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Resolving the status of the families Vesicomyidae and Kelliellidae (Bivalvia: Venerida), with notes on their ecology

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ABSTRACT

The bivalve family Vesicomyidae comprises two subfamilies: Pliocardiinae and Vesicomyinae. The Pliocardiinae include conspicuous mostly large- and medium-sized clams, which live in symbiosis with chemoautotrophic bacteria and often dominate chemosynthetic communities in the deep sea. The Vesicomyinae comprise poorly-studied tiny bivalves, which at first sight differ considerably from their better known, large-sized relatives. Vesicomyines have a worldwide distribution from mid-slope to hadal depths and reach abundances of thousands of specimens in one trawl catch in deep-sea trenches. The genus *Vesicomya* is morphologically very similar to the genus *Kelliella*, the type genus of family Kelliellidae. This fact has long caused taxonomic ambiguities and it has been suggested that *Vesicomya* and *Kelliella*, as well as their respective nominate families, should be synonymized. In this paper we study the relationship between *Vesicomya* and *Kelliella*, for the first time using not only morphological characters but also genetic divergence based on the mitochondrial cytochrome *c* oxidase subunit I (COI) gene. Our molecular data indicate that the genera *Vesicomya* and *Kelliella* are clearly distinct and that *Kelliella* is distantly related to the Vesicomyidae. Results of morphological analysis support the molecular inferences. We provide further evidence for the relationship of vesicomyines and pliocardiines and propose an evolutionary scenario according to which Vesicomyinae is the less derived group and Pliocardiinae the more derived. We provide the first information on stable carbon and nitrogen isotopic composition of soft tissues of *Vesicomya* and *Kelliella*. These data do not suggest involvement of chemosynthetically fixed carbon in the nutrition of either *Vesicomya* or *Kelliella*. We revise current usage of these two genera and provide lists of the species of each, with details of their distribution. A new species, *Vesicomya alleni*, is described on the basis of morphological and molecular characters.

INTRODUCTION

The family Vesicomyidae constitutes morphologically diverse, widely distributed, deep-sea bivalves, including conspicuous large-sized clams from hydrothermal vents and hydrocarbon seeps. The family comprises two subfamilies, Vesicomyinae Dall & Simpson, 1901 and Pliocardiinae Woodring, 1925, which in some respects differ significantly from each other (Krylova & Sahling, 2010). Pliocardiines include mainly large- and medium-sized clams, which live in symbiosis with chemoautotrophic, sulphur-oxidizing bacteria (Fisher, 1990) and often dominate chemosynthetic communities in the deep sea (Sibuet & Olu, 1998). By contrast the Vesicomyinae are represented by tiny bivalves, which at first sight have little in common with their better known large-sized relatives. The distribution of vesicomyines ranges from mid-slope to deep-water trench depths and they are among the most common bivalves in the abyssal and ultra-abyssal zones of the World Ocean (Knudsen, 1970; Belyaev, 1972; Belyaev & Mironov, 1977; Allen, 2001; Linse, 2004; Kamenev, 2015). They are recognized as an important component of deep-water communities, from which thousands of specimens can be recovered with single trawl catches (Filatova, 1971, 1974; Vinogradova *et al.*, 1993). It is unclear whether or not vesicomyines are symbiotrophic. Transmission electron microscopy (TEM) has indicated the presence of bacteria in the gills of *Vesicomya sergeevi* from the Kuril-Kamchatka Trench, but the relationship between the bacteria and the clam remains unresolved (Krylova, Drozdov & Mironov, 2000). Studying the relationship between the two subfamilies within the Vesicomyidae may shed light on the evolutionary path that led from heterotrophic deep-sea clams to highly specialized hosts harbouring autotrophic bacteria, which allow exploitation of sulphide-rich sediments.

At present the Vesicomyinae include only one genus, *Vesicomya* Dall, 1886. It should be noted that throughout this paper we use the generic name *Vesicomya* in the strict sense of being the sole genus of the subfamily Vesicomyinae. In contrast, in the literature several pliocardiine species have been termed '*Vesicomya*', because of ambiguity in the generic composition of the family. With improving resolution of pliocardiine genera (Von Cosel & Salas, 2001; Krylova & Sahling, 2006; Von Cosel & Olu, 2008, 2009; Krylova, Sahling & Janssen, 2010; Krylova & Von Cosel, 2011; Krylova *et al.*, 2014; Hansen *et al.*, 2017; Johnson *et al.*, 2017), this broad usage of '*Vesicomya*' for pliocardiine clams should decrease. The resolution of the taxonomic diversity of vesicomyines is as yet unsatisfactory. They include 15 named species, but some need taxonomic revision, and recent morphological and molecular data indicate that vesicomyines are more diverse and might have a more complicated generic structure than currently recognized (Krylova *et al.*, 2015).

Morphological differences obviously separate vesicomyines and pliocardiines, but recent molecular data suggest that vesicomyines and pliocardiines form sister phylogenetic clades (Krylova *et al.*, 2015; Johnson *et al.*, 2017). Molecular data for *Vesicomya s. s.* are scarce. Audzijonyte *et al.* (2012) used a species of *Vesicomya* (wrongly assigned to *V. atlantica*, though closely related) as the outgroup in a phylogenetic tree of pliocardiines based on the mitochondrial cytochrome *c* oxidase subunit I (COI) gene. Bieler *et al.* (2014) published sequences of five molecular marker genes (including COI) of a species they referred to as *Kelliella* sp., but that is a species of *Vesicomya* (see their Fig. 4C and arguments of Krylova *et al.*, 2015). COI gene sequences from four specimens of *V. pacifica* were published by Krylova *et al.* (2015). Finally, the sister relationship between the *Vesicomya* and pliocardiine clades was recently shown through analysis of COI and five nuclear genes (H3, Ant, Cal, 18 S and 28 S rRNA) by Johnson *et al.* (2017). These authors suggested that the lineages leading to pliocardiines and *Vesicomya* split during the Late Cretaceous to early Cenozoic eras.

The genus *Vesicomya* is morphologically highly similar to the genus *Kelliella* M. Sars, 1870. Both *Vesicomya* and *Kelliella* comprise small-sized heterodont bivalves with swollen shells and rounded shell outline. This resemblance has long caused taxonomical ambiguities and the suggested synonymy of *Vesicomya* and *Kelliella*. As both are type genera for the corresponding families, their synonymy would lead to nomenclatural changes, Kelliellidae P. Fischer, 1887 having priority over Vesicomyidae Dall & Simpson, 1901. Many authors have argued for the synonymy of *Vesicomya* and *Kelliella* (Thiele, 1935; Knudsen, 1970; Studencka, 1987; Bernard, 1989; Hayami & Kase, 1993; Allen, 2001; Huber, 2010; Raines & Huber, 2012), while others have considered them to be distinct (Dall, 1908; Odhner, 1960; Boss, 1968; Filatova, 1969, 1971; Scarlato, 1981; Von Cosel & Salas, 2001; Krylova & Sahling, 2010; Janssen & Krylova, 2012; Krylova *et al.*, 2015). Reduction of body sizes in both genera probably resulted in significant morphological convergences, and this in turn limits the value of many morphological characters for systematics. Molecular data for *Kelliella* has not been available until now.

In this study, we attempt to resolve the relationship between *Kelliella* and *Vesicomya*, based on morphological and molecular characters using the COI gene. We provide lists of species of *Vesicomya* and *Kelliella*, which have been used in the current literature, but without taxonomical revision of these species. Critical revision of the species composition of both genera needs further effort and additional material, and is beyond the scope of this paper. We aim to stimulate further investigations of the two genera by providing information on their ecology, both by reviewing published data and providing our own observations on stable carbon and nitrogen isotopic compositions of their soft tissues.

The genus Vesicomya

Vesicomya was introduced by Dall (1886: 272) as a subgenus of *Callocardia* and was typified by *Callocardia* (?) *atlantica* (see Table 3 for authorities of species of *Vesicomya s. s.*). Together with the type species, *Vesicomya* included *C.* (?) *pacifica*, *C.* (?) *adamsi*, *C. (V.) pilula* Dall, 1881 and *C. (V.) venusta* Dall, 1886. Later, Smith (1900) confirmed that *C. (?) atlantica*, *C. (?) pacifica* and *C. (?) adamsi* differ from *Callocardia* Adams, 1864 and "should be placed in *Vesicomya*" (Smith, 1900: 81). Smith (1900) elevated *Vesicomya* to generic level and included additional species such as *albida*, *smithii*, *stearnsii*, *lepta*, *ovalis*, *gigas*, *dalli*, *leeana* and *angulata*, on the basis of similarity of the hinge margins. Dall & Simpson (1901) placed *Vesicomya* in a new family Vesicomyacidae (=Vesicomyidae), which they established on the basis of the gill structure of *V. stearnsii*, studied previously (Dall, 1895). Subsequently, some new species such as *ticaonica*, *brevis*, *indica*, *solidissima* and others were added to *Vesicomya* (Smith, 1904; Dall, 1908; Thiele & Jaeckel, 1931; Prashad, 1932). However, these species differ considerably in shell shape, size and pallial scar arrangement from the type species of *Vesicomya*, and their inclusion obscured the limits of the genus. As a result *Vesicomya* became a voluminous taxon combining phylogenetically distantly related species.

Fossil records of *Vesicomya s. s.* are not known.

The genus Kelliella

M. Sars established the genus *Kelliella* and typified it by a new species *Kelliella abyssicola* from Norwegian fiords (M. Sars, 1870), which had previously been mistaken by Jeffreys (1869) as juveniles of *Isocardia cor* (now *Glossus humanus*). Later G.O. Sars (1878) confirmed that *K. abyssicola* is not a juvenile and synonymized this species with *Venus*? *miliaris* described by Philippi (1844) from Sicily from Pleistocene fossil specimens. Forbes (1844) introduced another name, *Kellia abyssicola*, for a Recent species from the Aegean Sea, and some authors have used it as a name for the type species of *Kelliella*. But Janssen & Krylova (2012) showed that *miliaris* Philippi, 1844 has a priority over *abyssicola* Forbes, 1844, since the paper of Philippi was published several months earlier. G.O. Sars (1878) placed *Kelliella* in the family Cyamiidae. Later, Fischer (1887) placed *Kelliella* in a separate family, Kellyellidae (=Kelliellidae).

Fossil records include: *K. barbara* Studencka, 1987, Middle Miocene, Poland (Studencka, 1987); *K. miliaris*, Early Pleistocene, Sicily (Philippi, 1844), France (Janssen & Krylova, 2012); Middle Pleistocene, Sicily (Janssen & Krylova, 2012).

Understanding of generic names Vesicomya *and* Kelliella *by different authors*

Similarity of the genera *Vesicomya* and *Kelliella* and their possible synonymy have been discussed since the establishment of *Vesicomya*. When introducing *Vesicomya*, Dall (1886: 272) indicated as the main distinguishing character the presence of a "distinct" hinge without "angular arrangements noticeable in *Kelliella miliaris*". Some authors considered this feature insufficient for keeping *Vesicomya* and *Kelliella* separate. For example, Thiele (1935) suggested *Vesicomya* to be a subgenus of *Kelliella*. Odhner (1960: 373) suggested that the genera *Vesicomya* and *Kellyella* (=*Kelliella*) "may be kept distinct" (p. 373), but in the same family Kellyellidae (=Kelliellidae). Boss (1968) maintained the separation of *Vesicomya* and *Kelliella*, although he repeatedly suggested that "future research will show that the small Vesicomyas…. constitute an assemblage which is congeneric with *Kelliella*" (Boss, 1968: 77). Filatova (1969, 1971) argued for the validity of the genus *Vesicomya*, describing three new species from deep-sea trenches on the basis of conchological similarity with the type species of the genus, *V. atlantica*.

Clausen (1958) performed a detailed anatomical and histological study of *K. miliaris*, which provided a basis for using soft-body features as taxonomic characters. Knudsen (1970) described four new species from the abyssal zones of the Indian and Pacific Oceans (*K. galatheae*, *K. indica*, *K. sundaensis* and *K. tasmanensis*) and gave their anatomical characters. All these species have two siphonal apertures, in contrast to *K. miliaris* which has only one. Despite these anatomical differences, Knudsen (1970) assigned the four new species to *Kelliella* on the basis of shell characters. Bernard (1989) described a new species, *K. elegantula*. He compiled a list of 14 species, which he suggested belonged to *Kelliella*, including the type species of *Vesicomya*, *V. atlantica*, and thus *de facto* synonymized *Kelliella* and *Vesicomya*. Bernard (1989) underlined that the conchological characters of all these species are remarkably uniform, while noting that significant anatomical differences suggest that the species with a single siphonal aperture (typical *Kelliella*) may be separated at the generic level from the deep-water species with both inhalant and exhalant apertures. Allen (2001) synonymized *Kelliella* and *Vesicomya*, and thereby also the families Kelliellidae and Vesicomyidae, on the basis of morphological similarity, but suggested that 'large-sized vesicomyids' could be separated from *Kelliella* at least at subfamilial level. He described five new species from the Atlantic Ocean under the name *Kelliella* and reported general anatomical data. However, among those newly described species there were three very different ones (*K. concentrica*, *K. elongata* and *K. tenina*), which lack outer demibranchs and have a large foot. In *K. elongata*, Von Cosel & Salas (2001) recognized a representative of the genus *Isorropodon* Sturany, 1896 (Pliocardiinae).

Von Cosel & Salas (2001) redescribed the type material of *V. atlantica* and provided new information on the anatomy of this species. In discussing the affinity of *Vesicomya* to *Kelliella*, they stressed their differences and concluded that these genera "must be maintained as separate genera, at least until a more general picture of the phylogeny of these groups emerges…" (Von Cosel & Salas, 2001: 339).

For the first time since the original figure by Philippi (1844), Janssen & Krylova (2012) presented images of topotypes of *K. miliaris*. They discussed the affinity of *Kelliella* to *Waisiuconcha*, a genus of Vesicomyidae (Pliocardiinae), showed the difference between these groups and transferred the species *ruggierii* described as *Kelliella* (Ceregato & Tabanelli, 2001) to *Waisiuconcha*.

Okutani & Fujiwara (2013) described a small-sized bivalve that was collected from sediments near a sunken whale carcasses as '*Kelliella*' *ossisocia*. This species has a hinge that clearly resembles the 'pliocardiine' type (Okutani & Fujiwara, 2013: Figs 2 and 3). Nevertheless, "preliminary molecular phylogenetic analyses of partial … COI sequence of the present specimen proved it to be an out-group of the Vesicomyidae clade (Fujiwara *et al.*, unpublished)" (Okutani & Fujiwara, 2013: 224). Therefore, the authors tentatively allocated this species to *Kelliella*.

The world register of marine species (Worms Editorial Board, 2016) listed 12 Recent species of *Kelliella*, including *V. atlantica*, which is the type of *Vesicomya*. It is clear that the relationship of *Kelliella* and *Vesicomya* is not yet resolved and both these groups need a thorough revision.

MATERIAL AND METHODS

Material included 17 species of *Vesicomya* (six of which are undescribed), two species of *Kelliella*, two species of the vesicomyid subfamily Pliocardiinae at the early postlarval stage of development and two species which were originally included in *Vesicomya* by Dall (1886)—*Diplodonta pilula* and *Callocardia* (*Vesicomya*) *venusta* (Table 1). The type material of ten described species of *Vesicomya* was examined. All except *Kelliella* sp. were available as live-collected specimens. The gross anatomy was studied on preserved live-taken specimens. Prodissoconchs and morphological details were investigated by scanning electronic microscopy (SEM) using standard methods of material preparation. Abbreviations used in shell descriptions: H, height; L, length; LV, left valve; RV, right valve; W, width (1 valve).

