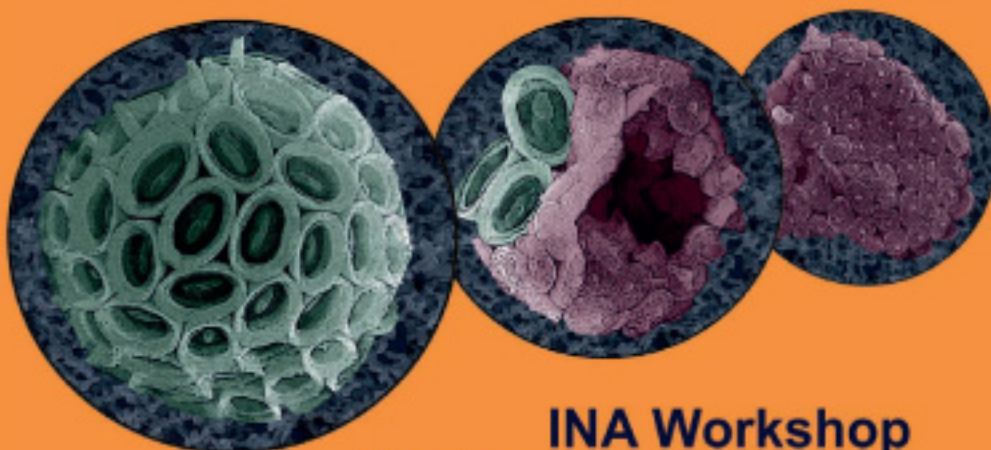


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COCCOLITHOPHORES 2014



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Searching for cells: the potential of fossil coccospheres in coccolithophore research

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Abstract: The majority of fossil coccolithophore studies are based on disaggregated coccoliths but preserved complete coccospheres provide documentation of true cellular traits (cell size, numbers of coccoliths per cell and calcite quotas) and represent a relatively untapped archive of palaeobiological information. Coccospheres are more frequently present when coccolith preservation is good or exceptional. Their preservation is dependent on a variety of taphonomic factors that combine to minimize the destructive effects of grazing and sinking, seafloor bioturbation and, finally, carbonate diagenesis. Clay-rich hemipelagic sediments that have not been deeply buried are particularly productive. Herein, we highlight the occurrences and potential of these coccosphere fossils and illustrate the range of morphologies we have so far encountered, predominantly from the Paleogene interval. Our observations show that coccosphere morphology is generally a conservative, long-lived character, with fossil representatives of living taxa (e.g., *Braarudosphaera*, *Coccolithus*, *Helicosphaera*, *Reticulofenestra*), all showing very similar coccosphere style back through their evolutionary history. In addition, we have also observed a variety of sphere shapes (ovoid, ellipsoidal, cylindrical) and significant coccolith polymorphism and varimorphism across a number of different families and in taxa for which fossil coccospheres have not previously been known. Fossil *Acanthoica* and *Calciosolenia* spheres, for example, indicate that polymorphism is a long-lived characteristic of the Syracosphaerales group. Lastly, by combining morphometric data from both fossil and living populations we show that coccosphere geometries (coccosphere size, number of coccoliths per coccosphere and coccolith size) show systematic trends (e.g., larger cells have larger coccoliths) but there is significant divergence from this trend that reflects intrinsic, taxon-specific factors (e.g., coccolith shapes and packing) and growth phase of the population. Although our preliminary coccosphere studies have uncovered new, surprising and useful observations we are still far from understanding the fundamental controls on cell size, coccosphere geometry and architecture.

Keywords: fossil coccospheres, Paleogene, Mesozoic

1. Introduction

Palaeontologists studying the long fossil record of coccolithophores have predominantly gathered stratigraphic, taxonomic, palaeoecological and palaeobiological information based on the documentation of disaggregated coccoliths, because this is the most common state in which their cellular remains are found in sea floor sediments. However, complete coccospheres are also preserved in the fossil record and with increasing numbers of studies aiming to understand fossil assemblages as representations of communities of reproducing cells, there is a strong incentive to seek out these complete fossils. Fossil coccospheres enable the documentation of cellular traits that can be directly compared with living cells, including cell size, numbers of coccoliths per cell and cellular calcite quotas (e.g., Henderiks & Pagani, 2007; Henderiks, 2008; Gibbs *et al.*, 2013). These fossils therefore provide an invaluable archive of important palaeobiological information that can inform all aspects of coccolithophore science, including classification (e.g., through observation of coccolith morphology across entire coccospheres), palaeo-growth rates or phase, species-specific calcite quotas and production rates, and biomineralogical responses to changes in palaeoenvironmental conditions including ocean chemistry.

