

A REVIEW OF EUROPEAN 'MYSELLA' SPECIES (BIVALVIA, MONTACUTIDAE), WITH DESCRIPTION OF *KURTIELLA* NEW GENUS

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ABSTRACT

The type species of the genera *Mysella* Angas, 1877, *Rochefortia* Vélain, 1878, *Rochefortula* Finlay, 1927 and *Altenaeum* Spink, 1972 are illustrated and discussed. A new genus *Kurtiella* is introduced for '*Mysella*' *bidentata* (Montagu, 1803) and other European species currently placed in *Mysella*. These species display a unique diagnostic character state in having the cardinal platform deeply receding to house the internal ligament, along with an array of more general montacutid traits. At the species level, diagnostic characters are given for the type species *K. bidentata*, and for other included species *K. ovata* (Jeffreys, 1881), *K. pellucida* (Jeffreys, 1881), *K. triangularis* (Watson, 1897) and *K. tumidula* (Jeffreys, 1866), based mostly on characters of the prodissoconch and on shell outline. *Montacuta simillima* Smith, 1892, from St Helena, is considered a junior synonym of *K. pellucida*. The loss of labial palps in *K. tumidula* is interpreted as a further derived character, which does not conflict with the generic placement in *Kurtiella*.

INTRODUCTION

The Montacutidae are a family of small bivalves that live in association with a variety of benthic invertebrates, commonly with echinoderms (Pelseneer, 1925; Boss, 1965; Gage, 1966; Morton & Scott, 1989). The level of association with the host is extremely variable, ranging from partly free-living to permanently attached. Several species of this family, currently assigned to the genus *Mysella* Angas, 1877, have been reported from European seas. The most common and widespread, '*Mysella*' *bidentata* (Montagu, 1803), is found from northern Norway to Morocco and in the Mediterranean. It lives on the continental shelf in loose association with burrowing ophiurids (Ockelmann & Muus, 1978; Kunitzer, 1989), and possibly with other invertebrates (Pelseneer, 1925; Prevedelli, Simonini & Ansaloni, 2001). The other European species, seldom reported on after their original description, were reviewed by van Aartsen (1996) based on the very limited material available at that time.

Recent exploration of the northeastern Atlantic seamounts has yielded extensive material for two species hitherto known by hardly more than the type material. These are '*Mysella*' *pellucida* (Jeffreys, 1881), originally described from the Adventure Bank in the strait of Sicily, and '*Mysella*' *ovata* (Jeffreys, 1881), originally described from off southwestern Portugal. Examination of this material revealed unambiguous species-specific characters and therefore provided elements for the species-level revision presented in this paper. However, the current generic assignment of this species-group to *Mysella* appeared to be questionable and is here reconsidered.

MATERIAL AND METHODS

Most of the material examined herein belongs to the malacology collections in Muséum National d'Histoire Naturelle, Paris (hereafter MNHN). The material from the Lusitanian seamounts and Galicia bank was collected during 'Seamount 1' expedition, conducted in September/October 1987 by Philippe

Bouchet (65 dredge hauls and 15 beam trawl operations on Gorringe, Josephine, Ampère, Lion and Seine seamounts; 11 dredge hauls and 1 beam trawl operation on Galicia Bank; see Bouchet & Métivier, 1988). The 'Seamount 2' expedition was conducted in January/February 1993 by the first author and investigated the Great Meteor bank, Hyères, Irving, Cruiser, Plato, Atlantis and Tyro seamounts (69 dredge hauls and 16 beam trawl operations shallower than 1,000 m; see Gofas, 1993). The material from the Seamount expeditions was sorted to the species level, on board for the coarser fraction and later at the lab down to the 0.5 mm mesh. The largest part consisted of shells, and these were taken into account in the mollusc counts. The material from Seamount 1 is shared between the Swedish Museum of Natural History, Stockholm (SMNH), and MNHN; that of Seamount 2 is deposited in MNHN.

Other material belongs to the general collection in MNHN, some of which is from the first author's own collecting in Europe and Morocco. The details of material examined for the European species are given in the Appendix and summarized along with the species-level systematic treatment. In addition, the following material was examined:

Rochefortia australis Vélain, 1878: Ile St Paul, 3 spm. (syntypes MOLL5541, 2.30 × 1.62 to 2.84 × 2.00 mm), MNHN.

Rochefortula reniformis (Suter, 1908): Auckland, New Zealand, 1 spm. (4.35 × 3.05 mm) and 8 v. (3.40 × 2.35 to 4.70 × 3.05 mm), coll. P. Serre 1924; Mangonui (35°00'S, 173°34'E), 3 spm. (5.25 × 3.50 mm to 5.70 × 3.75 mm), coll. P. Serre 1925, MNHN.

Altenaeum dawsoni (Jeffreys, 1864): N of Gardaskaga, Iceland (64°08'N, 22°38'W, 25–45 m), 2 spm. (1.63 × 1.24 mm, 1.55 × 1.18 mm), leg. Bogason 15.03.1990 (SMNH).

Epilepton clarkiae Clark, 1852: Calahonda, Spain (36°29.4'N, 04°41.8'W, 0–2 m), 2 sh. (1.70 × 1.41, 1.90 × 1.54 mm).

Live-collected specimens of '*Mysella*' *bidentata* and '*M.*' *tumidula* originally fixed in formalin and preserved in 70% ethanol, were cut open, critical-point dried and examined under SEM. Shells were cleaned by soaking for 10–15 min in 10% sodium

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lauryl sulphate solution and rinsed; those that were not exceedingly fragile were also subject to a brief ultrasonic cleaning for about 1–2 s.

THE NEED FOR A NEW GENUS

The species originally described as *Mya bidentata* Montagu, 1803 was placed in the genus *Montacuta* Turton, 1822 (including unjustified emendation *Montaguia* by Locard, 1886) by classical XIXth century and early XXth century authors (Turton, 1822; Forbes & Hanley, 1849; Jeffreys, 1864; Locard, 1886; Pelseneer, 1925; Lebour, 1938; Popham, 1940). The placement in the family Montacutidae is correct, but the thoroughly different arrangement of the hinge teeth in the type species of *Montacuta*, with anterior laterals present in both valves and no posterior laterals, indicate that this generic assignment is not tenable.

In the recent literature (e.g. Tebble, 1966; Ockelmann & Muus, 1978; Ó Foighil *et al.*, 1984; Seaward, 1990; van Aartsen, 1996; Jespersen & Lützen, 2001), it is consistently cited in the combination *Mysella bidentata* following a lead by Winckworth (1932). This has hardly been questioned although Bowden & Heppell (1968) admit to having ‘left the three British species in *Mysella* ... until satisfactory evidence for their generic placement elsewhere is forthcoming’.

The type species of *Mysella* (Fig. 1) is the Australian *Mysella anomala* Angas, 1877 (p. 176, pl. 26, Fig. 22). Examination of the syntypes reveals important discrepancies which make questionable the current generic placement of ‘*Mysella*’ *bidentata* and the group of species treated herein. *Mysella anomala* has a solid hinge platform underlying the ligamental pit as is usual in most bivalves. Conversely, in ‘*M.*’ *bidentata* there is a complete regression of the hinge plate beneath the umbones at the site of insertion of the ligament, to the point that some of the more

fragile shells spontaneously crack across the umbo when drying (see e.g. Fig. 11E). The teeth of the right valve are markedly unequal in *M. anomala*, making a further difference with ‘*M.*’ *bidentata* in which they are subequal. Other genus-level names to be considered are *Rochefortia* Vélain, 1878, *Rochefortula* Finlay, 1927 and *Altenaeum* Spaink, 1972.

Rochefortia is generally considered as a synonym of *Mysella*, following in this the view of Dall (1900). The name first appears as a *nomen nudum* in Vélain (1876: 285) and was described only two years later (Vélain, 1878) with *R. australis* Vélain, 1878 as type species by monotypy. *Rochefortia* has seldom been used in combination with the specific epithet *bidentata* (but e.g. Cerulli-Irelli, 1908).

Vélain’s (1878) description and drawings (and likewise the reproduction of these drawings by Chavan in Moore, 1969) are confusing and difficult to relate with the actual specimens (Fig. 2). Vélain describes the ‘right valve’ of *Rochefortia* as having two unequal laterals and, between these and the dorsal edge, two grooves to accommodate the laterals of the opposite valve; in addition he mentions (in translation) ‘sort of a small tooth abutting against anterior lateral’. He mentions both cardinals and laterals on the ‘left valve’. This wording suggests that he assumed an orientation opposite to what is suggested here. Also, as will be discussed below, we assume the alleged cardinals on the ‘left valve’ (here considered right valve) to be laterals, and the alleged laterals to be merely the dorsal edge of the cardinal platform. This view makes irrelevant Vélain’s argument that (in translation) ‘the arrangement and number of cardinals precludes to bring them aside with the *Montacuta*, *Erycina*, *Tellimya*, *Scintilla*, etc.’ The supposed small tooth abutting against the lateral was probably a piece of the ligament, which is prone to shear into vertically oriented pieces as seen on Figure 2E.

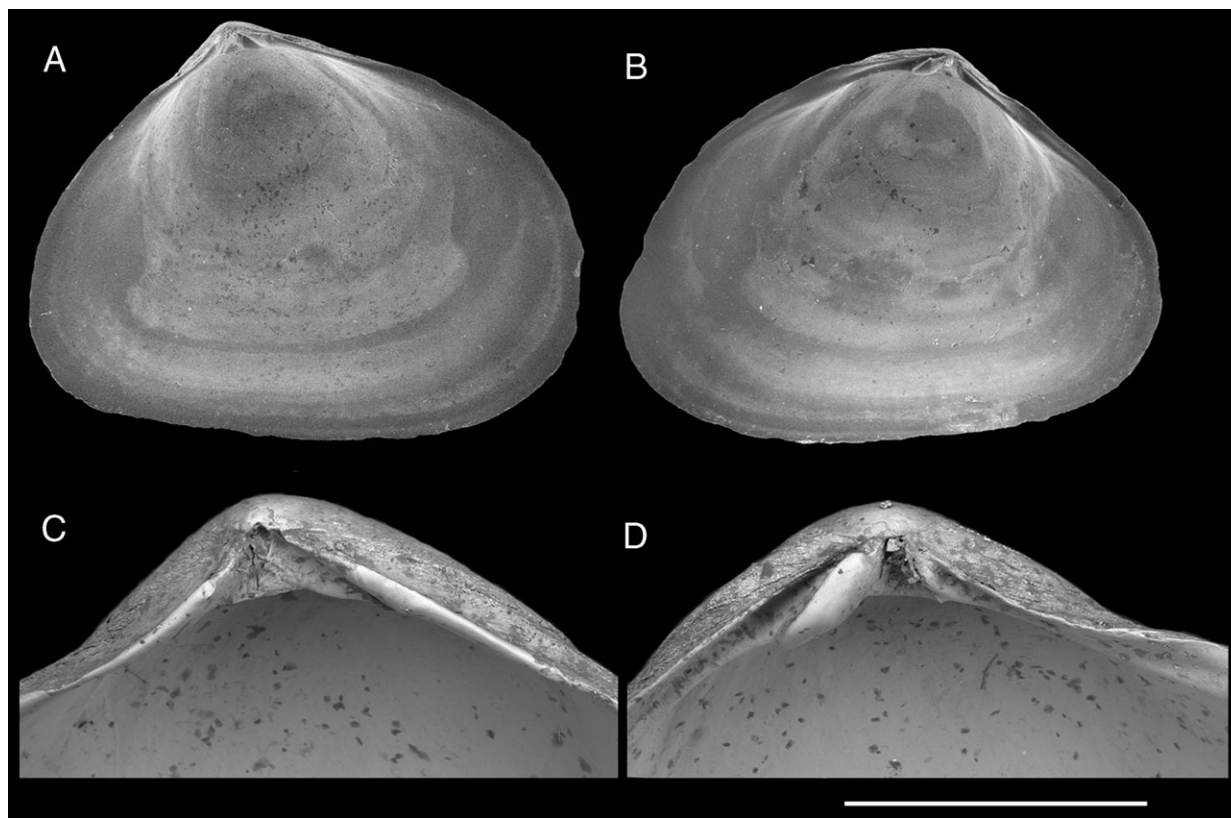


Figure 1. One of the two syntypes of *Mysella anomala* Angas, 1877, from Shark Island, Port Jackson, Australia, in black mud 12 fathoms (leg. G. Angas, BMNH reg. 77.5.12.108). **A, B.** Inside of left and right valves, length of valves 8.2 mm. **C, D.** Detail of the hinge. Scale bar = 1 mm.



