ORIGIN OF THE EOCENE PLANKTONIC FORAMINIFER *HANTKENINA* BY GRADUAL EVOLUTION

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Abstract: *Hantkenina* is a distinctive planktonic foraminiferal genus characterized by the presence of tubulospines (robust hollow projections) on each adult chamber, from Middle and Upper Eocene marine sediments worldwide. Here we illustrate its evolutionary origin using *c.* 150 specimens from 30 stratigraphic intervals in two sediment cores from Tanzania. The specimens, which span an estimated time interval of 300 ka, show four intermediate steps in the evolution of the tubulospines that amount to a complete intergradation from *Clavigerinella caucasica*, which does not possess them, to *Hantkenina mexicana*, which does. Stable isotope analyses indicate that the transitional forms evolved in a deep planktonic habitat not occupied at that time by other species of planktonic foraminifera. We discuss the morphogenetic constraints involved in the evolutionary transition and propose an ecological/adaptive model for the selective pressures that resulted in the evolution of tubulospines. We compare our record with similar, recently described assemblages from Austria and Italy, and we update the biostratigraphy and systematic taxonomy of the key morphospecies involved in the transition.

Key words: *Hantkenina singanoae*, evolution, foraminifera, Eocene, Tanzania.

THE mineralizing plankton of the oceans have provided some of the best examples of evolutionary transition in stratigraphically ordered sequences because they are abundant, broadly distributed and can be found in continuously deposited deep-sea sediments (Norris 2000; Lazarus 2011). Most studies published to date demonstrate relatively simple changes in size or shape, for example (in planktonic foraminifera) the degree of test compression, the number of chambers per whorl or the development or loss of peripheral thickenings (e.g. Malmgren and Kennett 1981; Malmgren *et al.* 1983; Norris *et al.* 1996; Kucera and Malmgren 1998; Hull and Norris 2009). Here we examine the evolutionary origin of the fossil planktonic foraminifer *Hantkenina*, focusing on the record from two sediment cores obtained by us from Tanzania and in the light of other recently published records from Austria (Rögl and Egger 2010, 2011) and Italy (Coccioni and Bancalà 2012). The example is interesting in that it encompasses the evolution of a relatively complex structure known as a tubulospine *de novo* that demands an adaptive explanation.

Planktonic foraminifera are heterotrophic protists that produce a test ('shell') of calcite that is usually composed of successive chambers arranged in a spiral form with interconnecting foramina. The genus *Hantkenina* (reviewed most recently by Coxall and Pearson 2006) is a highly distinctive, albeit minor, component of Middle and Upper Eocene assemblages. Unlike the primary chamber wall, the tubulospines of hantkeninids are externally smooth or striated and lack the mural pores that generally occur on the walls of planktonic foraminifera (Fig. 1). The internal canals of the tubulospines sometimes open out at the distal end via a small circular aperture (Fig. 1M–P). The first species to occur widely in the fossil record, *Hantkenina mexicana*, commonly possesses flaring calcite pustules at the end of each tubulospine, arranged in a so-called coronet structure (Ramsay 1962, p. 82; Blow 1979, p. 1168; see Fig. 1A, K). Structures similar to the tubulospines of hantkeninids are known from other unrelated genera in the Cretaceous and have been cited as an example of iterative evolution (Coxall *et al.* 2007).

Blow (1979, p. 1165) noticed that the tubulospines of some early hantkeninids taper into the chambers at their bases and commonly show a transition over a few microns from the nonporous tubulospine surface to the fully porous chamber wall (see also Fig. 1K). He concluded from this that they are structurally contiguous
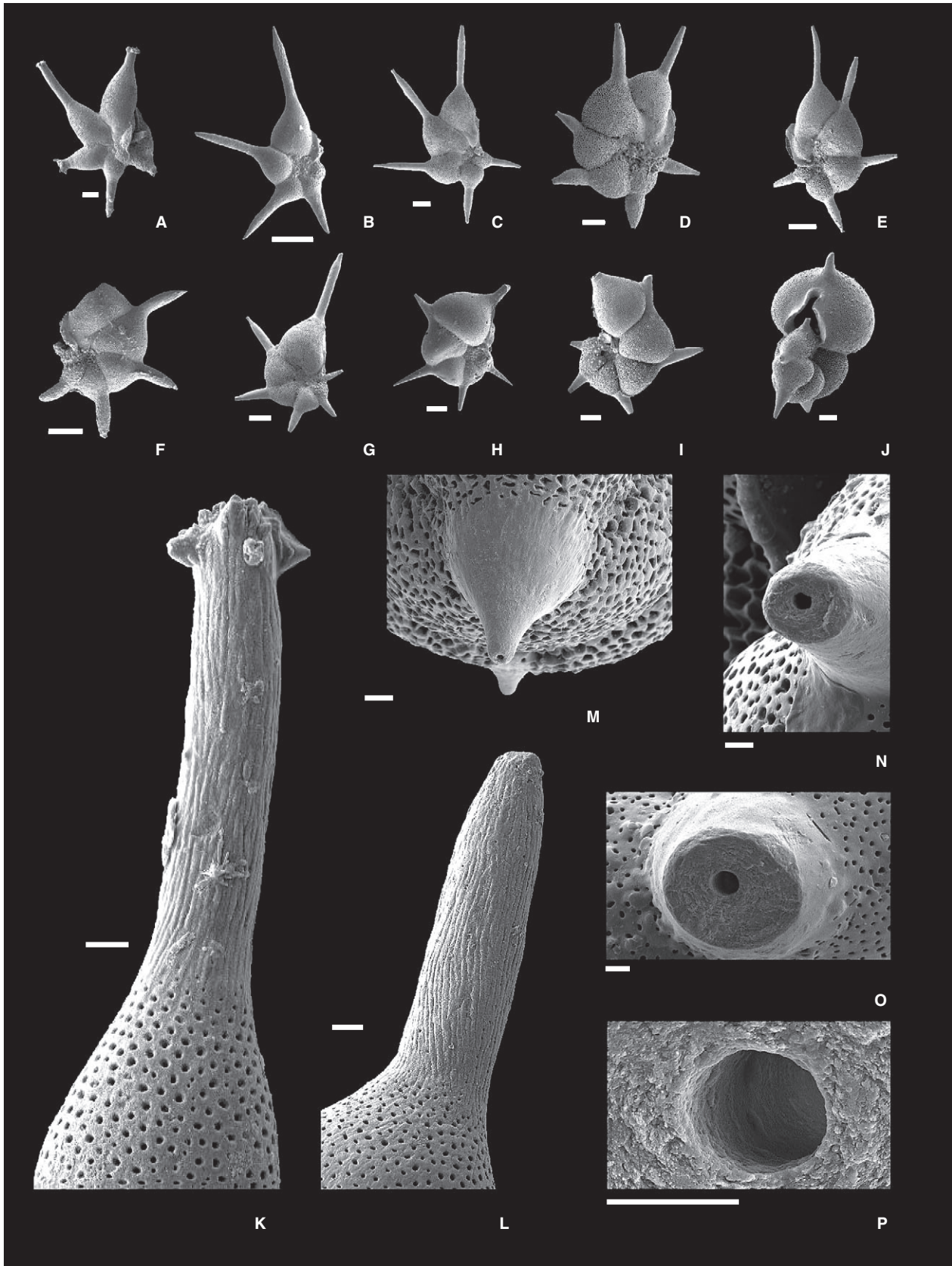
with the primary chamber wall rather than being separate constructions, as is the case with the acicular 'true spines' of some modern species. From this, he inferred that the structures must have evolved by constriction and extension of the primary chamber wall, loss of pores along the tubular constrictions and other modifications such as the development of the coronet structure. Despite these inferences, the evolution of *Hantkenina* in the Eocene was for many years regarded as abrupt and something of a mystery, and several very different ancestors have been proposed (Cushman and Wickenden 1930; Shokhina 1937; Blow and Banner 1962; Benjamini and Reiss 1979; Blow 1979; Banner and Lowry 1985; Pearson 1993). On the basis of comparative ontogeny and test ultrastructure as revealed by dissections and X-rays, Coxall *et al.* (2003) showed that the origin of *Hantkenina* must have been in the genus *Clavigerinella* as had been earlier proposed by Shokhina (1937) and Benjamini and Reiss (1979) and not *Pseudohastigerina* as had been proposed by Blow (1979), Banner and Lowry (1985) and Pearson (1993), among others. Coxall *et al.* (2003) also illustrated eight apparently 'transitional' specimens from Austria that had originally been collected by K. Gohrbandt and F. Aberer in the 1950s, which had been donated to us by F. Rögl (Museum of Natural History, Vienna).

PREVIOUS INVESTIGATIONS

Very well-preserved assemblages of 'early' hantkeninids were described by Blow and Banner (1962), Ramsay (1962) and Blow (1979) from a locality near Kilwa Masoko in Tanzania (see Fig. 2 for palaeogeography of this and other key sites). In 2002, shortly after we sent the paper of Coxall *et al.* (2003) to the press, we drilled a borehole (Tanzania Drilling Project (TDP) Site 2) at this classic site using continuous coring to a total depth of 92.78 m. One of the objectives of this drilling was to attempt recovery of the postulated evolutionary origin of
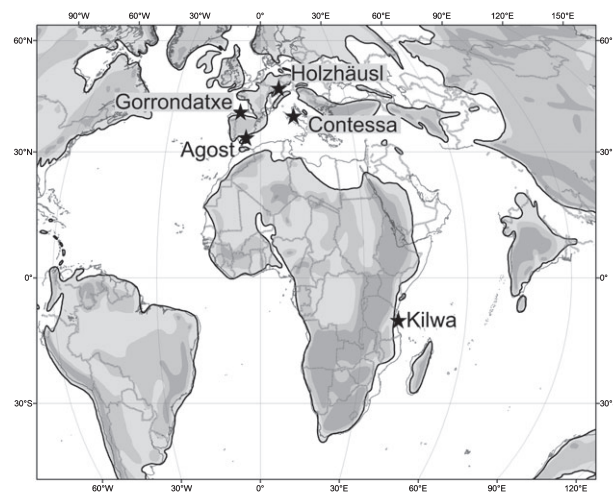

FIG. 2. Eocene palaeogeographical map modified from Markwick *et al.* (2000) showing key localities discussed in the text.

Hantkenina, and in this, we were successful. The lithostratigraphy, biostratigraphy and chemostratigraphy of this site were described by Pearson *et al.* (2004). Initial investigation of the foraminiferal assemblages from TDP Site 2 (Pearson *et al.* 2004) led us to propose that the immediately ancestral species of *Hantkenina* was a little-known form that had been described by Subbotina (1958) from the Belaya River section in the Caucasus as *Clavigerinella caucasica*. This was instead of *C. eocanica*, as we had previously suggested (Coxall *et al.* 2003), the two species having generally been regarded as synonyms (e.g. Blow 1979; Pearson 1993). *Clavigerinella caucasica* has somewhat pointed chamber ends, reminiscent of an airship in shape, whereas in *C. eocanica,* they are bulbous and rounded. Pearson *et al.* (2004) illustrated two specimens of *C. caucasica* and three specimens labelled as 'transitional *Hantkenina*' from TDP Site 2.

Despite containing these apparently transitional specimens, the biostratigraphy of TDP Site 2 was problematic for us because there was a substantial mismatch between

FIG. 1. Hantkeninids of various species and their tubulospines. A, *Hantkenina mexicana*, Tanzania Drilling Project (TDP) 2/4/2, 63–75 cm, Tanzania (re-illustrated from Pearson *et al.* 2004, plate 2, fig. 22). B, *Hantkenina liebusi*, TDP 2/5/1, 80–88 cm, Tanzania (re-illustrated from Pearson *et al.* 2004, plate 2, fig. 23). C, *Hantkenina liebusi*, TDP 13/16/2, 50–60 cm (re-illustrated from Coxall and Pearson 2006, plate 8.9, fig. 15). D, *Hantkenina dumblei*, ODP 865B/4H/3, 100–108 cm (re-illustrated from Coxall and Pearson 2006, plate 8.7, fig. 10). E, *Hantkenina dumblei*, ODP 865C/5H/6, 110–112 cm, Tanzania. F, *Hantkenina australis*, ODP 647/50/5, Labrador Sea (note recurved tubulospines; re-illustrated from Coxall and Pearson 2006, plate 8.5, fig. 14). G, *Hantkenina dumblei*, TDP 13/ 15/2, 30–40 cm, Mkazambo, Tanzania (re-illustrated from Coxall and Pearson 2006, plate 8.7, fig. 16). H, *Hantkenina alabamensis*, TDP 12/14/1, 81–83 cm, Tanzania. I, *Hantkenina alabamensis*, TDP 17/42/2, 61–68 cm, Tanzania. J, *Hantkenina nanngulanensis*, TDP 11/25/3, 10–20 cm (same specimen as Coxall and Pearson 2006, plate 8.11, fig. 11). K, tubulospine of *H. mexicana*, TDP 2/4/2, 63–75 cm, Tanzania, showing striations and coronet structure. L, tubulospine of *H. liebusi*, TDP 2/4/2, 63–75 cm, Tanzania, showing striations. M, tubulospine of *Cribrohantkenina inflata*, TDP 12/46/2, 56–66 cm, Tanzania, showing conical shape and small terminal aperture. N, tubulospine of *Cribrohantkenina inflata*, TDP 12/42/1, 36–46 cm, Tanzania, showing terminal aperture. O and P, tubulospine of *Cribrohantkenina inflata*, TDP 17/44/2, 0–12 cm, Tanzania, showing terminal aperture. Scale bars represent 100 μm (A–J) and 10 μm (K–P).

the planktonic foraminifer and nannofossil biostratigraphies in relation to the then standard correlation schemes (e.g. Berggren *et al.* 1995; Luterbacher *et al.* 2004). The basic problem was that the *Hantkenina* first appearance, although convincing enough in itself (to us), was stratigraphically far higher than expected, only just below the first occurrence of the planktonic foraminifer *Globigerinetheka* and within the range of the nannofossil *Chiasmolithis gigas*. The mismatch between foraminifera and nannofossil ages was about three million years, which at the time we thought barely possible. To help resolve this problem, we suggested that: (1) there may have been a cryptic hiatus at TDP Site 2 just above the first appearance of *Hantkenina*; and (2) *C. gigas* may have appeared much earlier in hemipelagic environments than in the open ocean (Pearson *et al.* 2004, p. 49). We now know from subsequent studies by others of several sections in Europe (described below, but see especially Payros *et al.* 2007) that it was the standard correlation that was at fault, so there is now no need to invoke anomalous ranges and a cryptic hiatus to explain the record in Tanzania.

