

Patterns of spatio-temporal distribution as criteria for the separation of planktic foraminiferal species across the Danian–Selandian transition in Spain

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Danian–Selandian (D–S) planktic foraminiferal taxonomy and paleoecology, including the most problematic index-species of biochronological schemes, are here revised based on qualitative and quantitative data from the Caravaca and Zumaia sections, Spain. As a first step the morphological and microtextural diagnostic characters are revised in order to achieve appropriate morphological distinctions of the investigated species. The analysis of latitudinal preferences of the planktic foraminiferal species deduced from a comparison of their relative abundances at Caravaca (western Tethyan subtropical waters) and Zumaia (central North Atlantic warm temperate waters) in suite with a statistical comparison of quantitative stratigraphic distributions of the species at Caravaca have shown several divergences in their patterns of spatio-temporal distribution (i.e., in their latitudinal preferences and quantitative stratigraphic distributions). This analysis allowed taxonomical separation of 41 species from the following genera: *Eoglobigerina*, *Subbotina*, *Parasubbotina*, *Globanomalina*, *Luterbacheria*, *Acarinina*, *Igorina*, *Morozovella*, *Praemurica*, *Chiloguembelina*, and *Zeauvigerina*. Morphologically convergent species pairs such as *Acarinina trinidadensis* and *Praemurica inconstans*, *Acarinina praecursoria* and *Acarinina uncinata*, *Morozovella conicontruncata* and *Morozovella angulata*, or *Morozovella* cf. *albeari* and *Igorina albeari*, are well differentiated using aforementioned criteria. Since some of the species are index-taxa, the taxonomic refinements are essential to clarify and compare the planktic foraminiferal zonation from the Danian–Selandian transition. A new lower/higher (L/H) latitude taxa ratio is proposed for paleoclimatic interpretations based on the paleoecological and quantitative studies. Fluctuations in L/H ratio in the Caravaca section suggest three climate warming events during the D–S transition, one of them probably occurring at the D–S boundary.

Key words: Foraminifera, taxonomy, index-species, paleoecology, Paleocene, Spain.

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Introduction

The Danian/Selandian (D–S) boundary has been defined in the Zumaia section, northern Spain, using a radiation of the calcareous nannofossil group, *Fasciculithus*, as event for global, marine correlation (Schmitz et al. 2011). The position of the D–S boundary in the planktic foraminiferal stratigraphic scale could not be clarified because taxonomic problems caused uncertainties in correlation of the Paleocene zones (Arenillas et al. 2008).

The reference biozonation for most of the current Paleocene planktic foraminiferal stratigraphers is that of Berggren and Pearson (2005), which is based on the systematics of Berggren and Norris (1997) and Olsson et al. (1999). Some of their conclusions contradicted previous taxonomies, such as those of Luterbacher (1964), Stainforth et al. (1975), Blow (1979), Toumarkine and Luterbacher (1985), and Arenillas (1996), but they had the advantage of photographing the holotypes of most Paleocene species by means of Scanning

Electronic Microscope (SEM). The SEM images prevent some subjective interpretations made from the original drawings and descriptions of these holotypes. However, these images reflect deficiencies in the preservation of many specimens, by impeding the observation of the original wall-texture and ornamentation, both of which are important features in planktic foraminiferal systematics.

In addition, reconciliation between splitter and lumpers morphological taxonomies is still a long-awaited outcome. Until an invariable and unique species concepts exist, the number of species proposed for a given time interval (number of morphospecies) and the number of evolutionary species within anagenetic series (number of chronospecies within a given lineage) will continue to be a matter of arbitrary judgment. This subjectivity and discrepancy in the proposed taxonomies have caused and probably will continue to cause uncertainty in the biostratigraphic scales. The classic use of morphological and microtextural diagnostic characters for the distinction of planktic foraminiferal species has

made it possible to show convincingly how many species there are in a certain time period. Morphostatistical analyses such as those by Arenillas and Arz (2007), and Arz et al. (2010), have proved valuable for morphospecies discrimination within planktic foraminifera. Paleocological analysis and studies on the quantitative stratigraphic distributions of the species should also be valid in taxonomy, assuming that differences in their patterns of spatio-temporal distribution are criteria for the separation of species.

A revision of the D–S planktic foraminiferal taxonomy and paleoecology are documented herein. Divergences in latitudinal preferences of the species as well as statistical comparisons of their quantitative stratigraphic distributions are used as criteria for the taxonomical separation of species. These patterns of spatio-temporal distribution were inferred comparing relative abundances of the species at Caravaca and Zumaia (Spain) and analyzing their fluctuations in abundance across the D–S transition at Caravaca. The main purposes of the taxonomic refinements are to better clarify the stratigraphic position of the biozones established by the different planktic foraminiferal specialists for the D–S transition, and propose a new paleoclimatic ratio (lower/higher latitude taxa ratio), which is able to recognize fluctuations in temperature across the D–S transition.

Institutional abbreviation.—MPZ, Museo Paleontológico de the Universidad de Zaragoza, Aragon Government, Spain.

Other abbreviations.—D–S, Danian–Sealandian transition; FOD, first occurrence data; L/H, lower/higher latitude, LOD, last occurrence data.

Material and methods

The D–S planktic foraminiferal taxonomic and paleoecological revision is based mainly on the Caravaca and Zumaia sections, Spain (Fig. 1). The Caravaca section is located in the Subbetic Zone of the Betic Cordilleras (western Tethys), to the south of the town Caravaca de la Cruz (southeastern Spain). D–S sediments belong to the Jorquera Formation, consisting of grey marls and calcareous marls of middle–lower bathyal depths (Ortiz et al. 2008). The planktic foraminiferal stratigraphic record of the Caravaca section was studied by Arenillas (1996) and Arenillas and Molina (1997). The Zumaia/Zumaya section is located in the western Pyrenees (paleo-Bay of Biscay, North-central Atlantic), to the northwest of the village of Zumaia (northern Spain). The D–S transition at Zumaia spans the upper part of the Danian Limestone Formation, consisting of greyish limestone–reddish marly couplets, and the lower part of the Itzurun Formation, of red to grey marls (Arenillas et al. 2008). According to Ortiz in Arenillas et al. (2008), D–S sediments were also deposited at middle–lower bathyal depths. The planktic foraminiferal stratigraphic record of the Zumaia section was studied by Arenillas (1996) and Arenillas and Molina (2000), and recently revised by Arenillas et al. (2008).

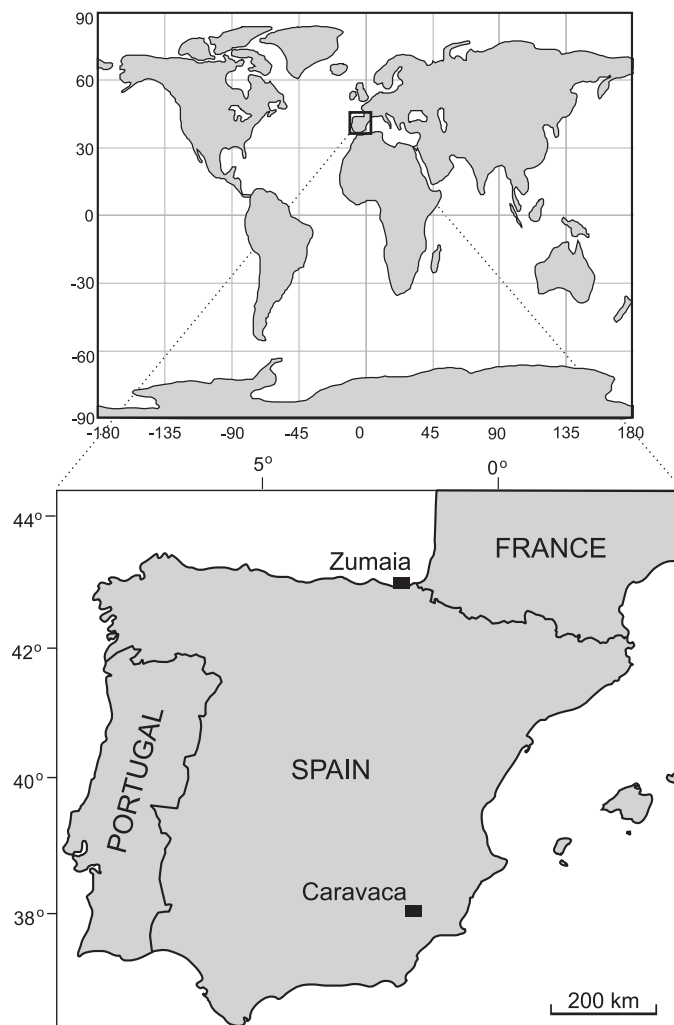


Fig. 1. Geographical location of the Caravaca and Zumaia sections (Spain).

The revision takes into account previously reported taxonomies, mainly those of Beckmann (1957), Luterbacher (1964), Stainforth et al. (1975), Blow (1979), Toumarkine and Luterbacher (1985), Arenillas (1996), Berggren and Norris (1997), and Olsson et al. (1999). Most of the illustrated planktic foraminiferal specimens come from the Caravaca section. Specimens were obtained from samples disaggregated in tap water and diluted H_2O_2 , then washed and sieved into 63–106 μm and $\geq 106 \mu m$ size fractions, and dried at 50°C. Representative splits of about 300 specimens of planktic foraminifera from $\geq 106 \mu m$ size fraction were chosen from each sample, using an Otto microsplitter, to obtain quantitative data (relative abundance of the species). All the representative specimens were selected and mounted on microslides for a permanent record and identification. These microslides were deposited in the Museo Paleontológico de the Universidad de Zaragoza, Spain, with repository numbers MPZ.

To analyse the latitudinal preferences of planktic foraminiferal species, previous paleobiogeographical and isotopic studies (e.g., Boersma and Premoli Silva 1989, 1991; Shackleton et al. 1985; Arenillas 1996; Olsson et al. 1999) and relative

Table 1. Average relative abundances of the species in the *Acarinina uncinata* Zone from both Caravaca and Zumaia sections, and probable latitudinal preferences. Data obtained from Arenillas (1996), Arenillas and Molina (1997, 2000), and Arenillas et al. (2008). Note that the *A. uncinata* Zone of Caravaca stratigraphically continues below with respect to the samples shown in Figs. 3 and 5, and Tables 4 and 5.

Species	Caravaca	Zumaia	Latitudinal preferences
<i>Eoglobigerina fringa</i>	0.60	2.23	middle-high
<i>Eoglobigerina cf. trivialis</i>	5.18	2.54	low
<i>Eoglobigerina tetragona</i>	1.07	1.62	middle-high
<i>Eoglobigerina edita</i>	1.82	1.14	low
<i>Eoglobigerina spiralis</i>	0.28	0.53	middle-high
<i>Subbotina triloculinoides</i>	2.58	14.52	middle-high
<i>Subbotina triangularis</i>	5.19	7.89	middle-high
<i>Subbotina compressaformis</i>	1.79	0.74	low
<i>Globanomalina compressa</i>	2.23	4.44	middle-high
<i>Globanomalina haunsbergensis</i>	5.14	5.71	middle-high
<i>Globanomalina chapmani</i>	1.18	2.68	middle-high
<i>Luterbacheria ehrenbergi</i>	5.84	1.56	low
<i>Parasubbotina pseudobulloides</i>	3.69	6.45	middle-high
<i>Parasubbotina quadrilocula</i>	18.16	21.32	middle-high
<i>Praemurica inconstans</i>	7.94	3.75	low
<i>Acarinina trinidadensis</i>	5.11	3.48	low
<i>Acarinina uncinata</i>	11.10	6.83	low
<i>Acarinina praecursoria</i>	1.29	1.33	middle-high
<i>Acarinina hansbollii</i>	2.46	2.05	low
<i>Acarinina indolensis</i>	2.49	1.43	low
<i>Acarinina arabica</i>	0.51	0.25	low
<i>Acarinina praepentacamerata</i>	7.50	6.00	low
<i>Acarinina praeaequa</i>	0.88	0.12	low
<i>Igorina tadjikistanensis</i>	0.55	0.47	low
<i>Chiloguembelina taurica</i>	0.44	0.01	low
<i>Chiloguembelina midwayensis</i>	3.19	0.68	low
<i>Chiloguembelina cf. subcylindrica</i>	0.36	0.11	low
<i>Zeauvigerina teuria</i>	0.32	0.01	low
<i>Globoconusa daubjergensis</i>	0.58	0.00	low
<i>Globoconusa conusa</i>	0.24	0.00	low

abundance were considered in both the Caravaca and the Zumaia sections. The average relative abundance of species was calculated for the stratigraphic intervals corresponding to the *Acarinina uncinata* and *Morozovella cf. albeari* zones in both sections (Tables 1, 2). Since the Caravaca section is situated at lower latitudes (subtropical Tethyan region), the species which are more abundant in Caravaca than in Zumaia were considered to be lower-latitude dwellers, preferably tropical-subtropical, whereas the rest were considered to be higher-latitude dwellers, i.e., widely cosmopolitan. The D–S transition in Zumaia is characterized by large cyclical fluctuations in planktic foraminiferal assemblages (Arenillas et al. 2008), from warmer to cooler, but the average relative abundances of species should reflect its latitudinal position.

In addition, the quantitative stratigraphic distributions of the species across the D–S transition of Caravaca (Tables 3, 4) were compared to evaluate the difference in their patterns

of temporal distribution, and to use these differences as criteria for the taxonomic separation of species. The cluster analyses based on Morisita's index measures have been used to find groupings that represent similar ecological requirements and/or biological behaviours, and as a method for taxonomic separation of those morphologically similar species.

Danian–Selandian taxonomic and biostratigraphic controversy

Planktic foraminiferal stratigraphic controversy.—Taxonomic problems have recently caused uncertainties in the D–S biostratigraphy (Arenillas et al. 2008; Sprong et al. 2009), which impeded the exact placement of the D–S boundary within planktic foraminiferal stratigraphic scales. Figure 2 shows the most probable correlation of some of these planktic foraminiferal zonations.

The D–S transition was initially divided into the *Acarinina uncinata*, *Morozovella angulata*, and *Igorina pusilla* zones, using the first occurrence data (FODs) of the nominate species

Table 2. Average relative abundances of the species in the *Morozovella cf. albeari* Zone from both Caravaca and Zumaia sections, and probable latitudinal preferences. Data obtained from Arenillas (1996), Arenillas and Molina (1997, 2000), and Arenillas et al. (2008). Note that the *M. cf. albeari* Zone of Caravaca stratigraphically continues above with respect to the samples shown in Figs. 3 and 5, and Tables 4 and 5.

