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Revalidation of the genus *Chiloguembelitria* Hofker: implications for the evolution of early Danian planktonic foraminifera

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ABSTRACT

Guembelitria is the only planktonic foraminiferal genus whose survival from the mass extinction event of the Cretaceous/Paleogene (K/Pg) boundary has been clearly proven. The evolution of *Guembelitria* after the K/Pg boundary led to the appearance of two guembelitriid lineages in the early Danian: one biserial, represented by *Woodringina* and culminating in *Chiloguembelina*, and the other trochospiral, represented by *Trochoguembelitria* and culminating in *Globoconusa*. We have re-examined the genus *Chiloguembelitria*, another guembelitriid descended from *Guembelitria* and whose taxonomic validity had been questioned, it being considered a junior synonym of the latter. Nevertheless, *Chiloguembelitria* differs from *Guembelitria* mainly in the wall texture (pustulate to rugose vs. pore-mounded) and the position of the aperture (umbilical-extraumbilical to extraumbilical vs. umbilical). *Chiloguembelitria* shares its wall texture with *Trochoguembelitria* and some of the earliest specimens of *Woodringina*, suggesting that it played an important role in the evolution of early Danian guembelitriids, as it seems to be the most immediate ancestor of both trochospiral and biserial lineages. Morphological and morphostatistical analyses of *Chiloguembelitria* discriminate at least five species: *Chg. danica*, *Chg. irregularis*, and three new species: *Chg. hofkeri*, *Chg. trilobata* and *Chg. biseriata*.

Keywords: Guembelitriids, wall texture, K/Pg boundary, morphostatistical analysis, Tunisia.

1. Introduction

The mass extinction event of the Cretaceous/Paleogene (K/Pg) boundary 66 million years ago eliminated almost all species of Maastrichtian planktonic foraminifera (Smit

1990; Arenillas *et al*. 2002; Molina *et al*. 2006, 2009), leaving vacant most of the pelagic niches and triggering in the early Danian the most important radiation in their evolutionary history. One of the most passionate debates in the Earth Sciences focuses on the paleobiological and paleoenvironmental changes that occurred before, during and after this extinction, as well as its relation with the massive eruptions in the Deccan volcanic province in India (Chenet et al. 2007; Schoene et al. 2015) and/or with the Chicxulub asteroid impact on Yucatan in Mexico (Hildebrand et al. 1991; Schulte et al. 2010).

Numerous new species of trochospiral and biserial planktonic foraminifera originated after the K/Pg boundary (Luterbacher and Premoli Silva 1964; Smit 1982; Canudo et al. 1991; Liu and Olsson 1992; Molina et al. 1998). This evolutionary radiation happened in two pulses (Arenillas et al. 2000b, 2004). The first occurred between approximately 5 and 20 kyr after the K/Pg boundary (Arenillas et al. 2016b), with the appearance of species belonging to the parvularugoglobigerinids (*Parvularugoglobigerina* Hofker, 1978, and *Palaeoglobigerina* Arenillas, Arz and Náñez, 2007) and biserial taxa (*Woodringina* Loeblich and Tappan, 1957, and *Chiloguembelina* Loeblich and Tappan, 1956). The second evolutionary radiation occurred between approximately 37 and 80 kyr after the K/Pg boundary, giving rise to species belonging to *Trochoguembelitria* Arenillas, Arz and Náñez, 2012, *Eoglobigerina* Morozova, 1959, *Parasubbotina* Olsson, Berggren and Liu, 1992, *Globanomalina* Haque, 1956, and *Praemurica* Olsson, Hemleben, Berggren and Liu 1992 (Arenillas et al. 2010, 2012; Arenillas and Arz 2013a, 2013b, 2016a). Other genera appear shortly afterwards, such as *Subbotina* Brotzen and Pozaryska, 1961, and *Globoconusa* Khalilov, 1956.

One of the presumed ancestors of the earliest Danian taxa was *Guembelitria* Cushman, 1933, the only planktonic foraminiferal genus whose survival from the K/Pg mass extinction event has been clearly proven (Smit 1982; Olsson et al. 1999; Arenillas et al. 2000a; Ashckenazi-Polidova et al. 2014; Arenillas et al. 2016a). There is a general consensus that *Guembelitria* is the ancestor of microperforate genera such as *Woodringina* and *Globoconusa* (Olsson et al. 1999; Arenillas and Arz 2000; Arenillas et al. 2010; Koutsoukos 2014). For the latter, Arenillas et al. (2012, 2016b) proposed the evolutionary lineage *Guembelitria-Trochoguembelitria-Globoconusa*, instead of the more direct derivation of *Globoconusa* from *Guembelitria*. *Woodringina*, with a mixed triserial-biserial test, is in turn the ancestor of the wholly biserial genus *Chiloguembelina*.

Guembelitria species were r-strategy opportunists that inhabited surface-water environments (Nederbragt 1991) and bloomed during the stressful times of Maastrichtian global warming events associated with the Deccan Traps eruptions (Pardo and Keller 2008). *Guembelitria* also bloomed immediately after the Chicxulub impact, during approximately the first 10 or 15 kyr of the Danian (acme-stage PFAS-1 of Arenillas et al. 2006). Another, later bloom of triserial guembelitriids has been recognized in the early Danian of Egypt, Israel, Tunisia and India. This was related to a global warming episode linked to the last phase of Deccan volcanism (Punekar et al. 2014).

The main object of the present study is *Chiloguembelitria* Hofker, 1978, another guembelitriid that originated in the first evolutionary radiation and whose taxonomic validity has been questioned, it being considered a junior synonym of *Guembelitria* (e.g. D'Hondt 1991; MacLeod 1993). However, *Chiloguembelitria* may be key to elucidating the evolutionary relationships among the earliest Danian guembelitriids. Arenillas et al. (2010) suggested that *Chiloguembelitria* includes at least three species: *Chg. danica* Hofker, 1978, *Chg. irregularis* (Morozova, 1961) and *Ch.* cf. *cretacea*. However, studies of its morphologic variability and species diversity have not been conducted so far.

In this paper, we document new specimens assignable to the genus *Chiloguembelitria* mainly from the El Kef section (Tunisia) in order to assess its taxonomic validity, advance the understanding of its phylogenetic relationships with *Guembelitria*, *Woodringina* and other genera, and determine its species diversity. This review will also help to date and correlate the climatic warming episodes of the early Danian. The bloom of triserial guembelitriids linked to the last volcanic phase of the Deccan has been ascribed to *Guembelitria* (Punekar et al. 2014). Nevertheless, it could in fact be an acme of *Chiloguembelitria*, which replaced *Guembelitria* in the early Danian, occupying the same ecological niche. Considering *Chiloguembelitria* and *Guembelitria* as separate genera will make it possible to differentiate more easily the possible Danian blooms of *Chiloguembelitria* from the PFAS-1 episode (acme of *Guembelitria* inmediately after the K/Pg boundary), recognize and calibrate possible hiatuses in lower Danian sections, and interpret and correlate more accurately the paleoenvironmental changes occurring after the K/Pg boundary extinction event.

2. Material and Methods

Samples for this study were selected from the lower Danian of the El Kef section, Tunisia, which is the Global boundary Stratotype Section and Point for the base of the Danian Stage (Molina et al. 2006). All studied rock samples were disaggregated in water with diluted H_2O_2, washed through a 63 μm sieve, then oven-dried at 50°C. Analyzed specimens were mounted on microslides for a permanent record and identification. Planktonic foraminifera were picked from the residues and selected for scanning electron microscopy (SEM), using the JEOL JSM 6400 and Zeiss MERLIN

FE-SEM of the Electron Microscopy Service of the Universidad de Zaragoza (Spain). The type-specimens of the new species described in this paper were deposited in the Museo de Ciencias Naturales of the Universidad de Zaragoza (Aragon Government, Spain). In addition to El Kef, specimens from other localities have also been taken into account for taxonomic studies, such as those from Elles and Aïn Settara (Tunisia), Caravaca and Agost (Spain), Ben Gurion (Israel), Lynn Creek (Mississippi), Nye Klov (Denmark) and Bajada del Jagüel (Argentina).

For taxonomical and evolutionary studies, we have relied on morphological, morphostatistical, ontogenetic and textural criteria, and a high-resolution biostratigraphy. The morphostatistical studies were based on 124 specimens of *Chiloguembelitria* randomly chosen from lower Danian sample KF19.50 of El Kef (Table 1), 7.5 m above the K/Pg boundary. The foraminiferal preservation in El Kef is good enough to analyze the wall texture, although corroded and recrystallized surfaces can be observed. The ranges of the studied taxa were established after reviewing the high-resolution biostratigraphic data from the El Kef section (Arenillas et al. 2000a), which allowed us to pinpoint the first appearance of the taxa. We 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 greatly expanded Tunisian and Spanish K/Pg sections such as El Kef, Aïn Settara, Elles, Caravaca, Agost and Zumaia (see Molina et al. 2009). Biomagnetochronological calibrations allowed Arenillas et al. (2004) to date the zonal boundaries of their biochronological scale (Figure 1). The section studied at El Kef spans only up to the *Subbotina triloculinoides* Subzone (*Parasubbotina pseudobulloides* Zone) of Arenillas et al. (2004), or Subzone P1b of Berggren and Pearson (2005). For this reason, the range tops of some species have been determined after reviewing previous biostratigraphic studies at Spanish localities such as Caravaca, Agost and Zumaia (see Molina et al. 1998).

[Figure 1 near here]

3. Taxonomic and phylogenetic remarks

All the planktonic foraminiferal taxa studied here have usually been considered to belong to the family Guembelitriidae Montanaro-Gallitelli, 1957, except for *Chiloguembelina* of the family Chiloguembelinidae Reiss, 1963 (Loeblich and Tappan 1987; Olsson et al. 1999), and *Trochoguembelitria* and *Globoconusa*, which have recently been included in the family Globoconusidae BouDagher-Fadel, 2012 (see Arenillas et al. 2016b). Guembelitriidae traditionally includes to planktonic foraminifers with triserial tests, at least in their juvenile stage. Its type-genus, *Guembelitria*, is the only one universally accepted as belonging to it. The other genera included within guembelitriids show serial reduction (*Woodringina*) or proliferation (*Guembelitriella* Tappan, 1940) throughout their ontogeny. *Guembelitriella* was proposed to include irregular multiserial forms in the adult stage, being triserial in the early stage. However, the systematic position of this genus is problematic, since Longoria (1974) and Georgescu (2009) considered that its type-species, *Guembelitriella graysonensis* Tappan, 1940, exhibits a trochospirally coiled test and is morphologically closer to benthic *Praebulimina* Hofker, 1953, than to *Guembelitria*. The *Guembelitriella*-type multiserial forms of the K-Pg transition, assigned to *Guembelitriella postcretacea* Pandey, 1981, were not considered in the taxonomies of Arenillas et al. (2007) and Arz et al. (2010) because they apparently belong to aberrant forms of *Guembelitria*.

According to these authors, all survivor guembelitriids from the K/Pg boundary event belong to *Guembelitria*.

3.1. Upper Cretaceous triserial guembelitriids

Guembelitria is characterized by a test that is wholly triserial (Figure 2), microperforate and with a pore-mounded wall texture (Loeblich and Tappan 1987; Olsson et al. 1999; Georgescu et al. 2011), its type-species being *Guembelitria cretacea* Cushman, 1933. After carrying out a morphostatistical analysis, Arz et al. (2010) proposed three species in *Guembelitria* for the upper Maastrichtian: *G. cretacea* (Figure 2(a)–(d)), *G. blowi* Arz, Arenillas and Náñez, 2010 (Figure 2(e)–(g)), and *G. dammula* Voloshina, 1961 (Figure 2(h)–(k)). Before being described, *G. blowi* was usually named as *Guembelitria trifolia* (Morozova, 1961) because Blow (1979) used the specific name *trifolia* for the low-spired triserial morphotypes. However, the holotype of *Globigerina* (*Eoglobigerina*) *trifolia* Morozova, 1961, is an early Danian trochospiral form that Olsson et al. (1999) later considered to be *Globoconusa*. On the other hand, Cretaceous specimens of *G. dammula* have usually been attributed to *Guembelitria danica* (Hofker, 1978) (e.g. MacLeod 1993). Arenillas et al. (2007) and Arz et al. (2010) pointed out the possible existence of two pseudocryptic species among Danian high-spired *Guembelitria*, both usually referred to *Guembelitria danica* but one exhibiting pore-mounds (*G. danica* sensu MacLeod 1993, and *G. dammula* sensu Arz et al. 2010) and the other imperforate pustules and rugosities (*Chiloguembelitria danica* sensu Hofker 1978). The same applies to the species *Guembelitria irregularis*, herein referred to as *Chiloguembelitria irregularis*, which includes triserial tests of irregular appearance.

[Figure 2 near here]

It is traditionally believed that the chronostratigraphic range of *Guembelitria* spans from the upper Albian to the lower Danian (Loeblich and Tappan 1987; Kroon and Nederbragt 1990). However, Georgescu (2009) restricted its range from the upper Santonian to the lower Daniana, considering that the triserial taxa of the upper Albian to Turonian triserial taxa belong to a different genus, *Archaeoguembelitria* Georgescu, 2009. Georgescu (2009) argued that *Archaeoguembelitria* and *Guembelitria* are not phylogenetically related, and that the first derived from the buliminid *Praeplanctonia* Georgescu, 2009. *Archaeoguembelitria* was excluded from the family Guembelitriidae and assigned to the new family Archaeoguembelitriidae Georgescu, 2009, within the buliminid superfamily Praeplanctonioidea Georgescu, 2009.

A relevant species for the evolutionary history of *Guembelitria* may be *G.*? *turrita* Kroon and Nederbragt, 1990, which ranges from the upper Campanian to the lower Maastrichtian. Georgescu (2009) considered that *G. cretacea* evolved from *G.*? *turrita* during the upper Campanian. However, *G.*? *turrita* has triangular pustules that do not tend to result pore-mounds (Georgescu et al. 2011). In addition, it usually has a buliminid-shaped, asymmetrical aperture (Kroon and Nederbragt 1990), and therefore it may represent a separate lineage of triserial planktonic foraminifera descending from some still unknown buliminid (Georgescu et al. 2011). The benthic species *Neobulimina newjerseyensis* Georgescu, Arz, Macauley, Kukulski, Arenillas and Pérez-Rodríguez, 2011, which exhibits small pustules and incipient circular pore-mounds, may represent a major challenge in deciphering the origin of *Guembelitria*. The evolution of *Guembelitria* from *Neobulimina* would be similar to that from *Praeplanctonia* to *Archaeoguembelitria* in the late Albian. However, the occurrence of clear *G. cretacea* specimens in Santonian sediments means that additional studies are required to define more adequately the stratigraphical distributions of *G.*? *turrita* and *N. newjerseyensis* as presumed ancestors of *G. cretacea* (see Georgescu et al. 2011).

3.2. Biserial and trochospiral lineages of Danian guembelitriids

The Paleogene biserial lineage descending from *Guembelitria* includes *Woodringina* and *Chiloguembelina* (Figure 3). *Woodringina* clusters Danian species with a triserial juvenile stage followed by biserially arranged chambers. Its type-species is *W. claytonensis* Loeblich and Tappan, 1957. The description of its wall texture has varied from one author to another, but it is usually considered to be pustulate with a variable density of pustules, giving an appearance that is smoother if low density or more muricate if high density. Although Loeblich and Tappan (1957) described it as very finely hispid, Loeblich and Tappan (1987) later depicted it as smooth. Olsson et al. (1999) and BouDagher-Fadel (2012, 2015) also suggested a smooth wall for *Woodringina*, though sometimes bearing pore-mounds, at least in the juvenile stage. Arenillas et al. (2007) proposed for *Woodringina* a papillate wall, with imperforate blunt pustules, and suggested that its pustules are ontogenetically linked to modified pore-mounds, which are only present in the most primitive forms (assigned herein to *Chiloguembelitria biseriata* sp. nov.). *Woodringina* is considered the intermediate taxon between *Guembelitria* and *Chiloguembelina* (Olsson et al. 1999). *Chiloguembelina* is characterized by a wholly biserial test, and its wall texture was originally described as smooth or hispid (Loeblich and Tappan 1956), or as granulate by Loeblich and Tappan (1987). Olsson et al. (1999), Huber et al. (2006) and BouDagher-Fadel (2012, 2015) described it as having with numerous small pustules, and Arenillas et al. (2007) as having a finely or moderately papillate surface, with blunt pustules. Four species of *Woodringina* and *Chiloguembelina* have been considered here: *W. claytonensis*

Loeblich and Tappan, 1957 (Figure 3(a), 14(e)–(h)), *W. hornerstownensis* Olsson, 1960 (Figure 3(b)–(f)), *Ch. taurica* Morozova, 1961 (Figure 3(g)–(i)), and *Ch. midwayensis* (Cushman, 1940) (Figure 3(j)–(k)).

[Figure 3 near here]

Various trochospiral genera from the earliest Danian have also been linked to or included in the family Guembelitriidae (Olsson et al. 1999; Arenillas et al. 2007, 2012), such as *Parvularugoglobigerina*, *Palaeoglobigerina*, *Trochoguembelitria*, and *Globoconusa*. The first two have recently been excluded from the guembelitriids (BouDhager-Fadel 2012; Arenillas and Arz 2013a, 2013b), and a benthic origin has been proposed for them (Brinkhuis and Zachariasse 1988; Arenillas and Arz 2016). The Paleogene trochospiral lineage descending from *Guembelitria* includes to *Trochoguembelitria* and *Globoconusa* (Figure 4). The genus *Trochoguembelitria*, whose type-species is *Guembelitria? alabamensis* Liu and Olsson, 1992, was proposed by Arenillas et al. (2012) in order to include trochospiral specimens with a pustulate to rugose wall texture (with decentred pore-mounds and perforate rugosities) previously assigned to *Parvularugoglobigerina* (e.g. Olsson et al. 1999), restricting the latter genus only to species with a smooth wall texture, such as *Pv. eugubina* (Luterbacher and Premoli Silva, 1964) and *Pv. longiapertura* (Blow, 1979). *Trochoguembelitria* may be triserial in the juvenile stage, at least in some specimens of *T. alabamensis*, revealing its triserial evolutionary origin. Arenillas et al. (2012) suggested that *Trochoguembelitria* is the ancestor of the pustulate-walled *Globoconusa*. After carrying out a morphostatistical analysis of *Trochoguembelitria*, Arenillas et al. (2016b) proposed four species: *T. alabamensis* (Liu and Olsson, 1992) (Figure 4(a)–(c)), *T. extensa* (Blow, 1979) (Figure

4(d)–(e)), *T. liuae* Arenillas, Arz and Náñez, 2016 (Figure 4(f)), and *T. olssoni* Arenillas, Arz and Náñez, 2016 (Figure 4(g)). Moreover, three species have been considered in *Globoconusa*: *Gc. daubjergensis* Brönnimann, 1953 (type-species, Figure 4(h)–(i)), *Gc. conusa* Khalilov, 1956 (Figure 4(j)), and *Gc. victori* Koutsoukos, 2014 (Figure 4(k)). The classification of BouDagher-Fadel (2012, 2015) still retained the genus *Postrugoglobigerina* Salaj, 1986, basing it on characters similar to those attributed to *Trochoguembelitria*. However, *Postrugoglobigerina* has been regarded as a *nomen dubium non conservandum* due to the holotypes and type-material of its species have been lost and are of doubtful application (see discussion in Arenillas et al. 2012). Olsson et al. (1999) and Arenillas et al. (2012, 2016b) considered *Postrugoglobigerina* a junior synonym of *Parvularugoglobigerina*. The latter has also usually been included in Guembelitriidae because *Guembelitria* was considered its direct ancestor (Olsson et al. 1999), but recent taxonomic proposals include it, together with *Globanomalina*, in the family Globanomalinidae Loeblich and Tappan, 1984 (e.g. BouDagher-Fadel 2012).

