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Calcareous nannofossils from the Paleocene/Eocene Thermal Maximum interval of southern Tanzania (TDP Site 14)

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Abstract The Tanzania Drilling Project Site 14 corehole recovered the Paleocene/Eocene boundary interval in claystones that host exceptional calcareous nannofossil preservation and high diversities. This paper describes and illustrates the calcareous nannofossils from this site, including descriptions of two new genera (*Craticullithus* and *Kilwalithus*), nine new species (*Bomolithus aquilus, Braarudosphaera perampla, Campylosphaera differta*, *Coccolithus pauxillus*, *Craticullithus cancellus*, *C. clathrus*, *C. laminus*, *Fasciculithus lobus* and *Kilwalithus cribrum*), one new subspecies (*Zygrhablithus bijugatus maximus*) and two new combinations (*Craticullithus cassus* and *Bomolithus megastypus*).

Keywords Paleocene, Eocene, PETM, taxonomy, calcareous nannofossils

1. Introduction

The Tanzania Drilling Project (TDP) is a palaeoclimate research programme whose primary aim has been the recovery of mid-Cretaceous to Oligocene sediments with exceptionally-preserved calcareous microfossils (Pearson *et al*., 2004, 2006; Nicholas *et al*., 2006). The high quality foraminiferal (and organic carbon) preservation has led to significant improvements in the interpretation of tropical stable isotope palaeotemperature proxy data (Pearson *et al*., 2001, 2007, 2008; Handley *et al*., 2008), but it is the extraordinarily diverse and exquisitely preserved assemblages of Paleogene calcareous nannofossils that justifies the status of Konservat-lagerstätte for the Kilwa Group (Bown *et al*., 2008; Dunkley Jones *et al*., 2009). One of the main stratigraphic targets of the project has been the Paleocene-Eocene boundary interval and this has been recovered at TDP Sites 7, 14 and 16. Initial light microscope (LM)-based taxonomic and biostratigraphic work from these sections was included in Bown (2005), Bown & Dunkley Jones (2006), Nicholas *et al*. (2006) and Bown *et al*. (2008). We have since carried out integrated geochemical, sedimentological and palaeontological studies, principally using the TDP Site 14 corehole (Handley *et al*., 2008; Bown & Pearson, 2009), and the nannofossil assemblages, including 12 new taxa, are documented here.

2. Material and methods

The Site TDP 14 corehole was drilled near Pande in southern Tanzania (9˚16'59.89"S, 39˚30'45.04"E; Figure 1) and comprises a 35.2m section of Late Paleocene-Early Eocene age (Nicholas *et al*., 2006). The lithology is homogeneous dark claystones, with varying amounts of silt, which display no visible cyclicity and no obvious change across the Paleocene-Eocene Thermal Maximum (PETM). The PETM interval is 6.8m thick and distinguished by a striking carbon isotope excursion (CIE) (Handley *et al*., 2008) as well as biotic indicators, including nannofossil and foraminiferal excursion taxa (Bown & Pearson, 2009). The site was located at around 19˚S palaeolatitude in the Eocene and deposited in a bathyal, outer shelf to upper slope environment at water depths of 300-500m (Nicholas *et al*., 2006).

Nannofossils were viewed in simple smear-slides (Bown & Young, 1998), using transmitted-light microscopy in cross-polarised (XPL) and phase-contrast (PC)

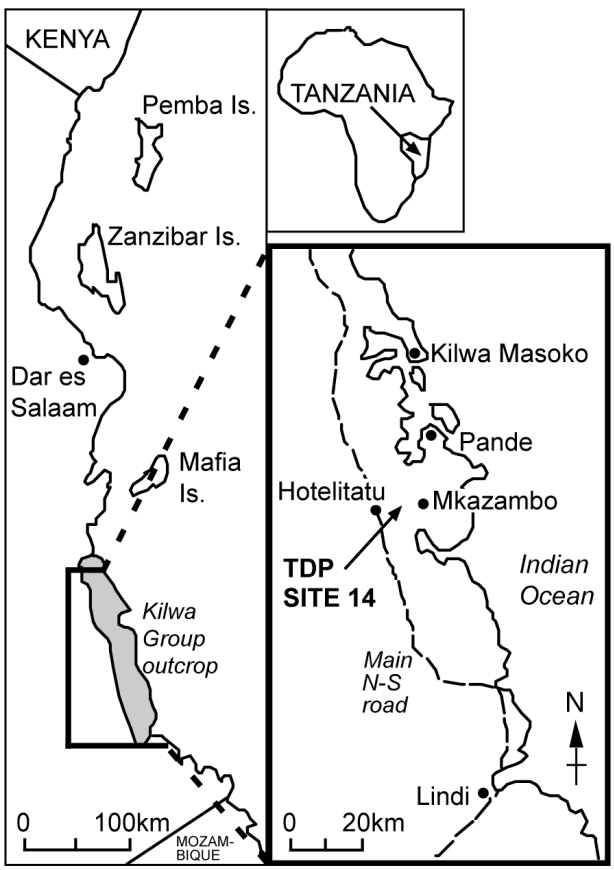

Figure 1: Location of study area

Table 1: Stratigraphic range-chart of selected nannofossil taxa from TDP Site 14. The taxa shown include those that are new, dominant or biostratigraphically significant

| TDP14 | Eocene | | |

light, and on broken rock-surfaces using scanning electron microscopy (SEM) (Lees *et al*., 2004). Both semi-quantitative and quantitative data have been collected, and in total all light microscope slides were studied for at least one hour, and for many hours in the SEM.

3. Results

The nannofossils are rare to abundant and often significantly diluted by clay. Preservation of the nannofossils is uniformly good and often exceptional. The assemblages have high species richness values, which are significantly higher than previously encountered in coeval sections (Bown *et al*., 2008). A total of 162 separate taxa were logged through the NP9 biozone interval, and single-sample species richness reaches 107 species (full stratigraphic range-charts can be found in Bown & Pearson, 2009). This compares with 88 species for biozone NP9 from the global compilation of Bown *et al*. (2004), a maximum of 63 species from other shelf sections and 14-48 species from carbonate-rich deep-sea sections (Bown *et al*., 2008). The quality of preservation is demonstrated not only by enhanced diversity, but also by the conservation of small (<3.0μm) and delicate coccoliths, complete coccospheres, delicate central structures, and taxa that are prone to post-mortem dissolution.

The exquisite nature of the preservation only becomes fully apparent when the material is viewed using SEM to observe unprocessed, broken rock-surfaces. This methodology avoids the dissolution or fragmentation of small and/or fragile taxa that may occur during wet-processing preparation techniques. Although this SEM method is time-consuming and does not suit all sample types, we have consistently achieved good results from the claystones of the Kilwa Group. The nannofossils occur disaggregated and dispersed throughout the sediment fabric, but more rarely are found in concentrations that most likely represent undisturbed marine snow aggregates or faecal pellets. The lack of disturbance is demonstrated by the presence of placolith coccospheres (see Plates 1-4) and collapsed coccospheres of non-placolith taxa (see Pl.5, fig.11). These concentrations show little sign of any modification by overgrowth or dissolution, contain no cement and often include abundant *Gladiolithus* liths and other minute coccoliths, such as *Kilwalithus* gen. nov. (Pl.4, figs 19, 20) and *Pocillithus spinulifer* Dunkley Jones *et al*., 2009 (Pl.12, fig. 8). At TDP Site 14, the abundance of *Gladiolithus* is striking in most samples, and it is often the most abundant taxon in the concentrations. Nannoplankton preservation is also good within the very low abundance assemblages of the PETM interval, and includes fragile coccoliths and coccolith structures that are normally lacking in less well-preserved coeval material (*e.g*. Pl.1, fig.5; Pl.5, fig.13).

The PETM interval is characterised by a 6-7‰ negative CIE in plant-derived *n*-alkanes (Handley *et al*., 2008) and the occurrence of nannofossil and planktonic foraminiferal excursion taxa, such as *Coccolithus bownii* and *Acarinina africana*. The CIE is sharp at both top and bottom, contrasting with other PETM sections, where the onset is rapid, but followed by gradual recovery of carbon isotope values (*e.g*. Kelly *et al*., 2005; Sluijs *et al*., 2007). The sharp top may be due to the presence of a hiatus that terminated the sediment record prior to the isotope recovery or event top. A short hiatus would also explain a cluster of nannofossil appearances seen at this level (*Discoaster mahmoudii*, *D. diastypus*, *Bomolithus aquilus* sp. nov., *Holodiscolithus macroporus*), though equally it could be interpreted as a biotic response at the cessation of the PETM perturbation (Table 1).

The background assemblages have typical Early Paleogene community structure and are dominated by *Toweius* and *Coccolithus*. Other aspects of the assemblages are less typical, in particular, the consistent presence of fragile taxa (holococcoliths, *Gladiolithus*, *Calciosolenia, Blackites* and the new genera, *Craticullithus* and *Kilwalithus*), the common occurrence of recently described forms, such as *Umbilicosphaera jordanii* (>5%) and *Coccolithus bownii* (often >25%), and the presence of taxa typically reported as originating at higher stratigraphic levels, for example, *Pontosphaera* spp., *Blackites* spp. and *Umbilicosphaera bramlettei*. The extant taxon *Gladiolithus* is abundant in the majority of slides. Conversely, there are diagnostic PETM components that are not present at Site TDP14, most notably the excursion taxon *Discoaster araneus*, and *Rhomboaster* spp. are rare.

Major assemblage shifts occur at both the PETM onset and top, and the intra-PETM assemblages are wholly distinct from those above or below. These shifts are described and discussed in Bown & Pearson (2009), but the principal changes from background to intra-PETM include overall abundance and diversity decline, extinction of at least eight species, and a switch in the dominant taxon from *Toweius* to *Coccolithus*. The PETM assemblages are characterised by abundant *C. bownii* and relatively higher abundances of *Discoaster salisburgensis*, *Bomolithus supremus*, *Neochiastozygus imbriei, Fasciculithus lobus* sp. nov. and rare occurrences of the excursion species *Discoaster anartios*. Above the PETM, there is a return to 'normal' assemblage compositions, *i.e*. *Toweius*-dominated, although a number of first appearances occur at this level (see above).

4. Biostratigraphy

Biostratigraphically, the lower part of TDP Site 14 falls within zone NP9, based on the presence of *Discoaster multiradiatus* (also *Campylosphaera dela*). The FO of *Rhomboaster* spp. (usually *R. cuspis* or *R. calcitrapa*) is used by some authors to define an NP9b subzone (*e.g*. Aubry, 1999; and equivalent to the CP8b subzone definition used by Raffi *et al*., 2005), and occurs at 13.7m; however, *Rhomboaster* spp. are rare in Tanzania. The upper 9.1m of the borehole also falls within NP9, but belongs to an older/lower part of the zone, as evidenced by the presence of large *Ericsonia robusta* (Raffi *et al*., 2005) and *Cruciplacolithus frequens*. This older stratigraphy is probably the result of a small fault. TDP Sites 16A and 16B were

drilled close to Site 14, but were poorly recovered, and so we have focussed on the latter core (Nicholas *et al*., 2006), although images from the other coreholes are included within this paper. TDP Sites 7A and 7B, drilled near Kilwa Kivinje (Pearson *et al*., 2006), recovered a succession stratigraphically immediately above that of Site 14, but was terminated before the PETM interval was reached, due to coring difficulties (Nicholas *et al*., 2006). These cores spanned zones NP9 and 10, with the FO of *Rhomboaster bramlettei* (marking the base of NP10) recorded at 105.2m at TDP Site 7B.

5. Systematic palaeontology

The aim of this section is to provide images of the principal taxa from the TDP Site 14 section and to describe the 12 new taxa. Remarks are only provided where additional information has come to light since the LM-based taxonomic studies of Bown (2005), Bown & Dunkley Jones (2006) and Bown *et al*. (2007, 2008). The descriptive terminology follows the guidelines of Young *et al*. (1997). The higher taxonomy essentially follows the scheme for extant coccolithophores of Young *et al*. (2003) and, for the extinct taxa, the scheme of Young & Bown (1997). All new taxonomic names are derived from Latin and the meaning is given in each case. Range information is given for stratigraphic distributions in the Tanzanian sites. Morphometric data are given for all new taxa. Only bibliographic references not included in Perch-Nielsen (1985), Bown (1998) or Jordan *et al*. (2004) are included in the reference list. The following abbreviations are used: SEM – scanning electron microscope, LM – light microscope, XPL cross-polarised light, PC – phase-contrast illumination, L – length, H – height, W – width, D – diameter. Type material and images are stored in the Department of Earth Sciences, University College London.

The nannofossil taxa from TDP Site 14 are illustrated in Plates 1-12. The SEM images are reproduced at variable magnifications, but a 1μm scale-bar is provided beside each image, unless otherwise noted (only the *Braarudosphaera* plate has a number of 5μm scale-bars). The LM images are reproduced at constant magnification (approx. x2180) and a 1μm scale-bar is provided beside at least one of the images on each plate. The sample information is provided using the following notation: Core (3m lengths)-Section (1m subdivisions of each core), depth in section in cm, for example, 4-1, 60cm is TDP Site 14, Core 4, Section 1, at a depth of 60cm and represents a subsurface depth of 9.6m (see Pearson *et al*., 2004, for details of drilling methods). When the sample is from either TDP Site 7 or 16, where two holes were drilled, then 'A' or 'B' is added as a prefix, for example, 16B/22-2, 9cm.

PLACOLITH COCCOLITHS

Order ISOCHRYSIDALES **Paascher, 1910**

Family **PRINSIACEAE** Hay & Mohler, 1967 emend. Young & Bown, 1997

Genus *Toweius* Hay & Mohler, 1967

Pl.1, figs 1-21. **Remarks**: The dominant *Toweius* species at TDP Site 14 is *T. pertusus*, a name applied here to small- to medium-sized, elliptical to subcircular forms with finely-perforate central-area grills, where the perforations are small and may be difficult to resolve in the LM. SEM observations show that this grouping contains a high degree of variability, in terms of the grill structure and coccolith size and shape (see cluster in Pl.1, fig.1). This is perhaps not surprising, considering the subtle and/or distinct morphological variability that is observed in the more recent descendant placolith groups, such as *Gephyrocapsa* and *Emiliania*; like those groups, this likely represents true biological diversity (Bollmann, 1997; Geisen *et al*., 2004). In the larger species, *T. eminens* and *T. occultatus*, the central grills comprise coarse distal perforations and more delicate proximal nets (Pl.1, figs 13-16), a feature also seen in the closely-allied Family Noelaerhabdaceae.

Toweius eminens (Bramlette & Sullivan, 1961) Perch-Nielsen, 1971
Pl.1, figs 13-16
Toweius occultatus (Locker, 1967) Perch-Nielsen, 1971
Pl.1, fig.20

Toweius pertusus (Sullivan, 1965) Romein, 1979
Pl.1, figs 1-12. **Remarks**: See *Toweius* remarks above.

Toweius rotundus Perch-Nielsen *in* Perch-Nielsen *et al*., 1978
Pl.1, figs 17-19
Toweius serotinus Bybell & Self-Trail, 1995
Pl.1, fig.21

Family **NOELAERHABDACEAE** Jerkovic, 1970 emend. Young & Bown, 1997

Cyclicargolithus? *luminis* (Sullivan, 1965) Bukry, 1971
Pl.1, fig.22

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

Family **COCCOLITHACEAE** Poche, 1913 emend. Young & Bown, 1997

Coccolithus pelagicus (Wallich, 1877) Schiller, 1930
Pl.2, figs 1-8. **Remarks**: *C. pelagicus* shows a high degree of morphological variability, most basically in coccolith size (at this site, ranging from 3.5 to 12.0μm), but also in outline (elliptical to subcircular), and size of the central opening. The well-preserved specimens from the Kilwa Group also commonly exhibit delicate central-area axial crosses (Pl.2, figs 5, 6), which are not visible in LM. This morphology is similar, or possibly identical, to the 'species'

Cruciplacolithus tenuiforatus, described from the Upper Miocene (Clocchiatti & Jerkovic, 1970). As with the modern *Coccolithus*, now considered to represent at least two biological species or subspecies, this coccolith variability most likely reflects true biological diversity (*e.g.* Geisen *et al.*, 2004). The fossil species concept therefore likely represents a plexus of several species, with only the more obviously different morphotypes having been separately distinguished, *e.g.* circular (*Coccolithus formosus* (Kamptner, 1963) Wise 1973), or very large forms (*Coccolithus eopelagicus* (Bramlette & Riedel, 1954) Bramlette & Sullivan, 1961 and *miopelagicus* Bukry, 1971).

