

A NEW SPECIES OF POECILOSCLERID SPONGE (PORIFERA) FROM BATHYAL METHANE SEEPS IN THE GULF OF MEXICO

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A new species of poecilosclerid sponge from methane seeps on the Louisiana Slope, Gulf of Mexico, USA is described. This thickly encrusting sponge grows around vestimentiferan tubes and has a very patchy distribution. The skeletal structure and the spicule set match those characterizing the genus *Ectyomyxilla*. The new species, *Ectyomyxilla methanophila* sp. nov., is distinguished from the remaining species in the genus by the structure of its ectosomal skeleton, where small acanthostyles are never present, and by its choanosomal skeleton, which is barely reticulate and has echinated main tracts. The small size of the choanocyte chambers suggests occurrence of nutritional benefits derived from association with chemoautotrophic symbiotic bacteria. However, the presence of oscules, ostioles, aquiferous canals and choanocyte chambers indicates that this sponge also relies partly on filtration for its nutrition. This is the first record of the genus *Ectyomyxilla* in the northern hemisphere, and the first non-carnivorous demosponge known to exploit methane-rich marine environments.

INTRODUCTION

Regions of the deep sea floor where methane gas seeps from underlying hydrocarbon deposits often support dense populations of animals (McDonald et al., 1989; Kennicutt et al., 1985; Juniper & Sibuet, 1987), some of which can convert methane or sulphide into usable sources of reduced carbon (Childress et al., 1986) and energy (Cary et al., 1988) with the aid of chemosynthetic endosymbiotic bacteria. The resulting high productivity at methane seeps attracts a diversity of animals from the surrounding communities (McDonald et al., 1989; Carney, 1994), which take advantage of the enhanced food. Methane is also exploited by free-living bacteria, which in turn become available as food for filter-feeders (Olu et al., 1996), and deposit feeders on the sea-floor. Because sponges are capable of removing bacteria from suspension (Reiswig, 1975; Pile et al., 1997), they might be expected to occur in great numbers where seeps fuel high bacterial populations. It is surprising, therefore, that only two marine sponges, which still remain taxonomically undescribed, are known to occur near marine methane seeps. One of them is a member of the deep sea family Cladorhizidae (Vacelet et al., 1995, 1996). Unlike most sponges, this species is not a

filter-feeder, but rather a methanotrophic carnivore which depends on chemosynthetic symbionts for its nutrition, and transmits the symbionts to the next generation by means of the embryos (Vacelet et al., 1995, 1996).

The other sponge was first mentioned, though not identified, in a study of the spatial distributions of seep organisms by McDonald et al. (1989) and shown to have a very light (-32.8) $\delta^{13}\text{C}$ value consistent with methanotrophic nutrition. Chemoautotrophic bacteria have also been reported to occur in the mesohyl of this sponge by Harrison et al. (1994), who preliminarily regarded it as an undescribed species in the genus *Hymedesmia*. This sponge, a new species of a genus previously known only from Antarctic and subantarctic seas, *Ectyomyxilla*, is described here. This species, which lives as an epibiont of vestimentiferan tube worms at bathyal methane seeps on the Louisiana Slope, is entirely capable of filter-feeding. We suggest that it obtains its nutrition in part by feeding on free-living chemoautotrophic bacteria associated with the methane seeps, and in part by symbiosis with chemoautotrophic bacteria.

MATERIALS AND METHODS

Sponges were collected during September 1995 from 500–600 m depths at Bush Hill (27°46.95'N 91°30.49'W) and nearby sites in the Green Canyon Block of the Gulf of Mexico (Louisiana Slope), using a manipulator arm on the manned submersible 'Johnson-Sea-Link I'. *In situ* photographs were taken with an externally mounted, laser-aimed 35 mm benthos camera with 85 mm lens.

Material was fixed in 10% seawater formalin then preserved in 70% ethanol. Skeletal mounts and histological sections for light microscopy were prepared according to standard techniques (Rützler, 1978). Scanning electron micrographs were taken with a Hitachi S-2300 SEM. The type material and additional specimens are deposited in the Porifera collection of the Smithsonian National Museum of Natural History (USNM).

