

On the last occurrence of *Marginella* Lamarck, 1799 (Gastropoda, Marginellidae) in the Mediterranean: description of a new species from the Early Pleistocene and paleoceanographic implications

Rafael LA Perna

Dipartimento di Scienze della Terra e GeoAmbientali, Università di Bari,
via Orabona 4, I-70125 Bari (Italy)
rafael.laperna@uniba.it

Angelo Vazzana

Museo di Biologia Marina e Paleontologia di Reggio Calabria,
via Strad. Prima Giuffrè 32, I-89122 Reggio Calabria (Italy)
angelovazzana@tin.it

Published on 30 September 2016

[urn:nbn:zoobank.org:pub:EC4EA93F-AB85-4C7F-BA09-9CB0AB2A1B38](http://urn.nbn:zoobank.org:pub:EC4EA93F-AB85-4C7F-BA09-9CB0AB2A1B38)

La Perna R. & Vazzana A. 2016. — On the last occurrence of *Marginella* Lamarck, 1799 (Gastropoda, Marginellidae) in the Mediterranean: description of a new species from the Early Pleistocene and paleoceanographic implications. *Geodiversitas* 38 (3): 451–461. <http://dx.doi.org/10.5252/g2016n3a5>

ABSTRACT

A new species of *Marginella* Lamarck, 1799 is described from the Early Pleistocene of the Messina Strait area, *M. seguenzai* n. sp. The remarkable variability in shell size and shape required a preliminary morphometric analysis, which provided evidence of a single species. This is the last known representative of the genus *Marginella* in the Mediterranean, today highly diverse in the tropical and subtropical shallow waters of West Africa, up to about 28°N. The genus *Marginella* was thought to have disappeared from the Mediterranean and the adjacent Atlantic after the Early Pliocene, due to early cooling phases. Anyway, *Marginella seguenzai* n. sp. was a deep water species, and its extinction was most probably due to the loss of psychrosphere, in the Early Pleistocene, rather than to climatic deterioration. The remarkable closeness between the new species and a deep water living species, endemic to three seamounts in the NE Atlantic, suggests a common origin for both species. High productivity seems to have been a key factor in the Mediterranean distribution of *Marginella*, either in shallow and deep waters.

RÉSUMÉ

Sur la dernière occurrence de Marginella Lamarck, 1799 (Gastropoda, Marginellidae) en Méditerranée: description d'une nouvelle espèce du Pléistocène inférieur et implications paléocénographiques.

Marginella seguenzai n. sp. est décrite du Pléistocène inférieur du Détrit de Messine. La variation considérable dans la taille et la forme de la coquille, a demandé une analyse préliminaire morphométrique, qui ont fourni des preuves d'une seule espèce. En Méditerranée, c'est la dernière occurrence du genre *Marginella* Lamarck, 1799, aujourd'hui très diversifié dans les eaux peu profondes, tropicales et subtropicales, d'Afrique de l'Ouest, jusqu'à environ 28°N. On croyait que le genre *Marginella* avait disparu de la Méditerranée et de l'Atlantique adjacente depuis le Pliocène inférieur, en raison des premiers épisodes de refroidissement. *Marginella seguenzai* n. sp. était une espèce d'eaux profondes, et son extinction est plus probablement due à la disparition de la psychrosphère, dans le Pléistocène inférieur, plutôt que de à la détérioration climatique. La similitude entre l'espèce nouvelle et une espèce profonde, endémique de trois monts sous-marins de l'Atlantique du Nord, suggère une origine commune pour les deux espèces. La haute productivité semble être un facteur clé dans la distribution de *Marginella* dans la Méditerranée, en eaux profondes et peu profondes.

KEY WORDS

Marginella,
shape analysis,
Early Pleistocene,
Messina Strait,
Mediterranean,
paleoceanography,
new species.

MOTS CLÉS

Marginella,
analyse de contours,
Pléistocène inférieur,
Détrit de Messine,
Méditerranée,
paléocénographie,
espèce nouvelle.

INTRODUCTION

In the well-known work on the “Tertiary formations” in the area of Reggio Calabria, Seguenza (1879) described an “Astian” locality, Gallina, from which he reported an unusually rich molluscan fauna. The Astian stage of Seguenza includes a chronostratigraphic interval ranging from Late Pliocene to Early Pleistocene (La Perna & D’Abramo 2010). The deposits of Gallina are Early Pleistocene in age.

A survey on the Marginellidae Fleming, 1828 and Cystiscidae Stimpson, 1865 (marginelliform gastropods *sensu* Coovert & Coovert 1995) from this locality, led to the identification of some species of the genera *Granulina* Jousseaume, 1888 and *Gibberula* Swinson, 1840. Actually, Seguenza (1879) reported seven marginelliform species from Gallina, including a new species, *M. ovulaeformis*, currently under study. Unexpectedly, an undescribed species of the genus *Marginella* Lamarck, 1799 was also encountered: it is well distinct from the co-occurring marginelliforms, and also fairly common in the assemblage. The reason why it was not reported by Seguenza remains obscure, unless it was confused with *Volvarina mitrella* (Risso, 1826), superficially similar in size and shape.

The genus *Marginella* is richly diverse in the tropical and subtropical shallow waters of West Africa (Gofas & Fernandes 1988, 1994; Fernandes & Rolán 1991; Coovert & Coovert 1995; Goud & Neefs 1996; Cosignani 2006), up to c. 28°N. According to literature data, its last occurrence in the Mediterranean dates back to the Early Pliocene. Therefore, the presence of a species of the genus *Marginella* in the Pleistocene was even more unexpected.

RECORDS OF *MARGINELLA* FROM THE EUROPEAN PLIO-QUATERNARY

Until recently, the only species known from the Mediterranean Pliocene was *Marginella aurisleporis*, described by Brocchi (1814: 320, pl. 4, fig. 11) from the Early Pliocene of Tabiano (Northern Italy). In addition to the illustration and re-description of the type material (Rossi Ronchetti 1955), there are several illustrated records, all from the Italian Pliocene, such as Cossman (1899), Pelosio (1966), Malatesta (1974), Forli & Dell’Angelo (2000) and Chirli (2002).

Another species of *Marginella*, coeval with *M. aurisleporis*, was described by Forli & Dell’Angelo (2000) from the surroundings of Siena (Tuscany), *Marginella misae*. The species was said to be very similar to *M. aurisleporis*, from which it differs by being slightly more inflated, with a lower spire and a thinner lip, lacking the internal denticulations. The morphometric study provided by Forli & Dell’Angelo (2000: figs 3, 4) actually supports the separation of *M. misae* from *M. aurisleporis* but, as discussed by Landau *et al.* (2006a), they seem ecological morphs related to different substrates or depth ranges. This led Landau *et al.* (2006a) to consider *M. misae* a junior synonym of *M. aurisleporis*.

An astonishing association of shallow water marginelliforms was reported by Muñiz Solis (2002) and Landau *et al.* (2006a) from the Early Pliocene (Zanclean-Early Piacenzian) of Estepona, Southern Spain. Eight species of *Marginella*, including *M. aurisleporis*, are present at Estepona, in addition with genera never recorded from the Mediterranean Pliocene: *Eratoidea* Weinkauff, 1879, *Dentimargo* Cossmann, 1899, *Prunum* Hermannsen, 1852 and *Persicula* Schumacher, 1817. Though Estepona belongs geographically to the Mediterranean, its fauna is markedly different from the fauna from coeval deposits known all through the Mediterranean. It is unusually diverse and rich in thermophilic taxa, as well documented by the occurrence and diversity of several groups, such as the Olividae (Landau & Da Silva 2006), the Cancellarioidea (Landau *et al.* 2006b), etc. Such a high diversity and richness in thermophilic taxa has been attributed either to the tropical conditions in the Early Pliocene, with the tropical zone ending at the latitudes of southern Iberian Peninsula (Landau & Da Silva 2006; Monegatti & Raffi 2007; Landau *et al.* 2007), and to local conditions of high productivity (Landau *et al.* 2006a, b; Landau & Da Silva 2006). Currently, the complex hydrodynamics of the Gibraltar Strait, including an upwelling system in the north-western part of the Alboran Sea, off Estepona (Bárcena & Abrantes 1998; Sarhan *et al.* 2000), strongly enhances productivity and diversity (Gómez *et al.* 2000).