Coccolithus bownii Jiang & Wise, 2007

Pl.2, figs 9-11. **Description**: Medium- to large-sized, elliptical to subcircular placolith coccoliths with a broad, open central area that may be spanned by a fragile axial cross (see Pl.2, fig.9). The LM image comprises a wide, dark outer cycle and a narrow, bright inner cycle. The LM image is typical of *Coccolithus*, but the central area is wider than in *C. pelagicus*, and the inner cycle is narrower than in *C. foraminis* Bown, 2005 and *C. latus* Bown, 2005. **Remarks**: At TDP Site 14, this species is often the dominant coccolith within the PETM assemblages, and appears to be restricted to the CIE interval, hence it is considered a PETM 'excursion species'. It was described from Demerara Rise (Jiang & Wise, 2007), but probably has a widespread distribution that has been obfuscated by inconsistent taxonomy, having been called various different names, for example, *Markalius apertus* Perch-Nielsen, 1979; *Ericsonia subpertusa* Hay & Mohler, 1967, *Coccolithus subpertusus* (Hay & Mohler, 1967) (*e.g.* Jiang & Wise, 2006; Agnini *et al.*, 2007; Knox *et al.*, 2003). **Occurrence**: PETM interval; TDP Sites 14, 16A and 16B.

Coccolithus pauxillus nom. nov. pro *Coccolithus minimus* Bown, 2005 *non* Kamptner, 1963

Coccolithus minimus Bown, 2005, p.27, pl.3, fig.13 (Bown, P.R. 2005. *J. Nannoplankton Research*, **27**: 21-95) is a later homonym of *Coccolithus minimus* Kamptner (Kamptner, E. 1963, figs 14a, b. *Naturhistorisches Museum in Wien, Annalen*, **66**: 139-204). *Coccolithus pauxillus* is here proposed as a replacement for *Coccolithus minimus* Bown, 2005.

Not figured. **Derivation of name**: From '*pauxillus*', meaning 'small', referring to the small size of this *Coccolithus* species. **Original diagnosis**: Small (<5μm), circular *Coccolithus* coccoliths with a narrow, open central-area.

Ericsonia robusta (Bramlette & Sullivan, 1961) Edwards & Perch-Nielsen, 1975

Pl.2, figs 12, 13, 15, 16. **Remarks**: The large and small forms of this taxon appear to be stratigraphically distinct. The large form (>6μm) has a last occurrence in the latest Paleocene (Romein, 1979; Raffi *et al.*, 2006), the small morphotype continues into the Eocene (pers obs., 2008).

Ericsonia staerkeri Bown, 2005

Pl.2, fig.14

Coccolithus sp.

Pl.2, figs 17-19. **Remarks**: The first appearance of the circular species *Coccolithus formosus* is typically cited as Lower Eocene, but near-circular coccoliths of *Coccolithus* are found in the Upper Paleocene at TDP Site 14. There are also subcircular *Coccolithus*-like coccoliths with wide central-areas (Pl.2, figs 18, 19) that are similar in appearance to *Ericsonia*.

Campylosphaera dela (Bramlette & Sullivan, 1961) Hay & Mohler, 1967

Pl.3, figs 1-3

Campylosphaera differta sp. nov.

Pl.3, figs 4, 6. **Derivation of name**: From '*differta*', meaning 'full', referring to the filled central-area of these placolith coccoliths. **Diagnosis**: Medium to large, elliptical to oblong *Campylosphaera*, with a relatively narrow central-area filled with broad cross-bars. **Differentiation**: Distinguished from other *Campylosphaera* species by the broad cross-bars that fill the central area, and the bright inner cycle is reduced. **Dimensions**: L = 6.8-5.8μm. **Holotype**: Pl.3, fig.4. **Paratype**: Pl.3, fig.6. **Type locality**: TDP Site 14, Pande, Tanzania. **Type level**: Upper Paleocene, Sample TDP14/4-1, 60cm (NP9). **Occurrence**: NP9b-10; TDP Sites 3, 7A, 7B, 8, 14, 16A, 16B.

Campylosphaera eroskayi (Varol, 1989) Bown, 2005

Pl.3, fig.5

Cruciplacolithus latipons Romein, 1979

Pl.3, fig.7

Cruciplacolithus frequens (Perch-Nielsen, 1977) Romein, 1979

Pl.3, fig.9

Cruciplacolithus inseadus Perch-Nielsen, 1969

Pl.3, figs 10-14 and Figures 2, 3. **Remarks**: Described from the Danian of Denmark, but also figured from the Danian of Alabama (Bramlette & Martini, 1964) and Upper Eocene of JOIDES Hole 5 (Roth, 1970, as *Sollasites tardus*), but rarely documented since. This placolith has a distinctive central-area grill that is identical in form to the Mesozoic *Sollasites lowei* (Bukry, 1969), but also the Jurassic murolith coccolith *Vacherauvillius mirus* Goy, 1981, undescribed Paleogene muroliths (pers. obs., 2008) and extant pappospheraceans (*e.g.* Young *et al.*, 2003, pl.35, figs 7-9), indicating that this grill-architecture occurs across biologically-distant taxonomic groups. Although it has not been distinguished in the LM, *C. inseadus* is consistently observed in the SEM throughout the Paleocene-Oligocene Kilwa Group samples (*e.g.* Figure 3).

Cruciplacolithus primus Perch-Nielsen, 1977

Pl.3, fig.15 and Figure 2. **Remarks**: Although *Crucipla-*

colithus coccoliths are rarely documented in rocks younger than Late Paleocene, there is an extant species, *C. neohelis,* which is comparable in coccolith and coccosphere morphology to *C. primus*, which was an early species of the genus that first appeared in the Danian (this similarity was initially noted by the describing authors, McIntyre & Bé, 1967). Both taxa are characterised by small, elliptical placolith coccoliths with axial cross-bars and reticulate grills, although the grills are only seen in the Paleocene forms when the preservation is excellent (*e.g.* see Mai *et al*., 1997, pl.5, fig.5). *Cruciplacolithus* coccoliths are consistently present in the Eocene (LM) of the Kilwa Group, and various different species have been observed in the SEM (see *C. inseadus*, above, and Figure 2). It should be noted that *Bramletteius serraculoides* Gartner, 1969 is essentially a *C. primus*-like coccolith with a diagnostic sail-like 'spine', and it can be a common component of Middle Eocene to Early Oligocene assemblages, thus further supporting the extended range of the *Cruciplacolithus* group. The *Cruciplacolithus* specimen shown in Pl.3, fig.15 is very similar to modern *C. neohelis* (McIntyre & Bé, 1967) Reinhardt, 1972 and suggests that the Eocene to Neogene ghost-range that currently exists for *Cruciplacolithus* is a fossil record artefact due to the fragility of the post-Paleocene forms or, alternatively, reflects a significant switch in ecology to the coastal strategy that is a feature of the extant species (see also discussion in Medlin *et al*., 2008). Miocene occurrences of *C. neohelis* in Tanzania further support this view (pers obs., 2008).

Chiasmolithus bidens (Bramlette & Sullivan, 1961) Hay & Mohler, 1967
Pl.3, figs 16, 17
Chiasmolithus californicus (Sullivan, 1964) Hay & Mohler, 1967
Pl.3, figs 19, 20
Chiasmolithus consuetus (Bramlette & Sullivan, 1961) Hay & Mohler, 1967
Pl.3, fig.18
Chiasmolithus nitidus Perch-Nielsen, 1971
Pl.3, figs 21, 22

Genus *Craticullithus* gen. nov.
Pl.4, figs 1-15. **Type species**: *Craticullithus cancellus* sp. nov. **Derivation of name**: From '*craticula*', meaning 'grill', referring to the distinctive central-area structures of these placolith coccoliths, and '*lithus*', meaning 'stone'.. **Diagnosis**: Placolith coccoliths with a wide central area typically spanned by multi-element, lattice-like grills or imperforate plates. The distal shield elements show distinctly kinked and stepped sutures, and the rim structure in general appears to be coccolithacean (*i.e.* typical of the Family Coccolithaceae), although the centro-distal cycle is variably developed. The rim and central structures are similar to those of *Cruciplacolithus*, and so this genus is placed within the Family Coccolithaceae, although their rim structure is also comparable with coccoliths currently classified within the Calcidiscaceae.

Craticullithus cancellus sp. nov.
Pl.4, figs 1-3. **Derivation of name**: From '*cancellus*', meaning 'lattice', referring to the diagnostic grill that spans the central area of this placolith coccolith. **Diagnosis**: Medium- to large-sized, elliptical placolith coccoliths with broad central-areas spanned by lattice-like grills that are dominated by transverse bars. The distal shield is formed from elements with distinctly kinked and stepped sutures, and the proximal shield appears to be unicyclic and formed from elements joined along strongly clockwise-twisting sutures. Around 12-25 lath-like bars make up the central grill, with one central, longitudinal bar, several smaller longitudinal bars, and multiple transverse bars forming the rest of the structure. The coccoliths have not been unequivocally observed in the LM, but they may correspond to low-birefringence placoliths with open central areas, the central-area laths being too small or non-birefringent to be visible (*e.g.* Pl.4, fig.7). **Differentiation**: One coccosphere has been found which shows consistent central-area morphology across the sphere, suggesting that the similar morphologies described below do represent separate morphospecies. The shields, in general, are similar to *Cruciplacolithus* coccoliths, but with more complex central-area grills and a reduced centro-distal cycle. It is notable, however, that several *Cruciplacolithus* species with more complex central areas have been rarely documented, *e.g. C. inseadus* (see above) and *C. filigranus* (Mai, 2001), both originally from the Danian, but both species have been found in the Upper Paleocene and Eocene of the Kilwa Group (*e.g.* Pl.3, figs 10-14 and Figure 2). The presence of these forms with dissolution-prone, delicate central grills is therefore most likely highly sensitive to preservation state. **Dimensions**: L = 3.7-5.9μm. **Holotype**: Pl.4, fig.1. **Paratypes**: Pl.4, figs 2, 3. **Type locality**: TDP Site 14, Pande, Tanzania. **Type level**: Upper Paleocene, Sample TDP14/9-1, 20cm (NP9). **Occurrence**: NP9; TDP Site 14, 16B.

Craticullithus clathrus sp. nov.
Pl.4, figs 4, 5. **Derivation of name**: From '*clathrus*', meaning 'lattice or bars', referring to the grill that spans the central area of these coccoliths. **Diagnosis**: Medium- to large-sized, elliptical placolith coccoliths with broad central areas spanned by lattice-like grills that are dominated by longitudinal bars. The distal-shield elements show distinctly kinked and stepped sutures. Around 12 lath-like bars make up the central grill, with one to four central, transverse bars, and three to five longitudinal bars, forming the rest of the structure. The coccoliths have not been unequivocally observed in the LM (see comments for *C. cancellus*). **Differentiation**: Similar to *C. cancellus*, but with a central grill dominated by longitudinal bars. **Dimensions**: L = 4.0-5.0μm. **Holotype**: Pl.4, fig.4. **Paratype**: Pl.4, fig.5. **Type locality**: TDP Site 16B, Pande, Tanzania. **Type level**: Upper Paleocene, Sample TDP16B/12-2, 9cm (NP9). **Oc-**

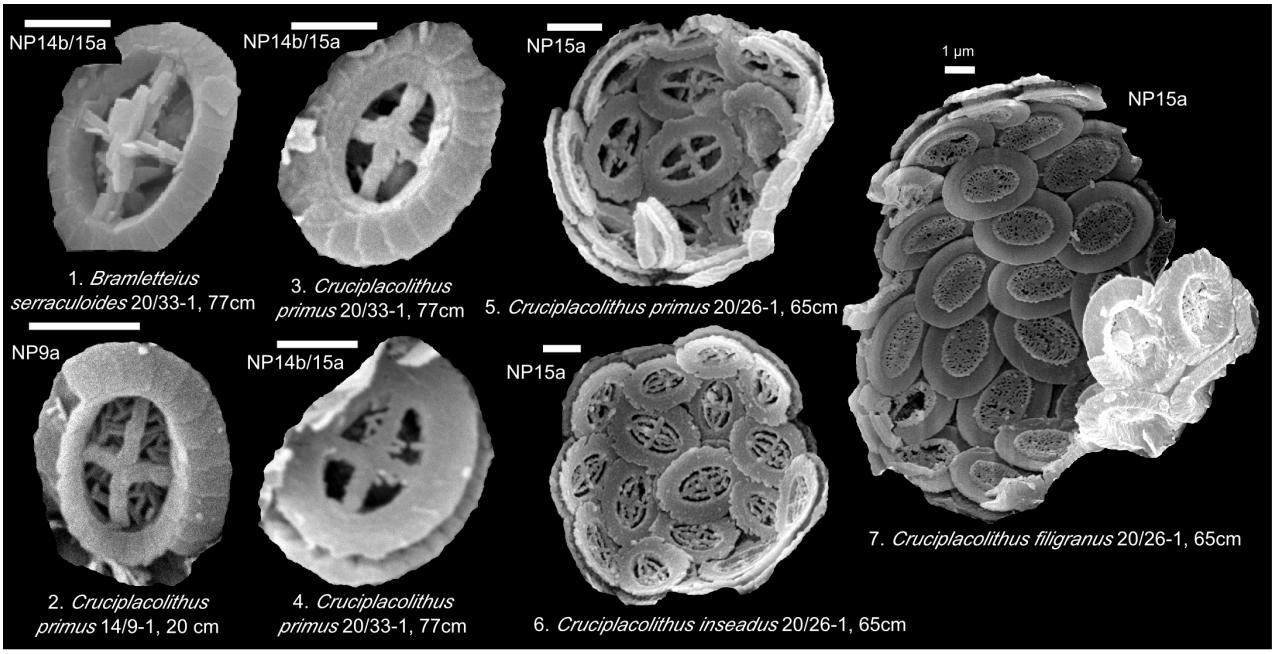

Figure 2: SEM images of *Cruciplacolithus* and *Bramletteius* coccoliths from the Kilwa Group of Tanzania (TDP Sites 14 and 20)

currence: NP9; TDP Site 16B.

Craticullithus cf. *C. clathrus* sp. nov.

Pl 4, fig.6. **Remarks**: Like *C. clathrus*, but the central grill has only one transverse bar, and is therefore similar to the central structure of the Mesozoic *Sollasites horticus* Stradner *et al*., 1966. **Occurrence**: NP9; TDP Site 14.

Craticullithus lamina sp. nov.

Pl.4, figs 8-10. **Derivation of name**: From '*lamina*', meaning 'plate', referring to the granular structure which spans the central area of these coccoliths. **Diagnosis**: Medium- to large-sized, elliptical placolith coccoliths with broad central areas spanned by a plate formed from small, non-aligned, rectangular elements. The distal-shield elements show distinctly kinked and stepped sutures and there is no centro-distal cycle. The coccoliths have not been unequivocally observed in the LM (see comments for *C. cancellus* and questionable specimen Pl.4, fig.11). **Differentiation**: The rim structure is similar to other species of *Craticullithus*, but the central-area structure is an imperforate plate. The wide central area and lack of central-area perforations distinguishes them from *Clausicoccus* Prins, 1979 and *Hughesius* Varol, 1989. **Dimensions**: L = 7.0-7.7μm. **Holotype**: Pl.4, fig.8. **Paratype**: Pl.4, fig.9. **Type locality**: TDP Site 16B, Pande, Tanzania. **Type level**: Upper Paleocene, Sample TDP16B/12-2, 9cm (NP9). **Occurrence**: NP9; TDP Sites 14 and 16B.

Craticullithus? *cassus* (Bown, 2005) comb. nov.

Basionym: *Cruciplacolithus*? *cassus* Bown, 2005, p.28, pl.6, fig.1. (Bown, P.R. 2005. *J. Nannoplankton Research*, **27**: 21-95.)

Pl.4, figs 12, 13. **Remarks**: Medium-sized, elliptical placolith coccoliths with central areas spanned by a perforate plate. The distal shield appears to be bicyclic: the outer cycle elements are joined along distinctly kinked sutures; the inner cycle appears to have a smooth upper surface and the sutures are less clear, but are broadly radial. The central area is spanned by a perforate plate formed from small elements. The overall shape and appearance suggests that these coccoliths correspond to the *Cruciplacolithus*? *cassus* species described by Bown (2005) from LM images. As this species has a complex central-area grill and coccolithacean rim, the species is here recombined into the new genus *Craticullithus*. **Differentiation**: Similar to species of *Craticullithus*, but the distal shield is distinctly bicyclic. **Occurrence**: NP7-11; TDP Sites 3, 7A, 14, 19.

