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Serpuloidea (Annelida: Polychaeta) from Milos, an island in the Aegean Sea with submarine hydrothermalism

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Serpuloidea were collected by diving within 45 m depth, by indirect sampling in deeper waters (50 and 81 m), and among the fouling settled on oceanographic instruments at various depths (10, 50, 80 and 83 m depth). A total of 33 species or subspecific taxa was found: 25 Serpulidae and eight Spirorbidae. All the species collected are already known for the western Mediterranean and have Atlantic–Mediterranean or worldwide distribution. Several of these, however, may be species-complexes hiding species with restricted geographic ranges. No Lessepsian migrants were found. The number of species found at vent sites was significantly higher than that found at non-vent sites, although no vent-obligate species were recognized. Hydrothermal vents might influence serpuloidean richness through four main mechanisms: (i) increasing food sources to these filter-feeders, due to the chemiosynthetic production by vent microbiota; (ii) enhancing the development of biogenic carbonate mounds, which provide habitats for encrusting and cryptic species; (iii) inducing advective mechanisms that concentrate larval stages in the vicinity of vents and thus favouring recruitment; (iv) creating, through the periodic emission of toxic fluids, a regime of 'intermediate disturbance' that allows a larger number of species to coexist.

INTRODUCTION

Many shallow seabed areas with strong hydrothermal activity occur in the Hellenic Volcanic Arc, Aegean Sea. Hydrothermal vents off Milos, one of the islands along the Arc, have been intensively studied in recent years (Dando et al., 1995; Morri et al., 1999). The sessile epibenthic fauna around vents was unexpectedly rich and comprised, among others, many species of Serpuloidea (Bianchi et al., 1999). Serpulidae (but not Spirorbidae) are a common element in deep-water hydrothermal communities (Olu et al., 1996; Desbruyères et al., 1985) and also comprise species unique to those habitats (ten Hove & Zibrowius, 1986). On the contrary, the Serpuloidea living near vents at shelf depths have never been studied.

Information of the serpuloidean fauna of the Aegean Sea is poor (Fassari, 1982), especially compared to the western Mediterranean (Zibrowius, 1968; Bianchi, 1979a). Bellan (1961, 1964) examined the Serpulidae collected at numerous stations in most of the Aegean during the scientific cruises of the 'Calypso'. Bailey (1969) studied Spirorbidae from Chios (eastern Aegean Islands). Knight-Jones et al. (1991) reported on Serpuloidea from the Turkey's Aegean coast. Arvanitidis & Koukouras (1994) collected the Serpulidae associated with the coral *Cladocora caespitosa* at the Chalkidiki Peninsula.

Besides providing a first account on the serpuloidean species living in a subtidal vent area, this paper aims to contribute towards the faunal knowledge of the Aegean Sea.

MATERIALS AND METHODS

Serpuloideans were collected at various depths in ten sites off the south-east coast of Milos (Figure 1). Although all sites were situated in a hydrothermally active area, only SR*, CR*, VS*, L*, PL* and C* were close (5–10 m) to the actual vents. Most samples were taken by snorkelling (SR*) and SCUBA diving (W, ST, CR*, VS*, S) within 45 m depth, but additional material came from a box corer at 81 m (PL*) and from the fouling of oceanographic instruments at 10–83 m depth (A, C*, L*). Serpuloideans were preserved in 4% seawater formaline and sorted a few weeks later. Specimens are deposited in the authors' reference collection. Species were identified mostly according to Bianchi (1981) and Nelson-Smith et al. (1990), adopting the taxonomy of Bianchi (1979a) who considered the Serpuloidea as a superfamily comprised of the two families Serpulidae s. str. and Spirorbidae (the latter are considered as a subfamily of the former by other authors). Individual species names follow the checklist of the Italian fauna (Castelli et al., 1995). Species were grouped using cluster analysis (van der Maarel coefficient, complete linkage) on a presence–absence data matrix.

SYSTEMATICS

SERPULIDAE

Serpula vermicularis L.
Occurrence: C*, L*, S, VS*, W.

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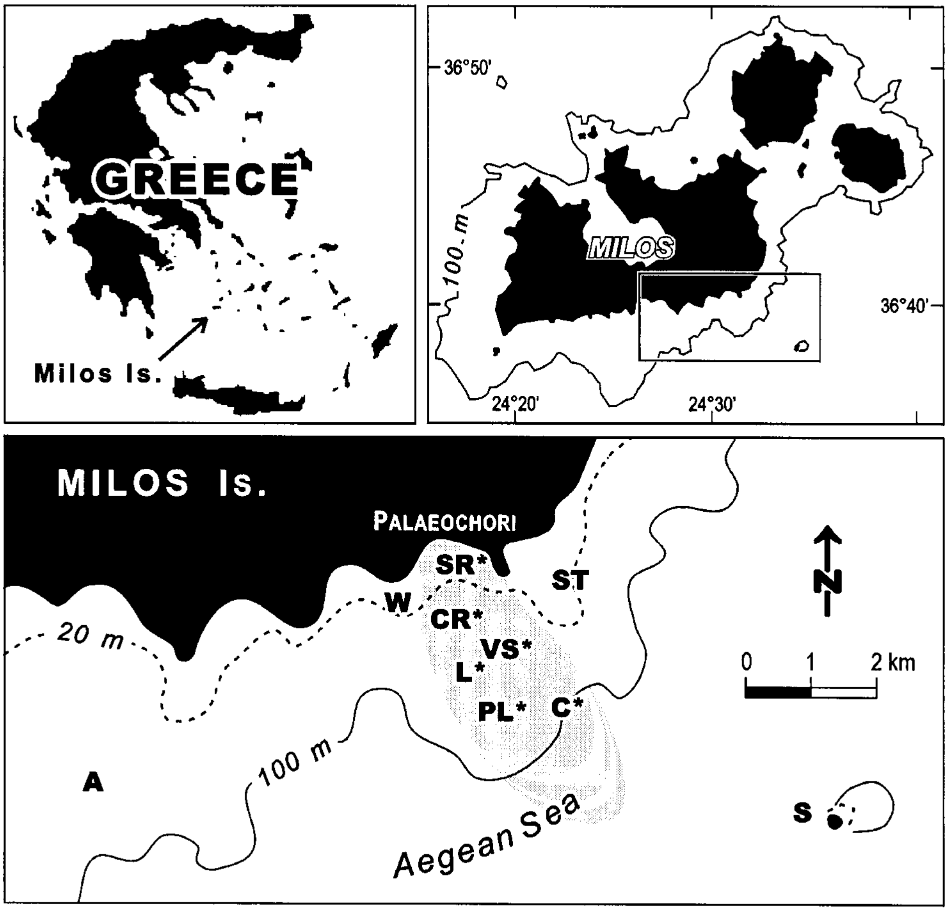

