ORIGIN AND MORPHOLOGY OF THE EOCENE PLANKTONIC FORAMINIFER *HANTKENINA*

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ABSTRACT

Study of the origin and early evolution of the tubulospine-bearing planktonic foraminiferal genus *Hantkenina* reveals that it evolved gradually from the clavate species *Clavigerinella eocanica* in the earliest middle Eocene and is unrelated to the genus *Pseudohastigerina*.

Clavigerinella eocanica and the lower middle Eocene species *Hantkenina nuttalli* share many morphologic features and show similar developmental patterns but differ significantly in these aspects from *P. micra*. Rare, transitional *Clavigerinella-Hantkenina* forms from the Helvetikum section of Austria bridge the gap between clavate and tubulospinose morphologies, providing direct, stratigraphically-ordered evidence of the evolutionary transition between *Hantkenina* and *Clavigerinella*. Clavigerinellid ancestry is traced to a previously undescribed low-trochospiral species, *Parasubbotina eoclava* sp. nov., at Ocean Drilling Program Site 865.

We speculate that *Hantkenina* originated through competition for limited food resources in a deep, oxygen-deficient habitat below the thermocline. The tubulospines may represent a structural adaptation to this new trophic strategy, allowing the organism to harvest a greater volume of water at minimal metabolic cost. The abrupt occurrence of *Hantkenina* in pelagic sediment cores from the central Pacific and other regions of the world ocean may represent immigration into these areas following speciation within the hydrographically evolving Tethys Seaway. Alternatively, cladogenesis may have occurred over a wider area, but due to a contemporaneous global hiatus the fossil record of this bioevent is poorly preserved.

INTRODUCTION

One of the most distinctive bioevents in Cenozoic planktonic foraminifera evolution was the origin of the genus *Hantkenina*, which involved the acquisition of conspicuous hollow 'tubulospines'. Since Cushman described *Hantkenina* in 1924, the question of its origin and phylogeny has received attention from a number of authors. Commonly its first appearance in the lower middle Eocene has been regarded as one of the few punctuated events in the evolution of planktonic foraminifera (e.g., Banner and Lowry, 1985; Pearson, 1993). Yet, there have also been occasional reports of transitional clavate-tubulospinose morphologies (Premoli Silva and Spezzaferri, 1990; Fred Rögl, oral communica-

tion, *in* Pearson, 1993), intimating that the evolution of *Hantkenina* involved gradual morphological transition. Due to the scarcity of *Hantkenina* near its first appearance level and a shortage of suitable stratigraphic records of appropriate age, these assertions have been difficult to substantiate and the details of the origination and probable ancestor have not been satisfactorily demonstrated. The major hypotheses that have been proposed to explain *Hantkenina* phylogeny are presented in Figure 1.

Here we present an investigation into the origin of *Hantkenina* and its evolutionary relationships with other Eocene planktonic foraminifera using stratigraphic records that were unavailable to earlier workers. By using comparative morphologic observations, ontogenetic morphometric analysis, stable isotopes, and documenting rare, transitional hantkeninid material from Austria, we demonstrate that *Hantkenina* is a monophyletic taxon that evolved by gradual transition from the genus *Clavigerinella*. The question of clavigerinellid ancestry is also addressed and traced to the low-trochospiral genus *Parasubbotina*. We speculate on the speciation processes involved and suggest that the origin of *Hantkenina* involved divergence of populations within the same depth habitat into a new nutritional niche.

PALEONTOLOGY OF *HANTKENINA*, *CLAVIGERINELLA* AND *PSEUDOHASTIGERINA*

The tubulospinose hantkeninids had a worldwide distribution at low and mid latitudes, and their extinction at 33.7 Ma denotes the Eocene/Oligocene boundary (Coccioni and others, 1988; Berggren and others, 1995). The earliest species, *H. nuttalli* (Toumarkine, 1981), is distinctly stellate in outline and, although relatively rare, is conspicuous when present in microfossil assemblages. The early stellate hantkeninids gave rise to a continuously evolving clade that can be divided into a number of biostratigraphically useful taxa, including the late Eocene monospecific genus *Cribrohantkenina*, which is characterized by additional areal apertures (Fig. 2). The principal morphological characters used to differentiate the various species discussed in this paper are summarized in Table 1. Stable isotope analysis indicates that early Eocene forms occupied a deep sub-thermocline habitat but the group later shifted into warmer waters of the surface mixed-layer, while undergoing substantial morphological evolution, in the middle Eocene (Coxall and others, 2000).

The genus *Clavigerinella* is known from a relatively small number of localities and therefore the stratigraphic ranges and evolutionary relationships of the recognized species, *C. eocanica*, *C. akersi*, *C. jarvisi* and *C. colombiana*, are poorly understood. *Clavigerinella eocanica* has the least specialized morphology and is considered the most likely ancestor of *Hantkenina*. Moreover, we regard the bulbous,

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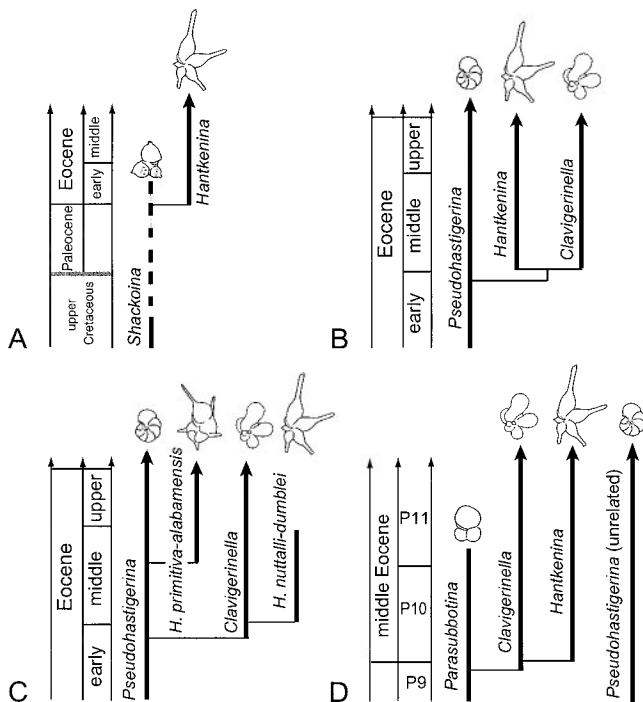
FIGURE 1.   The various hypotheses on *Hantkenina* phylogeny. A, *Hantkenina* is monophyletic and evolved from Cretaceous tubulospinose genus *Shackoina* (Pl. 2, Fig. 1) in the early middle Eocene (e.g. Cushman and Wickenden, 1930; Cushman, 1933; Thalmann, 1932, 1942; Rey, 1939; Brönnimann, 1950; Bolli and others, 1957). B, *Hantkenina* is monophyletic and evolved directly from genus *Pseudohastigerina* at the base of the middle Eocene (intermediates unknown), *Clavigerinella* is sister taxon to *Hantkenina* (Banner and Lowry 1985, Pearson, 1993). C, *Hantkenina* is polyphyletic and middle and late Eocene groups evolved independently from different pseudohastigerinid ancestors (Blow and Banner, 1962; and Blow, 1979; Berggren and others, 1967) Stellate early middle Eocene forms are linked to the proposed ancestor *Pseudohastigerina* via intermediate morphotype *Clavigerinella*, which is considered sister taxon to *Hantkenina*. A similar relationship was proposed by Dieni and Proto Decima (1964) and Steineck (1971). D, *Hantkenina* is monophyletic. It evolved from *Clavigerinella* and is unrelated to *Pseudohastigerina* (Shockina, 1937; Benjamini and Reiss, 1979; this study).

FIGURE 2.   The stratigraphic distribution of the hantkeninid species recognized in this study, including the probable ancestor of *Hantkenina, Clavigerinella eocanica*. The first appearance of *Hantkenina* (49.0 Ma) marks the base of tropical planktonic foraminiferal Biozone P10 (Berggren and others, 1995). This datum was calibrated in the Contessa Highway Section, Italy, by M. Toumarkine (Lowrie and others, 1982). It is presumed to be globally synchronous, however, the timing is not well constrained outside of the calibration locality. Stratigraphic data indicate that *Clavigerinella* ranges from the uppermost lower Eocene to the upper Eocene (Stainforth, 1948; Bolli, 1957; Blow, 1979; Pearson and Chaisson, 1997).

pointed and paddled shaped chambers of *C. akersi, C. jarvisi* and *C. colombiana,* respectively, as developments of the more moderate *C. eocanica* morphology, and therefore evolutionary side branches to the *C. eocanica-H. nuttalli* transition. *Clavigerinella eocanica* was originally described by Nuttall (1928) as *Hastigerinella eocanica.* We place this taxon in genus *Clavigerinella* Bolli, 1957, together with other Eocene clavate forms, following the taxonomic schemes of Blow (1979) and Toumarkine and Luterbacher (1985). Limited isotopic data indicate that *C. eocanica* was a deep-dwelling species that lived within or below the oceanic thermocline (Pearson and others, 1993, Coxall and others, 2000).

Pseudohastigerina, by contrast with *Hantkenina* and *Clavigerinella,* occurs in the high as well as low-latitudes. It evolved in lower Eocene Zone P8 and ranges across the Eocene/Oligocene boundary (Berggren and others, 1967). *Pseudohastigerina micra* is the longest ranging and most morphologically conservative pseudohastigerinid species. No elongation of chambers into tubulospine-like structures
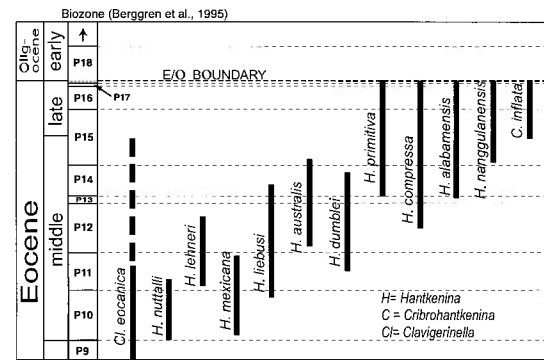
has been observed in *Pseudohastigerina* (Berggren and others, 1967).

MATERIALS AND METHODS

SAMPLE LOCALITIES
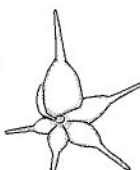
The early middle Eocene Zone P9–P10 transition, which would be expected to contain clues to the origin of *Hantkenina,* occurs in a stratigraphic interval that is often poorly represented in the deep-sea sediment record (e.g., Premoli Silva and Boersma, 1986; McGowran, 1986; Olsson and Wise, 1987; Aubry, 1995). This phenomenon has been linked with a major sea-level fall (Haq and others, 1987; Vail and Hardenbol, 1979; Aubry, 1991, 1995) and contemporaneous widespread occurrence of siliceous biofacies, suggesting increased levels of ocean productivity at that time (McGowran, 1989). However, in recent years new material has become available that has helped fill at least some of the gaps (Table 2).

The principal study material is a suite of core samples from Ocean Drilling Program (ODP) Site 865 and a subsurface sample collected in coastal Tanzania. The cornerstone evidence in our evolutionary arguments is based on a series of SEM micrographs produced by R. Olsson, Rutgers University, and F. Rögl, Museum of Natural History, Vienna, in 1991 (unpublished), documenting the gradual transition of *Hantkenina* from *Clavigerinella* in the Austrian Helvetikum section.

ODP Site 865

ODP Site 865 contains one of the most stratigraphically complete middle to upper Eocene sections available. However, as in most deep-sea sections, biostratigraphic evidence suggests the presence of a hiatus at the critical Zone P9-P10 boundary interval (Bralower and others, 1995; Norris and Nishi, in press; this study). Despite this problem, the section contains some of the best preserved and most numerous

TABLE 1. The external morphologic characters of the species discussed in this study. *H* = *Hantkenina*, *C.* = *Clavigerinella*, *P.* = *Pseudohastigerina*. Taxonomic concepts selectively follow Blow (1979) and Toumarkine and Luterbacher (1985). The taxonomy of the hantkeninids is currently under revision by the Eocene Planktonic Foraminifera Working Group. * Refers to tubulospines of *Hantkenina* on the final 2 or 3 chambers of the last whorl only. ** The tubulospines are always inclined forwards, in the direction of coiling. N.B. 'tubulospine position' and estimated 'angle of inclination' is measured with respect to the chamber central axis.

	H. nuttalli	*H. mexicana*	*H. liebusi*	*H. dumblei*	*H. compressa*	*C. eocanica*	*P. micra*
peripheral outline (side view, exc. tubulospines)	stellate, deep incisions between chambers	stellate, deep incisions between chambers	stellate/lobed, incisions between chambers	lobed/smooth, no incisions between chambers	lobed/angular, no incisions between chambers	clavate, deep incisions between chambers	smooth/rounded, no incisions between chambers
aperture	equatorial arched slit + wide lip	equatorial arched slit + wide lip	equatorial arched slit + wide lip	equatorial arched slit + wide lip	equatorial arched slit + wide lip	equatorial arched slit + wide lip	equatorial low arch + thin lip
external 'relict' aperture	often seen as 'sutural webs' in final whorl	often seen as 'sutural webs' in final whorl	none	none	none	often seen as 'sutural webs' in final whorl	none
wall	smooth, robust rel. large pores	smooth, robust rel. large pores	smooth, robust rel. large pores	smooth, robust rel. large pores	smooth, robust rel. large pores	smooth/ pseudocancellate rel. large pores	smooth, small, sparse pores
*tubulospine position	central/radial	central/radial	close to anterior suture	close to or at anterior suture	spanning or overlapping anteroir suture	N/A	N/A
*tubulospine morphology	broad-based robust, blunt-ending	narrow-based slender, narrows at tip	narrow-based slender, narrows at tip	narrow-based, slender, long, narrows at tip	narrow-based, slender/triangular narrows at tip	N/A	N/A
tubulospine tips	distal projections +/- terminal aperture	+/- small distal projections, terminal aperture	+/- small distal projections, terminal aperture	simple points, terminal aperture	simple points, terminal aperture	N/A	N/A
*tubulospine inclination**	(~0°)	(~0°)	slight (~0-45°)	moderate (~45-70°)	moderate (~45-70°)	N/A	N/A
chamber morphology	radially elongate-cylindrical	radially elongate	triangular	elongate triangular	triangular/ polygonal	rounded/ clavate	rounded/ 'kidney-shaped'
coiling	low trochospiral-planispiral	planispiral	planispiral	planispiral	planispiral	low trochospiral-planispiral	planispiral
degree of chamber inflation	rel. compressed or cylindrcal	rel. compressed or cylindrcal	compressed	compressed	slightly inflated	slightly inflated	rel. compressed - slightly inflated
Type reference	Toumarkine 1980 (=*H. aragonensis* Nuttall, 1930)	Cushman 1924	Shokhina 1937	Weinzierl & Applin 1929	Parr 1947	Cushman 1930 (=*Hastigerinella eocanica*)	Colle, 1927 (=*Nonion micrus*)

specimens of *Clavigerinella* and early *Hantkenina* ever recovered, and is thus an important source of specimens for comparative analysis. Two 20 cm³ samples per core section were taken through a Zone P9-P10 time slice, spanning the first appearance datum (FAD) of *H. nuttalli*. Sample information and the stratigraphic distribution of key species at this site are shown in Table 3. Additional samples from the middle-late Eocene were also used in this study. These are given in the text.

Tanzania

This area became historically important in micropaleontological studies following Ramsay's (1962) account of the hantkeninids from Kilwa Masoko and Kitunda and the detailed taxonomic and biostratigraphic work of Blow and Banner (1962) and Blow (1979). Continuous stratigraphic sections are rare in Tanzania and therefore systematic biostratigraphic work is not possible. However, the pristine shell preservation of the Tanzanian foraminifera enables a rare opportunity for studying shell microstructure and obtaining stable isotope data that have not been affected by diagenetic processes (Pearson and others, 2001). Sample PPK-2 contained a diverse foraminiferal assemblage, including *H. nuttalli* and *P. micra*. Large samples (~100 cm³) were processed owing to heavy dilution of microfossils by sand and clay material.

TABLE 2. Localities of studied material.

Locality	Latitude	Longitude	Biozones
ODP Hole 865B, Allison Guyot, western tropical Pacific	18°26'N	179°33'W	P9–P10
Helvetikum Section, Austria	47°58'N	13°06'W	P9–P10
Kilwa Masoko Prison, coastal Tanzania: Sample PPK-2	08°55.178'N	13°30.228'W	P10

Austrian Helvetikum Section

The Helvetikum comprises a sequence of Lower Cretaceous to upper Eocene sediments overthrusted by tens of kilometers of flysch and represents part of the northern most peripheral tectonic unit of the Alps (Hagn, 1960; Gorhbandt, 1967; Wagner, 1998). Lower middle Eocene sediments occur within the older 'Ultra Helvetikum' (Cretaceous to middle Eocene), which lies to the south of the North Helvetikum (middle to late Eocene) and South Helvetikum (Cretaceous to uppermost middle Eocene) units (Burkhard and Sommaruga, 1998). The uppermost lower Eocene to basal middle Eocene is represented by the Buntmergelserie sub-division. It consists of marls that crop out discontinuously north of Salzburg near the village of Mattsee (Hagn, 1960; Gorhbandt, 1967). This section appears to be one of the few in the world in which at least part of the lower-middle Eocene transition is preserved and is unique in containing a series of specimens transitional in morphology between *Clavigerinella* and *Hantkenina.* Sample data and the occurrence of *Hantkenina* and *Clavigerinella* are shown in Table 4.