As a contribution to the *Atlas of Eocene Planktonic Foraminifera* (Pearson *et al.* 2006), we reviewed the taxonomy of all species of *Clavigerinella* and *Hantkenina* (Coxall and Pearson 2006). We illustrated Subbotina's holotype of *Clavigerinella caucasica* in SEM for the first time. We also illustrated six more transitional specimens from TDP Site 2 and, based on these specimens, suggested that the evolutionary transition first involved: (1) the development of pointed chamber ends, as in *Clavigerinella caucasica*; (2) the evolution of a 'terminal nub' or constriction on the chamber ends; (3) the extension of the chamber ends into a roughly tubular structure, still porous like the rest of the chamber surface, which we called a 'proto-tubulospine'; and (4) the development of this into a true tubulospine by its becoming smooth and nonporous and in some cases having a coronet structure, as in *Hantkenina mexicana*. We noted that for stage 2, the 'distal chamber ends can be inclined in an anterior, posterior or dorsoventral direction', and for stage 3, proto-tubulospines 'are commonly bent' (Coxall and Pearson 2006, p. 252). We named a new species, *Hantkenina singanoae* Pearson and Coxall, to accommodate transitional forms that possess either terminal nubs or proto-tubulospines, choosing not to oversplit what was evidently quite a plastic population of forms. We assigned our new species to *Hantkenina* rather than *Clavigerinella* on the grounds that, in our view, the terminal nubs and proto-tubulospines are essentially homologous with, and 'ancestral' to, true tubulospines, while at the same time noting that the morphological transition appears gradual, and hence, taxonomic divisions are necessarily arbitrary to some extent. We assigned one of the transitional

specimens from Austria that was previously illustrated by Coxall *et al.* (2003) to *H. singanoae* and the others to *C. caucasica*.

Meanwhile, investigations by others were devoted to studying the biostratigraphy and magnetostratigraphy of several sections in Europe with a view to establishing a stratotype for the base of the Lutetian Stage (and, hence, of the Middle Eocene). Bernaola *et al.* (2006) presented the first results from a spectacular section at Gorrondatxe in the Basque country of the western Pyrenees, Spain, which has clear magnetostratigraphy. In that section, they recorded the first *Hantkenina* (which they called *H. nuttalli*, regarded here as a synonym of *H. mexicana*) well within the stratigraphic range of the nannofossil *Chiasmolithus gigas*. As in Tanzania, this was a much higher level than expected, but Bernaola *et al.* (2006) noted that the species is rare in the section and so the level might not record its true first occurrence. However, further consideration of the problem by the same research group (Payros *et al.* 2007) with reference to various sections around the world, including Tanzania, led to a radical new proposal: the true level of origin of *Hantkenina* was within nannofossil zones CP13b and Chron C20r as opposed to CP12a and the base of C21r as previously thought (e.g. Lowrie *et al.* 1982; Napoleone *et al.* 1983; Berggren *et al.* 1995; Luterbacher *et al.* 2004; Berggren and Pearson 2005). This solution was further evidenced from other stratigraphic sections in the Basque region (Payros *et al.* 2009) and now seems to have been accepted by all involved (see especially Molina *et al.* 2011; Wade *et al.* 2011).

Larrasoaña *et al.* (2008) and Ortiz *et al.* (2008) presented two related papers on the detailed magnetostratigraphy and biostratigraphy of another excellent Early–Middle Eocene section from Spain, this time at Agost in the Betic Cordillera. Once again, the first occurrence of hantkeninids was found to be within the range of *Chiasmolithus gigas* and within Chron C20r. Just below the first occurrence of *Hantkenina* (recorded as *H. nuttalli* by Larrasoaña *et al.* 2008, and *H. mexicana* by Ortiz *et al.* 2008; see the systematic taxonomy for a discussion of these names), they recorded a single sample containing '*Hantkenina* cf. *singanoae*', which they described as showing 'gradual transition to *H. nuttalli*' (Larrasoaña *et al.* 2008, p. 401). They also recorded the presence of *Clavigerinella eocanica* and *Clavigerinella jarvisi* at a similar level. These authors did not illustrate the transitional *Hantkenina*, nor did they indicate why it was recorded as 'cf. *singanoae*'. Nevertheless, the presence of transitional specimens is important because it implies that the Agost section approximates the true first occurrence and not a later immigration.

Rögl and Egger (2010, 2011) published two papers on the *Clavigerinella–Hantkenina* transition from the Hol-

zhäusl section near Mattsee in Austria, the same area as was originally collected and described by Gohrbandt (1967). The first paper (Rögl and Egger 2010) indicated a complex evolutionary scenario, in which *Clavigerinella eocanica* gave rise to *C. jarvisi* (an evolutionary dead end), and *C. caucasica*. *Clavigerinella caucasica* then gave rise to *Hantkenina singanoae* (another dead end), and a transitional form called *Hantkenina* nov. spec. (not formally named in that paper) which then gave rise to '*Hantkenina nuttalli*' (their quotation marks). This taxon was the supposed ancestor of *H. mexicana* and another form, *H.* cf. *mexicana*. These hypotheses of ancestry were supported by some illustrations (two of *C. caucasica*, one of *H. singanoae* and three of *Hantkenina* nov. spec.). The various taxa were not formally described or differentiated, but the authors did comment that '*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' (Rögl and Egger 2010, p. 25). Although they did not specifically make the point, their concept of *Hantkenina* is polyphyletic with the terminal nub evolving twice: in a 'bent' form in *H. singanoae* and straight in their *H.* nov. spec.

This scenario was further elaborated in the second paper (Rögl and Egger 2011), in which 12 more transitional specimens were illustrated in SEM and three in thin section. The species *Hantkenina gohrbandti* was formally described for the '*H.* nov. spec.' of Rögl and Egger (2010). This species was distinguished from *H. singanoae* because 'the straight and pointed chamber ends differ clearly from the cylindrical, hood-like chamber ends in *H. singanoae*' (Rögl and Egger 2011, p. 5). Rögl and Egger (2010) also suggested that fully formed tubulospines first appeared in the juvenile stages of some specimens of *Hantkenina gohrbandti*.

Coccioni and Bancalà (2012) have also investigated the evolutionary origin of *Hantkenina*, using samples from the Contessa Highway section near Gubbio, Italy, which is especially useful because the section contains rhythmic sedimentary variations related to Earth's orbital cycles and hence provides an astronomical calibration for the critical interval. They recognize the following relevant species: *Clavigerinella eocanica*, *C. caucasica*, *Hantkenina gohrbandti* (morphotypes 1–3), *H. singanoae*, *H.* cf. *mexicana* 'forma *nuttalli* Toumarkine' and *H. mexicana*. They illustrated 32 specimens distributed among these species and morphotypes, which they regarded as representing a single gradual evolutionary transition with one side branch to *H. singanoae*. Like Rögl and Egger (2010, 2011), they described *H. gohrbandti* as 'the real ancestor of *Hantkenina*' (Coccioni and Bancalà 2012, p. 71), considering it unlikely that straight tubulospines could have evolved from bent chamber ends. Also like Rögl and

Egger (2010, 2011), the genus *Hantkenina* is polyphyletic in their scheme, with both *H. gohrbandti* and *H. singanoae* descended separately from *C. caucasica*. They also noted that specimens with long tapering proto-tubulospines like those illustrated by Coxall and Pearson (2006) from Tanzania were not found in Italy or Austria and so might be interpreted as a local ecological adaptation in Tanzania.

The various suggestions of Rögl and Egger (2010, 2011) and Coccioni and Bancalà (2012) are revisited below in the light of our new and much more extensive evidence from Tanzania. The systematic taxonomy of all relevant specimens that have been illustrated is then reviewed in the final section.

PALAEOCLIMATE, HABITAT AND ISOTOPE PALAEOECOLOGY

The peak of Cenozoic warmth was in the Early Eocene, whereupon a gradual global cooling trend set in that (notwithstanding some plateaus and reversals) persisted until the Early Oligocene when a large ice cap first appeared on Antarctica (Zachos *et al.* 2008). The cooling was predominantly in the high latitudes but also affected deep-ocean water masses sourced at those latitudes (Pearson *et al.* 2007; Bijl *et al.* 2009). The cooling of oceanic deep waters would have caused gradual changes in the structure of the oceanic water column worldwide. One aspect of this cooling that may have been important for pelagic niche partitioning relates to the rates of remineralization of sinking organic matter. In the very warm Early Eocene, organic carbon would have been much more efficiently remineralized in the upper water column because of more active bacterial metabolism (Olivarez Lyle and Lyle 2007; John *et al.* in press). This would have produced a shallower, more focused oxygen minimum zone with a more vertically condensed pelagic ecosystem above it (John *et al.* in press). We suggest that as subthermocline waters cooled in the Middle Eocene, bacterial metabolic rates would have slowed at depth allowing sinking organic particles to descend further, on average, than they did before, and in consequence, the oxygen minimum zone would have become less intense and more spread out. This process could have opened up new niches for deep-dwelling zooplankton that were able to tolerate relatively low levels of oxygen. We speculate that the evolution of *Clavigerinella* and *Hantkenina* was related to this global cooling process. Pulses of deep-water anoxia may also have spurred this evolution (Coccioni and Bancalà 2012).

A number of studies have published stable isotope ratios of hantkeninid and clavigerinellid tests in relation to other species to investigate the depth habitats of the

group (Boersma *et al.* 1987; Pearson *et al.* 1993, 2001; van Eijden 1995; Coxall *et al.* 2000; Wade and Pearson 2008). Coxall *et al.* (2000) showed that the earliest hantkeninids (*Hantkenina mexicana*) lived in a deep planktonic environment, although subsequent species migrated to shallower depths. The development of elongate chambers has occurred several times independently in the long history of planktonic foraminiferal evolution, seemingly always in deep, oxygen-poor environments; the basic reason for this may be a general tendency for foraminifera in those habitats to optimize food harvesting and to maximize their surface-area-to-volume ratio to more efficiently take up oxygen (Coxall *et al.* 2007; Coccioni and Bancalà 2012).

Modern digitate planktonic foraminifera also live in deep planktonic habitats (Bradshaw 1959; Hemleben *et al.* 1989). Hull *et al.* (2011) recently described the first detailed observations of living deep-dwelling planktonic foraminifera based on observations and collections made by a remotely operated vehicle (ROV) in Monterey Bay, California. They found *Hastigerinella digitata* and another related species living at depths of 150–500 m, with a clear peak in abundance at *c.* 320 m above the core of the local oxygen minimum zone. These species are carnivorous, preying on deep-dwelling copepods that also peak in abundance at this depth, as does mesopelagic biomass in general (Hull *et al.* 2011). Hull *et al.* (2011, p. 573) described *Hastigerinella* as 'planktivorous sit-and-wait predators' that prey mainly on copepods year round with a peak population density of about one individual per 5 m³ of water. Not all deep-dwelling planktonic foraminifera are this specialized, however; others feed on sinking phytodetritus or are omnivorous (Hemleben *et al.* 1989).

As part of this study, we subjected the tests of transitional hantkeninids (*H. singanoae*) to stable isotope analysis for the first time alongside a suite of co-occurring planktonic species and a single sample of benthic foraminifera (Fig. 3; all data are presented in Table 1). The various species were divided into depth habitats following the classification of Pearson *et al.* (2001), and their carbon isotope ratios were interpreted following the model of Pearson and Wade (2009). Oxygen isotope palaeotemperatures were determined using the equation of Kim and O'Neil (1997) assuming a palaeolatitude correction of +0.83‰ (Zachos *et al.* 1994) and a global ice volume correction of −0.8‰ (Cramer *et al.* 2011) (see Pearson 2012, for discussion of these assumptions; the Kim and O'Neil 1997, equation is preferred because it is calibrated to warmer temperatures than common foraminifer-specific equations). The results (Fig. 3) indicate a sea surface temperature of *c.* 33°C and a bathyal sea floor temperature of *c.* 20°C at the Tanzania outer shelf/slope site. The array of species produces very similar results to other samples from TDP Site 2 and nearby outcrops (Pearson *et al.* 2001, 2007). Significantly, *Hantkenina singanoae* does not cluster with any other species. Its oxygen isotope palaeotemperature (*c.* 24°C) and relatively depleted $\delta^{13}C$ indicate a deep subthermocline habitat, identical to the descendant species *H. mexicana* (Pearson *et al.* 2001). When fitted to a reconstructed water column temperature profile extracted from an Eocene general circulation model using the method of John *et al.* (in press) (Fig. 3B; National Center for Atmospheric Research model with 4000 ppm atmospheric pCO_2 forcing; Huber and Caballero 2011, data extracted by Matthew Huber, pers. comm. 2012), this indicates a mean depth of calcification at *c.* 250 m. These data suggest that the evolution of *Clavigerinella* and *Hantkenina* was driven primarily in response to challenging environmental conditions as they invaded a new mesopelagic habitat rather than by direct competition with other species of planktonic foraminifera.

