

1 **Do morphological and functional traits of free-living marine**
2 **nematodes mirror their taxonomical diversity?**

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15 **Abstract**

16

17 The taxonomical structure or diversity of nematode assemblages are the main attributes

18 analyzed in ecology, but their adaptations to the habitats are still under studied.

19 Accordingly, a survey on some known and other newly proposed morpho-functional traits

20 was carried out in order to: understand if the morpho-functional diversity may mirror the

21 taxonomical one and assess potential nematode adaptations to granulometry and

22 hydrodynamic stress. All the morpho-functional traits showed significant differences in

23 relation to these environmental parameters. Medium-coarse sands (M-CS) and medium

24 energy level (MEL) revealed the highest taxonomical and morpho-functional diversity. M-

25 CS and MEL were likely richer in micro-habitats and subject to a low selective pressure

26 hosting nematodes with a wide range of adaptations. The mirroring of the morpho-
27 functional diversity with taxonomical one is crucial for the future growth in the use
28 nematodes in biomonitoring because the only study of the morpho-functional traits could
29 be hypothesized reducing efforts and costs.

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31 **Key-words:** Nematoda; granulometry; morpho-functional diversity; physical stress;
32 adaptations.

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1. Introduction

Nematodes are arguably the most successful free-living metazoans on Earth (Da Rocha et al., 2006; Boufahja et al., 2015). They have colonized all climatic regions and environments, even the most extreme ones. For instance, *Halicephalobus mephisto*, a free-living terrestrial nematode, was found at a depth of 3.6 kilometers under the earth's crust (Borgonie et al., 2011). This phylum is considered "plastic" because it is able to change or adapt itself under selective pressures or stressful conditions (Tahseen, 2012; Semprucci and Balsamo, 2014a). They are key organisms in marine ecosystems with a documented role in trophic chains and recirculation of nutrients (Zeppilli et al., 2015; Semprucci et al., 2016a).

In the last decades, the interest in the application of marine nematodes in ecological assessment as bioindicators has greatly increased (see Semprucci et al., 2015 for review). In this regard, the taxonomical structure of their assemblages and the indices of diversity are often used as tools of comparison in the ecological studies. The nematodes' adaptations, that allow them to live in specific ecological conditions or survive to perturbations, are not well studied although they are very important in understanding the ecology of the group. For instance, there is evidence that the loss in nematode trophic diversity is closely related to the loss of marine ecosystem functioning (Danovaro et al., 2008). Thus, to make a proper use of nematodes possible in monitoring programs, it is crucial to collect all the information about how their morphological and functional traits vary by the changing of ecological conditions, especially of the natural variables. It is documented that nematode assemblages may be influenced by various environmental parameters (Raes et al., 2007; Giere, 2009), but especially the relationship between sediment features and nematode assemblage composition has been a central theme in meiobenthic ecology (Fonseca et al. 2014). The sediment type is recognized to affect both

62 horizontal and vertical distribution of the meiobenthic assemblages (e.g. Vanaverbeke et
63 al., 2002; Steyaert et al., 1999, 2003; Semprucci et al., 2010b; Boufahja et al., 2016). In
64 turn, sedimentological characteristics of a study area are closely linked to its hydrodynamic
65 conditions that allow the deposition or the removal of sediments and thus indirectly create
66 the micro-habitat in which meiofauna live (Semprucci et al., 2010a, 2011).

67 Several morpho-functional traits of free-living nematodes are thought to be related to
68 important ecological functions. Wieser (1959) was the first nematologist that associated
69 morphological characters of nematode species with their habitat features in studying
70 material collected during the Chile expedition (1948-49). He first created functional groups
71 of nematodes based on the morphology of the buccal cavity (Wieser, 1953). hypothesizing
72 that the different buccal structures of marine nematodes might be related to different
73 trophic roles in the ecosystem. This classification has then been widely applied in
74 nematode ecology even if Moens and Vincx (1997) underlined the need of laboratory
75 experiments to document the real trophic style of each species, and also the difficulty in
76 assigning the trophic group to a given specimen only on the base of the mouth features.
77 Despite these criticisms, Wieser's classification has been the only applied so far in field
78 studies.

79 Tail shape is another nematode trait that seems to play an important role in locomotion,
80 feeding, and reproduction. Thistle and Sherman (1985) divided nematodes species into 11
81 categories on the base of the tail shape and Thistle et al. (1995) subsequently reduced this
82 number to 4 categories.

83 Life-style is an important biological and ecological character of nematodes, on which
84 Bongers (1990) and Bongers et al. (1991) created a classification, distinguishing the trait
85 of colonizer (c) species from that of persister (p) species in 5 classes. He classified
86 nematode species along a scale from extreme *r*-strategists (short life cycle, high
87 reproduction rates, high colonization ability, and tolerance to stress) to *k*-strategists (long

88 life cycle, few offspring, low colonization ability and sensitivity to stress). C–p ranking is
89 mainly recognized as a functional trait, but it is also related to a different body size of
90 nematodes: *r*–strategists are generally small-sized, while *k*–strategists show greater body
91 dimensions.

92 Other morpho-functional traits may have an adaptive role and can be easily identified
93 because they are diagnostic characters for the taxonomical identification. Among them,
94 amphids are the largest and most complex sensorial organs of the nematode cephalic
95 region (Decraemer et al., 2014). They are chemioreceptor organs used during the search
96 of food and partner. It has been observed that terrestrial nematodes have small,
97 sometimes punctiform amphids likely because they inhabit environments with a rich food
98 supply, while large amphids are generally more frequent in open fresh waters where
99 chemical information travels greater distances (see Cesaroni et al., 2017). Despite their
100 importance, there are not data about possible occurrence of amphids related to particular
101 habitat features in marine environment. In our study, we recognized numerous types of
102 amphids that we have subdivided in 7 main categories on the basis of the shape of the
103 amphideal fovea and the extension of exposure surface to chemical information.

104 Body cuticle is a morphological trait that numerous literature data relate with sediment
105 type and hydrodynamic conditions, even if so far no functional category is recognized on
106 this base (i.e. Raes et al., 2007; Semprucci et al., 2014a). According to this observed
107 relation, we have characterized 6 categories of the body cuticle morphology, basing on the
108 observations carried out under light and electron scanning microscopy.

109 Therefore, the present study aims to test how some selected nematode traits may
110 change over the spectra of both sediment grain-size and hydrodynamic energy level.
111 Some traits cited above have already found a wide application in marine ecology as
112 functional categories (e.g. trophic groups, tail shapes, c-p classes) (see Schratzberger et

113 al., 2007 for review), whereas amphids have never been investigated in their relation with
114 the habitat and cuticles were studied only in pioneer studies (Wieser, 1959).

115 For this analysis, we selected a geographical area, the Maldivian archipelago, where
116 some localities characterized by a low level of anthropogenic disturbance were previously
117 studied (Semprucci et al., 2014a), and a wide data set (a total of 29 stations) on nematode
118 assemblages was available (see Semprucci and Balsamo, 2014b for review). To avoid
119 potential overlap effects with depth, the data set used in this study were only those from
120 shallow subtidal stations collected with the same sampling process (Fonseca et al., 2014).
121 All these points are fundamental to discriminate the effects from natural or anthropogenic
122 factors as best as possible.

123 Thus, we have put three main questions: are morpho-functional traits of nematodes
124 influenced by the sediment grain-size variations? Are morpho-functional traits influenced
125 by different levels of hydrodynamic conditions? Does morpho-functional diversity mirror the
126 taxonomical diversity trends?

127

128 **2. Materials and Methods**

129 **2.1. Study area**

130

131 Maldives comprises a double chain of 22 atolls and more than 1,200 islands in the
132 central part of the Indian Ocean (6°57'N to 0°34'S) (Fig. 1). The Maldivian archipelago is
133 situated on a carbonate bank that rises from the deep ocean to an approximate depth of
134 2000 m (Kench et al., 2008). The sediments found here are completely of carbonate origin
135 and due to the erosion of the coral reefs (Semprucci et al., 2010a).

136 In detail, the first study was carried out at South Malé and North and East Felidhoo
137 atolls in May 2005 (Semprucci et al., 2010a). Samples were collected from three transects
138 along three back-reef platforms located on the eastern rim. A total of 18 stations were

139 sampled at a water depth that ranged from 0.40 to 5 m (Fig. 1). The texture of the
140 sediments showed a range from very coarse to fine sands, thus, the samples were marked
141 as VCS (very coarse sands), CS (coarse sands), MS (medium sands, FS (fine sand)
142 (Table 1). Since the back-reef platforms were characterized by a scarce wave and current
143 rework of the sediments, the trends observed in this study only reflected the relationship
144 between fauna and sediment grain size.

