UNIVERSITEIT GENT

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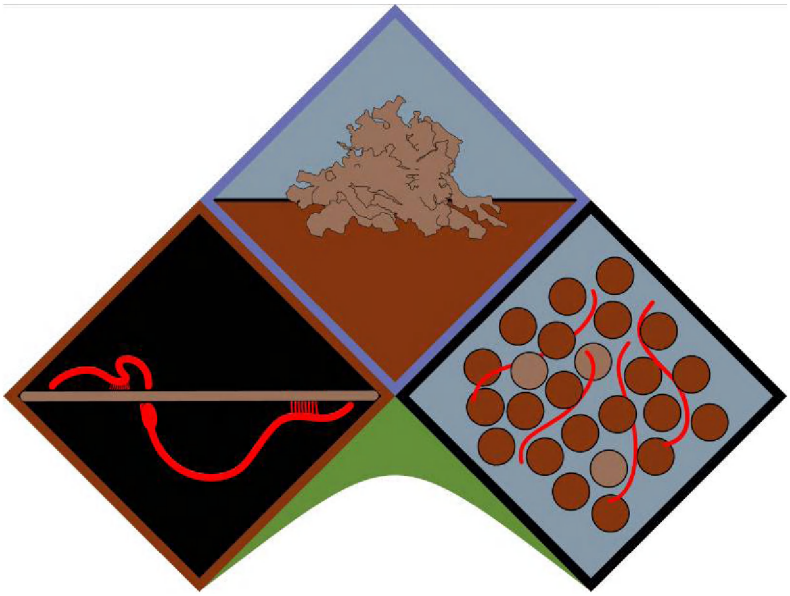
Krijgslaan 281-S8, B-9000 Gent, BELGIUM

AN ECOLOGICAL AND TAXONOMICAL STUDY OF THE FREE-LIVING MARINE NEMATODES ASSOCIATED WITH COLD-WATER AND TROPICAL CORAL STRUCTURES

Een ecologische en taxonomische studie van de vrijlevende mariene nematoden geassocieerd met koudwater- en tropische koraalstructuren



Maarten Raes

Promotor: Prof. Dr. Ann Vanreusel
Co-promotor: Prof. Dr. Wilfrida Decraemer

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In Loving Memory of

MARTHA DE CRAENE (1917 - 2006)
RAYMOND RAES (1913 - 1998)

To whom I owe so much.

"I want to know God's thoughts. The rest are details."

ALBERT EINSTEIN (1879 - 1955)

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DANKWOORD

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Maarten.

SUMMARY – SAMENVATTING

SUMMARY

It is widely accepted that tropical coral reefs are characterised by a high biological diversity (Reaka-Kudla, 1997). Most studies dealing with these reefs have focused on the coral species themselves or the associated macro- and megafauna (Sale, 1977; Connell, 1978; Rogers, 1993; McClanahan, 1994; Hughes *et al.*, 2002; Roberts *et al.*, 2002; Bellwood *et al.*, 2003; Karlson *et al.*, 2004, amongst others). The smaller size fraction known as meiofauna (between 32 µm and 1 mm) living in association with tropical coral reefs is however much less studied. Although the living coral is considered not to be a suitable habitat for meiofauna, the presence of dead coral fragments and other degradation products of the coral skeleton in and on the reef-associated sediment could have a profound influence on the structure and diversity of the meiofauna, especially when bearing in mind that small changes in sediment characteristics are able to alter marine benthic communities. These degradation products are found in a zone adjacent to the reef where dead coral material is progressively degraded: the coral degradation zone.

Coral degradation zones are also found in association with cold-water coral reefs (Mortensen *et al.*, 1995; Freiwald *et al.*, 2002). Although cold-water corals are already known to science for two and a half centuries now (Pontoppidan, 1755), the cold-water coral reef (or bank) ecosystem is still relatively poorly studied. However, some studies indicate a considerably high diversity of coral and sponge species, and of the associated macro- and megafauna (Jensen & Frederiksen, 1992; Rogers, 1999 and references herein; Fosså *et al.*, 2002; Roberts & Hirshfield, 2004; Heifetz *et al.*, 2005). The meiofauna in this ecosystem was unknown until now and this is the first comprehensive study dealing with nematodes associated with cold-water corals.

Cold-water coral degradation zones were investigated in the Belgica mound region of the Porcupine Seabight (North-East Atlantic), at a depth around 1000 m. Shallow, tropical coral degradation zones were investigated on the south coast of Kenya and the east coast of Zanzibar (Tanzania) (Indian Ocean).

Attention is focused on nematodes, which usually dominate the meiofauna both in abundance and biomass (Giere, 1993).

In CHAPTER 2, the nematofauna associated with a cold-water coral degradation zone is investigated. This study mainly aimed to investigate the influence of microhabitat type on nematode community structure. Three distinct microhabitats for nematodes were distinguished: dead coral fragments, glass sponge skeletons and the underlying sediment. The nematode assemblages associated with these three microhabitats were significantly different from each other. The fact that coral and sponge substrata lie relatively unprotected on the seafloor and are more subjected to strong currents compared to the underlying sediment resulted in a higher abundance of taxa that are less vulnerable and more adapted to physical disturbance. In contrast, the underlying sediment housed more typically slender, sediment-dwelling taxa. Typically epifaunal taxa, such as Epsilonematidae and Draconematidae, were especially abundant on dead coral fragments, where they are thought to feed on the microbial biofilm which covers the coral surface. A lower abundance of typically epifaunal taxa on sponge skeletons compared to coral fragments was attributed to more efficient sediment trapping

by the former structures. The underlying sediment was dominated by taxa typical for slope sediments. A considerable degree of overlap between the communities of each microhabitat was observed and was attributed to sediment infill between the coral branches and sponge spicules. It is assumed that the nematofauna associated with large biogenic substrata is composed of a typically sediment-dwelling background community, supplemented with taxa adapted to an epifaunal life strategy. Selective deposit feeders were dominant on sponge skeletons (50.6%) and in the underlying sediment (40.0%). Coral fragments were dominated by epistratum feeders (45.4%), which is explained by the presence of a microbial biofilm on these fragments. Densities in the underlying sediment were low (166-429 ind/10 cm²) in comparison with other studies, but biodiversity was higher here (N_0 = 106; H' = 3.86) than on the coral and sponge fragments (N_0 = 93 for both microhabitats; H' = 3.69 for coral fragments and 3.67 for sponge skeletons), which was attributed to lower disturbance. Nevertheless, the large biogenic substrata provide a microhabitat for rare, epifaunal taxa and fragments of both substrata within the sediment increase habitat complexity and hence biodiversity.

The nematode assemblages at four sites in tropical coral degradation zones along the African east coast, *i.c.* Watamu and Tiwi Beach on the south coast of Kenya and Matemwe and Makunduchi on the east coast of Zanzibar, are investigated in CHAPTER 3. A distinction was made between three microhabitat types: coralline sediment, coral gravel and coral fragments. General nematode community composition was comparable to that in other studies for the same type of habitat. The presence of a common genus pool in coral degradation zones was reflected in the considerable similarities between the samples. However, the addition of coral fragments as a habitat for nematodes resulted in an increased importance of taxa typical for coarse sediment and large substrata. Local and regional turnover were of the same order of magnitude (β_{sim} = approx. 0.2), but the structuring effect of microhabitat type clearly overrode the effect on a local and regional scale. Differences in sediment characteristics were also more important in structuring the nematode assemblages than differences between the coralline sediment and coral fragments. There was no effect related to the three-dimensional structure of coral fragments. Differences between nematode assemblages in the coralline sediment and on coral fragments are attributed to the exposed nature of the latter habitat, its large surface area for epifaunal taxa and its microbial or algal cover. Differences in available food sources were reflected in nematode trophic composition.

The community structure, habitat preferences, biogeography and biodiversity of the typically epifaunal Epsilonematidae and Draconematidae in both cold-water and tropical coral degradation zones are discussed in CHAPTER 4. These nematodes were collected from the Porcupine Seabight and from a north-to-south transect along the coast of Kenya. Communities from different microhabitat types were compared: coral fragments, sponge skeletons and sediment in the Porcupine Seabight; coral fragments and coral gravel in Kenya. Coral fragments were recognised as more favourable substrata for these typically epifaunal nematodes and also housed a community significantly different from that of the other microhabitats. Species-specific habitat preferences could be explained by fine-tuned morphological adaptations. An examination of the biogeography of Epsilonematidae and Draconematidae indicated that cosmopolitan species could very well be cryptic species. Coral degradation zones were recognised as an important source for new species from both typically

epifaunal nematode families. Coral fragments were characterised by the highest diversity and a lower average similarity, which was reflected in a relatively high turnover between coral samples from different locations. Turnover between gravel samples from different locations was generally low, although values of β_{sim} were not significantly lower compared to turnover between microhabitats within each location and between coral samples from different locations. Additive partitioning showed that α-diversity was the principal contributor to total diversity when working with abundance data (71.2%). The contribution of β-diversity related to the turnover between locations was high for presence-absence data (44.5%) but was considerably reduced when adding abundance information, indicating that the addition of sampling locations contributed to the total number of species although the added species were generally rare.

In terms of both genus richness and evenness, the cold-water coral degradation zones were characterised by a similar or even slightly higher diversity on coral fragments (E*G* (100) = 38.4; N_{inf} = 11.2) and in the underlying sediment (E*G* (100) = 43.3 ; N_{inf} = 10.9) compared to the tropical coral degradation zones (E*G* (100) = 35.2 and 41.7, respectively; N_{inf} = 4.4 and 10.8, respectively). Although the sediment was proven to be most favourable for the majority of nematodes, the coral fragments were recognised as highly diverse for Epsilonematidae and Draconematidae, and as an important source for many new species belonging to these families. Genus area curves showed that especially the coral fragments add considerably to the total number of genera. This is an important finding and an argument for the conservation of coral degradation zones.

In CHAPTER 5, three new species of Epsilonematidae are described from a cold-water coral degradation zone in the Porcupine Seabight. *Glochinema trispinatum* Raes, Vanreusel & Decraemer, 2003 is characterised by three dorsal thorns in the pharyngeal region. This species was also found on the Antarctic shelf. *Epsilonema multispiralum* Raes, Vanreusel & Decraemer, 2003 is characterised by a multispiral amphidial fovea consisting of 3.25 coils. *Bathyepsilonema lopheliae* Raes, Vanreusel & Decraemer, 2003 can be distinguished by its body length, the position and relative width of the amphidial fovea and the nature of the cuticular ornamentation. Within the subfamily Glochinematinae Lorenzen, 1974, the number and arrangement of ambulatory setae was considered not to be of diagnostic importance. The former species *Metaglochinema strigosum* Gourbault & Decraemer, 1993 was therefore classified under the genus *Glochinema* Lorenzen, 1974. The original genus diagnosis of *Metaglochinema*, now a monotypic genus, is adjusted.

A new species of *Akanthepsilonema* and the first stage juvenile of *Glochinema trispinatum* are described in CHAPTER 6. Furthermore, additional morphological information is provided for *Triepsilonema tripapillata*. Specimens originated from a cold-water coral degradation zone in the Porcupine Seabight. *Akanthepsilonema sinecornibus* sp. n. differs from *A. helleouetae* in the number of body annules, the sexual dimorphism in size of the amphidial fovea, the absence of copulatory thorns in males, the absence of large spines and horns, the shape of the copulatory apparatus and the position of the ambulatory setae relative to the vulva in females. The genus diagnosis for *Akanthepsilonema* was adjusted to incorporate the new species: *Akanthepsilonema* mainly differs from every other genus in the family by the combination of six rows of ambulatory setae situated around the vulva in females and eight subcephalic setae not displaced towards the anterior part of the

head capsule. Small differences between the Papua New Guinea and the Porcupine Seabight populations of *T. tripapillata* indicated minimal intraspecific variability. Second stage juveniles from Papua New Guinea have two rows of three ambulatory setae whereas Porcupine Seabight specimens have two rows of four ambulatory setae. First and fourth stage juveniles of *T. tripapillata* were described for the first time. Literature data and personal observations showed that the moulting of first stage juveniles into second stage juveniles and of third stage juveniles into fourth stage juveniles involves a decrease in the number of body rings resulting in a loss of flexibility, which is possibly compensated by the development (I-II) or the doubling of the number of rows (III-IV) of ambulatory setae. This decrease was also linked with the formation of the head capsule and the smooth tail tip, although intergeneric variability was evident. The moulting of second stage juveniles into third stage juveniles and of fourth stage juveniles into adults was also subject to intergeneric variability. The variability in the number and orientation of caudal gland outlets among different nematode taxa is discussed. The presence of separate outlets for the caudal glands seems to be widespread within the family Epsilonematidae and had also been observed in various other, unrelated taxa of free-living aquatic nematodes, although their arrangement in Epsilonematidae is opposite. This aberrant arrangement is probably related to the aberrant locomotory pattern in this family.

In CHAPTER 7, a new species of *Tenuidraconema* is described from a cold-water coral degradation zone in the Porcupine Seabight. *Tenuidraconema parvospermis* sp. n. is distinguished from all other species of *Tenuidraconema* by the combination of 10 CAT located posterior to amphidial fovea, SIAT alternately long and short, amphidial fovea in males composed of an inner and outer loop with ventral arm of the inner loop equally long as high, compact, jagged sperm cells with large, refractile inclusions, the shape of the gubernaculum and the number of tail rings. Additional information is provided for *T. koreensis* from specimens found in the Porcupine Seabight, and the fourth stage juvenile of this species is described for the first time. The biogeography of *T. koreensis* in the North Atlantic is discussed in view of its occurrence on the Great Meteor Seamount. A dichotomic identification key to the four species of *Tenuidraconema* is provided.

Two new and closely related species of *Cygnonema* are described from a coral degradation zone in the Porcupine Seabight in CHAPTER 8. Both species differ from *C. steineri* Allen & Noffsinger, 1978 by more pronounced pharyngeal and posterior swellings, a smaller body, a shorter pharynx in relation to body length, a higher number of CAT and the absence of a dorsal tooth. *Cygnonema verum* sp. n. differs from *C. belgicae* sp. n. because it is larger, because of a relatively larger head capsule, a higher number of CAT, a more anteriorly positioned anteriormost laterodorsal CAT, a higher number of PAT, the presence of setiform external labial sensilla, a higher number of subcephalic setae and a more anterior position of the amphidial fovea on the head capsule. Males of *C.verum* sp. n. are easily recognised by the presence of two large, subventral, precloacal corniform setae. They also differ from males of *C. belgicae* sp. n. in the larger amount of cytoplasm in the sperm cells, a knob-like capitulum (in contrast to the beak-shaped capitulum in *C. belgicae* sp. n.) and a relatively shorter tail tip. The genus diagnosis was adjusted and a dichotomic identification key is provided.

This study has provided a first comprehensive overview of the nematode communities associated with cold-water corals. It has also revealed the important role of coral degradation products in

structuring the nematode community composition. Moreover, the study shows that especially the larger coral fragments add considerably to the total number of genera in coral degradation zones. Remarkably, cold-water coral degradation zones are at least as diverse as tropical coral degradation zones. Coral degradation products were also recognised as an important source of new species of Epsilonematidae and Draconematidae, which are typically epifaunal taxa. Four new species of Epsilonematidae and four new species of Draconematidae are described, and additional information is provided on biogeography, relationships between taxa, intraspecific variability and the delineation of diagnostic features.

SAMENVATTING

Het is algemeen aanvaard dat tropische koraalriffen gekenmerkt worden door een hoge biologische diversiteit (Reaka-Kudla, 1997). De meeste studies over koraalriffen hebben zich toegespitst op de koralen zelf of de geassocieerde macro- en megafauna (onder andere Sale, 1977; Connell, 1978; Rogers, 1993; McClanahan, 1994; Hughes *et al.*, 2002; Roberts *et al.*, 2002; Bellwood *et al.*, 2003; Karlson *et al.*, 2004). De grootteklasse gekend als meiofauna (tussen 32 µm en 1 mm) in tropische koraalriffen is echter veel minder gekend. Hoewel het levende koraal zelf niet wordt beschouwd als een geschikt habitat voor meiofauna kan de aanwezigheid van dode koraalfragmenten en andere afbraakproducten van het koraalskelet in en op het sediment nabij het rif een grote invloed hebben op de structuur en diversiteit van de aanwezige meiofauna, vooral gezien kleine verschillen in sedimenteigenschappen reeds in staat zijn om de mariene benthische gemeenschappen te wijzigen. Deze afbraakproducten worden teruggevonden in een zone grenzend aan het rif waar dood koraalmateriaal progressief wordt afgebroken: de koraalafbraakzone.

Koraalafbraakzones worden ook gevonden in associatie met koudwaterkoraalriffen (Mortensen *et al.*, 1995; Freiwald *et al.*, 2002). Hoewel koudwaterkoralen al twee en een halve eeuw gekend zijn voor de wetenschap (Pontoppidan, 1755), is het koudwaterkoraal-rif (of -bank) ecosysteem nog steeds onvoldoende bestudeerd. Sommige studies wijzen echter op een vrij hoge diversiteit aan koraal- en sponssoorten, alsook aan geassocieerde macro- en megafauna (Jensen & Frederiksen, 1992; Rogers, 1999 en referenties hierin; Fosså *et al.*, 2002; Roberts & Hirshfield, 2004; Heifetz *et al.*, 2005). De meiofauna in dit ecosysteem was tot nu toe onbekend en dit is ook de eerste uitgebreide studie over de nematoden geassocieerd met koudwaterkoralen.

Koudwaterkoraal-afbraakzones werden bestudeerd in de Belgica mound regio van de Porcupine Seabight (Noord-Oost Atlantische Oceaan), op een diepte van ongeveer 1000 m. Ondiepe, tropische koraalafbraakzones werden onderzocht aan de zuidkust van Kenia en de oostkust van Zanzibar (Tanzania) (Indische Oceaan).

In deze studie richt de aandacht zich op nematoden, die over het algemeen het dominante taxon zijn in meiofauna, zowel wat betreft aantallen als wat betreft biomassa (Giere, 1993).

In HOOFDSTUK 2 wordt de nematofauna geassocieerd met koudwaterkoraal-afbraakzones onderzocht. Het onderzoek richtte zich vooral op de invloed van het microhabitat type op de structuur van de nematodengemeenschappen. Drie verschillende microhabitats voor nematoden werden onderscheiden: dode koraalfragmenten, skeletten van glassponzen en het onderliggende sediment. De nematodengemeenschappen geassocieerd met deze drie microhabitats waren significant verschillend van elkaar. Het feit dat koraal- en sponssubstraten relatief onbeschermd op de zeebodem liggen en dus in vergelijking met het sediment meer onderhevig zijn aan sterke stromingen, resulteerde in een hoger aantal minder gevoelige taxa die beter aangepast zijn aan fysische verstoring. In tegenstelling tot deze grote substraten herbergde het onderliggende sediment vooral typisch slanke, sediment-bewonende taxa. Typisch epifaunale taxa, zoals Epsilonematidae en Draconematidae, waren vooral sterk vertegenwoordigd op dode koraalfragmenten, waar ze verondersteld worden zich te voeden met de microbiële biofilm die het koraaloppervlak bedekt. Het

lagere aantal typisch epifaunale taxa op sponsskeletten in vergelijking met koraalfragmenten kon verklaard worden door een efficiënter opvangen en vasthouden van sediment door de sponsskeletten. Het onderliggende sediment werd gedomineerd door taxa typisch voor sedimenten van de continentale helling. Een behoorlijke mate van overlap werd waargenomen tussen de gemeenschappen in elk van deze microhabitats en dit werd toegeschreven aan de ophoping van sediment tussen de koraaltakken en sponsspiculen. Er wordt verondersteld dat de nematofauna geassocieerd met grote biogene substraten is opgebouwd uit een typische sediment-bewonende achtergrondgemeenschap, aangevuld met taxa aangepast aan een epifaunale levenswijze. Selectieve bezinkseleters waren dominant op sponsskeletten (50.6%) en in het onderliggende sediment (40.0%). De koraalfragmenten werden echter gedomineerd door epistratumeters (45.4%), hetgeen verklaard kon worden door de aanwezigheid van een microbiële biofilm op deze fragmenten. Densiteiten in het onderliggende sediment waren laag (166-429 ind/10 cm²) in vergelijking met andere studies. De biodiversiteit was echter hoger in het sediment (N_0 = 106; H' = 3.86) dan op de koraal- en sponsfragmenten (N_0 = 93 voor beide microhabitats; H' = 3.69 voor koraalfragmenten and 3.67 voor sponsskeletten), hetgeen verklaard werd door een beperktere verstoring. Hoedanook verschaffen de grote biogene substraten een microhabitat voor zeldzame, epifaunale taxa en verhoogt de aanwezigheid van fragmenten van beide substraten in het sediment de habitatcomplexiteit en biodiversiteit.

De nematodengemeenschappen in tropische koraalafbraakzones op vier locaties langs de Afrikaanse kust, *i.c.* Watamu en Tiwi Beach aan de zuidkust van Kenia en Matemwe en Makunduchi aan de oostkust van Zanzibar, worden onderzocht in HOOFDSTUK 3. Een onderscheid werd gemaakt tussen drie microhabitat-types: coralligeen sediment, koraalgruis en koraalfragmenten. De samenstelling van de nematodengemeenschappen was vergelijkbaar met deze in andere studies over hetzelfde type habitat. De aanwezigheid van een gemeenschappelijke genus*pool* in koraalafbraakzones werd weerspiegeld in de aanzienlijke similariteiten tussen de stalen. De toevoeging van koraalfragmenten als een habitat voor nematoden resulteerde echter in een toename van het aantal taxa typisch voor grove sedimenten en grote substraten. Locale en regionale *turnover* waren van dezelfde grootteorde (β_{sim} = ca. 0.2) hoewel het structurerende effect van het microhabitat type overheerste over het effect op locale en regionale schaal. Verschillen in sedimenteigenschappen waren zelfs belangrijker in het structureren van de nematodengemeenschappen dan verschillen tussen het coralligeen sediment en de koraalfragmenten. Er werd geen effect waargenomen gerelateerd aan de driedimensionale structuur van de koraalfragmenten. De verschillen tussen de nematodengemeenschappen in het coralligeen sediment en op de koraalfragmenten werden toegeschreven aan de onbeschutte aard van het laatste habitat, het grotere oppervlak voor epifaunale taxa en de bedekking met bacteriën of algen. Variatie in beschikbare voedselbronnen werd weerspiegeld in de trofische samenstelling van de nematodengemeenschappen.

De gemeenschapsstructuur, habitat preferenties, biogeografie en biodiversiteit van de typisch epifaunale Epsilonematidae en Draconematidae in zowel koudwaterkoraal- als tropische koraalafbraakzones worden bediscussieerd in HOOFDSTUK 4. Deze nematoden werden verzameld in de Porcupine Seabight en langs een noord-zuid transect aan de kust van Kenia. Gemeenschappen

geassocieerd met verschillende microhabitattypes werden vergeleken: deze op koraalfragmenten, op sponsskeletten en in het sediment in de Porcupine Seabight; deze op koraalfragmenten en in koraalgruis in Kenia. Koraalfragmenten werden beschouwd als geschiktere substraten voor deze typisch epifaunale nematoden en herbergden ook een gemeenschap significant verschillend van deze in de andere microhabitats. Soortspecifieke habitatpreferenties konden verklaard worden aan de hand van specifieke morfologische aanpassingen. Een analyse van de biogeografie van Epsilonematidae en Draconematidae toonde aan dat de cosmopoliete soorten wel eens cryptische soorten zouden kunnen zijn. Koraalafbraakzones werden beschouwd als een belangrijke bron van nieuwe soorten behorend tot beide, typisch epifaunale, nematodenfamilies. De koraalfragmenten waren gekenmerkt door de hoogste diversiteit en een lagere gemiddelde similariteit, hetgeen tot uiting kwam in een relatief hoge *turnover* tussen de koraalstalen van verschillende locaties. *Turnover* tussen koraalgruis-stalen van verschillende locaties was over het algemeen laag, hoewel β_{sim}-waarden niet significant lager waren in vergelijking met *turnover* tussen microhabitats binnen elke locatie en tussen koraalstalen van verschillende locaties. Additieve verdeling van de diversiteit toonde aan dat α-diversiteit de belangrijkste bijdrage leverde tot de totale diversiteit wanneer men werkte met abundantiegegevens (71.2%). De bijdrage van β-diversiteit, gerelateerd aan de *turnover* tussen locaties, was hoog voor aanwezigheid-afwezigheid data (44.5%), maar was aanzienlijk gereduceerd wanneer informatie over abundaties werd toegevoegd. Dit toonde aan dat de toevoeging van staalnamelocaties bijdroeg tot het totaal aantal soorten, hoewel de toegevoegde soorten over het algemeen zeldzaam waren.

In termen van genusrijkdom en equitabiliteit waren koudwaterkoraal-afbraakzones gekarakteriseerd door een vergelijkbare of zelfs hogere diversiteit op koraalfragmenten (E*G* (100) = 38.4; N_{inf} = 11.2) en in het onderliggende sediment (E*G* (100) = 43.3 ; N_{inf} = 10.9) in vergelijking met tropische koraalafbraakzones (E*G* (100) = 35.2 and 41.7, respectively; N_{inf} = 4.4 and 10.8, respectively). Hoewel het sediment beschouwd werd als een geschikter habitat voor de meerderheid van de nematoden, werden de koraalfragmenten gekenmerkt door een hoge diversiteit aan Epsilonematidae en Draconematidae en werden ze tevens gezien als een belangrijke bron van verschillende nieuwe soorten behorend tot deze families. Genus oppervlakte-curves toonden aan dat vooral de koraalfragmenten een aanzienlijk aantal genera toevoegden. Dit is een belangijk gegeven en een argument voor de bescherming van koraalafbraakzones.

In HOOFDSTUK 5 worden drie nieuwe soorten Epsilonematidae beschreven van een koudwaterkoraal-afbraakzone in de Porcupine Seabight. *Glochinema trispinatum* Raes, Vanreusel & Decraemer, 2003 is gekenmerkt door drie dorsale doornen in de faryngeale regio. Deze soort werd ook teruggevonden op het Antarctisch continentaal plat. *Epsilonema multispiralum* Raes, Vanreusel & Decraemer, 2003 is gekenmerkt door een multispiralige *fovea amphidialis* bestaande uit 3.25 windingen. *Bathyepsilonema lopheliae* Raes, Vanreusel & Decraemer, 2003 kan onderscheiden worden van andere soorten binnen het genus door zijn lichaamslengte, de positie en relatieve breedte van de *fovea amphidialis* en de aard van de cuticulaire ornamentatie. Er werd vastgelegd dat het aantal en de organisatie van de ambulatorische setae binnen de onderfamilie Glochinematinae Lorenzen, 1974 geen diagnostische waarde heeft. De vroegere soort *Metaglochinema strigosum*

Gourbault & Decraemer, 1993 werd daarom ondergebracht in het genus *Glochinema* Lorenzen, 1974. De originele genusdiagnose van *Metaglochinema*, nu een monotypisch genus, werd aangepast.

Een nieuwe soort behorend tot het genus *Akanthepsilonema* en het eerste juvenile stadium van *Glochinema trispinatum* worden beschreven in HOOFDSTUK 6. Verder wordt bijkomende morfologische informatie verschaft voor *Triepsilonema tripapillata*. De specimens werden verzameld in een koudwaterkoraal-afbraakzone in de Porcupine Seabight. *Akanthepsilonema sinecornibus* sp. n. verschilt van *A. helleouetae* in het aantal lichaamsringen, het sexueel dimorfisme in de afmetingen van de *fovea amphidialis*, de afwezigheid van copulatorische doornen in mannetjes, de afwezigheid van grote stekels en hoornen, de vorm van het copulatorische apparaat en de positie van de ambulatorische setae in relatie tot de vulva in wijfjes. De genus diagnose voor *Akanthepsilonema* werd aangepast om de nieuwe soort te integreren: *Akanthepsilonema* verschilt vooral van elk ander genus in de familie door de combinatie van zes rijen van ambulatorische setae gesitueerd rond de vulva in wijfjes en acht subcefale setae die niet naar de voorzijde van het kopkapsel verplaatst zijn. Kleine verschillen tussen de populaties van *T. tripapillata* in Papua Nieuw Guinea en de Porcupine Seabight duidden op een beperkte intraspecifieke variabiliteit. Juvenielen behorende tot het tweede juveniele stadium hebben twee rijen van drie ambulatorische setae in Papua Nieuw Guinea en twee rijen van vier ambulatorische setae in de Porcupine Seabight. Eerste en vierde juveniele stadia van *T. tripapillata* werden voor het eerst beschreven. Literatuurdata en persoonlijke observaties toonden aan dat het vervellen van juvenielen van het eerste juveniele stadium tot juvenielen van het tweede juveniele stadium en van juvenielen van het derde juveniele stadium tot juvenielen van het vierde juveniele stadium een afname in het aantal lichaamsringen tot gevolg heeft, hetgeen resulteert in een verminderde beweeglijkheid, die mogelijks gecompenseerd wordt door de ontwikkeling (I-II) of het verdubbelen van het aantal rijen (III-IV) van ambulatorische setae. Deze afname is ook verbonden met de vorming van het kopkapsel en de gladde staarttip, hoewel intergenerische variabiliteit voorkomt. De vervelling van juvenielen van het tweede juveniele stadium tot juvenielen van het derde juveniele stadium en van juvenielen van het vierde juveniele stadium tot adulten is ook onderhevig aan intergenerische variabiliteit. De variabiliteit in het aantal en de orientatie van de uitmondingen van de caudale klieren in verschillende nematodentaxa werd bediscussieerd. De aanwezigheid van afzonderlijke uitmondingen voor de caudale klieren bleek algemeen voor te komen binnen de Epsilonematidae en werd ook waargenomen in verscheidene andere, niet-verwante taxa van vrijlevende, aquatische nematoden. De ordening van de uitmondingen is echter tegengesteld in Epsilonematidae. Deze afwijkende ordening is mogelijks gerelateerd aan de aberrante voortbewegingswijze in deze familie.

In HOOFDSTUK 7 wordt een nieuwe soort *Tenuidraconema* beschreven van een koudwaterkoraal-afbraakzone in de Porcupine Seabight. *Tenuidraconema parvospermis* sp. n. is gekenmerkt door de combinatie van 10 CAT vóór de *fovea amphidialis* gelegen, afwisselend lange en korte SIAT, een *fovea amphidialis* opgebouwd uit een binnenste en een buitenste lus in mannetjes, met de ventrale arm van de binnenste lus even lang als hoog, compacte, hoekige spermacellen met grote, refractiele inclusies, de vorm van het gubernaculum en het aantal staartringen. Additionele informatie werd verschaft voor *T. koreensis*, afkomstig van specimens gevonden in de Porcupine Seabight. Het vierde

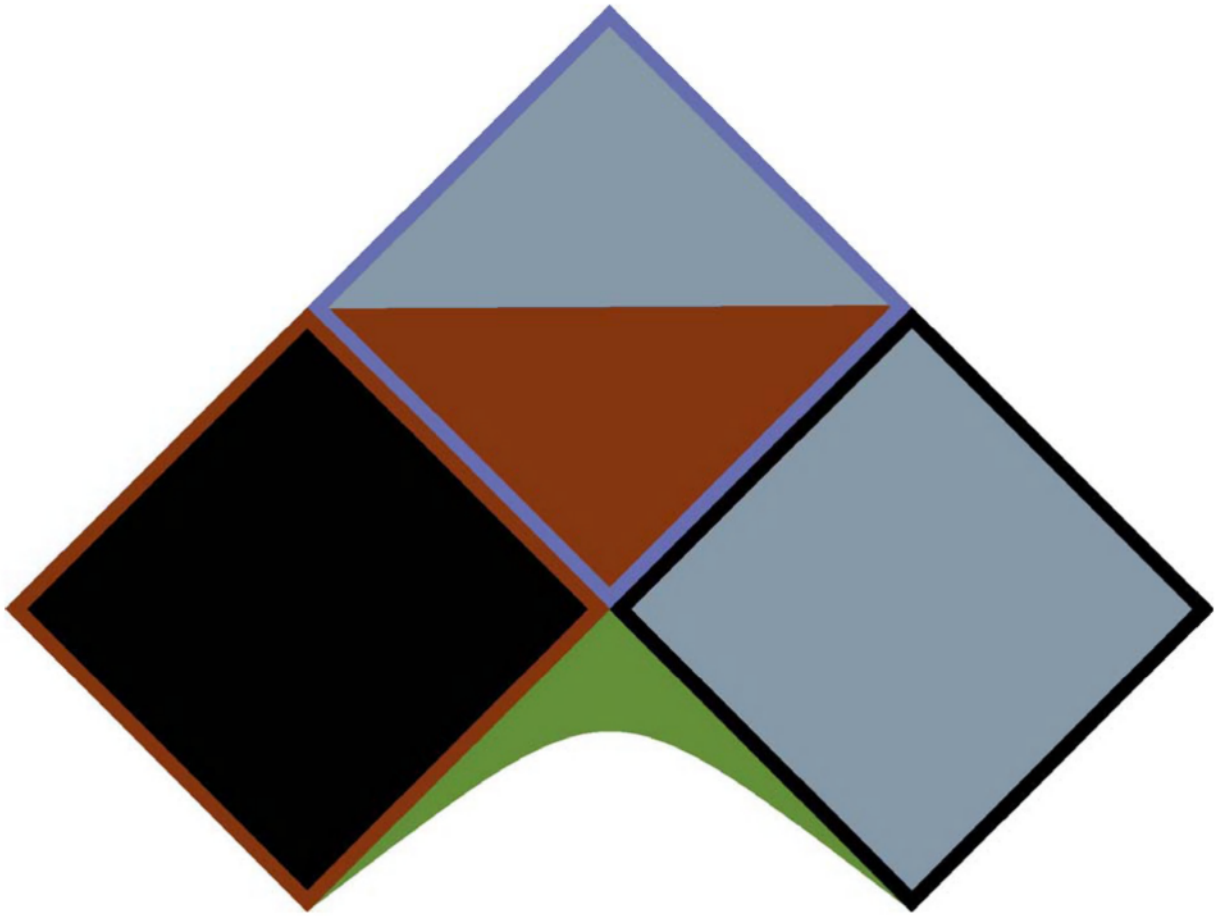
juveniele stadium van deze soort werd voor het eerst beschreven. De biogeografie van *T. koreensis* in de Noord-Atlantische Oceaan werd bediscussieerd met betrekking tot zijn voorkomen op de Great Meteor Seamount. Een dichotome identificatiesleutel tot de vier soorten binnen het genus werd verschaft.

Twee nieuwe en sterk verwante soorten van het genus *Cygnonema* worden beschreven van de koudwaterkoraal-afbraakzone in de Porcupine Seabight in HOOFDSTUK 8. Beide soorten verschillen van *C. steineri* Allen & Noffsinger, 1978 door meer uitgesproken verdikkingen in de faryngeale en posterieure regio, een kleiner lichaam, een relatief kortere farynx, een hoger aantal CAT en de afwezigheid van een dorsale tand. *Cygnonema verum* sp. n. verschilt van *C. belgicae* sp. n. in een grotere lichaamslengte, een relatief groter kopkapsel, een hoger aantal CAT, een meer vooraan gepositioneerde voorste laterodorsale CAT, een hoger aantal PAT, de aanwezigheid van setiforme externe labiale sensillen, een hoger aantal subcefale setae en een meer anterieure ligging van de *fovea amphidialis* op het kopkapsel. Mannetjes van *C. verum* sp. n. kunnen makkelijk herkend worden aan de twee grote subventrale, precloacale, corniforme setae. Ze verschillen ook van de mannetjes van *C. belgicae* sp. n. in de grotere hoeveelheid cytoplasma in de spermacellen, een knopvormig capitulum (in tegenstelling tot het snavelvormig capitulum in *C. belgicae* sp. n.) en een relatief kortere staarttip. De genusdiagnose werd aangepast en een dichotome identificatiesleutel werd verschaft.

Deze studie heeft een eerste uitgebreid overzicht verschaft van de nematodengemeenschappen geassocieerd met koudwaterkoralen. Het heeft ook onthuld dat koraal-afbraakproducten een belangrijke rol spelen in het structureren van de samenstelling van de nematodengemeenschappen. Daarnaast toonde de studie aan dat vooral de grotere koraalfragmenten een aanzienlijke bijdrage leveren tot het totale aantal genera in koraal-afbraakzones. Opvallend genoeg blijken koudwaterkoraal-afbraakzones minstens even divers te zijn als tropische koraalafbraakzones. Koraal-afbraakproducten werden erkend als een belangrijke bron van nieuwe soorten Epsilonematidae en Draconematidae, welke typisch epifaunale taxa zijn. Vier nieuwe soorten Epsilonematidae en vier nieuwe soorten Draconematidae werden beschreven en additionele informatie werd verschaft over biogeografie, de relaties tussen taxa, intraspecifieke variabiliteit en de afbakening van diagnostische kenmerken.

CHAPTER 1

GENERAL INTRODUCTION, AIMS AND THESIS OUTLINE



1.1. CORAL REEFS: DIVERSITY AND CONSERVATION

The high biological diversity associated with tropical coral reefs is widely accepted (Reaka-Kudla, 1997). However, most studies dealing with tropical coral reef diversity have focused on the coral species themselves (Connell, 1978; Rogers, 1993; Hughes *et al.*, 2002; Karlson *et al.*, 2004, amongst others) or on the large macro- and megafauna associated with them, mainly fishes (Sale, 1977; McClanahan, 1994; Hughes *et al.*, 2002; Roberts *et al.*, 2002, Bellwood *et al.*, 2003, amongst others). Although the local diversity is strongly influenced by the regional species pool (Cornell & Karlson, 1996; Karlson *et al.*, 2004), local processes and disturbance on a local scale are known to have an important effect on coral reef diversity. For example, associated fish diversity is influenced by biological interactions (*e.g.* competition with sea urchins), reef complexity and anthropogenic activities such as intensive fishing (McClanahan, 1994). Disturbance affecting the corals and associated fish fauna has either a biological, physical or anthropogenic source. According to Connell (1978) and Rogers (1993), high diversity of corals in tropical reefs is maintained in a non-equilibrium state as a result of intermediate disturbance, *i.e.* intermediate in frequency, intensity and scale. Frequent or long-term, intense and/or large-scale stresses on coral reefs, such as hurricanes, will lead to a decrease in their diversity, although this also depends on the ecological history and morphology of the reef (Rogers, 1993). On the other hand, human-induced disturbance, such as overfishing (Polunin & Roberts, 1996; Bellwood *et al.*, 2003), pollution from agriculture and land development (Roberts *et al.*, 2002), and global climate change (Goreau *et al.*, 2000) are an important threat to the survival of coral reefs (Hughes *et al.*, 2003). Climate change increases the frequency of climate-related disturbance (*e.g.* hurricanes), leading to a shorter time for recovery of the reef and its fauna (Hughes *et al.*, 2003). Increased sea surface temperatures, related to global climate change and severe ENSO events, may also result in coral bleaching and may stimulate infectious diseases (Goreau *et al.*, 2000; Reaser *et al.*, 2000; Harvell *et al.*, 2002; Hughes *et al.*, 2003). Concerns related to these threats and declines in coral reef diversity have stimulated the debate on coral reef conservation (Reaser *et al.*, 2000; Roberts *et al.*, 2002; Baird *et al.*, 2002; Hughes *et al.*, 2002; Hughes *et al.*, 2003).

Although cold-water corals have been known to science since the 18th century (Pontoppidan, 1755), their biodiversity and associated fauna have not been studied as intensely as they have for tropical corals. This is in part due to methodological difficulties associated with research of these deep-water organisms. The 'deep-water' corals thrive at great water depths under cold and dark environmental conditions. They lack zooxanthellae, *i.e.* the unicellular, symbiotic algae living in the gastrodermis of corals, which provide energy through photosynthesis and facilitate the deposition of $CaCO_3$ to form the coral skeleton (Davies, 1992). Nevertheless, cold-water corals are known to build extensive reefs (Freiwald *et al.*, 2002) and there are reports of considerably high diversity of coral and sponge species (Heifetz *et al.*, 2005; mainly soft corals), and of associated macro- and megafauna (Jensen & Frederiksen, 1992; Rogers, 1999 and references herein; Fosså *et al.*, 2002; Roberts & Hirshfield, 2004). This high diversity, together with the increased habitat complexity resulting from the presence of the coral framework, is a strong argument for the conservation of cold-water coral banks and reefs. Moreover, these reefs provide protection from currents and predators, and are feeding,

breeding and spawning areas for commercially important fish and shellfish species (Baker *et al.*, 2001; Reed, 2002; Roberts & Hirshfield, 2004). Growing concerns have arisen about the impact of (1) destructive fishing practices in deep waters, especially by large trawling nets, (2) hydrocarbon drilling and seabed mining and (3) ocean acidification related to increased atmospheric carbon dioxide levels (Rogers, 1999; Fosså *et al.*, 2002; Roberts & Hirshfield, 2004; The Royal Society, 2005; Guinotte *et al.*, 2006; Roberts *et al.*, 2006). The impact of deep-sea trawling activities has been clearly demonstrated by Hall-Spencer *et al.* (2002). These and numerous other reports about the anthropogenic destruction of cold-water coral reefs have finally produced some first results in terms of conservation and management, including a complete closure of coral reefs and banks to bottom fishing (*e.g.* Reed, 2002; Roberts & Hirshfield, 2004).

1.2. CORAL DEGRADATION ZONES

The term 'coral degradation zone' has been established here (see Addendum 1) to emphasise the dynamic character of the zone adjacent to a living coral bank or reef, where coral material is gradually broken down to smaller pieces, eventually producing sediment or merging into it. The general character of this zone is comparable in the vicinity of tropical and cold-water coral reefs, although environmental conditions are different. The structure of both cold-water coral and tropical coral degradation zones is briefly discussed below.

1.2.1. COLD-WATER CORAL DEGRADATION ZONES

In view of the geographical position of the sampling sites treated in this thesis, only literature sources dealing with cold-water coral reefs from the North-East Atlantic will be considered here. The most important reef-building coral in this region is the scleractinian *Lophelia pertusa* (Linnaeus, 1758), a species with a wide geographical distribution (globally as well as in the North-East Atlantic: Rogers, 1999; Freiwald *et al.*, 2004; Fig. 1) and a bathymetric distribution between 39 and 3380 m depth (Mortensen, 2000). *Lophelia pertusa* has a dendroid branching skeleton and is able to form three-dimensionally complex colonies, ranging from irregular small bushes to large, hemispherical 'cauliflower' forms (Mortensen, 2000). Data on the different facies/habitats associated with *Lophelia* reefs come from Norwegian waters, *i.c.* the Sula Reef Complex. Mortensen *et al.* (1995) distinguished five habitats in and around the reef: (1) silty and clayey sediments surrounding the bioherm, (2) scattered stones on soft bottom, (3) *Lophelia* rubble, (4) dead *Lophelia* colonies and (5) living *Lophelia* colonies (Fig. 2). Only the habitats 3-5 are considered part of the cold-water coral bioherm; the first two habitats constitute the background. The bioherm itself can be subdivided in a lower zone of dead *Lophelia* and an upper zone of living *Lophelia*. Living coral is always present as a complex framework ('coral thickets'), whereas the dead coral appears either as a framework or as eroded coral rubble. This eroded rubble is often found accumulated in and on the sediment near the base of the bioherm and its coverage of the sediment gradually decreases away from the centre of the bioherm.

In a later study, Freiwald *et al.* (2002) reported a more complex zonation pattern from a geological perspective. They distinguish seven different facies. The two off-reef facies, (1) bioturbated silty sand

and (2) sponge-rich boulder ground, are similar to the first two habitats proposed by Mortensen *et al.* (1995). The second facies type forms islands within the first. The bioherm itself (on-reef) can be subdivided in five facies: (3) pebbly sand facies; (4) coral rubble facies; (5) sediment-clogged coral framework; (6) exposed dead coral framework and (7) living coral framework (Fig. 3). The pebbly sand facies forms the transition between on-reef and off-reef facies and is littered with worn fragments of *Lophelia*. In the sediment-clogged coral framework facies, the coral is still present as a three-dimensional framework, although with considerable infill from sediment, enriched with shelly remains and bio-eroded sponge chips. Facies types 4, 6 and 7 are similar as those described by Mortensen *et al.* (1995). The whole bioherm, from the live coral framework to the pebbly sand facies with scattered small coral remains, can be regarded as a dynamic system where living coral dies off and is progressively degraded, from the living coral framework facies up to the pebbly sand facies.

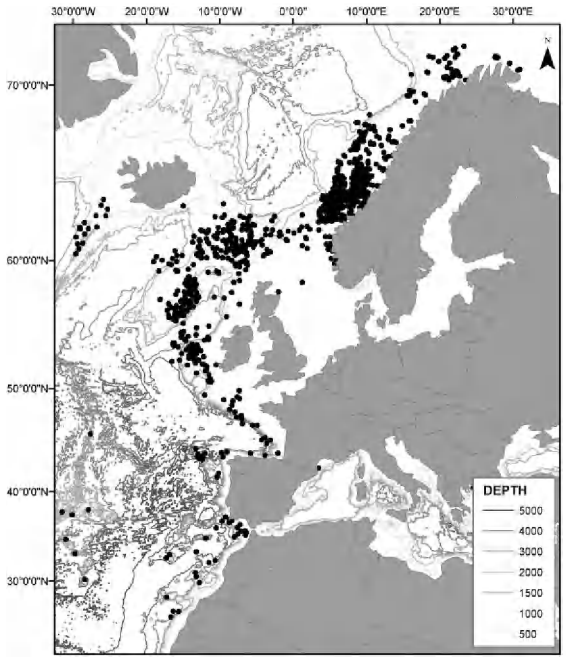


Fig. 1. Map showing the distribution of *Lophelia pertusa* in the northeast Atlantic (modified from Freiwald *et al.* (2004) by Andrew Davies (SAMS)).

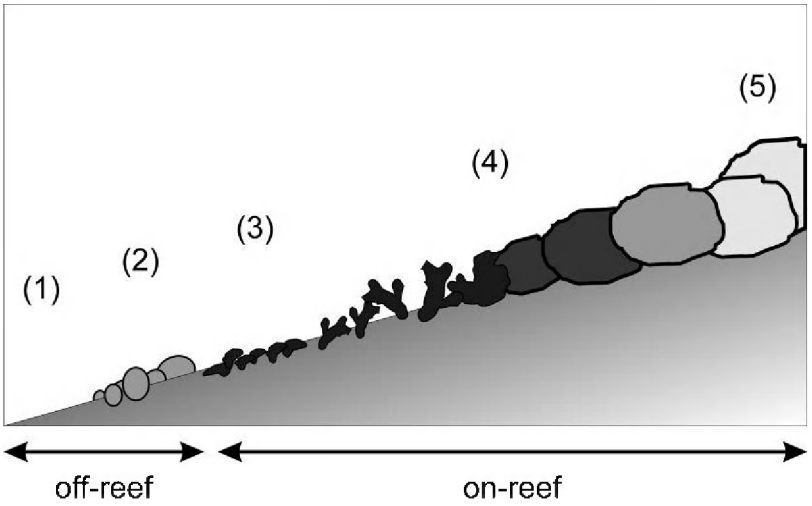


Fig. 2. *Lophelia* reef habitats, according to Mortensen *et al.* (1995). Numbers correspond with habitat numbers in the text.

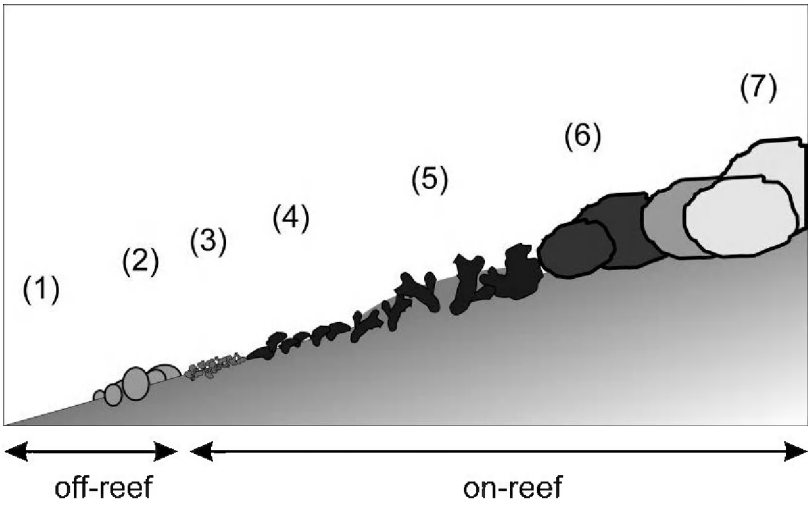


Fig. 3. *Lophelia* reef habitats, according to Freiwald *et al.* (2002). Numbers correspond with habitat numbers in the text.

1.2.2. TROPICAL CORAL DEGRADATION ZONES

Given that the tropical coral degradation zones that are dealt with in this thesis are associated with fringing reefs, the focus will be here on this type of reef. Fringing reefs are the most common type of reef on East-African coasts and project seaward directly from the shore. The zone between the tropical fringing reef bioherm and the shore is considered here as the coral degradation zone, a zone with erosion products of coral fragments and scattered seagrass meadows. It corresponds well with what is generally called a 'tropical coral reef lagoon' in literature. Although the term 'lagoon' is typically used for barrier reefs, the reef flat between the reef crest and shore may become so deep that it can be regarded as a lagoon. Moreover, the reef flat and lagoon are not always clearly separated from each other. Ólafsson *et al.* (1995) even used the term 'intertidal lagoon flat' for the back reef flat of the fringing reef in Zanzibar, which is also relevant to the subject of the presented study. Patch reefs are often found scattered in the lagoon. Extensive seagrass beds may cover large areas of the coral degradation zone.

In comparison with cold-water coral degradation zones, there is no clear zonation of different facies in tropical coral degradation zones (Fig. 4a, b). Therefore, the term 'habitat' is used here instead of 'facies'. The different erosion products of coral fragments are not discussed in literature but the following habitats were distinguished by personal observation: (1) living coral framework; (2) dead coral framework (fragments); (3) coral rubble; (4) coral gravel and (5) coralline sediment. The living coral framework is mainly found on the reef front and as patch reefs in the lagoon. All other habitat types can be found in the lagoon. After the death of the living coral, the coral framework is attacked by boring organisms and the coral fragments become progressively more eroded and smaller in the sequence from habitat type 2 to 5. This process also involves loss in three-dimensional complexity of the coral structures.

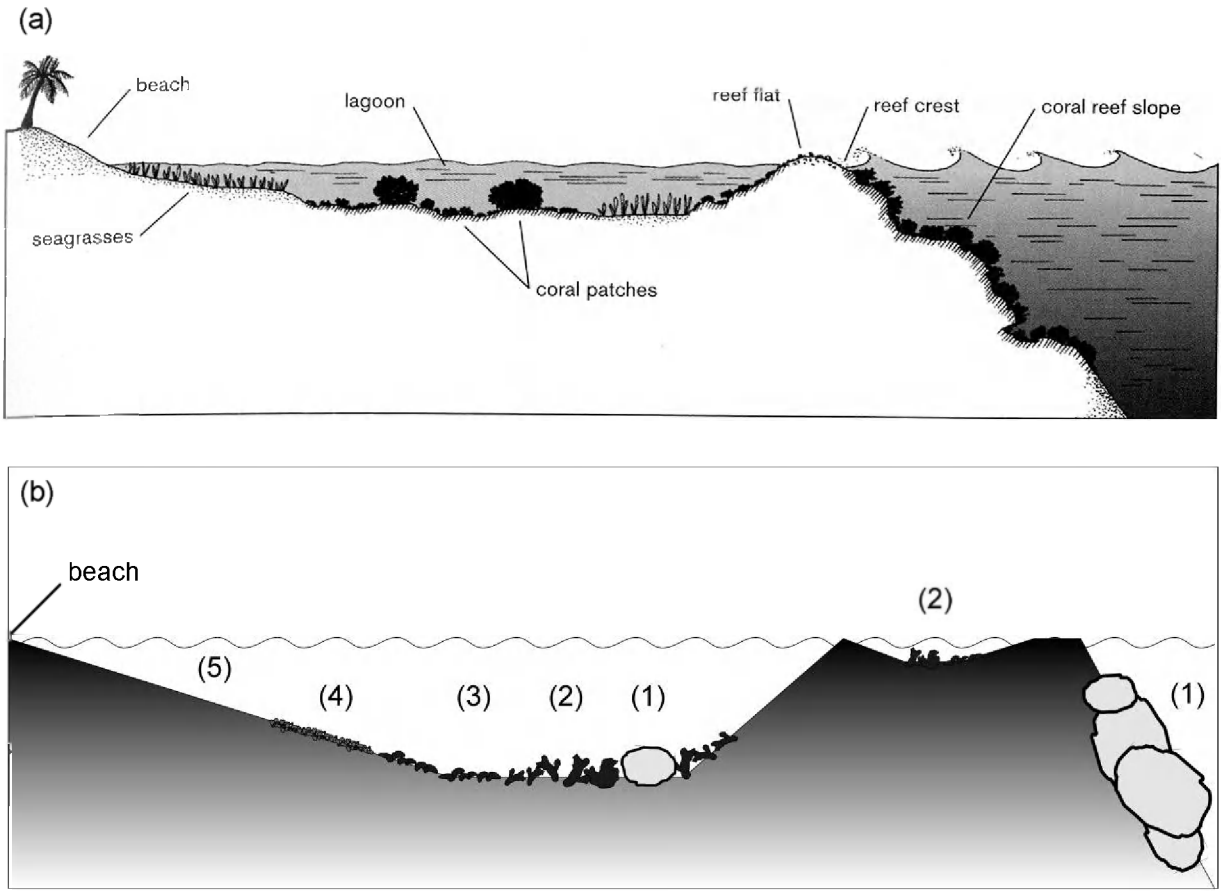


Fig. 4. (a) Cross section of a typical fringing reef and lagoon, as seen during low tide (From Richmond, 2002). (b) Tropical coral reef habitats. Numbers correspond with habitat numbers in the text.

1.3. MEIOFAUNA IN DEEP-SEA SEDIMENTS OF THE NORTH-EAST ATLANTIC

The meiofauna associated with *Lophelia pertusa* reefs in the North-East Atlantic has never been studied in detail before. The present study is the first comprehensive survey of the cold-water coral reef associated meiobenthos (*i.c.* nematofauna). One of its aims (see Section 1.9.) is to investigate the structuring effect of microhabitat type, *i.c.* coral degradation products, and the contribution of these microhabitats to the total biodiversity of the ecosystem. In order to assess both their effect and contribution, it is important to know and understand the background community in the same region, *i.e.* the community living in North-East Atlantic deep-sea sediments that are not associated with these biogenic structures. The composition, density and diversity of the meiobenthos of the deep North-East Atlantic has been reviewed by Vincx *et al.* (1994). Soetaert & Heip (1995) reviewed nematode densities and assemblage structure in the North Atlantic and Mediterranean. Information assembled from these sources is summarised here without unduly repeating the references themselves or references cited therein, except where deemed really essential. This information is supplemented below with more recent information from the North-East Atlantic region. All depth zones deeper than 200 m, *i.e.* from the shelf break up to the abyssal plain, are considered. Only the metazoan, *i.e.*

multicellular, meiobenthos will be discussed here; information on Foraminifera is not provided. A distinction is made between total meiofauna and nematode data, two types of information relevant to the study at hand.

Table 1 and Fig. 5 list the study areas which are explicitly mentioned in the text. For an overview of the areas reviewed in Vincx *et al.* (1994), see Fig. 1 and Table 1 in that publication; for an overview of the areas reviewed in Soetaert & Heip (1995), see Table 1 in that publication. For the study of Soltwedel (1997), only the two transects that are located in the North-East Atlantic are indicated.

	Location	Depth	Data	Source
1	Bay of Biscay	2000-4700 m	meiofauna/ Nematoda	a: Dinet & Vivier (1977); b: Dinet &Vivier (1979)
2	Norwegian Sea	970-3294 m	Nematoda	Jensen (1988)
3	Bay of Biscay	190-325 m	meiofauna/ Nematoda	Vanreusel *et al.* (1992)
4	Porcupine Abyssal Plain	4850 m	Nematoda	Vanreusel *et al.* (1995a)
5	Cape Verde Abyssal Plain	4650 m	Nematoda	Vanreusel *et al.* (1995a)
6	off northwestern Spain	120-300 m	meiofauna	Vanreusel *et al.* (1995b)
7	Porcupine Seabight	600-1500 m	meiofauna	Vanreusel *et al.* (1995b)
8	Porcupine Seabight	1320-1362 m	meiofauna	Gooday *et al.* (1996)
9	Goban Spur	206-2760 m	meiofauna/ Nematoda	a: Soetaert *et al.* (1997); b: Vanaverbeke *et al.* (1997)
10	off Guinea	37-4327 m	meiofauna	Soltwedel (1997) (transects 1-2)
11	Darwin Mounds	904-960 m	meiofauna/ Nematoda	Van Gaever *et al.* (2004)

Table 1. Sampling locations of the studies on deep-sea meiobenthos in the North-East Atlantic that are explicitly mentioned in Section 1.3., except those reviewed in Vincx *et al.* (1994) and Soetaert & heip (1995). The depth range and type of data are indicated.

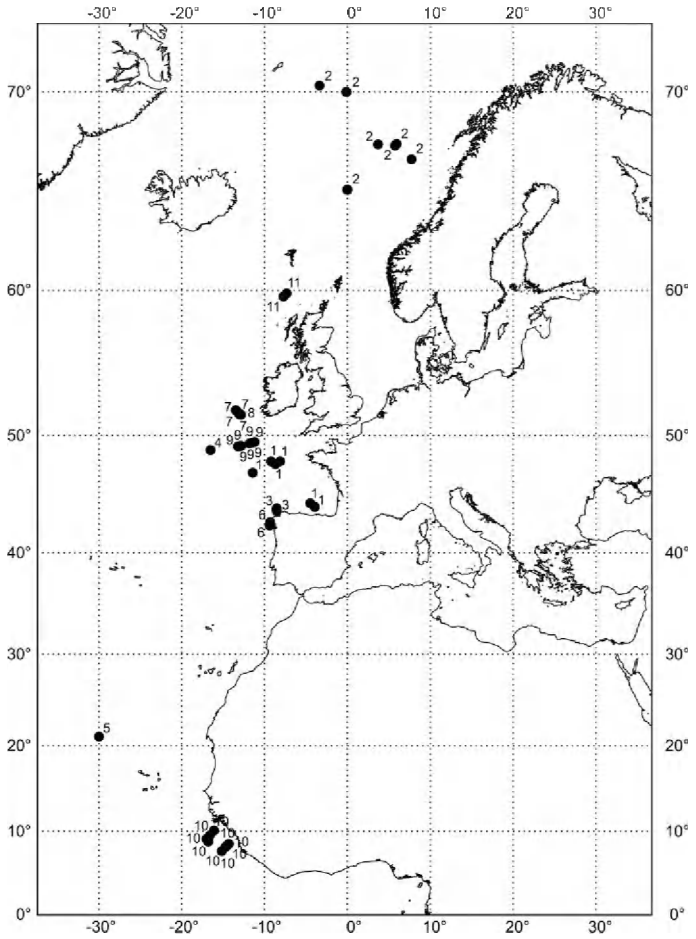


Fig. 5. Sampling locations of the studies on deep-sea meiobenthos in the North-east Atlantic that are explicitly mentioned in Section 1.3., except those reviewed in Vincx *et al.* (1994) and Soetaert & heip (1995). The numbers correspond with those in Table 1.

1.3.1. MEIOFAUNA

Composition

Nematodes are always the dominant taxon in North-East Atlantic meiobenthos, comprising between 41.1% (Bay of Biscay; Vanreusel & Vincx (unpublished in Vincx *et al.*, 1994)) and 98.6% (Gulf of Biscay; Dinet & Vivier, 1977) of the total meiobenthic abundance. Harpacticoid copepods are generally the second most abundant taxon. Their relative abundance ranges between 0% (off Morocco (Dinet, unpubl. in Vincx *et al.*, 1994) and Gulf of Biscay (Dinet & Vivier, 1977)) and 30.9% (Bay of Biscay; Vanreusel & Vincx (unpublished in Vincx *et al.*, 1994)). An overview of all meiofaunal taxa (higher-taxon level) encountered in the North-East Atlantic is provided in Table 2. In total, 25 taxa have been found in this region. The number of taxa per study varies between 8 and 21, although in two studies only the dominant taxa were provided (Table 3). Global trends in the percentage composition of the meiofauna are not straightforward. However, the relative abundance of nematodes usually increases with bathymetric depth (Soltwedel, 2000). Correspondingly, the relative abundance of the other taxa decreases with depth. According to Carney *et al.* (1983), these trends are related to physiological parameters (temperature, salinity, oxygen concentration and hydrostatic pressure), sediment characteristics (sediment tends to become finer at greater depths) and resources that either decrease in availability with depth (food) or increase in availability with depth (space). Sediment grain size is regarded as one of the most important factors determining the composition of the meiobenthos (Coull, 1988).

Taxon	Vincx *et al.* (1994)	8	9b	10	11
Amphipoda	X			X	X
Aplacophora				X	X
Bivalvia	X	X		X	X
Bryozoa				X	
Cladocera					X
Cnidaria	X			X	
Cumacea				X	
Echinodermata					X
Gastropoda				X	
Gastrotricha	X			X	X
Halacarida	X			X	
Harpacticoida	X	X	X	X	X
Isopoda	X		X	X	
Kinorhyncha	X	X	X	X	X
Loricifera	X				
nauplii*	X	X	X	X	X
Nematoda	X	X	X	X	X
Oligochaeta	X				X
Ostracoda	X	X	X	X	X
Polychaeta	X	X	X	X	X

Table 2. Meiofauna higher taxa from the North-East Atlantic deep sea: presence-absence data. Numbers in the first row correspond with those in Table 1.

	Number of taxa	Lowest dominance	Highest dominance
2		88% (Nematoda)	92% (Nematoda)
Vincx *et al.* (1994)	17*	41.1% (Nematoda)	98.6% (Nematoda)
6, 7		53% (Nematoda)	more than 90% (Nematoda)
8	8*	71.2% (Nematoda)	97.6% (Nematoda)
9b	11	87.6% (Nematoda)	95.2% (Nematoda)
10	21	53% (Nematoda) (average value)	65% (Nematoda) (average value)
11	17	93.9% (Nematoda)	95.5% (Nematoda)

Table 3. Taxon richness and dominance in North-East Atlantic deep-sea meiobenthos. *: only the dominant taxa were mentioned in this study. Numbers in the first column correspond with those in Table 1.

	Meiofaunal densities
Vincx *et al.* (1994)	7-2656 ind/10 cm²
4, 5	139-638 ind/10 cm² (average values)
6, 7	368-1523 ind/10 cm² (average values)
8	491-2763 ind/10cm²
9b	178-969.5 ind/10 cm²
10	182-1564 ind/10 cm²
11	666-864 ind/10 cm²

Table 4. Densities of North-East Atlantic deep-sea meiobenthos. Numbers in the first column correspond with those in Table 1.

Densities

Densities of the metazoan meiofauna in the North-East Atlantic deep sea range between 7 ind/10 cm² (Gulf of Biscay; Dinet & Vivier, 1977) and 2763 ind/10 cm² (Porcupine Seabight; Gooday *et al.*, 1996) (Table 4). There is a general tendency for metazoan meiobenthic densities to decrease with increasing bathymetric depth (Vincx *et al.*, 1994; Soetaert *et al.*, 1997; Soltwedel, 1997; Vanaverbeke *et al.*, 1997; Soltwedel, 2000), although the meiofauna:macrofauna ratio increases linearly with depth (Flach *et al.*, 1999). Highest densities are generally recorded in the shallowest deep-sea areas (< 1000 m; mean per area up to 2000 ind/10 cm²), lowest densities at abyssal depths (mean per area ≤ 600 ind/10 cm²) (Vincx *et al.*, 1994). In general, densities are related to (1) food availability, (2) hydrodynamic disturbance, (3) sediment grain size, (4) sediment heterogeneity, (5) sediment oxygen concentration, (6) sediment $CaCO_3$ content and (7) predation pressure. Food availability is generally regarded as the most important modifying factor for deep-sea meiobenthic abundance (Thiel, 1983) and meiobenthos standing stocks reflect the availability of food supply, bacterial biomass, food quality and organic matter mineralisation (Vanreusel *et al.*, 1995a; Vanreusel *et al.*, 1995b; Soetaert *et al.*, 1997; Pfannkuche *et al.*, 1999). On the other hand, Gooday *et al.* (1996) found no clear response of the metazoan meiobenthos on phytodetrital inputs, which was attributed to behavioural and reproductive aspects of the communities. The food that sustains deep-sea benthic communities originates mainly from surface water primary production and fluxes seasonally to the ocean floor. A decline with increasing depth in the amount of food reaching the ocean floor is an important explanation for the observed negative correlation between meiofaunal density and depth. This correlation is summarised in the function Y = 2241 – 227*ln (depth) (where Y is meiofaunal density) (Vincx *et al.*, 1994). Food availability directly depends on the surface productivity in the region, *e.g.* associated with upwelling, and the distance off-shore (for food originating from land). Furthermore, it is also determined by hydrodynamic disturbance, as strong currents will keep detrital food in suspension and will therefore impede sedimentation (Soltwedel, 2000). Bacteria, which are an important food source for the meiobenthos, are less abundant in coarse sediments (Vanreusel *et al.*, 1995b). On the other hand, oxygen concentrations are much lower in finer sediments. Meiofaunal densities increase with increasing food supply, but are limited by the relatively poor oxygen availability in fine sediment and deeper sediment layers (Vanreusel *et al.*, 1995b).

Densities tend to be much more variable on a small scale than on a regional scale, which is partially due to the presence of biogenic structures (burrows, depressions, mounds, etc.) from macrofauna and the patchy distribution of particulate organic matter. Both aspects are also related to each other. Temporal patterns in meiobenthic abundance are related to the seasonality of the

phytodetritus flux following surface primary production, and the rate at which the taxa respond to it (Gooday *et al.*, 1996; Pfannkuche *et al.*, 1999).

Diversity

The total number of meiofauna higher taxa and the extent of dominance of nematodes in each study is provided in Table 3. Nematode dominance is usually very high, which indicates that the relative abundance of nematodes is very important in determining the diversity of the deep-sea meiobenthos. Indeed, meiobenthic diversity tends to decrease with increasing depth, which is due to the higher dominance of nematodes at greater depths. Coarser sediments generally support a more diverse fauna, which is again related to the reduced dominance of nematodes (Coull, 1988).

1.3.2. NEMATOFAUNA

Composition

First data on nematode community composition comes from the abyssal plain and shelf break of the Gulf of Biscay. On the abyssal plain (Dinet & Vivier, 1979), the most abundant nematode families were Monhysteridae, Chromadoridae, Oxystominidae, Desmoscolecidae, Microlaimidae and Axonolaimidae. At the shelf break (Vanreusel *et al.*, 1992), the nematode community was dominated by Xyalidae, Chromadoridae, Oxystominidae, Desmoscolecidae and Microlaimidae. The most abundant genera on the abyssal plain were *Theristus*, *Halalaimus*, *Microlaimus*, *Acantholaimus*, *Leptolaimus*, *Diplopeltula* and *Sabatieria.* At the shelf break, *Theristus* was replaced by *Daptonema* and *Trichotheristus*. According to Soetaert & Heip (1995), who compared these data with information from the Mediterranean and West-Atlantic, *Theristus*, *Acantholaimus* (+ *Spiliphera*), *Halalaimus* and several monhysterid genera are dominant genera in abyssal and continental rise stations, whereas *Sabatieria*, *Daptonema* and *Richtersia* are more abundant at the shelf-break. The continental slope is characterised by an intermediate community, mainly composed of *Sabatieria*, Monhysteridae, *Acantholaimus* and *Amphimonhystrella*. Vanaverbeke *et al.* (1997) provided an extensive overview of the most abundant nematode genera in seven continental slope stations of the Goban Spur. They found a decrease in the relative abundance of *Daptonema* with increasing depth along the slope and an increased importance of *Acantholaimus* and *Monhystera* in the deepest stations (lower slope; below 670 m). *Sabatieria* was only abundant in the shallowest stations (upper slope; up to 1425 m). This is considered a typical nematode for shallow waters and the genus gradually decreases in abundance with depth (Soetaert & Heip, 1995). *Sabatieria* is typically found in muddy sediments with only limited oxygen penetration. The increased oxygen penetration depth with bathymetric depth was introduced as an explanation for the observed trend by Soetaert & Heip (1995) and Vanaverbeke *et al.* (1997). According to Vanaverbeke *et al.* (1997), *Desmoscolex*, *Leptolaimus* and *Oxystomina* are also frequently found in deep-sea areas. The Darwin mounds, which are large topographic structures on the sea floor to the north of the British Isles, were dominated by *Microlaimus*, *Molgolaimus* and *Sabatieria*, three taxa known from reduced habitats (Van Gaever *et al.*, 2004). Nematode community structure is mainly determined by (bathymetric) depth-related factors, such as (1) availability of food

sources (decreases with depth), (2) oxygen penetration in the sediment (deeper penetration at greater depths) and (3) bioturbation activity (decreases with depth).

The most abundant trophic groups in the North-East Atlantic deep sea are the selective and non-selective deposit feeders (Rutgers van der Loeff & Lavaleye, 1986; Jensen, 1988; Soetaert & Heip, 1995) and epistratum feeders (Jensen, 1988). Predatory and scavenging nematodes are generally rare, which is attributed to a lack of freshly deposited dead organisms (Jensen, 1988; Soetaert & Heip, 1995). The distribution of feeding types is related to (1) the availability of appropriate food sources and competition for the bacterial-based food source, (2) current activity and (3) sediment composition (Tietjen, 1971).

Densities

Nematode densities in the North-East Atlantic deep sea range between 5 ind/10 cm² (Dinet & Vivier, 1977 (Gulf of Biscay)) and 2500 ind/10 cm² (Soetaert & Heip, 1995) (Table 5). The same environmental factors influencing the densities of the total meiofauna are active here, and the availability of food is again the most important modifying factor. Especially nematodes feeding on bacteria are able to quickly respond to the variable food input at great depths. The nematode community exhibits the same trend of decreasing densities with increasing bathymetric depth as the total meiofauna (Soetaert *et al.*, 1997; Vanaverbeke *et al.*, 1997).

Diversity

The total number of families, genera and species in different studies is provided in Table 6; other diversity indices are listed in Table 7. The highest number of genera was found on the Darwin Mounds by Van Gaever *et al.* (2004). At the Bay of Biscay (Dinet & Vivier, 1979; Vanreusel *et al.*, 1992), diversity was high, both in terms of richness and evenness. Jensen (1988) also found low dominance on seven locations in the Norwegian Sea. Nematode species diversity is directly related to (1) sediment heterogeneity, (2) predictability of the environment, (3) surface productivity and (4) bioturbation. Sediment heterogeneity (factor 1) may be caused by bioturbation (factor 4). Large-scale disturbance also has a negative effect on deep-sea nematode biodiversity (Lambshead *et al.*, 2001). Not only is the local diversity high, the very low levels of overlap in species composition between adjacent sites (Jensen, 1988) also contribute to a high regional diversity in the deep sea. Although regional deep-sea nematode diversity may be very high, Lambshead & Boucher (2003) warn against exaggeration. A positive latitudinal gradient in deep-sea nematode diversity was attributed to a complex pattern of productivity (Lambshead *et al.*, 2000).

	Nematode densities
2	20-204 ind/10 cm² (average values)
Vincx *et al.* (1994)	5-2382 ind/10 cm²
Soetaert & Heip (1995)	up to 2500 ind/10 cm²
4, 5	89-254 ind/10 cm² (average values)
9a, b	156-898.5 ind/10 cm²
10	111-869 ind/10 cm²

Table 5. Densities of North-East Atlantic deep-sea nematofauna. Numbers in the first column correspond with those in Table 1.

	Number of families	Number of genera	Number of species
1b	35	109	20-50 (317)
2			92
3		79	
9b		35-72	
11		72-91 (155)	

Table 6. Family, genus and species richness in North-East Atlantic deep-sea nematofauna, either indicated as total numbers for the entire study or as a range (per sample) with the total number between brackets. Numbers in the first column correspond with those in Table 1.

	N_1 (genera)	N_2 (genera)	N_{inf} (genera)	EG (100) (genera)	H' (species)	J'
2					3.79-5.01	0.85-0.95
9b	8.96-34.18	13.41-20.60	4.77-10.20	31.2-39.4		

Table 7. North-East Atlantic deep-sea nematofauna: diversity numbers. Numbers in the first column correspond with those in Table 1.

1.4. METHODOLOGY FOR SAMPLING DEEP-SEA MEIOFAUNA

The study of the deep-water fauna is generally known to suffer from methodological difficulties related to (1) the distance between the research vessel (the investigator) and the sea floor, and (2) the uncertainty about the environmental conditions (*e.g.* current velocity, angle of inclination, presence of hard substrates, etc.) at the site of interest on the sea floor. Whereas shallow-water sampling can be more easily controlled and adjusted, remote sampling mainly relies on the suitability and technical aspects of the sampling device. This section will give an overview of the devices that can be used in the collection of deep-sea meiofauna and the associated practical problems.

For some studies (*e.g.* preliminary surveys, studies aiming to formulate faunistic lists, collection of specimens for culturing and for physiological or taxonomical analyses), samples taken in an unpredictable, variable, biased and not-quantified (or unquantifiable) way may be already adequate. Such qualitative sampling of deep-sea meiobenthos can be carried out with small dredges, such as the meiobenthic sled (Fleeger *et al.*, 1988). However, most studies dealing with this fauna aim to describe their temporal and spatial distribution or attempt to test specific hypotheses. In both cases, sampling is critical to the quality of the answer obtained, and unbiased, quantitative samples are required. Several devices are suitable for taking (relatively) unbiased and undisturbed samples. Grab samplers (*e.g.* van Veen grab) consist of two large jaws which close when penetrating the sediment, taking out a 'bite' of material. Although grabs have been used for quantitative meiofaunal sampling, jaw penetration and closure of the grab are known to disturb and compress the sediment. Moreover, grabs often do not close properly. During their descent, the open jaws can create a strong bow wave, resulting in the loss of superficial material (see below) (Ankar, 1977). Therefore, it is not advisable to use grab samplers for quantitative sampling (Blomqvist, 1991).

Deep-sea studies have generally avoided the use of grab samplers and have instead relied upon box corers and, more recently, multiple corers. In soft sediments, coring is indeed the best quantitative sampling technique (Fleeger *et al.*, 1988; Blomqvist, 1991). Corers are devices with a known surface area and are usually cylindrical. They are able to collect a fixed surface area and a measurable

volume without considerable disturbance of the sediment, especially when compared to grabs. Moreover, all depths layers of the sediment are equally represented in the core and the whole fauna present before sampling is captured when the corer is used with care. However, there are several sources of bias associated with core sampling:

1. loss or relocation of the sediment if the corer is not closed immediately after emergence from the sediment;
2. the 'bow wave effect', a problem arising from the presence of a 'bow wave' preceding the orifice of the corer in its descent and washing away fine surface material or even the upper sediment layers before the core reaches the bottom;
3. the size of the corer in relation to the patchy distribution of the meiofauna;
4. compaction, core shortening or draw-down of material due to friction between the sediment and the corer walls when the corer is forced into the sediment;
5. disturbance during closure or retrieval of the core;
6. disturbance through repenetration;
7. skewed entry in the sediment due to strong current activity.

In a shallow situation, these problems can be avoided by manually guiding the core to ensure slow penetration of the sediment (*e.g.* manually pushing Perspex cores into sediment at shallow intertidal sites, during skin or scuba diving (see Section 1.7.)). Such a direct manipulation of the core at the sediment surface is clearly impossible when sampling the deep sea, except when using submersibles or ROV's (Remotely Operated Vehicles) with dynamic arms and visual observation. The only way to tackle the aforementioned problems with large corers is the technical improvement of the device itself. Efforts are continually made to understand sampler bias and to design gear that takes the best samples possible.

In the present study, deep-sea samples are taken with a cylindrical box corer (diameter 30 cm). A box or spade corer consists of an open box which penetrates the sediment under its own weight. When the box is pulled from the sediment, a lever is turned that causes a spade to cut through the sediment below the box, thus closing the corer at its bottom (see Hessler & Jumars, 1974). An upper lid closes off the top of the corer. Because a box corer penetrates the sediment at a moderate speed, the bow wave effect is modest and the upper layer of the sediment may be left undisturbed. According to Barnett *et al.* (1984), however, box corers seldom produce a sample with an undisturbed surface layer. In general, it is clear that box corers do not routinely take samples with a quality equal to deliberate corers. Deliberate corers are devices consisting of a supporting frame and a movable sampling unit. After arrival of the corer on the sea floor, the sampling unit is gently lowered into the sediment, thus limiting the bow wave effect and compaction. The supporting frame also ensures more stability and a more controlled entry of the sampling unit into the sediment, in this way avoiding skewed entry in the sediment and repenetration. The SMBA (Scottish Marine Biological Association) multiple corer (Barnett *et al.*, 1984) is an example of a deliberate corer frequently used in deep-sea meiobenthic research. According to Elliot (1977), many small cores provide a better density estimate than a small number of large cores. In this regard, the multiple corer is also able to avoid the third source of bias listed above.

Bett *et al.* (1994) investigated the influence of sampler type (either box corer or multiple corer) on quantitative estimates of deep-sea meiobenthos and concluded that box corers are less efficient collectors of meiobenthos than multiple corers. According to Blomqvist (1991), the SMBA corer even seems to be the best device available for general sampling of open-sea, soft-bottom sediments at present. However, the slow and gentle approach of the multiple corer is no longer suitable when sampling in areas with hard substrates, such as cold-water coral degradation zones, as the sampling unit will have difficulties penetrating the sediment. Furthermore, the supporting frame will not be positioned in a stable way on the erratic, coral-littered surface. Box corers, however, utilise their own velocity and weight and are able to break through the large coral fragments (pers. obs.). Moreover, the coral and sponge fragments in these coral degradation zones cover the sediment and may therefore prevent the resuspension of the upper sediment layers, thus avoiding the bow wave effect produced by the box corer. In conclusion, box corers appear to be more suitable for sampling the meiofauna in cold-water coral degradation zones than multiple corers.

Given the small size of meiobenthic organisms, it is usually not necessary to collect the entire content of the corer. Therefore, subsamples are taken with smaller, hand-held 'corers'. In most cases, straws, cut-off syringes or Perspex meiocores are used for subsampling. Perspex cores are round, plastic cores with an internal diameter of 36 mm. These cores have a surface area of 10 cm^2 and are therefore very useful when densities have to be calculated (meiobenthic densities are usually expressed as individuals per 10 cm^2). Subsampling is also carried out when more than one analysis has to be done on a single core sample (*e.g.* faunal sampling, grain size analysis, chemical analyses).

1.5. MEIOFAUNA IN TROPICAL CORAL REEF LAGOONS

In the present study, attention will be focused, among other things, on dead coral fragments as a habitat for the meiofauna in tropical coral degradation zones. All previous studies on tropical marine meiofauna have however dealt with either infaunal (from mud to very coarse sediment) or epiphytic (mainly on seagrasses) biota. In order to interpret the results of this thesis, an overview of the knowledge concerning the meiofauna in tropical reef associated lagoons is provided here. This overview will thus provide an immediate background for comparison (see Chapter 3). It will mainly focus on the processes and environmental variables that (are thought to) influence the composition, density and diversity of meiobenthic communities in these environments. Comparing the results of this thesis with those of other studies in the same type of habitat will make it possible (1) to verify whether the meiobenthic communities in the present study are representative or exceptional and (2) to examine whether and how the meiofauna reacts to the presence of coral fragments.

Although seagrasses can occupy large parts of the sediment surface in coral reef lagoons, only sedimentary habitats that are not associated with seagrass beds are considered in this section. Epiphytic assemblages will be discussed in Section 1.6, although a short mention will be provided here where appropriate. Several studies have focused on the taxonomy of meiofauna (especially Nematoda) in tropical coral reefs (*e.g.* for nematodes: Gerlach, 1958, 1962, 1963, 1964; Inglis, 1968; Boucher, 1973; Decraemer, 1974, 1977, 1982, 1987, 1988, 1989; Gourbault & Decraemer, 1992,

1993; Gourbault & Vincx, 1994). Furthermore, a number of studies have dealt with the ecology of reef-associated meiofauna and/or nematofauna, and the results from these studies are summarised here. The vast majority of them has been carried out in the South Pacific (Salvat & Renaud-Mornant, 1969 (Mururoa: French Polynesia); Renaud-Mornant *et al.*, 1971 (Maturei Vavao: French Polynesia); Thomassin *et al.*, 1982 (Moorea: French Polynesia); Alongi, 1986 (Great Barrier Reef); Guzmán *et al.*, 1987 (Costa Rica); Gourbault & Renaud-Mornant, 1989 (Fangataufa: French Polynesia); St.John *et al.*, 1989 (Great Barrier Reef); Gourbault & Renaud-Mornant, 1990 (Fangataufa: French Polynesia); Tietjen, 1991 (Great Barrier Reef); Boucher & Kotta, 1996 (Fiji); Boucher, 1997 (New Caledonia); Boucher *et al.*, 1998 and Kotta & Boucher, 2001 (both Moorea)). Only one study was carried out in the North Pacific (Kotta & Boucher, 2001 (Miyako Island: Japan)), three in the North Atlantic (Coull, 1970 (Bermuda); Boucher & Gourbault, 1990 (Guadeloupe); de Jesús-Navarrete, 2003 (Mexico)), one in the South Atlantic (Netto *et al.*, 1999 and Netto *et al.*, 2003 (Rocas Atoll)), two in the Red Sea (Grelet, 1984 and Grelet *et al.*, 1987 (Gulf of Aqaba); Arlt, 1995 (Eritrea)) and three in the Indian Ocean (Thomassin *et al.*, 1976 (Madagascar); Ólafsson *et al.*, 1995 (Zanzibar); Ndaro & Ólafsson, 1999 (Zanzibar)).

Because (1) some of these studies made a comparison between the lagoon and the reef itself, (2) the lagoon is always closely connected to other habitats (*e.g.* the reef crest and reef flat, reef pools, intertidal reef-flats, coral heads, etc.) and (3) the distinction between these habitats is sometimes unclear, information on other coral reef habitats will also be added where necessary.

Table 8 and Fig. 6 give an overview of the sampling locations considered in this section.

1.5.1. MEIOFAUNA

Composition

A total of 28 different taxa has been encountered in coral reef lagoons (Table 9), ranging from 9-18 per study (Table 10). Incomplete taxon lists ('Rest') and differences in approach, *e.g.* the insertion or not of the number of nauplii into the Harpacticoida counts, of Archiannelida into Polychaeta (due to changes in the systematic position of this taxon) and of protozoans (Foraminifera, Ciliata, Rhizophora) into total meiobenthic density, may interfere with the comparison between studies.

The meiofauna in reef lagoons is either dominated by nematodes (Salvat & Renaud-Mornant, 1969; Coull, 1970; Renaud-Mornant *et al.*, 1971; Thomassin *et al.*, 1982; Guzmán *et al.*, 1987; Gourbault & Renaud-Mornant, 1989; St.John *et al.*, 1989; Boucher & Gourbault, 1990; Gourbault & Renaud-Mornant, 1990; Ólafsson *et al.*, 1995; Boucher & Kotta, 1996; Boucher, 1997; Boucher *et al.*, 1998; Ndaro & Ólafsson, 1999; Netto *et al.*, 1999; Netto *et al.*, 2003), harpacticoid copepods (Thomassin *et al.*, 1976; Thomassin *et al.*, 1982; Guzmán *et al.*, 1987; Gourbault & Renaud-Mornant, 1989; Gourbault & Renaud-Mornant, 1990; Ndaro & Ólafsson, 1999; Netto *et al.*, 1999; Kotta & Boucher, 2001; Netto *et al.*, 2003), nauplii (Thomassin *et al.*, 1976), polychaetes (Thomassin *et al.*,

		Region	Location	Habitat
1	Salvat & Renaud-Mornant (1969)	South Pacific	Mururoa (Tuamotu)	coral reef lagoon (atoll)
2	Coull (1970)	North Atlantic	Bermuda	platform
3	Renaud-Mornant *et al.* (1971)	South Pacific	Maturei Vavao (Tuamotu)	coral reef lagoon
4	Thomassin *et al.* (1976)	Indian Ocean	SE Madagascar (Toliara)	coral reef lagoon
5	Thomassin *et al.* (1982)	South Pacific	Moorea (Polynesia)	reef flat/reef lagoon
6	Grelet (1984); Grelet *et al.* (1987)	Red Sea	Gulf of Acaba	coral reef and lagoon
7	Alongi (1986)	South Pacific	Great barrier Reef	reef crest/reef flat/reef lagoon
8	Guzmàn *et al.* (1987)	South Pacific	Costa Rica	coral reef lagoon
9	Gourbault & Renaud-Mornant (1989)	South Pacific	Fangataufa (Tuamotu)	coral reef lagoon (atoll)
10	St.John *et al.* (1989)	South Pacific	One Tree Reef (Great Barrier Reef)	coral reef lagoon
11	Boucher & Gourbault (1990)	North Atlantic	Guadeloupe	subtidal sediment
12	Gourbault & Renaud-Mornant (1990)	South Pacific	Fangataufa (Tuamotu)	coral reef lagoon (atoll)
13	Tietjen (1991)	South Pacific	Great Barrier Reef	coral reef lagoon
14	Arlt (1995)	Red Sea	Massawa	coral reef lagoon
15	Olafsson *et al.* (1995)	Indian Ocean	Zanzibar	coral reef lagoon + seaweed farms
16	Boucher & Kotta (1996)	South Pacific	Fiji	coral reef lagoon
17	Boucher (1997)	South Pacific	New Caledonia	lagoon
18	Boucher *et al.* (1998)	South Pacific	Moorea (Polynesia)	coral reef lagoon
19	Netto *et al.* (1999)	South Atlantic	Rocas Atoll	atoll lagoon, reef pools etc.
20	Ndaro & Olafsson (1999)	Indian Ocean	Zanzibar	intertidal lagoon
21	Kotta & Boucher (2001)	North Pacific	Miyako Island (Japan)	coral reef lagoon
22	Netto *et al.* (2003)	South Atlantic	Rocas Atoll	intertidal reef-flats
23	de Jesus-Navarrete (2003)	North Atlantic	Banco Chinchorro (Mexico)	coral reef lagoon (atoll)
24	This study (2006)	Indian Ocean	Kenyan Coast	coral reef lagoon
25	This study (2006)	Indian Ocean	Zanzibar	coral reef lagoon

Table 8. Sampling locations of the studies on meiofauna in tropical coral reef lagoons discussed in Section 1.4., supplemented with the present study. Habitat type discussed in the respective is indicated.

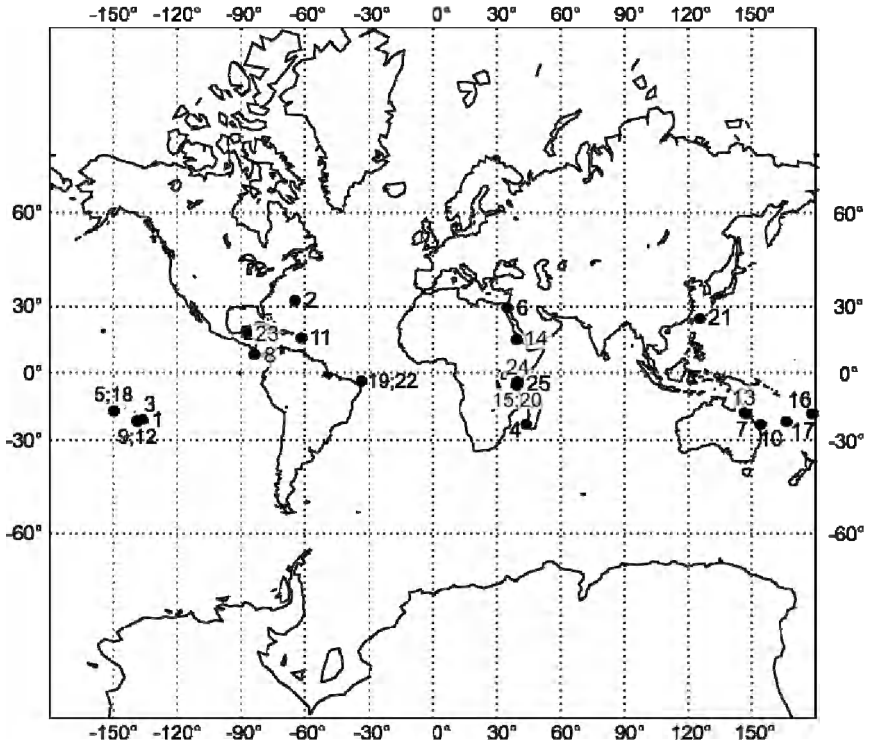


Fig. 6. Sampling locations of the studies on meiofauna in tropical coral reef lagoons discussed in Section 1.4., supplemented with the location of the present study. The numbers correspond with those in Table 8.

1982; Netto *et al.*, 2003) or gastropods (Guzmán *et al.*, 1987). Nematodes, copepods and polychaetes are generally the three most abundant taxa (*e.g.* Kotta & Boucher, 2001) and nematodes or copepods are the dominant taxa in most cases (Table 10, 11). Globally, harpacticoid copepods are usually the second most abundant taxon in marine sediments, after free-living nematodes (Hicks & Coull, 1983). The relative abundance of harpacticoids in tropical reef lagoons is mainly determined by their trophic requirements and oxygen needs. First of all, these crustaceans prefer habitats that guarantee an easy access to benthic diatoms, which are a major food source (Hicks & Coull, 1983; Thomassin *et al.*, 1976). As a result, copepods tend to assemble in the upper sediment layers (Fenchel & Riedl, 1970). Another reason why harpacticoid copepods are particularly found in the upper layers of the sediment is their sensitivity to decreasing oxygen levels (McLachlan, 1978; Ansari & Ingole, 1983; Moodley *et al.*, 1997; Wetzel *et al.*, 2001). In fact, they have to remain above the sediment's RPD (Redox Potential Discontinuity) layer. To summarise, they prefer well-oxygenated sediments where benthic diatoms are abundant. It is known that harpacticoid copepods become numerically more abundant as the particle size of the sediment increases and they are often the dominant meiobenthic taxon in coarse sediments (Hicks & Coull, 1983). The harpacticoid copepods are especially abundant in coarse, biogenic, carbonate sands, both subtidal and intertidal (Coull, 1970; Thomassin *et al.*, 1976; Thomassin *et al.*, 1982; Renaud-Mornant & Gourbault, 1984; St.John *et al.*, 1989; Kotta & Boucher, 2001). According to Asmus & Bauerfeind (1994), epipsammic diatoms, which are benthic diatoms attached to sand grains, dominate in more dynamic, sandy sediments. Strong oxygenation and penetration by sunlight improves conditions for primary production and consequently stimulates diatom reproduction and growth. In their study of the temperate Molenplaat (Westerschelde estuary), Hamels *et al.* (1998) reported that sandy sediments accommodate a very diverse diatom community, especially when compared to nearby silty sediments.

Nematodes generally exhibit a high tolerance to oxygen deficiency compared to other meiofaunal taxa and especially to crustaceans, which are much less resistant to reduced oxygen concentrations (Moodley *et al.*, 1997; Wetzel *et al.*, 2001). According to Renaud-Mornant & Gourbault (1984), the dominance of nematodes in calm, undisturbed waters may be due to an elevation of the water temperature and the consequent lower solubility of oxygen. In the study of the coral sediments at Tiahura Reef by Thomassin *et al.* (1982), copepods were dominant in exposed, clean and coarse sands whereas nematodes dominated in sheltered zones with accumulated detrital food. The decomposition (respiration) of accumulated phytodetritus contributes to the depletion of oxygen in the bottom and will therefore favour nematodes. A clear separation should be made here between (1) fresh organic material (*in situ* primary production and macrophytes) and (2) degraded organic material (detritus). The presence of fresh organic material, *i.c.* diatoms (as a food source) and macrophytes (as a habitat), will favour harpacticoid copepods, while decomposing organic material will favour nematodes.

The fact that harpacticoid copepods are less abundant in fine, homogenic sediments is also attributed to the difficulty for relatively larger and plumper taxa (*e.g.* the larger Harpacticoida) to penetrate the denser sandmass. This is in contrast with smaller animals, such as Tardigrada, or taxa well-adapted to interstitial life, such as Gastrotricha and Nematoda and typical burrowers, such as

Priapulida (Renaud-Mornant & Gourbault, 1984; Kotta & Boucher, 2001). Furthermore, the relative quantity of silt in the sediment is responsible for the degree of sediment pore space filling, which determines the size limit of the interstitial taxa (Tita *et al.*, 1999). Hence, a higher proportion of silt will positively influence the relative abundance of nematodes (Gourbault & Renaud-Mornant, 1989; 1990). According to Kotta & Boucher (2001), Tardigrada are associated with coarser sediment and Priapulida with a higher silt content. The former result is unexpected given the above reasoning.

According to Thomassin *et al.* (1976), nauplii follow the same pattern in relative abundance and densities as the adult copepods. The same author observed that polychaetes reach their maximal densities in fine, enriched sediments. St.John *et al.* (1989), however, observed highest oligochaete and polychaete abundances in coarse sediments. Thomassin *et al.* (1976) also observed that nematodes became dominant in the proximity of *Thalassia testudinum* Banks & Soland ex Koenig seagrass beds. This indicates that the presence of macrophytes also influences meiobenthic community structure.

Geographical and temporal aspects are also to be considered. Kotta & Boucher (2001) found that meiobenthic assemblage structure was determined by the geographical position of the sampling location. Species composition also fluctuated greatly on a monthly scale, which was explained by changes in climate conditions (monsoons). Guzmán *et al.* (1987) observed a peak in abundance of temporary meiofauna (*e.g.* Gastropoda) during or towards the end of the rainy season, while the permanent meiofauna peaked during the dry season.

To sum up, meiobenthic community structure is determined by the following environmental aspects: (1) mean sediment grain size, (2) relative quantity of silt in the sediment, (3) sediment oxygen content, (4) extent of *in situ* primary production, (5) macrophytal biomass, (6) phytodetritus content in the sediment, (7) depth, (8) geographical position and (9) seasonality.

Taxon	2 (CHD)	4	5	8	9*	10*	11	12	15	17*	19	20
Amphipoda				X		X	X		X			X
Bivalvia	X		X	X		X		X				
Chaetognatha		X										
Cnidaria								X	X			X
Cumacea				X					X			X
Cyclopoida									X			X
Echinodermata				X								
Gastropoda			X	X		X		X				X
Gastrotricha		X	X				X	X		X		
Gnathostomulida			X									
Halacarida	X	X		X			X	X			X	
Harpacticoida	X	X	X	X	X	X	X	X	X	X	X	X
Insecta			X									X
Isopoda		X		X								
Kinorhyncha	X	X						X		X	X	
Megalopa				X								
nauplii*		X			X					X		
Nematoda	X	X	X	X	X	X	X	X	X	X	X	X
Nemertini			X					X				
Oligochaeta			X			X	X	X	X		X	X
Ostracoda	X	X	X	X		X	X	X	X	X	X	X
Polychaeta	X	X	X	X		X	X	X	X	X	X	X
Priapulida	X											
Rotifera								X				
Sipunculida				X								
Tanaidacea	X	X	X			X	X	X		X	X	
Tardigrada		X					X	X		X	X	
Turbellaria			X	X	X			X	X			X
REST	X			X	X		X	X			X	

Table 9. Meiofauna higher taxa in tropical coral reef lagoons: presence-absence data. Numbers in the first row correspond with those in Table 8. CHD = Castle Harbor Deep Station. *: nauplii included in Harpacticoida count.

	Number of taxa	Lowest dominance	Highest dominance
2 (CHD)	9*	63.7% (Nematoda)	94.8% (Nematoda)
4	8-12 (12)	32.5% (Copepoda)	56.1% (Nauplii)
5	4-9 (13)	45.9% (Polychaeta)	70.9% (Nematoda)
8	8-13* (14*)	15.3% (Nematoda)	43.0% (Gastropoda)
11	3-8* (10*)	51.0% (Nematoda)	96.3% (Nematoda)
12	3-12* (15*)	31% (Nematoda)	92% (Nematoda)
15	10	68% (Nematoda) (average value)	87% (Nematoda) (average value)
17	18	42.9% (Nematoda)	56.0% (Nematoda)
19	14	43.2% (Nematoda) (average value)	51.8% (Copepoda) (average value)
20	12	45% (Nematoda) (average value)	97% (Nematoda) (average value)
22		44% (Copepoda)	55% (Polychaeta)

Table 10. Taxon richness and dominance of meiofauna in tropical coral reef lagoons, indicated as total numbers for the entire study or as a range (per sample) with the total number between brackets. *: only the dominant taxa were mentioned in this study. Numbers in the first column correspond with those in Table 8. CHD = Castle Harbor Deep Station.

	Dominant taxa
1	Nematoda (52-56%)
2 (CHD)	Nematoda (63,7-94,8)
3	Nematoda (16-61%)
4	Nauplii (28,1-56,1%), Copepoda (21,6-44,5%) or Nematoda (9,7-34,6%)
5	Polychaeta (11,4-61,3%), Copepoda (7,6-55,6%) or Nematoda (8,8-70,9%)
6	Nematoda (32-91%)
8	Nematoda (9,9-30,5%), Gastropoda (1,7-43,0%) or Copepoda (9,9-41,4%)
9	Nematoda (19-92%) or Copepoda (2-44%)
10	Nematoda (56,83%)
11	Nematoda (51,0-96,3%)
12	Nematoda (19-92%) or Copepoda (2-44%)
15	Nematoda (68-87%) (average values)
16	Nematoda
17	Nematoda (42,9-56,0%)
18	Nematoda
19	Nematoda (23,4-45,6%) or Copepoda (38,3-51,8%) (average values)
20	Nematoda (13-97%) or Copepoda (2-77%) (average values)
21	Copepoda
22	Nematoda (45%), Copepoda (44%) or Polychaeta (55%)

Table 11. Dominant taxa in the meiofauna of tropical coral reef lagoons. Numbers in the first column correspond with those in Table 8. CHD = Castle Harbor Deep Station.

	Meiofaunal densities
1	144-517 ind/10 cm²
2 (CHD)	306-1187 ind/10 cm²
3	90-616 ind/10 cm²
4	325-609.5 ind/ 10cm²
5	38.7-120.3 ind/10 cm²
8	99-575 ind/10 cm² (average values) (including forams!)
9	528-7001 ind/ 10 cm²
11	678-9989 ind/10 cm²
12	528-7001 ind/ 10 cm²
17	1224-3275 ind/10 cm² (average values)
19	540.3-1179.7 ind/10 cm² (average values)
20	219-3422 ind/10 cm² (average values)
22	278-4165 ind/10 cm²

Table 12. Densities of meiofauna in tropical coral reef lagoons. Numbers in the first column correspond with those in Table 8. CHD = Castle Harbor Deep Station.

Densities

Meiobenthic densities range from 38.7 ind/10 cm² (Thomasssin *et al.*, 1982) to 9989 ind/10 cm² (Boucher & Gourbault, 1990) (Table 12). The very low densities reported by Thomassin *et al.* (1982) may be the result of the very wide mesh size (250 µm) used to collect the meiofauna (see Section 1.7). High densities of meiofauna in tropical lagoon environments are due to the high potential of meiofauna to partition available resources. This is for example demonstrated by the adaptive trophic strategies of nematodes (see below). According to Renaud-Mornant *et al.* (1971), Thomassin *et al.* (1976) and Grelet *et al.* (1987), these densities are positively influenced by the organic carbon and nitrogen content, and hence the amount of detritus, in the sediment. Meiobenthic distribution and densities are particularly determined by the availability of organic food particles, *i.e.* by the food supply from the water column and the abundance of food present within the sediment. The meiobenthos exploits both the phytodetritus itself as well as the rich bacterial communities that are involved in the microbial decomposition of the detrital aggregates. This leads to the conclusion that meiobenthic densities are highest in undisturbed sediments with accumulated phytodetritus. These are also the conditions with increased nematode relative abundances. Boucher & Gourbault (1990) indeed found that highest densities were found where nematode occurrence was high.

The texture and high porosity of coarse sediment, *i.c.* the presence of large cavities between the sand grains, improves oxygenation and penetration of sunlight, hence improving conditions for primary production (Thomassin *et al.*, 1976). Clavier & Garrigue (1999) found that in a reef lagoon in New Caledonia, overall mean primary production was almost as high as overall mean respiration, and mean primary production even exceeded mean respiration in coarser sediments (sand vs. mud). Clearly, coarse sediments are not ideal for the decomposition of organic material. Nevertheless, the areas of the lagoon that are more protected from strong hydrodynamic activity will be characterised by more accumulated detritus and thus higher densities of the meiofauna. It is essential to note that the influence of mean sediment grain size on meiobenthic density may actually be an effect of increased hydrodynamics, which will reduce food input and cause coarsening as well as better oxygenation of the sediment. When hydrodynamic stress becomes too vigorous, physical erosion will also lower meiobenthic abundance. A link between densities and sediment grain size is proposed by Renaud-Mornant *et al.* (1971) in their study of Maturei Vavao, where meiofaunal density increased with decreasing grain size. Grelet *et al.* (1987) and Ndaro & Ólafsson (1999) also found higher densities in fine sand habitats compared to sediment with a larger mean grain size. Surprisingly however, the opposite was found by Boucher (1997): in his study of a reef in New Caledonia, he found much higher densities in coarse, very hydrodynamic sediments adjacent to the reef itself than in sediments closer to the beach, although the latter were much more enriched with terrestrial inputs.

The nature of the sediment, *i.e.* whether carbonate or not, may also provide an explanation for differences in nematode densities, as $CaCo_3$ has a low sorption capacity and usually a low organic content (Guzmán *et al.*, 1987). On the other hand, Grelet *et al.* (1987) found no significant variation in meiobenthic densities with the (biogeneous or terrigeneous) nature of the sediment.

Netto *et al.* (1999) found proof for a negative correlation between temperature and meiobenthic densities. Oxygen depletion related to a decreased solubility of the gas may be an essential factor

here. According to Ndaro *et al.* (1995), sediment porewater biochemistry is also a factor which varies substantially on a small scale and influences meiobenthic abundance.

Renaud-Mornant *et al.* (1971) observed an increase in meiobenthic density with increasing water depth. On the other hand, Gourbault & Renaud-Mornant (1990) found lowest densities in the deepest stations of Fangataufa Atoll. This was however the result of long-term dredging activities. Grelet *et al.* (1987) reported some conflicting results regarding the depth:density relationship for meiobenthos. These authors attributed the observed trends to differences in hydrodynamic conditions (related to bottom topography) and the presence of a seagrass meadow. In contrast, Tietjen (1969) stated that shallow waters often support more meiofauna than deeper waters.

According to Renaud-Mornant *et al.* (1971), Thomassin *et al.* (1982) and Alongi (1986), bioturbation and predation by macrobenthic animals, such as the holothuroid *Halodeima atra* Jaeger, 1833 and the ghost shrimp *Callianassa kraussi* Stebbing, 1900, may negatively influence the colonisation, establishment and growth of a meiobenthic community. The presence of bioturbators also alters the vertical penetration and seasonal fluctuations of the meiobenthos. Ólafsson *et al.* (1995) attributed the lower abundance of the meiobenthos inside seaweed farms along the Zanzibar east coast at least partly to the predation by juvenile fish, in particular the Mojarra *Gerres oyena* (Forsskål, 1775). In contrast, St.John *et al.* (1989) found no effect of the predatory goby *Valenciennea longipinnis* (Lay & Bennett, 1839) on meiobenthic abundance.

Finally, temporal fluctuations in densities have been observed by Guzmán *et al.* (1987), who attributed the increased density in the month of September to an increased supply of organic matter from precipitation and landslides.

Diversity

The origin of the sediment may be an important factor determining meiobenthic diversity, as the higher permeability and porosity of carbonate sediments enables more water exchange and stimulates the movement of interstitial fauna (Gray, 1974). Moreover, angular carbonate sands allow for increased interstitial space (Renaud-Debyser, 1963). Guzmán *et al.* (1987) indeed observed a higher diversity in sediment with a higher $CaCO_3$ content. Furthermore, poorly sorted sediment can maintain an even higher diversity as a mixture of fine and coarse sediment offers more potential niches for meiofauna (Gray, 1981).

Decreasing oxygen levels will lead to a taxon-poor sediment with a manifest dominance of nematodes and a much lower percentage or even the absence of other taxa. This may be the case in calm, undisturbed waters, where water temperatures may rise quickly, or in conditions with large amounts of decomposing phytodetritus. These are the conditions where the meiobenthos tends to become most dense. Moreover, increased hydrodynamic stress may lead to low densities (see above), but also to high diversity due to reduced competition. This suggests an inverse relationship between diversity and density, an idea that has been confirmed by several studies (Renaud-Mornant *et al.*, 1971; Rao & Misra, 1983; Netto *et al.*, 1999).

The extent of disturbance is also very important: frequent or continuous, strong and/or large-scale disturbance will have a negative effect on the diversity of the meiobenthos, whereas sporadic, less vigorous and small-scale disturbance will have the opposite effect (Ólafsson *et al.*, 1995).

According to Renaud-Mornant *et al.* (1971), meiobenthic diversity decreases with increasing depth.

1.5.2. NEMATOFAUNA

Although the focus will be here on the structuring role of abiotic factors on the composition and diversity of nematode assemblages, biotic interactions also play an important role, especially in physically undisturbed environments (Coull, 1970; Kotta & Boucher, 2001). These biotic interactions are however much less documented and will therefore not be discussed below. Moreover, abiotic factors are expected to be the most important structuring factors in tropical carbonate sands, as these are known to be subjected to frequent disturbance (Connell, 1978).

Composition

The wide range of contrasting approaches and considerable differences in scale and sampling effort between the few studies that concentrate on nematode community composition, pose a considerable problem in comparing nematode data from different studies. Sampling effort is expressed as the number of samples that was taken, the total collected surface area and simply as the size of the sampling area. Another problem is the nature of the composition data. Just as for the meiobenthos on a higher taxon level, some studies only report the dominant taxa, with the result that only partial comparisons can be made. Problems may also arise when different authors rely on a different taxonomy, either due to contrasting traditions or related to changes in taxonomical knowledge over the years. Despite all these problems, some clear patterns do arise.

In the sediment of a coral reef in New Caledonia, Inglis (1968) observed that all species were new to science, whereas all genera and families were not. This was explained by the fact that genera at least tend to be cosmopolitan while species do not, which was confirmed in the studies of Boucher & Gourbault (1990), Gourbault & Renaud-Mornant (1990), Tietjen (1991) and Boucher (1997). Moreover, Boucher (1997) argued that most taxa in lagoonal sediments belong to the same families and genera as those of most temperate, sublittoral sands. Contrasting to the idea of Inglis (1968), Alongi (1986) found that the nematode communities in the tropical lagoon at Davies Reef were comprised of species that had already been found in other environments (mangroves, tropical beaches) of the South Pacific. Furthermore, up to 30.6% of the species found in the study of de Jesús-Navarrete (2003) were already described from other regions of the world. The importance of cosmopolitism evidently increases with each study on the subject. The study of Tietjen (1991) is an exception in the opposite way: here only 93 out of 135 genera were already known to science. Still, the dominance of Desmodoridae, Chromadoridae, Xyalidae and Cyatholaimidae in tropical, lagoonal sediments seems to be consistent over most studies (Grelet, 1984; Renaud-Mornant & Gourbault, 1984; Gourbault & Renaud-Mornant, 1990; Boucher & Gourbault, 1990; Tietjen, 1991; Boucher, 1997; Ndaro & Ólafsson, 1999; Kotta & Boucher, 2001), although some other families, or representatives of other families, may also become

very abundant (*i.c.* Axonolaimidae, Comesomatidae, Ethmolaimidae, Linhomoeidae, Microlaimidae, Oncholaimidae, Oxystominidae) (Table 13). Chromadoridae usually dominate in terms of number of genera (Alongi, 1986; Ndaro & Ólafsson, 1999).

The importance of these families is very well reflected in the nature of the dominant species and genera. Grelet (1984) observed a dominance of *Microlaimus* (Microlaimidae), but the second and third most abundant genera were representatives of Desmodoridae (*Spirinia*) and Chromadoridae (*Spilophorella*). The dominant species in the study of Gourbault & Renaud-Mornant (1989; 1990) were representatives of the families Xyalidae (*Daptonema fistulatum* (Wieser & Hopper, 1967), *Paramonohystera* sp. 1, *P.* sp. 2), Ethmolaimidae (*Gomphionema* sp. 1), Chromadoridae (*Ptycholaimellus* sp. 1) and Cyatholaimidae (*Pomponema* sp.). This is very much in correspondence with the study of Boucher & Gourbault (1990), where the dominant species belonged to Desmodoridae (*Metachromadora* sp., *Spirinia parasitifera* (Bastian, 1865)), Xyalidae (*Daptonema miamiensis* (Hopper, 1969), *Rhynchonema* sp. 1) and Ethmolaimidae (*Gomphionema* sp.). Tietjen (1991) observed a dominance of *Theristus* (Xyalidae), *Spilophorella* (Chromadoridae) and *Halalaimus* (Oxystominidae). The dominant species in the study of Boucher (1997) was *Laxus cosmopolitus* Ott, Bauer-Nebelsick & Nvotny, 1995 (Desmodoridae). Next to *Laxus*, the most abundant genera were *Daptonema* (Xyalidae), *Ptycholaimellus* and *Spilophorella* (both Chromadoridae). The most abundant species in the study of Kotta & Boucher (2001), who compared four geographically distant locations, were again representatives of Desmodoridae (*Paradesmodora* sp. 1, *Laxus cosmopolitus*), Chromadoridae (*Chromadorita* sp. 3) and Cyatholaimidae (*Marylynnia annae* (Wieser & Hopper, 1972)). The most abundant species in the study of de Jesús-Navarrete (2003) were *Paracomesoma inaequale* Jensen & Gerlach, 1977 (Comesomatidae), *Meyersia major* Hopper, 1967 (Oncholaimidae), *Spirinia hamata* Wieser & Hopper, 1967 (Desmodoridae), *Odontophora* sp. (Axonolaimidae) and *Rhynchonema hirsuta* Hopper, 1961 (Xyalidae). Finally, Netto *et al.* (2003) reported *Chromaspirina* sp. 1 (Desmodoridae), *Metoncholaimus* sp. 1 (Oncholaimidae), *Gomphionema* sp. 1 (Ethmolaimidae) and *Paralinhomoeus* sp. 2 (Linhomoeidae) as the most abundant species. It is clear from the above that despite of the pronounced geographical separation of the study sites, the dominant taxa are generally the same (families, genera) or closely related (genera).

The following ten studies examined nematode community composition and performed at least some kind of multivariate analysis (whether agglomerative or divisive) on nematode data to define distinct species assemblages and to unravel the effect of the different environmental variables listed below (the mention of each of these variables in a particular study is indicated with its number in superscript): Alongi, 1986[1,7]; Boucher & Gourbault, 1990[2,4,5,6]; Gourbault & Renaud-Mornant, 1990[1,2,4,9]; Tietjen, 1991[1,6]; Ólafsson *et al.*, 1995[1,7,8]; Boucher, 1997[2,6,8]; Ndaro & Ólafsson, 1999[1,3,6]; Netto *et al.*, 1999[1,3,4,6,9], Kotta & Boucher, 2001[1,2,9,10,11,12], de Jesús-Navarrete, 2003. Nematode assemblage structure is determined by (1) mean sediment grain size, (2) sediment composition (*i.c.* clay-silt content), (3) sediment sorting, (4) sediment oxygen content, (5) position of RPD (Redox Potential Discontinuity) layer in the sediment, (6) the amount of accumulated phytodetritus (*i.e.* organic content of the sediment), (7) the extent of bioturbation by macrobenthos, (8) macrofloral biomass (*i.c.* proximity of macrophytes), (9) depth, (10) longitude, (11) latitude and (12) sampling scale. The first

five factors are clearly interrelated with each other and the first six are clearly related to the hydrography of the reef water column. Intensified hydrodynamics, whether by tidal currents or waves, will produce coarser and better sorted sediment with lower clay-silt content and it will also guarantee better oxygenation of the sediment. Grain size has an indirect control on interstitial space and a direct control on total grain surface areas, which affects the presence of biofilms and bacterial abundances. It is very important to emphasise that although these variables have all been correlated with nematode community structure, it is not evident to verify which of these factors exerts the actual structuring role for a given assemblage. Furthermore, Kotta & Boucher (2001) found that the combined effect of several environmental variables often gave a better explanation of the variability of nematode assemblages. This indicates the complexity of the matter.

According to Alongi (1986) and Netto *et al.* (1999), nematode communities are distinct in different functional zones of a coral reef (resp. lagoon/reef flat/reef crest and outer reef/reef pools/tidal flats). Ndaro & Ólafsson (1999) were also able to delimit distinct communities in accordance with differences in sediment grain size. Boucher (1997) found a more subtle zonation pattern, characterised by a gradual change of nematode assemblages from the reef (offshore) to the beach (onshore).

Although all authors stress the existence of distinct communities, the composition of these communities is seldom discussed and preferences are difficult to discover. Taxa associated with silty sediments are *Gomphionema* (Gourbault & Renaud-Mornant, 1990), *Terschellingia*, *Marylynnia*, *Cyartonema* and the family Comesomatidae (Boucher & Gourbault, 1990; Wieser & Hopper, 1967). Moreover, *Gomphionema* and *Marylynnia*, together with *Sabatieria* (Comesomatidae) and two Linhomoeidae genera were found to be typical taxa for fine sediments (Ndaro & Ólafsson, 1999). Taxa associated with low oxygen levels are *Molgolaimus*, *Perspiria*, *Steineria* (Boucher & Gourbault, 1990), *Chromaspirina* and *Metoncholaimus* (Netto *et al.*, 1999). Taxa associated with strong hydrodynamic disturbance are *Viscosia*, *Metoncholaimus* and the families Cyatholaimidae and Comesomatidae (Alongi, 1986; Boucher, 1997). This reveals an important discrepancy regarding the occurrence of Comesomatidae. Monhysteridae were found to be much more abundant in muddy sediments than in coarse, coralline sediment, whereas *e.g.* Epsilonematidae were clearly much more abundant in the reefal white sands than in the more onshore sediments (Boucher, 1997). Epsilonematidae and the related Draconematidae were indicated as typical outer reef taxa in the study of Netto *et al.* (1999), who attributed their success in the high energy environment of the outer reef subtidal to adaptations to high substratum instability. Ndaro & Ólafsson (1999) also found *Epsilonema* (Epsilonematidae) to be much more abundant in coarse sediment. The morphological adaptations of representatives of these families to a life in coarse sediments and on larger surfaces will be discussed below (see Section 1.8.3). The presence of macrophytic substrata also has an effect on the assemblage structure of the nematode fauna, as pointed out by Ólafsson *et al.* (1995), who reported a preference of *Paracyatholaimus* for cultivated seaweeds. Whether morphological (cuticle structure, number and length of setae) or ecological (trophical, locomotory) adaptations of nematodes to differences in habitat structure and environmental conditions are important in explaining community structure still remains to be seen.

Tietjen (1991) found evidence of differences in species composition on a temporal scale (*i.c.* between January and October), both on the genus and species level: *Spirinia*, *Molgolaimus* and *Paracanthonchus* were more abundant in January, while *Sabatieria*, *Paracomesoma* and *Metacomesoma* were more abundant in October. Strikingly, the former three genera are all epigrowth feeders, while the latter three are non-selective deposit feeders. This observation provides evidence for the hypothesis that community composition is also structured by changes in trophic composition, which is in turn determined by the amount of accumulated phytodetritus. Nevertheless, Tietjen (1991) refuted the existence of seasonal changes in nematode trophic composition and attributed the irregular, short-term fluctuations to changes in sediment temperature. A higher temperature results in a lower oxygen content of the sediment.

Kotta & Boucher (2001) mentioned scale, longitude and latitude as principal determining factors for nematode community structure. Sampling scale, in contrast to sample size, will influence the number of taxa that is found, as more (micro)habitats will be sampled when the sampling scale is larger.

Epigrowth feeders (Wieser group 2A) and/or non-selective deposit feeders (Wieser group 1B) are generally the dominant trophic groups (according to Wieser, 1953) in subtidal coralline sediments (Coull, 1970; Alongi, 1986; Gourbault & Renaud-Mornant, 1989; Gourbault & Renaud-Mornant, 1990; Tietjen, 1991; Ólafsson *et al.*, 1995; Boucher, 1997; Ndaro & Ólafsson, 1999). There is no consensus in literature data on the modifying function of sediment granulometry on the trophic composition of nematode assemblages. Alongi (1986), Ólafsson *et al.* (1995) and Ndaro & Ólafsson (1999) found that epigrowth feeders dominated medium to very coarse sediment, whereas non-selective deposit feeders dominated finer, less disturbed sediments. Epigrowth feeders possess teeth with which they can rasp food particles off large sand grains and crack open algal cells. According to Suess (in Coull, 1970), carbonate grains tend to aggregate organic matter into thick, visible, stainable layers. As already discussed above, benthic diatoms may also be more abundant in coarse sand. The significantly higher abundance of non-selective deposit feeders in finer, less disturbed sediments, where bacterial populations and particulate detritus are more abundant than in coarser sediment, may be attributed to the ability of these nematodes to consume a variety of food particles of different sizes. The supply of detrital food appears to be a major factor in determining the trophic composition of nematodes. Remarkably, Gourbault & Renaud-Mornant (1990) found exactly the opposite trend as Alongi (1986): deposit feeders were most abundant in clean sands, while epigrowth feeders were most numerous in fine, silty sands. Furthermore, the relative abundance of either of the trophic groups did not even differ with sediment type or grain size in the study of Boucher (1997). So, it can be concluded that sediment grain size is not determinant for the trophic structure of nematodes, whereas availability/accumulation of phytodetritus probably is. Strikingly, Alongi (1986) and Netto *et al.* (2003) found predators/omnivores (Wieser Group 2B) to be dominant on the reef crest and in several intertidal reef-flat pools, respectively. This result is not well understood; the precise nature of Wieser Group 2B may be varied (Moens & Vincx, 1997).

An interesting aspect of the trophic habits of lagoonal nematodes is the existence of ectosymbiosis, which was observed in representatives of the Stilbonematinae (family Desmodoridae),

such as the dominant *Laxus cosmopolitus* in the study of Boucher (1997). Although Stilbonematinae are well-known for their ectosymbiotic relationships with bacteria (Ott *et al.*, 1991; Ott, 1995; Ott *et al.*, 2005), symbiosis does also occur in other taxa, *e.g. Daptonema*, *Pomponema* and *Calomicrolaimus* (Gourbault & Renaud-Mornant, 1989). This shows the importance of alternative feeding strategies.

