	6
82. Number of dorsal cerebral commissures	None (P)	0
	One	1
	Two (P)	2
83. Distinct outer neurilemma of cerebral ganglion (Figs 4B, 16)	Absent	0
	Present	1
84. Inner neurilemma of cerebral ganglion (Fig. 16)	Absent	0
	Present	1
85. Statocysts in brain tissue (Fig. 16)	Absent	0
	Present	1
86. Lateral nerve cords (H) (Figs 4C, 11)	Without accessory lateral nerve	0
	With accessory lateral nerve	1
87. Accessory lateral nerve (H)	Reaches no farther back than into foregut region of body	0
	Extends posterior to foregut region but not reaching posterior portion of body	1
	Extending all or most of body length	2
88. Four large nerves in head region (P)	Absent	0
	Associated with cephalic glands	1
	Not associated with cephalic glands	2
89. Number of dorsal nerves (P) (Fig. 11)	Upper dorsal nerve only	0
	Pair of upper dorsal nerves	1
	Both upper and lower dorsal nerve	2
90. Posterior junction of lateral nerve cords	Subintestinal	0
	Supraintestinal	1
91. Neurochord cells in brain (Fig. 16)§	Absent	0
	One pair	1
	More than one pair	2
92. Neurochords in lateral nerve cords (Fig. 16)¶	Absent	0
	Present	1
93. Myofibrillae in lateral nerve cords (Figs 4C, 11)	Absent	0
	Present	1

APPENDIX *Continued*

Nervous system		
94. Position of myofibrillae in lateral nerve cords (H)	Within fibrous core	0
	In cellular part	1
	Between fibrous core and cellular part	2
95. Buccal nerves	Absent	0
	Paired	1
	Unpaired	2
Excretory system		
96. Excretory system	Absent	0
	Present	1
97. Extent of system	Confined to foregut region of body	0
	Extending through most of body, including in front of cerebral ganglion (H)	1
98. Excretory canal (P)	Canal inside inner circular muscle	0
	Canal outside inner circular muscle	1
	Several systems ('cephalothrix'- type)	2
99. Nephridial gland (P) (Figs 6D, 11)	Absent	0
	Present	1
100. Flame cells (H) (Fig. 17)	No flame cells distinguished	0
	Simple mononucleate	1
	Binucleate, without support bars	2
	Binucleate, with transverse support bars only	3
	Binucleate, with transverse and longitudinal support bars	4
101. Glandular components in excretory tubules	Absent	0
	Present	1
102. Number of nephridiopores	Limited to one or two on each side of body	0
	Numerous, opening all over body surface	1
103. Position of nephridiopores	Anterior, close to or alongside brain, in anterior region of excretory system	0
	Mid-excretory system	1
	Posterior, at or near posterior Region of excretory system	2
Reproductive system		
104. Nature of sexes	Separate sexes	0
	Simultaneous hermaphroditic	1
	Protandrous hermaphroditic (H)	2
105. Gonad arrangement in heterogamous taxa (Fig. 15)	Single gonad alternating with intestinal diverticula	0
	Groups of gonads alternating with intestinal diverticula	1
	Clustered above each other (P)	2
	In lateral rows/groups diverticula absent	3
106. Gonad arrangement in hermaphroditic taxa (H)	Testes and ovaries in different regions of body	0
	Testes and ovaries distributed in same regions of body, gonads composed of ovotestes	1
	Testes and ovaries distributed in same regions of body, ovaries and testes separate	2
107. Testes	Simple	0
	Bilobate	1
108. Sexual colour dimorphism (H)	Absent	0
	Present	1

