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Esperiopsis koltuni sp. nov. (Demospongiae: Poecilosclerida: Esperiopsidae), a carnivorous sponge from deep water of the Sea of Okhotsk (North Pacific)

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Esperiopsis koltuni, a new species of the sponge family Esperiopsidae, is described from deep water of the Sea of Okhotsk. The new species has a unique growth form: there is a basal plate with radiating cylindrical branches, whose oval flat distal parts bear filament-like outgrowths. Megascleres are arranged differently in the main part of branches and in their distal flat parts. The dermal membrane contains isochelae with protruding alae and abundant sigmancistras. Microscleres are represented by large anchorate spatuliferous isochelae, small isochelae, sigmas and sigmancistras. *Esperiopsis koltuni* sp. nov. is hermaphroditic, with parenchymella larva. The larval skeleton consists only of sigmas and sigmancistras. *Esperiopsis koltuni* sp. nov. can be easily distinguished from other *Esperiopsis* species by dimensions and combination of spicule types. In particular, it is the only species in the genus with three different size categories of styles. The new species lacks the aquiferous system, has a characteristic body plan with symmetrical lateral expansions, an unusual arrangement of microscleres in the dermal membrane and true sigmancistras. Moreover, prey capture by a filament-like outgrowth of the flat distal part was observed. All of these characteristics indicate that *Esperiopsis koltuni* sp. nov. is a carnivorous sponge.

INTRODUCTION

The family Esperiopsidae, introduced by Hentschel in 1923, currently comprises 43 valid species found at depths between 5 and 2928 m in all oceans (Lehnert et al., 2006). The family diagnosis reads: 'Encrusting, massive, lobate, flabellate or cup-shaped sponges. … Skeleton a reticulation of tracts of styles ending at the surface in brushes or single spicules, no special ectosomal structures. Exclusively styles as megascleres… Microscleres palmate isochelae and sigmas…' (van Soest & Hajdu, 2002). Four genera within the Esperiopsidae are considered valid by van Soest & Hajdu, 2002: *Amphilectus* Vosmaer, 1880, *Esperiopsis* Carter, 1882, *Semisuberites* Carter, 1877 and *Ulosa* de Laubenfels, 1936.

Sponges from the genus *Esperiopsis* are characterized by an anastomosing skeleton of thick spicule tracts condensed in the interior and running upwards to the surface; desma-like spicules may occur occasionally; microscleres are represented by chelae and sigmas (van Soest & Hajdu, 2002). In the North Pacific, eight *Esperiopsis* species, one of them with two varieties, have been described: *E. chindoensis* Sim, 1995 (Korea), *E. digitata digitata* (Miklucho-Maclay, 1870) (North Pacific), *E. digitata infundibula* Koltun, 1956 (north-west Pacific), *E. flagrum* Lehnert, Stone, Heimler, 2006 (Aleutian Islands), *E. laxa* Lambe, 1892 (Pacific coast of Canada), *E. lingua* Koltun, 1970 (north-west Pacific), *E. plumosa* Tanita, 1965 (Japan), *E. stipula* Koltun, 1958 (NW Pacific), *E. uncigera*

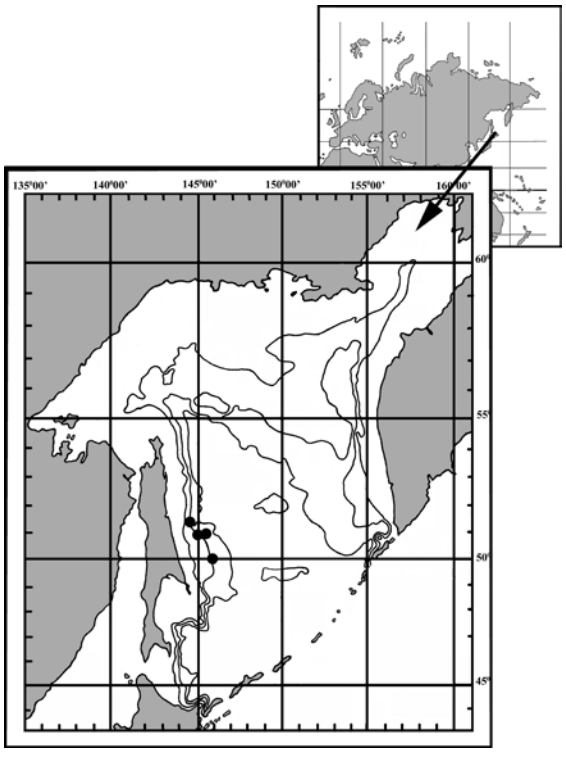

Figure 1. Location of the collection sites of *Esperiopsis koltuni* sp. nov. in the Sea of Okhotsk (North Pacific Ocean). The circles indicate the exact collecting sites.

