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Notes

The missing link in the evolutionary origin of the foraminiferal genus *Hantkenina* and the problem of the lower-middle Eocene boundary

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ABSTRACT

The initial appearance of the planktonic foraminiferal genus *Hantkenina* has been used for about fifty years to recognize the base of the Lutetian and middle Eocene. However, probably as a result of incomplete stratigraphic records, discrepant ranges of *Hantkenina* have been reported by various investigators at many Eocene sections. Here we report the first complete evolutionary transition from *Clavigerinella* to *Hantkenina*, from the northwestern Tethyan deep-water section at Holzhäusl (Salzburg, Austria). A newly discovered species, *Hantkenina* nov. sp., is the link between *Clavigerinella caucasica* and *Hantkenina mexicana*. This finding unequivocally heralds the initial entry of *Hantkenina*, which is correlated to the upper part of calcareous nannoplankton Subzone NP15b (*Sullvania gigas* Subzone), to be defined. This indicates a mismatch of ~4.5 m.y. between the base of the Lutetian at the type locality, which has been placed within Subzone NP14b, and the first appearance datum of *Hantkenina*. Consequently, the first occurrence of *Hantkenina* can no longer be used as a marker for the base of the middle Eocene.

INTRODUCTION

The first appearance date of *Hantkenina* is an important stratigraphic marker. Since the basic work of Bolli (1957), the first occurrence (FO) of the genus *Hantkenina* has been used to recognize the base of both the middle Eocene and the Lutetian Stage. According to standard stratigraphic procedures, the Ypresian-Lutetian boundary must be defined near the base of the Lutetian stratotype, which has been proposed at St. Leu d'Esserent ~50 km north of Paris, France (Blondeau, 1981). There, as at many other areas, the Ypresian-Lutetian-boundary is an unconformity that encompasses a major stratigraphic gap. The upper surface of this unconformity (the base of the type Lutetian) is in calcareous nannoplankton Subzone NP14b (Aubry, 1991), which has been thought to be consistent with the first occurrence (FO) of *Hantkenina* (see Molina et al., 2006, for a review).

This is in contrast to the results of Toumarkine and Bolli (1975) and Proto-Decima et al. (1975) from the Possagno section, where the FO of *Hantkenina* was found in the *Nannotetrina fulgens* Zone (NP15). Similar results were obtained in Tanzanian sections, where the FO of *Hantkenina singanoae* occurs in Subzone NP15b; however, Pearson et al. (2004) considered this to be an effect of problems in the correlation of calcareous nannoplankton and foraminiferal zonation schemes. Additional uncertainties arise because the sedimentary record at Kilwa is punctuated by stratigraphic gaps. At the Gorrondatxe and Agost sections in Spain, the first *Hantkenina* was also found in Subzone NP15b (Payros et al., 2007, 2008; Larrasoña et al., 2008). There, this mismatch to the standard stratigraphic framework has not been interpreted as evidence for a true late appearance of *Hantkenina*, but as a result of the overall scarcity of *Hantkenina*.

These taxonomic and stratigraphic problems make it necessary to reevaluate the enigmatic initial entry of *Hantkenina*. For this reason, a high-resolution study was performed at the Austrian Holzhäusl section, where the transition between *Clavigerinella* and *Hantkenina* was

described for the first time (Coxall et al., 2003). In this paper we demonstrate that the newly discovered *Hantkenina* nov. sp. is the real ancestor of the genus *Hantkenina* and we correlate its first occurrence with the standard Cenozoic calcareous nannoplankton zonation (Martini, 1971), which was refined by Aubry (1991).