Craticullithus spp.

Pl.4, figs 14, 15. **Remarks**: Several less consistently observed *Craticullithus* coccoliths have the same rim structure, but differ in the details of the central-area grill.

Genus *Kilwalithus* gen. nov.

Pl.4, figs 19, 20 and Figure 3. **Type species**: *Kilwalithus cribrum* sp. nov. **Derivation of name**: From the Kilwa area (southern Tanzania), from where these coccoliths are described. **Diagnosis**: Placolith coccoliths, typically small (*c*.3μm), with a central area spanned by a finely-perforate net. The distal shield is typically bicyclic and the rim structure appears to be coccolithacean. The main distal shield elements are joined along kinked suture lines.

Kilwalithus cribrum sp. nov.

Pl.4, figs 19, 20 and Figure 3. **Derivation of name**: From '*cribrum*', meaning 'sieve', referring to the net that spans the central area of these coccoliths. **Diagnosis**: Small, el-

liptical placolith coccoliths with central areas spanned by a perforate net. The distal shield is bicyclic and the rim structure appears to be coccolithacean. **Remarks**: The coccoliths have not been unequivocally observed in the LM, presumably because of their small size (*c*.3μm or less), but they have been frequently observed in the SEM from the Upper Paleocene and Lower to Upper Eocene, often as intact coccospheres. In middle Eocene samples, the coccospheres are distinctly varimorphic, with apical and antapical coccoliths that have long distal processes (Figure 3). **Differentiation**: Similar rim stucture to *Cruciplacolithus* and *Craticullithus*, but the central-area structure is a perforate net. *Toweius* coccoliths of the same age also have perforate nets, *e.g*. *T. pertusus* (see above), however the *Kilwalithus* rim structure is not prinsiacean. **Dimensions**: L = 1.6-2.2μm. **Holotype**: Pl.4, fig.19. **Paratype**: Pl.4, fig.20. **Type locality**: TDP Site 16B, Pande, Tanzania. **Type level**: Upper Paleocene, Sample TDP16B/12-2, 9cm (NP9). **Occurrence**: NP9; TDP Sites 14, 16B.

Tetralithoides symeonidesii? Theodoridis, 1984

Pl.4, figs 16, 17. **Remarks**: Small, inconspicuous (in LM) placoliths with four-part central-area plates have been observed in the LM, and occasionally in the SEM, throughout the Kilwa Group (Upper Paleocene-Lower Eocene). These coccoliths are similar to *T. symeonidesii* described from the Miocene (Theodoridis, 1984) and the extant *T. quadrilaminata* (Okada & McIntyre, 1977) Jordan *et al*., 1993. The latter species is a lower photic zone taxon (Young & Andruleit, 2006).

Tetralithoides? sp.

Pl.4, fig.18. **Remarks**: Small placolith with a central-area plate that is similar in overall form to the 'narrow-rimmed placolith' group of Young *et al*. (2003, pl.32, especially the species *Calyptrosphaera sphaeroidea* HET).

Family **CALCIDISCACEAE** Young & Bown, 1997

Calcidiscus? sp.

Pl.3, fig.8. **Remarks**: Small, low-birefringence placoliths are occasionally seen in the Upper Paleocene of TDP Site 14. Other PETM studies have documented occurrences of *Biscutum* coccoliths (a Mesozoic genus), which may be comparable with the form shown here, but they have not been illustrated (Bralower, 2002; Gibbs *et al*., 2006a).

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

Pl.3, fig.23. **Remarks**: See Bown *et al*. (2006).

Umbilicosphaera bramlettei (Hay & Towe, 1962) Bown *et al*., 2006

Pl.3, fig.24. **Remarks**: See Bown *et al*. (2006).

Umbilicosphaera jordanii Bown, 2005

Pl.3, figs 25, 26. **Remarks**: See Bown *et al*. (2006).

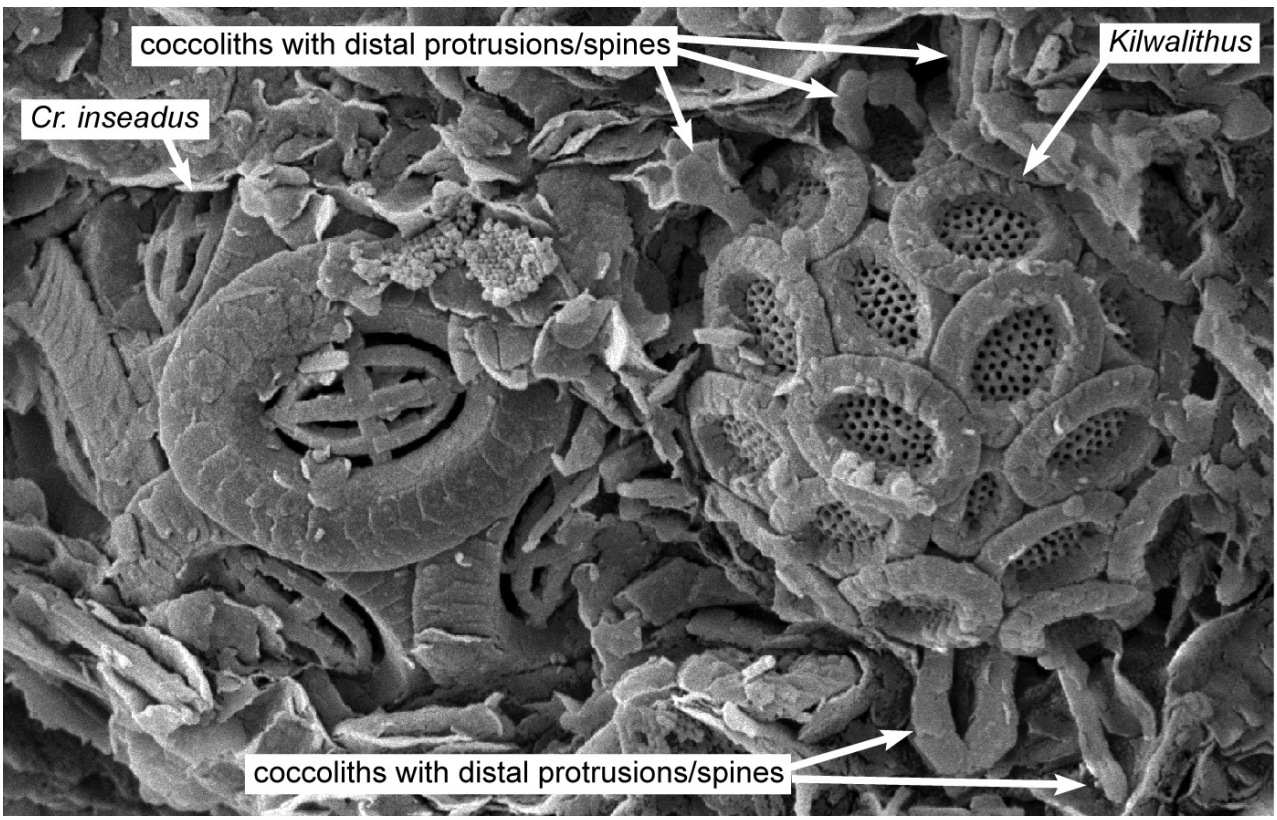

Figure 3: SEM image of *a Kilwalithus* coccosphere from TDP Site 13 (Sample TDP13/20-1, 40cm, Middle Eocene, NP15b). To the left is a coccosphere of *Cruciplacolithus inseadus*

PLACOLITHS OF UNCERTAIN AFFINITY (INCERTAE SEDIS)

Genus *Ellipsolithus* Sullivan, 1964
Pl.5, figs 1-10. **Remarks**: The placolith coccoliths of *Ellipsolithus* have a structure that is quite distinct from the principal Cenozoic placolith Orders Coccolithales and Isochrysidales. They comprise unicyclic distal shields built from numerous (>50) narrow elements joined along highly 'frilled' suture lines. The central area is spanned by perforate (*E. anadoluensis*) or imperforate (*E. macellus*) plates and may have additional bars (*E. distichus*). *E. anadoluensis* has elevated distal shields and is frequently observed in side view (Pl.5, figs 3, 5).

Ellipsolithus anadoluensis Varol, 1989
Pl.5, figs 1-5
Ellipsolithus bollii Perch-Nielsen, 1977
Pl.5, fig.7
Ellipsolithus distichus (Bramlette & Sullivan, 1961) Sullivan, 1964
Pl.5, figs 6, 8
Ellipsolithus macellus (Bramlette & Sullivan, 1961) Sullivan, 1964
Pl.5, figs 9, 10

MUROLITH COCCOLITHS

Mesozoic survivor muroliths

Order EIFFELLITHALES **Rood *et al*., 1971**

Family **CHIASTOZYGACEAE** Rood *et al*., 1973

Jakubowskia leoniae Varol, 1989
Pl.6, fig.2
Neocrepidolithus grandiculus Bown, 2005
Pl.6, fig.1
Staurolithites primaevus Bown, 2005
Pl.6, fig.3
Zeugrhabdotus sigmoides (Bramlette & Sullivan, 1961) Bown & Young, 1997
Pl.6, figs 4-6

Cenozoic muroliths

Order ZYGODISCALES **Young & Bown, 1997**

Family **PONTOSPHAERACEAE** Lemmermann, 1908

Pontosphaera exilis (Bramlette & Sullivan, 1961) Romein, 1979
Pl.6, figs 7-9
Pontosphaera plana (Bramlette & Sullivan, 1961) Haq, 1971
Pl.6, figs 10, 11
Pontosphaera versa (Bramlette & Sullivan, 1961) Sherwood, 1974
Pl.6, fig.12

Family **ZYGODISCACEAE** Hay & Mohler, 1967

Lophodolithus nascens Bramlette & Sullivan, 1961
Pl.6, figs 22-24
Neochiastozygus distentus (Bramlette & Sullivan, 1961) Perch-Nielsen, 1971
Pl.5, fig.17

Neochiastozygus imbriei Haq & Lohmann, 1975
Pl.5, figs 11-14. **Remarks**: *N. imbriei* is used here for small *Neochiastozygus* coccoliths that have asymmetric crossbars rotated from axial by 10-20˚. In the SEM, these coccoliths consistently show the presence of additional lateral bars and therefore resemble the Danian species *Chiastozygus ultimus* Perch-Nielsen, 1981, *Neochiastozygus denticulatus* (Perch-Nielsen, 1969) and *N. primitivus* Perch-Nielsen, 1981, which were informally grouped as the *Neochiastozygus* 'asymmetrical species' by van Heck & Prins (1987). *N. imbriei* is consistently documented through the Paleocene/Eocene boundary interval of the Kilwa Group and is a conspicuous species (~10% relative abundance) within the PETM interval. The similarity between these coccoliths and the Danian forms is intriguing, as quite a number of typically Danian taxa become conspicuous again around the PETM interval, including *Biantholithus*, *Neocrepidolithus*, *Markalius*, *Hornibrookina* and *Zeugrhabdotus sigmoides* (*e.g*. see Bybell & Self-Trail, 1995; Gibbs *et al*., 2006a, b; Angori *et al*., 2007). The cluster of specimens shown in Plate 5, fig.11 may represent a single collapsed coccosphere, and, if so, indicates varimorphism across the cell that includes changes in coccolith size and bar orientation.

Neochiastozygus junctus (Bramlette & Sullivan, 1961) Perch-Nielsen, 1971
Pl.5, figs 15, 16
Neochiastozygus pusillus Bown & Dunkley Jones, 2006
Pl.5, fig.19
Neochiastozygus rosenkrantzii (Perch-Nielsen, 1971) Varol, 1989
Pl.5, fig.18
Neococcolithes protenus (Bramlette & Sullivan, 1961) Black, 1967
Pl.5, fig.20
Zygodiscus cearae (Perch-Nielsen, 1977) Bown & Dunkley Jones, 2006
Pl.6, figs 19-21
Zygodiscus multiforus Bown & Dunkley Jones, 2006
Pl.6, fig.18
Zygodiscus plectopons Bramlette & Sullivan 1961
Pl.6, figs 15, 16

Zygodiscus cf. *Z. plectopons* Bramlette & Sullivan, 1961
Pl.6, fig.17. **Remarks**: Large, thick-rimmed specimens.

Zygodiscus sheldoniae Bown, 2005
Pl.6, figs 13, 14

Zygodiscus cf. *Z. sheldoniae* Bown, 2005
Pl.6, fig.25. **Remarks**: Large, thick rimmed specimens with blocky bar.

Order SYRACOSPHAERALES **Hay, 1977 emend. Young *et al*., 2003**

Family **CALCIOSOLENIACEAE** Kamptner, 1927

Calciosolenia aperta (Hay & Mohler, 1967) Bown, 2005
Pl.7, figs 22-24

Calciosolenia fossilis (Deflandre *in* Deflandre & Fert, 1954) Bown *in* Kennedy *et al*., 2000
Pl.7, figs 25-27. **Remarks**: Morphologically comparable with the extant *C. brasiliensis* (Lohmann, 1919), but fossil specimens have tended to be classified as *Calciosolenia* (or *Scapholithus*) *fossilis*. The extant species show considerable varimorphism across their coccospheres, and there is evidence of similar variability in the Kilwa Group (*e.g.* Bown *et al*., 2008, fig.3K).

Family **RHABDOSPHAERACEAE** Haeckel, 1894

Genus *Blackites* Hay & Towe, 1962
Pl.7, figs 1-21. **Remarks**: *Blackites* diversity comprises around eight species in the Paleocene/Eocene boundary interval of TDP Site 14, although this rises considerably in the Middle and Late Eocene of the Kilwa Group (*e.g.* Bown, 2005; Dunkley Jones *et al*., 2009). If the cluster of coccoliths shown below (Figure 4) represents a collapsed coccosphere, then this indicates considerable morphological variability across the cell, ranging from typical *morionum*-like forms with domed spines, through *Algirosphaera*-like coccoliths with low-lying central processes, to *Syracosphaera*-like coccoliths with multi-lath central-area grills. This is somewhat consistent with observations of extant Rhabdosphaeraceae, which frequently exhibit strong coccosphere vari- or polymorphism, which is mostly expressed in spine length, or spine presence or absence (Kleijne, 1992; Young *et al*., 2003).

Blackites gamai Bown, 2005
Pl.7, fig.5
Blackites herculesii (Stradner, 1969) Bybell & Self-Trail, 1997
Pl.7, fig.8
Blackites morionum (Deflandre *in* Deflandre & Fert, 1954) Varol, 1989
Pl.7, figs 1-4
Blackites perlongus (Deflandre, 1952) Shafik, 1981
Pl.7, figs 6, 7, 9, 10
Blackites turritus Bown, 2005
Pl.7, figs 12-14

Blackites sp. A
Pl.7, fig.11. **Remarks**: *Blackites* with a tall, tapering spine that has a collar at its base. Similar to *Blackites creber* (Deflandre *in* Deflandre & Fert, 1954), but the rim is typical of the *B. morionum* group, rather than the *B. gladius* group (see Bown, 2005).

Blackites sp. B
Pl.7, fig.20. **Remarks**: A small *Acanthoica*-like coccolith (*i.e.* lacking the multicyclic spines of typical *Blackites*) that has a rim, radial cycle and lamellar cycle that forms a low cone (see terminology in Young *et al*., 2003 and Dunkley Jones *et al*., 2009). The specimen figured was found amongst typical *Blackites* coccoliths and may represent just one of a variety of morphologies that was present on these Paleocene rhabdolith cells.

Blackites sp. C
Pl.7, fig.21. **Remarks**: A *Blackites*-like coccolith with a spine that extends from a central grill formed from numerous near-radial, small laths.

Blackites bases
Pl.7, figs 15-19. **Remarks**: *Blackites* coccoliths with low bosses/spines or no spines. They are rare in the TDP Site 14 material, but become common in the Middle Eocene, and names exist for some of these forms, *e.g.* *Blackites amplus* Roth & Hay *in* Hay *et al*., 1967 and *Blackites furvus* Bown & Dunkley Jones, 2006. It is possible that these 'bases' represent coccoliths from which the spines have been detached, or simply spineless forms that occurred alongside spinose forms on varimorphic coccopheres.

