

# Smooth and rugose wall textures in earliest Danian trochospiral planktic foraminifera from Tunisia

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With 8 figures

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**Abstract:** New scanning electron microscopy (SEM) photographs of planktic foraminiferal specimens from Tunisian sections (El Kef, Aïn Settara, Elles) have revealed the occurrence of two lineages of primitive trochospiral species in the lowermost Danian. The first lineage to appear, which evolves at the P0–Pa transition, exhibits a smooth and/or granular wall texture (with pore-murals), and its species were attributed to the parvularugoglobigerinids (*Parvularugoglobigerina* and *Palaeoglobigerina*). The second to appear at the Pa–P1 transition has a rugose wall texture (with rugosities and isolated irregular pore-mounds) and is herein assigned to the new genus *Trochoguembelitra*. Both lineages co-occur in the upper part of Pa (middle-upper part of *Eoglobigerina simplicissima* Subzone), containing quasi-homeomorph species – pseudocryptic under stereomicroscopy – only differentiated under SEM by their wall texture (e.g., *Palaeoglobigerina alticonusa* vs *Trochoguembelitra alabamensis*). The data at our disposal suggest *Trochoguembelitra* derived from triserial *Guembelitra* and its species evolved in parallel with the parvularugoglobigerinids in the earliest Danian.

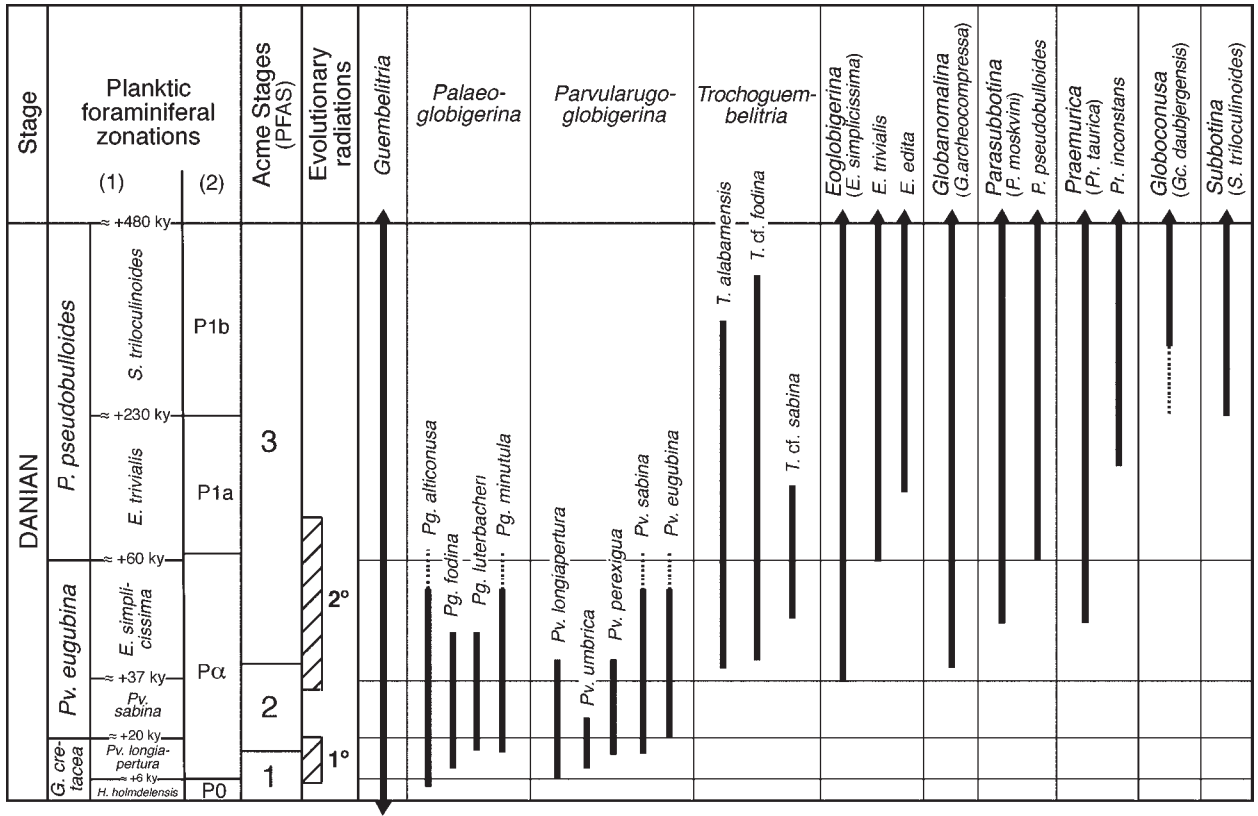
**Key words:** Planktic foraminifera, guembelitrids, parvularugoglobigerinids, new genus.

## 1. Introduction

An “explosive” evolutionary radiation of new trochospiral and biserial planktic foraminifera has been widely documented after the greatest mass extinction in the planktic foraminiferal history, the Cretaceous/Paleogene (K/Pg) boundary event (LUTERBACHER & PREMOLI SILVA 1964; SMIT 1982; CANUDO et al. 1991; LIU & OLSSON 1992; MOLINA et al. 1998). The most probable common ancestor of the first Cenozoic taxa is *Guembelitra* CUSHMAN, 1933, the only genus whose survival from the K/Pg extinction event has been clearly proven (SMIT 1982; ARZ et al. 1999; OLSSON et al. 1999; ARENILLAS et al. 2000a). *Guembelitra* bloomed immedi-

ately after the K/Pg boundary, during approximately 10–15 ky, and significantly diversified during the early Danian. This episode was recorded as an acme-stage called planktic foraminiferal acme-stage 1 (PFAS1) by ARENILLAS et al. (2006).

The earliest Danian planktic foraminifera evolutionary radiation occurred in two pulses (ARENILLAS et al. 2000b, 2010; Fig. 1): the first occurring around 5–20 ky after the K/Pg boundary (transition between the Zones P0 and Pa of BERGGREN & PEARSON 2005), and the second around 35–80 ky (transition between the Zones Pa and P1a of BERGGREN & PEARSON 2005). Small trochospiral species of *Palaeoglobigerina* ARENILLAS, ARZ & NÁJUEZ, 2007, and *Parvularugoglo-*



**Fig. 1.** Biostratigraphical ranges of *Palaeoglobigerina*, *Parvularugoglobigerina* and *Trochoguembelitra* species in Tunisia sections (based mainly on the El Kef stratotype), compared with those of triserial *Guembelitra* and other lowermost Danian trochospiral planktic foraminiferal taxa. Planktic foraminiferal zonation of ARENILLAS et al. (2004) (1), and BERGGREN & PEARSON (2005) (2). Stratigraphic position and approximated calibration of the acme-stages PFAS and evolutionary radiation intervals by ARENILLAS et al. (2006, 2010). Dotted lines: stratigraphic distribution not supported by SEM-photographed specimens from Tunisian sections.

*bigerina* HOFKER, 1978, as well as biserial species of *Woodringina* LOEBLICH & TAPPAN, 1957, evolved during the earliest evolutionary pulse. The first two genera dominated the planktic foraminiferal assemblages for about 30 ky following PFAS1, being recorded as an acme-stage called PFAS2 by ARENILLAS et al. 2006. In the second pulse, other more modern genera evolved, including the biserial *Chiloguembelina* LOEBLICH & TAPPAN, 1956; pitted and/or cancellate trochospiral *Globanomalina* HAQUE, 1956; *Praemurica* OLSSON, HEMLEBEN, BERGGREN & LIU, 1992; *Eoglobigerina* MOROZOVA, 1959; *Parasubbotina* OLSSON, HEMLEBEN, BERGGREN & LIU, 1992; and probably the pustulate trochospiral *Globoconusa* KHALILOV, 1956. In addition, ARENILLAS et al. (2010) suggested that trochos-

piral taxa with a rugose wall texture first appeared or, at least, increased suddenly in abundance during this last evolutionary pulse. This bioevent occurred approximately when *Woodringina* and *Chiloguembelina* began to dominate the planktic foraminiferal assemblages, starting the acme-episode called PFAS3 (ARENILLAS et al. 2006).

The small trochospiral species of the lowermost Danian are often included within the genus *Parvularugoglobigerina*, whose type species *Parvularugoglobigerina eugubina* (LUTERBACHER & PREMOLI SILVA, 1964) is used as index species in the biochronological scales (e.g., TOUMARKINE & LUTERBACHER, 1985). Other trochospiral genera proposed for this time interval were *Postrugoglobigerina* SALAJ, 1986 (today consid-

ered as a junior synonym of *Parvularugoglobigerina*), and *Palaeoglobigerina* ARENILLAS, ARZ & NÁÑEZ, 2007. However, none of them present the characteristics of the rugose trochospiral morphotypes described here, which were already documented by LIU & OLSSON (1992, 1994), and OLSSON et al. (1992, 1999). In the lowermost Danian, ARENILLAS et al. (2010) demonstrated the occurrence of two trochospiral lineages including species which were probably pseudocryptic (i.e., cryptic species only *a posteriori* distinguished as morphospecies by small textural or morphological details). The rugose species appeared later than the smooth species, with textural features that do not seem to fit in with those of *Parvularugoglobigerina* or *Palaeoglobigerina* (ARENILLAS et al. 2010).

Herein we report the occurrences of both lineages in Tunisia (mainly based on the El Kef section), and define a new genus, *Trochoguembelitra*, to include species of the rugose trochospiral lineage. Such SEM-based, high-resolution study helps in understanding the evolution and phylogeny of the first Cenozoic trochospiral planktic foraminiferal taxa, and its impact on the lowermost Danian taxonomy and biostratigraphy.

## 2. Material and methods

We revised in detail the Tunisian sections of El Kef, Aïn Settara and Elles, preferably the former for its continuous and widely expanded record, and the good preservation of its planktic foraminifera. The El Kef section is the K/Pg boundary stratotype, and the other two sections have been proposed as K/Pg auxiliary sections (MOLINA et al. 2006, 2009). We conducted high-resolution sampling of the lowermost Danian, quantitatively analysing 25 samples of El Kef, 21 of Aïn Settara and 24 of Elles. The rock samples were disaggregated in water with diluted H<sub>2</sub>O<sub>2</sub> (10%), washed through a 63- $\mu$ m sieve, then oven-dried at 50 °C. Specimens were picked from the residues and selected for scanning electron microscopy using a JEOL JSM 6400 SEM at the Electron Microscopy Service of the Universidad de Zaragoza (Spain). Over 1000 SEM-photographs were taken of 291 specimens from Tunisian sections, including the different test views and surface details.

