

New sponge species of the family Vulcanellidae (Demospongiae: Tetractinellida) from the Piip submarine volcano and adjacent areas (Bering Sea, NW Pacific)

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ABSTRACT

Four new species of vulcanellid sponges (Demospongiae: Tetractinellida), *Poecillastra malyutini* sp. nov., *Vulcanella koltuni* sp. nov., *V. commander* sp. nov. and *V. grebelnyi* sp. nov., are described from the Piip submarine volcano and adjacent area (the Bering Sea, North Pacific). This work includes materials sampled using the ROV *Comanche 18* during the cruises of the RV *Akademik M.A. Lavrentyev* in 2016 and 2018. These specimens were studied and illustrated using light and electron (SEM) microscopy and micro-computed tomography (micro-CT). The distribution of species is characterized by pronounced vertical zoning. In areas of hydrothermal vents and on their periphery, Demospongiae are abundant with a pronounced dominance of a single species, *V. koltuni* sp. nov. The $\delta^{13}\text{C}$ value for *V. koltuni* sp. nov. and *P. malyutini* sp. nov. from the volcano summits were almost 2-fold lower than for *V. commander* sp. nov. collected outside the areas of hydrothermal activity. These isotopic signatures indicate the organic matter of chemosynthetic origin in the diet of *V. koltuni* sp. nov. and *P. malyutini* sp. nov. Phylogenetic analysis based on 18S rDNA does not confirm the phylogenetic relationship of *Lamellomorpha* Bergquist, 1968 with the family Vulcanellidae Cárdenas, Xavier, Reveillaud, Schander & Rapp, 2011.

1. Introduction

Deep-sea Demospongiae Sollas, 1885 inhabit a variety of habitats in the world's oceans where they often not only dominate in abundance and biomass but are also known to be ecosystem-forming species (Maldonado et al., 2016; Gonzalez-Mirelis et al., 2021). In deep-sea waters, aggregations of sponges often become biogenic habitats providing substrate and creating favorable conditions for the existence of associated fauna (Hogg et al., 2010).

Demospongiae are common on rocky substrates of seamounts, including habitats near hydrothermal vents and methane seeps (Vacelet et al., 1995, 1996; Vacelet, 2006; Kelly and Rowden, 2019; Georgieva et al., 2020). Furthermore, sponges associated with hydrothermal vents and cold seeps demonstrate carbon and nitrogen isotopic signatures consistent with contributions to nutrition from chemosynthesis (McDonald et al., 1989; Vacelet et al., 1996; Georgieva et al., 2020).

Sponges are known to harbor dense and diverse microbial communities including sulfide and methaneoxidizing bacteria as part of their microbiome (Webster and Taylor, 2011). Chemoautotrophic symbiosis has been confirmed both for various filter-feeders and for carnivorous sponge species (Nishijima et al., 2010; Arellano et al., 2012; Hestetun et al., 2016; Rubin-Blum et al., 2019; Georgieva et al., 2020).

Studies of hydrothermal vent-associated fauna conducted in the Northwest (NW) Pacific are limited mainly to the southern part of this region, which is distinguished by numerous faults and submarine volcanoes (Watanabe et al., 2010, 2019; Nakajima et al., 2014). In the northern NW Pacific, the only known area of communities developing on deep-sea hydrothermal vent fields is the summits of the Piip submarine volcano (Seliverstov, 2009; Galkin and Ivin, 2019; Galkin et al., 2019). There is currently a lack of data on the fauna of demosponges from these ecosystems.

Despite the rather long history of exploration of deep-sea

Abbreviations: IO RAN, Shirshov Institute of Oceanology, Russian Academy of Sciences, Moscow, Russia; MIMB, Museum of the A.V. Zhirmunsky National Scientific Center of Marine Biology FEB RAS; NSCMB FEB RAS, A.V. Zhirmunsky National Scientific Center of Marine Biology, FEB RAS, Vladivostok, Russia.

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communities in the NW Pacific, the knowledge of sponge biodiversity and pattern of distribution there still remains fragmentary (Downey et al., 2020). The expeditions aboard the R/V *Vityaz* that provided a significant collection of sponge specimens, in particular Demospongiae (Koltun, 1959, 1966, 1970), provided a breakthrough in the study of deep-sea communities in the 20th century. These works are still considered seminal for the northwestern Pacific Ocean. Since 2010, four international integrated deep-sea expeditions have been conducted in the NW Pacific, which made it possible to collect extensive material to investigate the macrofauna of the region, including the diversity and distribution patterns of Demospongiae (Downey and Janussen, 2015; Downey et al., 2018, 2020). Unfortunately, deep-sea Demospongiae from the western Bering Sea were largely undescribed in all the above-mentioned works.

Out of the 43 currently recognized species of Vulcanellidae Cárdenas et al. (2011) (de Voogd et al., 2022), 26 have been found in the Pacific Ocean, and only three species of the genus *Poecillastra* Sollas, 1888 and five species of *Vulcanella* Sollas, 1886 have been recorded from the NW Pacific (Tables 2 and 3). The first Vulcanellidae species from the NW Pacific, *Poecillastra tenuilaminaris* (Sollas, 1886), was described by Sollas from Sagami Bay in 1886 (Sollas, 1886). Subsequently, five more species were described in the period 1898–1914: *P. japonica* (Thiele, 1898), *Vulcanella doederleini* (Thiele, 1898), *V. cribriporosa* (Lebwohl, 1914), *V. nethides* (Lebwohl, 1914), and *V. porosa* (Lebwohl, 1914). The last two described species of Vulcanellidae from the NW Pacific were *V. acanthoxea* Sim and Kim (1995) and *P. wondoensis* described by Tanita and Hoshino (1989). The initially determined distribution ranges of the species were then substantially extended. Thus, Koltun (1966) noted the presence of *V. porosa* off the Southern Kuril Islands and *P. japonica* off the Pacific coasts of the Kuril Islands, in the Sea of Japan, Sea of Okhotsk, and Bering Sea. Rho and Sim (1976) found *P. japonica* in the Korea Strait. Downey et al. (2020) summarize information on the distribution of *P. japonica* in the northern Pacific Ocean: between the latitudes 36°–54° N and the longitudes 151° E to 129° W. *P. tenuilaminaris* also proved to be a widespread species: in addition to Japan, the species is found off the California coast, in the Gulf of Alaska, and the eastern Bering Sea (Laubenfels, 1932; Dickinson, 1945; Green and Bakus, 1994; Stone et al., 2011) (Table 2).

It should be particularly noted that out of the eight above-listed species, six were found for the first time for the well-studied Sagami Bay, and only one for a much larger area – for the deep waters of the western Bering Sea and adjacent waters. This may be evidence of a much greater actual diversity of the family Vulcanellidae.

The present paper provides new information about sponges of the Vulcanellidae from the Piip submarine volcano (Bering Sea) with descriptions of new species and remarks on their ecology.

2. Materials and methods

2.1. Study area and sampling

The material was collected during the 75th and 82nd research cruises aboard the R/V *Akademik Lavrentiev* to the area of the Volcanologists Massif, Bering Sea, in 2016 and 2018. Detailed information on the environmental parameters and communities was published previously (Seliverstov, 2009; Galkin et al., 2019; Polonik, 2019; Demina et al., 2021) and is also provided in the present special issue (Rybakova et al., 2022). Active hydrothermal venting occurring at both summits of the volcano supports diverse biological communities, including obligate or potentially obligate to reducing environment species (bivalves *Calypotoga pacifica* Dall, 1891; gastropods *Parvaplustrum wareni* Chaban et al., 2022 and *Provanna* sp.; amphipods *Onesimoides* sp., leptostracans *Nebalia* sp., polychaetes *Neosabellides uschakovi* (Kuznetsov & Levenstein, 1988), *Ophryotrocha* sp. and *Harmothoe globosa* Pettibone, 1990). Thermal waters come to the bottom surface through numerous cracks, seep through the collapse of blocks of lava flows. In places where thermal water seeps, numerous “moires” are observed, due to the difference in temperatures of thermal and sea waters. Widespread development of bacterial mats is associated with seepages of thermal waters; at the Northern summit, there are areas of continuous coverage of the bottom with bacterial mats with an area of up to 100 m² (Seliverstov, 2009). The hydrothermal fluids are enriched with methane (88–95%) and also contain carbon dioxide, hydrogen sulphide and ethane (Sagalevich et al., 1992; Taran et al., 1992; Polonik, 2018). The chemical and isotopic composition of gas and carbonates indicates the significant role of hydrocarbons from the sedimentary layers which, during the low-temperature stage, stimulate the processes of bacterial sulphate reduction (Torokhov and Taran, 1994).

The studied specimens were collected using the manipulator of a ROV *Comanche-18* (Sub-Atlantic, UK) from the summits and slopes of the Piip submarine volcano and adjacent areas of the seafloor (Fig. 1; Table 1). Photo and video footage was collected during the ROV dives. The collected material was also photographed on board and fixed in 96% ethanol. Before fixation, individuals were washed with chilled filtered sea water to remove epifauna and potential adherent sediments and small samples were taken for stable isotope ration analysis (approximately 1 cm³ from individual, rinsed twice with distilled water, dried at 57 °C for 24 h) and molecular studies (approximately 1 cm³ from individual, chilled to –20 °C in 96% ethanol, and kept in a –20 °C freezer for at least 48 h for subsequent DNA studies).

The type material is deposited at MIMB, the Museum of the A.V. Zhirmunsky National Scientific Center of Marine Biology FEB RAS (NSCMB FEB RAS), formerly Institute of Marine Biology FEB RAS, Vladivostok, Russia. The taxonomy used in the present study is in accordance with the World Porifera Database (De Voogd et al., 2022). The descriptions were carried out in accordance with the terminology adopted in Boury-Esnault and Rützler (1997). Abbreviations in Table 2 are 3 are in accordance with Carvalho et al. (2011).

Table 1
List of the species and location data.

Sample	Station	Date	Latitude, °N	Longitude, °E	Depth, m	Species	δ ¹⁵ N, ‰	δ ¹³ C, ‰
1	LV75-10-3	June 20, 2016	55.417	167.275	411	<i>V. koltuni</i> sp. nov.		
2	LV75-13-2	June 23, 2016	55.383	167.260	472	<i>V. koltuni</i> sp. nov.		
3	LV75-15-3	June 26, 2016	55.382	167.261	467	<i>V. koltuni</i> sp. nov.		
4	LV75-18-3	June 28, 2016	55.438	167.265	1569	<i>V. grebelnyi</i> sp. nov.		
5	LV82-1-5	June 13, 2018	55.416	167.276	382	<i>P. malyutini</i> sp. nov.	13.8	–27.2
6	LV82-3-2	June 14, 2018	55.382	167.261	469	<i>V. koltuni</i> sp. nov.	13.0	–31.1
7	LV82-4-1	June 14, 2018	55.381	167.261	471	<i>V. koltuni</i> sp. nov.		
8	LV82-6-1	June 16, 2018	55.695	167.124	3753	<i>V. commander</i> sp. nov.		
9	LV82-6-2	June 16, 2018	55.692	167.120	3599	<i>V. commander</i> sp. nov.	14.9	–17.0
10	LV82-7-2	June 17, 2018	55.369	167.266	981	<i>V. grebelnyi</i> sp. nov.		
11	LV82-8-1	June 17, 2018	55.381	167.262	469	<i>V. koltuni</i> sp. nov.		
12	LV82-8-2	June 17, 2018	55.382	167.262	472	<i>V. koltuni</i> sp. nov.	13.8	–29.0

Table 2

Comparative micrometric, habit, distribution and depth data for the species of *Poecillastra* known from Pacific and some species from the surrounding regions. Measurements are expressed in μm , as minimum-(mean)-maximum length $\times$ width value whenever available (modified from [Carvalho et al., 2011](#)).

Species	Oxeas	Triakens	Microxeas	Asters	Habit; distribution; depth
<i>Poecillastra malyutini</i> sp. nov.	I. 1062.4-(2230.5)-3399.7 $\times$ 29.2-(53.2)-76.9 II. >8366.4 $\times$ 10.5-(16.2)-23.7 III. styles (up to subtilostyles) 584.3-(1714.4)-2483.4 $\times$ 45.1-(79.6)-116.6 IV. strongyles 1168.6-(1540.5)-1859.2 $\times$ 45.1-(61.0)-68.9	Ca: 398.4-(513.1)-743.7 $\times$ 34.2-(41.2)-52.6 Pg (to Or): rhabdome 225.8-(338.4)-411.7 $\times$ 28.9-(44.9)-57.9; clad 398.4-(599.7)-916.3 $\times$ 31.6-(49.9)-60.5 De; Mo; Mo irregular	121.9-(156.0)-212.0 $\times$ 5.0-(6.1)-7.2	Sp (sometimes smooth): 13.2-(19.6)-23.7; Pl: 17.1-(24.6)-32.9	Plate-like; Bering Sea, the northern and southern peaks of the Piip volcano; 347–470 m
<i>P. antonbruinae</i> Carvalho et al., 2011 (orig. descr.)	I. 972-(1924.2)-3060 $\times$ 14-(36.9)-53 II. 262-(401.6)-621 $\times$ 10-(14.6)-24	Ca: 242-(423.4)-572 $\times$ 17-(27.4)-36	73-(99.9)-136 $\times$ 4-(4.6)-6	Sp: 15-(17.7)-24	Lamellate; Chile; 290–450 m
<i>P. ciliata</i> Wilson (1925) (orig. descr.)	I. 2000–3500 $\times$ 70–80 II. 850–8	Di: rhabdome 450 $\times$ 70; protocladi 100 $\times$ 70; deuterocladi 360	I. 160–220 $\times$ 6 II. 32–40 $\times$ 4 (dermal)	St (am/pl): 16–30	Lamellate; Philippines; 622 m
<i>P. compressa</i> (Bowerbank, 1866), sensu Sollas (1888)	I. 1600–1900 $\times$ 30–45 II. slender 2500 $\times$ 16 (american specimen)	Or, Ca: 170–320 $\times$ 250 (cladi)	140–200	Pl: 28 Sp: 20	Plate-shaped or cup-like; Shetland, west of Scotland and Hebrides, Queen Charlotte Islands, N America; 203 m
<i>P. cribraria</i> Wilson (1904) (orig. descr.)	I. 2500 $\times$ 40 II. 3500 $\times$ 10	Or (rare): cladi 380 $\times$ 30; rhabdome 200 $\times$ 30	180 $\times$ 4	Sp: 16 Pl: 24	Plate-like; Galapagos; 97 m
<i>P. cribraria</i> Wilson (1904) , sensu Desqueyroux-Faúndez and Van Soest (1997)	448-(1554)-2000 $\times$ 18-(22)-35	Or (rare): cladome 500-(579)-664; rhabdome 100–200 $\times$ 13-(18)-26	112-(136)-171 $\times$ 2-(3)-5	Sp: 10-(12)-13 Pl: 13-(18)-26	Lamellate, linguiform; Galapagos; 95 m
<i>P. ducitriaena</i> Kelly & Cárdenas, 2019 (orig. descr.)	I. 1150-(1725)-2271 $\times$ 8-(16)-22 II. curved 1095–(1801)-2671 $\times$ 5-(13)-17	Or (rare): clad 200-(232)-250; rhabdome 260-(290)-300	sometimes centrotyle 28-(38)-46 $\times$ 2-(3)-4	Sp: 5–7 Me to Am: 5-(8)-12	Multilamellate, foliose, fan, stalked; Subantarctic region of New Zealand, east of Snares Island Platform; 125–213 m
<i>P. incrustans</i> Sollas (1888) , sensu Lévi and Lévi, 1983	770–1400 $\times$ 8–17	Ca: 40–400 $\times$ 45	centrotiles	Sp, Me	Crust; Tristan da Cunha; Gough Island (Antarctic); 180 m. Philippines; 183, 185 m
<i>P. japonica</i> (Thiele, 1898) (orig. descr.)	I. 5000 $\times$ 65 II. 3000–3500 $\times$ 110 III. 2500 (with lateral appendages)	Ca: 750 $\times$ 550	180–270 $\times$ 8 (microrabd)	Sp: 15–20	Form not specified, fragment; Japan, Sagami Bay, Enoshima; 300 m
<i>P. japonica</i> (Thiele, 1898), sensu Koltun (1966) as <i>P. compressa japonica</i>	I. 3000–3500 $\times$ 110 II. up to 5000 $\times$ 65 (thin) III. Oxeas with lateral appendages IV. styles	Ca: rays up to 750 $\times$ 55 Or: rays up to 750 $\times$ 55 (rhabdome shortened) Mo	often centrotiles 134–270 $\times$ 8	Sp: 14–20 Me: 60–70 (diameter)	Plate-like; The Bering, Okhotsk and Japan Seas, the East Coast of Japan and the Kuril Islands, the Pacific coast of Canada; 32–301, up to 2440 m (near the Komandorski Islands)
<i>P. japonica</i> (Thiele, 1898), sensu Rho and Sim (1976)	I. 1000–4000 $\times$ 56 II. 115 $\times$ 23	Ca	14 $\times$ 7	Sp	Plate-like; Korea, Korea Strait; Japan, Enoshima; depth not given
<i>P. laminaris</i> (Sollas, 1886), sensu Sollas (1888)	I. 3500 $\times$ 51.6 II. 5300 $\times$ 8	Ca: 636 $\times$ 63 Or: rhabdome 678 $\times$ 60; cladi 357 $\times$ 60	145 $\times$ 4	Sp: 19.7 Me (to Pl): 19.7	Lamellate; off Indonesia, 1830 m
<i>P. laminaris</i> , sensu Lévi and Lévi (1983)	I. 1800–3800 $\times$ 40–60 II. to 7500 $\times$ 7–15	Or(Ca): rhabdome and clads 200–550 $\times$ 15–40	140–160 or 170–200 $\times$ 3–6	Me: 10–30 Sp: 12–20 (multi-turn)	Lamellate; Indonesia (Banda Sea); 1829 m
<i>P. laminaris</i> , sensu Lévi and Lévi (1983)	2700–4400 $\times$ 50–100	Ca: rhabdome 500–1000 $\times$ 45–90; cladi 500–800 $\times$ 45–90	140–160 $\times$ 3	Me: 20–25 Sp: 15–20	Lamellate; Indonesia (Amboine), New Caledonia; 185–198 m
<i>P. macquariensis</i> Kelly & Cárdenas, 2019 (orig. desc.)	I. True oxeas (no measures) II. Sinuous 2125–(3725)-5750 $\times$ 30-(53)-70	Or (to pseudocalthrops): rhabdome (slightly curved) 550-(852)-1225; clads 450–(578)-680	260-(332)-420 $\times$ 5-(7)-8	Sp (to metastar-like streptasters): 15-(19)-20; Pl: overall 57-(67)-100, ray length 25-(37)-60	Part of the stalk; Subantarctic region of New Zealand, Macquarie Ridge; 462–524 m;
<i>P. marentana</i> Carvalho et al., 2011 (orig. desc.)	I. 1516–3432 $\times$ 24-(42.2)-54 II. 315–1401 $\times$ 10-(21.6)-34 III. >4600 $\times$ 5-(10.2)-12	Ca: 272-(494.2)-776 $\times$ 19-(30.5)-39	106-(126.1)-158 $\times$ 2-(4.4)-5	Sp: 14-(16.5)-22 Pl I: 26-(45.5)-74 Pl II: 17-(24.3)-31	Lamellate; Chile; 338–414 m
<i>P. rickettsi</i> de Laubenfels, 1930 , sensu de Laubenfels, 1932	I. 3700 $\times$ 65 II. 17000 $\times$ 15–30	Ca: 450–650 $\times$ 50–70	170–270 $\times$ 4–5	Sp or Me: 10–13 Pl: 14–18 Toxas (proper?)	Plate-like; California; 800 m
<i>P. sinetridens</i> Carvalho et al., 2011 (orig. descr.)	3003-(4253.4)-5720 $\times$ 48-(68.4)-82	Absent	97-(213.9)-349 $\times$ 2-(4.9)-8	Sp: 17-(19.2)-22 Pl: 15-(24.0)-32	Lamellate; Chile; 300 m
<i>P. stipitata</i> Lévi, 1993 (orig. desc.)	I. 2400–3000 $\times$ 22–28 II. 800–1300 $\times$ 8–20	Oc and Pc: 250–500 $\times$ 20–40	150–270 $\times$ 4–5	Me Sp: 15–20 Me Pl: 18–35 (actines)	Erect, pedunculate; New Caledonia; 675–700 m
<i>P. tenuilaminaris</i> (Sollas, 1886), sensu Sollas (1888)	3400 $\times$ 42	Ca/Or: 500 (rhabdome); 464 (cladi)	136 $\times$ 5	Me (to Pl): 23.7	Lamellate; Japan, Sagami Bay; 1417 m
<i>P. tenuilaminaris</i> , sensu Lebwohl (1914)	1050–3600 $\times$ 25–70	Ca: 105–645 $\times$ 15–70 Ca irregular	130–165 $\times$ 4–6	Me: diameter 15–37, ray length 6–29, shaft 2–7	Lamellate; Japan, Sagami Bay; 200 m
	1350–2500 $\times$ 35–45	Ca: 350 $\times$ 40	135 $\times$ 3	Pl: 20–28 Me: 14–16	