There are some Pliocene records of *Marginella* from the Atlantic façade: Vale de Freixo, in the Mondego Basin, west-central Portugal (Da Silva 2002; Landau *et al.* 2007; Da Silva *et al.* 2011). The age is referred to the uppermost Zanclean-lower Piacenzian (Da Silva *et al.* 2010, 2011). Two species of *Marginella* occur in the Mondego Basin, one identified as *M. aurisleporis*, the other as *M. iberica* Landau, La Perna & Marquet, 2006, one of the species described from Estepona. The few available shells referred to as *M. aurisleporis* (Da Silva *et al.* 2011: figs 3, 2.1-2.4) are smaller (40-45 mm) and more inflated than the Italian material, but for the moment being *M. aurisleporis* seems the best identification for the Portuguese material.

No Pleistocene record of *Marginella* was available before the present one, and no species occurs in the Mediterranean, but *M. glabella* (Linnaeus, 1758), distributed from Morocco to Senegal, has recently been recorded from the Málaga harbour, as an alien species of anthropic origin (Luque *et al.* 2012).

LOCATION AND GEOLOGICAL SETTING

Gallina, municipality of Reggio Calabria, is located about 4 km from the Calabrian coast of the Messina Strait (Fig. 1A, B). The outcrop, small and poorly exposed, is in the north-western part of Gallina (38°51'10.4"N, 15°40'30.8"E) (Fig. 1B, C).

The study material is from a richly fossiliferous bed (Fig. 1B, C), about 20 cm thick, consisting of yellowish clayey fine sand. It overlays a greyish sandy-clayey bed exposed for about 60 cm (Fig. 1C[a]), containing a scant molluscan fauna including the Boreal Guest (*sensu* Raffi 1986) *Pseuda-*

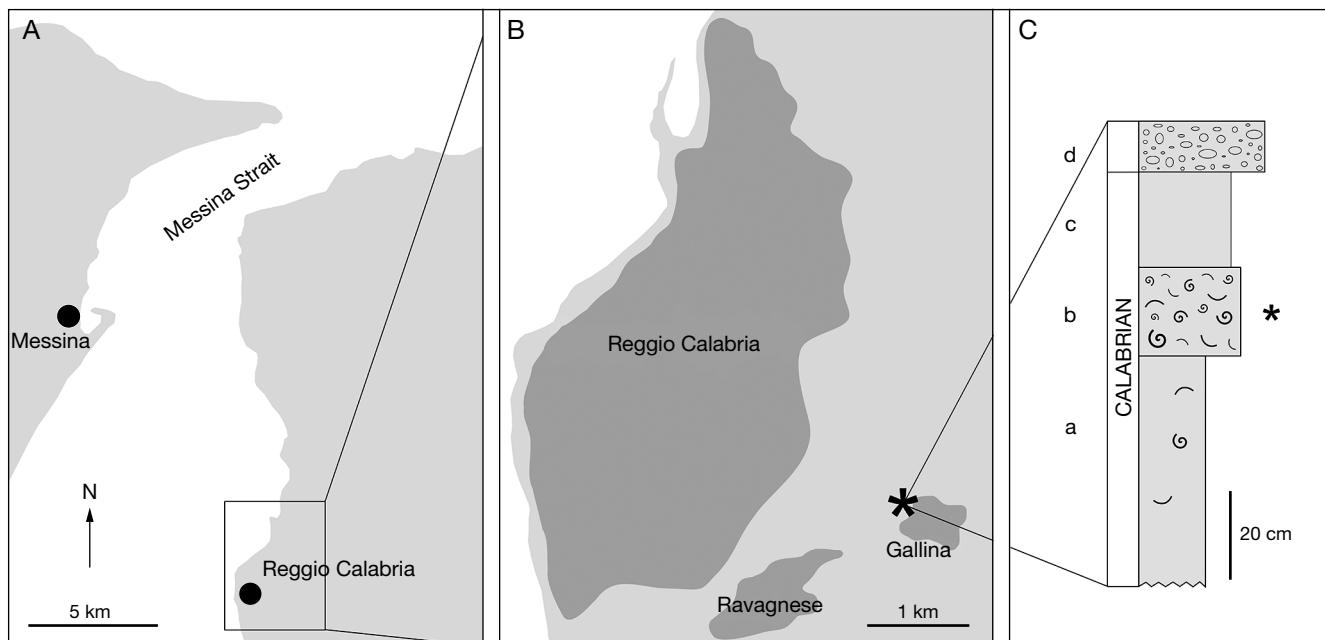


FIG. 1. — **A**, Map of the Messina Strait; **B**, location of the outcrop; **C**, schematic stratigraphy of the outcrop (asterisk indicates the sampled bed). Abbreviations: see text.

mussium septemradiatum (O. F. Müller, 1776). The richly fossiliferous bed is overlaid by about 30 cm of silty sands (Fig. 1C[c]), without evident macrofossils. The section is topped by Late Pleistocene-Holocene terrace deposits and soil (Fig. 1C[d]). There are evidences of lateral variations: in a nearby outcrop, about 10 m from the first, the richly fossiliferous bed is replaced by greyish clayey sands rich in brachiopods, mainly *Terebratula scillae* Seguenza, 1871 and *Gryphus sphenoideus* (Philippi, 1844).

The calcareous nannofossil content of the richly fossiliferous bed (Fig. 1C[b]) is poorly preserved and consists of abundant Neogene reworked taxa, whereas the basal greyish bed (Fig. 1C[a]) can be unambiguously referred to the large *Gephyrocapsa* Zone, and the top silty sandy bed (Fig. 1C[c]) to the small *Gephyrocapsa* Zone (respectively, MNN19d and MNN19e Zones of Rio *et al.* 1990) (M. Marino pers. comm.). The fossiliferous bed can therefore be referred to the Calabrian stage, Early Pleistocene.

Seguenza (1879: 240, 241) devoted some special comments to the fossil fauna from Gallina. He remarked on its richness (over 700 molluscan species, about 40 of which were described as new) and its unusual composition, a mixture of the three types of Astian assemblages known from the area of Reggio Calabria: “*facies degli abissi*”, “*facies littorale*” and “*facies a Brachiopodi*” (“Così i depositi di Gallina riescono del più alto interesse paleontologico e geologico, e costituiscono un facies che io direi misto”). According to Seguenza, the composition of the Gallina fauna, including deep and shallow water species, was indicative of “intermediate depth”, between shelf and slope. Actually, the molluscan fauna contains several shelf species, such as *Bittium reticulatum* (da Costa, 1778), *Manzonia crassa* (Kanmscher, 1798), *Pteromeris minuta* (Scacchi, 1836), *Digitaria digitata*

(Linnaeus, 1758), etc., but for the most part it consists of species (mainly small gastropods), with a generically deep water distribution (outer shelf to slope). Several typically bathyal species are also present, such as *Solariella marginulata* (Philippi, 1844), *Alvania testae* (Aradas & Maggiore, 1844), *Amphissa acutecostata* (Philippi, 1844), *Ennucula corbuloides* (Seguenza, 1877), *Yoldiella messanensis* (Jeffreys, 1876), *Cyclopecten hoskynsi* (Forbes, 1844), etc., known from Pleistocene bathyal deposits in Southern Italy (Di Geronimo & La Perna 1997).