145 The second investigation was carried out in the South Malé, Rasdhoo and Thoddoo
146 atolls (Central Eastern and Western Maldivian Archipelago) during May 2007 (Semprucci
147 et al., 2011). Samples were collected at three back-reef platforms characterized by a
148 different exposure to wave energy (Fig. 1). Accordingly, transects may be regarded as
149 characterized by an increasing level of hydrodynamic conditions from T107 (LEL) to T307
150 (HEL) (Table 1). The sediments were collected from a total of 10 stations. In this study
151 case, the different current and wave exposure of the areas selected allowed to well
152 discriminate the effect of the hydrodynamic conditions on the nematode assemblages and
153 consequently the detection of potential adaptations to physical stress.

154 The nominal labels of each station studied for the sediment type and hydrodynamic
155 condition and used for statistical analysis were reported in Table 1.

156

157 **2.2. Field sampling and sample processing**

158

159 At each station, three sample replicates of sediment were collected for meiofaunal
160 analysis by a SCUBA diver equipped with a corer tube (diameter 2 cm); an additional
161 sample per station was taken for the sediment characterization. Each sample was added
162 first with Magnesium chloride 7% in aqueous solution for narcotizing meiofauna then with
163 formalin (formaldehyde 4% buffered solution) and Rose Bengal solutions (2 g of Rose
164 Bengal in 1000 ml of ethyl alcohol) (Danovaro et al., 2004). During the sampling, a visual

165 census was carried out in each sampling transect in order to collect information about the
166 most relevant sedimentological processes and hydrodynamic conditions of the study areas
167 (Semprucci et al., 2011).

168

169 **2.3. Sedimentological analysis**

170

171 Sedimentological analysis was performed using a vibro-siever for fractions larger than
172 63 μm , and an X-ray analyzer (Sedigraph 5200) for those smaller than 63 μm . The
173 sediment samples were statistically characterized according to Folk and Ward (1957) and
174 finally classified in accordance with the Wentworth scale (Buchanan, 1984).

175

176 **2.4. Study of the nematode community and morpho-functional traits**

177

178 After meiofaunal extraction (see Semprucci et al., 2010a for details), about 100
179 nematode specimens from each replicate were taken randomly and mounted in permanent
180 slides under stereo-microscope (Seinhorst, 1959). The specimens were identified under a
181 100x oil immersion objective (Optiphot-2 Nikon) using Platt and Warwick (1983, 1988) and
182 Warwick et al. (1998) pictorial keys and the NeMys online identification key (Guilini et al.,
183 2016). The traits of each specimen (i.e. trophic guild, amphideal shape, cuticle
184 morphology, tail shape, life-strategy) were identified on about 8,700 animals.

185 In detail, trophic guild was identified following Wieser's classification according to the
186 various buccal cavity structures: group 1A, selective deposit feeders; 1B, non-selective
187 deposit feeders; 2A, epigrowth feeders; and 2B, predators and omnivores Wieser (1953).

188 Tail shape was defined according to the revision of Thistle et al. (1995) into 4
189 categories: short/round, elongated/filiform, conical, clavate/conical-cylindrical.

190 Life-style (c–p classes) was assigned following Bongers et al. (1991) classification.
191 According to this subdivision, each nematode was classified along a scale of 1 to 5 (from
192 extreme *r*–strategists to *k*–strategists). When a genus was not present in the Bongers’s
193 list, it was assigned to the *taxon* the c–p score at family level.

194 Amphids and cuticle are the only traits for which no data are available on the possible
195 relation between occurrence and a particular environmental feature or type of marine
196 habitat. As for amphids, we hypothesized a division on the basis of the shape of the
197 amphideal fovea and its exposure surface to chemical cues. The numerous types of
198 amphids observed in this study have been grouped into 7 main categories: indistinct, slit-
199 like, pocket-like, rounded or elongate loop, circular, blister-like, longitudinal slit.

200 The cuticle morphology has been categorized in the following 6 types: smooth, with
201 desmens, with a bacteria covering, punctuated or annulated with or without lateral
202 differentiation, punctuated or annulated with longitudinal structures for the whole body
203 length, with wide body annules and longitudinal ridges. We discriminate them on the basis
204 of the most different morphologies using the information obtained both by light and
205 electron scanning microscopy (Cesaroni et al., 2017) (see Supplementary Material 1 for
206 details).

207

208 **2.5. Statistical routine**

209

210 The statistical analysis was based on a total of 84 study cases (28 stations × 3
211 replicates). Possible differences of morpho-functional traits between sediments types and
212 the different hydrodynamic conditions were evaluated using an Analysis of Variance (One-
213 way ANOVA). When significant differences ($p < 0.05$) were noticed, Tukey’s test was used
214 for the pair-wise comparisons. SPSS v.21 program was utilized for the univariate analyses
215 of the data. Dominance curves were performed for each morpho-functional trait both in

216 relation to sediment type and level of hydrodynamic energy. SIMPER test (cut-off of 90%,
217 none transformation) was used to detect the traits that mainly contributed to the
218 differences between the factors analyzed. All the multivariate analyses were performed
219 with the PRIMER software, v.5 (Clarke and Gorley, 2001; Clarke and Warwick, 2001).

220

221 **3. Results**

222 **3.1. Morphological and functional adaptations to sediment types**

223

224 Four amphideal morphotypes resulted significantly different (ANOVA): circular, slit-like,
225 rounded and elongate loop, and indistinct (Table 2). In detail, circular amphids were
226 significantly more abundant in FS (ANOVA, $p < 0.01$; Tukey's test, $p < 0.01$), rounded and
227 elongate loops in MS (ANOVA, $p < 0.01$; Tukey's test, $p < 0.05$), while slit-like and indistinct
228 amphids were more abundant in VCS (ANOVA, $p < 0.001$; Tukey's test, $p < 0.01$).

229 Only two trophic groups resulted significantly different between sediment types. The
230 guild 1B showed significant differences between the sediments with highest abundances in
231 FS (ANOVA, $p < 0.001$; Tukey's $p < 0.001$), while 2B the lowest ones (ANOVA, $p < 0.01$;
232 Tukey's $p < 0.01$) (Table 2).

233 Regarding the cuticle, ANOVA revealed significant differences of smooth ($p < 0.05$),
234 wide body annules and longitudinal ridges ($p < 0.01$), presence of bacteria covering
235 ($p < 0.05$) and punctuation or annulation with longitudinal structures ($p < 0.01$) (Table 2).
236 Smooth cuticle was significantly abundant in CS especially if compared to FS (Tukey's
237 test, $p < 0.05$). Wide body annules and longitudinal ridges as well as punctuation or
238 annulation with longitudinal structures were more abundant in MS especially if compared
239 to CS and FS (Tukey's test, $p < 0.05$ and $p < 0.01$). Nematodes with the presence of a
240 bacteria covering were significantly more abundant in the comparison MS vs. VCS
241 (ANOVA, $p < 0.05$; MS > VCS, Tukey's test, $p < 0.01$).

242 Only conical and clavate conical-cylindrical tails showed significant differences
243 between sediments (ANOVA, $p<0.001$): conical tails were less abundant in FS (Tukey's
244 test, $p<0.01$), while clavate conical-cylindrical tails were more abundant (Tukey's test,
245 $p<0.01$) (Table 2).

246 All colonizer–persister (c-p) classes were represented in the sediments analysed, but
247 only c-p 2, c-p 3 and c-p 4 resulted significantly different. In detail, the class c-p 2 was
248 more abundant in FS especially if compared with M-CS (medium-coarse sands)(ANOVA,
249 $p<0.001$; Tukey's test, $p<0.01$), c-p 3 was more represented in MS especially if compared
250 to CS and FS (ANOVA, $p<0.01$; Tukey's test, $p<0.05$) and c-p 4 was significantly low in
251 FS (ANOVA, $p<0.001$; Tukey's test, $p<0.01$) (Table 2).

252

253 **3.2. Morphological and functional adaptations to hydrodynamic conditions**

254 As concerns amphideal types, circular, rounded and elongate loop, slit-like, longitudinal
255 slit and indistinct amphids resulted significantly different between the different
256 hydrodynamic conditions. In detail, circular amphids were less abundant in the HEL
257 (ANOVA, $p<0.001$; Tukey's test $p<0.001$), while rounded and elongate loops resulted more
258 abundant in the same hydrodynamic condition (ANOVA, $p<0.01$; Tukey's test $p<0.01$).
259 Both slit-like and indistinct amphids resulted more abundant in MEL especially if compared
260 to HEL (ANOVA, $p<0.01$ and $p<0.05$, respectively; Tukey's test $p<0.01$ and $p<0.05$,
261 respectively), while longitudinal slit resulted significantly different in the comparison MEL
262 vs. LEL (MEL>LEL Tukey's test $p<0.05$) (Table 3).

263 The most represented trophic groups were 2A and 1A. Only 1A and 1B were
264 significantly different in the comparison (ANOVA, $p<0.05$ and $p<0.001$, respectively). Non-
265 selective deposit feeders (1B) were significantly low in number and 1A high in the HEL
266 (Tukey's test $p<0.01$ and $p<0.05$, respectively) (Table 3).