Species	Caravaca	Zumaia	Latitudinal preferences
<i>Subbotina triloculinoides</i>	2.19	10.50	middle-high
<i>Subbotina triangularis</i>	6.46	10.90	middle-high
<i>Subbotina compressaformis</i>	1.57	10.05	middle-high
<i>Globanomalina haunsbergensis</i>	1.45	1.78	middle-high
<i>Globanomalina chapmani</i>	0.34	1.83	middle-high
<i>Luterbacheria ehrenbergi</i>	7.72	2.25	low
<i>Parasubbotina quadrilocula</i>	20.67	25.92	middle-high
<i>Praemurica inconstans</i>	1.12	0.25	low
<i>Acarinina uncinata</i>	0.36	0.34	low
<i>Acarinina hansbollii</i>	0.98	2.23	middle-high
<i>Acarinina praepentacamerata</i>	2.16	0.71	low
<i>Acarinina praeaequa</i>	1.12	2.34	middle-high
<i>Igorina tadjikistanensis</i>	0.74	0.41	low
<i>Morozovella angulata</i>	11.42	6.72	low
<i>Morozovella conicotruncata</i>	9.19	11.58	middle-high
<i>Morozovella simulatilis</i>	6.45	3.84	low
<i>Morozovella cf. albeari</i>	14.14	2.52	low
<i>Morozovella lacerti</i>	6.22	0.21	low
<i>Morozovella aequa</i>	0.20	0.01	low
<i>Chiloguembelina midwayensis</i>	3.38	0.62	low
<i>Ch. cf. subcylindrica</i>	0.62	0.69	middle-high
<i>Chiloguembelina crinita</i>	0.15	0.30	middle-high
<i>Ch. subtriangularis</i>	0.76	0.01	low
<i>Zeauvigerina teuria</i>	0.14	0.03	low
<i>Zeauvigerina aegyptiaca</i>	0.04	0.01	low

Series	Stage	Magnetozone	Planktic foraminiferal index species stratigraphic data └ FOD └ LOD	Planktic foraminiferal zonation		
				Toumarkine and Luterbacher 1985	Arenillas and Molina 1997	Berggren and Pearson 2005
PALEOCENE	SELANDIAN (lower part)	C26r	<i>L. pseudomenardii</i>			
			<i>M. occlusa</i>	<i>Planorotalites pusilla pusilla</i>	<i>Igorina albeari</i>	P3
			<i>M. velascoensis</i>			
			<i>I. albeari</i>			
			<i>I. pusilla</i>	(*)	<i>Morozovella crosswicksensis</i> (= <i>M. cf. albeari</i>)	
	<i>M. cf. albeari</i>					
	<i>M. angulata</i>	<i>Morozovella angulata</i>	<i>Morozovella angulata</i>	<i>Igorina albeari</i>		
	DANIAN (upper part)	C27n	<i>A. praepentacamerata</i> (= <i>A. praeangulata</i>)	<i>Morozovella uncinata</i>	<i>Acarinina uncinata</i>	P2
	C27r		<i>A. uncinata</i>			

Fig. 2. Comparison of some planktic foraminiferal zonation proposed for the D–S transition in low and middle latitudes. Correlation with the chronostratigraphic and magnetostratigraphic scales based on data from the Zumaia stratotype. (*) Probable biostratigraphic position of the base of the *Igorina pusilla* Zone by Toumarkine and Luterbacher (1985), and Canudo and Molina (1992), based on data from Zumaia. (**) Biostratigraphic position of the P3a/P3b boundary by Berggren and Pearson (2005), assuming that their species concept of *I. albeari* includes *Morozovella crosswicksensis* by Blow (1979) and Arenillas and Molina (1997) and/or *M. cf. albeari* by Arenillas et al. (2008). FOD, first occurrence data; L/H, lower/higher latitude, LOD, last occurrence data.

to place their lower boundaries (Bolli 1966; Toumarkine and Luterbacher 1985; Canudo and Molina 1992). The upper boundary of the *Igorina pusilla* Zone was placed at the FOD of *Luterbacheria pseudomenardii* (= *Planorotalites pseudomenardii*) according to Toumarkine and Luterbacher (1985). Although the transitional forms between these species and their ancestors appear to have caused confusion, the taxonomic concepts of *A. uncinata* (Bolli, 1957), *M. angulata* (White, 1928), and *L. pseudomenardii* (Bolli, 1957) have not changed over time, except for their generic assignment. Toumarkine and Luterbacher (1985) included *A. uncinata* in the genus *Morozovella*, and *I. pusilla* and *L. pseudomenardii* in the genus *Planorotalites*. The species *I. pusilla* (Bolli, 1957) became more problematic, so Berggren et al. (1995) and Arenillas and Molina (1997) excluded it as index species.

The alphanumeric zonation of Berggren et al. (1995) and Berggren and Pearson (2005) divided the D–S transition in two biozones: P2, equivalent to the *A. uncinata* Zone, and P3, equivalent to the *M. angulata* and *I. pusilla* zones. These authors subdivided P3 into two subzones: P3a and P3b, the P3a/P3b boundary being the FOD of *Igorina albeari*. The upper boundary of P3b (or P3b/P4 boundary) is also the FOD of *Luterbacheria pseudomenardii* (= *Globanomalina pseudomenardii*) according to Olsson et al. 1999).

Arenillas (1996) and Arenillas and Molina (1997) used the FODs of *Morozovella crosswicksensis* and *Igorina albeari* to subdivide the previous P3 or *M. angulata* Zone into three biozones: *M. angulata*, *M. crosswicksensis*, and *I. albeari* zones. Since Olsson et al. (1999) considered *M. crosswicksensis* (Olsson, 1960) to be a junior synonym of *Morozovella occlusa* (Loeblich and Tappan, 1957), the lowermost Selandian *M. crosswicksensis*-type specimens (Blow 1979; Arenillas 1996) were renamed *Morozovella cf. albeari* by Arenillas et al. (2008). The *M. crosswicksensis*-type specimens were interpreted by Olsson et al. (1999) and Sprong et al. (2009) as belonging to *Igorina albeari*, so P3a/P3b boundary corresponds to the *M. angulata*/*M. cf. albeari* boundary recognized by Arenillas and Molina (1997).

The biostratigraphical distributions of the most part of the D–S transition index-species are debatable. Figure 3 shows the stratigraphical position of the biozones proposed by Arenillas and Molina (1997, modified) and by Berggren and Pearson (2005) in the Caravaca section, taking into account that the former relied on the taxonomy of Arenillas (1996) and the latter on that of Olsson et al. (1999).

Planktic foraminiferal taxonomic controversy.—Taxonomic differences regarding the taxonomic concept of certain species, including some of the index-species, and their generic assignments, have emerged among specialists which in turn has caused biostratigraphic controversy. The D–S planktic foraminiferal taxonomy reported here (SOM_1: Supplementary Online Material available at http://www.app.pan.pl/archive/published/SOM/app57-Arenillas_SOM.pdf) build upon the work of Arenillas (1996), which was largely based on the work of Luterbacher (1964), Stainforth et al. (1975), Blow (1979), and Toumarkine and Luterbacher (1985). This taxonomic proposal is compared with that of Olsson et al. (1999) (Table 5).

Arenillas (1996) grouped the species of the D–S transition into the following genera: *Eoglobigerina* Morozova, 1959, *Subbotina* Brotzen and Pożaryska, 1962, *Parasubbotina* Olsson, Berggren, and Liu, 1992, *Globanomalina* Haque, 1956, *Luterbacheria* Canudo, 1994, *Acarinina* Subbotina, 1953, *Igorina* Davidzon, 1976, *Morozovella* McGowran, 1964, *Praemurica* Olsson, Berggren, and Liu, 1992, *Chiloguembelina* Loeblich and Tappan, 1956, and *Zeauvigerina* Finlay, 1939. This generic classification was shared by Berggren and Norris (1997) and Olsson et al. (1999), except for *Luterbacheria* which was included within *Globanomalina*.

Eoglobigerina includes the following species (Fig. 4): *E.*

Table 3. Average relative abundances of the species in the Caravaca section from sample 1 to sample 9.5. In bold, lower latitude dwellers; * species that apparently changed their latitudinal preferences; ** insufficient data. Note that the change in latitudinal preference of *Chiloguembelina* cf. *subcylindrica* occurs in the *Acarinina uncinata* Zone but below sample 1.

Biozone	Acarinina uncinata Zone										Morozovella angulata Zone										
	1	1.5	2	2.5	3	3.5	4	4.5	5	5.5	6	6.5	7	7.5	8	8.5	9	9.25	9.5		
<i>Eoglobigerina fringa</i>	1.4	1.6	0.2	0.3	0.7	0.5	0.4	0.2	0.3	0.3	0.9										
<i>Eoglobigerina</i> cf. <i>trivialis</i>	8.2	4.9	7.3	4.2	6.1	6	5.5	7.2	2.5	3.3	3	4.5	1.4	0.2		0.3	0.9	0.3	0.3		
<i>Eoglobigerina tetragona</i>	0.7	2.3	1.6	0.6	0.5	1.7	0.4	1.8	0.6	0.9	0.9	0.6	1.7	0.7	0.2	1.8	0.3		1.6		
<i>Eoglobigerina edita</i>	0.2	1.6	1.9	0.6	0.9	1.4	1.2	1.3	0.3	0.6	0.5	0.6	0.8	1.2	0.5	0.6	0.3				
<i>Eoglobigerina spiralis</i>		0.7	x		0.5	0.5	0.2	0.2	0.6		0.7		0.6			0.9					
<i>Subbotina triloculinoidea</i>	1.4	2.3	1.9	2.4	1.6	0.7	1.2	2.9	4.4	2.4	3.5	1.6	3	0.7	2.7	3.7	3.5	3.5	2.9		
<i>Subbotina triangularis</i>	4.3	2.6	3.5	4.2	5.2	1.2	5.1	7	2.5	6.4	4.9	2.5	5.8	9.9	7.9	9.5	9	3.8	11.9		
<i>Subbotina compressaformis</i> *	2.7	1.2	3.3	3.6	1.9	2.1	1.8	3.1	2.2	2.1	2.1	2.2	0.8	2.9	0.2	4.9	2	2.9	2.1		
<i>Globanomalina compressa</i>	2.9	3.5	3.5	1.2	3.8	2.6	1.6	2	1.9	1.2	3	2.5	0.3	1.9	2.2	1.5	2.6	0.9	0.8		
<i>Globanomalina haunsbergensis</i>	8.7	2.6	1.6	6.3	5.2	6.9	4	4.7	6.3	7.3	3.5	6.4	3.9	6.3	2.5	7.3	3.5	4.9	2.1		
<i>Globanomalina chapmani</i>	1.9	1.2	0.7	0.9	1.9	2.9	1.6	1.3	1.9	1.5	0.5	1.9	x	1		2.1	2.9	0.3	0.8		
<i>Luterbacheria ehrenbergi</i>	7.0	7.7	9.2	11.3	8.7	5.7	4.3	6.3	6.9	7.9	4.2	2.9	7.7	3.6	6.7	2.7	9	6.4	7.5		
<i>Parasubbotina pseudobulloidea</i>	0.7	1.6	2.3	1.8	2.8	4.3	0.6	1.1	2.2	1.8	0.2	1.6	1.7	1.7	0.5	0.9					
<i>Parasubbotina quadrilocula</i>	16.9	24.6	19	17	19.3	19.3	2.6	18.8	23.8	25.5	23.7	2.4	27.8	19.5	13.6	18.9	16	2.9	2.5		
<i>Parasubbotina variospira</i>												0.3									
<i>Praemurica inconstans</i>	3.1	4	3.1	4.5	7.8	3.1	2.6	2.7	3.1	2.7	3.5	1.3	2.5	2.2		1.5	0.6	2	3.1		
<i>Acarinina trinidadensis</i>	2.7	6.3	4.9	6.6	2.1	5.2	2.6	3.1	1.6	0.9	0.7	1.6	0.6	0.7	1.5	2.7	1.2	1.7	0.3		
<i>Acarinina uncinata</i>	11.1	8.5	14.8	6	11.8	8.8	14	11.2	2.7	9.1	13.1	1.5	8.3	6.7	9.2	5.5	7.8	4.6	5.7		
<i>Acarinina praecursoria</i>	1.2	1.2	1.2	2.4	0.2	x	0.8	0.9	0.6	0.6	0.5	x			0.7	0.6	0.3	3.8	0.3		
<i>Acarinina hansbollii</i> *	1.4	1.2	3.1	3.6	1.9	1.9	3.6	2	0.9	5.5	3	2.9	3.3	3.4	3	3.4	5.2	2.9	1.3		
<i>Acarinina indolensis</i>	3.6	2.3	2.8	1.8	0.9	2.9	5.9	2	1.6	4.8	5.2	6.4	2.8	4.3	3	3	0.6	3.8	1		
<i>Acarinina arabica</i>	1.2	0.5	0.7	0.6	0.7	0.7	0.8	0.4	0.9	0.6	0.2	0.6	0.6	0.5	0.2	0.6	0.6	2.9			
<i>Acarinina praepentacamerata</i>	8.0	7.5	8.7	11.9	6.6	7.4	13.6	13.7	9.4	1.6	11.5	17.5	11.3	14.5	28.3	12.2	6.1	15.1	1.9		
<i>Acarinina praeaequa</i> *	1.0	0.7	1.4	1.5		0.5	2	1.1	0.3	0.9	3.7	2.9	5.5	2.7	5.7	0.9	4.4	2.3	2.3		
<i>Igorina tadjikistanensis</i>	0.7		1.4	0.6		0.2	1	0.9	0.3	0.3	2.8	1	1.7	2.4	2.5	1.8	4.7	1.4	1.3		
<i>Morozovella angulata</i>														3.2	1.9	3.1	4	3.7	4.9	7.8	8.8
<i>Morozovella conicotruncata</i>														0.3	2.2	1	1.2	2.6	0.9	4.7	
<i>Morozovella simulatilis</i>															1.2	0.2	x	1.2	0.9	2.1	
<i>Morozovella</i> cf. <i>albeari</i>																					
<i>Morozovella lacerti</i>														0.3	1.2	0.7	1.2	2.3	0.9	2.3	
<i>Morozovella aequa</i>																		x	0.3		
<i>Chiloguembelina taurica</i>	0.2	2.1	0.2	0.3	1.2	0.5	0.6	0.4	0.3		0.7	0.3	0.8	0.2	0.2	0.3			0.3		
<i>Chiloguembelina midwayensis</i>	7.0	5.9	1.2	5.7	6.4	3.6	3.4	2.2	3.1	2.4	3	2.9	3.6	4.6	1.5	5.2	6.1	4.3	4.7		
<i>Chiloguembelina</i> cf. <i>subcylindrica</i>*	1.0	0.2	0.5	0.3	0.5	0.5	0.4	0.4	0.3	0.3	0.2	0.6	0.6	0.5	0.7	0.6	1.2	0.6	0.3		
<i>Chiloguembelina crinita</i>																					
<i>Chiloguembelina subtriangularis</i>																					
<i>Zeauvigerina teuria</i>	0.7	0.9			0.9			0.7	0.3				0.3	0.8		0.2	0.3	0.3		0.3	
<i>Zeauvigerina aegyptiaca</i>																					
<i>Eoglobigerina</i>	1.5	11.1	11	5.7	8.7	1.1	7.7	1.7	4.3	5.1	6	5.7	4.5	2.1	0.7	3.6	1.5	0.3	1.9		
<i>Subbotina</i>	8.4	6.1	8.7	1.2	8.7	13	8.1	13	9.1	1.9	1.5	6.3	9.6	13.5	1.8	18.1	14.5	1.2	16.9		
<i>Globanomalina</i>	13.5	7.3	5.8	8.4	1.9	12.4	7.2	8	1.1	1	7	1.8	4.2	9.2	4.7	1.9	9	6.1	3.7		
<i>Luterbacheria</i>	7.0	7.7	9.2	11.3	8.7	5.7	4.3	6.3	6.9	7.9	4.2	2.9	7.7	3.6	6.7	2.7	9	6.4	7.5		
<i>Parasubbotina</i>	17.6	26.2	21.3	18.8	22.1	23.6	21.2	19.9	26	27.3	23.9	22.3	29.5	21.2	14.1	19.8	16	2.9	2.5		
<i>Praemurica</i>	3.1	4	3.1	4.5	7.8	3.1	2.6	2.7	3.1	2.7	3.5	1.3	2.5	2.2		1.5	0.6	2	3.1		
<i>Acarinina</i>	3.2	28.2	37.6	34.4	24.2	27.4	43.3	34.4	36	33	37.9	42.4	32.4	32.8	51.6	28.9	26.2	37.1	21.8		
<i>Igorina</i>	0.7		1.4	0.6		0.2	1	0.9	0.3	0.3	2.8	1	1.7	2.4	2.5	1.8	4.7	1.4	1.3		
<i>Morozovella</i>														3.2	2.5	7.7	5.9	6.1	11	1.8	17.9
<i>Chiloguembelina</i>	8.2	8.2	1.9	6.3	8.1	4.6	4.4	3	3.7	2.7	3.9	3.8	5	5.3	2.4	6.1	7.3	4.9	5.3		
<i>Zeauvigerina</i>	0.7	0.9			0.9			0.7	0.3				0.3	0.8		0.2	0.3	0.3		0.3	
L/H ratio	54.7	52.4	56.7	54.4	54.6	46	55.9	52.5	51.3	49	51.6	57.1	49.8	53.4	62.6	50.5	55	58.8	52.3		

Table 4. Average relative abundances of the species in the Caravaca section from sample 9.75 to sample 14.25. In bold, lower latitude dwellers; * species that apparently changed their latitudinal preferences; ** insufficient data.

