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Mediterranean Pliocene protobranchs: the genera *Jupiteria* Bellardi, 1877, *Ledella* Verril & Bush, 1897 and *Zealeda* Marwick, 1924 (Mollusca, Bivalvia)

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Abstract

Six protobranch species of the genera *Jupiteria* Bellardi, 1875, *Ledella* Verrill & Bush, 1897 and *Zealeda* Marwick, 1924, that occur in the Pliocene deposits of Italy, are considered here. The type species of *Jupiteria*, *J. concava* (Bronn, 1831), is redefined. It is common in deep shelf and epibathyal deposits. *J. fissistriata* (Foresti, 1897) is less common and only occurs in shelf deposits. It has been previously misidentified as *J. concava*. A third species, *J. gibba* (Seguenza, 1877), often co-occurs with *J. concava* in epibathyal deposits. These species are also present in Pleistocene deposits. The genus *Ledella* is represented by *L. seminulum* (Seguenza, 1877) and *L. nicotrae* (Seguenza, 1877). *L. seminulum* is often misidentified as *L. messanensis* (Jeffreys, 1876), which seems not to be present in the Pliocene. It was a typically bathyal species with a limited distribution in the Pleistocene. *L. nicotrae*, so far known only from Pleistocene deposits, is difficult to distinguish from *L. messanensis*, but had a shallower distribution. The genus *Zealeda*, previously used only for Australian and New Zealand species, is represented by *Z. elegans* n.sp., a typical bathyal species known only from the Pliocene. It is hypothesised that *Jupiteria* and *Zealeda* have Tethyan origins.

Riassunto

Protobranchi pliocenici Mediterranei: i generi *Jupiteria* Bellardi, 1877, *Ledella* Verrill & Bush, 1897 e *Zealeda* Marwick, 1924 (Mollusca, Bivalvia). Nel presente lavoro sono trattate sei specie di protobranchi, una delle quali nuova, presenti nei depositi pliocenici italiani. I generi rappresentati sono *Jupiteria* Bellardi, 1875, *Ledella* Verrill & Bush, 1897 e *Zealeda* Marwick, 1924. Il genere *Jupiteria* è stato prevalentemente usato in maniera non corretta e nel presente lavoro viene posta enfasi sui suoi caratteri distintivi. La specie tipo, *J. concava* (Bronn, 1831), è frequente nei depositi pliocenici di piattaforma profonda ed epibatiali. Un'altra specie, *J. fissistriata* (Foresti, 1897), meno comune e presente solo in depositi di piattaforma, è stata finora confusa con *J. concava*. Una terza specie è *J. gibba*, spesso associata a *J. concava* in depositi epibatiali. Tutte e tre le specie sono presenti anche nel Pleistocene. Il genere *Ledella* è rappresentato da *L. seminulum* (Seguenza, 1877) e da *L. nicotrae* (Seguenza, 1877). La prima, spesso confusa con *L. messanensis* (Jeffreys, 1876) che invece non sembra presente nel Pliocene, è tipicamente batiale e limitatamente presente anche nel Pleistocene. La seconda, sebbene ponga problemi di separazione morfologica da *L. messanensis*, aveva una distribuzione batimetrica più superficiale (piattaforma profonda-epibatiale). *L. nicotrae* era precedentemente nota solo per il Pleistocene. Il genere *Zealeda*, finora utilizzato solo per specie dell'area australiana e neozelandese, è rappresentato da *Z. elegans* n.sp., a distribuzione batiale e nota solo per il Pliocene. Si ipotizza che *Jupiteria* e *Zealeda* possano rappresentare degli elementi faunistici di origine tetidea.

Key words

Protobrachia, *Jupiteria*, *Ledella*, *Zealeda*, Pliocene, Mediterranean, bathyal, systematics, new species.

Introduction

Bivalves of the subclass Protobranchia, order Nuculoida, are well represented in the deep-sea benthos, where they have formed typical assemblages at least since the Eocene (Hickman, 1984). Because of its conservatism (low diversity of form and paucity of distinctive features, morphological convergence, etc.), it is a taxonomically difficult group and the classification is much debated (*e.g.* Allen & Hannah, 1986; Maxwell, 1988a; Ockelmann & Warén, 1998; Coan *et al.*, 2000).

Although the fossil record of the Mollusca is mostly from continental shelf deposits, some widely outcropping deep-sea deposits allow us to have a "glance" at ancient deep-sea assemblages and environments. Some studies (e.g. Robba, 1981; Tabanelli, 1993; Di Geronimo & La Perna, 1997; Di Geronimo *et al.*, 1997; Ceregato & Tabanelli, 2001; La Perna, 2003), focusing on fossil molluscs from the Pliocene and Pleistocene of Italy, go some way to fill the gap in the knowledge of the deep-sea constituents of the Mediterranean. Further, these studies allow a better understanding of the Plio-Quaternary history of the deep-sea benthos (La Perna, 2003, in press a).

The Pleistocene and Recent Mediterranean protobranch fauna is fairly well known (La Perna, 2003, in press a, with references), but the knowledge of the Pliocene and older protobranchs is still poor. In the present work, three genera occurring in the Pliocene deposits of Italy are studied: *Jupiteria* Bellardi, 1875, *Ledella* Verrill & Bush, 1897 and *Zealeda* Marwick, 1924. Out of six species considered, five are from deep-sea deposits.

Abbreviations

The following abbreviations are used:

v(s) = valve(s); sh(s) = shell(s); MCI = Museo Civico di Imola; MPUR = Museo di Paleontologia dell'Università di Roma; MRSN = Museo Regionale di Scienze Naturali di Torino; MZB = Laboratorio di Malacologia, Museo di Zoologia dell'Università di Bologna; RL, AC, CT coll. = authors' collections.

Systematics

Class **Bivalvia** Linné, 1758

Order **Nuculoida** Dall, 1889

Family **Nuculanidae** H.& A. Adams, 1858

Genus **Jupiteria** Bellardi, 1875
(Type-species: *Nucula concava* Bronn, 1831, SD Dall, 1898)

The type species of *Jupiteria* was described from the Pliocene of Italy. *Jupiteria* has been mostly considered as a subgenus of *Nuculana* Link, 1807 and even synonymised with it, as well as with *Saccella* Woodring, 1925 and *Teretileda* Iredale, 1929. Full generic rank for *Jupiteria* was adopted by Maxwell (1988a, b), Kilburn (1994), Kafanov & Savizky (1995) and La Perna (1998). A poor knowledge of the type species of *Jupiteria* and the absence of living representatives in European waters have contributed to the misinterpretation and confusion. La Perna (1998) provided evidence for keeping *Jupiteria* distinct from *Nuculana* and *Saccella*, as reported in the present work (Tab. 1). Apart from significant differences in shell shape, particularly the trigonal shape of *Jupiteria* and the wide concave postero-dorsal margin, *Jupiteria* has a smooth prodissoconch (La Perna, 1998), distinct from the net-like sculptured prodissoconch of *Nuculana* (Ockelmann & Warén, 1998) and *Saccella* (La Perna, 1998). Juveniles of *Jupiteria* are similar to those of *Ledella* Verrill & Bush, 1897 and suggest a closer relationship between *Jupiteria* and *Ledella*, rather than with *Nuculana* and *Saccella*.

Because of the confused usage of *Jupiteria*, the Recent biogeographical distribution is problematical. However, no living European species can be assigned to this genus. It seems to have a mainly West Pacific distribution (La Perna, 1998) which, together with the occurrence in the Late Tertiary of Europe suggests a Tethyan origin. This is supported by the occurrence in the Tertiary of New Zealand, of several species which can be confidently assigned to *Jupiteria* (Maxwell, 1988b; Beu & Maxwell, 1990).

Teretileda Iredale, 1929, described on a Recent species from Southern Australia, appears to be similar to *Jupiteria*, or possibly a synonym. This genus was briefly discussed by Maxwell (1969), who reported the following diagnostic features: "...robust, trigonal shell with rather weak concentric sculpture and long hinge plate with a deep triangular resilifer". We refrain from adopting a definite position on this matter.