	Dominant families
6	Desmodoridae (19.8%), Chromadoridae (14.8%), Xyalidae (13.6%)
11	Desmodoridae (40.3%), Xyalidae (23.3%), Cyatholaimidae (8.2%), Chromadoridae (6.7%)
12	Xyalidae (45.0%), Ethmolaimidae (21.8%), Chromadoridae (9.2%)
13	Chromadoridae (15.6%), Desmodoridae (12.7%), Comesomatidae (11.6%), Xyalidae (11.5%)
16	Desmodoridae (26.1%)
17	Desmodoridae (20.5%), Chromadoridae (20.4%), Xyalidae (11.7%), Cyatholaimidae (7.4%)
18	Desmodoridae (28.7%)
20	Desmodoridae (19.8%), Linhomoeidae (16.3%), Chromadoridae (11.3%)
21	Chromadoridae (46.0%)
22	Desmodoridae (40%), Oncholaimidae (19%), Ethmolaimidae (11%), Linhomoeidae (10%)
23	Desmodoridae, Comesomatidae

Table 13. Dominant nematode families in tropical coral reef lagoons. Numbers in the first column correspond with those in Table 8.

	Nematode densities
1	74.9-289.5 ind/10 cm²
2 (CHD)	195-958 ind/10 cm²
3	14-345 ind/10 cm²
4	46.3-181.3 ind/10 cm²
5	5.6-50.8 ind/10 cm²
7	35-399 ind/10 cm² (average values)
8	12.5-130.2 ind/10 cm² (average values)
10	121.5-152.9 ind/10 cm² (average values)
11	434-6728 ind/10 cm²
12	173-6451 ind/10 cm²
13	310-1250 ind/10 cm²
15	438-875 ind/10 cm² (average values)
17	685-1404 ind/10 cm² (average values)
19	206.8-508 ind/10 cm² (average values)
20	29-3039 ind/10 cm² (average values)
22	53-2592 ind/10 cm²
23	3.2-18.3 ind/10 cm²

Table 14. Nematode densities in tropical coral reef lagoons. Numbers in the first column correspond with those in Table 8. CHD = Castle Harbor Deep Station.

Densities

Nematode densities range from 3.2 ind/10 cm² (de Jesús-Navarrete, 2003) to 6728 ind/10 cm² (Boucher & Gourbault, 1990) (Table 14). In contrast to the aforementioned reasoning that meiobenthic densities may increase with decreasing grain size of the sediment, Alongi (1986) found that at Davies Reef, nematode densities were not at all correlated with sediment grain size. There was also no correlation with water depth. In the study of Boucher (1997), however, nematode densities increased together with the overall meiobenthic densities, *i.c.* in medium to coarse sands subjected to strong hydrodynamic forces. Ndaro & Ólafsson (1999) even mentioned 'the overwhelming dominance of sediment grain size as a factor influencing meiofaunal density'. According to Alongi (1986), nematode densities are highest in undisturbed sediments, which concurs with the aforementioned negative effect of hydrodynamics on nematode relative abundance and meiobenthic density. It is important to repeat here that in undisturbed conditions with increased temperature, meiobenthic density tends to increase. The availability of detrital food is the main determining factor here and sediment grain size is not

directly influential to meiofaunal densities. In this context, the accumulation of food and the size of the sand grains can be regarded as two independent variables, both structured by the hydrodynamics in the lagoon. Decomposing phytodetritus is also more abundant in the vicinity of seagrass beds. This is confirmed in the studies of Thomassin *et al.* (1976) and Ndaro & Ólafsson (1999), where nematodes reached higher densities in the proximity of, or in, seagrass beds. Again, the study of Boucher (1997) is an exception here.

Just as for meiobenthic densities, the presence of bioturbators and predators has shown to negatively affect nematode densities (Alongi, 1986; Ólafsson *et al.*, 1995).

	# families	# genera	# species	*H'* (species)	Margalef's SR	*J'*
2 (CHD)			197			
6				5.09±0.18	11.36±0.42	85±3
7	16	39	6-25 (50)	0.76-1.65		
9			57	1.85-3.68 (2.65±0.11)	1.74-4.56 (3.02±0.19)	55.78-86.71 (68.67±1.79)
11	30		18-38 (156)	2.28-4.58 (3.76±0.76)	2.56-5.57 (3.87±0.95)	55-89 (79.25±11.36))
12	19	54	62	2.64±0.49	2.99±0.83	68.73±8.29
13	17-21 (28)	135	248			
15			51			
16			31.6 (average value)	4.28 (average value)	6.64 (average value)	86 (average value)
17	10.3-20 (33)	21.3-38.7 (172)	22.7-41.3 (369)	4.15±0.15 - 4.60±0.09 (4.45±0.07)	6.01±0.45 - 7.79±0.22 (7.10±0.22)	86.09±1.72 - 89.59±0.83 (88.23±0.73)
18			16.0 (average value)	2.88 (average value)	3.26 (average value)	73 (average value)
19			109			
20		100	25			
21			22.2 (average value)	3.44 (average value)	4.60 (average value)	77 (average value)
22			61			
23	21	65	14-47 (98)	5.03		91

Table 15. Diversity numbers of the nematofauna in tropical coral reef lagoons, indicated as total numbers for the entire study or as a range (per sample) with the total number (sometimes supplemented with standard deviation) between brackets. Numbers in the first column correspond with those in Table 8. CHD = Castle Harbor Deep Station.

Diversity

Total numbers of families, genera and species, as well as other diversity indices from different studies, are provided in Table 15. According to Alongi (1986), Ólafsson *et al.* (1995) and Boucher (1997), nematode diversity is much lower in real carbonate sands compared to quartz sands, especially when the latter are influenced by terrestrial inputs. This implies that in carbonate reef sand habitats nematode diversity is low. As already argued above, the coarser carbonate sands are characterised by efficient microphytobenthic primary production, which promotes copepods at the expense of nematodes. Boucher (1997) therefore suggested an inverse relationship between nematode diversity and productivity. Sediment that is rich in degraded organic matter, on the other hand, is much more ideal for nematodes, and should therefore accommodate a more diverse nematode community. This explains the remarkably low species diversity of nematodes in the lagoonal sands of Davies Reef (Alongi, 1986), where low rates of deposition of organic material to the seabed may have lead to subsequent competition for food resources and thus a lowering of the diversity. Just

like for their density, the diversity of nematodes is highest in the shallow, protected parts of the lagoon, which is due to the high abundance of accumulated detritus. Strangely, Tietjen (1991) found no significant differences in bacterial abundance, bacterial production, chlorophyll a or phaeopigment concentrations between carbonate and quartz sands. Sediment grain size alone is also not a determinant factor, as Boucher & Gourbault (1990) found no clear correlation between diversity and sediment granulometry. Differences in sediment properties (*e.g.* sorption capacity, clay-silt content) and the extent of terrigenous inputs have been proposed as possible explanations (Tietjen, 1991; Kotta & Boucher, 2001). In the study of Kotta & Boucher (2001), silt content of the sediment had a positive effect on the total number of nematode species. Whether this is a direct effect (altering of interstitial space) or an indirect effect (higher clay-silt content in more protected parts of the lagoon) is not clear. The same authors have also listed literature sources for both an increase and a decrease in nematode diversity with increasing silt content. The reduction of interstitial space and the extent of sediment sorting may also play an important role here, even in combination with each other. Nematodes with a maximal body width 0.16 times smaller than the sediment grain diameter will be able to slide through the interstitia (interstitial life strategy), whereas nematodes with a larger body width will have to push away the grains (burrowing life strategy). A median grain size of 120-125 µm is thought to be the lower limit for an interstitial lifestyle (Wieser, 1959; Coull, 1988). However, this is very much dependent on the clay-silt fraction within the sediment, as an increased clay-silt fraction will result in a shift from interstitial nematodes to burrowing nematodes (Tita *et al.*, 1999). As already mentioned, this may result in either a decrease or an increase in nematode diversity. This is where sediment sorting may provide an explanation. Poorly sorted sediments are more prone to increased diversity, as increased microhabitat diversity is beneficial for the diversity of sediment-dwelling nematodes. High microhabitat complexity relaxes competition and permits coexistence of many species.

Boucher & Gourbault (1990) introduced the intermediate disturbance hypothesis (Connell, 1978) to explain the higher diversity in relatively calm, undisturbed areas compared to areas influenced by strong hydrodynamic forces. Disturbance, for example from anthropogenic activities, will result in decreased diversity when it is too frequent or too strong, but it can also have a positive effect on diversity when it is more sporadic and less vigorous (Tietjen, 1991). The presence of macrobenthic bioturbators, however, appears to have a distinctly negative effect on nematode diversity (Alongi, 1986). This effect could also be coupled with predation and competition by the macrofauna (Tietjen, 1991).

High generic richness may not only be sustained by a high number of spatial microhabitats, but also by the variety of food sources in the sediment, such as phytodetritus, bacteria and an organic coating which covers the $CaCO_3$ particles (Suess, 1968; Tietjen, 1991). Niche segregation is also reflected in the high relative importance of both non-selective deposit feeders and epistratum feeders.

In the overview of Kotta & Boucher (2001), diversity indices increased with depth. This is in sharp contrast with the findings of Renaud-Mornant *et al.* (1971) regarding meiobenthic diversity.

1.6. THE NEMATOFAUNA ASSOCIATED WITH SEAGRASS BEDS

For reasons of comparison, a short overview of seagrass-associated nematode community structure, densities and diversity will be provided hereafter. Literature data on the nematode assemblages in seagrass beds, both within the sediment and on the plants themselves, are summarised. The importance of this section lies in the comparison of epifaunal nematode assemblages on two different types of substratum: a comparison between coral-associated and seagrass-associated nematofauna will make it possible (1) to seek for parallels between the structuring role of both types of substratum and (2) to assess the effect of small-scale differences of the substratum's surface on the composition of the nematofauna. However, as seagrass meadows are only of interest for comparison and as they are not part of the core question of this thesis, the meiofauna on a higher taxon level will not be considered here. The focus will be only on the structuring factors that are directly related to the presence of the seagrasses. Other factors influencing subtidal nematode communities have already been discussed in Section 1.5.

Most studies on meiofauna and/or nematodes associated with seagrasses have been carried out in temperate and subtropical regions (see review of Bell *et al.*, 1984a; Decho *et al.*, 1985; Danovaro & Gambi, 2002), although some research has also been carried out in tropical regions (Den Hartog, 1967; De Troch *et al.*, 2001; Fisher, 2003; Fisher & Sheaves, 2003). In most cases, the Turtle Grass *Thalassia testudinum* has been the subject of research (Hopper & Meyers, 1967a, b; Lewis & Hollingworth, 1982; Bell *et al.*, 1984b; Decho *et al.*, 1985). Other examined species are *Thalassia hemprichii* (Ehrenbergii) Ascherson 1871; *Zostera marina* L.; *Syringodium filiforme* Kutzing; *S. isoetifolium* (Ascherson) Dandy 1939; *Halophila* ovalis (R. Brown) Hooker F., 1858; *H. stipulacea* (Forsskal) Ascherson 1867; *Halodule wrightii* Ascherson, 1868; *H. uninervis* (Forssk.) Ascherson and *Posidonia oceanica* (L.) (see review of Bell *et al.*, 1984a; De Troch *et al.*, 2001; Danovaro & Gambi, 2002; Fischer, 2003).

Nematodes are either dominant in seagrass beds (Lewis & Hollingworth, 1982), co-dominant with copepods (Bell *et al.*, 1984a; Danovaro & Gambi, 2002), or second most abundant behind copepods (Bell *et al.*, 1984a). Bell *et al.* (1984a) observed that nematode densities on seagrass blades are lower than in the sediment. These vary from 58.2-4811 ind/10 cm² in the sediment and from 0.6-1403.9 ind/10 cm² on the leaves (Bell *et al.*, 1984a; Danovaro & Gambi, 2002; Fisher, 2003). It is important to mention here that the high diversity in techniques (see below) for sampling leaf-associated fauna may prove to be an important limitation when comparing these data. Several studies have nevertheless reported increased nematode densities in the coralline sediment of tropical lagoons near seagrass beds (Thomassin *et al.*, 1976; Coull, 1970, Grelet *et al.*, 1987; Ndaro & Olafsson, 1999). Alongi & Christofferson (1992) attributed higher densities in seagrass beds to the higher quality of the seagrass detritus. Nematode densities, both in the sediment and on the leaves, fluctuate seasonally (Bell *et al.*, 1984b).

The proximity of macrophytes is important in structuring the nematode communities in tropical lagoons. This is either a direct effect (presence of substrata, shelter against macrofauna) or an indirect effect (elevated organic content in the sediment due to the deposition of leaf litter; see Danovaro &

Gambi, 2002). Heip *et al.* (1985) confirms that macrophytes may be beneficial for a rich nematode community, as their presence results in an enormous increase in food availability, habitat complexity and shelter from macrofauna. Hopper & Meyers (1967a) observed decreasing numbers of *Metoncholaimus scissus* in parallel with the decline of the seagrass community. The hypothesis here was that *M. scissus* uses the leaves of *Thalassia testudinum* as a substratum for egg attachment. This implies a very close link between the nematode species and the distribution and health of the seagrass bed. It is important to notice that a substantial seagrass cover, possibly produced in relation to seasonal changes in temperature and exposure, may have both a positive and a negative influence on the sediment-dwelling nematofauna beneath the seagrasses. The positive effect lies in the stabilisation of the sediment, in this way allowing further, undisturbed settlement of detritus. The negative effect lies in the detritus-trap function of the seagrass leaves: the removal of the plants from the bottom has been shown to result in an increase in the amount of detritus and a better settlement of epiphytic micro-algae on the sediment surface (Paula *et al.*, 2001; Fisher, 2003).

Leaf nematodes are believed to be associated with the epiphytic flora that covers the seagrass leaves (Kikuchi & Pérès, 1977). Larger epiphytes provide (1) shelter for meiofaunal taxa, (2) a direct food source for herbivores and (3) phytodetritus for detritus-feeders. Epiphytic algae are also able to effectively trap detritus for meiofaunal utilisation. Furthermore, the presence of these algae may increase the available surface area with one order of magnitude (Reyes-Velasques, 1970) and in that way cause higher habitat complexity. Epifaunal taxa on leaves are generally permanent residents, small and limited in mobility (Lewis & Hollingworth, 1982).

In the study of Hopper & Meyers (1967a), the nematode community in the sediment of a subtropical Turtle Grass bed was dominated by *Metoncholaimus scissus* Wieser & Hopper, 1967, *Theristus fistulatus* Wieser & Hopper, 1967, *Spirinia parasitifera* (Bastian, 1865) and *Gomphionema typica* Wieser & Hopper, 1966. Typical species on the seagrass leaves in the same area were *Oncholaimus dujardinii* de Man, 1876, *Chromadora macrolaimoides* Steiner, 1915, *Paracanthonchus platypus* Wieser & Hopper, 1967, *Chromadorina epidemos* Hopper & Meyers, 1967 and *Acanthonchus cobbi* Chitwood, 1951 (Hopper & Meyers, 1967b). *Microlaimus*, *Desmodora* and *Daptonema* were the most abundant genera in the sediment of a *Posidonia oceanica* seagrass bed (Danovaro & Gambi, 2002). Linhomoeidae, Xyalidae, Chromadoridae, Desmodoridae and Comesomatidae were the most abundant families, *Terschellingia*, *Metalinhomoeus* and *Catanema* the most abundant genera and *Terschellingia longicaudata* de Man, 1907 the dominant species in the study of Fischer (2003) and Fisher & Sheaves (2003). This study compared estuarine seagrass communities with more marine seagrass communities in a coral reef environment. The nematode communities in the coral-reef associated seagrass beds were dominated by *Catanema* sp. 1, *Spirinia parasitifera* (Bastian, 1865), *Actinonema* and *Prochromadorella*. The high abundance of *Terschellingia* in tropical seagrass meadows has been confirmed by Ndaro & Ólafsson (1999), who found a dominance of *Chromaspirina*/*Spirinia*, *Terschellingia*, *Daptonema*, *Leptolaimus* and *Spilophorella* in a seagrass bed in Paje (Zanzibar). *Terschellingia* is a typical representative of a climax community in undisturbed, silty sediments.

Relative abundances of separate species and nematode assemblages were found to fluctuate seasonally (Hopper & Meyers, 1967a; Fisher, 2003). In the study of Fisher (2003), temporal variability was even much greater than within-site spatial variability.

Hopper & Meyers (1967a) observed that the dominant species in Turtle Grass associated sediment represented different trophic levels, either feeding on bacteria, diatoms or even higher algae. Epistratum feeders are generally the most abundant feeding category in seagrass beds, both in the sediment (Danovaro & Gambi, 2002) and on the leaves (Lewis & Hollingworth, 1982). Nevertheless, both deposit feeders and omnivores/predators may also become very abundant (Danovaro & Gambi, 2002; Fisher & Sheaves, 2003). According to Danovaro & Gambi (2002), nematode trophic structure is tightly coupled with the availability of different food sources: organic matter, microphytobenthos and bacteria. Epistratum feeders are known to graze on epiphytic diatoms, while deposit feeders utilise the phytodetritus that originates from larger epiphytes or phytodetritus that has been trapped by these structures. A decrease in seagrass cover will therefore have a positive effect on the abundances of infaunal epistratum feeders and deposit feeders (see above). In the study of Danovaro & Gambi (2002), the relative abundance of non-selective deposit-feeders was indeed closely related to the concentration of labile organic detritus although, strangely, the abundance of epigrowth feeders was not correlated with chloropigment concentrations but with the number of dividing bacteria. These authors also found that the biomass of predator nematodes was significantly correlated with the biomass of other nematodes. The high relative abundance of predator nematodes in this study could easily be explained given the observed high nematode densities in seagrass beds. Nematode trophic structure also shows temporal changes as a result of seasonal changes in food quality (Danovaro & Gambi, 2002; Fisher, 2003).

Diversity of nematode communities in seagrass sediments is characterised by homogeneity, high dominance and relatively low species richness. Homogeneity and high dominance have been attributed to the sheltering function of seagrasses against hydrodynamic disturbance and low number of available microhabitats (Hopper & Meyers, 1967a; Fisher, 2003; Fisher & Sheaves, 2003). Pioneer seagrass beds are however much more disturbed and yield more heterogeneous nematode communities (De Troch *et al.*, 2001). The higher heterogeneity of this habitat and still relative amelioration of physical disturbance may render these pioneer meadows into 'hotspots of diversity' (Fisher & Sheaves, 2003). High physical stress and disturbance by macrofauna in intertidal zones also leads to a lower diversity (Moore, 1972; Fisher, 2003). Nematode species diversity displays evident temporal changes (Danovaro & Gambi, 2002; Fisher, 2003). High concentrations and highly heterogeneous composition of food sources, as well as the high quality of seagrass detritus, are potential causes for high biodiversity in seagrass beds.

1.7. METHODOLOGY FOR SAMPLING MEIOFAUNA IN TROPICAL SUBTIDAL HABITATS

Throughout the years, different methodologies and sampling devices have been developed and used to sample tropical subtidal habitats for meiofauna. The choice for a certain method or device has mainly been influenced by (1) the type of (micro)habitat that is sampled, (2) practical considerations and (3) personal (or lab) preferences. Obviously, the removal of meiofauna from coral fragments or seagrass leaves will require a different approach than the sampling of sediment (see below). In fact, differences in sediment grain size may already demand the use of different sampling techniques. Practical considerations may include water depth, habitat, grain size, and the availability of sampling tools.

Thomassin *et al.* (1976) mentioned practical problems with pushing Perspex meiocores (plastic cores, internal diameter 36 mm) into coralline sediment: not only did the coral fragments and large grain size in the sediment prove to be a major obstacle for pushing down the meiocore, the fluidity and high water content of the coarse sediment also caused the sediment to pour out of the core during removal from the bottom. As an alternative, these authors simply scooped off and collected the uppermost 1.5 cm of the sediment. The tool utilised for removal of the sediment was not mentioned for this study. Thomassin *et al.* (1982) collected meiofauna by scooping a cylindrical jar horizontally into the upper 3 cm of the sediment. In more recent studies, however, meiocores of various diameters were usually applied. Alongi (1986) used plastic cores with a surface of 4.9 cm² (25 mm inner diameter), Guzmán *et al.* (1987) used cores with a surface of 5.31 cm² (26 mm inner diameter), St.John *et al.* (1989) with a surface of 19.6 cm² (50 mm inner diameter), Boucher & Gourbault (1990) with a surface of 5.72 cm² (27 mm inner diameter), Gourbault & Renaud-Mornant (1989; 1990) with a surface of 10 cm² (36 mm inner diameter), Ólafsson *et al.* (1995) with a surface of 9.6 cm² (35 mm inner diameter), Boucher & Kotta (1996), Boucher (1997) and Boucher *et al.* (1998) with a surface of 10 cm² (36 mm inner diameter), Ndaro & Ólafsson (1999) with a surface of 9.6 cm² (35 mm inner diameter), Netto *et al.* (1999) and Netto *et al.* (2003) with a surface of 4.9 cm² (25 mm inner diameter), Kotta & Boucher (2001) with a surface of 10 cm² (36 mm inner diameter) and de Jesús-Navarrete (2003) with a surface of 19.6 cm² (50 mm inner diameter).

To tackle the problem of sediment outflow, Alongi (1986) placed the cores directly in plastic jars while still underwater. St.John *et al.* (1989) applied a piston to seal the core. Tietjen (1991) used a Bouma boxcorer (surface: 270 cm²) to obtain undisturbed sediment samples. Subsamples from the boxcores were taken by means of plastic cores with a surface of 6.6 cm² (2.9 cm inner diameter).

The use of SCUBA divers to sample the reef sediment, especially at greater depths, has been a common practice (Thomassin *et al.*, 1982; Alongi, 1986; Guzmán *et al.*, 1987; Boucher & Gourbault, 1990; Gourbault & Renaud-Mornant, 1990; Boucher & Kotta, 1996; Boucher, 1997; Boucher *et al.*, 1998; Netto *et al.*, 1999; Kotta & Boucher, 2001; de Jesús-Navarrete, 2003; Netto *et al.*, 2003). In these studies, water depths varied between 1-10 m (Thomassin *et al.*, 1982), 2-16 m (Alongi, 1986), 5-10 m (Guzmán *et al.*, 1987), 4-38 m (Gourbault & Renaud-Mornant, 1990), 8-40 m (Boucher & Kotta,

1996), 6-16 m (Boucher, 1997), 0.8-2.5 m (Boucher *et al.*, 1998), 1.5-4.4 m (Netto *et al.*, 1999), 2.5-4 m (Kotta & Boucher, 2001), 3.5-20 m (de Jesús-Navarrete, 2003) and 1.5-3.3 m (Netto *et al.*, 2003).

In the study at hand, the focus is no longer only on the sediment as a habitat: a comparison will be made with meiofauna on large biogenic substrata. The collection of epifauna from various large substrata implies even more methodological problems, especially when quantitative sampling is required. The methods and devices usually used to sample sediments, *e.g.* Perspex meiocores, are no longer applicable for this type of research. This is for example clear from seagrass studies. Hopper & Meyers (1967b) developed a method which consisted of breaking the seagrass leaves free at the sediment surface, placing them in labeled bags while still under water, emptying and rinsing the bags and leaves at the laboratory and the analysis of this residue. This method, or an adapted version of it, has also been applied by other authors (*e.g.* Lewis & Hollingworth, 1982). Nevertheless, techniques for sampling seagrass leaves have remained diversified and inconsistent. As a result, Bell *et al.* (1984a; b) have pleaded for the use of comparable sampling techniques. These authors used a plastic tube sampler, which they filled with filtered seawater, corked it, opened it again under water, placed it over a single seagrass leave, clipped off the blade near the sediment, corked the tube again and analysed the collected meiofauna.

Another main problem in comparing meiofauna studies is the wide array of sieve mesh sizes that is used by different researchers to separate the macrofauna from the meiofauna (upper limit for meiofauna) and the meiofauna from the microfauna (lower limit for meiofauna). Only Alongi (1986) (500 µm), Guzmán *et al.* (1987) (500 µm), Boucher & Gourbault (1990) (250 µm), Tietjen (1991) (500 µm), Ólafsson *et al.* (1995) (500 µm), Ndaro & Ólafsson (1999) (500 µm) and Netto *et al.* (2003) (500 µm) reported which meshes they used as an upper limit. Regarding the lower limit, it is obvious that the use of sieves with a larger mesh size will result in a lower figure for meiobenthic densities. Striking differences can be found in studies of tropical, lagoonal meiobenthos: Thomassin *et al.* (1976), Alongi (1986), Guzmán *et al.* (1987), St.John *et al.* (1989), Boucher & Gourbault (1990), Tietjen (1991), Ólafsson *et al.* (1995), Ndaro & Ólafsson (1999), Netto *et al.* (1999) and Netto *et al.* (2003) used small mesh sizes (40, 45, 63, 11, 40, 45, 40, 40, 63 and 63 µm respectively), whereas Thomassin *et al.* (1982) used a sieve with much wider meshes (250 µm). As already put forward above, this has clearly influenced the density values in their study. Boucher & Kotta (1996), Boucher (1997), Boucher *et al.* (1998) and Kotta & Boucher (2001) did not mention the mesh size that was used, but it can be deduced from the text that these authors manually picked out all the meiofauna from the centrifugation residue. In the studies of Gourbault & Renaud-Mornant (1989; 1990) and de Jesús-Navarrete (2003), mesh sizes were also not communicated.

Kotta & Boucher (2001) examined (1) sample size (*i.e.* the number of individuals that is identified), (2) taxonomic level and (3) size of the sediment column as potential causes of incomparability between studies. These authors found that significant differences in the structure of the species assemblage could not be detected between samples of 100, 200 and 300 individuals. The patterns of nematode assemblages at species and genus level were also not different in this study, although distinct changes were found when working with higher taxonomic levels. Due to the vertical zonation of

different species in the sediment column, size of the sediment column has an effect on the observed community structure.

1.8. EPSILONEMATIDAE AND DRACONEMATIDAE

Epsilonematidae and Draconematidae are two closely related families of nematodes, characterised by an aberrant body shape, unique locomotory structures and a typical, crawling locomotion. These nematodes are particularly found in biotopes with fixed surfaces, on which they can attach themselves or on which they can crawl: *e.g.* coarse sand, gravel, algae and the cavities between sessile animals (see Section 1.8.3.). Coral fragments and other degradation products of the coral skeleton (coral gravel, coarse coralline sand) are regarded as suitable substrates for, and a source of, many species and individuals of these nematodes. Given their peculiar morphology and ecology, which is clearly linked to the presence of large substrates, special attention is given to these taxa in the ecological part of this thesis and they were also selected as subject for the taxonomical study.

1.8.1. GENERAL MORPHOLOGY

A representation of a typical epsilonematid and a typical draconematid is given in Fig. 7, in order to point to some important morphological features of these peculiar nematodes. However, 'typical' is relative here, as both families are characterised by a multitude of different body shapes. Within each family, the genera and species differ in numerous morphological features, such as the overall body shape, the structure and appendices of the cuticle, the morphology of the head region, the shape of the sensory organs, etc. Epsilonematids and draconematids are epsilon- (ε-) or s-shaped, and clearly enlarged at the level of the pharynx and the posterior body region. Both families can be distinguished from each other by (1) the distinction between ambulatory setae and adhesion tubes and (2) the position of the vulva relative to these structures. Ambulatory setae (Epsilonematidae) and adhesion tubes (Draconematidae) are structures that are essential in locomotion. While adhesion tubes are robust, hollow structures associated with adhesive glands, ambulatory setae are fine, hair-like structures and are apparently not associated with epidermal glands. Moreover, adhesion tubes occur both on or near the head capsule (cephalic adhesion tubes) and in the posterior body region (posterior adhesion tubes), whereas ambulatory setae are only present in the posterior part of the body. Representatives of the subfamily Glochinematinae (Epsilonematidae) are somewhat different in having longer ambulatory setae and 'cephalic' thorns. Nevertheless, they are clearly epsilonematids as inferred from the position of the vulva (Fig. 8). In Epsilonematidae, the vulva is either surrounded by the ambulatory setae or positioned posterior to these structures, *i.e.* at the level of the second dorsal curvature. In Draconematidae, the vulva is always positioned far anterior to the posterior adhesion tubes, *i.e.* in between both dorsal curvatures (Lorenzen, 1974).

The different body shapes of Epsilonematidae and Draconematidae are summarised in the review articles of Gourbault & Decraemer (1996) and Decraemer *et al.* (1997).

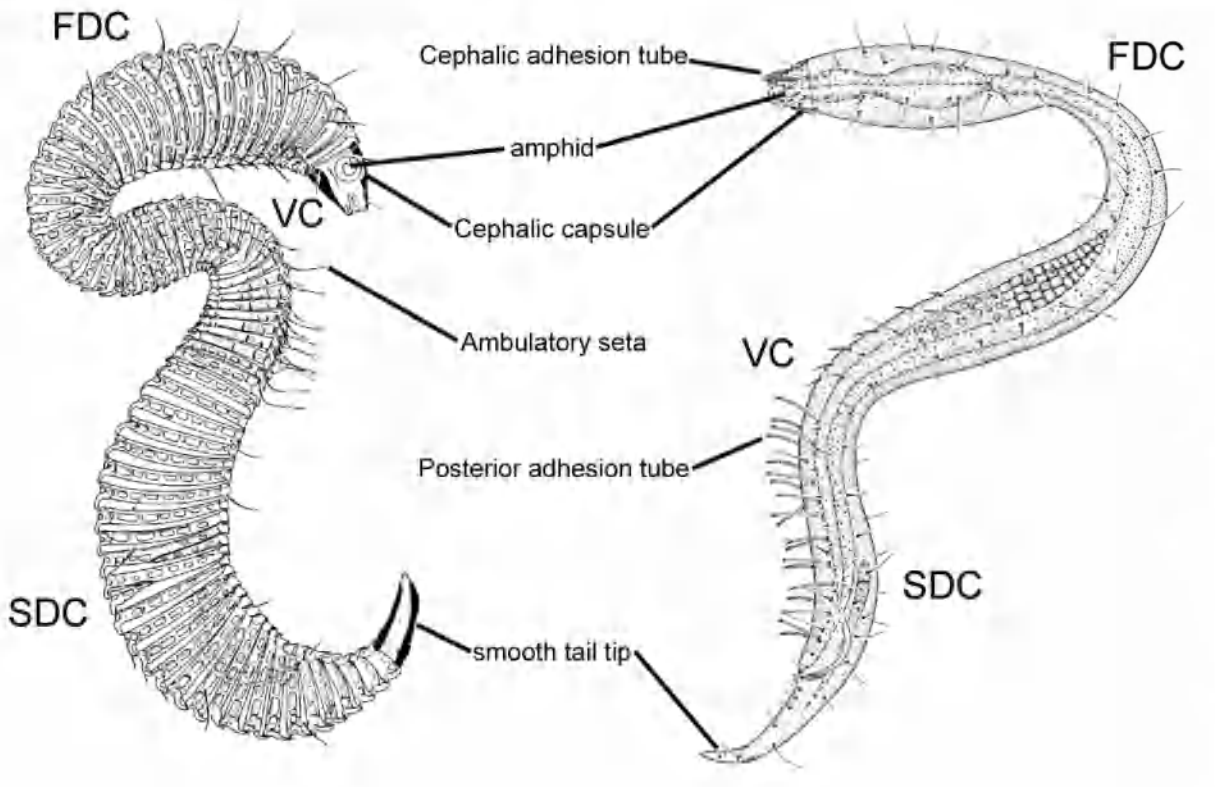


Fig. 7. Generalised morphology of Epsilonematidae (*Bathyepsilonema dermoglyphum* Gourbault & Decraemer, 1987; left) and Draconematidae (*Dracograllus timmi* Allen & Noffsinger, 1978; right) . Both are males. FDC = First dorsal curvature; VC = ventral curvature; SDC = second dorsal curvature.

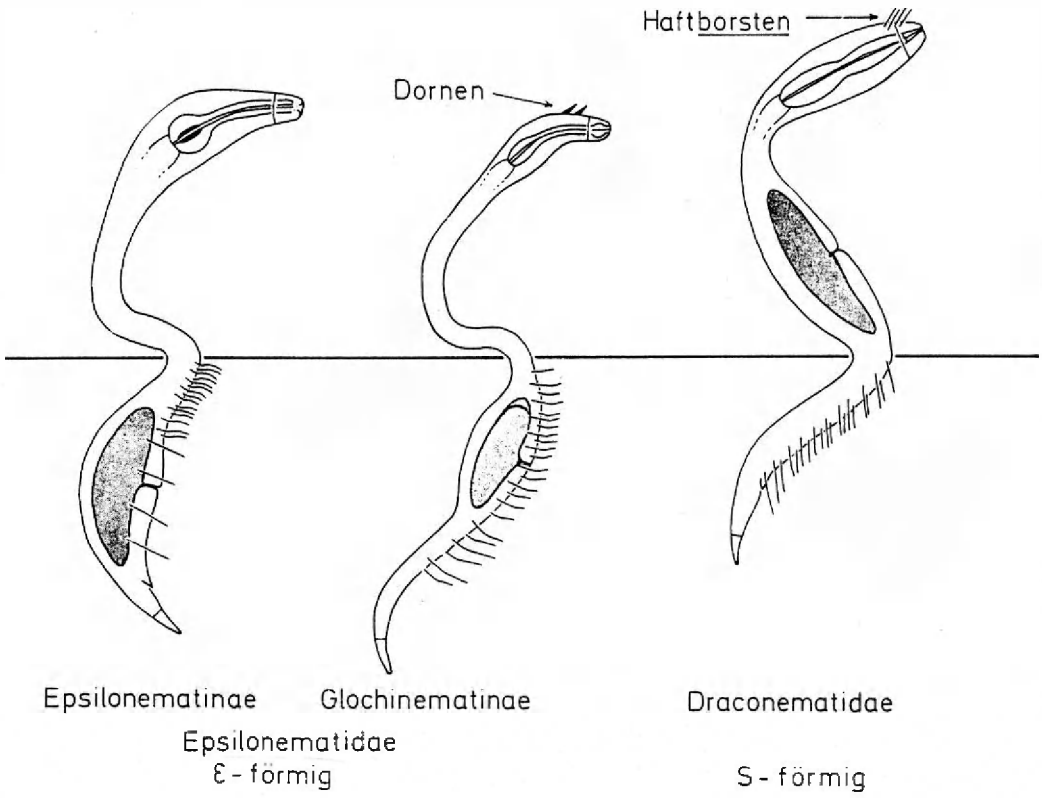


Fig. 8. Location of the vulva relative to the ambulatory setae or adhesion tubes in Epsilonematidae and Draconematidae (from Lorenzen, 1974).

1.8.2. TAXONOMY AND SYSTEMATICS

The families Epsilonematidae Steiner, 1927 and Draconematidae Filipjev, 1918 are closely related to the family Desmodoridae Filipjev, 1922. Together, they form the holophyletic superfamily Desmodoroidea Filipjev, 1922. The holophyly of this superfamily is established by the holapomorphy that only the anterior testis is present (Lorenzen, 1994). An overview of the classification within these two families, supplemented with the diagnoses for the different subfamilies and genera and an analysis of the phylogenetic relations between the genera, is provided in Gourbault & Decraemer (1996) and Decraemer *et al.* (1997). The genus identification keys included in these review articles are now also available online (www.nemys.ugent.be; Deprez *et al.*, 2004). The family Epsilonematidae is subdivided into three subfamilies: Epsilonematinae Steiner, 1927, Glochinematinae Lorenzen, 1974 and Keratonematinae Gourbault & Decraemer, 1986. The family Draconematidae consists of the subfamilies Draconematinae Filipjev, 1918 and Prochaetosomatinae Allen & Noffsinger, 1978.

Since the publication of these two review articles, the following new species have been described:

1. Epsilonematidae:

- *Leptepsilonema antonioi* Decraemer & Gourbault, 2000 (Decraemer & Gourbault, 2000a)
- *Leptepsilonema dauvini* Decraemer & Gourbault, 2000 (Decraemer & Gourbault, 2000a)
- *Leptepsilonema horridum* Decraemer & Gourbault, 2000 (Decraemer & Gourbault, 2000a)
- *Polkepsilonema guirali* Decraemer & Gourbault, 2000 (Decraemer & Gourbault, 2000a)
- *Metepsilonema volutum* Decraemer & Gourbault, 2000 (Decraemer & Gourbault, 2000b)
- *Metepsilonema amphidoxum* Decraemer & Gourbault, 2000 (Decraemer & Gourbault, 2000b)
- *Metepsilonema comptum* Decraemer & Gourbault, 2000 (Decraemer & Gourbault, 2000b)
- *Metepsilonema corrugatum* Decraemer & Gourbault, 2000 (Decraemer & Gourbault, 2000b)
- *Glochinema bathyperuvensis* Neira, Gad, Arroyo & Decraemer, 2001 (Neira *et al.*, 2001)
- *Glochinema kentrosaurides* Gad, 2002 (Gad, 2002)
- *Glochinema trispinatum* Raes, Vanreusel & Decraemer, 2003 (Raes *et al.*, 2003)
- *Epsilonema multispiralum* Raes, Vanreusel & Decraemer, 2003 (Raes *et al.*, 2003)
- *Bathyepsilonema lopheliae* Raes, Vanreusel & Decraemer, 2003 (Raes *et al.*, 2003)
- *Glochinema spinithorni* Neira, Decraemer & Backeljau, 2005 (Neira *et al.*, 2005)

2. Draconematidae:

- *Tenuidraconema koreensis* Rho & Kim, 2004 (Rho & Kim, 2004)
- *Dinetia orientalis* Rho & Kim, 2005 (Rho & Kim, 2005a)
- *Dracogalerus koreanus* Rho & Kim, 2005 (Rho & Kim, 2005b)
- *Paradraconema jejuense* Rho & Kim, 2005 (Rho & Kim, 2005c)
- *Draconema brasiliensis* Venekey, Monteiro Lage & Da Fonsêca-Genevois, 2005 (Venekey *et al.*, 2005)
- *Draconema fluminensis* Venekey, Monteiro Lage & Da Fonsêca-Genevois, 2005 (Venekey *et al.*, 2005)
- *Tenuidraconema philippinensis* Rho & Kim, 2005 (Rho & Kim, 2005d)

This brings the present total number of epsilonematid species on 95 and of draconematid species on 77.

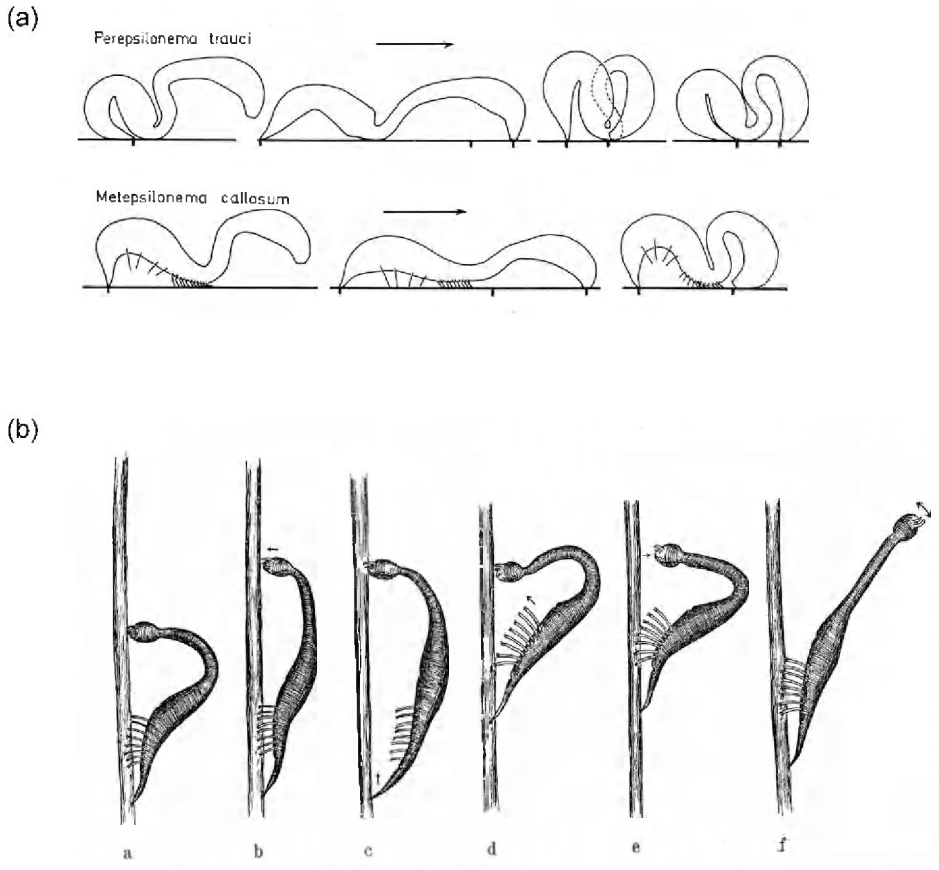


Fig. 9. Locomotion in (a) Epsilonematidae (from Lorenzen, 1973a) and (b) Draconematidae (from Stauffer, 1924).

1.8.3. LOCOMOTION, ECOLOGY AND DEPTH DISTRIBUTION

Locomotion of Epsilonematidae and Draconematidae has been extensively discussed by Stauffer (1924) and, for Epsilonematidae, by Lorenzen (1973a). Contrasting to the undulating movement exhibited by most, slender, nematodes, representatives of these families move forward like a geometrid caterpillar over the surface of a substratum. During this crawling locomotion, the anterior and posterior end of the body are alternately released from the substratum and moved forward (Fig. 9a, b). There are three major anchor points: (1) the anterior end (head capsule), (2) the region of ambulatory setae or posterior adhesion tubes and (3) the posterior end (tail tip). The anterior end of the body may be fixed to the substratum by suction (mouth and pharynx; Epsilonematidae) or with the cephalic adhesion tubes (Draconematidae), which are hollow, tube-like structures associated with adhesive glands (see Section 1.8.1.). The adhesive glands located in the tail discharge through the outlets on/at the terminal part of the tail tip. In contrast to the posterior adhesion tubes in Draconematidae, which are similar in structure and function as the cephalic adhesion tubes, ambulatory setae are apparently not associated with glands and can only be used as stilts or for clinging on to a substratum. This last function can be found in taxa where the distal tip of the ambulatory setae is hook-shaped, *e.g.* in *Epsilonema espeeli* Verschelde & Vincx, 1994 and

Metepsilonema bermudae Lorenzen, 1973 (Verschelde & Vincx, 1994). In some taxa, additional structures, such as supporting setae, spines, thorns, etc. may increase stability while crawling.

As a result of their looper-caterpillarlike locomotion, these taxa are particularly found in biotopes where they can find fixed surfaces for attachment, such as coarse sand, gravel, algae and the cavities between sessile animals (Lorenzen, 1973a; Decraemer *et al.*, 2001). For example, the cavities between the byssus threads of *Aucalomya ater* Molina, 1782 are the microhabitat from which *Epsilonema byssicola* Lorenzen, 1973 was described. Lorenzen (1973a) stated that Epsilonematidae are not found in silty sediments. However, a representative of the subfamily Glochinematinae has been recently described from muddy, deep-sea sediments: *Glochinema bathyperuvensis* Neira, Gad, Arroyo & Decraemer, 2001 (Neira *et al.*, 2001). According to Neira *et al.* (2001) and Gad (2002), the conspicuous cuticular appendages of this species (spines, thorns, blade-like protrusions) are adaptations to the fine, muddy habitat, increasing the body area/body mass ratio for enhanced oxygen diffusion in this oxygen-poor habitat and enabling the animal to swim in the uppermost soupy mud layers. On the other hand, Gad (2004) found another new species of *Glochinema* in deep-sea fine sand with a large clay fraction, but without such morphological adaptations. He concluded that Glochinematinae could have a much wider distribution than other Epsilonematidae in terms of suitable microhabitats.

Most Epsilonematidae and Draconematidae have been found in littoral or shallow subtidal sand. Until recently, Epsilonematidae were even unknown from deep-sea habitats (Decraemer *et al.*, 2001). However, more and more species are being described from deep-sea areas. Deep-sea epsilonematids have been described from the South-East Pacific (Neira *et al.*, 2001), the North-East Pacific (Neira *et al.*, 2005) and the North Atlantic (Gad, 2002); deep-sea draconematids from the North Pacific (Kito, 1983), the East Pacific (Bussau, 1993; Decraemer & Gourbault, 1997), the West Pacific (Decraemer & Gourbault, 1997), the Central Pacific (Decraemer & Gourbault, 1997) and the North Atlantic, South Atlantic, Laptev Sea, Scotia Sea, Mediterranean and New Ireland Basin (Gad, *in press*).

1.9. AIMS AND THESIS OUTLINE

Most preceding studies on marine meiofauna have focused on the meio-infauna. The few studies that dealt with meio-epifauna focused on the fauna associated with macro-algae and seagrasses (see Section 1.6 for an overview of the nematofauna associated with seagrasses). This thesis, however, focuses on the degradation products of dead coral, such as coral fragments and coral gravel. Living coral is assumed not to be a suitable substratum for meiofauna, as it responds to the settlement of sessile organisms by an increase in mucus production and selective sclerenchyme precipitation (Freiwald & Wilson, 1998). The dead coral degradation products discussed in this thesis originate from coral degradation zones, which are found adjacent to the coral reef or bank (for a definition, see Section 1.2.). Data from both deep-sea and tropical coral degradation zones will be compared.

Although cold-water corals have been known to science since the 18th century (Pontoppidan, 1755), the study of the biology of these corals and the fauna associated with the coral banks or reefs they produce is still in its infancy. This is mainly due to methodological difficulties. However, recent

studies have already reported considerably high biodiversity of the corals themselves (Heifetz *et al.*, 2005; mainly soft corals) and of the associated macro- and megafauna (Jensen & Frederiksen, 1992; Rogers, 1999 and references herein; Fosså *et al.*, 2002), and some of these studies suggest that cold-water coral reef biodiversity could be comparable with that of tropical coral reefs, which are known as hotspots of biodiversity. Moreover, these cold-water reefs are known as rich sources for commercially important fish and shellfish species (Roberts & Hirshfield, 2004). Although the first data on the fish fauna and macrofauna associated with these reefs are becoming available, one important hiatus remains: meiofauna. Meiofauna is known as a major component of especially deep-sea, benthic ecosystems, both in terms of metabolism (food consumption), density and biomass (Thiel, 1983; Flach *et al.*, 1999). Moreover, it plays an important role in the marine benthic ecosystem (Heip *et al.*, 1985; Coull, 1988), is characterised by high species richness (Heip *et al.*, 1985; Lambshead, 1993) and may serve as food for other organisms (Thiel, 1983; Coull, 1988).

Nematodes usually dominate the meiofauna both in abundance and biomass (Giere, 1993). Although information on the meiofauna at higher taxon level is given in Addenda 1 and 2, this thesis will focus only on the nematofauna.

The first part of this thesis deals with the ECOLOGY of the nematode communities associated with cold-water and tropical coral structures. The aims of the ecological study are:
(1) to provide the first comprehensive study dealing with the nematofauna associated with cold-water coral reefs; (2) to characterise the nematode communities associated with cold-water and tropical coral degradation zones; (3) to investigate the structuring effect of microhabitat type, *i.c.* coral degradation products and associated microhabitats, on nematode community and trophic composition; (4) to verify whether coral degradation zones harbour a nematode community typical for the habitat or typical for the region; (5) to compare turnover at local and regional scales; (6) to calculate and compare the biodiversity of the nematode communities in cold-water and tropical coral degradation zones and (7) to examine the community structure, habitat preferences, biodiversity and biogeography of the typically epifaunal Epsilonematidae and Draconematidae.

In the second part of this thesis, four new species of Epsilonematidae and three new species of Draconematidae are described from a cold-water coral degradation zone and additional information is provided for another species of Epsilonematidae. Next to the descriptions, the TAXONOMICAL part of this thesis also aims (1) to provide information on the biogeography of these species, (2) to critically discuss the taxonomical position of these species and their relationships with closely related taxa, (3) to provide new insights into intraspecific variability of features and the suitability of the features currently considered to be of diagnostic value.

CHAPTER 2 of this thesis describes the nematofauna associated with sediment-clogged cold-water coral framework in the Porcupine Seabight. It mainly aims to investigate the influence of microhabitat type on nematode community structure. Three microhabitat types are considered: (1) dead coral fragments, (2) glass sponge skeletons and (3) the underlying sediment. Habitat preferences, densities and diversity will be discussed.

The structuring role of different microhabitats is also the main topic in CHAPTER 3, which deals, however, with tropical coral degradation zones from Kenya and Zanzibar. The three examined

microhabitats are dead coral fragments, coral gravel and coralline sediment. This study aims to answer the following three research questions: (1) do coral degradation zones harbour a typical nematode community?, (2) how strong is turnover in taxonomic composition operating at local and regional scales? and (3) is microhabitat structure an additional source for variation in nematode community composition?

The samples that were analysed for this study yielded considerable numbers of typically epifaunal nematodes: representatives of Epsilonematidae and Draconematidae. These animals are well-known from coarse sand and different types of substratum (see Section 1.8.). In CHAPTER 4, the community structure, fine-tuned habitat preferences, biogeography and biodiversity of these typically epifaunal taxa are discussed, based on material from both cold-water coral and tropical coral degradation zones. Cosmopolitanism of nematode species is extensively discussed. Turnover on a microhabitat and local scale is also compared.

ADDENDUM 1 focuses on the meiofauna associated with a cold-water coral degradation zone, at a higher taxon level. Again, aspects of habitat preferences, densities and biodiversity will be discussed. The same microhabitat types as in Chapter 2 will be considered here. Parallel with this first addendum, ADDENDUM 2 discusses the community structure of the meiofauna in a tropical coral degradation zone from two locations in Kenya, and the structuring effect of microhabitats and locations. Microhabitat types are the same as in Chapter 3. This addendum also provides information on the biodiversity of the nematode and copepod communities in this habitat and therefore complements Chapter 2. The contribution of coral degradation products to the total diversity of the system and the use of higher-taxon (*i.c.* family-level) surrogacy are also examined.

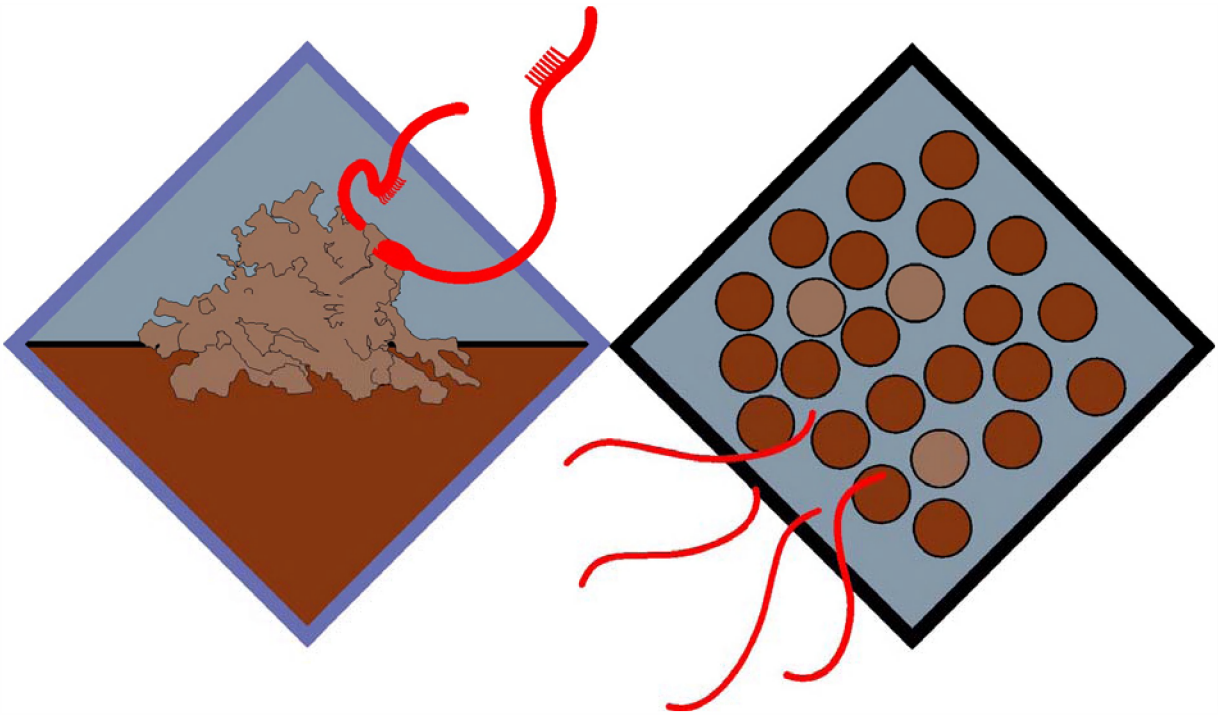
In CHAPTER 5, three new species of Epsilonematidae are described from a cold-water coral degradation zone: *Glochinema trispinatum* sp. n., *Epsilonema multispiralum* sp. n. and *Bathyepsilonema lophelia* sp. n. The status of the genus *Metaglochinema* Gourbault & Decraemer, 1986 is discussed. Additional information is given regarding the biogeography of Epsilonematidae.

CHAPTER 6 includes the description of *Akanthepsilonema sinecornibus* sp. n., a new epsilonematid species, the redescription of *Triepsilonema tripapillata* Decraemer, 1982 with additional information, and the description of the first stage juvenile of *Glochinema trispinatum.* Next to this, the postembryonic morphology in Epsilonematidae and the taxonomic importance of caudal glands and their outlets is thoroughly discussed.

In both CHAPTER 7 and CHAPTER 8, new species of Draconematidae are described. In Chapter 7, additional information is provided for the species *Tenuidraconema koreensis* Rho & Kim, 2004 and a new, closely related species, *T. parvospermis* sp. n. is described. The biogeography of *T. koreensis* and the use of sperm cell structure in taxonomy are discussed. Chapter 8 deals with two new, closely related species of the genus *Cygnonema* Allen & Noffsinger, 1978: *C. verum* sp. n. and *C. belgicae* sp. n. The coexistence of both species is briefly discussed. In both chapters, a key to the species within the respective genera is provided.

CHAPTER 2

MICROHABITAT TYPE DETERMINES THE COMPOSITION OF NEMATODE COMMUNITIES ASSOCIATED WITH SEDIMENT-CLOGGED COLD-WATER CORAL FRAMEWORK IN THE PORCUPINE SEABIGHT



Paper *in press*

Raes, M., Vanreusel, A.

Microhabitat type determines the composition of nematode communities associated with sediment-clogged cold-water coral framework in the Porcupine Seabight

Deep-Sea Research I

2.1. ABSTRACT

The nematofauna associated with a cold-water coral degradation zone in the Porcupine Seabight (NE Atlantic) was investigated. This is the first comprehensive study of nematodes associated with cold-water corals. This research mainly aimed to investigate the influence of microhabitat type on nematode community structure. Three distinct microhabitats for nematodes were distinguished: dead coral fragments, glass sponge skeletons and the underlying sediment. The nematode assemblages associated with these three microhabitats were significantly different from each other. Coral and sponge substrata lie relatively unprotected on the seafloor and are consequently more subjected to strong currents than the underlying sediment. As a result, both large biogenic substrata were characterised by higher abundances of taxa that are less vulnerable and more adapted to physical disturbance, whereas the underlying sediment housed more typically slender, sediment-dwelling taxa. Typically epifaunal taxa, such as Epsilonematidae and Draconematidae, were especially abundant on dead coral fragments, where they are thought to feed on the microbial biofilm which covers the coral surface. Several epifaunal genera showed significant preferences for this microhabitat, and *Epsilonema* (Epsilonematidae) was dominant here. Sponge skeletons are thought to act as efficient sediment traps, resulting in a lower abundance of epifaunal taxa compared to coral fragments. The underlying sediment was dominated by taxa typical for slope sediments. The considerable degree of overlap between the communities of each microhabitat is attributed to sediment infill between the coral branches and sponge spicules. It is assumed that the nematofauna associated with large biogenic substrata is composed of a typical sediment-dwelling background community, supplemented with taxa adapted to an epifaunal life strategy. The extent to which these taxa contribute to the community depends on the type of the substratum. Selective deposit feeders were dominant on sponge skeletons and in the underlying sediment, whereas coral fragments were dominated by epistratum feeders. The presence of a microbial biofilm on the coral fragments is proposed as an explanation for the significant preference of epistratum feeders for this microhabitat. Densities in the underlying sediment were low in comparison with other studies, but biodiversity was higher here than on the coral and sponge fragments, a difference which is attributed to lower disturbance. Nevertheless, the large biogenic substrata provide a microhabitat for rare, epifaunal taxa, and fragments of both substrata within the sediment increase habitat complexity and hence biodiversity.

Key words: cold-water corals, meiobenthos, nematodes, community composition, microhabitats, biodiversity, northeast Atlantic, Porcupine Seabight

2.2. INTRODUCTION

Until recently, most studies on deep-sea meiofauna focused on the interstitial and mud-dwelling meio-infauna. The term 'meio-epifauna' was introduced by Raes & Vanreusel (2005) to define the meiofauna living epifaunally on well-defined surfaces of diverse origin (biogenic debris, seagrasses, macro-algae, coral fragments, sponge skeletons, manganese nodules, pebbles etc.). According to

their definition, suitable substrata for meio-epifauna (1) should be discrete and well-defined structures of at least about 5 mm in diameter and (2) should not be completely covered with sediment, implying that at least part of the surface area remains in contact with the water column. In the present study, suitable surfaces were found on large biogenic substrata, namely dead coral fragments of the framework building cold-water coral *Lophelia pertusa* (Linnaeus, 1758) and skeletons of the glass sponge *Aphrocallistes bocagei* Schultze, 1886.

Dead coral fragments are the result of a bioerosion process that starts with the death of *L. pertusa* colonies due to the persistent attack by fouling organisms, the formation of a microbial biofilm and endolithic fungal infestation, followed by colonisation of the coral skeleton by sessile invertebrates such as sponges and octocorals (Freiwald & Wilson, 1998). Locally intense sponge excavation results in skeletal loss, and the *in situ* collapsing of the dead *L. pertusa* framework. On the other hand, the encrusting sponges speed up the closure of gaps in the open coral framework and foster sediment-trapping, resulting in the strengthening of the framework architecture. This facies type is called sediment-clogged coral framework (Freiwald *et al.*, 2002). In a final stage of the degradation process, intensified bioerosion results in accumulation of centimetre-sized coral rubble. Because of the dynamic origin of the habitat between living coral thickets and coral rubble, it is referred to as a 'coral degradation zone'.

Because of the sheltering function and higher habitat complexity of three-dimensionally branched coral skeletons, the diversity of megafauna living in the zones with living or dead coral framework is higher than that in the coral rubble zone (Mortensen *et al.*, 1995). According to Mortensen *et al.* (1995) and Jensen & Frederiksen (1992), the dead coral framework harbours the most diverse macro- and megafauna. Healthy, living *L. pertusa* responds to the settlement of sessile organisms by (1) an increase in mucus production and (2) selective sclerenchyme precipitation (Freiwald & Wilson, 1998). These protective properties have proven to be rather successful antifouling measures against macrofauna (Mortensen, 2000). For the same reasons, living coral is assumed not to be a suitable substratum for meiofauna.

Cold-water corals have been known to science since the 18th century (Pontoppidan, 1755). Nevertheless, the associated fauna has by no means been studied as intensively as it has for tropical corals. Moreover, most studies dealing with epifauna on either living or dead *L. pertusa* focused on the macro- and megafauna (Dons, 1944; Le Danois, 1948; Burdon-Jones & Tambs-Lyche, 1960; Jensen & Frederiksen, 1992; Mortensen *et al.*, 1995; Fosså & Mortensen, 1998; Rogers, 1999).

The present paper provides a first overview of the nematode communities inhabiting cold-water coral degradation zones. Additionally, we aim to determine whether the trends observed by Raes & Vanreusel (2005) across the entire meiofaunal community on a higher taxon level can be specifically extended to a lower taxonomic level, *i.e.* within the nematode community. As in the case of deep-sea sediments that are not associated with large biogenic structures, nematodes are the dominant metazoan meiofaunal taxon in this deep-sea habitat.

The main topic of interest is the influence of habitat type on nematode community structure. For nematodes the conditions within the sediment are different from those on a complex elevated structure on the sea floor. Next to this distinction between large biogenic substrata and the underlying sediment

as a habitat, small differences in microhabitat structure could also influence the nematode community composition. Skeletons of dead *L. pertusa* in the Porcupine Seabight area are highly branched, dendroid structures with slender but solid branches and well-developed, cup-shaped corallites. The surface of the branches is smooth, although calcified tubes of the polychaete *Eunice norvegica* (Linnaeus, 1767) may be attached to the skeleton, and the coral surface is sometimes covered with a thin layer of bryozoan colonies. In contrast, skeletons of the glass sponge *A. bocagei* form a dense, complex, three-dimensional latticework of fine silica spicules. The underlying sediment in the area consists of Foraminifera-rich silty sand or soupy, foraminiferal sand, with a high sand content. In the vicinity of coral banks the sediment becomes littered with coral fragments and other biogenic debris.

2.3. MATERIALS AND METHODS

2.3.1. SAMPLING SITES AND PROCEDURE

Material was obtained by means of a round NIOZ (Netherlands Institute for Sea Research) box corer (ø 32 cm). Two box cores were taken during the 9-19 June 2000 sampling campaign on the RV Belgica at 51°24'48.2" N 11°45'55.4" W and 51°24'49.4" N 11°45'55.9" W. A third box core was taken at the same location during the 2-11 May 2001 sampling campaign on the same vessel, at 51°25'7.7" N 11°46'9.3" W. All material originates from the top and slope of a single seabed mound at depths between 972 and 1005 m, located in the Belgica mound province of the Porcupine Seabight (Fig. 1). The Porcupine Seabight is a large embayment of the European continental slope, located in the North-East Atlantic Ocean, southwest of Ireland. In this area numerous seabed mounds occur, grouped in three so called 'mound provinces': the Hovland mound province, the Magellan mound province and the Belgica mound province (Fig. 1). The Belgica mound province is the most southern of the seabed mound provinces. The mounds in this province are known to be associated with deep-water coral banks, constructed mainly by the framework builder *L. pertusa* and associated fauna such as the glass sponge *A. bocagei*.

The presence of transversal sand dunes in the Belgica mound region indicates very high current velocities, up to 100 cm/s (De Mol, 2002). Although these very high velocities are probably exceptional, normal current speeds are still considered high: about 10-25 cm/s (White, *in press*) or even 40-50 cm/s (V. Huvenne, pers. comm.). High current speeds are attributed to the combination of strong, northward along-slope bottom currents, internal tides and waves, and the presence of mounds (Rice *et al.*, 1991; Van Rooij *et al.*, 2003; White, *in press*).

The Porcupine Seabight area is also known to be subject to substantial phytodetrital deposition (Billett *et al.*, 1983; Lampitt, 1985; Gooday *et al.*, 1996). The detritus itself, as well as the bacteria and protozoa that rapidly colonise it, are the main food source for deep-sea meiofauna. Taking into account both timing of surface blooms in 2000 and 2001 as well as sinking rates (Billett *et al.*, 1983), it was calculated that phytodetritus should have been present on the bottom on both sampling dates. It is, however, not clear whether this deposited material was available for the benthic fauna in the Belgica mound region, as strong bottom currents will certainly cause resuspension and relocation of the organic material. Down-slope and along-slope variability of phytodetrital deposition in this region

makes generalisations even more difficult (D. Billett, pers. comm.). Our samples did not show any evidence of a detrital layer covering the sediment or the large biogenic substrata (pers. obs.).

In all cases, the surface of the sediment was partly or entirely covered with several fragments of dead corals (*L. pertusa*) and dead sponge skeletons (*A. bocagei*). Only a very small amount of living coral was present. The large coral and sponge fragments were collected separately. After removal of the large biogenic substrata, three sediment cores (10 cm^2) were pushed into the underlying sediment of each box core. All material was fixed with 4% buffered formalin. Each coral fragment, sponge fragment and sediment core is indicated here as a subsample.

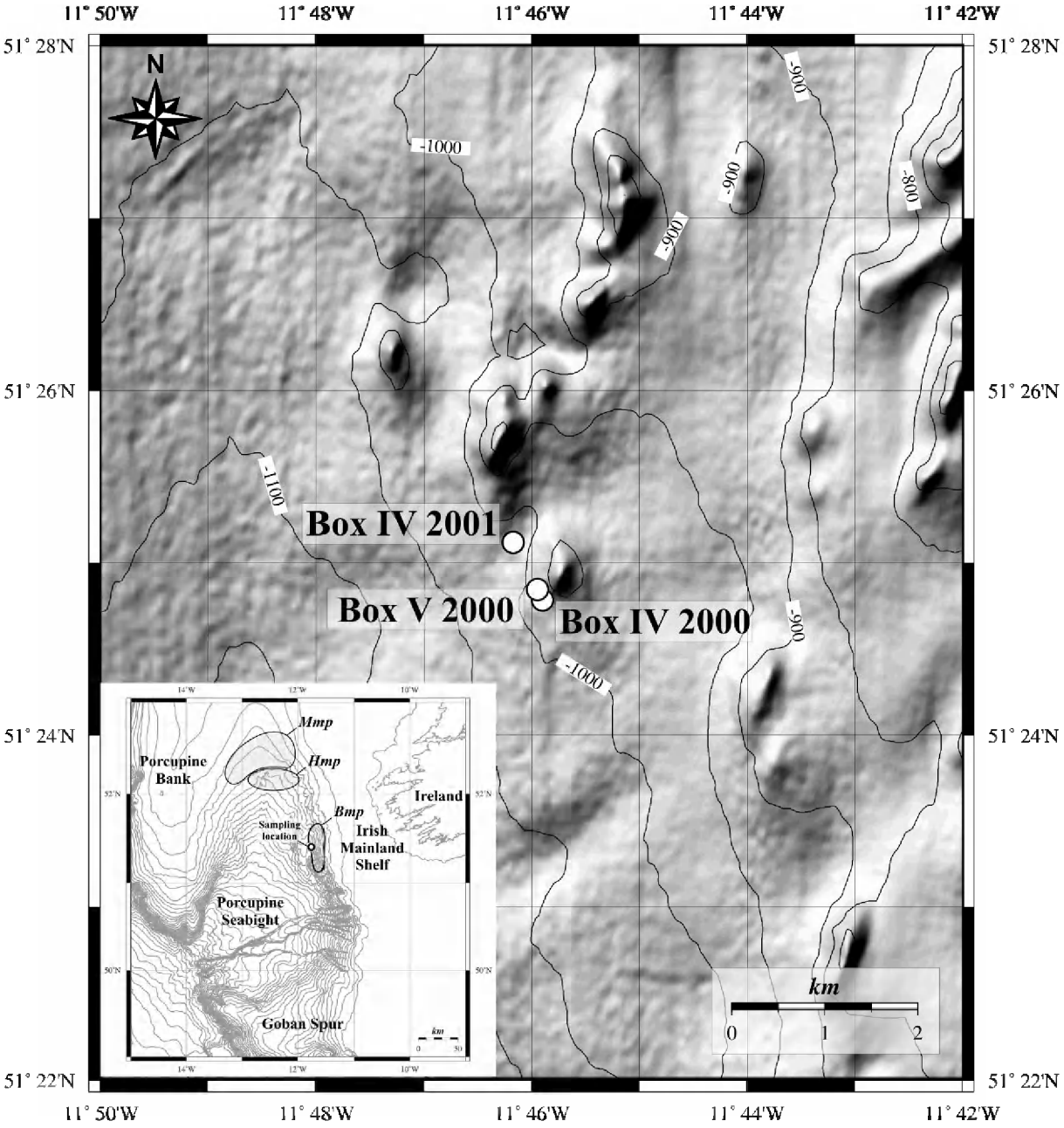


Fig. 1. Map of the Porcupine Seabight area and a detail showing the ridge of mounds in the Belgica mound province with indication of the exact box core locations (bathymetry after Beyer *et al.*, 2003). (*Mmp* = Magellan mound province; *Hmp* = Hovland mound province; *Bmp* = Belgica mound province)

2.3.2. MATERIAL

In total, 28 subsamples were examined: 18 subsamples were collected in the first box core from 2000, six subsamples in the second box core from 2000 and another four subsamples in the box core from 2001. After thorough examination of its content, each subsample was classified into one of the following groups, each of them representing a microhabitat type: (1) dead coral fragments, (2) dead sponge skeletons (*i.e.* the two large biogenic substrata), (3) underlying sediment and (4) mixed substratum. The underlying sediment consisted of fine to medium sand (median 194.9 µm) with a small fine silt fraction and a high amount of planktonic Foraminifera. It was observed that this was a poorly sorted sediment, also containing small fragments of both large biogenic substrata, as well as some small mollusc shells and echinoid spines. Subsamples belonging to the mixed substratum-group contained coral fragments as well as sponge skeletons and some sediment.

2.3.3. LABORATORY ANALYSES

Each *Lophelia* and *Aphrocallistes* fragment was rinsed thoroughly over sieves with mesh sizes of 1 mm and 32 µm to separate macrofauna and meiofauna. Meiofauna was extracted from the underlying or remaining sediment by density gradient centrifugation, using Ludox (a colloidal silica polymer; specific gravity 1.18) as a flotation medium (Heip *et al.*, 1985; Vincx, 1996). From each subsample 200 nematodes (or a lower number when less than 200 nematodes were present in the examined subsample) were randomly picked out. They were subsequently mounted onto slides using the formalin-ethanol-glycerol technique described by Seinhorst (1959) and Vincx (1996), and identified to the genus level. Volumes of coral fragments and sponge skeletons were calculated by means of immersion.

The trophic composition of the nematode community was analysed according to the classification of Wieser (1953) for reasons of comparability with other studies, although its practical application is no doubt questionable, and new feeding type classifications have been proposed (Moens & Vincx, 1997; Moens *et al.*, 2004). Representatives of the families Benthimermithidae Petter, 1980 and Rhaptothyreidae Hope & Murphy, 1969 were eliminated from the trophic analysis because they are parasitic in their larval stages and the adults lack a buccal cavity.

2.3.4. STATISTICAL ANALYSES

The PRIMER5 software (Plymouth Marine Laboratory; Clarke & Gorley, 2001) was used to calculate Bray-Curtis similarities between all subsamples, ultimately resulting in a test statistic R reflecting within-microhabitat as well as between-microhabitat similarities. The obtained similarity matrix was applied to produce a non-metric multidimensional scaling two-dimensional plot (MDS). The stress value gives a measure for goodness-of-fit of the MDS ordination: a low stress value (<0.2) indicates a good ordination with no real prospect for a misleading interpretation (Clarke, 1993). One-way Analysis of similarities (ANOSIM) was performed to test for significant differences ($p < 0.05$) in the nematode community structure between the different microhabitats. Similarity of percentages (SIMPER) was carried out to investigate which genera were responsible for these differences. All absolute data were square root transformed prior to the analysis.

Several biodiversity indices were calculated: The Shannon-Wiener index *H'* (Log base = e) and Pielou's evenness *J* (Pielou, 1975) are mainly included for reasons of comparability with other studies. Hill's diversity numbers (Hill, 1973) gradually change from indices of species richness to indices of dominance with increasing number: N_0 is identical to the number of species, N_1 = exp (*H'*) and N_∞ reflects evenness. The Expected number of Genera for a theoretical sample of 100 individuals E*G* (100) was calculated in analogy with the Expected number of Species (Hurlbert, 1971). E*G* (n)-values were also used to construct rarefaction curves.

Indicator genus analysis was performed using the PC-ORD4 software, by analogy with the indicator species analysis of Dufrêne & Legendre (1997). For this type of analysis, absolute data were used without transformation. The mixed substratum subsamples were omitted from the analysis and only the dominant genera (>0.5%) were considered. Calculated indicator values were tested for statistical significance using a Monte Carlo test.

Parametric (one-way ANOVA) and non-parametric (Kruskal-Wallis ANOVA by ranks) analysis of variance was performed using the STATISTICA6 software. Bartlett's and Cochran's test were used to verify the homogeneity of variances prior to the analysis.

2.4. RESULTS

2.4.1. NEMATODE COMMUNITY COMPOSITION AND HABITAT PREFERENCES

In total, 5036 nematodes belonging to 136 different genera (see Appendix) and 38 different families were included in the analysis. Of these 136 genera, 10 are considered new to science. Only 69 genera out of 136 were present in both the coral fragments, sponge skeletons and underlying sediment microhabitat. Table 1 lists the relative abundances of the 20 most abundant nematode genera for the coral, sponge, mixed and sediment microhabitats, calculated as the average of the relative abundance per subsample. All microhabitats, except for the coral fragment microhabitat, were dominated by *Desmoscolex*. *Sabatieria* was the second most abundant genus in the underlying sediment and *Pselionema* the second most abundant genus on sponge skeletons. The genus *Epsilonema* was dominant on dead coral fragments, but was not found among the 20 most abundant genera either on sponge skeletons or within the underlying sediment. *Desmoscolex* was the second most abundant genus on coral fragments.

Representatives of the closely related families Epsilonematidae and Draconematidae, which are characterised by an aberrant body shape, were found in all microhabitats and were especially abundant on the coral fragments. Three genera of Epsilonematidae (*Epsilonema*, *Triepsilonema* and *Glochinema*) and two genera of Draconematidae (*Tenuidraconema* and *Cygnonema*) were found amongst the 20 most abundant genera on coral fragments. Epsilonematids were much more abundant on coral fragments (16.8%) and sponge skeletons (6.1%) than in the underlying sediment (2.7%). Draconematidae were also more abundant on coral fragments (4.7%) and sponge skeletons (1.4%) than in the underlying sediment (0.5%). Only the epsilonematid *Glochinema* was found abundantly on both coral fragments, sponge skeletons and within the underlying sediment.

Coral fragments (10)		Sponge skeletons (8)		Mixed substratum (4)		Underlying sediment (6)	
genus	%	genus	%	genus	%	genus	%
Epsilonema	8.51	*Desmoscolex*	7.85	*Desmoscolex*	9.66	*Desmoscolex*	9.01
Desmoscolex	7.71	*Pselionema*	7.56	*Pselionema*	6.06	*Sabatieria*	8.27
Halalaimus	6.84	*Halalaimus*	6.59	*Ceramonema*	4.96	*Acantholaimus*	6.78
Acantholaimus	6.70	*Actinonema*	6.15	*Acantholaimus*	4.88	*Desmodora*	5.68
Anticoma	4.94	*Ceramonema*	5.19	*Halalaimus*	4.62	*Halalaimus*	4.10
Theristus	4.40	*Tricoma*	4.84	*Anticoma*	3.64	*Microlaimus*	3.09
Triepsilonema	3.69	*Calomicrolaimus*	4.75	Araeolaimoidea sp.1	3.52	*Tricoma*	3.04
Tricoma	3.48	*Acantholaimus*	4.61	*Epsilonema*	3.23	*Syringolaimus*	3.03
Prochromadorella	2.97	*Anticoma*	4.17	*Theristus*	3.23	*Bathynox*	2.92
Actinonema	2.77	*Glochinema*	3.43	*Sabatieria*	2.81	*Ceramonema*	2.85
Tenuidraconema	2.63	*Desmodora*	2.67	*Tricoma*	2.40	*Molgolaimus*	2.17
Cyatholaimus	2.50	*Paracantonchus*	2.50	*Desmodora*	2.37	*Calomicrolaimus*	2.15
Calomicrolaimus	2.34	*Sabatieria*	2.37	*Actinonema*	2.11	*Paracantonchus*	2.01
Glochinema	2.17	*Monhystera*	2.30	*Triepsilonema*	2.09	*Aegialoalaimus*	1.94
Paracantonchus	2.13	*Microlaimus*	1.83	*Paracantonchus*	2.08	*Halichoanolaimus*	1.82
Monhystera	2.13	*Dichromadora*	1.62	*Monhystera*	2.03	*Monhystera*	1.80
Innocuonema	2.12	*Prochromadorella*	1.57	*Prochromadorella*	1.99	*Glochinema*	1.64
Dichromadora	2.08	Araeolaimoidea sp.1	1.42	*Procamacolaimus*	1.90	Araeolaimoidea sp.1	1.58
Chromadorina	1.67	*Theristus*	1.29	*Viscosia*	1.46	*Anticoma*	1.54
Ceramonema	1.64	*Metadasynemella*	1.17	*Microlaimus*	1.37	*Metadesmolaimus*	1.36
Average density	8914.7 ± 2890.6 ind/l*		49952.1 ± 40660.0 ind/l		23038.9 ± 19710.6 ind/l		301 ± 101.6 ind/10 cm²

Table 1. Relative abundances of the 20 most abundant nematode genera and overall average densities (with standard deviations) of the nematofauna associated with cold-water coral degradation zones, per distinguished microhabitat. Representatives of the epifaunal families Epsilonematidae and Draconematidae are underlined. *: for one substratum the volume could not be measured; average densities based only on the subsamples with known volume.

Although a certain degree of overlap between the different microhabitats in terms of associated nematofauna composition was obvious from the MDS graph (stress 0.15) given in Fig. 2, there was a clear trend in three directions, distinguishing between the three most distinct microhabitats: coral fragments, sponge skeletons and the underlying sediment (see arrows in Fig. 2). The mixed substratum subsamples took up a central position between these three microhabitats in the MDS

graph. This distinction between microhabitats in terms of community structure was confirmed by a one-way Analysis of similarities (ANOSIM): overall differences between all 4 microhabitats were very highly significant (p = 0.001). Pairwise tests revealed the absence of significant differences only between (1) the mixed substratum and sponge skeletons and between (2) the mixed substratum and the underlying sediment (Table 2). R values were generally low, which was due to the observed overlap between the microhabitats (see MDS). Nevertheless, the number of actual permutations (between 210 and 999) was high enough to trust the significance levels.

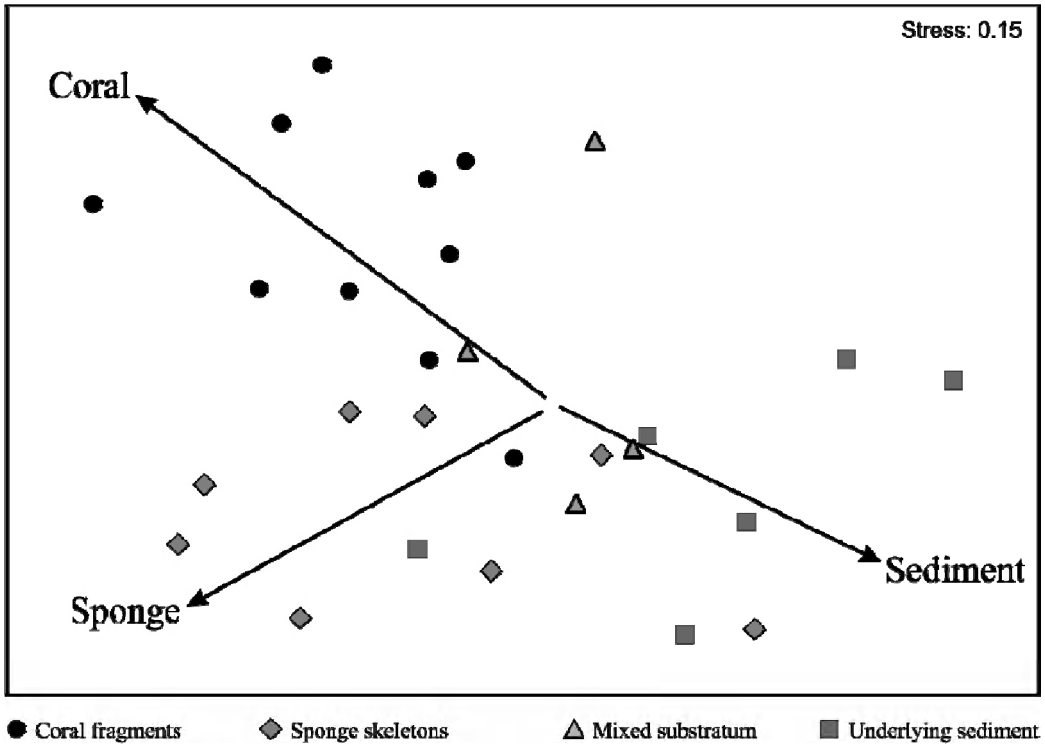


Fig. 2. Multidimensional Scaling (MDS) two-dimensional plot of all subsamples. The trend in three directions, reflecting different communities in the three distinct microhabitats as mentioned under Section 2.4.1, is visualised here with three arrows radiating from the center.

	Coral fragments	Sponge skeletons	Mixed substratum	Underlying sediment
Coral fragments		✶✶✶	✶	✶✶✶
Sponge skeletons	**0.44**		-	✶
Mixed substrate	**0.357**	**0.026**		-
Underlying sediment	**0.715**	**0.314**	**0.075**	

Table 2. Results of ANOSIM pairwise test: values of the R statistic and corresponding p-levels are indicated. ***: $p \leq 0.001$; *: $0.01 < p \leq 0.05$; -: $p > 0.05$.

Attention will be focused now on the coral fragments, the sponge skeletons and the underlying sediment. The average dissimilarity in community composition between sponge skeletons and the underlying sediment was 47.7% and mainly attributed to the higher abundance of *Sabatieria* in the underlying sediment (explains 3.4% of the dissimilarity) and *Pselionema* on the sponge skeletons (explains 3.1% of the dissimilarity), as indicated by SIMPER. The average dissimilarity between coral fragments and sponge skeletons was 46.6%, mainly explained by *Epsilonema* (4.4%, more abundant

on coral fragments) and *Pselionema* (3.6%, more abundant on sponge skeletons). The average dissimilarity between the underlying sediment and the coral framework, in terms of community composition, was the highest (51.9%). This dissimilarity was mainly explained by *Epsilonema* (3.9%, more abundant on coral fragments) and *Sabatieria* (3.2%, more abundant in the interstices of the sediment).

All significant microhabitat preferences, as indicated by an indicator genus analysis, are summarised in Table 3. The analysis confirmed the above proposed habitat preferences: *Sabatieria* within the underlying sediment (p = 0.006), *Pselionema* on sponge skeletons (p = 0.006) and *Epsilonema* on dead coral fragments (p = 0.001). This analysis also indicated the preference of several representatives of the closely related families Epsilonematidae and Draconematidae, for the coral substratum: *Akanthepsilonema* (p = 0.003), *Epsilonema* (both Epsilonematidae), *Cygnonema* (p = 0.002) and *Tenuidraconema* (p = 0.001) (both Draconematidae). *Bathyepsilonema* was the exception here: this epsilonematid genus preferred sponge skeletons (p = 0.02).

Genus	Preferred microhabitat	IV	Significance level
Actinonema	sponge skeletons	59	0.004 (**)
Aegialoalaimus	underlying sediment	57	0.024 (*)
Akanthepsilonema	coral fragments	66	0.003 (**)
Bathyepsilonema	sponge skeletons	60	0.020 (*)
Ceramonema	sponge skeletons	58	0.014 (*)
Cygnonema	coral fragments	74	0.002 (**)
Epsilonema	coral fragments	89	0.001 (***)
Halichoanolaimus	underlying sediment	64	0.004 (**)
Innocuonema	coral fragments	79	0.002 (**)
Molgolaimus	underlying sediment	61	0.011 (*)
Prochromadorella	coral fragments	56	0.005 (**)
Pselionema	sponge skeletons	66	0.006 (**)
Sabatieria	underlying sediment	71	0.006 (**)
Syringolaimus	underlying sediment	76	0.002 (**)
Tenuidraconema	coral fragments	67	0.001 (***)
Theristus	coral fragments	63	0.004 (**)

Table 3. Microhabitat preferences, as indicated by an indicator genus analysis. Only the statistically significant preferences are shown. Significance level is indicated. IV = Indicator Value. (*): $0.01 < p \leq 0.05$; (**): $0.001 < p \leq 0.01$; (***): $p \leq 0.001$.

All microhabitats were dominated either by selective deposit feeders (Wieser group 1a) or epistratum feeders (Wieser group 2a). Predators/omnivores (Wieser group 2b) always constituted the least abundant group (Fig. 3). There were, however, small differences between the microhabitats; selective deposit feeders were the dominant trophic group in all microhabitats except for the coral fragments, which were dominated by epistratum feeders. This observed preference of epistratum feeders for the coral fragment microhabitat was statistically highly significant (ANOVA; df = 1; p = 0.002) and mainly attributed to *Epsilonema* (IV = 65; p = 0.001) as pointed out by an indicator genus analysis. The relative importance of both non-selective deposit feeders (Wieser group 1b) and predators/omnivores was clearly higher in the underlying sediment compared to both large biogenic substrata, with the mixed substratum taking up an intermediate position. The prevalence of predators/omnivores in the underlying sediment, in contrast to other microhabitats, was proven to be statistically very highly significant (ANOVA; df = 1; $p < 0.001$) and was mainly attributed to *Syringolaimus* (IV = 67; p = 0.001).

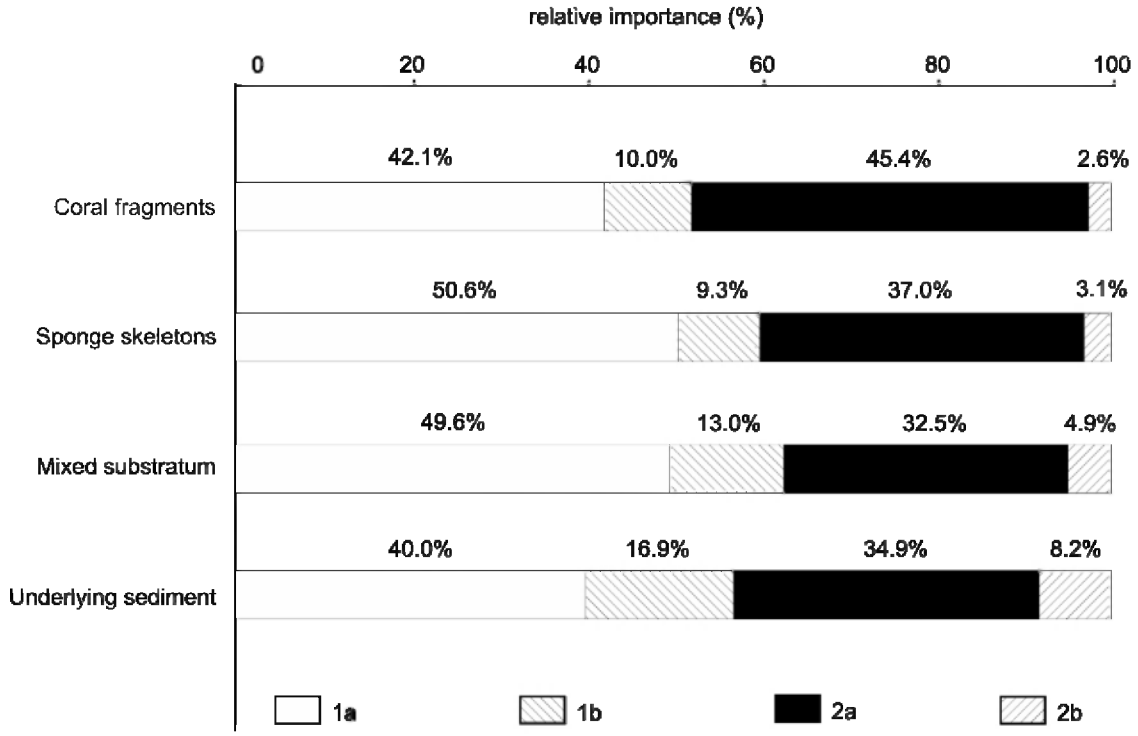


Fig. 3. Composition of Wieser (1953) feeding types for each microhabitat: selective deposit feeders (1a), non-selective deposit feeders (1b), epistratum feeders (2a) and predators/omnivores (2b).

2.4.2. DENSITIES

Average nematode densities and standard deviations for each microhabitat are given in Table 1. Nematode densities are expressed as ind/l on the substrata and as ind/10 cm² in the sediment for reasons of comparison with other studies. Densities tended to differ to a large extent between subsamples of the same microhabitat type as standard deviations were high. Nevertheless, the sponge skeletons were characterised by significantly higher densities of nematodes than the coral fragments (Kruskal-Wallis ANOVA; df = 1; $p < 0.001$).

2.4.3. BIODIVERSITY

For all microhabitats, a whole spectrum of biodiversity indices, ranging from indices of genus richness (N_0, E*G* (100)) to indices of evenness (J, N_∞), is given in Table 4. Dominance was generally low and there were no significant differences between microhabitats in terms of evenness (ANOVA; J and N_∞). The sediment clearly harboured the highest number of genera N_0, whereas the other microhabitats had more or less the same number of genera. It should be noted that the coral fragments and sponge skeletons yielded nevertheless the highest number of individuals. It was found that on average, both substrata were characterised by a significantly lower number of genera compared to the underlying sediment and the mixed substratum (Kruskal-Wallis ANOVA; df = 1; p = 0.016). This was confirmed by a comparison of the E*G* (100) values (Kruskal-Wallis ANOVA; df = 1; p = 0.02). Moreover, Hill's N_1 (ANOVA; df = 1; p = 0.004) and the Shannon-Wiener index H' (ANOVA; df = 1; p = 0.005) were also significantly higher for the sediment and mixed substratum microhabitats than for both separate substrata.

The rarefaction curves for the total community associated with each microhabitat and for the entire community combined over all microhabitat types (pooled data) (Fig. 4) show that the expected number of genera for coral fragments and sponge skeletons falls below that of the sediment and the mixed substratum. The presence of these substrata even lowers the value for the added-up community in comparison with the sediment. This combined community is not to be interpreted as a representation of the natural situation as it is not possible to calculate the relative importance of the three microhabitats in the cold-water coral degradation zone.

		N_0	EG (100)	N_1	H'	J	N_∞
Coral fragments	(a)	40.60 ± 8.78	33.47 ± 5.07	26.48 ± 5.85	3.25 ± 0.23	0.88 ± 0.03	8.03 ± 2.10
	(b)	93	38.41	40.13	3.69	0.81	11.24
Sponge skeletons	(a)	42.38 ± 10.81	33.70 ± 5.04	25.63 ± 6.38	3.22 ± 0.25	0.86 ± 0.04	7.51 ± 1.96
	(b)	93	38.00	39.44	3.67	0.81	12.41
Mixed substratum	(a)	53.25 ± 4.57	40.34 ± 5.52	34.09 ± 5.53	3.52 ± 0.16	0.89 ± 0.03	9.43 ± 1.48
	(b)	91	43.40	47.20	3.85	0.85	10.67
Underlying sediment	(a)	51.00 ± 2.45	40.26 ± 2.48	32.16 ± 3.98	3.46 ± 0.13	0.88 ± 0.04	8.36 ± 2.95
	(b)	106	43.29	47.26	3.86	0.83	10.94
p-level		0.02 (*)	0.03 (*)	0.04 (*)	0.05 (*)	0.58 (NS)	0.56 (NS)

Table 4. Biodiversity indices: Hill's diversity numbers N_0, N_1 and N_∞, the expected number of genera for 100 individuals EG (100), the Shannon-Wiener diversity index H' and Pielou's evenness J. Under (a) the average value over all subsamples, with its standard deviation, is given, under (b) the value for the pooled data of all subsamples for the respective microhabitat. The p-level indicates the overall statistical significance level for the observed differences between microhabitats. (NS): not significant ($p > 0.05$); (*): significant ($0.01 < p \leq 0.05$).

2.5. DISCUSSION

The present paper is part of the first comprehensive study dealing with the community structure, habitat preferences and biodiversity of the metazoan meiofaunal community associated with cold-water coral degradation zones (Raes & Vanreusel, 2005). The main conclusions of this study, which dealt with meiofauna at higher (*i.e.* coarser) taxonomic levels, are briefly as follows. The meio-infaunal community composition in the sediment beneath the large biogenic substrata was similar to that of other slope sediments. However, the meio-epifaunal community associated with the large biogenic substrata was significantly different from the meio-infauna: it was characterised by a lower dominance of nematodes and higher abundances of several other taxa. This indicates a positive influence of large

biogenic substrata on the number of taxa present in the whole ecosystem. Especially coral fragments housed a characteristic community which was significantly different from that in the sediment. Nevertheless, the meio-epifauna was composed of a typical sediment-dwelling background community, supplemented with taxa adapted to an epifaunal life strategy. This was attributed to the presence of sediment infill within the framework of both substrata and the close contact with the underlying sediment. Densities in the underlying sediment were low. In contrast, both large biogenic substrata were thought to be low disturbance habitats, rich in food and hence densely populated. Because of these properties of the two substratum types, the high microhabitat diversity and the low dominance of nematodes, cold-water coral degradation zones were assumed to be biologically diverse. Of all microhabitat types, coral fragments supported the most diverse communities, whereas the underlying sediment was the least diverse.

Whether the same conclusions can be drawn for the nematode community on a generic level will be discussed next.

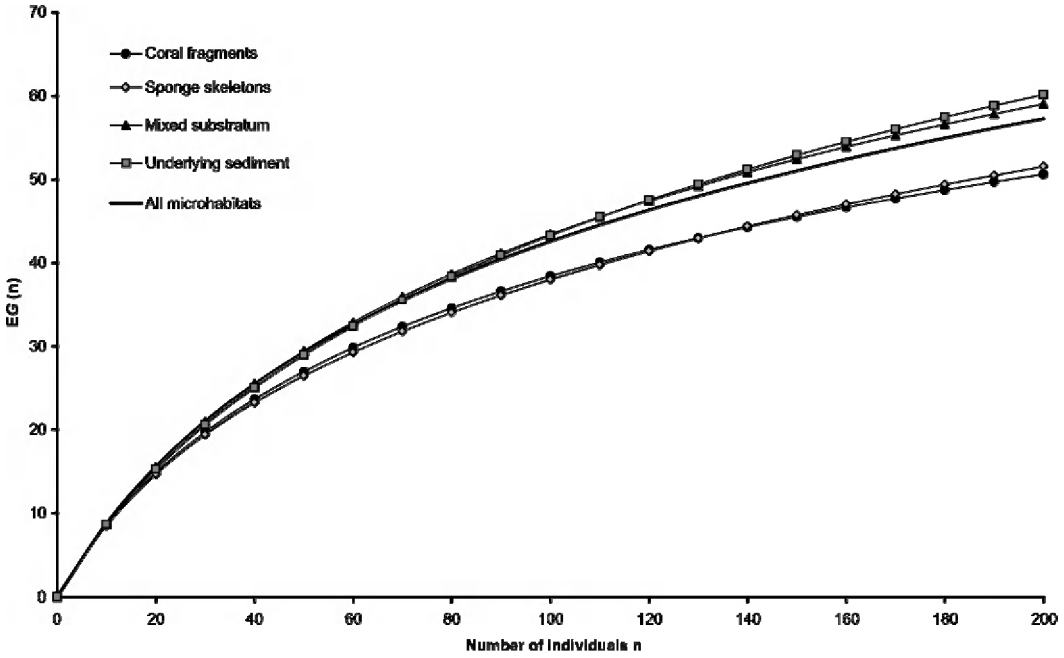


Fig. 4. Rarefaction curves for the pooled data per microhabitat and for the combined community over all microhabitats.

2.5.1. NEMATODE COMMUNITY COMPOSITION AND HABITAT PREFERENCES

Dead coral fragments and sponge skeletons lie relatively unprotected on the sea floor. The fauna associated with these substrata could therefore be strongly influenced by the vigorous bottom currents which prevail in the area (White, *in press*). The danger of physical erosion and removal by these hydrodynamic forces prevents most nematode taxa from living here. However, taxa that are able to withstand the currents' eroding effect will have an advantage in these exposed habitats. Coral fragments were dominated by *Epsilonema*, a nematode belonging to the family Epsilonematidae. SIMPER showed that *Epsilonema* was the main explanatory taxon for the dissimilarity between coral fragments on the one hand and sponge skeletons and sediment on the other hand. This is remarkable

given that Epsilonematidae were, until recently (Neira *et al.*, 2001; Gad, 2002; Raes *et al.*, 2003; Gad, 2004; Neira *et al.*, 2005; Raes *et al.*, *in press*), unknown from deep-sea habitats (Decraemer *et al.*, 2001). Moreover, both Epsilonematidae and the closely related Draconematidae were much more abundant on coral fragments than in either of the other microhabitats and an indicator genus analysis revealed significant preferences of two epsilonematid and two draconematid genera for the coral fragment microhabitat. Due to their peculiar locomotory pattern and morphology, Epsilonematidae and Draconematidae are well-adapted to living with physical disturbance. First of all, representatives of both families are known to move forward over a substratum just like looper-caterpillars, alternately attaching and releasing the anterior and posterior end of the body (Stauffer, 1924; Lorenzen, 1973a). To perform this kind of locomotion, they possess typical locomotory structures known as cephalic and posterior adhesion tubes (Draconematidae) or ambulatory setae (Epsilonematidae), which they can use together with the caudal glands to attach themselves firmly to a substratum and, hence, better withstand removal by current activity. Next to this, most Epsilonematidae (*e.g. Epsilonema*) are stout, heavily cuticularised nematodes, which makes them more stable and less vulnerable to physical damage. The idea that small, short and stout nematodes, which are characterised by higher growth rates and a reduced age at first breeding, and which are more able to withstand different types of disturbance, act as opportunists in shallow and ocean margin areas, has been proposed by several authors (Soetaert *et al.*, 2002; Vanaverbeke *et al.*, 2004). *Desmoscolex* is also a stout nematode with a cuticle strengthened by bands of secretion and foreign material, called desmen. According to Stauffer (1924), *Desmoscolex* also moves forward like a caterpillar, using specialised setae associated with glands, which are located subdorsally[1]. In this way, *Desmoscolex* is able to firmly attach itself to a substratum, which might partly explain its high abundance on both large biogenic substrata. On the other hand, *Desmoscolex* was also the dominant genus in the underlying sediment. This nematode is considered a typical sediment-dwelling genus for these depths (Soetaert & Heip, 1995; Vanaverbeke *et al.*, 1997) and its importance on both large biogenic substrata could well be the result of considerable sediment infill.

The nematofauna inhabiting the underlying sediment is relatively protected from current activity by the substrata that cover it, which means that its composition is not fundamentally structured by physical disturbance. As a result, the opportunistic Epsilonematidae and Draconematidae are much less abundant here in comparison with the substrata and most nematodes in the sediment-dwelling community belong to the slender morphotype typical for an interstitial microhabitat (Giere, 1993). This is thought to be the reason why the sediment communities and coral communities are so different from each other. Only Vanaverbeke *et al.* (1997) have described the nematode genus composition in sediment not associated with large biogenic structures at a nearby location (Goban Spur) and at a comparable depth. Station B in their study was located at a depth of 1034 m and is therefore our main source for comparison. The nematode community at this station appears to be dominated by *Acantholaimus* and *Sabatieria*. However, the genera *Desmoscolex* and *Pareudesmoscolex* were counted separately in this study, although *Pareudesmoscolex* is considered a subgenus of *Desmoscolex* (Decraemer, 1985) and was accordingly identified in our study. Thus, when the relative abundances of these two genera at station B of Vanaverbeke *et al.* (1997) are added up, a co-

[1]This mode of locomotion is not used by all desmoscolecids: *e.g. Tricoma* does not move forward like a caterpillar.

dominance of *Desmoscolex* (9.8%), *Acantholaimus* (9.8%) and *Sabatieria* (9.3%) arises. This corresponds relatively well with what was found in the underlying sediment of our study. *Sabatieria* and *Acantholaimus* are considered typical slope genera for the North Atlantic and Mediterranean (Soetaert & Heip, 1995). According to Vanaverbeke *et al.* (1997), *Acantholaimus* and *Desmoscolex* are typical deep-sea genera that are also frequently found on the lower slope (*i.e.* station B and deeper stations), whereas *Sabatieria* is more abundant in shallower stations (see also Soetaert & Heip, 1995). Except for *Desmodora*, the eight most abundant genera in the underlying sediment of our study were also found among the 20 most abundant genera in station B of Vanaverbeke *et al.* (1997). It can be concluded that, despite the presence of small fragments of both large biogenic substrata, mollusc shells and echinoid spines within the underlying sediment in cold-water coral degradation zones, the nematode communities are still dominated by typical soft sediment slope taxa. In contrast to normal slope sediments which are not supplemented with these biogenic structures, epsilonematids and draconematids were still relatively well-represented in the underlying sediment of our study. Nevertheless, the only epsilonematid among the 20 most abundant genera here was *Glochinema* (subfamily Glochinematinae). This is a long and slender nematode, supported by long and fine ambulatory setae, and is therefore less stable and more vulnerable to current activity than most other, shorter and thicker Epsilonematidae. So this might be more of a sediment-dweller, taking advantage of the presence of smaller substrata within the underlying sediment. On the other hand, several representatives of the subfamily Glochinematinae have been found in soft sediments (Gad, 2004). *Sabatieria* plays an important role in the underlying sediment. The dissimilarity between the sediment and both other microhabitats was mainly attributed to this genus and indicator genus analysis revealed significant preferences of *Sabatieria* for the sediment microhabitat. As already argued above, *Sabatieria* is a typical slope genus. According to Soetaert & Heip (1995), *Sabatieria* also has a preference for suboxic or anoxic environments. This is very interesting, given that the depth distribution of cold-water coral reefs in the Porcupine Seabight coincides with the OMZ (Oxygen Minimum Zone) layer in this area (Freiwald, 2003).

Although sponge skeletons are also large biogenic structures that stick out from the sediment, they house a community significantly different from the one associated with coral fragments (Table 2; Fig. 2). Moreover, this microhabitat does not favour the epifaunal taxa as strongly as the coral fragments. As in the underlying sediment, the only abundant epsilonematid here is *Glochinema*. We propose a structural explanation for this discrepancy. Due to its complex, three-dimensional latticework of fine silica spicules, a glass sponge skeleton is probably able to trap more sediment than a dead coral framework. It was observed that the dead sponge skeletons were coloured greyish-brown and that a considerable amount of sediment was accumulated in the central spongocoel. In contrast, only a small amount of sediment was accumulated in the felty layer of bryozoan colonies which covered parts of the surface of the coral fragments (M.R., pers. obs.). As a result, the sponge microhabitat is more suitable for slender, sediment-dwelling taxa than the coral habitat. Nematodes could also be slightly more protected from physical erosion in this microhabitat, which means that opportunistic epifaunal taxa will have fewer advantages here. On the other hand, the spicules might still serve as a suitable substratum for epifaunal nematodes, as indicated by the observed preference

of *Bathyepsilonema* for sponge skeletons. The indicator genus analysis revealed only two other indicator genera for this microhabitat: *Pselionema* and *Ceramonema*. Both ceramonematids are heavily armoured nematodes, which is again interpreted as an adaptation to physical disturbance by hydrodynamic forces. However, it must also be mentioned here that Ceramonematidae are not uncommon in slope soft sediments (Vanaverbeke *et al.*, 1997).

Although the communities in different microhabitats were significantly dissimilar from each other, the MDS-biplot (Fig. 2), the low R-values (ANOSIM; Table 2) and the low average dissimilarity numbers (SIMPER) indicate a considerable degree of overlap. Accumulation of sediment between the sponge spicules or coral branches and the presence of small fragments of both biogenic substrata within the sediment are introduced here as explanations. Sediment infill is caused either by close contact between the biogenic substrata and the underlying sediment or by the deposition of suspended material. It is assumed that the nematofauna associated with large biogenic substrata in cold-water coral degradation zones is composed of a typical slope sediment-dwelling, interstitial background community, supplemented with taxa adapted to an epifaunal life strategy. The extent to which these epifaunal taxa contribute to the community depends on the substratum type. The central position of the mixed substratum subsamples on the MDS biplots also reflects the combined effect of the three microhabitat types on the nematode community structure.

The nematode communities on the continental slope are usually dominated by selective and non-selective deposit feeders (Soetaert & Heip, 1995). Strangely, in station B of Vanaverbeke *et al.* (1997) there was a co-dominance of these two trophic groups and the epistratum feeders. Thus, the trophic composition of the nematode communities in the present study can be considered normal for this location and this depth. The statistically significant preference of epistratum feeders for coral fragments is attributed to the presence of a microbial biofilm which covers the surface of these structures (Freiwald & Wilson, 1998) and might act as an important food source here. This preference was mainly attributed to *Epsilonema*. Indeed, when epsilonematids or draconematids 'walk' over the dead coral fragments, their buccal cavity is ideally positioned for feeding on the biofilm. The prevalence of predators/omnivores in the underlying sediment could be related to the presence of a more stable community in this relatively undisturbed microhabitat.

2.5.2. DENSITIES

As nematode densities on both substrata in our study are expressed as individuals per unit of volume (*i.c.* ind/l), comparison with other studies dealing with epifauna, *e.g.* on seagrasses or macro-algae, is impossible as densities are usually expressed as individuals per unit of surface area. Due to the irregularity and three-dimensional complexity of the substrata at hand it was impossible to measure the exact surface area. Moreover, the accumulation of sedimented material on the substrata obscures the concept of total available surface area. The significantly higher densities of nematodes on sponge skeletons compared to the dead coral fragments can be explained by the higher degree of sediment infill in the former substratum. The presence of interstitial microniches is considered essential for nematode colonisation (Danovaro & Fraschetti, 2002) and sediment infill might therefore be essential to build a well-developed, and hence dense, nematode community. Moreover, Giere

(1993) stated that most nematodes are morphologically more adapted to move between the sand grains than to crawl over a substratum.

According to Raes & Vanreusel (2005), the sediment-clogged coral framework and associated glass sponge skeletons could be densely populated by meiofauna as a result of low disturbance, low predation pressure and abundant food. However, the nematode data contradict low disturbance on these substrata. Moreover, the same authors observed significantly lower abundances of nematodes on these substrata.

In the underlying sediment, densities varied between 166 and 429 ind/10 cm². This number is consistently lower than in the studies of Pfannkuche (1985) (Porcupine Seabight - 960 m, 1429 ind/10 cm²; 1492 m, 820 ind/10 cm²), Vanaverbeke *et al.* (1997) (Goban Spur - 670 m, 580 ind/10 cm²; 1034 m, 587.5 ind/10 cm²; 1425 m, 482 ind/10 cm²) and Gooday (unpubl. in Vincx *et al.*, 1994) (Porcupine Seabight - 1340 m, 1026-1211 ind/10 cm²). All of these studies were carried out on nearby locations, at comparable depths and, in the case of the study by Pfannkuche (1985), at a similar time in the year. Raes & Vanreusel (2005) proposed several potential explanations for the low meiofaunal densities in the underlying sediment: (1) effect of different sampling gear; (2) limited food supply due to phytodetritus-trapping by the coral framework which covers the sediment or (3) due to strong currents; (4) physical removal by strong currents; (5) presence of biogenic structures in the sediment or (6) high predation pressure. As already argued above, the erosive effect of current activity (fourth explanation) is thought to be rather limited in the underlying sediment.

2.5.3. BIODIVERSITY

Several indices (N_0, E*G* (100), N_1, *H'*) indicated a significantly higher diversity in the underlying sediment compared to both large biogenic substrata, despite of the expected higher habitat complexity of the branched coral fragments and the network of sponge spicules compared to the interstitial habitat, especially when taking into account the sediment infill between these structures. As mentioned above, both substrata, especially the coral fragments, are rather hostile environments for most nematodes and that the majority of nematodes is better adapted to an interstitial life strategy (Giere, 1993). The interstitial habitat of the underlying sediment is a more suitable one for nematodes than the substratum surface and is relatively undisturbed, enabling a more diverse community to establish itself in the former habitat. Consistently with this idea, Gage *et al.* (1995) found that macrofaunal species diversity was markedly depressed by high current energy in the deep sea. It appears that only a few, well-adapted nematodes can thrive on the substrata whereas the other genera are dependent on the presence of sediment infill, especially for sponge skeletons. This is, however, not reflected in the indices of evenness. Thus it seems that although fewer genera are able to live in these more disturbed microhabitats, the community is not merely dominated by the best adapted ones. Our results also indicate that the presence of a higher number of epifaunal genera on these substrata is not able to compensate for the loss in genus richness due to the physical erosion by strong currents.

The presence of small biogenic structures in the underlying sediment considerably adds to its habitat complexity and heterogeneity and therefore its biodiversity. Hence, both interstitial and epifaunal taxa will be present here and their combined presence increases genus richness. This is

confirmed by the high N_0-value of the sediment. Furthermore, this value is much higher than for the Goban Spur stations I, B and II in Vanaverbeke *et al.* (1997) (106 vs. 45-72), although fewer individuals were identified. The same is true for N_1 and E*G* (100).

The higher genus richness of the nematode community on the mixed substratum can easily be explained as this community recruits from both the sponge and coral communities, each with a different genus composition.

Both coral fragments and sponge skeletons provide a microhabitat for representatives of the Epsilonematidae and Draconematidae, which are rare or not yet recorded elsewhere along the continental margin and in the deep sea (Decraemer *et al.*, 2001; Gad, 2004), and small degradation products of the two substrata positively influence the biodiversity in the underlying sediment. The importance of such 'habitat islands' for deep-sea fauna has been confirmed by Gage (1996), who states that they attract aggregations of species, including many specialist taxa that are very rare in the background community.

In conclusion, the nematode data largely confirm the hypotheses proposed by Raes & Vanreusel (2005) for taxa at a higher taxonomic level. However, these data contradict low disturbance on the large biogenic substrata. In addition, the nematode community in the underlying sediment is significantly more diverse than on the coral fragments whereas the opposite is true for the meiofaunal community on a higher taxon level.

2.6. ACKNOWLEDGEMENTS

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Acantholaimus Allgén, 1933
Acanthonchus Cobb, 1920
Actinonema Cobb, 1920
Aegialoalaimus de Man, 1907
aff. *Antarcticonema*
aff. *Diplolaimella*
aff. *Linhystera*
Laimella Cobb, 1920
Leptolaimoides Vitiello, 1971
Leptolaimus de Man, 1876
Linhystera Juario, 1974
Litinium Cobb, 1920
Longicyatholaimus Micoletzky, 1924
Manganonema gen. n.

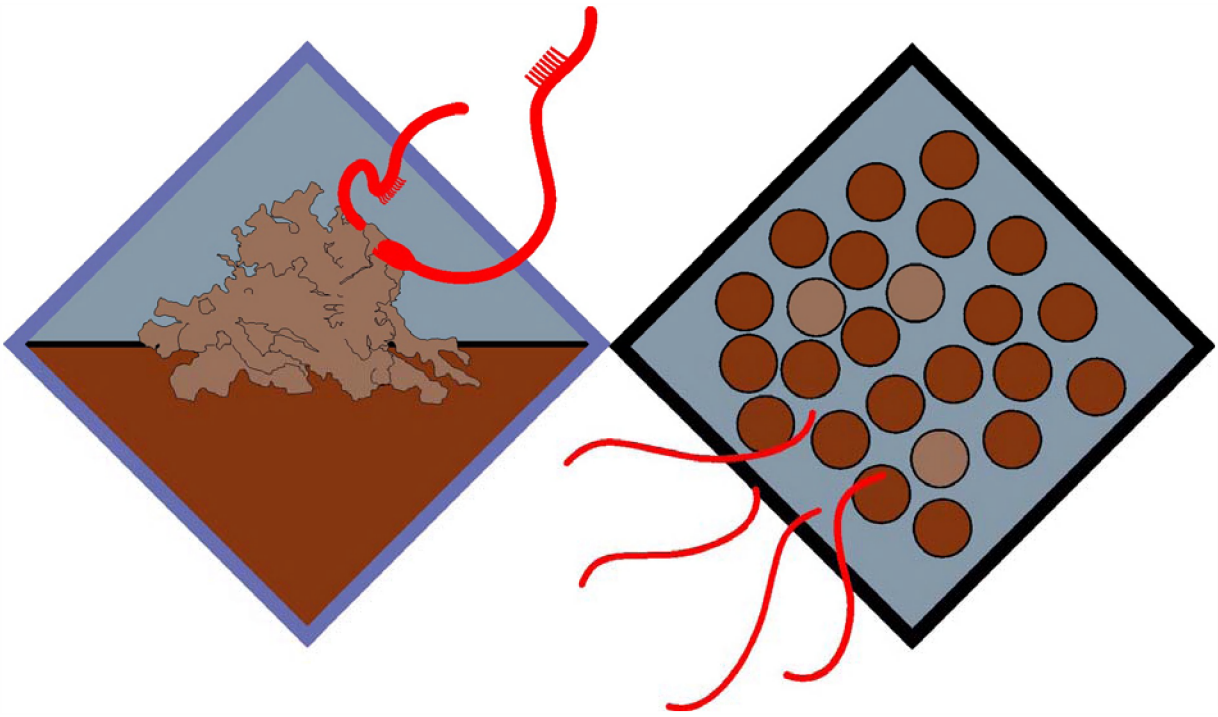
aff. *Noffsingeria*
aff. *Odontolaimus*
aff. Sphaerolaimidae
aff. *Trefusia*
Akanthepsilonema Gourbault & Decraemer, 1991
Alaimella Cobb, 1920
Amphimonhystera Allgén, 1929
Amphimonhystrella Timm, 1961
Anoplostoma Bütschli, 1874
Anticoma Bastian, 1865
Antomicron Cobb, 1920
Araeolaimoidea sp.1
Araeolaimus de Man, 1888
Ascolaimus Ditlevsen, 1919
Bathyepsilonema Steiner, 1931
Bathynox Bussau & Vopel, 1999
Benthimermis Petter, 1980
Calomicrolaimus Lorenzen, 1976
Calyptronema Marion, 1870
Camacolaimus de Man, 1889
Campylaimus Cobb, 1920
Ceramonema Cobb, 1920
Cervonema Wieser, 1954
Chaetonema Filipjev, 1927
Chromadora Bastian, 1865
Chromadorella Filipjev, 1918
Chromadorina Filipjev, 1918
Chromadorita Filipjev, 1922
Coninckia Gerlach, 1956
Crenopharyngidae sp.1
Cricolaimus Southern, 1914
Cyartonema Cobb, 1920
Cyatholaimus Bastian, 1865
Cygnonema Allen & Noffsinger, 1978
Daptonema Cobb, 1920
Desmodora de Man, 1889
Desmodorella Cobb, 1933
Desmodorinae sp.1
Desmoscolex Claparède, 1863
Dichromadora Kreis, 1929
Diplolaimella Allgén, 1929
Diplopeltis Cobb in Styles & Hassal, 1905
Diplopeltoides Gerlach, 1962
Diplopeltula Gerlach, 1950
Dorylaimopsis de Coninck, 1965
Dracograllus Allen & Noffsinger, 1978
Eleutherolaimus Filipjev, 1922
Elzalia Gerlach, 1957
Enoplus Dujardin, 1845
Epsilonema Steiner, 1927
Eubostrichus Greeff, 1869
Fenestrolaimus Filipjev, 1927
Gammanema Cobb, 1920
Glochinema Lorenzen, 1974
Marylynnia Hopper, 1977
Mesacanthion Filipjev, 1927
Metacomesoma Wieser, 1954
Metacyatholaimus Stekhoven, 1942
Metadasynemella de Coninck, 1942
Metadasynemoides Haspeslagh, 1973
Metadesmolaimus Stekhoven, 1935
Metalinhomoeus de Man, 1907
Metoncholaimus Filipjev, 1918
Microlaimus de Man, 1980
Minolaimus Vitiello, 1970
Molgolaimus Ditlevsen, 1921
Monhystera bastian, 1865
Monhystrella Cobb, 1918
Nannolaimus Cobb, 1920
Nemanema Cobb, 1920
Neochromadora Micolezky, 1924
Oxystomina Filipjev, 1921
Paracanthonchus Micoletzky, 1924
Parachromadorita Blome, 1974
Paracyatholaimus Micoletzky, 1922
Paradesmodora Stekhoven, 1950
Paralongicyatholaimus Stekhoven, 1950
Paramonohystera Steiner, 1916
Paratricoma Gerlach, 1964
Pareurystomina Micoletzky, 1930
Pierrickia Vitiello, 1970
Pomponema Cobb, 1917
Procamacolaimus Gerlach, 1954
Prochromadora Filipjev, 1922
Prochromadorella Micoletzky, 1924
Pselionema Cobb, 1933
Pterygonema Gerlach, 1954
Retrotheristus Lorenzen, 1977
Rhabdocoma Cobb, 1920
Rhaptothyreus Hope & Murphy, 1969
Rhips Cobb, 1920
Rhynchonema Cobb, 1920
Richtersia Steiner, 1916
Sabatieria Rouville, 1903
Siphonolaimus de Man, 1893
Southerniella Allgén, 1932
Sphaerolaimus Bastian, 1865
Spiliphera Bastian, 1865
Spilophorella Filipjev, 1917
Stephanolaimus Ditlevsen, 1918
Symplocostoma Bastian, 1865
Synonchus Cobb, 1894
Syringolaimus de Man, 1888
Tarvaia Allgén, 1934
Tenuidraconema Decraemer, 1989
Terschellingia de Man, 1888
Thalassironinae sp.1
Thalassoalaimus de Man, 1893

Gnomoxyala Lorenzen, 1977
Greeffiella Cobb, 1922
Halalaimus de Man, 1888
Halaphanolaimus Southern, 1914
Halichoanolaimus de Man, 1886
Haptotricoma Lorenzen, 1977
Innocuonema Inglis, 1969
Theristus Bastian, 1865
Trefusia de Man, 1893
Tricoma Cobb, 1894
Triepsilonema Decraemer, 1982
Viscosia de Man, 1890
Wieseria Gerlach, 1956
Xenella Cobb, 1920

Appendix. List of identified genera. Taxonomy after Lorenzen (1994) and original genus descriptions.

CHAPTER 3

THE STRUCTURING ROLE OF MICROHABITAT TYPE IN CORAL DEGRADATION ZONES: A CASE STUDY WITH MARINE NEMATODES FROM KENYA AND ZANZIBAR



Paper *submitted*

Raes, M., De Troch, M., Ndaro, S.G.M., Muthumbi, A., Guilini, K., Vanreusel, A.

