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Vesicomomyinae (Bivalvia: Vesicomomyidae) of the Kuril–Kamchatka Trench and adjacent abyssal regions

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ABSTRACT

Keywords:

Abyssal
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Morphology
New species
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Vesicomomya

Representatives of the subfamily Vesicomomyinae (Bivalvia, Vesicomomyidae) are tiny deep-sea molluscs distributed worldwide and reaching huge abundances of hundreds and thousands of specimens in trawl catches. During the German–Russian deep-sea expedition KuramBio (R/V *Sonne*, 2012) for the first time two vesicomomyin species were collected from the abyssal plain adjacent to the Kuril–Kamchatka Trench from the depths of 4861–5787 m, *Vesicomomya pacifica* (Smith, 1885) and “*Vesicomomya*” *filatovae* sp.n. Two species of vesicomomyins, *V. sergeevi* Filatova, 1971 and *V. profunda* Filatova, 1971, which were previously reported from the hadal of the Kuril–Kamchatka Trench, were not collected at the abyssal depth despite of the close geographical proximity of the sampling area to their distribution ranges. Altogether nine species of vesicomomyins are recorded now from the West and Indo-West Pacific; data on distribution and morpho-anatomical characters of these species are provided. Taxonomic description of *V. pacifica* is revised including information on its soft part anatomy, new localities and COI sequences. For the first time for a vesicomomyin bivalve molecular data is given for a species with an explicit morphological description and unambiguous taxonomic affiliation. Molecular analysis of 160 published COI sequences of vesicomomyids and newly obtained molecular data on *V. pacifica* showed that *V. pacifica* and two undescribed vesicomomyin species forming a monophyletic clade which exhibits sister relationships with the Pliocardiinae, the group of chemosymbiotic vesicomomyids. “*Vesicomomya*” *filatovae* sp.n. is provisionally assigned to the genus *Vesicomomya* (s.l.) until additional morphological and molecular data are obtained. It differs from *Vesicomomya* s.s. by a broader hinge margin with more radiating teeth and the presence of only one pair of demibranchs.

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1. Introduction

Vesicomomyins comprise tiny mostly deep-sea bivalves distributed in all large oceanic basins (Krylova and Sahling, 2010). They are an important component of abyssal plain and hadal trench communities where they were recovered in huge abundances of hundreds and thousands of specimens in trawl catches (Filatova,

1971; Linse, 2004; Vinogradova et al., 1993). Vesicomomyins are a little-known group with obscure way of life; adaptations, which could help to support high abundance at the abyssal and hadal zones, have yet to be investigated.

Vesicomomyins have been often considered as a synonym of the family Kelliellidae P. Fischer, 1887 (Knudsen, 1970; Allen, 2001). Krylova and Sahling (2010) proposed that the Vesicomomyinae Dall and Simpson, 1901 be one of the two subfamilies of the family Vesicomomyidae Dall and Simpson, 1901. The other subfamily, Pliocardiinae Woodring, 1925, includes chemosymbiotic large-sized molluscs. The phylogenetic relationships of the vesicomomyins with the pliocardiiins are still problematic. At present vesicomomyins include only the genus *Vesicomomya* Dall, 1886 with 14 described species (Krylova and Sahling, 2010) of which some require taxonomic revision. Vesicomomyins are frequently millimetric in size with maximum shell length up to 14 mm. In contrast to the larger-sized pliocardiiins, which are living in symbiosis with sulphide-oxidizing bacteria, chemosymbiotrophy has not yet been proved

Abbreviations: AGT, Agassiz trawl; EBS, epibenthic sledge; *H*, shell height; *L*, shell length; MIMB, Museum of the Institute of Marine Biology, Vladivostok, Russia; MNHN, Museum National d'Histoire Naturelle, Paris, France; NHMUK, the Natural History Museum, London, UK; NMNS, National Museum of Nature and Science, Tokyo, Japan; SMF, Senckenberg Forschungsinstitut und Naturmuseum, Frankfurt am Main, Germany; Spm(s), specimen(s); St., station; *W*, shell width; ZMMU, Zoological Museum of Moscow State University, Moscow, Russia

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for vesicomysins despite that bacteria were discovered in gills of *V. sergeevi* (Krylova et al., 2000; Krylova and Sahling, 2010).

Three species of vesicomysins have been recorded from the Northwestern Pacific so far: *Vesicomya pacifica* (Smith, 1885), *V. profundus* Filatova, 1971 and *V. sergeevi* Filatova, 1971. The former species is known from the abyssal Mid-North and Northwestern Pacific at depths of 4130–5440 m (Smith, 1885; Okutani and Kawamura, 2002) and the two latter occur in the hadal zone of the Kuril–Kamchatka Trench, *V. profundus* at depths of 7120–9050 m and *V. sergeevi* at depths of 7600–9530 m. Additionally, *V. profundus* is recorded in the Aleutian Trench at depth of 7246 m (Filatova, 1971). During the recent German–Russian deep-sea expedition KuramBio on board of R/V *Sonne* to the abyssal plain adjacent to the Kuril–Kamchatka Trench new material of vesicomysin bivalves was collected from depths of 4861–5787 m. Morphological analyses of the specimens has shown that the collection includes two species; one of them previously described as *V. pacifica*, and the other is an undescribed species.

In this paper we provide data on distribution and morpho-anatomical characters of all nine vesicomysin species recorded from the West Pacific and Indo-West Pacific. We refine the taxonomic description of *V. pacifica* providing new information on its anatomy, morphological variations, localities and *COI* sequences. For the first time for a vesicomysin bivalve molecular data is given for a species with an explicit morphological description and unambiguous taxonomic affiliation. In our paper we compare 160 published *COI* sequences of vesicomysids with newly obtained molecular data on *V. pacifica* in a preliminary attempt to assess relationships between vesicomysins and pliocardiids. We also describe the new species “*Vesicomya*” *filatovae* sp.n. on the basis of conchological and anatomical characters. “*Vesicomya*” *filatovae* sp.n. differs from the type species of the genus, *V. atlantica* (Smith, 1885), in many respects and is only provisionally assigned to the genus *Vesicomya* (s.l.) until additional morphological and molecular data are obtained.

2. Material and methods

2.1. Sampling and morphological analysis

The study was based on the material collected by the German–Russian deep-sea expedition KuramBio (Kuril–Kamchatka Biodiversity Study) in July–September 2012 during the cruise no. 223 of R/V “*Sonne*” (Fig. 1). The material was obtained from the abyssal plain of the Pacific Ocean adjacent to the Kuril–Kamchatka Trench from the depths of 4861–5787 m by epibenthic sledge and Agassiz trawl and live-collected specimens of two species were preserved in 96% ethanol (Table 1). In addition, the type material of four earlier described species of *Vesicomya* and non-type material of two species were studied (Table 2). For the morphological description standard valve measurements were made and the terminology for the hinge teeth was used as previously described (Cosel and Salas, 2001; Krylova and Sahling, 2006). Gross anatomy was observed on preserved specimens. For scanning electron microscopy, shells were cleaned of traces of soft tissues and periostracum in a diluted commercial bleach, washed in distilled water and dried. They were mounted to aluminium stubs using adhesive tape and coated with platinum for examination with a EVO 40XVP. The material is stored in the Institute of Marine Biology, Vladivostok, Russia and Zoological Institute and Zoological Museum, Hamburg, Germany. Type specimens are deposited in the Museum of the Institute of Marine Biology, Vladivostok, the Senckenberg Forschungsinstitut und Naturmuseum, Frankfurt am Main, Germany, Zoological Institute and Zoological Museum, Hamburg and the Zoological Museum of Moscow State University, Moscow, Russia.

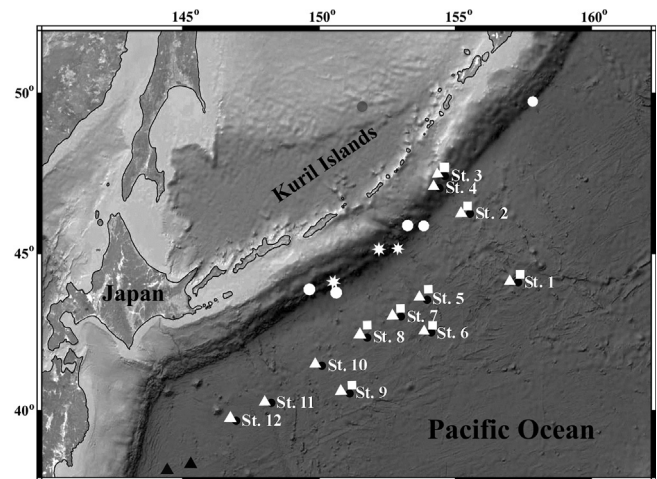


Fig. 1. Distribution of vesicomysins in the Kuril–Kamchatka Trench and adjacent abyssal regions. Designations: KuramBio 2012 stations – black circles; “*Vesicomya*” *filatovae* sp.n., collected by KuramBio – white squares; *V. pacifica* (Smith, 1885), collected by KuramBio – white triangles; *V. pacifica*, collected by R/V *Soyo Maru*, 1978 (Okutani and Kawamura, 2002) – black triangles; *Vesicomya profundus* Filatova, 1971, collected by R/V *Vityaz*, 1953, 1955, 1956 – white circles; *Vesicomya sergeevi* Filatova, 1971, collected by R/V *Vityaz*, 1953, 1954, 1966 (Filatova, 1971) – white stars.