Figure 2. One of the three syntypes of *Rochefortia australis* Vélain, 1878, from Ile St Paul, intertidal (leg. C. Vélain, MNHN MOLL5541). **A, B.** Inside of left and right valves, length of valves 2.8 mm. **C, D.** Detail of the hinge. **E.** Detail of the ligament on the left valve, showing vertical shearing. Scale bars: **C, D** = 500 μm ; **E** = 100 μm .

Although Morrison (1962), Chavan in Moore (1969) and Coan, Scott & Bernard (2000) attempted to distinguish *Rochefortia* from *Mysella*, it seems therefore correct to consider them as synonyms. In the type species of both genera, the right valve has unequal laterals and both valves have a continuous cardinal platform holding a large triangular pit for the internal ligament. Unless further data regarding anatomy should disprove the relationship, we can see no reason to question it from the shell characters alone.

Rochefortula was separated from *Rochefortia* by Finlay (1927) with *Rochefortia reniformis* Suter, 1908 (Fig. 3) as type species by original designation. Finlay only stated that it 'differs in texture, solidity and somewhat in the hinge', which can be qualified here. The hinge on the right valve of *Rochefortula reniformis* resembles that of *Mysella anomala* except for having subequal anterior and posterior teeth. However the left valve is very different, bearing very short laterals well defined as teeth, in contrast with the elongate laterals merging into the cardinal platform in *Mysella*. The area just posterior to the beaks is depressed and shows a weak external ligament not seen in *Mysella* or *Rochefortia*. Therefore, *Rochefortula* appears so far as a monotypic genus, which may be valid, but which is still more inappropriate than *Mysella* for the European species.

Altenaeum Spink, 1972 is based on a fossil species of Pleistocene (Eemian) age from the southern North Sea, *Altenaeum nortoni* Spink, 1972. This species has been later placed in synonymy with *Montacuta dawsoni* Jeffreys, 1864 (Baceljau *et al.*, 1984; Fig. 4 herein). The hinge of the right valve (Fig. 4D) bears two distinct teeth of which the homology to those in *Mysella anomala* or '*Mysella*' *bidentata* is unclear. By comparison with '*Mysella*' *maltzani* (Verkrüzen, 1875) (see Baceljau *et al.*, 1984; Fig. 4), or with *Epiplepton* (see Fig. 7 herein), the large anterior tooth of the right valve could be interpreted as a cardinal whereas the delicate ridge parallel to the anterior dorsal margin would be a lateral; the left valve clearly shows an elongate anterior lateral. Posterior to the ligament pit, there is a lateral in each valve.

Type specimens of *Montacuta dawsoni* were figured by Waren (1980). Bowden & Heppell (1968) and van Aartsen (1996) pointed out that Jeffreys (1876) and some subsequent authors

confused the Arctic species '*Mysella*' *sovaliki* MacGinitie, 1959, with *Montacuta dawsoni*. True '*M.*' *sovaliki* shows much similarity, including the architecture of the hinge platform, with '*M.*' *bidentata* and is therefore probably related to it. Nordsieck (1969) transferred *Montacuta dawsoni* to *Mysella*, without an explanation, but may have been influenced by the erroneous concept including therein '*M.*' *sovaliki*.

SYSTEMATIC DESCRIPTIONS

Kurtiella n. gen.

Type species: *Mya bidentata* Montagu, 1803 (Figs 5–8).

Etymology: The generic name honours Dr Kurt Ockelmann, as one of the foremost taxonomists to have studied European bivalves and especially the small species in the Galeommatoida and related groups.

Description: Shell small, somewhat longer than high and moderately inflated, equivalve, inequilateral with beaks within the posterior half. Prodissoconch lens-shaped, not very inflated, with or without a differentiated prodissoconch 2. Dissoconch with a sculpture of fine commarginal lines and, more rarely, radial microsculpture of indistinct divergent striae. Ventral margins of valves smooth and tightly appressed. Cardinal platform extending dorsally on either sides of beaks, over approximately half of the shell length, interrupted beneath the beaks by a notch in which is lodged a large internal ligament. Lower part of ligament with small calcified portion constituting a lithodesma. Left valve with indistinct laterals, one anterior and one posterior, usually expressed as mere swelling of cardinal platform; right valve with two short but very distinct laterals bordering ligament anteriorly and posteriorly, separated from dorsal margin by distinct grooves, their termination bulging ventrally from cardinal platform. Anterior and posterior muscle scars subequal. Pallial line thick, irregular, entire. Shell colour white on dissoconch, white or brownish on prodissoconch.

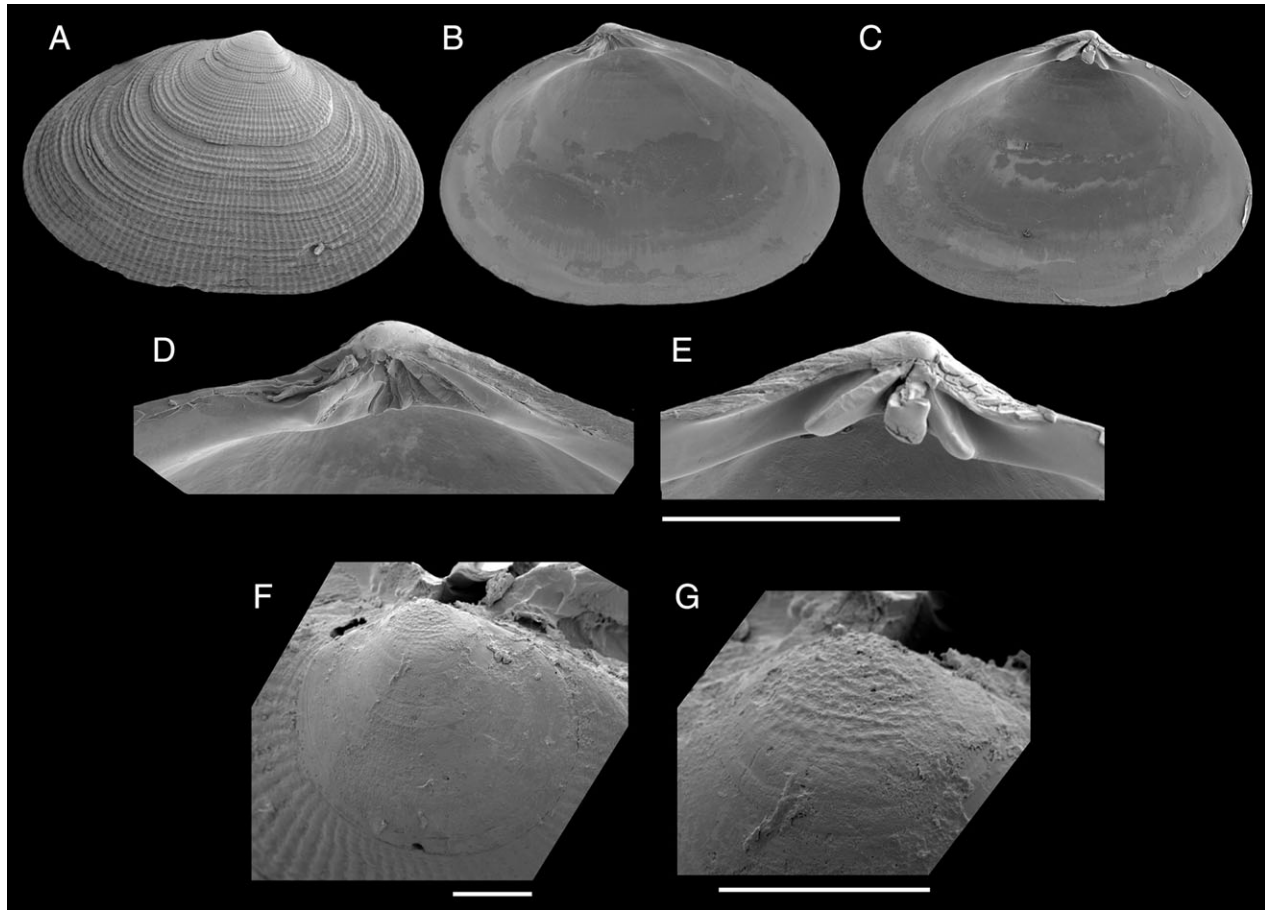


Figure 3. Specimens of *Rochefortula reniformis* (Suter, 1908) from Mangonui, North Island, New Zealand. (coll. M. Serres, MNHN). **A.** Exterior of a left valve, length 5.7 mm. **B, C.** Interior of left and right valves of another specimen, length 5.4 mm. **D, E.** Detail of the hinge. **F.** Prodissoconch, same specimen as A. **G.** Detail of prodissoconch 1 showing pitted microsculpture and well defined limit. Scale bars: **D, E** = 1 mm; **F, G** = 100 μ m.

Mantle extending hardly more than edge of valves when animal is fully extended, not reflected over outer surface. Mantle lobes with three distinct marginal folds, fused for very short distance postero-ventrally along inner fold. Pallial cavity with ctenidia comprising inner demibranch only, with or without two pairs of labial palps. Foot hatchet shaped, keeled ventrally.

Remarks: The homology of the teeth of *Kurtiella* with laterals is concluded (Fig. 7) from comparison with the hinge of the related *Epilepton clarkiae* (Clark, 1852), where the small structure forming a hook-shaped compound tooth is interpreted as a cardinal, and the elongate structures parallel to the hinge margin therefore as laterals. A further clue to considering the teeth in *K. bidentata* as laterals is that cardinals normally cluster anteriorly to the chondrophore (e.g. in Mactridae); we do not know of any heterodont bivalve where cardinals would be situated on either side of an internal ligament. Our view agrees with Tebble (1966) and Chavan in Moore (1969), but conflicts with the interpretation as cardinal teeth by Holmes, Gallichan & Wood (2006) for the present species, by Morton & Scott (1989) for *Mysella anomala*, and by Coan *et al.* (2000) and Boyko & Mikkelsen (2002) for similar West American species.

The calcified portion of the ligament was seen in *K. bidentata* by Lovén (1847:196, as *Mesodesma exiguum*) and in *K. verrilli* by Allen (2000), and may be also a diagnostic character; however this character remains to be checked in other species of this group and in other Montacutidae.