APPENDIX *Continued*

Reproductive system		
109. Gonoduct position	Lateral	0
	Ventrolateral	1
	Dorsolateral	2
	Both ventrolateral and dorsolateral	3
110. Nature of reproduction	Oviparous	0
	Ovoviviparous, young emerge from gonads via external gonopores (H)	1
	Ovoviviparous, young emerge via anus (H)	2
Sensory organs		
111. Apical organ	Absent	0
	Present	1
112. Typical cephalic glands	Absent	0
	Confined to anterior half of head	1
	Extend to brain but not behind brain	2
	Extend behind brain	3
113. Cephalic gland type (P)	Forming distinct lobules	0
	Scattered between muscle fibres of head	1
	Scattered between muscle fibres in anterior part of head, forming distinct lobules further back	2
114. Opening of cephalic glands	Via apical organ	0
	Through numerous independent ducts	1
115. Position of cerebral sensory organs in relation to brain	Organs absent	0
	Close to tip of head	1
	Close in front of brain	2
	Alongside brain	3
	Behind brain	4
116. Position of cerebral sensory organs in relation to epidermis	Ciliated pits or ciliated canals in epidermis (P)	0
	Inner part of the organ positioned in the lateral blood vessel (P)	1
	Separate from blood vessels under body wall muscle layers	2
117. Size of cerebral sensory organs	Less than half size of brain lobes	0
	More than half size of brain lobes	1
118. Ciliated cerebral canal (H) (Fig. 16)	Unforked	0
	Forked	1
119. Side organs (P)	Absent	0
	Present	1
120. Sensory pits in head region (P)	Absent	0
	Present	1

*A third character state may be distinguished, 'composed of a number of ocelli'. Here we consider this state as simple eye morphology.

†Structures appearing as rhynchocoelic caeca may be artefacts. A good way to tell if the structure is a caecum is to check the rhynchocoel muscle layers. If muscle layers end abruptly at the caecum as in Figure 6C it is probably a true structure, if not it is probably an artefact.

‡This character refers to the gland cells of the stomach.

§This character state is seen in e.g. *Geonemertes rodericana* (Pantin, 1969: 287, fig. 22).

¶Here we consider neurochord cells as having a membrane structure surrounding the cell while the neurochord lacks such a structure.

Figure 8. Stylet and stylet basis of ***Raygibsonia bergi*** **gen.** et **sp. nov.**

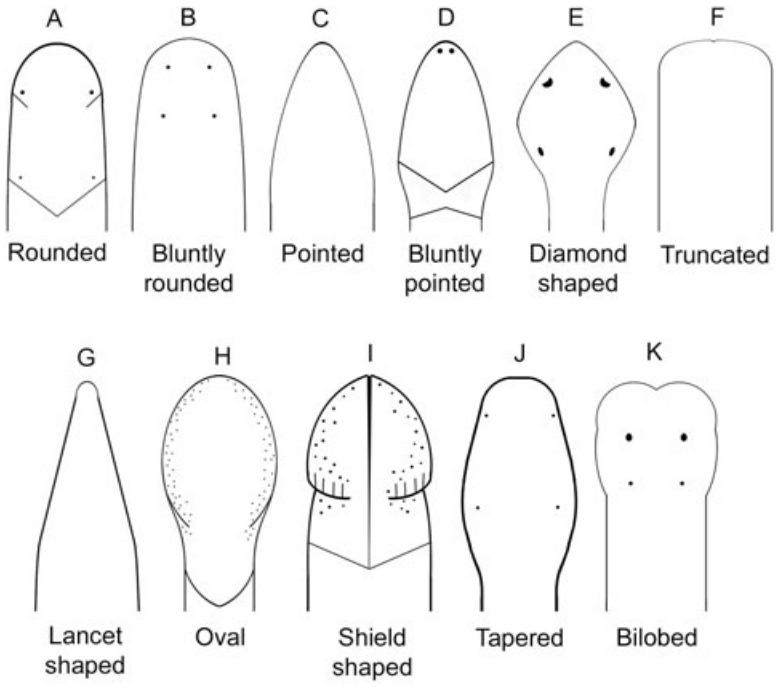

Figure 9. Nemertean head shapes, cephalic furrows, and eye distribution. A, *Nemertopsis flavida* with two pairs, anterior and posterior, cephalic furrows and eyes in rectangle; B, *Oerstedia dorsalis* with eyes in square; C, *Callinera monensis*; D, *Amphiporus bioculatus* with anterior V-shaped and posterior Λ-shaped cephalic furrows. However, different authors have described the furrows of this species in other ways (McIntosh, 1873–74). Also note the two eyes at the anterior tip of the head; E, *Tetrastemma cephalophorum*; F, general representation of truncated head shape; G, *Tubulanus inexpectatus*; H, *Amphiporus dissimulans* with anterior and posterior U-shaped cephalic furrows. Also note the eyes arranged in lateral rows on each side of head; I, *Nipponnemertes pulchra* with secondary grooves of anterior cephalic furrows. Eyes as H; J, *Tetrastemma flavidum*; K, *Prosorhochmus claparedii*, note the distinct anterior eyes. (Redrawn from Gibson, 1974.)