Institutional abbreviations:

BAS	British Antarctic Survey
IORAS	Shirshov Institute of Oceanology, Moscow
MNHN	Muséum National d'Histoire Naturelle, Paris
NHMUK	Natural History Museum, London
NSCMB	National Scientific Center of Marine Biology, Vladivostok
SMF	Forschungsinstitut und Naturmuseum Senckenberg, Frankfurt a. M.
SMNH	Swedish Museum of Natural History, Stockholm
ZMB	Museum für Naturkunde der Humboldt-Universität, Berlin
ZMBN	Zoological Museum, University of Bergen, Bergen
ZMUC	Zoological Museum, University of Copenhagen, Copenhagen
ZMMU	Zoological Museum of Moscow State University, Moscow.

The COI gene was analysed from two specimens of *Kelliella miliaris* and two specimens of *Vesicomya alleni* n. sp. (Table 1). Due to the lack of properly preserved material, we could not use the type species of *Vesicomya*, *V. atlantica*, for molecular investigation. However, the studied species resembles *V. atlantica* in the presence of rounded inflated valves with an escutcheon, a large pitted prodissoconch, thin teeth more or less parallel to the shell dorsal margin, presence of inhalant and exhalant siphonal apertures and two pairs of gills.

Genomic DNA was extracted from clam tissues using the DNeasy blood and tissue kit (QIAGEN, Hilden, Germany) according to the instruction manual. COI was amplified using TaKaRa Taq DNA polymerase (Clontech Laboratories, CA), the primers LCO1490 (5′-GGTCAACAAATCATAAAGATATTGG-3′) and HCO2198 (5′-TAAACTTCAGGGTGACCAAAAAATCA-3′) (Folmer *et al.*, 1994) and the following amplification parameters: initial denaturation at 95 °C for 5 min, 40 cycles of 1 min, 95 °C, 1.5 min, 42 °C, 2 min, 72 °C and final elongation at 72 °C for 10 min. PCR products were purified with the QIAquick PCR Purification Kit (QIAGEN, Hilden, Germany), using the microcentrifuge protocol. Purified PCR products served for direct sequencing of COI using an ABI PRISM 3100 genetic analyser (Applied Biosystems, Foster City, CA) with ABI BigDye and the same primers as in the amplification reaction. Quality-checked COI sequences were aligned against published sequences of vesicomyid, venerid, dreissenid and corbulid species with BioEdit (Hall, 1999) and trimmed to a final alignment of 502 nc. Maximum likelihood (ML) phylogenies were calculated using the PhyML algorithm (Guindon & Gascuel, 2003) as implemented in the Geneious software (http://www.geneious.com; Kearse *et al.*, 2012) using the TN93+G nucleotide substitution model, which was determined as the best fitting model by MEGA v. 7 (Kumar, Stecher & Tamura, 2016). Pairwise genetic distances were calculated based on the Kimura 2-parameter (K2P) model using MEGA v. 7. The sequences were deposited at GenBank under the accession numbers MF542321-MF542324 (Supplementary Material Table S1).

The stable carbon and nitrogen isotopic composition of *Vesicomya* species (*V. adamsi*, *V. sergeevi* and two undescribed species) and *K. miliaris* were analysed using soft tissues that had been preserved since their collection (Table 1) in different concentrations of ethanol (70–96%). The tissues were transferred into distilled water for 24 h and dried at 60 °C for 24 h. Although stable isotope determinations are typically made on fresh or dried soft tissues, tests on the use of ethanol preserved material suggest that only minor modification of the results is apparent after 12 months of storage (Carabel, Verísimo & Freire, 2009; Fanelli *et al.*, 2010) (see Discussion). Analyses of $\delta^{13}C$ and $\delta^{15}N$ were performed by mass spectrometry at the Museum für Naturkunde (Berlin). When enough organic material was available, two measurements per sample were performed. The values are given in the standard delta notation as per mil (±0.01‰) relative to the

Table 1. Species studied and methods used: stereo light microscopy (LM) for study of general morphology, scanning electron microscopy (SEM), stable δ^{13}C and δ^{15}N isotopic composition (isotopes) and COI sequencing.

Species	Source of material	Region	Storage, status	Method (no. of studied spms)
Vesicomya atlantica (Smith, 1885)	*Challenger* Stn 73, 38°30′N, 31°14′W, 1852 m	Azores, Atlantic O.	NHMUK 1887.2.9.2712 lectotype, fragments	LM
V. atlantica	*Challenger* Stn 78, 37°26′N, 25°13′W, 1852 m	Azores, Atlantic O.	NHMUK1887.2.9.2713 paralectotype, fragments	LM
V. atlantica	*Jean Charcot*, INCAL Stn OS07, 47°32′N, 09°34′W, 4249 m, 10 Aug 1976	NE Atlantic O.	MNHN	LM (2), SEM (2)
V. atlantica	*Jean Charcot*, BIAÇORES Stn D3130, 38°54′N, 33°22′W, 2940–2966 m, 24 Oct 1971	E Atlantic O.	MNHN	LM (1)
V. adamsi (Smith, 1885)	*Challenger* Stn 384, 03°10′N, 14°05′W, 4410 m, 2 April 1876	S of Sierra Leone, Atlantic O.	NHMUK,1998175, holotype	LM
V. adamsi	*Meteor*–63 Stn 91, 0°50.92′N, 05°38.35′ W, 5140 m, 21 March 2005	Gulf of Guinea, Atlantic O.	SMF	LM (3), isotopes (3)
V. bruuni Filatova, 1969	*Vityaz* Stn 3827, 28°53′S, 176°01′W, 8928–9174 m, 2 Jan 1958	Kermadec Trench, Pacific O.	ZMMU, syntypes	LM (2)
V. galatheae (Knudsen, 1970)	*Galathea* Stn 724, 05°44′N, 79°20′W, 2950–3190 m, 12 May 1952	E Pacific O.	ZMUC, holotype	LM
V. indica (Knudsen, 1970)	*Galathea* Stn 280, 01°56′N, 77°05′E, 4350 m, 9 April 1951	Central Indian O.	ZMUC, holotype	LM
V. pacifica (Smith, 1885)	*Challenger* Stn 244, 35°22′N, 169°53′E, 5220 m, 28 June 1875	Mid N Pacific O.	NHMUK 1887.2.9.2710-11, holotype	LM
V. pacifica	*Sonno*, KURAMBIO Stn 5, 43°13′N, 153°58′E, 5375–5379 m, 9–12 Aug 2012	E of the Kuril Is, NW Pacific O.	IORAS	LM (5)
V. profundi Filatova, 1971	“Vityaz”, St. 5611, 45°48′N, 153°21′, 7600–7710 m, 25 July1966	Kuril-Kamchatka Trench, NW Pacific O.	ZMMU Ld 2935, paratypes	LM (5)
V. sergeevi Filatova, 1971	*Vityaz* Stn 5612, 45°25′N, 153°07′E, 8185–8400 m, 27 Aug 1966	Kuril-Kamchatka Trench, NW Pacific O.	ZMMU, syntypes	LM (5), isotopes (4)
V. sundaensis (Knudsen, 1970)	*Galathea* Stn 465, 10°20′S, 109°55′E, 7000-6900 m, 5 Sept 1951	Sunda Trench, Indian O.	ZMUC, holotype	LM
V. tasmanensis (Knudsen, 1970)	*Galathea* Stn 601, 45°51′S, 164°32′E, 4400 m, 14 Jan 1952	Tasman Sea	ZMUC, holotype	LM
V. alleni n. sp.	*Polarstern* Stn PS67/021-7-E, 47°38.73′S, 4°15.20′E, 4555 m, 29 Jan 2005	S Atlantic O.	IORAS	LM (1), SEM (2), COI (2)
Vesicomya sp.	*Polarstern* Stn PS67/016-10-S, 41°7.06′S, 9°54.88′E, 4687 m, 26 Jan 2005	S Atlantic O.	IORAS	LM (1)
Vesicomya sp.	*Polarstern* Stn PS67/080-9-E, 70°39.07′S, 14°43.36′W, 3103 m, 23 Feb 2005	Antarctic O.	IORAS	LM (1), SEM
Vesicomya sp.	*Dmitri Mendeleev*–16, Stn 1300, 57°18′S, 157°18′E, 5950–5970 m, 28 Jan 1976	S Pacific O.	IORAS	LM (1), isotopes (1)
Vesicomya sp.	*Dmitri Mendeleev*–20, Stn 1636, 07°56′S, 81°10′W, 5770–5800 m, 7 March 1978	Peru Trench, E Pacific O.	IORAS	LM (4), isotopes (4)
Vesicomya sp.	Ecological Research Associates, 27°45.17 N, 90°47.38′W, 748 m,13 Oct 1984	Gulf of Mexico	USNM 1068830	LM (2)
Vesicomya sp.	*Akademik Kurchatov* Stn 7, 0° 11′S, 18°21′W, 7200 m, 16 Jan 1967	Romanch Deep, Atlantic O.	IORAS	LM (2)
Kelliella miliaris (Philippi, 1844)		Middle Pleistocene, Sicily: Ficarazzi near Palermo	SMF	LM (2)
K. miliaris	*Håkon Mosby* Stn 24, 62°27,456′N, 06°45,141′E, 628 m, 10 Nov 2005	Norwegian Sea	ZMBN	LM (10), SEM (5), isotopes (3), COI (2)

Continued

Table 1. *Continued*

Species	Source of material	Region	Storage, status	Method (no. of studied spms)
K. miliaris	n/a	Dröbak, Oslofjord, Norwegian Sea	USNM 201313, studied by Jeffreys (1869)	LM (1)
K. miliaris	*Meteor*–36, Stn 97, 25°30.2′N, 16°00.7′W, 409–417 m, 23 Feb1975	Off Canary Is, Atlantic O.	SMF	LM (2)
Kelliella sp.	*Alis* Stn CP 1858, 9°37 S, 160°42′E, 435–461 m, 7 Oct 2001	Solomon Is, SW Pacific	MNHN	LM (many)
Pliocardiinae sp., probably *'Calyptogena (Ectenagena)' fossajaponica* Okutani, Fujikura & Kojima, 2000	*Sonne*–110, Stn 40/1, TV box corer, 54° 18.17′N, 157°11.82′W, 4808 m, 2 Aug 1996	Aleutian Trench, N Pacific O.	IORAS	SEM (1)
Pliocardiinae sp., probably *Abyssogena phaseoliformis* (Métivier, Okutani & Ohta, 1986)	*Sonne*–110, Stn 40/1, TV box corer, 54° 18.17′N, 157°11.82′W, 4808 m, 02 Aug1996	Aleutian Trench, N Pacific O.	IORAS	SEM (1)
Diplodonta pilula Dall, 1881	*Blake* Stn 43, 718 m	Caribbean Sea	USNM 64224, holotype	LM
Callocardia (Vesicomya) venusta Dall, 1886	32°40′N, 76°40′W, 1442 m	Off N Carolina, W Atlantic O.	USNM 64041, holotype	LM

standards Pee Dee Belemnite for carbon and atmospheric nitrogen gas (air) for nitrogen.

RESULTS

Morphology of Vesicomya

All species of *Vesicomya* studied here (Table 1) have basically similar conchological and anatomical features. Common characters include relatively large prodissoconch with pitted structure, presence of lunule and escutcheon, absence of a ridge or furrow along shell margin, presence of both pairs of demibranchs, two siphonal apertures and z-shaped course of the gut. Differences can be found in shell sculpture, thickness of hinge margin, number of gill filaments, and number and arrangement of siphonal tentacles (Krylova *et al.*, 2015). Below we provide data on shell and anatomy of some species of *Vesicomya*, including the type species, *V. atlantica*.

***Vesicomya atlantica* (Smith, 1885)**
(Figs 1, 2)

Callocardia (?) *atlantica* E.A. Smith, 1885: 157, pl. 6, Figs 8–8b.

Synonymy: see Janssen & Krylova (2014).

Material examined: Description based on type material of *V. atlantica* as well as additional specimens collected from the region close to the type locality and morphologically coinciding with the types (Table 1).

Shell (Figs 1, 2): Shell small, L to 5 mm, outline subcircular, inflated, thin, nearly equivalve. Periostracum thin, glossy, translucent. Sculpture of concentric threads and low subregular ribs more conspicuous at posterior margin (Fig. 2F). Lunule large, heart-shaped, delimited by narrow incision (Fig. 1B). Escutcheon well defined (Fig. 1B). Inequilateral, umbo situated in anterior 20% of valve. Umbones prominent, prosogyrate, beak enrolled. All margins evenly rounded except postero-dorsal margin which is slightly convex and creates obtuse angle with posterior margin. Internal shell surface white, with faint concentric and radial striation. Pallial scars weak; pallial line close to margins, without sinus; anterior adductor scar oval–elongated, posterior adductor scar oval, lying below end of posterior dorsal shell margin. Shell margin with very weak striae along its length. Nymph weak, with smoothly sloping posterior end (Fig. 2A). Fibrous layer of ligament occupying about 10% of valve length and about 65% of posterior lamellar layer. Dentition of RV (Fig. 2A, B, E): ventral cardinal (1) and subumbonal cardinal (fused 3a and 3b). Tooth 1 short, thin, parallel to dorsal shell margin, located in front of tooth 3a+b. Tooth 3a+b nearly three times longer, thin, undulate, extending from posterior part of (1) to middle of ligament more or less parallel to dorsal margin. Dentition of LV (Fig. 2C–E): subumbonal cardinal tooth with two rami (2a and 2b) and elongated postero-dorsal cardinal tooth (4b); 2a-ramus short, located close to dorsal shell margin, connected with lateral surface of 2b-ramus; 2b-ramus elongated, thin, undulating. Prodissoconch D-shaped, nonumbonate, with pitted structure, about 180 μm in diameter, delimited by belt with faint radial and commarginal striae of about 33 μm in width (Figs 1D, 2G).

Soft parts: Mantle lobes thin and transparent, except at margins. Outer, middle and inner mantle folds present. Mantle fusion forms three pallial apertures, the pedal gape and two posterior openings. Pedal gape occupies entire ventral edge from middle of frontal surface of anterior adductor to base of inhalant opening. Inhalant aperture a little larger than exhalant one. Exhalant aperture has internally directed, thin, transparent sleeve. Around inhalant and exhalant apertures there are tiny tentacles; poor condition of material did not allow determination of their exact number. Anterior and posterior adductor muscles small, posterior muscle oval in section, anterior adductor muscle more elongate. Foot small, often entirely concealed by gills. Aperture of small byssal gland located slightly anterior to heel. Anterior and posterior pedal retractor muscles bifurcate before attaching to shell; anterior pedal retractor muscles insert on shell just posterior and dorsally to anterior adductor muscle, posterior pedal retractor muscles insert on shell dorsally to posterior adductor muscle. Ctenidia non-plicate, comprising inner and outer demibranchs, latter shorter than former. Interfilamental junctions not numerous. Ventral margin of demibranch with shallow food groove. Labial palps small, mouth small, rounded, located beneath posterior face of anterior adductor, opening into thin-walled oesophagus. Oesophagus enters anterior part of small stomach. Anterior half of stomach covered by digestive gland. Stomach thin-walled, elongate. Midgut leaves postero-ventral end of stomach, running nearly straight, then up and forward and, after curving upward, passing through visceral mass to penetrate pericardial cavity. Rectum ends in anus located on posterior surface of posterior adductor muscle.

