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REVIEW

The state of knowledge on deep-sea nematode taxonomy: how many valid species are known down there?

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Abstract All available information from literature sources dealing with deep-sea nematode species was analyzed, in order to obtain an overview of the state of knowledge in deep-sea nematode taxonomy and answer the question of how many valid nematode species are known from the deep sea so far. One hundred and twenty-seven taxonomic and ecological literature sources reported a total of 638 valid species belonging to 175 genera and 44 families, from 474 deep-sea stations at depths of 400–8,380 m. This number is less than 16% of all known marine nematode species, whereas the deep sea comprises about 91% of the ocean bottom. Of these species, 71% were initially described from the deep sea. Most of the valid species have been reported from the North Atlantic, including the Mediterranean. The rest of the World Ocean, including the Pacific, Indian, Arctic and Antarctic oceans, is considerably less studied. The largest numbers of valid species were reported from the continental slope and the abyssal plains, while information on valid species from trenches, deep-sea canyons, and seamounts is extremely scanty. Some deep-sea families are much more investigated than others in proportion to their relative species abundances in the deep sea, i.e., the percentage of valid species from these families among all valid deep-sea species is much higher than the real percentage of species from these families reported in faunistic studies (e.g., Desmoscolecidae, Comesomatidae, Sphaerolaimidae, Benthimermithidae, Leptosomatidae, and Draconematidae). On the other hand, the families Xyalidae, Oxystominidae, and Monhysteridae were recognized as the most "underinvestigated," as, in spite of their high species abundance in the deep sea, there are quite a few taxonomic studies on these taxa. Some deep-sea nematode species were reported from two or three oceans, and can be considered probable cosmopolitan species. Some number of probable eurybathic species were also found (the difference between minimum and maximum depth was from 1 km to more than 5 km).

Keywords Abyss · Continental slope · Cosmopolitan · Eurybathic · Deep-sea habitats · Marine free-living nematodes · Valid species

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Introduction

Nematodes are the most numerous multicellular animals on Earth (Heip et al. 1985). This is especially true for the marine environment. Among meiobenthic metazoans inhabiting sediments of marine bottoms, nematodes usually comprise 70–90%; their density in one square meter of marine bottom can amount to more than one million individuals (Mokievsky et al. 2004, 2007). About 4,000–5,000 species of marine nematodes are known to date (Tchesunov 2006), and new taxa are constantly being described as outcomes from ongoing projects.

Even so, most marine nematode species were discovered and described from shallow waters or the intertidal zone. Meanwhile, according to the most conservative estimate (Mokievsky and Azovsky 2002), the total number of marine nematode species is about 10,000–20,000, and a considerable part of them are presumed to inhabit the deep-sea bottom. Shallow-water habitats (this term is used here to refer to the intertidal and subtidal zones down to ca. 200 meters) cover only about 9% of the total bottom surface of the World Ocean, and the other 91% is below 200–400 m and belongs to the ocean floor, which is regarded here as deep sea. The latter includes large-scale habitats, such as the continental slope (12% of the bottom surface) and abyssal plains or basins (60%). Our knowledge and understanding of deep-sea life has increased considerably in recent years, and even more due to large, current projects, such as the Census of Marine Life (CoML) (http://www.coml.org). Rather than being a wide marine desert (as it was suggested just 50 years ago), the deep-sea bottom is a mosaic of different habitats. Beside vast deep-sea habitats, including the continental shelf below 400 m, continental slope, abyssal plains or basins, trenches, canyons, and channels, there are also not so spacious or just local habitats such as hydrothermal vents, cold seeps, mud volcanoes, the oxygen-minimum zone, cold-water coral reefs, manganese nodules, whale and log falls, etc. With the investigation of each of these habitats, which are still understudied (see results), new information about their specific nematode communities is to be expected.

In addition, deep-sea habitats display the highest evenness and α-diversity in nematode assemblages, which has been found only in the tropical sublittoral zone (Boucher and Lambshead 1995). The exploration of each new deep-sea habitat has been consistently accompanied by the discovery of new faunal communities. The species richness of these communities has exceeded all scientific expectations, especially the high diversity of marine nematodes. For example, from 200 to 325 nematode morphotypes were identified in samples of about 2,000 individuals from different abyssal regions (Bussau 1993; Lambshead et al. 2003; Miljutina et al. 2010), and 246 nematode genera were found in a total sample of 18,000 individuals from a deep-sea nodule field of the Clarion-Clipperton Fracture Zone (Pacific) (Radziejewska et al. 2001; Dr. V.V. Galtsova, pers. obs.) Therefore, it must be considered that the deep-sea bottom contains a surprisingly diverse community of nematodes, and at present it is impossible to judge the true extent of their species diversity, and what future studies will reveal about this most abundant meiobenthic group.

However, species of deep-sea nematodes are still described more rarely than shallow-water species, for several reasons. First, the nematofauna of shallow waters has been intensively studied since the 1880s–1890s, while almost no studies were done on deep-sea nematodes in the same period. This may have been caused by the lack of appropriate sampling gear and extraction methods to obtain deep-sea meiobenthic organisms at the end of the nineteenth century. Second, most deep-sea nematodes are much smaller than shallow-water ones, and their morphology was not successfully discerned before the development of modern light microscopes. Another problem of taxonomic work with deep-sea nematodes is related to the high evenness in their assemblages. It is often quite difficult to select enough specimens of the same species for species descriptions: several hundreds of unknown species can be found in a sample of 1,000 nematodes, but most of them may be represented by only a few or even one specimen.

The difficulties in nematode identification led to the situation that deep-sea nematodes are usually identified only to family or genus level in the majority of ecological studies, or to similar species, and the results of such identifications are sometimes doubtful and disputable. In most of the ecological studies, which are carried out at species level, the nematodes are usually identified as putative species, so-called "morphotypes," or as "working species" (e.g., *Acantholaimus* sp.1, *Acantholaimus* sp.2, etc.). These working species do not have a true taxonomic status, and therefore the results of these ecological studies cannot be used for comparative analysis of nematode assemblages from different locations. Obviously, these studies can be only considered as interim, making it impossible to discern the true species diversity and species interrelationships without their identifications.

The aim of the present paper is to bring together all available information from literature sources dealing with deep-sea species of nematodes, to obtain an overview of the recent knowledge on their taxonomy and geographical distribution and an answer to the question of how many valid species are known so far. Furthermore, the main gaps and problems in the taxonomy of deep-sea nematodes are discussed. It is shown how the existing data extracted from the available literature are distributed within the deep-sea bottoms, which oceans and depths are better investigated than others, and to what extent the described species represent the diversity in different families and orders of deep-sea nematodes.

Materials, methods, and analyses of literature sources

Taxonomic and ecological literature sources mentioning any valid deep-sea nematode species were sought. Only papers published to the end of 2008 were used in the present review.

In this paper, a nematode species is considered as a deep-sea species if it was described or reported below 400 m depth. At present, investigation of the depth at which the shallow-water nematofauna is substituted by the deep-sea nematofauna has not been still performed on a global scale. The 400-m isobath was chosen because the average individual biomass of nematodes sharply decreases below this depth (Udalov et al. 2005). This fact was interpreted here as an indirect sign of an abrupt change in environmental conditions which are significant for nematodes.

To evaluate the state of investigations of deep-sea nematode species in different parts of the World Ocean, the latter was subdivided into 23 geographical regions (Fig. 1). The boundary lines between the regions were drawn so that the regions would be more or less comparable in their sizes and their names would be in common usage (e.g., North-Eastern Atlantic, etc.). Five main deep-sea habitats are identified, which have the largest extent across the ocean bottoms: the continental shelf below 400 m depth and the continental slope; abyssal plains or basins; trenches; deep-sea canyons; channels; and seamounts. Attention was also paid to some more rare or local habitats listed in the Introduction.