GEOLOGICAL SETTING

The Holzhäusl section (47°58'26"N; 13°07'09"E) consists of a number of temporary outcrops resulting from the erosion of a small tributary to Lake Mattsee and is located 20 km north of the town of Salzburg in Austria (Fig. 1). The pelagic sediments are part of the informal lithostratigraphic unit "Buntmergelserie" and were deposited in the northwestern Tethyan realm at paleolatitude ~35°N. They consist of bathyal deposits of the passive southern margin of the European plate. In previous studies of the section, abundant and diverse tropical planktonic foraminiferal assemblages were recorded that indicate open marine environments (Hagn, 1960; Gohrbandt, 1967). In the Oligocene, the slope deposits were detached from their substratum and became part of the Ultrahelvetic thrust unit, which tectonically overlies the sedimentary infilling of the Alpine Molasse Basin.

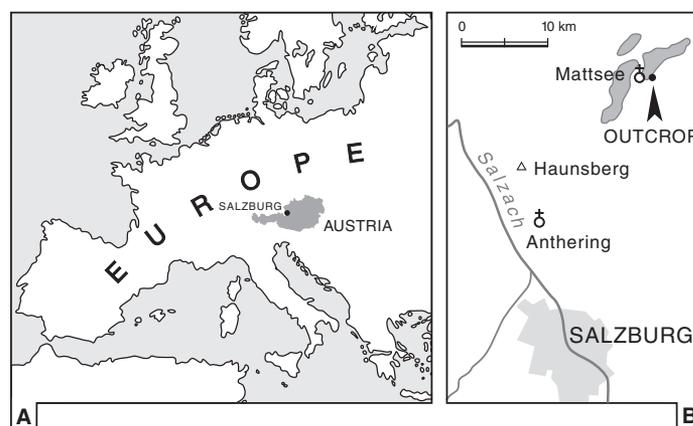


Figure 1. Location of studied section in Austria.

METHODS AND MATERIAL

We studied 32 samples spanning 16 m of section for planktonic foraminifera and calcareous nannoplankton (Fig. 2). The samples are gray marlstones with an average carbonate content of 58%. The sample resolution varies from 10 samples/m in the interval showing the transition between *Clavigerinella* and *Hantkenina* (between samples A2a to A2k; due to limited space, only 3 of 12 samples are indicated in Fig. 2) to 1 sample/m in the remainder of the section. For calcareous nannofossil studies, smear slides were studied with the light microscope at a magnification of 1000×. Foraminifera were studied in washed and sieved residues from the marlstone. The holotype of *Hantkenina* nov. spec. will be housed in the collection of the Museum of Natural History in Vienna.

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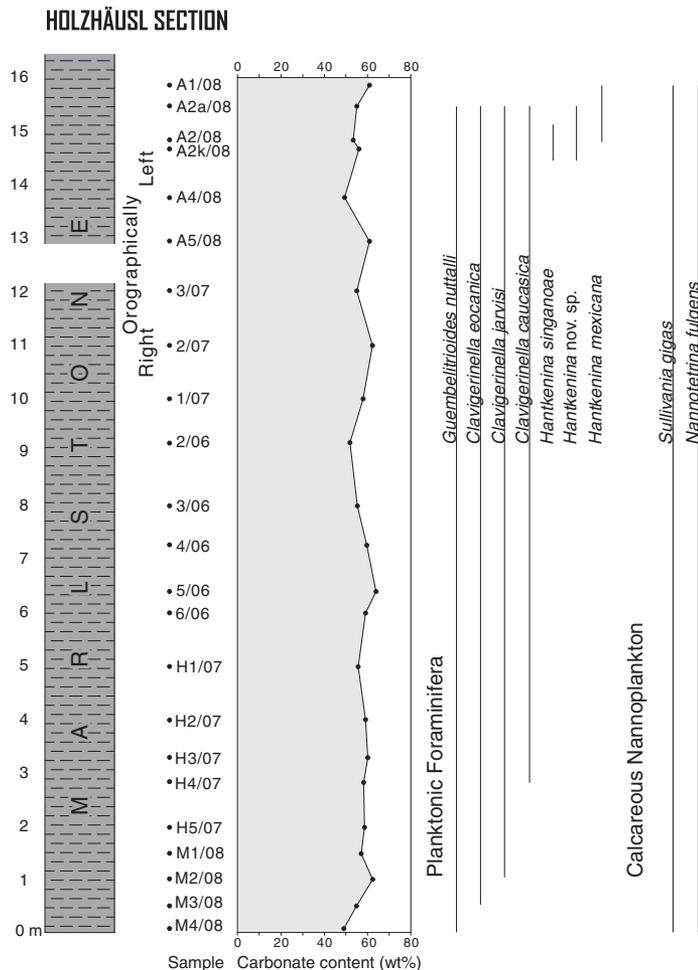