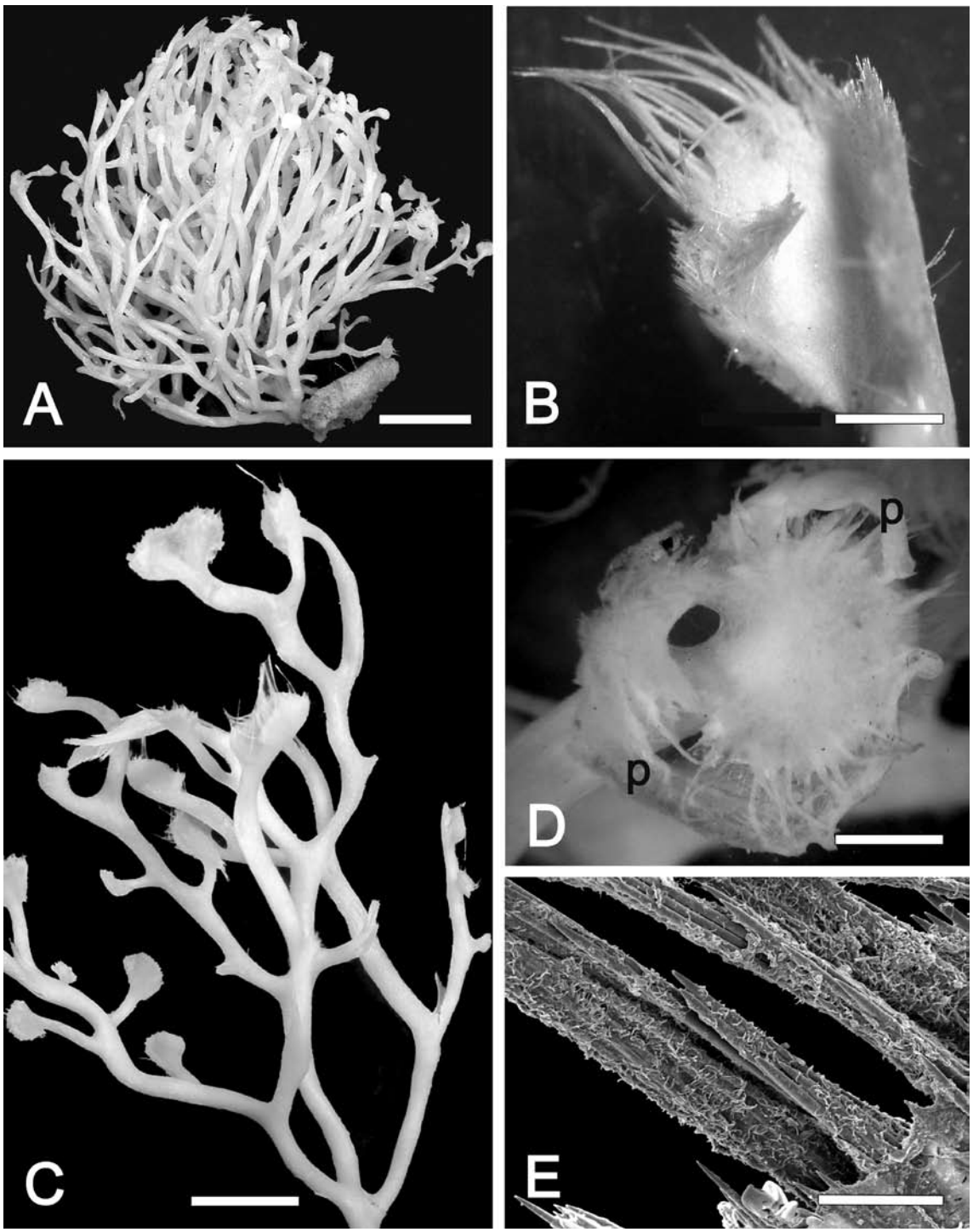

Figure 2. External morphology of *Esperiopsis koltuni* sp. nov. (A) Photograph of the type specimen with even surface; (B) flat distal part with thin outgrowths; (C) photograph of a branch terminating in an oval flat distal part; (D) flat distal part of a branch with a prey (p) captured with the filament-like outgrowth; (E) proximal part of thin outgrowth, made up by a bunch of megascleres. Scale bars: A, 2 cm; B, 25 mm; C, 12 mm; D, 2.5 μm; E, 120 μm.

Topsent, 1928 (Japan). This paper describes a new *Esperiosis* species found living attached to hard substrates in deep water along the western slope of the Sea of Okhotsk.

MATERIALS AND METHODS

Esperiopsis specimens were collected by deep-water dredging from the western slope of the Sea of Okhotsk during a scientific expedition on the 'Novoulyanovsk' trawler in October 1984 (Figure 1). Sponges were fixed in 70% ethanol and Bouin fixative. The material obtained is kept in the collections of the Zoological Institute of the Russian Academy of Sciences in Saint-Petersburg.

The spicules were studied as dissociated spicule mounts. To make them, sponge fragments were boiled in concentrated HNO_3. The resultant spicule suspensions were washed and centrifuged five times and mounted in Canada balsam.