The images we present here come from ongoing fossil coccosphere studies, but we would like to highlight the occurrences and potential of these fossils and illustrate the range of morphologies we have so far encountered, predominantly in the Paleogene interval.

2. Preserving coccospheres

Coccolithophore coccospheres fall into two main groups: those capable of maintaining structural integrity after death and those that collapse into constituent parts once the cell and organic binding material has been removed. The former type is limited to cells with placolith-type coccoliths (Pl. 1, figs 1-5; Pls 3-10), which both overlap and interlock, forming a mechanically robust structure, and these are not uncommon in fossil material (e.g., Mai *et al.*, 1997). The second group form spheres from non-interlocking, murolith-type coccoliths that sit side-by-side on the cell surface (Pl. 1, figs 6-9; Pl. 8, fig. 10) and such spheres have rarely been seen in the fossil record, with observations limited to a small number of rock surface scanning electron microscope images, such as Covington (1985), Lambert (1987, Pl. 4, 9, 10) and Bown (2010, Pl. 5, fig. 11). In very rare cases these coccospheres are complete and retain their shape, but more commonly they are collapsed: we consider them coccospheres if they form a discrete group of numerous coccoliths in close contact. Finally, non-coccolith (nannolith) or atypical-coccolith forming groups tend not to have interlocking coccospheres but can still be preserved as fossils, e.g., *Braarudosphaera* (Pl. 7, figs 1-6) and *Gladiolithus* (Pl. 8, fig. 11).

The frequency of placolith coccosphere occurrence is highly variable in the fossil record and moderate to poorly preserved assemblages typically include very few or no specimens. However, it is becoming increasingly apparent that the abundance of preserved coccospheres is closely

linked to the overall quality of nannofossil preservation more generally, and well known examples of sediments that host exceptionally preserved nannofossils also typically contain frequent coccospheres. The abundance of coccospheres is usually apparent in both light microscope and scanning electron microscope preparations.

In our recent work (e.g., Bown *et al.*, 2008; Bown, 2010; Gibbs *et al.*, 2013) we have focused on the best preserved fossil coccolithophore material, most typically found in clay-rich hemipelagic sediments that have not been deeply buried (e.g., Tanzanian Cretaceous-Paleogene Kilwa Group, New Jersey Paleogene Malboro Clay, Californian Paleogene, Gulf Coast Paleogene Yazoo Clay). In all of these materials we have observed enhanced levels of coccosphere preservation. This is perhaps not surprising, but the preservation of coccospheres is the result of several distinct taphonomic factors. Coccosphere disintegration can occur at any stage from initial cell death to final preparation of the sample, through both physical and chemical processes. The mostly likely points of loss include initial grazing of the cell and through recycling processes within the photic zone, during sinking and export from the photic zone, during sedimentation and burial at the seafloor (in particular, if bioturbation is intense) and finally during lithification and diagenesis, through compaction and dissolution (e.g., Honjo, 1976; Wise, 1977; Andruleit *et al.*, 2004). Plankton and trap studies suggest that most coccospheres are lost through upper water column processes, but that preservation may be favoured by initial high abundances (e.g., blooms) and rapid sedimentation. If coccosphere export to the seafloor is achieved, it is clear that clay-rich but organic-carbon-poor sediment composition is an important factor in both coccolith and coccosphere preservation, as impermeable clays minimize the destructive effects of carbonate diagenesis (Dunkley Jones *et al.*, 2009), and higher sedimentation rates may aid this effect. However, relatively low seafloor oxygen levels may also play a role, as such conditions reduce the activity of metazoan bioturbators that would otherwise both churn and ingest sediment and increase the probability of physical coccosphere destruction, especially the non-placolith forms. Our observations of unprocessed sediment/rock surfaces in SEM show undisturbed coccolith- and coccosphere-rich lamina and pellets (Pl. 2), suggesting little or no bioturbation has occurred. Finally, shelf-sea settings with shorter export paths and efficient fecal pellet production may also reduce coccosphere destruction rates during export.