The structuring role of microhabitat type in coral degradation zones: a case study with marine nematodes from Kenya and Zanzibar

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3.1. ABSTRACT

Nematode genus assemblages were identified from four locations in coral degradation zones along the African tropical east coast: Watamu and Tiwi Beach on the coast of Kenya and Matemwe and Makunduchi on the east coast of Zanzibar Island. A distinction was made between three microhabitat types: coralline sediment, coral gravel and coral fragments. Nematode community composition was comparable to that of other studies in a similar habitat, mainly from other oceans. The presence of a common genus pool in coral degradation zones was reflected in the considerable similarities between the samples. However, the addition of coral fragments as a habitat for nematodes resulted in an increased importance of taxa typical for coarse sediments and large substrata. Local and regional turnover were of the same order of magnitude and the structuring effect of microhabitat type clearly overrode the effect on a local and regional scale. Differences in sediment characteristics were also more important in structuring the nematode assemblages than differences between the coralline sediment and coral fragments. There was no effect related to the three-dimensional structure of coral fragments. Differences between nematode assemblages in the coralline sediment and on coral fragments were attributed to the exposed nature of the latter habitat, its large surface area for epifaunal taxa and its microbial or algal cover. Differences in available food sources were reflected in nematode trophic composition.

Key words: coral reefs, coral degradation zones, nematodes, microhabitats, spatial turnover, Indian Ocean, Kenya, Zanzibar

3.2. INTRODUCTION

Numerous studies have investigated the major factors that structure nematode community composition in coral reef associated sediments (Alongi, 1986; Boucher & Gourbault, 1990; Gourbault & Renaud-Mornant, 1990; Tietjen, 1991; Ólafsson *et al.*, 1995; Boucher, 1997; Ndaro & Ólafsson, 1999; Netto *et al.*, 1999, Kotta & Boucher, 2001, de Jesús-Navarrete, 2003). These efforts have produced a list of variables that are, at least potentially, determinant: (1) mean sediment grain size, (2) sediment clay-silt content, (3) sediment sorting, (4) sediment oxygen content, (5) position of RPD layer in the sediment, (6) organic content of the sediment, (7) extent of bioturbation by macrobenthos, (8) macrofloral biomass, (9) water depth, (10) longitude, (11) latitude and (12) sampling scale. The vast majority of these factors is related to sediment characteristics.

Coral reef associated sediments can be found in all functional zones of the reef, *e.g.* the reef crest, reef flat, outer reef, reef pools, reef lagoon etc. Most of the studies mentioned above have however focused on lagoons, which separate the reef platform from the adjacent land mass. In this zone, dead coral material coming from the main reef or from scattered coral thickets in the lagoon itself (*e.g.* from patch reefs), is progressively degraded into smaller pieces (coral gravel) until it becomes coralline sediment. Because of the dynamic character of this functional zone, the term coral degradation zone will be used throughout the text when referring to the lagoon between the reef and

the coast. As a result of this gradual process of degradation, the coral degradation zone sediment will obviously be mixed with coral fragments of different sizes and shapes. The presence of coral degradation products on and in the sediment may have a profound effect on nematode assemblage structure on a local scale. So far, these coral degradation products have not yet been considered as an ecologically valuable habitat in tropical coral degradation zones.

The present study contributes to the knowledge of nematode assemblages in coral degradation zones of the Indian Ocean, a subject investigated in only a limited number of studies (Thomassin *et al.*, 1976 (Madagascar); Ólafsson *et al.*, 1995 (Zanzibar); Ndaro & Ólafsson, 1999 (Zanzibar)).

In our study, three distinct microhabitat types (*i.c.* coralline sediment, coral gravel and coral fragments) are distinguished. This unique given makes it possible to investigate how changes in community composition resulting from the structuring role of microhabitat structure compares to the changes due to turnover on a local and regional scale. The key questions here are: (1) do coral degradation zones harbour a typical nematode community?; (2) how strong is turnover in taxonomic composition operating at local and regional scales? and (3) is microhabitat structure an additional source for variation in nematode community composition?

3.3. MATERIALS AND METHODS

3.3.1. SAMPLING SITES, PROCEDURE AND MICROHABITATS

Meiofauna samples were collected in the coral degradation zone of the fringing reefs stretching along the south coast of Kenya and along the east coast of Zanzibar Island (Unguja, Tanzania) (Fig. 1). In Kenya, samples were taken on two locations: Watamu, the northernmost location (03°23' S, 40°00' E; 27/02/2002), and Tiwi Beach, more to the south (4°14' S, 39°36' E; 22-23/02/2002). In Zanzibar, samples were taken in Matemwe, located in the north of the island (5°52' S, 39°21' E; 24/08/2004 and 31/08/2004), and Makunduchi (6°28' S, 39°32' E and 6°25' S, 39°34' E; 15/08/2004 and 25/08/2004), located in the south of the island. Distance between both Kenyan locations is 104 km, between Tiwi Beach and Matemwe 183.5 km and between both Zanzibar locations 70 km.

At each location, coralline sediment and coral fragments were collected. Coral gravel was collected in Watamu, Matemwe and Makunduchi, but not in Tiwi Beach due to the absence of this microhabitat in the sampled area. Coral gravel can easily be distinguished from coralline sediment because small pieces of coral can still be recognised in this microhabitat, whereas this is no longer true for the sediment (Fig. 2). The dead coral fragments were either compact or branched, unaffected or eroded. In Zanzibar, different coral morphotypes were collected, which were identified as *Fungia*, *Goniastrea*, *Pocillopora*, *Tubipora* and *Porites*/*Stylophora*. *Porites* and *Stylophora* were considered as the same morphotype in this study, based on their robustness and branching morphology. All sampling was carried out under water. Sediment samples were taken with a Perspex sediment core (10 cm²), coral gravel was gently scooped out with a spoon or sediment core and coral fragments were taken out manually. Coral gravel and coral fragments were put directly into firm plastic bags or buckets. At each location, two or more replicate samples were taken for each available microhabitat type.

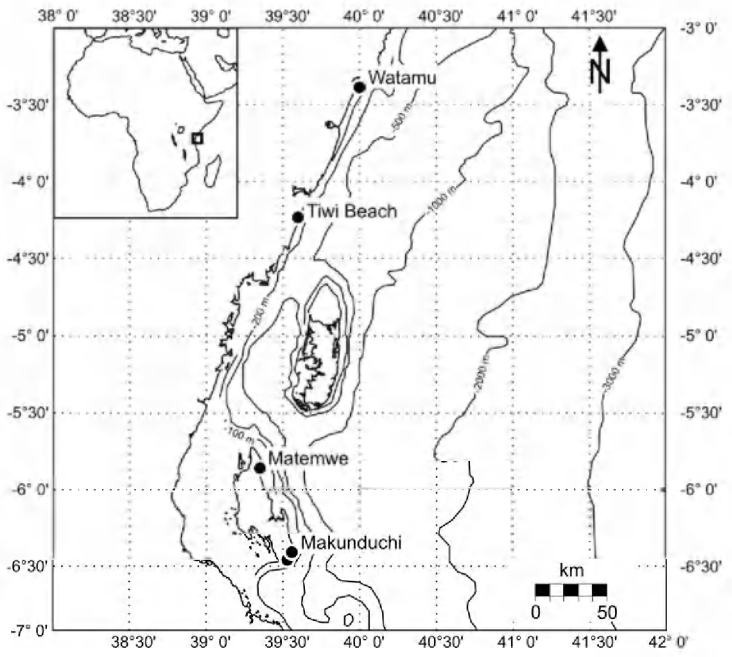

Fig. 1. Map of the study area; location of sampling sites is indicated. The northernmost island is Pemba, the southernmost island is Unguja (Zanzibar Island).

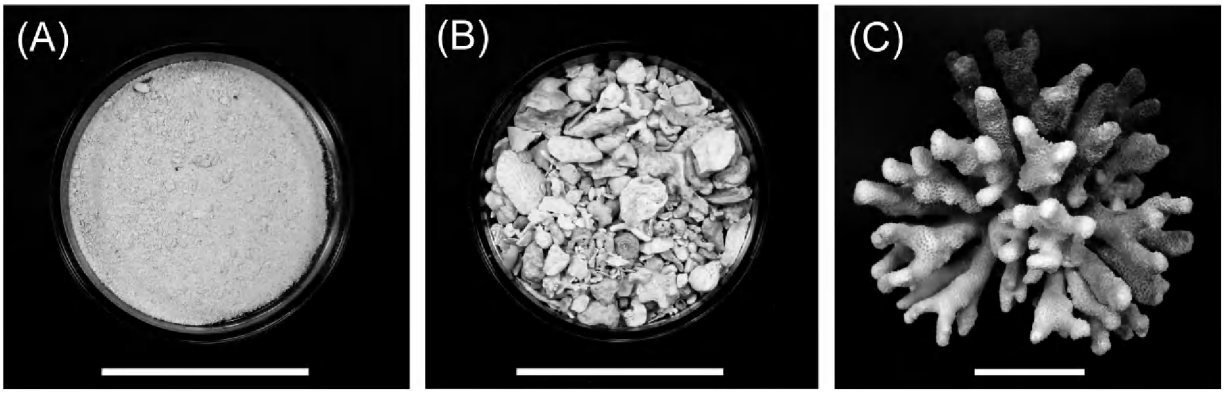

Fig. 2. The three microhabitats. (A) coralline sediment; (B) coral gravel; (C) coral fragment (*Stylophora* is given as an example). Scale bars: 5 cm.

3.3.2. LABORATORY ANALYSES

Meiofauna extraction from coralline sediment and coral gravel was done by decantation with filtered seawater over a 1 mm and a 32 µm sieve and subsequent centrifugation. Coral fragments were rinsed off thoroughly, also with filtered seawater, over the same sieves. The material collected on the 32 µm sieve was then subjected to density gradient centrifugation, using Ludox (a colloidal silica polymer; specific gravity 1.18) as a flotation medium (Heip *et al.*, 1985; Vincx, 1996). All material was fixed with 4% buffered formalin and stained with Rose Bengal. From each sample 200 nematodes (or all nematodes when less than 200 individuals were present in the examined sample) were randomly picked out. They were subsequently mounted onto slides using the formalin-ethanol-glycerol technique of Seinhorst (1959) and Vincx (1996), and identified up to the genus level, using Lorenzen (1994), Warwick *et al.* (1998), the Desmodoridae key in NeMys (Deprez *et al.*, 2004), and original

descriptions. The trophic composition of the nematode community was analysed according to the classification of Wieser (1953).

3.3.3. STATISTICAL ANALYSES

The PRIMER5 software (Plymouth Marine Laboratory; Clarke & Gorley, 2001) was used to calculate Bray-Curtis (dis)similarities between all samples. Samples were grouped together in three ways, concordantly with three spatial scales: (1) both regions (Kenya/Zanzibar: regional scale), (2) the different sampling locations (Watamu/Tiwi Beach/Makunduchi/Matemwe: local scale) and (3) the different habitats (coralline sediment/coral gravel/coral fragments: microhabitat scale). The obtained similarity matrix was used to produce non-metric multidimensional scaling two-dimensional plots (MDS). The stress value gives a measure for goodness-of-fit of the MDS ordination: a low stress value (<0.2) indicates a good ordination with no real prospect for a misleading interpretation (Clarke, 1993). One-way Analysis of Similarities (ANOSIM) was carried out to test for significant differences in the nematode community structure between different groups that were delimited beforehand. Similarity of Percentages (SIMPER) was used to investigate which genera were responsible for these differences. Due to differences in sample size, relative data were used per sample and these data were Log (x+1)-transformed prior to the analysis.

The Pcord4 software (McCune & Mefford, 1999) was applied to perform an Indicator Species Analysis (ISA) on the dominant genera (*i.e.* with a relative abundance >0.5%). Calculated indicator values were tested for statistical significance using a Monte Carlo test (Dufrêne & Legendre, 1997). The same software was also used for TWINSPAN analysis, which is a divisive classification method (Hill, 1979; Gauch & Whittaker, 1981). Calculated cut levels were 0.0; 0.5; 1.2; 3.0; 6.0; 53.0. For both ISA and TWINSPAN, relative data were used without transformation.

Parametric (one-way ANOVA) and non-parametric (Kruskal-Wallis ANOVA by ranks) analysis of variance was performed using the STATISTICA6 software. Bartlett's and Cochran's test were used to verify the homogeneity of variances prior to the analysis.

Turnover on a regional, local and microhabitat scale is visualised in a ternary plot (Koleff *et al.*, 2003). The values of a', b' and c' (*i.e.* the percentage of shared species a, the percentage of species exclusively present in the neighbouring sample b and the percentage of species exclusively present in the focal sample c) are plotted against a background of β_{sim}-values (Lennon *et al.*, 2001). This technique has already been successfully used for nematodes by Fonseca *et al.* (*submitted*).

3.4. RESULTS

A total of 7087 nematodes belonging to 149 different genera and 35 different families were included in the analysis. The coral gravel, coral fragments and coralline sediment yielded 89, 108 and 127 genera, respectively. A list of all encountered genera is provided in Appendix 1.

3.4.1. ARE THERE CHARACTERISTIC NEMATODE COMMUNITIES FOR THE DIFFERENT REGIONS, LOCATIONS AND MICROHABITATS? WHAT IS THE STRUCTURING ROLE OF MICROHABITAT STRUCTURE?

The MDS biplot of all samples (Fig. 3A) shows both a separation of the samples from the two regions (dashed line) and a separation of the coral samples from the sediment samples (dotted line), although the separation between regions is not as clear-cut as the separation between the two microhabitats. Nevertheless, ANOSIM calculated a very highly significant (p = 0.001) departure from the null hypothesis that assemblage differences between samples from Kenya and Zanzibar do not occur. Differences between the nematode communities in different microhabitats were also very highly significant (p = 0.001); pairwise tests revealed very highly significant differences between sediment and coral samples (p = 0.001) and highly significant differences between coral gravel and coral samples (p = 0.004). However, there were no significant differences between sediment and gravel samples. The gravel samples are also found scattered between samples from both other microhabitats in the MDS plot (Fig. 3A). Therefore, the gravel samples were omitted in further analyses. On the MDS plot, the coral samples were clearly clustered more closely together than the sediment samples. Furthermore, it is clear from Fig. 3A that the two sediment samples in the top left corner of the plot, which originate from Matemwe (Zanzibar), have a community composition different from that of the other sediment samples.

Although no clear separation of groups of samples from the four different sampling locations could be observed from the plot (not shown), ANOSIM calculated significant differences in community structure between Watamu and the two Zanzibar locations (in both cases p = 0.001), between Tiwi Beach and Watamu and between Tiwi Beach and Makunduchi (in both cases p = 0.005), but not between Tiwi Beach and Matemwe.

To define the most important structuring factor for the nematode communities, the effect of (1) local forces within both microhabitats and regions, (2) regional forces within both microhabitats and (3) microhabitat structure within all locations and both regions was investigated with ANOSIM (Table 1, Figs. 3B-E). The highest significance levels were found for the structuring effect of microhabitat structure within each region and the effect of locations and regions within each microhabitat. There was no significant separation between the coral samples from Watamu and those from Tiwi Beach (R = -0.3), which is also obvious from Fig. 3B. A TWINSPAN dendrogram (Fig. 4) revealed that at a first level the two sediment samples from Matemwe (TWIN group 1) branch off from the other samples. *Richtersia* was specified as a TWINSPAN indicator genus for group 1. At a second level, the other sediment samples (TWIN group 3) are separated from the coral samples (TWIN group 2). *Atrochromadora*, *Chromadora* and *Chromadorina* were specified as TWINSPAN indicator genera for group 2 whereas *Neochromadora* was specified as a TWINSPAN indicator genus for group 3.

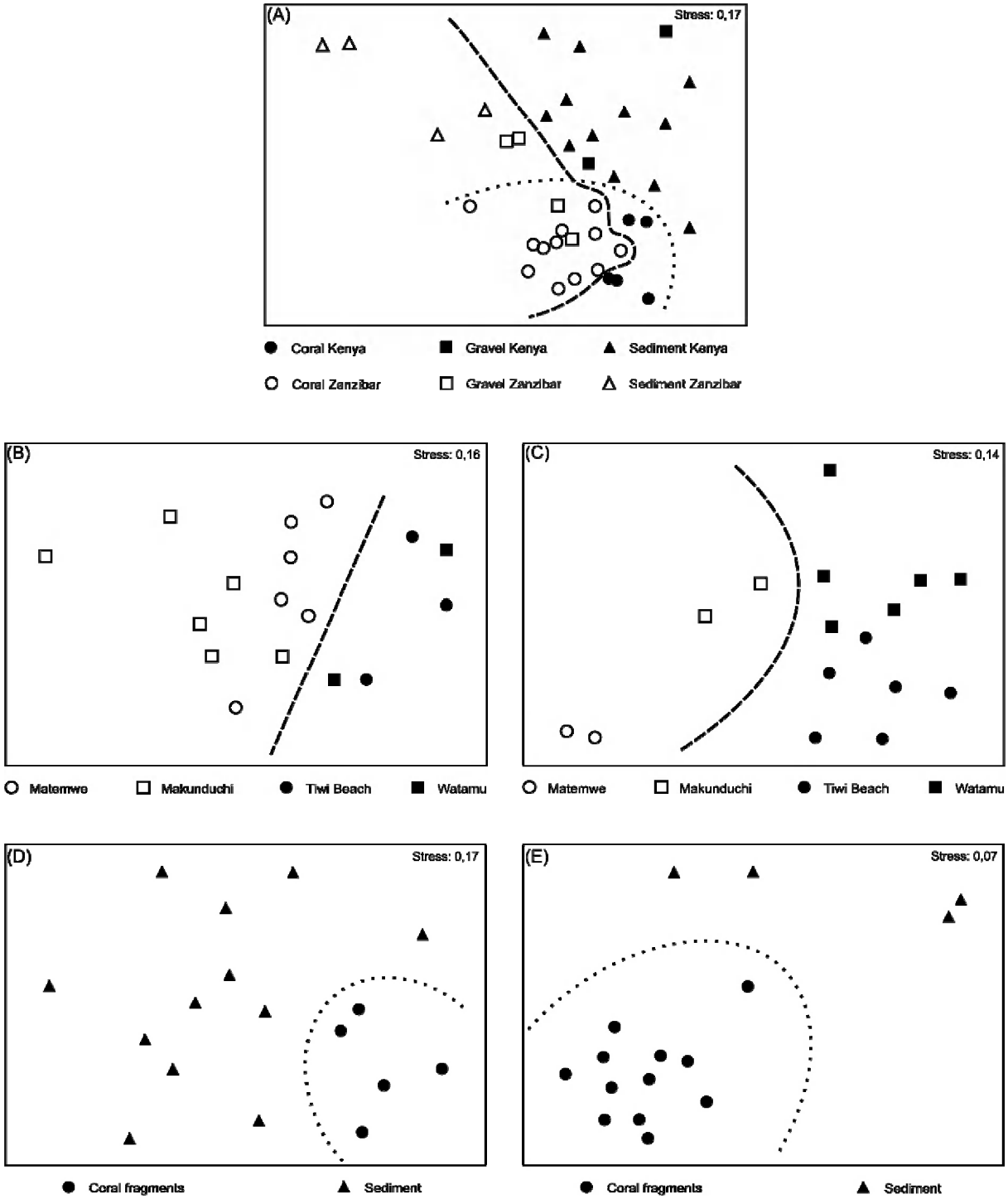

Fig. 3. MDS two-dimensional ordination plots. Stress values are indicated. (A) all samples; (B) coral samples; (C) sediment samples; (D) Kenya samples; (E) Zanzibar samples. The dashed lines separate samples from different regions (Kenya-Zanzibar); the dotted line separates sediment samples from coral samples.

selected samples \ effect		Regions	Locations	Microhabitats
Regions	Kenya		0.041	0.003
	Zanzibar		0.077	0.001
Locations	Watamu			0.357
	Tiwi Beach			0.012
	Matemwe			0.036
	Makunduchi			0.036
Microhabitats	Coral fragments	0.004	0.001	
	Coralline sediment	0.001	0.001	

Table 1. Significance levels of the effects on different spatial scales (see text for details). A black box stands for a very highly significant effect ($p \leq 0.001$), a dark grey box for a highly significant effect ($0.001 < p \leq 0.01$), a light grey box for a significant effect ($0.01 < p \leq 0.05$) and a white box for the absence of a significant effect ($p > 0.05$).

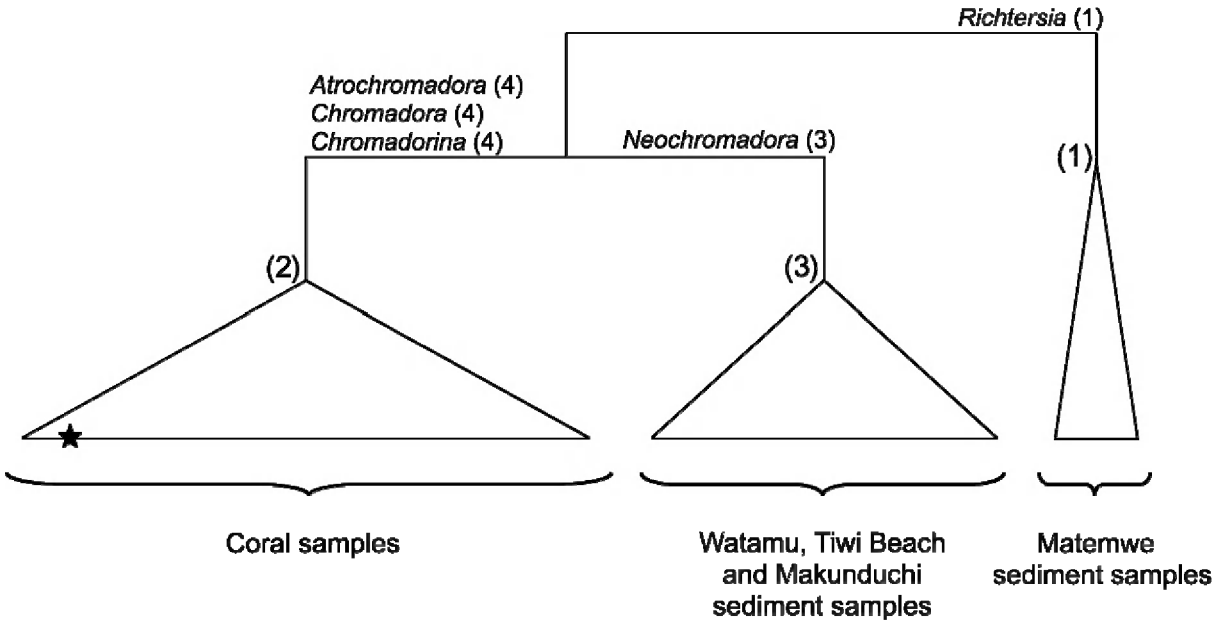

Fig. 4. TWINSPAN dendrogram based on relative abundances of nematode genera in each sample. Only sediment and coral fragment samples are considered. The star figure indicates a mismatched sediment sample in the coral samples TWIN group. TWINSPAN indicator genera for each TWIN group are indicated with their signs.

The ternary graph (Fig. 5) shows that turnover (β_{sim}) between coral and sediment within the same location (grey squares) is generally higher than the turnover between locations within the same region (black circles) and between locations from different regions (white triangles). Due to a lower value for the turnover between the microhabitats in Watamu, these differences were not significant ($p = 0.4$). Local and regional turnover are however clearly of the same order of magnitude, with a β_{sim} value around 0.2.

An MDS plot (not shown) and subsequent ANOSIM analysis demonstrated the absence of an effect of the three-dimensional build-up of different coral morphotypes on the nematode community composition. These analyses were carried out within each location in order to avoid interference by any regional and local effects.

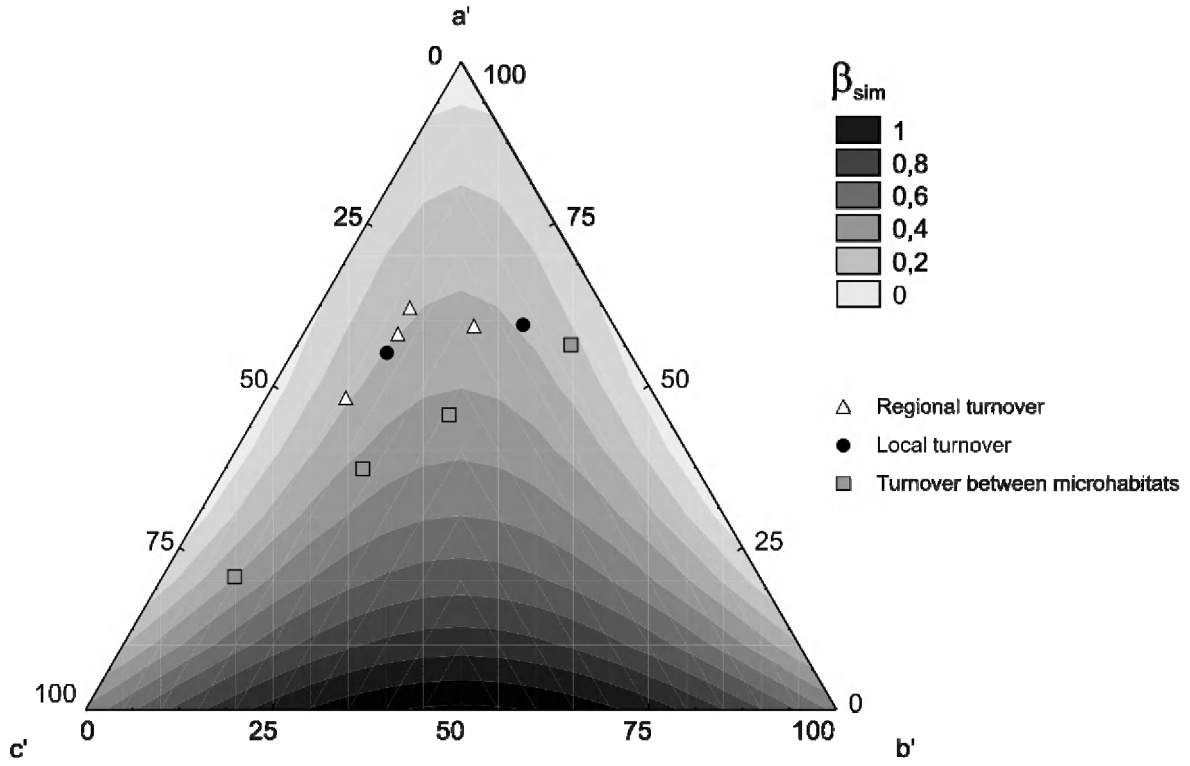

Fig. 5. Ternary plot representing species turnover between coral and sediment within the same location (turnover between microhabitats), between locations within the same region (local turnover) and between locations from different regions (regional turnover). Shading visualises the values of β_{sim}.

3.4.2. How unique and specific are the nematode communities in the different regions and microhabitats?

Even though the communities inhabiting coral fragments and coralline sediment in both regions are significantly different from each other, they do not make up distinct, clear-cut groups (Fig. 3A). Moreover, each group has at least half of its genera in common with other groups (Fig. 6). This effect is independent of the region. The lowest number of shared genera, as derived from the surface of the radar chart, was found for the sediment in Zanzibar, which was also characterised by the lowest number of genera (*i.e.* 72) (Fig. 6A). The highest number of shared genera was found for the sediment in Kenya (Fig. 6C), which was characterised by the highest number of genera (*i.e.* 115). Average dissimilarity (SIMPER analysis) between the four groups varied between 53.2% (Kenya coral-Zanzibar coral) and 82.8% (Kenya coral-Zanzibar sediment). Coral samples from both regions are relatively comparable in terms of associated nematode communities, whereas sediment samples from both regions are much more dissimilar from each other (average dissimilarity: 75.4%). On the other hand, the average similarity of samples within each group is relatively low: between 38.1% (Zanzibar sediment) and 52.9% (Zanzibar coral). Overall, average similarity of coral samples (50.2%) was higher than for sediment samples (33.9%).

The specificity of the nematode communities in the same four groups was evaluated in terms of uniqueness of genera, *i.e.* whether and how many genera are restricted to a certain microhabitat or region (Fig. 7). Although more stations were sampled for both Kenya sediment (11) and Zanzibar coral

(12) (Fig. 7A), this was only reflected in a higher number of unique genera in the sediment from Kenya (Fig. 7B). The detailed distribution shows that most of the unique genera are restricted to 1 or, to a lesser extent, 2-3 samples within a group (Fig. 7C). Moreover, the number of unique genera corresponds well with the distribution of singletons (*i.e.* unique genera found in only one sample). There were no genera unique for Kenya and only three genera unique for Zanzibar. Within Kenya, 11 and 24 genera were unique for coral fragments and sediment respectively whilst in Zanzibar 5 and 7 genera were restricted to coral fragments and sediment, respectively.

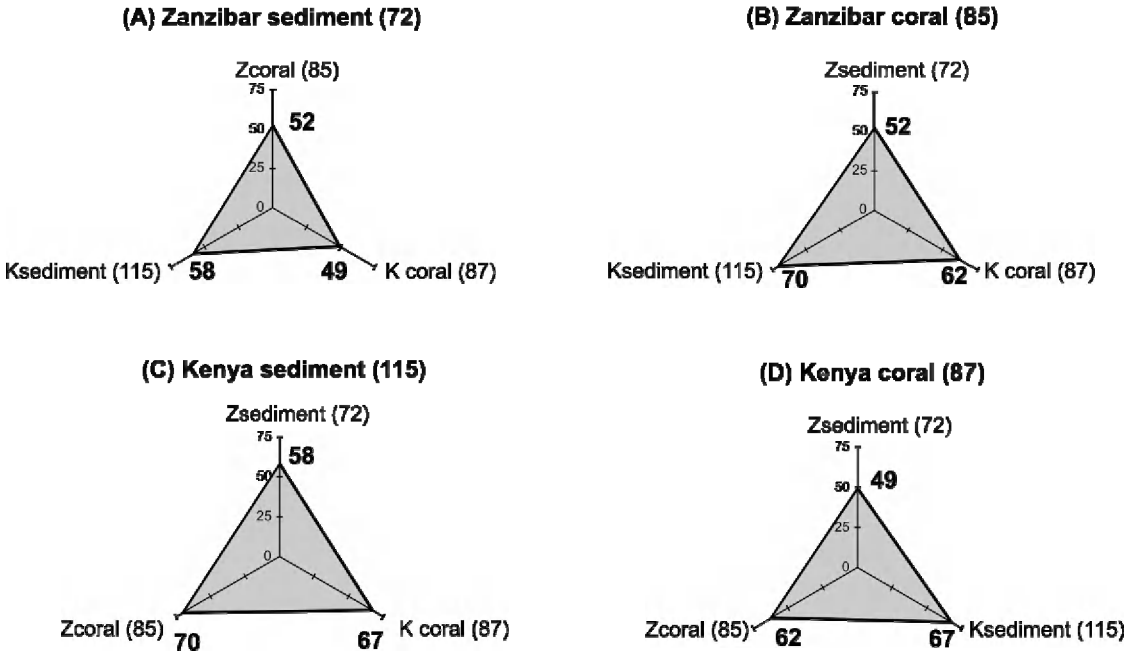

Fig. 6. Radar charts depicting the number of nematode genera shared between a certain microhabitat type in one of the regions (indicated above each graph) on the one hand and the other microhabitats in both regions (Z = Zanzibar, K = Kenya) on the other hand. The total number of genera in each microhabitat is indicated between brackets.

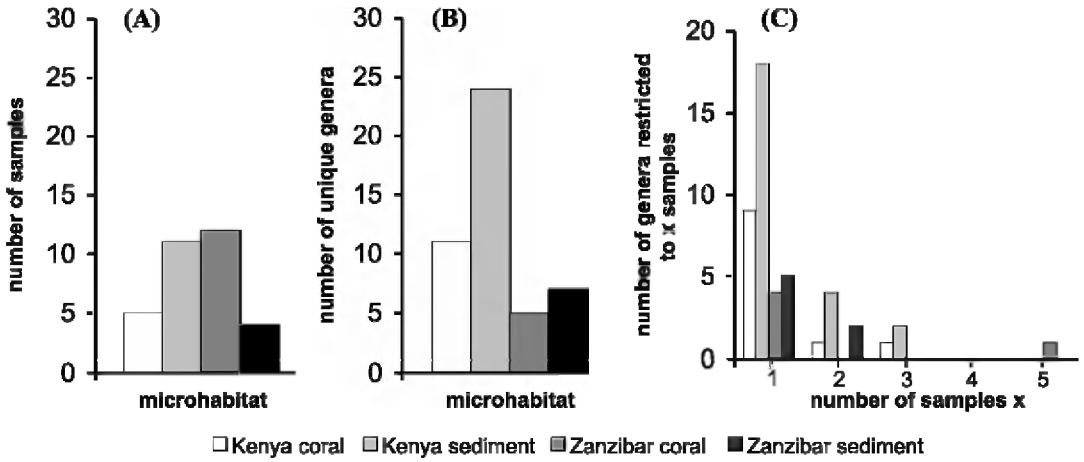

Fig. 7. Stacked columns depicting the number of nematode genera unique for a certain microhabitat type in one of the regions. (A) comparison of sampling intensity; (B) number of unique genera and (C) detailed distribution of unique genera.

3.4.3. CHARACTERISATION OF THE NEMATODE COMMUNITIES

An overview of the most abundant genera characteristic for coral and sediment samples from both regions is given in Fig. 8A and Fig. 8B, respectively (see also Appendix 2). For the coral samples, all genera with a relative abundance >2%, calculated over all coral samples, and occurring in at least 75% of the coral samples were selected. For the sediment samples, all genera with a relative abundance of >2%, calculated over all sediment samples, and occurring in at least 50% of the sediment samples were selected. This difference in procedure is due to the low abundances of the dominant genera in the sediment samples. In this way 46.5%, 50.5%, 60.5% and 66.5% of the Zanzibar sediment, Kenya sediment, Zanzibar coral and Kenya coral communities is shown in the stack bars, respectively.

The three most abundant genera in the coral samples belong to the families Chromadoridae (*Atrochromadora*, *Chromadora*) and Epsilonematidae (*Epsilonema*), whereas those in the sediment samples are representatives of the families Desmodoridae (*Chromaspirina*, *Spirinia*) and Chromadoridae (*Neochromadora*). Strikingly, the five most abundant families for both microhabitats are the same: Chromadoridae, Cyatholaimidae, Desmodoridae, Epsilonematidae and Xyalidae. Chromadoridae is the dominant family on corals, with Desmodoridae the second most abundant. The opposite is the case in the coralline sediment.

All genera exhibiting significant indicator values are listed in Table 2. The highest indicator values and highest significance levels for the coral fragments are found in representatives of the family Chromadoridae (*Atrochromadora*, *Chromadorina*, *Chromadora*) and for the coralline sediment they are found in representatives of both Desmodoridae (*Eubostrichus*, *Metachromadora*, *Bolbonema*) and Chromadoridae (*Neochromadora*). For coral fragments, the same results were found within each region. Nine out of the 10 genera featured in Fig. 8A are also indicator genera for coral fragments. This correspondence is not clear for the sediment samples. The four indicator genera for coralline sediment in Kenya belong to four different families, but none belongs to the Desmodoridae.

The list of genera that explain most of the average similarity within each of these four groups, as pointed out by a SIMPER analysis (not shown), corresponds well with the list of indicator genera (Table 2) and the genera provided in Fig. 8. Only for the overall coralline sediment group, some considerable differences with the list of indicator genera were observed.

Marylynnia, *Metadesmolaimus*, *Paracomesoma* and *Molgolaimus* are the significant indicator genera for the sediment in Matemwe (Zanzibar). The importance of these genera in the distinction between the Matemwe sediment samples and all other samples is confirmed by a SIMPER analysis.

Epistratum feeders were the dominant trophic group in each microhabitat (65.6% in coralline sediment; 75.2% on coral fragments). No obvious structuring effect on either regional, local or microhabitat scale was found. However, some significant effects on the individual trophic groups were detected with an analysis of variance. For example, the relative abundance of non-selective deposit feeders (Wieser group 1b) was significantly higher in the sediment (p = 0.01) and the relative abundance of epistratum feeders (Wieser group 2a) was significantly higher on coral fragments (p = 0.005).

Coral fragments		Coralline sediment	
Indicator genus	Indicator Value	Indicator genus	Indicator Value
Atrochromadora	89.2***	*Eubostrichus*	69.5**
Chromadorina	82.2***	*Neochromadora*	69.0**
Chromadora	79.8***	*Metachromadora*	56.7**
Paradraconema	72.6***	*Bolbonema*	53.3**
Daptonema	59.5***	*Perepsilonema*	56.1*
Euchromadora	74.7**	*Chromadorita*	56.0*
Acanthonchus	72.8**	*Ptycholaimellus*	52.0*
Epsilonema	72.5**	*Dracognomus*	46.0*
Spilophorella	69.6**	*Paracomesoma*	43.4*
Calomicrolaimus	54.8**		
Paracanthonchus	53.7**		
Syringolaimus	61.6*		
Halalaimus	48.3*		

Kenya coral		Kenya sediment	
Chromadora	68.6***	*Theristus*	49.6**
		Neochromadora	69.6*
		Perepsilonema	59.0*
		Dracognomus	56.0*

Zanzibar coral		Zanzibar sediment	
Chromadorina	64.0***	*Chromaspirina*	71.1***
Atrochromadora	58.4**	*Paracomesoma*	94.3**
Daptonema	56.9**	*Marylynnia*	71.1**
Halalaimus	51.7*	*Metadesmolaimus*	63.5*
Epsilonema	47.1*	*Molgolaimus*	52.1*
		Spirinia	51.5*

Table 2. Indicator genera for each separate microhabitat and for each microhabitat within a region, as specified by an indicator species analysis. Only genera with a significant microhabitat preference are listed. Indicator values and significance levels are provided. ***: $p \leq 0.001$; **: $0.001 < p \leq 0.01$; *: $0.01 < p \leq 0.05$.

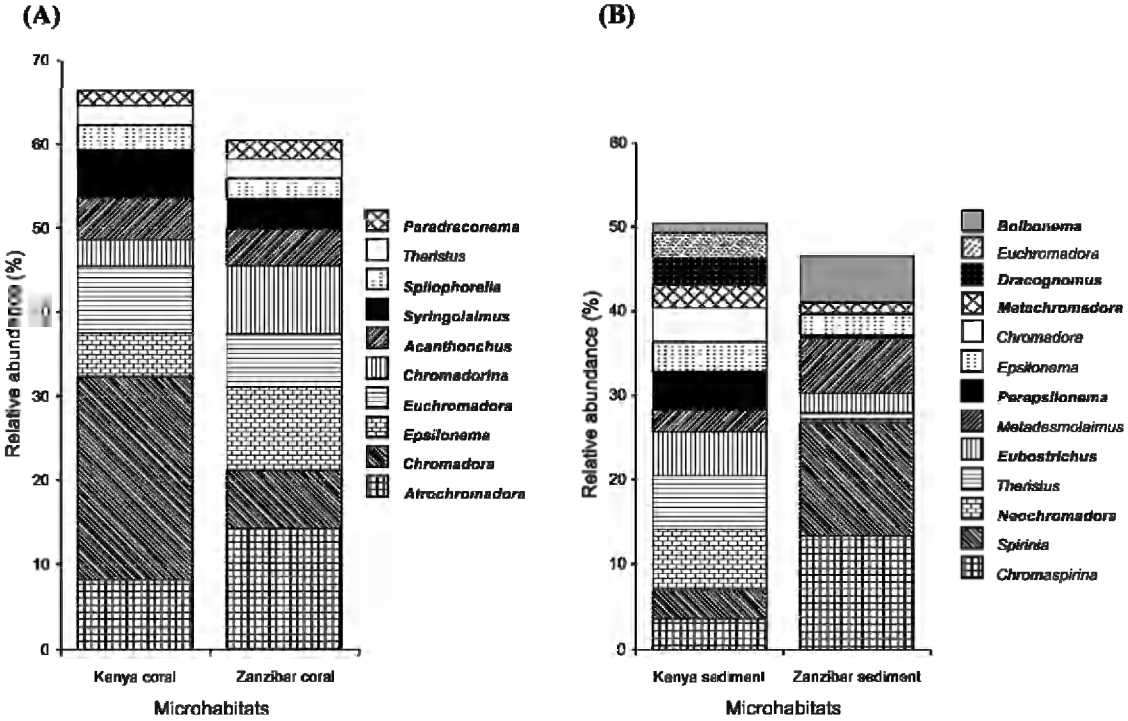

Fig. 8. Dominant nematode genera in coral and sediment samples from both regions. (A) coral fragments: genera with a relative abundance >2% of the total coral community and occurring in at least 75% of the coral samples; (B) sediment samples: genera with a relative abundance >2% of the total sediment community and occurring in at least 50% of the sediment samples. Indicator genera for either coral fragments or coralline sediment, as specified by an indicator species analysis, are printed in bold type.

3.5. DISCUSSION

3.5.1. DO CORAL DEGRADATION ZONES HARBOUR A TYPICAL NEMATODE COMMUNITY?

Desmodoridae, Chromadoridae, Xyalidae and Cyatholaimidae dominated both the sediment and coral fragments in our study area. This is consistent with most studies in tropical, reef-associated sediments (Grelet, 1984; Renaud-Mornant & Gourbault, 1984; Gourbault & Renaud-Mornant, 1990; Boucher & Gourbault, 1990; Tietjen, 1991; Boucher, 1997; Ndaro & Ólafsson, 1999; Kotta & Boucher, 2001). This general trend is also reflected in the genus composition of these sediments, and this is also the case in our study. A comparison with complete genus lists in similar environments (Alongi, 1986; Gourbault & Renaud-Mornant, 1990; de Jesús-Navarrete, 2003) has shown that, respectively, 90, 80 and 77 % of the genera encountered in Australia, French Polynesia and the Caribbean were also found along the East African coast. It should be added here that the total number of genera in these studies was rather low (35, 43 and 56). Nevertheless, these high percentages suggest similar (iso)communities in coral degradation zones all over the world. However, most taxa in lagoonal (coral degradation zone) sediments belong to the same families and genera as those in most temperate, sublittoral sands (Boucher, 1997). Especially Chromadoridae, Desmodoridae and Xyalidae become increasingly more important in gradually coarser sediments (Heip *et al.*, 1985). Furthermore, very coarse sands yield high abundances of taxa belonging to the families Epsilonematidae and/or Draconematidae (Willems *et al.*, 1982; Ndaro & Ólafsson, 1999). The dominant families in our study are thus explained solely by grain size and are not specific for this particular habitat.

Communities associated with the coral fragments in coral degradation zones are considered for the first time in our study. This resulted in an increased importance of typical coarse sand/coarse substratum taxa such as Chromadoridae and Epsilonematidae.

Nematode communities in the sediment of seagrass meadows documented in literature are very much comparable with the sediment-dwelling fauna in our study: the dominant genera here were *Chromaspirina*/*Spirinia*, *Terschellingia*, *Daptonema*, *Leptolaimus* and *Spilophorella* (Ndaro & Ólafsson, 1999 in Paje, nearby Makunduchi) or *Spirinia*, *Catanema*, *Actinonema* and *Prochromadorella* (Fisher, 2003; Fisher & Sheaves, 2003 in Australia). *Chromaspirina* and *Spirinia* are the dominant genera in our sediment samples, whereas *Eubostrichus*, a genus closely related to *Catanema*, is an indicator genus for the coralline sediment microhabitat. The communities associated with seagrass blades in a subtropical region (Hopper & Meyers, 1967a), which provide large surfaces just like the coral fragments, were also relatively comparable to the assemblages on the coral fragments in our study. The dominant species were representatives of the families Oncholaimidae (*Oncholaimus dujardinii* de Man, 1876), Chromadoridae (*Chromadora macrolaimoides* Steiner, 1915; *Chromadorina epidemos* Hopper & Meyers, 1967) and Cyatholaimidae (*Paracanthonchus platypus* Wieser & Hopper, 1967; *Acanthonchus cobbi* Chitwood, 1951). The last two families are also abundant on coral fragments (especially Chromadoridae) and both *Chromadora* and *Chromadorina* are indicator genera for coral fragments.

We did not find any new families or genera in our samples. This is consistent with the observation by Inglis (1968) that in coral reef sediment samples from New Caledonia, all species were new to

science, whereas all genera and families were already described, which was explained by the fact that genera at least tend to be cosmopolitan while species do not. This observation has been confirmed in the studies of Boucher & Gourbault (1990), Gourbault & Renaud-Mornant (1990), Tietjen (1991) and Boucher (1997). It can be concluded that coral degradation zones do not harbour a typical community in terms of taxa restricted to this system or in terms of new taxa above species level. However, many new species of Epsilonematidae and Draconematidae were found within our study area along the Kenyan Coast (Raes *et al.*, *submitted* a).

3.5.2. Is microhabitat structure an additional source for variation in nematode community composition?

Our study clearly shows that microhabitat structure is the main factor structuring the nematode assemblages in coral degradation zones along the coast of Kenya and the east coast of Zanzibar, as its effect on the nematode community structure overrides that of local or regional turnover. The nematode communities in coral degradation zones seem to have a patchy distribution, determined by small-scale differences in microhabitat structure. The assemblages are even more affected by changes in sediment grain size than by the structural differences between sediment and coral fragments, which was evidenced by the separation of the Matemwe sediment samples from both the coral samples and the coarser sediment samples in the TWINSPAN dendrogram. A granulometric analysis of the Zanzibar sediment samples revealed that the sediment in Matemwe had a much smaller coarse sand fraction and a larger medium and fine sand fraction than the coarser Makunduchi sediment. Several studies have indeed shown that nematode assemblages in coral degradation zones are mainly determined by sediment characteristics (Alongi, 1986; Boucher & Gourbault, 1990; Gourbault & Renaud-Mornant, 1990; Tietjen, 1991; Ólafsson *et al.*, 1995; Boucher, 1997; Ndaro & Ólafsson, 1999; Netto *et al.*, 1999, Kotta & Boucher, 2001, de Jesús-Navarrete, 2003). The explanation for the separation of the finer sediments at Matemwe may be related to food availability, oxygen availability and hydrodynamics: finer sediment is found in calm, undisturbed conditions, which are characterised by higher abundances of deposited food and a higher RPD layer, whereas coarser sediment is typically found in conditions characterised by strong hydrodynamic stress, resulting in removal of the phytodetritus on the sediment surface and better oxygenation. These three variables are known to influence nematode community composition in coral degradation zones (Boucher & Gourbault, 1990; Gourbault & Renaud-Mornant, 1990; Tietjen, 1991; Boucher, 1997; Ndaro & Ólafsson, 1999; Netto *et al.*, 1999). In addition, the indicator genera for fine/medium Matemwe sediment have been recognised as typical taxa for fine, silty sediments (*Marylynnia*, Comesomatidae: Boucher & Gourbault, 1990; Wieser & Hopper, 1967) and oxygen depleted conditions (*Molgolaimus*: Boucher & Gourbault, 1990).

Furthermore, the differences between the communities in the coralline sediment and those on the coral fragments were proven to be very highly significant. Taking into account the TWINSPAN dendrogram, it can be concluded that there is (1) a principal distinction between fine/medium sediment communities and coarse habitat communities and (2) a distinction between coarse sediment communities and coral fragment communities on a secondary level. There are no significant

differences between sediment and gravel samples and coral gravel is also significantly different from coral fragments.

It has been observed that the coral samples cluster more closely together in the MDS biplots than the sediment samples and that average similarity is higher between coral samples whereas average dissimilarity is higher between sediment samples. This could either be explained by (1) differences between sediment samples due to variation in grain size or (2) a lack of structuring effect of the three-dimensional build-up of the coral fragments. The latter explanation has been confirmed in our study despite the considerable differences in surface structure of the finely branched *Pocillopora* compared to *e.g.* the solid surface of *Goniastrea*, the grooved surface of *Fungia* or the complex tubular habitus of *Tubipora*. Govaere *et al.* (1980) and Vanaverbeke *et al.* (2002) have demonstrated that slight differences in grain size, even within the same size class, can fundamentally influence nematode community composition. Moreover, as the majority of nematodes are typically slender, sediment dwelling organisms (Giere, 1993) which live in the interstitia between the sand grains, they are more prone to changes in sediment composition than to changes in the three-dimensional build-up of the large biogenic substratum they are associated with.

The differences between coral associated communities and (coarse) sediment associated communities can be attributed to (1) the more exposed nature of the coral microhabitat, (2) differences in available surface area for epifaunal taxa and (3) the presence of a microbial biofilm and algal cover on the dead coral's surface. The fauna living on the surface and/or between the branches of the coral fragments, which lie relatively unprotected on the bottom and protrude from the sediment, is much more exposed to physical erosion by current activity than the fauna in the sediment. Hydrodynamic stress was indeed considerable on most sampling locations (M.R., pers. obs.). As a result, dead coral fragments are to be considered preferable habitats only for those nematodes that are able to withstand the current's eroding effect, such as the epifaunal Epsilonematidae and Draconematidae. Representatives of these two nematode families are morphologically and ecologically well-adapted to physical disturbance (Willems *et al.*, 1982; Raes & Vanreusel, *in press*). They are able to walk over different types of substratum like inchworms (Stauffer, 1924; Lorenzen, 1973a), attaching themselves to the surface with specialised setae, adhesive tubes and/or caudal glands with specially adapted outlets (Raes *et al.*, *in press*). In accordance with this hypothesis, the genera *Paradraconema* (Draconematidae) and *Epsilonema* (Epsilonematidae) were recognised as indicator genera for coral fragments and both genera are also among the dominant genera on corals. Moreover, short, fat and heavily cuticularised nematodes such as Epsilonematidae are also more able to withstand different types of disturbance (Soetaert *et al.*, 2002; Vanaverbeke *et al.*, 2004).

The shift in dominance from Chromadoridae on corals to Desmodoridae in the sediment is at present not well understood, although the larger body size of desmodorids might be a limiting factor on coral fragments as larger animals tend to be washed away more easily from the coral surface. Trophic segregation might not play a role here as most Chromadoridae and most Desmodoridae are epistratum feeders according to Wieser (1953). The desmodorid *Eubostrichus* (subfamily Stilbonematinae), which is the most pronounced indicator genus for the coralline sediment, is known as a sediment-dweller carrying ectosymbiotic, sulphide-oxidising chemoautotrophic bacteria on its

cuticle in order to survive in the deeper, oxygen depleted layers of the sediment (Ott, 1995; Ott *et al.*, 2005). Another representative of the Stilbonematinae, *Laxus cosmopolitus* Ott, Bauer-Nebelsick & Nvotny, 1995, was dominant in the lagoonal sediment studied by Boucher (1997) and Kotta & Boucher (2001).

Epifaunal diatoms or an organic coating cover calcium carbonate structures such as coral fragments after the death of the living tissue (Suess, 1968). The significantly higher relative abundance of epistratum feeders on coral fragments indicates the importance of these food sources on the coral surface, whereas the significantly lower abundance of non-selective deposit feeders in this microhabitat is attributed to the low amount of detrital material on the exposed coral fragments due to removal and resuspension by hydrodynamic activity. Epigrowth feeders and/or non-selective deposit feeders are generally the dominant trophic groups in subtidal coralline sediments (Alongi, 1986; Gourbault & Renaud-Mornant, 1989; Gourbault & Renaud-Mornant, 1990; Tietjen, 1991; Ólafsson *et al.*, 1995; Boucher, 1997; Ndaro & Ólafsson, 1999).

Next to the differences between communities in both microhabitats, the similarities between these assemblages are also considerable. Our analysis of the number of shared genera has shown that at least 50% of the genera living in the sediment are also found on corals, even between different regions. The five most abundant families are also the same in both microhabitats. As already discussed above, this background community on family and genus level is typical for coarse, subtidal sands. The relatively low number of unique genera in each microhabitat also supports this idea. At least part of the similarity between coral fragments and the coralline sediment can be explained by sediment-trapping between the coral branches. It is clear that the different communities associated with corals and coralline sediments from Kenya and Zanzibar, respectively, are based in particular on different contributions of the genera that are present and not on the presence of unique, very specific genera restricted to a particular region or microhabitat.

3.5.3. How strong is the turnover in taxonomic composition operating at local and regional scales?

Our results suggest that the extent of spatial turnover on a local and regional scale is very much comparable, notwithstanding the separation of Zanzibar Island from the African mainland by the Zanzibar Channel. The only indication that a regional effect may be more important than a local effect lies in the absence of clear-cut groups in Fig. 3B and the absence or low significance of local effects within regions (Table 1). Nevertheless, differences in nematode community structure between regions are relatively small in our survey, given the high number of shared genera between the microhabitats of both regions and the absence or very low number of unique genera for Kenya or Zanzibar, respectively. This could be related to the cosmopolitan nature of nematode genera (see above). Considering the limited structuring effect of localities within regions, the low average similarities between samples within the same group (Zanzibar sediment, Kenya sediment, Zanzibar coral and Kenya coral) are attributed to patchiness.

High turnover on a regional scale has been observed for nematodes by Kotta & Boucher (2001), who found distinct and significantly different communities in different regions, with spatially closer

regions having higher generic affinity. These regions (New Caledonia, Fiji, Moorea, Japan, Great Barrier Reef, Davies Reef, Guadeloupe, Indian Ocean and Red Sea) were however much more geographically distant from each other than the two regions in our study. Turnover on a local (km) scale may have either a negligible (Heip *et al.*, 1979) or a significant (Li *et al.*, 1997; Netto *et al.*, 2003) effect on nematode assemblage structure. Other studies also provide evidence for significant turnover between different areas or functional zones of a reef, *i.e.* on a scale of hundreds of meters to kilometers (Alongi, 1986; Netto *et al.*, 1999; Netto *et al.*, 2003). These differences were however attributed to different environmental conditions in the lagoon, the reef flat, reef crest, outer reef, reef pools and tidal flats. Kotta & Boucher (2001) also found that environmental variables such as grain size, silt content and water depth contributed most to the variability of nematode assemblages on a local scale, whereas variability on a regional scale was mainly determined by the geographical position of the sampling stations. Boucher (1997) and Kotta & Boucher (2001) observed that the extent of turnover between replicates often exceeded variability between regions and concluded that the pattern of nematode distribution is relatively homogeneous over tens of kilometers. This signifies that the variation in community composition within locations, due to small-scale differences in sediment characteristics and environmental conditions, exceeds the variation between localities on this scale.

A remarkable example of the substantial effect of local changes in environmental conditions was provided from one of the sediment samples from Watamu (Kenya). This sample was notably dominated by two species of the genus *Rhabditis*: *Rhabditis* (*Pellioditis*) *marina* Bastian, 1865 and *Rhabditis* (*Crustorhabditis*) *scanica* Allgén, 1949. Both species are known to co-occur on decaying seaweeds deposited on Kenyan beaches and *R. scanica* has also been found in coastal groundwater (Sudhaus, 1974a; Sudhaus, 1974b). The same sample contained three nematodes belonging to the family Cephalobidae Filipjev, 1934 and one individual of *Aphelenchoides* Fischer, 1894. Moreover, a rotylenchulid (Rotylenchulidae) was found on a coral fragment from the same location. All these taxa are known as soil nematodes, freshwater nematodes or plant parasites. The samples in question were however taken 500 m off the coast and at a depth of around 4 m, between coral rocks. As all formalin used for fixation was diluted with seawater filtered over a 32 µm sieve, contamination with freshwater during sample treatment can be excluded. This remarkable finding could however indicate seepage of groundwater at the sampling location. Groundwater outflow has indeed been reported from the Watamu area by Kamermans *et al.* (2002). Moreover, outwelling groundwater can be a major source of nutrients in oligotrophic waters such as these coastal waters, which could also explain the dominance of both *Rhabditis*-species, known as typical opportunists that thrive in enriched environments with high microbial activity (Sudhaus, 1974a; Sudhaus, 1974b; Bongers & Bongers, 1998).

Our survey has shown that variations in the structure of the microhabitat and differences in environmental conditions occur on very small spatial scales and that these small-scale differences are the predominant factors determining the structure of nematode assemblages in coral degradation zones.

3.6. ACKNOWLEDGEMENTS

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Acanthonchus Cobb, 1920
Acanthopharynx Marion, 1870
Actinonema Cobb, 1920
Aegialoalaimus de Man, 1907
aff. *Leptosomatum*
aff. *Nannolaimoides*
Alaimella Cobb, 1920
Ammotheristus Lorenzen, 1977
Anticoma Bastian, 1865
Aphelenchoides Fischer, 1894
Araeolaimoidea sp. 1
Araeolaimus de Man, 1888
Atrochromadora Wieser, 1959
Axonolaimus de Man, 1889
Bathyepsilonema Steiner, 1931
Bolbolaimus Cobb, 1920
Bolbonema Cobb, 1920
Calomicrolaimus Lorenzen, 1976
Calyptronema Marion, 1870
Camacolaimus de Man, 1889
Cephalobidae gen. 1
Ceramonema Cobb, 1920
Cervonema Wieser, 1954
cf. *Aegialoalaimus*
cf. *Rhynchonema*
cf. *Rotylenchulus*
Cheironchus Cobb, 1917
Chitwoodia Gerlach, 1956
Chromadora Bastian, 1865
Chromadorella Filipjev, 1918
Chromadorina Filipjev, 1918
Chromadorita Filipjev, 1922
Chromaspirina Filipjev, 1918
Comesomoides Gourbault, 1980
Cricolaimus Southern, 1914
Croconema Cobb, 1920
Cyartonema Cobb, 1920
Cyatholaimus Bastian, 1865
Daptonema Cobb, 1920
Litinium Cobb, 1920
Longicyatholaimus Micoletzky, 1924
Marylynnia Hopper, 1977
Mesacanthion Filipjev, 1927
Metachromadora Filipjev, 1918
Metacyatholaimus Stekhoven, 1942
Metadesmolaimus Stekhoven, 1935
Metalinhomoeus de Man, 1907
Metepsilonema Steiner, 1927
Metoncholaimus Filipjev, 1918
Microlaimus de Man, 1980
Molgolaimus Ditlevsen, 1921
Monhystera Bastian, 1865
Monhystrella Cobb, 1918
Nannolaimus Cobb, 1920
Neochromadora Micoletzky, 1924
Odontophora Bütschli, 1874
Odontophoroides Boucher & Helléouet, 1977
Omicronema Cobb, 1920
Onchium Cobb, 1920
Oncholaimus Dujardin, 1845
Onyx Cobb, 1891
Oxystomina Filipjev, 1921
Papillonema Verschelde, Muthumbi & Vincx, 1995
Paracanthonchus Micoletzky, 1924
Paracomesoma Home & Murphy, 1972
Paracyatholaimoides Gerlach, 1953
Paracyatholaimus Micoletzky, 1922
Paradraconema Allen & Noffsinger, 1978
Paralinhomoeus de Man, 1907
Paramesacanthion Wieser, 1953
Paramonohystera Steiner, 1916
Pareurystomina Micoletzky, 1930
Parodontophora Timm, 1963
Paroxystomina Micoletzky, 1924
Perepsilonema Lorenzen, 1973
Phanoderma Bastian, 1865
Polkepsilonema Verschelde & Vincx, 1992
Polygastrophora de Man, 1922

Dasynemoides Chitwood, 1936
Desmodora de Man, 1889
Desmodorella Cobb, 1933
Desmoscolex Claparède, 1863
Dichromadora Kreis, 1929
Didelta Cobb, 1920
Diodontolaimus Southern, 1914
Diplopeltis Cobb in Stiles & Hassal, 1905
Diplopeltula Gerlach, 1950
Dolicholaimus de Man, 1888
Dracognomus Allen & Noffsinger, 1978
Dracograllus Allen & Noffsinger, 1978
Draconema Cobb, 1913
Eleutherolaimus Filipjev, 1922
Enoplida gen. n. 1
Enoplida sp. 1
Enoploides Ssaweljev, 1912
Enoplolaimus de Man, 1893
Enoplus Dujardin, 1845
Epacanthion Wieser, 1953
Epsilonema Steiner, 1927
Eubostrichus Greeff, 1869
Euchromadora de Man, 1886
Eurystomina Filipjev, 1921
Gammanema Cobb, 1920
Gomphionchus Platt, 1982
Halalaimus de Man, 1888
Halichoanolaimus de Man, 1886
Innocuonema Inglis, 1969
Laimella Cobb, 1920
Latronema Wieser, 1954
Leptepsilonema Clasing, 1983
Leptolaimoides Vitiello, 1971
Leptolaimus de Man, 1876
Leptonemella Cobb, 1920
Linhomoeus Bastian, 1865
Praeacanthonchus Micoletzky, 1924
Procamacolaimus Gerlach, 1954
Prochromadora Filipjev, 1922
Prochromadorella Micoletzky, 1924
Promonhystera Wieser, 1956
Pseudochromadora Daday, 1899
Pseudonchus Cobb, 1920
Pternepsilonema Verschelde & Vincx, 1992
Ptycholaimellus Cobb, 1920
Rhabditis Dujardin, 1845
Rhinema Cobb, 1920
Rhips Cobb, 1920
Rhynchonema Cobb, 1920
Richtersia Steiner, 1916
Sabatieria Rouville, 1903
Southerniella Allgén, 1932
Spilophorella Filipjev, 1917
Spirinia Gerlach, 1963
Steineria Micoletzky, 1922
Stylotheristus Lorenzen, 1977
Symplocostoma Bastian, 1865
Synonema Cobb, 1920
Syringolaimus de Man, 1888
Terschellingia de Man, 1888
Thalassironus de Man, 1889
Thalassoalaimus de Man, 1893
Theristus Bastian, 1865
Trefusia de man, 1893
Trichotheristus Wieser, 1956
Tricoma Cobb, 1893
Trissonchulus de Man, 1889
Trochamus Boucher & Bovée, 1972
Tubolaimoides Gerlach, 1963
Viscosia de Man, 1890
Zalonema Cobb, 1920

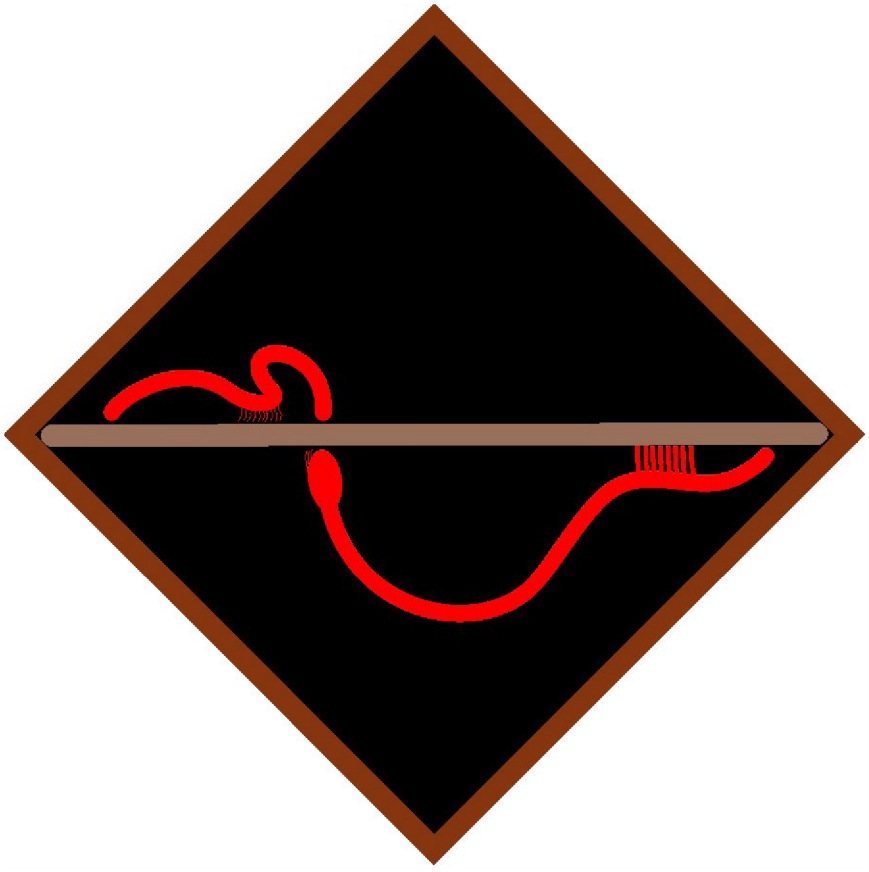
Appendix 1. List of identified genera. Taxonomy after Lorenzen (1994) and original genus descriptions.

Coral fragments				Coralline sediment			
Kenya		Zanzibar		Kenya		Zanzibar	
genus	%	genus	%	genus	%	genus	%
Chromadora	22.93	*Atrochromadora*	14.22	*Perepsilonema*	7.23	*Marylynnia*	14.25
Atrochromadora	8.70	*Spirinia*	9.66	*Neochromadora*	6.73	*Spirinia*	13.14
Euchromadora	8.01	*Epsilonema*	9.62	*Theristus*	5.42	*Chromaspirina*	12.92
Syringolaimus	6.31	*Chromadorina*	8.13	*Eubostrichus*	4.82	*Paracomesoma*	11.02
Acanthonchus	5.20	*Chromadora*	6.97	*Dracograllus*	4.62	*Metadesmolaimus*	6.79
Epsilonema	5.12	*Euchromadora*	6.59	*Chromadora*	3.82	*Bolbonema*	5.01
Chromadorina	3.07	*Acanthonchus*	4.35	*Epsilonema*	3.61	*Odontophora*	3.01
Spilophorella	2.98	*Syringolaimus*	3.61	*Chromaspirina*	3.51	*Richtersia*	2.56
Theristus	2.47	*Spilophorella*	2.53	*Spirinia*	3.41	*Epsilonema*	2.34
Paradraconema	1.88	*Paradraconema*	2.24	*Euchromadora*	3.21	*Eubostrichus*	2.34
Paracanthonchus	1.53	*Theristus*	2.24	*Metadesmolaimus*	2.91	*Chromadorita*	1.89
Prochromadorella	1.53	*Calomicrolaimus*	2.16	*Rhynchonema*	2.91	*Calomicrolaimus*	1.67
Zalonema	1.02	*Microlaimus*	1.91	*Metachromadora*	2.51	*Enoplolaimus*	1.45
Acanthopharynx	0.94	*Chromaspirina*	1.74	*Dracognomus*	2.31	*Molgolaimus*	1.34
Desmodora	0.85	*Desmoscolex*	1.45	*Atrochromadora*	2.21	*Omicronema*	1.34
Desmoscolex	0.85	*Prochromadorella*	1.41	*Metepsilonema*	2.11	*Metachromadora*	1.11
Procamacolaimus	0.85	*Tricoma*	1.37	*Microlaimus*	1.91	*Metepsilonema*	1.00
Ptycholaimellus	0.85	*Daptonema*	1.29	*Viscosia*	1.91	*Paramonhystera*	1.00
Metachromadora	0.77	*Actinonema*	1.24	*Acanthonchus*	1.71	*Stylotheristus*	1.00
Monhystera	0.77	*Paracanthonchus*	1.20	*Prochromadorella*	1.71	*Chitwoodia*	0.89

Appendix 2. Relative abundances of the 20 most abundant nematode genera associated with coral fragments and coralline sediment in both regions.

CHAPTER 4

WALKING WITH WORMS:
CORAL-ASSOCIATED EPIFAUNAL NEMATODES



Paper *submitted*

Raes, M., Decraemer, W., Vanreusel, A.

Walking with worms: coral-associated epifaunal nematodes

Journal of Biogeography

4.1. ABSTRACT

The community structure, habitat preferences, biogeography and biodiversity of Epsilonematidae and Draconematidae in cold-water and tropical coral degradation zones are discussed. These typically epifaunal nematodes were collected from the Porcupine Seabight (North-East Atlantic; continental slope) and from a north-to-south transect along the coast of Kenya (Indian Ocean; shallow lagoon). Communities from different microhabitat types were compared: coral fragments, sponge skeletons and sediment in the Porcupine Seabight, and coral fragments and coral gravel in Kenya. Coral fragments were recognised as more favourable substrata for typically epifaunal nematodes than the other microhabitats. They also housed a community distinctly and significantly different from that of these other microhabitats. Species-specific habitat preferences were explained by fine-tuned morphological adaptations. The biogeography of Epsilonematidae and Draconematidae and the putative cosmopolitanism of some specific taxa are discussed. Our results indicate that cosmopolitan species could very well be cryptic species and this explanation for the existence of morphologically identical nematodes in geographically distant areas was weighed up against other plausible explanations. Coral degradation zones were recognised as an important source for new species from both typically epifaunal nematode families. Coral fragments were characterised by the highest diversity and a lower average similarity. Low average similarity was reflected in a relatively high turnover between coral samples from different locations. Turnover between gravel samples from different locations was generally low, although values of β_{sim} were not significantly lower compared to turnover between microhabitats within each location and between coral samples from different locations. Additive partitioning showed that α-diversity was the principal contributor to total diversity when working with abundance data. The contribution of β-diversity related to the turnover between locations was high for presence-absence data but was considerably reduced when adding abundance information. This indicated that the addition of sampling locations contributed to the total number of species although the added species were generally rare.

Key words: Epsilonematidae, Draconematidae, habitat preferences, biogeography, biodiversity, North-East Atlantic, East African coast

4.2. INTRODUCTION

Marine, free-living nematodes are typically known as fine and slender worms which slide through the interstitia of the sediment with undulations of the body. However, aberrant body shapes do occur in a number of families, *e.g.* the short, stout Desmoscolecidae and the epsilon- or s-shaped Epsilonematidae and Draconematidae, which usually have pronounced enlargements at the level of the pharynx and posterior body region. Nematodes belonging to either of these two latter families are also characterised by the presence of unique locomotory structures: Epsilonematidae have so-called ambulatory setae on the ventral side of their posterior body and Draconematidae have both cephalic and posterior adhesion tubes. Together with the caudal glands, these structures enable the

nematodes to attach themselves to a large substratum and/or crawl over its surface in a fashion which is most comparable to that of a geometrid caterpillar (Stauffer, 1924; Lorenzen, 1973a). As a result of these adaptations, Epsilonematidae and Draconematidae are almost exclusively found in coarse sand and on larger substrata such as seagrass leaves and coral fragments. Hereafter, they will be referred to as typically epifaunal nematodes.

The species within both families are characterised by a whole spectrum of different body shapes and sizes, as well as differences in other morphological features such as cuticular ornamentation and cuticular appendages (*e.g.* Verschelde & Vincx, 1994).

Two recent studies on the ecology of the nematofauna in cold-water coral (Porcupine Seabight; Raes & Vanreusel, *in press*) and tropical coral (Kenyan coast; Raes *et al.*, *submitted* b) degradation zones have indicated that Epsilonematidae and Draconematidae have a pronounced preference for dead coral fragments. Comparisons between coral fragments and underlying sediment in both environments have revealed that the presence of these typically epifaunal nematodes on coral fragments is very important in explaining the differences between the nematode assemblages in both microhabitats. Furthermore, these nematodes make up a considerable proportion of the total nematode community on coral fragments. Consequently, a substantial number of epsilonematid and draconematid species has been collected from these environments.

The fact that Epsilonematidae and Draconematidae have been found abundantly in a deep water and shallow coral-associated environment has enabled a comparison between the communities from both extremely different environments. The study at hand focuses on the habitat preferences, biogeography and diversity of the typically epifaunal nematode communities in coral degradation zones. This means that in this study only the subset of the total nematode community consisting of Epsilonematidae and Draconematidae is considered, which can be justified given the relatively high number of specimens and species found in both environments. Such a selection enables us to evaluate the fine-tuned habitat preferences of species within these two families. Our study also provides new data on the biogeography of marine, free-living nematodes.

A final part focuses on biodiversity. First, the diversity of communities associated with different microhabitats will be compared. Meiofaunal samples from coral fragments and coral gravel were collected from 7 locations along a north-to-south transect on the south coast of Kenya. This provided us with the opportunity to compare the turnover between the typically epifaunal nematode communities from different microhabitat types and between the communities form different locations. The contribution of both α-diversity (sample diversity) and β-diversity (turnover) to the total (γ) diversity (additive partitioning) will also be discussed.

4.3. MATERIALS AND METHODS

4.3.1. SAMPLING SITES, MICROHABITATS AND LABORATORY ANALYSES

Biological samples were collected from a cold-water coral degradation zone in the Porcupine Seabight and a tropical coral degradation zone along the coast of Kenya (Fig. 1).

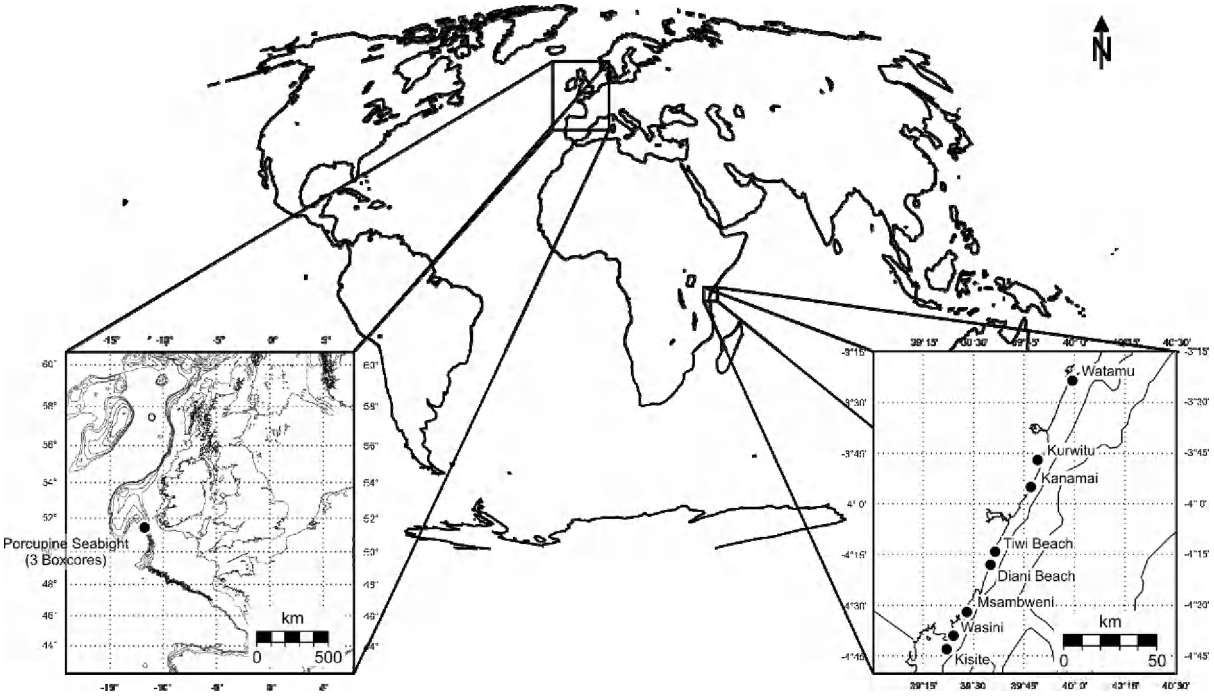


Fig. 1. Geographical position of the sampling locations, with details of the two regions of interest.

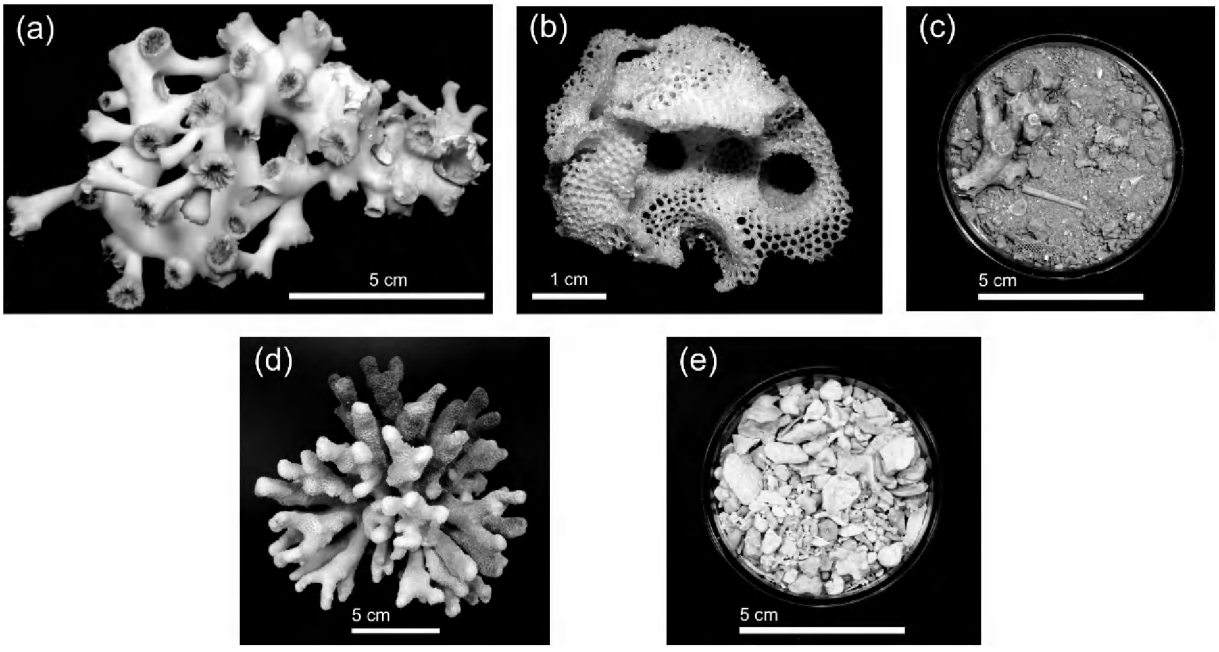


Fig. 2. Microhabitat types. Porcupine Seabight: (a) dead fragment of the coral *Lophelia pertusa*; (b) skeleton of the glass sponge *Aphrocallistes bocagei*; (c) sediment. Kenya: (d) dead coral fragment (*i.c. Stylophora*); (e) coral gravel.

	Area	Latitude	Longitude	Depth
Box IV 2000	Porcupine Seabight	51° 24' 48,2" N	11° 45' 55,4" W	1005 m
Box V 2000	Porcupine Seabight	51° 24' 49,4" N	11° 45' 55,9" W	1000 m
Box IV 2001	Porcupine Seabight	51° 25' 7,7" N	11° 46' 9,3" W	972 m
Watamu	Kenya	3° 23' 32" S	39° 59' 21" E	2-3 m
Kurwitu	Kenya	3° 47' S	39° 49' E	1 m
Kanamai	Kenya	3° 55' S	39° 47' E	0.5 m
Tiwi Beach	Kenya	4° 14' 10" S	39° 36' 25" E	1 m
Diani Beach	Kenya	4° 18' S	39° 35' E	0.3-2 m
Msambweni	Kenya	4° 32' S	3° 28' E	2-3 m
Wasini	Kenya	4° 39' S	39° 24' E	3-4 m
Kisite	Kenya	4° 43' S	39° 22' E	3-6 m

Table 1. coordinates and depth of the sampling locations.

The Porcupine Seabight is a large embayment of the European continental slope, located southwest of Ireland (North-East Atlantic). Material was obtained by means of NIOZ box corers (cylindrical; ø 32 cm) on the 17th of June 2000 (2 boxcores: Box IV 2000 and Box V 2000) and the 7th of May 2001 (1 boxcore: Box IV 2001) (Table 1). Distance between Box IV 2000 and Box IV 2001 is 659 m. Sampling depth ranges between 972 and 1005 m. A detailed description of the sampling location and governing environmental conditions is given in Raes & Vanreusel (2005). The surface of the sediment in each boxcore was partly or entirely covered by several fragments of dead corals (*Lophelia pertusa* (Linnaeus, 1758)) and dead sponge skeletons (*Aphrocallistes bocagei* Schultze, 1886). Recolonisation of the debris by small colonies of living coral was observed, although only to a small extent. Coral and sponge fragments were collected separately. After removal of these structures three cores (10 cm^2) were pushed into the sediment of each box core. This sediment consisted of poorly sorted, fine to medium sand (median 194.9 µm) with a small fine silt fraction, a high amount of globigerine forams and littered with small sponge and coral fragments, mollusc-shells and echinoid radiolas (Fig. 2c).

Eight sites were selected on the Kenyan coast, from Watamu in the north to Kisite in the south (Table 1). Distance between Watamu and Kisite is 162.5 km. Sampling depth varied between 0.3 and 6 m. At each location, large amounts of coral gravel were scooped out with a small shovel and coral fragments were removed by hand, either during snorkelling or skin diving. Material was carefully collected in large plastic bags while underwater. Coral gravel is characterised by the presence of small pieces of coral which can still be recognised (in contrast to coralline sediment) (Fig. 2e). The coral fragments are compact or branched, fresh (but always dead) or eroded. Different morphotypes were distinguished, some of which could be identified up to genus level: *Fungia*, *Stylophora*, *Lobophyllia*, *Porites*, *Pocillopora*, *Tubipora*. These morphotypes differ in robustness, branching complexity and surface microstructure.

All material was fixed with 4% buffered formalin.

Each coral and sponge fragment was rinsed thoroughly with filtered seawater over sieves with a mesh size of 1 mm and 32 µm, in order to separate macrofauna and meiofauna. The large amounts of coral gravel were decanted with filtered seawater over the same sieves prior to centrifugation. Meiofauna was extracted from the sediment or residue by density gradient centrifugation, using Ludox (a colloidal silica polymer; specific gravity 1.18) as a flotation medium (Heip *et al.*, 1985; Vincx, 1996). Meiofauna was stained with Rose Bengal. All Epsilonematidae and Draconematidae were picked out

from each sample, up to a maximum of 1000 individuals, mounted onto slides using the formalin-ethanol-glycerol technique of Seinhorst (1959) and Vincx (1996), and identified up to species level using original descriptions.

4.3.2. STATISTICAL ANALYSES

Only samples with more than 3 individuals were selected for analysis. For the Kenya samples, only adults were considered for analysis, due to the impossibility of identifying the juveniles of some of the most abundant species. Bray-Curtis (dis)similarities between the samples were calculated using the PRIMER5 software (Plymouth Marine Laboratory; Clarke & Gorley, 1993). All data were standardised (*i.e.* relative data were used) and log (x+1) transformed prior to the analysis. Samples were grouped together using the factors 'Microhabitat' (*i.e.* either coral fragments, sponge fragments and sediment (Porcupine Seabight) or coral fragments and coral gravel (Kenya)) and 'Fine-tuned microhabitat' (*i.e.* with indication of different coral morphotypes; only for Kenya samples). The obtained similarity matrix was used to produce a non-metric multidimensional scaling two-dimensional plot (MDS). The stress value gives a measure for goodness-of-fit of the MDS ordination: a low stress value (<0.2) indicates a good ordination with no real prospect for a misleading interpretation (Clarke, 1993). A cluster analysis (furthest neighbour) was carried out to confirm the MDS results. One-way Analysis of Similarities (ANOSIM) was carried out to test for significant differences in the community structure between the different groups, Similarity of Percentages (SIMPER) to verify which genera were responsible for these differences.

Parametric (ANOVA) and non-parametric (Kruskal-Wallis ANOVA by ranks) analysis of variance was performed using the STATISTICA6 software. Bartlett's and Cochran's test were used to verify the homogeneity of variances prior to the analysis.

Rarefaction curves were constructed from values of the Expected number of Species ES (n) (Hurlbert, 1971). The additive partitioning of species diversity along the Kenyan coast into measures of α- and β-diversity (Veech *et al.* 2002; Crist *et al.*, 2003) was conducted with the PARTITION software. A ternary plot was constructed to measure and compare turnover between microhabitats within locations and between locations within microhabitats, as recommended by Koleff *et al.* (2003). The values of a', b' and c' (*i.e.* the percentage of shared species a, of species exclusively present in the neighbouring sample b and of species exclusively present in the focal sample c) are plotted against a background of β_{sim}-values (Lennon *et al.*, 2001).

4.4. RESULTS

A total of 811 epsilonematids and draconematids was collected from the Porcupine Seabight, while in Kenya 4293 specimens were assembled. In the Porcupine Seabight 17 species were found (12 Epsilonematidae, 5 Draconematidae: Appendix 1), belonging to 8 genera (5 Epsilonematidae, 3 Draconematidae). At the time of sampling, 70.6% of these species was new to science. Since then (2001), 5 of these species have however been described: 4 species were described from our sampling location (Raes *et al.*, 2003; Raes *et al.*, *in press*) and one was described from Korea (Rho & Kim

2004). As a result, only 41.2% of the species is undescribed at present. In Kenya, 58 species (39 Epsilonematidae, 19 Draconematidae: Appendix 2), belonging to 12 genera (8 Epsilonematidae, 4 Draconematidae) were identified; 60% of the species were new to science.

Three species were found in both sampling locations: *Dracograllus demani* Allen & Noffsinger, 1978, *Epsilonema margaritatum* Decraemer & Gourbault, 1987 and *Triepsilonema tripapillata* Decraemer, 1982. A list of all 30 currently described species encountered in our study area, and their known distribution, is provided in Table 2. These species have been found in a multitude of microhabitats such as fine, medium and coarse sand (either coralline, shelly or otherwise), coralline, green and other algae, coral fragments, sponges, sponge spicule mats, bryozoan debris, polychaete tubes, diverse macro-epifauna, crabs and bottom debris. Some of the species we found in the Porcupine Seabight have also been recorded in the North Sea, on the Iberian Margin, on the Great Meteor Seamount, in the Mediterranean Sea, North Pacific Ocean, South Pacific Ocean, Indian Ocean, Caribbean and in Antarctica. The Porcupine Seabight has most of its Epsilonematidae and Draconematidae in common with the Iberian Margin (3 species), Kenya (3 species) and Papua New Guinea coasts (3 species). There is considerable variation on a bathymetric scale, as some of the species (*D. demani*, *E. margaritatum* and *B. spongiosum* Clasing, 1986) occur on sandy beaches as well as in the deep sea. Analogous observations were made for the species we found along the Kenyan coast. They were already known from other geographical areas such as Indonesia, The Philippines, the North Pacific Ocean, South Pacific Ocean, North Atlantic Ocean, South Atlantic Ocean, Caribbean, Gulf of Mexico, Mediterranean and Red Sea. Seventy-four percent of these species also live in littoral zones. The community was mainly composed of species that are known to live along the Kenyan coast (8), but also of species from Laing Island, Papua New Guinea (9) and from Guadeloupe (4).

4.4.1. PORCUPINE SEABIGHT

Both the cluster dendrogram (Fig. 3a) and MDS (Fig. 3b) showed that the coral samples were relatively well separated from the other microhabitats. There were only three 'mismatched' samples (one sediment sample and two sponge samples in the coral fragments cluster) in the cluster dendrogram. This clear-cut distinction was confirmed by the significant dissimilarities between coral fragments and sponge fragments (p = 0.001) and between coral fragments and the sediment (p = 0.003). There were no significant differences between replicates or sampling years. Average dissimilarities between coral fragments and sponge skeletons on the one hand and between coral fragments and sediment on the other hand were low (around 50%). *Epsilonema multispiralum* Raes, Vanreusel & Decraemer, 2003, *Cygnonema belgicae* sp. n. and *Triepsilonema tripapillata* Decraemer, 1982 appeared to be the most important species separating the communities on coral fragments from those of the other microhabitats, according to the SIMPER analysis (Table 3). *Bathyepsilonema lopheliae* Raes, Vanreusel & Decraemer, 2003 explained most of the separation of the sponge communities and *Glochinema trispinatum* Raes, Vanreusel & Decraemer, 2003 was very important in the sponge and sediment communities as opposed to the coral-inhabiting communities. This last species appeared to be abundant in all three habitats, although it was only dominant on sponges and

in the sediment (Table 4). *E. multispiralum* and *T. tripapillata* were the dominant species on coral fragments. Coral fragments yielded a significantly higher Draconematidae/Epsilonematidae ratio (0.1-0.8) when compared to the other two microhabitats (p = 0.0072).

Rarefaction curves indicated that the communities on coral fragments were more diverse than those on sponge skeletons and in the sediment (Fig. 4a).

4.4.2. KENYA

The number of individuals per sample was higher in the tropical coral degradation zone in Kenya than in the cold-water coral reef samples, although this resulted in considerable differences in sample size: between 7-565 individuals (without juveniles). There was a very clear and significant (p = 0.001) separation of the coral fragment samples and the coral gravel samples, both in the cluster dendrogram (Fig. 3c) and in the MDS biplot (Fig. 3d). Average similarity between gravel samples (46.8) was higher than between coral samples (40.2). The average dissimilarity between both microhabitats was relatively high and mainly attributed to *Epsilonema parvospina* Decraemer, 1982 and *Paradraconema* sp. 4 sp. n., two species with clearly higher relative abundances on coral fragments, and to *Perepsilonema papulosum* Lorenzen, 1973, *Dracognomus annae* Verschelde & Vincx, 1993 and *Dracognomus* sp. 2 sp. n., which were more abundant in the coral gravel (Table 3). These results were confirmed by the dominance of these taxa in the respective microhabitats (Table 4). Within the gravel samples, no differences between sampling locations were observed. Coral fragment samples from the neighbouring locations Diani Beach and Tiwi Beach were however significantly different from each other. There was no obvious effect of coral morphotypes on community structure as evidenced by an MDS biplot, although important differences were found between the communities on eroded rubble and on *Porites* (p = 0.032), and between *Porites* and the finely branched *Pocillopora* (low number of actual permutations; R = 0.764). We found no significant difference in Draconematidae/Epsilonematidae ratio between coral fragments and coral gravel.

Rarefaction curves indicated a higher diversity on the coral fragments although the values for ES (50) in coral samples were not significantly higher than those in coral gravel (p = 0.92) (Fig. 4b).

Total species richness of the tropical coral degradation zone in Kenya (γ) was mainly determined by local diversity (α; 38.2%) and the turnover between localities (44.5%). The contribution of the α-component to total diversity in terms of the Shannon-Wiener index was very high (71.2%), while β-diversity contributed little (Fig. 5).

Although β_{sim} values of turnover between microhabitats on the one hand and between locations on the other hand (pairwise comparison of neighbouring locations from north to south; for both microhabitats) were not significantly different (p = 0.15), it can be observed on the ternary plot (Fig. 6) that turnover between microhabitats and between coral samples from different localities was higher than turnover between locations for gravel samples. The extent of turnover at different levels was however highly variable.

	Species	Localities	Reference	Habitat	Microhabitat
SHARED SPECIES	*Dracograllus demani* Allen & Noffsinger, 1978	Marseille (France)	Allen and Noffsinger (1978)	sublittoral	
		Laing Island; Duangi Reef (Papua New Guinea)	Decraemer (1988)	reef flat, littoral, sublittoral	polychaete tubes; coralline algae; green algae; coarse coralline sand; dead coral fragments
		Watamu (Kenya)	Verschelde and Vincx (1993a)	littoral	coarse coralline sand
		Porcupine Seabight	new data	cold-water coral degradation zone (continental margin)	sponge skeletons
		Watamu; Kurwitu; Kanamai; Tiwi beach; Diani Beach; Msambweni; Wasini; Kisite Island (Kenya)	new data	tropical coral degradation zone (sublittoral)	coral gravel; coral fragments
	Epsilonema margantatum Decraemer & Gourbault, 1987	Guadeloupe; Jamaica (Caribbean)	Decraemer and Gourbault (1987)	littoral/lagoon	medium coralline sand
		Papua New Guinea	Decraemer *et al.* (2001)	littoral/lagoon	coarse sand
		the English Channel	Decraemer *et al.* (2001)	sublittoral	coarse sand
		Marseille (France)	Decraemer *et al.* (2001)	sublittoral	coarse sand
		Porcupine Seabight	Raes *et al.* (2003)	cold-water coral degradation zone (continental margin)	sponge skeletons
		Watamu; Kurwitu; Kanamai; Tiwi beach; Diani Beach; Msambweni; Kisite Island (Kenya)	new data	tropical coral degradation zone (sublittoral)	coral gravel; coral fragments
	Thepsilonema tripapillata Decraemer, 1982	Laing Island (Papua New Guinea)	Decraemer (1982)	lagoon	associated with *Halimeda*
		Porcupine Seabight	Raes *et al.* (*in press*)	cold-water coral degradation zone	fine to medium sand; coral fragments; sponge skeletons
		Kurwitu (Kenya)	Raes *et al.* (*in press*)	tropical coral degradation zone (sublittoral)	coral fragments
PORCUPINE SEABIGHT	*Akanthepsilonema sinecornibus* Raes, Decraemer & Vanreusel, 2005	Porcupine Seabight	Raes *et al.* (*in press*)	cold-water coral degradation zone (continental margin)	fine to medium sand; coral fragments
	Bathyepsilonema lophellae Raes, Vanreusel & Decraemer, 2003	Porcupine Seabight	Raes *et al.* (2003)	cold-water coral degradation zone (continental margin)	fine to medium sand; coral fragments; sponge skeletons
		off San Ciprian (Iberian Margin)	new data	cold-water coral degradation zone (continental margin)	coral fragments
	Bathyepsilonema spongiosum Clasing, 1986	Quellon Viejo; Talcan Island; Huelmo (Chile)	Clasing (1986)	littoral	coarse sand
		Porcupine Seabight	Raes *et al.* (2003)	cold-water coral degradation zone (continental margin)	coral fragments; sponge skeletons
	Epsilonema oxynoides (Metschnikoff, 1867) Gerlach & Riemann, 1931	Salerno; Naples; Ischia (Italy); Rovinj (Croatia)	several authors in Decraemer *et al.* (2001)	sublittoral	algae
		Kiel Bay (Germany); Bergen; Barents Sea (Norway)	several authors in Decraemer *et al.* (2001)	sublittoral	algae
		Porcupine Seabight	Raes *et al.* (2003)	cold-water coral degradation zone (continental margin)	coral fragments
	Epsilonema multispiralum Raes, Vanreusel & Decraemer, 2003	Porcupine Seabight	Raes *et al.* (2003)	cold-water coral degradation zone (continental margin)	fine to medium sand; coral fragments; sponge skeletons
		off San Ciprian (Iberian Margin)	new data	cold-water coral degradation zone (continental margin)	coral fragments
	Glochinema trispinatum Raes, Vanreusel & Decraemer, 2003	Porcupine Seabight	Raes *et al.* (2003)	cold-water coral degradation zone (continental margin)	fine to medium sand; coral fragments; sponge skeletons
		Kapp Norvegia (Antarctica)	new data	bryozoan and sponge spicule mats	sponges ; sponge spicules, bryozoan debris ; diverse macro-epifauna
		off San Ciprian (Iberian Margin)	new data	cold-water coral degradation zone (continental margin)	coral fragments
	Tenuidraconema koreensis Rho & Kim, 2004	Namae (South Korea)	Rho and Kim (2004)	shelf (150-250 m)	coarse sediment; crabs; sponges; bryozoans
		Porcupine Seabight	Raes *et al.* (*submitted a*)	cold-water coral degradation zone (continental margin)	fine to medium sand; coral fragments; sponge skeletons
		Great Meteor Seamount	G. Gad (pers. comm.)	Seamount	biogenic coarse sand (with coral fragments)

Table 2. Distribution of currently described species found in the study at hand.

	Species	Localities	Reference	Habitat	Microhabitat
KENYA	*Apenodraconema chlidosis* Allen & Noffsinger, 1978	Tahiti (Society Islands)	Allen and Noffsinger (1978)	sublittoral	red coralline algae; algae
		Fangataufa Atoll (Polynesia)	Gourbault and Decraemer (1992)	sublittoral	coarse sand
		Watamu; Tiwi beach, Diani Beach (Kenya)	new data	tropical coral degradation zone (sublittoral)	coral gravel; coral fragments
	Bathyepsilonema compactum Clasing, 1984	Galapagos Islands	Clasing (1984)	littoral	medium to coarse sand
		Watamu; Kurwitu; Kanamai; Tiwi beach; Diani Beach; Msambweni; Kisite Island (Kenya)	new data	tropical coral degradation zone (sublittoral)	coral gravel; coral fragments
	Dracognomus annae Verschelde & Vincx, 1993	Gazi (Kenya)	Verschelde and Vincx (1993a)	mangrove	sediment
		Watamu; Kurwitu; Tiwi beach; Diani Beach; Msambweni (Kenya)	new data	tropical coral degradation zone (sublittoral)	coral gravel; coral fragments
	Dracognomus dermatoglyphus Verschelde & Vincx, 1993	Gazi (Kenya)	Verschelde and Vincx (1993a)	mangrove	sediment
		Watamu; Kisite Island (Kenya)	new data	tropical coral degradation zone (sublittoral)	coral gravel
	Dracograllus eira (Inglis, 1968) Allen & Noffsinger, 1978	St. Vincent's bay (New Caledonia)	Inglis (1968)	littoral	
		Laing Island; Talia Point (Papua New Guinea)	Decraemer (1988)	reef flat; littoral; sublittoral	polychaete tubes; coarse coral sand; dead coral fragments
		Watamu (Kenya)	Verschelde and Vincx (1993a)	littoral	coarse coralline sand
		Watamu; Kurwitu; Kanamai; Tiwi beach; Diani Beach; Msambweni (Kenya)	new data	tropical coral degradation zone (sublittoral)	coral gravel; coral fragments
	Dracograllus laingensis Decraemer, 1988	Laing Island (Papua New Guinea)	Decraemer (1988)	reef flat; littoral; sublittoral	polychaete tubes; coarse coral sand; dead coral fragments
		Watamu; Kurwitu; Kanamai; Tiwi beach; Msambweni; Kisite Island (Kenya)	new data	tropical coral degradation zone (sublittoral)	coral gravel; coral fragments
	Dracograllus papuensis Decraemer, 1988	Laing Island (Papua New Guinea)	Decraemer (1988)	reef flat; sublittoral	polychaete tubes; green algae; dead coral fragments
		Kurwitu; Kanamai; Tiwi beach; Msambweni; Wasini; Kisite Island (Kenya)	new data	tropical coral degradation zone (sublittoral)	coral gravel; coral fragments
	Draconema clapareidi (Metschnikoff, 1867) Filipjev, 1918	Salerno (Italy)	Metschnikoff (1867)	sublittoral	
		Marseille (France)	Allen and Noffsinger (1978)		
		Naples (Italy)	Schepotieff (1907, 1908)		
		English Channel	Allen and Noffsinger (1978)		
		Roscoff (France)	Giard and Barrois (1874)		
		Clare Island (Ireland)	Southern (1914)	sublittoral	shelly sand
		Norway	Schepotieff (1907, 1908)		
		Menorca (Spain)	Palacin (1985); Masalles (1985)	littoral	algae
		Watamu; Tiwi beach; Msambweni; Kisite Island (Kenya)	new data	tropical coral degradation zone (sublittoral)	coral fragments
	Draconema haswelli (Irwin-Smith, 1918) Kreis, 1938	Port Jackson (Australia)	Irwin-Smith (1918)	sublittoral	associated with bottom debris
		Broken Bay (Australia)	Allen and Noffsinger (1978)		
		Red Sea	Allen and Noffsinger (1978)		
		Indonesia	Kreis (1938)		
		Watamu; Kurwitu; Kanamai; Tiwi beach; Diani Beach; Msambweni; Kisite Island (Kenya)	new data	tropical coral degradation zone (sublittoral)	coral gravel; coral fragments
	Epsilonema parvospina Decraemer, 1982	Laing Island (Papua New Guinea)	Decraemer (1982)	lagoon; reef flat	associated with *Halimeda*
		Watamu (Kenya)	Verschelde and Vincx (1994)	littoral	coarse coralline sand
		Watamu; Kurwitu; Kanamai; Tiwi beach; Diani Beach; Msambweni; Wasini; Kisite Island (Kenya)	new data	tropical coral degradation zone (sublittoral)	coral gravel; coral fragments

Table 2. Distribution of currently described species found in the study at hand (continued).

	Species	Localities	Reference	Habitat	Microhabitat
KENYA	*Leptepsilonema richardi* Verschelde & Vincx, 1992	Watamu (Kenya)	Verschelde and Vincx (1992)	littoral	coarse coralline sand
		Watamu; Kurwitu; Kanamai; Tiwi beach; Diani Beach; Msambweni (Kenya)	new data	tropical coral degradation zone (sublittoral)	coral gravel; coral fragments
	Metepsilonema chilotum Clasing, 1986	Quelon Viejo; Quinchao Island (Chile)	Clasing (1986)	littoral	coarse sand
		Watamu; Kurwitu; Kanamai (Kenya)	new data	tropical coral degradation zone (sublittoral)	coral gravel
	Metepsilonema hardyi Decraemer & Gourbault, 1992	Guadeloupe; La Désirade (Caribbean)	Decraemer and Gourbault (1992b)	littoral	medium coralline sand
		Tiwi beach; Diani Beach; Msambweni (Kenya)	new data	tropical coral degradation zone (sublittoral)	coral gravel
	Metepsilonema striatulum Decraemer & Gourbault, 1990	Guadeloupe; Iles des Saintes; La Désirade (Caribbean)	Decraemer and Gourbault (1990a)	littoral	medium to coarse coralline sand
		Kanamai; Tiwi beach; Diani Beach; Msambweni; Kisite Island (Kenya)	new data	tropical coral degradation zone (sublittoral)	coral gravel; coral fragments
	Paradraconema floridense Allen & Noffsinger, 1978	Coral Key; Bear Cut (Florida, USA)	Allen and Noffsinger (1978)	sublittoral	associated with *Halimeda*
		Port Jackson (Australia)	Allen and Noffsinger (1978)		
		Solano (Colombia)	Allen and Noffsinger (1978)		
		Ibusuki; Shimoda (Japan)	Allen and Noffsinger (1978)		
		Galeta Beach; Panama City (Panama)	Allen and Noffsinger (1978)		
		Little Santa Cruz Island; Malabungkay; Zamboanga (The Philippines)	Allen and Noffsinger (1978)		
		Samoa ; Pago pago	Allen and Noffsinger (1978)		
		Tiarei ; Tahiti ; Uturoa ; Raiatea (Society Islands)	Allen and Noffsinger (1978)		
		Laing Island (Papua New Guinea)	Decraemer (1982)	lagoon, reef flat	associated with *Halimeda*, coralline sand, sand
		Watamu; Kurwitu; Diani Beach; Kisite Island (Kenya)	new data	tropical coral degradation zone (sublittoral)	coral fragments
	Perepsilonema kellyae Gourbault & Decraemer, 1988	Guadeloupe; La Désirade (Caribbean)	Gourbault and Decraemer (1988)	littoral	fine to medium coralline sand
		Gazi (Kenya)	Verschelde and Vincx (1991)	littoral	
		Thio; Amédée (New Caledonia)	Decraemer *et al.* (2001)	littoral	fine to medium sand
		Djakarta; Bali (Indonesia)	Decraemer *et al.* (2001)	littoral	coarse sand
		Recife (Brasil)	Decraemer *et al.* (2001)	sublittoral	coarse sand
		Watamu; Kanamai (Kenya)	new data	tropical coral degradation zone (sublittoral)	coral gravel; coral fragments
	Perepsilonema moineaui Gourbault & Decraemer, 1992	Moorea Island; Fangataufa Atoll (Polynesia)	Gourbault and Decraemer (1992)	littoral, sublittoral (coral reef)	coarse sand
		Watamu; Kurwitu; Kanamai; Tiwi beach; Diani Beach; Msambweni (Kenya)	new data	tropical coral degradation zone (sublittoral)	coral gravel; coral fragments
	Perepsilonema papulosum Lorenzen, 1973	Puerto Montt (Chile)	Lorenzen (1973)	littoral	coarse sand
		Galapagos Islands	Clasing (1984)	littoral	medium to very coarse sand
		Kouaré (New Caledonia)	Decraemer *et al.* (2001)	littoral	fine to medium sand
		One Tree Island (Australia)	Decraemer *et al.* (2001)	littoral	
		Bora Bay (Japan)	Decraemer *et al.* (2001)	lagoon	fine to medium sand
		Watamu; Kurwitu; Kanamai; Tiwi beach; Diani Beach; Msambweni; Kisite Island (Kenya)	new data	tropical coral degradation zone (sublittoral)	coral gravel; coral fragments
		Laing Island (Papua New Guinea)	Decraemer (1982)	littoral	between *Halimeda*
	Polkepsilonema mombassae Verschelde & Vincx, 1992	Watamu (Kenya)	Verschelde & Vincx (1993b)	littoral	coarse coralline sand
		Diani Beach; Msambweni (Kenya)	new data	tropical coral degradation zone (sublittoral)	coral gravel; coral fragments
	Pternepsilonema servaesae Verschelde & Vincx, 1992	Watamu (Kenya)	Verschelde & Vincx (1993b)	littoral	coarse coralline sand
		Watamu; Kurwitu; Kanamai; Tiwi beach; Diani Beach (Kenya)	new data	tropical coral degradation zone (sublittoral)	coral gravel; coral fragments

Table 2. Distribution of currently described species found in the study at hand (continued).

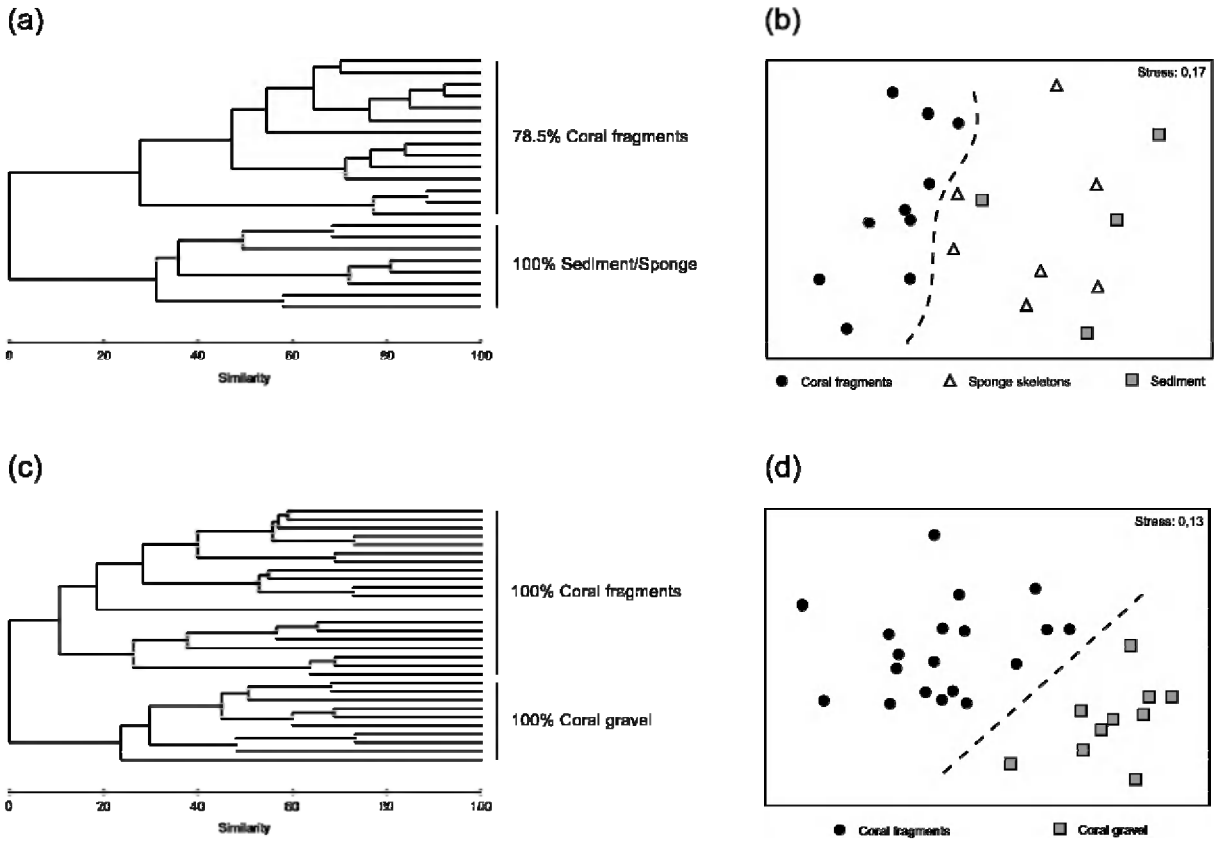


Fig. 3. Multivariate analyses. (a) cluster dendrogram of the Porcupine Seabight samples; (b) non-metric multidimensional scaling biplot of the Porcupine Seabight samples; (c) cluster dendrogram of the Kenya samples; (d) non-metric multidimensional scaling biplot of the Kenya samples. The percentage of equally classified samples in each cluster of the dendrograms is indicated.

Porcupine Seabight

	Coral fragments	Sponge fragments
	Average dissimilarity: 52.21	
Epsilonema multispiralum Raes, Vanreusel & Decraemer, 2003	13.58%	
Bathyepsilonema lopheliae Raes, Vanreusel & Decraemer, 2003		12.16%
Glochinema trispinatum Raes, Vanreusel & Decraemer, 2003		11.66%
Cygnonema belgicae sp. n.	9.81%	
Triepsilonema tripapillata Decraemer, 1982	9.45%	

	Coral fragments	Sediment
	Average dissimilarity: 56.94	
Epsilonema multispiralum Raes, Vanreusel & Decraemer, 2003	17.33%	
Glochinema trispinatum Raes, Vanreusel & Decraemer, 2003		15.58%
Cygnonema belgicae sp. n.	12.24%	
Triepsilonema tripapillata Decraemer, 1982	11.41%	

Kenya

	Coral fragments	Coral gravel
	Average dissimilarity: 78.95	
Epsilonema parvospina Decraemer, 1982	8.40%	
Perepsilonema papulosum Lorenzen, 1973		5.89%
Dracognomus annae Verschelde & Vincx, 1993		5.59%
***Dracognomus* sp. 2** sp. n.		5.45%
***Paradraconema* sp. 4** sp. n.	4.68%	

Table 3. SIMPER results for the three pairs of groups considered in this study. The following data are provided: the average dissimilarity between the two groups, the species most important in explaining this dissimilarity, their procentual contribution to the dissimilarity (> 9% in Porcupine Seabight; > 4% in Kenya) and their habitat preference.

	Species	%
Porcupine Seabight		
Coral fragments	***Epsilonema multispiralum*** Raes, Vanreusel & Decraemer, 2003	41.9
	Triepsilonema tripapillata Decraemer, 1982	22.9
	Glochinema trispinatum Raes, Vanreusel & Decraemer, 2003	7.3
	Akanthepsilonema sinecornibus sp. n.	6.7
	Cygnonema belgicae sp. n.	5.5
	Tenuidraconema koreensis Rho & Kim, 2004	5.0
Sponge skeletons	***Glochinema trispinatum*** Raes, Vanreusel & Decraemer, 2003	42.6
	Epsilonema multispiralum Raes, Vanreusel & Decraemer, 2003	16.8
	Triepsilonema tripapillata Decraemer, 1982	14.2
	Bathyepsilonema lopheliae Raes, Vanreusel & Decraemer, 2003	11.6
Sediment	***Glochinema trispinatum*** Raes, Vanreusel & Decraemer, 2003	56.5
	Triepsilonema tripapillata Decraemer, 1982	17.4
	Epsilonema multispiralum Raes, Vanreusel & Decraemer, 2003	6.5
	Tenuidraconema koreensis Rho & Kim, 2004	6.5
Kenya		
Coral fragments	***Epsilonema parvospina*** Decraemer, 1982	36.6
	***Epsilonema* sp. 12** sp. n.	12.6
	***Paradraconema* sp. 4** sp. n.	9.5
	***Epsilonema* sp. 10** sp. n.	7.0
Coral gravel	***Perepsilonema papulosum*** Lorenzen, 1973	19.1
	Dracognomus annae Verschelde & Vincx, 1993	15.5
	***Dracognomus* sp. 2** sp. n.	12.9
	***Epsilonema* sp. 15** sp. n.	9.2
	Epsilonema margaritatum Decraemer & Gourbault, 1987	6.0

Table 4. Dominant species within the Epsilonematidae and Draconematidae (relative abundance > 5%), per microhabitat in each region.

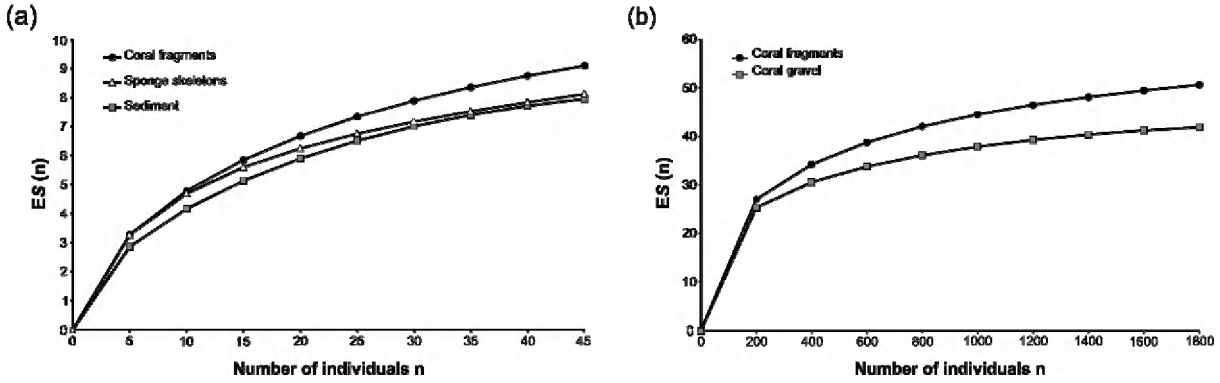


Fig. 4. Rarefaction curves. (a) Porcupine Seabight; (b) Kenyan coast. Note the different scales on the x- and y axis.

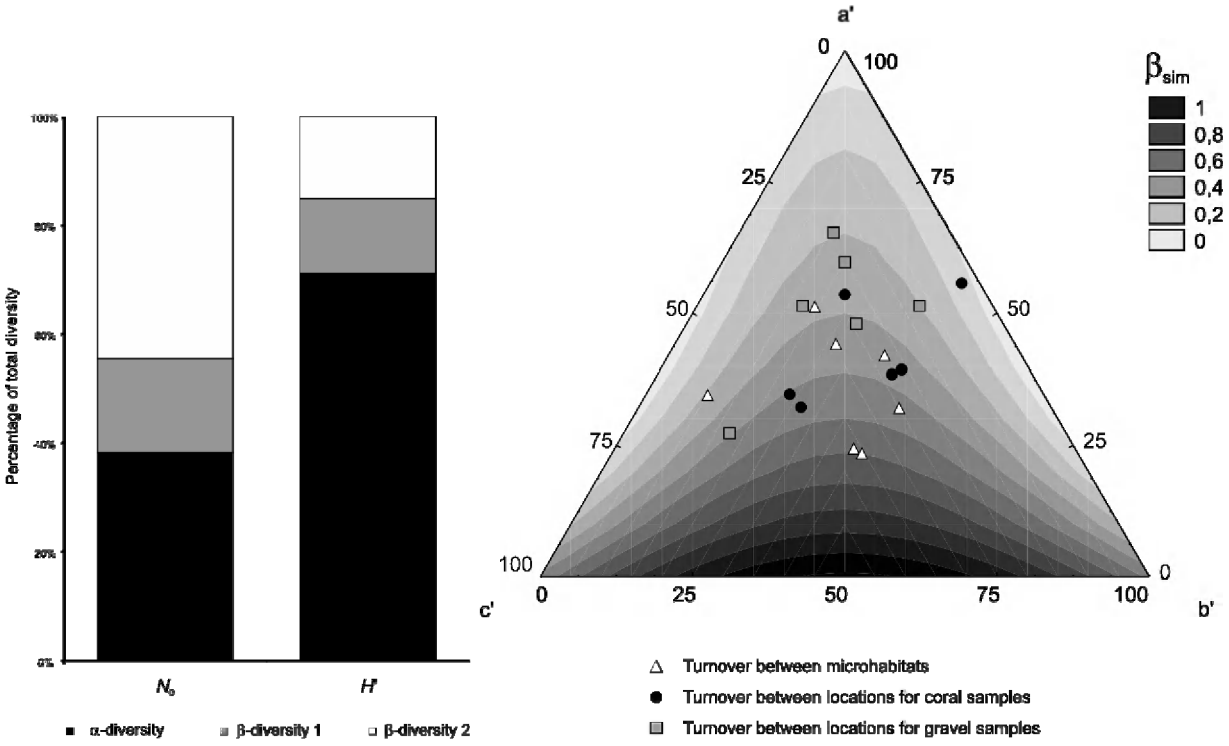


Fig. 5. Additive partitioning of total diversity for the number of species N_0 and Shannon-Wiener diversity H'. β-diversity 1 is the fraction of β-diversity resulting from differences between microhabitats; β-diversity 2 is the fraction of β-diversity resulting from differences between locations.

Fig. 6. Ternary plot representing species turnover between microhabitats within each location and between locations for both coral and gravel samples. Shading visualises the values of β_{sim}.

4.5. DISCUSSION

4.5.1. HABITAT PREFERENCES

Our results concerning the distinction between microhabitats and the communities which inhabit them in the Porcupine Seabight area agree to a large extent with a previous study on the total nematode community of this area, which was however conducted with genus level identifications (Raes & Vanreusel, *in press*). In contrast to the present survey, the sponge and sediment communities in that study were also significantly dissimilar from each other. Nevertheless, even on the genus level coral fragments were dominated by *Epsilonema* and characterised by high abundances of Epsilonematidae and Draconematidae, whereas both sponge skeletons and the sediment yielded much lower numbers of taxa belonging to these families. In the study of Raes & Vanreusel (*in press*), this relative comparability of sponges and sediment was attributed to the sediment-trapping capacity of the three-dimensional framework of sponge spicules, a hypothesis which could well explain the absence of significant differences between these microhabitats in the present study. Epsilonematidae are known to thrive in coarse sediments which are subject to strong hydrodynamic forces (Willems *et al.*, 1982; Vanaverbeke *et al.*, 2004). In our study, only the animals living on the coral fragments are thought to be subjected to considerable erosion by current activity, as the others are more protected in the sediment. Consequently, coral fragments can be considered a more favourable substratum for epifaunal nematodes. This is confirmed in the present study by the fact that, except for two species, all epsilonematid and draconematid species show a preference for coral fragments. *Glochinema trispinatum* is a slender nematode supported by long, fine ambulatory setae and therefore believed to be much more vulnerable to physical disturbance by the strong currents which govern in this ocean margin ecosystem. On the other hand, the preference of *Bathyepsilonema lopheliae* for sponge skeletons may be related to the hook-shaped tip of the ambulatory setae in this species, which could be important in clinging on to the smooth substratum of the sponge spicules. However, a hook-shaped tip has also been observed in several other Epsilonematidae and may be not so exceptional. Sediment infill between the coral branches and the addition of coral fragments in the sediment explain the low average dissimilarities between the microhabitats.

