*GEOLOGICA CARPATHICA*, JUNE 2013, 64, 3, 237–251 doi: 10.2478/geoca-2013-0016

# New evidence on the origin of non-spinose pitted–cancellate species of the early Danian planktonic foraminifera

IGNACIO ARENILLAS and JOSE ANTONIO ARZ

Departamento de Ciencias de la Tierra, and Instituto Universitario de Investigación en Ciencias Ambientales de Aragón, Universidad de Zaragoza, E-50009 Zaragoza, Spain; ias@unizar.es; josearz@unizar.es

*(Manuscript received July 24, 2012; accepted in revised form December 11, 2012)*

**Abstract:** Intermediate forms identified in some of the most continuous lower Danian sections allow a better understanding of the origin and evolution of pitted (*Globanomalina*) and cancellate (*Praemurica*) planktonic foraminifera. Both *Globanomalina* and *Praemurica* are part of a major Paleocene lineage, namely the "non-spinose lineage", which started to diverge in the early Danian. Transitional specimens strongly suggest the evolution from *Parvularugoglobigerina* to *Globanomalina*, and then to *Praemurica*. These evolutionary turnovers were quite rapid (probably lasting less than 10 kyr), and seem to have begun in the time equivalent of the lower part of the *E. simplicissima* Subzone, namely the middle part of the standard Zone Pa. The initial evolutionary trends within this non-spinose lineage were the increase of test size and lip thickness, and the evolution from tiny pore-murals to large pore-pits, and from smooth to pitted and finally cancellate walls. Biostratigraphic data suggest that evolution of the wall texture preceded the morphological evolution within each genus. The oldest species of both *Globanomalina* and *Praemurica*, namely *G. archeocompressa* and *Pr. taurica*, initially retained the external morphology of the ancestral *Parvularugoglobigerina eugubina*. Since their divergence, *Globanomalina* and *Praemurica* followed a separate evolutionary path, evolving into morphologically different species.

**Key words:** Paleocene, phylogeny, planktonic foraminifera, wall texture, *Parvularugoglobigerina*, *Globanomalina*, *Praemurica*.

## Introduction

After the Cretaceous/Paleogene (K/Pg) boundary mass extinction event a planktonic foraminiferal evolutionary radiation led to the origin to some of the main Early Paleogene lineages (Premoli Silva 1977; Smit 1982; D'Hondt 1991; Liu & Olsson 1992; MacLeod 1993; Olsson et al. 1999; Apellániz et al. 2002; Arenillas et al. 2010). One of these leads to the genus *Globanomalina* Haque, 1956, and another to *Praemurica* Olsson, Hemleben, Berggren & Liu, 1992. They were designated "non-spinose lineages" by Olsson et al. (1999). Both exhibit >1 μm-diameter pore-pits (also called pore-funnels). These are pores ending in a funnel-shaped depression in the external test wall enlarging externally the pore. However, while *Praemurica* develops honeycomb-like surface ridges (interpore ridges) typical of a cancellate or reticulate wall, *Globanomalina* exhibits a less ornamented wall, so its texture has been traditionally described as smooth. None of them have spines, papillas and/or pustules.

The phylogenetic origin of these genera has been the subject of several studies, in particular those of Olsson et al. (1992, 1999) and Liu & Olsson (1994). They supported the previous hypotheses of Berggren (1962, 1977), Olsson (1963, 1970) and Blow (1979), suggesting that the normal perforate Danian planktonic foraminifera (i.e. pitted and cancellate walls) derived from *Hedbergella* Brönnimann & Brown, 1958 with pitted walls. According to them, the cancellate (spinose and non-spinose) species derived from *H. monmouthensis* Olsson, 1960, and the pitted-smooth one from *H. holmdelensis* Olsson, 1964. In contrast, Arenillas & Arz (1996, 2000) and Arenillas et al. (2010) suggested the alternative perspective that *Palaeoglobigerina* Arenillas, Arz & Náñez, 2007, was the ancestor of the spinose lineage, whereas *Parvularugoglobigerina* Hofker, 1978 was the forerunner of the non-spinose lineage, first giving rise to *Globanomalina* and then to *Praemurica*. A similar phylogenetic hypothesis had already been proposed by Premoli Silva (1977), who considered that *Globanomalina*, in particular *Globanomalina compressa* (Plummer, 1927) derived from *Parvularugoglobigerina*, specifically from *Parvularugoglobigerina eugubina* (Luterbacher & Premoli Silva, 1964).

Following an intensive search of transitional lowermost Danian specimens, this study proposes an alternative phylogenetic hypothesis on the origin of the non-spinose lineage, suggesting an evolutionary relationship between smooth *Parvularugoglobigerina* and pitted *Globanomalina*, and between the latter and the cancellate *Praemurica*. In addition, we propose phylogenetic relationships among species based on textural and external morphological criteria and high resolution biostratigraphic data. In order to carry out this study, we have used specimens from some of the most continuous and expanded stratigraphic sections available from the lower Danian.

## Material and methods

For the analysis of the biostratigraphic ranges of the studied taxa and their transitional specimens, we have revised the lower Danian in the El Kef and Aïn Settara sections (Tunisia) and in the Caravaca and Agost sections (Spain). We also have taken into account biostratigraphic data from other sec-

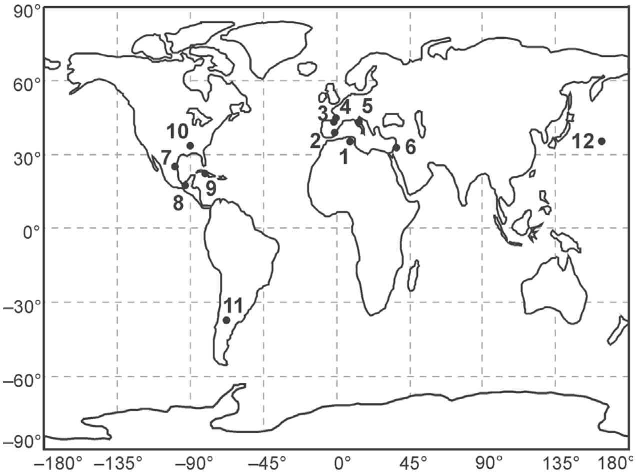

**Fig. 1.** Geographical location of the lower Danian sections mentioned in the text: **1** — El Kef, Aïn Settara and Elles (Tunisia); **2** — Caravaca and Agost (S Spain); **3** — Zumaia, Osinaga and San Sebastián (N Spain); **4** — Bidart (France); **5** — Gubbio (Italy); **6** — Ben Gurion (Israel); **7** — El Mulato, El Mimbral and La Lajilla (NE Mexico); **8** — Bochil and Guayal (S Mexico); **9** — Loma Campiro (Cuba); **10** — Lynn Creek (Mississippi); **11** — Bajada del Jagüel (Argentine); **12** — DSDP Site 305 (North Pacific).

tions such as Elles (Tunisia), Ben Gurion (Israel), Gubbio (Italy), Zumaia, Osinaga and San Sebastián (Spain), Bidart (France), El Mulato, El Mimbral, La Lajilla, Bochil and Guayal (Mexico), and Loma Capiro (Cuba). The geographical location of the analysed sections is shown in Fig. 1.

We used the lower Danian planktonic foraminiferal zonations by Arenillas et al. (2004) and Berggren & Pearson (2005); their equivalence is shown in Fig. 2. The zonation of Arenillas et al. (2004) includes the three classical lower Danian *Guembelitria cretacea*, *Parvularugoglobigerina eugubina* and *Parasubbotina pseudobulloides* Zones, and divides each of these biozones into two Subzones: *Hedbergella holmdelensis* and *Parvularugoglobigerina longiapertura* Subzones for the *G. cretacea* Zone, *Parvularugoglobigerina sabina* and *Eoglobigerina simplicissima* Subzones for the *Pv. eugubina* Zone, and *Eoglobigerina trivialis* and *Subbotina triloculinoides* Subzones for *P. pseudobulloides* Zone. We have included in this paper a third subzone in the upper part of the *P. pseudobulloides* Zone: the *Globanomalina compressa* Subzone, which was given the rank of Zone by Arenillas & Molina (1997). As shown in Fig. 2, Berggren & Pearson's (2005) Zone P0 is equivalent to the *H. holmdelensis* Subzone, the Zone Pa approximately spans both the *P. longiapertura* Subzone and the *Pv. eugubina* Zone, and P1a, P1b and P1c are roughly equivalent to the *E. trivialis*, *S. triloculinoides* and *G. compressa* Subzones respectively. The ranges of species shown in Fig. 2 are based on biostratigraphic data from the sections mentioned above.

For morphological analysis, we also checked other sections and boreholes (Fig. 1) such as Elles (Tunisia), Ben Gurion (Israel), Bajada del Jagüel (Argentine), Lynn Creek (Mississippi) and DSDP Site 305 (Shatsky Rise, North Pacific). Specimens were chosen mainly from El Kef and Aïn Settara samples, which were disaggregated in water with diluted $H_2O_2$, and washed through a 63-μm sieve. The foraminiferal preservation in these sections is good enough to analyse the wall texture, although corroded and recrystallized surfaces can be observed in some specimens ("frosty" specimens according to the terminology of Sexton et al. 2006). Wall textures were examined under scanning electron microscopes (SEM), trademarks JEOL JSM 6400 and Zeiss MERLIN FE-SEM, at the Electron Microscopy Service of the Universidad de Zaragoza (Spain). Over 600 SEM-photographs, including different views of whole specimens, were taken of 170 specimens, some of which are morphotypes transitional between species. Except for type-specimens of other authors, all the specimens illustrated in Figs. 3 to 8 are deposited in the Departamento de Ciencias de la Tierra of the Universidad de Zaragoza (Spain).

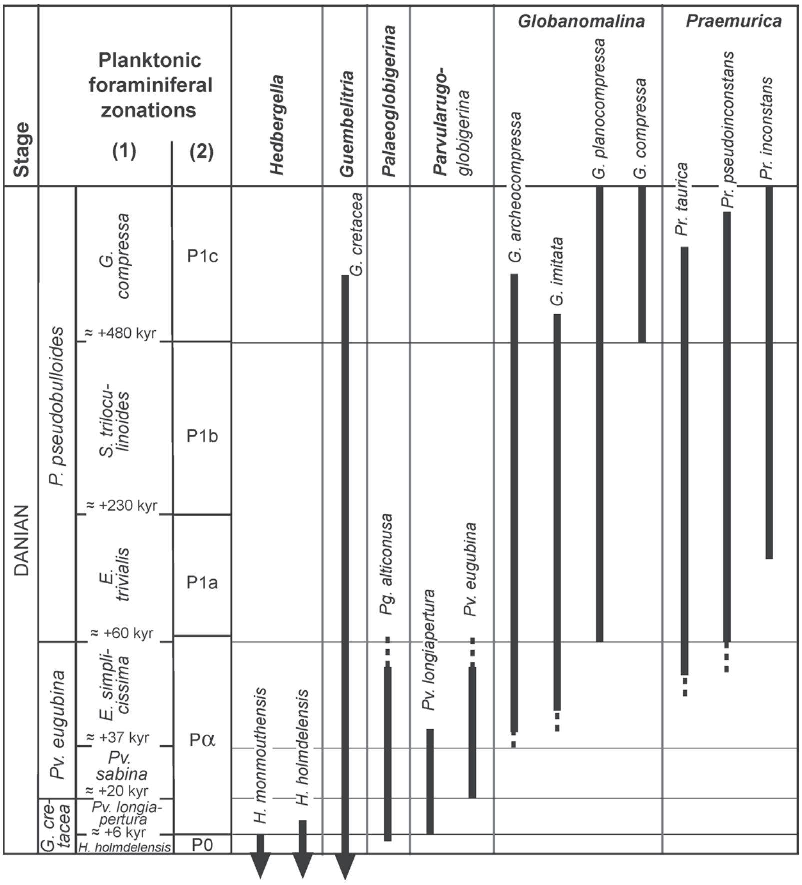

**Fig. 2.** Biostratigraphic ranges of analysed species: **1** — planktonic foraminiferal zonation of Arenillas et al. (2004 modified); **2** — planktonic foraminiferal zonation of Berggren & Pearson (2005); dotted lines mean doubtful biostratigraphic distribution (not supported by SEM-photographed specimens).