The planktic foraminiferal zonations for the lower Danian shown in Fig. 1 are those of ARENILLAS et al. (2004) and BERGGREN & PEARSON (2005). The species are biostratigraphically distributed mainly across the *Guembelitra cretacea*, *Parvularugoglobigerina eugubina* and *Parasubbotina pseudobulloides* Zones.

## 3. Discussion

### 3.1. Wall texture of lowermost Danian trochospiral planktic foraminifera

Based on detailed analyses of the K-Pg transition guembeltriids, ARENILLAS et al. (2010) suggested three major wall textures for the lowermost Danian trochospiral specimens: (1) smooth (Fig. 2A, B), with tiny pore-murals; (2) jagged-granular (Fig. 2C), showing minute sutured calcite crystallites similar to small pustules; (3) rugose (Fig. 2D, E), with pore-mounds coalescing to form rugosities (Fig. 2D) and isolated irregular pore-mounds (papillae with pores decentred); the rugosities and papillae tend to be imperforate (Fig. 2E), and some papillae are sharp.

These wall textures differ from those identified in similar Cretaceous trochospiral *Guembelitra* (generally pore-mounded, Fig. 2F); *Rugoglobigerina* BRÖNNIMANN, 1952 (rugose, with costae or aligned rugosities, Fig. 2G); and *Hedbergella* BRÖNNIMANN & BROWN, 1958 (smooth to pustulate, with pore-pits and abundant pustules, Fig. 2H); as well as in Danian *Globoconusa* (pustulate, usually with sharp pustules, Fig. 2J); *Globanomalina* (smooth, with pore-pits = pitted, Fig. 2K); *Eoglobigerina-Parasubbotina* (spinose cancellate, Fig. 2L); and *Praemurica* (non spinose cancellate, Fig. 2M).

**Parvularugoglobigerinid wall texture:** The trochospiral genera *Palaeoglobigerina* and *Parvularugoglobigerina* belong to the informal parvularugoglobigerinid group. *Parvularugoglobigerina* is characterized here by a smooth wall texture with pore-murals of small diameter < 1  $\mu$ m (Figs. 3-4). The smooth surface is often covered by a granular crust (Figs. 3L, 4D, F), so, *Parvularugoglobigerina* usually presents a jagged-granular wall texture with minute sutured calcite crystallites. For the definition of the genus *Parvularugoglobigerina*, HOFKER (1978) indicated that its wall has small pustules and fine pipelike pores (i.e., granular wall with tiny pore-murals). However, he also proposed that the pustules are often found in rows as in Cretaceous *Rugoglobigerina*, causing some confusion. TOUMARKINE & LUTERBACHER (1985) pointed out that the types of *Pv. eugubina* do not show the characteristics considered by HOFKER for *Parvularugoglobigerina*. The *Pv. eugubina* wall textures initially described as rugose, rough or finely pustulate (LUTERBACHER & PREMOLI SILVA 1964; HOFKER 1978) were later attributed to fossildiagenetic recrystallization (SMIT 1982; LOEBLICH & TAPPAN 1987; LIU & OLSSON 1992; OLS-

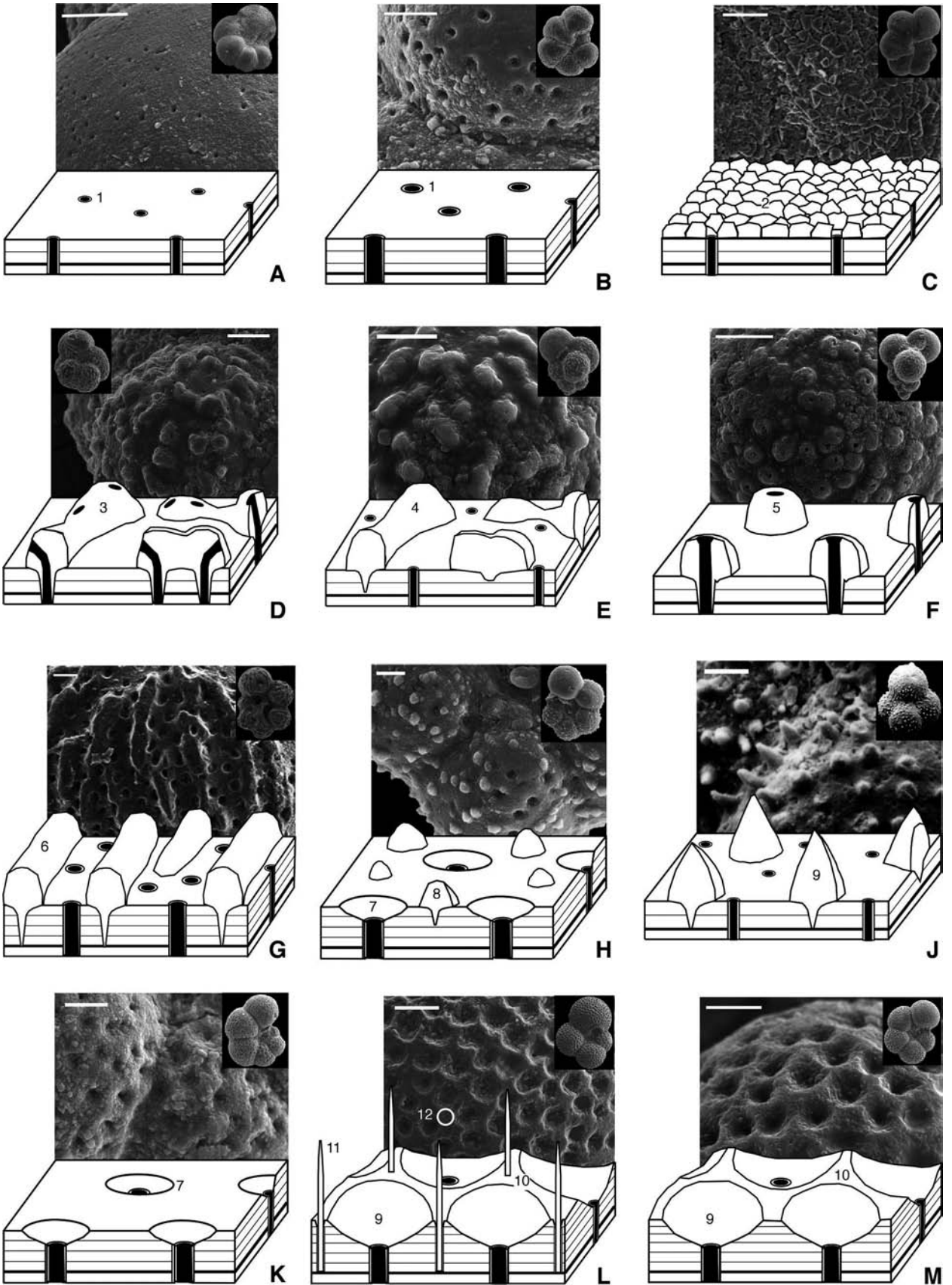


Fig. 2.

SON et al. 1999). Without ruling out the recrystallization processes (“frosty” specimens according to the terminology of SEXTON et al. 2006), ARENILLAS et al. (2010) suggested that the granular wall is related to gametogenetic calcification, i.e., to a secondary outer calcite crust covering the normal smooth wall. BLOW (1979) showed well-preserved specimens of *Parvularugoglobigerina* and *Palaeoglobigerina* (classified as *Globorotalia* (*Turborotalia*) and *Eoglobigerina* respectively) with a granular wall. Smooth and/or granular specimens were later reported by BRINKHUIS & ZACHARIASSE (1988), KELLER (1988), KELLER et al. (1995) and LI et al. (1995) among many others. According to ARENILLAS et al. (2007), *Parvularugoglobigerina* includes *Pv. longiapertura* (BLOW, 1979), *Pv. umbrica* (LUTERBACHER & PREMOLI SILVA, 1964), *Pv. perexigua* LI, MCGOWRAN & BOERSMA, 1995, *Pv. sabina* (LUTERBACHER & PREMOLI SILVA, 1964), *Pv. eugubina* (LUTERBACHER & PREMOLI SILVA, 1964), and *Pv. cf. hemisphaerica* (sensu BLOW 1979).

*Palaeoglobigerina*, whose type species is *Pg. fodina* (BLOW, 1979), has a wall texture identical to that of *Parvularugoglobigerina*. ARENILLAS et al. (2007) separated this taxon from *Parvularugoglobigerina* to group the species previously classified as primitive *Eoglobigerina* or *Globoconusa* (BLOW 1979; CANUDO et al. 1991; KELLER 1988; KELLER et al. 1995; ARENILLAS & ARZ 2000). It includes the most primitive trochospiral species of the Paleogene, and differs from *Parvularugoglobigerina* for its fewer number of chambers, both in the first spire whorl (3.5 to 4 instead of 4 to 4.5) and in the last (3 to 4 instead of 4 to 9). According to ARENILLAS et al. (2007), *Palaeoglobigerina*

includes *Pg. alticonusa* (LI, MCGOWRAN & BOERSMA, 1995), *Pg. fodina* (BLOW, 1979), *Pg. minutula* (LUTERBACHER & PREMOLI SILVA, 1964), *Pg. luterbacheri* ARENILLAS & ARZ, 2007, and possibly *Pg.? extensa* (BLOW, 1979).

***Postrugoglobigerina* controversy:** This genus has usually been considered a junior synonym of *Parvularugoglobigerina* (OLSSON et al. 1999; ARENILLAS & ARZ 2000). SALAJ (1986) described two *Postrugoglobigerina* species in El Kef: *Pt. haryana* (type-species) and *Pt. praedaubjergensis*, and described their wall texture as rugose, i.e., with abundant pustules often pierced by pores. In addition, SALAJ (1986) considered that *Pt. praedaubjergensis* was the ancestor of *Globoconusa daubjergensis* BRÖNNIMANN, 1953. For these reasons, these taxa could have been good candidates to name the specimens with rugose wall, such as had already been suggested by ARENILLAS et al. (2010). Unfortunately, original illustrations are inadequate and the holotypes and type material of both *Postrugoglobigerina* species have been lost (STEFAN JOZSA, pers. comm.), and these taxa must be considered a *nomen dubium non conservandum*.

