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## The genus *Kelliella* (Bivalvia) in the Atlantic Ocean

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### ABSTRACT

*Kelliella* M. Sars, 1870 is a genus of small epibenthic bivalves inhabiting muddy bottoms of the outer shelf and slope worldwide, commonly in habitats that are oxygen-poor or enriched in organic carbon. Currently, there are five accepted species of *Kelliella* with an Atlantic type locality, and six more Atlantic species, including *Vesicomya atlantica* (Smith, 1885), the type species of *Vesicomya* Dall, 1886, were at some time placed in *Kelliella*. In this work, we revise the genus *Kelliella* from the North Atlantic waters, based on large amounts of new material from both sides, and describe a new species from Martinique (*Kelliella madininae* n. sp.). We here propose, after revision of the shell morphology, the synonymy of *K. biscayensis* Allen, 2001 with *K. miliaris* (Philippi, 1844), and consider a single West European and Mediterranean species of *Kelliella*. The fossil “*Kelliella*” *barbara* is also excluded from the genus *Kelliella* and reallocated as *Coralliophaga barbara* (Studencka, 1987) n. comb. In the Atlantic margin of America, we consider that *Diplodonta pilula* Dall, 1881 remains a *nomen dubium*. The type material of *K. concentrica* Allen, 2001 is figured, and this species considered a member of the Vesicomyninae. The new Caribbean species, *K. madininae*, resemble *K. brasuca* Passos, Machado & Fantinatti, 2017 from southeastern Brazil. We recorded new localities for *Kelliella goesi* Odhner, 1960, so far known only from its original description. Diagnostic characters discriminating *Vesicomya* from *Kelliella*, stated by Krylova *et al.* (2018), *Journal of Molluscan Studies*, 84: 69–91, are discussed, and we consider the hinge architecture as the most robust.

### INTRODUCTION

*Kelliella* M. Sars, 1870 is a genus of small epibenthic bivalves inhabiting muddy bottoms of the outer shelf and slope worldwide, commonly in habitats that are oxygen-poor or enriched in organic carbon. Currently, there are five accepted species of *Kelliella* with an Atlantic type locality (MolluscaBase Eds, 2023), by chronological order: *Kelliella miliaris* (Philippi, 1844) from Pleistocene of Sicily, but still living along the European margin; *K. goesi* Odhner, 1960 from the Lesser Antilles; *K. biscayensis* Allen, 2001 from off W. Ireland; *K. concentrica* Allen, 2001 from deep water off New England; and *K. brasuca* Passos, Machado & Fantinatti, 2017 from Brazil. In addition, there is a fossil *Kelliella barbara* Studencka, 1987 from the Miocene of Poland. Six more Atlantic species, including *Vesicomya atlantica* (Smith, 1885), the type species of *Vesicomya* Dall, 1886, were at some time placed in *Kelliella* but are currently placed in *Vesicomya* or other vesicomimid genera.

Clausen (1958) made a thorough morphological, histological and biological study of *Kelliella miliaris*, indicating the presence of a comparatively thick byssus thread, extending from the byssus duct to a network of short byssus threads able to maintain the specimens hanging from the water surface. Clausen also noted that the species is able to move on the sediment by the aid of an elongated and powerful foot, but he never observed it burrowing, nor to attempt to do so. According to Krylova *et al.* (2018), reduction of body sizes in both *Kelliella* and *Vesicomya* probably resulted in significant morphological convergences, and this in turn limits the value of many morphological characters for systematics.

Due to the morphological resemblance between *Kelliella miliaris* and *Vesicomya atlantica*, there is an ongoing debate regarding whether the families Kelliellidae and Vesicomimidae should be considered as synonyms (Knudsen, 1970; Allen, 2001; Huber, 2010) with priority to the former because Kelliellidae P. Fischer, 1987 is earlier than Vesicomimidae Dall & Simpson, 1901, or whether *Kelliella* should

constitute a separate monotypic family Kelliellidae (Krylova *et al.*, 2018). According to their molecular data, the genera *Vesicomya* and *Kelliella* are clearly distinct and *Kelliella* is only distantly related to the Vesicomidae. Results of their morphological analysis support the molecular inferences, and consequently, Kelliellidae must be considered sister to but distinct from Vesicomidae.

In this work, we will revise the genus *Kelliella* from the Atlantic Ocean, based on large amounts of new material from both sides of the North Atlantic (including the Mediterranean and Caribbean seas), and summarize the characters that diagnose *Kelliella* and *Vesicomya* s.s. in the light of this new material.

## MATERIAL AND METHODS

We examined specimens of *Kelliella* mostly from the collections of Muséum National d'Histoire Naturelle (MNHN), Paris. Eastern Atlantic material is from Norway, the western European margin, the Ibero-Moroccan Gulf; Mediterranean material is from the Alboran Sea and the Gulf of Lion, in a depth range 100–500 m and also a sample from the Last Glacial Maximum deposit in the Alboran Sea. Western Atlantic material proceeds from the MNHN expeditions Karubenthos (2–30 May 2012, chief scientist Philippe Bouchet) around Guadeloupe from shore to 258 m depth, Madibenthos (5 September–11 October 2016, chief scientist Philippe Bouchet) around Martinique from shore to 100 m depth and Proteus Guyane (30 November–4 December 2017) off French Guyana in the depth range 75–155 m. The material examined is detailed in [Supplementary Material Table S1](#) and summarized under each species heading. In addition to this, we re-examined the material of *Vesicomya atlantica* listed in [Cosel & Salas \(2001\)](#), and enquired about type material housed in the Natural History Museum, London, Museum of Comparative Zoology (MCZ), Harvard, and National Museum of Natural History (NMNH), Smithsonian Institution, Washington, DC.

Illustrations were prepared mostly using a JEOL SM 6490LV scanning electron microscope (SEM) at the University of Málaga. Specimens of *V. atlantica* and *Kelliella miliaris* (one each) were critical-point dried after opening the valves and removing one mantle lobe in order to observe the morphology of soft parts. Shells were cleaned by soaking for *c.* 15 min in a 10% aqueous solution of sodium lauryl sulphate (a pH-neutral detergent), then mildly sonicated in water, dried, mounted on conductive copper tape and coated for SEM observation. Shells were measured using the calibrated scale of the SEM, but this was cross-checked with measuring the whole specimen under a stereomicroscope equipped with an ocular micrometer. The length of the hinge was measured from the anterior edge of cardinal 2a to the posterior edge of cardinal 4 on left valves, and from the anterior edge of cardinal 1 to the posterior edge of cardinal 3b (see [Fig. 1](#)) on right valves.

## RESULTS

### SYSTEMATIC DESCRIPTIONS

#### Family KELLIPELLIDAE P. Fischer, 1887

#### Genus *Kelliella* M. Sars, 1870

*Kelliella abyssicola* M. Sars, 1870, the type species of the genus by monotypy, has formally been introduced as “n. gen., n. sp.” and therefore is a self-standing taxon with a type locality in Norway, regardless of the possibility that the choice of the name may have been influenced by *K. abyssicola* Forbes, 1844. Forbes's *K. abyssicola* was known to G. O. Sars (1878), but he followed [Jeffreys \(1870\)](#) in considering that it could fit just as well with the thyasirid *Axinus ferruginosus* (Forbes, 1844) as with *Kelliella*. He, however, disagreed with [Jeffreys'](#) view that *Kelliella* was the juvenile stage of the glossid

*Isocardia cor* (Linnaeus, 1758). [Janssen & Krylova \(2012: 91\)](#) discussed the use of the names *miliaris* vs *abyssicola* for the type species of *Kelliella* and figured a topotype of *Venus miliaris* Philippi, 1844 from the Pleistocene of Ficarazzi (Sicily).

Species once placed in *Kelliella* ([Knudsen, 1970](#); [Allen, 2001](#); [Huber, 2010](#)) but now placed ([Krylova & Sahling, 2010](#); [Krylova \*et al.\*, 2018](#)) in *Vesicomya* include *V. abyssicola* ([Allen, 2001](#)) from deep water off Surinam [primary homonym of *K. abyssicola* M. Sars, 1870 and secondary homonym of *K. abyssicola* (Forbes, 1844)], *V. adamsii* (Smith, 1885) from off Sierra Leone, *V. albida* (Dall, 1890) from off Brazil and *V. atlantica* (Smith, 1885) from off the Azores [type species of *Vesicomya*; synonym *K. nitida* Verrill, 1885]. *Kelliella elongata* [Allen, 2001](#) from off Angola and *K. tenina* [Allen, 2001](#) from off Namibia are currently placed in the genus *Isorropodon* [Sturany, 1896](#) ([Cosel & Salas, 2001](#); [Rodrigues \*et al.\*, 2012](#)). Finally, *Diplodontia pilula* [Dall, 1881](#), of uncertain generic placement, was placed in *Kelliella* by [Huber \(2010\)](#) and could belong to *Kelliella* or *Vesicomya*

#### *Kelliella miliaris* (Philippi, 1844)

([Figs 1–8](#))

*Venus miliaris* Philippi, 1844 [April]: 36, pl. 14, fig. 15.

*Kellia abyssicola* Forbes, 1844 [June]: 192 (in part).

*Kelliella abyssicola* M. Sars, 1870: 201–209, pl. 11, fig. 11–15, pl. 13.