	Jupiteria	**Nuculana**[1]	**Saccella**[2]
shell shape	trigonal-ovate	ovate-elongate	ovate-elongate
shell convexity	strong	moderate	moderate
rostrum shape	rather short, pointed	long, blunt, two-keeled	rather long, pointed
rostrum position[3]	low	median	median
postero-dorsal area[4]	wide, mainly concave	wide, mainly convex	narrow, mainly flat
umbo orientation	opisthogyrate	opisthogyrate	opisthogyrate
concentric sculpture[5]	present to lost	present to ill-defined	present
anterior ridge[6]	absent	absent	present
shell wall	thick	moderately thick	moderately thick
ligament[7]	inner, with small external anterior component	inner, with small external amphidetic component	inner, with small external amphidetic component
inner rostral ridge[8]	absent	present	ill-defined
pallial sinus	shallow	deep	deep
resilifer	triangular	triangular, oblique	triangular
prodissoconch	smooth	net-like sculpture	net-like sculpture

[1] Many rostrate nuculanids are usually and conservatively allocated to *Nuculana*. In the present work, this genus is restricted to the type species *N. pernula* (Müller, 1771) and to closely allied species.
[2] *Saccella* is a poorly known group and the characters reported here are those of the type species *S. commutata* (Philippi, 1844) (Aartsen & Carrozza, 1987; Carrozza, 1987).
[3] The rostrum position refers to the antero-posterior midline.
[4] The postero-dorsal area is a wide well-defined escutcheon bordered by the rostral ridge.
[5] There is a tendency to the loss of commarginal sculpture among protobranchs (Maxwell, 1988a, b) and this character seems to have a little taxonomic wheight at supraspecific level.
[6] An external ridge extending antero-ventrally from umbo is present in *Saccella*.
[7] A small external portion of ligament may occur in nuculanids as a relict of an early mainly external ligament, which moves inwards with growth (Ockelmann & Warén, 1998).
[8] A thin ridge on the internal side of the rostrum is present in *Nuculana*. According to Savitsky (1974) it compensates for the incomplete closure of the inhalant siphon (see also Yonge, 1939). In *Saccella* the inner rostral ridge is reduced to a small, tubercle-like relief, close to the ventral margin.

Table 1. Comparison of shell features of *Jupiteria*, *Nuculana* and *Saccella*.

Tabella 1. Confronto fra i caratteri conchigliari di *Jupiteria*, *Nuculana* e *Saccella*.

Jupiteria concava (Bronn, 1831)
(**Figs 1A–L, Fig. 2M**)

1831 – *Nucula concava* Bronn: 109.
1876 – *Leda erctensis* Brugnone: 9, fig. 8.
1876 – *Leda striatella* Ponzi: 21, pl. 2, figs 7, b.
1877a – *Leda (Jupiteria) trigona* Seguenza: 94.
1877b – *Leda (Jupiteria) trigona* - Seguenza: 14, pl. 2, figs 12, 12a, 12b.
1998 – *Jupiteria erctensis* - La Perna: 227, pl. 1, figs 1-12, pl. 2, fig. 3.
2003 – *Jupiteria erctensis* - La Perna: 24, pl. 2, fig. 4.

Examined material

Tabiano Bagni (Parma), Emilia Romagna, Early Pliocene, 4 vs, 1 sh (topotypes), Della Bella coll. Bordighera (Genova), Middle Pliocene, 14 vs, 1 sh, MRSN, Bellardi & Sacco coll., BS.123.04.001, BS.123.04.002, BS.123.04.003. Rio Albonello (Imola), Emilia Romagna), Middle Pliocene, 21 vs, 3 shs, CT coll. Rometta (Messina), northeastern Sicily, Middle Pliocene, 1 v (topotype of *Leda trigona*), RL coll. Grammichele, southeastern Sicily, Pleistocene, 18 vs, 3 shs, RL coll. Bovalino Superiore, southern Calabria, 2 vs, RL coll. Fiumefreddo di Sicilia, northeastern Sicily, Pleistocene, 2 vs, RL coll.

Description

Shell thick-walled, strongly convex, ovate-trigonal. Rostrum low, short, blunt. Umbo median, large, opisthogyrate. Antero-dorsal margin convex, smoothly curving to form a well-rounded anterior end. Ventral margin weakly convex to almost straight in its median part. Posterior margin consisting of a well-defined, rounded, slightly curved keel from umbo to rostrum tip, producing a large and concave postero-dorsal area. Lunule small, not distinct. Sculpture of raised wide-spaced concentric ridges, numbering 5-6 per millimetre. Hinge-plate thick. Anterior row convex, posterior one straight to slightly concave. Teeth chevron-shaped, numbering 15-16 anteriorly and 10-11 posteriorly in 6 mm valves. Resilifer deep, triangular, slightly inclined, dividing hinge-plate. Anteriorly, a short, ill-defined semi-external ligament furrow. Anterior adductor scar larger and roundish, posterior one ovate, both impressed. Pallial line not well-defined, sinus shallow. Prodissonconch D-shaped, ca. 180 µm long. Maximum length 7.5 mm in length.

Distribution

The examined material ranges from Early Pliocene to Pleistocene. The Late Miocene records (Doderlein, 1864, *fide* Bellardi, 1875) need to be confirmed. *J. concava* is found associated with a deep-shelf and epibathyal fauna (La Perna, 1998; Ceregato *et al.*, submitted).

Remarks

The complex history of *Jupiteria concava* is reported under the following species.

Jupiteria fissistriata (Foresti, 1897, ex Meneghini ms)
(**Figs 1A–L, Fig. 2M**)

1875 – *Leda (Jupiteria) concava* var. A Bellardi: 21, fig. 15.
1897 – *Leda* (*Jupiteria*) *fissistriata* Foresti: 215, pl. 9, fig. 1.

