Benthic origin and earliest evolution of the first planktonic foraminifera after the Cretaceous/Paleogene boundary mass extinction

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Abstract

There are several hypotheses on the origin and evolution of the earliest Danian planktonic foraminifera. Most experts suggest that they descended from a few opportunist planktonic foraminifera species, mainly of the genera *Guembelitria* and *Hedbergella*, which are usually considered to be survivors of the Cretaceous/Paleogene (K/Pg) boundary mass extinction. Nevertheless, early Danian specimens of *Guembelitria* and *Hedbergella* remained morphologically well separated from the associated parvularugoglobigerinids (i.e. *Parvularugoglobigerina* and *Palaeoglobigerina*), the first trochospiral planktonic foraminifera appearing after the K/Pg boundary event. The most likely alternative is a benthic origin for the parvularugoglobigerinids, which would be consistent with molecular phylogenetic

studies that have suggested several episodes of benthic-planktonic transitions in the evolutionary history of planktonic foraminifera. A review of material from the El Kef section and other Tunisian sections supports the previous hypothesis that the buliminid genus *Caucasina* is the ancestor of the first parvularugoglobigerinids (i.e. *Parvularugoglobigerina longiapertura* and *Palaeoglobigerina alticonusa*), on the basis of similarities in test and apertural morphologies and wall texture. The intermediate morphotypes between caucasinids and parvularugoglobigerinids, which appeared approximately 3-5 kyr after the K/Pg boundary, are assigned to *Pseudocaucasina antecessor* gen. nov. sp. nov.

Keywords: Parvularugoglobigerinids, *Caucasina*, evolution, earliest Danian, Tunisia

1. Introduction

Several times during the evolutionary history of planktonic foraminifera, large-scale environmental changes in pelagic habitat have caused the extinction of the specialized, K-strategy species, allowing the survival of only opportunist or generalist, r-strategy species, which are in general minute and globular (Caron and Homewood 1983; Bolli 1986; Molina 2015). The mass extinction event of the Cretaceous/Paleogene (K/Pg) boundary 66 million years ago eliminated almost all species of planktonic foraminifera (Smit 1982, 1990; Arenillas et al. 2002; Molina et al. 2006, 2009; BoudDagher-Fadel, 2012, 2015), and opened up the pelagic domain for a new foraminiferal colonization. A number of new minute microperforate, globigeriniform species rapidly invaded the oceanic pelagic domain after the K/Pg boundary event (Luterbacher and Premoli Silva 1964; Smit 1982; Li and Radford 1991; Olsson et al. 1992). The evolutionary origin of these species is controversial, and both benthic and planktonic ancestors have been

proposed (e.g. Brinkhuis and Zachariasse 1988, and Liu and Olsson 1992). Most experts

suggest that they descended from a few opportunist planktonic foraminiferal species

that survived the catastrophic mass extinction event of the K/Pg boundary, such as

Guembelitria cretacea Cushman, 1933, *Hedbergella holmdelensis* Olsson, 1964, and

Hedbergella monmouthensis Olsson, 1960 (see Olsson et al. 1999, and Aze et al. 2011).

By contrast, Brinkhuis and Zachariasse (1988) postulated that the first Tertiary

planktonic foraminiferal species evolved in the earliest Danian from the benthic

foraminiferal genus *Caucasina* Khalilov, 1951, with mutation giving rise to an

enhancing buoyancy. In recent years, a number of papers have suggested a benthic

origin for several planktonic lineages and a more gradual boundary between benthic and

planktonic modes of life (Liu et al. 1998; Hart et al. 2003; Huber et al. 2006; Ujiié et al.

2008; Georgescu 2009; Darling et al. 2009; Leckie 2009; BoudDagher-Fadel, 2012,

2015). Studies based on ribosomal DNA sequences suggest that the earliest Danian

foraminifera may have evolved from benthic taxa (Darling et al. 1997; De Vargas et al.

1997; Aurahs et al. 2009), although the molecular phylogenetic data are not conclusive.

Darling et al. (2009) provided further genetic evidence to support the polyphyletic

origin of the planktonic foraminifera, and suggested that the tychopelagic mode of life,

i.e. foraminifera that are usually benthic but can survive and actively grow as

planktonic, may be reminiscent of the evolution of planktonic foraminifera from benthic

foraminifera. Another evolutionary vestige of this benthic-planktonic transition may be

the meroplanktonic mode of life, i.e. benthic foraminifera adopting the planktonic mode

for a part of their life cycle, mainly during the reproductive stage (see BouDagher-Fadel

2012, 2015). These lifestyles allow species to take advantage of both the pelagic and

benthonic environments (Casey et al. 1981), and would have facilitated the jump to the

holoplanktonic mode of life on numerous occasions.

The aim of this study is to analyze the hypotheses proposed for the origin of the earliest Danian planktonic foraminifera, in view of the biostratigraphical, textural and morphological evidence obtained from the El Kef section, i.e. the Global Boundary Stratotype Section and Point (GSSP) for the base of the Danian Stage, and from other auxiliary Tunisian sections such as Elles and Aïn Settara (Molina et al. 2009). The study has mainly focused on the first genera of planktonic foraminifera to appear after the K/Pg boundary extinction event, *Parvularugoglobigerina* Hofker, 1978, and *Palaeoglobigerina* Arenillas, Arz and Náñez, 2007, as well as on the previously proposed ancestors, such as *Guembelitria* Cushman, 1933, *Hedbergella* Brönnimann and Brown, 1958, and the benthic genus *Caucasina* Khalilov, 1951.

2. Material and Methods

For the analysis of the biostratigraphic ranges of the studied taxa, we have revised the lowermost Danian of the El Kef section, Tunisia. The ranges of planktonic foraminiferal species at the El Kef section are based on Arenillas et al. (2000a, b) and Molina et al. (2006), and include the stratigraphic distribution of species originating in the Cretaceous and considered as probable survivors of the K/Pg boundary extinction event (Figure 1). At this section, the lowermost Danian begins with a 50-cm-thick blackish clay, overlain by a 50-cm-thick dark grey clay (Molina et al. 2006). This dark clay is informally known as the 'KT Boundary Clay', and its base is characterized by a one-to-three-mm-thick rust-coloured ferruginous layer, usually referred to as the 'KT airfall layer'. The GSSP of the Danian Stage, or K/Pg boundary, was defined at the base of this clay, specifically at the base of the airfall layer characterized by an iridium anomaly, Ni-rich spinels and shocked quartz, and coincident with the mass extinction horizon of planktonic foraminifera at the K/Pg boundary (Smit 1990, 1999; Arenillas et

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al. 2000a, b; Molina et al. 2009). Benthic foraminiferal studies support an outer sublitoral-uppermost bathyal depth of deposition for the El Kef section (see Alegret et al. 2004). We have used the planktonic foraminiferal zonations of Arenillas et al. (2004) and Berggren and Pearson (2005); their equivalence is shown in Figure 1. Notably, the former is based on complete and very expanded Tunisian and Spanish K/Pg sections such as El Kef, Aïn Settara, Elles, Caravaca, Agost and Zumaia. Biomagnetostratigraphic calibrations (Figure 1) have made it possible to estimate the age of the first appearance of the Danian index species after the K/Pg boundary and to calibrate the zonal boundaries in accordance with Arenillas et al. (2004).

For the taxonomic studies, specimens were picked mainly from El Kef samples, but also from Aïn Settara and Elles samples, which were disaggregated in water with diluted H_2O_2 and washed through a 63-μm sieve. The quantitative planktonic foraminiferal analysis of El Kef (Figure 2; Table 1) was based on representative splits (using a modified Otto microsplitter) of approximately 300 specimens larger than 63 μm. All the specimens were mounted on microslides for a permanent record and identification. The foraminiferal preservation in these sections is good enough to analyze the wall texture, although corroded and recrystallized surfaces can be observed in some specimens. Wall textures were examined under JEOL JSM 6400 and Zeiss MERLIN FE-SEM scanning electron microscopes (SEM) at the Electron Microscopy Service of the Universidad de Zaragoza (Spain). Type-specimens are deposited in the Museo de Ciencias Naturales of the Universidad de Zaragoza (Gobierno de Aragón, Spain).