267 As for cuticle, smooth aspect and wide body annules and longitudinal ridges were the
268 only two morphologies that resulted significantly different between the three levels of
269 hydrodynamic conditions (ANOVA, $p < 0.01$), but Tukey's test revealed significant
270 differences only in relation to the smooth cuticle ($p < 0.01$) that was higher in the MEL
271 (ANOVA, $p < 0.01$) (Table 3). Notwithstanding, the morphology with wide body annules and
272 longitudinal ridges did not appear significantly different in the pair-wise comparisons, and
273 appeared more abundant in the HEL.

274 The tail with clavate conical-cylindrical shape was the only significant trait between the
275 different hydrodynamic conditions and, in particular, this morphology was more abundant
276 in the MEL (ANOVA, $p < 0.05$; Tukey's test $p < 0.05$).

277 As for classes, the class c-p 2 was low and c-p 4 high in relation to high
278 hydrodynamism (ANOVA, $p < 0.001$; Tukey's test, $p < 0.001$ and $p < 0.01$) (Table 3).

279

280 **3.3. Morpho-functional diversity patterns**

281 In the data set of 2005, the curves of dominance carried out directly on the morpho-
282 functional traits revealed that M-CS were characterized by the greatest diversity of
283 amphids followed by VCS and FS (Fig. 2a). SIMPER routine (cut-off of 90%) showed that
284 the main differences of FS *versus* the other sediment types were the dominance in FS of
285 the circular amphids (over 60%) and a low number of rounded and elongate loop and slit-
286 like amphids. Also the trophic guilds showed the best diversity pattern in M-CS, in which
287 they were mainly represented by 2A, followed by VCS and FS (Fig. 2b). FS was
288 dominated over 54% by 1B that contributed to characterize this sediment type (SIMPER).
289 The diversity curves of the cuticle morphotypes showed a remarkable dominance in all the
290 grain sizes. Nevertheless, it was possible to observe that M-CS showed a better diversity
291 level followed by FS and VCS (Fig. 2c). Despite the cuticle with punctuation or annulation
292 with or without lateral differentiation was dominant in all the sediments types, it contributed

293 especially to distinguish FS along with smooth cuticle (SIMPER). Dominance curves of the
294 tails revealed a notable dominance with a slight better diversity recorded in FS. Here, an
295 equal abundance of clavate conical-cylindrical and conical tails was, in fact, recorded
296 (SIMPER) (Fig. 3a). Regarding the c-p classes, CS showed the best diversity curve
297 followed by VCS, MS and FS (Fig. 3b). CS were especially characterized by c-p 4, while
298 FS by c-p 2 (SIMPER).

299 When the dominance curves were compared for hydrodynamic level of energy, a generally
300 higher diversity in the MEL followed by LEL and HEL was observed (Fig. 4 and 5). This
301 was more evident in relation to amphids and c-p classes, but the curves of MEL showed
302 also in the other traits a less rapid pattern of growth if compared to the other hydrodynamic
303 conditions. In detail, the MEL was distinguished by the high abundance of circular and slit-
304 like amphids, while rounded and elongate loop and spiral amphids were dominant in the
305 HEL (SIMPER) (Fig. 4a). Trophic guilds showed a very low diversity in high hydrodynamic
306 conditions due to the high abundance of 1A (SIMPER) (Fig. 4b). Punctuation or annulation
307 with or without lateral differentiation was the type of cuticle more abundant in HEL that
308 contributed to distinguish it from LEL and MEL), while a low abundance of bacteria
309 covering on the cuticle was revealed at HEL (SIMPER). The dominance curves of c-p
310 classes showed a greater diversity in relation to the MEL, mainly distinguished by c-p 2,
311 while the lowest diversity was revealed in the LEL where the differences were mainly due
312 to c-p 2 and c-p 3 (Fig. 5b). Dominance plots showed a very strong dominance of tail
313 shapes in all the hydrodynamic conditions (Fig. 5a). SIMPER revealed that conical tails
314 were characteristic of the HEL, while clavate conical cylindrical tails were more
315 characteristic of the other conditions. The other types of tails did not contribute in any case
316 to distinguish the three habitats.

317

318 **4. Discussion**

319 There are several morpho-functional traits of free-living nematodes thought to be
320 related to important ecological functions. Wieser was the first nematologist that related
321 morphological characters to the habitat features and created a morpho-functional group on
322 mouth morphology (Wieser, 1953, 1959). Among the '80 and '90 years, other pioneers of
323 the nematology proposed morpho-functional traits based on tail shapes and life strategies
324 (Thistle and Sherman, 1985, Bongers, 1990), but they did not find the same popularity of
325 the trophic groups (e.g. Thistle et al., 1995; Semprucci and Balsamo, 2014b; Semprucci et
326 al., 2017; Jouili et al., in press).

327 The relations between environment and morpho-functional traits of marine nematodes
328 have often been discussed on the base of the presence or relative abundance of a specific
329 family or genus, but only Schratzberger et al. (2007) and Armenteros et al. (2009) directly
330 utilized morpho-functional traits to test possible their relationships with the habitat.
331 However, they did not consider traits such as cuticle and amphid even if these features
332 seem to be affected both by sediment typology and hydrodynamic conditions (Wieser,
333 1959; Neira et al., 2001; Gad, 2002; Vanreusel et al., 2010; Cesaroni et al., 2017).

334

335 **4.1.Are morphological and functional features related to sediment types?**

336

337 Arguably, chemioreceptors such as amphids may perform a different role in the
338 various habitats. It seems that inconspicuous amphids are more frequent in soil waters rich
339 in salts and dissolved organic matter (DOM) probably because the chemical information
340 needs to travel for short distances (a few mm). On the contrary, amphids appear to be
341 well-developed in open fresh waters (usually less rich in DOM), where chemical
342 information travels long distances (Aldo Zullini, personal communication). No data are
343 available about a different occurrence of the amphids in marine habitats, but these
344 observations seem to match our findings because inconspicuous amphids were found in

345 the VCS that were likely rich in food sources. The VCS of the study area were deposits
346 from a strong storm occurred four months before the sampling and not reworked
347 (Semprucci et al., 2010a). Thus, in spite of the coarse granulometry, also detritus
348 progressively deposited along with sediments. Furthermore, the VCS of the reef system
349 are often represented by coral fragments that in turn are rich in biofilm made of bacteria
350 and algae available for nematodes (Raes and Vanreusel, 2006).

351 Epigrowth feeders (2A) did not result significantly associated to particular sediment
352 types even if they appeared more abundant in the M-CS. This trophic guild is generally
353 abundant in carbonate sediments for the high primary production and great abundance of
354 diatoms of this typology of substratum (Boucher, 1997; Raes et al., 2007). Instead, 1B
355 resulted prevalent in muddy sediments because the bacterial growth as well as the
356 deposition of organic detritus increase along with silt and pelite fractions of sediments
357 (Semprucci et al., 2014b). Predators/omnivores (2B) are commonly documented as
358 abundant in the M-CS as was the case of this study that showed them numerous
359 especially in the MS (Netto et al., 1999). This is probably due to high number and variety
360 of preys that this trophic group finds here. Furthermore, Oncholaimidae species (2B),
361 abundant in MS, are only facultative predators and therefore they are also able to feed on
362 detritus (Moens and Vincx, 1997).

363 Raes and Vanreusel (2006) and Vanreusel et al. (2010) documented the high
364 abundance of species with sculptured cuticles as the consequence of the advantage of
365 possessing this strong body covering for survival in coarse and physically harsh substrata.
366 In the present survey, heavily sculptured ornamentations (i.e. wide body annules and
367 longitudinal ridges and punctuation or annulation with longitudinal structures in families
368 Ceramonematidae and Monoposthiidae, respectively) appeared mainly associated to MS
369 probably because these cuticular morphologies may confer a peculiar flexibility and
370 mechanical resistance of the body for moving through small interstitial spaces.

371 Longitudinal ridges or structures like spines may allow flexion of the cuticle during
372 locomotion and be anchorages (Lee, 2002). Also nematodes with a bacteria covering (sub-
373 family Stilbonematinae) were mainly related to the MS, likely due to the symbiotic
374 consortium that needs a relatively sheltered micro-habitat. Stilbonematinae are, in fact,
375 frequently found in intertidal and subtidal porous sediments poorly disturbed by wave
376 action (Tchesunov et al., 2012). The smooth cuticle showed a positive relation with CS as
377 reported by Wieser (1959) that documented a prevalence of smooth cuticles in the
378 exposed littoral sands.

379 Statistical analysis showed a significant abundance of clavate conical-cylindrical tails in
380 FS in accordance with the trends revealed in a tropical semi-enclosed basin of the
381 Caribbean Sea (Armenteros et al., 2009) and in the southwestern North Sea in which they
382 appeared closely linked to sediments rich in silt fraction (Schratzberger et al., 2007).
383 Instead, no relationship was detected between filiform tails and FS as reported by other
384 authors (Riemann, 1974; Schratzberger et al., 2007). This is likely related to the fact that
385 these types of tails do not confer an advantage in carbonate sediments.