Moreover, the taxonomic interpretation of *Postrugoglobigerina* raised several questions mainly related to its wall texture and stratigraphic position in El Kef. Although he described the wall texture as rugose, considering it apparently derived from that of Cretaceous *Rugoglobigerina*, most of the *Postrugoglobigerina* specimens illustrated by SALAJ (1986) exhibit a smooth and/or granular wall similar to that of parvularugoglobigerinid species (ARENILLAS et al. 2007, 2010). The

**Fig. 2.** SEM images and schemes of the wall textures analyzed in this paper (scale bars of detail SEM-micrographs = 10 µm). **A-B** – Smooth wall texture, two pore-sizes: A, < 1 µm, from specimen of *Parvularugoglobigerina eugubina* (LUTERBACHER & PREMOLI SILVA, 1964); B, 1–4 µm, from specimen of *Parvularugoglobigerina eugubina* (LUTERBACHER & PREMOLI SILVA, 1964), transitional to *G. archeocompressa* (BLOW, 1979). **C** – jagged-granular wall texture, from specimen of *Parvularugoglobigerina eugubina* (LUTERBACHER & PREMOLI SILVA, 1964). **D-E** – Rugose wall texture; D, rugosities and/or papillae perforate, from specimen of *Trochoguembeltria cf. sabina* (LUTERBACHER & PREMOLI SILVA, 1964); E, rugosities and/or papillae imperforate, from specimen of *Trochoguembeltria cf. fodina* (BLOW, 1979). **F** – Pore-mounded wall texture, from specimen of *Guembeltria cretacea* CUSHMAN. **G** – Costellae-rugose wall texture, from specimen of *Rugoglobigerina hexacamerata* BRÖNNIMANN, 1952. **H** – Smooth to pustulate wall texture, from specimen of *Hedbergella holmdelensis* OLSSON, 1964. **J** – Pustulate wall texture, from specimen of *Globoconusa daubjergensis* BRÖNNIMANN 1953. **K** – smooth wall texture, from specimen of *Globoconusa daubjergensis* (BLOW, 1979). **L** – Spinose cancellate wall texture, from specimen of *Eoglobigerina simplicissima* BLOW 1979. **M** – Non-spinose cancellate wall texture, from specimen of *Praemurica taurica* MOROZOVA, 1961. (1) pore-murals; (2); minute sutured calcite crystallites; (3) perforate rugosities; (4) imperforate rugosities; (5) pore-mounds or perforate papillae; (6) costae or aligned rugosities; (7) pore-pits; (8) blunt pustules; (9) sharp pustules; (10) interpore ridges; (11) spines; (12) spine holes.

holotypes for both species are surely juvenile specimens (with sizes < 85 µm). Illustrations are poor, and the wall texture and even coiling mode are not clear, preventing an unambiguous identification. In addition, the stratigraphic position proposed by SALAJ (1986) for *Postrugoglobigerina* suggests another more plausible interpretation. He identified both *Postrugoglobigerina* species at the top of his *Pt. praedaubjergensis* Zone in El Kef, i.e., first biozone of the Danian (approximately equivalent to the *H. holmdelensis* Subzone of ARENILLAS et al. 2004 or P0 of BERGGREN & PEARSON 2005). However, we have found no trochospiral specimens with rugose wall in Zone P0 of the Tunisian sections such as El Kef; on the contrary, scarce specimens of smooth and/or granular wall assignable to *Palaeoglobigerina*, as well as pore-mounded wall with smoothed pore-mounds assignable to anomalous *Guembelitra* are identified (ARENILLAS et al. 2010). OLSSON et al. (1999) and ARENILLAS et al. (2007) considered that, since *Pt. haryana* is a junior synonym of *Pv. eugubina* (according to the first) or of *Pv. sabina* (according to the latter), *Postrugoglobigerina* is a junior synonym of *Parvularugoglobigerina*. Given its stratigraphic position and wall texture (smoothed pore-mounded), another more accurate interpretation would be that the *Pt. haryana* holotype was a juvenile specimen of irregular, multiseriate or aberrant *Guembelitra*, frequent in Zone P0 (COCCIONI & LUCIANI 2006).

**Early Danian rugose wall texture:** LIU & OLSSON (1992) and OLSSON et al. (1999) included specimens

with both wall texture types, smooth-granular and rugose, in *Parvularugoglobigerina*. They indicated that the well-preserved, pristine parvularugoglobigerinids exhibit a pore-mounded surface, and illustrated this with rugose trochospiral specimens from the Pa and Pla of Millers Ferry, Alabama (Fig. 5A-C). They also indicated that the recrystallization obscures the normal wall texture of these taxa. According to OLSSON et al. (1999), *Parvularugoglobigerina* includes three species: *Pv. eugubina* (for specimens with low to moderate spire height, more than 4 chambers in the last whorl and elongate aperture), *Pv. alabamensis* (for specimens with high spire, semicircular umbilical aperture and 3.5 to 4 chambers in the last whorl), and *Pv. extensa* (for specimens with moderately high spire, aperture often elongate and asymmetrical and 3.5 to 4 chambers in the last whorl). This taxonomic interpretation is consistent with pore-mounded *Guembelitra* as ancestor of the parvularugoglobigerinid group.

However, parvularugoglobigerinids identified in horizons equivalent to the top of P0 and the lower part of Pa from the Tunisian sections exhibit only a smooth and/or granular wall (ARENILLAS et al. 2007; ARZ & ARENILLAS 2007), as shown in Figs. 3-4. This wall texture is similar to that described by STAINFORTH et al. (1975) and BLOW (1979), and is widely reported in the lowermost Danian (KELLER 1988; KELLER et al. 1995; LI et al. 1995; MOLINA et al. 1998; ARENILLAS et al. 2000a, b). After analyzing the holotypes of *Pv. eugubina*, *Pv. sabina*, *Pv. umbrica*, and *Pg. minutula* in the Naturhistorisches Museum of Basel (Switzer-

**Fig. 3.** SEM images of *Palaeoglobigerina* and *Parvularugoglobigerina* species of the lowermost Danian (scale bar = 100 µm; scale bar of detail SEM-micrographs = 10 µm). **A** – *Palaeoglobigerina alticonusa* (LI, MCGOWRAN & BOERSMA, 1995), from lower *E. simplicissima* Subzone, El Kef, Tunisia: A1, axial view; A2, spiral view. **B** – *Pg. alticonusa*, from lower *E. simplicissima* Subzone, El Kef, Tunisia: B1, spiral view; B2, axial view. **C** – *Palaeoglobigerina fodina* (BLOW, 1979), from *Pv. longiapertura* Subzone (*G. cretacea* Zone), Aïn Settara, Tunisia: C1, axial view; C2, umbilical view. **D** – *Palaeoglobigerina minutula* (LUTERBACHER & PREMOLI SILVA, 1964), from *Pv. sabina* Subzone, Aïn Settara, Tunisia: D1, umbilical view; D2, spiral view. **E** – *Palaeoglobigerina luterbacheri* ARENILLAS & ARZ, 2007, holotype, from *Pv. sabina* Subzone, El Kef, Tunisia: E1, spiral view; E2, axial view; E3, umbilical view. **F** – *Parvularugoglobigerina longiapertura* (BLOW, 1979), from *Pv. sabina* Subzone, Elles, Tunisia: F1, umbilical view; F2, axial view; F3, spiral view. **G** – *Parvularugoglobigerina perexigua* LI, MCGOWRAN & BOERSMA, 1995, from *Pv. sabina* Subzone, Elles, Tunisia: G1, spiral view; G2, axial view; G3, umbilical view. **H** – *Parvularugoglobigerina longiapertura* (BLOW, 1979), from *Pv. sabina* Subzone, El Kef, Tunisia: H1, umbilical view; H2, axial view; H3, spiral view. **I** – *Parvularugoglobigerina sabina* (LUTERBACHER & PREMOLI SILVA), from *Pv. sabina* Subzone, Elles, Tunisia: I1, umbilical view; I2, axial view; I3, spiral view. **J** – *Parvularugoglobigerina eugubina* (LUTERBACHER & PREMOLI SILVA, 1964), from *Pv. sabina* Subzone, El Kef, Tunisia: J1, spiral view; J2, axial view; J3, umbilical view. **K** – *Parvularugoglobigerina eugubina* (LUTERBACHER & PREMOLI SILVA, 1964), from middle *E. simplicissima* Subzone, El Kef, Tunisia: K1, spiral view; K2, axial view; K3, umbilical view. **L** – *Parvularugoglobigerina eugubina* (LUTERBACHER & PREMOLI SILVA, 1964), from *Pv. sabina* Subzone, El Kef, Tunisia: L1, umbilical view; L2, axial view; L3, spiral view; L4, surface detail (granular wall texture in parvularugoglobigerinids).

