

The deep-water protobranch *Deminucula* (Bivalvia) in the Mediterranean Plio-Pleistocene and the contribution of palaeobiogeography to taxonomy

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Abstract

Three small nuculids from Plio-Pleistocene bathyal deposits in Southern Italy are allocated in *Deminucula* Iredale, 1931, namely *D. striatissima* Seguenza (1877), *D. seguenzai* nom. nov. and *D. calabra* n. sp. The status of *Deminucula* is debated (synonym of *Nucula* Lamarck, 1799 or full genus) and in the present work evidences are brought about its taxonomic validity. The type species of *Deminucula* is an extant species from Southeastern Australia and fossil species of this genus are known from the Cenozoic of New Zealand. In the present work, it is hypothesised that *Deminucula* had a wide east-west distribution, until the Early-Middle Miocene, when the final separation of the post-Tethyan eastern sectors (Atlantic and Mediterranean) from the eastern ones (Indo-Pacific) occurred. Discussion focuses on the importance of (paleo)biogeographic data and of a less conservative taxonomic approach to improve the systematics of complex groups, such as the Nuculidae.

Riassunto

Il genere *Deminucula* Iredale, 1931 comprende piccoli nuculidi a distribuzione batiale, con conchiglia triangolare, subequilaterale, liscia, a margine ventrale crenulato. La fossetta ligamentare è particolarmente piccola e sono presenti linee radiali di natura strutturale che producono l'impressione di una sottile scultura radiale. La specie tipo è *Nucula praetenta* Iredale, 1924, dell'Australia sud-orientale. Oltre a questa specie attuale, sono note alcune specie fossili nel Cenozoico (Eocene e Miocene) della Nuova Zelanda. La distribuzione attuale di *Deminucula*, comunque, sembra essere più ampia, anche se esclusivamente pacifica. La validità tassonomica di *Deminucula* è controversa, potendosi trattare di un sinonimo di *Nucula* Lamarck, 1799 oppure di un genere a sé stante. In questo lavoro, tre nuculidi del Plio-Pleistocene mediterraneo, provenienti da depositi batiali dell'Italia meridionale, sono riferiti a *Deminucula*: *D. striatissima* Seguenza (1877), *D. seguenzai* nom. nov. e *D. calabra* n. sp. La presenza di *Deminucula* in un'area oggi completamente separata da quella dove il genere è presente sin dall'Eocene è spiegata attraverso le ricostruzioni paleogeografiche basate sulla tettonica delle placche. Si ipotizza che *Deminucula* avesse un'ampia distribuzione da est (Pacifico) ad ovest (Mediterraneo) fino al Miocene inferiore-medio, quando i settori post-tetidei occidentali furono definitivamente isolati dall'Indo-Pacifico. L'ampia distribuzione biogeografica e stratigrafica, unitamente ai caratteri morfologici, danno sostegno all'ipotesi che *Deminucula* rappresenti un distinto gruppo di nuculidi. Si sottolinea l'importanza del contributo che la paleobiogeografia può dare per migliorare la sistematica di gruppi complessi, quali la famiglia Nuculidae, assieme ad un approccio tassonomico non eccessivamente conservativo.

Key words

Nuculidae, *Deminucula*, new species, Mediterranean, Plio-Pleistocene, deep-water molluscs, systematics, palaeobiogeography.

Introduction

Paucity of taxonomically useful characters, disagreement about the taxonomic application of these characters at genus and even at familial and subfamilial level (e.g. Allen & Hannah, 1986; Maxwell, 1988a; Ockelmann & Warén, 1998; Gofas & Salas, 1996), a poor knowledge of the soft part anatomy, all these problems make the classification of the protobranch bivalves difficult and unstable.

The extant and fossil representatives of the large family Nuculidae are generally clustered into few genera, of which *Nucula* Lamarck, 1799 is the largest one. Examples of these conservative taxonomic views are given by Allen & Hannah (1986), Bergmans (1978, 1991), Salas (1996) and Villaruel & Stuardo (1998). However, some efforts are made to develop a less conservative taxono-

my which tries to emphasize some shell characters (primarily shape, hinge, ligament and sculpture), as done by Maxwell (1988 a, b) and Kilburn (1994, 1999).

Protobranchs are typical components of the deep-sea benthos and the present work deals with a poorly known, debated deep-sea nuculid genus, focusing on taxonomy and biogeography.

Geological setting and methods

The present work is based on material collected over several years in the bathyal deposits of Plio-Pleistocene age cropping out in Southern Italy, particularly in the Messina Strait area. In this area, the strong Plio-Quaternary tectonics split the substrate in fault controlled, sinking compartments, on which deep-sea sediments were deposited (Barrier, 1987; Montenat & Barrier,

1987). More distal Tyrrhenian and Jonian sectors, have been affected by less intense tectonics but strong vertical displacements are documented by the bathyal sequences cropping out near the coast.

The study material is from four localities (Fig. 1). Age ranges from Middle Pliocene (Rometta) to Early-Middle Pleistocene (Fiumefreddo di Sicilia, Vallone Catrica, Bovalino Superiore). The molluscan fauna from these bathyal beds is rich in protobranch bivalves and other typically deep-sea taxa, allowing paleodepths from the shelf/slope transition to some 500-600 m to be inferred (Di Geronimo & La Perna, 1997; Di Geronimo *et al.*, 1997; La Perna, 2003 and unpubl. data).

Besides the well known prodissoconch and dissoconch, a third term, interdissoconch, is used in the present work. It was introduced by Bergmans (1978) to indicate the early post-larval stage, smooth or with a fine sculpture different from that of the dissoconch and with a distinct margin.

