



New species of the genus *Trochoguembelitra* from the lowermost Danian of Tunisia – biostratigraphic and evolutionary implications in planktonic foraminifera

by

IGNACIO ARENILLAS, JOSÉ ANTONIO ARZ and CAROLINA NÁÑEZ

with 4 plates, 7 text-figures and 1 table

Abstract

Two lineages of primitive trochospiral species emerged in the earliest Danian after the Cretaceous/Paleogene (K/Pg) mass extinction event, one exhibiting a smooth wall texture with mural pores and the other, a pustulate to rugose wall texture consisting of blunt pustules and small rugosities, imperforate or with decentred pores, and scattered pore-mounds. This evolutionary scenario is based on Tunisian sections, particularly the El Kef section, whose continuity, completeness, abundance and excellent preservation of the foraminifera make it the best locality worldwide for analyzing the taxonomy and evolution of the early Danian planktonic foraminifera. The first lineage appeared about 5 kyr after the K/Pg boundary catastrophic mass extinction and is attributed to the parvularugoglobigerinids (*Parvularugoglobigerina* and *Palaeoglobigerina*). The second lineage appeared approximately 35 kyr after the K/Pg boundary event and is assigned to *Trochoguembelitra* ARENILLAS, ARZ & NÁÑEZ, 2012. Morphological and morphostatistical analyses of *Trochoguembelitra* discriminate at least four species, two of them usually assigned to parvularugoglobigerinids: *T. alabamensis* (LIU & OLSSON, 1992) and *T. extensa* (BLOW, 1979); and two new species: *T. liuae* sp. nov. and *T. olssoni* sp. nov.

Keywords: planktonic foraminifera, taxonomy, morphostatistics, Paleocene, Tunisia

Contents

1. Introduction	6. Discussion
2. Material and methods	7. Systematic palaeontology
3. Biostratigraphy and Biochronology	Acknowledgements
4. Morphology, biometry and morphostatistical analysis ..	References
5. Descriptive morphology and results of morphostatistical analysis	Explanation of the plates

1. Introduction

After the catastrophic mass extinction of the planktonic foraminifera at the Cretaceous/Paleogene (K/Pg) boundary, an evolutionary radiation of new planktonic foraminifera species has been widely documented (LUTERBACHER & PREMOLI SILVA 1964, SMIT 1982, BRINKHUIS & ZACHARIASSE 1988, CANUDO et al. 1991, D'HONDT 1991, OLSSON et al. 1996,

MOLINA et al. 1998). This evolutionary radiation occurred in two pulses: the first one at approximately 5–20 kyr after the K/Pg boundary extinction event, and the second one at approximately 35–80 kyr (ARENILLAS et al. 2000a, b, 2010, 2012). Minute trochospiral species of *Palaeoglobigerina* ARENILLAS, ARZ & NÁÑEZ, 2007, and *Parvularugoglobigerina* HOFKER, 1978, both usually included in *Parvularugoglobi-*

Authors' addresses:

Ignacio Arenillas and José Antonio Arz, Departamento de Ciencias de la Tierra, and Instituto Universitario de Investigación en Ciencias Ambientales de Aragón (IUCA), Universidad de Zaragoza, E-50009 Zaragoza, Spain, e-mail: ias@unizar.es, josearz@unizar.es

Carolina Nánéz, Servicio Geológico Minero Argentino and CONICET, Benjamín Lavaisse 1194, C1107BJD Buenos Aires, Argentina, e-mail: carolina.nanez@yahoo.com

gerina (e.g., OLSSON et al. 1999), as well as biserial species of *Woodringina* LOEBLICH & TAPPAN, 1957, evolved during the earlier evolutionary pulse. In the second pulse, more modern genera evolved, including *Chiloguembelina* LOEBLICH & TAPPAN, 1956, *Eoglobigerina* MOROZOVA, 1959, *Parasubbotina* OLSSON, HEMLEBEN, BERGGREN & LIU, 1992, *Globanomalina* HAQUE, 1956, *Praemurica* OLSSON, HEMLEBEN, BERGGREN & LIU, 1992, and *Trochoguembelitra* ARENILLAS, ARZ & NÁJUEZ, 2012. Finally, other significant genera of the early Danian, such as *Globoconusa* KHALILOV, 1956, and *Subbotina* BROTZEN & POZARYSKA, 1961, evolved later around 150–250 kyr after the K/Pg boundary event.

Although microperforate trochospiral species of the lowermost Danian have usually been included in *Parvularugoglobigerina*, a detailed analysis of Tunisian sections suggested that two lineages of quasi-homeomorph species but of a different wall texture can be recognized. The first lineage exhibits a smooth wall texture with mural pores (e.g., SMIT 1982, BRINKHUIS & ZACHARIASSE 1988, LI & RADFORD 1991, LI et al. 1995) and evolved during the first evolutionary pulse. Its species were attributed by ARENILLAS et al. (2012) to the parvularugoglobigerinids (*Parvularugoglobigerina* and *Palaeoglobigerina*), such as *Parvularugoglobigerina eugubina* (LUTERBACHER & PREMOLI SILVA, 1964) and *Palaeoglobigerina alticonusa* (LI, MCGOWRAN & BOERSMA, 1995).

The second lineage has a pustulate to rugose wall texture. The rugosity is caused by coalescing pore-mounds and/or blunt pustules, generating small, not aligned rugae or ridges. Pustules and rugosities are imperforate or with decentred or peripherally associated pores. Scattered irregularly shaped pore-mounds can also be observed. This type of wall texture evolved during the second Danian evolutionary radiation. Wall texture and biostratigraphic data suggest that this is a lineage different from the parvularugoglobigerinids, and both probably derived independently from different ancestors. This second lineage was assigned to a new genus, *Trochoguembelitra* ARENILLAS, ARZ & NÁJUEZ, 2012, with *Guembelitra? alabamensis* LIU & OLSSON, 1992, as the type-species. However, detailed qualitative and morphostatistical studies of the morphological variability of *Trochoguembelitra* remained to be performed. In the present study, we statistically analyze new biometric data of *Trochoguembelitra* and its phenotypic variability. This enables us to discriminate species within *Trochoguembelitra*, re-assess its

phylogenetic relationships with other early Danian planktonic foraminiferal lineages, and analyze the biostratigraphic implications of these findings.

2. Material and Methods

Samples for this study were selected from the lower Danian of the El Kef section, Tunisia, the Global boundary Stratotype Section and Point (GSSP) for the base of the Danian Stage (MOLINA et al. 2006). The lowermost Danian begins with a 50 cm-thick black clay, overlain by 50 cm-thick dark grey clay (Text-fig. 1). This 100 cm-thick dark clay is informally known as the “K/T Boundary Clay” or K/Pg boundary Clay, and its base is characterized by a 1–3 mm-thick rust-coloured ferruginous layer, usually referred to as the “K/T airfall layer”. The K/Pg boundary was formally defined at the base of this clay, i.e., at the base of the airfall layer, which contains impact evidence, such as high concentration of iridium, shocked quartz and microspherules. It coincides with the catastrophic mass extinction of the planktonic foraminifera (SMIT 1990, 1999, ARENILLAS et al. 2000a, b, MOLINA et al. 2009). At El Kef, the “K/T Boundary Clay” is overlain by a 1 m-thick grey, clay-rich shale, followed by > 10 m-thick white to grey clayey marls. The original proposal and the revision of this GSSP including detailed stratigraphical and micropalaeontological descriptions can be found in MOLINA et al. (2006).

Eighty-four *Trochoguembelitra* specimens from lower Danian El Kef samples KF18.50, KF20.50 and KF24.80 (see Text-fig. 1), respectively 6.5, 8.5 and 12.8 m above the K/Pg boundary, were randomly chosen for the morphostatistical analysis. All studied rock samples were disaggregated in water with diluted H₂O₂, washed through a 63 µm sieve and oven-dried at 50 °C. Specimens were picked from the residues and selected for scanning electron microscopy using JEOL JSM 6400 SEM and Zeiss MERLIN FE-SEM at the Microscopy Service of the Universidad de Zaragoza (Spain). Figured specimens are deposited in the Museo de Ciencias Naturales de la Universidad de Zaragoza (Gobierno de Aragón, Spain). The preservation of the planktonic foraminifera is good (excellent at some samples), although corroded and recrystallized surfaces can be observed in many specimens. No evidence of selective dissolution affecting only cancellate or rugose species has been identified either in El Kef or other Tethyan sections (SMIT 1982, BRINKHUIS & ZACHARIASSE 1988, ARENILLAS et al. 2000a, b).

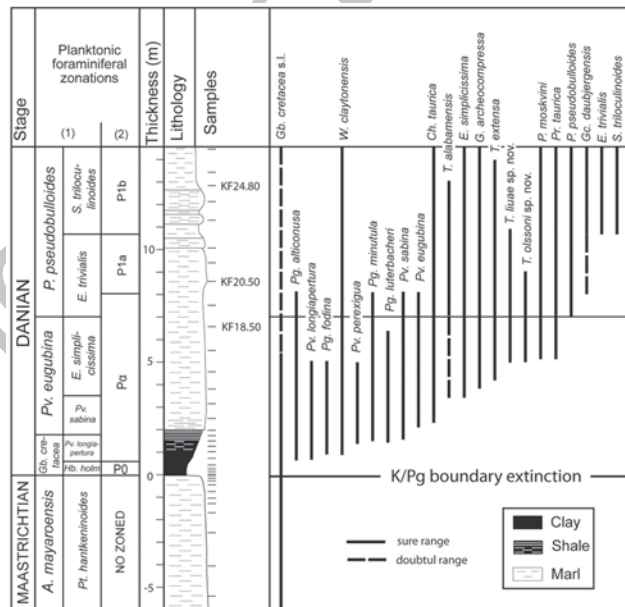
MOLINA et al. (2006, 2009) demonstrated that El Kef is – based on its continuity, exposure, completeness, and abundance and preservation of foraminifera – the best section worldwide for analyzing the taxonomy and evolution of the lowermost Danian planktonic foraminifera.

3. Biostratigraphy and Biochronology

The biozonation is based on that proposed by ARENILLAS et al. (2004) for the lower Danian (Text-fig. 1). It includes the three classical lower Danian biozones, i.e., the *Guembelitra cretacea*, *Parvularugoglobigerina eugubina* and *Parasubbotina pseudobulloides* Zones (SMIT 1982, TOUMARKINE & LUTERBACHER 1985, SMIT & ROMEIN 1985), and divides each of these biozones into two subzones: the *Hedbergella holmdelensis* and *Parvularugoglobigerina longiapertura* Subzones in the *G. cretacea* Zone, the *Parvularugoglobigerina sabina* and *Eoglobigerina simplicissima* Subzones in the *Pv. eugubina* Zone, and the *Eoglobigerina trivialis* and *Subbotina triloculinoides* Subzones in the *P. pseudobulloides* Zone. The lower boundaries of these subzones and their calibration to the numerical time scale according to ARENILLAS et al. (2004) are the following: (1) highest stratigraphic

cal occurrence (HSO) of *Plummerita hantkeninoides* and/or *Abathomphalus mayaroensis* for the base of the *H. holmdelensis* Subzone (coinciding with the K/Pg boundary, 66.0 Ma according to GRADSTEIN et al. 2012), (2) lowest stratigraphical occurrence (LSO) of *Pv. longiapertura* for the base of the homonymous subzone (about 6 kyr after the K/Pg boundary), (3) LSO of *Pv. eugubina* for the base of the *Pv. sabina* Subzone (about 18 kyr after the K/Pg boundary), (4) LSO of *E. simplicissima* for the base of the homonymous subzone (about 35 kyr after the K/Pg boundary), (5) LSO of *P. pseudobulloides* for the base of the *E. trivialis* Subzone (about 55 kyr after the K/Pg boundary) and (6) LSO of *S. triloculinoides* for the base of the homonymous subzone (about 220 kyr after the K/Pg boundary). This planktonic foraminiferal succession is recorded in complete and continuous sections in Tunisia, Spain and southeastern Mexico (ARENILLAS et al. 2004, 2006).

In Text-fig. 1, a correlation with the biozonation of BERGGREN & PEARSON (2005) is made assuming that the LSO of *Pv. longiapertura* marks the P0/Pa boundary, the HSO of *Pv. eugubina*, the Pa/P1a boundary, and the LSO of *S. triloculinoides*, the P1a/P1b boundary. Nevertheless, this equivalence can be



Text-fig. 1. Biostratigraphic ranges of some of the analyzed planktonic foraminifera species: (1) zonation of ARENILLAS et al. (2004), and (2) zonation of BERGGREN & PEARSON (2005).

compromised by the varying taxonomic conceptions of *Pv. eugubina*. The BERGGREN & PEARSON (2005) biozonation is based on the taxonomy of OLSSON et al. (1999), who amended the genus *Parvularugoglobigerina* to include specimens with both smooth and pore-mound wall textures and regarded *Pv. longiapertura* as a junior synonym of *Pv. eugubina*. However, *Parvularugoglobigerina* had usually been interpreted as having a smooth wall texture (SMIT 1982, BRINKHUIS & ZACHARIASSE 1988, LI & RADFORD 1991, LI et al. 1995, ARENILLAS & ARZ 2000). The top of Zone P α of BERGGREN & PEARSON (2005) may be higher than illustrated in Text-fig. 1, as it would encompass species with pustulate to rugose wall texture, here included in *Trochoguembelitra*.