[Figure 4 near here]

4. Textural variability in lower Danian guembelitriids

The wall texture of upper Maastrichtian guembelitriids is usually described as pore-mounded (Loeblich and Tappan 1987; Olsson et al. 1999; Georgescu et al. 2011). The typical pore-mounds of *Guembelitria* are blunt pustules (papilla-type) marked by a more or less centered pore (Figure 5(a)). However, Loeblich and Tappan (1987) and Arenillas et al. (2007, 2010) reported that the microtextural variability among guembelitriids of the lowermost Danian is greater than in the upper Maastrichtian. For example, the most immediate descendants from *Guembelitria*, i.e. *Woodringina* (Figure 5(e)) and

Trochoguembelitria (Figure 5(d)), already had a different type of wall texture (a pustulate or rugose wall), although this clearly evolved from the typical pore-mounded wall of *Guembelitria* (Arenillas et al. 2012, 2016b).

These textural variations may consist of irregular pore-mounds with decentered pores, imperforate pustules that may be blunt or sharp, and a high or low density of pore-mounds and/or imperforate pustules on the surface. Moreover, pore-mounds and blunt pustules can coalesce, generating small, non-aligned rugae or ridges (a rugose wall). Some of these variations can be mixed in a single specimen. In the case of triserial guembelitriids, these other types of wall texture have usually been considered part of the microtextural variability in *Guembelitria* (e.g. Olsson et al. 1999). Although part of this variability could have an ecophenotypic or ontogenetic origin, it has also been related to pseudocryptic speciation, which resulted in species only distinguished by their wall surface under the scanning electron microscope (Arenillas et al. 2010).

[Figure 5 near here]

4.1. Wall textures in lower Danian guembelitriids

Arenillas et al. (2007, 2010, 2012) and Arz et al. (2010) studied and illustrated the textural variability of the guembelitriids of the K-Pg transition, including examples of wall texture assignable to *Chiloguembelitria*. Among the earliest Danian guembelitriids, the following wall textures were recognized:

1) Pore-mounded wall, or papillate wall with pore-mounds (Figure 5(a)): wall texture characterized by blunt pore-mounds irregularly distributed, generally with one pore per papilla, approximately centered (regular pore-mounds), and sometimes two pores per papilla; the density of pore-mounds is variable and, when the density is high, the pore-

mounds can be fused at their bases; this is the wall surface typical of Maastrichtian specimens of *Guembelitria* from tropical to temperate latitudes in both oceanic and neritic environments, and also in lowermost Danian specimens.

2) Pustulate/papillate to rugose wall, with irregular, decentered pore-mounds, imperforate blunt pustules (papilla-type), and imperforate and perforate rugosities (Figure 5(c)–(d)): wall surface characterized mainly by rugosities with or without multiple pores, produced by the coalescence of pore-mounds or imperforate blunt pustules; the pustules may also be sharp (Figure 5(g)); it is microperforate with tiny pores within the rugosities and isolated pore-mounds, and in the smooth surface; pores in rugosities and pore-mounds are very decentered, often situated in the basal part of the ridges or mounds; in specimens with a higher pore density, the rugosities tend to be smaller and more crowded (muricate-type); all these types of pustules and rugosities may be found in a single specimen; this is typical of *Chiloguembelitria* and *Trochoguembelitria*.

3) Pustulate wall, with small blunt pustules (Figure 5(e)–(f)): wall surface with blunt pustules and tiny pores scattered over the smooth surface of the wall; this is typical of *Woodringina* and *Chiloguembelina*; in specimens – mainly of *Woodringina* – with higher pore density, the pustules tend to be smaller and more crowded (muricate-type); in specimens – mainly of *Chiloguembelina* – with low pustule density or smaller pustule size, the wall surface looks smooth.

4) Pustulate wall, with sharp pustules (Figure 5(h)): wall surface with sharp pustules and small pores scattered over the smooth surface of the wall; the pustules may also be blunt; both sharp and blunt pustules may be found in a single specimen; the density of pustules is usually low; this is typical of *Globoconusa*.

Additionally, Loeblich and Tappan (1987) and Arenillas et al. (2010) distinguished a granular or granulate wall in guembelitriids or in evolutionarily and/or ecologically associated taxa (e.g. *Chiloguembelina* and/or *Parvularugoglobigerina*). This is characterized by minute calcite crystallites with in a mosaic or jagged shape over the entire test surface (Figure 5(b)). Salaj (1986) defined at El Kef two new Danian species of *Guembelitria* (*G. besbesi* and *G. azzouzi*) that were also described as having small pustules, referring probably to a granulate wall texture. Although these species were later considered junior synonyms of *G. cretacea* (Olsson et al. 1999) and should be regarded as *nomina dubia non conservanda* like the *Postrugoglobigerina* species (see discussion in Arenillas et al. 2012), this is not the last time that this wall texture has been recognized in guembelitriids. Arz et al. (2010) and Arenillas et al. (2010) suggested that – unlike the specimens of other taxa in the same samples of Tunisian sections – the wall surface of many Maastrichtian and Danian specimens of *Guembelitria* is covered by a secondary granular crust (Figure 2(c), (g)). Without ruling out the recrystallization processes which are usual in Tunisian sections, the authors postulated that the granular wall could also be related to gametogenetic calcification, i.e. a secondary outer calcite crust covering the normal pore-mounded surface. Some specimens of guembelitriids show a granulate surface in all chambers except in the last ones (e.g. Figure 2(l)), suggesting the likelihood of such a proposal. However, due to the inability to demonstrate the difference between the diagenetically modified gametogenetic calcification and the recrystallization itself, the suggestion of a granular crust is here considered highly speculative for now.

4.2. Wall texture in Chiloguembelitria

Loeblich and Tappan (1987) considered that the main diagnostic character of *Chiloguembelitria* is its wall texture, which made it possible to differentiate it from

Guembelitria. Hofker (1978) specified its wall texture by studying the type-species *Chg. danica*, describing it as having small blunt pustules. Studying topotypes of *Chg. danica,* Loeblich and Tappan (1987) concluded that *Chiloguembelitria* has a surface that is finely pustulose but lacks pore-mounds. Later, Arenillas et al. (2010) described it as papillate to rugose, with perforate or imperforate pustules and rugosities, and BouDagher-Fadel (2012, 2015) as muricate, i.e. surface possessing high density of pustules.

Kroon and Nederbragt (1990), D'Hondt (1991), MacLeod (1993), Jenkins et al. (1998) and Olsson et al. (1999) among others have proposed, however, that *Chiloguembelitria* is a junior synonym of *Guembelitria,* claiming that both genera bear pore-mounds. MacLeod (1993) illustrated Maastrichtian specimens assigned to *Guembelitria danica* exhibiting well-developed pore-mounds, and suggested that both *G. cretacea* and *Chg. danica* – although distinct species – belong to the genus *Guembelitria*, *Chiloguembelitria* being a junior synonym. However, Maastrichtian specimens morphologically similar to the holotype of *Chg. danica* have recently been attributed to *G. dammula* (Arz et al. 2010). Because the holotype of *Chg. danica* cannot found (depository not given by the author), Jenkins et al. (1998) chose topotypes of *Chg. danica* and designated a neotype. They conclude that these type-specimens bear pore-mounds similar to those of *Guembelitria*, supporting the idea that the two genera are synonymous. However, the specimens that they illustrated are poorly preserved and seem to have imperforate pustules and rugosities, including the neotype of *Chg. danica* selected by them. For these reasons, Arz et al. (2010) concluded that the presence of regular pore-mounds in *Chg. danica* is very dubious, and proposed that their taxonomy should be clarified by carrying out a more profound study of the wall texture and morphology of this genus and other Danian guembelitriids.

5. Morphological variability in lower Danian guembelitriids

5.1. Gross morphology

At the genus level, the serial guembelitriids were usually classified in accordance with their chamber arrangement (Figure 6(a)), distinguishing the wholly triserial forms (*Guembelitria*) and the triserial-biserial mixed forms (*Woodringina*). The types of wall texture identified seemed to fit well with these two genera, *Guembelitria* having a pore-mounded wall (usually with regular pore-mounds) and *Woodringina* a papillate or pustulate wall (usually with a high density of blunt pustules).

At the species level, the main diagnostic criterion used in guembelitriids is the spire height, bearing in mind that triserial and biserial are spiral forms with three and two chambers per whorl respectively (Tyszka 2006; Figure 6). In *Guembelitria* (Arz et al. 2010), three species were distinguished according to whether they are low-spired (*G. blowi*, or *G. trifolia* for some authors), medium-spired (*G. cretacea*), or high-spired (*G. dammula*, or *G. danica* for some authors). Triserial guembelitriids of irregular appearance (twisted test) have usually been classified within *G. irregularis* (herein *Chiloguembelitria irregularis*). The separation of regular and "irregular" triserial guembelitriids can be established using the rotation angle β, so that when β is approximately between 120º and 130º they have a regular appearance (with some twisting when further away from 120º) and when more than 130º they have an irregular appearance (Figure 6(a)). In the adult stage, the spire height of *Chg. irregularis* is great, similar to that of *G. dammula* or that of the original holotype of *Chg. danica*.

[Figure 6 near here]

In *Woodringina* (Olsson et al. 1999; Arenillas et al. 2007), two species have been distinguished according to whether they are low-spired (*W. claytonensis*) or high-spired (*W. hornerstownensis*). The triserial juvenile stage of many specimens of *W. claytonensis* and *W. hornerstownensis*, mainly the most modern ones, is greatly shrunken (pseudotriserial, β ≈ 140-170º) or absent (biserial, β ≈ 170-180º) (Figure 6(a)). Those that have a gross morphology similar to *W. claytonensis* have been assigned to *Woodringina kelleri* MacLeod, 1993, and those similar to *W. hornerstownensis* have usually been assigned to *Chiloguembelina morsei* (Kline, 1943) or *Chiloguembelina* cf. *morsei* (e.g. D'Hondt 1991; Olsson et al. 1999; Arenillas and Arz 2000; Arenillas et al. 2000a, 2000b). MacLeod (1993) remarked that *W. kelleri* differs from *W. claytonensis* in its laterally compressed adult chambers, and especially in its large, elongate aperture. Olsson et al. (1999) considered *W. kelleri* to be a junior synonym of *W. claytonensis* adducing that the differences proposed by MacLeod (1993) appear insufficient to warrant maintenance of *W. kelleri* as a separate taxon. Arenillas et al. (2007) considered *Ch. morsei* (Figure 3(l)) to be a junior synonym of *Chiloguembelina midwayensis* (Cushman, 1940), since their holotypes are almost indistinguishable, and re-assigned the high-spired specimens with a shrunken triserial initial stage within the morphological variability of *W. hornerstownensis*.

Considering how species are discriminated in *Guembelitria* and *Woodringina*, it is consistent to expect the existence of several species within *Chiloguembelitria* distinguishable only by the spire height, as proposed Arenillas et al. (2010). In addition to *Chg. danica* (sensu the original holotype of Hofker, 1978) and *Chg. irregularis*, Arenillas et al. (2010) suggested the existence of a new pseudocryptic species in the early Danian similar to *G. cretacea* but with rugose wall, which was provisionally named *Ch.* cf. *cretacea* (assigned herein to *Chg. danica* sensu the neotype of Jenkins et al., 1998).

5.2. Aperture position and shape

Another of the criteria used to distinguish *Guembelitria* and *Chiloguembelitria* is the position and shape of the aperture (Hofker 1978), because the *Chiloguembelitria* aperture was originally described as more similar to that of *Chiloguembelina* than to that of *Guembelitria*. Following the terminologies of Li (1987), Li et al. (1992) and BouDagher-Fadel (2012) for describing the position and morphology of the aperture, Arenillas et al. (2016b) considered two types of apertural position in triserial-trochospiral tests: umbilical and umbilical-extraumbilical (Figure 6(b)), subdividing the first into two subtypes: intraumbilical and anterio-intraumbilical, and the second into another two subtypes: intra-extraumbilical and umbilical-peripheral. The apertures outside the umbilicus may also be subdivided into three other subtypes (Figure 6(b)): extraumbilical, equatorial (in spiral tests) and lateral (in biserial tests). According to this terminology, most of the *Chiloguembelitria* specimens present umbilical-peripheral or extraumbilical (rarely intra-extraumbilical) apertures, or lateral ones if they have a more developed biserial stage. This diagnostic character separates *Chiloguembelitria* from *Guembelitria*, whose species usually have intraumbilical or anterio-intraumbilical apertures.

The apertures of the studied planktonic foraminifera have the following morphologies: (a) a rounded, wide arch, (b) a marginally/laterally elongate, wide arch, and (c) a high arch (like a loop). Most of the *Chiloguembelitria* specimens exhibit apertures with a marginally or laterally elongate, wide arch, but rounded apertures similar to those of *Guembelitria* and *Trochoguembelitria* are also frequent. The apertural shape in *Chiloguembelitria* is almost identical to that of *Woodringina*, although species of the latter tend to acquire an aperture with a higher arch, as in *Chiloguembelina*. The aperture of all these genera is surrounded by a thin imperforate lip, although some tend to acquire a thicker lip as in *Chiloguembelina*.

6. Morphostatistical analysis of wholly triserial *Chiloguembelitria*

The biometric and morphostatistical analysis has been applied to "regular", wholly triserial specimens (Figure 6(a)) of *Chiloguembelitria*. The identification of other species in *Chiloguembelitria* was based on qualitative morphological criteria, i.e. their gross morphology: a strongly twisted, triserial test for *Chg. irregularis*, and a biserial final stage for *Chg. biseriata* sp. nov.

6.1. Biometric parameters and indices and morphostatistical analyses

The biometric parameters used to delimit species are the following (Figure 6(c)–(d); Table 1): convexity angle (α) measured in axial view; length (L), width (W) and height (H) of the test; and length (CL), width (CW) and height (CH) of the chamber, used to calculate the chamber average diameter $CAD = (CL \times CW \times CH)^{1/3}$. In addition, we used the biometric indices H/L and CAD/H (Table 1). Other biometric indices have been explored, but these have not given consistent results for separating species.

[Table 1 near here]

For morphostatistical analyses, the software used was the program PAST, version 3.11, by Hammer et al. (2001). The biometric parameters and indices were treated statistically using the following analyses:

1) Univariate analyses: Two of the above-mentioned biometric indices (α and H/L) were analyzed in an univariate manner in order to ascertain whether these biometric variables are useful for discriminating species; the results of the univariate analyses were displayed as histograms of 20 bins (Figure 7). Mixture analysis was applied to each biometric variable in order to identify two or more univariate normal distributions (Gaussian bell-shaped curves) based on a pooled univariate sample; this method is used to identify species and study differences between them; Kernel density estimates were also plotted on histograms.

2) Bivariate analyses: Variables α vs H/L were used to make bivariate analyses. Kernel density estimates allowed us to make smooth maps of point density in XY graphs (Figure 8); the density estimate is based on a Gaussian function, and scales give an estimate of the number of points per area, not a probability density.

3) Multivariate analyses: R-mode cluster analysis and principal component analysis (PCA) were used; the cluster analyses were based on Bray-Curtis index measures among all specimens using the values of the above-mentioned biometric indices/parameters (α, H/L and CAD/H) in order to find groupings that might represent species (Figure 9). The PCA was applied to the values of the three biometric indices/parameters (original variables). Such an analysis finds hypothetical variables (components) that account for as much of the variance in the multidimensional data as possible by reducing the data set to two variables (the two most important components) through a routine that finds eigenvalues and eigenvectors (i.e. components) of the variance-covariance correlation matrix. All the original data points were plotted as an XY graph in the coordinate system given by the two most important components (PC1 and PC2) to enhance visualization of the data sets representing the possible species (Figure 10); 95% confidence ellipses, which assume a bivariate normal distribution, and

convex hulls, which are the smallest convex polygons containing all points, were presented in the scatter diagram.

6.2. Results of the morphostatistical analysis

The morphological and morphostatistical analyses discriminate at least three species within *Chiloguembelitria*. Whether or not the statistically identified morphogroups are biological species is a question that we do not intend to clarify. Nevertheless, there is no doubt that the three identified species fall within the concept of morphospecies, which is based on overall morphological similarity, and defined as the smallest morphogroup that is consistently and persistently distinct.

[Figure 7 near here]

[Figure 8 near here]

Frequency distributions of the univariate analyses (Figure 7), calculated for all measured specimens and represented in plot histograms of 20 bins, suggest three morphogroups of *Chiloguembelitria*, as also suggested by Gaussian bells and Kernel density estimates. Both α and H/L variates seem to distinguish three groups, a low-spired group, assigned to *Chg. trilobata* sp. nov., a medium-spired group, assigned to *Chg. danica*, and a high-spired group, assigned to *Chg. hofkeri* sp. nov.. Bivariate analyses (Figure 8) also strongly suggest that the genus *Chiloguembelitria* contains the three above-mentioned species; these are well observable in the Kernel density maps.

[Figure 9 near here]

Cluster analysis (Figure 9), based on the Bray-Curtis similarity index, produced dendrograms with two primary clusters, one grouping the morphotypes with a low-spired test (*Chg. trilobata* sp. nov.), and the other those with a high-medium-spired test, which is subdivided into two sub-clusters, one grouping medium-spired (*Chg. danica*) and the other high-spired morphogroups (*Chg. hofkeri* sp. nov.). The two resulting dendrograms, one based on α and H/L variables (Figure 9(a)) and the other on α, H/L and CAD/H variables (Figure 9(b)), made it possible to discriminate the three above-mentioned species. The principal component analysis (PCA) based on α, H/L and CAD/H variables showed similar results to those of the cluster analysis (Figure 10). The principal component PC1 explains 94.5% of the variance. The PCA scatter diagram, where X and Y are the principal components PC1 and PC2, distinguishes three sets of points of higher density. We specified three groups of specimens, clustering them subjectively by their gross morphology. These are approximately equivalent to those obtained by the PCA. Except for the intermediate and/or anomalous specimens, the convex hulls and 95% confidence ellipses clearly delimit the three above-mentioned species. Their main characteristics are easily recognizable under the stereomicroscope.

[Figure 10 near here]

7. Paleontological systematics

Olsson et al. (1999) showed that the phyletic relationship of *Trochoguembelitria* (*Parvularugoglobigerina* according to them), *Globoconusa*, *Woodringina*, and *Chiloguembelina* with *Guembelitria* indicates that trochospiral and biserial chamber arrangements evolved divergently within the planktonic foraminifera. Such relationships are not clearly accounted for by taxonomic schemes, which separate serial and trochospiral morphotypes at the superfamily level (e.g. Loeblich and Tappan 1987). It is broadly accepted that *Chiloguembelina* is lineally derived from *Guembelitria*, via *Woodringina* (Olsson 1970; Li and Radford 1991; Liu and Olsson 1992; D'Hondt 1991). The phylogenetic relationship between *Chiloguembelina* and *Guembelitria* indicates that Guembelitriidae constitutes a paraphyletic family because it does not include descendant species assigned to the family Chiloguembelinidae (Olsson et al. 1999). Moreover, BouDagher-Fadel (2012, 2015) assigned the trochospiral guembelitriiids *Trochoguembelitria* (*Postrugoglobigerina* according to the author) and *Globoconusa* to the family Globoconusidae.