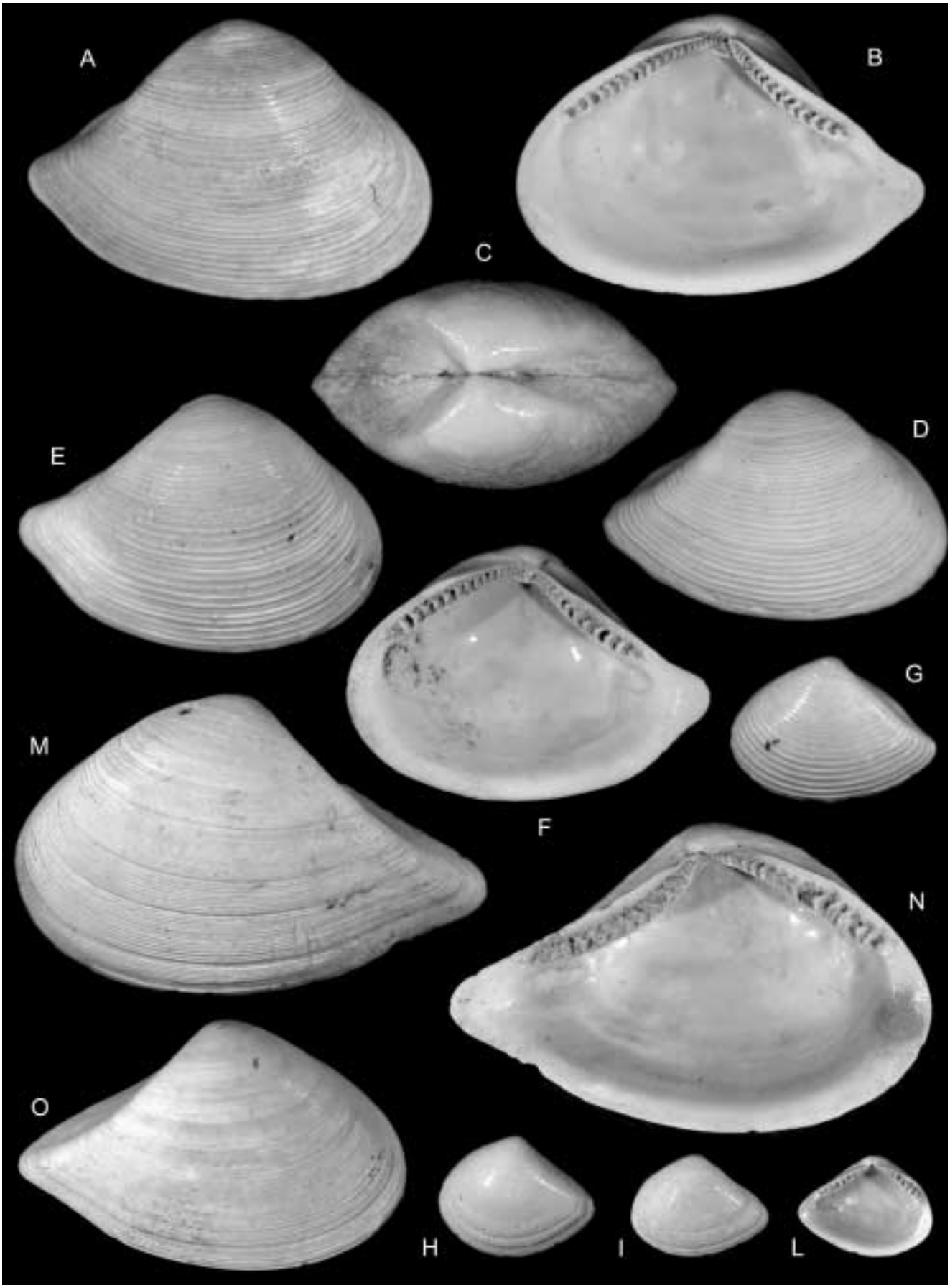

Fig. 1. A-L. *Jupiteria concava* (Bronn, 1831). A-D. Tabiano Bagni, Early Pliocene (A, B: 8.0 mm, MZB31001; C: 7.3 mm, MZB31001; D: 7.0 mm, MZB31001). E-G. Rio Albonello, Middle Pliocene (E, F: 7.5 mm, MZB31002; G: 4.2 mm, MZB31002). H. Grammichele, Pleistocene (3.0 mm, MZB31003). I, L. Campore, Middle Pliocene (2.5 mm). M-O. *Jupiteria fissistriata* (Foresti, 1897). Santa Maria in Ceperano, Late Pliocene (M, N: 9.5 mm, MZB31004; O: 8.0 mm, MZB31004).

Fig. 1. A-L. *Jupiteria concava* (Bronn, 1831). A-D. Tabiano Bagni, Pliocene inferiore (A, B: 8,0 mm, MZB31001; C: 7,3 mm, MZB31001; D: 7,0 mm, MZB31001). E-G. Rio Albonello, Pliocene medio (E, F: 7,5 mm, MZB31002; G: 4,2 mm, MZB31002). H. Grammichele, Pleistocene (3,0 mm, MZB31003). I, L. Campore, Pliocene medio (2,5 mm). M-O. *Jupiteria fissistriata* (Foresti, 1897). Santa Maria in Ceperano, Pliocene superiore (M, N: 9,5 mm, MZB31004; O: 8,0 mm, MZB31004).

1898 – *Portlandia (Jupiteria) concava* var. *longolaevis* Sacco: 56, pl. 12, figs 4, 5.
1995 – *Nuculana concava* - Tabanelli: 286.

Examined material

Genova, Middle Pliocene, 1 v, MRSNT, Bellardi & Sacco coll., BS 123.04.001 (type of *Leda concava* var. A and var. *longolaevis*). Rio Gamballaro (Imola), Emilia Romagna), Middle Pliocene, 3 vs, MCI, Foresti-Scarabelli coll., 9194 (types of *Leda fissistriata*). Santa Maria in Ceperano (Imola), Emilia Romagna, Late Pliocene, 4 vs, CT coll. Altavilla Milicia (Palermo), Sicily, Middle Pliocene, 1 v, RL coll. Monte Mario (Rome), Pleistocene, 12 vs, MPUR, Cerulli-Irelli coll.

Description

Shell thick-walled, strongly convex, ovate-trigonal, slightly elongated. Rostrum low, rather short and blunt. Umbo median, large, opisthogyrate. Antero-dorsal margin convex, smoothly curving to form a well-rounded anterior end. Ventral margin weakly convex, forming a poorly defined subrostral sinus. Posterior margin consisting of a well-defined, rounded, slightly curved keel from umbo to rostrum tip, producing a large and concave postero-dorsal area. Lunule small, not distinct. Sculpture of fine close-set commarginal ridges, numbering 16-18 per millimetre, becoming coarser, wide-spaced and irregularly oblique on posterior keel and anterior side, almost lost on a narrow area immediately anterior to keel. Hinge-plate thick. Anterior row convex, posterior one concave. Teeth chevron-shaped, numbering 16-17 anteriorly and 13-14 posteriorly in 8 mm valves. Resilifer deep, triangular, inclined, dividing hinge-plate. Anteriorly, a short, ill-defined semi-external ligament furrow. Anterior adductor scar large and roundish, posterior ovate and smaller, both impressed. Pallial line ill-defined to faintly impressed, sinus shallow. Prodissoconch not seen. Maximum length about 10 mm.

Distribution

The examined material is Middle Pliocene to Pleistocene in age. *J. fissistriata* cannot be considered a true deep-sea species, as it occurred in the outer shelf. It was less common than *J. concava*.

Remarks

The identity of *Nucula concava* Bronn, 1831, was confused in the late nineteenth century, whereas *Leda fissistriata* Foresti, 1898 remained practically ignored after its description. The history of these two species can be summarised as follows:

1. Bronn (1831) described, without illustration, *Nucula concava* on the basis of material from Tabiano (Parma, North Italy). This material was from Early Pliocene clays exposed in the area (Pelosio, 1967).
2. Bellardi (1875) illustrated Bronn's species from Early Pliocene material from Liguria. He also introduced the "variety A", briefly described as being less inflated and more finely ridged than *Leda concava*. Both taxa were assigned to the new "section" *Jupiteria*, in the genus *Leda*.
3. Brugnone (1876) described and illustrated *Leda erctensis* from Pleistocene beds in Sicily (Monte Pellegrino, Palermo). Although the description and the illustration are poor, a trigonal concentrically ridged protobranch shell can be recognised (La Perna, 1998).
4. Ponzi (1876) described and illustrated *Leda striatella* from Monte Vaticano (Rome). This material was most probably from Pliocene deposits (La Perna, 1998).
5. Seguenza (1877a, b) described and illustrated *Leda trigona* from Plio-Pleistocene deep-sea beds in Southern Italy (Messina and Calabria area). It was said to be similar to *Leda concava*, which was believed to be typical of shallow-water deposits. *L. trigona*, *L. concava* and its variety A of Bellardi were placed in the "section" *Jupiteria*.
6. Foresti (1897) described and illustrated *Leda (Jupiteria) fissistriata* from Pliocene clayey beds of Rio Gamballaro (Romagna, Northern Italy). The species was said to differ from *Leda (Jupiteria) concava* by having much finer concentric sculpture, anteriorly and posteriorly becoming coarser and somewhat irregular.
7. Sacco (1898) reported *Portlandia (Jupiteria) concava* and named the variety A of Bellardi as var. *longolaevis*, which he remarked had a rather irregular lateral sculpture ("resembling that of *Nucula sulcata*").
8. La Perna (1998) synonymised *Leda erctensis* Brugnone, 1876, *L. striatella* Ponzi, 1876, and *L. trigona* Seguenza, 1877 and proved Brugnone's name to be the oldest synonym. *Jupiteria concava* was believed to be a distinct species, with more elongated, flatter valves and a finer closely-spaced sculpture (*i.e. J. fissistriata*, according to the present work).

We examined material of *Leda concava* from its type locality (where it is the sole species of *Jupiteria* present: Pelosio, 1967; Della Bella, pers. comm.), material referred to *Leda concava* and its varieties by Bellardi (1875) and Sacco (1898), the type material of *Leda fissistriata* and material of *L. trigona* from some of the localities reported by Seguenza (1877b). These allowed the following identities to be ascertained: 1) *L. trigona* Seguenza, 1877 = *Leda concava* Bronn, 1831; 2) *Leda concava* var. *longolaevis* Sacco, 1898 = *L. fissistriata*, Foresti, 1897 = *L. concava* var. A Bellardi, 1875. About the synonymy between *L. erctensis* Brugnone, 1876 and *L. striatella* Ponzi, 1876, see La Perna (1998).

Summarising, two similar species were present in the Pliocene, *i.e. J. concava* and *J. fissistriata*. The latter differs by being a little larger, more elongated, less convex, with a slightly more slender rostrum and finer sculpture that becomes coarser laterally, as described by Foresti (1897) and Sacco (1898). Both species where also present in the Early Pleistocene (Calabrian-Emilian).