Kurtiella bidentata (Montagu, 1803)

(Figs 5–8)

Mya bidentata Montagu, 1803: 44-45 (Salcombe, England).

Mysella bidentata—Ockelmann & Muus, 1978 (biology and behaviour).

Erycina nucleola Récluz, 1844: 328 (Cherbourg, France).

Arcinella laevis Philippi, 1844: 54, pl. 16 Fig. 10 (Palermo, Sicily, Pleistocene fossil).

Mesodesma exiguum Lovén, 1846: 196 (Bohuslan, Sweden).

Material examined: France, Brittany, 315 live collected specimens; Southern Iberian Peninsula, 95 live collected specimens, 19 complete shells and 457 valves; Morocco, 3 live-collected specimens, 1 shell and 530 valves (see Supplementary Data for details).

Species-specific diagnostic characters: Shell up to nearly 4 mm in length with mean l/h ratio 1.4, beaks situated towards the posterior 1/3, very slightly opisthocline. Prodissoconch 400-480 μ m in diameter, with distinct, smooth, elongate prodissoconch 1 and prodissoconch 2 with faint growth lines. Dissoconch with sculpture of fine commarginal lines and, rarely, radial microsculpture of indistinct divergent striae. Anterior part of cardinal platform straight, sloping down gently; posterior part slightly concave, sloping more abruptly.

Lateral teeth well marked and diverging *ca.* 100° on right valve, hardly more than a swelling of cardinal platform and diverging *ca.* 120° on left valve. Shell colour white on dissoconch and prodissoconch, with yellowish periostracum.

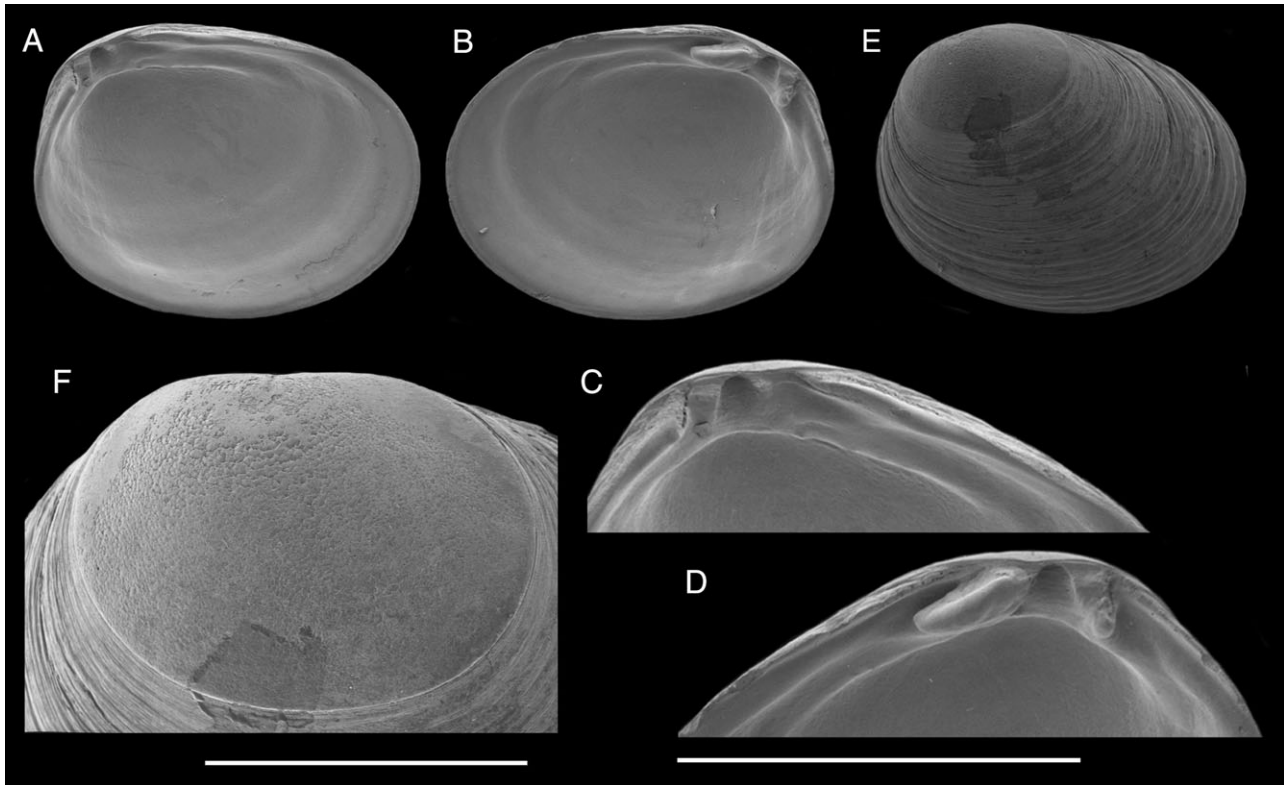


Figure 4. Specimens of *Altonaem dawsoni* (Jeffreys, 1864) from Gardaskaga, Iceland. **A, B.** Interior of left and right valves, length 1.63 mm. **C, D.** Detail of the hinge, same specimen. **E.** Exterior of the right valve of another specimen, length 1.55 mm. **F.** Detail of the prodissococonch, same valve as **E**, showing continuous shell surface without a distinct prodissococonch 2. Scale bars: **C, D** = 1 mm; **F** = 500 μ m.

Pallial cavity with well developed inner demibranch and two well developed pairs of labial palps. Foot with conspicuous pedal gland seen by transparency on ventral edge.

Distribution: Known with certainty from northern Norway to southern Morocco, and throughout the Mediterranean Sea. There are no positive records from Atlantic islands, for which published statements may be based on *K. triangularis* (see that species). West African records also need confirmation and may be based on undescribed species presently under study.

Habitat: On a broad variety of bottoms from the intertidal to the continental shelf in more than 100 m depth. The most trustworthy report of an association is with burrows of various species of Ophiuroidea (Ockelmann & Muus, 1978), whereas other reported associations may be accidental.

Remarks: It may be debated whether more than one species is present among the broad array of populations assigned to *Kurtiella bidentata* herein and in the literature. Ockelmann & Muus (1978) found two morphologically distinct forms living in nearby localities in the northern Øresund, Denmark. There are notable variations in the outline, which may be more or less elongate, more or less evenly rounded on the posterior margin (*vs* somewhat truncated), and with more or less salient beaks. The external surface is smooth, albeit never glossy, on most specimens, but sometimes displays a tenuous microsculpture of divergent threads perpendicular to the shell margin (Fig. 8H, I). However, in the large amount of material examined, there is no evidence that any of these traits are correlated nor that they provide the basis for recognition of more than one species. In all cases, these variations were found in association with the type of prodissococonch illustrated in Figure 8C, D, with a small, smoothish prodissococonch 1 clearly demarcated

from the larger, lens shaped prodissococonch 2. This does not demonstrate that all specimens are conspecific, but indicates a planktotrophic larval development and therefore the possibility of large scale gene flow. Therefore, if any differentiation should

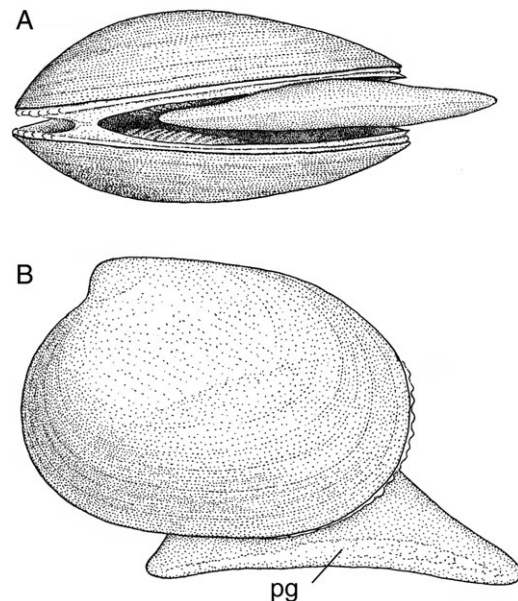


Figure 5. *Kurtiella bidentata* (Montagu, 1803), living animal from Rocquaine Bay, Guernsey (shell length 2 mm). **A.** Ventral view, anterior side to the right. **B.** Lateral view from the right. Abbreviation: pg, pedal gland.