The new evidence reported here indicates that it is advisable to reconsider the validity of the genus *Chiloguembelitria*, as its wall texture is distinguishable from those of *Guembelitria*, and very similar to those described in *Trochoguembelitria* and in some of the earliest specimens of *Woodringina*. Furthermore, the position of its aperture also differs from that of *Guembelitria*. *Chiloguembelitria* should be assigned to the family Guembelitriidae together with *Guembelitria* and *Woodringina*. The proposed phylogenetic relationships of these genera are illustrated in Figure 11.

[Figure 11 near here]

The family Guembelitriidae is usually included in the superfamily Heterohelicoidea Cushman, 1927, which has been excluded from the order Globigerinida Lankaster, 1885, in more recent taxonomies (e.g. BouDagher-Fadel 2012), and included separately in the order Heterohelicida Fursenko, 1958. However, if it is confirmed that *Guembelitria* evolved from the benthic *Neobulimina* or a similar buliminid, as

Georgescu et al. (2011) proposed, the family Guembelitriidae should also be excluded from the superfamily Heterohelicoidea and the order Heterohelicida.

? Order **Heterohelicida** Fursenko, 1958

? Superfamily **Heterohelicoidea** Cushman, 1927

Family Guembelitriidae Montanaro-Gallitelli, 1957

Genus ***Chiloguembelitria*** Hofker, 1978, emended

Type species. *Chiloguembelitria danica* Hofker, 1978

Type description. Test small, elongate, wholly triserial. All foramina and the aperture are placed axially and perpendicular to the sutures, are slit-like elongate, with a distinct lip which is crenulate at the axial side of the border of the apertures, as in *Chiloguembelina*. It is like a *Guembelina* in which the biserial part is not yet developed, and may be the true ancestor of that genus. Both *Chiloguembelitria* and *Chiloguembelina* are monolamellar.

Emended description. Test small, subconical, wholly triserial tending to biserial, or with an undeveloped biserial final stage. Chambers subspherical or globular. Outline lobate, with incised sutures. Aperture interiomarginal, umbilical-extraumbilical to extraumbilical (in the middle part of the suture between the last and the penultimate chamber), rounded or elongate arch, generally asymmetrical, with an imperforate lip. Wall calcareous, hyaline, microperforate, pustulate to rugose, with irregular or decentered pore-mounds, imperforate blunt pustules (papilla-type), occasionally sharp pustules, and both perforate and imperforate rugosities; rugosities and pustules irregularly distributed.

Remarks. *Chiloguembelitria* was originally described in the lower Danian as having a wholly triserial test, as *Guembelitria*, but with an aperture more similar to that of the biserial genus *Chiloguembelina*. Hofker (1978) and Loeblich and Tappan (1987) showed that the main diagnostic characters of *Chiloguembelitria* are its aperture shape (similar to *Chiloguembelina*) and its wall texture with imperforate blunt pustules. Kroon and Nederbragt (1990), D'Hondt (1991), MacLeod (1993), Jenkins et al. (1998) and Olsson et al. (1999) suggested that *Chiloguembelitria* is a junior synonym of *Guembelitria*, after concluding that its species bear pore-mounds similar to those of *Guembelitria*. However, well-preserved Danian specimens of *Chg. danica* from DSDP Site 47.2, Shatsky Rise (North Pacific) exhibit imperforate blunt pustules and rugosities (Loeblich and Tappan 1987), which is different from the wall texture of Maastrichtian specimens. Arz et al. (2010) and BouDagher-Fadel (2012, 2015) argued that *Chiloguembelitria* is a valid taxon, since its wall texture and apertural position differ from *Guembelitria*. Arenillas et al. (2010) described its wall texture as pustulate/papillate to rugose, and BouDagher-Fadel (2012, 2015) as muricate (a surface with a high density of pustules).

***Chiloguembelitria danica* Hofker, 1978**

(Figure 5(g); Figs 12(c)–(g))

non 1978 *Chiloguembelitria danica* Hofker, p. 60, holotype: pl. 4, figs. 14.

non 1987 *Guembelitria danica* (Hofker); Loeblich and Tappan, p. 452, part, topotype: pl. 484, fig. 8.

non 1993 *Guembelitria danica* (Hofker); MacLeod, pl. 3, figs. 1, 5.

1998 *Guembelitria danica* (Hofker); Jenkins et al., p. 64, part, neotype: pl. 1, fig. 1; topotype: pl. 1, fig. 5.

non 2007 *Guembelitria danica* (Hofker); Arenillas et al., p. 38, figs. 13.14–17.

Type description. Test small, elongate, with triserially arranged chambers throughout. Chambers globular, with distinctly depressed sutures in between, gradually increasing in size so that the whole test remains slender. Walls thin, consisting of only one lamella, without secondary thickening. Walls finely perforate, with small blunt pustules. Aperture high, elongate, narrow, with protruding lip at the axial side of the aperture, as in *Chiloguembelina*. Length of test up to 0.1 mm; larger breadth near the apertural end 0.05 mm.

Emended description. Test subconical, medium-spired although higher than wide or long. Triserial arrangement, often slightly twisted, with 9–12 subspherical chambers distributed in 3–4 spiral whorls, with a moderate rate of chamber enlargement. Outline subtriangular, lobate, with incised sutures. Aperture interiomarginal, umbilical-extraumbilical to extraumbilical, rounded or elongate, generally asymmetrical, surrounded by an imperforate lip. Wall surface microperforate, pustulate to rugose, with isolated, decentered pore-mounds, perforate and/or imperforate rugosities, and blunt pustules (papilla-type) and/or sharp pustules. Adult size range 100–150 µm in height.

Occurrence. Lowermost Danian, from the upper part of Zone P0 to the lower part of Zone P1c of Berggren and Pearson (2005), i.e. from the upper part of the *Hedbergella holmdelensis* Subzone (*Guembelitria cretacea* Zone) to the lower part of the *Globanomalina compressa* Subzone (*Parasubbotina pseudobulloides* Zone) of Arenillas et al. (2004). It is very frequent in the *Eoglobigerina trivialis* Subzone (*Parasubbotina pseudobulloides* Zone), i.e. in P1a (Figure 1).

Remarks. Kroon and Nederbragt (1990) suggested that *Chg. danica* is a junior synonyms of *G. cretacea*, assuming that it bears pore-mounds. However, the presence of regular pore-mounds in *Chg. danica* is doubtful (Hofker 1978; Loeblich and Tappan 1987; Arz et al. 2010; Arenillas et al. 2010; BouDagher-Fadel 2012, 2015). Morphologically, *G. dammula* is very similar to the original illustration of the holotype of *Chg. danica*. Since many authors have considered that *Guembelitria* and *Chiloguembelitria* are synonymous genera, the Maastrichtian high-spired guembelitriids assigned to *Guembelitria dammula* Voloshina, 1961, by Arz et al. (2010) have frequently been named *Guembelitria danica* (e.g. MacLeod 1993). In any case, *G. dammula* was originally defined from Maastrichtian beds and has priority in date of publication over the species defined by Hofker (1978). The neotype selected by Jenkins et al. (1998) for *Chg. danica* (Figure 12(c)) has a medium-spired test similar to that of *G. cretacea*, thus not reflecting the original morphology (high-spired test) of the Hofker's holotype (Figure 12(a)). Nevertheless, the designated neotype has priority according to the Article 75 of International Code of Zoological Nomenclature, so that the name "*danica*" should be used to refer to *Chiloguembelitria* specimens with a medium-spired test.

[Figure 12 near here]

***Chiloguembelitria irregularis* (Morozova, 1961)**

(Figure 12(i)–(n))

1961 *Guembelitria irregularis* Morozova, p. 17–18, pl. 1, figs. 9–10.

1987 *Guembelitria danica* (Hofker); Loeblich and Tappan, p. 452, part, pl. 484, figs. 7, 9.

1993 *Guembelitria irregularis* Morozova; MacLeod, pt. 3, figs. 2–4, 6–7.

1998 *Guembelitria danica* (Hofker); Jenkins et al., p. 64, part, pl. 1, figs. 4, 6.

2007 *Guembelitria*? *irregularis* Morozova; Arenillas et al., p. 38-39, figs. 13.9–13.

Type description. Test high, height two to three times exceeding the diameter. Initial end pointed, initial angle about 30°. Apertural end rounded. Spire consists of seven to eight whorls. The number of chambers in each whorl is not uniform, sometimes two and a half, sometimes three, so the chambers do not form regular rows. In all mature forms there are 17–20 subspheroidal chambers. Sutures deep. Aperture semilunate, basal. Wall smooth, semitransparent. Surface weakly rough [Translation from the Russian].

Emended description. Test elongated, subconical, high-spired. Triserial arrangement, twisted with irregular appearance, with 11–17 subspherical chambers distributed in 3.5–5.5 spiral whorls, with low rate of chamber enlargement. Outline subtriangular, lobate, with incised sutures. Aperture interiomarginal, usually extraumbilical, rounded or elongate, generally asymmetrical, with an imperforate lip. Wall surface microperforate, pustulate to rugose, with isolated, decentered pore-mounds, perforate and/or imperforate rugosities, and blunt pustules (papilla-type). Adult size range 120–180 µm in height.

Occurrence. Lowermost Danian, from the lower part of Zone Pα to the middle part of Zone P1b of Berggren and Pearson (2005), i.e. from the lower part of the *Parvularugoglobigerina longiapertura* Subzone (*Guembelitria cretacea* Zone) to the middle part of the *Subbotina triloculinoides* Subzone (*Parasubbotina pseudobulloides* Zone) of Arenillas et al. (2004). It is frequent in the *Eoglobigerina trivialis* Subzone (*Parasubbotina pseudobulloides* Zone), i.e. in P1a (Figure 1).

Remarks. It differs from *Chg. danica* in the twisted triserial test that gives it an irregular appearance. It also differs from other *Chiloguembelitria* species with "regular" rather than twisted triserial tests (*Chg. hofkeri* sp. nov. and *Chg. trilobata* sp. nov.) in its higher spire, similar to *Chg. danica*. As was suggested by Arz et al. (2010), the species name *irregularis* may have been used as a “wastebasket” grouping earliest Danian species with a pustulate to rugose wall (Loeblich and Tappan 1987) and both Maastrichtian and Danian aberrant forms with different types of wall texture. *Chg. irregularis* should thus not be confused with aberrant forms or with some specimens of *Guembelitria* with a relatively twisted test.

***Chiloguembelitria hofkeri* sp. nov.**

(Figure 5(c); Figs 12(h); Figs 13(a)–(d))

1978 *Chiloguembelitria danica* Hofker, p. 60, pl. 4, figs. 14.

1987 *Guembelitria danica* (Hofker); Loeblich and Tappan, p. 452, part, pl. 484, fig. 8.

non 1993 *Guembelitria danica* (Hofker); MacLeod, pl. 3, figs. 1, 5.

2007 *Guembelitria danica* (Hofker); Arenillas et al., p. 38, figs. 13.14–17.

Type-specimens. Holotype MPZ 2016/108 (Figure 13(a)). Paratype MPZ 2016/109 (Figure 13(b)). MPZ 2016/110 (Figure 13(c)). Paratype MPZ 2016/111 (Figure 13(d)). Type-specimens deposited in the Museo de Ciencias Naturales de la Universidad de Zaragoza (Aragon Government, Spain).

Diagnosis. Test elongated, subconical, high-spired. Triserial arrangement, often slightly twisted, with 11–14 subspherical chambers distributed in 3.5–4.5 spiral whorls, with low rate of chamber enlargement. Outline subtriangular, lobate, with incised sutures. Aperture interiomarginal, umbilical-extraumbilical to extraumbilical, rounded or elongate, generally asymmetrical, with an imperforate lip. Wall surface microperforate, pustulate to rugose, with isolated, decentered pore-mounds, perforate and/or imperforate rugosities, and blunt pustules (papilla-type). Adult size range 120–180 µm in height.

Derivation of name. Species dedicated to Jan Hofker for the discovery and definition of the Danian genus *Chiloguembelitria*.

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

Type level. 7.50 m above the Cretaceous/Paleogene boundary of the El Kef section (sample KF19.50), in the lower part of Zone P1a, or the middle part of the *Eoglobigerina trivialis* Subzone (*Parasubbotina pseudobulloides* Zone), lower Danian.

Occurrence. Lowermost Danian, from the upper part of Zone P0 to the middle part of Zone P1b of Berggren and Pearson (2005), i.e. from the upper part of the *Hedbergella holmdelensis* Subzone (*Guembelitria cretacea* Zone) to the middle part of the *S. triloculinoides* Subzone (*Parasubbotina pseudobulloides* Zone) of Arenillas et al. (2004). It is very frequent in the *Eoglobigerina trivialis* Subzone (*Parasubbotina pseudobulloides* Zone), i.e. in P1a (Figure 1).

Remarks. It differs from *Chg. danica* in having a higher-spired test. The gross morphology of *Chg. hofkeri* sp. nov. is similar to the original holotype of *Chg. danica* illustrated by Hofker (1978). Nevertheless, because this holotype was invalidated (depository not given by the author), the name "*danica*" should be used to refer to *Chiloguembelitria* specimens with a medium-spired test, such as the neotype designated by Jenkins et al. (1998). The difference in spire height of *Chg. hofkeri* sp. nov. from *Chg. danica* and *Chg. trilobata* sp. nov. is similar to that of *Guembelitria dammula* from *G. cretacea* and *G. blowi* (Arz et al. 2010). These two triplets of species differ from each other in the wall texture and the position and shape of the aperture. Danian specimens of *Chg. hofkeri* sp. nov. have commonly been attributed to *G. cretacea* (MacLeod 1993; Olsson et al. 1999; Arenillas et al. 2000a, 2000b), but Arenillas et al.

(2007) and Arz et al. (2010) have already pointed out the possible existence in the early Danian of a pseudocryptic species similar to *Guembelitria* spp. but with a rugose wall.

[Figure 13 near here]

***Chiloguembelitria trilobata* sp. nov.**

(Figure 13(e)–(h))

Type-specimens. Holotype MPZ 2016/112 (Figure 13(e)). Paratype MPZ 2016/113 (Figure 13(f)). MPZ 2016/114 (Figure 13(g)). Paratype MPZ 2016/115 (Figure 13(h)). Type-specimens deposited in the Museo de Ciencias Naturales de la Universidad de Zaragoza (Aragon Government, Spain).

Diagnosis. Test short subconical, low-spired. Triserial arrangement, often slightly twisted, with 8–11 subspherical chambers distributed in 2.5–3.5 spiral whorls, with a high rate of chamber enlargement. Outline subtriangular, lobate, with incised sutures. Aperture interiomarginal, umbilical-extraumbilical to extraumbilical, generally rounded and asymmetrical, with an imperforate lip. Wall surface microperforate, pustulate to rugose, with isolated, decentered pore-mounds, perforate and/or imperforate rugosities, and blunt pustules (papilla-type) and/or sharp pustules. Adult size range 90–120 µm in height.

Derivation of name. Latin term *trilobata* referring to the shape of *three lobes* in the equatorial outline.

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

Type level. 7.50 m above the Cretaceous/Paleogene boundary of the El Kef section (sample KF19.50), in the uppermost part of Zone Pα, or the lower part of the *Eoglobigerina trivialis* Subzone (*Parasubbotina pseudobulloides* Zone), lower Danian.

Occurrence. Lower Danian, from the lower part of Zone Pα to the upper part of Zone P1b of Berggren and Pearson (2005), i.e. from the uppermost part of the *Parvularugoglobigerina longiapertura* Subzone (*Guembelitria cretacea* Zone) to the lower part of the *Globanomalina compressa* Subzone (*Parasubbotina pseudobulloides* Zone) of Arenillas et al. (2004). It is very frequent in the *Eoglobigerina trivialis* Subzone (*Parasubbotina pseudobulloides* Zone), i.e. in P1a (Figure 1).

Remarks. It differs from *Chg. danica* in having a lower triserial test. Specimens of *Chg. trilobata* sp. nov. have been probably attributed to *Guembelitria blowi* (or *G. trifolia* for some authors; MacLeod 1993; Arenillas et al. 2000a, 2000b) or *G. cretacea* (Olsson et al. 1999). Nevertheless, Arenillas et al. (2007) and Arz et al. (2010) pointed out the possible existence of pseudocryptic species of *Guembelitria* spp. in the lower Danian, referring to some of the *Chiloguembelitria* species defined here. The gross morphology and size of *Chg. trilobata* sp. nov. resemble those of *Trochoguembelitria alabamensis*, with which it shares the wall texture but from which it differs in the chamber arrangement (triserial vs. trochospiral).

[Figure 14 near here]

Chiloguembelitria biseriata sp. nov.

(Figure 14(a)–(d))

? 1998 *Guembelitria danica* (Hofker); Jenkins et al., p. 64, part, pl. 1, fig. 3.

? 1999 *Woodringina claytonensis* Loeblich and Tappan; Olsson et al., p. 242, pl. 68, fig. 1.

Type-specimens. Holotype MPZ 2016/116 (Figure 14(a)). Paratype MPZ 2016/117 (Figure 14(b)). MPZ 2016/118 (Figure 14(c)). Paratype MPZ 2016/119 (Figure 14(d)). Type-specimens deposited in the Museo de Ciencias Naturales de la Universidad de Zaragoza (Aragon Government, Spain).

Diagnosis. Test subconical to flaring, with 7–10 subspherical chambers and a medium-to-high rate of chamber enlargement. Triserial juvenile stage with 5–6 chambers distributed in 1.5–2 spiral whorls, and biserial final stage with 1–2 pairs of chambers in a twisted plane of biseriality. Outline subtriangular, lobate, with incised sutures. Aperture interiomarginal, lateral, rounded or elongate, generally asymmetrical, with an imperforate lip. Wall surface microperforate, pustulate to rugose, with isolated, decentered pore-mounds, perforate and/or imperforate rugosities, and blunt pustules (papilla-type). Adult size range 120–160 µm in height.

Derivation of name. Latin term *biseriata* referring to the *biserial* final stage of its ontogeny.

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

Type level. 8.50 m above the Cretaceous/Paleogene boundary of the El Kef section (sample KF20.50), in the lower part of Zone P1a, or middle part of the *Eoglobigerina trivialis* Subzone (*Parasubbotina pseudobulloides* Zone), lower Danian.

Occurrence. Lowermost Danian, from the lower part of Zone Pα to the upper part of Zone P1a of Berggren and Pearson (2005), i.e. from the lower part of the *Parvularugoglobigerina longiapertura* Subzone (*Guembelitria cretacea* Zone) to the upper part of the *Subbotina trivialis* Subzone (*Parasubbotina pseudobulloides* Zone) of

Arenillas et al. (2004). It is not abundant, and is easily confused with *Woodringina claytonensis* (Figure 1).

Remarks. It differs from other *Chiloguembelitria* species in its final biserial stage. The species *Chg. biseriata* sp. nov. has previously gone unnoticed because it is morphologically very similar to *Woodringina claytonensis*. However, *W. claytonensis* differs in its wall surface (pustulate or muricate rather than rugose, and without pore-mounds) and its reduced triserial initial stage (single whorl of three-chambered stage, usually pseudotriserial rather than triserial). Olsson et al. (1999) included these morphotypes within the phenotypic variability of *W. claytonensis*, adducing that some specimens of *Woodringina* bear scattered pore-mounds. However, typical *W. claytonensis* has a pustulate wall like other species of *Woodringina* and *Chiloguembelina*, consisting of small imperforate blunt pustules (papilla-type). Many pustules in the wall of *Woodringina* may have the same ontogenetic origin as the pore-mounds in *Guembelitria*, although others perhaps may not.

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References

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

Arenillas I, Arz JA. 2013a. Origin and evolution of the planktic foraminiferal Family Eoglobigerinidae Blow (1979) in the early Danian (Paleocene). Rev. Mex. Cienc. Geol. 30(1):159–177.