## Taxonomic and phylogenetic notes

The taxonomy used here is based mainly on that of Arenillas (1996), with some modifications. The species analysed were: *Hedbergella monmouthensis* Olsson (1960; Fig. 3A–B), *Hedbergella holmdelensis* Olsson, 1964 (Fig. 3C–I), *Parvularugoglobigerina longiapertura* (Blow 1979; Fig. 3J–K), *Parvularugoglobigerina eugubina* (Luterbacher & Premoli Silva 1964; Fig. 3L–O), *Globanomalina archeocompressa* (Blow 1979; Fig. 4A–F), *Globanomalina imitata* (Subbotina 1953; Fig. 4G–J), *Globanomalina planocompressa* (Shutskaya 1965; Fig. 4K–4N), *Globanomalina compressa* (Plummer 1927; Fig. 5A–B), *Praemurica taurica* (Morozova 1961; Fig. 5C–D), *Praemurica pseudoinconstans* (Blow 1979; Fig. 5E–G), and *Praemurica inconstans* (Subbotina 1953; Fig. 5H–L). The diagnostic characteristics of these species are given in Appendix.

Wall texture has been widely considered when analysing the taxonomy and phylogeny of planktonic foraminifera. It is allowing taxa to be distinguished at the genus rank (e.g. Nederbragt 1991; Olsson et al. 1992; Liu & Olsson 1992, 1994; Georgescu 2007, 2009a,b; Arenillas et al. 2010). Olsson et al. (1999) differentiated two major lineages in the Danian based on textural criteria: the “non-spinose lineage” (*Globanomalina* and *Praemurica*) and the “spinose lineage” (*Eoglobigerina* Morozova, 1959, *Subbotina* Brotzen & Pozaryska, 1961, and *Parasubbotina* Olsson, Hemleben, Berggren & Liu, 1992). They also proposed two lineages within the lower Danian non-spinose: “smooth-walled lineage” (*Globanomalina*) and “praemuricate lineage” (*Praemurica*). These lineages are referred to here as “non-spinose pitted” and “non-spinose cancellate” respectively because *Globanomalina* exhibits a pitted rather than smooth wall texture (i.e. its pore-pits are always larger than 1 μm in diameter, and can easily be observed under the stereomicroscope), and the term “praemuricate” is not descriptive enough. Defined in this way, the *Globanomalina* wall texture can be distinguished from the smooth wall of *Parvularugoglobigerina* and the non-spinose cancellate wall of *Praemurica*.

Blow (1979) ascribed non-spinose pitted and cancellate Early Paleogene taxa to the large traditional family Globorotaliidae Cushman, 1927, specifically to *Globorotalia* (*Turborotalia*) Cushman & Bermúdez, 1949. He suggested that *Hedbergella* was the ancestor of these early “turborotaliids”, based mainly on similarities with the Danian *pseudobulloides*-group (currently separated from the non-spinose lineage and assigned to *Parasubbotina* by Olsson et al. 1999). Blow (1979) proposed that some earliest Danian species with smooth wall texture, such as *Pv. longiapertura* (Blow 1979; Fig. 3J–K), should be included in *Globorotalia* (*Turborotalia*). However, this group of primitive species had been assigned previously to the earliest Danian genus *Parvularugoglobigerina* Hofker, 1978. Olsson et al. (1999) excluded *Parvularugoglobigerina* from Globorotaliidae, after suggesting close relationships between parvularugoglobigerinids and guembelitriids and ascribed it to the family Guembelitriidae Montanaro Gallitelli, 1957.

Loeblich & Tappan (1987) classified *Globanomalina* in the family Globanomalinidae Loeblich & Tappan, 1984, which was defined as comprising Paleogene species with non-spinose “smooth” wall and low trochospiral to planispiral coiling. This macrotaxonomic classification was adopted by Arenillas (1996). However, Olsson et al. (1999) concluded that *Globanomalina* was derived from the Late Maastrichtian hedbergellids, and consequently included it in the family Hedbergellidae Loeblich & Tappan, 1961. The wall of *Hedbergella* is similar to that of *Globanomalina*, namely pitted-smooth, but displays small scattered pustules, which are frequently very abundant over the first chambers of the test (Fig. 3A–I). Olsson et al. (1999) and Apellániz et al. (2002) suggested *H. holmdelensis* was the ancestral species of *Globanomalina*, the former Danian species being *G. archeocompressa*. According to this hypothesis, the morphological characters of *Globanomalina* species (compressed test with an imperforate peripheral band, and an umbilical-extraumbilical aperture bordered by a narrow lip) were derived directly from the ancestral species.

*Praemurica*, whose type-species is *Pr. taurica*, was defined in order to group Lower Paleocene species with low trochospiral and well-developed cancellate wall texture (Olsson et al. 1992). It was the first non-spinose, cancellate taxa to evolve after the K/Pg boundary mass extinction (Olsson et al. 1999). Others authors (e.g. Arenillas 1996) included it in the family Truncorotaloididae Loeblich & Tappan, 1961. Olsson et al. (1999) also suggested a hedbergellid origin for *Praemurica*, but independently of the *Globanomalina* origin, proposing *H. monmouthensis* as the ancestral species, and *Pr. taurica* as its first species to appear. A similar phylogenetic scenario was proposed by Apellániz et al. (2002), but they suggested that *Praemurica* derived from *H. holmdelensis*, with *Pv. eugubina* as an intermediary step.

Arenillas & Arz’s (1996) hypothesis proposed alternatively that *Parvularugoglobigerina* was the ancestor of the entire non-spinose lineage and the genus *Globanomalina* the first one to evolve. Arenillas (1996) therefore ascribed *Parvularugoglobigerina* to the family Globanomalinidae together with *Globanomalina*. These authors also suggested that *Praemurica* evolved somewhat later deriving from *G. archeocompressa*, with *Pr. taurica* being its first species. According to this hypothesis, *Parvularugoglobigerina* had previously derived from *Hedbergella*, in particular from earliest Danian dwarfed *H. holmdelensis*, based on morphological similarities and biostratigraphic data. However, a more detailed morphological and textural analysis (Arenillas et al. 2007, 2010) indicated that *Parvularugoglobigerina* derived from *Palaeoglobigerina*, which in turn evolved from *Guembelitria* Cushman, 1933.

Olsson et al. (1999) and Arenillas et al. (2007) disagree on the wall structure of the parvularugoglobigerinids. This first group of authors claims that parvularugoglobigerinids have an irregularly pore-mounded wall; the second group maintains that their wall is smooth. The discrepancy is not caused by poor preservation, since smooth walled specimens and specimens with more ornamented walls (i.e. pore-mounded *Guembelitria*, and/or rugose *Woodringina*) are found in the same samples and exposed to the same diagenetic conditions (Arenillas et al. 2010). Recently, Arenillas et al. (2012) have suggested the co-occurrence of two groups of primitive

