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Umbilicosphaera jordanii Bown, 2005 from the Paleogene of Tanzania: confirmation of generic assignment and a Paleocene origination for the Family Calcidiscaceae

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Abstract Scanning electron microscope images of the recently described Paleogene coccolith *Umbilicosphaera jordanii* Bown, 2005*,* allow detailed comparison of its structure to that of extant *Umbilicosphaera*. The morphological and crystallographic evidence strongly support the inclusion of *U. jordanii* within *Umbilicosphaera,* and so confirms a Paleocene origination time for the extant Family Calcidiscaceae. We also recombine the species *Cyclolithus bramlettei* Hay & Towe, 1962 within *Umbilicosphaera*, based on similar considerations of shield morphology and crystallography.

Keywords *Umbilicosphaera*, Calcidiscaceae, taxonomy, Paleogene, Kilwa Group, Tanzania

1. Introduction

Umbilicosphaera jordanii was described from the Lower Eocene of coastal Tanzania (Bown, 2005) and is a conspicuous and common component (>5%) of much of the Paleogene Kilwa Group succession (Upper Paleocene-Oligocene). The species was described using light-microscopy and tentatively placed in the extant genus *Umbilicosphaera*, based on the overall character of its appearance. Here, we present new scanning electron microscope (SEM) images of *U. jordanii*, which allow detailed comparison of its structure to that of extant *Umbilicosphaera*, as described in detail by Young *et al.* (2004). This comparison strongly supports the inclusion of *U. jordanii* in *Umbilicosphaera,* and so confirms a Paleocene origination time for the extant Family Calcidiscaceae.

2. Methods and materials

The Kilwa Group (Cretaceous-Oligocene) of Tanzania has been studied in core material as part of a palaeoclimate research programme, the Tanzania Drilling Project (TDP). An overview of the TDP project, describing field techniques, geological setting, drilling objectives and stratigraphic results, is given in Pearson *et al.* (2004, 2006, in prep.) and Nicholas *et al.* (2006), and detailed nannofossil taxonomic inventories of the Paleogene material, based on light-microscopy, have been presented in Bown (2005) and Bown & Dunkley Jones (2006).

Nannofossils were viewed in smear-slides (Bown & Young, 1998) using a Zeiss Axiophot light-microscope (LM) at x1000-1250 magnification in cross-polarised (XPL) and phase-contrast (PC) light, and on broken rock-surfaces using a JEOL Digital JSM-6480LV SEM (see Lees *et al.*, 2004 for discussion of this technique). Descriptive terminology follows Young *et al.* (1997).

3. Results

Umbilicosphaera jordanii was described from LM images that show circular coccoliths with broad shields and wide, open central areas (Pl.1, figs 9-13). The rim displays low birefringence, with a bright tube-cycle crossed by diagonal extinction lines, consistent with an ultrastructure of V-units forming the distal shield, and R-units forming the proximal shield and part of the tube. The species was tentatively assigned to the genus *Umbilicosphaera*, as both the overall morphology and crystallography of the coccoliths are comparable to those of the extant species *U. foliosa*, and extinct Neogene species such as *U. jafari* and *U. rotula*.

We have now imaged multiple specimens of *U. jordanii* in the SEM, and a representative set of images is given in Plate 1, together with those of extant *Umbilicosphaera* species, to allow a direct comparison. The distal shield is formed from elements joined along near-radial sutures in their outer part, but at the shield crest the sutures kink, at which point they often show bead-like projections (Pl.1, fig.2). Individual elements can be directly traced from the distal shield into the tube (*e.g.* Pl.1, figs 1, 4), showing that a single cycle of crystal units forms the entire distal shield and tube, as in modern *Umbilicosphaera* (Pl.1, figs 3, 5). Around the inner edge of the distal surface, there may be an area with indistinct sutures, (Pl.1, figs 1, 2), a feature also seen in *U. foliosa* (Pl.1, fig.5). Above this zone of obscure sutures, the well-developed flat crystal faces seen on *U. jordanii* are almost certainly the {100} faces of rhombohedral calcite, as is the case on modern *Umbilicosphaera* (Young *et al.*, 2004). Closer examination reveals that the crystal edges between these rhombohedral faces in *U. jordanii* show exactly the same orientation as those in extant *Umbilicosphaera*, implying that they have identical *a*- and *c*-axis orientations (see annotation on Pl.1, figs 1, 3).