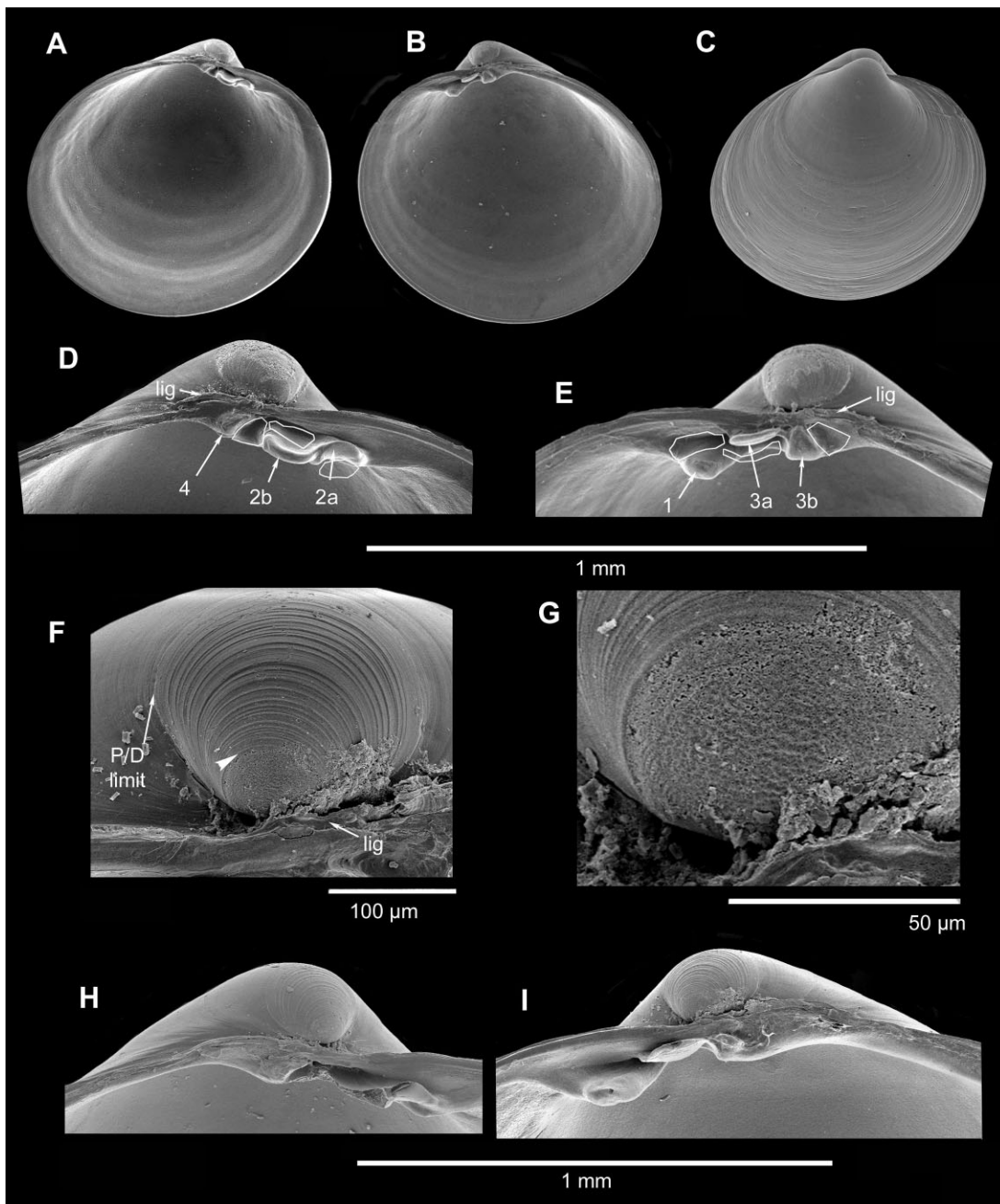
*Kelliella miliaris* (Philippi, 1844)—G.O. Sars, 1878: 65. [Allen, 2001](#): 201–203, figs 1, 2.

*Kelliella biscayensis* [Allen, 2001](#): 218–221, figs 24–26, new synonym.

*Type material*: *Venus miliaris* was reported as lost ([Janssen & Krylova, 2012](#)) but [Odhner \(1960\)](#) reported “co-types” from the Museum of Geology, Palermo, these having been presented to SMNH, Stockholm. A topotype was illustrated by [Janssen & Krylova, 2012](#). *Kelliella abyssicola* Forbes, 1844: reported as lost ([Janssen & Krylova, 2012](#)) but examined by [Jeffreys \(1870\)](#), who concluded that syntypes belonged in part to the thyasirid *Axinus ferruginosus* [now *Mendicula ferruginosa* (Forbes, 1844)] lacking their oxide crust and in part to the present species.

*Kelliella biscayensis*, holotype from off W. Ireland, 51°54.7', 12°27.3'W; 1015 m; 18 August 1972; R/V “Chain” cruise 106, sta. 314; NHMUK 1998177/1–3. The NHMUK catalogue (<https://data.nhm.ac.uk/dataset/collection-specimens/resource/05ff2255-c38a-40c9-b657-4ccb55ab2feb/record/2755676/1695254400000>) mentions a “holotype and two paratypes” and the ledger reads “the three specimens were in the same tube when presented”. However, [Allen \(2001\)](#) only designated a holotype. The other two specimens have no status as types, but there is no clue to which (of two complete with soft parts and one disarticulated paired shell) was intended as the holotype (all three specimens are illustrated in [Passos \*et al.\*, 2017](#), fig. 5). A large lot (see below) from the same haul as the holotype is held at MCZ, Harvard, Malacology, and was used in this work.

*Summary of other material examined* (see [Supplementary Material Table S1](#) for details): W. Norway, 52 specimens and 2 valves (300–500 m). Off W. and S.W. Ireland, *c.* 1,500 specimens (identified by J. Allen as *K. biscayensis*) from R/V “Chain” cruise 106, sta. 314 (1,015 m), MCZ 357515 and 357532; 244 specimens and 48 valves (identified by J. Allen as *K. miliaris*) from R/V “Thalassa” 1973 cruise (480–1,175 m); 18 specimens and 137 valves from R/V “Thalassa” Procet 1 (207–1,085 m). W. France, 16 specimens and 9 valves (identified by J. Allen as *K. miliaris*) from Thalassa 1973 cruise (330–1,870 m); *c.* 1,500 specimens and 40 valves from various sources (164–1,240 m). N. Spain, 645 specimens from R/V “Thalassa” 1971 and from Lagardère 1967–1971 (463–1,080 m). W. Portugal, 23 specimens from R/V “Thalassa” 1972 (320–820 m). S. Portugal, 148 specimens and 4 valves from R/V “Cryos” Balgim 1984 (452–1,523 m). S.W. Spain, 264 specimens from R/V “Cryos” Balgim 1984 (250–398 m) and other sources. W. Morocco, 20 specimens and 67 valves from R/V “Cryos” Balgim 1984



**Figure 1.** *Kelliella miliaris* (Philippi, 1844) from Korsfjorden, off Bergen, Norway, 500 m. **A, B.** Inside of left and right valves (length 1.75 mm). **C.** External view from the right of another specimen (length 1.60 mm). **D, E.** Hinge of the specimen shown in **A** and **B**, with a white outline indicating the insertion of the teeth of the opposite valve. **F, G.** Prodissoconch (right valve) of another specimen, 2.3 mm in length. **G.** Detail of prodissoconch 1. **H, I.** Hinge (same specimen as **F** and **G**). 1, 2a, 2b, 3a, 3b, 4, cardinal teeth; lig, ligament; P/D limit, prodissoconch/dissoconch limit. The arrowhead points to the prodissoconch 1/prodissoconch 2 limit. Scale bars: **D, E, H, I** = 1 mm; **F** = 100 µm; **G** = 50 µm.

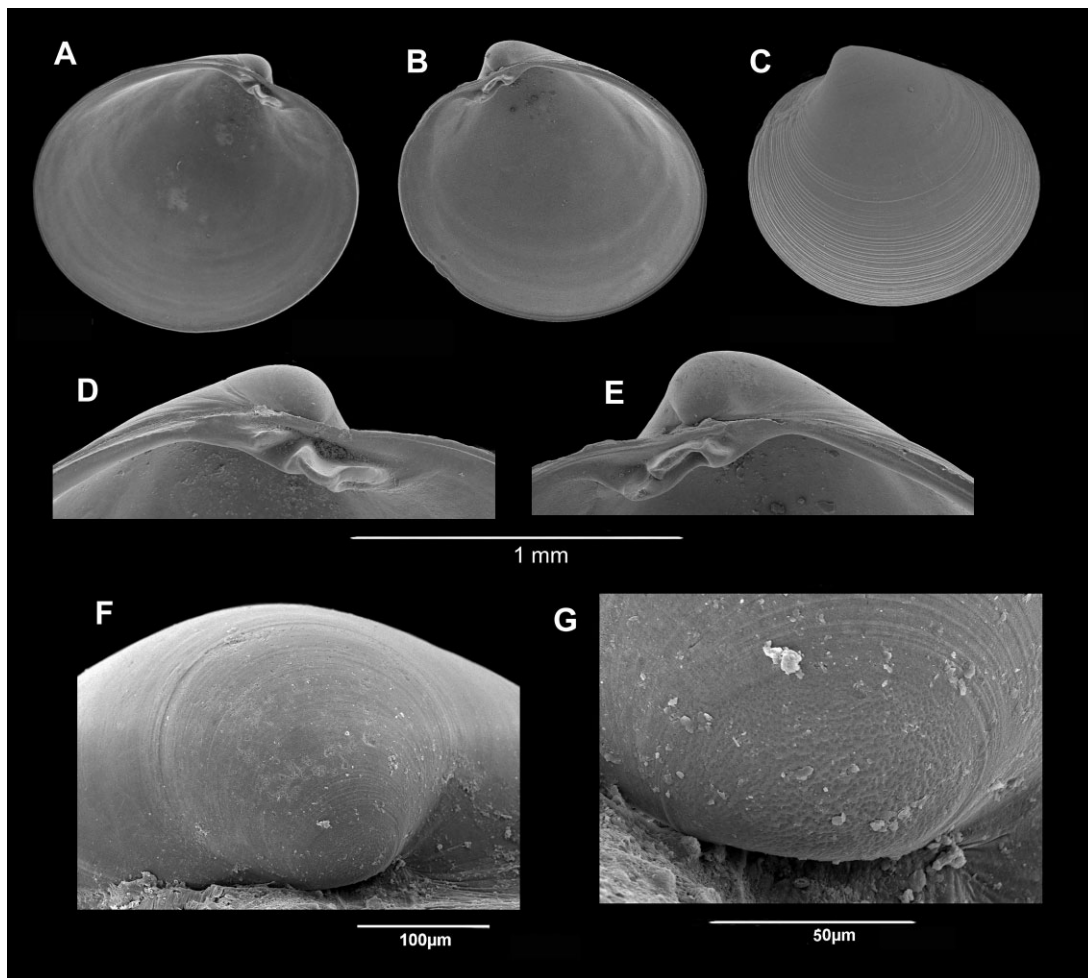
(155–1,222 m) and other sources. Spain, Alboran Sea, *c.* 1,700 specimens and 300 valves from various sources (97–998 m), 5 shells + *c.* 50 valves, subfossil. Mediterranean coast of France, 7 valves. Sicily, 2 shells. Greece, 4 valves.

**Description:** Shell minute (up to 2.5 mm in length but usually less than 1.6 mm), thin, translucent when fresh, inflated (length/width ratio 1.5–1.7), equivalve, not gaping. Outline rounded (length/height 1.05–1.11), slightly inequilateral, with slightly protruding, prosogyrous umbos situated at the anterior 1/3. Ventral margin uniformly rounded and continuous with anterior and posterior margins.

Lunule delimited anteriorly by a weak groove on each valve, starting at a short distance from the beginning of dissoconch. No escutcheon. Periostracum inconspicuous, colourless. Outer surface of the valves nearly smooth except for microscopic growth lines.

Prodissoconch 1 small (length *c.* 74–79 µm), ovate, with rugose surface; prodissoconch 2 (length *c.* 190–240 µm), rounded, with commarginal striae of variable intensity. Limits P1/P2 and P2/dissoconch clearly demarcated, as visible under SEM. Inner margins of valves smooth, with a narrow groove all along the inner shell margin of the right valve; and corresponding ridge on the left valve.