Jupiteria gibba (Seguenza, 1877)
(**Figs 2A–I**)

1877a – *Leda (Jupiteria) gibba* Seguenza: 286.
1877b – *Leda (Jupiteria) gibba* – Seguenza: 15, pl. 3, figs 13, 13a, b.
1897 – *Leda (Junonia) sinuata* Foresti, ex Meneghini ms. (partim): 216: pl. 9, fig. 2.
1993 – *Ledella gibba* - Tabanelli, fig. 11.
1998 – *Jupiteria gibba* - La Perna: 232, pl. 2, figs 1-14; pl. 3 figs 2, 4.
2003 – *Jupiteria gibba* - La Perna: 24, pl. 2, fig. 5.

Examined material

Rometta (Messina), northeastern Sicily, Middle Pliocene, 41 vs, 16 shs (topotypes), RL coll. Rio Gamballaro (Imola), Middle Pliocene, 22 vs, MCI, Foresti-Scarabelli coll., 9180 (types of *Leda sinuata*). Monte Besdone, Emilia Romagna, Middle Pliocene, 7 vs, 3 shs, CT coll. Bovalino Superiore, southern Calabria, Pleistocene, 3 vs, RL coll. Grammichele, southeastern Sicily, 1 v, RL coll.

Description

Shell thick-walled and markedly inflated, ovate-trigonal. Rostrum low, rather pointed. Umbo median, large, opisthogyrate. Postero-dorsal margin convex, smoothly curving to form well-rounded anterior end. Posterior margin consisting of a well-defined, rounded and curved keel from umbo to rostrum tip, producing a wide and markedly concave postero-dorsal area. Ventral margin evenly convex. Lunule well-defined. Sculpture of faint to obsolete concentric striae or growth lines. Hinge plate thick. Anterior row convex, posterior concave. Teeth chevron-shaped, numbering 11-12 anteriorly and 13-14 posteriorly in 5 mm valves. Resilifer deep, triangular, breaking through hinge plate. Anteriorly, a semi-external short, ill-defined ligament furrow. Anterior adductor scar large, roundish, posterior ovate and smaller, both impressed. Pallial line well-defined, sinus shallow. Prodissoconch ovate, about 160 µm long. Maximum length ca. 5 mm.

Distribution

The material examined ranges from the Middle Pliocene to Pleis-

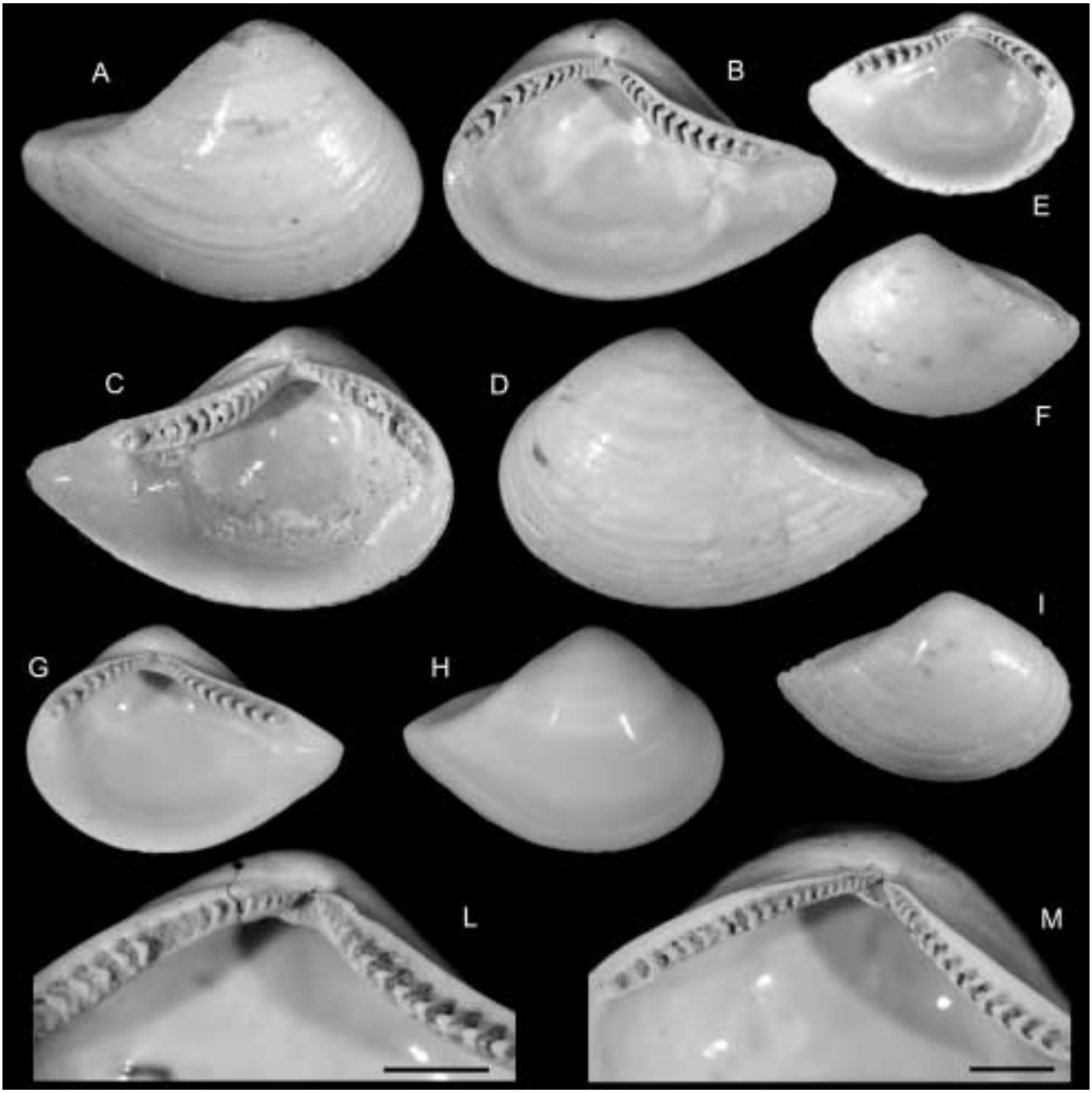

Fig. 2. A-I. *Jupiteria gibba* (Seguenza, 1877). A-F. Rometta, Middle Pliocene (A, B: 4.7 mm, MZB31005; C, D: 5.0 mm, MZB31005; E, F: 3.1 mm, MZB31005). G, H. Monte Besdone, Middle Pliocene (3.7 mm, MZB31006). I. Grammichele, Pleistocene (3.4 mm, MZB31007). L. *Jupiteria fissistriata* (Foresti, 1897). Santa Maria in Ceperano, Late Pliocene, hinge detail of Fig. 1O, scale bar = 1 mm. M. *Jupiteria concava* (Bronn, 1831), hinge detail of Fig. 1B, scale bar = 1 mm.

Fig. 2.. A-I. *Jupiteria gibba* (Seguenza, 1877). A-F. Rometta, Pliocene medio (A, B: 4,7 mm, MZB31005; C, D: 5.0 mm, MZB31005; E, F: 3,1 mm, MZB31005). G, H. Monte Besdone, Pliocene medio (3,7 mm, MZB31006). I. Grammichele, Pleistocene (3,4 mm, MZB31007). L. *Jupiteria fissistriata* (Foresti, 1897). Santa Maria in Ceperano, Pliocene superiore, dettaglio della cerniera di Fig. 1O, scala = 1 mm. M. *Jupiteria concava* (Bronn, 1831), dettaglio della cerniera di Fig. 1B, scala = 1 mm.

tocene. *Jupiteria gibba* is uncommon in the Pleistocene deposits, where it is found with an epibathyal fauna, together with *J. concava* (La Perna, 1998). In the Pliocene, it was more common and probably had a deeper distribution, as is indicated by the associated fauna.

Remarks

The lack of sculpture distinguishes *Jupiteria gibba* from *J. concava* and *J. fissistriata*. *J. gibba* is smaller, more elongate and with a sharper rostrum. However, because of its smooth surface, *J. gibba* can be confused with species of *Ledella*. This resemblance is even more striking in juveniles, where the rostrum has a median position, a posterior keel and a posterior "concavity" are not yet developed. *J. gibba* is similar to *J. isikela* Kilburn, 1994 from South Africa, which differs mainly by being less elongate and with a more inclined umbo.

The lack of concentric sculpture in *J. gibba* poses some taxonomic problems. According to Maxwell (1988a, b) there is a tendency to lose concentric sculpture among protobranchs but this seems to have little taxonomic weight at the supraspecific level. Apart from the other shell characters, it is worth noting that *J. gibba* shares with *J. concava* and *J. fissistriata* a *Ledella*-like juvenile shape.