2.2. Molecular methods

Four specimens of *Vesicomya pacifica* from 4 stations were used in the molecular analysis (Table 1). Approximately 20 mg tissue sample of each specimen was grinded and then lysed in a proteinase K buffer. DNA was extracted using Macherey–Nagel NucleoSpin® Tissue kit according to manufacturer’s protocol. Total DNA was used as a template in a polymerase chain reaction (PCR) carried out with Encyclo Plus PCR kit (Eurogene, Moscow, Russia). To amplify fragments of mitochondrial gene for cytochrome oxidase c subunit I (*COI*) the primer pair vesCOF – vesCOR was used, with vesCOF identical to the primer 1490F (Folmer et al., 1994), and the sequence of vesCOR was modified from sequence of VeshCO primer (5′-TCACCYARACCAGCRGGATC-3′) (Peek et al., 1997). The conditions for PCR were: incubation at 94 °C for 2 min followed by 30 cycles of 94 °C for 30 s, 45 °C for 30 s, 72 °C for 1 min, and 72 °C for 10 min. After running through 1% agarose gel the amplified fragments were excised and purified from agarose by DNA purification kit (Cytokine, SPb, Russia, www.cytokine.ru). Purified PCR products for *COI* were directly sequenced using an ABI PRISM 3100 genetic analyser (Applied Biosystems, Foster City, CA, USA) with ABI BigDye and the same primers as were in the amplification reaction. Newly obtained sequences were submitted to GenBank (accession numbers KM 388731 – KM 388734).

2.3. Phylogenetic analyses

Four newly generated sequences were incorporated into the set of 160 vesicomysid sequences extracted from GenBank and aligned using MUSCLE (Edgar, 2004). *COI* sequences of species from other veneroid families, as close relatives on the basis of molecular results (Bieler et al., 2014) were included into alignment as outgroup taxa: *Mercenaria mercenaria* (Linnaeus, 1758), U47648 and *Venus crebriculca* Lamarck, 1818, DQ458498 (Veneridae Rafinesque, 1815); *Dreissena blanci* Westerlund, 1890, EF414492 (Dreissenidae Gray, 1840); *Mactra chinensis* Philippi, 1846, JN674635 (Macrtridae Lamarck, 1809). After removing completely identical sequences with help of the RaxML programme (Stamatakis, 2006; Silvestro and Michalak, 2012) the final set consisted of 164 sequences. Phylogenetic analyses were performed by four

Table 1

Sampling locations and examined specimen numbers for *Vesicomya pacifica* (Smith, 1885) and "*Vesicomya*" *filatovae* sp.n. collected on R/V "Sonne" cruise no. 223. Specimen numbers in brackets give the number of sequenced specimens.

Station number	Coordinates	Depth (m)	Date	<i>V. pacifica</i>	" <i>Vesicomya</i> " <i>filatovae</i> sp.n.
1	43°58.26'N 157°19.68' E 43°58.33'N 157°17.98' E	5379–5427	29–31.07.2012	77	128
2	46°13.60'N 155°33.42' E 46°14.93'N 155°32.57' E	4861–4869	1–3.08.2012	120	1
3	47°13.83'N 154°41.88' E 47°14.87'N 154°43.18' E	4977–4998	4–6.08.2012	20	11
4	46°57.83'N 154°32.37' E 46°58.49'N 154°33.39' E	5687–5787	6–8.08.2012	28	–
5	43°35.50'N 153°57.89' E 43°34.30'N 153°58.18' E	5375–5379	9–12.08.2012	17	11
6	42°29.58'N 154°02.22' E 42°28.47'N 153°59.67' E	5290–5307	12–15.08.2012	17	20
7	43°02.87'N 152°59.45' E 43°01.50'N 152°58.35' E	5216–5223	16–18.08.2012	90 (1)	14
8	42°14.69'N 151°44.05' E 42°14.26'N 151°42.49' E	5112–5130	19–22.08.2012	79 (1)	9
9	40°27.29'N 150°59.92' E 40°40.84'N 151°00.62' E	5259–5412	22–25.08.2012	74 (1)	14
10	41°12.47'N 150°05.64' E 41°11.18'N 150°05.61' E	5236–5258	25–28.08.2012	20	–
11	40°13.26'N 148°06.24' E 40°12.37'N 148°05.43' E	5347–5352	28–31.08.2012	29 (1)	–
12	39°43.80'N 147°10.16' E 39°42.49'N 147°09.37' E	5217–5243	31.08–01.09.2012	22	–

methods: maximum parsimony (MP), maximum likelihood (ML), neighbor-joining (NJ) and Bayesian inference (BI). MP, ML, and NJ trees were inferred in MEGA6 (Tamura et al., 2013), and BI tree was constructed in MrBayes v. 3.2.2. (Ronquist et al., 2012). The optimal model of sequence evolution was identified using Bayesian information criterion (BIC) or Akaike Information Criterion (AIC) as implemented in MEGA6. For the MP all sites were treated as unordered characters with equal weight using the heuristic search method with random addition of sequences and branch swapping (TBR branch swapping algorithm). ML analysis was carried out using the GTR+G substitution model of sequence evolution. Initial tree(s) for the heuristic search were obtained by applying the NJ method to a matrix of pairwise distances estimated using the Maximum Composite Likelihood (MCL) approach. A neighbor-joining (NJ) tree was reconstructed for the complete dataset using the maximum composite likelihood method (Tamura et al., 2004). Robustness of each branch was evaluated by the bootstrapping method with 500 replications for MP and ML and 1000 replications for NJ analyses. For Bayesian analysis, two independent MCMC runs were performed using with 10 million generations each and sampling every 400th tree. Convergence was reached after 6 000 000 generations (average standard deviation of split frequencies < 0.01), and the first 15 000 sampled trees were discarded from the analysis (burnin=15 000). The remaining sampled trees were used to construct the phylogram based on the majority rule and posterior probability for the nodes. Average evolutionary divergences over sequence pairs between and within groups distinguished on the base of phylogenetic analyses were estimated using MEGA6 software (Tamura et al., 2013). Analyses were conducted using the Kimura 2-parameter model of sequence evolution (Kimura, 1980). The rate variation among sites was modelled with a gamma distribution (shape parameter=0.7).

3. Results

3.1. Systematics

Class Bivalvia Linnaeus 1758

Order Veneroida H. and A. Adams 1856

Superfamily Glossoidea Gray 1847

Family Vesicomylidae Dall and Simpson 1901

Subfamily Vesicomylinae Dall and Simpson 1901

Vesicomylinae – Krylova and Sahling, 2010: 5.

Genus *Vesicomya* Dall 1886

Vesicomya Dall, 1886, p. 272; Cosel and Salas, 2001, p. 336;

Krylova and Sahling, 2010, p. 5.

Kelliella – Knudsen, 1970, p. 107 (partim); Allen, 2001, p. 201 (partim).

Type species: *Callocardia atlantica* Smith, 1885 (by original designation).

Distribution of the genus: throughout the Atlantic Ocean; Indian Ocean: central part and Eastern (Sunda Strait); throughout the Pacific Ocean; Antarctic: Eastern Weddell Sea; 108–9530 m.

Vesicomya pacifica (Smith, 1885)

Figs. 2, 3 and 7E, F

Callocardia pacifica Smith, 1885, p. 156, pl. 6, Figs. 9, 9a.

Kelliella pacifica – Okutani and Kawamura, 2002, p. 12, Figs. 4D and 5A.

Type material: R/V "Challenger", St. 244, 35°22'N, 169°53'E, 5220 m, Mid-North Pacific, holotype, NHMUK, 1887.2.9.2710-11.

Material examined: Holotype; material, collected by R/V "Soyomaru" (Table 2); R/V "Sonne", cruise no. 223, St. 1, 2, 3, 4, 5, 6, 7, 8, 9, 10, 11, 12; for details see Table 1.

Type locality: Mid-North Pacific Ocean, 5220 m.

Diagnosis: *Vesicomya*-species with *L* to 8.2 mm, *H/L*=0.91–0.97, *W/L*=0.36–0.39, surface lustrous with sculpture consisting of regular very thin commarginal lines complemented with shallow grooves towards periphery; shallow escutcheon, lunular incision present, umbo situated at anterior 26–38%, prosogyrate beaks, 1-tooth locates in front of 3a-ramus and not overlapped by 3a.

Description: Shell small-sized, *L* to 8.2 mm, fragile, thin, subcircular in outline, *H/L*=0.91–0.97, *W/L*=0.36–0.39 (Table 3), equivalve; right valve slightly overlapped left valve postero-dorsally. Surface lustrous, sculpture consisting of regular very thin commarginal lines complemented with shallow grooves towards periphery. Escutcheon shallow, delimited by rounded keel. Lunule broad, distinctly demarcated by incision. Inequilateral, anterior margin much shorter, umbo situated at anterior 26–38% of valve. Umbones prosogyrate, protruding. Antero-dorsal margin nearly straight or slightly convex, anterior and ventral margins regular and evenly rounded, postero-dorsal margin evenly slightly convex, forming obtuse angle with posterior margin. All pallial scars hardly visible. Pallial line without pallial sinus. Anterior adductor scar narrow, elongated in outline, not impressed. Anterior pedal retractor scar not impressed, located dorsally to and fused with anterior adductor scar. Posterior adductor scar oval, slightly larger than anterior adductor scar, not impressed. Inner edge of valve margin thin, bearing incision parallel to shell margin. Nymph short. Ligament small, opisthodontic. Hinge plate narrow. Dentition of right valve: ventral cardinal (1) thin, short, not parallel to antero-dorsal shell margin, locates in front of 3a-ramus and not overlapped by 3a; 3a-ramus thin, elongated, parallel to antero-dorsal shell margin, fused in its proximal part with anterior edge of 3b-

Table 2
Additional vesicomycin species studied.