Arenillas I, Arz JA. 2013b. New evidence on the origin of nonspinose pitted-cancellate species of the early Danian planktonic foraminifera. Geol. Carpath. 64(3):237–251.

Arenillas I, Arz JA. 2016. Benthic origin and earliest evolution of the first planktonic foraminifera after the Cretaceous/Paleogene boundary mass extinction. Hist. Biol. 1–18, doi: 10.1080/08912963.2015.1119133.

Arenillas I, Arz JA, Molina E, Dupuis C. 2000a. An independent test of planktic foraminiferal turnover across the Cretaceous/Paleogene (K/P) boundary at El Kef, Tunisia: Catastrophic mass extinction and possible survivorship. Micropaleontology 46(1):31–49.

Arenillas I, Arz JA, Molina E, Dupuis C. 2000b. The Cretaceous/Paleogene (K/P) boundary at Aïn Settara, Tunisia: sudden catastrophic mass extinction in planktic foraminifera. J. Foramin. Res. 30(3):202–218.

Arenillas I, Arz JA, Molina E. 2002. Quantifying the evolutionary turnover across the K/T boundary catastrophic planktic foraminiferal extinction event at El Kef, Tunisia. GFF 124:121–126.

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

Arenillas I, Arz JA, Grajales-Nishimura JM, Murillo-Muñetón G, Alvarez W, Camargo-Zanoguera A, Molina E, Rosales-Domínguez C. 2006. Chicxulub impact event is Cretaceous/Paleogene boundary in age: new micropaleontological evidence. Earth Planet. Sc. Lett. 249(3–4):241–257.

Arenillas I, Arz JA, Náñez C. 2007. Morfología, Biometría y Taxonomía de foraminíferos planctónicos del Daniense basal: *Palaeoglobigerina* n. gen. [Morphology, biometry and taxonomy of the lowermost Danian planktonic foraminifera: *Palaeoglobigerina* n. gen.]. Rev. Esp. Paleontol. 22(1):21–62. Spanish.

Arenillas I, Arz JA, Náñez C. 2010. Diversidad y evolución de la textura de la pared en guembelítridos (foraminíferos planctónicos) en el tránsito Cretácico-Paleógeno [Textural diversity and evolution of guembelitriids (planktic foraminifera) across the Cretaceous-Paleogene transition]. Rev. Esp. Paleontol. 25(2):87–105. Spanish.

Arenillas I, Arz JA, Náñez C. 2012. Smooth and rugose wall textures in earliest Danian trochospiral planktic foraminifera from Tunisia. N. Jb. Geol. Paläont. Abh. 266(2):123–142.

Arenillas I, Arz JA, Grajales-Nishimura JM, Rojas-Consuegra R. 2016a. The Chicxulub impact is synchronous with the planktonic foraminifera mass extinction at the Cretaceous/Paleogene boundary: new evidence from the Moncada section, Cuba. Geologica Acta 14(1):35–51.

Arenillas I, Arz JA, Náñez C. 2016b. New species of genus *Trochoguembelitria* from the lowermost Danian of Tunisia - biostratigraphic and evolutionary implications in planktonic foraminifera. Palaeontographica Abteilung A 305(4-6):133–160.

Arz JA, Arenillas I, Náñez C. 2010. Morphostatistical analysis of Maastrichtian populations of *Guembelitria* from El Kef, Tunisia. J. Foramin. Res. 40(2):148–164.

Ashckenazi-Polivoda S, Rak C, Almogi-Labin A, Zsolt B, Ovadia O, Abramovich S. 2014. Paleoecology of the K-Pg mass extinction survivor Guembelitria (Cushman): isotopic evidence from pristine foraminifera from Brazos River, Texas (Maastrichtian). Paleobiology 40(1):24–33.

Berggren WA, Pearson PN. 2005. A revised tropical to subtropical Paleogene planktonic foraminiferal zonation. J. Foramin. Res. 35(4):279–298.

Blow WH. 1979. The Cainozoic Globigerinidae. A study of the morphology, taxonomy, evolutionary relationship and the stratigraphical distribution of some Globigerinidae (mainly Globigerinacea). Ed. EJ. Brill, Leiden, Netherlands, Vol. 1: xv+752 pp.; Vol. 2: 1413 pp.; Vol. 3: xxi, 264 pls.

BouDagher-Fadel MK. 2012. Biostratigraphic and geological significance of planktonic foraminifera (1st edition). Dev. Palaeontol. Stratigr. 22:1–289.

BouDagher-Fadel MK. 2015. Biostratigraphic and geological significance of planktonic foraminifera (3rd edition). UCLPress, London, 298 pp, 12 charts.

Brinkhuis H, Zachariasse WJ. 1988. Dinoflagellate cysts, sea level changes and planktonic foraminifers across the Cretaceous-Tertiary boundary at El Haria, Northwest Tunisia. Mar. Micropaleontol. 13(2):153–191.

Canudo JI, Keller G, Molina E. 1991. Cretaceous/Tertiary boundary extinction pattern and faunal turnover at Agost and Caravaca, SE Spain. Mar. Micropaleontol. 17(3–4):319–341.

Chenet AL, Auidelleur X, Fluteau F, Courtillot VY, Bajpai S. 2007. ^{40}K-^{40}Ar dating of the main Deccan large igneous province: Further evidence of KTB age and short duration. Earth Planet. Sc. Lett. 263:1-15.

D'Hondt SL. 1991. Phylogenetic and stratigraphic analysis of earliest Paleocene biserial and triserial planktonic foraminifera. J. Foramin. Res. 21(2):168–181.

Georgescu MD. 2009. On the origins of superfamily Heterohelicacea Cushman, 1927 and the polyphyletic nature of planktic foraminifera. Rev. Esp. Micropal. 41(1–2):1–38.

Georgescu MD, Arz JA, Macauley RV, Kukulski RB, Arenillas I, Pérez-Rodríguez I. 2011. Late Cretaceous (late Santonian-Maastrichtian) serial planktic and benthic foraminifera with pore mounds or pore mound-based ornamentation structures. Rev. Esp. Micropal. 43(1–2):109–139.

Hammer Ø, Harper DAT, Ryan PD. 2001. PAST: Paleontological Statistics Software Package for Education and Data Analysis. Palaeontol. Electron. 4(1):9 p.

Hildebrand AR, Penfield GT, Kring DA, Pilkington M, Camargo ZA, Jacobsen SB, Boynton WV. 1991. Chicxulub crater: a possible Cretaceous/Tertiary boundary impact crater on the Yucatan Peninsula, Mexico. Geology 19:867-871.

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

Huber BT, Olsson RK, Pearson PN. 2006. Taxonomy, biostratigraphy, and phylogeny of Eocene microperforate Planktonic foraminifera (*Jenkinsina*, *Cassigerinelloita*, *Chiloguembelina*, *Streptochilus*, *Zeauvigerina*, *Tenuitella*, and *Cassigerinella*) and Problematica (*Dipsidripella*). In: Pearson PN, Olsson RK, Huber BT, Hemleben C., Berggren WA. (eds.) Atlas of Eocene Planktonic Foraminifera, Cushman Foundation Special Publication, 41:461–508, Virginia, U.S.A.

Jenkins DG, Whittaker JE, Curry D. 1998. Palaeogene triserial planktonic foraminifera: J. Micropalaeontol. 17:61–70.

Koutsoukos EA. 2014. Phenotypic plasticity, speciations, and phylogeny in Early Danian planktic foraminifera. J. Foramin. Res. 44(2):109–142.

Kroon D, Nederbragt AJ. 1990. Ecology and paleoecology of triserial planktic foraminifera. Mar. Micropaleontol. 16(1–2):25–38.

Li Q. 1987. Origin, phylogenetic development and systematic taxonomy of the *Tenuitella* plexus (Globigerinitidae, Globigerinina). J. Foramin. Res. 17:295–320.

Li Q, Radford SS. 1991. Evolution and biogeography of Paleogene microperforate planktonic foraminifera. Palaeogeogr. Palaeoclimtol. Palaeoecol. 83(1–3):87–115.

Li Q, Sally S, Radford SS, Banner FT. 1992. Distribution of microperforate Tenuitellid planktonic foraminifers in Holes 747a and 749b, Kerguelen Plateau. Proc. Ocean Drill. Program Sci. Res. 120:569–594.

Li Q, McGowran B, Boersma A. 1995. Early Paleocene *Parvularugoglobigerina* and late Eocene *Praetenuitella*: does evolutionary convergence imply similar habitat? J. Micropaleontol. 14(2):119–134.

Liu C, Olsson RK. 1992. Evolutionary radiation of microperforate planktonic foraminifera following the K/T mass extinction event. J. Foramin. Res. 22(4):328–346.

Loeblich AR Jr, Tappan H. 1956. *Chiloguembelina*, a new Tertiary genus of Heterohelicidae (Foraminifera). J. Wash. Acad. Sci. 46:39–40.

Loeblich AR Jr, Tappan H. 1957. Planktonic foraminifera of Paleocene and early Eocene age from the Gulf and Atlantic coastal plains. B. U. S. Nat. Mus., 215:173–198.

Loeblich AR Jr, Tappan H. 1987. Foraminiferal general and their clasification. Van Nostrand Reinhold Company, New York, 2 Vol., 970 pp., 847 pls.

Longoria JF. 1974. Stratigraphic, morphologic and taxonomic studies of Aptian planktic foraminifera. Rev. Esp. Micropaleontol. Extr. Number:11-107.

Luterbacher HP, Premoli Silva I. 1964. Biostratigraphia del limite Cretaceous-Terciario nell Apennino Centrale [Biostratigraphy of the Cretaceous-Tertiary boundary in Central Apennines]. Riv. Ital. Paleontol. S. 70:67–128. Italian.

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

Molina E, Arenillas I, Arz JA. 1998. Mass extinction in planktic foraminifera at the Cretaceous/Tertiary boundary in subtropical and temperate latitudes. B. Soc. Geol. Fr. 169(3):351-363.

Molina E, Alegret L, Arenillas I, Arz JA, Gallala N, Hardenbol J, von Salis K, Steurbaut E, Vandenberghe N, Zaghbib-Turki D. 2006. The Global Stratotype Section and Point of the Danian Stage (Paleocene, Paleogene, “Tertiary”, Cenozoic) at El Kef, Tunisia: original definition and revision. Episodes 29(4):263–278.

Molina E, Alegret L, Arenillas I, Arz JA, Gallala N, Grajales-Nishimura M, Murillo-Muñetón G, Zaghbib-Turki D. 2009. The Global Boundary Stratotype Section and Point for the base of the Danian Stage (Paleocene, Paleogene, "Tertiary", Cenozoic): auxiliary sections and correlation. Episodes 32(2):84–95.

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

Olsson RK. 1970. Planktonic foraminifera from base of Tertiary, Millers Ferry, Alabama. J. Paleontol. 44:598–604.

Olsson RK, Hemleben C, Berggren WA, Huber BT. 1999. Atlas of Paleocene Planktonic Foraminifera. Smithsonian Contrib. Paleobiol. 85:1–252.

Pandey J. 1981. Cretaceous foraminifera of Um Sohryngkew River section, Meghalaya: J. Paleontol. Soc. India 25:53–74.

Pardo A, Keller G. 2008. Biotic effects of environmental catastrophes at the end of the Cretaceous and Early Tertiary: *Guembelitria* and *Heterohelix* blooms. Cretaceous Res. 29:1058–1073.

Punekar J, Mateo P, Keller G. 2014. Effects of Deccan volcanism on paleoenvironment and planktic foraminifera: A global survey. GSA Special Paper 505, doi: 10.1130/214.2505(04).

Salaj J. 1986. The new *Postrugoglobigerina praedaubjergensis* Zone at the base of the stratotype of the marine Paleocene (El Kef, Tunisia). Geol. Zbornik, Geol. Carpath. Bratislava 37:35–58.

Schoene B, Samperton KM, Eddy MP, Keller G, Adatte T, Bowring SA, Khadri SFR, Gerch B. 2015. U-Pb geochronology of the Deccan Traps and relation to the end-Cretaceous mass extinction. Science 347(6218):182-184.

Schulte P, Alegret L, Arenillas I, Arz JA, Barton PJ, Bown PR, Bralower TJ, Christeson GL, Claeys P, Cockell CS, Collins GS, Deutsch A, Goldin TJ, Goto K, Grajales-Nishimura JM, Grieve RAF, Gulick SPS, Johnson KR, Kiessling W, Koeberl C, Kring DA, MacLeod KG, Matsui T, Melosh J, Montanari A, Morgan JV, Neal CR, Norris RD, Pierazzo E, Ravizza G, Rebolledo-Vieyra, M, Reimold WU, Robin E, Salge T, Speijer RP, Sweet AR, Urrutia-Fucugauchi J, Vajda V, Whalen MT, Willumsen PS. 2010. The Chicxulub asteroid impact and mass extinction at the Cretaceous-Paleogene boundary. Science 327(5970):1214-1218.

Smit J. 1982. Extinction and evolution of planktonic foraminifera after a major impact at the Cretaceous/Tertiary boundary. GSA Special Paper 190:329–352.

Smit J. 1990. Meteorite impact, extinctions and the Cretaceous-Tertiary Boundary. Geol. Mijnbouw 69:187–204.

Tyszka J. 2006. Morphospace of foraminiferal shells: results from the moving reference model. Lethaia 39:1–12.

Figure captions

Figure 1. Stratigraphic ranges at El Kef, Tunisia, of analyzed early Danian species of *Guembelitria, Chiloguembelitria, Woodringina, Chiloguembelina, Trochoguembelitria* and *Globoconusa*, as well as of index-species of the planktonic foraminiferal zonation of Arenillas et al. (2004); (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); dotted lines indicate uncertain range, based probably on reworked specimens or not supported by SEM-photographed specimens; shaded intervals indicate first and second early Danian evolutionary radiations at the El Kef section.

Figure 2. Holotypes and specimens of *Guembelitria* spp. (scale bar = 100 microns; scale bar of detail SEM-micrographs = 10 microns). (a) *Guembelitria cretacea* Cushman, holotype, Upper Cretaceous, Guadalupe County, Texas, U.S.A. (SEM-micrograph from Olsson et al. 1999). (b) *Guembelitria cretacea* Cushman, sample KF13.50 (1.5 m above K/Pg boundary), *Pv. longiapertura* Subzone (*G. cretacea* Zone), El Kef, Tunisia. (c) *Guembelitria cretacea* Cushman, sample KF11 (1 m below K/Pg boundary), *P. hantkeninoides* Subzone (*A. mayaroensis* Zone), El Kef, Tunisia. (d) *Guembelitria cretacea* Cushman, sample KF 12.05 (5 cm above K/Pg boundary), *H. holmdelensis* Subzone (*G. cretacea* Zone), El Kef, Tunisia. (e) *Guembelitria blowi* Arz, Arenillas and Náñez, holotype, sample KF4.50 (7.5 m below K/Pg boundary), *P. hantkeninoides* Subzone (*A. mayaroensis* Zone), El Kef, Tunisia. (f) *Guembelitria blowi* Arz, Arenillas and Náñez, hypotype, sample JA680 (19 cm below K/Pg boundary), *A. mayaroensis* Zone, Bajada del Jagüel, Argentina. (g) *Guembelitria blowi* Arz, Arenillas and Náñez, hypotype, sample KF11 (1 m below K/Pg boundary), *P. hantkeninoides* Subzone (*A.

mayaroensis Zone), El Kef, Tunisia. (h) *Guembelitria dammula* Voloshina, holotype, Maastrichtian, Volin-Podolsk Plateu, western Russia. (i) *Guembelitria dammula* Voloshina, sample KF11 (1 m below K/Pg boundary), *P. hantkeninoides* Subzone (*A. mayaroensis* Zone), El Kef, Tunisia. (j) *Guembelitria dammula* Voloshina, sample KF13.00 (1 m above K/Pg boundary), *Pv. longiapertura* Subzone (*G. cretacea* Zone), El Kef, Tunisia. (k). *Guembelitria dammula* Voloshina, sample KF13.25 (1.25 m above K/Pg boundary), *Pv. longiapertura* Subzone (*G. cretacea* Zone), El Kef, Tunisia.

Figure 3. Holotypes and specimens of *Woodringina* spp. and *Chiloguembelina* spp. (scale bar = 100 microns; scale bar of detail SEM-micrographs = 10 microns). (a) *Woodringina claytonensis* Loeblich and Tappan, holotype, lower Danian, Clayton Fm., Alabama, U.S.A. (SEM-micrograph from Olsson et al. 1999). (b) *Woodringina hornerstownensis* Olsson, holotype, upper Danian, Hornerstown Fm., New Jersey, U.S.A. (SEM-micrograph from Olsson et al. 1999). (c) *Woodringina hornerstownensis* Olsson, sample AEA 6.90 (5.9 m above K/Pg boundary), *S. triloculinoides* Subzone (*P. pseudobulloides* Zone), Elles, Tunisia. (d) *Woodringina hornerstownensis* Olsson, sample KF 20.50 (8.5 m above K/Pg boundary), *E. trivialis* Subzone (*P. pseudobulloides* Zone), El Kef, Tunisia. (e) *Woodringina hornerstownensis* Olsson, sample KF 19.50 (7.5 m above K/Pg boundary), *E. trivialis* Subzone (*P. pseudobulloides* Zone), El Kef, Tunisia. (f) *Woodringina hornerstownensis* Olsson, sample KF 19.50 (7.5 m above K/Pg boundary), *E. trivialis* Subzone (*P. pseudobulloides* Zone), El Kef, Tunisia. (g) *Chiloguembelina taurica* Morozova, holotype, lower Danian, Tarkhankhut Peninsula, eastern Crimea. (h) *Chiloguembelina taurica* Morozova, sample KF 21.95 (9.95 m above K/Pg boundary), lower part of the *E. trivialis* Subzone (*P. pseudobulloides* Zone), El Kef, Tunisia. (i) *Chiloguembelina*

taurica Morozova, sample 14cc, *P. pseudobulloides* Zone, Site 305 Shatsky Rise, North Pacific. (j) *Gümbelina midwayensis* Cushman, holotype, Eocene, Midway Fm., Alabama, U.S.A. (SEM-micrograph from Olsson et al. 1999). (k) *Chiloguembelina midwayensis* (Cushman), sample KF 19.50 (7.5 m above K/Pg boundary), *E. trivialis* Subzone (*P. pseudobulloides* Zone), El Kef, Tunisia. (l) *Gümbelina morsei* Kline, holotype, Danian, Porters Creek Clay (Midway series), Alabama, U.S.A. (SEM-micrograph from Olsson et al. 1999).