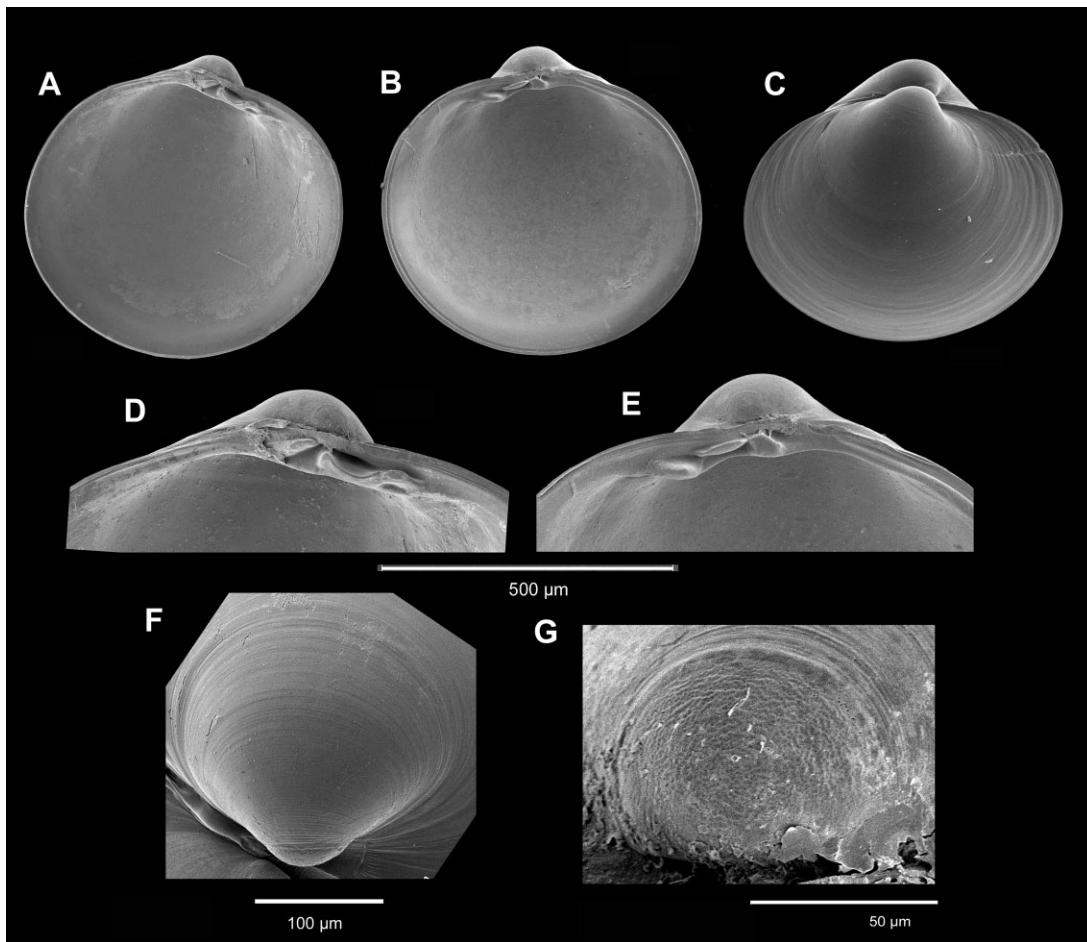
**Figure 2.** *Kelliella miliaris* (Philippi, 1844), fossil from the Last Glacial, Alboran Sea, off Oued Laou, 35°37.45'N, 04°55.8'W, 440 m depth, 664–666 cm down core (R/V Catherine Laurence “ALBOSED II-86”, core K10). **A.** Inside of a left valve (length 2.5 mm). **B.** Inside of a right valve (length 2.5 mm). **C.** External view of another left valve (length 2.4 mm). **D., E.** Hinge (same valves as **A** and **B**). **F.** Prodissoconch (same left valve as **D**). **G.** Detail of prodissoconch 1. Scale bars: **D, E** = 1 mm; **F** = 100 μm; **G** = 50 μm.

Hinge plates narrow, short (ratio length of hinge/total length: 0.16–0.21), with  $c$  3/5 of its extension anterior to the umbos. Hinge with three cardinals in each valve. Left valve with anterior cardinals 2a and 2b concatenated, nearly fused, narrow and elongate; the anteriormost 2a arched for fitting ventrally the cardinal 1 of right valve; cardinal 2b curved with a dorsal concavity to accommodate cardinal 3a of the right valve; posterior cardinal 4 small, pointing downwards and backwards, anteriorly separated from 2b by a broad pit accommodating cardinal 3b of the right valve, and posteriorly with a ridge merging into the hinge plate margin. Right valve with anterior cardinal tooth 1 short and bulging, situated more ventrally than the other teeth; cardinal 3a narrow and elongate, starting just beneath the umbo and directed forward, nearly horizontal; cardinal 3b short, directed downwards and therefore at an angle of about 90° to 3a. No lateral teeth. Ligament external, short, inserted at the edge of the hinge plates just behind the umbo. Adductor muscles scars indistinct, small, subequal in size.

Mantle margins forming exhalant and inhalant apertures within the posterior half. Exhalant aperture situated posteriorly, just below the horizontal midline of the shell, delimited by a short fusion of the mantle lobes and provided with an extremely thin, extensible sheath. Inhalant aperture broad and rounded, not separated from the rest of the pedal gape but neatly delimited in life by the mantle lobes abutting against each other. Minute tentacles (two to seven

posterior to exhalant, one on each lobe between exhalant and inhalant and four to six anterior to inhalant) surrounding these apertures. Foot well developed, with the anterior part able to extend to a distance surpassing the shell length, whereas the posterior part forms a distinct heel.

*Observed variability:* The umbonal area is more or less protruding from the rounded outline of the valves in lateral view; some specimens from Capbreton canyon (Fig. 3A, B) and Malaga Bay have the least protruding umbos. Thickness of cardinal plate and correlative of the teeth varies including among specimens from the same sample (compare Fig. 1D, E and H, I); some of the specimens from relatively shallow water in the Bay of Malaga were unusually thick (Fig. 4A, B, D, E). Prodissoconch 1 is quite constant in size (74–79 μm) and sculpture, but there is some variation in prodissoconch 2; commarginal lines are more conspicuous on the specimens from Bergen, and diameter is larger in the lot from off W. Ireland corresponding to *K. biscayensis* (240 μm vs 190–210 μm elsewhere). Shape of cardinal 3b varies from a neatly protruding, triangular tooth (e.g. Fig. 1E) to a rather shapeless structure more or less fused anteriorly to 3a (e.g. Fig. 1I). Specimens from Bergen and fossils from the last Glacial reach a slightly larger maximum size,  $c$  2.6 mm, whereas in the Bay of Biscay, the Iberian margin and the Mediterranean, most specimens grow to about 1.5 mm length and none reach 2 mm.



**Figure 3.** *Kelliella miliaris* (Philippi, 1844) from Capbreton canyon, Bay of Biscay, 43°35.9'N, 1°47.8'W, 761 m (SEDICAN TS26 sta. E, leg. Sorbe). **A, B.** Inside of left and right valves (length 1.1 mm). **C.** External view from the right of another specimen (length 1.1 mm). **D, E.** Hinge (same specimen as A and B). **F.** Prodossoconch (left valve) of another specimen, 1.1 mm in length. **G.** Detail of prodossoconch 1 (same right valve as **E**). Scale bars: **D, E** = 1 mm; **F** = 100  $\mu$ m; **G** = 50  $\mu$ m.

The number of tentacles surrounding the siphonal apertures is variable. Dissection of a large specimen (2.5 mm) from Bergen showed clusters of 7 tentacles posterior to the exhalant aperture and 6 anterior to the inhalant, still with only one pair at the divide between apertures. A specimen 1.4 mm long from the type locality of *K. biscayensis* (Fig. 7A) and a specimen 1.5 mm long from Capbreton canyon (Fig. 8A), critical-point dried and examined under SEM, also had three pairs of tentacles anteriorly and one pair on the divide. The specimens examined alive from Bay of Malaga with 1–1.2 mm length had only one pair of tentacles posterior to the exhalant aperture, one pair on the divide and two pairs on the ventral margin anterior to the inhalant aperture.

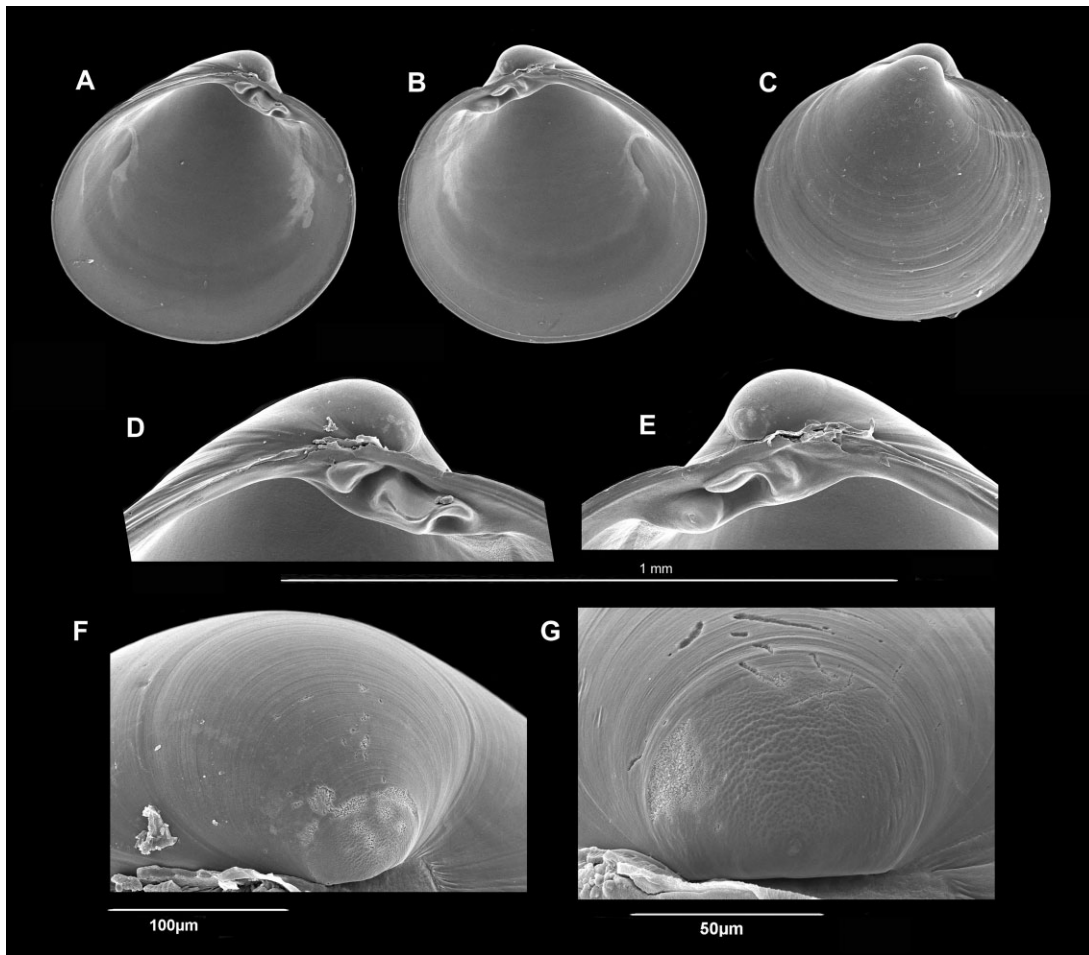
**Distribution:** European and N.W. African continental margin, in the Atlantic from Norway (70°N, R/V “Jean Charcot” NORBI CP11) to Morocco (33.7°N, R/V Cryos “Balgim” DR81), but not reported (Seaward, 1990) in the North Sea outside Norwegian waters; also absent in the Baltic Sea and the English Channel. In the Mediterranean Sea, from the Alboran Sea to the Eastern basin, the Aegean Sea and Marmara Sea (Öztürk *et al.*, 2014) but not reported from the Black Sea. Despite an intensive sampling effort in the appropriate depth interval, no specimen of *Kelliella* was found in the South Azorean Seamount Chain (69 dredge hauls and 16 beam trawl operations from 280 to 1,000 m; Caballero-Herrera *et al.*, 2023) in the Lusitanian seamounts (Beck *et al.*, 2006) or on Galicia Bank (51 samples between 615 and 1,768 m, Gofas *et al.*, 2021). There is a

report from Madeira (Segers *et al.*, 2009) based on a single valve from Funchal Bay (no further data) in the Frank Swinnen collection, which we consider insufficient to indicate the presence of the species. Conversely, there is an isolated record from off the Western Sahara (R/V “Meteor” cruise 36, sta. 97, 25.5°N, 409–417 m, Krylova *et al.*, 2018) and Mauritania (R/V “Meteor” cruise 60 SUBTROP EX 82, sta. KG960 and KG961, 17.3°N, 87–88 m, L. Hoffman, personal communication) but the latter corresponds to box cores and may not necessarily represent a Recent occurrence.

