

SPECIES, DISTRIBUTION AND A MICROHABITAT THEORY FOR MARINE MUD DWELLING COMESOMATIDAE (NEMATODA) IN EUROPEAN WATERS

by

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Résumé

Espèces, distribution et théorie des microhabitats des Comesomatidae (Nématodes) des sédiments marins vaseux des eaux européennes.

Le groupe de Nématodes le plus abondant dans les sédiments vaseux marins Comesomatidae est analysé en tenant compte de son mode de spéciation, de distribution et de ses éventuels microhabitats dans les eaux européennes. Les espèces de *Sabatieria* sont caractérisées et séparées en deux groupes suivant leur morphologie et leurs microhabitats.

Le groupe *S. pulchra* (*S. pulchra*, *S. punctata*, *S. granulosa* et *S. clavicauda*) vit essentiellement dans la zone réduite du sédiment. Il est géographiquement isolé respectivement dans le Sound, le Kattegat, la Mer du Nord, la Méditerranée et la Mer Noire. *S. pulchra* est le seul Comesomatidae mésohalin et constitue, de plus, l'un des rares Métazoaires supportant les sévères déficits en oxygène de la Baltique. *S. vulgaris* nécessite une redescription et pourrait être une espèce polyhaline au cœur du groupe *S. pulchra*. *S. breviseta* présente une préférence pour les sables vaseux.

Les membres du groupe *S. ornata* (*S. ornata*, *S. proabyssalis* et *S. abyssalis*) vivent dans les sédiments riches en oxygène. Ils apparaissent géographiquement isolés comme pour les trois espèces du groupe *pulchra* dans le Sound, le Kattegat, la Mer du Nord (*D. punctata* et *C. macramphix* et la Méditerranée (*D. mediterranea* et *C. tenuicauda*). Il en est de même des espèces des genres *Dorylaimopsis* et *Cervonema*.

Ces assemblages d'espèces géographiquement distincts appuient la théorie des communautés parallèles et fournissent l'indice d'une liaison entre métabolisme et mode de vie des espèces les plus communes.

Introduction

A morphological and systematic revision of the nematode family Comesomatidae was recently given by Jensen (1979 a). They are free-living benthic inhabitants (Jensen, 1978) and so far only *Sabatieria pulchra* and may be *S. vulgaris* are known to penetrate environments with low salinities (Jensen, 1979 b) and only two species *S. scotlandia* Inglis, 1961 and *S. lyonessa* Warwick, 1977 do not inhabit sediment, being found on *Laminaria*.

In this paper, attention is focused on the mud dwelling members found in European waters. Between one to three species of the family

usually make up more than 40 percent of the total nematode population in this habitat. Therefore, a more detailed investigation of the species, distribution and possible microhabitats of these quantitatively important animals was initiated in 1975 to detect possible natural patterns which might reflect their sensitivity to the specific conditions in their environment.

Material and methods

The animals were collected at nineteen muddy sites in the Baltic, the Sound, the Kattegat, the North Sea, the Mediterranean and the Black Sea (Fig. 1, Table 2). The species have been reported from other locations than these (see Gerlach and Riemann, 1973), but their identity is questionable and, since the original material is not available for a reexamination, these animals are excluded from this study. The material was examined (sites 1, 3-5, 8-10) or reexamined (sites 2, 6-7, 12-16) by the author, whilst the remaining information on the species is from the cited literature.

Details of the collecting sites are as follows:

Baltic.

1. Krogarviken (Tvärminne zoological Station), 1.5m depth (type locality of *S. pulchra*), collected 1978-79. Byviken (T.z.S.), 2m depth, collected 1978-79.
2. Storfjärden (T.z.S.), 5m and 31m depth, Keynäs and Keynäs (1978).
3. Gulf of Finland (Ajax sampling position), 78m depth, collected July 1978. LL 7, 92m depth; LL 12, ca. 100m depth; LL 15, 128m depth; collected May 1979, leg. K.P.
4. Bothnian Bay, 2-81m depth, no comesinatids present (Schiemer, Jensen and Riemann, in prep.), collected August 1976, 1979.
5. Baltic Sea (Bornhom Depth), 81m depth, collected September 1971, leg. E.L.
6. Baltic Sea (Askö), 48m depth, Elmgren (1976).
7. Wismar Bucht, down to ca. 20m depth, Brenning (1973).

The Sound.