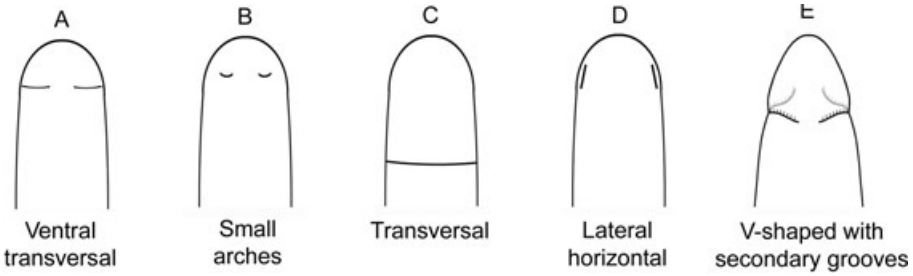

Figure 10. Schematic views of different cephalic furrows. A, ventral transversal furrows; B, small arches; C, posterior transversal furrow; D, lateral horizontal furrows; E, V-shaped furrows with secondary grooves (ghosted furrows show ventral distribution). See also Fig. 8.

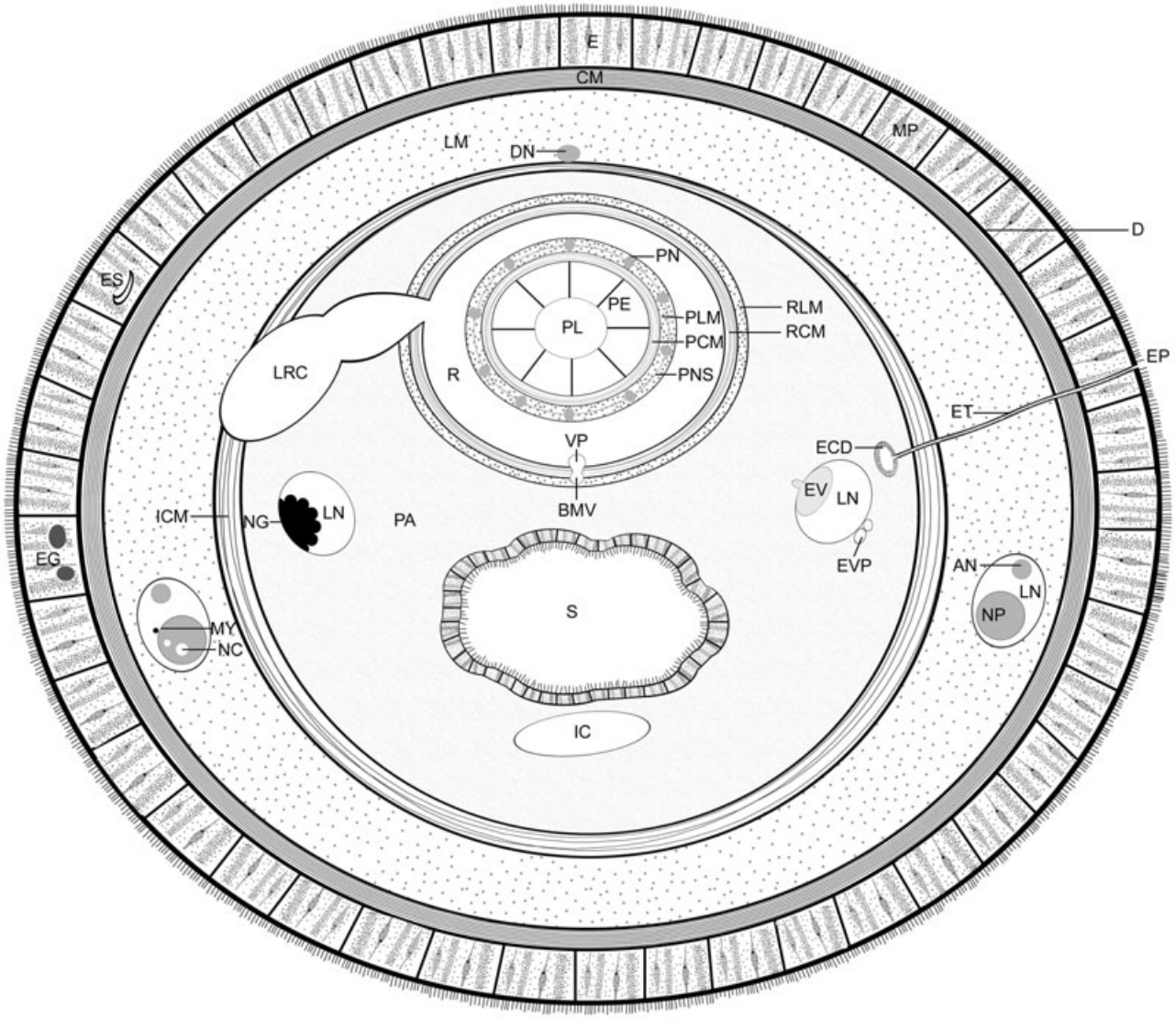

Figure 11. General view of transverse section through the stomach region of a nemertean to show the various organs and tissues mentioned in the character matrix. Abbreviations: Layers and structures of the body wall: E, ciliated epidermis; D, thin dermis; CM, outer circular muscle layer; LM, longitudinal muscle layer; ICM, inner circular muscle layer; PA, parenchyma; EP, epidermal spicule; EG, epidermal pigment granules; MP, muscle processes from dermis into epidermis. Alimentary system: S, stomach; IC, intestinal caecum. Proboscis apparatus: RLM, thynchocoel longitudinal muscle layer; RCM, thynchocoel circular muscle layer; R, thynchocoel; PLM, proboscis longitudinal