

## New carnivorous sponges (Porifera, Poecilosclerida) collected from manned submersibles in the deep Pacific

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Nine new species of carnivorous sponges, namely *Cladorhiza segonzaci*, *Chondrocladia koltuni*, *Chondrocladia lampadiglobus*, *Asbestopluma agglutinans*, *Asbestopluma (Helophloeina) formosa*, *Abyssocladia huitzilopochtli*, *Abyssocladia inflata*, *Abyssocladia dominalba* and *Abyssocladia naudur*, are described. The subgenus *Helophloeina* Topsent, 1929 and the genus *Abyssocladia* Lévi, 1964 are revived and redefined, with an identification key for *Abyssocladia* which at present includes seven species. Eight of the sponges were collected from the French IFREMER manned submersible Nautile near active hydrothermal sites of the East Pacific Rise and of the North Fiji and Lau Basins, one from the Russian submersible Mir 2 in the Northwest Pacific near Bering Island, and one from the US submersible Alvin south of Easter Island. Their life conditions are described from direct observations from the submersibles. Some remarks are presented on the taxonomy of Cladorhizidae and more generally of carnivorous Poecilosclerida. The study suggests a very high degree of diversity in the deep Pacific carnivorous sponges. © 2006 The Linnean Society of London, *Zoological Journal of the Linnean Society*, 2006, 148, 553–584.

ADDITIONAL KEYWORDS: *Abyssocladia* – *Asbestopluma* – *Chondrocladia* – *Cladorhiza* – Cladorhizidae – deep-sea vents – Demospongiae – East Pacific Rise – new species – taxonomy.

### INTRODUCTION

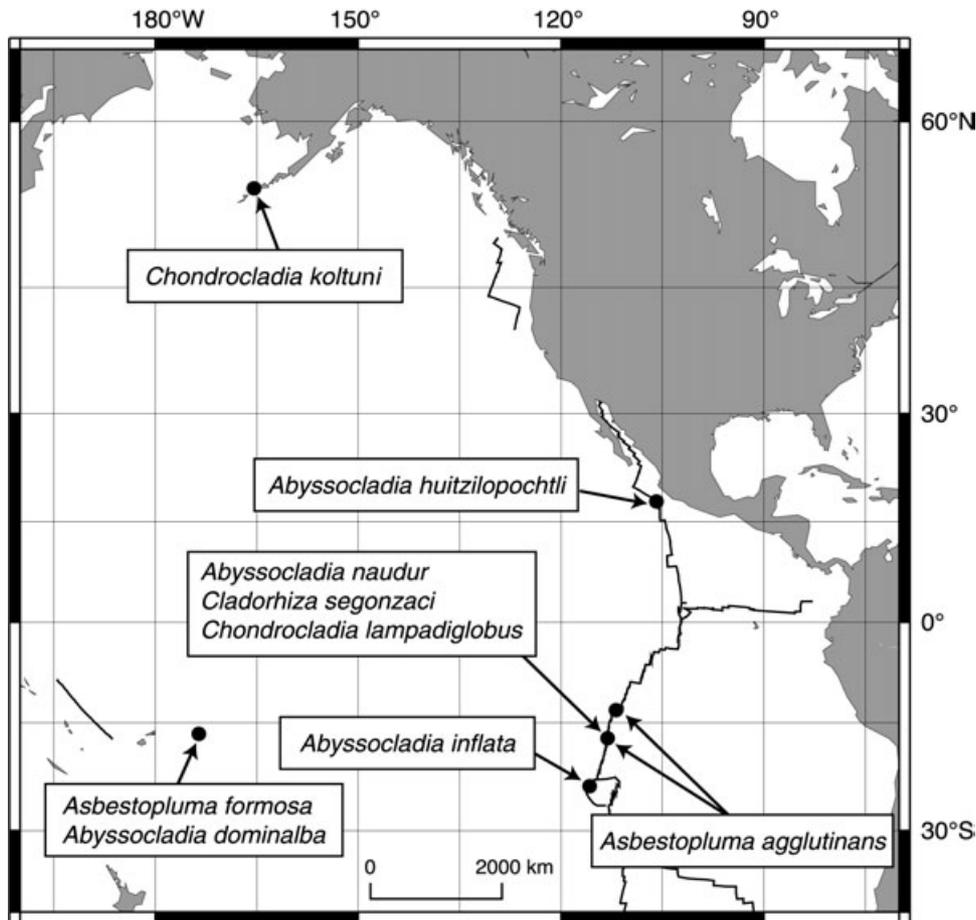
A carnivorous feeding habit has been discovered in representatives of the Demospongiae Cladorhizidae (Vacelet & Boury-Esnault, 1995; Kübler & Barthel, 1999; Vacelet & Dupont, 2004). The members of this deep-sea family display an unusual morphology, generally erect, with a pinnate or symmetrical shape, and a deletion or modification of the aquiferous system characteristic of the phylum Porifera. Their various microsclere spicules, hook-like in shape, show a special arrangement allowing the capture of hairy invertebrate prey. The family, mostly based on the morphology and including genera with various microsclere spicules, is probably polyphyletic (Hajdu & Vacelet, 2002). Furthermore, their erect morphology, apparent absence of aquiferous system and special arrangement of microscleres also occur in

several deep-sea representatives of other poecilosclerid families, such as the Guitarridae and Mycalidae, suggesting that a carnivorous habit is more frequent in deep-sea sponges than thought hitherto, and has been developed in several poecilosclerid lineages.

Several cruises by manned submersibles in the deep Pacific (Fig. 1), a huge area in which sponges have been poorly sampled, yielded collections and observations on several sponges with a morphology and taxonomic affinities suggesting a carnivorous feeding habit. Some of the most remarkable are described here. The cruises were primarily designed for the study of active hydrothermal sites and volcanic activity in zones of ultra-fast spreading ridges, up to 15–16 cm yr<sup>-1</sup> in the area explored during the Naudur expedition (Charlou *et al.*, 1996).

Although this study suggests a different classification scheme for the cladorhizid sponges and allied forms, I use the main lines of the consensual classification adopted in Hooper & Soest (2002), as evidence for a more phylogenetic scheme is still insufficient.

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**Figure 1.** Collection localities for new Pacific Cladorhizidae.

## MATERIAL AND METHODS

The specimens (Fig. 1) were collected during the NAUDUR (Geistdoerfer *et al.*, 1995), STARMER I, STARMER II (Auzende *et al.*, 1989; Desbruyères, Alayse-Danet & Ohta, 1994), PITO (Segonzac *et al.*, 1997; Naar *et al.*, 2004), BIOSPEEDO, GARRETT and NAUTIMATE cruises (see [http://www.ifremer.fr/sismer/UK/catal/campagne/campagne\\_UK.htm](http://www.ifremer.fr/sismer/UK/catal/campagne/campagne_UK.htm)) by the manned submersible Nautille operated by Ifremer. One specimen was collected from the Russian manned submersible Mir 2, and another from the US submersible Alvin (cruise PAR5). For most species, the environmental conditions were observed on the videos and photographs taken during the dives. Underwater pictures were taken by the camera of the submersible or extracted from low-definition VHS videos or when possible from high-definition BVU or BETACAM tape. The specimens were generally preserved in formalin, conserved in ethanol and sorted by the sorting centre Centob, Laboratoire Environnement Profond (Ifremer, Brest).

The type material has been deposited in the Museum National d'Histoire Naturelle in Paris, except the holotype of *Chondrocladia koltuni*, which has been deposited at the Institute of Oceanology in Moscow.

The skeletal architecture was studied by light microscopy on whole mounts, hand-cut tangential sections or thick polished sections obtained by sawing specimens embedded in Araldite® with a low-speed saw using a diamond wafering blade, and wet-ground on polishing discs. Living tissue and embryos of one species were observed after embedding in Araldite and either on non-desilicified polished sections or on semi-thin sections of desilicified tissue stained with toluidine blue.

For the study of spicules, a rapid method adapted from classical methods was used for both light and scanning electron microscopy (SEM). A small piece of sponge was boiled in a few drops of nitric acid on a microscopic glass slide, renewing the acid two or three times before complete drying. After drying and enough cooling to avoid breakage of the slide, the slide was

rinsed with several drops of distilled water and drained. Boiling in nitric acid and rinsing were repeated if necessary to obtain a sufficiently clean slide. The slide was then either mounted in Araldite for light microscopy or sputter-coated with gold–palladium, then observed under a Hitachi S570 SEM. Slides that are too large for the chamber of an electron microscope may be broken after cutting with a diamond pencil down to the required size. After SEM, the slides can be mounted in Araldite, observed under a light microscope and permanently stored. This rapid method gives reasonably clean preparations that have the advantage of allowing both light microscopy and SEM. It is especially successful with sponges such as those of the present study in which the living tissues are relatively poor as compared with the spicule skeleton. Loss of some large megascleres can occur during rinsing, but is generally limited.

### SYSTEMATICS

ORDER POECILOSCLERIDA TOPSENT, 1928

FAMILY CLADORHIZIDAE DENDY, 1922

*Diagnosis*, from Hajdu & Vacelet (2002): Sponges usually small, symmetrical, mostly in deep water, with

diagonal, radiating supporting processes and basal root adaptations for living in soft sediments. Axial skeleton composed of monactinal or diactinal megascleres, from which radiating extra-axial tracts diverge to the ectosome. Microscleres include (an)isochelae, sigmas, forceps or micro(subtylo)styles (microspined, spear-shaped in a few cases). Considerable reduction to complete loss of the choanocyte layer is known for some species, being associated with an adaptation to carnivory, preying on relatively large food items.

CLADORHIZA SARS, 1872

*Type species*: *Cladorhiza abyssicola* Sars, 1872 (by monotypy).

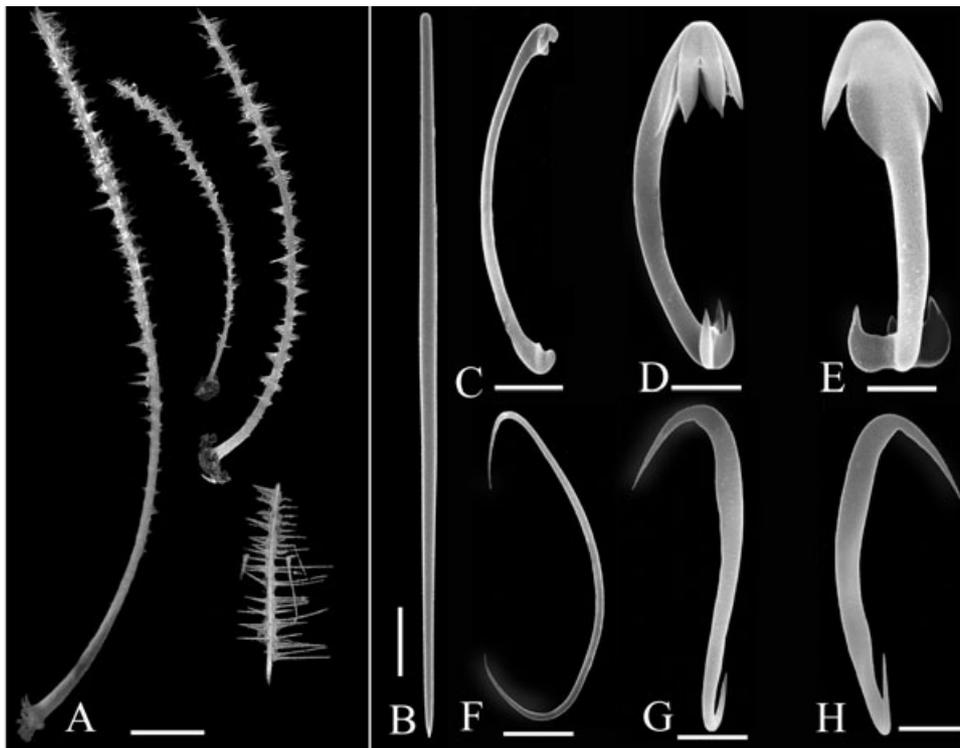
*Diagnosis*, from Hajdu & Vacelet (2002): Cladorhizidae with anchorate/unguiferate anisochelae.

**CLADORHIZA SEGONZACI SP. NOV.**

(FIGS 2, 17F)

*Type material*

*Holotype*: NAUDUR ND 5 (7-1B), 10/12/1993, 17°23.11'S, 113°11.60'W, 2581 m. Muséum National d'Histoire Naturelle, Paris, no. MNHN D JV 79.



**Figure 2.** *Cladorhiza segonzaci* sp. nov. A, view of the holotype (left), two paratypes and a fragment of a paratype (scale bar: 3 mm). B, style (scale bar: 90  $\mu$ m). C, developmental stage of anisochela (scale bar: 3.1  $\mu$ m). D, anisochela (scale bar: 3.7  $\mu$ m). E, anisochela, back view (scale bar: 3.2  $\mu$ m). F, sigma (scale bar: 12  $\mu$ m). G, sigmancistra (scale bar: 5.3  $\mu$ m). H, sigmancistra (scale bar: 5.3  $\mu$ m).

*Paratypes*: NAUDUR ND 5 (7-1B), 10/12/1993, 17°23.11'S, 113°11.60'W, 2581 m. Muséum National d'Histoire Naturelle, Paris, no. MNHN D JV 80.

#### *Etymology*

Dedicated to Michel Segonzac who organized the sorting and distribution of the biological specimens from the Ifremer cruises.

#### *Locality and habitat*

East Pacific Rise, north of Easter Island, 10/12/1993, 17°23.11'S, 113°11.60'W, 2581 m on a dead smoker. The sample was collected from the top of the highest chimney (up to 6 m high) of an inactive site, a few metres from some active black smokers with a relatively dense population of the sea anemone *Chondrophellia* sp. The sponges were attached to the vertical face of the chimney comprising sulfide deposits. The sample fragment also bore the sponge *Abyssocladia naudur* sp. nov., some hydroids and about 20 specimens of small white sea anemones.

#### *Description*

Eleven specimens or fragments of a small erect sponge, attached to the solid substratum by an enlarged base 2–3 mm in diameter, and forming an unbranched slender spicular axis with numerous lateral processes, arranged at right angles around the entire main axis, more rarely arranged irregularly in two lateral rows. Holotype (Fig. 2A) 32 mm high with a 10-mm-long basal part of the axis devoid of lateral processes. Axis 0.4–0.5 mm in diameter, lateral processes conical, up to 0.9 mm long for 0.3–0.4 mm in diameter at the base. Paratypes (Fig. 2A) smaller, the largest 24 mm high with the same diameter as the holotype, with similar lateral processes up to 4.2 mm maximum length. On specimens observed *in situ*, axis with an abrupt end and long lateral processes more numerous than on preserved samples. No visible aquiferous system. Colour white in life, cream to clear brown in alcohol, most often darker in the basal portion of the stem, base blackish.

*Skeleton*: Axis of fusiform styles longitudinally arranged, the thinner styles generally at the centre of the axis, from which arises the skeletal axis of the lateral processes. Axis of the processes conical at the base, with the styles anchored by their head reaching the centre of the stem and the point outwardly directed. Living tissue poorly preserved, forming a thin layer around the axis of the lateral processes and at their base, containing a huge number of anisochelae

dispersed without order in the present state of preservation of the specimens.

#### *Spicules*

1. Styles (Fig. 2B) of the axis of the stem and of the lateral processes, straight or rarely feebly curved, slightly fusiform, with a short, acerate tip. Size 380–990 × 14–23 µm, with a variable length/thickness ratio, some short and thick (for instance 380 × 22 µm) and others long and slender (930 × 15 µm). Some spicules, mostly localized in the centre of the skeletal axis, of same length but only 3–10 µm thick.
2. Anchorate/unguiferate anisochelae (Fig. 2D, E), extremely numerous, with a curved shaft, five lanceolate alae and well-developed fimbriae at the large end, three fang-like, sharply curved alae at the small end. Size 15–17.5 µm. Developmental stages (Fig. 2C) with two equal ends and alae appearing as small nodules.
3. Sigmas (Fig. 2F), moderately abundant, C or S shaped, very thin. Size 50–80 × 1–1.5 µm, the largest rare in the holotype.
4. Sigmancistras (Fig. 2G, H), uncommon, not observed in one specimen, contorted, with acerate tips, without notch. Size 20–25 µm × 2.0 µm.

#### *Remarks*

Underwater pictures taken from the submersible after collection of the tip of the chimney on which sponges were attached (Fig. 17F) probably represent this species, although it could be confused with *Abyssocladia naudur* sp. nov. described below, which was attached to the same rock sample. The two sponges are very similar in gross morphology (see Fig. 15A), and they were confused during the primary sorting operation and in the first spicule preparations. However, *C. segonzaci* is more irregular, with shorter and thicker filaments arranged in two opposite series, non-alternating along the axis, and has no lateral buds.

The sponge is very fragile, and many lateral filaments were broken upon examination in the laboratory. The filaments were most certainly longer in living specimens (Fig. 17F).