TAXONOMIC DESCRIPTION

Order POECILOSCLERIDA Topsent, 1928

Family MYXILLIDAE Hentschel, 1923

Ectyomyxilla Lundbeck, 1909

Synonymy

Crellomyxilla Dendy, 1924.

Diagnosis

Myxillidae with anchorate isochelae whose ectosomal skeleton consists of tangential diactines (tylotes or tornotes) and acanthostyles. Choanosomal skeleton consisting of an irregular to isodictyal or square-meshed reticulation. Choanosomal network made of smooth or spined styles, with accessory acanthostyles that may

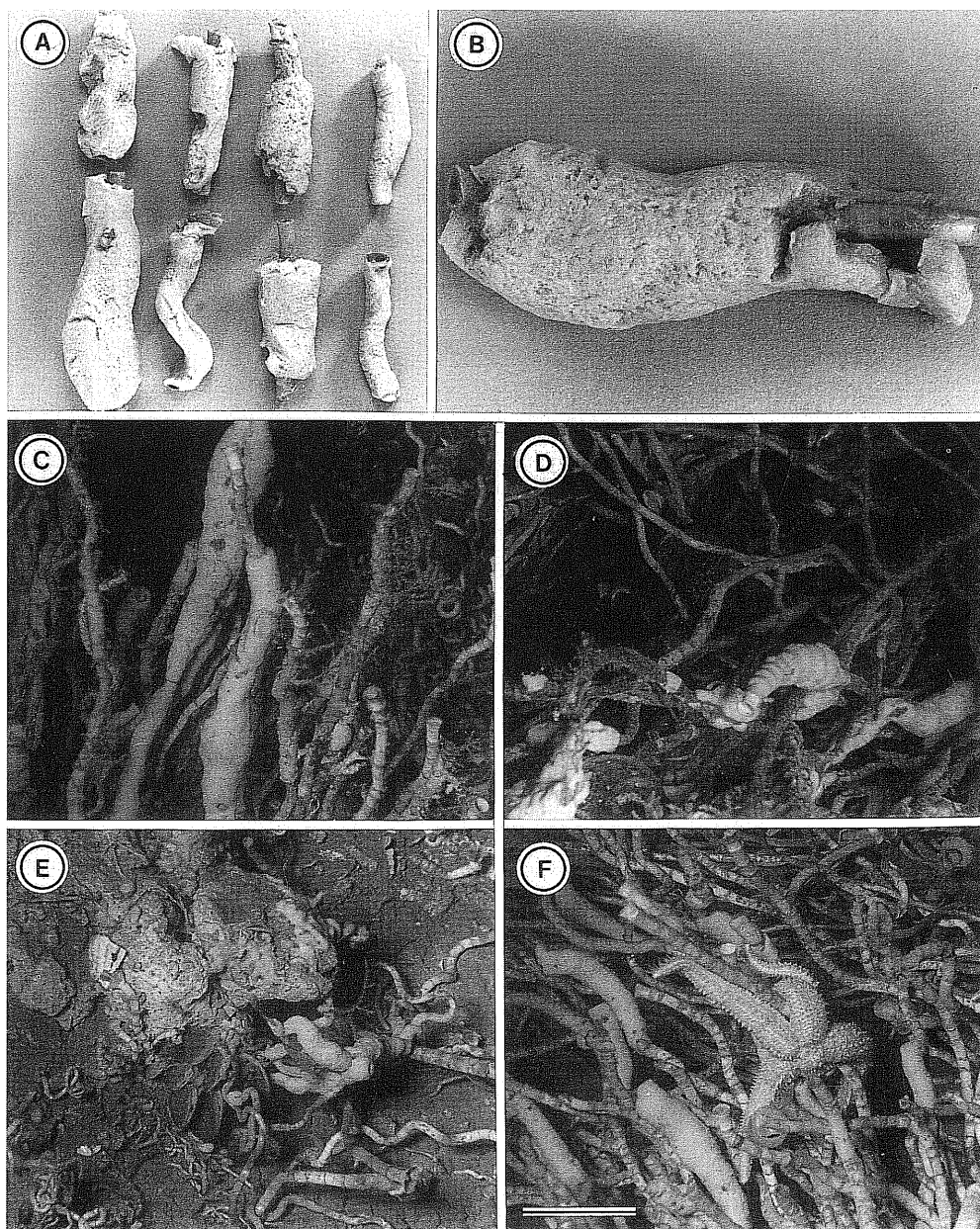


Figure 1. (A) Material of *Ectyomyxilla methanophila* collected from 500–600 m depths at Bush Hill. (B) Oscules and ostioles are shown on the surface of the holotype (USNM-39721). (C) Individuals of *E. methanophila* growing on the tubes of the large vestimentiferan tube worm *Lamellibrachia* sp. (D) Sponge individuals growing on the tubes of the small vestimentifera tube worm *Escarpia* sp. Shells of the mussel *Bathymodiolus* sp., consistently lacking sponge cover, are shown on the background. (E) Sponge individuals growing directly on rocks at the periphery of the seeps are quite uncommon. (F) An individual of the starfish *Sclerasterias* cf. *tanneri* wrapped around the vestimentiferan tubes in regions where the sponges were common. Scale bar in F: A, 4 cm; B, 1.7 cm; C–F, 7 cm.

echinate the tracts. Microscleres are anchorate-unguiferate, three-toothed isochelae in one or more size categories; sigmata are also present (*sensu* Bergquist & Fromont, 1988).

Remarks

The concept of *Ectyomyxilla* given by Bergquist & Fromont (1988) is followed here, rather than the recent proposal by Desqueyroux-Faúndez & van Soest (1996) regarding *Ectyomyxilla* as a subgenus of *Myxilla*. These latter authors diagnosed *Ectyomyxilla* as '*Myxilla* with echinating strongly spined styles'. Such a diagnosis may actually be invalid, because it is in conflict with the skeletal features of the type species, *Ectyomyxilla kerguelensis* Hentchel, 1914, that lacks echinating acanthostyles.

Ectyomyxilla methanophila sp. nov.

Holotype

Specimen USNM-39721 (Figure 1A,B).

Paratype