For evolutionary studies, we have relied on ontogenetic, morphological and textural criteria and a high-resolution biostratigraphy, which has allowed us to pinpoint the first appearance of the studied Danian taxa. Up to three ontogenetic stages have been

recognized from the embryonic stage or proloculus of the studied taxa: juvenile stage, i.e. initial stage following the proloculus in the first whorls; neanic stage, i.e. progressive acquisition of adult characters in the intermediate whorls; and adult stage, i.e. full expression of adult characters in the last whorls (Figure 3). The analyses of ontogeny were based on changes in the number of chambers during the development of the test (Table 2; Figure 4).

3. Biostratigraphic, taxonomic and phylogenetic remarks

3.1 Potential planktonic survivors

Besides *Guembelitria*, other Cretaceous genera such as *Heterohelix* Ehrenberg, 1843, *Pseudoguembelina* Brönnimann and Brown, 1953, *Globigerinelloides* Cushman and ten Dam, 1948, and *Hedbergella*, have frequently been reported in the lowermost Danian (e.g. Canudo et al. 1991; Keller et al. 1995; Olsson et al. 1992; Liu and Olsson 1994; Arenillas et al. 2000a, b, 2004; Paul 2005; Gallala 2014; Molina 2015). However, there are many doubts about whether these specimens are *in situ*, as their occurrence may be due to reworking and bioturbation (Huber 1996; Kaiho and Lamolda 1999; Minoletti et al. 2005; Molina et al. 2006; Rodríguez-Tovar et al. 2010). The relative abundance of these doubtful K/Pg survivors decreases sharply in the upper part of the *H. holmdelensis* Subzone or Zone P0 (Figure 2; Table 1). Their decline occurs at the beginning of a global *Guembelitria* acme, or Planktonic Foraminiferal Acme-Stage 1 (PFAS-1) of Arenillas et al. (2006), as opposed to what might be expected of opportunist and/or generalist survivors such as *Heterohelix* and *Hedbergella* in a period of paleoenvironmental recovery (Sepulveda et al. 2009; Molina 2015). Their stratigraphic distribution in the lower Danian may thus be based on reworked specimens. Although this hypothesis requires more rigorous studies, *Guembelitria* might be the only

planktonic foraminiferal survivor, as was originally proposed by Smit (1982), since its relative abundance increased sharply after the K/Pg boundary (see Arenillas et al. 2004, and references therein) and is generally accepted as the ancestor of certain Danian taxa (Olsson et al. 1999). Like *Guembelitria*, *Hedbergella* could also play a role in the phylogeny of Danian taxa (Liu and Olsson 1994; Olsson et al. 1999; Arenillas and Arz 2000; Apellaniz et al. 2002; Aze et al. 2011; BouDagher-Fadel 2012, 2015), but this scenario has recently been questioned (Arenillas and Arz 2013a, b).

3.2 The beginning of the Danian evolutionary radiation

The first trochospiral planktonic foraminifera species to appear after the K/Pg extinction event belong to the genera *Parvularugoglobigerina* and *Palaeoglobigerina* (Figure 1, 5), approximately 5 to 6 kyr after the K/Pg boundary. At El Kef, an acme of parvularugoglobigerinids or PFAS-2 is recorded above the acme of *Guembelitria* or PFAS-1, approximately from the upper part of the *Pv. longiapertura* Subzone to the lower part of the *E. simplicissima* Subzone (Figure 2). During the transition between PFAS-1 and PFAS-2, between approximately 5 and 20 kyr after the K/Pg boundary, a first evolutionary radiation is recorded (Figure 1), including first appearances of numerous species belonging to parvularugoglobigerinids, and serial *Woodringina* Loeblich and Tappan, 1957, and *Chiloguembelina* Loeblich and Tappan, 1956. Above PFAS-2, an increase in serial *Woodringina* and *Chiloguembelina*, or PFAS-3, is recorded (Figure 2). During the transition between PFAS-2 and PFAS-3, between approximately 37 and 80 kyr after the K/Pg boundary, a second evolutionary radiation (Figure 1) includes first appearances of more modern and larger species belonging to *Eoglobigerina* Morozova, 1959, *Parasubbotina* Olsson, Berggren and Liu, 1992, *Globanomalina* Haque, 1956, and *Praemurica* Olsson, Hemleben, Berggren and Liu

1992. Other genera appear shortly afterwards (Figure 1), such as *Subbotina* Brotzen and Pozaryska, 1961, and *Globoconusa* Khalilov, 1956.

The wall texture of parvularugoglobigerinids has been described as smooth or with superficial pore-mounds when specimens are well preserved (Liu and Olsson 1992; Olsson et al. 1999; Arenillas et al. 2007). However, Arenillas et al. (2012) ascertained that parvularugoglobigerinids in fact exhibit a smooth wall texture with tiny mural-pores of < 1 μm in diameter. They assigned earliest Danian trochospiral specimens with pore-mounds to a new genus (Figure 6(f),(g)), *Trochoguembelitria* Arenillas, Arz and Náñez, 2012, with *Guembelitria*? *alabamensis* Liu and Olsson, 1992, as its type-species (see discussion in Arenillas et al. 2015). Unlike parvularugoglobigerinids, the first appearance of *Trochoguembelitria* is in the second evolutionary radiation, approximately 35 kyr after the K/Pg boundary, and its maximum abundance occurs higher in PFAS-3, i.e. in the *E. simplicissima* and *E. trivialis* Subzones (Arenillas et al. 2012, 2015). *Parvularugoglobigerina* has been suggested as the ancestor of the 'non-spinose lineage' of Olsson *et al*. (1999), which includes the Danian genera *Globanomalina* and *Praemurica* (Arenillas and Arz 2000, 2013a; BouDagher-Fadel 2012, 2015). *Palaeoglobigerina*, whose type-species is *Eoglobigerina*? *fodina* Blow, 1979, was separated from *Parvularugoglobigerina* by Arenillas et al. (2007) to include the species previously identified as primitive *Eoglobigerina* Morozova, 1959, or *Globoconusa* Khalilov, 1956 (Blow 1979; Brinkhuis and Zachariasse 1988; Canudo et al. 1991; Keller et al. 1995; Arenillas and Arz 2000). It differs from *Parvularugoglobigerina* by its lower number of chambers (Figure 3, 4, 5), both in the first whorl (3.5 to 4 instead of 4 to 4.5) and in the last one (3 to 4 instead of 4 to 9). *Palaeoglobigerina* has been suggested as the ancestor of the 'spinose lineage' of Olsson et al. (1999), which includes the Danian genera *Eoglobigerina*, *Parasubbotina* and

Subbotina (Arenillas and Arz 2013b). The latter genera have spinose cancellate wall, and differ solely by the number and size of chambers, as well as the position of the aperture (Olsson et al. 1999).

3.3 Two possible planktonic ancestors: Guembelitria and Hedbergella

Since *Guembelitria* species are the only planktonic foraminifera survivors that crossed the K/Pg boundary in substantial numbers (Figure 2), undergoing a sharp increase in their relative abundance (acme-stage of *Guembelitria* or PFAS 1 of Arenillas 2000a), this genus has been suggested as the most obvious ancestor of earliest Danian planktonic foraminifera (Smit 1982; Olsson et al. 1992; Li et al. 1995; Arz et al. 2010; Arenillas et al. 2010, 2012; Arenillas and Arz 2013a, b; Koutsoukos 2014). *Guembelitria* is characterized by a triserial test (Figure 6(d),(e)), which is microperforate and with a pore-mounded wall texture (Loeblich and Tappan 1987; Georgescu et al. 2011). It comprises opportunist, r-strategy species of mainly shallow, neritic habitat (Smith and Pessagno 1973; Kroon and Nederbragt 1990; D'Hondt 1991; Koutsoukos 1994). There is a general consensus that *Guembelitria* is the ancestor of early Danian microperforate genera such as *Woodringina* and *Globoconusa* (Olsson et al. 1999; Arenillas and Arz 2000; Arenillas et al. 2010, 2012; Koutsoukos 2014). For the latter case, Arenillas et al. (2012) have proposed the evolutionary lineage *Guembelitria-Trochoguembelitria-Globoconusa*, instead of the more direct derivation of *Globoconusa* from *Guembelitria*. The ancestry of *Guembelitria* for the biserial lineage *Woodringina-Chiloguembelina* and the trochospiral lineage *Trochoguembelitria-Globoconusa* is corroborated by their similar wall textures, and by the triserial juvenile stage in *Woodringina* and in the first species of *Trochoguembelitria* to appear, *T. alabamensis*. Olsson et al. (1999) proposed that *Parvularugoglobigerina*

also derived directly from *Guembelitria*, but this hypothesis was questioned by Arenillas and Arz (2000) and BouDagher-Fadel (2012, 2015).