Another factor that may influence the correlation between biozones is the presence of hiatuses in those reference sections on which the biozonations have been based. For example, hiatuses affecting at least the *H. holmdelensis* Subzone and the “K/T Boundary Clay” are frequent in most of the K/Pg boundary sections in the region of the Gulf of Mexico (ARENILLAS et al. 2006, MOLINA et al. 2009). In Tethyan sections, the *H. holmdelensis* Subzone spans much of the “K/T Boundary Clay”, and is characterized exclusively by the presence of *Guembelitra* and other possible Cretaceous survivors of the K/Pg boundary extinction event. According to its original definition (SMIT 1982, SMIT & ROMEIN 1985), the Zone P0 contains no planktonic foraminiferal species originating in the early Danian. The occurrence of rugose *Trochoguembelitra*, pitted *Globanomalina* and cancellate *Eoglobigerina*, *Parasubbotina* and *Praemurica* just above the K/Pg boundary is indicative that the section has a hiatus corresponding to the lowermost Danian, probably the *H. holmdelensis*, *Pv. longiapertura* and *Pv. sabina* Subzones. Consequently, the *H. holmdelensis* Subzone of ARENILLAS et al. (2004) can be correlated with the Zone P0 of SMIT (1982) and SMIT & ROMEIN (1985), but probably not with the Zone P0 of OLSSON et al. (1999), since they record representatives of the genera *Globanomalina*, *Eoglobigerina* and *Praemurica*.

At El Kef, the LSO of *Trochoguembelitra* is in the transition between the *Pv. sabina* and *E. simplicissima* Subzones, i.e. in the middle part of Zone P α (Text-fig. 1). The first *Trochoguembelitra* species to appear seems to be *T. alabamensis*, about 35 kyr after the K/Pg boundary event according to the biochronology by ARENILLAS et al. (2004). This datum coincides ap-

proximately with the LSOs of *Eoglobigerina* and *Globanomalina* and the beginning of the second evolutionary radiation after the mass extinction at the K/Pg boundary. At El Kef, the HSO of *Trochoguembelitra* is in the lower part of the *S. triloculinooides* Subzone, approximately 300 kyr after the K/Pg boundary. This datum coincides with the HSO of *Pv. eugubina* (top of Zone P α) as suggested by BERGGREN & PEARSON (2005), approximately 280 kyr after the K/Pg boundary according to the biochronological calibrations proposed by GRADSTEIN et al. (2012). Although it should be further clarified, this datum supports the hypothesis that the top of the Zone P α of BERGGREN & PEARSON (2005) is based on the HSO of *Trochoguembelitra* species such as *T. liuae* sp. nov. and *T. olsoni* sp. nov., which is in agreement with the wider taxonomic conception of *Pv. eugubina* of these authors. The highest record of smooth-walled *Pv. eugubina* occurs in the lower part of the *E. trivialis* Subzone at El Kef and other Tethyan, Gulf of Mexico and Caribbean sections, i.e. approximately 60 kyr after the K/Pg boundary.

4. Morphology, biometry and morphostatistical analysis

As mentioned above, *Trochoguembelitra* species show morphological similarities with some species of *Palaeoglobigerina* and *Parvularugoglobigerina*, to which they have been attributed in previous studies (see references in ARENILLAS et al. 2012). For comparison, Plate 1 illustrates the most important *Palaeoglobigerina* and *Parvularugoglobigerina* species according to ARENILLAS et al. (2007, 2012), and Plate 2 the *Trochoguembelitra* species discussed in the present paper. In order to distinguish the *Trochoguembelitra* species, we have mainly used the following qualitative and quantitative morphological characters (see Text-fig. 2):

1) Aperture position and shape

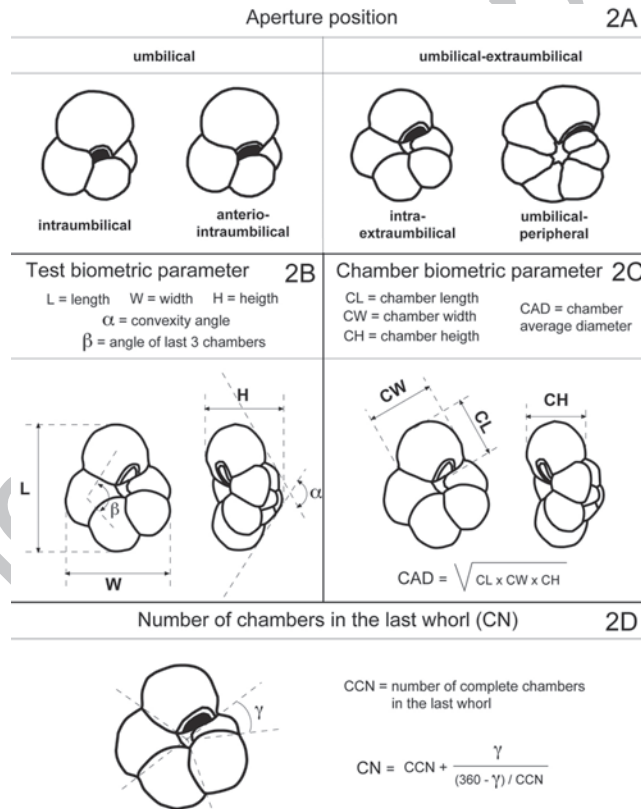
We have followed the traditional terminologies of LOEBLICH & TAPPAN (1987) to describe the position and shape of the aperture (Text-fig. 2). According to these authors, there are three types of apertural position in spiral tests: (1) umbilical (or intraumbilical), if the aperture opens completely into the umbilicus; (2) umbilical-extraumbilical (or extraumbilical-umbilical), if it extends from the umbilicus towards the periphery of the test; and (3) extraumbilical, if it is not connected with the umbilicus; the latter includes the

peripheral or equatorial position, if it opens completely in the periphery. All of them are interiomarginal, i.e. with the aperture located at the basal margin of the final chamber (LOEBLICH & TAPPAN 1987). The umbilical position is typical of high trochospiral and triserial tests, the umbilical-extraumbilical position of low trochospiral tests, and the peripheral or equatorial position of planispiral tests.

Since all planktonic foraminifera discussed in this paper are trochospiral (Plates 1–4), we have used a more precise terminology for the location of the aperture based mainly on LI (1987) and BOUDAGHER-FADEL (2012). We have subdivided the types of apertural position in trochospiral tests into two subtypes each (Text-fig. 2A): intraumbilical and antero-intraumbilical for umbilical apertures, and intra-extraumbilical and umbilical-peripheral for umbilical-extraumbilical apertures. Their definition is as follow:

(1a) intraumbilical, if the aperture is centred in the umbilicus; (1b) antero-intraumbilical, if the aperture is located in the umbilicus but is slightly asymmetrical and tends to warp towards the periphery; (1c) intra-extraumbilical, if the aperture is located in the umbilical area extending towards the periphery but does not reach it; and (1d) umbilical-peripheral, if it extends from the umbilicus up to the periphery.

The apertures of the planktonic foraminifera discussed in this paper have the following morphologies: (a) a semicircular, wide arch, (b) a elongate, wide arch, and (c) a narrow, high arch (like a loop). *Trochoguembelitra*, usually has wide-arched apertures surrounded by a thin lip, generally being rounded in intraumbilical and antero-intraumbilical apertures, and marginally elongate in intra-extraumbilical and umbilical-peripheral apertures. In *Globoconusa*, the aperture is intraumbilical but smaller. In the lowermost Danian,



Text-fig. 2. A: Types of aperture position. B: Biometric parameters, abbreviations and descriptive terms used in the morphological analysis of the *Trochoguembelitra* tests. C: Biometric parameters, abbreviations and descriptive terms used in the morphological analysis of the *Trochoguembelitra* chambers.

Table 1. Biometric measurements (in microns) of *Trochoguembelitra* specimens, and biometric index 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; β : angle made by centres of the last three chambers; CN: number of chambers in the last whorl.

<i>Trochoguembelitra alabamensis</i>								
Specimen	L	W	H	CAD	a	b	CN	CAD/H
1	112	94,9	126,2	73,1	79,8	81,7	3,7	57,9
2	106,7	87,2	140,1	81,1	61,3	67,3	3,3	57,9
3	148,6	121,3	163,5	100,5	76,9	68,1	3,3	61,5
4	92,5	78,4	99,9	66,3	81,3	69,3	3,0	66,4
5	92,9	88,9	99,8	62	84,1	85,2	3,6	62,2
6	109,6	85,5	128,1	82	75,7	81,4	3,5	64,0
7	99,4	83,8	104,8	67,4	92,3	86,5	3,7	64,4
8	108,8	91,4	123,2	76,4	78,7	77,1	3,4	62,0
9	126,5	108,3	143,2	88,6	74,2	70,3	3,4	61,9
10	110,3	93,3	127,3	80,6	80,0	73,2	3,3	63,3
Average	110,7	93,3	125,6	77,8	78,4	76,0	3,4	62,1
<i>Trochoguembelitra extensa</i>								
Specimen	L	W	H	CAD	a	b	CN	CAD/H
1	125,8	103,2	97,8	77,7	112,7	83,4	3,8	79,4
2	162,1	137,2	141,3	102,9	106,7	85,0	3,8	72,8
3	174,0	145,2	133,8	106,3	117,2	86,2	3,6	79,5
4	132,5	123,5	88,6	80,1	130,4	78,0	3,7	90,4
5	176,9	149,3	138,1	106,4	116,3	91,8	3,9	77,1
6	116,3	117,9	114,5	76,9	100,4	77,3	3,7	67,2
7	178,3	158,5	133,0	105,2	119,8	79,5	3,6	79,2
8	176,2	147,6	120,4	105,2	131,1	86,4	3,8	87,4
9	186,9	152,6	120,9	105,4	147,0	91,3	3,7	87,2
10	155,6	161,4	164,1	105,3	104,2	72,7	3,6	64,2
11	170,1	139,4	148,9	104,3	113,3	91,4	3,8	70,1
12	157,3	143,6	162,3	109,2	98,3	80,1	3,7	67,3
13	137,3	121,8	144,6	92,3	106,0	76,0	3,0	63,9
14	104,3	92,5	95,4	61,0	101,4	76,2	3,8	63,9
15	113,8	95,0	106,2	81,0	114,8	77,2	3,3	76,2
16	92,3	84,1	93,5	60,1	108,4	81,0	3,5	64,2
17	99,7	74,9	83,0	63,1	108,8	87,1	3,3	76,1
18	153,3	148,6	163,7	112,0	108,2	74,4	3,8	68,4
19	136,4	125,2	141,3	94,3	115,5	80,7	3,9	66,8
20	107,0	94,5	104,2	74,2	116,8	76,6	3,6	71,2
21	102,2	90,9	101,6	73,4	100,0	74,8	3,5	72,2
22	107,6	86,7	105,4	73,5	104,3	79,7	3,1	69,8
23	110,4	87,6	117,8	75,8	114,8	84,4	3,5	64,3
24	127,4	105,5	123,5	85,8	105,9	85,0	3,7	69,5
25	138,5	121,2	123,2	89	108,7	81,7	3,6	72,2
26	152,1	146,4	136,4	101,5	109,7	82,3	3,7	74,4
27	124,8	107,8	112,4	82,6	109,2	81,9	3,5	73,5
28	141,8	127,4	130,2	95	105,2	78,3	3,5	73,0
29	135,2	115,4	116,4	88,2	112,3	83,2	3,6	75,7
Average	137,8	120,9	122,8	89,2	112,0	81,5	3,6	73,0

<i>Trochoguembelitra liuae</i> sp. nov.								
Specimen	L	W	H	CAD	a	b	CN	CAD/H
1	103,4	85,8	69,4	64,3	137,9	99,0	4,6	92,7
2	116,3	96,0	79,5	71,7	135,2	99,5	4,4	90,1
3	158,6	130,6	103,3	86,8	147,1	101,1	4,5	84,0
4	132,9	108,8	95,9	79,4	129,9	101,9	4,5	82,8
5	130,4	97,4	87,7	71,7	130,7	111,1	4,4	81,7
6	174,3	158,0	133,8	106,9	118,7	102,3	5,3	79,9
7	137,5	118,0	94,0	80,3	131,3	94,2	4,1	85,5
8	132,2	109,8	99,9	74,4	124,2	110,3	4,8	74,5
9	154,6	137,7	122,8	91,5	125,8	97,2	4,5	74,5
10	109,3	102,3	85,5	60,8	123,7	101,9	4,7	71,1
11	108,4	81,9	73,1	59,1	132,2	107,2	5,0	80,9
12	187,2	160,7	148,1	103,6	118,2	101,7	4,5	70,0
13	165,4	133,5	100,3	91,6	132,1	104,2	4,7	91,3
14	207,0	162,2	139,7	109,2	140,1	104,5	4,7	78,1
15	184,3	162,1	121,2	102,0	136,7	101,0	4,5	84,2
16	153,3	128,7	114,0	88,2	115,6	111,6	4,7	77,3
17	174,2	138,4	131,2	102,3	118,8	103,2	4,4	78,0
18	196,9	172,1	134,6	106,4	122,6	114,2	5,0	79,0
19	218,8	190,0	175,9	124,4	123,6	105,1	4,7	70,7
20	90,3	85,9	66,5	52,9	117,9	103,9	4,8	79,6
21	123,2	111,3	90,5	72,6	120,0	104,3	4,8	80,2
22	136,3	111,4	91,4	77,0	132,1	108,8	4,7	84,2
23	132,0	116,1	91,5	77,7	144,4	109,2	4,4	85,0
24	192,6	161,6	139,2	117,9	138,9	96,9	4,4	84,6
25	132,6	123,9	100,5	71,0	134,9	101,5	4,5	70,7
26	93,8	86,6	69,6	55,8	131,2	92,3	4,7	80,2
27	150,9	128,1	106,3	86,0	122,4	108,7	4,6	80,9
28	140,3	123,0	108,7	86,6	124,1	90,1	4,3	79,6
29	146,4	124,0	103,5	83,9	131,4	104,5	4,6	81,0
30	131,0	114,1	94,3	75,9	127,7	104,5	4,7	80,5
31	161,4	133,6	112,7	92,8	136,1	105,4	4,5	82,3
32	158,9	143,7	114,6	96,0	124,6	92,6	4,3	83,8
Average	148,0	126,2	106,2	85,0	129,1	102,9	4,6	80,6
<i>Trochoguembelitra olssoni</i> sp. nov.								
Specimen	L	W	H	CAD	a	b	CN	CAD/H
1	139,5	115,8	85,5	71,8	164,6	123,0	5,5	83,9
2	210,0	171,9	132,6	106,6	151,3	121,6	5,1	80,4
3	172,4	150,4	110,3	89,5	158,8	130,9	5,2	81,2
4	143,9	114,1	89,0	83,7	167,5	117,2	5,0	94,0
5	139,3	115,9	84,1	75,4	158,8	118,6	4,7	89,7
6	208,7	187,0	134,5	100,4	146,6	127,1	5,4	74,6
7	146,5	122,3	89,5	75,6	151,3	126,7	5,3	84,5
8	113,2	93,8	85,3	70,7	128,1	126,7	4,9	82,9
9	124,8	97,2	77,1	67,0	144,5	125,1	5,4	86,9
10	147,9	129,3	102,7	81,4	133,9	118,4	4,8	79,3
11	161,6	134,6	100,2	86,0	155,2	125,7	5,3	85,8
12	168,3	138,5	107,2	93,8	157,3	119,7	5,1	87,5
13	152,9	129,6	93,6	79,9	149,2	125,2	5,2	85,4
Average	156,1	130,8	99,4	83,2	151,3	123,5	5,1	84,3

high-arched, narrow apertures are typical of many species of parvularugoglobigerinids (e.g., *Pv. longiapertura*). Thin lips are typical of the species considered in this paper, usually slightly projecting above and along the aperture. More modern Danian genera, such as *Eoglobigerina*, *Parasubbotina*, *Subbotina*, *Globanomalina* or *Praemurica*, have a thicker lip, usually transformed into a porticus or a tooth.