Biozone	Morozovella cf. albeari Zone																		
Sample	9.75	10	10.25	10.5	10.75	11	11.25	11.5	11.75	12	12.25	12.5	12.75	13	13.25	13.5	13.75	14	14.25
<i>Eoglobigerina fringa</i>																			
<i>Eoglobigerina cf. trivialis</i>	x	x																	
<i>Eoglobigerina tetragona</i>	0.8	1.3	0.3	0.5															
<i>Eoglobigerina edüta</i>																			
<i>Eoglobigerina spiralis</i>																			
<i>Subbotina triloculinoides</i>	5.1	3.8	3.3	1.8	4.4	1.9	3	1.8	1.4	4	1.9	2.9	3.3	0.5	3.4	1.9	0.6	1.2	
<i>Subbotina triangularis</i>	5.3	6.6	4.9	7.1	6.4	9.6	7.3	6.7	7.2	4.9	6.5	6.2	4.9	8.1	4.9	6	5.5	6.7	7
<i>Subbotina compressaformis</i> *	0.3	2.8	3	0.8	1.7	3.9	0.8	2.7	2.3	1.5	0.6	2.2	1.4	0.8	0.9	0.3	0.3	1.8	1.7
<i>Globanomalina compressa</i>	1.3	1.9																	
<i>Globanomalina haunsbergensis</i>	3.2	2.2	3	2	2.2	2.2	1.1	4	2.3	2.1	0.3	2.4	0.5	0.3	0.9	0.5	0.3	x	0.6
<i>Globanomalina chapmani</i>	1.1	0.3	0.9	0.3	1.4	0.3	x	0.3	x		0.3	0.5	0.8		0.3	0.3	0.3		
<i>Luterbacheria ehrenbergi</i>	7.4	12.9	1.3	8.1	7.8	3.6	8.9	11.9	8.7	5.5	7.1	5.5	8.8	8.4	1	7.9	5.8	5.2	7.8
<i>Parasubbotina pseudobulloides</i>																			
<i>Parasubbotina quadrilocula</i>	19.7	17.4	25.8	11.9	2.5	22.3	24.9	19.8	14.5	21	21.4	19.7	27.1	21.7	22.9	16	21.6	16.2	24.1
<i>Parasubbotina variospira</i>																			
<i>Praemurica inconstans</i>	0.3	0.6	0.3	2	1.1	0.6	2.2	0.9	0.6	2.4	0.6	1.4	1.4	0.5	1.7	1.6	0.9	0.9	
<i>Acarinina trinidadensis</i>																			
<i>Acarinina uncinata</i>	2.7	4.1	0.9	2.3	0.3	1.1								0.3	0.6		0.3		0.3
<i>Acarinina praecursoria</i>	1.3	0.3	0.3																
<i>Acarinina hansbollü*</i>	1.1	1.6	1.2	1.5	1.1	1.9	0.8	0.9	0.9	1.8	0.3	0.2	0.3	1.8	1.7	1.1	0.3	0.3	0.6
<i>Acarinina indolensis</i>	1.3	2.8	0.6	0.5	0.3	0.8	x	0.3		0.3									
<i>Acarinina arabica</i>	1.6	0.6		2		0.6													
<i>Acarinina praepentacamerata</i>	6.6	6.3	5.2	6.6	2.2	3.9	3.8	3.3	1.7	1.8	0.3	4.3	0.5	1.8		1.1			0.3
<i>Acarinina praeaequa</i>*	3.2	1.6	1.5	1.8		1.7	0.3	1.2	1.2	0.6	0.9	1	1.4	1.3	0.9	0.5	2.9	1.2	0.6
<i>Igorina tadjikistanensis</i>	0.5	6.3	0.6	2	0.8	1.7	1.6	0.9	0.3	1.5	0.3	0.7		0.5	1.1	0.5	x		
<i>Morozovella angulata</i>	11.7	9.5	14.9	11.4	18	7.4	1.3	11.6	14.5	8.2	6.8	1.6	9	6.5	1	16.3	13.5	1.1	15.1
<i>Morozovella conicotruncata</i>	3.2	5.4	4	9.3	4.2	9.4	4.6	5.5	6.4	4.9	1.2	8.4	12.3	9.4	7.4	9.5	1.7	28.4	11.6
<i>Morozovella simulatilis</i>	8.8	1.9	3.6	17.9	5.3	1.5	8.1	3.6	7.2	6.4	4	7.4	2.5	4.7	4	6.8	8.1	5.2	4.4
<i>Morozovella cf. albeari</i>			3.3	1.8	4.4	7.4	11.4	16.1	2.6	27.1	28.5	18.5	14.8	15.7	2.3	17.3	15.6	8.6	9
<i>Morozovella lacerti</i>	6.4	2.2	6.1	0.5	8.9	2.8	5.1	3	4.1	3	5.9	3.6	4.9	12.8	4.6	1.3	7.5	9.8	12.8
<i>Morozovella aequa</i>	x		x		x		0.5	x	x		x	x	0.3	0.5	0.3	0.3	0.9	x	0.6
<i>Chiloguembelina taurica</i>		0.3																	
<i>Chiloguembelina midwayensis</i>	3.5	5.7	4	6.8	5.8	6.1	3.3	4.6	3.5	1.5	3.1	3.6	4.4	1.8	2.3	1.9	2.6	1.5	0.6
<i>Chiloguembelina cf. subcylindrica</i> *	0.3	1.3	1.2	0.8	1.4	0.6	1.1	0.6	0.6	0.3	0.6	0.7	0.3		0.6			0.3	1.5
<i>Chiloguembelina crinita</i>	0.3		0.3	0.3	0.3						0.3	0.2		0.3			0.3	0.6	
<i>Chiloguembelina subtriangularis</i>	2.7		0.3	0.3	1.7		0.8		2				0.8	2.1	0.3		1.4	1.8	1.5
<i>Zeauvigerina teuria</i>	0.5	0.3				x		0.3		0.3			0.3	0.3	0.3		0.9		
<i>Zeauvigerina aegyptiaca</i>				x		x				0.6							x		
<i>Eoglobigerina</i>	0.8	1.3	0.3	0.5															
<i>Subbotina</i>	1.7	13.2	11.2	9.7	12.5	15.4	11.1	11.2	1.9	1.4	9	11.3	9.6	9.4	9.2	8.2	6.4	9.7	8.7
<i>Globanomalina</i>	5.6	4.4	3.9	2.3	3.6	2.5	1.1	4.3	2.3	2.1	0.6	2.9	1.3	0.3	1.2	0.8	0.6	x	0.6
<i>Luterbacheria</i>	7.4	12.9	1.3	8.1	7.8	3.6	8.9	11.9	8.7	5.5	7.1	5.5	8.8	8.4	1	7.9	5.8	5.2	7.8
<i>Parasubbotina</i>	19.7	17.4	25.8	11.9	2.5	22.3	24.9	19.8	14.5	21	21.4	19.7	27.1	21.7	22.9	16	21.6	16.2	24.1
<i>Praemurica</i>	0.3	0.6	0.3	2	1.1	0.6	2.2	0.9	0.6	2.4	0.6	1.4	1.4	0.5	1.7	1.6	0.9	0.9	
<i>Acarinina</i>	17.8	17.3	9.7	14.7	3.9	1	4.9	5.7	3.8	4.5	1.5	5.5	2.2	5.2	3.2	2.7	3.5	1.5	1.8
<i>Igorina</i>	0.5	6.3	0.6	2	0.8	1.7	1.6	0.9	0.3	1.5	0.3	0.7		0.5	1.1	0.5	x		
<i>Morozovella</i>	3.1	19	31.9	4.9	4.8	37.5	4	39.8	52.8	49.6	55.4	48.5	43.8	49.6	46.6	6.5	56.3	62.1	53.5
<i>Chiloguembelina</i>	6.8	7.3	5.8	8.2	9.2	6.7	5.2	5.2	6.1	1.8	4	4.5	5.5	4.2	3.2	1.9	4.3	4.2	3.6
<i>Zeauvigerina</i>	0.5	0.3		x		x		0.3		0.9			0.3	0.3	0.3		0.9		
L/H ratio	55.7	59.2	55.5	65.3	60.8	54.6	59	61.9	68.2	62.8	59	59.7	51.1	59.8	59.6	65.9	61	46.7	56.8

Table 5. Comparison of taxonomies by Arenillas (1996 modified) and Olsson et al. (1999), and latitudinal preferences. (1) Taxonomy by Arenillas (1996 modified); (2) taxonomy by Olsson et al. (1999); (3) details of species SEM-images; (4) latitudinal preferences according to previous works; (5) latitudinal preferences proposed here; * near-shore dwellers; ** initially low latitude dwellers, finally higher latitude dwellers. Some species not were considered by Olsson et al. (1999), but they were probably included within the species concepts of *Luterbacteria ehrenbergi* (a), *Praemurica uncinata* (b, c), *Morozovella praeangulata* (d, f), and *Chiloguembelina midwayensis* (g).

Taxonomy			Latitudinal preferences	
(1)	(2)	(3)	(4)	(5)
<i>Eoglobigerina fringa</i>	<i>Eoglobigerina eobulloides</i>	Fig. 4E (holotype), F	cosmopolitan	middle-high
<i>Eoglobigerina</i> cf. <i>trivialis</i>	<i>Subbotina cancellata</i>	Fig. 4G (holotype)?, Fig. 4H, I, J	cosmopolitan	low
<i>Eoglobigerina edita</i>	<i>Eoglobigerina edita</i>	Fig. 4M (holotype), N	cosmopolitan	low
<i>Eoglobigerina tetragona</i>		Fig. 4K (holotype), L	cosmopolitan	middle-high
<i>Eoglobigerina spiralis</i>	<i>Eoglobigerina spiralis</i>	Fig. 4O (holotype), P, Q	cosmopolitan	middle-high
<i>Subbotina triangularis</i>	<i>Subbotina trivialis</i>	Fig. 4W (holotype), X	cosmopolitan	middle-high
<i>Subbotina triloculinoides</i>	<i>Subbotina triloculinoides</i>	Fig. 4R (holotype), S	cosmopolitan	middle-high
<i>Subbotina compressaformis</i> alternatively <i>S. eoacnica</i>		Fig. 4U (holotype), V, Fig. 4T (<i>S. eoacnica</i> holotype)	cosmopolitan	**middle-high
<i>Parasubbotina pseudobulloides</i>		<i>Parasubbotina pseudobulloides</i>	Fig. 4A (holotype), B	cosmopolitan
<i>Parasubbotina quadrilocula</i>	<i>Parasubbotina varianta</i>	Fig. 4C (holotype), D	cosmopolitan	middle-high
<i>Parasubbotina variospira</i>	<i>Parasubbotina variospira</i>	Fig. 5A (holotype), B	cosmopolitan	middle-high
<i>Globanomalina compressa</i>	<i>Globanomalina compressa</i>	Fig. 8A (holotype), B	cosmopolitan	middle-high
<i>Globanomalina haunsbergensis</i>	<i>Globanomalina chapmani</i>	Fig. 8C (holotype), D	low-middle	middle
<i>Globanomalina chapmani</i>		Fig. 8E (holotype), F	low-middle	low
<i>Luterbacteria ehrenbergi</i>	<i>Luterbacteria ehrenbergi</i>	Fig. 8G (holotype), H	cosmopolitan	low
<i>Luterbacteria troelseni</i>	not considered (a)	Fig. 8I (holotype), J	cosmopolitan	no analyzed
<i>Luterbacteria pseudomenardii</i>	<i>Luterbacteria pseudomenardii</i>	Fig. 8K (holotype), L	low-middle	no analyzed
<i>Praemurica inconstans</i>	<i>Praemurica inconstans</i>	Fig. 5C (holotype), D	low-middle	low
<i>Acarinina trinidadensis</i>		Fig. 5E (holotype), F, G	low-middle	low
<i>Acarinina uncinata</i>		Fig. 5H (holotype), I	low-middle	low
<i>Acarinina praecursoria</i>	<i>Praemurica uncinata</i>	Fig. 7J (holotype), K	low-middle	middle
<i>Acarinina arabica</i>	not considered (b)	Fig. 7L (holotype), M	low-middle	low
<i>Acarinina indolensis</i>	not considered (c)	Fig. 7H (holotype), I	low-middle	low
<i>Acarinina hansbollii</i>	not considered (d)	Fig. 7A (holotype), B, C, D	low-middle	**middle-high
<i>Acarinina praeaquea</i>	not considered (e)	Fig. 7E (holotype), F, G	low-middle	**middle-high
<i>Acarinina praepentacamerata</i>	<i>Morozovella praeangulata</i>	Fig. 5J (holotype), K, L, Fig. 5M (<i>A. praeangulata</i> holotype)	low-middle	low
<i>Morozovella angulata</i>	<i>Morozovella angulata</i>	Fig. 5N (holotype), O	low-middle	low
<i>Morozovella conicotruncata</i>	<i>Morozovella conicotruncata</i>	Fig. 7N (holotype), O, P?	low-middle	middle
<i>Morozovella velascoensis</i>	<i>Morozovella velascoensis</i>	Fig. 7Q (holotype), R	low-middle	no analyzed
<i>Morozovella aequa</i>	<i>Morozovella aequa</i>	Fig. 5R (holotype), S	low-middle	low
<i>Morozovella lacerti</i>		Fig. 5P (holotype), Q	low-middle	low
<i>Morozovella simulatilis</i>	not considered (f)	Fig. 6K (holotype), M, N, L	low-middle	low
<i>Morozovella occlusa</i>	<i>Morozovella occlusa</i>	Fig. 6Q (holotype), S	low-middle	no analyzed
<i>Morozovella</i> cf. <i>albeari</i> alternatively <i>M. pusilla</i>	<i>Igorina albeari</i>	Fig. 6P (holotype), Q, Fig. 6O (<i>M. crosswicksensis</i> holot.)	low-middle	low
<i>Igorina albeari</i>		Fig. 6H (holotype), I, J?	low-middle	no analyzed
<i>Igorina pusilla</i> alternatively <i>I. convexa</i>	<i>Igorina tadjikistanensis</i>	Fig. 6C (holotype)?, E, F, G, Fig. 6D (<i>I. convexa</i> holotype)	low-middle	no analyzed
<i>Igorina tadjikistanensis</i>	<i>Igorina pusilla</i>	Fig. 6A (holotype), B	low-middle	low
<i>Globoconusa daubjergensis</i>	<i>Globoconusa daubjergensis</i>	Fig. 8M	cosmopolitan*	low
<i>Globoconusa conusa</i>		Fig. 8N	cosmopolitan*	low
<i>Chiloguembelina taurica</i>	<i>Chiloguembelina morsei</i>	Fig. 8O (holotype), P	cosmopolitan	low
<i>Chiloguembelina crinita</i>	<i>Chiloguembelina crinita</i>	Fig. 8T (holotype), U	cosmopolitan	middle-high
<i>Chiloguembelina midwayensis</i>	<i>Chiloguembelina midwayensis</i>	Fig. 8P (holotype), Q	low-middle	low
<i>Chiloguembelina</i> cf. <i>subcylindrica</i>	not considered (g)	Fig. 8R (holotype), S	cosmopolitan	** middle-high
<i>Chiloguembelina subtriangularis</i>	<i>Chiloguembelina subtriangularis</i>	Fig. 8U (holotype), W	low-middle	low
<i>Zeauvigerina aegyptiaca</i>	<i>Zeauvigerina aegyptiaca</i>	Fig. 8Z (holotype), AA	low-middle	low
<i>Zeauvigerina teuria</i>	<i>Zeauvigerina teuria</i>	Fig. 8X (holotype), Y	low-middle	low