Arenillas and Arz (2000, 2013b) and Arenillas et al. (2010) hypothesized that *Parvularugoglobigerina* derived from *Hedbergella* and gave rise to *Globanomalina*, on the basis of morphological and ontogenetic similarities. Olsson et al. (1992) and Liu and Olsson (1994) had proposed that the first 'normal' perforate Danian planktonic foraminifera, i.e. *Globanomalina* and *Eoglobigerina*, were directly descended from *Hedbergella*, whereas *Parvularugoglobigerina* was an evolutionary dead-end derived from *Guembelitria*. The latter phylogenetic hypothesis has subsequently been held by Olsson et al. (1999) and Aze et al. (2011). Nevertheless, this scenario seems to contradict the high-resolution biostratigraphic data reported by Smit (1982), Brinkhuis and Zachariasse (1988), Arenillas et al. (2000a, b; 2006) and Molina et al. (2006, 2009) among others from Tunisian, Spanish and Mexican sections. Zone P0 is characterized exclusively by species ranging from the Cretaceous, mainly *Guembelitria* spp., so no species originating in the Danian is recorded in this biozone (see Arenillas et al. 2004, 2015). The appearance and evolution of the parvularugoglobigerinids occurred in the P0-Pα transition, i.e. from the uppermost part of the *H. holmdelensis* Subzone to the lower part of the *Pv. longiapertura* Subzone, approximately 5 to 6 kyr after the K/Pg boundary. By contrast, the appearance and evolution of more modern and larger genera, such as *Eoglobigerina* and *Globanomalina,* came about in the middle part of Zone Pα, i.e. in the lowermost part of the *E. simplicissima* Subzone, approximately 35 to 45 kyr after the K/Pg boundary. The beginning of the second evolutionary radiation occurred when some of the possible survivors of the K/Pg boundary mass extinction event, such as *Heterohelix* and *Hedbergella*, had already become extinct (Arenillas and Arz 2013a, b; Gallala 2014), and only a few reworked specimens remained (Figure 1). It should

also be kept in mind that *Globanomalina* and *Eoglobigerina* exhibit a pitted or cancellate wall from their first record in the *E. simplicissima* Subzone (Arenillas et al. 2004). However, *Hedbergella* species such as *H. holmdelensis* (Figure 6(a)-(c)), if they are *in situ*, continued to exhibit their typical pustulate wall texture during the earliest Danian (see Arenillas et al. 2007), and they are therefore very different not only from the parvularugoglobigerinids, but also from *Eoglobigerina* and *Globanomalina*. In fact, Huber and Leckie (2011) described the wall texture of these hedbergellids as muricate (characterized by coarse pustules that may cover the entire test), and defined a new genus: *Muricohedbergella*, including *H. holmdelensis* and *H. monmouthensis* among other species. Apellániz et al. (2002) proposed *Hedbergella hillebrandti* (Orue-Etxebarria, 1985) as another possible ancestor of Danian species, concretely of *Eoglobigerina* species, although there are doubts as to whether this species really is planktonic (Arenillas and Arz 2007). Orue-Etxebarria (1985) suggested that it could be a transitional form between benthic and planktonic foraminifera. Liu and Olsson (1994), by contrast, argued that it appears to be a benthic species, probably belonging to the genus *Quadrimorphina* Finlay, 1939, on the basis of its distinct umbilicus and aperture.

Koutsoukos (2014) has recently identified a new species, *Praemurica nikolasi*, from a piston core in the Campo Basin, offshore of Rio de Janeiro, southeastern Brazil, and suggested that it is the earliest recorded cancellate species, near the base of the Zone P0. According to Koutsoukos (2014), *Pr. nikolasi* evolved directly from *Hedbergella monmouthensis*, giving rise to all subsequent cancellate lineages of the early Danian (i.e. *Eoglobigerina* and *Parasubbotina,* in addition to *Praemurica*). However, the identification of cancellate species near the K/Pg boundary is indicative that the piston core studied by Koutsoukos (2014) has a hiatus corresponding to the lowermost Danian, probably the *H. holmdelensis, Pv. longiapertura* and *Pv. sabina*

Subzones (see Arenillas et al. 2004, 2015). The absence of PFAS-1, or acme of *Guembelitria*, in the Campo Basin core supports this assumption. The earliest Danian assemblages of trochospiral planktic foraminifera recorded in the Campo Basin core include *Parvularugoglobigerina, Praemurica, Eoglobigerina, Parasubbotina,* and *Globoconusa*, as well as *Palaeoglobigerina* and *Trochoguembelitria*. The latter two genera were not mentioned by Koutsoukos (2014) because both genera were probably included within the interspecific variability of *Parvularugoglobigerina* following the taxonomy of Olsson et al. (1999). These assemblages suggest that belong to the *Eoglobigerina simplicissima* Subzone, and therefore the existence of a hiatus corresponding to the Zone P0 and lower part of the Zone Pα. The stratigraphic ranges of species from the Campo Basin core are different to those reported in El Kef and other sections of Tunisia and Spain, which are the most complete and expanded sections known to date (see Molina et al., 2009). This suggests that the core samples studied by Koutsoukos (2014), consisting of unconsolidated muddy sediments, may also have problems of contamination and mixture of foraminifera, perhaps during drilling and/or retrieval operations.

3.4 Possible benthic ancestors

The traditionally accepted monophyletic character of the planktonic foraminifera has been losing ground in the light of several molecular phylogenetic studies (Darling et al. 1997). Testing different hypotheses on the phylogenetic relationships between and within the major groups of recent planktonic foraminifera using ribosomal DNA sequences, De Vargas et al. (1997) concluded that there have been at least three independent episodes of benthic-planktonic transition in the history of modern planktonic foraminiferal families (Globigerinidae Carpenter, Parker and Jones, 1862;

Globorotaliidae Cushman, 1927; and Candeinidae Cushman, 1927). Unlike the other families, which have a more recent origin, Globigerinidae could have originated shortly after the K/Pg boundary mass extinction (De Vargas et al. 1997; Aurahs et al. 2009). Molecular evidence indicates that the modern triserial planktonic species *Gallitellia vivans* Cushman, 1934, may have evolved in the Miocene from the benthic genera *Stainforthia* Hofker, 1956, and/or *Virgulinella* Cushman, 1932, and that the sporadic occurrence of triserial planktonic foraminifera in the fossil record reflects multiple transitions from a benthic to a planktonic mode of life (Ujiié et al. 2008). Darling et al. (2009) suggested that the radiation and repopulation of the pelagic realm after the end-Cretaceous mass extinction may at least in part have occurred from tychopelagic benthic species rather than from nerito-planktonic ones, a claim supported by the evidence that the extant biserial planktonic *Streptochilus globigerus* and the benthic *Bolivina variabilis* are one and the same biological species.