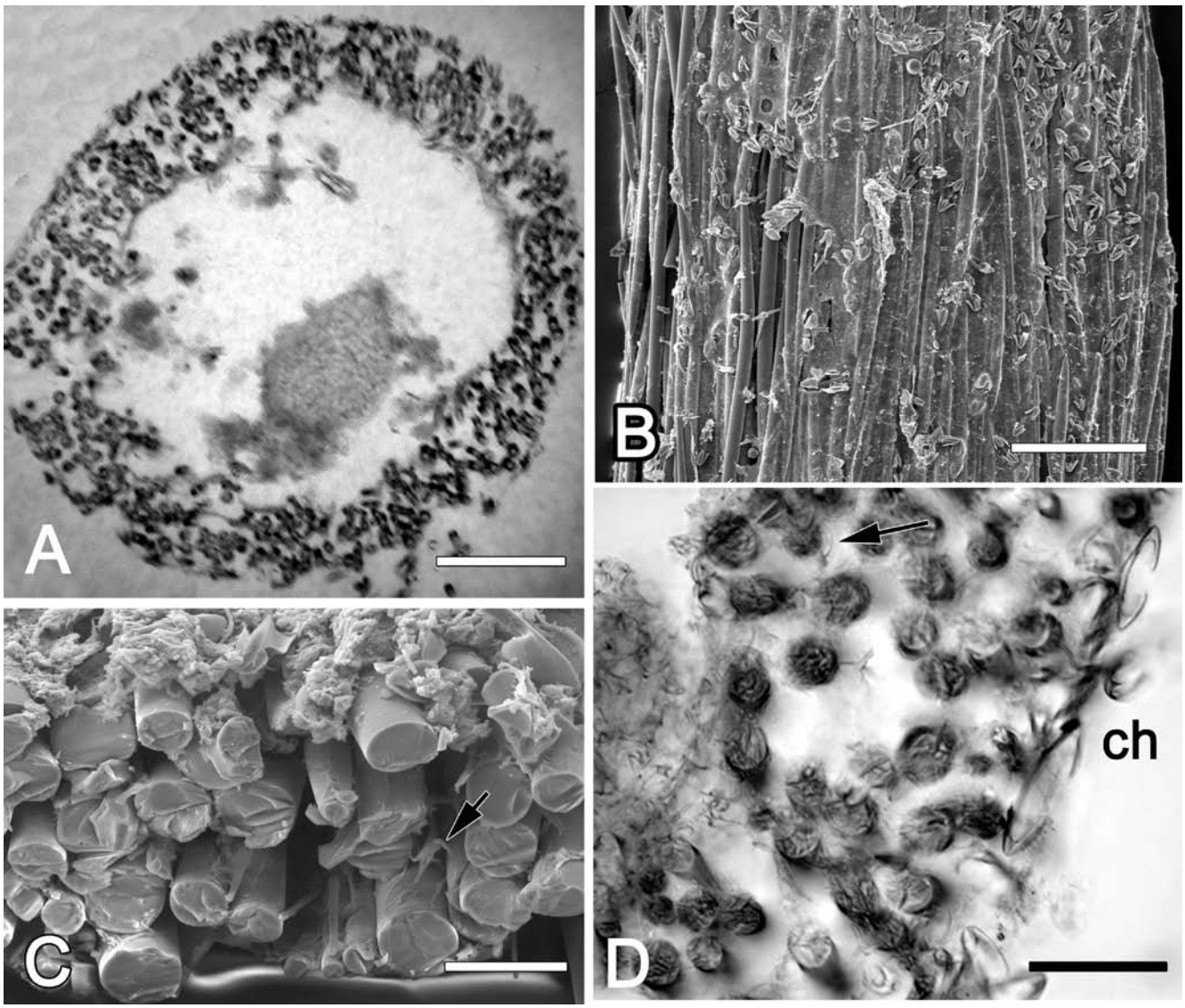

Figure 3. The skeleton of cylindrical branches of *Esperiopsis koltuni* sp. nov. (A) Polished section (perpendicular to surface), showing a branch wall consisting of densely packed styles, and the central part with the tissue; (B) dried external surface showing arrangement of styles along the axis of branch and dermal skeleton consist of anchorate spatuliferous isochelae (SEM); (C&D) polished (C) and SEM (D) sections perpendicular to the parts of a branch wall showing densely packed styles includes the sigmancistras (arrows) and dermal anchorate spatuliferous isochelae (ch). Scale bars: A, 850 μm; B, 240 μm; C, 40 μm; D, 70 μm.

For scanning electron microscopy (SEM), drops of spicule suspension were air-dried on SEM stubs, which were then sputtered with gold-palladium and examined under a XL30 ELSEM Philips SEM. The spicules were measured under the light microscope and on SEM photographs.

The material for histology was prepared as follows: tissue fragments fixed in Bouin solution were dehydrated in an ethanol series, placed into a celloidin-castor oil mixture, transferred to chloroform and then embedded in paraffin. Sections 6 μm thick were mounted on glass slides and stained with Mayer's hematoxylin, eosin and Heidenheim ferric hematoxylin.

Skeletal architecture was studied by light microscopy on polished sections. They were obtained by embedding a piece of sponge in Spurr's resin and cutting it at a low speed using a diamond wafering blade.

SYSTEMATICS

Order POECILOSCLERIDA Topsent, 1928
Suborder MYCALINA Hajdu, van Soest & Hooper, 1994
Family ESPERIOPSIDAE Hentschel, 1923
Genus *Esperiopsis* Carter, 1882
Esperiopsis koltuni sp. nov.
(Figures 2–6)

Type material

Holotype: ZIN RAS no. 10773 (50°52.3'–50.2'N 145°07.1'–10.2'E), Station 98, south-western slope of Sea of Okhotsk shelf, 500 m depth, silt ground with pebble and fragments of glass sponges. The material was fixed in 70% ethanol and Bouin solution. Zoological Institution of Russian Academy of Sciences, Saint-Petersburg. Collected by A.V. Ereskovsky, 09 October 1984, with trade trawl.