Rather than an assemblage formed at “intermediate depths”, the fauna from Gallina can be interpreted as being in part allochthonous, i.e. formed by means of downslope transport of sediment and shell material from the outer shelf. The Messina Strait area is characterised by a strong influence of tectonics and hydrodynamics on sedimentation (Barrier 1987; Mercier & Barrier 1987; Montenat *et al.* 1987). Gravity flows, erosional truncatures, hydraulic dunes, etc., are frequent characters of the Plio-Quaternary stratigraphy of the Messina Strait area. Dell'Angelo *et al.* (1998) assumed that the fauna from Gallina also included shells reworked from older sediments. Reworking is strongly suggested by the nannofossil assemblage but, at least in the case of *Marginella*, the conditions of preservation of shells do not support such an hypothesis.

MATERIAL AND METHODS

The study material consists of over 80 shells, all from bed b (Fig. 1C). It was collected either by manual picking on the outcrop and bulk samples (about 150 kg of sediments). Shells are generally fairly well preserved.

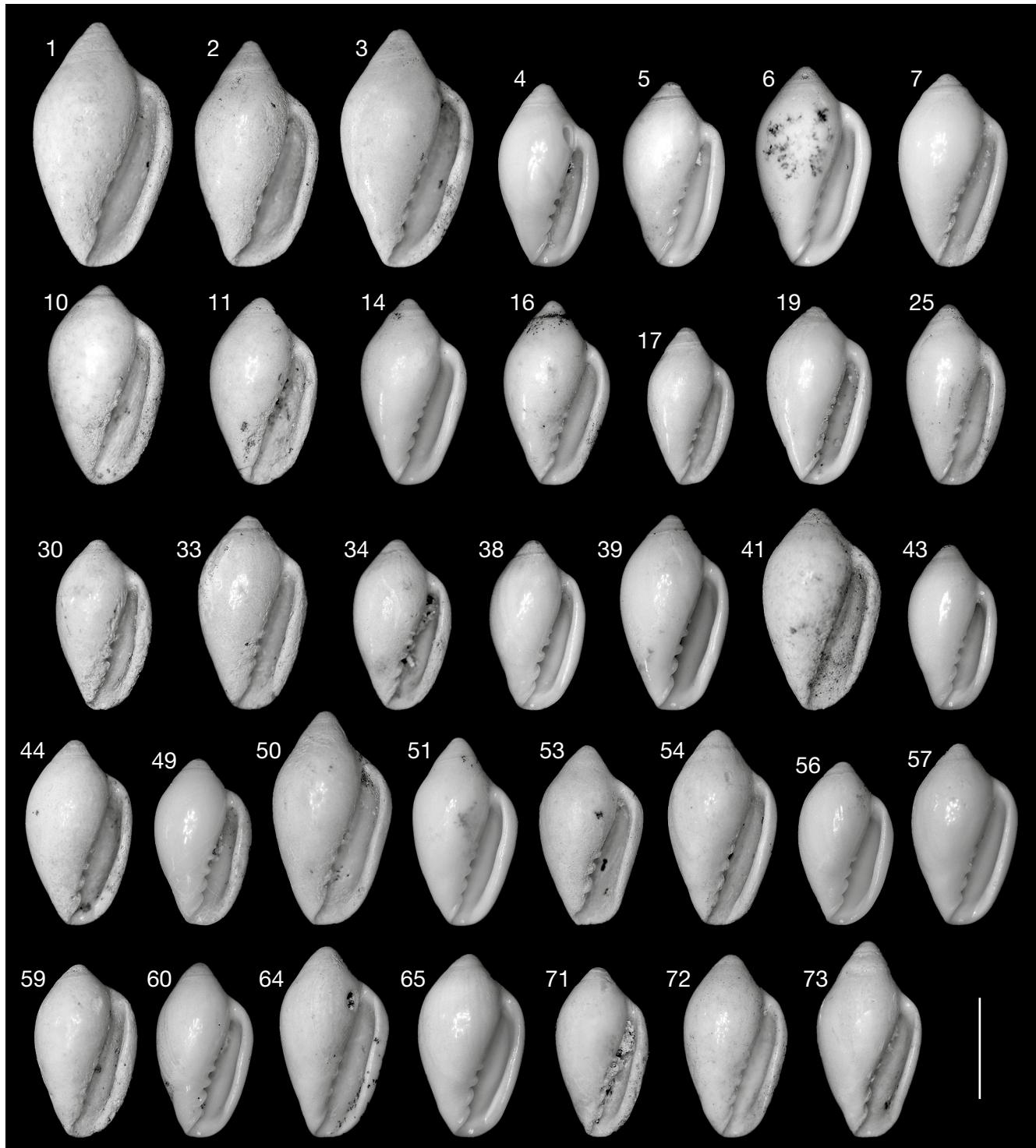


FIG. 2. — Sample of 36 shells used for morphometry and shape analysis, with identification number. Scale bar: 5 mm.

Because of the remarkable variability in size and shape shown by the shells of *Marginella*, a morphometric study, based on shell measurements and shape analysis, was performed to test the working hypothesis of a single species. The study was based on 36 shells (Fig. 2), all at full growth stage (with thick outer lip), whereas juveniles, sub-adults and worn shells were excluded. Each shell was photographed

with a low magnification digital microscope. Photographs were then used for shell measurements (height and maximum diameter) and for digitizing x/y coordinates around outlines. Outlines were digitized through 100 evenly spaced points, starting from shell apex. Points and their coordinates were obtained with the software tpsDig 2.12 (Rohlf 2010). Data analysis was performed using PAST

2.17 (Hammer *et al.* 2001). Outlines were standardized, removing size, position and rotation (Procrustes fitting), then submitted to harmonic decomposition with the Hangle method, based on the Fast Fourier Transform, proposed by Haines & Crampton (2000) as a competitor to the Elliptic Fourier Analysis. The coefficients of 9 harmonics (2 to 10, 97.88% of total power spectrum) were used in the Principal Component Analysis based on the covariance matrix.

ABBREVIATIONS AND ACRONYMS

The following abbreviations and acronyms are used in the present work:

H	shell height;
D	shell maximum diameter (shell width);
PCA	Principal Component Analysis;
PPCC	normal probability correlation coefficient;
SD	standard deviation;

Institutions

MNHN	Muséum national d'Histoire naturelle, Paris;
MBMPRC	Museo di Biologia Marina e Paleontologia, Reggio Calabria;
MZB	Museo di Zoologia dell'Università di Bologna.

MORPHOMETRY AND SHAPE ANALYSIS

Variability in the sample of 36 shells (Fig. 2) selected for morphometry and shape analysis can be summarized as follow: H ranges from 7.8 to 12.2 mm (SD 0.96), D from 4.4 to 7.0 mm (SD 0.55); the shell is more or less elongate (H/D 1.66-1.85, SD 0.04), with a more or less low spire and the maximum diameter more or less close to shell mid-height or slightly posterior to it. Conversely, lip and aperture are more constant in shape. Within such a variability some shells, such as nos 3, 10, 43, 73, etc., appear so much different from each other, that they could be identified as distinct species.

The bivariate scatter plot D vs H (Fig. 3) shows a single cloud of points, with a highly significant correlation coefficient ($r = 0.929$). Furthermore, H/D has a normal distribution, with a high PPCC (0.9911) (Fig. 3A[inset]). Normality tests (Shapiro-Wilk and Anderson-Darling) also support a normal distribution of H/D .