Species	Source of material
<i>Vesicomya atlantica</i> (Smith, 1885)	R/V "Challenger", St. 78, 37°26'N, 25°13'W, 1852 m, off Azores, Atlantic Ocean, paralectotype, fragments, NHMUK, N1887.2.9.2713.
<i>Vesicomya atlantica</i> (Smith, 1885)	R/V "Jean Charcot", St. OS07, 47°32'N, 09°34'W, 4249 m, 10.08.1976, Porcupaine, Eastnorthern Atlantic Ocean, 3 spms, MNHN.
<i>Vesicomya pacifica</i> (Smith, 1885)	R/V "Challenger", St. 244, 35°22'N, 169°53'E, 5220 m, Mid-North Pacific, holotype, NHMUK, 1887.2.9.2710-11.
<i>Vesicomya pacifica</i> (Smith, 1885)	R/V "Soyo-Maru", St. R17, 38°08.9'–38°09.4'N, 143°40.00'–143°37.2'E, 4130–4680 m, 23.06.1978, 3 spms, NMNS; St. R18, 38°29.3'–38°29.4'N, 145°41.1'–143°43.0'E, 5440 m, 26.06.1978, 10 spms, NMNS.
<i>Vesicomya sergeevi</i> Filatova, 1971	R/V Vityaz, St. 5627, 44°15'N, 150°46', 9170–9335 m, 27–28.08.1966, Kuril–Kamchatka Trench, syntypes, ZMMU Ld 2915; St. 5628, 43°54'N, 149°57', 9520–9530 m, 30.08.1966, Kuril–Kamchatka Trench, syntypes, ZMMU Ld 2916; St. 5631, 43°47'N, 149°43', 9070–9345 m, 4.09.1966, Kuril–Kamchatka Trench, syntypes, ZMMU Ld 2917.
<i>Vesicomya profundii</i> Filatova, 1971	R/V Vityaz, St. 3357, 52°26'N, 170°54', 7246 m, 7.06.1955, Aleutian Trench, paratypes, ZMMU Ld 2933; St. 5611, 45°48'N, 153°21', 7600–7710 m, 25.07.1966, Kuril–Kamchatka Trench, paratypes, ZMMU Ld 2935, St. 5632, 43°44'N, 149°52', 8240–8345 m, 4–5.09.1966, Kuril–Kamchatka Trench, paratypes, ZMMU Ld 2939.

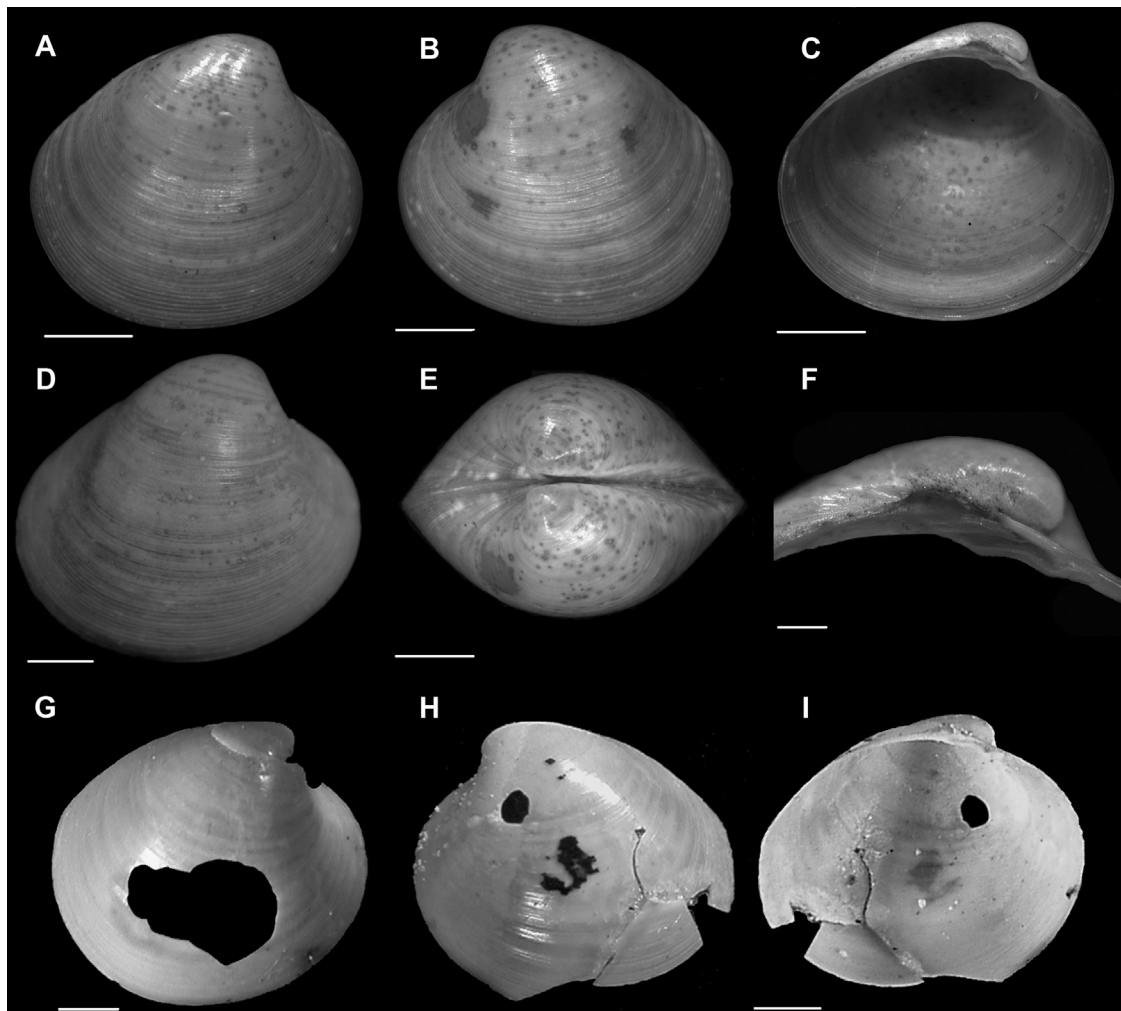


Fig. 2. (A–I) *Vesicomya pacifica* (Smith, 1885): (A–C, E, F) KuramBio, St. 11, IMB FEB RAS: (A) exterior of right valve, (B) exterior of left valve, (C) interior of left valve, (E) dorsal view, (F) hinge of left valve, (D) R/V "Soyo-Maru", St. R17, NSMT, exterior of right valve. (G–I) Holotype, NHMUK, 1887.2.9.2710-11: (G) exterior of right valve, (H) exterior of left valve and (I) interior of left valve. Scale bars: 1 mm.

ramus; 3b-ramus thin, elongated, subparallel to postero-dorsal shell margin. Dentition of left valve: 2a-ramus short, finger-like, along its postero-lateral margin fused with anterior edge of thin 2b-ramus; 2b curved anteriorly, in medial and posterior parts nearly parallel to postero-dorsal shell margin; 4b-tooth low, elongated, parallel to postero-dorsal shell margin. Prodissoconch with pitted sculpture,

about 180 μ m in diameter, margin sculptured with commarginal striae and irregular fine radial striation, about 30 μ m broad.

Soft parts: Mantle lobes thin, except at margins. Mantle fusion forming three pallial apertures, pedal gape and two posterior siphonal openings. Pedal gape occupying about two-thirds of the ventral edge from the middle of frontal surface of the anterior adductor to the base