Figure 2. Log of Holzhäusl section and distribution of important planktonic species.

RESULTS

Hantkeninid Evolution

The planktonic foraminiferal assemblages at the Holzhäusl section are characterized by *Clavigerinella* spp., *Guembeltrioides nuttalli*, *Morozovella aragonensis*, *Acarinina praetopilensis*, *Igorina broedermanni*, *Parasubbotina hagni*, *Turborotalia frontosa*, *Pseudohastigerina wilcoxensis*, and, in the upper part, by *Hantkenina mexicana*. The occurrences of common specimens of *Clavigerinella* and *Hantkenina* make this outcrop a prime site for the study of the transition between the two taxa.

The genus *Hantkenina* is characterized by planispiral coiling and nonporous hollow chamber extensions (tubulospines). It evolved gradually from the genus *Clavigerinella*, which shows radial elongate, clavate, or digitate chambers, but no tubulospines. This evolutionary trend and the transition from *Clavigerinella* to *Hantkenina* were demonstrated from the Austrian Holzhäusl section (Coxall et al., 2003) and from the Kilwa drill sites in Tanzania (Pearson et al., 2004). At both localities, a newly discovered species, named *Hantkenina singanoae* by Coxall and Pearson (2006), was considered to be the missing link between the two genera.

Contrary to this, our high-resolution study of the Holzhäusl section revealed a continuous development from the pointed chambers of *Clavigerinella caucasica* to the straight radial chamber extensions of a newly discovered *Hantkenina* nov. sp. (Fig. 3). The pointed chamber ends of this species show normal sized pores extending up to a nonporous nub (1 and