Other examples of benthic-planktonic transitions have been proposed in the evolutionary history of foraminifera. According to some authors (BouDagher et al., 1997; Hart et al. 2003), the first planktonic foraminiferal genus, *Conoglobigerina* Morozova, 1961, derived from an aragonitic benthic foraminifer of the family Oberhauserellidae Fuchs, 1970, although it has been recently refused (von Hillebrandt, 2012; Clemence and von Hillebrandt, 2013). Some Cretaceous serial planktonic genera are considered descendants of benthic ancestors. Georgescu (2009) erected the genus *Archaeoguembelitria* to include the latest Albian-earliest Turonian triserial planktonic foraminifera, regarded as phylogenetically unrelated to the late Cretaceous *Guembelitria*. *Archaeoguembelitria* includes both benthic and planktonic species, and may have derived from another, different ancestral benthic line: the buliminid *Praeplanctonia* Georgescu, 2009, which is also the proposed ancestor of the planktonic

biserial *Protoheterohelix washitensis* (Tappan, 1940). The ancestor of the late Cretaceous *Guembelitria* is unknown but may be the benthic genera *Praebulimina* Hofker, 1953, or *Pyramidina* Brotzen, 1948 (Georgescu 2009). Thus, buliminids appear to play a relevant role as ancestors of various serial or microperforate planktonic foraminifera.

Another example of benthic-planktonic transition could be the origin of parvularugoglobigerinids. The empty pelagic niche after the K/Pg mass extinction event may have favored repopulation from benthic ancestors. On the basis of a study of the El Kef section, Brinkhuis and Zachariasse (1988) postulated that the parvularugoglobigerinids evolved from the benthic genus *Caucasina*, approximately 5 kyr after the K/Pg boundary. They noted that guembelitriids and hedbergellids remained morphologically well separated from the earliest Cenozoic planktonic species. From their first appearance, parvularugoglobigerinids exhibit a clearly smooth wall surface with tiny mural-pores, and a trochospiral initial stage with 3.5 to 4.5 chambers in the first whorl. By contrast, guembelitriids are consistently triserial with a tapering test and pore-mounded surface when parvularugoglobigerinids appear. Hedbergellids differ markedly in their apertural shape and their wall texture, and they accordingly seem not to play any role in the phylogeny of earliest Danian taxa. Instead, Brinkhuis and Zachariasse (1988) found minute specimens of *Caucasina* sp. associated and nearly identical to the parvularugoglobigerinids (Figure 7(a)-(f)), suggesting a phylogenetic link between them.

4. Supporting the hypothesis of a benthic origin

The evolution of parvularugoglobigerinids from guembelitriids or hedbergellids is very questionable, since these latter two groups were very different from the former at

the time that such evolution had to occur, i.e. in the P0-Pα transition, approximately 5 to 6 kyr after the K/Pg boundary. A benthic origin for the parvularugoglobigerinids from a *Caucasina* species as proposed by Brinkhuis and Zachariasse (1988) appears a valid alternative. *Caucasina* is a buliminid genus recorded from the Campanian up to the uppermost Miocene (Bugrova 2012); it is an infaunal morphotype, an opportunist, phytodetritivore tolerant to nutrient-rich, dysoxic microhabitats (Poag 1989, 2012; Koutsoukos and Hart 1990). It includes species with an elongate, high trochospiral test, heteromorphic, with 4 to 8 chambers in the first whorl, reduced to 3 or fewer chambers in the last whorl, the wall texture smooth and finely perforate, and the aperture as an elongate narrow loop, bordered by a narrow lip extending up the face of the final chamber (Loeblich and Tappan 1987).

Another caucasinid morphologically close to the parvularugoglobigerinids is *Baggatella* Howe, 1939, similar to neanic forms of *Caucasina*. It is known from the Eocene to Miocene (Loeblich and Tappan 1987; Popescu and Crihan 2005), but also in the Maastrichtian and Paleocene (McGowran 1965; Malumián 1970; Aubert and Berggren 1976; Keller 1992; Náñez and Malumián 2008). We have not considered this genus, because of the absence of representative material in the studied Tunisian sections, but it could be another good candidate to be the ancestor of the parvularugoglobigerinids. *Antarcticella pauciloculata* (Jenkins, 1966), a Danian species from Austral high to mid latitudes, originally described as planktonic and later ascribed to a benthic habit (Liu et al. 1998), has a morphology close to low trochospiral parvularugoglobigerinids, mainly due to its globular chambers and the high-arched foramen that resembles some parvularugoglobigerinid apertures. Differences lie mainly in its umbilical flaps, the umbilical side partially covered by blunt pustules and the absence of a visible aperture, at least in some morphotypes (e.g. Papú et al. 2000;

Ballent et al. 2011). This species co-occurs with *Pv. eugubina* in an impoverished assemblage in New Zealand (Hollis and Strong 2003), but no transitional forms to parvularugoglobigerinids are known.

Thus, *Caucasina* sp. appears to be the most probable ancestor, according to the evidence known to date. It is very scarce at El Kef and the other Tunisian sections studied, and most specimens picked are juvenile. Brinkhuis and Zachariasse (1988) worked with a size-fraction of >37 μm, and illustrated caucasinid and parvularugoglobigerinid specimens with sizes of 50 to 70 μm (Figure 7(d)-(j)). The different size fraction studied may explain the slight differences in the morphology and the stratigraphic ranges proposed by Brinkhuis and Zachariasse (1988) compared to those of Arenillas et al. (2000a) in the same locality (El Kef).

Specimens exhibiting characteristics intermediate between *Caucasina* and parvularugoglobigerinids are identified in the P0-Pα transition of the three studied Tunisian sections (Figure 7(k)-(r); Figs 8(a)-(c)). These intermediate specimens cannot be assigned to any species or genera known to date in the earliest Danian, such as *Caucasina*, *Parvularugoglobigerina* or *Palaeoglobigerina*, so they have been assigned to a new genus and species: *Pseudocaucasina antecessor*. At El Kef, 55 specimens of the new species were recovered, mainly from sample KF12.70 (70 cm above the K/Pg boundary). Its first record occurs about 40 cm above the K/Pg boundary at El Kef (in the upper part of the *H. holmdelensis* Subzone), approximately 3-5 kyr after the mass extinction event. Its highest occurrence is in the top of the *Pv. longiapertura* Subzone, approximately 18 kyr after the K/Pg boundary event, although specimens, probably reworked, are found up to the lower part of the *E. simplicissima* Subzone (Figure 1). Its maximum relative abundance occurs in the transition between the *H. holmdelensis* and *Pv. longiapertura* Subzones, but is masked by the acme of *Guembelitria* in PFAS-1

(Figure 2; Table 1). In this short interval, its relative abundance increases from less than 0.3% in sample KF12.40 to 8% in sample KF12.70, which initiates the subsequent acme of parvularugoglobigerinids or PFAS-2. The swift evolution of *Palaeoglobigerina* and *Parvularugoglobigerina* and their rapid diversification in PFAS-2 caused a sharp reduction in the relative abundance of *Pc. antecessor* gen. nov. sp. nov. and its early disappearance.

Like *Caucasina* sp., *Pc. antecessor* gen. nov. sp. nov. is heteromorphic with two markedly different ontogenetic stages (Figure 3, 4), but exhibiting 4.5 to 5 chambers in its first whorl (juvenile stage) and 3 chambers in its last whorl (adult stage). The transition from the juvenile to the adult stage is more abrupt than in *Caucasina*, missing out the neanic stage almost entirely. Thus, there was an evolutionary trend to reduce the number of chambers in its juvenile stage, and to increase it in its adult stage, separating *Pseudocaucasina* gen. nov. from the caucasinids, and bringing it closer to the parvularugoglobigerinids. The juvenile stage of *Pc. antecessor* gen. nov. sp. nov. strongly resembles *Pv. longiapertura*, which retains related features from the juvenile form into adulthood, suggesting paedomorphosis by post-displacement. Conversely, its adult stage resembles *Pg. alticonusa*, which implies the earlier onset of neanic/adult characters in the juvenile stage, suggesting peramorphosis by pre-displacement. The other characters, such as wall texture, aperture shape, test size, etc., are similar in all these genera. *Pc. antecessor* gen. nov. sp. nov. displays a narrow, high-arched, loop-shaped aperture in the slightly depressed face of the final chamber, similar to both caucasinids and some of the earliest parvularugoglobigerinids. Its wall texture is smooth with tiny pore-murals (Figure 7, 8), also identical to those of both caucasinids and parvularugoglobigerinids. Some specimens illustrated by Brinkhuis and Zachariasse (1988) and assigned to *Globoconusa minutula* and *Parvularugoglobigerina fringa*

(Figure 7(g)-(j)) are interpreted here as probable juvenile/neanic forms of this intermediate species.