386 The species of class c–p 2, as opportunistic, increase in number in adverse
387 environmental conditions (Bongers et al., 1991; Schratzberger et al., 2007; Semprucci et
388 al., 2010b, 2015). Indeed, they resulted more abundant in fine sediments in which hypoxia
389 or anoxia conditions occur more frequently (Frontalini et al., 2014; Semprucci et al.,
390 2014b). The increase in c–p values recorded with the parallel increase in grain size was
391 probably related to the great abundance of Draconematidae and Epsilonematidae (both c–
392 p 4) just related to the grain size increase. Several authors have suggested that the
393 relation of these two families with increasing grain-size is favoured by their peculiar
394 locomotory movements, stout body and annulated cuticle sometimes even covered with
395 small spines (Stauffer, 1924; Lorenzen, 1973).

396

397 **4.2.Are morphological and functional features related to hydrodynamic conditions?**

398

399 When amphids were considered, it was found that rounded and elongate loops were
400 mainly related to the high action of water currents. Indeed, the intense scouring of
401 sediments and food therein can have led to a development of larger chemioreceptors in
402 nematodes. Accordingly, small amphids (slit-like, indistinct, and circular) were here
403 comparatively all less abundant. The removal or resuspension of the organic material from
404 the area with the HEL can be indirectly confirmed by the low number of 1B. The negative
405 relationship between 1B and high physical stress was also suggested by Raes et al.
406 (2007) in the coral degradation zones of Kenya and Zanzibar. The only trophic group that
407 appeared advantaged by the physical stress was the 1A, represented by families
408 Draconematidae and Epsilonematidae, known to be able to withstand even the effects of
409 current erosion (Willems et al., 1982; Raes et al., 2007).

410 Smooth cuticle and cuticle with wide body annules and longitudinal ridges were the
411 only ones that resulted significantly different between the three levels of energy, but pair-
412 wise comparisons revealed significant differences only in relation to the smooth cuticles
413 that could be a possible advantage in relation to the MEL along with clavate conical
414 cylindrical tails. Wide cuticular body annules and longitudinal ridges resulted almost
415 significant and more abundant in the HEL suggesting the high versatility of this cuticle type
416 and its advantage in physically disturbed habitats as documented for instance by
417 Vanreusel et al. (2010). In this physical condition, it was revealed also a low number of
418 nematodes with a bacteria covering on the cuticle confirming that sheltered habitats are an
419 advantage for the bacteria consortium of the Stilbonematinae (Tchesunov et al., 2012; Ott
420 et al., 2014).

421 In contrast to the Bongers's model, the r -strategists resulted numerically lower and k -
422 strategists significantly more abundant where the hydrodynamic stress was strong.

423 However, this unexpected trend was due to the high abundance of Epsilonematidae and
424 Draconematidae (both classified as c–p 4) that, as said above, are well-adapted to
425 physical stress (Semprucci et al., 2011, 2016b). Furthermore, as reported by Losi et al.
426 (2012), representatives of the Epsilonematidae family could be, for some aspects,
427 considered c–p 2 being small and stout nematodes and showing in some cases a
428 tolerance to various types of disturbances (Vanaverbeke et al., 2004; Losi et al., 2012).

429

430 **4.3. Do morpho-functional diversity mirror the taxonomical diversity?**

431

432 When the curves of dominance were analysed, the diversity of morpho-functional traits
433 was higher in M-CS supporting the trends documented by the analysis of the only
434 taxonomical structure of the nematode assemblages (Semprucci et al., 2010a). This is an
435 important goal for the ecology of the phylum because if the morpho-functional diversity
436 may efficiently mirror the changes in the taxonomical diversity, we could reduce the
437 timings and costs of the ecological surveys. The highest diversity of the M-CS is not
438 astonishing because these sediments are characterized by a high number of ecological
439 niches and a wide food availability (see Giere, 2009 and literature therein). The highest
440 richness of trophic niches in the M-CS was further confirmed by the dominance curves of
441 the trophic groups that showed the best trends in the M-CS followed by VCS and FS. The
442 only real exception to the general diversity trends was observed in relation to the tail
443 shapes. Indeed, this trait showed the highest diversity in the FS due to an equal proportion
444 of clavate conical-cylindrical and conical tails.

445 The dominance curve patterns in the three different hydrodynamic conditions generally
446 revealed the highest diversity of traits in relation to the MEL that seems to mirror also in
447 this case the pattern that was documented by the taxonomical structure of the nematode
448 assemblages (Semprucci et al., 2011). Thus, the area with a MEL appears the richest of

species as well as of biological traits. Instead, the LEL and especially the HEL were colonized by species with few, more specific adaptations to these environments. As suggested by Connell (1978), the specialization for living in a habitat characterized by a frequent and intense disturbance is one of the most common causes of diversity reduction followed by competition. Accordingly, the most resistant and adapted species to physical disturbance such as those of families Epsilonematidae and Draconematidae are certainly in advantage over the other nematode species in the HEL and become dominant with a consequent decrease of diversity. Only the shapes of the tails revealed a different trend in both these studies showing the highest diversity in the LEL.

458

459 **5. Conclusions**

All the morpho-functional traits, cuticles and amphids included, resulted significantly different in different conditions of sediment grain size and physical stress. This is very important because further studies could highlight that also other morphological features of nematodes could be adaptive to these habitat features.

M-CS and MEL revealed not only the highest taxonomical diversity, as documented in previous investigations, but also the greatest variety of morpho-functional traits. Thus, both these environmental conditions are characterized by a notable heterogeneity of the micro-habitats and niches leading nematodes to develop a wide range of adaptations to inhabit them. Instead, where the habitat is more selective, the species characterized by a series of more suitable adaptations become dominant and lead to a reduction of the overall diversity.

The mirroring of the morpho-functional diversity with the taxonomical diversity is not only important from an evolutionary point of view, but it may be an important issue for the modern ecology because ecologists could use only the biological traits in the ecological surveys reducing the efforts and costs during the monitoring programs.

475

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477

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Figure 1. Map with the location of the sampling transects. The colour of the dots highlight the different period of the sampling cruises (white: 2005; grey: 2007).

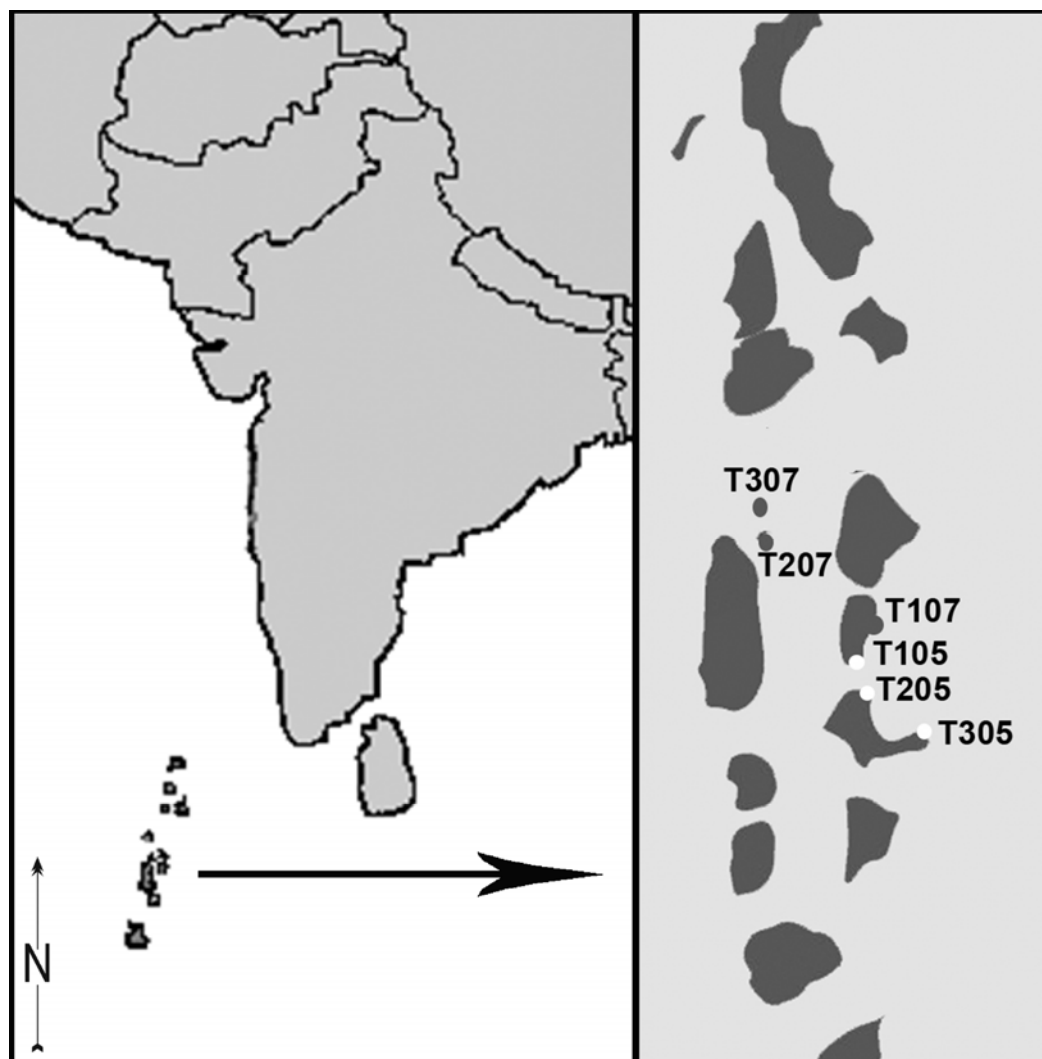


Figure 2. Curves of cumulative dominance obtained using amphideal fovea (a), buccal ~~cavities~~ cavity (b) and cuticles (c) in relation to the sediment types.