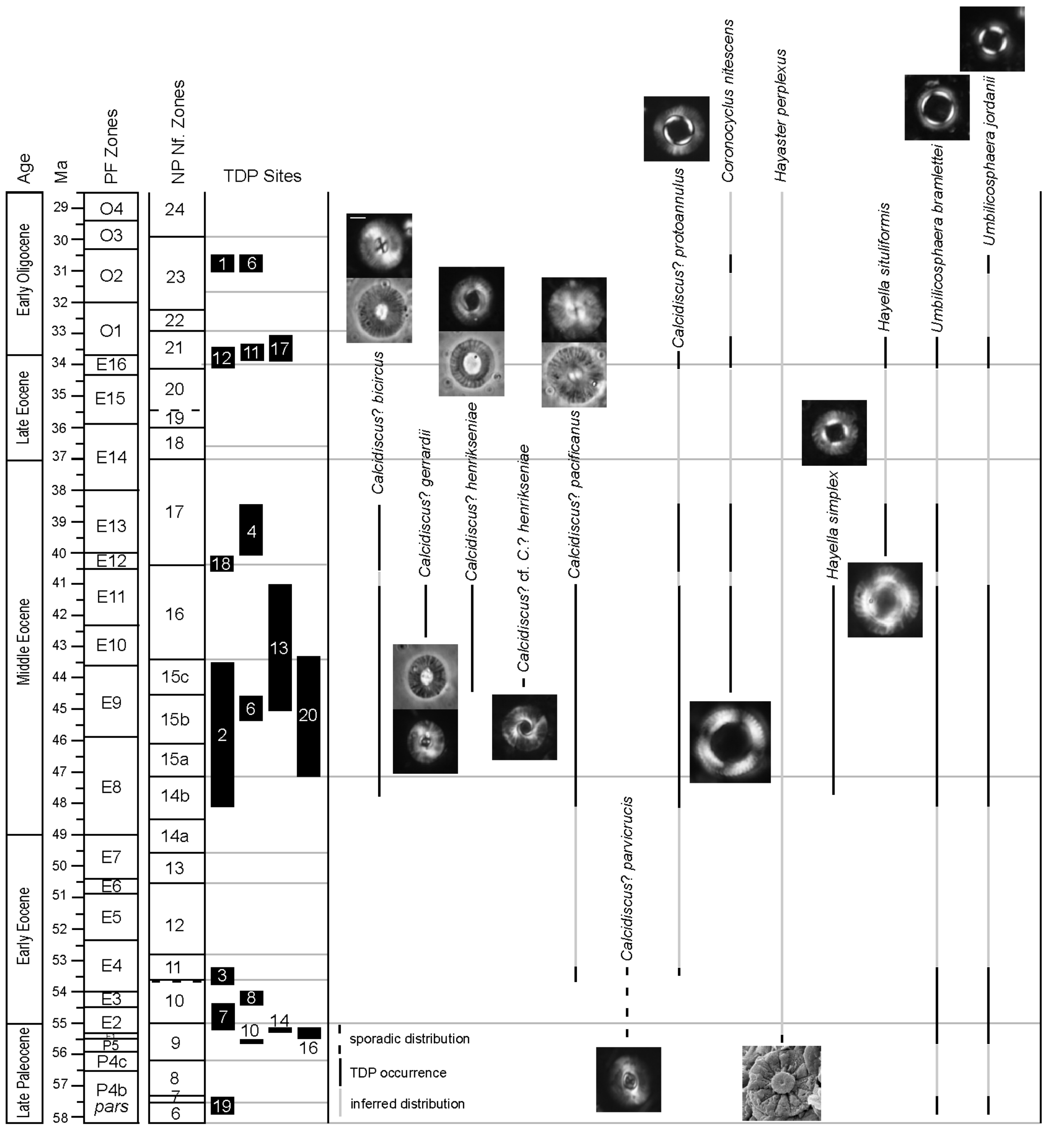

Figure 1: Stratigraphic distribution of Calcidiscaceae taxa from the Paleogene of Tanzania. Nannofossil biozonation from Martini (1971), planktonic foraminifera biozonation from Berggren & Pearson (2005). Correlation of the two plankton biozonation schemes and time-scale are from the latter. Stratigraphic extent of TDP cores shown to the left of the diagram