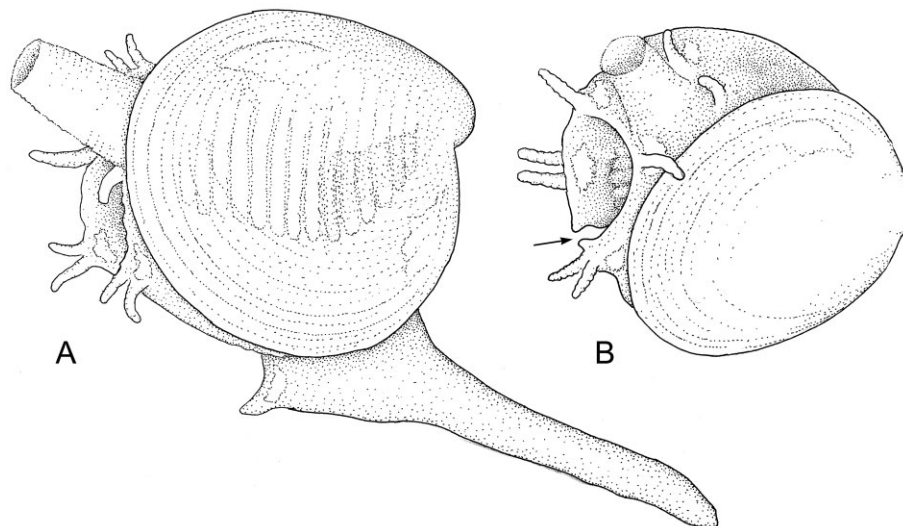
Depth range 100 m (Clausen, 1968) to 500 m (present material) in Norway; 200–1,400 m off Ireland and Brittany (present material); 140–1,240 m in Bay of Biscay; 250–1,520 m off W. Iberian Peninsula; 91–998 m in the Alboran Sea.

**Remarks:** The well differentiated prodossoconch 1 and prodossoconch 2 indicate planktotrophic development. Among hundreds of live-taken specimens observed with the animal visible by transparency, brooding of eggs, embryos or juveniles was never observed.

In our material, despite some variability described above, we could never distinguish more than one morphological species at any particular locality. This observation also holds for *K. biscayensis* (Allen, 2001). Despite its name, this nominal species has a type locality off Western Ireland in 1,015 m water depth, but was also recorded in the original description from Bay of Biscay within the Capbreton canyon (R/V “Sarsia”, sta. S40, 860 m and S56, 641 m). Allen (2001) reported *K. miliaris* living only from Norway

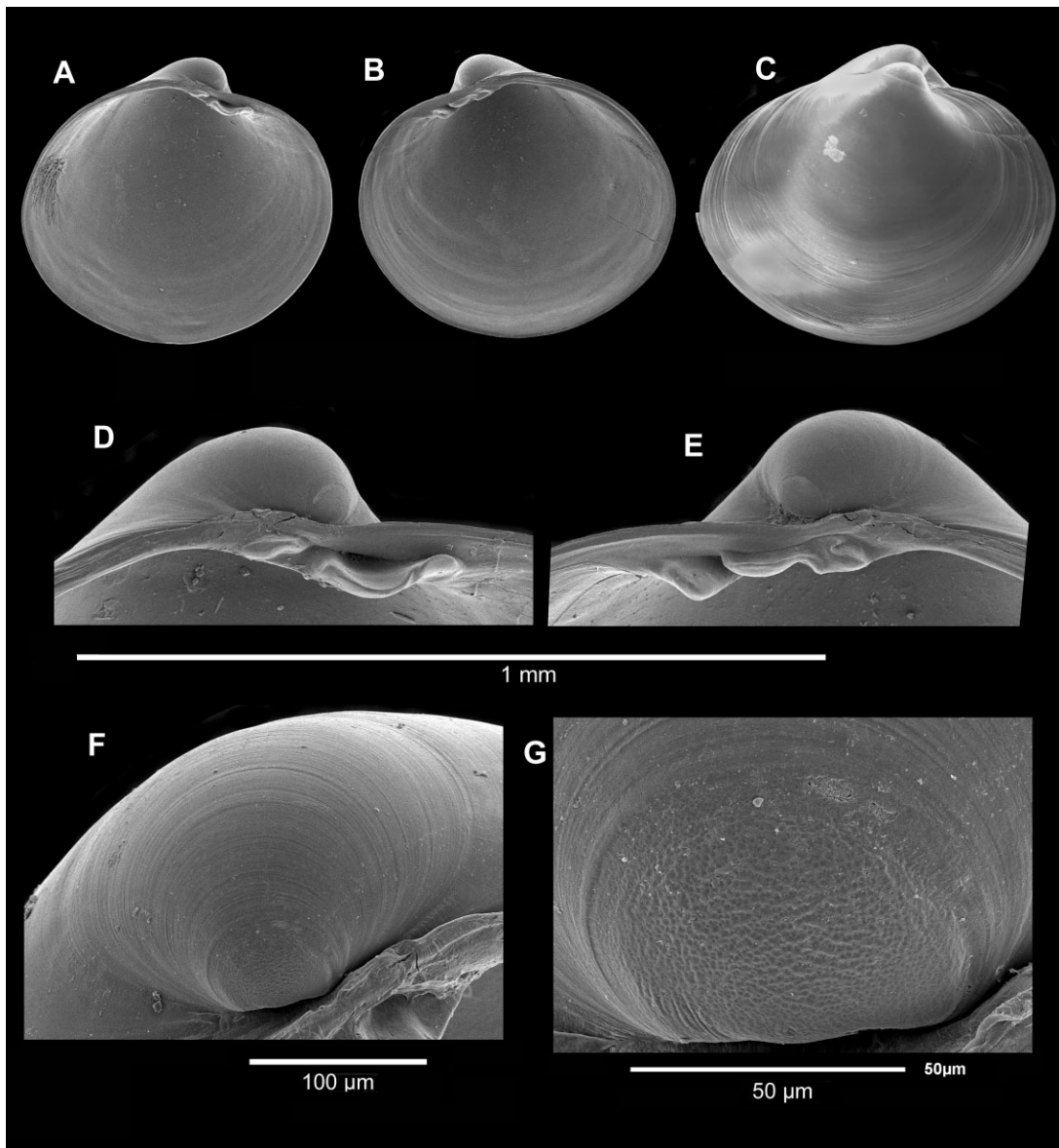


**Figure 4.** *Kelliella miliaris* (Philippi, 1844) from the Alboran Sea, Bay of Málaga, 36°36.83'N, 04°21.70'W, 94–124 m (R/V “Isla de Alborán” sta. BV68, leg. Gofas). **A, B.** Inside of left and right valves (length 1.1 mm). **C.** External view from the right of another specimen (length 1.0 mm). **D, E.** Hinge (same specimen as **A** and **B**). **F.** Prodissoconch (left valve, same as **D**). **G.** Detail of prodissoconch 1 of another left valve, 1.2 mm in length. Scale bars: **D, E** = 1 mm; **F** = 100  $\mu$ m; **G** = 50  $\mu$ m.



**Figure 5.** *Kelliella miliaris* (Philippi, 1844). Living specimen from the Alboran Sea (same sample as shown in Fig 4). **A.** View from right side, with completely extended foot and siphon. **B.** Postero-ventral view to show cleft of inhalant aperture (arrow). Diameter of shell *c.* 1 mm.





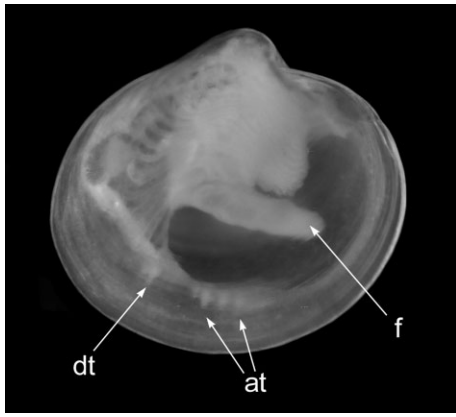
**Figure 6.** *Kelliella miliaris* (Philippi, 1844), specimen identified by J. Allen as *K. biscayensis*, from the same sample as the holotype, off W. Ireland, 51°54.7', 12°27.3'W; 1015 m (R/V “Chain” cruise 106, sta. 314; MCZ 357532). **A, B.** Inside of left and right valves (length 1.40 mm). **C.** External view from the right of another specimen (length 1.60 mm). **D, E.** Hinge (same specimen as **A** and **B**). **F.** Prodissoconch (right valve) of another specimen, 1.65 mm in length. **G.** Detail of prodissoconch 1. Scale bars: **D, E** = 1 mm; **F** = 100 µm; **G** = 50 µm.

and northern Scotland and as a fossil in its Mediterranean type locality, therefore holding all the West European occurrences as belonging to the new species. Based on this, some authors (e.g. [Martinez et al., 2007](#); [Galparsoro et al., 2020](#); [Rodríguez et al., 2021](#)) started to use the name *biscayensis* for material from the Bay of Biscay, always reporting on a single species in the local population.

The variation in the number of tentacles surrounding the siphonal apertures calls for some comments. [Clausen \(1958: 148\)](#) noted that “the number increases with the size of the bivalve” and could reach seven posteriorly and six anteriorly ([Clausen, 1958: fig. 12](#)). [Krylova & Sahling \(2010\)](#), also from material from the Norwegian Sea, noted 3 tentacles dorsally above the exhalant opening, 2 pairs of tentacles between openings, and 2–3 pairs anteriorly to the inhalant aperture. [Allen \(2001\)](#) noted for *K. biscayensis*, 4 pairs of tentacles anteriorly, 2 pairs between apertures (these numbers may be exaggerated, see [Figure 7](#) where the fourth apparent tentacle on the anterior side belongs to the opposite lobe) and 7 posteriorly

even though the specimen on his fig. 26 is only 1.3 mm long. It is therefore the shallow water specimens from Bay of Malaga ([Fig. 5](#)), with very few tentacles, which deviate most from the pattern of the Norwegian specimens.

