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PHENOTYPIC PLASTICITY, SPECIATION, AND PHYLOGENY IN EARLY DANIAN PLANKTIC FORAMINIFERA

EDUARDO A. M. KOUTSOUKOS

Geologie-Paläontologie Institut für Geowissenschaften, Universität Heidelberg, Im Neuenheimer Feld 234, DE-69120 Heidelberg, Germany.
E-mail: ekoutsoukos@gmail.com

ABSTRACT

A piston core drilled at a water depth of 2809 m off Rio de Janeiro, southeastern Brazil, recovered a 1.83-m thick section of unconsolidated muddy sediments, representing a complete stratigraphic succession across the Cretaceous–Paleogene (K/Pg) boundary. The sediments yielded abundant, strikingly pristine tests of planktic and benthic foraminifera, unaffected by diagenetic alteration or recrystallization.

The sedimentary record ranges from the uppermost Maastrichtian (*P. hantkeninoides* Zone) to the lower Danian (zones P0–P1c), spanning a time interval of about 3–4 Myr through the K/Pg transition. A detailed taxonomic appraisal of the recovered planktic foraminiferal assemblages is presented, together with an evaluation of lineage relationships, phylogenetic trends, and the sequence of evolutionary events that took place among the Globigerinina at the beginning of the Cenozoic.

The numerous recent taxonomic studies of Danian planktic foraminifera notwithstanding, the significance of phenotypic varieties has never been assessed in a paleoecological context. Whereas the cancellate-walled, low trochospiral, large-sized *Praemurica* (Truncorotaloididae) and *Parasubbotina* and *Subbotina* (Globigerinidae) lineages evidently underwent rapid speciation over a relatively narrow phenotypic range, the small-sized *Praemurica,* the distinctly elevated trochoid *Eoglobigerina* (Globigerinidae), the *Parvulorugoglobigerina,* and the coiled to elongate morphotypes of the *Guembelitria* and *Woodringina* (all members of the family Guembelitriidae) and *Chiloguembelina* (Chiloguembelinidae) lineages show phenotypic plasticity over a much broader range. This dichotomy correlates with inferred differences in life-history parameters among these planktic taxa, including pelagic-dwelling preferences, related to reproductive and feeding strategies and to water-mass trophic levels.

Two new early Danian planktic foraminiferal species are established herein: *Praemurica nikolasi* n. sp., the earliest recorded Truncorotaloididae and cancellate species, likely evolved directly from *Hedbergella monmouthensis* near the base of Zone P0 and probably giving rise to all subsequent cancellate lineages of the early Danian; and *Globoconusa victori* n. sp., evolved from *Globoconusa daubjergensis* within Zone P1c.

INTRODUCTION

Stage boundaries are characterized by significant geological and paleobiological events that leave distinct signatures in the stratigraphic record. They incorporate key criteria for attaining refined stratigraphic correlations and for understanding how ecosystems have reacted to and recovered from catastrophic events. Accordingly, the study of boundary sections reveals the sequential patterns of extinction, survival, and speciation among various fossil groups, thus enhancing understanding of the complexity of evolutionary patterns and processes. Hence, their importance in the geosciences can scarcely be understated.

The Late Cretaceous witnessed one of the highest recorded long-term sea levels in geological history (Miller et al., 2005; Müller et al., 2008), and as a consequence, Cretaceous-Paleogene (K/Pg) boundary sections occur worldwide in oceanic and marginal basins, commonly with a stratigraphically complete pelagic record. Nonetheless, there is a dearth of sections in which exceptional preservational conditions have resulted in fossils unaffected by compaction, diagenesis, and recrystallization.

Throughout their evolutionary history the Globigerinina have shown a remarkably high degree of phenotypic plasticity with commonly recurring general morphologies appearing in response to global variations in oceanographic conditions over time. Though widely documented, these morphological changes and their forcing mechanisms are as yet poorly understood. This probably points not to a single cause, but rather to a combination of minor biotic and abiotic variables which are difficult to estimate, model, and predict. However, taken as a whole, general evolutionary patterns and related environmental conditions may be inferred for the Globigerinina.

Early Danian planktic foraminifera characteristically show a high degree of speciation and phenotypic plasticity, which are evolutionary strategic modes enabling a particular taxon to populate a broad ecological setting, such as the widespread neritic and oceanic pelagic niches rendered vacant as a consequence of the K/Pg mass extinction. Notwithstanding numerous recent taxonomic studies, the significance of these phenotypic varieties has not been assessed in a paleoecological context.

A piston core drilled at a water depth of 2809 m in the Campos Basin, offshore of Rio de Janeiro, southeastern Brazil (Fig. 1), recovered a 1.83 m-thick interval of unconsolidated muddy sediments, representing a complete stratigraphic succession across the Cretaceous–Paleogene (K/Pg) boundary. The sediments yielded abundant, strikingly pristine tests of planktic and benthic foraminifera, unaffected by diagenetic alteration or recrystallization. The profuse and superbly preserved foraminiferal assemblages present a unique window to the past. They provide an outstanding basis for a detailed taxonomic appraisal, together with an evaluation of lineage relationships, phylogenetic trends, and the sequence of evolutionary events manifested among the Globigerinina at the beginning of the Cenozoic.

GEOLOGICAL SETTING

The Campos Basin is located off southern Brazil between latitudes 21–23°S. It is a typical passive Atlantic-type

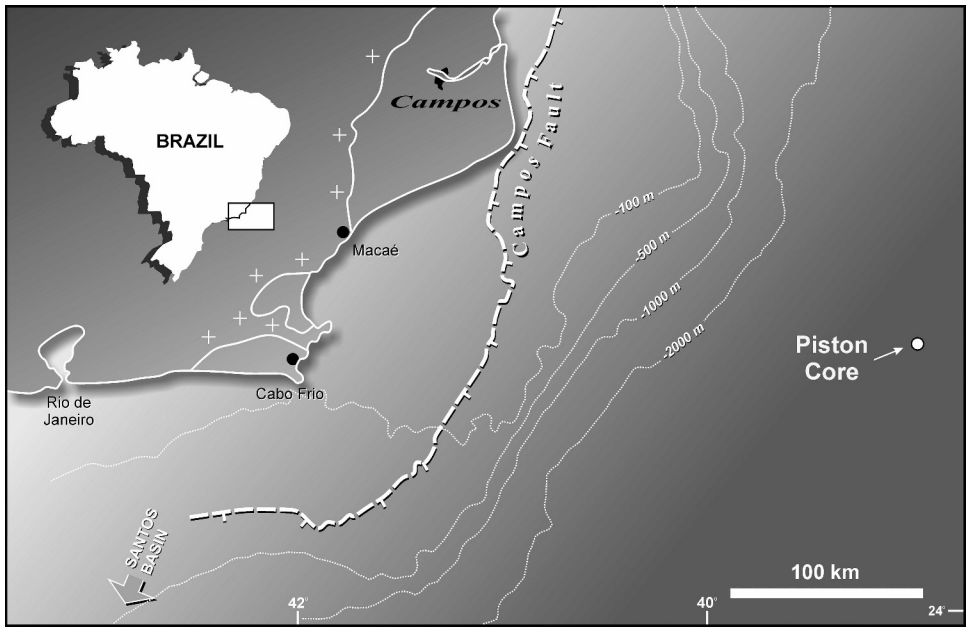


FIGURE 1. Map showing location of the piston core (latitude: 22°49′12″S; longitude: 39° 4′33″W) at a water depth of 2809 m in the Campos Basin, offshore of Rio de Janeiro, southeastern Brazil.

marginal basin formed during the rift and drift/spreading phases of the opening of the northern South Atlantic during the Late Jurassic–Early Cretaceous and Cenozoic. Its lithostratigraphic succession closely reflects the tectono-sedimentary evolution, which has been described elsewhere (e.g., Winter et al., 2007; Mohriak et al., 2008).

The K/Pg succession comprises shales and marlstones of the Tamoios Member of the Ubatuba Formation (Winter et al., 2007), which are represented in the presently studied piston-core interval, and subordinately by turbiditic sandstones of the Carapebus Formation, all of which mostly accumulated in bathyal settings along the continental margin.

MATERIAL AND METHODS: THE PISTON CORE

The piston core was drilled on the NE–SW flank of a huge ''piercement-type'' salt dome that uplifted the overlying K/Pg boundary section, which locally outcrops along submarine escarpments on the sea floor of the Campos Basin (Fig. 1). The uplift process effectively sequestered the sediments from the combined effects of lithostatic pressure, compaction, and diagenesis so that the sediments retained their unconsolidated state with their hosted microfossils superbly preserved.

The uppermost Maastrichtian is represented by a carbonate-rich, pale cream marl, ~20-cm thick at the core base. The K/Pg boundary is marked by a yellowish cream boundary layer, about 1–2-cm thick, positioned at a steep (60°) angle across the core (Fig. 2). The inclined bedding plane is likely due to post-depositional deformation caused by the dome uplift. With the exception of the tilted beds, the K/Pg boundary interval is virtually undisturbed and biostratigraphically complete, with no evidence of an unconformity (see below). The overlying Danian interval is represented by generally homogeneous, thin-bedded grayish-brown muds ~160-cm thick. The high biogenic content of all the samples, consisting primarily of planktic foraminifera, indicates that they represent predominantly a deep-sea pelagic or hemipelagic ooze. Lighter calcareous muds occur sparsely in the core, and appear to be burrow-mottled. They are particularly localized in the uppermost layers of the Maastrichtian marly ooze and in lowermost Zone P0, just at the K/Pg boundary, and at around 140–145 cm, in lower Zone Pα (Fig. 2). Immediately after drilling, parts of the core (the top 3 cm and the interval between 90–120 cm) were extracted for detection of natural hydrocarbon-seepage anomalies in the sea floor, and are thus unavailable. Sample intervals in the piston core represent depths (in cm) below the seafloor.

A quarter slice of the core, corresponding to the thickest-recovered Danian interval (~160 cm), was thoroughly sampled and carefully measured at 1–3-cm intervals. Samples were washed over a 63-μm sieve. Minimum counts of 300 planktic specimens were taken from each individual sample, and relative abundances were estimated for all the identified planktic foraminiferal species relative to the total planktic assemblage per sample.

A comprehensive SEM study of several hundreds of selected specimens (see below) enabled a detailed taxonomic reappraisal of the planktic foraminifera, intra- and interspecific variations, and phylogenetic affinities.

MICROSPHERULES FROM THE K/PG BOUNDARY LAYER

Abundant micotektite-like glossy black microspherules, ~300–800 μm in diameter, were recovered from the K/Pg bounday layer, which is ~1–2-cm thick (interval 162–164 cm; Fig. 2). This interval is hereafter called the impact layer. Electron microprobe (SEM/EDS) analysis of the

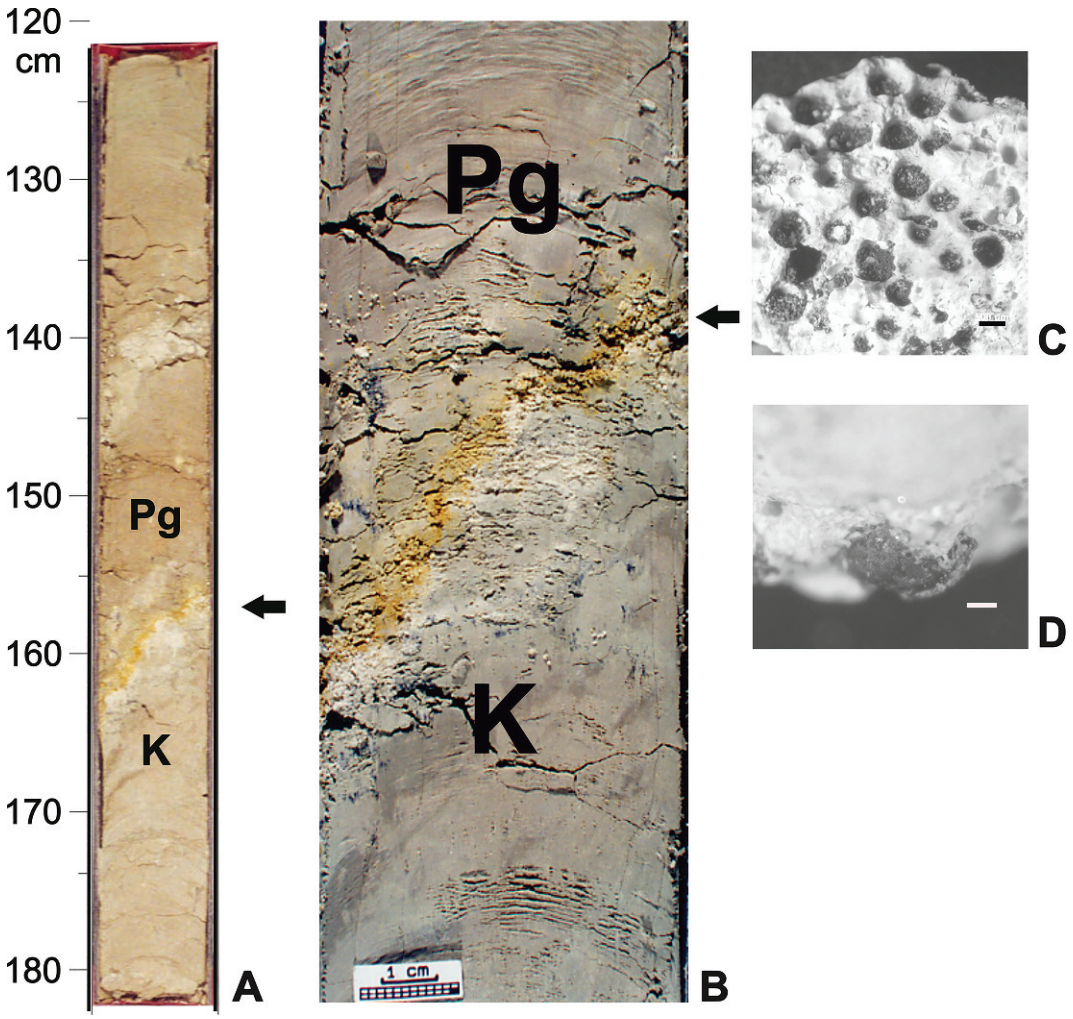


FIGURE 2. **A** Detail of the lower part (interval 122–183 cm) of the piston core, showing changes in lithology across the diagonal K/Pg boundary (K: carbonate-rich pale cream marls; K/Pg boundary layer: yellowish-cream marls; Pg: grayish-brown muds). **B** Close-up of the K/Pg boundary layer. **C, D** Optical photomicrographs of the impact layer (interval 162–164 cm) showing details of the embedded microtektite-like microspherules; C scale bar = 500 μm, D scale bar = 200 μm.

microsperules reveals that they are silica-rich (Fig. 3), roughly andesitic in composition, and show oxide compositional variations similar to K/Pg boundary microspherules in Beloc, Haiti, and Mimbral, Mexico (Sigurdsson et al., 1991; Glass et al., 1993; Bohor & Betterton, 1995) with residual tektite-like glass cores. They are also similar to known Cenozoic microtektites and impact glasses (Koeberl, 1986). The very high SiO_2 (66–69%) and Al_2O_3 (17–20%) content, moderately high Fe_2O_3 (4–9%), an unusually high MgO/CaO ratio (>3), and an average Na_2K/K_2O ratio (>1) characterize these microspherules. They are interpreted as fallout from the Chicxulub impact structure on the Yucatan Peninsula.

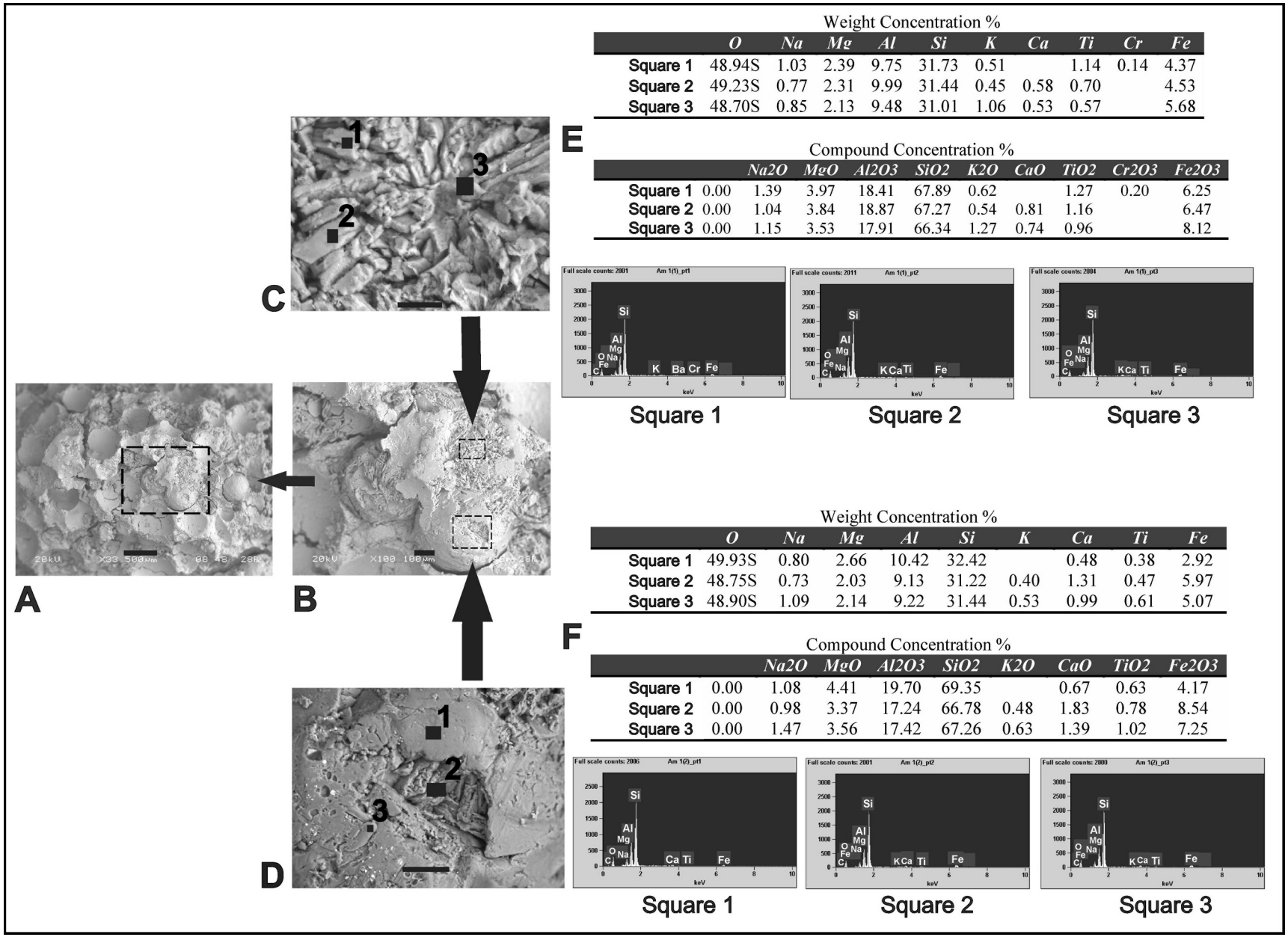
FORAMINIFERAL RECORD

BIOSTRATIGRAPHY

The continuous sedimentary record ranges from the uppermost Maastrichtian (*Plummerita hantkeninoides* Zone; Appendix 1) to the lower Danian (zones P0–P1c), spanning a time interval of about 3–4 Myr across the K/Pg transition. The rich and highly diverse foraminiferal assemblage yielded nearly all planktic species known from these zones plus two new ones, thus facilitating a detailed reconstruction of the sequence of ecological-evolutionary events that occurred over that critical time interval.

The distribution and relative abundance of uppermost Maastrichtian planktic foraminiferal species across the K/Pg transition in the piston core (interval 122–166 cm) are shown in Appendix 2. Apart from a few well-known Cretaceous survivor species (see below), very rare scattered occurrences of probably reworked Cretaceous planktic foraminifera were recorded in the lowermost Danian interval, which demonstrates the severity of the mass extinction event for the Gobigerinina.

The stratigraphic distribution and relative abundance estimates of the newly evolved lower Danian planktic foraminiferal species are shown in Figures 4 (families Guembelitriidae and Chiloguembelinidae) and 5 (families Globigerinidae and Truncorotaloididae).



Weight Concentration %

	O	Na	Mg	Al	Si	K	Ca	Ti	Cr	Fe
Square 1	48.94S	1.03	2.39	9.75	31.73	0.51		1.14	0.14	4.37
Square 2	49.23S	0.77	2.31	9.99	31.44	0.45	0.58	0.70		4.53
Square 3	48.70S	0.85	2.13	9.48	31.01	1.06	0.53	0.57		5.68

Compound Concentration %

	Na2O	MgO	Al2O3	SiO2	K2O	CaO	TiO2	Cr2O3	Fe2O3
Square 1	0.00	1.39	3.97	18.41	67.89	0.62		1.27	0.20	6.25
Square 2	0.00	1.04	3.84	18.87	67.27	0.54	0.81	1.16		6.47
Square 3	0.00	1.15	3.53	17.91	66.34	1.27	0.74	0.96		8.12

Weight Concentration %

	O	Na	Mg	Al	Si	K	Ca	Ti	Fe
Square 1	49.93S	0.80	2.66	10.42	32.42		0.48	0.38	2.92
Square 2	48.75S	0.73	2.03	9.13	31.22	0.40	1.31	0.47	5.97
Square 3	48.90S	1.09	2.14	9.22	31.44	0.53	0.99	0.61	5.07

Compound Concentration %

	Na2O	MgO	Al2O3	SiO2	K2O	CaO	TiO2	Fe2O3
Square 1	0.00	1.08	4.41	19.70	69.35		0.67	0.63	4.17
Square 2	0.00	0.98	3.37	17.24	66.78	0.48	1.83	0.78	8.54
Square 3	0.00	1.47	3.56	17.42	67.26	0.63	1.39	1.02	7.25

FIGURE 3. **A–D** SEM micrographs of microtektite-like microspherules embedded at the K/Pg boundary impact layer; A scale bar = 500 μm, B scale bar = 100 μm, C scale bar = 25 μm, D scale bar = 50 μm; solid black boxes in C and D show the spots selected for EDS analysis. **E, F** SEM/EDS elemental analysis of microtektite-like microspherules recovered from the piston core; E, spot EDS results for squares 1, 2, and 3 located in C; F, spot EDS results for squares 1, 2, and 3 located in D. Results for each element are shown in weight-concentration values, in compound concentrations, and in graphical representations of the EDS elemental spectrum.

