

Remarks on marine interstitial nemertines and key to the species

Jon L. Norenburg

Frenchman Bay Biological Laboratory, Salsbury Cove, ME 04672, USA

Key words: Nemertina, interstitial, mesopsammon, taxonomy, key

Abstract

Interstitial nemertines are highly specialized members of the phylum. All four orders are represented, but the hoplonemertines dominate in diversity and abundance. New genera and higher taxa are still being discovered. Brief reviews published during the last two decades summarize various aspects of the nature of interstitial nemertines. This presentation augments these reviews and provides a key designed for use with living interstitial nemertines. A procedure is advocated for formal topographic description of the cephalic ciliary cirri, thereby enhancing their potential taxonomic utility.

Interstitial nemertines inhabit the pore space between sediment particles. They can pass through a 0.5 mm mesh sieve and, in general, occupy sediments that are relatively coarse and in which the pore space contains little silt and organic particulate matter. In such sediments these worms need not displace sediment in order to move and cilia can be the principal propulsive agent. As is the case with mesopsammonic representatives of other major taxa, interstitial nemertines constitute a unique biological grouping recognizable by specializations that are characteristic of mesopsammon (see Swedmark, 1964, for review of the nature of interstitial organisms). Most of the represented genera and at least some of the families of nemertines are exclusively interstitial. This degree of taxonomic insularity contrasts with the situation found in small mud-dwelling or epibenthic nemertines that by virtue of size may be regarded as meiofauna, but which are not set apart from macrofaunal nemertines by shared specializations.

Kirsteuer (1971) provided the first integrated synopsis of the interstitial nemertine fauna of marine sand, listing 27 species and describing aspects of their specialized biology. This synopsis was updated recently and expanded upon by inclusion of method-

ology and further discussion of taxonomic characteristics (Norenburg, 1988). Other material of a review nature includes Gerner's (1969) taxonomic account of 4 of the 5 interstitial species of *Cephalothrix* Oersted, and two reviews of the genus *Ototyphlonemertes* Diesing (Müller, 1968; Kirsteuer, 1977). Müller (1968) summarized the literature and provided a key to 14 of the species of *Ototyphlonemertes* known at the time. Kirsteuer (1977), based on additional species descriptions and his own comparative work on *Ototyphlonemertes*, provided an important summary of various morphologic characters and discussed their potential taxonomic utility. Kirsteuer (1986) also discussed the subject of interstitial nemertines as potential stygofauna.

Thirty species of interstitial nemertines have been described; six archinemertines in two genera, one palaeonemertine, no heteronemertines, and 23 hoplonemertines in five genera. Relatively few of the many new species of interstitial nemertines discovered in the last decade have been formally named and described. About ten species, probably valid but unnamed, are described to various extents in the literature (Table 1); this includes the first report of a truly interstitial heteronemertine (Norenburg, 1982, 1985). Many more species are known but un-

Table 1. List and known distribution of interstitial nemertines referenced in key or in previous literature but not listed by Kirsteuer (1971, 1986).

Heteronemertina

Norenburg sp. 59; Richmond Beach, Puget Sound, intertidal

Hoploneimertina

Annuloneimertes minusculus Berg, 1985; Tromsø, Norway, 45–90 m depth

Otocyphlonemertes Gerner (1969) sp.; Canet Plage, France, intertidal

Otocyphlonemertes Mock & Schmidt (1975) sp. 1; Floreana, Galapagos

Otocyphlonemertes Mock & Schmidt (1975) sp. 2; Puerto Nuñez, Galapagos

Otocyphlonemertes Kirsteuer (1977) sp. 1; North Carolina

Otocyphlonemertes Kirsteuer (1977) sp. 11; Brazil, several Caribbean sites

Otocyphlonemertes Kirsteuer (1977) sp. III; Colombia

Otocyphlonemertes Kirsteuer (1977) sp. IV; Massachusetts

Otocyphlonemertes Kirsteuer (1977) sp. A; several islands, Galapagos, at low-water level and sublittoral