Figure 1. Geographical location of the Island of Milos in Greece and location of the sites where Serpuloidea were collected. Sites marked with an asterisk were close to actual hydrothermal vents. The principal area of vent occurrence is stippled.

On biogenic substrata (dead *Myriapora*, *Mesophyllum*, bases of *Cystoseira*) between 8 and 45 m depth, and on recovered instruments, 50–83 m depth. Small animals were pale whitish in white tubes, the largest ones were intensely pigmented with red, especially on the operculum, in pink tubes. Tubes were cylindrical with a dorsal keel, sometimes subtriangular in cross-section.

Serpula vermicularis echinata Philippi

Occurrence: A, CR*.

On a *Spondylus* shell and within a bryozoan nodule at 31 m depth. Also as a fouler at 80 m. Tube always pink, with five to seven toothed keels, worm always whitish. *Serpula vermicularis* should be regarded as a 'species complex' in need of revision (Kupryanova, 1999). We followed Bellan (1961) in keeping *echinata* apart because of its easily distinguished tube, but Zibrowius (1968) underlined its great variability. Whether differences in tube morphology may be of intra- or interspecific level is not clear at present (Ben-Eliahu & Fiege, 1996).

Serpula concharum Langerhans

Occurrence: CR*, S, W.

Always on biogenic substrata, such as corals (*Phyllangia mouchezi*) and coralline algae (*Mesophyllum lichenoides*, basal portion of the thallus of *Amphiroa rigida*), at 12–38 m depth. Tube white and rounded, with five toothed keels. Worms with an obvious dark spot on the thorax. Both characters are typical of the infralittoral 'form' of the species (Bianchi, 1981).

Serpula sp.

Occurrence: VS*.

A single animal, on a stone at 50 m depth. Tube white and much longer than the worm, rectangular in cross-section, with two stout and smooth lateral keels and a less evident central one. Worm thin and delicate (as compared to *S. concharum* above), tentacle crown fragile (the two lobes parted easily), operculum elongate, peduncle very long and slender, club-shaped pseudoperculum short (Figure 2). This species is distinct from what we are calling *S. concharum* above. The authors' reference collection contains specimens from both the Mediterranean (Cape Leuca, Tuscan Archipelago) and the north-east Atlantic (off Roscoff), from depths between 40 and 100 m. A. Poluzzi (Bologna) showed us fragments of a serpulid conglomerate, formed almost exclusively by tubes of this kind and collected at corresponding depths in the middle Adriatic. Both the species here called *Serpula concharum* and *Serpula* sp. are known from the eastern Mediterranean but their preferred depth range is said to be just the opposite (Ben-Eliahu & Fiege, 1996).

Serpula lobiancoi Rioja

Occurrence: PL*.

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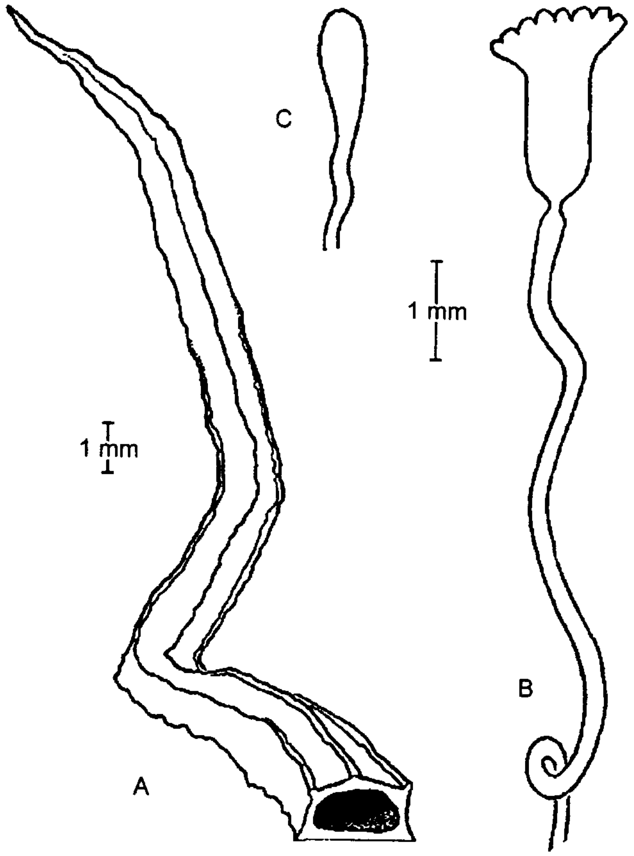

Figure 2. *Serpula* sp.: (A) tube; (B) operculum with peduncle; (C) pseudoperculum.

A single animal, with a large pink tube coiled in a double spire. The worm occupied the lower spire.

Hydroides norvegicus Gunnerus
Occurrence: A, VS*.