HOLOCOCCOLITHS

Family **CALYPTROSPHAERACEAE** Boudreaux & Hay, 1967

The higher taxonomy of holococcoliths is problematical due to their generalised morphologies, and in light of recent advances demonstrating that many extant holococcolithophores have a separate heterococolith-bearing life-cycle equivalent (*e.g.* Geisen *et al*., 2004). The taxonomy applied here attempts to maintain consistency with previous taxonomic monographs (*e.g.* Perch-Nielsen, 1985; Aubry, 1988), applying established generic names where possible, and for the most part inferring only limited phylogenetic information.

Clathrolithus ellipticus Deflandre *in* Deflandre & Fert, 1954
Pl.8, figs 1-9. **Remarks**: Used here for large, solid, elliptical and 'C'-shaped holococcoliths that have honeycomb-like ridges on one surface. These coccoliths have complex, three-dimensional structure and exhibit high variability, including plate-like and domed forms. In the LM, they are distinguished by the diagnostic raised ridges.

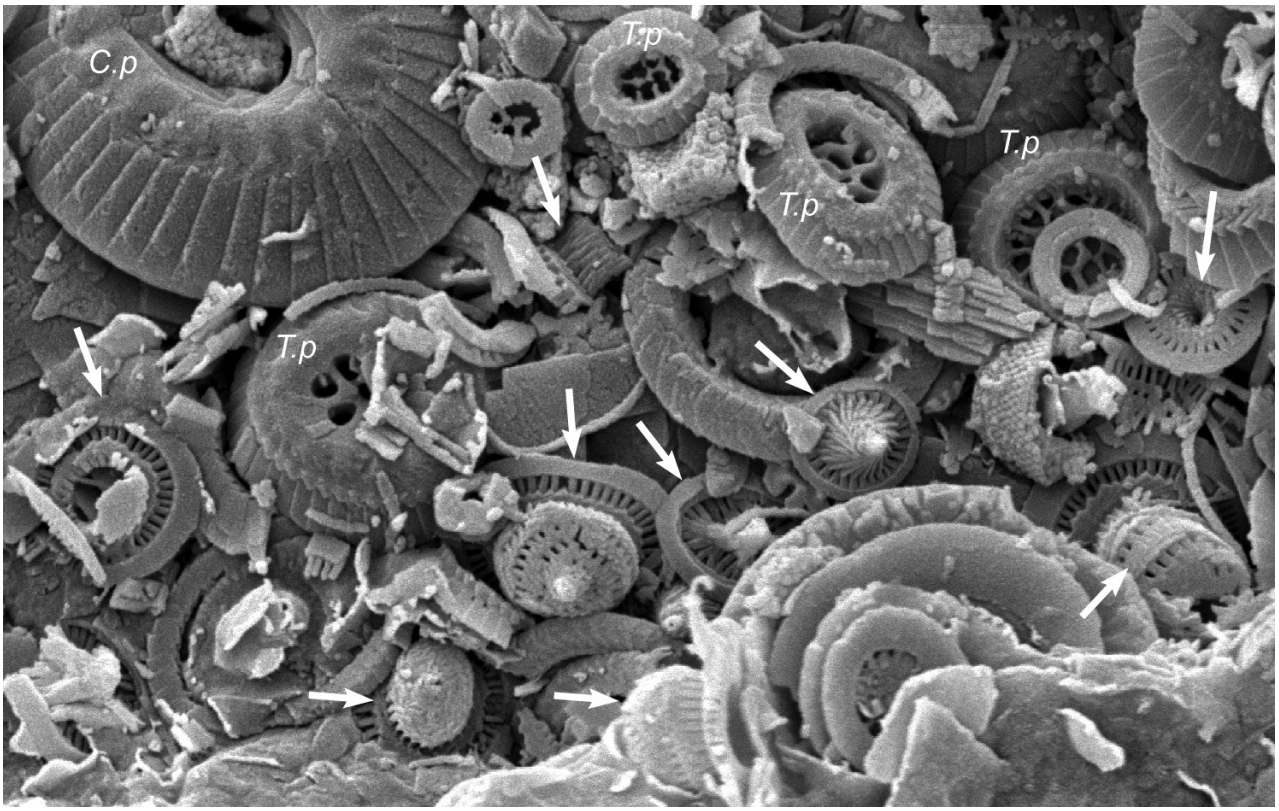

Figure 4: SEM image of a cluster of *Blackites* coccoliths that may represent a collapsed, variomorphic coccosphere. From TDP Site 14 (Sample TDP14/4-2, 20cm, NP9b)

Holodiscolithus geisenii Bown, 2005
Pl.8, fig.14
Holodiscolithus macroporus (Deflandre *in* Deflandre & Fert, 1954) Roth, 1970
Pl.8, figs 15, 16
Holodiscolithus solidus (Deflandre *in* Deflandre & Fert, 1954) Roth, 1970
Pl.8, figs 11-13
Semihololithus biskayae Perch-Nielsen, 1971
Pl.8, figs 17-20
Semihololithus cf. *S. biskayae* Perch-Nielsen, 1971
Pl.8, fig.22
Semihololithus dimidius Bown, 2005
Pl.8, fig.21
Semihololithus kanungoi Bown, 2005
Pl.8, fig.23
Zygrhablithus bijugatus (Deflandre *in* Deflandre & Fert, 1954) Deflandre, 1959 ssp. *bijugatus*
Pl.8, figs 24-26

Zygrhablithus bijugatus (Deflandre *in* Deflandre & Fert, 1954) Deflandre, 1959 ssp. *maximus* ssp. nov.
Pl.8, figs 27-29. **Derivation of name**: From '*maximus*', meaning 'large', referring to the tall spine that characterises this holococcolith. **Diagnosis**: *Z. bijugatus*-like holococcoliths with tall spines (height >2x width) that display relatively low birefringence in XPL, although brighter ridges are present on most specimens. **Differentiation**: *Z. bijugatus* is currently differentiated into forms with moderately-sized spines (*Z. bijugatus bijugatus*), short spines (*Z. bijugatus nolfii* Steurbaut, 1990; *Z. sileensis* Varol, 1989), and spines with lateral horns (*Z. bijugatus cornutus* (Deflandre *in* Deflandre & Fert, 1954)). *Z. bijugatus maximus* has tall spines, which are rather dark in XPL and may be restricted in stratigraphic range to the uppermost Paleocene and lowest Eocene. **Dimensions**: Coccolith base L = 4.5-5.5μm; H = 11.25-17.0μm. **Holotype**: Pl.8, fig.27. **Paratypes**: Pl.8, figs 28, 29. **Type locality**: TDP Site 14, Pande, Tanzania. **Type level**: Upper Paleocene, Sample TDP14/9-1, 20cm (NP9). **Occurrence**: NP9; TDP Site 14, 16B.

HAPTOPHYTE NANNOLITHS

Family **BRAARUDOSPHAERACEAE** Deflandre, 1947

Braarudosphaera bigelowii (Gran & Braarud, 1935) Deflandre, 1947
Pl.9, figs 1, 5, 6, 8, 9. **Remarks**: The *B. bigelowii* liths show a wide range of sizes, but the large forms are especially conspicuous, and are described separately below. The thickness of the liths is also variable, for example, compare Pl.9, figs 5 and 6.

Braarudosphaera perampla sp. nov.
Pl.4, figs 2-4, 7, 10. **Derivation of name**: From '*perampus*', meaning 'very large', referring to the size of these pentaliths. **Diagnosis**: Large (>12μm) *Braarudosphaera* with pentaliths that have slightly rounded corners and con-

vex upper surfaces. The convexity is due to the decreasing width of the constituent laminae. The laminae also change shape from stellate at the shortest width and most distal, to straight-edged at the maximum width. **Dimensions**: Maximum lith diameter L = 12.0-20.7μm. **Holotype**: Pl.9, fig.7. **Paratypes**: Pl.9, figs 4, 10. **Type locality**: TDP Site 16B, Pande, Tanzania. **Type level**: Upper Paleocene, Sample TDP16B/12-2, 9cm (NP9). **Occurrence**: NP6-23; TDP Sites 1, 2, 3, 6, 7, 12, 13, 14, 16B, 19.

Pentalith side views
Pl.9, figs 11-13. **Remarks**: Pentaliths that are equal, or greater, in height than width, and therefore often seen in side view in the LM, occur in both *Braarudosphaera* and *Micrantholithus* (also the younger genus, *Pemma*). These forms appear to be less common in *Braarudosphaera*, although moderately thick liths are commonly seen in *B. bigelowii* and larger types at Site TDP 14 (*e.g.* Pl.9, figs 2-4, 6, 7). The specimens on Pl.9 (figs 11-13) are likely *Braarudosphaera*, as these are the only large, robust pentaliths seen in this material.

Micrantholithus attenuatus Bramlette & Sullivan, 1961
Pl.9, fig.17
Micrantholithus bramlettei Deflandre *in* Deflandre & Fert, 1954
Pl.9, fig.15
Micrantholithus breviradiatus Bown, 2005
Pl.9, fig.14
Micrantholithus discula (Bramlette & Riedel, 1954) Bown, 2005
Pl.9, figs 18, 19
Micrantholithus pinguis Bramlette & Sullivan, 1961
Pl.9, fig.16

EXTINCT NANNOLITHS

Order DISCOASTERALES **Hay, 1977 emend.**
Pls 10, 11. **Emended diagnosis**: Radially symmetrical nannoliths formed from one to several separate cycles of elements and including disc-like (discoasters), stellate (discoasters), cylindrical (fasciculiths, helioliths and sphenoliths) and conical (fasciculiths and sphenoliths) morphologies. **Remarks**: Hay (1977) described the Order Discoasterales as a broad taxonomic group that included most radial and stellate Mesozoic and Cenozoic nannoliths. The order is emended here to a narrower taxonomic concept that incorporates the type family, the Discoasteraceae, together with the other Paleocene radial nannolith groups, the Heliolithaceae, Fasciculithaceae and Sphenolithaceae, which originated within 4Myr of one another, and have common morphological features, suggesting phylogenetic affinity. This concept was also used in the classification of Young & Bown (1997).

Family **DISCOASTERACEAE** Tan, 1927

Discoaster anartios Bybell & Self-Trail, 1995
Pl.10, fig.17. **Remarks**: This species has been identified as a PETM excursion taxon, but specimens often appear to represent poorly-preserved *Discoaster salisburgensis* liths, with the ragged outline due to etching. Very rare within the PETM and post-PETM interval at TDP Site 14.

Discoaster binodosus Martini, 1958
Pl.11, figs 1, 2
Discoaster falcatus Bramlette & Sullivan, 1961
Pl.11, figs 4, 6
Discoaster cf. *D. falcatus* Bramlette & Sullivan, 1961
Pl.11, fig.7
Discoaster lenticularis Bramlette & Sullivan, 1961
Pl.10, fig.19
Discoaster cf. *D. lodoensis* Perch-Nielsen, 1981
Pl.11, fig.11
Discoaster mahmoudii Perch-Nielsen, 1981
Pl.11, figs 9, 10
Discoaster mediosus Bramlette & Sullivan, 1961
Pl.11, fig.3
Discoaster multiradiatus Bramlette & Riedel, 1954
Pl.10, figs 11-14
Discoaster salisburgensis Stradner, 1961
Pl.10, figs 15, 16, 18
Discoaster splendidus Martini, 1960
Pl.11, fig.8

Family **FASCICULITHACEAE** Hay & Mohler, 1967

Fasciculithus Bramlette & Sullivan, 1961
Pl.11, figs 12-28. **Remarks**: The single genus within this family exhibits a high degree of morphological variability and this is reflected in a plethora of published species names. Here, I recognise four basic morphogroups:
***involutus* group**: cylindrical forms with a convex upper surface – *F. involutus*;
***alanii* group**: tapering forms – *F. alanii* (narrow and strongly tapered, with straight or concave sides), *F. thomasii* (broad and tapering), *F. lilianiae* (tapered with straight or convex sides and a distinct 'shoulder' on the upper surface);
***schaubii* group**: forms with a discrete column and distal tapering cone - *F. richardii* (wide column, which may broaden distally to angular terminations), *F. schaubii* (narrow, tapering column);
***lobus* group**: tapering forms with a concave upper surface - *F. lobus* sp. nov.

Fasciculithus alanii Perch-Nielsen, 1971
Pl.11, figs 13, 14
Fasciculithus involutus Bramlette & Sullivan, 1961
Pl.11, figs 18, 20
Fasciculithus lilianiae Perch-Nielsen, 1971
Pl.11, figs 16, 17
Fasciculithus richardii Perch-Nielsen, 1971
Pl.11, figs 25-27

Fasciculithus lobus sp. nov.

Pl.11, figs 21-23. **Derivation of name**: From '*lobus*', meaning 'lobe', referring to the lobate morphology of this nannofossil. **Diagnosis**: Medium-sized fasciculith with concave top and bottom surfaces and a tapering column that has at least two deep indentations, resulting in a lobate outline. Overall, it has a rather angular, blocky outline. **Differentiation**: Distinguished from most other fasciculiths by the concave top/distal surface, but also by its sloping and strongly lobate column. **Remarks**: At TDP Site 14, this taxon appears to be restricted to the PETM interval and may represent an excursion species. **Dimensions**: D = 5.2-6.5μm; H = 5.5-6.0 μm. **Holotype**: Pl.11, fig.21. **Paratype**: Pl.11, fig.22. **Type locality**: Upper Paleocene, Sample TDP14/5-1, 20cm (NP9, PETM CIE). **Occurrence**: NP9; TDP Site 14.

Fasciculithus thomasii Perch-Nielsen, 1971
Pl.11, fig.15
Fasciculithus tonii Perch-Nielsen, 1971
Pl.11, fig.12
Fasciculithus schaubii Hay & Mohler, 1967
Pl.11, fig.28
Fasciculithus sidereus Bybell & Self-Trail, 1995
Pl.11, fig.24

Family **HELIOLITHACEAE** Hay & Mohler, 1967

Pl.10, figs 1-10. **Remarks**: Group of nannoliths closely allied to the discoasters, and probably transitional between typically *V/R* heterococcolith morphology and the more derived, single-crystal-unit form of the latter group. The taxonomy of the group is rather poor at both generic and species levels, and high-quality images of the taxa are lacking in the literature. Typically, the genus *Heliolithus* Bramlette & Sullivan, 1961 is used for taxa that have birefringent images, *Bomolithus* for forms with a single, birefringent cycle that is narrower than the diameter of the nannolith (although simply the possession of three cycles, not the crystallography, has been used as a diagnostic criterion by some, *e.g*. Romein, 1979), and both *Discoaster* and *Bomolithus* have been used for taxa where the birefringent cycle is narrow. The genus *Discoasteroides* Bramlette & Sullivan, 1961 has also been used for this latter group, but its type species is *Discoaster keupperi*, which is a relatively typical discoaster, albeit with a tall, robust boss. There appears to be an evolutionary/stratigraphic trend, first towards reduction in the width of the birefringent (*R*-unit) cycle (in *Bomolithus*) and, second, towards loss of cycles, until only one, the *V*-unit, remains (in *Discoaster*) (Figure 5). Here, *Bomolithus* is used for taxa where the birefringent cycle is narrower than the diameter of the nannolith, but I also include a new species, *Bomolithus aquilus*, where several cycles are present, but they are non-birefringent.

Bomolithus aquilus sp. nov.

Pl.10, figs 1-4. **Derivation of name**: From '*aquilus*', meaning 'dark-coloured', referring to the LM appearance of this nannofossil. **Diagnosis**: Medium-sized, circular heliolith with at least two discernible cycles in the LM, both of which are dark in XPL. The cycles comprise around 40 visible radial elements, and the central area is typically closed. **Differentiation**: Distinguished from other *Heliolithus* and *Bomolithus* species by the absence of a birefringent cycle. **Dimensions**: D = 8.2-9.0μm. **Holotype**: Pl.10, fig.2. **Paratype**: Pl.10, fig.3. **Type locality**: TDP Site 14, Pande, Tanzania. **Type level**: Upper Paleocene, Sample TDP14/4-2, 20cm (NP9b). **Occurrence**: NP9b, above the PETM CIE; TDP Sites 7, 14.

Bomolithus elegans Roth, 1973
Pl.10, fig.5
Bomolithus megastypus (Bramlette & Sullivan, 1961) comb. nov.
Pl.10, figs 6, 7

Basionym: *Discoasteroides megastypus* Bramlette & Sullivan, 1961, p.163, pl.13, fig.14. (Bramlette, M.N. & Sullivan, F.R. 1961. *Micropaleontology*, **7**: 129-188.)