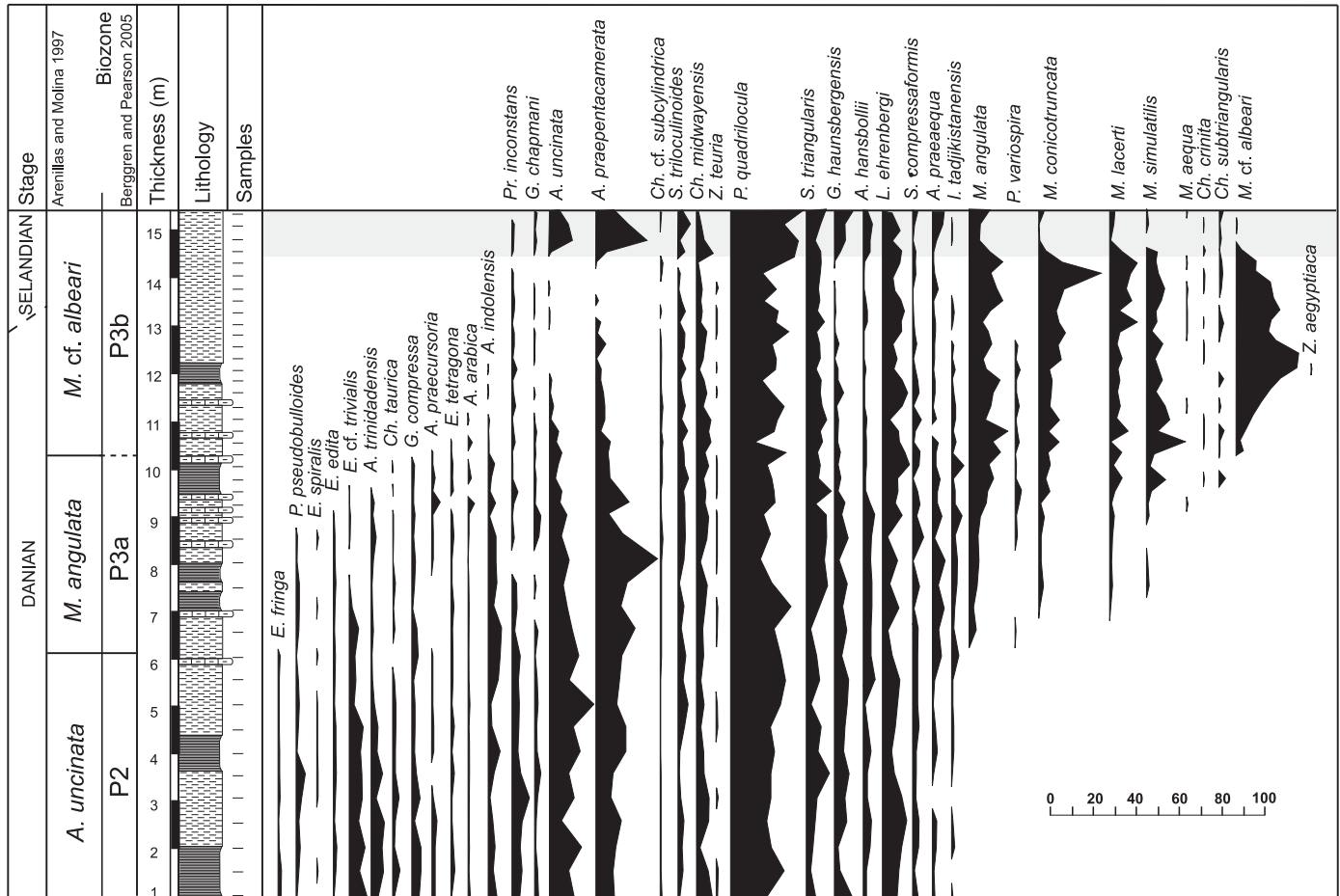
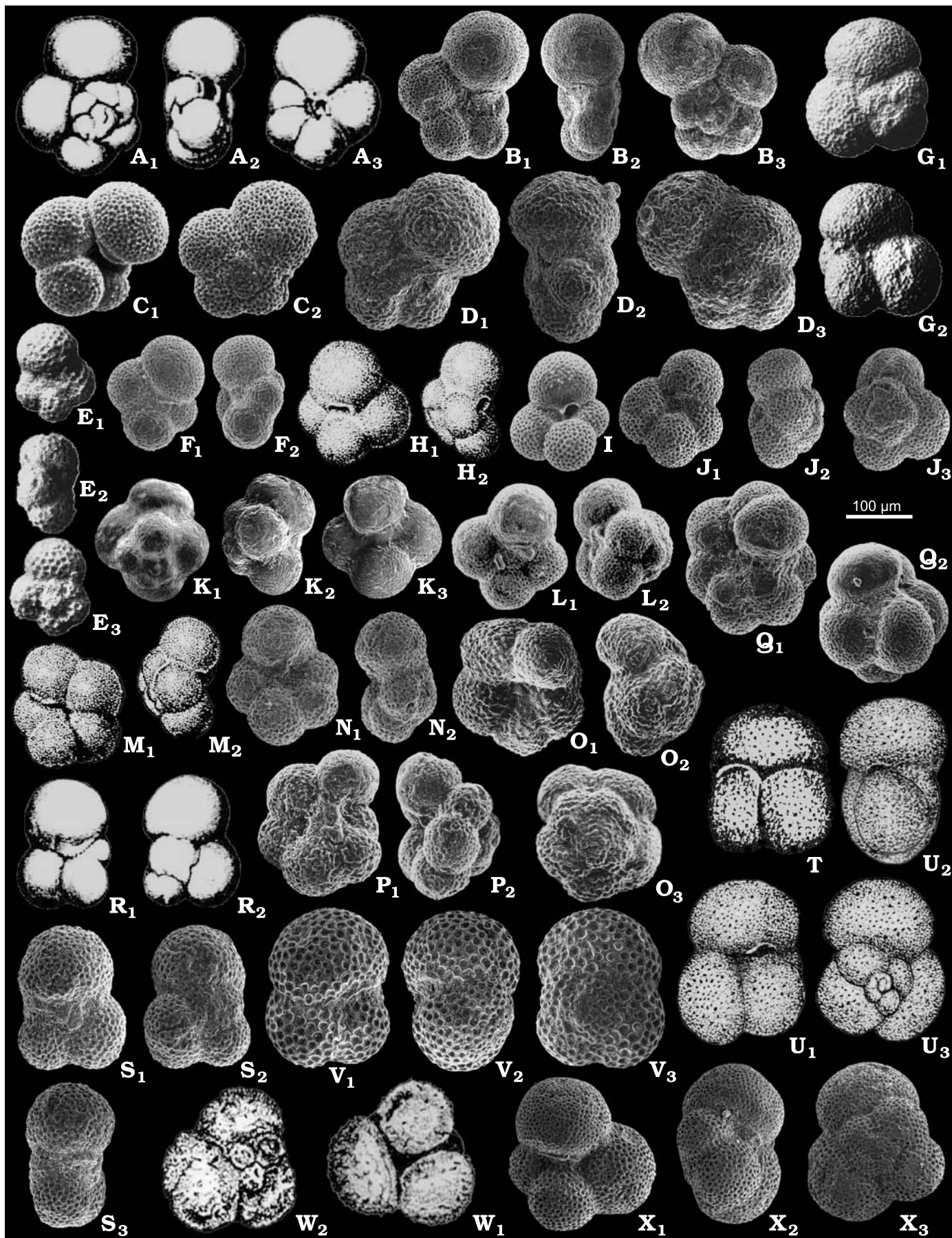


Fig. 3. Quantitative stratigraphic distribution of planktic foraminiferal species across the Danian–Selandian transition at Caravaca. The shown stratigraphic interval does not include the lower part of the *A. uncinata* Zone, where *Globoconusa* species were found (see Arenillas and Molina 1997).

Fig. 4. SEM images of Danian–Selandian species of planktic foraminifera *Parasubbotina*, *Eoglobigerina*, and *Subbotina* from the Caravaca section (B, D, F, J, L, N, P, Q, S, V, X), as well as original drawings and SEM-images of holotypes. **A.** Holotype* of *Globigerina pseudobulloides* Plummer (1927), spiral (A₁), axial (A₂), and umbilical (A₃) views, from Danian, Wills Point Formation, Midway Group, Navarro Co., Texas. **B.** *Parasubbotina pseudobulloides* (Plummer, 1927), umbilical (B₁), axial (B₂), and spiral (B₃) views, from *A. uncinata* Zone (sample CAR94-18, repository number MPZ 2012/352). **C.** Holotype (C₁) and paratype (C₂) of *Globorotalia (Turborotalia) quadrilocula* Blow (1979), umbilical (C₁) and spiral (C₂) views, from Selandian, DSDP Leg 6, Station 47/2, Core 10, Section I, Shatsky Rise, northwestern Pacific. **D.** *Parasubbotina quadrilocula* (Blow, 1979), umbilical (D₁), axial (D₂), and spiral (D₃) views, from *Morozovella cf. albeari* Zone (sample CARA98D/S-14.25, repository number MPZ 2012/423). **E.** Holotype* of *Globigerina fringa* Subbotina (1953), umbilical (E₁), axial (E₂), and spiral (E₃) views, from Danian, Anapa, northwestern Caucasus, Russia. **F.** *Eoglobigerina fringa* (Subbotina, 1953), umbilical (F₁) and axial (F₂) views, from *A. uncinata* Zone (sample CAR94-40, repository number MPZ 2012/358). **G, H, M.** Danian, Kuban River, northwestern Caucasus, Russia. **G.** Holotype* of *Globigerina trivialis* Subbotina (1953), umbilical (G₁) and spiral (G₂) views. **H.** “Original” (topotype) of *Globigerina trivialis* Subbotina (1953), axial (H₁) and umbilical (H₂) views. **I.** Hypotypes of *Eoglobigerina trivialis* (Subbotina, 1953) by Blow (1979), umbilical view, from Danian, DSDP Leg 6, Station 47/2, Core 11, Section I, Shatsky Rise, northwestern Pacific. **J.** *Eoglobigerina cf. trivialis* (Subbotina, 1953), umbilical (J₁), axial (J₂), and spiral (J₃) views, from *A. uncinata* Zone (sample CAR94-40, repository number MPZ 2012/358). **K.** Holotype* of *Globigerina (Eoglobigerina) tetragona* Morozova (1961), spiral (K₁), axial (K₂), and umbilical (K₃) views, from Danian, Novouzensk, cis-Caspian Basin, Russia. **L.** *Eoglobigerina tetragona* (Morozova, 1961), umbilical (L₁) and axial (L₂) views, from *P. pseudobulloides* Zone (sample CAR94-12, repository number MPZ 2012/349). **M.** Holotype of *Globigerina edita* Subbotina (1953), umbilical (M₁) and axial (M₂) views. **N.** *Eoglobigerina edita* (Subbotina, 1953), umbilical (N₁) and axial (N₂) views, from *A. uncinata* Zone (sample CAR94-48, repository number MPZ 2012/360). **O.** Holotype* of *Globigerina spiralis* Bolli (1957), umbilical (O₁), axial (O₂), and spiral (O₃) views, from Danian, Lizard Springs Formation, Trinidad. **P.** *Eoglobigerina spiralis* (Bolli, 1957), umbilical (P₁) and axial (P₂) views, from *A. uncinata* Zone (sample CAR94-58, repository number MPZ 2012/363). **Q.** *Eoglobigerina spiralis* (Bolli, 1957), umbilical (Q₁) and axial (Q₂) views, from *A. uncinata* Zone (sample CAR94-58, repository number MPZ 2012/363). **R.** Holotype of *Globigerina triloculinooides* Plummer (1928), umbilical (R₁) and spiral (R₂) views, from Danian, Wills Point Formation, Midway Group, Navarro Co., Texas. **S.** *Subbotina triloculinooides* (Plummer, 1928), umbilical (S₁), axial (S₂), and spiral (S₃) views, from *M. angulata* Zone (sample CARA97D/S-8, repository number MPZ 2012/400). **T.** Holotype of *Globigerina eoacenaica* Terquem (1882), umbilical view. **U.** Holotype of *Globigerina compressaformis* Khalilov (1956), umbilical (U₁), axial (U₂), and spiral (U₃) views, from upper Paleocene–lower Eocene, northeastern Azerbaijan. **V.** *Subbotina compressaformis* (Khalilov, 1956), umbilical (V₁), axial (V₂), and spiral (V₃) views, from *I. albeari* Zone (sample CAR94-86, repository number MPZ 2012/382). **W.** Holotype of *Globigerina triangularis* White (1928), spiral (W₁) and umbilical (W₂) views, from Danian, Velasco Formation, Tampico Embayment, Mexico. **X.** *Subbotina triangularis* (White, 1928), umbilical (X₁), axial (X₂), and spiral (X₃) views, from *A. uncinata* Zone (sample CAR94-40, repository number MPZ 2012/358). * SEM-images by Olsson et al. (1999).



edita (Subbotina, 1953), *E. fringa* (Subbotina, 1950), *E. cf. trivialis* (*E. trivialis* Subbotina, 1953, sensu Blow, 1979), *E. spiralis* (Bolli, 1957), and *E. tetragona* Morozova, 1961. This proposal for *Eoglobigerina* is similar to that of Blow (1979), and partially shared by Olsson et al. (1999) who validated only the first four, considering *E. fringa* and *E. tetragona* junior synonyms of *E. eobulloides* (Morozova, 1959) and *E. edita* respectively. Arenillas (1996) used the species concept of *E. trivialis* sensu Blow (1979) (Fig. 4H, I), but this is a junior synonym of *Subbotina triangularis* (Fig. 4G) as shown by Olsson et al. (1999). The *E. trivialis*-type specimens of Blow (1979), here considered *E. cf. trivialis*, were probably included in *Subbotina cancellata* Blow, 1979 by Olsson et al. (1999).

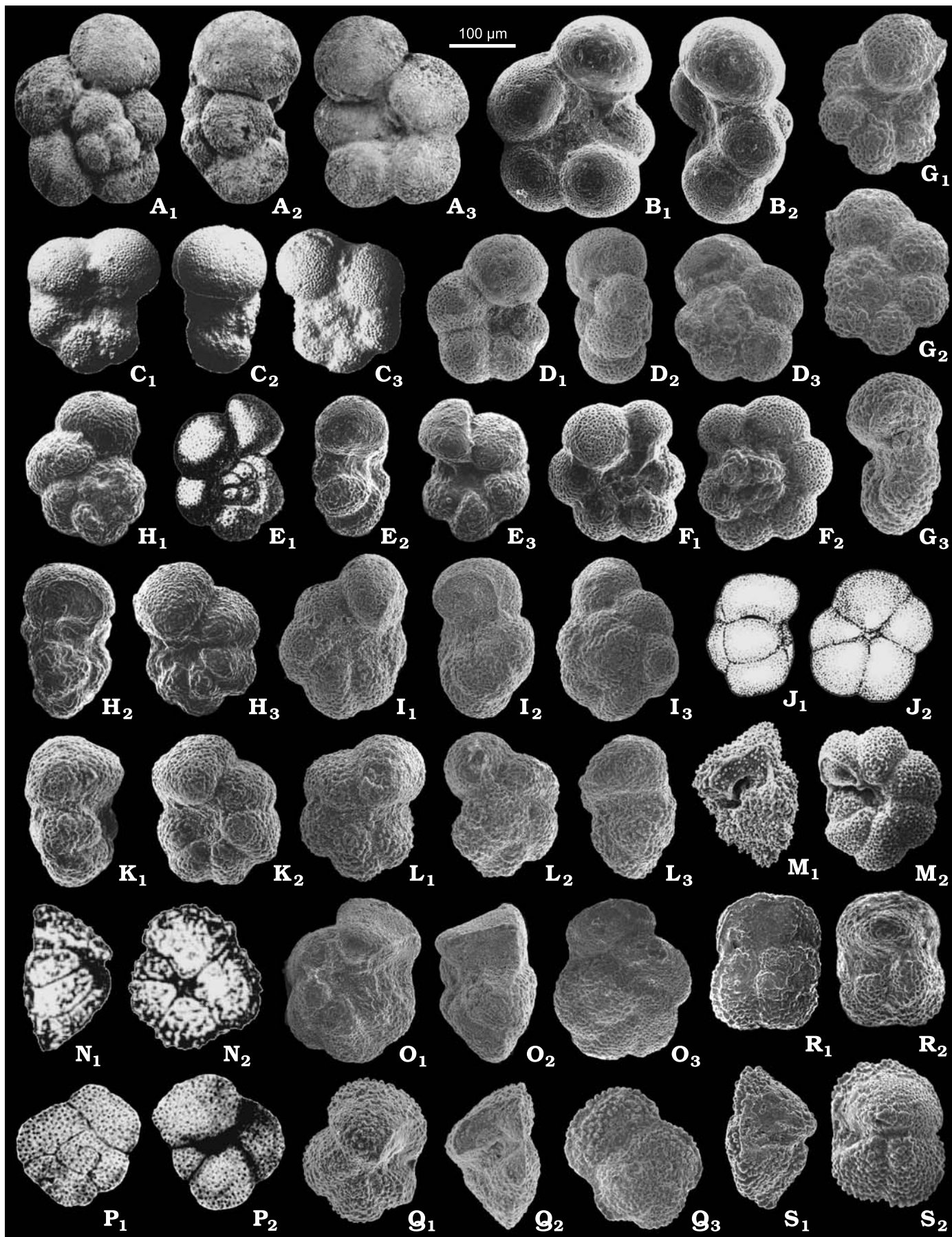
Subbotina (Fig. 4) includes the following species: *S. triangularis* (White, 1928), *S. triloculinoides* (Plummer, 1927), and *S. compressaformis* (Khalilov, 1956). This *Subbotina* classification is similar to that of Blow (1979), who recognized two subspecies in *S. triangularis triangularis* and *S. t. cancellata*, the last of which was raised to full species by Olsson et al. (1999). Although *S. eocaenica* (Terquem, 1882) must be considered as nomen dubium non conservandum, Blow (1979) and Arenillas (1996) retained this name for *Subbotina* with inflated-chambers occurring from the middle Paleocene to the Eocene (Fig. 4T). These forms are now re-named *S. compressaformis* (Fig. 4U, V). Olsson et al. (1999) included them in *S. triloculinoides*, although due to their different morphologies, stratigraphic ranges and patterns of spatio-temporal distribution, it appears reasonable to continue considering them as distinct species.

In the D–S transition, *Parasubbotina* (Fig. 4) includes the following species: *P. pseudobulloides* (Plummer, 1927), *P. quadrilocula* (Blow, 1979), and *P. variospira* (Belford, 1984). The second one was considered by Olsson et al. (1999) a junior synonymous of *P. varianta* (Subbotina, 1953), but Are-

nillas (1996) used the name *P. varianta* for lower–middle Danian forms with high rate of chamber enlargement. Arenillas (1996) also used the species *Parasubbotina ferreri* (Orue-Etxebarria and Apellaniz, 1991), but apparently this species is a junior synonym of *P. variospira*.