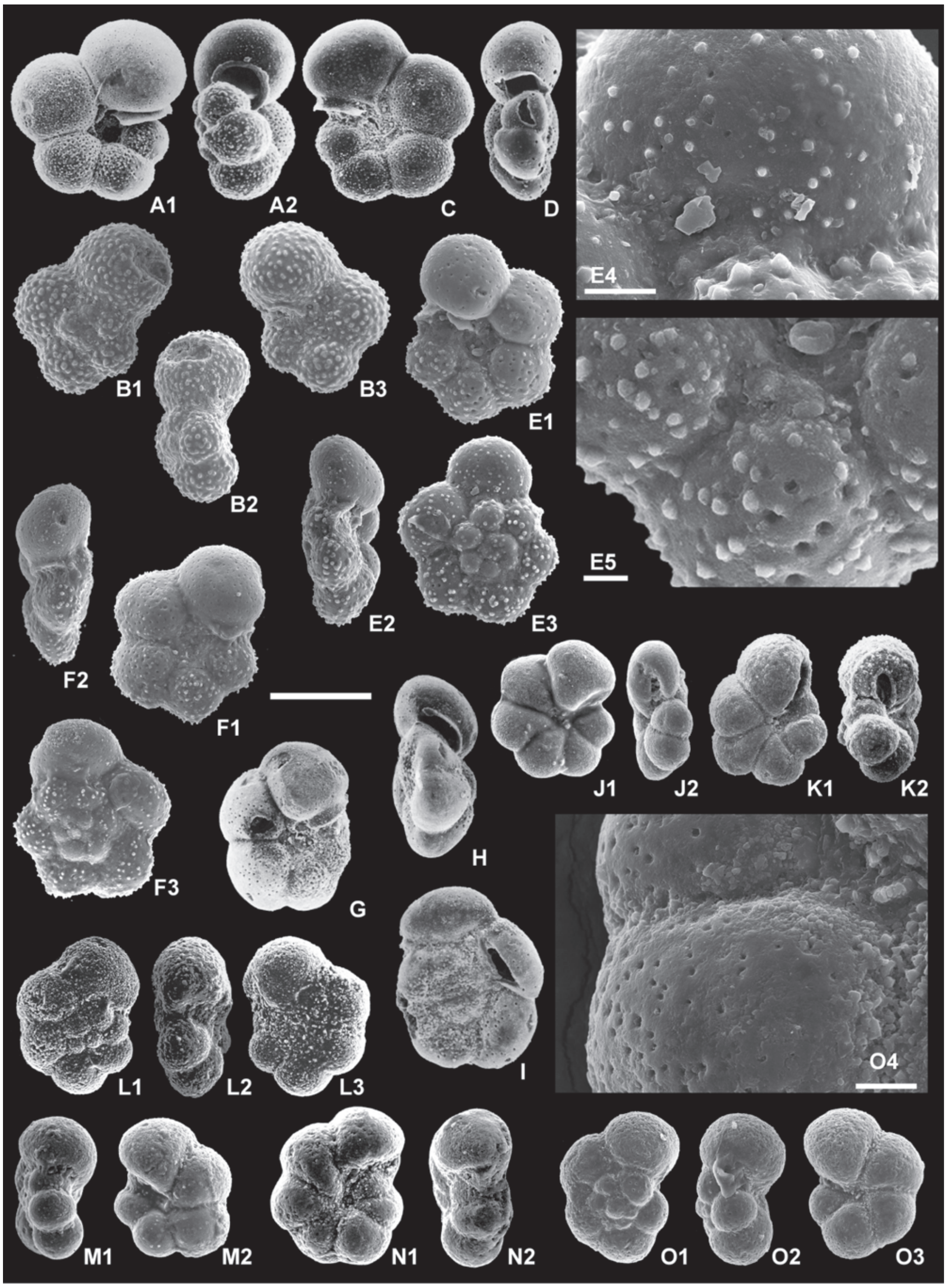

**Fig. 3.** SEM images of *Hedbergella* Brönnimann & Brown, 1958, and *Parvularugoglobigerina* Hofker, 1978, species of the K-Pg transition (scale bar = 100 µm; scale bar of SEM-micrographs illustrating details = 10 µm). **A** — *Hedbergella monmouthensis* Olsson, 1960, topotypes from Olsson et al. (1999), from the upper Maastrichtian, Redbank Fm, New Jersey: 1 — umbilical view, 2 — axial view. **B** — *H. monmouthensis*, from the *H. holmdelensis* Subzone (*G. cretacea* Zone), Aïn Settara, Tunisia: 1 — spiral view, 2 — axial view, 3 — umbilical view. **C, D** — *Hedbergella holmdelensis* Olsson, 1964, two topotypes of Olsson et al. (1999), from the upper Maastrichtian, Redbank Fm, New Jersey: C — umbilical view, D — axial view. **E** — *H. holmdelensis*, from the *Pv. longiapertura* Subzone (*G. cretacea* Zone), Aïn Settara, Tunisia: 1 — umbilical view, 2 — axial view, 3 — spiral view, 4, 5 — details of surface. **F** — *H. holmdelensis*, from the *H. holmdelensis* Subzone (*G. cretacea* Zone), Aïn Settara, Tunisia: 1 — umbilical view, 2 — axial view, 3 — spiral view. **G, H, I** — *H. holmdelensis*, three specimens from Olsson et al. (1999) assigned to *Globanomalina archeocompressa* (Blow, 1979), from the Zone P0, Millers Ferry, Alabama: G — umbilical view, H — axial view, I — spiral view. **J** — *Parvularugoglobigerina longiapertura* (Blow, 1978), from the *Pv. longiapertura* Subzone (*G. cretacea* Zone), Aïn Settara, Tunisia: 1 — umbilical view, 2 — axial view. **K** — *Pv. longiapertura*, type-specimens from Blow (1979), from the Zone Pa, DSDP Leg 6, South Pacific: 1 — holotype, umbilical view, 2 — paratype, axial view. **L** — *Parvularugoglobigerina eugubina* (Luterbacher & Premoli Silva, 1964), "*Pv. eugubina*" type-sample, from the lowermost Danian, Ceselli, Italy: 1 — spiral view, 2 — axial view, 3 — umbilical view. **M** — *Pv. eugubina*, from the *E. simplicissima* Subzone (*Pv. eugubina* Zone), Aïn Settara, Tunisia: 1 — axial view, 2 — umbilical view. **N** — *Pv. eugubina* (Luterbacher & Premoli Silva), from the *E. simplicissima* Subzone (*Pv. eugubina* Zone), Agost, Spain: 1 — umbilical view, 2 — axial view. **O** — *Pv. eugubina*, from the *Pv. sabina* Subzone (*Pv. eugubina* Zone), El Kef, Tunisia: 1 — spiral view, 2 — axial view, 3 — umbilical view, 4 — detail of surface (granular wall texture in parvularugoglobigerinids).

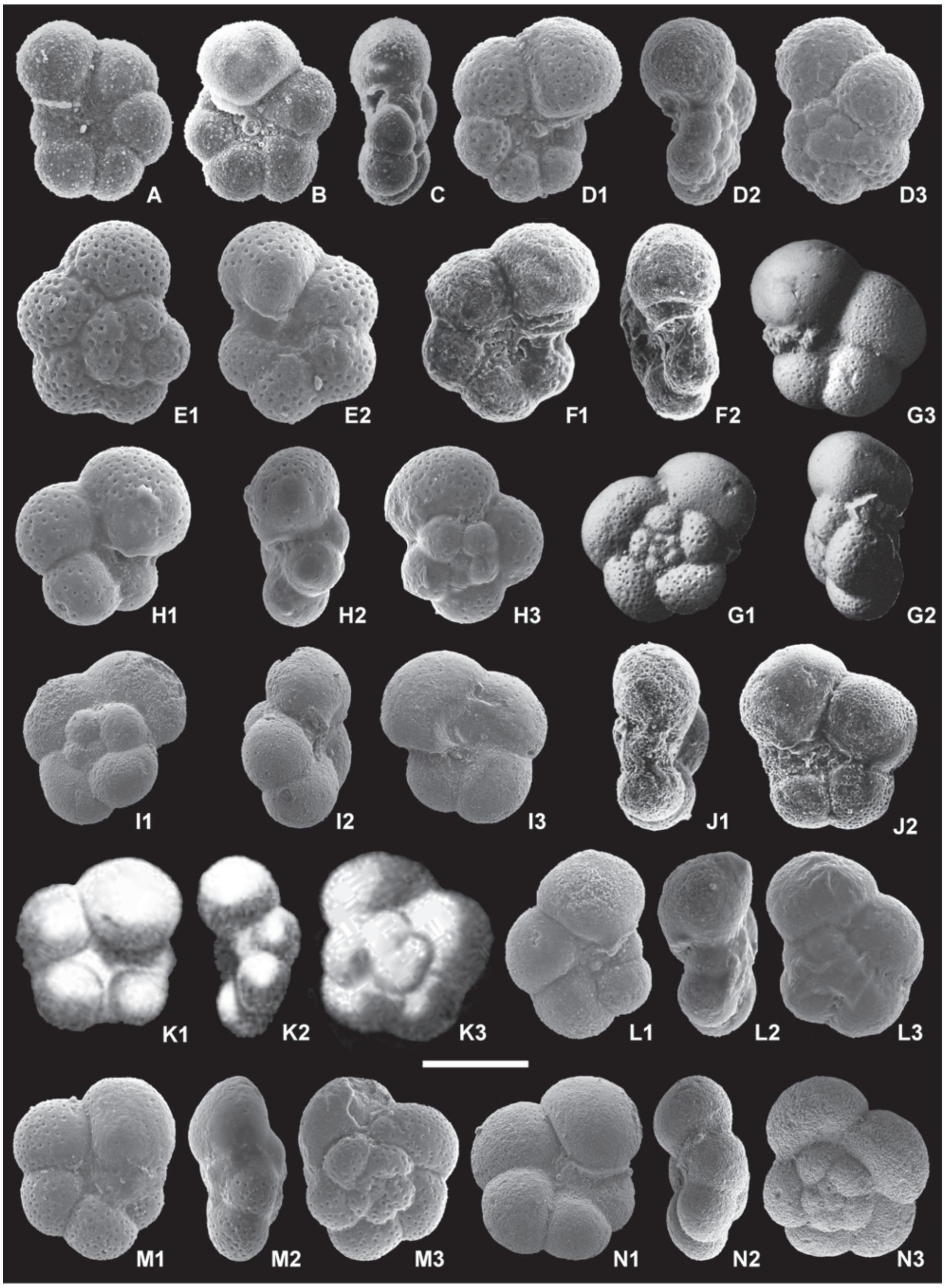

**Fig. 4.** SEM images of *Globanomalina* Haque (1956) species of the lower Danian (scale bar=100 μm). **A** — *Globanomalina archeocompressa* (Blow, 1979), paratype, Zone Pa, DSDP Leg 6, South Pacific (Blow 1979): umbilical view. **B** — *G. archeocompressa*, holotype, from the Zone Pa, DSDP Leg 6, South Pacific: umbilical view. **C** — *G. archeocompressa*, paratype, from Zone Pa, DSDP Leg6, South Pacific: axial view. **D** — *G. archeocompressa*, from the *S. triloculinoides* Subzone (*P. pseudobulloides* Zone), El Kef, Tunisia: 1 — umbilical view, 2 — axial view, 3 — spiral view. **E** — *G. archeocompressa*, from the *E. trivialis* Subzone (*P. pseudobulloides* Zone), Aïn Settara, Tunisia: 1 — spiral view, 2 — umbilical view. **F** — *G. archeocompressa*, from the *G. compressa* Subzone (*P. pseudobulloides* Zone), Caravaca, Spain: 1 — umbilical view, 2 — axial view. **G** — *Globanomalina imitata* (Subbotina, 1953), holotype, from Danian, Kuban River, northern Caucasus, Russia (SEM-image from Olsson et al. 1999): 1 — spiral view, 2 — axial view, 3 — umbilical view. **H** — *G. imitata*, from the *S. triloculinoides* Subzone (*P. pseudobulloides* Zone), El Kef, Tunisia: 1 — umbilical view, 2 — axial view, 3 — spiral view. **I** — *G. imitata* (Subbotina), from the *E. trivialis* Subzone (*P. pseudobulloides* Zone), El Kef, Tunisia: 1 — spiral view, 2 — axial view, 3 — umbilical view. **J** — *G. imitata*, transitional to *G. planocompressa*, from the *E. trivialis* Subzone (*P. pseudobulloides* Zone), Osinaga, Spain: 1 — axial view, 2 — umbilical view. **K** — *Globanomalina planocompressa* (Shutskaya, 1965), holotype, from the Danian, Khazni-don River, North Osetia, Russia: 1 — umbilical view, 2 — axial view, 3 — spiral view. **L** — *G. planocompressa* (Shutskaya), from the *S. triloculinoides* Subzone (*P. pseudobulloides* Zone), El Kef, Tunisia: 1 — umbilical view, 2 — axial view, 3 — spiral view. **M** — *G. planocompressa*, transitional to *G. compressa*, from the *S. triloculinoides* Subzone (*P. pseudobulloides* Zone), El Kef, Tunisia: 1 — umbilical view, 2 — axial view, 3 — spiral view. **N** — *G. planocompressa*, transitional to *G. compressa*, from the *E. trivialis* Subzone (*P. pseudobulloides* Zone), Aïn Settara, Tunisia: 1 — umbilical view, 2 — axial view, 3 — spiral view.