An animal epiphyte on *Sargassum acinarium* at 50 m depth and numerous others on recovered instruments at 80 and 83 m, in white tubes tightly coiled in flat spirals. Spines of the upper opercular crown long and sharpened, with numerous lateral denticles.

Hydroides pseudouncinatus pseudouncinatus Zibrowius
Occurrence: ST, CR*, W.

Common between 8 and 29 m depth, on corals (*Phyllangia mouchezi*) and especially on bryozoans (*Myriapora truncata*, *Rhyncozoon* sp., *Schizoporella longirostris*). Numerous very small animals together with larger empty tubes at CR*. The presence of a small tooth, turned towards the inside, on the spines of the opercular basal funnel was observed in all the worms examined.

Vermiliopsis infundibulum (Philippi)
Occurrence: VS*, W.

Several animals at 41–45 m on bioconcretion, stones and leathery algae (*Osmundaria volubilis*), and a small aggregation of tubes (mostly dead) on bryozoans on a cave roof at 8 m depth. Operculum variable, occasionally very high. Two main morphologies were recognized (Figure 3): (A) distal horny part distinctly domed to elongate, bearing a stout and rounded process on the top; (B) distal horny part short and flat-topped. Form A was found at 41–45 m, form B at 8 m. The possibility that these forms are of taxonomic value cannot be excluded.

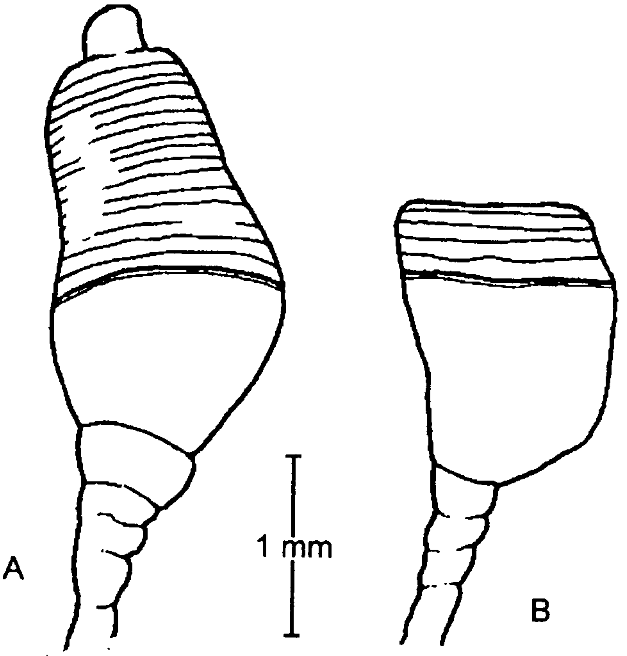

Figure 3. Opercular variability in *Vermiliopsis infundibulum*: (A) commonest shape at 41–45 m; (B) a specimen from 8 m depth.

Vermiliopsis striaticeps (Grube)
Occurrence: SR*, W.

A few animals among algae at shallow depths (3 and 12 m).

Vermiliopsis labiata (O.G. Costa)
Occurrence: ST, CR*, PL*, S, VS*, W.

Many animals at various depths from 8 to 81 m, on a shell of *Spondylus gaederopus*, at the base of *Cystoseira schiffneri*, and especially on the corals *Phyllangia mouchezi* and *Madracis pharensis* and within the interstices of mounds of *Mesophyllum lichenoides*. In these mounds, empty tubes remain to participate in the bioconcretion.

Vermiliopsis monodiscus Zibrowius
Occurrence: PL*, W.

Although more abundant at 81 m, the species was also observed in shallow water (8 and 12 m), always within bioconcretion. All the opercula bore a stout conical tooth or a small spine on the outer concave side of the opercular horny plate.

Metavermilia multicristata (Philippi)
Occurrence: CR*, PL*, VS*.

Found at depths between 31 and 81 m, on stones and shells but more commonly within the interstices of *Mesophyllum lichenoides* mounds. Tube long compared to the worm body, opercular cap elongate.

Semivermilia torulosa (Delle Chiaje)
Occurrence: PL*.

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Two worms and many empty tubes participating in the bioconcretion of *Mesophyllum lichenoides*.

Semivermilia agglutinata (Marenzeller)
Occurrence: VS*.

Within the interstices of a *Mesophyllum lichenoides* mound. Tube white, triangular in cross-section, with a toothed median keel and at least two side-keels. Horny distal plate of the operculum disc-shaped and relatively thick.

Semivermilia pomatostegoides (Zibrowius)
Occurrence: CR*.

A single animal, within bioconcretion.

Semivermilia crenata (O.G. Costa)
Occurrence: A, CR*, PL*, S, VS*, W.

Abundant at VS* but also common at other sites. On different substrata, but especially within *Mesophyllum* mounds, between 8 and 80 m. Opercular distal spine very variable; absent in small animals, seems to increase in length with worm size. In a worm nearly 10 mm long, the spine was as broad as and longer than the operculum.

Filogranula calyculata (O.G. Costa)
Occurrence: CR*, ST, VS*, W.

On *Mesophyllum* mounds, bryozoans and especially corals (*Polycyathus muelleri* and *Phyllangia mouchezi*), 8–45 m depth. Numerous empty tubes, some showing scissiparity, participate in bioconstruction at VS*.

Filogranula gracilis Langerhans
Occurrence: W.

A small animal on a valve of *Lithophaga lithophaga* in a rock crevice.

Janita fimbriata (Delle Chiaje)
Occurrence: CR*, VS*, PL*.

Abundant within the interstices of *Mesophyllum* mounds and corals (*Polycyathus muelleri* and *Madracis pharensis*), between 31 and 81 m. Numerous empty tubes (and only few worms) at PL.

Spirobranchus polytrema (Philippi)
Occurrence: A, C*, CR*, L*, S, ST, VS*.