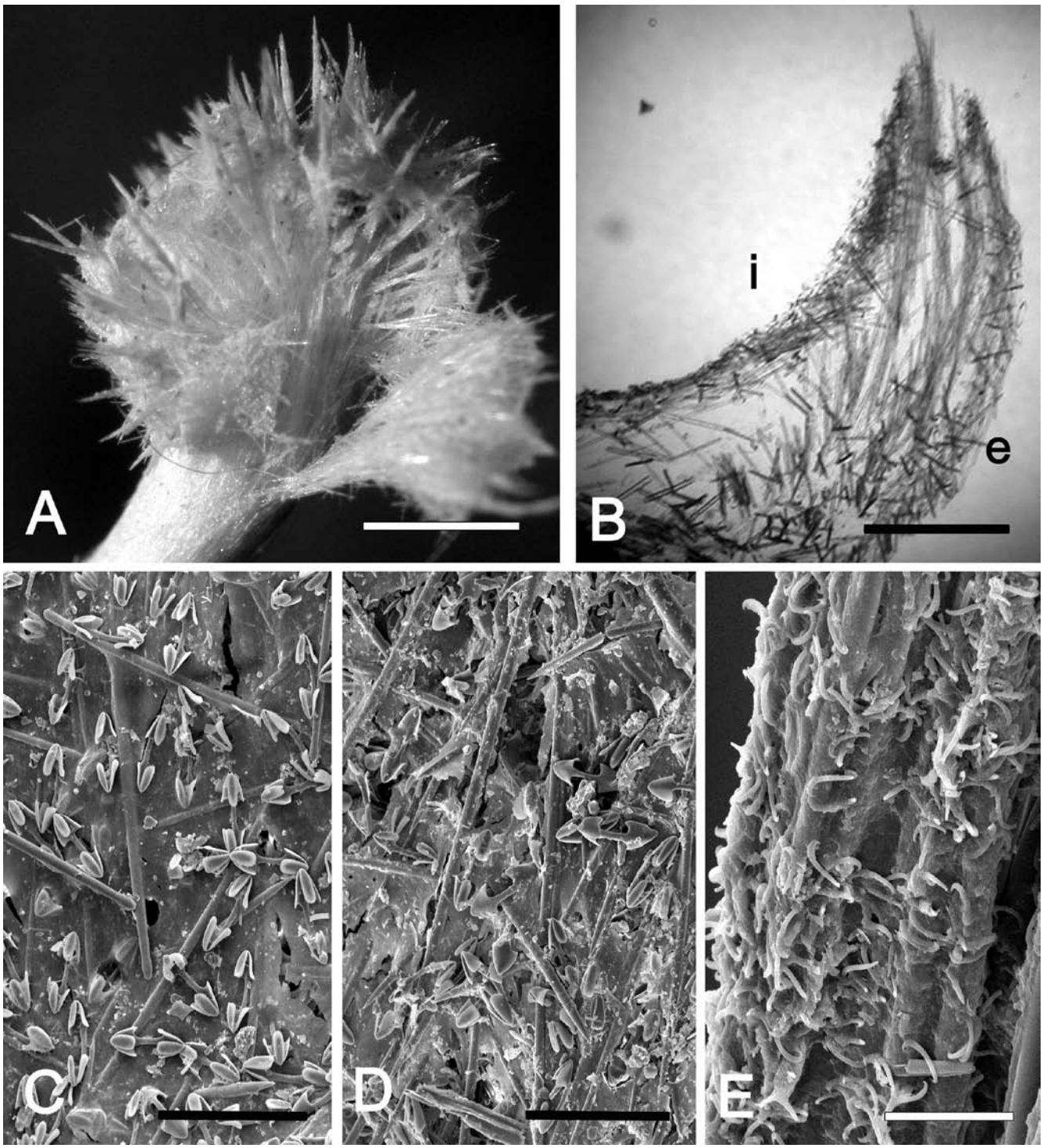

Figure 4. The skeleton of a flat distal parts of *Esperiopsis koltuni* sp. nov. (A) Photograph of the principal skeleton; (B) polished section (perpendicular to the flat distal part), showing external parts of principal skeleton: internal (i) and external (e); (C & D) dermal skeleton of internal (C) and external (D) parts of the flat distal part, showing a tangential chaotic network of smaller styles and isochelae (SEM); (E) external surface of filament-like outgrowths, showing numerous sigmancistras (SEM). Scale bars: A, 2.5 cm; B, 900 μm; C, D, 135 μm; E, 30 μm.

Paratypes: ZIN RAS no. 10774, five sponges and some fragments; south-western slope of Sea of Okhotsk shelf, (50°52.3'–50.2'N 145°07.1'–10.2'E), Station 98, south-western slope of Sea of Okhotsk shelf, 500 m depth, silt ground with pebble and fragments of glass sponges. The material was fixed in 70% ethanol. Zoological Institution of Russian Academy of Sciences, Saint-Petersburg. Collected by A.V. Ereskovsky, 09 October 1984, with trade trawl.