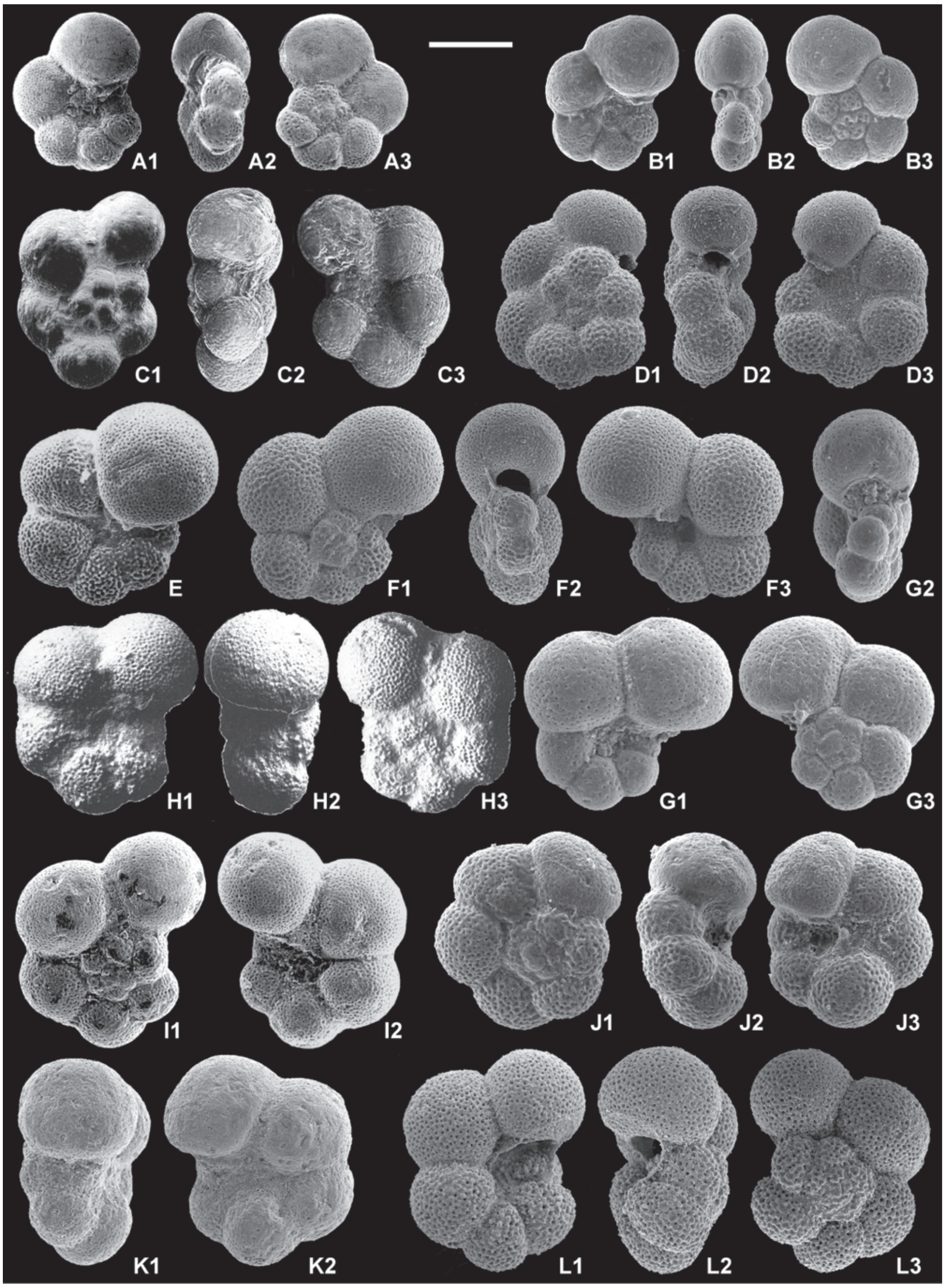

**Fig. 5.** SEM images of *Globanomalina compressa* (Plummer, 1927) and *Praemurica* Olsson, Hemleben, Berggren & Liu, 1992 species of the Danian (scale bar = 100 μm). **A** — *G. compressa*, holotype, from the Danian, Midway Formation, Navarro County, Texas (SEM-image from Olsson et al. 1999): 1 — umbilical view, 2 — axial view, 3 — spiral view. **B** — *G. compressa*, from the *G. compressa* Subzone (*P. pseudobulloides* Zone), Ben Gurion, Israel: 1 — umbilical view, 2 — axial view, 3 — spiral view. **C** — *Praemurica taurica* (Morozova, 1961), holotype, from the lower Danian, Tarkhankhut Peninsula, Crimea, Ukraine (SEM-image from Olsson et al. 1999): 1 — spiral view, 2 — axial view, 3 — umbilical view. **D** — *Pr. taurica*, from the Danian, Site 305, Shatsky Rise, North Pacific: 1 — spiral view, 2 — axial view, 3 — umbilical view. **E** — *Praemurica pseudoinconstans* (Blow, 1979), holotype, from Zone P1, DSDP Leg 6, South Pacific: umbilical view. **F** — *Pr. pseudoinconstans*, from the Danian, DSDP Site 305, Shatsky Rise, North Pacific: 1 — spiral view, 2 — axial view, 3 — umbilical view. **G** — *Pr. pseudoinconstans*, from the *S. triloculinoides* Subzone (*P. pseudobulloides* Zone), El Kef, Tunisia: 1 — umbilical view, 2 — axial view, 3 — spiral view. **H** — *Praemurica inconstans* (Subbotina, 1953), holotype, from Danian, Kuban River, Northern Caucasus, Russia (SEM-image from Olsson et al. 1999): 1 — umbilical view, 2 — axial view, 3 — spiral view. **I** — *Pr. inconstans*, from the *S. triloculinoides* Subzone (*P. pseudobulloides* Zone), Aïn Settara, Tunisia: 1 — spiral view, 2 — umbilical view. **J** — *Pr. inconstans*, from *S. triloculinoides* Subzone (*P. pseudobulloides* Zone), El Kef, Tunisia: 1 — spiral view, 2 — axial view, 3 — umbilical view. **K** — *Pr. inconstans*, from the *E. trivialis* Subzone (*P. pseudobulloides* Zone), Loma Capiro, Cuba: 1 — axial view, 2 — umbilical view. **L** — *Pr. inconstans*, from the Danian, DSDP Site 305, Shatsky Rise, North Pacific: 1 — umbilical view, 2 — axial view, 3 — spiral view.

trochospiral species in the earliest Danian, one with a smooth wall texture (with pore-murals) and other with a rugose wall texture (with rugosities and irregular pore-mounds). The former evolved at the P0–Pα transition, and was attributed to the parvularugoglobigerinids. The latter evolved at the Pα–P1 transition, and was assigned to the new genus *Trochoguembelitria* Arenillas, Arz & Náñez, 2012. On the contrary, Olsson et al. (1999) claim that the latter group belongs to *Parvularugoglobigerina*, and that its wall texture is irregular pore-mounded. However, textural and biostratigraphic data suggest that the two groups represent two different lineages, *Parvularugoglobigerina* appearing earlier than *Trochoguembelitria*.

## Evolution at the genus level

Specimens with intermediate characteristics have been recorded in El Kef and Aïn Settara (Figs. 6–8), illustrating transitions that indicate an evolution from *Parvularugoglobigerina* to *Globanomalina*, and then to *Praemurica*. Transitional specimens suggest the following initial evolutionary trends within this lineage: (1) increase of test size; (2) increase of lip thickness; (3) increase of pore size; (4) evolution from tiny pore-murals to large pore-pits; and (5) evolution from smooth to cancellate wall. These evolutionary steps are recorded in the lower part of the *E. simplicissima* Zone, occurring quite rapidly in terms of geological time (probably in less than 10 kyr according to the biochronological calibrations by Arenillas et al. 2004; see Fig. 2). Within the genera, changes in the overall shape of the test of the species seem to be preceded by the changes of the wall textures. Our data suggest an evolution from the smooth wall of *Parvularugoglobigerina* to the pitted wall of *Globanomalina*, and finally to the cancellate wall of *Praemurica* (Fig. 9).

The increase in test and pore sizes preceded the evolution of wall texture. Several *Pv. eugubina* specimens show a progressive change from 100–130 μm-length tests with < 1 μm-diameter mural pores (Fig. 6A–B; similar to the diagram in Fig. 9A) to 150–180 μm-length tests with 1–2 μm-diameter mural pores (Fig. 6D; similar to diagram in Fig. 9B). The latter are clearly intermediate morphotypes between *Pv. eugubina* and *G. archeocompressa*, which still retains primitive characters such as mural pores instead of pore-pits and a smooth instead of a pitted wall.

In the lower part of the *E. simplicissima* Subzone, some *Globanomalina* specimens show different degrees of the development of a pitted wall (Fig. 7). Ancestral morphotypes of *G. archeocompressa* (Fig. 7A) offer examples of the evolution from mural pores of parvularugoglobigerinids to pore-pits typical of the non-spinose lineage (as in Fig. 9C). The specimen in Fig. 7A still retains an aperture with primitive features, namely an unusually high arch with a thin lip and therefore it could also belong to *Pv. eugubina* or to *Pv. longiapertura* with modern textural characters. The apertural shape of this specimen is more common in the morphotypes intermediate between *Pv. longiapertura* (Fig. 3J–K) and *Pv. eugubina* (Fig. 3L–O) than in those between *Pv. eugubina* and *G. archeocompressa*. Blow (1979) illustrated a paratype of *G. archeocompressa* (Fig. 4A) with almost globular chamber and a thick lip and considered it as a “primitive” morphotype. This specimen seems to be an intermediate form between *Pv. eugubina* and *G. archeocompressa*. Other specimens, like that in Fig. 7B, are typical examples of *G. archeocompressa* (with pitted wall, low-arched aperture, thick lip, and imperforated peripheral band in the first chambers of the last whorl), showing different stages of development of pore-pits as exemplified in Fig. 9C and 9D. The external funnel-shaped depressions of these pores can reach up to about 5 μm in diameter (larger than in the holotype of *G. archeocompressa*). These morphotypes did not develop interpore ridges, which mean a cancellate wall, but the degree of pore-pit development in some of them (e.g. specimen in Fig. 7C) strongly supports an evolution from *Globanomalina* to *Praemurica*, particularly from *G. archeocompressa* to *Pr. taurica*.

Typical *Pr. taurica* specimens are illustrated in Fig. 8 — the degree of development of praemuricate cancellate wall varies from one specimen to another. Interpore ridges in the specimens of Fig. 8A–B are still underdeveloped, but there is a clear tendency to develop a coarsely cancellate wall as exemplified in Fig. 9E. The overall morphology of primitive specimens of *Pr. taurica* is almost identical with that of *Pv. eugubina* and *G. archeocompressa* (Figs. 6–7). All three species have subglobular chambers which may be compressed in some specimens.

Species of the non-spinose lineage (*Globanomalina* and *Praemurica*) usually exhibit 5 to 6 chambers in the first whorl (neanic stage). This character separates them from other cancellate Paleocene taxa such as *Eoglobigerina* or *Parasubbotina* with 3.5 to 5 neanic chambers (Arenillas & Arz 2013). This difference is similar to that which enabled Arenillas et al. (2007) to separate *Palaeoglobigerina* (3.5 to 4 neanic chambers) from *Parvularugoglobigerina* (4 to 4.5 chambers, or even 5 in the neanic stage). This morphological feature again suggests that both *Globanomalina* and *Praemurica* are phylogenetically related, and that the non-spinose lineage originated from *Parvularugoglobigerina*, with only a slight increase in the number of chambers in the neanic stage.