Illustrated material and types are deposited in the Laboratorio di Malacologia, Museo di Zoologia dell'Università di Bologna (MZB).

Systematics

Classis BIVALVIA Linnaeus, 1758

Subclassis PROTOBRANCHIA Pelseneer, 1889

Ordo NUCULOIDA Dall, 1889

Familia NUCULIDAE Gray, 1824

Genus *Deminucula* Iredale, 1931

The type species of *Deminucula* is *Nucula praetenta* Iredale, 1924 (replacement name for *Nucula umbonata* Smith, 1891, non Seguenza, 1877) from off Sydney, Southeastern Australia (Fig. 2). Schenck (1934) questioned the nuculid affinities of *N. praetenta* because of the apparent lack of a ligament pit and this led Vokes (1980) to include *Deminucula* in the Mallettiidae (Bergmans, 1978). The type material of *N. praetenta* (apparently, the only material so far known for this species) was studied by Bergmans (1978), within a revision of the Australian nuculids, with the conclusion that *Deminucula* is a synonym of *Nucula*. More recently, Maxwell (1988 a, b) advocated the validity of *Deminucula* as a full genus.

The characters of *Deminucula* are a bluntly trigonal, subequilateral shape, small size (not exceeding 5 mm in length), small, inconspicuous ligament pit, not projecting below the hinge plate, almost smooth surface, fine structural radiating lines, which give impression of a true radial sculpture, and a finely crenulate margin. Shells tend to be somewhat sturdy, inflated and with a relatively strong hinge, with stout to indistinctly chevron-shaped teeth.

Structural radiating lines are seen in several nuculids with a marginal crenulation, but in *Demicula* they are much more obvious. Crenulation is due to the exposed terminal part of radial rods of aragonitic prisms in the outer shell-layer and partly encased in the inner layer (Van de Poel, 1955; Taylor *et al.*, 1969: pp. 64-67). Probably, well distinct radial lines are due to a particularly



Fig. 1. Map of Calabria and Sicily with collecting sites (solid dots).

Fig. 1. Mappa di Calabria e Sicilia con le località di raccolta.

thin external layer. A major subdivision of the Nuculidae is traditionally based on the presence/absence of crenulation (Schenck, 1934; Van de Poel, 1955; Maxwell, 1988b). However, Gofas & Salas (1996) suggested that the smooth margin is a symplesiomorphic character, related to the loss of the radial rods. As remarked by Kilburn (1999), rods and crenulation may have been independently lost in distinct nuculid lineages.

A trigonal, subequilateral shape is uncommon among nuculids. *Brevinucula* Thiele, 1934 has a deeply triangular shape, but the shell is unusually flat and sturdy, with a smooth ventral margin. Nuculids with a strongly posterior umbo tend to have an elongate, oblique and projecting resilifer (i.e. leaning out below the hinge plate). However, a projecting resilifer can be present in species with a subequilateral shape.

In *Deminucula* the interdissoconch is well distinct. Unfortunately, in most literature the interdissoconch stage is overlooked or even confused with the larval stage and this prevent from drawing conclusions about its occurrence within the family and its possible taxonomic meaning.

Besides the type species, three fossil species from New Zealand are currently assigned to *Deminucula* (Maxwell, 1988a, Beu & Maxwell, 1990, Maxwell, 1992), namely *D. bergmansii* Maxwell, 1988, *D. totangiensis* (Marwick,

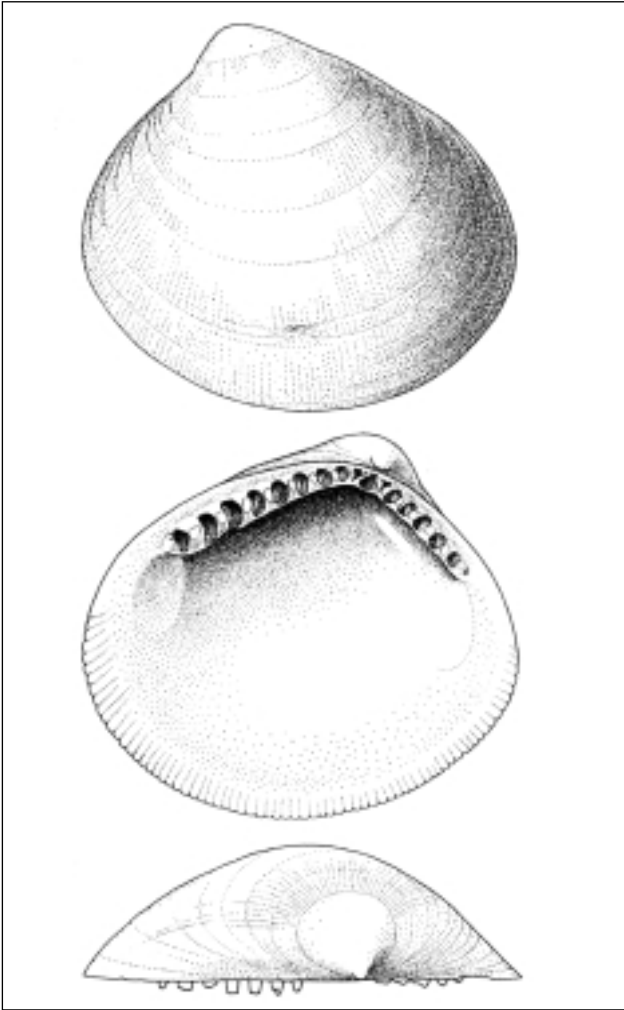


Fig. 2. Lectotype of *Nucula praetenta* Iredale, 1924, 3.37 mm (after Bergmans, 1978, modified).