Specimen USNM-39740 (Figure 1A).

Type locality

Bush Hill, Green Canyon Lease Block on the Louisiana Slope, Gulf of Mexico (27°46.95'N 91°30.49'W) 542 m depth.

Additional material

Specimens USNM-39747, USNM-40619, USNM-406121, USNM-40632 (Figure 1A).

Etymology

The species refers to the close relation of this species with the methane seeps. Methano = methane gas, Phila = loving.

External morphology

Thickly encrusting sponges, between 5 and 8 cm long, and between 0.2 and 0.6 cm thick, growing around vestimentiferan tubes (Figure 1A–F). Living individuals are cream colour and have a soft, crumbly texture. The sponge surface is smooth to the touch, although slightly uneven in places and microhispid in some areas. Oscules and ostioles are simple pore-like perforations, scattered across the sponge surface (Figure 1B). Although oscules are difficult to distinguish from ostioles in fixed animals, major oscules can usually be identified by the presence of a surrounding radial pattern of transparent excurrent canals. Major oscules range from 300–800 μm in diameter. The remaining perforations on the sponge surface range from 150 to 400 μm , and correspond to either smaller oscules, ostioles or inhalant canals where the ectosome is broken or retracted by fixation. The smaller oscules are sometimes very close together, especially when sharing a common subectosomal space. In such cases, they are separated from each other only by thin exopinacothelial strands.

Spicules

The spicule set (Figures 2 & 3) is as follows.

Tornotes. Straight or slightly undulated, more or less isodiametric, with symmetrical ends being smooth, sharply pointed and slightly lanceolate, measuring $190\text{--}230 \times 3\text{--}6 \mu\text{m}$ (Figures 2A,B & 3A).

Acanthostyles-I. Slightly curved, showing a higher spine concentration towards the round end, while spines are more sparse or even absent toward the spicule point. Spine morphology is extremely variable; they may be large or small, straight or curved, conical and pointed or thick and blunt (Figure 2C). Spicules measure $234\text{--}257 \times 9\text{--}13 \mu\text{m}$.