8. Hornbäk region, 28m depth (type locality of *S. ornata*, *D. punctata*, *C. macramphis* and a similar habitat for *S. punctata*), Jensen (1979 a).

Kattegat.

9. Gullmarfjorden, 31m depth, collected June 1978, Widbom (unpubl.).

North Sea.

10. Ringköbing Fjord, 1-3m depth, collected October 1979.
11. Elbe Estuary, ca. 15m depth, Riemann (1966).
12. Lynher Estuary, intertidal mudflat, Warwick and Price (1979).
13. Coast of Northumberland, 81m depth, Warwick and Buchanan (1970).
14. Ems-Dollart Estuary, intertidal mudflat, Bouwman (1978).
15. German Bight, 20-25m depth, Lorenzen (1974).

Mediterranean.

16. Banyuls-sur-Mer, 35m depth (type locality of *S. granulosa*, *S. proabyssa-lis* and a similar habitat for *D. mediterranea* and *C. tenuicauda*), Vitiello et Boucher (1972), Boucher (1972), de Bovée (pers. comm.).

17. Golfe de Fos, 49-80m depth, Vitiello (1974).

Black Sea.

18. Sevastopol area, ? depth (type locality of *S. clavicauda*, *S. abyssalis*), Filipjev (1918).

19. Coast of Rumania, 55-87m depth, Groza-Rojancovski (1973).

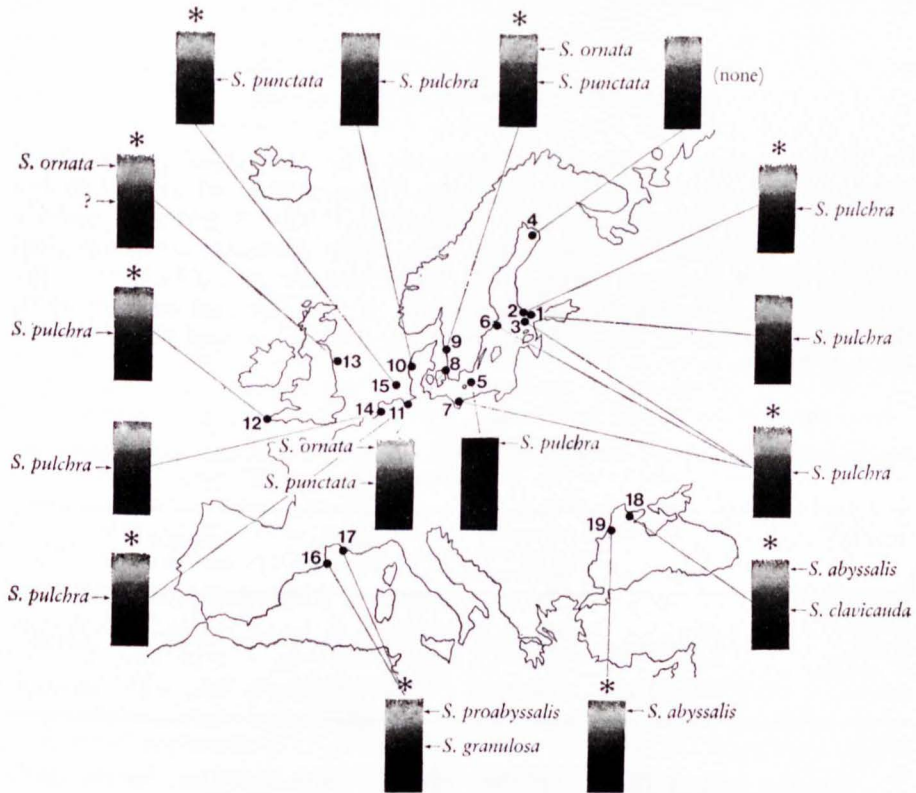


FIG. 1

Species, distribution and position of the microhabitats of mud dwelling *Sabatieria* species (nematodes) in European waters in relation to the redox potential discontinuity (RPD) layer.

*: microhabitat to be substantiated.

The designation of the redox potential discontinuity (RPD) layer (Fenchel and Riedl, 1970) is based on both actual measurements of the redox potentials in the sediments and observing the colour patterns of sectional cores collected by scuba diving. These methods were used at sites 1, 3, 8 and 10; at site 5, the sediment is known to be frequently oxygen deficient (see reviews in Andersin *et al.*, 1978; Jansson, 1978), so that the RPD layer is most likely at the surface or even periodically totally absent (see also Fenchel, 1978).