SAMPLE PREPARATION AND ANALYSIS

Samples were gently disaggregated in water on a mechanical agitating table, wet-sieved and dried over a hot

TABLE 3. Stratigraphic range of key species in the latest-early Eocene-lower middle Eocene of ODP Hole 865B, including *Hantkenina* spp., *Clavigerinella eocanica, Pseudohastigerina micra* and the P9 zonal marker *Planorotalites palmerae.* The range of new species *Parasubbotina eoclava* is also shown. Biostratigraphy follows the zonation scheme of Berggren and others (1995). During the Eocene this site was located between 2°W and 6°N with an estimated paleodepth of 1300–1500 m and sedimentation rates of ~1/cm k. y. (Bralower and others, 1995).

Epoch	Sample	Depth (mbsf)	Biozone	Planorotalites palmerae	Pseudohastigerina micra	Parasubbotin eoclava	Clavigerinella eocanica	Hantkenina nuttalli	Hantkenina mexicana	Hantkenina liebusi
MIDDLE EOCENE	865B-7H-3, 110-112 cm	60.1	P10							R
	865B-7H-4, 63-65 cm	61.13	P10		C				R	R
	865B-7H-4, 110-112 cm	61.6	P10		C				R	
	865B-7H-5, 56-58 cm	63.54	P10		C			R	R	
	865B-7H-6, 55-57 cm	63.55	P10		C		R	R	R	
	865B-7H-6, 57-59 cm	63.53	P10			R	R	R	R	
	865B-7H -CC	-	P10		C	R	R	R	R	
	865B-8H-1, 5 5-57 c m	66.05	P10		C	R	R	R		
	865B-8H-1, 1 10-112 cm	66.6	P10		C	-	-	R		
LOWER EOCENE	865B-8H-2, 54-56 cm	67.54	P9		C	-	-			
	865B-8H-2,110-112 cm	68.1	P9		C	-	-			
	865B-8H-3, 54-56 cm	69.04	P9		C	-	-			
	865B-8H-3, 128-130 cm	69.78	P9		C	-	-			
	865B-8H-4, 53-55 cm	70.53	P9			R	R			
	865B-8H-4 , 55-57 cm	70.55	P9		C	-	R			
	865B-8H-4 , 57-59 cm	70.57	P9			R	R			
	865B-8H-4, 1 37-139 cm	71.37	P9		C	-	R			
	865B-8H-5, 59-61 cm	72.09	P9		C	R	R			
	865B-8H-5, 1 32-134 cm	72.82	P9		C	R	-			
	865B-8H-6, 10-12 cm	73.05	P9			R	R			
	865B-8H-6, 35-37 cm	73.35	P9		C	-	-			
	865B-8H-6, 75-77 cm	73.73	P9			R	R			
	865B-8H-6, 85- 87 cm	73.85	P9			R	R			
	865B-8H-6, 87-88 cm	73.85	P9		C	R	R			
	865B-9H-1, 30-32 cm	75.3	P9		C	-				
	865B-9H-2, 90-92 cm	77.4	P9		C	R				
	865B-9H-3, 90-92 cm	78.9	P9	C	C					

C=common, R=rare   ⁓⁓⁓⁓ indicates position of probable hiatus

TABLE 4.   Helvetikum section samples and hantkeninid species occurrences from F. Rögl and R. K. Olsson (unpublished). Sample 64/1-36/0 was collected by F. Aberer, November 16, 1647. Samples 64/1-36/1 to 64/1-36/4b were collected by K. Gohrbandt and F. Aberer, May 20, 1960. *C-H* transitions = forms intermediate in morphology between *Clavigerinella* and *Hantkenina*. * Indicates the first stratigraphic occurrence of hantkeninid tubulospines.

Sample	Sample position (m)	*H. nuttalli*	*C. eocanica*	*C-H transitions*
64/1-36/0	?		√	√
64/1-36/4b	19.6	√	√	√
64/1-36/4a	15.5		√	
64/1-36/3	9.5	√*	√	√
64/1-36/2	4.4		√	
64/1-36/1	0		√	

plate before examination under light microscope and by SEM. Specimens from ODP Site 865 were X-rayed and a smaller subset dissected. Morphometric analysis was performed on digital microradiographs using the public domain NIH-image software. Measurement precision was determined to be ± 2 μm at × 160 magnification (Huber, 1994). The biometric variables are illustrated in Figure 3.

ONTOGENETIC MORPHOMETRICS

Various authors have demonstrated the importance of ontogenetic information for resolving questions of phylogeny and taxonomy in recent and fossil planktonic foraminifera (e.g., Huang, 1981; Sverdlove and Bé, 1985; Brummer and others, 1987; Huber, 1994). Drawing on techniques used in these previous studies, an ontogenetic study was undertaken to compare the early developmental stages of *Hantkenina, Clavigerinella*, and *Pseudohastigerina*. The most practical methods for examining internal whorl morphology in isolated foraminiferal shells are microradiography and micro-dissection. These techniques are described in detail by Huber (1994).

RESULTS

Five species of *Hantkenina*, representing different stages in the lineage evolution, were compared to *Clavigerinella eocanica* and *Pseudohastigerina micra.*

EXTERNAL MORPHOLOGY

Hantkenina

The genus *Hantkenina* is characterized by having tubulospines on some or all of the chambers in the adult whorls (Pl. 1, Figs. 1–7). Gross morphologies of the species examined are summarized in Table 1 and the external shell ultrastructure is described below. X-ray views and dissections confirm the tubulospines to be hollow elongations of individual chambers (e.g., Pl. 2, Figs. 9–13; Pl. 3, Figs. 11, 12). These structures are rather delicate and have a tendency to break off during burial or sample processing (Pl. 1, Figs. 2–7), making them unreliable taxonomic features. The tubulospines surfaces are usually imperforate or scattered with small occasional pores and commonly ornamented with spiral grooves (Ramsay, 1962; Blow, 1979). The middle Eocene species *H. compressa*, by contrast to *H. nuttalli* and
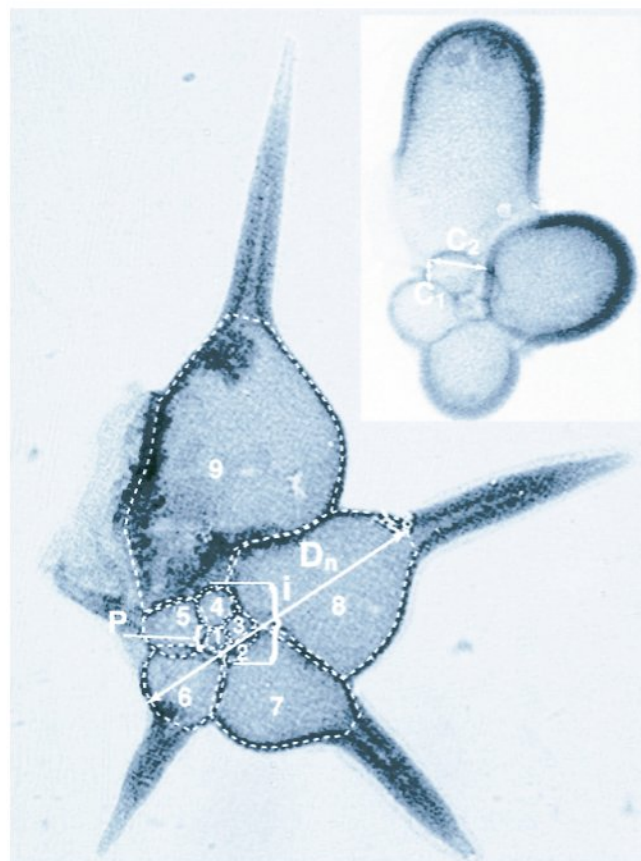

FIGURE 3.   Morphometric variables measured from X-rays. The dashed line traces the perimeter of each chamber. U, number of chambers in the ultimate whorl = 'whole number of chambers in ultimate whorl' + $[C1/(C1+C2)]$. D_n = maximum test diameter at chamber n, i = initial whorl, P = proloculus (= chamber$_1$).

H. mexicana, has a more continuous shell periphery (Pl. 1, Figs. 6–7).

Hantkenina nuttalli has ~4.5 chambers in the final whorl (mean = 4.42, see Table 5), which increase rapidly in height during ontogeny. The wall is usually smooth, robust and perforated by relatively large pores (Pl. 1, Fig. 8) that disappear abruptly at the tubulospine bases. In well-preserved material pores are often flush to the surface, whereas in even slightly dissolved material, dissolution around pore openings can give the wall a rather misleading 'pseudocancellate' appearance. However, it may be that some specimens also have original biogenic inter-pore ridges. Absolute pore size and density varies considerably across the test, through ontogeny and between individuals. Pustules are common on the earliest chambers of the final whorl close to the aperture, particularly in younger morphospecies.

Despite many dissections and studies of external wall morphology, no true spines have been found in any species of *Hantkenina* or *Cribrohantkenina* and no unequivocal spine holes have been identified. However, it has been argued (Hemleben and Olsson, oral communication, 2001) that rare probable spine holes are occasionally seen. This would support our overall thesis in uniting the *Hantkenina* group with the spinose parasubbotinids, which we contend were ancestral (see below). At this stage the present authors
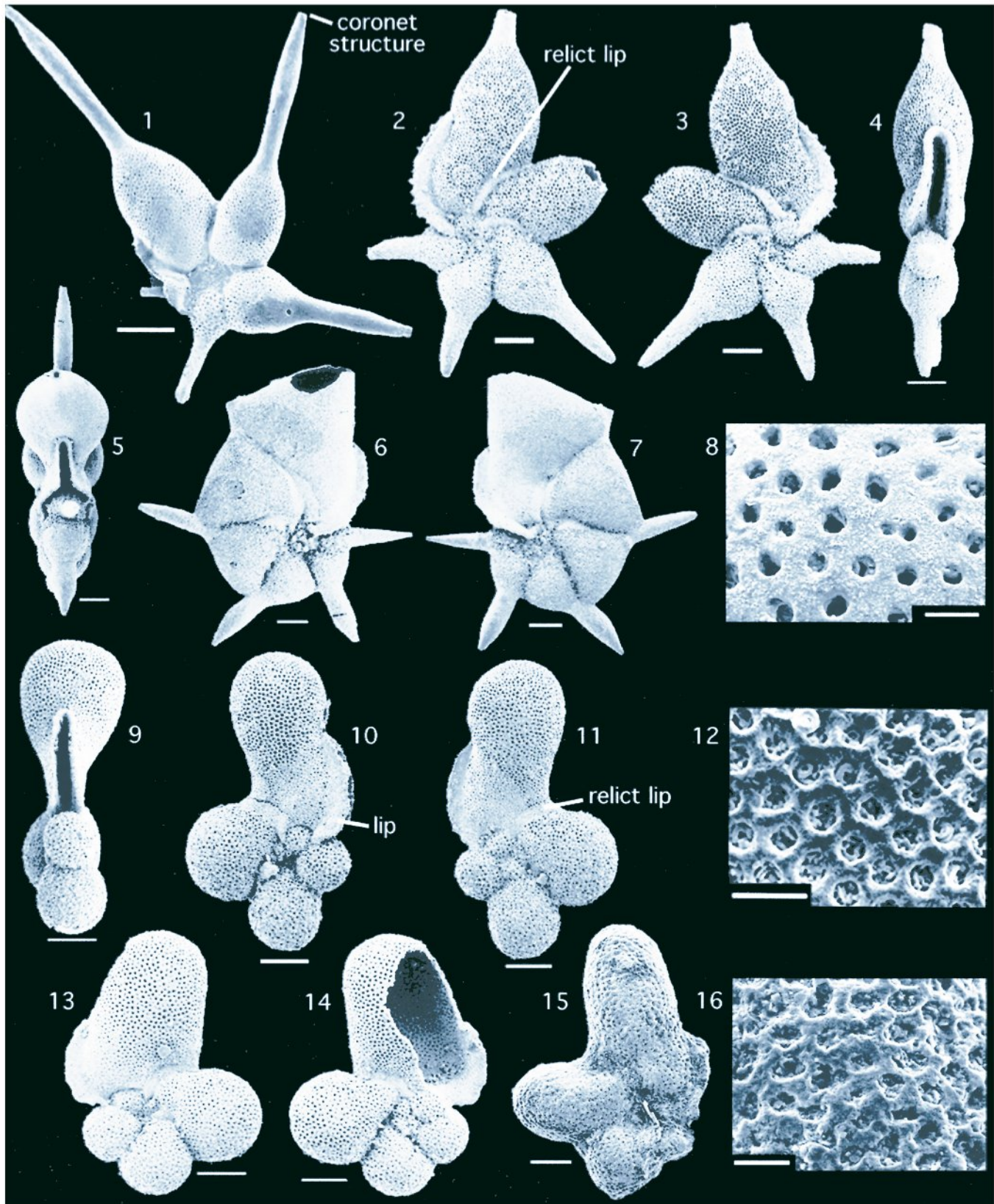
PLATE 1

External morphology. **1** and **8** *Hantkenina mexicana,* Tanzania, Sample PPK-2, Zone P11, Fig. 8 view of wall. **2–4** *Hantkenina nuttalli*, ODP Sample 865B-7H-6, 57–59 cm, Zone P10, same specimen. **5–7** *Hantkenina compressa* ODP Sample 865B-4H-3, 54–56 cm Zone P14, same specimen. **9–14** *Clavigerinella eocanica,* ODP Sample 865B-8H-6, 87–89 cm, **9–11** three views of same specimen, Fig. 12 view of wall, Fig. 13 and 14 same specimen. **15, 16** *Clavigerinella eocanica,* Helvetikum Section, Austria, 64/1-36/4b, Zone P9–P10, Fig. 16 view of wall. Scale bar: **1–7, 9–11, 13–16** = 100 μm; **8** = 10 μm; **12** = 30 μm; **16** = 20 μm.
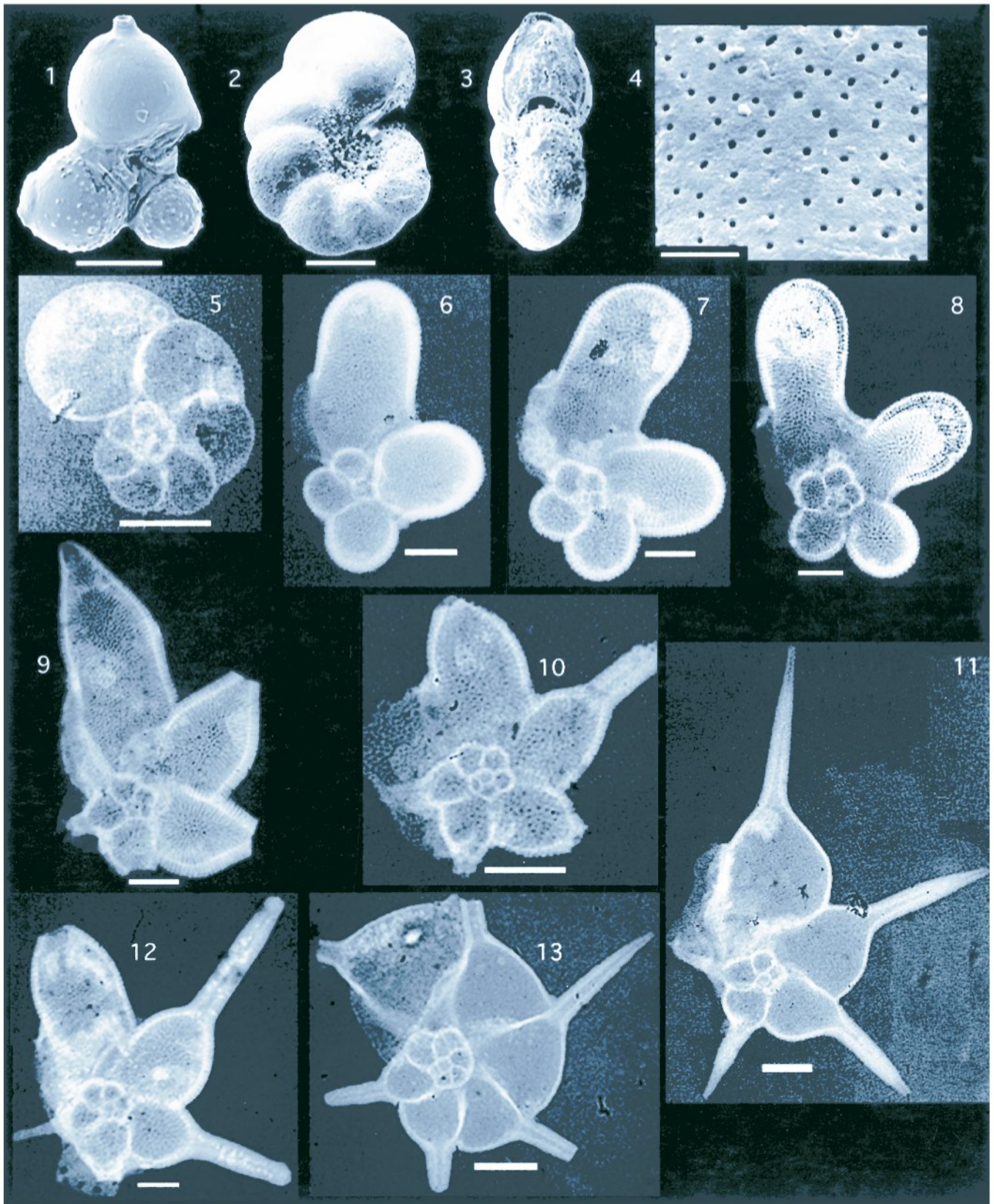
PLATE 2