The literature sources were divided into taxonomic papers (with species descriptions only) and ecological papers (where valid species were mentioned). This subdivision was made because there are no taxonomic descriptions in the ecological sources, and the reliability of species identifications in these studies is less than in taxonomic works. Data for possible candidates of cosmopolitan species and for eurybathic species were not searched in ecological sources. When searching for eurybathic species, taxonomic papers on shallow-water valid nematode species were also used if species which were found in the deep sea had been recorded in shallow waters as well.

Among the ecological papers, so-called "faunistic" works were noted. They represent the ecological papers devoted to nematode assemblages, in which the authors attempted to identify all species in the assemblage from some localities, at least to putative "working" species. Such faunistic papers were used to calculate average relative taxonomic abundance (number of species) of different nematode taxa in the deep sea.

In total, data from 127 sources (116 taxonomic and 11 ecological studies) were extracted, in which valid species of deep-sea nematodes were mentioned. For the whole list of species and associated sampling stations and literature souces, see Supplementary material (MS Excel file).

The data were entered into the ACCESS database, in which imprints of publications, coordinates and depths of stations, and species names were fixed. The reduced version (only species recorded deeper than 2,000 m) of this nematode database is a part of the CoML database on all abyssal benthic species findings (available at http://www.cedamar.org/Biogeography/ and http://www.iobis.org/Welcome.htm).

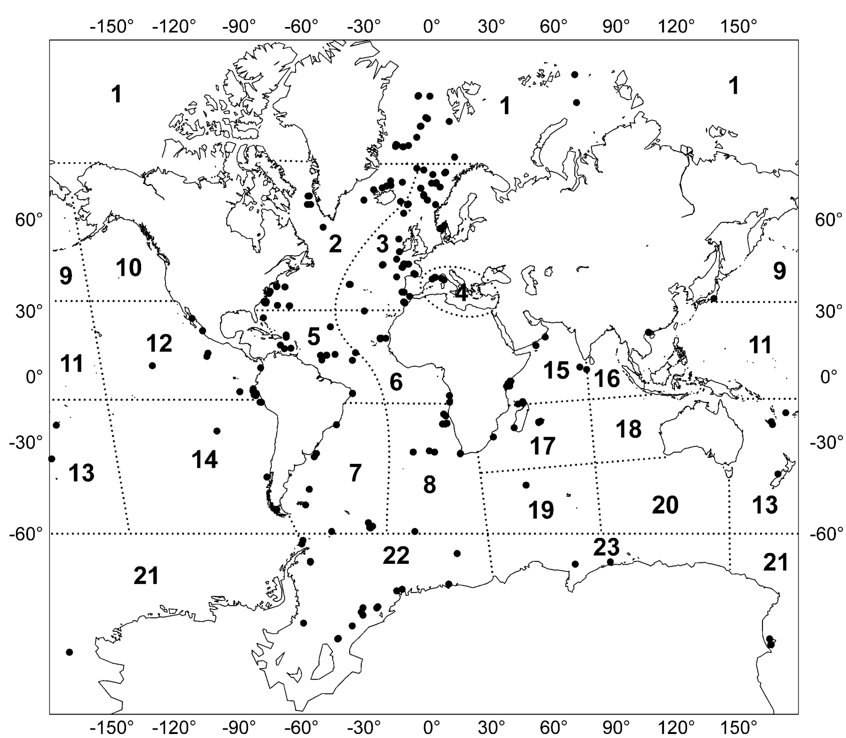


Fig. 1 Map of the World Ocean divided into 23 geographical regions, and the locations of 474 deep-sea stations (marked by *black dots*) from which valid nematode species have been recorded. Figure legend: *1* Arctic Ocean; *2* North-Western (NW) Atlantic; *3* North-Eastern (NE) Atlantic; *4* Mediterranean; *5* Central-Western (CW) Atlantic; *6* Central-Eastern (CE) Atlantic; *7* South-Western (SW) Atlantic; *8* South-Eastern (SE) Atlantic; *9* NW Pacific; *10* NE Pacific; *11* CW Pacific; *12* CE Pacific; *13* SW Pacific; *14* SE Pacific; *15* NW Indian Ocean; *16* NE Indian Ocean; *17* CW Indian Ocean; *18* CE Indian; *19* SW Indian Ocean; *20* SE Indian Ocean; *21* Pacific sector of Antarctic Ocean; *22* Atlantic sector of Antarctic Ocean; *23* Indian sector of Antarctic Ocean

Results

Historical review of deep-sea nematode studies

The investigation of the deep-sea benthic fauna is traditionally considered to begin with the famous cruise of the British corvette *HMS Challenger* in 1872–1876. However, for benthic sampling, this vessel was only equipped with trawls and dredges, and no meiobenthic animals were caught (Thomson 1880).

The earliest paper on deep-sea nematodes that has been found is dated 1926, concerning the results of the expedition across the North Atlantic in 1895–1896 by the Danish cruiser *Ingolf*, and it contains the descriptions of 26 species, 22 of them new (Ditlevsen 1926). The early papers by C. Allgén (1929, 1932, 1934, 1954, 1955), J. Shuurmans Stekhoven (1946), I. Filipjev (1946), W. Wieser (1956), and P. Mawson (1956, 1958) should also be mentioned. Most of them are devoted to North-Atlantic nematodes, but there are also descriptions of nematodes from the Antarctic region and the Pacific. This initial period of deep-sea nematode taxonomy provides a number of descriptions of large species occasionally collected from various sites, mainly during macrobenthic studies.

The relative increase of interest in deep-sea nematode taxonomy and ecology began in the mid-1960s (Table 1; Fig. 2). During this period, valid nematode species were described or identified all over the World Ocean. This second period started with two expeditions especially devoted to deep-sea meiobenthos (Wigley and McIntyre 1964; Thiel 1966). Since then, research vessels have been equipped with special gear for meiobenthic studies, such as multicorers and box corers of different types (for further details see Higgins and Thiel 1988). The new approaches for meiobenthos processing were implemented, with special attention to small-sized organisms. The mesh sizes used for nematode extraction decreased from the conventional 70–100 µm down to 40 and 32 µm (Higgins and Thiel 1988; Giere 2009). It was shown (Thiel 1975) and later confirmed (Udalov et al. 2005) that meiobenthic animals in the deep sea are generally much smaller than those in shallow water. Many nematodes of the smallest size classes have been missed before. As can be seen in Fig. 2, the intensity of taxonomic studies increased shortly after these first deep-sea meiobenthic cruises, in the 1970s.

Since the 1980s, the number of samples from stations at depths of more than 2,000 m has increased considerably, which was followed by an increase of the number of nematode species found and described from these depths (Fig. 2). The largest number of papers was published in the 1970s and 1980s.

About 95% of the studies deal with deep-sea nematode species based on material obtained during 30 research cruises carried out since 1895 (Table 1). In total, we counted about 50 cruises from which samples were used for studying deep-sea nematodes (most of the samples were obtained with French and German vessels). Unfortunately, the sources of the material examined were not mentioned in some of the earlier papers. As the most important cruises, from which large numbers of valid species were recorded or described, P. Vitiello's project (unfortunately, all attempts to find the name and dates of this cruise failed), the Mediterranean transect, BIOGAS, and DISCOL/ECO-BENT should be mentioned.