The most abundant species in this collection. Found from 2 to 80 m depth, but especially in shallow water, on a variety of substrata, including different algae (*Cystoseira*, *Sargassum*, *Corallina*, *Lobophora*) and ascidian tests (*Microcosmus sabatieri*, *Halocynthia papillosa*). Hundreds of individuals settled on a flotation buoy at 10 m at site C. The numerous specimens collected showed variability in both tube and operculum (Table 1). According to the tube colour, white or pink varieties could be distinguished. White tubes occurred at a larger depth range and number of sites; pink tubes apparently characterized well-lit habitats, and were usually less sculptured. Whatever the colour, tube was sinuous to coiled (e.g. in crowded fouling population), generally subtriangular in cross-section and provided with toothed keels. Operculum showed three distinct morphologies, always concerning the dorsal ornaments of the distal calcareous plate (Figure 4): (A) two symmetric stout tubercles; (B) a single median tubercle (less frequently observed); (C) a high subconical process, slightly curved inward (possibly a derivation of B). In *Spirobranchus* cf. *polytrema* from the South China Sea, Fiege & Sun (1999) described opercula with a calcareous cone, perhaps comparable to our form C, in pink (small specimens) or white triangular tubes; and opercula with a lower distal calcareous part in specimens inhabiting white rounded tubes. Despite forms B and C being more frequently found within pink tubes, no convincing relation between tube and operculum variability was established in the Milos material.

Pomatoceros triqueter (L.)
Occurrence: C*, L*

Several animals on recovered instruments (50 and 83 m depth) and a large one on the bivalve *Anomia*

Table 1. Spirobranchus polytrema*: variability in tube and operculum according to tube colour, and environmental correlation.*

	White variety	Pink variety
Tube colour	Completely white.	At least partially pink, more frequently on the upper/outer side, sometime with two distinct longitudinal side bands parallel to the median keel.
Tube shape	(Sub)triangular in cross-section (rarely subcircular), always distinctly keeled. Keels toothed to (rarely) laciniate. Tube wall alveolate, often with Folliculina. Tube sometime coiled.	Subcircular to (sub)triangular in cross section, always with toothed keels. Tube wall smooth to alveolate. Tube often coiled.
Operculum	Biturbercolate or high subconical, sometime monotubercolate.	High subconical perhaps more frequent than bitubercolate. Monotubercolate comparatively abundant.
Sites	SR*, W, CR*, S, VS*, A, C*, L*	W, CR*, C*
Depth range (m)	2–90.	10–31
Substratum	Bioconcretion, algae, corals, shells, fouling.	Algae, fouling, bioconcretion, shells.

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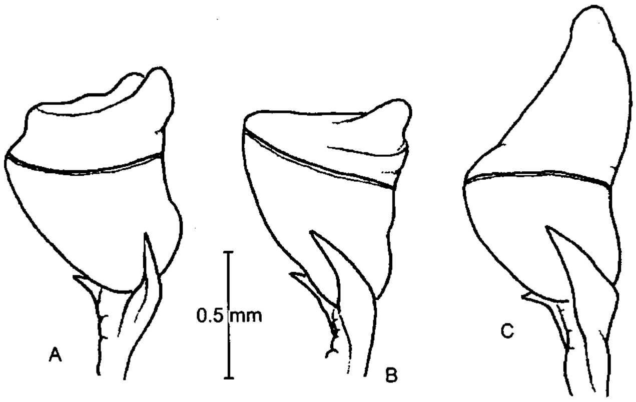

Figure 4. Three morphologies of the opercular plate in *Spirobranchus polytrema*. (A) bitubercolate; (B) monotubercolate; (C) high subconical.

ephippium settled on the same instruments. Opercular calcareous plate variable within the same population, from smooth and elongate to conical with two distal-lateral tubercles, to tridentate, as illustrated using scanning electron microscopy by Dixon et al. (1998).

Protula tubularia (Montagu)
Occurrence: L*, S, ST.
On rock, at 21–31 m depth. A small animal, probably a juvenile, among the fouling at 50 m. Tube cylindrical, relatively slender, worm with extensive thoracic membranes. Identification follows ten Hove & Pantus (1985).

Apomatus similis Marion & Bobretsky
Occurrence: CR*, L*.
A large animal from a *Mesophyllum* mound at 31 m depth and three on a recovered instrument at 50 m. The largest tube had up to six longitudinal, fine but regular and well defined ridges. Colour of freshly fixed worms was a bright orangered. Identification follows ten Hove & Pantus (1985).

Salmacina dysteri (Huxley)
Occurrence: A, CR*, L*, PL*, S, SR*, VS*.
Common on various substrata at 4–80 m, tending to form aggregations at the base of *Cystoseira* and other algae (*Beckerella mediterranea*, *Amphiroa rigida*). Very abundant among the fouling, producing cordons through asexual reproduction. The species was identified by the swollen radiole tips and the lenticular clusters on the rachis (Nelson-Smith et al., 1990).

Josephella marenzelleri Caullery & Mesnil
Occurrence: CR*, PL*, S, ST, VS*, W.
Numerous animals on various substrata, including algae (*Cystoseira*, *Sargassum*, *Lobophora*, *Osmundaria*), 8–81 m. Tubes very long and thin, flexible, isolated or in small skein, with distal part sometime erect.

SPIRORBIDAE

Protolaeospira striata (Quiévreux)
Occurrence: CR*, W.
Several animals, always on bryozoans (*Myriapora truncata*, *Schizoporella longirostris*), at 8 and 29 m depth. Never found incubating.

Janua pagenstecheri (Quatrefages)
Occurrence: S, VS*, W.
On fleshy algae (*Sargassum*, *Flabellia*, *Osmundaria*), 6–50 m depth. Tube keeled and rather subtriangular in cross-section, last whorl usually coiling up. Distal calcareous plate flat in both primary and secondary opercula.