Figure 4. Holotypes and specimens of *Trochoguembelitria* spp. and *Globoconusa* spp. (scale bar = 100 microns; scale bar of detail SEM-micrographs = 10 microns). (a) *Trochoguembelitria alabamensis*, holotype, Millers Ferry, Alabama, U.S.A. (SEM-micrograph from Liu and Olsson, 1992). (b) *Trochoguembelitria alabamensis*, sample KF24.80 (12.8 m above the K/Pg boundary), *S. triloculinoides* Subzone (*P. pseudobulloides* Zone), El Kef, Tunisia. (c) *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. (d) *Trochoguembelitria extensa*, holotype, Zone P1, DSDP Leg 6, South Pacific (SEM-micrographs from Blow 1979). (e) *Trochoguembelitria extensa*, sample KF18.50 (6.5 m above the K/Pg boundary), upper part of the *E. simplicissima* Subzone (*Pv. eugubina* Zone), El Kef, Tunisia. (f) *Trochoguembelitria liuae*, holotype, sample KF20.50 (8.5 m above the K/Pg boundary), middle part of the *E. trivialis* Subzone (*P. pseudobulloides* Zone), El Kef, Tunisia. (g) *Trochoguembelitria olssoni*, holotype, sample KF20.50 (8.5 m above the K/Pg boundary), middle part of the *E. trivialis* Subzone (*P. pseudobulloides* Zone), El Kef, Tunisia. (h) *Globoconusa daubjergensis* (Brönnimann), sample BG1000-4.25, *S. triloculinoides* Subzone (*P. pseudobulloides* Zone), Ben Gurion, Israel. (i) *Globoconusa*

daubjergensis, sample BJ56+110, middle part of the *E. trivialis* Subzone (*P. pseudobulloides* Zone), Bajada del Jagüel, Argentina. (j) *Globoconusa conusa* Khalilov, sample BG1000-4.25, *S. triloculinoides* Subzone (*P. pseudobulloides* Zone), Ben Gurion, Israel. (k) *Globoconusa victori* Koutsoukos, sample BJ56+110, middle part of the *E. trivialis* Subzone (*P. pseudobulloides* Zone), Bajada del Jagüel, Argentina.

Figure 5. Wall textural details of *Guembelitria*, *Chiloguembelitria*, *Trochoguembelitria*, *Globoconusa*, *Woodringina* and *Chiloguembelina* (scale bars = 10 µm). (a) *Guembelitria cretacea* Cushman, sample KF13.5 (1.5 m above K/Pg boundary), *Pv. longiapertura* Subzone (*G. cretacea* Zone), El Kef, Tunisia. (b) *Guembelitria dammula* Voloshina, sample KF13.00 (1 m above K/Pg boundary), *Pv. longiapertura* Subzone (*G. cretacea* Zone), El Kef, Tunisia. (c) *Chiloguembelitria hofkeri* sp. nov., sample KF 20.50 (8.5 m above K/Pg boundary), *E. trivialis* Subzone (*P. pseudobulloides* Zone), El Kef, Tunisia. (d) *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. (e) *Woodringina hornerstownensis* Olsson, sample KF 19.50 (7.5 m above K/Pg boundary), *E. trivialis* Subzone (*P. pseudobulloides* Zone), El Kef, Tunisia. (f) *Chiloguembelina taurica* Morozova, sample 14cc, *P. pseudobulloides* Zone, Site 305 Shatsky Rise, North Pacific. (g) *Chiloguembelitria danica* Hofker, Paratype MPZ 2016/109, sample KF 20.50 (8.5 m above K/Pg boundary), *E. trivialis* Subzone (*P. pseudobulloides* Zone), El Kef, Tunisia. (h) *Globoconusa daubjergensis*, sample BJ56+110, middle part of the *E. trivialis* Subzone (*P. pseudobulloides* Zone), Bajada del Jagüel, Argentina.

Figure 6. (a) Types of chamber arrangement. (b) Types of aperture position. (c–d) Biometric parameters, abbreviations and descriptive terms used for the morphological analysis of the *Chiloguembelitria* tests.

Figure 7. Univariate analyses based on biometric variables α and H/L to delimit the *Chiloguembelitria* species, displayed as histograms of 20 bins; thick dotted lines are the Kernel density estimations; fine dot lines are univariate normal distributions (Gaussian beel-shaped curves) based on mixture analysis.

Figure 8. Bivariate analyses based on Kernel density estimations from paired variables α vs. H/L, and plotted in smooth map of point density; colour scale with deep red for highest density and dark blue for lowest.

Figure 9. R-mode cluster analysis based on Bray-Curtis index and applied to the values of the biometric variables measured in all SEM-photographed *Chiloguembelitria* specimens. (a) Cluster for biometric variables α and H/L; (b) Cluster for biometric variables α, H/L and CAD/H. D_{jk} = Bray-Curtis index value between specimen j and specimen k; x_{ij} = value of the variable i (biometric index/parameter i) of the specimen j; x_{ik} = value of the variable i (biometric index/parameter i) of the specimen k.

Figure 10. Principal components analysis (PCA), applied to the values of biometric variables (α, H/L and CAD/H) in all *Chiloguembelitria* specimens.

Figure 11. Proposed phylogenetic relationships of *Guembelitria, Chiloguembelitria, Trochoguembelitria, Globoconusa*, *Woodringina* and *Chiloguembelina* based on

evidence reported here and previous phylogenetic studies (see Arenillas et al. 2012, 2016b); thick dotted lines indicate doubtful range, based probably on reworked specimens. (1) Arenillas et al. (2004); (2) Berggren and Pearson (2005).

Figure 12. Holotypes and specimens of *Chiloguembelitria danica* Hofker and *Chiloguembelitria irregularis* Morozova (scale bar = 100 microns; scale bar of detail SEM-micrographs = 10 microns). (a) *Chiloguembelitria danica* Hofker, invalid holotype (considered here as *Chg. hofkeri* sp. nov.), middle Danian, DSDP Leg 6 Shatsky Rise, northern Pacific. (b) *Chiloguembelitria danica* Hofker (considered here as *Chg. hofkeri* sp. nov.), topotype of Loeblich and Tappan (1987), Danian, DSDP Site 47.2, Shatsky Rise, northern Pacific. (c) *Chiloguembelitria danica* Hofker, neotype of Jenkins et al. (1998), Danian, DSDP Leg 6, Shatsky Rise, northern Pacific. (d) *Chiloguembelitria danica* Hofker, sample KF 20.50 (8.5 m above K/Pg boundary), *E. trivialis* Subzone (*P. pseudobulloides* Zone), El Kef, Tunisia. (e) *Chiloguembelitria danica* Hofker, sample KF 20.50 (8.5 m above K/Pg boundary), *E. trivialis* Subzone (*P. pseudobulloides* Zone), El Kef, Tunisia. (f) *Chiloguembelitria danica* Hofker, sample KF 20.50 (8.5 m above K/Pg boundary), *E. trivialis* Subzone (*P. pseudobulloides* Zone), El Kef, Tunisia. (g) *Chiloguembelitria danica* Hofker, sample KF 20.50 (8.5 m above K/Pg boundary), *E. trivialis* Subzone (*P. pseudobulloides* Zone), El Kef, Tunisia. (h) *Chiloguembelitria hofkeri* sp. nov., sample KF 20.50 (8.5 m above K/Pg boundary), *E. trivialis* Subzone (*P. pseudobulloides* Zone), El Kef, Tunisia. (i) *Guembelitria irregularis* Morozova, Holotype, lower Danian, Tarkhankut, Crimea (SEM-micrographs from Olsson et al. 1999). (j) *Chiloguembelitria irregularis* (Morozova), sample KF 20.50 (8.5 m above K/Pg boundary), *E. trivialis* Subzone (*P. pseudobulloides* Zone), El Kef, Tunisia. (k) *Chiloguembelitria irregularis* (Morozova), sample STW+45+47 (46

cm above K/Pg boundary), *Pv. longiapertura* Subzone (*G. cretacea* Zone), Aïn Settara, Tunisia. (l) *Chiloguembelitria irregularis* (Morozova), sample KF 20.50 (8.5 m above K/Pg boundary), *E. trivialis* Subzone (*P. pseudobulloides* Zone), El Kef, Tunisia. (m) *Chiloguembelitria irregularis* (Morozova), sample KF 19.50 (7.5 m above K/Pg boundary), *E. trivialis* Subzone (*P. pseudobulloides* Zone), El Kef, Tunisia. (n) *Chiloguembelitria irregularis* (Morozova), sample KF 19.50 (7.5 m above K/Pg boundary), *E. trivialis* Subzone (*P. pseudobulloides* Zone), El Kef, Tunisia.

Figure 13. Type-specimens of *Chiloguembelitria hofkeri* sp. nov. and *Chiloguembelitria trilobata* sp. nov (scale bar = 100 microns; scale bar of detail SEM-micrographs = 10 microns). (a) *Chiloguembelitria hofkeri* sp. nov., Holotype MPZ 2016/108, sample KF 19.50 (7.5 m above K/Pg boundary), *E. trivialis* Subzone (*P. pseudobulloides* Zone), El Kef, Tunisia. (b) *Chiloguembelitria hofkeri* sp. nov., Paratype MPZ 2016/109, sample KF 20.50 (8.5 m above K/Pg boundary), *E. trivialis* Subzone (*P. pseudobulloides* Zone), El Kef, Tunisia. (c) *Chiloguembelitria hofkeri* sp. nov., Paratype MPZ 2016/110, sample KF 20.50 (8.5 m above K/Pg boundary), *E. trivialis* Subzone (*P. pseudobulloides* Zone), El Kef, Tunisia. (d) *Chiloguembelitria hofkeri* sp. nov., Paratype MPZ 2016/111, sample KF 19.50 (7.5 m above K/Pg boundary), *E. trivialis* Subzone (*P. pseudobulloides* Zone), El Kef, Tunisia. (e) *Chiloguembelitria trilobata* sp. nov., Holotype MPZ 2016/112, sample KF 19.50 (7.5 m above K/Pg boundary), *E. trivialis* Subzone (*P. pseudobulloides* Zone), El Kef, Tunisia. (f) *Chiloguembelitria trilobata* sp. nov., Paratype MPZ 2016/113, sample KF 19.50 (7.5 m above K/Pg boundary), *E. trivialis* Subzone (*P. pseudobulloides* Zone), El Kef, Tunisia. (g) *Chiloguembelitria trilobata* sp. nov., Paratype MPZ 2016/114, sample KF 21.25 (9.25 m above K/Pg boundary), *E. trivialis* Subzone (*P. pseudobulloides* Zone), El Kef,

Tunisia. (h) *Chiloguembelitria trilobata* sp. nov., Paratype MPZ 2016/115, sample KF 20.50 (8.5 m above K/Pg boundary), *E. trivialis* Subzone (*P. pseudobulloides* Zone), El Kef, Tunisia.

Figure 14. Type-specimens of *Chiloguembelitria biseriata* sp. nov. and comparison with specimens of *Woodringina claytonensis* Loeblich (scale bar = 100 microns; scale bar of detail SEM-micrographs = 10 microns). (a) *Chiloguembelitria biseriata* sp. nov., Holotype MPZ 2016/116, sample KF 20.50 (8.5 m above K/Pg boundary), *E. trivialis* Subzone (*P. pseudobulloides* Zone), El Kef, Tunisia. (b) *Chiloguembelitria biseriata* sp. nov., Paratype MPZ 2016/117, sample KF 19.50 (7.5 m above K/Pg boundary), *E. trivialis* Subzone (*P. pseudobulloides* Zone), El Kef, Tunisia. (c) *Chiloguembelitria biseriata* sp. nov., Paratype MPZ 2016/118, sample KF 19.50 (7.5 m above K/Pg boundary), *E. trivialis* Subzone (*P. pseudobulloides* Zone), El Kef, Tunisia. (d) *Chiloguembelitria biseriata*, Paratype MPZ 2016/119, sample KF 18.50 (6.5 m above K/Pg boundary), *E. simplicissima* Subzone (*Pv. eugubina* Zone), El Kef, Tunisia. (e) *Woodringina claytonensis* Loeblich and Tappan, sample KF 20.50 (8.5 m above K/Pg boundary), *E. trivialis* Subzone (*P. pseudobulloides* Zone), El Kef, Tunisia. (f) *Woodringina claytonensis* Loeblich and Tappan, sample KF 19.50 (7.5 m above K/Pg boundary), *E. trivialis* Subzone (*P. pseudobulloides* Zone), El Kef, Tunisia. (g) *Woodringina claytonensis* Loeblich and Tappan, sample KF 19.50 (7.5 m above K/Pg boundary), *E. trivialis* Subzone (*P. pseudobulloides* Zone), El Kef, Tunisia. (h) *Woodringina claytonensis* Loeblich and Tappan, sample KF24.00 (12 m above the K/Pg boundary), *S. triloculinoides* Subzone (*P. pseudobulloides* Zone), El Kef, Tunisia.

Table caption

Table 1. Biometric measurements (in microns) of *Chiloguembelitria* specimens, and biometric indices H/L and CAD/H. Arithmetic means in bold type. L, test length; W, test width; H, test height; CAD, chamber average diameter; α, test convexity angle measured in axial view.

Chiloguembelitria danica

Specimen	L	W	H	CAD	α	H/L	CAD/H
1	83.4	83.0	104.7	57.2	64.4	125.6	54.6
2	102.5	104.8	146.3	69.1	60.9	142.7	47.2
3	102.4	101.6	137.0	62.2	65.5	133.8	45.4
4	96.8	92.1	121.3	60.6	69.5	125.3	49.9
5	88.1	85.1	124.7	65.0	63.6	141.6	52.2
6	87.8	84.7	122.3	59.0	59.9	139.2	48.2
7	85.4	86.2	121.7	57.8	72.9	142.5	47.5
8	107.5	90.7	140.9	70.0	68.9	131.0	49.7
9	88.1	81.4	110.0	61.3	71.2	125.0	55.7
10	87.1	87.8	115.7	56.6	68.7	132.8	48.9
11	97.8	102.0	123.1	61.7	68.6	125.9	50.1
12	89.1	87.2	127.1	57.7	60.4	142.6	45.4
13	79.8	79.4	111.7	57.7	67.4	140.0	51.7
14	80.9	85.6	112.1	57.0	65.3	138.5	50.8
15	90.4	88.4	113.1	60.9	72.8	125.1	53.9
16	80.2	82.5	102.0	58.6	73.6	127.1	57.5
17	89.6	90.2	125.0	65.3	70.4	139.5	52.3
18	94.1	94.7	134.6	64.4	67.7	143.1	47.9
19	94.2	89.9	128.6	63.8	70.3	136.5	49.6
20	70.4	70.4	92.6	44.0	65.3	131.5	47.5
21	83.6	83.4	120.7	59.3	62.8	144.3	49.1
22	77.3	67.1	103.7	53.0	69.3	134.2	51.1
23	77.1	69.5	97.6	50.8	68.6	126.6	52.0
24	92.9	89.9	130.4	68.3	65.0	140.4	52.4
25	75.2	76.1	104.0	45.6	60.4	138.3	43.8
26	88.9	85.5	126.2	61.8	70.2	142.0	49.0
27	72.6	74.4	95.9	46.5	66.7	132.2	48.5
28	74.7	77.0	106.1	50.9	69.4	142.1	48.0
29	85.1	83.6	123.4	59.8	60.5	144.9	48.4
30	80.3	71.4	106.9	53.3	70.0	133.1	49.9
31	73.9	69.3	104.0	46.2	61.5	140.7	44.5
32	78.3	79.4	107.0	51.8	61.8	136.7	48.4
33	103.7	106.7	151.3	63.0	69.6	145.8	41.6
34	92.0	92.2	133.1	51.9	65.5	144.7	39.0
35	80.2	83.4	110.2	51.2	62.3	137.4	46.5
36	90.0	96.8	126.4	61.6	67.1	140.4	48.7
37	103.3	97.3	128.2	62.6	67.7	124.1	48.9
38	84.0	85.1	119.7	56.3	64.8	142.5	47.1
39	108.8	104.1	139.6	70.0	67.8	128.4	50.1
40	99.6	95.9	138.1	64.0	64.2	138.7	46.3
41	90.7	89.5	121.9	56.1	67.1	134.4	46.0
42	89.1	86.1	116.0	50.9	69.5	130.1	43.9
43	93.9	88.9	127.4	66.2	64.6	135.7	52.0
44	104.8	104.8	136.7	64.0	64.7	130.4	46.8
45	88.7	91.6	126.5	64.2	70.4	142.6	50.7
46	84.0	80.2	105.3	52.5	63.6	125.5	49.9
47	94.1	93.5	117.3	51.0	65.9	124.7	43.5
48	75.7	58.2	108.8	51.0	68.7	143.7	46.9
49	83.0	77.8	112.6	56.0	62.6	135.6	49.7
50	77.8	88.1	112.6	54.1	62.5	144.7	48.1

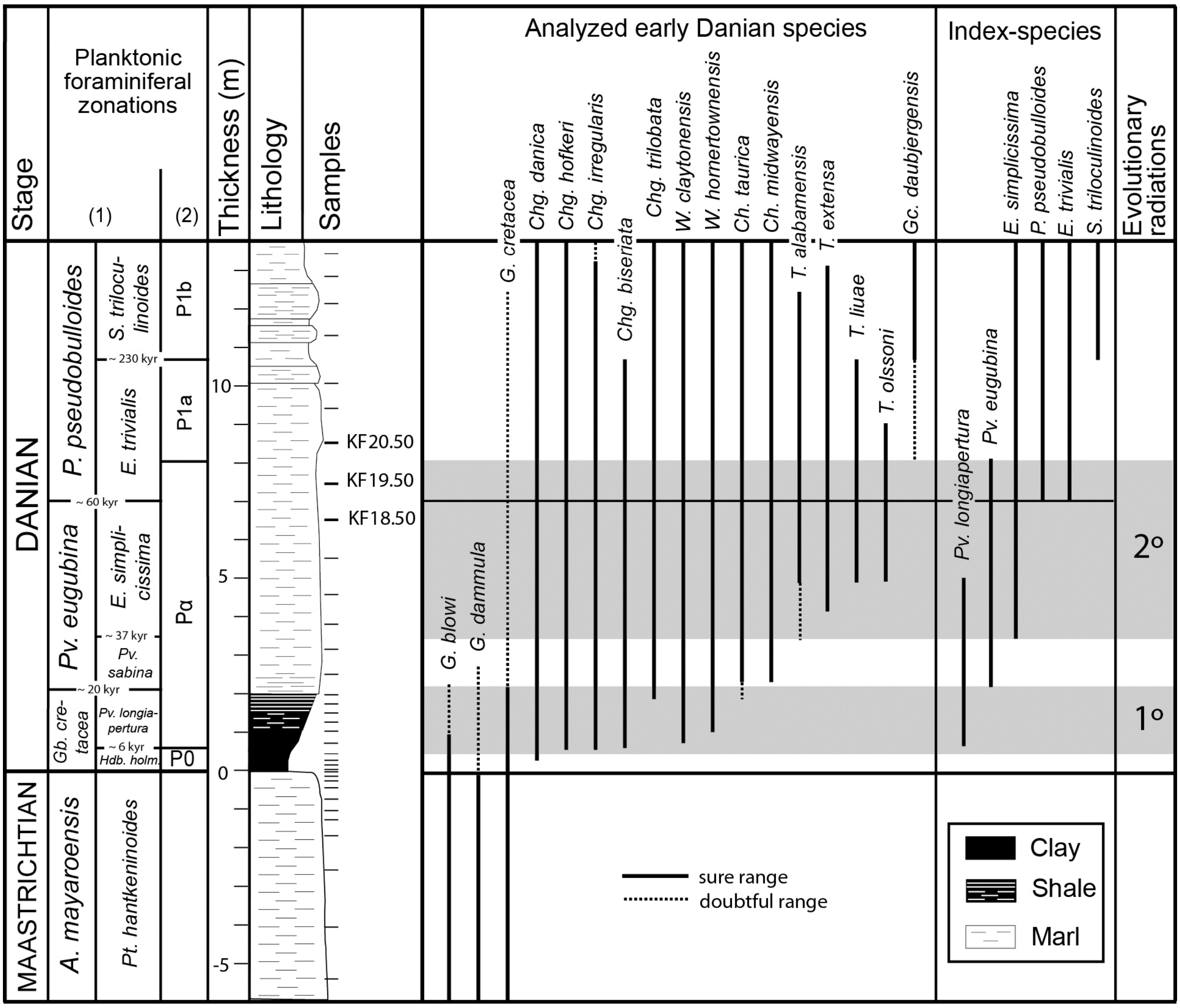
51	92.2	91.0	130.8	61.3	63.8	141.9	46.8
52	97.4	96.4	132.2	58.0	63.9	135.6	43.9
53	84.7	88.9	122.3	49.4	69.6	144.3	40.4
54	107.7	102.8	154.1	78.7	65.9	143.1	51.1
55	89.6	93.1	127.2	67.9	69.8	142.0	53.4
56	104.0	107.0	134.9	69.0	66.7	129.7	51.1
57	102.5	92.1	134.0	63.9	67.9	130.7	47.7
58	99.0	82.5	132.8	63.0	66.3	134.2	47.5
59	82.0	83.9	114.8	57.0	68.3	140.1	49.7
60	101.6	102.0	139.2	69.1	64.8	137.0	49.6
61	87.9	85.8	122.5	52.2	65.1	139.5	42.6
62	91.4	88.2	124.7	63.5	67.4	136.5	50.9
63	104.5	102.7	139.8	63.4	66.2	133.8	45.4
64	91.8	93.0	130.3	67.1	64.3	141.9	51.5
65	88.9	88.2	118.0	57.9	66.4	132.8	49.1
66	88.5	89.1	121.1	59.1	66.1	136.9	48.7
67	92.5	88.2	127.1	59.6	67.6	137.3	46.9
Average	**89.6**	**87.9**	**122.1**	**59.2**	**66.5**	**136.3**	**48.6**