The proximal shields are rather flat and, in some cases, larger than the distal shields, as also seen in *U. sibogae* (Pl.1, figs 1, 3). The proximal shield elements show strong clockwise obliquity, and there is a raised collar and narrow smoother area around the inner edge (Pl.1, fig.6). A narrow, outer proximal-shield cycle is complexly intergrown with the main proximal-shield elements (Pl.1, fig.7). These proximal-shield characters are directly comparable to modern *U. foliosa* (Pl.1, fig.8) and many other, although not all, Calcidiscaceae and Coccolithaceae.

4. Discussion

The Order Coccosphaerales (Coccolithaceae and Calcidiscaceae) form placolith coccoliths with V-unit distal shields, R-unit proximal shields and embedded proto-coccolith rings (Young *et al*., 2003). Coccolithaceae coccoliths further have a complex tube formed from R-units in the upper part and V-units in the lower part. Calcidiscaceae coccoliths typically comprise monocyclic distal shields with strongly curving sutures, and proximal shields that can be mono- or bicyclic. *Umbilicosphaera* is distinguished from *Calcidiscus* by its wide central opening, kinked distal-shield sutures and birefringent tube-cycle. While these distinctions are not particularly great, the separation of the two genera is, nevertheless, supported by genetic analysis (Saez *et al*., 2003).

The morphological and crystallographic observations presented above and in Plate 1 provide unambiguous evidence that *U. jordanii* possesses a structure typical of the Calcidiscaceae, that is, proximal shield and lower tube R-units, distal shield and upper tube V-units, exactly the same chirality of elements, and the proto-coccolith ring embedded inside the tube (V/R alternation is not seen on the proximal surface). The kinked sutures and bead-like projections of the distal shield, and larger, bicyclic proximal shields with clockwise chirality, are all features seen in the extant species *U. foliosa* and *U. sibogae*, and support the inclusion of *U. jordanii* within *Umbilicosphaera*. We also recombine the species *Cyclolithus bramlettei* Hay & Towe, 1962 within *Umbilicosphaera*, based on similar considerations of shield morphology and crystallography (see below and Pl.2, figs 1-4, 7-12).

Previous palaeontological records of *Umbilicosphaera* placed its origination in the Early Neogene (*e.g.* zone NN2, ~22Ma, according to Young, 1998), but the Tanzanian Kilwa Group occurrences extend its fossil record by 36Ma, to at least the Late Paleocene (Figure 1). The species *U. jordanii* has been found in the oldest Paleogene drilled by the TDP (TDP Site 19, zone NP6: Nicholas *et al*., 2006) and it is consistently found throughout the Paleocene to Early Oligocene. One important test of the generic classification applied here is whether we will be able to trace lineages from our youngest Oligocene representatives of *U. jordanii* to the Miocene *U. jafari* or *U. rotula*.

The common and consistent presence in the Kilwa Group of other coccoliths with comparable morphologies, for example, *U. bramlettei* and *Hayaster perplexus* (Pl.2, fig.5), has now established, beyond doubt, that the Calcidiscaceae extended into the Paleocene and were a significant component of placolith assemblages throughout the Paleogene interval (Figure 1). There is no stratophenetic evidence for the origin of the Calcidiscaceae, but coccolith structure and molecular genetics both suggest they evolved from the Coccolithaceae. Since the first Coccolithaceae occur in the Early Paleocene, it is reasonable to infer that the Calcidiscaceae originated subsequent to this, and so within the Paleocene. Other taxa that are tentatively included within the genus *Calcidiscus* (see Figure 1) have yet to be studied in detail using the SEM, but their LM images suggest affinities with the Family Calcidiscaceae. The taxonomy of Paleogene Coccolithaceae and Calcidiscaceae is in need of revision, not least since there are numerous poorly-characterised species in the literature. We intend to use the exceptionally preserved material from the TDP to revise this group and so enhance our knowledge of coccolithophore palaeodiversity and phylogeny.