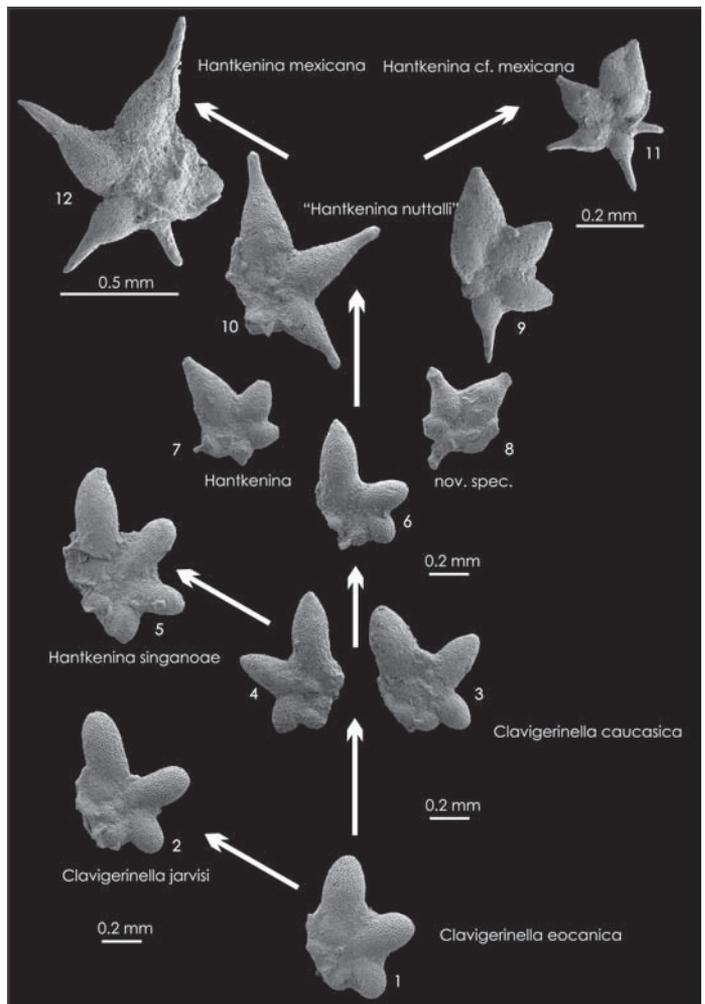


Figure 3. Evolutionary lineage from *Clavigerinella* to *Hantkenina*. 1—*Clavigerinella eocanica* (Nuttall), typical development with club-shaped chambers. 2—*C. jarvisi* (Cushman), elongated cylindrical chambers with rounded ends. 3, 4—*C. caucasica* (Subbotina), later chambers with pointed perforate distal chamber ends. 5—*Hantkenina singanoae* Coxall and Pearson, later chambers ending in hood-like nub. 6–8—*H. nov. sp.* later chambers with pointed non-perforated chamber end (6), primary chamber of final whorl with distinct tubulospine, second chamber with pointed end, later chamber probably with tubulospines (broken off) (7), chambers ending in proto-tubulospines with short thickened tips (8). 9, 10—“*Hantkenina nuttalli*” variation of *H. mexicana*, with broad strongly appressed chambers ending in a distal tubulospine (9), with slender chambers ending in tubulospines that show perforations nearly up to short nonperforated ends, similar to those of 8. 11—*Hantkenina cf. mexicana* Cushman. Form with true tubulospines but broad strongly appressed chambers. 12—*H. mexicana* Cushman. Typical development with slender chambers and long tubulospines.

2 in Fig. 4). In this evolutionary transition, the first true (nonporous) tubulospines appear in the juvenile stage (3 in Fig. 4), whereas the chambers of the final whorl still end in a nonporous tip or a thickened nub (3 and 4 in Fig. 4). In the next step, longer tubulospines developed also in the final whorl. This form of *H. mexicana* with broad appressed chambers was originally described as *H. nuttalli* (Toumarkine, 1981). It connects *Hantkenina* nov. sp. with *H. mexicana* sensu stricto, characterized by well-developed long tubulospines and slender chambers.

The evolution between *C. caucasica* and *H. mexicana* occurs in a 2-m-thick part of the Holzhäusl section. Rare specimens of *H. singanoae*

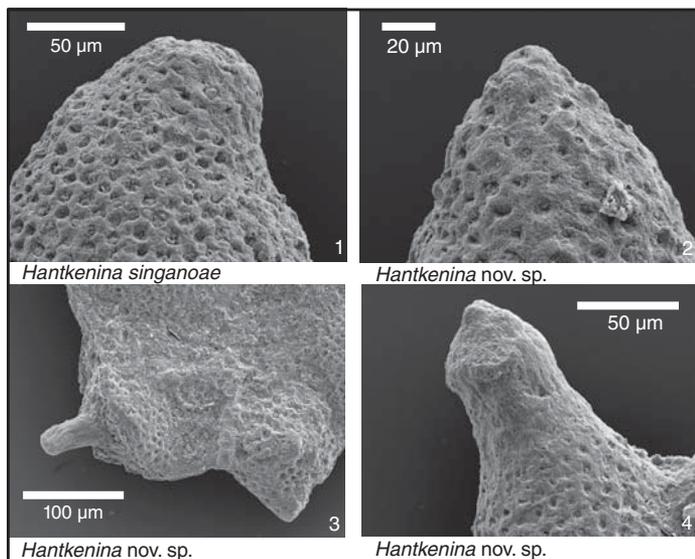


Figure 4. Evolution of tubulospines. 1—*Hantkenina singanoae* Coxall and Pearson (detail of 5 in Fig. 3), distal chamber ends with terminal nub. 2—*Hantkenina* nov. sp. (detail of 6 in Fig. 3), distal chamber ends with an acute nub. 3—*Hantkenina* nov. sp. (detail of 7 in Fig. 3), first chamber of final whorl has short tubulospine and acute nub at distal end of second chamber. 4—*Hantkenina* nov. sp. (detail of 8 in Fig. 3), chambers end in short tubulospines with thickened conical tip.