The papers mentioning valid deep-sea nematode species can be subdivided into three groups. The first, and largest, group consists of taxonomic papers containing substantial numbers of deep-sea species descriptions. These may be completely devoted to deep-sea nematodes (e.g., Gourbault 1980a, b; Decraemer 1983a, b, 1984a, b; 1985; Gourbault and Vincx 1985a, b, c), or also contain the descriptions of shallow-water species. As a rule, authors of these papers intentionally chose some taxonomic group of nematodes within a genus or family, in which they specialize.

The second group also includes taxonomic papers with nematode descriptions, but they attempt to describe the entire nematofauna of some deep-sea area or point. Such papers could be termed "ideal faunistic work". An example of this type of study is the doctoral thesis of C. Bussau (1993), in which he reported 324 species of nematodes and described 110 species (97 of them as new) from the nodule-bearing area of the Peru basin (CE Pacific). Unfortunately, the collection of the holotypes was never deposited in a repository institution, and therefore a considerable number of nematologists consider these species as invalid. Only a few of the species were formally described (Bussau 1995; Bussau and Vopel 1999). Nevertheless, the value of this work is still enormous because of its completeness and carefulness. Many of Bussau's species were rediscovered 5,200 km from their original location (Miljutina et al. 2010). The other example in this context is the set of Vitiello's papers that contain descriptions of 85 species from the upper slope of the Mediterranean (Vitiello 1969a, b, 1970a, b, c, d, 1971, 1975, 1976; Vitiello and Haspeslagh 1972).

The third group of papers represents ecological sources devoted to the structure of deep-sea nematode assemblages at species level. Several "faunistic" works also belong to this group. Most nematodes in these papers are usually identified as putative species, morphotypes, or "working species." However, nematodes were sometimes identified as known, valid species in these sources. Chronologically, the oldest paper of this type is the work of Tietjen (1971) on the NW Atlantic slope. Other important studies were carried out by Vitiello (1976) and Vivier (1976) on the Mediterranean canyons; Dinet and Vivier (1979) at depths of 2,000–4,700 m in the Bay of Biscay (NE Atlantic); and Soetaert et al. (1995) on the Mediterranean slope. Equally,

Table 1 List of the main marine research cruises from which samples have been used for studying deep-sea nematodes. The references with the total number of valid species mentioned are given for each cruise (only cruises with more than two species are included; publications that do not mention the source of the material studied have been omitted; *?* indicates no data available)

Year	Region	Depth, m	Research vessel	Ship owner	Campaign, cruise	References	No. of species
1895–1896	Atlantic, N	446–3,474	*Ingolf*	Denmark	Danish Ingolf Expedition	Ditlevsen (1926)	26
1901–1903	Antarctica	920	Antarctic	Sweden	Swedish Antarctic Expedition	Allgen (1959, 1960)	4
1923–1924	Antarctica	550	?	Germany	Ross Sea Expedition	Allgen (1929)	8
1929–1931	Antarctica	1,266–2,286	Discovery	Great Britain	BANZARE	Mawson (1956, 1958)	3
1937–1940	Arctic Ocean	410–510	*G.Sedov*	USSR	Glavsevmorput drifting expedition	Filipjev 1946	6
1948	Atlantic, N	4590	*Albatross*	Sweden	Albatross Expedition	Allgen (1954, 1955)	4
1950–1952	Atlantic, N	1,048–2,160	*Galathea*	Denmark	Galathea Expedition	Wieser (1956)	16
1965	Pacific, E	520–6,200	*Anton Bruun*	USA	11th	Timm (1970); Freudenhammer (1975b); Gerlach et al. (1979)	14
1966	Atlantic, W	939–3,806	*Atlantis II*	USA	24th, 31th	Hope (1988); Hope and Murphy (1969, 1970); Miljutin et al. (2006)	5
1966	Mediterranean	410–650	?	?	?	Vitiello (1969a, b, 1970a, b, c, d, 1971, 1975, 1976); Vitiello and Haspeslagh (1972).	96
1967	Atlantic, NE	510–4,354	*Meteor*	Germany	8th	Freudenhammer (1970, 1975a, b); Gerlach et al. (1979)	20
1971	Antarctica	443–1,729	*Academic Kurchatov*	USSR	11th	Chesunov (1988a, b); Platonova and Tchesunov (1989)	6
1971	Atlantic, NE	520–651	*Meteor*	Germany	23th	Riemann (1974); Riemann and Schrage (1977)	3
1971	Atlantic, E	2,063–4,308	*Jean Charcot*	France	VALDA	Gourbault (1980a, b); Gourbault and Boucher (1981); Gourbault and Petter (1985); Gourbault and Vincx (1985a, b, c)	20
1973–1981	Atlantic, NE	1,960–4,725	*Jean Charcot*	France	BIOGAS	Dinet and Vivier (1979); Decraemer, (1983a, b, 1984b, 1985), Vivier (1985)	84
1975	Arctic ocean	2,502–3,713	*Jean Charcot*	France	NORBI	Petter (1981a, b, 1982a, 1983, 1987)	11
1977	Indian, W	400–3,700	*Suriot*	France	BENTHEDI	Decraemer (1983b, 1984a, 1985)	12
1978	Atlantic, CW	4,550–5,210	*Jean Charcot*	France	WALVIS	Petter (1982b); Miljutin (2004)	4
1980	Atlantic, W	4,434–4,850	*Jean Charcot*	France	DEMERABY	Decraemer (1983a); Miljutin (2004)	13
1983–1986	Mediterranean	530–1,250	*Recteur Dubuisson*	France	different cruises	Timm (1970); Soetaert (1989); Soetaert and Vincx (1987, 1988); Soetaert and Decraemer (1989); Soetaert et al. (1995)[a]; Decraemer and Soetaert (1989)	63
1986	Arctic ocean	970–3,294	*Meteor*	Germany	2nd	Jensen (1988a, b, 1991, 1992)	17
1988	Arctic ocean	1,245–1,425	*Meteor*	Germany	MET 7/4	Jensen (1991, 1992)	15
1989	Antarctica	600–1,985	*Polarstern*	Germany	EPOS	Vermeeren et al. (2004); Fonseca et al. (2006a, b)	10
1989	Pacific, CE	4,100–4,201	*Sonne*	Germany	DISCOL/ECOBENT	Bussau (1993, 1995); Bussau and Vopel (1999)	99
1992	Indian, CW	500–2,179	*Tyro*	Netherlands	A1–A2	Muthumbi and Vincx (1996, 1997, 1998a, b, 1999); Muthumbi et al. (1997)	38
1994	Pacific, S	440–550	*Victor Hensen*	Germany	Joint Chilean-German-Italian Magellan Campaign	Chen and Vincx (1998, 1999, 2000a, b)	8
1998	Antarctica	423–1,028	Polarstern	Germany	EASIZ-2	Vermeeren et al. (2004); Fonseca et al. (2006a)	9

Table 1 (continued)

Year	Region	Depth, m	Research vessel	Ship owner	Campaign, cruise	References	No. of species
2000	Arctic ocean	5,416–5,569	*Polarstern*	Germany	ARK-XVI	Tchesunov and Miljutina (2005); Tchesunov and Mokievsky (2005); Tchesunov and Miljutin (2006)	9
2000	Atlantic, NE	1,005–1,250	*Belgica*	Belgium	Porcupine-Belgica 2000	Raes et al. (2003); Fonseca et al. (2006b)	4
2002–2003	Atlantic, SW	750–1,950	*Prof. W.Besnard*	Brazil	OCEANPROF I and II	Botelho et al. (2007)	4

[a] The data on species composition in the nematode assemblages described in this article were provided by Dr. K. Soetaert (Ghent University, Belgium)

the monograph by Bussau (1993) can be referred to this type of paper, as in addition to the taxonomic part, it contains a wide spectrum of ecological data and analyses. Several other ecological sources on the deep sea mention smaller numbers (two to four) of identified valid species (Tietjen 1984, 1989; Jensen 1988b; Vermeeren et al. 2004). Authors of the latter papers attempted to identify only the most abundant species.