Bomolithus supremus Bown & Dunkley Jones, 2006
Pl.10, figs 8?, 9, 10

SMALL COCCOLITHS OF UNCERTAIN AFFINITY (INCERTAE SEDIS)

Gladiolithus flabellatus (Halldal & Markali, 1955) Jordan & Chamberlain, 1993

Pl.12, figs 1-4. **Remarks**: Disaggregated tube coccoliths, lepidoliths and complete collapsed coccospheres are consistently present throughout the Paleogene Kilwa Group. The morphology, and several new Paleogene species, of *Gladiolithus* are described in Bown *et al*. (2009). **Occurrence**: NP6-23, all Paleogene TDP sites.

Murolith indet. 1

Pl.12, fig.5. **Remarks**: Miniscule to very small murolith coccoliths with high, narrow walls and central areas spanned by a granular plate with a central spine-base. Rare, but present in Upper Paleocene and Middle Eocene samples. **Occurrence**: NP9-21; TDP Sites 2, 12, 13, 14, 16B.

Murolith indet. 2

Pl.12, fig.6. **Remarks**: Miniscule to very small simple coccolith with a narrow rim, plain central-area plate and small central spine/boss. **Occurrence**: NP9; TDP Site 16B.

Murolith indet. 3

Pl.12, fig.7. **Remarks**: Miniscule to very small murolith coccolith with a narrow rim and a central-area plate made up of small, angular elements. **Occurrence**: NP9; TDP Site 16B.

Pocillithus spinulifer Dunkley Jones *et al*., 2009

Pl.12, fig.8. **Remarks**: Miniscule to very small murolith coccoliths with high, narrow walls and central areas

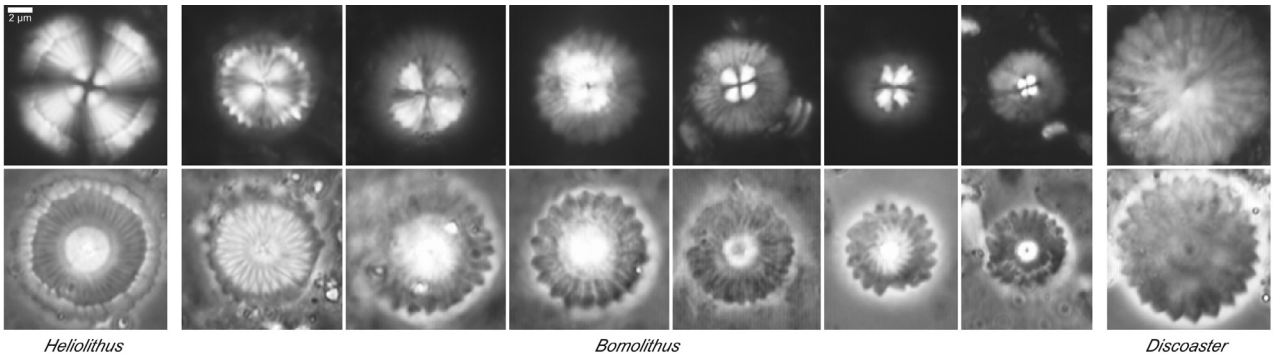

Figure 5: LM images (upper row XPL, lower row PC) representing the range of morphologies seen in the genera *Heliolithus* (two furthest left images), *Bomolithus*, and *Discoaster (*two furthest right images). Images from TDP Site 19 (NP6), except for last four on the right, which are from TDP Site 14 (NP9)

spanned by an axial cross bearing tall, hollow, near-parallel-sided spines. The outer rim cycle comprises non-imbricate elements (protoliths of Bown, 1987), and the spines are typically square in cross-section. The coccoliths have not been unequivocally observed in the LM, due to small size, but are consistently present in SEM samples through the Paleogene Kilwa Group. They are similar to the simple murolith coccoliths of the Early Mesozoic, but also share characters with the extant Pappposphaeraceae, *i.e*. small, murolith coccoliths, often tall-spine-bearing with square cross-section, but quite unlike any previously described Paleogene forms. **Occurrence**: NP9-21; TDP Sites 2, 12, 13, 14, 16B.

Family **RHOMBOASTERACEAE** Bown, 2005

Rhomboaster cuspis Bramlette & Sullivan, 1961
Pl.12, figs 9-10
Rhomboaster calcitrapa Gartner, 1971
Pl.12, figs 11, 12

NANNOLITHS INCERTAE SEDIS

Biantholithus flosculus Bown, 2005
Pl.12, fig.13

Calcispheres
Pl.12, figs 14-18

Ascidian spicules
Pl.12, fig.19

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Plate 1

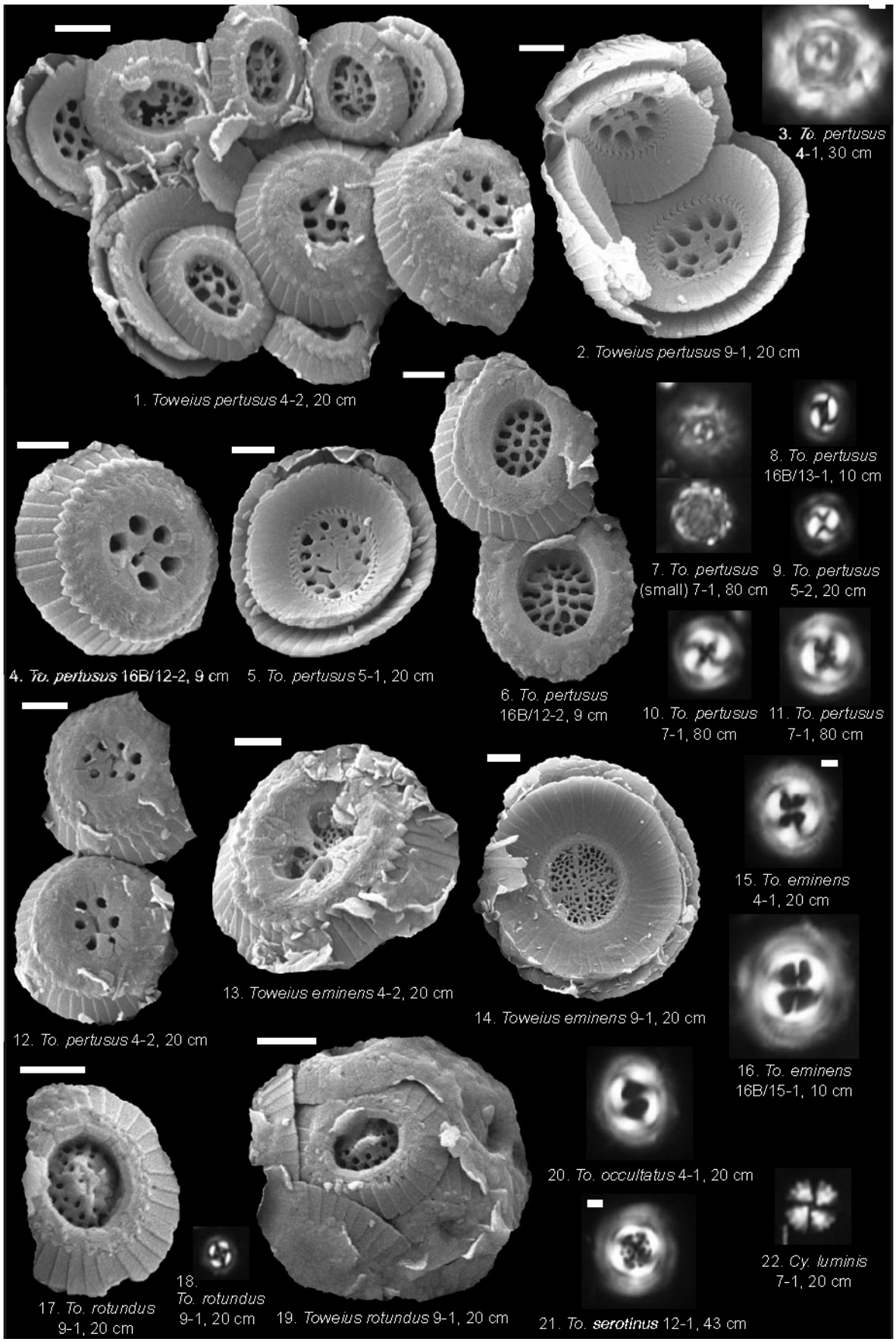

1. Toweius pertusus 4-2, 20 cm
2. Toweius pertusus 9-1, 20 cm
3. To. pertusus 4-1, 30 cm
4. To. pertusus 16B/12-2, 9 cm
5. To. pertusus 5-1, 20 cm
6. To. pertusus 16B/12-2, 9 cm
7. To. pertusus (small) 7-1, 80 cm
8. To. pertusus 16B/13-1, 10 cm
9. To. pertusus 5-2, 20 cm
10. To. pertusus 7-1, 80 cm
11. To. pertusus 7-1, 80 cm
12. To. pertusus 4-2, 20 cm
13. Toweius eminens 4-2, 20 cm
14. Toweius eminens 9-1, 20 cm
15. To. eminens 4-1, 20 cm
16. To. eminens 16B/15-1, 10 cm
17. To. rotundus 9-1, 20 cm
18. To. rotundus 9-1, 20 cm
19. Toweius rotundus 9-1, 20 cm
20. To. occultatus 4-1, 20 cm
21. To. serotinus 12-1, 43 cm
22. Cy. luminis 7-1, 20 cm

Plate 2

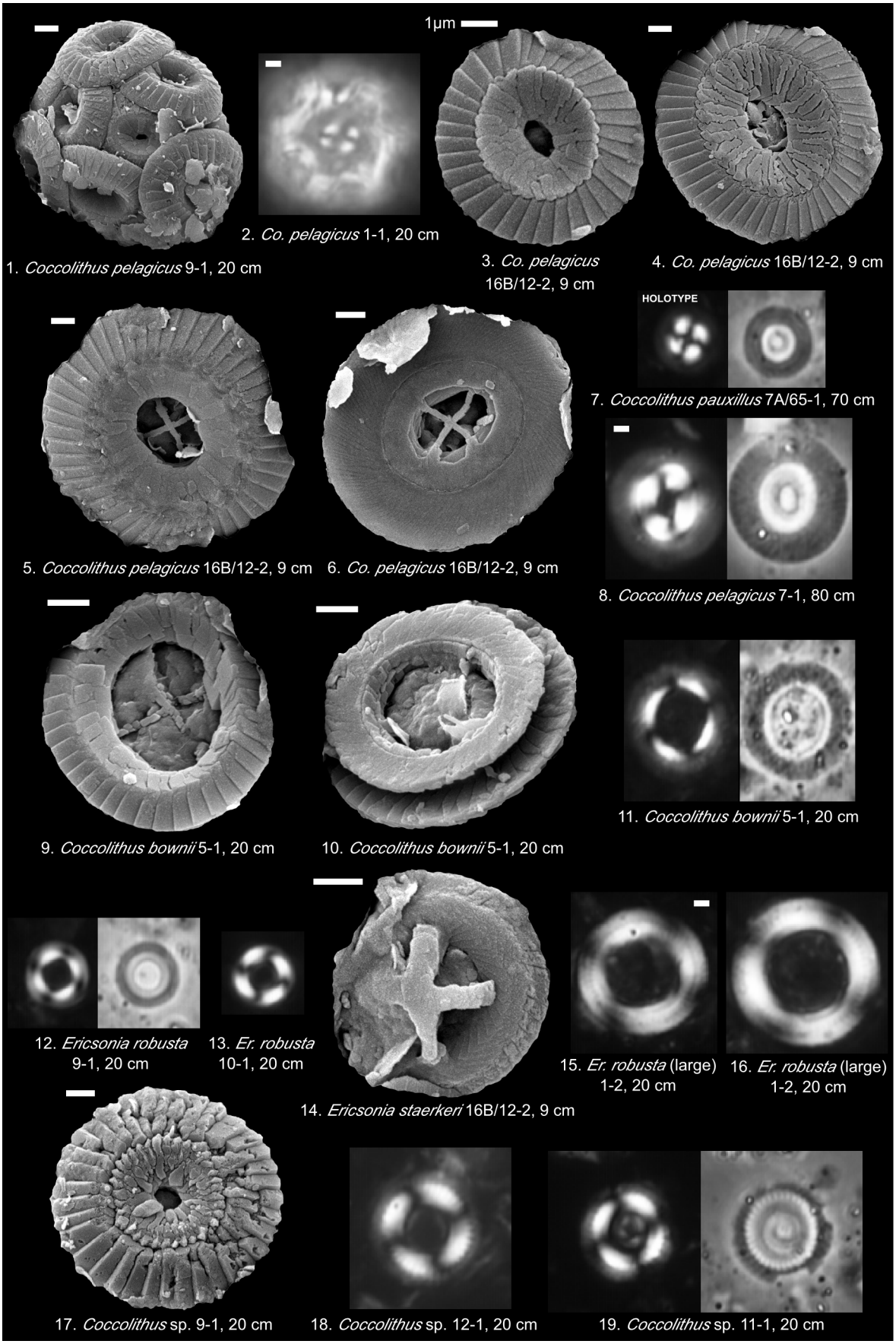

1µm
1. *Coccolithus pelagicus* 9-1, 20 cm
2. *Co. pelagicus* 1-1, 20 cm
3. *Co. pelagicus* 16B/12-2, 9 cm
4. *Co. pelagicus* 16B/12-2, 9 cm
5. *Coccolithus pelagicus* 16B/12-2, 9 cm
6. *Co. pelagicus* 16B/12-2, 9 cm
HOLOTYPE
7. *Coccolithus pauxillus* 7A/65-1, 70 cm
8. *Coccolithus pelagicus* 7-1, 80 cm
9. *Coccolithus bownii* 5-1, 20 cm
10. *Coccolithus bownii* 5-1, 20 cm
11. *Coccolithus bownii* 5-1, 20 cm
12. *Ericsonia robusta* 9-1, 20 cm
13. *Er. robusta* 10-1, 20 cm
14. *Ericsonia staerkeri* 16B/12-2, 9 cm
15. *Er. robusta* (large) 1-2, 20 cm
16. *Er. robusta* (large) 1-2, 20 cm
17. *Coccolithus* sp. 9-1, 20 cm
18. *Coccolithus* sp. 12-1, 20 cm
19. *Coccolithus* sp. 11-1, 20 cm

