

# ***Granulina* (Gastropoda, Marginellidae) from the Pliocene of Málaga (southern Spain) with descriptions of four new species**

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The Lower Pliocene shelf deposits that crop out near Estepona (Málaga) have yielded nine species of the marginellid genus *Granulina* Jousseume, 1888, six of which [*G. iberica* n. sp., *G. detruncata* n. sp., *G. malacitana* n. sp., *G. longa* n. sp., *G. clandestina* (Brocchi, 1814), and *Granulina* sp. sensu Gofas, 1992] are extinct, while *G. marginata* (Bivona, 1832), *G. boucheti* Gofas, 1992 and *G. guttula* La Perna, 1999 still occur in the Mediterranean to this day. Differences in species composition in the Pliocene of Italy are thought to be due mainly to the typically restricted distribution and endemicity of *Granulina* and of marginellids in general. Affinities between Pliocene representatives of *Granulina* from the Mediterranean and Recent West African species confirm the 'warm-temperate' to 'warm' character of this genus. Subsequent to the Middle-Late Pliocene and Pleistocene cooling events, the species with warmer affinity mostly went extinct, the genus evolved a more temperate character and diversity amongst shallow-water species decreased.

KEY WORDS: Pliocene, Gastropoda, Marginellidae, new species, Spain, Mediterranean, systematics, palaeobiogeography.

## **Introduction**

Until a few years ago, two fossil/extant Mediterranean species of the genus *Granulina* were listed in the literature, viz. *G. occulta* (Monterosato, 1869) and *G. clandestina*. However, several recent papers have been devoted to extant species from the Mediterranean and Gibraltar (Gofas, 1992; Smriglio & Mariottini, 1996, 1999; Smriglio *et al.*, 1998; La Perna, 1999) and to Pliocene and Pleistocene representatives from the Mediterranean (La Perna, 1999, 2000). Contrary to previous views, the genus *Granulina* has turned out to be well diversified in the Recent Mediterranean (12 species), three of which are endemic to the Gibraltar area. Similarly, during the Pleistocene, it was well represented, with four extinct and five extant forms having been recorded from Italy. Numerous Pliocene Mediterranean species probably still remain to be studied; four are known from the Pliocene of Italy, one of which survives to the present day. Comparably, many species have recently been recorded from off the West African coast and from the Ibero-Moroccan Gulf south to the Guinea Gulf, including the Canary and Cape Verde Islands (Fernandes, 1987; Gofas & Fernandes, 1988; Fernandes & Rolán, 1991; Gofas, 1992; Pin & Boyer, 1995; Rolan & Fernandes, 1997; Boyer & Rolán, 1999; Smriglio *et al.*, 2001; Boyer, 2001).

Although most species of *Granulina*, or at least the better known ones, are from shallow-water settings, a

marked ecological trend to the deep shelf and upper slope has recently been noted (La Perna, 1999). However, the 'warm-temperate' to 'warm' biogeographic affinity of this genus is beyond doubt. In the eastern Atlantic its northern limit is along the Iberian coasts, which holds true for both the shallow- and deep-water species.

The present paper attempts to fill the gap in our knowledge of Pliocene species of *Granulina*, on the basis of material collected from Lower Pliocene deposits exposed near Estepona (Málaga Basin, southern Spain). These new data are of particular interest. Not only do they increase our knowledge of the genus, they also provide additional data on the geographical position, close to the Strait of Gibraltar, of a gateway that has controlled biotic exchanges between the Atlantic and Mediterranean since the Late Cainozoic.

For stratigraphic, tectonic and palaeogeographical data on the Málaga Basin, situated in the western sector of the Internal Zones of the Betic Cordillera, reference is made to Sanz de Galdeano & López Garrido (1991). During the Tortonian (Miocene), an extended seaway existed from the Mediterranean (Málaga area) to the Atlantic, through the Guadalquivir and Ronda basins. In contrast, the Pliocene basin was much smaller, extending inland for c. 30 km from the present-day Málaga-Torremolinos area. Pliocene sediments also crop out along the coast, south to Estepona. This series consists of conglomerates and sands, which are laterally replaced by

bluish grey marls and clays, in turn overlain by yellowish white sands, to a maximum thickness of *c.* 400 m in the easternmost areas. The age ranges from Early-Middle to early Late Pliocene. The uppermost Pliocene and Quaternary sediments are terrestrial.

Lozano Francisco (1998) studied the bivalves from several outcrops in the Málaga area. Most associations proved to be indicative of infralittoral and circalittoral environments with coarse- to fine-grained substrates. Only in recent years have these extremely fossil-rich deposits received attention in the literature, with the emphasis on molluscs (*e.g.*, Véra-Peláez *et al.*, 1995; Lozano Francisco, 1998; Muñiz-Solís, 1999; Landau & Marquet, 1999, 2000). Not only are they exceptionally rich, with over 700 species of gastropod (BL, pers. obs.), but the unique geographical position of these deposits also is reflected in the faunal composition. As could be expected, there are many species typical of an Early Pliocene Mediterranean fauna, as found in Italy. There is also a strong Atlantic influence with typically northern species, such as *Scaphella lamberti* (J. Sowerby, 1816), as well as a more southerly influence, exemplified by the recent discovery of the gastropod genus *Cymbium* at Velerín (Landau & Marquet, 2000). Amongst a fairly large number of new species, most of which have yet to be described, a few appear to be endemic to the west-