(continued on next page)

Table 2 (continued)

Species	Oxeas	Triacenes	Microxeas	Asters	Habit; distribution; depth
<i>P. tenuilaminaris</i> , sensu de Laubenfels (1932)					Lamellate; California, USA; depth not given
<i>P. tenuilaminaris</i> , sensu Dickinson (1945)	3870 × 60	Ca: 450 × 50	145 × 3	Pl: 30 Me: 15	Thin, stiff, smooth; California, USA; depth not given
<i>P. tenuilaminaris</i> , sensu Green and Bakus (1994)	I. 1550-(2052)-2525 × 8-(16)-26 II. 530-(705)-1100 × 13-(20)-31 III. 1475-(2207)-2750 × 29-(47)-78 IV. 675-(1796)-2500 × 39-(53)-72 (styles)	Ca: 260-(433)-700 × 21-(36)-62 310-(444)-600 × 29-(42)-68 (derived triactines)	86-(129)-151 × 3-(4)-5	Me and Sp: 10-(23)-34	Lamellate; California, USA; 69–73.5 m
<i>P. tenuilaminaris</i> , sensu Stone et al. (2011)	1240–2650 × 32–47	Ca: 320–540 × 35–48 Tr: rays of the same size	117–157 × 3–5 (always bent in the middle)	St: 14–28	Plate-like or lamellar; Bering Sea; 149–486 m; Gulf of Alaska; 71–486 m
<i>P. wondoensis</i> Sim and Kim (1995) (orig. desc.)	I. 1320–1820 × 30–80 II. 1800–3500 × 3–10 III. 730–1120 × 38–75 (styles)	Ca: 110–500 × 10–50 Pr: 2500 (clade 80)	I. 150–250 × 5–10 II. 48–80 × 2.5	Me: 15–20 Sp: 15	Thickly encrusting; Korea; 15–25 m
<i>P. compressa antarctica</i> , sensu Boury-Esnault and van Beveren (1982) as <i>P. compressa</i>	1033-(2839)-5075 × 12-(31)-52	Ca: 227-(679)-1247 × 26-(30)-40	76-(149)-221 × 5-(6)-7	Me: 12-(15.6)-31 Sp: 8-(15)-19 Pl: 42-(56)-83 (4–5 actines), actines 10-(27.5)-51	Erect, vasiform or digitate; Kerguelen; 172–315 m
<i>P. tenuirhabda</i> Lendenfeld (1907) (as <i>Chelotropaea</i>) (orig. desc.)	I. 7000–10000 × 8–25 II. 3200–4600 × 35–100 (styles and subtylostyles)	Ca: 300–900 × 30–70 Pg: 600–1400 × 40–75; cladi 200–400; cladome 320–630 Di: 420–900 × 30–80 (+ derivative forms)	I. 90–300 × 7–10 II. 125–200 × 1–2	Me	Massive; St. Paul (S Indian Ocean); 672 m

Legend ([Carvalho et al., 2011](#)): Ca, calthrops; Oc, orthocalthrops; Pc, plagioalthrops; Tr, triod; Or, orthotriaene; Di, dichotriaene; Pg, plagiotriaene; Pr, prototriaene; De, diaene; Mo, monaene; St, streptaster; Sp, spiraster; Pl, plesiaster; Am, amphistaster; Me, metastar.

2.2. Microscopy

Specimens were identified on the basis of mounts of spicules and sections through the sponge body. To make the mounts, a small fragment of sponge was treated in a sodium hypochlorite solution until soft tissues were completely dissolved. Then the spicules were washed five times with distilled water and twice with ethyl alcohol. After each washing, the suspension was left to settle for 25–30 min. Then the spicules were applied to a glass slide, dried, and embedded in Canada balsam. Two mounts were made: from the ectosomal and choanosomal parts of the sponge. A total 25 (unless otherwise specified) randomly selected spicules of each type were measured. The minimum, mean, and maximum dimensions (length and width) were taken into account. The width of oxeas was measured in the middle part; rays of calthrops and triacenes, at the base; styles, in their widest part. For microscleres (except microxeas), only length was taken into account. To study the skeleton structure, sections perpendicular to the surface of the body or tangential sections from the surface were made manually with a scalpel, then were dried and embedded in Canada balsam. The methods for preparing permanent mounts of sponge spicules and tissues followed those described in detail by [Rützler \(1978\)](#), [Hooper \(2003\)](#), [Hooper and Van Soest \(2006\)](#), and [Van Soest et al. \(2014\)](#). The material was processed, and images were taken under an Axio Imager.Z2 light microscope equipped with a digital camera.

For scanning electron microscopy (SEM), a suspension of spicules was applied onto the microscope stub, dried, carbon-coated, and observed and imaged on a Zeiss Sigma 300 VP scanning electron microscope.

2.3. Micro-computed tomography

For micro-computed tomography (micro-CT), material was fixed in 96% ethanol and air dried overnight (according to [Urgorri and Diaz-Agras, 2019](#) with some modifications). Scans were made on a SkyScan 1272 system with the following parameters: 50 kv, 200 μ A, no Filter, rotation step 0.2 deg, image pixel size 3.8 μ m (low resolution) and 1.8 μ m (high resolution). All samples were rotated 180°. The X-ray

projection images obtained during scanning were reconstructed with the NRecon software (Bruker, Belgium), and the CTvox software (Bruker, Belgium) was used to get 3D representations. All micro-CT images represent sections cut from the outer edge through the flat sponge body perpendicular to the surface. The orientation of the section, being single for all species, is shown in [Fig. 2B](#).

2.4. Molecular analyses

Altogether, 8 specimens belonging to four species were used in the analyses: 4 specimens of *Vulcanella koltuni* sp. nov., 2 specimens of *V. commander* sp. nov., 1 specimen of *V. grebelnyi* sp. nov. and 1 specimen of *Poecillastra malyutini* sp. nov. Total DNA was extracted using the Qiagen DNeasy extraction kit according with the protocol. PCR mixture contained 5 μ L Go Taq Green Master Mix (Promega corp, Madison, WI, USA), 0.5 μ M of each primer, 3 μ L of nuclease free water (Ambion) and 1 μ L of genomic DNA. Fragments of the nuclear ribosomal DNA (18S rDNA and 28S rDNA) and the mitochondrial cytochrome oxidase c subunit 1 (COI) genes were tried to amplify. For 18S rDNA, we used the primer set SSU_F_11 and SSU_R_81 ([Blaxter et al., 1998](#)) which amplifies a fragment of ca 1100 bp. The D2-D3 region of the 28S ribosomal DNA was amplified using the primers 28Sa ([Whiting et al., 1997](#)) and D3b ([Nunn, 1992](#)), the length of the obtained amplicon was 500 bp whereas additional D4.8-D7 region of 28S rDNA was amplified using primers 28Srd4.8a and 28Srd7b1 ([Schwendinger and Giribet, 2005](#)) with length of amplicon 1200 bp. For COI, we used the primers LCO1490 and HCO2198 ([Folmer et al., 1994](#)). PCR products were visualized on an 1.5% agarose gel with Ethidium bromide after electrophoresis. Unfortunately, 18S rDNA and D4.8-D7 region of 28S rDNA was amplified only for 5 specimens belonging to three species (*V. koltuni* sp. nov., *V. commander* sp. nov., and *P. malyutini* sp. nov.); the D2-D3 region of 28S rDNA was amplified for 2 specimens (*V. koltuni* sp. nov., *V. commander* sp. nov.); the COI Folmer fragment could not be amplified. Single bands were purified with Exonuclease I and Thermosensitive Alkaline Phosphatase (ThermoFisher Scientific). Purified PCR products were sequenced directly in both directions using an automated sequencer (ABI 3130xl Genetic Analyzer Sequencer; Applied Biosystems, USA) at

Table 3

Comparative micrometric, habit, distribution and depth data for the species of *Vulcanella* known from Pacific. Measurements are expressed in μm , as minimum-(mean)-maximum length $\times$ width value whenever available (modified from [Carvalho et al., 2016](#)).

Species	Oxeas	Trianaes	Microxeas	Asters	Habit; distribution; depth
<i>Vulcanella koltuni</i> sp. nov.	I. 823.4-(1649.9)-3320.0 $\times$ 13.5-(33.4)-54.0 II. >9864.0 $\times$ 5.3-(15.9)-28.9	Or, Pg: rhabdome 225.8-(299.1)-411.7 $\times$ 31.6-(45.4)-52.6; clad 531.2-(715.0)-916.3 $\times$ 34.2-(47.9)-55.2; Or irregular; De	100.7-(128.9)-174.9 $\times$ 5.0-(5.8)-6.6	Sp: 16.2-(18.9)-22.8 Me: 16.9-(19.5)-23.8	From plate-like to cup-shaped; Bering Sea, The northern and southern peaks of the Piip volcano; 347–486 m
<i>Vulcanella commander</i> sp. nov.	I. 1328.0-(3231.8)-5046.4 $\times$ 25.0-(41.7)-60.5 II. 1460.8-(2415.9)-3452.8 $\times$ 10.5-(15.3)-19.5 III. >6108.8 $\times$ 11.0-(15.5)-21.0	Ca: 557.8-(729.3)-863.2 $\times$ 47.7-(54.1)-61.0 Or, Pg: rhabdome 225.8-(388.6)-491.4 $\times$ 37.1-(53.6)-63.6; clad 332.0-(630.5)-929.6 $\times$ 31.8-(53.6)-63.6; Mo, De, De and Or with forked clads	52.6-(60.9)-68.4 $\times$ 2.6-(3.5)-4.7	Sp: 18.4-(24.1)-28.9 Pl I: 26.3-(39.0)-49.0	Plate-like; Bering Sea, Graben Commander; 3599 and 3753 m
<i>Vulcanella grebelnyi</i> sp. nov.	I. 2058.4-(3184.5)-4050.4 $\times$ 39.8-(55.0)-68.9 II. 982.7-(1482.0)-2523.2 $\times$ 10.6-(17.4)-26.5 III. >10225.6 $\times$ 10.6-(17.4)-21.7	Or, Pg: rhabdome 199.2-(283.5)-332.0 $\times$ 31.6-(48.2)-58.7; clad 584.3-(810.1)-969.4 $\times$ 36.8-(51.2)-60.5; De, Or with forked clad (rare)	118.4-(152.5)-210.4 $\times$ 5.8-(7.4)-10.5	Sp: 22.4-(25.6)-28.9 Pl I: 44.7-(58.8)-84.2 Pl II: 21.0-(30.4)-47.3	Plate-like; Bering Sea, slopes of Piip volcano; 981 and 1569 m
<i>V. aberrans</i> (Maldonado and Uriz, 1996) (orig. desc.)	I. 1500–3115 $\times$ 23–70 II. 3500–6000 $\times$ 9–20	Or–Pg: rhabdome 565–1125 $\times$ 9–15; cladome 150–350 $\times$ 7–15	I: 150–315 $\times$ 3–7 II: 65–140 $\times$ 2–2.5	Me: 18–25 Sp: 6–21	Plate-like; W Mediterranean; 70–120 m
<i>V. acanthoxea</i> (Tanita and Hoshino, 1989) (orig. desc.)	I. 1550–5000 $\times$ 33–120 II. >5000 $\times$ 5	Pg: 550–990 $\times$ 70–110 (rhabdome <150, wht rounded end)	I. 95–190 $\times$ 2–6 II. 300–440 $\times$ 10–23 (achantoxeas)	Sp: <20 Me: <25	Fragment (lamellate ?); Japan, Sagami Bay; 300 m
<i>V. bifacialis</i> (Wilson, 1925) (orig. desc.)	I. 2500–4500 $\times$ 60–90 (редко до 1800 $\times$ 35) II. 1500–12000 $\times$ 10–20, common lengths 2000–7000	Or: rhabdome 250–350 $\times$ 50–70; clad 500-(900)-1110 $\times$ 50-(60)-80	250 $\times$ 4	Me: 24 (ray length 12) Sp: 16–20 (ray length 6–8) St: 16–40 Pl I: 40 (ray length 25) Pl II: 32 (ray length 14–20)	Massive; Eastern Philippines; 296 m
<i>V. cribrifera</i> (Sollas, 1888) (orig. desc.)	I. 3035 $\times$ 67 II. >7500 $\times$ 32 Strongyles: 357 $\times$ 28	Or: rhabdome 1000/40 clad 250 $\times$ 32 Ca: 286–636 $\times$ 39.5–80	110	Me: 11.8 (rays) Sp: 16–20	Egg-shaped; Brazil, South Region; Cape Verde; 186–238
<i>V. cribriporosa</i> (Lebwohl, 1914) (orig. desc.)	I. 1900–3300 $\times$ 40–67 II. Up to 5000 $\times$ 7–10	Pg: rhabdome 480–760 $\times$ 35–50; clad 150–340; Or: rhabdome 180–540 $\times$ 22–55; clad 210–590 $\times$ 22–55; Ca: rhabdome 250–690 $\times$ 38–85; clad 240–690 $\times$ 38–85	100–190 $\times$ 4–6	Me: 21–38 Sp: 16–20	Plate-like; Sagami Bay, Japan; 300–400 m (in the habitat area)
<i>V. doederleini</i> (Thiele, 1898) (orig. desc.)	I. 1750–2500 $\times$ 65 II. 4000 $\times$ 15	Present Pg, Or, De, Mo; Ca: 300–450 $\times$ 65	I. 270 $\times$ 12 II. 70–90	Sp	Plate-like; Japan; depth not given
<i>V. gracilis</i> (Sollas, 1888) (orig. desc.)	I. 3800 $\times$ 100 II. 5600 $\times$ 15	Ca: 830 $\times$ 64	350 $\times$ 11.5 140 $\times$ 4 (smooth)	Me: 12 (rays) Sp: 15	Incrusting; Cape Verde; Mediterranean; 186–238 m
<i>V. gracilis</i> (Sollas, 1888) sensu Sarà (1958)	I. 2880 $\times$ 32; 2850 $\times$ 64; 3392 $\times$ 48 II. 9600 $\times$ 12	Ca: 536 $\times$ 48–53	250 $\times$ 9.8 148 $\times$ 3.8 (smooth)	Me: 22 (diameter) 10 (rays) Sp: 15 (diameter) 5 (rays)	Plate-like; Gulf of Genoa; 770 m
<i>V. horrida</i> (Schmidt, 1870) sensu Sollas (1888)	5000 $\times$ 142	Ca and Tr: 1060 $\times$ 106	I: 500 II: 180	Sp: 22	Thick plate; N Atlantic, Florida; 206–422 m
<i>V. horrida</i> (Schmidt, 1870) sensu Maldonado (2002)	I. up to 3000 $\times$ 35 II. up to 5000 $\times$ 142	Ca: 400–1100 $\times$ 40–100	I: 200–500 $\times$ 8–13 II: 100–180 $\times$ 3–4.5	Sp: 12–18	Thick plate; N Atlantic, Florida and Azores; 60–2500 m
<i>V. netheides</i> (Lebwohl, 1914) (orig. desc.)	I. 750–3500 $\times$ 18–150 II. 4000–7000 $\times$ 12–13 III (tylostyles). 550–2550 $\times$ 35–170 IV (strongyles, subtylotes). 2000–2600 $\times$ 100	Pg: rhabdome 590–795 $\times$ 30–52; clad 90–220 Or: rhabdome (often rounded): 40–140 $\times$ 40–115; clad 240–840 $\times$ 30–110	60–405 $\times$ 2.5–18	Me: 19–34 Sp: 14–23	Plate-like; Japan, Sagami Bay; depth not given
<i>V. orthotriaena</i> (Lévi and Lévi, 1983) (orig. desc.)	2400–3600 $\times$ 12–80	Or–Di (almost calthrops): rhabdome 900–1200 $\times$ 45–50; clads 500–700 $\times$ 40–50 (rare dichotriaenes of the same dimensions)	270–400 $\times$ 5–8	St: 15–20 (ray length) $\times$ 45 (diameter) Sp: no measures	Cushion-shaped; New Caledonia; 360–365 m; 500–515 m (Lévi, 1993)
<i>V. osculanigera</i> (Dickinson, 1945) (orig. desc.)	I. 2100 $\times$ 75 II. 800 $\times$ 2	410 $\times$ 95	375 $\times$ 10	Asters: 15	Cushion-shaped; Gulf of California, Tepoca Bay, Mexico; 13 m
<i>V. porosa</i> (Lebwohl, 1914) (orig. desc.)	I. 800–3800 $\times$ 30–125 II. 12000 $\times$ 16 III. styles and tylostyles	Pg: rhabdome 500–1100 $\times$ 30–50; clad 90–260 $\times$ 70–75 Or: clad 300–850 (clads is twice as long as rhabdome)	100–405 $\times$ 3–14 100–405 $\times$ 3–14	Me: 11–22	Plate-like; Japan, Sagami Bay; depth not given