2) Biometric parameters and indices

The biometric parameters used to delimit species are the following: convexity angle (α) measured in axial view; angle (β) made by centres of the last three chambers in umbilical and/or spiral view; maximum diameter or 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 $CAD = (CL \times CW \times CH)^{1/3}$ (see Text-fig. 2B, C, and Table 1). In addition, we used the biometric index CAD/H. The latter and the biometric variable α are measures of test convexity whereas β , together with the number of chambers (CN), are measures of the morphology of the equatorial outline (Table 1). Other biometric indices have been explored as measures of test convexity, such as L/H or CH/H, and outline morphology, such as W/L, but these have not given consistent results for separating species.

The number of chambers (CN, "Chamber Number") in the last whorl is a character used to distinguish taxa mainly at the species level, but also at the genus level, as is the case with *Subbotina* and *Eoglobigerina*. The number of chambers in the last whorl in the lower Danian planktonic foraminifera varies between 3 and 8, and between 3.5 and 5.5 for *Trochoguembelitra*. To calculate the number of chambers, we have counted the number of complete chambers in the last whorl, and the percentage of the first chamber of the last whorl visible on the umbilical side. This observable percentage was calculated using the angle (γ) between the umbilical centre and the sutures of the chamber, and dividing by the average angle of the other chambers (Text-fig. 2D). The observable percentage was also calculated by measuring the length of the first chamber of the last whorl on the umbilical side divided by the length of the same chamber on the spiral side. The results are similar in both cases, therefore we opted for the first method of calculation (Table 1).

3) Morphostatistical analyses

For morphostatistical analyses, the software used was the program PAST, version 2.17c, by HAMMER et al.

(2001). The biometric parameters and indices were treated statistically using the following analysis:

- i Univariate analyses: Three above-mentioned biometric indices (α , β and CAD/H) and the number of chambers (CN) 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 15 bins (Text-fig. 3). 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.
- ii Bivariate analyses: Paired variables were used to make four bivariate analyses: CN vs. α , β vs. α , CN vs. β , and CAD/H vs. α . Kernel density estimates allowed us to make smooth maps of point density in XY graphs (Text-fig. 4); 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. Given that the variables cover a large range of values, the measures were transformed logarithmically to reduce the wide range to a more manageable size.
- iii 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 , β , CAD/H and CN) in order to find groupings that might represent species (Text-fig. 5). The PCA was applied to the values of the four 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 (Text-fig. 6); 95%-confidence ellipses, which assume a bivariate normal distribution, and convex hulls, which are the

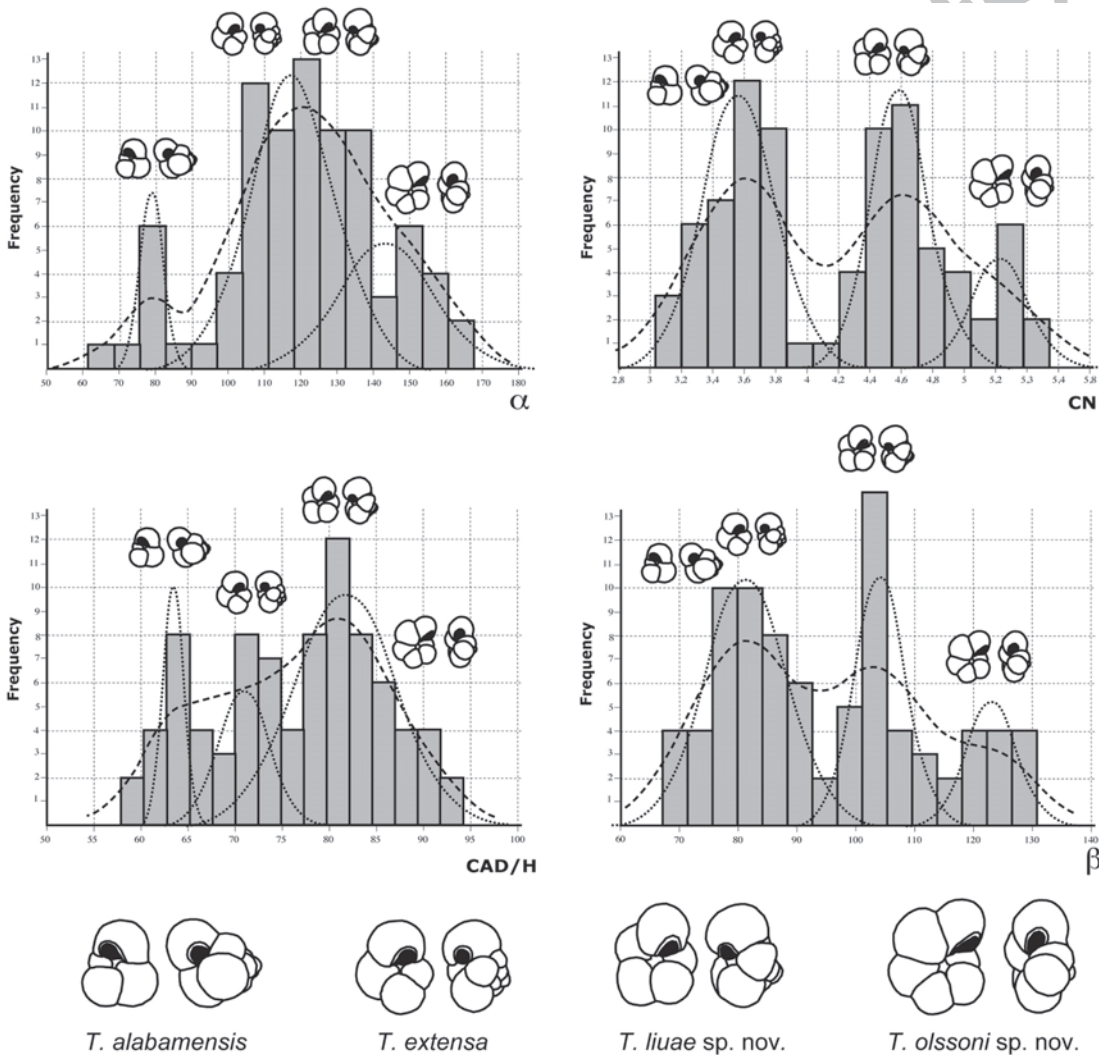
smallest convex polygons containing all points, were presented in the scatter diagram. As in the case of bivariate analyses, measures were transformed logarithmically.

5. Descriptive morphology and results of morphostatistical analysis

The morphological and morphostatistical analyses discriminate at least four species within *Trochoguembeli-*

tria. 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 four 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.

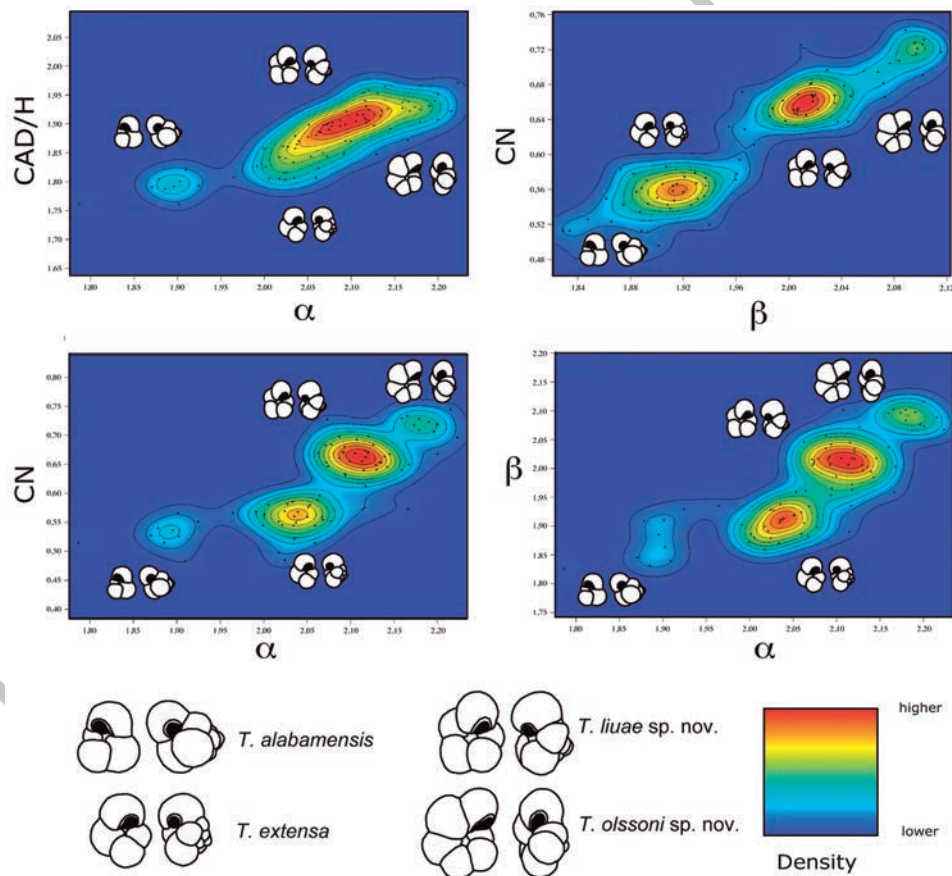
Frequency distributions of the univariate analyses (Text-fig. 3), calculated for all measured specimens



Text-fig. 3. Univariate analyses based on biometric variables α , CN, CAD/H and β to delimit the *Trochoguembelitra* species, displayed as histograms of 15 bins; thick dotted lines are the Kernel density estimations; fine dot lines are univariate normal distributions (Gaussian bell-shaped curves) based on mixture analysis.

and represented in a plot histogram of 15 bins, suggest four morphogroups of *Trochoguembelitra*. The biometric variables of test convexity (α and CAD/H) suggest at least two morphogroups (high-trochospiral, and low- or medium-trochospiral), as suggested by Kernel density estimates. The high-trochospiral morphogroup is assigned to *T. alabamensis* (LIU & OLSSON, 1992). Histograms and Gaussian bells enable us to recognize three other morphogroups, here assigned to the species *T. extensa* BLOW (1979), *T. liuae* sp. nov. and *T. olssoni* sp. nov. The α variable seems to distinguish two groups, a low-trochospiral group, which can be assigned to *T. olssoni* sp. nov., and a medium-trochospiral group, which can be assigned to either *T. extensa* or *T. liuae* sp. nov. By contrast, the CAD/H variable indicates that both *T. liuae* sp. nov. and *T.*

olssoni sp. nov. have a low trochospire, whereas *T. extensa* is separated by the medium height of its trochospire. In order to separate the latter three morphogroups simultaneously it is more useful to analyze the biometric variables of the equatorial outline (β and CN). Univariate Kernel density estimates based on these latter variables indicate at least three morphogroups, which are also observable in the histograms and Gaussian bells. The first morphogroup includes specimens subtriangular or subquadrangular in outline and averaging 3.6 chambers in the last whorl, which can be assigned to either *T. alabamensis* or *T. extensa*. The second morphogroup includes specimens subpentagonal in outline and averaging 4.6 chambers in the last whorl, which are assigned to *T. liuae* sp. nov. Finally, the third morphogroup includes specimens

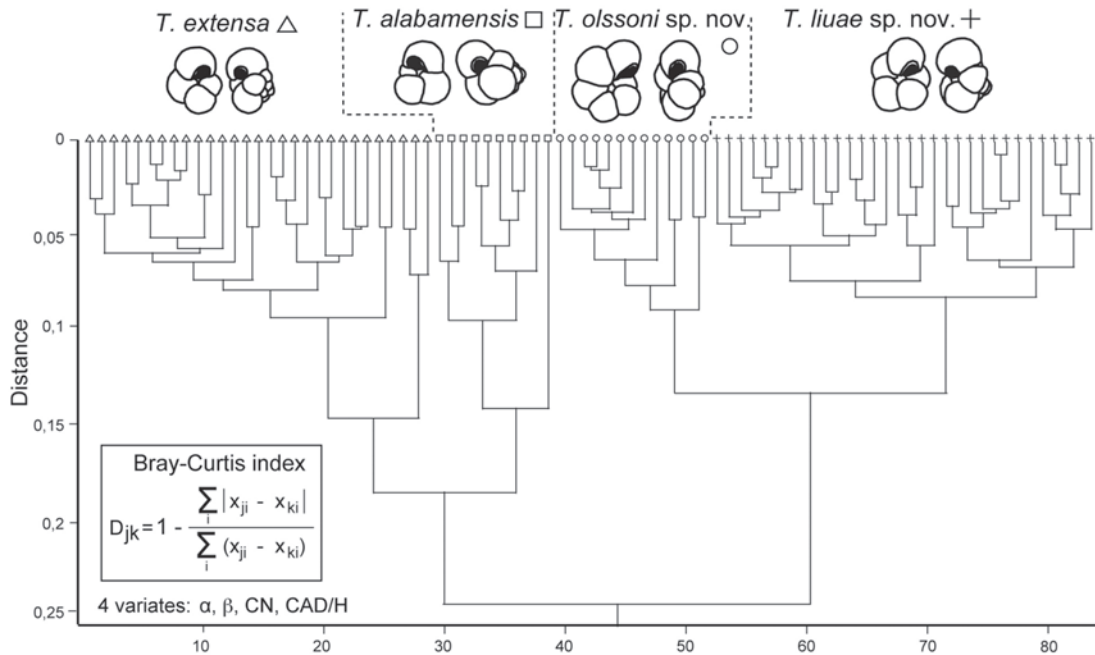


Text-fig. 4. Bivariate analyses based on Kernel density estimations from paired variables (CN vs. α , β vs. α , CN vs. β , CAD/H vs. α) and plotted in smooth maps of point density; colour scale with deep red for highest density and dark blue for lowest.

subcircular in outline and averaging 5.1 chambers in the last whorl, which are assigned to *T. olssoni* sp. nov.