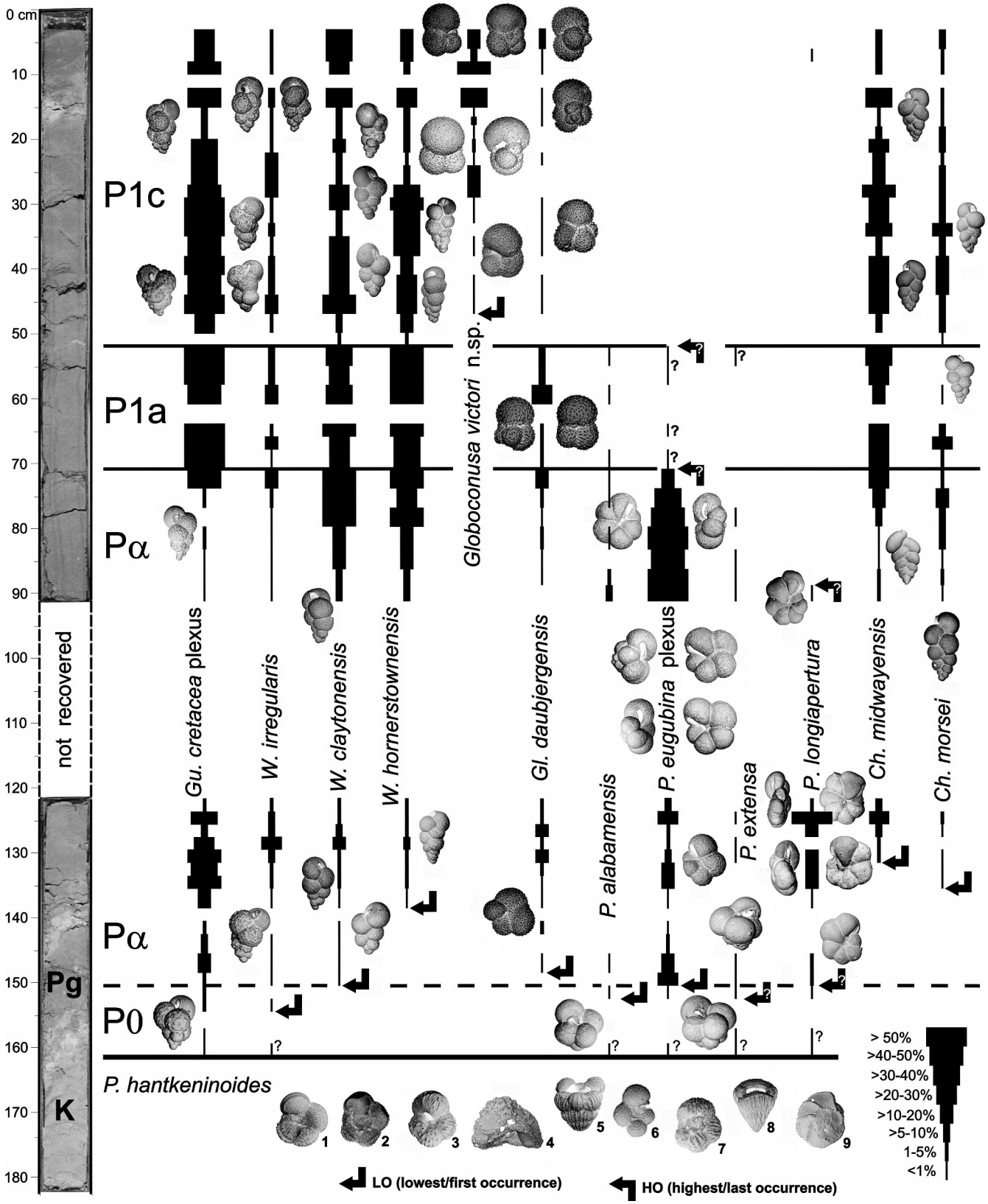


FIGURE 4. Biostratigraphic distribution and relative abundance estimates of key planktic foraminiferal species of the families Guembelitriidae (*Globoconusa* = *Gl.*, *Guembelitria* = *Gu.*, *Parvularugoglobigerina* = *P.*, and *Woodringina* = *W.*) and Chiloguembelinidae (*Chiloguembelina* = *Ch.*) in the lower Danian of the piston core. Excepting *Gu. cretacea,* which is the best-known and longest-lasting Cretaceous survivor, all others are newly evolved Danian species. Numbered specimens are illustrated from the uppermost Maastrichtian *Plummerita hantkeninoides* Zone: 1, *Abathomphalus mayaroensis* (180.5–183 cm); 2, *Ab. mayaroensis* (169–171 cm); 3, *Ab. intermedius* (180.5–183 cm); 4, *Contusotruncana contusa* (169–171 cm); 5, *Pseudotextularia intermedia* (180.5–183 cm); 6, *Globigerinelloides subcarinatus* (180.5–183 cm); 7, *Rugoglobigerina rugosa* (180.5–183 cm); 8, *Pseudotextularia elegans* (180.5–183 cm); 9, *Globotruncanita stuartiformis* (180.5–183 cm).

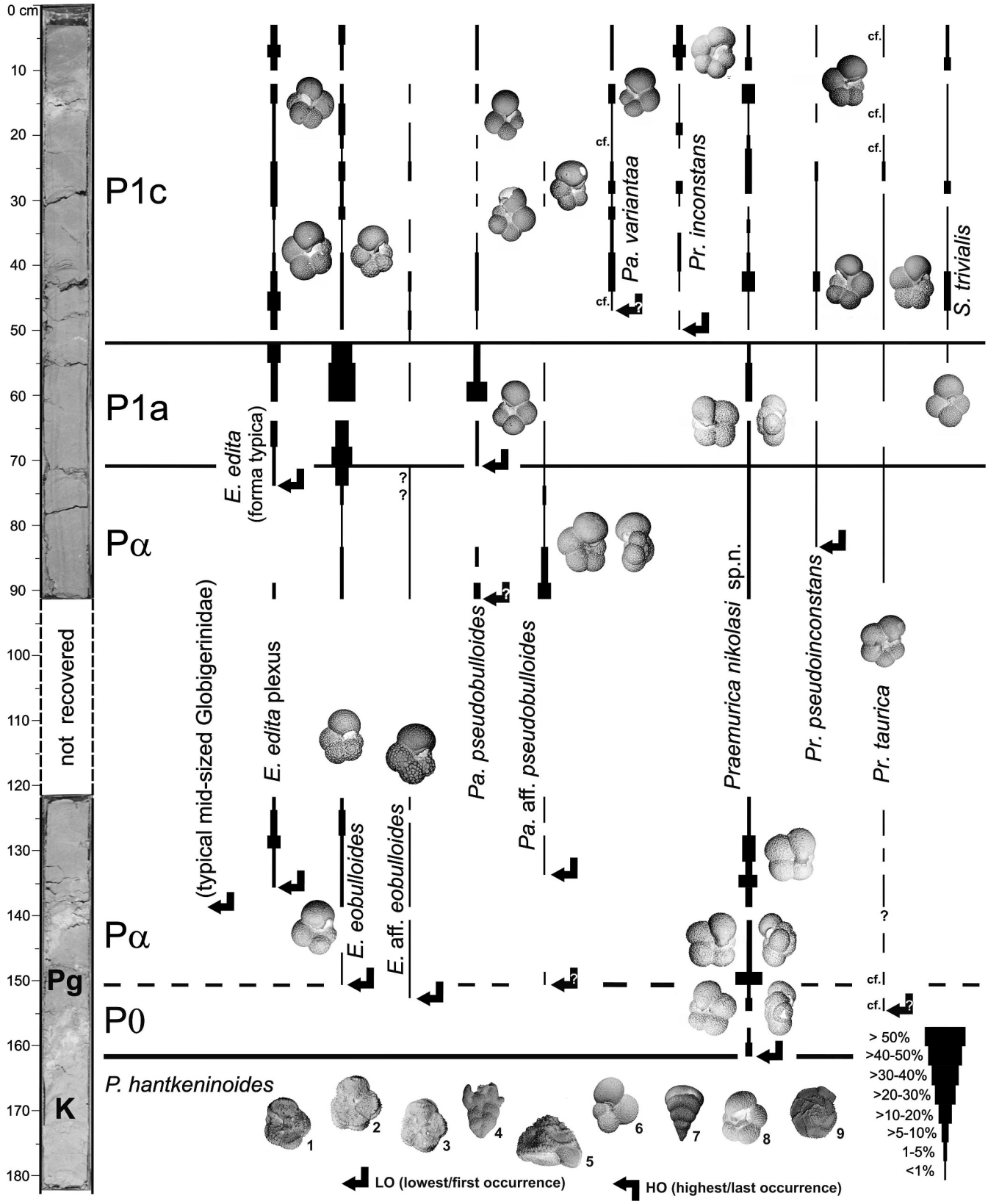


FIGURE 5. Biostratigraphic distribution and relative abundance estimates of newly evolved key planktic foraminiferal species of the families Globigerinidae (*Eoglobigerina* = *E.*, *Parasubbotina* = *Pa.*, and *Subbotina* = *S.*) and Truncorotaloididae (*Praemurica* = *Pr.*) in the lower Danian of the piston core. Numbered specimens are illustrated from the uppermost Maastrichtian *Plummerita hantkeninoides* Zone: 1, *Abathomphalus mayaroensis* (169–171 cm); 2, *Ab. mayaroensis* (180.5–183 cm); 3, *Ab. mayaroensis* (180.5–183 cm); 4, *Pseudoguembelina hariaensis* (180.5–183 cm); 5, *Contusotruncana contusa* (169–171 cm); 6, *Globotruncanella petaloidea* (180.5–183 cm); 7, *Pseudotextularia nuttali* (169–171 cm); 8, *Rugoglobigerina rugosa* (180.5–183 cm); 9, *Globotruncanita stuartiformis* (169–171 cm).

Paleoenvironmental Setting

The studied site is located in the southernmost part of the northern South Atlantic, which was likely under the influence of a tropical to subtropical oceanic water-mass during the end Cretaceous and early Paleogene, at approximately 30°S paleolatitude (Hay et al., 1999). A highly diverse, uppermost Maastrichtian planktic foraminiferal assemblage (Appendix 1) is known to characterize the tropical Tethyan Realm, which extended southwards between 0–30°S paleolatitude (Sliter, 1972, 1977).

Benthic foraminifera recovered from all samples indicate upper lower-bathyal to lower middle-bathyal depths (Koutsoukos, 2010), with deep-water calcareous taxa such as *Allomorphina conica* Cushman & Todd, *A. trochoides* (Reuss), *Aragonia velascoensis* (Cushman), *Bolivinoides delicatulus* Cushman, *B. decoratus* (Jones), *Bulimina midwayensis* Cushman & Parker, *Nuttallides truempyi* (Nuttall), *Nuttallinella florealis* (White), *Osangularia velascoensis* (Cushman), *Pyramidina szajnochae* (Grzybowski), *Stensioina beccariiformis* (White), and *Tappanina selmensis* (Cushman). As at other deeper-water K/Pg boundary sites (deposited in middle-bathyal and deeper settings), such as at El Mulato, NE Mexico (Alegret et al., 2002), Agost, SE Spain (Alegret et al., 2003), Blake Nose Plateau, western North Atlantic (Alegret & Thomas, 2004), and Walvis Ridge, eastern South Atlantic (Alegret & Thomas, 2007), the benthic foraminiferal assemblages recorded across the boundary transition do not reflect any marked extinction and environmental change. This contrasts with shallower K/Pg boundary sites (deposited in deep neritic to upper/middle-bathyal settings) that have recorded a distinct ecological-driven shift in the benthic foraminiferal community structure, such as at Caravaca, SE Spain (middle-bathyal environment; Coccioni & Galeotti, 1994), coupled with a significant sea-level fall across the K/Pg transition, such as at El Kef, Tunisia (Speijer & van der Zwaan, 1994, 1996), and at the Poty section, NE Brazil (Koutsoukos, 1996b, 2005, 2006). The paleobathymetric interpretation thus clearly supports a paleo-location in a distant offshore oceanic setting, away from the high-energy influence of coastal and shelf depositional processes. The cored stratigraphic interval is most likely representative of continuous deep-oceanic pelagic sedimentation, of great sensitivity to global climatically induced oceanographic changes. Hence the observed ecological-evolutionary variations and the sequence of bioevents likely represent a true global record.

TAXONOMIC NOTES AND PHYLOGENY OF THE EARLY DANIAN GLOBIGERININA

The general taxonomic classification of the planktic foraminifera identified in this study follows the work of Olsson et al. (1999) with a few exceptions. Some species previously considered as having equivocal taxonomic status are here considered valid based on detailed observations of the pristinely preserved representatives. In addition, two new planktic species recovered in the core are described below. The noted stratigraphic ranges refer to the species record in the piston core, not the total global range, which may differ mostly due to partial incompleteness of the local biostratigraphic record (lack of Zone P1b), ecological exclusion, and/or rarity of occurrence. The concept of plexus is here adopted to represent a species group characterized by large phenotypic variability, which resulted in increased taxonomic complexity and the attribution of diverse taxonomic names to morphological variants within the plexus.

A few, very rarely occurring species (members of the Hedbergellidae and *Subbotina triloculinoides*) were not illustrated, and their distribution is not shown in Figure 4. For these species, synonymies are kept to a minimum, and their sampling distribution within the core is reported along with their stratigraphic ranges.

All illustrated SEM micrographs are of planktic foraminifera recovered from the piston core. All type and illustrated specimens, together with additional unillustrated topotypes of the new species, are reposited at the National Museum of Natural History (NMNH), Smithsonian Institution, Washington, D.C., under the collection numbers USNM 545300–545329 and USNM 597300–597437, respectively. The assigned museum numbers are given after each species in Figs. 6–15.

Alphabetical list of standard abbreviations of generic names for the Globigerinina discussed in this paper: *Abathomphalus* = *Ab.*, *Archaeoglobigerina* = *Ar.*, *Chiloguembelina* = *Ch.*, *Contusotruncana* = *Cont.*, *Eoglobigerina* = *E.*, *Globigerina* = *G'ina*, *Globigerinelloides* = *Gllo.*, *Globanomalina* = *G.*, *Globoconusa* = *Gl.*, *Globotruncana* = *Gtru.*, *Globotruncanella* = *Gtre.*, *Globotruncanita* = *Gtri.*, *Guembelitria* = *Gu.*, *Hedbergella* = *Hd.*, *Heterohelix* = *Hx.*, *Laeviheterohelix* = *L.*, *Parasubbotina* = *Pa.*, *Parvularugoglobigerina* = *P.*, *Planoglobulina* = *Plg.*, *Plummerita* = *Pl.*, *Praemurica* = *Pr.*, *Pseudoguembelina* = *Psgu.*, *Pseudotextularia* = *Pstx.*, *Rugoglobigerina* = *Rugl.*, *Subbotina* = *S.*, *Turborotalita* = *T.*, *Woodringina* = *W.*, *Zeauvigerina* = *Z.*

Supergroup RHIZARIA Cavalier-Smith, 2002
Class FORAMINIFERA d'Orbigny, 1826
Order GLOBIGERININA Delage & Hérouard, 1896
Family GUEMBELITRIIDAE Montanaro Gallitelli, 1957
Genus *Guembelitria* Cushman, 1933
Type species: *Guembelitria cretacea* Cushman, 1933.

Guembelitria cretacea Cushman, 1933, plexus
Figs. 6.1–6.6

Guembelitria cretacea Cushman, 1933, p. 37, pl. 4, figs. 12a, b; Olsson et al., 1999, p. 79, 80, pl. 13, fig. 3 (reillustrated holotype), pl. 63, figs. 1–11.

Remarks. Specimens assigned to *Gu. cretacea* are consistently triserial with a large arched aperture, slightly pinched/folded inward at one side, situated at the base of the last-formed chamber symmetrically over the first two chambers of the last whorl. The height/diameter ratio of the tests is highly variable, from trochoid to elongate morphotypes. The various morphotypes of *Gu. cretacea* intergrade and fall within the range of morphological/ecophenotypic variability of the plexus, are coeval and/or reappear stratigraphically at different levels, and thus have not been accorded discrete taxonomic status herein. Test surface microperforate, covered extensively with perforation cones.

Stratigraphic range. Maastrichtian–Zone P1c (lower Danian; Fig. 4).

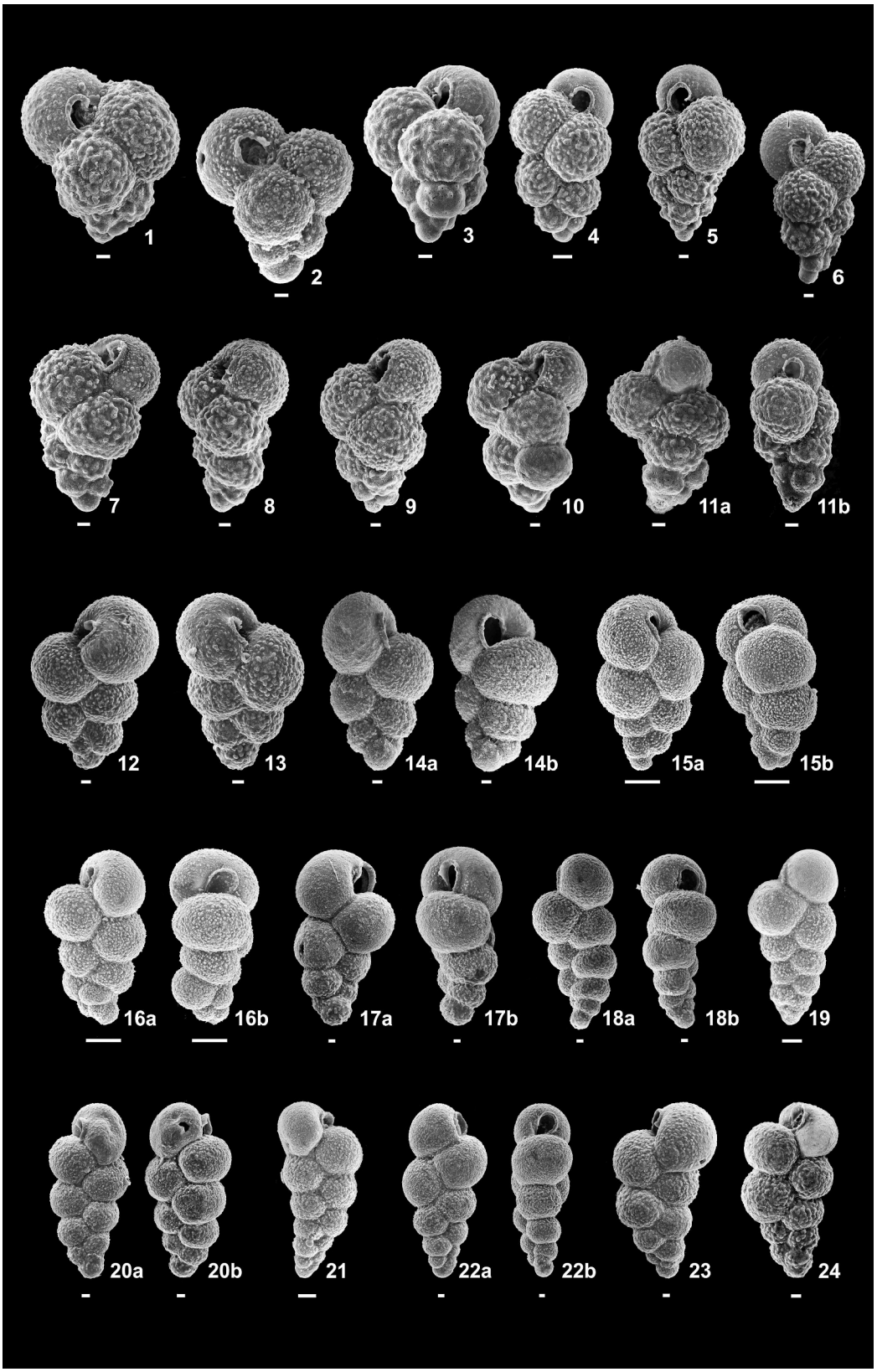


FIGURE 6. SEM micrographs of species of the family Guembelitriidae recovered from the piston core; scale bars = 10 μm unless stated otherwise. **1–6** *Guembelitria cretacea* plexus: 1 (USNM 597300), 3 (USNM 597302), 5 (USNM 597304), 58–61 cm (Zone P1a); 2 (USNM 597301), 6 (USNM 597305), 122–124 cm (lower Zone Pα); 4 (USNM 597303; scale bar = 20 μm), 24–27 cm (Zone P1c). **7–11** *Woodringina irregularis*: 7 (USNM 597306), 8 (USNM 597307), 9 (USNM 597308), 10 (USNM 597309), 58–61 cm (Zone P1a); 11 (USNM 597310), 132–134 cm (lower Zone Pα). **12–15** *Woodringina claytonensis*: 12 (USNM 597311), 13 (USNM 597312), 14 (USNM 597313), 58–61 cm (Zone P1a); 15 (USNM 597314; scale bar =

Genus *Woodringina* Loeblich & Tappan, 1957
Type species: *Woodringina claytonensis* Loeblich & Tappan, 1957

Woodringina irregularis (Morozova, 1961), emended
Figs. 6.7–6.11

Guembelitria irregularis Morozova, 1961, p. 17, pl. 1, fig. 9; Olsson et al., 1999, pl. 8, figs. 1–3 (reillustrated holotype).
Guembelitria cretacea ex interc. *Woodringina claytonensis* Loeblich & Tappan. Liu & Olsson, 1992, p. 338, pl. 1, fig. 3.
Guembelitria cretacea Cushman. Olsson et al., 1999, pl. 63, fig. 12.