(continued on next page)

Table 3 (continued)

Species	Oxeas	Trianaes	Microxeas	Asters	Habit; distribution; depth
<i>V. porosa</i> (Lebwohl, 1914), sensu Koltun (1966)	I. 800–3800 × 30–125 II. 12000 × 16–30 III. (tylostyles): 1200–2000 × (head) 120–134	Pg: rhabdome 500–1470 × 30–80; clad 90–670 Or: 300–800 (clads is twice as long as rhabdome) Ca: 300–800 De, Mo		Sp (up to Me) 15– 28	Plate-like; Japan, Sagami Bay; Southern Kuril Islands; 137 m
<i>V. stylifera</i> Carvalho et al. (2016) (orig. desc.)	I. 3375–(3897)–4540 × 40– (44)–46 II. 5770–(7000)–11496 × 23–(30)–38 Exotyles: 2403–(3125)– 3780 × 66–(69)–75 Styles: 1850–(2095)–2525 × 10–(15)–27.5	Or: rhabdome 875–(1329)–1725 × 50–(65)–75 cladome 529–(801)– 1120 × 44–(46)–48	130–(350)–446 × 1.9– (2.1)–2.5	Sp: 28–(34)–40 Me: 43–(45)–48	Encrusting or cushion- shaped; Campos Basin (SE Brazil); 1059–1130 m
<i>V. theaides</i> (Burton, 1959) (orig. desc.)	I. 6000–8000 × 40–56	Or (rhabdome = cladome): 480–800 × 32–50 Di: rare Or (with reduced rhabdome): clads 700–1000	no	St: 22–50 4–5 (rays)	Subspherical; Indian Ocean; 878 m
<i>V. tricornis</i> (Wilson, 1904) (orig. desc.)	I. 2500–5000 × 85–135 II. up to 25000 III. 3000–5000 × 12	Or (with reduced rhabdome): clads 700–1000	I: 400–500 × 8–16 II: 120 (nearly smooth)	Me: 20; ray length 8 Sp I: 20; ray length 2–3 Sp II: 24–26; ray length 7–8	Plate-like; Galápagos Islands; 713 m
<i>V. tricornis</i> (Wilson, 1904), sensu Desqueyroux-Faúndez and Van Soest (1997)	I. up to 7000 × 18 II. 2500–3500 × 170–180	Ca: rhabdome 30–55–100; clads 440–860; cladome up to 1000	I. 205–(298)–450 × 8 II. 64–(85)–128 × 3	Sp: 9–(10)–14 Pl: 10–(13)–16	Cushion-shaped; Galápagos Islands; 95 m

Legend (Carvalho et al., 2011): Ca, calthrops; Oc, orthoclathrops; Pc, plagioclathrops; Tr, triod; Or, orthotriaene; Di, dichotriaene; Pg, plagiotriaene; Pr, prototriaene; De, diaene; Mo, monaene; St, streptaster; Sp, spiraster; Pl, plesiaster; Me, metaster.

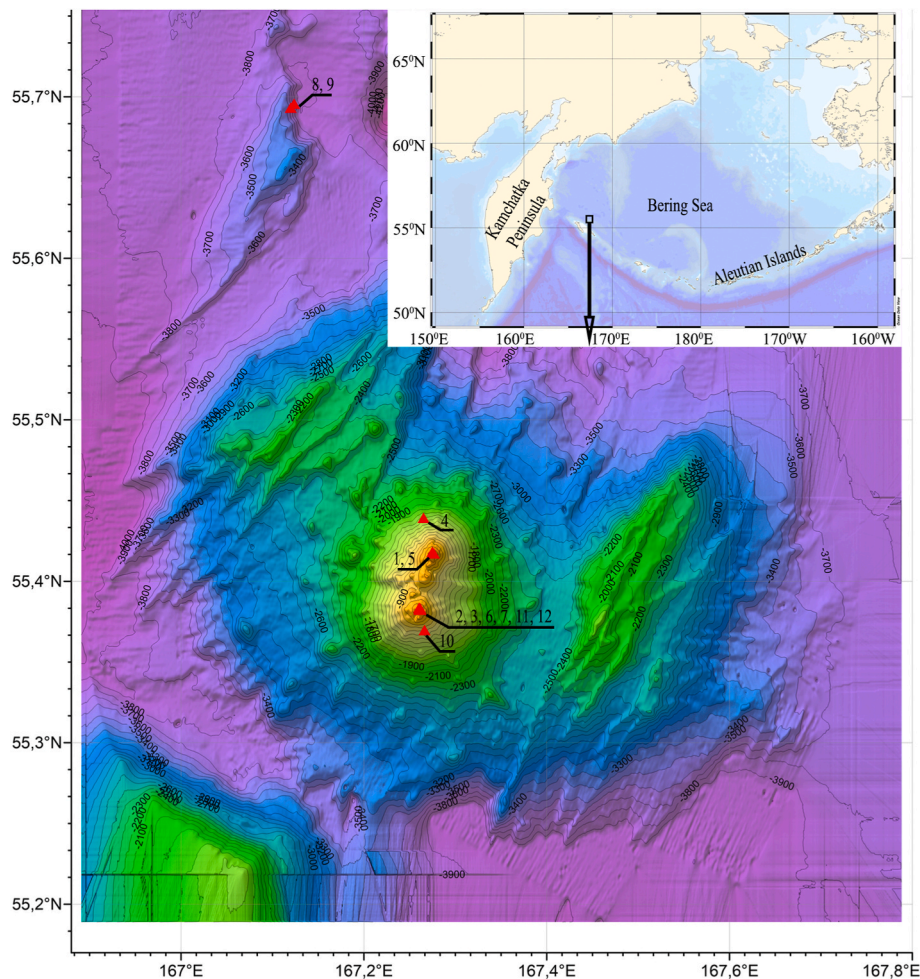


Fig. 1. Map of the investigated area. *Poecillastra malyutini* sp. nov. – sample 5; *Vulcanella koltuni* sp. nov. – samples 1, 2, 3, 6, 7, 11, 12; *V. commander* sp. nov. – samples 8, 9; *V. grebelnyi* sp. nov. – samples 4, 10.

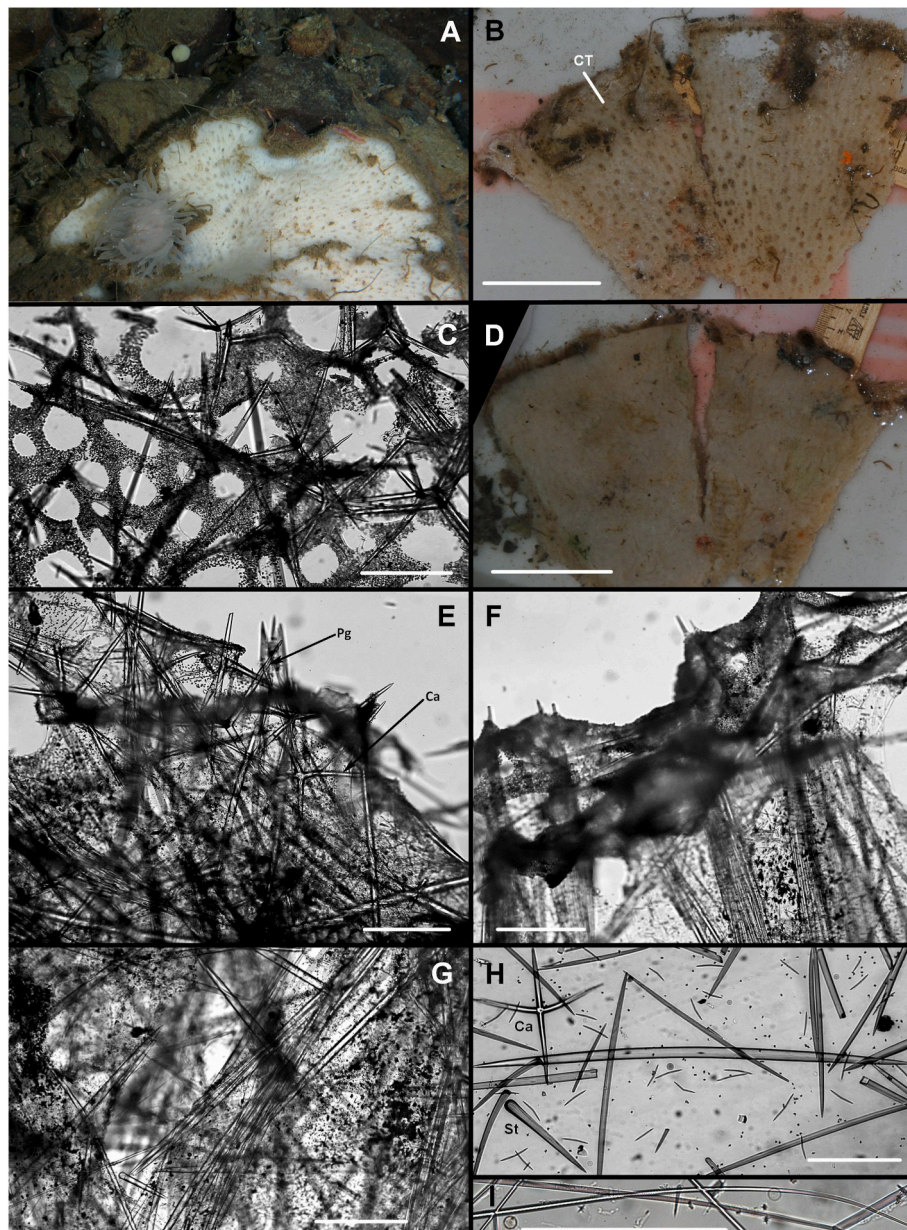


Fig. 2. *Poecillastra malyutini* sp. nov., Holotype MIMB43733: (A) *in situ* image; (B) oscule side (CT – cut direction); (D) pore side; (C) ectosomal skeletal, tangential section, pore side; (E) section perpendicular to the surface, oscule side (Ca – calthrop, Pg – plagiotriaene); (F) section perpendicular to the surface, pore side; (G) choanosomal skeletal; images of spicules: (H) calthrop (Ca), style (St) end oxeas I; (I) oxeas II. Scale bars: B, D – 5 cm; C, E–I – 500 μ m.

department of Cell Biology and Genetics of Far Eastern Federal University.

Forward and reverse sequences were manually assembled and edited using Finch TV (Geospiza Inc., Seattle, WA) and MEGA 7 (Kumar et al., 2016). Alignment of the DNA sequences were performed using the T-Coffee algorithm (Notredame et al., 2000). Base frequencies and molecular character statistics were calculated in MEGA 7.

Phylogenetic trees were constructed using Maximum Likelihood (ML) and Bayesian inference (BI) approaches. The optimal nucleotide substitution model for BI was selected using Partition Finder 2.1.1 (Lanfear et al., 2012) while for the ML analysis was used GTR (Tavaré, 1986) + G (Gamma distribution). The best model of nucleotide substitution for large subunit rDNA was SYM + I (a proportion of invariable sites) + G (Zharkikh 1994) while the best model for small subunit rDNA was GTR + G. ML analysis was performed in RAxML v. 8.2.4 using bootstrapping with 1000 replications (Stamatakis, 2006). BI was carried out using Markov Chain Monte Carlo (MCMC) randomization in

MrBayes v3.2.7 (Ronquist and Huelsenbeck, 2003). Four Markov chains (three heated chains, one cold) were run for 5 million generations, with the first 25% of sampled trees discarded as burn-in. Moreover, trace files were visually inspected in Tracer 1.7 (Rambaut et al., 2018) and then the consensus tree was visualized in FigTree v. 1.4.4. Bayesian posterior probabilities and ML bootstrap values were used to evaluate branch support. We show only a Bayesian tree with the addition bootstrap supports in the branch nodes of ML tree with the same topology. In addition to our sequences, we used GenBank data and only sequences longer than 1600 bp and 700 bp were included in the final SSU and LSU phylogenetic analyses respectively. D4.8-D7 region of 28S rDNA was used only for calculation interspecific distances.

Sequences of *V. koltuni* sp. nov., *V. commander* sp. nov. and *P. malyutini* sp. nov. obtained in this study have been deposited in GenBank (under the accession numbers ON569795, ON569801–ON569804 for 18S rDNA and ON569796, ON569799 for 28S rDNA).

2.5. Stable isotope analysis

For isotope analysis, samples were dried at 60°C for 48 h and ground in an agate mortar. Powdered samples were weighed (~0.6 mg) into tin caps and analyzed at the Laboratory of Stable Isotopes, Far Eastern Geological Institute, FEB RAS, on a FlashEA 1112 elemental analyzer coupled to a MAT 253 isotope mass spectrometer (ThermoQuest, Germany) by a ConFlo IV interface. It has been shown that acidification of samples as a pre-treatment for isotopic analysis is not useful for marine organisms without calcareous structures and is necessary only when the sampled parts contain significant amounts of carbonate (Vafeiadou et al., 2013; Schlacher and Connolly, 2014; Pires-Teixeira et al., 2020). Samples were not acidified, and the lipids were not chemically extracted. Sample isotopic ratios were calculated and expressed in the conventional δ notation as parts per thousand (‰) by the following equation:

$$\delta^{13}\text{C} \text{ or } \delta^{15}\text{N} = [(R_{\text{sample}} - R_{\text{standard}}) / R_{\text{standard}}] \times 1000,$$

where $R = {}^{13}\text{C}/{}^{12}\text{C}$ or ${}^{15}\text{N}/{}^{14}\text{N}$. The δ values were expressed relative to the international reference standards of Pee Dee Belemnite for carbon and atmospheric N_2 for nitrogen. The internal laboratory standard was measured after every sixth sample during analysis for data quality control purposes. Based on the SD of the replicates of the laboratory standard, the internal precision was $\pm 0.1\text{‰}$ for both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$.

3. Results

3.1. Systematic descriptions

Phylum Porifera Grant, 1836

Class Demospongiae Sollas, 1885

Subclass Heteroscleromorpha Cárdenas et al., 2012

Order Tetractinellida Marshall, 1876

Suborder Astrophorina Sollas, 1887

Family Vulcanellidae Cárdenas et al., 2011.

Diagnosis (from Kelly et al., 2019). Astrophorina with calthrops, short-shafted triaenes or long-shafted triaenes, in addition to large oxeas and contorted or sinuous stronglyxeas. Microscleres include several categories of streptasters (spirasters, metasters, amphisters, and pleiasters). Monaxonic spicules consist of one to three categories of spiny microxeas or microstrongyles.

Genus *Poecillastra* Sollas, 1888.

Diagnosis (from Cárdenas et al., 2011). Vulcanellidae with spiny microxeas in a single category, triaenes are pseudocalthrops and/or short-shafted triaenes.

Type species:

Poecillastra compressa (Bowerbank, 1866)

Poecillastra malyutini new species Shilov, Kamenev, Semenchenko.