muscle layer; PCM, proboscis circular muscle layer; PE, proboscis epithelium; PL, proboscis lumen; PN, proboscis nerve; PNS, proboscis peripheral neural sheath; LRC, lateral rhynchocoelic caecum. Nervous system: LN, lateral nerve cord; NP, neuropil; AN, accessory lateral nerve; MY, myofibrillae; NC, neurochord; DN, dorsal nerve. Circulatory system: LN, lateral blood vessel; EVP, extravascular pouch; EV, extravascular valve; BMV, branch of mid-dorsal vessel; VP, vascular plug. Excretory system: NG, nephridial gland; ECD, collecting duct of excretory system; ET, efferent tubule of excretory system; EP, excretory pore.

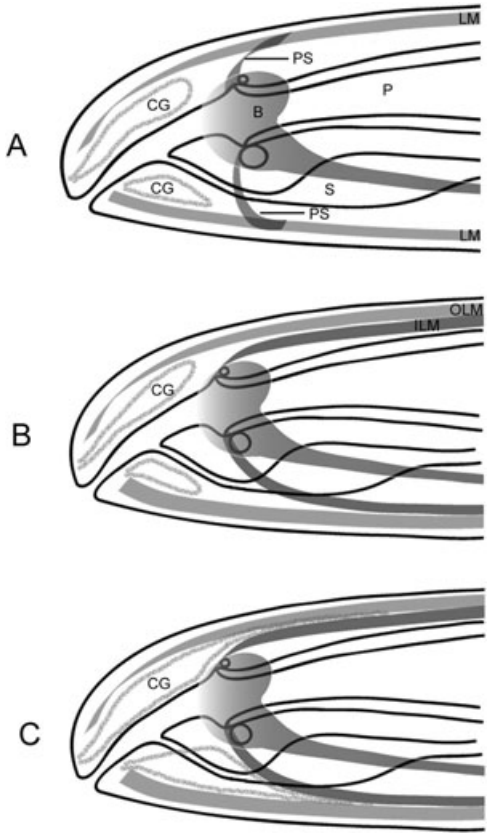

Figure 12. The different states of division of body wall longitudinal muscle layers. A, not divided. B, divided by connective tissue; C, divided by cephalic glands. Abbreviations: B, brain; CG, cephalic glands; ILM, inner longitudinal muscle layer; LM, longitudinal muscle layer; OLM, outer longitudinal muscle layer; P, proboscis; PS, precerebral septa; S, stomach.