Emended description. The species has a triserial test followed by a final biserial stage, with the aperture positioned over the penultimate chamber. Test small; the axis of coiling is commonly twisted, which gives the impression in some morphotypes that the specimen is set to uncoil. The maximum height/diameter ratio is always close or equal to 2. Test wall microperforate, covered by small perforation cones.

Phylogenetic relationships. Intermediate specimens are associated with *Woodringina claytonensis*, its derivative species. *Woodringina irregularis* was considered by Olsson et al. (1999, p. 79) as "indistinguishable" from *Guembelitria cretacea* and thus regarded as a junior synonym of that species. However, the holotype clearly shows an asymmetrical aperture positioned over the penultimate chamber and a hint of biseriality in the last two formed chambers. These features have never been seen in any Cretaceous specimens of *Gu. cretacea* or, for that matter, any species in the genus *Guembelitria.* It is obviously a novel phenotypic trait (uncoiling trend) that evolved during the earliest Danian, thus providing further support to the taxonomic status of the species and of its generic placement in *Woodringina.* Specimens assigned to *W. irregularis* have their first occurrence within Zone P0. The species evolved from *Gu. cretacea* through rudimentary uncoiling of the triserial arrangement, a phenotypic evolutionary trend that continues to develop progressively into the various *Woodringina* and then *Chiloguembelina* species.

Stratigraphic range. Upper Zone P0–Zone P1c (lower Danian; Fig. 4).

Woodringina claytonensis Loeblich & Tappan, 1957
Figs. 6.12–6.15

Woodringina claytonensis Loeblich & Tappan, 1957, p. 39, figs. 1a–d; Olsson et al., 1999, p. 86, 87, pl. 13, figs. 6–8, pl. 68, figs. 2–4.

Remarks. Woodringina claytonensis has a small and relatively short, tapered test that increases rapidly in size from its short, initial triserial stage to the latter 3–4 biserially arranged inflated chambers, which extend for ~¾ of the test height.

Phylogenetic relationships. The species evolved from *W. irregularis* around the P0/Pα zonal boundary.

Stratigraphic range. Zone Pα–Zone P1c (lower Danian; Fig. 4).

Woodringina hornerstownensis Olsson, 1960
Figs. 6.16–6.24

Woodringina hornerstownensis Olsson, 1960, p. 29, pl. 4, figs. 18, 19; Olsson et al., 1999, p. 87, 88, pl. 13, figs. 4, 5, pl. 68, figs. 8–14.

Remarks. Woodringina hornerstownensis differs from *W. claytonensis* by having a more elongated, less tapering test with ~ 5–8 chambers in the later biserial stage.

Phylogenetic relationships. The species evolved from *W. claytonensis* in lower Zone Pα.

Stratigraphic range. Zone Pα–Zone P1c (lower Danian; Fig. 4)

Genus *Globoconusa* Khalilov, 1956
Type species: *Globoconusa conusa* Khalilov, 1956
(= *Globigerina daubjergensis* Brönnimann, 1953).

Globoconusa victori Koutsoukos, n. sp.
Figs. 7.1–7.10, 8.1–8.7

Globigerina kozlowskii Brotzen & Pozaryska, 1961, p. 162, pl. 1, figs. 1, 2?, 7, 8 (ex interc.?).
Globoconusa tripartita Morozova et al., 1967, pl. 5, figs. 6a–c (paratype; ex interc.).
Globastica daubjergensis (Brönnimann). Blow, 1979, p. 1235, pl. 256, fig. 4 (ex interc.?).
Globoconusa daubjergensis (Brönnimann). Olsson et al., 1999, pl. 64, figs. 5?, 6 (ex interc.).

Description. Test small; low, compact trochospiral, tightly coiled; spiral side slightly flattened to somewhat depressed, slightly concave in outline, umbilical side inflated, and thickness ~⅔ the diameter. Last whorl composed of 3–3½ globular chambers increasing rapidly in size; ultimate chamber is characteristically highly inflated (globular), commonly occupying from ~½–⅔ of test size (~40–60%). Equatorial outline is typically trilobate. Axial periphery broadly rounded. Sutures are straight to slightly curved, depressed on umbilical side, and nearly flush/indistinct (in the early ontogenetic stage) to slightly depressed on the spiral side. Primary aperture a very low, elongate arch or low-arched slit, extraumbilical-umbilical in position. Test microperforate, pores widely dispersed, with a distinct hispid/pustulose surface, covered by scattered to abundant blunt to more commonly sharp-pointed small pustules (enlarged view in Fig. 7.1b).

Holotype (USNM 545313; Fig. 7.1): maximum diameter 121 μm, thickness 87 μm, proloculus indistinct; paratypes: maximum diameter 120–180 μm (averaging 144 μm), thickness 88–125 μm (averaging 108 μm).

Remarks. The species is characterized by its small trilobate form with a distinctive test surface. It is distinguished from its ancestral species, *Globoconusa daubjergensis*, in having a compact, trilobate form with a flattened to somewhat depressed spiral side, rather than a high trochospire; a highly inflated ultimate chamber occupying from ½–⅔ of test size; and a distinct extraumbilical-umbilical (rather than umbilical) aperture. Intermediate specimens occur with overall similar trilobate morphology, but with a slightly higher spire and an aperture varying from more extraumbilical and slit-like (see Olsson et al., 1999, pl. 64, fig. 6) to slightly

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50 μm), 24–27 cm (Zone P1c). **16–24** *Woodringina hornerstownensis*: 16 ((USNM 597315; scale bar = 50 μm), 19 ((USNM 597318; scale bar = 20 μm), 21 (USNM 597320; scale bar = 20 μm), 3–6 cm (Zone P1c); 17 (USNM 597316), 18 (USNM 597317), 20 (USNM 597319), 22 (USNM 597321), 23 (USNM 597322), 24 (USNM 597323), 58–61 cm (Zone P1a).

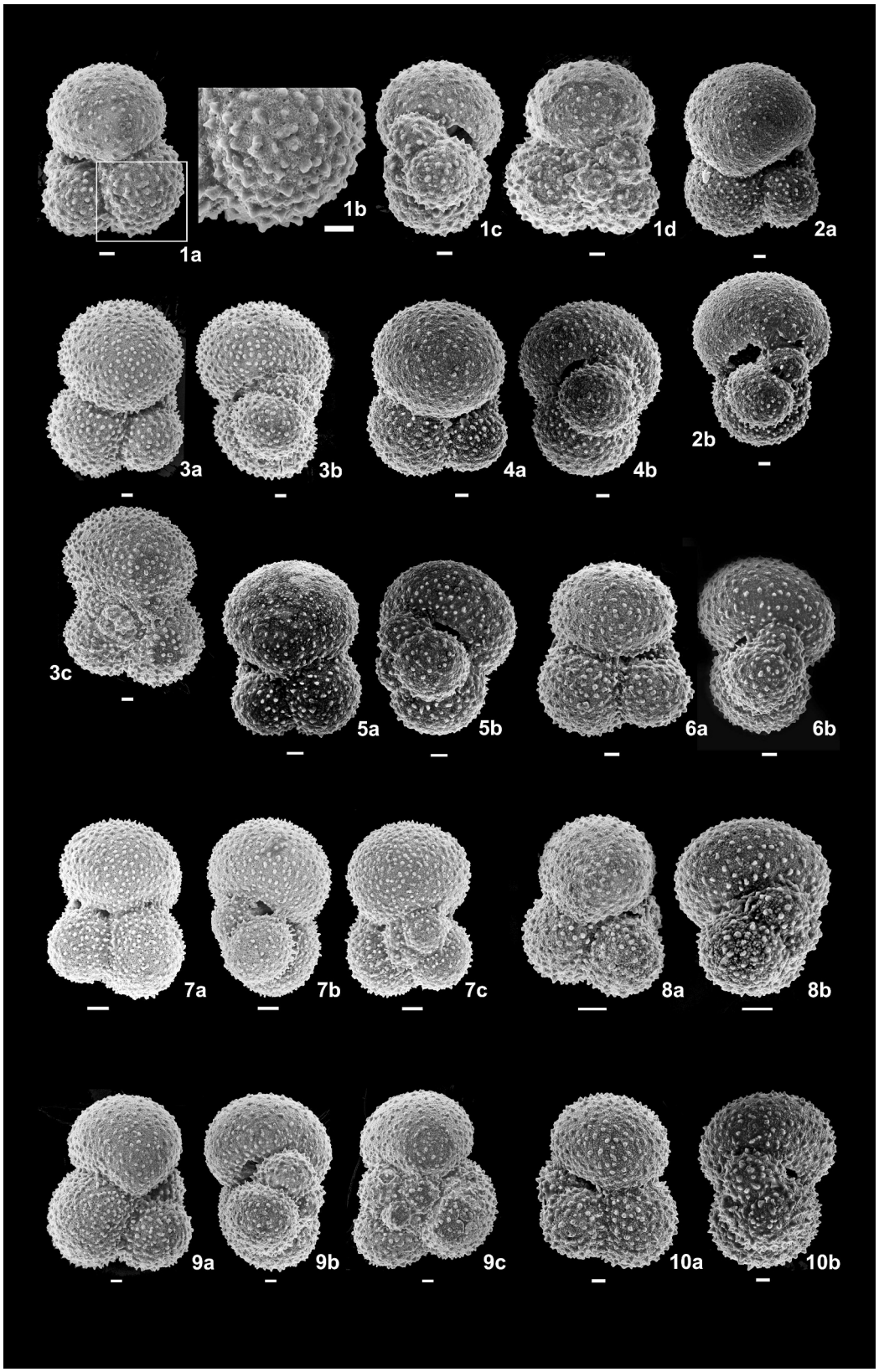


FIGURE 7. **1–10** *Globoconusa victori* n. sp. from the lower Danian (Zone P1c), all except 7 from 6–8 cm; scale bars = 10 μm unless stated otherwise: 1 (USNM 545313), holotype, 1b, detail of penultimate chamber showing microperforate wall texture covered by abundant poreless small pustules; 2 (USNM 545314), paratype; 3 (USNM 545315), paratype; 4 (USNM 545316), paratype; 5 (USNM 545317), paratype; 6 (USNM 545318), paratype; 7 (USNM 545319; scale bar = 20 μm), paratype, 3–6 cm; 8 (USNM 545320; scale bar = 20 μm), paratype; 9 (USNM 545321), paratype; 10 (USNM 545322), paratype.

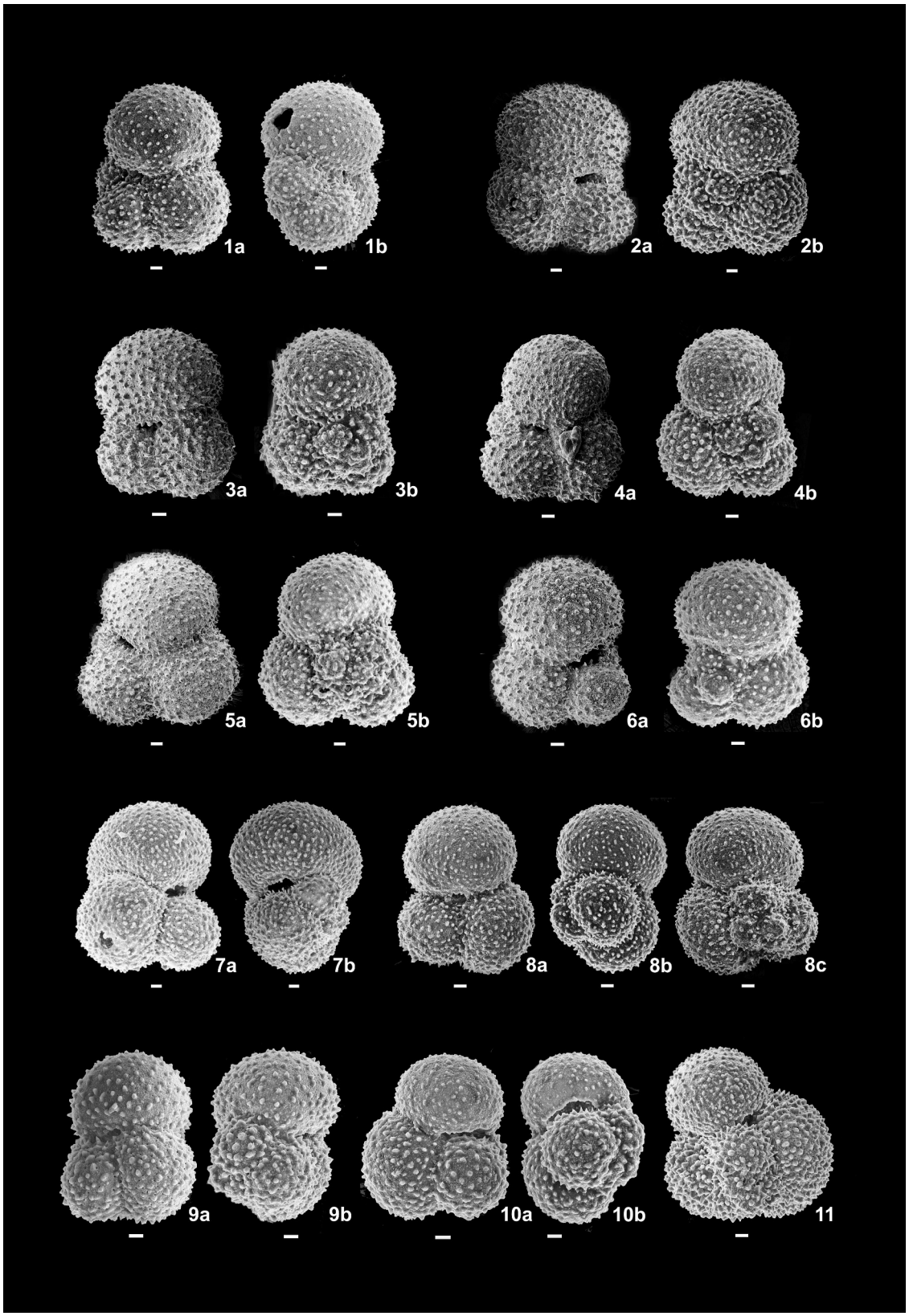


FIGURE 8. *Globoconusa* species from the lower Danian (Zone P1c); scale bars = 10 μm unless stated otherwise. **1–7** *Globoconusa victori* n. sp., all from 6–8 cm: 1 (USNM 545323), paratype; 2 (USNM 545325), paratype; 3 (USNM 545326), paratype; 4 (USNM 545327), paratype; 5 (USNM 545328), paratype; 6 (USNM 597324), paratype; 7 (USNM 597325), paratype. **8** *Globoconusa victori* n. sp. ex. interc. *Gl. daubjergensis* (USNM 597326), 6–8 cm, transitional specimen with higher spire and an umbilical to slightly extraumbilical but arched aperture close to that of *Gl. daubjergensis.* **9–11** *Globoconusa daubjergensis*, all from 6–8 cm: 9 (USNM 597327); 10 (USNM 597328); 11 (USNM 597329).

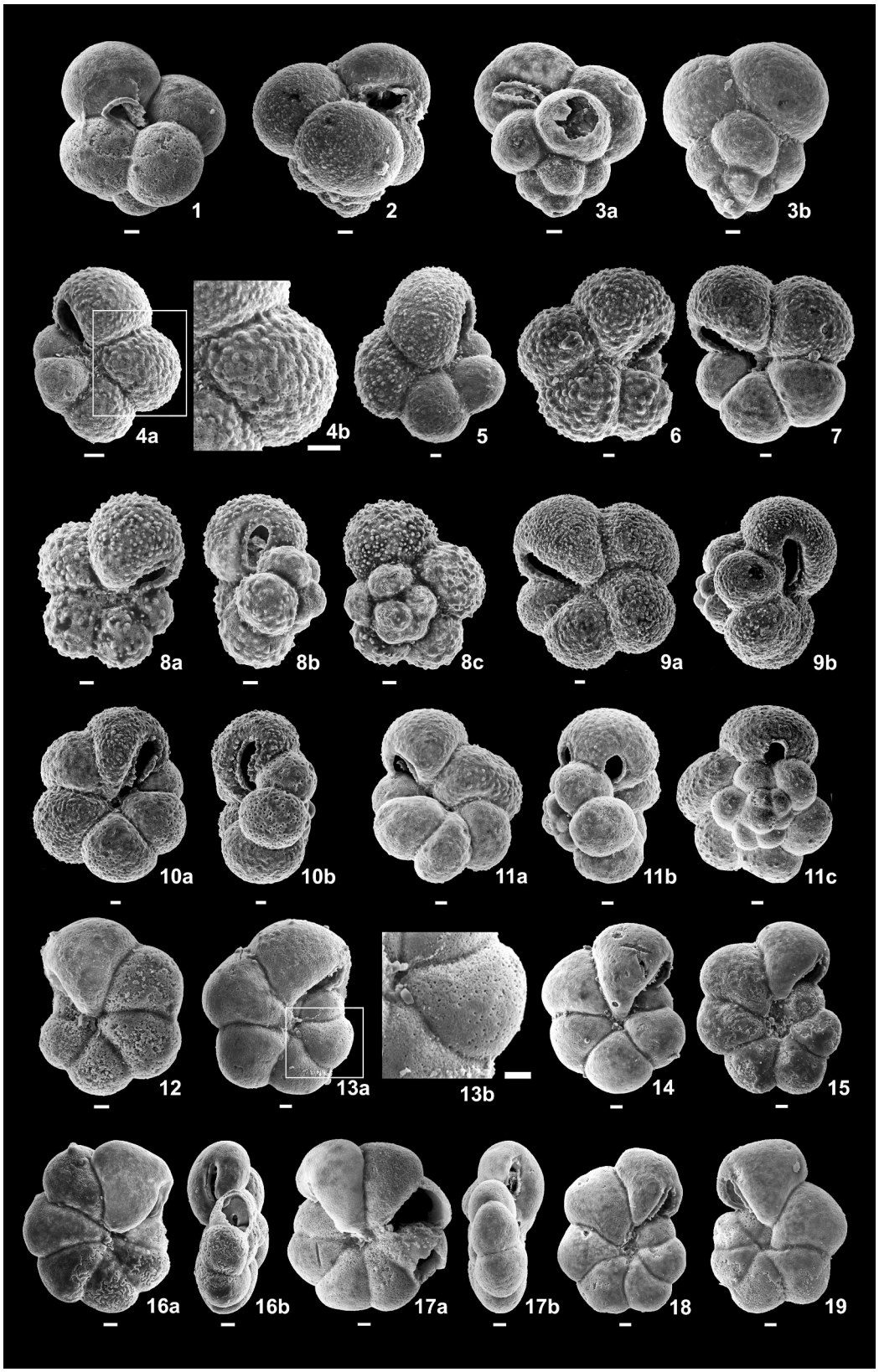


FIGURE 9. *Parvularugoglobigerina* species from Zone Pα; scale bars = 10 μm unless stated otherwise. **1** *Parvularugoglobigerina alabamensis* (USNM 597330), 146–149 cm (lowermost Zone Pα). **2, 3** *Parvularugoglobigerina extensa*: 2 (USNM 597331), 122–124 cm (lower Zone Pα); 3 (USNM 597332), 130–132 cm (lower Zone Pα). **4–11** *Parvularugoglobigerina eugubina* plexus: 4 (USNM 597333; scale bar = 20 μm), 5 (USNM 597334), 122–124 cm (Zone Pα); 4b, detail of penultimate chamber showing microperforate pustulose wall texture covered by finely developed perforation cones; 6 (USNM 597335), 71–74 cm (uppermost Zone Pα); 7 (USNM 597336), 9 (USNM 597338), 10 (USNM 597339), 11 (USNM 597340), 80–83.5 cm

extraumbical but arched, close to *Gl. daubjergensis* (Fig. 8.8; see also Morozova et al., 1967, pl. 5, figs. 6a–c).

Repository. Holotype USNM 545313 and paratypes USNM 545314–545323, USNM 545325–545328 (in October 2011), USNM 597325, and USNM 597326 deposited at the National Museum of Natural History, Smithsonian Institution, Washington, D.C. Additional unpublished topotypes are deposited in the NMNH collections with the curatorial numbers USNM 545324, USNM 545329, USNM 597385, and USNM 597423–597427.

Etymology. Named after my son Victor de Souza Koutsoukos, who accompanied me during a research period (1986–1990) in Plymouth, U.K.

Phylogenetic relationships. The species evolved from *Gl. daubjergensis* (Brönnimann) within Zone P1c through the development of a more compact trilobate test with a much larger highly inflated last chamber, and by the sharp decrease of spiral height to produce a flattened or somewhat depressed profile.

Stratigraphic range. Zone P1c (lower Danian; Fig. 4). The total range is unknown because the core is short and at its base Zone P1c unconformably overlies Zone P1a sediments.

Geographic distribution. This initial report of *Gl. victori* n. sp. in a deep-water core implies a preference for tropical to subtropical conditions, but this requires confirmation from additional sites.

Stable isotope paleobiology. Currently unrecorded.

Globoconusa daubjergensis (Brönnimann,1953)
Figs. 8.9–8.11

Globigerina daubjergensis Brönnimann, 1953, p. 340, text-fig. 1.
Globigerina kozlowskii Brotzen & Pozaryska, 1961, p. 162, pl. 3, figs. 1a–c (holotype).
Globoconusa tripartita Morozova et al., 1967, pl. 5, figs. 4a–c (holotype), 5a–c.
Globastica daubjergensis (Brönnimann). Blow, 1979, p. 1235, pl. 74, figs. 7–9, pl. 256, figs. 1–9, pl. 257, figs. 3, 4.
Globoconusa conusa Khalilov. Blow, 1979, p. 1386, pl. 257, figs. 10, 11.
Globoconusa daubjergensis (Brönnimann). Olsson et al., 1999, p. 81, 82, pl. 8, figs. 4–6, pl. 15, figs. 13, 14 (reillustrated holotype), pl. 64, figs. 1–12.

Phylogenetic relationships. The species clearly evolved from *Guembelitria cretacea* in earliest Zone Pα, to which transitional forms link it (see Liu & Olsson, 1992, pl. 1, fig. 9).