In accordance with the above reasoning, a difference between the exposed nature of coral fragments and the relatively lower exposition within the coral gravel may also explain the differences in community composition between the two microhabitats on the coast of Kenya. Again, this has been proven to be the case for the total nematode community on genus level (Raes *et al.*, *submitted* b). In that study, the genera *Paradraconema* (Draconematidae) and *Epsilonema* (Epsilonematidae) were recognised as indicator genera for coral fragments. The present study confirms this on the species level. The absence of ambulatory setae in *Perepsilonema papulosum* and the smaller, finer adhesion tubes without a bell-shaped tip in both *Dracognomus annae* and *D.* sp. 2 hampers the attachment to the substratum, which allows selective advantage on the surface of the coral fragments, and is provided here as an explanation for the preference of these species for the somewhat calmer coral gravel microhabitat. If we continue on this reasoning that the morphology of the specialised locomotory structures in both families plays an important role in explaining habitat preferences, we would expect a

significantly higher relative abundance of Draconematidae on the more exposed coral fragments, as draconematids have adhesion tubes associated with glands with which they can attach themselves better to the substratum. A significantly higher Draconematidae/Epsilonematidae ratio on corals was however only found in the Porcupine Seabight community, even when *Dracognomus* was added to the Epsilonematidae group in Kenya.

4.5.2. BIOGEOGRAPHY

Decraemer *et al.* (2001) established that cosmopolitism in Epsilonematidae is common. Our data confirm and endorse this observation and reveal that the same is true for Draconematidae. Although our list of occurrences only includes those species that have been found in the study at hand, the geographical and bathymetrical range over which some species occur is astonishing and inspires reflection on the biogeography of marine nematodes.

First of all, one should be aware of the fact that sampling effort and exploration intensity greatly influences our view on the distribution of these epifaunal nematodes. The taxonomical record of Epsilonematidae and Draconematidae has grown considerably in recent years thanks to numerous descriptions by a limited group of researchers and from a limited number of sampling locations. The description of several species from the Kenyan coast by Verschelde & Vincx (1992; 1993a, b; 1994), from Laing Island, Papua New Guinea by Decraemer (1982; 1988) and from Guadeloupe by Decraemer & Gourbault (1987; 1990a, b) and Gourbault & Decraemer (1988) have considerably influenced the general results emerging from Table 2. For example, the communities along the Kenyan coast are composed to a great extent of species described or recorded from Papua New Guinea. Indeed, on a total of 174 currently described species of Epsilonematidae and Draconematidae, 20 have been found in Papua New Guinea (*i.e.* 11.5%). This emphasises the importance of and the need for comprehensive studies in areas where suitable substrata for epifaunal nematodes are available.

The occurrence of morphologically identical meiofaunal taxa in completely divergent areas, even at lower systematic levels, has been an unsolved enigma for many years now. The solution to this 'meiofauna paradox' (Giere, 1993), in this context adopted for nematodes, should either be looked for in (1) the dispersive opportunities and mechanisms of nematodes, (2) the existence of cryptic species and conservative morphology of nematodes or (3) the eventuality of parallelism. There are five possible explanations for the existence of morphologically identical nematodes in geographically distant areas: (1) they belong to the same species and genetic and morphological equality is maintained by active gene flow between the populations; (2) they belong to the same species, the populations are isolated from each other but the morphology and genetic structure in both populations is conserved; (3) they belong to different cryptic species; (4) they belong to different pseudo-sibling species *sensu* Knowlton (1993) or (5) they belong to different species which have obtained the same morphology due to parallel evolution.

Several studies have reviewed the mechanisms and opportunities of meiobenthic dispersal (Gerlach, 1977; Palmer, 1988; Giere, 1993). Only few meiobenthic taxa have pelagic larvae and nematodes are especially recognised as taxa with limited mobility, poor swimming capacity (Hopper &

Meyers, 1966) and a conservative reproductive method (*i.e.* lack of dispersive stages), characterising them as biogeographically localised organisms (Castillo-Fernandez & Lambshead, 1990). As already mentioned in the introduction, Epsilonematidae and Draconematidae are characterised by a crawling locomotion distinctly different from the undulating movement of most other nematodes, rendering them more mobile on larger substrata (Stauffer, 1924; Lorenzen, 1973a). This type of locomotion can however only be used to bridge short distances. Dispersal of meiobenthic organisms over larger spatial scales has to go through the water column: either by rafting on drifting material, in sediment used as ballast for ships or via currents (Gerlach, 1977). This latter possibility is clearly the most common and most generally available one as it is not determined by the coincidental presence of suitable transports. Meiofauna is indeed regularly found in the water column (Hagerman & Rieger, 1981). Chandler & Fleeger (1983) have experimentally proven the colonisation of meiofauna through the water column. Meiofauna may leave the sediment either through active emergence or through passive erosion by hydrodynamic activity (Palmer, 1988). Organisms dwelling near the sediment surface or on substrata such as seagrasses (or corals, as in our study) are more susceptible to passive erosion than infaunal animals (Palmer, 1984; 1988). Nevertheless, Hicks (1986) has shown that meiofauna dispersal from seagrass beds is primarily an active process. It should be remarked here that the sediment surface and seagrass dwelling meiofauna in the aforementioned studies were mainly composed of copepods, which are relatively good swimmers. It seems however plausible that although epifaunal nematodes such as Epsilonematidae and Draconematidae are not good swimmers, they are able to actively let go of the substratum by releasing their ambulatory setae or adhesion tubes. In this way, they may control their own dispersal. All this indicates that the coral fragment-inhabiting nematodes investigated in our study are prone to easy and frequent dispersive events. Yet, we did not find any indication that the coral-dwelling nematodes were more widely distributed than the sediment/gravel-dwelling ones. Furthermore, most of the species given in Table 2 live in both microhabitats.

Although meiofauna settlement is considered largely a passive process, active habitat selection may be expected in seagrass beds according to Palmer (1988). Ullberg & Ólafsson (2003) have experimentally shown that marine, free-living nematodes may actively choose suitable habitats. Given the clear-cut distinction between coral and gravel communities of epifaunal nematodes and the exposed nature of the coral fragments (and, to a lesser extent, the surface of the coral gravel) in the study at hand, we assume that a combination of passive (erosion and resuspension) and active processes (active emergence and active habitat inspection/selection after settlement by crawling) determines colonisation of these microhabitats by nematodes.

It is not clear whether dispersal via the water column can sustain active gene flow between geographically distant areas such as the Porcupine Seabight and the coast of Kenya. The biogeography of a species like *Tenuidraconema koreensis* Rho & Kim, 2004, which is found in the Porcupine Seabight and on the coast of Korea, is even more astonishing and suggests that the populations could be isolated from each other, at least to some extent. This is attributed not only to mere geographical distance, but also to the complexity of the dispersion routes that link both populations and, moreover, the difficulties associated with bridging a bathymetric boundary of 750-850

m. On a smaller spatial scale, the occurrence of *T. koreensis* populations in the Porcupine Seabight and on the Great meteor Seamount has been explained by passive transport via Meditteranean Outflow Water and stepping stones, *i.e.* following the same trajectory as the larvae of the coral *Lophelia pertusa* on which they occur (Raes *et al.*, *submitted* c).

From Table 2, it is clear that *T. koreensis* is not the only species with a putative cosmopolitan distribution. Following the above reasoning, populations of such species could be genetically different from each other or even consist of different species. This implies that morphologically similar nematodes may belong to different biological species, *i.e.* they could be reproductively isolated. Actual tests for reproductive isolation of marine nematode populations are however hampered by difficulties associated with culturing these animals. Nevertheless, a comparison with mitochondrial sequence data could already indicate whether these animals, which are morphologically identical, molecularly belong to the same species or whether they represent different cryptic species. Recent studies have indicated that some meiobenthic 'species' are actually complexes of cryptic species and, as a result, that putatively cosmopolitan species have more limited geographical ranges (Schmidt & Westheide, 2000; Rocha-Olivares *et al.*, 2001; Derycke *et al.*, 2005). Such complexes are especially prominent in small invertebrates with few taxonomically diagnostic characters. The prevalence of cryptic species indicates that morphological stasis persists after speciation events, while species continue to diverge genetically in the absence of morphological differentiation. Evidence for such a decoupling of molecular and morphological evolution is summarised by Rocha-Olivares *et al.* (2001). In contrast, the discovery of two pairs of morphologically very similar (but with distinctly different sperm cell morphology) sympatric species (*Tenuidraconema koreensis* and *T. parvospermis*; *Cygnonema verum* and *C. belgicae*) indicates that morphological evolution is not that slow and even goes on when gene flow is still active (via Mediterranean Outflow Water) (Raes *et al.*, *submitted* c; d). This paradox clearly complicates the discussion on whether nematode morphology is either conserved or variable. According to Knowlton (1993), the establishment of many sibling species has resulted from failure to recognise subtle morphological distinctions between existing species, which are therefore referred to as 'pseudo-sibling species'. This problem has arisen from the inadequate definition of diagnostic features, the inadequate identification of homologous structures and intraspecific variability, and is especially acute in taxa with few morphological features, such as nematodes. However, as the morphology of the identified species in this study was thoroughly examined, the pitfall of inadequate morphological observation can be ruled out for the present study.

The five explanations for finding morphologically identical nematodes in geographically distinct areas given above can now be assessed. The first (same species, with gene flow between populations), second (isolated populations with conserved morphology and genetic structure) and fourth (different pseudo-sibling species) explanations can be ruled out based on arguments provided above. The assumption that they are cryptic species appears very plausible, although molecular analysis is needed. A final possibility is that they are closely related, but different species, which have obtained a similar morphology as a response to similar environmental conditions (*i.c.* similar microhabitats). A completely independent development of such an exceptional and specialised morphology as *e.g.* in *T. tripapillata* seems unlikely, although some functional morphological features

of epsilonematids may have evolved several times in different taxa because their morphological information is enclosed in the genetic code of these animals. This could easily be the case for the three papillae on the terminal tip of the tail, each with the separate outlet of one of the three caudal glands (Raes *et al*., *in press*). Such papillae are thought to be important for improved attachment to the substratum and could therefore have arisen in response to strong hydrodynamic stress on coral fragments.

4.5.3. DIVERSITY

Coral degradation zones, both in temperate deep and tropical shallow environments, are clearly an important source of new species of Epsilonematidae and Draconematidae. The higher diversity on coral fragments compared to the other microhabitats, as evidenced by the rarefaction curves in Fig. 4, confirms the aforementioned statement that coral fragments can be considered a more favourable substratum for typically epifaunal nematodes. This shows that these typically epifaunal nematodes are able to establish more extensive and diverse communities on coral fragments, which is due to the fact that they are morphologically and ecologically well-adapted to a life in this exposed habitat, which is less suitable for most other nematodes. However, the differences between the E*G* (n) values for coral fragments and coral gravel were not significant in Kenya, indicating that a higher overall diversity on coral fragments may also be caused by the more considerable differences in community structure between coral samples, resulting in a high total number of species. This is confirmed by the lower average similarity values within this microhabitat. The typically epifaunal nematode communities in Kenya are clearly more diverse than those in the Porcupine Seabight area, although this may be due to the pronounced difference in sampling scale (three boxcores at the same location in the Porcupine Seabight area vs. a whole transect along the Kenyan coast).

It is clear from our analysis of additive partitioning that sample (α) diversity is by far most important in contributing to the total diversity when working with abundance data (*H'*). This is however no longer true when working with presence-absence data. Furthermore, the contribution of different locations to the total diversity is high when working with species richness but is completely reduced when adding abundance information. This indicates that the addition of sampling locations considerably contributes to the total number of species, although the added species are generally rare. The contribution of β-diversity related to differences between microhabitats to the total diversity is low, both for presence-absence and abundance data. In contrast, turnover between microhabitats appears to be generally higher than turnover between locations for gravel samples. This could have been expected given the important structuring role of microhabitats for the communities, which was observed in our study. However, turnover between coral samples also appears to be generally high. This is in agreement with the more considerable differences in community structure between coral samples. In this regard, this result confirms the observation from the rarefaction curve from Kenya that coral fragments contribute more to the total diversity than gravel samples. The unusually high value of β_{sim}-value (0.39) for the one grey square marker comparing gravel samples from Msambweni with those from Kisite in the lower left corner of the ternary plot may be attributed to an effect of the relative isolation of the Kisite Island. Indeed, a' was markedly lower than for the other comparisons. The high contribution of α- or

sample-diversity, and hence the importance of variability between samples irrespective of their microhabitat or location, is reflected in the scattered position of the markers on the ternary graph.

In conclusion, this study investigated a subset of the meiofauna in comparable microhabitats from very different ecosystems, which are geographically and bathymetrically separated from each other. Despite of these striking environmental differences, similar (and in some cases even identical) species where found. This emphasises the importance of microhabitat type in structuring the nematode community but also raises questions about the extent of genetic divergence between morphologically identical nematodes in geographically distant areas.

4.6. ACKNOWLEDGEMENTS

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Porcupine Seabight
Coral fragments
Akanthepsilonema sinecornibus sp. n.
Akanthepsilonema sp. 2 sp. n.
Bathyepsilonema lopheliae Raes, Vanreusel & Decraemer, 2003
Bathyepsilonema spongiosum Clasing, 1986
Bathyepsilonema sp. 3 sp. n. (PSB)
Epsilonema cf. *byssicola* sp. n.
Epsilonema cf. *lasium* sp. n.
Epsilonema cygnoides (Metschikoff, 1867) Gerlach & Riemann, 1931
Epsilonema multispiralum Raes, Vanreusel & Decraemer, 2003
Glochinema trispinatum Raes, Vanreusel & Decraemer, 2003
Triepsilonema tripapillata Decraemer, 1982
Cygnonema belgicae sp. n.
Cygnonema verum sp. n.
Tenuidraconema koreensis sp. n.
Tenuidraconema parvospermis sp. n.
Sponge skeletons
Bathyepsilonema lopheliae Raes, Vanreusel & Decraemer, 2003
Bathyepsilonema sp.3 sp. n. (PSB)
Bathyepsilonema spongiosum Clasing, 1986
Dracograllus demani Allen & Noffsinger, 1978
Epsilonema margaritatum Decraemer & Gourbault, 1987
Epsilonema multispiralum Raes, Vanreusel & Decraemer, 2003
Glochinema trispinatum Raes, Vanreusel & Decraemer, 2003
Triepsilonema tripapillata Decraemer, 1982
Cygnonema belgicae sp. n.
Tenuidraconema koreensis sp. n.
Tenuidraconema parvospermis sp. n.
Sediment
Akanthepsilonema sinecornibus sp. n.
Bathyepsilonema lopheliae Raes, Vanreusel & Decraemer, 2003
Epsilonema multispiralum Raes, Vanreusel & Decraemer, 2003
Glochinema trispinatum Raes, Vanreusel & Decraemer, 2003
Triepsilonema tripapillata Decraemer, 1982
Cygnonema belgicae sp. n.
Tenuidraconema koreensis sp. n.
Tenuidraconema parvospermis sp. n.

Appendix 1. List of epsilonematid and draconematid species associated with the three microhabitats in the Porcupine Seabight.

Kenya	
coral fragments	coral gravel
Bathyepsilonema compactum Clasing, 1984	*Bathyepsilonema compactum* Clasing, 1984
Bathyepsilonema sp. 3 sp. n. (Kenya)	*Bathyepsilonema* sp. 2 sp. n.
Bathyepsilonema sp. 5 sp. n.	*Epsilonema margaritatum* Decraemer & Gourbault, 1987
Epsilonema margaritatum Decraemer & Gourbault, 1987	*Epsilonema parvospina* Decraemer, 1982
Epsilonema parvospina Decraemer, 1982	*Epsilonema* sp. 1 sp. n.
Epsilonema sp. 1 sp. n.	*Epsilonema* sp. 3 sp. n.
Epsilonema sp. 3 sp. n.	*Epsilonema* sp. 6 sp. n.
Epsilonema sp. 3' sp. n.	*Epsilonema* sp. 7 sp. n.
Epsilonema sp. 6 sp. n.	*Epsilonema* sp. 8 sp. n.
Epsilonema sp. 7 sp. n.	*Epsilonema* sp. 10 sp. n.
Epsilonema sp. 8 sp. n.	*Epsilonema* sp. 11 sp. n.
Epsilonema sp. 10 sp. n.	*Epsilonema* sp. 12 sp. n.
Epsilonema sp. 11 sp. n.	*Epsilonema* sp. 15 sp. n.
Epsilonema sp. 12 sp. n.	*Epsilonema* sp. 16 sp. n.
Epsilonema sp. 13 sp. n.	*Leptepsilonema richardi* Verschelde & Vincx, 1992
Epsilonema sp. 13' sp. n.	*Leptepsilonema* sp. 2 sp. n.
Epsilonema sp. 14 sp. n.	*Metepsilonema chilotum* Clasing, 1986
Epsilonema sp. 15 sp. n.	*Metepsilonema hardyi* Decraemer & Gourbault, 1990
Leptepsilonema richardi Verschelde & Vincx, 1992	*Metepsilonema striatulum* Decraemer & Gourbault, 1990
Leptepsilonema sp. 2 sp. n.	*Metepsilonema* sp. 6 sp. n.
Metepsilonema striatulum Decraemer & Gourbault, 1990	*Perepsilonema kellyae* Gourbault & Decraemer, 1988
Metepsilonema sp. 2 sp. n.	*Perepsilonema moineaui* Gourbault & Decraemer, 1992
Metepsilonema sp. 4 sp. n.	*Perepsilonema papulosum* Lorenzen, 1973
Metepsilonema sp. 6 sp. n.	*Perepsilonema* sp. 2 sp. n.
Metepsilonema sp. 8 sp. n.	*Perepsilonema* sp. 2' sp. n.
Perepsilonema kellyae Gourbault & Decraemer, 1988	*Perepsilonema* sp. 3 sp. n.
Perepsilonema moineaui Gourbault & Decraemer, 1992	*Perepsilonema* sp. 4 sp. n.
Perepsilonema papulosum Lorenzen, 1973	*Polkepsilonema mombasae* Verschelde & Vincx, 1992
Perepsilonema sp. 2 sp. n.	*Pternepsilonema servaesae* Verschelde & Vincx, 1992
Perepsilonema sp. 3 sp. n.	
Perepsilonema sp. 4 sp. n.	
Polkepsilonema mombasae Verschelde & Vincx, 1992	
Triepsilonema tripapillata Decraemer, 1982	
Dracognomus annae Verschelde & Vincx, 1993	*Dracognomus annae* Verschelde & Vincx, 1993
Dracognomus sp. 1 sp. n.	*Dracognomus dermatoglyphus* Verschelde & Vincx, 1993
Dracognomus sp. 2 sp. n.	*Dracognomus* sp. 1 sp. n.
Dracograllus cf. *minutus* sp. n.	*Dracognomus* sp. 2 sp. n.
Dracograllus demani Allen & Noffsinger, 1978	*Dracograllus* cf. *minutus* sp. n.
Dracograllus eira (Inglis, 1968) Allen & Noffsinger, 1978	*Dracograllus demani* Allen & Noffsinger, 1978
Dracograllus laingensis Decraemer, 1988	*Dracograllus eira* (Inglis, 1968) Allen & Noffsinger, 1978
Dracograllus papuensis Decraemer, 1988	*Dracograllus laingensis* Decraemer, 1988
Dracograllus sp. 4 sp. n.	*Dracograllus papuensis* Decraemer, 1988
Dracograllus sp. 5 sp. n.	*Dracograllus* sp. 4 sp. n.
Dracograllus sp. 6 sp. n.	*Draconema haswelli* (Irwin-Smith, 1918) Kreis, 1938
Draconema claparedii (Metschnikov, 1867) Filipjev, 1918	*Paradraconema* sp. 2 sp. n.
Draconema haswelli (Irwin-Smith, 1918) Kreis, 1938	*Paradraconema* sp. 3 sp. n.
Paradraconema floridense Allen & Noffsinger, 1978	*Paradraconema* sp. 4 sp. n.
Paradraconema sp. 2 sp. n.	
Paradraconema sp. 3 sp. n.	
Paradraconema sp. 4 sp. n.	
Paradraconema sp. 5 sp. n.	

Appendix 2. List of epsilonematid and draconematid species associated with the two microhabitats in Kenya.

ADDENDUM 1

THE METAZOAN MEIOFAUNA ASSOCIATED WITH A COLD-WATER CORAL DEGRADATION ZONE IN THE PORCUPINE SEABIGHT (NE ATLANTIC)

Paper *published*

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ABSTRACT

The metazoan meiofauna associated with *Lophelia pertusa* reef degradation zones in the Belgica mound province (Porcupine Seabight, North-East Atlantic) was studied in the framework of the Atlantic Coral Ecosystem Study (ACES; EC Fifth Framework Research Program). Attention was focused on the influence of and differences between different microhabitat types: dead coral fragments, glass sponge skeletons and the underlying sediment. This study demonstrates the importance of dead *Lophelia pertusa* framework and associated substrates for meiofauna along the European continental margins. The presence of these large biogenic structures on the sea floor of the continental margin (1) enables more taxa to be present and (2) particularly favours harpacticoid copepods, naupliar larvae and polychaetes. The meio-epifaunal community on these substrates significantly differs from the meio-infaunal community in the underlying sediment. This is mainly due to a much lower dominance of nematodes and a higher relative abundance of most other taxa, especially harpacticoids, naupliar larvae and polychaetes, in the latter habitat. This situation is comparable to that of epiphytic assemblages. Dominance of nematodes is low. The meio-infaunal assemblage in the underlying sediment is characterised by low densities. There are clear indications that cold-water coral degradation zones are biologically very diverse, in terms of species richness as well as equitability. Of all microhabitat types, coral fragments support the most diverse communities, whereas the underlying sediment is the least diverse.

Key words: cold-water corals, dead coral framework, meiofauna, community structure, microhabitats, biodiversity

INTRODUCTION

MEIO-EPIFAUNA: A NEW CHAPTER IN COLD-WATER CORAL RESEARCH

Although the existence of cold-water corals is already known to science since the 18th century (Pontoppidan, 1755), the associated fauna has by no means been studied as intensely as for tropical corals. Most preceding studies dealing with real epifauna on either living or dead *Lophelia pertusa* (Linnaeus, 1758) have focused on the macrofauna; some studies dealt with the associated fauna in a broader sense and examined the animals that could be identified on live images or photographs from ROV, defined as megafauna (Dons, 1944; Le Danois, 1948; Burdon-Jones & Tambs-Lyche, 1960; Jensen & Frederiksen, 1992; Mortensen *et al.*, 1995; Fosså & Mortensen, 1998; Rogers, 1999; Van Gaever, 2001 (*unpublished data*); De Backer, 2002 (*unpublished data*)). Until today, there is almost no knowledge on the composition and diversity of the smaller fraction, known as meiofauna, associated with *Lophelia pertusa* reefs (except for the study of Jensen & Frederiksen, 1992). Obviously, this is an important hiatus in our understanding of cold-water coral associated fauna. Meiofauna is known to play an important role in the marine benthic ecosystem (Heip *et al.*, 1985; Coull 1988) and it serves as

food for other organisms (Thiel, 1983; Coull, 1988). Furthermore, as meiofaunal organisms occur in high abundances and because they are characterised by high species richness (Heip *et al.*, 1985; Lambshead, 1993), they are very suitable for biodiversity studies.

For the first time, the meiofauna associated with cold-water corals has been intensively studied. Three years of study on this topic will be presented here, highlighting the most important and striking aspects of this formerly unknown fauna and underlining its particular nature and relevance.

The present study deals only with metazoan meiofauna. In this paper, meiofauna is defined as the fauna that passes through a 1 mm mesh sieve but that is retained on a 32 µm mesh sieve. The 32 µm limit is used primarily in deep-sea studies because of the smaller size of deep-sea meiofauna (Thiel, 1975; Thiel, 1983; Pfannkuche, 1985; Soetaert & Heip, 1989). Next to the interstitial and mud-dwelling meiofauna (here referred to as meio-infauna), there is a large group of meiofauna living epifaunally on well-defined surfaces from diverse origin, ranging from large biogenic debris to seagrasses, macro-algae, larger coral fragments, sponge skeletons, manganese nodules and pebbles, to name a few. The term meio-epifauna will be used here to cover this unit of the meiofauna. For meiofauna living on seagrasses and macro-algae, the terms 'epiphytic' and 'foliicolous' have already been used in literature. A suitable substrate for meio-epifauna (1) should be a discrete and well-defined structure of at least about 5 mm in diameter and (2) is not completely covered with sediment, implying that at least a part of the surface area is in contact with the water column. Although it is expected that these surfaces will provide higher numbers of typical epifaunal taxa than any other habitat, there is of course no exclusive relationship in either way. This is because the surfaces are always in close contact with the sediment to a certain extent (physical contact with sediment surface, infill from sedimentation and resuspension), and because several typical epifaunal taxa (*e.g.* representatives from the epifaunal nematode families Epsilonematidae and Draconematidae: Fig. 4) are also found in coarse and poorly sorted sediments. Recently, a representative of the family Epsilonematidae (*Glochinema bathyperuvensis* Neira, Gad, Arroyo & Decraemer, 2001) has even been found living in fluffy, muddy sediments (Neira *et al.*, 2001). In the present study, suitable surfaces for meio-epifauna are found on dead coral fragments of the framework builder *Lophelia pertusa* (Linnaeus, 1758) and skeletons of the glass sponge *Aphrocallistes bocagei* Schultze, 1886, both abundantly present in the cold-water coral degradation zones.

Most preceding studies on marine meiofauna have focused on the meio-infauna. The few studies that dealt with meio-epifauna focused on the fauna associated with macro-algae and seagrasses (*e.g.* Lewis & Hollingworth, 1982; Coull *et al.*, 1983; Bell *et al.*, 1984a; Hall & Bell, 1993; Jarvis & Seed, 1996; De Troch *et al.*, 2001). The present study focuses on dead coral fragments and the dead glass sponge skeletons that are associated with them. Living coral is assumed not to be a suitable substrate for meiofauna, although the absence of meiofauna has not yet been verified. It was observed that the healthy coral responds to the settlement of sessile organisms by (1) an increase in mucus production and (2) selective sclerenchyme precipitation (Freiwald & Wilson, 1998). These protective properties have proven to be rather successful antifouling measures against macrofauna (Mortensen, 2000).

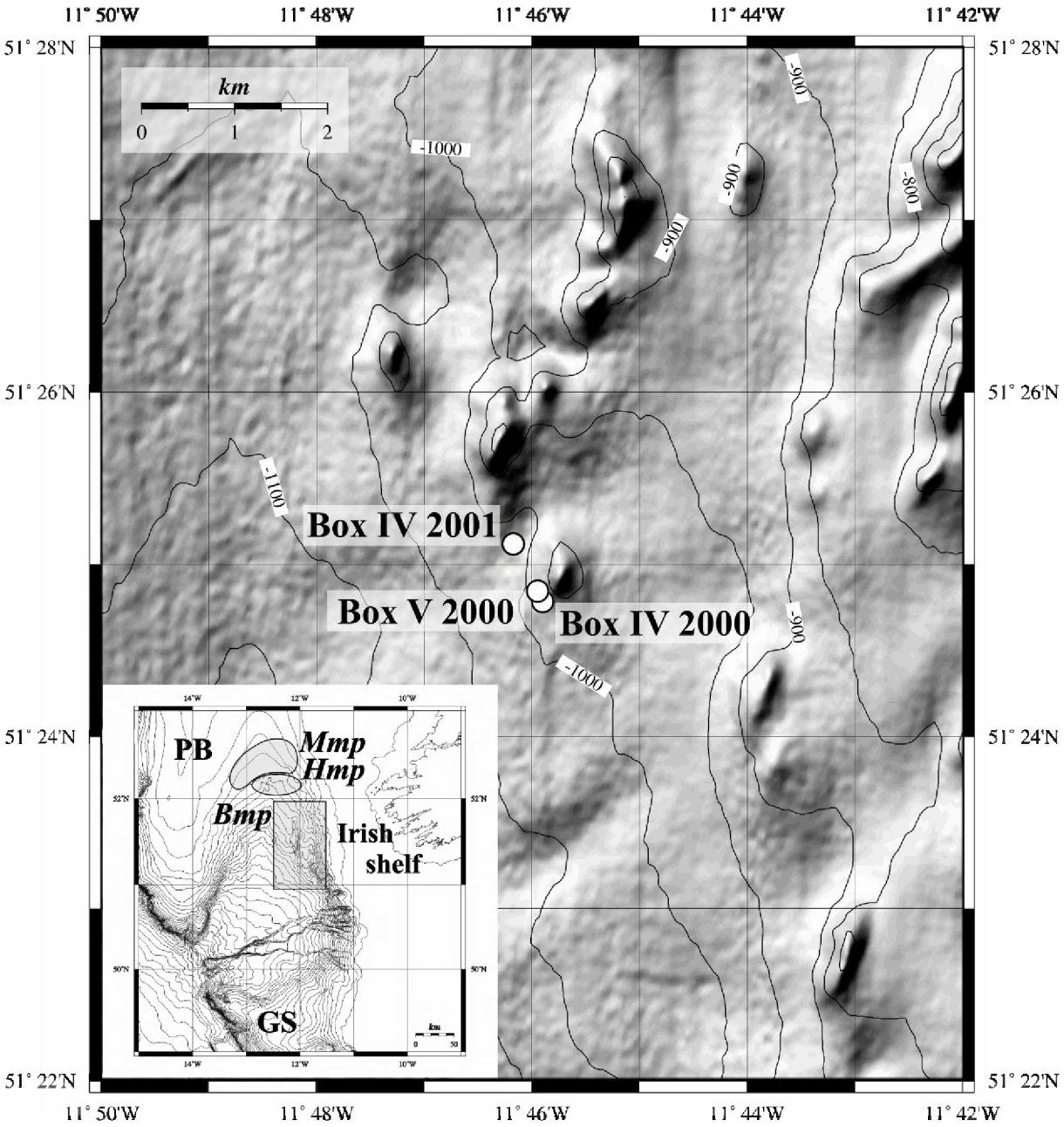

Fig. 1. Map of the Porcupine Seabight area, with a detail showing the ridge of mounds in the Belgica mound province where the analysed samples originate from (bathymetry after Beyer *et al*., 2003). Boxcore locations are indicated. (PB= Porcupine Bank; *Mmp*= Magellan mound province; *Hmp*= Hovland mound province; *Bmp*= Belgica mound province; GS= Goban Spur).

	Area	Coordinates		Depth (m)	Observed density (ind/10 cm^2)	Calculated density (ind/10 cm^2)
		Latitude	Longitude			
Box IV 2000	Porcupine Seabight	51°24'48.2" N	11°45'55.4" W	1005	376 ± 54	672
Box V 2000	Porcupine Seabight	51°24'49.4" N	11°45'55.9" W	1000	328 ± 178	673
Box IV 2001	Porcupine Seabight	51°25'7.7" N	11°46'9.3" W	972	291	679
Station 511-03 (Pfannkuche, 1985)	Porcupine Seabight	51°47'0" N	13°08'36" W	960	1593 ± 143	682
Station 511-04 (Pfannkuche, 1985)	Porcupine Seabight	51°21'24" N	13°03'18" W	1492	943 ± 127	582
Vanreusel et al. (1995)	Porcupine Seabight	51°46'12.8" N	13°13'2.4" W	900	1523 ± 267	697
Vanreusel et al. (1995)	Porcupine Seabight	51°39'2.4" N	12°59'1.8" W	1200	1500 ± 270	632
Station I (Vanaverbeke et al., 1997)	Goban Spur	49°24'43.2" N	11°31'51.6" W	670	612 ± 76	764
Station B (Vanaverbeke et al., 1997)	Goban Spur	49°21'59.4" N	11°48'5.4" W	1034	619 ± 47	665
Station II (Vanaverbeke et al., 1997)	Goban Spur	49°11'12.0" N	12°49'10.8" W	1425	509 ± 72	593

Table 1. An overview of the exact sampling location and depth, as well as the observed and calculated densities of the sediment-dwelling meiofauna found in the underlying sediment of the present study and in sediments from nearby localities at a comparable depth. Artificial values for the respective depths were calculated using the function Y = 2241-227*ln depth (Vincx *et al.*, 1994: Fig. 4).

LOCATION AND ENVIRONMENTAL CONDITIONS

The information compiled in this study is based on three box core samples. The box cores were taken on the top and slope of a single seabed mound at depths between 972 and 1005 m (Fig. 1; Table 1). This mound is located in the Belgica mound province of the Porcupine Seabight. The Porcupine Seabight is a large embayment of the European continental slope, located in the North-East Atlantic Ocean, southwest of Ireland. It is bordered by the Slyne Ridge in the north, the Goban Spur in the south, the Porcupine Bank in the west and the Irish Mainland shelf in the east. In this area numerous seabed mounds occur, grouped in three so called 'mound provinces': the Hovland mound province, the Magellan mound province and the Belgica mound province (Fig. 1). The Belgica mound province is the most southern of all seabed mound provinces. It is characterised by large outcropping or buried, conical (sometimes composite) mounds with well-exposed downslope sides (De Mol *et al.*, 2002), aligned in four along-slope-trending ridges (Van Rooij *et al.*, 2003). In total, 21 outcropping

mouds are present. These mounds are known to be associated with deep-water coral banks, mainly constructed by the framework builder *Lophelia pertusa* (Linnaeus, 1758) and associated fauna such as the glass sponge *Aphrocallistes bocagei* Schultze, 1886. Only on the basinward flanks of the mounds, these cold-water corals are present (De Mol *et al.*, 2002). The presence of these mounds as well as the reefs that are associated with them alters the local hydrodynamic and sedimentary regime.

The presence of transversal sand dunes in the Belgica mound region indicates very high current velocities, up to 100 cm/s (De Mol, 2002). These very high velocities are probably exceptional but normal current speeds are still rather high (about 10-25 cm/s (White, *in press*) or even 40-50 cm/s (V. Huvenne, pers. comm.)). High current speeds are attributed to the combination of strong, northward along-slope bottom currents, internal tides and waves, and the presence of mounds (Rice *et al.*, 1991; Van Rooij *et al.*, 2003; Wheeler *et al.*, *in press*; White, *in press*). Strong current activity is known to affect meiofaunal abundance and community structure (Thistle & Levin, 1998; Thistle *et al.*, 1999; Aller, 1989; Aller, 1997). Currents are less vigorous upslope, to the east of the mounds (Van Rooij *et al.*, 2003).

According to De Mol *et al.* (2002) and Van Rooij *et al.* (*in press*), the upper 10 cm of the sediment in the Belgica Mound region can be defined as Foraminifera-rich silty sand or soupy, foraminiferal sand, with a high sand content decreasing towards a depth of 10 cm. Below this, the sediment becomes more clayey (pers. obs.), defined as olive grey silty clay by Van Rooij *et al.* (*in press*). In the vicinity of the mounds, the sediment becomes littered with coral fragments and other biogenic debris (see below).

The Porcupine Seabight is known to be subject to substantial phytodetrital deposition (Billett *et al.*, 1983; Lampitt, 1985; Gooday *et al.*, 1996). The detritus itself as well as the bacteria and protozoa that rapidly colonise it are the main food source for deep-sea meiofauna. Taking into account both timing of surface blooms in 2000 and 2001, as well as sinking rates, it was calculated that phytodetritus should have been present on the bottom at both sampling occasions. It is however difficult to judge whether this material already had a relevant impact on the meiobenthos, as response speed by benthic organisms may be taxon-specific, or even guild-specific: smaller species that utilise the organic matter directly show a more rapid response than larger species on a higher trophic level (Graf *et al.*, 1982; Gooday *et al.*, 1996). Next to this, it is not even clear if this deposited material was available for the benthic fauna in the Belgica mound region, an area subject to strong bottom currents. These currents will certainly cause resuspension and relocation of the material. Down-slope and along-slope variability of phytodetrital deposition in this region makes generalisations even more difficult (D. Billett, pers. comm.).

Food supply is known to influence meiofaunal abundance and biomass (Graf *et al.*, 1982; Thiel *et al.*, 1990; Gooday & Lambshead, 1989; Pfannkuche & Thiel, 1987; Pfannkuche, 1993; Vanreusel *et al.*, 1995a; Gooday, 2002), metabolic activity (Graf *et al.*, 1982; Pfannkuche, 1993; Gooday, 2002), community structure (Gooday, 1988), reproductive cycles (Gooday *et al.*, 1996; Gooday, 2002) and size spectra (Thiel, 1975; Soetaert & Heip, 1989; Vanreusel *et al.*, 1995a; Soltwedel *et al.*, 1996) in the

deep sea. Our samples did not show any evidence of a detrital layer covering the sediment or the large biogenic substrates (pers. obs.).

COLD-WATER CORAL DEGRADATION ZONES

As already mentioned above, this study deals mainly with dead coral skeletons. These structures are the result of a bioerosion process that starts with the death of *Lophelia pertusa* colonies due to persistent attack by fouling organisms. The progress of this bioerosion process is visible in the zonation of the deep-water reef mound environment. Although each reef has its own characteristic zonation pattern with its own succession of typical facies (Freiwald *et al.*, 1997; Freiwald *et al.*, 2002), the two zones described by Mortensen *et al.* (1995) can be distinguished in most cases: according to these authors, a cold-water bioherm can be divided into two zones of approximately equal height: (1) a living coral zone on the summit and the upper flanks, and (2) a lower zone of dead corals. The centre of a deep-water bioherm indeed consists of living coral framework. According to Freiwald & Wilson (1998), the *Lophelia pertusa* bioerosion process starts with the formation of a microbial biofilm and endolithic fungal infestation, followed by colonisation of the coral skeleton by sessile invertebrates such as sponges and octocorals. The microbial biofilm might serve as a food source for small microvores including some meiofauna. As already mentioned above, this meiofauna is a food source for higher trophic levels (macrofauna and megafauna). Thus, the development of such a biofilm might enable an entirely new food web to be established, although there is still no evidence for this. In the reef's zonation pattern the living coral framework is flanked by the dead coral framework.

In a next stage, locally intense sponge excavation results in skeletal loss, and the *in situ* collapsing of the dead *Lophelia pertusa* framework. Conversely, the encrusting sponge communities also speed up the closure of the gaps in the open coral framework and catalyse sediment-trapping, resulting in the strengthening of the framework architecture and the origin of large topographic features (De Mol *et al.*, 2002). The dead coral framework gradually changes into a zone composed of smaller and more biodegraded coral skeletons with a rich associated fauna. The gaps between the skeletons and their branches are filled up with sediment (Freiwald *et al.*, 2002). In this type of habitat (sediment-clogged coral framework) our samples were taken. The sediment infill in our samples seemed however rather limited, probably due to the high current velocities and the resulting resuspension of the sediment (see above). Because of the dynamic origin of this habitat, it is more generally referred to as a 'coral degradation zone' in the present study.

In a final stage, intensified bioerosion will result in accumulations of centimetre-sized coral debris. This so-called coral rubble pavement (Freiwald *et al.*, 1997) then grades into the soft bottom background. The diversity of megafauna living in this *Lophelia pertusa* rubble zone has been found to be lower than that of the zones with living or dead coral colonies (Mortensen *et al.*, 1995). Dead coral colonies accommodate the most diverse macro- and megafauna (Mortensen *et al.*, 1995; Jensen & Frederiksen, 1992). This can be attributed to the sheltering function and higher habitat diversity of

branched dead coral skeletons (framework) in contrast to the very small fragments in the *Lophelia pertusa* rubble zone.

In the immediate vicinity of the seabed mound examined in this study, every stage between dead coral framework and the coral rubble pavement is present. The dead framework however occurs only in small patches. Live coral framework in this region is present on the ridge directly to the north of the examined mound, from the nearby Therèse mound to Galway mound farther north (A. Foubert, pers. comm.). As the seabed mound in question is considered to be the most southern mound of this ridge, it is expected that this structure also contains live coral patches.

The present paper aims to describe the metazoan meiofaunal community structure associated with cold-water coral degradation zones for the first time, investigate the importance of different microhabitats for meiofauna in this area by checking for habitat preferences and compare the observed community structure with the composition of epiphytic assemblages. Next to this, densities of the meio-infauna in the underlying sediment will be compared with available data from preceding studies on meiofauna in the northeast Atlantic and the biodiversity of this formerly unknown fauna will be extensively discussed.

METHODS USED TO STUDY THE MEIOFAUNA

SAMPLING PROCEDURE

Material was obtained by means of a NIOZ (Netherlands Institute for Sea Research) box corer (ø 32 cm). In total, three box cores were examined. Two box cores were taken during the 9-19 June 2000 sampling campaign on the RV Belgica. A third box core was taken on the same location and brought to the surface during the 2-11 May 2001 sampling campaign on the same vessel (Fig. 1). In all cases, the surface of the sediment was partly or entirely covered with several fragments of dead corals (*Lophelia pertusa* (Linnaeus, 1758)) and dead sponge skeletons (*Aphrocallistes bocagei* Schultze, 1886). Only a very small amount of living coral was present. The larger sponge and coral fragments were collected separately. After removal of the large biogenic substrates three sediment cores (10 cm^2) were pushed into the underlying sediment of each box core. All material was fixed with 4% neutralised formalin.

MICROHABITATS

The main aim of this study is to examine the differences in community structure due to the presence of different microhabitat types. Obviously, for meiofaunal organisms the conditions within the sediment are clearly different from those on a complex elevated structure on the sea floor, and this in terms of food supply and food quality as well as in terms of the physical influence of strong bottom currents. These differences should have their effect on the presence and abundance of meiofaunal taxa. Next to this obvious distinction between large biogenic substrates and the underlying sediment as a habitat, small differences in microhabitat structure should also influence meiofaunal community

composition as meiofauna is known to respond acutely to minor environmental changes. In this respect the rough surface of the branches of *Lophelia pertusa* (Linnaeus, 1758), sometimes covered with a thin layer of bryozoan colonies, is quite dissimilar from the complex three-dimensional build-up of spicules in the glass sponge *Aphrocallistes bocagei* Schultze, 1886 (Fig. 2).

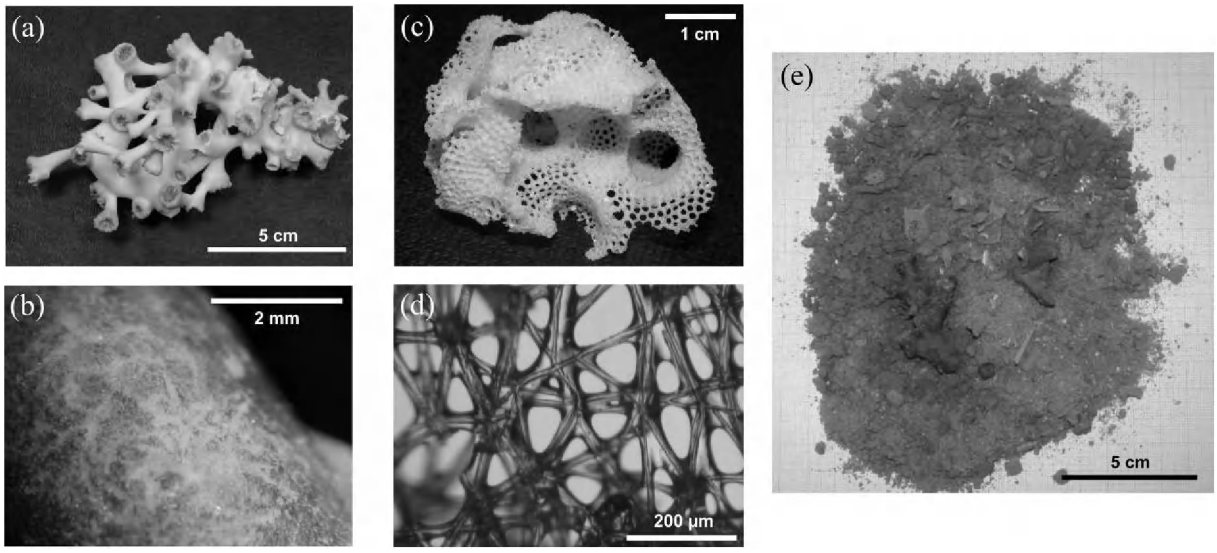

Fig. 2. An overview of the three major microhabitat types: (a) a dead *Lophelia pertusa*-fragment; (b) detail of the fragment's surface; (c) a dead *Aphrocallistes bocagei*-skeleton; (d) detail of the complex three-dimensional sponge spicule framework; (e) the underlying sediment. Note that small coral and sponge debris is present in the underlying sediment, as well as small bivalve and gastropod shells and echinoid radiolas.

In total, 28 subsamples were examined: 18 subsamples were collected in the first box core (2000), six subsamples in the second box core (2000) and another four subsamples in the box core from 2001. After thorough examination of their contents, the subsamples were classified into one of the following groups, each of them representing a microhabitat type (Fig. 2): (1) coral fragments, (2) sponge skeletons (*i.e.* the two large biogenic substrates), (3) the underlying sediment and (4) a mixed substrate. Subsamples belonging to the *mixed substrate*-group contained coral fragments as well as sponge skeletons. The underlying sediment consisted of fine to medium sand (median 194.9 µm) with a small fine silt fraction and a high amount of globigerine forams. It was observed that this was a poorly sorted sediment, also containing small fragments of both large biogenic substrates, as well as some small mollusc-shells and echinoid-radiolas (Fig. 2e). The second sample from 2000 did not yield any 'sponge skeletons'-subsamples and the sample from the 2001-campaign did not yield any 'mixed substrate'-subsamples.

LABORATORY ANALYSES

Each *Lophelia* and *Aphrocallistes* fragment was rinsed thoroughly over a 1 mm and a 32 µm sieve to separate the macrofauna from the meiofauna fraction. Meiofauna extraction from the underlying or remaining sediment was done by density gradient centrifugation, using Ludox (a colloidal silica polymer; specific gravity 1.18) as a flotation medium (Heip et al. 1985; Vincx 1996). All metazoan

meiofauna was stained with Rose Bengal, counted in small counting trays and identified up to higher taxonomic level under a stereomicroscope. Meiofauna was classified into several taxonomic groups, ranging from orders to phyla. Most larvae however were difficult to associate with a single taxon and therefore they were referred to by using the name of their larval stage: nauplii (Crustacea), zoea (Crustacea), metazoea (Crustacea) and trochophora larvae (Polychaeta).

Volumes of all examined large biogenic substrates were measured by immersion. This method only provides a value for the volume of each substrate and not its surface area, but volume can be used as a proxy for surface area: only an extra mathematical factor describing branching complexity of corals or three-dimensional structure of sponge skeletons is needed. The use of volumes results from the absence of such a factor and the lack of good alternatives. Each sediment subsample represented 10 cm^2 of sediment.

STATISTICAL ANALYSES

The PRIMER5 software was used for most statistical analyses. With this software Bray-Curtis (dis)similarities between all subsamples are calculated, ultimately resulting in a test statistic reflecting within-microhabitat as well as between-microhabitat similarities. The resulting similarity matrix was applied to perform a non-metric multidimensional scaling analysis (MDS; stress 0.11). The stress value gives a measurement of goodness-of-fit of the MDS ordination. A low stress value (<0.2) indicates a good ordination with no real prospect for a misleading interpretation (Clarke, 1993). ANalysis Of SIMilarities (ANOSIM) was used to test the statistic for significant differences ($p < 0.05$) between meiofaunal community structure in the different microhabitats and to investigate which taxa were responsible for these differences (SIMilarity of PERcentages: SIMPER). In this study all absolute data were square root transformed prior to the analysis.

Indicator species analysis (ISA; Dufrêne & Legendre, 1997) was performed using the PC-ORD4 software. For this type of analysis absolute data were used without any transformation. Calculated indicator values were tested for statistical significance using the Monte Carlo test.

Parametric (one-way ANOVA) and non-parametric (Kruskal-Wallis) analysis of variance were performed using the STATISTICA6 software. Bartlett's and Cochran's test were used to verify the homogeneity of variances prior to the analysis.

Several biodiversity indices were calculated to obtain an extensive overview of taxon diversity of the analysed samples: The Shannon-Wiener index *H'* and Pielou's evenness *J* (Pielou, 1975) are mainly included for reasons of comparability with other studies. Hill's diversity numbers (Hill, 1973) gradually change from indices of species richness to indices of dominance with increasing number: N_0 is identical to the number of species, $N_1 = \exp(H')$ and N_∞ reflects evenness. The *Expected number of Taxa* for a theoretical sample of 100 individuals E*T* (100) was derived from the *Expected number of Species* (Hurlbert, 1971).

(a)

Entire community (28)	
taxon	%
Nematoda	67,04
Harpacticoida	12,57
Nauplii	7,14
Polychaeta	5,19
Tardigrada	2,67
Gastrotricha	1,51
Ostracoda	0,81
Turbellaria	0,79
Aplacophora	0,62
Trochophora-larvae	0,56
Acari	0,45
Isopoda	0,21
Oligochaeta	0,10
Sipuncula	0,07
Bivalvia	0,04
Unknown juvenile arthropod	0,04
Cumacea	0,02
Kinorhyncha	0,02
Loricifera	0,02
Pycnogonida	0,02
Tantulocarida	0,02
Chaetognatha	0,01
Priapulida	0,01
Tanaidacea	0,01
Amphipoda	0,01
Cladocera	0,01
Echiura	0,01
Holothuroidea	0,01
Metazoea	0,01
Rotifera	0,01
Zoea	0,01
# of individuals	16392
Average density meio-epifauna	35932 ind/l
Average density meio-endofauna	346 ind/10 cm^2

(b)

Coral fragments (10)		Sponge skeletons (8)		Mixed substrate (4)		Underlying sediment (6)	
taxon	%	taxon	%	taxon	%	taxon	%
Nematoda	56,59	Nematoda	77,18	Nematoda	78,89	Nematoda	85,83
Harpacticoida	17,85	Harpacticoida	10,59	Harpacticoida	8,30	Harpacticoida	5,48
Nauplii	8,72	Polychaeta	6,07	Polychaeta	4,86	Polychaeta	2,96
Polychaeta	8,09	Tardigrada	2,30	Tardigrada	2,46	Nauplii	2,53
Tardigrada	2,47	Nauplii	1,60	Nauplii	1,35	Tardigrada	0,72
Gastrotricha	2,00	Aplacophora	0,55	Turbellaria	1,20	Gastrotricha	0,62
Ostracoda	0,99	Gastrotricha	0,53	Ostracoda	0,54	Ostracoda	0,59
Aplacophora	0,72	Ostracoda	0,39	Acari	0,53	Aplacophora	0,30
Turbellaria	0,67	Acari	0,32	Gastrotricha	0,47	Acari	0,23
Acari	0,66	Isopoda	0,18	Unknown juvenile arthropod	0,28	Turbellaria	0,19
Trochophora-larvae	0,64	Oligochaeta	0,11	Aplacophora	0,21	Kinorhyncha	0,14
Isopoda	0,25	Turbellaria	0,10	Isopoda	0,17	Cumacea	0,08
Oligochaeta	0,07	Sipuncula	0,06	Oligochaeta	0,17	Oligochaeta	0,08
Tanaidacea	0,07	Pycnogonida	0,02	Pycnogonida	0,15	Trochophora-larvae	0,06
Sipuncula	0,07	Kinorhyncha	0,01	Loricifera	0,14	Metazoea	0,05
Bivalvia	0,05			Sipuncula	0,09	Zoea	0,04
Tantulocarida	0,04			Bivalvia	0,05	Loricifera	0,04
Holothuroidea	0,01			Cladocera	0,05	Rotifera	0,04
Priapulida	0,01			Priapulida	0,05	Isopoda	0,02
Chaetognatha	0,01			Tantulocarida	0,05		
Amphipoda	0,01						
Echiura	0,01						
Cumacea	0,01						
# of individuals	7226		4695		1815		2656
Average density	15919 ind/l *		63192 ind/l		26443 ind/l		346 ind/10 cm^2

Table 2. Relative abundances and overall average densities of the meiofauna associated with cold-water coral degradation zones. (a) entire community; (b) separate microhabitats. Taxa found exclusively on a certain substrate are underlined. *: for 1 substrate the volume is not known, average densities were measured using only the samples with known volumes.

ASSOCIATED MEIOFAUNA: COMMUNITY STRUCTURE, DENSITIES AND THE INFLUENCE OF SUITABLE SUBSTRATES

As mentioned above, only the metazoan meiofauna was considered in this study. It is however relevant to mention that intact ciliates and foraminiferans were encountered in our samples.

In this study a total of 16547 metazoan meiofaunal organisms was counted, divided into 16 phyla and 33 groups (*i.e.* taxonomic groups as well as larval stages). The number of phyla represented here is quite high, especially taking into account that only 22 metazoan phyla (in the traditional sense) have representatives in the meiobenthos (Coull, 1988). Because a full taxon list is seldom given in literature, it is difficult to compare the number of taxa. In total, only 31 of the 33 groups were included in the analysis: Hydrozoa and Calanoida were excluded for different reasons. A large number of hydrozoans was found: either individual polyps or branched pieces of hydrocaulus with several polyps still attached. It was reasoned that large branched colonies of Hydrozoa would be withheld on a 1 mm sieve and that therefore the number of individual polyps counted as meiofauna was not an accurate reflection of the natural situation. Calanoida on the other hand are pelagic copepods that have an aggregated spatial distribution in the water column. Therefore, their occurrence in the overlying water of a box core is highly coincidental. As a result, the presence of 29 Calanoida in two subsamples from the same box core and their absence in all the other subsamples indicates that these 29 individuals originated from a swarm of calanoids in the overlying water of this box core and can therefore be considered as contamination. It should be remarked here that a large number of other taxa found in our samples is also capable of permanent or temporary residence in the overlying water (*e.g.* Chaetognatha, Cladocera, and most larvae), especially when the high current velocities in the region (see above) are taken into account.

A considerable number of larvae or juveniles was encountered. Next to the crustacean and polychaete larvae already mentioned above, an unknown juvenile arthropod, which is probably a recently hatched juvenile amphipod, was encountered. It should be mentioned here that direct development resulting in hatching as a juvenile, *i.e.* without a nauplius larva, is a feature of all Peracarida (*e.g.* Amphipoda, Isopoda, Tanaidacea, and Cumacea) and of Cladocera (Williamson, 1982). This means that the nauplii encountered in our samples are either from harpacticoid copepods, ostracods or from crustaceans that belong to the macrofauna. Therefore, unlike for most other studies, nauplii will be considered separately from harpacticoid copepods here. Judging by their size, the zoea and metazoea are larvae from crustaceans of macrofaunal size and in this respect they are regarded as temporary meiofauna. Loricifera, Tantulocarida and Bivalvia were only represented by their larvae (Loricifera: 'Higgins-larvae'; Tantulocarida: 'Tantulus-larvae') or juveniles (Bivalvia).

An overview of the relative abundances and overall average densities of the meiofauna taxa and larvae associated with cold-water coral degradation zones is given in Table 2a. Overall, the meiofaunal population was dominated by nematodes which made up 67.0% of the total metazoan meiofaunal community on average. Harpacticoida constituted the second most abundant taxon,

comprising 12.6% of all meiofauna on average. Nauplii were the third most abundant group: they accounted for 7.1% of the total meiofauna. These results correspond relatively well with the available information on deep-sea meio-infaunal community composition (compiled by Vincx *et al.*, 1994 and Soltwedel, 2000), although the observed relative abundance of nematodes is lower than for the meio-infauna in the Porcupine Seabight (Pfannkuche, 1985). This relative abundance varies strongly, between 32.7 and 94.7%, which is due to differences in the type and amount of large biogenic substrates present in the subsamples. These substrates accommodate a community characterised by a significantly lower dominance of nematodes (see below) and higher relative abundances of most other taxa. When only the underlying sediment is considered, nematodes comprise between 71.6 and 94.7% of the total meiofaunal community, a situation more similar to that of the deep-sea meiobenthos not associated with large biogenic structures on the seafloor (Vincx *et al.*, 1994). Moreover, there are no relevant differences between the meiofaunal community composition on higher taxon level in the underlying sediment of this study and in other deep-sea soft sediments not covered by dead coral framework, at least not for the most abundant taxa.

Next to the three taxa already mentioned, only polychaetes, tardigrades and gastrotrichs have a relative importance of more than 1%. According to Vincx *et al.* (1994), polychaetes are indeed the third most abundant taxon in the northeast Atlantic deep-sea meio-infauna (after nematodes and the combined harpacticoids-nauplii).

Only the densities of the meio-infauna in the underlying sediment could be compared with existing data, because no comparable density measurements (ind/l) were made for meio-epifauna in preceding studies and because the accumulation of sedimented material on the substrates obscures the concept of total available surface area for meio-epifaunal organisms. The overall meio-infaunal density of 346 ind/10 cm^2 found in the present study is below that expected for a depth of 1000 m as indicated by the 'best regression' in Vincx *et al.* (1994: Fig. 4). This is even more obvious when applying the function given by the same authors, describing the relationship between metazoan meio-infaunal density and depth in the northeast Atlantic, and given as Y = 2241 – 227 * ln depth. The mean densities (and standard deviations) of the meio-infauna for each examined box core, compared with calculated values for the respective depths, are given in Table 1. It is clear that the observed values are consistently far below the calculated values. Moreover, the mean densities in the Porcupine Seabight area (given as areas 1 and 2 in the considered graph) appear to have a position far above the 'best regression' trendline depicted in Vincx *et al.* (1994: Fig. 4), indicating that this area is normally characterised by very high densities. In a final attempt to confirm that the densities found in the present study are exceptionally low, they are compared with data from three studies dealing with samples from the Porcupine Seabight and nearby Goban Spur at a similar depth (Pfannkuche, 1985; Vanreusel *et al.*, 1995b; Vanaverbeke *et al.*, 1997). For optimal comparison, it was attempted each time to select the stations from each study that are most comparable in depth with the samples from the present study, *i.e.* around 1000 m. The average densities, standard deviations and the corresponding calculated values are given in Table 1. The highest mean density in our samples (376

ind/10 cm^2: Box IV 2000) is still markedly lower than the lowest value found in literature (509 ind/10 cm^2: station II in Vanaverbeke et al. 1997). Moreover, station II in Vanaverbeke *et al.* (1997) is situated much deeper (1425 m) than Box IV 2000 (1005 m) and therefore the low observed densities in the former are probably due to an effect of depth-related density decrease. Vanaverbeke *et al.* (1997) attributed their lower density values compared to sites in the Porcupine Seabight to (1) a difference in deposited amount of phytodetritus and (2) differences in sampling gear. Indeed, the Porcupine Seabight is considered an area with exceptionally high organic food input (Billett *et al.*, 1983; Lampitt, 1985; Gooday *et al.*, 1996), resulting in very high meiofaunal densities. This contrasts sharply with the low densities observed in our study. Without taking in consideration the current uncertainty about the extent of phytodetrital deposition in the Belgica mound region, there are several potential explanations for this discrepancy.

Differences in sampling gear and the low efficiency of box corers in collecting meiobenthos may be of importance here, as the studies of Pfannkuche (1985) and Vanreusel *et al.* (1995b) are based on multiple corer samples. On the other hand, the coral and sponge fragments present at the sample site might act as a sediment trap, preventing resuspension of the sediment and therefore limiting the bow-wave effect generated by box corers. The relative limpidity of the overlying water seems to confirm this last hypothesis. In this case, the presence of large biogenic structures on the sea floor affects the meio-infaunal densities on the sampling site in a positive way. However, their presence may also cause a decline in meiofaunal densities in the underlying sediment as it is thought that the collapsed coral framework and associated substrates act as a kind of 'net', successfully trapping most of the seasonally supplied phytodetritus and in this way limiting the amount of food supplied to the underlying sediment. The high amount of food trapped by the biogenic structures is made unavailable for the fauna in the underlying sediment. It has already been mentioned that meiobenthic densities decrease with decreasing food availability.

Although these large biogenic structures are thought to protect the underlying meio-infauna from physical erosion and removal by strong currents and enable other taxa to dwell among the coral branches, it is not clear to what extent they are able to reduce the impact of strong currents on the underlying sediment. Strong bottom flow may not be adequately decreased under the sediment-clogged cold-water coral framework. Lower meio-infaunal abundances may therefore be an effect of physical removal of the meiofauna in the upper sediment layers (keeping the fauna in suspension until a time of decreased flow) or an effect of lower microbial biomass due to decreased deposition of food. The relative limpidity of the overlying water as argued above, as well as the presence of a well-established meio-epifaunal community associated with the *Lophelia pertusa*-framework as proven by the present study, are however inconsistent with this idea. One should always keep in mind that because of the diurnal and semi-diurnal nature of tidal currents (Rice *et al.*, 1991) the impact on meiobenthos will fluctuate on a short time-scale. This is because the frequently changing current speeds will result in periodic cycles of erosion and deposition. During the latter periods, sediment, food

and organisms are redeposited on the seabed and meiofaunal abundances will increase (Aller, 1989; Aller, 1997).

The presence of small biogenic structures (coral fragments, sponge skeletons, sponge spicules, echinoid radiolas, gastropod and bivalve shells) in the sediment may also have its effect on meiofaunal density. The coarsening of the sediment might particularly affect typical interstitial taxa, such as the dominant nematodes and gastrotrichs, because of its influence on the dimensions of interstitial free space and because the biogenic structures are probably obstacles for organisms crawling between the sand grains. A decrease in nematode density will then directly affect total meiofaunal density. Decreased meiobenthic densities in the underlying sediment can also be explained by high predation pressure by the abundant and diverse macrofaunal community found in association with the sediment-clogged coral framework (Jensen & Frederiksen, 1992). A more intense comparison with background sediments is needed to confirm or falsify these and other hypotheses.

In contrast with the underlying sediment, the sediment-clogged coral framework itself is thought to be more densely populated. Because this framework is able to trap sedimented organic food, it can be regarded as a hotspot of abundant food in a generally food-limited environment. Limitation of food is not proven here: on the contrary, fast flows should provide a constant supply of food. It is argued however that fast flows may also interfere with deposition of food and that sediment resuspension due to strong currents makes deposited food less accessible for meiobenthos (see also: Lampitt, 1985). This is based on the observed decrease in microbial biomass due to faster flow by Thistle & Levin (1998). As complex biogenic structures may also provide shelter against predation, conditions should be ideal for the development of a rich meio-epifaunal community: low disturbance, low predation pressure and abundant food enable a specific community to be established on and in between the coral branches and sponge skeletons.

HABITAT PREFERENCES

Within this relatively protected habitat, significant differences in meiofaunal community structure were found between the different microhabitats that were distinguished. Only twelve taxa occurred in all four microhabitats (Table 2b). Moreover, on a total of 31 taxa, five taxa were found exclusively on coral fragments, although not in all subsamples. In contrast, only three were found exclusively in the sediment, two on the mixed substrate and not a single taxon was restricted to sponge skeletons. There were no taxa showing an obligate association with a certain microhabitat in the sense that when a taxon occurred in only one microhabitat it was never found in all subsamples.

The MDS graph given in Fig. 3 plots all subsamples relative to each other. There is a high degree of overlap between the different microhabitats in terms of community composition, although on the MDS plot a trend from the upper left corner to the lower right corner (coral fragments - sponge skeletons - underlying sediment) is present. Overall, the image seems rather complex.

ANOSIM showed highly significant (p = 0.005) overall differences between the microhabitats. Pairwise tests were carried out and revealed significant differences between the coral microhabitat and all other microhabitats in terms of community composition. It can therefore be concluded that the coral microhabitat houses a very typical and rather unique meiofaunal community. Very highly significant differences (p = 0.001) were found between the coral microhabitat and the underlying sediment. This result is in good agreement with the number of taxa found exclusively in each of these microhabitats and the image given by the MDS analysis: the coral fragment subsamples can be clearly separated from the sediment subsamples on the ordination graph.

At this point, attention will be focused only on these two extremes. Average dissimilarity (29.7%) is low, probably because of the large differences between the subsamples within one microhabitat type. More than 50% of this dissimilarity is caused by four taxa: Harpacticoida (16%), Nematoda (14%), nauplii (13.5%) and Polychaeta (8.5%). Only nematodes had a significantly higher average relative abundance (p = 0.0007) in the sediment subsamples compared to the coral subsamples; all other taxa were relatively more abundant on coral fragments. An indicator species analysis was carried out on all subsamples (including the sponge and mixed subsamples) to elucidate habitat preferences. This yielded three taxa with significant indicator values for coral fragments: nauplii (IV = 74); Harpacticoida (IV = 53) and Polychaeta (IV = 47). Kinorhyncha was the only significant indicator for the sediment subsamples (IV = 40). Nematodes were not identified as indicators for the sediment, although this was put forward by SIMPER and the observed significantly lower relative abundance of this taxon on coral fragments. This is due to the fact that nematodes were still the dominant group on this substrate.

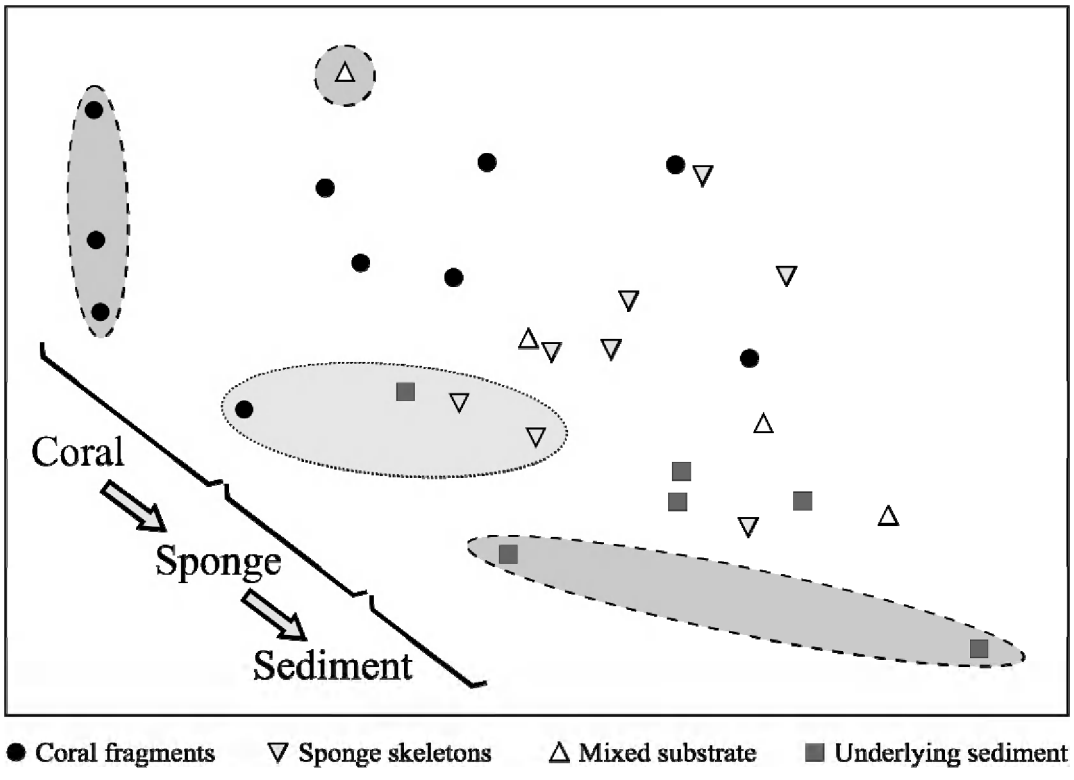

Fig. 3. Multidimensional Scaling (MDS) two-dimensional plot (stress: 0.11) of all subsamples. The subsamples in a pale field surrounded by a dotted line are from the 2001-box core. The subsamples in a darker field surrounded by a dashed line are from the second box core taken in 2000. The trend mentioned in the text is visualized in the lower left corner.

Although nematodes are the dominant group in all microhabitats, they are relatively more important in sedimentary habitats. Because most nematodes are long and slender organisms, they are morphologically more adapted to move between the sand grains than to crawl over a large surface (Giere, 1993). Moreover, the presence of interstitial microniches is essential for nematode colonisation (Danovaro & Fraschetti, 2002). So the presence of sediment is probably essential to ensure a well-developed nematode community. Only those nematodes belonging to the epifaunal families Epsilonematidae and Draconematidae are morphologically adapted to 'walk' over hard substrates. These nematodes are known to have a looper caterpillar-like locomotion using ventral setae (*ambulatory setae*: Epsilonematidae) or tubes (*posterior adhesion tubes*: Draconematidae) on their posterior body region, sometimes together with tubes on or near the head capsule (*cephalic adhesion tubes*: Draconematidae) (Fig. 4). Raes & Vanreusel (*in press*) report a predominance of representatives of these two families on dead *Lophelia pertusa*-fragments. The lower dominance of nematodes on coral fragments results in a higher relative abundance of all other taxa. Although some of these taxa are known to be typically interstitial (*e.g.* Gastrotricha and Tardigrada), only kinorhynchs were found to have a clear habitat preference for the underlying sediment. According to Higgins (1988), kinorhynchs are frequently found in the interstitia of medium to coarse sand or gravel. On the other hand, Coull (1988) stated that Kinorhyncha, being for the most part burrowing organisms in muddy sediments, are excluded from interstitial habitats.

The fact that nematodes are still the dominant group on the coral substrate is mainly attributed to the sediment infill between the fragments and coral branches: these substrates are still in close association with the underlying sediment. The community composition of meio-epifauna on cold-water coral fragments is therefore in a broad sense somewhat comparable to the composition of the infauna, however with some important differences as already argued above. On higher taxon level, a meio-epifaunal community is composed of a sediment-dwelling background community (predominantly nematodes) but with several groups that are more adapted to a life on large biogenic surfaces than nematodes (evidently Harpacticoida, naupliar larvae and Polychaeta from our Indicator Species Analysis), showing a significantly increased importance. Although communities found in the sediment are significantly different from those on cold-water coral fragments (see above), it is almost impossible to distinguish between 'typical interstitial' and 'typical epifaunal' taxa on a higher taxonomic level.

Some dead coral structures may be partly covered with a felty layer of bryozoan colonies that very effectively traps sedimented material. It can be stated that the coral substrate provides a complex habitat for meiofauna because it can possibly be subdivided into even smaller microhabitats: the felty bryozoan encrustation probably combines sediment-dwelling and substrate-crawling taxa; the sediment infill between branches harbours an interstitial fauna; the coral surface is covered with a microbial biofilm and will therefore mainly attract obligate microbial-feeding meio-epifauna, and the cavities within the coral fragments (*e.g.* those constructed by *Eunice norvegica*) are maybe home to still other communities. These differences within one microhabitat type (*i.c.* dead coral fragments) could then explain the scattered distribution of the coral subsamples in the MDS ordination graph.

Analysis of all these very specific microhabitats should be a subject for future research. In the present study, relatively fine-tuned habitat preferences on family-level have been found for nematodes (families Epsilonematidae, Draconematidae in Raes & Vanreusel, *in press*) and harpacticoid copepods (families Tegastidae and Laophontidae (H. Gheerardyn, pers. comm.)).

Several studies dealing with epiphytic meio-epifauna revealed that this fauna was often dominated by nematodes. In those cases, their relative abundances were rather low, especially compared to infaunal communities (Lewis & Hollingworth, 1982; De Troch *et al.*, 2001). Harpacticoida and naupliar larvae are always abundant in epiphytic communities (Lewis & Hollingworth, 1982; Jarvis & Seed, 1996; De Troch *et al.*, 2001) and several authors reported a shift to a predominance of these two groups in epiphytic samples, especially on seagrass leaves and on macro-algae (Coull *et al.*, 1983; Bell *et al.*, 1984a; Hall & Bell, 1993 and authors cited herein). These results confirm the observed importance of these two groups as indicator epifauna. The high abundance of naupliar larvae (and copepodites) in seagrass beds has also been attributed to a potential nurseries function (Lewis & Hollingworth, 1982; Hall & Bell, 1993). It is difficult to say whether this is also the case for cold-water coral degradation zones, although the assumed low disturbance, low predation pressure and abundant food might provide a suitable habitat for larvae and juveniles. Most meiofaunal taxa, and especially nematodes, turned out to be associated with the filamentous epiphytic flora covering the macro-algae and seagrasses (Lewis & Hollingworth, 1982; Bell *et al.*, 1984a; Hall & Bell, 1993; Jarvis & Seed, 1996). Algae that accumulate sediment and detritus have a richer nematode community because the sediment provides the interstitial microniches that are crucial for nematodes (Heip *et al.*, 1985). This is an interesting idea, especially when applied to cold-water coral fragments were the coral surface is sometimes covered with a felty layer of bryozoans.

Finally, a comparison between soft-bottom and hard-bottom meiofauna carried out in a shallow environment on the Mediterranean coast (Danovaro & Fraschetti, 2002) produced SIMPER-results that are comparable with ours: harpacticoid copepods were identified as the taxon characterising hard-bottom assemblages and nematodes were identified as responsible for the differences between hard- and soft-bottom community composition.

From the MDS graph given in Fig. 3 it is clear that the community structure on sponge skeletons is intermediary between that from coral fragments and that from the sediment, indicating the presence of both infaunal and epifaunal organisms. Because of their intricate structure, these sponge skeletons are able to trap a lot of sediment, in this way stimulating the presence of interstitial taxa. On the other hand, the sponge spicules may act as a substrate for epifaunal forms or as a three-dimensional maze for crawling taxa.

The high number of taxa encountered in this study is attributed to the presence of a large number of different microhabitats that were extensively discussed above. It is hypothesised here that each of these microhabitats favours a community with a different life style and a different composition. The sum of all these separate communities results in a high number of taxa.

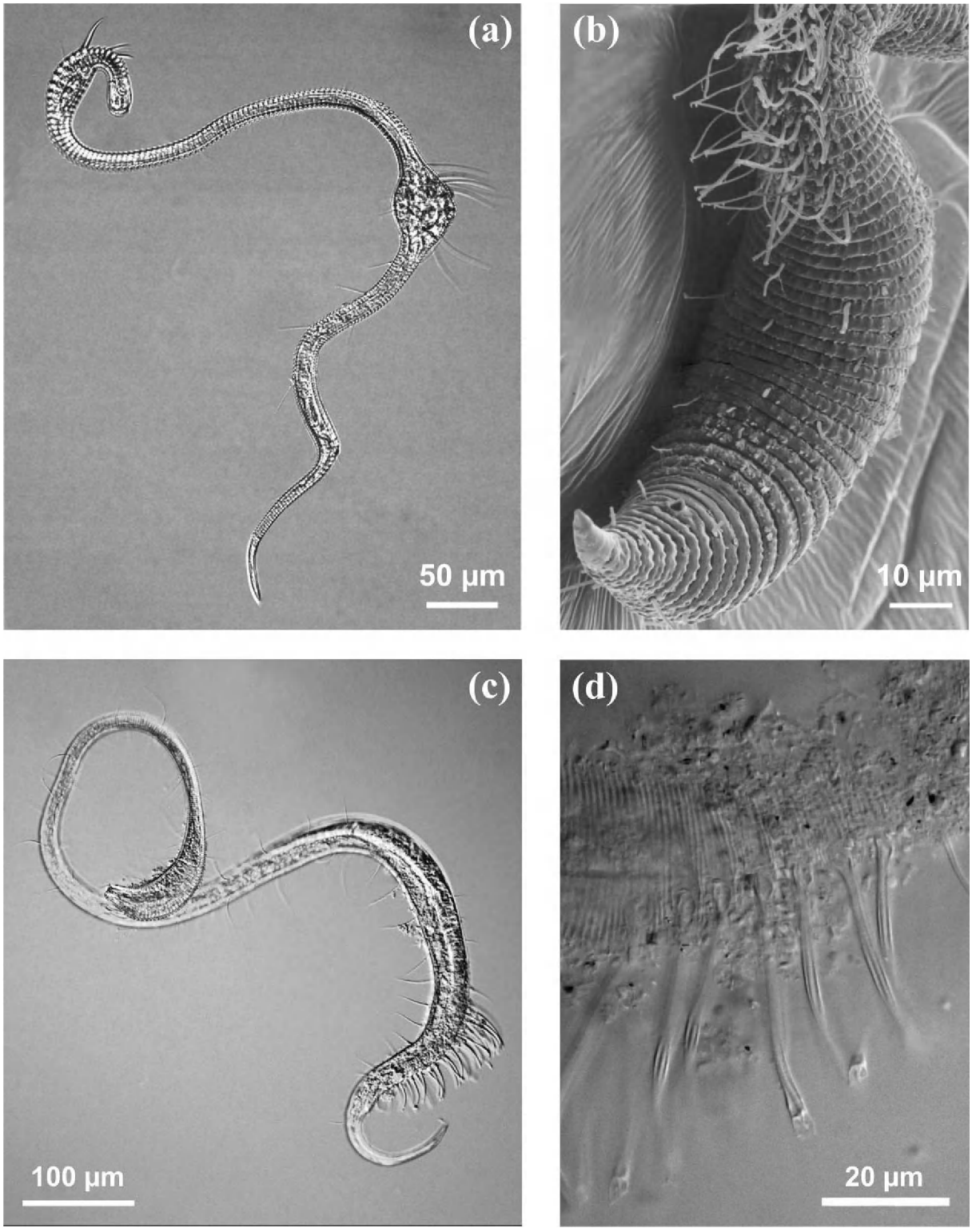

Fig. 4. Some representatives of the nematode families Epsilonematidae and Draconematidae found in the Porcupine Seabight area, and their morphological adaptations to an epifaunal life strategy. (a) *Glochinema trispinatum* Raes, Vanreusel & Decraemer, 2003: habitus; (b) *Bathyepsilonema lopheliae* Raes, Vanreusel & Decraemer, 2003: ambulatory setae; (c) *Tenuidraconema* sp. n.: habitus; (d) *Cygnonema* sp. n.: posterior adhesion tubes.

BIODIVERSITY

The statement by Jensen & Frederiksen (1992) that the associated fauna of *Lophelia pertusa* is as rich and diverse as that of hermatypic branching species of coral has lead to increased efforts to describe the biological diversity of cold-water coral reefs. Although the correctness of this idea is not yet fully proven, for example because tropical coral reefs are much older than cold-water coral reefs and because their diversity is increased by the presence of a higher number of coral species, the presence of coralline algae and a higher diversity of food sources, cold-water coral reefs are without doubt diversity hotspots in the deep sea. Mortensen *et al.* (1995) found that diversity is three times higher on the reefs than in the surrounding soft-bottom. In the present study attention is only focused on the dead *Lophelia pertusa* and associated substrates. According to both Jensen & Frederiksen (1992) and Mortensen *et al.* (1995), the fauna associated with living *Lophelia* colonies is generally poorer than that on dead colonies.

In the foregoing, some strong indications for high taxon diversity, as well as a number of favourable conditions promoting high biodiversity have already been put forward:

1. A total number of 33 groups (taxa and larvae) was identified. This high taxon richness is attributed to the cumulative effect of different communities associated with a large number of different microhabitats due to the process of niche segregation, and due to the lower dominance of nematodes. A possible effect on an even smaller scale (microhabitats within microhabitats) opens up even more perspectives on this subject.

2. Low dominance of the most abundant taxon, Nematoda, and the resulting higher relative abundances of all other taxa was observed. This is thought to be due to the preference of nematodes for interstitial habitats resulting from their morphological (slender body shape) and ecological (feeding strategy, locomotion) adaptations to a life between the sandgrains.

3. It is hypothesised that cold-water coral degradation zones are characterised by high habitat complexity for meiofauna, and that each of the large number of microhabitats favours a certain life style among meiofauna. As each of these life styles require some highly specialised morphological adaptations, several habitat-specific taxa were found, at least on the family level (Nematoda: Epsilonematidae, Draconematidae; Harpacticoida: Tegastidae, Laophontidae).

4. The Porcupine Seabight is an area known to be subject to exceptionally high organic food input (Billett *et al.*, 1983; Lampitt, 1985; Gooday *et al.*, 1996). Abundant food might support a higher number of individuals as well as a higher number of taxa. It is however still not clear whether this is also the case for the Belgica mound region.

5. Large biogenic structures might also act as an efficient food trap. This leads to the idea that cold-water coral degradation zones are possible food hotspots, but associated with an impoverished underlying sediment. Although high food concentrations may support enriched, diverse communities, they can also have a negative effect on biodiversity by creating intensified competitive exclusion of species. According to Lambshead (1993), the occurrence of a spatiotemporal mosaic of small-scale

patches, low disturbance and a low amount of nutrients keeps evenness high and prevents competitive exclusion of species, thus resulting in a high regional species pool. In the underlying sediment these three conditions are fulfilled, implying that this sediment may be home to a very diverse meiobenthic community.

6. Moreover, the food deposited in cold-water coral degradation zones will become patchily distributed between the substrate fragments, in this way adding to the process of niche segregation.

7. These biogenic structures are also thought to provide a low-disturbance environment in which the meiofauna is protected against physical erosion (currents) and predation from higher trophic levels. Frequent large-scale disturbances resulting from strong bottom currents might lead to (1) a high-dominance community or (2) destruction of life and/or habitats. High predation intensity will result in competitive exclusion and therefore a community characterised by high dominance.

8. Turnover is known to be very high in meiofauna, especially in nematodes. High turnover rates are attributed to the limited mobility and conservative reproductive method (*i.e.* lack of larvae with dispersive capacities) in nematodes, characterising them as biogeographically localised organisms with high speciation rates (Castillo-Fernandez & Lambshead, 1990). Combined with the presence of a whole spectrum of small-scale patches within and in between coral and sponge fragments, this could ultimately lead to a high number of species on a small or medium spatial scale.

In conclusion, there is a lot of evidence indicating that cold-water coral degradation zones constitute a highly diverse habitat for deep-sea meiofauna. Diversity values for the entire meiofauna community associated with this habitat (on higher taxon level) are given in Table 3. At present, no diversity measurements on a higher taxonomic level are present for comparison.

		N_0	ET (100)	N_1	H'	N_2	J	N_∞
Coral fragments	(a)	11.30 ± 3.65	7.96 ± 1.58	3.97 ± 1.28	1.33 ± 0.34	2.82 ± 1.00	0.55 ± 0.10	1.90 ± 0.57
	(b)	23	9.65	4.89	1.59	3.24	0.51	2.00
Sponge skeletons	(a)	8.75 ± 2.05	6.25 ± 1.23	2.32 ± 0.33	0.83 ± 0.15	1.63 ± 0.17	0.39 ± 0.06	1.30 ± 0.08
	(b)	15	7.06	2.40	0.88	1.58	0.32	1.27
Mixed substrate	(a)	10.50 ± 6.46	6.81 ± 3.55	2.56 ± 1.36	0.84 ± 0.52	1.68 ± 0.60	0.36 ± 0.14	1.30 ± 0.25
	(b)	20	8.04	2.46	0.90	1.56	0.30	1.26
Underlying sediment	(a)	10.00 ± 2.37	5.93 ± 1.65	1.92 ± 0.60	0.61 ± 0.29	1.37 ± 0.28	0.26 ± 0.11	1.17 ± 0.12
	(b)	19	6.76	2.10	0.74	1.42	0.25	1.20
Entire community		31	8.70	3.46	1.24	2.11	0.36	1.49
p-level		0.52 (NS)	0.16 (NS)	0.0057 (**)	0.0011 (**)	0.0015 (**)	0.000051 (***)	0.0018 (**)

Table 3. Biodiversity indices: Hill's diversity numbers N_0, N_1, N_2 and N_∞, the expected number of taxa for 100 individuals ET (100), the Shannon-Wiener diversity index H' and Pielou's evenness J. Under (a) the average value over all subsamples with its standard deviation is given. Under (b) the value for the total community associated with the respective microhabitat is given. (NS): not significant; (**): highly significant; (***): very highly significant.

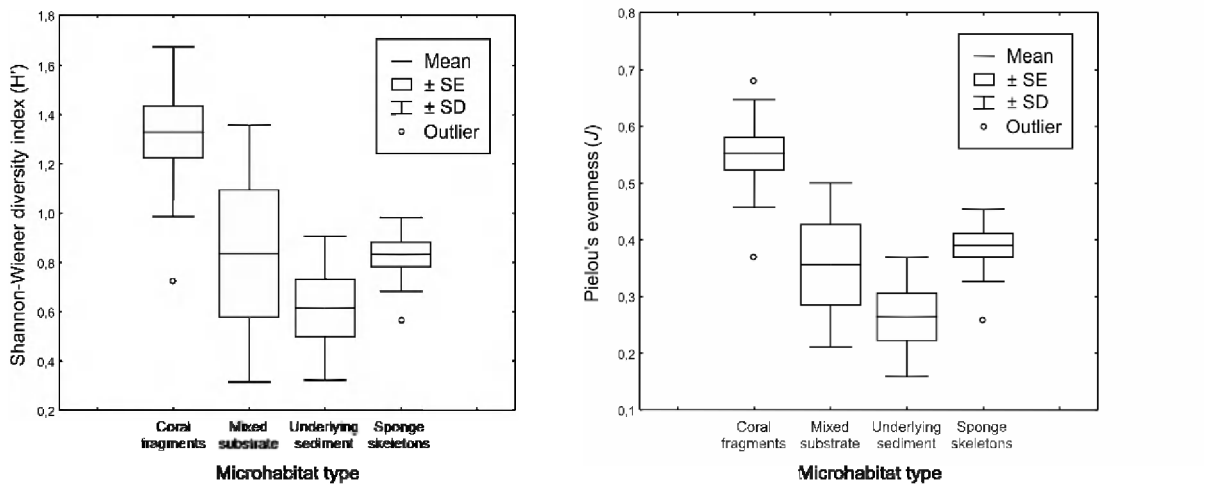

Fig. 5. Box and Whisker plots comparing the microhabitats for the Shannon-Wiener diversity index (*H'*) and Pielou's evenness *J*, a typical equitability index.

Another interesting question is: which microhabitat type harbours the most diverse meiofaunal community? A whole spectrum of biodiversity indices, ranging from indices of taxon richness (N_0) to indices of evenness (N_∞ and *J*), is given in Table 3. An obvious difference in taxon richness between the different microhabitats can also be seen in Table 2b. The exact number of taxa per microhabitat type is given by the overall (b) N_0 in Table 3. Although there are of course differences in microhabitat volume, N_0 gives a good first impression of differences in terms of taxon richness. Clearly, coral fragments house the highest number of taxa (N_0 = 23) whereas sponge skeletons are characterised by the lowest number of taxa (N_0 = 15). The expected number of taxa for 100 individuals E*T* (100), an index not influenced by differences in sample size, is also highest on coral fragments. The same is true for *H'*. Differences between microhabitats are visualised by Box and Whisker plots for *H'* and *J* in Fig. 5. As expected, equitability (*J*) is highest on coral fragments and lowest in the underlying sediment, where nematodes exhibit a high dominance. Except for N_0, all indices indicate that the sediments are the least diverse and that coral fragments support the most diverse communities. All differences were statistically highly or very highly significant, with the exception of N_0 and E*T* (100).

It is also very conspicuous that the entire community has much more taxa than either of the separate microhabitats. This result confirms the statement that the combination of all separate communities results in a high number of taxa (see above).

CONCLUSIONS

1. The presence of large biogenic structures on the sea floor of the continental margin (1) enables more taxa to be present and (2) particularly favours harpacticoid copepods, naupliar larvae and polychaetes. The nematode community responds by a shift to a predominance of typical epifaunal nematodes on the coral fragments.

2. The large biogenic substrates are characterised by a meio-epifaunal community that is significantly dissimilar from the meio-infaunal community in the underlying sediment.

3. The meio-epifaunal community is composed of a sediment-dwelling background community (predominantly nematodes); however with several groups that are more adapted to a life on large biogenic surfaces showing a significantly increased importance.

4. The meio-infaunal community in the underlying sediment is characterised by low densities.

5. Cold-water coral degradation zones are assumed to be biologically diverse. This high biodiversity is attributed to:

a) lower physical disturbance by strong bottom currents and lower predation pressure by higher trophic guilds,

b) a high microhabitat diversity resulting in a high degree of niche segregation. Combined, the communities associated with each microhabitat type give rise to high taxon richness,

c) low dominance of nematodes,

d) assumed abundant food from seasonally deposited phytodetritus, partly resulting from the suggested efficient food trapping function of the biogenic substrates.

6. Of all four microhabitat types, coral fragments support the most diverse communities, whereas the underlying sediments are the least diverse.

ACKNOWLEDGEMENTS

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ADDENDUM 2

SPATIAL DIVERSITY OF NEMATODE AND COPEPOD GENERA OF THE CORAL DEGRADATION ZONE ALONG THE KENYAN COAST, INCLUDING A TEST FOR HIGHER-TAXON SURROGACY

ABSTRACT

Meiofaunal composition, as well as copepod and nematode diversity were examined in the coral degradation zone along the Kenyan coast. Communities from three microhabitat types (coralline sediment, coral gravel and coral fragments) at two locations (Watamu and Tiwi Beach) were analysed. The total number of meiofaunal taxa was higher than in any other tropical coral degradation zone studied so far, but lower than in a cold-water coral degradation zone. Meiofaunal community composition was mainly structured on a local scale, although microhabitat type also had an effect in Watamu. Copepod and nematode communities exhibited comparable trends in biodiversity. The coralline sediment was generally characterised by higher genus richness than the other microhabitats and coral fragments were consistently low in evenness. Differential susceptibility to hydrodynamic disturbance is proposed as an explanation. Coral fragments contributed considerably to the total number of nematode and copepod genera. It is recommended to include this microhabitat in future biodiversity studies on tropical lagoons. Trends in biodiversity were similar for genera and families. The use of family-level identifications in fast screening and comparison of biological diversity is therefore endorsed by our study.

INTRODUCTION

In the marine environment, coral reefs are known as diverse ecosystems in terms of structural habitat complexity and a high variety of associated organisms, determined by both local and regional processes (Cornell & Karlson, 1996; Karlson *et al.*, 2004). Where local processes determine the upper limits of species richness, species richness mainly reflects productivity, climate or disturbance regime, and, ultimately, the number of available niches (MacArthur & MacArthur, 1961, Brown *et al.*, 2001). At local scales, complex habitats are normally richer in species (Downes *et al.*, 1998) because of the increased availability of microhabitats (McNett & Rypstra, 2000), the modification of biotic interactions (Finke & Denno, 2003) and changes in resource partitioning and niche breadth (May & MacArthur, 1972).

In the lagoon between the reef and the adjacent land mass, dead coral material originating from the main reef is progressively degraded until it eventually produces coralline sediment. As a result of this degradation process, a large variety of microhabitat types, each with its typical habitat structure and complexity, is present in this coral degradation zone. The increased level of habitat complexity may have a strong influence on the local diversity of the coral degradation zone ecosystem. Given that small changes in sediment grain size and clay-silt content are able to alter marine benthic communities, the presence of coral degradation products on and in the sediment may also have a profound effect on benthic diversity.

Information on the composition of meiobenthic communities in tropical reef lagoons of the Indian Ocean is scarce (Thomassin *et al.*, 1976; Ólafsson *et al.*, 1995; Ndaro & Ólafsson, 1999). In a first part of this study, the assemblage structure of the meiofauna will be discussed on a higher taxon level, with indication of the local factors that influence it. In a second part, a dual-taxon approach (copepods and

nematodes) will be employed on the genus level to unravel the diversity patterns associated with different microhabitat types. This comparison will be extended to the family level to test for higher-taxon surrogacy, *i.e.* the usefulness of family level diversity information as a proxy of the diversity patterns on a lower taxonomic level (*i.c.* genus level). Both copepods and nematodes are typically characterised by a high species richness, but also by a complex taxonomy and intraspecific and intrageneric variability, whereas identification on the family level is much easier, even for non-specialists.

The importance of this study lies in (1) the dual-taxon approach and (2) the inclusion of coral gravel and coral fragments as potential habitats in tropical meiofauna diversity research. The contribution of these two microhabitats to the total diversity of the coral degradation zone system will be discussed.

MATERIALS AND METHODS

STUDY SITE, SAMPLING PROCEDURE AND TREATMENT OF THE SAMPLES

Meiofauna samples were collected in the coral degradation zone at two locations along the Kenyan coast: Watamu (3°23' S, 40°00' E, collected on 27/02/2002) and Tiwi Beach (4°14' S, 39°36' E, collected on 22-23/02/2002) (Fig. 1). These sampling sites are 104 km apart. At each site, two replicate cylindrical metal cores with a diameter of 30 cm were placed onto the sea floor to delimit a sampling area. Within each of these sampling areas, three microhabitats were sampled: coralline sediment, coral gravel and dead coral fragments (Fig. 2). Coral gravel was, however, not present in our sampling area at Tiwi Beach. Coral gravel differs from coralline sediment because small pieces of coral can still be distinguished in the former microhabitat, whereas this is not so for the coralline sediment. The dead coral fragments were compact and eroded. They constitute the coarsest microhabitat type in this study.

Sampling was carried out under water during snorkeling or skin diving. Within each cylindrical core, three sediment samples were taken with a Perspex sediment core (10 cm^2; up to a depth of 4 cm), coral gravel was gently scooped out with a spoon and the available coral fragments were taken out manually. Coral gravel and coral fragments were put immediately into firm plastic bags or buckets. $MgCl_2$ was added to the bags with coral fragments in order to stun the attached fauna. Subsequently, the fragments were rinsed off thoroughly over sieves with mesh sizes of 1 mm and 32 µm to separate the macrofauna and the meiofauna. The same sieves were used to collect the meiofauna from the coralline sediment and coral gravel. The material collected on the 32 µm sieve was then subjected to density gradient centrifugation, with Ludox (specific gravity 1.18) as a flotation medium (Heip *et al.*, 1985; Vincx, 1996). Meiofauna was fixed with 4% buffered formalin and stained with Rose Bengal. Meiofauna taxa were identified and enumerated under a stereoscopic microscope. From each sample, 200 nematodes and 100 copepods (or all individuals when the number of individuals in the sample was lower than the required number) were picked out at random. Nematodes and copepods were mounted onto glycerol slides. The formalin-ethanol-glycerol technique of Seinhorst (1959) and Vincx (1996) was used for nematodes and a direct transfer to glycerol for copepods. Both nematodes and

copepods were identified to genus level using original descriptions and the following identification keys and reference books: Warwick *et al.* (1998), Lorenzen (1994) and the Desmodoridae key in NeMys (Deprez *et al.*, 2004) for nematodes; Boxshall & Halsey (2004) and Lang (1948, 1965) for copepods.

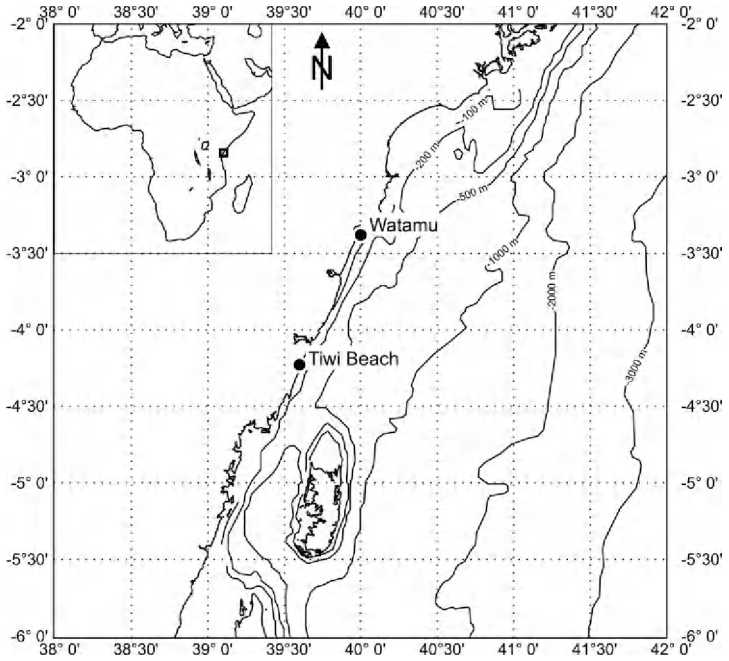


Fig. 1. Map of the Kenyan south coast, with indication of both sampling locations.

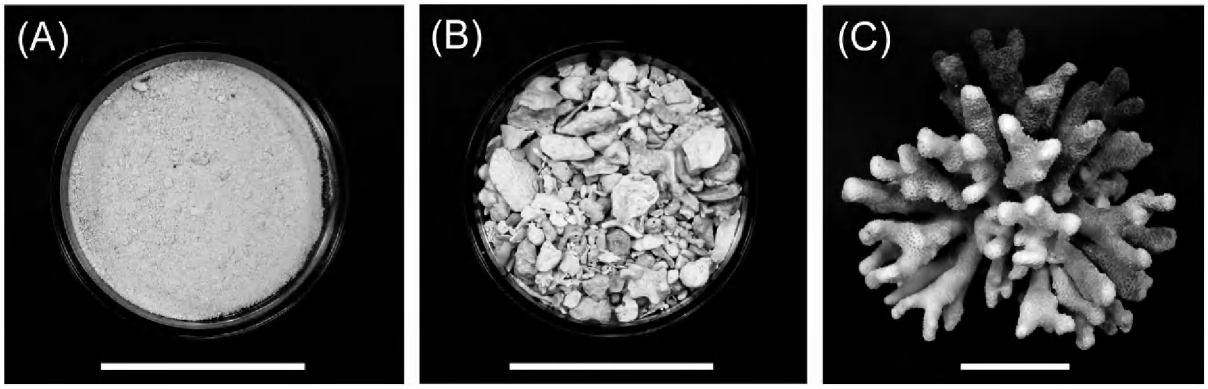


Fig. 2. The three microhabitats. (A) coralline sediment; (B) coral gravel; (C) coral fragment (*Stylophora* is given as an example). Scale bars: 5 cm.

STATISTICAL ANALYSES

The PRIMER5 software (Plymouth Marine Laboratory; Clarke & Gorley, 2001) was used to calculate Bray-Curtis (dis)similarities between all samples. The obtained similarity matrix was used to produce a non-metric multidimensional scaling two-dimensional plot (MDS). The stress value gives a measure for goodness-of-fit of the MDS ordination: a low stress value (<0.2) indicates a good ordination with no real prospect for a misleading interpretation (Clarke, 1993). One-way Analysis of similarities (ANOSIM) was carried out to test for significant differences in the community structure between different groups that were delimited beforehand. Due to large differences in sample size, the

data were standardised and Log(x+1)-transformed prior to the analysis. Similarity of percentages (SIMPER) was used to investigate which taxa were responsible for these differences. The same software was also used to produce genus area plots, based on non-transformed data. The first marker, *i.e.* the one on the Y-axis, gives the number of genera in the coralline sediment. The samples from increasingly coarser microhabitats (first coral gravel, then coral fragments) were subsequently added. The second marker gives the number of genera in all sediment and gravel samples, the third marker for all microhabitats combined.

Parametric (one-way ANOVA) analysis of variance was performed using the STATISTICA6 software. Bartlett's and Cochran's test were used to verify the homogeneity of variances prior to the analysis.

Several biodiversity indices were calculated: the Shannon-Wiener index *H'* and Pielou's evenness *J* (Pielou, 1975), Hill's diversity numbers (Hill, 1973) and the Expected number of Genera for a theoretical sample of 100 individuals E*G* (100). N_0 is identical to the number of species, N_1 = exp (*H'*) and N_∞ reflects evenness. The Expected number of Genera and the Expected number of Families were calculated in analogy with the Expected number of Species (Hurlbert, 1971). Both indices were also used to construct rarefaction curves.

RESULTS

COMPOSITION OF THE MEIOFAUNA

A total of 65337 individuals was counted and 23 meiofaunal groups belonging to 13 phyla were distinguished. The highest number of individuals (24805) and taxa (20) was found in the sediment of Tiwi Beach, whereas the coral fragments from the same location yielded the lowest number of taxa (15) (Table 1). Meiofauna was generally dominated by copepods, except for the sediment samples from Watamu, where nematodes were dominant (Fig. 3; Table 1). The relative abundance of copepods was comparable in different microhabitat types. Adult copepods, their naupliar larvae and nematodes always constituted the three dominant groups. There were considerable differences in the relative abundance of these three groups between both locations (although only significantly so for nematodes (ANOVA; $p = 0.009$) and copepods (ANOVA; $p = 0.02$)), which is especially clear for the sediment samples (Fig. 3). These differences and the importance of copepods in the studied coral degradation zone were also reflected in the low nematode/copepod (N/C) ratios (Fig. 4). In 47.4% of the samples this ratio was below 0.5, *i.e.* there were more than twice as much copepods than nematodes in those samples. There were no significant differences between the N/C ratios of different microhabitats (ANOVA; $p = 0.62$). Overall, polychaetes were the fourth most abundant taxon.

Tiwi Beach sediment (6)		Tiwi Beach coral fragments (3)		Watamu sediment (6)		Watamu gravel (2)		Watamu coral fragments (2)	
taxon	%	taxon	%	taxon	%	taxon	%	taxon	%
Copepoda	55,29	Copepoda	48,15	Nematoda	42,27	Copepoda	56,43	Copepoda	54,09
nauplii	33,59	Nematoda	32,33	Copepoda	29,00	nauplii	23,01	nauplii	19,33
Nematoda	5,49	nauplii	14,48	nauplii	11,02	Nematoda	13,92	Nematoda	18,32
Halacarida	2,06	Polychaeta	2,41	Gastrotricha	5,70	Ostracoda	2,32	Polychaeta	4,26
Amphipoda	1,18	Turbellaria	1,05	Polychaeta	3,95	Polychaeta	1,37	Ostracoda	1,24
Polychaeta	0,88	Halacarida	0,68	Ostracoda	2,80	Gastrotricha	0,77	Amphipoda	0,63
Turbellaria	0,42	Tanaidacea	0,37	Amphipoda	1,32	Amphipoda	0,73	Tanaidacea	0,59
Gastrotricha	0,31	Amphipoda	0,21	Turbellaria	1,10	Tanaidacea	0,38	Tardigrada	0,53
Rotifera	0,18	Ostracoda	0,13	Tardigrada	0,66	Gastropoda	0,31	Halacarida	0,27
Tanaidacea	0,14	Rotifera	0,09	Tanaidacea	0,55	Tardigrada	0,24	Gastrotricha	0,23
Oligochaeta	0,13	Oligochaeta	0,07	Gastropoda	0,44	Turbellaria	0,14	Cumacea	0,16
Kinorhyncha	0,13	Kinorhyncha	0,02	Oligochaeta	0,38	Halacarida	0,10	Oligochaeta	0,09
Ostracoda	0,12	Gastrotricha	0,02	Halacarida	0,33	Bivalvia	0,10	Turbellaria	0,08
Isopoda	0,03	Tardigrada	0,01	Rotifera	0,16	Oligochaeta	0,04	Gastropoda	0,06
Tardigrada	0,02	Isopoda	0,01	Syncarida	0,16	Cumacea	0,04	Isopoda	0,05
Cumacea	0,02			Kinorhyncha	0,05	Isopoda	0,04	Kinorhyncha	0,04
Bivalvia	0,01			Cumacea	0,05	Rotifera	0,03	Bivalvia	0,02
Gastropoda	0,004			Isopoda	0,05	Kinorhyncha	0,01	Priapulida	0,01
Ophiuroidea	0,004					Cnidaria	0,01	Rotifera	0,01
Bryozoa	0,004								
# of individuals	24805		12572		1824		9430		16706

Table 1. Relative abundances of meiofaunal taxa within each microhabitat at both locations, and the total number of individuals per group. The number of samples within each group is indicated between brackets.

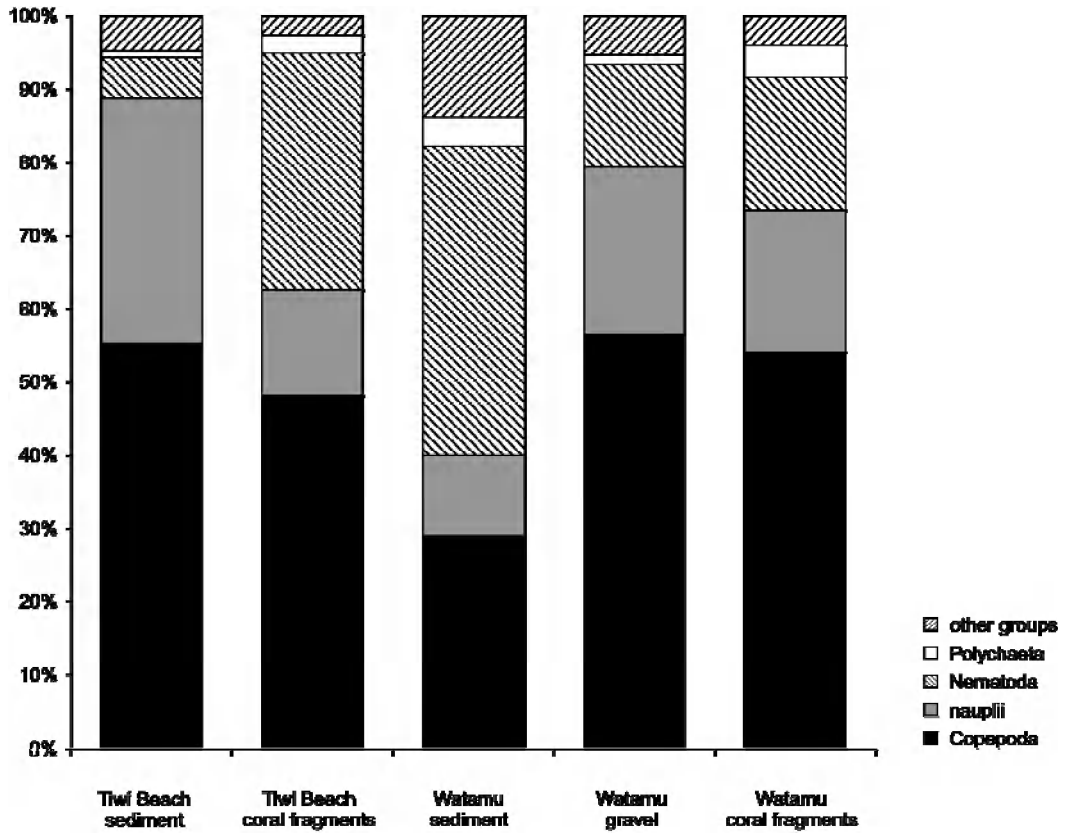


Fig. 3. Stacked columns depicting the composition of the meiofauna and the proportions of the four most abundant meiofaunal groups in the different microhabitats at each location.

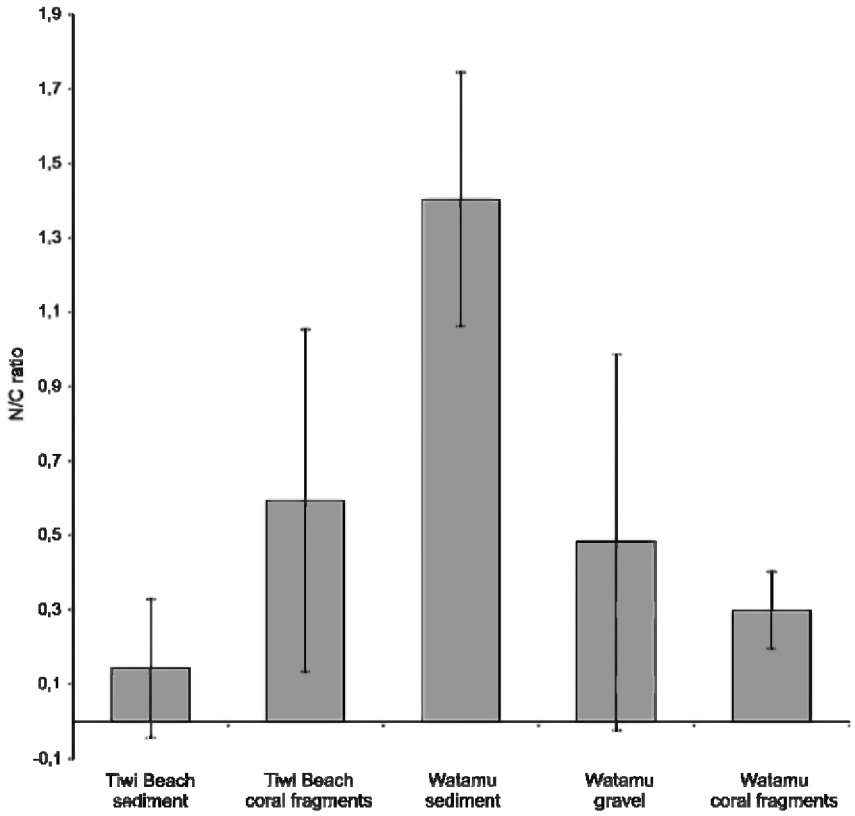


Fig. 4. Nematode/copepod ratios in each microhabitat at both locations (average value and standard deviations).

The meiofaunal communities in Tiwi Beach were significantly dissimilar from those in Watamu (p = 0.001), as pointed out by ANOSIM. Average dissimilarity was low (33.8%) and mainly attributed to nematodes (33.1%; more abundant in Watamu), copepods (23.8%; more abundant in Tiwi Beach) and nauplii (21.8%; more abundant in Tiwi Beach). Only within Watamu a significant structuring effect of microhabitat was observed. At this location, the sediment-dwelling communities were significantly dissimilar from the communities in the other microhabitats (p = 0.029), although average dissimilarity was again low (31.70%). This dissimilarity was mainly attributed to nematodes (12.6%; more abundant in sediment), copepods (28.8%; more abundant in the other microhabitats) and nauplii (16.4%; more abundant in the other microhabitats). The dissimilarities which are mentioned above are visualised in an MDS biplot (Fig. 5).

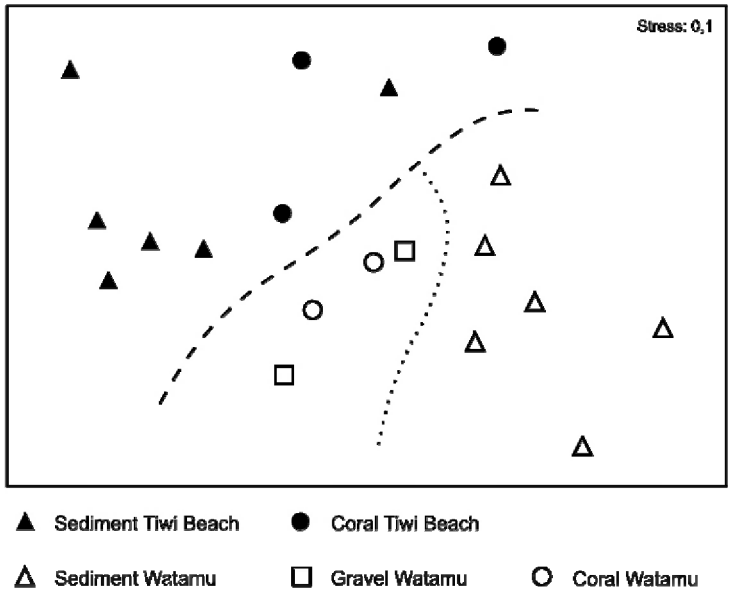


Fig. 5. MDS two-dimensional ordination plot. Stress value is indicated. The dashed line separates samples from different locations (Tiwi Beach – Watamu); the dotted line separates sediment samples from both coral and gravel samples.

		N_0	EG (100)	N_1	H'	J	N_{inf}
Coral fragments	(a)	14.00 ± 4.06	14.00 ± 4.06	8.30 ± 2.85	2.07 ± 0.33	0.79 ± 0.06	3.19 ± 0.93
	(b)	31	18.51	12.08	2.49	0.73	3.59
Coral gravel	(a)	15.50 ± 6.36	15.50 ± 6.36	9.29 ± 5.06	2.15 ± 0.57	0.79 ± 0.09	4.03 ± 2.16
	(b)	24	18.77	11.94	2.48	0.78	4.06
Coralline sediment	(a)	16.33 ± 2.57	16.33 ± 2.57	11.44 ± 2.34	2.42 ± 0.23	0.87 ± 0.05	5.09 ± 1.43
	(b)	46	25.99	21.11	3.05	0.80	8.00
p-level		0.44 (NS)	0.44 (NS)	0.11 (NS)	0.09 (NS)	0.02 (*)	0.06 (NS)

Table 2. Biodiversity indices for copepod communities. Under (a) the average value over all samples and the standard deviation are given. Under (b) the value for the pooled data is given per microhabitat. p-levels are provided for the differences between microhabitats. (NS): not significant; (*): significant ($0.01 < p \leq 0.05$).

		N_0	EG (100)	N_1	H'	J	N_{inf}
Coral fragments	(a)	44.80 ± 11.90	30.74 ± 8.62	20.60 ± 11.64	2.89 ± 0.59	0.76 ± 0.11	4.54 ± 2.65
	(b)	87	35.18	27.98	3.33	0.75	4.36
Coral gravel	(a)	43.50 ± 12.02	30.62 ± 7.31	22.39 ± 7.92	3.08 ± 0.36	0.82 ± 0.04	7.26 ± 1.78
	(b)	64	35.34	32.04	3.47	0.83	11.9
Coralline sediment	(a)	31.33 ± 10.69	28.91 ± 8.36	19.69 ± 7.02	2.91 ± 0.39	0.86 ± 0.09	6.40 ± 2.51
	(b)	115	41.68	46.73	3.84	0.81	10.8
p-level		0.07 (NS)	0.90 (NS)	0.91 (NS)	0.88 (NS)	0.18 (NS)	0.31 (NS)

Table 3. Biodiversity indices for nematode communities. Under (a) the average value over all samples and the standard deviation are given. Under (b) the value for the pooled data is given per microhabitat. The differences between microhabitats were not significant.

LOCAL DIVERSITY OF COPEPODS AND NEMATODES

Lists of identified copepod families and genera are provided in Appendix. All nematode identifications can be found in Chapter 3. For both copepods and nematodes, an overview of several biodiversity indices per microhabitat is given in Table 2 and Table 3, respectively. Moreover, N_0, H', J' and N_{inf} values per microhabitat within each location are visualised in Fig. 6. Only the differences between J-values for the copepod communities of different microhabitats were statistically significant. However, some general and consistent trends were observed. Despite of the dominance of copepods at both locations and in all microhabitats, nematodes yielded a much higher number of genera (Fig. 6a, e). The total number of copepod and nematode genera (N_0; Fig. 6a, e) was highest in the coralline sediment and lowest in the coral gravel. Average values were highest in the sediment for copepods and lowest in the sediment for nematodes. Remarkably, the total number of nematode genera was higher on coral fragments than in the coralline sediment in Tiwi beach (Fig. 6e). The sample size-independent index EG (100) provided similar results, although the lowest total number of expected genera was found on coral fragments instead of coral gravel, and this for both taxa. For copepods, the N_1 and H' values were highest in the coralline sediment, both when working with total and average values. Total values were lowest in coral gravel and average values on coral fragments. For nematodes, total N_1 and H' values were highest in the coralline sediment and average values were highest in coral gravel. Lowest total values were found on coral fragments, lowest average N_1 in the coralline sediment and lowest average H' on coral fragments. Figs. 6b and 6f confirm the comparable behaviour of total H' values for both taxa.

Evenness (J and N_{inf}) in copepod communities was highest in the coralline sediment and lowest on coral fragments, both for total and average values. In nematode communities, the coral fragments were always characterised by the lowest total and average values for both indices and the highest total values were always found in the coral gravel. Highest average values for J were found in the coralline sediment while average N_{inf} values were highest in the coral gravel. The behaviour of these two equitability indices was more or less comparable for both taxa and at both locations (Figs. 6c, d and 6g, h), indicating that the extent of dominance was similar for both copepods and nematodes.

The rarefaction curves (Fig. 7a, b) indicate that, for both taxa, the coralline sediment is clearly more diverse than the other two microhabitats. This is especially clear for copepods. Furthermore, the curves for coral fragments and coral gravel level off more quickly towards higher numbers of individuals than the curve for coralline sediment. Curves for both fragments and gravel are almost identical in copepods and intersect around 100 individuals in nematodes.

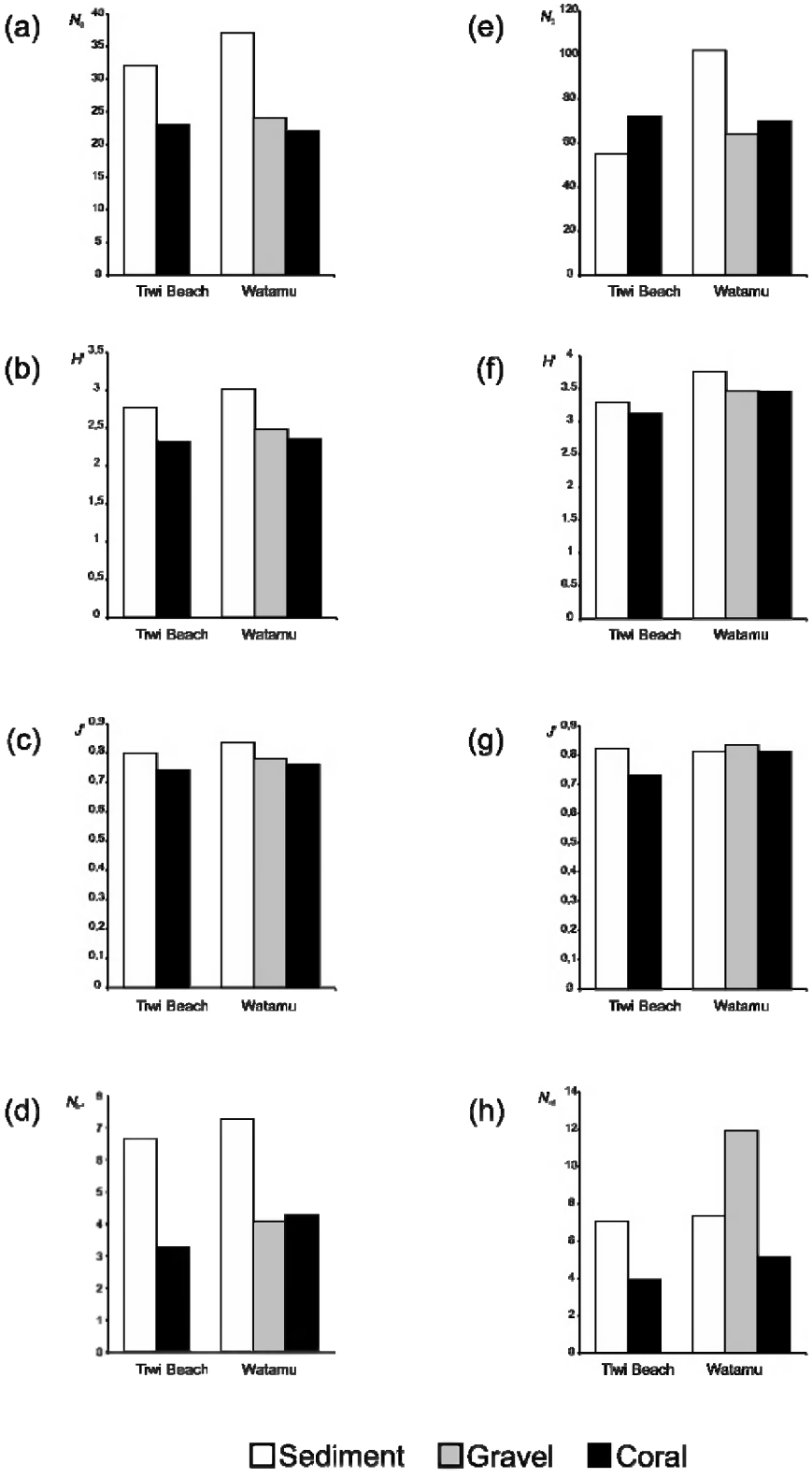


Fig. 6. Clustered columns of N_0, H', J' and N_{inf} values for each microhabitat per location. (a) - (d): total copepod community; (e) - (h): total nematode community.