Statistics of data extraction from literature sources

In total, 638 valid species of deep-sea nematodes were reported in the 127 sources considered (116 taxonomic and 11 ecological), representing 175 genera and 44 families (as it is inferred from the methods used, genera and families are only meant here, which have valid deep-sea species reported or described in the literature sources). Among them, 454 species (71%) are only known from the deep sea, and 184 species (29%) were initially described from the shallow waters. The nematodes were collected worldwide from 474 deep-sea stations in the depth range from 400 to 8,380 m. Taxonomic sources reported 548 species, representing 166 genera (Table 2).

The largest numbers of valid species are recorded from the deep sea of the Mediterranean (175), the NE Atlantic (131), and the CE Pacific (130). The largest numbers of new species described per publication are from the CE Pacific, the Mediterranean, and the NE Atlantic (Table 3).

The great majority of publications concerns nematodes from the NE Atlantic (25 studies), the Mediterranean (18), and the Arctic (19) (Table 3). There is information on only one valid deep-sea species from the NW and CW Pacific, and the NE Indian Ocean. There are no records of deep-sea nematodes from the CE and SE Indian Ocean. Considering the number of deep-sea stations, the best-studied regions of the World Ocean so far are the NE Atlantic (79 stations) and the CE Pacific (75 stations). The large number of stations in the latter region, however, is a result of only one point of investigation, a manganese nodule area in the Peru basin (Bussau 1993, 1995; Bussau and Vopel 1999). The best-investigated deep-sea habitats are the low continental shelfs and slopes below 400 m (212 stations, 318 species) and the abyssal plains (226 stations, 297 species) (Table 3). The least-studied habitats are trenches (five stations, nine species) and seamounts (one station, one species).

Of the rest of the habitats listed in the introduction, we found only three publications devoted to the nematofauna of abyssal nodule fields, with mention of 55 stations and 110 valid species (Bussau 1993, 1995; Bussau and Vopel 1999); three publications on nematodes from deep-sea hydrothermal vents, with eight stations and nine species (Decraemer and Gourbault 1997; Verschelde et al. 1998; Zekely et al. 2006); one publication on a cold-water coral reef, with two stations and three species (Raes et al. 2003);

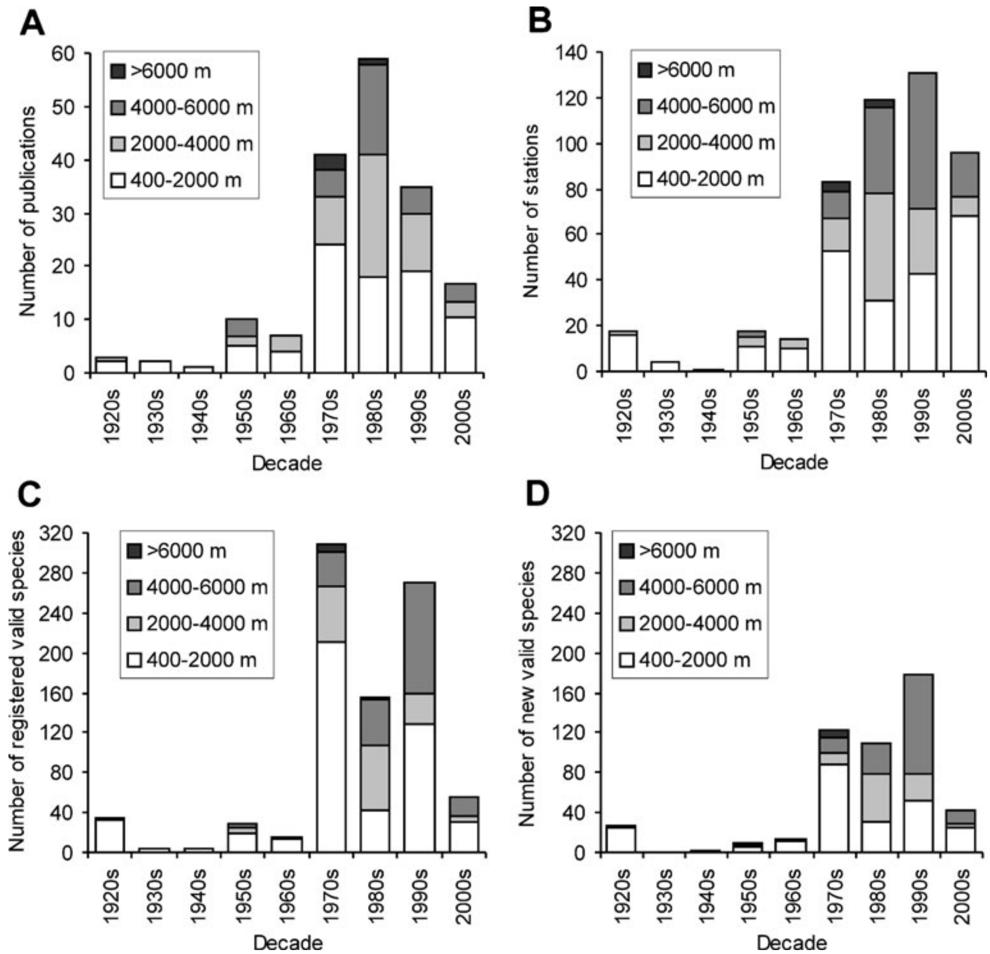


Fig. 2 a–d Data on valid species of deep-sea nematodes, subdivided into four depth ranges, by decade. **a** Number of publications devoted to valid species of deep-sea nematodes; **b** number of deep-sea stations where valid species of deep-sea nematodes were reported or new species were described; **c** total number of valid deep-sea species found; **d** number of new species only

one publication on the oxygen-minimum zone, with one station and one species (Neira et al. 2005); and one publication on a mud volcano, with one station and one species (Van Gaever et al. 2006).

About 52% of all descriptions or mentions of unique valid species were made from the depth range of 400–2,000 m; 21% from the depth of 2,000–4,000 m; 26% from the depth of 4,000–6,000 m; and about 1% from the depth of more than 6,000 m. All deep-sea species from the Mediterranean, the SW Atlantic, the NW and NE Pacific, the Pacific and Indian sectors of the Arctica are from the depth 400–2,000 m; the most species from the CE Pacific (about 88%) were reported from the depth range 4,000–6,000 m (Fig. 3). Species from a depth of more than 6,000 m were mentioned only in five regions: the CW Atlantic, the CE, SW, and SE Pacific, and the CW Indian Ocean (Fig. 3).

One hundred species inhabiting a wide depth diapason (the difference between the minimum and maximum depths, where the species was recorded, is more than 1,000 m) were found (Table 4) among taxonomic papers (including taxonomic papers on shallow-water valid nematode species). Of them, six species were recorded from the depths with the deviation more than 4,000 m (Table 5).

There are 46 deep-sea species that have been recorded in more than one ocean (Table 6). The families Benthimermithidae (with five *Trophomera* species), Chromadoridae (among them, seven *Acantholaimus* species), Desmoscolecidae (among them, nine *Desmoscolex* species), and Meyliidae (among them, three *Quadricoma* and three *Tricoma* species) possess the most numbers of valid deep-sea species found in two oceans. *Cervonema tenuicaudatum* Schuurmans Stekhoven 1946 (Comesomatidae) is the only species, which has the widest distribution, across three oceans. The distribution maps of the 12 most widespread species are presented in Fig. 4.