Janua pagenstecheri gnomonica (Bailey)
Occurrence: VS*, W.
On *Myriapora truncata* on a rock overhang at 8 m and on *Mesophyllum lichenoides* at 45 m depth. Distal opercular plate little or not calcified, except the eccentric distal process. Only three big eggs inside the incubatory chamber of secondary opercula. *Spirorbis (Janua) gnomonicus* was described by Bailey (1969) from Chios, and later synonymized with *Janua pagenstecheri* by Knight-Jones et al. (1975). We prefer to keep this form apart for having distinct ecological requirements: it seems to prefer dim-light or circalittoral biotopes (Belloni & Bianchi, 1982; Sanfilippo, 1991) and might be characteristic of warm localities (Knight-Jones et al., 1975).

Neodexiospira pseudocorrugata (Bush)
Occurrence: CR*, SR*, VS*.
Usually an epiphyte of different algae (*Anadyomene stellata*, *Corallina elongata*, *Flabellia petiolata*, *Sargassum acinarium*), but also collected on stones and bryozoan nodules (*Schizoporella longirostris*), from 1 to 50 m depth. Both primary and secondary opercula, with eggs in the brooding chamber, were commonly observed.

Pileolaria militaris Claparède
Occurrence: PL*.
Two large animals, both with secondary operculum. The dark spot on the worm's thorax seems a constant feature of this species (as in *Serpula concharum* above).

Pileolaria heteropoma (Zibrowius)
Occurrence: VS*.
A few incubating animals on a *Schizoporella* nodule.

Vinearia koehleri (Caullery & Mesnil)
Occurrence: CR*, VS*, W.
The most abundant spirorbid, especially on bryozoans (*Myriapora truncata*, *Schizoporella longirostris*, and other encrusting species) but also on *Vermetus granulatus* (which in turn settled on bryozoans), corals (*Madracis pharensis*) and *Mesophyllum lichenoides*, 8–45 m depth. Gregarious: small tubes were settled on larger ones. Both primary and secondary opercula were observed, the latter was commonly found incubating.

Nidificaria clavus (Harris)
Occurrence: PL*, S, VS*.
Several animals, always on *Mesophyllum lichenoides* in rather deep water (38–81 m). Tube smooth, nearly quadrangular in cross-section. Most worms with primary operculum, a few with the secondary, incubating 2–3 eggs in the ampulla.

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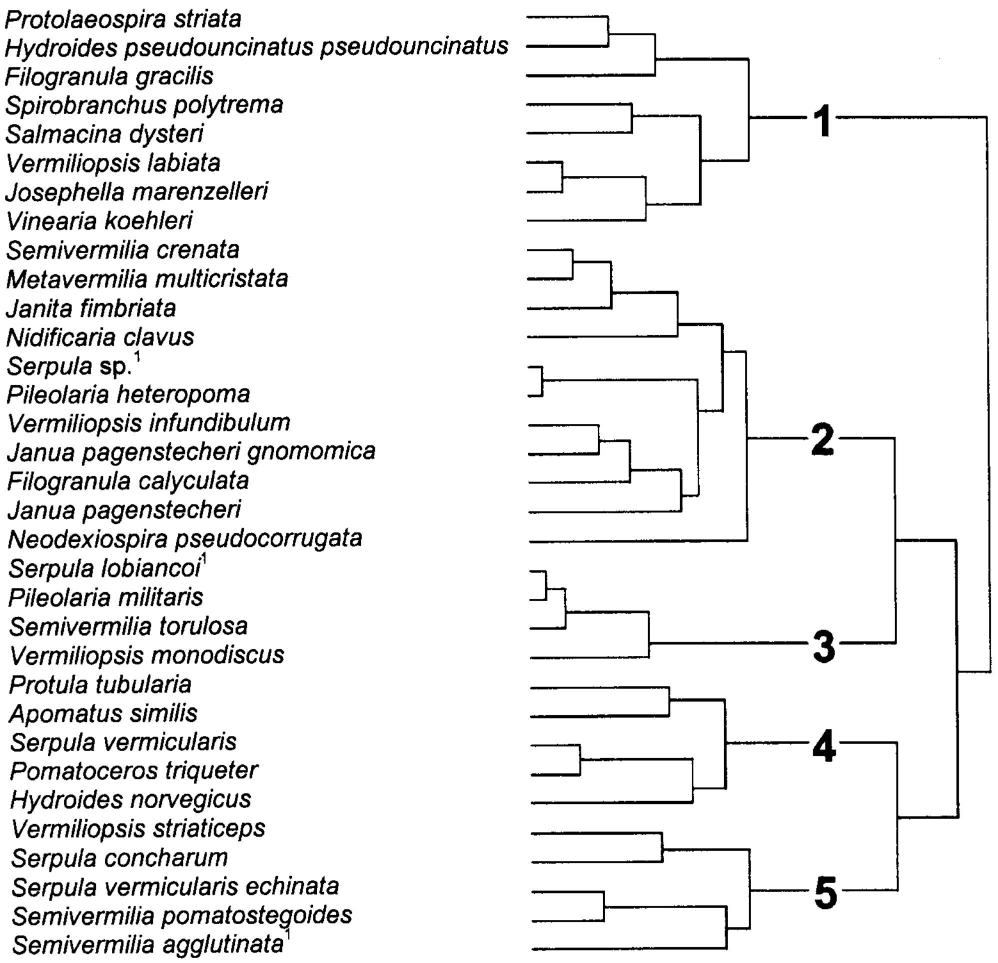

Figure 5. Dendrogram of species affinity, van der Maarel coefficient, complete linkage. Bold numbers indicate species clusters. [1], species found only once.

BIODIVERSITY

A total of 33 species (or subspecific taxa) were found: 25 Serpulidae and eight Spirorbidae. This figure corresponds to about half the species known in the Mediterranean Sea. If we exclude brackish-water species and species typically thriving in harbours, which would obviously not occur in the present collection, then the relative proportion is still higher. Finding more than half the species of the Mediterranean in a small area with a comparatively low sampling effort, supports recent claims that the Aegean biodiversity is not as low as previously believed (Bianchi et al., 1999).