Acanthostyles-II. Straight or slightly curved and entirely spiny (Figure 2D). They measure $137\text{--}158 \times 7\text{--}9.5 \mu\text{m}$.

Isochelae-I. Spatuliferous, anchorate, three-toothed type (Figures 2F & 3D); sometimes appearing unguiferate (the latter may be underdeveloped spicules; Figures 2E & 3D). Teeth showing a slightly marked groove on the external side and a crest-like reinforcement on the internal one (Figure 3C). Alae always present, flanking the shaft. Spicules measure $47\text{--}54 \mu\text{m}$ in length.

Isochelae-II. Spatuliferous, anchorate, three-toothed type. Teeth are fused with each other at their bases, showing an appearance intermediate between anchorate and palmate (Figures 2G & 3E). Teeth long relative to the shaft, and lacking both the external groove and the internal crest characterizing the larger isochelae-I. Alae are always present. Spicules measure $14.3\text{--}19 \mu\text{m}$ in length.

Sigmata. S-shaped and varying widely in size, from 25×2 to $50 \times 3 \mu\text{m}$ (Figures 2H & 3F).

Internal organization and skeleton

The ectosome is an epithelium-like, bright, translucent membrane that is not easily detached, and which contains abundant tornotes, large acanthostyles and numerous microscleres of all three types (isochelae-I, II and sigmata). Tornotes and large acanthostyles are tangential, without forming any particular reticulation or any relevant tract pattern within the ectosomal plane. Small acanthostyles are never present in the ectosomal membrane. The endosomal region is soft, fleshy, with small aquiferous canals ($<1 \text{mm}$ in diameter), and relatively few unevenly distributed choanocyte chambers. Choanocyte chambers are oval, measuring from 7.5×15 to $17.5 \times 26 \mu\text{m}$ in histological sections. All eight sponge individuals examined contained developing embryos and spermatogonia. Embryos were at various stages of development, and ranged in size (length \times width) from 275×244 to $336 \times 275 \mu\text{m}$. Extracellular rod-like bacteria ($<1 \mu\text{m}$ in length) were common in the sponge mesohyl.