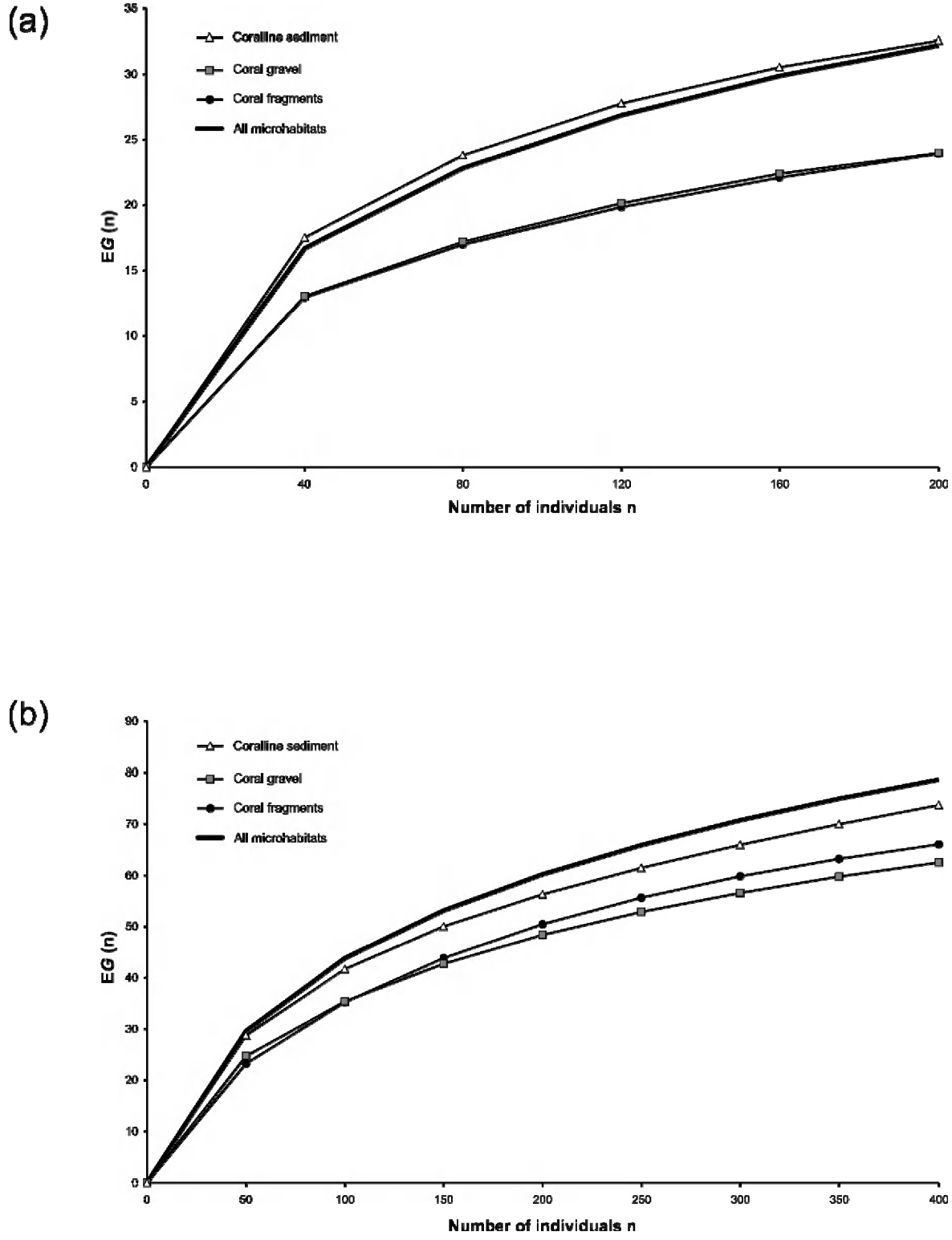


Fig. 7. Rarefaction curves for the pooled data per microhabitat and for the combined community over all microhabitats. (a) copepod genera; (b) nematode genera.

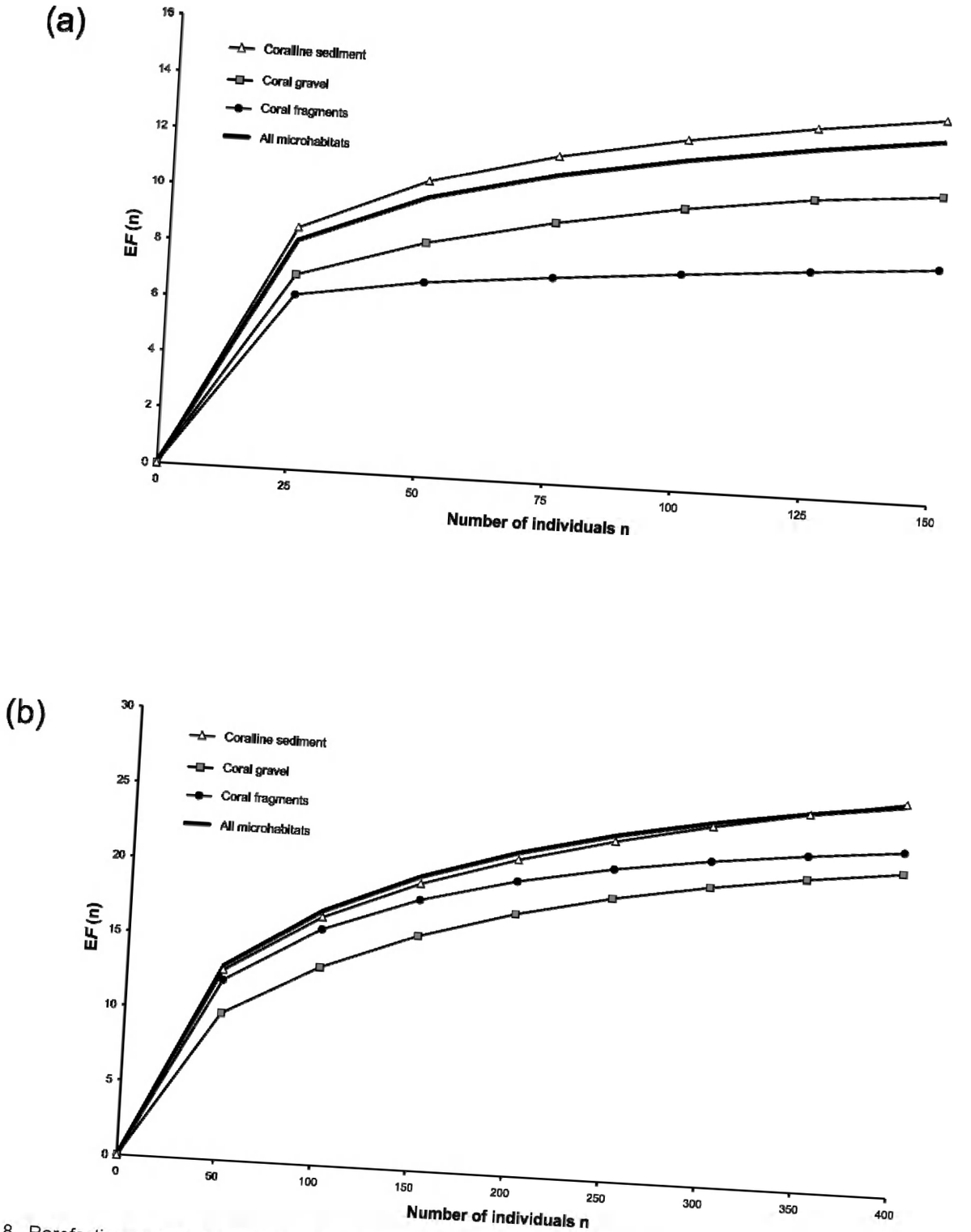


Fig. 8. Rarefaction curves for the pooled data per microhabitat and for the combined community over all microhabitats. (a) copepod families; (b) nematode families.

HIGHER-TAXON SURROGACY

Similar as for the genus data, the number of nematode families is higher than the number of copepod families in each microhabitat: 35 vs. 19 in the coralline sediment, 22 vs. 11 in the coral gravel and 27 vs. 11 on coral fragments. Again, the highest number of nematode families was found in the coralline sediment and the lowest number in coral gravel. The highest number of copepod families was also found in the coralline sediment whereas the coral gravel and coral fragments yielded the same number.

Rarefaction curves based on family level identifications confirm the trends observed on the genus level (Fig. 8a, b). Again, the sediment is clearly more diverse than the other two microhabitats. Furthermore, the curves for coral fragments level off more quickly than the other ones. In contrast to the trend in Fig. 7a, however, the copepod communities on family level are characterised by a clearly higher diversity in the coral gravel than on the coral fragments.

ADDITIVE IMPORTANCE OF MICROHABITATS TO THE LOCAL DIVERSITY OF COPEPODS AND NEMATODES

Rarefaction curves were constructed for the total community added up over all microhabitats, both on the genus and family level (Figs. 7, 8). Only for nematode genera the curve for the total community was higher than for the coralline sediment, and when working with copepod families it was even lower than the sediment curve. In both other cases, the curves were very closely together.

Genus area plots for both copepods (Fig. 9a) and nematodes (Fig. 9b) clearly indicate that coral gravel and coral fragments contribute to the total number of genera in the system. Coral gravel adds only little to the total N_0 in copepod communities (1 genus) while coral fragments add more (6 genera). For the nematode communities, both microhabitats add more or less the same number of genera (10 and 11 genera, respectively). Nevertheless, the contribution of these microhabitats to the number of genera already present in the sediment is rather low: 13% for copepods and 15.5% for nematodes.

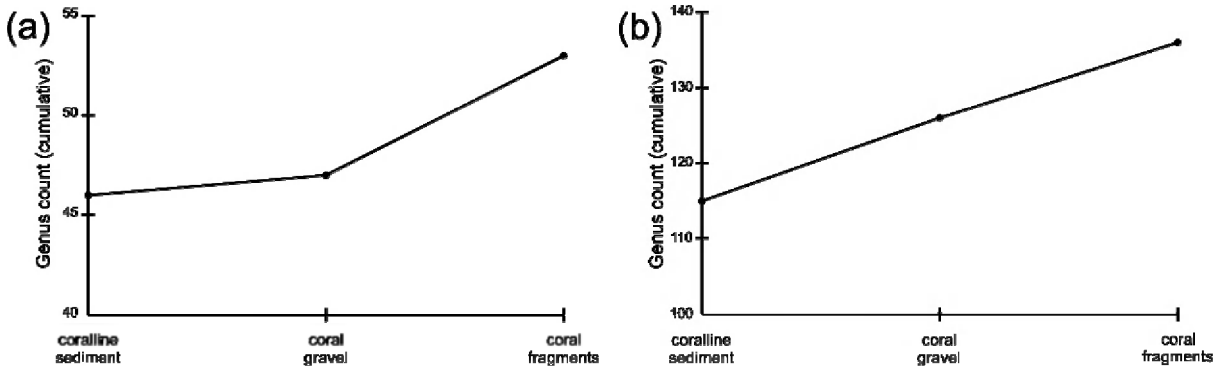


Fig. 9. Genus area plots for the additive importance of microhabitats. (a) copepod genera; (b) nematode genera.

DISCUSSION

COMPOSITION OF THE MEIOFAUNA

The total number of meiofaunal taxa encountered in our study (23) is higher than in any other study on the meiofaunal communities in tropical coral reef-associated lagoons (coral degradation zones). In other surveys, only 10 (Ólafsson *et al.*, 1995) to 18 (Boucher, 1997) taxa was found. This high taxon richness can not only be attributed to the addition of previously unstudied microhabitats in tropical coral degradation zones (*i.c.* coral gravel and coral fragments), as in our study the sediment alone already yielded 21 taxa. Furthermore, it is also not related to a larger sampling area, *i.e.* the additive effect of two distant sampling locations, as we found already 20 taxa in the sediment at Tiwi Beach alone. This is also the first study where Syncarida and Bryozoa are reported. On the other hand, comparison with literature data is not evident because many sources only report the most abundant taxa.

The coralline sediment in tropical coral degradation zones is usually dominated by nematodes (*e.g.* Boucher & Gourbault, 1990; Boucher & Kotta, 1996; Boucher *et al.*, 1998) or copepods (Coull, 1970; Kotta & Boucher, 2001). Other taxa may become locally dominant, such as Polychaeta (Thomassin *et al.*, 1982; Netto *et al.*, 2003) or Gastropoda (Guzmàn *et al.*, 1987). Nevertheless, nematodes, copepods and polychaetes are generally the three most abundant taxa. This is confirmed in our study when the nauplii are added to the total copepod count. Globally, harpacticoid copepods are generally the second most abundant taxon in marine sediments, whereas nematodes are usually dominant (Hicks & Coull, 1983). The relative abundance of harpacticoids increases in coarser, better oxygenated sediments, which is related to their trophic requirements (*i.c.* benthic diatoms; Hicks & Coull, 1983; De Troch *et al.*, 2006) and their sensitivity to low oxygen levels (McClachlan, 1978; Wetzel *et al.*, 2001). According to Hicks & Coull (1983), they are often the dominant meiobenthic taxon in coarse sediments. The dominance of nematodes in the sediment samples from Watamu could thus be related to a lower average grain size. Although average grain size of the sediment has a profound effect on copepod relative abundance, it is clear from our study that even coarser microhabitats such as coral gravel and coral fragments do not exhibit higher abundances of copepods or significantly lower N/C ratios. This could indicate that the amount of food and the extent of oxygenation in coarse sediments is already optimal to establish a well-developed copepod community. Nevertheless, the dominance of copepods in the sediment from Tiwi Beach (89% if nauplii are added) is extraordinary; it is the highest copepod dominance ever recorded in tropical coral degradation zones.

In contrast to the tropical coral degradation zone examined in the study at hand, all microhabitats in a coral degradation zone associated with cold-water coral reefs on the European continental margin were dominated by nematodes, whereas copepods were always the second most abundant taxon (Raes & Vanreusel, 2005). Nevertheless, the coral fragments in that study were characterised by a significantly lower abundance of nematodes compared to the underlying sediment. This was fine-to-medium sediment and therefore the relative abundance of copepods was low. The fact that nematodes were still the dominant taxon on the coral fragments was attributed to sediment infill between the fragments and their branches. Moreover, Vincx *et al.* (1994) and Soltwedel (1997) have

observed an increase of the relative abundance of nematodes with increasing water depth. Of all the taxa encountered in our study only Gastropoda, Syncarida, Ophiuroidea and Bryozoa were not found in the cold-water coral meiofauna, whereas Aplacophora, Sipuncula, Loricifera, Pycnogonida, Tantulocarida, Chaetognatha, Cladocera, Echiura, Holothuroidea and Rotifera were taxa found in the cold-water coral system but not in our tropical system. The total number of taxa in the cold-water coral degradation zone (31) was also higher than in the tropical coral degradation zone of our study (23), despite of the smaller sampling area (only one location on the European margin) and lower number of individuals (only 16547 ind.). This could be related to the higher spatial cover in the study of Raes & Vanreusel (2005) compared to our study. Latitudinal and bathymetric trends may also play a role, either separately or in combination. A latitudinal trend is contradicted by Kotwicki *et al.* (2005), who reported much more meiofaunal taxa on tropical beaches compared to cold regions. On the other hand, the deep-sea is characterised by high diversity (Gage, 1996).

In our sampling area, microhabitat structure was by far the most important structuring factor for nematode assemblages on the genus level, while turnover on a local scale was low in comparison (Raes *et al.*, *submitted* b). On a higher taxon level, however, the communities at different locations are significantly dissimilar from each other and a significant effect of microhabitats was only present in Watamu. The dissimilarity between both locations was mainly attributed to a higher relative abundance of nematodes in Watamu, which is consistent with the high abundance of nematodes in the sediment samples at this location. This high abundance of nematodes in the Watamu sediment is also the main reason why the meiofaunal community in the sediment is significantly dissimilar from that in the other microhabitats at the same location. The low average dissimilarities between meiofaunal communities at each location and between microhabitats at Watamu indicate either limited differences between locations/microhabitats or considerable differences within a location/microhabitat.

LOCAL DIVERSITY OF NEMATODES AND COPEPODS AND THE ADDITIVE IMPORTANCE OF MICROHABITATS

The copepod and nematode communities exhibited similar trends in biodiversity when comparing the three microhabitat types. For some indices the trends were even identical. On the other hand, the trends of values for the total community were sometimes different from the trends of the average values. The low average N_0 values for nematodes in the sediment can be explained by the low number of individuals per sediment sample, especially in comparison with gravel and coral samples. Moreover, most trends were not significant. This indicates that considerable differences occur between samples within the same microhabitat, which could be related to different conditions on a small scale or to differences in sample size. Nevertheless, the sediment was generally characterised by higher genus richness for both taxa. Given that harpacticoid copepods and nematodes react in opposite ways to increased sediment grain size, it is remarkable that they exhibit similar patterns in genus richness. However, diversity of both copepods and nematodes in tropical lagoons is known to be higher in relatively calm, undisturbed areas compared to areas characterised by high physical, mainly hydrodynamic, stress (Coull, 1970; Villiers & Bodiou, 1996; Boucher & Lambshead, 1995). In analogy, the higher diversity in the coralline sediment could reflect lower disturbance, *i.c.* in the deeper parts of

the sediment. Coral fragments are rather large biogenic substrata that lie relatively unprotected on the sea floor, and coral gravel was collected only from the surface. These microhabitats could therefore be more subjected to hydrodynamic stress than the deeper portions of the sediment. Although the surface layers of the sediment may be disturbed to the same extent as the other microhabitats, the deeper parts are not and this could result in higher diversity measures in our sediment samples. The sampling sites were indeed characterised by considerable current activity (M.R., pers. obs.). Strong currents will keep a lot of the organic food in suspension and will therefore deprive the meiofauna associated with the surface of our microhabitats of a stable food source. Furthermore, frequent erosion by currents will also have a direct physical effect on the animals. Because of their elevated position on the sea floor, coral fragments are thought to be most exposed to hydrodynamic disturbance. This is confirmed by the low observed evenness on coral fragments for both nematodes and copepods.

Due to the irregular shape of its biogenic particles, microhabitat complexity is high in marine carbonate sand because angular carbonate grains allow for increased interstitial space. This promotes copepod diversity (Coull, 1970). On the other hand, nematode diversity is much lower in carbonate sands than in quartz sands (Alongi, 1986; Ólafsson *et al.*, 1995; Boucher, 1997), which is probably related to the more irregular structure of the interstitia.

Although the pooled, combined community (Fig. 7: all microhabitats) is not a true reproduction of the natural situation (because the prevalence of the sediment in the natural system was not accounted for), it can still be used to investigate to what extent the coral gravel and coral fragments contribute to the diversity of the system. It is clear from Fig. 7b that the addition of structurally complex microhabitats to the local habitat has a positive effect on nematode diversity. For copepods this is not so clear, as the total community (*i.e.* all microhabitats combined) is slightly less diverse than the sediment in terms of E*G* (n). This is due to the much lower copepod diversity in the added microhabitats, which causes lower E*G* (n) values when added to the total community. Nevertheless, increased habitat complexity should have a positive effect on diversity. For example, it is known that micro-spatial complexity of marine algae allows for significant linearly related increases in associated harpacticoid species number and diversity (Hicks, 1980). On the other hand, the addition of habitat structure may lead to increased copepod diversity as a result of increased surface area rather than increased complexity, which was demonstrated by an artificial seagrass plants experiment (Jenkins *et al.*, 2002). Genus area curves were more successful in visualising the additive effect of all microhabitats. It is clear that although the sediment alone already harbours most of the taxa present at the sampling locations, both microhabitats do contribute to genus richness. Whereas coral gravel only adds one genus to the total copepod genus pool, the contribution of coral fragments is considerable for both taxa. This is an important argument to recommend that coral fragments should also be considered when calculating copepod and nematode diversity in coral degradation zones. The fact that this microhabitat has been ignored in previous studies could therefore have had its effect on the calculated diversity numbers.

HIGHER-TAXON SURROGACY

According to Somerfield & Clarke (1995) and Kotta & Boucher (2001), the patterns of nematode abundance and assemblage structure at the levels of species and genera are similar, although aggregations at an even higher taxonomic level result in a notable shift in assemblage structure. This would mean that higher-taxon surrogacy for analysing abundance and assemblage structure is only applicable for the two lowest taxonomical units. Herman & Heip (1988), however, observed that for both copepods and nematodes, family data still allowed for a more or less clear separation of stations in multivariate analyses. For nematodes, the same was even true when working with orders. The authors concluded that for a multivariate analysis of the communities, taxonomical grouping allows for results that are just as good as, but not better than, the species data. Our approach was different, in that we did not compare community composition or abundance, but diversity. Our results indicate that family-level identifications could be sufficient to unravel the major trends in diversity of nematodes and copepods. The resemblance between the rarefaction curves for nematode genera and families is especially striking. This can have far-reaching consequences in terms of the time and intensity of identification. It also endorses the use of family-level identifications for fast assessment and comparison of biological diversity, *e.g.* in conservation planning. It could even be a good alternative for molecular barcoding, another fast screening method used for biodiversity assessment, which is however less suitable in marine ecosystems because of the difficulties associated with the sequencing of marine nematodes. Analogous results were obtained by Vincx (1990) for North Sea nematodes, which confirms the use of family-level identification to unravel diversity trends. However, the usefulness of diversity patterns on family level as a proxy for the patterns of species or genus level biodiversity is not yet confirmed for other meiobenthic taxa or for other environments. For example, an analogous comparison with terrestrial organisms has shown that family-level surrogacy for species-based biodiversity information is not always applicable (van Jaarsveld *et al.*, 1998).

Ameiridae Monard, 1927	Miraciidae Dana, 1846
Canthocamptidae Sars, 1906	Orthopsyllidae Huys, 1990
Canuellidae Lang, 1944	Paramesochridae Lang, 1944
Cletodidae T. Scott, 1905	Parastenheliidae Lang, 1936
Ectinosomatidae Sars, 1903	Porcellidiidae Boeck, 1865
Harpacticidae Dana, 1846	Tegastidae Sars, 1904
Laophontidae T. Scott, 1905	Tetragonicipitidae Lang, 1944
Longipediidae Sars, 1903	Thalestridae Sars, 1905
Louriniidae Monard, 1927	Tisbidae Stebbing, 1910
Metidae Sars, 1910	

Appendix 1. List of identified copepod families. Taxonomy after Boxshall & Halsey (2004).

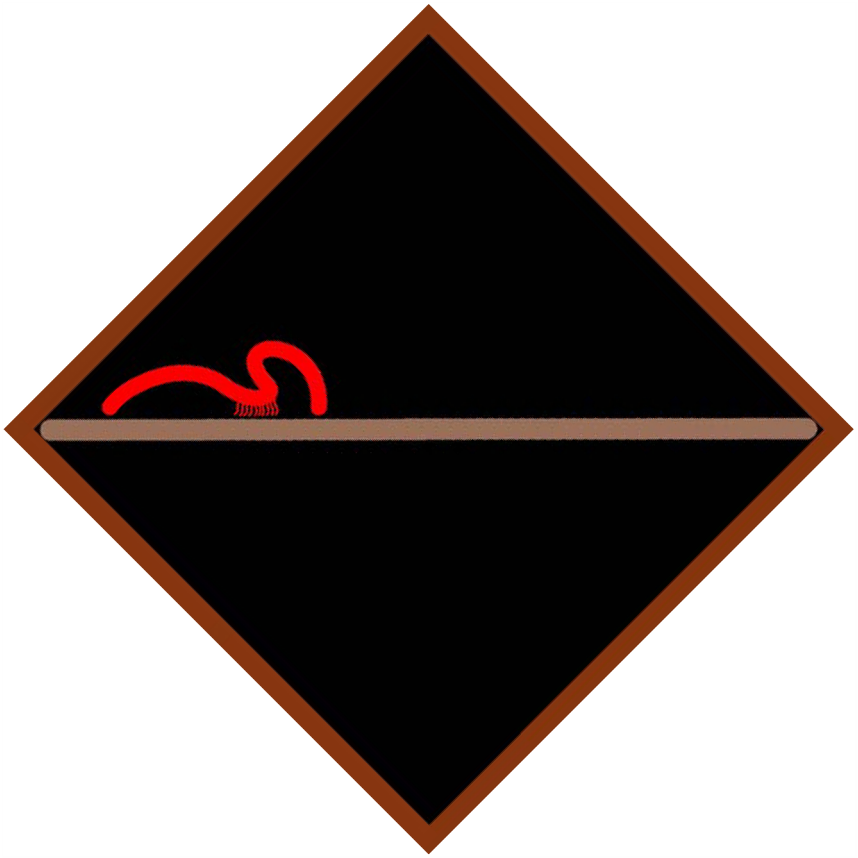
Ameira Boeck, 1865	*Orthopsyllus* Brady & Robertson, 1873
Amphiascus Sars, 1905	*Paradactylopodia* Lang, 1944
Apodopsyllus Kunz, 1962	*Paralaophonte* Lang, 1944
Bradya Boeck, 1873	*Paramesochra* T. Scott, 1892
Brianola Monard, 1927	*Parastenhelia* Thompson & A. Scott, 1903
Canthocamptus Westwood, 1836	*Peltidiphonte* Gheerardyn, Fiers, Vincx & De Troch, 2006
Cletodes Brady, 1872	*Phyllocamptus* Sars, 1911
Cyclopoida sars, 1866	*Phyllopodopsyllus* T. Scott, 1906
Dactylopusis Norman, 1903	*Phyllothalestris* sars, 1905
Diagoniceps Willey, 1930	*Porcellidium* Claus, 1860

Diarthrodes G.M. Thomson, 1883
Diosaccus Boeck, 1873
Echinolaophonte Nicholls, 1941
Ectinosoma Boeck, 1865
Enhydrosoma Boeck, 1873
Eudactylopus A. Scott, 1909
Harpacticus Milne Edwards, 1840
Heterolaophonte Lang, 1944
Idomene Philippi, 1843
Kliopsyllus Kunz, 1962
Laophonte Philippi, 1840
Longipedia Claus, 1862
Lourinia C.B. Wilson, 1924
Mesochra Boeck, 1865
Metis Philippi, 1843
Mwania Fiers & De Troch, 2000
Nitokra Boeck, 1865
Robertgurneya Lang, 1944
Schizacron Gee & Huys, 1996
Schizopera sars, 1905
Scottopsyllus Kunz, 1962
Scutellidium Claus, 1866
Stenhelia Delavalia (Brady, 1869)
Stenhelia Melima (Por, 1964)
Stenocopia Sars, 1907
Stylicletodes Lang, 1936
Tegastes Norman, 1903
Tetragoniceps Brady, 1880
Thalestris Claus, 1862
Tisbe Lilljeborg, 1853
Typhlamphiascus Lang, 1944
Zaus Goodsir, 1845
Zausodes C.B. Wilson, 1932

Appendix 2. List of identified copepod genera. Taxonomy after Boxshall & Halsey (2004).

CHAPTER 5

EPSILONEMATIDAE (NEMATODA) FROM A COLD-WATER CORAL ENVIRONMENT IN THE PORCUPINE SEABIGHT, WITH A DISCUSSION ON THE STATUS OF THE GENUS *METAGLOCHINEMA* GOURBAULT & DECRAEMER, 1986



Paper published

Raes, M., Vanreusel, A., Decraemer, W. (2003)

Epsilonematidae (Nematoda) from a cold-water coral environment in the Porcupine Seabight, with a discussion on the status of the genus *Metaglochinema* Gourbault & Decraemer, 1986

Hydrobiologia 505, 49-72

(original manuscript)

5.1. ABSTRACT

Thirteen species of nematodes from the family Epsilonematidae Steiner, 1927 were found to be associated with a cold-water coral reef in the Porcupine Seabight. Among them, four species were already known from various locations such as Chile and Papua New Guinea. Three new species are described here: *Glochinema trispinatum* sp. n. is recognised by three dorsal thorns in the pharyngeal region. This species was also recovered from the Antarctic shelf. *Epsilonema multispiralum* sp. n. is characterised by a multispiral amphid consisting of 3.25 coils. *Bathyepsilonema lopheliae* sp. n. is characterised by its body length, the position and relative width of the amphids and the nature of the cuticular ornamentation. Within the subfamily Glochinematinae Lorenzen, 1974, the number and arrangement of ambulatory setae is considered not to be of diagnostic importance. The former species *Metaglochinema strigosum* Gourbault & Decraemer, 1993 is therefore classified under the genus *Glochinema* Lorenzen, 1974. The original genus diagnosis of *Metaglochinema*, now a monotypic genus[1], is adjusted. The geographic distribution of epsilonematid nematodes is briefly discussed.

Key words: Epsilonematidae, Glochinematinae, cold-water corals

5.2. INTRODUCTION

Epsilonematidae are marine nematodes with a characteristic ε-shaped body. The family is composed of 3 subfamilies: Epsilonematinae Steiner, 1927, Glochinematinae Lorenzen, 1974 and the monospecific Keratonematinae Gourbault & Decraemer, 1986. They occur frequently in the marine interstitial fauna but until recently, epsilonematid nematodes were unknown from deep-sea habitats (Decraemer *et al.*, 2001). In 2001, a new species *Glochinema bathyperuvensis* Neira *et al.*, 2001 was found in oxygen-limited bathyal sediments from the Peru margin (Neira *et al.*, 2001). Another species of the same genus (*G. kentrosaurides* Gad, 2002) was found recently on the plateau of the Great Meteor Seamount at 455 m depth (Gad, 2002). Epsilonematidae are known to have a looper-caterpillarlike locomotion (Lorenzen, 1973a). This infers a preference for habitats providing fixed anchor points, such as coarse sands, carbonate sands and biogenic structures. Although coral fragments can be regarded as ideal substrates for epifaunal nematodes such as Epsilonematidae and Draconematidae, the meiofauna associated with cold-water corals has never been studied before. Degradation processes in coral reefs provide fragments of different sizes and shapes, resulting in a very high habitat complexity, especially when mixed with the sediment.

Nine new and four known species of Epsilonematidae were found to be associated with the cold-water coral *Lophelia pertusa* (Linnaeus, 1758). Three new species are described here, completed with SEM photos.

[1]Type species of *Metaglochinema* is *M. globicephalum* Gourbault & Decraemer, 1986.

5.3. MATERIALS AND METHODS

Material was obtained with a NIOZ box corer (ø 32 cm) during the 9-19th June 2000 sampling campaign on the RV Belgica. The examined boxcore was collected on the 17th of June 2000, from the top of a coral mound in the Belgica Mounds region (Porcupine Seabight, coordinates: 51°24'48,2" N and 11°45'55,4" W). The boxcore penetrated about 15 to 20 cm into the sediment. The surface of the sediment was totally covered with several pieces of dead sponges (*Aphrocallistes bocagei* Schultze, 1886) and dead corals (*Lophelia pertusa* (Linnaeus, 1758)). The larger sponge and coral fragments were collected separately and fixed with 4% formaldehyde. Three bulk sediment cores of 10 cm^2 were taken.

A first stage juvenile of *Bathyepsilonema lopheliae* sp. n. was found in samples obtained from the same location during a may 2001 sampling campaign on the RV Belgica.

The *Lophelia* and sponge material was rinsed over a 1 mm and a 32 µm sieve. Meiofauna extraction from the sediment was done by density gradient centrifugation, using Ludox (density 1.18) as a flotation medium (Heip *et al.*, 1985; Vincx, 1996). Nematodes were picked out individually and mounted on slides for detailled morphological observation with a Leica DMLB light microscope.

An image analysis apparatus (consisting of a Leitz Dialux 20 microscope, a Sanyo CCD videocamera and the Quantimet 500 software) was used to perform the measurements of several type specimens.

Scanning electron microscopic pictures were taken from formalin fixed specimens. After an ultrason treatment (to remove detritus attached to the body) the specimens were transferred in OsO_4, dehydrated, dried (*critical point drying*) and coated with gold particles.

Type material is stored in the collection of Ghent University, Museum voor Dierkunde (UGent), the Koninklijk Belgisch Instituut voor Natuurwetenschappen in Brussel (KBIN) and the Natural History Museum in London (NHM).

5.4. ABBREVIATIONS USED

L: total body length
N: number of cuticular rings, smooth tail tip not included
cs: length of the cephalic setae
dcs: distance from the anterior edge to the cephalic setae
Hdw: maximal width of the head capsule
Hdl: length of the head capsule
Amphw: amphidial width
Amph%: (Amphw / Hdw)*100
Ph: pharyngeal length, measured from the anterior end of the head capsule to the posterior border of the pharyngeal bulb, cardia not included
Asl: length of the anteriormost ambulatory seta of the outer subventral row
sup: length of the supporting setae

mvAsl: length of the middle medioventral or subventral ambulatory seta on the posterior body enlargement

mlvAsl: length of the middle lateroventral ambulatory seta on the second body enlargement

tail: tail length

tmr: length of the non-annulated tail tip

mbd ph: body diameter at the level of the pharyngeal bulb

mbd: maximal diameter of the posterior body region

(mbd): minimal body diameter

mbd/(mbd): proportion of the minimal body diameter to the maximal body diameter

ABD: anal body diameter

spic: length of the spicule, measured along the central axis of the structure

gub: length of the gubernaculum, measured along the central axis of the structure

V%: position of the vulva as a percentage of the total body length, measured from the anterior end

a: de Man a-ratio, *i.e.* L / mbd

b: de Man b-ratio, *i.e.* L / ph

c: de Man c-ratio, *i.e.* L / tail

5.5. DESCRIPTIONS

* Remark regarding the descriptions: terminology concerning cuticular appendages was adapted from Verschelde & Vincx (1994).

Family **Epsilonematidae Steiner, 1927**

Subfamily **Glochinematinae Lorenzen, 1974**

Genus ***Glochinema* Lorenzen, 1974**

***Glochinema trispinatum* sp. n.** (Figures 1-4)

Type specimens

Holotype male on slide RIT 676. Paratype males, females and juveniles on slide numbers RIT 677-681, 683, 688 (KBIN), MDNC 4021-4025, 4032, 4035 (UGent), other paratypes 2003.329-2003.334, 2003.336, 2003.337 and 2003.340-343 are stored at NHM.

Type locality. Porcupine Seabight, Belgica mounds, at a depth of 1005 m. Coordinates: 51°24'48,2" N and 11°45'55,4" W.

Other representatives were found in the Belgica mound region at 51°25'7.74" N and 11°46'9,32" W, and in Antarctica (see second remark).

Date of collection. 17th of june 2000.

Type habitat. Deep sea environment, on the top of a coral mound. Associated with cold-water coral reef degradation zones. Epifaunal on sponge and coral fragments, as well as in the sediment.

Relative abundance. This species comprises 3.43% of the total nematode community at the type locality.

Etymology. The name refers to the number of pharyngeal thorns present in this new species. *Tri* comes from the Latin *tres, tria* (three); *spinatum* comes from the Latin noun *spina, spinae* (thorn).
Measurements: Table 1

Males

The body is elongated, slender and clearly epsilon-shaped, with a very long anterior body region (Fig. 1D). There are pronounced enlargements at the level of the pharynx and in the posterior body region, at the level of the testis. At this last level the body reaches its maximal body diameter. The head and the first part of the pharyngeal region are curved ventrally, behind them the first dorsal curvature is situated. Along this curvature, the body is straight and slender. The first dorsal curvature is followed immediately by the ventral curvature. Behind this conspicuous 'S', the second body enlargement is situated, followed by the second dorsal curvature. There is a very thin and long tail clearly oriented dorsally.

The cuticle is built up of 245-271 broad cuticular annules, counted dorsally. This number includes the partial annules present on the tail. Scanning electron micrographs indicate the presence of a zone with longitudinal rods (just as found on body annules) at the posterior edge of the head capsule (Fig. 3A). With a light microscope this 'first annule' cannot even be distinguished, so we do not consider this structure a separate annule.

The anteriormost annules are directed anteriorly. There are three inversions of orientation (►) along the body, so that in the posterior body region the annules are directed posteriorly. The location of these inversion sites is highly variable: the first inversion occurs somewhere between the annules 72 and 88 on the ventral side and between annules 76 and 92 on the dorsal side; the second inversion between annules 89 and 105 ventrally and between annules 84 and 104 dorsally; the third inversion occurs somewhere between annules 116 and 128 ventrally and between annules 116 and 137 dorsally. It was found that there is a certain correlation between the position of these inversion sites and the total number of body annules (indeed when the number of annules is higher, inversion sites occur further down the body, *i.e.* on annules of higher number. This can also be seen in the relative position of the inversion sites and the combs (see below)). Only a limited degree of overlap was observed between the annules, especially in the pharyngeal region and at the level of the ventral curvature. Body annules are narrowest posterior to the ventral curvature, especially at the level of the second enlargement. Very broad annules are found in the pharyngeal region, and around the cloacal opening. All annules are ornamented with longitudinal ridges, which are actually local elevations of the cuticle. Such elevations are most pronounced on the anterior edge of the annule, sometimes forming small protruding spines. This is obvious on the anterior annules (Fig. 3A) and in the cloacal region, but especially at the level of the ventral curvature (on annules 88-103 in the holotype male) were the (elongated and bent) spines group on the ventral side to form comb-like structures (Figs. 3B-D). These combs tend to occur immediately behind the first ventral inversion site.

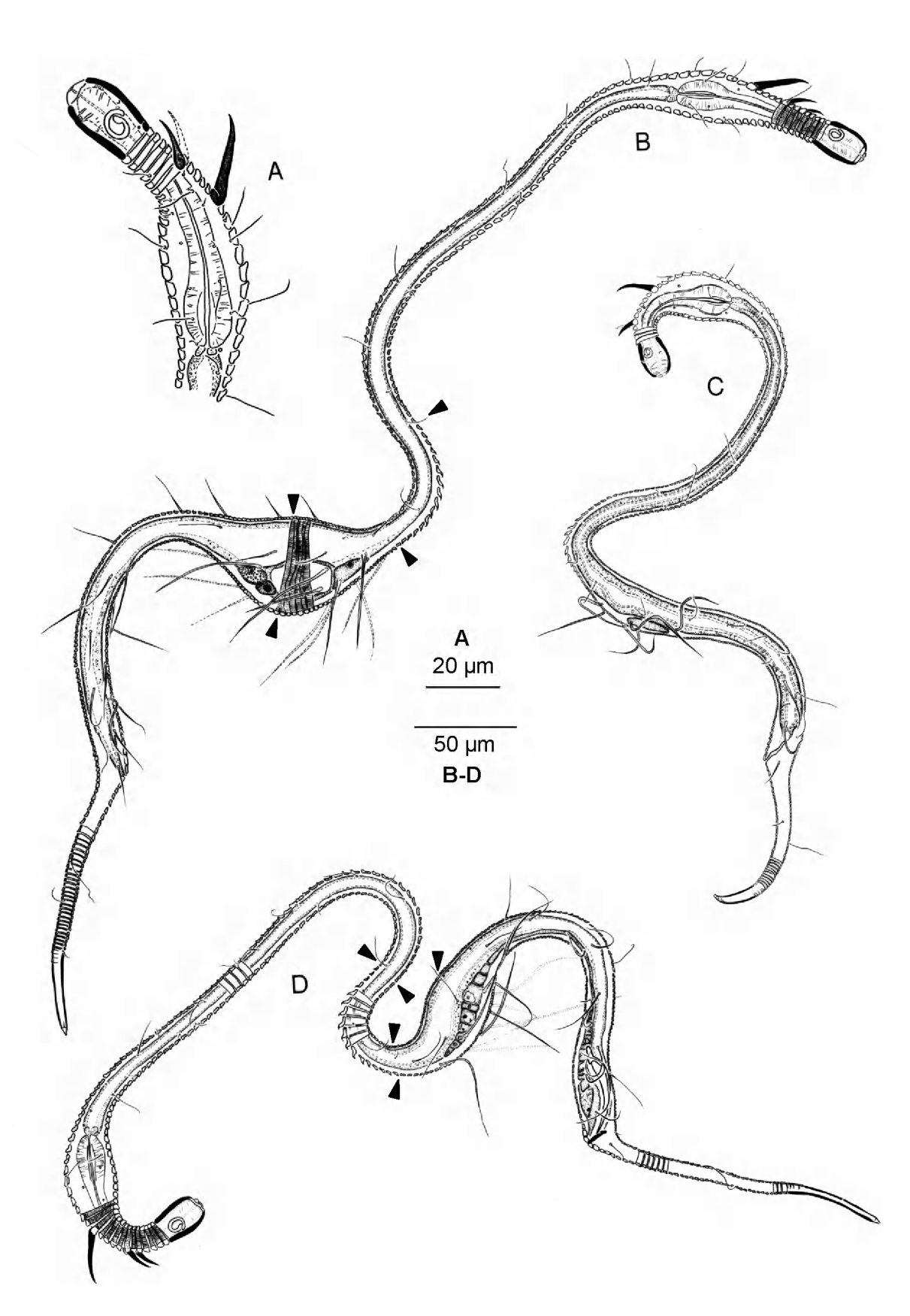


Fig. 1. *Glochinema trispinatum* sp. n. (A) paratype ♂, head and pharynx. Cephalic and subcephalic setae only represented by their insertion sites; (B) paratype ♀, habitus. The mid body is slightly turned, which makes the vulva unclear; (C) juvenile IV, habitus; (D) holotype ♂, habitus. One cephalic seta only represented by its insertion site. Inversion sites are indicated with arrows.

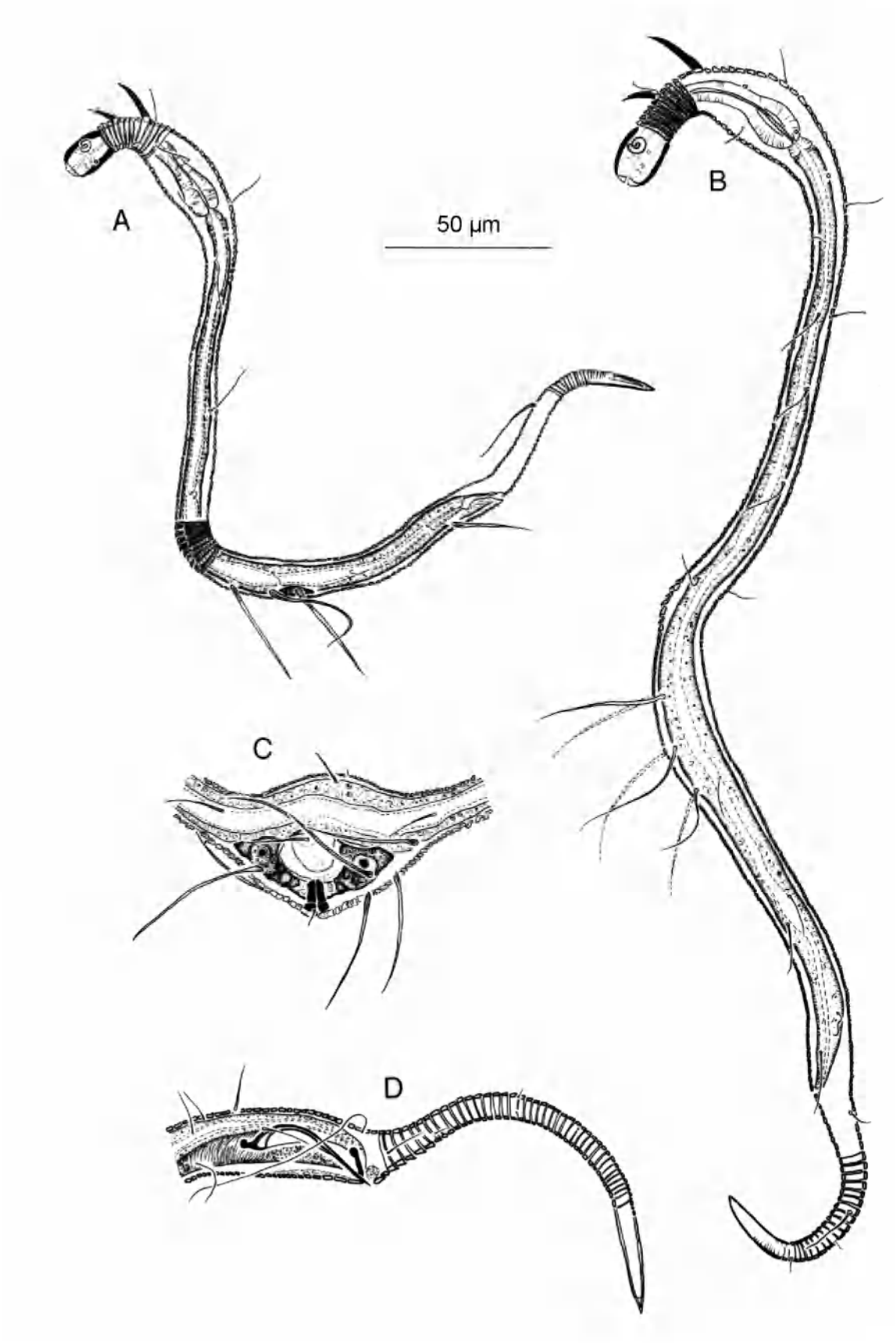


Fig. 2. *Glochinema trispinatum* sp. n. (A) juvenile II, habitus; (B) juvenile III, habitus. One supporting seta not present in this specimen; (C) paratype ♀, detail of reproductive system; (D) paratype ♂, spicular apparatus and tail in surface view.

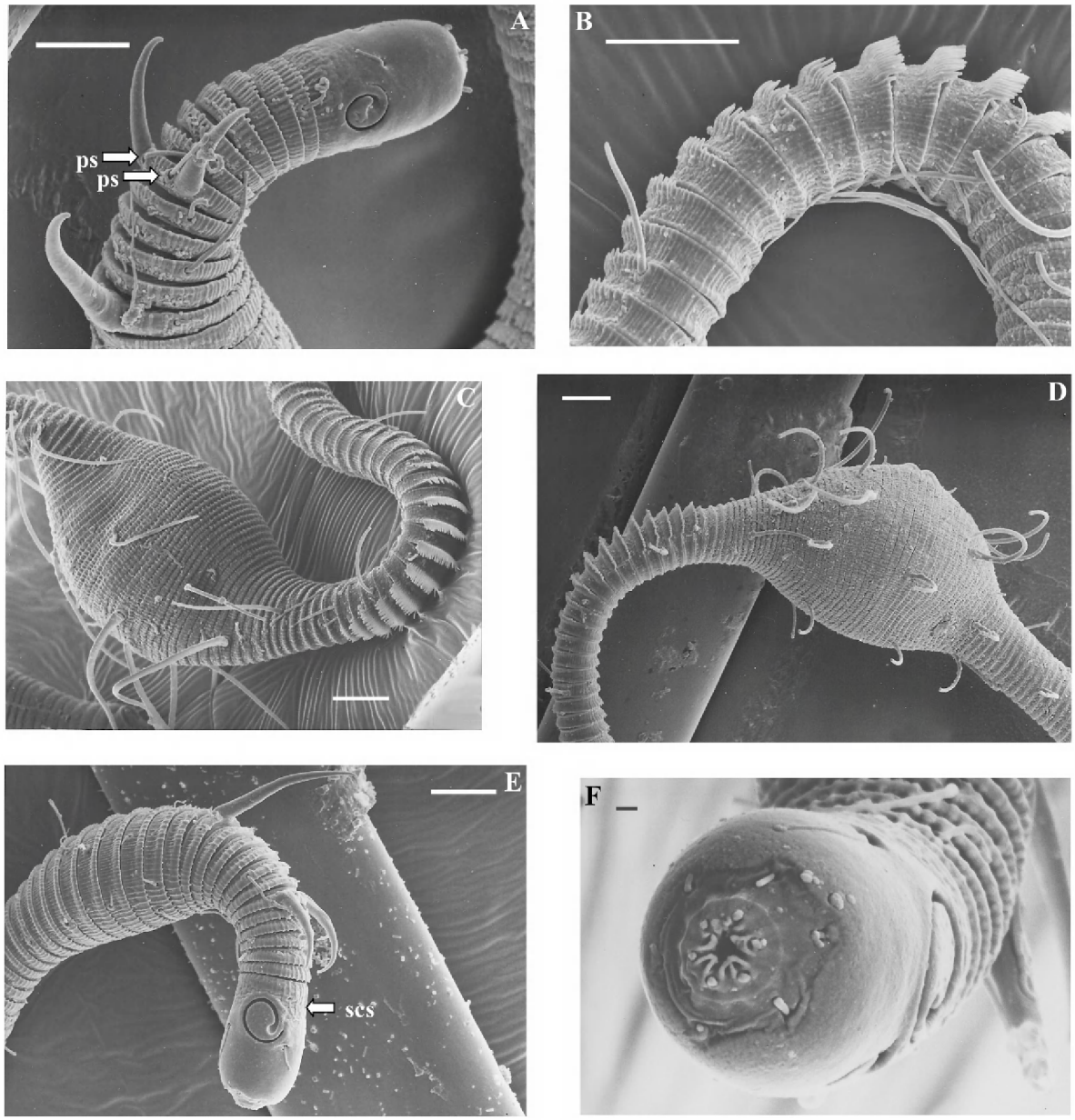


Fig. 3. *Glochinema trispinatum* sp. n. (A) ♀, head capsule and anterior part of pharyngeal region: lateral-dorsal view; (B) ♂, comb-like cuticular appendages: lateral view; (C) ♂, ventral curvature and posterior body enlargement: lateral-ventral view; (D) ♀, ventral curvature and posterior body enlargement: lateral view; (E) ♂, head capsule and pharyngeal region: lateral view; (F) ♂, labial region: en face view. 'ps': see text; scs = subcephalic setae. Scale bars: A,B,C,D and E: 10 µm; F: 1 µm.

The most conspicuous cuticular appendages however are the three thorns in the cervical-pharyngeal region (Figs. 3A, E). Each thorn is associated with a seta (**ps** in Fig. 3A) at its insertion site. In most cases there are two small subdorsal thorns located on the same annule and a larger, mediodorsal thorn situated posteriorly to these two thorns. In 24 males, 29 females and 43 juveniles this normal pattern with three thorns was observed. Only one male, two females, one third stage juvenile and four fourth stage juveniles differed from this pattern as they had a higher (four to six) or lower (two) number of thorns. When the annules are given a number (starting behind the head, not counting the 'first annule' attached to the head as argued above), it is possible to formulate a certain

'configuration'. For example, when the two smaller thorns are situated on the seventh annule and the larger thorn is situated on the twelfth annule, the configuration would be 7 7 12. For every specimen this kind of configuration was formulated. The results are depicted in a graph (Fig. 5). Variability in the position of pharyngeal thorns will be further discussed below.

In the pharyngeal region, the somatic setae are arranged in nine rows: one mediodorsal row, two subdorsal rows, two laterodorsal rows, two lateroventral rows and two subventral rows. Immediately behind the head capsule there is also a mediolateral pore present, on the left side. A study of the precise distribution of the somatic setae in this region revealed that somatic setae keep their relative position (in relation to the location of the pharyngeal thorns) even when pharyngeal thorns occur on different annules.

Between the pharyngeal region and the dorsal curvature a very large number of setae is present, arranged on four rows: two laterodorsal-subdorsal rows and two lateroventral-subventral ones. A single subventral seta was also found in this region. Between the dorsal curvature and the second body enlargement, setae are arranged on two subventral rows and two subdorsal rows, although also one lateroventral and one laterodorsal seta occur on each side.

There are two mediolateral rows of somatic setae present on the posterior body enlargement. They appear to be part of a series of setae including similar setae in front of the enlargement and behind it. In the same region there are also subdorsal, laterodorsal and lateroventral setae present.

The pattern that is present in the region behind the second body enlargement is similar to that in females, but in males it is subject to a greater amount of variability. Therefore it will be discussed only in females.

The ambulatory setae (Figs. 3C, D) are all of the same type: very long, robust, slightly curved and pointed at their distal end. They are arranged on four or five rows. There are two lateroventral rows each consisting of three to four ambulatory setae and two subventral rows each consisting of two to three ambulatory setae. Sometimes there are one or two single medioventral setae.

In the region behind the enlargement there are several long and robust supporting setae, but again their distribution has shown to be variable. In females there was a more consistent pattern which will be discussed below.

The head capsule is barrel-shaped: more or less cylindrical but slightly swollen anteriorly. Around the mouth opening there are six triangular lips (Fig. 3F). The papilliform internal labial sensilla are inserted at the base of each of these lips (Figs. 3F, 4A). There are six short but setiform external labial sensilla, situated on the same radius as the internal ones. There is a great distance between the lip region and the four cephalic setae. The latter are inserted at the anterior border of the amphids: two of them are inserted subdorsally, the other two subventrally. There are two subdorsal subcephalic setae (**scs**) located at the base of the head (Fig. 3E). The amphidial fovea is an open spiral, oval in outline: ventrally wound, slightly more than one turn. Amphids are large: in males they take up half of the head width. The buccal cavity is narrow and long, teeth are absent. The pharynx is slender, swollen in the anterior part of the head (muscles attaching the pharynx to the head capsule can be clearly observed here) and at its posterior end, forming an elongated bulbus (Fig. 1A). The cardia is triangular and small.

The male reproductive system is monorchic; the testis is outstretched, located ventrally to and on the left of the intestine. It extends as far as the second enlargement. The vas deferens is narrow. The spicules are very slender and arcuate (Fig. 2D). The capitulum bears a knob-like appendix, directed to the anterior end. Because of this, the capitulum resembles the head of a human femur. The velum is obscure. The gubernaculum is short, but has a knob-like enlargement at its distal end. A thin cuticular flap covers the cloacal opening.

The tail is very long and slender (Fig. 1D). The number of annules on the tail varies from 39 to 50. This number includes the five to nine partial annules situated on the dorsal side of the tail tip. The tail tip is also remarkably long.

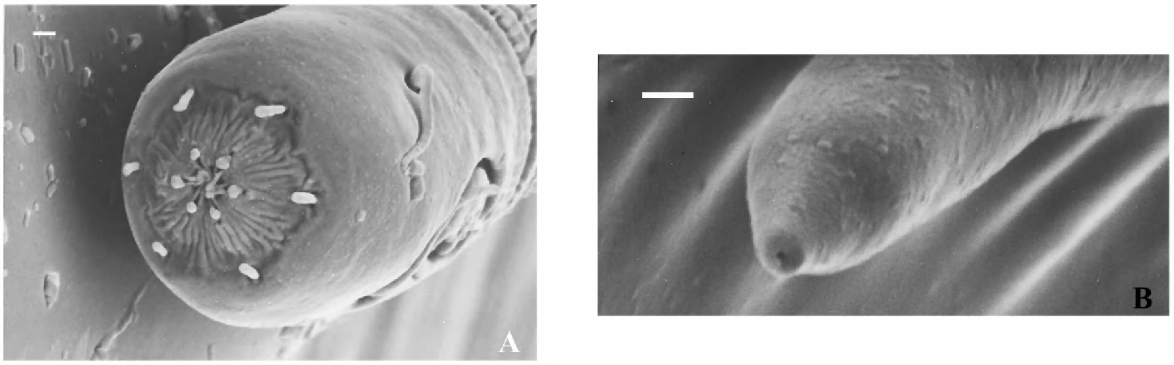


Fig. 4. *Glochinema trispinatum* sp. n. (A) ♀, head capsule: en face view. The labial region is more retracted here than in Fig. 3F; (B) ♀, non-annulated tail tip with terminal pore. Scale bars: 1 µm.

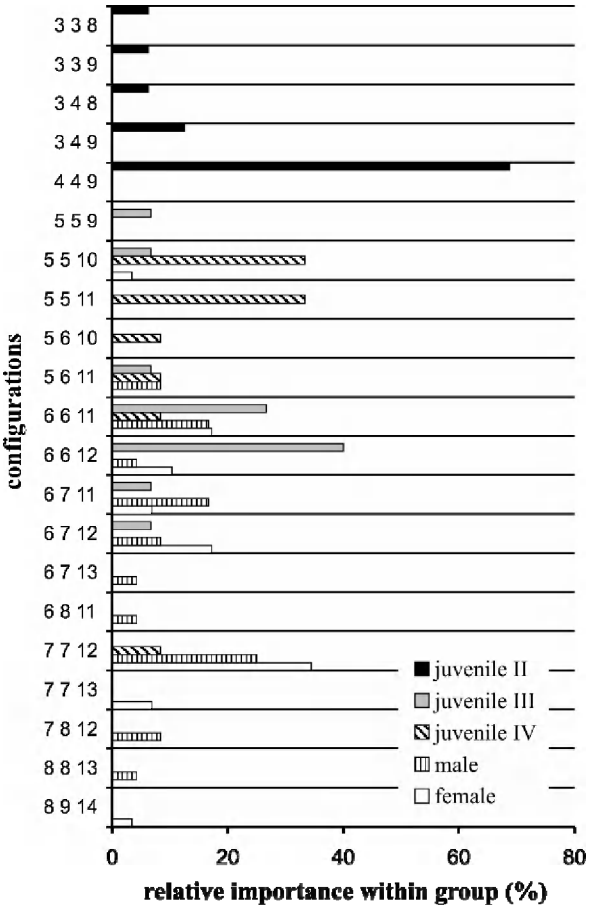


Fig. 5. Distribution of pharyngeal thorns in *Glochinema trispinatum* sp. n. The length of the bars indicate the relative importance of each configuration within a group (*i.e.* juv II, juv III, juv IV, male and female) in percentage.

Females

They resemble the males in most respects. The second body enlargement is well developed in gravid females (Figs. 1B, 2C). The number of annules is comparable to that in males: 241-257 counted subdorsally. The first ventral inversion (►) occurs somewhere between annules 73 and 81, the second one between annules 87 and 97, the third ventral inversion is positioned around the vulva (between annules 114 and 127). Dorsally only one inversion site was found, somewhere between the annules 116 and 129. Cuticular ornamentation is similar as in males. The number and position of pharyngeal thorns is also comparable to that in males (see below). In the pharyngeal region and between the pharyngeal region and the second enlargement, the arrangement of somatic setae is similar as in males.

On the second body enlargement, two mediolateral rows of somatic setae are present. They form a continuous series together with mediolateral setae in front of the enlargement and behind it. In the same region there are also subdorsal and laterodorsal setae present, as well as four smaller setae near the vulva (two on each side).

Between the second body enlargement and the cloaca, several long mediodorsal and (sometimes) medioventral somatic setae are present. The series of mediolateral setae mentioned above splits into four rows: two laterodorsal rows of long somatic setae and two lateroventral rows of six to seven long and stronger built supporting setae. These supporting setae are shorter and not as strongly built as the ambulatory setae on the second body enlargement. In most cases they are straight.

The mediolateral setae at the level of the second body enlargement are not considered to be ambulatory, because they are not markedly longer or stronger built than the other somatic setae. The ambulatory setae are arranged in three or five rows: there are two lateroventral rows of three very long, robust and slightly curved ambulatory setae, a row of four long and unpaired medioventral setae, or three unpaired setae and a pair of subventral setae.

The reproductive system is didelphic and amphidelphic, with antidromously reflexed ovaries. It is positioned ventrally to the intestine (Fig. 2C). The uterus is often well-developed, the ovaries however are always short. The vulva is surrounded by a smooth region in the cuticula, the vagina is heavily cuticularised and consists of one piece.

There are 5-11 incomplete annules on the tail tip. Caudal glands are inconspicuous but scanning electron micrographs have shown that they end in a single pore (Fig. 4B).

Juveniles

First stage juveniles: not found[2]

Second stage juveniles (Fig. 2A)

Seventeen specimens were found. There is only an obvious thickening of the body in the pharyngeal region, the second body enlargement is nearly absent. There are 197 to 213 body annules, which is clearly less than in adults. The tail consists of 35 to 47 annules and the non-

[2]The first stage juvenile of this species is described in Chapter 6.

annulated tail tip. The amphids are similar to those in adults, although they are more circular and narrower. There are no subcephalic setae.

In the pharyngeal region, somatic setae are arranged on five rows: one mediodorsal row, two subdorsal rows and two subventral rows. In the posterior body region (in this case the whole region behind the ventral curve is meant) there are two dorso-sublateral rows of somatic setae. Two subventral rows of three long ambulatory setae are present and there is only one pair of supporting setae, situated anterior to the anus.

Third stage juveniles (Fig. 2B)

Twenty-one specimens were found. Except for the absence of a clear second body enlargement, the body resembles that of adults. The number of annules (237-258) is higher than in juvenile stage II, but it is still lower than in adults. The tail consists of 30 to 36 annules and the tail tip. This number includes the four to eight partial annules. Amphids are not so narrow wound as in second stage juveniles, but they are still relatively circular in contour. There are no subcephalic setae present.

Just as in second stage juveniles, somatic setae in the pharyngeal region are arranged on one mediodorsal row, two subdorsal rows and two subventral rows. Similar as in adults, a series of (in this case laterodorsal instead of mediolateral) somatic setae is present around the second body enlargement. There are two subventral rows of three long ambulatory setae. In the posterior body region there are two laterodorsal rows of somatic setae, and two lateroventral rows of three supporting setae.

Fourth stage juveniles (Fig. 1C)

Nineteen specimens were found. A second body enlargement is present here, although not as well-developed as in adults. The number of body annules (254-262) is only slightly lower than in adults. The tail consists of 44 to 47 annules and the tail tip. This number includes the five to nine partial annules. Subcephalic setae are absent.

The arrangement of somatic setae in the pharyngeal region is comparable to that in adults, although the number of setae is smaller. At the level of the enlargement, somatic setae are arranged on one mediodorsal row and two mediolateral rows. As in adults, the mediolateral setae form a series together with similar setae in front of and behind the enlargement. There are two lateroventral rows of three ambulatory setae and three long and unpaired medioventral ambulatory setae. Behind the enlargement, the series of long somatic setae splits into four rows just like in the adults. There are two laterodorsal rows of somatic setae, and two lateroventral rows of three to five supporting setae. In addition, a few small laterodorsal and lateroventral somatic setae are present in the posterior body region.

Diagnosis

Glochinema trispinatum sp. n. is characterised by its large size (length in males 770 µm on average, in females 775 µm on average), the large number of annules (in males between 245 and 271, in females between 241 and 257), the slender body with a very long tail oriented dorsally and 2+1

thorns in the pharyngeal region. Comb-like cuticular appendages are present on the ventral curvature. In males, ambulatory setae are arranged in two lateroventral rows of three to four setae, two subventral rows of two to three setae and sometimes one or two medioventral setae. In females, there are three to five rows of ambulatory setae: two rows of three lateroventral setae and next to this four medioventral setae, or only three medioventral setae and two subventral setae (one on each side). In the region behind the enlargement there are two lateroventral rows of six to seven supporting setae. The head capsule is barrel-shaped, the amphid is an oval spiral consisting of one loop; there are two subdorsal subcephalic setae. The males are characterised by their long and slender spicules (48.22 µm on average) with a capitulum bearing a knob-like appendix.

Differential diagnosis, with a discussion on the systematic position within the subfamily Glochinematinae Lorenzen, 1974

According to Gourbault & Decraemer (1986), the genus *Metaglochinema* Gourbault & Decraemer, 1986 differs from *Glochinema* Lorenzen, 1974 in the number of rows of ambulatory setae, the presence of two types of ambulatory setae instead of only one type, and in the number of subcephalic setae. In *Metaglochinema*, the ambulatory setae are arranged on five rows: the setae on the ventral row and those on the two subventral rows are bent and pointed at their distal end, but those on the two 'dorsosublateral' rows are short, fine and tubular. In *Glochinema*, the ambulatory setae are all bent and pointed at their distal end. They are arranged in four subventral rows. In *Metaglochinema* there are only two subcephalic setae, in *Glochinema* four to seven.

The diagnosis of both genera had to be adjusted because of difficulties to distinguish medioventral setae from subventral setae (Gourbault & Decraemer, 1993). This influences the interpretation of row numbers and therefore the distinction between the 2 genera.

In overall appearance, *Glochinema trispinatum* sp. n. is closest to *Metaglochinema strigosum* Gourbault & Decraemer, 1993. The two species can be distinguished by the presence of three pharyngeal thorns in *G. trispinatum* sp. n., the shape of its tail and the structure of the spicules. As in species of the genus *Metaglochinema*, this new species has two rows of long laterodorsal ('dorsosublateral') setae. However, these setae are not short and tubular here. Moreover, we do not consider these setae in *G. trispinatum* sp. n. and in *M. strigosum* to be ambulatory, because there are no clear differences with somatic setae. Laterodorsal setae similar to these can be found in *G. bathyperuvensis* Neira *et al.*, 2001, in *G. kentrosaurides* Gad, 2002 (where they are indicated as extremely long, sensory setae), in *G. agile* Lorenzen, 1974 and in *G. chilense* Lorenzen, 1974. Only in *M. globicephalum* Gourbault & Decraemer, 1986 these setae appear to be clearly tubular.

In *G. trispinatum* sp. n., there are three to five rows of ambulatory setae (depending on the sex). It is obvious that the correct interpretation of setae arrangement is crucial here to find out to which genus this new species belongs. One can also observe that in *G. kentrosaurides* Gad, 2002 the number of rows of ambulatory setae is identical to that in *G. trispinatum* sp. n., a species very close to *M. strigosum*. In short, it appears to us that the arrangement of ambulatory setae is not a good feature to distinguish the two genera in the subfamily Glochinematinae. As argued by Gad (2002) there is also an overlap in the number of subcephalic (or additional cephalic) setae, a feature of great diagnostic

importance in Epsilonematidae. In *G. kentrosaurides* there are two subcephalic setae in the males, a number until now only found within *Metaglochinema.* In *G. bathyperuvensis* there are even no subcephalic setae present.

We conclude that *M. strigosum* shows more similarities with species of *Glochinema* than with *M. globicephalum.* The features used to argue its systematic position within *Metaglochinema* have little diagnostic value. Therefore, this species is transferred to the genus *Glochinema*. The genus *Metaglochinema* is maintained for *M. globicephalum*, a species well defined by the presence of strongly built, tubular, dorsosublateral ambulatory setae. The original genus diagnosis by Gourbault & Decraemer (1986) is adjusted:

Metaglochinema Gourbault & Decraemer, 1986 is morphologically similar to *Glochinema* Lorenzen, 1974. However, it can be distinguished from this genus by the presence of strongly built, tubular, dorsosublateral ambulatory setae in addition to the medioventral and subventral rows of ambulatory setae already present in *Glochinema.*

At present, the genus *Glochinema* is thus comprised of seven species:

1. *Glochinema agile* Lorenzen, 1974
2. *Glochinema chilense* Lorenzen, 1974
3. *Glochinema phaleratum* Gourbault & Decraemer, 1993
4. *Glochinema strigosum* (Gourbault & Decraemer, 1993)
5. *Glochinema bathyperuvensis* Neira *et al.*, 2001
6. *Glochinema kentrosaurides* Gad, 2002
7. *Glochinema trispinatum* sp. n.

Remarks

1. Pharyngeal thorns (Fig. 5)

Observation of 25 males, 31 females, 16 second stage juveniles, 16 third stage juveniles and 16 fourth stage juveniles showed that the position of the pharyngeal thorns is highly variable. On the graph (Fig. 5) it can be seen that in males as well as in females the most common configuration is 7 7 12, while in juveniles (when considered as one group) it is 4 4 9. Generally, in juveniles the pharyngeal thorns tend to occur more frequently on annules that are situated more anteriorly than in adults. There seems to be a clear backward shift in the position of the pharyngeal thorns during ontogeny, probably due to the formation of new annules anteriorly. However, this trend is not clear when the different juvenile stages are compared. In juvenile II specimens, the most common configuration is 4 4 9, in juvenile III it is 6 6 11 and 6 6 12 (this is still consistent with the hypothesis), but in juvenile IV it is 5 5 11. At present, this can not be explained.

	Holotype male	Paratype males (n = 5)	Paratype females (n =5)	Juvenile stage II (n = 8)	Juvenile stage III (n = 7)	Juvenile stage IV (n = 7)
L	830	735-790 (760)	750-830 (775)	335-425 (380) [17]	430-560 (505) [21]	475-755 (625) [19]
N	266	245-271 (261)	241-257 (249)	197-213 (205) [5]	237-258 (247) [5]	254-262 (258) [5]
dcs	12.3	11.6-15.3 (13.3)	11.2-14.3 (12.6)			
Hdw	15.5	14.9-15.7 (15.5)	14.9-16.5 (15.6)	10.3-12.6 (11.1)	11.3-16.1 (14.0) [6]	13.7-17.3 (14.8)
Hdl	23.2	23-28.5 (25.0)	20.8-24.9 (22.9)	13.9-17.0 (15.8)	16.3-20.5 (18.2) [6]	19.9-22.5 (21.6)
Amphw	7.6	6.9-8.1 (7.5)	6.6-7.6 (7.3)	3.4-4.5 (4.0)	4.6-5.9 (5.1) [6]	5.0-6.4 (5.9)
Amph%	48.9	46.4-51.8 (48.3)	42.1-50.7 (46.5)	25.3-41.0 (34.6)	31.5-40.6 (36.4) [6]	27.1-44.4 (38.6)
ph	98.0	92.6-97.4 (94.8)	93.1-100.3 (97.1)	58.5-72.2 (64.4)	67.8-89.8 (77.6)	77.9-99.6 (85.7)
mvAsl	38.8	42.3-46.8 (44.2)	35.4-50.7 (42.3)			32.2-40.3 (37.6)
mlvAsl	74.7	44.6-65.6 (56.3)	39.2-68.8 (55.7)	34.3-42.3 (39.9)	42.0-47.9 (44.3)	31.7-55.7 (47.8)
tail	160.6	126.8-137.7 (131.9)	127.7-161.1 (136.7)	65.2-81.0 (71.7)	84.1-104.3 (93.8)	95.6-126.3 (113.1)
tmr	50.5	32.3-37.4 (34.8)	34.7-40.1 (37.2)		19.1-28.6 (24.9) [4]	27.2-33.9 (30.6) [2]
mbd ph	25.6	23.0-24.2 (23.8)	23.4-24.4 (24.1)	15.6-19.7 (18.2)	19.4-24.0 (22.0)	23.2-27.4 (25.2)
mbd	33.6	34.7-42.0 (38.6)	41.6-49.8 (46.8)	10.4-14.8 (13.2)	15.5-19.3 (17.3)	20.8-30.6 (26.7)
(mbd)	12.4	10.1-12.6 (11.4)	10.8-12.4 (11.5)	7.3-9.2 (8.3)	7.9-10.9 (9.8)	10.1-12.7 (11.4)
mbd/(mbd)	2.7	3.0-3.9 (3.4)	3.7-4.6 (4.1)	1.4-1.8 (1.6)	1.6-2.0 (1.8)	2.1-2.8 (2.4)
ABD	16.4	16.4-18.3 (17.2)	13.4-14.6 (13.9)	8.1-10.5 (9.7)	9.8-13.4 (11.9)	13.4-17.9 (15.1)
spic	54.8	42.9-53.8 (46.9)				
gub	9.8	7.3-7.9 (7.6)				
V%			55.9-58.7 (57.3)			
a	24.7	17.6-22.1 (19.8)	18.2-21.0 (19.5)	26.3-32.7 (29.0)	27.4-32.9 (29.8)	22.1-30.2 (25.9)
b	8.4	7.7-8.3 (8.0)	8.9-9.9 (9.4)	5.4-6.7 (5.9)	6.1-7.2 (6.6)	6.9-9.8 (8.1)
c	5.2	5.6-5.8 (5.8)	5.8-7.0 (6.7)	5.0-5.8 (5.3)	5.3-5.8 (5.5)	5.7-6.6 (6.1)

Table 1. Measurements of specimens of *Glochinema trispinatum* sp. n. All absolute values are in µm. The number of specimens that was measured, when different from the total number of specimens, is indicated between brackets in superscript.

2. Antarctica specimens

Some material obtained from the Antarctic shelf in 1996 and 1998 also contained several specimens of *Glochinema trispinatum* sp. n. The samples were taken near Kapp Norvegia at depths of 182 m and 805 m. In this case, the substrate consisted of sponge spicules (forming spicule mats) and bryozoan debris. The microhabitat is roughly comparable to that in the Porcupine Seabight, especially to the underlying sediment consisting of a mixture of sponge fragments (and spicules), small coral fragments and sediment.

The animals found in Antarctica are morphologically similar to those in the North Atlantic: they also have three pharyngeal thorns and the arrangement of ambulatory and supporting setae, as well as the shape of the head capsule and spicules is identical. There are however certain morphometrical differences: the Antarctica specimens are longer and more slender than those from the type location. The amphids are also relatively larger, and the number of annules is slightly higher. One male was measured: L: 1213.3 µm; spic: 48.9 µm; N: 284; Amph%: 56.6; mbd/(mbd): 3.8; de Man a: 27.0; de Man b: 9.2; de Man c: 5.5.

Family **Epsilonematidae Steiner, 1927**
Subfamily **Epsilonematinae Steiner, 1927**
Genus ***Epsilonema*** **Steiner, 1927**
Epsilonema multispiralum **sp. n.** (Figures 6-7)

Type specimens

Holotype male on slide RIT 681. Paratype males, females and juveniles on slide numbers RIT 681-684, 688 (KBIN), MDNC 4026-4030, 4034 (UGent), other paratypes 2003.335, 2003.338, 2003.339, 2003.344 and 2003.345 are stored at NHM.

Type locality. Porcupine Seabight, Belgica mounds, at a depth of 1005 m. Coordinates: 51°24'48,2" N; 11°45'55,4" W. *Remark:* other representatives were found in the Belgica mound region at 51°25'7,74" N and 11°46'9,32" W.

Date of collection. 17th of june 2000.

Type habitat. Deep sea environment, on the top of a coral mound. Associated with cold-water coral reef degradation zones. Epifaunal on sponge and coral fragments. These nematodes showed a clear preference for coral fragments as a substrate.

Relative abundance. This species comprises 2.96% of the total nematode community at the type locality.

Etymology. The name refers to the shape of the amphids, consisting of 3.25 coils. From the Latin adverb *multus, a, um* (much) and the Latin adjective *spiralis* (coiled).

Measurements: Table 2

Males

These are small nematodes with a distinct ε-shaped body. The body is enlarged at the level of the pharynx and at the level of the testis, but the first enlargement is often less conspicuous (Figs. 6A, 7C). The ventral curvature is usually sharp.

There are 136-149 body annules. Ventrally, the inversion of orientation (►) occurs between annules 45 and 46 (or 47 and 48), dorsally between annules 62 and 63 (or 65 and 66). The first annules behind the head capsule and those at the level of the second body enlargement are narrow. In the pharyngeal region and around the cloacal opening the annules are broadest. Only a limited degree of overlap was observed. Each annule is ornamented with vacuoles: these are actually indentations of the body cuticle, separated by cuticular ridges. A row of vacuoles occupies more than half the annule length, the other half of the annule is smooth. On the first annules, vacuoles are less obvious. Vacuoles are more pronounced dorsally than ventrally, especially in the posterior body region. In the region posterior to the ventral curvature and on the tail, the ventral side of the body is covered with hair-like spines protruding from the posterior edge of the annules. Medioventrally these structures are much finer than lateroventrally, where they are relatively short and thick (Figs. 7A, B). The same type of spines is found also on the lateral and dorsal side of the second enlargement (Fig. 7C). There are seven rows of somatic setae in the pharyngeal region: only one mediodorsal seta, two subdorsal rows, two mediolateral rows and two subventral rows. A few more somatic setae occur scattered in this region.

In the region of the ambulatory setae, somatic setae are arranged on two subdorsal, almost mediodorsal rows. In the region of the supporting setae there are a few mediodorsal, subdorsal and medioventral setae.

The ambulatory setae are quite short and clearly bent in a posterior direction. Their distal end is knicked. They are positioned in four subventral rows: the inner rows each consist of ten to eleven setae, the outer rows of 10-12 setae.

Between the ambulatory setae and the cloacal opening two ventrosublateral, longitudinal rows of three straight and robust supporting setae were found.

The head capsule is triangular, truncated anteriorly (Figs. 6D, 7D). Because in fixed specimens the lip region is usually retracted, the internal and external sensilla are inconspicious, even on SEM micrographs. The lip region consists of several radial, cuticular ridges (Fig. 7E). There are four cephalic setae, 4 µm in length (holotype male). There are six subcephalic setae, situated at the level of the amphids: one subventral, one ventrolateral and one subdorsal (nearly mediodorsal) pair (Fig. 7D). The amphids are whirled ventrally, multispiral with 3.25 coils. They are located near the base of the head capsule, clearly shifted dorsally. In males they take up 64.75% of the head width on average. The buccal cavity is relatively narrow (however in some cases the buccal cavity can become wider due to fixation) and bears a large dorsal tooth (Fig. 6D). The pharynx is short but has a strong muscular posterior bulb with strongly cuticularised valves. The cardia is small.

The tail consists of fifteen to seventeen annules and the tail tip. No partial annules were observed. The tail is short and the overall shape is conical. The caudal glands are not obvious, but an SEM micrograph shows that they end in three separate pores (Fig. 7F).

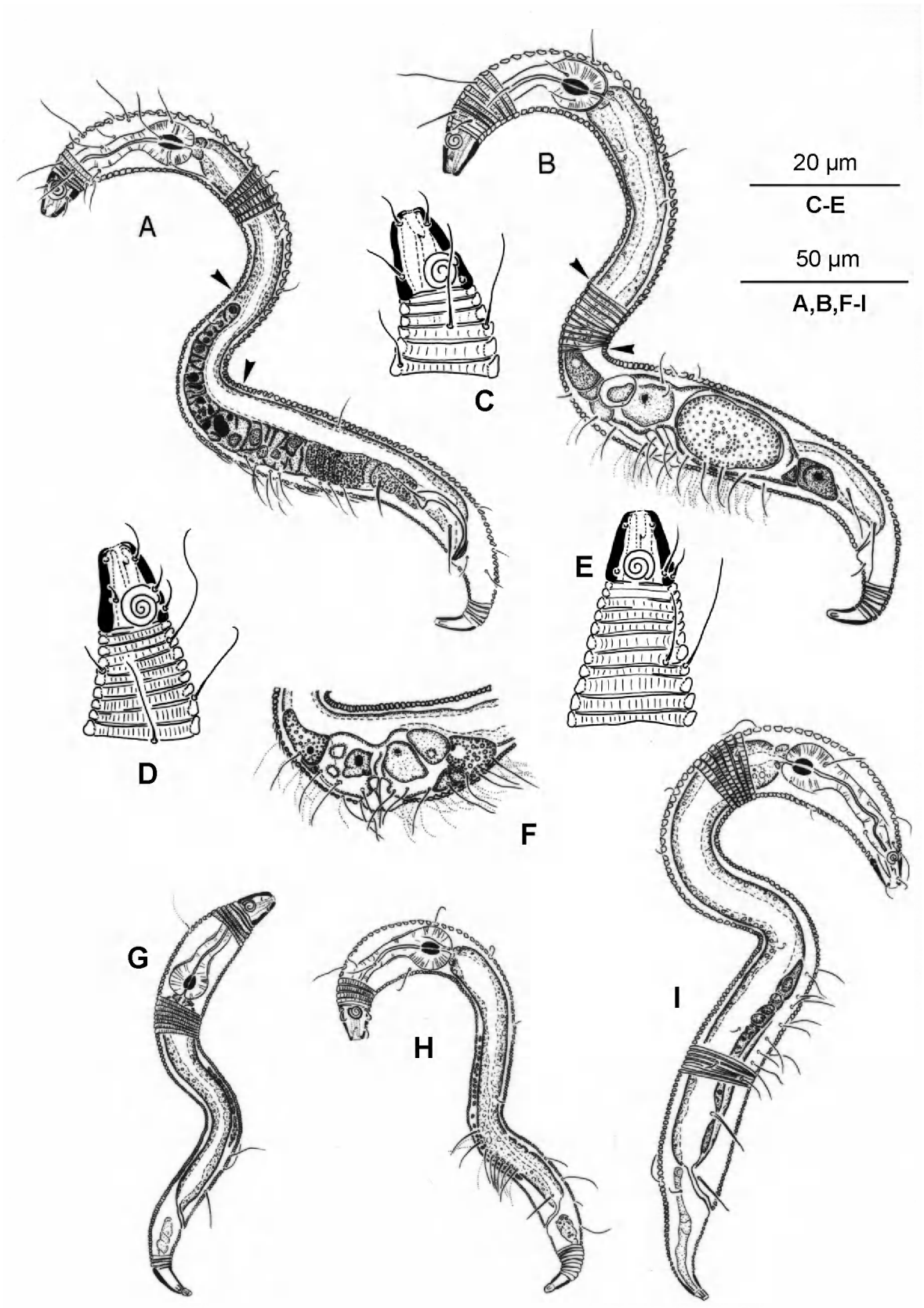


Fig. 6. *Epsilonema multispiralum* sp. n. (A) holotype ♂, habitus; (B) paratype ♀, habitus; (C) paratype ♀, surface view of head capsule; (D) paratype ♂, surface view of head capsule; (E) juvenile IV, surface view of head capsule; (F) paratype ♀, detail of reproductive system; (G) juvenile II, habitus; (H) juvenile III, habitus; (I) juvenile IV, habitus. Inversion sites are indicated with arrows.

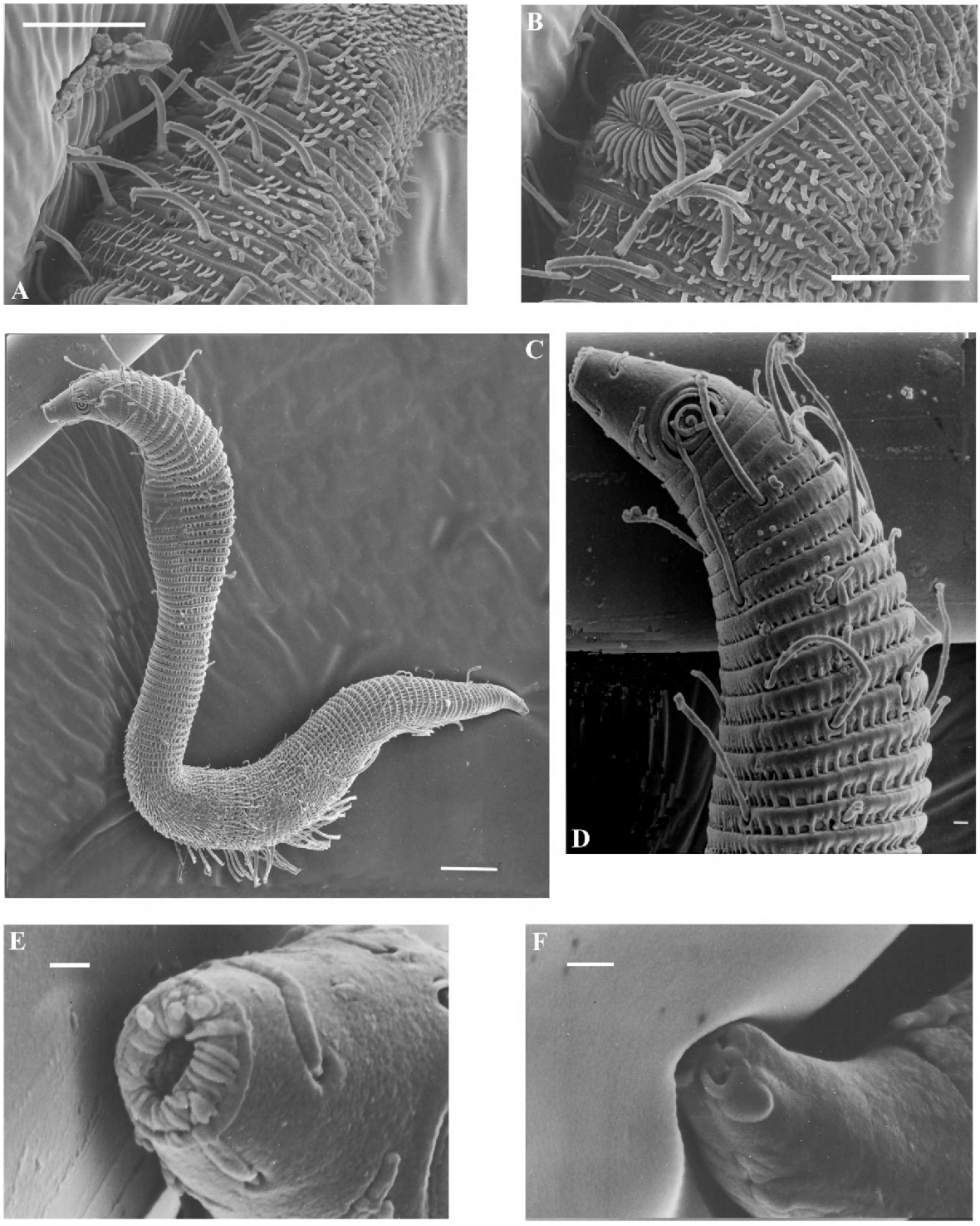


Fig. 7. *Epsilonema multispiralum* sp. n. (A) ♀, cuticle in front of the vulva, with ambulatory setae: lateral-ventral view; (B) ♀, cuticle around the vulva: lateral-ventral view; (C) ♂, habitus; (D) ♂, head capsule and pharyngeal region: lateral view; (E) ♂, labial region: en face view; (F) ♂, tail tip. Scale bars: A,B,C: 10 µm; D,E & F: 1 µm.

There is one outstretched testis extending into the ventral curve (anterior to the ambulatory setae), positioned ventrally of the intestine. The spicules are slightly curved and slender, velum obscure, with a triangular capitulum pointing ventrally (Fig. 6A). The gubernaculum is 4 µm long (in the holotype male), lying adjacent to the spicules. Copulatory thorns were not observed.

Females

The females resemble the males in most respects (Figs. 6B, C). However, the second enlargement of the body is more pronounced than in the males, especially in gravid females. The number of annules is also comparable (138-145). The tail consists of thirteen annules (including the tail tip). Ventrally, the inversion (►) occurs between the annules 46-47, 47-48 or 48-49. Dorsally the inversion is not clear, probably it is between annules 58-60 or 62-63. Cuticular ornamentation is similar as in males.

The position of the somatic setae in the pharyngeal and posterior body region, as well as the position and number of subcephalic setae, is comparable to that in males.

There are four rows of ambulatory setae: two outer rows of ten to twelve setae and two inner rows of ten to eleven setae.

The number and location of supporting setae is identical to that in males.

The reproductive system is situated on the ventral side of the intestine: it is didelphic and amphidelphic (Fig. 6F). The vulva is surrounded externally by a large number of radial cuticular ridges (Fig. 7B). In some cases, the vulva is bulged out markedly. At the level of the vulva, thread-like spines are finer than on the rest of the body.

Juveniles

First stage juveniles: not found

Second stage juvenile (Fig. 6G)

Only a single, moulting specimen was found. Moulting was inferred from the presence of a double distal part of the tail tip. Second stage juveniles are clearly smaller than adults. The body is not as slender as in adults, where the body region between the first dorsal curvature and the ventral curvature is clearly more elongated. There is no posterior enlargement. There are 161 body annules: this is far more than in the adults. Annules are also narrower compared to those in adults. In the pharyngeal region each annule is ornamented with a single row consisting of a large number of small vacuoles. In the posterior body region the annules are even thinner than in the pharyngeal region (as a result, vacuoles can no longer be distinguished). The ratio amphids-head width is slightly lower than in adults. The amphids consist of 2.25 turns. There are no subcephalic setae.

In the pharyngeal region only a single long subdorsal seta (on the left) and a very short medioventral seta were found. Ambulatory setae were difficult to observe; probably there are four setae on a single row. The most posterior seta is straight and in this respect it resembles a supporting seta. In the posterior region, no somatic setae were found.

Third stage juveniles (Fig. 6H)

Four specimens were found. Compared to second stage juveniles their overall body shape is more similar to that of adults, however they are smaller and the posterior body enlargement is still absent. The number of annules varies from 146 to 154, which is still more than in adults. The tail consists of seventeen to eighteen annules plus the tail tip. Cuticular ornamentation is similar to that in second stage juveniles, however vacuoles tend to be larger and fewer in number. Only three subcephalic setae were observed: a medium-sized mediodorsal one and two short subventral setae (one on each side).

In the pharyngeal region there are mediodorsal, laterodorsal and subventral somatic setae. There are two rows of eight bent ambulatory setae (the last one is slightly shifted more dorsally), followed by one pair of robust ventrosublateral supporting setae. On each side, a long subdorsal seta is situated immediately behind the most posterior ambulatory setae. Next to this, several short setae are found in the posterior body region.

Fourth stage juveniles (Figs. 6E, I)

Twelve specimens were examined, most of them older individuals. They resemble adults in most respects, however they are slightly smaller and have still got a larger number of annules (between 141 and 166). The tail consists of seventeen annules and the tail tip. There are five subcephalic setae: one pair of subventral setae (however in most cases only one seta was actually observed), one pair of ventrolateral setae and a single long mediodorsal seta.

In the pharyngeal region somatic setae are arranged in five rows: one mediodorsal row, two laterodorsal rows and two lateroventral rows. Sometimes there is a single short mediolateral seta situated immediately behind the head capsule. The bent ambulatory setae are arranged in four subventral rows: the outer rows consist of nine setae, the inner rows of six setae. In the posterior body region, there are two pairs of long and straight supporting setae and several subdorsal setae.

Diagnosis

Epsilonema multispiralum sp. n. is a small nematode (length of males 300 µm on average, females 295 µm on average), characterised by the combination of the following characters: the cuticle consists of a large number of narrow annules (in males between 136 and 149, in females between 138 and 145), the cuticular ornamentation is made up of a single row of large vacuoles. It has large, dorsally shifted amphids consisting of 3.25 whirls. Males are characterised by slightly curved and slender spicules with a triangular capitulum and no clear velum. Copulatory thorns are absent.

Differential diagnosis

The amphids of *Epsilonema multispiralum* sp. n. resemble those of *E. meunierorum* Decraemer & Gourbault, 1987 in size and the number of coils. However, there are markedly fewer body annules in the latter species (in males on average: 139 in *E. multispiralum* sp. n. vs 88 in *E. meunierorum* Decraemer & Gourbault, 1987). The new species is clearly smaller (males of *E. multispiralum* sp. n. have an average body length of 299.4 µm, those of *E. meunierorum* Decraemer & Gourbault, 1987

have an average body length of 385 µm) and it bears no precloacal copulatory thorns. Next to this, the cuticle of *E. meunierorum* Decraemer & Gourbault, 1987 has only an obscure vacuolar ornamentation where in this new species large vacuoles occur. All other species of this genus have amphids of different size and shape.

	Holotype male	Paratype males (n = 5)	Paratype females (n =5)	Juvenile stage II (n = 1)	Juvenile stage III (n = 4)	Juvenile stage IV (n = 12)
L	305	285-310 (300)	275-315 (295)	150	180-215 (200)	210-275 (245)
N	149	136-144 (139)	138-145 (141)	161	146-154 (150)	141-166 (153)
cs	4.0		4.1-5.8 (5.0) [2]			3.6-5.7 (4.5) [6]
dcs	2.1	3.0 [1]	1.7-2.1 (1.9) [2]	3.3	3.3 [1]	3.2-4.9 (3.9) [8]
Hdw	9.8	9.3-10.6 (9.9)	9.4-11.3 (10.1)	8.7	7.9-9.1 (8.4)	8.0-9.7 (9.3)
Amphw	6.0	6.0-6.8 (6.4)	5.1-6.2 (5.5)	4.1	3.5-4.4 (3.9)	3.9-5.2 (4.5)
Amph%	61.8	59.7-70.3 (65.4)	50.4-58.7 (54.5)	47.0	41.8-55.7 (46.2)	40.7-55.4 (48.1)
ph	57.5	59.0-68.2 (63.4)	56.4-62.8 (60.0)	42.1	48.4-55.2 (51.7)	49.0-62.2 (56.0)
Asl	12.2	11.4-13.9 (12.7)	10.9-13.6 (12.5)	10.3	11.5-13.6 (12.7)	9.5-17.9 (12.5)
sup	15.4	14.6-21.1 (17.2)	13.5-20.4 (16.0)	14.2	12.2-16.2 (14.2)	10.5-15.9 (14.2) [11]
tail	35.3	35.0-38.2 (36.6)	31.7-36.4 (33.7)	25.1	24.3-30.3 (26.9)	28.5-38.3 (30.3)
tmr	12.6	8.2-12.4 (10.4)	11.1-12.0 (11.6)	5.7	7.8-10.3 (8.5)	7.7-9.9 (8.7)
mbd ph	19.0	18.2-20.5 (19.0)	18.5-20.9 (20.0)	16.2	16.1-18.2 (17.2)	18.0-22.0 (20.3)
mbd	25.0	20.8-23.1 (21.9)	29.0-32.3 (30.5)	11.9	12.0-15.8 (14.2)	15.7-21.6 (18.9)
(mbd)	14.1	13.2-14.9 (14.0)	14.7-15.9 (15.3)	10.9	10.7-13.5 (12.5)	13.4-17.4 (15.6)
mbd/(mbd)	1.8	1.5-1.7 (1.6)	1.9-2.1 (2.0)	1.1	1.1-1.2 (1.1)	1.1-1.3 (1.2)
ABD	14.4	13.9-16.3 (14.8)	11.2-13.5 (12.7)	10.3	10.4-12.5 (11.4)	10.3-16.2 (13.5)
spic	35.1	33.0-41.3 (37.3)				
gub	14.5					
V%			40.1-65.3 (55.1)			
a	12.2	13.1-14.3 (13.6)	9.0-10.9 (9.7)	12.8	13.2-14.8 (14.0)	11.8-14.5 (13.0)
b	5.3	4.5-5.1 (4.7)	4.7-5.1 (4.9)	3.6	3.3-4.1 (3.9)	3.7-4.8 (4.4)
c	8.7	7.4-8.7 (8.2)	7.8-10.0 (8.8)	6.0	7.0-7.6 (7.4)	6.9-8.4 (8.4)

Table 2. Measurements of specimens of *Epsilonema multispiraturn* sp. n. All absolute values are in µm. When different from the total number, the number of specimens that was measured is indicated between brackets in superscript.

Family **Epsilonematidae Steiner, 1927**

Subfamily **Epsilonematinae Steiner, 1927**

Genus ***Bathyepsilonema* Steiner, 1931**

***Bathyepsilonema lopheliae* sp. n.** (Figures 8-11)

Type specimens

Holotype male on slide RIT 685. Paratype males, females and juveniles on slide numbers RIT 687-688 (KBIN), MDNC 4022, 4031-4036 (UGent), other paratype 2003.346 is stored at NHM.

Type locality. Porcupine Seabight, Belgica mounds, at a depth of 1005 m. Coordinates: 51°24'48,2" N; 11°45'55,4" W. *Remark:* other representatives were found in the Belgica mound region at 51°25'7.74" N and 11°46'9.32" W.

Date of collection. 17th of june 2000.

Type habitat. Deep sea environment, on the top of a coral mound. Associated with cold-water coral reef degradation zones. Epifaunal, preferably on sponge fragments.

Relative abundance. This species comprises 0.57% of the total nematode community.

Etymology. The name refers to the unique substrate on which it lives: the deep-water coral *Lophelia pertusa* (Linnaeus, 1758).

Measurements: Table 3

Males

The body is relatively stout and clearly epsilon-shaped, with conspicuous enlargements in the pharyngeal region and at the level of the second dorsal curvature (Figs. 8A, 10A). The first dorsal curvature and the ventral curvature are most pronounced: as a result the anterior body region often lies adjacent to the mid-body region. The posterior body region is hardly bent at all. There is a short tail ending in a conical tail tip (Fig. 10F).

The cuticle is built up of 89-93 broad cuticular annules, clearly overlapping in the pharyngeal and posterior body region. Ventrally (in the holotype male), the inversion of orientation (►) occurs between annules 31 and 32, dorsally between the 44th and 45th annule. The annules are ornamented with vacuoles (Figs. 8E, F), except on the first two annules (Fig. 10C). Along the tail the pattern of vacuoles fades away, resulting in a more irregular pattern of cuticular ripples.

The somatic setae in the pharyngeal region are long and arranged on six rows: two subdorsal rows, two laterodorsal rows also and two subventral rows.

On the posterior body region, behind the ambulatory setae, the somatic setae are positioned in four to five rows: two subdorsal rows, two subventral rows and sometimes a few very long mediodorsal setae.

The ambulatory setae are all located on the ventral curvature, restricted to a small region extending between the ventral curvature and the anterior tip of the testis. The setae are clearly arranged in six longitudinal rows. Each row consists of twelve to thirteen setae, although the exact number is difficult to determine. The proximal part of each seta lies adjacent to the body, oriented in a

posterior direction. The distal end bears two small hooks forming a bifid appendix attached to the seta at a right angle (Fig. 10B, D). No supporting setae were observed.

The head capsule is dome-shaped and heavily cuticularised (Figs. 8B, 10C). The amphids are very large and surrounded by a cuticular rim, causing the head to flatten off laterally (Fig. 10E). In males, the amphids take up 61.8% of the total head width on average. They are circular in shape, spiral with two turns and in some cases the corpus gelatum is protruded (Fig. 11D). The internal and external labial sensilla are not obvious (even on SEM micrographs) because in most specimens the lip region is retracted. There are four cephalic setae, situated at the anterior end of the amphids. There are eight subcephalic setae (Fig. 10C): two short subdorsal setae can be found at the level of the amphidial fovea. The other subcephalic setae are situated at the posterior border of the head capsule: on each side there is one long subdorsal seta and one shorter lateroventral seta. There is also an unpaired, very short laterodorsal seta and a single short lateroventral seta. These two unpaired setae are both situated on the right side of the head capsule. It is very important to notice that the two subcephalic setae at the level of the amphid are only visible using SEM, not with a light microscope. The buccal cavity is not clear because the lip region is always retracted. Teeth were not observed though this can again be due to the retraction of the lip region. The pharynx shows two enlargements: there is a small swelling in the middle of the pharynx and a well-developed muscular end bulb. The pharynx lumen is strongly cuticularised. The cardia is flattened.

The tail is short and conical, bearing six (sometimes seven) annules without distinct vacuoles. The tail endring is quite irregularly shaped at its base, but becomes more smooth and cylindrical posteriorly. At its tip a small spinneret can be observed. The caudal glands end in one pore and a curved slitlike opening (situated dorsally of this pore) at the terminal end of the tail tip (Fig. 11B). A pair of strongly built setae is positioned just before the tail tip.

There is one broad, outstretched testis extending between the ventral and second dorsal curvature (Fig. 8A). The spicules are slender and they describe an angle of 90°. The capitulum is triangular, the proximal part of the calomus is clearly broader than the distal part. There is a fine but clear velum. The gubernaculum is small and slender. Small copulatory thorns were observed in front of the cloacal opening (Fig. 10B).

Females

The females are similar to the males in most respects (Fig. 8C, D), though the second enlargement is more pronounced (Fig. 11A). The cuticle consists of 91-94 annules. Inversion (►) occurs ventrally between annules 28 and 29, dorsally between annules 42 and 43. Cuticular ornamentation is similar as in males.

The arrangement of somatic setae in the pharyngeal region is comparable to that in males. At the level of the second enlargement, behind the ambulatory setae, the somatic setae are positioned on four to five rows: a row of very long mediodorsal setae, two subdorsal rows and two subventral rows.

The position of ambulatory setae is identical to that in males. In this case this also means that the ambulatory setae are all positioned in front of the vulva. No supporting setae were observed.

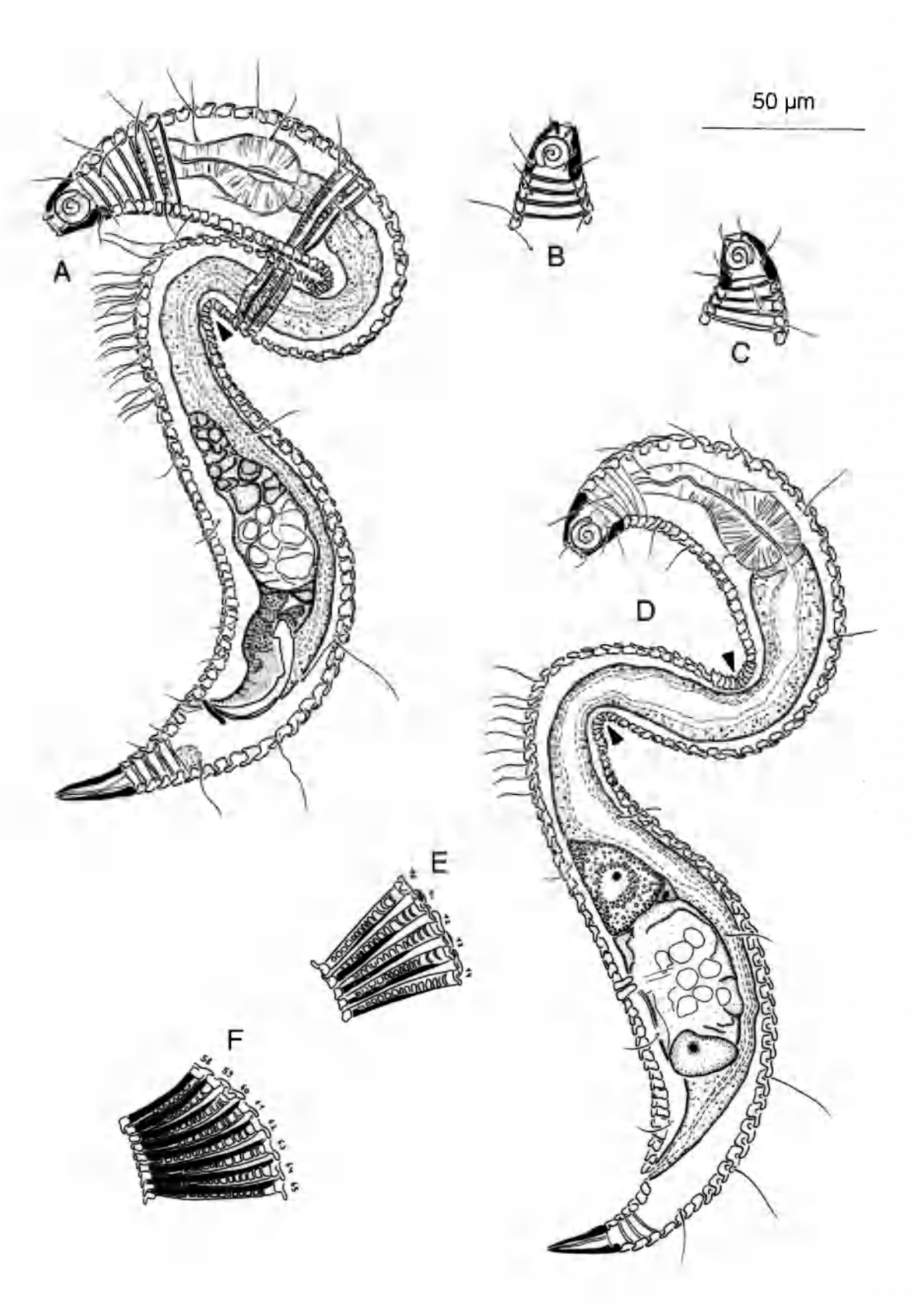


Fig. 8. *Bathyepsilonema lopheliae* sp. n. (A) holotype ♂, habitus; (B) paratype ♂, surface view of head capsule; (C) paratype ♀, surface view of head capsule; (D) paratype ♀, habitus; (E) paratype ♂, detail of cuticular ornamentation in pharyngeal region; (F) paratype ♂, detail of cuticular ornamentation in posterior body region. Inversion sites are indicated with arrows.

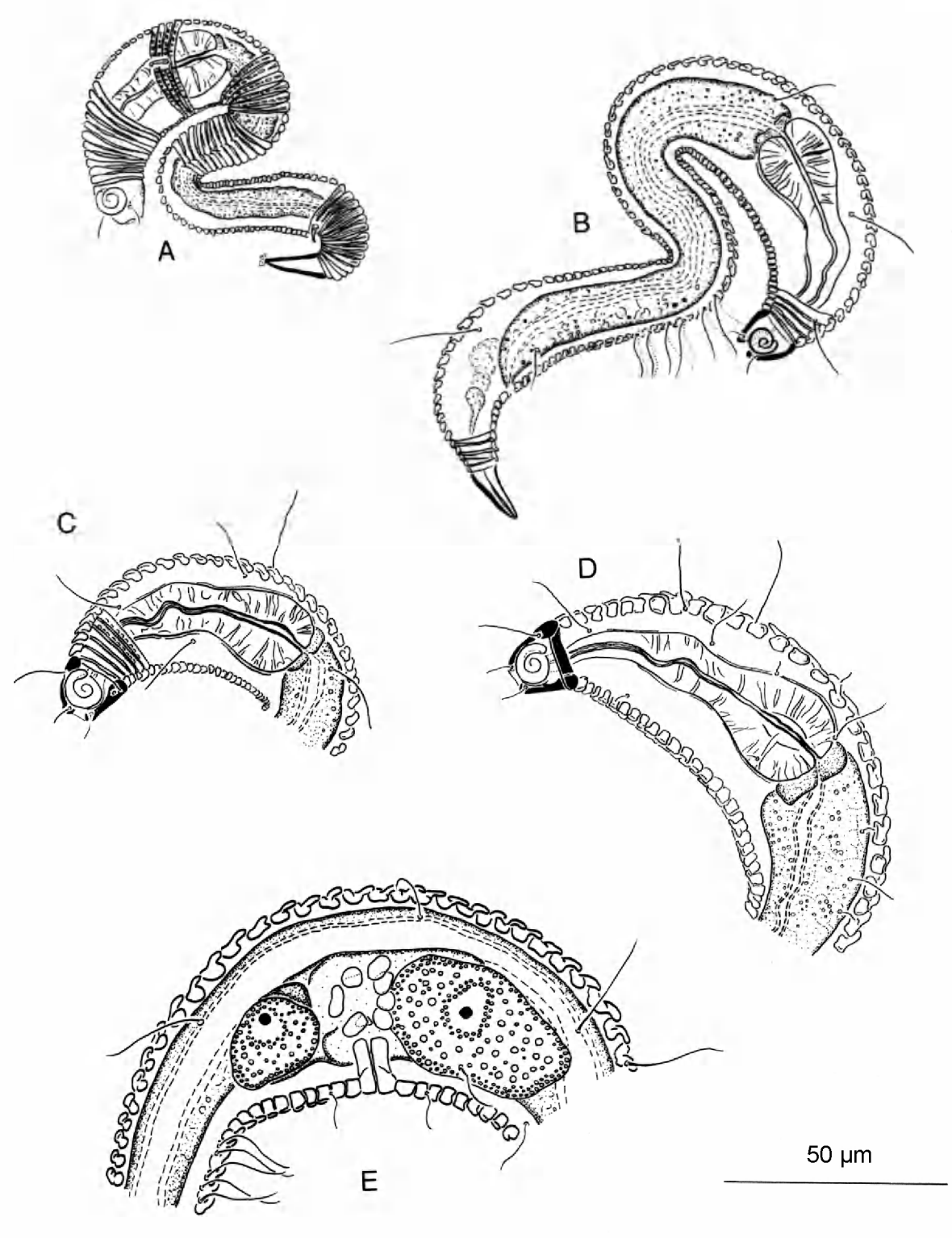


Fig. 9. *Bathyepsilonema lopheliae* sp. n. (A) juvenile I, habitus and surface view of cuticle; (B) juvenile II, habitus; (C) juvenile III, head and pharyngeal region; (D) juvenile IV, head and pharyngeal region; (E) paratype ♀, detail of reproductive system.

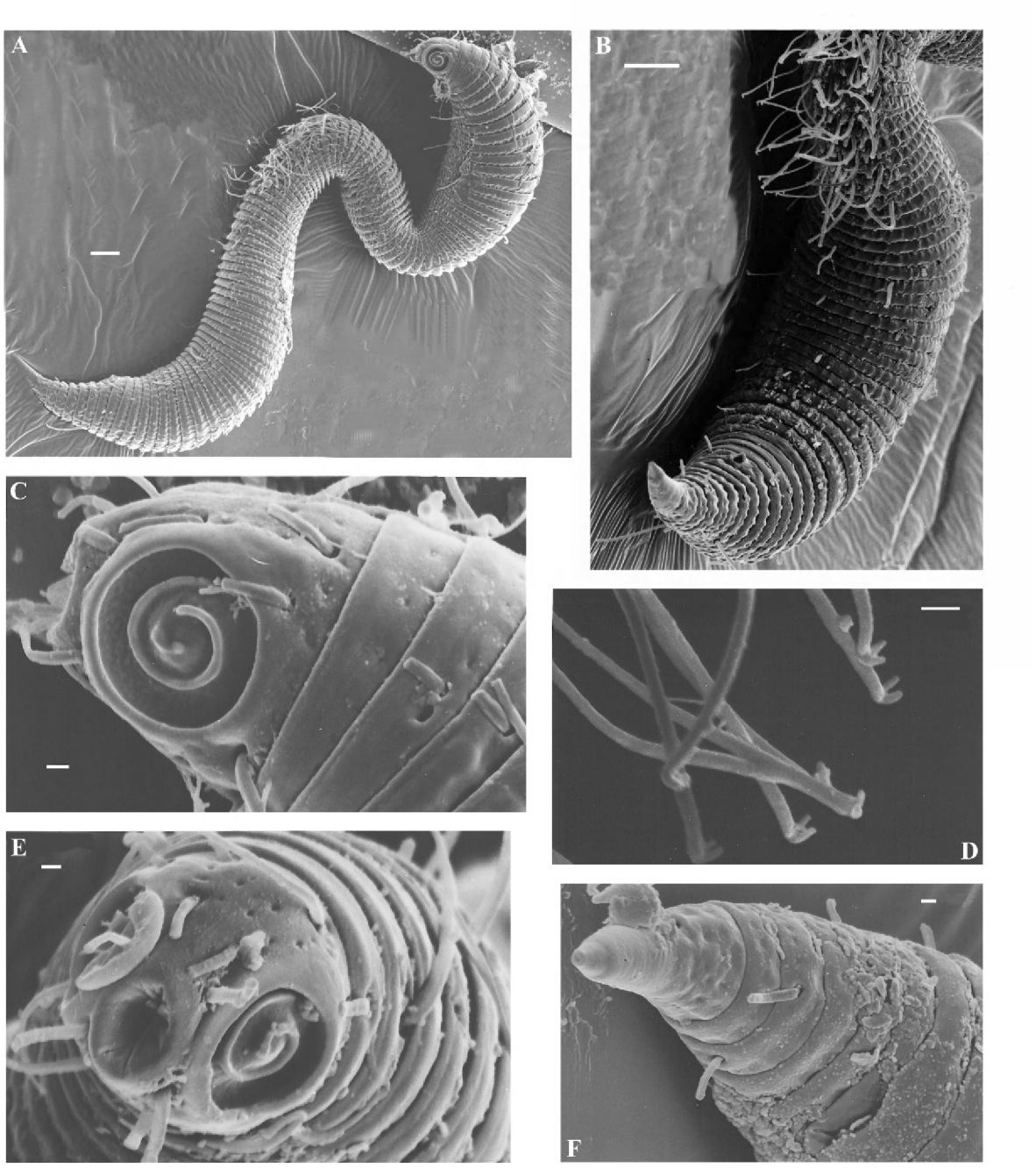


Fig. 10. *Bathyepsilonema lopheliae* sp. n. (A) ♂, habitus; (B) ♂, posterior body region: lateral-ventral view; (C) ♂, head capsule: lateral view; (D) ♂, distal end of ambulatory setae; (E) ♀, head capsule: en face view; (F) ♀, anus and tail tip. Scale bars: A,B: 10 µm; C,D,E & F: 1 µm.

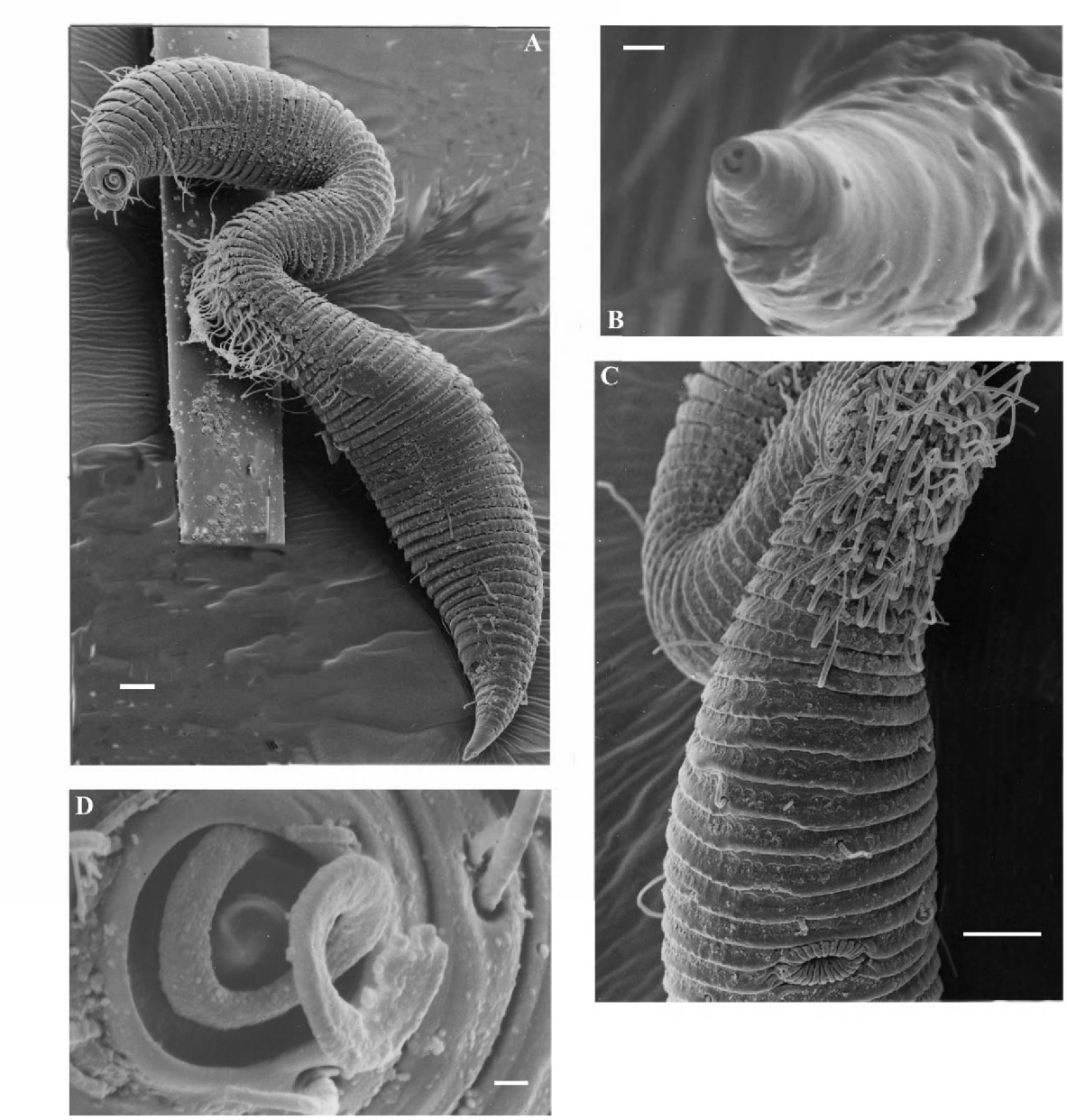


Fig. 11. *Bathyepsilonema lopheliae* sp. n. (A) ♀, habitus; (B) ♂, tail tip with terminal pore and slit-like opening; (C) ♀, vulva and ambulatory setae: ventral view; (D) ♂, protruded corpus gelatum. Scale bars: A,C: 10 µm; B & D: 1 µm.

	Holotype male	Paratype males (n = 2)	Paratype females (n =4)	Juvenile stage I (n = 1)	Juvenile stage II (n = 1)	Juvenile stage III (n = 1)	Juvenile stage IV (n = 4)
L	420	415-420 (415)	414-440 (420)	165	220	230	310-360 (350)
N	91	89-93 (91)	91-94 (93)	100	94	87	87-92 (90)
cs	7.1	5.5-8.1 (6.8)	5.8-7.2 (6.7)	6.6	3.6	4.8	4.2-6.2 (5.2)
dcs	1.2	2.1-2.7 (2.4)	1.5-2.0 (1.8)	3.9	1.2	2.2	0.9-1.7 (1.2)
Hdw	16.4	15.9-17.2 (16.6)	16.6-16.9 (16.8)	10.9	11.4	12.6	14.6-15.6 (15.1)
Amphw	10.5	9.4-10.6 (10.0)	8.8-10.2 (9.5)	6.9	6.7	8.0	8.3-9.9 (8.9)
Amph%	64.2	54.7-66.3 (60.5)	53-61.5 (56.7)	62.9	58.8	63.5	55.1-65.2 (59.3)
ph	83.3	89.2-91.2 (90.2)	80.4-87.5 (84.0)	57.4	59.8	66.8	76.9-82.5 (80.3)
Asl	24.2	20.9-21.4 (21.1)	20.9-23.6 (22.4)		16.3	19.5	17.0-21.1 (18.5)
tail	59.9	50.7-50.7 (50.7)	42.0-44.5 (43.2)	28.4	39.7	39.0	39.9-46.8 (45.6)
tmr	27.8	24.4-26.9 (25.7)	19.4-23.0 (21.6)	15.3	12.7	16.3	18.1-21.5 (20.4)
mbd ph	40.0	34.7-34.7 (34.7)	37.0-38.0 (37.4)	21.2	27.5	25.2	32.1-36.8 (35.1)
mbd	41.5	35.8-37.2 (36.5)	45.1-46.5 (45.6)	12.8	20.3	19.0	26.1-34.5 (32.0)
(mbd)	24.8	22.3-24.6 (23.5)	22.3-24.0 (23.4)	11.8	15.5	15.6	20.7-23.7 (22.7)
mbd/(mbd)	1.7	1.5-1.6 (1.6)	1.9-2.0 (2.0)	1.1	1.3	1.2	1.3-1.5 (1.4)
ABD	22.0	21.3-23.1 (22.2)	19.9-20.7 (20.2)	13.5	17.9	16.8	18.2-23.5 (20.8)
spic	55.9	51.1-52.4 (51.8)					
gub	7.1	9.6 [1]					
V%			67.9-71.3 (69.8)				
a	10.1	11.2-11.7 (11.4)	9.0-9.5 (9.3)	13.0	11.0	12.0	10.4-11.9 (11.0)
b	5.1	4.6-4.7 (4.6)	4.8-5.4 (5.0)	2.9	3.7	3.4	3.9-4.7 (4.3)
c	7.0	8.2-8.3 (8.2)	9.4-10.1 (9.8)	5.8	5.6	5.8	7.3-7.9 (7.7)

Table 3. Measurements of specimens of *Bathyepsilonema lopheliae* sp. n. All absolute values are in µm. The number of specimens that was measured, when different from the total number of specimens, is indicated between brackets in superscript.