Bivariate analyses (Text-fig. 4) also strongly suggest that the genus *Trochoguembelitra* contains four species; these are well observable in the Kernel density maps. If we match the log-transformed variables of test convexity (α and CAD/H), two morphogroups can be distinguished, one composed by low- or medium-trochospiral groups (*T. extensa*, *T. liuae* sp. nov. and *T. olssoni* sp. nov.) and the other by the high-trochospiral group (*T. alabamensis*). As regards the biometric variables of equatorial outline (β and CN), three morphogroups are well distinguishable in the Kernel density map, which comprise those subtriangular or subquadrangular in outline (*T. alabamensis* and *T. extensa*), subpentagonal (*T. liuae* sp. nov.), and subcircular (*T. olssoni* sp. nov.). If the biometric variables for different geometrical information are matched, such as CN vs. α and β vs. α , four morphogroups emerge clearly, allowing us to discriminate the four above-mentioned species.

Cluster analysis (Text-fig. 5), based on the Bray-Curtis similarity index and the log-transformed variables α , CAD/H, β and CN, produced dendrograms with two primary clusters, one grouping the morphotypes with less than 4 chambers in the last whorl (*T. alabamensis* and *T. extensa*) and the other those with more than 4 chambers (*T. liuae* sp. nov. and *T. olssoni* sp. nov.). Each of these clusters is further subdivided into two sub-clusters, which are well differentiated by their equatorial outline and test convexity. The first cluster is subdivided in medium-trochospiral and high-trochospiral morphogroups, which are assigned to *T. extensa* and *T. alabamensis* respectively. The second cluster is subdivided into subpentagonal specimens with 4–4.5 chambers in the last whorl represented by *T. liuae* sp. nov. and subcircular specimens with more than 4.5 chambers represented by *T. olssoni* sp. nov. Except for anomalous specimens or intermediate morphotypes, the identified clusters correspond to morphogroups that can be distinguished under the stereomicroscope.



Text-fig. 5. R-mode cluster analysis based on Bray-Curtis index and applied to the values of the biometric variables (α , β , CAD/H and CN) measured in all *Trochoguembelitra* specimens photographed by SEM. D_{jk} = Bray-Curtis index value between specimen j and specimen k; x_{ji} = value of the variable i (biometric index/parameter i) of the specimen j; x_{ki} = value of the variable i (biometric index/parameter i) of the specimen k.

The principal component analysis (PCA) shows similar results as those of the cluster analysis (Text-fig. 6). The principal component PC1 explains 85.8% of the variance, and the PC2 9.9%. The PCA scatter diagram, where X and Y are the principal components PC1 and PC2, distinguish four sets of points of higher density. We specified four groups of specimens, clustering them subjectively by their gross morphology. They are approximately equivalent to those obtained by the PCA. Except for the intermediate and/or anomalous specimens, convex hulls and 95%-confidence ellipses clearly delimit the four species above-mentioned. Their main characteristics are easily recognizable under the stereomicroscope.

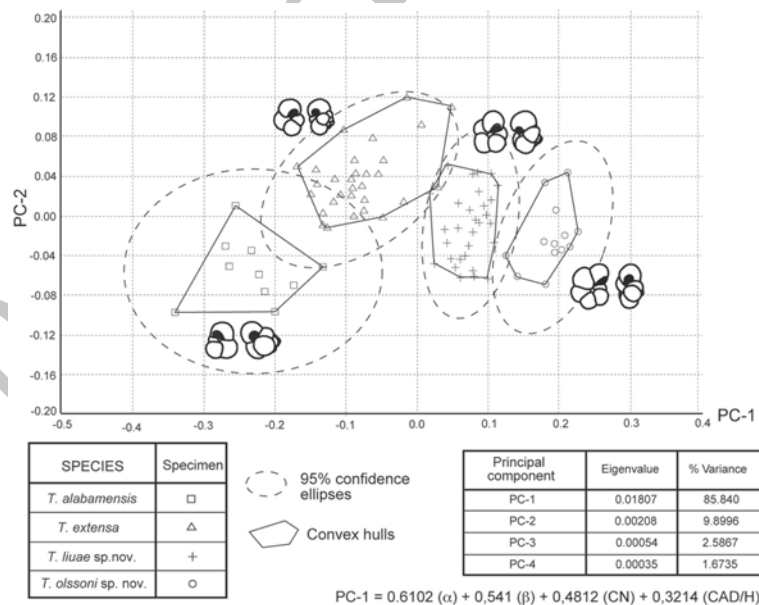
The position of the aperture in *Trochoguembelitra* varies from intraumbilical to umbilical-peripheral. The lesser the number of chambers the specimen has in the last whorl, the more centred is the aperture in the umbilicus. In general, *T. alabamensis* has an intraumbilical aperture, *T. extensa* an anterio-intraumbilical aperture, *T. liuae* sp. nov. an intra-extraumbilical aperture, and *T. olssoni* sp. nov. an umbilical-peripheral aperture. The shape of the aperture is usually similar to that of *Guembelitra*, i.e. large and semicircular but asymmetric due to its elongation toward the

periphery and up apertural face. The more peripheral the aperture, the more elongated it is.

6. Discussion

Textural, biometric and morphostatistical analyses discriminate four species within the genus *Trochoguembelitra*: *T. alabamensis* (LIU & OLSSON, 1992), *T. extensa* (BLOW, 1979), *T. liuae* sp. nov. and *T. olssoni* sp. nov. The first two species were originally attributed to *Guembelitra*? and *Eoglobigerina*?, respectively. Blow (1979) regarded *T. extensa* and *Globoconusa daubjergensis* (BRÖNNIMANN, 1953) as quite closely related on the basis of similarities in wall texture, coiling mode and chamber shape. FORDHAM (1986) suggested the lineage *T. extensa*-*Gc. daubjergensis* descended from *G. cretacea*, as also proposed by other authors (e.g., BANG 1969, OLSSON 1970, OLSSON et al. 1999).

For similar reasons, ARENILLAS et al. (2012) also suggested that *Trochoguembelitra* is a descendent of the pore-mound walled, triserial *Guembelitra* and the ancestor of the pustulate-walled, trochospiral *Globoconusa*. These authors illustrated intermediate specimens between *T. cf. fodina*, here *T. extensa*, and *Gc. daubjergensis* from the *E. trivialis* and *S. triloculinoides*



Text-fig. 6. Principal components analysis (PCA), applied to the values of biometric variables (α , β , CAD/H and CN) in all *Trochoguembelitra* specimens.

Subzones, exhibiting a similar gross morphology and a transitional wall texture. The wall texture of these intermediate specimens has pustules sharper than usual in *Trochoguembelitra*, resembling those of *Globoconus*, and suggesting a tendency in *Trochoguembelitra* to increasingly develop acuminate pustules. At El Kef and other Tethyan sections, the LSO of *Gc. daubjergensis* s.s. is in the *S. triloculinooides* Subzone (= P1b), but its real LSO might be lower as suggested by data from other sections and cores (e.g., KOUTSOUKOS 2014).

Eoglobigerina? fodina BLOW, 1979, here assigned to *Palaeoglobigerina*, was also included by both BLOW (1979) and FORDHAM (1986) in the lineage descending from *Guembelitra*. However, the holotypes of *Pg. fodina* and *T. extensa*, described from Zone Pa and Zone P1 respectively (BLOW 1979), differ in size and shape. The holotype of *Pg. fodina* (Plate 1, Fig. 4) is approximately 100 µm in length, whereas the holotype of *T. extensa* (Plate 2, Fig. 5) is approximately 200 µm long. BLOW (1979) described a similar wall texture for both species, i.e. finely perforate with very widely and sparsely developed mural pores, and pustules that may be the bases of normal spines. However, the holotypes are recrystallized, so the pustules appear as rather calcite crystals. In addition, there are conspicuous differences in the shape of the aperture. BLOW (1979) noticed that the aperture of *Pg. fodina* is extremely peculiar and does not match with any other species included either in *Eoglobigerina* or *Globastica* BLOW, 1979, this latter being a junior synonym of *Globoconusa*. According to BLOW (1979), it is described as circular, but it has a fairly high arch extending from the umbilicus. It is very similar to the aperture in other species of *Parvularugoglobigerina* (e.g., *Pv. longiapertura*) and *Palaeoglobigerina* (e.g., *Pg. alticonusa*). The almost rectangular shape of the aperture of the holotype of *T. extensa* is probably a teratological deformation (Plate 2, Fig. 5). Nevertheless, it may be inferred that it is wider than the aperture of the holotype of *Pg. fodina*. Given the plasticity of the morphology and location of the aperture in these taxa, OLSSON et al. (1999) considered that such differences are insufficient to maintain *T. extensa* and *Pg. fodina*, and other similar species, as separate taxa, and therefore reduced *Pg. fodina* to a junior synonym of *T. extensa*. However, better-preserved specimens from Tunisian sections allowed ARENILLAS et al. (2012) not only to observe differences between *Pg. fodina* and *T. extensa* in apertural shape and initial spiral arrangement, but

also in the wall texture (smooth vs. rugose). BLOW (1979) indicated that unlike *T. extensa*, *Pg. fodina* has a fairly low trochospire. Given the textural and morphological differences in well-preserved specimens, we retain *Pg. fodina* in *Palaeoglobigerina* and assign *T. extensa* to *Trochoguembelitra*.

No intergradation between the pustulate to rugose wall texture of *Trochoguembelitra* and the typically smooth wall texture of parvularugoglobigerinids was observed and consequently both groups are regarded as separate lineages. The occurrence of the minute, smooth-walled parvularugoglobigerinids in the lowermost Danian of Tunisia has been indicated by SMIT (1982), BRINKHUIS & ZACHARIASSE (1988), and other authors. BRINKHUIS & ZACHARIASSE (1988) noted that *Parvularugoglobigerina* is a very unfortunate generic name for species that have a smooth wall texture and no affinity with Upper Cretaceous *Rugoglobigerina* BRÖNNIMANN, 1952, and suggested that a more appropriate name would have been *Planoconus* as opposed to *Globoconusa*, in which they included the globular species subsequently assigned to *Palaeoglobigerina* by ARENILLAS et al. (2007).

SALAJ (1986) defined the genus *Postrugoglobigerina* in the lowermost Danian of El Kef, composed of the species *Pt. haryana* and *Pt. praedaubjergensis*, and based it on characters similar to those later attributed to *Trochoguembelitra*. *Postrugoglobigerina* was reported by LOEBLICH & TAPPAN (1987), and more recently by BOUDAGHER-FADEL (2012) to have a trochospiral test and a microperforate and muricate wall texture. This taxon could have been a good candidate to name the *Trochoguembelitra* specimens, but the holotypes and type-material of both *Postrugoglobigerina* species have been lost, are of doubtful application, and must be regarded as *nomen dubium non conservandum* (see discussion in ARENILLAS et al. 2012). The taxonomic interpretation of *Postrugoglobigerina* raises several questions, such as the true nature of its wall texture, the coiling mode of the holotypes of its species, and its biostratigraphic position. This genus should therefore be invalidated, or at least regarded as a junior synonym of *Parvularugoglobigerina* as proposed by OLSSON et al. (1999), since its type-species (*Pt. haryana*) is probably a junior synonym of *Pv. sabina*.

After a detailed re-examination with a SEM-microscope of El Kef samples previously studied by traditional stereomicroscopy, we have noticed that some specimens have to be placed in the genus *Trochoguembelitra*. They had been previously attributed to quasi-

homeomorph species belonging to the genera *Parvularugoglobigerina*, *Palaeoglobigerina*, *Eoglobigerina*, *Globanomalina* and *Praemurica* (see morphological similarities in Text-fig. 7).