External morphology. **1** *Shackoina multispinata,* Kerguelen Plateau, ODP Sample 1135-34R-CC, Campanian. **2–4** *Pseudohastigerina micra,* Tanzania, Sample PPK-2, Zone P11, same specimen, Fig. 4 view of wall. X-rays. **5** *Pseudohastigerina micra,* ODP Sample 865-7H-6H, 57–59 cm, P10. **6–8** *Clavigerinella eocanica,* ODP Sample 865-8H-6, 87-89 cm, Zone P9–P10. **9, 12** *Hantkenina nuttalli,* Tanzania, Sample PPK-2, Zone P11. **10** *Hantkenina nuttalli,* Guayabal Fm. Mexico, lower middle Eocene. **11** *Hantkenina mexicana,* Tanzania, Sample PPK-2, Zone P11. **13** *Hantkenina compressa,* ODP Sample 865B-4H-1, 60–62 cm, Zone P14. Scale bar: **1** = 50 μm; **2–3, 5–11** = 100 μm; **4** = 10 μm.
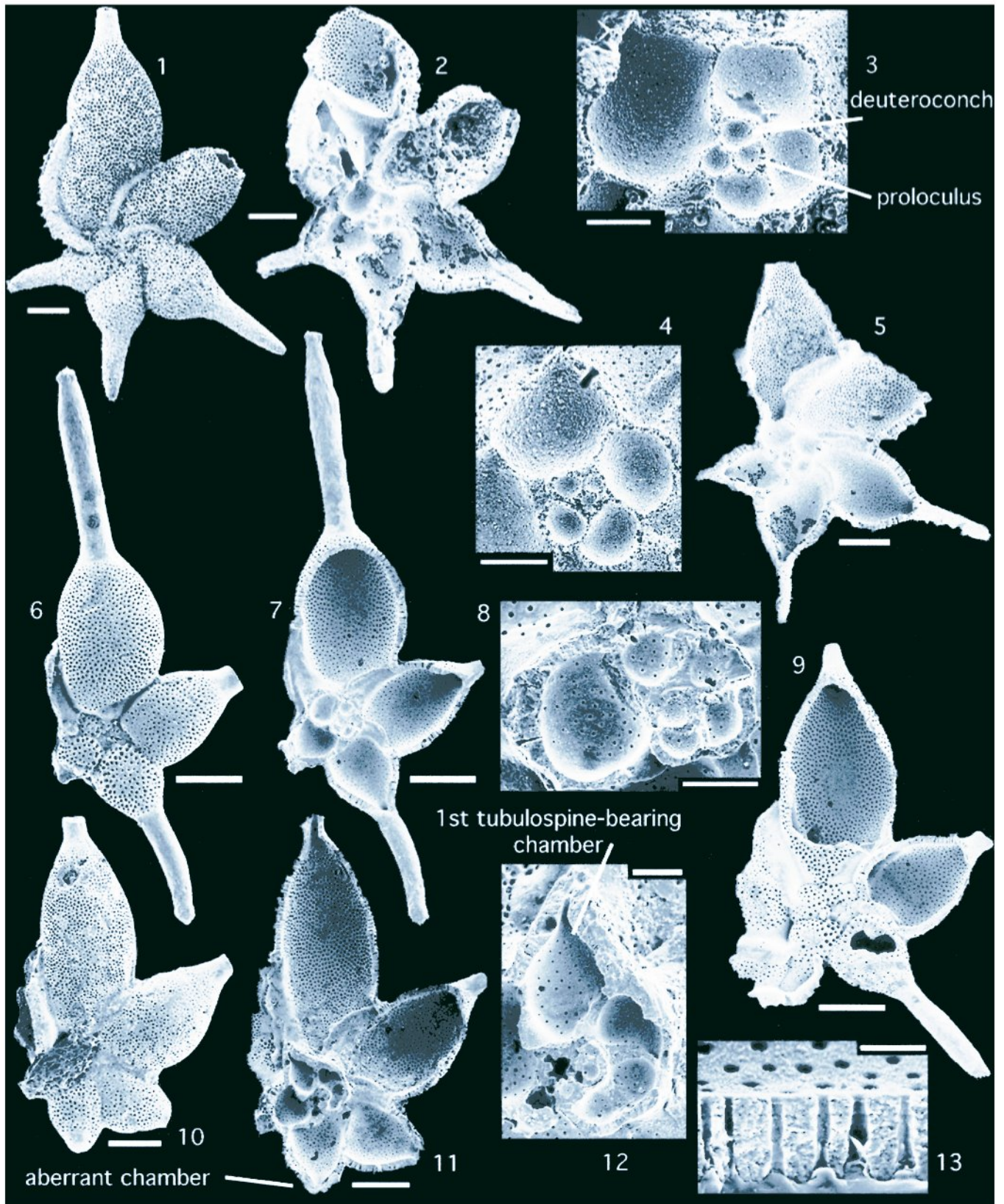
PLATE 3

External views and serial dissections. **1–3, 4–5** *Hantkenina nuttalli,* ODP Site 865B-7H-6, 55–57 cm, Zone P10. **6–8** *Hantkenina mexicana,* Sample PPK-2, Zone P10, **9–13** *Hantkenina nuttalli,* Sample PPK-2, Zone P10 Fig. 13 wall cross-section. ODP Sample 865B-4H-1, 60–62 cm, Zone P14. Scale bar: **1, 2, 5–7, 9–11** = 100 μm; **3, 4, 8, 12** = 30 μm; **13** = 10 μm.

TABLE 5. Biometric variables measured from microradiographs: T = total number of chambers in shell, U = ultimate whorl number of chambers (See Fig. 3).

Species/sample	Depth (mbsf)	Zone	T (Mean)	U (Mean)	n
C. eocanica ODP-865B-8H-6, 85–87 cm	73.85	P9	10.75	4.35	14
H. nuttalli/mexicana ODP-865B-7H-6, 57–59 cm	63.55	P10	10.60	4.42	20
H. nuttalli/mexicana ODP-865B-7H-5, 55–56 cm	61.60	P10	10.54	4.36	14
H. compressa ODP-865B-4H-3, 60–62 cm	31.10	P14	11.17	5.15	45
H. compressa ODP-865B-4H-1, 60–62 cm	28.10	P14	11.50	5.17	46
P. micra ODP-865B-4H-1, 60–62 cm	28.10	P14	14	7.67	1

are unconvinced, and the presence of true spines in hant-keninids has yet to be demonstrated.

Clavigerinella

Clavigerinella eocanica is similar in size to early *Hantkenina* (usually 250–500μm). It has approximately 4.5 chambers in the final whorl (mean = 4.35; Table 5) but lacks tubulospines. The final two or occasionally three chambers of the adult whorl are elongated into sub-cylindrical or 'clavate' extensions (Pl. 1, Figs. 9–11, 13–15). *Clavigerinella eocanica* has many features in common with *Hantkenina* (Table 1). In slightly dissolved or recrystallized material, as in some specimens of *Hantkenina,* the wall can have a pseudo-cancellate appearance (Pl. 1, Fig. 12). Specimens from the Helvetikum Section show slightly better preservation of the primary wall texture than most deep-sea core material (Pl. 1, Fig. 16) and appear to have a smooth or weakly cancellate wall as in *H. nuttalli.* It has been observed that in some examples of *Clavigerinella* the wall looks genuinely more cancellate than in *Hantkenina* and may be considered to be transitional between a truly cancellate and smooth-to-normal perforate texture (Benjamini and Reiss, 1979).

As is the case of *Hantkenina,* the presence of true spines in *Clavigerinella* has yet to be demonstrated. However, it is possible that the whole group was initially spinose with spines becoming much reduced or absent about the time of evolution of *Clavigerinella.*

Pseudohastigerina

Pseudohastigerina is a smaller species (~100–300μm) with a relatively continuous or slightly lobed peripheral outline, and a significantly different wall texture to *Hantkenina* and *Clavigerinella* (Table 1; Pl. 2, Figs. 2–4). It has 6–8 closely spaced chambers in the final whorl (Table 5), which increase gradually in size (Pl. 2, Fig. 2). This genus is fully planispiral but it probably evolved from a low trochospiral ancestor (probably *Globanomalina chapmani*) in the early middle Eocene (Berggren and others, 1967). It is unequivocally non-spinose.

INTERNAL MORPHOLOGY

X-ray images reveal the arrangement of internal whorl chambers (Pl. 2, Figs. 5–11). Serial dissection confirms these morphologies and allows examination of initial whorl ultrastructure (Plates 3–5). Dissections of *H. mexicana, C. eocanica* and *P. micra* were performed. In addition, specimens of *H. liebusi, H. dumblei* and *H. compressa* were dissected to investigate the hypothesis that the upper Eocene

forms evolved independently in the upper middle Eocene from a second pseudohastigerinid ancestor (Blow and Banner, 1962; Berggren and others, 1967; Blow, 1979). The individual dissections are described below and internal morphologic characters are summarized in Table 6.

Hantkenina

Hantkenina mexicana and *H. nuttalli* are shown in Plate 3. The initial whorl morphologies of the dissected specimens are very similar. Tubulospines are absent from the first-formed chambers in the early whorl and do not occur until the 7th or 8th chamber (Pl. 3, Figs, 2, 5, 7, 11; also see X-rays: Pl. 2, Figs 9–11). Magnified views of the initial whorl morphologies reveal tiny pore openings beginning in the second or third chamber (Pl. 3, Figs, 3, 4, 8, 12).

The initial whorl microstructure is best preserved in the Tanzanian specimens (Pl. 3, Figs. 6–13). Dissections show that the chamber wall thickness increases markedly from the 6th chamber, and that pores are distributed evenly across internal chamber surfaces after the 3rd chamber (Pl. 3, Figs., 8, 12). The proloculus appears to be imperforate. Plate 3 (Fig. 9) shows a partially dissected specimen revealing the exterior morphology and pore distribution on chambers in the initial whorl. Plate 3 (Figs. 10–12) illustrates a large specimen of *H. nuttalli* with an aberrant chamber in the final whorl. The 6th or 7th chamber of this specimen has been successfully dissected to reveal the narrow central canal running through the first-formed tubulospine (Pl. 3, Fig. 12). The view of the external morphology (Pl. 3, Fig. 10) and whorl-shell dissection (Pl. 3, Fig. 11) shows that the second chamber of the last whorl does not possess a tubulospine and instead terminates in a blind-ending imperforate stub. A magnified view of the dissected wall of *H. nuttalli* (Pl. 3, Fig. 13) reveals funnel-shaped pore canals, with the external openings being wider than the interior openings.

Plate 4 shows further dissections of the subsequent middle Eocene species *Hantkenina liebusi, H. dumblei* and *H. compressa.* Plate 4 (Figs. 1–3) shows *H. liebusi,* in which the first tubulospine appears at the 8th chamber-stage. The complete dissections (Pl. 4, Figs. 2, 3, 7, 11, 14) show that the tubulospines of early ontogenetic stages are positioned centrally on each chamber, as in *H. nuttalli,* but shift to a more anterior position in later growth stages, thus reflecting phylogeny in their ontogeny. Plate 4 (Figs. 4, 5, 7, 8) shows dissections of *H. liebusi-dumblei* transitions. The middle to upper Eocene species *H. compressa* is shown in Plate 4 (Figs. 10–15). In particular, Plate 4 (Figs. 13 and 15) shows the migration of tubulospines to a more forward position on each chamber during ontogeny.

Chamber arrangements in these younger morphospecies

tubulospine
canal
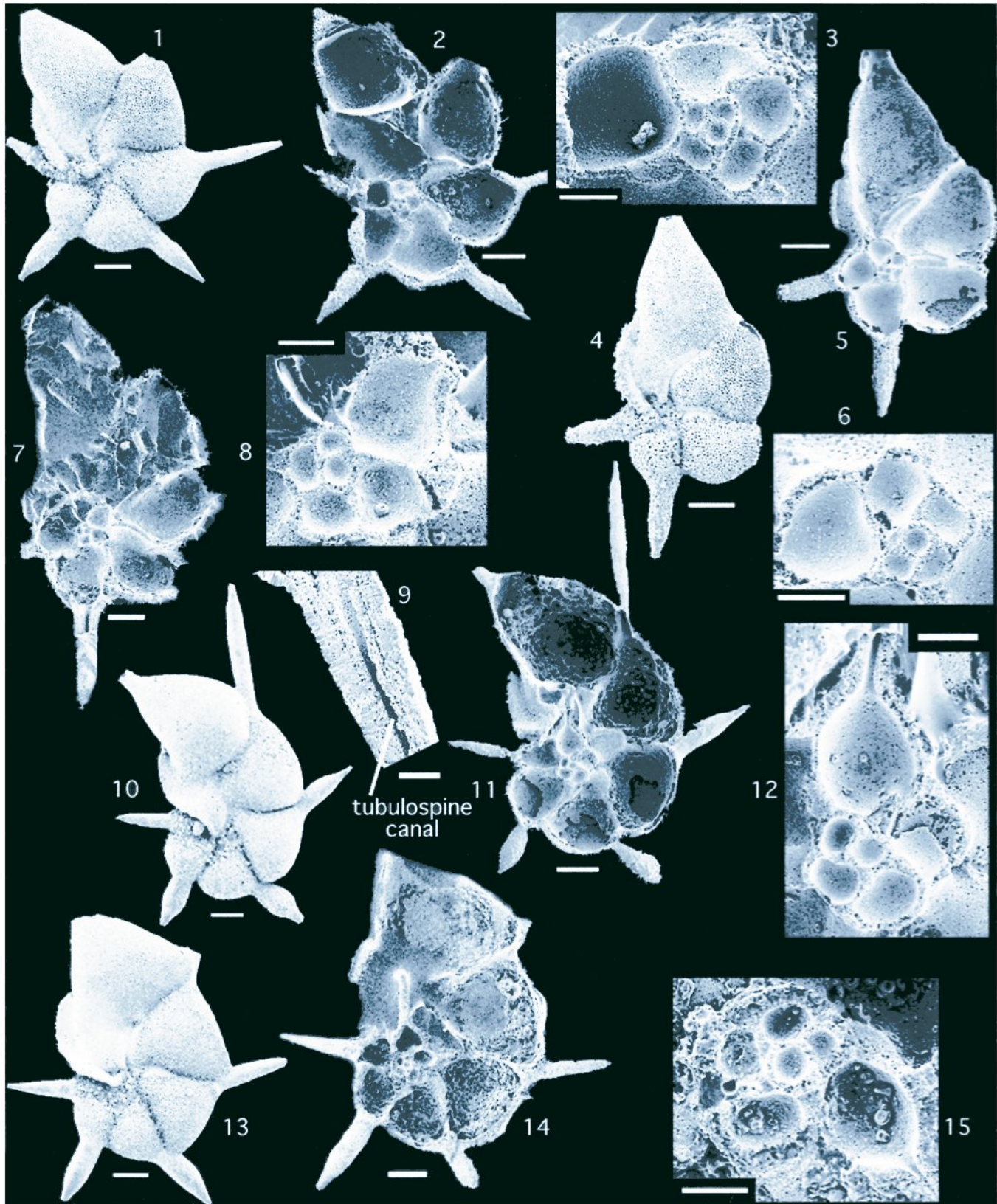
PLATE 4

External views and serial dissections. **1–3** *Hantkenina liebusi,* ODP Site 865B-5H-5, 78–80 cm, Zone P12. **4–6** *Hantkenina liebusi-dumblei* transition, ODP Sample 865B-6H-5, 52–54 cm, Zone P11. **7, 8** *Hantkenina liebusi,* ODP Sample 865B-5H-5, 54–56 cm, Zone P12. **9** *Hantkenina liebusi* section through tubulospine, ODP Sample 865B-6H-5, 52–54 cm, Zone P12. **10–12, 13–15** *Hantkenina compressa,* ODP Site 865B-4H-3, 60–62 cm, Zone P14. Scale bar: **1–2, 4, 5–7, 10, 11, 13, 14** = 100 μm; **3, 6, 8, 12, 15** = 30 μm; **9** = 10 μm.

PLATE 5

External views and serial dissections. **1–8** *Clavigerinella eocanica*, ODP Sample 865B-8H-6, 87–89 cm, Zone P9–P10. **9, 10** *Pseudohastigerina micra*, ODP Sample 865-3H-2, 75–77 cm, Zone P16. Scale bar: **1, 2, 4, 5, 7–9** = 100 μm; **3, 6, 10** = 30 μm; **10** = 10 μm.

are similar to the earlier forms except that the first tubulo-spine tends to occur earlier in ontogeny (usually on the 6th chamber) and the proloculus tends to be larger than in *H. nuttalli* and *H. mexicana* (Table 6).