Vesicomya pacifica **(Smith, 1885)**
(Fig. 3)

Callocardia (?) *pacifica* E.A. Smith, 1885: 156, pl. 6, figs 9, 9a.

Synonymy: see Krylova *et al.* (2015).

Shell: This species is conchologically and anatomically very close to *V. atlantica*. Prodissoconch about 180 µm diameter. For complete description see Krylova *et al.* (2015).

Soft parts: As in *V. atlantica*, two siphonal apertures (Fig. 3A, B); inhalant opening a simple slit and exhalant siphon a short conical tube inverted into mantle cavity (Fig. 3F). 4–5 pairs of tentacles at lateral margins at base of inhalant opening, 2–3 pairs of tentacles at lateral margins of exhalant openings, 3–5 tentacles dorsally above exhalant opening; tentacles are of different size; among tentacles of inhalant siphon the smallest located most ventrally. Foot well developed, nevertheless in some specimens it can be concealed by gills. Ctenidia thin, well-developed, both inner and outer demibranchs consisting of about 50 filaments (Fig. 3C, D).

Vesicomya alleni **new species**
(Figs 4–6)

Vesicomya atlantica, Audzijonyte *et al.*, 2012: 406.
Vesicomya sp. 1, Johnson *et al.*, 2017: 351.

ZooBank registration: urn:lsid:zoobank.org:act:D8992F47-6EA7-422A-99C4-3F99E7CDFCE6

Etymology: Dedicated to J.A. Allen in acknowledgement of his investigations of deep-sea bivalve molluscs.

Type material: Holotype: ZMMU 3043 (both valves of same spm without soft parts). Paratypes: ZMMU 3044 (3 paratypes: 2 spms with soft parts; RV with soft parts); SMF 349236 (3 paratypes: 1 spm with soft parts, 2 spms as paired valves without soft parts). Type locality: South Atlantic Ocean, 47°38.73′S, 4°15.20′E, 4555 m, 29 January 2005 (RV *Polarstern*, Stn 67/021-7-E, EBS).

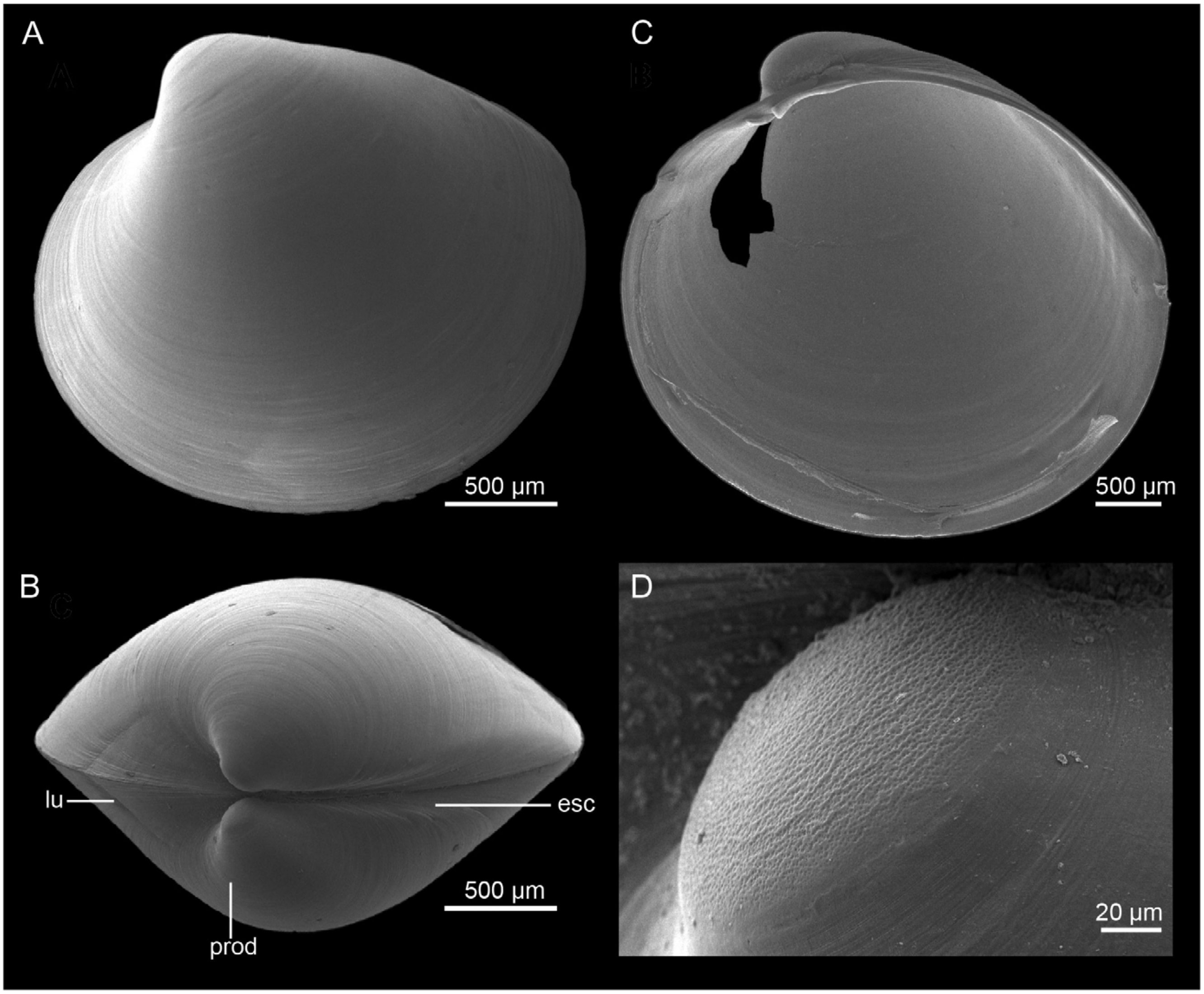


Figure 1. *Vesicomya atlantica* (Smith, 1885), RV *Jean Charcot* Stn OS07 (MNHN), SEM. **A.** Exterior of LV. **B.** Interior of RV. **C.** Dorsal view. **D.** Prodissoconch. Abbreviations: esc, escutcheon; lu, lunule incision; prod, prodissoconch border.

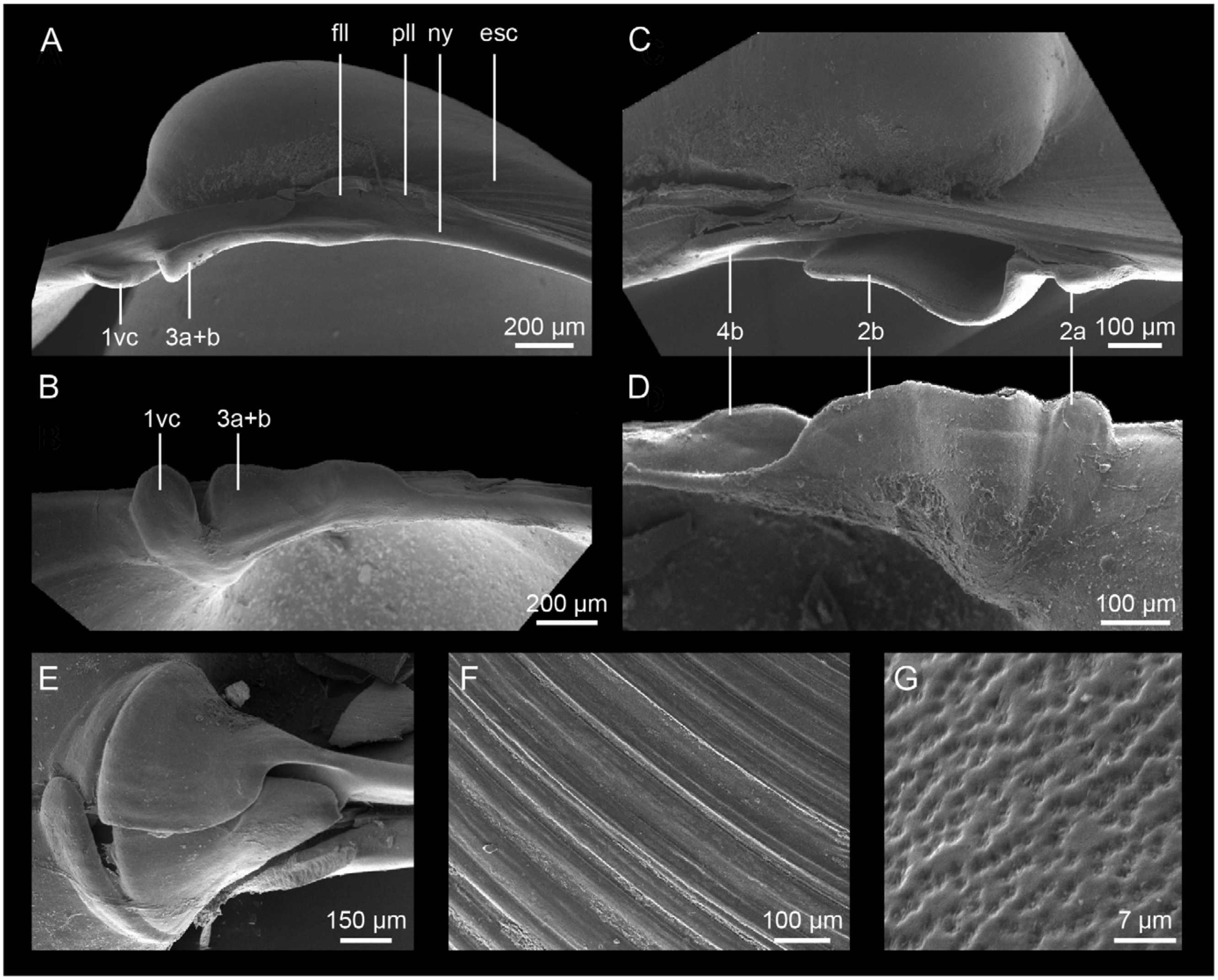


Figure 2. *Vesicomya atlantica* (Smith, 1885), RV *Jean Charcot*, Stn OS07 (MNHN), SEM. **A, B.** RV hinge plate: **A.** Lateral view, **B.** Ventral view. **C, D.** LV hinge plate. **C.** Lateral view, **D.** Ventral view. **E.** Hinge of both valves, LV above, ventral view. **F.** Exterior shell sculpture. **G**. Sculpture of prodissoconch. Abbreviations: 1vc, ventral cardinal tooth; 2a, 2b, anterior and posterior rami of subumbonal cardinal tooth of LV; 3a+b, fused 3a and 3b rami of subumbonal cardinal tooth of RV; 4b, posterodorsal cardinal tooth; esc, escutcheon; fll, fibrous ligament layer; ny, nymph; pll, posterior lamellar ligament layer.

Material examined: Type material. RV *Polarstern*, Stn 67/021-7-E: 3 spms studied with SEM, 23 spms, 15 V.

Diagnosis: *Vesicomya* with L to 4 mm, thin, semitransparent, subcircular shell in larger specimens, more oval-triangular in smaller, H/L = 0.81–0.97, W/L = 0.25–0.30; sculpture consisting of low regular commarginal ribs separated by thin furrows, lunule and escutcheon present; umbo situated at anterior 33–40%, prosogyrate beaks, nymph short, in left valve 4b-tooth of the same length as nymph; low proximal part of 1-tooth located under 3a-ramus; with two pairs of demibranchs.

Shell: Shell small, L to 4 mm, fragile, thin, subcircular outline, H/L = 0.81–0.97, W/L = 0.25–0.30, equivalve. RV holotype: L = 3.3 mm, H = 3.2 mm, W = 1.0 mm. Periostracum thin, glossy, translucent. Sculpture of commarginal threads and low regular ribs separated by thin furrows. Escutcheon well defined (Fig. 4B). Lunule demarcated by incision, sometimes not very distinctly. Inequilateral, anterior margin shorter, umbo situated at anterior 33–40% of valve. Umbones prosogyrate, protruding. Antero-dorsal margin nearly straight, anterior, ventral and postero-ventral margins regular and evenly rounded, postero-dorsal margin straight or slightly convex, forming obtuse angle with long posterior margin. All pallial scars hardly visible. Pallial line without pallial sinus. Nymph short. Ligament small, opistodetic. Hinge plate narrow. Dentition of RV: ventral cardinal (1) wedge-like, subparallel to antero-dorsal shell margin, its elongated lower proximal part located under 3a-ramus; 3a-ramus thin, elongated, parallel to antero-dorsal shell margin, fused in its proximal part with anterior part of 3b; 3b-ramus thicker than 3a, radiated posteriorwards. Dentition of LV: 2a-ramus short, along postero-lateral margin fused with anterior edge of 2b; 2b-ramus elongated, undulating; 4b-tooth elongated, parallel to postero-dorsal shell margin. Prodissoconch with pitted structure, about 160 µm diameter with margin, about 20 µm broad, sculptured by commarginal striae and fine radial striation (Fig. 4F–H).

Soft parts: 3 pairs of tentacles at lateral margins at base of inhalant opening, 1 pair of tentacles and 1 pair of small papillae at lateral margins between siphons, and 5 tentacles dorsally above exhalant opening. Ctenidia thin; in spm of L 2.9 mm inner demibranch of about 25 filaments and outer demibranch 18; last 7 filaments of outer demibranchs not reflected. In larger specimens the number of filaments increases and outer demibranchs reflected.

Distribution: Type locality.