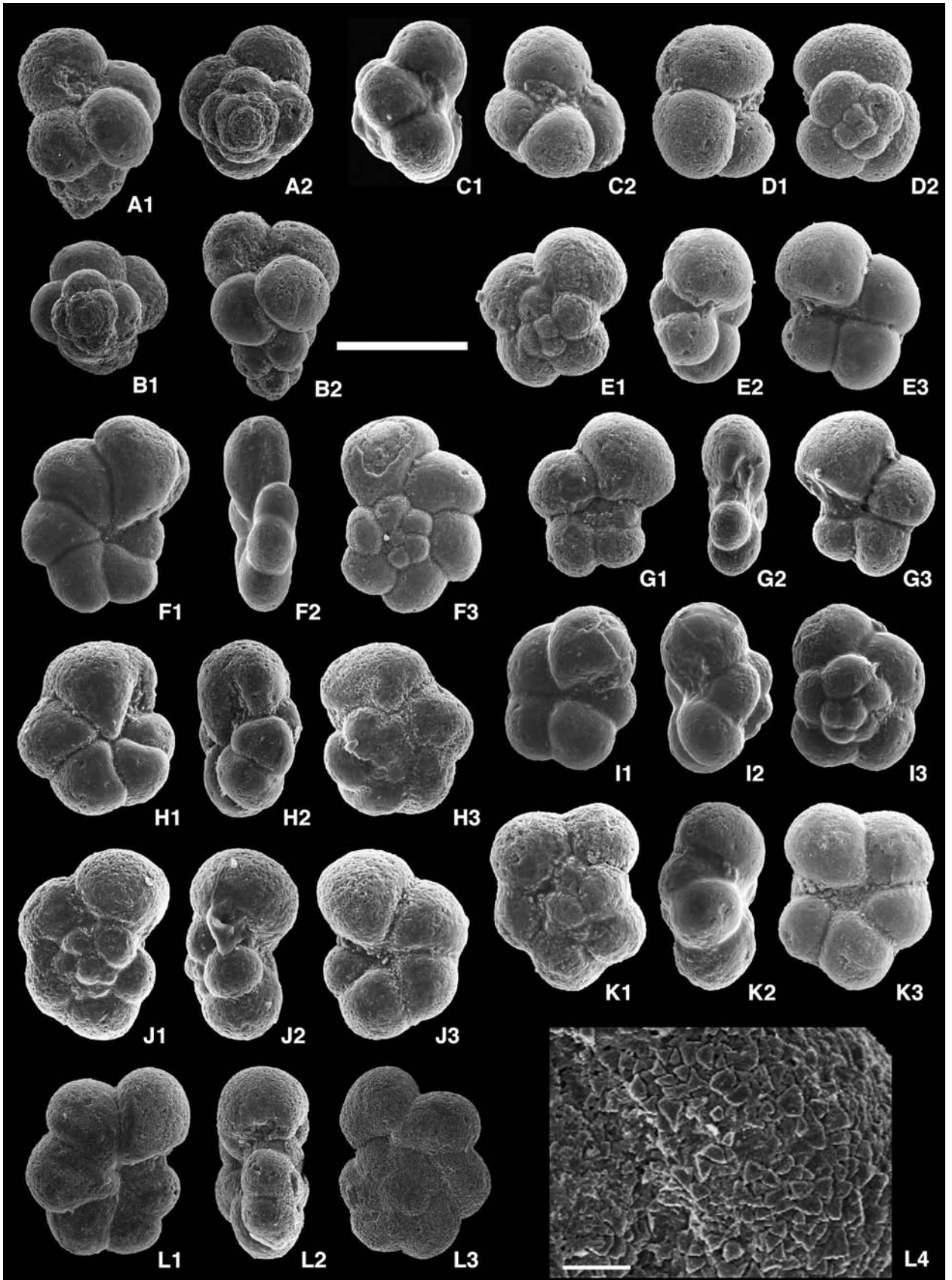


Fig. 3.

land), and studying their type sample from the type locality (Ceselli, Italy), ARENILLAS & ARZ (2000) also concluded that all these species have a smooth wall. According to the planktic foraminiferal assemblage identified by these authors, the type-sample is placed in the lowermost part of Pa, i.e., in the lower part of the *Pv. sabina* Subzone. Planktic foraminiferal preservation in Ceselli is unfortunately very poor, which raises doubts regarding the true wall texture of these holotypes. Nevertheless, the best-preserved specimens from Ceselli have jagged-granular wall similar to those described for the holotypes. Holotypes of *Pv. longiapertura*, *Pg. alticonusa* and *Pg. luterbacheri* also exhibit a smooth and/or granular wall texture (BLOW 1979; LI et al. 1995; ARENILLAS & ARZ 2007). We therefore propose that smooth-granular trochospiral species continue to be assigned to *Parvularugoglobigerina* and/or *Palaeoglobigerina*.

On the contrary, the rugose trochospiral specimens (Figs. 5-6) exhibit textural features that do not fit in with those of *Parvularugoglobigerina* or *Palaeoglobigerina* (Figs. 3-4). Their wall surface is characterized by wrinkles, creases or warts with multiple pores (pore-rugosities), originated by coalescing pore-mounds; isolated pore-mounds can also be observed, many with the pores decentred and somewhat sharp; in specimens with higher pore density, the rugosities tend to be smaller and more crowded. Some specimens have imperforate rugosities and papillae (e.g., Fig. 6A, F, G), showing inter-rugosity pore-murals and apparently relict pores within the ridges. Other specimens have a granular surface (Fig. 6C, H) due perhaps to gametogenetic calcification as in other guembelitrids or to fossilidiagenetic recrystallization. There are however, similar morphotypes in both lineages (compare Fig. 3A vs Fig. 5D, Fig. 3C vs Fig. 5E, or Fig. 3I vs

Fig. 5H), so their distinction seems to be possible only with textural criteria. Differences between smooth and rugose wall textures can be clearly seen in Fig. 7.

### 3.2. Biostratigraphic and phylogenetic implications

ARENILLAS et al. (2010) indicated that rugose and pore-mounded trochospiral specimens are abundant only from the *E. simplicissima* to the *E. trivialis* Subzone, i.e., from the upper part of Pa to the lower part of Pl<sub>1a</sub>. We summarize here the stratigraphic distributions of both lowermost Danian trochospiral lineages in the Tunisian sections (Fig. 1). Data support different biostratigraphic ranges for both lineages, as proposed by ARENILLAS et al. (2010). The first to appear were the parvularugoglobigerinids with a smooth-granular wall, at the top of P0. The rugose trochospiral specimens appeared later (ARENILLAS et al. 2007), probably in the middle part of Pa.

El Kef data suggest that the rugose trochospiral species almost completely replaced parvularugoglobigerinids from the middle part of the *E. simplicissima* Subzone, i.e., from the upper part of Pa upwards (Fig. 1). In *Pv. longiapertura* and *Pv. sabina* Subzones (lower and middle part of Pa), SEM photographs of trochospiral specimens, excluding *Guembelitra*, indicate that only smooth-granular wall texture occurs in this interval (about 37 photographed specimens of *Pv. longiapertura*, *Pv. umbrica*, *Pv. eugubina*, *Pv. sabina*, *Pg. alticonusa*, *Pg. fodina* and *Pg. luterbacheri*). In the lower part of the *E. simplicissima* Subzone (upper part of Pa), almost all SEM-photographed specimens exhibit a smooth wall (about 71 specimens of *Pv. longiapertura*, *Pv. eugubina*, *Pv. sabina*, *Pv. cf. hemisphaerica*, *Pg. alticonusa*, *Pg. fodina* and *Pg. luterbacheri*),

**Fig. 4.** Detail of smooth wall texture of *Palaeoglobigerina* and *Parvularugoglobigerina* (scale bars = 10 µm); note tiny pore-murals < 1 µm in the smooth surfaces, and minute sutured calcite crystallites in the granular surfaces attributed to gametogenetic calcification (secondary outer calcite crust) and/or fossilidiagenetic recrystallization. **A** – *Palaeoglobigerina alticonusa* (LI, MCGOWRAN & BOERSMA, 1995), from lower *E. simplicissima* Subzone, El Kef, Tunisia. **B** – *Palaeoglobigerina luterbacheri* ARENILLAS & ARZ, 2007, paratype, from *Pv. sabina* Subzone, El Kef, Tunisia. **C** – *Parvularugoglobigerina perexigua* (LI, MCGOWRAN & BOERSMA, 1995), from *Pv. sabina* Subzone, Ain Settara, Tunisia. **D** – *Palaeoglobigerina alticonusa* (LI, MCGOWRAN & BOERSMA, 1995), from *Pv. longiapertura* Subzone, Settara, Tunisia. **E** – *Parvularugoglobigerina longiapertura* (BLOW, 1979), from *Pv. sabina* Subzone, Elles, Tunisia. **F** – *Parvularugoglobigerina longiapertura* (BLOW, 1979), from *Pv. sabina* Subzone, El Kef, Tunisia. **G** – *Parvularugoglobigerina eugubina* (LUTERBACHER & PREMOLI SILVA, 1964), from *Pv. sabina* Subzone, El Kef, Tunisia. **H** – *Parvularugoglobigerina eugubina* (LUTERBACHER & PREMOLI SILVA, 1964), from lower *E. simplicissima* Subzone, El Kef, Tunisia.



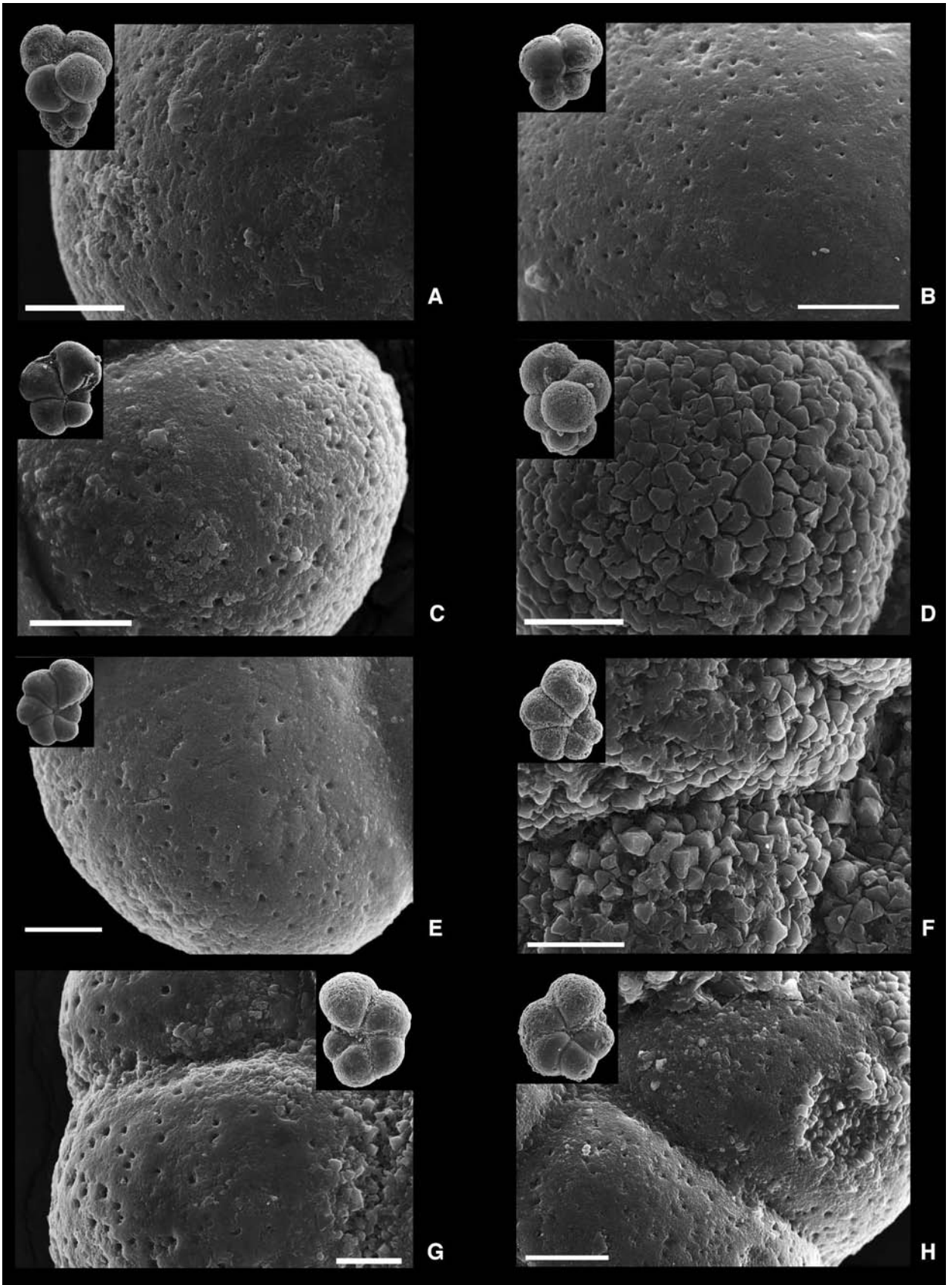


Fig. 4.

except for one rugose (assignable to *alabamensis*). However, in the middle-upper part of the *E. simplicissima* Subzone (uppermost part of Pa), almost all SEM-photographed specimens exhibit a rugose wall (about 31 specimens), and only 5 have a smooth wall (assignable to *Pv. eugubina*, *Pv. sabina*, *Pg. alticonusa*, and *Pg. luterbacheri*). In *E. trivialis* and *S. triloculinoides* subzones (P1a and P1b respectively), only rugose wall trochospiral specimens have been SEM-photographed (about 17 specimens). This pattern seems to be also identified in the other Tunisian sections (Aïn Settara and Elles), raising doubts as to whether the parvularugoglobigerinid stratigraphic range reaches the *P. pseudobulloides* Zone.