The ontogenetic development of *Pc. antecessor* gen. nov. sp. nov. is similar to that of *Caucasina* sp. with two distinctly different stages though less pronouncedly so (Figure 3, 4). The morphological differences between juvenile and adult stages in *Pv. longiapertura* and *Pg. alticonusa* are greatly reduced (Figure 3), decreasing the number of chambers in the first whorl and maintaining it approximately the same throughout ontogeny (with small differences in each *Parvularugoglobigerina* and *Palaeoglobigerina* species). The neanic stage virtually disappears in *Pc. antecessor* gen. nov. sp. nov., *Pv. longiapertura* and *Pg. alticonusa* (Figure 3). The ontogenetic development of the other species included in Figure 4 seems to diverge from those of *Parvularugoglobigerina* and *Palaeoglobigerina*, although the ontogeny and morphology of *H. holmdelensis* and *G. cretacea* are similar to those of *Pv. longiapertura* and *Pg. alticonusa* respectively. These similarities have already been noted by other authors (Li et al. 1995; Arenillas and Arz 2000; BouDagher-Fadel 2012, 2015), and led to some of the phylogenetic hypotheses described above. However, other characters (e.g. wall texture, size of test and proloculus, apertural shape, etc.) do not support the latter phylogenies.

Transitional specimens between *Pc. antecessor* gen. nov. sp. nov. and parvularugoglobigerinids are illustrated in Figure 9. Several morphotypes seem to represent transitional forms between *Pc. antecessor* gen. nov. sp. nov. and *Pg. alticonusa*; e.g. specimens assigned to *Pg.* aff. *alticonusa* with fewer chambers (3.5 to 4 chambers) in the juvenile stage than *Pc. antecessor* gen. nov. sp. nov. (Figure 9(a)), or with more chambers (3.5 to 4 chambers) in the adult stage (Figure 9(b)). The latter specimen may also be an intermediate form between *Pc. antecessor* gen. nov. sp. nov.

and *Pv. longiapertura*. Morphotypes of *Pv. longiapertura* with a convex spiral side (*Pv. aff. longiapertura* in Figure 9(c)-(e) may likewise represent a transition from *Pc. antecessor* gen. nov. sp. nov). These morphotypes are mainly recorded from the basal part of the *Pv. longiapertura* Subzone, but are very scarce.

Given this new evidence, we support the hypothesis put forward by Brinkhuis and Zachariasse (1988) that *Caucasina* is the origin of the parvularugoglobigerinids, with *Pc. antecessor* gen. nov. sp. nov. as the intermediate taxon. The mode of life of this new species is unknown, but it was probably holoplanktonic, as evidenced by the globular form of its chambers and, unlike *Caucasina*, its marked increase in abundance after its first record in the transition between the *H. holmdelensis* and *Pv. longiapertura* Subzones. Alternatively *Pc. antecessor* gen. nov. sp. nov. could be tychopelagic, or more likely meroplanktonic with a benthic juvenile stage and a planktonic adult stage. The latter possibility may be reflected by the heteromorphic test due to an ontogenetic change from the more numerous chambers in the earlier whorls to the triserial final stage with globular chambers. However, the lack of dimorphism caused by the alternation of micro- and macrospheric generations in *Pc. antecessor* gen. nov. sp. nov. suggests a fully planktonic mode of life.

5. Paleontological systematics

The implications of Brinkhuis and Zachariasse's hypothesis for planktonic foraminiferal taxonomy of major rank are not analyzed here in detail. Nevertheless we note that, except for *Guembelitria* and its Danian descendants, the Cenozoic planktonic foraminifera seem unrelated with those of the Cretaceous. The grouping of all planktonic foraminifera in the order Globigerinida Lankaster, 1885, and, except for some minor groups, the division of Cenozoic taxa into two major superfamilies (the

superfamilies Globigerinoidea Carpenter, Parker and Jones, 1862, and Globorotalioidea Cushman, 1927) seem to be artificial. Loeblich and Tappan (1987) considered there to be four superfamilies in the lower Danian (Table 3), separating the taxa of the Cretaceous (Heterohelicoidea Cushman, 1927, and Rotaliporoidea Sigal, 1958) from those of the Paleogene (Globorotalioidea Cushman, 1927, and Hantkeninoidea Cushman, 1927).

In the Danian, BouDagher-Fadel (2012, 2015) considered there to be four superfamilies of trochospiral taxa in the order Globigerinida (Table 3): Eoglobigerinoidea BouDagher-Fadel, 2012 (*Eoglobigerina*, *Parasubbotina* and *Subbotina*), Globigerinitoidea BouDagher-Fadel, 2012 (*Parvularugoglobigerina* and *Globanomalina*), Truncorotaloidinoidea BouDagher-Fadel, 2012 (*Praemurica*), and Globoconusoidea BouDagher-Fadel, 2012 (*Globoconusa*). She also mentions a fifth superfamily, Globigerinoidea Carpenter, Parker and Jones, 1862, which includes apparently unrelated taxa of the Cretaceous (e.g. *Hedbergella*) and Eocene-Holocene. Furthermore, the family Guembelitriidae Montanaro Gallitelli, 1957 (*Guembelitria*) and the family Chiloguembelinidae Loeblich and Tappan, 1956 (*Woodringina* and *Chiloguembelina*) were grouped by BouDagher-Fadel (2012) in the superfamily Heterohelicoidea Cushman, 1927, and included separately in the order Heterohelicida Fursenko, 1958.

BouDagher-Fadel (2012, 2015) assigned *Globoconusa* to the family Globoconusidae BouDagher-Fadel, 2012 (Table 3), and considered it to be a descendant from *Guembelitria*. This classification is compatible with those proposed by Olsson et al. (1999) and Arenillas et al. (2012), although the latter grouped *Globoconusa* in the family Guembelitriidae. We suggested that Globoconusidae should also include *Trochoguembelitria*, but be assigned to the order Heterohelicida along with the

guembelitriids. On the other hand, BouDagher-Fadel (2012, 2015) included

Parvularugoglobigerina in the family Globanomalinidae Loeblich and Tappan, 1984,

and *Praemurica* in the family Truncorotaloididae Loeblich and Tappan, 1961 (Table 3).

This classification is supported by Arenillas and Arz (2013b), but contradicts that of

Olsson et al. (1999), who included *Parvularugoglobigerina* in the family

Guembelitriidae and *Globanomalina* in the family Hedbergellidae Loeblich and

Tappan, 1961, because they believed that *Parvularugoglobigerina* descended directly

from *Guembelitria* and *Globanomalina* from *Hedbergella* (Table 3). Furthermore, we

postulate that the family Eoglobigerinidae Blow, 1979, should also include

Palaeoglobigerina in addition to *Eoglobigerina*, *Parasubbotina* and *Subbotina* (Table

3).

   BouDagher-Fadel's classification seems to be a better approach towards a more

natural classification of Danian planktonic foraminifera, except for the phylogenetic

origin of the parvularugoglobigerinids. BouDagher-Fadel (2012), like Olsson et al.

(1999) and Aze et al. (2011), suggested a hedbergellid origin for eoglobigerinids (and

hence for *Palaeoglobigerina*) and globanomalinids (and hence for

Parvularugoglobigerina sensu Arenillas et al. 2012, and BouDagher-Fadel 2012). By

contrast, we support a benthic origin for parvularugoglobigerinids, which would be

better reassigned to a new ancestral family of earliest Cenozoic planktonic foraminifera.