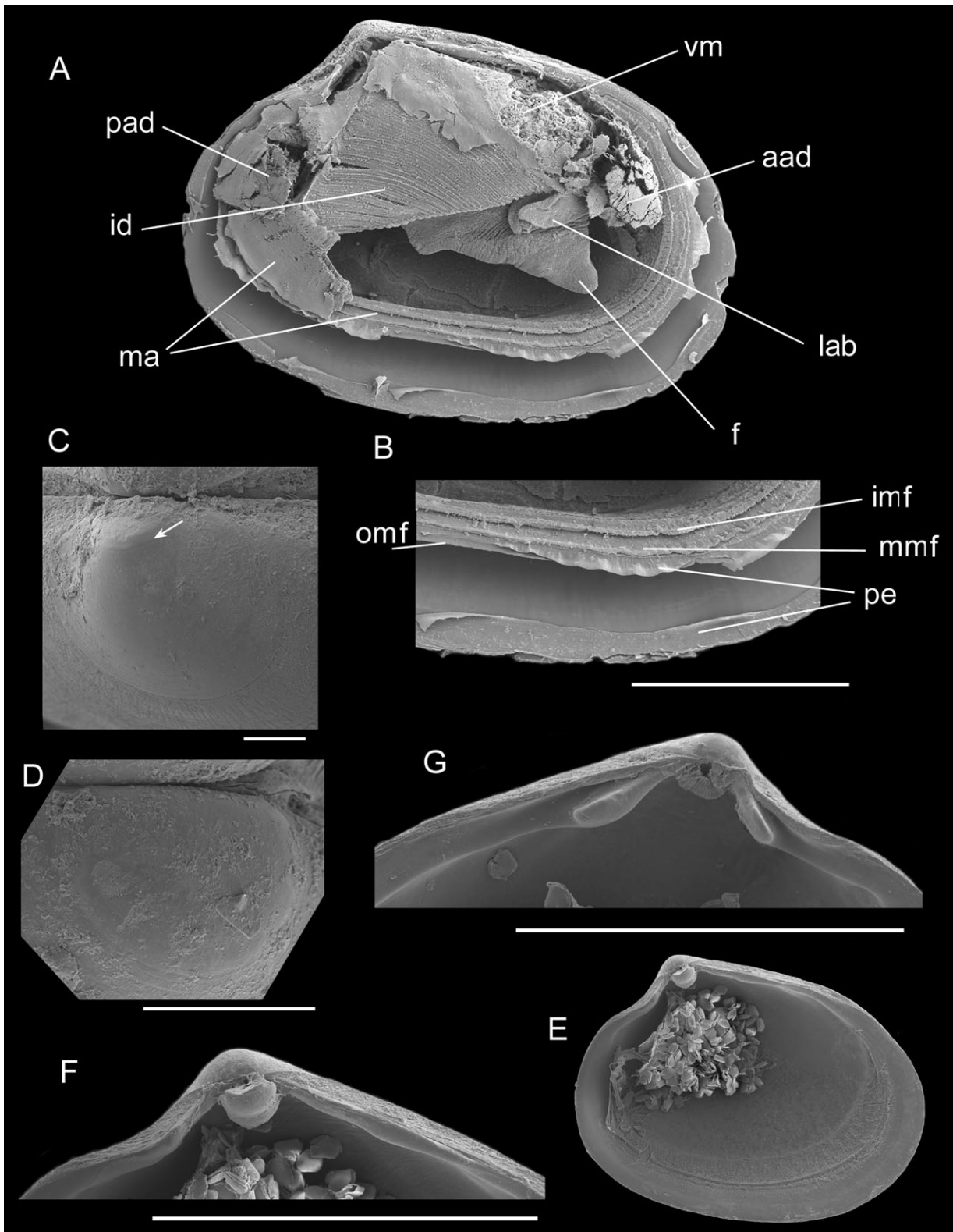


Figure 6. *Kurtilia bidentata* (Montagu, 1803), specimens from Roscoff area, Brittany. **A.** Critical-point dried specimen from Chenal de l'Île Verte, with right valve and right mantle lobe removed, length of shell 3.60 mm. Abbreviations: aad, anterior adductor muscle; id, inner demibranch; f, foot; lab, labial palps; ma, mantle; pad, posterior adductor muscle; vm, visceral mass. **B.** Detail of the ventral mantle edge. Abbreviations: imf, inner mantle fold; mmf, middle mantle fold; omf, outer mantle fold; pe, periostracum. **C.** Prodossoconch of a specimen from Cochons Noirs. Arrow indicates the limit between prodossoconch 1 and prodossoconch 2. **D.** Detail of prodossoconch 1 of another specimen, same locality. **E.** Interior of left valve of a specimen from Cochons Noirs, length 2.06 mm; note prodossoconchs of brooded specimens adhering to mantle lobe. **F, G.** Detail of hinge of same specimen. Scale bars **B, F, G** = 1 mm; **C, D** = 100 μ m.

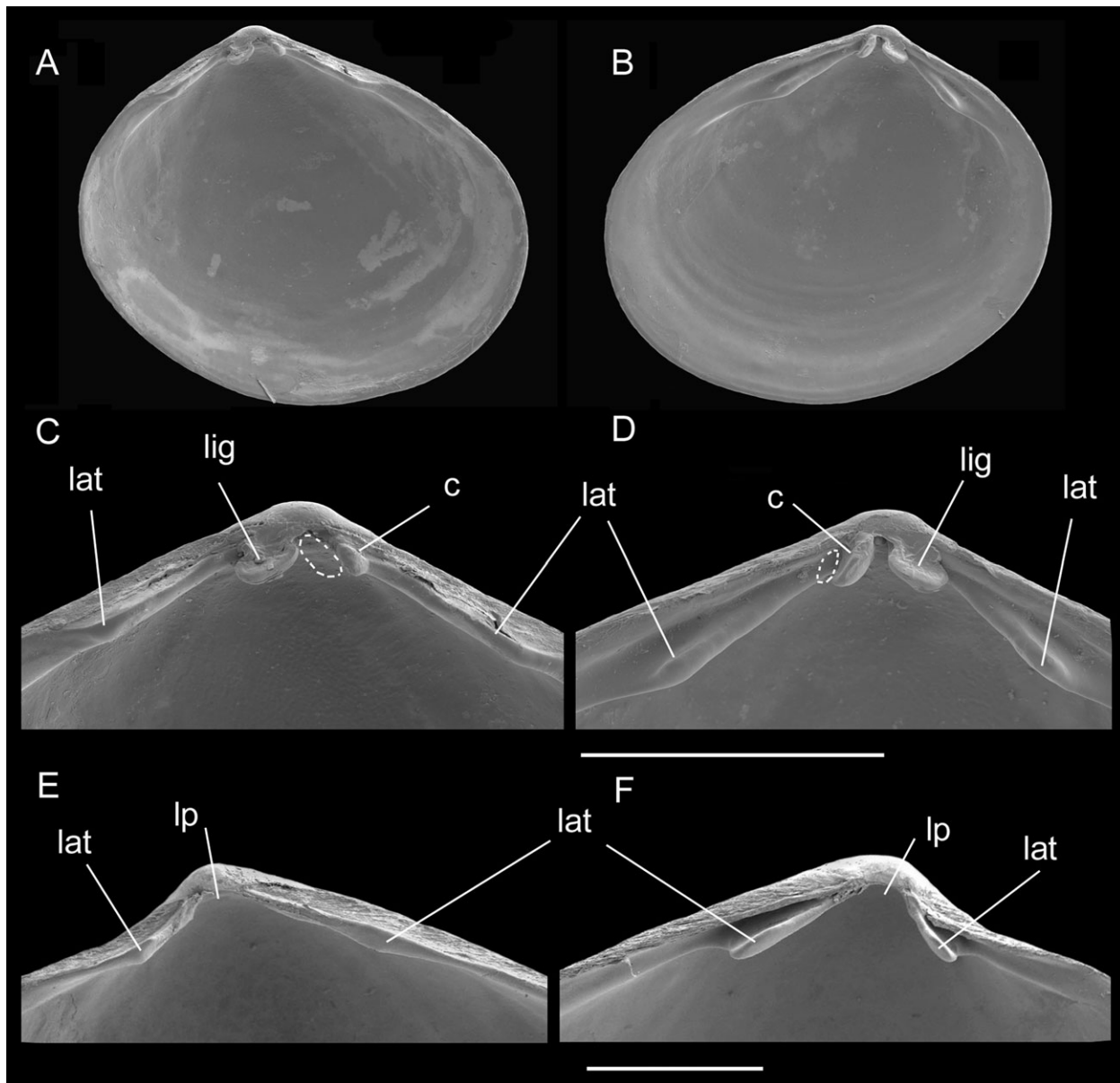


Figure 7. Hinges of *Epilepton clarkiae* (Clark, 1852) and *Kurtiella bidentata* compared. **A, B.** Interior of left and right valves of a specimen of *E. clarkiae* from Calahonda, Spain, length 1.70 mm. **C, D.** Detail of hinge; dashed line indicates insertion of opposite cardinal. **E, F.** Detail of hinge of specimen of *Kurtiella bidentata* from Sotogrande, Spain. Abbreviations: c: cardinal teeth; lat, lateral teeth; lig, ligament; lp, ligamental pit. Scale bars **C–F** = 500 μm .

have occurred, it may have required sympatric speciation processes, which could be envisaged if host selection were decisive in the settlement of larvae and aggregation of adults.

There is some variation in the maximum diameter of the prodissoconch. Ockelmann & Muus (1978) reported, for the reared larvae of Danish populations, a diameter of 135–150 μm for freshly released veligers and 400–440 μm at the time of metamorphosis; for specimens collected in the wild the diameter of prodissoconch 2 reached 580 μm . In our specimens from Spain and Northern Morocco the diameter of prodissoconch 2 ranges from 400 to 480 μm , but in a large lot examined from off Agadir, southern Morocco, the diameter of the prodissoconch does not exceed 400 μm .

It is noteworthy that the left valve of juvenile *Thracia* spp., particularly *T. phaseolina* (Poli, 1791) and *T. villosiuscula* (MacGillivray, 1827) resemble *Kurtiella bidentata* to the point

that they may be misidentified as such. This misleading similarity would explain why '*Rochefortia fontemaggii* Conti, 1864 (a junior synonym of *Thracia phaseolina*)' was compared to '*R. bidentata*' by Cerulli-Irelli (1908)

***Kurtiella ovata* (Jeffreys, 1881)**

(Fig. 9)

Montacuta ovata Jeffreys, 1881: 698, pl. 61 Fig. 4 (type locality not designated, cited localities *Porcupine* 1870 stn 24 (W of Cape St Vincent 37°19'N, 9°13'W, 292 fathoms), 27 (Gulf of Cadiz 36°37'N, 07°33'W, 322 fathoms) and 30 (36°15'N, 06°52'W, 386 fathoms).

Mysella ovata—van Aartsen, 1996: 36 (lectotype designated and figured).

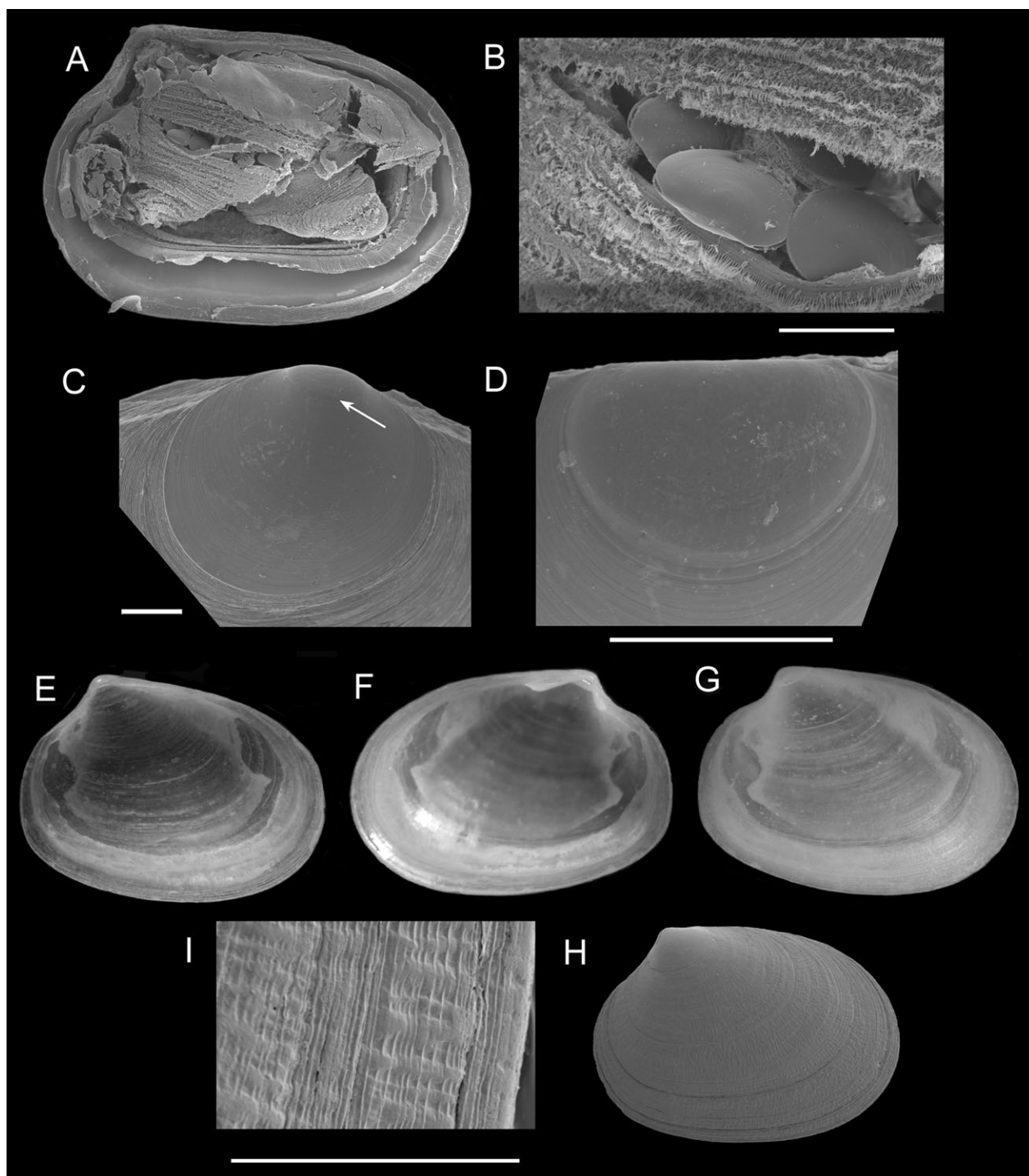


Figure 8. *Kurtiella bidentata* (Montagu, 1803), specimens from southern Spain. **A.** Critical-point dried specimen from Calahonda, with right valve and right mantle lobe removed, length of shell 2.27 mm; note more elongate outline and rounded posterior end. **B.** Detail of brooded larvae showing between gill filaments. **C.** Prodissoconch of another specimen, same locality. Arrow indicates the limit between prodissoconch 1 and prodissoconch 2. **D.** Detail of prodissoconch 1, same specimen. **E.** Inside of left valve from Sotogrande, Strait of Gibraltar, length 2.72 mm. **F.** Inside of right valve, same locality, length 2.84 mm. **G.** Outside of same right valve. **H.** Outside of right valve from Tarifa, Strait of Gibraltar, with antimarginal microsculpture, length 2.0 mm. **I.** Detail of microsculpture, shell margin towards right border of image. Scale bars **B, C, D, I** = 100 μ m.