3. Coccosphere and palaeobiological observations

Fossil coccosphere observations are the only definitive way in which we can determine cell size and shape (using the coccosphere architecture) and assess morphological variability of coccoliths associated with single cells. Overall, our observations suggest that coccosphere morphology is generally a conservative, long-lived

character, with fossil representatives of living taxa (e.g. *Acanthoica*, *Braarudosphaera*, *Calciosolenia*, *Coccolithus*, *Gladiolithus*, *Helicosphaera*, *Reticulofenestra*), all showing very similar coccosphere style back through their evolutionary history (Pl. 3-8). Architecturally, the majority of fossil coccospheres that we have observed are spherical, monomorphic, placolith-bearing types, and include those of the dominant taxa *Watznaueria* (Jurassic-Cretaceous), *Toweius* (Paleocene-early Eocene) and *Reticulofenestra* (early Eocene and younger) (Pls 1, 2, 5, 6). Across these individual fossil cells the coccoliths are identical or exhibit very similar shape and size. However, we have also observed different shaped spheres (ovoid, ellipsoidal and cylindrical) and significant coccolith polymorphism (multiple coccolith types) and varimorphism (varying morphology related to position on the coccosphere) across a number of families (see Young *et al.*, 1997 for coccosphere terminology). Today, polymorphism is largely restricted to coccospheres of specific taxonomic groups, especially the Syracosphaerales (Syracosphaeraceae, Calciosoleniaceae and Rhabdosphaeraceae) (e.g., Young *et al.*, 2003, 2005). We have observed fossil examples of the Syracosphaerales exhibiting polymorphism, e.g., subtle varimorphic coccolith size and spine length variations in Paleogene *Acanthoica* (Pl. 8, fig. 8; Dunkley Jones *et al.*, 2009, Pl 8, figs 2; Pl 9, figs 10) and both Cretaceous and Paleogene specimens of *Calciosolenia* show varimorphism, with subtle variations in coccolith length and width (Pl. 1, fig. 8). These *Acanthoica* and *Calciosolenia* observations are similar to the morphologies seen in modern species (e.g., Malinverno, 2005; Kleijne, 1992) and suggest that polymorphism is a long-lived characteristic of the Syracosphaerales group. In terms of other non-placolith taxa, we also see variations in coccolith size in Paleogene *Neochiastozygus* (Zygodisciales, Zygodiscaceae) (Pl. 8, fig. 10; Bown, 2010 Pl. 5, fig. 11). Remarkably, coccospheres of the extant nannolith bearing species *Gladiolithus flabellatus* show that the dimorphic sphere morphology has been conserved over at least 58 million years (Pl. 8, fig. 11; Bown *et al.*, 2009; Bown, 2010, Pl. 12, 1-4). These fossil coccospheres show that both lepidoliths and tube coccoliths occur, confirming the same dimorphism as living forms (Young & Poulton, this volume). This dimorphism relates to a bowl-shaped morphology in the modern coccospheres and so it is reasonable to assume that the coccosphere geometry was the same in the fossil forms.

Fossil placolith taxa with polymorphic coccospheres include the common Mesozoic species *Biscutum constans*, which has ovoid coccospheres with varimorphic coccoliths that reduce in size towards each end of the 'sphere' (Pl 1, fig. 2). Unusual 'coccocylinder' morphologies have also been reported within this genus (Pl 1, fig. 1; Covington, 1985). Similarly, the Paleogene *Biscutum braloweri*, frequently seen in the Paleocene-Eocene thermal maximum (PETM) interval, also displays this ovoid morphology with varying coccolith sizes (Pl. 9), and

this may be a coccosphere architecture feature of placolith coccoliths with relatively narrow elliptical shapes. The small Paleogene placolith *Kilwalithus* has a large number of coccoliths per coccosphere and displays striking dimorphism, with a subset of coccoliths possessing blade-like, arched appendages (Pl. 10).

As well as preserving the ‘finished’ cell covering, the preservation of intact coccospheres also includes snapshots of growing coccoliths. In both LM and SEM observation, specimens containing proto-coccolith rings are frequently observed, revealing the partially formed coccoliths formed within intracellular vesicles prior to completion of growth and exocytosis onto the cell surface. Such specimens were originally reported by Young & Bown (1991) and used to reconstruct the ontogeny of Mesozoic *Watznaueria*, but we have now found proto-coccolith rings in almost all the Paleogene placolith taxa (e.g., *Toweius* - Pl 11; *Coccolithus* - Pl.3, fig. 1, *Reticulofenestra* - Pl. 6, figs 1, 2, 4, 7).