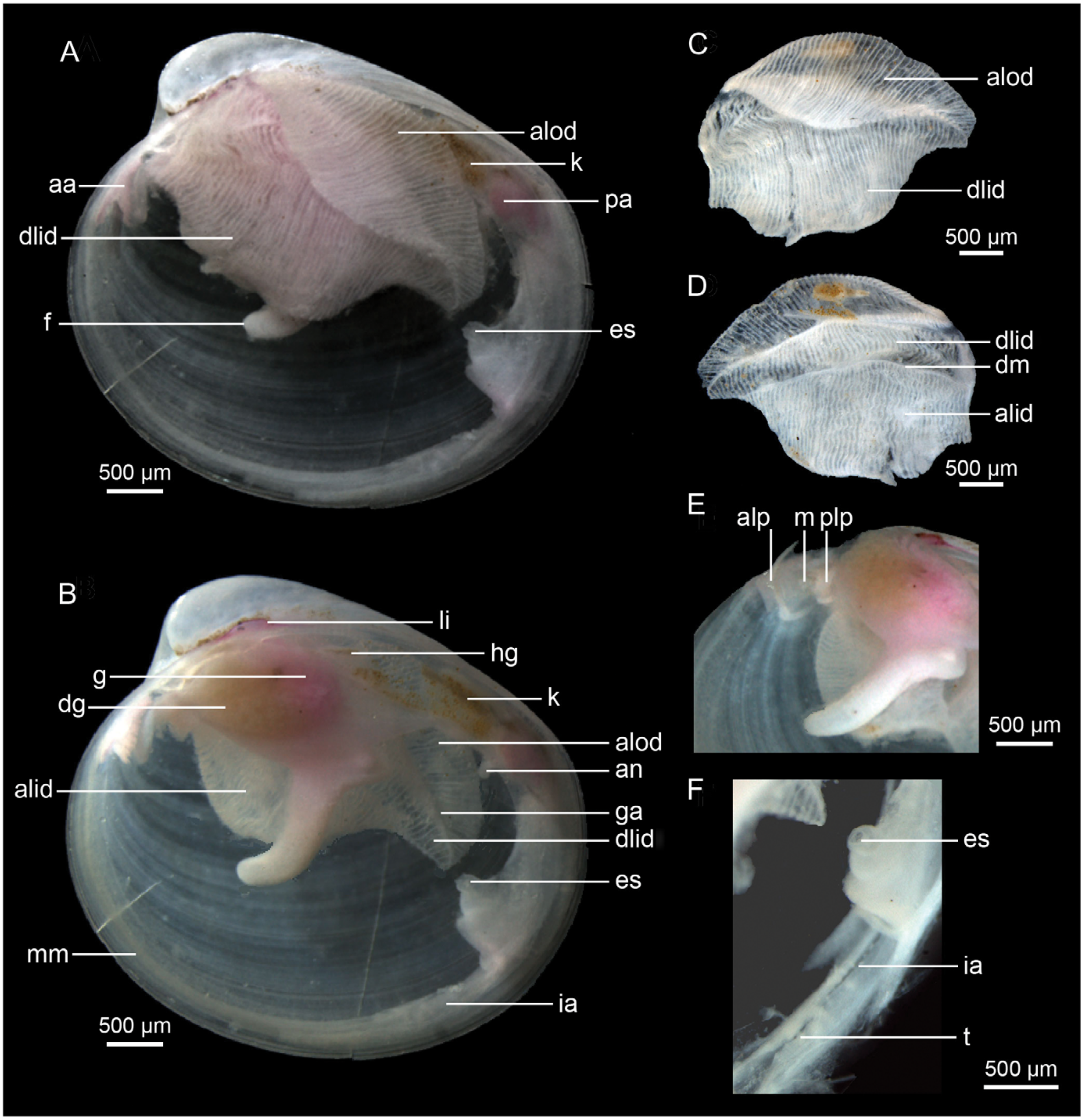


Figure 3. *Vesicomya pacifica* (Smith, 1885), RV *Sonne* cruise 223, KuramBIO Stn 5 (IORAS), L = 4.7 mm. Stained with Rose Bengal. **A.** Body seen from left. **B.** Body seen from left, left gills removed. **C, D.** Gills. **C.** Exterior view. **D.** Interior view (with fragment of hindgut and ventricle). **E.** Lateroventral view of body. **F.** Laterodorsal view of exhalant siphon. Abbreviations: aa, anterior adductor muscle; alid, ascending lamella of inner demibranch; alod, ascending lamella of outer demibranch; alp, anterior labial palps; an, anus; dg, digestive gland; dlid, descending lamella of inner demibranch; dm, dorsal margin of ascending lamella of inner demibranch; es, exhalant siphon; f, foot; g, gonad; ga, gill axis; hg, hindgut; ia, inhalant aperture; k, kidney; li, ligament; m, mouth; mm, mantle margin; pa, posterior adductor muscle; plp, posterior labial palps; t, tentacles.

Remarks: Shell shape can vary from oval-triangular in smaller specimens to more subcircular in larger specimens. Commarginal sculpture can be more or less prominent. The lunule is more conspicuous in larger specimens. The relative length of 3a- and 3b-rami in RV can vary.

The hinge margin of *V. alleni* differs from that of *V. atlantica* and *V. pacifica* in that it is a little wider, 3a+b thicker, with tooth 1 located in front of and beneath the 3a-ramus, whereas in both *V. atlantica* and *V. pacifica* tooth 1 is located just in front of 3a-ramus. In its wider hinge margin and arrangement of 1 and 3a teeth, *V. alleni* is similar to *V. sergeevi* and *V. profundi* from the Pacific, from which differs by shell outline, sculpture and number of siphonal tentacles (Krylova *et al.*, 2015). The new species is similar in shell outline to *V. sirenkoi* described from the Weddell Sea (Egorova, 1998). In contrast to *V. alleni*, *V. sirenkoi* has a relatively thicker-walled shell with more distinct commarginal ribs and deeper escutcheon separated by a strong rib.

Morphology of Kelliella *M.Sars, 1870*

K. miliaris (**Philippi, 1844**)

(Table 1, Figs 7–9)

Venus (?) *miliaris* Philippi, 1844: 36, pl. 14, fig. 15.

Synonymy: see Allen (2001).

Material examined: From type locality, the Middle Pleistocene of Sicily (Philippi, 1844) and from Norwegian Sea, from where one of the synonyms, *K. abyssicola*, was described (M. Sars, 1870) (Table 1). See Janssen & Krylova, 2012 for a discussion of type locality and images of topotype.

Shell (Figs 7, 8): Shell small, L to 3 mm, thin, circular in outline, nearly equivalve. Periostracum thin, glossy, translucent. Sculpture of faint concentric threads. Lunule large, heart-shaped, delimited by broad groove. Escutcheon very shallow, hardly discernible. Inequilateral, umbo situated in anterior 20% of valve. Umbones prominent, prosogyrate. All margins rounded. Internal shell surface white, with faint concentric and radial striation. Inner shell margin of RV has a furrow parallel to margin and inner shell margin of LV a corresponding ridge. Pallial scars hardly discernible; posterior adductor scar located lower than anterior one; pallial line somewhat distant to margins, without sinus. Nymph very weak, short, fibrous layer of ligament occupying less 10 % of L. Dentition of RV (Fig. 8A, B): ventral cardinal (1) and subumbonal cardinal (3), of two rami, 3a and 3b. Tooth 1 upright, strong, wedge-shaped, bluntly pointed. 3a lower that 1, thin, parallel to dorsal margin. 3b shorter, diverging at about 90° from 3a. Dentition of LV (Fig. 8C, D): subumbonal cardinal tooth with two rami (2a and 2b) and posterodorsal cardinal tooth (4b); 2a+b thin, undulated, more or less parallel to dorsal margin; 2a two times shorter than 2b and connected by its dorsal surface with ventral side of 2b. 4b tooth upright, short, stout. Prodissoconch (Fig. 7F) of small prodissoconch I, about 60 µm in diameter, with pitted structure, and prodissoconch II, about 220 µm in diameter, with commarginal sculpture.

Soft parts (Fig. 9): Mantle lobes thin and transparent, except at margins. Outer, middle and inner mantle folds present. Inner mantle fold strongly developed (Fig. 9F). Mantle fusion forms two pallial apertures, the pedal gape and one posterior (exhalant) opening. Pedal gape occupies entire ventral edge from middle of frontal surface of anterior adductor to base of exhalant opening. Exhalant aperture simple; 3 tentacles dorsally above exhalant opening, 2 pairs of tentacles at lateral margins at base of exhalant opening, and 2–3 pairs of tentacles at lateral margins of middle mantle fold ventrally. Anterior and posterior adductor muscles similar in size, oval in section. Foot well developed, never concealed by gills. Aperture of small byssal gland located slightly anterior to heel. Anterior and posterior pedal retractor muscles bifurcate before attaching to shell; anterior pedal retractor muscles insert on shell just posterior and dorsally to anterior adductor muscle, posterior pedal retractor muscles insert on shell dorsally to posterior adductor muscle. Ctenidia non-plicate, comprising inner and outer demibranchs, both with ascending and descending lamellae (Fig. 9C, D). In spms of L 1.5 mm inner demibranch of about 30 filaments and outer about 20. Length of outer demibranch about 1/3 of inner demibranch, beginning at approximately mid-length of inner demibranch. Interfilamental junctions not numerous. Labial palps small, covered with cilia, mouth rounded (Fig. 9E), located beneath posterior face of anterior adductor, opening into thin-walled oesophagus. Oesophagus enters anterior part of stomach. Anterior half of stomach covered by digestive gland. Stomach large, vertically orientated. Midgut leaves postero-ventral end of stomach, running nearly straight, then up and forward and, after curving upward, passing through visceral mass to penetrate pericardial cavity. Rectum ends in an anus located on posterior surface of posterior adductor muscle.

Morphological comparisons between Vesicomya, Kelliella *and pliocardiines*

The morphology of examined species of *Vesicomya* and *Kelliella* is summarized in Table 2. Although *Vesicomya* and *Kelliella* show considerable resemblance, there are numerous distinguishing features (see Discussion). For comparison, the morphological characters of *Waisiuconcha* sp., a representative of pliocardiines, is included in Table 2, based on the studies of Janssen & Krylova (2012). In addition, juvenile specimens of selected species of pliocardiines were studied including '*Calyptogena* (*Ectenagena*)' *fossajaponica* Okutani, Fujikura & Kojima, 2000 and *Abyssogena phaseoliformis* (Métivier, Okutani & Ohta, 1986) (Figs 10, 11).

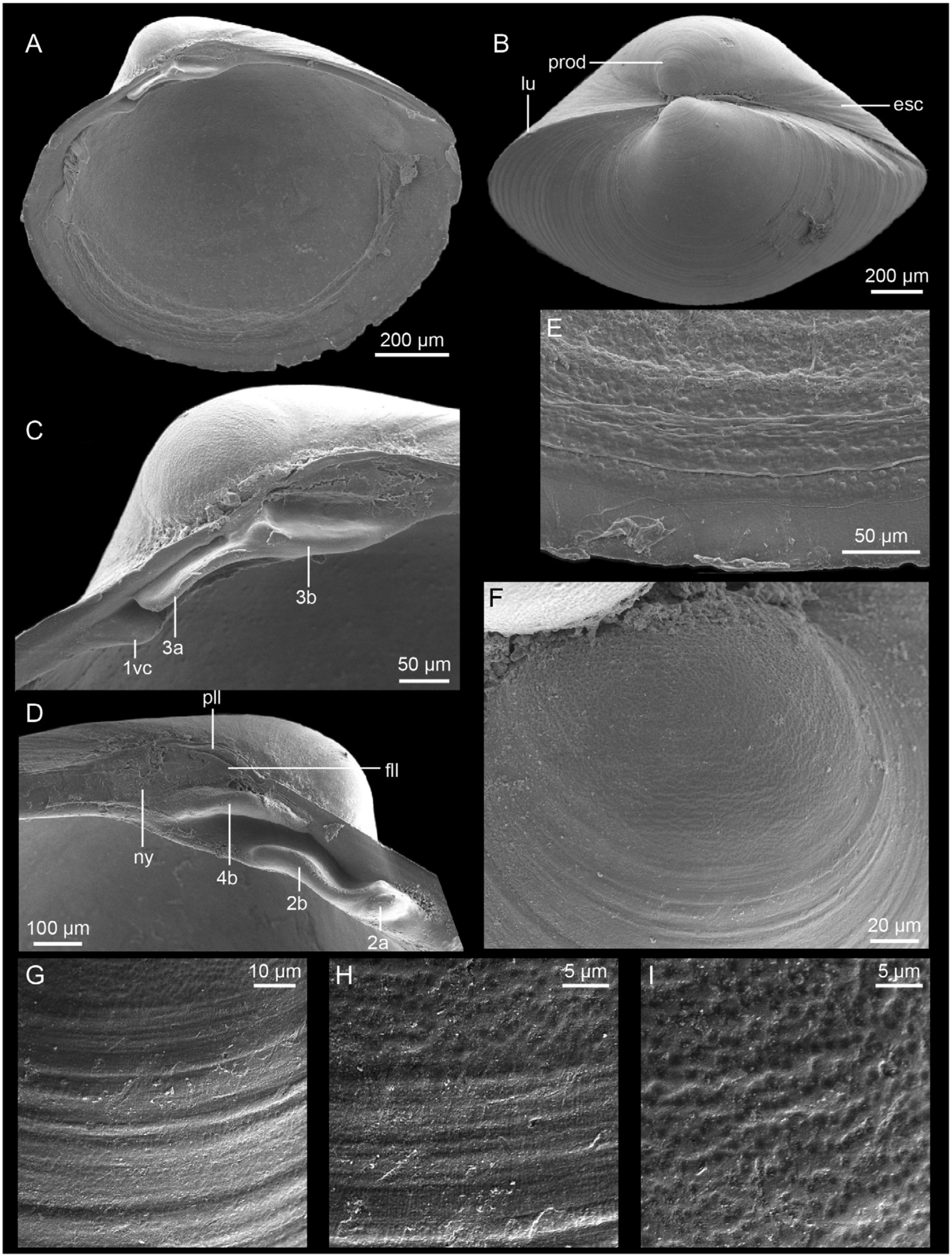
Composition of the genus Vesicomya

Based on our studies, we propose that the genus *Vesicomya* comprises 15 named Recent species (Table 3). Comparison of the type species *V. atlantica* with species originally assigned to *Vesicomya, Kelliella* or *Callocardia*, shows that some of them correspond well morphologically with *V. atlantica*. Common features of these species include having an inflated rounded shell with an escutcheon, narrow hinge line with teeth mainly parallel to dorsal margin, large prodissoconch with pitted structure (Figs 1, 2, 4, 6), thin gills comprising both inner and outer demibranchs, the presence of three pallial apertures and short inverted exhalant siphon (Figs 3, 5). Some of these species (Table 3) have a thicker hinge margin and are thereby considered closely related to each other, e.g. *V. sergeevi*, *V. profundi* and *V. alleni* n. sp. However, only future comprehensive study of freshly preserved material can further resolve the taxonomic structure of the genus.

We have not included *K. concentrica* or '*V.*' *filatovae* in this list of *Vesicomya* species because, in contrast to *Vesicomya s. s.*, these two species lack outer demibranchs (Allen, 2001; Krylova *et al.*, 2015). The generic assignment of these species requires further study and a new genus should probably be established for them. Nevertheless, we consider them as representatives of the subfamily Vesicomyinae (Table 4). We have not included *K. ossisocia* Okutani & Fujiwara, 2013, *K. elongata* Allen, 2001 or *K. tenina* Allen, 2001 in Vesicomyinae, because available information on anatomical and molecular characters is at present insufficient for a clear decision. We also hesitated to include *V. sumatrana* and *V. rotunda* in Vesicomyinae. Despite some similarities of *V. sumatrana* with *Vesicomya s. s.* (e.g. small rounded inflated shell with thin lamellate teeth located parallel to hinge margin), there are also considerable differences, i.e. the pallial line of *V. sumatrana* has a very shallow pallial sinus (Boss, 1970; Krylova, unpublished), while *Vesicomya* lacks any pallial sinus. '*Vesicomya*' *sumatrana* may be assigned to the pliocardiines. As for '*V.*' *rotunda*, we provisionally assign it to *Kelliella* as discussed below. We also have not included *Diplodonta pilula* or *V. venusta*, which were assigned to *Vesicomya* by Dall (1886). Our examination of the holotype of *D. pilula* (Table 1) showed that the teeth are arranged very differently and this species is not a vesicomyid. '*Vesicomya*' *venusta* may be considered a pliocardiine. More morphological and molecular studies are needed to unravel the yet uncertain generic structure of Vesicomyinae.