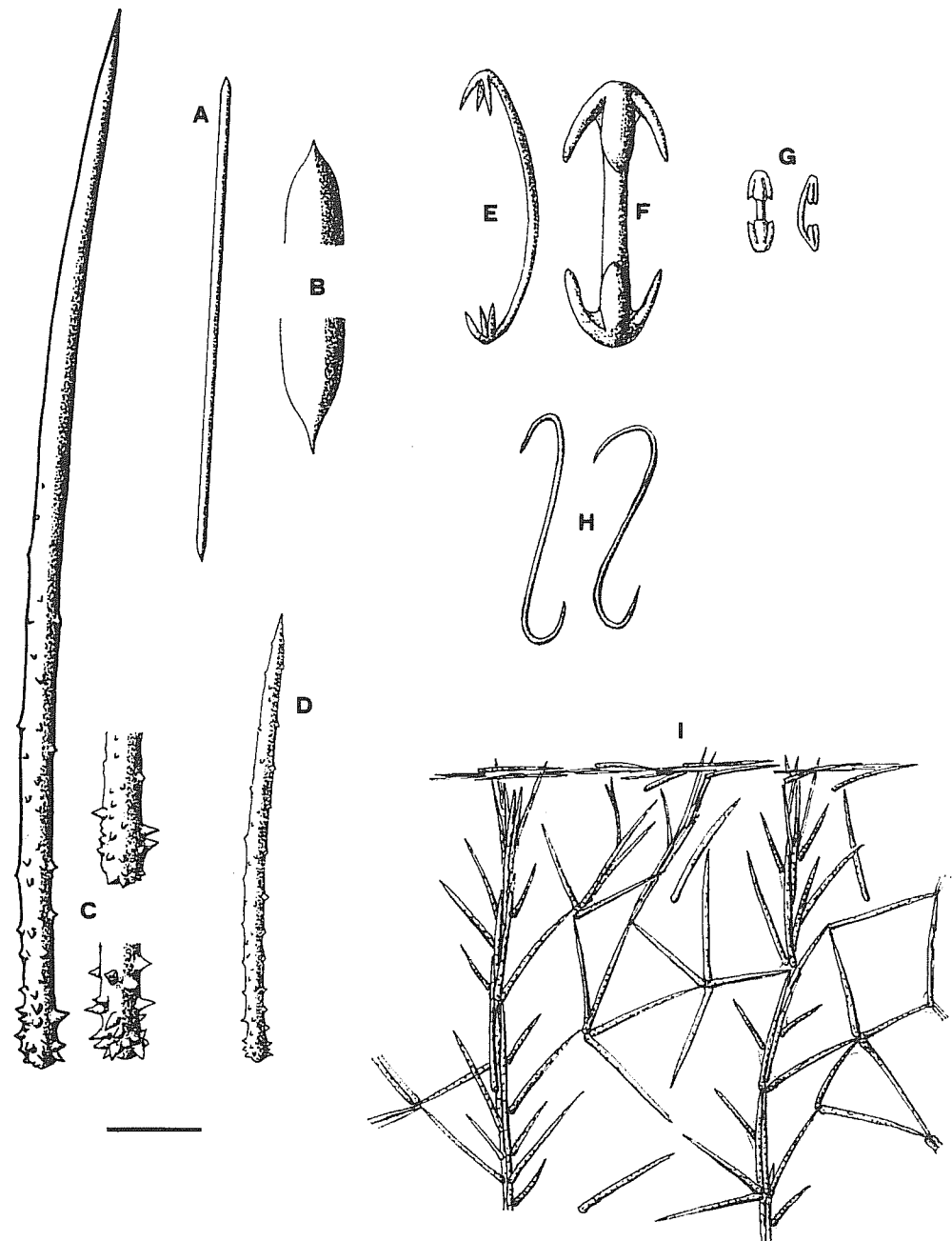


Figure 2. Spicule set and skeleton of *Ectyomyxilla methanophila*: (A) ectosomal tornote; (B) detail of the mucronate ends; (C) acanthostyle-I and details of the spines on the rounded end; (D) acanthostyle-II; (E) lateral view of an under-developed isochela-I; (F) frontal view of a well-developed isochela-I; (G) frontal and lateral views of an isochela-II; (H) S-shaped sigmata; and (I) general skeletal arrangement. Scale bar: A, 40 μm ; B, 3.5 μm ; C, 21 μm ; D, 30 μm ; E-H, 18 μm ; I, 190 μm .