Praemurica raises more taxonomical problems, because Olsson et al. (1999) included some species that Blow (1979) and Arenillas (1996) considered as belonging to the genus *Acarinina*. According to the latter, *Praemurica* includes only *Pr. inconstans* (Subbotina, 1953) in the D–S transition, whereas *Acarinina* includes (Figs. 5–7): *A. arabica* (El Nagg, 1966), *A. hansbollii* (Blow and Banner, 1962), *A. indolensis* Morozova, 1959, *A. praeaquia* Blow, 1979, *A. praecursoria* Morozova, 1957, *A. praepentacamerata* (Shutskaya, 1956), *A. trinidadensis* (Bolli, 1957), and *A. uncinata* (Bolli, 1957). Olsson et al. (1999) considered that *A. uncinata* comes under the genus *Praemurica*, and *A. trinidadensis* and *A. praecursoria* are junior synonyms of *Pr. inconstans* and *Pr. uncinata* respectively. Nevertheless, Blow (1979), Toumarkine and Luterbacher (1985), and Arenillas (1996) showed that these species have a more or less developed muricate wall (instead of a cancellate wall as in *Praemurica*), which makes them more appropriate for grouping within the genus *Acarinina*. Arenillas (1996) considered that *A. praeangulata* (Blow, 1979) to be a more evolved morphotype of *A. praepentacamerata*, as both do not present peripheral muricocarinata. Other authors considered that *A. praeangulata* was the first member of *Morozovella* (e.g., Berggren and Norris 1997; Olsson et al. 1999). In addition, Blow (1979) and Arenillas (1996) showed two evolutionary trends within *Acarinina*: one towards reducing the number of chambers (*A. hansbollii* and *A. praeaquia*), and one towards the trochospire raise and the aperture migration in intraumbilical position (*A. indolensis* and *A. arabica*), but these were not considered by Olsson et al. (1999).

Fig. 5. SEM images of Danian–Selandian species of planktic foraminifera *Parasubbotina*, *Praemurica*, *Acarinina*, and *Morozovella* from the Caravaca section (D, F, G, I, L, N, Q, S), as well as original drawings and SEM-images of holotypes. **A.** Holotype of *Globigerina (Turborotalia) variospira* Belford (1984), spiral (A₁), axial (A₂), and umbilical (A₃) views, from Thanetian, Lagaip River, Papua New Guinea. **B.** *Parasubbotina variospira* (Belford, 1984), umbilical (B₁) and axial (B₂) views, from *M. cf. albeari* Zone, Zumaia, Basque Country, Spain (SEM-images by Arenillas 1996). **C.** Holotype* of *Globigerina inconstans* Subbotina (1953), umbilical (C₁), axial (C₂), and spiral (C₃) views, from Danian, Kuban River, northwestern Caucasus, Russia. **D.** *Praemurica inconstans* (Subbotina, 1953), umbilical (D₁), axial (D₂), and spiral (D₃) views, from *A. uncinata* Zone (sample CAR94-40, repository number MPZ 2012/358). **E, H, P.** Danian, Lizard Springs Formation, Trinidad. **E.** Holotype* of *Globorotalia trinidadensis* Bolli (1957), spiral (E₁), axial (E₂), and umbilical (E₃) views. **H.** Holotype* of *Globorotalia uncinata* Bolli (1957), spiral (H₁), axial (H₂), and umbilical (H₃) views. **P.** Holotype of *Globorotalia lacerti* (Cushman and Renz, 1956), axial (P₁) and umbilical (P₂) views. **F.** *Acarinina trinidadensis* (Bolli, 1957), umbilical (F₁) and spiral (F₂) views, from *A. uncinata* Zone. **G.** *Acarinina trinidadensis* (Bolli, 1957), umbilical (G₁), axial (G₂), and spiral (G₃) views, from *A. uncinata* Zone (sample CAR94-52, repository number MPZ 2012/361). **I.** *Acarinina uncinata* (Bolli, 1957), umbilical (I₁), axial (I₂), and spiral (I₃) views, from *M. angulata* Zone (sample CARA97D/S-8, repository number MPZ 2012/400). **J.** Holotype of *Globorotalia angulata* (White, 1928) var. *praepentacamerata* Shutskaya (1956), axial (J₁) and umbilical (J₂) views, from Danian, Kheu River, Kabardino-Balkar Republic, central Caucasus, Russia. **K.** *Acarinina praepentacamerata* (Shutskaya, 1956), axial (K₁) and umbilical (K₂) views, from *M. angulata* Zone (sample CAR94-67, repository number MPZ 2012/371). **L.** *Acarinina praepentacamerata* (Shutskaya, 1956), umbilical (L₁), axial (L₂), and spiral (L₃) views, from *M. angulata* Zone (sample CARA97D/S-8, repository number MPZ 2012/400). **M.** Holotype (M₁) and paratype (M₂) of *Globorotalia (Acarinina) praeangulata* Blow (1979), axial (M₁) and umbilical (M₂) views, from Selandian, DSDP Leg 6, Station 47/2, Core 10, Section 2, Shatsky Rise, northwestern Pacific. **N.** Holotype of *Globigerina angulata* White (1928), axial (N₁), and umbilical (N₂) views, from Danian, Velasco Formation, Tampico Embayment, Mexico. **O.** *Morozovella angulata* (White, 1928), spiral (O₁), axial (O₂), and umbilical (O₃) views, from *M. cf. albeari* Zone (sample CARA97D/S-13, repository number MPZ 2012/418). **Q.** *Morozovella lacerti* (Cushman and Renz, 1956), spiral (Q₁), axial (Q₂), and umbilical (Q₃) views, from *M. cf. albeari* Zone (sample CARA98D/S-12.75, repository number MPZ 2012/417). **R.** Holotype* of *Globorotalia crassata* (Cushman) var. *aequa* (Cushman and Renz, 1942), spiral (R₁) and umbilical (R₂) views, from lower Eocene, Soldado Formation, Trinidad. **S.** *Morozovella aequa* (Cushman and Renz, 1942), axial (S₂) and umbilical (S₃) views, from *M. cf. albeari* Zone (sample CARA97D/S-13, repository number MPZ 2012/418). * SEM-images by Olsson et al. (1999).



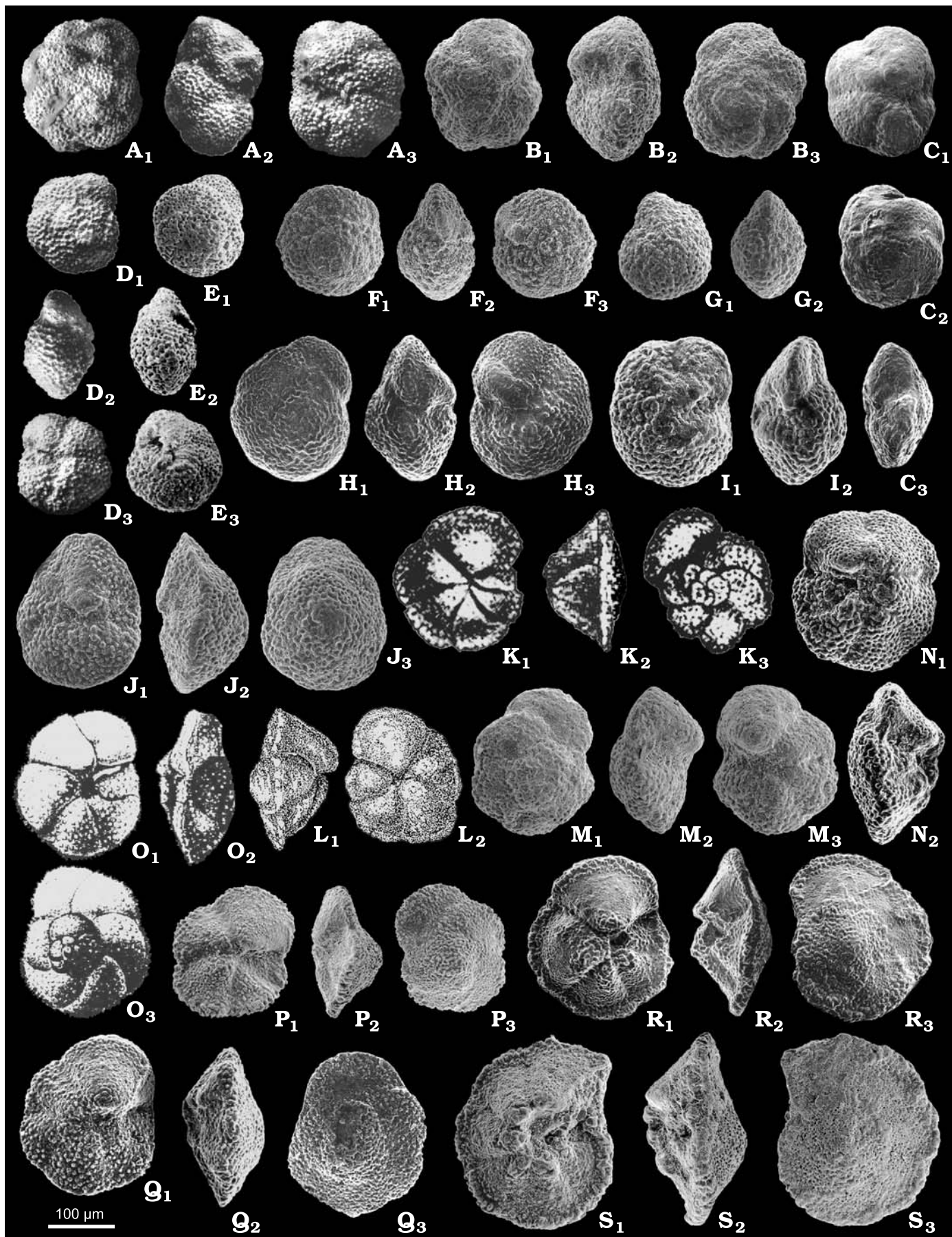
Igorina includes the following species: *I. albeari* (Cushman and Bermúdez, 1949), *I. pusilla* (Bolli, 1957), and *I. tadjikistanensis* (Bykova, 1953) (Fig. 6). The most problematic one is *I. pusilla*. Bolli (1957) defined *I. pusilla* as a biconvex globorotalid with a smooth wall and angular axial margin, but no keel. Stainforth et al. (1975) and Toumarkine and Luterbacher (1985) indicated that well-preserved specimens of this species have a strong perforated wall, and included it in the genus *Planorotalites*. Davidzon (1976) proposed this species as belonging to his new genus *Igorina*, along with other species such as *I. tadjikistanensis* (Bykova, 1953) and *I. laevigata* (Bolli, 1957). Blow (1979) assigned to *Globorotalia (Acarinina) convexa convexa* Subbotina, 1953 the taxonomic concept of *I. pusilla* by Stainforth et al. (1975) and Davidzon (1976), noting that these specimens have a muricate wall. Finally, Arenillas (1996) and Olsson et al. (1999) set the current concept of *Igorina* (i.e., biconvex forms with a muricate wall), but they opposed the concepts of *I. tadjikistanensis* and *I. pusilla*.

Morozovella groups the following species in the D–S transition (Figs. 5–7): *M. aequa* (Cushman and Renz, 1942), *M. angulata* (White, 1928), *M. conicotruncata* (Subbotina, 1947), *M. cf. albeari* (= *M. crosswicksensis* Olsson, 1960, sensu Blow, 1979), *M. lacerti* (Cushman and Renz, 1946), and *M. simulatilis* (Schwager, 1883, sensu Luterbacher 1964). This taxonomic framework is based on the studies of Luterbacher (1964) and Blow (1979), but it differs substantially from that of Olsson et al. (1999) who only considered three species for this time interval: *M. angulata* and *M. conicotruncata*, in addition to *M. praeangulata*. However, Arenillas (1996) showed two trends within *Morozovella* developing through the D–S transition: one towards reducing the chamber number (*M. lacerti* and *M. aequa*) and one towards a compressed biconvex shape (*M. simulatilis* and *M.*

cf. albeari). In the lower Selandian, transitional forms (Fig. 7P) between *M. conicotruncata* (Fig. 7N, O) and *M. velascoensis* (Cushman, 1925) are also encountered (Fig. 7Q, R). This variety (attributed to *M. conicotruncata* by Arenillas 1996) was considered a new species, *Morozovella proto-carina*, by Corfield (1989).

Blow (1979) and Arenillas (1996) named *M. crosswicksensis* the specimens assigned herein to *M. cf. albeari*. However, Olsson et al. (1999) considered that the former was a junior synonym of *Morozovella occlusa* (Loeblich and Tappan, 1957). According to Blow (1979), *M. occlusa* differs from *M. crosswicksensis* by having a muricate circum-umbilical rim, well-developed muricocarina and almost a muricae-free wall (Fig. 6). Since Olsson et al. (1999) synonymized both species, the lowermost Selandian *M. crosswicksensis*-type specimens were reconsidered to be *M. cf. albeari* by Arenillas et al. (2008). These latter wanted to note with this name the probable difficulty in distinguishing *M. cf. albeari* from *I. albeari* (e.g., specimen in Fig. 6J). According to Arenillas (1996), the first one evolved from the lineage *M. angulata*–*M. simulatilis* developing an ever more compressed biconvex shape, whereas the second one evolved from the lineage *A. praepentacamerata*. *tadjikistanensis*–*I. pusilla* developing circumcameral muricocarina in the most evolved forms. The *M. crosswicksensis*-type specimens of Blow (1979) and Arenillas et al. (2008) were included in *I. albeari* by Olsson et al. (1999) and by Sprong et al. (2008), introducing a new focus of taxonomic and biostratigraphic controversy. According to the taxonomy by Arenillas (1996), *I. albeari* differs from *M. cf. albeari* by having sutures generally covered with muricae, poorly developed (or absent) circumcameral muricocarina and being generally masked by the dense muricae, and aperture tending towards an intraumbilical position (SOM_1). Nevertheless, the SEM image (by Olsson et al. 1999) of the *I. pusilla*

Fig. 6. SEM images of Danian–Selandian species of planktic foraminifera *Igorina* and biconvex *Morozovella* from the Caravaca section (B, F, G, I, J, M, N, P, Q, S), as well as original drawings and SEM-images of holotypes. **A.** Holotype* of *Globorotalia tadjikistanensis* Bykova (1953), spiral (A₁), axial (A₂), and umbilical (A₃) views, from Suzakian Stage (given as Eocene), Tadjhik Basin, Ak-Tau, Kazakhstan. **B.** *Igorina tadjikistanensis* (Bykova, 1953), umbilical (B₁), axial (B₂), and spiral (B₃) views, from *A. uncinata* Zone (sample CAR94-63, repository number MPZ 2012/367). **C.** Holotype* of *Globorotalia pusilla pusilla* Bolli (1957), umbilical (C₁), axial (C₂), and spiral (C₃) views, from Selandian, Guayaguayare well 159, Trinidad Leaseholds, Ltd., Lizard Springs Formation, Trinidad. **D.** Holotype of *Globorotalia convexa* Subbotina (1953), spiral (D₁), axial (D₂), and umbilical (D₃) views, from lower Eocene, Nalchik-Kheu River, northern Caucasus, Russia. **E.** *Igorina pusilla* (Bolli, 1957), specimen by Stainforth et al. (1975), spiral (E₁), axial (E₂), and umbilical (E₃) views, from Selandian, northwestern South Atlantic. **F.** *Igorina pusilla* (Bolli, 1957), spiral (F₁), axial (F₂), and umbilical (F₃) views, from *L. pseudomenardii* Zone (sample CAR94-92, repository number MPZ 2012/385). **G.** *Igorina pusilla* (Bolli, 1957), umbilical (G₁) and axial (G₂) views, from *L. pseudomenardii* Zone (sample CAV90-13, repository number MPZ 2012/314). **H.** Holotype* of *Globorotalia (Globorotalia) albeari* Cushman and Bermudez (1949), spiral (H₁), axial (H₂), and umbilical (H₃) views, from Thanetian, Madruga Formation, Habana Province, Cuba. **I.** *Igorina albeari* (Cushman and Bermudez, 1949), umbilical (I₁) and axial (I₂) views, from *I. albeari* Zone (sample CAR94-90, repository number MPZ 2012/384). **J.** *Igorina albeari?* (Cushman and Bermudez, 1949), umbilical (J₁), axial (J₂), and spiral (J₃) views, from *L. pseudomenardii* Zone (sample CAV92-4.5, repository number MPZ 2012/303). **K.** Holotype of *Discorbina simulatilis* Schwager (1883), umbilical (K₁), axial (K₂), and spiral (K₃) views, from Thanetian? (given as Eocene), El Guss Abu Said, Farafra Oasis, Western Desert, Egypt. **L.** *Globorotalia simulatilis* (Schwager, 1883) sensu Luterbacher (1964), axial (L₁) and umbilical (L₂) views, from Selandian–Thanetian transition, Gubbio, Italy. **M.** *Morozovella simulatilis* (Schwager, 1883), spiral (M₁), axial (M₂), and umbilical (M₃) views, from *M. cf. albeari* Zone (sample CAR98D/S-14.25, repository number MPZ 2012/423). **N.** *Morozovella simulatilis* (Schwager, 1883), umbilical (N₁) and axial (N₂) views, from *M. cf. albeari* Zone (sample CAR94-74, repository number MPZ 2012/376). **O.** Holotype of *Globorotalia crosswicksensis* Olsson (1960), umbilical (O₁), axial (O₂), and spiral (O₃) views, from Selandian (given as lower Eocene), Hornerstown Formation, New Jersey. **P.** *Morozovella cf. albeari*, umbilical (P₁), axial (P₂), and spiral (P₃) views, from *I. albeari* Zone (sample CAR94-90, repository number MPZ 2012/384). **Q.** *Morozovella cf. albeari*, umbilical (Q₁), axial (Q₂), and spiral (Q₃) views, from *I. albeari* Zone. **R.** Holotype* of *Globorotalia occlusa* Loeblich and Tappan (1957), umbilical (R₁), axial (R₂), and spiral (R₃) views, from Thanetian, Velasco Formation, New Jersey. **S.** *Morozovella occlusa* (Loeblich and Tappan, 1957), umbilical (S₁), axial (S₂), and spiral (S₃) views, from *L. pseudomenardii* Zone (sample CAV90-8, repository number MPZ 2012/309). * SEM-images by Olsson et al. (1999). →



holotype (Fig. 6C) might suggest another interpretation: although its preservation is poor, it could have a muricate wall and muricocarina, and be reassigned to *Morozovella* as was suggested by Yassini (1979). In this case, (1) the D–S *M. crosswicksensis*-type specimens could be attributed to *Morozovella pusilla*, and (2) the taxonomic concept of *I. pusilla* sensu Stainforth et al. (1975), Davidzon (1979), and Toumarkine and Luterbacher (1985) could now be attributed to *Igorina convexa* (Subbotina, 1953) in agreement with the opinion of Blow (1979) (Fig. 6D).