5. Systematic palaeontology

Only bibliographic references not included in Perch-Nielsen (1985) and Bown (1998) are included in the reference list. All sample material, slides, stubs and images are curated in the Micropalaeontology Unit of the Department of Earth Sciences at UCL.

Order COCCOSPHAERALES **Haeckel, 1894** emend. **Young & Bown, 1997**

Family **CALCIDISCACEAE** Young & Bown, 1997

Hayaster perplexus (Bramlette & Riedel, 1954) Bukry, 1973

Pl.2, figs 5, 6. **Remarks**: Large, circular coccoliths with a small number of large, triangular distal-shield elements and a diminutive proximal shield with sutures that display clockwise chirality and pronounced kinking towards the centre. There is little to distinguish these Paleogene forms from the modern species. **Occurrence**: Rare, Upper Paleocene (NP9); TDP Site16B.

Umbilicosphaera bramlettei (Hay & Towe, 1962) comb. nov.

Pl.2, figs 1-4, 7-12. **Basionym**: *Cyclolithus bramlettei* Hay & Towe, 1962, p.500, pl.5, fig.6; pl.7, fig.2. *Eclogae Geol. Helv*., **55**: 497-517. **Remarks**: Small- to medium-sized (3.5-7.5μm), narrow, ring-shaped coccoliths, distinctly bicyclic in XPL. The two cycles are similar in width, and the bright inner cycle is crossed by non-axial extinction lines. It forms distinctive cubic coccospheres, seen in the LM (Pl.2, figs 11, 12). The distal-shield elements are strongly kinked, and show distinctly stepped edges across the outer half of the shield, but straight edges across the inner half, a feature identical to the extant species *U. sibogae*. The proximal shield elements show strongly clockwise obliquity and are kinked near the inner edge. **Differentiation**: Similar to *Coronocyclus nitescens* in LM appearance, but has a more clearly defined, bright tube-cycle in XPL and lacks the characteristic serrated outline. *Coronocyclus* also appears to have significantly modified placolith structure, unlike typical calcidiscids. Comparable to *U. jordanii* and *Calcidiscus*? *protoannulus*, but the two rim-cycles are similar in width and the tube-cycle details are distinct, being more clearly defined than the former, and crossed by straighter, more diagonal extinction lines than the latter. **Occurrence**: Upper Paleocene to Lower Oligocene (NP6-21); TDP Sites 2-4, 7A, 7B, 8, 10-14, 16-19.

Umbilicosphaera jordanii Bown, 1985

Pl.1, figs 1, 2, 4, 6, 7, 9-13. **Remarks**: The distal-shield sutures are distinctly kinked and, like the modern species of *Umbilicosphaera*, this may be explained by relatively simple, single crystal-units whose surfaces interact obliquely with the sloping shield surface (Young & Henriksen, 2003; Young *et al*., 2004). The proximal shields are relatively large and flat, as in *U. sibogae*, where this feature is related to large coccosphere size. For further ultrastructural detail, see above. **Occurrence**: Upper Paleocene to Oligocene (NP6-23); TDP Sites 1, 3, 7A, 7B, 8, 10-14, 16-19. Common in the Late Paleocene-Early Eocene, and Late Eocene-Early Oligocene, but may be rarer or absent in parts of the Middle Eocene.