The species differs from most other representatives of *Cladorhiza* in the small size of the anisochelae. The only other species with anisochelae smaller than 20 µm, *C. microchela* Lévi, 1964, from the South China Sea (4330 m), has anisochelae not exceeding 13 µm and differs from the new species in the larger size of the styles, and the absence of sigmas and sigmancistras. The peculiar shape of the small end of the anisochelae, with three fang-like alae, is rather unusual, although it resembles that of the anisochelae of *C. pentacrinus* Dendy, 1887 (Dendy, 1887) from New Zealand. This species, however, differs in external

shape, larger size of all spicule categories and absence of sigmancistra.

*CHONDROCLADIA THOMPSON, 1873*

*Type species: Chondrocladia virgata* Thompson, 1873 (by monotypy).

*Diagnosis*, modified from Hajdu & Vacelet (2002): Cladorhizidae with anchorate isochelae.

The diagnosis has been slightly modified by adding 'anchorate' to isochelae in order to avoid confusion with *Abyssocladia* Lévi, 1964.

***CHONDROCLADIA KOLTUNI SP. NOV.***

(FIG. 3)

*Type material*

*Holotype*: IORAS 5/2/1 (Institute of Oceanology of Russian Academy of Sciences, Moscow). St. 2298 of submersible MIR-2, 26/07/1990, near Bering Island, 54°59.25'N, 165°42.50'E, 5249 m.

*Etymology*

Dedicated to the memory of the late Professor V. Koltun, in honour of his contribution to the knowledge of deep Pacific sponges.

*Locality and habitat*

Near Bering Island in the north part of Kuril Trench, 54°59.25'N, 165°42.50'E, 5249 m. Cruise 22 of R/V 'Akademic Mstislav Keldysh', dive of MIR-2, St. 2298, 26/07/1990. The sponge was rooted in muddy sediment.

*Description*

Large stalked sponge (Fig. 3A, B), 40 cm high, composed of a rooting system, a cylindrical stalk ending in an enlarged body from which radiate in all directions 15 secondary branches, each ending in a translucent sphere in the living animal, in an irregular swelling when preserved. Rhizoids anchoring the sponge in the mud, more than 60 mm long, richly ramified, composed of thick fibres of fusiform styles, very thin at their end. Stalk 30 cm high and 5–7 mm in diameter, rigid, made of thick fibres of longitudinally arranged fusiform styles with a less dense central part and a coating of smaller styles. Secondary axis similar to the main stalk, rigid, with two internal canals approximately 1 mm in diameter, straight and ending in a translucent sphere, 30–38 mm in diameter in life according to *in situ* photograph, slightly curved and ending in an irregular, shrunken bulge 5–10 mm in

diameter after preservation. Long, thin appendages of most probably bathypelagic crustaceans present on the shrunken bulges, sometimes included in the bulges. Apertures not visible. Consistency fleshy, rather hard. Colour yellowish white to clear brown in life and in alcohol, root system brownish.

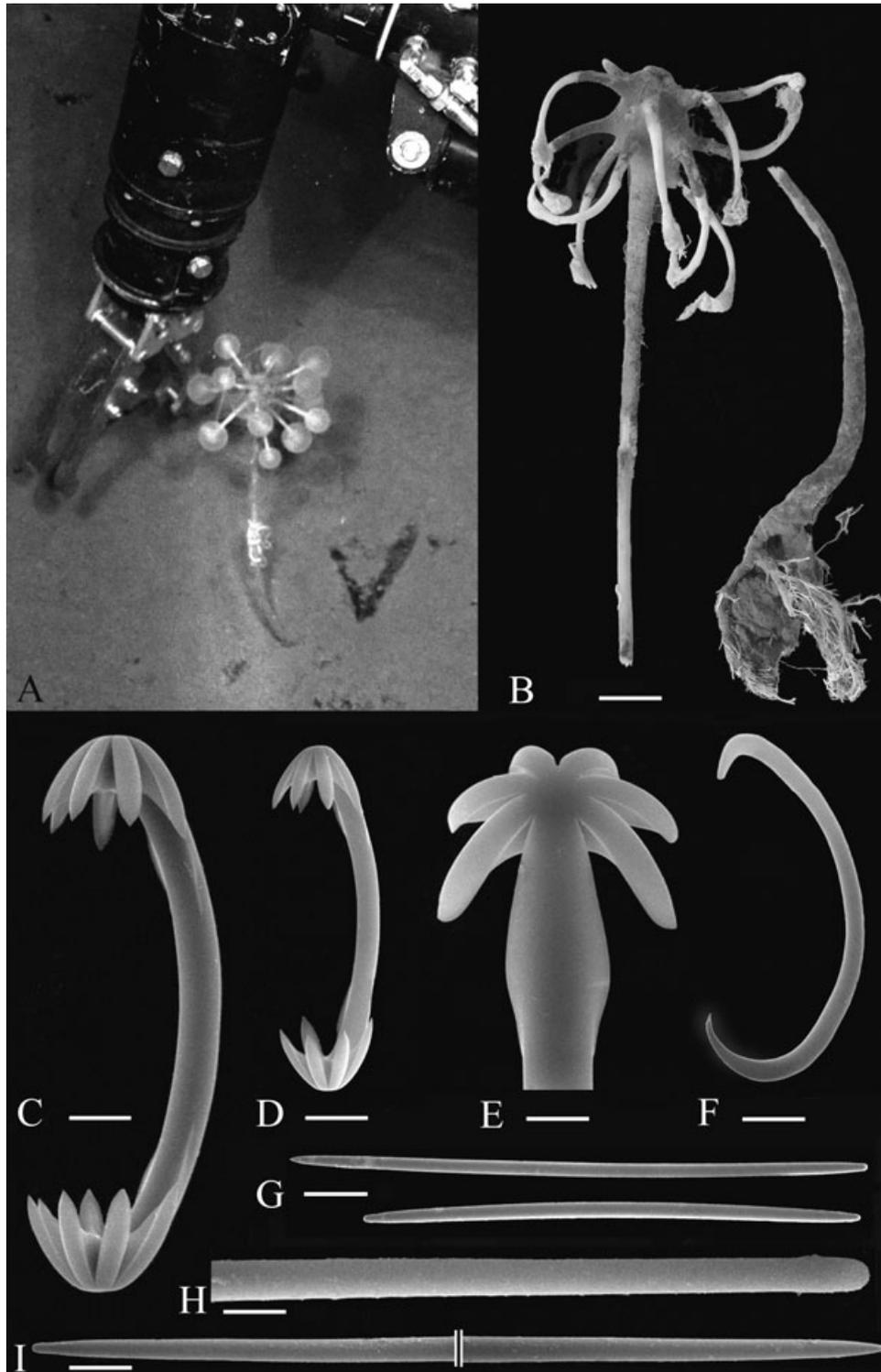
*Skeleton*: rhizoids made of thick fibres of large fusiform styles linked by spongin. Stalk made of similar fibres of spicules, spirally twisted, and covered by a 300–400- $\mu$ m-thick coating of smaller styles irregularly arranged, forming an irregular hispidation in which some sediment is included. Secondary branches with a coating of small styles forming an irregular palisade, with an axis made of fibres similar to those of the main stalk ending at the extremity of the bulge. Bulges with irregularly radiating fascicles of relatively small styles and a thick cover of extremely numerous isochelae 1 perpendicular to surface, lining the surface and the internal folds.

*Spicules*:

1. Styles of the stalk (Fig. 3G, I), secondary axis, body and rhizoids, strongly fusiform, sometimes nearly oxea (for instance in a spicule 500  $\mu$ m long, head 10  $\mu$ m and middle part 30  $\mu$ m in diameter, or in a spicule 4500  $\mu$ m long, head 25  $\mu$ m and middle part 50  $\mu$ m in diameter), with an abrupt shrinking near the head and a short acerate tip. Overall size 420–5000  $\times$  14–50  $\mu$ m, possibly longer. Longest spicules found in the main stalk, those of the body and of the rhizoids being usually less than 2000  $\mu$ m. Styles of the inflatable bulges more regular and smaller, usually 630–800  $\times$  14–17  $\mu$ m.
2. Styles or subtylostyles (Fig. 3H) from an external layer of the body and of the stalk, absent in the rhizoids and in the inflatable bulges, generally smooth, sometimes with very faint rare spines. Size 500–750  $\times$  6–10  $\mu$ m.
3. Anchorate isochelae 1 (Fig. 3C, E), rare or absent from the stalk and rhizoids, common in the body and very abundant in the inflatable bulges, with six alae, more rarely five, at each end, curved shaft with fimbriae. Size 98–105  $\mu$ m, shaft 7.5–8  $\mu$ m thick.
4. Anchorate isochelae 2 (Fig. 3D), rare in the stalk, common in the rhizoids, absent in the body and the inflatable bulges. Same shape as isochelae 1, with six or five alae, but smaller. Size 55–70  $\mu$ m, shaft 3.5–4.2  $\mu$ m thick.
5. Sigma 1, rare in body and stalk. Size 92–110  $\mu$ m.
6. Sigma 2 (Fig. 3F). Size 40–46  $\mu$ m, some in the rhizoids only 30  $\mu$ m.

*Remarks*

This large specimen of *Chondrocladia* has been figured and commented on without specific assignation



**Figure 3.** *Chondrocladia koltuni* sp. nov. A, sampling of the holotype by the manned submersible MIR, 5249 m depth, photo J. Volodin. B, holotype after preservation (scale bar: 13 mm). C, anchorate isochela 1 (scale bar: 12.3  $\mu\text{m}$ ). D, anchorate isochelae 2 (scale bar: 12.3  $\mu\text{m}$ ). E, anchorate isochelae 1, back view (scale bar: 7.6  $\mu\text{m}$ ). F, sigma 2 (scale bar: 7.3  $\mu\text{m}$ ). G, two styles from rhizoid (scale bar: 170  $\mu\text{m}$ ). H, head of a style from the cover of the stalk (scale bar: 93  $\mu\text{m}$ ). I, style of the stalk (scale bar: 106  $\mu\text{m}$ ).

several times since its observation and collection by the manned submarine MIR-2 (Tendal, Barthel & Tabachnik, 1993; Tendal & Sahling, 1997; Hajdu & Vacelet, 2002). Being the first to be observed *in situ* and collected at the same time, it resolved the problem of a deep-sea organism whose nature long remained enigmatic owing to the striking difference in morphology between the *in situ* observations and the collected animals (Tendal *et al.*, 1993). The presence of several long, thin appendages of crustaceans on the shrunken bulges, with some of the setae trapped in the alae of the isochelae 1, and of crustacean debris within the sponge, clearly demonstrated in other species of *Chondrocladia* (Kübler & Barthel, 1999).

The species evidently belongs to the *concrescens* group (Topsent, 1930). It differs from the specimens of north-west Pacific identified as *C. concrescens* Schmidt, 1880 by Koltun (1970), a species first described from the Caribbean and whose records from the Pacific are doubtful (see Remarks for the following species). It also differs from *C. lampadiglobus* sp. nov. in the styles of the cover, which are nearly smooth here, and the size and characters of the isochelae.

Another specimen with the same external morphology, possibly belonging to the same species, has been photographed *in situ* by Tendal & Sahling (1997), from 4900 m depth, in a nearby area of the North Pacific, 550 km apart.

#### **CHONDROCLADIA LAMPADIGLOBUS SP. NOV.**

(FIGS 4, 17A–D)

##### *Type material*

*Holotype*: NAUDUR ND 06 (9-1B), 11/12/1993, East Pacific Rise, 17°24.10'S, 113°13.75'W, 2714 m, Muséum National d'Histoire Naturelle, Paris, no. MNHN D JV 81.

##### *Etymology*

From *lampas*, *lampadis*, Latin, noun fem. lamp, lantern, and *globus*, *globi*, Latin, noun masc. ball, sphere. Referring to the resemblance of the sponge to a street-light with several spherical glass globes.

##### *Locality and habitat*

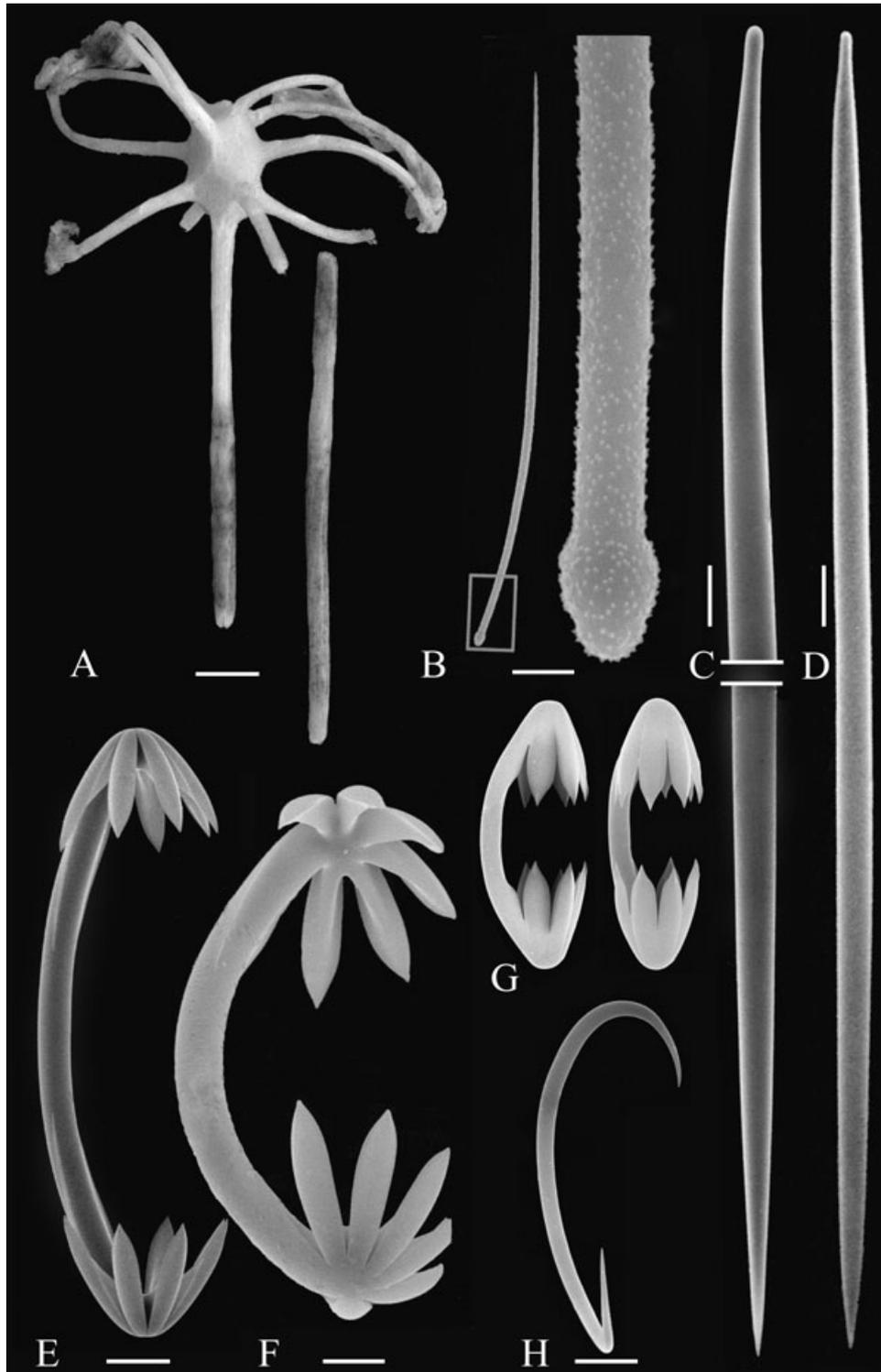
East Pacific Rise, 17°24.10'S, 113°13.75'W, 2714 m, 11/12/1993, 16:30, near the thermal site 'Rehu'. The holotype was rooted in sediment between pillow lava, near active hydrothermal sites, but in an area still with low density of animal life. Several other specimens possibly belonging to the same species have been observed from submersibles during several cruises on the East

Pacific Rise under similar conditions, approximately 2600–3000 m depth, either rooted in a thick sediment layer or directly attached to pillow lava with a thin sediment cover (Fig. 17C, D), always at some distance from the rich animal communities of the active hydrothermal sites. These observations, which have been made over a large area of the East Pacific Rise extending from 23°32'S to 13°N, are presented and discussed in the Remarks below.