Additional material

ZIN RAS no. 10775, Station 92 (49°57.7'–50°00.6'N 145°51.3'–49.1'E), 600 m depth, 08 October 1984, five juvenile sponges; ZIN RAS no. 10777, Station 99 (50°59.2'–51°02.2'N 145°21.2'–19.2'E), 620–645 m depth, 10 October 1984, three sponges; ZIN RAS no. 10776, Station 106 (51°21.3'–18.3'N 144°42.1'–44.8'E), 500 m depth, 11 October 1984, four sponges. All collected by A.V. Ereskovsky.

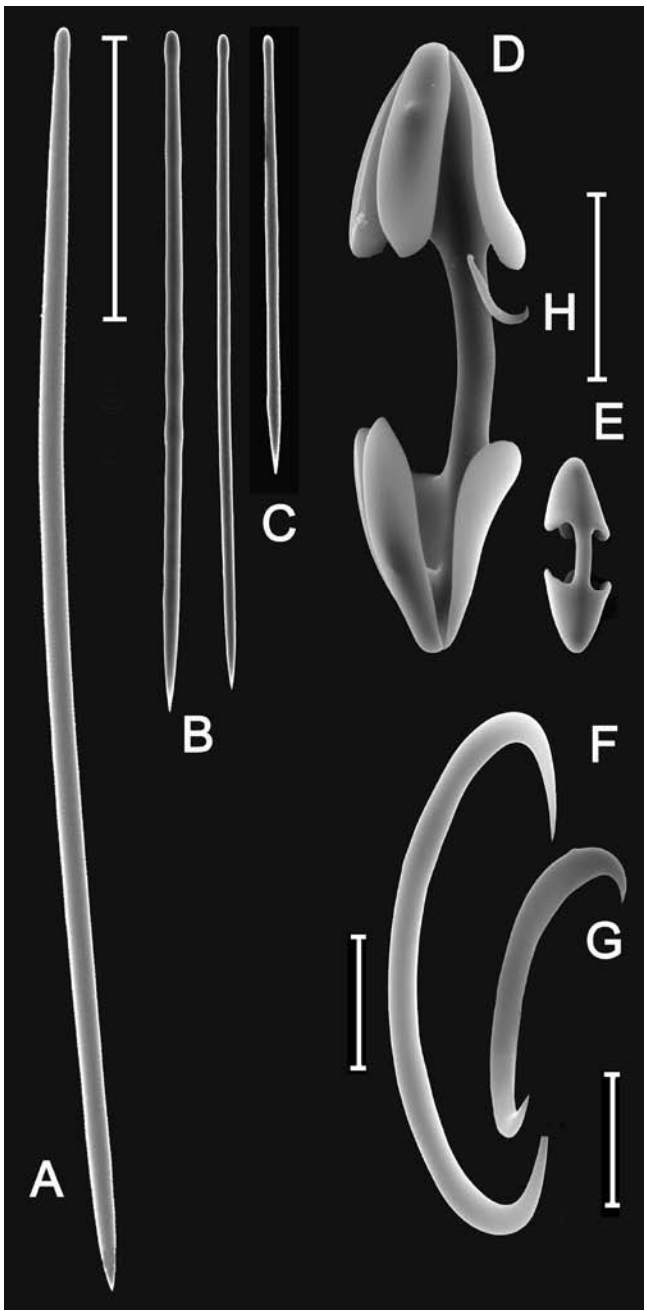

Figure 5. SEM micrographs of the spicules of *Esperiopsis koltuni* sp. nov. (A) Style of principal skeleton; (B & C) styles of dermal skeleton; (D) big anchorate spatuliferous isochela; (E) small arcuate isochela; (F) sigma; (G & H) sigmancistras. Scale bars: A–C, 200 μm; D, E, H, 25 μm; F, 15 μm; G, 5 μm.

Diagnosis

Body consisting of basal plate and radiating cylindrical branches. The branches anastomose and their distal parts are oval and flat, with filament-like outgrowths. Principal skeleton of distal parts modified, with a particular category of styles. Arrangement of microscleres in dermal membrane characteristic, with protruding alae and crochets all over sponge body. *Esperiopsis koltuni* sp. nov. differs from other species of the genus in having three size categories of styles (length×width; minimum–maximum) first: 575.3–906.2×17.1–27.5 μm (mean 717.4×23.45 ±44.7×0.3), second: 474–579.6×10.6–15.4 μm (mean 546.3×13.6 ±24.7×3.4) and third: 286–398.2×7.7–10.4 μm (mean 346.8×9.2 ±44.7×0.3).

Description

The holotype is a complete branching specimen 7–12 cm high (Figure 2A). It is attached to a thin plate, 12 mm in the largest dimension. The branches ramify dichotomously, sometimes anastomosing. Their diameter varies from 4 mm at the base to 0.25 mm in the apical part. The branch wall is about 85–115 μm thick. Distal parts of the branches are oval and flat, their diameter varies from 1.5 mm in 'young' sponges to 7 mm in 'adults' (Figure 2B,C). Flat distal parts can be slightly bent or slightly funnel-shaped (Figure 2C). On their edges there are thin filament-like outgrowths, each consisting of a bunch of megascleres incorporated into exopinacoderm (Figure 2E). The outgrowths are 2.2–3.5 μm long, their diameter varies from 71–110 μm at the base to 15–50 μm in the distal part. New branches are formed by division of flat distal parts (Figure 2C). Most of the sponge surface is smooth, but the basal part of the stalk is finely hispid. The dermal membrane is present. There are no oscula. All the specimens examined are white or light yellow. An instance of prey capture by the flat distal part was observed (Figure 2D). The prey (a crustacean) was attached to a filament-like outgrowth, which was shorter than the others, and enveloped by the dermal membrane.