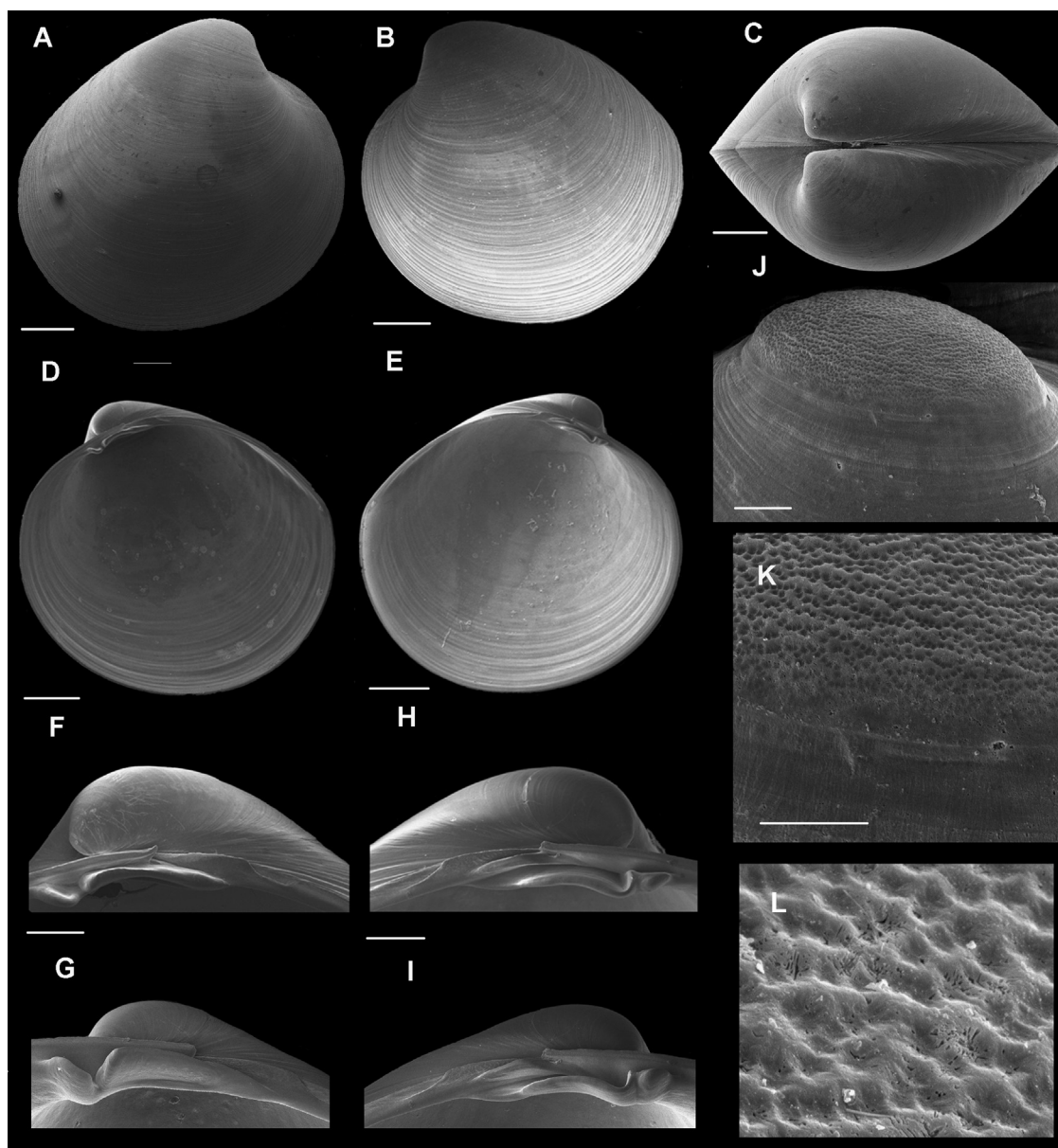


Fig. 3. (A–L) *Vesicomya pacifica* (Smith, 1885), Kurambio, St. 11, IMB FEB RAS: (A) exterior of right valve, (B) exterior of left valve, (C) dorsal view, (D) interior of right valve and (E) interior of left valve. (F, G) Hinge of right valve, lateral and latero-ventral view. (H, I) Hinge of left valve, lateral and lateroventral view. (J) Prodissoconch. (K, L) Detail of prodissoconch sculpture. Scale bars: A–E, 1 mm; F–I, 00 μ m; J, K, 20 μ m; L, 4 μ m.

of inhalant opening. Inhalant opening is simple slit; exhalant siphon is short conical tube inverted into mantle cavity. Middle mantle fold bears 4–5 pairs of tentacles at the lateral margins at the base of inhalant opening, two–three pairs of tentacles at lateral margins of exhalant openings and 3–5 tentacles dorsally above exhalant opening. Tentacles are of different size; among tentacles of inhalant siphon the smallest locate most ventrally. Foot well developed.

Ctenidia thin, non-plicate, well-developed, comprising both inner and outer demibranchs; ascending lamella of outer demibranch approximately two times larger than descending lamella of outer demibranch and two times shorter than descending lamella of inner demibranch; both inner and outer demibranchs consisting of about 50 filaments. Labial palps small; outer palps consisting of thickened ridge, running along anteriormost part of ctenidia, posterior palps a little bit more developed.

Variation: Shell shape can vary from more triangular to more subcircular. Commarginal sculpture can be more or less prominent.

Number of siphonal tentacles varies; sometimes additional intercalary tentacles appear in the dorsal margin of exhalant siphon.

Distribution: Mid-North and Northwestern Pacific Ocean, 4130–5787 m.

Remarks: From the species occurring in the Kuril–Kamchatka Trench, *V. sergeevi* (Fig. 4) and *V. profunda* (Fig. 5), and from "*Vesicomya*" *filatovae* sp.n. (Fig. 6), *V. pacifica* differs by the shell shape, sculpture, hinge margin and number and location of siphonal tentacles (Tables 4 and 5). In contrast to *V. sergeevi* and *V. profunda*, *V. pacifica* has no overlapping teeth 1 and 3a in the right valve. Also, from *V. sergeevi* it differs by more inflated umbo, and from *V. profunda* by less conspicuous commarginal sculpture. Additional data is needed to decide if this species is conspecific with the population identified as *V. pacifica* (Coan et al., 2000) and distributed in the Eastern Pacific along the coast of America from off Oregon to off Valparaiso at 1200–6200 m. Compared to the Kuril–Kamchatka specimens, the eastern-pacific specimens

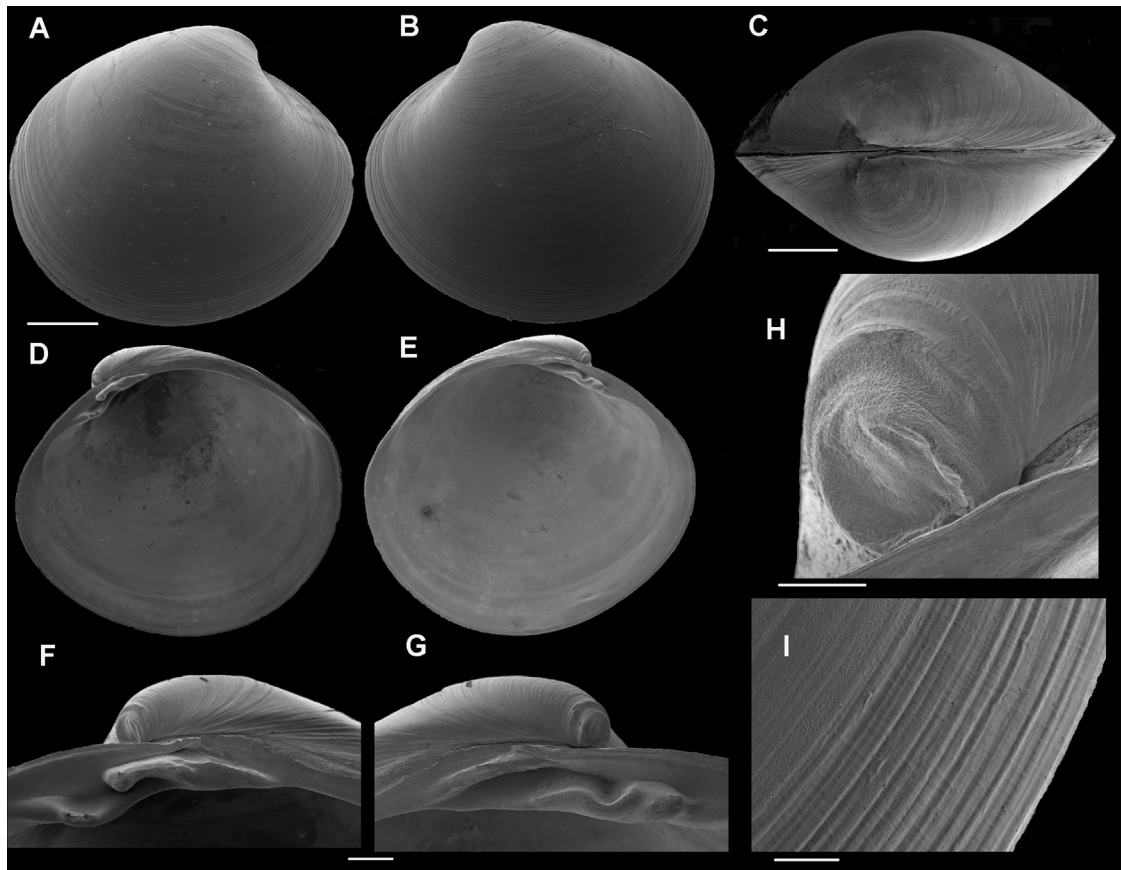


Fig. 4. (A–I) *Vesicomysa sergeevi* Filatova, 1971, R/V Vityaz, St. 5627, ZMMU, Ld 2915: (A) exterior of right valve, (B) exterior of left valve, (C) dorsal view, (D) interior of right valve, (E) interior of left valve, (F) hinge of right valve, (G) hinge of left valve, (H) prodissoconch and (I) detail of sculpture near shell margin. Scale bars: A–E, 1 mm; F, G, 200 μ m; H, I, 100 μ m.

characterised by a more protruding umbo, which locates in a more anterior position.

"Vesicomysa" filatovae Krylova and Kamenev sp.n.

Figs. 6, 7A D, and 8

Holotype: spm with soft parts (R/V "Sonne", cruise no. 223, St. 7–9, EBS, 43°01.50'–43°02.87'N, 152°58.35'–152°59.45'E, 5216–5222 m, 17.08.2012), MIMB 29210.