Stratigraphic range. Zone Pα–Zone P1c (lower Danian; Fig. 4).

Genus *Parvularugoglobigerina* Hofker, 1978
Type species: *Globigerina eugubina* Luterbacher & Premoli Silva, 1964

Parvularugoglobigerina alabamensis (Liu & Olsson, 1992)
Fig. 9.1

Guembelitria? alabamensis Liu & Olsson, 1992, p. 341, pl. 2, figs. 1–7.
Parvularugoglobigerina alabamensis (Liu & Olsson). Olsson et al., 1999, p. 83, pl. 65, figs. 1–6.

Remarks. Species has a minute high-trochospiral test with 3½–4 inflated subglobular chambers, and a low-arched umbilical aperture.

Stratigraphic range. Upper? Zone P0–Zone P1c (lower Danian; Fig. 4).

Parvularugoglobigerina extensa (Blow, 1979)
Figs. 9.2, 9.3

Eoglobigerina? *extensa* Blow, 1979, p. 1220, pl. 69, fig. 7, pl. 74, figs. 1, 2.
Parvularugoglobigerina aff. *eugubina* (Luterbacher & Premoli Silva). Liu & Olsson, 1992, p. 345, pl. 2, figs. 8–12.
Parvularugoglobigerina extensa (Blow). Olsson et al., 1999, p. 85, 86, pl. 65, figs. 7–13.

Remarks. Species has a minute high-trochospiral test with 3½–4 inflated subglobular chambers in the last whorl, and a distinctive elongate, loop-shaped to slit-like aperture that extends asymmetrically over the face of the last chamber.

Stratigraphic range. Upper Zone P0–Zone Pα (lower Danian; Fig. 4).

Parvularugoglobigerina eugubina (Luterbacher & Premoli Silva, 1964) plexus, emended
Figs. 9.4–9.11

Globigerina eugubina Luterbacher & Premoli Silva, 1964, p. 105, pl. 2, figs. 8a–c.
Parvularugoglobigerina eugubina (Luterbacher & Premoli Silva). Liu & Olsson, 1992, p. 345, pl. 3, figs. 1–7, 11, 12 (cf.); Olsson et al., 1999, pl. 66, figs. 1–6, 9; Arenillas & Arz, 2013a, figs. 3.M, 6.A–D.
Globanomalina archeocompressa? (Blow). Arenillas & Arz, 2013a, figs. 7.A1–3.

Emended description. The species is characterized by its typical inflated trochoidal test, commonly with 4–5½, up to 7, globular chambers in the last whorl; small size; strongly incised sutures; a highly variable spiral height, from a low, nearly flattened spire (Fig. 9.10b) to a moderately high spire (Figs. 9.8b, 9.9b); a distinctive slit-like arched areal aperture in the face of the last chamber; a microperforate test with very high pore density per unit area and very small pores; and a smooth to finely developed pustulose wall surface with perforation cones (see detail in Fig. 9.4b).

Remarks. It is common to find among the *P. eugubina* population well-preserved specimens where the first 2–3 chambers of the last whorl are rather smooth, covered by very weakly developed pustules and perforation cones (see Figs. 9.4a, 9.5, and 9.7), and the last 2–3 chambers have more finely developed pustules and perforation cones. This strongly suggests the presence of pustules in *P. eugubina* might be ontogenetically mediated, perhaps induced during gametogenesis (i.e., gametogenetic calcification).

Toward upper Zone Pα the species blooms, reaching a dense population of >50% of the total planktic foraminiferal assemblage (Fig. 4), and becomes highly plastic in morphology, with increased pustulose coarseness. Some

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(upper Zone Pα); 11, possibly a teratological form, note secondary aperture on the spiral side at the base of the last chamber; 8 (USNM 597337), 132–134 cm (lower Zone Pα). **12–19** *Parvularugoglobigerina longiapertura* plexus: 12 (USNM 597341), 13 (USNM 597342), 14 (USNM 597343), 15 (USNM 597344), 18 (USNM 597347), 19 (USNM 597348), 122–124 cm (lower Zone Pα); 13b, detail showing smooth and microperforate wall, with randomly distributed minute pores; 16 (USNM 597345), 134–136 cm (lower Zone Pα); 17 (USNM 597346), 146–149 cm (lowermost Zone Pα).

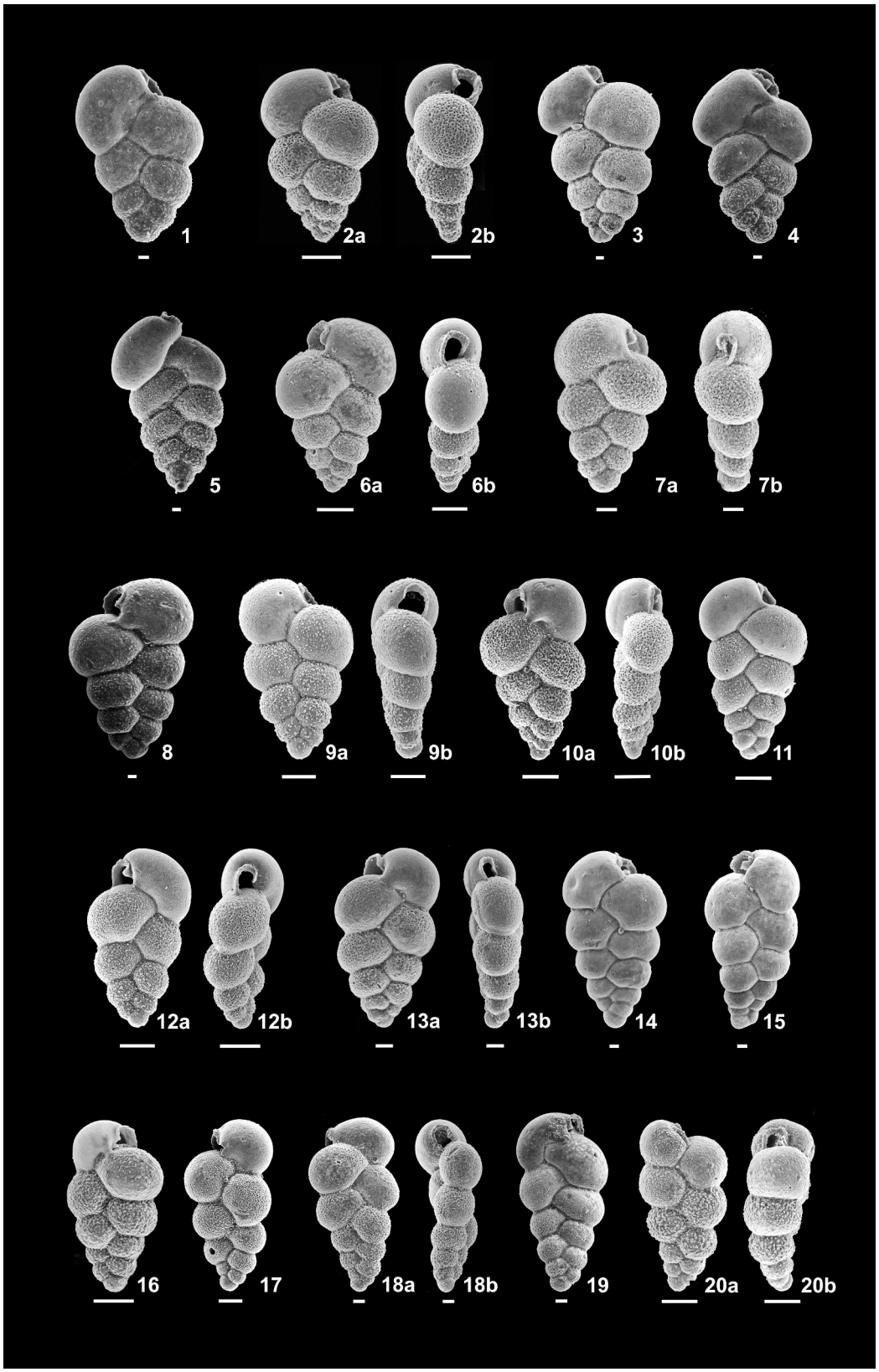


FIGURE 10. SEM micrographs of species of the families Chiloguembelinidae and Heterohelicidae; scale bars = 10 μm unless stated otherwise. **1–13** *Chiloguembelina midwayensis* plexus: 1 (USNM 597349), 3 (USNM 597351), 4 (USNM 597352), 5 (USNM 597353), 58–61 cm (Zone P1a); 2 (USNM 597350), 6 (USNM 597354), 9–13 (scale bars = 50 μm), 9 (USNM 597357), 10 (USNM 597358), 11 (USNM 597359), 12 (USNM 597360), 13 (USNM 597361), 24–27 cm (Zone P1c); 7 (USNM 597355; scale bar = 20 μm), 3–6 cm (Zone P1c); 8 (USNM 597356), 134–136 cm (lower Zone Pα). **14** *Chiloguembelina midwayensis* ex interc *Ch. morsei* (USNM 597362), 122–124 cm (lower Zone Pα), specimen with rather smooth microperforate

specimens are aberrant morphotypes (teratomorphic effect?) with inflated, distorted tests of 6–7 chambers in the last whorl, and several show a secondary aperture on the spiral side at the base of the last chamber (Figs. 9.11a–c; see also Olsson et al., 1999, pl. 66, figs. 6 and 9).

Phylogenetic relationships. The highly plastic microperforate/pustulose *P. eugubina* most likely evolved from *Guembelitria cretacea* through *P. extensa* near the P0/Pα zonal boundary, based on their guembelitriid surface texture (pustulose with perforation cones) and general morphology.

Stratigraphic range. Zone Pα (lower Danian; Fig. 4).

Parvularugoglobigerina longiapertura (Blow, 1979) plexus, emended
Figs. 9.12–9.19

Globorotalia (*Turborotalia*) *longiapertura* Blow, 1979, p. 1085, pl. 63, figs. 7, 8 (holotype), pl. 56, figs. 3, 4, pl. 58, figs. 3–5, pl. 63, figs. 1–3, 6, 9, pl. 68, fig. 3, pl. 72, fig. 1.
Globigerina eugubina Luterbacher & Premoli Silva. Smit, 1982, p. 339–341, fig. 9, pl. 1, figs. 1–13, 15–17, 19, 20; pl. 2, figs. 1–3, 5–8.
Parvularugoglobigerina eugubina (Luterbacher & Premoli Silva). Olsson et al., 1999, pl. 66, figs. 7, 8, 10–12.
Parvularugoglobigerina longiapertura (Blow). Arenillas & Arz, 2000, pl. 2, figs. 1–5, 8–10; Arenillas et al., 2004, figs. 4.G–H; Arenillas & Arz, 2013a, figs. 3.J, K.
Civisina euskalherriensis Apellaniz et al., 2002, p. 168–170, figs. 6.1–6.8 and 7.1–7.6.
Civisina longiapertura (Blow). Apellaniz et al., 2002, p. 170, 171, fig. 6.9 (not 6.10).

Emended description. Low spiral, laterally compressed, multi-chambered species commonly with 5–8 chambers in the last whorl and a very elongate, long slit-like areal aperture in the face of the last chamber over the peripheral margin. Test small to medium in size. Test surface smooth, microperforate, with very high pore density per unit area and minute pores (~0.3–0.5 μm in diameter), commonly somewhat masked by gametogenic overgrowth.

Remarks. The spiral side of *P. longiapertura*, which can be clearly seen in a slightly oblique peripheral view in Fig. 9.16b, shows the same smooth surface texture as the umbilical side. Specimens assigned to the *P. longiapertura* plexus differ from *P. eugubina* in having a test with smoother wall, less chamber inflation, a smaller spire height, commonly laterally compressed sides, and gradually increasing number of chambers in the last whorl. The complete absence of pustules and perforation cones in all recovered specimens of the plexus together with the consistent morphological features argue for discriminating it as a separate species within the *P. eugubina* lineage. The more laterally compressed specimens (Figs. 9.15–9.19) with 6–8 chambers in the last whorl were assigned by Apellaniz et al. (2002) to a new species *Civisina euskalherriensis*. However, the various morphotypes intergrade and are coeval, and are thus considered here to fall within the range of intraspecific variation (ecophenotypes and/or ontogenetic variants) of the *P. longiapertura* plexus.

Phylogenetic relationships. Transitional specimens between *P. longiapertura* and *P. eugubina* occur in lower Zone Pα. They characteristically have 5–6 chambers in the last whorl, an elongated aperture, and a slightly more inflated test, but still are completely smooth, lacking pustules or perforation cones. *Parvularugoglobigerina longiapertura* represents a more evolutionarily advanced form of, and is clearly derived from, *P. eugubina* (B. T. Huber, written communication, 2013).

Stratigraphic range. Lower Zone Pα (lower Danian; Fig. 4).

Family HEDBERGELLIDAE Loeblich & Tappan, 1961
Genus *Hedbergella* Brönnimann & Brown, 1958
Type species: *Anomalina lorneiana* d'Orbigny var. *trocoidea* Gandolfi, 1942

Hedbergella holmdelensis Olsson, 1964

Hedbergella holmdelensis Olsson, 1964, p. 160, pl. 1, figs. 1a–c (paratype), fig. 2a–c (holotype); Olsson et al., 1999, p. 35, pl. 30, figs. 1–17.

Stratigraphic range. Maastrichtian–lowermost Zone Pα (lowermost Danian). Extremely rare in piston-core samples at 143–146 cm, 153–155 cm, and 160–162 cm.

Hedbergella monmouthensis (Olsson, 1960)

Globorotalia monmouthensis Olsson, 1960, p. 47, pl. 9, figs. 22–24.
Hedbergella monmouthensis (Olsson). Olsson et al., 1999, p. 35–37, fig. 15, pl. 31, figs. 1–15.

Stratigraphic range. Maastrichtian–lowermost Zone Pα (lowermost Danian). Extremely rare in piston-core samples at 143–146 cm, 149–151 cm, 153–155 cm, and 160–162 cm.

Genus *Globanomalina* Haque, 1956, emended Olsson et al., 1999
Type species: *Globanomalina ovalis* Haque, 1956

Globanomalina archeocompressa (Blow, 1979)

Globorotalia (*Turborotalia*) *archeocompressa* Blow, 1979, p. 1049, pl. 56, figs. 1, 2, pl. 58, figs. 2, 6, 7, 8, 9 (holotype), pl. 64, figs. 5, 9, pl. 68, figs. 5, 6.
Globanomalina archeocompressa (Blow). Olsson et al., 1999, p. 37, 38, pl. 32, figs. 1–10.

Stratigraphic range. Zone P0–lowermost Zone Pα. Extremely rare in piston-core samples at 146–149 cm, and 160–162 cm.

Family CHILOGUEMBELINIDAE Reiss, 1963
Genus *Chiloguembelina* Loeblich & Tappan, 1956
Type species: *Gümbelina midwayensis* Cushman, 1940

Chiloguembelina midwayensis (Cushman, 1940) plexus
Figs. 10.1–10.13

Gümbelina midwayensis Cushman, 1940, p. 65, pl. 11, fig. 15.
Chiloguembelina midwayensis (Cushman). Olsson et al., 1999, p. 90, 91, pl. 13, figs. 9, 10 (reillustrated holotype), pl. 69, figs. 16–22.

Remarks. Specimens assigned to the *Ch. midwayensis* plexus have a rapidly tapering wholly biserial test that is compressed laterally, a characteristic chiloguembelinid

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wall. **15–19** *Chiloguembelina morsei*: 15 (USNM 597363), 122–124 cm (lower Zone Pα); 16 (USNM 597364; scale bar = 50 μm), 17 (USNM 597365; scale bar = 50 μm), 24–27 cm (Zone P1c); 18 (USNM 597366), 58–61 cm (Zone P1a); 19 (USNM 597367), 71–74 cm (Zone P1a). **20** *Zeauvigerina waiparaensis* forma *prolata* (USNM 597368; scale bar = 50 μm), 3–6 cm (Zone P1c).

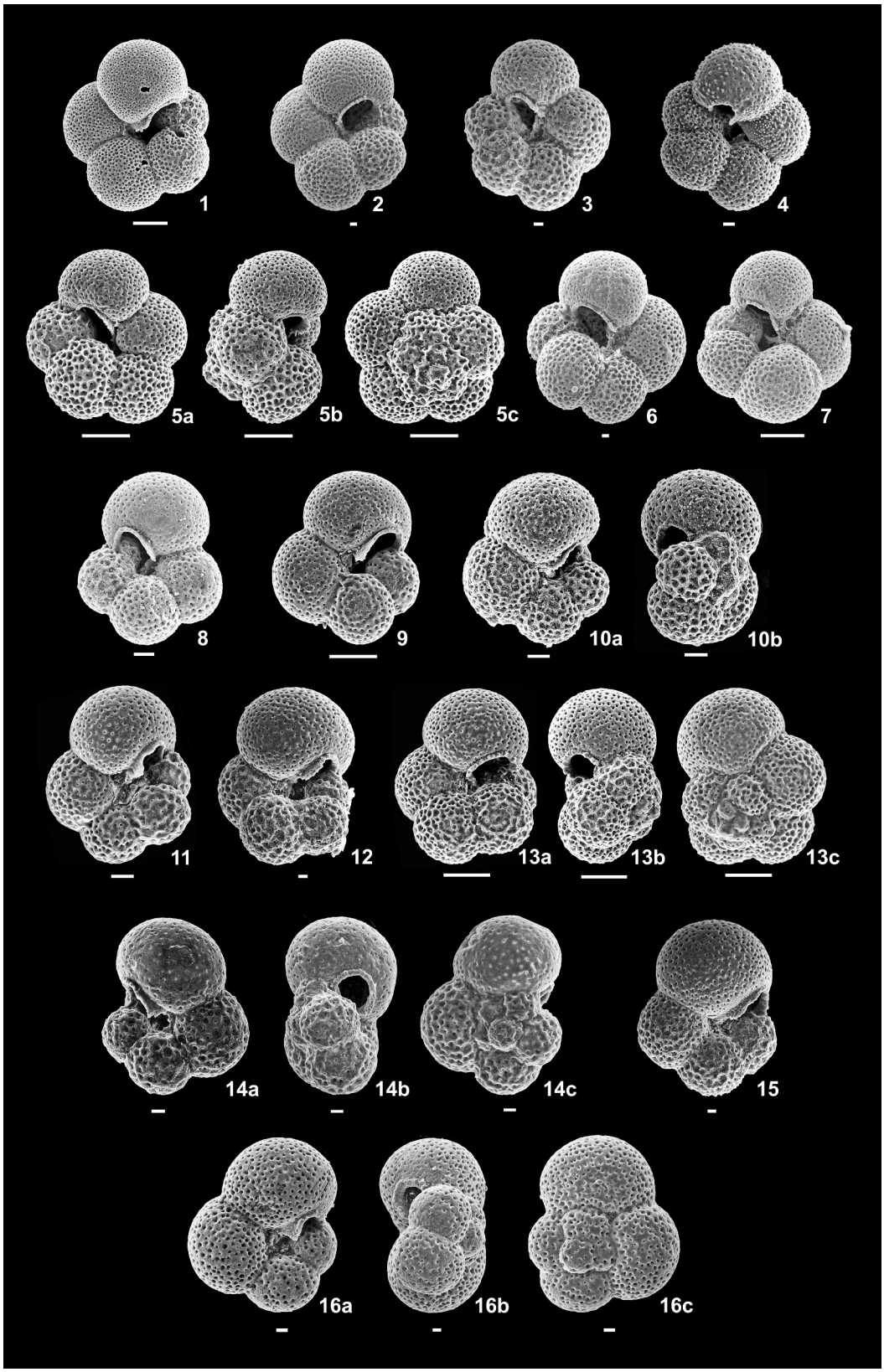


FIGURE 11. SEM micrographs of species of the family Globigerinidae; scale bars = 10 μm unless stated otherwise. **1–7** *Eoglobigerina edita*: 1 (USNM 597369; scale bar = 50 μm), 5 (USNM 597373 scale bar = 50 μm), 24–27 cm (Zone P1c); 2 (USNM 597370), 3 (USNM 597371), 6 (USNM 597374), 7 (USNM 597375), 3–6 cm (Zone P1c); 4 (USNM 597372), 122–124 cm (Zone Pα). **8–13** *Eoglobigerina eobulloides*: 8 (USNM 597376; scale bar = 20 μm), 3–6 cm (Zone P1c); 9 (USNM 597377; scale bar = 50 μm), 10 (USNM 597378; scale bar = 20 μm), 11 (USNM 597379; scale bar =

asymmetrical aperture, and a microperforate wall commonly covered with fine small pustules; last 1–2 chambers are rather smooth.

Phylogenetic relationships. The species evolved in early Zone Pα from *Chiloguembelina morsei*, to which it is linked by transitional morphotypes (Fig. 10.14).

Stratigraphic range. Zone Pα–Zone P1c (lower Danian; Fig. 4).

Chiloguembelina morsei (Kline, 1943)
Figs. 10.15–10.19

Gümbelina morsei Kline, 1943, p. 44, pl. 7, fig. 12.
Chiloguembelina morsei (Kline). Olsson et al., 1999, p. 91, 92, pl. 13, figs. 14, 15 (reillustrated holotype), pl. 69, figs. 9–15.

Remarks. The species has a wholly biserial test and a microperforate, smooth to finely pustulose wall with minute perforation cones. The specimens recovered from Zone P1a and upwards are commonly twisted in the last 4–6 chambers (see Figs. 10.18a, b). *Chiloguembelina morsei* differs from *Ch. midwayensis* in having a narrower, less tapering, elongated test with more globular chambers.

Phylogenetic relationships. The species evolved in earliest Zone Pα from *Woodringina* (d'Hondt, 1991; Olsson et al., 1999).

Stratigraphic range. Zone Pα–Zone P1c (lower Danian; Fig. 4).