   In accordance with the new data reported here and previous phylogenetic studies (see

Arenillas 2013a, b), we support Brinkhuis and Zachariasse's hypothesis that the benthic

genus *Caucasina* is phylogenetically related to the parvularugoglobigerinids, and

propose a new species as intermediate taxon (*Pc. antecessor* gen. nov. sp. nov.). We

tentatively suggest *Caucasina* sp. as the origin of the latter, and propose the phylogeny

of the earliest Danian planktonic foraminifera illustrated in the Figure 10. The

macrotaxonomic position of *Pc. antecessor* gen. nov. sp. nov. is uncertain because it cannot be assigned to caucasinids or to parvularugoglobigerinids, and it is difficult to determine exactly which family it belongs to. If it were to be incorporated into the family Caucasinidae, the new taxon should be included in the order Rotaliida Delage and Hérouard, 1896, or better in the order Buliminida Calkins, 1909. However, its mode of life, probably fully planktonic, supports its inclusion in the order Globigerinida. A more thorough review of the Danian planktonic foraminiferal macrotaxonomy should clarify this uncertainty, but we would agree to include *Pseudocaucasina* gen. nov., *Parvularugoglobigerina* and *Palaeoglobigerina* in a new ancestral family within the order Globigerinida.

? Order **Globigerinida** Lankaster, 1885

Family indet.

Genus ***Pseudocaucasina*** gen. nov.

Type species. *Pseudocaucasina antecessor* sp. nov.

Diagnosis. Test small, elongate, subcylindrical to flaring, high trochospiral, heteromorphic, initially with 4-4.5 chambers per whorl and finally triserial. Aperture intraumbilical emplaced in the slightly depressed apertural face of the last chamber, loop-shaped, bordered by a thin lip. Wall texture smooth, with tiny pores (< 1 μm in diameter).

Derivation of name. Prefix *pseudo-* (false, imitation) in order to indicate that it resembles, but it is not, the genus *Caucasina* Khalilov, 1951.

Occurrence. Lowermost Danian, from the upper part of Zone P0 to the lower part of Zone Pα, i.e. from upper part of the *Hedbergella holmdelensis* Subzone to the upper

part of the *Parvularugoglobigerina longiapertura* Subzone of the *Guembelitria cretacea* Zone of Arenillas et al. (2004).

Remarks. *Pseudocaucasina* gen. nov. differs from *Caucasina* in having more incised sutures, more globular chambers, and usually a lower number of chambers in the first whorl. *Parvularugoglobigerina* is low trochospiral throughout, and usually with fewer chambers in the first whorl, and a uniform number of chambers per whorl. *Palaeoglobigerina* has fewer chambers in the first whorl, and a uniform number of chambers per whorl. *Guembelitria* is triserial and has a wall texture with pore-mounds, and a more rounded aperture. *Trochoguembelitria* differs in having a pustulate to rugose wall texture and a wider aperture. *Globoconusa* differs in having a pustulate wall texture and fewer chambers in the first whorl.

Pseudocaucasina antecessor **sp. nov.**

(Figure 7(k)-(r); Figs 8(a)-(c))

1988 *Globoconusa minutula* (Luterbacher and Premoli Silva), Brinkhuis and Zachariasse, page 178, plate 2, figures 1-7, 13; juvenile morphotypes.

1988 *Parvularugoglobigerina fringa* (Subbotina), Brinkhuis and Zachariasse (part), pages 178-181, plate 2, figures 10-11, juvenile morphotypes.

Type-specimens. Holotype MPZ 2014/292 (Figure 8(a)). Paratype MPZ 2014/293 (Figure 8(b)). Paratype MPZ 2014/294 (Figure 8(c)). Depository indicated by prefix of specimen number : MPZ (Museo Paleontológico of the Universidad de Zaragoza, Aragón Government).

Diagnosis. Test small, a high trochospire, with 11-13 chambers, heteromorphic with

low trochospire in initial stage with 4.5-5 slightly compressed globular chambers in the first whorl, and high trochospire in final stage with three globular chambers in the last whorl. Low to moderate rate of chamber size increase. Outline lobate, with slightly depressed sutures in the first whorl and incised in the last whorls. Aperture intraumbilical, situated in the slightly depressed apertural face of the last chamber, a narrow, high arch, surrounded by a thin, partly cristate, lip. Wall texture smooth, with tiny pores (< 1 μm in diameter).

Derivation of name. Latin term *antecessor* referring to *predecessor*, *ancestor*, equivalent to *anteced-*.

Type locality. El Kef section, El Haria Formation, Tunisia.

Type level. 0.7 m above the Cretaceous/Paleogene boundary of the El Kef section (loc. KF12.70), in the upper part of Zone P0, or upper part of the *Hedbergella holmdelensis* Subzone (*Guembelitria cretacea* Zone), lowermost Danian.

Occurrence. Lowermost Danian, from the upper part of Zone P0 to the lower part of Zone Pα of Berggren and Pearson (2005), i.e. from the upper part of the *Hedbergella holmdelensis* Subzone to the top of the *Parvularugoglobigerina longiapertura* Subzone of the *Guembelitria cretacea* Zone of Arenillas et al. (2004).

Remarks. *Pseudocaucasina antecessor* sp. nov. differs from *Caucasina* sp. in having more incised sutures, and less numerous chambers in the first whorl (4.5-5 chambers rather than 5-6 chambers). *Parvularugoglobigerina longiapertura* has a compressed, low trochospiral test, usually fewer chambers in the first whorl (4-4.5 chambers rather than 4.5-5 chambers), and a more uniform number of chambers per whorl. *Palaeoglobigerina alticonusa* differs in having a lower number of chambers in the first whorl (3.5-4 chambers rather than 4.5-5), which remains constant in the following whorls. *Guembelitria cretacea* is fully triserial, has a pore-mounded wall texture, and a

rounded aperture. *Trochoguembelitria alabamensis* has a larger test, a pustulate to rugose wall texture, and a rounded aperture.

Order **Buliminida** Calkins, 1909

Family **Caucasinidae** Bykova, 1959

Genus *Caucasina* Khalilov, 1951

Caucasina **sp.**

(Figure 7(a)-(c))

Remarks. The scarce specimens recovered belong to different ontogenetic stages, the specimen shown in Figure 7(a) being its more adult form, with 2 to 3 chambers in the last whorl and a height of 120 μm. These specimens have more globular chambers and a more flaring test compared to the holotype of *Caucasina minuta* Loeblich and Tappan, 1964, a widespread species originally described from the Danian of California, USA (Figure 3). Specimens of *C. minuta* illustrated from the Danian of the Gafsa-Metlaoui area of Tunisia, from inner to middle sublittoral depths (Aubert and Berggren 1976), also have more elongated and cylindrical tests than the El Kef specimens. The *Caucasina* sp. illustrated by Brinkhuis and Zachariasse (1988) and partly reproduced in Figure 7(d)-(f) of this paper, is most probably the same species recovered in the present study, although no lateral views are available for comparison. As Brinkhuis and Zachariasse (1988) worked with a size-fraction of >37 μm, most of their illustrated specimens may be juvenile/neanic forms exhibiting 5 to 6 chambers per whorl in their juvenile stage and 3 to 4 in their neanic stage. They are also similar to *Baggatella* sp. cf. *B. coloradoensis* Malumián, 1970, illustrated by Aubert and Berggren (1976) from late

Paleocene shelf deposits of Tunisia, but much smaller. The specimens of *Caucasina* sp. recovered in the present study from the El Kef section have a higher and more cylindrical test than *Baggatella coloradoensis* and are better placed in *Caucasina*.

Stratigraphic range. Indeterminate; specimens identified in the basal part of the Danian at the El Kef and Aïn Settara sections, Tunisia, from Zone P0 to the lower part of Zone Pα of Berggren and Pearson (2005), i.e. from the *Hedbergella holmdelensis* Subzone (*G. cretacea* Zone) to the *E. simplicissima* Subzone (*Pv. eugubina* Zone) of Arenillas et al. (2004).

6. Conclusions

New high-resolution biostratigraphic, textural and morphological evidence from Tunisian sections, mainly from El Kef, supports the hypothesis that the earliest Danian planktonic foraminifera informally known as parvularugoglobigerinids (*Parvularugoglobigerina* and *Palaeoglobigerina*) evolved from the benthic buliminid genus *Caucasina*. A benthic origin for the parvularugoglobigerinids is consistent with studies of molecular phylogeny, which support the polyphyly of the planktonic foraminifera, suggesting several episodes of benthic-planktonic transition in the evolutionary history of planktonic foraminifera. *Pseudocaucasina antecessor* gen. nov. sp. nov. is proposed to include the intermediate morphotypes between *Caucasina* and parvularugoglobigerinids. The first appearance of *Pseudocaucasina* gen. nov. is approximately 3-5 kyr after the mass extinction event of the Cretaceous/Paleogene boundary.