As follows from the data in Fig. 5, the number of known valid species of higher-ranking taxa (order or family level) often does not correspond with the species diversity of this taxon. For example, according to faunistic studies (Vitiello 1976; Vivier 1976; Dinet and Vivier 1979; Tietjen 1984, 1989; Bussau 1993; Miljutina et al. 2010), when a nematode assemblage is studied thoroughly and most nematode individuals in samples are sorted to morphospecies, about 25% of all deep-sea nematode species belong to the order Monhysterida; whereas monhysterids represent only about 15% of all known valid nematode species. The same

Table 2 List of orders, families, genera, and number of species found at depths greater than 400 m (according to published literature sources). *A* number of species found in all literature sources (taxonomic and ecological); *T* number of species found only in taxonomic literature sources. Genera and families are only meant here, which have valid deep-sea species reported or described in the literature sources

Taxon	A	T
ARAEOLAIMIDA		
Comesomatidae		
Cervonema	9	9
Comesoma	1	1
Comesomoides	1	1
Dorylaimopsis	2	2
Hopperia	3	3
Kenyanema	1	1
Laimella	3	3
Pierrickia	2	2
Sabatieria	24	17
Coninckiidae		
Coninckia	1	1
Diplopeltidae		
Campylaimus	3	2
Diplopeltis	2	1
Diplopeltula	14	14
Intasia	1	1
Paraerolaimus	1	1
Pararaeolaimus	1	–
Southerniella	5	4
BENTHIMERMITHIDA		
Benthimermithidae		
Adenodelphis	1	1
Trophomera	28	28
CHROMADORIDA		
Axonolaimidae		
Odontophora	1	1
Chromadoridae		
Acantholaimus	32	30
Actinonema	5	5
Atrochromadora	1	1
Chromadora	1	1
Chromadorita	4	4
Dichromadora	9	4
Euchromadora	1	1
Hypodontolaimus	1	–
Prochromadorella	1	1
Rhips	1	1
Spiliphera	3	1
Trochamus	3	3
Cyatholaimidae		
Longicyatholaimus	5	3
Marylynnia	1	–
Metacyatholaimus	2	1
Minolaimus	2	2
Nyctonema	1	1
Chromaspirina	1	1
Desmodora	9	8
Desmodorella	3	2
Molgolaimus	21	20
Spirinia	1	1
Draconematidae		
Cephalochaetosoma	2	2
Dinetia	1	1
Eudraconema	1	1
Epsilonematidae		
Bathyepsilonema	1	1
Epsilonema	1	1
Glochinema	3	3
Microlaimidae		
Aponema	2	2
Bathynox	1	1
Bolbolaimus	3	2
Caligocanna	1	1
Calomicrolaimus	1	1
Ixonema	1	1
Microlaimus	11	7
Spirobolbolaimus	1	1
DESMOSCOLECIDA		
Desmoscolecidae		
Antarcticonema	2	2
Desmolorenzenia	1	1
Desmoscolex	48	46
Desmotricoma	1	1
Greeffiella	2	2
Paratricoma	1	–
Prototricoma	1	1
Protricoma	5	5
Quadricomoides	2	2
Spinodesmoscolex	1	1
Tricoma	36	31
Usarpnema	1	1
Meyliidae		
Erebus	1	1
ENOPLIDA		
Anticomidae		
Anticoma	1	1
Paranticoma	1	1
Enchelidiidae		
Bathyeurystomina	2	2
Eurystomina	1	1
Ledovitia	1	1
Pareurystomina	1	1
Deontostoma	4	4
Leptosomatides	1	1
Leptosomatina	1	1
Leptosomatum	2	2
Metacylicolaimus	1	1
Platycomopsis	2	2
Pseudocella	2	2
Synonchoides	1	1
Synonchus	2	2
Syringonomus	2	2
Thoracostoma	8	8
Oncholaimidae		
Curvolaimus	1	1
Filoncholaimus	3	2
Mononcholaimus	2	2
Oncholaimus	2	2
Pelagonema	1	1
Viscosia	1	1
Oxystominidae		
Cricohalalaimus	1	1
Halalaimus	20	13
Litinium	3	1
Oxystoma	1	1
Oxystomina	4	4
Thalassoalaimus	6	3
Wieseria	1	–
Phanodermatidae		
Crenopharynx	3	3
Micoletzkyia	4	4
Phanoderma	2	2
Phanodermella	2	1
Phanodermopsis	1	1
Rhabdodemaniidae		
Rhabdodemania	5	5
Thoracostomopsidae		
Epacanthion	1	1
Paramesacanthion	4	4
Trefusiidae		
Rhabdocoma	1	1
Trefusia	4	3
Trefusialaimus	1	1
Marimermithidae		
Ananus	1	1
Thalassonema	1	1
MERMITHIDA		
Mermithidae		
Thalassomermis	1	1

Table 2 (continued)

Taxon	A	T	Taxon	A	T	Taxon	A	T
Paracanthonchus	2	2	*Symplocostoma*	1	1	MONHYSTERIDA		
Paracyatholaimus	2	1	*Symplocostomella*	1	1	Bodonematidae		
Pomponema	4	3	Enoplidae			*Bodonema*	1	1
Neotonchidae			*Enoploides*	1	1	Linhomoeidae		
Neotonchus	2	2	*Enoplolaimus*	3	3	*Anticyclus*	2	2
Richtersiidae			*Enoplus*	5	5	*Didelta*	2	2
Richtersia	3	2	Ironidae			*Disconema*	3	1
Selachinematidae			*Parironus*	1	1	*Eleutherolaimus*	1	1
Gammanema	2	2	*Syringolaimus*	7	7	*Grahamia*	1	1
Halichoanolaimus	5	4	*Thalassironus*	2	2	*Metalinhomoeus*	6	3
Synonchiella	2	2	Leptosomatidae			*Paralinhomoeus*	3	3
DESMODORIDA			*Corythostoma*	1	1	*Terschellingia*	3	2
Desmodoridae			*Cylicolaimus*	3	3	*Thelonema*	1	1
Acanthopharyngoides	1	1						
Monhysteridae			*Elzalia*	1	–	*Pselionema*	3	2
Halomonhystera	2	1	*Enchonema*	1	1	*Pterygonema*	1	1
Monhystera	1	–	*Filipjeva*	2	1	Cyartonematidae		
Thalassomonhystera	15	15	*Manganonema*	5	5	*Cyartonema*	1	1
Siphonolaimidae			*Theristus*	11	6	Diplopeltoididae		
Siphonolaimus	3	3	*Xyala*	1	–	*Diplopeltoides*	2	2
Sphaerolaimidae			PLECTIDA			Haliplectidae		
Metasphaerolaimus	5	5	Aegialoalaimidae			*Setoplectus*	1	1
Parasphaerolaimus	1	1	*Aegialoalaimus*	1	1	Leptolaimidae		
Sphaerolaimus	17	16	Camacolaimidae			*Antomicron*	1	–
Subsphaerolaimus	2	2	*Camacolaimus*	6	5	*Leptolaimus*	7	4
Xyalidae			*Smithsoninema*	1	1	Tarvaiidae		
Amphimonhystera	3	3	Ceramonematidae			*Tarvaia*	1	1
Amphimonhystrella	1	1	*Ceramonema*	5	3	RHAPTOTHYREIDA		
Capsula	1	1	*Dasynemoides*	1	1	Rhaptothyreidae		
Daptonema	7	3	*Metadasynemella*	1	1	*Rhaptothyreus*	2	2

situation obtains in the order Chromadorida, and in certain families (Xyalidae, Oxystominidae, Monhysteridae, Axonolaimidae). For instance, according to faunistic studies, about 14% of all deep-sea nematode species belong to the family Xyalidae, but, among valid deep-sea species, they represent only approximately 4% of the species. Besides these "understudied" taxa, there are also some "much more studied" taxa, in which the percentage of described species is higher than the percentage of species of the same taxon in deep-sea nematode assemblages (orders Desmoscolecida and Benthimermithida, families Desmoscolecidae, Draconematidae, Comesomatidae, Benthimermithidae, Sphaerolaimidae).