(Figs. 2A–I, 3A–O, 4A–B)

Type material. Holotype: MIMB43733; R/V *Akademik M.A. Lavrentyev*, cruise 82, stn. 1, sample 5.

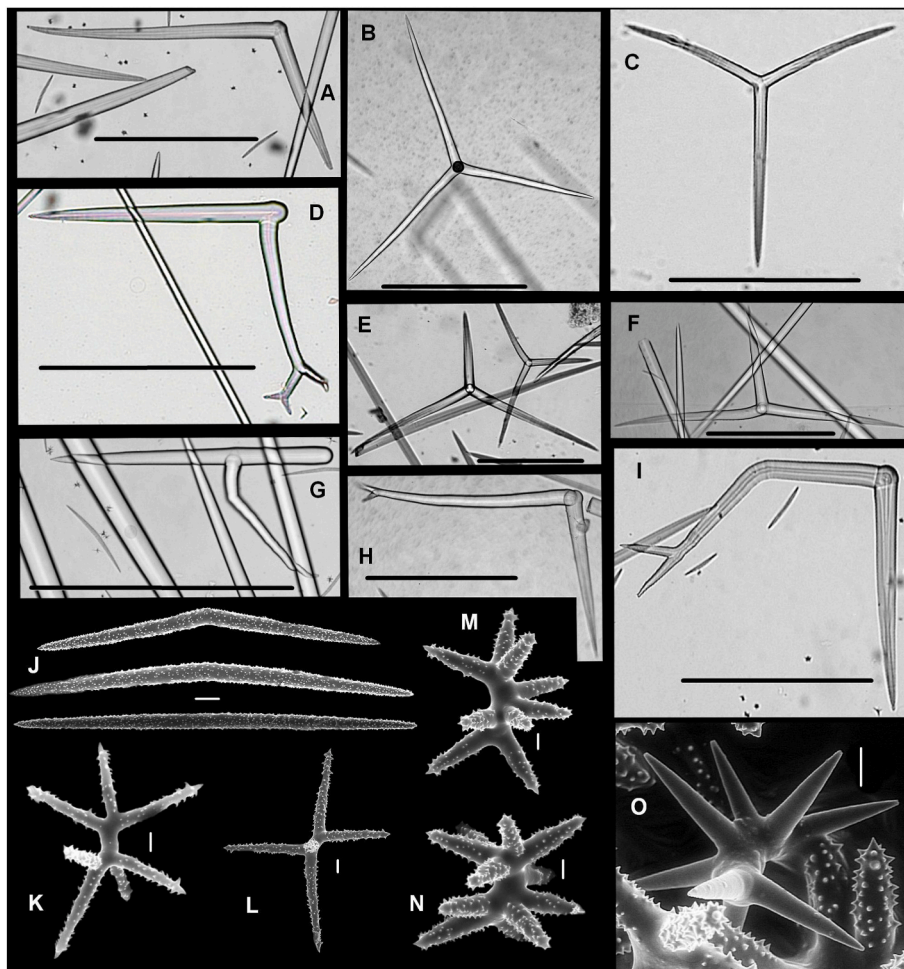


Fig. 3. *Poecillastra malyutini* sp. nov., images of spicules: (A) monaene; (B) calthrop; (C) diaene; (E) plagiatriaenes; (F) orthotriaene; (D, G–I) monaenes irregular; (J) acanthomicroxeas; (K, L) pleiasters; (M–O) spirasters. Scale bars: A–I – 500 μm ; J – 10 μm ; K–O – 2 μm .

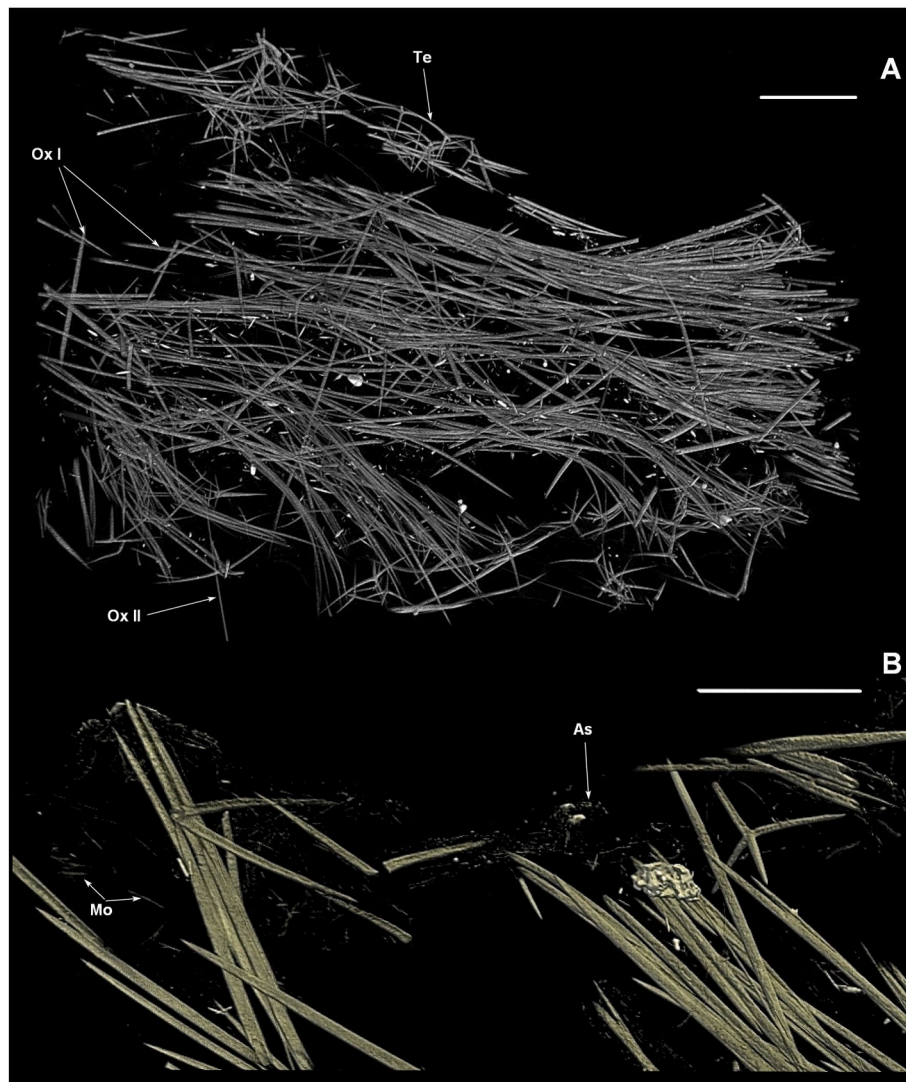


Fig. 4. *Poecillastra malyutini* sp. nov., Micro-CT image of skeleton of the Holotype. (A) section perpendicular to the surface (low resolution): Te – triaenes, Ox I – oxeas I, Ox II – oxeas II. (B) section perpendicular to the surface, oscule side (high resolution): Mo – microxeas, As – asters. Scale bars: A – 1 mm; B – 500 μ m.

Material examined. Type material.

Locality. Bering Sea, the northern summit of the Piip volcano, 55.4163° N, 167.2765° E, depth 382 m.

Etymology. The species is named in tribute to Dr. Andrey Malyutin (1960–2018), a member of the research team of the cruise 2018 to the area of the Piip submarine volcano.

Measurements. See Table 2 and text.

Sponge body (Fig. 2A) plate-like in shape, 25 $\times$ 30 cm. The examined fragment 13.5 cm wide, 15 cm tall, and 1.5 cm thick. The outer edge of the fragment 0.5 cm thick. Surface rough (microhispid) due to the protruding ends of oxeas I. Oscules of up to 2000 μ m in diameter concentrated on one side (Fig. 2B). The opposite side (Fig. 2D) bears large number of pores with a diameter of 120–270 μ m. Consistency hard but compressible. Color of live specimens white; alcohol-fixed specimens light beige. In the photographs taken *in situ*, the sediment on the upper side gives the sponge a dirty brown color.

Skeleton (Figs. 2C, E–G and 4A, B). Ectosome contains microscleres at a much greater concentration than choanosome (Figs. 2C and 3B). Sets of megascleres similar between ectosome and choanosome. Choanosomal skeleton consists of loose bundles of oxeas I (Figs. 2G and 4A). In ectosome of the lower sponge surface, bundles of oxeas I oriented perpendicular to the surface. Tips of oxeas I protrude up to 500 μ m above surface, supporting the ectosomal membrane and creating

microhispid texture of the surface (Figs. 2F and 4A, B). Calthrops and plagiotriaenes located irregularly in the choanosome and ectosome, with larger numbers in the ectosome (Figs. 2E and 4A, B). Oxeas II form an uneven, discontinuous palisade up to 5 mm wide along the outer edge of sponge, and also present in small numbers in ectosome and choanosome.

Spicules. Megascleres (Fig. 2H and I; 3A–I). Oxeas I (Fig. 2H) fusiform, slightly curved 1062.4–(2230.5)–3399.7 $\times$ 29.2–(53.2)–76.9 μ m. Styles (up to subtilostyles) (Fig. 2H) (N = 21) 584.3–(1714.4)–2483.4 $\times$ 45.1–(79.6)–116.6 μ m. Strongyles (rare, N = 5) 1168.6–(1540.5)–1859.2 $\times$ 45.1–(61.0)–68.9 μ m. Oxeas II (Fig. 2I) long, more than 8366.4 μ m in length and 10.5–(16.2)–23.7 μ m in width. Calthrops (Figs. 2H and 3B), rays 398.4–(513.1)–743.7 $\times$ 34.2–(41.2)–52.6 μ m. Plagiotriaenes (up to orthotriaenes) (Fig. 3E and F): rhabdome 225.8–(338.4)–411.7 $\times$ 28.9–(44.9)–57.9 μ m; clad 398.4–(599.7)–916.3 $\times$ 31.6–(49.9)–60.5 μ m. Rarely monaenes, diaenes, monaenes with forked or curved clads (Fig. 3A, C, D, H–I). Microscleres (Fig. 3J–O). Acanthomicroxeas (Fig. 3J), usually slightly curved, 121.9–(156.0)–212.0 $\times$ 5.0–(6.1)–7.2 μ m. Spirasters (Fig. 3M–O) (sometimes smooth) 13.2–(19.6)–23.7 μ m. Plesiasters (Fig. 3K, L) 17.1–(24.6)–32.9 μ m.

Diagnosis. *Poecillastra* with two categories of oxeas, subtylostyles, strongyles, calthrops and triaenes with short rhabdome. Acanthomicroxeas in one category, from straight to slightly curved, never

centrotylotes. Streptasters of two categories (spirasters and plesiasters).

Distribution and habitat. The northern and southern summits of the Piip volcano. In the images taken with the ROV *Comanche-18*, five specimens were observed on the northern summit of the Piip volcano within a depth range of 347.3–393.5 m and five on the southern summit at depths of 463–470 m. All specimens were located in the vent zone. Moreover, two specimens that externally resembled *Poecillastra malyutini* sp. nov. were found on the northern slope, at depths of 1308 and 1329 m; however, additional material is needed to confirm the identification of the species for complete certainty. The specimens were attached to the bedrock.

Relationships. The new species is distinguished by having two size categories of oxeas, of which one is thin and long ($>8366.4 \times 10.5$ – $23.7 \mu\text{m}$). Apart from the new species, only three other Pacific species of *Poecillastra* have long thin oxeas that are comparable in length and width to those of *P. malyutini* sp. nov.: *P. laminaris* (Sollas, 1886), *P. marentana* Carvalho et al., 2011, and *P. rickettsi* de Laubenfels, 1930 (see Table 2).

Poecillastra laminaris has oxeas in two categories, of which one is thin and long. However, oxeas II in *P. laminaris* do not reach the length of oxeas II in *P. malyutini* sp. nov. Trienes in *P. laminaris* are significantly smaller than those in *P. malyutini* sp. nov. In trienes, the rhabdome to clad length ratio is opposite. Spirasters in *P. laminaris* are multi-turn, with shorter rays.

Poecillastra marentana has oxeas in three categories, with the average width of the longest ones (III, $>4600 \mu\text{m}$) being only $10.2 \mu\text{m}$, whereas in *P. malyutini* sp. nov. it is $16.2 \mu\text{m}$. Furthermore, *P. marentana*, of four-ray spicules, has only calthrop but lacks plagiotriaenes, orthotriaenes, diaenes, and monaenes; microxeas are centrotylote and two categories of plesiasters are present.

The long ($17\,000 \mu\text{m}$) oxeas in *P. rickettsi* form palisades around oscular areas, which is a sign indicating that it belongs to the genus *Vulcanella*. It is likely that after a thorough re-examination of the holotype of *P. rickettsi* its status will change. In addition, the oxeas of the first category in *P. rickettsi* are longer and thicker, especially taking into account the fact that Laubenfels (1932) reported their average size. *P. rickettsi* has only calthrops, whereas the new species has hasplagiotriaenes, orthotriaenes, diaenes, and monaenes. There are also significant differences in size of microscleres.

Among geographically close species, of particular note are *P. japonica* (Thiele, 1898) and *P. tenuilaminaris* (Sollas, 1886). In *P. japonica* from the Bering Sea and the seas of Okhotsk and Japan (Koltun, 1966), oxeas are much thicker and do not reach the length recorded from *P. malyutini* sp. nov. Spirasters in *P. japonica* vary greatly in appearance, and metastars are significantly larger than plesiasters in *P. malyutini* sp. nov. Acanthomicroxeas *P. japonica* are frequently centrotylote, while *P. malyutini* sp. nov. lacks them.

Poecillastra tenuilaminaris also lacks long, thin oxeas. According to various authors, *P. tenuilaminaris* has smaller calthrops and lacks triene and their derivatives, except triods in *P. tenuilaminaris* sensu Stone et al. (2011) and orthotriaenes in *P. tenuilaminaris* sensu Sollas (1888). Furthermore, *P. tenuilaminaris* has shorter and thinner microxeas.

Among species from other regions of the ocean, *P. compressa antarctica* sensu Boury-Esnault and van Beveren (1982) and *P. tenuirhabda* (Lendenfeld, 1907) have thin, long oxeas, but there are also significant differences (see Table 2).

Poecillastra compressa antarctica sensu Boury-Esnault and van Beveren (1982) has oxeas in a single category, with their maximum width significantly greater than that of the new species. Of tetractins, only calthrops are present, while plesiasters are much larger than those in the new species.

Poecillastra tenuirhabda (Lendenfeld, 1907) has oxeas in a single category, with dichotriaenes present, microxeas in two categories, and lacks spiraster.

The new species is characterized by oxeas in two categories including thin, long, subtylostyles, strongyles, and a large number of triene

derivatives (diaenes and monaenes). Microxeas are never centrotylote. Smooth spirasters are present. Such a set of traits allows erecting *P. malyutini* sp. nov. into a separate species.

Nucleotide sequences. GenBank accession numbers ON569802 for 18S rDNA.

Vulcanella Sollas, 1886.

Diagnosis (from Cárdenas et al., 2011). Vulcanellidae with spiny microxeas in one to three categories, with a more or less conspicuous ringed ornamentation; trienes are calthrops and/or short-shafted trienes or long-shafted trienes.

Type species:

Vulcanella horrida (Schmidt, 1870)

Vulcanella koltuni new species Shilov, Kamenev, Semchenko. (Figs. 5A–I, 6A–J, and 7A–B)

Type material. Holotype: MIMB43742; R/V *Akademik M.A. Lavrentyev*, cruise 82, stn. 8, sample 1. Paratypes: R/V *Akademik M.A. Lavrentyev*, cruise 75: MIMB43738, stn. 10, sample 3; MIMB43737, stn. 13, sample 2; MIMB43734, stn. 15, sample 3, Sp. 1; MIMB43735, stn. 15, sample 3, Sp. 2; MIMB43736, stn. 15, sample 3, Sp. 3. R/V *Akademik M.A. Lavrentyev*, cruise 82: MIMB43744, stn. 3, sample 2; MIMB43741, stn. 3, sample 2, Sp. 1; MIMB43740, stn. 3, sample 2, Sp. 2; MIMB43743, stn. 4, sample 1, Sp. 1; MIMB43739, stn. 8, sample 2.

Material examined. Type material.

Locality. Bering Sea, the northern peak of the Piip volcano, 55.3814° N, 167.2617° E. Depth 469 m.

Etymology. The species is named in tribute to Dr. Vladimir Mikhailovich Koltun (1921–2004), a world-renowned Soviet and Russian spongiologist, commemorating the 100th anniversary birth.

Measurements. See Table 3 and text.

Sponge cup-shaped, ca. 25 cm in width (Fig. 5A). The studied fragment 25.5 cm wide, 19 cm tall, and 2 cm thick. The surface rough (microhispid) due to the protruding ends of oxeas I and II. Upper side (Fig. 5B) bears cribiporal oscules (Fig. 5C) irregular in shape, 14–42 mm, covered by membrane with apertures up to 1 mm in diameter and surrounded by palisade of oxeas II. A similar palisade of oxeas II encircles outer edge of the fragment (Fig. 5D). Consistency rather hard but compressible. Color of live specimens white; alcohol-fixed specimens light beige. In the photographs taken *in situ*, the sediment on the upper side gives the sponge a dirty brown color. Other specimens, according to photo and video materials, have a cup- or plate-like shape and are 5–30 cm in size.