Plate 3

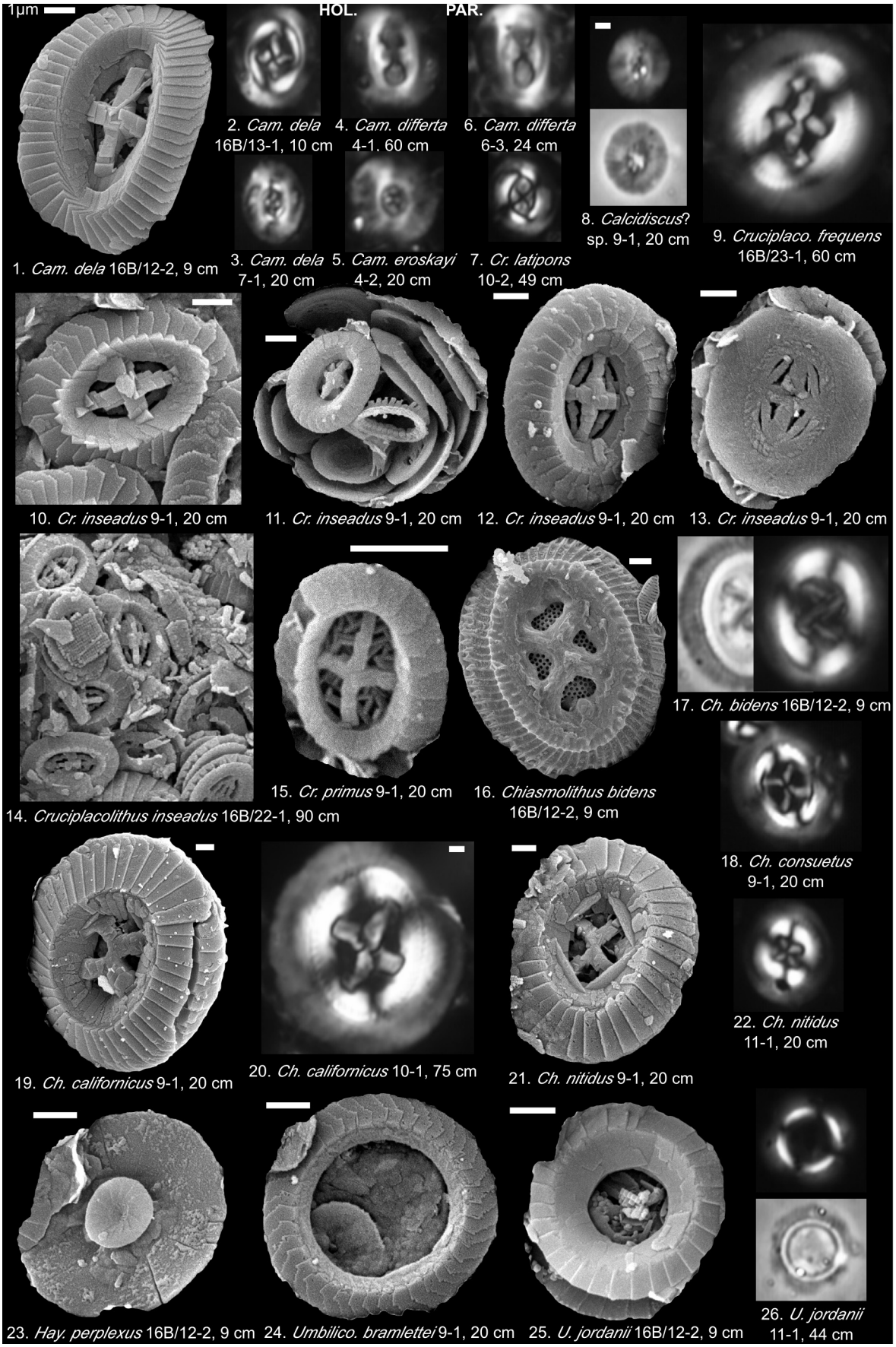

1µm
HOL.
PAR.
1. Cam. dela 16B/12-2, 9 cm
2. Cam. dela 16B/13-1, 10 cm
3. Cam. dela 7-1, 20 cm
4. Cam. differta 4-1. 60 cm
5. Cam. eroskayi 4-2, 20 cm
6. Cam. differta 6-3, 24 cm
7. Cr. latipons 10-2, 49 cm
8. Calcidiscus? sp. 9-1, 20 cm
9. Cruciplaco. frequens 16B/23-1, 60 cm
10. Cr. inseadus 9-1, 20 cm
11. Cr. inseadus 9-1, 20 cm
12. Cr. inseadus 9-1, 20 cm
13. Cr. inseadus 9-1, 20 cm
14. Cruciplacolithus inseadus 16B/22-1, 90 cm
15. Cr. primus 9-1, 20 cm
16. Chiasmolithus bidens 16B/12-2, 9 cm
17. Ch. bidens 16B/12-2, 9 cm
18. Ch. consuetus 9-1, 20 cm
19. Ch. californicus 9-1, 20 cm
20. Ch. californicus 10-1, 75 cm
21. Ch. nitidus 9-1, 20 cm
22. Ch. nitidus 11-1, 20 cm
23. Hay. perplexus 16B/12-2, 9 cm
24. Umbilico. bramlettei 9-1, 20 cm
25. U. jordanii 16B/12-2, 9 cm
26. U. jordanii 11-1, 44 cm

Plate 4

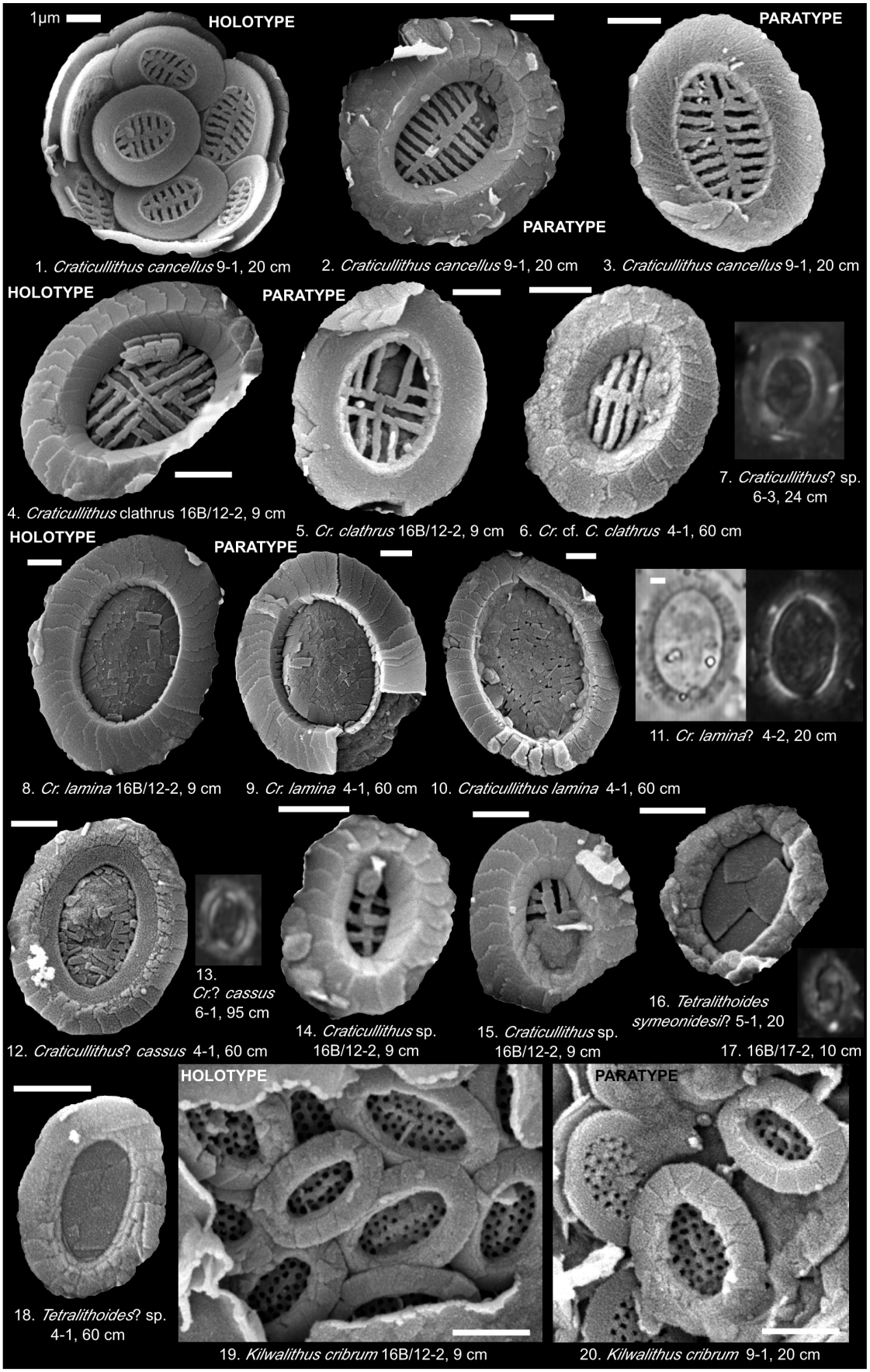

1µm
HOLOTYPE
PARATYPE
PARATYPE
1. Craticullithus cancellus 9-1, 20 cm
2. Craticullithus cancellus 9-1, 20 cm
3. Craticullithus cancellus 9-1, 20 cm
HOLOTYPE
PARATYPE
4. Craticullithus clathrus 16B/12-2, 9 cm
5. Cr. clathrus 16B/12-2, 9 cm
6. Cr. cf. C. clathrus 4-1, 60 cm
7. Craticullithus? sp. 6-3, 24 cm
HOLOTYPE
PARATYPE
8. Cr. lamina 16B/12-2, 9 cm
9. Cr. lamina 4-1, 60 cm
10. Craticullithus lamina 4-1, 60 cm
11. Cr. lamina? 4-2, 20 cm
12. Craticullithus? cassus 4-1, 60 cm
13. Cr.? cassus 6-1, 95 cm
14. Craticullithus sp. 16B/12-2, 9 cm
15. Craticullithus sp. 16B/12-2, 9 cm
16. Tetralithoides symeonidesi? 5-1, 20
17. 16B/17-2, 10 cm
18. Tetralithoides? sp. 4-1, 60 cm
HOLOTYPE
PARATYPE
19. Kilwalithus cribrum 16B/12-2, 9 cm
20. Kilwalithus cribrum 9-1, 20 cm

Plate 5

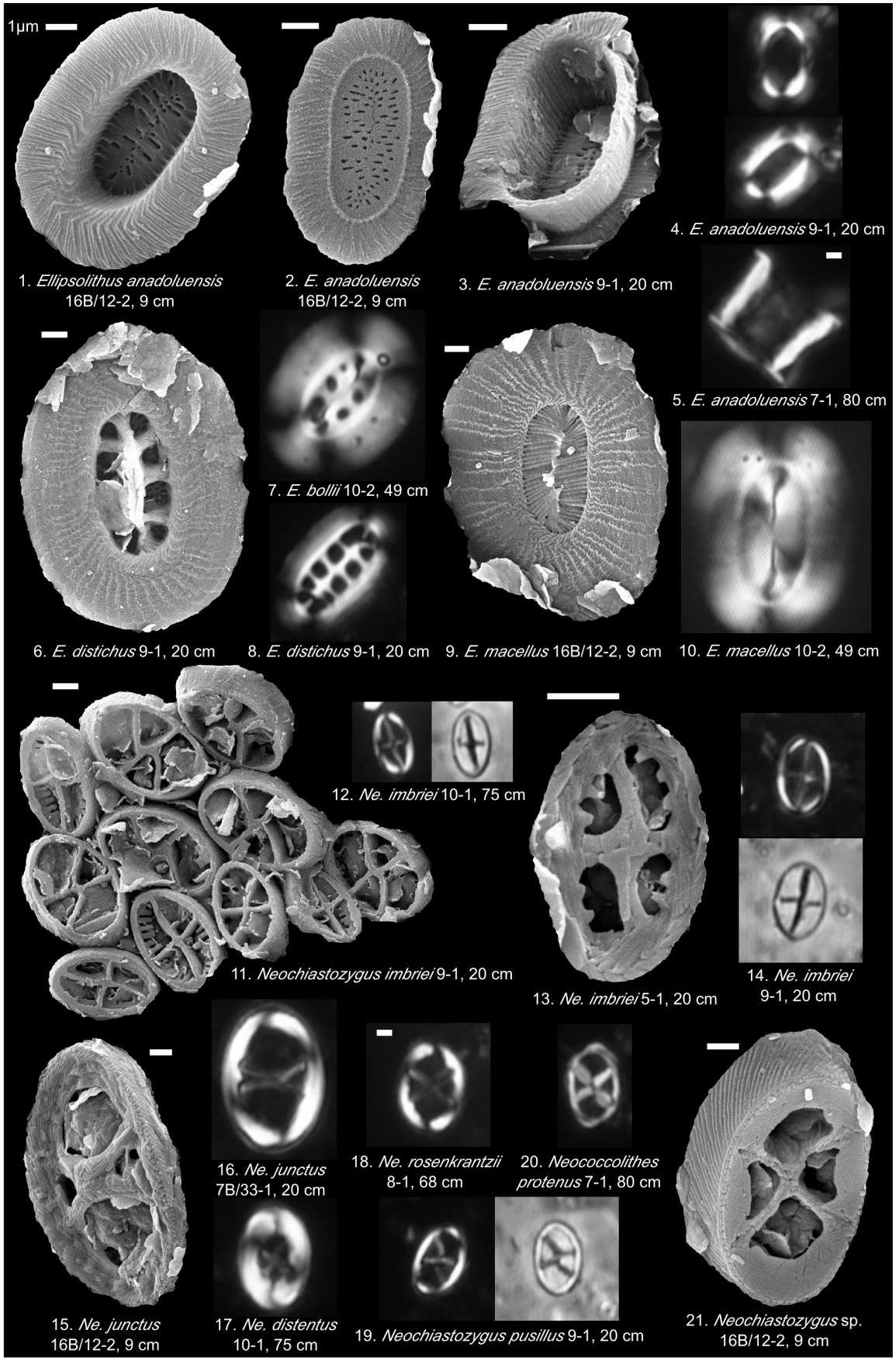

1µm
1. *Ellipsolithus anadoluensis* 16B/12-2, 9 cm
2. *E. anadoluensis* 16B/12-2, 9 cm
3. *E. anadoluensis* 9-1, 20 cm
4. *E. anadoluensis* 9-1, 20 cm
5. *E. anadoluensis* 7-1, 80 cm
6. *E. distichus* 9-1, 20 cm
7. *E. bollii* 10-2, 49 cm
8. *E. distichus* 9-1, 20 cm
9. *E. macellus* 16B/12-2, 9 cm
10. *E. macellus* 10-2, 49 cm
11. *Neochiastozygus imbriei* 9-1, 20 cm
12. *Ne. imbriei* 10-1, 75 cm
13. *Ne. imbriei* 5-1, 20 cm
14. *Ne. imbriei* 9-1, 20 cm
15. *Ne. junctus* 16B/12-2, 9 cm
16. *Ne. junctus* 7B/33-1, 20 cm
17. *Ne. distentus* 10-1, 75 cm
18. *Ne. rosenkrantzii* 8-1, 68 cm
19. *Neochiastozygus pusillus* 9-1, 20 cm
20. *Neococcolithes protenus* 7-1, 80 cm
21. *Neochiastozygus* sp. 16B/12-2, 9 cm

Plate 6

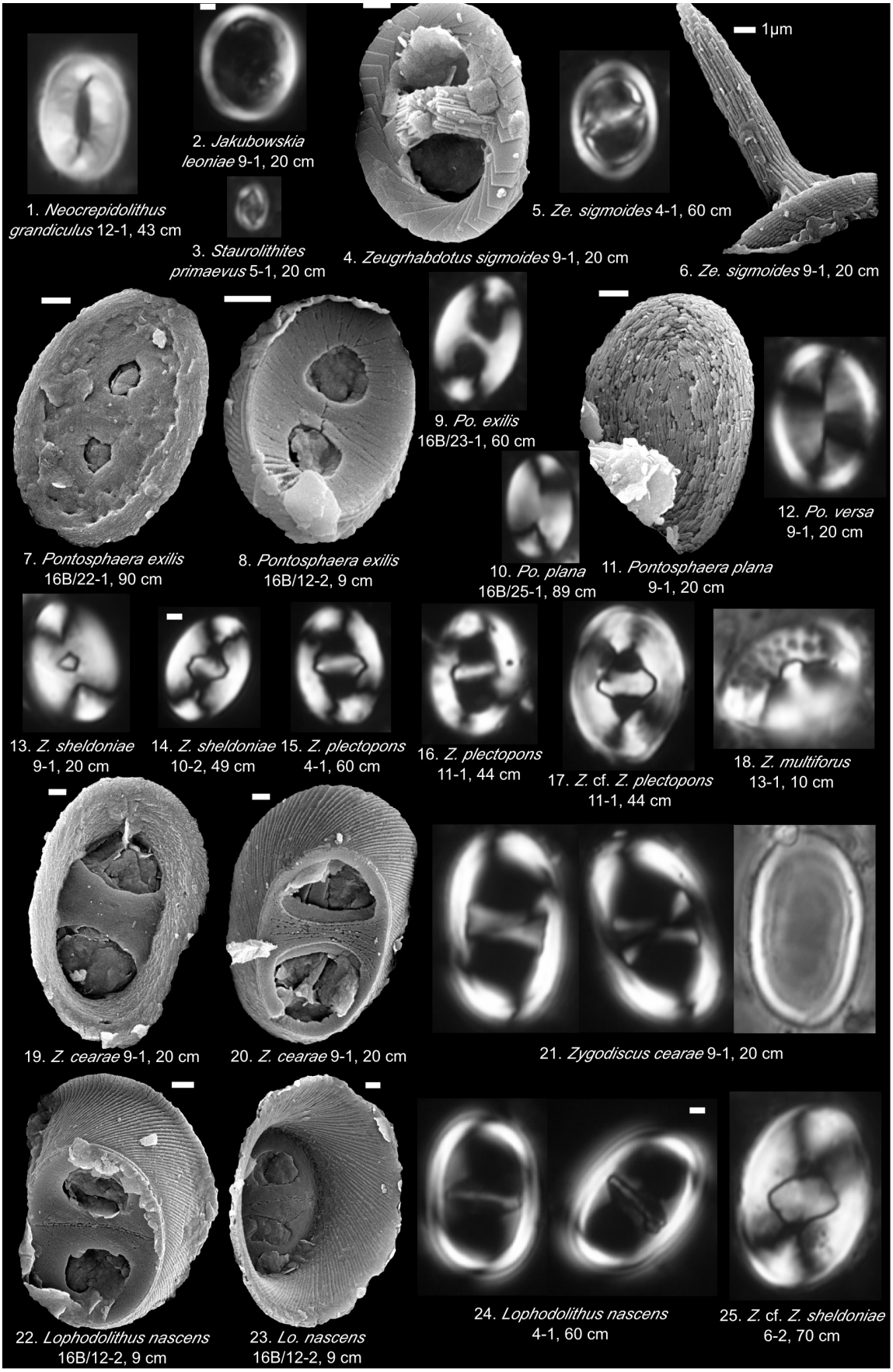

1µm
1. Neocrepidolithus grandiculus 12-1, 43 cm
2. Jakubowskia leoniae 9-1, 20 cm
3. Staurolithites primaevus 5-1, 20 cm
4. Zeugrhabdotus sigmoides 9-1, 20 cm
5. Ze. sigmoides 4-1, 60 cm
6. Ze. sigmoides 9-1, 20 cm
7. Pontosphaera exilis 16B/22-1, 90 cm
8. Pontosphaera exilis 16B/12-2, 9 cm
9. Po. exilis 16B/23-1, 60 cm
10. Po. plana 16B/25-1, 89 cm
11. Pontosphaera plana 9-1, 20 cm
12. Po. versa 9-1, 20 cm
13. Z. sheldoniae 9-1, 20 cm
14. Z. sheldoniae 10-2, 49 cm
15. Z. plectopons 4-1, 60 cm
16. Z. plectopons 11-1, 44 cm
17. Z. cf. Z. plectopons 11-1, 44 cm
18. Z. multiforus 13-1, 10 cm
19. Z. cearae 9-1, 20 cm
20. Z. cearae 9-1, 20 cm
21. Zygodiscus cearae 9-1, 20 cm
22. Lophodolithus nascens 16B/12-2, 9 cm
23. Lo. nascens 16B/12-2, 9 cm
24. Lophodolithus nascens 4-1, 60 cm
25. Z. cf. Z. sheldoniae 6-2, 70 cm