Paratypes: two spms with soft parts (the same station as the holotype), MIMB 29211;

two spms with soft parts, ZMMU Ld-3049, two spms with soft parts, Zoological Museum, Hamburg, and SMF 345013/2, (R/V "Sonne", cruise no. 223, St. 6–10, AGT, 42°29.00'–42°34.17'N, 154°00.09'–154°00.32'E, 5295–5309 m, 14–15.08.2012).

Type locality: Northwestern Pacific Ocean, to the east of the Kuril Islands, 43°01.50'–43°02.87'N, 152°58.35'–152°59.45'E, 5179–5222 m.

Other material examined: R/V "Sonne", cruise no. 223, St. 1, 2, 3, 5, 6, 7, 8, 9; for details see Table 1.

Diagnosis: Vesicomysinae-species with L to 1.6 mm, relatively solid, semitransparent, subcircular-ovoid shell, $H/L=0.88-0.94$, $W/L=0.31-0.38$, with sculpture consisting of thin thread-like regular commarginal ribs; well-defined escutcheon stretching along whole postero-dorsal margin, lunular incision present, umbo situated at anterior 24–33%, prosogyrate beaks, nymph short, in left valve 4b-tooth of the same length as nymph, with one pair of demibranchs.

Description: Shell small-sized, L to 1.6 mm, relatively solid, semitransparent, subcircular-ovoid in outline, $H/L=0.88-0.94$, $W/L=0.31-0.38$ (Table 4), equivalve; right valve slightly overlapped left valve posterodorsally. Sculpture consisting of thin

tread-like regular commarginal ribs, in umbonal region ribs get smaller and irregular located; number of ribs about 28 on a shell of about 1.5 mm length. External shell surface covered by very small irregular scattered pores, more densely aggregated on top of ribs. Escutcheon stretching along whole postero-dorsal margin, well-defined, delimiting keel in left valve sharper. Lunule broad, slightly depressed, distinctly demarcated by incision, occupying whole length of antero-dorsal margin. Inequilateral, anterior margin much shorter, umbo situated at anterior 24–33% of valve. Umbones prosogyrate, protruding. Antero-dorsal margin convex, anterior and ventral margins regular and evenly rounded, postero-dorsal margin long, evenly slightly convex, forming obtuse angle with ventral margin. Pallial line hardly visible, without pallial sinus. Anterior adductor scar ovately elongated in outline, dorsal margin of anterior adductor scar slightly impressed. Anterior pedal retractor scar impressed, located dorsally to anterior adductor scar, on thickening just below anterior part of hinge plate, fused with anterior adductor scar. Posterior adductor scar oval, slightly larger than anterior adductor scar, not impressed. In both valves low ridge running inside along postero-dorsal margin separated from margin by shallow furrow. Inner edge of valve margin thin, bearing furrow parallel to shell margin. Nymph weak and short. Ligament small, opisthodontic. Dentition of right valve: ventral cardinal (1) wedge-like, parallel to antero-dorsal shell margin; 3a-ramus thin, short, parallel to antero-dorsal shell margin, fused in its proximal part with anterior edge of 3b-ramus; 3b-ramus thicker than 3a, radiating posteriorwards. Dentition of left valve: 2a-ramus thin, fused in its proximal part with anterior edge of thicker 2b-ramus; both 2a and 2b nearly parallel to dorsal shell margin; 4b-tooth low, elongated, parallel to postero-dorsal shell margin.

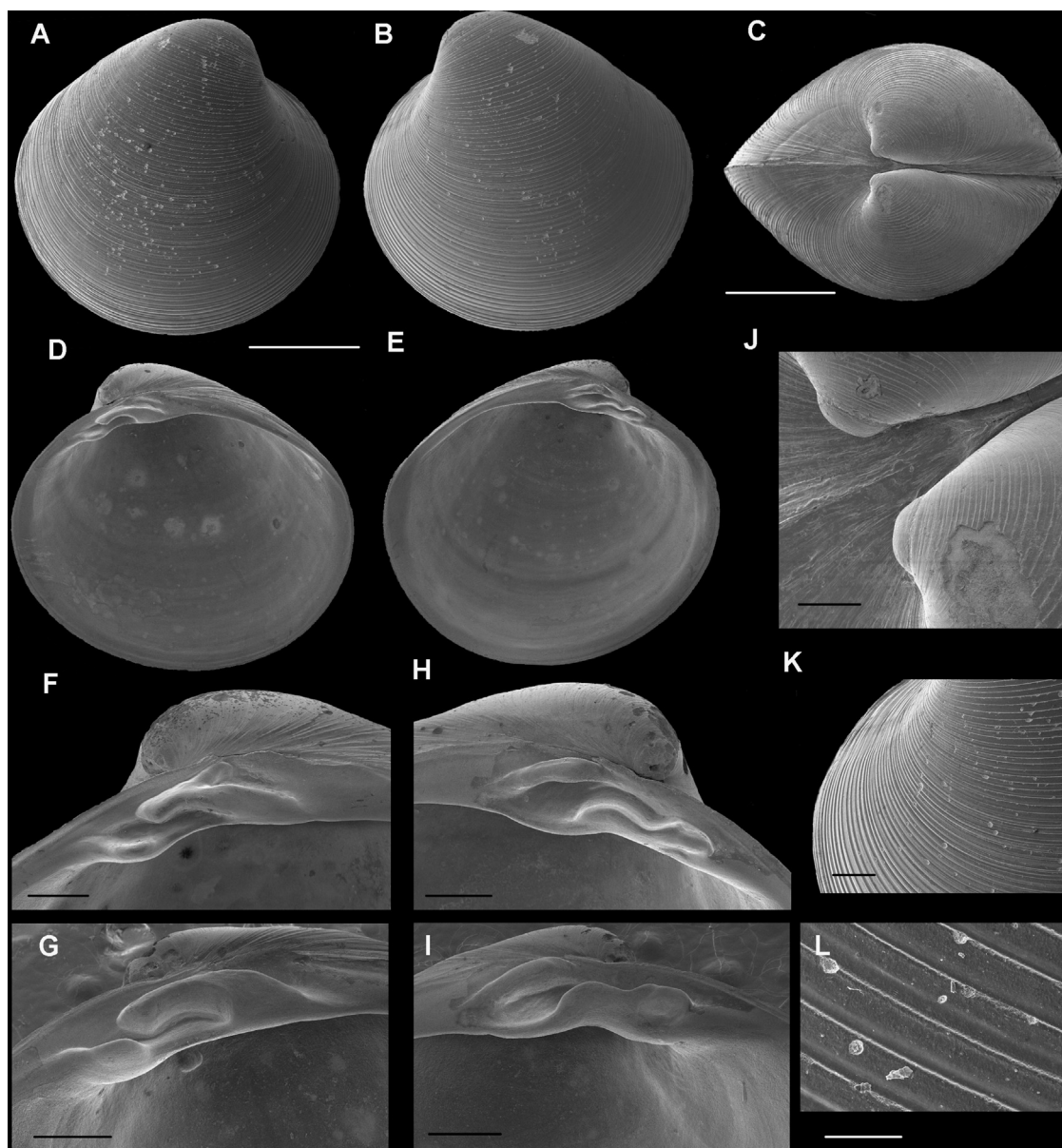


Fig. 5. (A–L) *Vesicomya profunda* Filatova, 1971, R/V Vityaz, St. 5632, ZMMU, Ld 2939: (A) exterior of right valve, (B) exterior of left valve, (C) dorsal view, (D) interior of right valve, and (E) interior of left valve. (F, G) Hinge of right valve, lateral and latero-ventral view. (H, I) Hinge of left valve, lateral and latero-ventral view. (J) Umbonal part of shell with prodissoconch. (K) Anterior part of shell with lunule. (L) Detail of sculpture. Scale bars: A–E, 1 mm; F–I, K, 200 μ m; J, L, 100 μ m.

Table 3
Measurements of shells of *Vesicomya pacifica* (Smith, 1885) (mm).

	L	H	W	H/L	W/L	Um %
1 spm, St. 9, MIMB	8.2	7.6	3.2	0.93	0.39	34
2 spm, St. 9, MIMB	6.5	6.3	2.5	0.97	0.38	38
3 spm, St. 9, MIMB	5.8	5.5	2.1	0.95	0.36	36
4 spm, St. 9, MIMB	5.1	4.9	1.9	0.96	0.37	26
5 spm, St. 9, MIMB	4.7	4.3	1.7	0.91	0.36	33

Table 4
Measurements of shells of "*Vesicomya*" *filatovae* sp.n. (mm).

	L	H	W	H/L	W/L	Um %
Holotype, St. 7, MIMB	1.6	1.4	0.5	0.88	0.31	29
Paratype, St. 7, MIMB	1.4	1.3	0.5	0.93	0.36	33
Paratype, St. 7, MIMB	1.4	1.3	0.45	0.93	0.32	24
Paratype, St. 6, ZMMU	1.6	1.5	0.6	0.94	0.38	–

Prodissoconch with pitted structure, about 160 μ m in diameter, with margin, about 20 μ m broad, sculptured by commarginal striae and irregular fine radial striation.

Soft parts: Mantle lobes thin, except at margins. Mantle fusion forming three pallial apertures, pedal gape and two posterior siphonal openings. Pedal gape occupying the entire ventral edge from the middle of frontal surface of the anterior adductor to the base of inhalant opening. Middle mantle fold bears one pair of tentacles at the ventral margin of inhalant opening, one pair of tentacles close to fusion between inhalant and exhalant openings and three tentacles dorsally above exhalant opening. Foot well developed.