Shape analysis results agree with the basic morphometry. The scatter plot on the PCA 1-PCA 2 plane (about 63% of total variance) shows an undifferentiated dispersion of data (Fig. 4). Shells are ordered mainly according to spire elevation (PCA 1, 48.60% of total variance), and secondly according to slenderness (PCA 2, 14.29% of total variance). It is worth remarking that both PCA 1 and PCA 2 scores show a normal distribution, with very high values of PPCC (confirmed by normality tests, as above), providing evidence of a single cluster.

In conclusion, in spite of the evident variability in size and shape, the study sample consists of a single entity, here dealt with as a single species.

A variability, similar to that herein documented, should be expected on many marginelliforms, usually studied or described on few shells or living specimens. It is worth remarking that a wide variability can also affects the colour pattern of soft parts (Wakefield 2003), usually considered as an important diagnostic character in marginelliform gastropods.

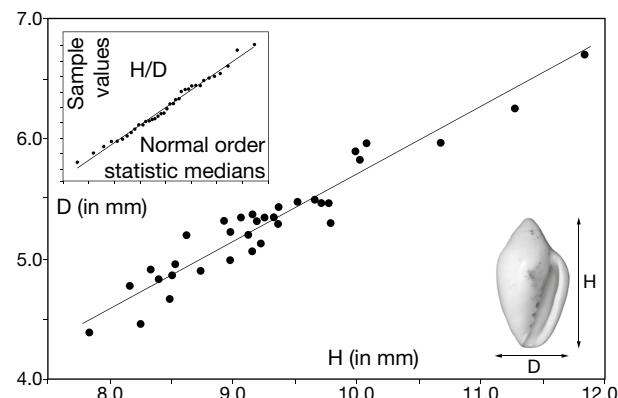


FIG. 3. — D vs H scatter plot and fitting mean-squares line. Inset shows the normal probability plot for H/D .

SYSTEMATICS

Family MARGINELLIDAE Fleming, 1828
Subfamily MARGINELLINAE Fleming, 1828

Genus *Marginella* Lamarck, 1799

TYPE SPECIES. — *Voluta glabella* Linnaeus, 1758 by monotypy.

Marginella sequenzai n. sp.
(Figs 2; 5A-L; 6A, B)

TYPE MATERIAL. — Holotype and five paratypes. Holotype: H 9.3 mm, D 5.3 mm (MZB60202). — Paratypes: Paratype 1, H 10.6 mm, D 5.9 mm (MZB60203); Paratype 2, H 9.7 mm, D 5.4 mm (MZB60203); Paratype 3, H 9.0, D 5.3 mm (MZB60203); Paratype 4, H 8.4 mm, D 4.8 mm (MBMPRC). Paratype 5, H 11.8 mm, D 6.7 mm (MBMPRC).

ETYMOLOGY. — After Giuseppe Seguenza (Messina 1833-1889), eminent Italian geologist and paleontologist.

MATERIAL EXAMINED. — Over 80 shells, all from the type horizon (MBMPRC).

TYPE HORIZON. — Bed b in the outcrop of Gallina, Reggio Calabria (Fig. 1C).

TYPE LOCALITY. — Gallina, Reggio Calabria, Calabrian, Early Pleistocene.

DIAGNOSIS. — A small *Marginella* species, biconical, moderately inflated, with last whorl making about 85% of shell height, maximum diameter at shell mid-height. Apex blunt, spire low, with two flat whorls. Aperture narrow, elongate, somewhat parallel-sided, with four columellar plications. Outer lip internally smooth, thickened by a wide outer rim.

DISTRIBUTION. — The new species is only known from the type locality. Because of the allochthonous character of the fauna from Gallina, *M. sequenzai* n. sp. could be a bathyal species, or a shelf species whose shells were transported to bathyal depths. *Marginella* mainly has a shallow water distribution, but some species are widely dis-

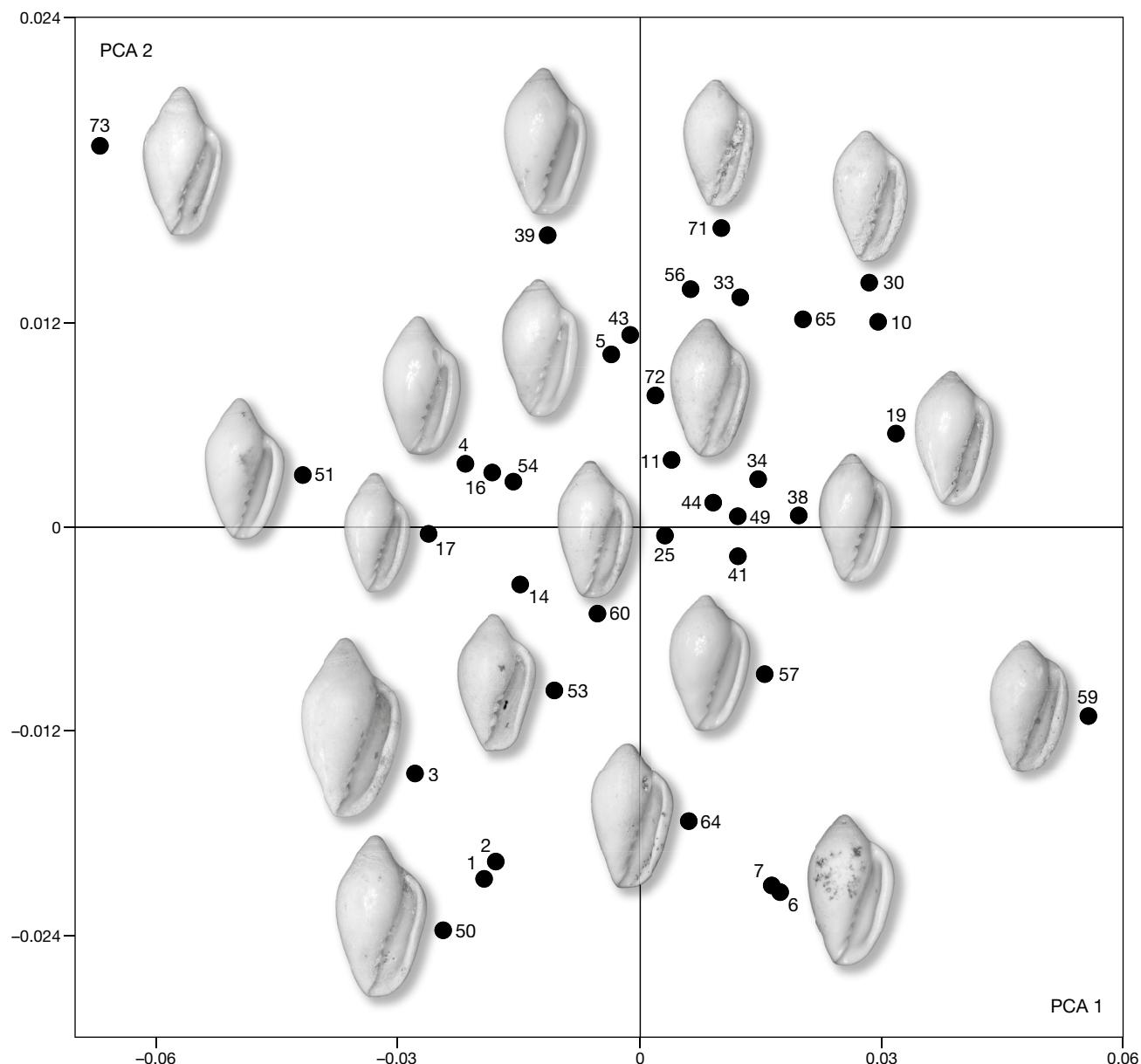


FIG. 4. — PCA based on harmonic decomposition of shell outline: plane PCA1-PCA2. Identification numbers as in Figure 2.

tributed bathymetrically (e.g. Goud & Neefs 1996), while few are only known from bathyal depths (e.g. Coomans 1975; Bouchet & Warén 1985). Considering the general good preservation of shells and the prevalent composition of the molluscan assemblage, it can be assumed that *M. seguenzai* n. sp was a deep water species. This hypothesis is also supported by close similarities occurring between the new species and a Recent deep water species from the NE Atlantic, as discussed in Distribution part.