Clavigerinella eocanica

Serial dissections of *C. eocanica* are presented on Plate 5 (Figs. 1–8). Magnified views of the initial whorl (Plate 5, Figs. 3, 6) shows that the chambers become clavate only in the ultimate and penultimate chambers of the final whorl. As in *Hantkenina,* the pores seem to be evenly distributed on the early chambers, although preservation is insufficient to determine whether the proloculus is porous or not.
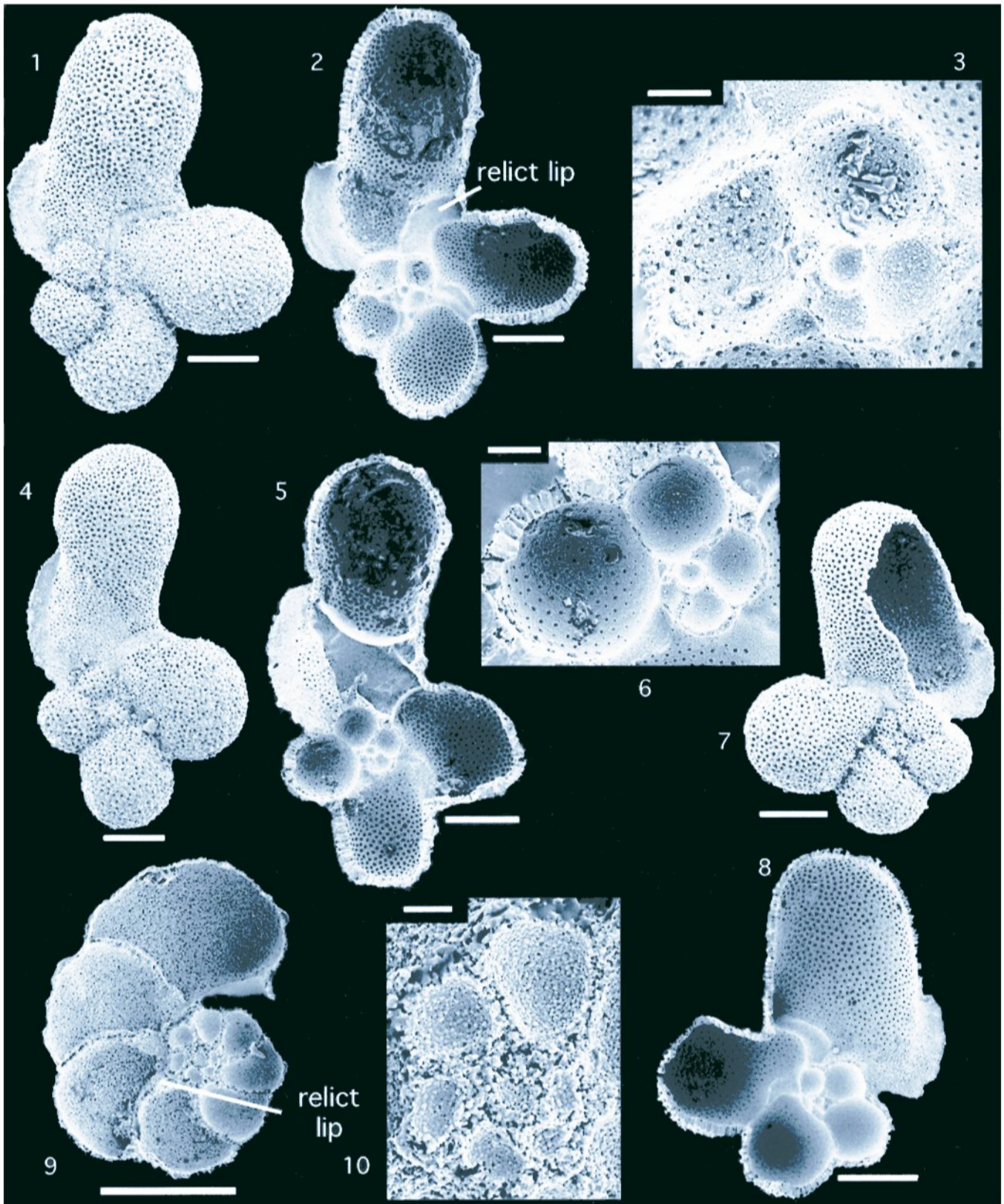
Pseudohastigerina micra

A single specimen of *P. micra* was dissected to reveal the morphology and arrangement of pre-adult chambers (Plate 5, Figs. 9, 10). The whole-shell dissection view shows that the initial whorl morphology is fundamentally different from *Hantkenina* and *Clavigerinella,* despite the fact that this specimen is not especially well preserved (Pl. 5, Fig. 9). There are approximately 7.5 sub-triangular to comma-shaped chambers in the ultimate whorl, which increase gradually in size through ontogeny and are separated by strongly curving sutures. By contrast to *Clavigerinella* and *Hantkenina, P. micra* shows no obvious increase in wall thickness or chamber height after the 6th or 7th chamber.

DEVELOPMENTAL MORPHOLOGY

Mean values for the final-whorl number of chambers (U) counted from the dissected and X-rayed specimens are shown in Table 5. Plots of the chamber-by-chamber increase in maximum test diameter are presented in Figure 4 (see also Appendix 1). *Hantkenina nuttalli* and *C. eocanica* show almost identical trends throughout ontogeny (Fig. 4A). The similarity of their best-fit exponential regression curves (slope value = 0.348 and 0.358, respectively) indicates that these species follow very similar ontogenetic growth paths. On the other hand the trend is clearly different in *P. micra.* The slope of the best-fit regression curve in this species is significantly lower (0.237), reflecting a more gradual increase in test diameter and thus chamber size through ontogeny. *Hantkenina compressa* (late Eocene) also shows a slower rate of ontogenetic increase in test diameter (0.255) compared to *H. nuttalli* (Fig. 4B). The approximate growth rates of *H. compressa* and *P. micra* are closely comparable, but consistently offset due to the larger size of individual chambers in *H. compressa.*

GEOCHEMISTRY

We compared the ecological preferences of the taxa under investigation using geochemical methods. The Helvetikum material has not been available for isotopic analysis; therefore, specimens from ODP Site 865 have been analyzed. Multispecies carbon and oxygen stable isotope data reported by Coxall and others (2000) are re-illustrated as carbon-oxygen cross plots (Fig. 5), supplemented with new data for *P. micra* and some additional reference species from the same interval (see also Appendix 2). *Clavigerinella eocan-*

TABLE 6. The internal morphologic characters of *Hantkenina, Clavigerinella* and *Pseudohastigerina* species examined in this study. The proloculus size is equivalent to the maximum diameter of chamber$_1$ (see Fig. 3 and Appendix 1).

|	H. nuttalli	H. mexicana	H. liebusi	H. dumblei	H. compressa	C. eocanica	P. micra
Initial whorl	~4 rounded, compressed chambers rapidly inc. in height	~4 rounded, compressed chambers rapidly inc. in height	~4 rounded, compressed chambers rapidly inc. in height	4–5 rounded, compressed chambers rapidly inc. in height	4–5 rounded, compressed chambers rapidly inc. in height	~4 rounded, compressed chambers rapidly inc. in height	6 small, round chambers, inc. gradually in size
Internal 'relict' aperture	'sutural webs' in final whorl often present	'sutural webs' in final whorl often present	none	none	none	'sutural webs' in final whorl often present	small-triangular 'flaps' in final whorl
First tubulospine	7th or 8th formed chamber	7th or 8th formed chamber	7th or 8th formed chamber	7th or 8th formed chamber	7th or 8th formed chamber	N/A	N/A
Proluculs size (mean)	17.8 μm (n = 8)	—	—	—	32.57 μm (n = 14)	18.6 μm (n = 6)	16.97 μm (n = 1)
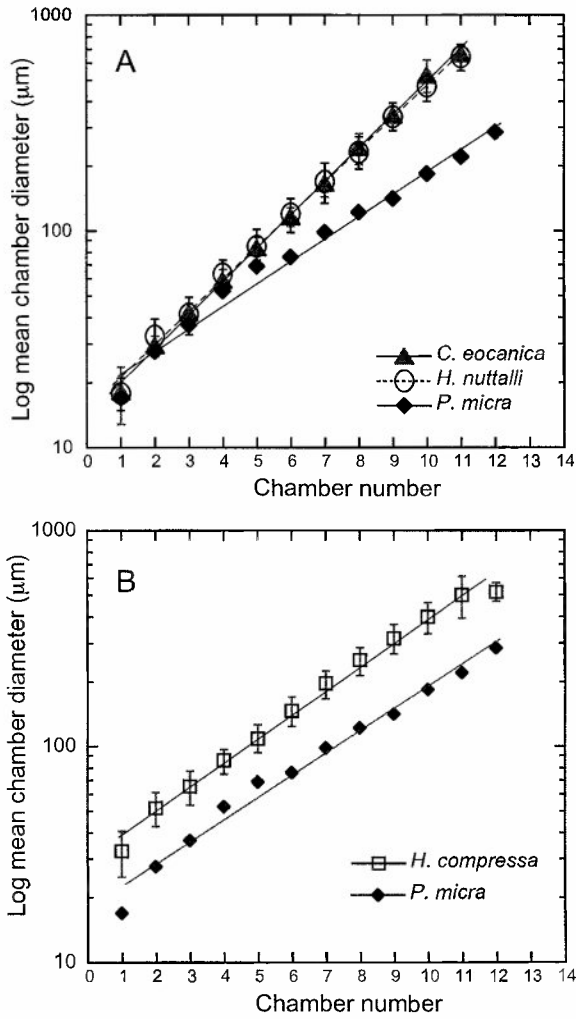
FIGURE 4. Logarithmic plots of the chamber-by-chamber increase in maximum test diameter in *Hantkenina* compared to proposed ancestral species *C. eocanica* and *P. micra* during the early middle Eocene (A) and P. micra in late Eocene (B). *H. nuttalli* and *P. micra*, ODP Sample 865B-7H-6, 57–59 cm, P10; *C. eocanica*, ODP Sample 865B-8H-6, 85–87 cm, P9; *H compressa* ODP Sample 865B-3H-5, 65–67 cm, P15. Error bars show one standard deviation about the mean values. The slopes of the regressions are presented as an approximation of the mean rate of increase in test diameter: *C. eocanica*, 0.358; *H. nuttalli*, 0.348; *H. compressa*, 0.255; *P. micra*, 0.237.

FIGURE 5. Multispecies carbon and oxygen stable isotope cross-plots. *Hantkenina* and suggested ancestors are compared to deep and shallow dwelling planktonic reference taxa during the lower middle Eocene (A) and late Eocene (B). C = illustrates isotopic signature of new species *Parasubbotina eoclava* compared to thermocline and surface mixed-layer reference taxa from the same sample. The data are from Coxall et al. (2000), supplemented with new data generated for this study. Additional analysis was carried out at the Godwin Laboratory, University of Cambridge and the Southampton Oceanography Centre. M = *Morozovella*, A = *Acarinina*, Gk = *Globigerinatheka*, T = *Turborotalia*, Ps = *Psuedohastigerina*, S = *Subbotina*, G = *Guembelitrioides*, C = *Clavigerinella*, H = *Hantkenina*, P = *Parasubbotina*.

ica and *H.nuttalli/mexicana* register the heaviest $\delta^{18}O$ values (~0–0.5‰) and lightest $\delta^{13}C$ values (1–1.5‰) of all the planktonic species (Fig. 5A). Both species form tight clusters in virtually the same position on the carbon-oxygen cross-plot, and are slightly heavier in $\delta^{13}C$ than the benthic species *Cibicidoides* and lighter in $\delta^{13}C$ below than the thermocline-dwelling reference taxon *Subbotina frontosa*. Hantkeninids from Biozones P14–P15 (Fig. 5B), which are represented by the species *H. compressa* and *H. alabamensis*, are lighter in $\delta^{18}O$ than the co-occurring thermocline-dweller *Subbotina linaperta*, which is more similar to the known shallow dwelling forms *Morozovella spinulosa* and *Acarinina pseudotopilensis*. In this sample, a single measurement of *P. micra* registers a $\delta^{18}O$ value of -0.1 ‰ and $\delta^{13}C$ value of 1.5 ‰, suggesting an intermediate depth habitat. This signature differs from *H. compressa* and *H. alabamensis*
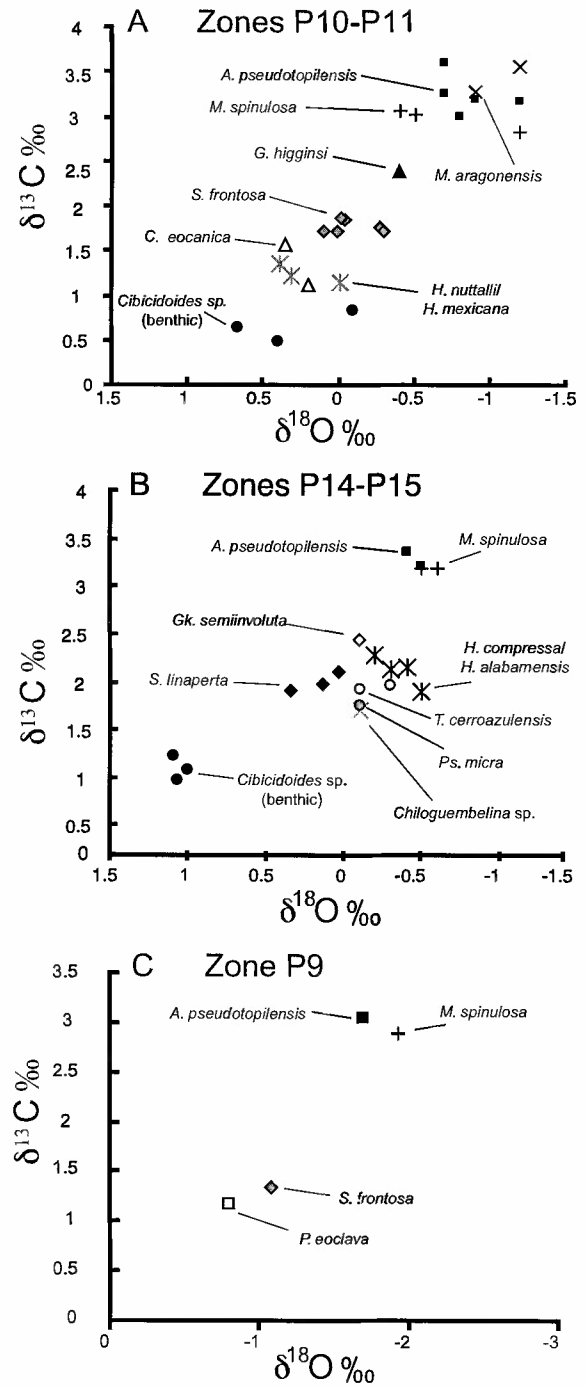
from the same assemblage in the unusually light $\delta^{13}C$, which is more similar to the values given by *Chiloguembelina* sp. This pattern is consistent with previous data for *Pseudo-hastigerina* (Premoli Silva and Boersma 1986; Pearson and others, 1993; Pearson and others, 2001). Coxall and others, (2000) have shown that at no stage in the lineage evolution do hantkeninid $\delta^{13}C$ values approach the very positive values of about 3‰ or exhibit an ontogenetic $\delta^{13}C$ enrichment trend (which have been interpreted as signatures of symbiosis), indicating that the hantkeninids did not have a symbiotic ecology.

THE *CLAVIGERINELLA-HANTKENINA* TRANSITION IN AUSTRIA

The most persuasive evidence that *Clavigerinella* is the ancestor of *Hantkenina* comes from the discovery of rare transitional forms in the lower middle Eocene Helvetikum of Austria (Pl. 6, Figs, 1–17). Gohrbandt (1967) recognized *C. akersi* and *C. jarvisi* in Helvetikum assemblages of latest early to early middle Eocene age. However, we regard all of Gohrbandt's clavigerinellids as referable to *C. eocanica* since they do not have particularly bulbous or unusually tall chambers. The stratigraphically lowest samples (64/1-36/1 and 64/1-36/2) contain *Clavigerinella* but no *Hantkenina* (Table 4; Pl. 6, Figs. 1–4). Stratigraphically higher, some specimens of *Clavigerinella* exhibit slightly constricted or pointed ends on some of the chambers (Pl. 6, Figs. 5–8). This feature is interpreted as representing an extremely rare transitional stage between clavate chambers and tubulo-spines. Stratigraphically higher again in the sequence (Sample 64/-36/3) the first recognizable *Hantkenina* appear. Like coexisting *Clavigerinella* these forms have approximately 4 chambers in the final whorl and a weakly cancellate wall texture. They are distinguished by having 'primitive' tubulospines, which at this stage in the lineage evolution emerged from broad shoulders, centered along the radial axis of each chamber, and lacked a terminal aperture (Pl. 6, Figs, 9–10, 16–17). In younger samples, forms recognizable as typical *H. nuttalli* occur, although the tubulospines are usually detached (Pl. 6, Figs. 9–12). The transitional forms are referred to as *H. nuttalli,* although they are not typical. The only other illustrated example of a possible *Clavigeri-nella-Hantkenina* transitional form that we could find is an SEM micrograph figured in Honigstein and others (1991; Pl. 3, Fig. 22) as *H. nuttalli,* from the early middle Eocene of the Jordan Valley, Israel. This specimen is similar to *H. nuttalli* but, as in some of the Helvetikum specimens, it possesses stunted points on the final whorl chambers in place of fully developed tubulospines. The possible exception is a specimen illustrated by Honigstein and others, (1991) as *H. nuttalli* (Plate 3, Fig. 22) from lower middle Eocene (Biozone P10) of the Jordan Valley, Israel.