The synonymy between *J. gibba* and *Leda sinuata* Foresti, 1897, is discussed under the following species.

Genus **Ledella** Verrill & Bush, 1897
(Type-species: *Ledella bushae* Warén, 1987, ICNZ, 1985)

La Perna (2003, in press a) commented on the taxonomy of *Ledella*, which should be kept distinct from the confused "*Yoldiella*" group. Several Recent and fossil species are known from the European area, all of them similar to *Ledella messanensis* (Jeffreys, 1876), the best known representative of this group.

Ledella seminulum (Seguenza, 1877)
(**Figs 3A–M**)

1877a – *Leda (Junonia) seminulum* Seguenza: 286.
1877b – *Leda (Junonia) seminulum* – Seguenza: 16, pl. 3, figs 14, 14a, b.
1897 – *Leda (Junonia) sinuata* var. *striata* Foresti, ex Meneghini ms: 216: pl. 9, fig. 2.
1981 – *Nuculana (Ledella) messanensis* – Robba: pl. 11, figs, 2-3.
1995 – *Yoldiella messanensis* – Tabanelli: 286.
2000 – *Leda (Junonia) seminulum* – Bertolaso & Palazzi: 33, figs 126-127 (type).

Examined material

Rometta (Messina), northeastern Sicily, Middle Pliocene, 34 vs, 16 shs (topotypes), RL coll. Rio Gamballaro (Imola), Emilia Romagna, Middle Pliocene, 16 vs, 28 shs, CT coll. Rio Gamballaro (Imola) Emilia Romagna, Middle Pliocene, MCI, Foresti-Scarabelli coll., 8 vs (types of *Leda sinuata* var. *striata*). Montalbano Jonico-Craco, Basilicata, Late Pliocene 21 vs, RL coll.

Description

Shell thick-walled, inflated, elongate-ovate. Rostrum median, moderately long, sharp. Umbo median, large, slightly opisthogyrate, protruding above shell outline. Antero-dorsal margin slightly concave, curving to form a narrowly rounded anterior end. Posterior margin concave near umbo, becoming convex towards rostrum tip. Rostral keel well-defined, rather sharp and slightly curving, extending from umbo to rostrum tip and bordering a rather wide convex postero-dorsal area. Lunule well-defined, escutcheon fading into postero-dorsal area. Sculpture particularly evident on the ventral half, consisting of well-defined concentric ridges, numbering ca. 13 per millimetre, and widely spaced, slightly stepped incremental scars. Hinge plate markedly thick. Teeth chevron-shaped, numbering ca. 11 anteriorly and posteriorly in 4 mm valves. Ligament pit rather deep, rounded. Anterior adductor scar large, rounded, posterior ovate and smaller, both impressed. Pallial line well-defined, sinus shallow. Prodissoconch ovate, ca. 210 μm long. Maximum length ca. 6 mm.

Distribution

Although the examined material is all Pliocene in age, *L. seminulum* has also been recorded from a Pleistocene locality (see Remarks). *L. seminulum* is found in association with a bathyal fauna (La Perna, unpubl.).

Remarks

Seguenza (1877b) remarked on the close similarities between *Leda seminulum*, *L. acuminata* Jeffreys, 1870 (=*L. messanensis*) and *L. rectidorsata* Seguenza, 1877. The differences he reported are confirmed (see also La Perna, 2003). The present species is more thick-walled and convex than *Ledella messanensis* (figs 3N, O) (and much more so than in *L. rectidorsata*), more elongate, with a sharper rostrum, a fairly well incised subrostral sinus and a different dorsal and umbonal outline. *L. messanensis* is mostly smooth or with ill-defined ridges close to the ventral margin, whereas true concentric sculpture is present in *L. seminulum*. *L. rectidorsata* has a straighter dorsal margin and sculpture of fine, close-set ridges.

Bertolaso & Palazzi (2000) illustrated a type of *Leda seminulum* (matching the present material) from Salice, a Pleistocene locality near Messina where this species is rare (La Perna, unpubl.). This species was also reported by Seguenza (1877b) from Rometta (Messina), where it is one of the most common protobranchs in bathyal beds of Middle Pliocene age. *L. messanensis* illustrated by Robba (1981) from the Early Pliocene of Northern Italy is *L. seminulum* and also the species reported by Lozano Francisco (1998) as *L. messanensis* from the Pliocene of Málaga has proved to be *L. seminulum* on examination of unpublished pictures.

Foresti (1897) described *Leda (Junonia) sinuata* from Early Pliocene clayey beds at Rio Gamballaro (Romagna, Northern Italy). Examination of type and topotype material proved this name to be based on two distinct species, namely *Jupiteria gibba* (juveniles) and *Ledella seminulum*. This is also evident from the description, where the occurrence of smooth (*J. gibba*) and concentrically sculptured specimens (*L. seminulum*) was remarked on. The sculptured specimens were referred to *Leda sinuata* var. *striata*.

Concentric sculpture is also present in the Late Miocene Mediterranean species, *L. peraffinis* (Seguenza, 1877) (figs 4O, P), which is much smaller than *L. seminulum* and has a different shape.

Ledella nicotrae (Seguenza, 1877)
(**Figs 4A–N**)

1877a – *Leda (Junonia) nicotrae* Seguenza: 94.
1877b – *Leda (Junonia) nicotrae* – Seguenza: 16, pl. 3, figs 14, 14a, b.
1997 – *Ledella nicotrae* - Di Geronimo & La Perna: 410, pl. 6, figs 7, 8.
2003 – *Ledella messanensis* - La Perna: 24, pl. 2, fig. 7.

Examined material

Monte Cerreto (Castrocaro), Emilia Romagna, Early Pliocene, 10 vs, 1 sh, CT coll. Campore (Parma), Emilia Romagna, Middle Pliocene, 13 vs, 2 shs, AC coll. Grammichele, southeastern Sicily, Pleistocene, >1000 vs, RL coll. Mineo, southeastern Sicily, Pleistocene, 56 vs, RL coll. Fiumefreddo di Sicilia, northwestern Sicily, Pleistocene, 103 vs, RL coll. Bovalino Superiore, southern Calabria, Pleistocene, 297 vs, RL coll.

Description

Shell moderately robust, rather inflated, ovate, almost equilateral. Umbo median, small, moderately protruding above shell outline, opistogyrate. Dorsal margin strongly convex; anterior margin well-rounded; posterior margin extended as a short, somewhat sharp rostrum. Ventral margin wide, strongly convex. A well-defined, obtuse keel