Otocyphlonemertes Kirsteuer (1977) sp. B; several islands, Galapagos, sublittoral

Otocyphlonemertes Norenburg sp. 21; Crow Neck, Maine; Portsmouth, New Hampshire; Manomet and Nantucket, Massachusetts, low to sublittoral

Otocyphlonemertes Norenburg sp. 30; Crow Neck, Maine; Portsmouth, New Hampshire; Manomet and Martha's Vineyard, Massachusetts, midlittoral

Otocyphlonemertes Norenburg sp. 39; Richmond Beach and Friday Harbor, Puget Sound, low to sublittoral

Otocyphlonemertes Norenburg sp. 41; Dangriga, Belize, at low water

Otocyphlonemertes Norenburg sp. 45; Martha's Vineyard, Massachusetts, midlittoral

Otocyphlonemertes Norenburg sp. 71; Nobska, Ellipsisville, Manomet, and Nahant, Massachusetts; Liberty Point, Maine, high to sublittoral

Norenburg sp. 11; Nahant, Massachusetts, low to sublittoral

described (unpub. obs. and pers. com. by Gibson, Kirsteuer & Riser).

Kirsteuer (1986) and others have noted that the taxonomy of nemertines is plagued by a high proportion of inadequate species descriptions. This is no less true for the interstitial nemertines. For instance, in more than half of the described species of *Otocyphlonemertes* we do not know the detailed distribution of cephalic cirri, a character that is now promising to be a valuable species diagnostic within that group (Kirsteuer, 1977; unpub. obs.). Thus, in

the key that follows, the distribution of cephalic cirri could provide the simplest means for distinguishing between *Otocyphlonemertes pallida* (Keferstein, 1862) (*sensu* Mock, 1978) and *Otocyphlonemertes santacruzensis* Mock & Schmidt, 1975. For the first we have a figure detailing the distribution of the cirri (Mock, 1978), whereas we have only the information that they are present for the second (Mock & Schmidt, 1975). In contrast, Bürger's (1895: Pl. 29, Fig. 14) sketch of the stylet of *Otocyphlonemertes macintoshi* Bürger, 1895, appears to be intended to portray a stylet that is spirally sculpted, yet he makes no verbal reference to it. Thus, Gerner (1969) was apparently unaware of that possibility when he reported the unique occurrence in Europe of a spirally sculpted stylet in an undescribed species of *Otocyphlonemertes* found at Canet Plage. I believe that the latter may be *O. macintoshi* on the evidence of stylet structure, characteristics of the proboscis and geographic proximity. Even when particular characters have been described, as with other nemertines, it is often difficult to evaluate the variability and, hence, taxonomic potential of these characters. Thus, characters such as number of statolith granules, distribution and number of cephalic cirri, and relative dimensions must be utilized with caution (Kirsteuer, 1977).

As more species are discovered, the diagnostic value of features that were considered to be significant in early works, such as length of rhynchocoel and number of granules in the statolith, though still important, can no longer be used in isolation. Although knowledge of internal anatomy based on histological study is essential to taxonomic work, the small size, transparency and specializations of most interstitial nemertines make observations on living material equally important and also convenient for specific identification by non-specialists. The key that follows is offered as a start in that direction, although it is limited by the often scant information in early publications and the many partially described and unnamed species in the literature. New species, genera and families of interstitial nemertines continue to be found as new geographic regions are explored (e.g. New Zealand; Riser, 1984), as well as in regions that have been examined previously. Most of the undescribed species alluded to above are