Type material: Lectotype (van Aartsen, 1996; rv ca. 3.3 mm, now broken) in BMNH 1885-11-5-829 and paralectotypes (rv, 3.32 mm, lv 2.84 mm, lv 2.78 mm) from *Porcupine* 1870 stn 24, 27, 30.

Other material examined: Galicia bank, 7 valves; Lusitanian seamounts, 4 live-collected specimens, 53 complete shells and nearly 2000 valves; Meteor group seamounts, 7 complete shells and 121 valves (see Supplementary Data).

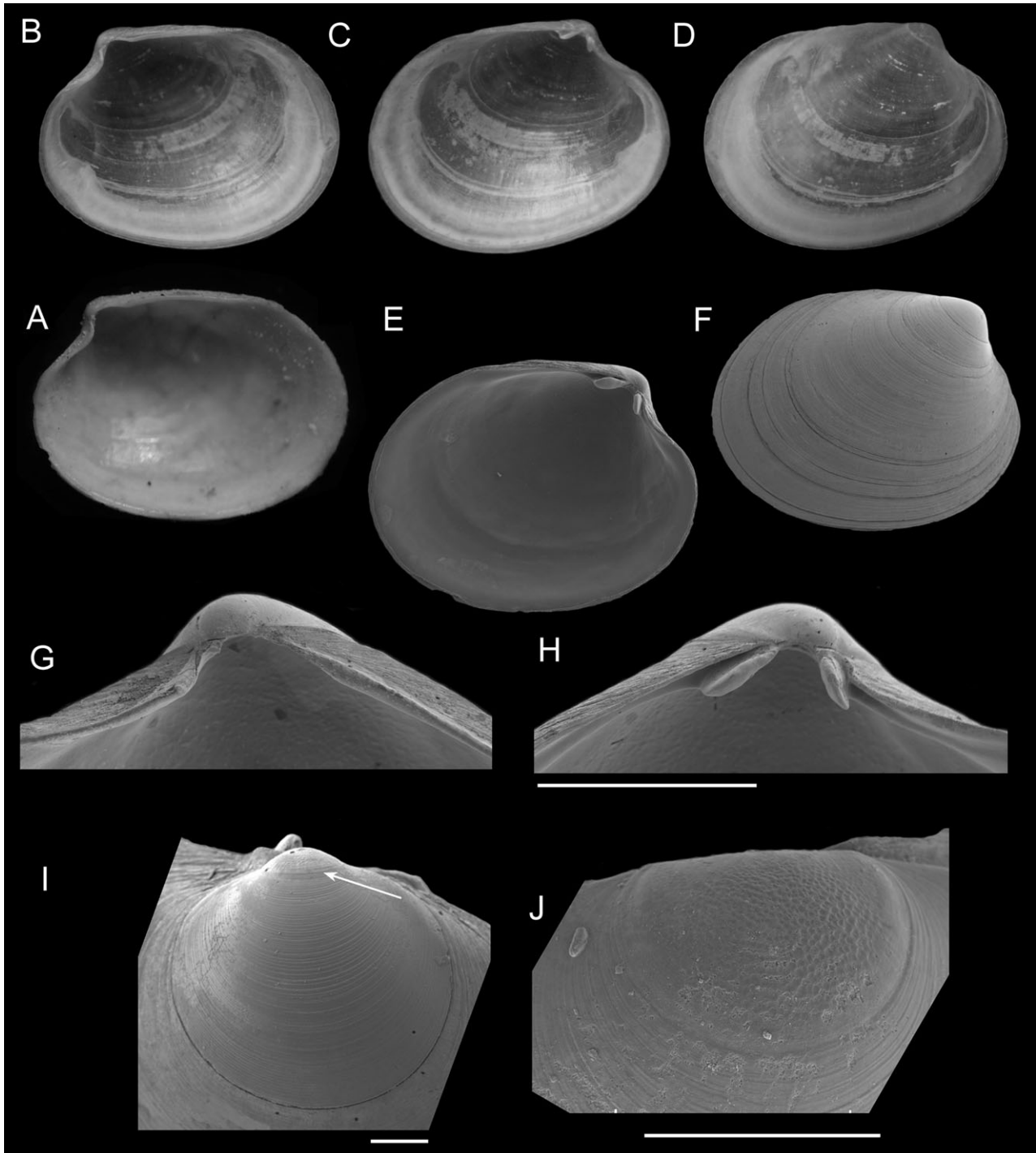


Figure 9. *Kurtiella ovata* (Jeffreys, 1881). **A.** Paralectotype, inside of left valve from *Porcupine* stn 24, 27, 30, length 2.78 mm. **B, C.** Inside of left and right valves of shell from Josephine Seamount DW61, length 2.6 mm. **D.** Outside of left valve, same shell. **E.** Inside of right valve from Gorringer Seamount CP20, length 2.2 mm. **F.** Outside of left valve from Gorringer Seamount DW06, length 2.0 mm. **G, H.** Detail of hinge of left and right valves of shell from Gorringer Seamount DW06. **I.** Prodissoconch of same shell. Arrow indicates limit between prodissoconch 1 and prodissoconch 2. **J.** Detail of prodissoconch 1, same shell. Scale bars: **G, H** = 1 mm; **I, J** = 100 μm .

Species-specific diagnostic characters: Shell up to nearly 4 mm in length with mean l/h ratio 1.4, beaks situated towards posterior 1/4 or further behind, markedly opisthocline. Prodissoconch 440–500 μm in diameter. Prodissoconch 1 distinct, elongate, ca. 120 μm long, with pitted microsculpture on central part and smooth ventral edge; prodissoconch 2 with faint growth

lines only. Dissoconch with sculpture of fine commarginal lines only. Anterior part of cardinal platform straight, sloping down gently; posterior part markedly bent inwards, sloping more abruptly and bordering distinct escutcheon. Lateral teeth well marked, diverging less than 90° on right valve, posterior tooth markedly overhanging cardinal platform; teeth hardly more

than a swelling of cardinal platform and diverging *ca.* 100° on left valve. Shell colour pale brown to yellowish on prodissoconch, whitish on dissoconch.

Distribution: As from types and material examined. The record of this species for the Alboran Sea in Peñas *et al.* (2006) is erroneous; SEM examination of the prodissoconchs revealed that it is based on juvenile *K. pellucida*.

Habitat: On deep bioclastic gravels from 180 to 700 m (mostly 200–400 m on the upper part of seamounts). Despite the large number of valves collected, only very few specimens were collected alive and a possible association with an invertebrate host could not be demonstrated.

Remarks: This species was hitherto known with certainty only from the type material, and appears to be widespread on the northeast Atlantic seamounts. The large amount of material and the SEM observations allow this species to be clearly distinguished from *K. bidentata*. It is diagnosed by its brownish prodissoconch (faded on most type specimens, but still apparent on one of the paralectotypes) with pitted microsculpture on prodissoconch 1, by the more markedly opisthoclinal and more posteriorly situated beaks, by the definite inward curvature of the posterior cardinal platform and by the distinct escutcheon (not so conspicuous in *K. bidentata*). The shape of the beaks is reminiscent of that in *K. tumidula* but the latter has a more inflated shell, with beaks still closer to the posterior end and is proportionally more elongate in general shape.

***Kurtiella pellucida* (Jeffreys, 1881)**

(Figs 10–12)

Montacuta pellucida Jeffreys, 1881: 697, pl. 61, Fig. 3 (Adventure Bank, Strait of Sicily).

Mysella pellucida—van Aartsen, 1996: 37–38.

Montacuta simillima Smith, 1892: 131, pl. 12, fig. 1 (St Helena).

Type material: Holotype (lv, 5.39 mm) in BMNH 1885-11-5-939 from Porcupine 1870 stn, Adventure Bank.

Other material examined: Alboran Sea, 1 live-collected specimen, 1 shell and 3 valves; Lusitanian seamounts, 94 valves; St Helena Island, 2 valves identified as ‘*Tellimya simillima* E. Smith’ in Jousseume collection, MNHN.

Species-specific diagnostic characters: Shell up to nearly 10 mm in length with mean l/h ratio over 1.4 in juveniles, tending to *ca.* 1.3 in large specimens; beaks situated towards the posterior 1/3 and very slightly opisthoclinal in juveniles, tending to become closer to midline and still less opisthoclinal in large specimens. Prodissoconch 380–480 µm in diameter. Prodissoconch 1 distinct, elongate, *ca.* 120–130 µm long, with microsculpture of 5–6 narrow radial threads on central part and smooth ventral edge; prodissoconch 2 with faint growth lines only. Dissoconch smooth or only with very fine commarginal growth lines, very fragile and translucent. Anterior and posterior parts of cardinal platform straight, sloping down gently, posterior one bordering a very narrow but distinct escutcheon. Lateral teeth well marked but very short, diverging slightly more than 90° on right valve; teeth hardly more than a swelling of cardinal platform and diverging broadly *ca.* 150° on left valve. Shell colour pale brown to yellowish on prodissoconch, whitish on dissoconch.

Distribution: As from types and material examined: Strait of Sicily, Alboran Sea, Lusitanian seamounts, and St Helena (see Remarks).

Habitat: On deep bioclastic gravels from 165 to 700 m (mostly 200–300 m on the upper part of seamounts), not collected alive on the NE Atlantic seamounts.

Remarks: There are some differences in outline between the holotype (single left valve from Adventure Bank, Fig. 10A, B) and the specimens found alive in the Alboran Sea (Peñas *et al.*, 2006, and Fig. 10J–M herein) assigned to this species. In particular, the posterior segment of the cardinal platform is markedly longer in the former. However, some specimens from the seamounts come close to the outline of the holotype and we find it more parsimonious to accept this as intraspecific variation and use the name for the species figured herein. The presence of delicate threads radiating from the umbo of the prodissoconch 1 is an unusual and diagnostic feature, which can only be seen using scanning electron microscopy and therefore could not be checked on the type.