##### *Description*

Large stalked sponge (Figs 4A, 17A–D), 27 cm high after preservation and loss of the basal part, approximately 50 cm high in life, composed of a rhizoid fixation system, a cylindrical stalk ending in an enlarged, ovoid body from which radiate in all directions secondary branches, each ending in an irregular swelling on the preserved specimen, a translucent sphere in the living animal. Fixation base not preserved, owing to the breakage of the lower part of the stalk, estimated at 6 cm long from Fig. 17A, B. Stalk 24.5 cm high and 5–6 mm in diameter, rigid, smooth near the base, rugose to the fingers near the body, made of longitudinally arranged fusiform styles and a coating of rugose tylostyles. Body ovoid, 30 × 20 mm, with a rugose surface, from which radiate 13 secondary axes, 2–4 mm in diameter. Five of the secondary axes broken more or less near the base, the other, 50 mm maximum length, somewhat curved, ending in an irregular bulge, which often coalesces with one or two of the bulges of the nearby extensions, sometimes forming a veil between the axes. Translucent spheres of variable diameter, estimated at 3–5 cm from the underwater pictures. Apertures not visible. Consistency rigid but easily broken. Colour yellowish white to clear brown in alcohol. Several unidentifiable crustacean debris fragments, up to 4 mm long, present on the surface of the body and more frequently on the surface of the bulges. Stalk bearing a comatulid crinoid, probably *Thaumatometra* sp. (M. Eleaume, MNHN, pers. comm.), and an unidentified ophiuroid. An unidentified worm, possibly a polychaete, gliding on one of the spheres visible on underwater pictures (Fig. 17A).

*Skeleton*: Stalk made of large fusiform styles arranged in parallel without any twisting, with a thick cover of rugose tylostyles arranged in a dense irregular felt-work. Cover devoid of microscleres in the most basal part of the stalk, with a few isochelae 1 near the body. Body and secondary branches with a rugose coating of styles smaller than those of the axis, including numerous microscleres. Bulges with a confused skeleton of fusiform styles, smaller than in the axis, and an outer cover of extremely numerous microscleres, especially isochelae 1.



**Figure 4.** *Chondrocladia lampadiglobus* sp. nov. A, holotype (scale bar: 17 mm). B, tylostyle of the cover of the stalk (scale bars: 42  $\mu\text{m}$  and 4.2  $\mu\text{m}$ ). C, style of the stalk (scale bar: 30  $\mu\text{m}$ ). D, style of the body surface (scale bar: 63  $\mu\text{m}$ ). E, anchorate isochelae 1 (scale bar: 14  $\mu\text{m}$ ). F, anchorate isochelae 1 (scale bar: 9.6  $\mu\text{m}$ ). G, two anchorate isochelae 2 (scale bar: 7  $\mu\text{m}$ ). H, sigma (scale bar: 10  $\mu\text{m}$ ).

*Spicules:*

1. Styles of the fibres in the body and the stalk (Fig. 4C), straight, strongly fusiform (for instance in a spicule 4750 µm long, head 20 µm and middle part 75 µm in diameter), with a head abruptly shrunken to 20 µm long and an acerate tip. Size 700–4750 × 15–75 µm.
2. Styles of the terminal swellings, fusiform, similar to those of stalk and body (Fig. 4D), but smaller. Size 510–580 × 17–30 µm.
3. Subtylostyles or tylostyles of the outer cover of stalk and of swellings (Fig. 4B), slightly curved or flexuous, often with a marked oval head, rugose with numerous short spines. Size 300–535 × 5–6 µm.
4. Anchorate isochelae 1 (Fig. 4E, F), rare or absent from the stalk, common in the body and very abundant in the swellings, with six alae at each end. Alae relatively short, lanceolate, sharp, with a well-marked hull on the underside. Shaft curved, with narrow fimbriae. Size 123–140 µm, shaft 6–7 µm thick, alae 25 µm long.
5. Anchorate isochelae 2 (Fig. 4G), rare in the stalk, moderately abundant in the body and the bulges, with six alae. Alae rather thick, lanceolate with a sharp point. Size 20–32 µm, shaft 2 µm thick, alae 10–11 µm long.
6. Sigmas (Fig. 4H), rare in the body and in the stalk, not seen in the bulges. Size 45–120 × 2–3 µm, possibly in two size categories, but with numerous intermediary forms.

*Remarks*

The identification of species of *Chondrocladia* of the 'conrescens type' is difficult, especially for the Pacific representatives, which are generally known from single or few specimens, giving no indication on specific variations. Furthermore, several specimens of Pacific *Chondrocladia* have been tentatively identified, probably incorrectly, either to *C. conrescens* Schmidt, 1880 or to *C. gigantea* (Hansen, 1885), originally described, respectively, from the Gulf of Mexico and the north-east Atlantic.

This species from the East Pacific Rise is very similar in external morphology to *Chondrocladia koltuni* sp. nov. Both have the same aspect with inflated spheres in life. The holotypes of the two species differ in the styles of the coating, which are rugose tylostyles in *C. lampadiglobus* and nearly smooth styles in *C. koltuni*, in the size and characters of the isochelae, and the thickness of the main styles. Both differ in several important spicule characters from the sponge from the deep north Pacific identified as *C. gigantea* by Koltun (1958). However, *C. lampadiglobus* appears very similar to the sponge identified as *C. conrescens* by Koltun (1970), who gathered under this name spec-

imens from the Gulf of Mexico, north Atlantic and north Pacific, while admitting extensive polymorphy. This 'species' appears to be common in the Okhotsk Sea and the South Kuril Islands, at 300–8860 m depth. Koltun did not comment on the variability of his numerous specimens, but according to his description they appear to differ from the type of *C. conrescens* from the Gulf of Mexico (Schmidt, 1880; Topsent, 1920) and probably belong to an undescribed species. The specimen here described as *C. lampadiglobus* has a rather similar spiculation, differing only in larger rough tylostyles, a clearer distinction between the two types of isochelae, and in the isochelae 2 with longer alae. (These isochelae 2 are reminiscent of those that characterize *C. conrescens*, with very long alae, although here the opposite alae are far from being in contact, as described by Schmidt, 1880 and Topsent, 1920.) The possibility that *C. lampadiglobus* belongs to the same species as Koltun's specimens from the north-west Pacific cannot be excluded, although the difference in the shape of anisochelae 2 and the large geographical distance make it rather unlikely. This will need to be confirmed when more is known of the variability of the spiculation of *C. lampadiglobus*, as discussed below.

The other species of *Chondrocladia* originally described from the Pacific, namely *C. asigmata* Lévi, 1964, *C. challengerii* Topsent, 1920, *C. clavata* Ridley & Dendy, 1886, *C. crinita* Ridley & Dendy, 1886, *C. pulvinata* Lévi, 1993, *C. scoloniema* Lévi, 1993 and *C. yatsui* Topsent, 1930, differ in spicule characters, which are admittedly rather subtle and whose constancy remains to be examined.

Specimens of *Chondrocladia* sp. with a similar morphology are rather common on the East Pacific Rise from 23°S to 13°N, but only one has been collected and it is at present unclear whether they all actually belong to the same species (Fig. 17C, D). During the NAUDUR cruise, the sponge was observed at the same depth in nearby areas of the type location or was recognized in the videos or photographs during PL04, PL16, PL17 and PL18. Observations were also made during BIOSPEEDO dive PL 1579, 19/04/2004, 17°24.86'S, 113°11.96'W, 2590 m (Jollivet *et al.*, 2004), during PARS5 cruise of the R/Atlantis (dive 4095 of submersible Alvin, 23°32.06'S, 115°34.17'W, 2596 m) and during GEOCYARISE 1 and 3 cruises also on the East Pacific Rise but at a location more than 3000 km distant to the north (around 13°N). Only one specimen has been collected very recently during cruise PARS5, from the southernmost location. A preliminary study of a single bulge and its axis was made during this work, with rather uncertain results for the specific identification. The spicules are rather similar to those of the holotype, although with a few significant differences. The rugose subtylostyles of the coat were not

observed, possibly because they are located only on the main stalk, not studied, and there are numerous sigmancistras 40–65 µm long, not found in the holotype. It is likely that these differences come under specific variability, especially given the geographically rather distant location of the holotype and the PARS5 specimen (725 km), implying a wide distribution of *C. lampadiglobus* on the East Pacific Rise. However, these differences are of the same order as those found between the holotype and the specimens from the North Pacific identified as *C. conrescens* by Koltun (1970). Accordingly, the identification of the PAR5 specimen and the uncollected specimens to the new species is made with reservation, pending collection of more individuals.

The collected pictures indicate that the sponge could have up to 16 spheres, and that it could be rooted either on patches of thick sediment between pillow lava or directly attached to lava. During the NAUDUR cruise, the sponge was reported by the observers, mostly geologists, as the 'arbre à boules' ('tree with spheres'). The number of 'arbres à boules' seen during dive PL06 (when the holotype was collected), and during PL17 (from 18°12.40'S, 113°22.10'W to 18°10.20'S, 113°20.90'W) has been reported by the observer (V. Ballu, unpubl. report of NAUDUR cruise, Ifremer), allowing a rough estimation of the abundance of the sponge. Seven individuals were observed in PL06 over a distance of 6 km, and 12 individuals including a small one during PL17 over a distance of 4.5 km, between 2586 and 2684 m depth. The sponge is never directly associated with the dense animal fauna of the active sites, but occurs at least several tens of metres from the active smokers, in areas with poor and highly dispersed macrofauna. It has never been observed in the zones where the increasing abundance of the sea anemone *Chondrophellia* introduces the 'oasis' of life surrounding the active smokers (Geistdoerfer *et al.*, 1995).

The video made before and during collection of the holotype shows that, contrary to what has been suspected from *in situ* photographs of a *Chondrocladia* sp. (Tendal & Sahling, 1997), there was no fast reaction of the sponges, such as contraction of the spheres, during the few minutes of observation and the spheres are still fully expanded during collection by the arm of the submarine (Fig. 17B).

The *in situ* observation of an unidentified worm, possibly a polychaete, on a sphere of the holotype of *C. lampadiglobus* is interesting in this carnivorous sponge. The worm is not a prey item trapped by the sponge spicules because it moved significantly during the video sequence. It is possible that it is a commensal feeding on the crustacean debris in the process of digestion observed at the surface of the contracted sphere. Commensalism by polynoid polychaetes has

been reported in deep-sea hexactinellid sponges (Martin, Rosell & Uriz, 1992).

#### ASBESTOPLUMA TOPSENT, 1901

*Type species: Cladorhiza pennatula* Schmidt, 1875 (by subsequent designation).

*Diagnosis*, from Hajdu & Vacelet (2002): Cladorhizidae with palmate anisochelae.

#### ASBESTOPLUMA AGGLUTINANS SP. NOV.

(FIG. 5)

##### *Type material*

*Holotype*: NAUDUR 15-2-1B, 20/12/1993, 18°15.90'S, 113°22.08'W, 2689 m, Muséum National d'Histoire Naturelle, Paris, no. MNHN D JV 82.

*Paratype*: GARRETT GN 19-07, 31/01/1991, East Pacific Rise, Garrett Segment, 13°22.50'S, 112°16'W, 2680 m, Muséum National d'Histoire Naturelle, Paris, no. MNHN D JV 83.

##### *Etymology*

From 'agglutinare', Latin, verb: to glue, referring to the collection by the sponge of numerous skeletons of protists.

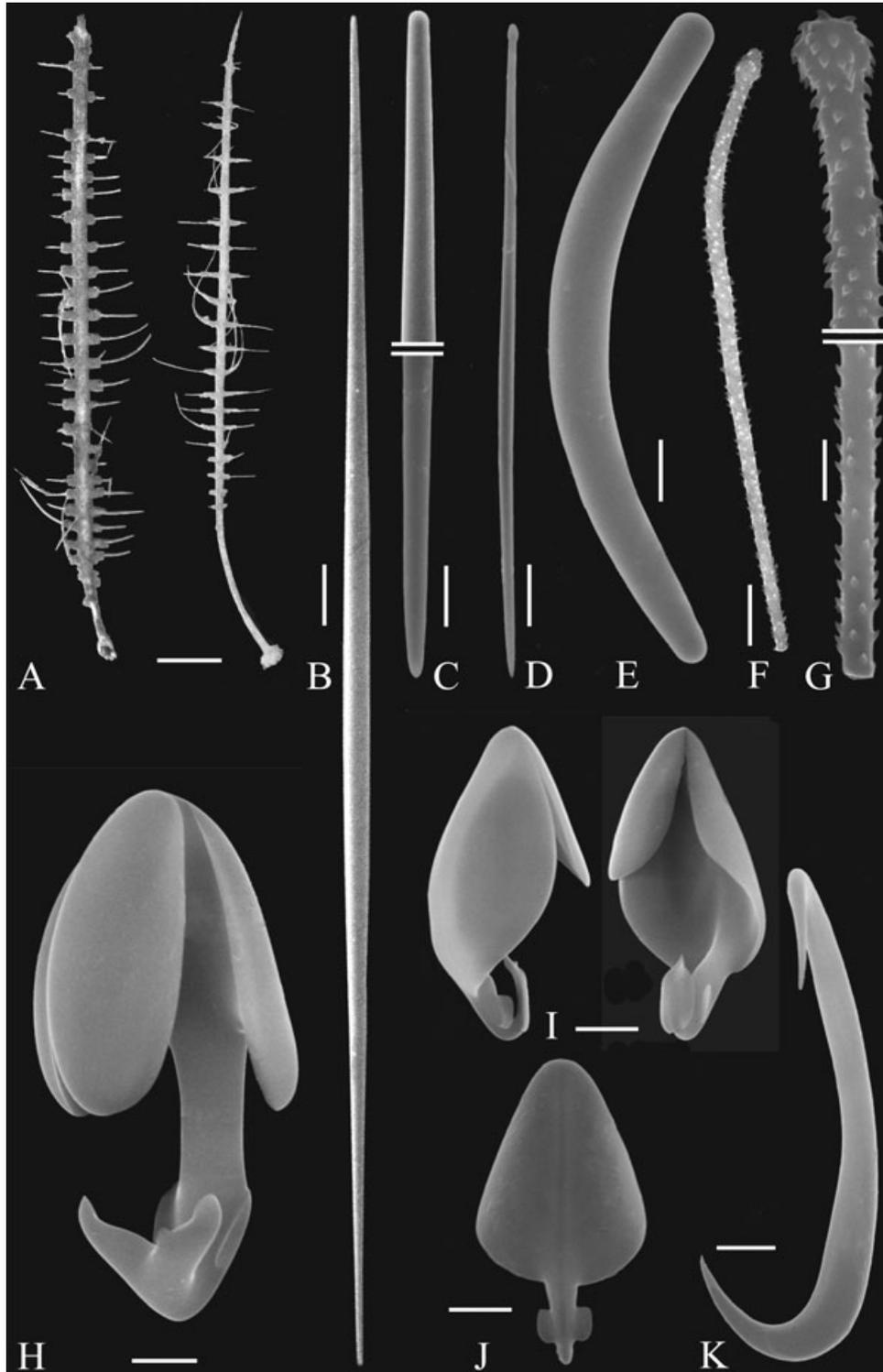
##### *Locality and habitat*

East Pacific Rise. NAUDUR 15-2, 20/12/1993, 18°15.90'S, 113°22.08'W, 2689 m, on a dead smoker. GARRETT GN 19-07, Garrett Segment, 31/01/1991, 13°22.50'S, 112°16'W, 2680 m, on a basalt fragment.

##### *Description*

Two small erect sponges (Fig. 5A), consisting of a somewhat flattened axis 4 cm high and 0.8–1 mm in diameter, smooth on the basal quarter, then with biserially arranged lateral filaments arising perpendicularly to the axis in two opposite series. Filaments frequently broken, up to 5 mm long, cylindrical and 1–1.5 mm in diameter at the base, abruptly reduced to a thin spicular axis at approximately 0.7 mm from the axis in the holotype, up to 6 mm long in the paratype in which the cylindrical base is generally longer and thinner. No aperture or aquiferous system visible. Colour brown in alcohol.

*Skeleton*: Main axis of large fusiform styles longitudinally arranged, surrounded by a dense feltwork of small acanthotylostrongyles including sediment and skeletons of radiolarians and foraminiferans. Axis of the lateral filaments made of smaller styles, with a



**Figure 5.** *Asbestopluma agglutinans* sp. nov. A, holotype (left) and paratype (scale bar: 3.8 mm). B, style of the axis (scale bar: 83  $\mu$ m). C, head and tip of a style of the axis (scale bar: 28  $\mu$ m). D, style of the filament axis (scale bar: 35  $\mu$ m). E, substrongyle of the base (scale bar: 37  $\mu$ m). F, acanthotylostrongyle (scale bar: 7.5  $\mu$ m). G, head and tip of an acanthotylostrongyle (scale bar: 2.3  $\mu$ m). H, anisochela 1 (scale bar: 4.1  $\mu$ m). I, anisochelae 2 (scale bar: 2  $\mu$ m). J, anisochela 2, back view (scale bar: 2  $\mu$ m). K, sigmancistra (scale bar: 2.9  $\mu$ m).

similar feltwork of acanthotylostrongyles and sediment in the thickened base. Fixation base with a cover of thick, more or less flexuous styles or substrongyles tangentially arranged. Microscleres very abundant in the tissue of stem and branches.