Skeleton (Figures 3–4)

The principal skeleton is subdivided into that of the cylindrical branches and that of the flat distal parts. The principal skeleton of the cylindrical branches consists of densely packed megascleres, located parallel to the long body axis (Figure 3A–D), and of the sigmas and sigmancistras located between the megascleres (Figure 3C). The dermal membrane of the cylindrical branches includes the anchorate spatuliferous isochelae with protruding alae and abundant sigmancistras (Figure 3B & D).

The principal skeleton of the flat distal parts consists of radiating bunches of greater styles, which lie inside the tissue (Figure 4A,B). These bunches protrude from the surface of the marginal zone forming filament-like outgrowths, bordering the flat distal parts (Figure 2C–E). A tangential chaotic network of smaller styles and isochelae with protruding alae forms the concave (internal) part of the principal skeleton (Figure 4B,C). The convex (external) part of the principal skeleton is similar to the concave one, but has more smaller styles (Figure 4B & D). Finally, the external surface of the filament-like outgrowths has many sigmancistras (Figure 4E).

Spicules (Figure 5)

Megascleres. Styles (Figure 5A–C): slightly curved, fusiform, with a slightly enlarged head. Size of the styles of the principal skeleton: length 575.3–906.2 μm (mean 717.4 ±44.7), width 17.1–27.5 μm (mean 23.5 ±0.3), head diameter 7.7–12 μm (mean 10 ±1.8). In the dermal skeleton there are two types of styles: greater and smaller (Figure 5B,C). Greater styles: length 474–579.6 μm (mean 546.3 ±24.7), width 10.6–15.4 μm (mean 13.6 ±3.4), head diameter 9.7–10.1–10.2 μm (mean 9.7 ±0.3). Smaller styles: length 286–398.2 μm (mean 346.8