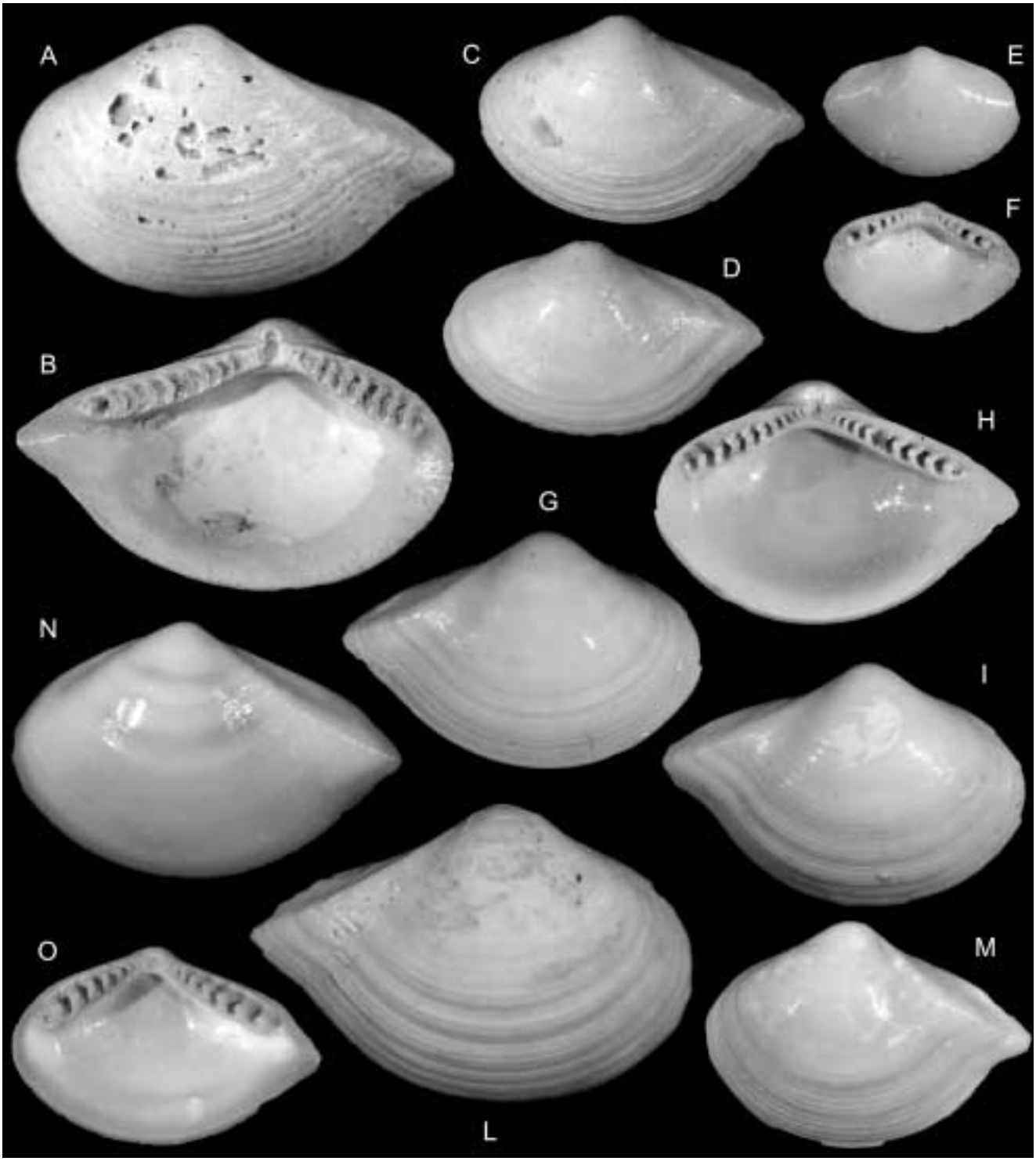

Fig. 3. A-M. *Ledella seminulum* (Seguenza, 1877). A-F. Rometta, Middle Pliocene (A, B: 4.8 mm, MZB31010; C: 3.6 mm, MZB31010; D: 3.2 mm, MZB31010; E, F: 1.9 mm, MZB31010). G-M. Rio Gamballaro, Middle Pliocene (G, H: 4 mm, MZB31011; I: 4 mm, MZB31011; L: 4.8 mm, MZB31011; M: 3.6 mm, MZB31011). N, O. *Ledella messanensis* (Jeffreys, 1876). Archi (southern Calabria) Pleistocene (N: 4.3 mm, MZB31012; O: 3.4 mm, MZB31012).

Fig. 3. A-M. *Ledella seminulum* (Seguenza, 1877). A-F. Rometta, Pliocene medio (A, B: 4,8 mm, MZB31010; C: 3,6 mm, MZB31010; D: 3,2 mm, MZB31010; E, F: 1,9 mm, MZB31010). G-M. Rio Gamballaro, Pliocene medio (G, H: 4 mm, MZB31011; I: 4 mm, MZB31011; L: 4,8 mm, MZB31011; M: 3,6 mm, MZB31011). N, O. *Ledella messanensis* (Jeffreys, 1876). Archi (Calabria meridionale) Pleistocene (N: 4,3 mm, MZB31012; O: 3,4 mm, MZB31012).

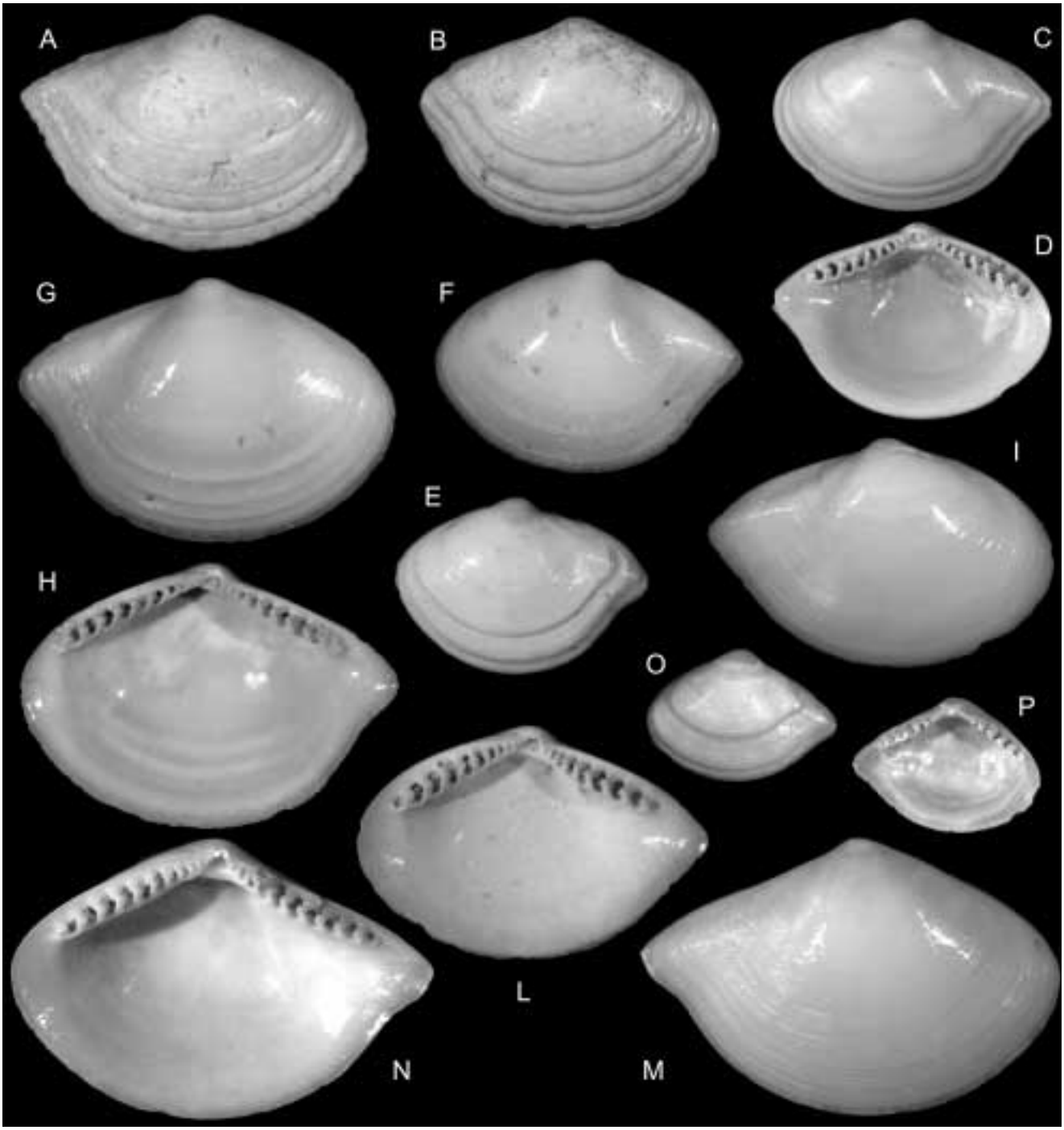

Fig. 4. A-N. *Ledella nicotrae* (Seguenza, 1877). A, B. Monte Cerreto, Early Pliocene (A: 3.4 mm, MZB31014; B: 3.0 mm, MZB31014). C-E. Campore, Middle Pliocene (C, D: 2.7 mm, MZB31015; E: 2.4 mm, MZB31015). F-H. Grammichele, Pleistocene (F: 3.0 mm, MZB31016; G, H: 3.7 mm, MZB31016). I-N. Transitional form to *L. messanensis*, Bovalino Superiore (southern Calabria), Pleistocene (I, L: 3.5 mm, MZB31022; M, N: 4.3 mm, MZB31022). O, P. *Ledella peraffinis* (Seguenza, 1877). Benestare (southern Calabria), Late Miocene (1.9 mm, MZB31013).