Few other species inventories for the eastern Mediterranean are available for comparison (Ben-Eliahu & Fiege, 1996). Ergen & Cinar (1997) listed 47 Serpulidae (ten Serpulidae and three Spirorbidae) from Antalya et al. (1999), 24 Serpulidae from Cyprus. Zibrowius (1969) collected 24 species (20 Serpulidae and four Spirorbidae) in the Gulf of Gabès and Tripolitania. Comparable records from the western Mediterranean include 28 species (20 Serpulidae and eight Spirorbidae) from the Ligurian Sea (Bianchi, 1979b); 23 species (16 Serpulidae and seven Spirorbidae) from Sardinia (Bianchi et al., 1984); 38 species (27 Serpulidae and 11 Spirorbidae) from Marseilles (Zibrowius, 1968); and 29 species (23 Serpulidae and six Spirorbidae) from northern Tunisia (Zibrowius, 1978).

ZOOGEOGRAPHY

All the species collected at Milos are already known for the western Mediterranean (Bianchi, 1981; Castelli et al., 1995). Most are Atlantic–Mediterranean species, the remaining have worldwide distribution. Some of these, however, may be species-complexes hiding species with restricted geographic ranges. This is almost certainly the case with *Serpula vermicularis* (Kupriyanova, 1999), *Vermiliopsis infundibulum* and *Spirobranchus polytrema* (Fiege & Sun, 1999), but might also apply to *Apomatus similis*, *Salmacina dysteri*, *Protula tubularia*, *Janua pagenstecheri* and other species as well.

The lack of Lessepsian migrants, that now characterize the Levant serpulid fauna (Ben-Eliahu, 1991; Ben-Eliahu & Payatis, 1999), is remarkable. Also remarkable is the absence from this collection of certain alien species long established in the Mediterranean, such as well known examples within the genus *Hydroides* (Zibrowius, 1971). Both absences may be explained, at least in part, by our collection coming from an area relatively far from harbours.

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Even excluding old and new migrants, *Hydroides* comprises many species in the Mediterranean, but was represented only by two in our collection. This seems to contrast with the geographical position of Milos, which should favour warm-water fauna, as are most *Hydroides* species. One of such species is *Hydroides niger*, considered thermophilic by Bianchi et al. (1984). Its absence from Milos and Israel (Ben-Eliahu & Fiege, 1996) apparently conforms to the alleged filtering-out of species from west to east in the Mediterranean Sea. *Hydroides niger*, however, is known from Cyprus (Ben-Eliahu & Payiatas, 1999) and Turkey (Knight-Jones et al., 1991).

SPECIES GROUPS

Cluster analysis revealed five groups of species (Figure 5). Group 1 is formed by eight species and includes all the most abundant and common, such as *Spirobranchus polytrema*, *Salmacina dysteri*, *Vermiliopsis labiata*, *Josephella marenzelleri* and *Vinearia koehleri*. They inhabited various substrata at depths ranging from 1 to 83 m. Their wide ecological distribution on continental shelf areas has been reported also for other sites of the Mediterranean (Zibrowius, 1968; Bianchi, 1981). Also the 11 species of group 2 were for the most part common and abundant, but all were especially found at vent sites (SR*, CR* and VS*), 1–45 m deep.

Group 3 comprises four species found mainly (*V. monodiscus*) or exclusively within bioconcretion at the deep site PL*. The five species of group 4 were joined by their apparent preference for the fouling assemblages settled on recovered instruments. All are already known as common open-water foulers in the Mediterranean (Relini et al., 1977; Bianchi, 1979b). Finally, group 5 includes five species that are more common in shallow water, although one (*Serpula vermicularis echinata*) was found also at 80 m depth. The two most abundant species of this group, *S. concharum* and *Vermiliopsis striaticeps*, are somehow characteristic of algal communities in shallow water (Bianchi, 1979b).

Table 2. *Observed depth distribution of the serpuloidean species collected. Species are ordered according to their apparent depth preference.*

Depth (m)	1 to 15	15 to 40	40 to 83
INFRALITTORAL			
Vermiliopsis striaticeps	+	–	–
Filogranula gracilis[1]	+	–	–
Protolaeospira striata	+	+	–
Hydroides pseudouncinatus pseudouncinatus	+	+	–
Serpula concharum	+	+	–
Spirobranchus polytrema	+++	++	+
INFRALITTORAL AND CIRCALITTORAL			
Neodexiospira pseudocorrugata	+	+	+
Filogranula calyculata	+	+	+
Vinearia koehleri	+	+	+
Janua pagenstecheri	+	+	+
Semivermilia crenata	+	+	+
Serpula vermicularis	+	+	+
Janua pagenstecheri gnomonica	+	–	+
Vermiliopsis infundibulum	+	–	+
Vermiliopsis monodiscus	+	–	+
Semivermilia pomatostegoides[1]	–	+	–
Salmacina dysteri	++	+++	++
Josephella marenzelleri	+	++	++
Vermiliopsis labiata	+	++	++
CIRCALITTORAL	–	+	+
Apomatus similis			
Nidificaria clavus	–	+	+
Serpula vermicularis echinata	–	+	+
Metavermilia multicristata	–	+	+
Protula tubularia	–	+	+
Janita fimbriata	–	+	++
Pileolaria heteropoma[1]	–	–	+
Serpula sp.*	–	–	+
Semivermilia agglutinata[1]	–	–	+
Pomatoceros triqueter	–	–	+
Hydroides norvegicus	–	–	+
Pileolaria militaris[1]	–	–	+
Serpula lobiancoi[1]	–	–	+
Semivermilia torulosa[1]	–	–	+

+, present (one to few specimens); ++, common (several specimens); +++, very common (tens to hundreds of specimens).