Family HETEROHELICIDAE Cushman, 1927
Genus *Zeauvigerina* Finlay, 1939
Type species: *Zeauvigerina zelandica* Finlay, 1939

Zeauvigerina waiparaensis (Jenkins, 1965)
Fig. 10.20

Chiloguembelina waiparaensis Jenkins, 1965, p. 1095, pl. 1, figs. 1–6.
Zeauvigerina waiparaensis (Jenkins) forma *prolata* Huber & Boersma, 1994, p. 278, pl. 1, figs. 4a–c, pl. 2, figs. 10a, b.
Zeauvigerina waiparaensis (Jenkins). Olsson et al., 1999, p. 97, 98, pl. 71, figs. 6–8 (forma *prolata*).

Remarks. The species differs from *Ch. morsei* in having a biserial test throughout with more globular, slightly-inflated chambers, and an interiomarginal off-center arched aperture, bordered by an equidimensional narrow lip; wall microperforate and finely pustulose.

Stratigraphic range. Zone P0–Zone P1c (lower Danian). Rare to common in piston-core samples at 8–10 cm, 12–15 cm, 18–20 cm, 20–22 cm, 41–44 cm, 44–47 cm, 47–50 cm, 50–52 cm, 134–136 cm, 146–149 cm, 151–153 cm, 153–155 cm, 157.5–160 cm, and 160–162 cm.

Family GLOBIGERINIDAE Carpenter, Parker & Jones, 1862
Genus *Eoglobigerina* Morozova, 1959
Type species: *Globigerina* (*Eoglobigerina*) *eobulloides* Morozova, 1959

Eoglobigerina edita (Subbotina, 1953)
Figs. 11.1–11.7

Globigerina edita Subbotina, 1953, p. 62, pl. 2, fig. 1a–c.
Eoglobigerina edita (Subbotina). Olsson et al., 1999, p. 19, 20, pl. 18, figs. 1–16.

Remarks. Species with commonly 4½–5 globular chambers in the last whorl; a moderately high trochospire; and a rounded arched umbilical to slightly extraumbilical aperture, but shifting to a more umbilical position.

Phylogenetic relationships. Eoglobigerina edita evolved from *E. eobulloides* within early Zone Pα by slightly increasing the number and inflation of chambers in the last whorl, which shifted the aperture towards a more umbilical position.

Stratigraphic range. Zone Pα–Zone P1c (lower Danian; Fig. 5).

Eoglobigerina eobulloides (Morozova, 1959)
Figs. 11.8–11.13

Globigerina (*Eoglobigerina*) *eobulloides* Morozova, 1959, p. 1115, text-fig. 1a–c.
Globigerina fringa Subbotina. Premoli Silva & Bolli, 1973, pl. 7, figs. 6, 9.
Eoglobigerina eobulloides simplicissima Blow, 1979, pl. 55, fig. 1.
Eoglobigerina fringa (Subbotina). Stott & Kennett, 1990, p. 559, pl. 1, figs. 5, 6; Arenillas & Arz, 2013b, figs. 4.2, 4.3, 6.4, 8.2, 8.3?.
Eoglobigerina eobulloides (Morozova). Olsson et al., 1999, p. 20–22, pl. 8, figs. 10–12 (reillustrated holotype), pl. 19, figs. 1–15; Arenillas & Arz, 2013b, figs. 7.1–7.3.
Eoglobigerina simplicissima Blow. Arenillas et al., 2004, figs. 4.L–M; Arenillas & Arz, 2013b, figs. 6.2, 6.3, 7.5, 9.1.
Eoglobigerina microcellulosa (Morozova). Arenillas & Arz, 2013b, figs. 3.10, 9.2, 9.3?.

Remarks. Species with 4–4½ globular chambers in the last whorl, a moderately elevated trochospire, and an umbilical to slightly extraumbilical low-arched aperture. Specimens with four chambers in the last whorl (Figs. 11.8, 11.9; see also Olsson et al., 1999, pl. 19, figs. 3, 4, 10, 11; Arenillas et al., 2004, figs. 4.L–M; Arenillas & Arz, 2013b, figs. 4.2, 4.3, 6.2–6.5, 7.5) resemble *E.* aff. *E. eobulloides*, from which they differ by having a larger size, a moderately elevated trochospire, more inflated globular chambers, deeper umbilical sutures, and a less developed cancellate wall.

Phylogenetic relationships. Eoglobigerina eobulloides apparently evolved directly from *Praemurica nikolasi* n. sp., or through *E.* aff. *E. eobulloides* in late Zone P0 (see further discussion below).

Stratigraphic range. Zone Pα–Zone P1c (lower Danian; Fig. 5).

Eoglobigerina aff. *E. eobulloides* (Morozova, 1959)
Figs. 11.14, 11.15

aff. *Globigerina* (*Eoglobigerina*) *eobulloides* Morozova, 1959, p. 1115, text-fig. 1a–c.
Eoglobigerina eobulloides (Morozova). Huber, 1991, p. 461, pl. 2, figs. 9–11; Olsson et al., 1999, pl. 19, fig. 8.
Eoglobigerina fringa (Subbotina). Koutsoukos, 1996a, figs. 8.1, 8.2; Arenillas & Arz, 2013b, figs. 6.5 (ex interc.?), 8.1.
Eoglobigerina simplicissima Blow. Arenillas & Arz, 2013b, fig. 6.1 (ex interc.?).

Description. The specimens assigned here to *E.* aff. *E. eobulloides* have a distinct minute 4–4½-chambered test, coarsely cancellate in the first 3 chambers of the last whorl, characteristically with a low to nearly flat spiral side, and a

←

20 μm), 13 (USNM 597381; scale bar = 50 μm), 24–27 cm (Zone P1c); 12 (USNM 597380), 58–61 cm (Zone P1a). **14, 15** *Eoglobigerina* aff. *E. eobulloides*: 14 (USNM 597382), 136–139 cm (lower Zone Pα), 15 (USNM 597384), 58–61 cm (Zone P1a); **16** *Eoglobigerina* aff. *E. eobulloides* ex. interc. *E. eobulloides* (USNM 597383), 136–139 cm (lower Zone Pα).

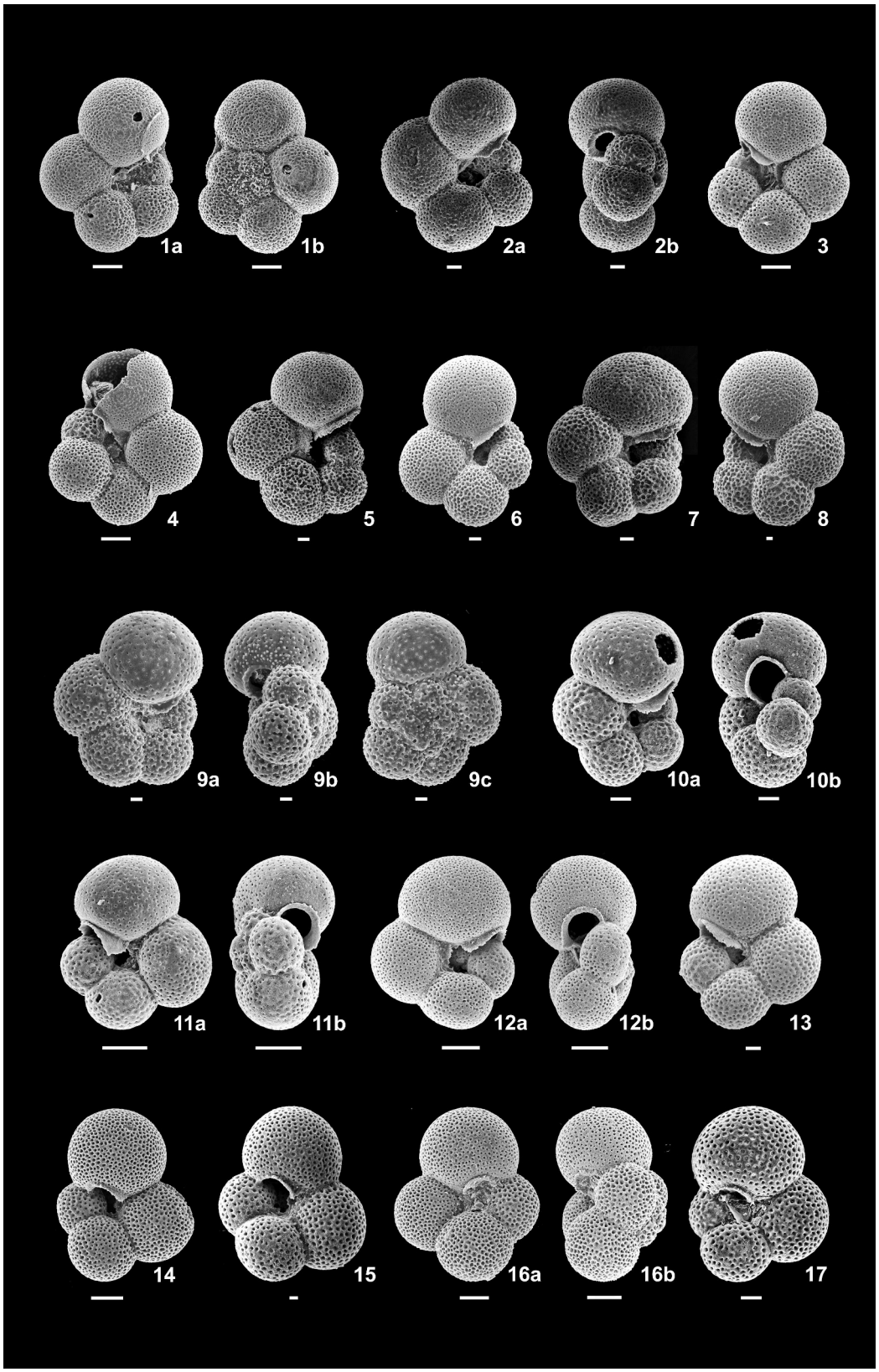


FIGURE 12. *Parasubbotina* and *Subbotina* species; scale bars = 50 μm unless stated otherwise. **1–8** *Parasubbotina pseudobulloides*: 1 (USNM 597386), 3 (USNM 597388), 4 (USNM 597389), 24–27 cm (Zone P1c); 2 (USNM 597387; scale bar = 20 μm), 71–74 cm (uppermost Zone Pα); 5 (USNM 597390; scale bar = 20 μm), 7 (USNM 597392; scale bar = 20 μm), 6–8 cm (Zone P1c); 6 (USNM 597391; scale bar = 20 μm), 3–6 cm (Zone P1c); 8 (USNM 597393; scale bar = 10 μm), 58–61 cm (Zone P1a). **9, 10** *Parasubbotina* aff. *Pa. pseudobulloides*: 9 (USNM 597394; scale bar = 10 μm), 132–134 cm (lower Zone Pα); 10 (USNM 597395; scale bar= 20 μm), 24–27 cm (Zone P1c). **11–13** *Parasubbotina varianta*: 11 (USNM 597396),

very low arched aperture, umbilical to slightly extraumbilical in position.

Remarks. Eoglobigerina aff. *E. eobulloides* differs from minute 4-chambered specimens of *E. eobulloides* by having a low to nearly flat spiral side, a very low extended apertural arch, and less depressed umbilical sutures. Specimens assigned to *E.* aff. *E. eobulloides,* with a well-developed cancellate wall, were recovered throughout the lower Danian, consistently from the lowermost Danian Zone Pα and upwards.

The holotype of *Globigerina fringa* Subbotina (reillustrated in Olsson et al., 1999, pl. 9, figs. 7–9) has 4½ chambers, a moderately low trochospire, very small size, an umbilical-slightly extraumbilical low-arched aperture, typical of *Eoglobigerina*, and a coarsely cancellate wall on all chambers. Olsson et al. (1999) tentatively placed *G'ina fringa* within *Subbotina cancellata,* based on its similar cancellate wall texture, which has its lowest occurrence in Zone P1c. However, the aperture of *G'ina fringa* is clearly low arched and umbilical to slightly extraumbilical in position, whereas in *S. cancellata* the aperture shifts to a more umbilical position. Though similar to *G'ina fringa* in test size and chamber arrangement, the morphotypes of *E.* aff. *E. eobulloides* "do not compare well with the holotype of *fringa,* which has a significantly lower pore density per unit area and a much smaller pore diameter than the piston core morphotypes" (R. K. Olsson, written communication, 2013).

Olsson et al. (1999, p. 29) argued that a coarsely cancellate wall texture is an advanced evolutionary development in the planktic foraminifera and is not present in Zone Pα. However, strongly cancellate mid-sized Globigerinidae, mostly *E. eobulloides,* were indeed recovered from lower Zone Pα (Fig. 5), together with coarsely cancellate minute-sized specimens assigned to *E.* aff. *E. eobulloides* (Fig. 11.14).

Phylogenetic relationships. Eoglobigerina aff. *E. eobulloides* possibly evolved directly from *Praemurica nikolasi* n. sp. in late Zone P0. Transitional specimens between *E.* aff. *E. eobulloides* and *E. eobulloides* (Fig. 11.16) occur in lower Zone Pα with a less-developed cancellate wall, four chambers, and a higher arched umbilical-slightly extraumbilical aperture. Some 4½-chambered specimens appear also to be morphologically transitional to *Parasubbotina* aff. *Pa. pseudobulloides,* differing mostly by the much smaller size, coarser cancellate wall, low-arched aperture, and less inflated chambers, increasing less rapidly in size. The definite taxonomic status of this controversial species is still a matter open to discussion, and would greatly benefit from a further detailed study of the morphological variation and stratigraphic occurrence of the so-called "*fringa*-like" morphotypes throughout the lower Danian.

Stratigraphic range. Upper Zone P0–Zone P1c (lower Danian; Fig. 5).

Genus *Parasubbotina* Olsson, Hemleben, Berggren & Liu, 1992
Type species: *Globigerina pseudobulloides* Plummer, 1926

Parasubbotina pseudobulloides (Plummer, 1926)
Figs. 12.1–12.8

Globigerina pseudobulloides Plummer, 1926, p. 133, pl. 8, figs. 9a–c.
Parasubbotina pseudobulloides (Plummer). Olsson et al., 1999, p. 24, 25, pl. 21, figs. 1–15.

Remarks. Species has a low trochospiral test with five globular to slightly ovate chambers in the last whorl, increasing rapidly in size; an umbilical-extraumbilical high-arched aperture with distinct narrow lip; and a well-developed cancellate spinose wall texture.

Phylogenetic relationships. The species evolved from *Parasubbotina* aff. *Pa. pseudobulloides* late in Zone Pα.

Stratigraphic range. Uppermost Zone Pα–Zone P1c (lower Danian; Fig. 5).

Parasubbotina aff. *Pa. pseudobulloides* (Plummer, 1926)
Figs. 12.9, 12.10

Parasubbotina aff. *pseudobulloides* (Plummer). Olsson et al., 1992, p. 197, pl. 4, figs. 1–4; Olsson et al., 1999, p. 25, 26, pl. 22, figs. 1–5.

Remarks. Species characterized by its small test (maximum diameter ~150–170 μm for illustrated specimens) with 4½–5 globular chambers, increasing rapidly in size; very low trochospire; a high-arched umbilical-extraumbilical aperture bordered by a distinct lip; and a finely developed cancellate wall texture.

Phylogenetic relationships. Parasubbotina aff. *Pa. pseudobulloides* possibly evolved directly from *Praemurica nikolasi* n.sp. or through *Eoglobigerina* aff. *E. eobulloides* (see comments above) in lowermost Zone Pα.

Stratigraphic range. Zone Pα–Zone P1c (lower Danian; Fig. 5).

Parasubbotina varianta (Subbotina, 1953)
Figs. 12.11–12.13

Globigerina varianta Subbotina, 1953, p. 63, pl. 3, figs. 5a–c (holotype)–7, 10–12, pl. 4, figs. 1–3.
Parasubbotina varianta (Subbotina). Olsson et al., 1999, p. 26–28, pl. 9, figs. 16–18 (reillustrated holotype), pl. 22, figs 6–16.

Remarks. Specimens assigned to *Pa. varianta* have a low trochospiral test with four subglobular to globular chambers in the last whorl, rapidly increasing in size; a high-arched umbilical-extraumbilical aperture bordered by a distinct lip; and a spinose cancellate wall texture. The species is distinguished from *Pa. pseudobulloides* by its smaller size with fewer chambers in the last whorl.

Phylogenetic relationships. The species evolved from *Pa. pseudobulloides* in Zone P1c (Olsson et al., 1999).

Stratigraphic range. Zone P1c (lower Danian; Fig. 5).

Genus *Subbotina* Brotzen & Pozaryska, 1961
Type species: *Globigerina triloculinoides* Plummer, 1926

Subbotina cancellata Blow, 1979

Subbotina triangularis cancellata Blow, 1979, p. 1284, pl. 80, figs. 2–9.

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24–27 cm (Zone P1c); 12 (USNM 597397), 13 (USNM 597398; scale bar = 20 μm), 3–6 cm (Zone P1c). **14–17** *Subbotina trivialis*: 14 (USNM 597399), 16 (USNM 597401; scale bar = 20 μm), 17 (USNM 597402; scale bar = 20 μm), 24–27 cm (Zone P1c); 15 (USNM 597400; scale bar = 10 μm), 3–6 cm (Zone P1c).

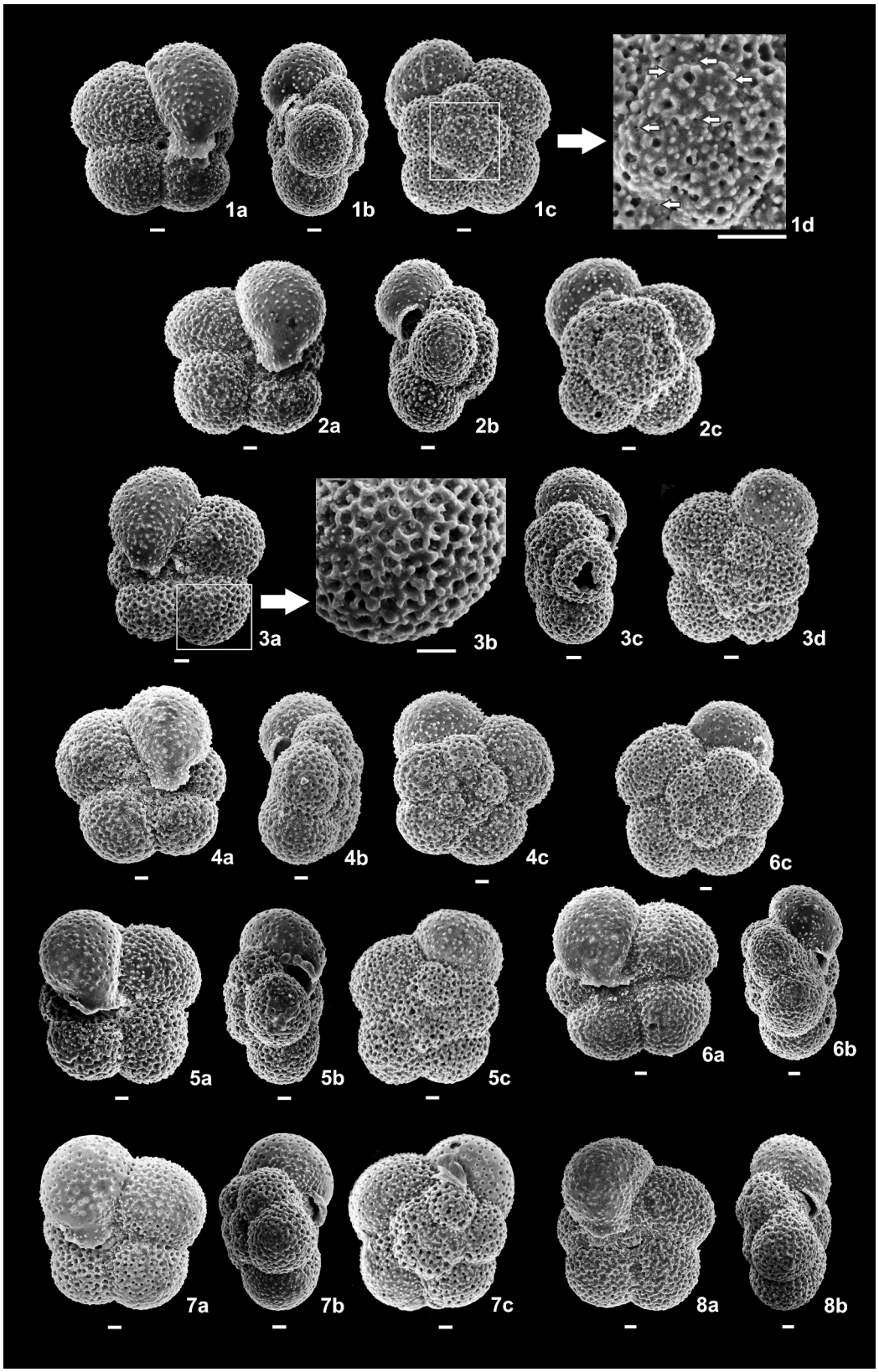


FIGURE 13. **1–8** *Praemurica nikolasi*, n. sp.; scale bars = 10 μm: 1 (USNM 545300), holotype, 134–136 cm (lower Zone Pα), 1d, magnified view of weakly developed praemuricate cancellate nonspinose wall texture on spiral side showing pustules coalescing around pores, structures similar to primitively developed small pores (white arrows) scattered next to pustules and to larger pores, and gametogenetic calcification; 2 (USNM 545301), paratype, 5 (USNM 545304), paratype, 6 (USNM 545305), paratype, 7 (USNM 545306), paratype, 8 (USNM 545307), paratype, 146–149 cm

Subbotina cancellata Blow. Olsson et al., 1999, p. 29, 30, pl. 25, figs. 1–15.

Stratigraphic range. Zone P1c (lower Danian). Very rare in piston-core samples at 20–22 cm, 27–29 cm, 35–38 cm, and 47–50 cm.

Subbotina triloculinoides (Plummer, 1926)

Globigerina triloculinoides Plummer, 1926, p. 134, pl. 8, figs. 10a–b.
Subbotina triloculinoides (Plummer). Olsson et al., 1999, p. 31, 32, pl. 14, figs. 15, 16, pl. 27, figs. 1–13.