Skeleton (Figs. 5E–G, 7). Ectosome contains a large number of microscleres, mainly spirasters (Fig. 5G). Metastars and acanthomicroxeas found in smaller numbers. Relative number of spirasters decreases with distance from surface. Trienes occur only in ectosome, on the side of cribiporal oscules (Figs. 5E and 7). Oxeas I and II permeate surface. Oxeas II form palisade around oscules and along the outer edge of sponge. Choanosomal skeleton (Figs. 5F and 7) formed by randomly confused loose bundles of oxeas I and, to a lesser extent, II, and also by single oxeas. Immediately below surface, a portion of oxeas oriented vertically and permeate dermal membrane (Fig. 7). Skeleton of membrane covering oscules consists of oxeas I and microscleres, mainly spirasters.

Spicules. Megascleres (Figs. 5H and I; 6A–D). Oxeas I (Fig. 5H) fusiform, slightly curved ($N = 100$) 823.4 – (1649.9) – 3320.0×13.5 – (33.4) – $54.0 \mu\text{m}$. Measurement of a large number of oxeas I showed the lack of their division into different size categories. Oxeas II (Fig. 5I) long and thin, more than $9864.0 \mu\text{m}$ in length and 5.3 – (15.9) – $28.9 \mu\text{m}$ in width. Orthotriaenes (plagiotriaenes) (Fig. 6A and B): rhabdome 225.8 – (299.1) – 411.7×31.6 – (45.4) – $52.6 \mu\text{m}$; clad 531.2 – (715.0) – 916.3×34.2 – (47.9) – $55.2 \mu\text{m}$. In a small amount of dienes and trienes with curved clads (Fig. 6A, C, D). Microscleres (Fig. 6E–J). Acanthomicroxeas (Fig. 6E and F) 100.7 – (128.9) – 174.9×5.0 – (5.8) – $6.6 \mu\text{m}$. In the middle part of acanthomicroxeas, spines form ringed ornamentation expressed to varying degrees. Spirasters (Fig. 6I and J) 16.2 – (18.9) – $22.8 \mu\text{m}$. Metastars (Fig. 6G and H) 16.9 – (19.5) – $23.8 \mu\text{m}$.

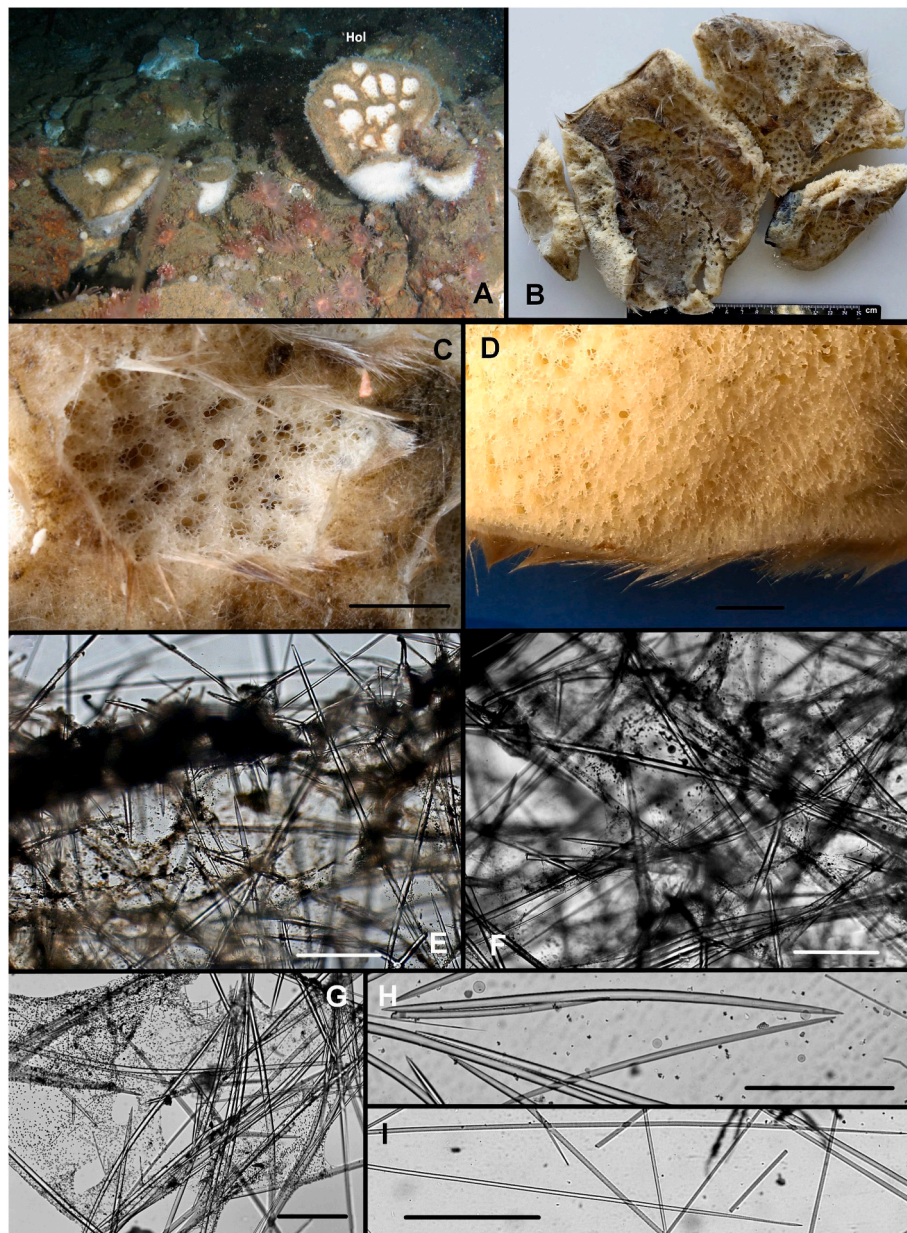


Fig. 5. *Vulcanella koltuni* sp. nov., Holotype MIMB43742: (A) *in situ* image (Hol); (B) oscule side; (C) oscule; (D) pore side; (E) section perpendicular to the surface, oscule side; (F) choanosomal skeletal; (G) ectosomal skeletal, tangential section, pore side; (H) oxeas I; (I) oxeas II. Scale bars: C, D – 1 cm; E-I – 500 μm.

Diagnosis. *Vulcanella* with two categories of oxeas, and triaenes with short rhabdome. Acanthomicroxeas with a ringed ornamentation in the middle, expressed to varying degrees. Streptasters of two categories (spirasters and metasters).

Distribution and habitat. The northern and southern peaks of the Piip volcano. The images and videos show 205 specimens on the northern peak of the Piip volcano within a depth range of 347–415 m and 163 specimens on the southern peak, at depths of 460–486 m. All specimens are located in the vent zone, with most of them being in the immediate vicinity to it. The substrate is bedrock and stones.

Relationships. In the composition of spicules, the new species is most similar to the species described in 1914 by Lebwahl for Sagami Bay, Japan: *V. cribriporosa*, *V. netheides*, and *V. porosa* (Table 3). At the same time, there are significant differences.

The new species differs from *V. cribriporosa* (Lebwahl, 1914) and *V. netheides* (Lebwahl, 1914) by much longer and thicker oxeas II. *V. koltuni* sp. nov. lacks tylostyles, strongyles or subtylotes that were

reported by Lebwahl (1914) for *V. netheides*. Triaenes of *V. koltuni* sp. nov. are with a very short rhabdome, whose average length is 2.4 times in clad length. In *V. cribriporosa* and *V. netheides*, the rhabdome to clad length ratio is inverse. *V. koltuni* sp. nov. is also distinguished by triaenes with curved rays and diaenes. The differences in the structure and size of microcleres are also pronounced. In microxeas of *V. koltuni* sp. nov., the ringed ornamentation is expressed to varying degrees only in the middle. Microxeas of *V. netheides* vary greatly in size, within 60–405 μm, and only larger ones have a clearly conspicuous ringed ornamentation. In *V. cribriporosa*, all microxeas have thickening in the middle. Metasters *V. koltuni* sp. nov. are significantly smaller in size than metasters in *V. cribriporosa* and *V. netheides*.

Vulcanella porosa (Lebwahl, 1914) and *V. porosa* sensu Koltun (1966) have long oxeas II, comparable in size to oxeas II in *V. koltuni* sp. nov. However, *V. porosa* is distinguished from the new species by the presence of tylostyles and plagiotriaenes with a long rhabdome. Microxeas of *V. porosa* are centrotylote and are larger in size than those of *V. koltuni*

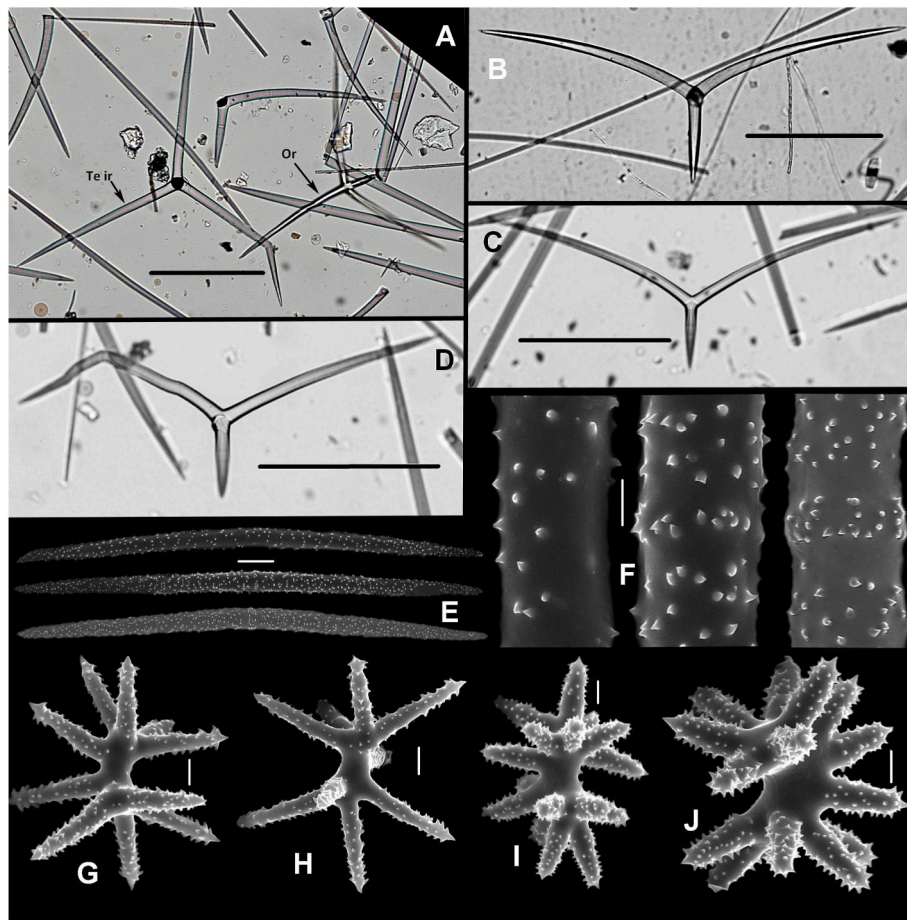


Fig. 6. *Vulcanella koltuni* sp. nov., images of spicules: (A) triaene irregular (Te ir) and orthotriaene (Or); (B) orthotriaene; (C) diaene; (D) plagiortriaene irregular; (E) acanthomicroxeas; (F) acanthomicroxeas, middle parts; (G, H) metasters; (I, J) spirasters. Scale bars: A-D – 500 µm; E – 10 µm; F-J – 2 µm.

sp. nov.

The new species has more significant differences from other *Vulcanella* species. Especially from *V. gracilis* (Sollas, 1888) from the North Atlantic and the Mediterranean Sea. However, of four-ray macroscleres, this species has only calthrops, and also two types of microxeas, including smooth ones.

Nucleotide sequences. GenBank accession numbers ON569795, ON569803, ON569804 for 18S rDNA and ON569799 for 28S rDNA.

***Vulcanella commander* new species** Shilov, Kamenev, Semenchenko.

(Figs. 8A–G, 9A–L, 10A–G, 11)

Type material. Holotype: MIMB43746; R/V *Akademik M.A. Lavrentyev*, cruise 82, stn. 6, sample 2. Paratype: MIMB43745; R/V *Akademik M.A. Lavrentyev*, cruise 82, stn. 6, sample 1.

Material examined. Type material.

Locality. Bering Sea, Graben Commander, 55.6922° N, 167.1199° E. Depth 3599 m.

Etymology. The species is named after the place of finding, the Commander Basin, north of the Piip volcano.

Measurements. See Table 3 and text.

Sponge plate-like in shape, 10 cm wide and 1.5 cm thick (Fig. 8A and B). Upper side (Fig. 8B) bristly (strongly hispid) due to protruding ends of oxeas I and II. Cribiporal oscules (Fig. 8D) on sponge upper side from 7 to 20 mm in size, covered by membrane with apertures up to 0.5–3.5 mm in diameter and surrounded by palisade of oxeas III. A similar palisade of oxeas III encircles outer edge of sponge. Lower side (Fig. 8C, E) covered by sieve with apertures up to 1 mm. Several bundles of oxeas III up to 10 mm long also present. Consistency rather hard but compressible. Oxeas on the upper side are covered by deposit that gives

the sponge a dirty brown color. The deposit is insoluble in sodium hypochlorite, but soluble in concentrated nitric acid.

Skeleton (Figs. 8F and G; 9A and B; 11). Ectosomal skeleton (Figs. 8F and 11) is formed by oxeas I and II, of which some are arranged radially and protrude 4–5 mm above the surface, and also by calthrops and triaenes. Ectosome contains a large number of spirasters, while plesiasters and acanthomicroxeas in smaller numbers. The relative number of spiraster decreases with distance from the surface. Calthrops and triaenes are found only in ectosome of the sponge upper side (Figs. 8F and 11). Choanosomal skeleton (Figs. 9A and 11) is formed by randomly arranged oxeas I and II, with the latter being in a small number. Membrane skeleton covering oscules (Fig. 8G) and sieve skeleton of the (Fig. 9B) on the sponge lower side are also formed by oxeas I and II and microscleres, mainly spirasters.

Spicules. Megascleres (Fig. 9C–L). Oxeas I (Fig. 9C) fusiform, slightly curved, sometimes turning into styles 1328.0–(3231.8)–5046.4 × 25.0–(41.7)–60.5 µm. Oxeas II (Fig. 9D) thin 1460.8–(2415.9)–3452.8 × 10.5–(15.3)–19.5 µm. Oxeas III (Fig. 9E) long and thin, more than 6108.8 µm in length and 11.0–(15.5)–21.0 µm in width. Calthrops (Fig. 9F), rays 557.8–(729.3)–863.2 × 47.7–(54.1)–61.0 µm. Orthotriaenes (up to plagiortriaenes) (Fig. 9G): rhabdome 225.8–(388.6)–491.4 × 37.1–(53.6)–63.6 µm; clad 332.0–(630.5)–929.6 × 31.8–(53.6)–63.6 µm. In a small number of monaenes, diaenes, diaenes, and triaenes with one or two forked clads (Fig. 9H–L). Microscleres (Fig. 10A–G). Acanthomicroxeas (Fig. 10A and B) from straight to strongly curved, many centrotylote, 52.6–(60.9)–68.4 × 2.6–(3.5)–4.7 µm. Spirasters (Fig. 10C–E) 18.4–(24.1)–28.9 µm. Plesiasters (Fig. 10F and G) with 3–8 rays, 26.3–(39.0)–49.0 µm.

Diagnosis. *Vulcanella* with three categories of oxeas, calthrops and

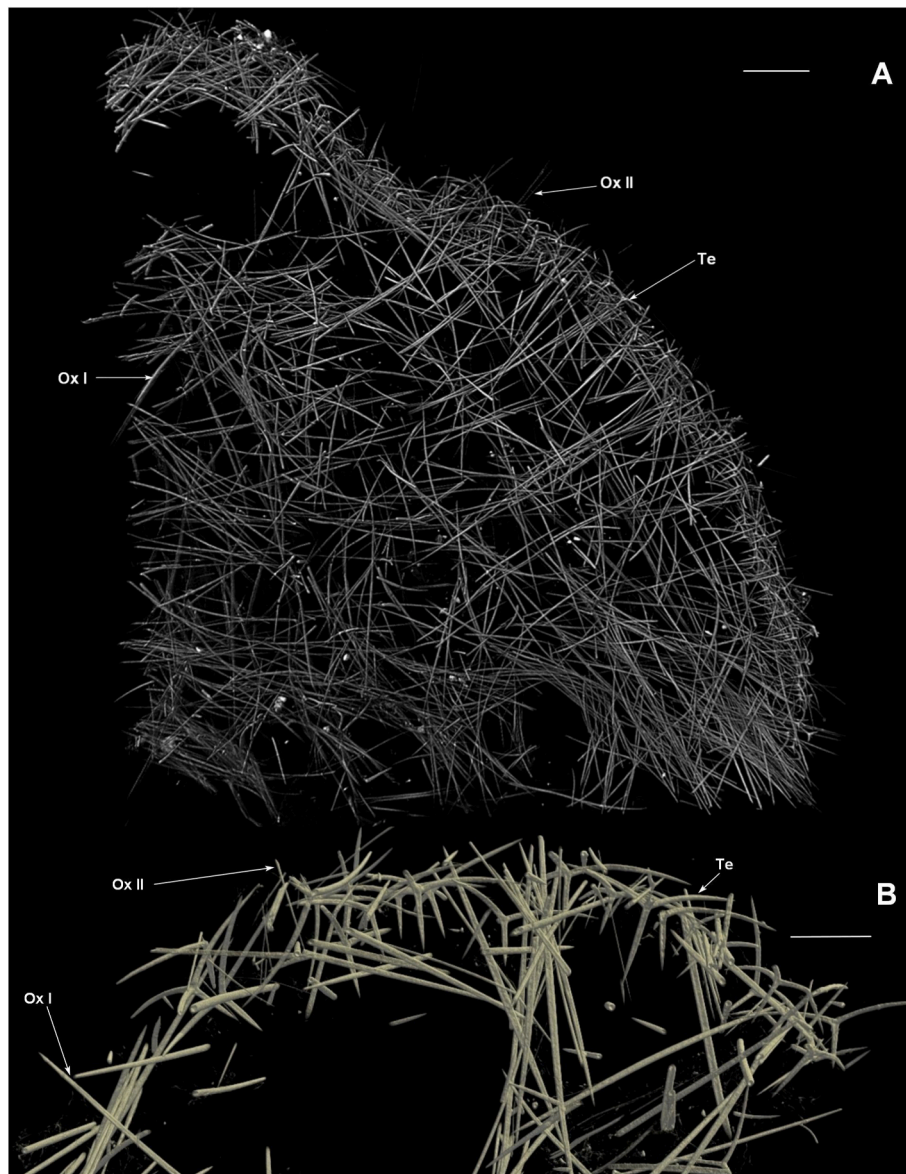


Fig. 7. *Vulcanella koltuni* sp. nov., Micro-CT image of skeleton of the Holotype. (A) section perpendicular to the surface (low resolution). (B) section perpendicular to the surface, oscule side (high resolution): Te – triaenes, Ox I – oxeas I, Ox II – oxeas II. Scale bars: A – 1 mm; B – 500 μ m.

triaenes with short rhabdome. Acanthomicroxeas in one category, from straight to strongly curved, many centrotylote. Streptasters of two categories (spirasters and plesiasters).