Longitudinal striations on tubulospines and adjacent chamber surfaces in *H. mexicana* and other hantkeninids indicate, by analogy with modern species, that they were
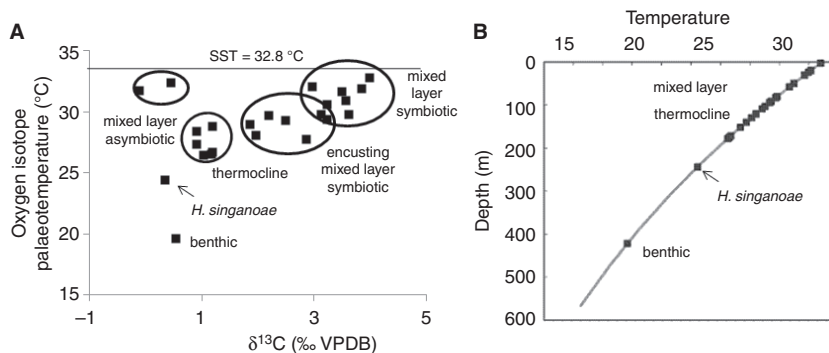

FIG. 3. Multispecies foraminifer stable isotope array from Tanzania Drilling Project Site 20 demonstrating the deep mesopelagic habitat of transitional *Hantkenina* (*H. singanoae*). For full list of species and size fractions, see Table 1. A, cross-plot of oxygen isotope palaeotemperature versus $\delta^{13}C$. Species are assigned to depth habitats according to the classification of Pearson *et al.* (2001). B, Reconstructed depth habitats based on an extracted general circulation model temperature/depth profile from Huber and Caballero (2011) for the Tanzania grid square. See text for discussion.

TABLE 1. Stable isotope data from sample Tanzania Drilling Project 20/24/3, 93–99 cm with palaeotempertature.

Species	Size fraction (μm)	$\delta^{13}C$	$\delta^{18}O$	PDB conversion	Ice volume correction (Cramer *et al.* 2011)	Latitude correction (Zachos *et al.* 1994)	Temperature (equation of Kim and O'Neil 1997) (°C)
Igorina broedermanni	250–300	3.99	−3.62	−0.27	−0.8	0.83	32.81
Planoglobanomalina pseudoageriana	150–212	0.45	−3.55	−0.27	−0.8	0.83	32.44
Acarinina pseudosubsphaerica	212–250	2.97	−3.49	−0.27	−0.8	0.83	32.13
Igorina broedermanni	212–250	3.84	−3.46	−0.27	−0.8	0.83	31.97
Pseudohastigerina micra	150–212	−0.11	−3.42	−0.27	−0.8	0.83	31.77
Morozovelloides bandyi	212–250	3.5	−3.41	−0.27	−0.8	0.83	31.71
Morozovelloides bandyi	250–300	3.56	−3.27	−0.27	−0.8	0.83	30.99
Acarinina praetopilensis	212–250	3.24	−3.21	−0.27	−0.8	0.83	30.67
Acarinina praetopilensis	300–355	3.62	−3.05	−0.27	−0.8	0.83	29.85
Morozovella aragonensis	300–355	3.13	−3.05	−0.27	−0.8	0.83	29.85
Guembelitrioides nuttalli	250–300	2.19	−3.03	−0.27	−0.8	0.83	29.75
Acarinina praetopilensis	250–300	3.23	−2.97	−0.27	−0.8	0.83	29.44
Acarinina bullbrooki	250–300	2.5	−2.95	−0.27	−0.8	0.83	29.34
Acarinina bullbooki	212–250	1.86	−2.89	−0.27	−0.8	0.83	29.03
Turborotalia frontosa	300–355	1.2	−2.85	−0.27	−0.8	0.83	28.82
Turborotalia frontosa	250–300	0.92	−2.77	−0.27	−0.8	0.83	28.42
Subbotinna senni	250–300	1.96	−2.71	−0.27	−0.8	0.83	28.11
Acarinina bullbrooki	300–355	2.87	−2.64	−0.27	−0.8	0.83	27.75
Turborotalia frontosa	212–250	0.92	−2.56	−0.27	−0.8	0.83	27.35
Subbotina crociapertura	300–355	1.19	−2.43	−0.27	−0.8	0.83	26.69
Subbotina crociapertura	250–300	1.17	−2.41	−0.27	−0.8	0.83	26.59
Subbotina crociapertura	250–300	1.03	−2.39	−0.27	−0.8	0.83	26.49
Hantkenina singanoae	300–355	0.35	−1.98	−0.27	−0.8	0.83	24.45
Cibicidoides spp.	300–355	0.55	−1.00	−0.27	−0.8	0.83	19.68

Palaeotemperature calculations are based on the equation of Kim and O'Neil (1997) and appropriate corrections for global ice volume and palaeolatitude.

remoulded in life by external cytoplasm flowing along their length (see Fig. 1K, L). From this, we propose that the tubulospines anchored large rhizopodial networks that would have streamed outward from the distal ends, probably with bidirectional flow to maintain a balanced distribution of cytoplasm (Hemleben *et al.* 1989, pp. 60–61). Analogous structures in which rhizopodia stream from terminal openings are seen in some living benthic foraminifera (e.g. Röttger and Krüger 1990). If *H. singanoae* was carnivorous like modern *Hastigerinella*, in which rhizopodia stream from the tips of true spines (Hull *et al.* 2011, p. 563), these networks would have been useful for catching and securing large prey such as copepods. Alternatively, if they were herbivorous, they could have been used for scavenging small food particles, such as sinking phytodetritus, from the surrounding water, which could then have been passed into the shell through the primary or even terminal aperture, if one was present. The diameter of the terminal aperture is always very small (*c.* 3–10 μm; see Fig. 1P); hence, any food passed into the test via that route must been very small also, suggesting

bacteria or minute algae. Although the ends of tubulospines are commonly found closed off by calcite, such closure may have occurred late in the life cycle associated with reproduction (gametogenesis) when, again by analogy with modern species (Hemleben *et al.* 1989, pp. 152–154), the test surface and fine-scale features were probably modified. Alternatively, in some species or specimens, closure of the canals may have been the normal state. Observation of specimens by X-ray shows that the internal canals of tubulospines extend to their very tips, even in the early species *H. mexicana* and *H. liebusi*, suggesting that they were probably open in life (Fig. 4).

Another possible function for the tubulospines has been suggested to us by Susan Goldstein (pers. comm. 2012) by analogy with species of benthic foraminifera (Dahlgren 1964; Sliter 1965), namely that they could have been used to increase the efficiency of gamete dispersal at reproduction. This possibility is not in conflict with the feeding hypothesis as both functions could have occurred at different stages in the life cycle as is the case in some canal-bearing benthic foraminifera (Röttger and Krüger 1990, p. 424).
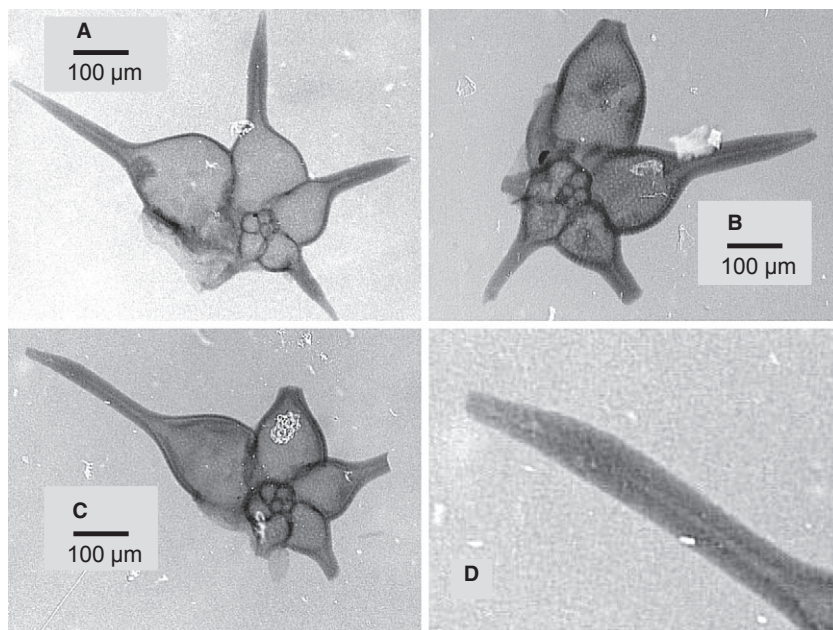
FIG. 4. X-ray exposures of three specimens of *Hantkenina* from a surface outcrop sample at Tanzania Drilling Project Site 2, made following the method of Huber (1994). Note that the internal canals extend to the very tips of the tubulospines suggesting that they opened via a terminal aperture in life. A, *H. liebusi*. B, *H. mexicana*. C, *H. mexicana*. D, Enlargement of the same specimen as C. All specimens from Sample PP98/K2, Kilwa Masoko prison, collected by P. N. Pearson, C. J. Nicholas and J. M. Singano.

Observations of many species by X-ray (Coxall 2000; see also Fig. 4) indicate that tubulospines only occur on the neanic and adult chambers and not in the earlier juvenile stage. Tubulospines were evidently key to the life strategy of all the various species of *Hantkenina* and *Cribrohantkenina* because they were never lost, which we speculate would have been 'easy' in an evolutionary sense, through heterochrony. The structures do, however, vary considerably between individuals and especially between species, in some of which they are long and slender, and in others short and stubby; they can be tapered or curved, and they may or may not possess a distal coronet structure (see Fig. 1; see also Coxall and Pearson 2006, for many more examples).

MORPHOGENETIC CONSTRAINTS

Chamber formation in a variety of modern spinose and nonspinose planktonic foraminifera has been studied in the laboratory (Bé *et al.* 1979; Hemleben *et al.* 1989). The sequence was summarized by Hemleben *et al.* (1989) as follows: (1) extrusion of a cytoplasmic bulge from the aperture; (2) organization of the bulge and extrusion of radiating rhizopodia to define the position of a perimeter called an outer protective envelope; (3) further extrusion of the cytoplasmic bulge to the line of the outer protective envelope and the construction of a primary organic membrane; and (4) calcification on both the inside and outside of the primary organic membrane. This mechanical extrusion of cytoplasm may explain why many foraminifera have relatively simple, globular, chamber shapes (Tyszka 2006). But from a consideration of these constructional aspects, it can be seen what a challenge it must have been for a foraminifer to produce tubulospines with hollow canals of almost machine-like precision and, in some species at least, minute terminal apertures. This presumably involved much more precise delineation of the outer protective envelope, and hence the resulting site of calcification (primary organic membrane), than is normal for most planktonic foraminifera. A simple cytoplasmic bulge would not easily suffice: a more complex scaffold of rhizopodia and, we speculate, rigid microtubules (e.g. Gull 2001) would seem to be necessary. Another problem for the foraminifera is that the distal chamber ends were laid down far away from the pre-existing test and aperture, which is inevitably an environment more prone to turbulence than the area immediately around the test.

With these theoretical constraints in mind, we turn to examine the full collection of transitional specimens from Tanzania.

THE COMPLETE COLLECTION FROM TANZANIA

Tanzania Drilling Project Site 2 (08°55.277′S, 039°30.219′E) was drilled near Kilwa Masoko in southern coastal Tanzania in 2002. The site was selected because excellently preserved assemblages of *H. mexicana* have previously been described from surface outcrops there (Blow and Banner 1962; Ramsay 1962 Pearson *et al.* 2001). A second hole, TDP Site 20 (08°55.269′S, 039°30.159′E), was drilled *c.* 300 m from it in 2005. The biostratigraphy of these cores was initially described by Pearson *et al.*

(2004) and Nicholas *et al.* (2006), respectively. Both holes penetrated from Middle Eocene (planktonic foraminifer Zone E9 and calcareous nannofossil Subzone NP15c) at the surface to Lower Eocene (planktonic foraminifer Zones E6/7 undifferentiated and calcareous nannofossil Subzones NP14b/NP15a undifferentiated) at total penetration depth. The primary lithology is relatively soft hemipelagic silty mudstone with occasional limestone turbidite interbeds. Bathyal benthic foraminiferal assemblages indicate a depositional depth of >350 m water depth (Nicholas *et al.* 2006), possibly as much as 1000 m (John *et al.* in press). Planktonic foraminifer shell preservation is generally excellent, although some levels are affected by infilling and overgrowth by calcite cements. As discussed above, we were confused by the apparently anomalous stratigraphic ranges of *Hantkenina*, *Globigerinatheka* and the nannofossil *Chiasmolithus gigas*, which led us to infer a possible hiatus in these cores (Pearson *et al.* 2004; Nicholas *et al.* 2006). We now know that the standard correlation schemes were almost certainly in error, and the successions are, as far as we can tell, continuous, although TDP Site 2 is substantially thicker in the critical interval.