Evidence for Helvetikum Paleoenvironments

Hagn (1960) and Gorhbandt (1967) record abundant, diverse, and typically tropical planktonic foraminifera assemblages in the Buntmergelserie of the Ultrahelvetikum sequence, indicating deposition in a relatively deep marine environment with connections to the open-ocean. The North Helvetikum and South Helvetikum also contain nummulitic limestones, suggesting shallower conditions at certain times

in these regions (Gorhbandt, 1967; Burkhard and Somma-ruga, 1998).

Also of note in Gohrbandt's (1967) report is the occurrence of a large ("0.58 mm") planktonic form occurring in relatively great abundance, which he describes as *Globigerina hagni.* Judging from the type description and illustrations of this morphotype, we suggest that this form probably belongs to the spinose cancellate genus *Parasubbotina,* due to the quadrate inflated morphology, extraumbilical-umbilical aperture, and the presence of an apertural lip. Like *Clavigerinella, Parasubbotina* tends to be rare in fully pelagic environments and sometimes occurs in large numbers in areas of upwelling along continental margins and topographic ocean highs (e.g., Petters, 1954; Mckeel and Lipps, 1972; Toumarkine and Luterbacher, 1985; Blow, 1979; Shipboard Scientific Party, 1996). We interpret the co-occurrence of *Globigerina hagni* and *Clavigerinella* in the Helvetikum section as indicating times of unusually productive hydrographic conditions in this region of Tethys during the latest early to earliest middle Eocene.

CLAVIGERINELLA ANCESTRY

One question that has been given little consideration in previous investigations of planktonic foraminifera evolution is the phylogenetic past of *Clavigerinella.* Toumarkine and Luterbacher (1985) noted that transitional morphologies to *Clavigerinella* are rare, and in many sections the genus appears rather abruptly. Pearson (1993) suggested that the sudden appearance of *Clavigerinella* was one of the best examples of punctuated cladogenesis among the Paleogene planktonic foraminifera. Several authors have linked *Clavigerinella* directly to *Pseudohastigerina* (e.g., Blow and Banner, 1962; Berggren and others, 1967; Blow, 1979; Pearson, 1993; see Fig. 2) but, as in the *Hantkenina-Pseudo-hastigerina* argument, large differences in wall texture and internal morphology suggest that this explanation is unlikely. An alternative hypothesis is that *Clavigerinella* descended from *Subbotina.* Benjamini and Reiss (1979) suggested *Clavigerinella* evolved from a form such as *S. triloculino-ides* (Pl. 7, Fig. 1), highlighting similarities between their shell microstructures. However, various differences in the morphology and stratigraphic range of *S. triloculinoides* compared to *Clavigerinella* (*S. triloculinoides* has a three-chambered, trochospiral, globigerinid morphology, and is thought to be restricted to the Paleocene) suggest that these species were not closely related. Other authors have suggested *Clavigerinella* evolved from the *S. inaequispira* group (Hillebrandt, 1976; Blow, 1979; Toumarkine and Luterbacher, 1985), noting that some specimens of *S. inae-quispira* exhibit considerably evolute and low-trochospiral coiling (Pl. 7, Fig. 2).

In the course of this study, we found a distinctive morphotype at ODP Site 865 that appears to be transitional between a cancellate "globigerine" morphology and *Clavigerinella.* The weakly cancellate wall texture of this species may also represent a transitional stage between truly cancellate and smoother wall textures as seen in the suggested descendent group *Clavigerinella.* This morphotype is not discussed specifically in the standard taxonomic works (e.g., Bolli and others, 1957; Jenkins, 1965; Blow, 1979; Tou-
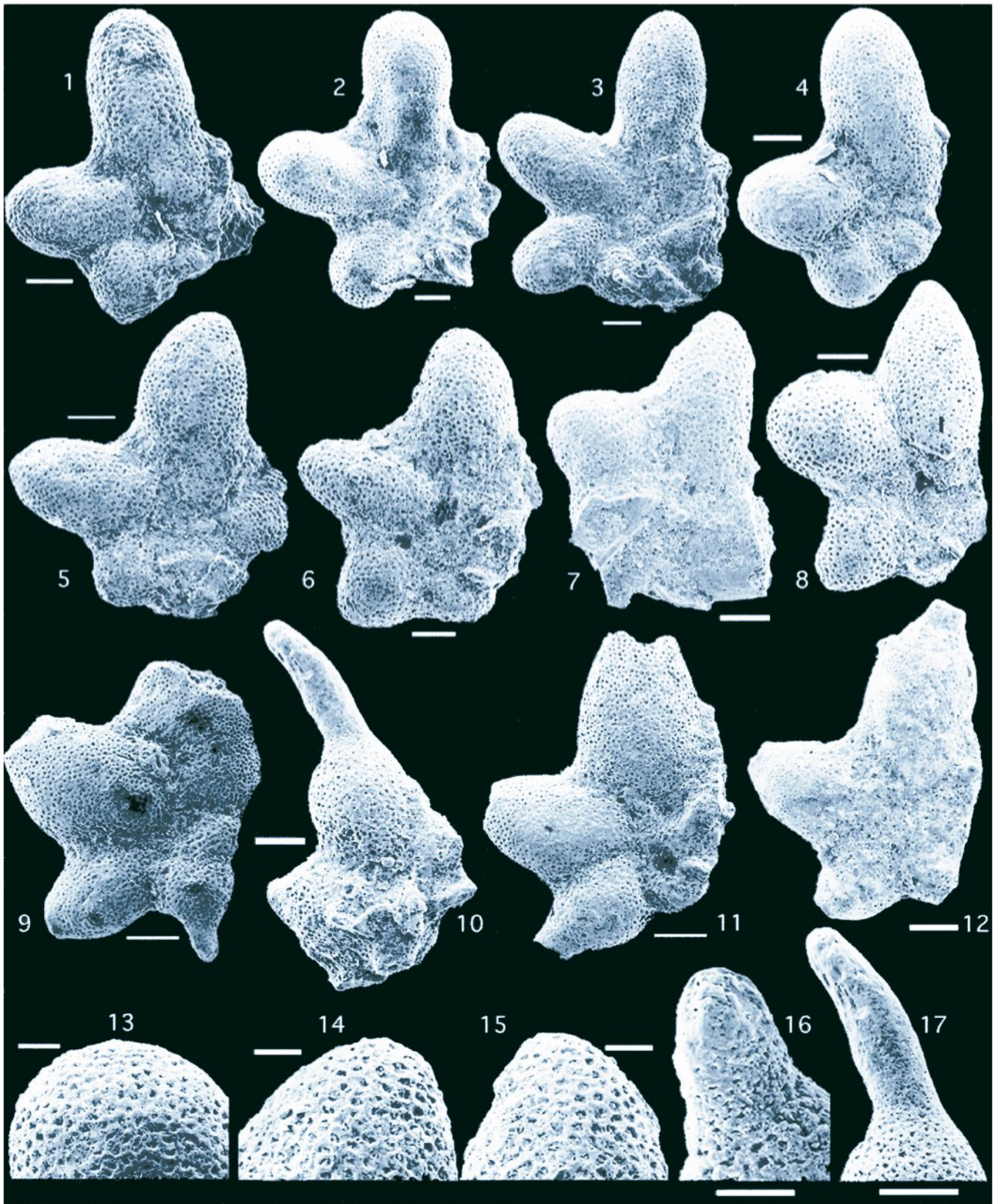
PLATE 6

Clavigerinella-Hantkenina morphological transition, Helvetikum Section Austria. **1–4** *Clavigerinella eocanica,* Fig. 1 Sample 64/1-36/2, Fig. 2, 4 Sample 64/1-36/1, Fig. 3 Sample 64/1-36/4a. **5–8** *Clavigerinella-Hantkenina* transitions, Fig. 5 Sample 64/1-36/4b, Fig. 6–8 Sample 64/1-36/0. **9–12** 'primitive' *H. nuttalli,* Sample 64/1-36/4b. **13–17** Chamber morphological-transition sequence Fig. 13 Sample 64/1-36/1, Fig. 14, 16, 17 64/1-36/4b, Fig. 15 Sample 64/1-36/0. Scale bar: **1–12, 17** = 100 μm; **13–16** = 40 μm.
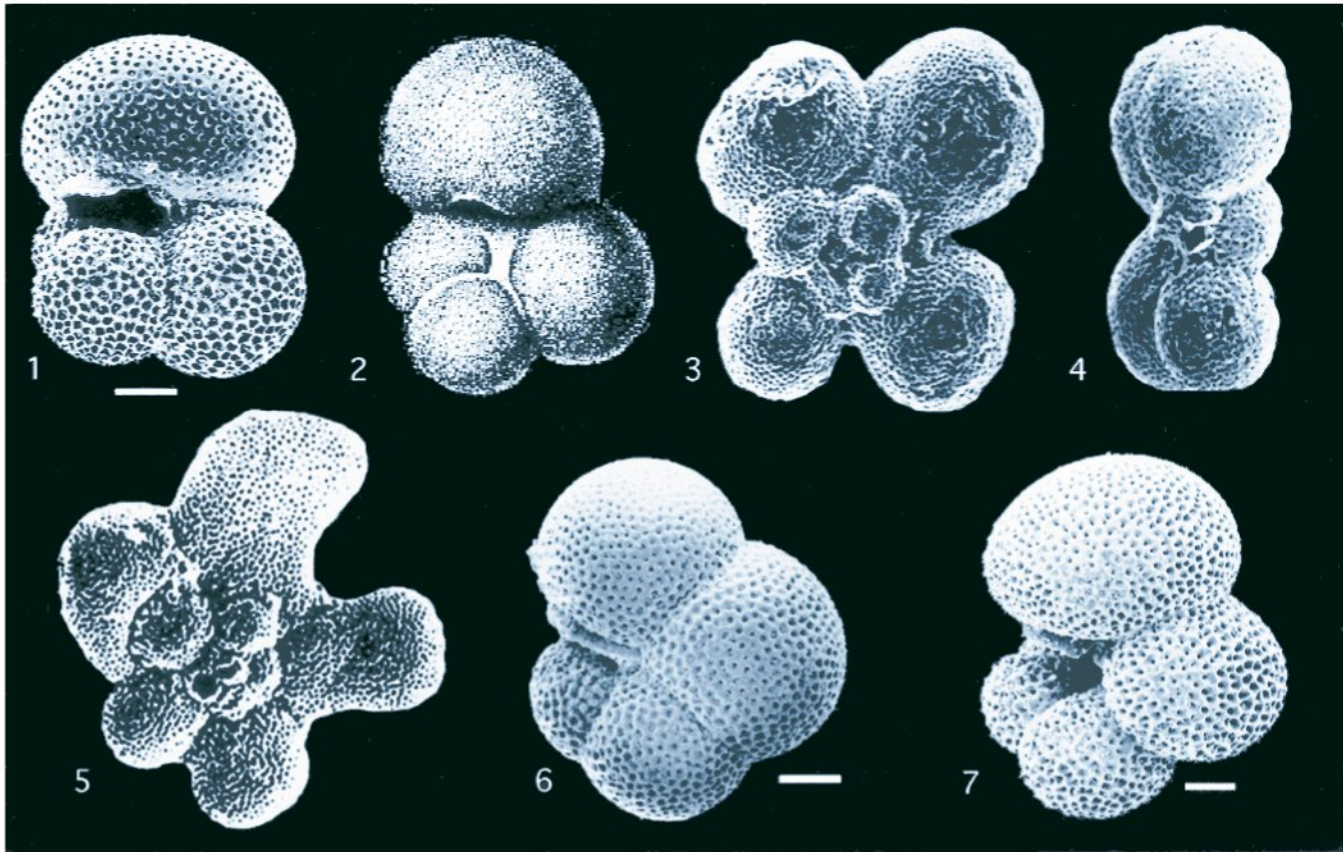
PLATE 7

Additional taxa for comparison with *Parasubbotina eoclava* new sp. **1** *Subbotina triloculinoides* (Zone P1, early Paleocene), **2** *Subbotina inaequispira* (re-illustration of Holotype, Subbotina, 1953) early Eocene, **3, 4** *Globigerina* (*Eoglobigerina*) *prebetica*, Paratype, early Eocene (re-illustrated, Martínez-Gallego, 1978, Pl. 1, Figs. 19, 24), **5** *Clavatorella paleocenica* Paratype (re-illustrated, de Klasz and de Klasz, 1987, Pl. 2, Fig. d) **6,** *Paragloborotalia griffinae*, early middle Eocene **7,** *Parasubbotina varianta*. Zone P2, early Paleocene. Scale bar: = 50 μm.

markine and Luterbacher, 1985) and therefore it is regarded as a new species, formally described below as *Parasubbotina eoclava* sp. nov. (see Systematic Taxonomy section below and Pl. 8).

At ODP Site 865 *P. eoclava* has a patchy occurrence, ranging from the topmost lower Eocene into the lowermost middle Eocene (Table 3). Its first appearance in Zone P9 pre-dates that of *C. eocanica* by one core sample (approximately 2.10 m of core, equivalent to ~200 Kyr), but it overlaps with *C. eocanica* at the top of its range. Juvenile specimens of *C. eocanica* may be difficult to distinguish from *P. eoclava*, except possibly by their smaller size.

Shell geochemistry provides evidence that *C. eocanica* and *P. eoclava* shared a similar ecology. The new morphotype occupies a similar position in a carbon and oxygen isotope cross-plot to *Clavigerinella* (i.e., more positive in $\delta^{18}O$ and more negative in $\delta^{13}C$ than the thermocline reference taxon *Subbotina frontosa*), suggesting that *P. eoclava* lived in a deep, sub-thermocline environment (Fig. 5C). Low abundance levels and the occurrence of the new species in the same localities as *Clavigerinella* provide further evidence to support this suggestion.

X-rays (Pl. 8, Figs 12–13) reveal the arrangement of chambers in the inner whorl and the tendency for final whorl chambers to become elongated, but the proloculus and ini-

tial whorl chambers are difficult to identify due to overlap of later formed chambers. Internal views of a serially dissected specimen better illustrate the morphology of these early chambers (Pl. 8, Fig. 14, 15). By contrast to *Clavigerinella*, the initial whorl chambers of *P. eoclava* form a relatively pronounced trochospiral. There are approximately 5 chambers in the penultimate whorl, which increase steadily in size. The ultimate whorl tends to have fewer chambers (4 to 4.5), corresponding with a more rapid rate of chamber expansion late in ontogeny.