Distribution and habitat. Two findings in the Graben Commander at depths of 3599 and 3753 m. The substrate is the skeleton of *Periphragella* sp. (Hexactinellida: Euretidae).

Relationships. A characteristic trait of *V. commander* sp. nov. is the presence of a continuous cover of long oxeas I and II protruding above the surface. Oscules are surrounded by palisade of even longer oxeas III. The zone containing pores on the sponge lower side is covered by a kind of sieve with small apertures. The sieve probably serves to protect the pores from clogging with silt particles that are abundant in sponge's habitat. A similar sieve covering the pores is characteristic of the family Theneidae. There are other traits characteristic of Theneidae. For example, acanthomicroxeas in *V. commander* sp. nov. resemble plesiasters reduced to two rays and are much larger than “ordinary” plesiasters (Cárdenas et al., 2011). In addition, some microxeas are strongly curved in the middle and their ends resemble plesiaster rays in structure (Fig. 9A and B). But the new species lacks triaenes with long rhabdome characteristic of Theneidae: anatriaenes, protriaenes, and dichotriaenes.

The body shape and the absence of root-like outgrowths also suggest affinity to the genus *Vucanella*.

The Pacific species of *Vulcanella* with long thin oxeas differ significantly from *V. commander* sp. nov. in the set and size of spicules (Table 3):

Vulcanella acanthoxea (Tanita and Hoshino, 1989) lacks calthrops and has only plagiotriaenes with short rhabdome. Two categories of microxeas, with asters shorter.

Vulcanella bifacialis (Wilson, 1925) lacks calthrops and has only orthotriaenes with short rhabdome. The length of the microxeas is 4-fold longer; the set of asters is more diverse: metasters, streptasters, and two categories of plesiasters.

Vulcanella cribriporosa (Lebwohl, 1914) has plagiotriaenes with rhabdome that are much longer than clads; microxeas are longer, while metasters and spirasters are smaller in size.

Vulcanella nethoides (Lebwohl, 1914), *V. porosa* (Lebwohl, 1914), and *V. porosa* sensu Koltun (1966) have styles, tylostyles, strongyles, and subtylostyles (depending on species); in plagiotriaenes, rhabdome is several times longer than clads; the maximum size of microxeas is six-fold larger; metasters and spirasters are smaller.

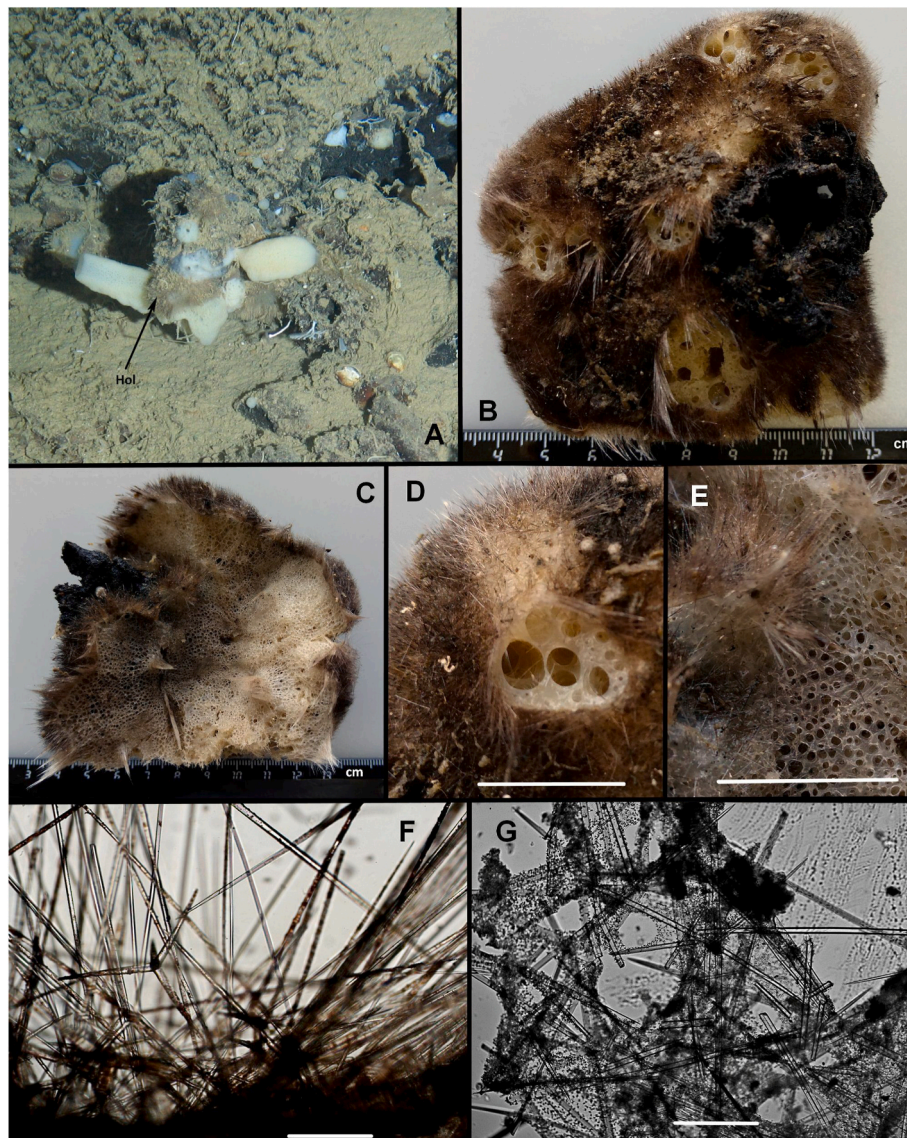


Fig. 8. *Vulcanella commander* sp. nov., Holotype MIMB43746: (A) *in situ* image (Hol); (B) oscule side; (C) pore side; (D) oscule; (E) pore side, fragment; (F) section perpendicular to the surface, oscule side; (G) the skeleton of the oscule membrane. Scale bars: D, E – 1 cm; F, G – 500 μm.

Vulcanella orthotriaena (Lévi and Lévi, 1983) has oxeas in a single category; rhabdome in triaenes is longer than clads; microxeas are much longer.

Vulcanella tricornis (Wilson, 1904) has only orthotriaenes with reduced rhabdome, two categories of microxeas and two categories of spirasters.

Vulcanella tricornis sensu Desqueyroux-Faúndez and Van Soest (1997) has only calthrops with a shortened rhabdome (rather plagiotriaenes), two categories of microxeas, spirasters and plesiasters of much smaller sizes.

All Pacific species, except *V. tricornis*, have oxeas in two categories.

The species from the Atlantic and the Mediterranean Sea also differ substantially from *V. commander* sp. nov.:

Vulcanella aberrans (Maldonado and Uriz, 1996) has triaenes with rhabdome significantly longer than clads, two categories of microxeas, and lacks calthrops.

Vulcanella cribrifera Sollas (1886) has triaenes with rhabdome significantly longer than clads.

Vulcanella gracilis (Sollas, 1888) lacks triaenes and has only calthrops; two categories of microxeas, of which one is smooth.

Vulcanella stylifera Carvalho et al. (2016) has exotyles and styles.

Rhabdome in triaenes is much longer than clads; calthrops are absent. The average size of microxeas is six times the size of microxeas in *V. commander* sp. nov.

Furthermore, *V. commander* sp. nov. is distinguished from all species of *Vulcanella* (except *V. porosa* sensu Koltun (1966)) by having three derivatives of triaenes: monaenes, diaenes, and also diaenes and triaenes with bifurcated clads.

Nucleotide sequences. GenBank accession numbers ON569801 for 18S rDNA and ON569796 for 28S rDNA.

***Vulcanella grebelnyi* new species** Shilov, Kamenev, Semchenko

(Figs. 12A–H, 13A–L, and 14)

Type material. Holotype: MIMB43749, R/V *Akademik M.A. Lavrentyev*, cruise 75, stn. 18, sample 3, Sp. 4. Paratypes: R/V *Akademik M.A. Lavrentyev*, cruise 75: MIMB43750, stn.18, sample 3, Sp. 5. R/V *Akademik M.A. Lavrentyev*, cruise 82: MIMB43747, stn. 7, sample 2, Sp. 13; MIMB43748, stn. 7, sample 2, Sp. 16.

Material examined. Type material.

Locality. Bering Sea, the northern slope of the Piip volcano, 55.4382° N, 167.2652° E. Depth 1569 m.

Etymology. The species was named in tribute to Dr. Sergey

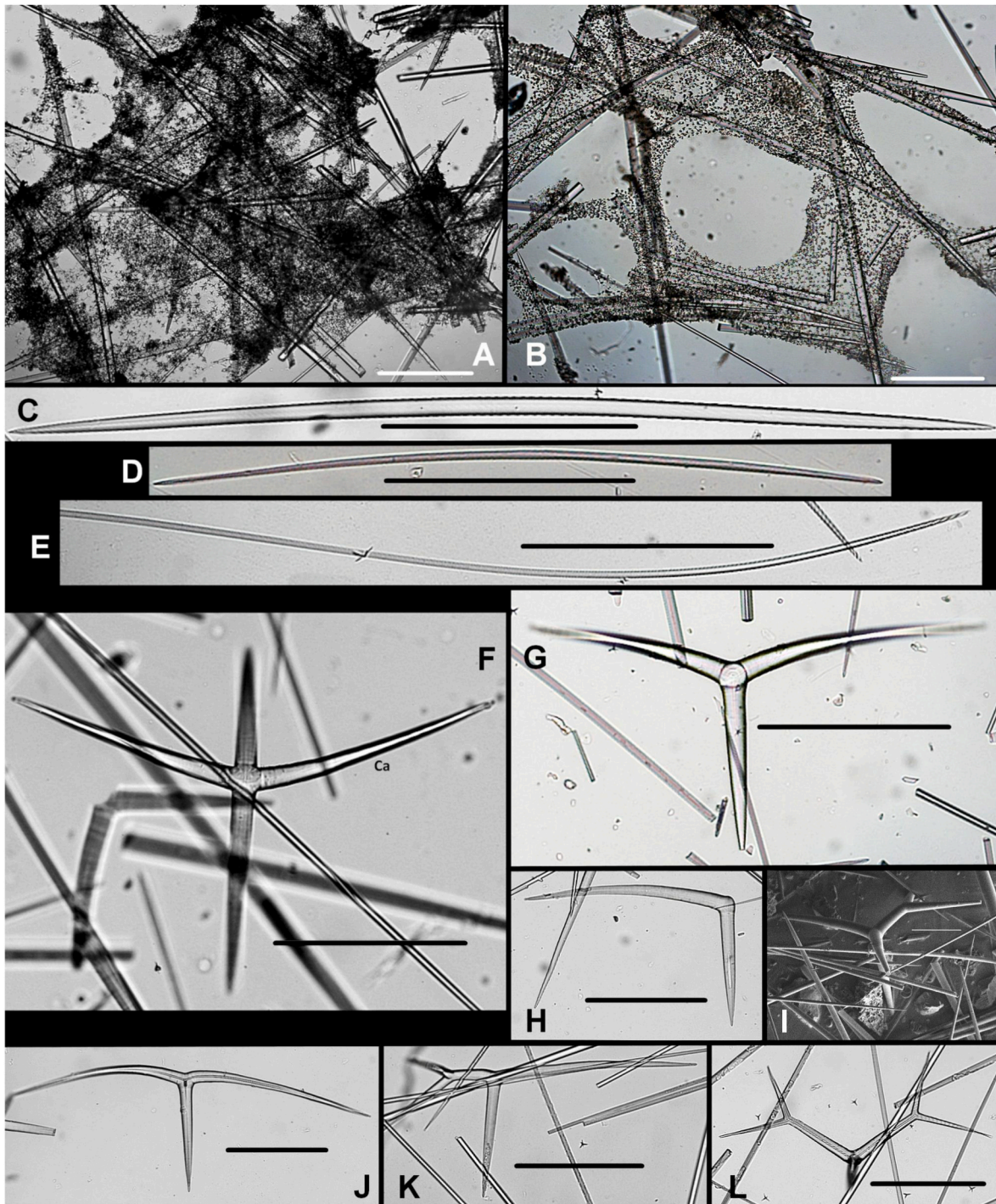


Fig. 9. *Vulcanella commander* sp. nov. 2: (A) choanosomal skeletal; (B) ectosomal skeletal, tangential section, pore side; images of spicules: (C) oxea I; (D) oxea II; (E) oxea III; (F) calthrop (Ca); (G) orthotriaene; (H) monaene; (I) orthotriaene with forked clad (J) diaene; (K, L) diaenes with forked clads. Scale bars: A-H, J-L – 500 µm; I – 200 µm.

Dmitrievich Grebelny, a researcher from the Zoological Institute, Russian Academy of Sciences, St. Petersburg.

Measurements. See Table 3 and text.

Sponge body plate-like in shape, 4×3.5 cm, up to 1 cm thick. Surface is rough (microhispid) due to the protruding ends of oxeas I and II. On upper side (Fig. 12A), an oscule of 1.5 cm in diameter surrounded by palisade of oxeas III and covered by netting with apertures of up to 0.6 mm in diameter. Fragments of a similar netting are also visible on the lower side (Fig. 12B). Unfortunately, the sponge is severely damaged, possibly with the ROV manipulator during sampling. Palisade of oxeas

III encircles the outer edge of the sponge. Color of alcohol-fixed specimens light brown from above and light beige from below.

Skeleton (Fig. 12C–F, 14). Ectosomal skeleton (Figs. 12C and 14) is formed by oxeas I and II, of which most are arranged radially and protrude 1–2 mm above the surface, and also by triaenes. Ectosome (Fig. 12F) contains a large number of spirasters and plesiasters II, while plesiasters I and acanthomicroxeas in smaller numbers. In choanosome, the relative number of plesiasters I and microxeas increases. Triaenes are located mainly in ectosome of the sponge upper side. Their cladomes lying on the surface; rhabdomes are arranged radially. A small number

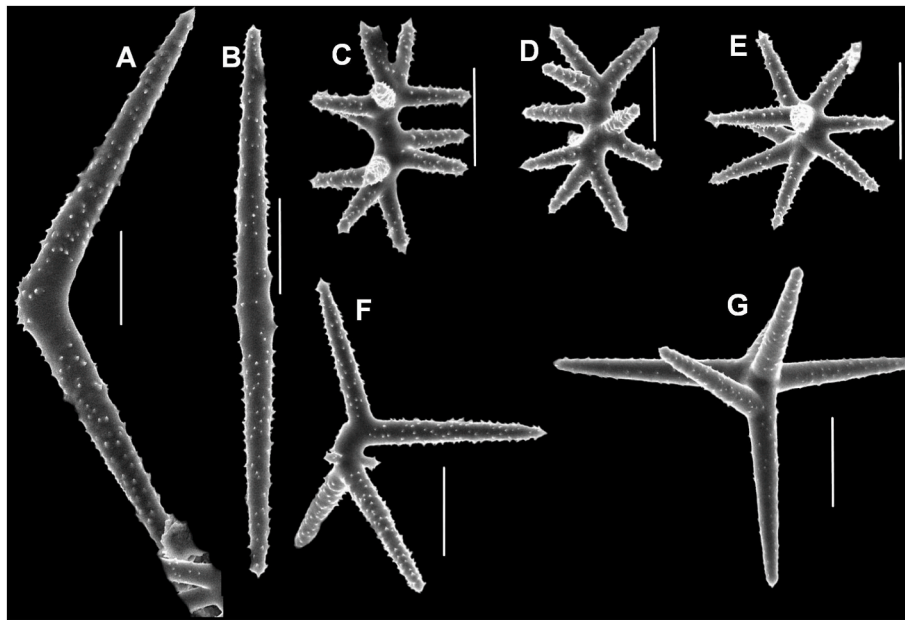


Fig. 10. *Vulcanella commander* sp. nov., images of spicules: (A, B) acanthomicroxeas; (C–E) spirasters; (F, G) plesiasters. Scale bars: A–G – 10 μ m.