Composition of the genus Kelliella

Among Recent species currently assigned to *Kelliella* there are five species (Table 5), which correspond morphologically to the type species *K. miliaris*: *K. goesi*, *K. japonica*, *K. rotunda sensu* Boss (1970), *K. rotunda sensu* Raines & Huber (2012) and *Kelliella* sp. (Warén, 2011). All these have small subcircular shells with rounded margins and clearly delimited lunule, and characteristically angulated right and tubercular left posterior teeth that lack conspicuous escutcheon. In *K. miliaris*, *K. japonica* and *Kelliella* sp., along the circumference of the


A
200 µm
B
prod
lu
esc
200 µm
C
3b
3a
1vc
50 µm
D
pll
fll
ny
4b
2b
2a
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50 µm
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H
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I
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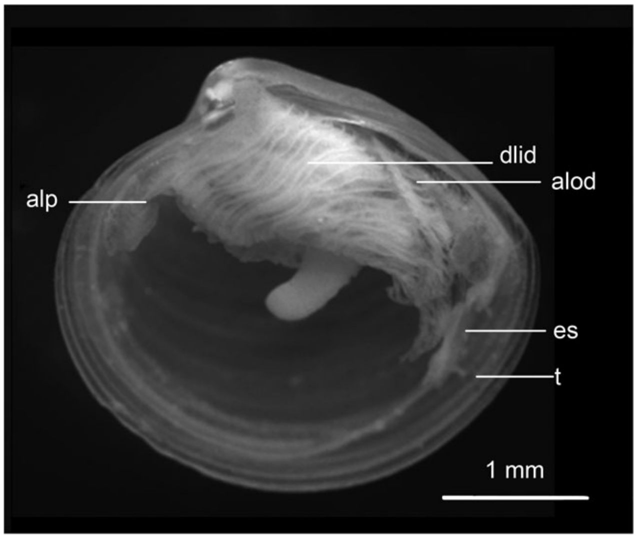

Figure 5. A. *Vesicomya alleni* n. sp., RV *Polarstern* Stn PS67/021-7-S (IORAS). Body as seen from left. Abbreviations: alod, ascending lamella of outer demibranch; alp, anterior labial palps; dlid, descending lamella of inner demibranch; es, exhalant siphon; t, tentacles.

inner margin of the right valve a regular clear furrow is present and in the left valve there is a corresponding ridge. The prodissoconch of *K. miliaris*, *K. japonica* and *Kelliella* sp. is distinctly divided into prodissoconch I and prodissoconch II. There are no data about inner shell margin and prodissoconch structure of *K. goesi*, *K. rotunda sensu* Boss (1970) and *K. rotunda sensu* Raines & Huber (2012). All these five species differ from each other only in small details of sculpture and hinge margin, and also relative location of beaks. *Vesicomya rotunda* Thiele & Jaeckel, 1931 also quite possibly could be assigned to *Kelliella*. The original description of *V. rotunda* was short and included the following characters: a subcircular shell outline, very thin sculpture, the presence of distinct lunule incision, a hinge margin similar to that of '*V.*' *sumatrana* (of L = 2 mm, H = 1.8 mm; Thiele & Jaeckel, 1931). Unfortunately, however, this information is not sufficient for explicit generic assignment. The type material of *V. rotunda* is fragmented and represented by small pieces (ZMB Moll 111.642). Boss (1970) redescribed *V. rotunda* not on the basis of the type material collected by RV *Valdivia* in the Siberut Strait, at 750 m in the eastern Indian Ocean (Thiele & Jaeckel, 1931), but on specimens collected by RV *Albatross I* near the Philippines from 1785 m, which he supposed to be *V. rotunda*. Raines & Huber (2012) recorded *K. rotunda* from around Easter Island, at depths of 30–150 m. Their '*K. rotunda*' differs from the bivalves described by Boss (1970) in the absence of the distinct concentric sculpture. Additionally, Raines & Huber (2012) synonymized *K. rotunda* and *K. japonica*, described from sublittoral caves of the Ryukyu Islands (Hayami & Kase, 1993). We prefer to keep all these species separate (Table 5) until thorough taxonomic revision of the genus *Kelliella* has been conducted. One more species that could be assigned to *Kelliella* is *K. biscayensis*, as it lacks an escutcheon and has a somewhat angulated right posterior tooth similar to *Kelliella*. Additionally, *K. biscayensis* has only one mantle fusion (Allen, 2001), similar to *K. miliaris*, but there are no data available about the prodissoconch and inner shell margin.

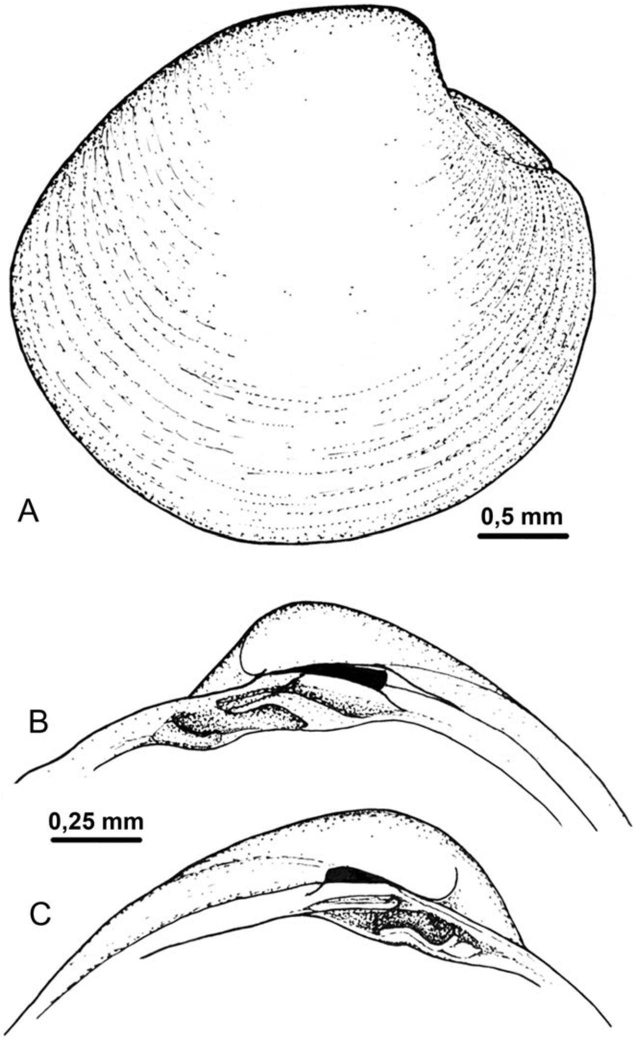

Figure 6. *Vesicomya alleni* n. sp., holotype, RV *Polarstern* Stn PS67/021-7-S (ZMMU). **A.** Exterior of RV. **B.** RV hinge plate. **C.** LV hinge plate.

COI sequence analysis

Phylogenetic analysis of the COI gene revealed that Vesicomyinae and Pliocardiinae are well supported sister clades (bootstrap proportion BS = 97.8%) while *K. miliaris* is placed next to Veneridae (BS = 100%). The split between the Vesicomyinae +Pliocardiinae clade and Veneridae+K. *miliaris* clade indicates that *Kelliella* is not closely related to Vesicomyidae (Fig. 12). Two specimens of *V. alleni* from the South Atlantic Ocean at 47°38.73′ S, 004°15.20′E (Table 1) cluster with *Vesicomya* sp. 1 from the same station, studied previously (Johnson *et al.*, 2017). A maximum K2P distance of only 0.007 between the three COI haplotypes of *Vesicomya* sp. 1 and *V. alleni* suggests their conspecific status.

Stable carbon and nitrogen isotopic composition

The stable carbon and nitrogen compositions of soft tissue are given in Table 6. The standard deviation of repeated measurement of δ^{13}C was small (<0.7‰), but larger for δ^{15}N (up to 2.7‰) (this may be the result of insufficient homogenization of the sample). In general, the values for δ^{13}C ranged between −16.34 and −19.96‰ and for δ^{15}N between 8.59 and 15.51‰.

Figure 4. *Vesicomya alleni* n. sp., RV *Polarstern* Stn PS67/021-7-S (IORAS). **A.** Interior of RV. **B.** Dorsal view, RV above. **C.** RV hinge plate. **D.** LV hinge plate. **E.** Inner view of shell margin. **F.** Prodissoconch. **G, H.** Margin of prodissoconch. **I.** Sculpture of prodissoconch. Abbreviations: 1vc, ventral cardinal tooth; 2a, 2b, anterior and posterior rami of subumbonal cardinal tooth of LV; 3a, 3b, anterior and posterior rami of subumbonal cardinal tooth of RV; 4b, posterodorsal cardinal tooth; esc, escutcheon; fll, fibrous ligament layer; lu, lunular incision; ny, nymph; pll, posterior lamellar ligament layer; prod, prodissococh border.

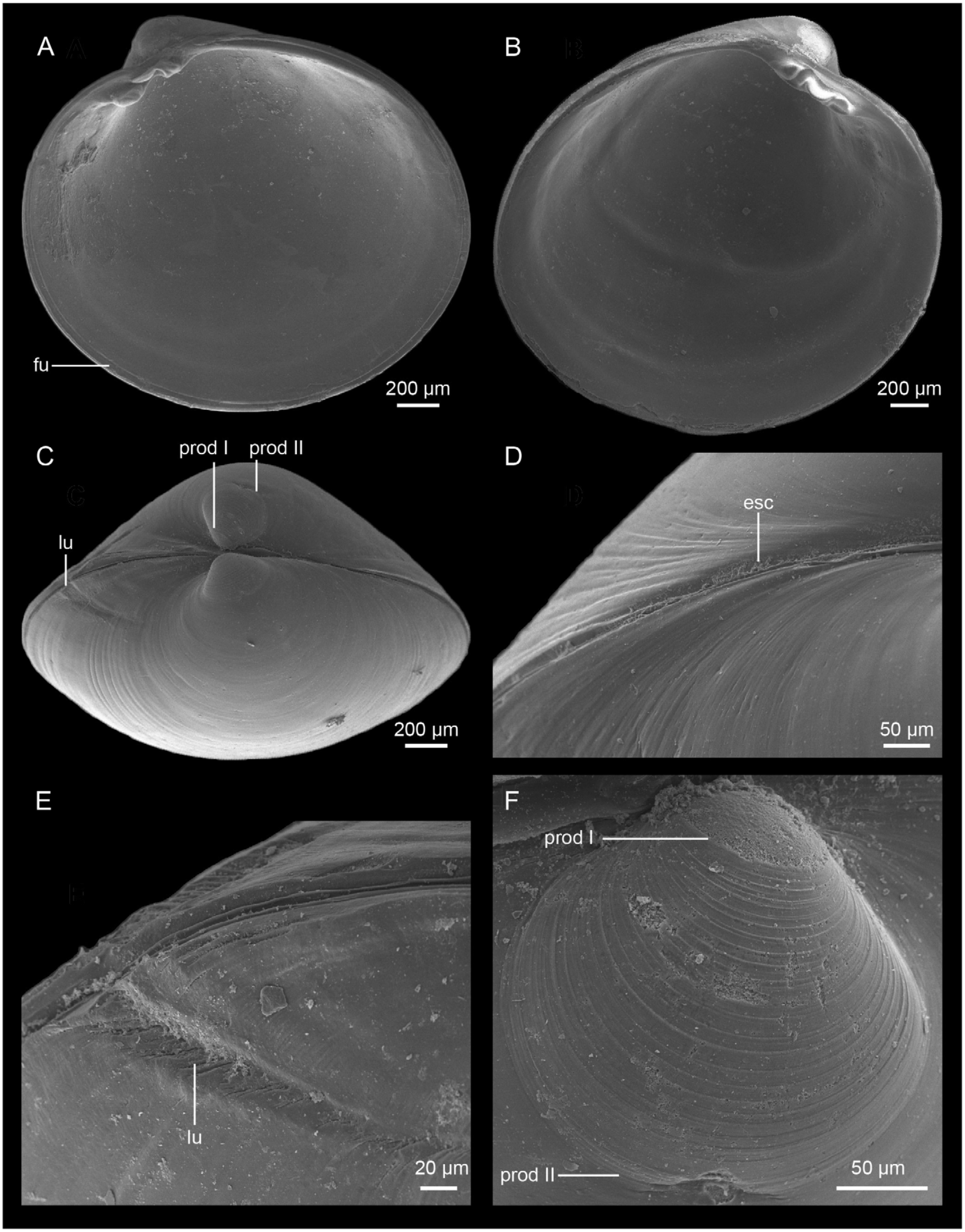

Figure 7. *Kelliella miliaris* (Philippi, 1844), RV *Håkon Mosby* Stn 24 (IORAS). **A.** Interior of RV. **B.** Interior of LV. **C.** Dorsal view, RV above. **D.** Posterodorsal margin of conjoined valves showing very shallow escutcheon. **E.** Lunule incision. **F.** Prodissoconch I and II. Abbreviations: esc, escutcheon, fu, furrow along inner margin of RV; lu, lunular incision; prod I, border between prodissococh I and II; prod II, distal limit of prodissococh II.

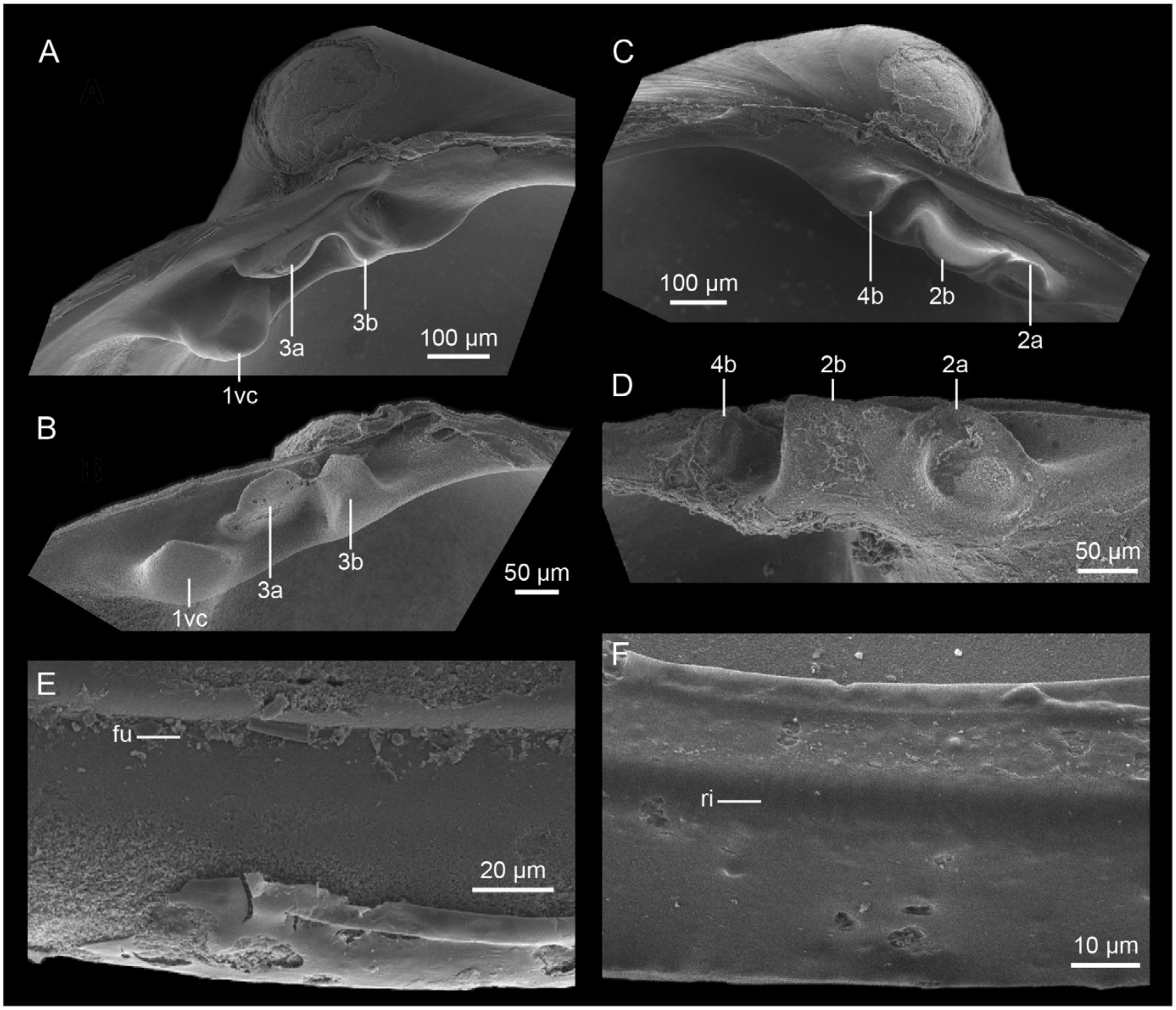

Figure 8. *Kelliella miliaris* (Philippi, 1844), RV *Håkon Mosby* Stn 24 (IORAS). **A, B.** Right hinge plate. **A.** Lateral view, **B.** Lateroventral view. **C, D.** LV hinge plate: **C.** Lateral view. **D.** Lateroventral view. **E.** Interior shell margin of RV. **F.** Interior shell margin of LV. Abbreviations: 1vc, ventral cardinal tooth; 2a, 2b, anterior and posterior rami of subumbonal cardinal tooth of LV; 3a, 3b, anterior and posterior rami of subumbonal cardinal tooth of RV; 4b, posterodorsal cardinal tooth; fu, furrow along inner margin of RV; ri, ridge along inner margin of LV.