The muddy sediment at site 16 (Banyuls-sur-Mer) is characterized having no distinct RPD layer nor colour changes down to 7cm depth (de Bovée, pers. comm.). Futural studies have to substantiate whether

this fact is a general rule in the muddy sediment in the Mediterranean; until then, it is considered here as a specific feature of the mud in Banyuls-sur-Mer.

The percentage composition of the Mediterranean comesomatid fauna presented in table 2 might be questioned (de Bovée, pers. comm.) since both authors treated their material, only counting the first 100-200 animals in each sample.

Systematic relationships and status

Jensen (1979 a) regarded *Sabatieria* as the stem group from which may be derived *Cervonema* with reduced characters and *Dorylaimopsinae* with differentiated characters. The *Sabatieria* species discussed here can be separated into two distinct morphological groups: the *S. pulchra* group and the *S. ornata* group based on the copulatory structures, the configuration of the preanal supplements, the arrangements of the anteriormost cervical setae and the shape of the tail (Table 1).

TABLE 1
Morphological characters differentiating the *Sabatieria pulchra* group from the *S. ornata* group.

	Copulatory apparatus		Preanal supplements	Cervical setae	Tail
	apophyses	gubernaculum			
<i>S. pulchra</i> group	dorsocaudal	indistinct	1+1+1+4	2+2	blunt
<i>S. ornata</i> group	caudal	distinct	4+1+1+1+...	not 2+2	slender

Species within the *S. pulchra* group recognized here were, until 1970, all considered synonymous with *S. pulchra*, being treated as a cosmopolitan species. *S. pulchra* was originally described in 1906 by G. Schneider as belonging to *Aphanolaimus*; Riemann (1970) correctly transferred it to *Sabatieria*. In the meantime, De Man (1907) described *S. vulgaris* (as *Parasabatieria*), Filipjev (1918) described *S. clavicauda* (as *Parasabatieria*), Kreis (1924) described *S. punctata* (as *Parasabatieria*) and finally Stekhoven (1935) described *S. breviseta* pro *S. quadripapillata* sensu De Coninck and Stekhoven, 1933.

Wieser (1954) synonymized *S. punctata* with *S. clavicauda* based on a literature study. Gerlach (1965) synonymized *S. clavicauda* with *S. vulgaris* after finding what was presumed to be *S. vulgaris* animals. Riemann (1970) compared the literature and concluded that *S. vulgaris* and *S. pulchra* were conspecific. Finally, Lorenzen (1974) concluded that *S. breviseta* was synonymous with *S. pulchra* after examining much material.

Unfortunately, none of these conclusions were based on a reexamination of *S. pulchra* from or close to its type locality, nor reexaminations of the other species in question. The redescription of *S. pul-*

chra from its type locality in Krogarviken (Jensen, 1979 b) has, however, shown that intraspecific variation in eleven adult characters is less than 10 percent. The specimens of *S. punctata* from the Tvärminne area (Gerlach, 1953) and from Wismar Bucht (Brenning, 1973) are, in fact, *S. pulchra*. Moreover, the *Sabatieria* aff. *pulchra* animals in Jensen (1978) are significantly different from *S. pulchra*; these animals were described as *S. punctata* in Jensen (1979 a). Similar animals were also found in Lorenzen's (1974) *S. pulchra*-material in addition to *S. breviseta*. *S. breviseta* is herein recognized as a valid species (1), different from *S. punctata* in the cuticular ornamentation and the accessory pieces of the copulatory apparatus. Unfortunately, Stekhoven apparently depicted the cloacal region (Fig. 7 D) from a sublateral view, which resulted in a rather strange figure of the preanal supplements and in overlooking the first (and small) preanal supplement level with the spicules (terminology sensu Jensen, 1979 b). In the rather poor figure of *S. clavicauda*, only the wide turns of the amphids can here be used as a morphological differentiating character; a redescription of this species is thus highly desirable. Although I have not been able to reexamine such material, *S. clavicauda* is here recognized as a valid species, since additional information on its distribution is available (see below). *S. vulgaris* was originally carefully described and depicted; its specific morphological characters are the body size (2-2.5mm) and a conical tail lacking the cylindrical portion; otherwise it is closely related to *S. pulchra* and *S. breviseta*. *S. vulgaris* is here recognized as a valid species. *S. vulgaris* from the Ems-Dollart Estuary (Oost Friese Plaat) (Bouwman, 1978) is, in fact, *S. pulchra*.

