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First record of the sponge genera *Crambe* and *Discorhabdella* for the eastern Pacific, with description of three new species

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Three new sponge species are described from the Pacific coast of Panama, namely *Crambe panamensis* n. sp., *Discorhabdella urizae* n. sp. and *Discorhabdella littoralis* n. sp. This is the first record of the genera *Crambe* and *Discorhabdella* for the eastern Pacific, which represents not only a considerable expansion in their known biogeographical distribution, but also empirical support for their Tethyan origin. The new species provide a better understanding of the skeletal evolution in these peculiar genera, representing a lineage in which aster-derived spicules occur within a typical poecilosclerid skeleton. The skeleton of *C. panamensis* consists of ectosomal subtylostyles, choanosomal tylostyles with smooth tyle, basal desmas of astroclone type only, and anchorate isochelae. The skeleton of *D. urizae* consists of ectosomal subtylostyles, choanosomal tylostyles with tuberose tyle, basal acanthostyles with aster-like tyle, anchorate isochelae, sigmas, and distinctive twisted microxeas. The skeleton of *D. littoralis* consists of ectosomal tylostyles, choanosomal tylostyles that occasionally show remains of tubercles in the tyle, basal acanthostyles with a tyle intermediate between aster-like and regular morphology, and sigmas. The skeletal affinities of *Crambe* and *Discorhabdella* with the genera *Lithochela* and *Monanchora* are discussed, and a new family concept based on all four genera is proposed. The name Crambeidae is proposed for such a family, to replace the pre-occupied name Crambidae.

KEYWORDS: Desmas, Poecilosclerida, spicule evolution, sponge taxonomy, Pacific fauna.

Introduction

The sponge fauna of the Pacific coasts of Central and South America is poorly known. Most of the few studies on the eastern Pacific fauna are concentrated on

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the coast of North America (e.g. de Laubenfels, 1926, 1932; Dickinson, 1945). Some attention has also been focused on the Pacific coast of Mexico (Carter, 1882; Green and Gómez, 1986; Gómez and Bakus, 1992; Gómez, 1998) and on the oceanic archipelago of the Galapagos Islands (Wilson, 1904; de Laubenfels, 1939; Desqueyroux-Faúndez and van Soest, 1996, 1997), yet the sponge fauna of this region remains superficially known. This lack of knowledge is most evident for the vast coastal area between Mexico and North Chile, where virtually no taxonomic study has been made aside from two assessments of conspecificity between sponges living at either end of the Panama Canal (de Laubenfels, 1936; Wulff, 1996). Such a lack of faunal information hinders not only our knowledge of biodiversity in the Porifera, but also our understanding of global patterns of biogeographical distribution and skeletal evolution in the phylum.

In the present study, we describe new species of *Crambe* Vosmaer, 1880 and *Discorhabdella* Dendy, 1924 from the Pacific coast of Panama. These two genera, which are here reported for the first time from the eastern Pacific, are characterized by peculiar spicules whose significance in the skeletal evolution of the order Poecilosclerida still remains the subject of intense debate (e.g. Lévi, 1960; Hajdu *et al.*, 1994; Uriz and Maldonado, 1995; Maldonado and Uriz, 1996; Maldonado *et al.*, 1999).

Materials and methods

The material described herein was collected during a cruise of the R/V *Seward Johnson* (Harbor Branch Oceanographic Institution, Fort Pierce, Florida, USA) to survey the Pacific coast of Panama in November 1995.

Specimens of *Crambe panamensis* n. sp. and *Discorhabdella littoralis* n. sp. were collected by scuba, whereas *Discorhabdella urizae* n. sp. was collected using the *Johnson-Sea-Link I* manned submersible. After collection, sponges were fixed in formalin for 24 h, then transferred to 70% ethanol. For the study of the skeleton, sponges were boiled in concentrated nitric acid and rinsed in distilled water; free spicules were then mounted on a brass stub and sputter-coated with gold-palladium. Observations were made with a Hitachi 2300 SEM.

Taxonomic interpretation and discussion of the new species are based on either recent or previous re-examination of material belonging to all extant species of the genera *Crambe*, *Discorhabdella* and *Vetulina* Schmidt, 1879 (see Maldonado and Uriz, 1996). We re-examined material stored in the Natural History Museum of London (NHML), Muséum National d'Histoire Naturelle, Paris (MNHN), Museo Civico de Storia Naturale, Genoa (MCSN), Museum of Monaco (MM), Station Marine d'Endoume, Marseille (SME), Landesmuseum Johanneum Graz, Steiermarkische (LMJG), and Centro de Estudios Avanzados de Blanes (CEAB), as follows: *Vetulina stalactites* Schmidt, 1879 (syntype in NHML); *Crambe crambe* (Schmidt, 1862) (slide from the holotype—as *Suberites crambe*—in NHML, paralectotype of *Suberites fruticosum* and *Suberites crambe* in LMJG, plus diverse Mediterranean material from SME and CEAB colls.); *Crambe acuata* (Lévi, 1958) (not type material, but CEAB collections from Namibia: Uriz, 1988); *Crambe tailliezi* Vacelet and Boury-Esnault, 1982 (not type material, but Mediterranean CEAB material from the Alboran and the Catalan seas: Uriz *et al.*, 1992; Maldonado, 1993); *Crambe tuberosa* Maldonado and Benito, 1991 (holotype in CEAB); *Crambe erecta* Pulitzer-Finali, 1992 (slides from the holotype in MCSN); *Discorhabdella incrustans* Dendy, 1924 (slides from the holotype in NHML); *Discorhabdella* *tuberosocapitata* (Topsent, 1892) (slides from the holotype in MM); *Discorhabdella hindei* Boury-Esnault, Pansini and Uriz, 1992 (slides from holotype in MNHN). Also re-examined was material stored in the NHML from related genera, such as *Lithochela* Burton, 1929 and *Monanchora* Carter, 1883, as follows: type series of *Lithochela conica* Burton, 1929; holotype of *Monanchora clathrata* Carter 1883; material of *Monanchora unguiculata* (Dendy, 1921a) from the Siboga Expedition; material of *Monanchora pulchra* (Lambe, 1894).