The first occurrence of rugose trochospiral species in Tunisia coincides approximately with those of *Eoglobigerina* and *Globanomalina* (Fig. 1). The biostratigraphical ranges proposed in previous studies (e.g., TOUMARKINE & LUTERBACHER 1985; ARENILLAS et al. 2000a, 2007; BERGGREN & PEARSON 2005) can be misleading as they fail to take into account the existence of such a cryptic variety. Rugose trochospiral species were probably misclassified as belonging to species of other genera, such as *Parvularugoglobigerina*, *Palaeoglobigerina*, *Globoconusa* or *Eoglobigerina*, because they include species that are apparently cryptic under the stereomicroscope. This pseudocryptic variety could have strong implications in the planktic foraminiferal stratigraphic scales, for example, in the definition of the *Pv. eugubina* Zone and its equivalent Pa. Based on TOUMARKINE & LUTERBACHER (1985) and MOLINA et al. (1996), ARENILLAS et al. (2004) defined the *Pv. eugubina* Zone as the interval between the first occurrence data of *Pv. eugubina* and *P. pseudobulloides*, whilst BERGGREN & PEARSON (2005) defined Pa as the total range of *Pv. eugubina*. For a strict recognition of the base of the *Pv. eugubina* Zone, and both the base and top of Pa, the texture of the specimens would have to be known.

An alternative hypothesis is to consider that the pore-mounded and rugose wall derived newly from the smooth wall in all species at a time, immediately after changing the palaeoenvironmental conditions at the beginning of the acme-episode PFAS3 (Fig. 1). The pore-mounds are projecting extensions of the wall, secondarily thickened during the test growth (Fig. 2F). The pore-mounded wall has also been observed independently on several planktic foraminiferal groups, which are phylogenetically unrelated (BANNER et al. 1993; LI et al. 1995): early Cretaceous *Blefuscuiana* BANNER & DESAI, 1988, and Oligocene-Miocene *Cas-*

*sigerinella* POKORNY, 1955. Both genera include species with different types of wall texture, some with pore-mounded wall and others with a smooth wall, with no morphological evidence to help decide whether or not they belong to the same genus, or even the same species (BANNER & DESAI 1988; PEARSON & WADE 2009). Something similar could have occurred between the earliest Danian trochospiral, so, the proposal of a new genus and pseudocryptic species might not be strictly necessary. Such a scenario supports OLSSON et al.'s (1999) hypothesis that both smooth and rugose walls are the same. According to this hypothesis, it should be speculated that smooth parvularugoglobigerinids were genetically prepared to redevelop pore-mounds or structures (rugosities) similar to that of their guembelitrid ancestors. Under this view, the parvularugoglobigerinid group was an evolutionary offshoot that became an evolutionary dead end, contradicting ARENILLAS & ARZ's (1996, 2000) hypothesis that *Palaeoglobigerina* was the ancestor of the *Eoglobigerina-Parasubbotina* lineage -with spinose pitted and/or cancellate wall-, and *Parvularugoglobigerina* of the *Globanomalina-Praemurica* lineage -with non spinose pitted and cancellate wall.

The marked difference between the smooth and rugose wall textures (Figs. 4, 6, 7) and their different biostratigraphic ranges suggest however, the two lineages separated taxonomically. The context of rapid evolution in wall textures seen in triserial and biserial in the earliest Danian (ARENILLAS et al. 2010), also support the recognition and splitting of smooth and rugose trochospiral. The test ornamentation and texture had been previously and successfully used to separate a number of genera in a group (see LIU & OLSSON 1992; OLSSON et al. 1992; GEORGESCU 2007, 2009a, b). For example, NEDERBRAGT (1991) proposed the genus *Laeviheterohelix*, separating it from *Heterohelix* EHRENBERG, 1843, – typically with striate or costate wall – by the smooth or pore-mounded surface. Later, GEORGESCU (2009a) emended *Laeviheterohelix* to include only species with small sized pore-mounds. Pore-mound shape and degree of development are important features that can be helpful in deciphering the evolutionary history of certain lineages of planktic and benthic foraminifera (GEORGESCU et al. 2011).

Both lower Danian trochospiral lineages probably evolved from *Guembelitria* but they appeared at different times, generating almost homeomorphic species. This represents a parallel evolution, i.e., the development of similar traits in related, but distinct, taxa descending from the same ancestor, but from different

clades. Species of both lineages coincided partly in time, recording pseudocryptic species in the *E. simplicissima* Subzone (or upper part of Pa). This hypothesis would imply a more complex evolution and a greater diversity in the earliest Danian trochospiral planktic foraminifera.

Parallel evolution of pseudocryptic species does not seem to be exclusively of the earliest Danian trochospiral. ARENILLAS et al. (2010) suggested pseudocryptic species in earliest Danian triserial *Guembelitra*, which include at least two wall textures: pore-mounded (assignable to *Guembelitra* s.s.) and rugose (assignable to *Guembelitra?* or perhaps to *Chiloguembelitra*). According to these authors, rugose walled *Guembelitra* were common in earliest Danian, appeared earlier than the rugose trochospiral lineage (during the PFAS1) and are their likely ancestor. The planktic foraminiferal evolutionary radiation after the K/Pg boundary mass extinction gave origin to various lineages, and the rugose trochospiral, which have not yet been formally described, seem to be one of them. ARENILLAS et al. (2010) also suggested that rugose trochospiral are in turn the ancestor of the pustulate walled *Globoconusa*, as some specimens exhibit an intermediate wall texture (Fig. 8). The wall of these specimens has imperforate papillae, either isolated or as part of rugosities, sharper than usual, which resembles the pustules of *Globoconusa* (compare specimens from El Kef, Tunisia, of the Fig. 8A-B and genuine *Globoconusa* specimen from Bajada del Jagüel, Argentina, of the Fig. 8C). In conclusion, current data from Tunisia strongly support the existence of two primitive trochospiral lineages in the earliest Danian, requiring the definition of a new genus for the rugose species.

#### 4. Systematic palaeontology

Order Foraminifera EICHWALD, 1830

Suborder Globigerinina DELAGE & HÉROUARD, 1896

Superfamily Heterohelicoidea CUSHMAN, 1927

Family Guembelitriidae MONTANARO GALLITELLI, 1957

Genus *Trochoguembelitra* nov.

**Type species:** *Guembelitra? alabamensis* LIU & OLSSON, 1992.

**Etymology:** The generic name, *Trochoguembelitra*, is derived from the Greek prefix trocho-, meaning wheel, which is added to the genus name *Guembelitra*. The prefix refers to the trochospiral coiling.

**Diagnosis:** Trochospiral test, initially triserial or trochospiral. Outline lobate, with incised sutures. Aperture intraumbilical or umbilical-extraumbilical, semicircular to slightly elongated and asymmetrical, with a thin imperforate lip. Wall calcareous hyaline, rugose by perforate and/or imperforate rugosities, and isolated pore-mounds and/or imperforate papillae, irregularly distributed. Secondary granular crust often covering the wall and ornamentation.

**Occurrence:** Lower Danian, from the *E. simplicissima* Subzone (middle part of the *Pv. eugubina* Zone) to the middle part of the *S. triloculinoides* Subzone (middle part of the *P. pseudobulloides* Zone), i.e., from the middle-upper part of Pa to the middle part of P1b of BERGGREN & PEARSON (2005).

**Remarks:** *Guembelitra* s. s. differs from *Trochoguembelitra* n. gen. in having pore-mounded wall texture and triserial arrangement throughout. ARZ et al. (2010) showed other wall texture types in *Guembelitra*, but they are not rugose. *Globoconusa* differs in having a pustulate wall texture, with sharp, more sparsely distributed pustules. *Parvularugoglobigerina* and *Palaeoglobigerina* differ in having smooth wall textures, also often covered with a secondary granular crust.

Trochospiral specimens with rugose wall texture first occur in the *E. simplicissima* Subzone (middle-upper part of the Zone Pa), but they are abundant only in the transition between *Pv. eugubina* (Pa) and *P. pseudobulloides* (P1) Zones. These specimens were already documented by LIU & OLSSON (1992, 1994) and OLSSON et al. (1992, 1999). However, they considered them as belonging to *Parvularugoglobigerina* after emending the genus. This emendation was proposed to redefine the type of wall texture, since they considered that *Parvularugoglobigerina* sometimes exhibit pore-mounds, illustrating trochospiral specimens with a pore-mounded rugose wall. We now include these rugose forms in *Trochoguembelitra* n. gen.