DISCUSSION

Our results indicate that *Kelliella* is phylogenetically distantly related to the family Vesicomyidae (which includes Vesicomyinae with at present the single genus *Vesicomya* and Pliocardiinae with the large-sized specialized genera). According to an evolutionary scenario outlined below, Vesicomyinae is the less derived group and Pliocardiinae the more derived.

Separation of Kelliellidae from Vesicomyidae based on morphology

The morphological resemblance of *Kelliella* and *Vesicomya* lies mainly in small body sizes and white, semi-transparent subcircular shells with heterodont dentition comprising only cardinal and no lateral teeth. The absence of lateral teeth is likely a convergent trait that resulted from a shell size reduction in both groups, and can be seen also in several groups of veneroids (Mikkelsen *et al.*, 2006). Nevertheless, there are important conchological and anatomical features discriminating *Kelliella* and *Vesicomya*. Firstly, there are differences in the details of the hinge margin; in *Kelliella* the posterior right tooth is angulated (fused 3a and 3b), while in *Vesicomya* it is more or less linear and parallel to the hinge margin. The posterior left tooth (4b) in *Kelliella* is short and stout, while in *Vesicomya* it is elongated and lamellate. Secondly, there are differences in other shell characters. The shell of *Kelliella* lacks an escutcheon or it is nearly indiscernible, whereas the shell of *Vesicomya* has a noticeable escutcheon. The inner ventral shell margin of *Kelliella* has a regular and clear incision in its right valve and a corresponding ridge in the left one, whereas *Vesicomya* bears only a faint stria in both valves. The prodissoconch of *Kelliella* is distinctly divided into small prodissoconch I and large prodissoconch II, but of *Vesicomya* is quite large and not separated into prodissoconch I and II. Thirdly, anatomical differences also support the separation of *Kelliella* and *Vesicomya*. In *Kelliella* there is only one mantle fusion, forming a single posterior exhalant siphon and an inhalant aperture that is not separated from the pedal gape. *Vesicomya* has two fusions forming both an inhalant and an exhalant aperture. *Kelliella* has longer posterior palps than *Vesicomya* and a more voluminous stomach that is

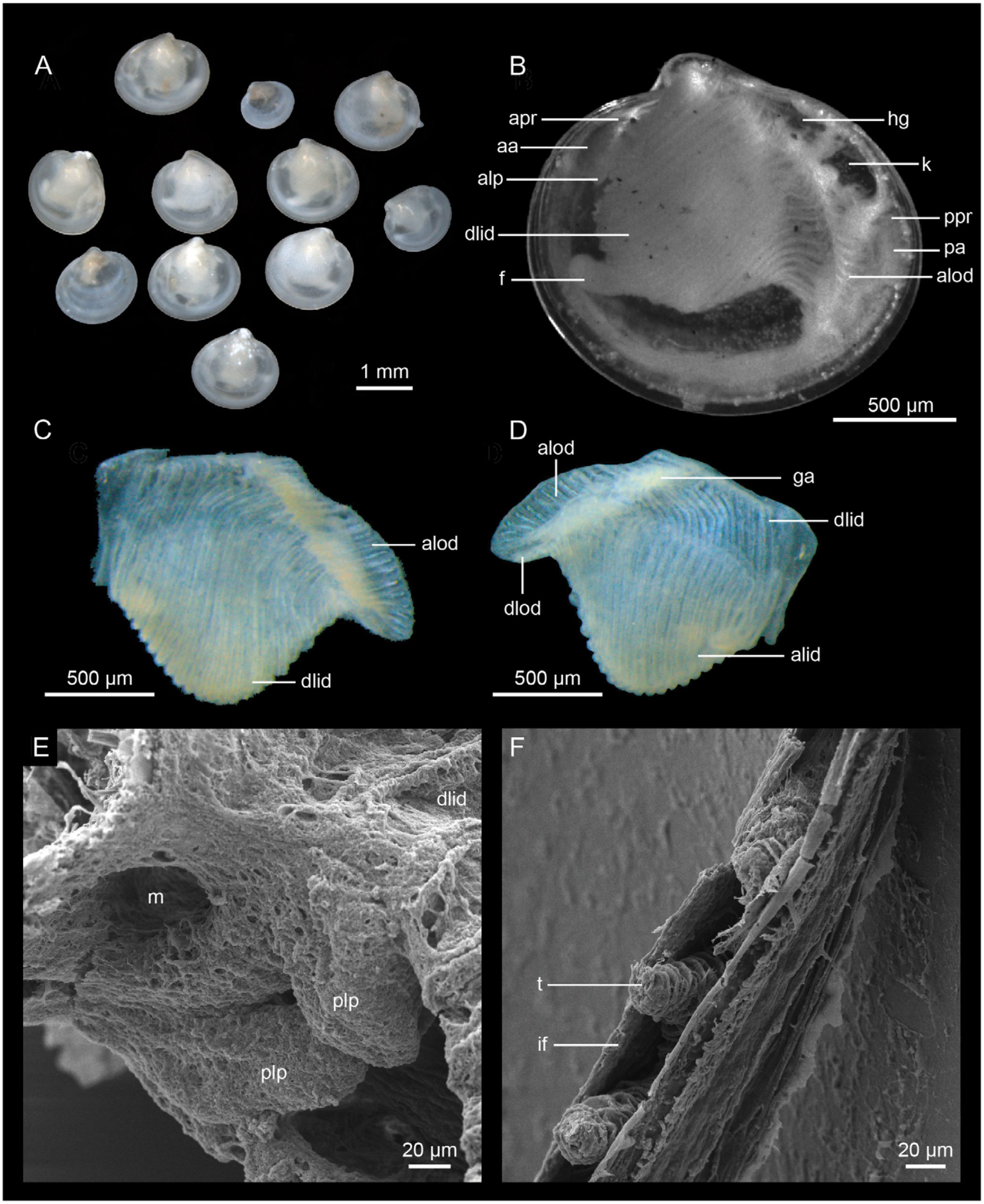

Figure 9. *Kelliella miliaris* (Philippi, 1844), RV *Håkon Mosby* Stn 24 (IORAS). Stained with Rose Bengal. **A.** General view of live-preserved specimens. **B.** Body as seen from left. **C, D.** Left gills. **C.** Exterior view. **D.** Interior view. **E.** Mouth and posterior palps. **F.** Tentacles of mantle margin with strongly developed inner mantle fold. Abbreviations: aa, anterior adductor muscle; alid, ascending lamella of inner demibranch; alod, ascending lamella of outer demibranch; alp, anterior labial palps; apr, anterior pedal retractor muscle; dlid, descending lamella of inner demibranch; dlod, descending lamella of outer demibranch; f, foot; ga, gill axis; hg, hindgut; if, inner mantle fold; k, kidney; m, mouth; pa, posterior adductor muscle; plp, posterior labial palps; ppr, posterior pedal retractor muscle; t, tentacles.

Table 2. Comparison of features of *Kelliella*, *Vesicomya*, '*Vesicomya' filatovae* and *Waisiuconcha*.

Taxa	Shell length, mm	Disposition of 3a and 3b rami	4 b tooth	Presence of lunule	Escutcheon	Presence of prodissoconch II	Incision in inner shell margin	Number of pairs of demibranchs	Number of pallial apertures	Relative size and location of stomach
Kelliella M.Sars, 1870	1.5–3	Diverge at about 90°	Stout short	Yes	Absent or very small	Yes	Regular furrow in RV, corresponding ridge in LV	2	2	Large, nearly vertically located
Vesicomya Dall, 1886	1.2–13	Linear or slightly arcuate	Lamellar elongated	Yes	Well developed	No	Very faint stria, same in both valves	2	3	Small, horizontally located
'*Vesicomya*' *filatovae*	1.6	Arcuate	Lamellar elongated	Yes	Well developed	No	1 shallow groove same in both valves	1	3	Small, horizontally located
Waisiuconcha, Beets, 1943	2–24	Diverge at 90° or more	Lamellar elongated	Yes	Well developed	No	1–2 shallow grooves, same in both valves	?	?	?

oriented in an oblique angle of *c.* 45° to the antero-posterior body axis (Clausen, 1958). In *Vesicomya* the stomach is small and its long axis parallels the antero-posterior axis of the animal. *Kelliella* has a better-developed foot than *Vesicomya*.

Some of the mentioned morphological features distinguishing *Vesicomya* and *Kelliella* do not necessarily imply a distant genetic relationship, but may be attributed to different lifestyles. For example, different structure of the prodissoconchs is generally not phylogenetically constrained, but indicates different types of larval development (Bouchet, 1990). In *Kelliella* the prodissoconch structure indicates a planktotrophic type of development, as typical for shallow-water groups, while *Vesicomya* larvae develop lecithotrophically like many other deep-sea bivalves. Nevertheless, the morphological differences discussed above suggest a separation of *Vesicomya* and *Kelliella*.

Kelliella shares common features with some pliocardiine genera, but in general the differences prevail. Among all the studied pliocardiines, *Kelliella* is most similar to *Waisiuconcha* Beets, 1943, which includes small-sized bivalves (3–24 mm L) with mainly subcircular shells characterized by the presence of an escutcheon and lunule (Table 2). The hinge of *Waisiuconcha*, as recorded by Von Cosel & Salas (2001), is less modified compared with other vesicomyids and very similar to that of young venerids such as *Pitar rudis*. The main difference of *Waisiuconcha* from young venerids is its absence of lateral teeth. The shape and arrangement of teeth in *Waisiuconcha* is very similar to that in *Kelliella*. However, *Waisiuconcha* differs from *Kelliella* by a thicker and more sculptured shell that possesses an escutcheon, by an inner shell margin bearing 1–2 shallow grooves, and by a prodissoconch that is not divided into prodissoconch I and II (Janssen & Krylova, 2012). The anatomy of *Waisiuconcha* has not been published, but according to our own unpublished data it has only one pair of demibranchs. This is in contrast to *Kelliella* that has two pairs. We consider that the similarity between *Kelliella* and *Waisiuconcha*, mainly expressed in the hinge structure, is homoplasious and does not suggest close phylogenetic relationship.

Kelliella is similar to *Christineconcha* Krylova & Von Cosel, 2011 with regard to the presence of only one mantle fusion instead of two. Although there is no ventral tissue fusion in *Christineconcha*, this part of the mantle margin can function as a 'usual' siphon with the help of strongly developed muscles at the base of the inhalant aperture and additional vascularized thickenings, which can be enlarged and then touch each other to form a complete tube (Krylova & Von Cosel, 2011). Therefore, despite the absence of a second mantle fusion in *Christineconcha*, the modifications of the inhalant aperture may provide similar functionality as the inhalant siphon in vesicomyids, guiding inhalant water flow into and pseudofaces removal from the mantle cavity (Krylova & Von Cosel, 2011). In *Kelliella* the entire pedal gape functions as an inhalant aperture and the inhalant current goes through the pedal gape anteriorly and ventrally; pseudofaeces are also removed ventrally (Clausen, 1958). In all respects *Christineconcha* is considerably distinct from *Kelliella*. It is large (up to 122 mm L), with elongated shell and one pair of demibranchs. So, in spite of some features shared by *Kelliella* and specialized chemosymbiotic vesicomyid genera, the overall differences call for a separation of the taxa at family level.

Relationship between Vesicomya *and pliocardiines based on morphology*

The morphological comparison of *Vesicomya* with the 'large-sized' genera belonging to the Pliocardiinae indicate affinities between these groups. The hinge of *Vesicomya* is very similar to hinges of adult specimens of several genera, e.g. *Isorropodon* Sturany, 1896 and *Callogonia* Dall, 1889. Furthermore, it has close resemblance to hinges of juveniles of pliocardiines, which all have modified hinges in their adult stages (Figs 10D, E, 11C). Prodissoconchs of all the studied pliocardiines are similar to that of *Vesicomya*: they