[1], species found only once.

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As a whole, clustering of species was related to their depth distribution, substratum preference, and perhaps also to some indirect effect of hydrothermalism.

DEPTH DISTRIBUTION

Although some species were only recorded once, most were found throughout the depth range investigated. Three main situations, however, can be distinguished (Table 2): (i) six species preferred shallow depths, common in less than 15 m, and can therefore be qualified as infralittoral species; (ii) 13 species inhabited mainly deeper sites, below 15 or 40 m, showing a clear circalittoral affinity; (iii) the remaining 14 species were equally present from shallow to deep water or preferred intermediate depths.

This depth zonation conforms for the most part to previous knowledge from other Mediterranean areas (Zibrowius, 1968; Bianchi, 1981; Ben-Eliahu & Fiege, 1996). A peculiar feature at Milos, however, was the frequent occurrence of comparatively deep-water species in shallow habitats. *Vermiliopsis monodiscus*, *Metavermilia multicristata*, *Filogranula calyculata* and others (e.g. most species of the genus *Semivermilia*) are more typically found at bathyal depths or in dark submarine caves (Bianchi, 1981; Belloni & Bianchi, 1982). Their occurrence in shallow sites at Milos may have two explanations. First, these species were always found in cryptic habitats, such as the microcavities within *Mesophyllum* mounds or under rock overhangs, which resemble cave habitats. Second, shelf topography south of Milos is such that bottom friction in the deeper water layers induces currents toward

Table 3. *Distribution of the serpuloideans on the different substrata sampled.*

	Epiphytes on algae			Participating in bioconstruction			Primary settlers		
	Cystoseira	*Sargassum*	Other algae	*Mesophyllum* mounds	Corals	Bryozoan colonies	Rock and stones	Shells	Fouling
Serpula vermicularis	+	–	+	–	+	+	–	–	++
S. vermicularis echinata	–	–	–	–	–	+		+	+
S. concharum	–	–	+	++	+	.	.	.	.
Serpula sp.[1]	–	–	–	–	.	.	+	.	.
S. lobiancoi	–	–	–	+	–	–		–	–
Hydroides norvegicus	–	+	–	–	–	–		–	+++
H. pseudouncinatus pseudouncinatus	–	–	–	–	+	+		–	–
Vermiliopsis infundibulum	–	–	+	+	–	+	+	–	–
V. striaticeps	–	–	+	–	–	–		–	–
V. labiata	+	–	–	++	++	–		+	–
V. monodiscus	–	–	–	++	–	+		–	–
Metavermilia multicristata	–	–	–	++	–	–	+	+	–
Semivermilia torulosa	–	–	–	++	–	–		–	–
*S. agglutinata**	–	–	–	+	–	–		–	–
*S. pomatostegoides**	–	–	–	+	–	–		–	–
S. crenata	++	–	–	+++	–	–		+	+
Filogranula calyculata	–	–	–	+	++	+		–	–
*F. gracilis**	–	–	–	–	–	–		+	–
Janita fimbriata	–	–	–	+++	++	–		–	–
Spirobranchus polytrema	++	+	+	++	+	++		+	+++
Pomatoceros triqueter	–	–	–	–	–	–		+	++
Protula tubularia	–	–	–	–	–	–	+	–	+
Apomatus similis			–	+	–	–		–	+
Salmacina dysteri	++	+	++	+	+	+	+	–	+++
Josephella marenzelleri	+	+	++	+++	++	+		++	–
Protolaeospira striata	–	–	–	–	–	+		–	–
Janua pagenstecheri	–	++	+++	–	–	–		–	–
J. pagenstecheri gnomonica	–	–	–	+	–	+		–	–
Neodexiospira pseudocorrugata	–	+	+++	++	–	–	++	–	–
Pileolaria militaris[1]	–	–	–	+	–	–		–	–
P. heteropoma[1]	–	–	–	–	–	+		–	–
Vinearia koehleri	–	–	–	+	+	++		–	–
Nidificaria clavus	–	–	–	+	–	–		–	–

+, present (one to few specimens); ++, common (several specimens); +++, very common (tens to hundreds of specimens);
[1], species found only once.

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the coast (Aliani & Bergamasco, 1999): these currents may well be the carrier of deep-water species larvae.

SUBSTRATUM PREFERENCE

The vast majority of the species collected at Milos inhabited the biogenic mounds formed by the coralline alga *Mesophyllum lichenoides* (Table 3), settling on the leafy calcareous surface or colonizing the interstices. Major examples of the latter case were *Vermiliopsis infundibulum*, *V. labiata*, *Semivermilia torulosa* and *Filogranula calyculata*. Serpuloidea participated in the bioconstruction, acting as binders, or adding their calcareous tubes to the build-up when simply acting as cavity-dwellers. Similar roles were played by species associated with bryozoan nodules (especially *Schizoporella longirostris*) and corals. For example, tubes of *V. labiata* living on *Phyllangia mouchezi* were embedded within the coral skeleton, a phenomenon more commonly reported for tropical species symbiotic with hermatypic corals (Nishi & Nishihira, 1996).

Serpulidae may also be primary builders themselves (Bianchi et al., 1995). At Milos we observed aggregations of tubes of *Salmacina dysteri*, often called colonies or pseudocolonies in the literature (e.g. Nishi & Nishihira, 1994), but they were fragile and did not show any significant constructional capacity.