*Trochoguembelitra alabamensis* (LIU & OLSSON, 1992)

Figs. 5A, D, 6A, G

- 1992 *Guembelitra? alabamensis* LIU & OLSSON, p. 341, pl. 2, figs. 1-7.  
 1999 *Parvularugoglobigerina alabamensis* (LIU & OLSSON). – OLSSON et al., p. 83, part, pl. 83, figs. 3, 5-6.  
 2007 *Guembelitra? alabamensis* LIU & OLSSON. – ARENILLAS et al., p. 39, fig. 14.1-14.5

**Original diagnosis:** Test small, 110-160 µm in height and 90-135 µm in largest diameter, height-width ratio 1.0-1.2; 10-13 globular or spherical chambers arranged in a high trochospire, triserial in the early and trochospiral in later ontogenetic stage, with 3 to 4, mostly 3.5 to 4 chambers in the last formed whorls; sutures deeply incised; umbilicus open, narrow and shallow; aperture semicircular, high, with a distinct narrow but thick lip, umbilical, symmetrically situated at the base of the last formed chamber. Wall microp-

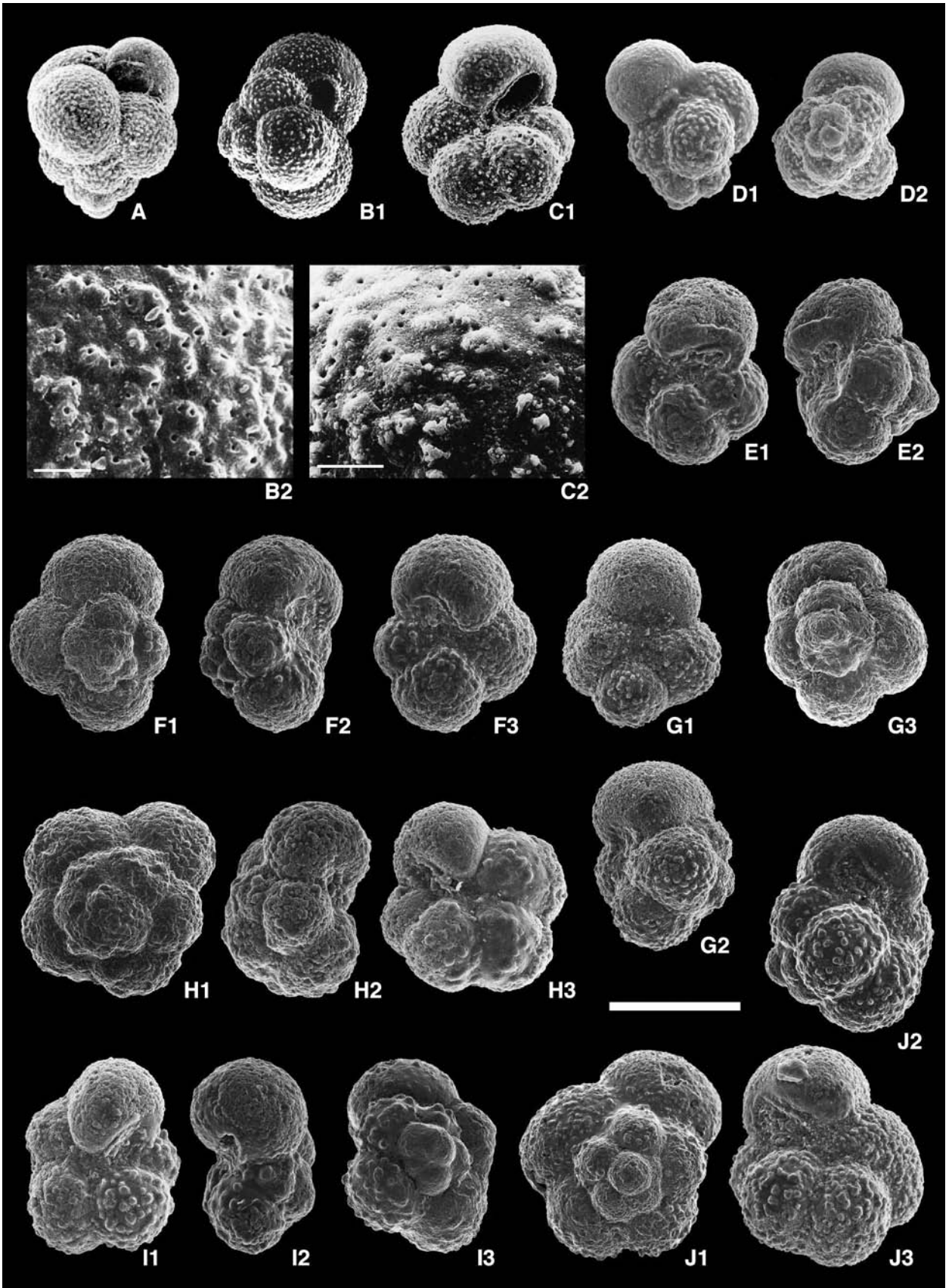


Fig. 5.

erforate, early chambers have intensive small pore-mounds, later chambers are covered with dense blunt pustules and less frequent pore-mounds.

**Description:** Triserial-tetraserial mixed or trochospiral test, with moderate to strong high spire (subconical), 9 to 13 spherical chambers in 3 spiral whorls, 3.5 to 4 chambers in the last whorl and low rate of size increase. Outline lobate, with incised sutures. Aperture intraumbilical, semicircular, with a thin imperforate lip. Wall calcareous hyaline, rugose by perforated and/or imperforated rugosities, and isolated pore-mounds and/or imperforated papillas, irregularly distributed. Adult size ranges 100-160  $\mu\text{m}$  in height and 90-150  $\mu\text{m}$  in length.

**Occurrence:** Lower Danian, from the *E. simplicissima* Subzone (middle part of the *Pv. eugubina* Zone) to the lower part of the *S. triloculoides* Subzone (middle part of the *P. pseudobulloides* Zone), i.e., from the middle-upper part of Pa to the lower part of P1b of BERGGREN & PEARSON (2005).

**Remarks:** *Trochoguembeltria* cf. *fodina* differs from *T. alabamensis* in having a lower trochospiral test (as *Gc. daubjergensis*). *Trochoguembeltria* cf. *sabina* differs in having a lower trochospiral test and greater number of chambers in the last whorl (4 to 5 instead of 3.5 to 4 chambers). *Gc. conusa* differs in being larger and having a pustulate wall texture, with sharp pustules, more sparsely distributed. *Pg. alticonusa* differs in being smaller and in having smooth-granular wall textures, and high arched aperture.

LIU & OLSSON (1992) tentatively included *T. alabamensis* in *Guembeltria*?, and indicated that *T. alabamensis* differs from *Guembeltria cretacea* CUSHMAN, 1933, by having a trochospiral test and poreless blunt pustules (= papillas) in the later ontogenetic stage. OLSSON et al. (1999) included it in *Parvularugoglobigerina* after emending the genus. They ranged this species up to Zone P3b (Selandian), but we could not confirm this occurrence.

*Trochoguembeltria* cf. *fodina* (BLOW, 1979)

Figs. 5B, E-G, 6B-C, 8A

cf. 1979 *Eoglobigerina?* *fodina* BLOW, p. 1221 f., pl. 57, figs. 5-6.

? 1986 *Postrugoglobigerina praedaubjergensis* SALAJ, p. 54, pl. 3, figs. 7-8.

1999 *Parvularugoglobigerina alabamensis* (LIU & OLSSON). – OLSSON et al., p. 83, part, pl. 63, fig. 4.

non 1999 *Parvularugoglobigerina extensa* (BLOW). – OLSSON et al., p. 85-86, part, pl. 65, figs. 7-13.

**Description:** Trochospiral test, slightly high spire, 9 to 12 spherical chambers in 3 spiral whorls, 3.5 to 4 chambers in the last spiral whorl, and moderate rate of size increase. Outline lobate, with incised sutures. Aperture intraumbilical, semicircular to slightly asymmetrical and elongated, with a thin imperforate lip. Wall calcareous hyaline, rugose by perforate and/or imperforate rugosities, and isolated pore-mounds and/or imperforate papillas, irregularly distributed. Adult size range 100-150  $\mu\text{m}$  in length.

**Occurrence:** Lower Danian, from the middle part of the *E. simplicissima* Subzone (upper part of the *Pv. eugubina* Zone) up to the middle part of the *S. triloculoides* Subzone (middle part of the *P. pseudobulloides* Zone), i.e., from the upper part of Pa to the middle part of P1b of BERGGREN & PEARSON (2005).

**Remarks:** The external morphology of *T. cf. fodina* resembles that of *Pg. fodina*, but the latter differs in being smaller and in having a smooth wall texture, usually covered with a secondary granular crust, and higher arched aperture. *T. alabamensis* differs from *T. cf. fodina* in having a higher trochospiral form (as *G. cretacea*). *Trochoguembeltria* cf. *sabina* differs in having more chambers in the last whorl (4 to 5 instead of 3.5 to 4 chambers). *Gc. daubjergensis* differs in being larger and in having a pustulate wall texture, with sharp pustules, sparsely distributed. *Eoglobigerina trivialis*

**Fig. 5.** Specimens of *Trochoguembeltria* n. gen. of the lower Danian (scale bar = 100  $\mu\text{m}$ ; scale bars of detail SEM-micrographs = 10  $\mu\text{m}$ ); note surface details showed by LIU & OLSSON, 1992, with pore-mounded and/or rugose wall texture typical in *Trochoguembeltria* n. gen. **A** – *Guembeltria?* *alabamensis* LIU & OLSSON, 1992, holotype, from Millers Ferry, Alabama, U.S.A. (SEM-micrographs from LIU & OLSSON 1992): axial view, showing typical high trochospire. **B** – *Guembeltria?* *alabamensis* LIU & OLSSON, 1992, from P1a Subzone, Millers Ferry, Alabama, U.S.A. (SEM-micrographs from LIU & OLSSON 1992): B1, axial view, showing low trochospire typical of *Trochoguembeltria* cf. *fodina* (BLOW, 1979); B2, surface detail, with pore-mounded and/or rugose wall texture typical in *Trochoguembeltria* n. gen. **C** – *Parvularugoglobigerina eugubina* (LUTERBACHER & PREMOLI SILVA, 1964), sensu LIU & OLSSON (1992), from Pa Zone, Ferry, Alabama, U.S.A. (SEM-micrographs from LIU & OLSSON 1992): C1, umbilical view, showing 4.5 chambers typical of *Trochoguembeltria* cf. *sabina* (LUTERBACHER & PREMOLI SILVA, 1964); C2, surface detail, with pore-mounded and/or rugose wall texture. **D** – *Trochoguembeltria alabamensis* (LIU & OLSSON, 1992), from lower *E. simplicissima* Subzone, Ain Settara, Tunisia: D1, axial view; D2, spiral view. **E** – *T. cf. fodina*, from upper *E. simplicissima* Subzone, El Kef, Tunisia: E1, umbilical view; E2, axial view. **F** – *T. cf. fodina*, from upper *E. simplicissima* Subzone, El Kef, Tunisia: F1, spiral view; F2, axial view; F3, umbilical view. **G** – *T. cf. fodina*, from upper *E. trivialis* Subzone, El Kef, Tunisia: G1, umbilical view; G2, axial view; G3, spiral view. **H** – *T. cf. sabina*, from upper *E. simplicissima* Subzone, El Kef, Tunisia: H1, spiral view; H2, axial view; H3, umbilical view. **I** – *T. cf. sabina*, from upper *E. simplicissima* Subzone, El Kef, Tunisia: I1, umbilical view; I2, axial view; I3, spiral view. **J** – *T. cf. sabina*, from middle *E. trivialis* Subzone, El Kef, Tunisia: J1, spiral view; J2, axial view; J3, umbilical view.