Holotypes of the species described herein are deposited in the National Museum of Natural History at Washington (NMNH) and paratypes at the Harbor Branch Oceanographic Museum, Fort Pierce (HBOM).

Taxonomic descriptions

ORDER *Poecilosclerida* Lévi

SUBORDER *myxillina* Hajdu, van Soest and Hooper, 1994

Poecilosclerida characterized by tridentate-derived chelae. Toxas never found. Ectosomal megascleres basically diactinal, although aniso-terminations are widespread. Terminal spination of ectosomal megascleres rare and, if present, usually coarse or irregular.

FAMILY *crambeidae* Lévi, 1963

(nomen novum pro Crambidae, preoccupied)

Diagnosis. Encrusting, tubular, ramose or massive growth forms distributed in four nominal genera: *Crambe*, *Discorhabdella*, *Monanchora* and *Lithochela*. Ectosomal megascleres consist of smooth subtylostyles in only one category, usually arranged in brushes or bundles perpendicular to the ectosome. Choanosomal megascleres are smooth or acanthose (tylo)styles in only one category, arranged in hymedesmioid, plumose or plumo-reticulate skeletal structures. Peculiar aster-like desmas (termed astroclones and spheroclones) or acanthostyles (termed pseudoastrose acanthostyles) may occur at the most basal skeletal stratum, depending upon the genus. Microscleres, when present, consist of unguiferous-anchorate isochelae (rarely spatulate) with three to eight teeth, C-shaped sigmas (probably derived from reduced isochelae), and microspiny microxeas, depending upon species in each genera.

Remarks. See section of Discussion for further information on family name and diagnosis.

Crambe Vosmaer, 1880

Diagnosis. Encrusting sponges characterized by having aster-like desmas (astroclones or sphaeroclones), along with a category of large choanosomal (tylo)styles, a category of small ectosomal subtylostyles, and one or two categories of anchorate-unguiferate isochelae. Irregularly spiny microxeas occur in some species.

Remarks. It has long been recognized that, for unknown reasons, most populations of *Crambe crambe* and some of *Crambe acuata* produce neither desmas nor isochelae (e.g. Boury-Esnault, 1971; Vacelet *et al.*, 1976). This fact has largely complicated both species and genus diagnoses in *Crambe*. However, it was recently found that laboratory populations of *C. crambe* reared in seawater experimentally enriched with silicic acid produce up to four spicule types, desmas and isochelae included, that were otherwise missing in most natural populations (Maldonado *et al.*, 1999). Therefore, it must be concluded that production of asteroid desmas and isochelae is a genetic trait shared by all individuals of all *Crambe* species. The skeletal reduction observed in many natural populations of *C. crambe* does not appear to have a genetic basis, but seems to be a phenotypic skeletal inhibition induced by limiting levels of silicic acid in sublittoral waters. Consequently, the presence/absence of desmas and isochelae must be used cautiously in the taxonomy of both *Crambe* and other crambeids.

The genus *Crambe* is here reported for the first time from the Pacific Ocean. It is noteworthy that it has not been reported to date from the well-known Caribbean sponge fauna or in nearby zones of the Central Pacific, such as the Galapagos Islands, which have recently been surveyed (Desqueyroux-Faúndez and van Soest, 1997; authors, unpublished data). Nevertheless, the presence of the genus in the western Pacific stratigraphic sediments can be inferred from the fossil sphaeroclones found in Lower Tertiary strata of Oamaru (New Zealand). Such characteristic sphaeroclones, though formerly attributed to the genus *Vetulina* by Hinde and Holmes (1892), most likely belong to a fossil species of *Crambe* (Uriz and Maldonado, 1995), namely *Crambe oamaruensis* (Hinde and Holmes, 1892).

Crambe panamensis n. sp.

Material collected. USNM 51470, paratype HBOM-003:00951.

Type locality. Pacific coast of Panama, Gulf of Chiriqui, Isla Montuosa 7°27.992′N, 82°15.629′W). Paratypes collected at a nearby site (7°27.932′N, 82°15.611′W).

Etymology. The species name refers to the geographical location of the type locality.

Description. The holotype is a 14 × 10 cm, encrusting sponge that was growing on a living thorny oyster. It was pinkish red when alive, and faded in ethanol. In the many living individuals observed *in situ*, the ectosome was epithelium-like, translucent, with spacious subectosomal cavities that collapse after fixation; oscula were distended, slightly raised, 1–2 mm in diameter; groups of exhalant canals converged towards the oscula showing a radial pattern, as typically seen in other species of *Crambe*. Ostia were not visible with the naked eye, but under magnification, they were visible in aerolated areas, 400–600 μm diameter, that were scattered all over the sponge surface. The surface is microscopically hispid.