Fig. 2. Lectotipo di *Nucula praetenta* Iredale, 1924, 3.37 mm (da Bergmans, 1978, modificato).

1931), both Late Miocene, and *D. infrequens* Maxwell, 1992, Eocene.

Deminucula has a deep-sea distribution. The type species is from 750 m depth and all the fossil species so far known are from outer shelf-bathyal deposits.

Deminucula striatissima (Seguenza, 1877)

Fig. 3 a-c; Fig. 4 a-f

Nucula striatissima Seguenza, 1877a: p. 92.

Nucula striatissima Seguenza, 1877b: p. 1166, pl. 1, figs. 1, 1a, 1b.

Deminucula striatissima - La Perna, 2003: p. 24.

Description

Shell bluntly trigonal, subequilateral, slightly elongate antero-posteriorly, inflated, thick-walled. Umbo large, opisthogyrate, posterior to midline. Dorsal margin notably short, convex. Anterior margin strongly convex, with an obscure antero-ventral angulation. Posterior margin moderately convex, passing with a smooth angulation into a broadly rounded ventral margin. Surface almost smooth, with only faint, irregularly spaced growth lines. Fine, closely set structural lines give impression of a

radial sculpture. Hinge plate robust, arched to obscurely angulose, with stout to barely chevron-shaped teeth in two series, the anterior slightly longer and stronger. Resilifer small, poorly distinct, not projecting. Adductor muscle scars poorly distinct. Inner ventral margin finely crenulate. Interdissoconch well distinct, about 0.70 mm in diameter. Prodissoconch roundish, about 200 µm in diameter. Maximum size 2.70 mm in antero-posterior length.

Types

Unknown. The Seguenza collection was mostly destroyed by the earthquake of Messina (1908).

Material examined

Rometta, Middle Pliocene, 24 valves (topotypic material).

Distribution

Nucula striatissima was originally reported (Seguenza, 1877 a, b) from Rometta and Salice, both near Messina and frequently mentioned by Seguenza. The Rometta hill consists mainly of bathyal marls, Middle Pliocene in age (Violanti, 1989). Salice is an Early Pleistocene locality (Di Stefano & Lentini, 1995).

Remarks

Jeffreys (1879) reported *Nucula striatissima* Seguenza from off Cape Mondego, Portugal, 740-1095 fathoms depth. He compared the "single but perfect specimen" with material of *Nucula trigona* sent by Seguenza, concluding that the latter was a variety of the former. Jeffreys applied several names of fossil species described by Seguenza from the Mediterranean Plio-Pleistocene to extant Northeast Atlantic species. His fixist views led him to an overemphasized idea that most tertiary species still exist (Warén, 1989; La Perna, 2004a), disregarding the real differences between fossil and extant species. However, the identity of this Atlantic species remains unknown.

Deminucula seguenzai nom. nov.

Fig. 3 d-f, Fig. 5 a-j

Nucula trigona Seguenza, 1877a: p. 92, non *Nucula trigona* Sowerby, 1818: p. 208, nec *Nucula trigona* Münster in Goldfuss, 1837: p. 155.

Nucula trigona - Seguenza, 1877b: p. 1167, pl. 1, figs. 2, 2a, 2b.

Deminucula trigona - La Perna, 2003: p. 24, pl. 1, fig. 6.

Types

Unknown. See under *D. striatissima*.

Material examined

Fiumefreddo di Sicilia, Early Pleistocene, about 100

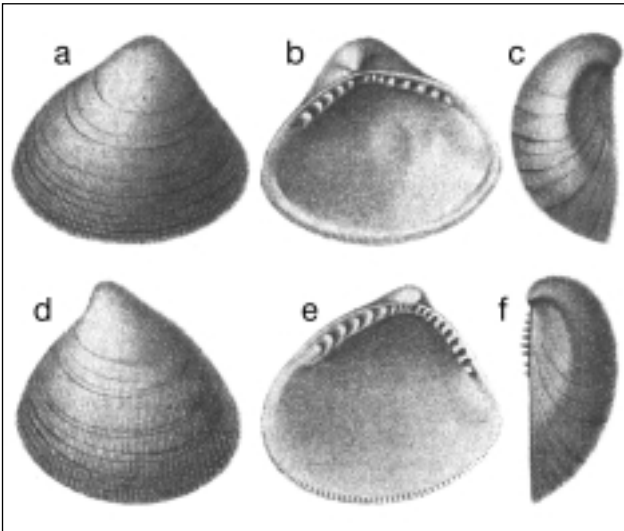


Fig. 3. Original illustrations of *Nucula striatissima* (a-c) and *Nucula trigona* (d-f) (after Seguenza, 1877b, modified).

Fig. 3. Illustrazioni originali di *Nucula striatissima* (a-c) e *Nucula trigona* (d-f) (da Seguenza, 1877b, modificato).

valves; Bovalino Superiore, Early Pleistocene, 11 valves and some fragments.

Description

Shell bluntly trigonal, equidimensional, subequilateral, moderately inflated and thick-walled. Umbo somewhat narrow, prominent, opisthogyrate, posterior to midline. Dorsal margin short, convex. Anterior margin evenly convex, with an obscure antero-ventral angulation. Posterior margin moderately convex, passing with a fairly distinct angulation into a broadly rounded ventral margin. Surface almost smooth, with faint, irregularly spaced growth lines. Few ill defined commarginal ridges near ventral margin only in fully growth valves.