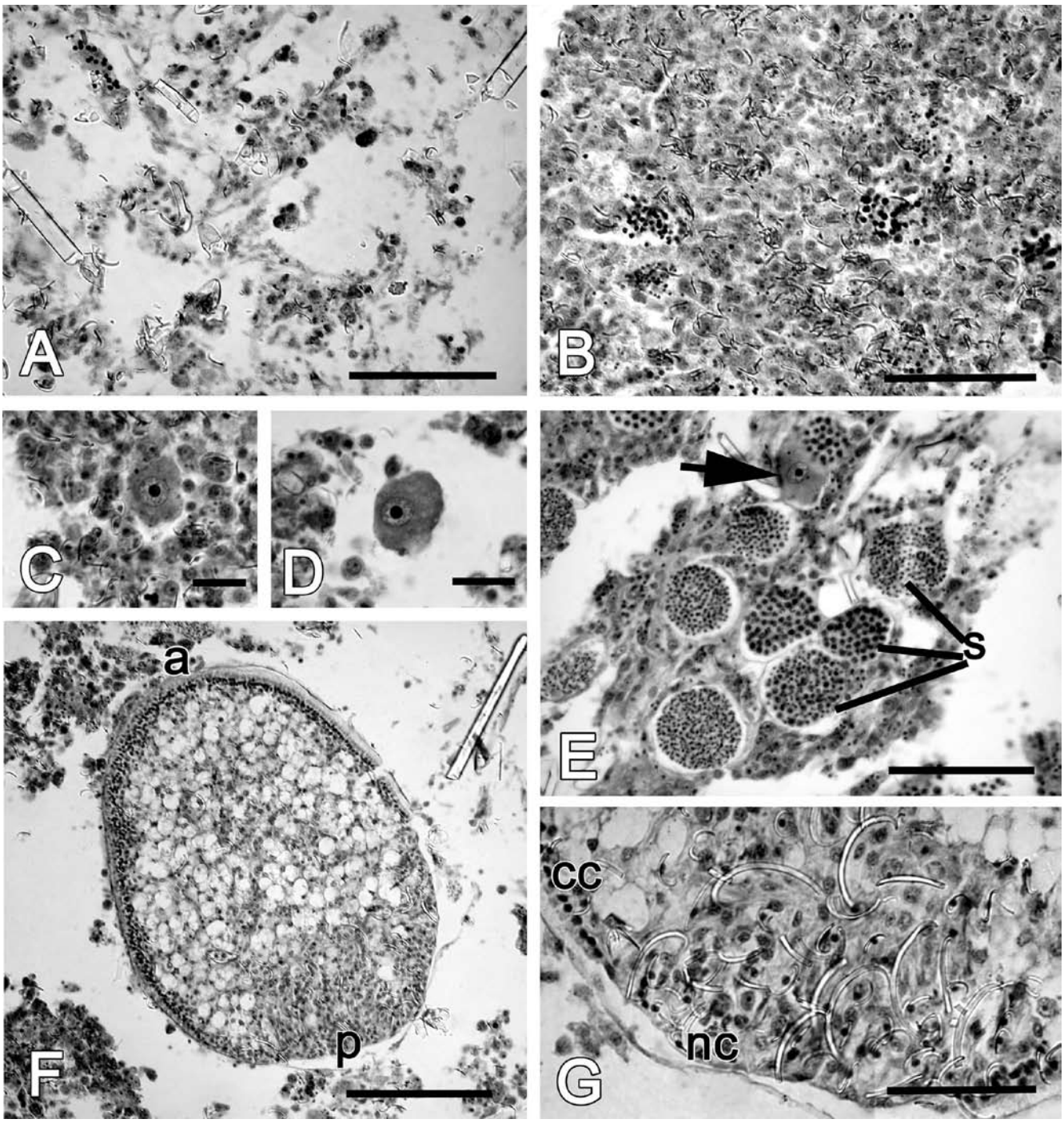

Figure 6. Histological sections of living tissue of *Esperiopsis koltuni* sp. nov. (A) Low cells density in the flat distal parts with dispersed microscleres; (B) high cell density inside the branch, with high concentration of sigmancistras; (C&D) early oocytes with nucleolated nucleus; (E) high density of spermatocysts (s) at different developmental stages and one early oocyte (arrow); (F) parenchymella larva with distinct anterior (a) and posterior (p) poles; (G) detail of posterior larval pole, showing a columnar epithelium of monociliated cells (cc), flat non-ciliated cells (nc) and larval microscleres: sigmancistras and sigmas. Scale bars: A, B, 10 μm; C, D, 30 μm; E, 100 μm; F, 150 μm; G, 60 μm.

±44.7), width 7.7–10.4 μm (mean 9.2 ±0.3), head diameter 7.7–9.9 μm (mean 8.8 ±0.3).

Microscleres. Anchorate spatuliferous isochelae (Figure 5D): the shaft is straight or slightly curved; each end has three alae 23.3–32.6 μm in length (mean 29.2 ±1.6). Fimbriae absent. Size: total length 58.2–82.6 μm (mean 75.8 ±10.25), width near the alae 26.1–30.5 μm (mean 28 ±3.1). There are rare small isochelae (Figure 5E) of the same shape as anchorate spatuliferous isochelae. Size: total length 30.5–46.3 μm (mean 37.5 ±3.6), width near the alae 15.2–20.1 μm (mean 16.6 ±2.5), alae length 11.3–19.5 μm (mean 15.3 ±1.6). Sigmas (Figure 5F): with equal ends in the same plane, abundant in tubes. Size: length 34.8–69.6 μm (mean 54.2 ±24.6), width 2.4–4.5 μm (mean 3.8 ±1.3). Sigmancistras (Figure 5G,H): with ends situated in different planes, less strongly bent than the sigmas; ends have different length;

the shaft is asymmetrical. Size: length 10.9–17.8 μm (mean 13.6 ±4.2), width 1.2–2.1 μm (mean 1.6 ±0.4).

Living tissue (Figure 6)

Histology. The tissue density is low in the flat distal parts (Figure 6A) and high in the cylindrical branches (Figure 6B). Neither subdermal cavities, nor canals lined with endopinacocytes, nor choanocyte chambers were revealed at histological sections of various sponge parts.

Reproduction. All the specimens investigated were reproducing. *Esperiopsis koltuni* sp. nov. sponges are simultaneous hermaphrodites: all stages of spermatogenesis and early oogenesis occur at the same time (Figure 6E). Gametogenesis and embryogenesis take place in the flat distal parts and in the cylindrical branches. Early oocytes are 16 to 28 μm in diameter (Figure 6C,D). Mature eggs were not found. Spermatogenesis occurs inside spherical spermatocysts (48–66 μm in diameter). Spermatogenesis is synchronous in the individual spermatocyst but asynchronous in neighbouring ones (Figure 6E).

Esperiopsis koltuni sp. nov. larvae are typical parenchymellae (Figure 6F). Their oval or oviform body (about 500×380 μm) is evenly covered by cilia of the same length. The posterior pole is not covered with cilia and there is no band of long cilia around it. The antero-lateral surface of the larva is made up by monociliated cells, which form a pseudo-stratified columnar epithelium (Figure 6F,G). The non-ciliated cells of the posterior pole are flat (Figure 6G). The larval skeleton consists only of microscleres: sigmancistras (length 10.8–13.2–16.7 μm and width 0.8–1.3–1.7 μm) and sigmas (length 41.7–47.2–50 μm and width 2.1–2.6–3.3 μm) concentrated near the posterior pole (Figure 6F,G). Rare microscleres are diffused evenly in the larva.

Noteworthy, while the larva develops, the parental tissue disintegrates only locally. General anatomical and histological organization of the parental sponge does not change.

Ecology and distribution

All the specimens of *Esperiopsis koltuni* sp. nov. were found attached to pebbles and fragments of the glass sponges (*Aphrocallistes* spp.) at the south-western slope of the Sea of Okhotsk shelf on silt ground, at a depth of 500–645 m (Figure 1).

Etymology

The species is named in honour of the late Dr Vladimir M. Koltun (1921–2005), a prominent Russian spongiologist.

DISCUSSION

Species composition of the genus *Esperiopsis* is a matter of some debate. Van Soest & Hajdu (2002) listed 50 *Esperiopsis* species. According to the latest revision by Lehnert et al. (2006), the genus includes 43 species distributed worldwide, six of them inhabiting the North Pacific. All the above authors noted high polymorphism of *Esperiopsis* sponges in respect to body shape and spicule composition.