The existence of quasi-homeomorph species and even pseudocryptic (i.e. cryptic species only *a posteriori* distinguished as morphospecies by wall texture or

small morphological details) has been tested in other Tunisian sections (ARENILLAS et al. 2010, 2012). KOUTSOUKOS (2014) has also reported new lower Danian species in *Globoconusa* (*Gc. victori*) and *Praemurica* (*Pr. nikolasi*), indicating that the morphological variability of lower Danian planktonic foraminiferal genera is greater than previously thought (Text-

	Subconical test	Globular test					Compressed test
	3-3.5 chambers 	3-3.5 chambers 	3.5-4 chambers 	4 chambers 	4-4.5 chambers 	4.5-7 chambers 	4.5-7 chambers 
Palaeoglobigerina Smooth wall	 <i>Pg. alticonusa</i>	 <i>Pg. minutula</i>	 <i>Pg. fodina</i>	 <i>Pg. luterbacheri</i>			
Parvularugoglobigerina Smooth wall					 <i>Pv. sabina</i>	 <i>Pv. eugubina</i>	 <i>Pv. longiapertura</i>
Trochoguembelitra Pustulate to rugose wall	 <i>T. alabamensis</i>		 <i>T. extensa</i>		 <i>T. liuae</i> sp. nov.	 <i>T. olssoni</i> sp. nov.	
Globoconusa Pustulate wall	 <i>Gc. conusa</i>	 <i>Gc. victori</i>	 <i>Gc. daubjergensis</i>				
Eoglobigerina Spinose cancellate wall	 <i>E. tetragona</i>		 <i>E. simplicissima</i>	 <i>E. fringa</i>	 <i>E. edita</i>		
Parasubbotina Spinose cancellate wall				 <i>P. moskvini</i>	 <i>P. pseudobulloides</i>		
Subbotina Spinose cancellate wall		 <i>S. triloculinooides</i>					
Globanomalina Non spinose pitted wall				 <i>G. imitata</i>	 <i>G. planocompressa</i>	 <i>G. archeocompressa</i>	 <i>G. compressa</i>
Praemurica Non-spinose cancellate wall					 <i>Pr. nikolasi</i>	 <i>Pr. taurica</i>	

Text-fig. 7. Morphological variability of lower Danian genera *Palaeoglobigerina*, *Parvularugoglobigerina*, *Trochoguembelitra*, *Globoconusa*, *Eoglobigerina*, *Parasubbotina*, *Subbotina*, *Globanomalina* and *Praemurica*, based on number of chambers in the final whorl of species and the shape of the test. Specimens are not to scale.

fig. 7). The lower Danian planktonic foraminiferal lineages show a broad phenotypic variability, and quasi-homeomorph species belonging to different genera may be rather common. For example, the variations in the number of chambers in the last whorl (3 to 3.5; 3.5 to 4; 4; 4 to 4.5; and more than 4.5) are commonly used to differentiate species, and even genera, among trochospirally coiled taxa (Text-fig. 7). As a result, species attributed to different genera may have nearly the same gross morphology. The stratigraphical ranges of the pseudocryptic species are therefore difficult to determine accurately because they may be underestimated in routine studies with a stereomicroscope.

Therefore, the biostratigraphic ranges proposed for the *Trochoguembelitra* species are, mainly in their upper part, still tentative (Text-fig. 1). The rugose wall texture is its main diagnostic character, but is hardly visible under stereomicroscopy or frequently masked by taphonomic and diagenetic processes. Other useful features for recognizing *Trochoguembelitra* specimens are a frequently protruding proloculus and, to a lesser extent, the shape of their aperture, which comprises a wide, rounded arch with a thin lip, similar to *Guembelitra*, in some species turning to an elongate, asymmetrical arch, reaching the periphery and extending up the apertural face. However, both these features may display great plasticity in early Danian planktonic foraminifera, and it is difficult to correctly identify these taxa with a stereomicroscope.

7. Systematic palaeontology

Order Foraminifera EICHWALD, 1830
Suborder Globigerinina DELAGE & HÉROUARD, 1896

Superfamily Heterohelicoidea CUSHMAN, 1927

Family Guembelitriidae MONTANARO-GALLITELLI, 1957

Genus *Trochoguembelitra* ARENILLAS, ARZ & NÁÑEZ, 2012

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

Occurrence: Lower Danian, from the *E. simplicissima* Subzone (middle part of the *Pv. eugubina* Zone) to the middle part of the *S. triloculinoides* Subzone (middle part of the *P. pseudobulloides* Zone), i.e., from the middle-upper part of $P\alpha$ to the middle part of P1b of BERGGREN & PEARSON (2005). They are common in the transition between *Pv. eugubina* ($P\alpha$) and *P. pseudobulloides* (P1) Zones.

Composition: *Trochoguembelitra alabamensis* (LIU & OLSSON, 1992), *Trochoguembelitra extensa* (Blow, 1979), *Trochoguembelitra liuae* sp. nov., and *Trochoguembelitra olsoni* sp. nov.

Description: Trochospiral test, initially triserial or trochospiral. Outline lobate, with incised sutures. Aperture relatively large, umbilical to umbilical-extraumbilical, semicircular to elongated and asymmetrical, with a thin imperforate lip. Wall calcareous hyaline, microperforate, pustulate to rugose consisting of blunt pustules that may coalesce to form small, not aligned rugosities, and scattered pore mounds; pustules and rugosities imperforate or with decentred or peripherally associated pores.

Remarks: *Guembelitra* s.s. differs from *Trochoguembelitra* in having a pore-mound wall texture and being triserial throughout. *Globoconusa* has a pustulate wall texture, with pointed, more sparsely distributed pustules. *Parvularuglobigerina* and *Palaeoglobigerina* are smaller and have a smooth wall texture with mural-pores (sensu BLOW, 1979, or simple pores according to LOEBLICH & TAPPAN, 1987). Similar specimens were documented by LIU & OLSSON (1992, 1994), and OLSSON et al. (1992, 1999), but assigned to *Parvularugoglobigerina* based on their emendation of this genus. ARENILLAS et al. (2012) included these specimens with blunt pustules, small rugosities and pore-mounds in *Trochoguembelitra*, retaining smooth-walled specimens in *Parvularugoglobigerina*.

Trochoguembelitra alabamensis (LIU & OLSSON, 1992)
(Plate 2, Figs 2–4)

- 1992 *Guembelitra? alabamensis* LIU & OLSSON, p. 341, pl. 2, figs 1–7.
1999 *Parvularugoglobigerina alabamensis* – OLSSON et al., p. 83, part, pl. 65, figs 3, 5–6.
2000 *Guembelitra? alabamensis* – PAPÚ et al., p. 28, pl. 2, figs 9–11.
2007 *Guembelitra? alabamensis* – ARENILLAS et al., p. 39, figs 14.1–14.5.
2012 *Trochoguembelitra alabamensis* – ARENILLAS et al., p. 133–135, figs 5A, D, 6A, G.

Biostratigraphic occurrence: Lower Danian, from the *E. simplicissima* Subzone (in the middle part of the *Pv. eugubina* Zone) to the lower part of the *S. triloculinoides* Subzone (middle part of the *P. pseudobulloides* Zone), i.e., from the middle-upper part of $P\alpha$ to the lower part of P1b of BERGGREN & PEARSON (2005).

Description: Trochospiral test, initially triserial, with moderate to very high spire, 9 to 13 spherical chambers in 3 spiral whorls, about 3.5 chambers in the last whorl and low rate of size increase. Outline lobate, subtriangular or subquadrangular, with incised su-

tures. Aperture umbilical (intraumbilical), semicircular, with a thin imperforate lip. Wall calcareous hyaline, microperforate, pustulate to rugose with blunt pustules and small rugosities, which are imperforate or with decentred or peripherally associated pores, and scattered pore-mounds. Adult size ranges 110–170 μm in height and 90–150 μm in maximum diameter.

Remarks: *T. extensa* differs from *T. alabamensis* in having a lower trochospiral test and an anterio-intraumbilical to intra-extraumbilical, semicircular to slightly asymmetrical and elongated aperture. *T. liuae* sp. nov. has a lower trochospiral test and a larger number of chambers in the last whorl (4 to 5 instead of 3.5 to 4 chambers). *Pg. alticonusa* is smaller and has a smooth to granular wall texture, and usually a narrow, high arched aperture. LIU & OLSSON (1992) tentatively included *T. alabamensis* in *Guembeltria?*, and indicated that *T. alabamensis* differs from *Guembeltria cretacea* CUSHMAN, 1933, by having a trochospiral test and poreless blunt pustules in the later ontogenetic stage. OLSSON et al. (1999) included it in *Parvularugoglobigerina* after emending this genus.

Trochoguembeltria extensa (BLOW, 1979)

(Plate 2, Figs 7–9)

- 1979 *Eoglobigerina?* *extensa* BLOW, p. 1220, pl. 69, fig. 7; pl. 74, figs 1–2.
 ? 1986 *Postrugoglobigerina praedaubjergensis* SALAJ, p. 54, pl. 3, figs 7–8.
 non 1999 *Parvularugoglobigerina extensa* – OLSSON et al., p. 85–86, pl. 65, figs 7–13.
 2012 *Trochoguembeltria* cf. *fodina* (BLOW). – ARENILLAS et al., p. 135–137, figs 5B, E–G, 6B–C, 8A.

Biostratigraphic occurrence: Lower Danian, from the middle part of the *E. simplicissima* Subzone (in the upper part of the *Pv. eugubina* Zone) up to the middle part of the *S. triloculinoides* Subzone (middle part of the *P. pseudobulloides* Zone), i.e., from the upper part of P2a to the middle part of P1b of BERGGREN & PEARSON (2005).

Diagnostic description: Trochospiral test, slightly high spire, 9 to 12 spherical chambers in 3 spiral whorls, 3.5 to 4 chambers in the last whorl, and moderate rate of size increase. Outline lobate, subtriangular or subquadrangular, with incised sutures. Aperture umbilical to umbilical-extraumbilical (anterio-intraumbilical to intra-extraumbilical), semicircular to slightly asymmetrical and elongated, with a thin imperforate lip. Wall calcareous hyaline, microperforate, pustulate to rugose with perforate and/or poreless small rugosities and blunt pustules, and scattered

pore-mounds. Adult size range 110–180 μm in maximum diameter.

Remarks: *T. extensa* resembles *Pg. fodina*, but the latter is smaller, has a smooth wall texture, and usually a higher arched, narrow aperture. *T. alabamensis* has a higher trochospiral test (as *G. cretacea*), and an intraumbilical, semicircular aperture. *T. liuae* sp. nov. has more chambers in the last whorl (4 to 5 instead of 3.5 to 4 chambers). *Gc. daubjergensis* is larger and has a pustulate wall texture, with sharp pustules, sparsely distributed. *T. extensa* should not be confused with *Parvularugoglobigerina extensa* according to OLSSON et al. (1999) since authors grouped into this taxon the trochospiral morphotypes with smooth to granular wall texture classified as *Pg. alticonusa*, *Pg. fodina* and *Pg. minutula* by LI et al. (1995), BLOW (1979) and LUTERBACHER & PREMOLI SILVA (1964) respectively, and assigned to *Palaeoglobigerina* by ARENILLAS & ARZ (2007) and ARENILLAS et al. (2007, 2012). *T. extensa* could be similar to *Postrugoglobigerina praedaubjergensis* SALAJ, 1986, i.e., high-trochospiral, intraumbilical aperture, and 4 chambers in the last whorl, but the holotype of *Pt. praedaubjergensis* has been lost and is of doubtful application, so it must be considered *nomen dubium non conservandum* (ARENILLAS et al., 2012). In addition, its wall texture and stratigraphical range do not coincide with those proposed herein for *T. extensa*.

Trochoguembeltria liuae sp. nov.

(Plate 2, Figs 11–12; Plate 3, Fig. 1 (holotype), Fig. 2 (paratype), Fig. 3 (paratype))

- ? 1986 *Postrugoglobigerina haryana* SALAJ, p. 53, pl. 3, figs 1–2.
 1999 *Parvularugoglobigerina eugubina* – OLSSON et al., p. 83–85, part, pl. 66, figs 1–3, 5, 6; pl. 67, figs 13–14.
 2012 *Trochoguembeltria* cf. *sabina* – ARENILLAS et al., p. 137, figs 5C, H–J, 6D–F, H, 7B, 8B.

Figured specimens and repository: Holotype MPZ 2014/295 (Plate 3, Fig. 1): maximum diameter or length = 187.2 μm , width = 160.7 μm , height = 148.1 μm ; Paratype MPZ 2014/296 (Plate 3, Fig. 2): length = 132.2 μm , width = 108.8 μm , height = 95.9 μm ; Paratype MPZ 2014/297 (Plate 3, Fig. 3): length = 208.7 μm , width = 187.0 μm , height = 134.5 μm . Holotype and paratypes are deposited in the Museo de Ciencias Naturales of the Universidad de Zaragoza, Gobierno de Aragón, Spain, with the prefix MPZ.

Etymology: Species dedicated to CHENGJIE LIU, one of the first in identifying these morphotypes.

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

Type level: 8.5 m above the Cretaceous/Paleogene boundary of the El Kef section (loc. KF20.50), in the lower part of Subzone P1a, or lower part of *Eoglobigerina trivialis* Subzone of *Parasubbotina pseudobulloides* Zone by ARENILLAS et al. (2004), lower Danian.

Biostratigraphic occurrence: Lower Danian, identified from the middle-upper part of the *E. simplicissima* Subzone (upper part of the *Pv. eugubina* Zone) to the *E. trivialis* Subzone (lower part of the *P. pseudobulloides* Zone), i.e., from the upper part of P α to the top of P1a of BERGGREN & PEARSON (2005).