DESCRIPTION

Shell small, up to c. 12 mm in height, moderately solid, biconical, with last whorl making about 85% of total height; maximum diameter at about mid-height to slightly posterior; apex blunt. Protoconch not well distinct from teleoconch, smooth, formed by about one whorl. Spire low, consisting of about two flat-sided whorls. Sutures shallow,

poorly impressed, distinct. Sometimes, the spire is slightly narrower, forming a stepped suture with last whorl. Last whorl regularly rounded, gently tapering anteriorly, rarely forming a poorly distinct basal constriction. Aperture elongate, narrow, somewhat parallel-sided, taking about 70% of shell height. Outer lip internally smooth; externally bordered by a well distinct, wide rim, making the lip uniformly thick; straight for most of its length, posteriorly arched; anterior notch shallow, moderately wide. Four columellar plications, all well distinct, not markedly prominent, the posterior one smaller. Sometimes a fifth false plication is present, as an elongate, weak tubercle or as a thin plait similar to a true plication. Columellar and parietal callus rather wide, forming a thin glossy lining near aperture, slightly thicker posteriorly.

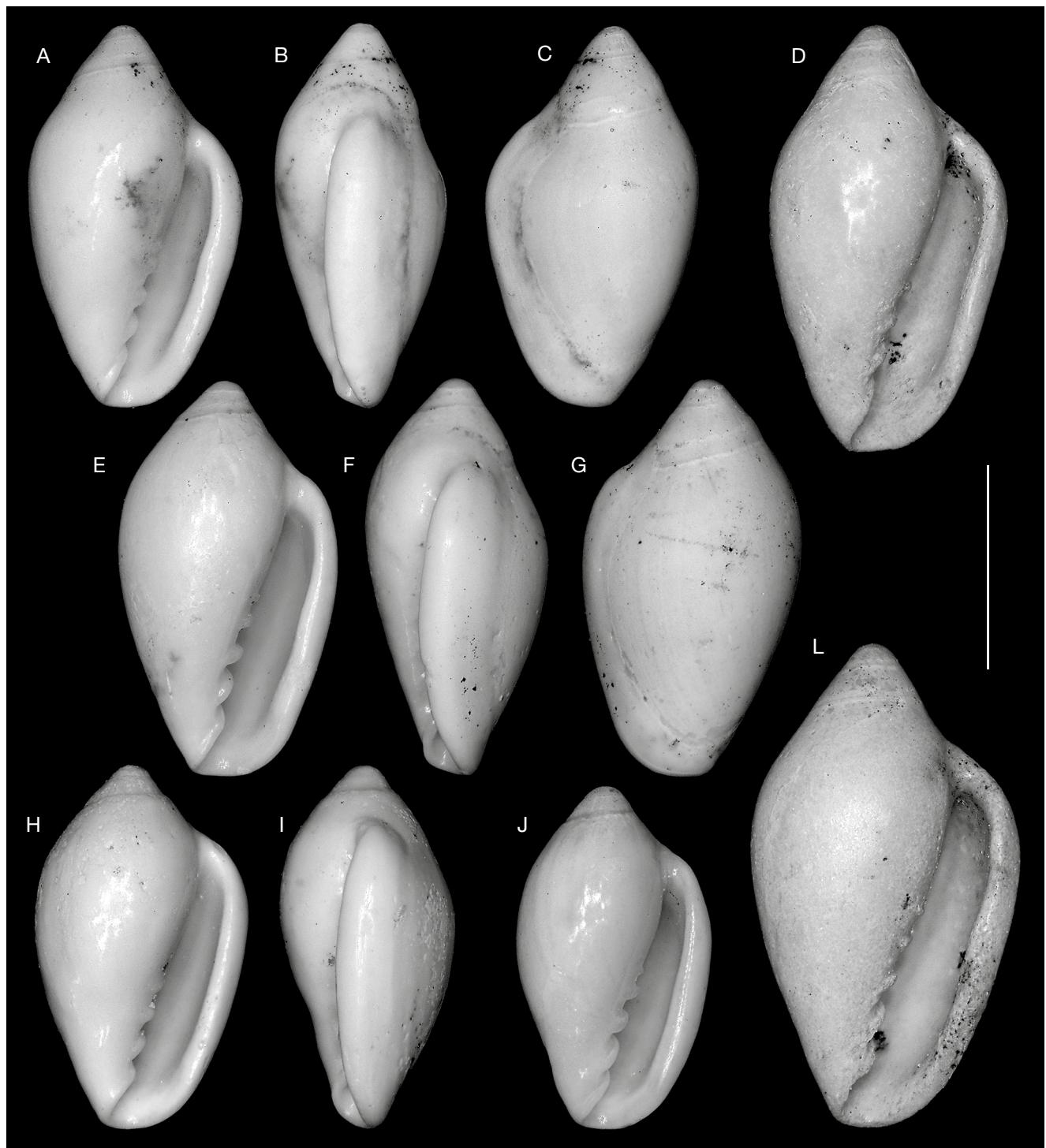


FIG. 5. — *Marginella sequenzai* n. sp.: A-C, holotype, H 9.3 mm (MZB60202); D, paratype 1, H 10.6 mm (MZB60203); E-G, paratype 2, H 9.7 mm (MZB60203); H, I, paratype 3, H 9.0 mm (MZB60203); J, paratype 4, H 8.4 mm (MBMPRC); L, paratype 5, H 11.8 mm (MBMPRC). Scale bar: 5 mm.

REMARKS

The genus *Marginella* typically includes species with brightly coloured shells, with a range of patterns (variously combined bands, flames, lineoles, blotches, dots, etc.) (Goud & Neefs 1996; Cossignani 2006), but several colourless species are also known, mainly from deep waters (Bouchet & Warén 1985; Goud & Neefs 1996). No preserved colour pattern was

observed in the material of *M. sequenzai* n. sp., either under daily light, or under UV light, but the uniform milky aspect of the shell surface suggests a colourless, or lightly coloured, original condition.

In addition to the variability in size and shape, another variable character was observed: some shells (about 20%) show a “false fifth plication” (Coovert & Coovert, 1995). In most

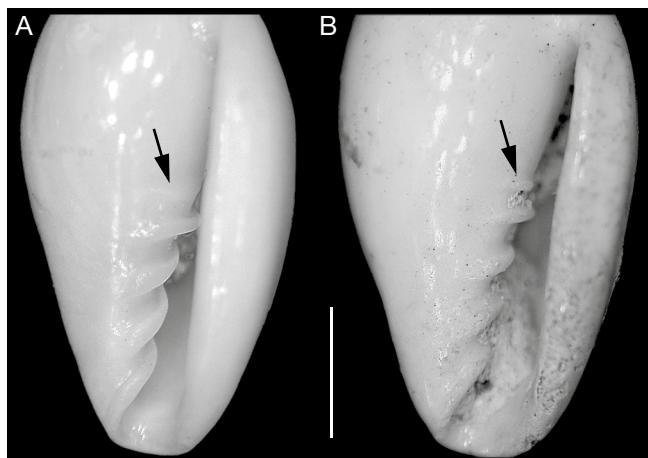


FIG. 6. — *Marginella sequenzai* n. sp.: shells with a fifth false plication (arrows): **A**, poorly developed fifth plication; **B**, well developed fifth plication. Scale bar: 2 mm.

cases it consists of a weak, elongate tubercle near the fourth (posterior) plication (Fig. 6A). Rarely, the false plication is more elongate and stronger, resembling a true, internally continuous, columellar plication ((Fig. 6B).