Many shells, unquestionably conspecific with those from Alboran, were found on all the Lusitanian seamounts along with *K. ovata*, but not in the Meteor group despite a similarly large sampling effort. There is a marked allometry in the growth: young specimens are rather compressed and markedly inequilateral like other species in the genus, but the Atlantic shells reach a large size, becoming quite triangular in shape with markedly convex valves.

A lot of two large valves from St Helena Island, in the MNHN collection and presumably originating from Turton, like the type specimens of the species, has been examined under SEM. These valves are similar in shape and size to the large valves collected on the Lusitanian seamounts, and one of them displays the diagnostic microsculpture of radial threads on the prodissoconch 1. It is nevertheless surprising that the same species could extend its range to such distant locality and yet be missing in the Meteor seamount group.

***Kurtiella triangularis* (Watson, 1897)**

(Fig. 13)

Montacuta triangularis Watson, 1897: 264–265, pl. 20, fig. 33 (Funchal and Ponta de São Lourenço, Madeira).

Mysella triangularis—van Aartsen, 1996: 34–35 (figs 13–14 labelled ‘*Mysella tumidula*’ in error).

Type material: Syntypes (one left valve and one right valve) in BMNH.

Other material examined: Spain, Alboran Island and Strait of Gibraltar, 5 complete shells and 11 valves; Morocco, 2 valves; Canary Is, 2 complete shells and 1 valve; Selvagen Is, 4 live collected specimens.

Species-specific diagnostic characters: Shell up to *ca.* 3 mm in length, rather solid for its size but translucent, with mean l/h ratio 1.4; beaks situated between the posterior 1/3 and 1/4, very slightly opisthoclinal. Prodissoconch ovate in outline, 440–530 µm in maximum diameter without definite prodissoconch 2, smooth or with indistinct concentric wrinkles near umbo. Dissoconch with sculpture of fine commarginal lines only. Anterior and posterior sections of cardinal platform straight. Lateral teeth well marked and diverging *ca.* 100° on right valve; teeth hardly more than a swelling of cardinal platform and diverging *ca.* 120° on left valve. Shell colour white on dissoconch and prodissoconch.

Distribution: Madeira, Selvagens, Canary Islands, Atlantic coast of Morocco, the Strait of Gibraltar and Alboran island in the Mediterranean. No species of *Kurtiella* were found on the shores of the Azores despite appropriate sampling in possible habitats.

Habitat: Intertidal among rocks and algal turf; association with benthic invertebrates not documented.

Remarks: The large, oval prodissoconch without any limit indicating the beginning of a prodissoconch 2 is unique among the European species here assigned to *Kurtiella*, and indicates a non-planktotropic development. A quite similar prodissoconch

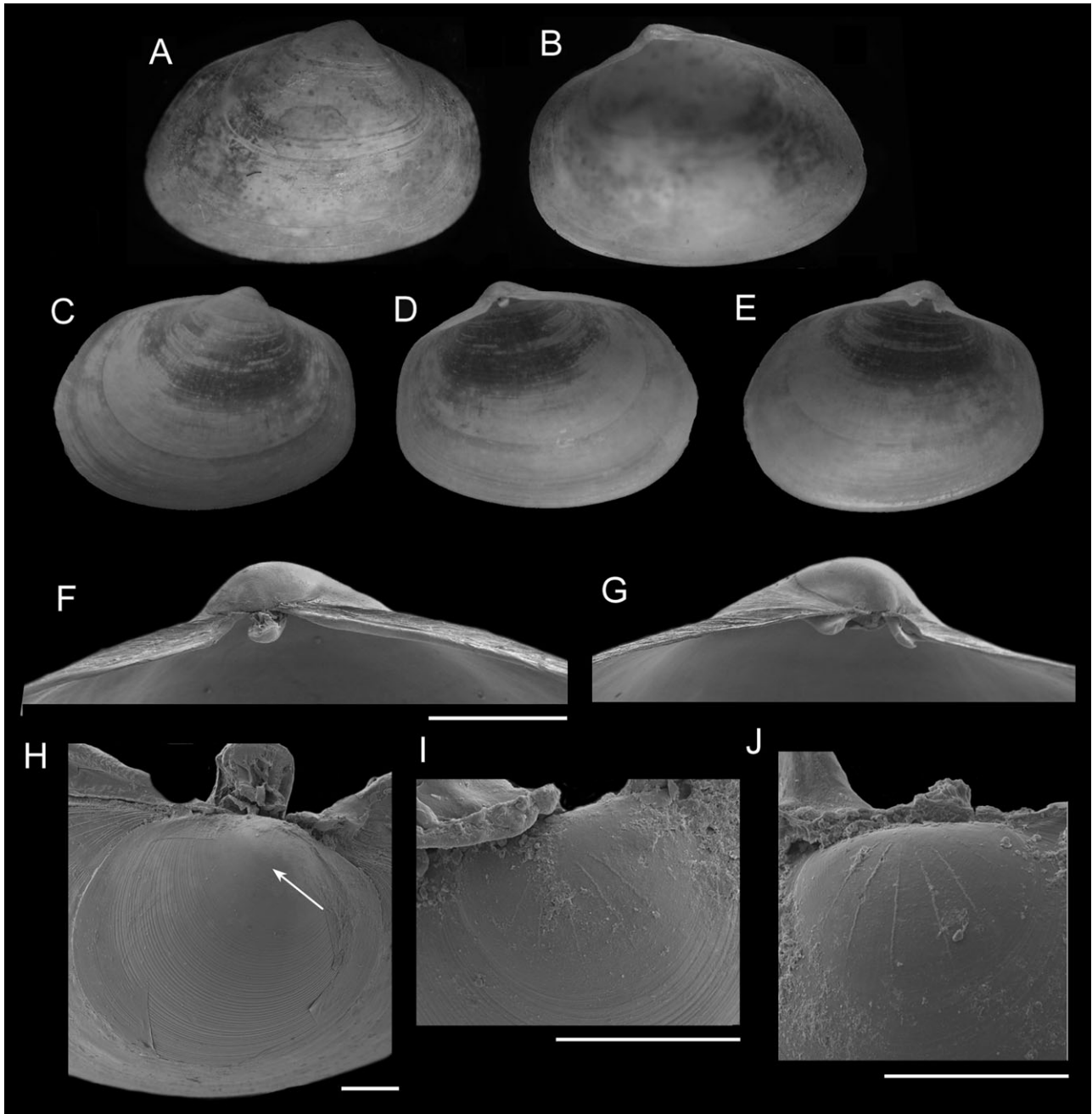


Figure 10. *Kurtiella pellucida* (Jeffreys, 1881) from Mediterranean. **A, B.** Holotype, outside and inside of left valve from *Porcupine* stn Adventure Bank, length 5.4 mm. **C.** Outside of the left valve of a specimen from Xauen Bank, Alboran Sea, *Balgim* stn DW136, length 3.5 mm. **D, E.** Inside of left and right valves of same specimen, with internal ligament still attached. **F, G.** Detail of the hinge of left and right valves, same specimen. **H.** Prodissoconch of same specimen. Arrow indicates limit between prodissoconch 1 and prodissoconch 2. **I.** Detail of prodissoconch 1, same specimen. **J.** Prodissoconch 1 of another valve from Alboran I., coll. A. Peñas. Scale bars: **F, G** = 500 μm ; **H, I, J** = 100 μm .

is seen in the boreal *Altenaeum dawsoni* (see Fig. 4F), but this does not show the characteristic concentric wrinkles of *K. triangularis*. Brooding is probable although not observed among the few live-collected specimens examined. This species is also distinguished from *K. bidentata* by the configuration of the hinge, where the posterior segment is rather straight, not curved inwards, and by the generally more solid construction of the shell.

This seems to be the sole representative of the genus on the shores of Atlantic islands. It is noteworthy that *K. bidentata* was

not recorded in any of the Macaronesian archipelagos and that existing reports are very general statements (e.g. Tebble, 1966; Nordsieck, 1969), not based on a particular material. The two species are nevertheless sympatric in the Strait of Gibraltar (van Aartsen, 1996, and material herein) and in Alborán Island (Peñas *et al.*, 2006). We were reluctant to accept that the same species with probably limited ability for dispersal, could be present in such widely separated mainland and insular localities, but cannot see any difference between specimens examined.

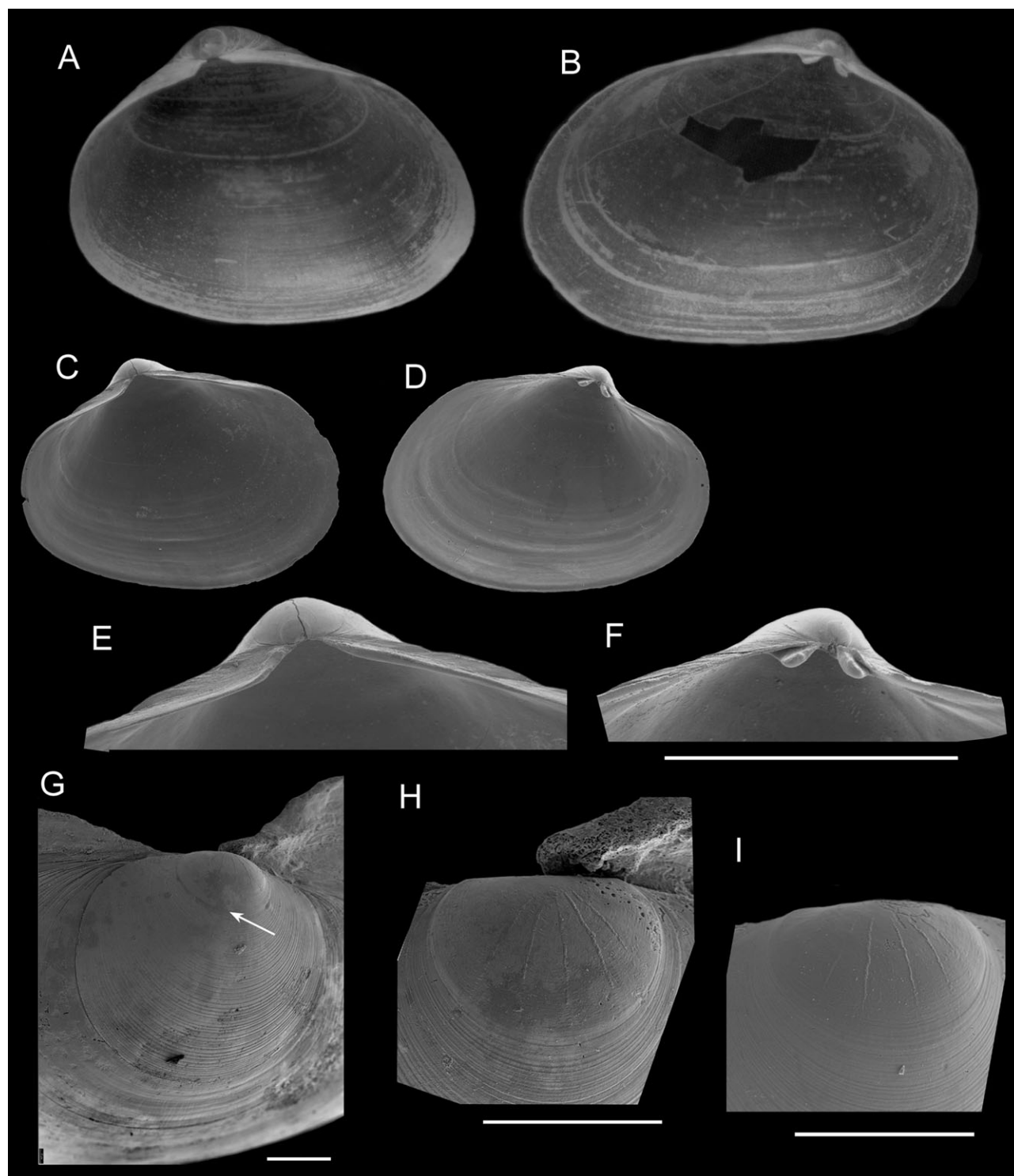


Figure 11. *Kurtiella pellucida* (Jeffreys, 1881) from the Lusitanian seamounts. **A, B.** Inside of left valve and of right valve from Gorringe Seamount CP20, length of both valves 4.5 mm. **C, D.** Inside of left and right valve of shell from Ampère Seamount CP99, length 3.6 mm. **E, F.** Detail of hinge of left and right valves, same shell. **G.** Prodissoconch of same shell. Arrow indicates limit between prodissoconch 1 and prodissoconch 2. **H.** Detail of prodissoconch 1, same shell. **I.** Prodissoconch 1 of another valve from Seine Seamount. Scale bars: **E, F** = 1 mm; **G, H, I** = 100 μ m.