The skeleton consists of four spicule types, as follows:

(1) Ectosomal subtylostyles: 117–208 μm × 2.5–3.5 μm; straight, relatively isodiametric, with an oval subtyle, and with a tapering, sharp point (figure 1a, b). Feeble vestiges of microspines, which are hard to see even under magnification, surround the point (figure 1b).

(2) Choanosomal tylostyles: 180–300 μm × 6.5–12 μm; straight or somewhat curved, slightly fusiform, with an irregularly shaped, well-marked tyle (figure 1c).

(3) Astroclone desmas: in a wide variety of growth stages (figure 1d–h). Fully formed desmas have a well-developed centrum, from which four to seven main actines radiate, along with one in four additional, shorter processes

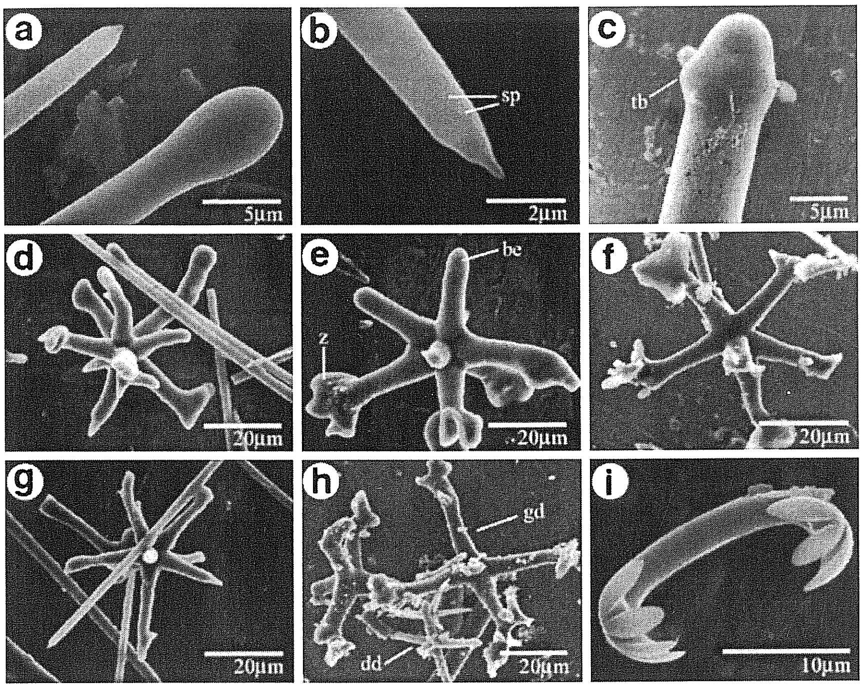

FIG. 1. Spicules of *Crambe panamensis* n. sp.: (a) point and tyle of an ectosomal subtylostyle; (b) point of a subectosomal subtylostyle with feeble spines (sp); (c) tyle of a choanosomal tylostyle, where vestiges of a tubercle (tb) can be seen; (d–f) fully grown astroclones with diversely developed actines that show both zygomes (z) and blunt ends (be); (g) early developing stage of an astroclone; (h) comparative view of fully grown desmas (gd) and early developing stages (dd); (i) isochela.

(actines or ornamental spines?), up to a maximum of eight radiating processes. Fully grown actines, if in contact with other desmas, develop a flat, terminal expansion called zygome plate (figure 1e–f); zygomes articulate inter-spicule contacts to build up a network of interlocked, but not fused, desmas. If actines contact no nearby spicule, actinal ends remain unexpanded and blunt (figure 1e). Early developing stages of astroclone desmas, which were fairly common in the sponges collected, resemble oxyasters with four to eight irregular, blunt actines (figure 1g, h). Fully grown desmas measure up to 65 µm in largest diameter, with some early developing stages as small as 26 µm across.

(4) Isochelae: 20–22 µm; with three to five well-formed, anchorate teeth (figure 1i). These spicules are infrequent in the sponges.

The arrangement of the spicule types within the sponges consists of a basal stratum of more or less interlocked astroclones that rests on a basal spongin layer from which short tracts of subtylostyles cored by one or several main choanosomal tylostyles ascend. Ascending tracts become hispid tufts when they reach the sponge surface. Isochelae are very scarce and occur mostly in the ectosome.

Habitat. This species is fairly common at the collection site (Isla Montuosa, Pacific coast of Panama), particularly on overhangs, vertical walls, and sites moderately exposed to sunlight, at depths of 10–30 m. It grows on rocks, but also overgrows living barnacles and oysters.

Taxonomic remarks. The fact that *Crambe panamensis* n. sp. produces desmas with only radiating arms (i.e. astroclones) clearly distinguishes this species from all three Mediterranen species (table 1), *Crambe crambe*, *Crambe tuberosa* and *Crambe tailliezi*, which produce only sphaeroclone desmas (i.e. desmas with all actines curved towards the substratum, when fully developed).

Astroclones similar to those of *Crambe panamensis* n. sp. occur in two other species, *Crambe erecta* and *Crambe acuata*. Because *C. erecta*, a species only known by its holotype from the East Coast of Africa (North Kenya Bank), produces isochelae in two size categories, whereas *C. panamensis* produces only one category, the specific distinction is clear.