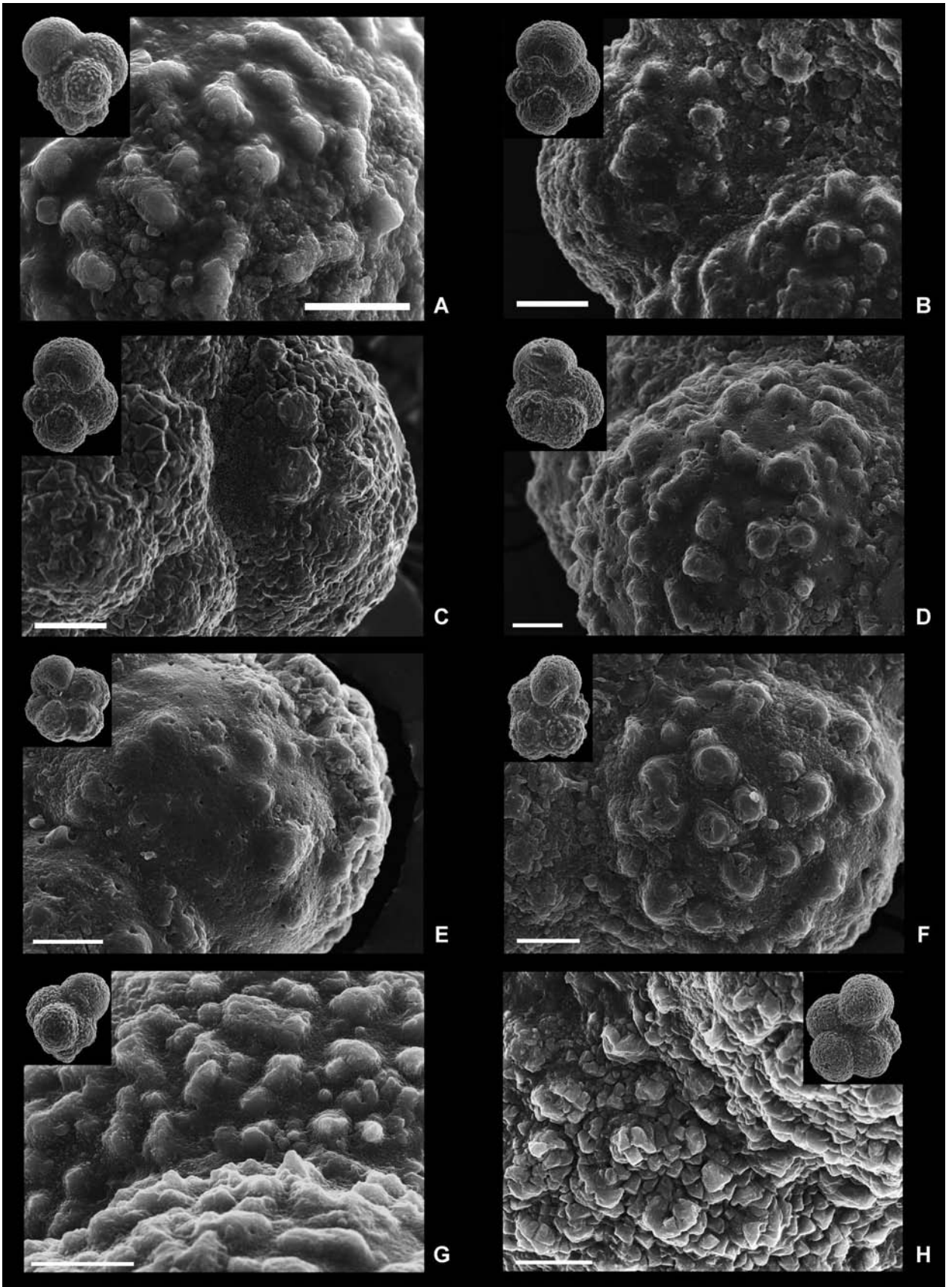


Fig. 6

(SUBBOTINA 1953) and *Eoglobigerina simplicissima* BLOW, 1979, mainly differ in having cancellate wall textures, spines, and often well-developed apertural lips.

The external characteristics of *T. cf. fodina* could be similar to those proposed by SALAJ (1986) for *Postrugoglobigerina praedaubjergensis* (i.e., high-trochospiral, intraumbilical aperture, and 4 chambers in the last whorl). Unfortunately, the holotype of *Pt. praedaubjergensis* has been lost, so it must be considered *nomen dubium non conservandum*. In addition, its wall texture and stratigraphical range seem to not coincide with those proposed for *T. cf. fodina* (see discussion above). OLSSON et al. (1999) included these low trochospiral morphotypes (Fig. 4B) in *Pv. alabamensis*. *T. cf. fodina* should not be confused with *Pv. extensa* according to OLSSON et al. (1999) since authors grouped into this taxon the trochospiral morphotypes with smooth-granular wall classified as *Pg. alticonusa*, *Pg. extensa*, *Pg. fodina* and *Pg. minutula* by ARENILLAS et al. (2007).

*Trochoguembelitra* cf. *sabina* (LUTERBACHER & PREMOLI SILVA, 1964)

Figs. 5C, H-J, 6D-F, H, 7B, 8B

cf. 1964 *Globigerina sabina* LUTERBACHER & PREMOLI SILVA, p. 108, pl. 2, figs. 1a-c, 6a-c, 7a-c.

? 1986 *Postrugoglobigerina haryana* SALAJ, p. 53, pl. 3, figs. 1-2.

1999 *Parvularugoglobigerina eugubina* (LUTERBACHER & PREMOLI SILVA). – OLSSON et al., p. 83-85, pl. 66, figs. 1-3, 5-6; pl. 67, figs. 13-14.

**Description:** Trochospiral test, slightly high spire, 10 to 12 spherical chambers in 3 spiral whorls, 4.5 to 5 chambers in the last spiral whorl, and low rate of size increase. Outline lobate, with incised sutures. Aperture umbilical to somewhat extraumbilical, semicircular to slightly asymmetrical and elongated, with a thin imperforate lip. Wall calcareous hyaline, rugose by perforate and/or imperforate rugosities, and isolated pore-mounds and/or imperforate papillas, irregularly distributed. Adult size ranges 110-160 µm in length.

**Occurrence:** Lower Danian, identified from the middle-upper part of the *E. simplicissima* Subzone (upper part of the *Pv. eugubina* Zone) to the *E. trivialis* Subzone (lower part

of the *P. pseudobulloides* Zone), i.e., from the upper part of Pa to the middle part of the P1a of BERGGREN & PEARSON (2005).

**Remarks.** The external morphology of *T. cf. sabina* resembles that of *Pv. sabina*, but the latter differs in being smaller and in having a smooth wall texture. *T. cf. fodina* differs from *T. cf. sabina* in having fewer chambers in the last whorl (3.5 to 4 instead of 4 to 5 chambers) and aperture intraumbilical. *T. alabamensis* differs in having a higher trochospiral test and lesser number of chambers in the last whorl. *Eoglobigerina edita* (SUBBOTINA, 1953) and *Eoglobigerina praedita* BLOW, 1979, mainly differ in having cancellate wall textures, spines (at least the first one), and often well-developed apertural lips.

The external morphology of this species could be similar to that described by SALAJ (1986) for *Postrugoglobigerina haryana* (i.e., low-trochospiral, intraumbilical aperture, and 5 chambers in the last whorl). As *praedaubjergensis*, the holotype of this species has been lost (*Pt. haryana* must be considered *nomen dubium non conservandum*) and its wall texture and stratigraphical range seem to not coincide with those of *Trochoguembelitra* cf. *sabina* (see discussion above). Specimens illustrated by OLSSON et al. (1999), with pore-mounded and/or rugose wall texture, and five chambers in the last whorl are included here in *Trochoguembelitra* cf. *sabina*. They classified these morphotypes as *Pv. eugubina*.

## 5. Conclusions

We have revised the trochospiral planktic foraminiferal assemblages of the lowermost Danian, and taken over 1000 SEM-photographs of 291 specimens from Tunisian sections (El Kef, Ain Settara, Elles), including wall surface details. SEM-photographs have revealed the occurrence of two groups of primitive trochospiral species, containing quasi-homeomorphic species – pseudocryptic under stereomicroscopy – only differentiated under SEM by their wall texture. The two groups have different stratigraphic ranges, although they co-occur in the upper part of Pa (middle-upper part of *Eoglobigerina simplicissima* Subzone).

The first group to appear exhibits a smooth and/or

**Fig. 6.** Detail of rugose wall texture of *Trochoguembelitra* n. gen. (scale bars = 10 µm); note perforate rugosities (pore-rugosities) and irregular pore-mounds, as well as imperforate rugosities and papillas in some specimens; also note specimens with granular texture covering rugosities and papillas. **A** – *Trochoguembelitra alabamensis* (LIU & OLSSON, 1992), from lower *E. simplicissima* Subzone, Ain Settara, Tunisia. **B-C** – *Trochoguembelitra* cf. *fodina* (BLOW, 1979), from upper *E. simplicissima* Subzone, El Kef, Tunisia. **D** – *Trochoguembelitra* cf. *sabina* (LUTERBACHER & PREMOLI SILVA, 1964), from middle *E. trivialis* Subzone; El Kef, Tunisia. **E** – *T. cf. sabina*, from upper *E. simplicissima* Subzone, El Kef, Tunisia. **F** – *T. cf. sabina*, from upper *E. simplicissima* Subzone, El Kef, Tunisia. **G** – *T. alabamensis* (LIU & OLSSON, 1992), from *S. trilocolinoides* Subzone, El Kef, Tunisia. **H** – *T. cf. sabina*, from upper *E. simplicissima* Subzone (*Pv. eugubina* Zone), El Kef, Tunisia.