Description: Trochospiral test, slightly high spire, 10 to 12 spherical chambers in 3 spiral whorls, 4.5 to 5 chambers in the last whorl, slowly increasing in size. Outline lobate, subpentagonal, with incised sutures. Aperture umbilical to umbilical-extraumbilical (anterio-intraumbilical to intra-extraumbilical), rounded, asymmetrical and elongated, with a thin imperforate lip. Wall calcareous hyaline, microperforate, pustulate to rugose consisting of blunt pustules that may coalesce to form small, not aligned rugosities; pustules and rugosities imperforate or with decentred or peripherally associated pores; scattered pore-mounds. Adult size ranges 120–200 μm in maximum diameter.

Remarks: *T. liuae* sp. Nov. strongly resembles *Pv. ostul*, but the latter is smaller and has a smooth wall texture. *T. extensa* differs from *T. liuae* sp. Nov. in having fewer chambers in the last whorl (3.5 to 4 instead of 4 to 5 chambers) and intraumbilical aperture. *T. alabamensis* has a higher trochospiral test and lesser number of chambers in the last whorl. *T. liuae* sp. Nov. also resembles *Eoglobigerina edita* (SUBBOTINA, 1953) and/or *Eoglobigerina praedita* BLOW, 1979, which have similar sizes, but these mainly differ in having cancellate wall texture, spines (at least the first one), and often well-developed apertural lips. The morphology of this species could be similar to that described by SALAJ (1986) for *Postrugoglobigerina haryana* (i.e., low-trochospiral, intraumbilical aperture, and 5 chambers in the last whorl). As *Pt. praedaubjergensis*, the holotype of this species has been lost and its identification becomes confusing so *Pt. haryana* should be considered *nomen dubium non conservandum*; its wall texture and stratigraphical range seem to not coincide with those of *T. liuae* sp. Nov. Specimens illustrated by OLSSON et al. (1999), with pore-mound and/or ostulate wall texture, and five chambers in the last whorl are herein included in *T. liuae* sp. Nov. They identified these morphotypes as *Pv. Eugubina*.

Trochoguembelitra olssoni sp. nov.

(Plate 2, Figs 13–14; Plate 4, Fig. 1 (holotype), Fig. 2 (paratype), Fig. 3 (paratype))

1992 *Parvularugoglobigerina eugubina* – LIU & OLSSON, p. 345, part. pl. 3, figs 5–6.

Figured specimens and repository: Holotype MPZ 2014/298 (Plate 4, Fig. 1): maximum diameter or length = 208.7 μm , width = 187.0 μm , height = 134.5 μm ; Paratype MPZ 2014/299 (Plate 4, Fig. 2): length = 139.5 μm , width = 115.8 μm , height = 85.5 μm ; Paratype MPZ 2014/300 (Plate 4, Fig. 3): length = 139.3 μm , width = 115.9 μm , height = 84.1 μm . Holotype and paratypes are deposited in the Museo de Ciencias Naturales of the Universidad de Zaragoza, Gobierno de Aragón, Spain, with the prefix MPZ.

Etymology: Species dedicated to Richard K. Olsson for his work on Danian planktonic foraminifera.

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

Type level: 6.5 m above the Cretaceous/Paleogene boundary of the El Kef section (loc. KF18.50), in the upper part of Zone P α , or upper part of *Eoglobigerina simplicissima* Subzone of *Parvularugoglobigerina eugubina* Zone by ARENILLAS et al. (2004), lower Danian.

Biostratigraphic occurrence: Lower Danian, identified from the middle-upper part of the *E. simplicissima* Subzone (upper part of the *Pv. eugubina* Zone) to the lower part of the *E. trivialis* Subzone (lower part of the *P. pseudobulloides* Zone), i.e., from the upper part of P α to the lower part of P1a of BERGGREN & PEARSON (2005).

Description: Low trochospiral test, 10 to 12 spherical chambers in 3 spiral whorls, 5 to 5.5 chambers in the last whorl, increasing slowly in size. Outline lobate, subcircular, with incised sutures. Aperture umbilical-extraumbilical (intra-extraumbilical to umbilical-peripheral), rounded, asymmetrical and elongated, with a thin imperforate lip. Wall calcareous hyaline, microperforate, pustulate to rugose consisting of blunt pustules that may coalesce to form small, not aligned rugosities; pustules and rugosities imperforate or with decentred or peripherally associated pores; scattered pore-mounds. Adult size ranges 120–210 μm in maximum diameter.

Remarks: Similar specimens to *T. olssoni* sp. nov. were already documented by LIU & OLSSON (1992), but identified as *Pv. eugubina*. *T. olssoni* sp. nov. resembles *Pv. eugubina*, but the latter is smaller and has a smooth wall texture.

Acknowledgements

We thank the reviewer Hanspeter Luterbacher for his thoughtful and useful comments. This research was funded by the Spanish Ministerio de Ciencia e Innovación projects CGL2011-23077 and CGL2011-22912 (both cofinanced by the European Re-

gional Development Fund), by the Aragonian Departamento de Educación y Ciencia (DGA group E05), and by the Consejo Nacional de Investigaciones Científicas y Técnicas (Argentina), projects PIP 0820 and PIP 0281. Authors would like to acknowledge the use of the Servicio General de Apoyo a la Investigación-SAI, Universidad de Zaragoza. The authors are grateful to Rupert Glasgow for improvement of the English text.

References

- ARENILLAS, I. & ARZ, J.A. (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, J.A. (2007): Análisis morfoestadístico del género *Palaeoglobigerina* (Foraminifera, Globigerinida) del Paleoceno basal, y descripción de una nueva especie. – *Rev. Esp. Micropaleontol.* **39** (1–2): 1–28.
- ARENILLAS, I. & ARZ, J.A. (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, J.A. (2013b): New evidence on the origin of nonspinoso pitted-cancellate species of the early Danian planktic foraminifera. – *Geol. Carpathica* **64** (3): 237–251.
- ARENILLAS, I., ARZ, J.A., 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, J.A., MOLINA, E. & DUPUIS, C. (2000b): The Cretaceous/Paleogene (K/P) boundary at Ain Settara, Tunisia: sudden catastrophic mass extinction in planktic foraminifera. – *J. Foramin. Res.* **30** (3): 202–218.
- ARENILLAS, I., ARZ, J.A. & MOLINA, E. (2004): A new high-resolution planktic foraminiferal zonation and subzonation for the lower Danian. – *Lethaia* **37**: 79–95.
- ARENILLAS, I., ARZ, J.A., GRAJALES-NISHIMURA, J.M., MURILLO-MUÑETÓN, G., ALVAREZ, W., CAMARGO-ZANOQUERA, A., MOLINA, E. & ROSALES-DOMÍNGUEZ, C. (2006): Chicxulub impact event is Cretaceous/Paleogene boundary in age: new micropaleontological evidence. – *Earth Planet. Sci. Lett.* **249**: 241–257.
- ARENILLAS, I., ARZ, J.A. & NÁJUEZ, C. (2007): Morfología, Biometría y Taxonomía de foraminíferos planctónicos del Daniense basal: *Palaeoglobigerina* n. gen. – *Rev. Esp. Paleontol.* **22** (1): 21–62.
- ARENILLAS, I., ARZ, J.A. & NÁJUEZ, C. (2010): Diversidad y evolución de la textura de la pared en guembelítridos (foraminíferos planctónicos) en el tránsito Cretácico-Paleógeno. – *Rev. Esp. Paleontol.* **25** (2): 87–105.
- ARENILLAS, I., ARZ, J.A. & NÁJUEZ, C. (2012): Smooth and rugose wall textures in earliest Danian trochospiral planktic foraminifera from Tunisia. – *Neues Jahrb. Geol. Palaeontol. Abh.* **266** (2): 123–142.
- ARZ, J.A., ARENILLAS, I. & NÁJUEZ, C. (2010): Morphostatistical analysis of Maastrichtian populations of *Guembelitra* from El Kef, Tunisia. – *J. Foramin. Res.* **40** (2): 148–164.
- BANG, I. (1969): Planktonic foraminifera and biostratigraphy of the type Danian. – In: BRÖNNIMANN, P. & RENZ, H.H. (eds): *Proceedings of the I International Conference on Planktonic Microfossils 1*: 17–25.
- BERGGREN, W.A. & PEARSON, P.N. (2005): A revised tropical to subtropical Paleogene planktonic foraminiferal zonation. – *J. Foramin. Res.* **35**: 279–298.
- BLOW, W.H. (1979): The Cainozoic Globigerinidae. A study of the morphology, taxonomy, evolutionary relationship and the stratigraphical distribution of some Globigerinidae (mainly Globigerinacea). – 3 vols., 1413 pp., E.J. Brill, Leiden, Netherlands.
- BOUDAGHER-FADEL, M.K. (2012): Biostratigraphic and geological significance of planktonic foraminifera. – *Developments in Palaeontology & Stratigraphy* **22**: 1–289.
- BRINKHUIS, H. & ZACHARIASSE, W.J. (1988): Dinoflagellate cysts, sea level changes and planktonic foraminifers across the Cretaceous-Tertiary boundary at El Haria, Northwest Tunisia. – *Mar. Micropaleontol.* **13**: 153–191.
- BRÖNNIMANN, P. (1952): Globigerinidae from the Upper Cretaceous (Cenomanian-Maastrichtian) of Trinidad. – *Bull. Amer. Paleontology* **34** (140): 1–30.
- BRÖNNIMANN, P. (1953): Note on planktonic foraminifera from Danian localities. – *Bull. Amer. Paleontology* **45**: 339–341.
- BROTZEN, F. & POZARYSKA, T. (1961): Foraminifères du Paléocène et de l'Éocène inférieur en Pologne septentrionale; remarques paléogéographiques. – *Rev. Micropaléontol.* **4**: 155–166.
- CANUDO, J.I., KELLER, G. & MOLINA, E. (1991): Cretaceous/Tertiary boundary extinction pattern and faunal turnover at Agost and Caravaca, SE Spain. – *Mar. Micropaleontol.* **17**: 319–341.
- CUSHMAN, J.A. (1927): An outline of a re-classification of the Foraminifera. – *Contributions from the Cushman Foundation for Foraminiferal Research* **3**: 1–105.
- DELAGE, Y. & HÉROUARD, E. (1896): *Traité de Zoologie Concrète*, vol. 1, La Cellule et les Protozoaires. – Schleicher Frères, Paris.
- D'HONDT, S.L. (1991): Phylogenetic and stratigraphic analysis of earliest Paleocene biserial and triserial planktonic foraminifera. – *J. Foramin. Res.* **21**: 168–181.
- EICHWALD, C.E., VON (1830): *Zoologia specialis*. – Vilnae: D.E. Eichwaldus **2**: 1–323.
- FORDHAM, B.G. (1986): Miocene-Pleistocene planktic foraminifers from D.S.D.P. Sites 208 and 77, and phylogeny and classification of Cenozoic species. – *Evolutionary Monographs* **6**: 200 pp., University of Chicago.
- GRADSTEIN, F.M., OGG, J.G., SCHMITZ, M.D. & OGG, G.M. (2012): *The Geological Time Scale*. – Elsevier, 2 vols, 1144 p.
- HAMMER, Ø., HARPER, D.A.T. & RYAN, P.D. (2001): PAST: Paleontological Statistics Software Package for Education and Data Analysis. – *Palaeontol. Electronica* **4** (1): 9 p.