Acknowledgements

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Calcidiscus Kamptner, 1950
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Calcidiscus? *gerrardii* Bown, 2005
Calcidiscus? *henrikseniae* Bown, 2005
Calcidiscus? *parvicrucis* Bown, 2005
Calcidiscus? *protoannulus* (Gartner, 1971) Loeblich & Tappan, 1978
Coccolithaceae Poche, 1913 emend. Young & Bown, 1997
Coccosphaerales Haeckel, 1894 emend. Young & Bown, 1997
Coronocyclus nitescens (Kamptner, 1963) Bramlette & Wilcoxon, 1967 [probably a junior synonym of *prinion* (Deflandre & Fert, 1954)]
Hayaster Bukry, 1973
Hayaster perplexus (Bramlette & Riedel, 1954) Bukry, 1973
Hayella simplex Bown & Dunkley Jones, 2006
Hayella situliformis Garter, 1969
Umbilicosphaera Lohmann, 1902
Umbilicosphaera anulus (Lecal, 1967) Young & Geisen *in* Young *et al*., 2003
Umbilicosphaera bramlettei (Hay & Towe, 1962) comb. nov.
Umbilicosphaera foliosa (Kamptner, 1963 *ex* Kleijne, 1993) Geisen *in* Sáez *et al*., 2003
Umbilicosphaera jafari Müller, 1974
Umbilicosphaera jordanii Bown, 2005
Umbilicosphaera rotula (Kamptner, 1956) Varol, 1982
Umbilicosphaera sibogae (Weber-van Bosse, 1901) Gaarder, 1970