occur together with *Hantkenina* nov. sp. In contrast to Pearson et al. (2006), *H. singanoae* is here considered to be an evolutionary side branch to the *Clavigerinella*-*Hantkenina* transition, since it is unlikely that the bent chamber ends of this species have developed into straight tubulospines.

Calcareous Nannoplankton Biostratigraphy

An inventory of the nannoplankton assemblages encountered will be given elsewhere. In this paper we report on the biostratigraphically important species to establish a correlation between the calcareous nannoplankton zonation of Martini (1971) and the first occurrence of the genus *Hantkenina*. For the taxonomy of calcareous nannoplankton, see Bown (2005).

The nannoplankton assemblages, which are dominated by *Reticulofenestra dictyoda*, *R. scrippsae*, *Coccolithus pelagicus*, and *Zygrhablithus bijugatus*, are diverse and show moderate preservation. Reworking of Cretaceous nannoplankton specimens is <1%. All samples display similar compositions of the nannoplankton assemblages, which are characterized by the occurrences of *Blackites spinosus*, *Chiasmolithus expansus*, *C. grandis*, *C. solitus*, *Coccolithus mutatus*, *Discoaster barbadiensis*, *D. gemmifer*, *D. saipanensis*, *D. tanii*, *D. wemmelensis*, *N. fulgens*, *N. cristata*, *R. umbilicus* (>14 µm), *Sphenolithus moriformis*, *S. spiniger*, *S. radians*, *Sullivania gigas*, and *Su. consueta*.

This assemblage is typical for the *N. fulgens* Zone, which is defined by the stratigraphic range of the marker fossil. The *N. fulgens* Zone represents Zone NP15 in the zonation scheme of Martini (1971) and Zone CP13 in the zonation scheme of Okada and Bukry (1980), who suggested a threefold subdivision of the *N. fulgens* Zone using the range of *Su. gigas* (Fig. 5), which is restricted to the middle part (CP13b) of the *N. fulgens* Zone. Aubry (1991) defined Subzone NP15a as the interval between the FO of *N. fulgens* and the FO of *Su. gigas*, Subzone NP15b as the total range of *Su. gigas*, and Subzone NP15c as the interval between the last occurrence (LO) of *Su. gigas* and the LO of *Rhabdosphaera gladius*. Using these criteria, the entire Holzhäusl section can be assigned to the *Su. gigas* Subzone.

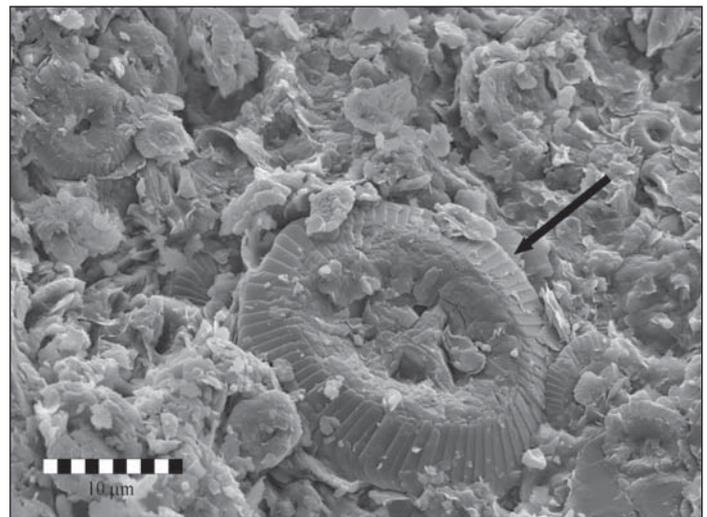


Figure 5. Scanning electron image of marlstone from Holzhäusl section (sample A2e/08) containing *Sullivania gigas* (arrow) beside abundant other calcareous nannoplankton specimens.