The *Clavigerinella–Hantkenina* group is always rare in early Middle Eocene foraminifer assemblages, probably because their deep-dwelling habitat did not support large numbers of individuals. For this reason, we cannot avail ourselves of the very large collection sizes that have been made in some other evolutionary investigations of foraminifera (e.g. Malmgren and Kennett 1981; Malmgren *et al.* 1983; Hull and Norris 2009). Moreover, the shells are also very delicate and prone to breakage during standard extraction procedures. The total collection described here consists of *c.* 150 'transitional' specimens from 30 core samples, plus more numerous undisputed representatives of *Hantkenina mexicana* and *H. liebusi* from higher in the core. Some of these specimens are fragmentary chambers that may belong to the same individual. A representative selection of these specimens is illustrated to a common scale in Figures 5–8. The entire collection of transitional forms is illustrated in Figures S1–S10 (available in the online Supporting Information). The images are assigned to morphospecies in Appendix S1 (available in the online Supporting Information), which also indicates which are the type specimens and other comments.

Despite full morphological intergradation across the transition, we have assigned specimens to four qualitatively recognizable stages:

1. *Clavigerinella caucasica* with radially elongate and slightly tapering chambers.
2. *Hantkenina singanoae* Type 1 (first transitional stage), with tapering chambers that end with a distinct terminal nub or constriction on at least one chamber. When well developed, these constrictions commonly appear slightly folded and often lean in an anterior or posterior direction.
3. *Hantkenina singanoae* Type 2 (second transitional stage), with radially elongate chambers that gradually taper into a 'proto-tubulospine' on at least one chamber, which is a cylindrical protuberance that is porous along its length but may show a reduction in pore density towards the distal end.
4. *Hantkenina mexicana* with radially elongate chambers that rapidly taper into at least one smooth or finely striated and largely nonporous cylindrical tubulospine. Tubulospines commonly end in a terminal coronet structure and may open at the end via a terminal aperture.

Populations may contain individuals of more than one of these stages or 'morphospecies' without implying the existence of more than one biospecies at any time (Pearson 1998). We note also that during growth, as chambers are added, a single individual may traverse more than one of these stages. In Figure 9, we show histograms of the four morphological stages against stratigraphic position in the more densely sampled drill core, TDP Site 2. Although considerable variability exists between individuals, we do not see any obvious morphological subdivisions at any stratigraphic level, and consequently, we regard the whole population as a single evolving lineage.

EVOLUTIONARY MODEL

We note the strong similarity of the Tanzanian forms to specimens from Europe (Rögl and Egger 2010, 2011; Coccioni and Bancalà 2012) and regard the entire known global population as a single genetically connected lineage inhabiting deep-water niches worldwide. Studies of modern planktonic foraminifera have shown that cryptic genetic variation is common, some of which may indicate cryptic species with substantial (multi-million year) divergence times in the past (e.g. DeVargas *et al.* 1999; Darling and Wade 2008). However, if genetic isolates occurred during the evolutionary origin of *Hantkenina*, they must have been very minor and short-lived in comparison, because the transitional morphotypes of *C. caucasica* and *H. singanoae* do not persist in the fossil record.

Considering the depth habitat, functional constraints and the morphoseries illustrated in Figures 4–8 and Figures S1–S10, we propose an adaptive scenario for the origin of the tubulospines (Fig. 10). The ancestral species, which we recognize as *Clavigerinella caucasica*, possessed radially elongate chambers with a tendency to taper at their ends, rather than ending in rounded, bulbous extremities as occurs in other members of the genus (e.g. *C. eocanica*, *C. akersi*). Individuals of *C. caucasica* with more pointed chamber ends must have had a slight
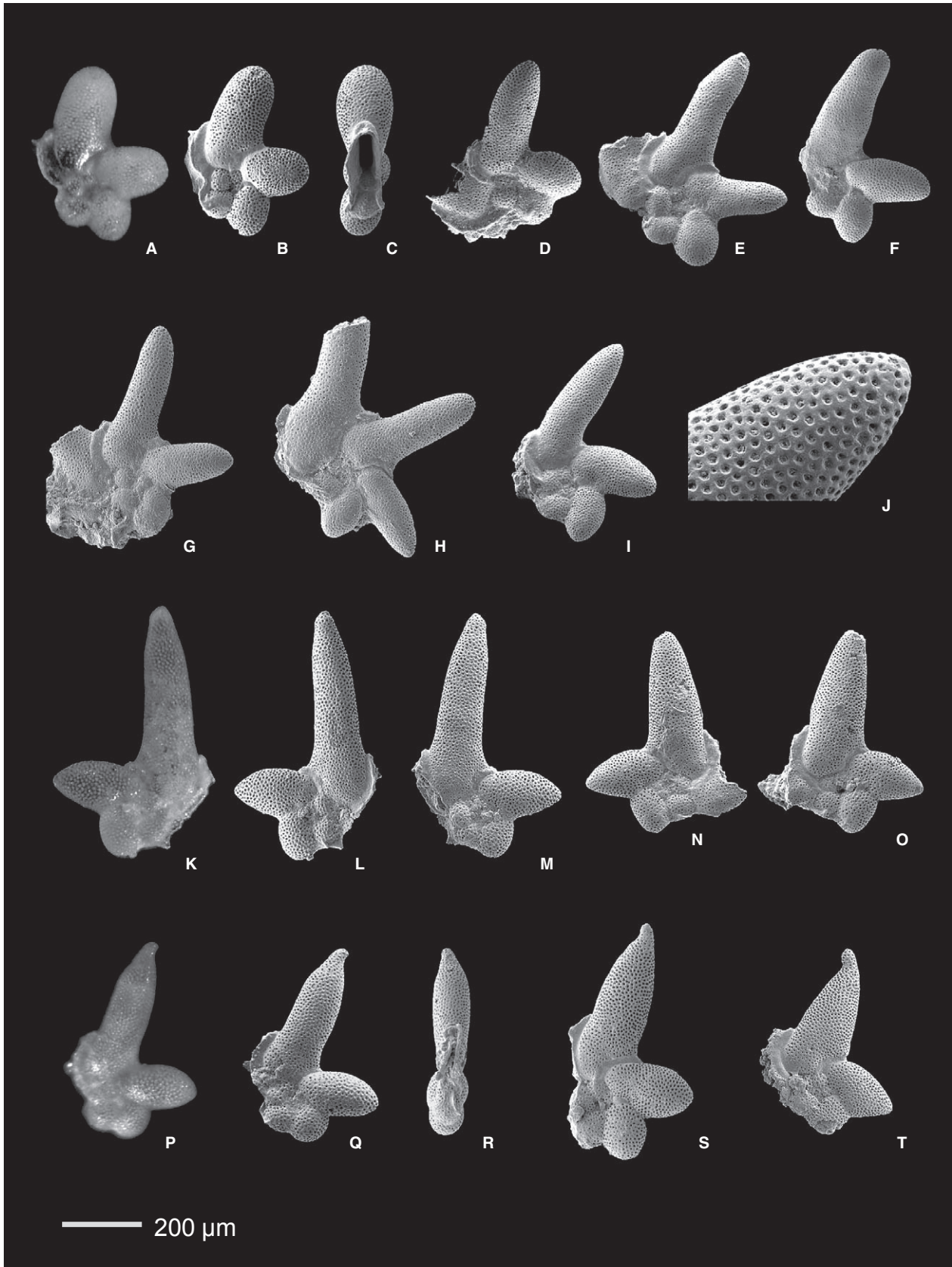
selective advantage with respect to their mode of life. This could have been because cytoplasm flowing over the outer surface of the shell would have flowed together and been more firmly anchored at the chamber tips, hence supporting a larger or more directed pseudopodial network than in other species. A large pseudopodial network may have been analogous to the trailing tentacles commonly found in modern mesopelagic and bathypelagic plankton. Food supply in deep planktonic habitats is usually intermittent and scarce; hence, individuals with flattened, stellate tests (having, consequently, high surface-area-to-volume ratios) and robust psuedopodial networks, further extending their reach, could have been able to harvest the surrounding water more efficiently at low metabolic cost and possibly exploit new food sources such as mesopelagic copepods (if carnivorous) or sinking aggregates of phytodetritus (if herbivorous). Food would have been passed over the chamber surface and through the primary aperture in the normal way. Once these selection pressures were initiated, the process may have led to further evolution in this direction among the population that would ultimately give rise to *Hantkenina*. We infer this from the apparently directional nature of the trend for tubulospine development, the fact that intermediate morphologies do not persist in the fossil record, and the observation that there are other species of *Clavigerinella* with rounded chamber ends that survived independently for many millions of years without undergoing this specialization.

In our scenario, the process of pseudopodial anchoring favoured elongation of the chambers and the development of a constriction or terminal nub at the chamber tips, leading to stage 2 described above. These terminal constrictions often lean in anterior, posterior or even sideways direction. We regard the bending of the chamber ends as adventitious, resulting from the position adopted by the primary organic membrane far from the site of cytoplasmic bulge extrusion. The exact shape of the membrane was difficult for the foraminifer to constrain and at the mercy of environmental turbulence before it was strengthened by calcification. The fact that no two specimens or even chambers are exactly alike during the evolutionary transition supports this idea. Extreme morphological plasticity is also seen in popula-

tions of the homeomorphic but unrelated Cretaceous digitate planktonic foraminiferal genera *Leupoldina* and *Shackoina* (Verga and Premoli Silva 2002). Both *Leupoldina,* which possesses bulbous, nub-like or proto-tubulospine-like tipped extensions of the chambers, and its probable descendant *Shackoina*, characterized by hantkeninid-like hollow tubulospines, show immense variability in the morphology, orientation and ontogeny of their chamber modifications suggesting similar challenges of test construction.

A continuation of these selection pressures, whether constant or intermittent, would have favoured more extreme degrees of chamber elongation. The chambers began to extend distally into long, hollow, tubular and porous extensions (stage 3 above). Their considerable variability of form suggests that the morphogenesis of these structures was still less precisely controlled than was later to be the case for the true tubulospines of subsequent hantkeninids. These 'proto-tubulospines' could have contained only a small volume of cytoplasm; hence, the pores for chemical exchange would have been redundant, and moreover, they structurally weakened the proto-tubulospine and so gradually disappeared with time. However, it was always mechanically necessary that the structures were hollow, in order for the organism to be able to lay down the organic template from the inside.

Foraminiferal shells often show irregular external pustules and protrusions that are secreted onto their outer surfaces from external cytoplasm. Exaggeration of surface roughening around the tubulospine ends would have helped fan the rhizopodial network away from the tips and possibly helped divide ingoing and outgoing flows. This, we suggest, is the most likely function of the coronet structure in *H. mexicana* (see Fig. 1K). At some point, the chamber ends became open via a small circular aperture. These apertures could have allowed the foraminifera to bring small food particles such as bacteria, some algae or possibly the digested remnants of large prey, directly into the test without taking the longer route via the primary aperture. This may have given bearers of this structure an immediate advantage.

The selection pressures that drove this evolution were evidently occurring during the adult phase of the life

FIG. 5. First of four figures showing selected specimens of *Clavigerinella* and *Hantkenina* from Tanzania arranged in stratigraphical order to illustrate the morphological transition. A–C, *Clavigerinella eocanica* (Tanzania Drilling Project (TDP) Site 20, 55.25 m) (same specimen illustrated in side view by light microscope and SEM and in edge view). D, *Clavigerinella caucasica* (TDP Site 2, 56.20 m). E–F, *Clavigerinella caucasica* (TDP Site 2, 55.75 m) (E, reproduced from Coxall and Pearson 2006, plate 8.2, fig. 7). G, *Clavigerinella caucasica* (TDP Site 2, 55.54 m). H–J, *Clavigerinella caucasica* (TDP Site 2, 55.10 m) (J, close-up view of final chamber; I, reproduced from Pearson *et al.* 2004, plate 2, fig. 16; J, reproduced from Coxall and Pearson 2006, plate 8.2, fig. 6). K–O. *Clavigerinella caucasica* (TDP Site 20, 54.25 m) (K–M, same specimen illustrated in side view by light microscope and SEM and other side; N–O, same specimen illustrated on both sides). P–R, *Hantkenina singanoae* Type 1(TDP Site 20, 54.25 m) (same specimen illustrated in side view by light microscope and SEM and in edge view; note distinct terminal nub to final chamber). S–T, *Hantkenina singanoae* Type 1 (TDP Site 2, 53.63 m).