There are two additional less well-known clavate species that predate *Clavigerinella* and *P. eoclava*. The first is a lower Eocene form, originally named *Globigerina* (*Eoglobigerina*) *prebetica* by Martínez-Gallego and Cremades (1978), herein emended to *Parasubbotina prebetica* (see Systematic Taxonomy section below). This species has not been reported outside of its type locality (Alicante, southern Spain). *Parasubbotina prebetica* probably belongs to the family of Eocene parasubbotinids that includes *P. eoclava*, *Paragloborotalia bolivariana*, *P. griffinae*, *P. wilsoni*, and *G. hagni*. Increasing paleoecologic evidence indicates that all of these forms may have been specialized to conditions of high productivity. This species can be distinguished from *C. eocanica* by its restricted, umbilical-extraumbilical ap-
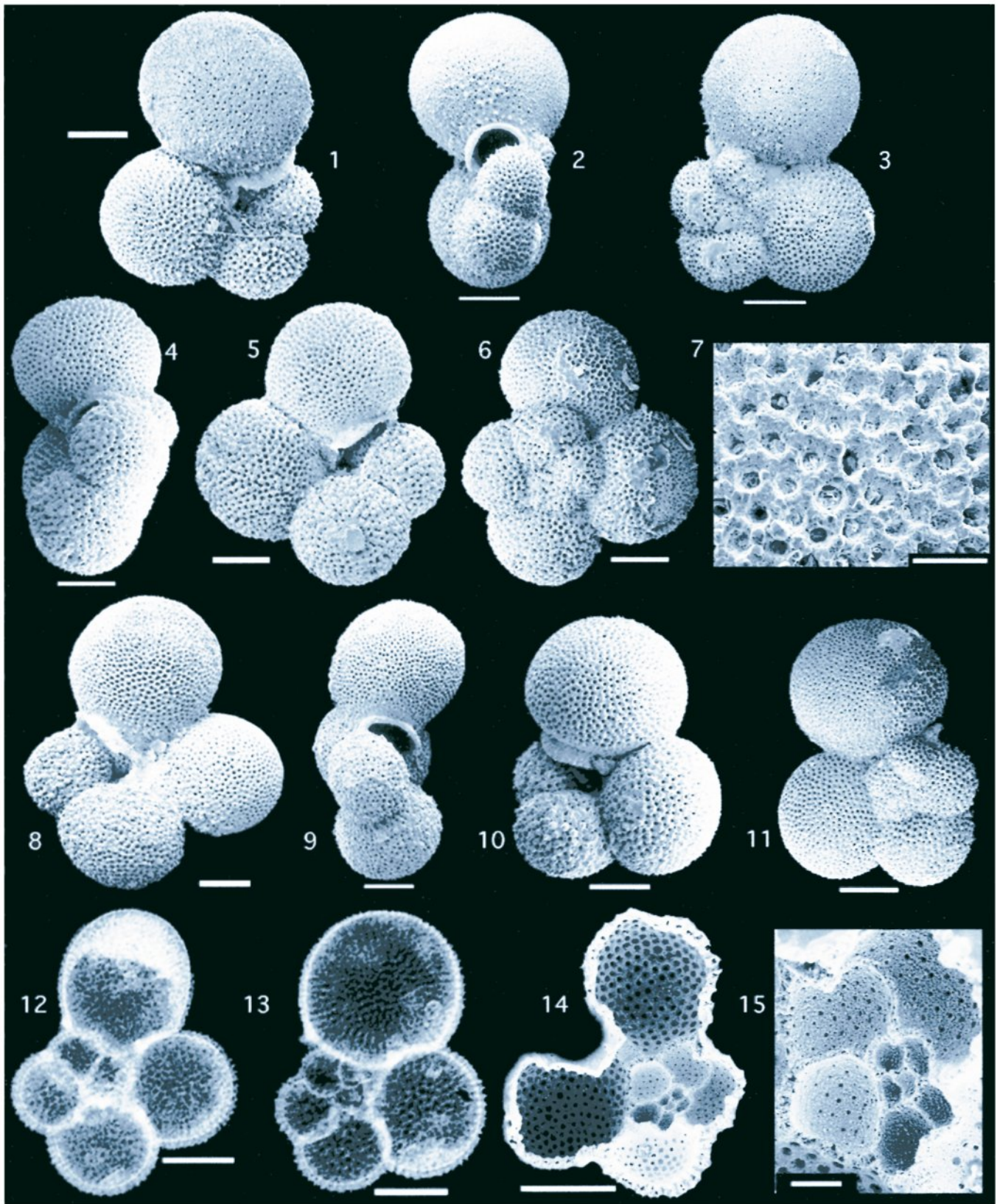
PLATE 8

Parasubbotina eoclava nov. sp., **1–11,** ODP Sample 865B-7H-5, 55–60 cm, Zone P10. **12–15** ODP Sample 865B-8H-6, 87–88 cm, Zone P9–P10. **1–3** Holotype (USNM 517714). **4–6** Paratype (USNM 517715). **7, 9** Wall texture view of Fig. 11. **8, 9** Paratype (USNM 517716). **10, 11** Paratype (USNM 517717), **12, 13** X-ray views. **14, 15** Complete dissection. Scale bar: **1–6, 8–14** = 100 μm; **9, 15** = 20 μm.

erture, more obvious trochospiral coiling and the quadrate arrangement of the final whorl chambers (Pl. 7, Figs. 3,4).

The second taxon, *Clavatorella paleocenica* de Klasz and de Klasz (1986), herein emended to *Parasubbotina paleocenica* (see Systematic Taxonomy section below), was described from the lower Paleocene of Senegal (de Klasz and de Klasz, 1986, 1987). It is not discussed in recent taxonomic works (e.g., Olsson and others, 1999) and to date the type reference represents the only record of a clavate species from the Paleocene. The principal differences between *P. paleocenica* and *C. eocanica* are the much earlier stratigraphic occurrence, the lack of an open arched aperture, and more obvious low-trochospiral coiling in *P. paleocenica* (Pl. 7, Fig. 5).

It is possible that *Clavigerinella*'s ancestry lies in a precursor clavate form such as *P. paleocenica* and *P. prebetica*, and that *P. eoclava* is an evolutionary side-branch of the *Parasubbotina* lineage. However, as mentioned above, the latter species have a very restricted stratigraphic and paleogeographic distribution and it is more likely that their similarity to *Clavigerinella* is the result of convergent evolution and homeomorphy. *Parasubbotina eoclava* on the other hand is stratigraphically and morphologically well placed as the putative ancestor of *Clavigerinella*.

HANTKENINA ANCESTRY AND TAXONOMIC REVISION

Multiple lines of evidence, including comparative morphology, ontogenetic morphometrics and the discovery of rare transitional forms, strongly indicate that *Clavigerinella* is the ancestor of *Hantkenina*. In addition, the discovery of likely morphological intermediates between *Parasubbotina* and *Clavigerinella* supports the view that *Clavigerinella*, and thus the hantkeninids, were descended from a cancellate spinose trochospiral group and not, as many workers in the past believed, from the smooth-walled, planispiral *Pseudohastigerina*.

Comparison of the gross test morphologies and microstructure reveals that *Hantkenina* and *Clavigerinella* have many shared characters. *Hantkenina nuttalli* and *C. eocanica* have radially elongated chambers in the ultimate whorl and an identical equatorial high arched primary aperture bordered by a well developed imperforate lip. Relict apertural lips from previous chambers can often be seen in the wide sutures between the chambers in both species, testifying to the equatorial position of the aperture during the earlier growth stages. *Hantkenina* and *Clavigerinella* share a generally smooth and robust wall, perforated by large pores, whereas *Pseudohastigerina* has much smaller, more sparsely distributed pores and a delicate wall.

Coiling in *C. eocanica* and *H. nuttalli* is usually considered to be fully planispiral, at least in the adult stages. However, we have observed asymmetry of the test in edge and side view in many individuals of *C. eocanica* and *H. nuttalli*, indicating very low trochospiral coiling and thus probable descent from a trochospiral rather than a fully planispiral ancestor. Later *Hantkenina* morphotypes appear to be more fully planispiral (cf. the symmetrical apertural systems in *Cribrohantkenina inflata*). Similar developments can be observed in the *Pseudohastigerina* lineage, with the earliest

forms having an asymmetrical equatorial aperture and low trochospire (i.e., *P. wilcoxensis*) and later morphotypes developing more perfect planispiral coiling (Berggren and others, 1967; Blow, 1979). We conclude that the planispiral body-plans of *Pseudohastigerina* and *Hantkenina* evolved independently, at different times during the early Eocene.

Complete shell dissections reveal that the initial whorl morphologies of *H. nuttalli*, *C. eocanica*, and *P. micra* are broadly similar, the main differences being that *P. micra* has ~6 chambers in the initial whorl, compared with ~4.5 in *H. nuttalli* and *C. eocanica*. At about the 6–7 chamber-stage, chambers of *C. eocanica* and *H. nuttalli* become noticeably taller and more loosely coiled, giving the shell a highly lobate periphery. This probably represents the onset of the neanic stage as identified in living and fossil planktonic foraminifera by Brummer and others (1987) and Huber (1994), respectively. In *Hantkenina*, this stage coincides with the appearance of the first tubulospine, implying that this structure was important throughout an individual's neanic and adult life and not merely a terminal-stage skeletal modification. Rapid ontogenetic increases in chamber expansion in *C. eocanica* and *H. nuttalli* compared to *P. micra* confirms that the former species have similar patterns of growth and are therefore probably closely related, whereas *P. micra*, which has smaller chambers, grows more gradually, adding more chambers to attain a similar size.

The initial whorl morphology of subsequent middle and late Eocene *Hantkenina* morphospecies is closely comparable to the early middle Eocene forms, although proloculus size and variation is greater in later Eocene morphospecies (i.e., *H. compressa*), and shells tend to possess one more chamber in adult specimens (~11–12, compared to 10–11 in earlier morphospecies). Ontogenetic increases in test diameter are also significantly different from the early Eocene forms and more similar to *P. micra*, corresponding with the decrease in chamber height that occurred during the lineage evolution. Based on this morphologic evidence and the knowledge from additional studies that middle and upper Eocene *Hantkenina* are linked by a series of intergrading morphologies (Barnard, 1954; Pearson, 1993), we reject the hypotheses of a polyphyletic origin (Blow and Banner, 1962; Blow, 1979; Berggren and others, 1967).

These results significantly improve our understanding of the position of *Hantkenina* in the Paleogene planktonic foraminifera phylogenetic tree, indicating that they belong to a line that branched from the Paleocene stem group *Eoglobigerina* rather than *Globanomalina*, as was previously believed. Consequently, we suggest that the family level taxonomy (last reviewed by Loeblich and Tappan, 1988) be revised to reflect these newly determined evolutionary relationships, and propose that *Clavigerinella* be removed from family Globanomalinidae to be united with *Hantkenina* and *Cribrohantkenina* in Family Hantkeninidae Cushman, 1927 (see Systematic Taxonomy section below). Finally, we consider it likely that the Oligocene and Miocene clavate species evolved independently after the extinction of *Clavigerinella* (cf. *Clavigerinella nazcaensis*, Quilty, 1976).

SPECIATION IN HANTKENININIDAE

Rare *Clavigerinella-Hantkenina* transitional morphologies from the Austrian Helvetikum Section provide good

evidence that *Hantkenina* evolved from *Clavigerinella* and is an indication of cladogenisis in this group. Furthermore, this transition provides important insights into the mode and tempo of the evolutionary processes involved in this origination, and the prevailing and changing environmental conditions under which *Hantkenina* evolved.

No transitional morphotypes have been found at ODP Site 865 or virtually any other lower middle Eocene site studied other that the Austrian Helvetikum, and possibly the Jordan Valley, Israel (Honigstein and others, 1991). This occurrence suggests that the evolution occurred locally in the ancient Tethys region and that the abrupt, or punctuated, occurrence of *Hantkenina* elsewhere in the world ocean is the result of subsequent migration. Alternatively, cladogenesis may have been repeated and widespread but, due to a global hiatus and sea level lowstand at the time (Haq and others, 1987; Olsson and Wise, 1987; Premoli Silva and Boersma, 1986; Norris and Nishi, in press), the fossil evidence is not preserved.

Evidence of speciation processes is derived from isotopically inferred paleoecologies and paleoenvironmental clues. The stable isotope signatures of *C. eocanica* and *H. nuttalli/mexicana* are very similar, and both indicate life in a deep-water habitat. This argument is supported by limited plankton tow and observational data that indicate modern homeomorphs of *Clavigerinella* i.e., *Hastigerinella digitata, Beella digitata,* and *Globigerinella adamsi*; (Bé, 1977; Hemleben et al., 1989; Hilbrect, 1996; S. Haddock, Monterey Bay Aquarium Research Institute, oral communication, 2001) are also all deep-dwelling forms. Consequently, we suggest that, unlike some examples of speciation in planktonic foraminifera (e.g., Norris and others, 1993; Schneider and Kennett, 1996), speciation did not involve a shift in depth habitat (see Pearson, 1998, for further discussion).

The evolution of *Hantkenina* occurred during the initial rapid phase of Cenozoic cooling, between 50 and 48 million years, which followed the extremely warm climatic optimum of the early Eocene (e.g., Shackleton and Kennett, 1975; Zachos and others, 1994; Zachos and others, 2001). If cladogenesis was geographically restricted to the Tethyan region, it is possible that speciation was controlled to some extent by unusual hydrographic conditions associated with the closure of this seaway. There are no detailed paleoenvironmental interpretations for the lower middle Eocene Tethys, but studies for the Late Paleocene-early Eocene (e.g., Pardo and others, 1999) indicate restricted circulation, involving periods of low oxygen conditions followed by upwelling, and it is likely that similar conditions existed in the middle Eocene. In this scenario, it is possible that restricted ocean basins within the "Tethys island region" provided initial hydrographic barriers to dispersal of deep-dwelling *Hantkenina,* maintaining genetic isolation long enough to allow allopatric speciation to occur. Regional subsidence and perhaps increased local sea level stands, accompanying the tectonic evolution during the early middle Eocene, may have subsequently permitted exchange and emigration of *Hantkenina* into the rest of the world ocean. A similar scenario has been suggested in the cladogenetic evolution of deep-dwelling species *Globorotalia truncatulinoides* from its ancestor *G. crassaformis* during the Late Pliocene in the Indonesian Island arc area (Spencer-Cervato and Thierstien, 1997).

Recent genetic studies of modern planktonic foraminifera indicate that, although species maybe specialized to particular hydrographic conditions, there are few hydrographic barriers to gene flow. Reproductive mechanisms and behavior must therefore play key roles in speciation rather than geographic barriers to dispersal (de Vargas and others, 1999; Darling and others, 2000; Norris, 2000). Furthermore, theoretical studies and models of speciation processes have suggested that sympatric speciation within the same ecological niche is a common speciation mechanism within pelagic ecosystems (Dieckmann and Dobeli, 1999). We can imagine that the evolution of *Hantkenina* involved divergence from the ancestral species *Clavigerinella eocanica* within a deep, cold, oxygen-starved, nutrient-rich but food-poor environment. It is possible that competition for food during adverse environmental conditions drove a *Clavigerinella* population to evolve strategies to use a different, less-sought-after food source, such as larger prey items (cf. Kondrasov and Kondrasov, 1999; Tregenza and Butlin, 1999). Pointed chambers and ultimately chambers extended into tubulospines may have provided skeletal support for robust food-gathering rhizopods, thus increasing increase effective shell size and feeding radius. Selection would favor morphotypes that were best adapted to exploit either the original or new food source, which may explain why intermediate morphologies are rare (see Norris, 2000, for discussion). Scarcity of *Clavigerinella* and *Hantkenina* during this interval suggests populations were small, and individuals perhaps long-lived. It is possible that *Clavigerinella* and initially *Hantkenina* were specialized for living under periodic or seasonal upwelling or conditions of low oxygen, but that skeletal adaptations acquired by *Hantkenina* subsequently enabled these morphotypes to utilize a wider range of food sources and thus diversify into broader oceanic realms than *Clavigerinella.*

Whatever scenario accounts for the origin of hantkeninid tubulospines, it appears that they remained advantageous for many millions of years, even when later forms migrated into a completely different surface mixed-layer habitat (Coxall and others, 2000).

CONCLUSIONS

Multiple lines of evidence demonstrate that *Hantkenina* evolved gradually from *Clavigerinella* in the earliest middle Eocene and, contrary to the long-held view, it is unrelated to *Pseudohastigerina.* Furthermore, our data indicate that the hantkeninids are a monophyletic group, disproving earlier suggestions that tubulospines evolved independently in the middle and late Eocene species. These results significantly improve our understanding of the position of *Hantkenina* in the Paleocene planktonic foraminiferal phylogenetic tree and facilitate a revision of the suprageneric taxonomy that more accurately reflects evolutionary patterns.

Determining the processes and mechanisms of speciation is more problematic. Isotopic paleoecological evidence indicates that speciation was not accompanied by a shift in depth habitat, but may instead have involved a change in

nutritional habitat that was associated with evolution of the elaborate tubulospine structures.

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SYSTEMATIC TAXONOMY

Order FORAMINIFERIDA Eichwald, 1830
Family HANTKENINIDAE Cushman, 1927

Clavigerinella Bolli, Loeblich and Tappan, 1957 (early–late middle Eocene)
Hantkenina Cushman, 1924 (middle–late Eocene)
Cribrohantkenina, Thalmann, 1942 (late Eocene)

Emended description. Test planispirally enrolled, chambers rounded to radially elongate, those of the final whorl clavate or with a distinct tubulospine arising form the peripheral margin; aperture a high interiomarginal and equatorial opening or may become cribrate. Early –late Eocene.

Family GLOBIGERINIDAE Carpenter, Parker and Jones, 1862
Genus *Parasubbotina* Olsson, Hemleben, Berggren and Liu, 1992

Type species. Globigerina pseudobulloides Plummer, 1926
Description. Test very low trochospiral with 10–12 chambers, and with 4 to 5 chambers in the ultimate whorl. The chambers, which are inflated globular and slightly ovoid in shape, increase rapidly in size. The aperture is an interiomarginal to extraumbilical, high rounded arch, boarded by a narrow lip. The umbilicus is deep, and open to the previous chambers. The wall is weakly to strongly cancellate and spinose. Spine holes are numerous and located at the juncture of and along the cancellate ridges. They may be obscured by gametogenetic and/or diagenetic calcification.

Parasubbotina eoclava sp. nov.

A new species of Parasubbotina distinguished by lateral compression of the test, very low trochospiral coiling, slight elongation of the final chambers and a prominent apertural lip
Plate 8, Figs. 1–15

Subbotina inaequispira (Subbotina)—Blow, 1979, Plate 163, Figs. 9, 10, [both specimens from Kane 9-C piston core, sample depth 42 cm, Echo Seamount, western equatorial Atlantic] [not Subbotina, 1953]
Clavigerinella ?*colombiana* (Petters)—Mckeel and Lipps, 1975, Plate 3, Figs. 8a–c [lower middle Eocene Tyee formation, Oregon Coast Range, California, sample D-3408]

Description of holotype. Type of wall: weakly cancellate, possibly spinose but spine holes are not visible in type the material. *Coiling mode:* very low trochospiral. *General morphology* test somewhat lat-erally compressed, lobulate-petaloid in outline; chambers globular and well separated with a tendency for the final chamber to become slightly radially elongated. *Umbilical view:* 4 chambers in the final whorl, increasing rapidly in size; umbilicus small, narrow and deep; sutures straight and slightly depressed. *Spiral view:* spiral surface flattened so that chambers of inner whorl are distinguishable; sutures straight, slightly depressed. *Edge view:* primary aperture a moderately high arch, interiomarginal, umbilical-extra umbilical, bordered by a well developed, asymmetrical flaring lip that extends from the umbilicus to the equatorial margin.