DISCUSSION

Berggren et al. (1985) give a review of the different opinions on the FO of *Hantkenina*, which has been placed within Zone NP14, at the NP14/15 boundary or within Zone NP15. Berggren et al. (1985) relied on the paper of Lowrie et al. (1982), who associated plankton zonation with the magnetic polarity stratigraphy at the Contessa Road section near Gubbio, Italy. According to this correlation, *Hantkenina* appeared in the youngest part of Chron C22n, which encompasses the lower part of Zone NP14. The same correlation was given in the latest standard stratigraphic framework by Berggren and Pearson (2005). They chose the first appearance of *G. nuttalli*, which is thought to be approximately synchronous to the FO of *H. mexicana*, to define the base of Zone E8. They used this event to recognize the base of the middle Eocene and placed the base of Zone E8 within calcareous nannoplankton Subzone NP14a.

Payros et al. (2007) and Larrasoña et al. (2008) were able to demonstrate that the long-established magnetobiostratigraphic framework is not reliable, because the FO of *G. nuttalli* has been found within magnetic polarity Chron C20r at the Gorrondatxe and Agost sections. This implies that the base of Zone E8 is ca. 2.5 m.y. younger than originally supposed and was placed within NP15a. The first *Hantkenina* has been found within Subzone NP15 in the Spanish sections, but this has been interpreted as a delayed entry, which does not reflect the true first appearance of the genus.

In contrast to the Tanzanian and Spanish sections, the Holzhäusl section is neither punctuated by stratigraphic gaps nor affected by the admixture of reworked specimens. *G. nuttalli* and *Su. gigas* occur throughout the section, which, therefore, can be attributed to planktonic foraminifera Zone E8 and calcareous nannoplankton Subzone NP15b. As at least 15 m of marlstone contain *G. nuttalli* and *Su. gigas* in the absence of *Hantkenina*, the first occurrence of *Hantkenina* must have been relatively high within Zone E8 and Subzone NP15b. The discovery of *Hantkenina* nov. sp., which is the missing link in the evolutionary lineage between *Clavigerinella* and *Hantkenina*, gives clear evidence that the FO of *Hantkenina* at Holzhäusl reflects the initial entry of the genus.

CONCLUSION

The morphological features of the test of the newly discovered *Hantkenina* nov. sp. are clear indicators that this species is the real ancestor of *H. mexicana*. The FO of this genus can be assigned to planktonic

foraminifera Zone E8 and the upper part of *Su. gigas* Subzone (NP15b). In the standard stratigraphic framework of Gradstein et al. (2004), the age of the base of this subzone is estimated at 45 Ma and the top at 43 Ma. Together with the data of the Holzhäusel section, this suggests that the first appearance date of *Hantkenina* was ca. 44 Ma or even slightly younger. As the base of the Lutetian is estimated at 48.6 Ma, a mismatch of ~4.5 m.y. occurs between the base of the Lutetian and the first appearance date of *Hantkenina*. Contrary to the long-held view, the FO of *Hantkenina* cannot be used for recognizing the stage boundary. As long as a Global Stratigraphic Section and Point (GSSP) is not defined for the Ypresian-Lutetian boundary, the base of calcareous nannoplankton Subzone NP14b can be used as a proxy for the determination of the lower-middle Eocene boundary, which approximately coincides with the age of the base of the type Lutetian in the Paris Basin (Aubry, 1991; Larrasoña et al., 2008).

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