Differentiation between the skeleton of *Crambe panamensis* n. sp. and that of *Crambe acuata* is somewhat more complicated. The latter species, known from the South Atlantic (Namibia and South Africa), the Red Sea and Madagascar, shows an enormous skeletal variability between populations (table 1). South Atlantic populations of *C. acuata* are characterized by ectosomal and choanosomal tylostyles, abundant astroclones, a single category of isochelae, and microxeas (Lévi, 1960, 1963; Uriz, 1988). Populations from the Red Sea and Aldabra (northern Madagascar) produce ectosomal and choanosomal tylostyles, isochelae in two size categories, very few astroclones (see Vacelet *et al.*, 1976) and no microxeas (Lévi, 1958, 1961). The population from Tulear (southern Madagascar) produces spicules as those described above, but with isochelae in a single size and microxeas in variable abundance, depending upon individuals (dubious species assignations, according to Vacelet *et al.*, 1976, are not considered here). Because of the skeletal differences explained above, the Indian Ocean populations of *C. acuata* were originally described as *Folitispa acuata* Lévi, 1958, whereas the South Atlantic populations were described as *Crambe chelastra* Lévi, 1960. This synonymy was proposed by Vacelet *et al.* (1976) and has been accepted ever since, although a review of such a taxonomic decision would be advisable if new material is collected (Maldonado and Uriz, 1996; Lévi, personal communiction).

The absence of microxeas in *C. panamensis* n. sp. differentiates it from the South Atlantic and Tulear populations of *Crambe acuata* (table 1). The new species can also be differentiated from Red Sea and Aldabran populations of *C. acuata*, because the latter two, though also lacking microxeas, produce isochelae in two size categories (Lévi, 1958, 1961), whereas only one size category is present in *C. panamensis* (table 1). Taxonomic differentiation is also supported by the widely disjunct geographical distribution between the eastern Pacific populations of the new species and the nearest populations of *C. acuata* in Madagascar and the Red Sea. Indeed, the presence of this new species on the Pacific coast of Panama, along with the occurrence of a New Zealand fossil species known from Tertiary strata, strongly suggest that the genus *Crambe*, also known from the Mediterranean, the eastern South Atlantic, the Red Sea and the western Indian Ocean, was perhaps once widespread in the Tethys Sea and has persisted to the Recent with relative success in some biogeographical regions. This idea is consistent with recent experimental work that has shown that concentration of silicic acid in surface waters of modern oceans is insufficient for the sublittoral species *Crambe crambe* to produce its desmas (Maldonado *et al.*, 1999). Such a finding suggests that the genus *Crambe*—or a direct, close ancestor—appeared in a shallow-water environment that was still rich

Table 1. Skeletal and biogeographical summary of the species in the genus *Crambe*. Measurements are spicule size ranges (length × width, or length only), in micrometres. Given the irregular form of desmas, only measurements for their largest diameter (∅) are considered.

Species	Recorded as	Author	Locality and depth	Ectosomal (tylo)styles	Choanosomal (tylo)states	Desmas	Chelae-I	Chelae-II	Raphides
C. oamaruensis	*Vetulina*, (fossil spicules)	Hinde and Holmes, 1892	Oamaru (New Zealand)	?	With tuberose tyle?	Sphaeroclones	?	?	?
C. crambe	*C. crambe*	Many sources, see Boury-Esnault, 1971	Mediterranean and the Canaries, sublittoral	Always present	Occasional presence	Occasional, scarce sphaeroclones	Occasional Presence	–	–
	C. crambe	Maldonado *et al.* (unpublished)	Mediterranean, laboratory population	Always, 120–185 × 2–5	Always, 270–470 × 14–17	Always, 50–130 ∅ sphaeroclones	Always 28–34	Occasional 8–11	–
C. acuata	*Folistipa* (holotype)	Lévi, 1958	Red Sea, 1–40 m	120 × 2	120–175 × 8–10	Scarce astroclones (Vacelet *et al.*, 1976)	20–22	8–10	–
	C. chelastra (holotype)	Lévi, 1960	South Atlantic (S. Africa), 0–17 m	200–300 × 6–7	300–650 × 16–18	110 ∅ astroclones	30–35	–	32–38
	F. acuata	Lévi, 1961	Madagascar (Aldraba), 42 m	150–250	250–400 × 4–12	Scarce astroclones (Vacelet *et al.*, 1976)	22–24	8	–
	C. chelastra	Lévi, 1963	South Atlantic (S. Africa), 2–13.5 m	200–300 × 6–7	300–650 × 16–18	110 ∅ astroclones	30–35	–	32–38
	C. acuata	Vacelet *et al.*, 1976	Madagascar (Tulear), 10–15 m	200–325 × 2.5–7	230–400 × 7.5–14	15–75 ∅ astroclones	22–30	–	16–90 or absent
	C. acuata	Uriz, 1988	Namibia, Sublittoral, 182 m	280–335 × 11–15	400–750 × 28–48	40–170 ∅ astroclones	33–40	–	35–48
C. tailliezi	Holotype	Vacelet and Boury-Esnault, 1982	Mediterranean (Port-Cross), 10–40 m	205–330 × 4–25	350–460 × 6–8	25–80 ∅ sphaeroclones	23–26	–	–
	C. tailliezi	Maldonado, 1993	Mediterranean (Alboran), 74 m	200–240 × 4–5	380–500 × 8–12	120 ∅ sphaeroclones	18–20	–	16–22
C. tuberosa	Holotype	Maldonado and Benito, 1991	Mediterranean (Alboran), 70–120 m	87–104 × 4–6	500–700 × 20–30	94–134 ∅ sphaeroclones	27–30	–	–
C. erecta	Holotype	Pulitzer-Finali, 1992	Off Kenia (Zanzibar), 110 m	230–340 × 6–9	350–500 × 14–38	120–180 ∅ astroclones	33	16–19	–
C. panamensis	Holotype	Present paper	Pacific coast of Panama, Sublittoral	117–208 × 2.5–3.5	180–300 × 6.5–12	26–65 ∅ astroclones	20–22	–	–

in dissolved silica, predating the chronic silicon exhaustion characteristic of surface water in modern oceans and that was caused by the expansion and diversification of the diatoms over the Cretaceous (Harper and Knoll, 1975; Maliva *et al.*, 1989; Maldonado *et al.*, 1999).