A small number of species was found on algae, but none were strict epiphytes. The two spirorbids *Janua pagenstecheri* and *Neodexiospira pseudocorrugata*, however, showed some preference for algae with leafy thalli (*Sargassum*, *Flabellia*, *Osmundaria*, *Anadyomene*, etc.). Many Spirorbidae are known to exhibit preference for and even specificity to distinct algae (Knight-Jones & Knight-Jones, 1977). No Mediterranean serpuloideans are known to exhibit such a specificity, and species settling on algae are mostly substratum generalists which are able to colonize algae due to their small size or tube flexibility, as in the case of *Josephella marenzelleri* (Sanfilippo, 1996). Morphological constraints, thus, seem more important than selective choice. None of the Serpuloidea primarily settled on stones, (dead) shells, and recovered instruments showed substratum preference.

INFLUENCE OF VENT PROXIMITY

The number of species found at vent sites was significantly (Mann–Whitney *U*-test; $Z=2.611$; $P=0.009$) higher than that found at non-vent sites (Figure 6). Species belonging to group 2 (see above) were found mainly at vent sites and some of them (e.g. *Metavermilia multicristata*, *Janita fimbriata* and *Neodexiospira pseudocorrugata*) were abundant and found exclusively there, thus suggesting a significant preference.

According to Barry et al. (1996), biota inhabiting vent areas include 'obligate' species, restricted to sites in direct proximity to fluids, and 'regional' species, which occupy both vent and neighbouring non-vent sites. All the serpuloidean species collected near shallow-water vents at Milos are already known from 'normal' sites in the Mediterranean Sea (Zibrowius, 1968; Bianchi, 1981) and, therefore, cannot be classified as obligate.

Four main explanations are possible for the higher serpuloidean diversity near vents at Milos.

Table 4. *Serpuloidea occurred amidst fouling assemblages on oceanographic instruments.*

Site/Depth (m)	L* 50	C* 10	C* 83	A 80
Oceanographic instrument	Probe supporter	Flotation buoy	Current meter	Current meter
Serpula vermicularis	++	–	++	–
S. vermicularis echinata	–	–	–	+
Hydroides norvegicus	–	–	+++	+
Semivermilia crenata	–	–	–	+
Spirobranchus polytrema	+	+++	–	+
Pomatoceros triqueter	+	–	++	–
Protula tubularia	+	–	–	–
Apomatus similis	++	–	–	–
Salmacina dysteri	+++	–	–	++

+, present (one to few specimens); ++, common (several specimens); +++, very common (tens to hundreds of specimens).

As filter-feeders, serpuloideans profit from the additional primary production by chemosynthetic bacteria (Olu et al., 1996). Desbruyères et al. (1985) have found filamentous bacteria attached to the digestive tubes of hydrothermal serpulids.

Deposition of carbonates is enhanced by the modified water chemistry at vents (Kulm & Suess, 1990). At Milos, *Mesophyllum lichenoides* mounds and other biogenic carbonate structures were more conspicuous near vents. They

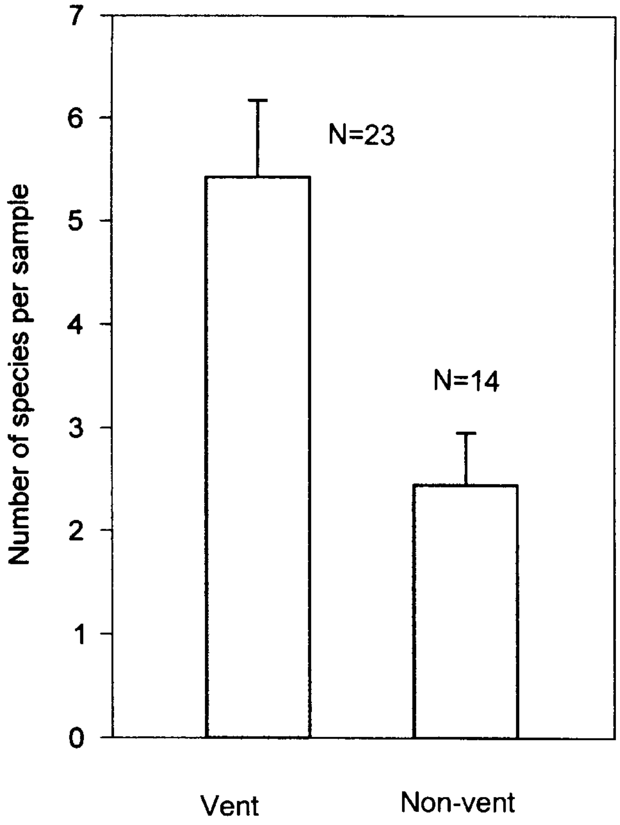

Figure 6. Serpuloidean species richness (mean ±SE) at vent and non-vent sites.

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provided newly formed secondary substrata for the settlement of encrusting organisms and numerous interstices and microcavities for the cryptic fauna. Both definitions apply to serpuloideans.

Fluid emission at vents may cause advective mechanisms concentrating larval stages in the vicinity of vents. Van Dover et al. (1988) observed higher levels of recruitment near hydrothermal vents. At Milos, the occurrence of many small-sized individuals of some species (e.g. *Hydroides pseudouncinatus pseudouncinatus*, *Semivermilia crenata* and *Vinearia koehleri*) at vent sites might suggest a similarly higher level of recruitment. A diverse serpuloidean fouling was found on oceanographic instruments, but differences between settlements at vent and non-vent sites were unclear (Table 4).

Emission of toxic fluids from vents causes episodic mass mortality of the benthic fauna (Dando et al., 1995). In vestimentiferan tube-worms at deep-sea hydrothermal vents, Tunnicliffe et al. (1990) observed a mortality rate of 44% in 26 days. Hypothetically similar high mortality rates in Serpuloidea at Milos might explain the finding of numerous empty tubes at vent sites (see for example, *Vermiliopsis labiata*, *Semivermilia torulosa*, *Filogranula calyculata* and *Janita fimbriata*). Episodic mass mortalities would free space for the settlement of other species and thus reset ecological succession of the epibenthic community. Vent activity may therefore act as an 'intermediate disturbance' (Connell, 1978), allowing for coexistence of a larger number of species.

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