No anatomical nor genetic characters were invoked in the species comparisons between *K. biscayensis* and *K. miliaris*. In the words of [Allen \(2001\)](#) “*K. biscayensis* most closely resembles *K. miliaris*, *K. nitida* and *K. [now Vesicomya] atlantica* but is distinguished from them by the paucity of co-marginal striation, by the more elongate somewhat lozenge-shaped lunule and by the unusually short and characteristic hinge plate”. The first stated character of external sculpture is relevant to *K. nitida* and *Vesicomya atlantica* only, therefore the difference from *K. miliaris* is based on essentially based on the shape of the lunule “more elongate somewhat lozenge-shaped” ([Allen, 2001: fig. 24B](#)), which we cannot see as being essentially different from that of Norwegian *K. miliaris* ([Fig. 1C](#)), and on the length of the hinge plate ([Fig. 6A–D](#)), which is similar to



**Figure 7.** *Kelliella miliaris* (Philippi, 1844), a whole ethanol-preserved specimen (MCZ 357532, length 1.4 mm) identified by J. Allen as *K. biscayensis*; same specimen as shown in Fig. 6A, B prior to preparation for SEM. Foot (f) and tentacles surrounding the siphonal openings are visible by transparency (at, tentacles anterior to inhalant opening; dt, tentacles on the divide between inhalant and exhalant aperture).

that of other populations examined for *K. miliaris*. So far, there were no data on the prodissoconch, leaving open the possibility that a sibling species to *K. miliaris* with non-planktotrophic development could exist. The type specimens in the NHMUK were not available for SEM study but the large lot at MCZ, Harvard, from the same dredge haul as the holotype, could be examined and we observed a prodissoconch (Fig. 6F, G) with a differentiated prodissoconch 1 and prodissoconch 2, denoting planktotrophic development like the other samples identified as *K. miliaris*. Consequently, we here propose the synonymy of *K. biscayensis* with *K. miliaris*, and consider a single West European and Mediterranean species of *Kelliella*. In line with this, Allen (2008) did cite *K. miliaris* from the northern Bay of Biscay (R/V “Sarsia” sta. S29, 119 m, 47°40.0’N, 05°00.0’W), and a large lot returned from him to MNHN in 2005 contained 261 specimens and 77 valves from 27 stations collected off W. Ireland to W. Brittany in a depth range of 330–1870 m (R/V “Thalassa”) in 1973, all identified as *K. miliaris* and none as *K. biscayensis*.

### *Kelliella madininae* new species

(Fig. 9)

**Type material:** Holotype, 1 live-taken specimen from Martinique, off Macouba, 14°55’N, 61°08.9’W, 80 m, 27 September 2016, Madibenthos AD275, MNHN-IM-2000–29030. Paratypes, 25 live-taken specimens, 10 shells and 30 valves, same data as for holotype, MNHN-IM-2000–29031.

**ZooBank registration:** urn:lsid:zoobank.org:act:D15469DC-8395-424A-99A4-741753F43F4C

**Etymology:** From Madinina, Amerindian name of the island of Martinique (after which the Madibenthos expedition was named).

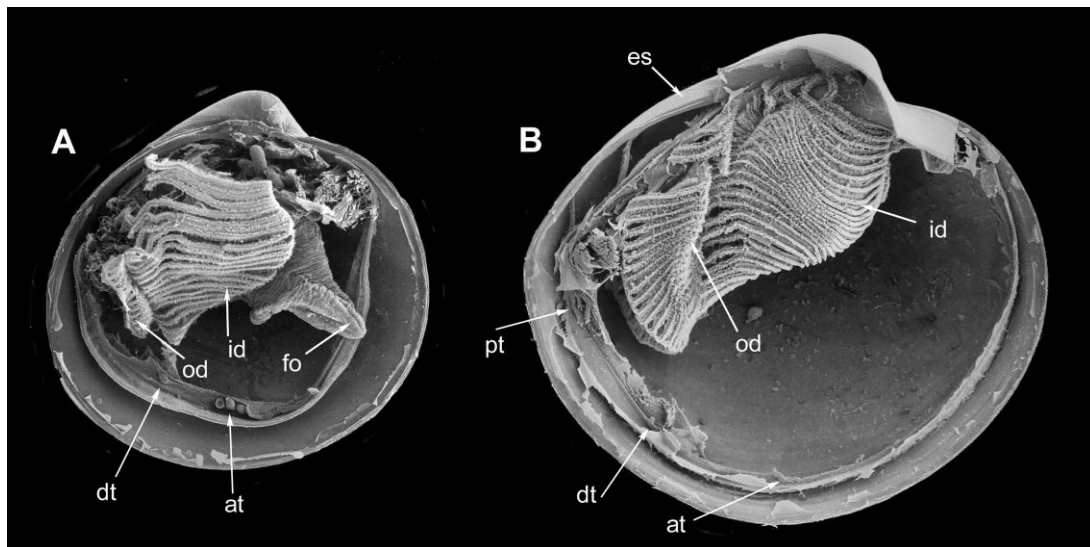
**Summary of other material examined** (see Supplementary Material Table S1 for details): Martinique, 84 specimens and 106 valves or shells from Madibenthos (44–80 m). Guadeloupe, 16 specimens and 37 valves or shells from Karubenthos 1 and 2 (49–150 m).

**Description:** Shell minute (up to 2.9 mm in length), moderately thin, opaque white to yellowish in colour, moderately inflated (length/width ratio: 1.4–1.5), equivalve, not gaping. Outline rounded (length/height 1.10), slightly inequilateral, with small, protruding, prosogyrous umbos situated at the anterior 1/3. Ventral margin uniformly rounded and continuous with anterior and posterior margins.

Lunule delimited anteriorly by a groove on each valve, starting at a short distance from the beginning of dissoconch. No distinct escutcheon, but an inconspicuous ridge running very close to the dorsal edge on the right valve only (Fig. 9E). Periostracum inconspicuous, colourless. Outer surface of the valves with distinct commarginal grooves spaced *c.* 10  $\mu$ m, and minute pustules randomly distributed, less than 1  $\mu$ m in size (Fig. 9K).

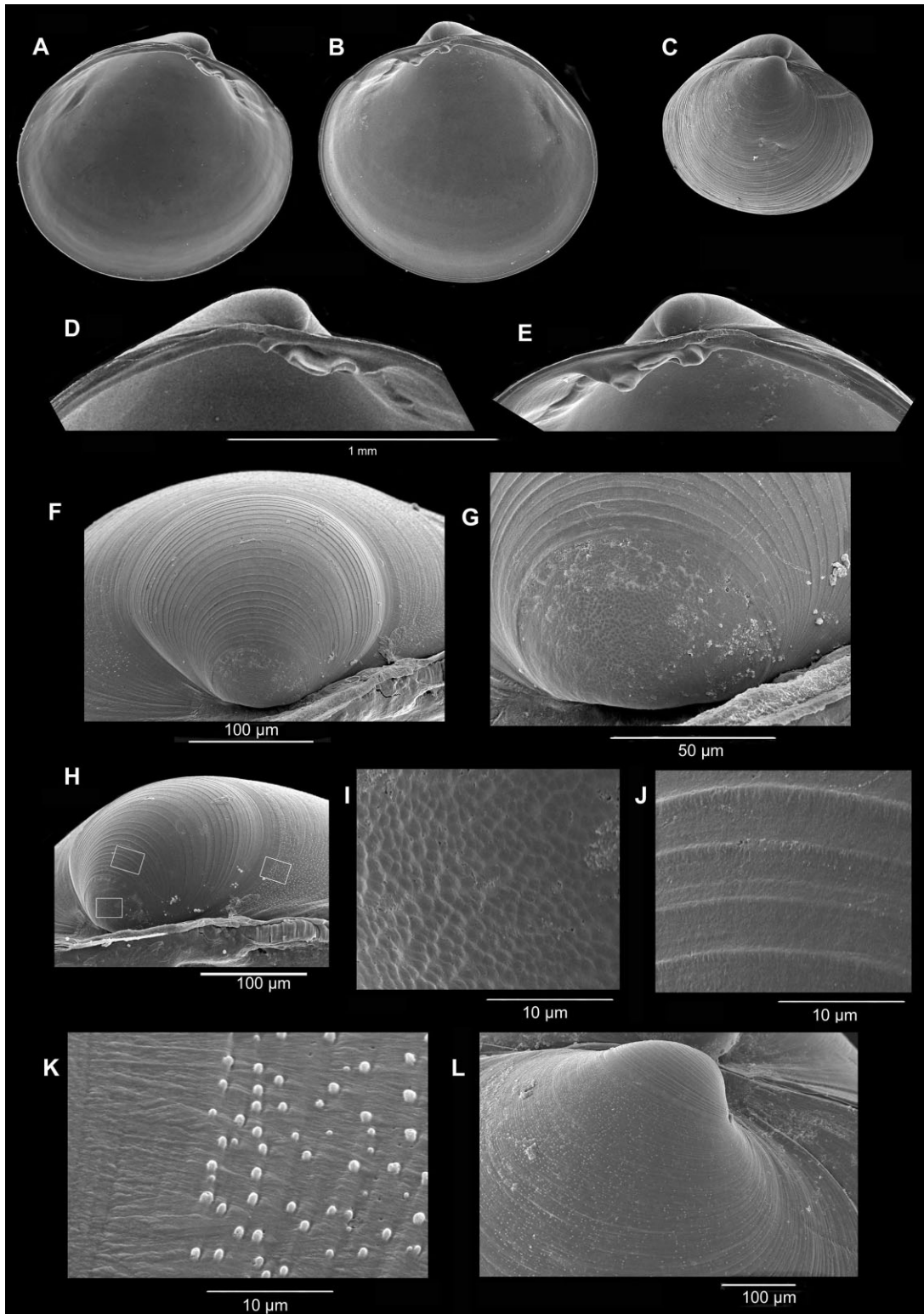
Prodissoconch 1 small (length *c.* 79  $\mu$ m), ovate, with distinctly pitted surface; prodossoconch 2 (length *c.* 200  $\mu$ m), rounded, with commarginal striae of variable intensity. Limits P1/P2 and P2/dissoconch clearly demarcated, as visible under SEM. Inner margins of valves smooth, with a narrow groove all along the inner shell margin of the right valve; and corresponding ridge on the left valve.