ernmost Mediterranean and adjacent Atlantic. The following taxa are found both at Velerín and in coeval Atlantic deposits at Huelva (Spain): *Crepidula lucenica* Landau, 1984, *Cyllene (Cyllenina) lucenensis* Landau & Marquet, 1999 and *Cymbium ibericum* Landau & Marquet, 2000. More interesting, as well as unexpected, is the occurrence of relict Miocene species, such as *Vermicularia milleti* (Deshayes, 1839), *Euthriofusus burdigalensis* (DeFrance in de Blainville, 1824), *Marginella (Eratoidea) eratoformis* Hoernes & Auinger, 1880, and *Perrona jouanneti* (Desmoulins, 1842), not recorded previously from other Lower Pliocene deposits of the Mediterranean.

### Material and methods

Five localities, Rio del Padrón, Velerín Carretera, Velerín Antena, 'Velerín Conglomerates' and Parque Antena (Table 1), between 5.5 and 9 km northeast of Estepona (see map in Véra-Peláez *et al.*, 1995), have been sampled by two of us (BL, RM). At each of these, bulk samples have been taken and sieved on a 1 mm, and from each, at least 5 kg of residue has been sorted out under a binocular microscope.

SPECIES	VCa	VA	PA	RP	VCo
<i>Granulina iberica</i> n. sp.	?	common			present
<i>Granulina detruncata</i> n. sp.	present				present
<i>Granulina malacitana</i> n. sp.	present			present	present
<i>Granulina ? longa</i> n. sp.	present		present		
<i>Granulina clandestina</i>	present				present
<i>Granulina marginata</i>					present
<i>Granulina boucheti</i>	present				present
<i>Granulina guttula</i>	present				
<i>Granulina</i> sp.				common	

**Table 1.** Distribution of *Granulina* in the Málaga area; VCa = Velerín Carretera, VA = Velerín Antena, PA = Parque Antena, RP Rio del Padrón, VCo = 'Velerín Conglomerates'.

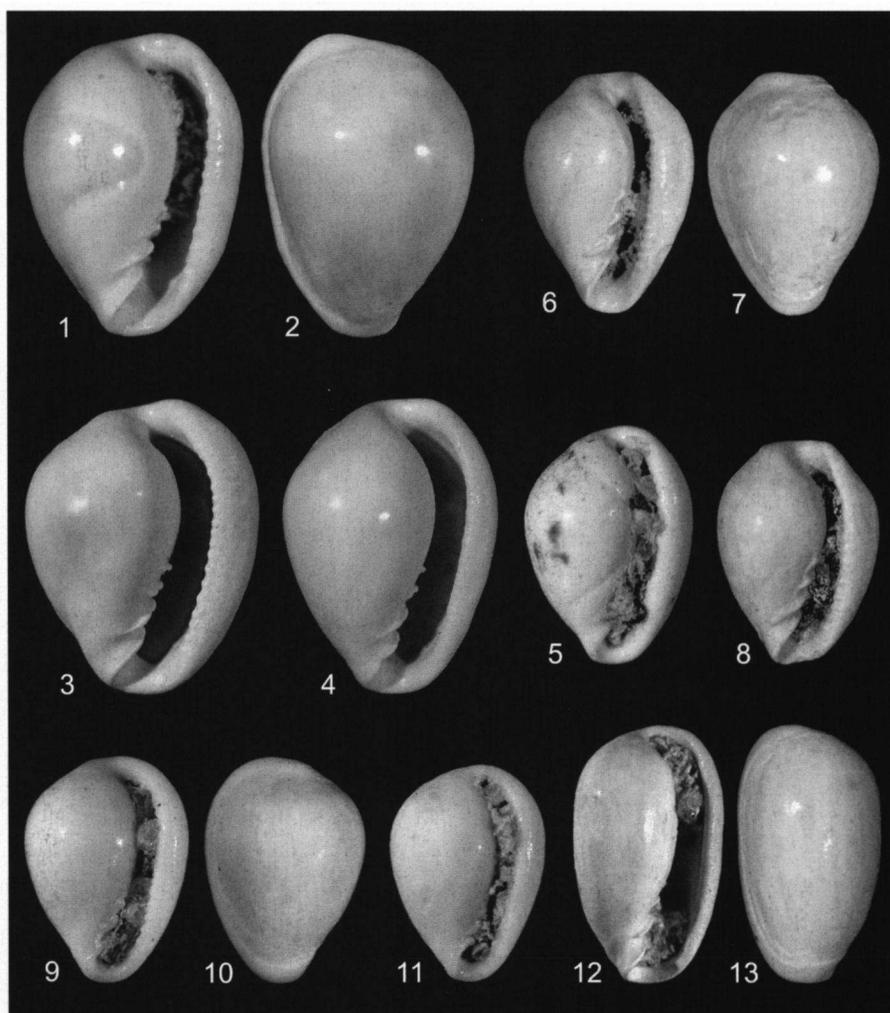
At Velerín Carretera, greyish sandy clays and clayey sands are exposed in a road-cutting about 4 m in height, with a scattered fauna, consisting mainly of small, superbly preserved molluscs. Velerín Antena is a disused quarry, exposing the same lithology as Velerín Carretera. The molluscan fauna generally is small sized and is dominated in number of specimens by bivalves, many of which are still articulated. Most species belong to the families Yoldiidae, Nuculanidae and Semelidae, which indicate a relatively deep-water (deep circalittoral) assemblage, which has experienced little or no transport.