200 μm
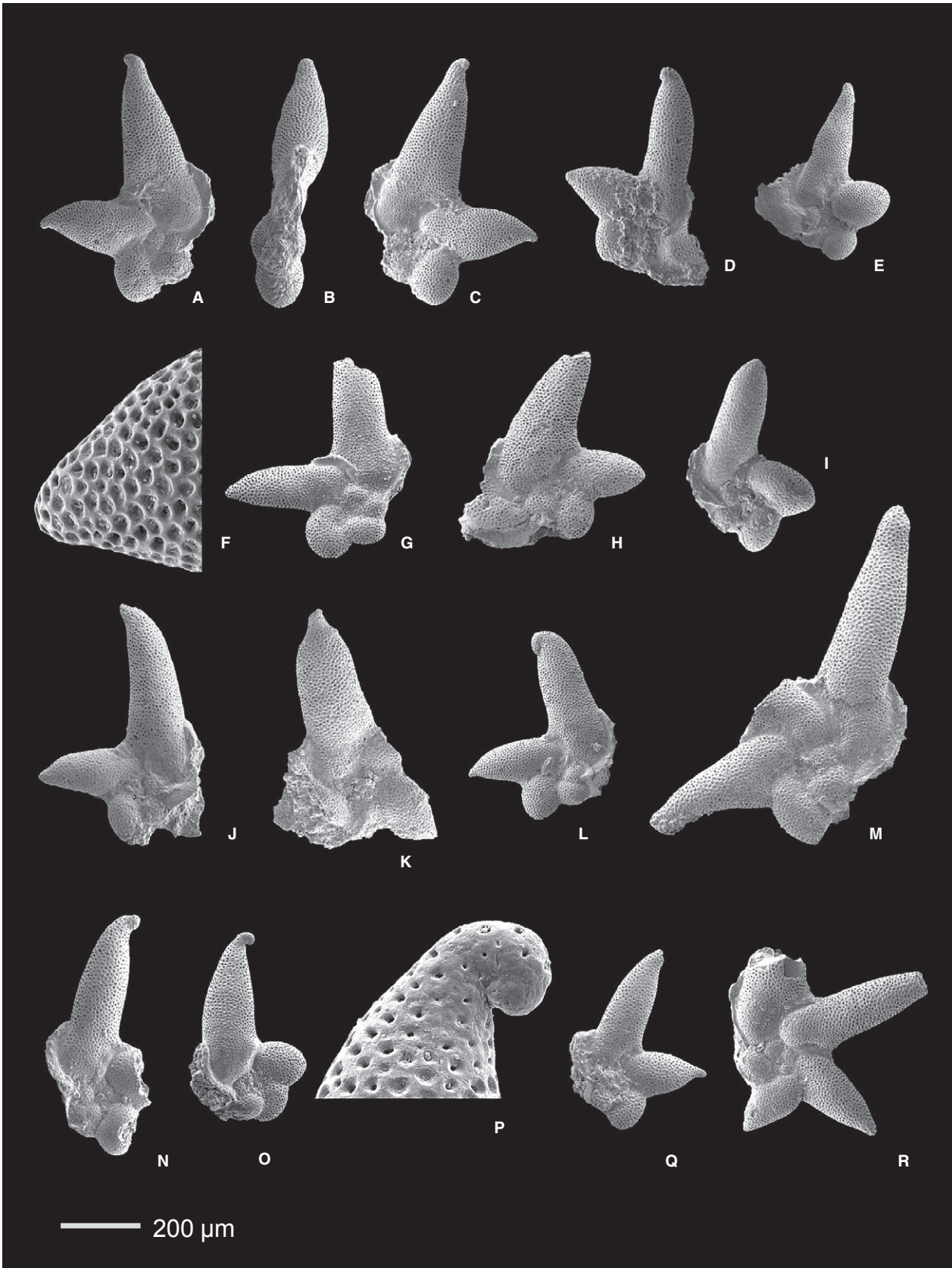
cycle because it is always on the last one to three chambers that the innovations are observed. Earlier chambers, by contrast, retain a simple morphology throughout the evolutionary transition (see, for example, Figs 5P, S, T, 6A, J, O, 7J, 8G, J, L). In later hantkeninids, however, tubulospines occur on up to six adult chambers (e.g. Fig. 1D), suggesting either that the instructions for their formation were passed forward in ontogeny, in a heterochronic process known as predisplacement, or that the lifespan was extended allowing extra chambers to be laid down (hypermorphosis; see McNamara (1986) for the terminology of heterochrony). Both processes probably occurred, and it would take further detailed studies of X-rays or dissections to determine the pattern in detail; however, hypermorphosis seems especially likely around the time of the first *H. mexicana* because specimens are typically larger than the transitional forms.

COMPARISONS WITH OTHER RECORDS

Professor F. Rögl has kindly showed us micropalaeontological residues from the Holzhäusl section and demonstrated the outcrops in the field. The section is monotonous marlstone about 16 m thick. Although currently poorly exposed along a wooded hillside, it was cleaned by trenching for the studies of Rögl and Egger (2010, 2011). The transitional hantkeninids are from several samples taken through about 1 m of stratigraphy near the top of the section (Rögl and Egger 2010, fig. 2). The illustrated specimens, which are from seven closely spaced samples, belong (according to our taxonomy) either to *Clavigerinella caucasica*, the Type 1 morphotype of *Hantkenina singanoae*, or to *H. mexicana*. The more 'advanced' Type 2 morphotype of *H. singanoae* has not been recorded from Austria.

The Italian Contessa Highway section is composed of marly limestones and calcareous marls bundled together into astronomical couplets. *Clavigerinella caucasica* occurs over approximately 2.5 m of section, but transitional hantkeninids occur only in about 0.5 m of stratigraphy.

Coccioni and Bancalà (2012, pp. 78–89) have split their transitional hantkeninids into four morphotypes, which they describe as follows:

1. *Hantkenina gohrbandti* morphotype 1, with 'pointed chamber ends with a nub that appears as a rounded, hollow and perforate structure in the younger chambers' (Coccioni and Bancalà 2012, p. 79).
2. *Hantkenina gohrbandti* morphotype 2, with a 'short, real tubulospine in the primary chambers of the final whorl. After developing a tubulospine in the inner whorl, the following chambers are pointed or with an acute nub' (Coccioni and Bancalà 2012, p. 79).
3. *Hantkenina gohrbandti* morphotype 3, with 'blunt tubulospines in different chambers of the final whorl. Other chambers of the final whorl are with pointed ends or thickened conical knobs' (Coccioni and Bancalà 2012, p. 79).
4. *Hantkenina singanoae,* with 'later chambers ending in a terminal, hood-like nub or cylindrical projection (proto-tubulospine). Proto-tubulospines are smooth and distinctly porous' (Coccioni and Bancalà 2012, p. 79).

Coccioni and Bancalà (2012) noted the absence of specimens with elongated final chambers similar to those illustrated by us from Tanzania (that is, corresponding to the Type 2 *H. singanoae* of this study). They envisaged the evolution of the 'real tubulospine' (by which they mean, like us, a nonporous cylindrical projection) to have occurred first on a single early chamber, then on several chambers in the final whorl and finally (in true *Hantkenina mexicana*) on all adult chambers. This hypothesis is similar to that of Rögl and Egger (2010, 2011). However, almost all the illustrated specimens of both these sets of authors have the delicate chamber tips broken off making it difficult or impossible to determine which morphologic variant many of the specimens belong to. We suggest that the few specimens that have been illustrated with true tubulospines in the early chambers and broken final chambers (Rögl and Egger 2011, pl. 2, fig. 4; Coccioni and Bancalà 2012, pl. 2, fig. 1) are most likely attributable to *Hantkenina mexicana* rather than to any transitional form. We have seen no such morphology in the more

FIG. 6. Second of four figures showing selected specimens of *Clavigerinella* and *Hantkenina* from Tanzania arranged in stratigraphical order to illustrate the morphological transition. A–E, *Hantkenina singanoae* Type 1 (Tanzania Drilling Project (TDP) Site 2, 52.63 m) A–C, holotype, Natural History Museum, London, 67215; same specimen shown on both sides and in edge view; note terminal nub on final two chambers; A, reproduced from Pearson *et al.* 2004, plate 2, fig. 18; B–C, reproduced from Coxall and Pearson 2006, plate 8.13, figs. 2–3. F–G, *Hantkenina singanoae* Type 1 (TDP Site 2, 50.00 m). (Marginal specimen; F, close-up view of penultimate chamber showing slight constriction or terminal nub that places this specimen in *Hantkenina*). H–I, *Clavigerinella caucasica* (TDP Site 20, 53.30 m). J–N, *Hantkenina singanoae* Type 1 (TDP Site 20, 53.30 m). O–P, *Hantkenina singanoae* Type 1 (TDP Site 2, 47.65 m) (Figured paratype, Natural History Museum, London, 67217; P, close-up view of final chamber showing bent terminal nub; O, reproduced from Coxall and Pearson 2006, plate 8.13, fig. 9). Q, *Hantkenina singanoae* Type 2 (TDP Site 2, 46.50 m) (Marginal specimen; note extended nub/rudimentary proto-tubulospine on penultimate chamber; reproduced from Coxall and Pearson 2006, plate 8.13, fig. 15). R. *Hantkenina singanoae* Type 1 (TDP Site 2, 46.50 m) (Marginal specimen; note slight terminal nubs on two early chambers).

200 μm
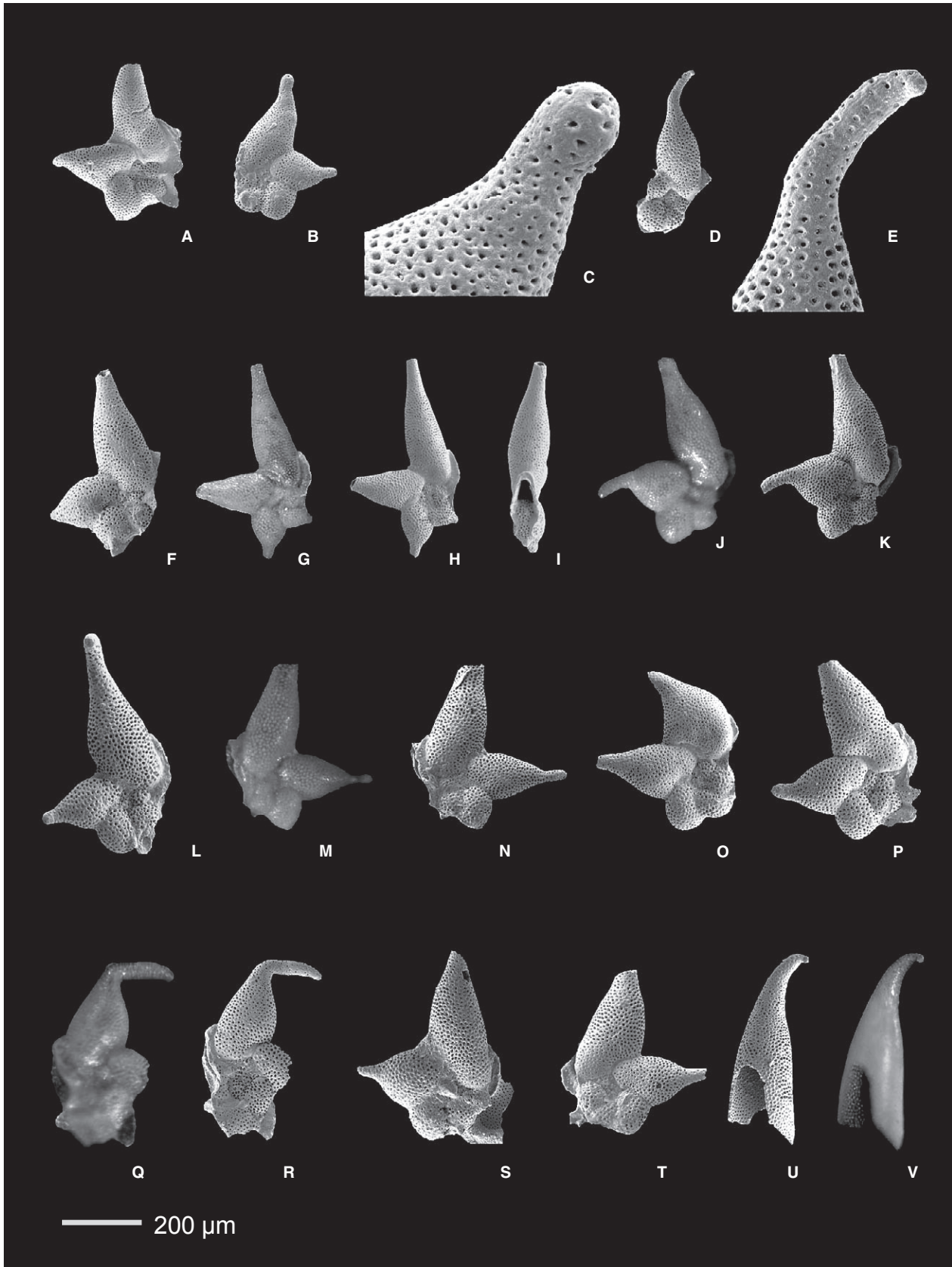
complete and better-preserved (Bown *et al.* 2008) Tanzanian record.

The new Tanzanian material indicates that the evolution of tubulospines was directly preceded by a proto-tubulospine stage affecting the final 1–3 chambers (*Hantkenina singanoae* Type 2). The fact that no specimens like these have been illustrated from either European section suggests to us that either those records are incomplete or the delicate morphology of such forms has not been preserved via the processing of the relatively hard lithologies (especially Contessa Highway). Another possibility is that the evolutionary transition is more fully represented at tropical sites in the centre of the geographical range of these forms. We note also that the evolutionary transition phase is much more expanded in the Tanzanian section (about 15 m of stratigraphy in TDP Site 2 compared with about 1 m in Austria and 0.5 m in Italy).