Remarks. Specimens of *S. triloculinoides*, the marker species of Zone P1b (cf. Berggren & Norris in Olsson et al., 1999, p. 9), were only found within Zone P1c. Its range is truncated at the bottom of the piston core by an unconformity separating Zone P1c from directly overlying Zone P1a sediments. The hiatus spans at least the entire Zone P1b, and perhaps also part of upper Zone P1a.

Stratigraphic range. Zone P1c (lower Danian). Rare to common in piston-core samples at: 6–8 cm, 8–10 cm, 12–15 cm, 15–18 cm, 18–20 cm, 22–23 cm, 27–29 cm, 29–31 cm, 33–35 cm, 35–38 cm, 38–41 cm, 41–44 cm, and 47–50 cm.

Subbotina trivialis (Subbotina, 1953)
Figs. 12.14–12.17

Globigerina trivialis Subbotina, 1953, p. 64, pl. 4, figs. 4–7.
Subbotina trivialis (Subbotina). Olsson et al., 1999, p. 32, 33, pl. 9, figs. 10–12 (reillustrated holotype), pl. 28, figs. 1–13.

Remarks. Species has 3½–4 chambers in the last whorl, a low to moderately high trochospire, an umbilical arched aperture bordered by a thin lip, and a spinose, weakly cancellate wall texture.

Phylogenetic relationships. Subbotina trivialis is considered the earliest representative of *Subbotina*. It probably evolved from 4-chambered morphotypes of *Eoglobigerina eobulloides* in Zone P1a, or earlier (cf. Olsson et al., 1992, 1999).

Stratigraphic range. Zone P1a–Zone P1c (lower Danian; Fig. 4).

Family TRUNCOROTALOIDIDAE Loeblich & Tappan, 1961
Genus *Praemurica* Olsson, Hemleben, Berggren & Liu, 1992
Type species: *Globigerina* (*Eoglobigerina*) *taurica* Morozova, 1961

Praemurica nikolasi Koutsoukos, n. sp.
Figs. 13.1–13.8, 14.1–14.9

Globigerina fringa Subbotina. Smit, 1982, p. 339, pl. 2, figs. 11A–C.
''Globorotalia'' (*Turborotalia*) cf. *tetragona* (Morozova). Stott & Kennett, 1990, p. 559, pl. 1, figs. 12, 13.
Eoglobigerina fringa (Subbotina). Huber, 1991, p. 461, pl. 2, fig. 8.

Description. Very small trochospiral test with 10–12 chambers, commonly with 4½–5 subglobular chambers in the last whorl, increasing gradually in size. Trochospire varying from low to moderately high; equatorial periphery lobate; axial periphery moderately compressed; very small, hardly discernible umbilicus; chambers on the spiral side are rounded to slightly elongate-oval, drawn out in the direction of coiling; chambers on the umbilical side are broadly triangular, somewhat angular in disposition; last chamber is inflated, balloon-shaped, subglobular, slightly offset toward the umbilicus, with a well-developed apertural lip projecting over the umbilicus and covering most of it. Sutures distinct, depressed, radial on the umbilical side, oblique to curved in the direction of coiling on the spiral side. Aperture developed as a low, wide umbilical-extraumbilical arch, bordered by a moderately thin, wide imperforate lip covered by scattered small pustules with a hispid/corrugated margin. Wall calcareous, microperforate, circular pores ~0.3–1.0 μm in diameter, with a nonspinose, weakly developed cancellate praemuricate texture, in varying developmental stages, from pustules coalescing around pores (Fig. 13.1d) to well-formed honeycomb ridges surrounding pores of a rather coarsely cancellate wall texture, distinctive under the SEM (Fig. 13.3b).

Detailed high-magnification SEM analyses of well-preserved specimens reveal a few scattered structures similar to primitive small pores developed next to pustules and occasionally to larger well-defined pores (see Figs. 13.1d, 14.6b). These small pores are not spine holes, are not related to the dissolution process, and are commonly obscured in specimens with better developed cancellate walls and by gametogenic overgrowth calcification.

Holotype (USNM 545300; Fig. 13.1a–d): maximum diameter 139 μm, thickness 81 μm, proloculus indistinct; paratypes: diameter 127–166 μm (averaging 149 μm), thickness/height 74–97 μm (averaging 86 μm).

Remarks. The new species is placed within the genus *Praemurica* by the development of a microperforate, nonspinose, weakly cancellate praemuricate wall texture.

Despite variations in spire height (e.g., holotype USNM 545300, Fig. 13.1, and paratype USNM 545301, Fig. 13.2) all specimens assigned to *Pr. nikolasi* n. sp. consistently share the same chamber arrangement, with 4½–5 subglobular chambers, an inflated, balloon-shaped, subglobular last chamber projecting over the umbilicus with a well-developed apertural lip largely obscuring it, and an umbical-extraumbilical aperture. The variety of morphotypes probably has established phylogenetic roots from which are derived all the subsequent earliest Danian cancellate species (see below).

Specimens with a distinct low, nearly flat trochospire, somewhat resemble *Globigerina* (*Eoglobigerina*) *theodosica* Morozova, 1961 (holotype reillustrated in Olsson et al., 1999, p. 20, pl. 8, figs. 16–18), a 5–chambered species with a moderately low elevated spiral side and fine cancellate wall, assigned by Olsson et al. (1999) to the *Eoglobigerina edita* plexus. *Praemurica nikolasi* n. sp. differs by the characteristic shape of the last chamber, fewer numbers of chambers in the last whorl, closed umbilicus, and aperture that is a low and wide arch, with a rim commonly bordered by a broad, imperforate corrugated lip. *Globigerina* (*Eoglobigerina*)

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(lowermost Zone Pα); 3 (USNM 545302), paratype, 134–136 cm (lower Zone Pα), 3b, detailed view of third chamber of the final whorl showing the better developed and rather coarse cancellate wall texture, with honeycomb ridges surrounding pores located at the center of the cells; 4 (USNM 545303), paratype, 151–153 cm (Zone P0).

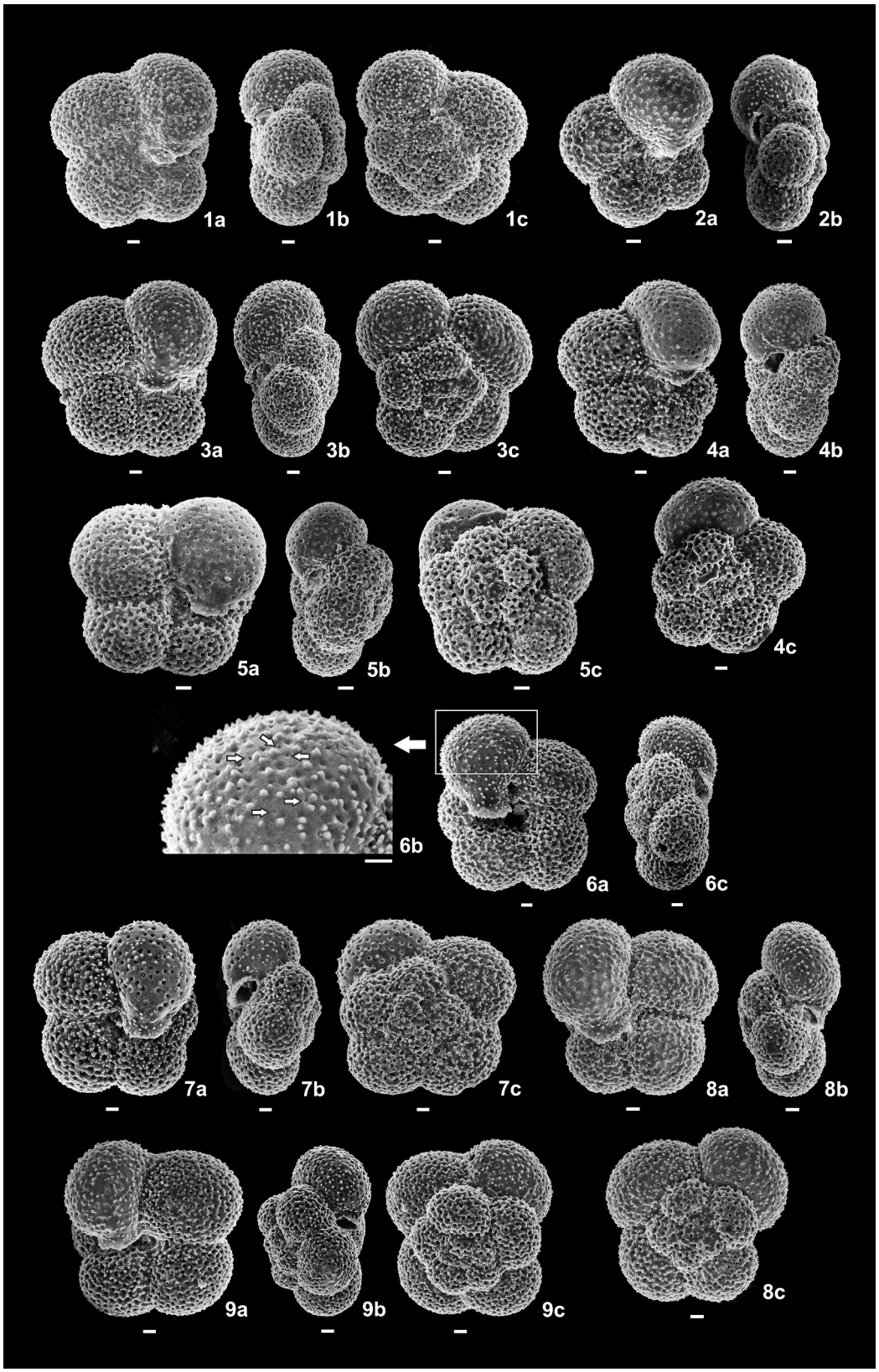


FIGURE 14. **1–9** *Praemurica nikolasi*, n. sp.; scale bars = 10 μm unless stated otherwise. 1 (USNM 545308), paratype, 151–153 cm (Zone P0); 2 (USNM 545309), paratype, 6 (USNM 597403), paratype, 146–149 cm (lowermost Zone Pα), 6b, detail of last chamber showing scattered pustules and possible primitively developed small pores (white arrows); 3 (USNM 545310), paratype, 4 (USNM 545311), paratype, 5 (USNM 545312), paratype, 160–162 cm (lowermost Zone P0); 7 (USNM 597404), paratype, 130–132 cm (lower Zone Pα); 8 (USNM 597405), paratype, 134–136 cm (lower Zone Pα); 9 (USNM 597406), paratype, 143–146 cm (lowermost Zone Pα).

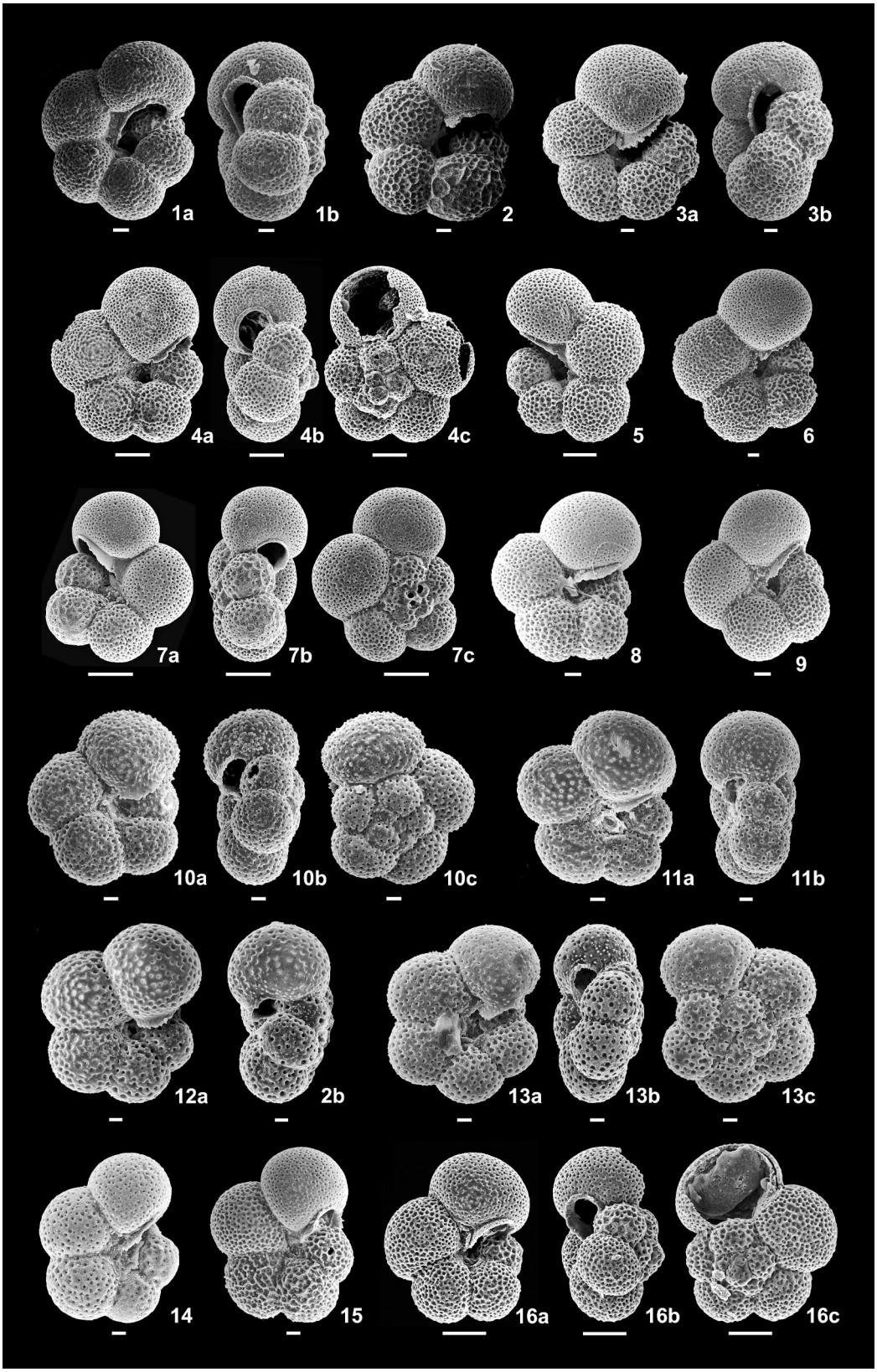


FIGURE 15. *Praemurica* species; scale bars = 20 μm unless stated otherwise. **1–3** *Praemurica inconstans* (Zone P1c): 1 (USNM 597407), 3 (USNM 597409), 3–6 cm; 2 (USNM 597408), 6–8 cm. **4–9** *Praemurica pseudoinconstans* (Zone P1c): 4 (USNM 597410; scale bar = 50 μm), 5 (USNM 597411; scale bar = 50 μm), 7 (USNM 597413; scale bar = 50 μm), 24–27 cm; 6 (USNM 597412), 8 (USNM 597414), 9 (USNM 597415), 3–6 cm. **10** *Praemurica nikolasi* n. sp. ex interc. *Pr. taurica* (USNM 597416; scale bar = 10 μm), 153–155 cm (upper Zone P0). **11–16** *Praemurica taurica*: 11 (USNM 597417; scale bar = 10 μm), 136–139 cm (lower Zone Pα); 12 (USNM 597418; scale bar = 10 μm), 134–136 cm (lower Zone Pα); 13 (USNM 597419; scale bar = 10 μm), 143–146 cm (lowermost Zone Pα); 14 (USNM 597420), 15 (USNM 597421), 16 (USNM 597422; scale bar = 50 μm), 3–6 cm (Zone P1c).

theodosica appears to be a morphotype of the *E. edita* plexus, as concluded by Olsson et al. (1999).

Specimens of *Pr. nikolasi* n. sp. with a moderately high to highly elevated trochospiral test are somewhat similar to *Eoglobigerina tetragona* Morozova, 1961 (holotype reillustrated in Olsson et al., 1999, p. 20, pl. 9, figs. 1–3), also placed within the *E. edita* plexus by Olsson et al. (1999). *Praemurica nikolasi* n. sp. also differs in apertural features and in having its characteristically offset, balloon-shaped last chamber projecting into the umbilicus.

The new species is practically homeomorphic with *Turborotalita quinqueloba* (Natland, 1938), which ranges from the Oligocene–Recent, and is very similar morphologically to *Turborotalita praequinqueloba* Hemleben & Olsson, 2006 (in Pearson et al., 2006, p. 165, pl. 6.20), a late Eocene species. It differs from *T. praequinqueloba* in having morphotypes typically with a low to highly elevated trochospire; 4½–5 (rather than 4–4½) globular chambers in the last whorl; chambers gradually increasing in size; a less lobate profile; an ultimate subglobular chamber nearly equal to or larger than the penultimate one (never reduced in size as often seen in *T. praequinqueloba*), typically projecting toward the umbilicus; an umbilical to slightly extraumbilical low-arched apertural opening commonly bordered by a thin corrugated imperforate lip; and a more weakly developed cancellate test, with minute circular pores (diameter ~0.3–1.0 μm). It differs from *T. quinqueloba* in having a less compact test, with a looser, more lobate equatorial periphery; a low to moderately high trochospire; and an invariably large final chamber.

Despite the high degree of morphological variablity, which can be observed among early Danian Globigerinina, *Pr. nikolasi* n. sp. is quite a stable morphospecies. It remarkably exhibits a consistent expression of its main morphological characters and common occurrence throughout the studied Danian interval, and can be easily distinguished from other globigerinacean species.

Repository. Holotype USNM 545300 and paratypes USNM 545301–545312 (in October 2011) and USNM 597403–597406 deposited at the National Museum of Natural History, Smithsonian Institution, Washington, D.C. Additional unpublished topotypes are deposited in the NMNH collections with the curatorial numbers USNM 597428–597437.

Etymology. Named after Nikolas Alves Koutsoukos, my son, who accompanied me during two research visits (March–June 2009 and March–May 2012) in Heidelberg, Germany.

Phylogenetic relationships. The species is the earliest recorded member of the Truncorotaloididae and of the cancellate lineages. It appears to descend directly from *Hedbergella monmouthensis*, from which it differs by having a microperforate test with a nonspinose weakly developed cancellate praemuricate wall texture, a more closed umbilicus with the last chamber protruding into and covering most of the umbilical area, generally fewer chambers in the last whorl, and a progressively higher trochospire.

Morphologically, in chamber arrangement (viewed both dorsally and ventrally) and variability in spiral height, *Praemurica nikolasi* n. sp. appears to be intermediate between the genera *Praemurica* (nonspinose, Truncorotaloididae) on the one hand and *Eoglobigerina* and *Parasubbotina* (spinose, Globigerinidae) on the other. Indeed transitional morphotypes are commonly seen within the population (see below), in some instances in blooms coeval or just about preceeding the first occurrence of the probable derived species. It could very well be the common progenitor-ancestor-species stock from which all early Danian cancellate lineages were derived (see further discussion below).

Stratigraphic range. Zone P0–Zone P1c (lower Danian; Fig. 5); range truncated here by the top of the piston core.

Geographic distribution. The occurrence of *Praemurica nikolasi* n. sp. in a deep-water core of the Campos Basin implies a preference for tropical to subtropical oceanic water masses at low to middle latitudes, but this needs to be confirmed from other sites.

Stable isotope paleobiology. Currently unrecorded.

Praemurica inconstans (Subbotina, 1953)
Figs. 15.1–15.3

Globigerina inconstans Subbotina, 1953, p. 58, pl. 3, figs. 1, 2.
Praemurica inconstans (Subbotina). Olsson et al., 1999, p. 73, 74, pl. 10, figs. 4–6 (reillustrated holotype), pl. 59, figs. 1–16.

Remarks. Species with a subcircular to oval test commonly with 5–6, up to 7, globular conical-shaped umbilical chambers in the last whorl, increasing gradually in size; low to high arched umbilical-extraumbilical aperture with distinct lip; wall texture nonspinose cancellate.

Phylogenetic remarks. Praemurica inconstans evolved from *Pr. pseudoinconstans* at around the P1b/P1c zonal boundary by developing a test with more inflated conical-shaped umbilical chambers.

Stratigraphic range. Zone P1c (lower Danian; Fig. 5).

Praemurica pseudoinconstans (Blow, 1979)
Figs. 15.4–15.9

Globorotalia (*Turborotalia*) *pseudoinconstans* Blow, 1979, p. 1105, pl. 67, figs. 3, 4, pl. 69, fig. 4.
Praemurica pseudoinconstans (Blow). Olsson et al., 1999, p. 74, 75, pl. 60, figs. 1–13.

Remarks. The species has a very low trochospire commonly with 5–5½ subglobular chambers in the last whorl, increasing gradually in size; straight umbilical sutures; aperture an umbilical to extraumbilical high arch bordered by a rather ragged imperforate lip; wall texture nonspinose weakly cancellate. It is distinguished from *Parasubbotina pseudobulloides* by having less inflated chambers in the last whorl, increasing less rapidly in size, and a nonspinose wall with a meandriform pattern of cancellate ridges, well-observed under the SEM, each containing one or more pores (see Olsson et al., 1999, pl. 60, fig. 13). It differs from *Praemurica taurica* by having moderately inflated chambers, which increase more rapidly in size in the last whorl.

Phylogenetic remarks. Praemurica pseudoinconstans evolved from *Pr. taurica* in Zone Pα by slightly increasing the rate of chamber growth and inflation in the last three chambers of the last whorl (Olsson et al., 1992, 1999).

Stratigraphic range. Zone Pα–Zone P1c (lower Danian; Fig. 5).

Praemurica taurica (Morozova, 1961)
Figs. 15.11–15.16

Globigerina (*Eoglobigerina*) *taurica* Morozova, 1961, p. 10, pl. 1, fig. 5a–c.

Praemurica taurica (Morozova). Olsson et al., 1999, p. 75, 76, pl. 10, figs. 1–3 (reillustrated holotype), pl. 61, figs. 1–15.

Remarks. Species has a very low trochospiral test commonly with 5–6 inflated subglobular chambers in the last whorl, increasing gradually in size; profile very lobate; aperture a low to high arch, umbilical–extraumbilical in position, bordered by a narrow lip; relatively broad and deep umbilicus; nonspinose, with a weakly cancellate praemuricate wall texture. Morphologically advanced forms (Figs. 15.13–15.15) have more conical-shaped umbilical chambers, increasing rapidly in size in the last whorl.