Parque Antena is a temporary building site, lithologically and palaeoecologically closely similar to the sequence seen at Velerín Carretera and Velerín Antena. Samples have been taken *c.* 5 m below the highest level

exposed, from a clayey sediment with scattered, well-preserved shells.

The Rio del Padrón outcrop is on the left bank of a river bed, mostly dry in summer, exposing a sequence of >15 m; it appears to represent an upward-shallowing trend with the main body of sediment consisting of clayey sand, with a sparse fauna, yielding white corals. The molluscan fauna, however, occurs at a level *c.* 5 m below the top of the section, containing coarse-grained sand with shells and occasional pockets of gravel. Shells are often abraded and bivalves occur mainly disarticulated, and are often decalcified.

The 'Velerín Conglomerates' are exposed close to Velerín Antena, and form a steep valley on the right bank of a small seasonal river.



**Figures 1-4.** *Granulina iberica* n. sp., from Velerín Carretera; 1, 2 - holotype (IRScNB IST 6422), H = 3.4 mm; 3 - paratype (IRScNB IST 6423), H = 3.4 mm; 4 - paratype (IRScNB IST 6424), H = 3.3 mm (SEM).

**Figure 5.** *Granulina* aff. *iberica* n. sp. (IRScNB IST 6439), from 'Velerín Conglomerates'; H = 2.8 mm (SEM).

**Figures 6-8.** *Granulina detruncata* n. sp., from Velerín Carretera; 6, 7 - holotype (IRScNB IST 6427), H = 2.8 mm; 8 - paratype (IRScNB IST 6428), H = 2.5 mm (SEM).

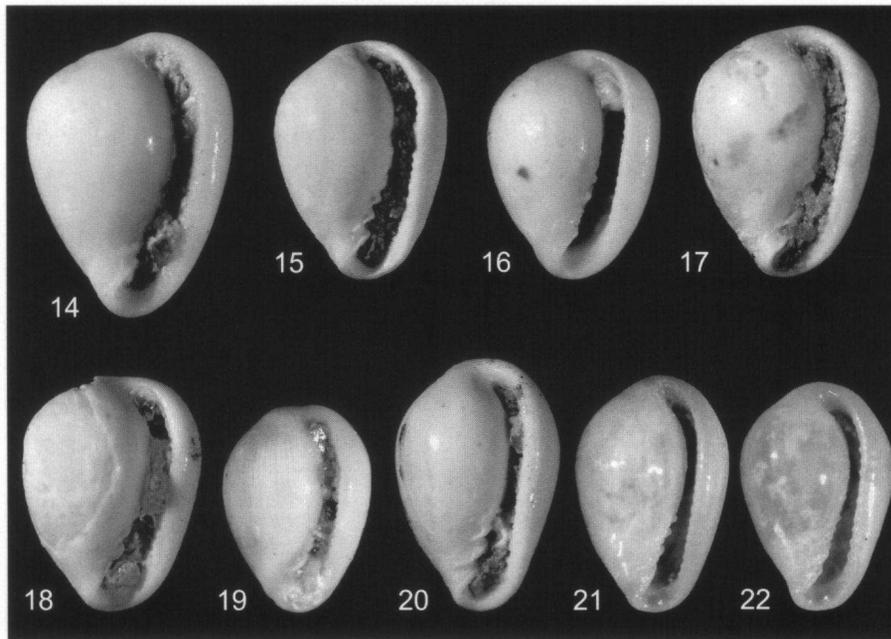
**Figures 9-11.** *Granulina malacitana* n. sp., from 'Velerín Conglomerates'; 9, 10 - holotype (IRScNB IST 6430), H = 2.1 mm; 11 - paratype (IRScNB IST 6431), H = 2.0 mm (SEM).

**Figures 12, 13.** *Granulina?* *longa* n. sp., from Parque Antena, holotype (IRScNB IST 6433), H = 2.9 mm (SEM).

The conglomerates contain coarse-grained, whitish to brown sand which may be indurated in parts, containing mainly eroded boulders up to 1 m in diameter. In some places rare pockets of yellowish brown sand occur. The molluscan fauna is very rich and is dominated by gastropods, which may attain a large size. Some bivalves are articulated, but most are not. Some specimens show but few traces of transport, others are strongly affected. In the eastern part of the same hill exposure, conglomerates contain small amounts of sand and barely eroded schist slabs; only very few molluscan species are present. These

conglomerates seem to represent a shingle beach deposit, containing an admixture of faunal elements of varying depths and environments.

Over 160 shells of *Granulina* have been examined, most of which have been identified to species. The remaining specimens were either too poorly preserved or too immature to be identified. Descriptions below are based on fully-grown shells. All types and illustrated specimens are housed in the collections of the Institut royal des Sciences naturelles de Belgique (Brussels).