Ctenidia thin, non-plicate, comprising inner demibranch only with descending and ascending lamellae; ascending lamella very short, consisting about one-sixth of height of descending lamellae. Descending lamella comprising about 12–15 filaments with one row of interfilamental junctions. Demibranch without interlamellar septa. Labial palps small; outer palps consisting of thickened ridge, running along anteriormost part of ctenidia, inner labial palps smaller.

Table 5
Morphological characters of vesicomysins from the Pacific and Indo-West Pacific.

Species	Maximal shell length (mm)	Number of siphonal tentacles	Teeth of right valve (x – 1- and 3a-teeth overlap, 0 – no overlapping)	Numbers of pairs of demibranchs	Distribution	Reference
<i>V. pacifica</i> (Smith, 1885) (type material)	4.5	?	0	?	Mid-North Pacific, 5220 m	Smith (1885)
<i>V. pacifica</i>	8.2	4–5 pairs near inhalant siphon, 2–3 pairs at lateral margins of exhalant siphon + 3–5 dorsal	0	2	Northwestern Pacific, to the east of the Kuril Islands, 4861–5787 m	This paper
<i>V. bruuni</i> (Filatova, 1969)	6.6	35–70 around both siphons	0	2	Kermadec trench, 5900–9200 m	Filatova (1969), Knudsen (1970)
<i>V. galathea</i> (Knudsen, 1970)	5.2	3 pairs ventral + 1 pair between siphons + 3 dorsal	0	2	Eastern Pacific from British Columbia to Gulf of Panama, 1760–4000 m	Knudsen (1970), Bernard (1989), Coan et al. (2000)
<i>V. sundaensis</i> (Knudsen, 1970)	3.9	3 pairs ventral + 3 pairs between siphons + 1–2 pairs lateral + 5 dorsal	0	2	Sunda Trench, 6900–7000 m	Knudsen (1970)
<i>V. tasmanensis</i> (Knudsen, 1970)	6.2	Up to 3 pairs ventral + 2 pairs lateral + 3 dorsal	0	2	Tasman Sea, 4400 m	Knudsen (1970)
<i>Vesicomys</i> sp.	–	1 pair ventral + 1 pair lateral	0	2	Kermadec Trench, 4540 m	Knudsen (1970)
<i>V. sergeevi</i> (Filatova, 1971)	4.8	2–3 pairs ventral + app. 10 pairs around exhalant siphon + 1 dorsal	x	2	Kuril–Kamchatka Trench, 7600–9530 m	Filatova (1971), this paper
<i>V. profundus</i> (Filatova, 1971)	5.5	5–6 pairs near inhalant siphon, about 6 pairs around exhalant siphon + 1 dorsal	x	2	Kuril–Kamchatka Trench, 7120–9050 m; Aleutian Trench, 7246 m	Filatova (1971), this paper
“ <i>V.</i> ” <i>filatovae</i> sp.n.	1.6	1 pair at the base of inhalant siphon + 1 pair near separation between siphons + 3 dorsal	x	1	North-western Pacific, to the east of the Kuril Islands, 4861–5427 m	This paper

Variation: Smaller specimens have relatively shorter postero-dorsal margin and consequently have more subquadrate shell shape.

Distribution: Northwestern Pacific Ocean, to the east of the Kuril Islands, 4861–5427 m.

Derivation of name: This species is dedicated to late Russian malacologist Zinaida A. Filatova in acknowledgement of her investigations of abyssal bivalve molluscs.

Relationships: The new species has considerable resemblance to small-sized species of the genus *Waisiuconcha* Beets, 1943 (Pliocardiinae), *W. haeckeli* Cosel and Salas, 2001 and *W. ruggierii* (Ceregato and Tabanelli, 2001) but differs from the type species of *Waisiuconcha*, *W. alberdinae* Beets, 1942, by smaller, more inflated and higher shell provided with well-developed concentric sculpture (Janssen and Krylova, 2012). *Waisiuconcha haeckeli* occurs in the Eastern Atlantic near Mauritania at depths of 600–1200 m (Cosel and Salas, 2001). *W. ruggierii* is a fossil species recorded from the Pliocene of Italy and France (Ceregato and Tabanelli, 2001; Janssen and Krylova, 2012). From both these species, “*Vesicomys*” *filatovae* sp.n. differs by the slender hinge margin with thinner teeth, by the absence of incisions in the inner shell margin and by the details of shell sculpture. Both *W. haeckeli* and *W. ruggierii* have a commarginal sculpture in which interstices are narrower than ribs while in “*Vesicomys*” *filatovae* sp.n. interstices are much wider than thin thread-like ribs. The anatomy of *W. haeckeli* and *W. ruggierii* is not known. Another species, which is very similar to “*Vesicomys*” *filatovae* sp.n. morphologically and probably closely related phylogenetically, is “*Kelliella*” *concentrica* Allen, 2001. “*Kelliella*” *concentrica* is also a very small-sized species with shell length of up to 2.5 mm which occurs in the Northwestern Atlantic in the North America Basin at depth 457–811 m. We put the generic name used by Allen (2001) in quotations because this species differs considerably from *Kelliella miliaris* (Philippi, 1844), the type species of the

genus *Kelliella* M. Sars, 1870 (discussion see in Janssen and Krylova, 2012). “*Kelliella*” *concentrica* has similar characteristics to “*V.*” *filatovae* sp.n. in the concentric sculpture, the strong hinge margin, the distinctly incised lunule, the well-developed escutcheon and the presence of inner demibranch only. “*Vesicomys*” *filatovae* sp.n. differs from “*Kelliella*” *concentrica* by a more convex postero-dorsal margin, in details of hinge margin (in the right valve *filatovae* has larger 3a and 3b-teeth and smaller 1-tooth, see Allen, 2001: 212, Fig. 14) and the smaller number of siphonal tentacles. “*Kelliella*” *concentrica* has about 15 tentacles while *filatovae* has 7. The generic assignment of “*Kelliella*” *concentrica* requires further study.

Remarks: The new species is only provisionally placed in the genus *Vesicomys*, as it differs from *V. atlantica* (Smith, 1885), the type species of the genus *Vesicomys*, in many respects.

In contrast to *V. atlantica*, the new species has a more solid shell with a stronger hinge margin. Teeth in “*Vesicomys*” *filatovae* sp.n. are thicker and more radiating than in *V. atlantica*. Besides that *V. atlantica* has two pairs of demibranchs while the new species has only one. Despite the conchological similarity with some species earlier assigned to the genus *Waisiuconcha* (Pliocardiinae), we do not allocate the new species to *Waisiuconcha* because of its anatomical differences from all described pliocardians. Representatives of the subfamily Pliocardiinae have gills with subfilamental interlamellar septa consisting of bacteriocytes while “*Vesicomys*” *filatovae* sp.n. has gills lacking subfilamental tissue. Further morphological study together with the molecular analysis, which is underway now, will help to clarify the position of “*Vesicomys*” *filatovae* sp.n. in the system of the Vesicomysinae.

3.2. Phylogenetic analysis

The part of cytochrome oxidase *c* subunit I (COI) gene for four individuals of putative species *V. pacifica* was sequenced. The lengths of the sequenced fragments were 582 bp for Ves 9.9, 624