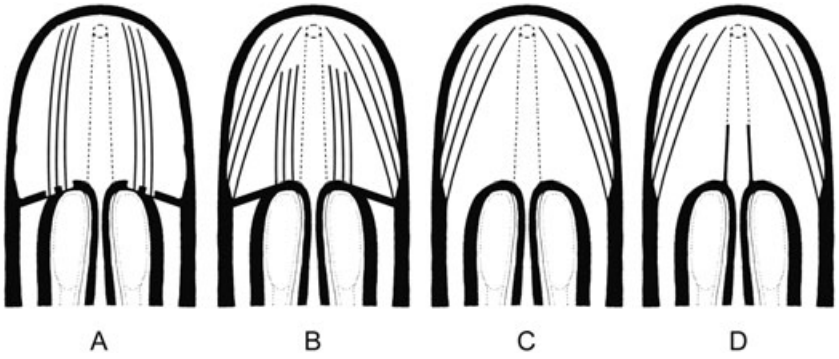

Figure 13. Schematic representation of different types of precerebral septa. A, semi-closed septum; B, closed septum; C and D, septum lacking. Revised and redrawn after Kirsteuer, 1974.

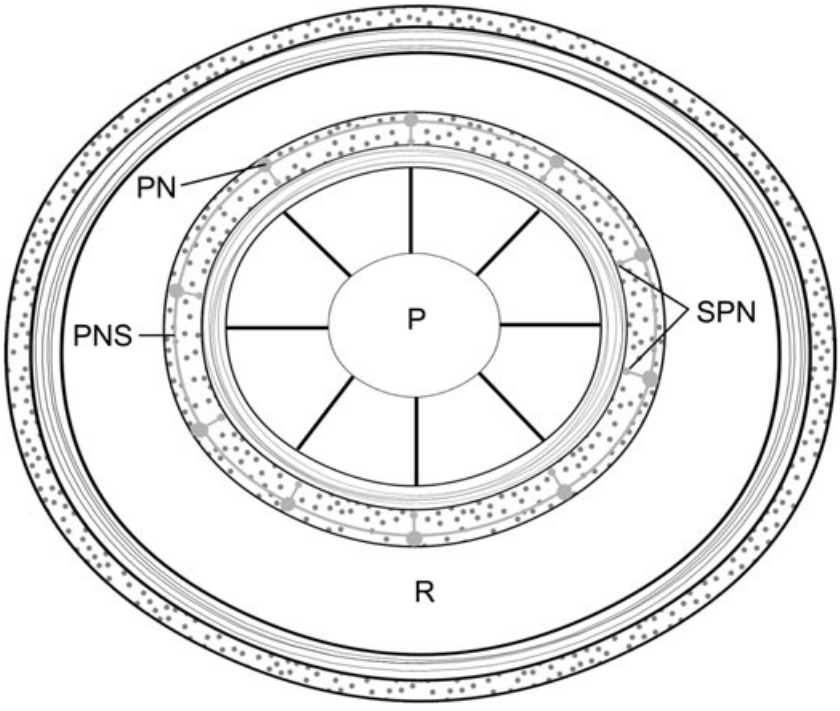

Figure 14. Schematic representation of the proboscis apparatus showing proboscis nerves. Abbreviations: P, proboscis; PN, proboscis nerves; PNS, peripheral neural sheath; R, rhynchocoel; SPN, secondary proboscis nerves.