**Figure 14.** *Granulina clandestina* (Brocchi, 1814) (IRScNB IST 6434), from 'Velerín Conglomerates'; H = 6 mm (SEM).

**Figure 15.** *Granulina* sp. (IRScNB IST 6438), from Rio del Padrón; H = 2.2 mm (SEM).

**Figures 16, 17.** *Granulina boucheti* Gofas, 1992 (IRScNB IST 6436) from 'Velerín Conglomerates'; H = 2.1 and 2.4 mm, respectively (SEM).

**Figure 18.** *Granulina marginata* (Bivona, 1832) (IRScNB IST 6435), from 'Velerín Conglomerates'; H = 2.1 mm (SEM).

**Figure 19.** *Granulina malacitana* n. sp., paratype (IRScNB IST 6432), from Velerín Carretera; H = 1.9 mm (SEM).

**Figures 20-22.** *Granulina guttula* La Perna, 1999; 20 - IRScNB IST 6437, from Velerín Carretera; H = 2.3 mm; 21, 22 - paratypes (UPMC collections), southeast Tyrrhenian Sea, depth 84 m; H = 2.2 and 2.1 mm, respectively (SEM).

For descriptive terminology and taxonomy of *Granulina*, we follow Coover (1988a), Gofas (1992), Coover & Coover (1995) and La Perna (1999). As previously discussed by La Perna (1999), the traditional placement of the genus *Granulina* in the family Marginellidae, rather than in the Cystiscidae as proposed by Coover & Coover (1995), is here maintained.

#### Systematic palaeontology

**Abbreviations** — H = shell height; D = maximum diameter; IRScNB = Institut royal des Sciences naturelles de Belgique (Brussels); UPMC = University Palaeontological Museum, Catania; RM = R. Marquet Colln; BL - B. Landau Colln.

Class Gastropoda Cuvier, 1797  
 Order Neogastropoda Thiele, 1929  
 Family Marginellidae Fleming, 1828  
 Genus *Granulina* Jousseaume, 1888

**Type species** — *Marginella pygmaea* Issel, 1869, by monotypy.

#### *Granulina iberica* n. sp.

Figures 1-4

**Type locality** — Velerín Carretera, Estepona (province of Málaga, Spain).

**Stratum typicum** — Zanclean (Lower Pliocene).

**Type material** — Holotype is IRScNB IST 6422; paratypes are IRScNB IST 6423-6426.

**Material examined** — 86 specimens from Velerín Carretera, including the types; 28 specimens from Velerín Antena; 3 specimens from 'Velerín Conglomerates'; all BL and RM collections, except for type specimens.

**Etymology** — Latin *ibericus*, in reference to the Iberian Peninsula.

**Description** — Shell small, with immersed spire, ovoid-pyriform in shape, maximum diameter posterior to mid-height of shell, H/D 1.18-1.36. Posterior end slightly obliquely truncated. Siphonal notch distinct. Lip strongly thickened in fully-grown stage, slightly bevelled posteri-

only. Lip denticulations fine, but well defined. Four blade-like columellar plications, slightly excavated inside aperture, the uppermost notably small. Parietal callus wide, distinct, forming a deep narrow sinus. Aperture relatively wide. Surface smooth, shiny, except for faint growth striae. Measurements of holotype are H 3.4 mm, D 2.5 mm; paratypes and other material: H 2.7-3.4 mm.

*Distribution* — Known exclusively from the Lower Pliocene of Málaga; the commonest species of *Granulina* at the localities sampled.

*Remarks* — The degree of thickening of the outer lip varies from weak to strong, with the denticulations poorly developed in the former stage (Figures 3, 4). This character is clearly related to the lip thickening in marginelliform gastropods, occurring late in ontogenetic development (Coovert & Coovert, 1995; Nehm, 2001). Live specimens as well as empty extant or fossil shells of *Granulina* are usually found with a well-developed lip varix, its strength remaining fairly constant within a species. Subadult specimens showing initial stages of lip thickening are less commonly found than juvenile shells. This would suggest a fairly rapid lip thickening in the adult stage, whereas in *G. iberica* the lip thickening was probably unusually slow for the genus. Size also is somewhat variable, yet there is no relationship to lip thickness.

A single shell (Figure 5) from the 'Velerín Conglomerates' differs in being more solid, more ovate and in having a notably thicker parietal callus, and is here referred to as *G. aff. iberica*.

Although this species is clearly distinct from other fossil and extant European species, to a certain extent it resembles the deep-water Mediterranean *G. tenuilabiata* La Perna, 1999 in shape and size, from which it differs mainly in having a thicker lip (when fully-grown), a much narrower sinus on the parietal callus and a distinct posterior truncation. Other species reminiscent of *G. iberica* and *G. tenuilabiata*, e.g., the Pleistocene *G. rosarioi* La Perna, 1999 and *G. ovulina* (Monterosato, 1881), and the extant *G. gofasi* Smriglio & Mariottini, 1996, all have particularly large (3.0-3.5 mm) and globose shells, with near-absent to fine lip denticulations and which lack any parietal callus ridge (see below). It is worth mentioning that these species have or had notably deep-water (circalittoral to epibathyal) ranges (La Perna, 1999, table 1). *Granulina iberica* probably had a mainly circalittoral distribution as well.