The shape of the head and amphid, as well as the number and position of subcephalic setae, is similar as in males.

The reproductive system is didelphic and amphidelphic (Fig. 9E). The vulva is surrounded externally by a large number of radial, cuticular ridges (Fig. 11C). The vagina consists of two parts, the distal part is heavily cuticularised. The caudal glands seem to end in one pore only: the curved opening that was found in males is not observed here (Fig. 10F).

Juveniles

First stage juvenile (Fig. 9A)

One individual was found in 2001 on the type location. This first stage juvenile is very small. Compared to adults, the anterior body region has a great relative length (de Man b is 2.9 compared to 4.8 in adult males on average). The relative proportion and the shape of the amphids is similar as in adults, although the amphids consist of one and a half turns only (instead of two). There are 100 cuticular annules, all of comparable size. Some annules are ornamented with a single transverse row of small vacuoles. Between the first dorsal curve and the ventral curve there seems to be a longitudinal, mediolateral ridge on both sides. No subcephalic setae were found.

There are two short but very thick laterodorsal somatic setae present at the level of the pharyngeal bulb (one on each side), and two thick and short mediolateral setae (one on each side) near the anus. There are no ambulatory setae present.

Second stage juvenile (Fig. 9B)

Only a single specimen was found. In overall appearance it resembles the adults, however it is clearly smaller. There are 94 body annules, a number comparable to that in adults. There are no subcephalic setae.

In the pharyngeal region there are subdorsal, mediolateral and lateroventral somatic setae present. In the posterior body region the somatic setae are located subdorsally, mediolaterally and subventrally.

The ambulatory setae are arranged in two subventral rows, each consisting of six setae.

Third stage juvenile (Fig. 9C)

Only a single specimen was found, in size comparable to the second stage juvenile. There are 87 body annules, which is slightly less than in adults and second stage juveniles. There is one long subdorsal subcephalic seta present at the right side of the head.

Compared to the distribution of somatic setae in the pharyngeal region in second stage juveniles, a mediodorsal row is added in third stage juveniles. In the posterior body region, the distribution of somatic setae is similar as in second stage juveniles, although there is a higher number of setae. The ambulatory setae are arranged in two rows, each consisting of twelve setae.

Fourth stage juveniles (Fig. 9D)

One young (future female) and three older fourth stage juveniles (one future male, two future females) were found. They resemble the adults in most respects (e.g. the number of annules), however they are somewhat smaller. There are two subcephalic setae: a subventral and a subdorsal one.

In the pharyngeal region, somatic setae are arranged on subdorsal and subventral rows, sometimes a long mediodorsal seta is also present. In the posterior body region there are mediodorsal, subdorsal, lateroventral, subventral and medioventral rows of somatic setae.
The ambulatory setae are arranged in four rows of approximately ten setae.

Diagnosis

Bathyepsilonema lopheliae sp. n. is characterised by its body length (in males 417 µm on average, in females 423 µm on average), the number of body annules (in males between 89 and 93, in females between 91 and 94), a dome-shaped head with large amphids (in males 61.75% on average, in females 56.71% on average) positioned centrally or slightly shifted anteriorly on the head capsule. There are eight subcephalic setae, of which two setae are only visible using SEM. The cuticle is ornamented with large vacuoles.

Differential diagnosis

Bathyepsilonema lopheliae sp. n. is very closely related to *B. brachycephalum* Steiner, 1931. There are nevertheless some important differences: in this new species, the amphids are clearly larger (for males: 43.2-52.0% of the head width in *Bathyepsilonema brachycephalum* Steiner, 1931 vs 54.7-66.3% in *B. lopheliae* sp.n) and they take up almost the entire head length. The new species also differs in the overall shape of the head capsule, its smaller body size (for males: 450-595 µm in *Bathyepsilonema brachycephalum* Steiner, 1931 vs 415-421 µm in *B. lopheliae* sp.n) and the number of body annules (for males: 95-99 in *Bathyepsilonema brachycephalum* Steiner, 1931 vs 89-93 in *B. lopheliae* sp.n). The cuticle shows no garland-like ornamentation delimiting faint vacuoles: there are large and clear vacuoles on one row at the level of both enlargements. In between these enlargements, the vacuoles are smaller and are not positioned in a single row.

Other Epsilonematidae associated with this cold-water coral environment

In total, thirteen species of Epsilonematidae belonging to five genera were found to be associated with *Lophelia* and *Aphrocallistes* skeletons in the Porcupine Seabight (samples from 2000 and 2001). Several new species of this family, other than those described above, were found but will not be described here because of the lack of an adequate number of specimens to examine.

The genus *Glochinema* is represented only by the new species described above.

The genus *Epsilonema* is represented by seven species: *Epsilonema multispiralum* sp. n., four other new species but also two known species. *Epsilonema margaritatum* Decraemer & Gourbault, 1987 was already known to be cosmopolitic. Until now it was reported from intertidal and lagoon habitats in the Caribbean Sea (Decraemer & Gourbault, 1987) and Papua New Guinea, as well as

from sublittoral habitats (the Channel and the Mediterranean Sea). In all cases, the substrate was coarse to medium sand (Decraemer *et al.*, 2001). *Epsilonema cygnoides* (Metschnikoff, 1867) was already reported from Norway (Barents Sea) and Kiel Bay, but there the substrate consisted of algae (Decraemer *et al.*, 2001).

The genus *Bathyepsilonema* is represented by three species: the new species *Bathyepsilonema lopheliae* sp. n., another new species and *B. spongiosum* Clasing, 1986. The last species is also known from intertidal coarse sand in Chile (Clasing, 1986).

A new species of the genus *Metepsilonema* Steiner, 1927 was found but will not be described here.

The monotypic genus *Triepsilonema* Decraemer, 1982 is also represented here. *Triepsilonema tripapillatum* Decraemer, 1982 has been described from a lagoon in Papua New Guinea (Decraemer, 1982). The substrate there was very coarse, consisting of fragments of the coralline alga *Halimeda.*

Discussion

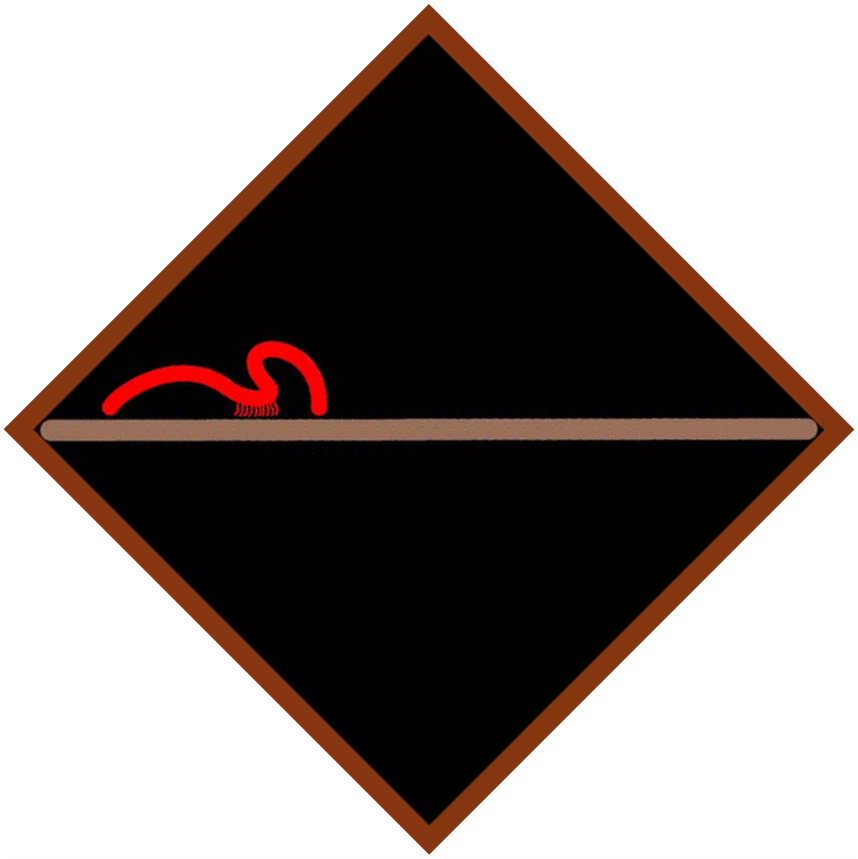
Based on these findings, one can assume that cosmopolitism in epsilonematid nematodes occurs more frequently than formerly accepted. However, more material has to be examined to improve our view on the geographical distribution of Epsilonematidae. The use of specific dispersion routes between oceans is another aspect that needs attention. Transoceanic dispersal occurs frequently among free-living marine nematodes. Marine benthic communities from the Antarctic shelf possess characteristics reminiscent of deep-sea communities (Aronson & Blake, 2001). The same is probably true for marine epifaunal communities. This hypothesis is supported by the geographical distribution of some epsilonematid nematodes. *Glochinema trispinatum* sp. n. for example occurs in the North-Atlantic deep-sea as well as on the Antarctic shelf. *Bathyepsilonema lopheliae* sp. n. is very closely related to *B. brachycephalum* Steiner, 1931, a species found in the Ross and Weddell Sea in Antarctica. The extent of morphological similarities and morphometrical differences between the specimens from Antarctica and those from the Porcupine Seabight indicates a certain genetic divergence, however it lies within the range of one species. This aspect can nevertheless only be fully understood by conducting a molecular phylogenetic survey.

5.6. ACKNOWLEDGMENTS

The authors wish to thank Prof Dr Jean-Pierre Henriet and the Renard Centre of Marine Geology, as well as the crew of the RV Belgica for a succesful collaboration. We are grateful to Prof Dr Magda Vincx and Drs Dominick Verschelde for their advice on some taxonomical questions and for their constructive comments on this article. Special thanks go to Rita Van Driessche for the excellent scanning micrographs. The authors wish to thank Drs Hee Joong Lee for providing the Antarctica-specimens of *Glochinema trispinatum* sp. n. The first author acknowledges an aspirant grant provided by the FWO-Vlaanderen, Belgium. Our research was conducted within the framework of the Atlantic Coral Ecosystem Study (ACES) (EC Fifth Framework Research Program).

CHAPTER 6

POSTEMBRYONIC MORPHOLOGY IN EPSILONEMATIDAE, WITH A DISCUSSION ON THE VARIABILITY OF CAUDAL GLAND OUTLETS



Paper *in press*

Raes, M., Decraemer, W., Vanreusel, A.

Postembryonic morphology in Epsilonematidae, with a discussion on the variability of caudal gland outlets

Journal of Nematology

6.1. ABSTRACT

A new species of *Akanthepsilonema* and the first stage juvenile of *Glochinema trispinatum* are described. Furthermore, additional morphological information is provided for *Triepsilonema tripapillata*. Animals originate from a cold-water coral degradation zone in the Porcupine Seabight area (North-East Atlantic Ocean). *Akanthepsilonema sinecornibus* sp. n. differs from *A. helleouetae* in the number of body annules, the sexual dimorphism in amphid size, the absence of copulatory thorns in males, the absence of large spines and horns, the shape of the copulatory apparatus and the position of the ambulatory setae relative to the vulva in females. The genus diagnosis for *Akanthepsilonema* is adjusted to incorporate the new species: *Akanthepsilonema* mainly differs from every other genus in the family by the combination of six rows of ambulatory setae situated around the vulva in females and eight subcephalic setae not displaced towards the anterior part of the head capsule. Small differences between the Papua New Guinea and the Porcupine Seabight populations of *T. tripapillata* indicate minimal intraspecific variability. Second stage juveniles from Papua New Guinea have two rows of three ambulatory setae whereas Porcupine Seabight specimens have two rows of four ambulatory setae. First and fourth stage juveniles of *T. tripapillata* are described for the first time. Literature data and personal observations showed that the moulting of first stage juveniles into second stage juveniles and of third stage juveniles into fourth stage juveniles involves a decrease in the number of body rings resulting in a loss of flexibility, which is possibly compensated by the development (I-II) or the doubling of the number of rows (III-IV) of ambulatory setae. This decrease is also linked with the formation of the head capsule and the smooth tail tip, although intergeneric variability is evident. The moulting of second stage juveniles into third stage juveniles and of fourth stage juveniles into adults is also subject to intergeneric variability. The variability in the number and orientation of caudal gland outlets among different nematode taxa is discussed. The presence of separate outlets for the caudal glands seems to be widespread within the family Epsilonematidae and has also been observed in various other, unrelated taxa of free-living aquatic nematodes, although their arrangement in Epsilonematidae is opposite. This aberrant arrangement is probably related to the aberrant locomotory pattern in this family.

Key words: Akanthepsilonema sinecornibus, caudal glands, cold-water corals, epsilonematids, *Glochinema trispinatum*, ontogeny, Porcupine Seabight, taxonomy, *Triepsilonema tripapillata*

6.2. INTRODUCTION

The family Epsilonematidae Steiner, 1927 is composed of three subfamilies: Epsilonematinae Steiner, 1927, Glochinematinae Lorenzen, 1974 and the monospecific Keratonematinae Gourbault and Decraemer, 1986. Epsilonematid nematodes are frequently found among the supralittoral or intertidal interstitial marine fauna and recently several species have also been found in the deep sea (Neira *et al.*, 2001; Gad, 2002; Raes *et al.*, 2003; Gad, 2004). Samples originating from a cold-water coral degradation zone in the Porcupine Seabight yielded a rich nematode community, including

several new species for this family (Raes *et al.*, 2003). Coral fragments, such as those of the framework building cold-water coral *Lophelia pertusa* (Linnaeus, 1758), can be regarded as ideal substrates for epifaunal nematodes such as Epsilonematidae. Nematodes belonging to this family are characterised by an ε-shaped body and the presence of ambulatory setae on the ventral side of their posterior body region. These structures are used in their looper-caterpillarlike locomotion (Stauffer, 1924; Lorenzen, 1973a).

A new species of *Akanthepsilonema* Gourbault and Decraemer, 1991, with aberrant features for the genus, will be described here. Additional information is given for *Triepsilonema tripapillata* Decraemer, 1982, a species originally described from an intertidal lagoon in Papua New Guinea based on only one male, one female, one second stage juvenile and one third stage juvenile. Clearly, there was a need for additional information to incorporate intraspecific variability. Strikingly, this species was found to be very abundant in the sampled cold-water coral degradation zone. The complete juvenile series is illustrated in this paper. *Glochinema trispinatum* Raes, Vanreusel and Decraemer, 2003 was originally described from the Porcupine Seabight area. New material from this area yielded a first stage juvenile. Because the present study produced a lot of new information on juvenile stages within the Epsilonematidae, the ontogenetic morphology of this family will be discussed. The redescription of *T. tripapillata*, a species with pronounced caudal papillae bearing the separate outlets of the caudal glands, resulted in an extensive review on the number and orientation of caudal gland outlets in nematodes.

6.3. MATERIALS AND METHODS

The epsilonematids studied in this paper originated from three NIOZ (Netherlands Institute for Sea Research) box corers (diam. 32 cm) that were collected with the RV Belgica during the June 2000 and May 2001 sampling campaigns. These box cores were taken on the top and slope of a seabed mound situated in the Belgica mound province of the Porcupine Seabight (Box IV 2000 (depth: 1005 m): 51°24'48,2" N - 11°45'55,4" W. Box V 2000 (depth: 1000 m): 51°24'49,4" N - 11°45'55,9" W. Box IV 2001 (depth: 972 m): 51°25'7,7" N - 11°46'9,3" W). The Porcupine Seabight is a large embayment of the European continental slope, located in the North-East Atlantic Ocean, southwest of Ireland (Fig. 1). The Belgica mound province is one of the three seamound provinces in this area, characterised by the presence of 21 large, outcropping and conical mounds, aligned on four along-slope-trending ridges (Van Rooij *et al.*, 2003). These mounds are known to be associated with cold-water coral banks, mainly constructed by the framework builder *Lophelia pertusa* (Linnaeus, 1758) and associated fauna such as the glass sponge *Aphrocallistes bocagei* Schultze, 1886. The samples used in the present study originated from a cold-water coral reef degradation zone, covered with sediment-clogged dead coral framework (Freiwald *et al.*, 2002) and skeletons of *Aphrocallistes bocagei*. Only a very small amount of living coral was present. After removal of these large biogenic substrates, three sediment cores (surface area: 10 cm^2) were collected from each box core. The sediment was poorly sorted, containing small coral and sponge fragments as well as some small mollusc-shells and echinoid radiolas. All material was fixed with 4% neutralised formalin.

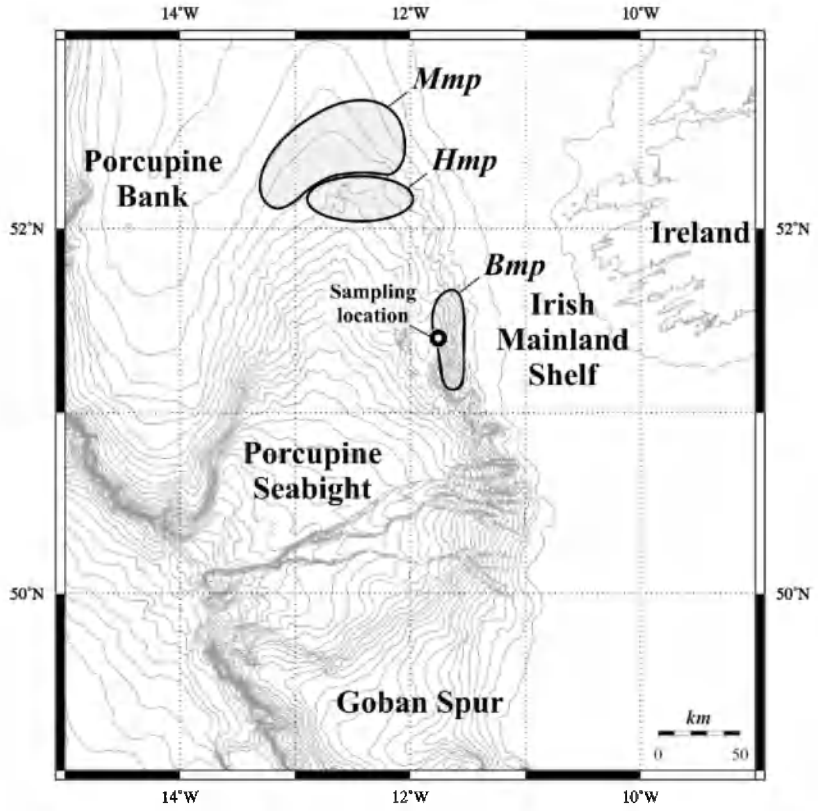


Fig. 1. Map of the Porcupine Seabight area (after Van Rooij *et al.*, 2003). The sampling location is indicated. A detailed overview of the Belgica mound province with an indication of the exact box core locations is given in Raes & Vanreusel (2005: Figure 1). *Mmp*= Magellan mound province; *Hmp*= Hovland mound province; *Bmp*= Belgica mound province.

Each *Lophelia* and *Aphrocallistes* fragment was rinsed thoroughly over a 1 mm and a 32 µm sieve to separate macrofauna and meiofauna. Meiofauna was extracted from the underlying or remaining sediment by density gradient centrifugation, using Ludox (a colloidal silica polymer; specific gravity 1.18) as a flotation medium (Heip *et al.*, 1985; Vincx, 1996). Some of the material was stained with Rose Bengal. Nematodes were picked out individually and subsequently mounted onto slides for detailed morphological observation with a Leica DMLB light microscope, using the formalin-ethanol-glycerol technique described by Seinhorst (1959) and Vincx (1996). A Leitz Dialux 20 microscope, Sanyo CCD video camera and the Quantimet 500 software were used to perform measurements. Scanning electron micrographs were taken from the formalin fixed specimens. After ultrasonic treatment (to remove detritus attached to the body) the specimens were transferred to OsO_4, dehydrated, subjected to critical point drying and coated with gold particles.

Type material is deposited in the collections of Ghent University, Museum voor Dierkunde (UGent), the Koninklijk Belgisch Instituut voor Natuurwetenschappen in Brussels (KBIN) and the Natural History Museum in London (NHM).

6.4. ABBREVIATIONS USED

L: total body length

N: number of cuticular rings, smooth tail tip included (remark: all annules counted dorsally)

dcs: distance from the anterior edge of the head capsule to the insertion point of the cephalic setae

hdw: maximal width of the head capsule

hdl: length of the head capsule

bda: body diameter at the level of the amphids

amphw: amphidial width

amph%: (Amphw / Hdw) X 100

ph: pharyngeal length, measured from the anterior end of the head capsule up to the posterior border of the pharyngeal bulb, lips (when protruding) and cardia not included

lvAsl: length of the anteriormost lateroventral ambulatory seta

osvAsl: length of the anteriormost ambulatory seta in the outer subventral rows

isvAsl: length of the anteriormost ambulatory seta in the inner subventral rows

asup: length of the anteriormost modified somatic or supporting seta

psup: length of the posteriormost modified somatic or supporting seta

tail: tail length

tmr: length of the smooth tail tip

mbd ph: body diameter at level of the pharyngeal bulb

mbd: maximal diameter of the posterior body region

(mbd): minimal body diameter

mbd/(mbd): proportion of the minimal body diameter to the maximal body diameter

abd: anal body diameter

spic: length of the spicule, measured along the arc

gub: length of the gubernaculum

V%: position of the vulva, expressed as a percentage of L, measured from the anterior end

a: de Man a-ratio, i.e. L / mbd

b: de Man b-ratio, i.e. L / ph

c: de Man c-ratio, i.e. L / tail

6.5. DESCRIPTIONS

Familia Epsilonematidae Steiner, 1927

Subfamilia Epsilonematinae Steiner, 1927

Genus *Akanthepsilonema* Gourbault and Decraemer, 1991

***Akanthepsilonema sinecornibus* sp. n.** (Figs. 2-4)

Type specimens.

Holotype male on slide RI 682 (KBIN). Paratype males on slides UGMD 104095 (UGent), RI 681, RI 677 (KBIN) and stored as 2005.2684 (NHM). Additional male: 2005.2657 (NHM). Allotype female on slide RI 681 (KBIN). Paratype females on slides UGMD 104093 (UGent), RI 681, RI 678 (KBIN) and stored as 2005.2675 (NHM). Paratype third stage juveniles on slides UGMD 104094 (UGent) and RI 678 (KBIN). Paratype fourth stage juveniles on slides UGMD 104092 (UGent), RI 676 (KBIN) and stored as 2005.2666 (NHM).

Type locality. Porcupine Seabight, Belgica mound province. Coordinates: 51°24'49,4" N - 11°45'55,9" W (material collected on 17/06/2000; depth: 1000 m).

Other localities. Porcupine Seabight, Belgica mound province. Coordinates: 51°24'48,2" N - 11°45'55,4" W (material collected on 17/06/2000; depth: 1005 m); 51°25'7,7" N - 11°46'9,3" W (material collected on 07/05/2001; depth: 972 m).

Date of collection. 17th of June 2000 and 7th of May 2001.

Type habitat. A cold-water coral degradation zone on the flank and near the top of a seabed mound. Associated with sediment-clogged framework of the cold-water coral *Lophelia pertusa* (Linnaeus, 1758). It was found on dead coral fragments and within the underlying sediment.

Relative abundance. This species comprises 0.46 % of the total nematode community at the type locality.

Etymology. The species name means 'without horns', as opposed to the key diagnostic feature formerly delimiting the genus: the presence of large mediodorsal horns just anterior to the ventral curvature. From the Latin preposition *sine* (without) and the ablative plural of the Latin noun *cornu, cornus* (horn).

Measurements. Table 1.

Males

Body typically epsilon-shaped, rather small and noticeably slender with only slight enlargements at level of pharynx and ambulatory setae. Region between anteriormost dorsal curvature and ventral curvature strikingly long and slender (Figs. 2A, 4A).

Body cuticle with 145-163 body annules (155 in holotype). Annules broadest at level of pharynx and cloaca and finest at level of ambulatory setae. Annules only minimally overlapping. Anteriormost annules with anteriorly directed margin. Ventrally, inversion of orientation between annules 56 and 67 (predominantly between annule 59 and 60; between 60 and 61 in holotype). Dorsally, inversion between annules 69 and 79 (predominantly between annule 77 and 78, as in holotype). Annules in pharyngeal region with irregular, sometimes mosaic-like pattern of heterogeneous vacuoles of various sizes (Fig. 2A). Annules in slender region posterior to pharynx with cuticular ornamentation comparable to that of pharyngeal region. Both regions dorsally with strongly built, longitudinal ridges delimiting more regularly shaped vacuoles. Annules at level of ambulatory setae ornamented with one transverse row of small vacuoles. Annules in posterior body region and anteriormost tail annules either with one row of irregular vacuoles or with mosaic of smaller heterogeneous vacuoles. More posteriorly on tail, vacuoles progressively smaller and 1-6 annules immediately anterior to tail tip completely

smooth or only with indistinct vacuoles. Ventral field of hair-like spines present anterior to ambulatory setae (Fig. 2A). Short spines present dorsally in region of ambulatory setae.

Somatic setae in pharyngeal region and region anterior to ambulatory setae arranged in 10 longitudinal rows: one mediodorsal row, two subdorsal rows, two laterodorsal rows, two lateroventral rows, two subventral rows and one medioventral row. Mediodorsal, subdorsal and laterodorsal setae especially long. Somatic setae at level of ambulatory setae arranged in five longitudinal rows: one mediodorsal row and two subdorsal rows with long setae and two mediolateral rows with short setae. In this region no somatic setae on ventral side of body. Ambulatory setae strongly built and slightly s-shaped, all with curved tip (see female in Fig. 4D) and arranged in six longitudinal rows: outer rows with 8-15 lateroventral setae, intermediate rows with 12-18 subventral setae and inner rows with 6-12 almost medioventral setae (Figs. 2A, 4G). Ambulatory setae in lateroventral row straighter than other ambulatory setae. Lateroventral row almost immediately followed by 4-5 lateroventral short, slender, straight, slightly modified somatic setae with straight, pointed tip. Slightly modified somatic setae gradually decreasing in length and width towards posterior end and eventually becoming indistinguishable from normal, subventral-lateroventral somatic setae on tail.

Head capsule a smooth truncated cone (Figs. 2B, 4B), often with lip region partially protruding. Head capsule with four cephalic setae and eight subcephalic setae, the latter all located at level of amphids. On each side of head capsule subcephalic setae arranged as follows: one subdorsal seta immediately anterior to amphid, one ventrosublateral seta at same level as subdorsal one, one lateroventral seta immediately posterior to sublateral seta and one subventral seta variable in position, i.e. at level of subdorsal and sublateral seta (as in holotype) (Fig. 2B), at level of lateroventral seta or in between sublateral and lateroventral seta. Amphids situated near base of head capsule and clearly shifted dorsally. Amphidial fovea a large (40.5% of corresponding head width in holotype), ventrally wound spiral usually consisting of 1.6 coils (1.8 coils in Fig. 2B). Buccal cavity very narrow. Two minute teeth (one dorsal, one ventral) present or absent where buccal cavity grades into pharyngeal lumen (Fig. 2B). Pharynx short, extending into well-developed, oval, muscular terminal bulb. Pharyngeal lumen wall strongly cuticularised, especially in posterior part of bulb where lumen wall is differentiated into well-developed cuticular valves (Fig. 3D). Cardia short and triangular. Intestine granular, with thick conspicuous brush border.

Male reproductive system (Fig. 3C) with single anterior, outstretched testis extending far into region between anteriormost dorsal curvature and ventral curvature. Testis positioned ventrally around intestine, sometimes shifted somewhat to left or right side. Narrow anterior germinal and growth zones followed by wider vesicula seminalis consisting of large, opaque sperm cells each with clear, round nucleus containing radiate pattern of small nucleoli. Spicules slender and strongly curved, with hook-shaped capitulum. Calomus thin, with small bulge at base of capitulum, where velum originates. Gubernaculum thin, slightly bent, adjacent to spicules except for proximal end. Copulatory thorns absent.

Tail short and conical, with 16-20 complete annules, including smooth tail tip (18 in holotype). Anterior end of conical tail tip dorsally with 1-5 incomplete annules (three in holotype). Anteriormost tail annule split ventrally around cloaca. Tail with subdorsal and subventral-lateroventral somatic setae.

Three caudal glands extending anteriorly beyond cloaca (Fig. 3C), up to two-thirds of spicule length. Each of these glands ending in a separate pore (Fig. 4H).

Females

Females similar to males in size and shape, although posterior body enlargement more pronounced (Figs. 2D, 4E). Cuticle composed of 151-163 annules (155 in allotype female), comparable to males. Inversion of orientation between annules 57 and 68 (between 60 and 61 in allotype female) ventrally and between annules 68 and 82 (between 80 and 81 in allotype female) dorsally. Cuticular ornamentation similar to that of males (Figs. 2C, 4F).

Position of rows of somatic setae in females identical to that of males, except for absence of medioventral row in pharyngeal region and presence of an additional medioventral seta immediately anterior to anus. Ambulatory setae similar to those of males, arranged in 6-7 longitudinal rows. Outer, lateroventral rows with 14-20 setae: 5-8 setae situated anterior to vulva, 8-11 setae posterior to vulva and in some cases one seta at level of vulva. Intermediate, subventral rows with 11-18 setae, of which 5-8 situated anterior to vulva, 5-10 posterior to vulva and one seta present or absent at level of vulva. Inner subventral rows with 7-10 setae: 1-5 setae anterior to vulva and 4-7 setae posterior to it. Ambulatory setae in lateroventral rows longer, straighter and more robust than those in subventral rows. As many as two medioventral setae may be present between both inner subventral rows. In total 27-38 setae situated anterior to vulva and 42-49 setae posterior to it. Number of ambulatory setae anterior to vulva always less than posterior to it. Each lateroventral row of ambulatory setae followed by two or three modified somatic setae considered supporting setae because they are longer (11-15.5 µm in females vs. 7.5-13 µm in males) and much more strongly built than the modified somatic setae in males. Each supporting seta similar to ambulatory setae in length and girth, but differing from them by being straight and usually lacking a curved tip, except for anteriormost supporting seta with minute, sometimes slightly curved, set-off tip. From anterior to posterior there is a gradual morphological transformation from ambulatory setae via supporting setae to normal somatic setae, expressed by changes in length, girth and structure of distal tip (Fig. 2D).

Sexual dimorphism evident from position of subcephalic setae and size and shape of amphids. Eight subcephalic setae: on each side one subdorsal seta, one lateroventral seta and one subventral seta immediately anterior to amphid and one laterodorsal seta immediately posterior to it (Fig. 2C). As a result, females with only six subcephalic setae at level of amphids. Amphids situated near base of head capsule and shifted dorsally. Amphids spiral, ventrally wound with 1.6 coils, but unlike males circular in outline and much smaller (28 % of corresponding head width in allotype female) (Fig. 4C).

Female reproductive system didelphic and amphidelphic, with antidromously reflexed ovaries, situated ventrally from intestine. Anterior ovary reflexed towards left side, posterior ovary reflexed towards right side. Vagina bipartite, with *pars distalis* shorter than, or as long as, *pars proximalis*. Uterus often filled with sperm cells (no. 10-24), recognisable by highly refractive nuclear material. Vulva surrounded externally by numerous radial cuticular ridges, ornamented with small tubercles (Fig. 4F). No somatic setae around vulva.

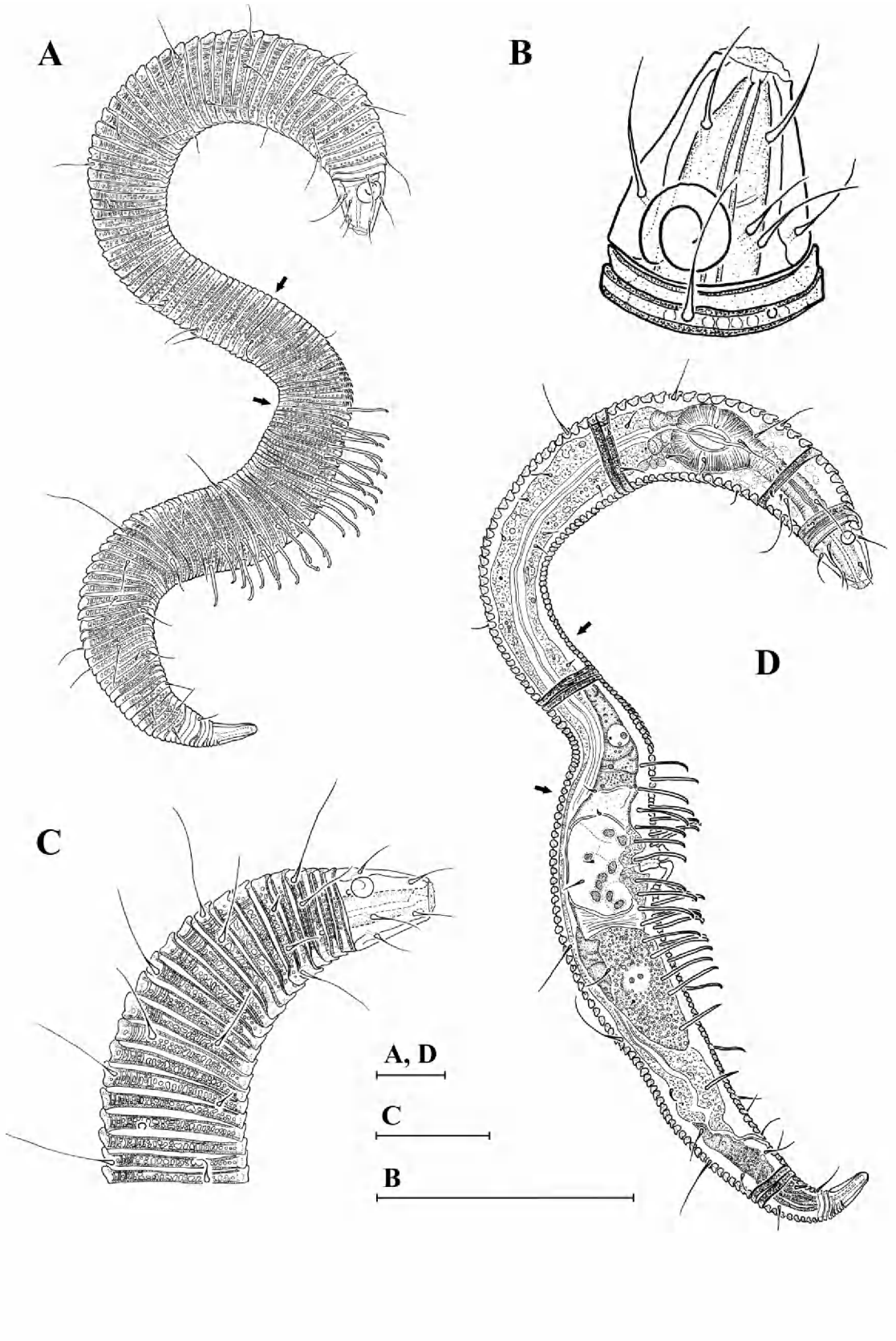


Fig. 2. *Akanthepsilonema sinecornibus* sp. n. A. holotype ♂, habitus; B. additional ♂, head capsule (lateral view); C. paratype ♀, pharyngeal region (lateral view); D. paratype ♀, habitus. Arrows indicate inversion of annular orientation. Scale bars: 20 µm.

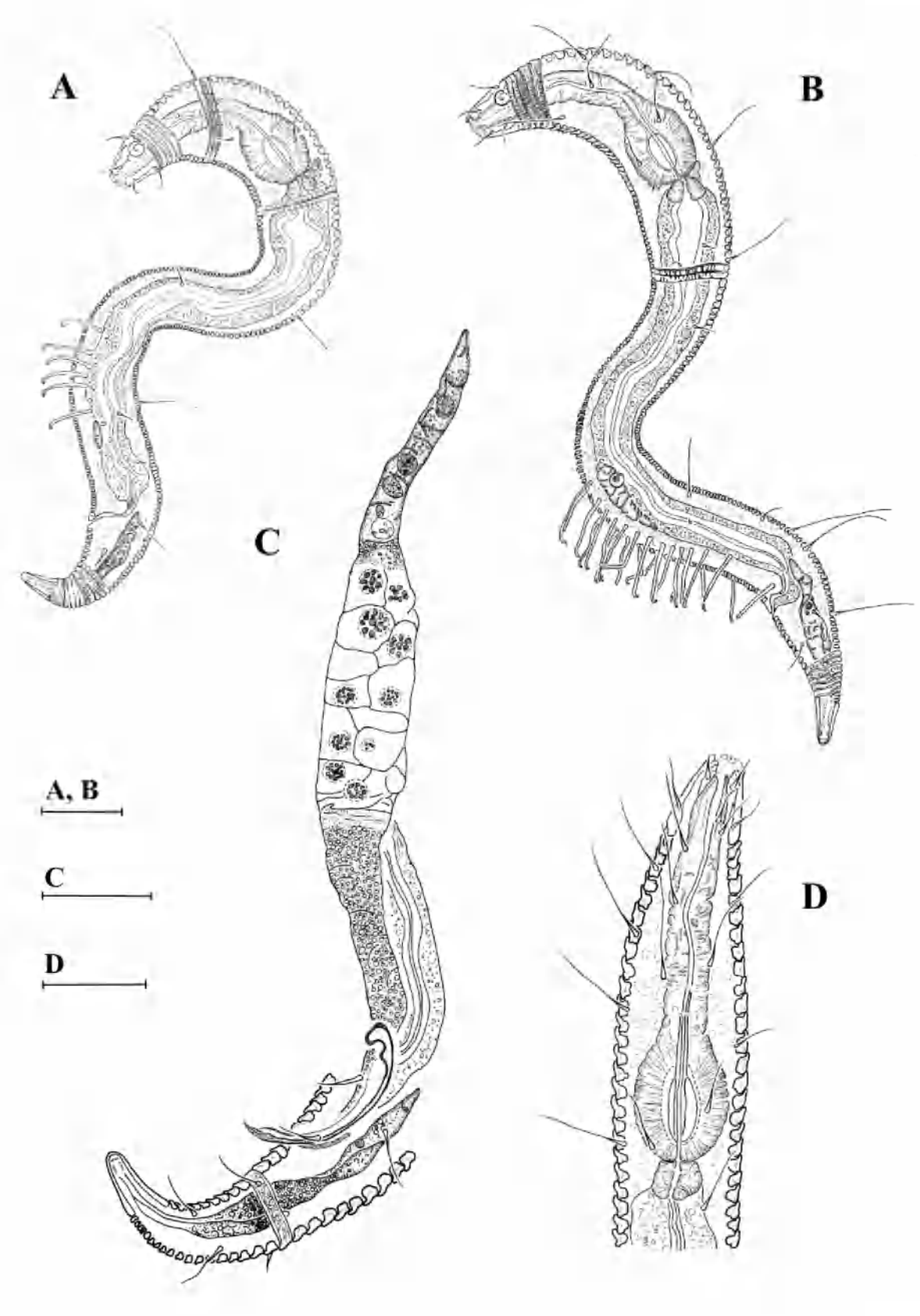


Fig. 3. *Akanthepsilonema sinecornibus* sp. n. A. third stage juvenile, habitus; B. fourth stage juvenile, habitus; C. paratype ♂, testis; D. paratype ♂, pharyngeal region (lateral view). Scale bars: 20 µm.

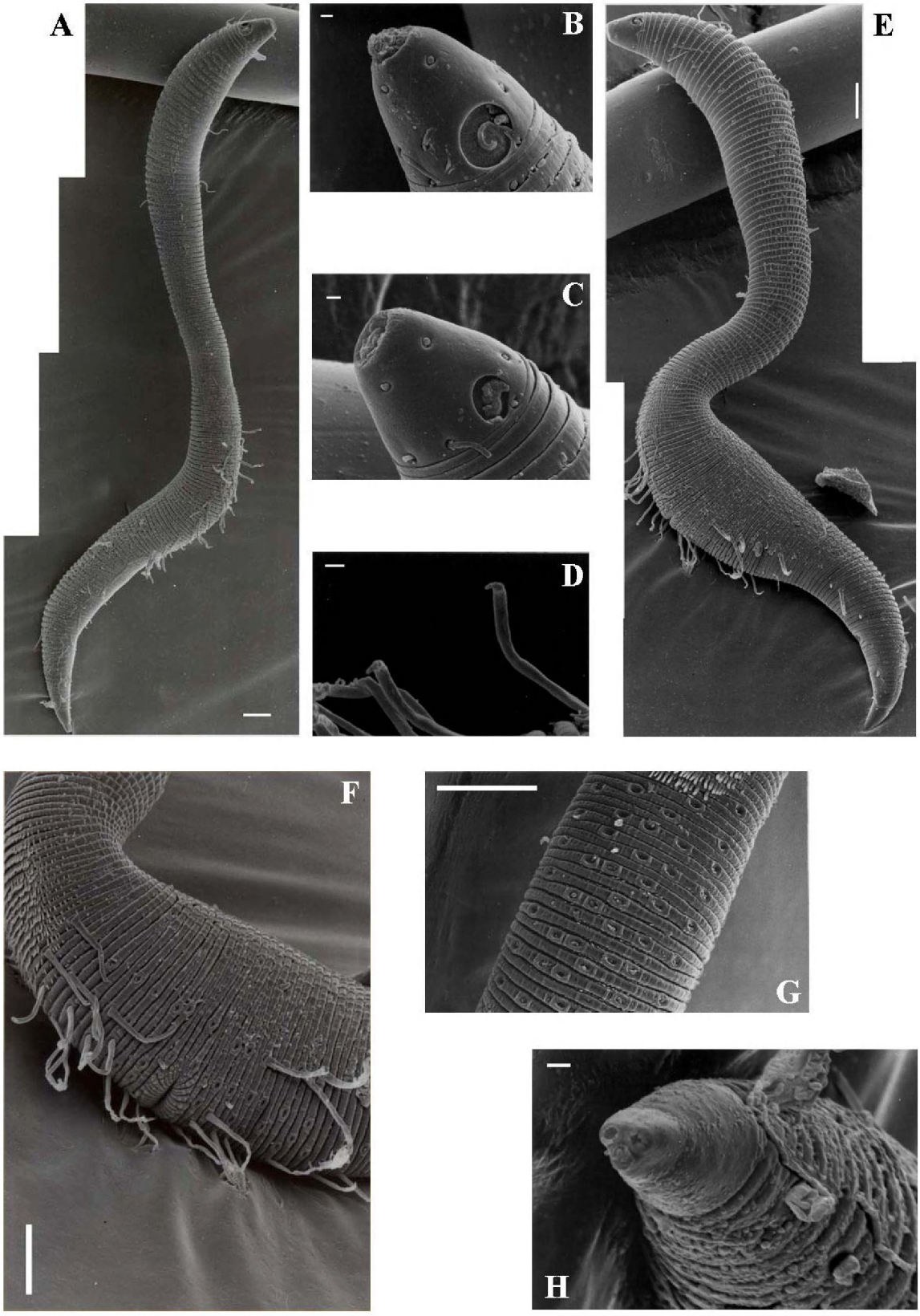


Fig. 4. *Akanthepsilonema sinecornibus* sp. n. A. ♂, habitus; B. ♂, head capsule (lateral view); C. ♀, head capsule (lateral view); D. ♀, ambulatory setae; E. ♀, habitus; F. ♀, vulva and ambulatory setae (lateral-ventral view); G. ♂, insertion sites of ambulatory setae (ventral view); H. ♂, tail tip with outlets of caudal glands. Scale bars: 10 µm in A, E, F and G; 1 µm in B, C, D and H.

Tail with 16-19 complete annules, including smooth tail tip (18 in allotype female). Conical tail tip with 1-5 incomplete annules on dorsal side (three in allotype female). As in males, anteriormost tail annule split around anus and separate outlets for each caudal gland.

Juveniles

First and second stage juveniles

Not found.

Third stage juveniles

Three juvenile males. Body comparable to male adults in shape (Fig. 3A), but smaller and with more constant body diameter. Cuticle with 166-185 narrow annules, which is more than in adults. Annules in pharyngeal region with one row of more or less irregular vacuoles occupying entire width of each annule. Annules in slender region posterior to pharynx with one row of tiny vacuoles. Annules smooth at level of ambulatory setae and in posterior body region. Anteriormost tail annules with one row of tiny vacuoles. Vacuoles larger and more irregular more posteriorly on tail.

Except for region of ambulatory and supporting setae, somatic setae arranged in five longitudinal rows: one mediodorsal row, two laterodorsal rows and two lateroventral rows. No lateroventral somatic setae in region of ambulatory and supporting setae. Two subventral rows with 10-11 slender, slightly s-shaped ambulatory setae with curved tip. Two posteriormost ambulatory setae on each side slightly broader and situated slightly more dorsally than other ambulatory setae, but distinguishable from supporting seta by presence of curved tip. One strongly developed, straight, dorsosublateral supporting seta with straight tip, situated just anterior to cloaca.

Five subcephalic setae, all situated near posterior edge of head capsule: one mediodorsal seta and on each side of head one laterodorsal and one lateroventral seta. Relative width of amphids comparable to that of females (29.5-32.5% of corresponding head width). Amphids with 1.6 coils.

Tail with 24-28 complete annules, including smooth tail tip, with one or two incomplete annules on dorsal side. As in adults, anteriormost tail annule split around anus.

Fourth stage juveniles

Four juvenile males and three juvenile females, all comparable to male adults in body shape, but smaller (Fig. 3B). Number of annules (162 to 171) comparable to that of third stage juveniles. Cuticular ornamentation in pharyngeal region as described in males. Annules in slender region posterior to pharynx ornamented with single row of vacuoles. Annules smooth at level of ambulatory setae. Annules in posterior body region and anteriormost tail annules with single row of rectangular vacuoles. More posteriorly on tail vacuoles becoming more irregular in shape.

Somatic setae in pharyngeal region and at level of anteriormost dorsal curvature arranged in five longitudinal rows as in third stage juveniles. Somatic setae in region of ambulatory setae and in caudal region arranged as follows: one row of mediodorsal setae, two dorsosublateral rows and two lateroventral rows. Five longitudinal rows of ambulatory setae: two outer subventral rows with 8-11 s-

shaped setae with curved tip, two inner subventral rows of 5-8 thinner and shorter s-shaped setae with curved tip and two medioventral setae at level of first two supporting setae, comparable in shape with inner subventral setae. Each outer subventral row of ambulatory setae followed by three more heavily built supporting setae with straight tip. Anteriormost supporting seta close to posteriormost ambulatory seta but distinguishable from ambulatory setae by its more robust appearance and absence of a distinctly curved tip.

Six to seven subcephalic setae: on each side, one subventral and one lateroventral seta always present. Juvenile males with two subdorsal setae, juvenile females with one mediodorsal seta and two laterodorsal setae posterior to amphid. Relative width of amphids comparable to that in adult females (26.5- 35.5 % of corresponding head width). Amphids spiral, consisting of 1.6 coils.

Tail with 17-25 complete annules, including smooth tail tip. Tail tip with 1-7 incomplete annules on dorsal side. As in adults, anteriormost tail annule split around anus.

Diagnosis

Akanthepsilonema sinecornibus sp. n. is characterised by 145-163 annules in males and 151-163 annules in females. Large spines or horns absent. Most ambulatory setae situated posterior to vulva. Amphids in females clearly smaller than in males. Spicules 37-44.5 µm in length, with hook-shaped capitulum. Copulatory thorns absent.

Differential diagnosis

Akanthepsilonema sinecornibus sp. n. resembles *A. helleouetae* Gourbault and Decraemer, 1991, the only other species within this genus, in the following features: (i) the elongation of the anterior body region; (ii) a maximum-to-minimum body diameter ratio lower than two; (iii) the cuticular ornamentation; (iv) the presence of eight subcephalic setae on the head capsule; (v) the presence of six rows of ambulatory setae in adults and (vi) supporting setae only differentiated in females and juveniles.

It differs from this species in the following features: (i) a higher number of annules; (ii) the total absence of large spines or horns; (iii) amphids wider in males than in females; (iv) shorter spicules with a hook-shaped capitulum in males; (v) absence of copulatory thorns in males and (vi) most ambulatory setae situated posterior to the vulva in females.

Relationships with other genera

The genus *Akanthepsilonema* Gourbault and Decraemer, 1991 was originally erected to accommodate *A. helleouetae*, an epsilonematid with conspicuous copulatory thorns, fine ventral and dorsal spines and large dorsal horns. This made *Akanthepsilonema* one of the easiest recognisable genera in the family.

However, the genus also differs from every other genus in the family by the combination of six rows of ambulatory setae situated around the vulva and eight subcephalic setae not displaced towards the anterior part of the head capsule. Given these features, the new species *A. sinecornibus* sp. n. clearly belongs to this genus. Moreover, Gad (2002) argued that cuticular protrusions such as spines

or dorsal horns can evolve in response to similar environmental conditions and similarities between species with such structures may therefore be interpreted as the result of convergent evolution. Therefore, the presence of such structures is of low diagnostic value and cannot be used to separate genera.

Except for the presence or absence of copulatory thorns, large spines and horns, there is one other important diagnostic character that separates both species: in *A. helleouetae* most ambulatory setae are situated anterior to the vulva whereas in *A. sinecornibus* sp. n. most ambulatory setae are situated posterior to the vulva. The arrangement of ambulatory setae in relation to the vulva was considered a character suitable for discriminating between genera by Gourbault and Decraemer (1996), with only the genus *Archepsilonema* Steiner, 1931 having more ambulatory setae posterior to the vulva. In contrast to *A. sinecornibus* sp. n. however, all ambulatory setae in *Archepsilonema* are situated at the level of the vulva or posterior to it and they are arranged in only four rows (Steiner, 1931).

Because the position of the ambulatory setae in relation to the vulva is a character that does not apply to males and juveniles, this character alone should not be used to erect a new genus. Therefore, *A. sinecornibus* is put in the genus *Akanthepsilonema*.

Within the subfamily Epsilonematinae Steiner, 1927 the only genera with ambulatory setae arranged in six longitudinal rows are *Akanthepsilonema*, *Bathyepsilonema* Steiner, 1931, *Leptepsilonema* Clasing, 1983, *Polkepsilonema* Verschelde and Vincx, 1992 and *Pternepsilonema* Verschelde and Vincx, 1992. Among these genera only *Akanthepsilonema*, *Bathyepsilonema* and *Leptepsilonema* possess eight subcephalic setae. However, we do not consider it advisable to draw any conclusions about relationships between genera within the family until molecular phylogenetic data are available to assess both the phylogenetic significance and the diagnostic value of morphological characters.

Emended genus diagnosis

Akanthepsilonema Gourbault and Decraemer, 1991. Epsilonematidae. This genus is characterised by the combination of an elongated anterior body region, a maximum-to-minimum body diameter ratio of less than two, six rows of ambulatory setae situated around the vulva, supporting setae only differentiated in females and juveniles and eight subcephalic setae not displaced towards the anterior part of the head capsule. Copulatory thorns, large spines and horns present or absent. The majority of the ambulatory setae is situated either anterior or posterior to the vulva.

Type species: *Akanthepsilonema helleouetae* Gourbault and Decraemer, 1991

Other species: *Akanthepsilonema sinecornibus* sp. n.

	Holotype male	Paratype males (n = 14)	Allotype female	Paratype females (n =15)	Juvenile stage III (n = 3)	Juvenile stage IV (n = 7)
L	435	335-500 (430)	435	345-475 (405) [14]	225-275 (255)	270-345 (305)
N	155	145-163 (154)	155	151-163 (155)	166-185 (178)	162-171 (166)
hdw	16	14-16 (15.0)	14.5	14-16 (14.9) [14]	11-12 (11.4)	12-13.5 (13.0)
hdl	16	13.5-16.5 (14.9) [13]	13.5	12.5-16 (14.4) [10]	10.5-12.5 (11.3) [2]	11-13.5 (12.0)
amphw	6.5	6-8 (6.7) [13]	4	4-5 (4.6) [13]	3-4 (3.6)	3.5-4.5 (4.1)
amph%	40.5	37.5-53.5 (44.7) [13]	28	28-35 (30.7) [13]	29.5-32.5 (31.2)	26.5-35.5 (31.3)
ph	77	66.5-83 (75.2)	79	69-86.5 (76.6) [13]	52-59 (56.1)	60.5-69.5 (65.1)
lvAsl	16	13-19.5 (16.9) [13]	15.5	13.5-19 (16.2) [12]		
osvAsl	12.5	11.5-16 (13.7) [12]	10	11.5-16 (13.8) [14]		16.5-18.5 (17.4) [5]
isvAsl	12	13-16 (14.0) [11]		11-16 (14.0) [12]	15.5-16 (15.7)	13.5-16.5 (15.1) [5]
psup	11	7.5-13 (10.8) [11]	11	11.5-15.5 (13.0)	13-15.5 (14.3)	13-15.5 (14.4) [6]
tail	48.5	40-55.5 (48.6) [13]	39.5	39-50.5 (45.2) [13]	35-37 (36.1)	37.5-45.5 (41.8)
tmr	14.5	12.5-16.5 (14.7) [13]		10.5-16 (13.5)	9.5-13 (11.0)	11.5-13 (12.6) [6]
mbd ph	26.5	25-27.5 (26.4)	26.5	25.5-28.5 (27.1)	20.5-23.5 (21.9)	24.5-27.5 (25.8)
mbd	26.5	23-28 (26.4)	36	26.5-38.5 (33.4)	14-18 (16.4)	19-26 (21.9)
(mbd)	19.5	17-19.5 (18.6)	20	18-20.5 (19.4)	14-17.5 (15.3)	16.5-20.5 (18.4)
mbd/(mbd)	1.3	1.3-1.5 (1.4)	1.8	1.4-1.9 (1.7)	1.0-1.2 (1.1)	1.1-1.3 (1.2)
abd	19.5	19-21 (19.6)	17	16-19 (17.4) [14]	13-16 (14.7)	16.5-19.5 (18.1)
spic	39.5	37-44.5 (41.1) [13]				
gub	10	6-9.5 (8.1) [12]				
V%			285.5	61.5-69 (64.1) [14]		
a	16.4	13.6-18.3 (16.3)	12.1	10.2-13.8 (12.0) [14]	15.1-16.0 (15.6)	13.4-14.8 (13.9)
b	5.6	5.0-6.5 (5.7)	5.5	4.4-5.9 (5.3) [14]	4.3-4.6 (4.5)	4.2-5.7 (4.7)
c	8.9	7.1-9.7 (8.9) [13]	11.0	7.8-10.0 (8.8) [13]	6.4-7.6 (7.0)	6.2-8.2 (7.3)

Table 1. Measurements of specimens of *Akanthepsilonema sinecornibus* sp. n. (ranges and means). All absolute values are in µm. The number of specimens that was measured, when different from the total number of specimens, is indicated between brackets in superscript.

Remark on juvenile stage III as described for A. helleouetae *Gourbault and Decraemer, 1991*

A detailed analysis of the arrangement of ambulatory setae in the juvenile stages of *A. sinecornibus* sp. n., *Bathyepsilonema* and *Leptepsilonema* showed that: (i) in all second stage juveniles of these genera the ambulatory setae are arranged in two rows of 3-8 setae; (ii) in all third stage juveniles of these genera the ambulatory setae are arranged in two rows of 8-15 setae; (iii) in all fourth stage juveniles of these genera the ambulatory setae are arranged in 4-5 rows with 4-11 setae in the internal rows and 7-16 setae in the external rows.

The third stage juvenile of *A. helleouetae* has four rows of ambulatory setae: the internal rows with four setae and the external rows with nine setae (Gourbault & Decraemer, 1991). This agrees with the above mentioned arrangement for a fourth stage juvenile and not with that of a third stage juvenile. Therefore we conclude that the third stage juvenile of *A. helleouetae* as described by Gourbault & Decraemer (1991) is actually a fourth stage juvenile.

Familia Epsilonematidae Steiner, 1927
Subfamilia Epsilonematinae Steiner, 1927
Genus *Triepsilonema* Decraemer, 1982
***Triepsilonema tripapillata* Decraemer, 1982** (Figs. 5-6)

Type specimens. Holotype male on slide RIT 27. Paratype female and juvenile III on slide RIT 28 and paratype juvenile II on slide RIT 29 (KBIN).
Additional specimens.
Additional males on slides UGMD 104092, UGMD 104096 and UGMD 104098 (UGent), RI 683 and RI 679 (KBIN), stored as 2005.2696, 2005.2706, 2005.2708-2005.2712 (NHM).
Additional females on slides UGMD 104096 and UGMD 104098 (UGent), RI 683 and RI 679 (KBIN), stored as 2005.2705, 2005.2707 (NHM).
Additional first stage juveniles on slides UGMD 104096, UGMD 104097 (UGent), RI 676 and RI 678 (KBIN), stored as 2005.2694 (NHM).
Additional second stage juveniles on slides UGMD 104096 (UGent), RI 677 (KBIN), stored as 2005.2662 and 2005.2693 (NHM).
Additional third stage juveniles on slides UGMD 104098 (UGent), RI 679 (KBIN), stored as 2005.2703 (NHM).
Additional fourth stage juveniles on slides UGMD 104096 and UGMD 104098 (UGent), RI 683 and RI 679 (KBIN), stored as 2005.2690, 2005.2695, 2005.2704 (NHM).
Type locality. Laing Island, Hansa Bay, Madang Province, Papua New Guinea.
New locality. Porcupine Seabight, Belgica mound province. Coordinates: 51°24'48,2" N - 11°45'55,4" W (material collected on 17/06/2000; depth: 1005 m); 51°24'49,4" N - 11°45'55,9" W (material collected on 17/06/2000; depth: 1000 m); 51°25'7,7" N - 11°46'9,3" W (material collected on 07/05/2001; depth: 972 m). It has also been recorded from 51°24'47,5" N - 11°45'55,7" W (material collected on 25/05/2003; depth: 994 m).

Date of collection. Type material: 5th of May 1977. Porcupine Seabight material: 17th of June 2000 and 7th of May 2001.

Type habitat. Between the marine alga *Halimeda*. Samples originated from a lagoon.

New habitat. A cold-water coral degradation zone on the flank and near the top of a seabed mound. Associated with sediment-clogged framework of the cold-water coral *Lophelia pertusa* (Linnaeus, 1758). It was found on dead coral fragments, on dead sponge skeletons (*Aphrocallistes bocagei* Schultze, 1886) and within the underlying sediment.

Relative abundance at new locality. This species comprises 2.0 % of the total nematode community in the Porcupine Seabight samples.

Measurements. Table 2.

Redescription and additional information

Males

Body slender, almost cylindrical and epsilon-shaped (Figs. 5A, 6C). No marked enlargements but widest at level of testis: body width gradually increasing from anterior end up to cloacal region and gradually decreasing again along tail. Posterior body region laterally often with large refractile bodies. Cuticle with 198 annules in holotype and 206-227 annules in Porcupine Seabight specimens. Annules fine, broadest at level of pharynx and on tail, finest at mid-body. Annules overlapping, with hyaline outer layer. Anteriormost annules with anteriorly directed margin. Ventrally, inversion of orientation on annule 42 in holotype and between annules 52 and 62 in Porcupine Seabight specimens (i.e. at level of anteriormost dorsal curvature), dorsally on annule 77 in holotype and between 79 and 90 in Porcupine Seabight specimens (i.e. at level of ventral curvature). Body rings in holotype male without ornamentation, except for a few tail annules with small, transversally elongated vacuoles. Porcupine Seabight specimens with scattered cuticular ornamentation. Anteriormost annules generally without ornamentation, although several small vacuoles may occur. Annules in pharyngeal region either smooth or ornamented with numerous tiny vacuoles, often gradually increasing in size until becoming transversally elongated and then gradually decreasing in size again. Annules at level of pharyngeal bulb either smooth or ornamented with tiny vacuoles. Annules between pharyngeal bulb and posterior body region always smooth. Annules anterior to cloaca with numerous tiny vacuoles, often gradually increasing in size until forming a network of transversally elongated vacuoles at level of cloaca and then gradually decreasing in size towards posterior end of tail. Posteriormost annules without ornamentation. Ventral field of hair-like spines present at level of ambulatory setae (Fig. 6E).

Somatic setae flattened. Somatic setae in pharyngeal region and region anterior to ambulatory setae arranged in eight longitudinal rows: two subdorsal rows, two laterodorsal rows, two lateroventral rows and two subventral rows. At level of ambulatory setae, somatic setae arranged in two dorsosublateral rows. Somatic setae at level of 'fine' (i.e. slightly modified somatic) setae situated in subdorsal, laterodorsal, dorsosublateral, lateroventral, subventral and medioventral position. Two fine somatic setae present immediately anterior to cloaca. Somatic setae on tail arranged in two subdorsal rows, two laterodorsal rows, two ventrosublateral-lateroventral rows and two subventral rows.

Ambulatory setae slender, slightly s-shaped, with curved tip, arranged in four longitudinal rows with some scattered setae in between (Fig. 6E): two outer subventral rows with 6-9 setae, two inner subventral rows with 8-13 setae and 2-6 setae scattered in between those two latter rows. Inner subventral rows converging towards cloaca. In holotype, outer subventral rows of ambulatory setae immediately followed by six (right side) and seven (left side) subventral, short, fine setae with straight and fine tip: three and four setae respectively anterior to cloaca, one seta at level of cloaca on right side and two and three setae respectively posterior to it, the latter gradually becoming shorter and finer. Porcupine Seabight specimens with 9-14 subventral fine setae: 5-10 setae anterior to cloaca, often one seta at level of cloaca and another 3-4 posterior to it, gradually becoming shorter and finer. Posteriormost subventral fine seta situated immediately anterior to smooth tail tip.

Head capsule a smooth, rounded, truncated cone, slightly lopsided with longer dorsal side (Fig. 6A). Labial region with two crowns of six labial papillae, often partially protruding and then partly surrounded by a small rim of the head capsule. Four cephalic and eight subcephalic setae. Subcephalic setae arranged on each side as follows: one subdorsal seta, one laterodorsal seta, one lateroventral seta and one subventral seta. All subcephalic setae located at anterior border of amphids except for laterodorsal setae, which are situated posterior to amphids at posterior edge of head capsule. Amphids situated near base of head capsule, slightly shifted dorsally (laterodorsal position). Amphidial fovea a small (29% of the corresponding head width in holotype), ventrally wound open spiral with 1.25 turns. Buccal cavity narrow and cylindrical. Two subventral tooth-like projections in lumen may be present, opposite with corresponding indentation of dorsal lumen wall, where buccal cavity grades into pharyngeal lumen. Pharynx long (88 µm in holotype male and 106.5-120 µm in Porcupine Seabight specimens) and slender, gradually widening into an oval, partly glandular terminal bulb. Terminal bulb ventrally, laterally and dorsally surrounded by glandular mass. Pharyngeal lumen wall slightly cuticularised. Cardia inconspicuous. Intestine often granular, although internal structure highly variable. Intestinal brush border conspicuous.

Male reproductive system with a single wide, anteriorly outstretched testis situated ventrally to intestine and extending beyond ventral curvature. Vesicula seminalis with several large, opaque sperm cells. Each sperm cell with a large round or slightly jagged nucleus containing numerous small nucleoli. Spicules often protruding (Fig. 5A), curved and rather robust, with triangular or beak-like capitulum and well-developed velum. Narrow, slightly s-shaped gubernaculum with clear triangular cuneus, adjacent to spicules, except for proximal part, which curves away from spicules. Copulatory thorns absent.

Tail short and conical, completely annulated, with 17-20 annules ventrally and 18-22 annules dorsally, including smooth tail tip. Smooth tail tip usually without incomplete annules. Three caudal glands extending anteriorly beyond cloaca. Caudal glands ending posteriorly in one medioventral and two laterodorsal, smooth papillae, 4-5 µm in length. Each papilla with terminal spinneret, forming a separate outlet for one of the three caudal glands (Fig. 8A).

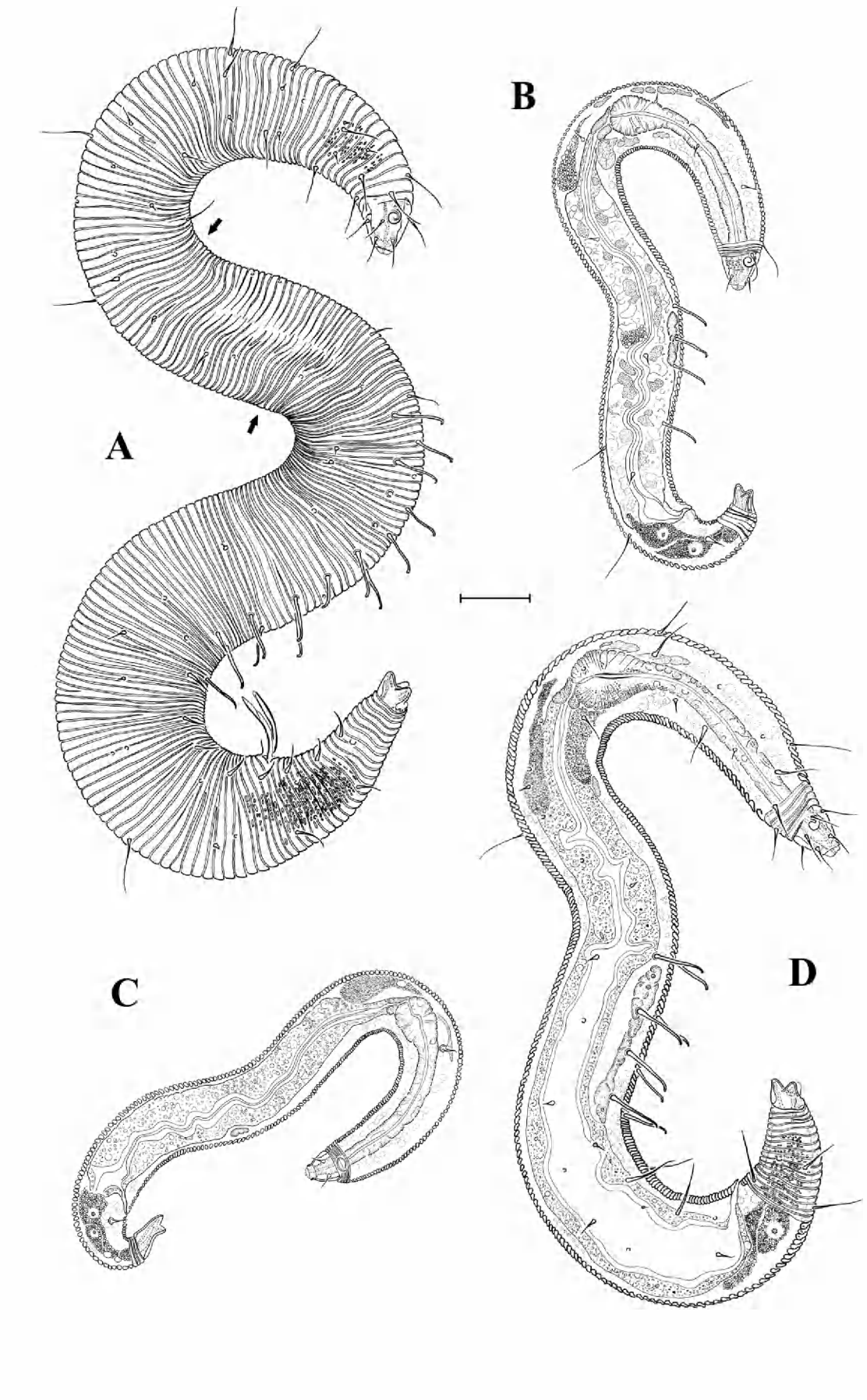


Fig. 5. *Triepsilonema tripapillata* Decraemer, 1982 (Porcupine Seabight specimens) A. ♂, habitus; B. second stage juvenile, habitus; C. first stage juvenile, habitus; D. fourth stage juvenile, habitus. Arrows indicate inversion of annular orientation. Scale bar: 20 µm.

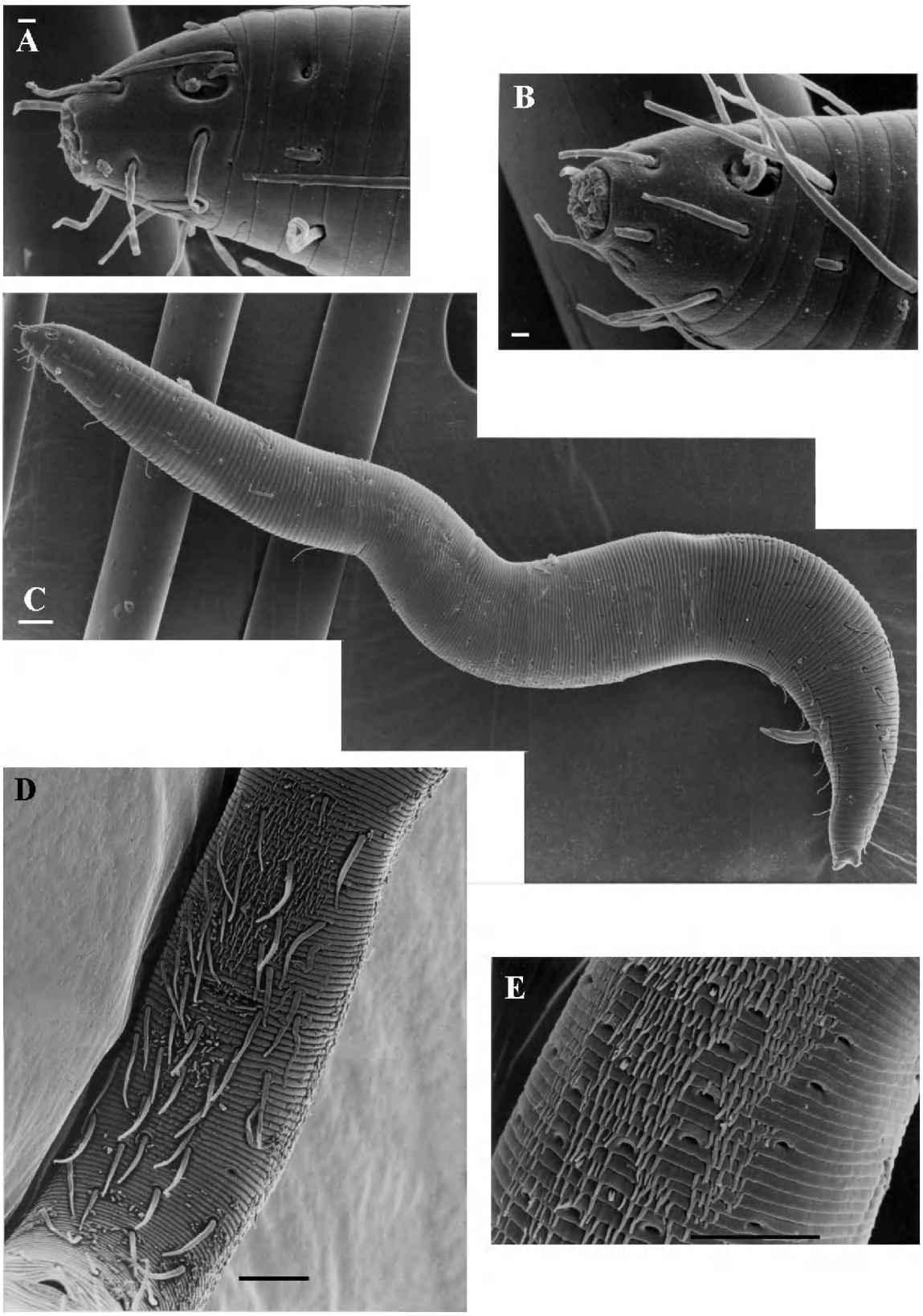


Fig. 6. *Triepsilonema tripapillata* Decraemer, 1982 (Porcupine Seabight specimens) A. ♂, head capsule (lateral view); B. ♀, head capsule (lateral view); C. ♂, habitus; D. ♀, vulva and ambulatory setae (ventral view); E. ♂, insertion sites of ambulatory setae (ventral view). Scale bars: 1 µm in A and B; 10 µm in C, D and E.

Females

Females similar to males in most respects. Body cuticle with 195 annules in Papua New Guinea specimen and 209-231 annules in Porcupine Seabight specimens, which is comparable to males. Inversion of orientation between annules 55 and 65 ventrally (i.e. at level of anteriormost dorsal curvature) and between annules 77 and 87 dorsally (i.e. at level of ventral curvature). Annules often smooth, sometimes ornamented with transversally elongated vacuoles in pharyngeal region and on tail. Ventral field of hair-like spines present in region of ambulatory setae (Fig. 6D).

Somatic setae flattened as in males. Number and position of longitudinal rows of somatic setae in females similar to that in males. Ambulatory setae slender, slightly s-shaped, with curved tip and arranged in four longitudinal rows with some scattered setae in between, as in males. No clear separation between ambulatory and fine (somatic) setae, but a gradual transition from the one type into the other, i.e. becoming finer, straighter and with a straighter distal tip (Fig. 6D). Somatic setae on tail posteriorly also becoming shorter. Two outer subventral rows with 14-18 setae, gradually changing from ambulatory setae anteriorly to somatic setae posteriorly: 4-6 setae anterior to vulva, sometimes one seta at level of vulva, 7-9 setae between vulva and anus, sometimes one seta at level of anus and 2-3 setae on tail. Posteriormost setae in outer subventral rows situated immediately anterior to smooth tail tip. Two inner subventral rows with 11-17 setae: 3-6 setae anterior to vulva, sometimes one seta at level of vulva and 7-10 setae between vulva and anus. Posteriormost setae in inner subventral rows clearly finer than setae situated more anteriorly. Four to seven ambulatory setae scattered between inner subventral rows: 1-5 anterior to vulva and 1-5 posterior to it.

Shape of head capsule, number and position of subcephalic setae, shape and size of amphids, buccal cavity and pharynx as in males (Fig. 6B).

Female reproductive system didelphic and amphidelphic with outstretched ovaries, situated ventrally to intestine. Anterior ovary shifted slightly to right side, posterior ovary to left side. In mature females, anterior ovary extending up to anteriormost dorsal curvature (close to pharyngeal bulb) and posterior ovary up to anus. Vagina bipartite, with cuticularised *pars distalis* shorter and narrower than *pars proximalis*, connected to anterior region of uterus. Uterus with or without large sperm cells, each with distinct nucleus. Spermathecae absent. Vulva situated at 50.5-60% of total body length from anterior, surrounded by several radial cuticular folds. Paravulval setae absent.

Tail with 15 annules ventrally and 16 annules dorsally in Papua New Guinea specimen and 17-19 annules ventrally and 18-22 annules dorsally in Porcupine Seabight specimens, always including smooth tail tip. Smooth tail tip without incomplete annules. Caudal glands ending separately in three smooth papillae as in males (Fig. 8B).

Juveniles

First stage juveniles

Twenty-one specimens, only from Porcupine Seabight area. Habitus as in adults, although smaller (Fig. 5C). Number of annules 179-200, which is slightly less than in adults. Annules thin, non-

overlapping and largely without ornamentation, except for some slightly broader annules on tail, ornamented with single row of small vacuoles.

Only four rather short and flattened somatic setae present along body: on each side one seta at level of pharyngeal bulb and one at level of anus. Each seta with distinct circular insertion site. Ambulatory setae absent.

Head capsule a short truncated cone, with four long (5.9 µm on average) cephalic setae. Subcephalic setae absent. Amphids positioned mediolaterally between annules one and five posterior to head capsule. Amphidial fovea small (average width: 4.0 µm; average length: 2.0 µm), antero-posteriorly flattened, oval and unispiral, dorsally wound with posterior aperture. Pharynx long and slender, partly glandular, with well-developed endbulb. Clear glandular structures laterally at level of pharyngeal bulb and dorsally posterior to pharyngeal bulb. Intestine granular. Genital primordium minute.

Tail with 16-18 annules ventrally and 19-24 annules dorsally, including smooth tail tip. Tail tip triangular, relatively longer than in adults due to an extended basis and without incomplete annules. Tail with three distinct caudal glands extending anterior to anus. Only two terminal papillae: ventral one (average length: 3.4 µm) longer than dorsal one (average length: 2.7 µm).

Second stage juveniles

One specimen originating from Papua New Guinea and 22 specimens from Porcupine Seabight area. General body shape as in adults (Fig. 5B). Body about equally wide, tapered towards both ends, 190-340 µm in length. Number of annules 163-193, which is slightly less than in first stage juveniles. Annules fine, non-overlapping and mostly smooth, except for some tail annules ornamented with one or two rows of small, oval vacuoles. Ventral field of small hair-like spines present anterior to ambulatory setae.

Somatic setae in pharyngeal region and region anterior to ambulatory setae arranged in five longitudinal rows: one mediodorsal row, two laterodorsal rows and two lateroventral rows. Anteriormost mediodorsal seta situated on second or third annule posterior to head capsule. Posterior body region with long mediodorsal setae and shorter laterodorsal setae. Tail with one lateroventral seta on each side. Somatic setae flattened, except mediodorsal ones. Two lateroventral rows of three (Papua New Guinea specimen) or four (Porcupine Seabight specimens) slender, slightly bent ambulatory setae with curved tip. Posteriormost ambulatory seta in Porcupine Seabight specimens slightly separated from other three setae.

Head capsule conical and truncated as in adults, with four cephalic setae and two long, laterodorsal subcephalic setae at base of head capsule, situated posterior to amphid and immediately anterior to first complete body ring. Labial sensilla apparently situated in two rows. Amphids similar to those of adults. Pharynx long and slender, partly glandular, with well-developed endbulb. Endbulb surrounded by glandular material. Intestine granular. Genital primordium small.

Tail with 12 annules ventrally and 19 annules dorsally in Papua New Guinea specimen, 14-17 annules ventrally and 19-25 annules dorsally in Porcupine Seabight specimens, including smooth tail

tip. Smooth tail tip without incomplete annules. Tail tip as in adults, ending on two small laterodorsal papillae and one longer medioventral papilla, each with the outlet of a caudal gland.

Third stage juveniles

One specimen originating from Papua New Guinea and 17 specimens from Porcupine Seabight area (sexes not evident). Habitus as in adults. Cuticle with 201 annules in Papua New Guinea specimen and 227-242 annules in Porcupine Seabight specimens. Annules fine, non-overlapping and mostly smooth, except for annules on tail, ornamented with numerous small, irregular (mostly elongated) vacuoles. Vacuoles inconspicuous (but present) in third stage juvenile from Papua New Guinea (RIT 28). Annules finest at mid-body, widest in pharyngeal region and tail region.

Somatic setae in pharyngeal region arranged in five longitudinal rows: one mediodorsal row, two laterodorsal rows and two lateroventral rows. Somatic setae in region between anteriormost dorsal curvature and ambulatory setae located in one mediodorsal and two laterodorsal rows. One short lateroventral seta on each side, immediately anterior to ambulatory setae. Several short dorsosublateral setae as well as some long mediodorsal setae present at level of ambulatory setae. One laterodorsal seta present on each side immediately anterior to anus. Tail on each side with one lateroventral seta and one mediodorsal seta immediately anterior to tail tip. Somatic setae flattened, except mediodorsal ones. Two lateroventral rows of seven almost straight ambulatory setae with curved tip. Posteriormost ambulatory seta situated anterior to anus, slightly finer than other ambulatory setae and with almost straight distal tip.

Head capsule a truncated cone, shorter in Papua New Guinea specimen (8 µm) than in Porcupine Seabight specimens (on average: 9.9 µm). Head with four cephalic and five subcephalic setae: one mediodorsal seta, two laterodorsal setae, one lateroventral seta and one medioventral seta. Lateroventral seta positioned on right side in Papua New Guinea specimen and predominantly on left side in Porcupine Seabight specimens. All subcephalic setae situated at base of head. Amphids as in adults. Pharynx long, slender, partly glandular and with well-developed endbulb. Endbulb surrounded by glandular material. Intestine granular. Genital primordium variable in size.

Tail with 15 annules ventrally and 16 annules dorsally in Papua New Guinea specimen, 18-22 annules ventrally and 19-24 annules dorsally in Porcupine Seabight specimens, including smooth tail tip. Tail tip without incomplete annules, ending on one medioventral and two laterodorsal papillae, all of equal size.

Fourth stage juveniles

Twelve juvenile male and nine juvenile female specimens, all from Porcupine Seabight area (Fig. 5D). Habitus as in adults. Cuticle with 215-239 annules, which is comparable to adults. Annules smooth, except for annules on tail ornamented with numerous elongated, irregular vacuoles. Annules finest at mid-body, widest in pharyngeal region and tail region.

Somatic setae in pharyngeal region and region between anteriormost dorsal curvature and ambulatory setae arranged in five longitudinal rows: one mediodorsal row, two laterodorsal rows and two lateroventral rows. Several short dorsosublateral and lateroventral setae, as well as some long

mediodorsal setae present at level of ambulatory and modified somatic setae. One medioventral, straight somatic seta usually present between posteriormost inner subventral ambulatory seta and anus. One laterodorsal seta on each side, immediately anterior to anus. Tail with one laterodorsal and one lateroventral somatic seta on each side and one mediodorsal seta.

Ambulatory setae arranged in two inner and two outer subventral rows. Each outer subventral row with 4-7 s-shaped ambulatory setae with curved tip, positioned closely together posterior to ventral curvature. More posteriorly, ambulatory setae followed by two setae gradually becoming more somatic, i.e. finer, straighter and with straighter distal tip. At level of anus, a subventral slightly modified somatic seta constitutes the endpoint of this progressive series. Inner subventral rows with 3-5 ambulatory setae, slightly shorter and finer than those of outer subventral rows.

Head capsule conical and truncated as in adults. Four cephalic and eight subcephalic setae, arranged as in adults. Amphids as in adults. Long, slender, partly glandular pharynx with well-developed endbulb. Endbulb surrounded by glandular material. Genital system in juvenile females variable in size: 41.5-57.5 µm.

Tail with 19-22 annules ventrally and 19-23 annules dorsally, including smooth tail tip. Tail tip without incomplete annules, ending on one medioventral and two laterodorsal papillae, all of equal size.

One aberrant specimen with vacuoles on head and pharyngeal region, similar to those on tail, and four papillae on smooth tail tip with small tubercle in between.

Emended diagnosis

Triepsilonema tripapillata Decraemer, 1982 is characterised by the three large caudal papillae, by the cuticular body rings, either lacking ornamentation or ornamented with transversally elongated vacuoles, and by the shape of the copulatory apparatus.

Emended genus diagnosis

Triepsilonema Decraemer, 1982. Epsilonematidae. Body almost cylindrical and slightly epsilon-shaped, with 200-230 body annules in adults. Ambulatory setae slender, slightly s-shaped, with bent tip, arranged in four longitudinal rows with some scattered setae in between. In males, ambulatory setae in outer subventral rows followed by short, fine setae. In females, outer subventral rows exhibiting a gradual transition from ambulatory setae to somatic setae towards the tail. Amphids rather small spiral structures with 1.25 turns; no sexual dimorphism. Head capsule with four cephalic and eight subcephalic setae in adults. Two crowns of labial sensilla. Pharynx long and slender, gradually widening into an oval, partly glandular terminal bulb. Ovaries outstretched. Three caudal glands extending anteriorly beyond cloaca, each with a separate outlet. Smooth tail tip very short, with one medioventral and two subdorsal, smooth papillae, each with the outlet of one of the caudal glands. First stage juveniles without ambulatory setae and with only two smooth papillae on tail tip. Second stage juveniles with two rows of three or four ambulatory setae and two subcephalic setae. Third stage juveniles with two rows of seven ambulatory setae and five subcephalic setae. Fourth stage juveniles with four rows of ambulatory setae and eight subcephalic setae.

Type species: *Triepsilonema tripapillata* Decraemer, 1982

Variability of features

Detailed observations on the type material from Papua New Guinea and the new material from the Porcupine Seabight showed that, although both populations are geographically and bathymetrically well isolated, they are morphologically remarkably similar. Whether this reflects either active gene flow or the conservation of character states is not clear, but the former seems unlikely. Nevertheless, a recent discovery of *T. tripapillata* on coral rubble from the Kenyan coast (Kurwitu) suggests that this species could be cosmopolitan (M. Raes, personal observation). The differences between both populations, although limited, might point to the presence of two cryptic species. This might well be the case, although in the absence of molecular (sequence) data for both populations it is inadvisable to discuss this matter here. Moreover, one should focus on the astonishing morphological similarity between both populations that live so distantly from each other, rather than on the differences.

The populations differ in: (i) size of females (clearly smaller in Papua New Guinea); (ii) length of the pharynx (clearly shorter in Papua New Guinea specimens); (iii) number of annules (slightly lower in Papua New Guinea specimens); (iv) inversion of annule orientation in males (more anterior in Papua New Guinea specimens); (v) ornamentation of annules (almost completely smooth in Papua New Guinea specimens); (vi) number of fine setae following outer subventral rows of ambulatory setae in males (clearly fewer in Papua New Guinea specimens); (vii) number of ambulatory setae in second stage juveniles.

Relationships with other genera

Decraemer (1982) considered *Triepsilonema* close to *Bathyepsilonema* mainly because both possess six rows of ambulatory setae. However, thorough observation of the new material and a subsequent re-examination of the type material revealed that the ventralmost ambulatory setae are not really arranged in two rows but they are rather scattered between the inner subventral rows (Fig. 6E). There are no obvious features linking *Triepsilonema* with any other epsilonematid, although its body shape may suggest some relation with *Archepsilonema*, a genus however characterised by only four rows of ambulatory setae. Nevertheless, the presence of three conical caudal papillae and outstretched ovaries in combination with an almost cylindrical body shape makes this genus rather unique within the family.

	Holotype male	Paratype female	Paratype juvenile stage II	Paratype juvenile stage III	Males (n = 10)	Females (n =10)	Juvenile stage I (n = 10)	Juvenile stage II (n = 10)	Juvenile stage III (n = 10)	Juvenile stage IV (n = 10)
L	400	370	190	295	365-575 (495)	480-580 (540)	185-280 (225)	210-340 (280)	270-395 (335)	365-505 (435)
N	198	195	164	201	206-227 (217)	209-231 (218)	179-200 (191)	183-193 (182)	227-242 (232)	215-239 (225)
hdw	12.5	12.5	12	12	13-14.5 (14.0)	13.5-15 (14.2)	8.5-9.5 (9.2)	10.5-12 (11.1)	11-13 (12.1)	12.5-13.5 (12.9)
hdl	12	11	10	8	10-13 (11.5)	10.5-15 (12.5)	5.5-8 (6.8) [6]	8.5-10 (9.4)	8.5-11.5 (9.9)	9.5-11.5 (10.9)
bda							11-12.5 (11.7)			
amphw	3.5	3.5	3.5	2.5	3-4 (3.8)	3.5-4 (3.8)	3.5-4.5 (4.0)	3.5-4 (3.8)	3.5-4.5 (3.9)	3.5-4 (3.8)
amph%	29	28.5	29	21.5	28-43 (33.4)	24.5-36 (30.8)	29.5-38 (34.1)	28.5-36.5 (34.0)	29-34.5 (32.4)	24.5-32.5 (29.6)
ph	88	93		82.5	106.5-120 (112.7)	104.5-122 (113.2)	69-78 (73.2)	67.5-87 (78.8)	76-98 (88.7)	92-108.5 (98.9)
osvAsl	17	14.5	10	11.5	16.5-19.5 (18.0) [3]	15.5-21 (17.4) [3]		10-15 (12.8)	12.5-16.5 (14.9)	15.5-16.5 (16.9)
isvAsl	13.5	13			13-15 (13.9) [6]	10.5-15 (12.7) [3]				11.5-14.5 (13.1)
asup	9.5				7.5-11 (9.6)					
tail	58.5	46	26	35.5	49.5-61.5 (55.8)	45.5-58.5 (50.5)	32.5-37.5 (35.2)	20.5-41 (33.1)	34.5-45 (38.9)	39.5-49 (44.9)
tmr	7	6	5.5	7	8.5-10 (9.3)	7.5-10.5 (9.6)	10.5-12.5 (11.6)	6.5-9 (7.7)	7.5-9 (7.9)	7.5-9.5 (8.5) [9]
mbd ph	25.5	36.5	25	30.5	29-34 (31.7)	30-38 (33.6)	18-24 (20.1)	19.5-29.5 (23.1)	23-31 (26.1)	25.5-35 (30.2)
mbd	38.5	48.5	25	38.5	37.5-47.5 (41.9)	42.5-57 (49.0)	19-25 (21.0)	19-34 (25.4)	25-37.5 (30.1)	29.5-52.5 (37.6)
(mbd)	29	38.5	23.5	33.5	30-35.5 (32.0)	30.5-39.5 (34.3)	18-23.5 (19.9)	18.5-30 (23.2)	22.5-30.5 (26.4)	25-39.5 (31.2)
mbd/(mbd)	1.3	1.3	1.1	1.1	1.2-1.4 (1.3)	1.3-1.6 (1.4)	1.0-1.1 (1.1)	1.0-1.2 (1.1)	1.1-1.3 (1.1)	1.1-1.3 (1.2)
abd	26.5	30.5	22	25.5	29-34.5 (31.2)	27-32 (30.3)	17.5-21 (19.2)	17.5-30 (21.5)	22-29.5 (25.1)	25-33.5 (28.6)
spic	42.5				42.5-49.5 (46.5)					
gub	11.5				12-15.5 (13.4)					
V%		58.5				50.5-60 (55.4)				
a	10.4	7.6	7.7	7.67	10.1-14.0 (11.8)	9.4-13.9 (11.6)	8.5-12.1 (10.7)	9.0-13.0 (11.0)	9.9-12.9 (11.2)	9.7-13.6 (11.7)
b	4.5	4.0		3.58	3.5-5.3 (4.4)	4.3-5.3 (4.8)	2.6-3.6 (3.1)	2.7-4.1 (3.5)	3.0-4.1 (3.8)	3.9-5.1 (4.4)
c	6.8	8.0	7.4	8.36	6.9-10.1 (8.8)	9.3-11.9 (10.7)	5.4-7.5 (6.3)	6.8-13.7 (8.6)	7.6-10.4 (8.6)	8.7-11.1 (9.7)

Table 2. Measurements of type specimens from Papua New Guinea (first four columns) and Porcupine Seabight specimens of *Triepsilonema tripapillata* Decraemer, 1982 (ranges and means). All absolute values are in µm. The number of specimens that was measured, when different from the total number of specimens, is indicated between brackets in superscript.

Familia Epsilonematidae Steiner, 1927

Subfamilia Glochinematinae Lorenzen, 1974

Genus *Glochinema* Lorenzen, 1974

***Glochinema trispinatum* Raes, Vanreusel and Decraemer, 2003** (Fig. 7)

One specimen juvenile stage I. Slide RI680 (KBIN).

Locality. Porcupine Seabight, Belgica mound province. Coordinates: 51°25'7,7" N - 11°46'9,3" W (material collected on 07/05/2001; depth: 972 m).

Date of collection. 7th of May 2001.

Habitat. A cold-water coral degradation zone on the flank and near the top of a seabed mound. Associated with sediment-clogged framework of the cold-water coral *Lophelia pertusa* (Linnaeus, 1758). It was found on dead coral fragments.

Measurements. Table 3.

First stage juvenile

One specimen. Small, with almost constant body diameter, except for enlarged pharyngeal region and more slender tail (Fig. 7). Pharynx remarkably long compared to adults. Cuticle with 227 fine annules, uniform in shape, non-overlapping and without ornamentation.

Only four somatic setae, all situated mediolaterally: on each side one seta at level of pharyngeal bulb and one seta on tail. Seta on left side of tail positioned more anteriorly than seta on right side. Head capsule short, with six labial sensilla at anterior end, of which four most dorsal sensilla hook-shaped and two most ventral sensilla only short, blunt protrusions. Four cephalic setae, situated at posterior edge of head capsule. Head capsule together with first eight body annules assumed to be positionally homologous with head capsule in second stage juveniles. Amphids small, oval, unispiral, situated at level of annules four to six. Pharynx slender with well-developed endbulb. Tail with 57 annules, including short smooth tail tip with long spinneret.

Remark regarding identification

Based on the combination of (i) the slender body with a slightly enlarged pharyngeal region, (ii) a slender pharynx with endbulb, (iii) the length and shape of the tail, (iv) the shape of the buccal cavity, (v) the shape of the amphid and (vi) the presence of broad annules, this first stage juvenile can only be attributed to two species: *Glochinema trispinatum* Raes, Vanreusel and Decraemer, 2003 and a new species of *Cygnonema* Allen and Noffsinger, 1978 (Draconematidae), which is also present in the same samples. However, the first stage juvenile of this latter species clearly differs from the one of *G. trispinatum* in having (i) a relatively shorter tail, (ii) a relatively longer pharynx, (iii) finer annules and (iv) an amphid situated on the head capsule.

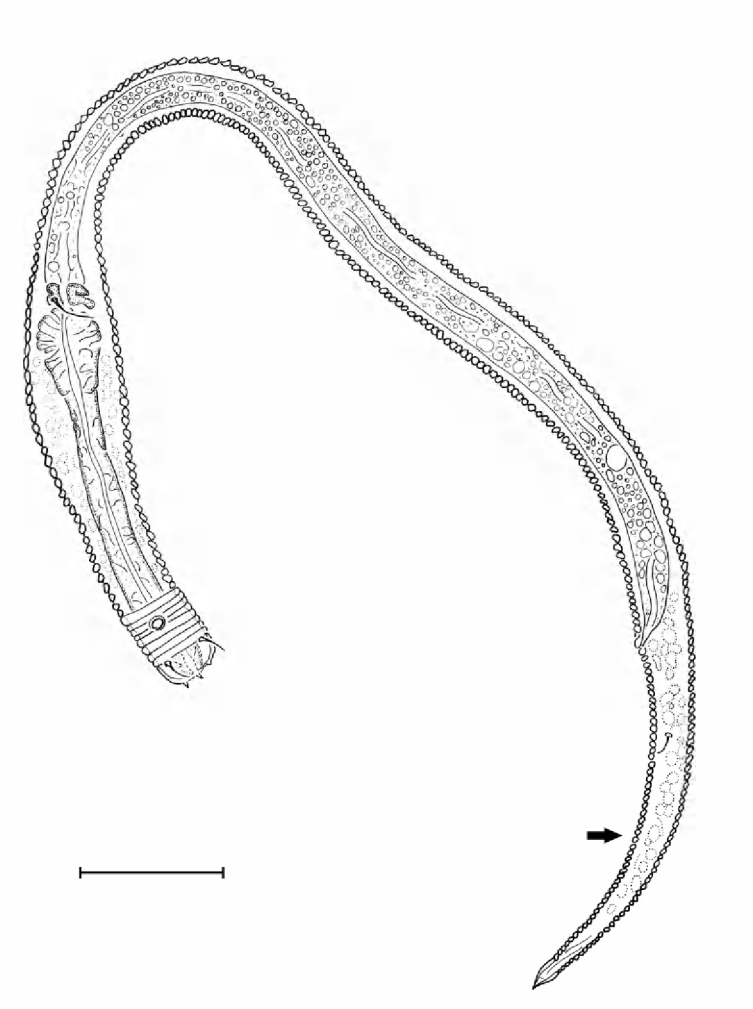


Fig. 7. *Glochinema trispinatum* Raes, Vanreusel and Decraemer, 2003. Habitus of first stage juvenile. The arrow indicates the position of the caudal somatic seta on the right side. Scale bar: 20 µm.

	Juvenile stage I (n = 1)
L	275
N	227
dcs	5.5
hdw	9
hdl	5.5
bda	9.5
amphw	1.5
amph%	15.5
ph	57.5
tail	58
tmr	3.5
mbd ph	14
mbd	10
(mbd)	7.5
mbd/(mbd)	1.3
abd	8.5
a	26.8
b	4.8
c	4.7

Table 3. Measurements of *Glochinema trispinatum* Raes, Vanreusel and Decraemer, 2003 first stage juvenile. All absolute values are in µm.

6.6. POSTEMBRYONIC MORPHOLOGY IN EPSILONEMATIDAE

Representatives of the family Epsilonematidae are characterised by several conspicuous features that change during ontogeny, *e.g.* the number (of rows) of ambulatory setae and the number of subcephalic setae. Because of this, juvenile stages are relatively easy to distinguish, making epsilonematids very suitable for ontogenetic studies. Lorenzen (1973a) published a short overview of some morphological changes during ontogeny, although his observations were based on only five genera (*Archepsilonema*, *Bathyepsilonema*, *Epsilonema* Steiner, 1927, *Metepsilonema* Steiner, 1927 and *Perepsilonema* Lorenzen, 1973). Changes in the number of cuticular annules, the shape of the head capsule, the length of the smooth tail tip and the position of the amphids will be discussed here.

Cuticular annules

Table 4 shows the changes in the number of cuticular annules at each moulting stage, based on literature data. It is clear that the transition from first to second stage juveniles always involves a decrease in the number of annules. The moulting of second stage juveniles into third stage juveniles is characterised by an increase in the number of body rings in *Epsilonema*, *Leptepsilonema*, *Triepsilonema* and *Glochinema* but a decrease in *Bathyepsilonema* and *Metepsilonema*. The moulting of third stage juveniles into fourth stage juveniles is subject to much more overlap between the number of annules in both stages, but there is a general decreasing trend. When fourth stage juveniles moult into adults the number of annules tends to increase in *Bathyepsilonema* and *Metepsilonema* whereas it decreases in *Akanthepsilonema*, *Epsilonema*, *Leptepsilonema*, *Perepsilonema* and *Triepsilonema*. Again there is a considerable degree of overlap. The observed overlap during the later moulting stages is explained by the fact that there are simply more data available. Variability is highest in *Polkepsilonema* and *Glochinema*.

Lorenzen (1973a) suggested that the pattern of change in the number of annules during ontogeny could be genus specific: he observed that the first two juvenile stages in *Epsilonema* and *Perepsilonema* have less and the last two stages more annules than the adults, whereas the opposite is true for *Bathyepsilonema*. For *Epsilonema* and *Bathyepsilonema* these observations are confirmed by other literature data on the changes during moulting from second stage juveniles into third stage juveniles and from fourth stage juveniles into adults (Table 4). The examples below also confirm intergeneric variability.

A general decrease in the number of body rings, as *e.g.* observed in the I-II and III-IV transitions, could be related to the creation of (i) broader annules, (ii) the head capsule or (iii) the tail tip. Indeed, annules in first stage juveniles are clearly narrower than in second stage juveniles. Moreover, there seems to be a positional homology of certain annules from first stage juveniles with parts of the annules, head capsule or tail tip in second stage juveniles. This can be clearly observed in moulting first stage juveniles. As the cuticle is presumably completely resynthesised during moulting, there will probably be no straightforward fusion of *e.g.* the annules of first stage juveniles into the annules of second stage juveniles during the process: either (i) a lower number of (broader) annules is newly formed or (ii) the same number of annules is formed and these annules apparently fuse in a later

stage of the moulting process. In the latter case, the observed body length increase during transitions between juvenile stages can only be explained by an additional broadening of body rings after or simultaneously with this annular fusion.

It is not entirely clear why these changes occur, although it is obvious that a higher number of annules in first stage juveniles (compared to second stage juveniles) allows for higher mobility, an important quality to free itself from the egg and to move forward without the help of ambulatory setae, which are absent in first stage juveniles. Something similar could be true for the III-IV transition in *Akanthepsilonema*, *Epsilonema*, *Leptepsilonema*, *Metepsilonema* and *Triepsilonema*, where the number of rows of ambulatory setae doubles from two to four (or five as in *Akanthepsilonema sinecornibus* sp. n.) resulting in increased stability and mobility, which might compensate for the loss in flexibility. In contrast, this decrease in the number of annules was also observed in *Perepsilonema* (absence of ambulatory setae) and *Polkepsilonema* (both third and fourth stage juveniles with four rows of ambulatory setae). Moreover, a similar decrease was not observed in representatives of the genus *Bathyepsilonema*, despite of the doubling in the number of rows of ambulatory setae.

Head capsule and position of the amphids

Judging by the position of the amphids, the cephalic setae and the cervical constriction, it was postulated that the head capsule and the eight anteriormost annules in the first stage juvenile of *Glochinema trispinatum* (Fig. 7) are positionally homologous with the head capsule in second stage juveniles. Indeed, the head capsule in the first stage juvenile of *G. trispinatum* is very short, the cephalic setae are at the base of this short head capsule and the amphids are positioned posterior to it, whereas this is no longer the case in second stage juveniles. The same was observed in *Epsilonema byssicola* Lorenzen, 1973 and *Triepsilonema tripapillata*. In contrast, the amphids in first stage juveniles of *Metepsilonema* and *Bathyepsilonema* are already situated on the head capsule, the head capsule is already well-developed and the cephalic setae are already situated anteriorly on the head capsule. Intergeneric variability is evident.

By way of comparison, intrageneric variability in the position of amphids and cephalic setae in first stage juveniles has been observed within *Desmodora*, a representative of the closely related family Desmodoridae: in first stage juveniles of *Desmodora minuta* Wieser, 1954 (Clasing, 1980) the cephalic setae are situated at the base of the head capsule and the amphids are situated in the annulated region posterior to the head capsule, whereas in first stage juveniles of *D. schultzi* Gerlach, 1950 cephalic setae and amphids are already situated anteriorly on the head capsule. In second stage juveniles of both species, amphids are located on the head capsule and cephalic setae are shifted to the anterior.

In first stage juveniles belonging to the closely related family Draconematidae cephalic setae are always at the posterior border of the head capsule and amphids are always surrounded by the anterior annules, posterior to the head capsule. Evidence for this has been found in *Dracograllus chiloensis* Clasing, 1980, *Draconema antarcticum* Allen and Noffsinger, 1978, *Cygnonema* sp. (a new species from the Porcupine Seabight) and *Tenuidraconema* sp. (a new species from the Porcupine Seabight). All these species are characterised by a well-developed head capsule in adults.

	juv. I ⇒ juv. II				juv. II ⇒ juv. III				juv. III ⇒ juv. IV				juv. IV ⇒ adults			
	↑	↓	→	*overlap*	↑	↓	→	*overlap*	↑	↓	→	*overlap*	↑	↓	→	*overlap*
Akanthepsilonema (2)										**1/1**		1/1		**2/2**		1/2
Archepsilonema (1)																
Bathyepsilonema (10)		**1/1**			1/6	**5/6**			4/7		3/7	3/7	**6/7**	1/7		3/7
Epsilonema (24)		**1/1**			**4/5**	1/5			3/11	**9/11**		2/11	2/15	**13/15**		4/15
Leptepsilonema (10)					**3/3**					**3/3**				**6/6**		
Metepsilonema (21)		**1/1**				**2/2**				**4/4**		2/4	**13/13**			3/13
Perepsilonema (13)					1/2	1/2			1/4	**3/4**				**3/3**		2/3
Polkepsilonema (3)					1/3	2/3				3/3	2/3		1/3	2/3	1/3	
Pternepsilonema (1)														1/1	1/1	
Triepsilonema (1)		**1/1**		1/1	**1/1**					**1/1**		1/1		**1/1**		1/1
Glochinema (7)		**1/1**			**2/2**				1/3	2/3		3/3	3/5	5/5	1/5	4/5
Metaglochinema (1)														1/1	1/1	1/1
Keratonema (1)																

Table 4. Changes in the number of body rings at each moulting stage, based on literature data. The number of species within each genus is given between brackets. The number of cases in which a certain pattern has been observed for a certain transition, divided by the number of times this transition could be examined in a certain genus, is given as a fraction. The arrows indicate an increase, decrease or stagnation in the number of annules. In case there is overlap between the number of body rings prior to and subsequent to moulting, this is indicated in the fourth column.

Tail tip

It is clear from Fig. 7 that the smooth tail tip in the first stage juvenile of *G. trispinatum* is very short compared to the tail tip in the second stage juvenile (Fig. 2A in Raes *et al.*, 2003). Again, there seems to be a positional homology of the tail tip together with several tail annules in first stage juveniles with the tail tip of second stage juveniles. In *Metepsilonema* the tail tip is also slightly shorter in first stage juveniles compared to second stage juveniles. In contrast, the smooth tail tip in first stage juveniles of *T. tripapillata* is longer than in second stage juveniles. In *Epsilonema*, the tail tip in first stage juveniles is also longer than in second stage juveniles. Again, intergeneric variability is present.

6.7. THE TAXONOMIC AND PHYLOGENETIC IMPORTANCE OF CAUDAL GLANDS

Within the family Epsilonematidae, the introduction of the new genus *Triepsilonema* by Decraemer (1982) was, apart from its habitus and the structure of its female reproductive system, mainly based upon the presence of separate outlets for the three caudal glands, with each outlet located at the end of a pronounced papilla (Figs. 8A, B). So far, caudal glands have been considered to be of great taxonomic importance at high taxonomic level (for example to distinguish between 'Adenophorea' and 'Secernentea') as well as at low taxonomic level (for example to distinguish certain genera such as *Ixonema* Lorenzen, 1971). Emphasis was put mainly on (i) the presence or absence of caudal glands, (ii) the number of gland cells and (iii) the presence of either a common outlet or separate outlets for the caudal glands.

Within the family Epsilonematidae (order Desmodorida), the presence of separate outlets for the three caudal glands seems relatively widespread. It has been observed in representatives of seven genera (*Akanthepsilonema*, *Bathyepsilonema*, *Epsilonema*, *Perepsilonema*, *Polkepsilonema*, *Pternepsilonema* and *Triepsilonema*). Current information is however based on few specimens per taxon and data on possible intrageneric variability, intraspecific variability or the presence of sexual dimorphism are rare.

The separate outlets of the three caudal glands in epsilonematids, when present, are arranged as follows: one medioventral outlet and two laterodorsal ones, as can be seen in Fig. 8C of a male of *Epsilonema multispiralum* Raes, Vanreusel and Decraemer, 2003 and Fig. 4H of a male of *Akanthepsilonema sinecornibus* sp. n. An SEM illustration by Karssen *et al.* (2000) shows three well developed papilliform structures in a male of *Epsilonema pustulatum* Lorenzen, 1973, which have a similar position as the caudal gland outlets in the species mentioned above (Fig. 8D). Males and females of *Pternepsilonema servaesae* Verschelde and Vincx, 1993 have been described with a spinneret bearing three separate pore-like outlets. SEM micrographs of a female specimen however show these outlets as short protruding tubes: a medioventral one and two laterodorsal ones (Fig. 8E).

The caudal gland outlets may show inter- and intraspecific differences in shape and number: *e.g.* in *Polkepsilonema mombasae* Verschelde and Vincx, 1993, males have been described with three times three pores, although it is clear from Fig. 8F that there are only three pores, filled with secretion particles. In contrast to males, females have seven, possibly eight or nine pores. The SEM micrograph

(Fig. 8G) shows a more or less triangular tail tip with the outlets arranged in three groups: a medioventral group with two pores and two laterodorsal groups with three pores each. In *Bathyepsilonema lopheliae* Raes, Vanreusel and Decraemer, 2003, sexual dimorphism in the nature of caudal gland outlets is also clear from SEM micrographs (Figs. 8H and I): the male shows a medioventral pore opposite a curved slit-like opening, which could be the result of fusion of the laterodorsal pores; the female on the other hand has only a single terminal pore. A single outlet has also been observed in a female of *Glochinema trispinatum* Raes, Vanreusel and Decraemer, 2003 (Fig. 4B in Raes *et al.*, 2003). In *Perepsilonema ritae* Verschelde and Vincx, 1994, males possess a spinneret provided with one medioventral and two laterodorsal groups of two pores each.

Within a species, the nature of caudal gland outlets may also differ between stages of development: the first stage juvenile of *Triepsilonema tripapillata* Decraemer, 1982 described in the current paper possesses only two caudal papillae (a medioventral and a mediodorsal one) whereas all later stages possess three caudal papillae.

SEM observations of two species belonging to the closely related family Draconematidae Filipjev, 1918, *i.c. Dracognomus simplex* (Gerlach, 1954) Allen and Noffsinger, 1978 (Karssen & Van Aelst, 2002) and a new, undescribed *Cygnonema* species (M. Raes, pers. obs.), show a single common outlet for the three caudal glands.

In spite of the taxonomic importance of caudal glands, little is known about their ultrastructure and physiology. For a long time, caudal glands have been considered to be of one type with a single secretory function, *i.e.* involved in the attachment of the nematode to the substrate. Later, a second function was attributed to caudal glands: the secretion of a sticky mucus that serves as a trap for food particles (Riemann & Schrage, 1978). Ultrastructural studies undertaken to better understand the locomotion of certain nematodes revealed the presence of two sets of caudal glands in several taxa, such as *Perepsilonema* (Adams & Tyler, 1980; Turpeenniemi & Hyvärinen, 1996). Both sets play a role in locomotion: one set of three viscid gland cells is responsible for attaching the nematode to the substrate and another set of smaller cells is responsible for releasing it from the substrate again. The ducts of both types of gland cells may have a common pore at the tail tip either with a spinneret apparatus (*Perepsilonema conifer* Lorenzen, 1973, Epsilonematidae) or without such an apparatus (*Theristus caudasaliens* Adams and Tyler, 1980, Xyalidae). In contrast, the ducts of the different gland cell types may open through different pores (*Sphaerolaimus gracilis* de Man, 1876, Sphaerolaimidae) (Turpeenniemi and Hyvärinen, 1996). Thus, the number and type of caudal gland outlets does not necessarily indicate the presence of one or two sets of caudal glands.

Caudal glands are present in the majority of aquatic nematodes belonging to the Enoplea and the non-rhabditidan (= non-secernentean) taxa of the class Chromadorea. In terrestrial forms there is a tendency towards reduction or absence of these structures.

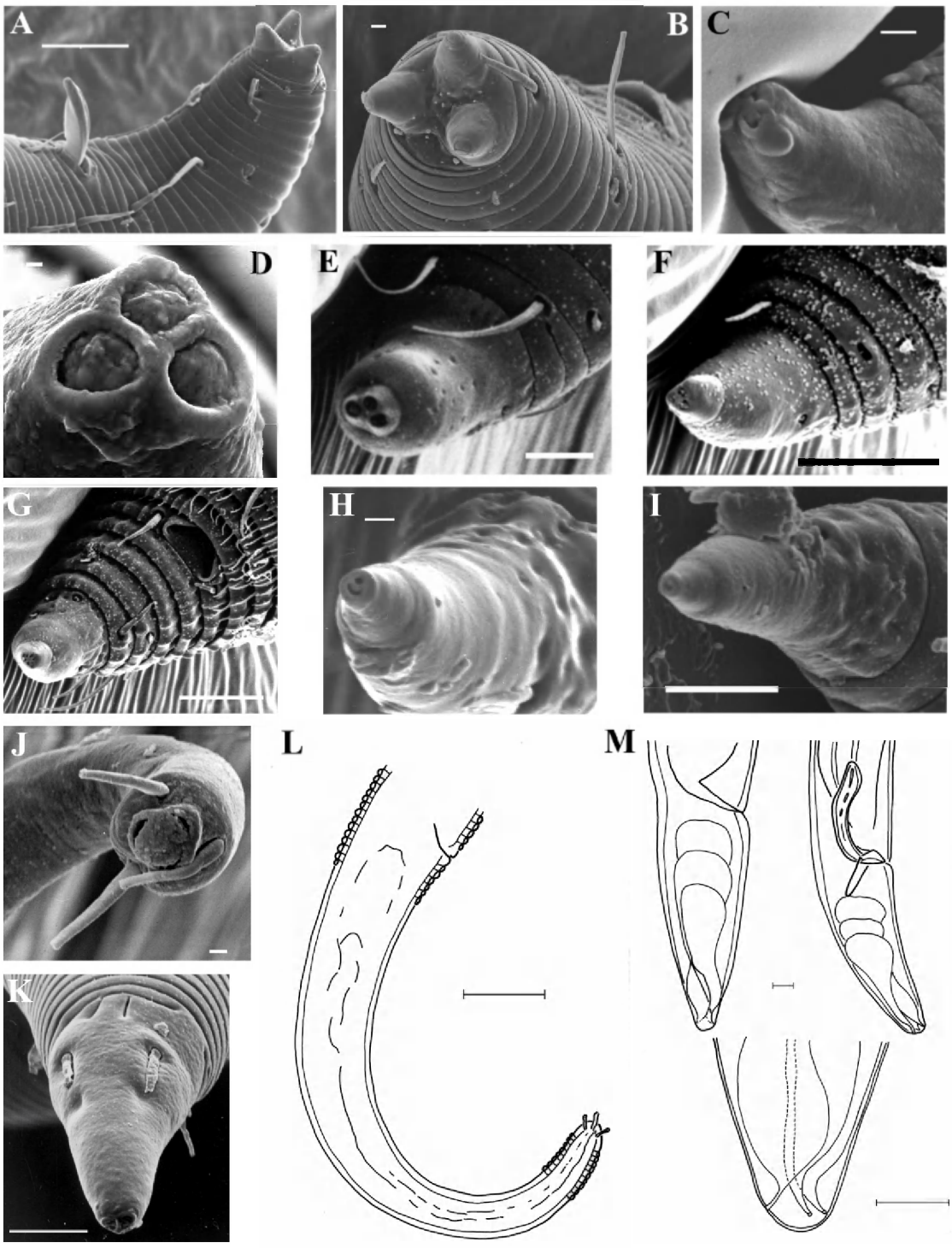


Fig. 8. Caudal gland outlets. A. *Triepsilonema tripapillata* Decraemer, 1982 (male); B. *Triepsilonema tripapillata* Decraemer, 1982 (female); C. *Epsilonema multispiralum* Raes, Vanreusel and Decraemer, 2003 (male) (after Raes, Vanreusel and Decraemer, 2003); D. *Epsilonema pustulatum* Lorenzen, 1973 (male) (after Karssen *et al.*, 2000); E. *Pternepsilonema servaesae* Verschelde and Vincx, 1993 (female) (after Verschelde and Vincx, 1993b); F. *Polkepsilonema mombasae* Verschelde and Vincx, 1993 (male) (after Verschelde and Vincx, 1993b); G. *Polkepsilonema mombasae* Verschelde and Vincx, 1993 (female) (after Verschelde and Vincx, 1993b); H. *Bathyepsilonema lopheliae* Raes, Vanreusel and Decraemer, 2003 (male) (after Raes, Vanreusel and Decraemer, 2003); I. *Bathyepsilonema lopheliae* Raes, Vanreusel and Decraemer, 2003 (female) (after Raes, Vanreusel and Decraemer, 2003); J. *Dorylaimopsis variabilis* Muthumbi, Soetaert and Vincx, 1997 (male) (after Muthumbi *et al.*, 1997); K. *Leptonemella vestari* Hoschitz, Buchholz and Ott, 1999 (female) (after Hoschitz *et al.*, 1999); L. *Deontolaimus papillatus* De Man, 1880 (female) (modified from Meyl, 1954); M. *Diplopeltula incisa* (Southern, 1914) (one female and two males) (modified from Gerlach, 1950). Scale bars: 100 nm in D; 1 µm in B, C, H and J; 5 µm in E, I and K; 10 µm in A, F, G, L and M.

According to Lorenzen (1978), caudal glands rarely open through separate ducts or pores except in the families Xyalidae (*e.g.* in *Echinotheristus cimbricus* Von Thun and Riemann, 1967 and *E. teutonicus* Von Thun and Riemann, 1967) and Sphaerolaimidae (Monhysteroidea), where separate outlets are more common. A single common duct and opening in the other family of the superfamily Monhysteroidea, the Monhysteridae, is regarded as a synapomorphy for this family.

Currently, separate outlets for the three caudal glands have been observed in various unrelated taxa of free-living aquatic nematodes. Within the order Araeolaimida, several taxa belonging to the superfamily Axonolaimoidea, *e.g. Diplopeltula incisa* (Southern, 1914) Gerlach, 1962, *D. breviceps* Gerlach, 1950 and *Pararaeolaimus nudus* (Gerlach, 1951) Timm, 1961 have separate caudal gland outlets. These data were gathered either by light microscopic observations (Diplopeltidae) or by SEM observations, *e.g.* of a male of *Dorylaimopsis variabilis* Muthumbi, Soetaert and Vincx (1997) (Comesomatidae) (Fig. 8J).

Within the order Desmodorida, separate outlets for the three caudal glands have been observed in representatives of the families Epsilonematidae (Desmodoroidea, see above), Desmodoridae (Desmodoroidea) and Microlaimidae (Microlaimoidea). Hoschitz *et al.* (1999) described three small separate pore-like outlets in *Leptonemella vestari* and illustrated this with an SEM micrograph of the tail tip (Fig. 8K). The orientation of the outlets was not described and could not be deduced from the illustration. A representative of the Microlaimidae, *Ixonema*, also possesses separate outlets, with each outlet located on a papilliform structure (M. Raes, pers. obs.).

Within the order Plectida sensu De Ley & Blaxter (2002), separate outlets were also observed: the caudal gland outlets in *Deontolaimus papillatus* de Man, 1880 (Camacolaiminae, Leptolaimidae) described by Meyl (1954) as one tube-like outlet next to two short papilliform structures, were later reinterpreted as three separate caudal gland outlets by Lorenzen (1973b) (Fig. 8L).

In contrast to the situation in the family Epsilonematidae, there are always one mediodorsal and two lateroventral outlets in former examples, as illustrated in Fig. 8J of *Dorylaimopsis variabilis* (Muthumbi *et al.*, 1997).

Lorenzen (1978) regarded the presence of three separate outlets for the caudal glands as a plesiomorphic character in nematodes, based upon the observations and hypotheses of Ossche (1955, 1958) and based on outgroup comparison, for example with the Gastrotricha. Ossche (1955, 1958) observed that in several secernentean species without caudal glands, the tail tip showed three protuberances, of which one was always mediodorsal in position and the remaining two always lateroventral. He interpreted these protuberances (currently termed mucrones or mucros) as rudiments of caudal gland openings, because this arrangement appeared constant and was similar to that of the three separate caudal gland openings in most free-living aquatic nematodes (*e.g. Diplopeltula incisa* (Southern, 1914) Gerlach, 1962 (Fig. 8M)). So, according to Ossche, the absence of caudal glands within the Secernentea is at a secondary rather than at a primary level.