Pseudocaucasina gen. nov. is likely to have had a fully planktonic habit, as suggested by the globular morphology of the test and, unlike *Caucasina*, the marked increase in abundance after its first appearance. *Pc. antecessor* gen. nov. sp. nov. is

proposed as a descendent of *Caucasina* sp., and the ancestor of both *Palaeoglobigerina alticonusa* and *Parvularugoglobigerina longiapertura*. *Guembelitria* is now regarded only as the ancestor of *Woodringina* and the biserial lineage that culminates with *Chiloguembelina*, and the ancestor of *Trochoguembelitria* and the trochospiral lineage that culminates with *Globoconusa*. It is also suggested that *Hedbergella* may have not played any role in the phylogeny of Danian taxa. To prove the hypothesis on the benthic origin of the earliest Cenozoic planktonic foraminifera, new high-resolution biostratigraphic studies in continuous and well-expanded sections as well as new studies based on ribosomal DNA sequences may be essential.

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Figure caption

Figure 1. Biostratigraphic ranges of selected planktonic foraminiferal species, including the first species to appear of each early Danian genus as well as Cretaceous-origin species considered to be probable survivors of the K/Pg boundary extinction event according to Arenillas et al. (2000a, b) and Molina et al. (2006); (1) planktonic foraminiferal zonation and calibrated numerical ages of the biozonal boundaries proposed by Arenillas et al. (2004), and (2) planktonic foraminiferal zonation after Berggren and Pearson (2005); thick dotted lines indicate doubtful range, based probably on reworked specimens; fine dotted lines indicate uncertain range, not supported by SEM-photographed specimens; shaded intervals indicate first and second early Danian evolutionary radiations at the El Kef section.

Figure 2. Quantitative stratigraphic distribution of planktonic foraminiferal genera at the El Kef section, and Planktonic Foraminifera Acme-Stages (PFAS) in the lowermost part of the Danian (modified from Molina et al. 2006). (1) Arenillas et al. (2004); (2) Berggren and Pearson (2005). Approximate calibrated numerical ages of the PFAS boundaries based on Arenillas et al. (2004).

Figure 3. Development of the test in spiral and umbilical/axial views, and ontogenetic stages of *Caucasina* sp., *Pseudocaucasina antecessor* gen. nov. sp. nov., *Palaeoglobigerina alticonusa* and *Parvularugoglobigerina longiapertura* (lower scale bar = 100 μm). (a) Holotype of *Caucasina minuta* Loeblich and Tappan, 1964, from the Danian of a core hole in the Panoche Hills, California.

Figure 4. Number of chambers during the test growth of *Pseudocaucasina antecessor* gen. nov. sp. nov., *Caucasina* sp., *Palaeoglobigerina alticonusa*, *Parvularugoglobigerina longiapertura*, *Guembelitria cretacea* and *Hedbergella holmdelensis*. The first point of each species is the chamber number in the first whorl; the following points are the chamber number after the addition of each new chamber during growth (see Figure 3).

Figure 5. SEM images of *Parvularugoglobigerina* and *Palaeoglobigerina* species (scale bar = 100 μm). (a) *Parvularugoglobigerina longiapertura*, sample STW84.2 (0.8 m above the K/Pg boundary), lower part of the *Pv. sabina* Subzone (*Pv. eugubina* Zone), Aïn Settara, Tunisia. (b) *Parvularugoglobigerina longiapertura*, sample KF13.00 (1 m above the K/Pg boundary), lower part of the *Pv. longiapertura* Subzone (*G. cretacea* Zone), El Kef, Tunisia. (c) *Parvularugoglobigerina perexigua*, sample STW84.2 (0.8 m above the K/Pg boundary), lower part of the *Pv. sabina* Subzone (*Pv. eugubina* Zone), Aïn Settara, Tunisia. (d) *Parvularugoglobigerina sabina*, sample KF14.50 (2.5 m above the K/Pg boundary), upper part of the *Pv. sabina* Subzone (*Pv. eugubina* Zone), El Kef, Tunisia. (e) *Parvularugoglobigerina eugubina*, sample KF14.00 (2 m above the K/Pg boundary), lower part of the *Pv. sabina* Subzone (*Pv. eugubina* Zone), El Kef, Tunisia. (f) *Parvularugoglobigerina eugubina*, sample KF14.00 (2 m above the K/Pg boundary), lower part of the *Pv. sabina* Subzone (*Pv. eugubina* Zone), El Kef, Tunisia. (g) *Palaeoglobigerina alticonusa*, sample KF15.75 (3.75 m above the K/Pg boundary), middle part of the *E. simplicissima* Subzone (*Pv. eugubina* Zone), El Kef, Tunisia. (h) *Palaeoglobigerina alticonusa*, sample KF16.50 (4.5 m above the K/Pg boundary), middle part of the *E. simplicissima* Subzone (*Pv. eugubina* Zone), El Kef, Tunisia. (i) *Palaeoglobigerina alticonusa*, sample KF16.50 (4.5 m above the K/Pg boundary),

middle part of the *E. simplicissima* Subzone (*Pv. eugubina* Zone), El Kef, Tunisia. (j) *Palaeoglobigerina alticonusa*, sample KF16.50 (4.5 m above the K/Pg boundary), middle part of the *E. simplicissima* Subzone (*Pv. eugubina* Zone), El Kef, Tunisia. (k) *Palaeoglobigerina fodina*, sample KF15.00 (3 m above the K/Pg boundary), lower part of the *E. simplicissima* Subzone (*Pv. eugubina* Zone), El Kef, Tunisia. (l) *Palaeoglobigerina fodina*, sample KF15.00 (3 m above the K/Pg boundary), lower part of the *E. simplicissima* Subzone (*Pv. eugubina* Zone), El Kef, Tunisia. (m) *Palaeoglobigerina minutula*, sample KF14.00 (2 m above the K/Pg boundary), lower part of the *Pv. sabina* Subzone (*Pv. eugubina* Zone), El Kef, Tunisia. (n) *Palaeoglobigerina luterbacheri*, sample KF15.00 (3 m above the K/Pg boundary), lower part of the *E. simplicissima* Subzone (*Pv. eugubina* Zone), El Kef, Tunisia.

Figure 6. SEM images of *Hedbergella, Guembelitria* and *Trochoguembelitria* species (scale bar = 100 μm). (a) *Hedbergella holmdelensis*, sample STW-5-7 (6 cm below the K/Pg boundary), lowermost part of the *P. hantkeninoides* Subzone (*A. mayaroensis* Zone), Aïn Settara, Tunisia. (b) *Hedbergella holmdelensis*, sample STW+8-10 (9 cm above the K/Pg boundary), upper part of the *H. holmdelensis* Subzone (*G. cretacea* Zone), Aïn Settara, Tunisia. (c) *Hedbergella holmdelensis*, sample KF12.70 (0.7 m above the K/Pg boundary) lower part of the *Pv. longiapertura* Subzone (*G. cretacea* Zone), El Kef, Tunisia. (d) *Guembelitria cretacea*, sample KF12.05 (5 cm above the K/Pg boundary), lower part of the *H. holmdelensis* Subzone (*G. cretacea* Zone), El Kef, Tunisia. (e) *Guembelitria blowi*, sample KF12.10 (10 cm above the K/Pg boundary), lower part of the *H. holmdelensis* Subzone (*G. cretacea* Zone), El Kef, Tunisia. (f) *Trochoguembelitria alabamensis*, sample KF24.80 (12.8 m above the K/Pg boundary), lower part of the *S. triloculinoides* Subzone (*P. pseudobulloides* Zone), El Kef, Tunisia.

(g) *Trochoguembelitria alabamensis*, sample KF20.50 (8.5 m above the K/Pg boundary), middle part of the *E. trivialis* Subzone (*P. pseudobulloides* Zone), El Kef, Tunisia.