The new evidence also leads us to reject the view of Rögl and Egger (2010, 2011) and Coccioni and Bancalà (2012) that the bent chamber terminations could not have evolved into straight tubulospines, and hence, *Hantkenina singanoae* should be regarded as an evolutionary offshoot from the main lineage. Our collection does not show two distinct populations with straight and bent chamber ends, respectively. As discussed above, the bending of the chambers is not likely to have been a heritable genetic feature; the pattern of bending is seldom similar on adjacent chambers of the same specimen, so it is much more likely adventitious, caused by the relatively loose morphogenetic constraints in these evolving forms. Only after some time were the hantkeninids able to reliably calcify straight and well-formed tubulospines on a relatively fixed template. For this reason, we regard *Hantkenina gohrbandti* to be a subjective junior synonym of *Hantkenina singanoae* (see Systematic Palaeontology).

BIOSTRATIGRAPHY

The '*Hantkenina* datum' has traditionally been used by foraminiferologists to recognize the base of the Lutetian Stage and hence the base of the Middle Eocene. Since the work of Payros *et al.* (2007), that view is now rightly discarded, and the base of the Lutetian Stage has been formally proposed at a much lower stratigraphic level in the Gorrondatxe section (Molina *et al.* 2011). Following Payros *et al.* (2007), Wade *et al.* (2011) suggested a revised numerical age of 44.5 Ma on the timescale of Cande and Kent (1995) for the first appearance of *Hantkenina*. Here we note that in Tanzania (Pearson *et al.* 2004), Agost in Spain (Larrasoaña *et al.* 2008; Ortiz *et al.* 2008) and Italy (Coccioni and Bancalà 2012), the first *H. mexicana* occurs slightly less than half way through the total range of the nannofossil *Chiasmolithus gigas*. If these biostratigraphic correlations are robust and the ages of 44.5 and 46.1 Ma for the top and base of the range of *C. gigas* (Berggren *et al.* 1995) are correct, this would indicate a revised age of about 45.4 Ma on the timescale of Cande and Kent (1995). The Gorrondatxe section in Spain (Payros *et al.* 2007) does not contain the full *C. gigas* zone, but extrapolation of sedimentation rates based on the top of *Discoaster sublodoensis*, base of *Guembelitrioides nuttalli*, base of Chron C20r and base of *C. gigas* in the section places the first *H. mexicana* in a similar position. This age is substantially older than suggested by Payros *et al.* (2007) and Wade *et al.* (2011), but still much younger than the previously accepted age of 49.0 Ma (Berggren *et al.* 1995; Berggren and Pearson 2005).

The best estimate for the duration of the evolutionary transition from *Clavigerinella caucasica* to *Hantkenina mexicana* is from the astronomically calibrated section at Contessa Highway at a little less than *c.* 300 kyr (Coccioni and Bancalà 2012). If the hantkeninids had monthly lifespans as is the case with some modern deep-dwelling planktonic foraminifera (Hemleben *et al.* 1989), this would indicate the passage of approximately 3–4 million generations as tubulospines were evolved.

DISCUSSION

Following their evolutionary origin, the hantkeninids were a successful component of pelagic ecosystems for over 15 million years until their eventual extinction at 33.7 Ma during the climatic changes that occurred at the end of the Eocene (Wade and Pearson 2008). Eleven distinct morphospecies (including one of *Cribrohantkenina*) have been described (Coxall and Pearson 2006), with a wide range of chamber morphologies, all of which were descended from the short-lived transitional forms

FIG. 7. Third of four figures showing selected specimens of *Clavigerinella* and *Hantkenina* from Tanzania arranged in stratigraphical order to illustrate the morphological transition. A, *Hantkenina singanoae* Type 2 (Tanzania Drilling Project (TDP) Site 20, 52.20 m). B–C, *Hantkenina singanoae* Type 2 (TDP Site 2, 45.00 m) (C, close-up view of final chamber showing short porous proto-tubulospine). D–E, *Hantkenina singanoae* Type 2 (TDP Site 2, 44.62 m) (figured paratype, Natural History Museum, London, 67217; E, close-up view of chamber showing bent proto-tubulospine; D, reproduced from Coxall and Pearson 2006, plate 8.13, fig. 10). F–V, *Hantkenina singanoae* Type 2 (TDP Site 20, 51.30 m) (G–I, same specimen in light microscope and SEM, in side and edge views; J–K, same specimen in light microscope and SEM; M–N, same specimen in light microscope and SEM; Q–R, same specimen in light microscope and SEM, note bent proto-tubulospine; U–V, same specimen in light microscope and SEM).
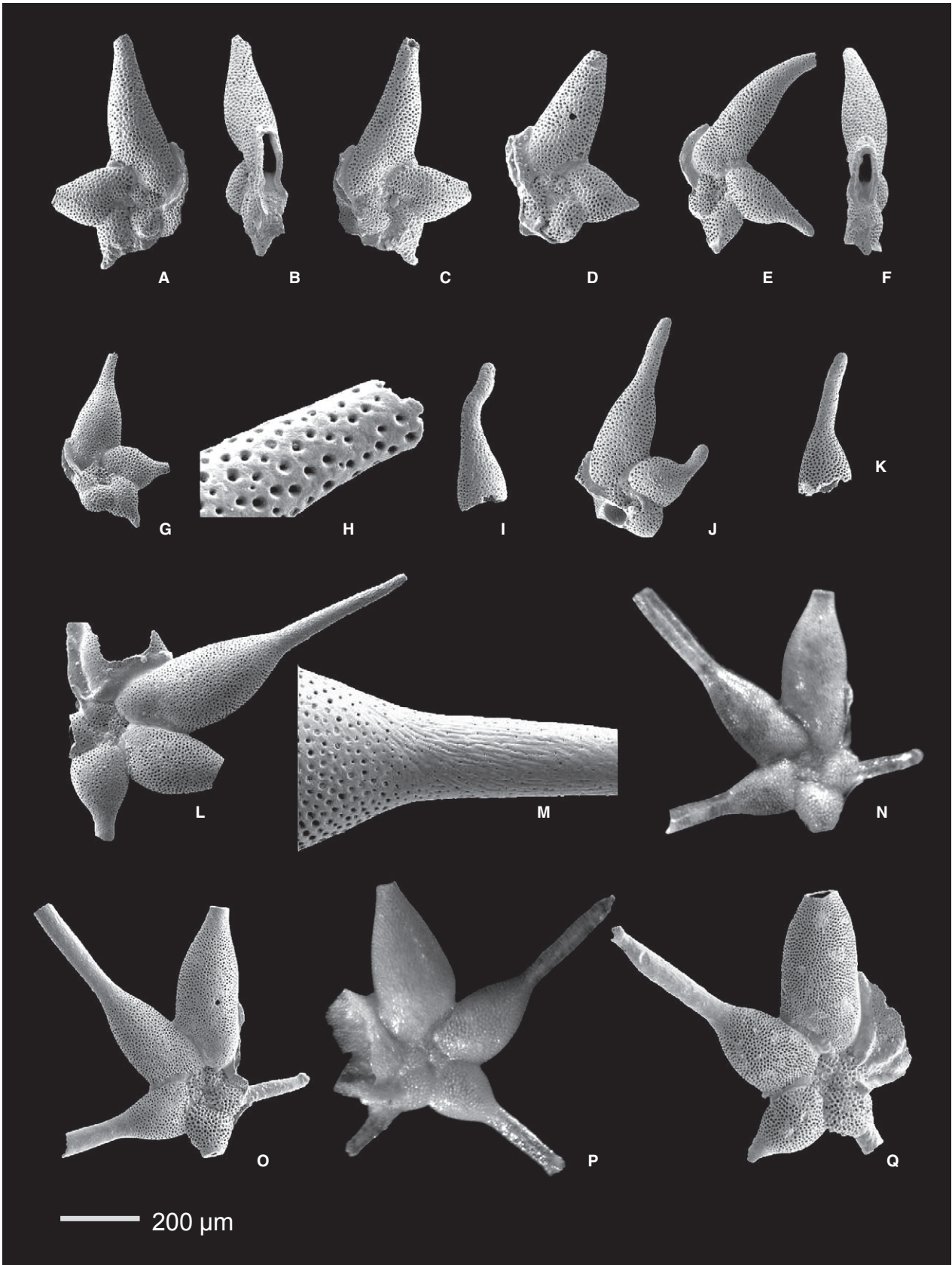
described in this article (see also Aze *et al.* 2011, for a breakdown of these morphospecies into proposed evolutionary lineages). Isotopic evidence suggests that by the late Middle Eocene, most descendant species lived in surface water habitats (Coxall *et al.* 2000) in contrast to the deep planktonic environment in which the genus evolved. However, the tubulospines evidently served useful purpose(s) throughout the history of the clade because they were retained by all subsequent species of *Hantkenina*.

It has sometimes been remarked that stratigraphic information is, in principle, of no use in inferring phylogenetic relationships and that tracing lines of ancestry and descent in the fossil record can never be justified (e.g. Gee 2000, p. 147). Our study demonstrates the opposite and that in favourable circumstances, the proactive sampling of a critical stratigraphic interval can produce new evidence and help resolve a disputed question of phylogeny. The evolutionary origin and phylogenetic position of *Hantkenina* have now been demonstrated unequivocally by targeted investigation of a precise stratigraphic interval by several research groups. The stratigraphic ordering provided by these studies gives us constraints on the pathway taken by evolution, its timescale and geographical range. The presence of 'transitional' *Hantkenina* in both Europe and East Africa suggests that the evolution did not occur in a peripheral isolate but rather across a broad area, as is perhaps to be expected in populations of oceanic plankton (Lazarus 2011). The current lack of evidence of transitional hantkeninids from the Pacific Ocean cannot be regarded as good evidence of absence because the relatively few sites that might yield such forms have not so far been sampled in sufficient detail (although we note in passing that our own detailed sampling of equatorial Pacific ODP Site 865 failed to yield transitional forms, possibly because of a small hiatus at the expected level).

The evolution of tubulospines by the hantkeninids must have involved a variety of developmental genetic innovations. Chief among these was the ability to lay down a precise organic template on which long, hollow, chamber extensions could be calcified with precision. It is likely that this mechanism involved a rigid scaffolding of microtubules. We cannot envisage that the genetic innovations necessary for tubulospine formation arose solely by drift or chance without the agency of selection. Experiments with diverse model organisms have shown the remarkable efficacy of artificial selection in producing rapid responses in populations in factors such as body size in mice, or bristle number in *Drosophila*, but the effectiveness of selection in producing such changes generally diminishes with time. Typically a barrier to directional evolution is reached as the variation produced by genetic recombination becomes exhausted (Bell 1997). Novel gene sequences are then required, presumably through mutation, and this process requires much longer periods of time. The fossil record can help determine how long real novelty, as opposed to allometric variations, takes to evolve in natural conditions. In the case discussed here, we note the largely unoccupied (at least by other planktonic foraminifera) but challenging deep planktonic niche in which *Hantkenina* evolved and the very long timescale of *c.* 3–4 million generations. This indicates that natural selection can produce distinct trends over vast periods of time when the innovations required are not straightforward.

We are aware that adaptive explanations for biological structures are notoriously difficult to prove because the myriad selective events that produced them are lost to history and a certain odium sometimes associates with 'adaptationist' thinking (following Gould and Lewontin 1979, although not necessarily in the spirit of that paper). Nevertheless, constraints on the likely evolutionary pathway and selective agencies are found when intermediate phases in the evolutionary process are discovered, as is the case in this study. We emphasize that our explanation for the evolution of tubulospines involves the interplay between natural selection in a challenging environment and morphogenetic constraints relating to chamber construction in foraminifera (the 'spandrels' of Gould and Lewontin). Our account of the origin of tubulospines is essentially similar to that predicted by Blow (1979), who was not aware of these intermediate forms and whose suggestion can therefore be regarded as having been supported and extended. We also note that the evolutionary