Globanomalina Haque, 1956 and *Luterbacheria* Canudo, 1994 group includes the following species (Fig. 8): *G. compressa* (Plummer, 1927), *G. haunsbergensis* (Gohrbandt, 1963), *G. chapmani* (Parr, 1938), and *L. ehrenbergi* (Bolli, 1957). Berggren and Norris (1997) and Olsson et al. (1999) considered both genera synonyms, since they belong to the same evolutionary lineage. However, Arenillas (1996) differentiated *Luterbacheria* from *Globanomalina* by the presence of a keel instead of an imperforate margin in the former, considering that similar criteria have been used for the separation of other genera (e.g., *Praemurica*–*Acarinina* from *Morozovella*). Haig et al. (1993) considered *G. haunsbergensis* to be a junior synonym of *G. chapmani*, although their holotypes differ in the number of chambers (Fig. 8C, D; see diagnostic characters in SOM_1). The keeled genus *Luterbacheria* includes other upper Paleocene species according to Canudo (1994) and Arenillas (1996), such as *L. troelsenii* (Loeblich and Tappan, 1957) (Fig. 8I, J) and *L. pseudomenardii* (Bolli, 1957) (Fig. 8K, L), whose taxonomical separation is debatable as the former is a transitional form between *L. ehrenbergi* and *L. pseudomenardii*.

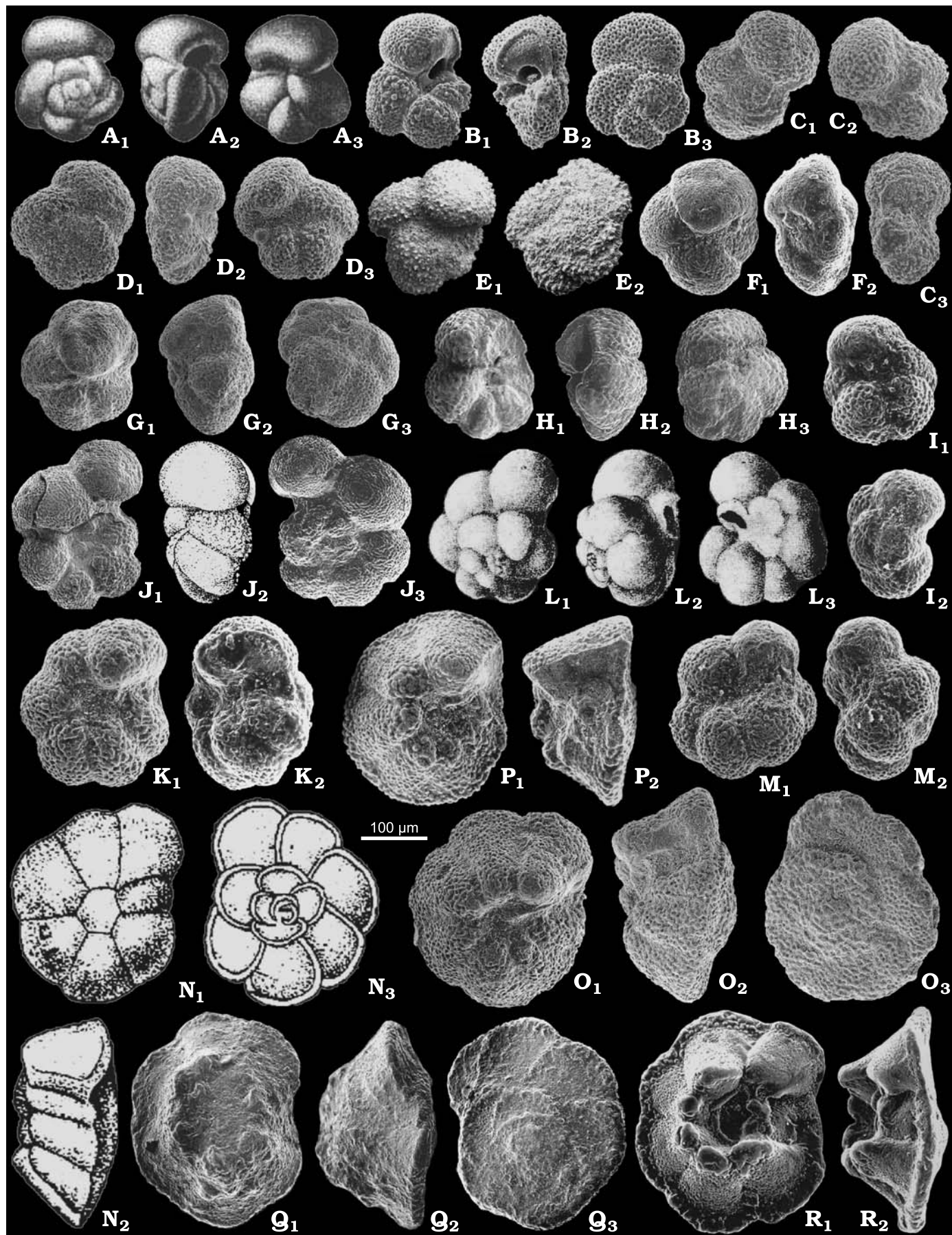
Globoconusa includes the following species (Fig. 8): *Gc. daubjergensis* (Brönnimann, 1953), and *Gc. conusa* Khalilov, 1956. Olsson et al. (1999) considered both species syn-

onymous, but they can be distinguished by the spire height, *Gc. conusa* being higher. Arenillas (1996) named the latter *Gc. kozlowskii* (Brotzen and Pożaryska, 1961), but apparently it is a junior synonym of *Gc. conusa*.

Chiloguembelina contains the following species in the D–S transition (Fig. 8): *Ch. crinita* (Glaessner, 1937, *Ch. midwayensis* (Cushman, 1940), *Ch. cf. subcylindrica* Beckmann (1957), *Ch. subtriangularis* Beckmann (1957), and *Ch. taurica* Morozova, 1961. This taxonomy was mainly based on Beckmann (1957) and subsequent studies of Arenillas (1996) and Olsson et al. (1999). The latter did not consider *Ch. cf. subcylindrica* (which is similar to *Ch. midwayensis* but with chambers more inflated) in the Paleocene. Moreover, they attributed to *Chiloguembelina morsei* (Kline, 1943) the taxonomic concept of *Ch. taurica*. Arenillas et al. (2007) showed that *Ch. morsei* is a junior synonym of *Ch. midwayensis*.

A genus probably related to *Chiloguembelina* is *Zeauvigerina* (Fig. 8), which groups the following species in the D–S transition: *Z. aegyptiaca* Said and Kenawy, 1956, and *Z. teuria* Finlay, 1947. It is doubtful that this taxon is planktonic (Loeblich and Tappan 1987), although taxonomists have considered it to be closely related to *Chiloguembelina* (Beckmann 1957; Huber and Boersma 1994; Arenillas 1996). However, others (e.g., Olsson et al. 1999) indicated that *Chiloguembelina waiparaensis* Jenkins, 1966 is a *Zeauvigerina* appearing in the Cretaceous, thereby unlinking *Zeauvigerina* from *Chiloguembelina* and raising new doubts about its pelagic habitat. In addition, although they inferred that it was planktonic based on quantitative data (high relative abundance compared with co-occurring benthic foraminifera), Huber and Boersma (1994) showed that this species yields stable isotopic values close to those of benthic foraminifera. Therefore, these forms probably were benthic with meroplanktonic behaviour.

Fig. 7. SEM images of other Danian–Selandian species of planktic foraminifera *Acarinina* and *Morozovella* from the Caravaca section (C, F, G, I, K, M, O, P, R), as well as original drawings and SEM-images of holotypes. **A.** Holotype of *Globorotalia (Turborotalia) hansbollii* Blow and Banner (1962), spiral (A₁), axial (A₂), and umbilical (A₃) views, from Thanetian, Lizard Springs Formation, Trinidad. **B.** Hypotype of *Globorotalia (Acarinina) hansbollii* (Blow and Banner, 1964) by Blow (1979), umbilical (B₁), axial (B₂), and spiral (B₃) views, from Selandian, DSDP Leg 6, Station 47/2, Core 10, Sections 5–6, Shatsky Rise, northwestern Pacific. **C.** *Acarinina hansbollii* (Blow and Banner), spiral (C₁), axial (C₂), and umbilical (C₃) views, from *A. uncinata* Zone (sample CARA97D/S-5.5, repository number MPZ 2012/395). **D.** *Acarinina hansbollii* (Blow and Banner, 1962), spiral (D₁), axial (D₂), and umbilical (D₃) views, from *M. angulata* Zone (sample CARA97D/S-8, repository number MPZ 2012/400). **E.** Holotype of *Globorotalia (Acarinina) praeaequa* Blow (1979), umbilical (E₁) and axial (E₂) views, from Danian, DSDP Leg 6, Station 47/2, Core 10, Sections 4–5, Shatsky Rise, northwestern Pacific. **F.** *Acarinina praeaequa* (Blow, 1979), umbilical (F₁) and axial (F₂) views, from *M. angulata* Zone (sample CAR94-68, repository number MPZ 2012/372). **G.** *Acarinina praeaequa* (Blow, 1979), umbilical (G₁), axial (G₂), and spiral (G₃) views, from *M. cf. albeari* Zone (sample CARA97D/S-13, repository number MPZ 2012/418). **H.** Holotype* of *Acarinina indolensis* Morozova (1959), umbilical (H₁), axial (H₂), and spiral (H₃) views, from Danian, Tarkhankhut Peninsula, Crimea, Ukraine. **I.** *Acarinina indolensis* Morozova (1959), umbilical (I₁) and axial (I₂) views, from *M. angulata* Zone (sample CAR94-65, repository number MPZ 2012/369). **J.** Holotype* of *Acarinina praecursoria* Morozova (1957), umbilical (J₁), axial (J₂), and spiral (J₃) views, from Danian, Khokodz' River, Northern Caucasus, Russia. **K.** *Acarinina praecursoria* Morozova (1957), umbilical (K₁) and axial (K₂) views, from *A. uncinata* Zone (sample CAR94-58, repository number MPZ 2012/363). **L.** Holotype of *Globigerina arabica* El-Naggar (1966), spiral (L₁), axial (L₂), and umbilical (L₃) views, from Danian, Gebel Owaina, Esna-Idfu region, Egypt. **M.** *Acarinina arabica* (El-Naggar, 1966), umbilical (M₁) and axial (M₂) views, from *A. uncinata* Zone (sample CAR94-60, repository number MPZ 2012/364). **N.** Holotype of *Globorotalia conicontruncata* Subbotina (1947), umbilical (N₁), axial (N₂), and spiral (N₃) views, from Selandian? (given as Danian), Kheu River, Kabardino-Balkar Republic, central Caucasus, Russia. **O.** *Morozovella conicontruncata* (Subbotina, 1947), umbilical (O₁), axial (O₂), and spiral (O₃) views, from *M. cf. albeari* Zone (sample CARA97D/S-13, repository number MPZ 2012/418). **P.** *Morozovella conicontruncata* (Subbotina, 1947), transitional to *Morozovella velascoensis* (Cushman, 1925) (= *Morozovella protocarina* Corfield, 1989), umbilical (P₁) and axial (P₂) views, from *M. cf. albeari* Zone (sample CAR94-80, repository number MPZ 2012/379). **Q.** Holotype* of *Pulvinulina velascoensis* Cushman (1925), umbilical (Q₁), axial (Q₂), and spiral (Q₃) views, from upper Paleocene (given as Upper Cretaceous), Velasco Formation, San Luis Potosí, Tampico Embayment, Mexico. **R.** *Morozovella velascoensis* (Cushman, 1925), umbilical (R₁) and axial (R₂) views, from *L. pseudomenardii* Zone (sample CAV90-10, repository number MPZ 2012/311). * SEM-images by Olsson et al. (1999). →



Paleoecological analysis

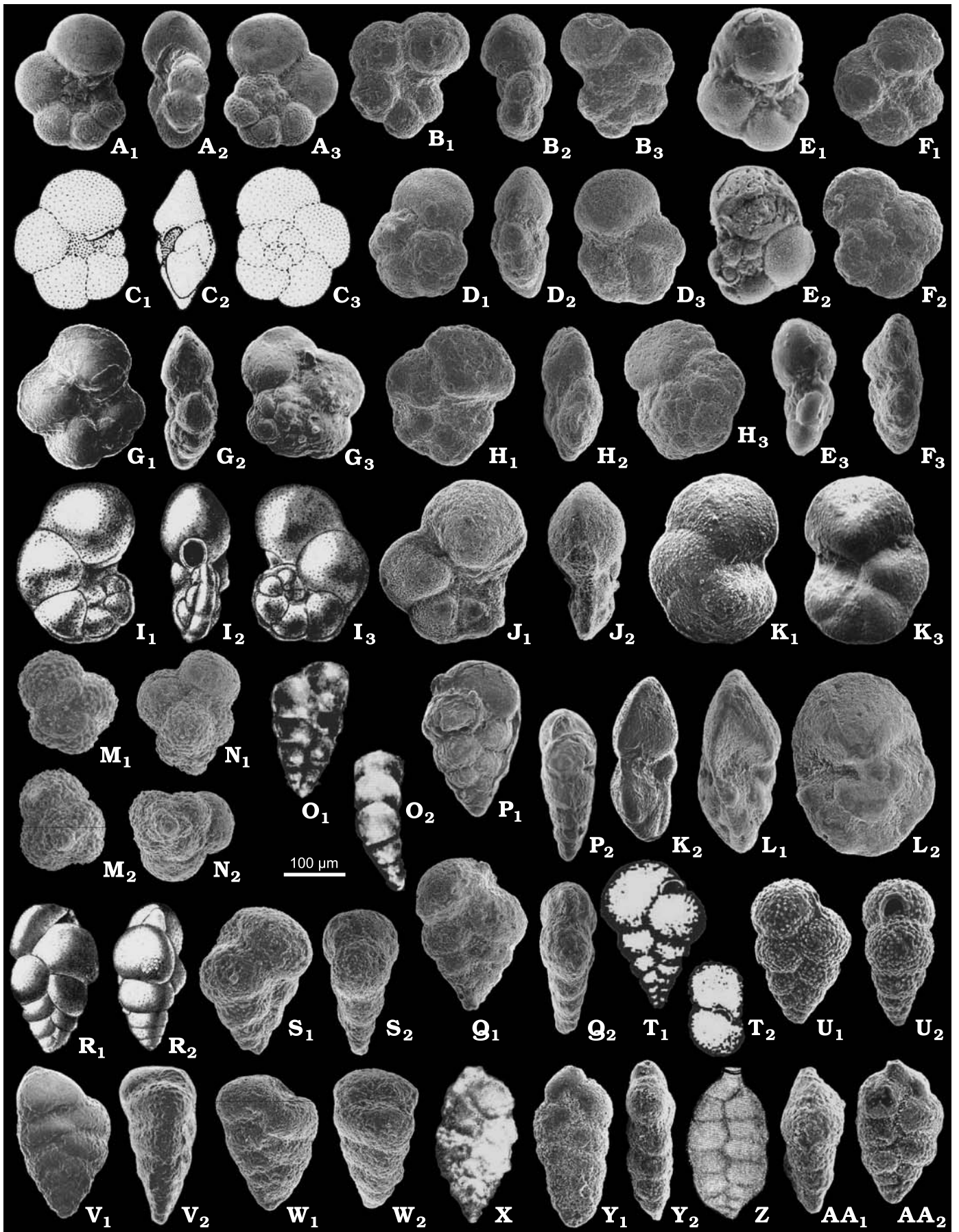
The principal factors influencing the biogeographical and bathymetric distribution, as well as the abundance of the planktic foraminiferal species, are both physical-chemical (temperature, nutrients, oxygenation, light, salinity, water density, turbidity, and pressure) and biotic factors (life cycles, algal symbionts, food supply, predations, and inter-specific relationships) in the pelagic realm. Most physical-chemical factors are in function of depth. Fluctuations in species abundance across the stratigraphic series are related to changes in one or more of these factors. Finding connections between species abundance fluctuations and changes in a particular ecological/biological factor is difficult due to the complexity of interactions between the controlling factors. However, it is feasible to assume that divergences in the quantitative stratigraphic distributions between two morphologically similar species are related to different ecological requirements and/or biological behaviors and therefore both belong to two—reproductively isolated—species.