Phylogenetic remarks. Praemurica taurica evolved from *Pr. nikolasi* n. sp. in late Zone P0, to which it is linked by transitional forms (see Fig. 15.10).

Stratigraphic range. Upper? Zone P0/Zone Pα–Zone P1c (lower Danian; Fig. 5).

BIOSTRATIGRAPHIC SEQUENCE AND EVOLUTIONARY EVENTS

The Danian planktic foraminiferal biozonation scheme adopted in this paper is based on Berggren & Norris (in Olsson et al., 1999, p. 8–10).

Plummerita hantkeninoides Zone — Uppermost Maastrichtian

The cream-colored, marly ooze recorded at the core base (interval 162–183 cm) marks the uppermost Maastrichtian (Figs. 4, 5). It yields a highly diversified planktic foraminiferal assemblage (Appendices 1, 2) characteristic of the *Plummerita hantkeninoides* Zone.

Very rare trans-K/Pg specimens appear scattered within the lowermost Danian interval, rapidly declining in numbers upward (Appendix 2). The total demise of the trans-K/Pg species is around upper Zone Pα. At that level the occurrences are mostly represented by extremely rare, isolated, and partially broken specimens, at a rate of about 1 K planktic /10,000 Pg planktic forams. These latter stray occurrences were likely reworked from nearby Cretaceous outcrops of unconsolidated muds episodically eroded by bottom currents. Though reworking is ubiquitous in some proportion in most K/Pg boundary sections (e.g., Huber, 1996; Kaiho & Lamolda, 1999; Huber et al., 2002), it is uncertain if the recovered trans-K/Pg specimens in the piston core are reworked or survivors.

Apart from the few well-known Cretaceous survivors, such as *Guembelitria cretacea* (the best known and longest-lasting survivor, recorded throughout the Danian), *Hedbergella holmdelensis*, *Hd. monmouthensis*, and *Zeauvigerina waiparaensis*, species with demonstrated close phylogenetic linkages to all Danian Globigerinina (cf. Liu & Olsson, 1992; Olsson et al., 1999), it is highly controversial that any other trans-K/Pg species could be a true survivor.

Zone P0 — Lowermost Danian

The characterization of the lowermost Danian Zone P0 in the studied piston core is not straightforward as it spans only about the first 10 cm above the K/Pg boundary layer (interval 162–151 cm). Its base is marked by the near-complete demise of Cretaceous planktic species, belonging to the genera *Abathomphalus*, *Contusotruncana*, *Globigerinelloides*, *Globotruncana*, *Gobotruncanella*, *Globotruncanita*, *Heterohelix, Laeviheterohelix, Planoglobulina*, *Plummerita*, *Pseudoguembelina*, *Pseudotextularia*, *Racemiguembelina*, *Rugoglobigerina*, and *Ventrilabrella* (Appendices 1, 2; Figs. 4, 5). Within the zonal interval, only a few probably reworked Cretaceous specimens have been recovered (Appendix 2), together with very rare specimens of *Gu. cretacea* (Figs. 6.1–6.6), *Hd. holmdelensis*, *Hd. monmouthensis*, and *Z. waiparaensis*, four among only a few known true survivors (see above). However, the interval is not devoid of newly evolving Danian species, which have their first occurrences at this very early interval (Figs. 4, 5), including *Parvularugoglobigerina alabamensis* (Fig. 9.1), *P. extensa* (Figs. 9.2, 9.3), *Woodringina irregularis* (Figs. 6.7–6.11), *Eoglobigerina* aff. *E. eobulloides* (Figs. 11.14–11.16), and, more remarkably, *Praemurica nikolasi* n. sp. (Figs. 13.1–13.8, 14.1–14.9), the earliest recorded member of the Truncorotaloididae and of the cancellate lineages, which occur persistently and continuously from the lowermost Danian upward. Stray, non-continuous occurrences of extremely rare Guembelitriidae specimens (*P. alabamensis, P. extensa, P. eugubina, P. longiapertura,* and *W. irregularis*) are recorded within lower Zone P0, but could represent some degree of mixing from an upper Zone P0 level, and are thus marked as questionable (Fig. 4). Apart from *Pr. nikolasi* n. sp., no other specimen of the Truncorotaloididae or Globigerinidae was recovered within lower Zone P0 (Fig. 5), which clearly demonstrates a preserved in situ record.

Even considering some degree of mixing in the lowermost Danian samples, the preserved record suggests that the starting point of recovery of the planktic foraminifera in the aftermath of the K/Pg boundary event, and the origination of the first Danian species, took place at a much faster pace than previously reported. The time span of Zone P0 is estimated to have been ~30 kyr (Berggren & Pearson, 2005). If so, the average sediment accumulation rate of the 10 cm-thick Zone P0 interval would be ~1 cm/3 kyr, which is considerably much slower than the average accumulation rate for modern deep-ocean pelagic sediments (~0.5–1.0 cm/1 kyr; Sverdrup & Armbrust, 2009, p. 114). Thus, the first occurrences recorded within the lowermost Danian samples would have taken place a few thousand years after the K/Pg boundary event, during an interval of ~3–6 kyr, and possibly even less.

Zone Pα — Lower Danian

The entire Zone Pα spans 80 cm (interval 151–71 cm) in the core; however, 30 cm within this interval that is approximately in the middle part of the core are missing due to prior geochemical sampling. The zone's base is marked by the first consistent occurrence in increasing numbers of the *Parvularugoglobigerina eugubina* plexus, together with the debut of *Woodringina claytonensis* (Figs. 6.12–6.15; Fig. 4).

The zone is characterized by the high abundance of the Guembelitriidae, such as *Gu. cretacea* and the *Woodringina* plexus, which blooms at the lower interval and at the upper zonal boundary, and particularly of trochospiral tests

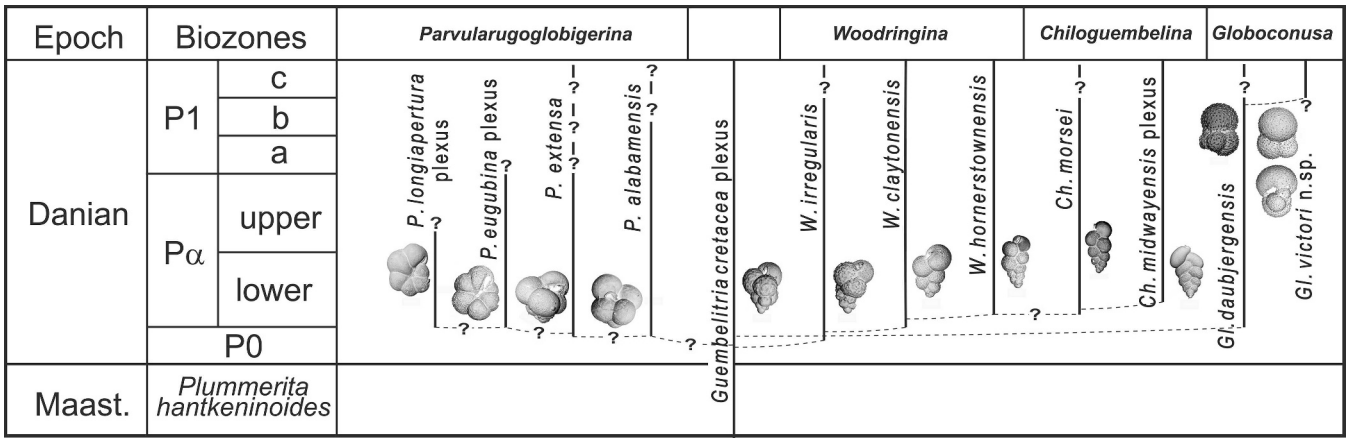


FIGURE 16. Stratigraphic ranges and phylogenetic relationships inferred for Danian species of *Parvularugoglobigerina*, *Guembelitria*, *Woodringina*, *Chiloguembelina*, and *Globoconusa*. The "?" on dashed thin lines represent uncertain phylogenetic relationships.

represented by variable morphotypes of the *P. eugubina* plexus (low to high trochospire with 4–5½, up to 7, chambers in the last whorl; Figs. 9.4–9.11), which are conspicuous throughout the interval (Fig. 4). *Parvularugoglobigerina longiapertura*, a compressed, smooth-walled low-spiral multichambered species, commonly with 6–8 chambers in the last whorl and a very elongated slit-like aperture (Figs. 9.12–9.19), blooms in the lower Zone Pα and has its last occurrence near the upper part of the zone at ~20 cm below the zonal boundary (Fig. 4). In addition, *Pr. nikolasi* n. sp. remarkably blooms in lower Zone Pα (Fig. 5), most likely coupled to radiation events from which originated the various cancellate lineages.

Typical mid-sized (>125–200 μm in maximum diameter) Globigerinidae specimens, mostly represented by the *E. edita* plexus (Figs. 11.1–11.7) and *E. eobulloides* (Figs. 11.8–11.13), make their first occurrence at ~15 cm above the zone's lower boundary (Fig. 5). The Globigerinidae (*Eoglobigerina* and *Parasubbotina*) and the other Truncorotaloididae, represented by *Praemurica pseudoinconstans* (Figs. 15.4–15.9) and *Pr. taurica* (Figs. 15.11–15.16), occur only subordinately within the zonal assemblages.

The Pα/P1a Zonal Boundary and The Dan-C2 Event

The Pα/P1a zonal boundary has been placed at a level where *P. eugubina* drops sharply in abundance (at 71 cm). The scattered occurrences in very rare numbers upward in the piston core may represent either reworked specimens or the last stragglers of a disappearing population. The peak abundance of *P. eugubina*, comprising >50% of the total planktic foraminiferal assemblage, is recorded toward the upper part of Zone Pα (interval 92–71 cm; Fig. 4). This abundance maximum is followed by a progressive stepwise decrease which culminates with the sharp decline at the zonal boundary. There is a consistent, strongly inverse relationship (Fig. 4) between the decreasing abundance of *P. eugubina* and the concomitant increasing blooms of *Guembelitria*, *Woodringina*, *Globoconusa*, and *Chiloguembelina* from uppermost Zone Pα to lowermost Zone P1a, along with associated blooms of *E. eobulloides* in lowermost Zone P1a (Fig. 5). A similar bloom of mostly *Gu. cretacea* was recorded in lower Zone P1a at Shatsky Rise (Premoli Silva et al., 2005). The peaks in abundance of the Guembelitiidae might suggest a more widespread event, associated with oceanic eutrophication in surface waters (e.g., Kroon & Nederbragt, 1990; Koutsoukos, 1996a; Keller, 2004; Keller & Pardo, 2004; Coccioni & Luciani, 2006; Pardo & Keller, 2008) across the Pα/P1a boundary transition. The latter was possibly related to the "Dan-C2" hyperthermal event, a transient greenhouse gas-driven warming episode, calibrated to fall in lowermost Zone P1a and close to the top of Chron 29r (cf. fig. 2 of Coccioni et al., 2012), which is recorded in the NW and SE Atlantic Ocean (Quillévéré et al., 2008) and the western Tethys (Coccioni et al., 2010) and thus of possible global extent. The onset of this warming event could have contributed to the decline and eventual demise of the *P. eugubina* population.

Zone P1a

Zone P1a occupies ~19 cm in the core (interval 71–52 cm). Larger (>200 μm) Globigerinidae specimens (mostly *Eoglobigerina* and *Parasubottina*; Fig. 5), such as *Pa. pseudobulloides* (Figs. 12.1–12.8), dominate the interval, together with very abundant, minute, serially coiled Guembelitriidae (mostly *Guembelitria* and *Woodringina*) and *Chiloguembelina*, marked by greater morphotypic variation (Fig. 4).

Zonal Boundary Unconformity

An unconformity (at 52 cm) eliminates Zone P1b, and perhaps also part of upper Zone P1a. No clear lithogical change is detected in the core at this position, apart from the ocurrence of fragments of a light carbonate-rich mud in the next overlying sample, but there is a sharp decline in the abundance of large-sized Globigerinidae above the unconformity (Fig. 5).

Zone P1c

Praemurica inconstans (Figs. 15.1–15.3), the biozonal marker of Zone P1c (cf. Berggren & Norris in Olsson et

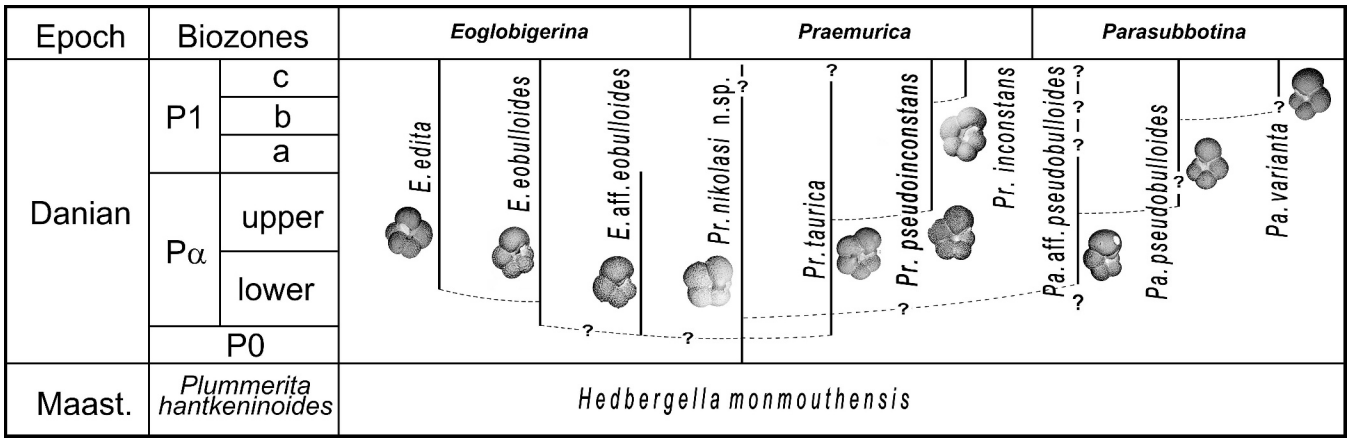


FIGURE 17. Stratigraphic ranges and phylogenetic relationships inferred for Danian species of *Eoglobigerina*, *Praemurica*, and *Parasubbotina*. The "?" on dashed thin lines represent uncertain phylogenetic relationships.

al., 1999, p. 9), together with *Parasubbotina varianta* (Figs. 12.11–12.13) have their first occurrences at 52–03 cm in the core (Fig. 5), thus confirming the assignment to Zone P1c. In accordance with Olsson et al. (1999, p. 3) the first occurrence of *Pa. varianta* is placed at about the P1b/P1c zonal boundary. The very rare presence of *Subbotina cancellata* in the samples further supports the zonal assignment (see Taxonomic Notes above). The interval also yielded scattered specimens of *Subbotina triloculinoides*, marker species of the missing Zone P1b.

Frequent specimens of a tiny trilobate species assigned herein to *Globoconusa victori* n. sp. (Figs. 7.1–7.10, 8.1–8.7; Fig. 4) first occur within the lower part of the interval, just above the boundary.

The zone is marked by common large tests of Globigerinidae (mostly *Eoglobigerina*, *Parasubbotina*, and S*ubbotina*) and Truncorotaloididae (*Praemurica*; Fig. 5), together with abundant minute, serially coiled Guembelitriidae (mostly *Guembelitria* and *Woodringina*) and *Chiloguembelina*, which dominate the assemblage (Fig. 4). Specimens of *Globoconusa* are subordinate components throughout the interval with only occasional blooms of *Gl. victori* n. sp. toward the upper part of the cored interval.

STRATOPHENETIC PHYLOGENY

PHYLOGENETIC REMARKS

The stratophenetic phylogeny of newly evolved Danian planktic foraminiferal species recovered from the piston core is shown in Figures 16 (families Guembelitriidae, and Chiloguembelinidae) and 17 (families Globigerinidae and Truncorotaloididae). Additional phylogenetic remarks are given under selected species in the Taxonomic Notes above (see also d'Hondt, 1991; Liu & Olsson, 1992; Olsson et al., 1992, 1999).

Six main lineages of minute-sized planktic foraminifera are characteristic of the Danian and jointly gave rise to nearly all the subsequent Globigerinina families: 1) the microperforate, with blunt pustules and perforation cones, triserial to biserial *Guembelitria-Woodringina* (Guembelitriidae) and *Chiloguembelina* (Chiloguembelinidae) lineage (Fig. 16); 2) the microperforate, hispid, with blunt to sharp-pointed pustules, trochoid to trilobate *Globoconusa* (Guembelitriidae) lineage (Fig. 16); 3) the microperforate, pustulose to smooth *Parvularugoglobigerina* (Guembelitriidae) lineage (Fig. 16); 4) the cancellate, nonspinose *Praemurica* (Truncorotaloididae) lineage (Fig. 17); 5) the cancellate, spinose *Eoglobigerina-Subbotina* (Globigerinidae) lineage (Fig. 17); and 6) the cancellate, spinose *Parasubbotina* (Globigerinidae) lineage (Fig. 17).

The highly plastic *Parvularugoglobigerina* likely evolved from *Guembelitria* based on their guembelitriid surface texture (smooth walled or bearing pustules with perforation cones) and general morphology. The lineage appears to be an evolutionary dead-end branch of the Guembelitriidae, most terminating at about the Pα/P1a zonal boundary (Figs. 4, 16).

Praemurica nikolasi n. sp., the earliest recorded Truncorotaloididae and cancellate species, likely evolved directly from *Hedbergella monmouthensis* near the base of Zone P0, and probably gave rise to all subsequent early Danian cancellate lineages (Figs. 17, 18). Furthermore, there is good stratophenetic linkage between *Pr. nikolasi* n. sp. with the other species of *Praemurica* in the piston core, indicating that the major phylogeny of this group took place in low paleolatitudes (R. K. Olsson, written communication, 2013). The main radiation events, coupled with peaks in abundance and morphological plasticity (Fig. 5), appear in the lowermost Pα and continue within the lower part of that zone.

The earliest Gobigerinidae (spinose, cancellate-walled, carnivorous; cf. Hemleben et al., 1991) recorded in the piston core is *Eoglobigerina* aff. *E. eobulloides*, which first occurs in latest Zone P0, and is followed by *E. eobulloides* at the P0/Pa zonal boundary (Fig. 5). *Eoglobigerina eobulloides* has a widespread paleogeographic distribution but appears in Zone P0 in mid-paleolatitudes (R. K. Olsson, written communication, 2013). It probably has a different origin from *Hedbergella*, evolving either directly from *Pr. nikolasi* n. sp. or through *E.* aff. *E. eobulloides* in late Zone P0 (Figs. 17, 18). Similarly, *Parasubbotina* aff. *Pa. pseudobulloides*, the earliest species of the *Parasubbotina* lineage, probably evolved directly from *Pr. nikolasi* n. sp. or through *E.* aff. *E. eobulloides* in the lowermost Zone Pα.