Holotype. ODP Sample 865B-8H-6, 10–12 cm. Pl. 8, Figs. 1–3. Dimensions; maximum diameter =481 μm, maximum breadth (edge view) =263 μm.

Paratypes. ODP Sample 143-865B-8H-6, 10–12 cm. Pl. 8, Figs. 4–6, 8–9, 10–11. Dimensions; maximum diameter = 418–526 μm; maximum breadth (edge view) =245–252 μm.

Type locality. ODP Hole 865B, Allison Guyot, central equatorial Pacific (18°26.425′N; 179°33.33′W)

Distingishing features. Parasubbotina eoclava is characterized by extremely low trochospiral coiling and an interiomarginal umbilical-extraumbilical aperture bordered by a broad, flaring apertural lip. It differs from *Subbotina inaequispira* (Subbotina, 1953) in the extraumbilical-umbilical position of the aperture, the possession of a distinctive lip, more compressed morphology and in the more rapid increase in chamber size through the final whorl. *Globigerina baylissi* Samanta is described as having a morphology similar to that of *P. eoclava* (Samanta, 1973). However, reexamination of the holotype specimen of this species reveals that the final chamber is not markedly radially elongate, as described, and the morphology falls within the range of variation permitted to *S. inaequispira,* with which it can probably be synonymized. The new taxon differs from *Clavigerinella eocanica* in consistently showing low trochospiral rather than planispiral coiling, having less-pronounced clavate chambers, a more asymmetrical, and lower arched aperture and a less-well developed apertural lip. It can be distinguished from *Parasubbotina prebetica* in having lower trochospiral coiling, a flat spiral side, 4–4.5 rather than 4.5–5 chambers in the final whorl, chambers increasing gradually in size in the final whorl that are considerable less bulbous than in *P. prebetica,* a small umbilicus and a more equatorial position and amore highly arched aperture. The *P. eoclava* morphology is possibly transitional between a trochospiral and planispiral coiling condition.

Stratigraphic range. Eocene Zone P9–P11?

Biogeographic distribution. From the few records available, it appears that *P. eoclava* had a wide distribution at low to mid latitudes but was restricted to certain oceanic paleoenvironments such as continental margins and topographic ocean highs. It is conspicuous but not common at its type locality and is generally rare in open ocean sites. Most of the recorded occurrences are in regions that were probably characterized by enhanced biological productivity during the lower Eocene. It is interesting to note that *P. eoclava* usually co-occurs with *Clavigerinella,* which itself has a sporadic and patchy distribution.

Repository. To be deposited in the U.S. National Museum, Washington D.C., USA. Collection numbers: Holotype, USNM 517714, Paratypes, USNM 517715–517716.

Discussion. The new morphotype is referred to the cancellate genus *Parasubbotina* Olsson, Hemleben, Berggren and Liu, 1992, on the basis of the honeycomb wall texture, low trochospiral coiling, and presence of a distinct apertural lip, and assigned the specific name *eoclava* from Latin: *eo* = dawn, *clava* = club. *Parasubbotina eoclava* resembles *Paragloborotalia griffinae* Blow (Pl. 7, Fig. 6) in general shape and its possession of 4 final-whorl chambers, but it has a more laterally compressed shell, more highly arched sub-symmetrical equatorial aperture and a broader, better developed apertural lip (Pl. 8, Figs. 1, 5, 8, 10). One of the most distinctive characteristics of the new species is a tendency for the final chambers to become radially elongate (Pl. 8, Figs. 1, 8, 12, 14). The morphology is also comparable to *P. varianta* (Pl. 7, Fig. 7). However, the latter species has more globular chambers, possesses an aperture situated closer to the umbilicus and it is thought to be restricted to the Paleocene.

It is possible that a number of specimens previously figured as *Subbotina inaequispira* belong to the new species. Blow (1979) recognized a sub-group within the "*S. inaequispira* plexus" that are closely comparable to our new species, *P. eoclava* (e.g., Blow, 1979; Plate 163, Figs. 9, 10). He notes that these forms differ from the typical *S.*

inaequispira in having an umbilical aperture and somewhat radially elongate globular chambers, and proposed that they may have led to an ancestral form from which *Clavigerinella* evolved. This is contradictory to Blow's (1979) suggestion elsewhere in the same work that *Clavigerinella* was a sister taxa to *Hantkenina,* which he believed evolved from *Pseudohastigerina.*

Parasubbotina prebetica (Martínez-Gallego and Cremades) new genus-species combination

Globigerina (Eoglobigerina) prebetica Martínez-Gallego and Cremades, 1978 (Plate 1, Figs. 1–2).

Type locality. Alicante, southern Spain
Type level. Lower Eocene
Discussion. This species has a distinctive low-trochospiral morphology with 4–5 bulbous to clavate chambers in the final whorl, an extraumbilical-umbilical aperture, a pronounced apertural lip and a cancellate wall. Based on these characters we assign the morphotype to genus *Parasubbotina. Parasubbotina prebetica* differs from *P. eoclava* sp. nov. in being more obviously trochospiral (with a distinctly raised initial whorl on the spiral side), usually having 4.5–5.0 chambers in the final whorl (rather than 4.0–4.5 in *P. eoclava*) that are distinctly bulbous and of equal size, a wide, square umbilicus, a less highly arched aperture, and a more pronounced apertural lip. The type illustrations also indicate modification of the lip into an umbilical tooth, as in some Paleocene species of *Parasubbotina.*

Parasubbotina paleocenica (de Klasz and de Klasz) new genus-species combination

Clavatorella paleocenica de Klasz and de Klasz, 1986

Type locality. The Madeleienes Formation, Dakar, Senegal
Type level. Lower Paleocene (Danian)
Discussion. As the original generic assignment suggests, the Paleocene form is similar in morphology to Miocene *Clavatorella bermudezi* although, the chambers are less clavate and the aperture is much more restricted compared to the Miocene form. More significantly, a large stratigraphic gap of ~40 million years separates the Paleocene form from *C. bermudezi,* implying that the similar morphologies are the result of iterative evolution and homeomorphy. Examination of de Klasz and de Klasz's (1986) SEM illustrations indicates that *C. paleocenica* shares a number of morphological characters with *Parasubbotina pseudobulloides,* with which it co-occurs in its type locality. Consequently, we assign the Paleocene clavate form to *Parasubbotina,* preserving *Clavatorella* as a monophyletic genus.

REFERENCES

AUBRY, M.-P., 1991, Sequence stratigraphy: Eustacy or tectonic imprint?: Journal of Geophysical Research, v. 96, p. 6641–6679.

———, 1995, From chronology to stratigraphy: Interpreting the lower and middle Eocene stratigraphic record in the Atlantic Ocean, *in* Berggren, W. A., Kent, D. V., and Hardebol, J., (eds.), Geochronology, Time Scales and global stratigraphic correlation: A unified Temporal Framework for an Historical Geology: Society of Economic Paleontologists and Mineralogists, Special Publication, v. 54, p. 213–274.

BANNER, F. T. and LOWRY, F. M., 1985, The stratigraphical record of planktonic foraminifera and its evolutionary implications: Special Papers in Palaeontology, v. 33, p. 117–130.

BARNARD, T., 1954, *Hantkenina alabamensis* Cushman and some related forms: Geological Magazine, v. 91, no. 5, p. 384–390.

BÉ, A. W. H., 1977, An ecological, zoographic and taxonomic review of Recent planktonic foraminifera, in Ramsay, A. T. S., (ed.), Oceanic Micropalaeontology, London, Academic Press, p. 1–100.

BENJAMINI, C. and REISS, Z., 1979, Wall-hispidity and perforation in Eocene planktonic foraminifera: Micropaleontology, v. 25, no. 2, p. 141–150.

BERGGREN, W. A., OLSSON, R. K., and REYMENT, R. A., 1967, Origin and development of the foraminiferal genus *Pseudohastigerina:* Micropaleontology, v. 13, no. 3, p. 265–288.

———, KENT, D. V., SWISHER, III. C. C. and AUBRY, M. P., 1995, A Revised Cenozoic Geochronology and Chronostratigraphy, in Berggren, W. A., Kent, D. V. and Hardenbol, J. (eds.), Geochro-

nology, Time Scales and global stratigraphic correlation: A unified Temporal Framework for an Historical Geology: Society for Economic Paleontologists and Mineralogists, Special Publication, v. 54, p. 129–212.

BLOW, W. H., 1979, The Cainozoic Globigerinida. A study of the morphology, taxonomy, evolutionary relationships and the stratigraphical distribution of some of the Globigerinida (mainly Globigerinacae): Leiden, E. J. Brill, 3 volumes: 1413.

——— and BANNER, F. T., 1962, The mid-Tertiary (upper Eocene to Aquitanian) Globigerinacae: in Eames, F. T. and others, (eds.), Fundamentals of mid-Tertiary stratigraphical correlation. London: Cambridge University Press, p. 61–151.

BOLLI, H. M., 1957, Planktonic foraminifera from the Eocene Navet and San Fernando formations of Trinidad, B. W. I., Bulletin of the U.S. National. Museum, v. 215, p. 155–172.

———, LOEBLICH, A. R. and TAPPAN, H., 1957, Planktonic foraminiferal families Hantkeninidae, Orbulinidae, Globorotalidae and Globotruncanidae: Bulletin of the U.S. National. Museum, v. 215, p. 3–50.

BRALOWER, T. J., ZACHOS, J. C., THOMAS, E., PARROW, M., PAULL, C. K., KELLY, D. C., PREMOLI SILVA, I., SLITER and W. V. LOHMAN, K. C., 1995, Late Paleocene to Eocene paleoceanography of the equatorial Pacific Ocean: Stable isotope record at Ocean Drilling Program Site 865, Allison Guyot: Paleoceanography, v. 20, p. 391–406.

BRÖNNIMANN, P., 1950, The genus *Hantkenina* Cushman in Trinidad and Barbados, B. W. I.: Journal of Paleontology, v. 24, p. 397–420.

BRUMMER, G. J. A., HEMLEBEN, C., and SPINDLER, M., 1987, Ontogeny of extant spinose planktonic foraminifera (Globigerinidae): A concept exemplified by *Globigerinoides sacculifer* (Brady) and *G. ruber* (d'Orbigny): Marine Micropaleontology, v. 12, p. 357–381.

BURKHARD, M., and SOMMARUGA, A., 1998, Evolution of the western Swiss mollasse basin: Structural relations with the Alps and the Jura belt, in Mascle, A., Puigdefabregas, C., Luterbacher, H. P., and Fernandez, M., (eds.), Cenozoic foreland basins of western Europe: Geological Society Special Publication, no. 134, p. 279–298.

CARPENTER, W. B., PARKER, W. K., and JONES, T. R., 1862, Introduction to the study of foraminifera: Royal Society Publications, London, p. 1–319 p.

COCCIONI, R., MONACO, P., MONECHI, S., NOCCHI, M. and PARISI, G., 1988, Biostratigraphy of the Eocene-Oligocene Boundary at Massignano (Ancona, Italy): International Subcomission on Paleogene Stratigraphy, E/O Meeting in Ancona, Italy, p. 59–75.

COXALL, H. K., PEARSON, P. N., SHACKLETON, N. J. and HALL, M. A., 2000, Hantkeninid depth adaptation: An evolving life strategy in a changing ocean: Geology, v. 28, no. 1, p. 87–90.

CUSHMAN, J. A., 1924, A new genus of Eocene foraminifera, Proceedings of the U.S. National Museum, v. 66, no. 30, p. 1–4.

———, 1927, Some characteristic Mexican foraminifera: Journal of Paleontology, v. 1, no. 2., p. 147–172.

———, 1933, Foraminifera, their classification and economic use: Special Publications of the Cushman Laboratory of Foraminiferal Research, 2nd edition.

———, and WICKENDEN, R. T., 1930, The development of *Hantkenina* in the Cretaceous with a description of a new species, Contributions from the Cushman Laboratory of Foraminiferal Research: v. 6, no. 2, p. 39–43.

DARLING, F. K., WADE, M. C., STEWART, I. A., KROON, D., and LEIGH BROWN, J. A., 2000, Molecular evidence for genetic mixing of Arctic and Antarctic subpolar populations of planktonic foraminifera: Nature, v. 405, p. 43–47.

DE KLASZ, I., and DE KLASZ, S., 1986, Description d'une nouvelle éspèce de Foraminifère planctonique (*Clavatorella paleocenica* n.sp.) du Danien du Sénégal: des Seances de l'Academie des Sciences, Serie 2: Mecanique-Physique, Chimie, Sciences de l'Univers, Sciences de la Terre, v. 302, p. 687–690.

DE KLASZ, I., DE KLASZ, S., and AUSSEIL-BADIE, J., 1987, Étude systématique des foraminifères du Danien de la Formation des Madeleines de Dakar (Sénégal): Cahiers de Micopaleontologie, v. 2, p. 29–38.

DE VARGAS, C., R., NORRIS, R., ZANINETTI, L., GIBB, W. S., and

PAWLOWSKI, J., 1999, Molecular evidence of cryptic speciation in planktonic foraminifers and their relation to oceanic province: Proceedings of the Natural Academy of Sciences, USA, v. 96, p. 2864–2868.

DIECKMANN, U. and DOBELI, M., 1999, On the Origin of species by sympatric speciation: Nature, v. 400, p. 351–354.

DIENI, I., and PROTO DECIMA, F. P., 1964, *Cribrohantkenina* ed atri *Hantkeninidae* nell'Eocene superiore di Castelnuovo (Colli Euganei): Rivista Italiana di Paleontologia e Stratigrafia v. 70, no. 3, p. 555–592.

EICHWALD, C. E. VON, 1830, Zoologica Specialis: v. 22, Vilnae, p. 1–323.

GOHRBANDT, K. H. A., 1967, Some new planktonic foraminiferal species from the Austrian Eocene: Micropaleontology, v. 13, no. 3, p. 319–326.

HAGN, H., 1960, Die stratigraphischen, paläographischen und tektonischen Beziehungen Zwischen Molasse und Helvetikum im östlichen Oberbayern: Geologica Bavarica, v. 44, p. 1–208.

HANTKEN, V. M., 1875, Die fauna der *Clavulina* szaboi-schichten. 1. Teil: Foraminifera, Mitth. Jahrb. ungar. geol. Anstalt, Budapest, v. 4, no. 1, p. 1–93.

HAQ, B. U., HARDENBOL, J., and VEIL, P. U., 1987, Chronology of fluctuating sea levels since the Triassic: Science, v. 235, p. 1156–1166.

HEMLEBEN, C., SPINDLER, M., and ANDERSON, O. R., 1989, Modern planktonic foraminifera: Springer-Verlag, New York, 363 p.

HILLEBRANDT, A. VON, 1976, Los foraminíferos planctonicos, nummulitidos y coccolitoforidos de la zona *Globorotalia palmerae* del Cuisiense (Eoceneo inferior) en el SE de España (Provincias de Murcia y Alicante): Revista Española Micropaleontolgía, v. 10, p. 337.

HILBRECHT, H., 1996, Extant planktic foraminifera and the physical environment in the Atlantic and Indian Oceans, v. 300: Zürich., Mitteilungen aus dem Geologischen Institut der Eidgen. Technischen Hochschule und der Universität Zürich, Neue Folge, 93 p.

HONIGSTEIN, A., ROSENFELD, A., and BENJAMINI, C., 1991, Ostracods and foraminifera from the early-middle Eocene of Qeren Sartaba, Jordan Valley: Journal of Micropalaeontology, v. 10, p. 95–107.

HUANG, C., 1981, Observations of the interior of some Late Neogene planktonic foraminifera: Journal of Foraminiferal Research, v. 11, p. 173–190.

HUBER, B. T., 1994, Ontogenetic morphometrics of some Late Cretaceous trochospiral planktonic foraminifera from the Austral Realm: Smithsonian Contributions to Paleobiology, no. 77, p. 1–85.

JENKINS, D. G., 1965, Planktonic foraminiferal zones and new taxa from the Danian to Lower Miocene of New Zealand: New Zealand Journal of Geology and Geophysics, v. 8, p. 1088–1126.

KONDRASOV, A. S. and F. A. KONDRASOV, 1999, Interactions among quantitative traits in the course of sympatric speciation: Nature, v. 400, p. 351–354.

LOEBLICH, A. R. JR. and TAPPAN, H., 1988, Foraminiferal genera and their classification, 970 p., 874 plates: Van Nostrand Reinhold, New York.

LOWRIE, W., ALVAREZ, W., NAPOLEONE, G., PERCH-NIELSON, K., PREMOLI SILVA, I., and TOUMARKINE, M., 1982, Paleogene magnetic stratigraphy in Umbrian pelagic carbonates rocks: Contessa sections, Gubbio: Geological Society of America Bulletin, v. 93, p. 414–432.

MARTINEZ-GALLEGO, J., and CREMADES, J., 1978, *Globigerina (Eoglobigerina) prebetica,* nueva especie de foraminífero planctonico del Eoceneo Inferior: Revista Española de Micropaleontología, v. 11, p. 95–98.

McGOWRAN, B., 1986, Cainozoic oceanic and climatic events: the Indo-pacific foraminifera biostratigraphic record: Palaeoceanography, Palaeoclimatology, Palaeoecology, v. 55, p. 247–256.