#### Spicules:

1. Styles of the main axis (Fig. 5B, C), straight, fusiform, with a blunt point. Size 1550–2100 × 30–35 µm.
2. Styles (mycalostyles) (Fig. 5D) of the axis of the lateral filaments, straight, moderately fusiform, with an oval head and a short, acerate tip. Size 370–780 × 8.5–17 µm.
3. Styles or substrongyles (Fig. 5E) found only at the fixation base, generally curved or more or less flexuous, sometimes vermiform, thicker in the middle, with unequal ends. Size 220–535 × 15–42 µm.
4. Acanthotylostrongyles (Fig. 5F, G) forming a feltwork around the main axis and the base of the filaments, straight or more often curved near the head, entirely covered by small spines curved toward the end near the head and toward the head near the end. Head roundish, end abruptly cut. Size 65–165 × 0.8–2.3 µm.
5. Anisochelae 1 (Fig. 5H). Head with large lateral alae attached to the shaft along approximately two-thirds of their length, frontal ala large, ovoid. Shaft feebly curved in the first part, then bearing two small fimbriae near the foot. Foot with two small diverging alae. Size 32–36 µm, shaft diameter 4.1–5 µm.
6. Anisochelae 2 (Fig. 5I, J). Head with large lateral alae attached to the shaft along their whole length. Shaft with a free part short, curved and bearing two small rectangular alae in the first part, then strongly bent and with a large ovoid ala ending in a short point. Size 9.8–10.5 µm, shaft diameter 0.8–1 µm.
7. Sigmancistras (Fig. 5K), with a 90° twisting and acerate points, without notch. Size 23–28 µm, 2.3 µm in maximum width.

#### Remarks

This species is remarkable in its morphology, with regular thickenings of the basal parts of the lateral filaments, and in the number of skeletons of various foraminiferans and radiolarians included in these thickened parts. This may suggest that protists are an important part of the diet of the sponge.

The nearest relative of this species among the *Asbestopluma* spp. of this area appears to be *A. biserialis* (Ridley & Dendy, 1886), which has been described and reported from the South Pacific. However, *A. biserialis* does not display the cylindrical thickenings of the base of the filaments, has no coating of spinose microtylostyles, has no vermiform basal spicules and the large anisochelae 1 are absent. The new

species more closely resembles the spicule characters of *A. pennatula* (Schmidt, 1875) and *A. quadriserialis* Tendal, 1973, from the North Atlantic and Arctic. It differs from these species, which are geographically very distant, in its external shape, larger styles, smaller anisochelae 1, which also show minor differences although their general shape is rather similar, and in the basal vermiform styles, which are rather straight strongyles in the two other species. *Asbestopluma quadriserialis* also differs in the presence of two sizes of sigmancistras.

Unlike the other sponges described here, this species is represented in the collection by two specimens from relatively distant localities (557 km). It is worth noting that the two specimens show no significant differences, either in morphology or in spicule characters.

#### ASBESTOPLUMA SUBGENUS HELOPHLOEINA TOPSENT, 1929

*Type species: Helophloeina stylivarians* Topsent, 1929 (by monotypy).

*Diagnosis*, modified from Topsent, 1929: *Asbestopluma* with a basal sheath of spear-shaped microtylostyles and microstrongyles, with styles or styles and oxeas which may be modified in desmas at the base.

#### ASBESTOPLUMA (HELOPHLOEINA) FORMOSA SP. NOV. (FIGS 6–8, 17E)

#### *Type material*

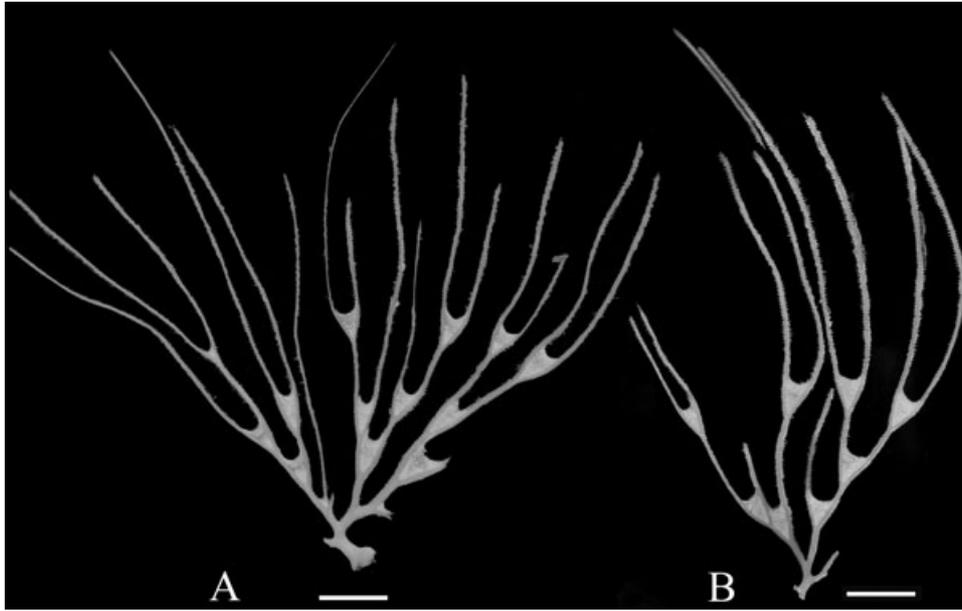
*Holotype*: STARMER I, PL 01, 12/06/1989, North-Fiji basin, 16°59.50'S, 173°55.47'W, 1997 m, Muséum National d'Histoire Naturelle, Paris, no. MNHN D JV 84, presently broken in several fragments.

#### *Etymology*

From *formosus*, Latin, adj. beautiful. Referring to the grace of the sponge.

#### *Locality and habitat*

Dive PL 01, 12/06/1989, North Fiji Basin, 16°59.50'S, 173°55.47'W, 1997 m. The sponge, which was tentatively identified *in situ* by the underwater geologist observer as 'a kind of gorgonian', was attached to a fossil chimney with red oxides, on which the density of sessile animals was very low, with only a few euplectellid sponges. The collection site is c. 50–100 m distant from the active site White Lady, a white chimney made of anhydrite emitting transparent hot (285 °C) fluids of low chlorine content, and harbouring a rich



**Figure 6.** *Asbestopluma (Helophloeina) formosa* sp. nov. Fragments of the holotype. A, scale bar: 10.3 mm. B, scale bar: 8 mm.

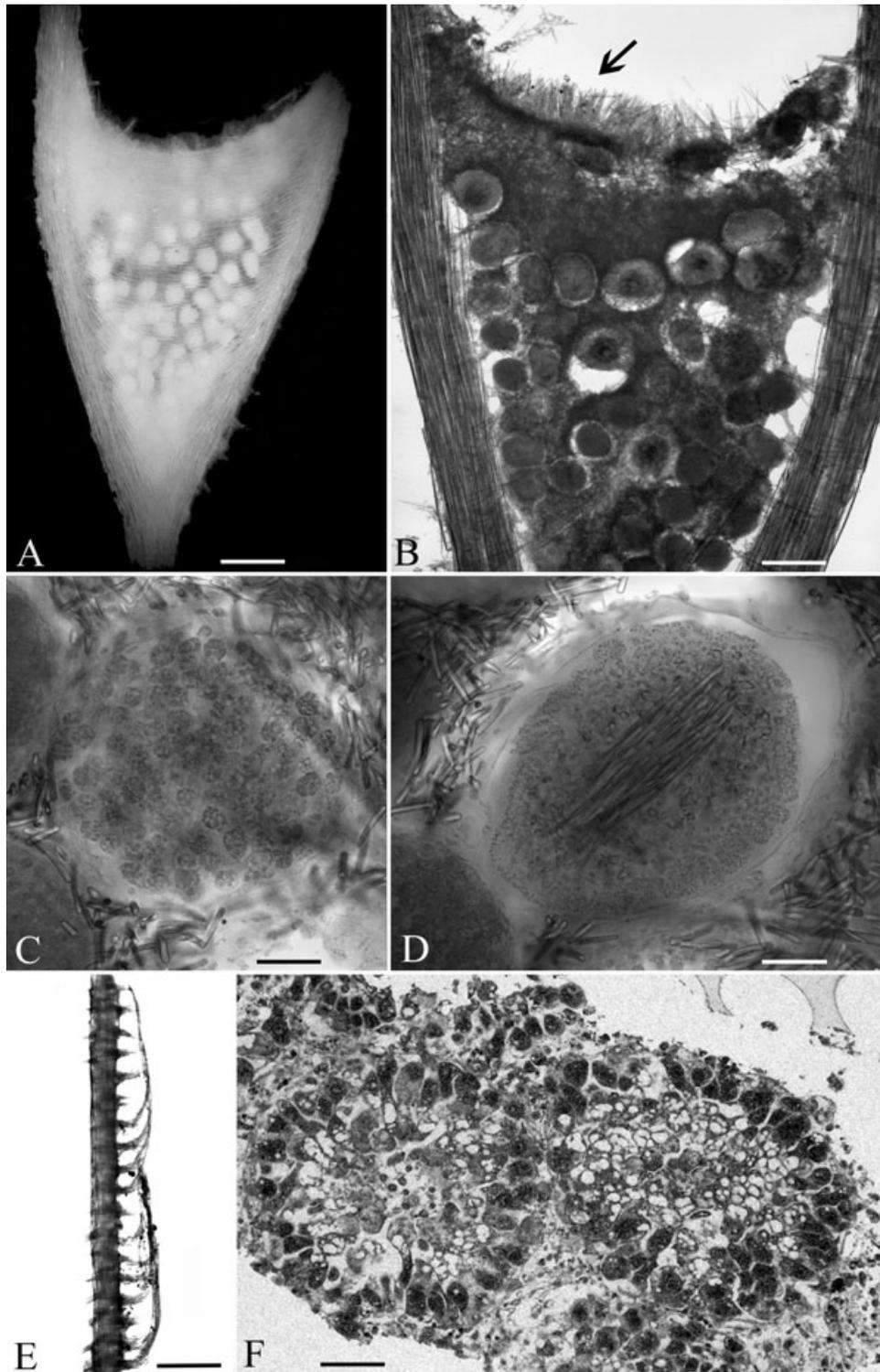
animal community (Auzende *et al.*, 1989; Desbruyères *et al.*, 1994).

#### Description

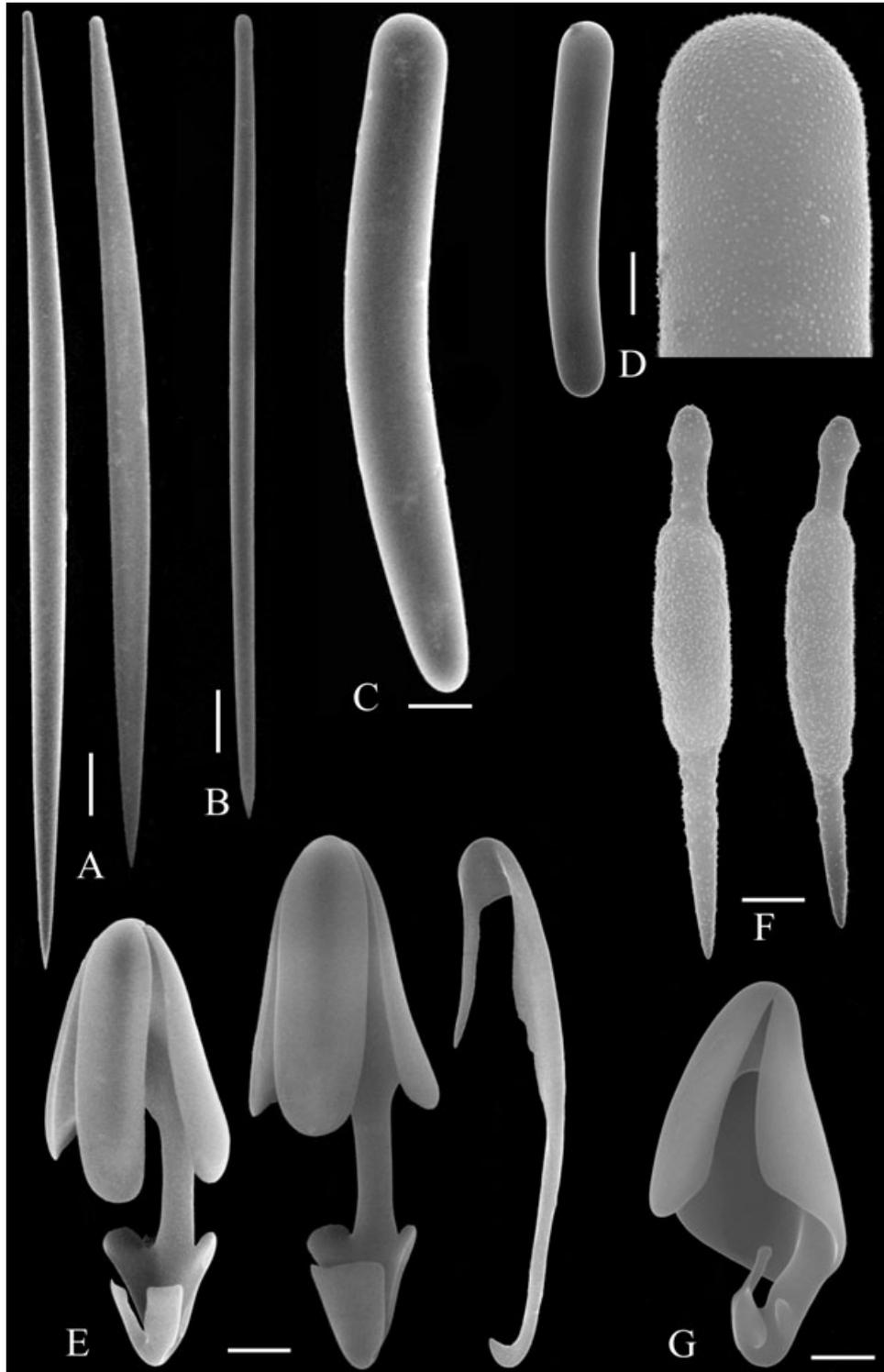
Erect, fan-shaped sponge (Fig. 6, 17E) consisting of a short stem from which arise branches which divide dichotomously three or four times in a single plane, the last branches being long and parallel. Dimensions in life approximately 8 cm high and 16 cm wide (evaluated from Fig. 17E). Holotype at present broken into several fragments, 80 mm high. Fixation base slightly enlarged, attached to a small rocky fragment. Primary stem contorted, smooth, 1 mm in diameter. Secondary branches flattened, bearing short lateral processes regularly arranged perpendicularly on both sides of the branch with a regular spacing of 0.5 mm. Tertiary branches similar to the secondary ones, but up to 45 mm long and 0.4–0.5 mm in diameter, covered by lateral processes regularly arranged on both sides, facing each other and 250–300 µm apart. Most lateral processes only 100–125 µm long, most probably broken, a few of them extending in a filament 2.5–3.7 mm long lying parallel to the branch (Fig. 7E). A flattened enlargement present at each point where the branches divide dichotomously, containing numerous oocytes or embryos (Fig. 7A–D, F). No visible aquiferous system, no visible aperture. Living tissue poorly represented in the present state of preservation, except at the branching points. Consistency rather rigid, but highly fragile. Colour pure white.

*Skeleton:* Stem and branches with an axis of large fusiform styles mixed with a few substrongyles especially near the base, covered on the lateral side of the flattened branches by a dense cover of microstrongyles, less developed on the enlarged side of the branches. Lateral processes with an axis of small styles, inserted on the main axis by an enlarged base and arising through the lateral cover of microstrongyles. Enlargements at the division points with on both sides a cover of fusiform styles and substrongyles parallel to the surface and pressed against each other, a dense feltwork of microstrongyles, and a palisade of slender styles of the same type as those of the axis of lateral processes on the edge (Fig. 7A, B). Base of the stem with a cover of numerous microtylostyles of a particular type, themselves covered by an external layer of short fusiform styles and substrongyles. Anisochelae dispersed on the branches, with no visible special arrangement except anisochelae 1, which are grouped in rosettes.

Embryos (Fig. 7A–D, F) numerous in every enlargement at branching points, each in a cavity surrounded by microstrongyles, 180–300 µm in diameter, showing various stages of development, most containing spicules as usual in embryos of *Asbestopluma* (Lundbeck, 1905). Earliest stages spherical, without spicules, made of blastomeres 20–22 µm in diameter filled with large vitelline inclusions and with a large nucleolated nucleus. In a probably more advanced stage, blastomeres more elongated and radially arranged near the border. Later stages made of poorly distinct cells,



**Figure 7.** *Asbestopluma (Helophloeina) formosa* sp. nov. A, embryos under a cover of fusiform styles in a branching enlargement (scale bar: 0.6 mm). B, non-desilicified polished section in a branching enlargement, showing embryos, axis of the branches and an outer palisade of small styles (arrow) (scale bar: 300  $\mu\text{m}$ ). C, enlargement of an embryo of B, early stage without spicule (scale bar: 50  $\mu\text{m}$ ). D, enlargement of an embryo of B, stage with a fascicle of styles and rosettes of anisochelae 2 (scale bar: 45  $\mu\text{m}$ ). E, remains of filaments on a branch (scale bar: 1 mm). F, semithin section of two desilicified embryos (scale bar: 28  $\mu\text{m}$ ).