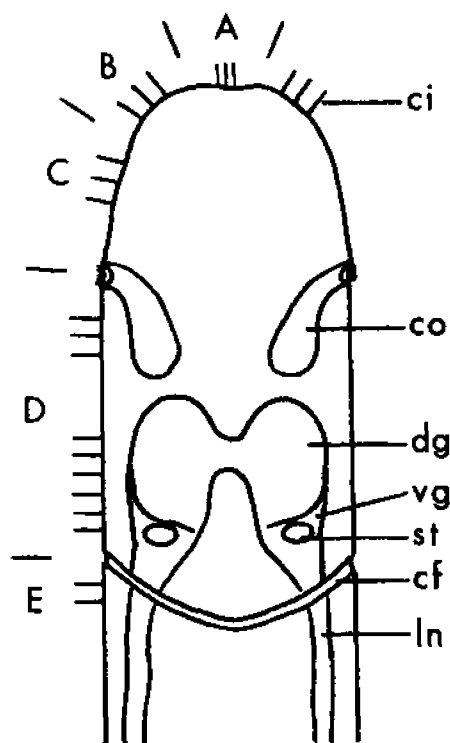


Fig. 1. Schematic illustration of the cephalic region of *Ototyphlonemertes*, demonstrating regions of cirri (A-F) on the left and structures referred to in the key on the right. ci = ciliary cirrus; cf = annular cephalic furrow; co = cerebral organ; dg = dorsal ganglion; ln = lateral nerve cord; st = statocyst; vg = ventral ganglion.

not included in the key because it would be difficult to distinguish them clearly from named species that are in the key but for which we have inadequate information.

Distribution of the ciliary cirri shows clear promise as a potent taxonomic character (Kirsteuer, 1977) but has not been used as such formally. Thus, a formal procedure is proposed here for describing position and number of those cirri that lie along the median horizontal plane (Fig. 1). In this procedure, for example, the number of cirri (x) at the cephalic tip (region A) is described by the formula $A = x$. The letters B through E refer to bilaterally symmetric regions that are successively more posterior. Region D can have discrete anterior (x) and posterior (x') cirri; this is presented in the form $D = x + x'$. Region E is considered here to extend no further than

the foregut; only *O. cirrula* Mock & Schmidt, 1975, is known to have a continuous distribution of cirri posterior to this. Other cephalic cirri having a fixed distribution on the dorsal surface are known from a few species (cf. Norenburg, 1982), but there is no comparable information in the literature. Caudal cirri appear to be present in most species but it is not evident at this time that they have taxonomic utility.

Most species of interstitial nemertines appear to have restricted geographic distributions (Kirsteuer, 1977; unpub. obs.); hence the key is most functional and intended to be used in conjunction with the known distributions. These are listed in large part by Kirsteuer (1971, 1986) and should be consulted. Distribution records for the species presented in the key but not listed by Kirsteuer (*ibid.*) are presented in Table 1. Further information and diagnoses for 'Norenburg' species may be found in Norenburg (1982) under manuscript names.

For purposes of this key several assumptions had to be made. The stylets of *Arenomertes microps* Friedrich, 1933, are assumed to be smooth because they are described in sufficient detail (Friedrich, 1933) to warrant the belief that Friedrich could and would have commented on something as unusual as spirally sculpted stylets. Similarly, proboscideal pseudocnidae were well known at the time of the description of *Procephalothrix kiliensis* Friedrich, 1935, but there is no mention of the proboscis in Friedrich's (1935) description. The species of *Annulonemertes* Berg, are not treated individually because I am at present unable to separate rigorously, within the scheme of this key, three potential congeners from the type species. For instance, an undescribed New England species assignable to the genus *Annulonemertes*, apparently can have two, one or no ocelli (Norenburg, 1982), whereas the only described species, *A. minusculus* Berg, 1985, appears to be eyeless (Berg, 1985). Likewise, *Arenonemertes minutus* Friedrich, 1949, has posterior pseudosegmentation and could be assigned to *Annulonemertes*, but, as noted by Berg (1985), we have insufficient data to do so unequivocally. Four species of *Ototyphlonemertes* are found at or near the type locale for *Ototyphlonemertes pellucida* Coe, 1943. The original species description of *O. pellucida* appears to include incompatible fea-