Fine, closely set structural lines give impression of a radial sculpture. Hinge plate relatively robust, subangulose to arched, with stout to barely chevron-shaped teeth in two series, the anterior slightly longer and stronger. Resilifer small, not projecting, roughly triangular at full growth stage. Adductor muscle scars poorly distinct. Inner ventral margin crenulate. Interdissoconch well distinct, 0.6 mm in diameter. Prodissoconch roundish, 200 μ m. Maximum size about 3.50 mm in antero-posterior length.

Etymology

The replacement name is a tribute to Giuseppe Seguenza (1833-1889), paleontologist from Messina, who greatly contributed to the knowledge of the Plio-Pleistocene molluscs from Southern Italy.

Distribution

The species was originally reported (Seguenza, 1877a) from "Astian" bathyal beds at Monasterace and Ardore (southern Calabria). Like for *Nucula striatissima*, this species was soon after (Seguenza, 1877b) illustrated, more detailed described and reported also from Riace, another "Astian" locality in southern Calabria. As discussed by Di Geronimo & La Perna (1997), the Astian of Seguenza covers a chronostratigraphic interval ranging from the Middle Pliocene to the Early-Middle Pleistocene.

The present material is only Pleistocene in age. Bovalino Superiore is a locality near Ardore and Monasterace (Jonian side of southern Calabria).

The molluscan fauna from both localities points to upper bathyal depths, probably slightly shallower than those of the Rometta deposits.

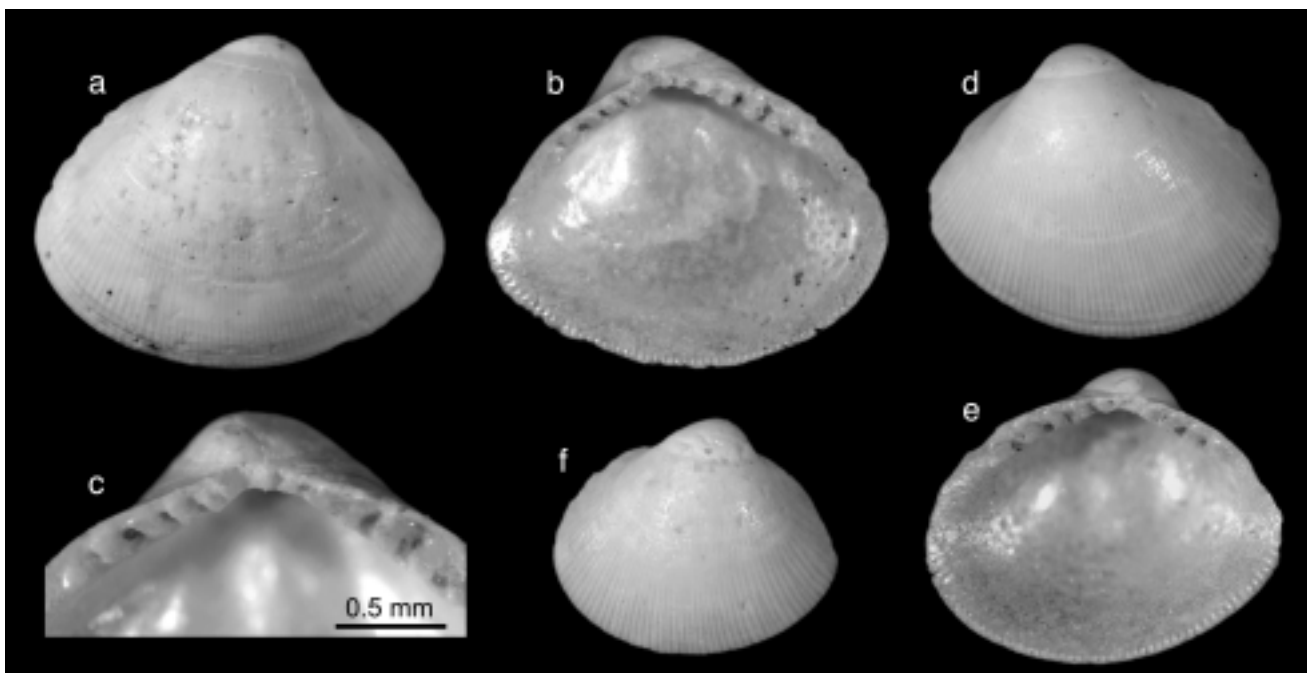


Fig. 4. *Deminucula striatissima* (Seguenza, 1877), Rometta: a-c. 2.70 mm (MZB 23630); d, e. 2.30 mm (MZB 23630); f. 1.85 mm (MZB 23630).

Fig. 4. *Deminucula striatissima* (Seguenza, 1877), Rometta: a-c. 2,70 mm (MZB 23630); d, e. 2,30 mm (MZB 23630); f. 1,85 mm (MZB 23630).

Remarks

The material of *Deminucula striatissima* and *D. seguenzai* matches well the original descriptions and illustrations (Fig. 3), but size is smaller than that reported by Seguenza (1877b). *Nucula striatissima* was said to be 5 mm and *Nucula seguenzai* 4.5 mm in length, whereas the maximum size within the present material does not exceed 3 mm for *D. striatissima* and 3.5 for *D. seguenzai*. However, the bar reported by Seguenza to indicate the real size of the illustrated valves is about 3 mm long, in agreement with the present material.

Deminucula striatissima and *D. seguenzai* differ from each other mainly in shape, convexity and wall thickness. The former is more inequilateral and elongate, more convex and thick-shelled than the latter. Younger valves of both species have a similar outline, but *D. seguenzai* has a thinner shell wall and a more convex dorsal margin.

Deminucula calabra n. sp.