## Discussion and conclusions

According to the textural, morphological and biostratigraphic data, we propose that the non-spinose lineage derived from *Parvularugoglobigerina eugubina* (near the base of the *Eoglobigerina simplicissima* Subzone; Fig. 10). *Globanomalina* was the first taxa of this lineage, developing pore-pits and acquiring a pitted wall texture. A short time later in evolutionary and geological terms (Fig. 2), cancellate walled *Praemurica* evolved from *Globanomalina* (in the upper part of the *E. simplicissima* Subzone; Fig. 10). According to this hypothesis, truncorotalids derived from globanomalinids, and these from parvularugoglobigerinids. Since their divergence, *Globanomalina* and *Praemurica* followed separate evolutionary paths that led to species of the two Paleocene non-spinose lineages, namely the “non-spinose pitted” (family Globanomalinidae) and the “non-spinose cancellate” (family Truncorotaloididae) lineages. The oldest species of

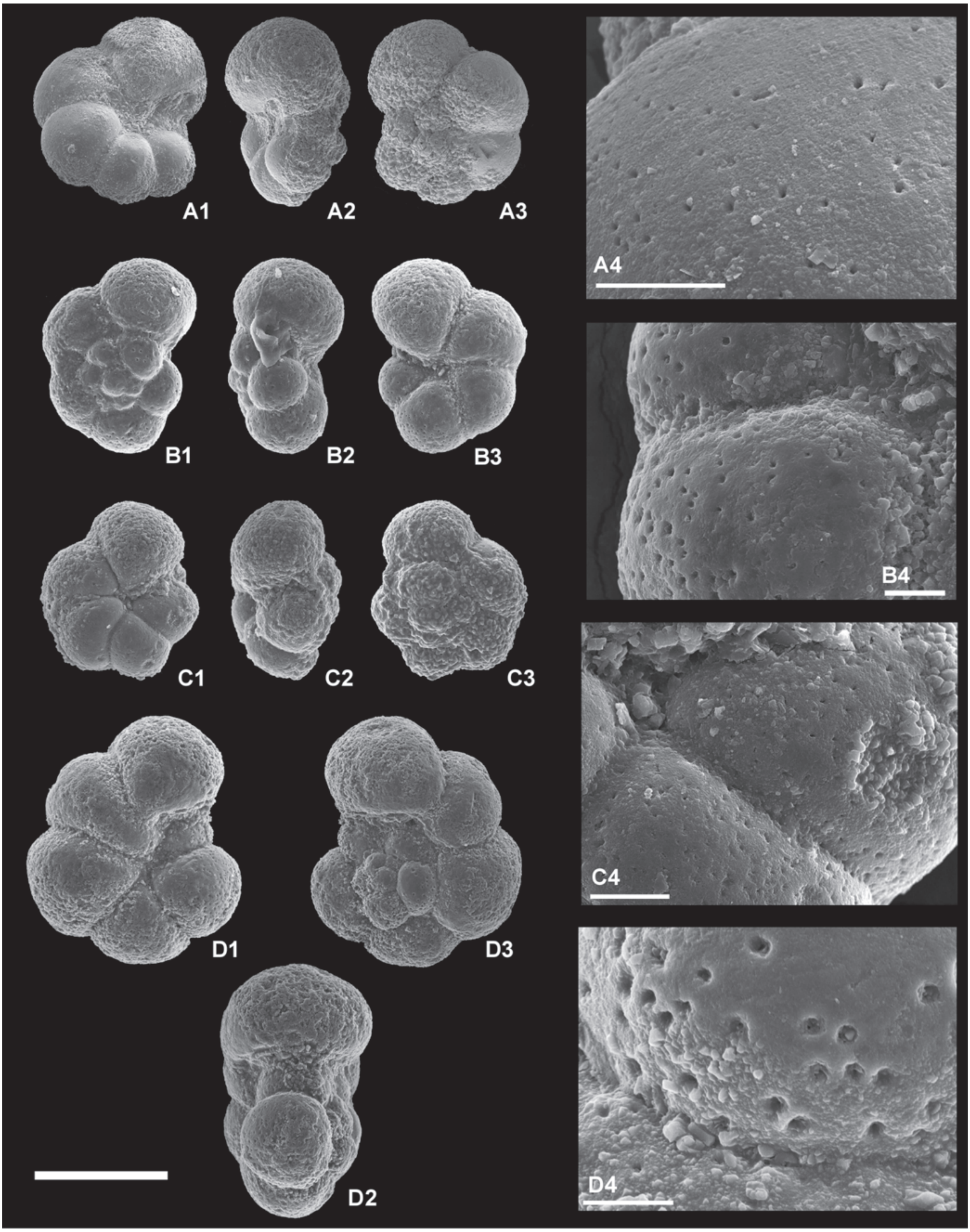

**Fig. 6.** SEM images of *Parvularugoglobigerina eugubina* specimens and details of their smooth wall texture, showing tiny pore-murals < 1 µm in the smooth surfaces (scale bar = 100 µm; scale bar of details = 10 µm). **A** — *Pv. eugubina*, from the *E. simplicissima* Subzone (*Pv. eugubina* Zone), Aïn Settara, Tunisia: 1 — umbilical view, 2 — axial view, 3 — spiral view, 4 — detail of surface. **B** — *Pv. eugubina*, from the *E. simplicissima* Subzone (*Pv. eugubina* Zone), El Kef, Tunisia: 1 — spiral view, 2 — axial view, 3 — umbilical view, 4 — detail of surface. **C** — *Pv. eugubina*, from the *E. simplicissima* Subzone (*Pv. eugubina* Zone), El Kef, Tunisia: 1 — umbilical view, 2 — axial view, 3 — spiral view, 4 — detail of surface. **D** — *Pv. eugubina*, specimen transitional to *G. archeocompressa* (Blow), from the *E. simplicissima* Subzone (*Pv. eugubina* Zone), El Kef, Tunisia: 1 — umbilical view, 2 — axial view, 3 — spiral view, 4 — detail of surface.

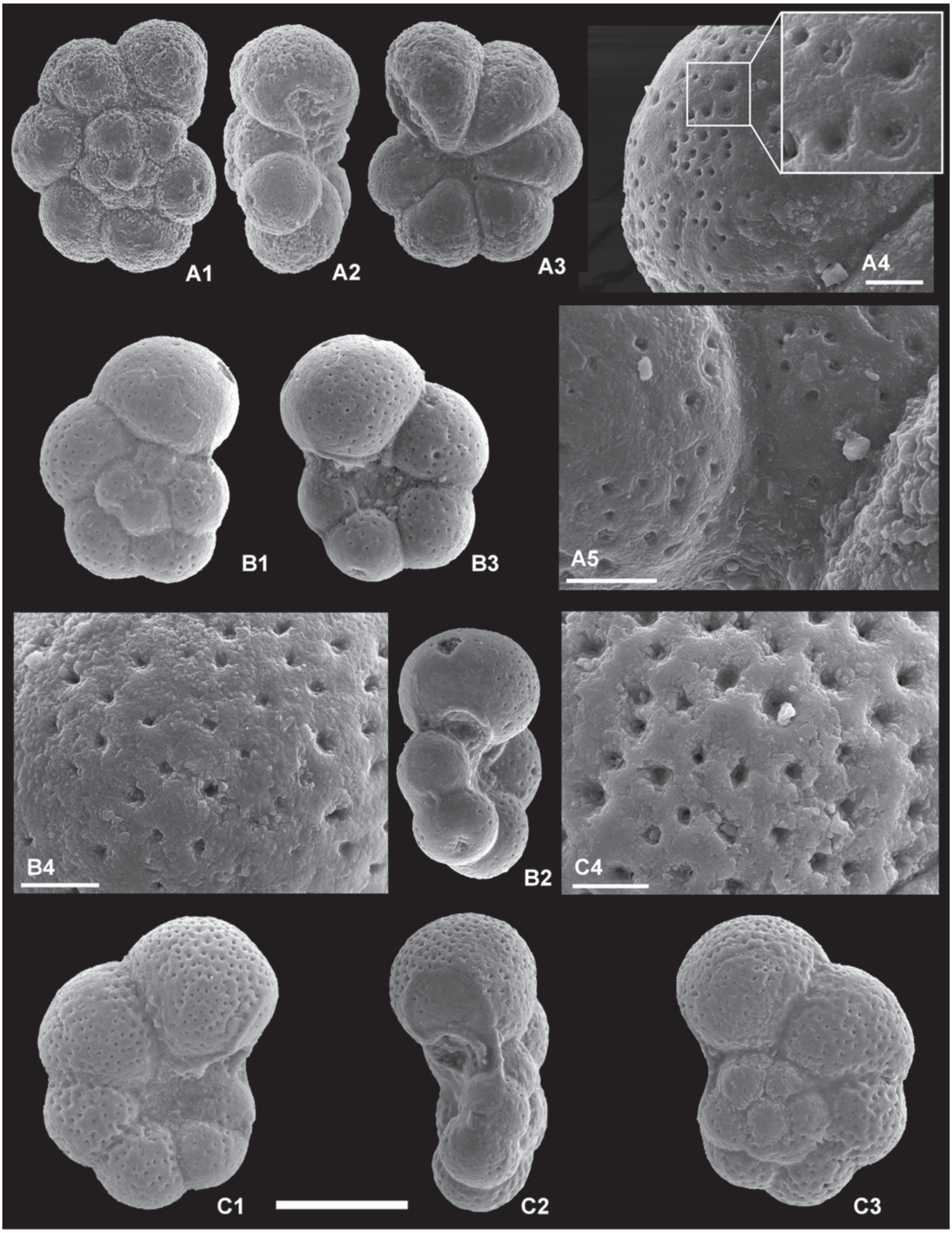

**Fig. 7.** SEM images of *Globanomalina archeocompressa* specimens and details of their smooth wall texture, showing pore-pits > 1 μm in the pitted surfaces (scale bar = 100 μm; scale bar of details = 10 μm). **A** — *G. archeocompressa*?, with primitive features similar to *Pv. longiapertura* and *Pv. eugubina*, from the *E. simplicissima* Subzone (*Pv. eugubina* Zone), El Kef, Tunisia: 1 — spiral view, 2 — axial view, 3 — umbilical view, 4, 5 — details of surface (with incipient pore-pits). **B** — *G. archeocompressa*, from the *S. triloculinoides* Subzone (*P. pseudobulloides* Zone), El Kef, Tunisia: 1 — spiral view, 2 — axial view, 3 — umbilical view, 4 — detail of surface. **C** — *G. archeocompressa*?, specimen transitional to *Pr. taurica*, from the *S. triloculinoides* Subzone (*P. pseudobulloides* Zone), El Kef, Tunisia: 1 — umbilical view, 2 — axial view, 3 — spiral view, 4 — detail of surface.