The following mud dwelling *Sabatieria* species are considered morphologically related and included in the *S. pulchra* group: *S. pulchra*, *S. punctata*, *S. granulosa* and *S. clavicauda* (Table 2). *S. granulosa* Vitiello and Boucher (1972) has the above characters of the *S. pulchra* group separating it from the *S. ornata* group. The main character separating it from the other species in question is the presence of a rather long cylindrical tail portion.

Three members of the *S. ornata* group are recognized: *S. ornata*, *S. proabyssalis* and *S. abyssalis* (Table 2); their specific differentiating characters were tabulated by Jensen (1979 a). *S. stekhoveni* pro *S. abyssalis* sensu Stekhoven, 1950 is related to the *S. ornata* group, but its habitat is most likely not muddy sediment (see below).

Of the eleven *Dorylaimopsis* species known (Jensen, 1979 a) only two occur in European waters: *D. punctata* and *D. mediterranea* (Table 2); their main differentiating characters are the structure of the spicules and the distribution of the caudal setae (see Jensen, 1979 a).

Only four *Cervonema* species are known (Jensen, 1979 a; Gourbault, 1980), two of them occur in European waters: *C. macramphis* and *C. tenuicauda* (Table 2). They differ in the amphids, cephalic setae and the spicules (see Jensen, 1979 a).

(1) A redescription is in preparation by Warwick and Platt.

TABLE 2

Parallel assemblages of closely related Comesomatids (Nematodes) and their relative abundances (percentage) compared with total nematodes number in muddy sediments in european waters.

	Region	Baltic	The Sound	Kattegat	North Sea	Mediterranean		Black Sea	
	Reference	Present study	Present study	Widbom (unpubl.)	Warwick and Buchanan (1970)	Boucher (1972)	Vitiello (1974)	Filipjev (1918)	Groza-Rojancowski (1973)
<i>Sabatieria pulchra</i>		5-98	—	—	—	—	—	—	—
<i>S. punctata</i>		—	1-13	ca. 6	?	—	—	—	—
<i>S. granulosa</i>		—	—	—	—	6	8	—	—
<i>S. clavicauda</i>		—	—	—	—	—	—	+	—
<i>S. ornata</i>		—	6-8	ca. 8	9	—	—	—	—
<i>S. proabyssalis</i>		—	—	—	—	26	24	—	—
<i>S. abyssalis</i>		—	—	—	—	—	—	+	dom.
<i>Dorylaimopsis punctata</i>		—	21-35	ca. 28	16	—	—	—	—
<i>D. mediterranea</i>		—	—	—	—	22	7	—	—
<i>Cervonema macramphis</i>		—	+	+	—	—	—	—	—
<i>C. tenuicauda</i>		—	—	—	—	+	+	—	—

—: not found; +: present; dom.: dominant; ?: as *S. cupida*.

General distribution

Sabatieria pulchra is the only comesomatid found in the Baltic (Fig. 1 and Table 2). Its distribution centre is within the muddy sediment and only occasionally individuals were found in muddy sand and single individuals on the submerged macrophytes. It inhabits such sediment independent of the water depth; its horizontal distribution pattern indicates that it is a mesohaline species. It is not found in the oligohaline areas of the Bothnian Bay (Fig. 1), Pohjo Viken at the Tvärminne zoological Station (Jensen, unpubl.) nor in the innermost part of the Gulf of Finland close to the river Neva (Filipjev, 1929 and 1930). Outside the Baltic, I found it in the mesohaline Ringkøbing Fjord (Fig. 1) and it also occurs in the Lynher Estuary, Ems-Dollart Estuary (Fig. 1) and in the Bay of Morlaix in Brittany (Renaud-Mornant et Gourbault, 1980; Gourbault, 1981; Jensen, pers. obs.). Most likely, it should also be found in the muddy sediments of the West German estuaries (Fig. 1). In the Mediterranean and the Black Sea, no mesohaline *Sabatieria* species have been reported so far. Thus, *S. pulchra* is to date the only mesohaline comesomatid in the European waters.

S. vulgaris may turn out to be a polyhaline, mud dwelling species. However, sampling and environmental data from the type locality are needed.