Fig. 6 g-i

Description

Shell bluntly trigonal, equidimensional, almost equilateral, moderately inflated, thin-walled but not brittle. Umbo moderately large, prominent, opisthogyrate, slightly posterior to midline. Dorsal margin short, convex. Anterior margin convex, becoming straighter antero-ventrally then smoothly passing to a moderately convex ventral margin. Posterior margin poorly convex to slightly truncate, with an obscure postero-ventral angulation. Surface almost smooth, with only faint, irregularly spaced growth lines. Fine, closely set structural lines give impression of a radial sculpture. Hinge plate relatively robust, arched, with stout teeth in two series of similar length and strength. Resilifer small, poorly distinct, not projecting. Adductor muscle scars not distinct. Inner ventral margin finely crenulate. Interdissoconch well distinct, 0.70 mm in diameter. Prodissoconch ovate, 140 µm. Maximum size 2.60 mm in antero-posterior length.

Etymology

After *calabrus*, referring to Calabria, the Southern Italy region from which the type material comes.

Type locality

Pleistocene beds cropping out at Vallone Catrica, on the Calabrian side of the Messina Strait (Fig. 1).

Type material

Holotype (MZB23632) and 4 paratypes (MZB 23633). Measurements in Tab. 1.

Other material examined

Type locality section, 30 valves.

	length	height	at	pt
Holotype	2.28	2.24	7	6
Paratype 1	2.48	2.39	8	6
Paratype 2	2.12	2.08	7	5
Paratype 3	1.94	1.83	6	5
Paratype 4	1.94	1.96	6	5

Tab. 1. Shell measurements and number of anterior and posterior teeth (at, pt.) in the type material of *Deminucula calabra* n. sp.

Tab. 1. Misura della conchiglia, numero di denti anteriori e posteriori (at, pt) nel materiale tipo di *Deminucula calabra* n. sp.

Distribution

Only known from the type locality. The molluscan assemblage is indicative of upper bathyal depths, probably not exceeding 500 m (Di Geronimo & La Perna, 1997; La Perna, 2004a).

Remarks

Deminucula calabra n. sp. differs markedly from *D. striatissima* in shape (the former is more rounded, equilateral and less elongate than the latter), convexity (*D. striatissima* is more inflated, somewhat gibbose) and in shell wall thickness (*D. striatissima* is much more sturdily built). It differs from *D. seguenzai* by being more equilateral and equidimensional, smaller, comparatively more convex and with a thinner shell wall. However, at similar size a narrow morphological overlap exist between the two species (compare Fig. 5 d and 6 h).

Discussion

Rhind & Allen (1992) assigned *Nucula atacellana* Schenck, 1939 (= *N. reticulata* Jeffreys, 1876, *N. cancellata* Jeffreys, 1881), a deep water Atlantic species, to *Deminucula*. This species has a wide distribution in the Eastern Atlantic, from Iceland (La Perna, unpubl. data) south to the Ibero-Moroccan Gulf (Salas, 1996) and the Angola Basin (Rhind & Allen, 1992). It also occurs in the Western Atlantic (North America Basin and Argentina Basin), with a bathyal to abyssal (1100-5000 m) range (Rhind & Allen, 1992; Allen & Sanders, 1996). This species actually has a roughly trigonal, subequilateral shape and a small size (Fig. 5 l; see also Schenck, 1939, pl. 5, figs. 4, 5, 9, 10, 13, 16), but a distinct commarginal sculpture and true radial riblets are present, giving a fine cancellate sculpture (Fig. 5 m). The ligament pit is small, but more developed than in *Deminucula*, even slightly projecting, and teeth are distinctly chevron-shaped (Fig. 5 n). As remarked by La Perna (2003), this species cannot be assigned to *Deminucula*. Nevertheless, the doubtful record of *Nucula striatissima* by Jeffreys (1879) (see above) prevent from excluding the occurrence of *Deminucula* from the Northeast Atlantic.

Nucula profundorum Smith, 1885, a deep water species ranging from Mid-North Pacific south to Mexico and