4. Coccosphere morphometric data

Our coccosphere morphometric data, first collected for early Paleogene *Toweius* and *Coccolithus*, (Gibbs *et al.*, 2013) show systematic relationships between coccosphere size (external diameter, \emptyset), number of coccoliths per coccosphere (C_N) and coccolith size (length, C_L), which we collectively refer to as cell geometry. There is an obvious trend of larger cells having larger coccoliths (previously documented by Henderiks, 2008) (see, for example, the *Reticulofenestra* and *Coccolithus* Pls 3 and 6) but we have recently shown that the relationship is also dependent on the number of coccoliths forming the coccosphere, as the same C_L can be associated with different \emptyset by having a variable C_N (Gibbs *et al.*, 2013; see Pl. 4). Certain taxa have geometries which diverge significantly from this norm, most strikingly seen in groups that have large numbers of smaller coccoliths per sphere (e.g., *Kilwalithus* - Pl. 10, *C. primus* - Pl. 4, fig. 20, small *Toweius* - Pl 5, fig. 6), where the relative size of the cell is particularly large compared with the coccoliths. There are also taxa whose coccolith shape or morphology results in distinctive packing structures, most extreme in the dodecahedra of *Braarudosphaera* (Pl 7, figs 1-6), but also cubiform spheres in *Umbilicosphaera bramlettei* (Pl 4, figs 22-23) and *Toweius pertusus* (Pl 5, figs 9, 12, 13). To some extent, coccosphere morphology will therefore be controlled by coccolith shape and also other factors intrinsic to the taxon (e.g., cell size), but we have also observed that coccosphere geometry is a function of growth phase of the population. Using both culture and field data we have shown that *Coccolithus* populations display a trend away from the general coccolith size to sphere size relationship at different phases of cell division, and a greater relationship between number of coccoliths on a cell *versus* its sphere size. Recently divided cells/coccospheres are smaller with fewer coccoliths (19-20 μ m, 8 coccoliths), growing cells prior to division

have large cells and enough coccoliths for the daughter cells (up to 26 microns, 14-16 coccoliths) and stalled, undividing cells show the largest size and (>26 microns) and greatest number of coccoliths (>16 coccoliths) (Gibbs *et al.*, 2013, Fig. 2b). These larger, pre-dividing cells can also be seen in fossil coccospheres (*Coccolithus* - Pl 3, fig. 9; *Reticulofenestra* - Pl 6, fig. 13).

These preliminary results from coccosphere research using fossil (and living) populations have uncovered new, surprising and useful observations but we are still far from understanding the fundamental controls on cell size, coccosphere geometry and architecture. We hope that this paper demonstrates the potential that is present in these fossil materials and inspires further discoveries in this new area of research. Furthermore, we hope it will stimulate the exploration and documentation of the relationships between coccolith size and shape, and coccosphere morphology in extant coccolithophores and encourage greater collaboration between those working on the fossil and living groups.

The Plates

The following plates predominantly illustrate the diversity of Paleogene coccospheres we have so far encountered, but there are also selected examples of Mesozoic taxa. The sample location abbreviations are as follows: 647 – ODP Leg 105, Site 647, NW Atlantic Ocean; 1052 – ODP Leg 171B, Site 1052, Blake Nose, NW Atlantic Ocean; BR – Bass River, New Jersey, USA; HB – Hampden Beach, New Zealand; LIN – Lindi, Tanzania; LO – Lodo Gulch, Californian, USA; MGr – Mossy Grove, Mississippi, USA; TDP – Tanzania Drilling Project sites, Tanzania; Tarf. – Tarfaya, Morocco; WL – Wilson Lake, New Jersey, USA. Sample age abbreviations are as follows: L. – Lower, M. – Middle, U. – Upper, Alb. – Albian, Eo. – Eocene, Mio. – Miocene, Oligo. – Oligocene, Pal. – Paleocene. The LM images are taken from standard smear slide preparations (Young and Bown, 1998) and the SEM images are mostly taken from unprocessed sediment surfaces (Bown *et al.*, 2008). Brief taxonomic notes are provided below where appropriate. Further information on the detailed morphometrics and coccosphere geometries of Paleogene *Toweius* and *Coccolithus* and modern *Coccolithus* and *Emiliania* are given in Gibbs *et al.* (2013).

Systematic Palaeontology

Taxa mentioned in the text or illustrated in the plates are listed below in alphabetical order. Remarks, mainly regarding coccosphere observations, are given where appropriate. Abundance information is qualitative but is provided as a guide to which taxa we have found most frequently in our best preserved materials. One new species, *Biscutum braloweri* (Pl. 9, figs 1-4), is described. See Perch-Nielsen (1985), Bown (1998) and the Nannotax website (ina.tmsoc.org/Nannotax3) for full bibliographic references.

New species

Biscutum braloweri Gibbs & Bown sp. nov.