According to de Vargas et al. (2001), heterochronic reproductive behaviors associated with niche adaptation may be a common mode of speciation in planktic foraminifera. Norris (2000) indicated that divergences in the timing and depth of reproduction are two important factors in the speciation of planktic foraminifera and other pelagic groups (seasonal sym-

patric and depth parapatric speciation, respectively). Thus many planktic foraminiferal species may have had narrower geographic ranges and ecological requirements than has been suspected, and very slight morphological differences may distinguish related species adapted to significantly different environments. In addition, biogeographic, ecological, and genetic studies on living specimens suggest that morphological taxonomies have underestimated the number of pelagic species (Darling et al. 2000).

Paleobiogeographic, quantitative and isotopic studies have been used to identify the latitudinal and bathymetric preferences of Paleocene planktic foraminiferal taxa. Summarizing the paleoecological data and interpretations by Boersma and Premoli Silva (1989, 1991), Shackleton et al. (1985), Corfield and Cartlidge (1992), D'Hondt and Zachos (1993), Arenillas (1996), Berggren and Norris (1997), and Olsson et al. (1999), the D–S planktic foraminiferal genera may be grouped into low-middle latitude (or tropical-subtropical), shallow water dwellers (*Praemurica*, *Acarinina*, *Morozovella*, and *Igorina*), and middle-high latitude (or cosmopolitan), intermediate-deep water dwellers (*Eoglobigerina*, *Subbotina*, *Parasubbotina*, *Globanomalina*–*Luterbacheria*, and *Chiloguembelina*). Nevertheless, particular species have paleoecological requirements and biological behavior that may be different from the norm within their genera. More data on the latitudinal preferences of planktic foraminiferal species is needed to refine the

Fig. 8. SEM images of Danian–Selandian species of planktic foraminifera *Globanomalina*, *Luterbacheria*, *Globoconusa*, *Chiloguembelina*, and *Zeauvigerina* from the Caravaca section (B, D, F, H, I, L, M, N, Q, S, W, Y, AA), as well as original drawings and SEM-images of holotypes. **A.** Holotype* of *Globigerina compressa* Plummer (1927), umbilical (A₁), axial (A₂), and spiral (A₃) views, from Danian, Midway Formation, Navarro Co., Texas. **B.** *Globanomalina compressa* (Plummer, 1927), umbilical (B₁), axial (B₂), and spiral (B₃) views, from *A. uncinata* Zone (sample CARA97D/S-2, repository number MPZ 2012/388). **C.** Holotype of *Globorotalia haunsbergensis* Gohrbandt (1963), umbilical (C₁), axial (C₂), and spiral (C₃) views, from Thanetian, north of Salzburg, Austria. **D.** *Globanomalina haunsbergensis* (Gohrbandt, 1963), spiral (D₁), axial (D₂), and umbilical (D₃) views, from *M. angulata* Zone (sample CARA97D/S-7.5, repository number MPZ 2012/399). **E.** Holotype* of *Globorotalia chapmani* Parr (1938), umbilical (E₁), axial (E₂), and spiral (E₃) views, from Thanetian, King's Park Shale, Perth, Australia. **F.** *Globanomalina chapmani* (Parr, 1938), umbilical (F₁), axial (F₂), and spiral (F₃) views, from *A. uncinata* Zone (sample CAR94-64, repository number MPZ 2012/368). **G.** Holotype* of *Globorotalia ehrenbergi* Bolli (1957), umbilical (G₁), axial (G₂), and spiral (G₃) views, from Selandian, Lizard Springs Formation, Trinidad. **H.** *Luterbacheria ehrenbergi* (Bolli, 1957), umbilical (H₁), axial (H₂), and spiral (H₃) views, from *A. uncinata* Zone (sample CARA97D/S-3, repository number MPZ 2012/390). **I.** Holotype of *Globorotalia troelseni* Loeblich and Tappan (1957), umbilical (I₁), axial (I₂), and spiral (I₃) views. **J.** *Luterbacheria troelseni* (Loeblich and Tappan, 1957), umbilical (J₁) and axial (J₂) views, from *I. albeari* Zone, from Thanetian, Nanafalia Formation, Wilcox Co., Alabama (sample CAR94-86, repository number MPZ 2012/382). **K.** Holotype* of *Globorotalia pseudomenardii* Bolli (1957), umbilical (K₁), axial (K₂), and spiral (K₃) views, from Thanetian, Guayaguayare well 159, Trinidad Leaseholds, Ltd., Lizard Springs Formation, Trinidad. **L.** *Luterbacheria pseudomenardii* (Bolli, 1957), axial (L₁) and umbilical (L₂), from *L. pseudomenardii* Zone (sample CAV92-3.5, repository number MPZ 2012/299). **M.** *Globoconusa daubjergensis* (Bronnimann, 1953), axial (M₁) and spiral (M₂), from *A. uncinata* Zone (sample CAR94-52, repository number MPZ 2012/361). **N.** *Globoconusa conusa* Khalilov (1956), axial (N₁) and spiral (N₂), from *A. uncinata* Zone (sample CAR94-48, repository number MPZ 2012/360). **O.** Holotype of *Chiloguembelina taurica* Morozova, frontal (O₁) and lateral (O₂) views, from Danian, Tarkhankhut Peninsula, Crimea, Ukraine. **P.** Holotype* of *Guembelina midwayensis* Cushman (1940), frontal (P₁) and lateral (P₂) views, from Paleocene, Midway group, Sumter Co., Alabama. **Q.** *Chiloguembelina midwayensis* (Cushman, 1940), frontal (Q₁) and lateral (Q₂) views, from *A. uncinata* Zone (sample CAR94-61, repository number MPZ 2012/365). **R.** Holotype of *Guembelina midwayensis* (Cushman, 1940) subs. *subcylindrica* Beckmann, 1957, frontal (R₁) and lateral (R₂) views, from lower Eocene, Lizard Springs Formation, Trinidad. **S.** *Chiloguembelina* cf. *subcylindrica* (Beckmann, 1957) by Arenillas (1996), frontal (S₁) and lateral (S₂) views, from *A. uncinata* Zone (sample CARA97D/S-2, repository number MPZ 2012/388). **T.** Holotype of *Guembelina crinita* Glaessner (1937), frontal (T₁) and aboral (T₂) views, from Paleocene–Eocene transition, Iiskaja oil field, northern Caucasus, Russia. **U.** *Chiloguembelina crinita* (Glaessner, 1937), frontal (U₁) and lateral (U₂) views, from *M. velascoensis* Zone, upper Paleocene (sample CAV90-20, repository number MPZ 2012/323). **V.** Holotype* of *Chiloguembelina subtriangularis* Beckmann (1957), frontal (V₁) and lateral (V₂) views, from Selandian, Lizard Springs Formation, Trinidad. **W.** *Chiloguembelina subtriangularis* Beckmann (1957), frontal (W₁) and lateral (W₂) views, from *A. uncinata* Zone (sample CARA98D/S-13.75, repository number MPZ 2012/421). **X.** Holotype of *Zeauvigerina teuria* Finlay (1947), frontal view, from Teurian (Danian), Te Uri Stream, North Island, New Zealand. **Y.** *Zeauvigerina teuria* Finlay (1947), frontal (Y₁) and lateral (Y₂) views, from *P. pseudobulloides* Zone (sample CAR94-12, repository number MPZ 2012/349). **Z.** Holotype of *Zeauvigerina aegyptiaca* Said and Kenawy (1956), frontal view, from Selandian, Esna shale, northern Sinai, Egypt. **AA.** *Zeauvigerina aegyptiaca* Said and Kenawy (1956), frontal (AA₁) and lateral (AA₂) views, from *M. cf. I. albeari* Zone (sample CAR94-78, repository number MPZ 2012/378). * SEM-images by Olsson et al. (1999).



paleoenvironmental indices used in studies of paleoclimatic and paleoceanographic fluctuations. In addition, such evidence can be used as a criterion to taxonomically separate species that had previously been synonymized by their morphological similarity.

Testing the latitudinal preferences of the species.—Species latitudinal preferences have been inferred by comparing their relative abundance (Tables 1, 2) between Caravaca and Zumaia. It is noteworthy that sediments of both sections were deposited at relatively similar depths (middle-lower bathyal), so the bathymetric factor should not influence the paleoecological interpretations.

Results indicate that species preferring low latitudes in the *A. uncinata* Zone (Table 1) were *E. cf. trivialis*, *E. edita*, *S. compressaformis*, *G. chapmani*, *L. ehrenbergi*, *Pr. inconstans*, *A. trinidadensis*, *A. uncinata*, *A. hansbollii*, *A. indolensis*, *A. arabica*, *A. praepentacamerata*, *A. praeaequa*, *I. tadjikistanensis*, *Ch. taurica*, *Ch. midwayensis*, *Ch. cf. subcylindrica*, *Z. teuria*, *Gc. daubjergensis*, and *Gc. conusa*. Species preferring middle latitudes, therefore being more cosmopolitan, were *E. fringa*, *E. tetragona*, *E. spiralis*, *S. triloculinooides*, *S. triangularis*, *G. compressa*, *G. haunsbergensis*, *P. pseudobulloides*, *P. quadrilocula*, and *A. praecursoria*.

In the *M. cf. albeari* Zone (Table 2), species preferring low latitudes (tropical-subtropical) were *L. ehrenbergi*, *Pr. inconstans*, *A. uncinata*, *A. praepentacamerata*, *I. tadjikistanensis*, *M. angulata*, *M. simulatilis*, *M. cf. albeari*, *M. lacerti*, *M. aequa*, *Ch. midwayensis*, *Ch. subtriangularis*, *Z. teuria*, and *Z. aegyptiaca*. Species preferring middle latitudes (temperate) were *S. triloculinooides*, *S. triangularis*, *S. compressaformis*, *G. haunsbergensis*, *G. chapmani*, *P. quadrilocula*, *A. hansbollii*, *A. praeaequa*, *M. conicotruncata*, *Ch. cf. subcylindrica*, and *Ch. crinita*.

Table 5 summarizes the latitudinal preferences of the species according to previous studies and compares with the results obtained here. Although both interpretations are consistent, some unexpected differences are noteworthy. Except for *Ch. crinita*, chiloguembelinids are more abundant in Caravaca, suggesting that they strongly preferred low latitudes. This result is consistent with paleobiogeographic studies by Beckmann (1957) and Olsson et al. (1999), who found chiloguembelinids preferably occur outside high latitudes.

Eoglobigerina and *Globanomalina*–*Luterbacheria* were considered essentially cosmopolitan (Arenillas 1996; Olsson et al. 1999), but data suggest that *E. cf. trivialis*, *E. edita*, and *L. ehrenbergi* preferred low latitudes. This result supports the suggestion that these species can be taxonomically separated from the morphologically similar species *E. tetragona*, *E. spiralis*, and *G. haunsbergensis* respectively, as was interpreted by Arenillas (1996). It suggests that high-spined *Eoglobigerina* and *Globanomalina* prefer temperate latitudes.

Among the acarininids and morozovellids, *A. praecursoria* and *M. conicotruncata* are more abundant in Zumaia, suggesting that (i) they preferred temperate latitudes, (ii) both species can be taxonomically differentiated from the morpho-

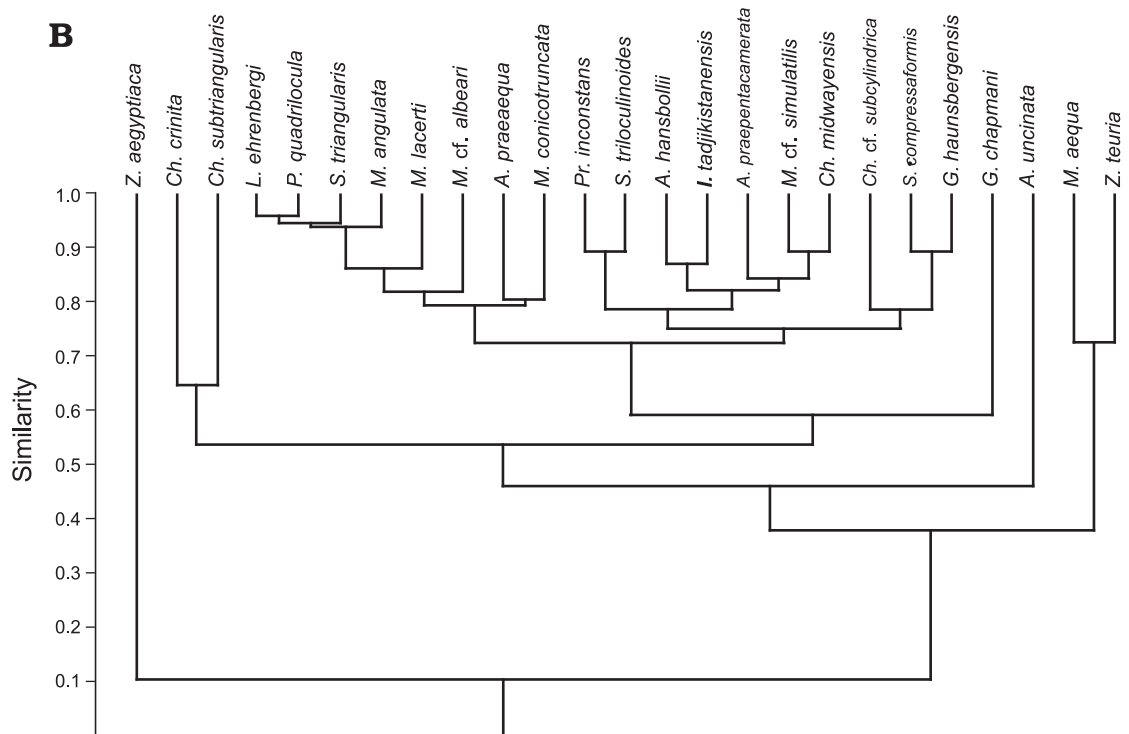
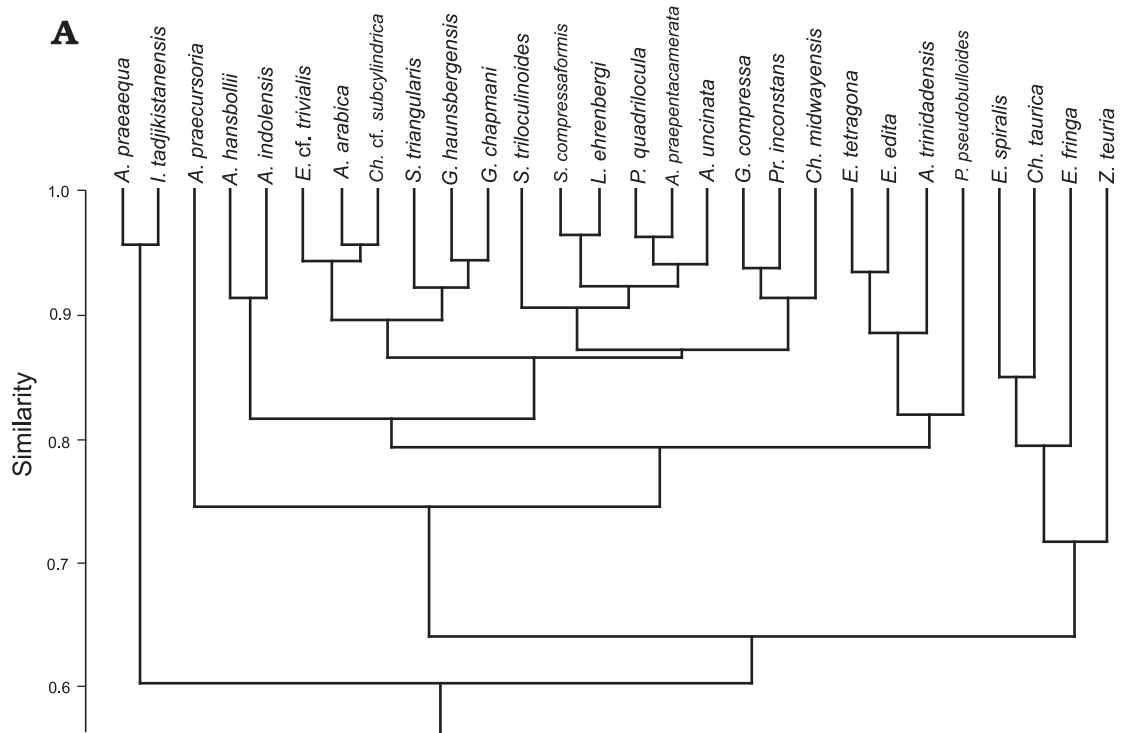
logically similar species *A. uncinata* and *M. angulata* respectively, and (iii) acarininids and morozovellids with many chambers in the last spire whorl preferred temperate latitudes.