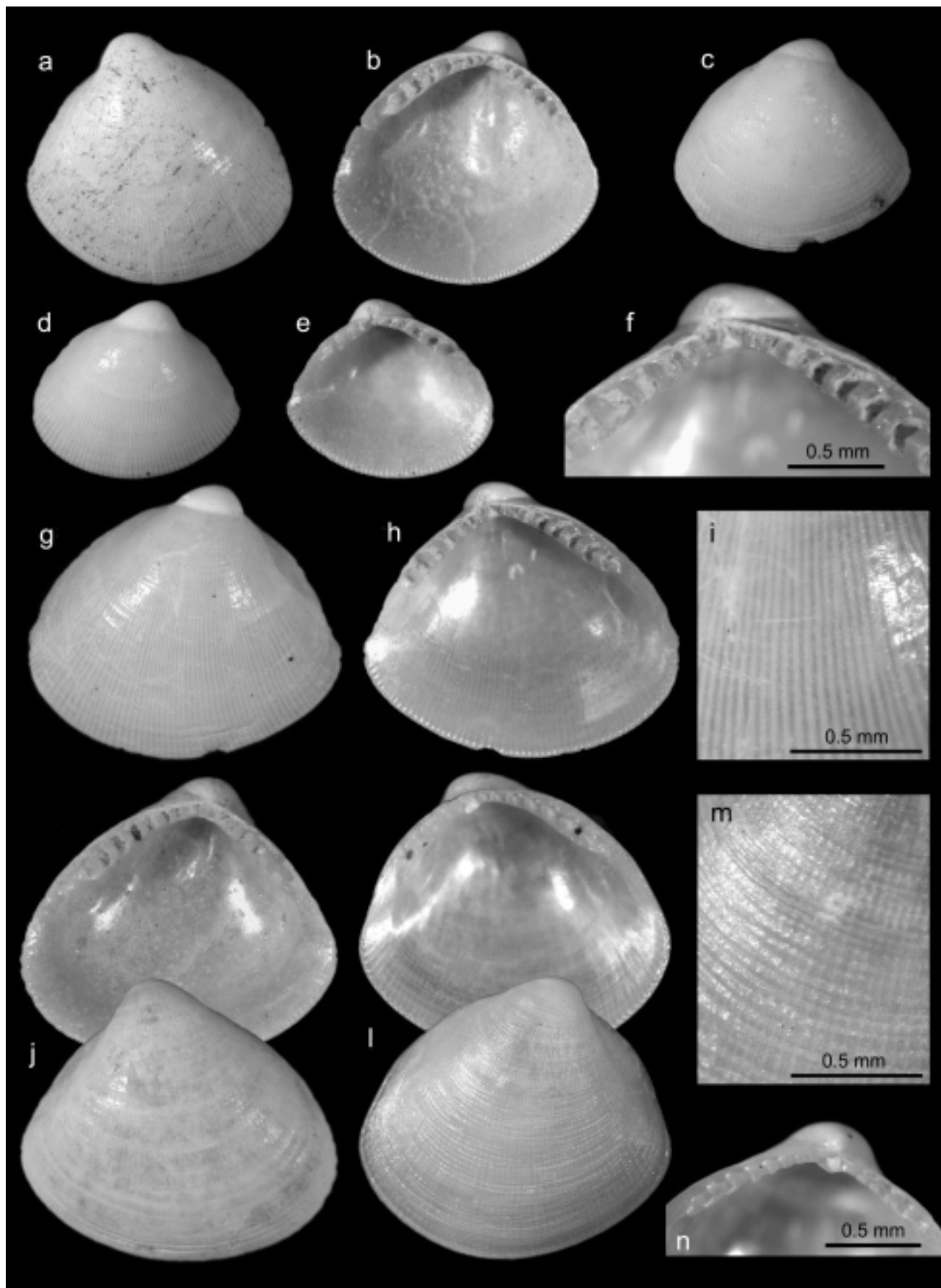


Fig. 5. a-j. *Deminucula seguenzai* nom. nov.: **a, b.** Fiumefreddo di Sicilia, 2,56 mm (MZB 23631); **c.** Bovalino Superiore, 2,25 mm (MZB 23631); **d, e.** Bovalino Superiore, 2,00 mm (MZB 23631). **f-i.** Fiumefreddo di Sicilia, 3,18 mm (MZB 23631). **j.** Fiumefreddo di Sicilia, 3,23 mm (MZB 23631). **l-n.** *Nucula atacellana* Schenck, 1939, Iceland, Bioice st. 731, N62°.34167, W16°.988333, 2,074 m (Icelandic Museum of Natural History, Reykjavik): **l, m.** 3,35 mm; **n.** 3,80 mm (hinge detail).

Fig. 5. a-j. *Deminucula seguenzai* nom. nov.: **a, b.** Fiumefreddo di Sicilia, 2,56 mm (MZB 23631); **c.** Bovalino Superiore, 2,25 mm (MZB 23631); **d, e.** Bovalino Superiore, 2,00 mm (MZB 23631). **f-i.** Fiumefreddo di Sicilia, 3,18 mm (MZB 23631). **j.** Fiumefreddo di Sicilia, 3,23 mm (MZB 23631). **l-n.** *Nucula atacellana* Schenck, 1939, Islanda, Bioice st. 731, N62°.34167, W16°.988333, 2,074 m (Icelandic Museum of Natural History, Reykjavik): **l, m.** 3,35 mm; **n.** 3,80 mm (dettaglio della cerniera).