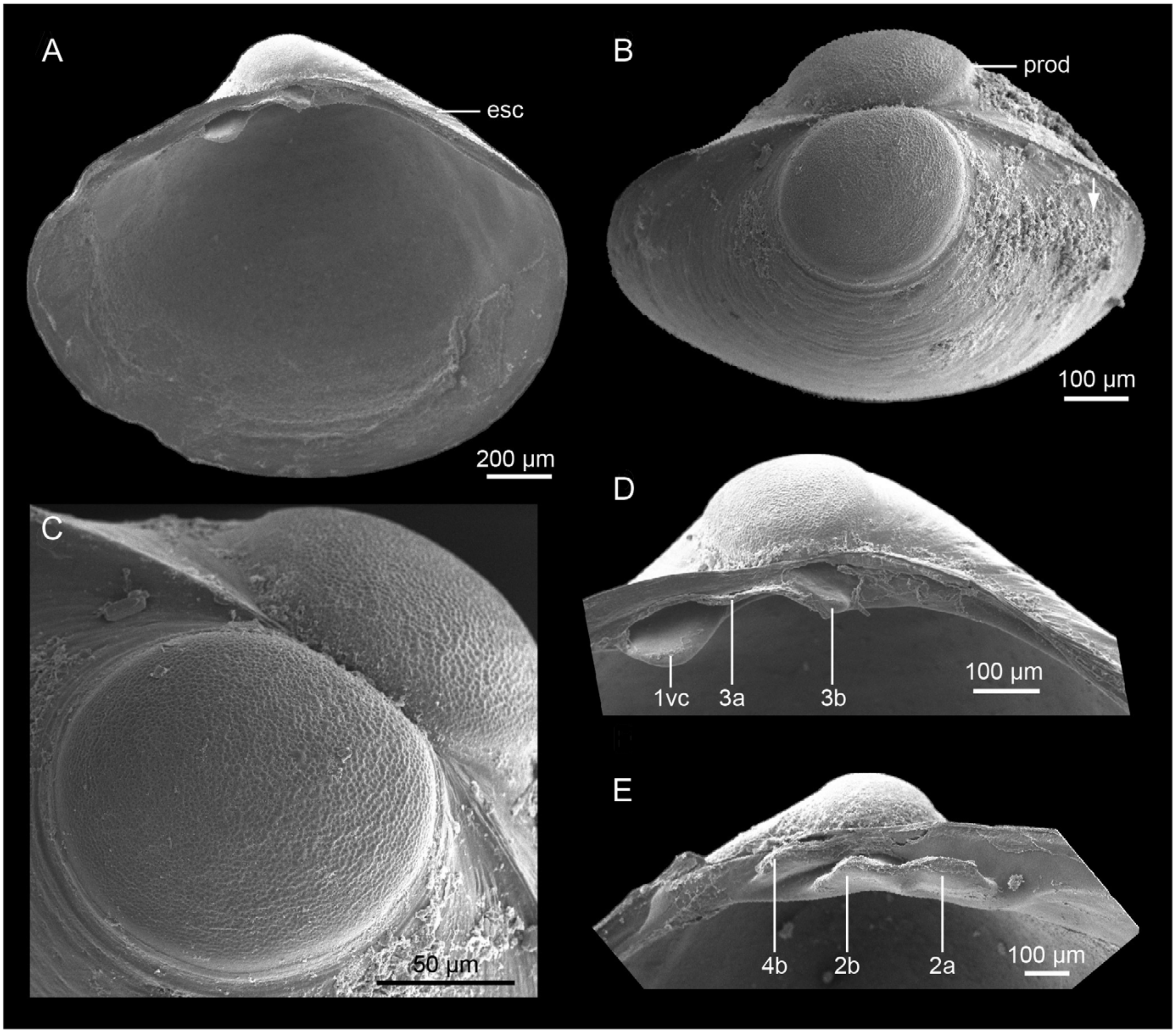

Figure 10. Pliocardiinae sp., probably '*Ectenagena*' *fossajaponica* Okutani, Fujikura & Kojima, 2000, RV *Sonne* cruise 110, Stn 40/1 (IORAS). **A.** Interior of RV. **B.** Dorsolateral view (RV mostly visible). **C.** Prodissoconch. **D.** RV hinge plate. **E**. LV hinge plate. Abbreviations: 1vc, ventral cardinal tooth; 2a, anterior ramus of subumbonal cardinal tooth; 2b, posterior ramus of subumbonal cardinal tooth; 3a, anterior ramus of subumbonal cardinal; 3b, posterior ramus of subumbonal cardinal; 4b, posterodorsal cardinal tooth; prod, prodissococh border; esc, escutcheon.

are large, have a pitted structure and are not divided into prodissoconchs I and II, implying lecithotrophic development (Figs 10C, 11A). The alimentary systems of pliocardiines show a considerable range of structural diversity (Johnson *et al.*, 2017), most likely reflecting a general tendency towards reduction that has reached various stages in the different genera. The least reduced conditions of the alimentary system are probably found in '*Calyptogena*' *ponderosa* Boss, 1968, '*V.*' *stearnsii* Dall, 1895 and species of the genus *Isorropodon* where the general configuration of the gut is very similar to that of *Vesicomya*. The labial palps are vestigial in both *Vesicomya* and pliocardiine genera.

The main morphological differences between *Vesicomya* and pliocardiines are probably connected with the adaptations of pliocardiines for symbiotrophy. To date, there is no evidence for a significant contribution of chemoautotrophic symbionts to the nutrition of *Vesicomya* (see below). The adaptations of pliocardiines for chemoautotrophic symbiosis are mainly the thickened ctenidia with frequently reduced outer demibranchs and large subfilamental tissue containing bacteriocytes, elongation of the body and development of a functional foot and siphons. The increase of body size and reduction of the alimentary system are also directly related to the chemosymbiotic lifestyle and can be considered as consequences of symbiotrophy. We hypothesize that these characters of the specialized Pliocardiinae are apomorphic and that the plesiomorphic states of anatomy and shell morphology are represented in Recent *Vesicomya* species.

COI-based phylogeny

Our phylogenetic analysis of mitochondrial COI confirmed recent results based on six genes (Johnson *et al.*, 2017), according to which *Vesicomya* and Pliocardiinae formed well defined sister clades (Fig. 12). This result agrees with the bivalve tree-of-life constructed from five gene fragments by Combosch *et al.* (2017). Accordingly to their tree, Vesicomyinae (as 'Kelliellidae') and Pliocardiinae

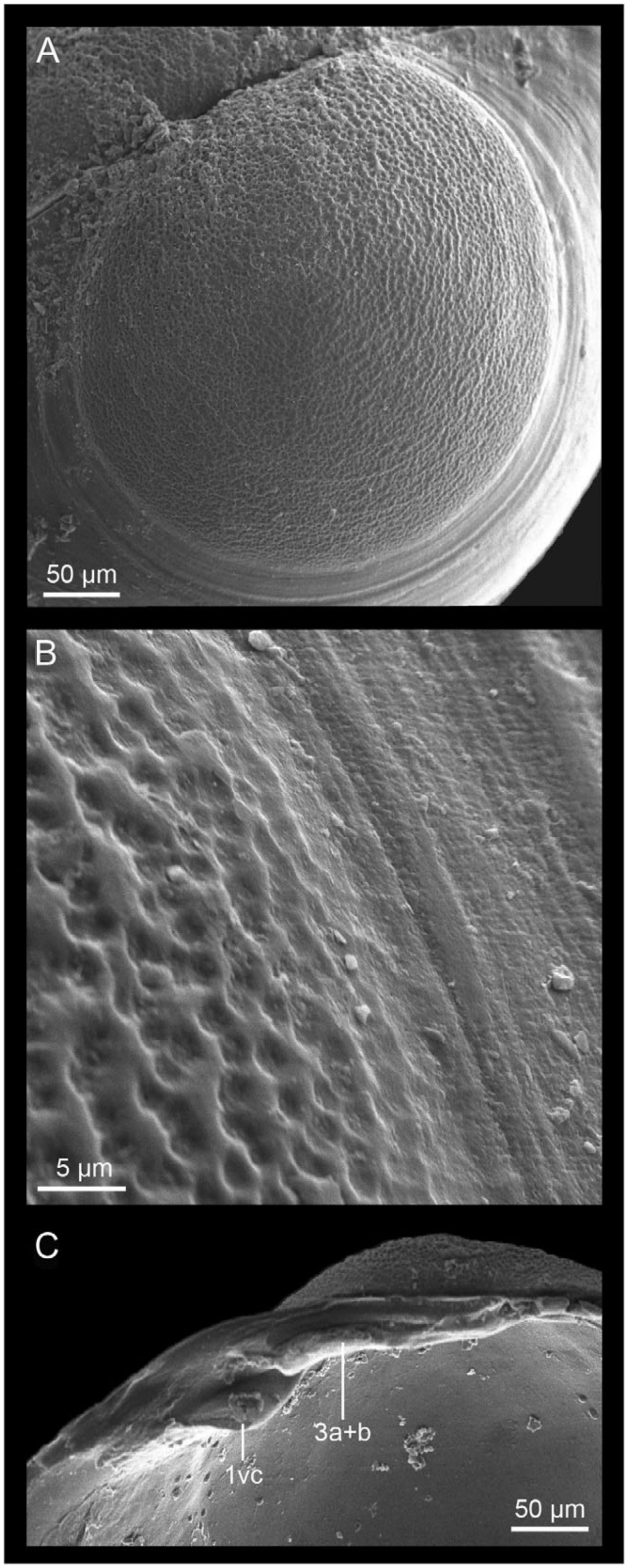

Figure 11. Pliocardiinae sp., probably *Abyssogena phaseoliformis* (Métivier, Okutani & Ohta, 1986), RV *Sonne* cruise 110, Stn 40/1 (IORAS). **A.** Prodissoconch. **B.** Margin of prodissoconch. **C.** Hinge plate of RV. Abbreviations: 1vc, ventral cardinal tooth; 3a+b, fused 3a and 3b rami of subumbonal cardinal tooth of RV.

(as 'Vesicomyidae') formed a well-supported clade, which appeared as sister group to Veneridae.

This finding is consistent with our interpretation of phylogenetic divergence of these taxa based on the morphological adaptations of all pliocardiines to the symbiotrophic lifestyle—such as modifications of the ctenidia that contain the bacterial endosymbionts, reduction of the alimentary system and an increase of body size. Our analysis of COI also revealed genetic divergence of *Kelliella* from the Vesicomyidae and thereby confirmed our interpretation of their distant relationship, based on the differences in shell and soft part morphology. The COI gene did not clearly resolve the deeper-branching relationship between *Kelliella* and Veneridae, and genetic support for the family status of Kelliellidae must await further analyses with nuclear genes.

Biology of Vesicomya

The fact that the small-sized *Vesicomya* are related to the large-sized symbiotrophic pliocardiines raises the question whether or not chemosymbiotic bacteria contribute to the nutrition of *Vesicomya*. An earlier TEM study of *V. sergeevi* recovered from the Kuril-Kamchatka Trench revealed bacteria-resembling cells in the gill filaments (Krylova *et al.*, 2000); however, whether these cells are symbiotic or pathogenic is difficult on the basis of the available ultrastructural images.

Our analyses of several *Vesicomya* species did not provide further evidence for a symbiotic lifestyle. On the contrary, there is a line of evidence that argues against a significant contribution of chemosynthetic bacteria to the nutrition of *Vesicomya*. As mentioned above, *Vesicomya* species possess a functional gut that is often filled with detritus-like particles, suggesting that these clams are detritus feeders. Furthermore, the gills are not enlarged as typical of bacteria-harbouring pliocardiines.

Finally, our measurements of stable isotope signatures in four *Vesicomya* species from different geographical locations (Table 6) suggest that these do not depend on chemoautotrophy, because the values are typical for deep-sea deposit feeders (Iken *et al.*, 2001; Bergmann *et al.*, 2009). Both carbon and nitrogen signatures are much more positive than those in pliocardiines with chemosynthetic endosymbionts, which usually show δ^{13}C values in the range of −30 to −40‰ and δ^{15}N values between −3.3 and 5.8‰ (Nelson & Fisher, 1995; Levin & Michener, 2002; Sahling *et al.*, 2003). Such low δ^{13}C values result from the specific C-isotope fractionation during carbon fixation by chemoautotrophic bacteria. The metabolic pathways that produce the low δ^{15}N values in pliocardiines are not yet known, but there are indications that their symbionts can assimilate inorganic nitrogen (Roeselers *et al.*, 2010).

It should be noted that we measured the stable isotopic composition on preserved specimens that had been stored in ethanol for up to 30 years, which may have influenced their isotopic composition. However, studies on the influence of ethanol on stable isotope signatures in animal tissues after preservation for 1 year revealed only minor effects (δ^{13}C less than 2‰, δ^{15}N 0‰; Carabel, Verísimo & Freire, 2009; Fanelli *et al.*, 2010). We therefore suggest that the effect of ethanol preservation in our samples is likely to have been small compared to the large differences between *Vesicomya* and pliocardiines outlined above, and that our data are a reliable indication of nutrition.

Proposed evolutionary trends in Vesicomyidae

It may be hypothesized that the ancestral group of vesicomyids were small clams that lived in the deep sea, similar to modern *Vesicomya*. For the symbiotrophic pliocardiines, an origin from deep-dwelling ancestors has recently received molecular support

Table 3. Described Recent species of *Vesicomya*.

Species	Original generic allocation	Maximum shell length (mm)	Distribution
V. abyssicola (Allen, 2001) (not *Kellia abyssicola* Forbes, 1844 or *Kelliella abyssicola* M. Sars, 1870)	*Kelliella*	3	N Atlantic to SW Ireland, Sierra Leone and Guyana Basin, 2185–4632 m (Allen, 2001)
V. adamsi (Smith, 1885)	*Callocardia?*	14	E Atlantic from off Sierra Leone (Smith, 1885), Romanche Deep (Odhner, 1960) to off Namibia, 4400–5300 m (Von Cosel & Salas 2001)
V. alleni n. sp.	*Vesicomya*	3.3	S Atlantic, 4555 m (this paper)
V. atlantica (Smith, 1885)	*Callocardia?*	4.6	N Atlantic from 53°55′N to Cape Verde Basin, off Azores, 1800–4249 m (Von Cosel & Salas 2001)
V. bruuni Filatova, 1969	*Vesicomya*	6.6	SW Pacific, Kermadec Trench, 5900–9200 m (Filatova, 1969; Knudsen, 1970)
V. elegantula (Bernard, 1989)	*Kelliella*	3.9	NE Pacific, W Triangle Island, 1760 m (Bernard, 1989)
V. galatheae (Knudsen, 1970)	*Kelliella*	5.2	E Pacific, off Central America, 2950–3570 m (Knudsen, 1970)
V. indica (Knudsen, 1970)	*Kelliella*	12.3	Central Indian O., 4350 m (Knudsen, 1970)
V. laevis (Pelseneer, 1903)	*Callocardia*	2.6	Antarctic (70–71° S, 80–88°W), 400–550 m (Pelseneer, 1903)
V. pacifica (Smith, 1885)	*Callocardia?*	8.2	Mid-N Pacific, NW Pacific E of Kuril Is, 4861–5787 m (Smith, 1885; Okutani & Kawamura, 2002; Krylova *et al.*, 2015)
V. profundi Filatova, 1971	*Vesicomya*	5.5	N Pacific, Kuril–Kamchatka Trench, 7120–9050 m; Aleutian Trench, 7246 m (Filatova, 1971)
V. sergeevi Filatova, 1971	*Vesicomya*	4.8	N Pacific, Kuril–Kamchatka Trench, 7600–9530 m (Filatova, 1971)
V. sirenkoi (Egorova, 1998)	*Kelliella*	3.7	Antarctic, Scotia and Weddell Seas, 2315–6348 m (Egorova, 1998; Linse, 2004)
V. sundaensis (Knudsen, 1970)	*Kelliella*	3.9	E Indian O., Sunda Trench, 6900–7000 m (Knudsen, 1970)
V. tasmanensis (Knudsen, 1970)	*Kelliella*	6.2	Tasman Sea, 4400 m (Knudsen, 1970)

Table 4. Recent representatives of Vesicomyinae that do not belong to the genus *Vesicomya s. s.* (Krylova *et al.*, 2015), but are included in the distribution map (Fig. 12B).

Species	Original generic allocation	Maximum shell length, mm	Distribution
concentrica Allen, 2001	*Kelliella*	2.5	Upper slope off New England, N American Basin (39°47′N, 70°56.4′W), 457–811 m (Allen, 2001)
filatovae Krylova & Kamenev, 2015	*'Vesicomya'*	1.6	NW Pacific O., E Kuril Is, 4861–5427 m (Krylova *et al.*, 2015)

Table 5. Recent named and undescribed species of *Kelliella*.