Hinge plates narrow, short (ratio length of hinge/total length: 0.15–0.17), with *c.* 3/5 of its extension anterior to the umbos. Hinge

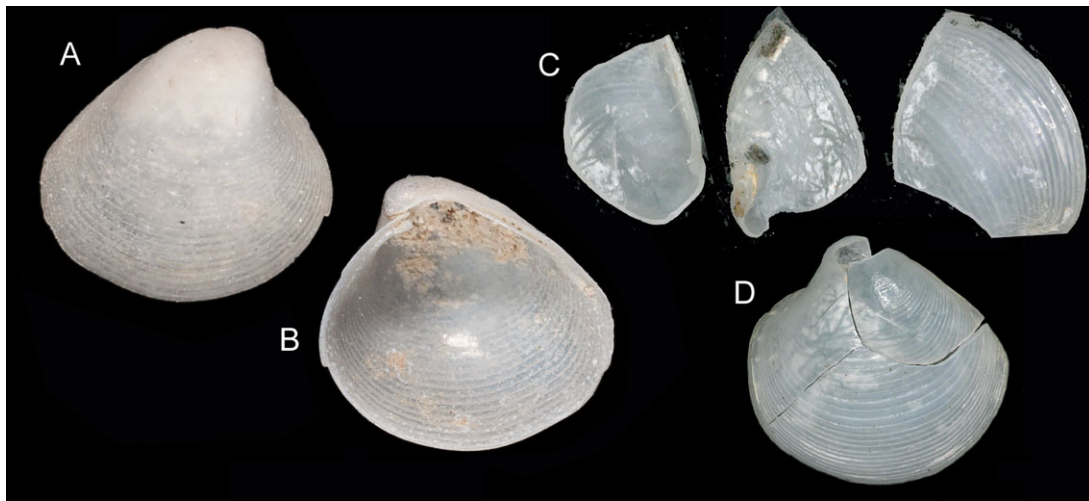


**Figure 8.** Critical-point dried specimens of *Kelliella* and *Vesicomya*, seen from right side, with right valve and mantle lobe removed. **A.** *Kelliella miliaris* (Philippi, 1844). Specimen from Capbreton canyon, 43°57.42’N, 02°05.16’W, 164 m, “Capbreton88” DE05 (length of valve 1.5 mm). **B.** *Vesicomya atlantica* (Smith, 1885). Specimen from W of São Miguel, Azores, 37°58’N, 26°07’W, 3215 m, “Biaçores” ChG171 (length of valve 2.6 mm). Abbreviations: fo, foot; id, inner demibranch; od, outer demibranch; es, escutcheon; at, tentacles anterior to inhalant opening; dt, tentacles on the divide between inhalant and exhalant aperture; pt, tentacles posterior to exhalant opening.





**Figure 9.** *Kelliella madininae* n. sp. from Martinique, 14°55'N, 61°08.9'W, 80 m (Madibenthos sta. AD275). **A**, **B**. Inside of left and right valves of the holotype (length 2.2 mm). **C**. External view from the right of a paratype (length 1.6 mm). **D**, **E**. Hinge of the holotype. **F**. Prodissoconch (right valve of the holotype). **G**. Detail of prodissoconch 1. **H**. Prodissoconch and early part of the dissoconch of the holotype (framed areas enlarged in **I**, **J** and **K**). **I**. Detail of microsculpture of prodissoconch 1. **J**. Detail of microsculpture of prodissoconch 2. **K**. Detail of early dissoconch showing micropustules. **L**. Prodissoconch and early part of dissoconch (same paratype as **C**). Scale bars: **D**, **E** = 1 mm; **F**, **H**, **L** = 100 μm; **G** = 50 μm; **I**, **J**, **K** = 10 μm.



**Figure 10.** Syntypes of *Diplodonta pilula* (Dall, 1881). **A, B.** Right valve (2.8 mm) from USA, West of Tortugas, 24°08'0''N, 82°51'0'' W, 339 fms (718 m), R/V Blake sta. 43, USNM 64,224, treated as “holotype” by Krylova *et al.* (2018). **C.** Fragmented left valve (inner view), same locality, MCZ: Mala: 7981. **D.** The same fragmented valve as **C** (outer view), reconstructed through image processing (c. 2.4 mm). Photo credits: **A, B,** NMNH, Smithsonian Institution (<http://www.nmnh.si.edu/>); **C, D,** Jennifer Trimble, MCZ, Harvard.

with three cardinals in each valve. Left valve with anterior cardinals 2a and 2b concatenated, nearly fused, narrow and elongate; the anteriormost 2a arched to fit ventrally to the right valve cardinal 1 of right valve; cardinal 2b curved with a dorsal concavity to accommodate cardinal 3a of the right valve; posterior cardinal 4 very small, pointing downwards and backwards, anteriorly separated from 2b by a broad pit accommodating cardinal 3b of the right valve, and posteriorly with a ridge merging into the hinge plate margin. Right valve with anterior cardinal tooth 1 short and bulging, situated more ventrally than the other teeth; cardinal 3a narrow and elongate, small, starting just beneath the umbo and directed forward, nearly horizontal; cardinal 3b short, directed downwards, therefore at an angle about 90° with 3a. No lateral teeth. Ligament external, short, inserted at the edge of the hinge plates just behind the umbo. Anterior adductor muscle scar small, well marked, bordered by a thickened rim; posterior adductor scar indistinct, similar in size to the anterior.

**Observed variability:** The material from off Martinique and Guadeloupe is very homogeneous. A few specimens reach 2.9 mm, but most are less than 2.5 mm in length.

**Distribution:** Caribbean Sea; so far known from around Martinique and Guadeloupe. A photograph of a specimen 2.9 mm in length from off Louisiana (28.061°N, 091.024°W, dredged in 57–65 m in coral rubble; García & Lee, 2010) was identified as *Vesicomya pilula* (Dall, 1881); we consider that it belongs to the present species and therefore we document its range to the northern Gulf of Mexico.

**Remarks:** The syntypes of *Diplodonta pilula* Dall, 1881 (Fig. 10) are definitely distinct from our specimens from Martinique and Guadeloupe, about twice as large, with a triangular outline and a more marked sculpture of commarginal ridges. Both valves are in poor condition: the best-preserved right valve lacks most of the hinge but the possible cardinal 1 remaining is elongate, more like *Vesicomya* (see Krylova *et al.*, 2018: fig. 4C) than like *Kelliella*. Unless better preserved material is collected near one of the type localities, *D. pilula* remains a *nomen dubium*.

*Kelliella brasuca* Passos, Machado & Fantinatti, 2017 is undoubtedly the most similar species but has more broadly spaced commarginal grooves (c. 40 on Passos *et al.*, 2017: fig. 2c vs c. 60 on a specimen of similar size in our Fig. 9C). The micropustules are widely spread out on the outer surface of the dissoconch, whereas

they are reported as restricted to the region near to the limit in the prodissoconch in *K. brasuca*. The most diagnostic character, however, is found in the hinge plate: in *K. brasuca*, it is much broader, forming a prominent crest-like plate anteriorly to the umbos (compare fig. 4b and g in Passos *et al.* with our Fig. 9D, E), and the cardinals terminate ventrally before reaching the edge of the hinge plate.

#### ***Kelliella brasuca* Passos, Machado & Fantinatti, 2017**

*Kelliella brasuca* Passos, Machado & Fantinatti, 2017: 207–219.

**Type material:** Holotype, 1 live-taken specimen from off Brazil, Rio de Janeiro State, 23°11'29''S, 41°0'50''W, 117 m; 21 February 2009, Habitats Project sta. HAB11 B-05 R2, Museum of Zoology Prof. Adão José Cardoso of the State University of Campinas, ZUEC-BIV 3237. Paratypes: State University of Campinas, Museum of Zoology of the University of São Paulo (MZSP) and in the National Museum of Rio de Janeiro (MNRJ), all from off Rio de Janeiro State in 39–147 m (see Passos *et al.*, 2017 for details).

**Distribution:** So far known only from a small stretch of the Brazilian continental shelf off Rio de Janeiro State.

**Remarks:** This species has been described in great detail by Passos *et al.*, (2017), to whom we refer. The tumidity (length/width ratio) is reported as being 1.11 by Passos *et al.*, but this value measured on their fig. 1b is 1.35.

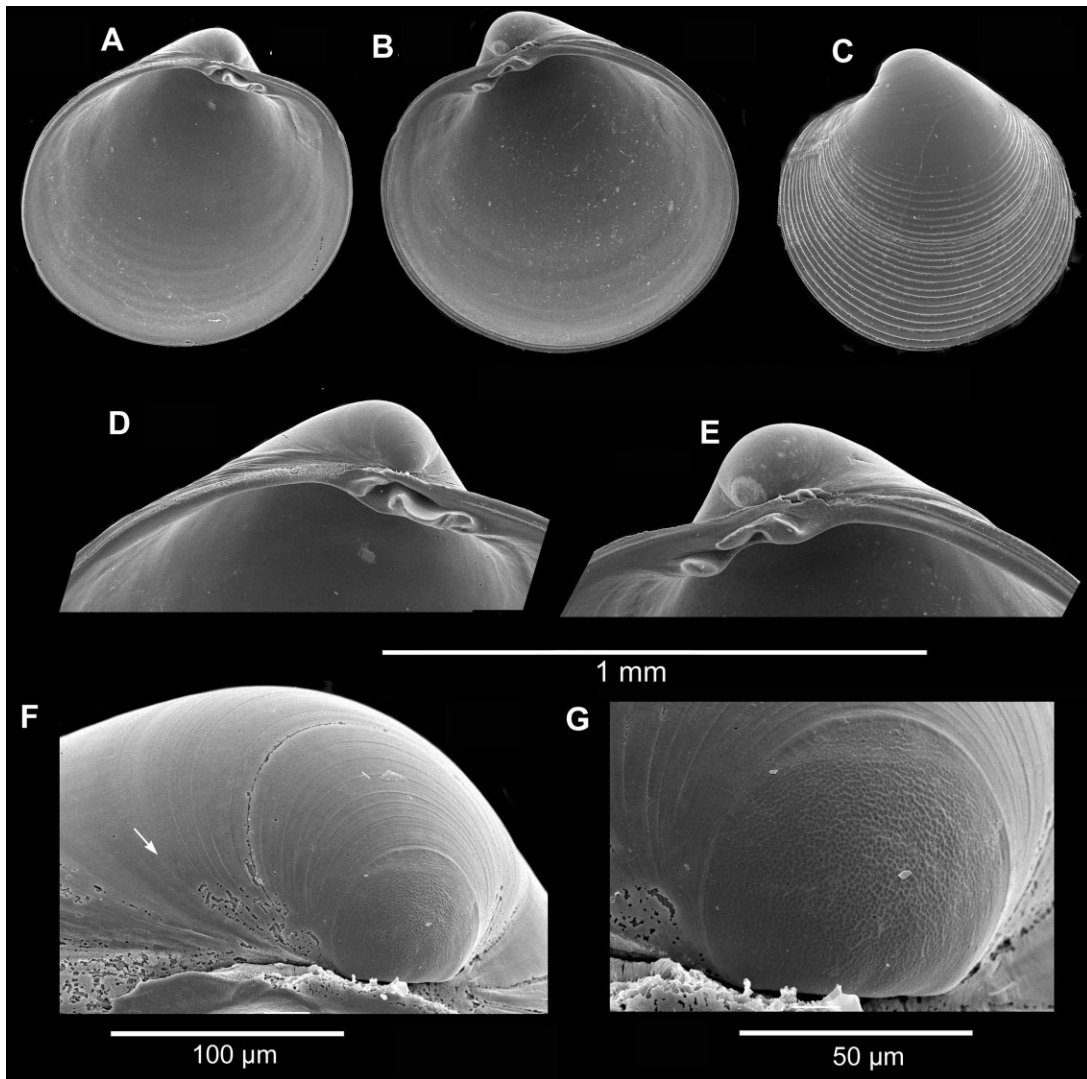
#### ***Kelliella goesi* Odhner, 1960**

(Fig. 11)

*Kelliella goesi* Odhner, 1960: pl. 2 fig. 24, 25.