**Figure 8.** *Asbestopluma (Helophloeina) formosa* sp. nov. A, two fusiform styles of the axis (scale bar: 65  $\mu$ m). B, style of the lateral processes (scale bar: 21.5  $\mu$ m). C, substrongyle (scale bar: 14.3  $\mu$ m). D, microstrongyle and detail of the head (scale bars: 6.2  $\mu$ m and 1.5  $\mu$ m). E, two anisochelae 1 and an immature one (scale bar: 10  $\mu$ m). F, two microtylostyles (scale bar: 4.3  $\mu$ m). G, anisochelae 2 (scale bar: 2  $\mu$ m).

including a few layers of small cells near the surface, with a central fascicle of styles varying from 1 to 4  $\mu\text{m}$  in thickness, to which are added in probably more advanced stages numerous rosettes of anisochelae 2.

#### Spicules:

1. Styles of the axis of stem and branches (Fig. 8A), strongly fusiform (for instance for a spicule 925  $\mu\text{m}$  long, diameter 11  $\mu\text{m}$  at the head and 40  $\mu\text{m}$  in the middle), straight or feebly curved, with a sharp point. Size 200–1025  $\times$  20–45  $\mu\text{m}$ .

2. Substrongyles of the axis (Fig. 8C), more numerous and smaller near the base, curved near the middle, sometimes double bent or even a little flexuous, with the two ends nearly equal. Size 80–500  $\times$  15–30  $\mu\text{m}$ .

3. Styles of the lateral processes and of the palisade of the enlargements (Fig. 8B), the larger slightly fusiform, straight, with a short, sharp point. Size 180–350  $\times$  7–9  $\mu\text{m}$ .

Microstrongyles (Fig. 8D), very numerous, slightly curved, some more sharply bent near the centre, most spicules covered by minute spines 0.04  $\mu\text{m}$  high not visible under the light microscope. Size 25–60  $\times$  5–7  $\mu\text{m}$ .

4. Microtylostyles (Fig. 8F) present only at the base where they are numerous, very peculiar in shape, resembling the 'spear-like' spicules figured by Ridley & Dendy (1887) for *Meliiderma stipitata* and by Topsent (1929) for *Helophloeina stylivarians*, with a round head, a short neck, an enlarged cylindrical body and a long point, the whole spicule covered by minute spines 0.1  $\mu\text{m}$  high more numerous on the enlarged 'body'. Size 25–45  $\times$  4–7  $\mu\text{m}$ .

5. Anisochelae 1 (Fig. 8E), grouped in rosettes with lateral alae attached to the shaft along most of their length. Frontal ala of the foot either simple or bifid. Size 72–90  $\mu\text{m}$ , shaft diameter 5–5.5  $\mu\text{m}$ .

6. Anisochelae 2 (Fig. 8G), very numerous and dispersed along the branches, grouped in rosettes in the more advanced embryos. Free part of the shaft very short, curved. Head with large lateral alae. Foot with two vestigial lateral alae, and a long frontal ala bearing two lateral expansions, strongly curved toward the shaft. Size 10–15  $\mu\text{m}$ .

#### Remarks

Like all these deep-sea sponges, the specimen is fragile, although the branches are rigid, and the holotype is at present broken into several fragments. Very likely the lateral processes are the remains of a well-developed system of long filaments which have been broken at their base except in a few places, as shown in Figure 7E. These filaments appear to be more numerous on a photograph taken soon after collection. Unfortunately, there is no available high-

definition *in situ* picture of the sponge. However, a low-definition video document taken during collection of the specimen shows that there is between the branches a regular arrangement of thin filaments (Fig. 17E). This morphology as well as the absence of a visible aquiferous system suggest a carnivorous feeding habit.

The sponge shows evident affinities with *Asbestopluma* in its erect shape, absence of aquiferous system and presence of anisochelae. However, it differs from other representatives of the genus in the gorgonian-like shape, the localization of the embryos, the presence of spear-shaped microscleres at the base, and the grouping in rosettes of the anisochelae. The particular microtylostyles of the base have a unique shape. There are only two other sponges with somewhat similar spicules, *Meliiderma stipitata* (Ridley & Dendy, 1886) and *Helophloeina stylivarians* Topsent, 1929, both with cladorhizid affinities. In *Meliiderma* Ridley & Dendy, 1887, which has anchorate isochelae, the spear-shaped spicules are clearly larger, although tentatively regarded as microscleres by Ridley & Dendy, and are packed in a single layer along the stem. This sponge has been returned by Hajdu & Vacelet (2002) to the genus *Chondrocladia* where it had originally been described and *Meliiderma* is rightly considered a synonym of *Chondrocladia*. The resemblances are greater with *Helophloeina stylivarians*, from the deep south-east North Atlantic (Canary Islands). This sponge, which has anisochelae of the *Asbestopluma* type, differs from the present species in shape (poorly known in the single known specimen), in the presence of desmas and a mixture of styles and oxeas, and in the smaller size of the microtylostyles. However, the two sponges, which have evident affinities with *Asbestopluma*, share two characters not found in the other species of the genus, i.e. the presence of microstrongyles and a sheath of spear-shaped microtylostyles. *Helophloeina* has been considered a synonym of *Asbestopluma* by Hajdu & Vacelet (2002), on the basis of the fact that there was a single species with these characters in the genus. I suggest reconsidering this position, as there are now two species sharing these characters, and reviving *Helophloeina* either as a genus within the Cladorhizidae or preferably as a subgenus of *Asbestopluma* with an emended diagnosis.

In *A. (H.) formosa* sp. nov., the grouping of the anisochelae in rosettes, which has not been reported in any other *Asbestopluma*, interestingly emphasizes the affinities of the genus with the Mycalidae, and more precisely *Mycale* Gray, 1867, already shown by the presence of palmate anisochelae and already emphasized for instance by Lundbeck (1905). However, the transfer of the genus to Mycalidae is not proposed here, pending more solid data that will allow a general

reassignment of all the members of the evidently polyphyletic Cladorhizidae (see Discussion).

#### ABYSSOCLADIA LÉVI, 1964

*Type species: Abyssocladia bruuni* Lévi, 1964 (by monotypy).

*Diagnosis*, modified from Lévi (1964): Cladorhizidae with abyssochelae and sigmancistras, most often pedunculate and disciform with a radial skeleton.

#### Remarks

The genus *Abyssocladia* Lévi, 1964 has been synonymized with *Phelloderma* Ridley & Dendy, 1886 by van Soest & Hajdu (2002b) based on a single shared character, i.e. a peculiar isochela with the two frontal alae nearly in contact for which they proposed the term 'abyssochela'. This measure appears unsound and will not be followed here. van Soest & Hajdu (2002b) mistakenly indicated that *Abyssocladia* was monotypic. It actually includes three species: *A. bruuni* Lévi, 1964, known by the type specimen and found again by Koltun (1970); *A. claviformis* Koltun, 1970; and *A. oxeata* Koltun, 1970. These three species, from the deep Pacific, have a thin stalk to which is attached a spherical or disc-shaped body with a radiate skeleton. They share a similar spicule complement, including styles, abyssochelae and sigmancistras to which may be added double bent microxea and subtylostyles. [In the type species, *A. bruuni*, Lévi (1964) reported sigmas, but from his description they are more likely sigmancistras.) By contrast, *Phelloderma radiatum* Ridley & Dendy, 1886, from the deep south-west Atlantic, while having rather similar spiculation, differs considerably in its sessile shape, the presence of oscules on small papillae and a cork-like cortex, suggesting to them (p. 113) that 'In the presence of a distinct cortex, and in the radiate arrangement of its skeleton, this genus approaches the Suberitidae . . .'. The organization of the three species previously described in *Abyssocladia* and which is also found in the four new species described below certainly cannot be assimilated to that of the suberitids. The shape of the isochelae alone cannot justify the merging of *Abyssocladia* with the poorly known, monotypic *Phelloderma*. As presently construed, with seven species including the four new species described below, the genus is well defined and homogeneous, the only exception being *A. nautur* sp. nov., which does not display the disciform pedunculate shape and possibly belongs to an undescribed genus or subgenus.

*Abyssocladia* was first assigned to Mycalidae by Lévi (1964). This assignment is not well justified, as the skeletal organization is different from that of the

Mycalidae (van Soest & Hajdu, 2002a), and the isochelae are rather of the arcuate type. Furthermore, the presence of sigmancistras in all representatives of the genus argues for affinities with Cladorhizidae (see Discussion). It seems more sound temporarily to classify the genus in the Cladorhizidae, although the family appears to be polyphyletic, pending more information before a general assignment of the various genera of the family can be made. The general organization, absence of a visible aquiferous system and microsclere spicule arrangement suggest a carnivorous habit, which is confirmed by the presence of crustacean debris in *A. huitzilopochtli* sp. nov.

#### ABYSSOCLADIA HUITZILOPOCHTLI SP. NOV.

(FIGS 9–11)

#### *Type material*

*Holotype*: NAUTIMATE NM 03-875-15, 21/01/1994, Middle America Trench (off Mexico), 18°17'N, 104°31'W, 3325 m, Muséum National d'Histoire Naturelle, Paris, no. MNHN D JV 85.

#### *Etymology*

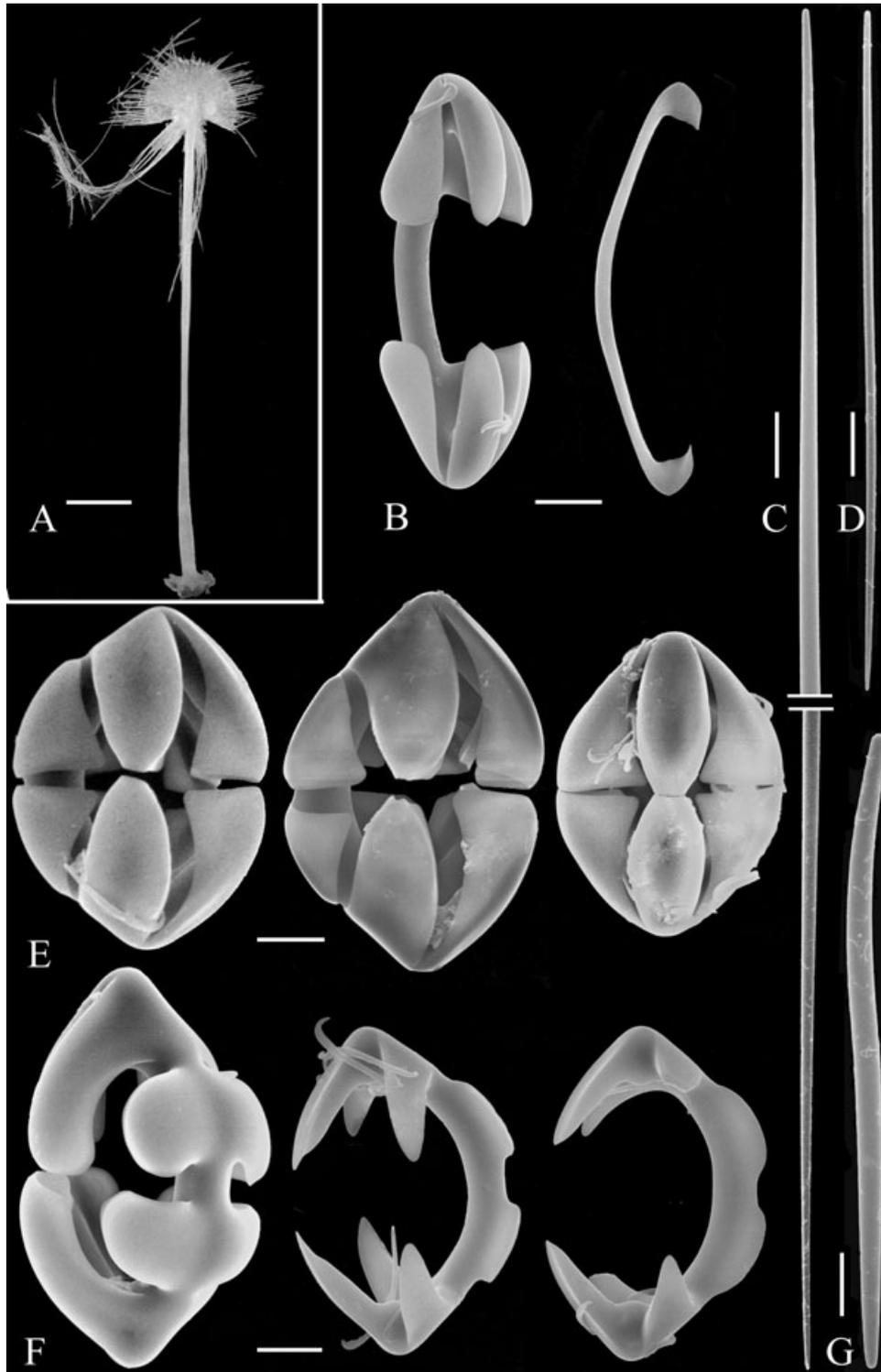
From 'Huitzilopochtli', the Aztecs' bloodthirsty god of the sun. Referring to the sun-like body shape of the sponge suggesting Aztec feather ornaments, and to Mexico off which this carnivorous sponge was collected.

#### *Locality and habitat*

Middle America Trench (off Mexico), 18°17'N, 104°31'W, 3325 m. Collected during NAUTIMATE cruise, dive NM 03 of the manned submersible Nautilie, on brown-green siltstone. No hydrothermal fluid emission was observed during dive NM 03. However, fluid emissions with associated fauna (*Calypptogena* sp., *Escarpia* sp.) were observed 16 km from the collection site, at 2600–3000 m depth.

#### *Description*

A single specimen of a pedunculate sponge consisting of a long thin peduncle and a flattened semicircular body (Fig. 9A). Peduncle 35 mm long, 1 mm thick near the base then varying from 0.3 to 0.6 mm, attached to a small rocky fragment by an enlarged base. Body in shape of a regular flattened disc, 7 mm in diameter and 0.3–0.5 mm thick, with free radiating spicule fascicles protruding from 2 to 4 mm and surrounded by a small amount of living tissue. Two extensions with flesh and spicule fascicles approximately 15 mm long on the lower part of the disc. A denser area, 0.5 mm in



**Figure 9.** *Abyssocladia huitzilopochtli* sp. nov. A, view of the holotype (scale bar: 4.8 mm). B, arcuate isochela 1 and developmental stage (scale bar: 12.4  $\mu$ m). C, head and tip of a substrongyle of the peduncle and of fascicles (scale bar: 95  $\mu$ m). D, small substrongyle (scale bar: 62  $\mu$ m). E, abyssochelae, front view (scale bar: 13  $\mu$ m). F, abyssochelae, dorsal view and developmental stages (scale bar: 13  $\mu$ m). G, substrongyle of the base (scale bar: 66  $\mu$ m).



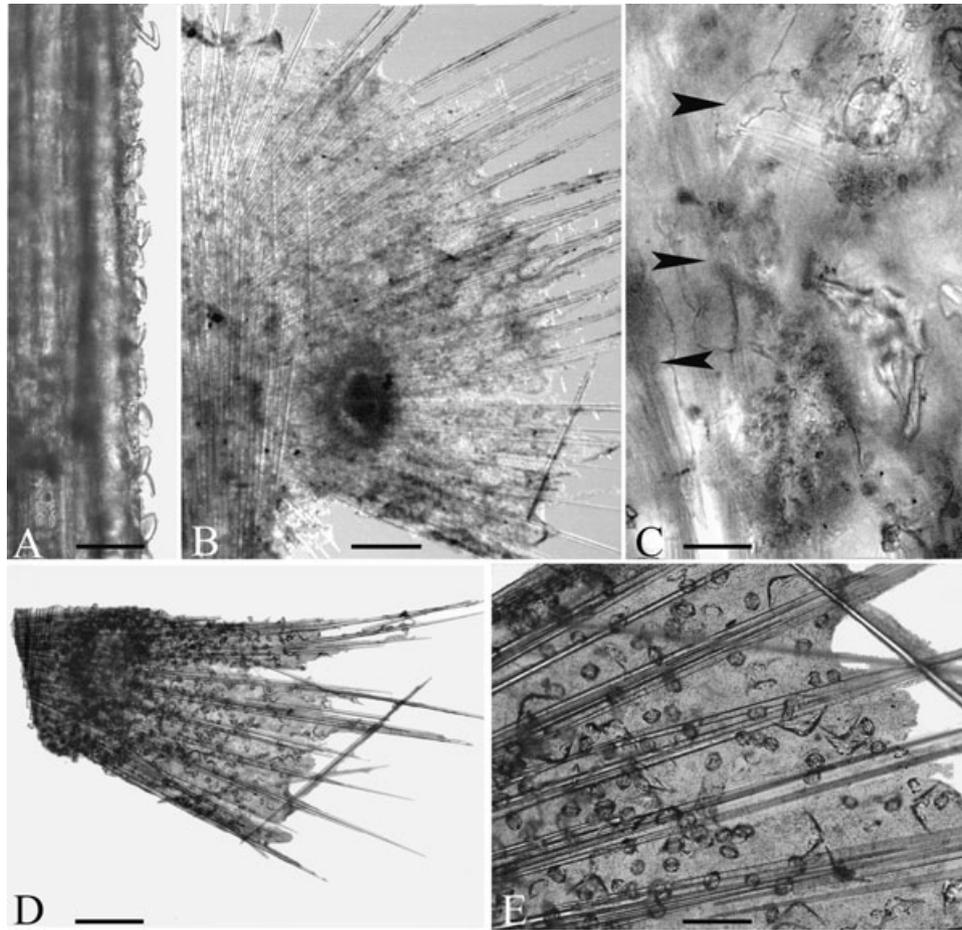
**Figure 10.** *Abyssocladia huitzilopochtli* sp. nov. A, orthancistras and developmental stage (scale bar: 24.5  $\mu$ m). B, sigmancistras 1 and 2 (scale bar: 3  $\mu$ m).

diameter, near the centre of the disc, comprising an unidentified clear mass surrounded by a dense concentration of microscleres, most likely the remains of prey (Fig. 11B, D). Several crustacean appendages included in the disc (Fig. 11C). No cortex, no visible aperture. Colour pure white.