### *Granulina detruncata* n. sp.

Figures 6-8

*Type locality* — Velerín Carretera, Estepona (province of Málaga, Spain).

*Stratum typicum* — Zanclean (Lower Pliocene).

*Type material* — Holotype is IRScNB IST 6427; paratypes are IRScNB IST 6428, 6429.

*Material examined* — 6 specimens from Velerín Carretera, including the types; 2 specimens from 'Velerín

Conglomerates'; all material, except type specimens, in BL and RM collections.

*Etymology* — Latin *detruncatus* meaning beheaded, in allusion to the clear-cut, 'upper' part of the shell.

*Description* — Shell minute, with immersed spire, ovoid-rhomboid in shape, maximum diameter slightly posterior to mid-height of shell, H/D 1.35-1.48. Posterior end strongly truncated and covered by a thick, slightly stepped callus, growing into a thin parietal ridge almost inside the aperture and extending to columellar plications. Siphonal notch distinct. Lip strongly thickened, markedly bevelled posteriorly, forming a wide, flattish and slightly rough surface with a somewhat sharp outer border. Lip denticulations fine but well defined. Four notably strong columellar plications, obscurely excavated inside aperture, the upper two notably smaller and connected by a thread-like callus. Parietal callus fairly distinct, forming a wide, shallow sinus. Aperture narrow. Surface smooth, but crossed by impressed growth striae. Measurements of holotype are H 2.8 mm, D 1.9 mm; paratypes and other material: H 2.3-2.5 mm.

*Distribution* — Known exclusively from the Lower Pliocene of Málaga.

*Remarks* — The strong posterior truncation, rhomboid outline and markedly thickened and wide lip clearly distinguish this species from all other fossil and Recent European *Granulina*. However, it may be compared with the shallow-water West African *G. ghanensis* Rolán & Fernandes, 1997. Specimens of *G. ghanensis* from Miama (Ghana) available to us are notably smaller, with a rounded posterior rostration and small, close-set plications, more deeply excavated inside the aperture by a shallow sulcus. This makes them appear almost 'double', a character also present in other species (Gofas, 1992; La Perna, 1999, 2000). These two species have the following features in common: the 'rhomboidal' shell outline, the wide lip surface, the well-developed posterior callus, notably thick in *G. detruncata*, thinner in *G. ghanensis* but forming a shallow pad near the posterior end, and the thin parietal callus ridge running from the posterior callus and joining the upper two to three plications. Another species apparently rather similar to *G. detruncata* and *G. ghanensis* is *G. africana* Gofas, 1992, from Senegal and the Ivory Coast. In *Granulina canariensis*, described recently from the Canary Islands (Boyer, 2001), also size, shape and apertural features are similar to those seen in *G. detruncata*, but the former has a narrower lip and a rather sharp posterior end.

An anomalous number of plications, 'about 5 small denticles', was recorded in the original description of *G. ghanensis* (Rolán & Fernandes, 1997) and 'three oblique pleats and 13-15 fine folds on the upper part' in *G. ocarina* (Fernandes, 1987), from the Cape Verde Archipelago. Topotypes of *G. ocarina* show a thin callus ridge joining the uppermost columellar folds, similar to that in *G. ghanensis* and *G. detruncata*. This ridge is a common feature in *Granulina* (Coovert, 1988b; Coovert & Coovert, 1995; La Perna, 1999, 2000) and, whenever slightly tuberculate, may give the appearance of more than four columellar-parietal plications.

***Granulina malacitana* n. sp.**  
Figures 9-11, 19

*Type locality* — 'Velerín Conglomerates', Estepona (province of Málaga, Spain).

*Stratum typicum* — Zanclean (Lower Pliocene).

*Type material* — Holotype is IRScNB IST 6430; paratype are IRScNB IST 6431, 6432.

*Material examined* — 12 specimens from 'Velerín Conglomerates', including the types; 3 specimens from Velerín Carretera; 3 specimens from Rio del Padrón; all material, except for type specimens, BL and RM collections.

*Etymology* — from the Spanish adjective malacitana, meaning 'of Málaga'.

*Description* — Shell minute, with immersed spire, markedly ovoid in shape, maximum diameter at mid-height of shell to slightly posterior, H/D *c.* 1.4. Posterior end obscurely truncated to regularly rounded, with a distinct callus producing a shallow rounded relief. Siphonal notch weakly developed. Lip thickened with fine denticulations. Four moderately strong columellar plications slightly excavated inside aperture, the upper two notably smaller. Parietal callus not particularly wide and poorly demarcated, forming a wide, shallow sinus. Thin parietal callus ridge inside aperture, with a slightly tuberculate appearance. Aperture narrow. Surface smooth, but crossed by fine axial striae, mostly appearing as thin, darker and lighter, regularly spaced bands lacking relief. Measurements of holotype are H 2.1 mm, D 1.6 mm; paratypes and other material: H 1.8-2.2 mm.

*Distribution* — Known only from the Lower Pliocene of Málaga.