tures of at least two of the four; none of these is unambiguously conspecific with *O. pellucida sensu* Corrêa (1961) (unpub. obs.). Hence, *O. pellucida sensu stricto* is not included in the key and its taxonomy awaits formal resolution (in prep.). It is assumed that *Ototyphlonemertes aurantiaca* (Du Plessis, 1891) lacks cephalic cirri, as Gerner (1969: 103) uses this as a feature distinguishing *O. aurantiaca* from *Ototyphlonemertes duplex* Bürger, 1895. However, it is not evident that he had adequate observations of living material to make such a claim. *O. duplex* and *O. santacruzensis* are widely separated geographically (Mediterranean and Galapagos) but are insufficiently described to separate them within the key; hence, they are coupled in the key. Body length is of dubious value as a descriptor, unless accompanied by information on how it was obtained and some sort of statistical qualifier, but it is included in the key because it may provide a useful fieldmark for some species. Most, if not all, length measures indicated refer to actively gliding specimens.

Key to interstitial nemertines

- 1a. Mouth ventral, proboscis simple tubular unit lacking central stylet Anopla 2
- b. Proboscis with 4 specialized regions, 1 with central armature Enopla Hoplonemertina 8
- 2a. Cephalic region long and pointed, without cerebral organs, mouth far posterior to cerebral ganglia Archinemertina 3
- b. Cerebral organs posterior to cerebral ganglia, mouth close to cerebral ganglia Palaeo- or Heteronemertina 7
- 3a. Proboscis with pseudocnidae *Cephalothrix* 4
- b. Pseudocnidae absent (?), dorsal blood vessel present (requires histological sections) *Procephalothrix kiliensis*
- 4a. Caudal adhesive plate present .. *C. pacifica*
- b. Adhesive plate absent 5
- 5a. Rhynchocoel with transverse septa *C. mediterranea*
- b. Septa absent 6
- 6a. Midbody triangular in cross-sectional profile, rhynchocoel two-thirds body length *C. atlantica*
- b. Midbody round in cross-sectional profile, rhynchocoel one-half body length *C. germanica*
- 7a. Cephalic region dorsoventrally flattened with broadly rounded margin, pigment discontinuity at posterior of foregut, cerebral statocysts present (?) ... *Carinina arenaria*
- b. Cephalic region elongate, not wider than foregut region, annular cephalic furrow between cerebral organs and mouth Norenburg sp. 59
- 8a. Intestinal region of body pseudosegmented by annular constrictions of body wall *Annulonemertes*
- b. Not pseudosegmented 9
- 9a. Ocelli present 10
- b. Ocelli absent, cerebral statocysts present ... *Ototyphlonemertes* 13
- 10a. Cerebral statocysts present *Otonemertes marcusii*
- b. Statocysts absent 11
- 11a. Four ocelli, stylets smooth 12
- b. Stylets spirally sculpted; ocelli two rows, each with 3-4 ocelli anterior and 1-3 ocelli posterior to cerebral organs, adults to 35 mm long Norenburg sp. 11.
- 12a. Ocelli reddish-brown, annular cephalic furrow precerebral, rhynchocoel full body length, adults 10-12 mm long *Prostomatella arenicola*
- b. Annular cephalic furrow absent (furrow of cerebral organ pores present), adults to 2-3 mm long *Arenonemertes microps*
- 13a. Stylet spirally sculpted 14
- b. Stylet smooth 25
- 14a. Cerebral organs absent 15
- b. Cerebral organs present 21
- 15a. Proboscis extremely short, rhynchocoel not extending beyond stomach 16
- b. Rhynchocoel more than one-third body length 17
- 16a. Anterior and lateral cephalic cirri present, adults to 5 mm long *O. lactea*
- b. Cephalic cirri absent, adults to 8 mm long *O. americana*
- 17a. Proboscis vesicle globose or its length less than