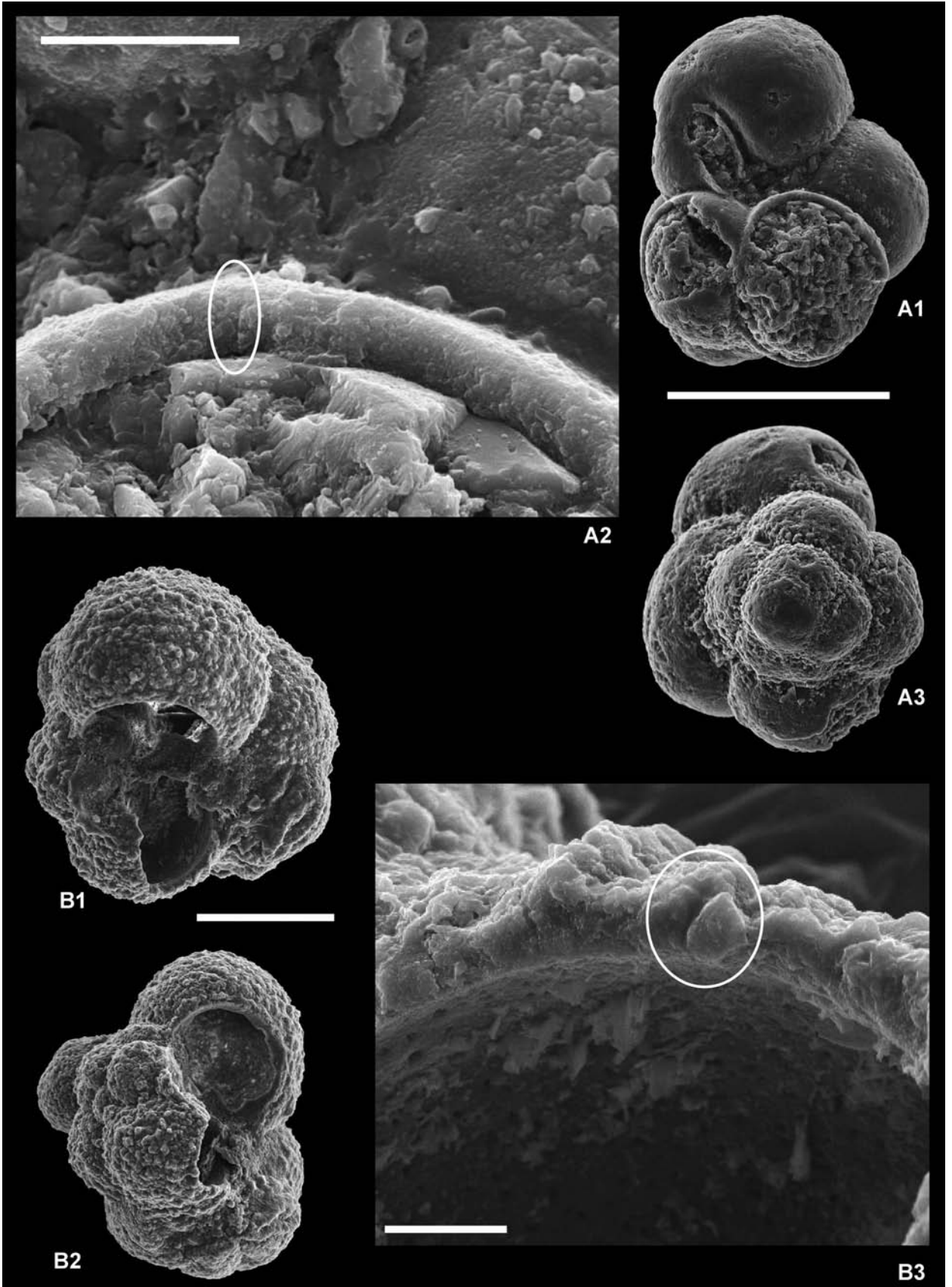


Fig. 7



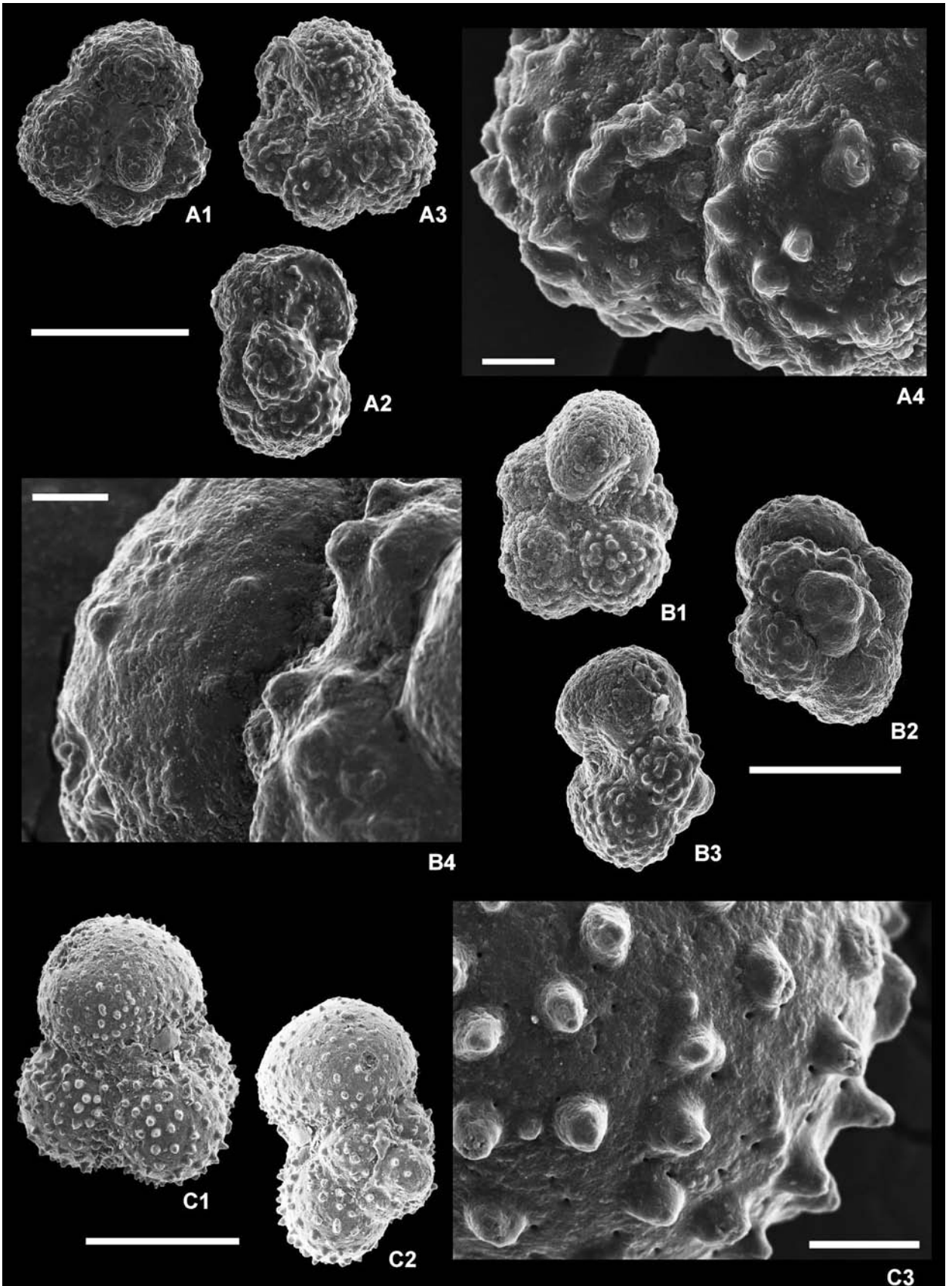


Fig. 8

granular wall texture (with pore-murals) and evolved at the P0-Pa transition (around 5-20 ky after the K/Pg boundary). Its species were herein attributed to the parvularugoglobigerinids (*Parvularugoglobigerina* HOFKER, 1978 and *Palaeoglobigerina* ARENILLAS, ARZ & NÁNEZ, 2007), such as *Parvularugoglobigerina eugubina* (LUTERBACHER & PREMOLI SILVA, 1964) and *Palaeoglobigerina alticonusa* (LI, MCGOWRAN & BOERSMA, 1995).

The second group has a rugose wall texture (with rugosities and isolated irregular pore-mounds) and evolved at the Pa-P1 transition (around 35-80 ky after the K/Pg boundary). Rugose and pore-mounded trochospiral specimens are abundant only from the *E. simplicissima* to the *E. trivialis* Subzone, i.e., from the upper part of Pa to the lower part of P1a. Textural and biostratigraphic data suggest that this group is a lineage different from that of the parvularugoglobigerinids, and both probably derived independently from triserial *Guembelitra*. This second group is herein assigned to the new genus *Trochoguembelitra*. We suggest the existence of at least three distinct species in this genus, one of them being *Trochoguembelitra alabamensis* (LIU & OLSSON, 1992).

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**Fig. 7.** Comparison of smooth (A) and rugose (B) wall textures in wall sections (scale bar = 100 µm; scale bars of detail SEM-micrographs = 10 µm). **A** – *Palaeoglobigerina alticonusa* (LI, MCGOWRAN & BOERSMA, 1995), from lower *E. simplicissima* Subzone, El Kef, Tunisia: A1, umbilical view; A2, spiral view; A3, detail of wall microstructure (ellipse indicates a pore-mural). **B** – *Trochoguembelitra* cf. *sabina* (LUTERBACHER & PREMOLI SILVA, 1964), aberrant specimen, from upper *E. simplicissima* Subzone, El Kef, Tunisia: B1, umbilical view; B2, spiral view; B3, detail of wall microstructure (ellipse indicates a pore-mound that is part of a rugosity).

**Fig. 8.** Comparison of *Trochoguembelitra* n. gen. (A-B) and *Globoconusa* KHALILOV, 1956 (C), wall textures. The first exhibits a wall texture intermediate to that of pustulate *Globoconusa*, with imperforate papillae sharper than usual, rather isolated, though also as part of rugosities (scale bar = 100 µm; scale bars of detail SEM-micrographs = 10 µm). **A** – *Trochoguembelitra* cf. *fodina* (BLOW, 1979), from *E. trivialis* Subzone, El Kef, Tunisia: A1, umbilical view; A2, axial view; A3, spiral view; A4, detail of wall texture. **B** – *Trochoguembelitra* cf. *sabina* (LUTERBACHER & PREMOLI SILVA, 1964), from upper *E. simplicissima* Subzone, El Kef, Tunisia: B1, spiral view; B2, axial view; B3, umbilical view; B4, detail of wall texture. **C** – *Globoconusa daubjergensis* (BRÖNNIMANN, 1953), from early Danian, Bajada del Jagüel, Argentina: C1, umbilical view; C2, spiral view; C3, detail of wall texture.

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