Plate 7

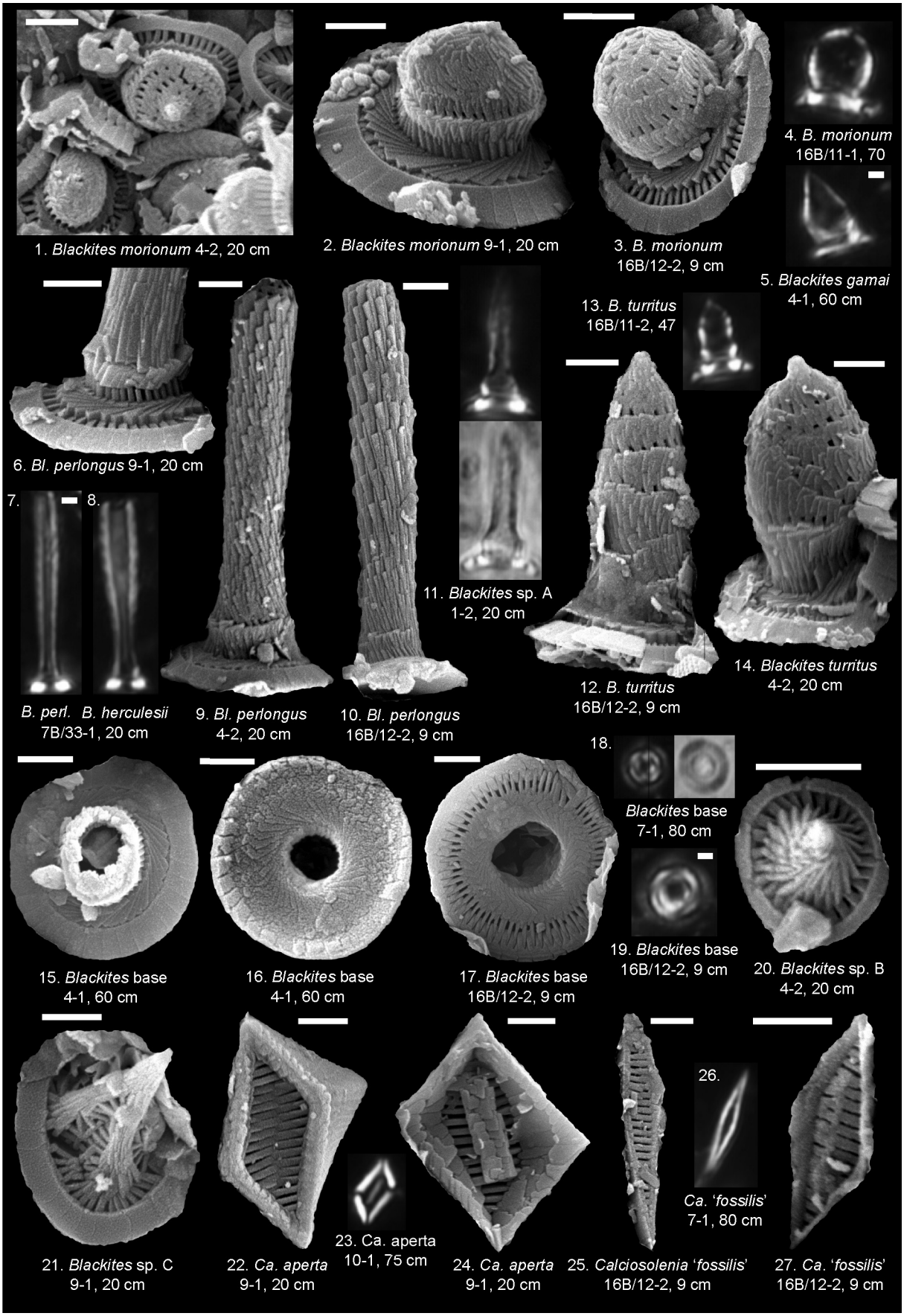

1. Blackites morionum 4-2, 20 cm
2. Blackites morionum 9-1, 20 cm
3. B. morionum 16B/12-2, 9 cm
4. B. morionum 16B/11-1, 70
5. Blackites gamai 4-1, 60 cm
6. Bl. perlongus 9-1, 20 cm
7.
8.
B. perl. B. herculesii 7B/33-1, 20 cm
9. Bl. perlongus 4-2, 20 cm
10. Bl. perlongus 16B/12-2, 9 cm
11. Blackites sp. A 1-2, 20 cm
12. B. turritus 16B/12-2, 9 cm
13. B. turritus 16B/11-2, 47
14. Blackites turritus 4-2, 20 cm
15. Blackites base 4-1, 60 cm
16. Blackites base 4-1, 60 cm
17. Blackites base 16B/12-2, 9 cm
18.
Blackites base 7-1, 80 cm
19. Blackites base 16B/12-2, 9 cm
20. Blackites sp. B 4-2, 20 cm
21. Blackites sp. C 9-1, 20 cm
22. Ca. aperta 9-1, 20 cm
23. Ca. aperta 10-1, 75 cm
24. Ca. aperta 9-1, 20 cm
25. Calciosolenia 'fossilis' 16B/12-2, 9 cm
26.
Ca. 'fossilis' 7-1, 80 cm
27. Ca. 'fossilis' 16B/12-2, 9 cm

Plate 8

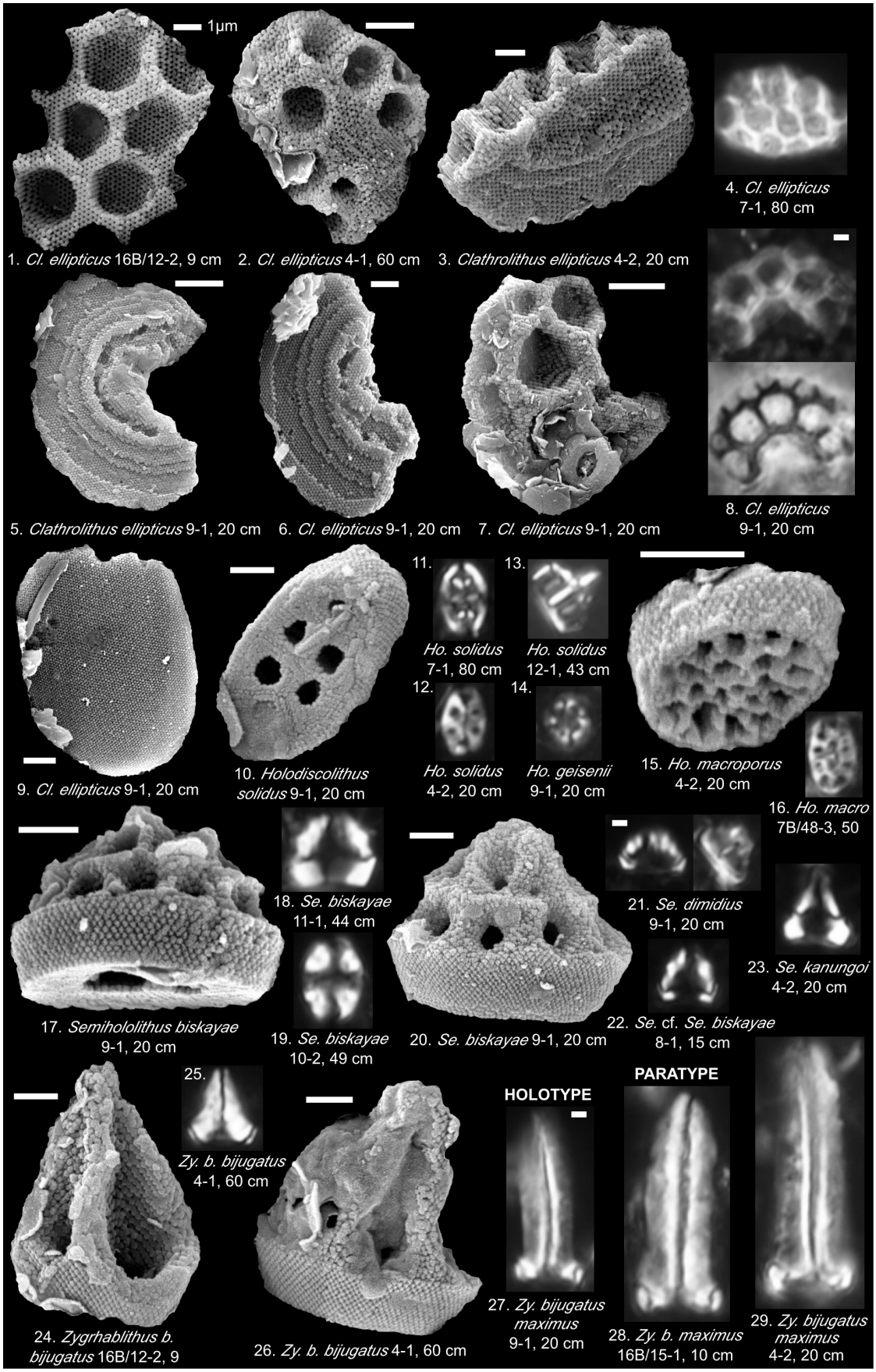

1µm
1. Cl. ellipticus 16B/12-2, 9 cm
2. Cl. ellipticus 4-1, 60 cm
3. Clathrolithus ellipticus 4-2, 20 cm
4. Cl. ellipticus 7-1, 80 cm
5. Clathrolithus ellipticus 9-1, 20 cm
6. Cl. ellipticus 9-1, 20 cm
7. Cl. ellipticus 9-1, 20 cm
8. Cl. ellipticus 9-1, 20 cm
9. Cl. ellipticus 9-1, 20 cm
10. Holodiscolithus solidus 9-1, 20 cm
11. Ho. solidus 7-1, 80 cm
12. Ho. solidus 4-2, 20 cm
13. Ho. solidus 12-1, 43 cm
14. Ho. geisenii 9-1, 20 cm
15. Ho. macroporus 4-2, 20 cm
16. Ho. macro 7B/48-3, 50
17. Semihololithus biskayae 9-1, 20 cm
18. Se. biskayae 11-1, 44 cm
19. Se. biskayae 10-2, 49 cm
20. Se. biskayae 9-1, 20 cm
21. Se. dimidius 9-1, 20 cm
22. Se. cf. Se. biskayae 8-1, 15 cm
23. Se. kanungoi 4-2, 20 cm
24. Zygrhablithus b. bijugatus 16B/12-2, 9
25. Zy. b. bijugatus 4-1, 60 cm
26. Zy. b. bijugatus 4-1, 60 cm
HOLOTYPE
27. Zy. bijugatus maximus 9-1, 20 cm
PARATYPE
28. Zy. b. maximus 16B/15-1, 10 cm
29. Zy. bijugatus maximus 4-2, 20 cm

Plate 9

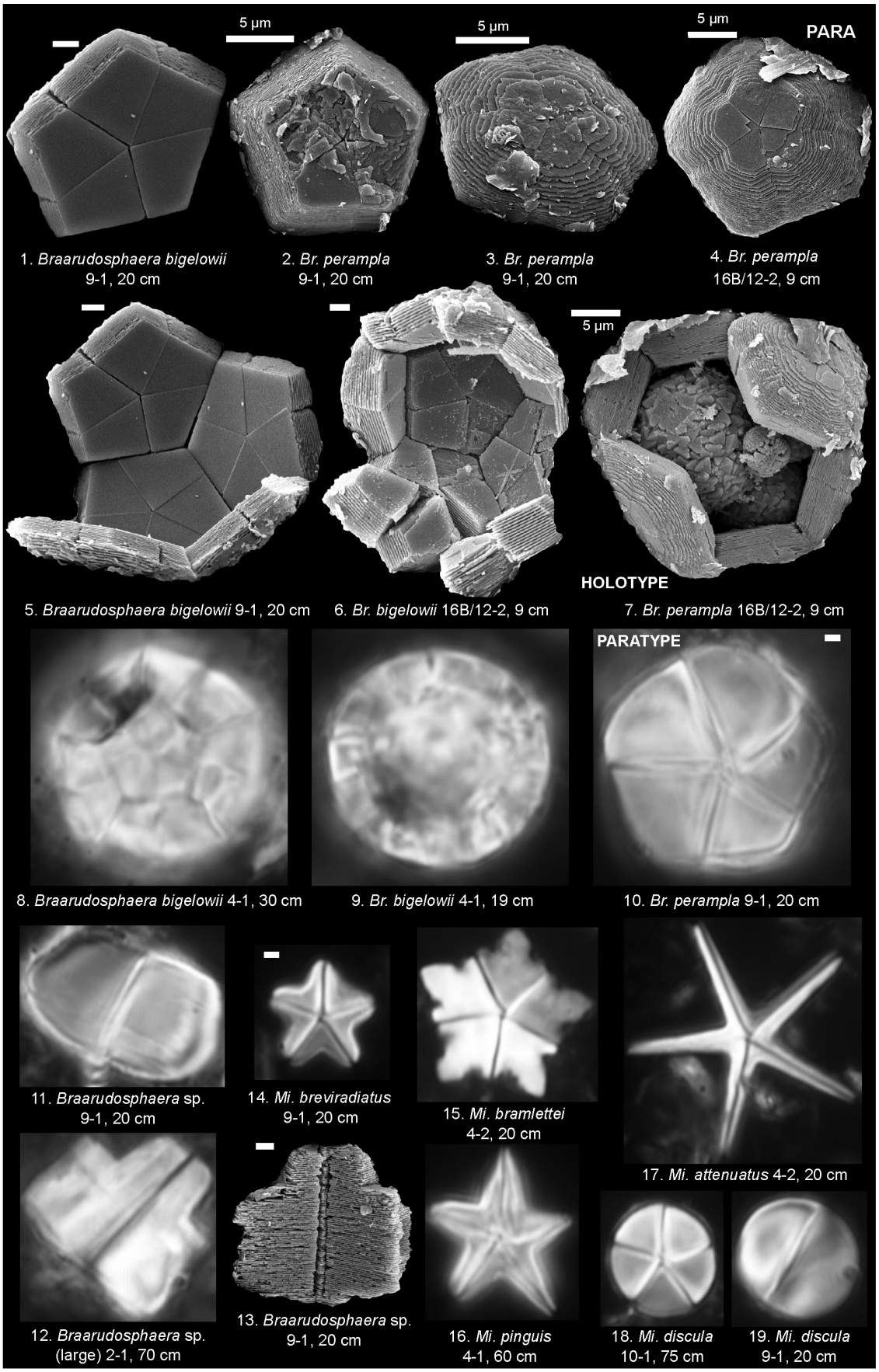

5 µm
5 µm
5 µm
PARA
1. Braarudosphaera bigelowii 9-1, 20 cm
2. Br. perampla 9-1, 20 cm
3. Br. perampla 9-1, 20 cm
4. Br. perampla 16B/12-2, 9 cm
5 µm
HOLOTYPE
5. Braarudosphaera bigelowii 9-1, 20 cm
6. Br. bigelowii 16B/12-2, 9 cm
7. Br. perampla 16B/12-2, 9 cm
PARATYPE
8. Braarudosphaera bigelowii 4-1, 30 cm
9. Br. bigelowii 4-1, 19 cm
10. Br. perampla 9-1, 20 cm
11. Braarudosphaera sp. 9-1, 20 cm
14. Mi. breviradiatus 9-1, 20 cm
15. Mi. bramlettei 4-2, 20 cm
17. Mi. attenuatus 4-2, 20 cm
12. Braarudosphaera sp. (large) 2-1, 70 cm
13. Braarudosphaera sp. 9-1, 20 cm
16. Mi. pinguis 4-1, 60 cm
18. Mi. discula 10-1, 75 cm
19. Mi. discula 9-1, 20 cm