- twice its width 18
- b. Proboscis vesicle length greater than twice its width 19
- 18a. Anterior and lateral cephalic cirri present, adhesive over most of body, statolith 7–10 granules, adults to 11 mm long Norenburg sp. 30 (*O. pellucida*, in part, *sensu* Coe, 1943)
- b. Cephalic cirri absent, caudal adhesion (plate observable in histological section) statolith 16–18 granules, adults to 11 mm long Norenburg sp. 41
- 19a. Accessory stylet sacs posterior to central basis, statolith approximately 16 granules, dorsal cephalic cirri present, adults to 20 mm long (sp. IV?; Kirsteuer, 1977) Norenburg sp. 71
- b. Accessory stylet sacs anterior or lateral to central basis 20
- 20a. Length of proboscis diaphragm (stylet chamber) about 2.5 times combined length of basis and stylet, cephalic cirri absent, statolith 8–12 granules, adults to 30 mm long *O. macintoshi*
- b. Length of proboscis diaphragm not much greater than diameter, vesicle length similar to that of anterior proboscis chamber, statolith 12–16 granules, adults to 5 mm long Mock & Schmidt sp. 1
- 21a. Pair lateral 'sensory' grooves in foregut region, proboscis vesicle elongate, rhynchocoel 1/4 body-length, adults to 50 mm *O. spiralis*
- b. Lateral 'sensory' grooves lacking, rhynchocoel 1/3 to 1/2 body-length 22
- 22a. Caudal adhesive plate present 23
- b. Caudal adhesive plate lacking 24
- 23a. Proboscis vesicle short but cylindrical, well developed cerebral organs, lateral nerve cords with 3–4 anterior swellings, proboscis papillae with 'rhabdites', adults to 20 mm long *O. fila*
- b. Proboscis vesicle globose, cerebral organs small, cephalic cirri A = 0, B = 0, C = 4, D = 1, E = 0, adults to 7 mm long Norenburg sp. 45
- 24a. Proboscis papillae squat and lacking 'rhabdites', cerebral organs well developed, cephalic cirri A = 4, B = 0, C = 6, D = 2, E = 1, adults to 12 mm long (*O. fila* of Mock & Schmidt, 1975) Kirsteuer sp. A
- b. Proboscis papillae with 'rhabdites', cerebral organs small pits, adults to 3 mm long, cephalic cirri unknown *O. parmula*
- 25a. Cerebral organs present 26
- b. Cerebral organs absent, rhynchocoel not reaching intestine, statolith about 10 granules, adhesive plate present, adults to 10 mm long *O. brevis*
- 26a. Statolith usually 2, 3 or 4 granules, rarely up to 10 27
- b. Statolith approximately 20 granules, cirri extend along entire length of body, adult at 3 mm long *O. cirrula*
- 27a. Pair brown pigment patches anterior to cerebral organs, adults to 20 mm long *O. brunnea*
- b. Without precerebral pair brown pigment patches 28
- 28a. Length of stylet to basis approximately 2:1 29
- b. Length of stylet to basis approximately 1:1 30
- 29a. Proboscis papillae with 'rhabdites', cephalic cirri A = 0, B = 6, C = 10, D = 5 + 6 (or E = 6?), adults to 12 mm long *O. erneba*
- b. Proboscis papillae without 'rhabdites', cephalic cirri A = 5, B = 0, C = 4, D = 0, E = 0, adults to 10 mm long *O. erneba* of Mock & Schmidt, 1975) .. Kirsteuer sp. B
- 30a. Caudal adhesive plate present 31
- b. Caudal adhesive plate absent 34
- 31a. Anterior proboscis chamber at least 2–3 times length of posterior chamber 32
- b. Anterior proboscis chamber only slightly longer than posterior chamber, adults to 7 mm long *O. antipai*
- 32a. Cephalic cirri present 33
- b. Cephalic cirri absent, adults to 10 mm long *O. aurantiaca*
- 33a. Rhynchocoel to one-half body length, cephal-