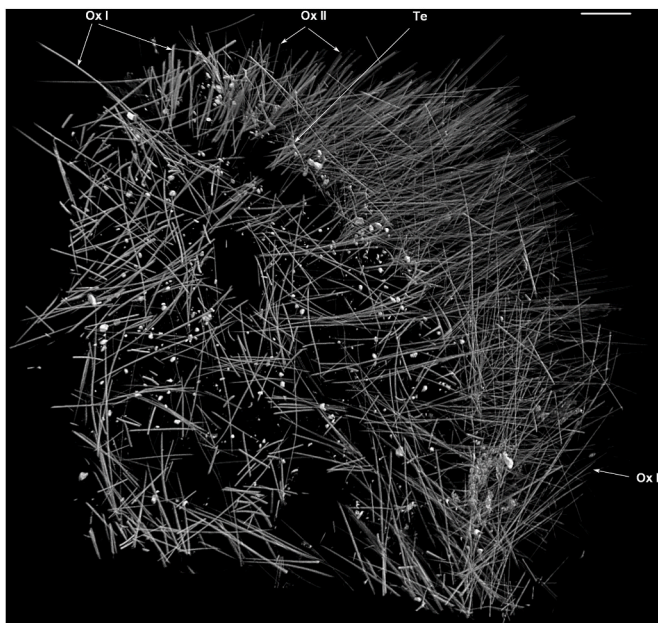


Fig. 11. *Vulcanella commander* sp. nov., Micro-CT image of skeleton of the Holotype. Section perpendicular to the surface (low resolution): Te – triaenes, Ox I – oxeas I, Ox II – oxeas II, Ox III – oxeas III (cropped). Scale bars: 1 mm.

of triaenes are found in ectosome of lower side and in choanosome. Choanosomal skeleton (Figs. 12D and 14) is formed by randomly arranged oxeas I and II, with the latter being in a small number. Oscular netting skeleton (Fig. 12E) also consists of oxeas I and II and microscleres, mainly spirasters.

Spicules. Megascleres (Fig. 12G and H; 13A–E). Oxeas I (Fig. 12G) thick, fusiform, slightly curved, $2058.4\text{--}(3184.5)\text{--}4050.4 \times 39.8\text{--}(55.0)\text{--}68.9 \mu\text{m}$. Oxeas II (Fig. 12G) thin, straight or slightly curved, $982.7\text{--}(1482.0)\text{--}2523.2 \times 10.6\text{--}(17.4)\text{--}26.5 \mu\text{m}$. Oxeas III (Fig. 12H) (up to styles and strongyles), long and thin, more than $10225.6 \mu\text{m}$ in length, $10.6\text{--}(17.4)\text{--}21.7 \mu\text{m}$ in width. Orthotriaenes (Fig. 13A and B) and plagiotriaenes (Fig. 13C): rhabdome $199.2\text{--}(283.5)\text{--}332.0 \times 31.6\text{--}(48.2)\text{--}58.7 \mu\text{m}$; clads $584.3\text{--}(810.1)\text{--}969.4 \times 36.8\text{--}(51.2)\text{--}60.5 \mu\text{m}$. Rarely

orthotriaenes with a forked clad (Fig. 13D), diaenes (Fig. 13E). Microscleres (Fig. 13F–L). Acanthomicroxeas (Fig. 13F and G), from straight to strongly curved, $118.4\text{--}(152.5)\text{--}210.4 \times 5.8\text{--}(7.4)\text{--}10.5 \mu\text{m}$. In the middle part of acanthomicroxeas, spines form ringed ornamentation expressed to varying degrees. Spirasters (Fig. 13K and L) $22.4\text{--}(25.6)\text{--}28.9 \mu\text{m}$. Plesiasters I (Fig. 13H) with 4–7 thick conical rays $44.7\text{--}(58.8)\text{--}84.2 \mu\text{m}$. Plesiasters II (Fig. 13I and J) with thin rays $21.0\text{--}(30.4)\text{--}47.3 \mu\text{m}$.

Diagnosis. *Vulcanella* with three categories of oxeas, and triaenes with short rhabdome. Acanthomicroxeas in one category, with ringed ornamentation in the middle. Streptasters of three categories (spirasters and two categories of plesiasters).

Distribution and habitat. Two findings on the northern slope of the Piip volcano at a depth of 1569 m and two on the southern slope at a depth of 981 m. The substrate is skeletons of *Farrea* sp. (Hexactinellida: Farreidae).

Relationships. In addition to the holotype, three more specimens of *V. grebelnyi* sp. nov. are available. Two of them, found on the southern slope of the Piip volcano at a depth of 981 m, are 5–6 mm specimens on a skeleton of *Farrea* sp.; however, it is impossible to judge about the shape and details of the external structure on their basis. The third, found near the holotype, is a fragment measuring $1.5 \times 4 \text{ cm}$. The upper side lacks oscules, but well-preserved details of the structure can be seen on the lower side of the fragment. Apertures of up to 1.5 mm in diameter are covered by a membrane with pores of ca. 0.4 mm. This matches the structure of the undamaged part of the lower surface of the holotype.

Vulcanella grebelnyi sp. nov. resembles *V. commander* sp. nov. in the composition and size of spicules, but with substantial differences as follows: in *V. grebelnyi* sp. nov., microxeas are much larger than those in *V. commander* sp. nov.; plesiasters are in two categories, of which one (I) is with straight conical rays.

The traits of the Pacific *Vulcanella* species with long, thin oxeas distinguishing them from *V. grebelnyi* sp. nov. are as follows:

Vulcanella acanthoxea (Tanita and Hoshino, 1989) has two categories of microxeas, with asters being shorter, and plesiasters absent.

Vulcanella bifacialis (Wilson, 1925) has a more diverse set of asters.

Vulcanella cribriporosa (Lebwohl, 1914) has plagiotriaenes with rhabdome significantly longer than clads; metastars and spiraster are smaller in size.

Vulcanella netheides (Lebwohl, 1914), *V. porosa* (Lebwohl, 1914), and *V. porosa* sensu Koltun (1966) have styles, tylostyles, strongyles, and

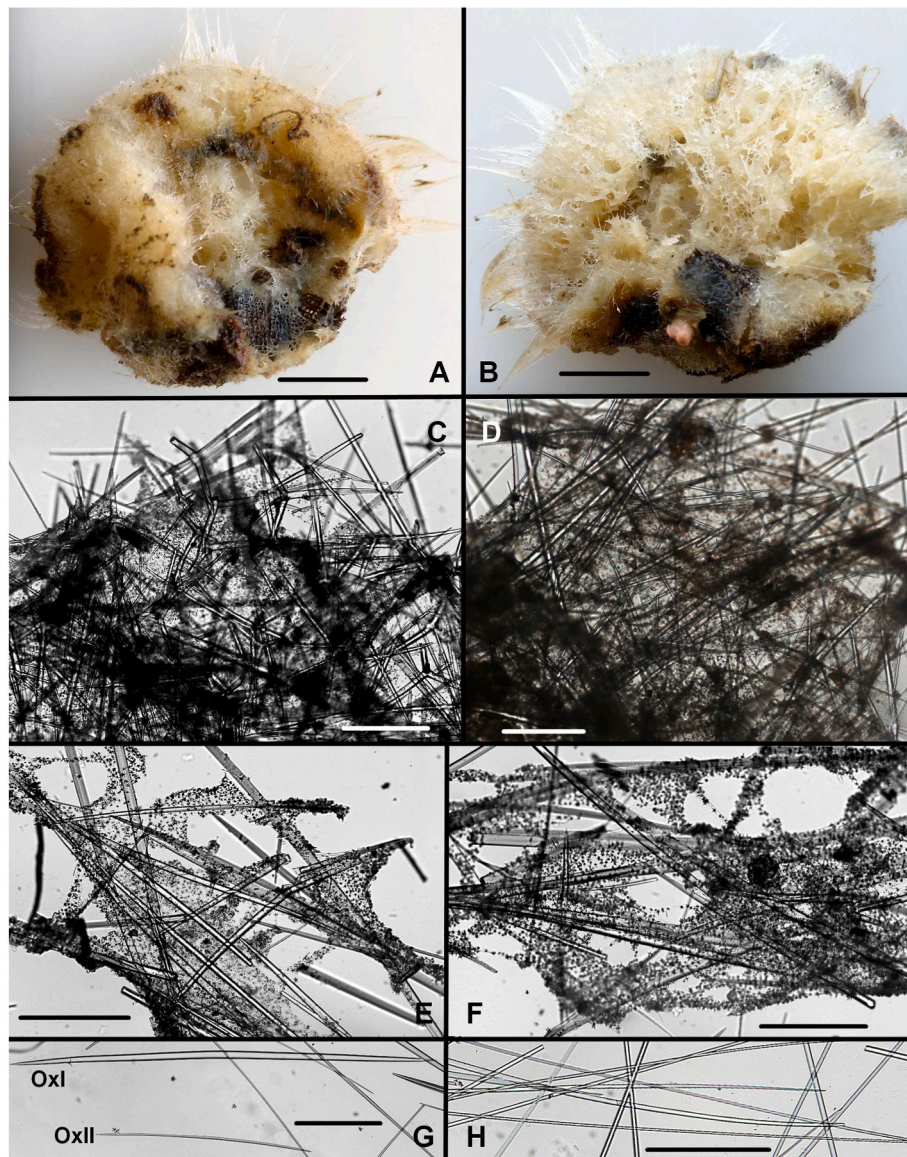


Fig. 12. *Vulcanella grebelnyi* sp. nov., Holotype MIMB43749: (A) oscule side; (B) pore side; (C) section perpendicular to the surface, oscule side; (D) choanosomal skeletal; (E) the skeleton of the oscule membrane; (F) ectosomal skeletal, tangential section, pore side; images of spicules: (G) oxaeas I and II; (H) oxaeas III. Scale bars: A, B – 1 cm; C–H – 500 μ m.

subtylotes (depending on species); in plagiotriaenes, rhabdome is several times longer than clads; the maximum size of microxeas is twice as large; metasters and spirasters are smaller in size. Judging by the illustrations from the descriptions, *V. netheides* and *V. porosa* lack clearly expressed plesiasters.

Vulcanella tricornis (Wilson, 1904) has orthotriaenes with reduced rhabdome, two categories of microxeas, and two categories of spiracles. Clearly expressed plesiasters are absent. Of the known *Vulcanella*, species, only *V. tricornis* has oxaeas in three categories and triaenes with bifurcated clads (dichotriaenes), but the differences with the new species are substantial in general.

Vulcanella tricornis sensu Desqueyroux-Faúndez and Van Soest (1997) has only calthrops with strongly shortened rhabdome (rather plagiotriaenes), two categories of microxeas, and one category of plesiasters. Spirasters and plesiasters are much smaller in size.

The differences of the Atlantic and Mediterranean *Vulcanella* species with long, thin oxaeas from *V. grebelnyi* sp. nov. are as follows:

Vulcanella aberrans (Maldonado and Uriz, 1996) has triaenes with rhabdome much longer than clads and two categories of microxeas.

Vulcanella cribrifera Sollas (1886) has strongyles, rhabdome in triaenes much longer than clads, and calthrops present.

Vulcanella gracilis (Sollas, 1888) and *V. gracilis* sensu Sarà (1958) has only calthrops and two categories of microxeas, including smooth ones.

Vulcanella stylifera Carvalho et al. (2016) has exotyles and styles. Rhabdome in triaenes is much longer than clads. The average size of microxeas is twice the size of microxeas in *V. grebelnyi* sp. nov.

3.2. Molecular analysis

In total, 3 specimens of *V. koltuni* sp. nov. and 1 specimens of *V. commander* sp. nov. and *P. malyutini* sp. nov. were sequenced. The sequence length of SSU rDNA after alignment was 1733 bp, 2 specimens of D2-D3 region of 28S rDNA was 521–546 bp while D4.8-D7 region of 28S rDNA was 911–1223 bp. The mean nucleotide base compositions were A 21.5%, C 24.0%, G 30.8%, and T 23.7% for 18S rDNA, A 18.0%, C 31.3%, G 36.6%, and T 14.1% for D2-D3 region of 28S rDNA while A 21.2%, C 25.6%, G 33.4%, and T 19.8% for D4.8-D7 region of 28S rDNA. Sequences of 18S rDNA for most specimens belonged to the same

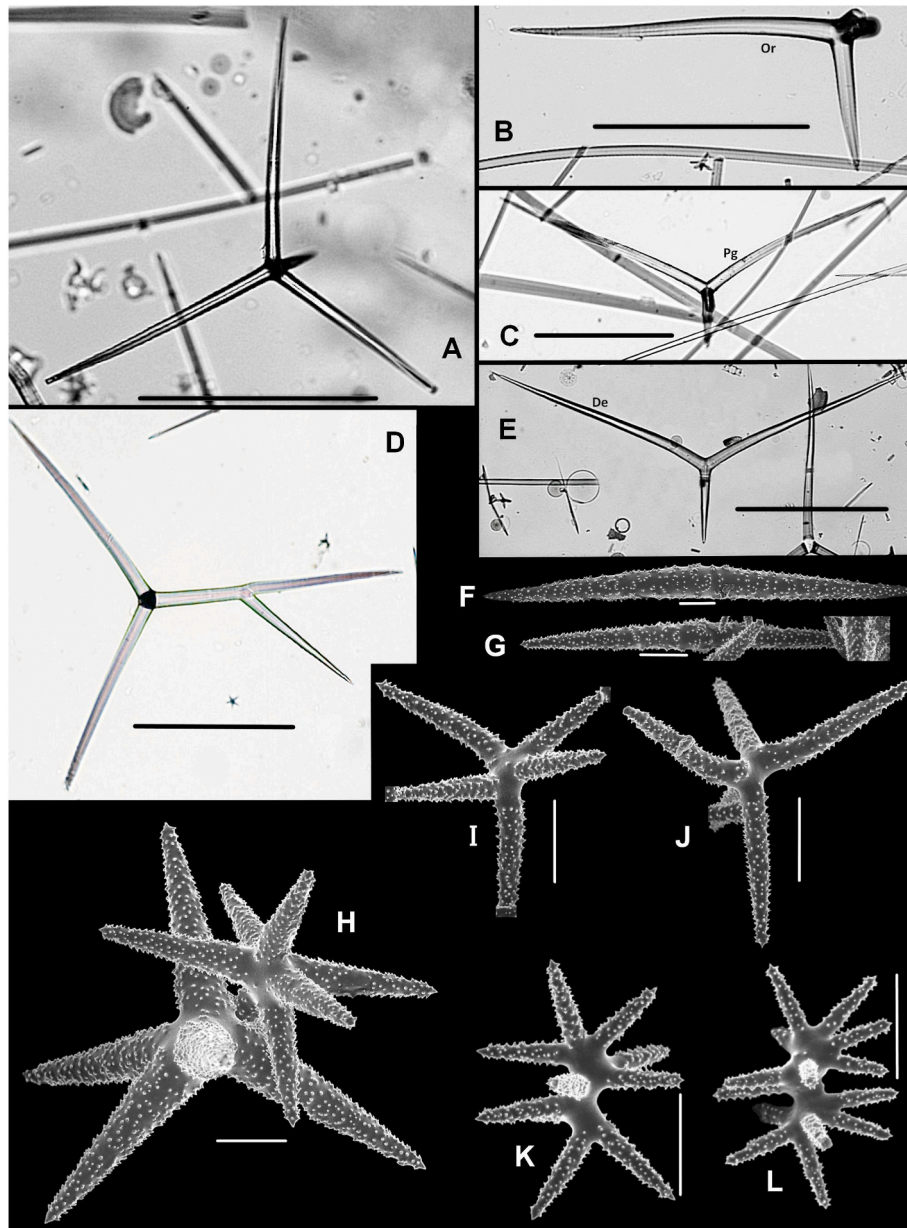


Fig. 13. *Vulcanella grebelnyi* sp. nov., images of spicules: (A) orthotriaene; (B) orthotriaene (Or), fragment; (C) plagiotriaene (Pg); (D) orthotriaene with diaenes with forked clad; (E) diaene (De); (F, G) acanthomicroxeas; (H) plesiasters I; (I, J) plesiasters II; (K, L) spirasters. Scale bars: A-E – 500 µm; F-L – 10 µm.

haplotype except *P. malyutini* sp. nov. which differed from the rest specimens by 0.06%. P-distance between *V. koltuni* sp. nov. and *V. commander* sp. nov. was 0.96% using D2-D3 region of 28S rDNA. D4.8-D7 region of 28S rDNA was conserved for 4 specimens of *V. koltuni* sp. nov. and *V. commander* sp. nov. while the average sequence divergence between this sequence and *P. malyutini* sp. nov. were 0.11%.

The BI phylogeny using 18S rDNA revealed two well supported primary clades, one including taxa placed in suborders Thoosina and Spirophorina (Bayesian Posterior Probability BPP = 1, Maximum likelihood bootstrap, ML = 74) and one including six families of suborder Astrophorina (BPP = 1, ML = 74) (Fig. 16). Members of family Vulcanellidae was the earliest branching lineage and sister to other clades. It is noteworthy that *Lamellomorpha strongylata* from New Zealand formed the separate clade from genera *Vulcanella* and *Poecillastra*, rendering that family paraphyletic. In turn, the sequences of clade that includes genera *Vulcanella* and *Poecillastra* (BPP = 0.87) were conservative and both genera were not monophyletic.

The unrooted phylogenetic tree reconstructed using D2-D3 region of 28S revealed two high supported clades (BPP = 1, ML = 100), one including two specimens of *P. amygdaloides* and *Tethyopsis mortenseni* and one includes the remaining members of Vulcanellidae (Fig. 17). Obtained species *V. koltuni* sp. nov. and *V. commander* sp. nov. were placed as sister to *P. compressa* (BPP = 1, ML = 100). At the same time, three other members of genus *Vulcanella* formed independent clades. Thus, *Poecillastra* and *Vulcanella* were shown to be polyphyletic.