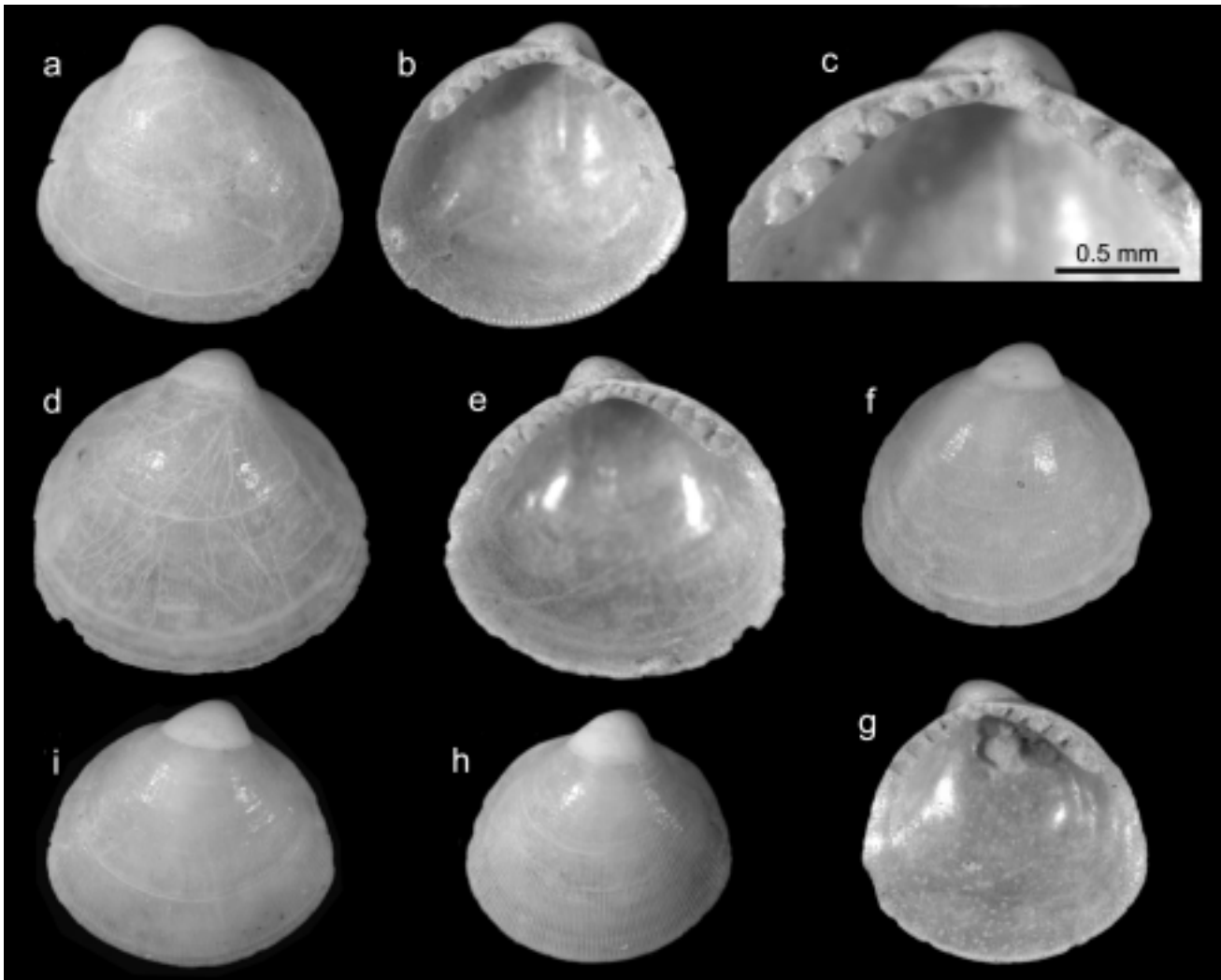


Fig. 6. *Deminucula calabra* n. sp., Vallone Catrica: **a-c.** Holotype, 2.30 mm (MZB 23632); **d, e.** Paratype 1, 2.48 mm (MZB 23633). **f, g.** Paratype 2, 2.10 mm (MZB 23633). **h.** Paratype 3, 2.11 mm (MZB 23633). **i.** Paratype 4, 1.93 mm (MZB 23633).

Fig. 6. *Deminucula calabra* n. sp., Vallone Catrica: **a-c.** Olotipo, 2,30 mm (MZB 23632); **d, e.** Paratipo 1, 2,48 mm (MZB 23633). **f, g.** Paratipo 2, 2,10 mm (MZB 23633). **h.** Paratipo 3, 2,11 mm (MZB 23633). **i.** Paratipo 4, 1,93 mm (MZB 23633).

Peru in 734–4,134 m (Coan *et al.*, 2000) has a trigonal, notably equilateral shape, a pseudo-sculpture of radiating lines, a small, not projecting resilifer and a small size (Coan *et al.*, 2000, p. 73, pl. 3). As suggested by La Perna (2003), this species may be a representative of *Deminucula*.

Nucula nitidulaformis Powell, 1971 from New Zealand and New Caledonia (Bergmans, 1991, p. 30, figs. 1, 2) could be another representative of *Deminucula*. It is an upper bathyal species with a small, bluntly trigonal shell, with structural radiating lines and a small, barely projecting resilifer.

New findings and a revision of well and little known fossil and living nuculids could be useful to better understand the morphologic, taxonomic and biogeographic range of this group.

The hypothesis supported by the present data is that *Deminucula* had a wide East-West distribution, i.e. from the eastern to the western sectors of the large biogeographic unit defined Tethys Realm by Harzhauser *et al.* (2002), until the late Early Miocene, when the final breakdown of the eastern sectors (Atlantic and Mediterranean) from the eastern ones (Indo-Pacific) occurred (Rögl, 1998; Harzhauser *et al.*, 2002) (Fig. 7). The Tethys

Realm is the direct biogeographic descendant of the Tethys Sea, which vanished during the Eocene (Berggren & Hollister, 1977; Rögl, 1998).

An important faunal exchange between the Eastern and the Western sectors of Tethys and subsequent disjunct distributions are fairly well known (e.g. Robba, 1987; Piccoli *et al.*, 1991), but mostly among the shallow water taxa. Recently, an Indo-Pacific affinity has been advocated for some protobranchs from the Plio-Pleistocene bathyal deposits of the Mediterranean. La Perna *et al.* (2004) described a Pliocene bathyal nuculanid as *Zealeda elegans*. *Zealeda* Marwick, 1924 is a deep-water genus with a geographic distribution similar to that of *Deminucula*, i.e. an extant species is known from Southern Australia and several others occur in the Late Cainozoic of New Zealand. This genus is also present in the Atlantic with some species, even though they are still conservatively allocated in *Ledella* Verrill and Bush, 1897 (Allen & Hannah, 1989). The distribution of another nuculanid genus, *Jupiteria* Bellardi, 1875, can serve as an interesting example (La Perna *et al.*, 2004): it was present in the Miocene and Plio-Pleistocene of the Mediterranean area, with shallow and deep-water species, in the Cainozoic of New Zealand and it most probably