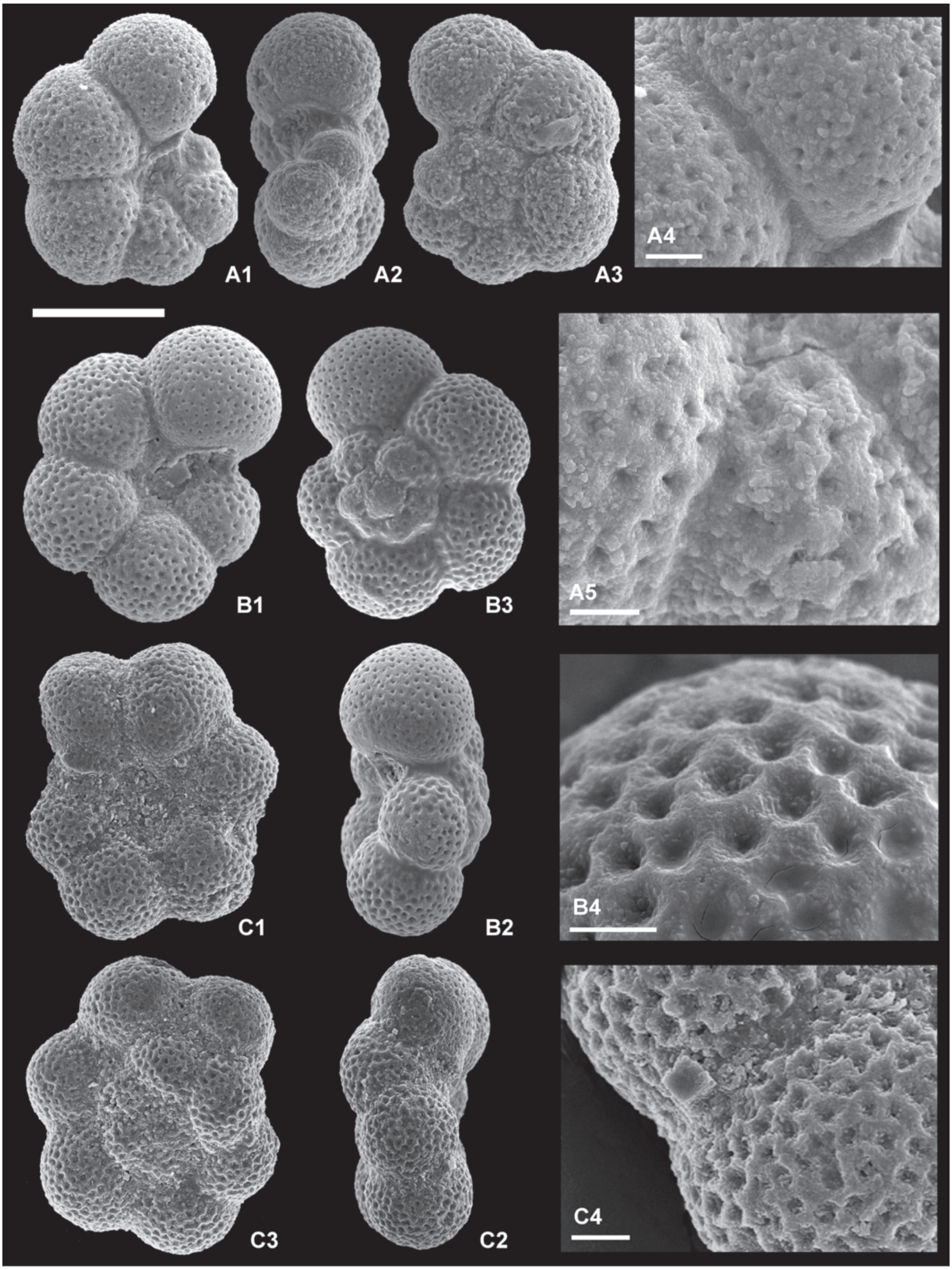

**Fig. 8.** SEM images of *Praemurica taurica* specimens and details of cancellate wall texture (scale bar = 100 μm; scale bar of details = 10 μm). **A** — *Pr. taurica*, specimen intermediate to *G. archeocompressa*, from the *S. triloculinoides* Subzone (*P. pseudobulloides* Zone), El Kef, Tunisia: 1 — umbilical view, 2 — axial view, 3 — spiral view, 4, 5 — details of surface (with incipient cancellate surface). **B** — *Pr. taurica*, from the *S. triloculinoides* Subzone (*P. pseudobulloides* Zone), El Kef, Tunisia: 1 — umbilical view, 2 — axial view, 3 — spiral view, 4 — detail of surface. **C** — *Pr. taurica*, from the *S. triloculinoides* Subzone (*P. pseudobulloides* Zone), El Kef, Tunisia: 1 — umbilical view, 2 — axial view, 3 — spiral view, 4 — detail of surface.

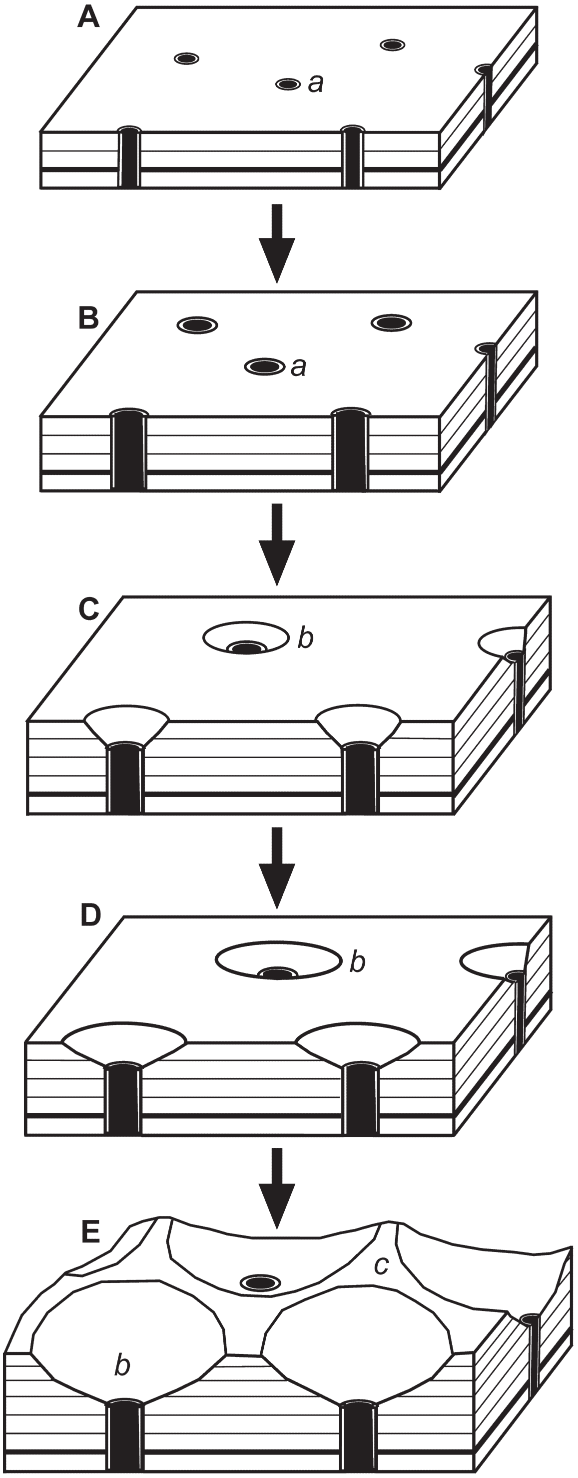

**Fig. 9.** Diagrams of wall textures illustrating the hypothetical evolution from the smooth wall of *Parvularugoglobigerina* to the pitted wall of *Globanomalina* and finally to the cancellate wall of *Praemurica*. **A** — smooth wall texture with tiny pore-murals (in typical *Parvularugoglobigerina*). **B** — smooth wall texture with larger pore-murals (in more evolved *Parvularugoglobigerina*). **C** — pitted wall texture with pore-pits (in ancestral *Globanomalina*). **D** — pitted wall texture with larger pore-pits (in typical *Globanomalina*). **E** — cancellate wall texture (in typical *Praemurica*). *a* — mural pores, *b* — pore-pits, *c* — interpore ridges.

both *Globanomalina* and *Praemurica*, namely *G. archeocompressa* and *Pr. taurica*, initially preserved a similar test shape of the ancestral *Pv. eugubina*.

Olsson et al. (1999) suggested *Hedbergella holmdelensis* as the ancestor of *Globanomalina* considering that *G. archeocompressa* exhibits similar features (mainly pitted smooth wall and the imperforated peripheral band). However, their illustrated specimens of *G. archeocompressa* (Fig. 3G to 3I) from Zone P0 at Millers Ferry (Alabama) do not fit well the diagnostic features of this species according to the original description of Blow (1979). These specimens might better be assigned to the earliest Danian *H. holmdelensis*, since they have smooth–pitted more or less pustulate walls, subconical chambers and planoconvex tests (compare with *H. holmdelensis* specimens of Fig. 3C to 3F). Blow (1979) described the chamber shape of *G. archeocompressa* as almost hemispherical, the latest chambers being subglobular (or slightly compressed) with little or no differentiation in the degree of inflation of their ventral and dorsal surfaces. Arenillas (1996) adopted Blow's concept, illustrating some *G. archeocompressa* specimens with essentially globular chambers in the last whorl similar to those of *Pv. eugubina*. Some of these morphotypes were probably considered by Blow (1979) and Olsson et al. (1999) as belonging to *G. planocompressa*.

Biostratigraphical, textural and morphological data seem to indicate that the evolutionary transition from *Parvularugoglobigerina* to *Globanomalina* is more plausible than from *Hedbergella*. High-resolution biostratigraphy in Tunisia and Spain suggested that the stratigraphic ranges of *Hedbergella* and *Globanomalina* do not overlap (Fig. 2), except for some questionable specimens of *Hedbergella* in the *Pv. eugubina* Zone, which were considered later as possibly reworked (Molina et al. 1996). The first *Globanomalina* specimens, assigned to *G. archeocompressa* by Arenillas (1996), exhibit subglobular — or slightly ovoid — chambers similar to *Pv. eugubina*. *Globanomalina* textural features seem to be more similar to those of *Hedbergella*, as proposed by Olsson et al. (1994, 1999), except for the presence of pustules in the latter.

According to our biostratigraphic data (Fig. 2), the order of appearance of the *Globanomalina* species was as follows: *G. archeocompressa* (base of *E. simplicissima* Subzone), *G. imitata* (lower part of *E. simplicissima* Subzone), *G. planocompressa* (base of *E. trivialis* Subzone) and *G. compressa* (base of *G. compressa* Subzone). The evolutionary relationships between them are not well known. We suggest two trends within early Danian *Globanomalina*: (1) one towards a reduction of the number of chambers (from *G. archeocompressa* to *G. imitata*); and (2) another one towards a compressed biconvex shape (from *G. archeocompressa* to *G. compressa*). Many specimens of these species also developed an imperforate peripheral band, especially among the more compressed species (*G. planocompressa*, *G. compressa*) and also in *G. archeocompressa* (Fig. 7B). This feature was considered by Olsson et al. (1992, 1999) to be directly derived from *H. holmdelensis*, but it could also be a character which reappeared in *Globanomalina*. Olsson et al. (1999) did not place *G. imitata* in the lower Danian, suggesting that it first occurred in the middle Danian (Zone P1c). Specimens