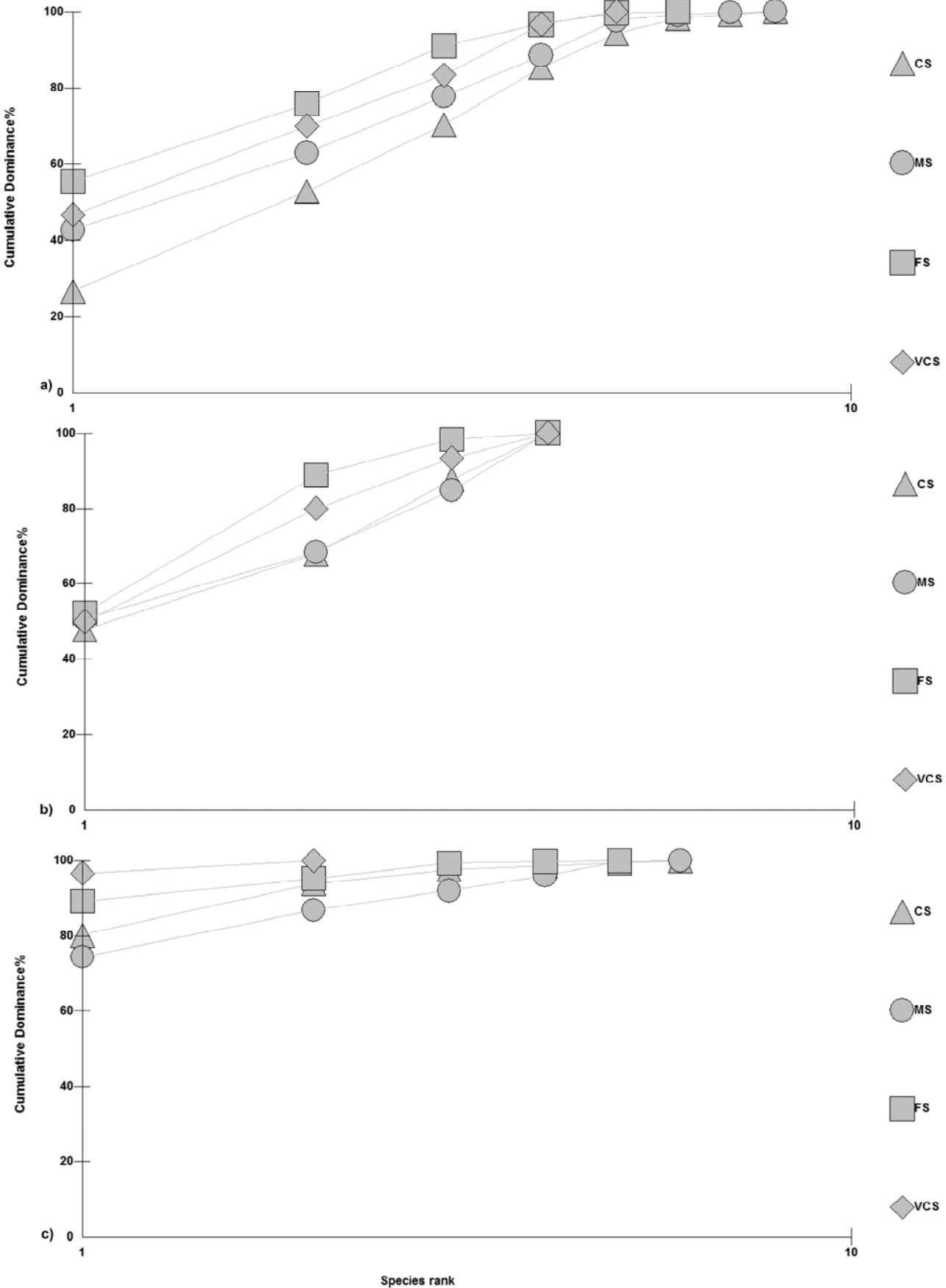


Figure 3. Curves of cumulative dominance obtained using tail (a), c-p classes (b) in relation to the sediment types.

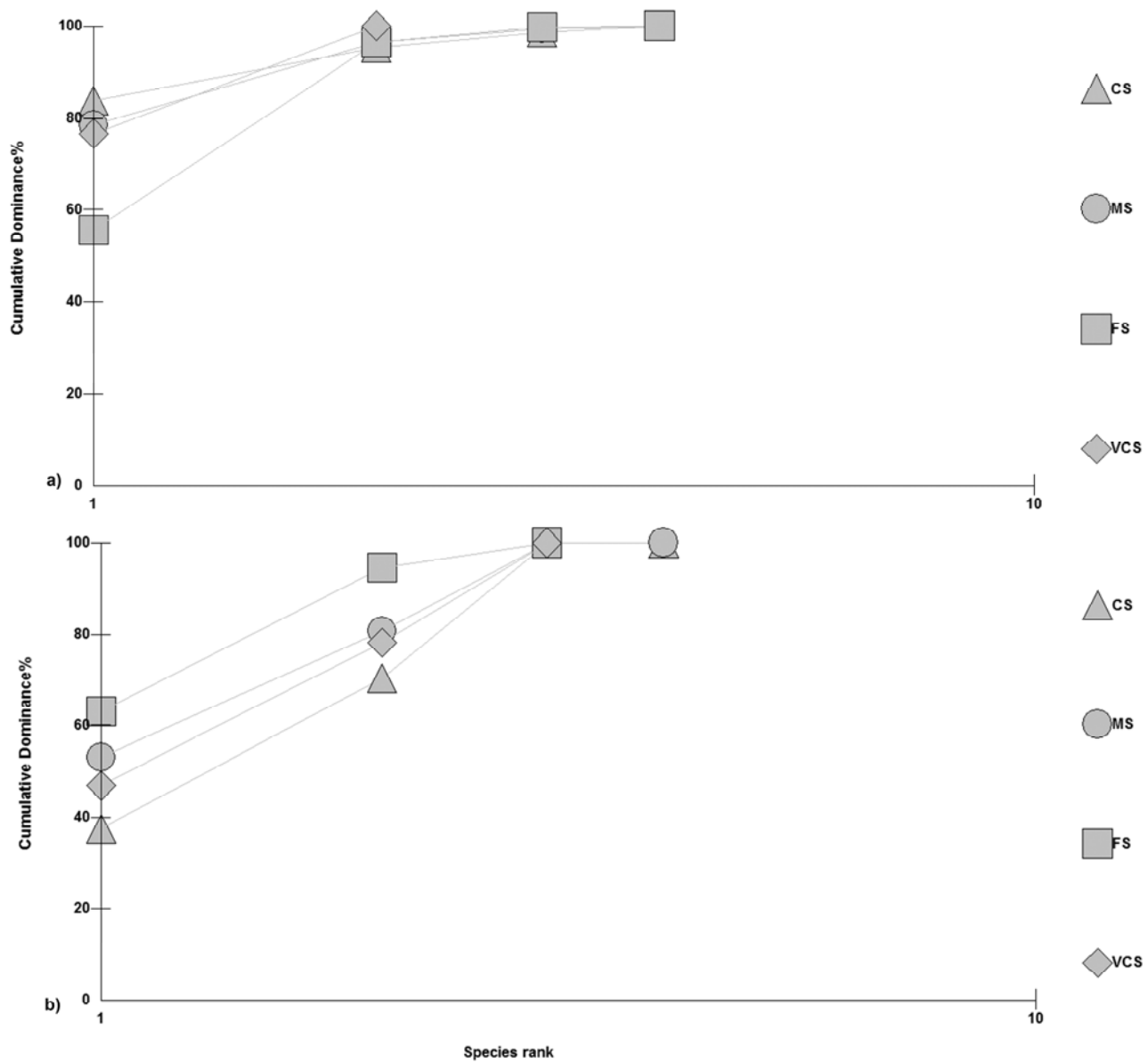


Figure 4. Curves of cumulative dominance obtained using amphideal fovea (a), buccal ~~cavities~~ cavity (b) and ~~cuticles~~ cuticle (c) in relation to the sediment types.