3.3. Stable isotopes analysis

The $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of sponges are provided in Table 1. The $\delta^{15}\text{N}$ signatures varied in a small range from 12.99 (*V. koltuni* sp. nov.) to 14.95‰ (*V. commander* sp. nov.). A pronounced difference between the species was found in the $\delta^{13}\text{C}$ values which varied from −31.12 (*V. koltuni* sp. nov.) to −16.63‰ (*V. commander* sp. nov.).

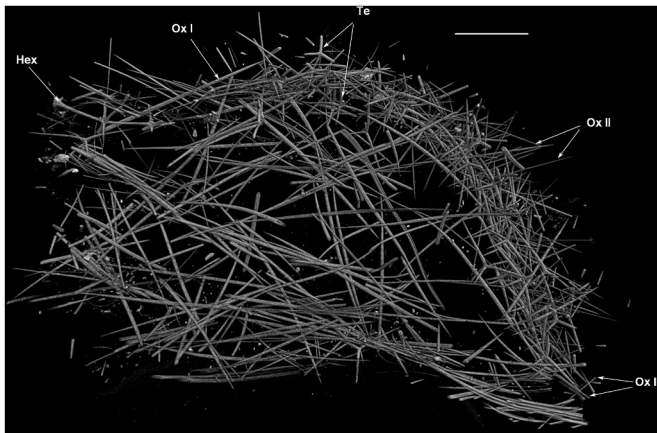


Fig. 14. *Vulcanella grebelnyi* sp. nov., Micro-CT image of skeleton of the Holotype. Section perpendicular to the surface (low resolution): Hex – skeleton of *Farrea* sp. (Hexactinellida: Farreidae), Te – triaenes, Ox I – oxeas I, Ox II – oxeas II, Ox III – oxeas III (cropped). Scale bars: 1 mm.

4. Discussion

The family Vulcanellidae currently includes three genera: *Lamellomorpha*, *Poecillastra*, and *Vulcanella*. The genus *Lamellomorpha* was established by Bergquist (1968) for *L. strongylata* and placed in the family Jaspidae de Laubenfels, 1936 (in the abandoned order Epipolāsida Sollas, 1888). The set of spicules in *Lamellomorpha* includes very large twisted strongyles, oxeas and strongyloxeas, as well as faintly spined microstrongyles and plesiasters, triaenes are completely absent. Due to difficulties in determining the exact taxonomic allocation, Hooper and Maldonado (2002) place *Lamellomorpha* in Astrophorida Incertae Sedis. After detailed morphological and molecular studies Kelly et al. (2019) proved the relationship of *Lamellomorpha* to the Vulcanellidae family. Our data contradict the results of Kelly et al. Unfortunately, we were unable to obtain sequences for COI and C1–C2 domains of the 28S rDNA.

The genera *Poecillastra* and *Vulcanella* are morphologically much closer to each other than to *Lamellomorpha*. The differences between *Poecillastra* and *Vulcanella* are clearly visible in external morphology and in skeletal structure. *Vulcanella* is characterized by the presence of cribporal oscules surrounded by a palisade of long oxeas and a more differentiated skeleton. Tetractinal megasclere in *Vulcanella* are located, with rare exceptions, only in the ectosome. Among the microsclera of *Vulcanella* there are microoxae with an annulated oxeas.

Most *Poecillastra* and *Vulcanella* species are deep-sea or eurybathic. Of the 27 valid species of *Poecillastra*, only half have been recorded from depths shallower than 200 m, with some of them living also at much greater depths: *P. compressa*, *P. c. antarctica*, *P. crassiuscula*, *P. cribraria*, *P. cumana*, *P. ducitriaena*, *P. fragilis*, *P. incrustans*, *P. japonica*, *P. laminaris*, *P. rudiastra*, *P. saxicola*, *P. tenuilaminaris*, and *P. wondoensis* (Carvalho et al., 2011, Table 2 in the text). Of the 15 *Vulcanella* species, *V. aberrans*, *V. cribrifera*, *V. gracilis*, *V. horrida*, *V. osculanigera*, *V. porosa*, and *V. tricornis* inhabit depths to 200 m. *V. horrida* is distributed to a depth of 2500 m, the greatest depth recorded for the known members of the family Vulcanellidae (Carvalho et al., 2016, Table 3 in the text). The rest of the *Poecillastra* and *Vulcanella* species occur only at depths greater than 200 m. The finding of *V. commander* sp. nov. at depths of 3599 and 3753 m substantially extends the known depth range for the family Vulcanellidae. Furthermore, the new species much increase the list of members of the family from the northwestern Pacific Ocean.

The spatial distribution of the above-described species is characterized by a pronounced vertical zonation. *V. commander* sp. nov. was found at depths greater than 3500 m; *V. grebelnyi* sp. nov., at depths of 981 m and 1569 m; and *P. malyutini* sp. nov. and *V. koltuni* sp. nov.,

immediately on the summits of the volcano in areas with abundant coverage of bacterial mats and on their periphery.

The Piip volcano summits are zones with hydrothermal activity. Hydrothermal vents are mainly found above the 450 m isobath at both peaks of the two-summit volcano; in this zone, extensive areas covered by bacterial mats and high concentrations of methane in water have been recorded (Galkin and Ivin, 2019; Galkin et al., 2019). The $\delta^{13}\text{C}$ value for *V. koltuni* sp. nov. and *P. malyutini* sp. nov. from the volcano summits were almost 2-times lower than for *V. commander* sp. nov. collected outside the areas of hydrothermal activity. Yasuda et al. (2016) found the $\delta^{13}\text{C}$ value for photosynthesis-derived organic matter in settling particles collected in the Bering Sea averaged $-22.5 \pm 1.6\text{‰}$. The carbon isotope ratios in microbial mats at the summits of Piip volcano ranged from -36.0‰ to -25.6‰ (Kiyashko & Mordukhovich, unpubl.). These isotopic signatures and literature data (Levin and Michener 2002; Levin, 2005) indicate the organic matter of chemosynthetic origin in the diet of *V. koltuni* sp. nov. and *P. malyutini* sp. nov. Brachiopods are also abundant on the summits of the volcano. The $\delta^{13}\text{C}$ value for this filter feeders was 19.3‰ (Kiyashko & Mordukhovich, unpubl.). In addition, the FAs composition of *V. koltuni* sp. nov. and *P. malyutini* sp. nov. tissues demonstrates an abnormally high content of 16:1n-7 (Rodkina, unpubl.), which is a marker of sulfur-oxidizing bacteria. Thus, the isotopic signatures for *V. koltuni* sp. nov. and *P. malyutini* sp. nov cannot be explained by consumption of POM and/or DOM only. These sponges seem to derive some part of their nutrition from symbiosis with sulphide-oxidizing bacteria.

V. commander sp. nov. has high $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values, which was previously found in other studies of deep-sea sponges (Polumin et al., 2001; Kahn et al., 2018; Hanz et al., 2022). The lack of data on isotopic signatures for potential food sources, as well as for cohabiting species, does not allow us to conduct a detailed nutritional analysis for this sponge. The high $\delta^{15}\text{N}$ value could indicate the internal recycling of nitrogen within the sponge tissue or in the sponge microbiome (Hanz et al., 2022).

Currently, there is ample evidence that sponges inhabiting the vent and seep zones benefit from the opportunity to use an additional food source such as symbiotic bacteria. Similar relationships are reported for members of various Porifera Grant, 1836 taxa (e.g., Cladorhizidae Dendy, 1922; Hymedesmiidae Topsent, 1928; Lubomirskiidae Weltner, 1895; Myxillidae Dendy, 1922; and Pachastrellidae Carter, 1875) (Harrison et al., 1994; Efremova et al., 1995; Vacelet et al., 1996; Maldonado and Young, 1998; Nishijima et al., 2010; Arellano et al., 2012; Rubin-Blum et al., 2019). Symbiotic bacteria allow the host sponge to adapt to the conditions of reducing habitats (Zhou et al., 2019). Due to their ability to pump a large amount of water through its system of water canals, sponges with symbionts can successfully exist even at some distance from hydrothermal vents and seeps, on their periphery (Kahn et al., 2015; Georgieva et al., 2020).

Of particular note is also the rather high abundance of *Vulcanella koltuni* sp. nov. A total of 368 representatives of this species were recorded from the summits of the Piip volcano using photo and video materials. Of these, 205 were spotted on the northern summit and 163 on the southern one. All specimens were located in the areas of hydrothermal vents or in the immediate vicinity of them (Figs. 5A and 15). In our case, the proximity to vents was evaluated by the distance to the bacterial mats clearly visible in photographs and still images. During a video transect on the northern slope, the first vent was found at a depth of 621 m, and the first representative of *V. koltuni* sp. nov. was encountered at 384 m. On the southern slope, these occurred at depths of 547 and 472 m, respectively. If bacterial mats had a sufficiently large area, several square meters or more, sponges grew on boulders at some distance from the floor, up to 0.5 m. In such conditions, there are probably some limiting factors that may act, in particular, during the settlement of sponge larvae.

No quantitative assessments for *V. koltuni* sp. nov. have been done to date, and the relationship between the large number of specimens on the

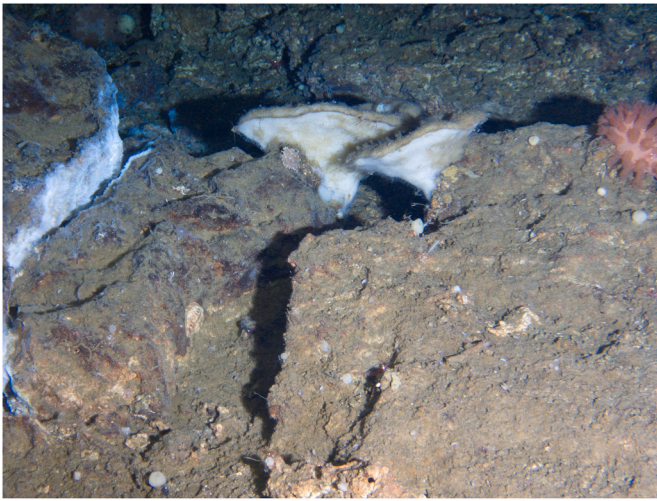


Fig. 15. *Vulcanella koltuni* sp. nov. in situ. The southern peak of the Piipa volcano, depth 469.5 m.

northern summit and the increased methane content cannot be considered proven. Nevertheless, such a relationship is suggested, as well as the existence of a symbiosis between *V. koltuni* sp. nov. and chemotrophic bacteria. It is worth mentioning that of the nine Pacific sponge species of the genus *Vulcanella* known to date, five species have been recorded from Sagami Bay (Pacific side of Honshu, Japan), where numerous methane seeps with beds of bivalve mollusks of the genus *Calyptogena* were found (Kitazato et al., 2009).

5. Concluding remarks

Four new species of vulcanellid sponges are described from the Piip submarine volcano and adjacent area. With further study of the seafloor communities in the Northwestern Pacific, the list of vulcanellid species and demosponges in general is expected to be significantly extended. The distribution of species is characterized by pronounced vertical zoning. In the areas of hydrothermal vents and on their periphery, demosponges form a high abundance with a pronounced dominance of a single species, *V. koltuni* sp. nov.

Our data indicate a possible contribution of chemosymbiotic bacteria to the nutrition *V. koltuni* sp. nov. and *P. malyutini* sp. nov. The high species richness and abundance of *Vulcanella* in various reducing habitats, may be due to the symbiotic relationships of these sponges with chemosynthetic bacteria.

Author contribution

Shilov V.A.: conceptualization, data curation, formal analysis, methodology, investigation, validation, visualization, writing - original draft, writing - review & editing.

Kamenev Y.O.: micro-computed tomography, visualization, writing - review & editing.

Semenchenko A.A.: molecular analyses, visualization, writing - review & editing.

Kiyashko S.I.: stable isotopes analysis, methodology, writing - review & editing.

Mordukhovich V.V.: validation, funding acquisition, project administration, writing - original draft, writing - review & editing.

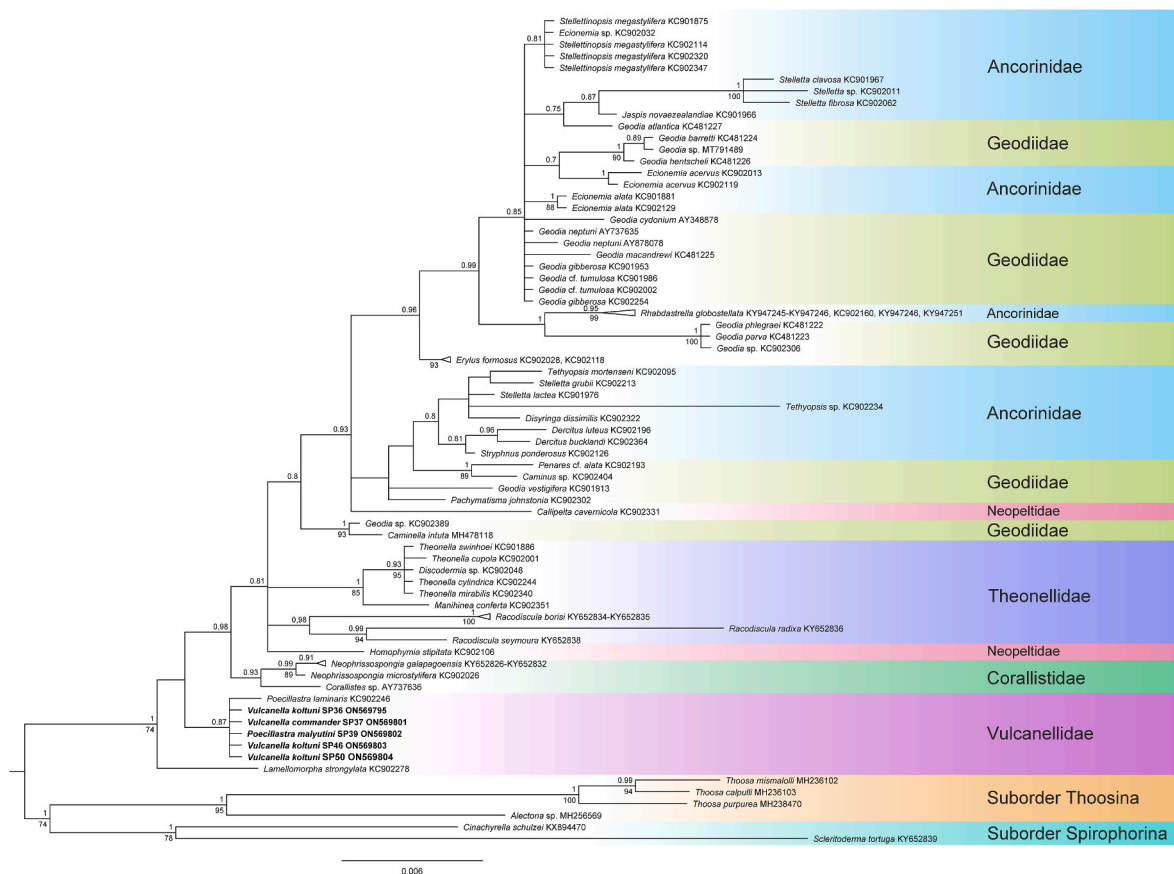


Fig. 16. Bayesian 18S rDNA phylogeny of the suborder Astrophorina, using the GTR + I + G model of nucleotide substitution. Bayesian posterior probabilities (PP) are given above tree nodes and bootstrap support values found in the ML analysis are shown below nodes.

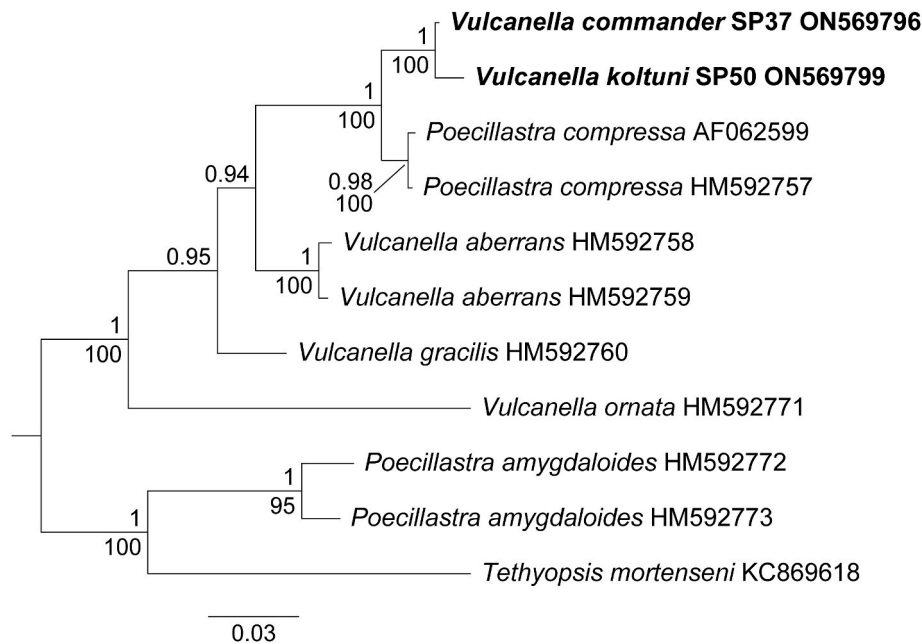


Fig. 17. Bayesian 28S rDNA phylogeny of the family Vulcanellidae, using the GTR + I + G model of nucleotide substitution. Specimens obtained in this study are in bold.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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