Fig. 4. A-N. *Ledella nicotrae* (Seguenza, 1877). A, B. Monte Cerreto, Pliocene inferiore (A: 3,4 mm, MZB31014; B: 3,0 mm, MZB31014). C-E. Campore, Pliocene medio (C, D: 2,7 mm, MZB31015; E: 2,4 mm, MZB31015). F-H. Grammichele, Pleistocene (F: 3,0 mm, MZB31016; G, H: 3,7 mm, MZB31016). I-N. Forma di transizione a *L. messanensis*, Bovalino Superiore (Calabria meridionale), Pleistocene (I, L: 3,5 mm, MZB31022; M, N: 4,3 mm, MZB31022). O, P. *Ledella peraffinis* (Seguenza, 1877). Benestare (Calabria meridionale), Miocene superiore (1,9 mm, MZB31013).

from umbo to rostrum tip defining a narrow convex posterior area. A fairly well impressed furrow behind rostrum, producing a shallow subrostral sinuation on postero-ventral margin. Lunule and escutcheon small, ill-defined. Concentric sculpture consisting of fairly well incised lines, somewhat irregularly spaced and stepped and intercalating growth lines, mostly on ventral half of valve. Hinge-plate moderately thick. Hinge taxodont; teeth chevron-shaped. Anterior and posterior row of similar length, both straight to barely curved. Teeth numbering 12 anteriorly and 11 posteriorly in valves 4 mm in length. Resilifer deep, roundish to roughly triangular. Anterior adductor scar smaller than posterior one, both ovate, not well distinct. Pallial line almost indistinct; pallial sinus rather deep. Prodissoconch ovate, ca. 215 μm long. Maximum length 4-5 mm.

Distribution

Pliocene and Pleistocene of Southern and Northern Italy. *L. nicotrae* was distributed from the deep shelf to the uppermost bathyal (La Perna, 2003).

Remarks

The taxonomic integrity of *Leda nicotrae* Seguenza, 1877 is questionable. Di Geronimo & La Perna (1997) remarked the difficulty of fully distinguishing *Ledella nicotrae* distinct from *L. messanensis*. This problem was again dealt with by La Perna (2003), who provided evidence of morphometric overlap among the Pleistocene populations of *L. nicotrae* and *L. messanensis*. The different palaeobathymetric distribution of *L. nicotrae* (deep shelf to epibathyal) and of *L. messanensis* (mesobathyal) in the Pleistocene deposits, led to the coclusion that the former is a shallower ecotype of the latter. The examination of Pliocene material necessitates revision of this hypothesis. There is no evidence of *L. messanensis s.s.* occurring in the Pliocene deposits, whereas material matching the Pleistocene *L. nicotrae* is found in association with deep-shelf to epibathyal fauna, like in the Pleistocene. Further studies may help to clarify this puzzle, but the present data suggest adoption of full species status for *L. nicotrae*, in spite of the difficulties for separating these two species. *L. nicotrae* is shorter, more expanded ventrally, less rostrate and generally more delicate than *L. messanensis*. It has a sculpture of well-incised growth lines and incremental scars, whereas *L. messanensis* is mostly smooth or with few ridges near the ventral margin. In conclusion, *L. nicotrae* was already present during the Pliocene and co-occurred with *L. messanensis* in the Pleistocene, at a different depths.

There are close similarities between *L. nicotrae* and *L. curvirostris* (Lehmann, 1885) from Middle Miocene of The Netherlands (Janse & Janssen, 1983). *L. curvirostris* seems to differ mainly by a slightly sharper rostral keel and a thicker shell-wall, otherwise it is notably similar to *L. nicotrae* in shape and sculpture.

Genus **Zealeda** Marwick, 1924

(Type-species: *Zealeda hamata* Marwick, 1924, OD)

Marwick (1924) proposed the genus *Zealeda* for a Pliocene species from New Zealand. Other species of *Zealeda* have since been described from the Late Tertiary of New Zealand (Fleming, 1966; Maxwell, 1988a; Beu & Maxwell, 1990). This genus is similar to *Ledella* in the general shell shape. The dorsal margin is somewhat straight, usually less arched than *Ledella*, and the postero-dorsal area is notably wide, giving a somewhat rectangular shell shape. The rostrum is median in position, short, moderately sharp, with a well-defined ridge extending from the umbo to rostrum tip. A rostral furrow and a subrostral sinuation is present. However, the most typical feature of *Zealeda* is represented by the sculpture, which consists of discontinuous, somewhat undulating or divaricating radial riblets, mostly present laterally, and of a regular pattern of fine close-set concentric ridges.

The distinction of *Zealeda* from *Ledella*, based on the presence of a distinct radial sculpture in the former, was stressed by Maxwell (1988a, b), who synonymised *Zealeda* with *Magaleda* Iredale, 1929 (type species *Ledella inopinata* Smith, 1885, Recent, South Australia). Although the taxonomic significance of sculpture in the protobranchs is not yet clear, the radial riblets of *Zealeda* are unusual. The sculpture is variable in strength among the New Zealand species of *Zealeda*, markedly coarse in *Z. crassicostata* Maxwell, 1988 to almost lost in *Z. concentrica* Marwick, 1931. However, the sculptural strength appears to be related to the general shell robustness, which is also variable, despite *Zealeda* being described as a thick-shelled species. A similar range of robustness is also present in species of *Ledella.*

A tortoiseshell pattern is sometimes preserved on the shell surface of *Z. elegans* n.sp. (fig. 5H). Allen & Hannah (1989) described a straw coloured periostracum, with a blistered appearance and leaving a tortoiseshell pattern for *Ledella pustulosa* (Jeffreys, 1876) (figs 5I, M). A blistered periostracum is also known for "*Magaleda*" *inopinata* (Smith, 1885) and *Ledellina* Filatova & Schileyko, 1984 (Filatova & Schileyko, 1984).

Zealeda has been never applied to any Atlantic protobranch, but there are some species or subspecies that should be assigned to this genus, the best known of which is *Ledella pustulosa*. Warén (1980, 1989) examined the type material and added comments on the shell morphology. Allen & Hannah (1989) distinguished four subspecies, namely *L. pustulosa pustulosa*, *L. pustulosa marshalli* Allen & Hannah, 1989 (both in the Northeast Atlantic), *L. pustulosa argentinae* Allen & Hannah, 1989 (Argentine basin) and *L. pustulosa hampsoni* Allen & Hannah, 1989 (West Africa). For the time being, these Atlantic taxa are conservatively maintained in *Ledella*, but their strong similarities to *Zealeda*, in shell shape, sculpture and periostracum, cannot be disregarded. The representatives of *Ledellina* (four species are known in the Pacific) are thin-shelled and closely recalling *L. pustulosa*, but the sculpture is only concentric (Filatova & Schileyko, 1984; Coan *et al.*, 2000). While additional study is needed, *Zealeda*, *Ledellina* and the group of *Ledella pustulosa* appear to be closely related to each other.

Zealeda elegans n.sp. ex Seguenza ms.

(**Figs 5A–H**)

1877a – *Leda (Junonia) pustulosa* – Seguenza: 17, pl. 3, figs 17a-d.
1993 – *Ledella pustulosa* – Tabanelli: 8, pl. 1, fig. 9.

Type locality

Savignano sul Panaro (Modena), Emilia Romagna, Middle Pliocene.

Type material

Holotype (1 v, MZB31008) and 5 paratypes (4 vs + 1 sh, MZB31009).

Other material

Type locality, 25 vs, 27 shs, Della Bella coll. Rometta (Messina), north-eastern Sicily, Middle Pliocene, 1 v and fragments, RL coll.

Etymology

From the Latin *elegans* (= graceful). It is the manuscript name used by Seguenza for the present species.