McGOWRAN, B., 1989, Silica burp in the Eocene: Geology, v. 17, p. 857–860.

McKEEL, D. R. and LIPPS, J. L., 1972, Calcareous plankton from the Tertiary of Oregon: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 12, p. 75–79.

——— and LIPPS, J. L., 1975, Eocene and Oligocene planktonic foraminifera from the central and southern Oregon coast range: Journal of Foraminiferal Research, v. 5 no. 4, p. 1–5.

NORRIS, R. D., CORFIELD, R. M. and CARTLIDEGE, J., 1993, Evolution of depth ecology in the foraminifera lineage *Globorotalia (Foshella)*: Geology, v. 21, p. 975–978.

NORRIS, R. D, 2000, Pelagic species diversity, biogeography and evolution: Palaeobiology, v. 26, p. 236–258.

——— and NISHI, H., 2001, Evolutionary trends in coiling of tropical Paleogene planktic foraminifera: Paleobiology, v. 27, p. 327–347.

NUTTALL, W. L. F., 1928, Notes on the Tertiary Foraminifera of southern Mexico: Journal of Paleontology, v. 2, p. 372–376.

OLSSON, R. K., HEMLEBEN, C., BERGGREN, W. A. and HUBER, B. T., (eds.), 1999, Atlas of Paleocene planktonic foraminifera: Smithsonian Contributions to Paleobiology, no. 65, p. 10–13.

———, ———, ———, and LIU, C., 1992, Wall texture classification of plantonic foraminifera genera in the lower Danian.

——— and WISE, S. W., 1987, Upper Paleocene to middle Eocene depositional sequences and hiatuses in the New Jersey Atlantic margin, in Ross, C.A. and Haman, D. (eds.), Timing and depositional history of eustatic sequences: constraints on seismic stratigraphy, Washington, D.C.: Cushman Foundation for Foraminiferal Research, v. 24, p. 99–112.

PARDO, A., KELLER, G., OBERHANSLI, H. and HSU, K. J., 1999, Paleoecologic and paleoceanographic evolution of the Tethyan realm during the Paleocene-Eocene transition: Journal of Foraminiferal Research, v. 29, no. 1, p. 37–57.

PEARSON, P. N., 1993, A lineage phylogeny for the Paleocene planktonic foraminifera: Micropaleontology, v. 39, no. 3, p. 193–232.

———, 1998, Stable isotopes and the study of evolution in planktonic foraminifera, in Manger, W. L., and Meeks, L.K., (eds.), Isotope paleobiology and paleoecology: Palaeontological Society Papers, v. 4, p. 138–178.

——— and CHAISSON, P., 1997, Late Paleocene to middle Miocene planktonic foraminifer biostratigraphy of the Ceara Rise, Proceedings of the Ocean Drilling Program Scientific Results, v. 154, Shackleton, N. J, Curry, W. B., Richter, C. and Bralower, T. J. (eds.): College Station, Texas (Ocean Drilling Program).

———, DITCHFIELD, P.W., SINGANO, J., HARCOURT-BROWN, K.G., NICHOLAS, C.J., OLSSON, R.K., SHACKLETON, N.J. and HALL, M.A., 2001, Warm Late Cretaceous and Eocene tropical sea-surface temperatures: Nature, v. 413, p. 481–487.

———, SHACKLETON N. J. and HALL, M. A., 1993, Stable isotope paleoecology of middle Eocene planktonic foraminifera and multispecies isotope stratigraphy, DSDP Site 523, south Atlantic: Journal of Foraminiferal Research, v. 23, no. 2, p. 123–140.

PETTERS, V., 1954, Tertiary and upper Cretaceous foraminifer from Colombia, S. A.: Contributions from the Cushman Foundation for Foraminiferal Research, v. 5, no. 1, p. 37–41.

PREMOLI-SILVA, I. and BOERSMA, A., 1986, Paleogene biofacies of the western North Atlantic, The western North Atlantic region: in P. R. Vogt and B. E. Tucholke (eds.), The Geology of North America: The Geological Society of America, Boulder, Colorado, v. M, p. 527–546.

——— and S. SPEZZAFERRI, 1990, Paleogene planktonic foraminifer biostratigraphy and paleoenvironmental remarks on Paleogene sediments from Indian Ocean sites, Leg 115. Duncan, R. A., Backmann, J., Peterson, L. C. and others (eds.), Proceedings of the ODP, Scientific Results, v. 115.: College Station TX, (Ocean Drilling Program), p. 227–314.

QUILTY, P. G., 1976, Planktonic foraminifera from DSDP Leg 34-Nazca Plate, in Yeats, R. D., Hart, S. R., and others, (eds.): Initial reports of the Deep Sea Drilling Project, v. 34, Washington, D.C., U.S. Govt. Printing Office, p. 650–651.

RAMSAY, W. R., 1962, Hantkeninidae in the Tertiary rocks of Tanganyika: Contributions from the Cushman Foundation for Foraminiferal Research, v. 13, p. 78–89.

REY, M., 1939, Distribution stratigraphique des Hantkenina dans le Nummulitique du Rharb (Maroc), Bulletin de la Société Géologique de France, v. 5, no.8, p. 321–341 (in French).

SAMANTA, B. K., 1973, Planktonic foraminifera from the Palaeocene-Eocene successionin the Rakhi Nala, Sulaiman Range, Pakistan: British Museum Natural History Bulletin, v. 22, no. 6, p. 436.

SCHNEIDER, C. E. and KENNETT, J. P., 1996, Isotopic evidence for interspecies habitat differences during the evolution of the Neogene planktonic foraminiferal clade *Globoconella*: Palaeobiology, v. 22, p. 282–303.

SHACKLETON, N. J., and P., K., 1975, Paleotemperature history of the Cenozoic and the initiation of Antarctic glaciation: oxygen and carbon isotope analysis in DSDP Sites 277, 279 and 281: *in* Kennett. J. P., Houtz R. E., and others, (eds.), Initial Reports of the Deep Sea Drilling Project, v. Vol. 29: Washington, D.C., U.S. Government Printing Office, p. 881–884.

SHIPBOARD SCIENTIFIC PARTY, 1996, Site 960, *in* Mascle, J., Lohmann, G.P., Clift, P.D., and others (eds.), Proceedings of the Ocean Drilling Program Initial Reports, v. 159: College Station, TX (Ocean Drilling Program), p. 151–215.

SHOKHINA, V. A., 1937, The genus *Hantkenina* and its stratigraphical distribution in the North Caucasus: Problems of Paleontology, Publication of the Laboratory of Palaeontology, Moscow University, v. 2–3, p. 425–452.

SPENCER-CERVATO, C. and THIERSTEIN H. R., 1997, First appearance of *Globorotalia truncatulinoides*: cladogenesis and immigration: Marine Micropaleontology, v. 30, no. 4, p. 267–291.

STAINFORTH, R. M., 1948, Applied micropaleontology in coastal Ecuador: Journal of Paleontology, v. 22, no. 3, p. 113–151.

STEINECK, P. L., 1971, Phylogenetic reclassification of paleogene planktonic foraminifera: The Texas Journal of Science, v. 23, p. 167–178.

SUBBOTINA, N. N., 1953, Fossil foraminifera of the U.S.S.R., Globigerinidae, Hantkeninidae and Globorotalidae: Trudy Vsesoyznogo Neftyanogo Nauchno-Issledovatel'skogo Geologo-Razvedochnogo Instituta (VNIGRI), v. 76, p. 1–296.

SVERDLOVE, M. S. and BÉ, A. W. H., 1985, Taxonomic importance of embryonic and juvenile planktonic foraminifera: Journal of Foraminiferal Research, v. 15, p. 253–241.

THALMANN, H. E., 1932, Die Foraminiferen-Gattung *Hantkenina* Cushman 1924 und ihre regional-stratigraphische Verbreitung: Ecolgae Geologicae Helvetiae, v. 25, p. 287–292.

——, 1942, Foraminiferal genus *Hantkenina* and its subgenera: American Journal of Science, v. 240, p. 809–820.

TOUMARKINE, M., 1981, Discussion de la validite de l'espeche *Hantkenina aragonensis*, Nuttall, 1930, Description de *Hantkenina nuttalli*, N. sp.: Cahiers De Micropalaeontologie, v. 4, p. 109–119.

—— and LUTERBACHER, H., 1985, Paleocene and Eocene planktonic foraminifera, in Bolli., H. M., Saunders, J. B. & Perch-Nielsen, K. (eds.), Plankton Stratigraphy, p. 87–154: Cambridge, UK, Cambridge University Press.

TREGENZA, T. and BUTLIN, R. K., 1999, Speciation without isolation: Nature, v. 400, p. 311–312.

VAIL, P. R., and HARDENBOL, J., 1979, Sea-level changes during the tertiary: Oceanus, v. 22, p. 171–179.

WAGNER, L., 1998, Tectono-stratigraphy and hydrocarbons in Puigdefabregas, in C., Luterbacher, H. P., and Fernandez, M., (eds.), Cenozoic foreland basins of western Europe: Geological Society Special Publication, no. 134, p.339–369.

ZACHOS, J. C., PAGANI, M., SLOAN, L. C., THOMAS, E., and BILLUPS, K., 2001, Trends, rhythms, and aberrations in global climate 65 Ma to present: Science, v. 292, p. 686–693.

ZACHOS, J. C., STOTT, L. D. and LOHMAN, K. C., 1994, Evolution of early Cenozoic marine temperatures: Paleoceanography, v. 9, no. 2, p. 358–387.

APPENDIX 1.   Biometric data for Fig. 4. Maximum diameter of individual chambers measured on foraminiferal X-rays. Lower case letters = specimen ID.

Chamber	a	b	c	d	e	f	g	h	i	j	k	l	m	n	Mean	std
C. eocanica, ODP Sample 865B-8H-6, 85–87 cm, P9 (maximum test diameter, mm) n = 6															
1	22	25	15	16	20	11									18	5
2	31	32	30	31	31	23									30	3
3	37	37	45	41	45	46									42	4
4	57	52	58	64	70	56									59	7
5	74	71	85	90	98	83									83	10
6	107	100	119	122	134	117									116	12
7	149	134	177	161	196	180									166	22
8	214	181	257	241	281	287									244	41
9	311	264	378	330	408	355									341	51
10	448	408	598	511	573	647									531	92
11	668	612		718											666	53
H. nuttalli, ODP Site 865B-7H-6, 57–59 cm, P10 (maximum test diameter, mm) n = 8															
1	18	22	13	16	17	18	18	22							18	3
2	37	43	25	28	30	33	30	37							33	6
3	46	46	29	34	41	41	38	55							41	8
4	65	71	49	50	58	70	63	77							63	10
5	97	89	61	65	83	98	86	105							85	16
6	153	126	93	89	111	136	124	132							120	22
7	209	197	127	115	156	205	164	185							170	35
8	299	253	190	173	219	266	221	242							233	41
9	388	372	310	254	357	381	323								341	48
10	494	532	446	360	548	522	404								472	71
			690	544			706								647	89
H. compressa, 865B-3H-5, 65–67 cm, P15 (maximum test diameter, mm) n = 14															
1	32	27	17	35	23	36	46	41	35	36	26	28	38	37	33	8
2	51	44	35	51	40	58	68	52	50	48	48	53	62	63	52	9
3	62	67	49	83	48	70	77	55	60	59	61	60	79	81	65	11
4	80	86	83	100	68	97	99	75	79	72	82	78	104	97	86	12
5	95	107	107	138	94	116	132	87	100	98	112	96	125	126	109	16
6	124	161	150	181	127	152	187	112	120	127	161	127	165	161	147	24
7	167	201	210	241	179	202	218	155	157	162	227	178	218	216	195	29
8	221	280	266	287	205	259	302	218	210	192	290	225	261	282	250	37
9	296	326	350	383	254	321	376	254	272	246	348	293	340	384	317	49
10	351	411	431	518	337	450		342	359	313	471	333	428	434	398	63
11	431	598	568	673		612		427	428	360		408			501	112
12	592							470	536			488			521	54
P. micra ODP Sample 865B-7H-6, 57–59 cm, P10															
1	17															
2	28															
3	37															
4	53															
5	68															
6	76															
7	98															
8	122															
9	142															
10	185															
11	219															
12	285															

APPENDIX 2. Carbon and oxygen stable isotope data and sample details for Fig. 5.

ODP Sample	mbsf	Zone	Species	δO18	δC18
865C/7H/6, 55–57	58.55	P11	*H. nuttalli/mexicana*	−0.40	2.39
865C/7H/6, 55–57	58.55	P11	*M. spinulosa*	0.00	1.19
865C/7H/6, 55–57	58.55	P11	*A. pseudotopilenis*	−1.20	2.84
865C/7H/6, 55–57	58.55	P11	*S. frontosa*	−0.70	3.62
865C/8H/1, 60–62	60.96	P11	*H. nuttalli/mexicana*	0.01	1.73
865C/8H/1, 60–62	60.96	P11	*M. spinulosa*	0.31	1.23
865C/8H/1, 60–62	60.96	P11	*S. frontosa*	−0.40	3.08
865C/8H/1, 110–112	61.40	P10–P11	*H. nuttalli/mexicana*	−0.04	1.85
865C/8H/1, 110–112	61.40	P10–P11	*M. spinulosa*	0.39	1.36
865C/8H/1, 110–112	61.40	P10–P11	*M. aragonensis*	−0.50	3.03
865C/8H/1, 110–112	61.40	P10–P11	*A. pseudotopilenis*	−0.90	3.29
865C/8H/1, 110–112	61.40	P10–P11	*T. pomeroli*	−0.70	3.27
865C/8H/1, 110–112	61.40	P10–P11	*S. frontosa*	−0.20	1.79
865C/8H/1, 110–112	61.40	P10–P11	*Cibicidoides* spp.	−0.02	1.87
865C/8H/2, 110–112	62.90	P10	*A. pseudotopilenis*	0.67	0.64
865C/8H/2, 110–112	62.90	P10	*S. frontosa*	−0.90	3.21
865C/8H/3, 70–72	62.90	P10	*C. eocanica*	0.20	1.11
865C/8H/3, 70–72	62.90	P10	*A. pseudotopilenis*	−1.20	3.19
865C/8H/3, 70–72	62.90	P10	*S. frontosa*	−0.27	1.77
865C/8H/3, 70–72	62.90	P10	*Cibicidoides* spp.	0.40	0.49
865C/8H/3, 110–112	64.40	P10	*C. eocanica*	0.35	1.56
865C/8H/3, 110–112	64.40	P10	*M. aragonensis*	−1.20	3.56
865C/8H/3, 110–112	64.40	P10	*A. pseudotopilenis*	−0.80	3.02
865C/8H/3, 110–112	64.40	P10	*S. frontosa*	−0.30	1.71
865C/8H/3, 110–112	64.40	P10	*Cibicides* spp.	−0.10	0.83
865C/8H/3, 110–112	64.40	P10	*G. higginsi*	−0.40	2.39
865C/4H/1, 110–112	23.40	P15	*H. compressa*	−0.30	1.92
865C/4H/1, 110–112	23.40	P15	*T. cerroazulensis*	−0.30	1.75
865C/4H/1, 110–112	23.40	P15	*S. linaperta*	0.13	1.76
865C/4H/1, 110–112	23.40	P15	*G. semiinvoluta*	−0.10	2.23
865C/4H/1, 110–112	23.40	P15	*Cibicides*	1.09	1.01
865B/3H/4, 66–68	23.15	P15	*Chiloguembelina* sp.	−0.11	1.50
865C/4H/3, 110–112	26.40	P14	*H. compressa*	−0.20	2.07
865C/4H/3, 110–112	26.40	P14	*M. spinulosa*	−0.50	2.99
865C/4H/3, 110–112	26.40	P14	*M. lehneri*	−0.50	2.80
865C/4H/3, 110–112	26.40	P14	*A. pseudotopilenis*	−0.50	3.01
865C/4H/3, 110–112	26.40	P14	*T. cerroazulensis*	−0.10	1.72
865C/4H/3, 110–112	26.40	P14	*S. linaperta*	0.03	1.88
865C/4H/3, 110–112	26.40	P14	*Cibicidoides* spp.	1.07	0.76
865C/4H/3, 110–112	26.40	P14	*P. micra*	−0.10	1.55
865C/4H/5, 110–112	29.40	P14	*H. compressa*	−0.40	1.94
865C/4H/5, 110–112	29.40	P14	*M. spinulosa*	−0.60	2.98
865C/4H/5, 110–112	29.40	P14	*A. pseudotopilenis*	−0.40	3.15
865C/4H/5, 110–112	29.40	P14	*T. cerroazulensis*	−0.10	1.72
865C/4H/5, 110–112	29.40	P14	*S. linaperta*	0.34	1.70
865C/4H/5, 110–112	29.40	P14	*Cibicidoides* spp.	1.00	0.86
865C/4H/6, 63–65	30.43	P14?	*H. compressa*	−0.50	1.70
		This study			
865B-8H-4, 137–139		P9–P10	*P. eoclava* nov. sp.	−0.77	1.19
865B-8H-4, 137–139		P9–P10	*M. spinulosa*	−1.93	2.90
865B-8H-4, 137–139		P9–P10	*A. pseudotopilensis*	−1.69	3.06
865B-8H-4, 137–139		P9–P10	*S. frontosa*	−1.08	1.34