All other comesomatids discussed here are fully marine inhabitants. From the Sound and Gullmarfjorden, one finds together *S. punctata*, *S. ornata*, *Dorylaimopsis punctata* and *Cervonema macramphis* (Fig. 1 and Table 2); the first species has an extremely patchy distribution in the Sound with an index of dispersion (Morisita's index) as high as 4.2. From a faunistically similar area, the Coast of Northumberland, both *S. ornata* and *D. punctata* are present (Fig. 1 and Table 2); *S. punctata* was not reported, but *S. cupida*. In my opinion *S. cupida*'s distribution center is muddy sand, whereas *S. punctata* is the mud dweller. Since the latter species, at least in the Sound, has an extremely patchy distribution, its presence in the muddy sediment along the Coast of Northumberland is not excluded, but probably it has not been detected because of the sampling strategy; the absence of *S. punctata* here could also be an indication of unfavourable conditions in deep waters (see Gullmarfjord). *S. punctata* animals are also found in the German Bight and constitute a population inhabiting the muddy sediment apparently together with *S. brevisetata*. Neither *D. punctata* nor *C. macramphis* were reported from the German Bight.

In the muddy sediments of the Mediterranean, Boucher (1973) found an assemblage of comesomatids which parallels that of the Sound, i.e. *S. granulosa*, *S. proabyssalis*, *D. mediterranea* and *C. tenuicauda* (Fig. 1 and Table 2). In the Black Sea only two *Sabatieria* species have so far been reported: *S. abyssalis* and *S. clavicauda* (Fig. 1 and Table 2).

In the Sound, there is a marked difference between the comesomatid fauna in muddy sediment and muddy sand despite the quality of the overlying water being the same and the habitats being at the

same depth and with a distance of less than 100 metres from each other. The density of *D. punctata* decreases and *S. punctata* is absent, but species of *Laimella* and *Comesoma* occur, as do *S. hilarula* and *S. aff. cupida*. With a further increase in the sandy fraction in the sediment, a new assemblage of comesomatids occurs with *S. celtica* and *S. strigosa* as the most abundant species and deeper down in the sediment, *S. longispinosa*. These species are also found outside the Sound (see Gerlach and Riemann, 1973) and most likely *S. breviseta* (North Sea) and *S. stekhoveni* (Mediterranean) belong to this muddy sand assemblage of *Sabatieria* species. In muddy sediment at 117m depth in the Gullmarfjord there also exists an abundant and differentiated comesomatid fauna Widbom (unpubl.). *D. punctata* is also present here, but the other comesomatids from the 31m depth are absent and a new *Cervonema* species occurs in addition to two or three *Sabatieria* species.

Microhabitats

Scuba diving samples from the shallow waters in the Tvärminne area and in the Ringköbing Fjord clearly revealed that *S. pulchra*'s microhabitat is in the RDP layer and deeper down (Fig. 1). In this sediment, *S. pulchra* animals might be found extremely abundant around the rhizome region of the submerged macrophyte *Potamogeton perfoliatus*. In the outermost archipelago of the Gulf of Finland (Ajax position) the *S. pulchra* animals are found in this black layer below the oxygenated brownish sediment inhabited by rather small nematode species (see Keynäs and Keynäs, 1978; Jensen, unpubl.). In the deepest areas of the Gulf of Finland and in the Bornholm Depth, *S. pulchra* may be, together with another nematode *Desmolaimus zeelandicus*, the only metazoan found in the totally reduced sediment (Fig. 1). Scuba diving sampling used in the sublittoral muddy sediment in the Sound showed that *S. punctata* was found most abundantly in this transition zone between aerobic and anaerobic sites, but very clumped (up to 55 individuals per ml sediment) (Fig. 1). From such cores in the Sound, it may further be concluded that the other comesomatids in question, i.e. *S. ornata*, *D. punctata* and *C. macramphis*, all occur significantly in the oxygenated portion, but beneath the surface sediment (Fig. 1). The presence of such related species in the same sediment layer could indicate interspecific competition for food, but since the size and armature of their buccal cavities are rather different (Jensen, 1979 a, Fig. 2), there may well be a size selection in searching for food. Of the other comesomatid reports cited herein only Boucher (1972) detected the distribution centres of the Banyuls-sur-Mer fauna. The centres are apparently similar to those found in the Sound, i.e. *S. granulosa* penetrates deepest; *S. proabyssalis* and *D. mediterranea* are found closer to the surface (Fig. 1). However, the vertical distribution of both *S. granulosa* and *S. proabyssalis* is, from a statistical point of view, not different in Banyuls-sur-Mer (de Bovée, pers. comm.).