Discussion

Although we may not have located all the papers containing any mention of valid deep-sea nematode species, undoubtedly, we examined the vast majority of them. This allows an estimation of the state of affairs in deep-sea nematology. Of about 4,000–5,000 known marine nematode species, less than 16% of them have been found in the deep sea. The deep sea is about 91% of the seabed surface, but the 473 deep-sea stations from which valid nematode species have been noted cover a bottom area of only 60–70 m^2. This clearly shows that deep-sea nematodes, as the most common and most dominant meiobenthic taxon in deep-sea sediments, are greatly understudied.

Among the vast habitats, the continental slope and the abyss are the most studied. Approximately equal numbers of nematode species have been described from each of them; however, as mentioned above, the bottom surface of the continental slope comprises only one-fifth of the abyss. Seamounts and trenches remain the least studied (Table 3), although the fields of trenches in the deep sea are quite extensive, and the number of deep-sea seamounts is

Table 3 Statistical summary of deep-sea nematode studies in different regions and habitats of the World Ocean. *P* number of publications; *S* number of stations; *V* total number of recorded valid species; *D* number of descriptions of new deep-sea species

Ocean region	Habitats																				Shared for all habitats			
	Shelf & slope				Abyssal basins & plains				Trenches				Canyons & deep-sea channels				Seamounts							
	P	S	V	D	P	S	V	D	P	S	V	D	P	S	V	D	P	S	V	D	P	S	V	D
Arctic Ocean	10	17	32	19	15	36	40	31	-	-	-	-	-	-	-	-	-	-	-	-	18	53	50	38
NW Atlantic	5	26	38	2	7	7	6	4	-	-	-	-	4	6	5	5	-	-	-	-	13	39	46	10
NE Atlantic	14	36	64	45	15	41	87	31	-	-	-	-	1	1	1	-	1	1	1	1	25	79	131	70
Mediterranean	8	10	65	18	-	-	-	-	-	-	-	-	12	8	128	61	-	-	-	-	19	18	175	79
CW Atlantic	3	4	3	2	5	32	20	11	1	3	4	-	-	-	-	-	-	-	-	-	8	39	23	13
CE Atlantic	6	3	10	6	8	21	19	11	-	-	-	-	-	-	-	-	-	-	-	-	9	24	21	13
SW Atlantic	5	46	9	8	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	5	46	9	8
SE Atlantic	3	3	4	3	9	11	25	19	-	-	-	-	-	-	-	-	-	-	-	-	12	14	29	22
NW Pacific	1	1	1	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	1	1	1
NE Pacific	1	1	3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	1	3	-
CW Pacific	1	1	1	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	1	1	1
CE Pacific	5	8	6	6	8	67	126	113	-	-	-	-	-	-	-	-	-	-	-	-	10	75	130	118
SW Pacific	3	2	3	1	2	4	3	3	-	-	-	-	-	-	-	-	-	-	-	-	5	6	6	4
SE Pacific	1	1	1	-	-	-	-	-	1	1	1	1	3	5	8	7	-	-	-	-	5	7	10	8
NW Indian	1	1	1	1	1	2	3	3	-	-	-	-	-	-	-	-	-	-	-	-	2	3	4	4
NE Indian	-	-	-	-	1	1	1	1	-	-	-	-	-	-	-	-	-	-	-	-	1	1	1	1
CW Indian	8	18	43	36	1	1	1	1	-	-	-	2	3	10	8	-	-	-	-	-	10	29	53	44
CE Indian	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
SW Indian	2	2	2	2	1	2	2	-	-	-	-	-	-	-	-	-	-	-	-	-	2	4	3	2
SE Indian	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Atlantic Antarctica	9	20	22	13	1	1	1	1	2	1	4	3	1	6	6	6	-	-	-	-	11	28	30	20
Pacific Antartica	3	4	25	12	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	3	4	25	12
Indian Antarctica	2	2	2	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	2	2	2
Shared for all regions	76	212	318	173	56	226	297	216	4	5	9	4	23	29	156	79	1	1	1	1	127	474	638	454

estimated at about 100,000 (Gubbay 2003; Mironov et al. 2006; Pitcher et al. 2007). The other deep-sea habitats are also very little known; only a small number of nematode species are known from them.

Among the regions of the World Ocean, those best studied for valid deep-sea nematode species are the NE Atlantic, the Mediterranean, and the CE Pacific. It is evident that the locations of the first two regions are correlated with the proximity to the densely populated countries with European culture, where the study of marine nematodes began.

The most intensive studies of deep-sea nematodes took place in the 1970s–1980s. The number of species described in the 1990s was still high; however, the tendency towards a decrease in deep-sea nematode taxonomy started at about that time. Nowadays, interest in the taxonomy of deep-sea nematodes seems to be decreasing, as inferred by the number of papers published over the last decade (Fig. 2). Obviously, to reach the rates of the 1990s, the number of valid deep-sea nematodes found or described for the next 2 years of the 2000s must be several times higher than the number of species described in the initial 8 years of the decade.

The substantial disproportion between species diversity in deep-sea nematode assemblages and the number of described species was revealed in many taxa at the order and family level (Fig. 5). There is no doubt that such "well-studied" and "understudied" taxa also exist at the genus level. Frequently, "understudied" taxa are small, deposit-feeding nematodes with no conspicuous anatomical features (i.e., having a narrow, tiny head; narrow, unarmed buccal cavity; thin, unornamented cuticle; little-visible internal structures). Such nematodes are challenging to describe, and consequently, nobody wants to describe them. In contrast, "well-studied" taxa possess some remarkable features (e.g., sculptured cuti-

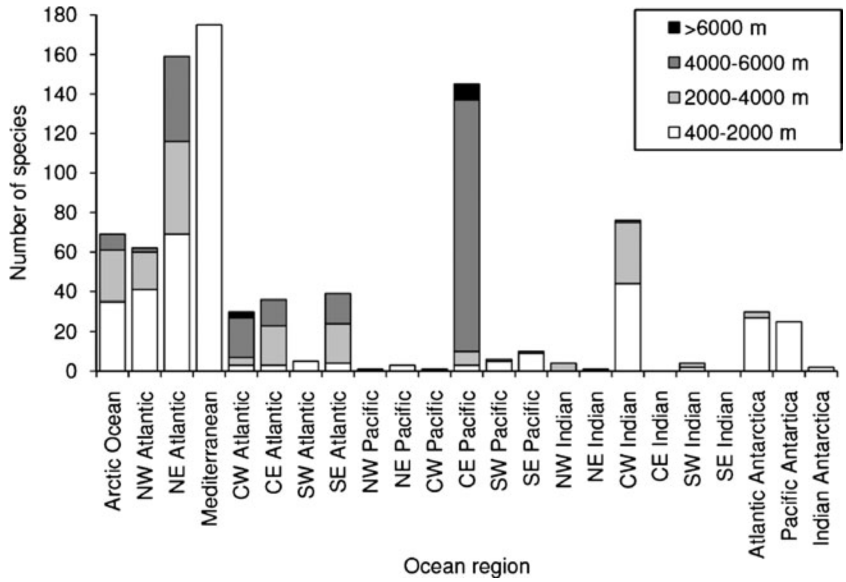


Fig. 3 Depth distribution of records of valid deep-sea nematode species, subdivided into regions of the World Ocean

cle, sclerotized stoma with tooth, etc.), making them more attractive to describe and recognizable among other nematode specimens.