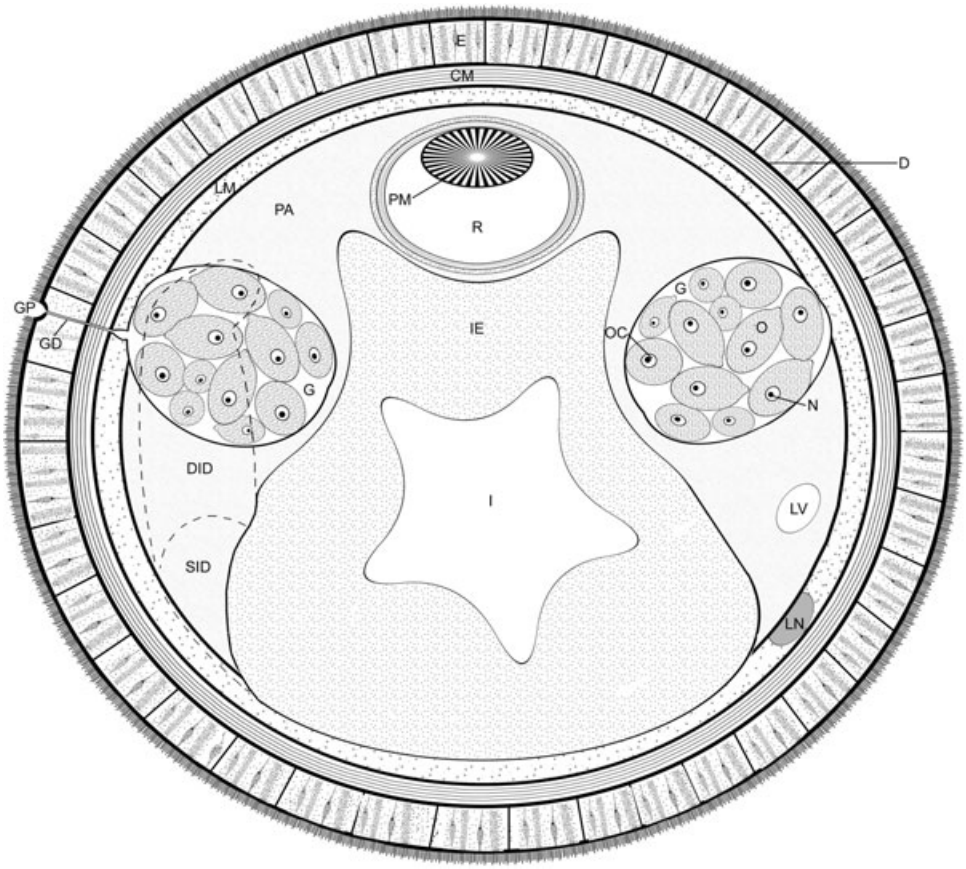

Figure 15. Schematic view of transverse section through the intestinal region of a nemertean to show the various organ systems mentioned in the character matrix list. The dashed lines show distribution of intestinal diverticulae alternating with the reproductive system. Abbreviations: Layers and structures of the body wall: E, epidermis; D, dermis; CM, circular muscle layer; LM, longitudinal muscle layer; PA, parenchyma. Proboscis apparatus: R, rhynchocoel; PM, proboscis retractor muscle. Alimentary system: I, intestine; IE, intestinal epithelium; SID, shallow intestinal diverticula; DID, deep intestinal diverticula. LN, lateral nerve cord; LV, lateral blood vessel. Reproductive system: G, gonad; O, ovary; OC, ovocyte; N, nucleolus; GD, gonoduct; GP, gonopore.