***Kurtiella tumidula* (Jeffreys, 1866)**
(Fig. 14)

Montacuta tumidula Jeffreys, 1866: 396–397 (NW coast of Rosshire, Scotland).

Mysella tumidula—van Aartsen, 1996: 35.

Material examined: Norway, 42 live-collected specimens and 1 valve. France, Mediterranean coast, 8 valves. Alboran Sea, 6 live-collected specimens. Azores, 1 valve identified as *Montacuta ovata* Jeffreys, 1881 in coll. H. Fischer, MNHN.

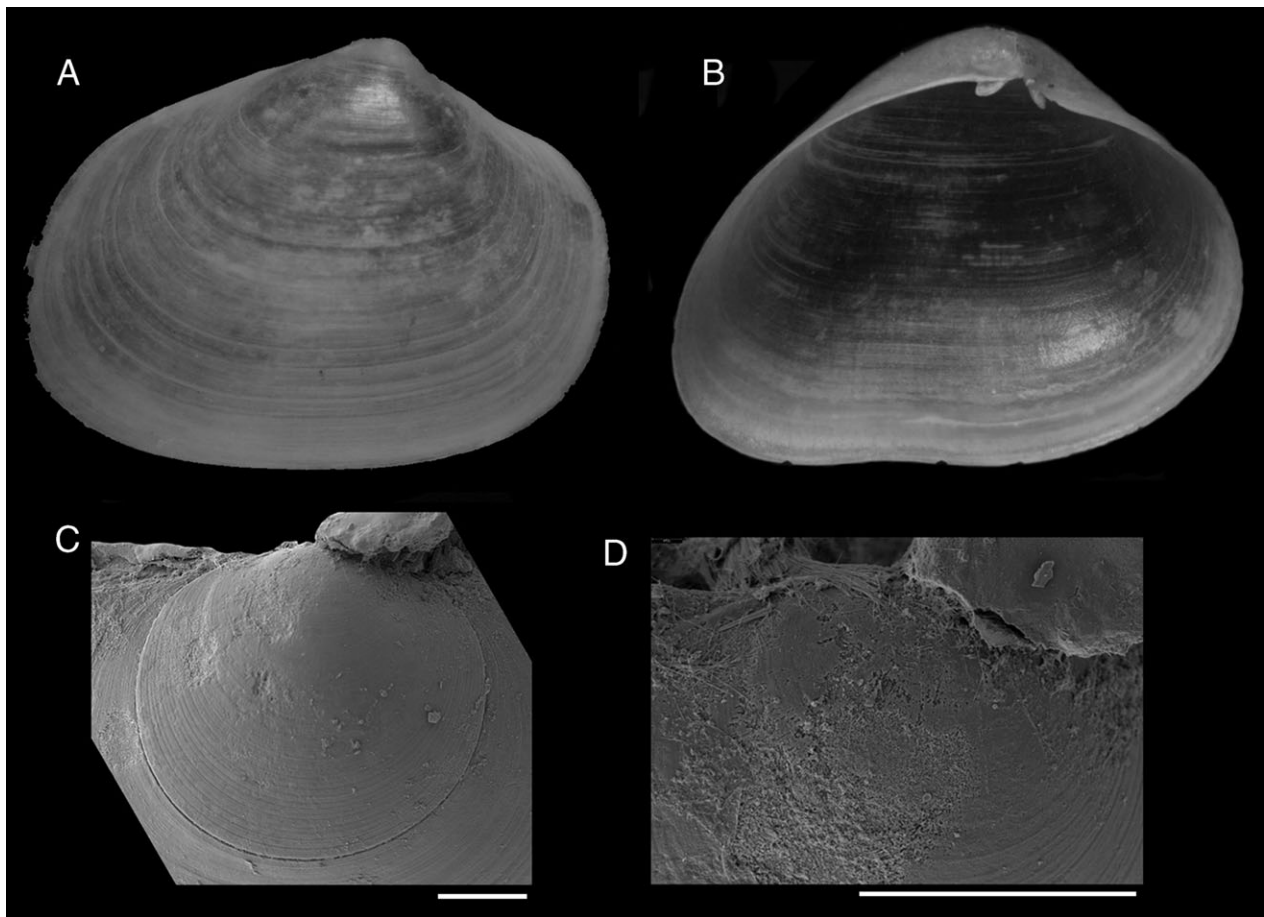


Figure 12. *Kurtiella pellucida* (Jeffreys, 1881), valves from St Helena Island identified as *Montacuta simillima* Smith, 1892 in Jouseaume collection, MNHN. **A.** Exterior of left valve, length 4.96 mm; **B.** Interior of a right valve, length 5.28 mm. **C.** Prodissoconch, same valve as B. **D.** Detail of prodissoconch 1 showing traces of radial threads.

Species-specific diagnostic characters: Shell up to ca. 2.6 mm in length with mean l/h ratio ca. 1.4; beaks situated towards the posterior 1/4, definitely opisthocline. Prodissoconch 360 μm in diameter, with distinct, elongate prodissoconch 1 and prodissoconch 2 with definite growth lines. Dissoconch with sculpture of fine commarginal lines and with periostracum forming a few, widely separated radial threads. Anterior part of cardinal platform slightly bent upwards, nearly horizontal; posterior part short, straight and sloping.

Lateral teeth well marked, broadly diverging ca. 110° on right valve, narrow and elongate but definite, diverging ca. 130° on left valve. Shell colour brown on prodissoconch, whitish on dissoconch, with yellowish periostracum.

Pallial cavity with only inner demibranch present, no labial palps.

Distribution: Known with certainty from northern Norway to the Strait of Gibraltar, and towards the entrance of the Mediterranean Sea. The valves collected off Mediterranean France, and more generally all records within the Mediterranean based on empty shells (e.g. the valves from off Palermo, Sicily, illustrated in van Aartsen, 1996), are old valves with a worn aspect. They are therefore likely to be Pleistocene fossils and do not indicate with certainty that the species is still living there.

Habitat: In deep water 200–800 m, not known with precision. A close association with an invertebrate host is likely but has not been demonstrated by observation.

Remarks: Concurring with the finding by Allen (2000) on specimens identified as *Mysella verrilli* Dall, 1899, we could not see any labial palps on the critical-point dried specimens of this species. We have not examined any American material and will not tackle the question of whether the populations from the Western Atlantic are specifically distinct from *K. tumidula*. Nevertheless we can see no reason to recognize more than one species among the material examined herein, and the occurrence of this species in the Azores strongly suggest that an amphiatlantic distribution is possible. Allen (2000) distinguishes *M. verrilli* on the grounds that the posterior end is more truncated, which could apply to our specimens from the Alboran Sea as well as to the specimens reported by Allen in the 'Western Mediterranean basin' (but the coordinates given $32^\circ 29.0' \text{N}$, $16^\circ 53.0' \text{W}$, 1446 m would situate the sample on the slope off Essaouira, Atlantic Morocco). Contrary to what is reported by Allen (2000: Fig. 8, but not Fig. 9) on a large (3.3 mm) specimen from the Western Atlantic, we could not see any indication of an outer demibranch, and the architecture of the gill appears essentially similar to that in *K. bidentata* except that there are much fewer filaments.

DISCUSSION

The new genus *Kurtiella* is represented in European waters by five species, ranging overall from the intertidal zone to the bathyal. Four of the species have a larval shell composed of a small,