Figure 7. SEM images of *Caucasina* and *Pseudocaucasina* gen. nov. species (scale bar = 100 μm). (a) *Caucasina* sp., adult specimen, sample KF12.10 (10 cm above the K/Pg boundary), lower part of the *H. holmdelensis* Subzone (*G. cretacea* Zone), El Kef, Tunisia. (b) *Caucasina* sp., juvenile to adult specimen, sample STW+8+10 (0.9 cm above the K/Pg boundary), upper part of the *H. holmdelensis* Subzone (*G. cretacea* Zone), Aïn Settara, Tunisia. (d) *Caucasina* sp., juvenile specimen, sample KF15.75 (3.75 m above the K/Pg boundary), middle part of the *E. simplicissima* Subzone (*Pv. eugubina* Zone), El Kef, Tunisia. (d-f), Juvenile/neanic specimens of *Caucasina* sp. by Brinkhuis and Zachariasse, 1988, probably in the lower-middle part of the *H. holmdelensis* Subzone (*G. cretacea* Zone), El Kef, Tunisia. (g-j), *Pseudocaucasina antecessor* gen. nov. sp. nov., Juvenile specimens by Brinkhuis and Zachariasse (1988), assigned to *Parvularugoglobigerina fringa* or to intermediates between *Globoconusa minutula* and *Parvularugoglobigerina fringa*, probably in the middle part of the *H. holmdelensis* Subzone (*G. cretacea* Zone), El Kef, Tunisia. (k) *Pseudocaucasina antecessor* gen. nov. sp. nov., sample KF12.70 (0.7 m above the K/Pg boundary), lower part of the *Pv. longiapertura* Subzone (*G. cretacea* Zone), El Kef, Tunisia. (l) *Pseudocaucasina antecessor* gen. nov. sp. nov., sample KF12.70 (0.7 m above the K/Pg boundary), lower part of the *Pv. longiapertura* Subzone (*G. cretacea* Zone), El Kef, Tunisia. (m) *Pseudocaucasina antecessor* gen. nov. sp. nov., sample KF12.70 (0.7 m above the K/Pg boundary), lower part of the *Pv. longiapertura* Subzone (*G. cretacea* Zone), El Kef, Tunisia. (n) *Pseudocaucasina antecessor* gen. nov. sp. nov., sample

STW+15+17 (16 cm above the K/Pg boundary), lower part of the *Pv. longiapertura* Subzone (*G. cretacea* Zone), Aïn Settara, Tunisia. (o) *Pseudocaucasina antecessor* gen. nov. sp. nov., sample AEA 1.60 (0.6 m above the K/Pg boundary), lower part of the *Pv. longiapertura* Subzone (*G. cretacea* Zone), Elles, Tunisia. (p) *Pseudocaucasina antecessor* gen. nov. sp. nov., Juvenile specimen, sample KF12.70 (0.7 m above the K/Pg boundary), lower part of the *Pv. longiapertura* Subzone (*G. cretacea* Zone), El Kef, Tunisia. (q) *Pseudocaucasina antecessor* gen. nov. sp. nov., Juvenile specimen, sample KF12.40 (0.4 m above the K/Pg boundary), upper part of the *H. holmdelensis* Subzone (*G. cretacea* Zone), El Kef, Tunisia. (r) *Pseudocaucasina antecessor* gen. nov. sp. nov., Juvenile specimen, sample KF12.70 (0.7 m above the K/Pg boundary), lower part of the *Pv. longiapertura* Subzone (*G. cretacea* Zone), El Kef, Tunisia.

Figure 8. SEM images of type-specimens of *Pseudocaucasina antecessor* gen. nov. sp. nov. (scale bar = 100 μm). (a) *Pseudocaucasina antecessor* gen. nov. sp. nov., Holotype MPZ 2014/292, sample KF12.70 (0.7 m above the K/Pg boundary) lower part of the *Pv. longiapertura* Subzone (*G. cretacea* Zone), El Kef, Tunisia. (b) *Pseudocaucasina antecessor* gen. nov. sp. nov., Paratype MPZ 2014/293, sample KF12.70 (0.7 m above the K/Pg boundary), lower part of the *Pv. longiapertura* Subzone (*G. cretacea* Zone), El Kef, Tunisia. (c) *Pseudocaucasina antecessor* gen. nov. sp. nov., Paratype MPZ 2014/294, sample KF13.00 (1 m above the K/Pg boundary), lower part of the *Pv. longiapertura* Subzone (*G. cretacea* Zone), El Kef, Tunisia.

Figure 9. SEM images of transitional specimens between *Pseudocaucasina antecessor* gen. nov. sp. nov. and *Pg. alticonusa* and *Pv. longiapertura* (scale bar = 100 μm). (a) *Pseudocaucasina* aff. *alticonusa* gen. nov. sp. nov., sample STW+30+32 (31 cm above

the K/Pg boundary), middle part of the *Pv. longiapertura* Subzone (*G. cretacea* Zone), Aïn Settara, Tunisia. (b) *Palaeoglobigerina* aff. *alticonusa*, sample STW+30+32 (31 cm above the K/Pg boundary), middle part of the *Pv. longiapertura* Subzone (*G. cretacea* Zone), Aïn Settara, Tunisia. (c) *Parvularugoglobigerina* aff. *longiapertura*, sample KF15.00 (3 m above the K/Pg boundary), lower part of the *E. simplicissima* Subzone (*Pv. eugubina* Zone), El Kef, Tunisia. (d) *Parvularugoglobigerina* aff. *longiapertura*, sample KF14.00 (2 m above the K/Pg boundary), lower part of the *Pv. sabina* Subzone (*Pv. eugubina* Zone), El Kef, Tunisia. (e) *Parvularugoglobigerina* aff. *longiapertura*, sample KF15.00 (3 m above the K/Pg boundary), lower part of the *Pv. longiapertura* Subzone (*G. cretacea* Zone), El Kef, Tunisia.

Figure 10. Proposed phylogenetic relationships of the main earliest Danian planktonic foraminiferal genera based on evidence reported here and previous phylogenetic studies (see Arenillas and Arz 2013a, b); a: adult form; j: neanic form; A, holotype of *Caucasina minuta* Loeblich and Tappan, 1964; thick dotted lines indicate doubtful range, based probably on reworked specimens. (1) Arenillas et al. (2004); (2) Berggren and Pearson (2005).

Table 1. Relative abundance of planktonic foraminiferal genera at the El Kef section (modified from Arenillas et al., 2000a); * Except *Guembelitria* and *Hedbergella*, Maastrichtian genera considered possible survivors of the K/Pg boundary extinction event according to Molina et al. (2006), i.e. *Heterohelix*, *Pseudoguembelina*, and *Globigerinelloides*; ** Other Danian genera (*Eoglobigerina*, *Globanomalina*, *Parasubbotina*, *Praemurica*, *Subbotina*, *Trochoguembelitria* and *Globoconusa*).

Table 2. Data for the calculation of the number of chambers during the growth of the test of *Caucasina* sp., *Ps. antecessor* gen. nov. sp. nov., *Pg. alticonusa*, *Pv. longiapertura*, *G. cretacea* and *H. holmdelensis*, based on representative specimens of each species (see Figure 4). 1. Angle γ_i = angle formed by the umbilical centre, the point of suture in the periphery between the first and second chamber of the whorl in question, and the point of suture in the periphery between first and last chamber of the whorl in question. 2. CCN_i = Complete chamber number in the whorl in question; 3. FC_i = portion of the first chamber belonging to the whorl in question, calculated as the division between angle γ and the average angle of the other chambers; and 4. CN_i = number of chambers during growth, calculated as the sum of CN_i and FC_i of the whorl in question.

Table 3. Macrotaxonomic frameworks of some of the main classifications of planktonic foraminifera for the lower Danian; [1] Taxa defined later or not considered; [2] This is a *nomen dubium non conservandum* and has been replaced by *Trochoguembelitria* Arenillas, Arz and Náñez, 2012; [3] This includes *Chiloguembelitria* Hofker, 1978; [4] This includes taxa later defined as *Palaeoglobigerina* Arenillas, Arz and Náñez, 2007, and *Trochoguembelitria* Arenillas, Arz and Náñez, 2012.