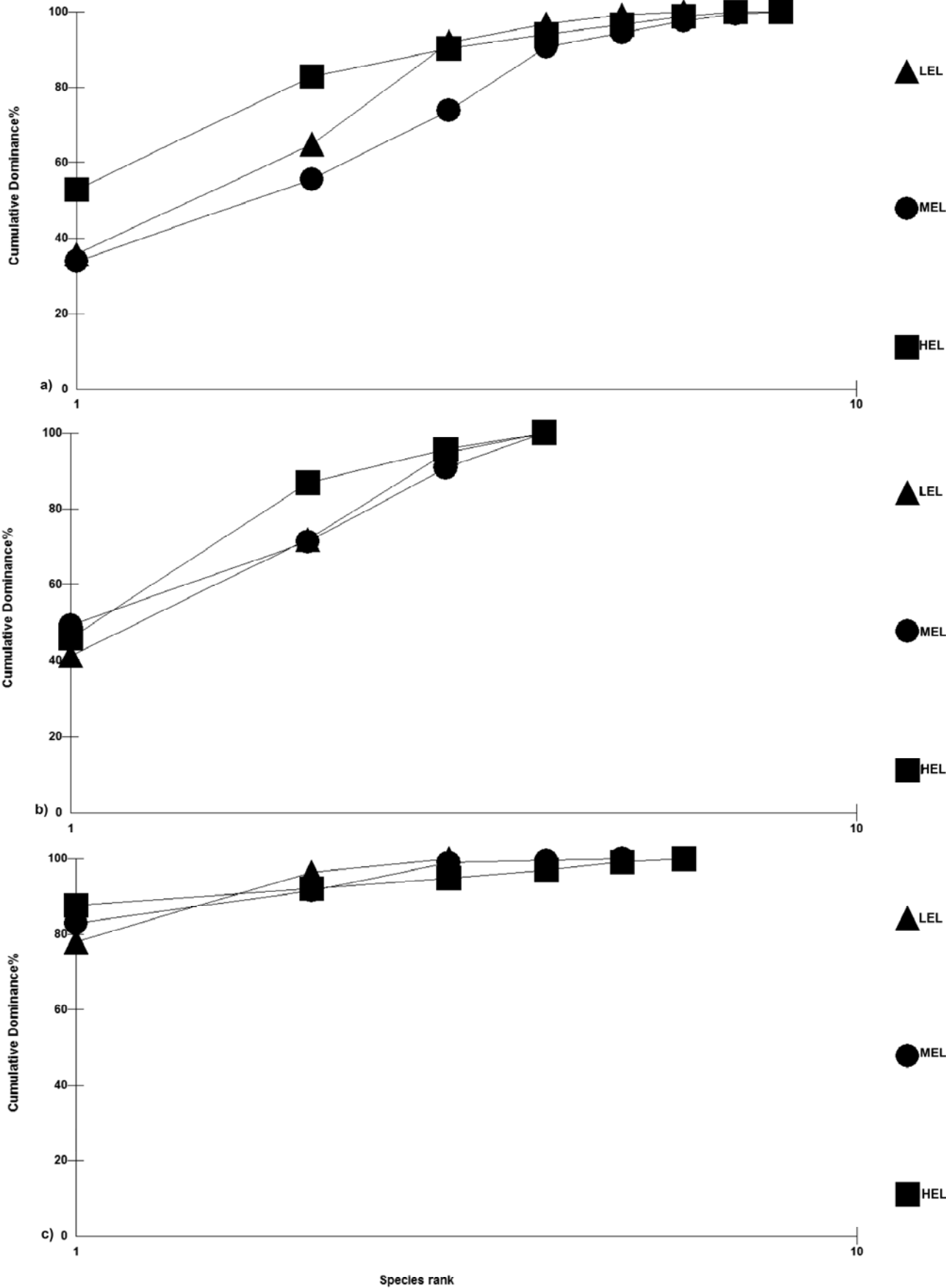


Figure 5. Curves of cumulative dominance obtained using tail (a), c-p classes (b) in relation to the sediment types.

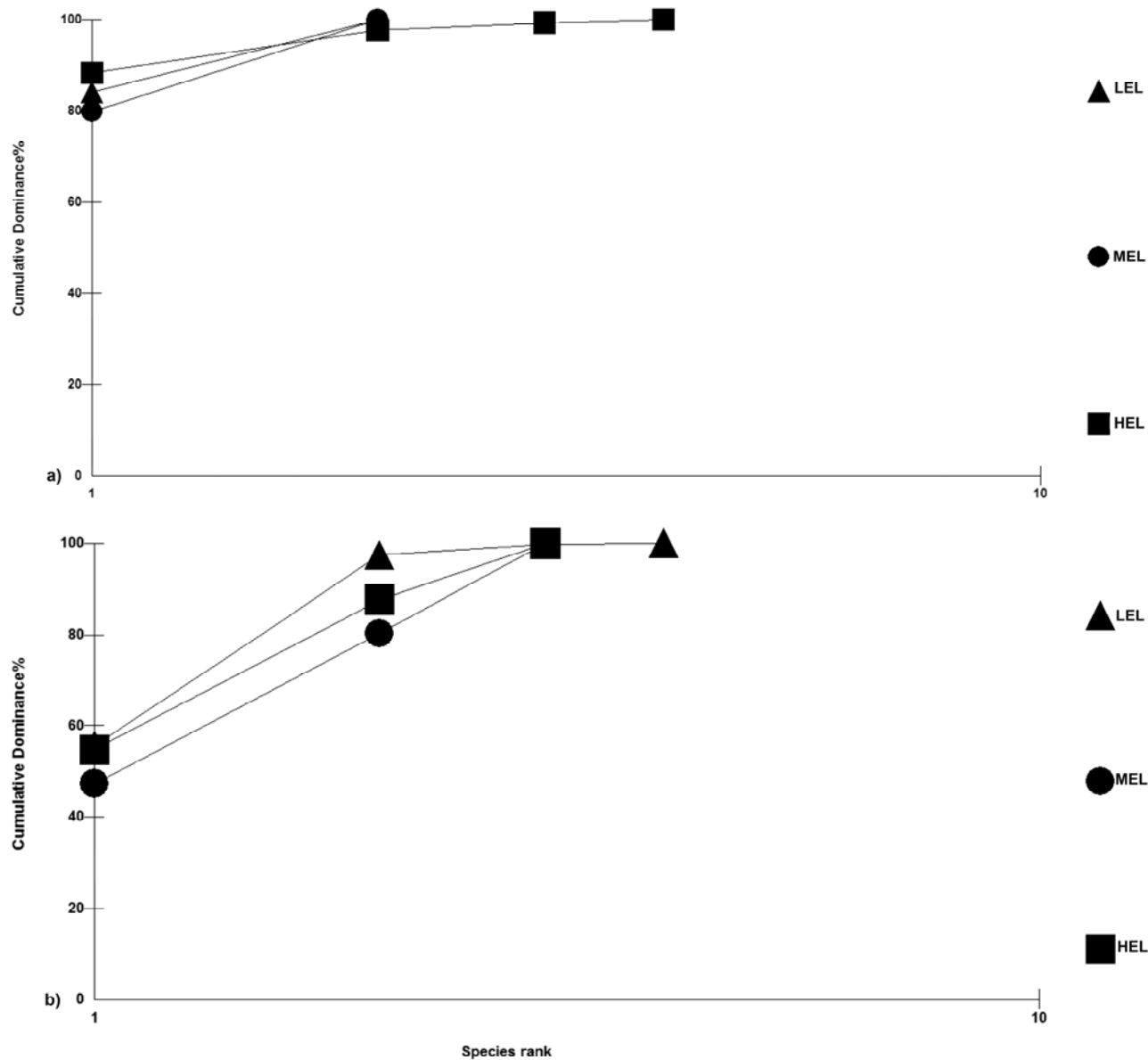


Table 1. Sedimentological parameters at each sampling transect and station of the scientific cruises in 2005 and 2007.

Transect	Station	Gravel %	Sand %	Mud %	Mean size Mz	Nominal label of the sample
T105	St. 1/105	15.32	83.02	1.66	0.00	CS
	St. 1/205	6.49	86.21	7.30	1.03	MS
	St. 1/305	3.49	94.41	2.10	0.99	CS
	St. 1/405	0.09	93.60	2.31	1.33	MS
	St. 1/505	9.77	85.61	4.63	0.87	CS
	St. 1/605	16.03	76.99	6.98	0.94	CS
T205	St. 2/105	11.57	88.36	0.07	0.23	CS
	St. 2/205	14.25	82.76	2.98	0.53	CS
	St. 2/305	1.01	89.06	9.93	2.27	FS
	St. 2/405	0.11	95.18	4.71	2.81	FS
	St. 2/605	16.61	82.03	1.36	-0.22	VCS
	St. 2/705	4.77	94.94	0.30	0.71	CS
T305	St. 2/805	9.23	89.35	1.42	1.19	MS
	St. 3/105	2.40	92.99	4.61	1.67	MS
	St. 3/205	1.54	96.47	2.00	1.90	MS
	St. 3/405	7.89	90.85	1.27	0.70	CS
	St. 3/505	8.47	90.75	0.77	0.76	CS
	St. 3/605	7.29	85.43	7.27	0.67	CS
T107	St. 1/107	13.67	83.61	2.71	0.24	LEL
	St. 1/207	16.37	80.75	2.88	0.3	LEL
	St. 1/307	7.64	89.81	2.55	0.77	LEL
T207	St. 2/107	12.76	84.99	2.25	0.49	MEL
	St. 2/207	11.08	87	1.92	0.71	MEL
	St. 2/307	9.79	88.18	2.03	0.68	MEL
T307	St. 3/107	2.02	93.84	4.14	0.98	HEL
	St. 3/207	13.65	83.73	2.62	0.38	HEL
	St. 3/307	5.13	91.33	3.54	1.02	HEL
	St. 3/407	0.85	96.61	2.54	0.09	HEL

Table 2. Results of the one-way ANOVA on the morphological and functional traits between sediment types (VCS= very coarse sands; CS= coarse sands; MS= medium sands; FS= fine sands; n.s.= not significant; p= level of significance).