Discussion

Although Ossche (1955, 1958) showed that tail tips with three protuberances are present in several secernentean taxa, these protuberances may be quite variable in number, position and shape

and may be accompanied by additional structures such as spines. The presence of protuberances may well be a useful diagnostic character at species level (*e.g.* within the genus *Chronogaster* in Chronogasteridae, Plectoidea), although the homology of mucrones with caudal gland outlets, as hypothesised by Ossche (1955), is questionable. The orientation of the three tail protuberances could be related to body symmetry and locomotion. The majority of nematodes have a slender, cylindrical body and usually crawl or swim with undulatory movements in a dorso-ventral plane (Stauffer, 1924; Decraemer & Hunt, *in press*). Aberrant body shapes may be related to an aberrant locomotory pattern as in Epsilonematidae and Draconematidae, which move like inchworms on their ventral side. The aberrant (i.e. opposite) arrangement of the separate outlets of the three caudal glands in Epsilonematidae taxa compared with other nematodes could be related to their aberrant mode of locomotion and is considered an apomorphy for this family of nematodes. It has already been mentioned above that Draconematidae only have a single outlet: caudal glands might not play an important role in locomotion here because locomotion in Draconematidae relies mainly on the presence of large locomotory adhesion tubes.

Within the family Epsilonematidae, the genus *Triepsilonema* differs from most other genera because of its more or less cylindrical body, comparable to most taxa within the Desmodorida. This character could be interpreted as primitive based upon outgroup comparison. If we accept Lorenzen's hypothesis that the presence of separate outlets for the caudal glands is a primitive character, this would provide an additional argument for the hypothesis that the genus *Triepsilonema* is a primitive genus within the family Epsilonematidae. On the other hand, *Triepsilonema* possesses the aberrant arrangement of caudal gland outlets typical for Epsilonematidae, which is a derived character. Next to that, *Triepsilonema* females differ from the other Epsilonematidae taxa by the possession of outstretched ovaries, a character considered as derived (Lorenzen, 1981; 1994). Based on the last two features it seems that the more cylindrical body shape in *Triepsilonema* is at a secondary (loss of aberrant body shape typical to all other Epsilonematidae) rather than at a primary (preservation of cylindrical body) level.

6.8. ACKNOWLEDGEMENTS

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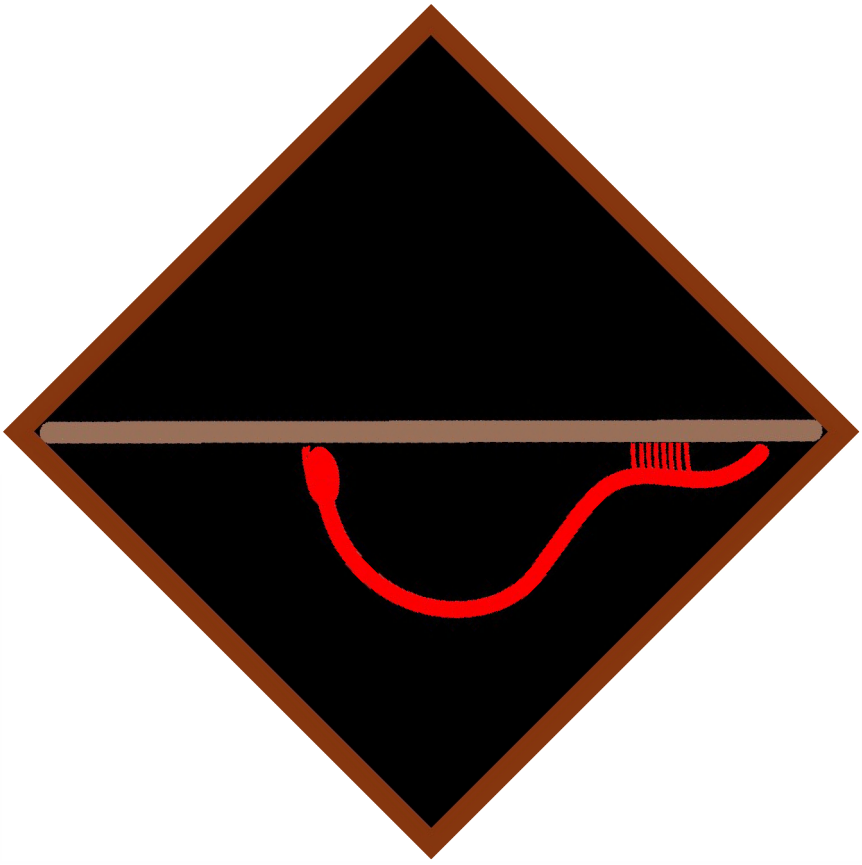
CHAPTER 7

DRACONEMATIDAE FROM COLD-WATER CORALS IN THE PORCUPINE SEABIGHT: THE GENUS *TENUIDRACONEMA* DECRAEMER, 1989



Paper *submitted*

Raes, M., Decraemer, W., Vanreusel, A.

Draconematidae from cold-water corals in the Porcupine Seabight: the genus *Tenuidraconema* Decraemer, 1989

Organisms, Diversity and Evolution

7.1. ABSTRACT

A new species of *Tenuidraconema* is described from a cold-water coral degradation zone in the Porcupine Seabight. *Tenuidraconema parvospermis* sp. n. is distinguished from all other species of *Tenuidraconema* by the combination of 10 CAT located posterior to amphidial fovea, SIAT alternately long and short, amphidial fovea in males composed of an inner and outer loop, with ventral arm of inner loop equally long as high, compact, jagged sperm cells with large, refractile inclusions, the shape of the gubernaculum and the number of tail rings. Additional information is provided for *T. koreensis*, from specimens found in the Porcupine Seabight and the fourth stage juvenile of this species is described for the first time. The biogeography of *T. koreensis* in the North Atlantic is discussed in view of its occurrence on the Great Meteor Seamount. A dichotomic identification key to the four species of *Tenuidraconema* is provided.

Key words: marine nematodes, taxonomy, *Tenuidraconema*, Porcupine Seabight, cold-water corals

7.2. INTRODUCTION

The present paper is part of an extensive study dealing with the nematofauna associated with a cold-water coral degradation zone in the Porcupine Seabight (continental slope, northeast Atlantic Ocean). This is an area where the living cold-water coral framework, which is present here, is gradually degraded due to a constant bioerosion process, resulting in the presence of dead fragments of the framework building coral *Lophelia pertusa* (Linnaeus, 1758) and skeletons of the glass sponge *Aphrocallistes bocagei* Schultze, 1886, clogged together with sediment. Compared to the associated sediment, the coral fragments themselves are characterised by higher abundances of typically epifaunal nematode taxa, such as Epsilonematidae and Draconematidae. Next to this, significant microhabitat preferences of several genera and species belonging to these two closely related families for dead *Lophelia* fragments have been found (Raes & Vanreusel, *in press*; Raes *et al.*, *submitted*). This is explained by the feeding behaviour and particular way of locomotion of these animals: they move forward over a certain surface like inchworms, alternately attaching and releasing the anterior and posterior end of the body (Stauffer 1924; Lorenzen 1973a). Draconematidae use both Cephalic Adhesion Tubes (CAT) and Posterior Adhesion Tubes (PAT) for attachment.

Only few Draconematidae have been described from the deep sea. Kito (1983) described two species of *Cephalochaetosoma* Kito, 1983 from a depth between 5549 and 5551 m in the western North Pacific. Subsequently, a new genus *Bathychaetosoma* Decraemer, Gourbault and Backeljau, 1997 was erected by Decraemer *et al.* (1997) to accommodate one of these species. Decraemer & Gourbault (1997) described a species of *Dinetia* Decraemer and Gourbault, 1997 from the East Pacific Rise (depth: 2600 m) and a new subspecies of *Cephalochaetosoma pacificum* Kito, 1983 from the West Pacific deep sea (depth: 1707 m). In his doctoral dissertation, Bussau (1993) described a new genus *Eudraconema* from the East Pacific (depth: 4100-4200 m). The same genus has since been encountered again by different authors: in the Central Pacific (depth: 4990 m; Decraemer & Gourbault,

1997), North Atlantic (depth: 4005 m), Laptev Sea (depth: 1140 m), Scotia Sea (depth: 2274-5194 m), Mediterranean, New Ireland Basin (depth: 1813 m) (Gad, *in press*) and has recently been described from the South Atlantic as *Bussauinema* gen. n. (depth: 5389-5505 m; Gad, *in press*).

Several new species of Epsilonematidae have already been described from the coral degradation zone in the Porcupine Seabight (Raes *et al.*, 2003; Raes *et al.*, *in press*). In the present paper, a new species of *Tenuidraconema* Decraemer, 1989 is described and additional information is provided for *T. koreensis* Rho & Kim, 2004. This species was originally described from the eastern coast of South Korea, where it was found at a depth of 150-250 m. Although a large number of individuals was examined, only few measurements on one male and one female were carried out. More information on intraspecific variability is added here and the original description is supplemented with more detailed observations on the different morphological features. Moreover, information on juvenile stages is provided for the first time. An identification key and an overview of the geographical distribution of the two species in question is also given.

7.3. MATERIALS AND METHODS

Type and additional material originate from dead coral fragments of *Lophelia pertusa* (Linnaeus, 1758) and, to a lesser extent, *Madrepora oculata* Linnaeus, 1758, skeletons of *Aphrocallistes bocagei* Scultze, 1886 and the sediment underlying these large biogenic substrata. Material was collected by means of a round box corer (diam. 32 cm) during two sampling campaigns with the RV Belgica. Box cores were taken on the top and slope of one seabed mound situated in the Belgica mound province of the Porcupine Seabight: Box IV 2000 (51°24'48,2"N 11°45'55,4"W; depth: 1005 m), Box V 2000 (51°24'49,4"N 11°45'55,9"W; depth: 1000 m) and Box IV 2001 (51°25'7,7"N 11°46'9,3"W; depth: 972 m). The Porcupine Seabight is a large embayment of the European continental slope, located in the North-East Atlantic, southwest of Ireland. Our samples were taken in the sediment-clogged cold-water coral framework facies (Freiwald *et al.*, 2002) and contained mainly dead coral and sponge material. After removal of the large biogenic substrata, three sediment cores (surface area: 10 cm^2) were pushed in the sediment of each box core. The sediment consisted of fine to medium sand and was poorly sorted. It contained small coral and sponge fragments, as well as some mollusc-shell fragments and echinoid radiolas. All material was fixed with a 4% neutralised formalin solution.

Each coral and sponge fragment was rinsed thoroughly over sieves with a mesh size of 1 mm and 32 µm, in order to separate macrofauna and meiofauna. Meiofauna was extracted from the underlying or remaining sediment by density gradient centrifugation, using Ludox (a colloidal silica polymer; specific gravity 1.18) as a flotation medium (Heip *et al.*, 1985; Vincx, 1996). Meiofauna was stained with Rose Bengal. Nematodes were individually picked out from the meiofauna and subsequently mounted onto slides, using the formalin-ethanol-glycerol technique described by Seinhorst (1959) and Vincx (1996). Detailed morphological observation was carried out with a Leica DMLB light microscope. A Leitz Dialux 20 microscope, Sanyo CCD video camera and the Quantimet 500 software were utilised for measurements. Scanning electron micrographs were taken from the glycerol fixed specimens. After

ultrasonic treatment (to remove detritus attached to the body) the specimens were transferred to OsO_4, dehydrated, subjected to critical point drying and coated with gold particles.

Type material is deposited in the collections of Ghent University, Museum voor Dierkunde (UGent), the Koninklijk Belgisch Instituut voor Natuurwetenschappen in Brussels (KBIN) and the Natural History Museum in London (NHM). Non-type material is indicated as 'additional material' throughout the text.

7.4. ABBREVIATIONS USED

L: total body length

Hdw: maximal width of head capsule

Hdl: length of head capsule

Bda: body width at level of amphidial fovea (in first stage juveniles only)

Amphw: width of amphidial fovea

Amphl: length of amphidial fovea

Amph%: (Amphw / Hdw)*100

ph: pharyngeal length, measured from anterior end of head capsule up to posterior border of pharyngeal bulb, lips (when protruding) and cardia not included

MdCAT: length of mediodorsal cephalic adhesion tube

MdCATa: length of anteriormost mediodorsal cephalic adhesion tube

MdCATp: length of posteriormost mediodorsal cephalic adhesion tube

SdCATa: length of anteriormost subdorsal cephalic adhesion tube

SdCATp: length of posteriormost subdorsal cephalic adhesion tube

LdCAT: length of laterodorsal cephalic adhesion tube

SlCATa: length of anteriormost sublateral cephalic adhesion tube

SlCATp: length of posteriormost sublateral cephalic adhesion tube

SlATa: length of anteriormost sublateral posterior adhesion tube

SlATp: length of posteriormost sublateral posterior adhesion tube

LvATa: length of anteriormost lateroventral posterior adhesion tube

LvATp: length of posteriormost lateroventral posterior adhesion tube

SvATa: length of anteriormost subventral posterior adhesion tube

SvATp: length of posteriormost subventral posterior adhesion tube

MvATa: length of anteriormost medioventral posterior adhesion tube

MvATp: length of posteriormost medioventral posterior adhesion tube

tail: tail length

tmr: length of tail tip

mbd ph: body diameter at level of pharyngeal bulb

mbd: maximal diameter of posterior body region

(mbd): minimal body diameter

mbd/(mbd): proportion of minimal body diameter to maximal diameter of posterior body region

abd: body diameter at level of anal or cloacal opening

spic: length of spicule, measured along the arc

gub: length of gubernaculum

V%: position of vulva, expressed as a percentage of L, measured from anterior end

a: de Man a-ratio, *i.e.* L / mbd

b: de Man b-ratio, *i.e.* L / ph

c: de Man c-ratio, *i.e.* L / tail

7.5. DESCRIPTIONS

Familia Draconematidae Filipjev, 1918

Subfamilia Draconematinae Filipjev, 1918

Genus *Tenuidraconema* Decraemer, 1989

***Tenuidraconema koreensis* Rho & Kim, 2004** (Figures 1, 2 and 5A)

Additional material. Eighteen males; 14 females; ten fourth stage juveniles.

Type locality. Namae, South Korea. Coordinates: 37°57'07"N 128°46'41"E (material collected on 21/04/2000; depth: 150-250 m).

Other localities. Porcupine Seabight, Belgica mound Province. Coordinates: 51°24'48,2"N 11°45'55,4"W (material collected on 17/06/2000; depth: 1005 m), 51°24'49,4"N 11°45'55,9"W (material collected on 17/06/2000; depth: 1000 m), 51°25'7,7"N 11°46'9,3"W (material collected on 07/05/2001; depth: 972 m) and 51°24'49"N 11°45'56.3"W (material collected on 25/05/2003; depth: 1004 m). Plateau of the Great Meteor Seamount. Coordinates: 30°02'00"N 28°32'00"W (Station 518; material collected on 14/09/1998; depth: 293 m), 30°06'00"N 28°24'18"W (Station 520; material collected on 14/09/1998; depth: 422 m), 29°53'54"N 28°22'00"W (Station 552; material collected on 18/09/1998; depth: 332 m).

Habitat at type locality. Subtidal coarse sediment and various invertebrates (hermit crabs, sponges and bryozoans).

Other habitats. (1) A cold-water coral degradation zone on the flank and near the top of a seabed mound. Specimens associated with sediment-clogged framework of the cold-water coral *Lophelia pertusa* (Linnaeus, 1758) and were found on dead coral fragments, on dead sponge skeletons (*Aphrocallistes bocagei* Schultze, 1886) and within the underlying sediment; (2) biogenic coarse sand, composed of coral fragments and mollusc shells.

Measurements. Tables 1 and 2.

Additional information

Males

Swollen pharyngeal region 8% (type material) or 11.3-13.2% (Porcupine Seabight specimens) of total body length. Thinnest body region immediately behind pharynx (Fig. 1B). Region between pharyngeal bulb and anterior tip of testis conspicuously long and slim. In some cases, sessile ciliates

attached to this region. Maximal body width at level of vesicula seminalis. Posterior to seminal vesicle body slightly decreasing in width again and body width maintained up to cloacal opening. Body width abruptly narrowing behind cloacal opening. Body with fine transverse striation, hereafter indicated as 'annulation'. Broadest annules at level of pharynx and in narrow region behind pharynx. Annules touching but not overlapping. Beginning 30-94 µm in front of anterior tip of testis, annules laterally interrupted by narrow lateral field, extending up to level of vesicula seminalis (Fig. 1B). Lateral interruption 166-250 µm in length and 2.2-3.0 µm in width, sometimes faint or absent. In region of lateral interruption annules gradually decreasing in width. Posterior to lateral field, annules very narrow and small annular width maintained up to cloacal opening. Along tail, annules slightly increasing in width again. Annules in pharyngeal region ornamented with numerous tiny, irregular vacuoles in one or two rows (Fig. 2B). Vacuoles sometimes faint. Annules in posterior body region with rough, somewhat granular edges and littered with detritus. Annules around cloacal opening occasionally ornamented with a single row of transversally elongated vacuoles. All other annules completely smooth.

Twelve slender CAT arranged in six longitudinal rows of two tubes (Figs. 2B,C). In one Porcupine Seabight specimen, two rows exceptionally carrying three tubes. Anteriormost CAT in each row at posterior border of head capsule (type and some Porcupine Seabight specimens) or on annules 1-3 (some Porcupine Seabight specimens): generally well posterior to amphidial fovea, sometimes at level of posterior border of amphidial fovea. Second CAT in each row located on annules 3-6. PAT long and relatively slender, with swollen base and conspicuous bell-shaped tip (Fig. 2D). Width of anteriormost SlAT 1.3-2.0 µm at 10 µm from base. PAT arranged in four rows: two rows of 8-12 SlAT (12 in type specimens) and two rows of 7-15 SvAT (15 in type specimens). SlAT slightly and gradually decreasing in length towards posterior. SvAT more strongly decreasing in length towards posterior. PAT clearly associated with glands, appearing as two longitudinal rows of several separate compartments at base of PAT. First PAT located at 56.5-81.5% of body length. Distance between first and last PAT 8.5-15.8% of total body length.

In pharyngeal region, somatic setae arranged in 12 or 14 longitudinal rows. one mediodorsal row, two subdorsal rows, two laterodorsal rows, two mediolateral or four sublateral rows, two lateroventral rows, two subventral rows and one medioventral row. Slender region behind pharyngeal bulb and region anterior to PAT with one mediodorsal row, two laterodorsal rows, two lateroventral rows and one medioventral row of somatic setae. In region of PAT, somatic setae in one mediodorsal row and two laterodorsal-sublateral rows. Sometimes one additional somatic seta in line with SlAT, just anterior to posteriormost or second last SlAT. Posterior to each posteriormost SlAT one lateroventral seta usually present. This seta usually followed by four (type specimens) or five (Porcupine Seabight specimens), subventral, pericloacal ('anal') setae: two (type specimens) or three (Porcupine Seabight specimens) pre-cloacal and two post-cloacal. Anteriormost pericloacal seta longest. In several smaller Porcupine Seabight individuals only three pericloacal setae present on each side: two pre-cloacal and one post-cloacal. Annulated tail on each side with two subventral setae and several subdorsal setae, including longest somatic setae on entire body (51.3 µm on average). These setae sometimes truncated and then 25.1 µm in length on average. Tail tip with one short lateroventral and one short subdorsal seta on each side.

Cephalic capsule a broad truncated cone, either smooth or ornamented with small vacuoles. Six small and setiform external labial sensilla, which may be visible when labial region protruded (which is rarely the case). Four cephalic and 21-24 subcephalic setae, arranged in eight rows: generally two subdorsal rows of three setae, two laterodorsal rows of five setae, two lateroventral rows of two setae and two subventral rows of two setae. Occasionally, additional scattered pores present near posterior border of cephalic capsule. Amphidial fovea long, 51.8-78.4% of length of cephalic capsule, located centrally on head capsule or near posterior border of head capsule; sometimes surrounded by first annule (Figs. 2B,C). Amphidial fovea composed of conspicuous outer loop and vague inner loop. Dorsal arm in outer loop shorter than ventral arm; dorsal arm in inner loop longer than ventral arm. Long arms of both loops joining at posterior border of head capsule, sometimes penetrating into first annules. Buccal cavity surrounded by four cephalic glands with gold coloured granules. Pharynx with elongated, muscular endbulb and two less pronounced anterior swellings divided by an indentation at level of posterior border of cephalic capsule. Large nerve ring situated immediately in front of terminal bulb. Cardia triangular or antero-posteriorly flattened. Intestine granular, with slightly thickened brush border. Cloacal flap present or absent.

Male reproductive system monorchic, with outstretched testis extending far anteriorly (testis tip located at 47.9-57.4% of total body length) (Fig. 2A). Germinal and growth zones finely granular, usually slender, forming broad band curved ventrally around intestine, slightly shifted to the left. Vesicula seminalis usually wider than former zones, located ventrally to and partially on left side of intestine. Seminal vesicle containing several large, irregularly shaped, elongated, opaque sperm cells, each with large amount of cytoplasm, narrow halo and one round or slightly jagged nucleus filled with numerous tiny nucleoli. Length of sperm cells 12 µm on average. Vas deferens granular, usually wide, located ventrally to and in most cases on right side of intestine. Percentage of spicule length to total body length 3.7-4.3%. Spicules slender and slightly curved, with set-off, ventrally oriented, triangular or beak-like capitulum and strongly cuticularised lamina usually bearing ventral apophysis at base of manubrium, connected with velum (Fig. 2E). Gubernaculum narrow. Distal part of gubernaculum parallel to lamina, proximal part bent away from spicules, sometimes hook-shaped.

Tail very slender and conico-cylindrical, with 54-78 complete annules, including long (34% of tail length in type specimens and 36.2-43.1% of tail length in Porcupine Seabight specimens) and pointed tail tip. Tail tip with tiny vacuoles on dorsal side. Tail tip sometimes with one incomplete annule dorsally or 1-5 incomplete annules ventrally (no incomplete annules in holotype). Caudal glands mostly inconspicuous, extending anteriorly to cloacal opening.

Females

Swollen pharyngeal region 9.9-16.4% of total body length. In most cases, lateral field absent or inconspicuous. When present, lateral field usually narrower than in males (width 1.5-2.8 µm) and extending from slightly anterior to genital system up to level of uterus (length 65-158 µm). Annulation and cuticular ornamentation as in males although one Porcupine Seabight specimen with decoration of fine vacuoles in slender region behind pharyngeal bulb.

Anteriormost CAT in each row at posterior border of head capsule (type and some Porcupine Seabight specimens) or on annules 1-3 (some Porcupine Seabight specimens): generally well posterior to amphidial fovea, sometimes at level of posterior border of amphidial fovea (Fig. 2F). Second CAT in each row situated on annules 1-6. Width of anteriormost SlAT 1.2-1.8 µm at 10 µm from base of tube. PAT arranged in four rows: two rows of 11-13 SlAT (13 in type specimens) and two rows of 7-19 SvAT: 19 in type specimens and 7-16 in Porcupine Seabight specimens (Fig. 1C). PAT gradually decreasing in length towards posterior.

In pharyngeal region, somatic setae arranged in 12 or 16 longitudinal rows: one mediodorsal row, two subdorsal rows, two or four laterodorsal rows, two mediolateral rows, two or four lateroventral rows, two subventral rows and one medioventral row. In slender region behind pharyngeal bulb, in region anterior to PAT and in region of PAT somatic setae arranged as in males, although with two subventral setae on each side at level of vulva and without medioventral setae in this region. Each side with or without one short seta between two posteriormost SlAT. Posterior to last SlAT, one or two short sublateral setae usually present on each side. One subventral anal seta on each side at level of anus or one medioventral setae anterior to anus. Tail on each side with one subventral seta, 3-4 laterodorsal setae and one very long subdorsal seta (37.5 µm in additional female from Porcupine Seabight). Tail tip on each side with one short lateroventral and 1-2 short subdorsal setae.

Shape of head capsule as in males, either smooth or ornamented with small vacuoles. Six labial sensilla, four cephalic setae and 21-29 subcephalic setae, arranged in eight rows: maximally two subdorsal rows of three setae, two laterodorsal rows of six setae (not entirely in one row but closely together), two lateroventral rows of three setae and two subventral rows of three setae. Sexual dimorphism obvious from shape of amphidial fovea: in females a large, longitudinally elongated, ventrally wound spiral consisting of 2.5-2.7 coils, situated centrally on cephalic capsule. Length of amphidial fovea 49.1-67.5% of head capsule length. Buccal cavity surrounded by gold coloured granules. Anal flap present or absent.

Female reproductive system situated ventrally to intestine: didelphic and amphidelphic, with antidromously reflexed ovaries (Fig. 1A). Anterior ovary reflexed along right side, posterior ovary reflexed along left side. Uterus often with numerous opaque sperm cells, each with considerable amount of cytoplasm and more condensed nucleus than in males. Vagina bipartite: proximal and distal part equal in length. Proximal part surrounded by strongly refractive contractor muscle. Four paravulval setae in type specimens, no paravulval setae in Porcupine Seabight specimens.

Tail with 50-76 complete annules, including long (39.2-46.7% of tail length) and pointed tail tip. Tail tip either without incomplete annules, with 1-3 incomplete annules dorsally (three in allotype) or with one incomplete annule ventrally.

Juveniles

First stage juveniles, second stage juveniles and third stage juveniles could not be distinguished from those of *T. parvospermis* sp. n.

Fourth stage juveniles (Fig. 5A)

Slender body, obviously enlarged at level of pharynx. Posterior swelling less pronounced, especially in juvenile males. Annules in pharyngeal region ornamented with one or two rows of irregular vacuoles. Slender region posterior to pharynx sometimes with one row of vacuoles. Remainder of annules smooth. Lateral field absent or present as lateral interruption of annules, anterior to genital system or at level of germinal and growth zones in some juvenile males.

Four slender CAT with swollen base and slightly swollen tip, located on posterior border of head capsule or on annules 1-5, always clearly posterior to amphidial fovea: two subdorsal and two laterodorsal tubes. One medioventral row of 7-9 PAT and two lateroventral rows of 6-7 PAT. PAT long, robust, with swollen base and well-developed bell-shaped tip, gradually decreasing in length towards posterior. Width of anteriormost LvAT 1.2-1.8 µm at 10 µm of base of tube.

Somatic setae in pharyngeal region arranged in eight rows: two subdorsal rows, two laterodorsal rows, two lateroventral rows and two subventral rows. Region between pharynx and PAT with one mediodorsal row, two laterodorsal rows, two lateroventral rows and one medioventral row of somatic setae. At level of PAT somatic setae in one mediodorsal and two sublateral rows in dorsal sector. On each side, one short subventral seta anterior to anus. Tail with one subventral and three subdorsal somatic setae on each side, including very long subdorsal setae. Tail tip with one short lateroventral and one short subdorsal seta on each side.

Cephalic capsule short truncated cone, ornamented with small vacuoles. Four cephalic and 11-17 subcephalic setae, arranged in two subdorsal rows, two laterodorsal rows, two lateroventral rows and two subventral rows. Amphidial fovea spiral, ventrally wound, consisting of 2-2.6 loops, usually longer than wide. Amphidial fovea located either centrally on head capsule or slightly shifted to anterior. Length of amphidial fovea 32.6-51.7% of length of cephalic capsule. Digestive system as in adults. Genital system well-developed in moulting individuals: juvenile females with reflexed ovaries.

Tail with 44-64 complete annules, including long (36.5-49.1% of tail length) and pointed tail tip. Tail tip with tiny vacuoles. Tail tip either without incomplete annules, with two incomplete annules dorsally or with one incomplete annule ventrally.

Emended species diagnosis

The species is characterised by the combination of the following character states: (1) all CAT located posterior to amphidial fovea, (2) 12 CAT, arranged in six longitudinal rows, (3) length of anteriormost SlAT 46-66 µm in males and 39-66 µm in females, (4) length of anteriormost SvAT 41-62.5 µm in males and 33.5-62 µm in females, (5) width of anteriormost SlAT 1.3-2.0 µm in males and 1.2-1.8 µm in females; (6) distance between first and last PAT 8.5-15.8% of total length in males, (7) external labial sensilla setiform, (8) amphidial fovea in males composed of an inner and an outer loop, with ventral arm of inner loop longer than high, (9) sperm cells elongated, irregularly shaped, with large amount of cytoplasm, narrow halo and one nucleus, 12 µm in length on average, (10) proximal part of gubernaculum hook-shaped, bent away from spicules, (11) well-developed cuticularised velum and (12) 54-78 tail rings in males and 50-76 tail rings in females.

Differential diagnosis

Differential diagnosis for this species is given under *T. parvospermis* sp. n.

	Males (n = 11)	Females (n = 10)	Juvenile stage IV (n = 9)
L	845-1405 (1190)	715-1485 (1075)	610-1030 (795)
Hdw	21.5-27 (23.2)	19.5-25 (23.1)	16.5-24.5 (21.1)
Hdl	15-20.5 (17.6)	12.5-20 (16.7) [9]	14-20 (15.9) [8]
Amphw	5.5-8 (6.9)	7-8 (7.5)	5-7.5 (6.5) [8]
Amphl	10-12.5 (11.3)	7.5-10.5 (8.9)	6-9 (7.3) [8]
Amph%	25.7-34.5 (29.9)	29.2-34.7 (32.3)	23.9-36.3 (31.4) [8]
ph	70-99.5 (88.8)	64.5-103 (83.7)	61-83.5 (75.6) [6]
MdCATa	17-22.5 (19.7)	15.5-21 (18.7) [8]	
MdCATp	22-30 (27.3)	20.5-29 (25.8) [8]	
SdCATa	18-22.5 (21.4)	17-24 (20.6) [9]	14-22 (18.7) [7]
SdCATp	23-31 (27.8)	22-29.5 (25.4) [9]	
LdCAT			17.5-25 (21.4) [7]
SlCATa	22-25.5 (23.8)	19-26.5 (22.8)	
SlCATp	25-30.5 (27.8)	22-31 (26.7)	
SlATa	46-66 (57.2)	39-66 (55.3)	
SlATp	30-44.5 (35.7)	31-46 (38.1)	
LvATa			33-53.5 (44.1)
LvATp			22-39.5 (34.1)
SvATa	41-62.5 (56.5)	33.5-62 (50.3) [9]	
SvATp	21.5-27.5 (24.4)	19.5-28 (24.6)	
MvATa			32-56 (43.4)
MvATp			14.5-27.5 (22.6)
tail	85-151 (128.9) [10]	106-161 (131.3)	82.5-116.5 (97.9)
tmr	40-58 (52.2) [10]	43.5-66.5 (55.2)	30-55.5 (44.1)
mbd ph	30-41 (34.2)	32.5-37 (34.3)	26-39 (33.5)
mbd	30-47 (38.6)	40-57.5 (47.4)	24.5-43.5 (32.3)
(mbd)	11.5-14 (13.4)	11.5-16 (13.6)	12-17 (14.3)
mbd/(mbd)	2.5-3.5 (2.9)	3.0-4.1 (3.5)	2.0-2.7 (2.3)
abd	16-22.5 (19.2)	14.5-18.5 (16.0)	14-18.5 (15.7)
spic	34-53 (47.6)		
gub	11-16 (14.1) [9]		
V%		54.0-67.7 (62.2)	
a	23.5-34.1 (30.8)	16.1-27.6 (22.4)	14.0-29.7 (25.2)
b	12.0-14.2 (13.3)	9.0-15.1 (12.7)	8.8-13.0 (10.8) [6]
c	8.3-12.3 (9.3)	6.0-9.8 (8.1)	6.4-10.6 (8.1)

Table 1. Measurements of Porcupine Seabight specimens of *Tenuidraconema koreensis* Rho & Kim, 2004. All absolute values in µm. The number of specimens measured, when different from the total number of specimens, is indicated between brackets in superscript.

Biogeography and dispersal

The species was originally described from Namae, South Korea, where it was collected from a depth of 150-250 m. It is remarkable that the same species, with only limited morphological differences, is now found in the North Atlantic at a depth of 1000 m. Due to the mere geographical and bathymetrical range, as well as the assumed complexity of dispersion routes that link both populations,

it is possible that these populations are genetically isolated from each other and may represent different cryptic species.

One male and one female specimen belonging to this species have been found on the plateau of the Great Meteor Seamount (measurements in Table 2). These individuals are morphologically and morphometrically almost identical to those of the type locality and Porcupine Seabight, although the number of tail annules is slightly lower: 49 in male and 43 in female. Moreover, another new species of *Tenuidraconema* has been found on this seamount (Gad, pers. comm.). These observations agree well with the hypothesis of Gad (2004) that cold-water coral reefs could be regarded as a source for the colonisation of the Great Meteor Seamount by Epsilonematidae and Draconematidae, and for genetic exchange. It is however still not clear how this takes place. According to Gad (2004) and Gad & Schminke (2004), the colonisation of the Great Meteor Seamount by meiofauna could occur through continuous transport by the outflow of Mediterranean water and between the Great Meteor Seamount and the north-western coast of Africa. According to these authors, this trans-oceanic colonisation is not the result of a single long-distance dispersive action but a gradual process using seamounts, the Canary Islands and the Island of Madeira as 'stepping stones', *i.e.* intermediate stations where a new population can be established, which can then again serve as a new source for colonisation. If this is the case, than the presence of *Lophelia pertusa* might be an essential aspect in this hypothesis. The plateau of the Great Meteor Seamount is known to be covered by biogenic coarse sand which is partially composed of coral fragments. Subfossil remains of the cold-water coral *Lophelia pertusa* have been found on this seamount and this coral species has also been recorded on the nearby Atlantis Seamount, near Madeira, near the Canary Islands and near the Azores (Rogers, 1999). The possibility that Mediterranean Outflow Water (MOW) may play a role in the distribution of *L. pertusa* and the dispersal of its larvae, both northward along the north-western European continental margin (up to the Norwegian Sea and also reaching the Porcupine Seabight at a depth of 800-1000 m) and westward across the Atlantic, has already been put forward by De Mol *et al.* (2002). According to Le Goff-Vitry *et al.* (2004), it could be the Shelf Edge Current (SEC), a surface current which follows the northward branch of the MOW and reaches the Porcupine Seabight at a depth of 100-200 m, that transports the larvae of *L. pertusa* along the continental margin from the Iberian margin up to the Norwegian Sea. However, only the MOW is able to reach both the Porcupine Seabight and the Great Meteor Seamount. We hypothesise here that at least part of the nematofauna associated with *L. pertusa* fragments follows the same trajectory as the larvae of this coral species, resulting in a co-occurrence of the coral and these nematodes. Following this hypothesis, the source for colonisation would be somewhere in the Mediterranean Sea or near the MOW outflow point in the North Atlantic. Moreover, this should ensure continuing long-distance genetic exchange, whether or not via stepping stones. It is however also possible that nematodes such as *T. koreensis* sp. n. are more widely distributed in the region but are only able to establish a population in the presence of *L. pertusa* fragments or other biogenic substrata.

	Male	Female
	Male	Female
L	1105	935
Hdw	22.5	22
Hdl	15	14.5
Amphw	6.5	8.5
Amphl	10.5	8
Amph%	28	38.4
ph	75.5	77.5
MdCATa	15	15
MdCATp	23.5	22
SdCATa	17	17
SdCATp	21.5	22.5
SlCATa	21.5	19
SlCATp	26.5	22.5
SlATa	51	46.5
SlATp	30	28
SvATa	42	34.5
SvATp	19	18
tail	111.5	108
tmr	43	49
mbd ph	31.5	32.5
mbd	32	45
(mbd)	13.5	13
mbd/(mbd)	2.4	3.4
abd	18.5	14.5
spic	51.5	
gub	11	
V%		66.2
a	34.8	20.8
b	14.6	12.1
c	9.9	8.7

Table 2. Measurements of Great Meteor Seamount specimens of *Tenuidraconema koreensis* Rho & Kim, 2004. All absolute values in µm.

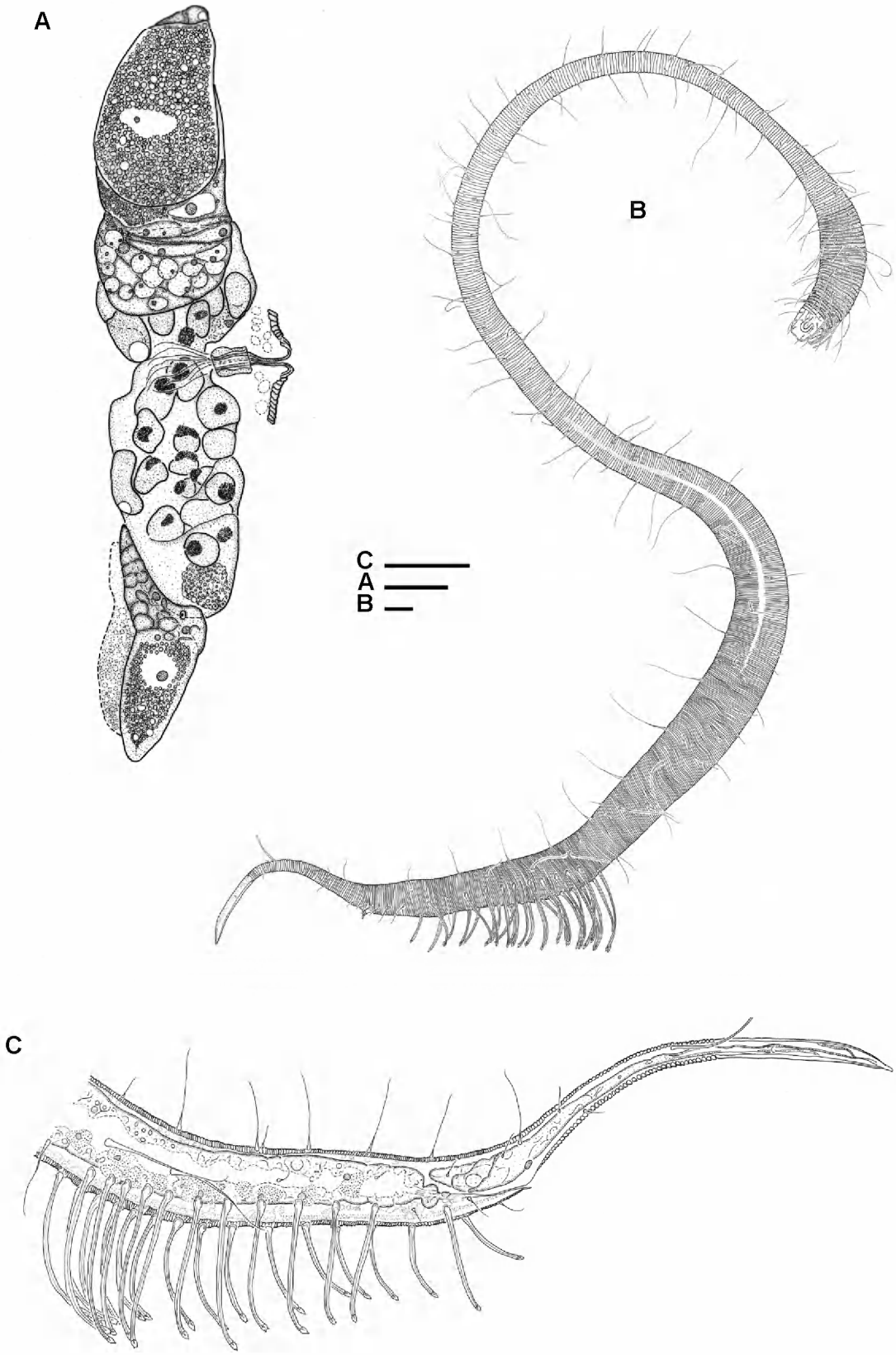


Fig. 1. *Tenuidraconema koreensis* Rho & Kim, 2004. (A) ♀, reproductive system; (B) ♂, habitus external; (C) ♀, posterior body region and tail. Scale bars 20 µm.

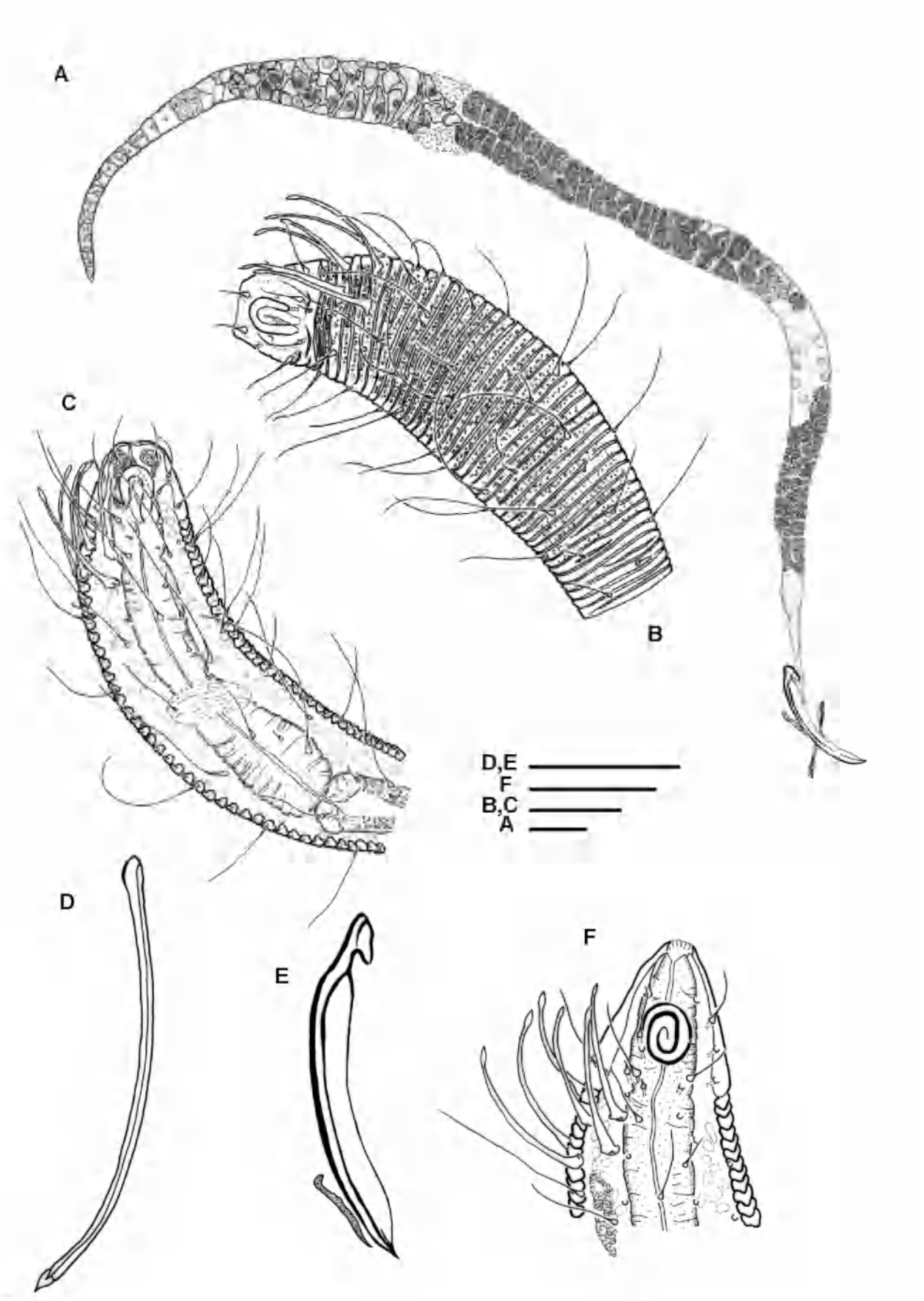


Fig. 2. *Tenuidraconema koreensis* Rho & Kim, 2004. (A) ♂, reproductive system; (B) ♂, head capsule and pharyngeal region external; (C) ♂, head capsule and pharyngeal region internal; (D) ♂, SIAT; (E) ♂, spicule and gubernaculum; (F) ♀, head capsule and CAT. Scale bars 20 µm.

Familia Draconematidae Filipjev, 1918

Subfamilia Draconematinae Filipjev, 1918

Genus *Tenuidraconema* Decraemer, 1989

***Tenuidraconema parvospermis* sp. n.** (Figures 3, 4, 5B, 6, 7)

Material. One holotype male ; seven paratype males ; four additional males; four paratype females; three additional females; three paratype fourth stage juveniles; seven additional fourth stage juveniles.

Type locality. Porcupine Seabight, Belgica mound Province. Coordinates: 51°24'48,2"N 11°45'55,4"W (material collected on 17/06/2000; depth: 1005 m).

Other localities. Porcupine Seabight, Belgica mound Province. Coordinates: 51°24'49,4"N 11°45'55,9"W (material collected on 17/06/2000; depth: 1000 m), 51°25'7,7"N 11°46'9,3"W (material collected on 07/05/2001; depth: 972 m) and 51°24'49"N 11°45'56.3"W (material collected on 25/05/2003; depth: 1004 m).

Habitat at type locality. A cold-water coral degradation zone on the flank and near the top of a seabed mound. Specimens were associated with sediment-clogged framework of the cold-water coral *Lophelia pertusa* (Linnaeus, 1758) and were found on dead coral fragments and on dead sponge skeletons (*Aphrocallistes bocagei* Schultze, 1886).

Other habitat. It was also found within the underlying sediment of the sediment-clogged coral framework.

Relative abundance. This species comprises 0.53% of the total nematode community at the type locality.

Etymology. The affix '*parvospermis*' is derived from the Latin adjective *parvus*, *parva*, *parvum*, which means 'small', and from the dative plural form of *sperma*, *spermae* (*i.e. spermis*), which reflects the observation that this species 'has small sperm cells'.

Measurements. Table 3.

Males

Body very slender, sigmoid, enlarged in pharyngeal region and at level of testis and vesicula seminalis (Figs. 3B, 6A). Swollen pharyngeal region 12.3-16.2% of total body length. Region between pharyngeal bulb and anterior tip of testis conspicuously long and slender: body width decreasing behind pharynx, reaching minimal width immediately posterior to pharyngeal bulb and slightly broadening again until reaching maximal width at level of vesicula seminalis. Posterior to seminal vesicle body slightly decreasing in width again and body width maintained up to cloacal opening. Abrupt decrease in body width at level of cloacal opening. Tail conico-cylindrical. Slender body region posterior to pharynx without attached ciliates.

Body completely annulated. Broadest annules in pharyngeal region and in narrow region behind pharynx. Annules not overlapping. Annules gradually decreasing in width along testis. Annules finest immediately anterior to PAT and at level of PAT. Posterior to PAT, annular width gradually increasing again and same width maintained on tail. Beginning at level of anterior tip of testis, annules laterally interrupted by narrow lateral field extending up to level of vesicula seminalis. Lateral field 67-154 µm in

length and 2.3-3.0 µm in width. Occasionally, lateral field present as local constriction of annules instead of actual interruption (Fig. 7C). One or two rows of numerous small and irregular vacuoles present on annules in pharyngeal region and slender anterior body region (Fig. 4B), one row at level of testis and around cloacal opening. Except for pharyngeal region, vacuoles may be faint and even inconspicuous. Annules in posterior body region with rough, somewhat granular edges and littered with detritus.

Ten CAT, arranged in five longitudinal rows, each row consisting of two very slender tubes with swollen insertion base and slightly swollen tip (Fig. 4B). Anteriormost CAT in each row located on posterior border of head capsule or on first annule, *i.e.* at posterior border of amphidial fovea. Second CAT in each row located either on head capsule or on annules 1-4. PAT very slender, bent backwards, with swollen base and bell-shaped tip (Fig. 3C). Width of anteriormost SlAT 0.8-1.0 µm at 10 µm from base. PAT arranged in four rows: two rows of 12-14 SlAT and two rows of 7-10 SvAT (Fig. 6C). First SlAT 38.5-53.5 µm in length, second SlAT either comparable in length or clearly shorter. Third SlAT always clearly shorter than first SlAT. Posterior to third SlAT, SlAT alternately long and short. SvAT gradually decreasing towards posterior. PAT clearly associated with glands, which appear as two longitudinal rows of several separate compartments located near insertion sites of PAT. First PAT located at 69.0-78.8% of body length. Distance between first and last PAT 10.9-15.4% of total body length.

In pharyngeal region, somatic setae arranged in 10 longitudinal rows: one mediodorsal row, two subdorsal rows, two laterodorsal rows, two lateroventral rows, two subventral rows and one medioventral row (Figs. 4B, 6E). Mediolateral setae sometimes present. Slender region posterior to pharyngeal bulb and region anterior to PAT with one mediodorsal row, two laterodorsal rows, two lateroventral rows and one medioventral row of somatic setae. Region of PAT with one mediodorsal row and two sublateral rows of somatic setae in dorsal sector. In some cases one subventral seta present in front of or behind posteriormost SlAT. Additionally, two lateroventral setae usually present behind posteriormost SlAT. These lateroventral setae usually followed by 4-5 subventral, pericloacal ('anal') setae: two pre-cloacal, two post-cloacal setae and sometimes one seta at level of cloacal opening. Anteriormost pericloacal seta slightly longer than other pericloacal setae. Tail on each side with several subventral setae and subdorsal setae, including longest somatic setae on entire body (62.5 µm in holotype). Tail tip with one short lateroventral and one short subdorsal seta on each side.

Cephalic capsule a broad truncated cone, either smooth or ornamented with small vacuoles, which may be faint (Figs. 4B, 7A). Labial sensilla papilliform. Four cephalic and 20-28 subcephalic setae, arranged in eight rows: generally two subdorsal rows of three setae, two laterodorsal rows of four setae, two lateroventral rows of two setae and two subventral rows of two setae. Next to this, scattered pores may be present near posterior border of cephalic capsule. Amphidial fovea long, between 52.4-76.0 % of length of cephalic capsule, located near posterior border of head capsule. Amphidial fovea composed of conspicuous outer loop and vague inner loop. Ventral arm in outer loop longer than dorsal arm; ventral arm in inner loop only a short bulge. Long arms of both loops join at posterior border of head capsule. Buccal cavity narrow and unarmed, surrounded by gold coloured granules. Pharynx cylindrical, with oval, muscular endbulb without thickened lumen wall. Large nerve ring

immediately in front of terminal bulb. Cardia antero-posteriorly flattened. Intestine granular, with slightly thickened brush border. Cloacal flap absent; cloacal opening sometimes ending on bulge.

Male reproductive system monorchic, with outstretched testis extending far anteriorly (testis tip located at 48.8-58.7% of total body length in holotype) (Fig. 4A). Germinal and growth zones finely granular, usually slender, situated ventrally to intestine: either medioventrally or shifted to the left or to the right. Vesicula seminalis only slightly wider than vas deferens, variable in length and located ventrally to and usually on left side of intestine. Sperm cells compact, jagged and opaque, with several large, refractive, spherical or rounded inclusions. Diameter of sperm cells 3.5 µm on average. Vas deferens granular, usually wide and located ventrally to and usually on right side of intestine. Percentage of spicule length to total body length 3.5-4.9%. Spicules arcuate, with set-off, ventrally oriented, usually beak-like capitulum (Fig. 4D). Velum well-developed, connected to base of capitulum. Gubernaculum narrow, slightly curved and parallel to spicules.

Tail very slender and conico-cylindrical, with 38-53 complete annules (49 in holotype), including long (32.8-45.4% of tail length) and pointed tail tip (Fig. 7F). Tail tip with tiny vacuoles on dorsal side and sometimes with one or two incomplete annules ventrally (one in holotype). Caudal glands inconspicuous, but ending in a common terminal outlet.

Females

Females similar to males in size and shape, although mid-body enlargement (at level of vulva) much more pronounced (Fig. 6B). Swollen pharyngeal region 12.8-16.3% of total body length. Annules broadest in pharyngeal region and in narrow region posterior to pharynx, gradually decreasing in width along anterior ovary. Finest annules at level of anterior PAT. Annules gradually increasing in width along tail. In most cases, lateral field absent or inconspicuous. When present, lateral field either as lateral interruption or lateral constriction of annules and extending from 9.6 µm in front of anterior ovary up to level of anterior ovary (width 3.0 µm; length 51 µm). Cuticular ornamentation similar as in males. Shape of CAT and PAT as in males (Fig. 7D). CAT arranged in five longitudinal rows on dorsal side, each consisting of two tubes. Anteriormost CAT in each row at posterior border of head capsule or on first annule, *i.e.* either well posterior to amphidial fovea or at level of posterior border of amphidial fovea. Second CAT in each row situated on annules 1-4. Width of anteriormost SlAT 0.9-1.2 µm at 10 µm from base of tube. PAT arranged in four rows: two rows of 12-17 SlAT and two rows of 8-13 SvAT (Figs. 3D, 6D). SlAT alternately long and short.

In pharyngeal region, somatic setae arranged in 12 or 14 longitudinal rows. Twelve rows arranged as follows: one mediodorsal row, two subdorsal rows, two laterodorsal rows, two mediolateral rows, two lateroventral rows, two subventral rows and one medioventral row. If somatic setae arranged in 14 rows, each mediolateral row replaced by one sublateral row of setae in dorsal sector and one sublateral row of setae in ventral sector. Slender region posterior to pharyngeal bulb, region anterior to PAT and region of PAT somatic setae arranged as in males, although with two subventral setae on each side at level of vulva and without medioventral setae in this region (Fig. 7E). Each side with one short seta behind posteriormost PAT. No anal setae. Tail on each side with three subventral setae and

five subdorsal setae, including longest somatic setae on entire body (47.0 µm in allotype) (Fig. 3D). Tail tip on each side with one short lateroventral and one short subdorsal setae.

Cephalic capsule a broad, truncated cone as in males, either smooth or ornamented with small vacuoles (Figs. 4C, 7B). Labial sensilla papilliform. Four cephalic setae and 23-28 subcephalic setae, arranged in eight rows: generally two subdorsal rows of three setae, two laterodorsal rows of five setae (not entirely in one row but closely together), two lateroventral rows of three setae and two subventral rows of two setae. Additional pores may be present near posterior border of head capsule. Sexual dimorphism obvious from shape of amphidial fovea: amphidial fovea in females a large, longitudinally elongated, ventrally wound spiral consisting of 2.5-2.7 coils, situated centrally on or at posterior border of cephalic capsule. Length of amphidial fovea 41.7-52.9% of head capsule length. Buccal cavity narrow and unarmed, surrounded by gold coloured granules. Digestive system as in males. Anal flap absent; anus sometimes ending on bulge.

Female reproductive system situated ventrally to intestine, slightly shifted to right side: didelphic and amphidelphic, with antidromously reflexed ovaries (Fig. 3A). Anterior ovary reflexed to posterior usually along left side, posterior ovary reflexed to anterior usually along right side. Uterus often with numerous small, jagged sperm cells with refractive rim. Vagina bipartite: proximal and distal part equal in length. Proximal part thin-walled but surrounded by strongly refractive contractor muscle. No paravulval setae.

Tail with 34-45 complete annules (42 in allotype), including long (40.5-52.4% of tail length) and pointed tail tip. Tail tip either without incomplete annules, with 1-2 incomplete annules dorsally or with one incomplete annule ventrally (no incomplete annules in allotype). Caudal glands ending in a common outlet (Fig. 7G).

Juveniles

First stage juveniles, second stage juveniles and third stage juveniles could not be distinguished from those of *T. koreensis*.

Fourth stage juveniles (Fig. 5B)

Very slender body, enlarged at level of pharynx, posterior body region only slightly swollen. Posterior swelling best developed in juvenile females. Annules in pharyngeal region ornamented with one row of irregular vacuoles. Slender region posterior to pharynx either smooth or with one row of faint vacuoles. Remainder of annules smooth. Lateral field absent, inconspicuous or present as lateral interruption of annules, located in front of genital primordium or at level of germinal and growth zones in males.

Four slender CAT (two subdorsal and two laterodorsal), with swollen base and slightly swollen tip, located on posterior border of head capsule or on annules 1-3, *i.e.* always clearly posterior to amphidial fovea. One medioventral row of nine PAT and two lateroventral rows of 6-7 PAT. PAT long, very slender, with swollen base and fine bell-shaped tip. MvAT gradually decreasing in width towards posterior. Long and short LvAT, not alternating. Width of anteriormost LvAT 0.8-1.1 µm at 10 µm of base of tube.

Somatic setae in pharyngeal region arranged in eight rows: two subdorsal rows, two laterodorsal rows, two lateroventral rows and two subventral rows. Region between pharynx and PAT with one mediodorsal row, two laterodorsal rows, two lateroventral rows and one medioventral row of somatic setae. At level of PAT somatic setae in one mediodorsal and two sublateral rows in dorsal sector. On each side, one short subventral seta sometimes present immediately in front of anus. Tail with one subventral and three subdorsal somatic setae on each side, including very long subdorsal setae. Tail tip with one short lateroventral and one short subdorsal seta on each side.

Cephalic capsule truncated cone, ornamented with small vacuoles. Four cephalic and 12-17 subcephalic setae, arranged in two subdorsal rows, two laterodorsal rows, two lateroventral rows and two subventral rows. Amphidial fovea spiral, ventrally wound, consisting of 2.1-2.6 loops, usually antero-posteriorly elongated. Amphidial fovea located centrally on head capsule. Length of amphidial fovea 34.8-49.8% of length of cephalic capsule. Digestive system as in adults. One moulting individual with fully developed spicules and spermatozoa as in males.

Tail with 35-39 complete annules, including long (51.1-58.4% of tail length) and pointed tail tip. Tail tip with tiny vacuoles. Tail tip either without incomplete annules, with 1-7 incomplete annules dorsally or with 3-6 incomplete annule ventrally.

Diagnosis

Tenuidraconema parvospermis sp. n. is characterised by the combination of the following character states: (1) all CAT located posterior to amphidial fovea; (2) 10 CAT, arranged in five longitudinal rows; (3) length of anteriormost SlAT 38.5-53.5 µm in males and 41-49 µm in females; (4) length of anteriormost SvAT 36-43.5 µm in males and 30.5-42 µm in females; (5) width of anteriormost SlAT 0.8-1.0 µm in males and 0.9-1.2 µm in females; (6) distance between first and last PAT 10.9-15.4% of total length in males; (7) SlAT alternately long and short; (8) labial sensilla papilliform; (9) amphidial fovea in males composed of an inner and an outer loop, with ventral arm of inner loop equally long as high; (10) sperm cells compact, jagged, with several large, refractive, spherical inclusions, diameter 3.5 µm on average; (11) proximal part of gubernaculum parallel to spicules and (12) 38-53 tail rings in males and 34-45 tail rings in females.

Differential diagnosis and discussion

At present, three species of *Tenuidraconema* are already described: *T. fiersi* Decraemer, 1989; *T. koreensis* Rho & Kim, 2004 and *T. philippinensis* Rho & Kim, 2005. Rho & Kim (2005d) compared the features they believed to be of diagnostic value for these three species. However, the results presented here show that some of those features are variable within a species. For example, the position of the anteriormost CAT may be on the head capsule or posterior to it in both *T. koreensis* and *T. parvospermis* sp. n. Next to this, in the Porcupine Seabight specimens of *T. koreensis*, the amphidial fovea may or may not reach the first body annules. Furthermore, the presence and position of somatic setae intermingled between the SlAT is variable in the males of *T. koreensis* from the Porcupine Seabight. The number of SlAT and SvAT is also variable and overlaps between species. Nevertheless, the different species can still be easily distinguished from each other:

Tenuidraconema fiersi shares with *T. philippinensis* the shape of the male amphidial fovea, which consists here of a single loop, whereas the fovea consists of an inner and outer loop in *T. koreensis* and *T. parvospermis*. Next to this, *T. fiersi* and *T. parvospermis* have papilliform external labial sensilla, while in the other species these sensilla are setiform. Nevertheless, *T. fiersi* clearly differs from all other species by the position of the CAT, *i.c.* all on the head capsule in *T. fiersi* and at least some located on the anteriormost annules in the other species.

Tenuidraconema philippinensis and *T. parvospermis* are clearly closely related, judging from the overall body shape and especially the shape, width and organisation of the SIAT, *i.c.* the fact that they are fine and alternating long and short. Nevertheless, *T. parvospermis* differs from this species in (1) the shape of the amphidial fovea in males, *i.c.* consisting of a double loop and (2) the tail shape (more slender in *T. philippinensis*). It also differs from both *T. philippinensis* and *T. koreensis* in the papilliform external labial sensilla and the number of CAT (10 compared to 12 in the other species). Furthermore, it can be clearly distinguished from *T. koreensis* in (1) the size and shape of the sperm cells (sperm cells in *T. koreensis* larger and with more cytoplasm), (2) the shape of the ventral arm of the inner loop in male amphidial fovea (longer in *T. koreensis*), (3) the location of the proximal part of the gubernaculum relative to spicules (bent away from spicules in *T. koreensis*) and (4) the number of tail rings (generally more in *T. koreensis*). It must be added here that the number of tail rings cannot be used as a diagnostic feature for Great Meteor Seamount specimens. Fourth stage juveniles of *T. koreensis* and *T. parvospermis* from the Porcupine Seabight area can be distinguished by (1) width of anteriormost SIAT and (2) number of tail rings. *Tenuidraconema koreensis* and *T. philippinensis* differ from each other in the shape of the male amphidial fovea and the shape, width and arrangement of the SIATs.

The four species of *Tenuidraconema* can easily be identified using the following identification key:

1) CAT located at level of amphidial fovea, *i.e.* on head capsule.....*T. fiersi* Decraemer, 1989
CAT located posterior to amphidial fovea, *i.e.* on posterior border of head capsule or posterior to head capsule.....2
2) Ten CAT, arranged in five longitudinal rows; papilliform external labial sensilla.....*T. parvospermis* sp. n.
Twelve CAT, arranged in six longitudinal rows; setiform external labial sensilla.....3
3) Amphidial fovea in males consisting of an inner and an outer loop; SIAT slender but robust, gradually decreasing in length towards the posterior.....*T. koreensis* Rho & Kim, 2004
Amphidial fovea in males consisting of a single loop; SIAT slender alternating long and short.....*T. philippinensis* Rho & Kim, 2005

According to Decraemer (1989), the genus *Tenuidraconema* Decraemer, 1989 is, among other character states, characterised by the presence of a lateral field. However, this feature should be utilised with caution as the lateral field may be inconspicuous or absent even in adults of both *T. koreensis* and *T. parvospermis* sp. n. Moreover, it may be present as either a lateral interruption of the

annules or as a lateral differentiation of the cuticle. The location of CAT relative to the head capsule is variable within the genus, which is an important observation given the diagnostic importance Decraemer *et al.* (1997) have given to this feature for the distinction between genera of the family Draconematidae. This is however also the case in the genus *Dracognomus* Allen & Noffsinger, 1978.

Light-microscopic morphology of sperm cells is not commonly used as a diagnostic feature in nematode taxonomy. Moreover, only few studies have attempted to construct a classification based on nematode sperm types (for an overview, see Justine, 2002) and in most cases phylogenetic studies based on nematode sperm deal with ultrastructural aspects and spermatogenesis (Yushin & Malakhov, 2004). However, sperm morphology can be used here as a diagnostic feature to distinguish between *T. koreensis* and *T. parvospermis*: the sperm cells of the se two species are strikingly different from each other and each type consequently occurs in individuals with either 10 or 12 CAT. The same is true for sperm cells found in the uterus of females of these two species.

Emended genus diagnosis

Draconematinae. Body slender, sigmoid, with swollen pharyngeal region, 8-16.4% of total body length. Body cuticle at level of pharynx, on slender body region posterior to pharynx, at level of testis and around cloacal opening with vacuolar ornamentation. Cuticle at mid-body interrupted by a conspicuous or inconspicuous lateral field. Ten or twelve CAT with widened base and slightly enlarged tip, located either on head capsule or within one head capsule width posterior to amphidial fovea. Amphidial fovea loop-shaped or consisting of an inner and an outer loop in males, spiral in females and juveniles. Pharynx cylindrical with elongated, muscular endbulb and with or without less pronounced anterior swellings, *i.c.* around mid-corpus and/or or at level of cephalic capsule. Endbulb without thickened lumen wall. Buccal cavity short and narrow, without teeth. Tail with numerous annules.

Juveniles

First, second and third stage juveniles of both *T. koreensis* and *T. parvospermis* sp. n. could not be distinguished from each other. These juvenile stages are described below (measurements in Table 4).

Material. Six first stage juveniles; 14 second stage juveniles; ten third stage juveniles.

First stage juveniles (Fig. 8A)

Slender body, slightly s-shaped and only slightly enlarged at level of pharynx. Body finely annulated. No adhesion tubes. On each side one mediolateral somatic seta at level of pharynx and one shorter mediolateral seta on tail. Head capsule short, anteriorly with six hook-shaped labial sensilla. Four cephalic setae; no subcephalic setae. Amphidial fovea a tiny circle (diameter 1.4-1.9 µm), situated posterior to head capsule.

Tail with 56-64 complete annules, including pointed tail tip. Tail tip smooth, with conspicuous spinneret, taking up only 6.3-12.5% of tail length. Tail tip either with four incomplete annules dorsally or with five incomplete annules ventrally.

Second stage juveniles (Fig. 8B)

Very slender body, enlarged at level of pharynx. Entire body finely annulated; no cuticular ornamentation. Lateral field absent or present either as local differentiation of cuticle or lateral interruption of annules, between first dorsal curvature and ventral curvature.

One robust, mediodorsal CAT, broadest at its base and gradually decreasing in width, with barely swollen tip, located on posterior border of head capsule or on annules 1-3, *i.e.* always well posterior to amphidial fovea. Two lateroventral rows of two PAT. PAT long and slender, with slightly swollen base and fine bell-shaped tip. Width of anteriormost LvAT 1.0-1.8 µm at 10 µm of base of tube.

Somatic setae in pharyngeal region arranged in six rows: one mediodorsal row, two laterodorsal rows, two lateroventral rows and one medioventral row. Region between pharynx and PAT with two laterodorsal rows and two lateroventral rows of somatic setae. At level of PAT somatic setae on two sublateral rows in dorsal sector. Immediately in front of anus, one lateroventral setae present on both sides. Tail with one very long subdorsal somatic seta on each side. Tail tip with one mediodorsal seta.

Cephalic capsule dome-shaped, sometimes ornamented with small vacuoles. Labial region usually clearly set-off immediately anterior to amphidial fovea. Four cephalic and four subcephalic setae: on each side one laterodorsal subcephalic seta immediately posterior to amphidial fovea and one subdorsal subcephalic seta at posterior border of cephalic capsule. Amphidial fovea ventrally wound spiral, consisting of 1.4-1.9 coils, located anteriorly on head capsule. Length of amphidial fovea 35.2-54.8% of length of cephalic capsule.

Tail with 30-52 complete annules, including long (42.6-54.8% of tail length) and pointed tail tip. Tail tip ornamented with vacuoles. Tail tip either without incomplete annules, with 1-11 incomplete annules dorsally or with three incomplete annule ventrally.

Third stage juveniles (Fig. 8C)

Slender body, enlarged in pharyngeal region. Annules in pharyngeal region sometimes with one row of tiny, irregular vacuoles. All other annules completely smooth. Lateral field absent or present either as lateral interruption or local differentiation of cuticle, extending up to anterior part of genital primordium.

Three slender CAT with swollen base and slightly swollen tip: one mediodorsal tube and two laterodorsal tubes. All CAT located on posterior border of head capsule or on annules 1-7, *i.e.* always posterior to amphidial fovea. Two lateroventral rows of 5 PAT. PAT long, relatively slender, with slightly swollen base and fine bell-shaped tip. Width of anteriormost LvAT 0.9-1.6 µm at 10 µm of base of tube. Somatic setae in pharyngeal region arranged in eight rows: two subdorsal rows, two laterodorsal rows, two lateroventral rows and two subventral rows. Region between pharynx and PAT with one mediodorsal row, two laterodorsal rows and two lateroventral rows of somatic setae. At level of PAT somatic setae on one mediodorsal and two sublateral rows in dorsal sector. Immediately in front of anus one short subventral seta present or absent on each side. Tail with two subdorsal setae on each side, including very long subdorsal seta. Tail tip with few short subdorsal and subventral setae.

Cephalic capsule truncated cone, ornamented with small vacuoles. Four cephalic and 7-10 subcephalic setae, arranged in two subdorsal rows, two laterodorsal rows, two lateroventral rows and

two subventral rows. Amphidial fovea spiral, ventrally wound, consisting of 2.1-2.2 coils. Amphidial fovea located centrally or anteriorly on head capsule. Length of amphidial fovea 36.1-57.8% of length of cephalic capsule. Digestive system as in adults.

Tail with 39-57 complete annules, including long (47.0-58.7% of tail length) and pointed tail tip. Tail tip ornamented with vacuoles. Tail tip either without incomplete annules, with 2-4 incomplete annules dorsally or with 1-2 incomplete annule ventrally.

	Holotype male	Males (n = 10)	Allotype female	Females (n = 6)	Juvenile stage IV (n = 9)
L	930	750-1060 (905)	895	810-965 (925)	445-735 (640)
Hdw	18.5	18.5-21 (19.8)	20.5	19.5-21 (20.6)	17.5-18.5 (18.0) [8]
Hdl	17.5	15-19 (16.7)	17	16.5-20 (18)	13-15.5 (14.3) [8]
Amphw	5.5	4.5-6 (5.5)	6.5	6-7.5 (7) (5)	5-6.5 (5.8) [8]
Amphl	10.5	9.5-11.5 (10.3)	9	8.5-9.5 (8.7)	5.5-7 (6.1) [8]
Amph%	29	24.4-30.1 (27.8)	31.2	29.6-38.3 (34.5) [5]	29.0-36.7 (32.1) [8]
ph	76	67.5-80.5 (74.8)	77	71.5-80.5 (74.8)	50-65 (61.0) [6]
MdCATa	16.5	15-19.5 (17.1) [9]	16.5	17-19.5 (18.1)	
MdCATp	24	20-25 (22.2) [9]	26.5	21-25 (22.9)	
SdCATa	17.5	17-21 (18.8) [9]	17.5	16.5-20 (18.5)	17-20.5 (18.1) [8]
SdCATp	22.5	21.5-26 (23.2) [9]	25.5	21.5-29 (24.2)	
LdCAT					18.5-24.5 (21.2) [7]
SlCATa	20.5	17-23.5 (21.1)	20	20.5-22 (21.2)	
SlCATp	21	23-29 (25.3)	22.5	24.5-27.5 (25.9)	
SlATa	46	38.5-53.5 (46.2)	54	41-49 (44.7)	
SlATp	27.5	25-46.5 (34.4)	39	28.5-41 (35.6)	
LvATa					29-47 (38.1)
LvATp					24-36 (31.2)
SvATa	40.5	36-43.5 (39.4)	37	30.5-42 (38.3)	
SvATp	19	17-24 (21.4)	19	16.5-22.5 (19.6)	
MvATa					24-37 (32.5)
MvATp					12.5-22.5 (18.8) [8]
tail	102.5	87.5-129.5 (111.1)	105	94.5-122.5 (107.7)	68-87 (79.5)
tmr	39	36-43 (41.3) [9]	53.5	49.5-53.5 (51.2)	40-49.5 (44.4)
mbd ph	30.5	21.5-31.5 (29.2)	31.5	29.5-33 (31.1)	25.5-36 (29.8)
mbd	32.5	25.5-37 (29.6)	51.5	38.5-52 (48.8)	19.5-38.5 (27.7)
(mbd)	12	11.5-13 (12.3)	12	12-13.5 (12.9)	10-15 (12.9)
mbd/(mbd)	2.7	1.9-3.0 (2.4)	4.3	2.9-4.4 (3.8)	1.5-2.7 (2.2)
abd	18	17.5-20 (18.8)	16.5	15-18 (15.7)	12.5-18.5 (14.8)
spic	38	31-39.5 (36.6)			
gub	12	8-12.5 (10.4)			
V%			64.7	63.3-64.6 (64.0)	
a	28.4	28.0-36.3 (30.8)	17.4	18.1-20.9 (19.1)	17.0-29.6 (24.0)
b	12.2	10.4-13.2 (12.1)	11.6	11.4-13.5 (12.4)	8.9-11.0 (10.3) [6]
c	9.1	7.6-10.2 (8.2)	8.5	7.8-9.1 (8.6)	6.4-9.3 (8.1)

Table 3. Measurements of *Tenuidraconema parvospermis* sp. n. All absolute values in µm. The number of specimens measured, when different from the total number of specimens, is indicated between brackets in superscript.

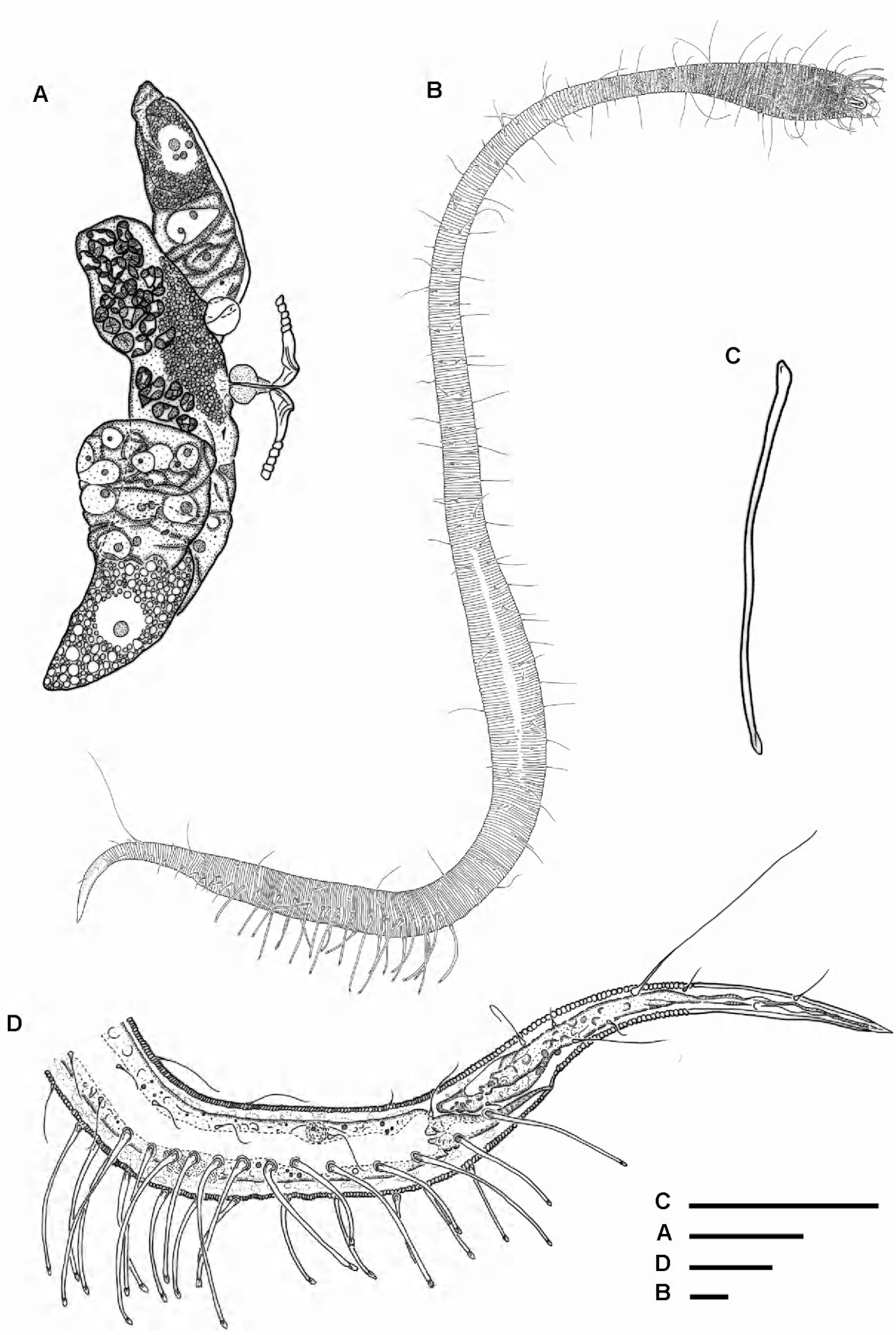


Fig. 3. *Tenuidraconema parvospermis* sp. n. (A) ♀, reproductive system; (B) ♂, habitus external; (C) ♂, SIAT; (D) ♀, posterior body region and tail. Scale bars 20 µm.

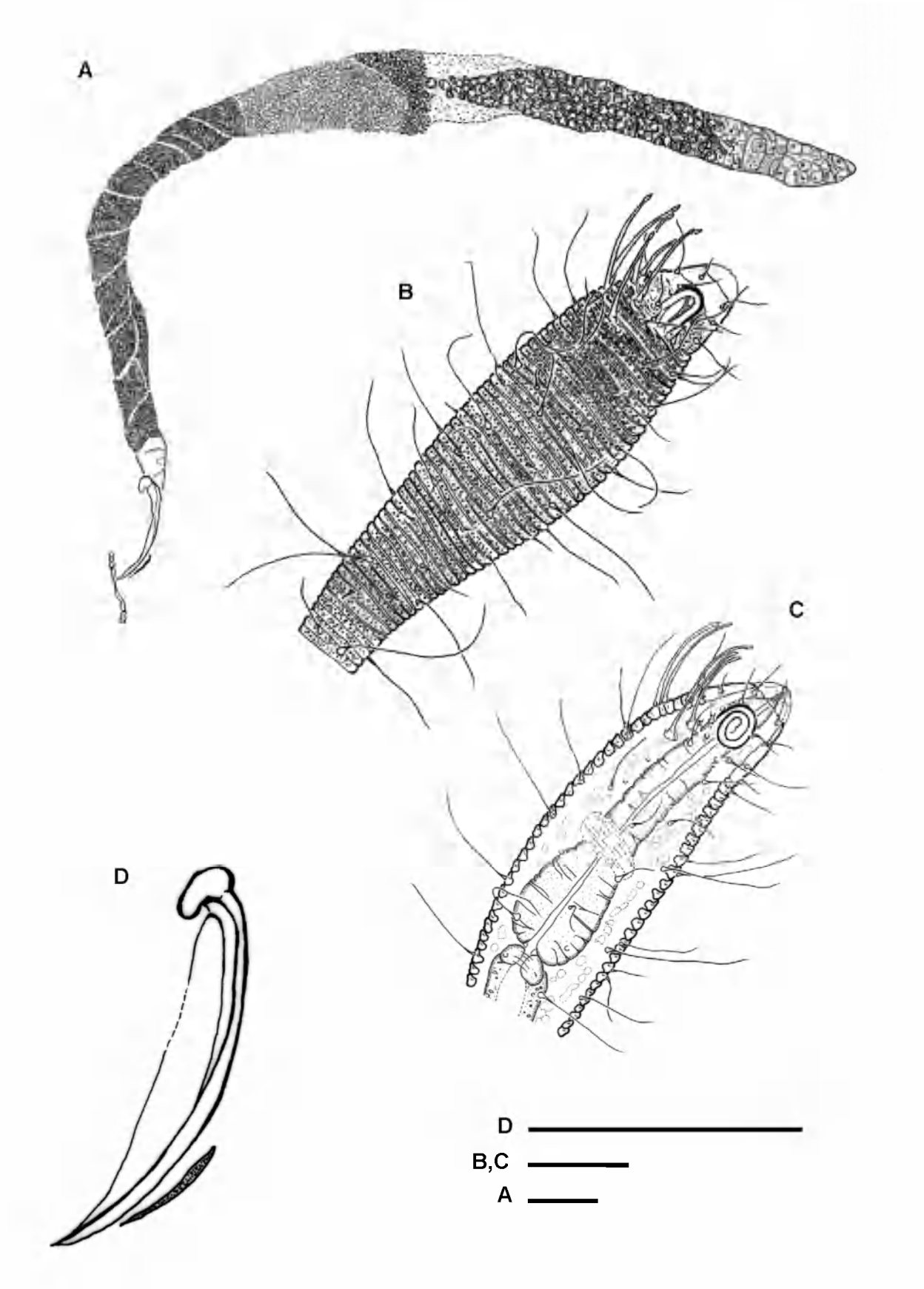


Fig. 4. *Tenuidraconema parvospermis* sp. n. (A) ♂, reproductive system; (B) ♂, head capsule and pharyngeal ragion external; (C) ♀, head capsule and pharyngeal region internal; (D) ♂, spicule and gubernaculum. Scale bars 20 µm.

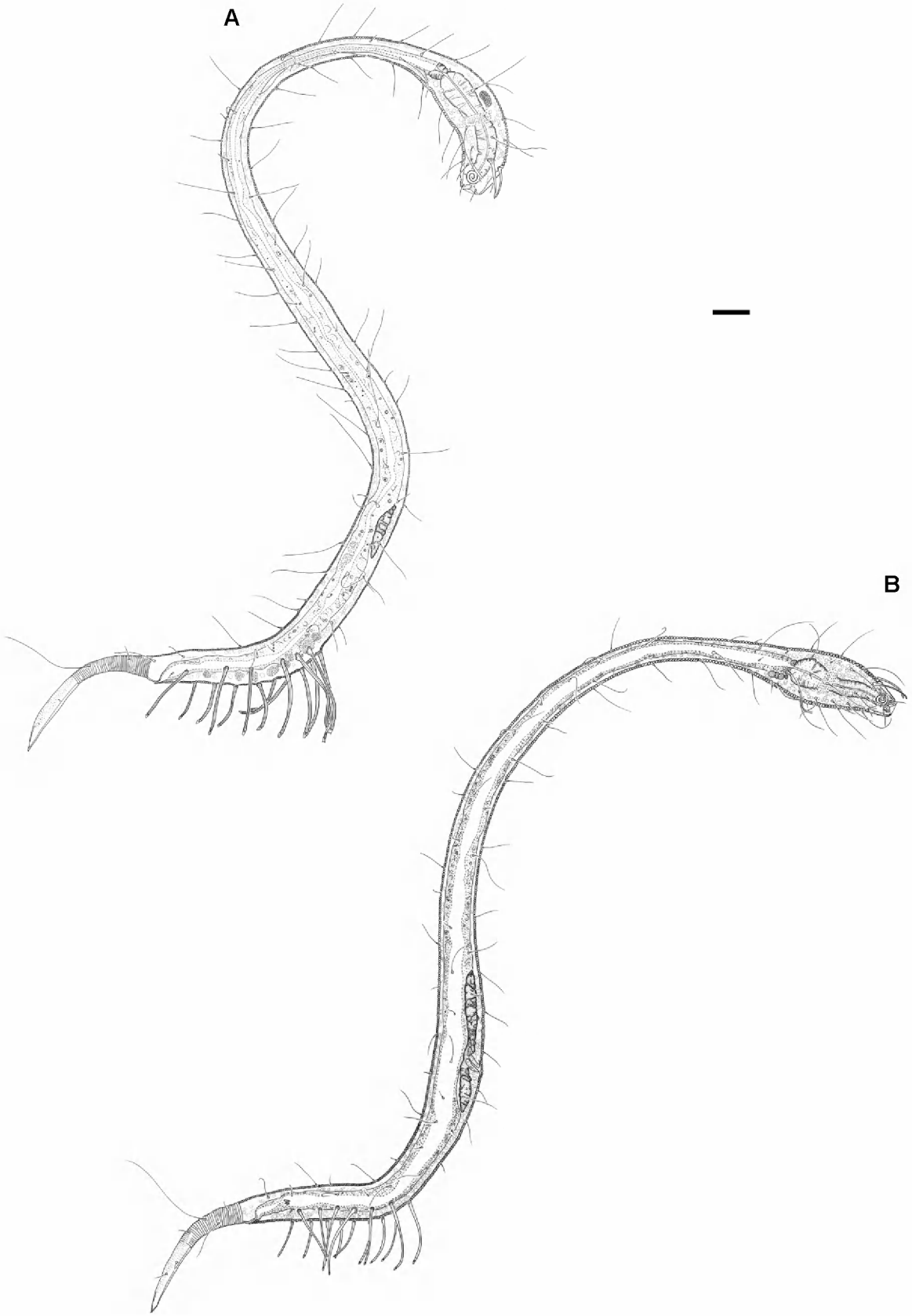


Fig. 5. (A) *Tenuidraconema koreensis* Rho & Kim, 2004, fourth stage juvenile; (B) *T. parvospermis* sp. n., fourth stage juvenile. Scale bar 20 µm.

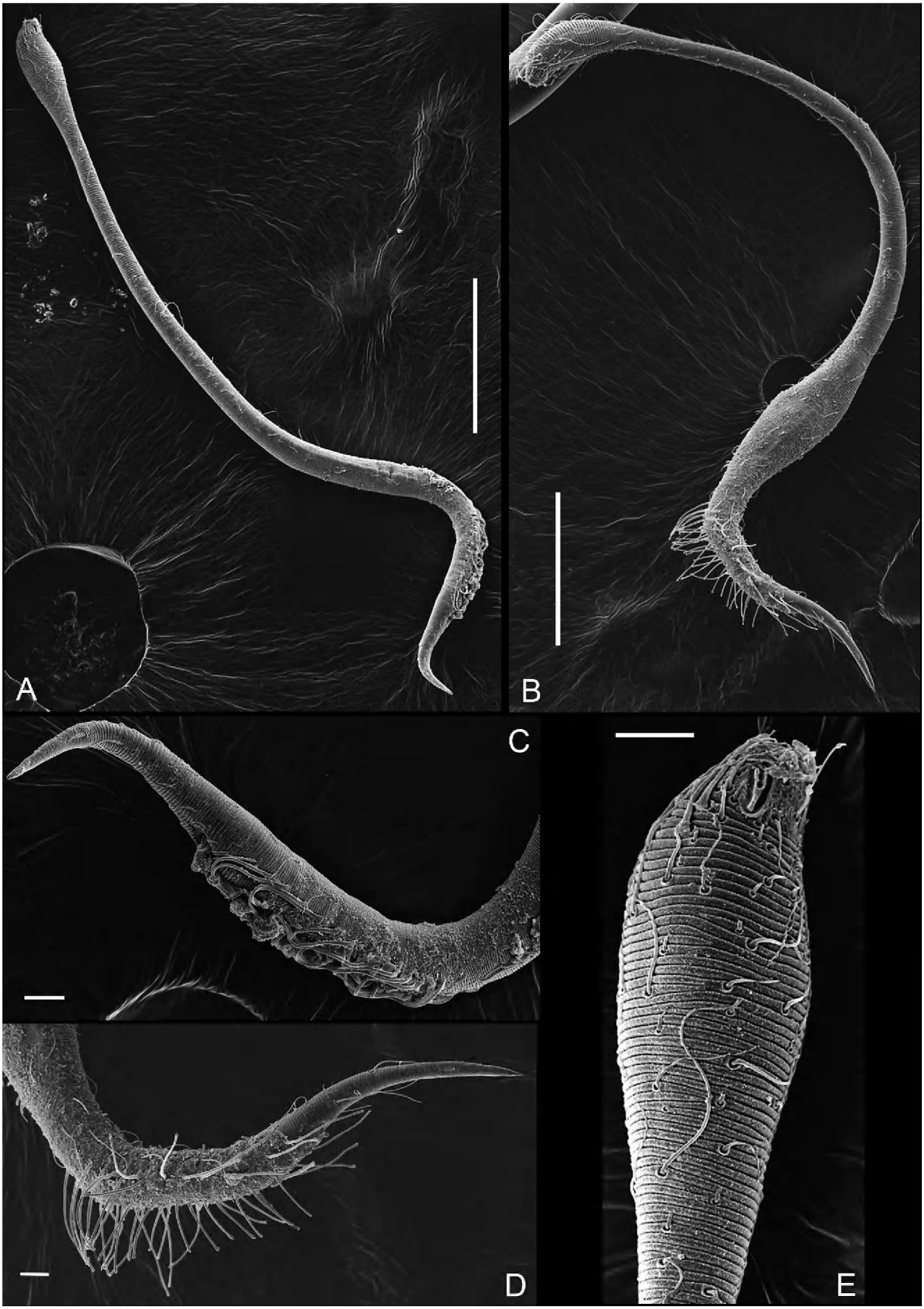


Fig. 6. *Tenuidraconema parvospermis* sp. n. (A) ♂, habitus; (B) ♀, habitus; (C) ♂, posterior body region and tail ; (D) ♀, posterior body region and tail; (E) ♂, head capsule and pharyngeal region. Scale bars: 100 µm (A,B); 10 µm (C-E).

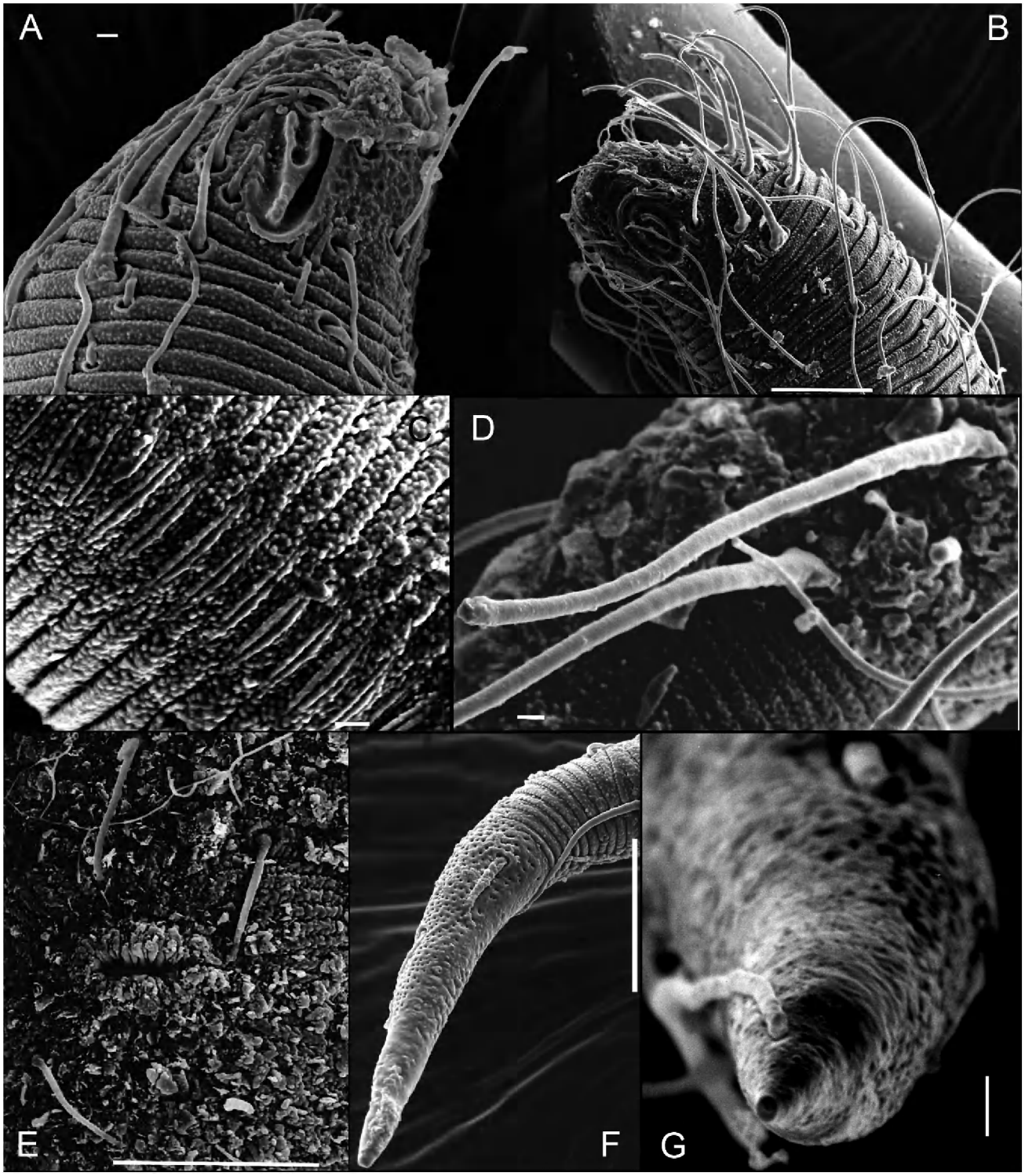


Fig. 7. *Tenuidraconema parvospermis* sp. n. (A) ♂, head capsule and CAT (lateral view); (B) ♀, head capsule and CAT (lateral view); (C) ♂, lateral field; (D) ♀, PAT; (E) ♀, vulva; (F) ♂, tail tip; (G) ♀, tail tip. Scale bars: 10 µm (B,E,F); 1 µm (A,C,D,G).

	Juvenile stage III (n = 10)	Juvenile stage II (n = 10)	Juvenile stage I (n = 5)
L	380-685 (555)	315-490 (380)	240-295 (260)
Hdw	15.5-19 (17.1) [9]	12.5-16 (14.3)	
Hdl	12.5-15 (13.7) [9]	7-13 (10.9) [9]	
Bda			10.5-13 (11.7) [4]
Amphw	4.5-7 (5.8) (9)	4-6 (4.8) [9]	1.4-1.6 (1.5) [3]
Amphl	5.5-8 (6.3) (9)	4-5.5 (4.6) [8]	1.4-1.9 (1.5) [4]
Amph%	29.4-38.9 (34.0) [9]	30.4-38.3 (33.6) [9]	13.1-13.4 (13.3) [3]
ph	56.5-69.5 (62.1) [9]	43.5-63 (53.6)	40.5-56 (48.8)
MdCAT	15-21.5 (18.5) [8]	13.5-19 (16.4) [9]	
LdCAT	16-23.5 (21.1) [9]		
LvATa	33-50 (42.7)	32-49 (40.9)	
LvATp	21-38.5 (30.2)	28.5-49 (39.1)	
tail	66.5-86 (77.3)	52.5-73 (60.5)	50.5-60 (54.9) [4]
tmr	32.5-45 (39.8)	24.5-35 (29.8)	3.5-6.5 (5.5)
mbd ph	20.5-29.5 (25.6)	18-26 (21.6)	16.5-23 (19.4)
mbd	14-23 (18.4)	12.5-19.5 (14.9)	12-14 (12.7)
(mbd)	8.5-13 (10.9)	9-12 (10.4)	9-14.5 (11.0)
mbd/(mbd)	1.6-1.9 (1.7)	1.3-1.6 (1.4)	1.2-1.4 (1.3)
abd	9.5-15 (12.4)	8.5-13.5 (11.1)	10-13 (10.9) [4]
a	16.4-37.4 (30.7)	16.2-35.4 (26.5)	17.7-22.5 (19.9)
b	6.5-10.1 (8.9)	5.9-7.8 (7.1)	4.9-6.2 (5.4)
c	5.7-8.3 (7.2)	5.6-7.9 (6.3)	4.5-5.0 (4.8) [4]

Table 4. Measurements of juveniles of *Tenuidraconema*. All absolute values are in µm. The number of specimens measured, when different from the total number of specimens, is indicated between brackets in superscript.

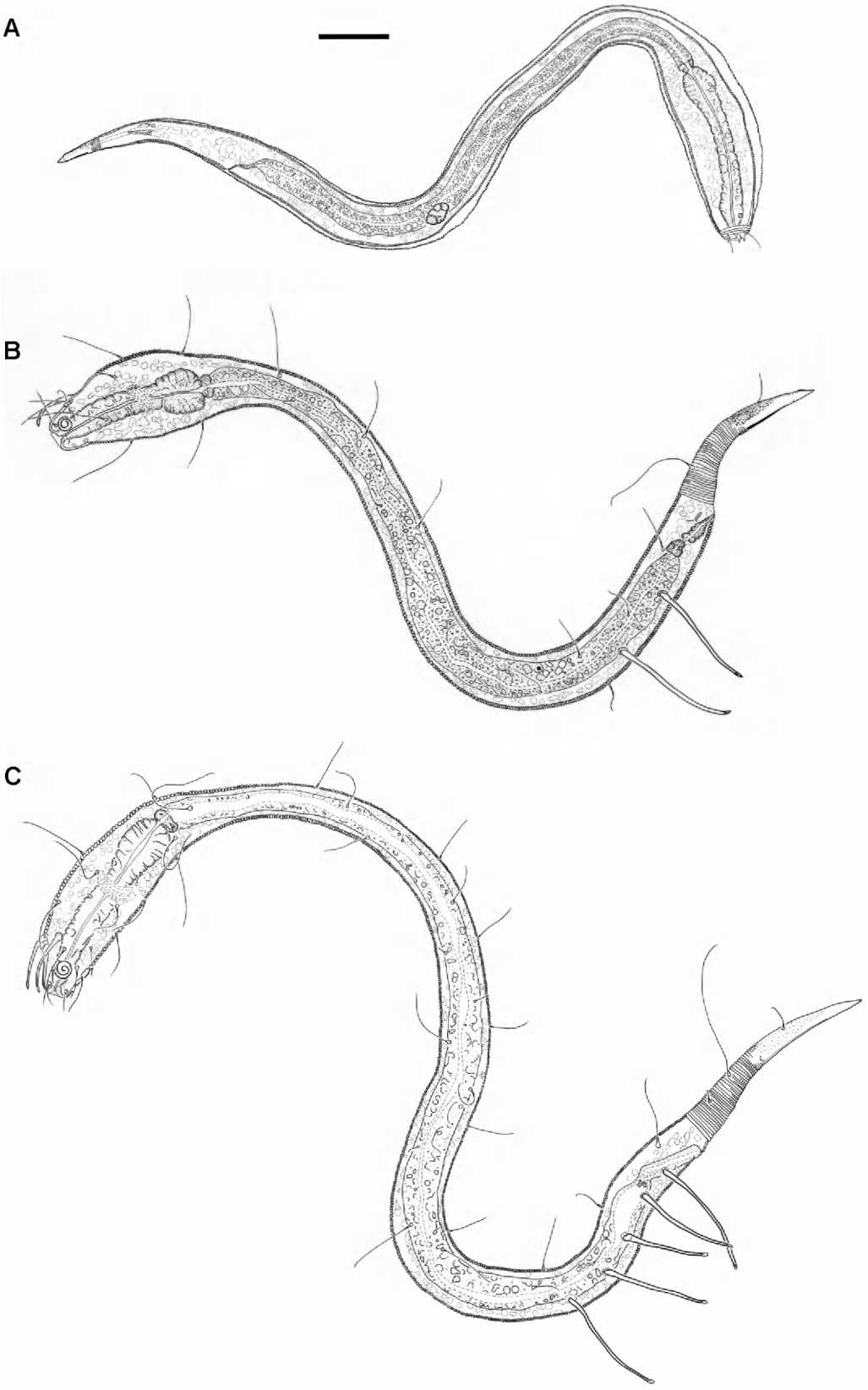


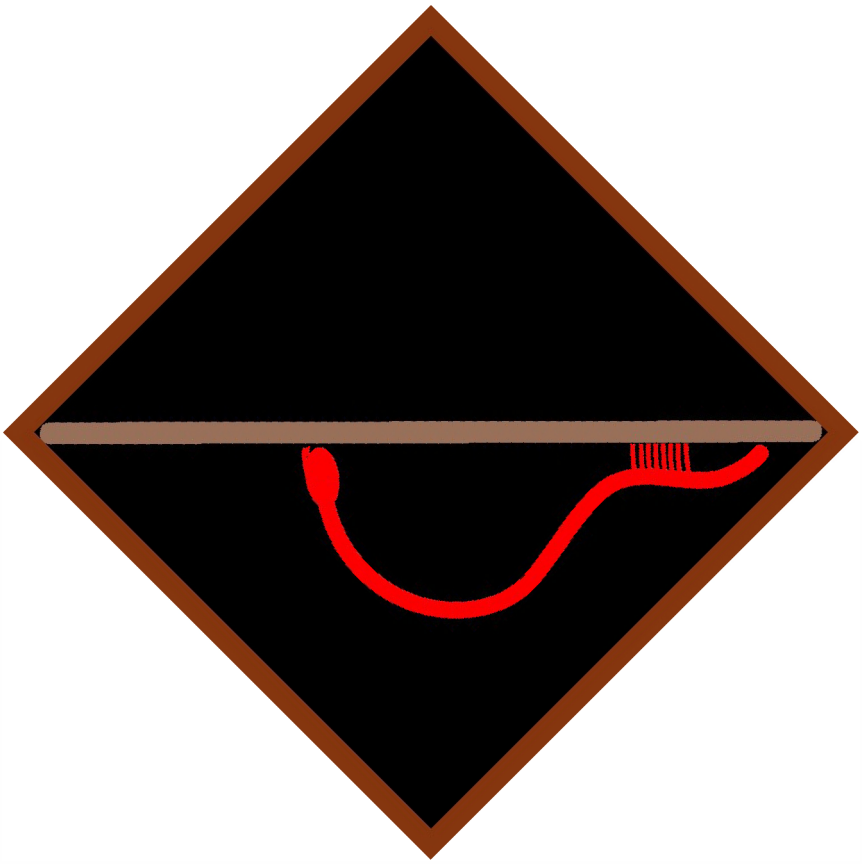
Fig. 8. *Tenuidraconema* sp. (A) first stage juvenile; (B) second stage juvenile; (C) third stage juvenile. Scale bar 20 µm.

7.6. ACKNOWLEDGEMENTS

The authors wish to thank the people from the Renard Centre of Marine Geology, as well as the crew of the RV Belgica, for a fruitful collaboration. Special thanks go to Dr Véronique Vanquickelberghe and Guy De Smet for their sampling efforts, Wies Gyselinck, Annick Van Kenhove and Bart Beuselinck for making lots of excellent Cobb slides and Rita Van Driessche for making high quality scanning micrographs. The authors are also very grateful to Dr Gunnar Gad for providing information and specimens from the Great meteor Seamount, and to Dr Vladimir Yushin for interesting discussions on sperm cell morphology. The first author acknowledges a Ph.D. grant provided by the Fund for Scientific Research (FWO-Flanders), Belgium. This research was supported by the HERMES project (EC Sixth Framework Research Programme under the priority 'Sustainable Development, Global Change and Ecosystems') and the national FWO research project G.0199.03.

CHAPTER 8

DRACONEMATIDAE FROM COLD-WATER CORALS IN THE PORCUPINE SEABIGHT: THE GENUS *CYGNONEMA* ALLEN & NOFFSINGER, 1978



Paper *submitted*

Raes, M., Decraemer, W., Vanreusel, A.

Draconematidae from cold-water corals in the Porcupine Seabight: the genus *Cygnonema* Allen & Noffsinger, 1978

Organisms, Diversity and Evolution

8.1. ABSTRACT

Two new and closely related species of *Cygnonema* are described from a cold-water coral degradation zone in the Porcupine Seabight (NE Atlantic). Both species differ from *C. steineri* Allen & Noffsinger, 1978 by more pronounced pharyngeal and posterior swellings, a smaller body, a shorter pharynx in relation to body length, a higher number of CAT and the absence of a dorsal tooth. *Cygnonema verum* sp. n. differs from *C. belgicae* sp. n. because it is larger, because of a relatively larger head capsule, a higher number of CAT, a more anteriorly positioned anteriormost laterodorsal CAT, a higher number of PAT, the presence of setiform external labial sensilla, a higher number of subcephalic setae and a more anterior position of the amphidial fovea on the head capsule. Males of *C.verum* sp. n. are easily recognised by the presence of two large subventral, precloacal corniform setae. They also differ from males of *C. belgicae* sp. n. in the larger amount of cytoplasm in the sperm cells, a knob-like capitulum (in contrast to the beak-shaped capitulum in *C. belgicae* sp. n.) and a relatively shorter tail tip. The genus diagnosis is adjusted and a dichotomic identification key is provided.

Key words: marine nematodes, taxonomy, *Cygnonema*, Porcupine Seabight, cold-water corals

8.2. INTRODUCTION

The monotypic genus *Cygnonema* Allen & Noffsinger, 1978 was originally described by Allen & Noffsinger (1978) from McMurdo Sound, Antarctica, where the type species *C. steineri* Allen & Noffsinger, 1978 was collected at a depth of 457 m. It is the most slender of all draconematid genera and can be distinguished by typical, non-modified cephalic adhesion tubes (*i.e.* with enlarged base), extending up to more than two head capsule diameters along the cervical region (Decraemer *et al.*, 1997).

This paper is part of an extensive study dealing with the nematofauna associated with a cold-water coral degradation zone in the Porcupine Seabight (continental slope, northeast Atlantic Ocean). Compared to the associated sediment, the coral fragments themselves are characterised by higher abundances of Epsilonematidae and Draconematidae (Raes & Vanreusel, *in press*), which is mainly attributed to their particular way of locomotion and capacity for attachment (Stauffer, 1924; Lorenzen, 1973a). Draconematidae use both Cephalic Adhesion Tubes (CAT) and Posterior Adhesion Tubes (PAT) for attachment to the coral surface. Several new species of Epsilonematidae have already been described from the same location (Raes *et al.*, 2003; Raes *et al.*, *in press*). In the present paper, two new and closely related species of *Cygnonema* are described and a dichotomic identification key for the genus is provided.

8.3. MATERIALS AND METHODS

The type material and additional specimens were collected from dead coral fragments of *Lophelia pertusa* (Linnaeus, 1758) and, to a lesser extent, *Madrepora oculata* Linnaeus, 1758, skeletons of *Aphrocallistes bocagei* Scultze, 1886 and the sediment directly beneath these large biogenic substrata. Material was collected with a NIOZ box corer (diam. 32 cm) during the June 2000 and May 2001 sampling campaigns of the RV Belgica. Box cores were taken on the top and slope of one seabed mound situated in the Belgica mound province of the Porcupine Seabight: Box IV 2000 (51°24'48,2"N 11°45'55,4"W; depth: 1005 m), Box V 2000 (51°24'49,4"N 11°45'55,9"W; depth: 1000 m) and Box IV 2001 (51°25'7,7"N 11°46'9,3"W; depth: 972 m). The Porcupine Seabight is a large embayment of the European continental slope, located in the North-East Atlantic, southwest of Ireland. Living cold-water coral framework (mainly *Lophelia pertusa*) and associated fauna is present on the mounds in the Belgica mound province. Our samples were taken in the sediment-clogged cold-water coral framework facies (Freiwald *et al.*, 2002) and contained mainly dead material. After removal of the large biogenic substrata, three sediment cores (surface area: 10 cm^2) were pushed in the sediment of each box core. The sediment consisted of fine to medium sand but was poorly sorted, containing small coral and sponge fragments as well as some mollusc-shell fragments and echinoid radiolas. All material was fixed with a 4% neutralised formalin solution.

Each coral and sponge fragment was rinsed thoroughly over a 1 mm and a 32 µm sieve to separate macrofauna and meiofauna. Meiofauna was extracted from the underlying or remaining sediment by density gradient centrifugation, using Ludox (a colloidal silica polymer; specific gravity 1.18) as a flotation medium (Heip *et al.*, 1985; Vincx, 1996). Material was stained with Rose Bengal. Nematodes were individually picked out from the meiofauna and subsequently mounted onto slides, using the formalin-ethanol-glycerol technique described by Seinhorst (1959) and Vincx (1996). Detailed morphological observation was carried out with a Leica DMLB light microscope. A Leitz Dialux 20 microscope, Sanyo CCD video camera and the Quantimet 500 software were utilised for measurements. Scanning electron micrographs were taken from the glycerol fixed specimens. After ultrasonic treatment (to remove detritus attached to the body) the specimens were transferred to OsO_4, dehydrated, subjected to critical point drying and coated with gold particles.

Type material is deposited in the collections of Ghent University, Museum voor Dierkunde (UGent), the Koninklijk Belgisch Instituut voor Natuurwetenschappen in Brussels (KBIN) and the Natural History Museum in London (NHM). Non-type material is indicated as 'additional material' throughout the text.

8.4. ABBREVIATIONS USED

L: total body length

Hdw: maximal width of head capsule

Hdl: length of head capsule

Bda: body width at level of amphidial fovea (in first stage juveniles only)

Amphw: width of amphidial fovea

Amphl: length of amphidial fovea

Amph%: (Amphw / Hdw)*100

ph: pharyngeal length, measured from anterior end of head capsule up to posterior border of pharyngeal bulb, lips (when protruding) and cardia not included

MdCAT: length of mediodorsal cephalic adhesion tube

SdCATa: length of anteriormost subdorsal cephalic adhesion tube

SdCATp: length of posteriormost subdorsal cephalic adhesion tube

LdCAT: length of laterodorsal cephalic adhesion tube

SlCATa: length of anteriormost sublateral cephalic adhesion tube

SlCATp: length of posteriormost sublateral cephalic adhesion tube

SlATa: length of anteriormost sublateral posterior adhesion tube

SlATp: length of posteriormost sublateral posterior adhesion tube

SvATa: length of anteriormost subventral posterior adhesion tube

SvATp: length of posteriormost subventral posterior adhesion tube

MvATa: length of anteriormost medioventral posterior adhesion tube

MvATp: length of posteriormost medioventral posterior adhesion tube

Corn-set: length of precloacal corniform setae

tail: tail length

tmr: length of tail tip

mbd ph: body diameter at level of pharyngeal bulb

mbd: maximal diameter of posterior body region

(mbd): minimal body diameter

mbd/(mbd): proportion of minimal body diameter to maximal diameter of posterior body region

abd: body diameter at level of anal or cloacal opening

spic: length of spicule, measured along the arc

gub: length of gubernaculum

V%: position of vulva, expressed as a percentage of L, measured from anterior end

a: de Man a-ratio, *i.e.* L / mbd

b: de Man b-ratio, *i.e.* L / ph

c: de Man c-ratio, *i.e.* L / tail

8.5. DESCRIPTIONS

Familia Draconematidae Filipjev, 1918

Subfamilia Prochaetosomatinae Allen & Noffsinger, 1978

Genus *Cygnonema* Allen & Noffsinger, 1978

***Cygnonema verum* sp. n.** (Figures 1-3)

Material. Holotype male; three paratype males; one allotype female; two paratype second stage juveniles; five paratype third stage juveniles; two paratype fourth stage juveniles.

Type locality. Porcupine Seabight, Belgica mound Province. Coordinates: 51°24'48,2"N 11°45'55,4"W (material collected on 17/06/2000; depth: 1005 m).

Habitat at type locality. A cold-water coral degradation zone on the flank and near the top of a seabed mound. Specimens were associated with sediment-clogged framework of the cold-water coral *Lophelia pertusa* (Linnaeus, 1758) and were found on dead coral fragments.

Relative abundance. This species comprises 0.26% of the total nematode community at the type locality.

Etymology. "*verum*" is derived from the Latin adjective *verus*, *vera*, *verum*, meaning "real". Compared to *Cygnonema steineri* Allen & Noffsinger, 1978 this new species, with its posteriorly more enlarged body and its broader pharyngeal region, has a more obvious resemblance with a floating swan (*Cygnonema* means: "swan nematode")

Measurements. Table 1.

Males

Body s-shaped, enlarged at level of pharynx and along reproductive system in posterior body half (Fig. 1A). Head capsule and anterior part of pharyngeal region conspicuously narrow. Width gradually increasing along pharynx, reaching maximal width immediately anterior to pharyngeal bulb (Fig. 2B). Behind this, body width gradually decreasing again and minimal body width reached immediately anterior to intestine. Posteriorly, body very slender but gradually increasing in width again until maximal width at level of vesicula seminalis. Posterior to vesicula seminalis body width constant, only decreasing again between corniform setae and tail. Tail conico-cylindrical. Swollen pharyngeal region 11.9-12.5% of total body length. Body with fine transverse striation, hereafter indicated as 'annulation'. Broadest annules immediately posterior to head capsule; finest annules at level of testis. All annules smooth. Posterior body region often littered with fine detritus.

CAT (14-16) arranged in four longitudinal rows: two laterodorsal rows consisting of two tubes and two subdorsal rows of 5-6 tubes (Fig. 2B). CAT slender but strongly built, with enlarged base; gradually decreasing in width up to the slightly swollen, fusiform tip. Anteriormost tubes in all four rows on annules 4-6. Posteriormost tubes in laterodorsal rows on annules 9-11 and posteriormost tubes in subdorsal rows on annules 23-32. Robust PAT with swollen base and well-developed bell-shaped tip, arranged in two rows of 9-12 SlAT and two subventral rows converging towards posterior, together consisting of 24-28 SvAT. Total number of PAT 48-51. Width of anteriormost SlAT 1.8-2.7 µm at 10µm from base of tube. PAT gradually decreasing in length towards posterior. Glands associated with PAT situated either on right or left side of vas deferens. Each gland with duct connecting it to PAT. Anteriormost PAT situated at 73.6-78.5% of body length. Region with PAT taking up 7.9-8.6% of total body length.

Somatic setae in pharyngeal region arranged in 12 rows: one mediodorsal row of short setae, two subdorsal and two laterodorsal rows of long setae, two mediolateral rows of short setae, two lateroventral and two subventral rows of long setae and one medioventral row of short setae (Fig. 2B). Some pores may be present between laterodorsal and mediolateral rows. Body between pharyngeal region and region of PAT with one mediodorsal row, two laterodorsal rows, two lateroventral rows and

one medioventral row of long somatic setae. Lateroventral setae alternating long and short. In region of PAT somatic setae arranged in one mediodorsal row, two sublateral rows in dorsal sector and two sublateral rows in line with SIAT. At level of corniform setae one or two sublateral setae and one subventral seta on each side. Two or four subventral setae between this subventral seta and cloacal opening on each side. On each side, one subventral seta at level of cloacal opening. One small lateroventral seta may be present anterior to cloacal opening on each side. Tail with four or six subventral setae, two very long (broken off in holotype; 57 and 66.5 µm in paratype male) subdorsal setae and several tiny subdorsal setae on each side. Tail tip on each side with one lateroventral and one tiny subdorsal seta.

Cephalic capsule smooth, bullet-shaped; labial region protruded (Fig. 2D). Head capsule length 16.1-16.9% of pharynx length; head capsule width 42.1-47.0% of pharynx width. Labial region with numerous small rod-like protrusions. Six small setiform external labial sensilla, four cephalic setae and 15-18 subcephalic setae. Subcephalic setae on each side located subdorsally, subventrally and at both sides of amphidial fovea. Additional setae may occur scattered on head capsule. Amphidial fovea question mark shaped, with longer dorsal arm, located centrally on head capsule. Length of amphidial fovea 30.9-34.6% of head capsule length. Buccal cavity tiny, elongated. Teeth absent. Anterior part of head capsule with gold-coloured granules. Pharynx long and cylindrical, with well-developed terminal bulb and slight swellings at level of cephalic capsule and immediately anterior to terminal bulb. Large nerve ring between both posteriormost swellings. Endbulb without thickened lumen wall. Cardia short. Intestine granular, with inconspicuous or thin brush border. Cloacal flap present (Fig. 1A, B).

Male reproductive system located ventrally to intestine: monorchic, with outstretched testis extending far anteriorly (*i.e.* tip of testis is located at 40.7-45.2% of total body length) (Fig. 2A). Germinal zone granular, with developing spermatogonia. Growth zone with several compact, fully grown spermatids with irregular border, 10 µm in diameter on average, without perceptible nucleus. Vesicula seminalis elongated, with large (19 µm on average), irregular spermatozoa. Each spermatozoon with marginal cytoplasm, well-developed halo and granular nucleus. Vas deferens slender and granular. Percentage of spicule length to total body length 5.5-6%. Spicules large, slender and curved (Figs. 1B, 2A). Capitulum set-off, knob-like. Conspicuous velum, starting at base of capitulum. Gubernaculum parallel to spicules. Two large subventral corniform setae with open tip and internal duct, located immediately behind posteriormost SvAT (Figs. 1A,C).

Tail conico-cylindrical, with 66-81 complete annules (81 in holotype), including tail tip. Tail tip 22.7-29.9% of tail length, dorsally with numerous tiny vacuoles and sometimes with one incomplete annule dorsally or two incomplete annules ventrally (one incomplete annule dorsally in holotype). Caudal glands extending up to halfway spicule length.

Female

Habitus similar to males, although body clearly more enlarged at level of female reproductive system. Swollen pharyngeal region 14.6% of total body length. Annulation as in males.

CAT morphology as in males; CAT arranged in two laterodorsal rows consisting of two tubes and two subdorsal rows of five tubes. Anteriormost LdCAT on annules 4 and 5, posteriormost LdCAT on

annules 7 and 10. Anteriormost SdCAT on annule 4, posteriormost SdCAT on annule 23. PAT morphology as in males; PAT arranged in two rows of 11-12 SlAT and two subventral rows converging towards posterior, together consisting of 25 SvAT. Total number of PAT 48. Width of anteriormost SlAT 1.9 µm at 10µm from base of tube. PAT gradually decreasing in length towards posterior.

Somatic setae in pharyngeal region, region anterior to PAT and region of PAT arranged as in males, except for the presence of subventral setae instead of medioventral setae around vulva. Between posteriormost SvAT and anal opening one medioventral seta, two lateroventral-subventral setae, two sublateral setae in dorsal sector and one subdorsal seta on each side. Tail with two short subdorsal setae, two very long (51 and 63 µm in allotype female) subdorsal setae and two short subventral setae on each side. Tail tip on each side with one lateroventral and one tiny subdorsal seta.

Shape of cephalic capsule as in males (Fig. 2C). Labial region protruded. Head capsule length 16.1% of pharynx length; head capsule width 50.7% of pharynx width. Eighteen subcephalic setae, arranged as in males. No sexual dimorphism in shape or location of amphidial fovea. Length of amphidial fovea 29.8% of head capsule length. Digestive system as in males. Anal flap present.

Female reproductive system situated ventrally to intestine: didelphic and amphidelphic, with antidromously reflexed ovaries (Fig. 1D). Anterior ovary reflexed along right side, posterior ovary reflexed along left side. Uterus with numerous sperm cells with condensed nucleus. Vulva bulged out. Vagina bipartite: proximal part surrounded by contractor muscles. Four paravulval setae.

Tail conico-cylindrical, with 54 complete annules, including tail tip. Tail tip 35.2% of tail length, dorsally with numerous tiny vacuoles. No incomplete annules.

Juveniles

First stage juvenile not found.

Second stage juveniles (Fig. 3A)

Posterior body region not enlarged; slight pharyngeal swelling. Body finely annulated. All annules smooth.

One slender, mediodorsal CAT with enlarged base and slightly swollen tip, located on annules 5-8. PAT slender, strongly cuticularised, with enlarged base and bell-shaped tip, arranged in two sublateral longitudinal rows, each consisting of two tubes. Width of anteriormost SlAT 1.8-1.9 µm at 10µm from base of tube.

Somatic setae in pharyngeal region arranged in 6 rows: one mediodorsal row, two laterodorsal rows, two lateroventral rows and one medioventral row, all with long setae. Between pharyngeal region and region of PAT two laterodorsal rows and two lateroventral rows of relatively long setae. In region of PAT, relatively long somatic setae in two sublateral rows in dorsal sector. Between posteriormost PAT and anus on each side one sublateral seta in dorsal sector and one lateroventral seta. Tail with one very long subdorsal seta on each side and one short, truncated lateroventral seta immediately anterior to tail tip. Tail tip with one short mediodorsal seta.

Shape of cephalic capsule and shape of amphidial fovea as in adults. Head capsule length 12.5-17.5% of pharynx length; head capsule width 41.5-50.1% of pharynx width. Six setiform labial sensilla,

four cephalic setae and two subcephalic setae: on each side of head capsule one seta situated dorsally to posterior end of amphidial fovea. Amphidial fovea located centrally on head capsule or slightly shifted to anterior. Length of amphidial fovea 41.8-53.7% of head capsule length.