Discussion

The present study has revealed some new morphological patterns in one of the most abundant group of nematodes, the *Sabatieria*, inhabiting muddy sediment in European waters (Table 1). Further studies might prove whether *S. pulchra* and *S. ornata* grouping presented here, is consistent for more *Sabatieria* species living in other sediments and also outside Europe. If such morphological features really turn out to be present in other *Sabatieria* species than herein recognized, one can argue to redefine *Parasabatieria* (type species *S. vulgaris*) including the *S. pulchra* group and describe a new genus including the *S. ornata* group. Above all, the characters of *S. cettensis* (type species of the genus) need a careful study before representatives of the genus are separated into other genera.

The geographical distribution of the herein recognized Comesomatidae species in European waters shows a marked pattern of parallel assemblages (Table 2) supporting the theory of isocommunities for the macrofauna (Thorson, 1957). This indication is most pronounced in the fauna from the Sound and from the Mediterranean where one representative from each of the four groups are present in the muddy sediment.

Investigations on the correlation between these animals, their vertical distribution centre and the redox potentials in the sediment have been carried out only in the Baltic, the Sound and in Ringkøbing Fjord. These results clearly showed that *S. ornata*, *D. ornata* and *C. macramphis* live in the oxygenated sediment, whereas *S. pulchra* and *S. punctata* are found deeper down with a distribution centre in the RPD layer. Since I recognize a parallel comesomatid fauna elsewhere in Europe, it is herein postulated that the oxygenated portion of the sediment is the microhabitat for the species of *Dorylaimopsis*, *Cervonema* and *Sabatieria ornata* group, as against the *S. pulchra* group with their microhabitat in the RPD layer.

The metabolic requirements for a nematode having its permanent life in the RPD layer are presently unknown. Warwick and Price (1979) have, however, presented a respiratory value for *S. pulchra* which strongly supports the above postulation and indicates an adaptation to life in oxygen deficient habitats as a facultative anaerobic animal. This may also turn out to be the case for the accompanying nematode fauna, i.e. the mesohaline *Desmolaimus zeelandicus* (see p. 238) and the fully marine *Terschellingia longicaudata*. Ecological studies on these abundant nematodes would be necessary.

Acknowledgements

Comparative material from the following is gratefully acknowledged: Drs. L. Bouwman, U. Brenning, R. Elmgren, K. Keynäs, E. Leppakoski, S. Lorenzen, K. Purasjoki, R. Warwick and B. Widbom. Skilled scuba diving assistance from I. Aagaard and E. Leskinen is greatly appreciated. Excellent working conditions provided at the Marine Biological Laboratory Helsingör and Tvärminne zoological Station is acknowledged. Drs G. Boucher, F. de Bovée and H. Platt kindly made linguistic corrections and provided fruitful comments on the manuscript. The study is a part of a project concerning the biology of aquatic nematodes from

the Baltic and Danish waters supported by grants from the Danish Natural Science Research Council, the Nordic Council for Marine Biology and the Faculty of Science, University of Copenhagen.

Summary

An analysis is made of the species, distribution and microhabitats of the Comesomatidae, the most abundant group of freeliving nematodes in muddy sediment of European waters. Each *Sabatieria* species is characterized and separated in two groups according to their morphology and microhabitats. The *S. pulchra* group (*S. pulchra*, *S. punctata*, *S. granulosa* and *S. clavicauda*) inhabits the RPD layer. *S. pulchra* is the only mesohaline comesomatid and is further characterized as being one of the few metazoans surviving the extreme oxygen-deficient sediments of the Baltic. The other three *Sabatieria* species are all fully marine species and geographically isolated in the Sound—the Kattegat—the North Sea, the Mediterranean and the Black Sea. *S. vulgaris* needs to be redescribed, and may turn out to belong to the *S. pulchra* group as a polyhaline species. *S. breviseta* is most probably a characteristic muddy sand dweller. Members of the *S. ornata* group (*S. ornata*, *S. proabyssalis* and *S. abyssalis*) live in the oxygenated sediment and, like the three *S. pulchra*-group species, are geographically isolated. *Dorylaimopsis* and *Cervonema* species live in the Sound—the Kattegat—the North Sea (*D. punctata* and *C. macramphis*) and the Mediterranean (*D. mediterranea* and *C. tenuicauda*). These geographically distinct assemblages support the theory of isocommunities and may provide an interesting background for further metabolic and life history investigations of these common benthic animals.

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