One-way ANOVA		Tukey's test	
Sediment type	F	Sig.	Pair-wise comparisons
Circular	5.546	0.002	FS>VCS, CS and MS; p<0.01
Pocket like	-	n.s.	-
Rounded and elongate loop	5.062	0.004	MS>VCS, CS and FS; p<0.05
Slit like	21.113	0.001	CS>MS, FS; p<0.001 and VCS>MS and FS; p<0.01
Spiral	-	n.s.	-
Blister-like	-	n.s.	-
Longitudinal slit	-	n.s.	-
Indistinct	9.217	0.001	CS>VCS, MS and FS; p<0.01
1A	-	n.s.	-
1B	29.09	0.001	FS>CS, MS; p<0.001
2A	-	n.s.	-
2B	4.99	0.01	FS<MS; p<0.01
Punctuation or annulation with or without lateral differentiation	-	n.s.	-
Smooth	4.018	0.012	CS>FS; p<0.05
Wide body annules and longitudinal ridges	4.819	0.005	MS>CS and FS; p<0.05
Desmens	-	n.s.	-
Presence of bacteria covering	3.487	0.022	MS>VCS; p<0.01
Punctuation or annulation with longitudinal structures for the whole length of the body	5.237	0.003	MS>CS and FS; p<0.01
Short/round	-	n.s.	-
Elongated/filiform	-	n.s.	-
Clavate conical cylindrical	7.864	0.001	FS>CS, MS; p<0.01
Conical	19.343	0.001	FS<VCS, CS and MS; p<0.01
C-p 1	-	n.s.	-
C-p2	7.355	0.001	FS>CS and MS; p<0.01
C-p3	5.469	0.002	MS>CS and FS; p<0.05
C-p4	18.802	0.001	FS<VCS, CS and MS; p<0.01
C-p5	-	n.s.	-

Table 3. Results of the one-way ANOVA on the morphological and functional traits between the different levels of hydrodynamic energy (HE= High Energy; ME= Medium Energy; LE= Low Energy; n.s.= not significant; p= level of significance).

One-way ANOVA		Tukey's test	
Level of hydrodynamic conditions	F	Sig.	Pair-wise comparisons
Circular	10.388	0.001	HEL<LEL and MEL; p<0.001
Pocket like	-	n.s.	-
Rounded and elongate loop	5.729	0.008	HEL>LE; p<0.01
Slit like	7.534	0.003	MEL>HEL; p<0.01
Spiral	-	n.s.	-
Blister-like	-	n.s.	-
Longitudinal slit	4.061	0.029	MEL>LEL; p<0.05
Indistinct	3.911	0.032	MEL>HEL; p<0.05
1A	3.073	0.05	HEL>LEL and MEL; p<0.05
1B	17.999	0.001	HEL<LEL and MEL; p<0.01
2A	-	n.s.	-
2B	-	n.s.	-
Punctuation or annulation with or without lateral differentiation	-	n.s.	-
Smooth	5.531	0.010	MEL>HEL; p<0.01
Wide body annules and longitudinal ridges	4.0227	0.030	n.s.
Punctuation or annulation without lateral differentiation	-	n.s.	-
Desmens	-	n.s.	-
Presence of bacteria covering	-	n.s.	-
Punctuation or annulation with longitudinal structures for the whole length of the body	-	n.s.	-
Short/round	-	n.s.	-
Elongated/filiform	-	n.s.	-
Clavate conical cylindrical	3.787	0.035	HEL<MEL; p<0.05
Conical	-	n.s.	-
C-p 1	-	n.s.	-
C-p2	13.139	0.001	HEL<MEL and LEL; p<0.001
C-p3	-	n.s.	-
C-p4	12.669	0.001	LEL<MEL and HEL; p<0.01

Supplementary material 1

Genus	Amphideal fovea	Buccal cavity	Cuticle	Tail	C-p class
Actinonema	rounded and elongate loop	2A	punctuation or annulation with lateral differentiation	conical	4
Aegialoalaimus	circular	1A	punctuation or annulation without lateral differentiation	conical	4
Alaimella	circular	1A	punctuation or annulation with longitudinal structures for the whole length of the animal	conical	3
Ammotheristus	circular	1B	punctuation or annulation without lateral differentiation	conical	2
Amphimonhystera	circular	1B	punctuation or annulation without lateral differentiation	clavate/conicalcylindrical	2
Anticoma	pocket like	1A	smooth	clavate/conicalcylindrical	2
Antomicron	rounded and elongate loop	1A	punctuation or annulation without lateral differentiation	clavate/conicalcylindrical	3
Ascolaimus	rounded and elongate loop	1B	punctuation or annulation without lateral differentiation	conical	2
Astomonema	circular	1A	punctuation or annulation without lateral differentiation	conical	3
Atrochromadora	slit like	2A	punctuation or annulation with lateral differentiation	conical	4
Axonolaimus	rounded and elongate loop	1B	punctuation or annulation without lateral differentiation	clavate/conicalcylindrical	2
Bolbonema	spiral	1A	punctuation or annulation without lateral differentiation	conical	3
Calomicrolaimus	circular	2A	punctuation or annulation without lateral differentiation	conical	2
Camacolaimus	spiral	2A	punctuation or annulation without lateral differentiation	clavate/conicalcylindrical	3
Campylaimus	rounded and elongate loop	1B	punctuation or annulation without lateral differentiation	clavate/conicalcylindrical	3
Cephalanticoma	pocket like	2A	smooth	clavate/conicalcylindrical	2
Ceramonema	rounded and elongate loop	1A	wide body annules and longitudinal ridges	conical	3
Chitwoodia	rounded and elongate loop	1A	punctuation or annulation without lateral differentiation	conical	3
Chromadora	slit like	2A	punctuation or annulation with lateral differentiation	conical	3
Chromadorella	slit like	2A	punctuation or annulation with lateral differentiation	conical	3
Chromadorina	slit like	2A	punctuation or annulation without lateral differentiation	conical	3
Chromadorita	slit like	2A	punctuation or annulation without lateral differentiation	conical	3
Chromaspirina	rounded and elongate loop	2B	punctuation or annulation without lateral differentiation	conical	4
Cobbia	circular	2A	punctuation or annulation without lateral differentiation	clavate/conicalcylindrical	3
Comesa	spiral	2A	punctuation or annulation with lateral differentiation	conical	3
Comesomatidae sp1	spiral	1B	punctuation or annulation without lateral differentiation	clavate/conicalcylindrical	2
Coninckia	rounded and elongate loop	1A	punctuation or annulation without lateral differentiation	clavate/conicalcylindrical	2
Crenopharynx	indistinct	1A	smooth	clavate/conicalcylindrical	4
Cyatholaimidae sp1	spiral	2A	punctuation or annulation with lateral differentiation	clavate/conicalcylindrical	3