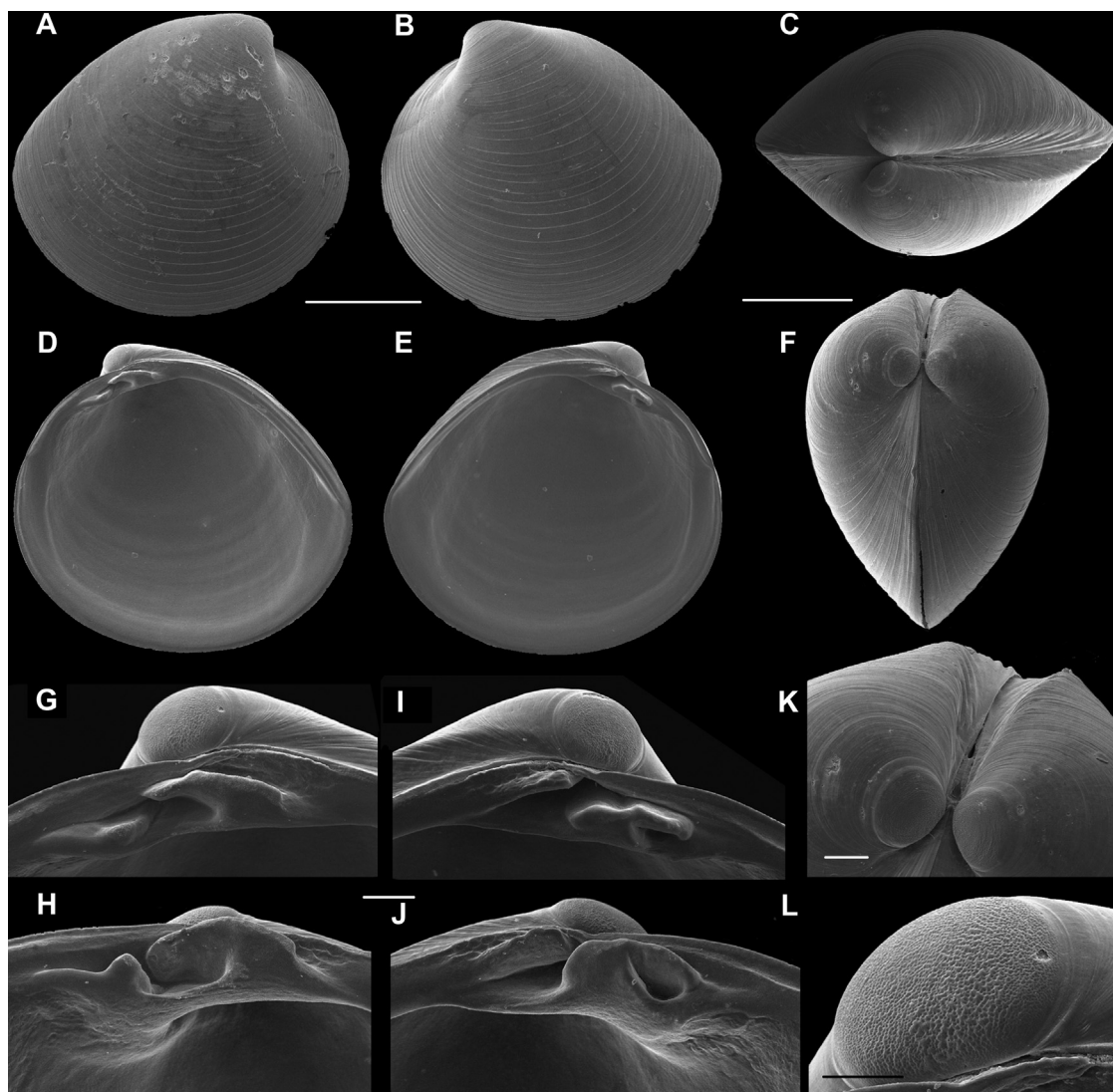


Fig. 6. (A–L) “*Vesicomya*” *filatovae* sp.n, KuramBio, St. 8, IMB FEB RAS: (A) exterior of right valve, (B) exterior of left valve, (C) dorsal view, (D) interior of right valve, (E) interior of left valve, and (F) anterio-dorsal view. (G, H) Hinge of right valve, lateral and latero-ventral view. (I, J) Hinge of left valve, lateral and latero-ventral view. (K) Umbonal part of shell with prodissoconch. (L) Prodissoconch. Scale bars: A–F, 500 μ m; G–J, K, 100 μ m; L, 50 μ m.

bp for Ves 11.9, and 658 bp for each Ves 7.9 and Ves 8.9. Because many of the sequences acquired from GenBank were shorter, all of our sequences were truncated to 513 bp for the present analyses. Examination of the inferred amino acid sequences revealed no indication to pseudogene involvement in the data (i.e. no stop codons or excess amino-acid substitutions). Within this alignment 326 positions were revealed as variable, among them 259 positions were assigned as parsimony informative and 67 positions were considered as singletons. There were no insertions or deletions specifically marking *V. pacifica* within COI locus. In the phylogenetic trees inferred by MP, ML, NJ and BI methods the dataset of four newly obtained COI sequences of *V. pacifica* together with 160 COI vesicomylid sequences taken from GenBank is splitted into two well supported monophyletic clades (Fig. 9). The major clade (BP=99/99/99%; PP=1) includes the following lineages, including one or more species: *Archivesica*, *Akebiconcha*, *Phreagena*, “*Calyptogena*” *magnifica*, “*cordata*”-group, *Ectenagena*, *Pliocardia*, *Abyssogena*, *Isorropodon*, *Calyptogena* (Table S1; “*cordata*”-group is a clade revealed in Audzijonyte et al., 2012, which will be formally described as a new genus elsewhere). The minor clade (BP= 72/72/82%; PP=0.65) includes the new sequences of *V. pacifica* and two GenBank sequences referring to *Kelliella* sp. (KC429129) and

Vesicomya sp. (JX196691). All four specimens of *V. pacifica* represent a tight cluster with a genetic divergence of $0.8\% \pm 0.3$ confirming their conspecific status. In this small vesicomylid dataset *V. pacifica* is sister to “*Kelliella*” sp. (KC429129) and this two species-clade in turn cluster as sister group to *Vesicomya* sp. (JX196691) although with lower support (for evolutionary distances see Table S2 in supplementary materials).

4. Discussion

Vesicomylids are among the most common bivalves in the abyssal zone of the World Ocean (Allen, 2001; Knudsen, 1970; Linse, 2004). In spite of their sometimes very small size, they can reach high biomasses due to huge abundances (Vinogradova et al., 1993). Biological features that promote the obvious success of vesicomylids in the deep-sea are not quite certain. In order to determine if bacterial symbiotrophy could be the trophic strategy for vesicomylids, the microstructure of gill filaments of *V. sergeevi* from the Kuril–Kamchatka Trench was previously studied (Krylova et al., 2000). The presence of bacteria in the gills was recorded, but a symbiotrophic nature was not proved.

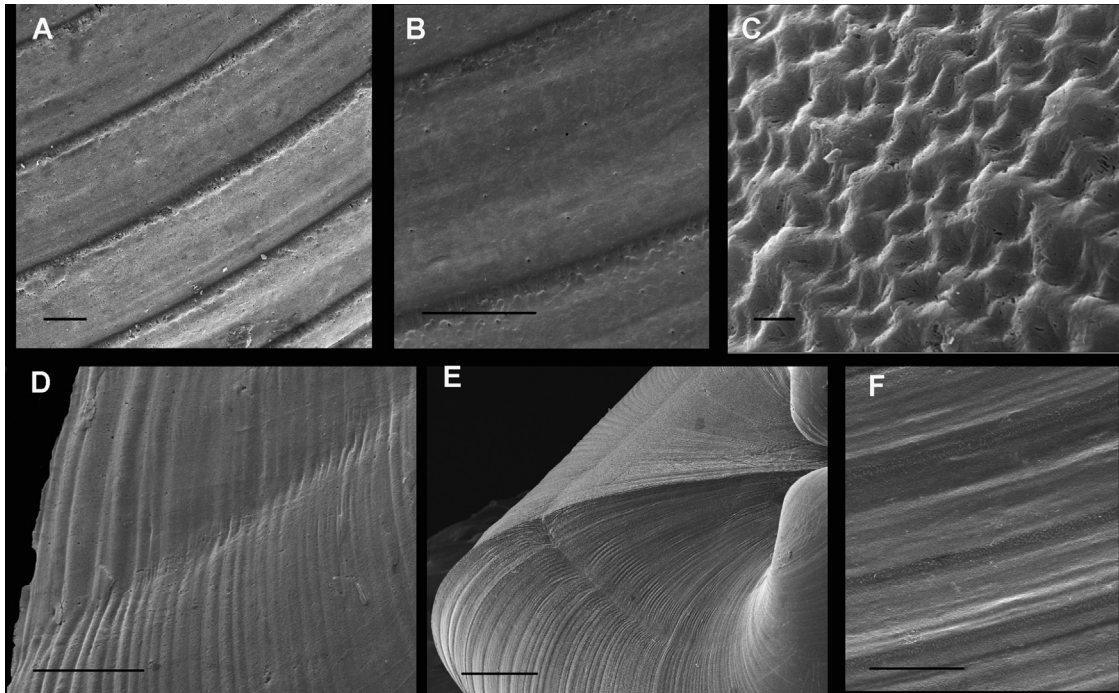


Fig. 7. (A–D) “*Vesicomya*” *filatovae* sp.n, KuramBio, St. 8, IMB FEB RAS: (A, B) Exterior shell sculpture. (C) Sculpture of prodissoconch. (D) Anterior part of shell with lunule insicion. (E, F) *Vesicomya pacifica*, KuramBio, St. 8, IMB FEB RAS. (E) Anterior part of shell with lunule. (F) Exterior shell sculpture near ventral margin. Scale bars: A, B, 20 μ m; C, 2 μ m; D, 50 μ m; E, 200 μ m; F, 100 μ m.

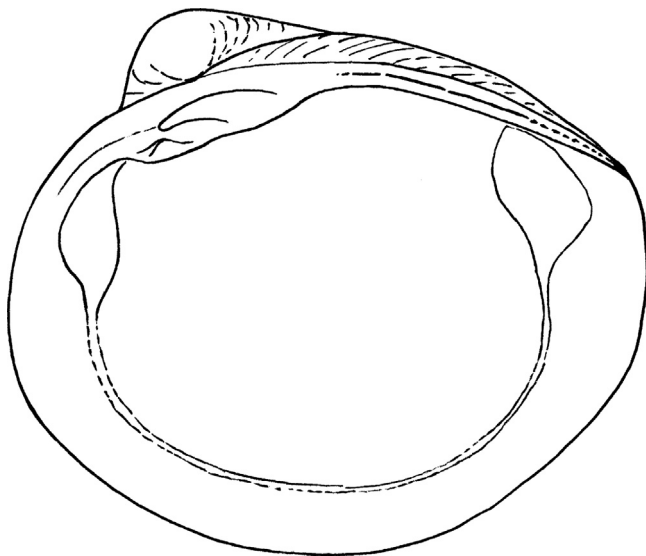


Fig. 8. “*Vesicomya*” *filatovae* sp.n, KuramBio, St. 8, IMB FEB RAS. Semi-schematic line drawing of right valve, L=1.6 mm.