Discorhabdella Dendy, 1924

Diagnosis. Encrusting poecilosclerids characterized by a category of small acanthostyles with a globate tyle and a short shaft with spines concentrated towards the end, along with a category of large choanosomal tylostyles with tuberose tyles, and a category of small ectosomal subtylostyles. A single category of anchorate-unguiferate isochelae occurs in all species, except one of the new species described herein. Microxeas and sigmas may also occur, depending upon species.

Remarks. The acanthostyle of *Discorhabdella* is highly characteristic in possessing a globate tyle, the hypertrophy of which is so important in some species that the spicule resembles an aster, and is termed a 'pseudoastrose acanthostyle' (Dendy, 1924). SEM observations reveal axial canals within the spines of the globate tyle, indicating that the presumed spines are actually actines and suggesting that these peculiar acanthostyles have evolved from a polyaxonid spicule, an ancestor most likely shared with the aster-like desmas of *Crambe* (Uriz and Maldonado, 1995; Maldonado and Uriz, 1996). The fact that *Crambe* and *Discorhabdella* share virtually identical spicule complement except for the aster-like desmas and the pseudoastrose acanthostyles is also consistent with the idea of aster-like desmas and pseudoastrose acanthostyles being homologous spicules. The alternative hypothesis that the pseudoastrose acanthostyles would not be non-polyaxonid in origin, but derived from regular diactinal acanthostyles is unlikely. From such an alternative view, the presence of axial canals in the aster-like tyles of *Discorhabdella* cannot be explained in agreement with the traditional actinal theory that distinguished between actines and spines in the spicules on the basis of the presence/absence of axial canals within the structure (Sollas, 1888; Dendy, 1921b, 1926). Furthermore, if aster-like desmas and pseudoastrose acanthostyles are considered non-homologous, the enormous similarity between *Crambe* and *Discorhabdella* in composition, structure and arrangement of the remaining spicule set would have to be explained by evolutionary convergence. Such a process is clearly unrealistic in probabilistic terms, given the large number of skeletal traits and micro-traits that should have converged (e.g. pattern of axial canals, spicule micro-ornamentation, spicule sizes and arrangement, etc.). It is also unsupported from any anatomic evidence.

Discorhabdella urizae n. sp.

Material collected. Holotype USNM-51470, paratype HBOM-003:00953.

Type locality. Off the Pacific coast of Panama, Gulf of Chiriqui, Banco Hannibal (7°23.644′N, 82°01.797′W).

Etymology. This species is named after spongiologist María J. Uriz, who has contributed greatly to the development of research on Porifera in Spain.

Description. Dark red, 5–15 cm^2, thinly encrusting colonies growing on a boulder collected between 55 and 73 m deep. Colonies, though physically isolated from each other, were very close, resulting either from fragmentation of a larger colony or gregarious larval settlement. The sponge surface is an epithelium-like ectosome, uniformly microhispid. Oscula measure about 100 μm in diameter, and are neither raised nor showing any appreciable pattern of exhalant canals; ostia are not visible.

The skeleton consists of six spicule types, as follows:

(1) Ectosomal subtylostyles: 180–220 μm × 5–7 μm; straight, with an oval subtyle and a tapering point surrounded by feeble microspines (figure 2a–c).

(2) Choanosomal tylostyles: 380–750 × 19–42 μm; with a somewhat curved, conical shaft, typically thickened immediately below the tyle, which is ornamented with tubercles (figure 1a, d, e).

(3) Pseudoastrose acanthostyles: 23–37 μm in length; with a hypertrophied, globate tyle (15–26 μm diameter) provided with blunt spines; the shaft is short, conical, ended in either a blunt or sharp point, which is surrounded by a subterminal group of marked spines (figure 2f–j).