Plate 10

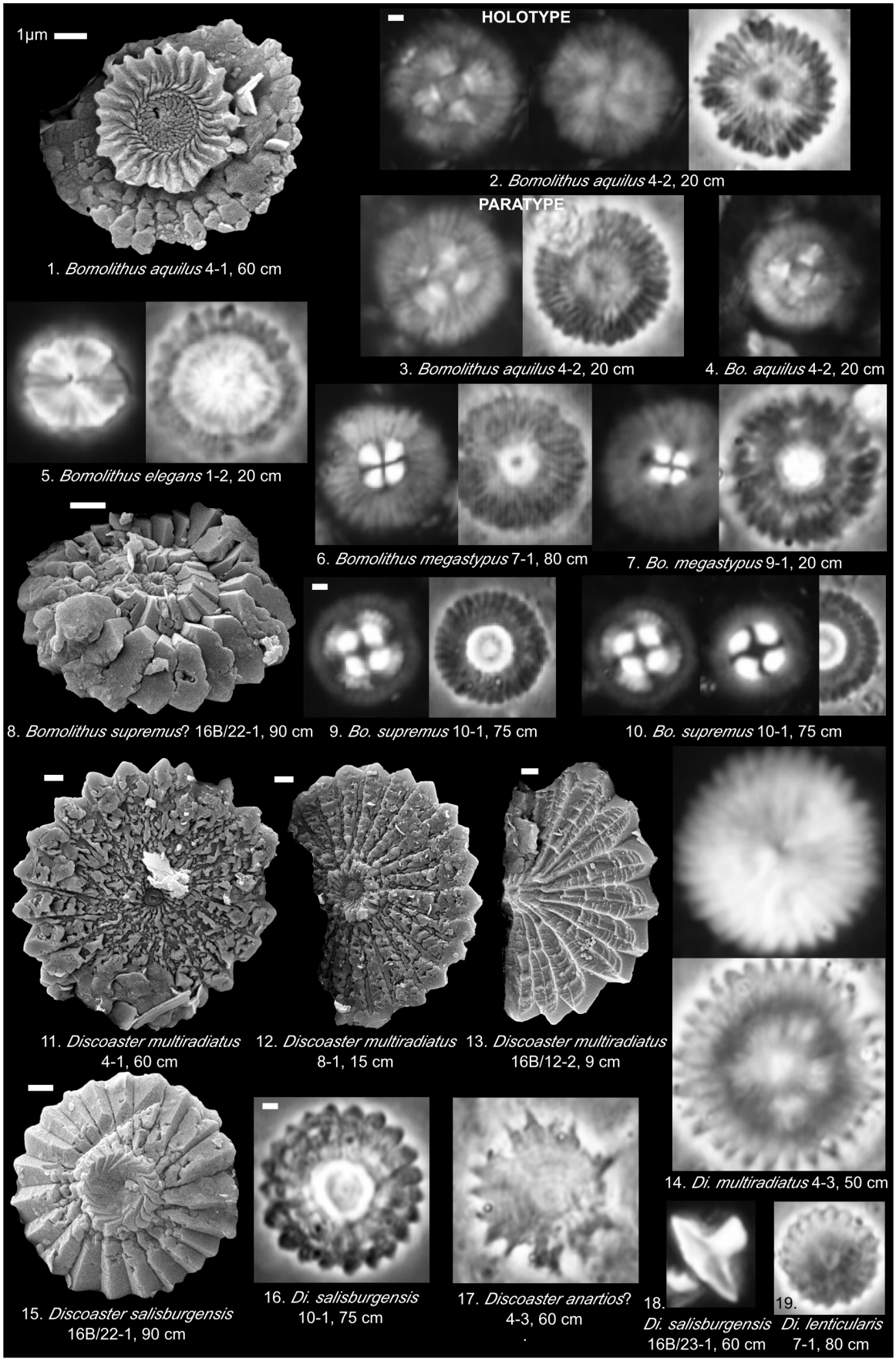

1µm
HOLOTYPE
2. Bomolithus aquilus 4-2, 20 cm
PARATYPE
1. Bomolithus aquilus 4-1, 60 cm
3. Bomolithus aquilus 4-2, 20 cm
4. Bo. aquilus 4-2, 20 cm
5. Bomolithus elegans 1-2, 20 cm
6. Bomolithus megastypus 7-1, 80 cm
7. Bo. megastypus 9-1, 20 cm
8. Bomolithus supremus? 16B/22-1, 90 cm
9. Bo. supremus 10-1, 75 cm
10. Bo. supremus 10-1, 75 cm
11. Discoaster multiradiatus 4-1, 60 cm
12. Discoaster multiradiatus 8-1, 15 cm
13. Discoaster multiradiatus 16B/12-2, 9 cm
14. Di. multiradiatus 4-3, 50 cm
15. Discoaster salisburgensis 16B/22-1, 90 cm
16. Di. salisburgensis 10-1, 75 cm
17. Discoaster anartios? 4-3, 60 cm
18. Di. salisburgensis 16B/23-1, 60 cm
19. Di. lenticularis 7-1, 80 cm

Plate 11

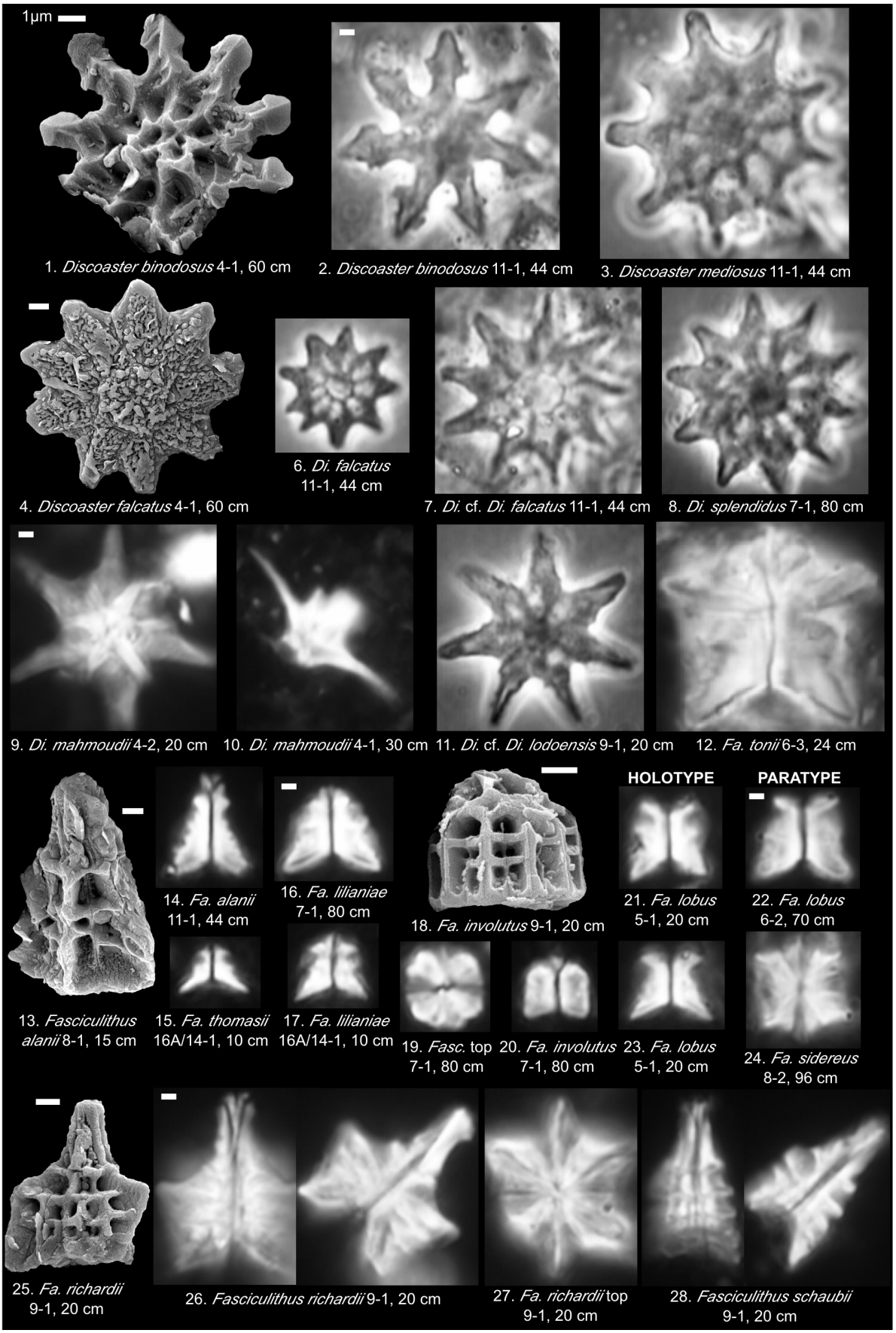
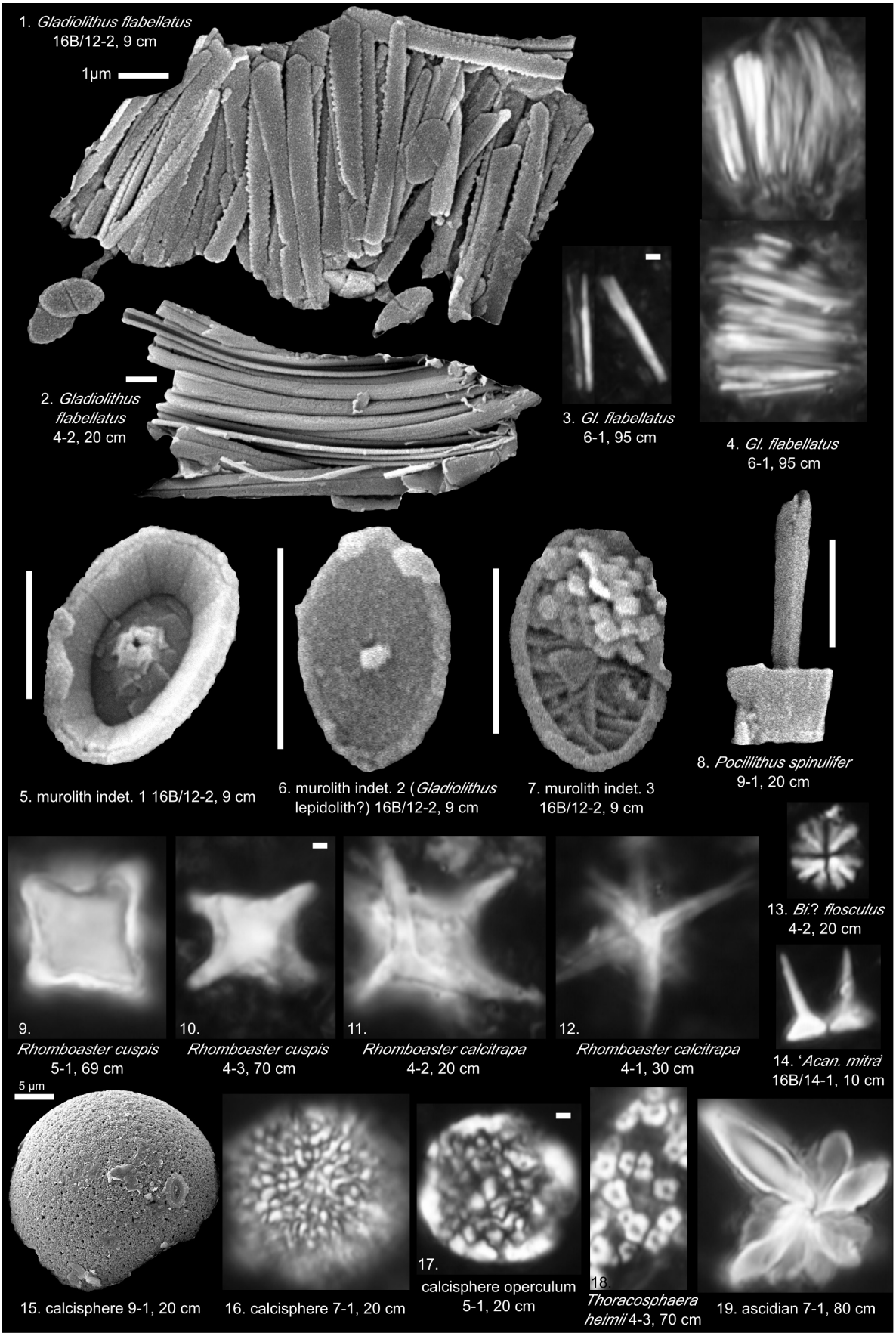

1µm
1. Discoaster binodosus 4-1, 60 cm
2. Discoaster binodosus 11-1, 44 cm
3. Discoaster mediosus 11-1, 44 cm
4. Discoaster falcatus 4-1, 60 cm
6. Di. falcatus 11-1, 44 cm
7. Di. cf. Di. falcatus 11-1, 44 cm
8. Di. splendidus 7-1, 80 cm
9. Di. mahmoudii 4-2, 20 cm
10. Di. mahmoudii 4-1, 30 cm
11. Di. cf. Di. lodoensis 9-1, 20 cm
12. Fa. tonii 6-3, 24 cm
13. Fasciculithus alanii 8-1, 15 cm
14. Fa. alanii 11-1, 44 cm
15. Fa. thomasii 16A/14-1, 10 cm
16. Fa. lilianiae 7-1, 80 cm
17. Fa. lilianiae 16A/14-1, 10 cm
18. Fa. involutus 9-1, 20 cm
19. Fasc. top 7-1, 80 cm
20. Fa. involutus 7-1, 80 cm
HOLOTYPE
21. Fa. lobus 5-1, 20 cm
23. Fa. lobus 5-1, 20 cm
PARATYPE
22. Fa. lobus 6-2, 70 cm
24. Fa. sidereus 8-2, 96 cm
25. Fa. richardii 9-1, 20 cm
26. Fasciculithus richardii 9-1, 20 cm
27. Fa. richardii top 9-1, 20 cm
28. Fasciculithus schaubii 9-1, 20 cm

Plate 12


1. *Gladiolithus flabellatus*
16B/12-2, 9 cm
1µm
2. *Gladiolithus flabellatus*
4-2, 20 cm
3. *Gl. flabellatus*
6-1, 95 cm
4. *Gl. flabellatus*
6-1, 95 cm
5. murolith indet. 1 16B/12-2, 9 cm
6. murolith indet. 2 (*Gladiolithus* lepidolith?) 16B/12-2, 9 cm
7. murolith indet. 3
16B/12-2, 9 cm
8. *Pocillithus spinulifer*
9-1, 20 cm
9. *Rhomboaster cuspis*
5-1, 69 cm
10. *Rhomboaster cuspis*
4-3, 70 cm
11. *Rhomboaster calcitrapa*
4-2, 20 cm
12. *Rhomboaster calcitrapa*
4-1, 30 cm
13. *Bi.*? *flosculus*
4-2, 20 cm
14. '*Acan. mitra*'
16B/14-1, 10 cm
5 µm
15. calcisphere 9-1, 20 cm
16. calcisphere 7-1, 20 cm
17. calcisphere operculum
5-1, 20 cm
18. *Thoracosphaera heimii* 4-3, 70 cm
19. ascidian 7-1, 80 cm