**Skeleton:** peduncle made of an axis of tightly packed, long substrongyles longitudinally arranged, reaching the centre of the disciform body and slightly diverging after the centre. Peduncle with a small amount of living material, entirely covered on the basal two-thirds by isochelae regularly attached by the dorsal surface with the teeth protruding outward (Fig. 11A). On the last third of the peduncle, cover of isochelae progressively replaced by a less dense cover of abyssochelae similarly arranged but more numerous on the two lateral sides. In the body, skeleton of radiating large substrongyles similar to those of the peduncle. Tissue of the body containing rare smaller substrongyles irregularly dispersed, a few isochelae, numerous orthancistras, numerous abyssochelae and extremely abundant sigmancistras (Fig. 11E). Protruding fascicles made of 5–10 megascleres with a few abyssochelae and orthancistras often dorsally attached to the fascicles.

#### *Spicules:*

1. Styles or substrongyles (Fig. 9C) of the peduncle and of the fascicles. Straight, with the two ends nearly equal, fusiform (for instance for a spicule 2450  $\mu$ m long, diameter 30  $\mu$ m in the middle, 10  $\mu$ m at the head and 8  $\mu$ m at the rounded tip). Size 1050–2500  $\times$  15–30  $\mu$ m.
2. Substrongyles (Fig. 9D) dispersed in the flesh and included in the fascicles. Straight, the longer slightly fusiform, with the two ends rounded and nearly equal. Size 260–660  $\times$  5–10  $\mu$ m.
3. Substrongyles (Fig. 9G) of the base. Ends nearly equal, often slightly flexuous, with a few intermediaries with the large fusiform substrongyles. Size 560–750  $\times$  21–30  $\mu$ m.
4. Isochelae 1 (Fig. 9B), arcuate or subpalmate, with lateral alae linked to the shaft along almost their entire length. Front alae ovoid. Developmental stages present in the body, showing a shaft of size similar to that of the mature spicule and more or less developed alae. Size 67–90  $\mu$ m.
5. Isochelae 2, found only on the basal part of the shaft. Same shape as isochelae 1 but smaller. Size 40–55  $\mu$ m.
6. Abyssochelae (Fig. 9E, F) of the terminal part of the shaft and of the body, absent in the distal parts of the filaments. Nearly spherical, with a shaft strongly



**Figure 11.** *Abyssocladia huitzilopochtli* sp. nov. A, peduncle near the base, showing lining by isochelae 1 and 2 (scale bar: 80  $\mu$ m). B, view of a part of the body, with a dense accumulation of microscleres surrounding an inclusion (scale bar: 1 mm). C, crustacean residue in the body (arrowheads); on the right, abyssochela, orthancistras and isochela 1 (scale bar: 55  $\mu$ m). D, section through the area of the body containing a dense inclusion shown in B (scale bar: 0.7 mm). E, section through the body, showing spicule fascicles, numerous abyssochelae, isochelae 1, orthancistras and sigmancistras (scale bar: 220  $\mu$ m).

curved, bearing two large lateral fimbriae roughly triangular, sometimes with a third smaller one in the middle. Lateral alae nearly in contact with the opposite alae, made of a thin lamella folded on the sides. Frontal ala long, nearly in contact with the opposite ala or sometimes bound to it, ovoid or occasionally bifid at the end. Developmental stages present in the body, with more or less developed conical alae and two thickening on the outer side of the shaft. Size 60–80  $\mu$ m long and 40–55  $\mu$ m wide.

7. Orthancistras (Fig. 10A) (new term for a peculiar microsclere spicule, from 'orth', Greek, perpendicular and 'ancistr', Greek, hook; referring to the general shape of the spicule with a roughly right angle between the two branches), found in the body and on the filaments. Symmetrical spicule arising from a rod

curved in the middle at roughly right angles and ending in two conical tips, on which develop lateral lamellae or expansions. Lamellae curved towards each other, increasing in width from the tip to the middle of the rod, cut in two hook-like spines. Two or more rarely three lateral expansions, roughly ovoid, near the middle of the rod. Immature spicules rather common in the body, the younger somewhat similar to an angular toxa, with a smooth shaft of irregular thickness, the later stages with more or less developed lateral lamellae or expansions. Size 150–195  $\mu$ m.

8. Sigmancistras 1 (Fig. 10B), extremely abundant everywhere. Contorted with the small end in a perpendicular plane, without notch. Size 20–24  $\mu$ m.

9. Sigmancistras 2 (Fig. 10B), extremely abundant everywhere. Contorted but with a smaller angle

than sigmancistras 1, with a well-marked notch. Size 11–12  $\mu\text{m}$ .

10. Microxeas, probably foreign, rare and found on a single slide, straight or slightly curved, the thicker sometimes fusiform. Size 30–95  $\times$  0.3–1  $\mu\text{m}$ .

#### Remarks

The sponge is more complete than the other species of the genus described below. It remains uncertain, however, if the radiating processes around the disc are complete or if they were similar in the live specimen to the two longer filaments of the base of the disc. The species is remarkable for its sophisticated organization, with a precise arrangement of the microscleres in the diverse parts of the body. The new type of spicule for which the term 'orthancistra' is proposed probably does not derive from chelae, as the tips of the juvenile spicules do not show enlargement, and the spicule seems to derive from a smooth angulate rod on which appear lateral expansions. Although their angulate shape is reminiscent of that of toxas, they do not appear to derive from this type of microsclere, which is rare in *Mycalina*.

The presence of crustacean debris in the body clearly indicates a carnivorous habit, which in the other species of *Abyssocladia* could be only inferred from the organization. The presence of a cover of isochelae along the peduncle, not found in the other *Abyssocladia* and more generally in other pedunculate carnivorous sponges, suggests that the peduncle plays a role in the capture of prey.

#### *ABYSSOCLADIA INFLATA* SP. NOV.

(FIGS 12, 13)

#### Type material

*Holotype*: PITO PI 17, 02/1993, East Pacific Rise, Easter microplate near Easter Island, 24°14.85'S, 115°39.70'W, 3142 m, Muséum National d'Histoire Naturelle, Paris, no. MNHN D JV 86. Spicule and skeleton slides only.

#### Etymology

From '*inflatus*', Latin, adj. swollen. Referring to the shape of the shaft of isochelae 1.

#### Locality and habitat

East Pacific Rise, Easter microplate, west of Eastern Island on the Terevaka fault, 24°14.85'S, 115°39.70'W, 3142 m. Collected during PITO cruise, dive PI 17 of the manned submersible *Nautile*, 02/1993 (Segonzac *et al.*, 1997; Naar *et al.*, 2004). Attached to a piece of

rock from a vertical cliff, with hanging sediment and very poor macrofauna, 423 km distant from the main hydrothermal venting of Pito Seamount.

#### Description

A single specimen of a small sponge (Figs 12A, 13) consisting of a thin peduncle 5 mm long, bearing a disciform body, 3.5 mm in diameter. Peduncle very thin (0.2–0.3  $\mu\text{m}$  in diameter), devoid of fixation base, made of longitudinally arranged fusiform styles, with extremely reduced living tissue. Body circular, flattened, with a skeleton of radiating styles protruding from the surface by 0.2–0.4  $\mu\text{m}$  (Fig. 13). No cortex present. Acanthomicroxeas and isochelae irregularly dispersed in the body, mostly near the surface. Consistency soft, highly fragile after preservation. Colour white. No visible aperture and aquiferous system.

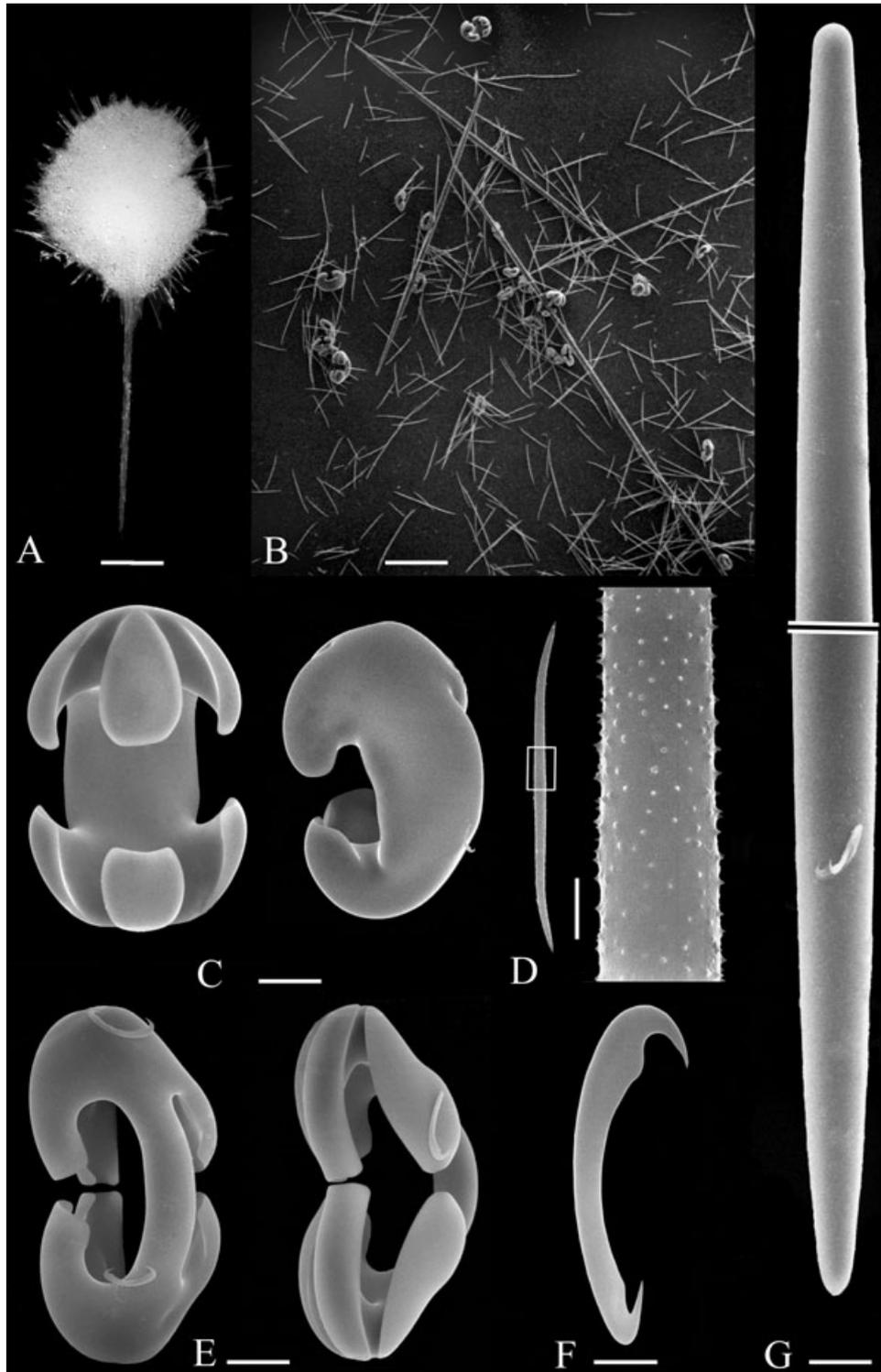
#### Spicules:

1. Styles of the peduncle and the radiating skeleton of the body (Fig. 12B, G), straight, with a short acerate tip, strongly fusiform (for instance, for a spicule 1250  $\mu\text{m}$  long, head 7  $\mu\text{m}$  and middle 22  $\mu\text{m}$ , or for a spicule 1500  $\mu\text{m}$  long, head 7  $\mu\text{m}$  and middle 26  $\mu\text{m}$ ). Size 1075–1800  $\times$  21–33  $\mu\text{m}$  in the middle.
2. Acanthomicroxeas (Fig. 12B, D), slightly fusiform, most often with a marked curve at both ends, some of the larger ones nearly straight. Surface finely rugose, with tiny conical spines 0.15  $\mu\text{m}$  high. Size 130–350  $\times$  3–5  $\mu\text{m}$ .
3. Arcuate isochelae (Fig. 12C), very stout. Shaft strongly curved, very thick, with a thin axial canal. Front alae ovoid, curved around the edges. Lateral alae large, flattened, partially attached to the shaft. Size 140–150  $\mu\text{m}$ , shaft 25–50  $\mu\text{m}$  in diameter.
4. Abyssochelae (Fig. 12E). Shaft strongly curved. Front alae long, curved, nearly in contact with the opposite ala, made of a thin lamella curved on the lateral sides and in the shape of a hollow chisel, abruptly cut at the end. Lateral alae partially attached to the shaft, more or less curved around half the free length. Immature spicules with a curved shaft and poorly developed alae. Size 80–100  $\mu\text{m}$ , shaft 6–11  $\mu\text{m}$  in diameter.
5. Sigmancistra (Fig. 12F), very numerous at the surface of the body, with a well-marked notch and acerate points. Size 15–18  $\mu\text{m}$ .

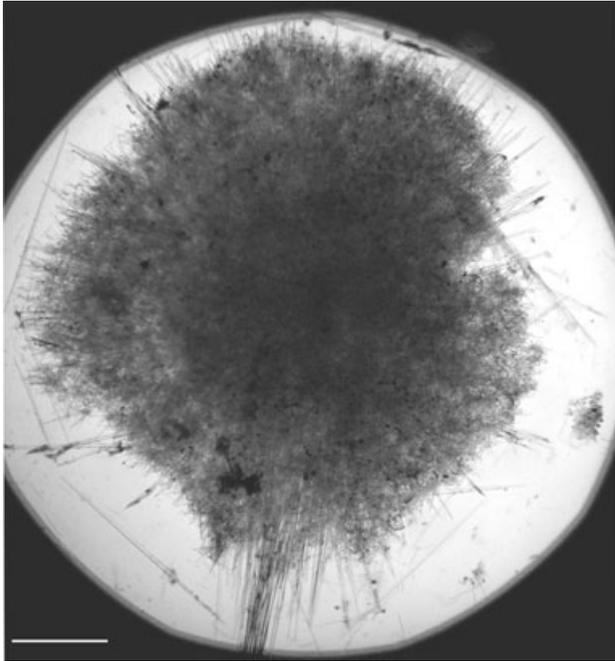
#### Remarks

This tiny sponge, very fragile, was entirely used in spicule and skeleton mounts.

The acanthomicroxeas are of relatively large size for microscleres. Although it has not been possible to observe their arrangement thoroughly owing to the



**Figure 12.** *Abyssocladia inflata* sp. nov. A, view of the holotype (scale bar: 1.4 mm). B, general view of the spicules (scale bar: 260  $\mu$ m). C, isochelae 1 (scale bar: 27  $\mu$ m). D, acanthomicroxea (scale bars: 25  $\mu$ m and 2.5  $\mu$ m). E, isochelae 2 (abyssochelae) (scale bar: 17  $\mu$ m). F, sigmancistra (scale bar: 3.3  $\mu$ m). G, style (scale bar: 18  $\mu$ m).



**Figure 13.** *Abyssocladia inflata* sp. nov. Microphotograph of the body and part of the peduncle (scale bar: 780  $\mu$ m).

size and the fragility of the specimen, they appear to have no apparent function in the main skeleton and are thus considered here as microscleres.

The new species resembles *A. oxedata* Koltun, 1970 in the presence of double bent microxeas of similar size. Koltun did not indicate a spination of these spicules, but this is visible only under SEM. *Abyssocladia oxedata* differs, however, by larger styles, absence of stout isochelae, and sigma 35  $\mu$ m long instead of small sigmancistra. The other species of the genus, *A. bruuni* Lévi, 1964, *A. claviformis* Koltun, 1970, *A. huitzilopochtli* sp. nov., *A. dominalba* sp. nov. and *A. naudur* sp. nov., do not have microxeas.