*Remarks* — The main distinctive features of *G. malacitana* are the marked egg shape, shallow posterior callus relief, small size and the axial 'ornament'. This last feature is reminiscent of the axial pattern seen in *G. vanharenii* van Aartsen *et al.*, 1984, endemic to Gibraltar (Gofas, 1992), in which the axial lines are slightly raised giving a 'chagriné' appearance (Gofas, 1992), whereas they are very shallow and mostly of chromatic nature (darker and lighter lines, see Figure 19) in *G. malacitana*. The true nature of this pattern is not understood. Under high magnification, very fine granulations are seen to cover the shell, giving the surface a satin appearance. Boyer & Rolán (1999) illustrated the same microsculptural pattern in *G. vanharenii* and in a new species, *G. fernandesi*, described from the Cape Verde Islands. As seen in SEM images, the pattern of granulation is somewhat different in the two. In addition, *G. malacitana* does not differ markedly in morphology from *G. vanharenii*, both species being notably small, egg-shaped and with a small posterior callus. However, the latter has a somewhat cylindrical shape and a marked anterior (siphonal) slope break. *Granulina fernandesi* also is particularly small and somewhat similar in shape to *G. vanharenii*.

Another species from West Africa, *G. mauretunica* Gofas, 1992, shows remarkable similarities in shell and soft parts to *G. vanharenii* (see Gofas, 1992), and is also

similar in shape and size to *G. malacitana*, but no data on the micro-ornament of the former are available.

***Granulina? longa* n. sp.**  
Figures 12, 13

*Type locality* — Parque Antena, Estepona (province of Málaga, Spain).

*Stratum typicum* — Zanclean (Lower Pliocene).

*Type material* — Holotype is IRScNB IST 6433.

*Material examined* — 1 specimen (holotype) from Parque Antena; 3 specimens (1 juv.) from Velerín Carretera; all material, except for type specimen, in BL and RM collections.

*Etymology* — Latin *longus*, meaning elongated.

*Description* — Shell small, with immersed spire, elliptical-subcylindrical, with maximum diameter at mid-height of shell, H/D *c.* 1.65. Posterior end somewhat truncated. Siphonal notch fairly well developed. Lip moderately thickened, roughly rectilinear in its median part. Denticulations very fine, indistinct. Four blade-like columellar plications, not excavated inside aperture. Parietal callus indistinct. Aperture moderately narrow. Surface smooth, shiny, except for very fine growth striae. Measurements of holotype are H 2.95 mm, D 1.75 mm.

*Distribution* — Known exclusively from the Pliocene of Málaga.

*Remarks* — The markedly subcylindrical shape and straight lip make allocation of this species within the genus *Granulina* rather doubtful. In addition, there are no fossil or extant European marginelliform gastropods that may be compared to the present species, except for '*Marginella*' *ovulaeformis* Seguenza, 1879, a poorly known Pleistocene species briefly commented on by La Perna (1999), which is much larger and pyriform in shape. Both species are reminiscent of representatives of the genus *Ovaginella* Laseron, 1957, from New Zealand and Australia (Coovert & Coovert, 1995), but the present material is too limited to examine inner shell features. Internal whorls are partially resorbed in *Granulina*, while they are unmodified in other marginellids.

***Granulina clandestina* (Brocchi, 1814)**

Figure 14

\*1814 *Voluta clandestina* Brocchi, p. 642, pl. 15, fig. 11.

1992 *Granulina clandestina* (Brocchi, 1814) — Gofas, p. 5, fig. 3.

2000 *Granulina clandestina* (Brocchi, 1814) — La Perna, p. 54, figs 8-10.

*Material examined* — 1 specimen from 'Velerín Conglomerates' (IRScNB IST 6434); 1 specimen from Velerín Carretera (BL colln).

*Distribution* — Pliocene, Mediterranean. This species is also known from the Pliocene of Italy (Gofas, 1992; La Perna, 2000), from where it was first described. Pleistocene records from Italy are in need of confirmation (La Perna, 1999).

**Remarks** — Its 'cordiform' shape is unique amongst fossil and extant Mediterranean species. However, *G. clandestina* is closely similar to the West African *G. parilis* Gofas & Fernandes, 1988 from the Guinea Gulf, which differs by having a more ovate and slightly subcylindrical shell, with a less marked 'cordiform' outline.

***Granulina marginata*** (Bivona, 1832)

Figure 18

- \*1832 *Volvaria marginata* Bivona, p. 24, pl. 3, fig. 5.
- 1992 *Granulina marginata* (Bivona, 1832) — Gofas, p. 6, figs 5-8, 25.
- 1999 *Granulina marginata* (Bivona, 1832) — La Perna, p. 38, figs 36-42.
- 2000 *Granulina marginata* — La Perna, figs 14, 15.

**Material examined** — from 'Velerin Conglomerates', 1 specimen (IRScNB IST 6435), and 2 specimens in BL colln.

**Distribution** — Pliocene-Recent, Mediterranean and Gibraltar. This species is also known from the Pliocene and Pleistocene of Italy (La Perna, 1999, 2000). In post-Pleistocene times, it is the commonest and most widely distributed, shallow-water species of the genus in the Mediterranean (Gofas, 1992; La Perna, 1999).

**Remarks** — The material examined is limited and poorly preserved. Identification is based on size and shell shape, as most apertural features are obscured by indurated matrix. *Granulina marginata* also has a parietal callus ridge, which is thin, often indistinct and faintly tuberculate.