Despite of their globally wide deep-sea distribution, vesicomys have not been known from the abyssal plain adjacent to the Kuril–Kamchanka Trench. As a result of the study in the collection obtained by the KuramBio expedition, two vesicomys species, *V. pacifica* and “*Vesicomya*” *filatovae* sp.n., were recorded from this region. In the material collected, *V. pacifica* was the most abundant bivalve species (Kamenev, 2015). On the basis of these new data the geographic range of *V. pacifica* was extended to the more northern regions of the Pacific by about 10° of latitude (Fig. 1).

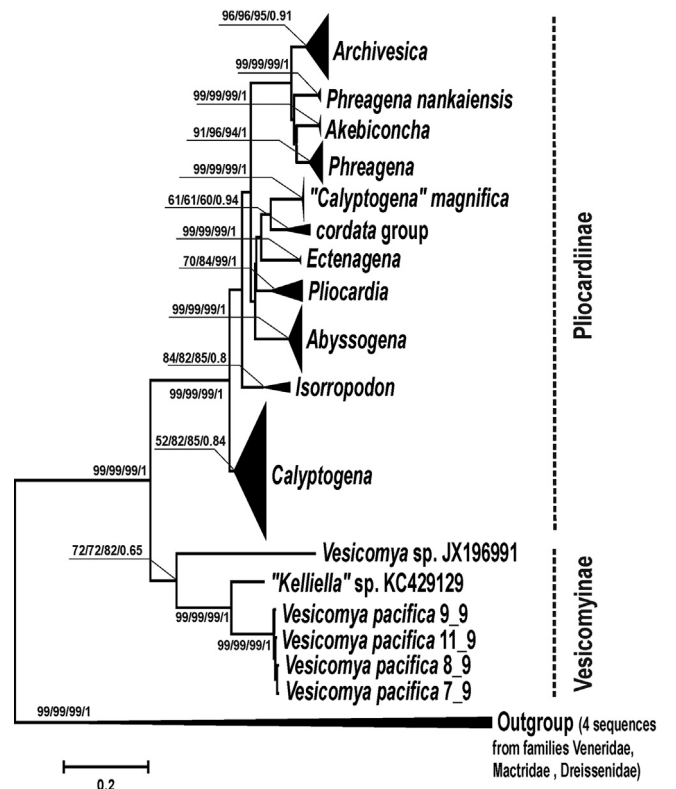


Fig. 9. Phylogenetic tree of Vesicomysidae based on COI nucleotide sequences listed in Table S1. This tree is a consensus of trees inferred by MP, ML, NJ and BI methods. Bootstrap values (MP/ML/NJ) and posterior probabilities (BI) are shown beside nodes. Operational taxonomic units (filled triangles) are expressed as the provisional generic names listed in Table S1. The tree is drawn to scale, with branch lengths measured in the number of substitutions per site.

Previously two species of vesicomys, *V. sergeevi* (7600–9530 m) and *V. profundus* (7120–9050 m), were described by Filatova (1971) from the Kuril–Kamchatka Trench. Despite of the geographical proximity of the distribution range of these hadal species with the species from the adjacent abyssal basin (Fig. 1) there is no overlap in their vertical distribution. This observation confirms the suggestion of Filatova (1971) on the existence of a specialized hadal complex of bivalve species in the Kuril–Kamchatka Trench and adds to evidence that the hadal zone has a fauna, which in many respects is distinct from the abyssal fauna (Belyaev, 1966, 1989; Vinogradova, 1997; Wolff, 1970). Notably, the restriction to hadal zone in this case does not mean a narrow geographic range: *V. profundus* is recorded also from the Aleutian Trench (Table 5).

To date the taxonomy and species composition of vesicomys are not clear. Many authors have synonymized the genera *Vesicomys* Dall, 1886 and *Kelliella* M. Sars, 1870 and consequently the families Vesicomysidae Dall and Simpson, 1901 and Kelliellidae P. Fischer, 1887 (Allen, 2001; Knudsen, 1970; Studencka, 1987). The problem of relationships between these taxonomic groups is beyond the scope of this paper and will be discussed in details in a separate study, which is currently underway (E. Krylova and H. Sahling). Here we follow Dall (1908), Woodring (1938), Cosel and Salas (2001), Krylova and Sahling (2010) and consider *Vesicomys* and *Kelliella* as separate genera belonging to the different families Vesicomysidae and Kelliellidae. The phylogenetic relationships of the genus *Vesicomys* to the large chalky chemosymbiotic clams from reducing habitats, e.g. *Calyptogena*, *Archivesica*, *Ectenagena*, which usually have been referred to as vesicomysids, also remain still questionable. Allen (2001) suggested that these large-sized chemosymbiotic clams differ from tiny vesicomysids at least at subfamilial level. Krylova and Sahling (2010) allocated the “large” clams to the subfamily Pliocardiinae Woodring 1925 in the family Vesicomysidae while the genus *Vesicomys* was assigned to the monotypic nominate subfamily Vesicomysinae Dall and Simpson, 1901. Morphological disparity between pliocardiaans and vesicomysids is prominent and the subfamilial level of their affinity needs to be approved by both morphological and molecular evidence. Comprehensive investigation of this problem is currently under work; nevertheless here we present the first results of a preliminary one-gene molecular analysis, which shows the position of *V. pacifica* in relation to two other vesicomysid species and the major groups of pliocardiaans. The results of the COI molecular analysis show low genetic divergence between four new vesicomysid sequences from specimens morphologically assigned to *V. pacifica* despite that all four specimens were from different stations and had some morphological disparities. Their calculated intra-group genetic distances of $0.8\% \pm 0.3$ fall in the intra-species divergence range estimated by different authors for vesicomysids as from 0.2 to 2.8% (Audzijonyte et al., 2012; Goffredi et al., 2003; Peek et al., 1997, 2000). For venerid species conspecific divergence values are shown to be in the range 0–3.17% (Chen et al., 2011). Analysis of COI and Cyt-b sequences from 22 266 populations and species across the animal kingdom testified for COI divergence levels of 0.89 ± 0.16 as conspecific, of 3.78 ± 1.18 as interspecies for cryptic species, and of 11.01 ± 0.53 for well distinguished morphospecies (Kartavtsev, 2013). Thus four new vesicomysid sequences belong to the same species, presumably *V. pacifica*.

According to the topologies resulting from the phylogenetic COI analysis (Fig. 9), *V. pacifica* together with “*Kelliella*” sp. (KC429129) and *Vesicomys* sp. (JX196991) form a monophyletic clade that corresponds to the proposed subfamily Vesicomysinae (Krylova and Sahling, 2010). In turn, this clade is sister to the cluster uniting all generic groups of “large” vesicomysids which are interpreted here as the subfamily Pliocardiinae. Special mention should be made

about the sister relationships of *V. pacifica* and the species which was registered in GenBank and used in the study of (Bieler et al., 2014) under the name of *Kelliella* sp. (KC429129). The material was unavailable for our examination, however we can suggest on the basis of the image (Fig. 4C in Bieler et al., 2014) that this species is actually *Vesicomys* s.s. since it has an escutcheon which is absent in *Kelliella miliaris*, the type species of *Kelliella* (Janssen and Krylova, 2012). An indirect indication for the change of the genus assignment is the depth of collection of the “*Kelliella*” (KC429129) material. This mollusc was collected in the Western Atlantic on the Gay Head-Bermuda transect at the depth of 3200 m (pers. com. of Prashant Sharma, 11.12.2013; Bieler et al., 2014). *Kelliella* usually occurs at sublittoral to upper bathyal depths with known vertical range 10–1170 m (Allen, 2001) and critically revised and confirmed species of *Kelliella* have yet not been recorded from the abyssal zone. *Vesicomys* sp. (JX196991) was collected from the abyssal depth (4580 m) of the southern Atlantic (Krylova and Sahling, in preparation).

Our new morphological and molecular data suggest that the Vesicomysinae, which have been considered as a monotypic subfamily, could have a more complicated taxonomic structure including several genera. *V. pacifica* and “*Kelliella*” sp. (KC429129) form a quite tight clade, which could be interpreted as *Vesicomys* s.s. (Table S2). Actually, *V. pacifica* morphologically is very similar to *V. atlantica* (Smith, 1885), which is the type species of the genus. Both species have narrow hinge line with teeth mainly parallel to the dorsal margin, short anterior tooth (1) in the right valve that is not overlapped with 3a-tooth, thin gills comprising both inner and outer demibranchs and short inverted to the mantle cavity exhalant siphon. Thus *V. pacifica* can be considered as an undoubted representative of the genus *Vesicomys*. *Vesicomys* sp. (JX196991) is genetically more diverged from the *V. pacifica* and “*Kelliella*” sp. and might represent a new generic group. Morphological evidence for this is that *Vesicomys* sp. (JX196991) has a thicker hinge margin with more radiating teeth and in the right valve an anterior tooth (1) being overlapped with 3a-tooth (see Fig. 1 in Krylova and Sahling, 2010). A very similar arrangement of teeth can be observed in *V. sergeevi* and *V. profundus* (Figs. 4F and 5F, G). Morphological and anatomical characteristics of “*Vesicomys*” *filatovae* sp.n. give more evidence for the suggestion of larger generic diversity in vesicomysids. The fact that “*Vesicomys*” *filatovae* sp.n. has only one pair of demibranchs instead of two pairs as recorded in all so far studied vesicomysids, may indicate the presence of a further genus in vesicomysids.

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This is KuramBio publication #8.

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at <http://dx.doi.org/10.1016/j.dsr2.2014.10.004>.

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