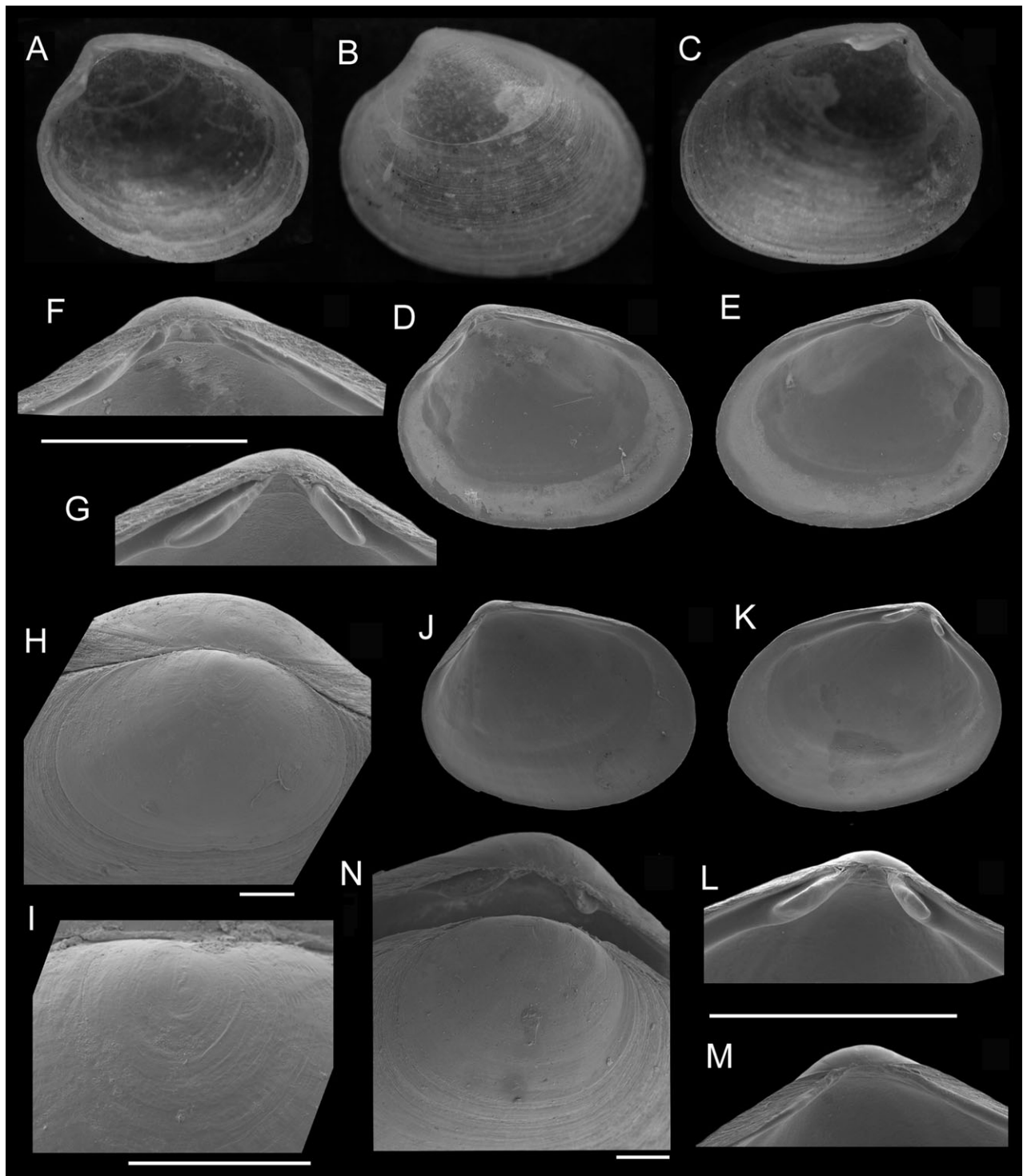


Figure 13. *Kurtiella triangularis* (Watson, 1897). **A.** Inside of a syntype (left valve), BMNH, length 2.93 mm. **B, C.** Outside and inside of a syntype (right valve), BMNH, length 3.26 mm. **D, E.** Inside of left and right valves of a specimen from Punta del Hidalgo, Tenerife, Canary Is, length 1.96 mm. **F, G.** Detail of hinge of left and right valves, same specimen. **H.** Prodissoconch of juvenile specimen, same locality. **I.** Detail of apical part of prodissoconch showing characteristic concentric wrinkles, same specimen. **J, K.** Inside of left and right valves of specimen from Getares, Strait of Gibraltar, length 1.5 mm. **L, M.** Detail of hinge of left and right valves, same specimen. **N.** Prodissoconch of another specimen, same locality. Scale bars **F, G, L, M** = 500 μm ; **H, I, N** = 100 μm .

well delimited prodissoconch 1 and a larger prodissoconch 2, suggesting that the pattern of larval development conforms to that documented for *K. bidentata*, i.e. brooding in the pallial cavity followed by a planktotrophic stage allowing long-distance

dispersal. The exception is *K. triangularis*, which does not display a differentiated prodissoconch 2 and is therefore inferred to lack a planktonic larval stage. This species nevertheless is able to bridge the distance between Canary Islands and the southwest

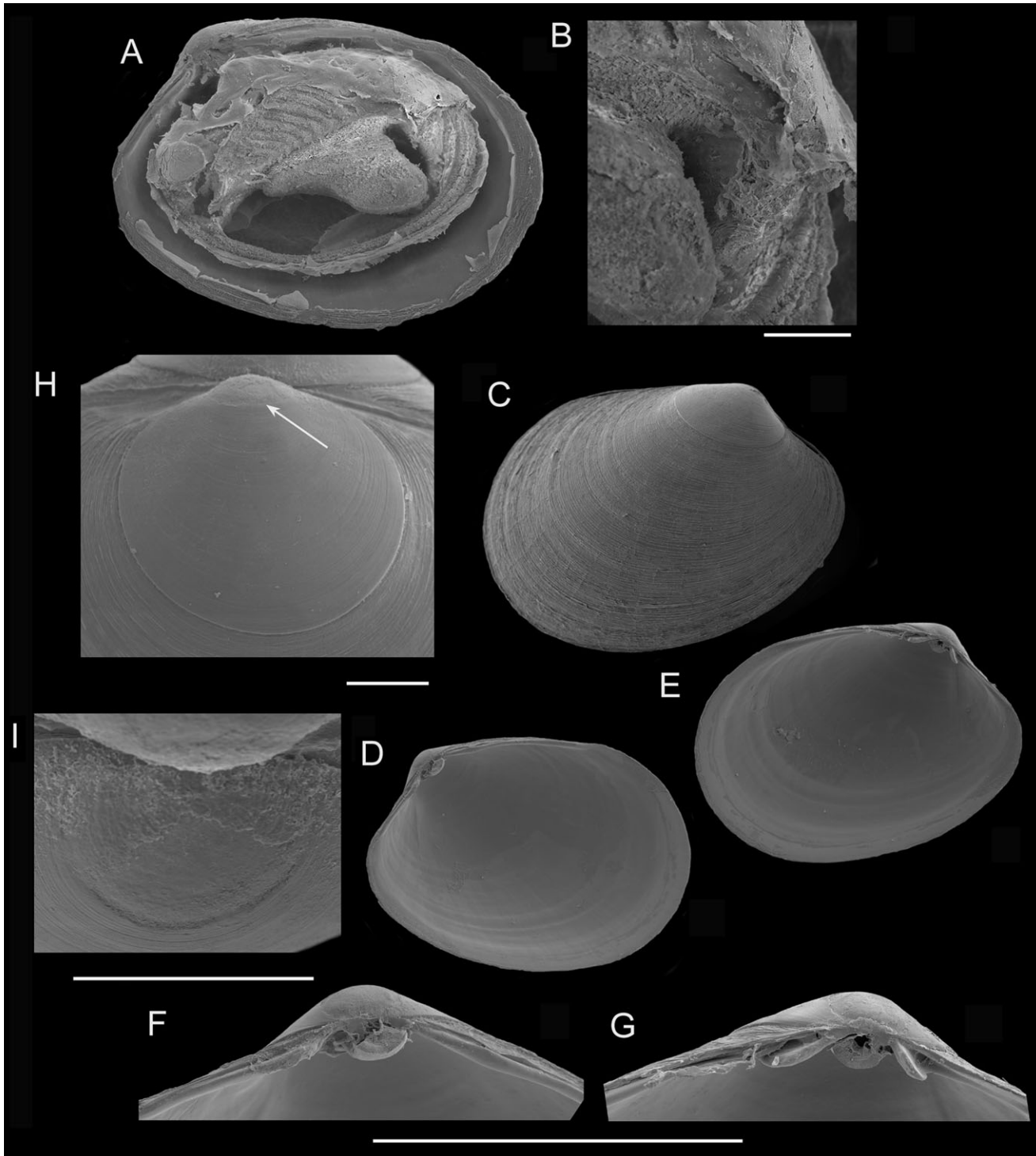


Figure 14. *Kurtiella tumidula* (Jeffreys, 1866). **A.** Critical-point dried specimen from Korsfjorden, Norway, with right valve and right mantle lobe removed, length of shell 1.42 mm. **B.** A tilted view of the area anterior to foot, where labial palps would be expected (see Fig. 6A). **C.** Exterior of specimen from Alboran Sea, Balgim DW147, length 1.20 mm. **D, E.** Inside of left and right valves of another specimen, same locality. **F, G.** Detail of the hinge of left and right valves, with ligament still attached, same specimen. **H.** Prodossoconch of specimen from Balgim DW128. Arrow indicates limit between prodossoconch 1 and prodossoconch 2. **I.** Detail of prodossoconch 1, same specimen. Scale bars: **F, G** = 500 μm ; **B, H, I** = 100 μm .

European mainland. The Antarctic species '*Mysella*' *charcoti* (Lamy, 1906), also non-planktotrophic, has been shown (Domaneschi *et al.*, 2002) to survive its passage in the digestive tract of demersal fish and to be passively dispersed a short distance in this way. This is not likely in the context of the algal

turf of the Atlantic islands, where intertidal fish are not expected to move far away from their habitat, and where rafting of seaweed seems the most probable alternative means of dispersal.

The generic characters outlined for the new genus *Kurtiella* are consistent with the placement in the family Montacutidae,

which is universally accepted for the type species *K. bidentata*. The Montacutidae are diagnosed (Pelseener, 1911; Chavan in Moore, 1969) as small sized heterodont bivalves, inequilateral with the anterior part most developed, with a well developed internal ligament situated below the beaks, subequal adductor muscle scars and an entire pallial line. Like the Galeommatidae and Leptonidae, and unlike most heterodonts, the mantle cavity of Montacutidae has a broad, anterior inhalant aperture which is continued into the pedal gape, and a smaller posterior exhalant aperture separated from the former by a small stretch of fused mantle lobes. However, contrary to Galeommatidae and Leptonidae, the Montacutidae show little, if any, development of mantle tentacles (see Fig. 5) and have only the inner demibranch developed. Brooding of the larvae in the pallial cavity (Figs 6E, 8B) seems to be a common trait if not a diagnostic character.

We agree with Allen (2000) that the loss of labial palps in *Kurtiella tumidula* and *K. verrilli* is an evolutionary change which does not preclude their generic assignment, because other diagnostic characters are present. This loss may be interpreted as a further derived condition which accompanies a tighter relationship with a host species, such as the shift between being a commensal and becoming a parasite.

Other genera assigned to the family Montacutidae are united by the presence of a strong internal ligament which plays a major role in the articulation of the shell, but display important variations regarding the arrangement of the hinge teeth. *Montacuta*, in its type species *M. substriata* (Montagu, 1808), has only the anterior laterals developed, quite evenly in both valves. Conversely in *Tellinomya* and *Planktomya* (see Gofas, 2000) each valve has one well defined cardinal anteriorly to the ligament, and no definite development of laterals. The recently erected *Coracuta* Holmes, Gallichan & Wood, 2006 resembles more *Epilepton* in having a small tubercle beneath the umbo anterior to the ligament (homologous with a cardinal of *Epilepton*) in the left valve, but not in the right valve.

Although it is not the scope of this paper to revise all the species which could be assigned to *Kurtiella* worldwide, it can be stated that a fair number of species currently classified in *Mysella* or *Rochefortia* should prove to belong to the new genus. We have checked specimens of the boreal Atlantic '*Mysella*' *sovaliki* MacGinitie, 1959 (see also van Aartsen, 1996: 36), of the Western Atlantic '*Mysella*' *planulata* (Stimpson, 1851) and of the South African '*Montacuta*' *natalensis* Smith, 1899, which all display the characteristic reduction of the cardinal platform under the umbo and, in the case of *Kurtiella planulata*, also the lithodesma. Examination of West African material in MNHN reveals at least three undescribed species which would bridge the distribution of the genus to South Africa. In the Eastern Pacific, in addition to *K. sovaliki*, species such as '*Mysella*' *pedroana* Dall, 1899 belong in this group (see Boyko & Mikkelsen, 2002). The genus seems therefore to be well represented in medium-high latitudes of both hemispheres. In the subantarctic area, '*Mysella*' *charcoti* (Lamy, 1906) studied by Passos, Domaneschi & Sartori (2005) and well figured by Dell (1990), somewhat resembles *Kurtiella* in the hinge, but its ligamental pit does not interrupt the cardinal platform, resembling more *Altenaeum* in this respect. We are surprised by the lack of references to species which could be assigned to *Kurtiella* in the Australian and Indo-West Pacific regions, but this must be taken with caution as there is still much to be discovered regarding micro-molluscs of these vast, species-rich areas.

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We extend our warmest thanks to the National Library of New Zealand and to the Royal Society of New Zealand for having made available the entire collection of *Transactions and Proceedings of the Royal Society of New Zealand 1868–1961* on the Internet <<http://rsnz.natlib.govt.nz/>>, including a wealth of malacological papers.

SUPPLEMENTARY MATERIAL

Supplementary material is available at Journal of Molluscan Studies online.

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