**ABYSSOCLADIA DOMINALBA SP. NOV.**

(FIG. 14)

*Type material*

*Holotype*: STARMER II, PL13, 08/07/1989, 16°59.50'S, 173°55.47'W, North-Fijian back-arc Basin, site White Lady, 1997 m. Muséum National d'Histoire Naturelle, Paris, no. MNHN D JV 87.

*Paratype*: STARMER II, PL 13, 08/07/1989, 16°59.50'S, 173°55.47'W, North-Fijian back-arc Basin, site White Lady, 1997 m. Muséum National d'Histoire Naturelle, Paris, no. MNHN D JV 88.

The two type specimens, small and fragile, have been permanently mounted in Araldite on a microscopic slide.

*Etymology*

From 'domina', Latin, noun fem. lady, sovereign, and *album*, Latin, adj. white. Referring to the active hydrothermal site 'White Lady' in the vicinity of which the sponge was living.

*Locality and habitat*

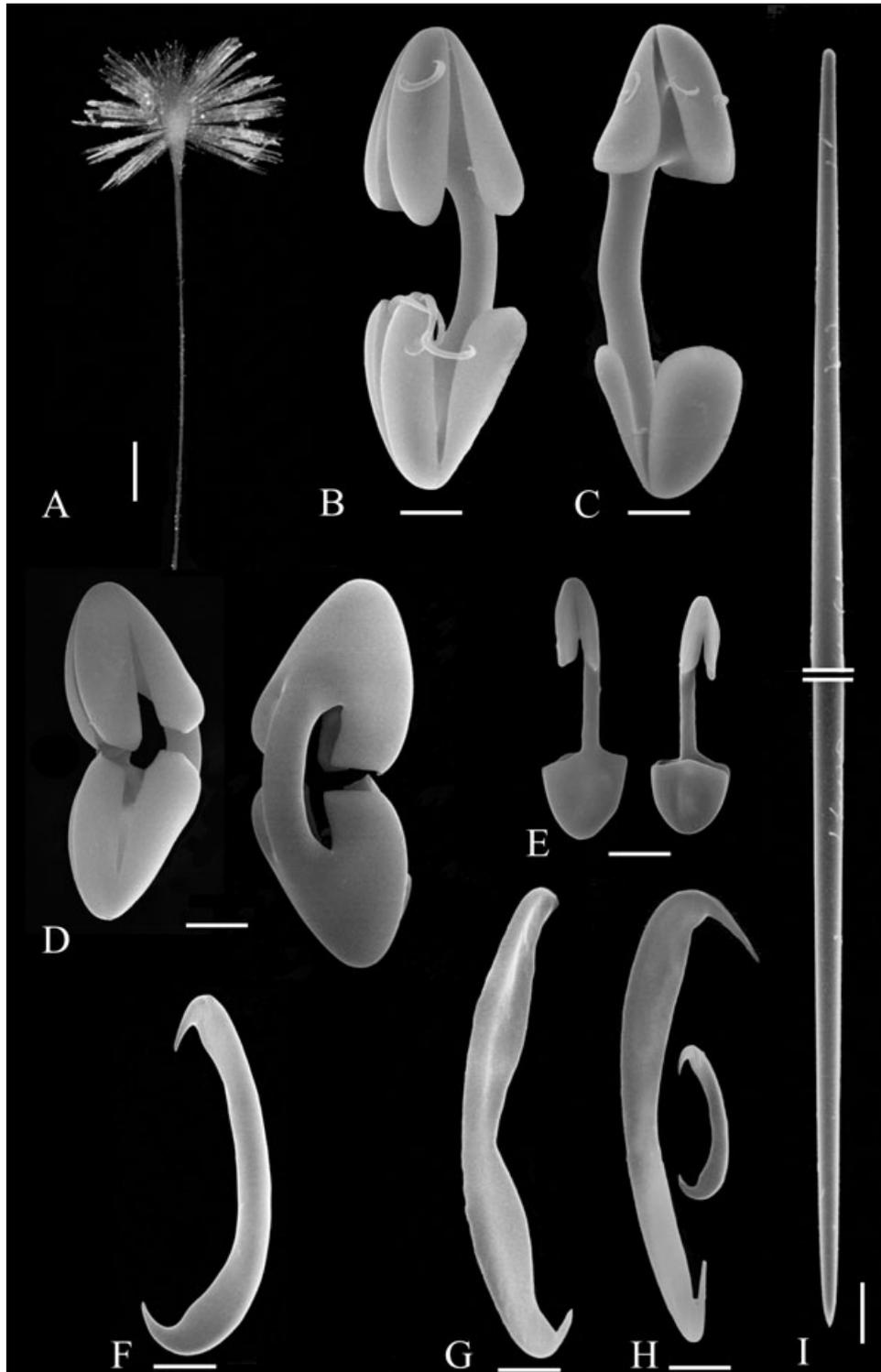
North-Fijian back-arc Basin, site White Lady, 16°59.50'S, 173°55.47'W, 1997 m. Collected during STARMER II cruise (Auzende *et al.*, 1989; Desbryères *et al.*, 1994), dive PL 13 (08/07/1989) of the manned submersible Nautilie, on a dead smoker near of the active site White Lady. Water temperature 2.6 °C at the site of collection.

*Description*

Two small pedunculate sponges (Fig. 14A), consisting of a thin peduncle bearing an ovoid or subspherical body with dense spicular fascicles laterally radiating. Body 3.5  $\times$  1.5 mm, with radiating fascicles up to 5 mm long. Peduncle 25–28 mm long, without attachment base, 0.3–0.5 mm in diameter, made of longitudinally arranged long fusiform styles. Living tissue poorly preserved, nearly absent in the paratype, containing numerous microscleres. Radiating fascicles made of fusiform styles and of smaller styles with the tip outwardly directed. Consistency very fragile after preservation. Colour white. No visible aperture or aquiferous system, no cortex.

*Spicules*:

1. Styles of the radiating fascicles and of the peduncle (Fig. 14I), straight, with two ill-defined categories. In the peduncle, spicules large and fusiform, with a rather blunt tip. In the body and radiating fascicles, smaller spicules, less fusiform and with an acerate short tip, in addition to styles of the peduncle type. Size 620–2500  $\times$  7–35  $\mu$ m.
2. Arcuate isochelae (Fig. 14B, C). Shaft curved. Alae ovoid, rather short. Size 80–170  $\mu$ m, shaft 8  $\mu$ m in diameter.
3. Abyssochelae (Fig. 14D). Shaft strongly curved. Front alae long, nearly in contact with the opposite ala, laterally curved, abruptly cut at the end. Lateral alae long, laterally curved. Size 40–45  $\mu$ m.
4. Anisochelae (Fig. 14E), moderately abundant, generally twisted, the plane of the two ends varying from a few degrees to 180°. Shaft straight. One end tridentate with the lateral alae cut away from the shaft and



**Figure 14.** *Abyssocladia dominalba* sp. nov. A, view of the holotype (scale bar: 3.4 mm). B, arcuate isochela 1 (scale bar: 12  $\mu$ m). C, arcuate isochela 1 (scale bar: 22  $\mu$ m). D, arcuate isochelae 2 (abyssochelae) (scale bar: 7.4  $\mu$ m). E, anisochelae (scale bar: 2.5  $\mu$ m). F, sigmancistra 2 (scale bar: 2.2  $\mu$ m). G, sigmancistra 1 (scale bar: 4.4  $\mu$ m). H, sigmancistras 1 and 2 (scale bar: 4.4  $\mu$ m). I, style (scale bar: 47  $\mu$ m).

the frontal ala bifid, the other end with fused alae. Size 9.5–11 µm.

5. *Sigmancistra* 1 (Fig. 14G, H), moderately abundant, most of them with the shaft laterally thickened in a lamella with a central depression, a few with the same shape as *sigmancistra* 2 but larger. Size 30–40 µm.

6. *Sigmancistra* 2 (Fig. 14F, H), very abundant. Shaft slightly contorted, the large end with a notch. Size 9.5–12.5 µm.

#### Remarks

This sponge has the same morphology and general organization as the representatives of the genus *Abyssocladia*, and its spiculation includes abyssochelae. It differs from the other species of the genus in the microscleres, especially in the presence of tiny anisochelae. These spicules are remarkable for the difference in the two ends, one being palmate and the other arcuate. Anisochelae are known in a member of the Mycalidae, *Anomomycale* Topsent, 1924, but they are arcuate, whereas in the new species the anisochelae are of an unusual type, both arcuate and palmate. The presence of anisochelae in otherwise typical representatives of *Abyssocladia* is one of the reasons temporarily to classify the genus within the Cladorhizidae, possibly indicating affinities with the Mycalidae as already found in *Asbestopluma*.

#### ABYSSOCLADIA NAUDUR SP. NOV.

(FIGS 15, 16)

#### Type material

*Holotype*: NAUDUR ND 5 (7-1B), 10/12/1993, 17°23.11'S, 113°11.60'W, 2581 m. Muséum National d'Histoire Naturelle, Paris, no. MNHN D JV 89.

*Paratypes*: NAUDUR ND 5 (7-1B), 10/12/1993, 17°23.11'S, 113°11.60'W, 2581 m, approximately 15 specimens or fragments, Muséum National d'Histoire Naturelle, Paris, no. MNHN D JV 90. NAUDUR ND 15 (4-1B), 20/12/1993, 18°15.90'S, 113°22.08 W, 2689 m, one specimen. Muséum National d'Histoire Naturelle, Paris, no. MNHN D JV 91.

#### Etymology

From the NAUDUR cruise ('NAUtile Dorsale Ultra Rapide') of Ifremer.

#### Locality and habitat

East Pacific Rise, North of Easter Island. NAUDUR ND 5, 17°23.11'S, 113°11.60'W, 10/12/1993, 2581 m, on a dead smoker. The sample was collected from the

top of the highest chimney (up to 6 m high) of an inactive site, a few metres from some active black smokers with a relatively dense population of the pink sea anemone *Chondrophellia* sp. The sponges were attached to the vertical face of the chimney, made of sulfide deposits, which also bears the sponge *Cladorhiza segonzaci* sp. nov. (see above), some hydroids and about 20 specimens of a small white sea anemone. NAUDUR ND 6, 17°24.85'S, 113°12.15'W, 11/12/1993, 2580 m, in a rich assemblage of Vesicomidae clams *Calypptogena*, mytilids *Bathymodiolus*, stalked barnacles *Neolepas*, etc. NAUDUR ND 15, 20/12/1993, 18°15.90'S, 113°22.08 W, 2689 m, on a dead chimney.

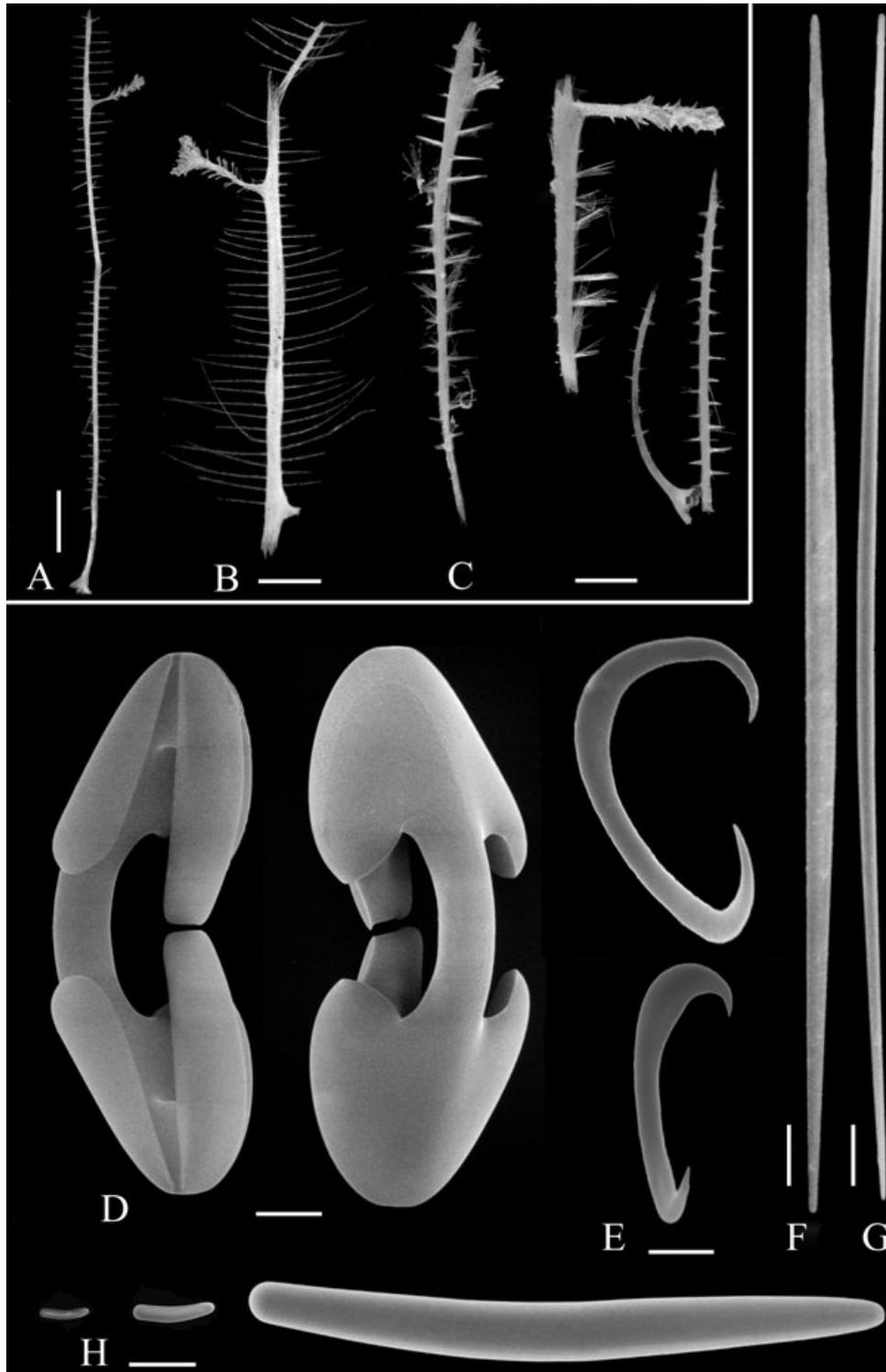
#### Description

Approximately 20 specimens or fragments of a small erect sponge (Fig. 15A–C), attached on a minute solid substratum by an enlarged base 2–3 mm in diameter, forming a slender, flattened spicular axis with numerous lateral filaments or processes, frequently with a bud-like larger branching process. Holotype 40 mm in total length, with a lateral bud and filaments 1.4 mm in maximum length. Paratypes more or less complete specimens, some with well-preserved thin filaments (Fig. 15B) up to 6 mm long, 170–200 µm in diameter at the base and one or two spicule thick at the end, others with only the base of the filaments. Filaments regularly arranged perpendicularly in two lateral rows along the axis, with a spacing of 0.3–0.6 mm, alternating on each side. Bud-like processes perpendicular or slightly oblique to the main axis, with a few short lateral processes on their axis, thickened at the end. No visible aquiferous system. Colour yellowish grey to clear brown.

*Skeleton*: Main axis of large fusiform styles longitudinally arranged, spirally twisted in the basal portion where the axis is lined by substrongyles. Axis of the filaments slightly conical at the base, with the styles anchored by their head and the point outwardly directed, entirely crossing the stem (Fig. 16), reduced to one or two styles near their end. Living tissue poorly preserved, containing numerous *sigmancistra*. Best preserved zones of the stem and of the base of the filaments with a continuous lining of isochelae, generally with the alae outwardly directed and the shaft lying parallel on the axis.

#### Spicules:

1. Styles or substrongyles of the main axis (Fig. 15F), straight, the larger strongly fusiform with a blunt point nearly similar to the head. Size 700–1600 × 10–37 µm.
2. Styles of the lateral branches (Fig. 15G), straight, the larger slightly fusiform, with a short acerate point. Size 330–1000 × 5–15 µm.



**Figure 15.** *Abyssocladia naudur* sp. nov. A, view of the holotype (scale bar: 4.3 mm). B, part of a paratype (scale bar: 3.4 mm). C, paratypes (scale bar: 2 mm). D, isochelae (scale bar: 5.5  $\mu$ m). E, sigmancistra 1 and 2 (scale bar: 1.4  $\mu$ m). F, style of the axis (scale bar: 64  $\mu$ m). G, styles of the lateral processes (scale bar: 40  $\mu$ m). H, diverse sizes of substrongyles of the base (scale bar: 33.4  $\mu$ m).

3. Styles, substrongyles or strongyles (Fig. 15H) from the base and from the coating of the main axis, very variable in size. The smaller located at the fixation base, slightly curved, sometimes with a double bend, with equal ends. The larger located along the basal part of the axis, often a little flexuous, fusiform, with unequal ends. Size  $30\text{--}825 \times 8\text{--}30 \mu\text{m}$ .