In some cases, the transition between spire and last whorl appears somewhat stepped, the spire being slightly narrower than the adjacent last whorl, as seen in Figure 5H, I.

None of the *Marginella* species known from the Pliocene of Estepona (Muñiz Solis 2002; Landau *et al.* 2006a) is particularly similar to the new species, all markedly differing in some respects (mainly size, shape and robustness).

Few of the many species known from Eastern Atlantic, deserve a comparison with the new species, such as *Marginella gloriosa* Jousseaume, 1884, *M. marocana* Locard, 1897, *M. bayay* Dautzenberg, 1910, *M. aronnax* Bouchet & Warén, 1985, *M. columborum* (Bozzetti, 1995) and *M. gilva* Goud & Neefs, 1996, but in most cases there are evident differences involving size and shape (convexity of spire whorls, spire elevation, shell slenderness, shape of outer lip, etc.). Of these species, only *M. columborum* shows an interesting overlap of characters with the new species. It was described from the Josephine Bank (Bozzetti 1995), a seamount in the North-East Atlantic, off Cape St. Vincent (Gubbay 2003). Though originally assigned to the genus *Prunum*, this species must be allocated in the genus *Marginella*. The species was examined on three shells from the type locality (Fig. 7A-D): the shell is colourless (actually very light pinkish, with the outer lip white), height close to that of *M. sequenzai* n. sp. also in the range (12.9-11.3 mm in the original description, 10.0-8.8 mm in the examined material), outer lip moderately thick, making a broad curve posteriorly, as in the new species. A remarkable difference from *M. sequenzai* n. sp. is the last whorl convexity, being *M. columborum* more inflated (H/D 1.70-1.86 in the examined material) than the new species, apparently without overlap. The shape of the aperture, rather parallel-sided in the new species and widening anteriorly in *M. columborum*, is another outstanding difference. Moreover, *M. columborum* has slightly convex spire whorls, whereas they are flat in the new species.

Marginella columborum has been also recorded from Seine and Ampère, other NE Atlantic seamounts (Beck *et al.* 2005). On WoRMS, Gofas (2015) added: “Endemic of Josephine, Seine and Ampère seamounts; common on Josephine, 270-335 m, rare on Seine and Ampère; a very similar if not identical species is found in the Italian Pleistocene”. The fossil species to which Gofas refers is *M. sequenzai* n. sp., of which he had examined some shells. Gofas’ view about the close similarity between *M. columborum* and the fossil species is confirmed, but they are evidently distinct species.

DISCUSSION

The genus *Marginella* was thought to have disappeared from Mediterranean and adjacent Atlantic (Landau *et al.* 2007; Da Silva *et al.* 2011), among many other thermophilic genera, due to the cooling trend which started in the early Late Pliocene, 3.0-3.2 Ma (Monegatti & Raffi 2001, 2007). Thermophilic groups suffered either local extinctions or contractions and shifting in their latitudinal range.

In the Early Pliocene, *Marginella* spread into the Alboran Sea, where it found favourable conditions of high productivity, forming a sort of Mediterranean “enclave” of NW African fauna. Out of the eight species known from Estepona, only *M. aurisleporis* was able to spread further into the Mediterranean, probably because not strongly depending on conditions of high productivity. It is also worth remarking that *Marginella* has limited dispersal abilities because of the direct larval development (Covert 1986; Gofas & Fernandes 1988; Covert & Covert 1995).

It must be emphasized that *M. aurisleporis* was a shallow water species, whereas *M. sequenzai* n. sp. was a deep water species, most probably adapted to cold water conditions. Actually, a tendency to colonize deep waters is known in several marginellid and cystiscid genera. Its history can be thus expected to differ notably from that of *M. aurisleporis*. Recent works have documented the richness of the deep Mediterranean benthos during the Pliocene-Early Pleistocene, due to two favourable conditions: hydrologic exchanges with the Atlantic much wider than today, thanks to a deeper Gibraltar sill, and cooling trend (Di Gerónimo & La Perna 1997; La Perna 2003). The Mediterranean benthos suffered a dramatic drop in diversity at about 0.9 Ma, when the uplift of the Gibraltar sill cut the basin out of the deep oceanic circulation (“loss of psychrosphere”) (La Perna 2004). *Marginella sequenzai* n. sp. was probably one of these bathyal species which became extinct when the deep water conditions switched to homeothermy.

The Messina Strait is an area of high productivity (Cescon *et al.* 1997) and high diversity (Vazzana 2010, 2011), with unusual ecological aspects, such as the occurrence of *Laminaria* meadows of Atlantic affinities (Drew 1974; Fredj & Giaccone 1987), evidently related with the dynamics (strong currents, turbulence, upwelling, etc.) of the Strait waters (De Domenico 1987). Due to its unique biological characters,

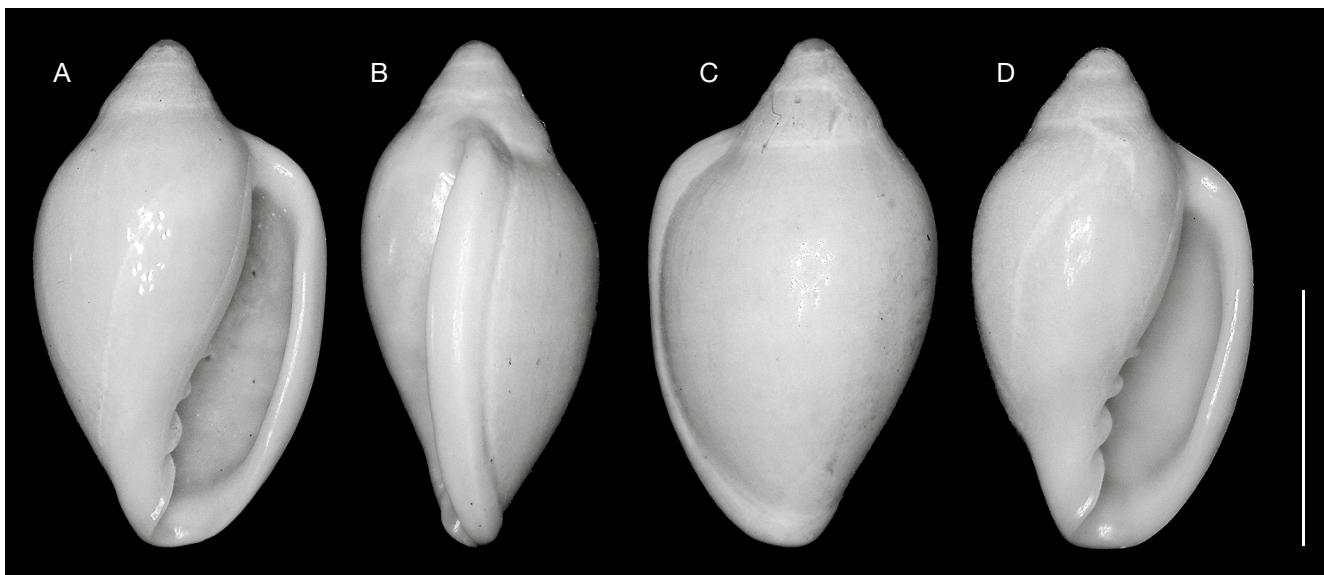


FIG. 7. — *Marginella colomborum* (Bozzetti, 1995), Josephine Bank, Seamount 1 Exp., St. DW37, 255–270 m, 36°42'N, 14°18'W, 4 Oct. 1988 (MNHN): A-C, H 10.0 mm; D, H 9.8 mm. Scale bar: 5 mm.

the Messina Strait was proposed by Bianchi (2007) as a distinct sector (the smallest one), within the biogeographic zonation of the Mediterranean. Hydrological and biological similarities between the Gibraltar Strait and the Messina Strait are evident, and probably the occurrence of *Marginella* in the Pliocene of Estepona and in the Pleistocene of Reggio Calabria shares a common base: high productivity. Interestingly, also the Josephine Seamount, and generally the oceanic seamounts, support high productivity and diversity (Boehlert & Genin 1987; Rogers 1994; Gubbay 2003; Morato *et al.* 2013).