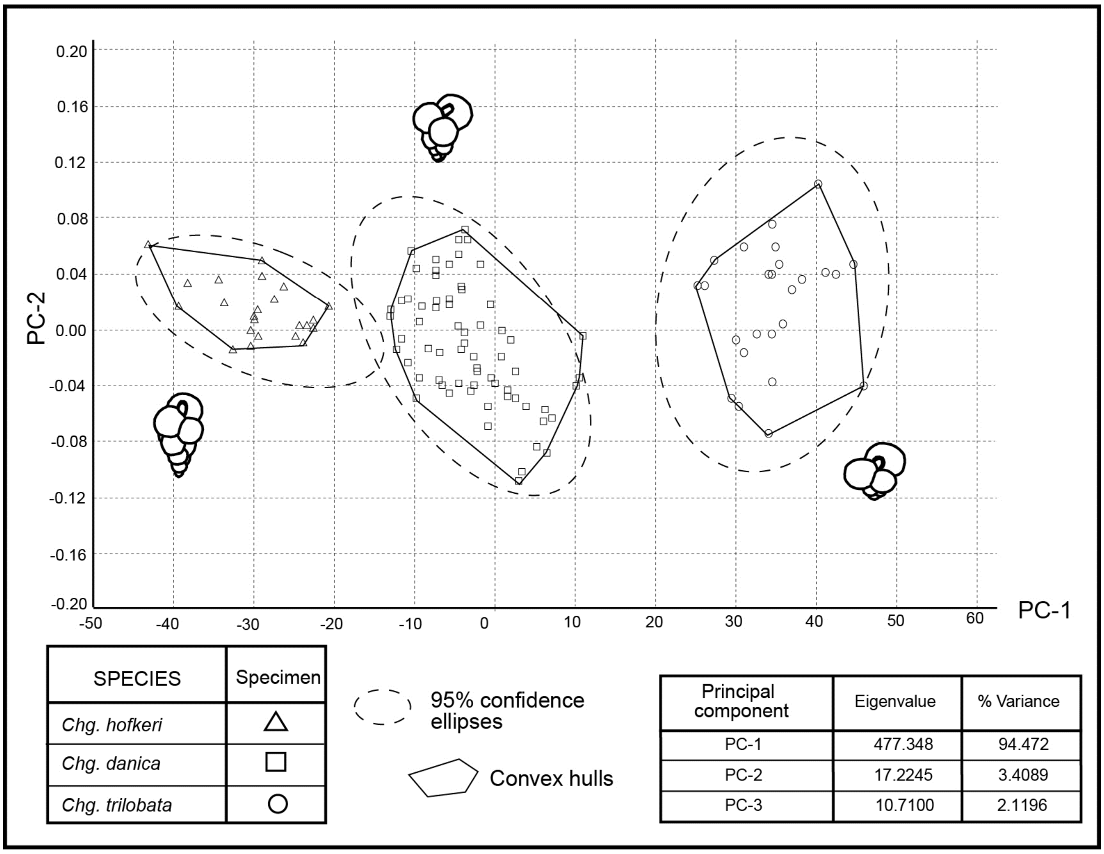
***Chiloguembelitria trilobata* sp. nov.**

Specimen	**L**	**W**	**H**	**CAD**	α	**H/L**	**CAD/H**
1	87.0	84.9	96.6	60.4	82.1	111.0	62.5
2	85.8	83.1	94.2	57.7	83.1	109.7	61.2
3	93.2	98.0	110.6	63.9	90.7	118.8	57.8
4	84.9	83.9	96.8	58.8	96.0	114.1	60.7
5	81.1	79.2	95.2	63.4	90.1	117.3	66.6
6	93.7	93.2	101.4	63.1	98.8	108.3	62.2
7	91.4	87.3	98.3	65.8	97.3	107.6	66.9
8	85.8	77.7	97.1	62.3	85.2	113.3	64.1
9	83.0	84.0	98.9	58.2	87.0	119.2	58.9
10	98.7	94.5	103.9	61.1	85.5	105.3	58.8
11	101.8	95.8	115.3	71.4	103.2	113.3	61.9
12	81.5	83.7	90.1	59.6	88.1	110.5	66.2
13	87.0	79.2	87.1	66.5	89.2	100.1	76.3
14	89.2	85.4	101.5	69.4	90.0	113.8	68.4
15	89.6	94.4	106.5	67.3	85.5	118.9	63.2
16	87.9	79.5	93.6	62.7	99.7	106.4	67.0
17	95.3	84.7	106.3	62.8	87.7	111.5	59.1
18	86.1	77.2	93.1	61.6	85.6	108.0	66.2
19	95.4	86.7	105.4	67.2	93.6	110.6	63.8
20	86.8	77.6	100.5	66.1	94.4	115.7	65.8
21	88.7	84.5	100.7	69.6	91.1	113.5	69.1
22	87.5	84.7	96.1	59.2	91.7	109.7	61.7
23	87.5	79.2	99.1	63.7	92.4	113.3	64.2
24	83.2	84.5	91.8	61.2	94.0	110.4	66.7
25	95.5	91.0	106.3	62.8	90.0	111.3	59.1
Average	**89.1**	**85.4**	**99.5**	**63.4**	**90.9**	**111.7**	**63.9**

***Chiloguembelitria hofkeri* sp. nov.**

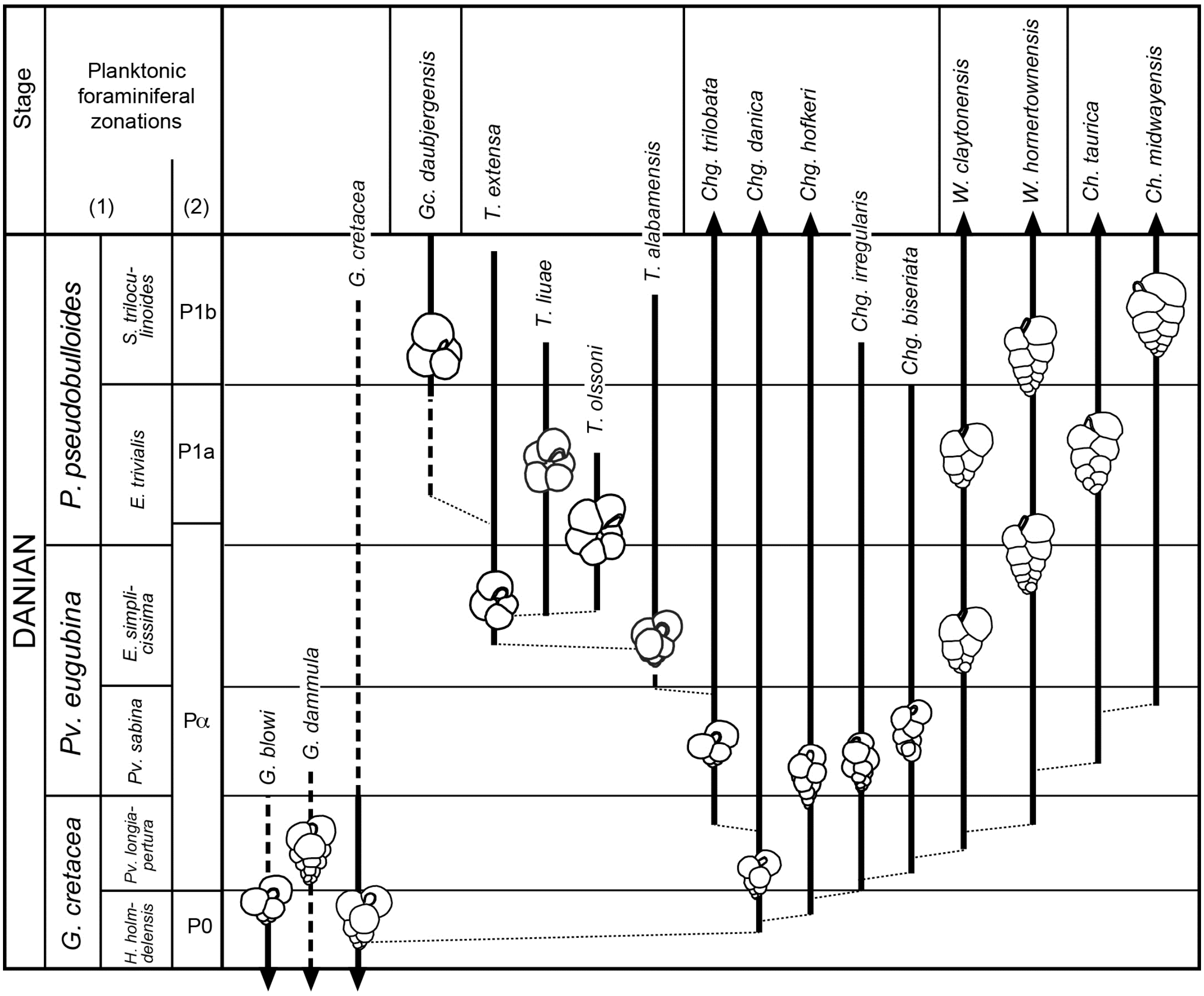
Specimen	**L**	**W**	**H**	**CAD**	**α**	**H/L**	**CAD/H**
1	92.7	91.6	140.4	64.3	53.2	151.4	45.8
2	86.1	92.9	141.9	59.7	45.6	164.8	42.1
3	89.9	99.6	141.5	65.7	48.0	157.4	46.4
4	90.5	92.6	148.6	58.9	44.3	164.2	39.7
5	106.0	105.6	170.0	70.9	48.0	160.4	41.7
6	78.4	77.4	119.7	59.5	49.4	152.7	49.7
7	80.9	75.2	126.9	53.1	50.8	156.9	41.8
8	94.0	94.1	159.9	61.7	45.5	170.0	38.6
9	82.5	77.8	128.4	53.1	48.3	155.8	41.4
10	95.3	98.3	149.8	59.0	47.4	157.2	39.4
11	84.0	82.6	126.8	56.4	56.7	150.9	44.5
12	98.9	97.0	154.7	61.1	51.4	156.5	39.5
13	76.4	78.1	115.6	48.3	55.8	151.3	41.8
14	84.9	85.3	128.5	55.8	52.8	151.2	43.4
15	82.3	85.8	125.3	53.1	53.9	152.3	42.4
16	88.9	92.1	138.7	60.6	52.3	156.0	43.7
17	80.9	81.9	125.9	54.6	54.1	155.8	43.3
18	80.2	85.1	127.6	56.8	52.8	159.2	44.5
19	81.3	81.6	123.3	54.2	53.9	151.7	44.0
20	102.2	103.6	158.9	67.2	49.4	155.5	42.3
21	110.7	114.1	179.1	69.1	50.4	161.7	38.6
22	90.3	95.3	142.9	63.6	52.1	158.3	44.5
23	107.2	110.0	167.7	66.0	50.3	156.4	39.4
Average	**89.8**	**91.2**	**141.0**	**59.7**	**50.7**	**156.9**	**42.5**

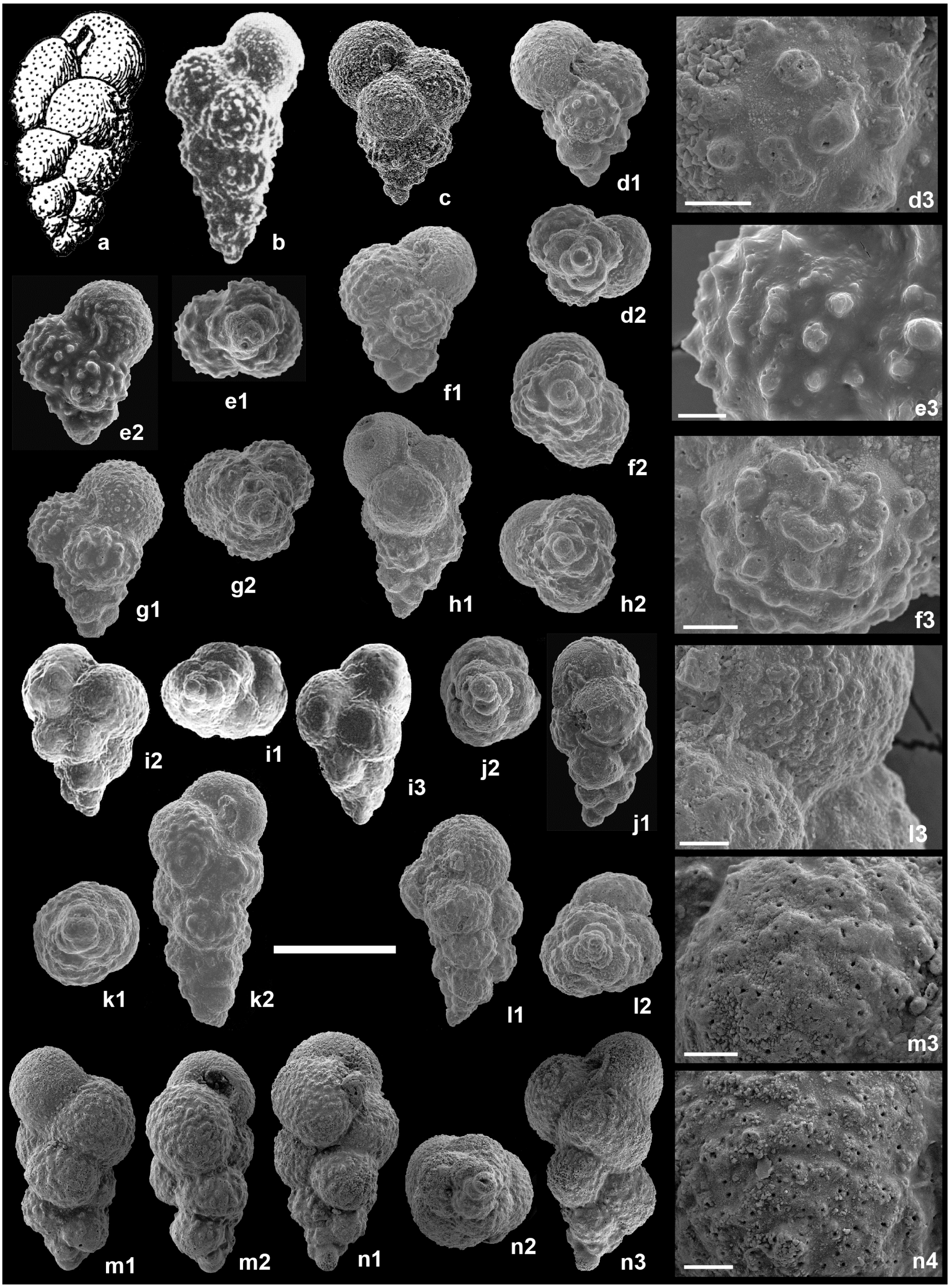

Stage
Planktonic foraminiferal zonations
(1)
(2)
Thickness (m)
Lithology
Samples
Analyzed early Danian species
Index-species
Evolutionary radiations
DANIAN
MAASTRICHTIAN
P. pseudobulloides
Pv. eugubina
Gb. cretacea
A. mayaroensis
S. triloculinoides
E. trivialis
E. simplicissima
Pv. sabina
Pv. longiapertura
Hdb. holm.
Pt. hantkeninoides
~ 230 kyr
~ 60 kyr
~ 37 kyr
~ 20 kyr
~ 6 kyr
P1b
P1a
Pα
P0
10
5
0
-5
KF20.50
KF19.50
KF18.50
G. blowi
G. dammula
G. cretacea
Chg. danica
Chg. hofkeri
Chg. irregularis
Chg. biseriata
Chg. trilobata
W. claytonensis
W. hornertownensis
Ch. taurica
Ch. midwayensis
T. alabamensis
T. extensa
T. liuae
T. olssoni
Gc. daubjergensis
Pv. longiapertura
Pv. eugubina
E. simplicissima
P. pseudobulloides
E. trivialis
S. triloculinoides
2º
1º
sure range
doubtful range
Clay
Shale
Marl