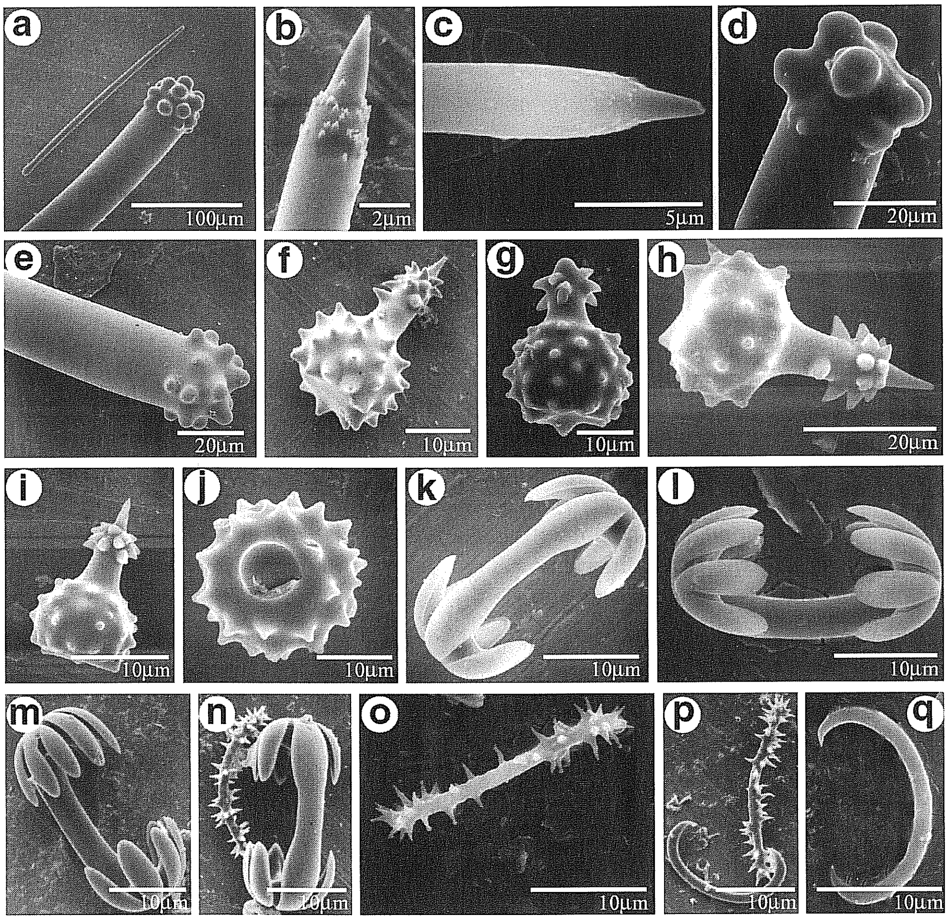

FIG. 2. Spicules of *Discorhabdella urizae* n. sp.: (a) comparative view of an ectosomal subtylostyle and a choanosomal tylostyle; (b, c) spiny point of ectosomal subtylostyles; (d, e) detail of the tuberose tyle of choanosomal tylostyles; (f–i) pseudoastrose acanthostyles; (j) tyle of a pseudoastrose acanthostyle, in which the shaft is broken, making it appear similar to a regular sphaeraster; (k–m) isochelae, in which differences in the number of teeth between and within spicules is seen; (n) comparative view of isochela and curved microxea; (o) curved microxea; (p) curved microxea and sigma; (q) sigma.

(4) Isochelae: 26–29 μm in length; with five anchorate teeth (figure 2k–n).
(5) Microxeas: 19–26 μm × 2–3 μm; slightly undulated (spiraster-like), entirely covered by irregularly scattered, long spines (figure 2n–p).
(6) Sigmas: 13–16 μm × 1 μm; symmetrical, C-shaped (figure 2p, q).

The skeletal arrangement consists of a single, basal stratum of densely packed, astrose acanthostyles that rest on a basal spongin layer, from which choanosomal tylostyles emerge in a hymedesmioid pattern. The ectosomal subtylostyles are arranged in bouquets around the point of the choanosomal tylostyles, which pierce the sponge surface. Sigmas and isochelae are abundant in the ectosome, whereas microxeas appear restricted to the choanosome.

Habitat. This species was common at the collection site, particularly on vertical substrata (submersible observations). It grew on rocks, overgrowing red crustose algae.

Taxonomic remarks. The new species is well characterized by its distinctive twisted microxeas, which are clearly differentiated from the straight microxeas with spines in two verticils that characterize the Indian Ocean *Discorhabdella incrustans*. Microxeas are absent in the two North Atlantic species, *Discorhabdella tuberosocapitata* and *Discorhabdella hindei*.

Discorhabdella littoralis n. sp.

Material collected. Holotype USNM-51472, paratype HBOM-003:00952.

Type locality. Pacific coast of Panama, Gulf of Chiriqui, Isla Montuosa (7°27.992′N, 82°15.629′W). Paratypes collected at a nearby site (7°27.932′N, 82°15.611′W).

Etymology. The name refers to the bathymetric distribution of this species, which is unusually shallow for the genus.

Description. Bright red-orange, approximately 5–30 cm in diameter, thinly encrusting colonies growing on rocky substrata. Oscula and ostia are not visible either in living individuals examined *in situ* or in fixed individuals examined microscopically. The sponge surface is uniformly microhispid, with spicules projecting about 200 μm beyond the ectosome. Aquiferous canals were not visible beneath the ectosome despite the thinly encrusting habit (about 1 mm thick).

The skeleton consists of four spicule types:

(1) Ectosomal tylostyles: 130–180 μm × 2.5–4 μm; straight or slightly curved, with an oval tyle (figure 3a), and with a smoothly sharpened point surrounded by feeble spines (figure 3b).
(2) Choanosomal tylostyles: 117–300 × 5–10 μm; somewhat curved, conical or fusiform, with a well-marked tyle that occasionally shows remains of tubercles (figure 3c).
(3) Pseudoastrose acanthostyles: 26–40 μm in length; with a moderately inflated tyle (10–18.5 μm diameter) that bears large spines, and with a short shaft, the spines of which are concentrated in a subterminal position (figure 3d–h). Spicules that are still in the process of formation have an axial canal (figure 3g, h) visible at the point of the spines (actines?) that radiate from the tyle.
(4) Sigmas: 13–15 μm × 1 μm; symmetrical, C-shaped (figure 3i).