Description

Shell markedly robust and inflated, ovate, almost equilateral. Umbo median, wide, moderately protruding above shell outline, ortogyrate to barely opistogyrate. Dorsal margin convex; anterior margin well-rounded; posterior margin extending in a short, rather blunt rostrum. Ventral margin strongly convex. A well-defined but not sharp keel from umbo to rostrum tip, producing a wide convex posterior area. Impressed furrow behind rostrum, giving a shallow subrostral sinuation to postero-ventral margin. Lunule and escutcheon small, well-defined. Radial sculpture of shallow, discontinuous, somewhat undulating riblets, becoming obsolete on central valve area. Concentric

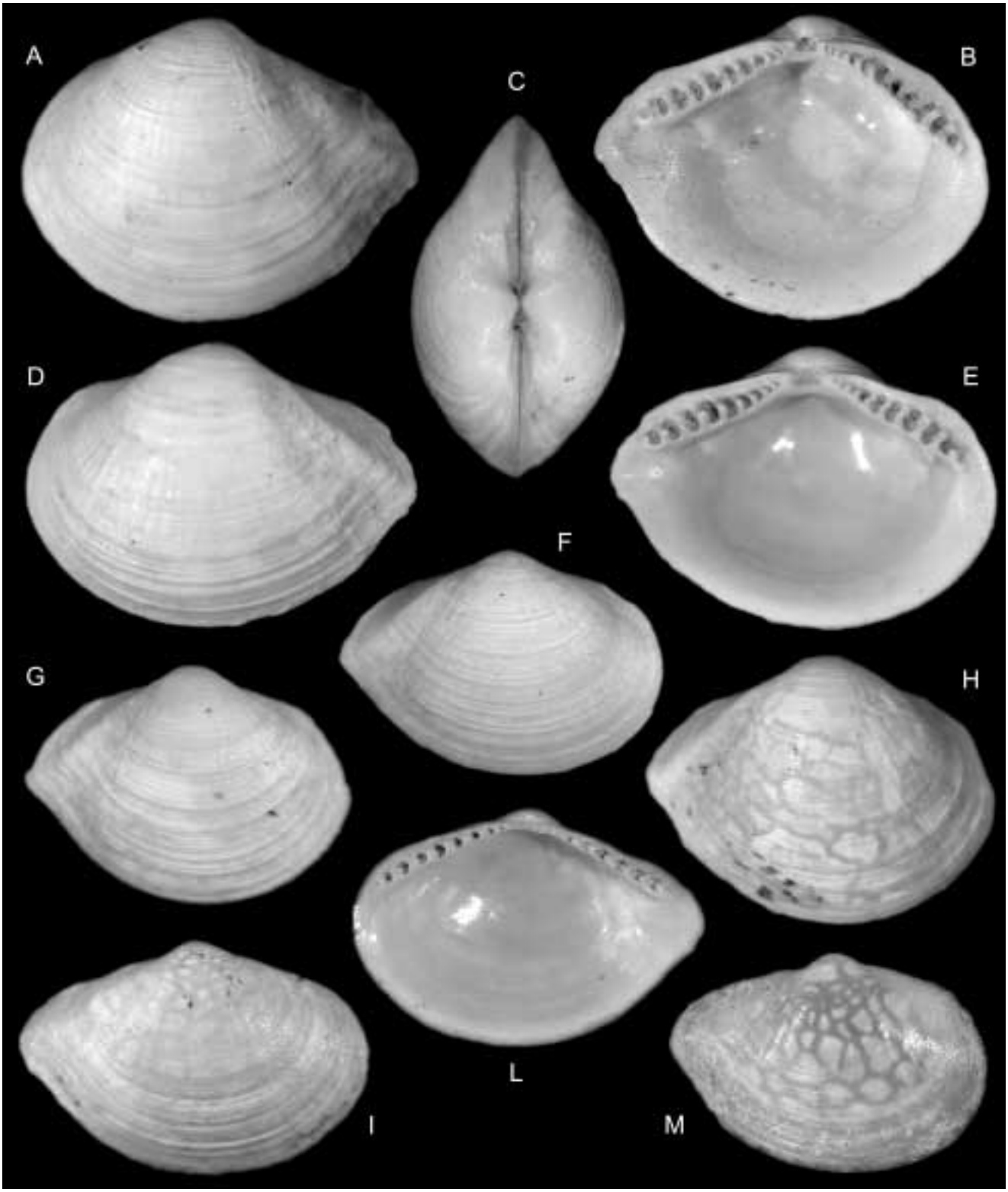

Fig. 5. A-H. *Zealeda elegans* n.sp. Savignano sul Panaro, Middle Pliocene. A, B. Holotype (4.0 mm, MZB31008). C. Paratype 1 (3.7 mm, MZB31009). D, E. Paratype 2 (4.0 mm, MZB31009). F. Paratype 3 (3.3 mm, MZB31009). G. Paratype 4 (3.3 mm, MZB31009). H. Paratype 5 (3.5 mm, MZB31009). I-M. *Ledella pustulosa* (Jeffreys, 1876). Iceland, BIOICE st. 728 (sample 2704), N 63°50'50"-W 27°42'80", 1295 m (I, L: 3.5 mm; M: 3.1 mm), Icelandic Museum of Natural History.

Fig. 5. A-H. *Zealeda elegans* n.sp. Savignano sul Panaro, Pliocene medio. A, B. Olotipo (4,0 mm, MZB31008). C. Paratipo 1 (3,7 mm, MZB31009). D, E. Paratipo 2 (4,0 mm, MZB31009). F. Paratipo 3 (3,3 mm, MZB31009). G. Paratipo 4 (3,3 mm, MZB31009). H. Paratipo 5 (3,5 mm, MZB31009). I-M. *Ledella pustulosa* (Jeffreys, 1876). Islanda, BIOICE st. 728 (sample 2704), N 63°50'50"-W 27°42'80", 1295 m (I, L: 3,5 mm; M: 3,1 mm), Icelandic Museum of Natural History.

sculpture consisting of well-defined close-set ridges, somewhat irregular in spacing and strength. Postero-dorsal area with growth lines only. Hinge-plate thick. Hinge taxodont; teeth not distinctly chevron-shaped. Anterior and posterior row of similar length, both straight. Teeth numbering 12 anteriorly and 11 posteriorly (holotype). Resilifer moderately deep, rounded. Anterior adductor scar smaller than posterior, both ovate, impressed. Pallial line fairly distinct; pallial sinus faint. Prodissoconch ovate, ca. 150 μm long. Holotype size: length 3.9 mm, height 3.0 mm, tumidity 1.1 mm. Paratypes and other material 3.0-4.3 mm in length.

Distribution

Only known from the Mediterranean Middle-Late Pliocene. *Zealeda elegans* n.sp. is found in association with a bathyal fauna (*Bathyspinula excisa*, *Ledella seminulum*, *Alvania diadema*, etc.), probably not deeper than 500-700 m.

Remarks

Seguenza (1877b) adopted the name *Leda pustulosa* Jeffreys for the species he had named *Leda elegans* in manuscript. The application of Jeffreys' names to fossil species by Seguenza, and *vice versa*, was frequent, since they corresponded and exchanged specimens (Warén, 1980; La Perna, in press a). Allen & Hannah (1989: fig. 17) illustrated a Pliocene valve from Sicily in the Jeffreys collection (U.S. National Museum), clearly belonging to *Z. elegans* n.sp.

The present species is not particularly similar to *Ledella pustulosa* (figs 5 I-M), from which it differs by being much more robust in all its parts, markedly ovate in shape, rather than somewhat rectangular, with a sharper rostral keel and a coarser sculpture. The West African *Ledella pustulosa hampsoni* Allen & Hannah, 1989 is thick-walled like *Z. elegans* n.sp., or even more so, and differs by having a straighter dorsal margin, a blunter rostrum and a less sharp rostral keel.

Discussion

Because of the poor knowledge of the Pliocene protobranchs, especially those from the deep-sea deposits, few aspects can be discussed in the present work.

Like the Pleistocene deep-sea fauna (Di Geronimo & La Perna, 1997; Di Geronimo *et al.*, 1997), the Pliocene fauna had a psychrospheric character, of which the Plio-Pleistocene protobranch *Bathyspinula excisa* (Philippi, 1844) probably is the best known "witness" (Di Geronimo & La Perna, 1996). The loss of the psychrosphere and the onset of deep homeothermic conditions during the Middle-Late Pleistocene caused the extiction of many deep-sea cold-water species, among them about 50% of the Pleistocene protobranchs (La Perna, 2003, in press a).

The Middle Pliocene cooling (Shackleton & Opdyke, 1977; Thunell & Williams, 1983), which caused a massive extinction of the shallow-water fauna (Monegatti & Raffi, 2001), must have controlled the deep-sea benthos too. Actually, evidence is accumulating for the appearance of cold deep-sea species in the Middle Pliocene (Tabanelli, 1993) and further studies may bring stronger evidence for this hypothesis.

The relationship between the Mediterranean and the Indo-Pacific fauna are worth studying. Whereas such relationships are fairly well known for the shallow-water fauna, the "Tethyan inheritance" in the Plio-Quaternary Atlantic and Mediterranean deep-sea fauna have been studied little. Both *Jupiteria* and *Zealeda* may have Tethyan origins and their distribution underwent a western-eastern disjunction because of the suppression of Tethys and the closure of the eastern seaway during the Early Miocene, as discussed elsewhere (La Perna, in press b). Because of the much lower degree of provincialism of the deep-sea fauna, we should expect a less clear disjunct pattern than within the shallow-water fauna.

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