***Granulina boucheti*** Gofas, 1992

Figures 16, 17

- \*1992 *Granulina boucheti* Gofas, p. 10, figs 9, 10, 26.
- 1999 *Granulina boucheti* (Gofas, 1992) — La Perna, p. 38, figs 38-40.

**Material examined** — 3 specimens from Velerin Carretera; from 'Velerin Conglomerates' 1 specimen (IRScNB IST 6436) and 3 specimens in BL colln.

**Distribution** — Pliocene-Recent, Mediterranean. After *G. marginata*, this is the second commonest extant species, also fairly common in the Pleistocene of Italy (Gofas, 1992; La Perna, 1999). The present record is the first from the Pliocene.

**Remarks** — The specimens from Estepona closely match extant shells. *Granulina boucheti* is another species with a thin, faintly tuberculate parietal ridge. A comparison of the soft parts and shell of this species with those of *G. marginata* was provided by Gofas (1992). These are two closely similar, often sympatric species, with a markedly shallow-water distribution. They may be related to *G. pierrepineaui* Pin & Boyer, 1995 from Senegal, which is similar to *G. boucheti* in shell and soft parts and which also has a markedly shallow-water distribution.

***Granulina guttula*** La Perna, 1999

Figures 20-22

- \*1999 *Granulina guttula* La Perna, p. 39, figs 13-16.

**Material examined** — from Velerin Carretera, 1 specimen (IRScNB IST 6437), 5 specimens in BL colln; type material is housed in the UPMC collections.

**Distribution** — Pliocene-Recent, Mediterranean, previously known only from the type locality, the eastern Tyrrhenian Sea, at a depth of 84 m.

**Remarks** — The present shells differ from the types in being slightly larger (maximum height 2.7 mm vs 2.25 mm in types) and slightly less rostrate. However, in view of our comparatively poor knowledge of *G. guttula* and the limited fossil material, we prefer to consider them conspecific. A certain difficulty in referring some fossil shells of *Granulina* to extant species was stressed by La Perna (1999), a fact related to the evolutionary pattern of this genus (see below).

In the original description, a noteworthy feature of this species was not recorded, *i.e.* the glossy and slightly iridescent appearance, despite the fact that the type material is not particularly fresh. This is in contrast with the more usual opaline appearance in shells of the genus *Granulina*. Two recently described species from north-west Africa, *G. cerea* and *G. crystallina* (Smriglio *et al.*, 2001), are characterised by a similar, particularly transparent shell wall, giving a glossy or waxy appearance. In addition, they are not markedly different from *G. guttula* in size, shape and apertural features, differing mainly in being more inflated and in having the maximum diameter located more posteriorly.

***Granulina* sp.**

Figure 15

compare

- 1992 *Granulina* sp. — Gofas, fig. 4.
- 2000 *Granulina* sp. — La Perna, p. 38, p. 54, figs 11-13.

**Material examined** — from Rio del Padrón, 1 specimen (IRScNB IST 6438) and 10 specimens in BL colln.

**Distribution** - Pliocene, Mediterranean. This was probably the commonest species of *Granulina* in the Mediterranean Pliocene.

**Remarks** — This species was first identified, but not named by Gofas (1992), and subsequently recorded from the Pliocene of Sicily by La Perna (2000). It is similar to *G. boucheti*, from which it may be distinguished by a sharper and 'symmetrical' posterior rostration. However, this species appears more closely related to the Pleistocene *G. jhomisiensis* La Perna, 1999. It will be formally named by La Perna & Smriglio (in prep.), on the basis of material from northern Italy (Tuscany).

**Discussion**

The present paper highlights some differences in composition of the genus *Granulina* between the Pliocene of Málaga (westernmost Mediterranean) and Italy (central Mediterranean). *Granulina iberica*, *G. detruncata*, *G. malacitana* and *G.? longa*, occurring at Málaga, are not known from Italy to date. On the other hand, *G. elliptica* La Perna, 2000, is known exclusively from the Pliocene of Sicily, while *G. guttula*, formerly known only as an extant species, occurs at Málaga. *Granulina marginata*, *G. boucheti*, *G. clandestina* and *Granulina* sp. are known from a much wider area, which may include the western and central Mediterranean. In this respect, it is worth noting the Recent wide distribution of *G. marginata* and *G. boucheti*. It seems unlikely that these compositional differences are related to distinct palaeoecological characters of the sites studied, as all Pliocene records of *Granulina* from Italy are from shelf deposits similar to those occurring in the Málaga area. Although such differences may in part be due to an incomplete knowledge

of the Pliocene fauna, the general pattern of distribution of the extant Mediterranean and West Atlantic species cannot be overlooked. The sole species with a genuinely Mediterranean to Atlantic (Ibero-Moroccan Gulf) distribution is *G. occulta*; three species are known only from the Gibraltar-Alboran Sea, while *G. guancha* (d'Orbigny, 1840) appears restricted to the Canary Islands, etc. This pattern may be biased by an incomplete knowledge of a number of species, described recently and often known only from the type locality; however, a high rate of endemism within the genus is beyond doubt. The same general pattern is found amongst marginellids and marginelliform gastropods; for instance, all nine species of the marginellid genus *Volvarina* recorded by Moreno & Burnay (1999) from the Cape Verde Islands are endemic to the archipelago. The exclusive intracapsular larval development of marginellids (Bouchet & Warén, 1985; Covert, 1986; Covert & Covert, 1995) strongly reduces the dispersal capabilities, thus promoting speciation, endemism and fast turn-over through (geological) time.