Among the taxonomic sources, there are 46 deep-sea species which could be considered as putatively cosmopolitan. Cosmopolitan species are known among shallow-water nematodes (see, e.g., Gerlach and Riemann 1973, 1974; Decraemer et al. 2001). However, because of extremely fragmentary reports on the geographic ranges of deep-sea nematode species, it is still a difficult task to find cosmopolitan species in deep-sea nematodes. The best candidate is *C. tenuicaudatum,* which was found with the widest distribution of all. Several genera are also represented by quite a big number of species. Obviously, this fact does not mean that these genera are actually spread wider than other deep-sea genera, but just indicates that these genera are studied better than other ones at the moment. Alongside with "cosmopolitan" species, some "eurybathic" species were revealed, which inhabit a wide depth diapason (the difference between minimum and maximum depth was more than 1,000 m).

Undoubtedly, the species identity of individuals from different localities or depths needs to be compared and verified. These morphological descriptions have been made without using methods of molecular taxonomy, which could reveal several cryptic species within the same morphology (Fonseca et al. 2008). Unfortunately, obtaining deep-sea material, suitable for DNA barcoding, is fraught with difficulties. The main problem is the identification of small deep-sea nematodes at the stage

Table 4 Number of valid nematode species recorded in the range of a depth deviation more than 1,000 m (difference between minimum and maximum recorded depths). Taxonomic papers both on deep-sea and shallow-water nematodes were used

Range of depth deviation, m	Number of species
5,000–6,000	1
4,000–5,000	5
3,000–4,000	24
2,000–3,000	18
1,000–2,000	52

Table 5 Six nematode species recorded in the widest range of depth deviation (more than 4,000 m). Taxonomic papers both on deep-sea and shallow-water nematodes were used

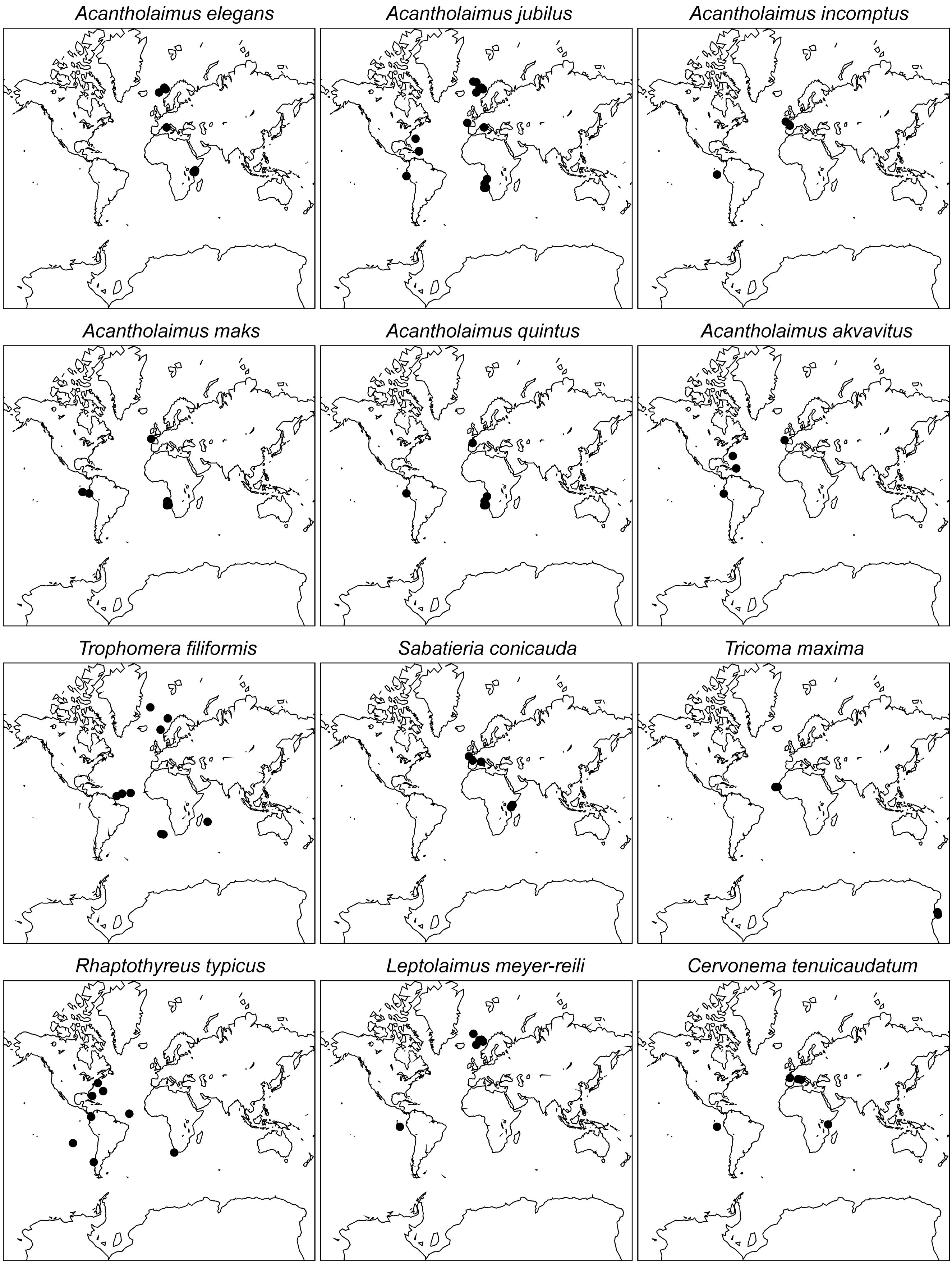
Species	Minimum depth, m	Maximum depth, m	Depth deviation, m
Desmolorenzenia desmoscolecoides (Timm 1970)	460 (Timm 1970)	6,200 (Timm 1970)	5,740
Trophomera marionensis (Petter 1983)	31 (Petter 1983)	4,440 (Miljutin 2004)	4,409
Acantholaimus quintus Gerlach et al. 1979	1,960 (Vivier 1985)	6,364 (Gerlach et al. 1979)	4,404
Halichoanolaimus minor Ssaweljev 1912	Tidal zone (Wieser 1954)	4,308 (Gourbault and Vincx 1985b)	4,308
Acantholaimus jubilus Gerlach et al. 1979	2,063 (Gourbault and Vincx 1985c)	6,313 (Gerlach et al. 1979)	4,250
Camacolaimus prytherchi Chitwood 1935	Tidal zone (e.g. Wieser and Hopper 1967)	4,154 (Bussau 1993)	4,154

Table 6 Deep-sea nematode species with a wider distribution in the world oceans, and therefore possible cosmopolitan deep-sea species according to literature sources. A + indicates occurrence in one of three oceans (including Arctic and Antarctic sectors)