Finally, it also is noteworthy that some species apparently changed their latitudinal preferences throughout the D–S transition. These are *S. compressaformis*, *A. hansbollii*, *A. praeaequa*, and *Ch. cf. subcylindrica*. Data suggest that they began as low latitude dwellers and ended up living at higher latitudes. Nevertheless, the relative abundances of the four species in Caravaca and Zumaia are very similar in the initial warmer period, suggesting that although they evolved in lower latitude waters, they soon adapted to cooler, higher latitudes.

Quantitative stratigraphic distributions as taxonomic criteria.

—The Fig. 3 shows the quantitative stratigraphical distribution of planktic foraminiferal species across the D–S boundary at Caravaca (data in Tables 3, 4), according to Arenillas (1996) and Arenillas and Molina (1997). These quantitative data were used to compare the patterns of temporal distribution of the species and to evaluate their differences. Applying cluster analyses based on Morisita's index measures (Fig. 9), species group into clusters that represent similar quantitative stratigraphic distributions (i.e., more or less coincidence of the maxima and minima in relative abundance). These analyses have been applied in both the *A. uncinata* (Fig. 9A) and *M. cf. albeari* zones (Fig. 9B), and the obtained clusters represent groups with similar ecological requirements and biological behaviours. If this interpretation is assumed, results indicate that the clustering involves an uncharacteristically poor result, grouping species of different latitudinal preferences almost indistinctly. Results suggest that the fluctuations in species relative abundance over time are controlled by several physical-chemical and biotic factors (in addition to the temperature) in a complex interaction.

Nevertheless, divergences in the quantitative stratigraphic distribution between two morphologically similar species could be interpreted as: (i) they have different ecological requirements and/or biological behaviours, and (ii) both could belong to two reproductively isolated species. Comparing the “splitter” taxonomy by Arenillas (1996, modified) and the “lumper” taxonomy by Olsson et al. (1999), the species pairs most conflictive by their morphological similarity to be taxonomically differentiated are: *S. compressaformis* from *S. triloculinooides*, *E. cf. trivialis* from *S. triangularis*, *E. spiralis* and *A. arabica*, *G. haunsbergensis* from *L. ehrenbergi*, *A. trinidadensis* from *Pr. inconstans*, *A. praecursoria* from *A. uncinata*, *M. conicotruncata* from *M. angulata*, *M. lacerti* from *M. aequa* and *Ch. cf. subcylindrica* from *Ch. midwayensis*. Their distant position within the cluster dendrogram suggests that the species comprising each pair are in fact different. This finding supports the hypothesis that slight morphological differences may distinguish closely related species adapted to different environments as suggested by Norris (2000) and Vargas et al. (2001). In the D–S stratigraphic interval, the comparison of other conflictive species pairs cannot be made, such as *M. cf. albeari* vs. *I. albeari*, *M. cf. albeari* vs. *M.*



Morisita's index

$$\lambda_1 = \frac{\sum_{i=1}^s (x_{ij} (x_{ij} - 1))}{\sum_{i=1}^s x_{ij} (\sum_{i=1}^s x_{ij} - 1)}$$

$$\lambda_2 = \frac{\sum_{i=1}^s (x_{ik} (x_{ik} - 1))}{\sum_{i=1}^s x_{ik} (\sum_{i=1}^s x_{ik} - 1)}$$

$$\text{Morisitaj}_k = \frac{2 \sum_{i=1}^s (x_{ij} x_{ik})}{(\lambda_1 + \lambda_2) \sum_{i=1}^s x_{ij} \sum_{i=1}^s x_{ik}}$$

Fig. 9. Cluster analyses based on Morisita's index for relative abundance data of species from Caravaca in the *Acarinina uncinata* Zone (4a) and in the *Morozovella cf. albeari* Zone (4b); λ_1 = Simpson's diversity index in sample j; λ_2 = Simpson's diversity index in sample k; x_{ij} = percentage of species i in sample j; x_{ik} = percentage of species i in sample k.

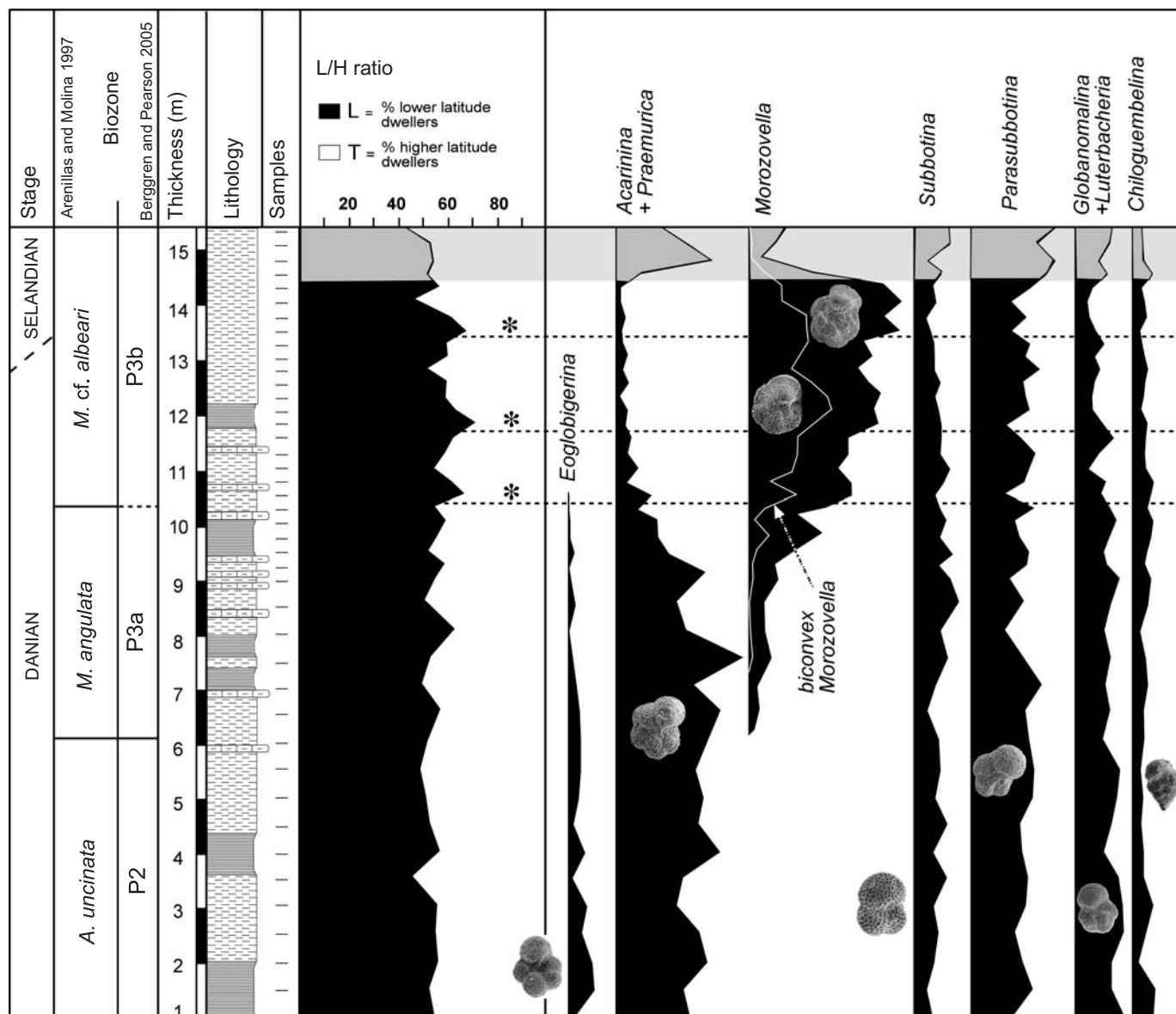


Fig. 10. Lower/higher (L/H) latitude taxa ratio and quantitative stratigraphic distribution of planktic foraminiferal genera across the Danian–Selandian transition at Caravaca. Asterisks indicate climate warming events identified here.

occlusa, *I. pusilla* vs. *I. albeari*, *L. ehrenbergi* vs. *L. troelseni*, and *L. troelseni* vs. *L. pseudomenardii*, since this comparison must be carried out in the Selandian–Thanetian (upper Paleocene) interval. As some of them are index-species and their taxonomic definition is uncertain, their diagnostic characters are also included in SOM_1.

A case-study from the Danian–Selandian transition of the Caravaca section

Taxonomical and paleoecological study allows a lower/higher (L/H) latitude taxa ratio to be proposed (Tables 3, 4).

The L/H ratio is the abundance in percentage of tropical-subtropical taxa with respect to the total, i.e., $L/H = [L/(L+H)] \times 100$, where L = relative abundance of species preferring lower latitudes, and H = relative abundance of species preferring higher (temperate-high) latitudes. Its fluctuations approximately reflect the variations of the temperature at the ocean surface, which is linked to the local climate.

Fluctuations in L/H ratio across the D–S transition at the Caravaca section are shown in Fig. 10. This figure also includes the quantitative stratigraphic distributions of the most abundant genera at Caravaca in order to compare results. The interval from meter 14.50 to 15.25 shows abundance values similar to those of the first 10 meters of the Caravaca section, suggesting reworked levels.

According to this L/H curve, three stratigraphic levels

stand out above the rest: meters 10.5, 12.0, and 13.5. In the three cases, the L/H ratio reaches maximum values (above 60%), suggesting climate warming events. Other relevant horizons are recorded at meters 3.5 and 8.0 (in the middle part of *M. angulata* Zone), the first characterized by a slight decrease of the L/H ratio and the latter by a very slight increase. Meter 3.5 (in the upper part of the *A. uncinata* Zone) is also characterized by a decrease in *Acarinina* (from 34% to 24%), suggesting climate-cooling event. Meter 10.5 (in the basal part of the *M. cf. albeari* Zone) is also characterized by a relevant increase of *Morozovella* (from 19% to 41%). A similar *Morozovella* acme-horizon was also identified at Tethyan sections such as Sidi Nasseur, ElKef, Elles, and Aïn Settara in Tunisia, Gebel Aweina in Egypt, and Ben Gurion in Israel (Arenillas 1996, 2008; Arenillas and Molina 1997). According to Arenillas et al. (2008), this horizon could correspond to a climate-warming event.

Meter 12.0 (in the lower part of the *M. cf. albeari* Zone) is characterized by another smaller increase in *Morozovella* (from 40% to 53%), mainly by biconvex morozovellids such as *M. cf. albeari*. Finally, meter 13.5 (in the lower part of the *M. cf. albeari* Zone) is also characterized by a slight increase in *Morozovella* (from 47% to 60%). As above, both horizons could correspond to climate-warming events. The latter could be related to the D–S boundary of the Zumaia stratotype. Arenillas et al. (2008) suggested that the D–S boundary at Zumaia corresponds to a low intensity hyperthermal event, since it coincides with the base of a red marly interval and a negative carbon isotopic excursion (CIE-DS2) similar to the P/E boundary also recorded at Zumaia (Schmitz et al. 1997, 1998; Arenillas and Molina 2000). However, unlike Caravaca, the *Morozovella* abundance decreases at Zumaia (Arenillas et al. 2008), suggesting the action of other paleoenvironmental factors in addition to surface oceanic temperature on the local planktic foraminiferal assemblages, such as fluctuations in sea-level, trophic conditions and/or salinity. Another hypothesis is that the D–S boundary at Caravaca is below or above meter 13.5, coinciding with the decline in the L/H ratio of meters 12.75 or 14.0.

Conclusions

In addition to classical morphological and microtextural diagnostic criteria, divergences in patterns of spatio-temporal distribution (i.e., in latitudinal preferences and quantitative stratigraphic distributions) have been applied as criteria for the taxonomical separation of the Danian–Selandian transition planktic foraminiferal species. These patterns have been inferred by comparing the average relative abundance of the species between Caravaca and Zumaia, and by using the quantitative stratigraphic distribution of the species at Caravaca. Morphologically convergent species pairs such as *Acarinina trinidadensis* and *Praemurica inconstans*, *Acarinina praecursoria* and *Acarinina uncinata*, *Morozovella conicontruncata*

and *Morozovella angulata*, or *Morozovella* cf. *albeari* and *Igorina albeari*, are now well taxonomically differentiated. The analysis allowed to recognize 41 planktic foraminiferal species from the D–S transitional interval. This taxonomic revision also suggest that the lower boundary of the Subzone P3b of Berggren and Pearson (2005), marked by the FOD of *I. albeari*, is approximately equivalent to the lower boundary of the *M. cf. albeari* Zone of Arenillas and Molina (1997) and Arenillas et al. (2008), marked by the FOD of *M. cf. albeari* (= *M. crosswicksensis* sensu Blow 1979 and Arenillas 1996), since the former grouped both morphospecies in the taxonomic concept of *I. albeari*.

Paleoecological analysis indicates that the species preferring lower latitudes (or tropical-subtropical waters) were *Eoglobigerina* cf. *trivialis* (= *E. trivialis* sensu Blow 1979), *E. edita*, *Globanomalina chapmani*, *Luterbacheria ehrenbergi*, *Praemurica inconstans*, *Acarinina trinidadensis*, *A. uncinata*, *A. praepentacamerata*, *A. indolensis*, *A. arabica*, *A. praepentacamerata* (= *A. praeangulata*), *Igorina tadjikistanensis*, *Morozovella angulata*, *M. simulatilis*, *M. cf. albeari*, *M. lacerti*, *M. aequa*, *Chiloguembelina taurica*, *Ch. midwayensis*, *Ch. cf. subcylindrica*, *Zeauvigerina teuria*, *Z. aegyptiaca*, *Gc. daubjergensis*, and *Globoconusa conusa*. Species preferring higher latitudes (temperate), therefore being more cosmopolitan, were *Eoglobigerina fringa*, *E. tetragona*, *E. spiralis*, *Subbotina trilocolinoides*, *S. triangularis*, *Globanomalina compressa*, *G. haunsbergensis*, *G. chapmani*, *Parasubbotina pseudobulloides*, *P. quadrilocula*, *Acarinina praecursoria*, *Morozovella conicontruncata*, and *Chiloguembelina crinita*. The analyzed data also suggest that *S. compressaformis* (= *S. eocaenica* sensu Blow 1979), *Acarinina hansbollii*, *A. praeaquea*, and *Chiloguembelina* cf. *subcylindrica* began as species preferring tropical-subtropical waters and ended up being more cosmopolitan.

Taxonomical and paleoecological study allows a lower/higher (L/H) latitude taxa ratio to be proposed. At Caravaca, three maxima (meters 10.5, 12.0, and 13.5) in the L/H ratio can be recognized, suggesting three climate warming events during the D–S transitional interval. The maximum warming event in meter 13.5 might be related to the D–S boundary because it has been found in the middle part of the *M. cf. albeari* Zone in the same interval as the D–S boundary in Zumaia.

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