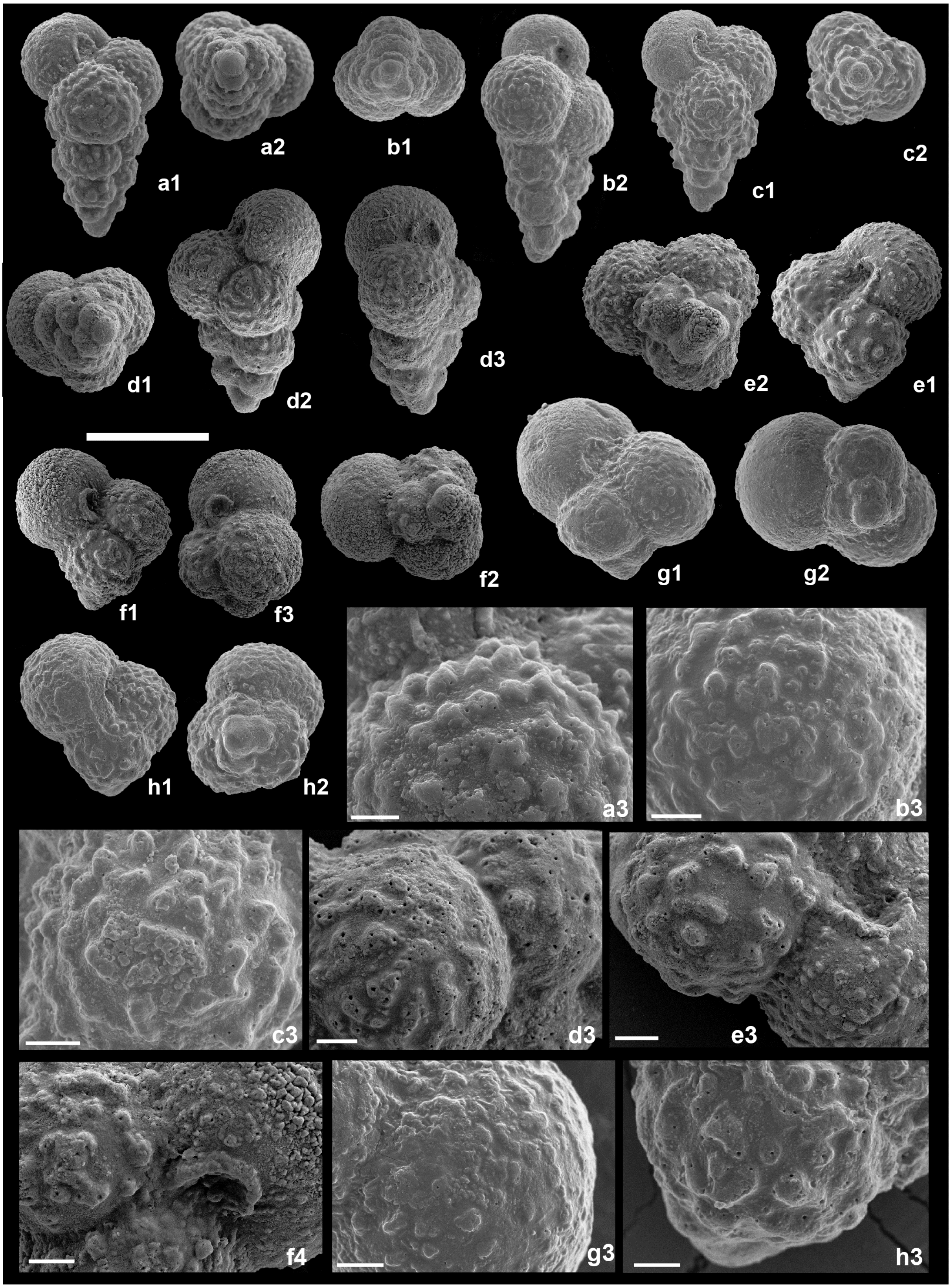


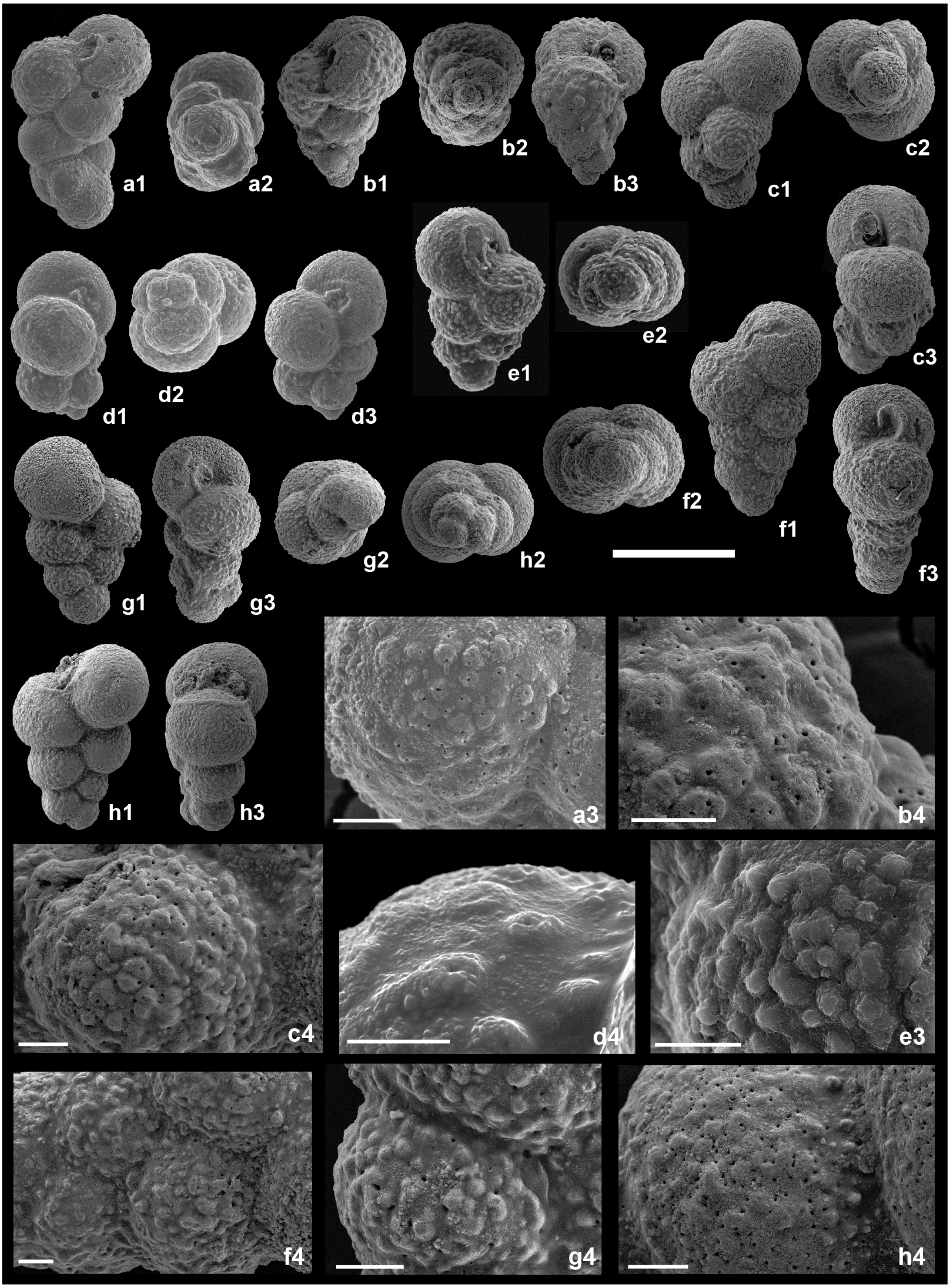
SPECIES	Specimen
Chg. hofkeri	△
Chg. danica	□
Chg. trilobata	○

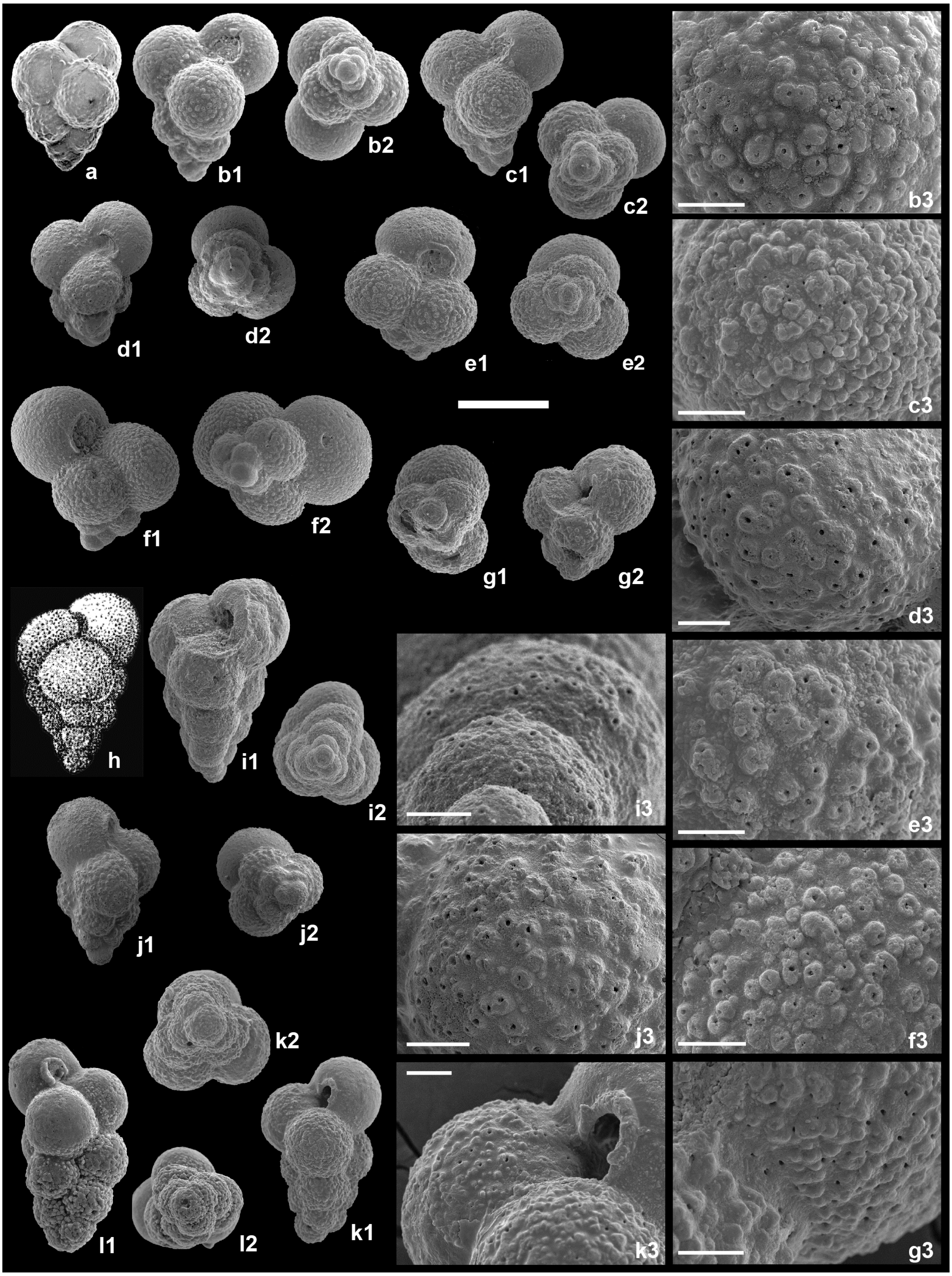
Principal component	Eigenvalue	% Variance
PC-1	477.348	94.472
PC-2	17.2245	3.4089
PC-3	10.7100	2.1196

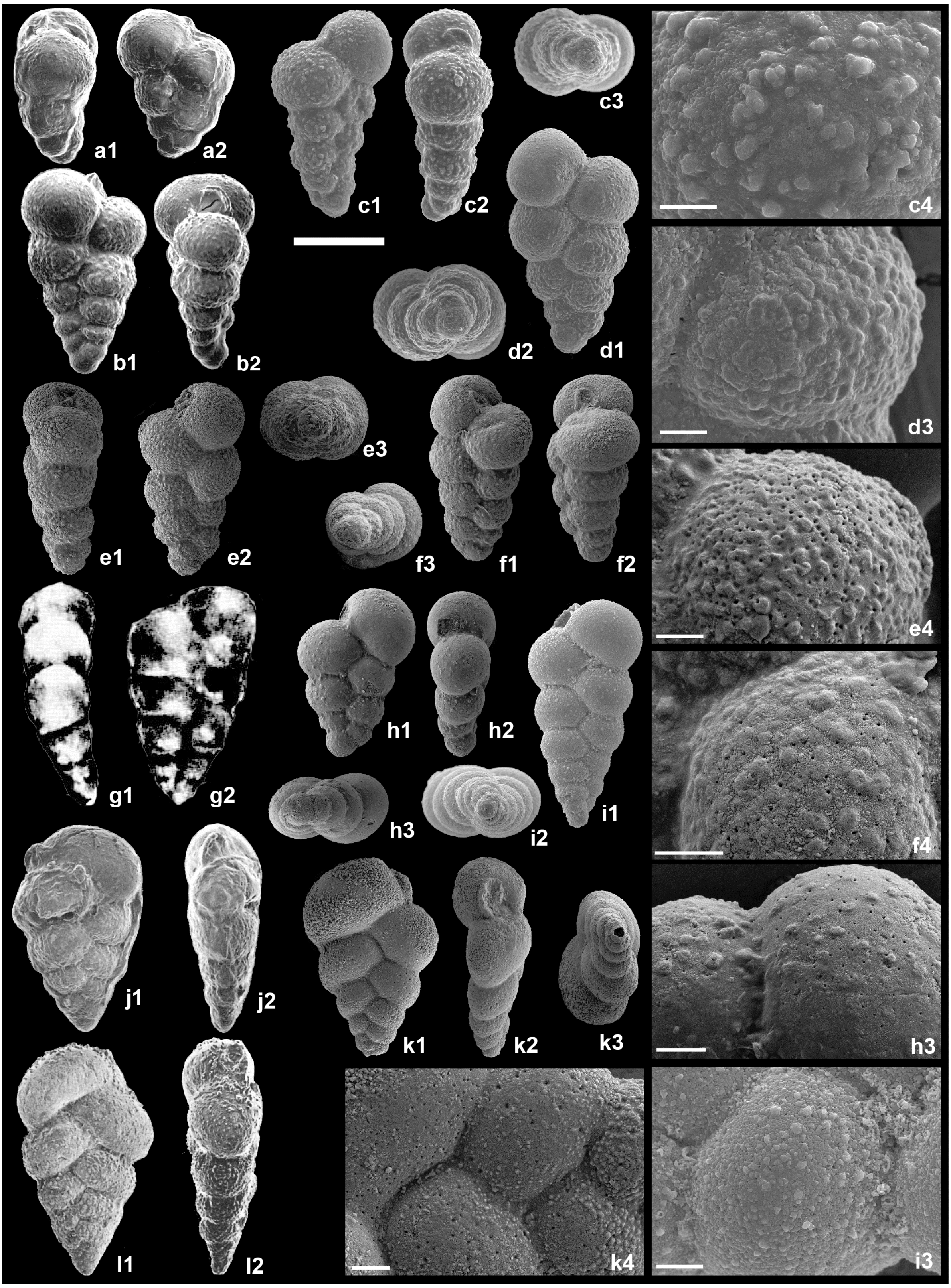

Stage
Planktonic foraminiferal zonations
(1)
(2)
DANIAN
P. pseudobulloides
Pv. eugubina
G. cretacea
S. triloculinoides
E. trivialis
E. simplicissima
Pv. sabina
Pv. longiapertura
H. holmdelensis
P1b
P1a
Pα
P0
G. blowi
G. dammula
G. cretacea
Gc. daubjergensis
T. extensa
T. liuae
T. olssoni
T. alabamensis
Chg. trilobata
Chg. danica
Chg. hofkeri
Chg. irregularis
Chg. biseriata
W. claytonensis
W. hornerstownensis
Ch. taurica
Ch. midwayensis

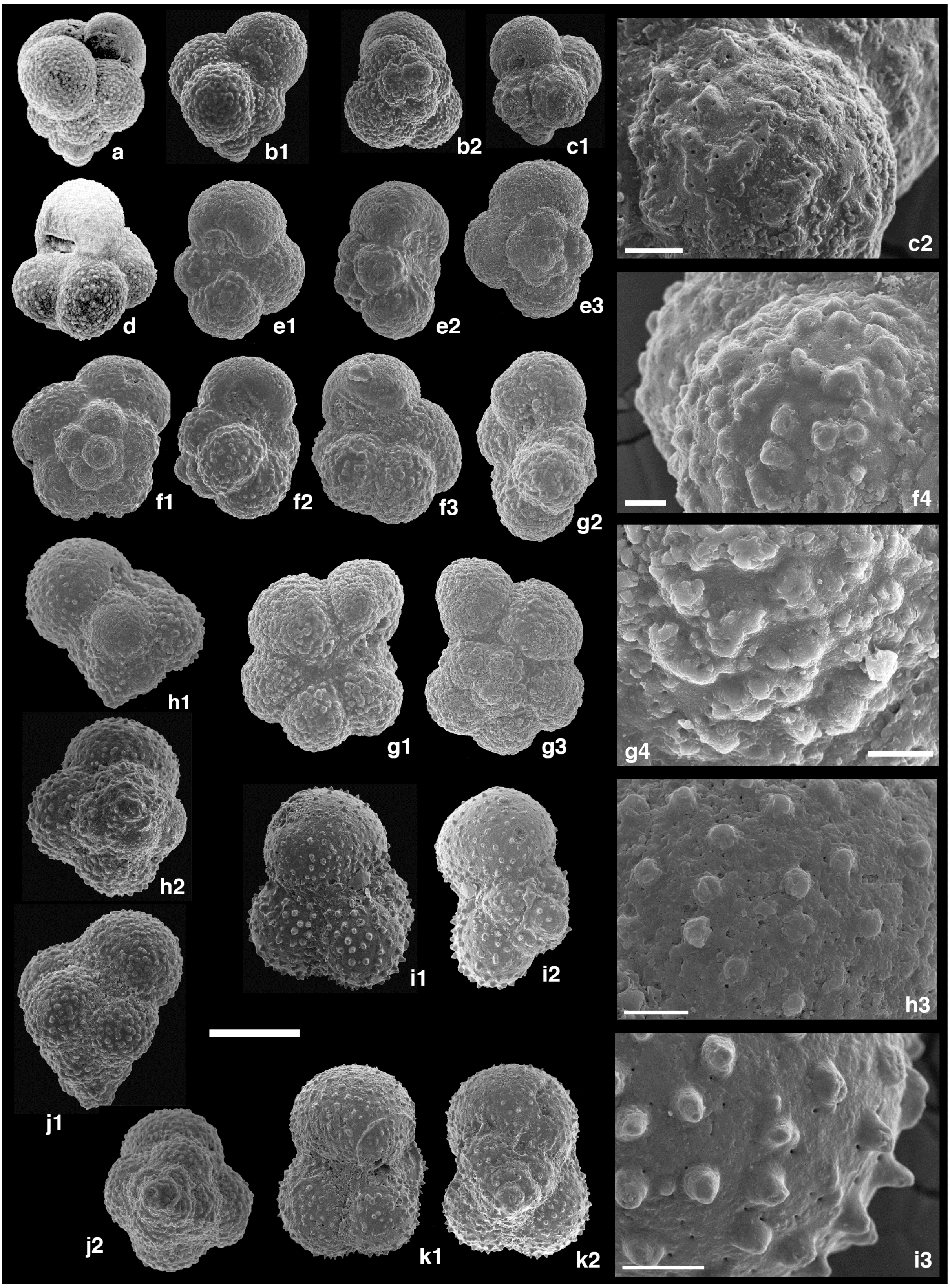

a
b
c
d1
d2
d3
e1
e2
e3
f1
f2
f3
g1
g2
h1
h2
i1
i2
i3
j1
j2
k1
k2
l1
l2
l3
m1
m2
m3
n1
n2
n3
n4