The skeletal arrangement consists of a stratum of densely packed acanthostyles that rests on a basal spongin layer from which the choanosomal tylostyles sparsely

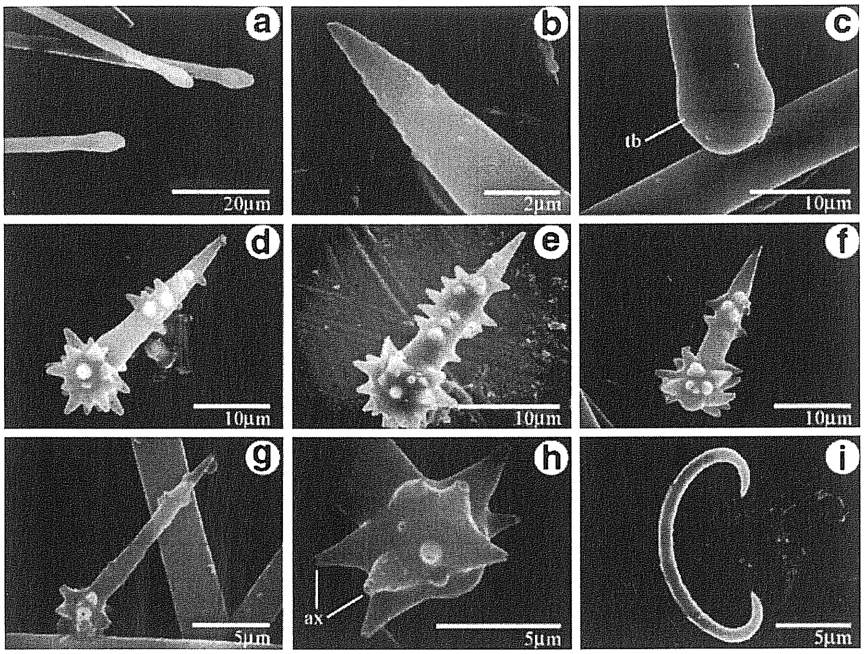

FIG. 3. Spicules of *Discorhabdella littoralis* n. sp.: (a) tyles of ectosomal subtylostyles; (b) feeble spines around the point of an ectosomal subtylostyle; (c) tyle of a choanosomal tylostyle, on which a slight tubercle (tb) is visible; (d–f) fully grown acanthostyles; (g, h) developing stages of acanthostyles, in which axial canals (ax) are visible in the tyle; (i) sigma.

emerge in a hymedesmioid pattern. The ectosomal subtylostyles are arranged in bouquets around the points of the choanosomal tylostyles, which pierce the sponge surface. Sigmas are found mostly in the ectosome.

Habitat. This species is abundant at the collection site, growing on both horizontal and vertical, rocky substrata, from 10 to 30 m depth. This is the shallowest occurring species of *Discorhabdella*, a genus that was previously known only from deep waters. This species sometimes shares habitat with *Crambe panamensis* and, though the latter grows commonly on barnacles and thorny oysters, *D. littoralis* was never seen overgrowing those living substrata.

Taxonomic remarks. The acanthostyles of the new species are not the typical pseudoastrose acanthostyles characterizing most species of *Discorhabdella*. However, evidence of a morphological relationship between the non-astrose acanthostyle of the new species and the typical astrose acanthostyle of other *Discorhabdella* species is provided by: (1) the polyaxonid pattern of axial canals in the acanthostyles of the former, (2) the confinement of its spines to a subterminal position in the shaft, and (3) the small size of the spicule. Several other skeletal traits strongly suggest affinity between the new species and other species in *Discorhabdella*: (1) vestiges of tubercles in the tyle of some choanosomal tylostyles of the new species, (2) the peculiar arrangement of the microspines that surround the point of its ectosomal styles, and (3) the symmetrical, C-shaped form of its sigmas. Therefore, we interpret this new species to be a modified, shallow-water species of *Discorhabdella* that has lost its chelae and slimmed its acanthostyles. Such a skeletal weakening is similar to that described in western Mediterranean populations of *Crambe crambe* as a consequence of chronic silicon limitation in sublittoral habitats (Maldonado *et al.*, 1999). Indeed, the skeletal weakening in this sublittoral *Discorhabdella* relative to the epibathyal and bathyal species in the genus may have been forced by the same environmental limitation.

This view is also consistent with the suggestion of Boury-Esnault *et al.* (1992) that the pseudoastrose acanthostyle characterizing species such as *Discorhabdella incrustans* would have evolved, becoming thinner and longer, to lead to the nearly regular acanthostyle that characterizes *Discorhabdella tuberosocapitata*. The finding of *D. littoralis* supports not only the hypothesis on acanthostyle evolution within the genus, but also substantially fills the gap between the extremes of this spicule's morphology, proving an intermediate stage to retrace the change in the graded morphological series. An alternative direction in the gradation series, i.e. that the pseudoastrose acanthostyles would be derived from regular, diactinal acanthostyles by shortening in the main axis and hypertrophy of the tyle, is unlikely. It explains neither the skeletal affinities with *Crambe* nor the presence of a polyaxonid pattern of axial canals in the tyle.