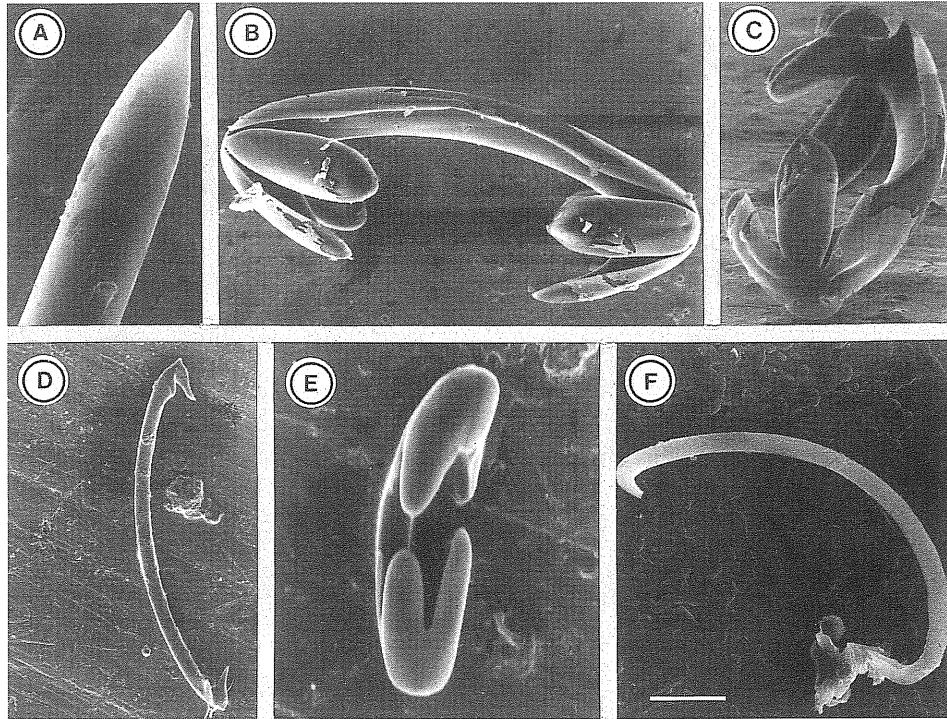


Figure 3. Scanning electron microscopy micrographs of some spicule types: (A) mucronate end of an ectosomal tornote; (B) isochela-I; (C) isochela-I showing a crest-like reinforcement on the internal side of the teeth and a groove on the external one; (D) under-developed isochela-I; (E) isochela-II; (F) sigmata. Scale bar: A, 2.5 μm ; B,C, 8 μm ; D, 10 μm ; E, 3.5 μm ; F, 7 μm .

The choanosomal skeleton is an ill-defined reticulation, with a vague sub-isodictyal, anisotropic pattern (Figure 2I). There are ill-defined, paucispiculate primary tracts made of large acanthostyles. Transverse connections describing a vague, triangular mesh, mostly consist of single spicules. The characteristic myxillioid, isodictyal pattern is barely recognizable, as many transversal spicules are loose and many network nodes are not completed. Primary tracts are mainly constructed of large acanthostyles, although they also contain a low proportion of tornotes, especially in their distal portion, near the ectosome. Primary tracts are irregularly echinate by small acanthostyles. Spongin is scarce, only being visible at the nodes and around the heads of the echinating, small acanthostyles. Microscleres, especially large isochelae, are abundant throughout the endosome.

Habitat and associated organisms

The biological community at the seeps was rich and predominantly composed of the chemosynthetic tube worms *Lamellibrachia* sp. and *Escarpia* sp., an undescribed methane-oxidizing mussel (*Bathymodiolus* sp.), as well as diverse non-chemosynthetic organisms (see MacDonald et al., 1989).

Ectomyxilla methanophila were found abundantly on the tubes of large vestimentiferan tube worms, most commonly *Lamellibrachia* sp. (Figure 1C), and less often on the smaller *Escarpia* sp. (Figure 1D). *Lamellibrachia* are among the most abundant animals found at cold methane/sulphide seeps on the Louisiana Slope. Distribution of the sponges was patchy on several scales; some tube worm stands had numerous sponges and others had few. Even within a dense stand of tube worms, sponges were not distributed uniformly. We never found them on the shells of the mussel *Bathymodiolus* sp., which forms the other major hard substratum in this habitat (Figure 1D), nor were they found on nearby rock outcroppings which were outside the direct influence of methane seepage. We did observe one rock lying within a few centimetres of an *Escarpia* aggregation which appeared to support a small *Ectomyxilla* individual as well as several other species of demosponge (Figure 1E). A large starfish, *Sclerasterias* cf. *tanneri* (identification by R. Carney, personal communication) was often seen wrapped around the vestimentiferan tubes in regions where the sponges were common (Figure 1F). Though at first sight it appeared that they were consuming the sponges, examination of gut contents of three individuals did not reveal the presence of sponge spicules.