Species	Original generic allocation	Maximum shell length, mm	Biotope	Distribution
? *K. biscayensis* Allen, 2001	*Kelliella*	1.5	?	E Atlantic, Bay of Biscay, 465–1015 m (Allen, 2001)
K. goesi Odhner, 1960	*Kellyella*	1.8	Clay (Odhner, 1960)	W Atlantic, St Martin, 360–540 m, Anguilla, 180–450 m (Odhner, 1960)
K. japonica Hayami & Kase, 1993	*Kelliella*	2.5	Sublittoral caves (Hayami & Kase, 1993)	W Pacific, Ryukyu Is (Hayami & Kase, 1993)
K. miliaris (Philippi, 1844)	?*Venus*	3	Soft sediments, common in fiords (M. Sars, 1870; Clausen, 1958; Warén, 1989; Allen, 2001)	NE Atlantic, Norwegian Sea, Mediterranean Sea, 10–1170 m (Allen, 2001)
? *K. rotunda* (Thiele & Jaeckel, 1931)	*Vesicomya*	2	?	E Indian O., Siberut Strait, S Sumatra, Indonesia, 750 m (Thiele & Jaeckel, 1931)
K. rotunda sensu Boss (1970)	*Vesicomya*	3	?	W Pacific, Philippines, 1785 m (Boss, 1970)
K. rotunda sensu Raines & Huber (2012)	*Kelliella*	3	Fine sand (Raines & Huber, 2012)	Central Pacific, Eastern Island, 30–150 m (Raines & Huber, 2012).
Kelliella sp.		2	Not precisely known; regularly obtained from washes of highly degraded driftwood (Warén, 2011)	SW Pacific, Vanuatu, 25 m (Warén, 2011)
Kelliella sp.		2	Soft sediments	W Pacific, Philippines, Panglao I., 35–139 m (E. Krylova, unpublished)
Kelliella sp.		2	Soft sediments	SW Pacific, Fiji, 260–1180 m (E. Krylova, unpublished)
Kelliella sp.		2	Soft sediments	SW Pacific, Solomon Is, 435–461 m (A. Warén, unpublished)

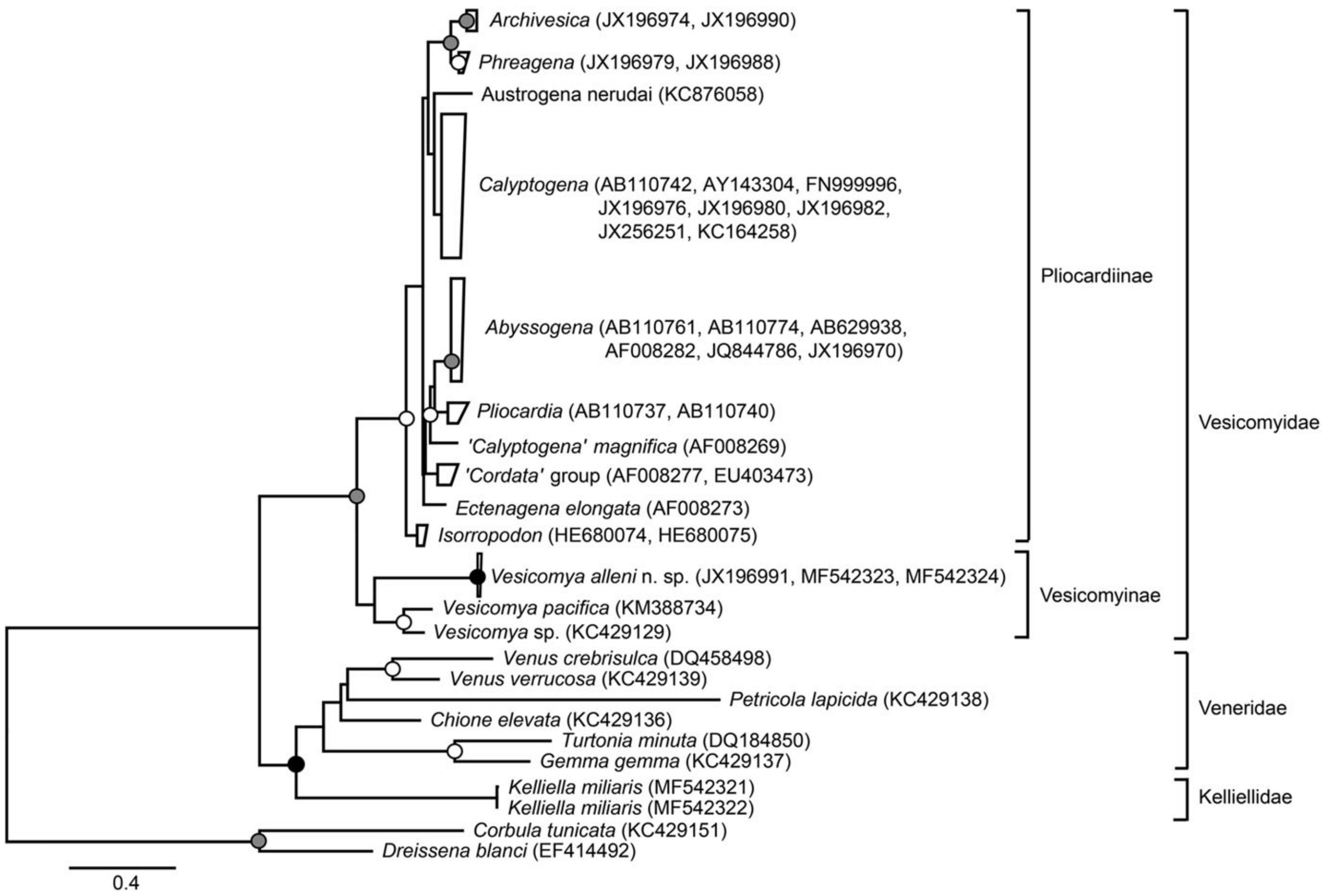

Figure 12. Phylogenetic reconstruction (ML) of Pliocardiinae, Vesicomyinae and *Kelliella* based on COI sequence data. Circles represent bootstrap probabilities: white >80%, grey >95%, black = 100% (1000 resamplings). *Vesicomya alleni* n. sp. is identical to *Vesicomya* sp. 1 of Johnson *et al.* (2017); *Vesicomya* sp. in this tree is identical to *Kelliella* sp. of Bieler *et al.* (2014) and *Vesicomya* sp. 2 of Johnson *et al.* (2017).

Table 6. Stable isotopic composition of soft tissues of species of *Vesicomya* and *Kelliella*.

Species	Comment	Cruise, Station	δ^{13}C	δ^{15}N
Vesicomya adamsi	1 individual, soft parts without gills	*Meteor* 63, Stn 91, 0°50.92′N, 05°38.35′W, 5140 m	−16.92‰	14.57‰
			−17.60‰	11.89‰
Vesicomya adamsi	2 individuals, gills	*Meteor* 63, Stn 91, 0°50.92′N, 05°38.35′W, 5140 m	−17.34‰	12.70‰
			−17.24‰	11.73‰
Vesicomya sp.	1 individual, soft parts	*Dmitri Mendeleev* Stn 1300, 57°18′S, 157°18′E, 5950–5970 m	−19.74‰	8.59‰
			−19.96‰	9.28‰
Vesicomya sergeevi	4 individuals, soft parts without gills	*Vityaz* Stn 5635, 45°25′N, 153°07′E, 8185–8400 m	−17.10‰	12.37‰
Vesicomya sp.	4 individuals, soft parts without gills	*Dmitri Mendeleev* Stn 1636, 07°56′S, 81°10′W, 5770–5800 m	−16.58‰	15.51‰
			−16.34‰	14.19‰
Kelliella miliaris	3 individuals, entire soft parts	*Håkon Mosby* Stn 24, 62°27,456′N, 06°45,141′E, 628 m	−18.71‰	11.47‰
			−19.39‰	11.36‰

Two measurements are presented in instances where there was sufficient material to make more than one analysis.

by the phylogenetic analysis of six mitochondrial and nuclear genes (Johnson *et al.*, 2017). In light of this, it is possible that early pliocardiines were physiologically preadapted to the environmental conditions in the deep sea and that this was a reason why this group radiated more successfully in the low-bathyal and abyssal zones than other chemosynthetic bivalves such as Lucinidae, Thyasiridae and Bathymodiolinae (Taylor & Glover, 2010; Lorion *et al.*, 2013; Johnson *et al.*, 2017).

We assume that the diversity of modern Vesicomyinae is much higher than currently recognized, but that the exploration of this diversity is hampered by difficulties of sampling and studying these small deep-sea bivalves with very fragile shells. The living species of *Vesicomya* occur worldwide (Fig. 13B) at 400–10,730 m depths in a variety of deep-sea settings, but reach especially high abundances in biotopes that receive high amounts of organic matter. It is possible that the ancestors of Pliocardiinae were also adapted to organic-rich deep-sea habitats. It is further feasible that symbiotrophy of the early Pliocardiinae developed in habitats in which microbial degradation of high loads of buried organic matter produced sulphide that in turn supported chemosynthetic microbes.

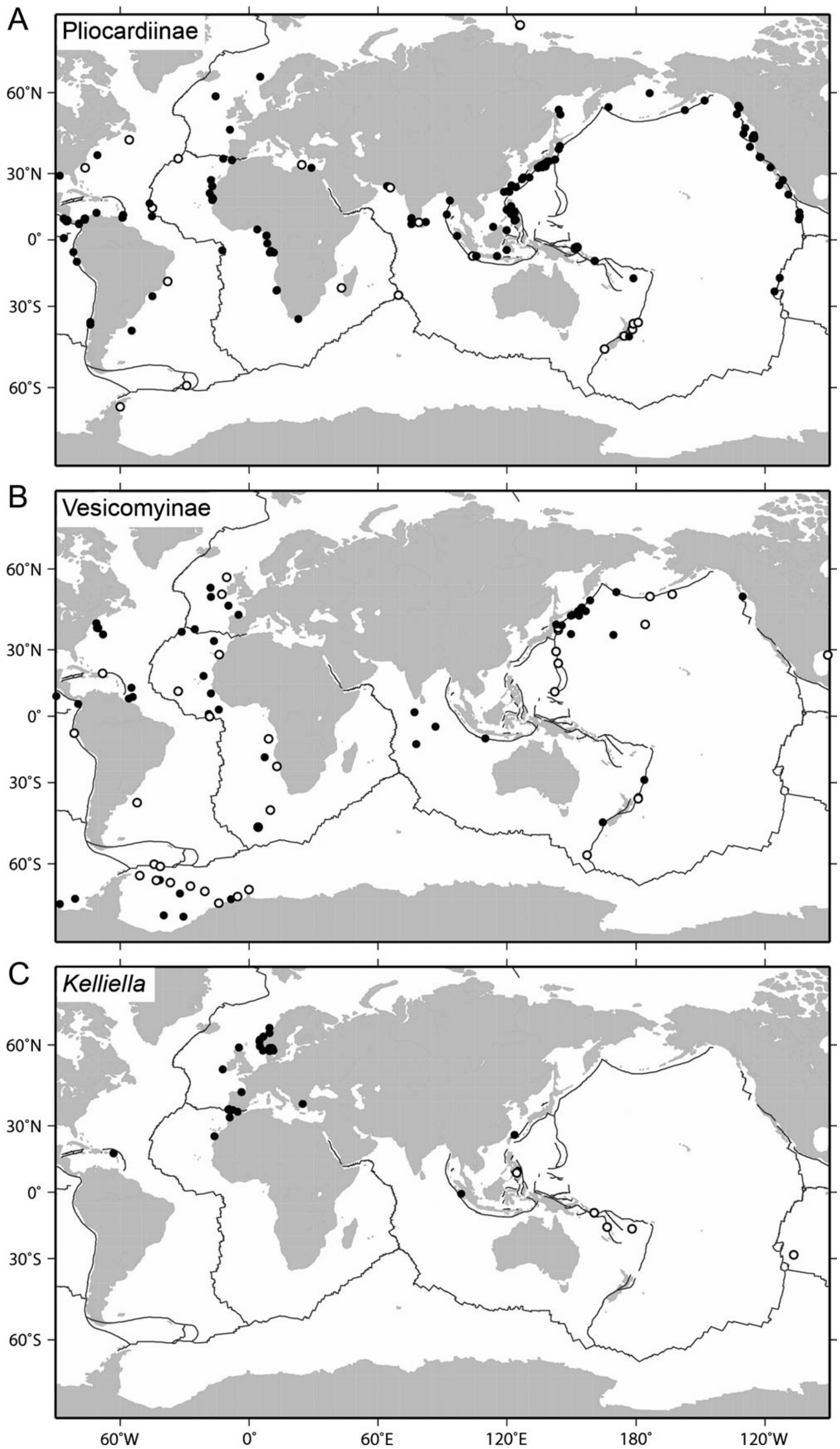

Figure 13. Distribution of named (filled circles) and unnamed (open circles) of species of Pliocardiinae (**A**), Vesicomyinae (**B**) and *Kelliella* (**C**). For details of geographical localities for Pliocardiinae see Krylova & Sahling (2006), Krylova *et al.* (2010, 2014), Audzijonyte *et al.* (2012), Decker *et al.* (2012), Oliver & Drewery (2013) and Johnson *et al.* (2017); for Vesicomyinae see Tables 1, 3 and 4 and Belyaev (1972), Filatova (1969, 1971, 1974), Knudsen (1970), Belyaev & Mironov (1977), Vinogradova *et al.* (1993), Allen (2001), Linse (2004), Krylova & Sahling (2010) and Krylova *et al.* (2015); for *Kelliella* see Tables 1 and 5.

Pliocardiines associated with chemoautotrophic bacteria could then have exploited other sulphidic deep-sea habitats, such as hydrocarbon seeps, which provided sulphide as an almost unlimited energy source for the chemosynthetic bacteria. Hydrocarbon seeps are present along almost all continental margins (Krylova & Sahling, 2010) and pliocardiines have successfully invaded these habitats worldwide (Fig. 13A). In the wake of a symbiotrophic lifestyle, the deep-sea pliocardiines became progressively independent from filter feeding on a limited resource of surface-derived phototrophic organic carbon. Their switch to a plentiful chemosynthetic carbon source provided by symbiotic bacteria resulted in a number of morphological modifications including an increase of body size, enlargement of the gills that contain the symbionts and reduction of the digestive tract.

Biology of Kelliella

Kelliella occurs from the sublittoral to 1785 m depth, but mainly on the continental shelf and upper slope shallower than 1000 m. Its known distribution is strongly biased towards European waters, as shown in the distribution map (Fig. 13C), but this is probably a result of intensive sampling and may not reflect the natural distribution. *Kelliella* species are small, with maximum shell lengths of 2–3 mm (Table 5). In general, they live on the surface of soft sediments. Clausen (1958: 154) studied living *K. miliaris* and noted that it “was never observed to burrow, nor to attempt to do so”. The structure of the alimentary system, the ciliation of the gills and the gut content all suggest that *K. miliaris* is a filter feeder on small organic particles (Clausen, 1958). The stable δ^{13}C and δ^{15}N isotopic composition of *K. miliaris* is similar to that of *Vesicomya* (Table 6), suggesting heterotrophy. Interestingly, some species of *Kelliella* occur in habitats that are enriched in organic carbon or are even exposed to reducing conditions. For example, *K. miliaris* can reach high abundances in sulphidic habitats where they co-occur with Pogonophora that harbour chemosynthetic endosymbionts (Southward *et al.*, 1981). *Kelliella* can co-occur with *Vesicomya* (A. Warén, personal communication; E. Krylova, unpublished). Other information on the biology of *Kelliella* is limited to a few observational interpretations. For example, an undescribed *Kelliella* species appears to live on driftwood, because it was regularly obtained from washes of highly degraded drifting logs (Warén, 2011). The distribution of *K. japonica* may be limited to sublittoral caves, because this species is exclusively known from dead shells collected in such caves (Hayami & Kase, 1993). The scarcity of data on the biology of *Kelliella* and in particular the fact that specimens have been observed in organic-rich, or even reducing, environments warrant further investigations of this group.

SUPPLEMENTARY MATERIAL

Supplementary material is available at *Journal of Molluscan Studies* online.

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