- HAQUE, A.F.M.M. (1956): The smaller Foraminifera of the Rankot and the Laki of the Nammal Gorge, Salt Range. – *Paleontol. Pakistanica, Geol. Surv. Pakistan* 1: 1–300.
- HOFKER, J. (1978): Analysis of a large succession of samples through the Upper Maastrichtian and the Lower Tertiary of Drill Hole 47.2, Shatsky Rise, Pacific, Deep Sea Drilling Project. – *J. Foramin. Res.* 8: 46–75.
- KHALILOV, D.M. (1956): O pelagicheskoy faune foraminifer Paleogenovykh otlozheniy Azerbaydzana. – *Trudy Instituta Geologii, Akademiya Nauk Azerbaydzhanskoj S.S.R., Baku* 17: 234–261.
- KOUTSOUKOS, E.A. (2014): Phenotypic plasticity, speciations, and phylogeny in Early Danian planktic foraminifera. – *J. Foramin. Res.* 44 (2): 109–142.
- LI, Q. (1987): Origin, phylogenetic development and systematic taxonomy of the *Tenuitella* plexus (Globigerinitidae, Globigerinina). – *J. Foramin. Res.* 17: 295–320.
- LI, Q. & RADFORD, S.S. (1991): Evolution and biogeography of Paleogene microperforate planktonic foraminifera. – *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 83: 87–115.
- LI, Q., MCGOWRAN, B. & BOERSMA, A. (1995): Early Paleocene *Parvularugoglobigerina* and late Eocene *Praetenuitella*: does evolutionary convergence imply similar habitat?. – *J. Micropaleontol.* 14: 119–134.
- LIU, C. & OLSSON, R.K. (1992): Evolutionary radiation of microperforate planktonic foraminifera following the K/T mass extinction event. – *J. Foramin. Res.* 22: 328–346.
- LIU, C. & OLSSON, R.K. (1994): On the origin of Danian normal perforate planktonic foraminifera from *Hedbergella*. – *J. Foramin. Res.* 24: 61–74.
- LOEBLICH, A.R., JR. & TAPPAN, H. (1987): Foraminiferal general and their classification. – *Van Nostrand Reinhold Company, New York*, 2 vol., 970 p., 847 plates.
- LUTERBACHER, H.P. & PREMOLI SILVA, I. (1964): Biostratigraphy of the Cretaceous-Tertiary boundary in Central Apennines. – *Riv. Ital. Paleontol. S.* 70: 67–128 (in Italian).
- MOLINA, E., ARENILLAS, I. & ARZ, J.A. (1998): Mass extinction in planktic foraminifera at the Cretaceous/Tertiary boundary in subtropical and temperate latitudes. – *B. Soc. Geol. Fr.* 169: 351–363.
- MOLINA, E., ALEGRET, L., ARENILLAS, I., ARZ, J.A., GALLALA, N., HARDENBOL, J., VON SALIS, K., STEURBAUT, E., VANDENBERGHE, N. & ZAGHBIB-TURKI, D. (2006): The Global Stratotype Section and Point of the Danian Stage (Paleocene, Paleogene, “Tertiary”, Cenozoic) at El Kef, Tunisia: original definition and revision. – *Episodes* 29 (4): 263–278.
- MOLINA, E., ALEGRET, L., ARENILLAS, I., ARZ, J.A., 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.
- MONTANARO-GALLITELI, E. (1957): A revision of the foraminiferal Family Heterohelicidae. – *Stud. Foramin., US Nat. Mus. Bull.* 215: 133–154.
- OLSSON R.K. (1970): Planktonic foraminifera from base of Tertiary Millers Ferry, Alabama. – *J. Paleontol.* 44: 598–604.
- OLSSON, R.K., HEMLEBEN, C., BERGGREN, W.A. & LIU, C. (1992): Wall texture classification of planktonic foraminifera genera in the Lower Danian. – *J. Foramin. Res.* 22: 195–213.
- OLSSON, R.K., LIU, C. & VAN FOSSEN, M. (1996): The Cretaceous-Tertiary catastrophic event at Millers Ferry, Alabama. – *Geol. Soc. Am. S.* 307: 263–277.
- OLSSON, R.K., HEMLEBEN, C., BERGGREN, W.A. & HUBER, B.T. (1999): Atlas of Paleocene Planktonic Foraminifera. – *Smith. C. Paleob.* 85: 1–252.
- PAPÚ, O.H., PRÁMPARO, M.B., NÁÑEZ, C. & CONCHEYRO, A. (2000): Palinología y micropaleontología de la Formación Jagüel (Maastrichtiano-Daniano), perfil Opasso, Cuenca Neuquina, Argentina. – In: Simposio Paleógeno de América del Sur (Buenos Aires, 1996), *Actas*. – Servicio Geológico Minero Argentino, *Anales* 33: 17–31.
- SALAJ, J. (1986): The new *Postrugoglobigerina praedaubjergensis* Zone at the base of the stratotype of the marine Paleocene (El Kef, Tunisia). – *Geol. Carpath.* 37: 35–58.
- SMIT, J. (1982): Extinction and evolution of planktonic foraminifera after a major impact at the Cretaceous/Tertiary boundary. – *Geol. Soc. Am. S.* 190: 329–352.
- SMIT, J. (1990): Meteorite impact, extinctions and the Cretaceous-Tertiary Boundary. – *Geol. Mijnbouw* 69: 187–204.
- SMIT, J. (1999): The global stratigraphy of the Cretaceous-Tertiary Boundary impact ejecta. – *Ann. Rev. Earth Pl. Sc.* 27: 75–113.
- SMIT, J. & ROMEIN, A.J.T. (1985): A sequence of events across the Cretaceous-Tertiary boundary. – *Earth Planet. Sci. Lett.* 74: 155–170.
- SUBBOTINA, N.N. (1953): Iskopaemye Foraminifery SSSR. Globigerinidy, Khantkeninidy i Globorotaliidy. – *Trudy Vsesoyuzhnyy Neftyanoy Nauchno-issledovatel'skiy Geologo-razvedochnogo Instituta (VNIGRI), Mikrofauna SSSR Sbornik* 6, 76: 1–296.
- TOUMARKINE, M. & LUTERBACHER, H.P. (1985): Paleocene and Eocene planktic foraminifera. – In: BOLLI, H.M., SAUNDERS, J.B. & PERCH-NIELSEN, K. (eds): *Plankton Stratigraphy*. – Cambridge University Press, 88–153.

Explanation of the plates

Plate 1

Scanning electron photographs of *Parvularugoglobigerina* and *Palaeoglobigerina* species (scale bar = 100 μ m).

- Fig. 1. *Palaeoglobigerina alticonusa*, holotype, Zone *Pa*, DSDP Site 152, Caribbean Pacific (SEM-micrograph from LI et al. 1995).
- Fig. 2. *Palaeoglobigerina alticonusa*, sample KF16.50 (4.5 m above the K/Pg boundary), middle part of the *E. simplicissima* Subzone (*Pv. eugubina* Zone), El Kef, Tunisia.
- Fig. 3. *Palaeoglobigerina alticonusa*, sample KF16.50 (4.5 m above the K/Pg boundary), middle part of the *E. simplicissima* Subzone (*Pv. eugubina* Zone), El Kef, Tunisia.
- Fig. 4. *Palaeoglobigerina fodina*, holotype, Zone *Pa*, DSDP Leg 6, South Pacific (SEM-micrographs from BLOW, 1979).
- Fig. 5. *Palaeoglobigerina fodina*, sample STW+50+52 (0.5 m above the K/Pg boundary), upper part of the *Pv. longiapertura* Subzone (*G. cretacea* Zone), Aïn Settara, Tunisia.
- Fig. 6. *Palaeoglobigerina fodina*, sample KF15.00 (3 m above the K/Pg boundary), lower part of the *E. simplicissima* Subzone (*Pv. eugubina* Zone), El Kef, Tunisia.
- Fig. 7. *Palaeoglobigerina minutula*, holotype, *Pv. eugubina* Zone, Ceselli, Italia (LUTERBACHER & PREMOLI-SILVA, 1964).
- Fig. 8. *Palaeoglobigerina minutula*, sample STW86 (2.6 m above the K/Pg boundary), lower part of the *E. simplicissima* Subzone (*Pv. eugubina* Zone), Aïn Settara, Tunisia.
- Fig. 9. *Palaeoglobigerina minutula*, sample STW84.2 (0.8 m above the K/Pg boundary), lower part of the *Pv. sabina* Subzone (*Pv. eugubina* Zone), Aïn Settara, Tunisia.
- Fig. 10. *Palaeoglobigerina luterbacheri*, holotype, sample KF15.00 (3 m above the K/Pg boundary), lower part of the *E. simplicissima* Subzone (*Pv. eugubina* Zone), El Kef, Tunisia.
- Fig. 11. *Parvularugoglobigerina longiapertura*, holotype, Zone *Pa*, DSDP Leg 6, South Pacific (SEM-micrographs from BLOW, 1979).
- Fig. 12. *Parvularugoglobigerina longiapertura*, sample STW84.2 (0.8 m above the K/Pg boundary), lower part of the *Pv. sabina* Subzone (*Pv. eugubina* Zone), Aïn Settara, Tunisia.
- Fig. 13. *Parvularugoglobigerina longiapertura*, sample KF14.00 (2 m above the K/Pg boundary), lower part of the *Pv. sabina* Subzone (*Pv. eugubina* Zone), El Kef, Tunisia.
- Fig. 14. *Parvularugoglobigerina perexigua*, holotype, Zone *Pa*, DSDP Site 152, Caribbean Pacific (SEM-micrograph from LI et al. 1995).
- Fig. 15. *Parvularugoglobigerina perexigua*, sample El4.50 (3.5 m above the K/Pg boundary), lower part of the *Pv. sabina* Subzone (*Pv. eugubina* Zone), Elles, Tunisia.
- Fig. 16. *Parvularugoglobigerina sabina*, holotype, *Pv. eugubina* Zone, Ceselli, Italia (LUTERBACHER & PREMOLI-SILVA, 1964).
- Fig. 17. *Parvularugoglobigerina sabina*, sample El6.00 (5 m above the K/Pg boundary), upper part of the *Pv. sabina* Subzone (*Pv. eugubina* Zone), Elles, Tunisia.
- Fig. 18. *Parvularugoglobigerina eugubina*, holotype, *Pv. eugubina* Zone, Ceselli, Italia (LUTERBACHER & PREMOLI-SILVA, 1964).
- Fig. 19. *Parvularugoglobigerina eugubina*, sample STW87 (3.6 m above the K/Pg boundary), middle part of the *E. simplicissima* Subzone (*Pv. eugubina* Zone), Aïn Settara, Tunisia.
- Fig. 20. *Parvularugoglobigerina eugubina*, sample STW87 (3.6 m above the K/Pg boundary), middle part of the *E. simplicissima* Subzone (*Pv. eugubina* Zone), Aïn Settara, Tunisia.

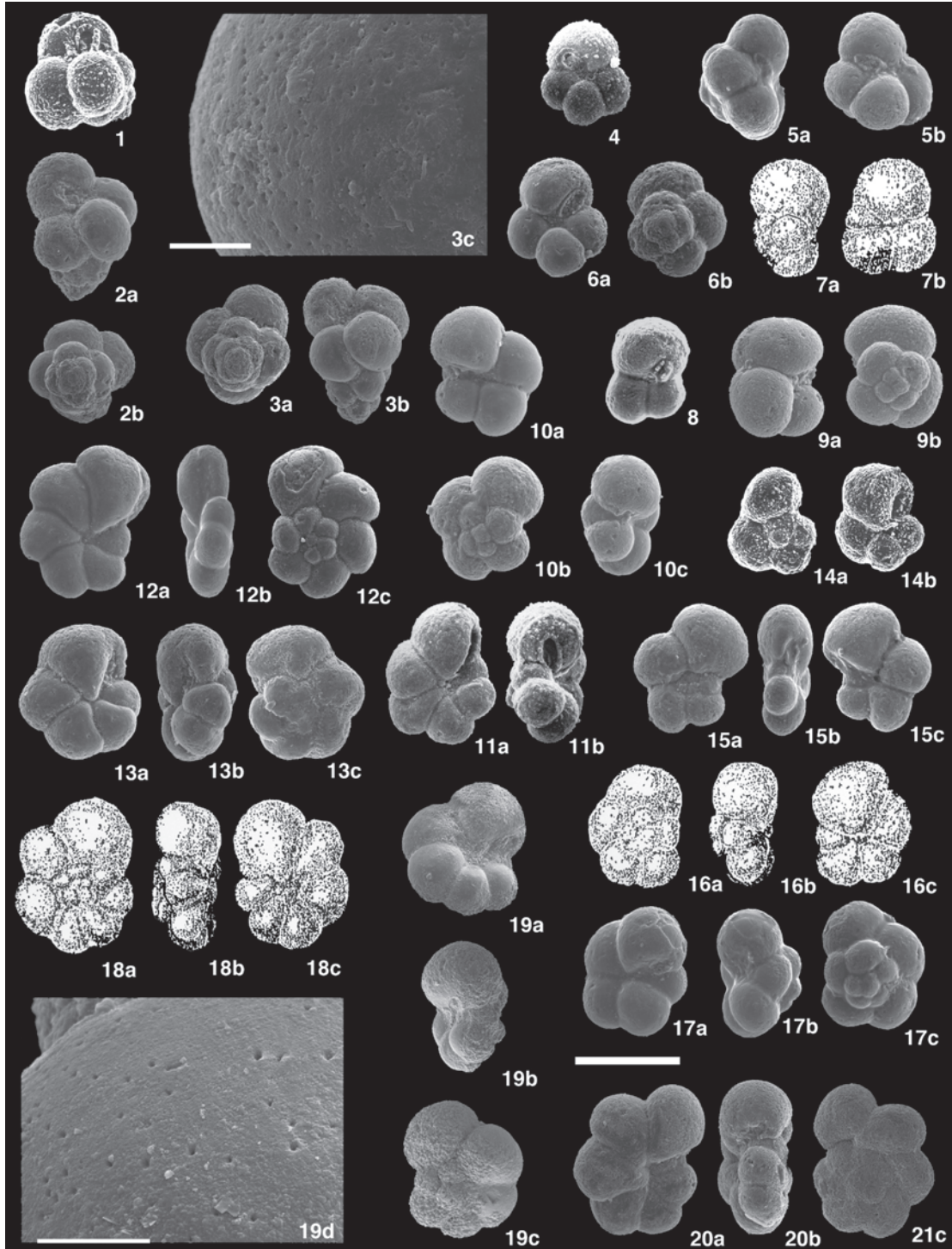


Plate 2

Scanning electron micrographs of *Trochoguembelitra* species (scale bar = 100 μm).

Fig. 1. *Trochoguembelitra alabamensis*, holotype, from Millers Ferry, Alabama, U.S.A. (SEM-micrograph from LIU & OLSSON, 1992).

Fig. 2. *Trochoguembelitra alabamensis*, sample KF24.80 (12.8 m above the K/Pg boundary), lower part of the *S. triloculinooides* Subzone (*P. pseudobulloides* Zone), El Kef, Tunisia.

Fig. 3. *Trochoguembelitra alabamensis*, sample STW87 (3.6 m above the K/Pg boundary), middle part of the *E. simplicissima* Subzone (*Pv. eugubina* Zone), Ain Settara, Tunisia.

Fig. 4. *Trochoguembelitra 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.

Fig. 5. *Trochoguembelitra extensa*, holotype, Zone P1, DSDP Leg 6, South Pacific (SEM-micrographs from BLOW, 1979).

Fig. 6. *Trochoguembelitra extensa*, paratype, Zone P1, DSDP Leg 6, South Pacific (SEM-micrographs from BLOW, 1979).

Fig. 7. *Trochoguembelitra 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.

Fig. 8. *Trochoguembelitra 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.

Fig. 9. *Trochoguembelitra 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.

Fig. 10. Specimen of *Trochoguembelitra liuae* sp. nov. of OLSSON et al. (1999), assigned to *Parvularugoglobigerina eugubina*.

Fig. 11. *Trochoguembelitra liuae* sp. nov., sample KF18.50 (6.5 m above the K/Pg boundary), upper part of the *E. simplicissima* Subzone (*Pv. eugubina* Zone), El Kef, Tunisia.