Apart from their morphological similarities, the relations between the Atlantic *M. colomborum* and the Mediterranean *M. seguenzai* n. sp. remain unclear. It can be hypothesised that both species belong to the same lineage with a NE Atlantic and Mediterranean distribution, mostly controlled by high rate of productivity, and whose dispersion and differentiation took place, so to say, by “jumping” from one seamount to the other one.

Acknowledgements

The authors gratefully acknowledge Paolo Crovato (Società Italiana di Malacologia, Naples), who indicated to one of us (A.V.) the location of the Gallina outcrop, Serge Gofas (Universidad de Málaga) for preliminary comments on the new species herein described and the loan of MNHN material of *Marginella colomborum* from the Josephine Bank, and Maria Marino (Università di Bari) for biostratigraphic data on the Gallina section. Bernard M. Landau (Naturalis Biodiversity Centre, Leiden) and Serge Gofas (Universidad de Málaga) are warmly acknowledged for their constructive criticism and suggestions on the manuscript.

Work supported by Fondi di Ricerca d’Ateneo 2015 (M. Marino).

REFERENCES

- BÁRCENA M. A. & ABRANTES F. 1998. — Evidence of high-productivity area off the coast of Málaga from studies of diatoms in surface sediments. *Marine Micropaleontology* 35 (1-2): 91-103. [http://dx.doi.org/10.1016/S0377-8398\(98\)00012-7](http://dx.doi.org/10.1016/S0377-8398(98)00012-7)
- BARRIER P. 1987. — Stratigraphie des dépôts pliocènes et quaternaires du Détrict de Messine. *Documents et travaux IGAL* 11: 59-81.
- BECK T., METZGER T. & FREIWALD A. 2005. — *BIAS. Biodiversity Inventory Atlas of Macrofaunal Seamount Animals*. OASIŚ, Hamburg, 118 p.
- BIANCHI C. N. 2007. — Biodiversity issues for the forthcoming tropical Mediterranean Sea. *Hydrobiologia* 580: 7-21. <http://dx.doi.org/10.1007/s10750-006-0469-5>
- BOEHLERT G. W. & GENIN A. 1987. — A review of the effects of seamounts on biological processes, in KEATING B., FRYER P., BATIZA R., BOEHLERT G. (eds), Seamounts, Islands and Atolls. *Geophysical Monograph* 47. American Geophysical Union, Washington, DC: 319-334.
- BOUCHET P. & WARÉN A. 1985. — Revision of the Northeast Atlantic bathyal and abyssal Neogastropoda excluding Turridae (Mollusca, Gastropoda). *Bollettino Malacologico* suppl. 1: 123-296.
- BOZZETTI L. 1995. — Tre nuove specie della famiglia Marginellidae Fleming, 1828 (Gastropoda, Prosobranchia) from the Indian and Atlantic Ocean. *World Shells* 14: 48-52 and errata corrigé 15: 62.
- BROCCHI G. 1814. — *Conchologia fossile subappennina, con osservazioni geologiche sugli Appennini e sul suolo adiacente*. Vols 1, 2. Stamperia Reale, Milano, 712 p.
- CESCON B., AZZARO F., CREAZZO S., DECEMBRINI F. & MAGAZZÙ G. 1997. — Processes affecting upwelling and primary productivity of the Messina Straits. *Bollettino di Geofisica Teorica ed Applicata* 38 (1-2): 137-147.
- CHIRLI C. 2002. — *Malacofauna Pliocenica Toscana. Vol 3. Superfamiglia Muricoidea-Cancellarioidea*. C. Chirli, Firenze, 92 p.
- COOMANS H. E. 1975. — *Marginella orstomi*, a new species from deeper water off the coast of West Africa (Gastropoda, Marginellidae). *Bulletin Zoologisch Museum Universiteit Van Amsterdam* 4 (12): 99-101.
- COOVERT G. A. 1986. — A review of marginellid egg capsules. *Marginella Marginalia* 1 (4):13-19.
- COOVERT G. A. & COOVERT H. K. 1995. — Revision of the supraspecific classification of marginelliform gastropods. *The Nautilus* 109 (2-3): 43-110.