Family	Species	Atlantic & Mediterranean	Pacific	Indian Ocean
Aegialolaimidae	*Aegialoalaimus elegans*	+	+	
	Diplopeltoides ornatus	+	+	
Benthimermithidae	*Trophomera filiformis*	+		+
	T. hureaui	+		+
	T. marionensis	+	+	
	T. minuta	+	+	
	T. turpicauda	+		+
Ceramonematidae	*Pselionema annulatum*	+	+	
Chromadoridae	*Acantholaimus akvavitus*	+	+	
	A. arminius	+	+	
	A. elegans	+		+
	A. incomptus	+	+	
	A. jubilus	+	+	
	A. maks	+	+	
	A. quintus	+	+	
	Actinonema longicaudatum	+		+
Comesomatidae	*Cervonema tenuicaudatum*	+	+	+
	Sabatieria conicauda	+		+
	S. pisinna	+		+
Cyatholaimidae	*Longicyatholaimus cervoides*	+	+	
Desmoscolecidae	*Desmoscolex amaurus*	+	+	
	D. articulatus	+	+	
	D. asetosus	+		+
	D. frigidus	+	+	
	D. gerlachi	+	+	
	D. labiosus	+	+	
	D. macrophasmata	+		+
	D. max	+	+	
	D. remifer		+	+
	Greeffiella antarctica	+	+	
Diplopeltidae	*Southerniella conicauda*	+	+	
Leptolaimidae	*Camacolaimus prytherchi*	+	+	
	Leptolaimus meyer-reili	+	+	
Meyliidae	*Antarcticonema comicapitatum*	+	+	
	Quadricoma avicapitata	+	+	
	Q. curvicaudata	+	+	
	Q. pontica	+	+	
	Tricoma maxima	+	+	
	T. nematoides	+	+	
	T. serpentrionalis	+	+	
	Usarpnema auriculatum	+	+	
Monhysteridae	*Thalassomonhystera molloyensis*	+	+	
	Th.oxycephalata	+	+	
Rhaptothyreidae	*Rhaptothyreus typicus*	+	+	
Xyalidae	*Amphimonhystrella bullicauda*	+	+	
	Manganonema pitilica	+	+	

antecedent to the use of methods of molecular genetics. They cannot be directly identified using a stereomicroscope, as can some large species from shallow waters. That is why, in the first step, they must be transferred to

Fig. 4 Worldwide distributions of 12 possibly cosmopolitan deep-sea nematode species. Black points mark the locations of deep-sea stations where these species were recorded ▶


Acantholaimus elegans
Acantholaimus jubilus
Acantholaimus incomptus
Acantholaimus maks
Acantholaimus quintus
Acantholaimus akvavitus
Trophomera filiformis
Sabatieria conicauda
Tricoma maxima
Rhaptothyreus typicus
Leptolaimus meyer-reili
Cervonema tenuicaudatum

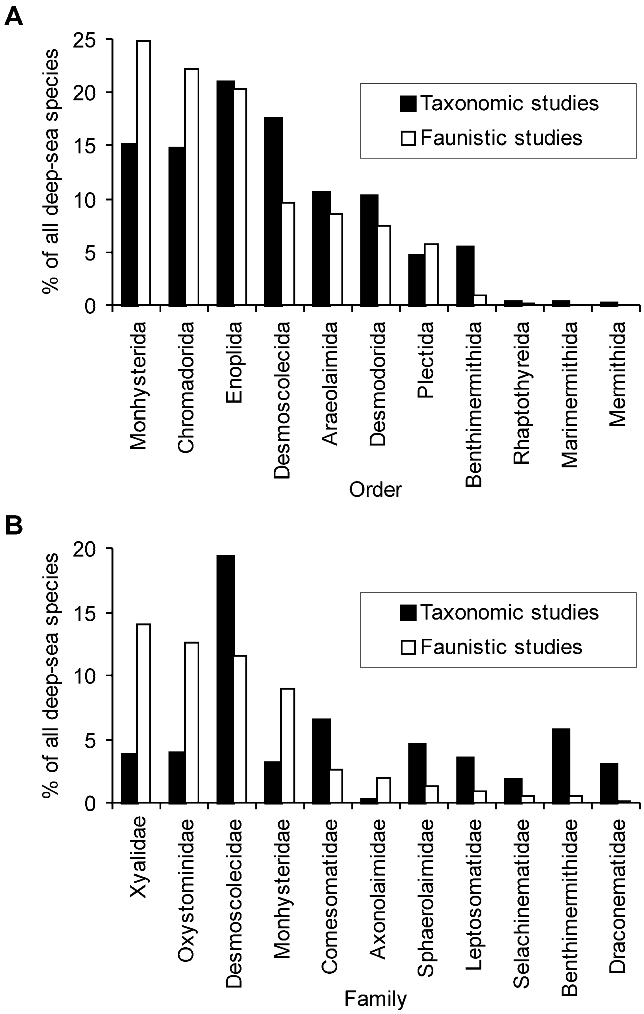


Fig. 5 a, b Differences between faunistic and taxonomic records of higher taxa of deep-sea nematodes. The graphs are based on the number of putative nematode species ("morphotypes" or "working species") from different taxa recorded in faunistic studies, and on the number of valid nematode species from different taxa described in the deep sea. **a** Order level; **b** family level (only the first ten families with the greatest differences between the faunistic and taxonomic data are shown)

a series of glycerol substances and mounted on slides to be finally identified prior to molecular analysis. This process is extremely time-consuming. In addition, most deep-sea nematode species have proved to be unknown to science.

Summary and main conclusions

1. Data from 127 taxonomic and ecological literature sources (116 taxonomic and 11 ecological papers) were summarized. Analysis of all the data resulted in finding 638 valid species of deep-sea nematodes belonging to 175 genera and 44 families. These nematodes have been recorded from 474 deep-sea stations (from 400 to 8,380 m) across the World Ocean. Of these species, 71% were initially known and described from the deep sea.
2. Less than 16% of about 4,000–5,000 known valid marine nematode species have been found in the deep sea below 400 m so far, although the deep sea comprises about 91% of the ocean bottom. Thus, the process of taxonomic description of the deep-sea nematofauna is still in a very early stage, and behind many other invertebrate groups discovered in abyssal depths.
3. The regions from which the most deep-sea nematodes have been reported are in the North Atlantic, including the Mediterranean, whereas the remaining parts of the World Ocean, the Pacific, Indian, Arctic, and Antarctic oceans, are considerably less well studied.
4. Among vast habitats, the largest numbers of valid species were reported from the continental slope and the abyssal plain in different parts of the World Ocean, whereas the information on valid species from trenches, deep-sea canyons, and seamounts is extremely scanty. There are only sporadic mentions of valid deep-sea nematode species from such habitats as cold-water corals, seamounts, hydrothermal vents, cold seeps, mud volcanoes, oxygen-minimum zones), although the nematode diversity in these habitats can be very high.
5. Some deep-sea nematode taxa are much more investigated than others in proportion to their relative abundances in the deep-sea, i.e., the percentage of valid species from these taxa among all valid deep-sea species is much higher than the true percentage of species from these taxa reported in faunistic studies (e.g., families Desmoscolecidae, Comesomatidae, Sphaerolaimidae, Draconematidae, Benthimermithidae). Contrariwise, the families Xyalidae, Oxystominidae, and Monhysteridae, which include the most common and abundant deep-sea nematodes, were recognized as the most "underinvestigated", as, in spite of their high abundance in the deep-sea, there are quite a few taxonomic studies on these taxa. Therefore, their true diversity is still hidden.
6. Several species of deep-sea nematodes were reported from two or three oceans, and may be considered as probable cosmopolitan species. Some number of probable eurybathic species were also found (the difference between minimum and maximum depth was from 1 km to more than 5 km).
7. The development of modern deep-sea nematode taxonomy is hampered by the small number of released taxonomic works based on morphological features such as DNA barcoding. On the whole, however, a decline of interest in deep-sea nematode taxonomy has been noted in last two decades.

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