The new species *E. koltuni* is remarkable in its morphology: anastomosing cylindrical branches terminate in oval flat parts. These distal parts are remarkably symmetrical, with filament-like outgrowths. Ramose form was described for *Esperiopsis laxa* Lambe, 1892 from the Pacific coast of Canada and for *E. digitata digitata* (Miclucho-Maclay, 1870) from the North Pacific. A stipitate shape with symmetrical lateral expansions were described for deep-sea *E. symmetrica* Dendy, Row, 1886 and *E. desmophora* Hooper, Lévi, 1989.

One of the characters of Esperiopsidae is the lack of an ectosomal skeleton (van Soest & Hajdu, 2002). However, *E. koltuni* sp. nov. has a modification of its principal skeleton in ectosomal zone of flat distal parts. The principal skeleton of the cylindrical branches, the main part of the sponge body, is not modified. Distribution of isochelae and sigmancistras, with protruding alae and crochets, deserves special mention. They are present in the dermal membrane all over the body and are especially numerous in the distal parts of the branches. This microsclere arrangement, unusual for Esperiopsidae, is characteristic of different carnivorous Poecilosclerida (Vacelet, 2006, in press).

In *E. koltuni* sp. nov. there are two categories of sigmas. Only seven *Esperiopsis* species were described with two categories of sigmas: *E. decora* Topsent, 1904 (Azores), *E. flagellum* Lundbeck, 1905 (Iceland), *E. flagrum* Lehnert, Stone, Heimler, 2006 (Aleutian Islands), *E. incognita* Stephens, 1916 (Ireland), *E. macrosigma* Stephens, 1916 (north-eastern Atlantic), *E. polymorpha* Topsent, 1892 (Azores), *E. praedita* Topsent, 1892 (Azores) and *E. novaezelandiae* Dendy, 1924 (New Zealand and New Caledonia).

Esperiopsis koltuni sp. nov. also has two categories of isochelae. There are four *Esperiopsis* species with combination of two categories of isochelae and two categories of sigmas: *E. flagellum* Lundbeck, 1905 (Iceland), *E. flagrum* Lehnert, Stone, Heimler, 2006 (Aleutian Islands), *E. incognita* Stephens, 1916 (Ireland) and *E. praedita* Topsent, 1892 (Azores).

Finally, *E. koltuni* sp. nov. has three size categories of styles, which is very unusual. Almost all the species of the genus have one size category of styles; two categories are present only in *E. polymorpha* Topsent, 1892 (Azores).

Four *Esperiopsis* species, one with two subspecies, were described from the Sea of Okhotsk and adjacent waters: *E. stipula* Koltun, 1958, *E. digitata digitata* (Miklucho-Maclay, 1870), *E. digitata infundibula* Koltun, 1956, and *E. lingua* Koltun, 1970. All of them differ from *E. koltuni* sp. nov. in growth form. *Esperiopsis stipula*, *E. digitata digitata*, *E. digitata infundibula* have only one microsclere type (isochelae), while the new species has three microsclere types. Similarly to the new species, *E. lingua* has three microsclere types and two isochelae categories; however, it has only one category of sigmas, while our species has two. Sexual development in *E. koltuni* sp. nov. proceeds, in general, similarly to that in the other Poecilosclerida (Ereskovsky, 2005). An infrequent feature of its larva is the absence of megascleres, which are present in most poecilosclerid larvae (Ereskovsky, 2005).

Thus, *Esperiopsis koltuni* sp. nov. can be easily distinguished from other species of the genus. Its distinguishing characters are modification of principal skeleton in distal parts of branches, arrangement of sigmoid and cheloid microscleres in the dermal membrane, with teeth and alae directed outwardly, and a comparable set of spicules.

Interestingly, *E. koltuni* sp. nov. has no aquiferous system: our histological study did not reveal any canals, ostia, oscula or choanocyte chambers. This curious feature, not

characteristic of sponges in general, has been associated only with carnivorous sponges (Vacelet & Boury-Esnault, 1995; Vacelet, 2006).

Carnivorous sponges share a number of morphological characters (Vacelet, 2006, in press). First, they either lack the aquiferous system or have a considerably modified version of it. Second, they have a characteristic body plan, with symmetrical lateral expansions. Finally, their microsclere arrangement is unusual, and they have a characteristic megasclere skeleton composed of more or less modified mycalostyles. All carnivorous sponges belong to the order Poecilosclerida and are the only poecilosclerids to possess true sigmancistras.

Carnivorous sponges are known with certainity in two poecilosclerid families: Cladorhizidae (the genera *Asbestopluma*, *Cladorhiza*, *Chondrocladia* and *Abyssocladia*) and Guitarridae (the genus *Eucheliplum*a). It has been supposed that *Esperiopsis symmetrica* Dendy & Row, 1886 and *Esperiopsis desmophora* Hooper & Lévi, 1989 from the family Esperiopsidae are also carnivorous (Vacelet, 2006, in press).

Our new species has most of the characters associated with carnivorous sponges: it lacks the aquiferous system, has a characteristic body plan and an unusual arrangement of microscleres in the dermal membrane, possesses true sigmancistras, and, finally, captures prey with the filament-like outgrowth. This combination of characters testifies that *Esperiopsis koltuni* sp. nov. is a carnivorous sponge.

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