- COSSIGNANI T. 2006. — *Marginellidae and Cystiscidae of the World. Atlas with over 2,600 photos*. L'Informatore Piceno, 408 p.
- COSSMANN M. 1899. — *Essais de Paléoconchologie comparée*. Livraison 3. Paris, 201 p.
- DA SILVA C. M. 2002. — Novos dados sobre os moluscos pliocénicos marinhos de Portugal: implicações paleoceanográficas e paleobiogeográficas. *Pliocénica* 2: 117-125.
- DA SILVA C. M., LANDAU B., DOMÈNECH R. & MARTINELL J. 2010. — Pliocene Atlantic molluscan assemblages from the Mondego Basin (Portugal): age and palaeoceanographic implications. *Palaeogeography, Palaeoclimatology, Palaeoecology* 285: 248-254.
- DA SILVA C. M., LANDAU B. & LA Perna R. 2011. — Biogeography of Iberian Atlantic Neogene marginelliform gastropods (Marginellidae, Cystiscidae): global change and transatlantic colonization. *Journal of Paleontology* 85 (6): 1052-1066. <http://dx.doi.org/10.1666/11-104.1>
- DE DOMENICO E. 1987. — Caratteristiche fisiche e chimiche delle acque nello Stretto di Messina. *Documents et travaux IGAL* 11: 223-235.
- DELL'ANGELO B., VAZZANA A. & BERTOLASO L. 1998. — Ritrovamento di piastre fossili di *Callistochiton* (Mollusca: Polyplacophora) nel Plio-Pleistocene della Calabria. *Bollettino Malacologico* 3 (9-12): 139-140.
- DI GERONIMO I. & LA Perna R. 1997. — Pleistocene bathyal molluscan assemblages from Southern Italy. *Rivista Italiana di Paleontologia e Stratigrafia* 103 (3): 389-426.
- DREW E. A. 1974. — An ecological study of *Laminaria ochroleuca* Pyl. growing below 50 metres in the Straits of Messina. *Journal of Experimental Marine Biology and Ecology* 15 (1): 11-24.
- FERNANDES F. & ROLÁN E. 1991. — The Marginellidae (Mollusca, Gastropoda) of Príncipe Island (República de São Tomé e Príncipe). *Journal of Conchology* 34: 85-90.
- FORLI M. & DELL'ANGELO B. 2000. — A new species of *Marginella* (Mollusca, Gastropoda) from the Italian Pliocene. *Bollettino Malacologico* 36 (5-8): 93-98.
- FREDJ G. & GIACCONI G. 1987. — Bionomie des fonds à Laminaires du Détrit de Messine. *Documents et travaux IGAL*, 11: 237-238.
- GOFAS S. 2015. — *Marginella columborum* (Bozzetti, 1995) in *MolluscaBase* (2015). Accessed through: World Register of Marine Species at <http://www.marinespecies.org/aphia.php?p=taxdetails&id=140321> on 2015-07-17.
- GOFAS S. & FERNANDES F. 1988. — The marginellids of São Tomé, West Afric. *Journal of Conchology* 33: 1-30.
- GOFAS S. & FERNANDES F. 1994. — The Marginellidae of Angola: the genus *Marginella*. *Journal of Conchology* 35: 103-119.
- GÓMEZ F., ECHEVARRÍA F., GARCÍA C. M., PRIETO L., RUIZ J., REUL A., JIMÉNEZ-GÓMEZ F. & VARELA M. 2000. — Microplankton distribution in the Strait of Gibraltar: coupling between organisms and hydrodynamic structures. *Journal of Plankton Research* 22 (4): 603-617. <http://dx.doi.org/10.1093/plankt/22.4.603>
- GOUD J. & NEEFS J. 1996. — The larger marginelliform gastropods (Cystiscidae and Marginellidae) collected during the CANCAP and MAURITANIA expeditions in the southern part of the North Atlantic Ocean. The genera *Persicula*, *Prunum*, *Dentimargo*, *Marginella* and *Glabella*. *Vita Marina* 43 (3-4): 25-50.
- GUBBAY S. 2003. — *Seamounts of the North East Atlantic*. WWF/OASIS, Bremen, 38 p.
- HAINES A. J. & CRAMPTON J. S. 2000. — Improvements to the method of Fourier shape analysis as applied in morphometric studies. *Paleontology* 43: 765-783. <http://dx.doi.org/10.1111/1475-4983.00148>
- HAMMER Ø., HARPER D. A. T. & RYAN P. D. 2001. — PAST: Paleontological statistics software package for education and data analysis. *Paleontologia Electronica* 4 (1): 9 p. http://paleo-electronica.org/2001_1/past/issue1_01.htm
- LA Perna R. 2003. — The Quaternary deep-sea protobranch fauna from the Mediterranean: composition, depth-related distribution and changes. *Bollettino Malacologico* 39: 17-34.
- LA Perna R. 2004. — The identity of *Yoldia micrometrica* Seguenza, 1877 and three new deep-sea protobranchs from the Mediterranean (Bivalvia). *Journal of Natural History* 38: 1045-1057. <http://dx.doi.org/10.1080/0022293021000056936>
- LA Perna R. & D'ABRAMO M. 2010. — Una collezione di G. Seguenza conservata presso l'Istituto Tecnico Commerciale "O.G. Costa" di Lecce. *Bollettino Malacologico* 46: 29-35.
- LANDAU B. & DA SILVA C. M. 2006. — The Early Pliocene Gastropoda (Mollusca) of Estepona, southern Spain. Part 9 Olividae. *Palaeontos* 9: 1-21.
- LANDAU B., LA Perna R. & MARQUET R. 2006a. — The Early Pliocene Gastropoda (Mollusca) of Estepona, Southern Spain. Part 10. Marginellidae, Cystiscidae. *Palaeontos* 9: 22-60.
- LANDAU B., PETIT R. & MARQUET R. 2006b. — The Early Pliocene Gastropoda (Mollusca) of Estepona, Southern Spain. Part 12: Cancellarioidea. *Palaeontos* 9: 61-101.
- LANDAU B., CAPELO J. C. & DA SILVA C. M. 2007. — Patterns of extinction and local disappearance of tropical marine gastropods; contrasting examples from across the North Atlantic. *Acoreana Suppl.* 5: 50-58.
- LUQUE A., BARRAJÓN A., REMÓN J. M., MORENO D. & MORO L. 2012. — *Marginella glabella* (Mollusca: Gastropoda: Marginellidae): a new alien species from tropical West Africa established in southern Mediterranean Spain through a new introduction pathway. *Marine Biodiversity Records* 5: e17. <http://dx.doi.org/10.1017/S1755267212000012>
- MALATESTA A. 1974. — Malacofauna pliocenica umbra. *Memorie per Servire alla Carta Geologica d'Italia* 13: 1-498.
- MERCIER D. & BARRIER P. 1987. — Les facteurs hydrodynamiques dans la sédimentation plio-quaternaire du Détrit de Messine. *Documents et travaux IGAL* 11: 171-183.
- MONEGATTI P. & RAFFI S. 2001. — Taxonomic diversity and stratigraphic distribution of Mediterranean Pliocene bivalves. *Palaeogeography, Palaeoclimatology, Palaeoecology* 165: 171-193. [http://dx.doi.org/10.1016/S0031-0182\(00\)00159-0](http://dx.doi.org/10.1016/S0031-0182(00)00159-0)
- MONEGATTI P. & RAFFI S. 2007. — Mediterranean-Middle Eastern Atlantic façade: molluscan biogeography & ecobiostratigraphy throughout the Late Neogene. *Acoreana Suppl.* 5: 126-139.
- MONTENAT C., BARRIER P. & DI GERONIMO I. 1987. — The Strait of Messina, past and present: a review. *Documents et travaux IGAL* 11: 7-13.
- MORATO T., KVILE K. Ø., TARANTO G. H., TEMPERA F., NARAYANASWAMY B. E., HEBBELN D., MENEZES G. M., WIENBERG C., SANTOS R. S. & PITCHER T. J. 2013. — Seamount physiography and biology in the north-east Atlantic and Mediterranean Sea. *Biogeosciences* 10: 3039-3054. <http://dx.doi.org/10.5194/bg-10-3039-2013>
- MUNIZ SOLIS R. 2002. — Estudio de las Familias Cystiscidae Stimpson, 1865 y Marginellidae Fleming, 1828 (Gastropoda, Neogastropoda) del Plioceno de Estepona (Málaga, España). *Pliocénica* 2: 263-306.
- PELOSIO G. 1966. — La malacofauna dello stratotipo del Tabianiano (Pliocene inferiore) di Tabiano Bagni (Parma). *Bollettino della Società Paleontologica Italiana* 5 (2): 101-183.
- RAFFI S. 1986. — The significance of marine boreal molluscs in the early Pleistocene faunas of the Mediterranean area. *Palaeogeography, Palaeoclimatology, Palaeoecology* 52: 267-289.
- RIO D., RAFFI I. & VILLA G. 1990. — Pliocene-Pleistocene calcareous nannofossil distribution patterns in the western Mediterranean, in KASTENS K. A., MASCLE J. et al. (eds), *Proceedings of the Ocean Drilling Program*. Scientific Results 107, College Station (TX): 513-533.
- ROGERS A. D. 1994. — The biology of seamounts, in BLAXTER J. H. S. & DOUGLAS B. (eds), *Advances in Marine Biology* 30: 305-350.
- ROHLF F. J. 2010. — tpsDig, digitize landmarks and outlines, version 2.16. Department of Ecology and Evolution, State University of New York at Stony Brook. Available at <http://life.bio.sunysb.edu/morph>

- ROSSI RONCHETTI C. 1955. — I tipi della Conchiologia Fossile Subappennina” di G. Brocchi. II. Gastropodi, Scafopodi. *Rivista Italiana di Paleontologia e Stratigrafia* 5 (2): 91-343.
- SARHAN T., GARCÍA LAFUENTE J., VARGAS M., VARGAS J. M. & PLAZA F. 2000. — Upwelling mechanisms in the northwestern Alboran Sea. *Journal of Marine Systems* 23: 317-331.
- SEGUENZA G. 1879. — Le formazioni terziarie della provincia di Reggio (Calabria). *Memorie della Reale Accademia dei Lincei*, Classe di Scienze Fisiche, Matematiche e Naturali 3, 6: 1-446.
- VAZZANA A. 2010. — La malacofauna del circalitorale di Scilla (Stretto di Messina). *Bollettino Malacologico* 46: 65-74.
- VAZZANA A. 2011. — *Biodiversità marina lungo le coste della provincia di Reggio Calabria*. Reggio Calabria, Laruffa Editore, 80 p.
- WAKEFIELD A. 2003. — A study of a population of *Mesoginella pygmaea* (Sowerby, 1846) (Gastropoda: Marginellidae) from the Bay of Islands, New Zealand. *Novapex* 4: 93-100.

*Submitted on 6 August 2015;
accepted on 3rd January 2016;
published on 30 September 2016.*