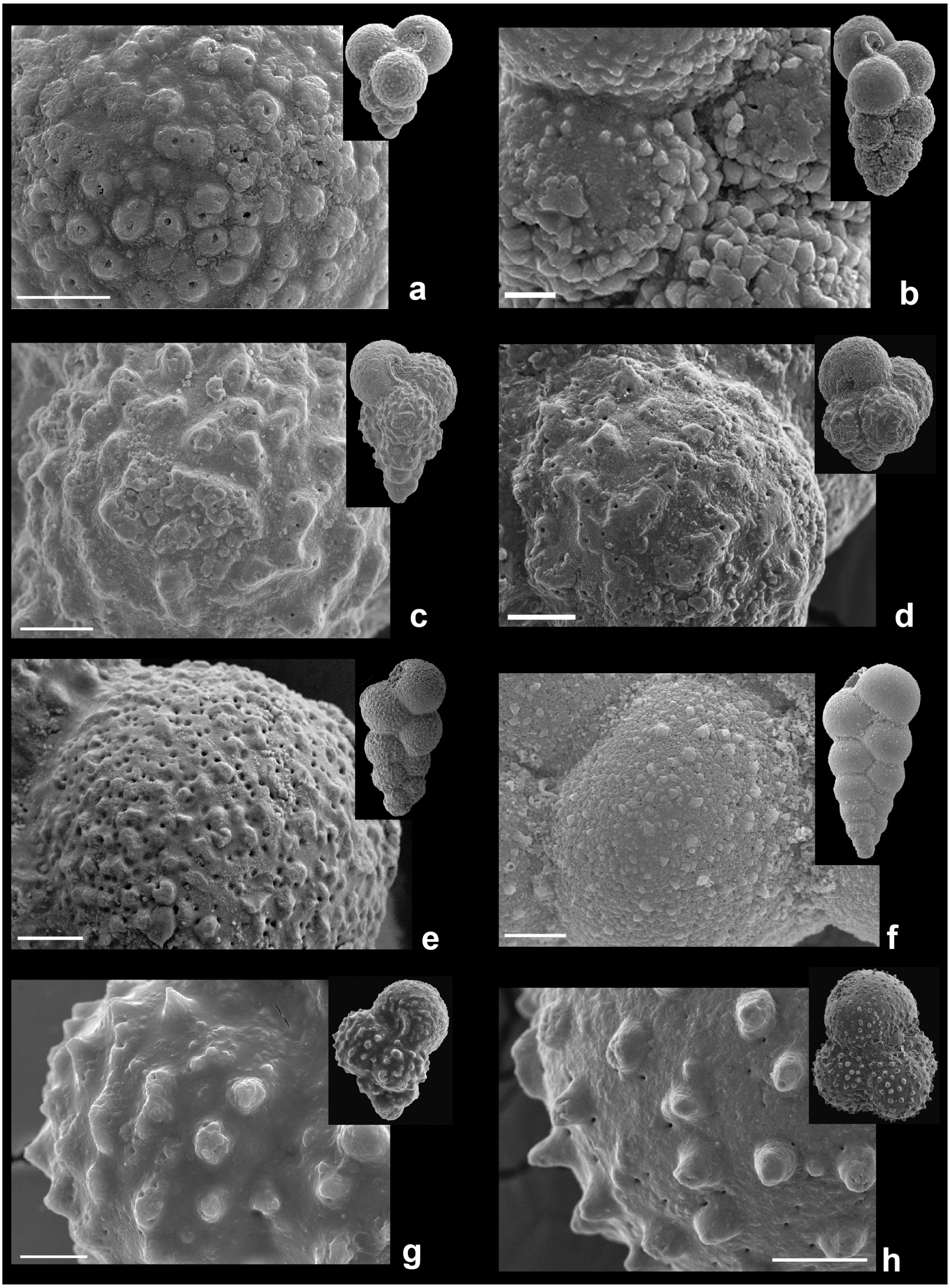

a1
a2
b1
b2
c1
c2
d1
d2
d3
e2
e1
f1
f3
f2
g1
g2
h1
h2
a3
b3
c3
d3
e3
f4
g3
h3

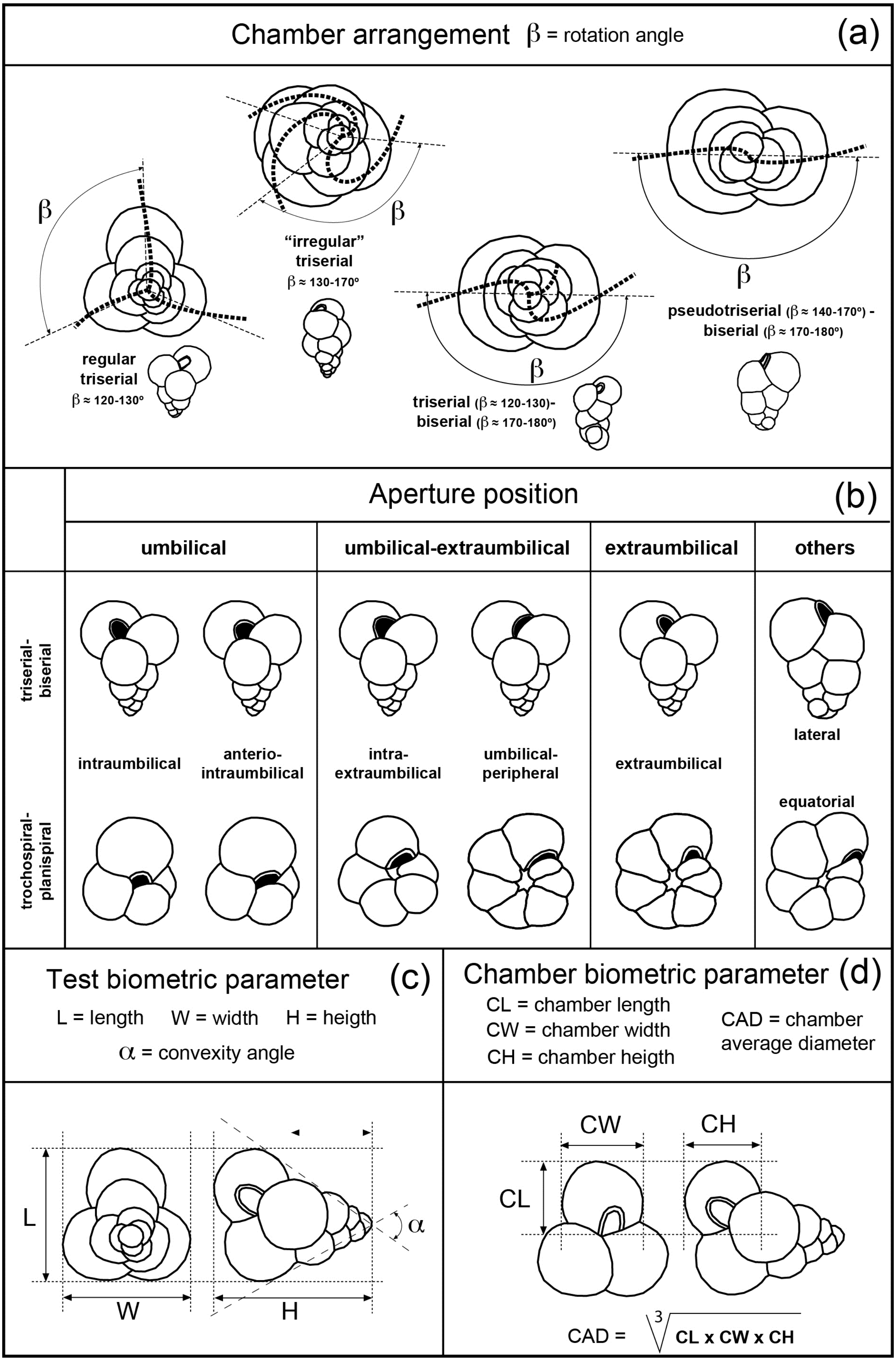

a1
a2
b1
b2
b3
c1
c2
e1
e2
c3
d1
d2
d3
f1
f2
f3
g1
g2
g3
h2
h1
h3
a3
b4
c4
d4
e3
f4
g4
h4

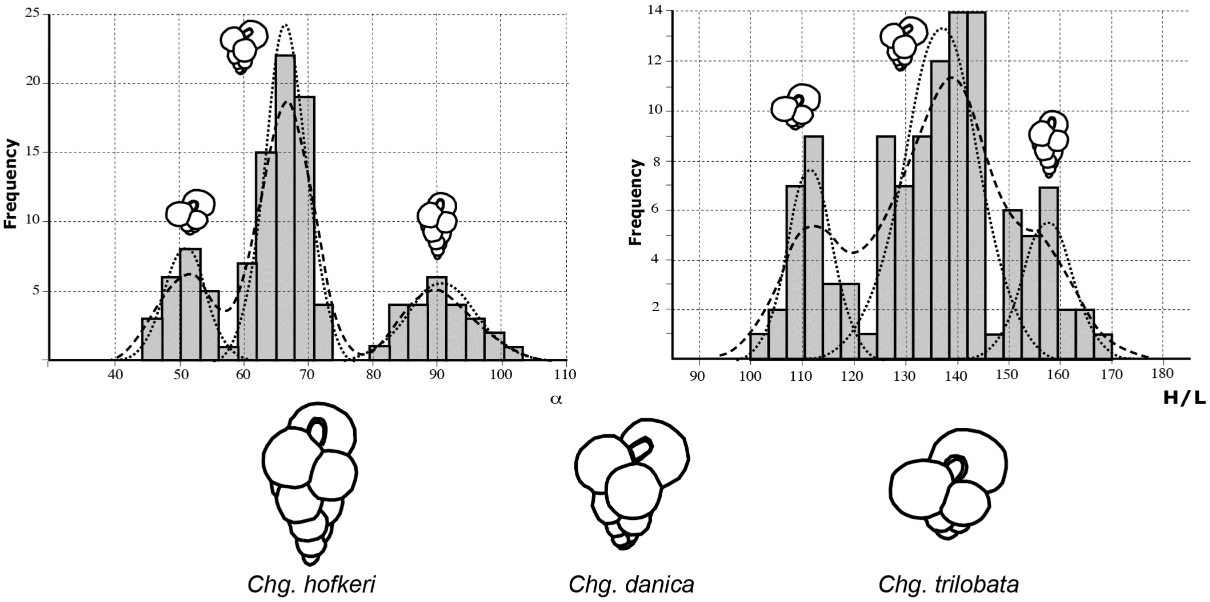

a
b1
b2
c1
c2
b3
d1
d2
e1
e2
c3
f1
f2
g1
g2
d3
h
i1
i2
i3
e3
j1
j2
j3
f3
k2
l1
l2
k1
k3
g3

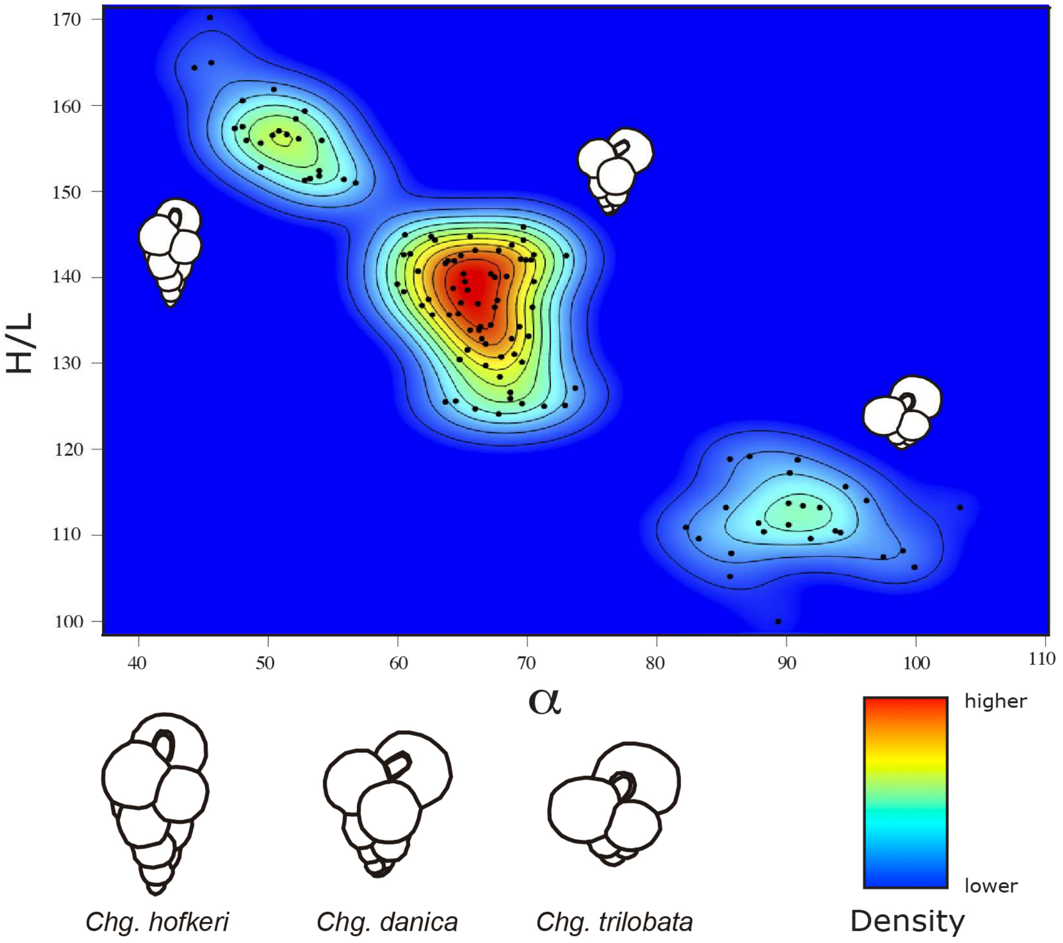

a1
a2
c1
c2
c3
c4
b1
b2
d2
d1
d3
e3
e1
e2
f3
f1
f2
e4
g1
g2
h1
h2
i1
f4
h3
i2
j1
j2
k1
k2
k3
h3
l1
l2
k4
i3

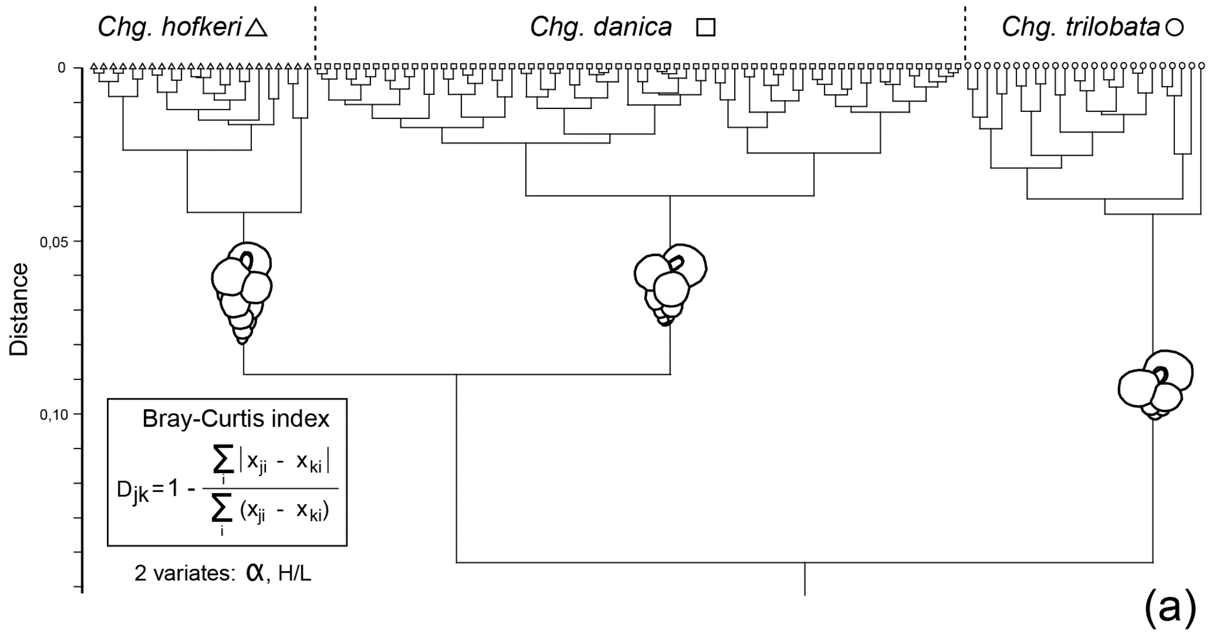

a
b1
b2
c1
c2
d
e1
e2
e3
f1
f2
f3
f4
g2
g1
g3
g4
h1
h2
h3
i1
i2
i3
j1
j2
k1
k2

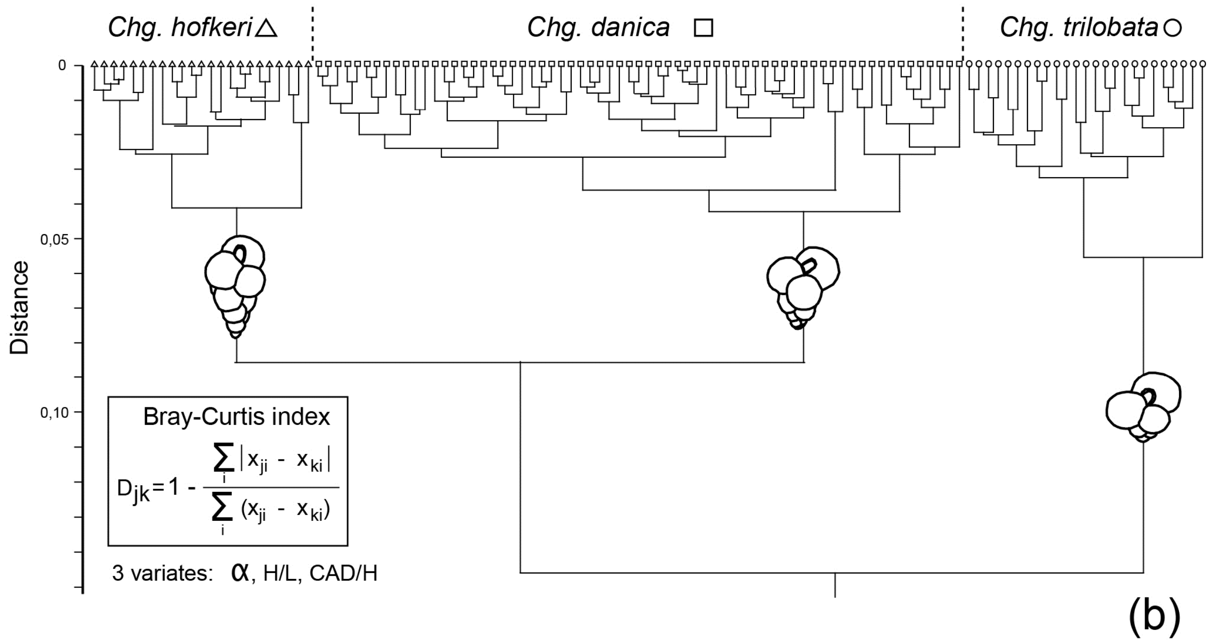

a
b
c
d
e
f
g
h


Chamber arrangement β = rotation angle
(a)
β
regular
triserial
β ≈ 120-130°
β
"irregular"
triserial
β ≈ 130-170°
β
triserial (β ≈ 120-130)-
biserial (β ≈ 170-180°)
β
pseudotriserial (β ≈ 140-170°) -
biserial (β ≈ 170-180°)
Aperture position
(b)
umbilical
umbilical-extraumbilical
extraumbilical
others
triserial-
biserial
trochospiral-
planispiral
intraumbilical
anterio-
intraumbilical
intra-
extraumbilical
umbilical-
peripheral
extraumbilical
lateral
equatorial
Test biometric parameter
(c)
L = length W = width H = heigth
α = convexity angle
Chamber biometric parameter (d)
CL = chamber length
CW = chamber width
CH = chamber heigth
CAD = chamber
average diameter
L
W
H
α
CW
CH
CL
CAD = $\sqrt[3]{CL \times CW \times CH}$


Frequency
25
20
15
10
5
40
50
60
70
80
90
100
110
α
Frequency
14
12
10
8
6
4
2
90
100
110
120
130
140
150
160
170
180
H/L
Chg. hofkeri
Chg. danica
Chg. trilobata


170
160
150
140
130
120
110
100
H/L
40
50
60
70
80
90
100
110
α
higher
lower
Density
Chg. hofkeri
Chg. danica
Chg. trilobata


Chg. hofkeri △
Chg. danica □
Chg. trilobata ○
0
0,05
0,10
Distance
Bray-Curtis index
$D_{jk}=1-\frac{\sum_i |x_{ji}-x_{ki}|}{\sum_i (x_{ji}-x_{ki})}$
2 variates: α, H/L
(a)


Chg. hofkeri △
Chg. danica □
Chg. trilobata ○
0
0,05
0,10
Distance
Bray-Curtis index
$D_{jk}=1-\frac{\sum_i |x_{ji}-x_{ki}|}{\sum_i (x_{ji}-x_{ki})}$
3 variates: α, H/L, CAD/H
(b)

HIGHLIGHTS

- The evolutionary radiation of earliest Danian guembelitriids was analysed.

- The genus *Chiloguembelitria* Hofker, 1978, is revalidated.

- Three new planktonic foraminifera species were identified.

- A new phylogenetic hypothesis is proposed based on the K/Pg boundary GSSP, Tunisia.