Fig. 12. *Trochoguembelitra liuae* sp. nov., sample KF18.50 (6.5 m above the K/Pg boundary), upper part of the *E. simplicissima* Subzone (*Pv. eugubina* Zone), El Kef, Tunisia.

Fig. 13. *Trochoguembelitra olsoni* sp. nov., sample KF17.50 (5.5 m above the K/Pg boundary), lower part of the *E. simplicissima* Subzone (*Pv. eugubina* Zone), El Kef, Tunisia.

Fig. 14. *Trochoguembelitra olsoni* sp. nov., sample KF18.50 (6.5 m above the K/Pg boundary), upper part of the *E. simplicissima* Subzone (*Pv. eugubina* Zone), El Kef, Tunisia.

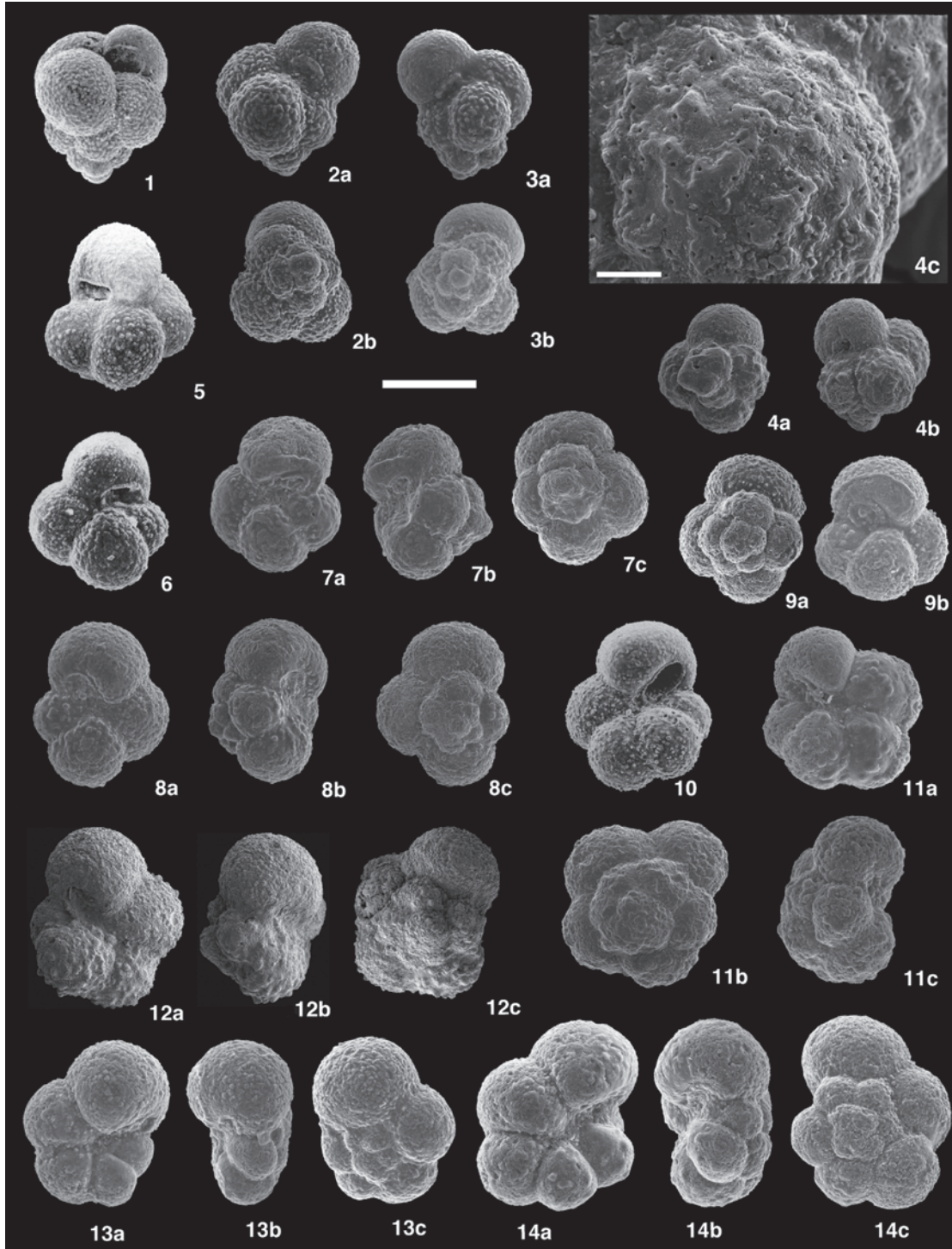


Plate 3

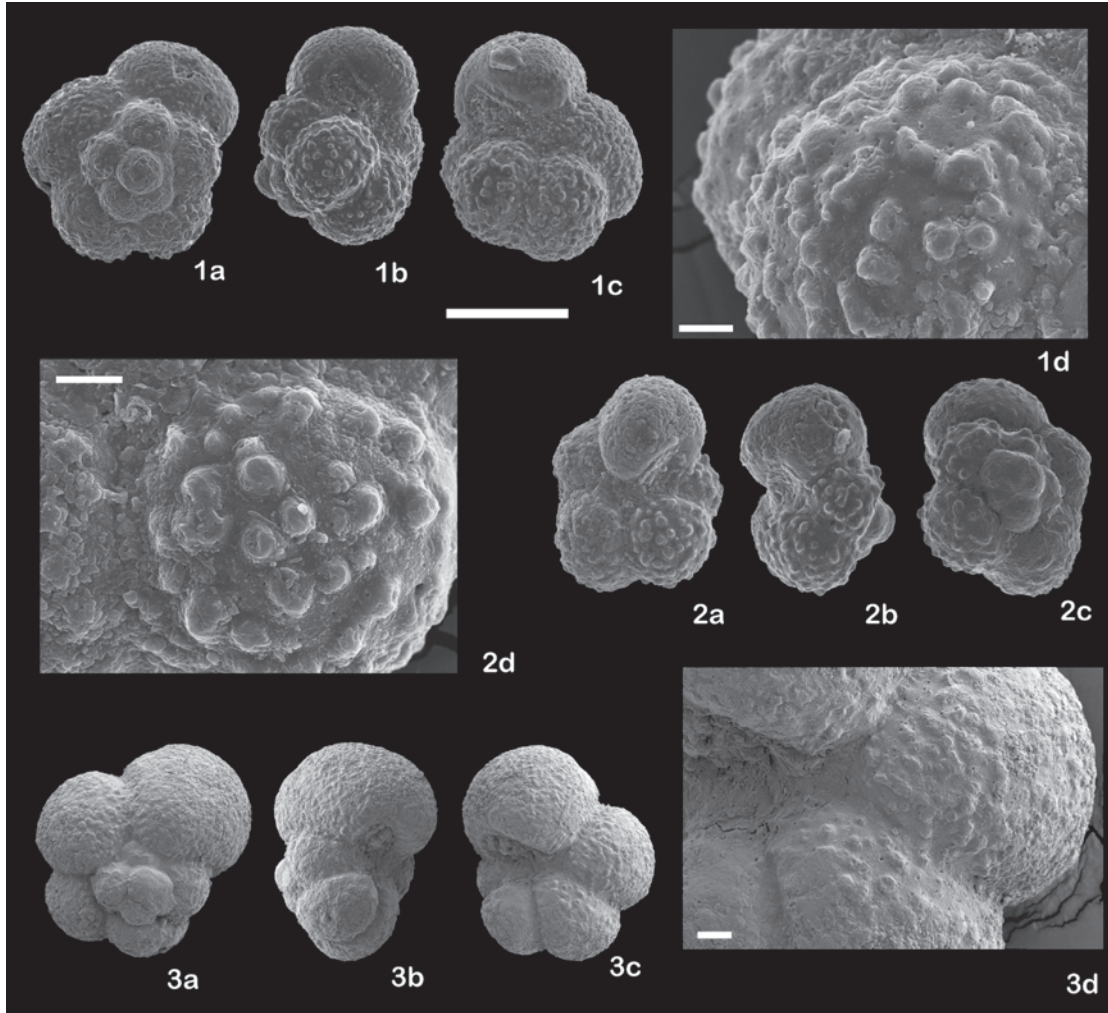
Scanning electron micrographs of the type-specimens of *Trochoguembelitra liuae* sp. nov. (scale bar = 100 μ m).

Fig. 1. *Trochoguembelitra liuae* sp. nov., holotype MPZ 2014/295, sample KF20.50 (8.5 m above the K/Pg boundary), middle part of the *E. trivialis* Subzone (*P. pseudobulloides* Zone), El Kef, Tunisia.

Fig. 2. *Trochoguembelitra liuae* sp. nov., paratype MPZ 2014/296, sample KF18.50 (6.5 m above the K/Pg boundary), upper part of the *E. simplicissima* Subzone (*Pv. eugubina* Zone), El Kef, Tunisia.

Fig. 3. *Trochoguembelitra liuae* sp. nov., paratype MPZ 2014/297, sample KF18.50 (6.5 m above the K/Pg boundary), upper part of the *E. simplicissima* Subzone (*Pv. eugubina* Zone), El Kef, Tunisia.

Uncorrected proofs



uncc

Plate 4

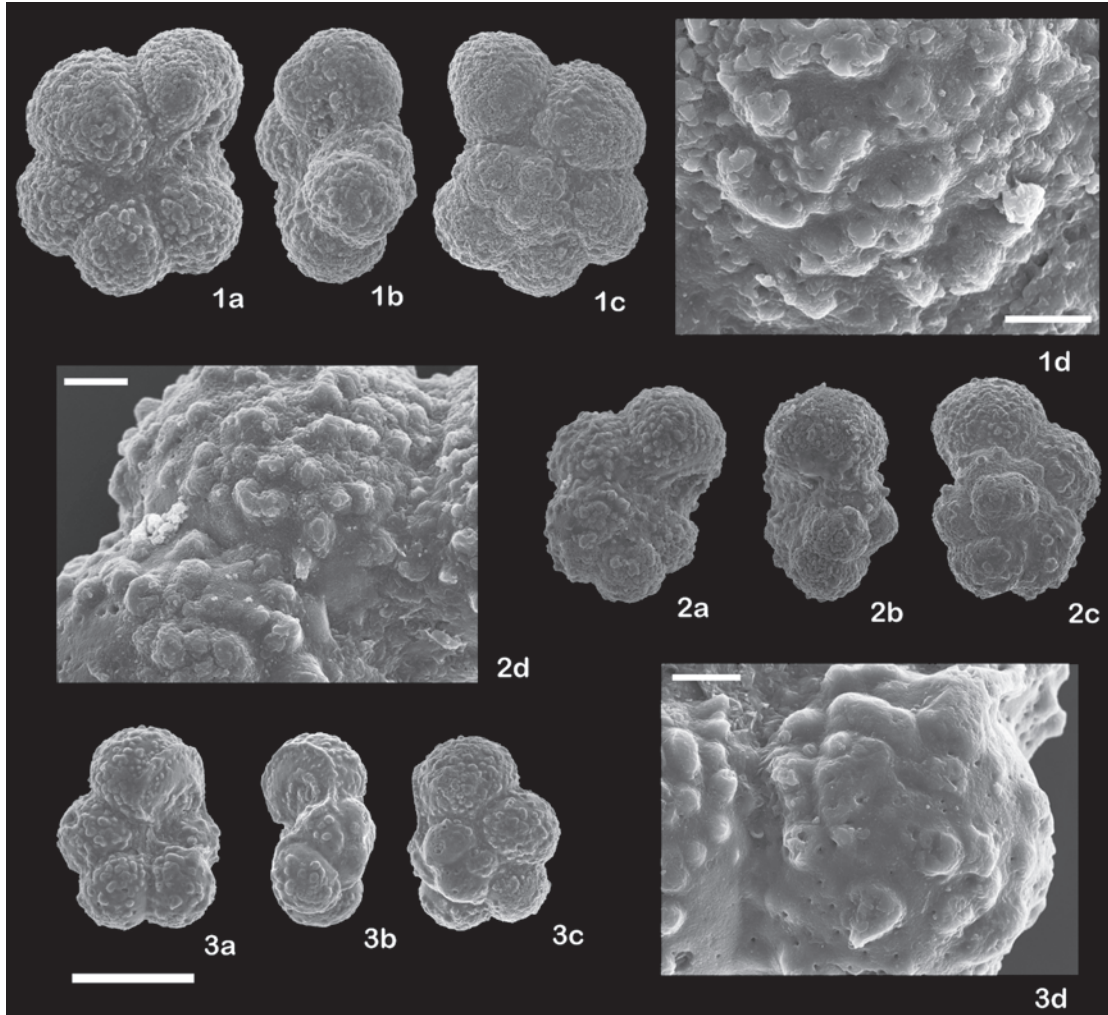
Scanning electron micrographs of the type-specimens of *Trochoguembelitra olssoni* sp. nov. (scale bar = 100 μ m).

Fig. 1. *Trochoguembelitra olssoni* sp. nov., holotype MPZ 2014/298, sample KF20.50 (8.5 m above the K/Pg boundary), middle part of the *E. trivialis* Subzone (*P. pseudobulloides* Zone), El Kef, Tunisia.

Fig. 2. *Trochoguembelitra olssoni* sp. nov., holotype MPZ 2014/299, sample KF18.50 (6.5 m above the K/Pg boundary), upper part of the *E. simplicissima* Subzone (*Pv. eugubina* Zone), El Kef, Tunisia.

Fig. 3. *Trochoguembelitra olssoni* sp. nov., holotype MPZ 2014/300, sample KF18.50 (6.5 m above the K/Pg boundary), upper part of the *E. simplicissima* Subzone (*Pv. eugubina* Zone), El Kef, Tunisia.

Uncorrected proofs



uncc

Uncorrected proofs