Discussion

Diverse problems have surrounded the suprageneric taxonomy of *Crambe* and *Discorhabdella*. In 1963, Lévi erected the monotypic family Crambidae to include only *Crambe*. Because Lévi (1963: 16) provided neither a diagnosis of such a taxon nor an explicit statement that he was erecting a new family, Maldonado and Benito (1991) incorrectly considered that the original family erection was invalid, based on a 'nomen nudum', and re-erected the family, providing an explicit diagnosis. However, Lévi's action was valid whereas Maldonado and Benito's was not, since the family diagnosis was validated by monotypy (Hooper, van Soest and Hajdu, personal communication). Moreover, a subsequent nomenclatorial problem has emerged, since the name Crambidae Lévi, 1963 was preoccupied by Crambidae Latreille, 1810 (Lepidoptera). Consequently, we propose to emend the sponge family name to Crambeidae, a spelling also suggested by Hajdu and van Soest (personal communication). Other spellings, such as Crambiidae, suggested by Hooper (personal communication) and published by Hajdu *et al.* (1994: 132) because of a probable misspelling, would be inadequate constructions for the genus name *Crambe*.

The taxonomic scope of this family is also a subject of debate. This family was originally erected to separate the genus *Crambe*, characterized by a distinct combination of aster-like desmas and anchorate-unguiferous isochelae, from other poecilosclerids. However, further skeletal studies showed that most of the spicule types of *Crambe* also occur in the genus *Discorhabdella*, except that there are desmas in *Crambe* and peculiar, pseudoastrose acanthostyles in *Discorhabdella* (Uriz and Maldonado, 1995; Maldonado and Uriz, 1996). Skeletal arrangements are also identical in both genera, and desmas and pseudoastrose acanthostyles occupy similar positions in their respective skeletons. The study of spicules at diverse growth stages (Lévi, 1960; Maldonado, 1993) has also revealed polyaxonid patterns for both the axial canals in desmas and acanthostyle tyles. Such traits strongly suggest that the astrose acanthostyle of *Discorhabdella* and the aster-like desma of *Crambe* are homologous spicules, probably evolved from a common polyactinal corpuscle (Uriz and Maldonado, 1995). Therefore, *Discorhabdella* and *Crambe* appear to be a monophyletic pair (Maldonado and Uriz, 1996) that can be reliably grouped into the family Crambeidae.

It is clear that some species of *Crambe* show an enormous intraspecific skeletal variability, so that many individuals or entire populations may consistently lack desmas and several other spicule types (e.g. Rützler, 1965; Boury-Esnault, 1971; Vacelet *et al.*, 1976). This unpredictable absence of desmas in *Crambe* has been used by some authors to suggest that other poecilosclerid genera that bear (tylo)styles and unguiferate isochelae, but lack aster-like desmas, could also be crambeids that have lost their desmas (Hajdu *et al.*, 1994). Such an assumption would allow the potential inclusion of genera such as *Monanchora* and *Lithochela* in Crambeidae, as well as *Leptosiopsis* Topsent 1927 and *Psammochela* Dendy, 1916, as tentatively suggested by Hooper (personal communication). On the one side, the plumo-reticulate skeletons and the spatulate isochelae of some *Monanchora* species, the absence of choanosomal (subtylo)styles and the monaxonic desmas of *Lithochela*, the polytylote styles in three size categories of *Leptosiopsis*, and the sand-reinforced reticulate skeleton of *Psammochela* will debase the evident monophyly of the group *Crambe-Discorhabdella*. On the other side, by neglecting the features shared between these genera and *Crambe* or *Discorhabdella*, we may provide a too conservative, incomplete family view, failing to recognize real crambeids that have experienced amounts of skeletal change greater than those in *Crambe* and *Discorhabdella*.

By balancing these two opposite views, we have opted to extend the content of Crambeidae to include the genera *Monanchora* and *Lithochela*, along with *Crambe* and *Discorhabdella*. The genus *Monanchora* is included because, although lacking aster-like desmas, most of its species contain ectosomal and choanosomal (subtylo)-styles, anchorate isochelae and spiny microxeas similar to those of *Crambe* (van Soest, 1990). In addition, cyclic guanidine alkaloids, such as crambescidin 800, are shared by some species of *Crambe* and *Monanchora* (van Soest *et al.*, 1996). The monotypic genus *Lithochela* is included in Crambeidae because of a combination of ectosomal styles, unguiferate five-tooth isochelae, and spiny microrhabds, the latter being recently discovered by SEM in the type (van Soest, in preparation). *Lithochela* has also desmas in two categories. The small desmas are irregular in shape, resembling sometimes the underdeveloped, polyaxonid desmas of *Crambe crambe*. The large desmas are clearly monaxonic, but they could be derived from the choanosomal (subtylo)styles, as illustrated by Burton (1929).

The taxonomic placement of the monotypic genus *Vetulina*, which is characterized by a massive skeleton made from astroclone and spheroclone desmas with spiny actines, remains complicated (e.g. Lévi, 1960; Maldonado and Benito, 1991; Kelly-Borges and Pomponi, 1994; Wiedenmayer, 1994). It is currently considered, along with a series of fossils, in the suborder Sphaerocladina, family Vetulinidae. Given that the genus has no spicules other than the desmas, inclusion in Poecilosclerida and the family Crambeidae is postponed until further evidence is provided.

Indeed, further investigation of recent and fossil sponges is needed to clarify the taxonomy of the sponges bearing aster-like desmas. This group originated and expanded in the upper Jurassic (Wiedenmayer, 1994), reaching Recent times with very few members. They are considered as 'living fossils' (Boury-Esnault *et al.*, 1992; Maldonado *et al.*, 1999), being hard to classify owing to their few skeletal connections with the bulk of recent sponges.

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