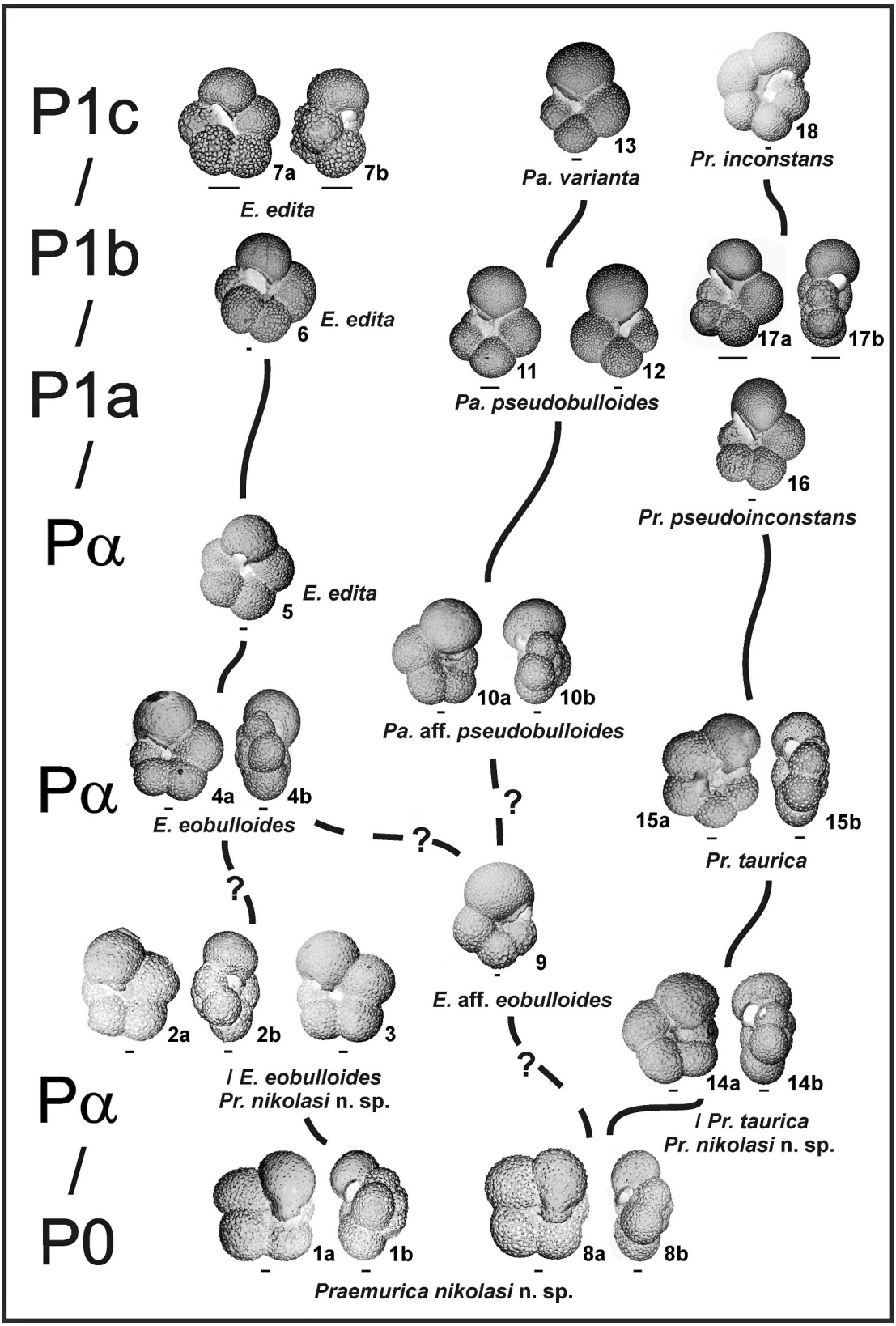


FIGURE 18. Schematic phylogenetic diagram illustrating the probable stratophenetic relationships of *Praemurica nikolasi* n. sp. to the cancellate lineages of the Truncorotaloididae and Globigerinidae in the early Danian; scale bars = 10 μm unless stated otherwise. **1–7** Lineage *Praemurica nikolasi* n. sp.-*Eoglobigerina eobulloides*-*E. edita*: 1, *Praemurica nikolasi* n. sp. (paratype USNM 545301; high-trochospiral morphotype), 146–149 cm (lower Zone Pα); 2, 3, *Praemurica nikolasi* n. sp. ex. interc. *E. eobulloides*: 2, 146–149 cm (lower Zone Pα); 3, 71–74 cm (uppermost Zone Pα); 4, *Eoglobigerina eobulloides*, 136–139 cm (lower Zone Pα); 5–7 *Eoglobigerina edita:* 5, 122–124 cm (Zone Pα); 6 (scale bar = 50 μm), 3–6 cm (Zone P1c);

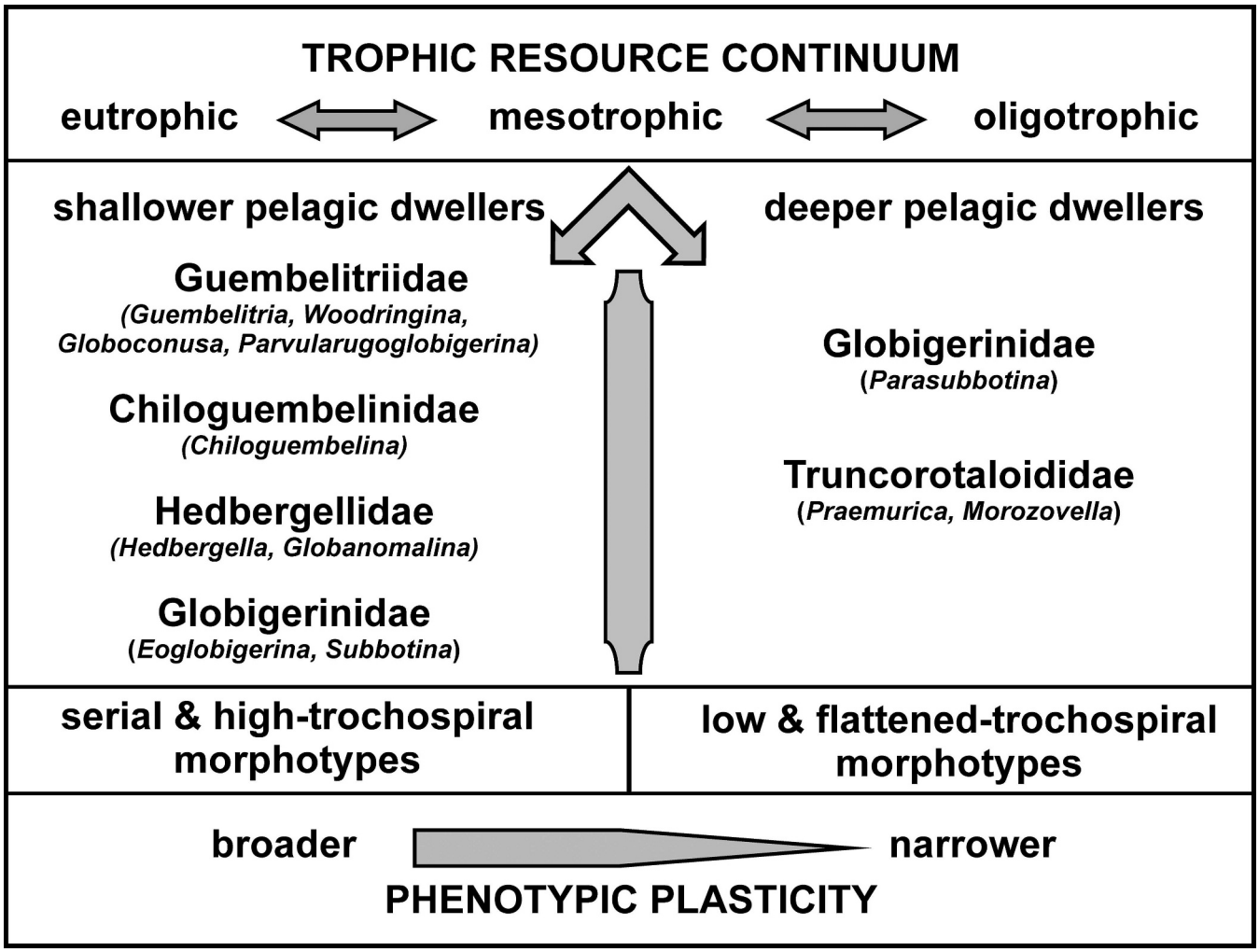


FIGURE 19. Theoretical diagram illustrating the relationships among the degree of adaptive phenotypic plasticity, inferred pelagic dwelling preferences, and water-mass trophic levels in the early Danian planktic foraminifera.

The near total absence of *Globanomalina* species in the piston core and elsewhere in the lower Danian record of the northern South Atlantic (e.g., Koutsoukos, 1996a, b) indicates that their early evolution took place in a different paleogeographic region. They are prominent in mid- to high paleolatitudes, as is *Subbotina triloculinoides* (R. K. Olsson, written communication, 2013; see also Boersma & Premoli Silva, 1983; Olsson et al., 1999).

Whereas the cancellate-walled, low trochospiral, large-sized *Praemurica* (Truncorotaloididae) and *Parasubbotina* and *Subbotina* (Globigerinidae) lineages evidently underwent rapid speciation over a relatively narrow phenotypic range, the small-sized *Praemurica*, the distinctly elevated trochoid *Eoglobigerina* (Globigerinidae), the *Parvularugoglobigerina*, and the coiled to elongate morphotypes of the *Guembelitria* and *Woodringina* (all members of the family Guembelitriidae) and *Chiloguembelina* (Chiloguembelinidae) lineages show phenotypic plasticity over a much broader range.

This dichotomy correlates with inferred differences in life-history parameters among these planktic taxa, including pelagic-dwelling preferences related to reproductive and feeding strategies and to water-mass trophic levels (see Fig. 19).

←

7, 24–27 cm (Zone P1c). **8–13** Lineage *Praemurica nikolasi* n. sp.-*Eoglobigerina* aff. *E. eobulloides*-*Parasubbotina* aff. *Pa. pseudobulloides*-*Pa. pseudobulloides*-*Pa. varianta*: 8, *Praemurica nikolasi* n. sp. (holotype USNM 545300; low-trochospiral morphotype), 134–136 cm (lower Zone Pα); 9, *Eoglobigerina* aff. *E. eobulloides*, 136–139 cm (lower Zone Pα); 10, *Parasubbotina* aff. *Pa. pseudobulloides*, 132–134 cm (lower Zone Pα); 11, 12, *Parasubbotina pseudobulloides*: 11 (scale bar = 50 μm), 24–27 cm (Zone P1c); 12 (scale bar = 20 μm), 3–6 cm (Zone P1c); 13, *Parasubbotina varianta* (scale bar = 20 μm), 3–6 cm (Zone P1c). **14–18** Lineage *Praemurica nikolasi* n. sp.-*Pr. taurica*-*Pr. pseudoinconstans*-*Pr. inconstans*: 14, *Praemurica nikolasi* n. sp. ex. interc. *Pr. taurica*, 153–155 cm (upper Zone P0); 15, *Praemurica taurica*, 143–146 cm (lowermost Zone Pα); 16, 17, *Praemurica pseudoinconstans*: 16 (scale bar = 20 μm), 58–61 cm (P1a Zone); 17 (scale bar = 50 μm), 24–27 cm (Zone P1c); 18, *Praemurica inconstans*, 6–8 cm (Zone P1c).

Epoch	Biozones		Ecological / Evolutionary Events	Main Radiation Events
Late Paleocene (Seladian)	P3		background water-mass conditions apparently fairly similar to those which existed at the end K with expanded surface-water oligotrophic settings and increased reliance on symbiosis	chiefly for the Truncorotaloididae
Early Paleocene (Danian)	P2		restructuring of nutrient levels within the water column	
	P1	c		
		b	progressive restabilization of water masses, with recovery of the surface water productivity and the oceanic C cycle	Globigeriniidae and Truncorotaloididae dominate
		a		
	Pα-P1a boundary		onset of Dan-C2 hyperthermal event	marked by extinction and radiation events
	Pα		rapid rate of recovery among pelagic communities, with increased speciation rates coupled with punctuated radiation events	chiefly for the Globigeriniidae
	P0			Guembelitriidae, Globigeriniidae & Truncorotaloididae

FIGURE 20. Schematic diagram summarizing the ecological and evolutionary (stratigraphic) responses of the main planktic foraminiferal lineages to oceanographic changes in the Paleocene.

PHYLOGENETIC TRENDS

Parallel evolutionary trends in Danian lineages seem to reflect adaptive feeding strategies caused by the changing availability of nutrients in the water column (Figs. 19, 20). For example, in the early Danian (Zones P0/Pα–P1b) the dominant planktic assemblages are largely herbivorous or passive grazers (probably most of the microperforate, pustulose Guembelitriidae and the biserial, smooth to pustulose Chiloguembelinidae), the nonspinose cancellate-walled Truncorotaloididae, and the finely perforate smooth Hedbergellidae, with subordinate omnivorous/carnivorous specimens (cancellate-walled spinose Globigerinidae; Hemleben et al., 1991).

In the aftermath of the K/Pg mass extinction event, the collapse of primary productivity in the earliest Danian coupled with reduced efficiency of the biological processes that transfer carbon from surface to deep waters (the marine biological pump) and promote nutrient cycling induced widespread oceanic eutrophication (to mesotrophic levels) of surface waters (e.g., Hsu & McKenzie, 1985; d'Hondt et al., 1998; Coxall et al., 2006; Alegret & Thomas, 2007; Fuqua et al., 2008). This may have inhibited the appearance of endosymbiont-bearing planktic taxa in the photic zone, initially favoring herbivorous and carnivorous feeding strategies (Hallock, 1982; Tappan & Loeblich, 1988; Hemleben et al., 1991; Koutsoukos, 1996a).

In the late Danian (Zones P1c–P2) there was full recovery of the planktic foraminiferal assemblages within the epipelagic layer (d'Hondt et al., 1998; Coxall et al., 2006; Fuqua et al., 2008) and a probable increasing reliance on symbiosis (likely the nonspinose, cancellate-walled, globular-chambered *Praemurica*/Truncorotaloididae; e.g., d'Hondt et al., 1994; Birch et al., 2012) under widespread oceanic low-nutrient conditions.

SUMMARY

After a near complete demise at the K/Pg boundary, the planktic foraminifera evidently recovered extremely rapidly, with newly evolved taxa appearing perhaps about every 3–6 kyr, or possibly even sooner, after the K/Pg boundary event, in the earliest Danian Zone P0 (Figs. 4, 5, 16, 17). These appearances support the concept of punctuated evolution in the micropaleontological record at certain time intervals, such as in the aftermath of mass-extinction events.

A marked bloom of the Guembelitriidae (*Guembelitria*, *Woodringina*, and *Globoconusa*), together with blooms of *Chiloguembelina* and *Eoglobigerina*, spanning uppermost Pα–lower Zone P1a, suggests widespread oceanic eutrophication of surface waters across the zonal transition that was likely related to the so-called Dan-C2 hyperthermal event. The progressive decline of the rich *Parvularugoglobigerina eugubina* population, culminating in its complete demise at the Pα/P1a boundary, appears to coincide with the onset of this event (Figs. 4, 5, 20).

The microperforate, pustulose to smooth *Parvularugoglobigerina* lineage, characteristically represented by the highly plastic *P. eugubina* and *P. longiapertura* plexuses, likely evolved from *Guembelitria* through *P. extensa.* It appears to be an evolutionary dead-end branch among the early Danian Guembelitriidae, most terminated at about the Pα/P1a zonal boundary.

Two new early Danian planktic foraminiferal species are established herein: 1) *Praemurica nikolasi* n. sp., the earliest recorded Truncorotaloididae and cancellate species, likely evolved directly from *Hedbergella monmouthensis* near the base of Zone P0, and probably gave rise to all subsequent cancellate lineages of the early Danian (Figs. 5, 13, 14, 17, 18); and 2) *Globoconusa victori* n. sp., evolved from *Gl. daubjergensis* within Zone P1c (Figs. 4, 7, 8, 16).

The good stratophenetic linkage between *Pr. nikolasi* n. sp. with other species of *Praemurica* in the piston core could

indicate that the major phylogeny of this group took place in low paleolatitudes.

Eoglobigerina eobulloides, the earliest spinose (carnivorous) cancellate species of the Globigerinidae to evolve in the early Danian, probably did not originate from *Hedbergella*, evolving either directly from *Pr. nikolasi* n. sp. or through *Eoglobigerina* aff. *E. eobulloides* in late Zone P0.

Parasubbotina aff. *Pa. pseudobulloides* probably evolved directly from *Pr. nikolasi* n.sp. or through *E.* aff. *E. eobulloides* in lowermost Zone Pα.

The near total absence of *Globanomalina* species in the piston core and elsewhere in the lower Danian record of the northern South Atlantic indicates that their early evolution took place in another paleogeographic region. They are prominent in mid- to high paleolatitudes.

The variably coiled to elongate morphotypes of the Guembelitriidae (*Guembelitria*, *Parvularugoglobigerina*, *Woodringina*, and *Globoconusa*; Figs. 6–9) and Chiloguembelinidae (*Chiloguembelina*; Fig. 10), the distinctly elevated trochoid earliest Globigerinidae (*Eoglobigerina*; Fig. 11), and the small-sized Truncorotaloididae (*Praemurica*; Figs. 13, 14) have the highest phyletic-phenotypic plasticicity and seem to have been opportunistic taxa with acmes during widespread oceanic mesotrophic conditions, such as in early Danian Zones P0, Pα, and P1a–b (Figs. 4, 5, 19, 20).

The cancellate-walled, low trochospiral spinose Globigerinidae (*Parasubbotina* and *Subbotina*) and the large-sized nonspinose Truncorotaloididae lineages (*Praemurica*; Figs. 12, 15) evince rapid speciation rates but with lesser phenotypic plasticity, and were likely equilibrium taxa thriving during mesotrophic-oligotrophic conditions, such as in late Danian Zones P1c–P2 (Figs. 19, 20).

The highly plastic morphology of the Danian planktic foraminifera allows for quite a large spectrum of intergrading and even recurring (cryptic species?) morphologies. Consequently precise intrageneric species definition often becomes blurred and must be based on much more flexible taxonomic criteria, while acknowledging the observed morphological variation. Still, distinctive patterns of test surface texture and ornamentation, being more stable characters, serve better to differentiate and demonstrate phylogenetic affinities among the various lineages.

FUTURE STUDIES

The study of the piston core is far from finished. The following research steps will be undertaken to evaluate the planktic and benthic foraminiferal assemblages comprehensively: 1) quantitatively study the smaller size fraction of the Zone P0 and early Zone Pα interval, primarily to better understand the evolutionary events within the Guembelitriidae and the early Truncorotaloididae and Globigerinidae in the lowermost part of the Danian; 2) continue the SEM analyses of all recovered species and variations, from the uppermost Maastrichtian–lower Danian, with emphasis on test wall structure and surface features; 3) analyze phyletic patterns of the early Danian planktic foraminifera; 4) analyze stable isotopes of all the recovered planktic taxa and of selected benthic taxa; 5) determine relative pelagic dwelling preferences among the planktics; 6) investigate the possible presence of symbiont photosynthetic activity in the planktic foraminifera of the latest Maastrichtian–early Danian; 7) determine the surface-to-deep-ocean carbon-isotope gradients; 8) determine the stratigraphic record of transient greenhouse climate shifts in the early Paleocene (e.g., Sprong et al., 2012) and the evolutionary response of the planktic lineages; and 9) determine if the trans-K/Pg planktic foraminifera in the piston core are either reworked or "in situ" survivors.

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APPENDIX 1

Species of planktic foraminifera recovered from the uppermost Maastrichtian (Zone *Plummerita hantkeninoides*) in the piston-core interval 162–183 cm.

Abathomphalus intermedius
Ab. mayaroensis
Contusotruncana contusa
Cont. cf. *plicata*
Cont. walfishensis
Globigerinelloides alvarezi
Gllo. messinae
Gllo. multispinus
Gllo. subcarinatus
Globotruncana aegyptiaca
Gtru. arca
Gtru. esnehensis
Gtru. gagnebini
Gtru. cf. *orientalis*
Gtru. rosetta
Globotruncanella havanensis
Gtre. minuta
Gtre. petaloidea
Gtre. pschadae
Globotruncanita stuarti
Gtri. stuartiformis
Guembelitria cretacea
Hedbergella holmdelensis
Hd. monmouthensis
Heterohelix globulosa
Hx. labellosa
Hx. planata
Heterohelix punctulata
Hx. rajagopalani
Hx. striata
Laeviheterohelix flabelliformis
L. glabrans
L. pulchra
Planoglobulina acervulinoides
Plg. brazoensis
Plg. carseyae
*Plummerita hantkeninoides**
Pseugoguembelina costellifera
Psgu. costulata
*Psgu. hariaensis**
Psgu. palpebra
Pseudotextularia elegans
Pstx. intermedia
Pstx. nuttalli
Racemiguembelina fructicosa
Rugoglobigerina hexacamerata
Rugl. macrocephala
Rugl. pennyi
Rugl. reicheli
Rugl. rugosa
Rugl. rotundata
Rugl. scotti
Ventrilabrella multicamerata

* = zonal marker species (Zone *P. hantkeninoides*)

APPENDIX 2

Distribution and relative abundance of uppermost Maastrichtian species of planktic foraminifera across the K/Pg transition in the piston-core interval 124–166 cm. VR = <1%, R = 1–5%, C = >5–10%, F = >10–20%, A = >20–30%, VA = >30–40%; gray columns indicate that taxon has not yet been recorded in the Danian.

Sample	*Abathomphalus intermedius*	*Ab. mayaroensis*	*Contusotruncana contusa*	*Co. cf. plicata*	*Co. walfishensis*	*Globigerinelloides alvarezi*	*Gllo. messinae*	*Gllo. multispinus*	*Gllo. subcarinatus*	*Globotruncana aegyptiaca*	*Gtru. arca*	*Gtru. esnehensis*	*Gtru. gagnebini*	*Gtru. cf. orientalis*	*Gtru. rosetta*	*Globotruncanella havanensis*	*Gtre. minuta*	*Gtre. petaloidea*	*Gtre. pschadae*	*Globotruncanita stuarti*	*Gtri. stuartiformis*	*Guembelitria cretacea*	*Hedbergella holmdelensis*	*Hd. monmouthensis*	*Heterohelix globulosa*	*Hx. labellosa*	*Hx. planata*	*Hx. punctulata*	*Hx. rajagopalani*	*Hx. striata*	*Laeviheterohelix flabelliformis*	*L. glabrans*	*L. pulchra*	*Planoglobulina acervulinoides*	*Plg. brazoensis*	*Plg. carseyae*	*Plummerita hantkeninoides*	*Pseugoguembelina costellifera*	*Psgu. costulata*	*Psgu. hariaensis*	*Psgu. palpebra*	*Pseudotextularia elegans*	*Ptx. intermedia*	*Ptx. nuttalli*	*Racemiguembelina fructicosa*	*Rugoglobigerina hexacamerata*	*Rugl. macrocephala*	*Rugl. pennyi*	*Rugl. reicheli*	*Rugl. rugosa*	*Rugl. rotundata*	*Rugl. scotti*	*Ventilabrella multicamerata*	MICROSPHERULES	Biozone	Stage
122–124 cm																						R																																		
124–126 cm	VR															VR						VA																								VR										
126–128 cm																						C																	VR																	
128–130 cm	VR										VR											A												VR					VR		VR	VR								VR		VR				
130–132 cm									VR													VA																			VR		VR													
132–134 cm																						VA																	VR		VR														P α	
134–136 cm								VR	VR							VR						VA																			VR									VR						
136–139 cm		VR																				F																			VR	VR														
139–141 cm																																																								
141–143 cm																						R																			VR															lower Danian
143–146 cm																						C	VR	VR		VR															VR															
146–149 cm																						F																																		
149–151 cm																						R		VR																		VR														
151–153 cm									VR													R																			VR															
153–155 cm																						R	VR	VR	VR		VR												VR		VR															
155–157.5 cm																																									VR														P 0	
157.5–160 cm		VR	VR						R					VR							VR	VR			VR		VR						VR	VR		VR			VR		VR								VR	R		VR				
160–162 cm	VR	VR				VR		R	R	R	R	R		R	R	VR	R				R	VR	VR	VR	R		R					R		R		R		R		VR	R	R		R		R			R	R		R				
162–164 cm	VR	**C**	R	VR	VR	VR	VR			R	R		R	R	R	**C**	R	R		R	R	VR	R		R		R	R	VR				R	R		**F**		R	R	**VR**	R	**F**	R	R	VR	R	R	R	R	**C**		R	R	**VA**	*Pl.*	*upper*
164–166 cm	R	C	C			VR		VR	VR		R	R				R				R	R	VR	R	R	R				VR		VR	C/F		R	VR	R	**VR**	R	**F**	**VR**	R	**C**	R	R	R			R	R	**C**	R	R	VR	**F**	*hantk.*	*Maastr.*