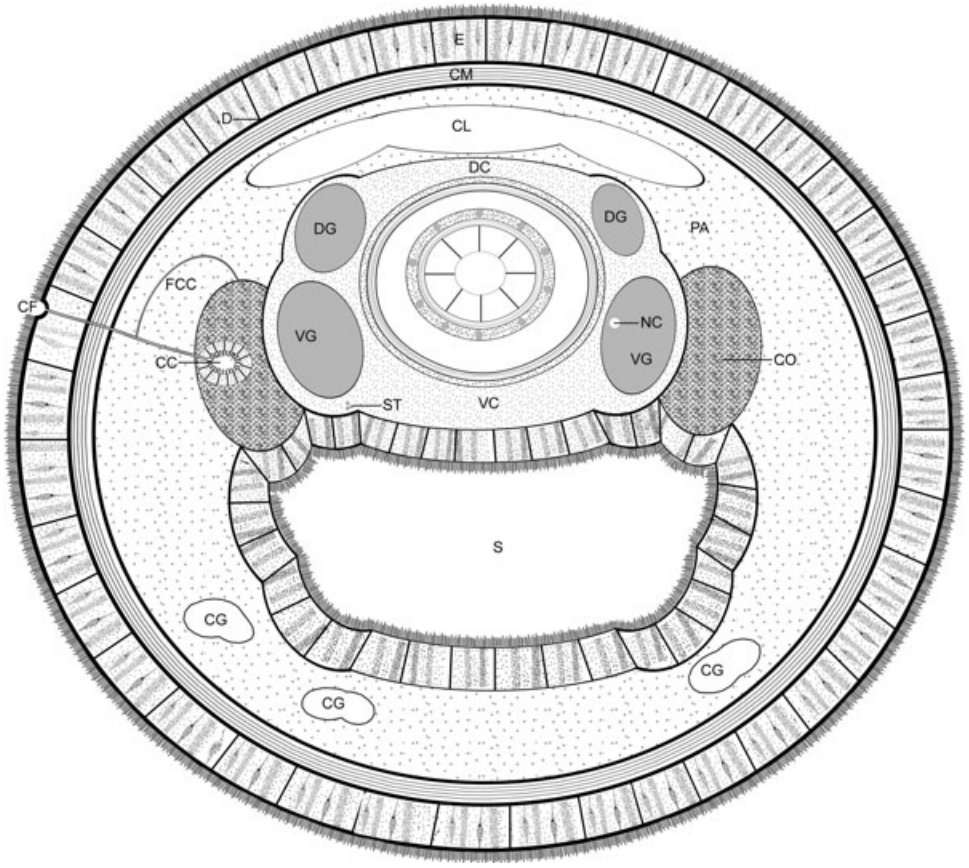

Figure 16. General scheme of the transverse section through the brain region of a nemertean to show the various organs and tissues mentioned in the character matrix. Abbreviations: Layers and structures of the body wall. E, epidermis; D, dermis; CM, circular muscle layer; LM, longitudinal muscle layer; CF, cephalic furrow. Nervous system and sensory organs: DG, dorsal ganglion; VG, ventral ganglion; VC, ventral commissure; DC, dorsal commissure; NC, neurochord cell; ST, statocyst; CO, cerebral organ; CC, ciliated cerebral canal; FCC, forked cerebral canal; CG, dorsolateral extensions of cephalic glands; CL, cephalic lacuna; S, stomach.

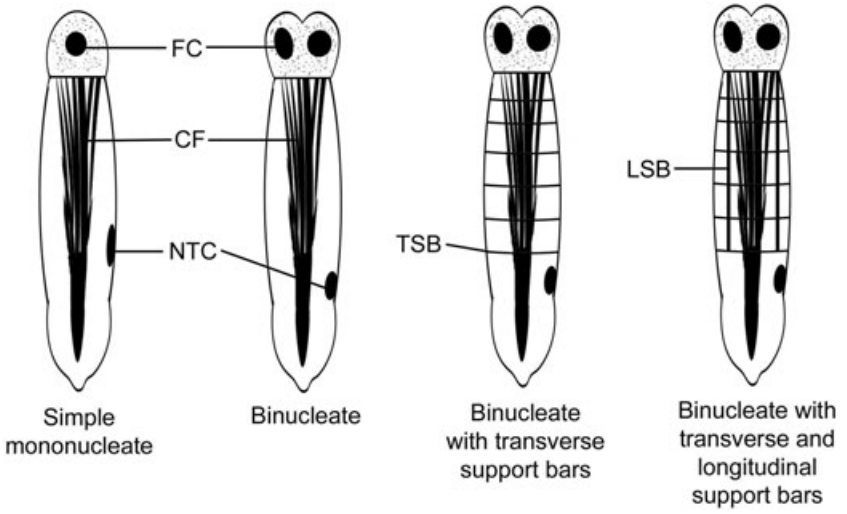

Figure 17. Schematic representation of different flame cell types present in nemerteans. Abbreviations: CF, ciliary flame; FC, flame cell; LSB, longitudinal support bar; NTC, nucleus of terminal chamber; TSB, transverse support bar. (Redrawn after Coe, 1930).