4. Abyssochelae (Fig. 15D) with a curved shaft approximately  $5 \mu\text{m}$  in diameter. Frontal ala roughly parallelepipedal, long, nearly in contact with the opposite frontal ala, with a broadly quadrangular section, abruptly cut at the end. Lateral alae large, linked to the shaft along almost their entire length. Size  $48\text{--}72 \mu\text{m}$ , most between  $60$  and  $65 \mu\text{m}$ , smaller in one specimen ( $30\text{--}65 \mu\text{m}$ ).

5. Sigmancistra 1 (Fig. 15E), with a slightly enlarged shaft. Size  $15\text{--}19 \mu\text{m}$ . Smaller sigma in one specimen, in which the size is only  $6.5\text{--}9.5 \times 1 \mu\text{m}$ .

6. Sigmancistra 2 (Fig. 15E), very abundant, without notch. Size  $5\text{--}8 \mu\text{m}$ .

#### Remarks

The sponge is very fragile, and several specimens were broken upon examination in the laboratory. Most specimens have the filaments reduced to short lateral processes. It cannot be separated with certainty from *Cladorhiza segonzaci* sp. nov. on the underwater pictures taken *in situ* after collection (Fig. 17F).

The sponge closely resembles *Cladorhiza segonzaci* from the same sample, and the two sponges were confused during the preliminary sorting operation and in the first spicule preparations. There are, however, some differences in gross morphology, which have been given in the description of *C. segonzaci*.

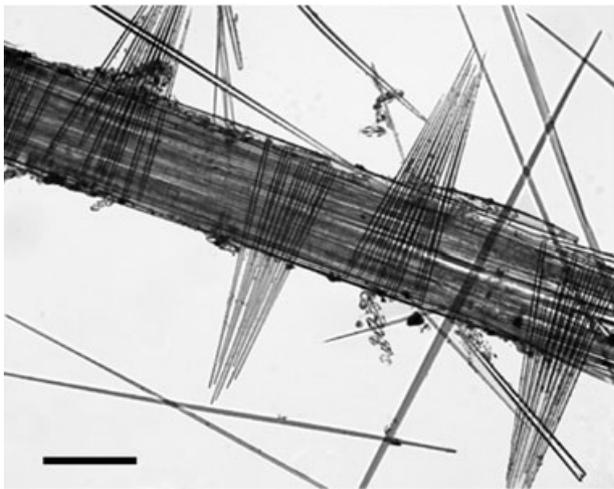
The spicule characters appear rather constant in the 20 available specimens or fragments. One specimen, however, differs slightly from the holotype and the other paratypes in smaller isochelae and small sigmas,  $6.5\text{--}9.5 \mu\text{m}$ , instead of sigmancistras,  $15\text{--}19 \mu\text{m}$ .

This species is classified in *Abyssocladia* as here redefined based on its spiculation, including abyssochelae. However, it does not display the typical pedunculate, disciform shape characteristic of the genus, but rather closely resembles the shape of some *Cladorhiza* or *Asbestopluma*. Furthermore, the abyssochelae have their lateral alae nearly palmate. Its inclusion in the genus is thus made with reservation and may be temporary.

## DISCUSSION

### FEEDING HABIT

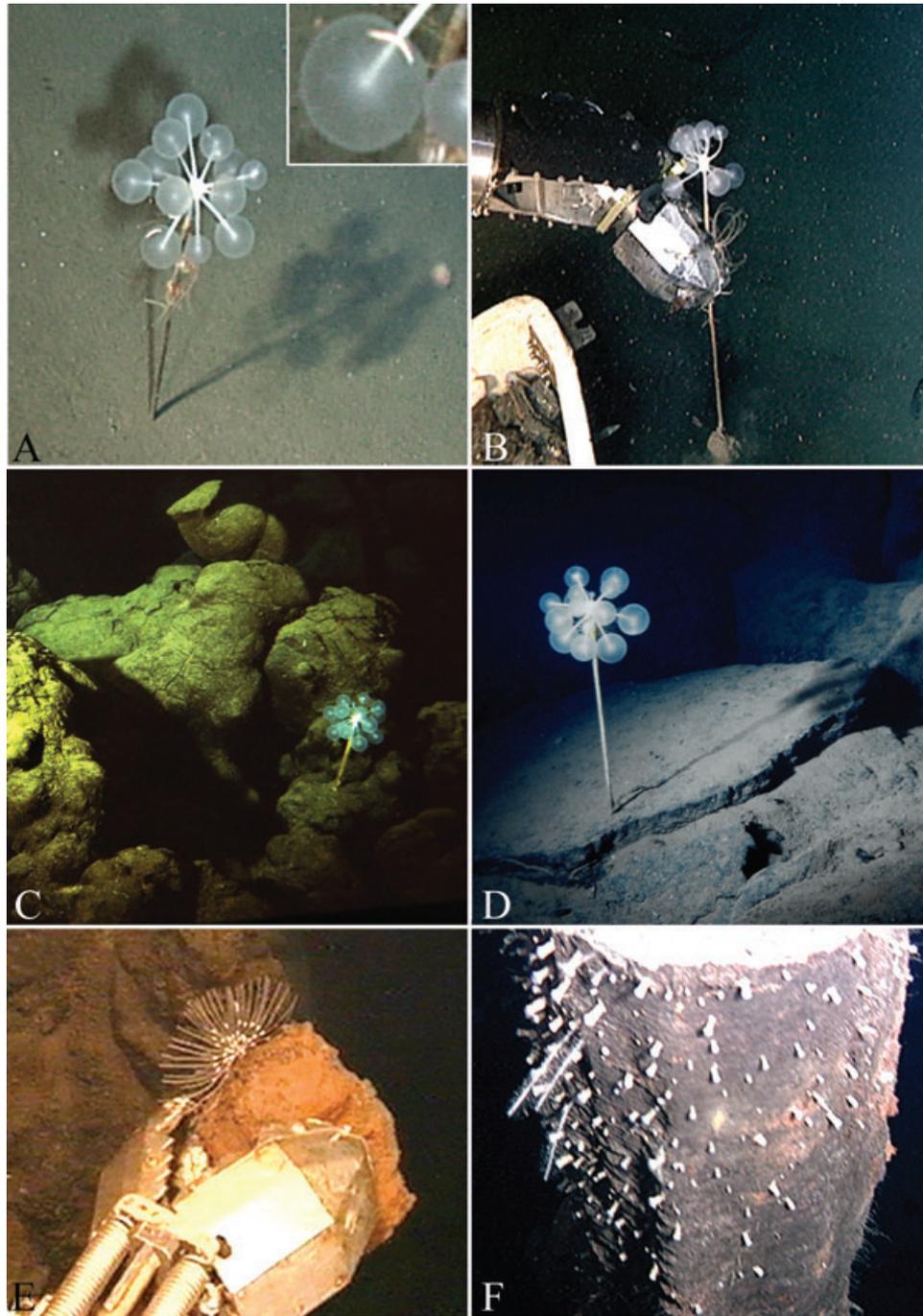
The carnivorous habit of these new sponges is indisputable in the case of the two *Chondrocladia* ssp. This feeding habit has been clearly demonstrated in



**Figure 16.** *Abyssocladia naudur* sp. nov. Microphotograph of the skeleton (scale bar:  $220 \mu\text{m}$ ).

### IDENTIFICATION KEY OF *ABYSSOCLADIA*

- |  |                                    |
|--|------------------------------------|
| 1. Body semispherical or disciform, attached to a thin stem . . . . .  | 2                                  |
| Erect main axis bearing lateral filaments regularly arranged . . . . . | <i>A. naudur</i> sp. nov.          |
| 2. Without rugose small oxeas curved at both end . . . . .             | 3                                  |
| With double-bend oxeas . . . . .                                       | 4                                  |
| 3. With small anisochelae . . . . .                                    | <i>A. dominalba</i> sp. nov.       |
| Without small anisochelae . . . . .                                    | 5                                  |
| 4. With isochelae with thick shaft . . . . .                           | <i>A. inflata</i> sp. nov.         |
| Without isochelae with thick shaft . . . . .                           | <i>A. oxeata</i> Koltun            |
| 5. With peculiar orthancistras . . . . .                               | <i>A. huitzilopochtli</i> sp. nov. |
| Without orthancistras . . . . .  | 6                                  |
| 6. With additional tylostyles . . . . .                                | <i>A. claviformis</i> Koltun       |
| Without additional tylostyles . . . . .                                | <i>A. bruuni</i> Lévi              |



**Figure 17.** A, *Chondrocladia lampadiglobus* sp. nov., holotype, 2714 m (Ifremer/Naudur). Inset: unidentified worm gliding on the lower left sphere of A, changing position during the video sequence. B, *C. lampadiglobus*, collection of the holotype by the arm of 'Nautile' submersible (Ifremer/Naudur). C, presumed *C. lampadiglobus*, GEOCYARISE 3 (CY 30), 2622 m, 12°54'N, 103°58'W (Ifremer/Geocyarize 3). D, presumed *C. lampadiglobus*, GEOCYARISE 1 (CY 07), 2623 m (Ifremer/Geocyarize 1). E, collection of *Abyssocladia formosa* sp. nov. by the arm of 'Nautile' submersible, 1997 m (Ifremer/Starmer 1). F, three presumed *Cladorhiza segonzaci* sp. nov. on a dead chimney on the tip of which was attached *C. segonzaci* and *Abyssocladia naudur* sp. nov. (Ifremer/Naudur).

*C. gigantea* (Hansen, 1885) (Kübler & Barthel, 1999), which has a general organization similar to that of the two new species described here. Furthermore, these new species display fragments of crustaceans in the process of digestion on their bulges. The evidence is less absolute for the other species, although their erect, symmetrical morphology, their general organization and the absence of a visible aquiferous system make such a feeding habit highly likely. This presumption is reinforced by the definite presence of crustacean debris in *Abyssocladia huitzilopochtli* (Fig. 11C). The arrangement of the diverse hook-like microscleres, able efficiently to capture the setae or thin appendages of crustaceans and of other hairy invertebrates, is generally less regular than in the certainly carnivorous *Asbestopluma hypogea* Vacelet & Boury-Esnault, 1996 (Vacelet & Boury-Esnault, 1996; Vacelet & Duport, 2004), which has been studied from well-preserved samples. This is most probably due to the poor preservation of the present specimens, which were collected near 3000 m depth in cold water and brought to the surface tropical water. The absence of visible prey on most of the studied specimens is not surprising, considering that these sponges do not eat frequently in the deep sea, and also that most of the fragile lateral filaments on which the prey are likely to have been lost.

#### ECOLOGY

It is rather difficult to determine whether these new sponges are directly linked to the hydrothermal vents. None was found in the rich animal communities that thrive in the immediate environment of the active smokers, and thus they cannot be considered as true members of the hydrothermal fauna (with the possible exception of *Cladorhiza segonzaci* and *Abyssocladia naudur*, which have been collected very near an active chimney). They rather occur at some distance from the active vents, in the outer rim where the sessile macrofauna is still poor but more stable (Desbruyères *et al.*, 1994; Geistdoerfer *et al.*, 1995) and includes a few filter feeders such as hexactinellid sponges. The remarkable *Chondrocladia lampadiglobus*, for instance, which is relatively common around the active sites, has never been observed in the area where a gradual increase in the population of the sea anemone *Chondrophellia* sp. foreshadows the proximity of the active smokers. As far as can be deduced from their distribution, the sponges described in the present study most probably do not depend directly on chemoautolithotrophic symbioses, such as those described for *Cladorhiza methanophila* Vacelet & Boury-Esnault, 2002 in the Barbados Trench, but may benefit from a general organic enrichment around the hydrothermal sites. It must be kept in

mind that these sponges were collected during dives aimed at the study of active sites and that their abundance or even presence at greater distances from hydrothermal zones has not been investigated by direct study from submersibles. It is unclear at present whether these species benefit from a general distant enrichment around the active vents or if they belong to a 'non-vent' fauna, taking advantage only of the presence of relatively recent basaltic lava issued at rapidly spreading areas and still feebly covered by sediment. More investigations are needed in this regard.

#### DIVERSITY

The diversity of deep Pacific carnivorous sponges appears remarkable. Lévi (1964), Koltun (1970) and several other authors have described a number of cladorhizids from various locations in the deep Pacific. None of these species was found in the present investigation, illustrating our present considerable underestimation of the biodiversity of the sponge fauna of the deep ocean. The uniqueness of the present collection can be explained by the fact that, unlike in previous studies, the cruises focused on areas of hydrothermal activity, frequently including solid substrata which are rare and difficult to sample in the deep sea, and have been conducted by means of manned submersibles instead of blind dredging or trawling. It must be emphasized that, except for the *Chondrocladia* spp. and *Asbestopluma formosa*, all the specimens are too small to be observed from the manned submersibles without particular attention, given that most of the scientists on board were geologists. Most specimens, sorted on board from rock samples collected for geological purposes, were collected by chance. Such samples certainly represent only a small fraction of the real sponge assemblages.

Most of the new species are represented by a single specimen, giving no indication of the possible variability in morphology and spicule characters. However, *Cladorhiza segonzaci* and *Abyssocladia naudur*, which were studied on several specimens from the same rock sample, display a rather low variation in spiculation (only one paratype of *C. segonzaci* differs by the apparent absence of sigmancistras, rare in the other specimens). The two specimens of *Asbestopluma agglutinans*, collected 557 km apart, also display low variability in morphology and spiculation. The case of *Chondrocladia lampadiglobus* is more puzzling. Numerous specimens of similar morphology have been observed in a large area from 23°S to 13°N of the East Pacific Rise, but only two were available for spicule study, and they show some differences, suggesting either that there are several species or that *C. lampadiglobus* has a somewhat variable spicula-

tion. More material of this remarkable species is needed.

#### CLASSIFICATION

It appears likely that most of the sponges currently classified in the Cladorhizidae, but also some other poecilosclerids with an arborescent, symmetrical shape and apparently devoid of an aquiferous system, actually have a carnivorous habit. Crustacean debris has been observed on diverse deep-sea *Cladorhiza* spp. Outside the Cladorhizidae, the morphology suggests that deep-sea sponges such as representatives of *Euchelipluma* Topsent, 1909, with a pinnate shape and in which the lateral filaments are covered by isochelae and placochelae forming a regular cover with the alae outwardly directed, are carnivorous. Indeed, according to unpublished observations, some specimens of *E. pristina* Topsent, 1909 have crustacean debris on their lateral filaments. Having typical placochelae, *Euchelipluma* species appear to be indisputable members of the Guitarridae (Uriz & Carballo, 2001; Hajdu & Lerner, 2002). This makes it evident that carnivory in sponges is not restricted to the various genera of the Cladorhizidae, but has been developed in several other evolutionary lines of the Poecilosclerida. Other examples could be *Esperiopsis symmetrica* Dendy & Row, 1886 and *Esperiopsis desmophora* Hooper & Lévi, 1989, deep-sea poecilosclerids in which shape and organization are highly suggestive of carnivory. Incidentally, the last example may suggest that such a feeding habit in sponges dates back to the Ordovician, given the similarities between *E. desmophora* and the Ordovician sponge *Saccospongia baccata* Bassler (Hooper & Lévi, 1989). The family Cladorhizidae as currently defined, with genera displaying various microsclere complements, is most likely polyphyletic and appears to include diverse adaptations to this deep-sea feeding habit (Hajdu & Vacelet, 2002). The addition to the Cladorhizidae of the genus *Abyssocladia*, as proposed here, increases the heterogeneity of the family, and it is evident that the diverse genera need to be classified in a more phylogenetic way. The presence of anisochelae in *Asbestopluma* suggests relationships with the Mycalidae. However, the possible affinities of the genera of Cladorhizidae with other families are not at present clear, and it seems preferable temporarily to maintain the Cladorhizidae, as proposed by Hajdu & Vacelet (2002), pending more information on the morphology and molecular characters of these poorly known deep-sea sponges. Two characters that are rather uncommon in Demosponges but which are shared by many of these poecilosclerids with an erect, symmetrical, often pinnate shape and a likely carnivorous habit are interesting to consider in this context.

First, several species have an outer coat of special spicules, especially developed on the stem and near the base. These spicules could be strongyles, tylostyles, microtylostyles or even monocrepid desmas in the case of *E. desmophora* and *A. (Helophloeina) stylivarians*. The presence of this spicule coat is probably a homoplasy, linked to the need for stem reinforcement in such thin, erect sponges, and is probably without any phylogenetic significance.

Secondly, sigmancistras are found in many of these sponges. True sigmancistras, which have been sometimes confused with sigmas, are rather uncommon in the Poecilosclerida. They are restricted to two families, Cladorhizidae and Guitarridae. In the Cladorhizidae as currently defined, they occur in all the four genera, but are not present in all species. Sigmancistras are reported for only two *Asbestopluma* spp. and four *Chondrocladia* spp., but their occurrence is more frequent in *Cladorhiza* and is general in *Abyssocladia*. In the Guitarridae, sigmancistras are found only in *Euchelipluma*, i.e. representatives of the family with a probably carnivorous habit. This character may be considered as a symplesiomorphy of the Cladorhizidae and Guitarridae, although has been lost in several of them.

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