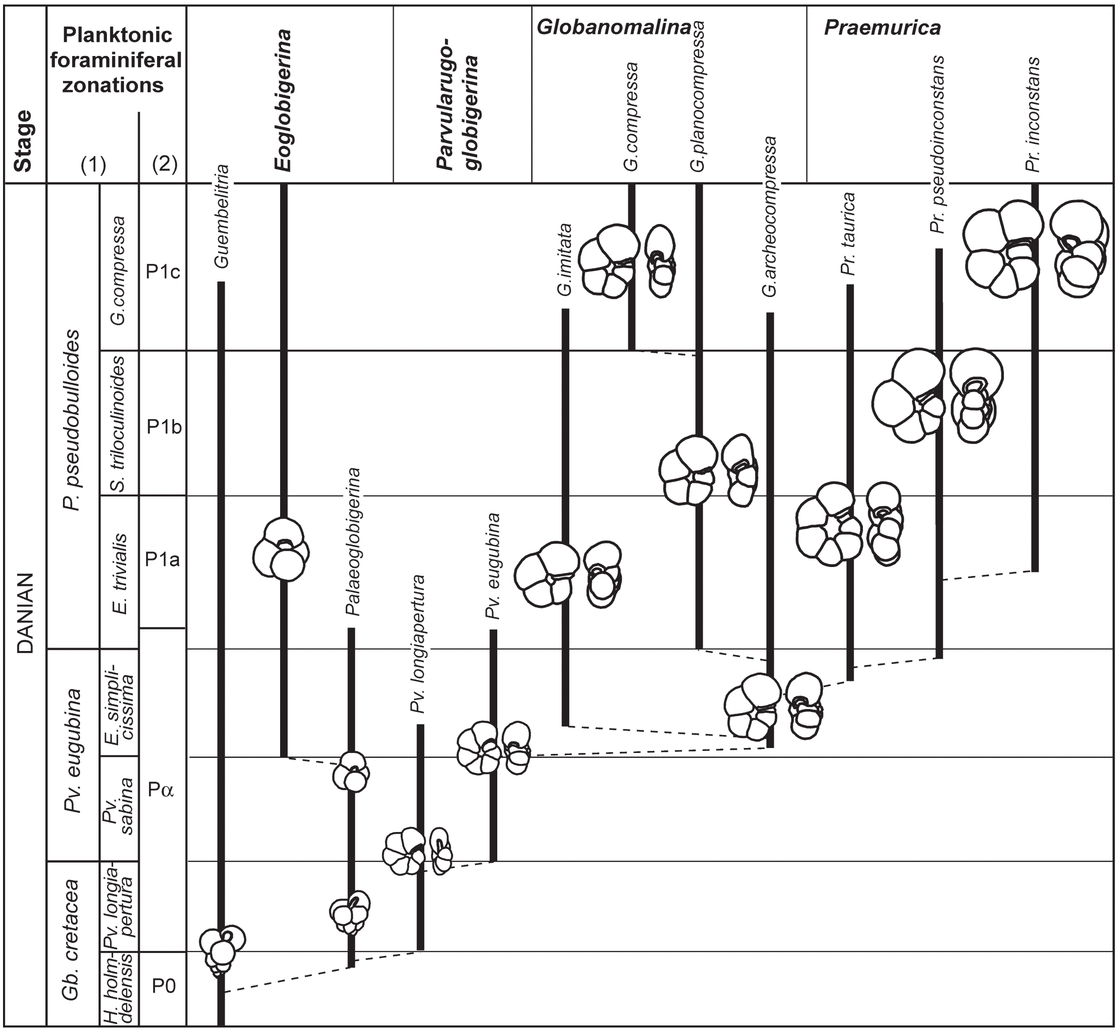

**Fig. 10.** Hypothetical phylogeny of the "non-spinose lineage" based on the textural and morphological characters. Phylogenetic relationships of *Guembelitria* Cushman, 1933, *Palaeoglobigerina* Arenillas, Arz & Náñez, 2007, *Eoglobigerina* Morozova, 1959 (oldest genus of the spinose lineage) and *Parvularugoglobigerina* are based on Arenillas et al. (2007, 2010).

assignable to this species, however, have been found in older stratigraphic levels (e.g. Fig. 4H–I), from the *E. simplicissima* Subzone, or upper part of Pa, according to Arenillas et al. (2004).

More uncertain is the evolutionary position of *G. planocompressa*, which seems to exhibit a morphological feature common to both trends. Its author, Shutskaya (1965), described the chambers of *G. planocompressa* with a broadly rounded periphery and a bluntly acute margin. Its quasi-planoconvex test seems to be similar to some specimens of *G. imitata*, suggesting an evolution from the latter to the first one. In addition, many *G. planocompressa* specimens, such as the holotype, have 4.5 chambers, suggesting that they derived from *G. imitata* by increasing again the number of chambers in the last whorl. However, we suggest that *G. planocompressa* is an intermediate step between *G. archeocompressa* and *G. compressa* (Fig. 10), leading to an ever more compressed test, because some *G. planocompressa* specimens (e.g. Fig. 4M) display shapes that already point to *G. compressa*. Identical phylogenetic relationships among these *Globanomalina* species were suggested by Apellániz et al. (2002).

Biostratigraphic data also seem to suggest that both *G. imitata* and *G. planocompressa* derived from *G. archeocompressa*, evolving in parallel to an increasingly compressed test. Consequently, the evolution of *G. compressa* from *G. planocompressa* is the most plausible hypothesis. Olsson et al. (1999) proposed a slightly different scenario, as they consider that both *G. planocompressa* and *G. compressa* derived independently from *G. archeocompressa* and evolved separately. These hypotheses are not contradictory, since the taxonomic concepts of *G. archeocompressa* and *G. planocompressa* of Olsson et al. (1999) differ from those of Arenillas (1996). They considered that *G. archeocompressa* had a planoconvex test and subconical chambers similar to *H. holmdelensis* (Fig. 3C–E), while *G. planocompressa* had subglobular to ovoid chambers, lumping morphotypes attributed to *G. archeocompressa* or *G. planocompressa* by Arenillas (1996) depending on the degree of compression of the latest chambers (see Appendix 1).

The evolution of the non-spinose cancellate lineage (*Praemurica*) shows an opposite trend to that of *Globanomalina*, namely the chambers became more and more inflated. The order of appearance of the *Praemurica* species is as follows: *Pr. taurica* (upper part of *E. simplicissima* Subzone), *Pr. pseudoinconstans* (top of *E. simplicissima* Subzone) and *Pr. inconstans* (middle part of *E. trivialis* Subzone). The second species displays a feature intermediate between *Pr. taurica* and *Pr. inconstans*. In *Pr. pseudoinconstans*, the last 2 or 3 chambers are strongly inflated, whereas the others are similar in size to those of *Pr. taurica*. In contrast, all chambers of the last whorl are inflated in *Pr. inconstans*. Olsson et al. (1999) suggested that the first appearance of *Pr. inconstans* is more modern, recorded at the base of Zone P1c. In contrast, we have identified abundant specimens of this species from the uppermost part of Zone P1a. This discrepancy is probably caused by different concepts of *Pr. inconstans* among authors (see Arenillas 2011). The separation of the different species of this lineage is somewhat arbitrary, since they are linked by transitional morphotypes and their original definitions are rather ambiguous. However, these discrepancies have no major phylogenetic implications. All authors agree that *Pr. taurica*, *Pr. pseudoinconstans* and *Pr. inconstans* represent successive evolutionary steps of the "non-spinose cancellate" lineage (Arenillas 1996; Olsson et al. 1999; Apellániz et al. 2002).

**Acknowledgments:** We thank Hanspeter Luterbacher, and an anonymous reviewer for helpful comments. We also thank Carolina Náñez for the previous review of the manuscript. This research was funded by the Spanish Ministerio de Ciencia e Innovación Projects CGL2011-23077 and CGL2011-22912 (both cofinanced by the European Regional Development Fund), and by the Aragonian Departamento de Educación y Ciencia (DGA group E05). The authors would like to acknowledge the use of the Servicio General de Apoyo a la Investigación — SAI, Universidad de Zaragoza. The authors are grateful to Richard Stephenson for improvement of the English text.

## References

Apellániz E., Orue-Etxebarría X. & Luterbacher H.P. 2002: Evolution of the early Paleocene planktonic foraminifera: a Basque point of view. *Neu. Jb. Geol. Paläont., Abh.* 225, 157–194.

Arenillas I. 1996: Planktic foraminifera of the Paleocene–lower Eocene: Systematic, biostratigraphy, chronostratigraphy and paleoceanography. *Ph.D. Thesis, Universidad de Zaragoza*, Spain, 1–513 (in Spanish).

Arenillas I. 2011: Paleoecological analysis of planktic foraminifera of the Danian-Selandian transition from Tethys and its taxonomic implications. *Rev. Española Micropaleont.* 43, 109–139 (in Spanish).

Arenillas I. & Arz J.A. 1996: Origin and phylogeny of the first planktic foraminiferal species of the basal Paleocene after the Cretaceous/Tertiary boundary. In: Perejón A. et al. (Eds.): *XII Bienal, Tomo extraordinario del 125 Aniversario de la Real Sociedad Española de Historia Natural*, Madrid, 267–27 (in Spanish).

Arenillas I. & Arz J.A. 2000: *Parvularugoglobigerina eugubina* type-sample at Ceselli (Italy): planktic foraminiferal assemblage and lowermost Danian biostratigraphic implications. *Riv. Ital. Paleont. Stratigr.* 106, 3, 379–390.

Arenillas I. & Arz J.A. 2013: Origin and evolution of the planktic foraminiferal Family Eoglobigerinidae Blow (1979) in the early Danian (Paleocene). *Rev. Mexicana de Ciencias Geol.,* 30, 1, 159–177.

Arenillas I. & Molina E. 1997: Quantitative analysis of the planktic foraminifera from Paleocene of Caravaca (Betic Cordillera): Biostratigraphy and faunal turnover. *Rev. Española Paleont.* 12, 2, 207–232 (in Spanish).

Arenillas I., Arz J.A. & Molina E. 2004: A new high-resolution planktic foraminiferal zonation and subzonation for the lower Danian. *Lethaia* 37, 79–95.

Arenillas I., Arz J.A. & Náñez C. 2007: Morphology, biometry and taxonomy of the lowermost Danian planktonic foraminifera: *Palaeoglobigerina* n. gen. *Rev. Española Paleont.* 22, 21–62 (in Spanish).

Arenillas I., Arz J.A. & Náñez C. 2010: Diversity and evolution of wall textures in guembelitriids (planktic foraminifera) across the Cretaceous-Paleogene transition. *Rev. Española Paleont.* 25, 2, 87–105 (in Spanish).

Arenillas I., Arz J.A. & Náñez C. 2012: Smooth and rugose wall textures in earliest Danian trochospiral planktic foraminifera from Tunisia. *Neu. Jb. Geol. Paläont., Abh.* 266, 123–142.

Berggren W.A. 1962: Some planktonic foraminifera from the Maestrichtian and type Danian stages of Southern Scandinavia. *Stockholm Contr. Geol.* 9, 1–18.

Berggren W.A. 1977: Atlas of Paleogene planktonic foraminifera. Some species of the genera *Subbotina, Planorotalites, Morozovella, Acarinina* and *Truncorotaloides*. In: Ramsay A.T.S. (Ed.): Oceanic micropaleontology. *Academic Press*, London, 250–299.

Berggren W.A. & Pearson P.N. 2005: A revised tropical to subtropical Paleogene planktonic foraminiferal zonation. *J. Foram. Res.* 35, 279–298.

Blow W.H. 1979: The Cainozoic Globigerinidae. A study of the morphology, taxonomy, evolutionary relationship and the stratigraphical distribution of some Globigerinidae (mainly Globigerinacea). *E.J. Brill*, Leiden, Netherlands 3, 1–1413.

Brotzen F. & Pozaryska T. 1961: Foraminifères du Paléocène et de l'Éocène inférieur en Pologne septentrionale; remarques paléogéographiques. *Rev. Micropaléont.* 4, 155–166.

Brönnimann P. & Brown N.K. Jr. 1958: *Hedbergella*, a new name for a Cretaceous planktonic foraminiferal genus. *J. Washington Acad. Sci.* 48, 15–17.