**Type material:** Syntypes, single valves “in great number” dredged off Sint Maarten or St. Martin, 200–300 fms (360–540 m) in clay, and from off Anguilla, odd valves and entire shells dredged in 100–250 fms (180–450 m), leg. A. Goës, 1869, Swedish Museum of Natural History.

**Summary of material examined** (see Supplementary Material Table S1 for details): Guadeloupe, 3 specimens and 33 valves or shells from Karubenthos 1 and 2 (130–360 m). Guyane, 17 valves from R/V Antea “Proteus Guyane” (82–129 m).



**Figure 11.** *Kelliella goesi* Odhner, 1960 from Guadeloupe, 16°25'N, 61°34'W, 258 m (Karubenthos sta. GN20). **A.** Inside of a left valve (length 1.2 mm). **B.** Inside of a right valve (length 1.3 mm). **C.** External view of a left valve (length 0.9 mm). **D, E.** Hinge (same valves as **A** and **B**). **F.** Prodissoconch (left valve, same as **D**; arrow points to putative prodissoconch/dissoconch limit). **G.** Detail of prodissoconch 1. Scale bars: **D, E** = 1 mm; **F** = 100 µm; **G** = 50 µm.

*Description:* Shell minute (up to 1.7 mm in length), rather thick for its size, colourless and somewhat translucent when fresh, very tumid (length/width ratio: 1.3–1.4), equivalve, not gaping. Outline rounded (length/height 1.10), slightly inequilateral, with distinctly protruding, prosogyrous umbos situated at the anterior 1/3. Ventral margin uniformly rounded and continuous with anterior and posterior margins.

Lunule delimited anteriorly by a groove on each valve, starting at a short distance from the beginning of dissoconch. No distinct escutcheon, but a very inconspicuous ridge running very close to the dorsal edge on both valves (Fig. 11D, E). Periostracum inconspicuous, colourless. Outer surface of the valves smooth on the earlier part (*c.* 0.3 mm from start of dissoconch), then with distinct commarginal grooves (about 25–35, spaced *c.* 20–25 µm).

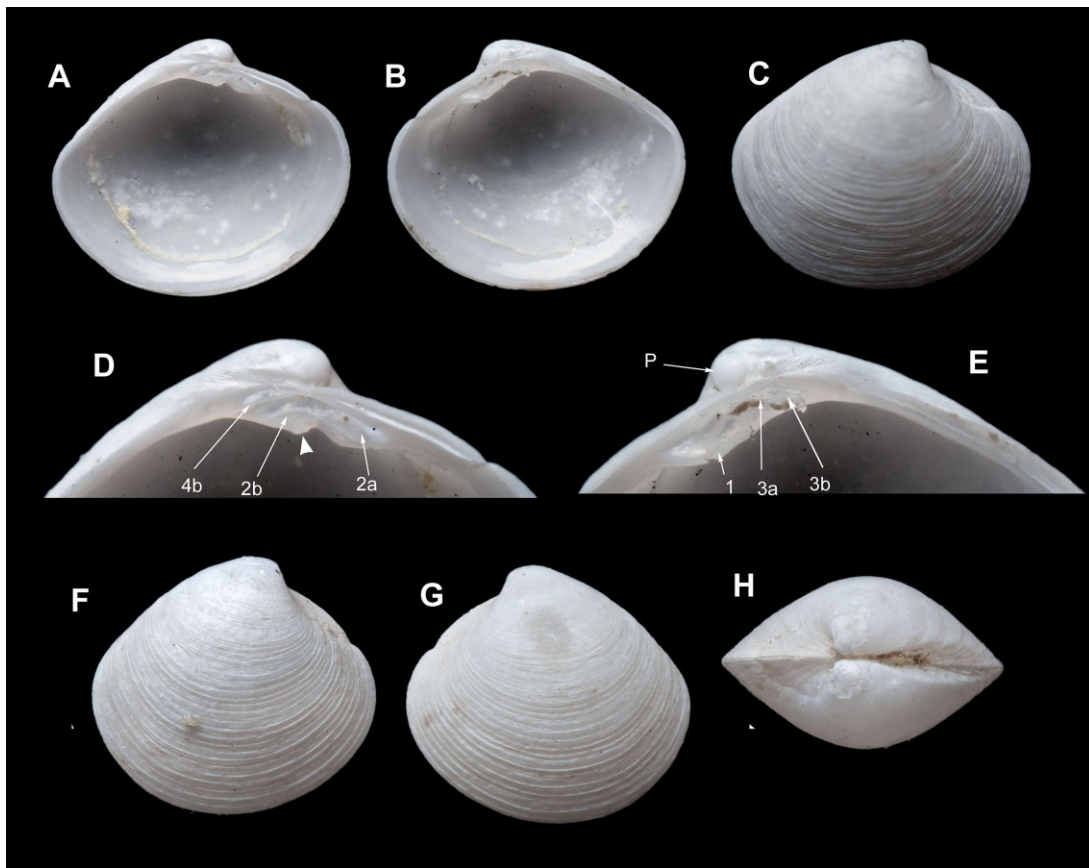
Prodissoconch 1 small (length *c.* 70–72 µm), ovate, with distinctly pitted surface; prodissoconch 2 (length *c.* 180–230 µm), rounded, with commarginal striae of variable intensity. Limit P1/P2 distinct, limit P2/dissoconch very indistinct even under SEM. Inner margins of valves smooth, with a narrow groove all along the inner shell margin of the right valve; and corresponding ridge on the left valve.

Hinge plates moderately broad, short (ratio length of hinge/total length: 0.18), with *c.* 3/5 of its extension anterior to the umbos.

Hinge with three cardinals in each valve. Left valve with anterior cardinals 2a and 2b concatenated, nearly fused, narrow and elongate; the anteriormost 2a arched to fit ventrally to the cardinal 1 of the right valve; cardinal 2b short, fitting above cardinal 3a of the right valve; posterior cardinal 4 small, pointing backwards, anteriorly separated from 2b by a broad pit accommodating cardinal 3b of the right valve, and posteriorly with a ridge merging into the hinge plate margin. Right valve with anterior cardinal tooth 1 short and bulging, situated more ventrally than the other teeth; cardinal 3a narrow and elongate, small, starting just beneath the umbo and directed forward, nearly horizontal and fused with cardinal 3b which is short, directed downwards and backwards, therefore at an angle about 120° to 3a. No lateral teeth. Ligament external, short, inserted at the edge of the hinge plates just behind the umbo. Adductor muscles scars not very distinct, small, subequal in size.

*Observed variability:* Specimens from Guadeloupe did not exceed 1.3 mm in length, whereas one specimen from Guyana reached 1.7 mm. There is much uncertainty as to the diameter of prodissoconch 2, which has been seen with conspicuous growth discontinuities whereas the limit with the smooth early part of the dissoconch is blurry.





**Figure 12.** *Kelliella concentrica* Allen, 2001 from off Rhode Island, 39°47.6'N, 70°56.4'W, 805–811 m (R/V “Chain” cruise 88, sta. 207). **A, B.** Inside of left and right valves of the holotype (BMNH no. 19980181/1; length 2.2 mm). **C.** External view from the right of the holotype. **D, E.** Hinge of the holotype. **F, H.** External views (right, left and dorsal) of the associated specimen (BMNH no. 19980181/2, length 2.2 mm), same sample as the holotype. 1, 2a, 2b, 3a, 3b, 4b, cardinal teeth; P, prodissoconch. The arrowhead points to the knob-like structure on the cardinal platform of the left valve of the holotype. Photo credit: Kevin Webb, NHM Image Resources, © Trustees of the Natural History Museum, London.

*Distribution:* Lesser Antilles off Sint Maarten or St Martin and off Antigua (type locality) and off Guadeloupe (depth range 130–520 m), also from the shelf of French Guyana (depth range 81–129 m).

*Remarks:* This is the first report of this species which was described in great detail but in a little-known publication. It occurs at greater depths than *K. madininae* although their bathymetric ranges may overlap.

**“*Kelliella*” *concentrica* Allen, 2001**  
(Fig. 12)

*Kelliella concentrica* Allen, 2001: 211–213.

*Type material:* Holotype from USA, off Rhode Island, 39°47.6'N, 70°56.4'W, 805–811 m, 22 February 1969, R/V “Chain” cruise 88, sta. 207, BMNH no. 19980181.1.

The NHMUK register (<https://data.nhm.ac.uk/media/b2b5da69-5688-472e-a01c-4089ecc39795>) mentions a “holotype and one paratype” and indicates “the two specimens were in the same tube when presented”. However, as was the case for *K. biscoyensis*, Allen (2001) only designated a holotype. The other specimen (NHMUK 1998181/2) has no status as a type.

*Remarks:* This species has never been reported since its original description. Janssen & Krylova (2012) suggested a placement in *Waisiuconcha* Beets, 1943. Later, based on the lack of an outer demibranch, Krylova et al. (2018) considered that the generic assignment

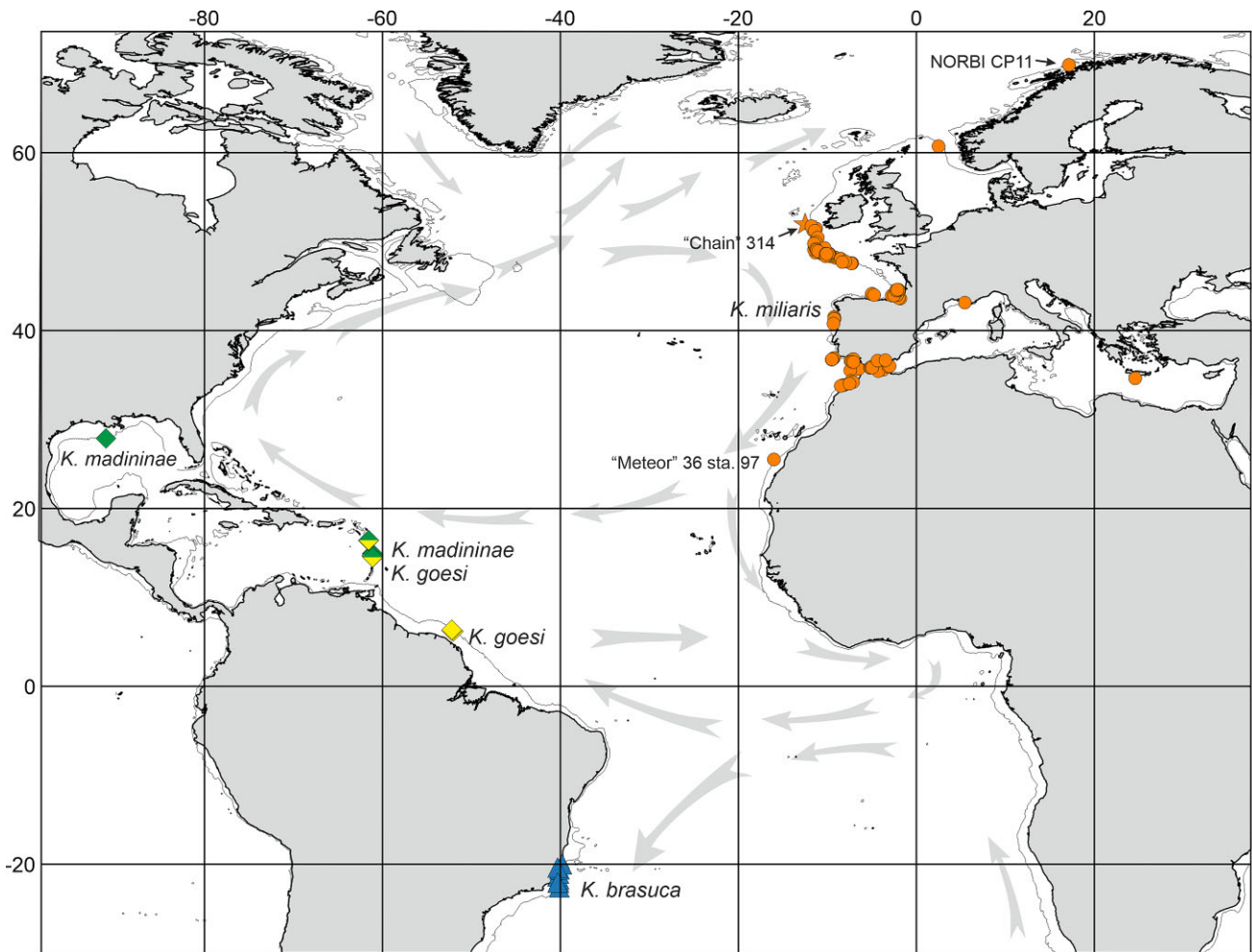
requires further study and a new genus should probably be established, but definitely placed it in the subfamily Vesicomyninae. The presence of a distinct escutcheon (Fig. 12H) and the aligned 3a and 3b teeth on the right valve (Fig. 12E) support this view and excludes this species from *Kelliella* as understood here. The unlabelled knob-like structure in the hinge of the left valve, between 2a and 2b, which appears on fig. 15 of Allen (2001), is also seen on the photographs (Fig. 12, arrowhead) but seems to be a lump on the basal part of the hinge plate rather than a tooth. The prodissoconch, about 150 µm in diameter, rounded and hourglass-shaped, is similar to that of several vesicomynid genera illustrated by Cosel & Salas (2001: figs 11, 29, 41) and denotes non-planktotrophic larval development.