occurs in Southern Australia (as *Teretileda* Iredale, 1929). A strong evidence of the eastern origin of *Jupiteria* is provided by its occurrence also in the Southern Indian Ocean (Kilburn, 1994). The malletiid genus *Neilo* Adams, 1854, original of the central West Pacific (Marshall, 1978), was present in the Mediterranean Plio-Pleistocene with two deep-water species, *Neilo isseli* Bellardi, 1875 and *N. dilatatus* (Philippi, 1844), whereas two extant species occur in the Atlantic (Sanders and Allen, 1985, as *Malletia*; see La Perna, 2003). The solemyoid protobranch *Nucinella* Wood, 1841, with a maximum diversity in the central West Pacific (La Perna, 2005) and two relict species in the Mediterranean Pleistocene (La Perna, 2004b) provides another evidence about the important contribution of Tethys and Indo-Pacific to the shallow and deep water Atlantic and Mediterranean fauna. Some recent studies remark the paleobiogeographic bearing of the closure of the Tethys on the deep-sea fauna, such as Ameziane & Roux (1997) and Grill & Zuschin (2001). The study of older (Miocene and Oligocene) deep-water faunas from the Mediterranean and European area could bring new and more detailed data about these paleobiogeographic relations. Unfortunately, the Indian Ocean, with its intermediate position between the Pacific and the Atlantic, is mostly absent in these paleobiogeographic reconstructions, mostly because of our poor knowledge of the modern and fossil fauna from this area.

The development and spreading of deep-sea taxa probably started with the appearance of world-wide psychros-

pheric conditions near the Eocene-Oligocene boundary (Benson, 1975; Dall'Antonia *et al.*, 2003). According to the reconstructions by Golonka (2004), slope and basinal areas were widely present between Eurasia and Africa during the Cainozoic, thus allowing the spreading of deep-water taxa between the eastern and western sectors. Finally, the striking differences between the deep Mediterranean protobranch fauna of the Plio-Pleistocene and the modern one are worthy of being reminded (Di Geronimo & La Perna, 1997; La Perna, 2003; La Perna, 2004b; La Perna *et al.*, 2004). The unusually poor modern fauna contrasts with the rich Plio-Pleistocene one, which is similar in diversity and composition to the Northeast Atlantic fauna. Probably, also the Mediterranean species of *Deminucula* were component of the postulated rich palaeoendemic stock, the extinction of which was due to the loss of the psychrosphere in the Late Quaternary (La Perna, 2004a).

Concluding remarks

There is an emerging discipline, the geobiology, defined by Lieberman (2005) as "that unifying discipline that seeks to span and link the geological and biological sciences". Within geobiology, paleobiogeography and biogeography provide data on the distribution of group of organisms across geological time and geographic space. Paleobiogeography and biogeography use the taxonomic units to define (paleo)biogeographic units and their changes through time. Of course, taxa cannot be defined on biogeographic grounds, but a feed-back between taxonomy-phylogeny and (paleo)biogeography is highly valuable, as shown by the present work.

Three species from the Plio-Pleistocene Mediterranean can be assigned to a genus known from the Australian-New Zealand area (but probably with a much wider Pacific distribution). Plate tectonics can explain such a widely separate distribution as a biogeographic disjunction caused by the closure of the East-West seaway, through which the genus ranged. The paleobiogeographic model then provides supporting evidences of a distinct genus-group with a wide geographic distribution and a relatively long history. If the three fossil species were conservatively allocated in *Nucula*, and thus "lost" in that enormous, undifferentiated genus, no contribution to the taxonomy of nuculids could be given and no paleobiogeographic pattern would emerge.

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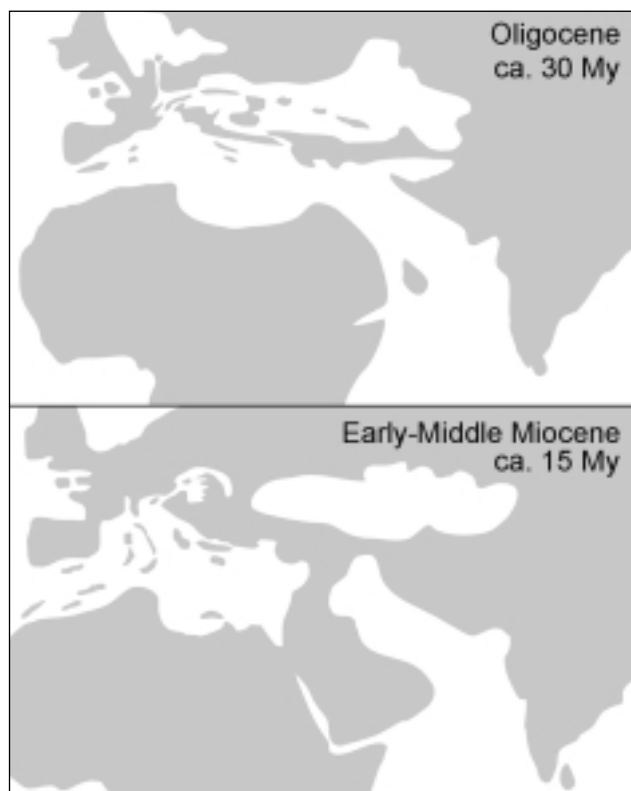


Fig. 7. Palaeogeographic map of the circum-Mediterranean area in the Oligocene and Middle Miocene (after Rögl, 1998 and Harzhauser *et al.*, 2002, modified).

Fig. 7. Mappe paleogeografiche dell'area circum-mediterranea nell'Oligocene e Miocene medio (da Rögl, 1998 e Harzhauser *et al.*, 2002, modificato).

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