Cushman J.A. 1927: An outline of a re-classification of the foraminifera. *Contr. Cushman Laboratory Foram. Res.* 3, 1–105.

Cushman J.A. 1933: Some new foraminiferal genera. *Contr. Cushman Laboratory Foram. Res.* 9, 32–38.

Cushman J.A. & Bermúdez P.J. 1949: Some Cuban species of *Globorotalia*. *Contr. Cushman Laboratory Foram. Res.* 25, 26–45.

D'Hondt S.L. 1991: Phylogenetic and stratigraphic analysis of earliest Paleocene biserial and triserial planktonic foraminifera. *J. Foram. Res.* 21, 168–181.

Georgescu M.D. 2007: Taxonomic re-evaluation of the Late Cretaceous serial planktonic foraminifer *Gümbelina punctulata* Cushman, 1938 and related species. *Rev. Española Micropaleont.* 39, 155–167.

Georgescu M.D. 2009a: Taxonomic revision and evolutionary classification of the biserial Cretaceous planktic foraminiferal genus *Laeviheterohelix* Nederbragt, 1991. *Rev. Mexicana Ciencias Geol.* 26, 315–334.

Georgescu M.D. 2009b: On the origins of Superfamily Heterohelicacea Cushman, 1927 and the polyphyletic nature of planktic foraminifera. *Rev. Española Micropaleont.* 41, 107–144.

Haque A.F.M.M. 1956: The smaller Foraminifera of the Ranikot and the Laki of the Nammal Gorge, Salt Range. *Paleontologica Pakistanica, Geol. Surv. Pakistan* 1, 1–300.

Hofker J. 1978: Analysis of a large succession of samples through the Upper Maastrichtian and the Lower Tertiary of Drill Hole 47.2, Shatsky Rise, Pacific, Deep Sea Drilling Project. *J. Foram. Res.* 8, 46–75.

Liu C. & Olsson R.K. 1992: Evolutionary radiation of microperforate planktonic foraminifera following the K/T mass extinction event. *J. Foram. Res.* 22, 328–346.

Liu C. & Olsson R.K. 1994: On the origin of Danian normal perforate planktonic foraminifera from *Hedbergella*. *J. Foram. Res.* 24, 61–74.

Loeblich A.R. Jr. & Tappan H. 1961: Suprageneric classification of the Rhizopodea. *Micropaleontology* 35, 245–330.

Loeblich A.R. Jr. & Tappan H. 1984: Suprageneric classification of the Foraminiferida (Protozoa). *Micropaleontology* 30, 1–70.

Loeblich A.R. Jr. & Tappan H. 1987: Foraminiferal genera and their classification. *Van Nostrand Reinhold Company*, New York, 2, 1–970.

Luterbacher H.P. & Premoli Silva I. 1964: Biostratigraphy of the Cretaceous-Tertiary boundary in Central Apennines. *Riv. Ital. Paleont. Stratigr.* 70, 67–128 (in Italian).

MacLeod N. 1993: The Maastrichtian-Danian radiation of triserial and biserial planktic foraminifera: Testing phylogenetic and adaptational hypotheses in the (micro) fossil record. *Mar. Micropaleont.* 21, 47–100.

Molina E., Alegret L., Arenillas I., Arz J.A., Gallala N., Hardenbol J., von Salis K., Steurbaut E., Vandenberghe N. & Zaghbib-Turki D. 2006: The global stratotype section and point of the Danian Stage (Paleocene, Paleogene, “Tertiary”, Cenozoic) at El Kef, Tunisia: original definition and revision. *Episodes* 29, 263–278.

Montanaro Gallitelli E. 1957: A revision of the foraminiferal Family Heterohelicidae. *Stud. Foram., United States Nat. Mus. Bull.* 215, 133–154.

Morozova V.G. 1959: Stratigraphy of the Danian-Montian deposits of the Crimea according to the foraminifera. *Doklady Akad. Nauk SSSR* 124, 1113–1116 (in Russian).

Morozova V.G. 1961: Planktonic foraminifera of Danian-Montian of the southern USSR. *Paleontologicheskiy Zhurnal* 1, 8–19 (in Russian).

Nederbragt A.J. 1991: Late Cretaceous biostratigraphy and development of Heterohelicidae (planktic foraminifera). *Micropaleontology* 37, 329–372.

Olsson R.K. 1960: Foraminifera of latest Cretaceous and earliest Tertiary age in the New Jersey Coastal Plain. *J. Paleontology* 34, 1–58.

Olsson R.K. 1963: Latest Cretaceous and earliest Tertiary stratigraphy of New Jersey Coastal Plain. *Bull. Amer. Assoc. Petrol. Geol.* 47, 643–665.

Olsson R.K. 1964: Late Cretaceous planktonic foraminifera from New Jersey and Delaware. *Micropaleontology* 10, 157–188.

Olsson R.K. 1970: Planktonic foraminifera from base of Tertiary Millers Ferry, Alabama. *J. Paleontology* 44, 598–604.

Olsson R.K., Hemleben C., Berggren W.A. & Liu C. 1992: Wall texture classification of planktonic foraminifera genera in the Lower Danian. *J. Foram. Res.* 22, 195–213.

Olsson R.K., Hemleben C., Berggren W.A. & Huber B.T. 1999: Atlas of Paleocene Planktonic Foraminifera. *Smithsonian Contr. Paleobiol.* 85, 1–252.

Plummer H.J. 1927: Foraminifera of the Midway formation in Texas. *Bull. Univ. Texas Bureau Econ. Geol. and Technology* 2644, 1–206.

Premoli Silva I. 1977: The earliest Tertiary *Globigerina eugubina* zone: Paleontological significance and geographical distribution. In: *Memorias del Segundo Congreso Latinomericano de Geología* 3, *Spec. Publ.* 7, 1541–1555.

Sexton P.F., Wilson P.A. & Pearson P.N. 2006: Microstructural and geochemical perspectives on planktic foraminiferal preservation: “Glassy” versus “Frosty”. *Geochemistry, Geophysics, Geosystems* 7, Q12P19.

Shutskaya E.K. 1965: Phylogenetic relations of the species of the group of *Globorotalia compressa* Plummer in Danian time and the Paleocene epoch. *Akad. Nauk SSSR, Voprosy Mikropaleont.* 9, 173–188 (in Russian).

Smit J. 1982: Extinction and evolution of planktonic foraminifera after a major impact at the Cretaceous/Tertiary boundary. *Geol. Soc. Amer., Spec. Pap.* 190, 329–352.

Subbotina N.N. 1953: Fossil Foraminifera of the USSR. Globigerinidae, Hantkeninidae and Globorotalidae. *Trudy Vsesoyuzhnyy Neftyanoy Nauchno-issledovatel’skiy Geologo-razvedochnogo Instituta (VNIGRI), Mikrofauna SSSR Sbornik* 6, 76, 1–296 (in Russian).

## Appendix

Diagnostic characters of the early Danian species of *Hedbergella* Brönnimann & Brown, 1958, *Parvularugoglobigerina* Hofker, 1978, *Globanomalina* Haque, 1956 and *Praemurica* Olsson, Berggren & Liu, 1992 mentioned in the text (Arenillas 1996, modified):

*Hedbergella monmouthensis* Olsson (1960): Trochospiral test, 5–6 hemispherical to subconical chambers in the first whorl, 4–5 subglobular chambers in the last whorl, moderate rate of chamber size increase, axial periphery rounded, aperture umbilical-extraumbilical, with thick lip, wall surface smooth, pustulate (Fig. 3A–B).

*Hedbergella holmdelensis* Olsson (1964): Trochospiral test, 5–6 hemispherical chambers in the first whorl, 5–6.5 moderately compressed hemispherical to subconical chambers in the last whorl, low rate of chamber size increase, axial periphery slightly angular, aperture umbilical-extraumbilical, with thick lip, wall surface smooth, pustulate (Fig. 3C–I).

*Parvularugoglobigerina longiapertura* (Blow 1978): Small trochospiral test, with low spire, 4–4.5 moderately compressed ovate to subglobular in the first whorl, 5–6.5 slightly to moderately compressed ovate chambers in the last whorl, low rate of chamber size increase, aperture extending up into the apertural chamber face, high arch, with lip thin, wall surface smooth or secondarily granular (Fig. 3J–K).

*Parvularugoglobigerina eugubina* (Luterbacher & Premoli Silva 1964): Small trochospiral test, with low spire, 4–4.5 subglobular chambers in the first whorl, 5–6.5 subglobular chambers in the last whorl, low rate of chamber size increase, aperture, umbilical-extraumbilical, low arch, with lip thin, wall surface smooth or secondarily granular (Figs. 3L–O, 6A–D).

*Globanomalina archeocompressa* (Blow 1979): Trochospiral test, with low spire, 4–4.5 subglobular chambers in the first whorl, 5.5–6.5 subglobular to slightly ovoid chambers in the last whorl, low rate of chamber size increase, aperture umbilical-extraumbilical, low arch, with lip moderately thick, wall surface pitted (Figs. 4A–F, 7A–C).

*Globanomalina imitata* (Subbotina 1953): Trochospiral test, with low spire, 4–4.5 subglobular to hemispherical chambers in the first whorl, 4 subglobular to hemispherical to planoconvex chambers in the last whorl, moderate rate of chamber size increase, aperture umbilical-extraumbilical, with lip moderately thick, wall surface pitted (Fig. 4G–J).

*Globanomalina planocompressa* (Shutskaya 1965): Trochospiral test, with flat spire, 4–4.5 hemispherical chambers in the first whorl, 4.5–5 ovoid to hemispherical chambers in the last whorl, low to moderate rate of chamber size increase, aperture umbilical-extraumbilical, with lip thick, wall surface pitted (Fig. 4K–N).

*Globanomalina compressa* (Plummer 1927): Trochospiral test, biconvex, 5–6 moderately compressed ovate chambers in the first whorl, 4.5–5.5 slightly to moderately compressed ovate chambers in the last whorl, low to moderate rate of chamber size increase, axial periphery rounded to slightly angular, with imperforate margin with poor developed or absent, aperture umbilical-extraumbilical, with lip thick, wall surface pitted to smooth (Fig. 5A–B).

*Praemurica taurica* (Morozova 1961): Trochospiral test, with low to flat spire, 5–6 subglobular chambers in the first whorl, 5.5–7 subglobular chambers in the last whorl, low rate of chamber size increase, aperture umbilical-extraumbilical, with lip thick, wall surface cancellate (Figs. 5C–D, 8A–C).

*Praemurica pseudoinconstans* (Blow 1979): Trochospiral test, with low to flat spire, 5–6 subglobular chambers in the first whorl, 5–5.5 subglobular chambers in the last whorl (2 or 3 last chambers very inflated), moderate to high rate of chamber size increase, aperture umbilical-extraumbilical, with lip thick, wall surface cancellate (Fig. 5E–G).

*Praemurica inconstans* (Subbotina 1953): Trochospiral test, with low to flat spire, 5–6 subglobular chambers in the first whorl, 5–6.5 inflated subglobular chambers in the last whorl, low to moderate rate of chamber size increase, aperture umbilical-extraumbilical, with lip thick, wall surface cancellate (Fig. 5H–L).