Cyatholaimus	spiral	2A	punctuation or annulation without lateral differentiation	conical	3
Cyartonema	circular	1A	punctuation or annulation without lateral differentiation	conical	3
Daptonema	circular	1B	punctuation or annulation without lateral differentiation	clavate/conicalcylindrical	2
Dasynemoides	rounded and elongate loop	1A	wide body annules and longitudinal ridges	conical	3
Demonema	spiral	2B	punctuation or annulation with lateral differentiation	clavate/conicalcylindrical	3
Desmodora	rounded and elongate loop	2A	punctuation or annulation without lateral differentiation	conical	2
Desmodoridae sp1	rounded and elongate loop	2A	punctuation or annulation without lateral differentiation	conical	2
Desmoscolex	blister-like	1A	desmens	conical	4
Dichromadora	slit like	2A	punctuation or annulation with lateral differentiation	conical	2
Didelta	rounded and elongate loop	1B	punctuation or annulation without lateral differentiation	clavate/conicalcylindrical	2
Disconema	rounded and elongate loop	1A	punctuation or annulation without lateral differentiation	clavate/conicalcylindrical	2
Dracognomus	slit like	1B	punctuation or annulation without lateral differentiation	conical	4
Dracograllus	rounded and elongate loop	1A	punctuation or annulation without lateral differentiation	conical	4
Draconema	slit like	1A	punctuation or annulation without lateral differentiation	conical	4
Epsilonema	spiral	1A	punctuation or annulation without lateral differentiation	conical	4
Epacanthion	indistinct	2B	smooth	conical	2
Eubostrichus	spiral	1A	presence of bacteria covering	conical	3
Euchromadora	slit like	2A	punctuation or annulation without lateral differentiation	conical	3
Eurystomina	pocket like	2B	smooth	conical	4
Gammanema	spiral	2B	punctuation or annulation without lateral differentiation	short/round	3
Gammarinema	circular	1B	smooth	conical	1
Gomphonema	spiral	2A	punctuation or annulation with lateral differentiation	conical	3
Gerlachius	circular	1A	punctuation or annulation without lateral differentiation	conical	4
Graphonema	slit like	2A	punctuation or annulation without lateral differentiation	conical	3
Halalaimus	longitudinal slit	1A	smooth	clavate/conicalcylindrical	4
Halichoanolaimus	spiral	2B	punctuation or annulation without lateral differentiation	clavate/conicalcylindrical	3
Innocuonema	slit like	2A	punctuation or annulation without lateral differentiation	conical	3
Latronema	spiral	2B	punctuation or annulation with longitudinal structures for the whole length of the animal	short/round	3
Leptepsilonema	spiral	1A	punctuation or annulation without lateral differentiation	conical	4
Leptolaimus	circular	1A	punctuation or annulation without lateral differentiation	clavate/conicalcylindrical	2
Leptonemella	rounded and elongate loop	1A	punctuation or annulation without lateral differentiation	conical	4
Linhomoeus	circular	1B	punctuation or annulation without lateral differentiation	conical	2
Linhystra	circular	1A	punctuation or annulation without lateral differentiation	clavate/conicalcylindrical	2
Litinium	rounded and elongate	1A	smooth	short/round	4

	loop				
Longicyatholaimus	spiral	2A	punctuation or annulation with lateral differentiation	clavate/conicalcylindrical	3
Marylynna	spiral	2A	punctuation or annulation with lateral differentiation	clavate/conicalcylindrical	3
Megadesmolaimus	circular	1B	punctuation or annulation without lateral differentiation	conical	2
Mesacanthion	indistinct	2B	smooth	clavate/conicalcylindrical	3
	rounded and elongate				
Metachromadora	loop	2B	punctuation or annulation without lateral differentiation	conical	2
Metacyatholaimus	spiral	2A	punctuation or annulation with lateral differentiation	clavate/conicalcylindrical	3
Metalinhomoeus	circular	1B	punctuation or annulation without lateral differentiation	conical	2
Metepsilonema	spiral	1A	punctuation or annulation without lateral differentiation	conical	4
Metoncholaimus	pocket like	2B	smooth	clavate/conicalcylindrical	4
Microlaimus	circular	2A	punctuation or annulation without lateral differentiation	conical	2
Molgolaimus	circular	1A	punctuation or annulation without lateral differentiation	clavate/conicalcylindrical	3
			punctuation or annulation with longitudinal structures for the whole length of the animal	conical	3
Monoposthia	circular	2A	punctuation or annulation with longitudinal structures for the whole length of the animal	conical	3
Monoposthoides	circular	2A	punctuation or annulation without lateral differentiation	conical	3
Nannolaimus	spiral	1A	punctuation or annulation without lateral differentiation	conical	3
Neochromadora	slit like	2A	punctuation or annulation with lateral differentiation	conical	2
Neotonchus	spiral	2A	punctuation or annulation with lateral differentiation	conical	2
Odontanticoma	pocket like	2A	smooth	clavate/conicalcylindrical	2
	rounded and elongate				
Odontophora	loop	1B	punctuation or annulation without lateral differentiation	conical	2
Onchium	spiral	2A	punctuation or annulation without lateral differentiation	clavate/conicalcylindrical	3
Oncholaimellus	pocket like	2B	smooth	clavate/conicalcylindrical	3
Oncholaimus	pocket like	2B	smooth	clavate/conicalcylindrical	4
Oxystomina	pocket like	1A	smooth	clavate/conicalcylindrical	4
Paracanthonchus	spiral	2A	punctuation or annulation without lateral differentiation	conical	2
Paracyatholaimoides	spiral	2A	punctuation or annulation without lateral differentiation	conical	3
Paracyatholaimus	spiral	2A	punctuation or annulation without lateral differentiation	conical	2
Paracomesoma	spiral	2A	punctuation or annulation without lateral differentiation	clavate/conicalcylindrical	2
	rounded and elongate				
Paradesmodora	loop	2A	punctuation or annulation without lateral differentiation	conical	3
	rounded and elongate				
Paradontophora	loop	1B	punctuation or annulation without lateral differentiation	clavate/conicalcylindrical	2
Paralinhomoeus	circular	1B	punctuation or annulation without lateral differentiation	clavate/conicalcylindrical	2
Paramicrolaimus	circular	2A	punctuation or annulation without lateral differentiation	conical	3
Paralongicyatholaimus	spiral	2A	punctuation or annulation without lateral differentiation	clavate/conicalcylindrical	3
Paramonhystera	circular	1B	punctuation or annulation without lateral differentiation	clavate/conicalcylindrical	2
Parapinnanema	slit like	2A	punctuation or annulation without lateral differentiation	conical	3

Paroxystomina	pocket like	1A	smooth	conical	4
Perepsilonema	rounded and elongate loop	1A	punctuation or annulation without lateral differentiation	conical	4
Perspiria	rounded and elongate loop	2A	punctuation or annulation without lateral differentiation	clavate/conicalcylindrical	3
Polygastrophora	indistinct	2B	smooth	conical	4
Pomponema	spiral	2B	punctuation or annulation with lateral differentiation	clavate/conicalcylindrical	4
Praeachantonchus	spiral	2A	punctuation or annulation with lateral differentiation	conical	4
Prochromadorella	slit like	2A	punctuation or annulation without lateral differentiation	conical	2
Psammonema	rounded and elongate loop	2A	punctuation or annulation with lateral differentiation	conical	3
Pselionema	rounded and elongate loop	1A	wide body annules and longitudinal ridges	conical	3
Pseudocella	pocket like	2A	smooth	short/round	5
Pseudonchus	rounded and elongate loop	2B	punctuation or annulation without lateral differentiation	conical	3
Ptycholaimellus	slit like	2A	punctuation or annulation with lateral differentiation	conical	3
Rhynchonema	circular	1B	punctuation or annulation without lateral differentiation	conical	3
Richtersia			punctuation or annulation with longitudinal structures for the whole length of the animal		3
Richtersia	spiral	1B		short/round	
Sabateria	spiral	1B	punctuation or annulation with lateral differentiation	clavate/conicalcylindrical	2
Sigmophoranema	rounded and elongate loop	2A	punctuation or annulation without lateral differentiation	conical	3
Siphonolaimus	circular	2B	punctuation or annulation without lateral differentiation	conical	3
Sphaerolaimus	circular	2B	punctuation or annulation without lateral differentiation	clavate/conicalcylindrical	3
Spilophorella	slit like	2A	punctuation or annulation with lateral differentiation	conical	2
Spirinia	rounded and elongate loop	2A	punctuation or annulation without lateral differentiation	conical	3
Stephanolaimus	slit like	1A	punctuation or annulation without lateral differentiation	conical	4
Stylotheristus	circular	1B	punctuation or annulation without lateral differentiation	clavate/conicalcylindrical	2
Subsphaerolaimus	circular	2B	punctuation or annulation without lateral differentiation	clavate/conicalcylindrical	3
Symplocostoma	pocket like	2B	smooth	conical	4
Synonema	circular	2A	smooth	conical	3
Tarvaia	rounded and elongate loop	1A	punctuation or annulation without lateral differentiation	conical	3
Terschellingia	circular	1A	punctuation or annulation without lateral differentiation	clavate/conicalcylindrical	3
Thalassironus	pocket like	2B	punctuation or annulation without lateral differentiation	clavate/conicalcylindrical	4
Thalassomonhystera	circular	1B	smooth	conical	1
Theristus	circular	1B	punctuation or annulation without lateral differentiation	conical	2
Trefusia	pocket like	1A	smooth	elongated/filiform	4
Tricoma	blister-like	1A	desmens	conical	4
Tripyloides	rounded and elongate loop	1B	smooth	clavate/conicalcylindrical	2

Trissonchulus	pocket like	2B	smooth	short/round	4
Tubolaimoides	circular	1A	punctuation or annulation without lateral differentiation	conical	3
Viscosia	pocket like	2B	smooth	conical	3
Xenella	slit like	1A	punctuation or annulation without lateral differentiation	conical	3
Zalonema	rounded and elongate loop	2A	punctuation or annulation without lateral differentiation	conical	3
Wieseria	rounded and elongate loop	1A	smooth	elongated/filiform	4