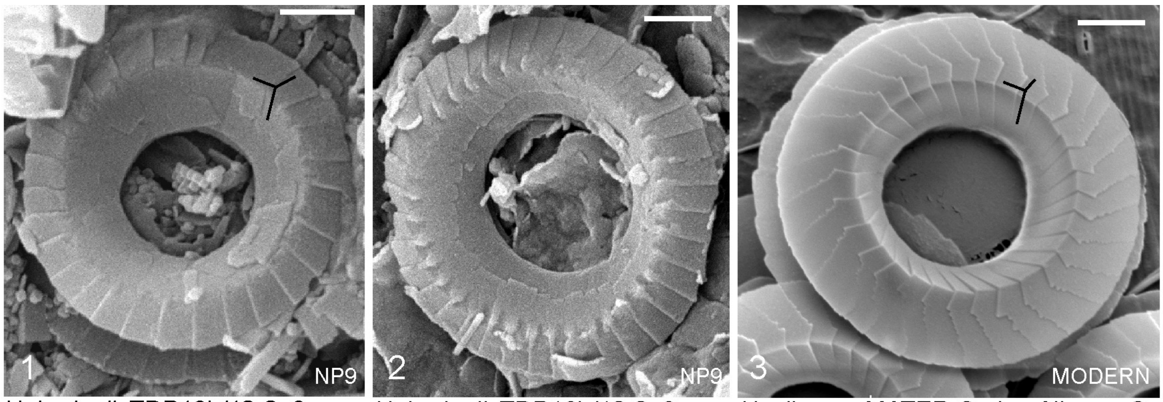
Plate 1

Comparison of *U. jordanii* with modern *U. foliosa* and *U. sibogae*

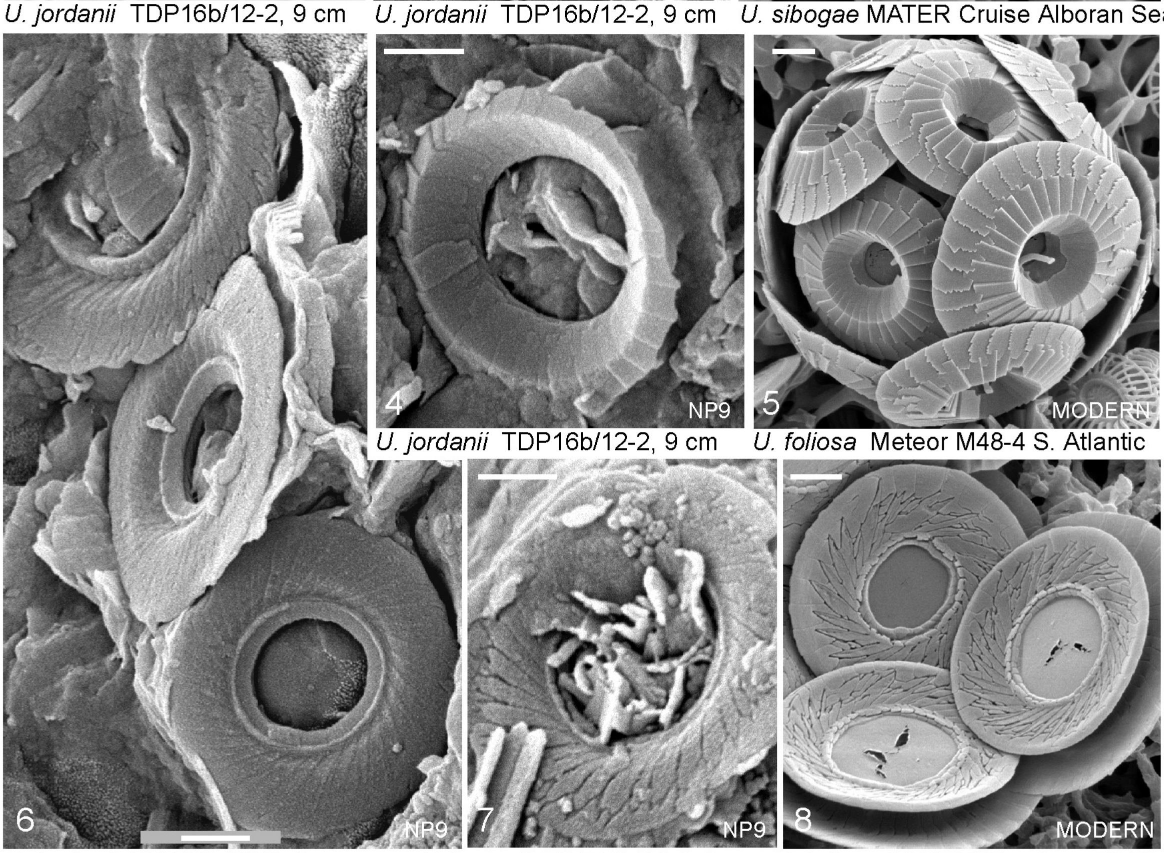
Black annotation lines on 1 and 3 trace crystal edges representing edges of the {100} faces of rhombohedral calcite