DISCUSSION

The spicule set of this new species closely matches that of the species complex *Ectomyxilla kerguelensis*–*Ectomyxilla chilensis*. *Ectomyxilla kerguelensis* Hentschel is known from Kerguelen Island (Hentschel, 1914; Boury-Esnault & Van Beveren, 1982), Antarctica (Burton, 1929), New Zealand (Brøndsted, 1923 as *Myxilla tornotata*; Dendy, 1924 as *Crellomyxilla intermedia*; Bergquist & Fromont, 1988), South Africa (Lévi, 1963), and the Atlantic coast of Brazil (Boury-Esnault, 1973). *Ectomyxilla chilensis* Thiele is known from the Pacific coast of Chile (Thiele, 1905; Desqueyroux-Faúndez, 1989; Desqueyroux-Faúndez & van Soest, 1996), Antarctica (Koltun, 1976), Kerguelen (Boury-Esnault & Van Beveren, 1982) and Namibia (Uriz, 1988). Some authors regard the two species as synonyms (Burton, 1932; Koltun, 1976) while others separate the species on the basis of differing sigmata sizes (Lévi, 1956; Boury-Esnault & Van Beveren, 1982). We have not examined the type material for these two species, but the information on skeletal structure available in the literature does not, in our opinion, justify separation of this complex into two species (Table 1). We regard these two species as synonymous, with the name *E. chilensis* having priority.

Although the spicule set of *E. methanophila* resembles that of *E. chilensis*, there are differences in the skeletal architecture of both the ectosome and the choanosome. The ectosomal skeleton in *E. chilensis* is mainly constructed of small acanthostyles and tornotes arranged in a reticulate pattern (e.g. Boury-Esnault & Van Beveren, 1982; Bergquist & Fromont, 1988), whereas the ectosomal skeleton in *E. methanophila* sp. nov. consists mainly of tornotes and large acanthostyles, mixed together without any apparent order, and lacking a reticulate pattern. Moreover, small acanthostyles are never present in the ectosome of the latter species. The choanosomal skeleton in *E. chilensis* consists of an irregular to isodiactyl reticulation of wide tracts of acanthostyles (sometimes with a typical, triangular-meshed, myxillioid pattern). This

Table 1. Summary of skeletal and distribution data of *Ectyomyxilla kerguelensis* and *Ectyomyxilla chilensis*. Skeletal measurements are in microns.

	Tornotes	Acanthostyles	Chelae	Sigmata	Locality	Depth
<i>Ectyomyxilla kerguelensis</i>						
Hentschel, 1914 (type)	152-184×5-6	176-225×14, 56-75×5-6	12.5-19	17-22×?	Kerguelen	?
Brøndsted, 1923 (as type of <i>Mixilla tornotata</i>)	130-156×4	90-140×8	10-26	32×2	New Zealand	Shallow-water 183 m
Dendy, 1924 (as type of <i>Crellomyxilla intermedia</i> *)	190-220×5-7	210-240×12-15, 90-135×7-9	25-32, 13-19	33-43×?	New Zealand	
Brøndsted, 1924 (as <i>C. intermedia</i>)	190-260×5-7	as Dendy's type	12-40	as Dendy's type	New Zealand	64 m
Burton, 1929	130×?	up to 150×?, up to 120×?	12-33	36×?	McMurdo Sound	335 m
Lévi, 1956	175-180×5	180-210×12, 110-120×8	13-21	35-45×3-4	Kerguelen	Intertidal
Lévi, 1963	170-175×5	190-220×?, 100-120×7	25, 12-13	12-13×?	South Africa	36 m
Boury-Esnault, 1973	217-259×3-6	218-250×3-9, 119-156×3-5	15-22	25-29×?	Brazil (Atlantic)	97-100 m
Boury-Esnault & Van Beveren, 1982	114-235×5-12	150-248×8-20, 37-1120×3-12	10-25	12-32×?	Kerguelen	5-315 m
Bergquist & Fromont, 1988	175-223×3-8	143-220×6-15, 90-130×5-8	38-46	11.5-18×?	New Zealand	10-30 m
<i>Ectyomyxilla chilensis</i>						
Thiele, 1905 (type**)	163-202×6-7	182-208×6-10, 102-134×6	20-35, 12-15	45-47×?	Chile (Pacific)	?
Boury-Esnault & Van Beveren, 1982	204-276×4-7	192-307×7-13, 102-172×5-10	16-30	44-58×?	Kerguelen	5-158 m
Desqueyroux-Faúndez, 1989	265×6	380-440×16-20	24-45, 16-22	48-56×2	Chile (south)	80 m
Desqueyroux-Faúndez & Van Soest, 1996	157-298×4-10	176-229×8-13, 83-144×3-6	18-45, 10-16	35-64×?	Chile (Pacific)	12-15 m
Uriz, 1988	190-210×5-7	165-210×8-11, 100-120×5-7	30-32, 12-15	25-32×?	Namibia	232 m