SPECIES CLUSTER	GEOGRAPHIC RANGE	STRATIGRAPHIC RANGE
<i>Granulina marginata</i> <i>Granulina boucheti</i> <i>Granulina pierrepineai</i>	Mediterranean Mediterranean northwest Africa	Pliocene - Recent Pliocene - Recent Recent
<i>Granulina clandestina</i> <i>Granulina parilis</i>	Mediterranean central West Africa	Pliocene Recent
<i>Granulina malacitana</i> <i>Granulina vanhareni</i> <i>Granulina fernandesi</i> <i>Granulina mauretunica</i>	Málaga Gibraltar Cape Verde Islands northwest Africa	Lower Pliocene Recent Recent Recent
<i>Granulina detruncata</i> <i>Granulina ghanensis</i> <i>Granulina africana</i> <i>Granulina canariensis</i>	Málaga central West Africa northwest Africa Canary Islands	Lower Pliocene Recent Recent Recent
<i>Granulina guttula</i> <i>Granulina crystallina</i> <i>Granulina cerea</i>	Mediterranean northwest Africa northwest Africa	Pliocene - Recent Recent Recent
<i>Granulina iberica</i> <i>Granulina tenuilabiata</i> <i>Granulina rosarioi</i> <i>Granulina ovulina</i> <i>Granulina gofasi</i>	Málaga Mediterranean Sicily Sicily Mediterranean	Lower Pliocene Pleistocene - Recent Pleistocene Pleistocene Pleistocene? - Recent
<i>Granulina</i> sp. <i>Granulina jhomisiensis</i>	Mediterranean Sicily	Pliocene Pleistocene

**Table 2.** Clusters of species of *Granulina* discussed in the present paper, with the exclusion of *G.? longa*, with indication of their geographical and stratigraphical distribution. 'Mediterranean' stands for fossil and extant species with recorded or inferred wide distribution within this basin (see text for additional comments).

As noted above, several cases of morphological similarity may be recognised amongst some species, both extant and fossil, as based on a number of shell features (size, shape, apertural features, micro-ornament, etc.). These similarities have importance for inferring phylo-

genetic relationships and for outlining the evolutionary and biogeographic history of the genus, allowing also a certain taxonomic differentiation at species-group level to be attempted. It is worth noting that marked similarities in soft parts occur between species with morphologi-

cally similar shells, as documented by Gofas (1992) for *G. marginata* and *G. boucheti*. On these grounds, some groups or 'lineages' may be tentatively recognised (Table 2).

*Granulina marginata* and *G. boucheti* represent an ancient stock which may have northwest African affinities, while *G. clandestina* and *G. sp.*, probably the most widely distributed Pliocene species, may be referred to two distinct lineages, the former pointing to a central West African affinity, while the latter may include the Pleistocene *G. jhomisiensis*, whose relationship with extant species is not yet clear. A similar 'southerly' affinity may also be proposed for *G. detruncata*, *G. malacitana* and *G. guttula*, each of them pointing to clearly distinct lineages. No living representatives of the *G. detruncata* lineage occur in the Mediterranean, while the lineage of *G. malacitana* never seems to have extended into the Mediterranean beyond Gibraltar and the Alboran Sea. *Granulina iberica* and 'allied' Pleistocene and extant species may represent an endemic stock of unclear affinity and with a marked preference for deep-water habitats. *Granulina elliptica* has a clear Atlantic affinity, as demonstrated by a 'sister' species recently found in Upper Pliocene strata of Portugal (La Perna *et al.*, in prep.).

Definition of such a model will be refined by further research. However, the present data support the 'warm-temperate' to 'warm' biogeographical character of *Granulina* and allow a general assessment to be made concerning the history of this genus in the Mediterranean. The Pliocene shelf species were characterised by an 'admixture' of 'warm-temperate' and 'warm' characters. Subsequent to the Middle-Late Pliocene and Pleistocene cooling events, the species with thermophilic affinity (the 'African lineages') mostly went extinct, new species appeared and earlier species with temperate affinity, such as *G. marginata* and *G. boucheti*, were more successful. The Mediterranean thus became the most northerly 'outpost' of *Granulina* in the eastern Atlantic. Of the twelve extant species known from the Mediterranean, only *G. marginata*, *G. boucheti* (entire Mediterranean), *G. vanhareni* and *G. torosa* (Gibraltar) have a typical shallow-water distribution. The first two also occurred in the Pliocene, where at least four species (*Granulina sp.*, *G. clandestina*, *G. malacitana* and *G. elliptica*) had a similar shallow-water distribution. This would imply that the diversity of *Granulina* in the shelf waters exceeded the modern one. However, as far as we know, the overall diversity did not change significantly, and this was probably related to an increased colonisation of deeper-water environments (outer shelf and upper slope).

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