Ages of specimens given in bottom right corner

Scale-bars = 1μm

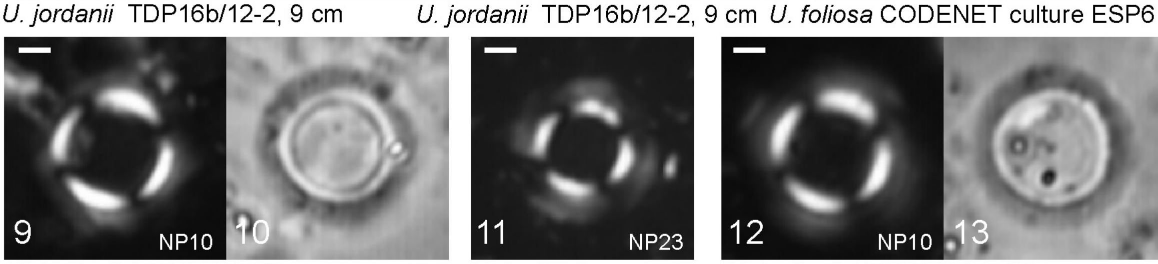


U. jordanii TDP16b/12-2, 9 cm — *U. jordanii* TDP16b/12-2, 9 cm — *U. sibogae* MATER Cruise Alboran Sea



U. jordanii TDP16b/12-2, 9 cm — *U. foliosa* Meteor M48-4 S. Atlantic

U. jordanii TDP16b/12-2, 9 cm — *U. jordanii* TDP16b/12-2, 9 cm — *U. foliosa* CODENET culture ESP6 M1



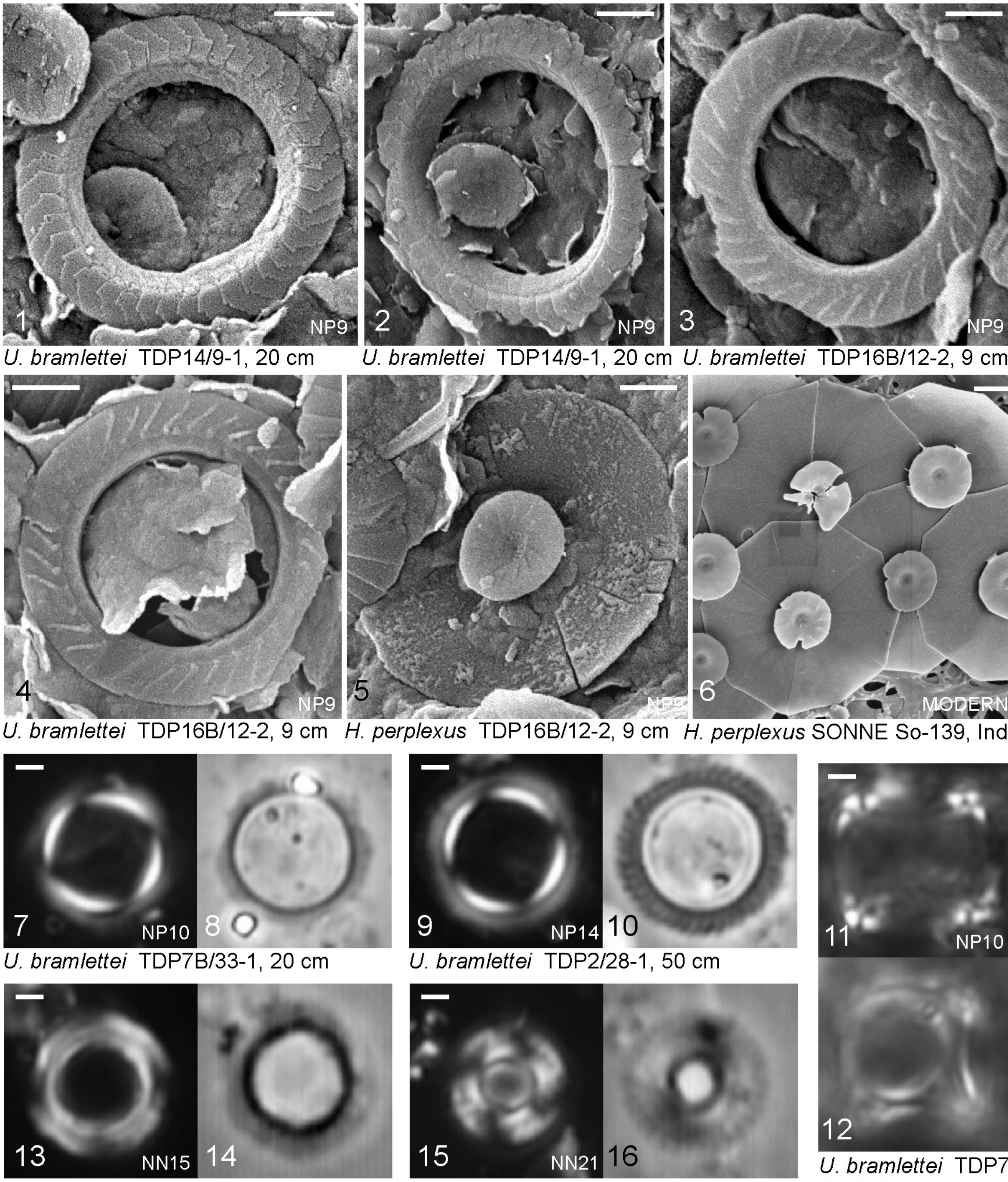
U. jordanii TDP8/1-1, 30 cm — *U. jordanii* TDP1/20-2, 30 cm — *U. jordanii* TDP7A/56-1, 18 cm

Plate 2

U. bramlettei, _Hayaster perplexus_ and other _Umbilicosphaera_ spp.

Ages of specimens given in bottom right corner

Scale-bars = 1µm



1: *U. bramlettei* TDP14/9-1, 20 cm

2: *U. bramlettei* TDP14/9-1, 20 cm

3: *U. bramlettei* TDP16B/12-2, 9 cm

4: *U. bramlettei* TDP16B/12-2, 9 cm

5: *H. perplexus* TDP16B/12-2, 9 cm

6: *H. perplexus* SONNE So-139, Ind. Oc.

7–8: *U. bramlettei* TDP7B/33-1, 20 cm

9–10: *U. bramlettei* TDP2/28-1, 50 cm

11–12: *U. bramlettei* TDP7B/38-1, 35 cm

13–14: *U. rotula* ODP1208-18CC

15–16: *U. foliosa* ODP1208-1-1, 15 cm