- ic cirri A = 0, B = 4, C = 5, D = 4 + 6, E = 0, adults to 20 mm long *O. pallida*
- b. Rhynchocoel approximately one-third body length, exact distribution of cephalic cirri unknown, adults to 10 mm long . . . *O. duplex* or *O. santacruzensis*
- 34a. Anterior proboscis chamber at least twice the length of posterior chamber 35
- b. Anterior and posterior proboscis chambers approximately equal lengths, cephalic cirri A = 2, B = 0, C = 2, D = 2, E = 0 (unpub. obs. on Florida specimens), adults to 30 mm long *O. evelinae*
- 35a. Intestine with single spiral constriction forming pseudo-diverticula, cephalic cirri A = 3, B = 4, C = 7, D = 6, E = 0, adults to 8 mm long Norenburg sp. 21
- b. Intestine with irregularly spaced, deep furrows, cephalic cirri A = 0, B = 4, C = 1, D = 2 + 2, E = 0, adults to 8 mm long Norenburg sp. 39

Acknowledgements

Presentation of this work at the 'Second International Meeting on Nemertean Biology' was supported by NSF award BSR-8603561 to Jon L. Norenburg and Pamela Roe.

References

- Berg, G., 1985. *Annulonemertes* gen. nov., a new segmented hoplonemertean. In S. C. Morris, J. D. George, R. Gibson & H. M. Platt (eds), *The Origins and Relationships of Lower Invertebrates*. Oxford University Press, NY: 200-209.
- Bürger, O., 1895. Nemertinen. *Fauna Flora Golf. Neapel* 22: 1-743.
- Coe, W., 1943. Biology of the nemerteans of the Atlantic Coast of North America. *Trans. Conn. Acad. Arts Sci.* 35: 129-328.
- Corrêa, D. D., 1961. Nemerteans from Florida and Virgin Islands. *Bull. mar. Sci.* 11: 1-44.
- Friedrich, H., 1933. Morphologische Studien an Nemertinen der Kieler Bucht, I und II. *Z. wiss. Zool.* 144: 496-509.
- Gerner, L., 1969. Nemertinen aus der Gattungen Cephalothrix und Ototyphlonemertes aus dem marinen Mesopsammal. *Helgoländer wiss. Meeresunters.* 19: 68-110.
- Kirsteuer, E., 1971. The interstitial nemertean fauna of marine sand. *Smithson. Contr. Zool.* 76: 17-19.
- Kirsteuer, E., 1977. Remarks on taxonomy and geographic distribution of the genus *Ototyphlonemertes* Diesing (Nemertina, Monostilifera). *Mikrofauna Meeresboden* 61: 167-181.
- Kirsteuer, E., 1986. Nemertina. In L. Botosaneanu (ed.), *Stygofauna Mundi. A faunistic, distributional, and ecological synthesis of the world fauna inhabiting subterranean waters (including the marine interstitial)*. E.J. Brill, Leiden: 77-75.
- Mock, H., 1978. *Ototyphlonemertes pallida* (Keferstein, 1862) (Hoplonemertini, Monostilifera). *Mikrofauna Meeresboden* 67: 1-14.
- Mock, H. & P. Schmidt, 1975. Interstitielle Fauna von Galapagos XIII. *Ototyphlonemertes* Diesing (Nemertini, Hoplonemertini). *Mikrofauna Meeresboden* 51: 1-40.
- Müller, G. J., 1968. Betrachtungen über die Gattung *Ototyphlonemertes* Diesing 1863 nebst Bestimmungsschlüssel der validen Arten (Hoplonemertini). *Senckenbergiana biol.* 49: 461-468.
- Norenburg, J. L., 1982. Comparative morphology of the nemertine integument: functional and phylogenetic interpretations. Ph.D. Diss., Northeastern Univ., Boston.
- Norenburg, J. L., 1985. Structure of the Nemertine Integument with Consideration of its Ecological and Phylogenetic Significance. *Am. Zool.* 25: 37-51.
- Norenburg, J. L., 1988. Nemertina. In R. Higgins & H. Thiele (eds), *Introduction to the Study of Meiofauna*. Smithsonian Institution Press, Washington, DC: (in press).
- Riser, N. W., 1984. General observations on the intertidal interstitial fauna of New Zealand. *Tane* 30: 239-250.
- Swedmark, B., 1964. The interstitial fauna of marine sand. *Biol. Rev.* 39: 1-42.