FIG. 8. Fourth of four figures showing selected specimens of *Clavigerinella* and *Hantkenina* from Tanzania arranged in stratigraphical order to illustrate the morphological transition. A–D, *Hantkenina singanoae* Type 2 (Tanzania Drilling Project (TDP) Site 20, 51.30 m) (A–C, same specimen viewed both sides and in edge view). E–F, *Hantkenina singanoae* Type 2 (TDP Site 2, 42.50 m) (Figured paratype, Natural History Museum, London, 67216; same specimen viewed in side and edge views; reproduced from Pearson *et al.* 2004, pl. 2, figs 20–21). G–K, *Hantkenina singanoae* Type 2 (TDP Site 2, 41.41 m) (H, close-up view of porous proto-tubulospine; G, figured paratype, Natural History Museum, London, 67219; reproduced from Pearson *et al.* 2004, pl. 2, fig. 19). L–O, *Hantkenina mexicana* (TDP Site 20, 49.57 m) (M, close-up view of tubulospine showing mostly smooth surface and spiral rifling but with minute pores; N–O, same specimen in light microscope and SEM, note internal canals). P–Q, *Hantkenina mexicana* (TDP Site 20, 48.68 m) (P, light microscope, note internal canals).
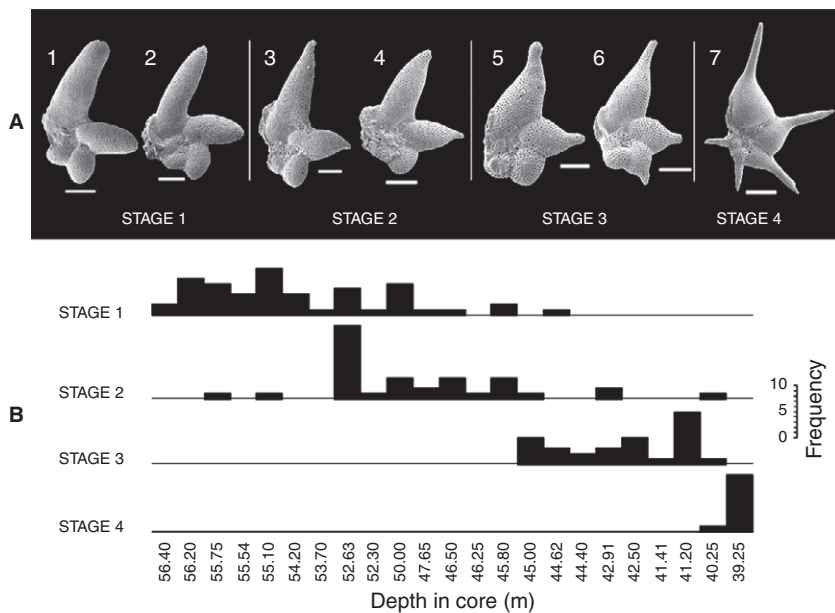
FIG. 9. Summary of the stratigraphic record in the more complete site, Tanzania Drilling Project Site 2. A, Selected specimens (1–7) to illustrate the four transitional stages. B, Frequency histograms of the four morphotypes against depth. Numbers represent the total number of specimens recovered from 10-cm half-round samples of core. The stratigraphic pattern is interpreted as gradual evolution along a single lineage which is artificially split into arbitrary but stratigraphically useful morphotaxa. Scale bars (A) represent 100 μm.
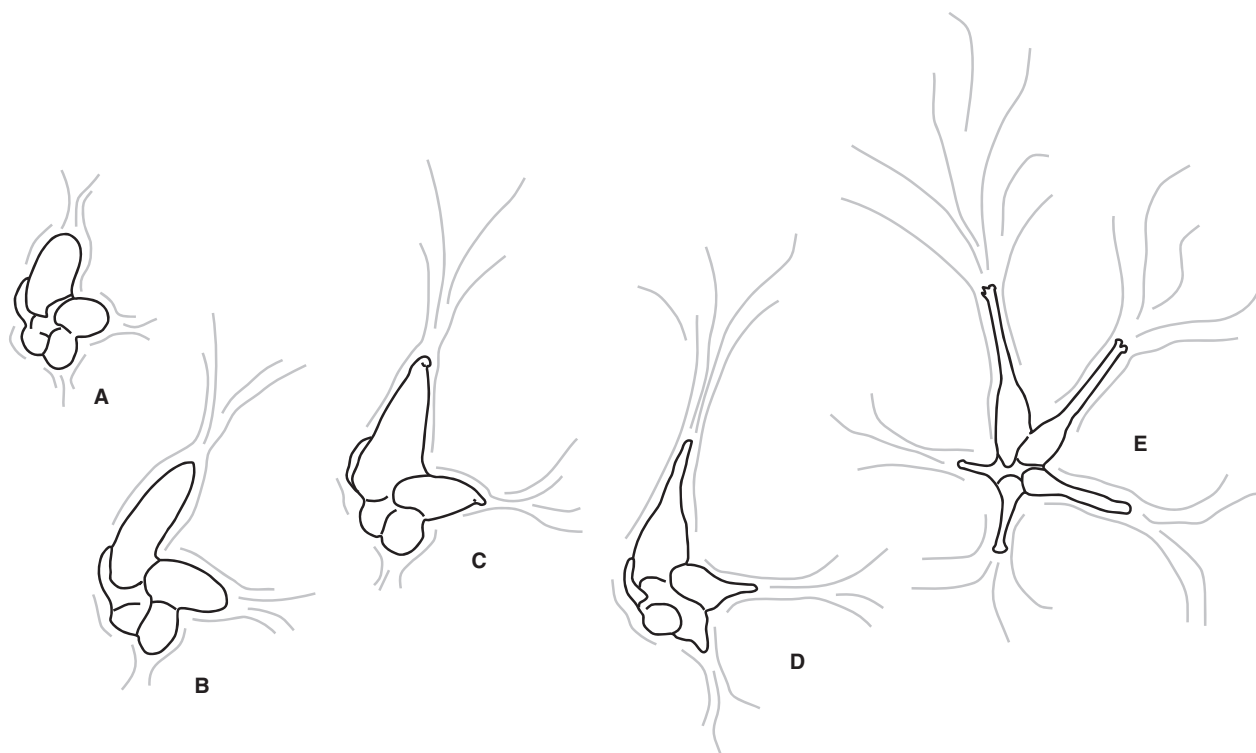

FIG. 10. Cartoon illustrating our concept of the evolution of tubulospines and the pseudopodial network as an adaptation for harvesting food in a deep mesoplanktonic habitat, spanning five morphotaxa in the gradual evolution from *Clavigerinella eocanica* to *Hantkenina mexicana*. A, *Clavigerinella eocanica*. B, *Clavigerinella caucasica*. C, *Hantkenina singanoae* Type 1. D, *Hantkenina singanoae* Type 2. E, *Hantkenina mexicana*.

model presented here could be falsified in various ways, most obviously by the unlikely discovery of an Early Eocene foraminifer with tubulospines homologous to those of *Hantkenina*.

SYSTEMATIC PALAEONTOLOGY

Remarks. Fuller synonymy lists for some of these taxa were provided by Coxall and Pearson (2006). Here we

focus on key synonymies and the recent literature pertaining to the *Clavigerinella–Hantkenina* transition.

Order FORAMINIFERIDA D'Orbigny, 1830
Superfamily GLOBIGERINOIDEA Carpenter, Parker and
Jones, 1862
Family HANTKENINIDAE Cushman, 1927

Genus CLAVIGERINELLA Bolli, Loeblich and Tappan, 1957

1980   *Eoclavatorella* Cremades Campos, p. 210; type species *Eoclavatorella benidormensis* Cremades Campos, 1980

Type species. Clavigerinella akersi Bolli, Loeblich and Tappan, 1957; from the Middle Eocene Navet Formation of Trinidad

Description. Wall weakly cancellate or smooth, normal perforate, possibly sparsely spinose. Test planispiral or pseudo-planispiral coiling, 4–5 chambers in the final whorl, increasing rapidly in size as added; final 2–3 chambers elongate, becoming clavate (club-shaped) or digitate (finger-like); distal chamber ends may be inflated, compressed or paddle-shaped with rounded, bulbous or pointed terminations; aperture is an elongated equatorial arch bordered by a distinctive flaring lip (modified from Coxall and Pearson 2006, p. 216).

Diagnostic features. Clavigerinella is distinguished from *Parasubbotina* by its pseudo-planispiral coiling and more elongate chambers and from *Hantkenina* by lacking tubulospines or homologous structures.

Discussion. The long-standing confusion in the literature regarding the possible synonymy of *Clavigerinella* Bolli *et al.* with *Hastigerinella* Rhumbler was resolved in a case brought before the International Commission on Zoological Nomenclature by Coxall (2003) with a decision passed as 'Opinion 2105' (ICZN 2005). The synonymy of *Eoclavatorella* Cremades Campos with *Clavigerinella* Bolli *et al.* follows from the synonymy of *Eoclavatorella benidormensis* Cremades Campos with *Clavigerinella eocanica* Nuttall as indicated by Coxall and Pearson (2006, p. 222) and also below. BouDagher-Fadel (2012, p. 151) recently resurrected *Eoclavatorella* as a distinct genus without discussion, but we stand by our earlier synonymy.

Clavigerinella caucasica (Subbotina, 1958)
Figures 5D–O

See also Figures S1.2–S1.3, S1.5–S1.11, S1.15–S1.22, S2.23–S2.24, S2.26–S2.35, S2.37–S2.38, S3.41–S3.42, S3.48, S3.55, S3.59–3.60, S4.69, S4.72–S4.74, S4.78–S4.79, S5.82–S5.86, S5.88–S5.89, S6.99.

1958   *Hastigerinella caucasica* Subbotina, p. 58, pl. 2, fig. 8a–b.
2003   *Clavigerinella–Hantkenina* transition, Coxall *et al.* (*pars*), p. 251, pl. 6, figs 5–8.
2006   *Clavigerinella caucasica* (Subbotina) 1958; Coxall and Pearson, pp. 218–221, pl. 8.1, figs 10–19.
2010   *Clavigerinella caucasica* (Subbotina); Rögl and Egger, fig. 3.3–3.4.
2011   *Clavigerinella caucasica* (Subbotina); Rögl and Egger, pl. 1, 8, pl. 4, fig. 1.
2012   *Clavigerinella caucasica* (Subbotina); Coccioni and Bancalà, pl. 1, figs 5–8.

Description. Wall smooth, normal perforate or weakly cancellate; characterized by pores with a wide range of diameters; possibly spinose. Test planispiral or pseudo-planispiral, evolute, biumbilicate or showing a slightly raised spiral side and very shallow umbilicus; 4–4½ rapidly enlarging chambers in the final whorl; early chambers rounded; final 1–4 chambers radially elongate, digitate peripheral outline strongly lobulate; distal chamber ends on final chambers acute, distinctly pointed; equatorial high-arched aperture, symmetrical or slightly asymmetrical, bordered by smooth broad imperforate lip; web-like relict apertural lips present along sutures; sutures shallow, straight, becoming curved in later stages, short compared with overall chamber length (description modified from Coxall and Pearson 2006, p. 218).

Dimensions. Diameter 0.75 mm; thickness 0.20 mm (Subbotina 1958).

Diagnostic features. The species is distinguished from other species of *Clavigerinella* by having adult chambers that taper into an acute or pointed tip (Subbotina 1958; Coxall and Pearson 2006). It is distinguished from *Hantkenina singanoae* principally by lacking a terminal constriction ('terminal nub'), which must be present on at least one adult chamber. The chambers are generally cylindrical rather than equatorially flattened and triangular as is common in *H. singanoae*. The species intergrades with both *Clavigerinella eocanica* and *Hantkenina singanoae*.

Discussion. This long-neglected species was included in the synonymy of *C. eocanica* by Blow (1979). Coxall and Pearson (2006) separated the two species on the basis of the distal chamber shape, which is rounded in *C. eocanica*, but slightly acute in *C. caucasica*. They illustrated the holotype of *C. caucasica* by SEM in three views for the first time, revealing the wall texture. They regarded it as a very short-ranging form which gave rise to *Hantkenina singanoae* by equatorial flattening of the chambers and the evolution of a distinct terminal constriction or 'nub' at the end of at least one chamber. Coxall and Pearson (2006) included in synonymy several specimens from

Austria that Coxall *et al.* (2003) had referred to as '*Clavigerinella–Hantkenina*' transition. Further specimens from Austria were illustrated by Rögl and Egger (2010, 2011) and from Italy by Coccioni and Bancalà (2012).

Clavigerinella eocanica (Nuttall, 1928)
Figures 5A–C

See also Figures S1.1a–c, S1.4, S1.13–1.14.

> 1928 *Hastigerinella eocanica* Nuttall, p. 376, pl. 50, figs 9–11.
> 1979 *Clavigerinella eocanica eocanica* (Nuttall); Blow, p. 1198–1203, pl. 151, figs 1–3, pl. 157, fig. 9, pl. 162, figs 1–3, 5–7.
> 1980 *Eoclavatorella benidormensis* Cremades Campos, p. 209, pl. 257, figs 1–3.
> 2006 *Clavigerinella eocanica* (Nuttall); Coxall and Pearson, p. 222–224, pl. 8.1, figs 10–19.
> 2012 *Clavigerinella eocanica* (Nuttall); Coccioni and Bancalà, pl. 1, figs 3–4.
> 2012 *Eoclavatorella benidormensis* Cremades Campos; BouDagher-Fadel, 2012, p. 151, pl. 5.3, fig. 6.

Description. Wall usually smooth, normal perforate, sometimes weakly cancellate; possibly spinose. Test planispiral or pseudoplanispiral, evolute, laterally compressed biumbilicate or showing a subtly raised spiral side and very shallow umbilicus; $4–4^1/_2$ rapidly enlarging chambers in the final whorl; early chambers rounded, final 2–3 adult chambers conspicuously elongated into club-shaped (clavate) extensions; highly lobular peripheral outline; distal chamber ends smoothly rounded; equatorial high-arched aperture, symmetrical or slightly asymmetrical, bordered by a smooth broad imperforate lip, relict apertural lips often preserved along sutures; sutures are shallow, straight, becoming curved in later stages, short relative to total chamber length (modified from Coxall and Pearson, 2006, p. 222).

Diagnostic features. This species is distinguished from others of the genus by possession of rounded to slightly bulbous clavate chambers.

Discussion. This was the first species of *Clavigerinella* to evolve and seems to have quickly given rise to a minor radiation of species including the *Clavigerinella caucasica–Hantkenina* lineage. According to Coxall *et al.* (2003), it evolved from *Parasubbotina inaequispira* via an intermediate species *Parasubbotina eoclava*. The evolution involved lowering of the height of the trochospire until a planispiral or near-planispiral arrangement was achieved and the development of extended clavate chambers in the adult. *Parasubbotina* was a spinose genus (Olsson *et al.* 2006), and it is possible that *Clavigerinella* or even *Hantkenina* retained a sparse distribution of true spines, but this has never been demonstrated, and it is more likely that spines were lost around the time of the evolution of *Clavigerinella* (Coxall and Pearson 2006).