Tail with 36-37 complete annules, including tail tip. Tail tip 40.7-43.6% of tail length, ornamented with numerous tiny vacuoles and with 1-2 incomplete annules dorsally.

Third stage juveniles (Fig. 3C)

Pharyngeal and posterior body region more swollen than in second stage juveniles; pharyngeal swelling and subsequent thin region conspicuous. Body finely annulated. All annules smooth.

Three slender CAT, broader at base and with slightly swollen tip: one mediodorsal tube and two laterodorsal tubes, all located on annules 6-10. PAT slender, strongly cuticularised, with enlarged base and bell-shaped tip, arranged in two sublateral longitudinal rows, each consisting of five tubes. Width of anteriormost SIAT 1.7-2.1 µm at 10µm from base of tube.

Somatic setae in pharyngeal region arranged in 8 rows: one mediodorsal row, two laterodorsal rows and two lateroventral rows with both long and short setae, two subventral rows with long setae and one medioventral row with short setae. Body between pharyngeal region and region of PAT with one mediodorsal row, two laterodorsal rows and two lateroventral rows of relatively long setae. In region of PAT somatic setae in one mediodorsal row of relatively long setae and two sublateral rows of short setae in dorsal sector. Between posteriormost PAT and anus one mediodorsal seta and on each side one laterodorsal seta and one short sublateral seta in ventral sector, in line with PAT. One short lateroventral seta at level of anus. Tail with one short and one very long subdorsal seta on each side. Tail tip on each side with one short subdorsal seta and one lateroventral truncated seta or pore.

Shape of cephalic capsule and shape of amphidial fovea as in adults. Head capsule length 13.6-18.2% of pharynx length; head capsule width 42.6-50% of pharynx width. Six setiform labial sensilla, four cephalic setae and two subcephalic setae, arranged as in second stage juveniles. Amphidial fovea located centrally on head capsule or slightly shifted to posterior. Length of amphidial fovea 36.7-44.5% of head capsule length.

Tail with 34-43 complete annules, including tail tip. Tail tip 42.3-50.1% of tail length, ornamented with numerous tiny vacuoles and either without incomplete annules, with 1-3 incomplete annules dorsally or with one incomplete annule ventrally.

Fourth stage juveniles

Two juvenile males; one juvenile moulting into adult (Fig. 3B). Posterior enlargement less pronounced than in adults. All annules smooth.

Six fine CAT with swollen base and slightly enlarged tip: four subdorsal tubes arranged in two longitudinal rows and two laterodorsal tubes at level of anteriormost subdorsal CAT. Anteriormost laterodorsal CAT on annule 8, anteriormost subdorsal CAT on annule 9 and posteriormost subdorsal CAT on annules 18-22. PAT robust, with slightly enlarged base and well-developed bell-shaped tip, arranged in three rows: two sublateral rows of 6-7 tubes and one medioventral row of 9 tubes. Total number of PAT 22-23. Width of anteriormost SIAT 2.3 µm at 10µm from base of tube.

Somatic setae in pharyngeal region arranged in 10 rows: one mediodorsal row of short setae, two subdorsal and two laterodorsal rows of long setae, two lateroventral and two subventral rows of long setae and one medioventral row of short setae. Body between pharyngeal region and region of PAT with one mediodorsal row, two laterodorsal rows, two lateroventral rows and one medioventral row of long somatic setae, as in adults. In region of PAT, somatic setae also arranged as in males. Between posteriormost PAT and anus, mediodorsal, laterodorsal, sublateral and lateroventral setae may be present, as well as one lateroventral seta immediately anterior to anus. Tail with two subventral setae, two very long subdorsal setae and several tiny subdorsal setae on each side. Tail tip on each side with one lateroventral and one subdorsal pore.

Shape of cephalic capsule and shape of amphidial fovea as in adults. Head capsule length 16.5% of pharynx length; head capsule width 42.6-49.2% of pharyngeal width. Six setiform labial sensilla, four cephalic setae and four subcephalic setae: on each side of head capsule one seta situated dorsally and one seta situated ventrally to amphidial fovea. Amphidial fovea located centrally on head capsule or slightly shifted to posterior. Length of amphidial fovea 32.4-34.7% of head capsule length. Digestive system as in adults. Male reproductive system already well-developed, especially in moulting specimen. Several spermatids and spermatozoa already present in this specimen.

Tail with 42-46 complete annules, including tail tip. Tail tip 38.3-44.2% of tail length, ornamented with numerous tiny vacuoles and with either two incomplete annules dorsally or two incomplete annules ventrally. Caudal glands may be unclear, extending in front of anus.

Diagnosis

Cygnonema verum sp. n. is characterised by (1) general body shape; (2) size (1325-1625 µm in males and 1415 µm in female); (3) percentage of head capsule length to pharynx length 16.1-16.9% in males and 16.1% in female; (4) percentage of head capsule width to pharynx width 42.1-47.0% in males and 50.7% in female; (5) 14-16 CAT; (6) anteriormost CAT located on annules 4-6; (7) 48-51 PAT; (8) setiform external labial sensilla; (9) 15-18 subcephalic setae; (10) amphidial fovea located centrally on head capsule; (11) spermatozoa with well-developed halo and only small amount of cytoplasm; (12) capitulum of spicules knob-like; (13) two large subventral corniform setae; (14) tail tip 22.7-29.9% of tail length in males.

Differential diagnosis

Differential diagnosis for this species is given under *C. belgicae* sp. n.

	Holotype male	Males (n = 3)	Allotype female	Juvenile stage II (n = 2)	Juvenile stage III (n = 5)	Juvenile stage IV (n = 2)
L	1625	1325-1525 (1440)	1415	450-480 (465)	580-770 (660)	1085-1125 (1105)
Hdw	20.5	19-20.5 (19.9)	21	12-13 (12.7)	15-16.5 (15.8)	17.5-20 (18.7)
Hdl	27	20.5-24.5 (22.6)	22	12-15 (13.4)	15.5-18.5 (16.9)	17.5-18.5 (17.9)
Amphw	5	5-6 (5.5)	5	3-3.5 (3.4)	3.5-4 (3.8)	3.5
Amphl	8.5	7-7.5 (7.5)	6.5	6-6.5 (6.3)	6-7.5 (6.7)	6
Amph%	23.3	26.5-29.1 (27.4)	22.7	26.5-27.5 (27.0)	21.7-24.9 (23.7)	17.2-19.8 (18.5)
ph	160.5	126-148.5 (137.5)	137.5	84.5-96.5 (90.5)	95-123.5 (105.6)	111 [(1)]
MdCAT				19.5-20.5 (20.0)	19-25.5 (22.4)	
SdCATa	25.5	25-26.5 (25.9)	27			25.5-26 (25.6)
SdCATp	43.5	33.5-39 (37.0)	35.5			30-31.5 (30,9)
LdCATa	31	25.5-29.5 (27.1)	28		24.5-25.5 (24.9)	27-28 (27.4)
LdCATp	36.5	32.5-35 (33.6)	39.5			
SlATa	56.5	54-56.5 (55.0)	52.5	32.5-35 (34.0)	34.5-41.5 (39.1)	40-42.5 (41.1)
SlATp	35.5	33.5-36.5 (35.4)	38.5	24-25.5 (24.8)	22.5-26 (24.1)	26.5-29 (27.8)
SvATa	39	35.5- 39 (36.9)	38.5			
SvATp	19.5	19.5-22 (20.9)	23.5			
MvATa						30-33 (31.5)
MvATp						17-19.5 (18.1)
Corn-set	10	10-12.5 (10.7)				
tail	165	121-148.5 (138.9)	123	56-60.5 (58.2)	95.5-75 (69.8)	86-91 (88,3)
tmr	37.5	36-36.5 (36.2)	43.5	24.5	29.5-34 (31.5)	35-38 (36.3)
mbd ph	49	42-46.5 (43.8)	41	26.5-29.5 (27.9)	32-37 (34.3)	35.5-46.5 (41.1)
mbd	65	35.5-64.5 (50.9)	61	20.5-21 (20.9)	25.5-33.5 (29.1)	36-40.5 (38.5)
(mbd)	16.5	15.5-19 (17.7)	16	15	15-16.5 (15.7)	15-17.5 (16.3)
mbd/(mbd)	3.9	2.3-3.5 (2.8)	3.8	1.4	1.7-2.0 (1.9)	2.3-2.5 (2.4)
abd	29.5	27-31 (29.4)	17	13.5-15 (14.3)	15-16.5 (15.9)	18-31 (24.4)
spic	85	79.5-85 (82.9)				
gub	24.5	20.5-25 (23.0)				
V%			60.2			
a	25.1	23.7-37.1 (29.6)	23.2	21.9-22.6 (22.2)	21.1-24.9 (22.7)	26.7-31.1 (28.9)
b	10.1	10.3-10.6 (10.5)	10.3	4.7-5.7 (5.2)	6.1-6.3 (6.2)	10.2 [(1)]
c	9.9	9.9-10.9 (10.4)	11.5	7.9-8.1 (8.0)	8.6-10.2 (9.4)	12.4-12.7 (12.5)

Table 1. Measurements of *Cygnonema verum* sp. n. All absolute values in µm. The number of specimens measured, when different from the total number of specimens, is indicated between brackets in superscript.

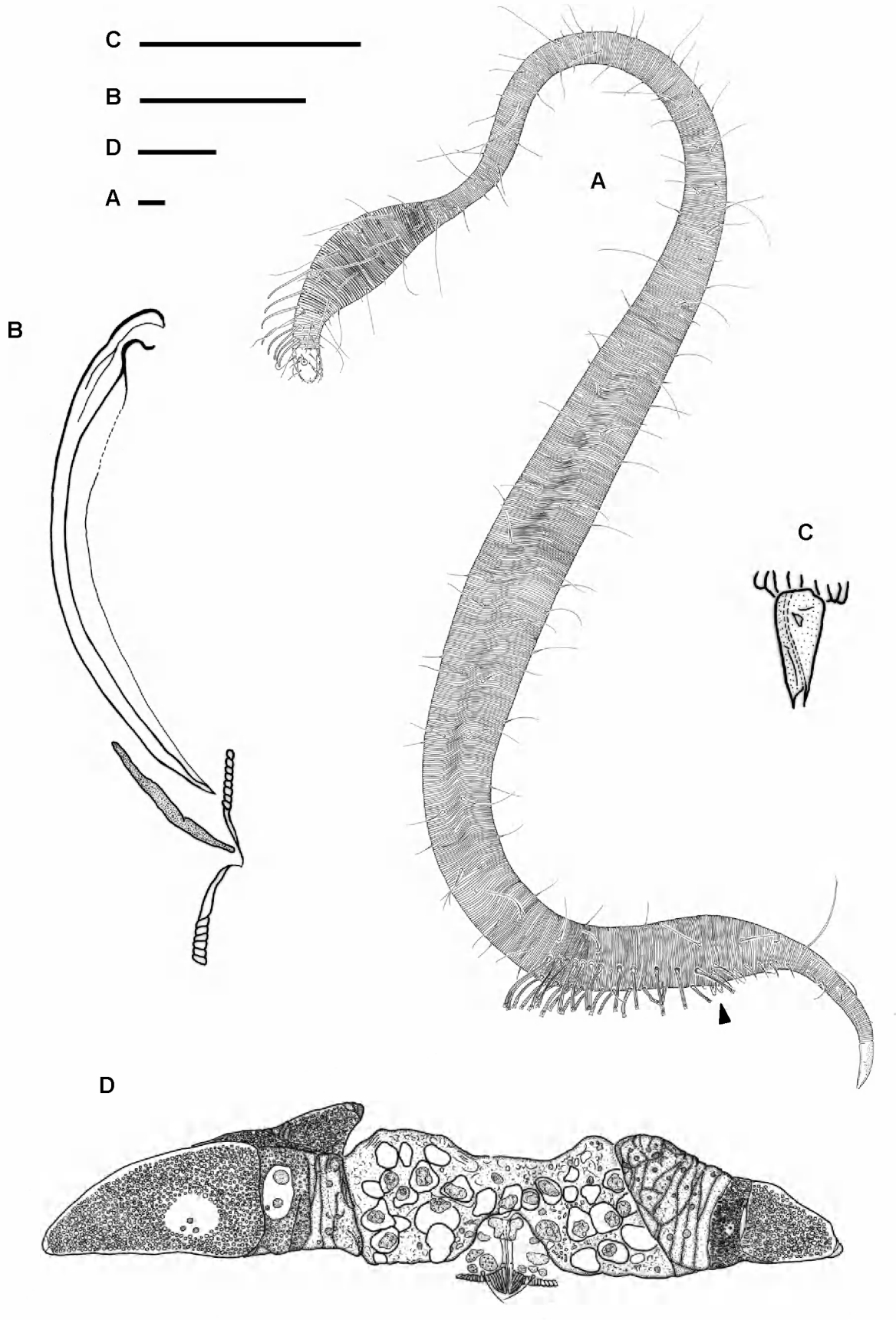


Fig. 1. *Cygnonema verum* sp. n. (A) holotype ♂, habitus external; (B) paratype ♂, spicule and gubernaculum; (C) paratype ♂, corniform seta; (D) allotype ♀, reproductive system. The arrow indicates the position of the corniform setae. Scale bars 20 µm.

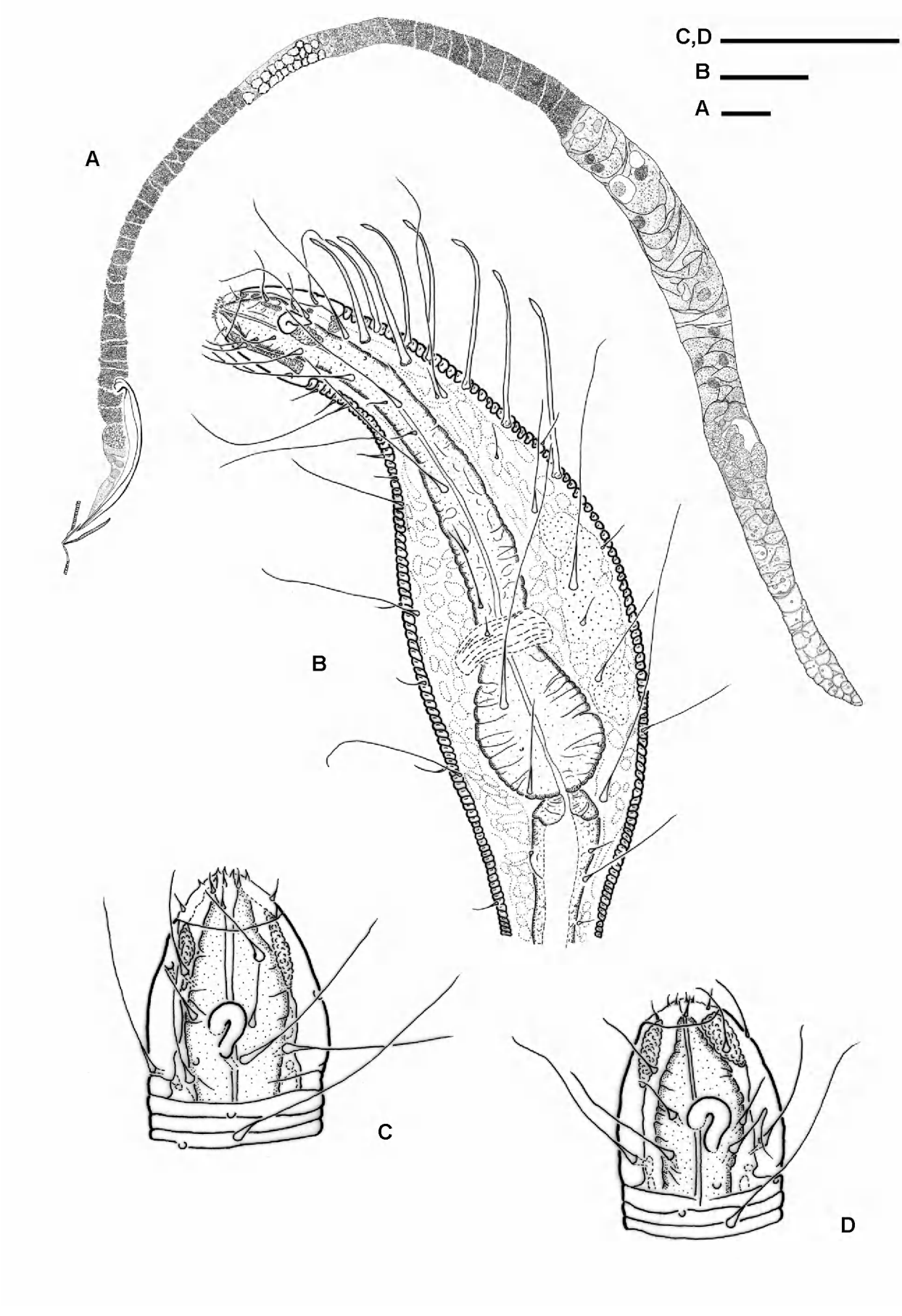


Fig. 2. *Cygnonema verum* sp. n. (A) paratype ♂, reproductive system; (B) holotype ♂, head capsule and pharynx; (C) allotype ♀, head capsule; (D) paratype ♂, head capsule. Scale bars 20 µm.

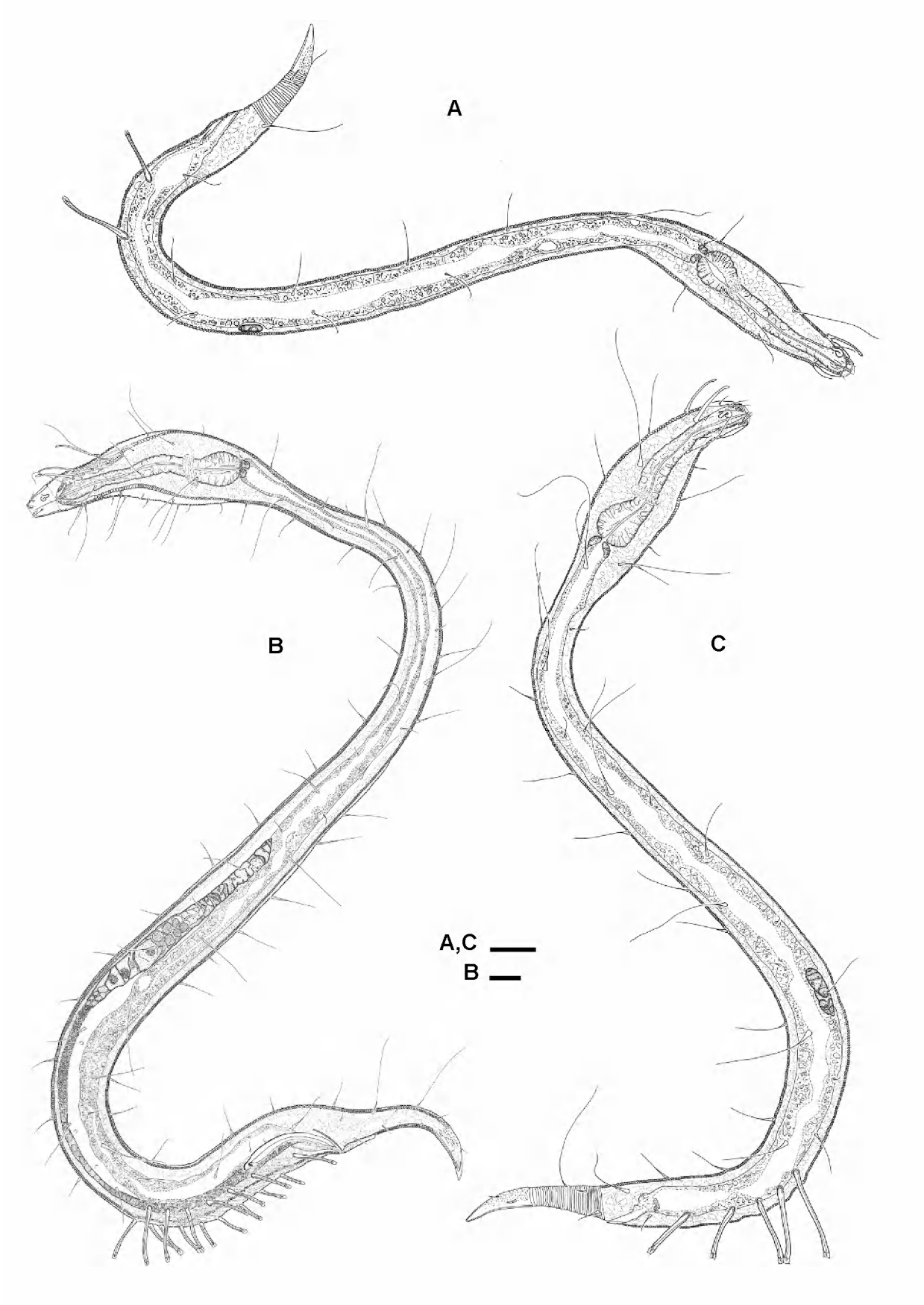


Fig. 3. *Cygnonema verum* sp. n. (A) second stage juvenile, habitus; (B) fourth stage juvenile, habitus; (C) third stage juvenile, habitus. Scale bars 20 µm.

Familia Draconematidae Filipjev, 1918

Subfamilia Prochaetosomatinae Allen & Noffsinger, 1978

Genus *Cygnonema* Allen & Noffsinger, 1978

***Cygnonema belgicae* sp. n.** (Figures 4-9)

Material. One holotype male; one paratype male; seven additional males; one allotype female; two paratype females; five additional females; one additional first stage juvenile; two paratype second stage juveniles; eight additional second stage juveniles; three paratype third stage juveniles; five additional third stage juveniles; seven additional fourth stage juveniles.

Type locality. Porcupine Seabight, Belgica mound Province. Coordinates: 51°24'49,4"N 11°45'55,9"W (material collected on 17/06/2000; depth: 1000 m).

Other localities. Porcupine Seabight, Belgica mound Province. Coordinates: 51°24'48,2"N 11°45'55,4"W (material collected on 17/06/2000; depth: 1005 m) and 51°25'7,7"N 11°46'9,3"W (material collected on 07/05/2001; depth: 972 m).

Habitat at type locality. A cold-water coral degradation zone on the flank and near the top of a seabed mound. Specimens were associated with sediment-clogged framework of the cold-water coral *Lophelia pertusa* (Linnaeus, 1758) and were found on dead coral fragments.

Other habitats. It was also found on dead sponge skeletons (*Aphrocallistes bocagei* Schultze, 1886) and within the underlying sediment.

Relative abundance. This species comprises 0.71% of the total nematode community at the type locality.

Etymology. The species is named in honour of the crew of the R.V. Belgica, in appreciation of their ready help on several sampling campaigns.

Measurements. Table 2.

Males

Slender s-shaped body, enlarged at level of pharynx and along reproductive system (Figs. 4A, 8A). Head capsule and anterior part of pharyngeal region strikingly narrow. Width gradually increasing along pharynx, reaching maximal width immediately anterior to nerve ring. Behind this, body width gradually decreasing again, reaching minimal body width immediately anterior to intestine. Posteriorly, body very narrow, slightly increasing in width again until reaching maximal width at level of vesicula seminalis. Posterior to vesicula seminalis body remaining wide, only decreasing again behind posteriormost SvAT. Tail slender, conico-cylindrical. Swollen pharyngeal region 13.0-15.1% of total body length. Body finely annulated. Broadest annules in pharyngeal region; finest annules at level of testis. All annules smooth. Posterior body region often littered with fine detritus (Fig. 8C).

CAT (12) arranged in four longitudinal rows: two laterodorsal rows consisting of two tubes and two subdorsal rows of four tubes (Figs. 5D, 8E, 9A). CAT slender, with enlarged base and gradually decreasing in width up to tip. Tip slightly swollen. Anteriormost tubes in laterodorsal rows on annules 7-10, posteriormost tubes in laterodorsal rows on annules 13-16. Anteriormost tubes in subdorsal rows on annules 11-14 and posteriormost tubes in subdorsal rows on annules 26-32. Robust PAT with

swollen base and well-developed bell-shaped tip, arranged in two rows of 8-11 SlAT and two subventral rows converging towards posterior, together consisting of 17-20 SvAT (Figs. 4A, 8C, 9E). Total number of PAT 34-41. Width of anteriormost SlAT 2.0-2.3 µm at 10µm from base of tube. PAT gradually decreasing in length towards posterior. Glands associated with PAT, situated either on right or left side of vas deferens. Anteriormost PAT situated at 71.9-76.9% of body length. Region with PAT taking up 7.8-11.8% of total body length.

Somatic setae in pharyngeal region arranged in 12 rows: one mediodorsal row of short setae, two subdorsal rows (only one seta on each side) and two laterodorsal rows of long setae, two mediolateral rows of short setae, two lateroventral and two subventral rows of long setae and one medioventral row of short setae (Fig. 5D). Mediolateral setae not always in one row. Body between pharyngeal region and region of PAT with one mediodorsal row, two laterodorsal rows, two lateroventral rows and one medioventral row of long somatic setae. In region of PAT, somatic setae arranged in one mediodorsal row and two sublateral rows in dorsal sector. Between posteriormost SlAT and cloacal opening three lateroventral-subventral somatic setae on each side. Tail with two or three subventral setae, two very long (46.5 and 59 µm in holotype) subdorsal setae and several tiny subdorsal setae on each side. Tail tip on each side with two lateroventral setae and one tiny subdorsal seta (Fig. 9F).

Cephalic capsule smooth, bullet-shaped; labial region protruded (Figs. 5A, 9C). Head capsule length 12.2-14.8% of pharynx length; head capsule width 36.7-41.7% of pharynx width. Labial sensilla short, inconspicuous. Four cephalic setae and 4-6 subcephalic setae: on each side one laterodorsal and one lateroventral seta; additional setae may be present. Amphidial fovea loop- or question mark-shaped with longer dorsal arm, located at or near posterior border of head capsule. Length of amphidial fovea 32.2-40.4% of head capsule length. Buccal cavity tiny and elongated. Teeth absent. Anterior part of head capsule with gold-coloured granules. Pharynx long and cylindrical, with well-developed terminal bulb (Fig. 5D). Large nerve ring immediately anterior to pharyngeal bulb. Endbulb without thickened lumen wall. Cardia short. Intestine granular, with inconspicuous or thin brush border. Cloacal flap may present or absent.

Male reproductive system located ventrally to intestine: monorchic, with outstretched testis extending far anteriorly (*i.e.* tip of testis located at 41.5-50.9% of total body length) (Fig. 5C). Germinal zone granular, with developing spermatogonia. Growth zone with several compact, fully grown spermatids with irregular border, 10.5 µm in diameter on average, without perceptible nucleus. Vesicula seminalis elongated, with large (15.5 µm on average) spermatozoa, each with large amount of cytoplasm, and granular nucleus. Vas deferens slender, granular. Percentage of spicule length to total body length 4.6-5.8%. Spicules large, slender, gently curved (Fig. 4B). Capitulum set-off, beak-shaped. Velum conspicuous, starting at base of capitulum. Gubernaculum parallel to spicules. No corniform seta.

Tail conico-cylindrical, with 75-81 complete annules (78 in holotype), including tail tip. Tail tip 31.0-36.6% of tail length, dorsally with numerous tiny vacuoles and sometimes with 1-2 incomplete annule dorsally or two incomplete annules ventrally (two incomplete annules dorsally in holotype). Caudal glands extending up to halfway spicule length, ending in a single, common outlet (Fig. 9F).

Females

Habitus as in males, although slightly more enlarged at level of reproductive system (Fig. 8B). Swollen pharyngeal region 12.3-17.3% of total body length. Body finely annulated. Annulation as in males.

Arrangement and structure of CAT as in males (Fig. 9B). Anteriormost tubes in laterodorsal rows on annules 8-13, posteriormost tubes in laterodorsal rows on annules 13-18. Anteriormost tubes in subdorsal rows on annules 9-15 and posteriormost tubes in subdorsal rows on annules 28-33. PAT structured as in males, arranged in two rows of 8-13 SlAT and two subventral rows converging towards posterior, together consisting of 18-22 SvAT (Fig. 8D). Total number of PAT 37-45. Width of anteriormost SlAT 1.8-2.2 µm at 10µm from base of tube. PAT gradually decreasing in length towards posterior.

Somatic setae in pharyngeal region, region anterior to PAT and region of PAT arranged as in males, except for presence of subventral setae instead of medioventral setae around vulva (Fig. 9H). Between posteriormost SvAT and anal opening one medioventral seta, 2-3 lateroventral-subventral setae, one sublateral seta in dorsal sector, one subdorsal seta and one mediodorsal seta on each side. Tail with several short subdorsal setae, two long (broken off in allotype female; 37 and 51.5 µm in one paratype female) subdorsal setae and one short subventral seta on each side. Tail tip on each side with one lateroventral and one subdorsal seta.

Shape of cephalic capsule similar as in males (Figs. 5B, 9D). Head capsule length 11.6-13.0% of pharynx length; head capsule width 34.9-42.1% of pharynx width. Four cephalic setae and 2-4 subcephalic setae, arranged as in males. Shape and location of amphidial fovea as in males. Length of amphidial fovea 29-35% of head capsule length. Digestive system as in males. Anal flap present or absent.

Female reproductive system situated ventrally to intestine: didelphic and amphidelphic, with antidromously reflexed ovaries (Fig. 4C). Anterior ovary reflexed along right side, posterior ovary reflexed along left side. Uterus often with numerous sperm cells, each with large amount of cytoplasm and condensed nucleus. Vagina bipartite: proximal and distal part equally long; proximal part surrounded by contractor muscle. Four paravulval setae.

Tail conico-cylindrical, with 65-74 complete annules (65 in allotype), including tail tip. Tail tip 31.8-38.7% of tail length, ornamented with numerous tiny vacuoles and sometimes with 1-3 incomplete annules ventrally (no incomplete annules in allotype). Caudal glands ending in a common outlet (Fig. 9G).

Juveniles

First stage juveniles (Fig. 6A)

One specimen, moulting into second stage juvenile (identification based upon features of second stage juvenile within cuticle). Body width almost uniform, with only slight pharyngeal swelling. Body finely annulated. All annules smooth.

Adhesion tubes absent. Only four somatic setae: on each side one mediolateral seta in pharyngeal region and one subdorsal seta at level of anus. Subdorsal setae broken off: only insertion sites visible. Cephalic capsule short. Six labial sensilla: two dorsalmost sensilla large (3.8 µm in length) and hook-shaped; other sensilla shorter, triangular. Amphidial fovea small, circular in outline, located posterior to head capsule.

Tail with 61 complete annules, including tail tip. Tail tip short (12.8% of tail length), smooth, conical, with well-developed spinneret.

Second stage juveniles (Fig. 6B)

Body width almost uniform; only slight pharyngeal swelling. Body finely annulated. All annules smooth.

One slender, mediodorsal CAT with enlarged base and barely swollen tip, located on annules 9-13. PAT slender, strongly cuticularised, with slightly enlarged base and bell-shaped tip, arranged in two sublateral longitudinal rows, each consisting of two tubes. Width of anteriormost SIAT 1.6-1.9 µm at 10µm from base of tube.

Somatic setae in pharyngeal region arranged in 6 rows: one mediodorsal row with relatively long setae, two laterodorsal rows with long setae, two lateroventral rows with short and long setae and one medioventral row with relatively long setae. Between pharyngeal region and region of PAT two laterodorsal rows and two lateroventral rows of relatively long setae. In region of PAT somatic setae in two sublateral rows of relatively long setae in dorsal sector. Between posteriormost PAT and anus on each side one sublateral seta in dorsal sector and one lateroventral seta. Tail with one very long subdorsal seta on each side and one short, truncated lateroventral seta immediately anterior to tail tip. This setae sometimes absent or located on tail tip. Tail tip also with one short mediodorsal seta.

Shape of cephalic capsule and shape of amphidial fovea as in adults. Head capsule length 15.1-19.8% of pharynx length; head capsule width 43.9-58.0% of pharynx width. Two subcephalic setae: on each side of head capsule one seta situated dorsally to posterior end of amphidial fovea. Amphidial fovea located posteriorly on and sometimes near posterior border of head capsule. Length of amphidial fovea 33.2-43.0% of head capsule length.

Tail with 36-42 complete annules, including tail tip. Tail tip 35.1-52.5% of tail length, ornamented with numerous tiny vacuoles and either without incomplete annules, with two incomplete annules dorsally or with 1-2 incomplete annules ventrally.

Third stage juveniles (Fig. 6C)

Body shape comparable to adults, although with less pronounced posterior enlargement. Body finely annulated. All annules smooth.

Three slender CAT, broader at base, gradually decreasing in width up to slightly swollen distal tip: one mediodorsal tube located on annules 14-16 and two laterodorsal tubes located more anteriorly: on annules 11-12. PAT slender, strongly cuticularised, with enlarged base and bell-shaped tip, arranged in two sublateral longitudinal rows, each consisting of five tubes. Width of anteriormost SIAT 1.7-2.0 µm at 10µm from base of tube.

Somatic setae in pharyngeal region arranged in 8 rows: one mediodorsal row, two laterodorsal rows and two lateroventral rows with both long and short setae, two subventral rows with long setae and one medioventral row with short setae. Body between pharyngeal region and region of PAT with one mediodorsal row, two laterodorsal rows and two lateroventral rows of relatively long setae. In region of PAT somatic setae in one mediodorsal row; two sublateral rows of short setae in dorsal sector may be present although these setae usually inconspicuous or absent. One mediodorsal seta present between posteriormost PAT and anus. At level of anus, one laterodorsal and one lateroventral seta present on each side. Tail with one short and one very long subdorsal seta on each side. Tail tip on each side with one short subdorsal seta and one lateroventral pore.

Shape of cephalic capsule and shape of amphidial fovea as in adults. Head capsule length 12.3-19.9% of pharynx length; head capsule width 38.3-48.0% of pharynx width. Two subcephalic setae: on each side of head capsule one seta situated dorsally to posterior end of amphidial fovea. Amphidial fovea located posteriorly on head capsule, near posterior border. Length of amphidial fovea 31.6-40.4% of head capsule length.

Tail with 39-47 complete annules, including tail tip. Tail tip 41.6-54.6% of tail length, ornamented with numerous tiny vacuoles and either without incomplete annules, with one incomplete annule dorsally or with 1-3 incomplete annule ventrally.

Fourth stage juveniles (Fig. 7)

Body slender as in adults, although slightly less enlarged posteriorly. All annules smooth.

Four slender CAT, gradually decreasing in width towards distal, slightly swollen, tip: two subdorsal and two laterodorsal tubes. Laterodorsal tubes located on annules 10-13; subdorsal tubes always located more posteriorly: on annules 14-17. PAT slender but strongly cuticularised, with enlarged base and well-developed bell-shaped tip, arranged in two sublateral rows and one medioventral row: each row with seven tubes. Total number of PAT 21. Width of anteriormost SIAT 1.8-2.0 µm at 10µm from base of tube.

Somatic setae in pharyngeal region arranged in 10 rows: one mediodorsal row of short setae, two subdorsal rows and two laterodorsal rows of long setae, two lateroventral and two subventral rows of long setae and one medioventral row of short setae. Somatic setae between pharyngeal region and posteriormost PAT arranged as in adults. Between posteriormost SIAT and anus one mediodorsal seta and on each side one subdorsal seta and two lateroventral setae; subdorsal seta and posteriormost lateroventral seta situated immediately anterior to anus or at level of anus. Tail usually with one subventral setae, two very long subdorsal setae and several tiny subdorsal setae on each side. Tail tip on each side with one subdorsal seta and one lateroventral pore.

Shape of cephalic capsule, shape and location of amphidial fovea as in adults. Head capsule length 10.7-15.4% of pharynx length; head capsule width 38.4-44.4% of pharynx width. Four subcephalic setae: on each side of head capsule one seta situated laterodorsally at level of amphidial fovea and one seta lateroventrally at posterior border of head capsule. Length of amphidial fovea 29.3-34.6% of head capsule length. Digestive system as in adults. Genital system in males long and slender; genital system in females small, although uterus and two ovaria already recognisable.

Tail with 52-60 complete annules, including tail tip. Tail tip 32.8-46.1% of tail length, ornamented with numerous tiny vacuoles and either with 1-3 incomplete annules dorsally or with 1-3 incomplete annules ventrally.

Diagnosis

Cygnonema belgicae sp. n. is characterised by (1) general body shape; (2) size (980-1195 µm in males and 1055-1305 µm in females; (3) percentage of head capsule length to pharynx length 12.2-14.8% in males and 11.6-13.0% in female; (4) percentage of head capsule width to pharynx width 36.7-41.7% in males and 34.9-42.1% in female; (5) 12 CAT; (6) anteriormost laterodorsal CAT located on annules 7-10 in males and on annules 8-13 in females; (7) 34-45 PAT; (8) 4-6 subcephalic setae in males and 2-4 subcephalic setae in females; (9) amphidial fovea located at or near posterior border of head capsule; (10) spermatozoa with large amount of cytoplasm; (11) beak-shaped capitulum; (12) tail tip 31.8-38.7% of tail length in males.

Differential diagnosis

Adults of *C. verum* sp. n. and *C. belgicae* sp. n. differ from the type species *C. steineri* Allen & Noffsinger, 1978 in (1) general body shape (*C. steineri* is much more slender), (2) size (*C. steineri* is larger: 1700-3100 µm vs. 1325-1625 µm in *C. verum* sp. n. and 980-1305 µm in *C. belgicae* sp. n.), (3) length of pharynx in relation to body length (pharynx in *C. steineri* is much longer: de Man b is 3.9-6.3 vs. 10.1-10.6 in *C. verum* sp. n. and 8.5-10.3 in *C. belgicae* sp. n.), (4) number of CAT (10 in *C. steineri* vs. 14-16 in *C. verum* sp. n. and 12 in *C. belgicae* sp. n.) and (5) absence of a dorsal tooth. Adults of *C. verum* sp. n. differ from those of *C. belgicae* sp. n. in (1) size (*C. verum* sp. n. is longer), (2) larger head capsule (percentage of head capsule length to pharynx length and percentage of head capsule width to pharynx width higher in *C. verum* sp. n.), (3) higher number of CAT, (4) position of anteriormost laterodorsal CAT (more anteriorly in *C. verum* sp. n.), (5) higher number of PAT, (6) presence of setiform external labial sensilla, (7) higher number of subcephalic setae and (8) location of amphidial fovea (centrally on head capsule and not near posterior border as in *C. belgicae* sp. n.). Moreover, males of *C. verum* sp. n. can easily be distinguished from those of the other species of this genus by the presence of two large subventral corniform setae immediately behind posteriormost SvAT. They differ from males of *C. belgicae* sp. n. in (1) the small amount of cytoplasm, (2) a knob-like capitulum instead of a beak-shaped capitulum and (3) a relatively shorter tail tip.

Fourth stage juveniles of *C. verum* sp. n. differ from those of *C. belgicae* sp. n. in (1) size (*cf.* adults), (2) width of head capsule (*cf.* adults), (3) location of amphidial fovea (*cf.* adults), (4) number of CAT (six in *C. verum* sp. n. vs. four in *C. belgicae* sp. n.) and (5) 9 MvAT vs. 7 MvAT in *C. belgicae* sp. n.

Earlier juvenile stages of *C. verum* sp. n. can be distinguished from those of *C. belgicae* sp. n. by (1) width of head capsule, (2) location of amphidial fovea and (3) location of MvCAT (at level of LdCAT in *C. verum* sp. n. and posterior to LdCAT in *C. belgicae* sp. n.).

The three species of *Cygnonema* can easily be identified using the following identification key:

1) Very slender body, only slightly swollen at base of pharynx; 1700 µm in length or larger; de Man b less than 7; 10 CAT; dorsal tooth evident……*C. steineri* Allen & Noffsinger, 1978
Slender body with conspicuous enlargement at level of pharynx; less than 1700 µm in length; de Man b more than 7; 12-16 CAT; teeth absent……2
2) 14-16 CAT; 48-51 PAT; setiform external labial sensilla; 15-18 subcephalic setae; amphidial fovea located centrally on head capsule; two large subventral corniform setae in males; spermatozoa with small amount of cytoplasm; capitulum knob-like……*C. verum* sp. n.
12 CAT; 34-45 PAT; external labial sensilla inconspicuous; 2-6 subcephalic setae; amphidial fovea located near posterior border of head capsule; corniform setae in males absent; spermatozoa with large amount of cytoplasm; capitulum beak-shaped……*C. belgicae* sp. n.

Emended genus diagnosis

Prochaetosomatinae. Nematodes 1.0-3.1 mm in length. Slender body, S-shaped, slightly enlarged at level of genital system and either with conspicuous enlargement at level of pharynx or only slightly swollen at base of pharynx. Annules smooth or with inconspicuous subcuticular granulation. CAT with enlarged base and with fine or slightly swollen tip. Number of CAT variable: between 10 and 16. All CAT posterior to cephalic capsule, extending up to more than two head capsule diameters posterior to head capsule and arranged in four longitudinal rows: two subdorsal rows and two sublateral rows. Two sublateral and two subventral rows of PAT with bell-shaped tip. Tail tip with 2-6 setae. Rostrum bullet-shaped, either smooth or with faint markings. Subcephalic setae present, variable in number (between 2 and 18). Amphidial fovea located centrally on head capsule or near posterior border of head capsule. Amphidial fovea in males loop-shaped with longer dorsal arm. Sexual dimorphism in shape of amphidial fovea present or absent: female amphidial fovea may be inconspicuous and tubular. Buccal cavity weakly developed, either without teeth or with conspicuous dorsal tooth. Pharynx long and cylindrical, with well-developed, oval or elongated terminal bulb and with slight anterior swellings. Endbulb without thickened lumen wall. Cloacal/anal flap may be present. Either four setiform or twelve short, truncated, tube-like paravulval setae in females. Two large subventral corniform setae in males present or absent.

	Holotype male	Males (n = 8)	Allotype female	Females (n = 7)	Juvenile stage I (n = 1)	Juvenile stage II (n = 10)	Juvenile stage III (n = 8)	Juvenile stage IV (n = 7)
L	1095	980-1195 (1100)	1275	1055-1305 (1215)	350	260-460 (385)	475-760 (590)	745-980 (840)
Hdw	12.5	12.5-13.5 (13.2)	13	13-13.5 (13.4)	7.5	10-11.5 (10.5)	10.5-12.5 (11.4)	11.5-13.5 (12.4)
Hdl	17.5	15-17 (15.8)	17	15-16.5 (15.6)	3.5	12-14 (13.3) [9]	12.5-15 (14.0)	13.5-17 (15.2)
Bda					9.5			
Amphw	4.5	3-4.5 (3.9)	3.5	3.5-4 (3.6)	3	3-4 (3.4) [9]	3-4 (3.5)	3.5-4 (3.7)
Amphl	6	5-6.5 (5.5)	5	4.5-5.5 (5.0)	4	4.5-6 (5.1)	4.5-5 (4.9)	4.5-5 (4.8)
Amph%	34.9	24.4-34.7 (29.7)	27.6	26.3-27.7 (27.2)	29.5	28.7-38.4 (32.3) [9]	26.9-35.1 (30.7)	26.9-34.2 (29.7)
ph	121	107-127 (119.3)	134.5	116-133.5 (126.1)	77	62.5-84 (76.7)	73.5-101 (91.0)	103-126.5 (111.4)
MdCAT						17.5-21 (18.5) [9]	13.5-20 (18.0) [7]	
SdCATa	16	16-19.5 (18.0)	15.5	17-19 (17.9) [6]				20-22 (21.0) [6]
SdCATp	28	25-29.5 (27.4)	28	25.5-28.5 (27.5)				
LdCATa	17	17-20.5 (18.5)	17	15.5-20 (18.2) [5]			13.5-19.5 (17.3)	16.5-23 (20.2) [6]
LdCATp	23	20-23 (21.5)	21	18-23.5 (21.3) [6]				
SlATa	49	44.5-50 (47.6)	50.5	47-54 (51.7)		34-38.5 (36.5) [9]	30-40.5 (36.6)	41-44 (42.8)
SlATp	27	27.5-32 (29.1)	26.5	23-30 (26.2)		25-29.5 (27.5) [9]	20-24.5 (22.2)	22.5-25.5 (23.7)
SvATa	38.5	33.5-39 (36.4)	39.5	35-40 (37.7)				
SvATp	19	15-20 (17.8)	17	14-19 (17.6) [6]				
MvATa								28.5-35 (33.3)
MvATp								14.5-18.5 (16.6)
tail	122	120-136.5 (128.0)	122.5	111-154 (136.4)	49	44.5-62.5 (53.9) [8]	57-77 (69.8)	79.5-117.5 (94.1)
tmr	42.5	40.5-47 (42.8)	44	43-50.5 (46.1)	6.5	22-25.5 (23.5) [9]	27-32.5 (31.1)	33.5-38.5 (36.9)
mbd ph	33.5	32-35 (33.7)	33.5	31.5-39 (33.6)	21	18-25 (21.2)	22.5-29.5 (26.3)	27.5-33.5 (30.1)
mbd	31.5	31.5-40.5 (36.4)	49.5	40-57.5 (48.0)	15	12.5-21 (16.8)	18.5-26.5 (22.2)	22-33.5 (28.7)
(mbd)	13	12.5-14 (13.2)	13.5	13-14 (13.3)	11.5	10-13.5 (11.9)	12-14.5 (12.8)	12-14.5 (13.2)
mbd/(mbd)	2.4	2.4-3.0 (2.8)	3.7	3.0-4.4 (3.6)	1.3	1.2-1.6 (1.4)	1.5-2.0 (1.7)	1.8-2.5 (2.2)
abd	18.5	18-20.5 (19.3)	16	14-17 (15.5)	13.5	9.5-14 (12.1) [8]	9.5-15 (12.9)	12-21.5 (15.4)
spic	57.5	54-64 (58.8)						
gub	17.5	15.5-19 (17.3)						
V%			63.2	57.5-61.9 (59.7)				
a	35.1	28.4-31.8 (30.2)	25.7	22.5-28.0 (25.5)	23.4	20.6-26.9 (23.1)	24.7-30.2 (26.6)	25.0-34.0 (29.5)
b	9.1	8.5-9.9 (9.2)	9.5	8.6-10.3 (9.7)	4.5	4.1-5.8 (5.0)	5.6-8.3 (6.5)	6.5-9.3 (7.5)
c	9	7.6-9.3 (8.6)	10.4	8.4-10.6 (9.0)	7.1	5.8-8.3 (7.2) [8]	6.9-9.9 (8.5)	8.3-9.7 (8.9)

Table 2. Measurements of *Cygnonema belgicae* sp. n. All absolute values in µm. The number of specimens measured, when different from the total number of specimens, is indicated between brackets in superscript.

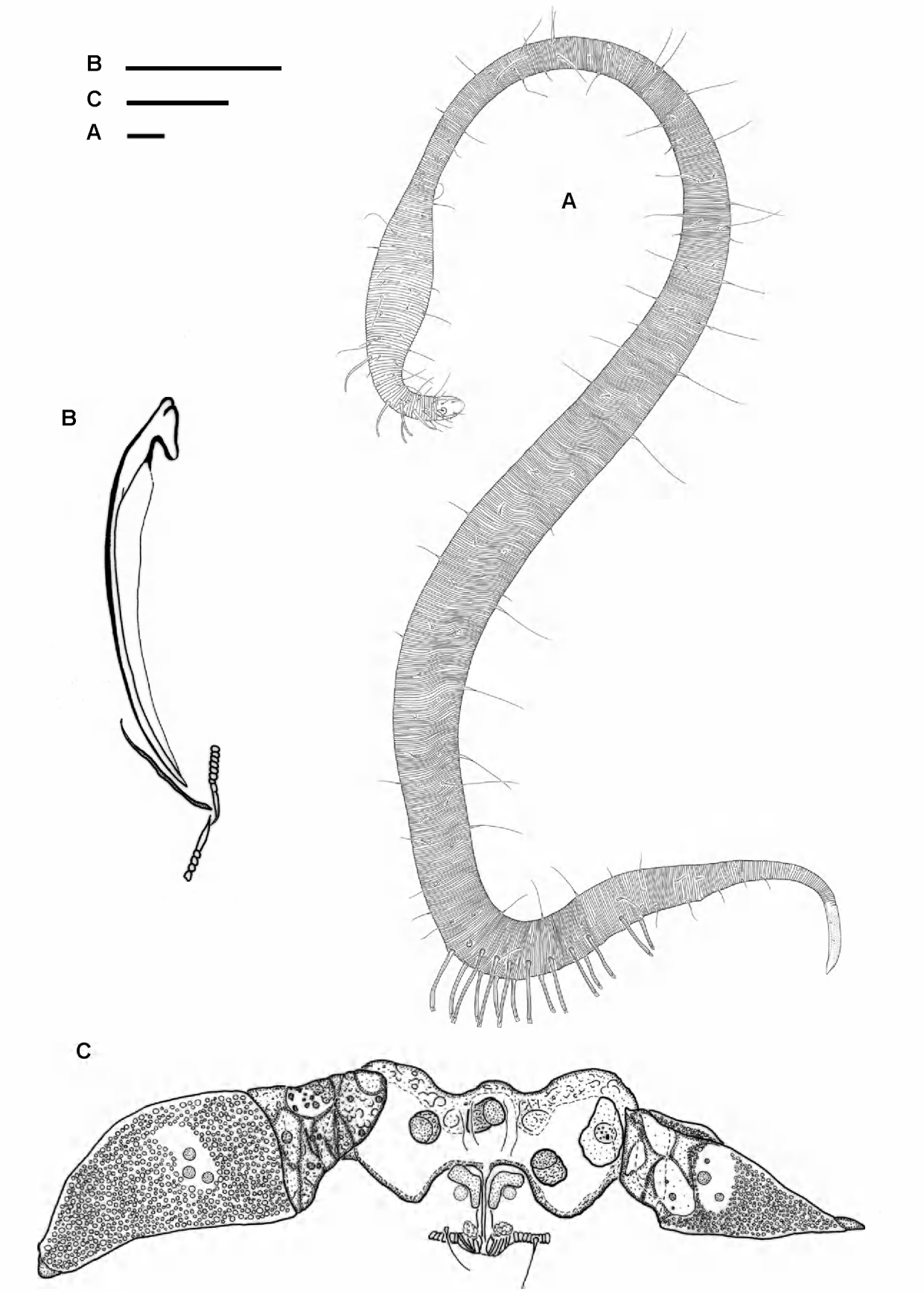


Fig. 4. *Cygnonema belgicae* sp. n. (A) holotype ♂, habitus external; (B) additional ♂, spicule and gubernaculum; (C) additional ♀, reproductive system. Scale bars 20 µm.

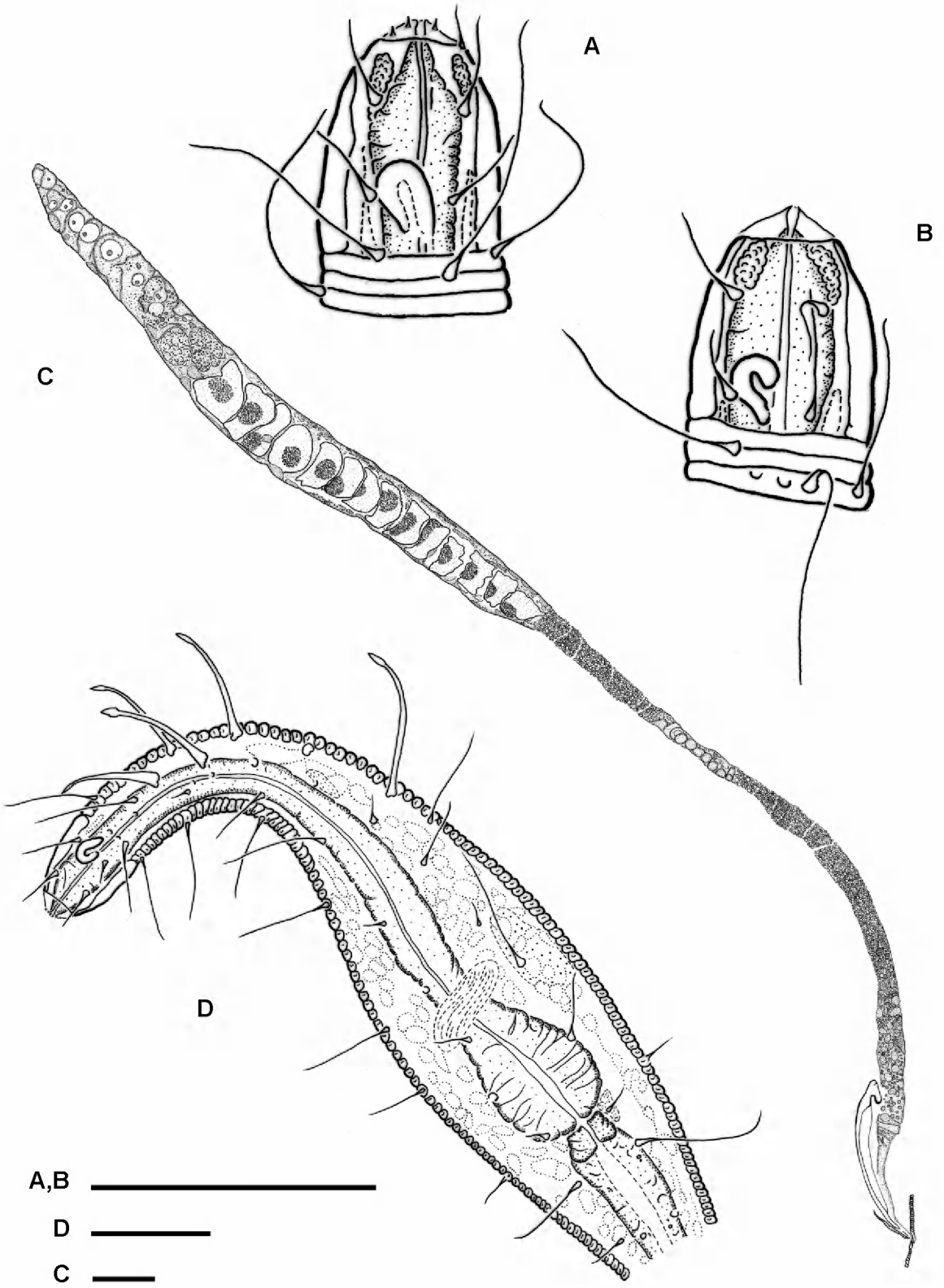


Fig. 5. *Cygnonema belgicae* sp. n. (A) additional ♂, head capsule; (B) additional ♀, head capsule; (C) additional ♂, reproductive system; (D) holotype ♂, head capsule and pharynx. Scale bars 20 µm.

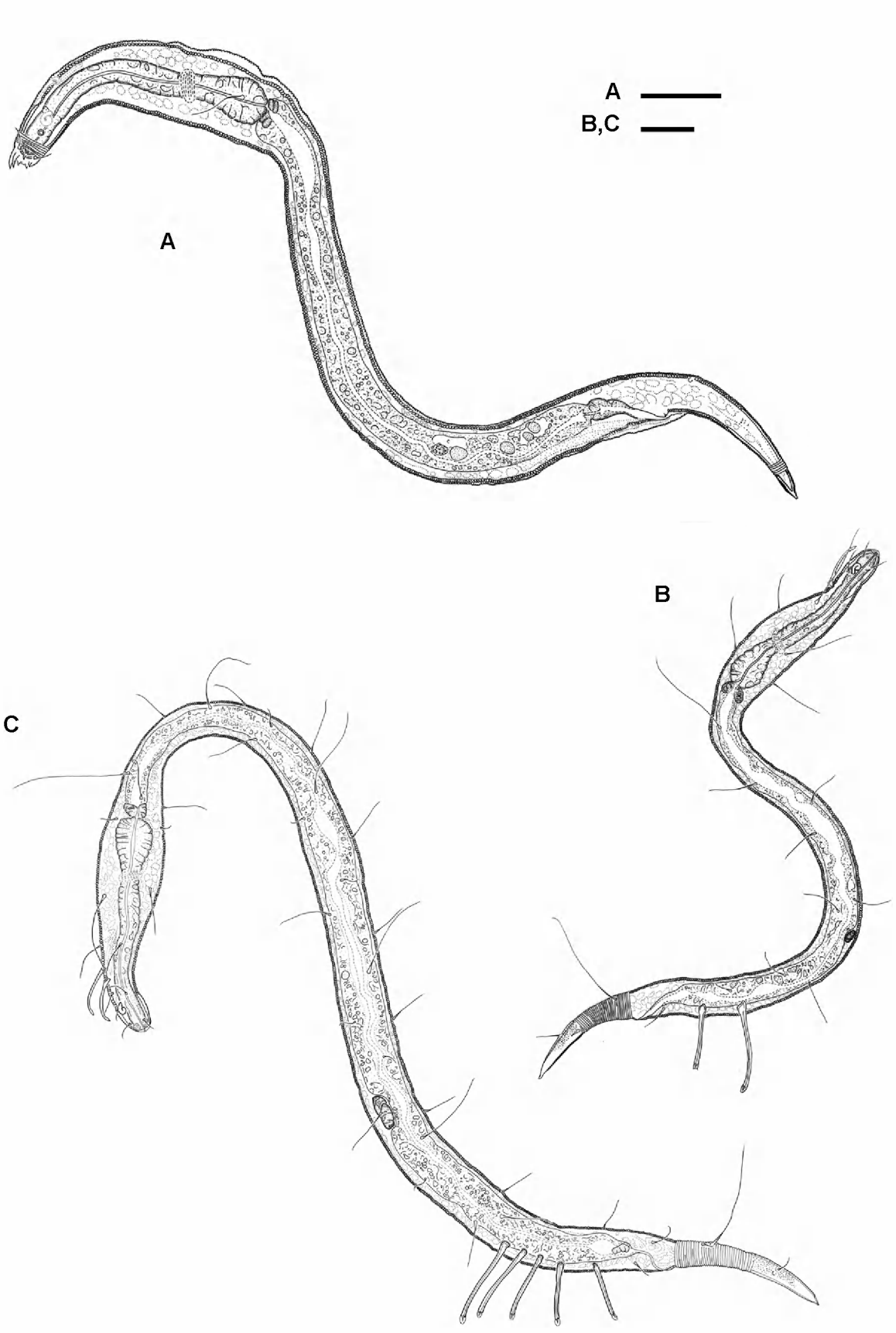


Fig. 6. *Cygnonema belgicae* sp. n. (A) first stage juvenile, habitus; (B) second stage juvenile, habitus; (C) third stage juvenile, habitus. Scale bars 20 µm.

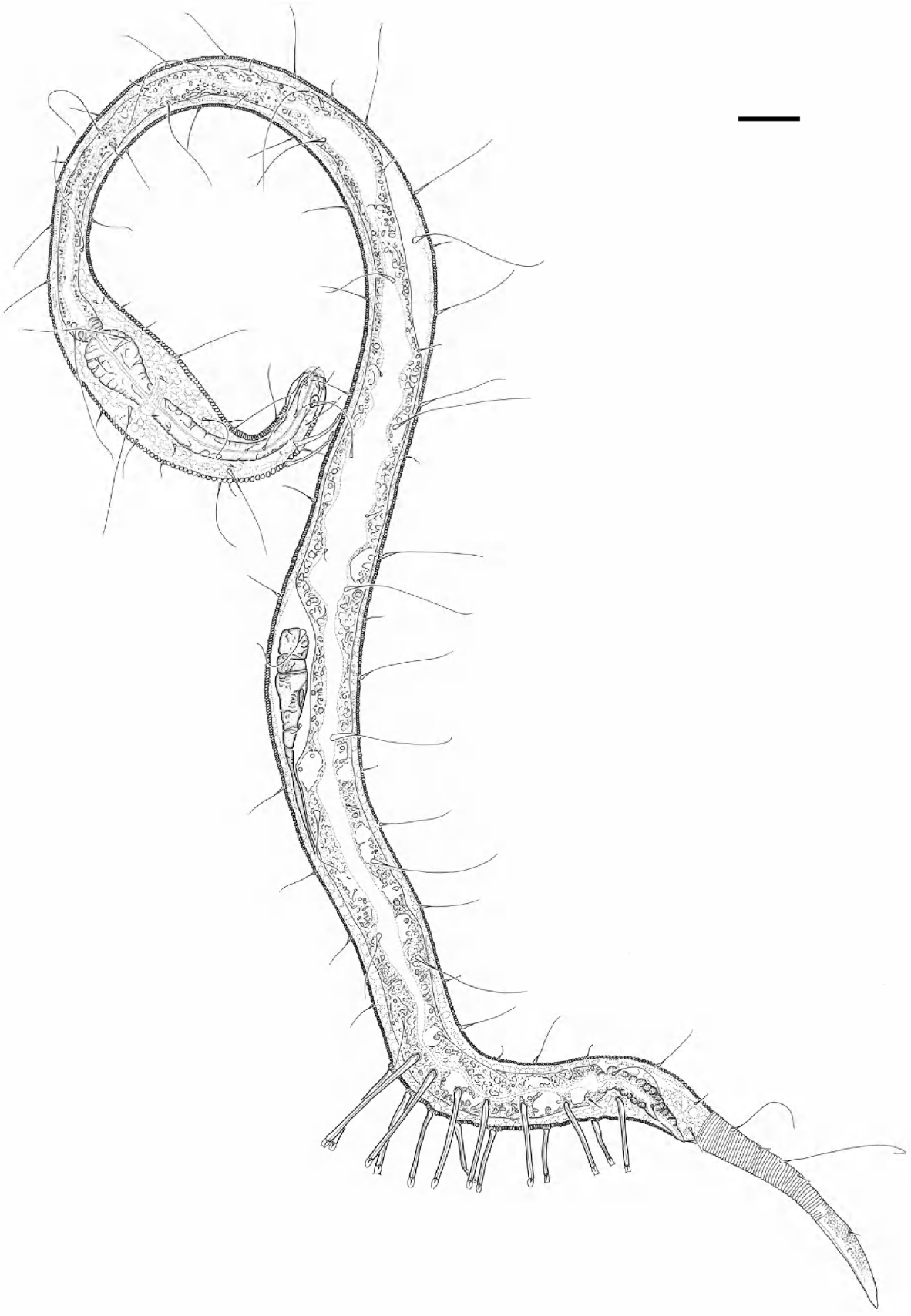


Fig. 7. *Cygnonema belgicae* sp. n. Fourth stage juvenile, habitus. Scale bar 20 µm.

Fig. 8. *Cygnonema belgicae* sp. n. (A) ♂, habitus; (B) ♀, habitus; (C) ♂, posterior body region; (D) ♀, posterior body region; (E) ♂, head capsule and pharyngeal region. Scale bars: 100 µm (A,B); 10 µm (C-E).

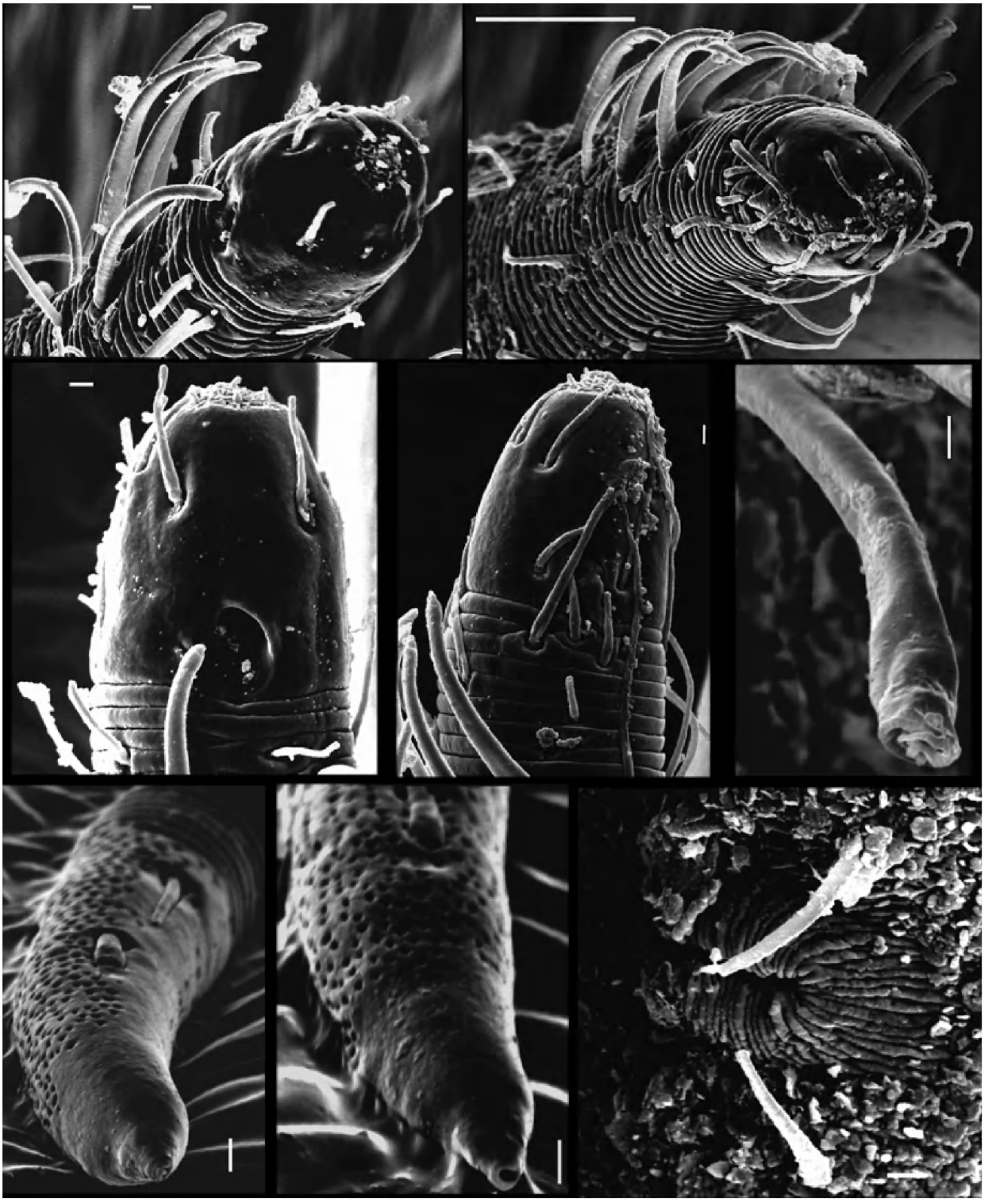


Fig. 9. *Cygnonema belgicae* sp. n. (A) ♂, anterior region (en face view); (B) ♀, anterior region; (C) ♂, head capsule (lateral view); (D) ♀, head capsule (lateral view); (E) ♂, PAT tip; (F) ♂, smooth tail tip; (G) ♀, smooth tail tip; (H) ♀, vulva. Scale bars: 1 µm (A,C-H); 10 µm (B).

8.6. ACKNOWLEDGEMENTS

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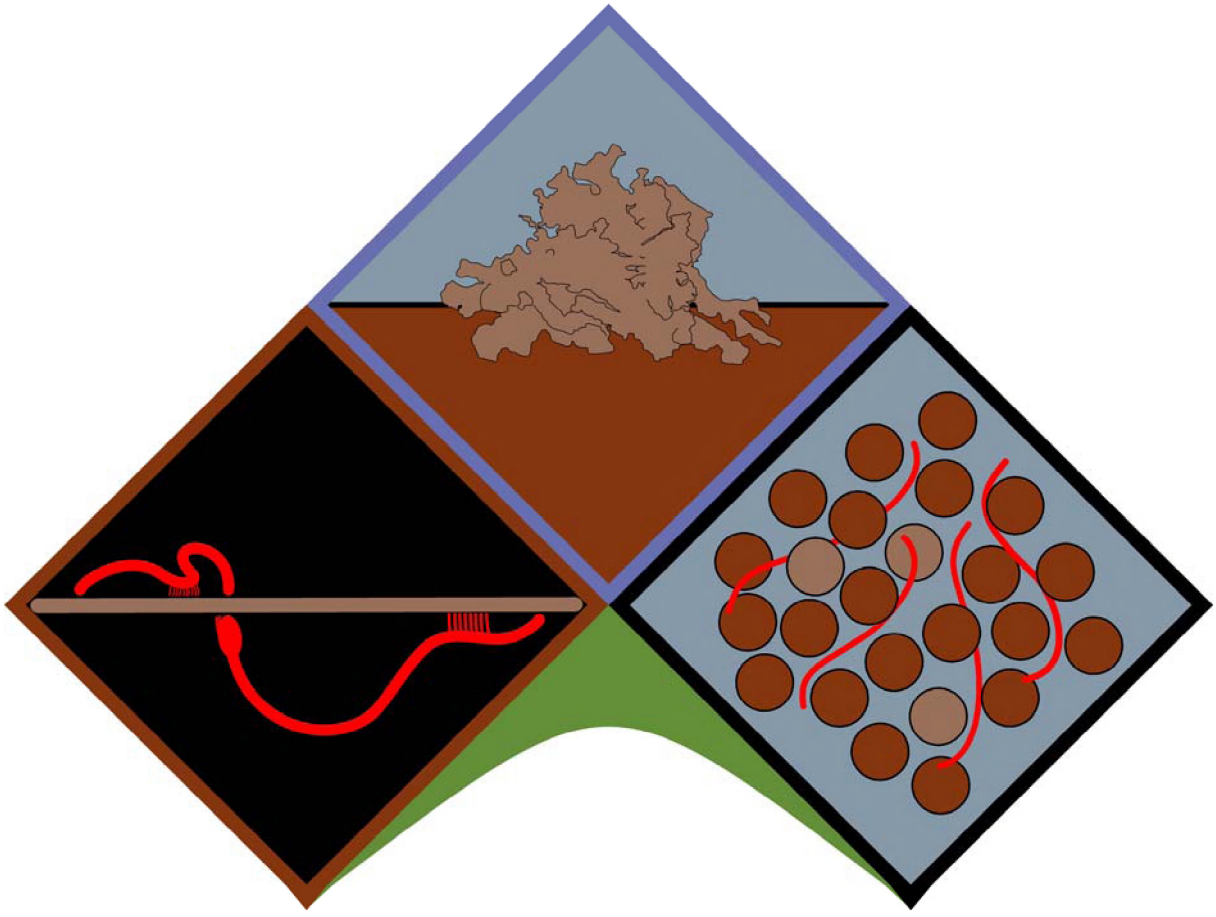
CHAPTER 9

GENERAL DISCUSSION AND FUTURE PERSPECTIVES



The present study discusses several aspects of the nematode communities associated with cold-water and tropical coral reefs. In this final chapter, the main results from the preceding chapters will be brought together in order to acquire an overview of the main contributions of this thesis and to compare the data from these two extreme environments. The first section shows that although the environmental conditions in both biotopes are fundamentally different, the nematode communities are determined by generally the same factors, such as microhabitat type, the influence of strong current activity and sediment infill. Morphological adaptations of the nematofauna to the structure of the microhabitat are also discussed. Section 9.2. discusses α-, β- and γ-diversity, the influence of microhabitat structure on the biodiversity of the associated fauna and the contribution of coral degradation products to the total diversity of the ecosystem. Biodiversity in both biotopes is compared. Again, some striking similarities become clear. In the next section, cosmopolitanism of meiofauna and the existence of cryptic species are briefly discussed and some prospects for future research on these topics are given. The present study has yielded new insights into the taxonomy of Epsilonematidae and Draconematidae, which are summarised in Section 9.4. In this section, the relationships between taxa, the delineation of diagnostic features, the assessment of character states and the problem of intraspecific variability within both families are critically discussed and the need for molecular support to unravel these issues is put forward. The final section indicates how this study contributes to our knowledge of the marine nematofauna and coral degradation zones. Future perspectives are briefly unfolded.

9.1. NEMATODE COMMUNITY STRUCTURE - STRUCTURING FACTORS

The nematode community composition and the factors which influence it are discussed in Chapters 2, 3 and 4. It is important to notice that although these three chapters deal with communities from distant regions and on different taxonomic levels, many of the results and discussion issues are the same. Therefore, the main results from these studies are brought together here in a concise way.

If there is anything clear from the comparison of these three chapters, it is that marine, free-living nematodes are in essence sediment-dwellers. The vast majority are characterised by a slender habitus and an undulating movement, which are suitable adaptations to a life in the interstitia between the sand grains. As a result, nematode communities are particularly structured by differences in sediment properties, *e.g.* median grain size. Differences in grain size were indeed proven more important in structuring the nematode communities in tropical coral degradation zones than the general distinction between sedimentary and substratum-based habitats. On the other hand, grain size is largely determined by hydrodynamics. Therefore, it is possible that the nematode community composition is not structured by the grain size itself, but by other environmental variables that are related to the hydrodynamic conditions, such as food and oxygen availability. The research at hand indicates a principal distinction between communities in fine/medium sediment on the one hand and communities in coarser habitats on the other hand, followed by a distinction within the coarser habitats: between coarse sediment communities and communities associated with large biogenic substrata. This last distinction has also been observed in cold-water coral degradation zones. Not only

is the sediment generally characterised by a higher relative abundance of nematodes in comparison to the large biogenic substrata, the results of this thesis also indicate that the slender morphotype is much less adapted to the strong hydrodynamic stress which is associated with these substrata. The conception that coral fragments and sponge skeletons on the deep ocean floor (Porcupine Seabight) or the shallow sea-floor (Kenya) are strongly influenced by erosive current activity, whereas the sediment is relatively undisturbed, has been put forward as the main explanation for the observed differences between nematode communities in sedimentary and substratum-based habitats. The rationale behind this idea is that large substrata, such as coral fragments and sponge skeletons, lie relatively unprotected on the sea floor and protrude from the sediment, whereas the sediment itself may be protected by the substrata that cover it. Disturbance by strong currents may lead to physical erosion and direct removal of meiofaunal animals and may successfully keep fine detrital food in suspension so that it is not available to the fauna associated with the large substrata. This idea is however contradicted by the results of the meiofauna community on a higher taxon level, which suggest that *i.c.* the coral fragments are low disturbance habitats characterised by low predation pressure and abundant food. The evidence for this last hypothesis was however rather circumstantial compared to the evidence for the first one and therefore I recant the latter hypothesis.

Given that the nematofauna on coral fragments and sponge skeletons is fundamentally structured by physical disturbance, taxa that are able to successfully withstand this perturbation have a competitive advantage here. A typical example is provided by the two closely related families Epsilonematidae and Draconematidae, which are morphologically and ecologically adapted to live in high-disturbance habitats. Draconematids are able to strongly attach themselves to the substratum with tubes associated with adhesive glands. Epsilonematids are able to cling onto the substratum with their ambulatory setae, they can attach themselves to the substratum with caudal glands, and they are short, stout, and heavily cuticularised. Analogous adaptations have been observed in the genus *Desmoscolex*. In fact, the research reported in this thesis proves that on different taxonomic levels, habitat preferences of individual taxa can be deduced from their morphology. On the higher taxon level, the slender shape of a generalised nematode is an adaptation to an interstitial life strategy; on the level immediately above family level (but not considering the Desmodoridae, which are also part of the same superfamily), the Epsilonematidae and Draconematidae stand out as taxa typically adapted to an epifaunal life strategy; on the family level, Epsilonematidae differ from Draconematidae in their adhesive attributes; on the genus level, *Sabatieria* (Comesomatidae, Araeolaimida) was recognised as a typical taxon for suboxic sediments, and at the species level, even more fine-tuned morphological adaptations were found (hooked setae for clinging onto sponge spicules (*Bathyepsilonema lopheliae* Raes, Vanreusel & Decraemer, 2003); absence of ambulatory setae in less disturbed habitats (*Perepsilonema papulosum* Lorenzen, 1973)...). It is clear that more *in situ* observations are needed to unravel the interaction between morphology, ecology and microhabitat structure in more detail.

The sediment is not fundamentally structured by physical disturbance and therefore the typically epifaunal Epsilonematidae and Draconematidae lose their competitive advantage here. As a result, the communities in the sediment of coral degradation zones are very much comparable to those from similar and/or nearby environments, even when these are not associated with corals (*i.c.* slope

sediments, other tropical lagoons). The fact that the large biogenic substrata are in close contact with the sediment, especially when it is resuspended and deposited between the coral branches or sponge spicules, has led to the conclusion that the meio-epifauna consists of a sediment-dwelling, interstitial background community, typical for the region or environment, supplemented with morphologically adapted typically epifaunal taxa. The contribution of these taxa to the total community depends on the microhabitat. Importantly, this has been found independently on a higher taxon level and within the nematode community. On an even lower taxonomic level (species within the two typically epifaunal families), it becomes clear that coral fragments are a favourable substratum for Epsilonematidae and Draconematidae, whereas this is not the case for sponge skeletons, which harbour a community more comparable to that in sediments. Again, a similar conclusion was drawn from the genus-level identifications.

In recent literature, there has been considerable debate on the relevance and applicability of the four 'trophic groups' proposed by Wieser (1953) (Moens & Vincx, 1997; Moens *et al.*, 2004). It is clear that only four possible trophic groups for such a diversity in buccal cavity shapes, food sources, microhabitats and life strategies, is grossly insufficient. Moreover, it is clear from *in situ* observations that a certain species may feed on different food sources and nematodes may even switch from one food source to another given the appropriate conditions (T. Moens, pers. comm.). However, the usefulness of this classification should also not be underestimated, as many statistically relevant differences in preferences of a certain Wieser-group have proven to be very useful in understanding the structuring effect of microhabitats.

Not only microhabitats are important in structuring the nematode communities. However, the structuring effect on a local and even regional scale is rather limited when compared to microhabitats, both on the genus level (Kenya) and on the species level (Epsilonematidae/Draconematidae Kenya). The fact that cold-water coral sediment, tropical coral sediment, coral gravel, sponge skeletons and coral fragments are all characterised by different nematode communities emphasises the importance of all the microhabitats considered in this study. Especially the dead coral fragments, which are recognised as an important source of new species of Epsilonematidae and Draconematidae (and most likely also other taxa) merit being included in the policy regarding coral reef conservation. Clearly, this also applies to the whole tropical and cold-water coral degradation zone as a habitat and as an ecosystem. The information assembled in this thesis is also essential for understanding the ecosystem functioning of the smaller size classes in these habitats.

9.2. NEMATODE BIODIVERSITY

It is obvious from literature that both tropical and deep-sea coral reefs (or banks) are characterised by a high biological diversity (see Section 1.1. for a more detailed discussion on this topic). Diversity numbers however come from either the coral species themselves, or from associated macro- and megafauna (mainly fish). One of the original aims of this study was to calculate meiofaunal diversity in order to confirm this statement for meiofauna as well. Such information could then be used as an additional argument for the conservation of these coral reefs. The issue is especially urgent for deep-

sea coral reefs, which are still largely unknown but already seriously in danger. There were however two reasons not to sample in the living reef itself. First of all, there was the issue of ethics: destroying a part of the reef by dropping a box corer onto it, and then claiming it is only necessary, collateral damage in order to achieve a higher cause (*i.e.* the protection of the reef), is at the very least a peculiar method. There was, however, also a more direct practical reason: the living coral tissue acts as an effective antifouling buffer, preventing meiofauna from living in association with the living coral framework. The main question is now: how diverse are the degradation zones adjacent to the reef in terms of meiofauna, and do they also deserve conservation? For macrofauna, a high diversity associated with dead coral framework has already been established (Jensen & Frederiksen, 1992; Mortensen *et al.*, 1995).

First of all, attention is again turned to the different microhabitats. On the higher taxon level, the sediment was found to be least diverse (Porcupine Seabight: E*T* (100) = 6.76; N_{inf} = 1.20), whereas the coral fragments were characterised by the highest taxon richness (E*T* (100) = 9.65) and evenness (N_{inf} = 2.00). This was however simply due to the high dominance of nematodes in the sediment, and the corresponding low number of other taxa. On the (nematode) genus level, the sediment was recognised as the most diverse microhabitat, both in tropical (N_0 = 115; *H'* = 3.84) and in cold-water coral (N_0 = 106; *H'* = 3.86) degradation zones (although not significantly so in the tropical region). This was unexpected at first, provided that the coral and sponge substrata were regarded as microhabitats with a high habitat complexity. The rationale here was that the 'large biogenic substratum microhabitat' is a combination of (1) the three-dimensionally complex coral or sponge skeleton microhabitat and (2) the sediment microhabitat, which was added through sediment infill. Even more potential 'microhabitats within microhabitats' were distinguished (*e.g.* a felty layer of bryozoans on cold-water coral skeletons, cavities in the skeletons…). Nevertheless, the large biogenic substrata are considered hostile, hydrodynamically disturbed microhabitats, which are not suitable for most nematodes. As already argued in Section 9.1., nematodes prefer the relatively calm, interstitial microhabitat of the sediment. Moreover, the large substrata are considered poor in particulate food, due to the constant resuspension of detritus. Only in the sediment, nematodes are able to establish a well-developed community, hence their high diversity in this microhabitat. On the species level, within the two typically epifaunal families, the situation was again opposite: coral fragments were most diverse (in comparison with coral gravel). This is not unexpected, as coral fragments have been indicated as a favourable microhabitat for these typically epifaunal taxa. For being nematodes, Epsilonematidae and Draconematidae are indeed aberrant in their microhabitat preferences.

This is the first study where coral degradation products are included as a potential habitat for meiofauna. Although the sediment has been proven to be most favourable for the majority of nematodes, the coral fragments are recognised as highly diverse for Epsilonematidae and Draconematidae, and as an important source for many new species belonging to these families. The sediment already harbours most of the genera in our study area along the Kenyan coast (*i.c.* 115), but genus area curves have shown that especially the coral fragments add considerably (*i.c.* 11) to the total number of genera. This is an important finding, as it can be used as an argument for conservation of coral degradation zones.

Biodiversity is traditionally subdivided in α- or sample-diversity, ß-diversity or turnover and γ-diversity or regional diversity. The contribution of α and ß diversity to γ diversity has only been examined on the species level for Epsilonematidae and Draconematidae. Sample diversity was clearly the most important contributor to regional diversity when abundances were considered (71.2%), whereas the different sampling locations added a large number of species, which were however generally rare. The high sample diversity indicates considerable patchiness in the distribution of the epifaunal nematodes.

There is one final question still to be answered: are cold-water coral degradation zones as diverse as tropical coral degradation zones for nematodes? Only the sediment and coral fragments can be compared here, as the other microhabitat types were only present in one of the regions. The total number of individuals identified in either of these four microhabitats was comparable, although a slightly higher number of specimens was analysed for the coral fragments in the Porcupine Seabight. The total number of genera associated with cold-water coral fragments (93) was more or less the same as on tropical coral fragments (87) and the same is true for the sediment (106 and 115 genera, respectively). To avoid any effect of sample size, the expected number of genera for 100 individuals is also compared. Both the sediment samples and the coral fragments from the Porcupine Seabight yielded a slightly higher number than the same microhabitats in Kenya (43.3 vs. 41.7 and 38.4 vs. 35.2, respectively). In terms of dominance, the diversity of cold-water coral fragments was even more explicitly higher than the diversity of the tropical coral fragments (N_{inf} = 11.2 and 4.4, respectively). For the sediment samples, evenness was almost identical. These results clearly show that cold-water coral degradation zones are at least as diverse as tropical coral degradation zones. They might even be slightly more diverse. On the other hand, the epsilonematid and draconematid communities along the Kenyan coast are noticeably more diverse than those in cold-water coral degradation zones. This difference has however been attributed to a difference in sampling scale: eight sites, 160 km apart along the Kenyan coast vs. only one location in the Porcupine Seabight.

It can be concluded that both tropical and cold-water coral degradation zones merit conservation, because they are a source of new species and because the dead coral fragments in these habitats considerably contribute to the total genus richness.

9.3. BIOGEOGRAPHY

With each description of a new species of Epsilonematidae and Draconematidae, some new information becomes available on the biogeography of these animals. However, a comprehensive analysis of the species composition in a certain region, such as provided in Chapter 4, yields much more information, as a higher number of species can be considered at once. In this regard, biogeography research will benefit from a shift from a species-oriented to a habitat-oriented approach. Of course, only animals with a clear-cut and known habitat preference qualify for such an approach. It is proven here that dead coral fragments and other coral degradation products are an important source for a rich Epsilonematidae and Draconematidae community. The proposed course of action is (1) to look for the appropriate habitat, (2) sample it in large quantities, and (3) analyse the associated

fauna within the desired taxonomical boundaries (*i.c.* within the two families of interest). This approach has been proven to be very useful for the purposes of the research at hand.

Although cosmopolitanism in marine, free-living nematodes is believed to be a common phenomenon, its unlikelihood has been thoroughly discussed in this thesis (Chapter 4). After weighing up the different possible explanations for the existence of morphologically identical nematodes in geographically and bathymetrically distant areas, the notion of cryptic species turned out to be the most plausible one for the time being. Several recent studies have shown that some meiobenthic 'species' are indeed complexes of cryptic species and that putatively cosmopolitan species have a much more restricted geographical distribution (Schmidt & Westheide, 2000; Rocha-Olivares *et al.*, 2001; Derycke *et al.*, 2005). Nevertheless, the study of population genetics in nematodes is still in its infancy and the amount of information on this topic is at the moment very limited. Epsilonematidae and Draconematidae could well be very suitable taxa for the investigation of cryptic speciation related to cosmopolitanism. In comparison with other nematode taxa, the delineation of morphological species within these two families is well-founded, as it can be based on a high number of distinct morphological and morphometrical criteria. A robust morphological species concept is imperative if one tries to compare with molecular data, in search for cryptic species. Moreover, it is also indispensable if one wants to refute the pseudo-sibling species concept.

Another aspect of nematode biogeography which merits more research is the mapping of potential dispersion routes, which could be important in permitting active gene flow between populations. As it is assumed here that active gene flow does not exist on a global scale, such dispersion pathways should only be considered on a local and regional scale. Whether gene flow is indeed active along these routes can again be tested through molecular analyses.

9.4. TAXONOMY, DIAGNOSTIC FEATURES AND RELATIONSHIPS BETWEEN SPECIES

In this thesis, seven new species of nematodes are described from the newly explored cold-water coral degradation zone habitat. These descriptions have provided new insights into the taxonomy of both Epsilonematidae and Draconematidae, and have elucidated some relationships at species and genus level. The emphasis has been on the adequate delineation of diagnostic features and the pitfall of intraspecific variability.

Gourbault & Decraemer (1996) and Decraemer *et al.* (1997) have attempted a phylogenetic analysis of genera belonging to the Epsilonematidae and Draconematidae respectively, based on morphological features. Although the choice of the utilised diagnostic features was thoroughly argued and clearly well-founded, their analyses fell short of indicating the relationships between the different genera in Epsilonematidae. For Draconematidae, the results were somewhat more satisfactory, as they clearly pointed to a classification of the genus *Tenuidraconema* in the subfamily Draconematinae. Nevertheless, only few branches were present and the relationships between most genera remained undetermined. Neira *et al.* (2005) attempted a similar analysis on the species level within the Epsilonematidae. Some extra diagnostic features were added and their usefulness was again

thoroughly argued. Nevertheless, the relationships among genera could again not be fully resolved with the phylogenetic analysis. These authors proposed that the dataset should be extended with additional ultrastructural and molecular features. A higher number of characters is indeed important to raise the consistency index, which was rather low in the analyses. However, the addition of more diagnostic features should not be at the expense of their quality. Moreover, the choice and delineation of diagnostic features should always be done conscientiously. In this context, the species descriptions in this thesis have yielded the following important results:

Epsilonematidae.

1. the arrangement of ambulatory setae and the number of subcephalic setae are not good diagnostic features to distinguish the two genera in the subfamily Glochinematinae (Epsilonematidae), whereas the presence of strongly built, tubular, dorsosublateral ambulatory setae is;
2. the genus *Akanthepsilonema* (Epsilonematidae) is characterised by the combination of an elongated anterior body region, a maximum-to-minimum body diameter ratio of less than two, six rows of ambulatory setae situated both anterior to and posterior to the vulva, supporting setae only differentiated in females and juveniles and eight subcephalic setae not displaced towards the anterior part of the head capsule;
3. the presence of conspicuous copulatory thorns, large spines and horns is not an adequate diagnostic feature to distinguish between genera in the family Epsilonematidae;
4. the position of the ambulatory setae relative to the vulva, *i.c.* whether the majority is situated anterior or posterior to it, is a feature intragenerically variable and should be used with caution to distinguish between genera in the family Epsilonematidae;
5. cuticular ornamentation may be variable within a species;
6. the number of rows of ambulatory setae in Epsilonematidae is prone to misinterpretation and should be examined conscientiously;
7. the number of caudal gland outlets is variable within a species, either between different stages of development or between sexes.

Draconematidae.

8. the position and number of CAT may vary within a genus in Draconematidae;
9. the size, shape and number of sperm cells may be considerably different between closely related species and is considered a useful diagnostic feature to distinguish between species within the same genus in Draconematidae;
10. within a species, lateral alae (or a lateral field) may be present or absent (inconspicuous);
11. the number of subcephalic setae can be an adequate diagnostic feature to distinguish species within the same genus of Draconematidae (*i.c. Cygnonema*).

Many of the features considered to be of diagnostic value for the distinction between genera in Epsilonematidae (Gourbault & Decraemer, 1996) or Draconematidae (Decraemer *et al.*, 1997) have

been proven here to be either unsuitable, or they should be used with caution: the number of rows of ambulatory setae, the number of subcephalic setae, the presence of conspicuous cuticular protrusions (*e.g.* in the pharyngeal region), the arrangement of ambulatory setae in relation to the vulva and the number of outlets of caudal glands in Epsilonematidae, the presence of lateral alae and the number and position of CAT in Draconematidae. The results of this thesis also indicate that certain features may be suitable for the distinction between genera within one subfamily, but not within another or for the distinction between species within one genus and not within another genus. It is also true that the most prominent features are not always the most suitable ones for distinction between taxa. An important example is the intraspecific variability in cuticular ornamentation. Personal observations have shown that the ornamentation of the cuticle in *Perepsilonema papulosum*, a species abundantly found along the coast of Kenya, is extremely variable: either with small, irregular vacuoles, with longitudinal striae or completely smooth. Cuticular ornamentation has however been used as a diagnostic feature to distinguish between species within this genus. Cuticular ornamentation was also observed to be variable in *e.g. Epsilonema parvospina* Decraemer, 1982 and *Pternepsilonema servaesae* Verschelde & Vincx, 1992. Intraspecific variability was also observed in the number, arrangement and size of copulatory thorns (*P. papulosum*; *E. parvospina*; *E.* sp. 12 sp. n.; *Bathyepsilonema* sp. 2 sp. n.;...). Extensive variability could however only be assessed when a large number of individuals from several locations was compared. Clearly, a large extent of intraspecific variability fundamentally influences and even hampers the distinction between species. Nevertheless, it is a real fact which should be taken into account, also in species description. Therefore, it is recommended here that species descriptions should be based on a considerable number of individuals, at least enough to assess intraspecific variability.

The delineation of diagnostic features and assessment of character states (*i.e.* whether plesiomorphic or apomorphic) can be facilitated through (1) outgroup comparison and (2) comparison between different stages of development. Epsilonematidae and Draconematidae are very suitable to study the different juvenile stages, as they can be relatively easily distinguished based on the number and arrangement of ambulatory setae (Epsilonematidae) or adhesion tubes (Draconematidae). As a result, the different juvenile stages are relatively well-known in both families and differences in morphological features between the one stage and the next have already provided a lot of information useful for assessing diagnostic features. It is recommended here that information on the morphology of the different juvenile stages, preferably beginning with the first stage juvenile, should always be added in future descriptions where possible.

Morphological features that have a definite ecological significance may be more suitable as diagnostic features. They are crucial for adaptive evolution in natural populations because of the importance of such features for the survival and/or competitive advantage of the animal. These features will respond more adequately to changes in the environment. Morphological structures related to reproduction, locomotion and feeding are relevant examples. Changes in the first type of characters also lead to reproductive isolation and therefore new species according to the biological species concept. Features associated with locomotion also included sensory organs and structures important in keeping the balance while crawling. Indeed, 13 of the 16 diagnostic features used to distinguish

between genera in the family Epsilonematidae can be related to one of the three ecological traits above. In Draconematidae this number is 8 out of 13. It is important to add here that features with ecological significance should be used with caution in taxonomy, as similar character states in different taxa could be the result of parallel evolution.

In order to test the significance of the diagnostic features that were selected, molecular support is needed. The rationale here is that if the phylogenetic tree based on morphological character states is completely supported by molecular (sequence) data, the selected characters are suitable as diagnostic features. Small subunit (SSU or 18S) rDNA sequences can be used here, as these have been proven very useful for phylogenetic analyses above population level in nematodes. Molecular phylogenetic analyses with 18S rDNA as a phylogenetic marker have already elucidated some of the relationships between nematode taxa on a higher taxonomical level (between classes, subclasses, orders, families - Blaxter *et al.*, 1998; De Ley & Blaxter, 2002; De Ley & Blaxter, 2003) and on a lower taxonomical level (between genera or species - *e.g.* Fitch *et al.*, 1995; De Ley *et al.*, 2002). The best way to unravel the phylogenetic relationships between taxa is, however, the combination of (1) a phylogenetic analysis based on morphological features and (2) a phylogenetic analysis based on molecular data. The results are considered most reliable when both resulting trees support each other and when the relationships can also be confirmed by ontogenetic observations. This means that all three sources of information are equally essential. Although the recent developments in molecular taxonomy have provided a powerful tool for analysis of phylogeny, the importance of classical (*i.e.* morphology-based) taxonomy should not be minimised. Moreover, it is still the only source of comprehensive species descriptions suitable for ecological research.

9.5. RELEVANCE AND FUTURE PERSPECTIVES

The innovative character of this thesis lies in the following facts:

1. this is the first comprehensive study dealing with cold-water coral associated meiofaunal and nematode communities;
2. this is the first study where different coral degradation products are considered as habitats for meiofauna and where the importance of these structures (1) in determining the meiofaunal and nematode community composition, (2) in contributing to the total biodiversity of the ecosystem, (3) as a source of new species and (4) as a rich source of Epsilonematidae and Draconematidae, is assessed and established;
3. this is to my knowledge the first study where the community structure and biodiversity of an ecologically defined subset (*i.c.* Epsilonematidae + Draconematidae) of a taxon (*i.c.* Nematoda) has been successfully analysed and has been proven to be relevant;
4. the high number of individuals belonging to the families Epsilonematidae and Draconematidae that was found in association with these coral degradation products, has enabled (1) a more thorough evaluation of intraspecific variability and (2) a better understanding of the biogeography of these taxa.

As already argued above, this study yielded many interesting results. Nevertheless, it has also revealed the need for a molecular support for the delineation of diagnostic features and for the assessment of phylogenetic relationships between taxa. Epsilonematidae and Draconematidae are clearly suitable taxa for such an analysis, as the number of potential diagnostic features is high and also because the coral degradation zones and general coarse sands provide a major source for large quantities of these taxa. Moreover, the presented research is also a strong plea for an increased effort in the production of comprehensive, well-founded and well-supported species descriptions. Species are the bricks of our tower of knowledge and should therefore be determined and described in a conscientious way.

To recapitulate, both tropical and cold-water coral degradation zones merit conservation, because they are a source of new species and because the dead coral fragments in these habitats considerably contribute to the total genus richness. The data presented in this thesis can be clearly used as an additional argument for conservation. However, the fact that these data come from meiofauna may be disadvantageous. Meiofauna is not known to the general public as it is not macroscopically observable and because it is not perceived as very charismatic. Nevertheless, public awareness and public concern are essential to get the message through that cold-water coral reefs are in danger and should urgently be protected from destructive anthropogenic activities. Some animals are known to capture the public attention and will always lead the campaign for conservation, regardless of biological concerns (*e.g.* giant panda; young harp seals...). Given their peculiar and dragon-like habitus, Epsilonematidae and Draconematidae may appeal more to the general public and could therefore be used as flagship taxa for meiofauna.

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GENUS AND SPECIES LIST

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Classification up to family level after De Ley & Blaxter (2003); below family level after Lorenzen (1994). Classification of Desmoscolecidae after Decraemer (1985); Epsilonematidae after Gourbault & Decraemer (1996); Draconematidae after Decraemer *et al.* (1997).

[1] : Porcupine Seabight

[2] : Kenya

[3] : Zanzibar

PHYLUM NEMATODA POTTS, 1932

INCERTAE SEDIS

ORDO BENTHIMERMITHIDA TCHESUNOV, 1995

Familia Benthimermithidae Petter, 1980

Benthimermis Petter, 1980[1]

ORDO RHAPTOTHYREIDA TCHESUNOV, 1995

Familia Rhaptothyreidae Hope & Murphy, 1969

Rhaptothyreus Hope & Murphy, 1969[1]

CLASSIS ENOPLEA INGLIS, 1983

SUBCLASSIS ENOPLIA PEARSE, 1942

ORDO ENOPLIDA FILIPJEV, 1929

Enoplida gen.1 gen. n.[2]

Enoplida sp. 1[2]

Subordo Enoplina Chitwood & Chitwood, 1937

Superfamilia Enoploidea Dujardin, 1845

Familia Enoplidae Dujardin, 1845

Enoplus Dujardin, 1845[1,2,3]

Familia Thoracostomopsidae Filipjev, 1927

Subfamilia Enoplolaiminae de Coninck, 1965

Enoploides Ssaweljev, 1912[2]

Enoplolaimus de Man, 1893[2,3]

Epacanthion Wieser, 1953[2,3]

Fenestrolaimus Filipjev, 1927[1]

Mesacanthion Filipjev, 1927[1,2]

Paramesacanthion Wieser, 1953[2]

Familia Anoplostomatidae Gerlach & Riemann, 1974

Subfamilia Anoplostomatinae Gerlach & Riemann, 1974

Anoplostoma Bütschli, 1874[1]

Subfamilia Chaetonematinae Gerlach & Riemann, 1974

Chaetonema Filipjev, 1927[1]

Familia Phanodermatidae Filipjev, 1927

Subfamilia Phanodermatinae Filipjev, 1927

Phanoderma Bastian, 1865[2,3]

Subfamilia Crenopharyngidae Platonova, 1976

Crenopharyngidae sp. 1[1]

Familia Anticomidae Filipjev, 1918

Anticoma Bastian, 1865[1,2,3]

Subordo Trefusiina Siddiqi, 1983

Superfamilia Trefusioidea Gerlach, 1966

Familia Trefusiidae Gerlach, 1966

Subfamilia Trefusiinae Gerlach, 1966

aff. *Trefusia*[1]

Rhabdocoma Cobb, 1920[1]

Trefusia de Man, 1893[1,3]

Familia Xenellidae de Coninck, 1965

Xenella Cobb, 1920[1]
Subordo Oncholaimina de Coninck, 1965
Superfamilia Oncholaimoidea Filipjev, 1916
Familia Oncholaimidae Filipjev, 1916
Oncholaimidae gen. 1[2]
Oncholaimidae gen. 4[2]
Subfamilia Oncholaimellinae de Coninck, 1965
Viscosia de man, 1890[1,2,3]
Subfamilia Oncholaiminae Filipjev, 1916
Metoncholaimus Filipjev, 1918[1,2]
Oncholaimus Dujardin, 1845[2]
Familia Enchelidiidae Filipjev, 1918
Calyptronema Marion, 1870[1,2]
Eurystomina Filipjev, 1921[2,3]
Pareurystomina Micoletzky, 1930[1,2]
Polygastrophora de Man, 1922[2,3]
Symplocostoma Bastian, 1865[1,2,3]
Subordo Ironina Siddiqi, 1983
Superfamilia Ironoidea de Man, 1876
Familia Ironidae de Man, 1876
Subfamilia Thalassironinae Andrassy, 1976
Dolicholaimus de Man, 1888[2,3]
Syringolaimus de Man, 1888[1,2,3]
Thalassironinae sp. 1[1]
Thalassironus de man, 1889[2,3]
Trissonchulus Cobb, 1920[2]
Familia Leptosomatidae Filipjev, 1916
Subfamilia Leptosomatinae Filipjev, 1916
aff. *Leptosomatum*[2]
Subfamilia Synonchinae Platonova, 1970
Synonchus Cobb, 1894[1]
Familia Oxystominidae Chitwood, 1935
Subfamilia Oxystomininae Chitwood, 1935
Litinium Cobb, 1920[1,3]
Nemanema Cobb, 1920[1]
Oxystomina Filipjev, 1921[1,2,3]
Thalassoalaimus de Man, 1893[1,3]
Wieseria Gerlach, 1956[1]
Subfamilia Halalaiminae de Coninck, 1965
Halalaimus de Man, 1888[1,2,3]
Subfamilia Paroxystomininae de Conicnk, 1965
Paroxystomina Micoletzky, 1924[2]

CLASSIS CHROMADOREA INGLIS, 1983
SUBCLASSIS CHROMADORIA PEARSE, 1942
ORDO DESMOSCOLECIDA FILIPJEV, 1929
Subordo Desmoscolecina Filipjev, 1934
Superfamilia Desmoscolecoidea Shipley, 1896
Familia Desmoscolecidae Shipley, 1896
Subfamilia Desmoscolecinae Shipley, 1896
Tribus Desmoscolecini Decraemer, 1985
Desmoscolex Claparède, 1863[1,2,3]
Tribus Greeffiellini Decraemer, 1985
Greeffiella Cobb, 1922[1]
Subfamilia Tricominae Lorenzen, 1969
aff. *Antarcticonema*[1]
Haptotricoma Lorenzen, 1977[1]
Paratricoma Gerlach, 1964[1]
Tricoma Cobb, 1894[1,2,3]
Familia Meyliidae De Coninck, 1965

aff. *Noffsingeria*[1]
Familia Cyartonematidae Tchesunov, 1990
Cyartonema Cobb, 1920[1,3]
ORDO CHROMADORIDA FILIPJEV, 1929
Subordo Chromadorina Filipjev, 1929
Superfamilia Chromadoroidea Filipjev, 1917
Familia Chromadoridae Filipjev, 1917
Subfamilia Spilipherinae Filipjev, 1918
Acantholaimus Allgén, 1933[1]
Spiliphera Bastian, 1865[1]
Subfamilia Chromadorinae Filipjev, 1917
Atrochromadora Wieser, 1959[2,3]
Chromadora Bastian, 1865[1,2,3]
Chromadorella Filipjev, 1918[1,2,3]
Chromadorina Filipjev, 1918[1,2,3]
Prochromadora Filipjev, 1922[1,2,3]
Prochromadorella Micoletzky, 1924[1,2,3]
Subfamilia Euchromadorinae Gerlach & Riemann, 1973
Actinonema Cobb, 1920[1,2,3]
Euchromadora de Man, 1886[2,3]
Rhips Cobb, 1920[1,2]
Trochamus Boucher & Bovée, 1972[2,3]
Subfamilia Hypodontolaiminae de Coninck, 1965
Chromadorita Filipjev, 1922[1,2,3]
Dichromadora Kreis, 1929[1,2,3]
Innocuonema Inglis, 1969[1,2,3]
Neochromadora Micoletzky, 1924[1,2,3]
Parachromadorita Blome, 1974[1]
Ptycholaimellus Cobb, 1920[2,3]
Spilophorella Filipjev, 1917[1,2,3]
Familia Neotonchidae Wieser & Hopper, 1966
Gomphionchus Platt, 1982[2]
Familia Cyatholaimidae Filipjev, 1918
Subfamilia Pomponematinae Gerlach & Riemann, 1973
aff. *Nannolaimoides*[2]
Minolaimus Vitiello, 1970[1]
Nannolaimus Cobb, 1920[1,2,3]
Pomponema Cobb, 1917[1]
Subfamilia Paracanthonchinae de Coninck, 1965
Acanthonchus Cobb, 1920[1,2,3]
Paracanthonchus Micoletzky, 1924[1,2,3]
Paracyatholaimoides Gerlach, 1953[2,3]
Paracyatholaimus Micoletzky, 1922[1,2]
Subfamilia Cyatholaiminae Filipjev, 1918
Cyatholaimus Bastian, 1865[1,2,3]
Longicyatholaimus Micoletzky, 1924[1,2,3]
Marylynnia Hopper, 1977[1,2,3]
Metacyatholaimus Stekhoven, 1942[1,2,3]
Paralongicyatholaimus Stekhoven, 1950[1]
Praeacanthonchus Micoletky, 1924[2,3]
Familia Selachinematidae Cobb, 1915
Cheironchus Cobb, 1917[3]
Gammanema Cobb, 1920[1,2,3]
Halichoanolaimus de Man, 1886[1,2,3]
Latronema Wieser, 1954[2,3]
Richtersia Steiner, 1916[1,3]
ORDO DESMODORIDA DE CONINCK, 1965
Subordo Desmodorina de Coninck, 1965
Superfamilia Desmodoroidea Filipjev, 1922
Familia Desmodoridae Filipjev, 1922

Subfamilia Desmodorinae Filipjev, 1922
Acanthopharynx Marion, 1870[2]
Bolbonema Cobb, 1920[2,3]
Croconema Cobb, 1920[2,3]
Desmodora de Man, 1889[1,2,3]
Desmodorella Cobb, 1933[1,2]
Desmodorinae sp. 1[1]
Paradesmodora Stekhoven, 1950[1]
Pseudochromadora Daday, 1899[2,3]
Zalonema Cobb, 1920[2,3]
Subfamilia Spiriniinae Gerlach & Murphy, 1965
Chromaspirina Filipjev, 1918[2,3]
Metachromadora Filipjev, 1918[2,3]
Onyx Cobb, 1891[2]
Papillonema Verschelde, Muthumbi & Vincx, 1995[2]
Spirinia Gerlach, 1963[2,3]
Subfamilia Pseudonchinae Gerlach & Riemann, 1973
Pseudonchus Cobb, 1920[3]
Subfamilia Stilbonematinae Cobb, 1936
Eubostrichus Greeff, 1869[1,2,3]
Leptonemella Cobb, 1920[2,3]
Subfamilia Molgolaiminae Jensen, 1978
Molgolaimus Ditlevsen, 1921[1,2,3]
Familia Epsilonematidae Steiner, 1927
Subfamilia Epsilonematinae Steiner, 1927
Akanthepsilonema Gourbault & Decraemer, 1991[1]
A. sinecornibus sp. n.[1]
A. sp. 2 sp. n.[1]
Bathyepsilonema Steiner, 1931[1,2,3]
B. compactum Clasing, 1984[2]
B. lopheliae Raes, Vanreusel & Decraemer, 2003[1]
B. spongiosum Clasing, 1986[1]
B. sp. 2 sp. n.[2]
B. sp. 3 sp. n. (PSB)[1]
B. sp. 3 sp. n. (Kenya)[2]
B. sp. 5 sp. n.[2]
Epsilonema Steiner, 1927[1,2,3]
E. cf. *byssicola* sp. n.[1]
E. cf. *lasium* sp. n.[1]
E. cygnoides (Metschnikoff, 1867) Gerlach & Riemann, 1931[1]
E. margaritatum Decraemer & Gourbault, 1987[1,2]
E. multispiralum Raes, Vanreusel & Decraemer, 2003[1]
E. parvospina Decraemer, 1982[2]
E. sp. 1 sp. n.[2]
E. sp. 3 sp. n.[2]
E. sp. 3' sp. n.[2]
E. sp. 6 sp. n.[2]
E. sp. 7 sp. n.[2]
E. sp. 8 sp. n.[2]
E. sp. 10 sp. n.[2]
E. sp. 11 sp. n.[2]
E. sp. 12 sp. n.[2]
E. sp. 13 sp. n.[2]
E. sp. 13' sp. n.[2]
E. sp. 14 sp. n.[2]
E. sp. 15 sp. n.[2]
E. sp. 16 sp. n.[2]
Leptepsilonema Clasing, 1983[2]
L. richardi Verschelde & Vincx, 1992[2]
L. sp. 2 sp. n.[2]

Metepsilonema Steiner, 1927[2,3]
M. chilotum Clasing, 1986[2]
M. hardyi Decraemer & Gourbault, 1990[2]
M. striatulum Decraemer & Gourbault, 1990[2]
M. sp. 2 sp. n.[2]
M. sp. 4 sp. n.[2]
M. sp. 5 sp. n.[2]
M. sp. 6 sp. n.[2]
M. sp. 8 sp. n.[2]
Perepsilonema Lorenzen, 1973[2,3]
P. kellyae Gourbault & Decraemer, 1988[2]
P. moineaui Gourbault & Decraemer, 1992[2]
P. papulosum Lorenzen, 1973[2]
P. sp. 2 sp. n.[2]
P. sp. 2' sp. n.[2]
P. sp. 3 sp. n.[2]
P. sp. 4 sp. n.[2]
P. sp. 5 sp. n.[2]
Polkepsilonema Verschelde & Vincx, 1992[2]
P. mombasae Verschelde & Vincx, 1992[2]
Pternepsilonema Verschelde & Vincx, 1992[2]
P. servaesae Verschelde & Vincx, 1992[2]
Triepsilonema Decraemer, 1982[1,2]
T. tripapillata Decraemer, 1982[1,2]
Subfamilia Glochinematinae Lorenzen, 1974
Glochinema Lorenzen, 1974[1]
G. trispinatum Raes, Vanreusel & Decraemer, 2003[1]
Familia Draconematidae Filipjev, 1918
Subfamilia Draconematinae Filipjev, 1918
Draconema Cobb, 1913[2,3]
D. claparedii (Metschnikov, 1867) Filipjev, 1918[2]
D. haswelli (Irwin-Smith, 1918) Kreis, 1938[2]
Dracograllus Allen & Noffsinger, 1978[1,2,3]
D. cf. *minutus* sp. n.[2]
D. demani Allen & Noffsinger, 1978[1,2]
D. eira (Inglis, 1968) Allen & Noffsinger, 1978[2]
D. laingensis Decraemer, 1988[2]
D. papuensis Decraemer, 1988[2]
D. sp. 4 sp. n.[2]
D. sp. 5 sp. n.[2]
D. sp. 6 sp. n.[2]
D. sp. 9 sp. n.[2]
Paradraconema Allen & Noffsinger, 1978[2,3]
P. floridense Allen & Noffsinger, 1978[2]
P. sp. 2 sp. n.[2]
P. sp. 3 sp. n.[2]
P. sp. 4 sp. n.[2]
P. sp. 5 sp. n.[2]
Subfamilia Prochaetosomatinae Allen & Noffsinger, 1978
Apenodraconema Allen & Noffsinger, 1978[2]
A. chlidosis Allen & Noffsinger, 1978[2]
Cygnonema Allen & Noffsinger, 1978[1]
C. belgicae sp. n.[1]
C. verum sp. n.[1]
Dracognomus Allen & Noffsinger, 1978[2,3]
D. annae Verschelde & Vincx, 1993[2]
D. dermatoglyphus Verschelde & Vincx, 1993[2]
D. sp. 1 sp. n.[2]
D. sp. 2 sp. n.[2]
Tenuidraconema Decraemer, 1989[1]

T. koreensis Rho & Kim, 2004[1]
T. parvospermis sp. n.[1]
Superfamilia Microlaimoidea Micoletzky, 1922
Familia Microlaimidae Micoletzky, 1922
Bathynox Bussau & Vopel, 1999[1]
Bolbolaimus Cobb, 1920[3]
Calomicrolaimus Lorenzen, 1976[1,2,3]
Microlaimus de Man, 1980[1,2,3]
Familia Aponchiidae Gerlach, 1963
Synonema Cobb, 1920[2,3]
Familia Monoposthiidae Filipjev, 1934
Rhinema Cobb, 1920[2]
ORDO MONHYSTERIDA FILIPJEV, 1929
Subordo Monhysterina de Coninck & Schuurmans Stekhoven, 1933
Superfamilia Monhysteroidea de Man, 1876
Familia Monhysteridae de Man, 1876
aff. *Diplolaimella*[1]
Diplolaimella Allgén, 1929[1]
Monhystera Bastian, 1865[1,2,3]
Monhystrella Cobb, 1918[1,2,3]
Superfamilia Sphaerolaimoidea Filipjev, 1918
Familia Xyalidae Chitwood, 1951
aff. *Linhystera*[1]
aff. *Rhynchonema*[2]
Ammotheristus Lorenzen, 1977[2,3]
Amphimonhystera Allgén, 1929[1]
Amphimonhystrella Timm, 1961[1]
Daptonema Cobb, 1920[1,2,3]
Elzalia Gerlach, 1957[1]
Gnomoxyala Lorenzen, 1977[1]
Linhystera Juario, 1974[1]
Manganonema gen. n.[1]
Metadesmolaimus Stekhoven, 1935[1,2,3]
Omicronema Cobb, 1920[2,3]
Paramonohystera Steiner, 1916[1,2,3]
Promonhystera Wieser, 1956[2,3]
Retrotheristus Lorenzen, 1977[1]
Rhynchonema Cobb, 1920[1,2,3]
Steineria Micoletzky, 1922[2]
Stylotheristus Lorenzen, 1977[2,3]
Theristus Bastian, 1865[1,2,3]
Trichotheristus Wieser, 1956[2,3]
aff. Sphaerolaimidae[1]
Familia Sphaerolaimidae Filipjev, 1918
Subfamilia Sphaerolaiminae Filipjev, 1918
Sphaerolaimus Bastian, 1865[1]
Subordo Linhomoeina Andrassy, 1974
Superfamilia Siphonolaimoidea Filipjev, 1918
Familia Siphonolaimidae Filipjev, 1918
Siphonolaimus de Man, 1893[1]
Familia Linhomoeidae Filipjev, 1922
Subfamilia Desmolaiminae Schneider, 1926
Metalinhomoeus de Man, 1907[1,2,3]
Terschellingia de Man, 1888[1,2,3]
Subfamilia Eleutherolaiminae Gerlach & Riemann, 1973
Eleutherolaimus Filipjev, 1922[1,2,3]
Subfamilia Linhomoeinae Filipjev, 1922
Didelta Cobb, 1920[2,3]
Linhomoeus Bastian, 1865[2,3]
Paralinhomoeus de Man, 1907[2,3]

ORDO ARAEOLAIMIDA DE CONINCK & SCHUURMANS STEKHOVEN, 1933
- Superfamilia Axonolaimoidea Filipjev, 1918
  - Araeolaimoidea sp. 1[1,2]
  - Familia Axonolaimidae Filipjev, 1918
    - *Ascolaimus* Ditlevsen, 1919[1]
    - *Axonolaimus* de Man, 1889[3]
    - *Odontophora* Bütschli, 1874[2,3]
    - *Odontophoroides* Boucher & Helléouet, 1977[2]
    - *Parodontophora* Timm, 1963[2]
  - Familia Comesomatidae Filipjev, 1918
    - Subfamilia Comesomatinae Filipjev, 1918
      - *Comesomoides* Gourbault, 1980[2]
      - *Metacomesoma* Wieser, 1954[1]
      - *Paracomesoma* Hope & Murphy, 1972[2,3]
    - Subfamilia Sabatieriinae Filipjev, 1934
      - *Cervonema* Wieser, 1954[1,2]
      - *Laimella* Cobb, 1920[1,2,3]
      - *Pierrickia* Vitiello, 1970[1]
      - *Sabatieria* Rouville, 1903[1,2]
    - Subfamilia Dorylaimopsinae de Coninck, 1965
      - *Dorylaimopsis* de Coninck, 1965[1]
  - Familia Diplopeltidae Filipjev, 1918
    - Subfamilia Diplopeltinae Filipjev, 1918
      - *Araeolaimus* de Man, 1888[1,2,3]
      - *Campylaimus* Cobb, 1920[1]
      - *Diplopeltis* Cobb in Styles & Hassal, 1905[1,2,3]
      - *Diplopeltula* Gerlach, 1950[1,2,3]
      - *Southerniella* Allgén, 1932[1,2,3]
  - Familia Coninckiidae Lorenzen, 1981
    - *Coninckia* Gerlach, 1956[1]

ORDO PLECTIDA MALAKHOV, 1982
- Superfamilia Leptolaimoidea Örley, 1980
  - Familia Leptolaimidae Örley, 1880
    - Subfamilia Leptolaiminae Örley, 1880
      - *Alaimella* Cobb, 1920[1,3]
      - *Antomicron* Cobb, 1920[1]
      - *Cricolaimus* Southern, 1914[1,2,3]
      - *Diodontolaimus* Southern, 1914[2]
      - *Halaphanolaimus* Southern, 1914[1]
      - *Leptolaimoides* Vitiello, 1971[1,2]
      - *Leptolaimus* de Man, 1876[1,2,3]
      - *Stephanolaimus* Ditlevsen, 1918[1]
    - Subfamilia Camacolaiminae Micoletzky, 1924
      - *Camacolaimus* de Man, 1889[1,2]
      - *Procamacolaimus* Gerlach, 1954[1,2,3]
      - *Onchium* Cobb, 1920[2,3]
  - Familia Aegialoalaimidae Lorenzen, 1981
    - aff. *Aegialoalaimus*[2]
    - *Aegialoalaimus* de Man, 1907[1,2,3]
    - *Diplopeltoides* Gerlach, 1962[1]
  - Familia Odontolaimidae Gerlach & Riemann, 1974
    - aff. *Odontolaimus* de Man, 1880[1]
- Superfamilia Ceramonematoidea Cobb, 1933
  - Familia Tarvaiidae Lorenzen, 1981
    - *Tarvaia* Allgén, 1934[1]
  - Familia Ceramonematidae Cobb, 1933
    - *Ceramonema* Cobb, 1920[1,2,3]
    - *Dasynemoides* Chitwood, 1936[2]
    - *Metadasynemella* de Coninck, 1942[1]
    - *Metadasynemoides* Haspeslagh, 1973[1]

Pselionema Cobb, 1933[1]
Pterygonema Gerlach, 1954[1]
Familia Tubolaimoididae Lorenzen, 1981
Chitwoodia Gerlach, 1956[3]
Tubolaimoides Gerlach, 1963[2,3]
ORDO RHABDITIDA CHITWOOD, 1933
Subordo Tylenchina Thorne, 1949
Infraordo Cephalobomorpha De Ley & Blaxter, 2002
Superfamilia Cephaloboidea Filipjev, 1934
Familia Cephalobidae Filipjev, 1934
Cephalobidae gen. 1[2]
Infraordo Tylenchomorpha De Ley & Blaxter, 2002
Superfamilia Aphelenchoidea Fuchs, 1937
Familia Aphelenchoididae Skarbilovich, 1947
Aphelenchoides Fischer, 1894[2]
Superfamilia Tylenchoidea Ôrley, 1980
Familia Hoplolaimidae Filipjev, 1934
Subfamilia Rotylenchulinae (Hussain & Khan, 1967)
aff. *Rotylenchulus*[2]
Subordo Rhabditina Chitwood, 1933
Infraordo Rhabditomorpha De Ley & Blaxter, 2002
Superfamilia Rhabditoidea Ôrley, 1880
Familia Rhabditidae Ôrley, 1880
Rhabditis Dujardin, 1845[2]