*, Type remeasured by Bergquist & Fromont (1988); **, type remeasured by Desqueyroux-Faúndez & van Soest (1996).

myxillioid skeletal pattern is barely recognizable in the choanosome of *E. methanophila*. In addition, the choanosomal tracts are clearly echinated in the new species but not in *E. chilensis*. It is also noteworthy that the isochelae-I of *E. methanophila* are larger than those of *E. chilensis*.

The choanosomal architecture of *E. methanophila* is somewhat closer to that described for *Ectyomyxilla ramosa* Bergquist & Fromont, 1988, from New Zealand, which has a square-sided mesh showing main tracts. This latter species is, however, clearly distinguishable by its bright red colour, its ramose growth habit, more extensive development of spongin fibres around the acanthostyles, and the small size of both its single category of acanthostyles and its single category of isochelae. *Ectyomyxilla methanophila* is also easily distinguished from other species in the genus, such as *Ectyomyxilla massa* (Ridley & Dendy, 1886), *Ectyomyxilla mariana* (Ridley & Dendy, 1887) and *Ectyomyxilla dracula* Desqueyroux-Faúndez & van Soest, 1996, all of which have ectosomal diactines with microspined ends. The new species also differs from *Ectyomyxilla tenuissima* (Thiele, 1905) and *Ectyomyxilla hentscheli* Burton 1929 that have a hymedesmioid-like skeletal pattern (Lévi, 1963; Desqueyroux-Faúndez, 1976; Desqueyroux-Faúndez & van Soest, 1996).

The location of these populations of *E. methanophila* in the Gulf of Mexico at more than 500 m is surprising both biogeographically and bathymetrically. To date, the distribution of all previous known species of the genus *Ectyomyxilla* was limited to the Antarctic region and adjacent subantarctic areas (South Africa, New Zealand, Chile, etc.), with only a single record for *E. kerguelensis* in a temperate region (Atlantic coast of Brazil; Boury-Esnault, 1973). Therefore, *E. methanophila* is the first record of the genus in the northern hemisphere. This is also the deepest record for this genus. Most other species have relatively wide bathymetric ranges, but all occur at depths less than 335 m.

The occurrence of *E. methanophila* in association with methane seeps is also noteworthy. To date, there is only one other marine sponge known from methane seeps, a methanotrophic-carnivorous sponge in the genus *Cladorhiza* (Vacelet et al., 1995). Cladorhizid sponges are not filter-feeders. They have lost the aquiferous system while developing alternative feeding mechanisms as an adaptation to the food-poor deep sea environment (Vacelet et al., 1995). By contrast, *E. methanophila* has anatomical features typical of shallow-water sponges and lacks any obvious morphological adaptation to deep sea or seep environments. Because the aquiferous system and choanocyte chambers seem to be functional, we assume that this species is a filter-feeder, like most other demosponges. The ratio $^{13}\text{C}/^{12}\text{C}$ (i.e. $\delta^{13}\text{C}$ value) for this sponge is very low (McDonald et al., 1989), suggesting that it obtains its carbon from hydrocarbons seeping from the sea-floor rather than photosynthetic products from the euphotic zone. This light $\delta^{13}\text{C}$ value could be indicative of nutritional benefits derived from symbiosis with chemoautotrophic bacteria living in the sponge tissues, but could also result from filter-feeding on free-living methanotrophic bacteria. The small size of the choanocyte chambers and its relative scarcity suggest the occurrence of a nutritional benefit from symbiotic bacteria, similar to the association between shallow-water sponges and photoautotrophic bacteria (Boury-Esnault et al., 1990;

Rützler & Muzik, 1993). Further electron microscopy studies and physiological experiments will still be required to determine whether symbiosis or filter-feeding is the primary mode of nutrition.

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