Genus HANTKENINA Cushman, 1924

> 1937 *Hantkenina (Sporohantkenina)* Bermudez, p. 151; type species *Hantkenina brevispina* Cushman, 1924.
> 1942 *Hantkenina (Aragonella)* Thalmann, p. 811; type species *Hantkenina mexicana* Cushman, 1924. Raised to the rank of genus by BouDagher-Fadel (2012, p. 151).
> 1942 *Hantkenina (Applinella)* Thalmann, pp. 812–814; type species *Hantkenina dumblei* Weinzierl and Applin, 1929.
> 1950 *Hantkenina (Hantkeninella)* Bronnimann, p. 399; type species *Hantkenina alabamensis* var. *primitiva* Cushman and Jarvis, 1929.

Type species. *Hantkenina alabamensis* Cushman, 1924; from the Upper Eocene *Zeuglodon* bed, Alabama.

Description. Wall smooth, normal perforate, probably nonspinose. Test planispiral, biumbilicate or showing a subtly raised spiral side and very shallow umbilicus; 4–7 chambers in the final whorl; chambers rounded in the early stages, adult chambers radially elongated, triangular, polygonal or spherical, laterally compressed to highly inflated; some or all of the adult chambers extend into hollow nonporous tubulospines, of variable length, shape and orientation or, in the case of *H. singanoae*, the chambers possess a distinct terminal nub or porous 'proto-tubulospine'; peripheral outline (excepting tubulospines) varies from stellate, with deep incisions between chambers, to angular, smooth, continuous or gently lobed; the aperture is a single equatorial arch bordered by a distinctive lip of variable width, symmetrical or slightly asymmetrical (modified from Coxall and Pearson, 2006, pp. 229–230).

Diagnostic features. This genus is distinguished from *Clavigerinella* by possessing tubulospines or, in transitional forms, homologous structures such as terminal nubs and proto-tubulospines. It is distinguished from *Cribrohantkenina* by lacking areal apertures.

Discussion. The synonymy of the various genera and subgenera listed above was discussed by Coxall and Pearson (2006, pp. 229–230). BouDagher-Fadel (2012) resurrected *Aragonella* and raised it to the rank of genus, but we regard this as unnecessary.

Hantkenina mexicana Cushman, 1924
Figures 8L–Q

See also Figures S9.154–S9.161, S10.162–S10.172.

> 1924 *Hantkenina mexicana* Cushman, p. 3, pl. 2, fig. 2.

1930 *Hantkenina mexicana* var. *aragonensis* Nuttall, p. 284, pl. 24, figs 2–3.

1981 *Hantkenina nuttalli* Toumarkine, p. 112, pl. 1, fig. 4.

2003 'primitive' *Hantkenina nuttalli* Toumarkine; Coxall *et al.*, p. 251 (*pars*), pl. 6, figs 10–12.

2006 *Hantkenina mexicana* Cushman; Coxall and Pearson, pp. 242–246, pl. 8.10, figs 1–21.

2006 *Hantkenina nuttalli* Toumarkine; Bernaola *et al.*, p. 88, fig. 10 h–i.

2008 *Hantkenina mexicana* Cushman; Larrasoaña *et al.*, fig. 4H (two views).

2010 '*Hantkenina nuttalli*' Toumarkine; Rögl and Egger, fig. 3.9–10.

2010 *Hantkenina mexicana* Cushman; Rögl and Egger, fig. 3.12.

2010 *Hantkenina* cf. *mexicana* Cushman; Rögl and Egger, fig. 3.11.

2010 *Hantkenina* nov. spec. Rögl and Egger (*pars*), fig. 3.7–3.8.

2011 *Hantkenina gohrbandti* Rögl and Egger (*pars*), pl. 2, figs 4–5, pl. 3, figs 10–11 (close-ups of the same specimens; note these paratypes are the same as those recorded as *Hantkenina* nov. spec. Rögl and Egger, figs 3.7–3.8), pl. 4, fig. 4 (thin section).

2011 *Hantkenina gohrbandti* – *H. mexicana* transition Rögl and Egger, pl. 2, figs 8–9.

2011 *Hantkenina mexicana* Cushman; Rögl and Egger, pl. 4, figs 2–3 (thin sections).

2011 *Hantkenina* cf. *mexicana* forma *H. nuttalli* Toumarkine; Rögl and Egger, pl. 3, fig. 14.

2012 *Hantkenina gohrbandti* Rögl and Egger morphotype 2; Coccioni and Bancalà, pl. 2, fig. 1. 2012 *Hantkenina* cf. *mexicana* Cushman 'forma *H. nuttalli* Toumarkine'; Coccioni and Bancalà, pl. 2, figs 8–12.

2012 *Hantkenina mexicana* Cushman; Coccioni and Bancalà, pl. 2, figs 13–15.

Description. Wall smooth, normal perforate and probably non-spinose; tubulospines imperforate or with small, scattered pores, smooth or finely striated with a well-defined zone of demarcation between the tubulospines and the chamber wall. Test planispiral, evolute, biumbilicate or showing a slightly raised spiral side and very shallow umbilicus; laterally compressed with 4–5 rapidly expanding chambers in the final whorl; final whorl chambers radially elongate or digitate, well separated, inflated peripherally and more compressed within the umbilical region; some specimens, including the holotype, exhibit anterior flexure of the final chamber; peripheral outline distinctly stellate; each chamber of the adult whorl extends gradually into a hollow tubulospine; aperture is a narrow, elongate equatorial arch bordered by an imperforate flaring lip, often with a crenulated and/or pustulose margin, relict apertural lips are sometimes preserved as 'webs' along the sutures; sutures straight, becoming curved in the final stages, only partially contacting adjacent chamber; tub-

ulospines variable in form, broad based and stout or long and slender, positioned centrally with respect to the radial chamber axis, directed radially between anterior and posterior chamber shoulders, distal ends commonly possess terminal finger-like projections (coronet structure of Ramsay, 1962) (description modified from Coxall and Pearson, 2006, p. 245).

Dimensions. Maximum diameter (excluding tubulospines) 0.5 mm, with tubulospines 0.75 mm or more.

Diagnostic features. This species is distinguished from later species of *Hantkenina* by the stellate outline and radially directed tubulospines that are positioned centrally on the chamber. It is distinguished from *H. singanoae* by possessing true nonporous tubulospines with a distinct demarcation in texture from the primary chamber wall.

Discussion. Coxall and Pearson (2006, pp. 243–246) introduced the synonymy of *Hantkenina mexicana* Cushman and *H. nuttalli* Toumarkine. The specimen chosen by Toumarkine (1981) as the holotype does not fit the type description well and has broken chamber ends on the last three chambers, making it impossible to determine their original state and hence base a reliable species concept. The four specimens from Austria described as 'primitive' *Hantkenina nuttalli* by Coxall *et al.* (2003) include one specimen that we assign tentatively to *Hantkenina singanoae* and three that we assign tentatively to *Hantkenina mexicana*. The reason for the uncertainty is that all the specimens are broken, and the original nature of the tubulospines or proto-tubulospines is uncertain. Rögl and Egger (2010, 2011) illustrated several specimens under different names that we assign to this species: the reason for including two of the specimens assigned to *Hantkenina* nov. spec. (initially, in 2010) and then to *Hantkenina gohrbandti* (in 2011, as paratypes of that taxon) is that both apparently show a nonporous tubulospine on an early chamber, but other chambers in the final whorl are broken or eroded so it is not possible to determine whether they possessed terminal nubs, proto-tubulospines or tubulospines; we think the latter is most likely given the tubulospines on the earlier chamber. Three specimens labelled as '*Hantkenina gohrbandti* – *H. mexicana* transition' by Rögl and Egger (2011) apparently each possess a nonporous tubulospine on the one complete chamber remaining of each specimen and so are assigned to this species. Similarly, the morphotype recorded as '*Hantkenina gohrbandti* Rögl and Egger morphotype 2' by Coccioni and Bancalà (2012) is probably a broken specimen of *H. mexicana* insofar as an earlier chamber appears to possess a true nonporous tubulospine according to the description of those authors.

Hantkenina singanoae Pearson and Coxall, 2006
Figures 5P–T, 6A–G, J–R, 7A–V, 8A–K

See also Figures S1.12, S2.25, S2.36, S3.40, S3.43–S3.47, S3.49–
S3.53, S3.55–S3.58, S3.61–S3.62, S4.63–S4.68, S4.70–S4.71,
S4.75–S4.77, S4.80, S5.81, S5.87, S5.90–S5.97, S6.98, S6.100–
S6.116, S7.117–S7.129, S8.130–S8.148, S9.149–S9.153.

2003 ?'primitive' *Hantkenina nuttalli* Cushman 1924;
Coxall *et al.*, p. 251 (*pars*), pl. 6, fig 9 (*non* pl. 6,
figs 10–12).

2004 transitional *Hantkenina* sp. Pearson *et al.*, p. 37,
pl. 2, figs 18–21.

2006 *Hantkenina singanoae* Pearson and Coxall *in* Coxall
and Pearson, pp. 252–253, pl. 8.13, figs 1–17.

2010 *Hantkenina singanoae* Pearson and Coxall; Rögl and
Egger, fig. 3.5.

2011 *Hantkenina gohrbandti* Rögl and Egger (*pars*), pl. 1,
fig. 1 (holotype), pl. 1, figs 2–7 (paratypes), pl. 2,
fig. 1–3 (paratypes), pl. 2, fig. 6 (paratype), pl. 3,
figs 1–9 (close-up views of various specimens from
pls 1 and 2), pl. 4, fig. 5 (thin section). Not pl. 1,
figs 4–5.

2011 *Hantkenina singanoae* Pearson and Coxall, pl. 1, fig.
9 (same specimen as Rögl and Egger 2010, fig. 3.5);
pl. 3, fig. 13 (re-illustration of holotype).

2011 ?*Hantkenina mexicana* Cushman; Rögl and Egger,
pl. 3, fig. 15. (Note this specimen has long slender
tubulospine-like projections, but they are porous
for most of their length, becoming smooth towards
their tips, making it in our taxonomy almost
exactly transitional between *H. singanoae* and
H. mexicana.

2012 *Hantkenina gohrbandti* Rögl and Egger morphotype
1; Coccioni and Bancalà, pl. 1, figs 9–16.

2012 *Hantkenina gohrbandti* Rögl and Egger morphotype
3; Coccioni and Bancalà, pl. 2, figs 2–6

2012 *Hantkenina singanoae* Pearson and Coxall; Coccioni
and Bancalà, pl. 2, fig. 7.

Description. Wall layered and perforate with a smooth or weakly
cancellate surface. Test planispiral or pseudo-planispiral, laterally
compressed, 4–5 rapidly expanding chambers in the final whorl;
final chamber and up to three of the preceding chambers radi-
ally elongate, at least one of these ending in either a terminal
nub or a cylindrical projection ('proto-tubulospine'); proto-tub-
ulospines are smooth and distinctly porous (although pore den-
sity may be reduced at the distal ends) in contrast to the true
tubulospines of *H. mexicana* and subsequent species, which are
usually imperforate; distal chamber ends can be inclined in an
anterior, posterior or dorsoventral direction, and proto-tubulos-
pines are commonly bent; aperture is a high equatorial arch with
a smooth, broad lip; lips of relict apertures are commonly
observed along the sutures of the final whorl; sutures are shallow
and usually curved in a posterior direction (description modified
from Coxall and Pearson, 2006, p. 252).

Dimension. Maximum diameter of holotype (excluding terminal
nubs) 0.63 mm.

Diagnostic features. This species is distinguished from all
other *Hantkenina* by lacking true nonporous tubulos-
pines and possessing instead a terminal nub to the
chamber or a porous proto-tubulospine in the sense of
Coxall and Pearson (2006). Subdivision of *H. singanoae*
from *C. caucasica* relies on the identification of the
slightest terminal constriction on at least one chamber
(see also Rögl and Egger 2011 and Coccioni and Bancalà
2012).

Discussion. Following Coxall and Pearson (2006), we take
a broad view of this morphospecies, including within it
specimens similar to *Clavigerinella caucasica* that possess
a terminal constriction or 'nub' (which we call Type 1;
the holotype is one such specimen) and those that possess
long, slender proto-tubulospines (Type 2). We see little
value in splitting the taxa formally based on minor details
given that the populations are so variable during the evo-
lutionary transition. The holotype and most of the para-
types of *Hantkenina gohrbandti* Rögl and Egger are of
Type 1, but only just, insofar as the terminal constriction
is very small on these specimens, and they are hence very
similar to *C. caucasica*.

Authors' contributions. PNP made the collection and wrote the
manuscript. HKC produced the X-rays and map and contributed
to the interpretation and writing.

Editor. Svend Stouge

SUPPORTING INFORMATION

Additional Supporting Information may be found in the online
version of this article:

Figs S1–S10. The complete collection of specimens from
Tanzania arranged in stratigraphic order, shown to a common
scale. Numbers next to specimens are the collection numbers
that are linked to Appendix S1.

Appendix S1. List of specimens illustrated in Figures 5–14
from the stratigraphic collection at TDP Sites 2 and 20.

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