## DISCUSSION

### *Kelliella* and *Vesicomya* compared

The morphological resemblance between the type species of *Kelliella* and *Vesicomya* (Fig. 8) has been seen by several authors as supporting the reunion of those two genera. Shared traits include a small, inflated shell with strongly prosogyrous umbos; a hinge with a deformed pattern of cardinal teeth departing from that of the family Veneridae, with three cardinals radiating from beneath the umbo; and the presence of two demibranchs, the outer one reduced in size.

Diagnostic characters discriminating *Vesicomya* from *Kelliella*, stated by Krylova et al. (2018) include:



**Figure 13.** Overview of the distribution of *Kelliella* spp. in the Atlantic Ocean, based mostly on the material we examined. Orange circles, *Kelliella miliaris* (orange star: type locality of *K. biscayensis*, see also Krylova *et al.* (2018) for additional localities off Norway; green diamonds, *K. madininae* n. sp.; yellow diamonds, *K. goesi*; partitioned green and yellow diamonds indicate sympatric occurrence of *K. madininae* n. sp. and *K. goesi*; blue triangles, *K. brasuca*. The light grey arrows indicate in a very simplified way the surface circulation pattern (redrawn from Pinet, 2008).

- cardinal teeth 3a–3b of right valve linear, slightly arcuate (*vs* diverging at *c.* 90° in *Kelliella*)
- presence of both lunule and escutcheon (*vs* no escutcheon in *Kelliella*)
- absence of a ridge or furrow along ventral shell margin (*vs* ridge on left valve fitting groove on right valve of *Kelliella*),
- a relatively large prodissoconch with pitted structure, in which there is no differentiated prodissoconch 2 (*vs* distinct p1 and p2 in *Kelliella*)
- two distinct siphonal apertures, the anterior (inhalant) separated from pedal gape by a mantle fusion (*vs* inhalant siphon continuous with pedal gape in *Kelliella*).

In addition to this, representatives of *Vesicomya atlantica* from abyssal area around the Azores (i.e. close to the type locality) studied by Cosel & Salas (2001) (Fig. 8B) lack a functional foot, and this organ is concealed beneath the gill in preserved specimens, whereas *Kelliella miliaris* has a large foot (Fig. 5) still visible on preserved specimens.

Some of the characters currently considered to discriminate *Kelliella* from *Vesicomya* are nevertheless debatable. The escutcheon, conspicuous in *Vesicomya*, is totally absent in *K. miliaris* but suggested in *K. madininae*, *K. brasuca* (right valve only) and *K. goesi* (both valves, but very inconspicuous). The presence of grooves along the ventral margins is not a clearcut character. In *V. atlantica*,

the valves are so thin that it cannot be expressed as clearly as in *K. miliaris*. The prodissoconch is indeed diagnostic, but this character of planktotrophic *vs* non-planktotrophic larval development has been discredited as a basis for generic separation, because loss of planktotrophy is known to occur repeatedly in distinct lineages (Bouchet, 1990; Duda & Palumbi, 1999; Collin, 2004).

Cosel & Salas (2001) and Krylova *et al.* (2018) reported that *Kelliella* has only one mantle fusion, forming a single posterior exhalant aperture, whereas the inhalant aperture is not separated from the pedal gape. Conversely, *Vesicomya* has two definite fusions forming both an inhalant and an exhalant aperture. This, however, must be qualified. The functional inhalant aperture of *Kelliella* is usually bound anteriorly by lobes of the mantle edge, which are tightly appressed at a point which is coincident with the small mantle tentacles (two or three on each side; Figs 5, 7). In one specimen from Capbreton canyon, this was seen as a delicate bridge of mantle tissue closing anteriorly the inhalant aperture. Such variability was observed also by Salas & Gofas (1998: 40) in *Neolepton sulcatulum* (Jeffreys, 1859), where most (26 out of 30) of the specimens observed alive had the tissue bridge broken but still had a functional inhalant siphon formed by the attitude of the mantle lobes which are touching each other in place of the tissue bridge. In *V. atlantica*, the mantle fusions delimiting the siphons are robust and did not split.

The foot is a diagnostic character only at the species level. Whereas, *V. atlantica* as understood here and by Cosel & Salas (2001) lacks a functional foot, the specimens figured by Allen (2001: 207, fig. 8) as *V. atlantica* do have a functional foot and certainly represent a different species.

In conclusion, the architecture of cardinal teeth 3a–3b seems to be the most robust morphological character to diagnose *Kelliella* from *Vesicomya*, in connection with the absence of a definite escutcheon. Incidentally, we noted that the middle Miocene fossil species “*Kelliella*” *barbara* (Studencka, 1987: plate 32, fig. 1, 2) does not have the hinge of a *Kelliella*, but instead conforms that of the genus *Coralliophaga* in the family Trapeziidae (see Supplementary Material Fig. S1), an identification that would be more consistent with its habitat in a shallow epicontinental sea. Therefore, we here exclude this species from the genus *Kelliella* and reallocate it as *Coralliophaga barbara* (Studencka, 1987) n. comb.

Whether these differences can support the placement in different families has to be considered in the framework of a phylogenetic hypothesis. In the BivaTOL phylogenetic reconstruction (Bieler et al., 2014: 85), “*Kelliella* sp.” clusters with the large vesicomid *Calyptogena magnifica*, and it clusters with *V. pacifica* (E.A. Smith, 1885) in a phylogeny presented by Krylova et al. (2015). The specimens sequenced (Bieler et al., 2014: fig. 4C), from a depth of 3,200 m along the Gay Head–Bermuda transect, were identified by Krylova et al. (2015) as species of *Vesicomya* s.s. based on the presence of an escutcheon. This is confirmed by the fact that true *Kelliella* have so far never been reported in that area and depth. In the phylogenetic reconstruction of Krylova et al. (2018), undoubted *K. miliaris* appear as a sister group of venerids rather than of vesicomids, with a bootstrap probability of 100%. This clearly places *Kelliella* close to the divergence between vesicomids and venerids, but it must be kept in mind that the topology could vary slightly if different genes or a different taxon sampling is considered. Therefore, our view is that the placement in two different families is tenable with the molecular data at hand, but the need for that separation is not robustly demonstrated. Morphologically, *Kelliella* retains plesiomorphic characters such as the presence of both demibranchs and the planktotrophic larval development, consistent with a basal position in the clade comprising venerids and vesicomids.

### Distribution

*Kelliella miliaris* shows a broad distribution in the Northeastern Atlantic (from Norway to the Gulf of Cádiz) and Mediterranean Sea (Fig. 13); however, the species is not present along the West African coastal area, despite the extensive sampling carried out in many countries (Cosel & Gofas, 2019), particularly in Senegal where many samples were studied in the 100–250 m depth interval. The habitat, muddy bottom with low level of oxygen, is present in many localities (Brandt et al., 2015), particularly offshore Mauritania where a strong upwelling is present under which a minimum oxygen zone has been observed (Gilly et al., 2013). In addition, it would be logical to think that the Canary Current could transport the larvae towards West Africa. One possible reason for the absence of transport of larva from the South Iberian Peninsula towards West Africa could be that beneath the near-surface flow towards the Equator of the Canary Current, a subsurface current flows polewards, counter to the general circulation and tightly bound to the continental slope between 300 and 500 m depth (Barton, 2001). It has been documented along the entire continental margin between the Gulf of Guinea and northwest Spain, and is a common feature of all eastern boundaries. Above the undercurrent, shallow equatorward flow predominates, while in layers deeper than 500 m, Antarctic intermediate water is carried northwards at depths of around 900 m. Where it meets the Canary Current separating from the coast, some of the poleward flow continues northwards (Barton, 2001).

The absence of true *Kelliella* on the North American Atlantic slope is striking, and sufficiently documented considering the amount of existing data. Regarding South America, the south equatorial current (from West Africa to Brazil) is split into two branches, one northwards and another southwards of Cape São Roque (Fig. 13). This divergence, together with the Amazon freshwater discharge, seems to represent a physical barrier for the exchange of larvae between the southeast Brazilian shelf (*K. brasuca*) and the Caribbean area (*K. madininae*, *K. goesti*). The scarcity of records in the Caribbean area, mostly limited to material collected recently by MNHN, Paris, could reflect a gap of knowledge in the outer shelf and slope of this area, which has been scarcely sampled in comparison with the European margin.

While the size of the prodissoconch 1 is very similar in all the examined specimens of *K. miliaris* (between 74 and 79 µm), there was variation in the size of prodissoconch 2, from 190 µm in specimens from the Bay of Málaga (southern Spain), living at the edge of the shelf (100–120 m), to 240 µm in specimens from off Ireland, collected at 1,015 m depth. This size range could be related to the vertical distribution and the time that the larvae take to reach the bottom.

## SUPPLEMENTARY MATERIAL

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

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## CONFLICT OF INTEREST

We declare that we have no conflict of interest.

## DATA AVAILABILITY

The list of material examined is presented in the Supplementary Material. Examined specimens are deposited in Muséum National d’histoire Naturelle, Paris, unless otherwise stated, and are available for study.



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