Pl. 9, figs 1-4

Derivation of name: Named after Timothy Bralower (Penn State University, USA), nannopalaeontologist, stratigrapher and palaeoceanographer. **Diagnosis:** Medium-sized elliptical bicyclic placolith with dark outer-shield image and bright tube-cycle image. The central area varies from closed to narrow with diffuse birefringence suggesting the presence of a grill or net. Coccospheres are ovoid to ellipsoidal. **Differentiation:** The coccosphere shape and variable central areas are diagnostic features. The coccoliths with open central areas are similar to *Toweius* and with closed central areas are similar to *Prinsius martinii* and *P. bisulcus*. **Dimensions:** Coccolith length ~ 6.0 µm. **Holotype:** Pl.9, fig.3. **Paratype:** Pl.9, fig. 1. **Type locality:** ODP 174X onshore drillsite at Bass River (New Jersey coastal plain, USA). **Type level:** Upper Paleocene, Sample BR85, depth 358.02 metres below surface (Zone NP9) Upper Vincetown Formation. **Occurrence:** Upper Paleocene to lowermost Eocene. Possible last occurrence recorded during the PETM CIE (Zone NP10) as *Biscutum?* sp. LO' in Gibbs *et al.* (2006). Also recorded as *Biscutum* sp. by Bralower (2002). Coccospheres found at Bass River and ODP Site 401 (Bay of Biscay, N. Atlantic Ocean), individual liths from New Jersey, Southern Ocean, Shatsky Rise (N. Pacific Ocean) and Bay of Biscay.

Taxon list

Acanthoica Lohmann, 1903

Acanthoica backmanii Dunkley Jones *et al.*, 2009

Pl. 8, fig. 8

Remarks: Collapsed coccospheres reveal coccoliths with and without spines.

Biantholithus Bramlette & Martini, 1964

Biantholithus astralis Steinmetz & Stradner, 1984

Pl. 7, figs 7-9

Remarks: Monomorphic spherical coccospheres.

Birkelundia Perch-Nielsen, 1971

Birkelundia arenosa Perch-Nielsen, 1971 Pl. 4, fig. 16
Remarks: Large placolith, but rarely reported since its first description. Large, monomorphic, spherical coccospheres.

Biscutum Black in Black and Barnes, 1959

Remarks: Rare coccospheres, usually on rock surfaces.

Biscutum braloweri Gibbs & Bown sp. nov.

Pl. 9, figs 1-4

Remarks: Coccospheres frequently observed in the PETM interval.

Biscutum constans (Górka, 1957) Black in Black and Barnes, 1959 Pl. 1, fig. 2

Remarks: Name used for a relatively broad range of coccolith morphologies, there are fewer observations on coccospheres but these are often ovoid to ellipsoidal

in shape and varimorphic, with coccoliths that become smaller towards each end.

Biscutum sp. *sensu* Covington, 1985 Pl. 1, fig. 1

Remarks: Rare, but forms striking cylindrical coccospheres.

Braarudosphaera Deflandre, 1947

Remarks: Relatively frequent coccospheres. This is a surprising given the fragility of the coccospheres (i.e., they are non-interlocking) and this may be due to the shallower water settings in which *Braarudosphaera* live or, speculatively, because they are resting cysts that sink to the seafloor after forming in the plankton. Furthermore, the absence of any proto-coccolith ring observations is suggestive of a mode of biomineralization different from the intracellular growth seen in heterococcoliths, with lith growth outside the cell wall but within a membrane most likely.

Braarudosphaera bigelowii (Gran & Braarud, 1935)

Deflandre, 1947 Pl. 7, figs 1-4

Remarks: Relatively frequent coccospheres.

Braarudosphaera aff. *B. bigelowii*

(Gran & Braarud, 1935) Deflandre, 1947

Pl. 7, figs 5-6; Pl. 8, fig. 9

Remarks: Many fossil *Braarudosphaera* specimens are similar in general form to the living species *Braarudosphaera bigelowii* but differ in lith size and sometimes in lith thickness, hence the informal designation given here. Some size variability is seen in modern *Braarudosphaera bigelowii* (Hagino *et al.*, 2009), and may reflect at least three separate species, however, far greater morphological diversity is seen in the fossil record, especially in the Paleogene.

Calcidiscus Kamptner 1950

Calcidiscus sp. Pl. 8, figs 5-6

Calciosolenia Gran, 1912

Calciosolenia fossilis (Deflandre in Deflandre & Fert, 1954) Bown in Kennedy *et al.*, 2000

Pl. 1, fig. 8

Remarks: Rare collapsed coccospheres seen on Cretaceous and Paleogene rock surfaces. Subtle variation in coccolith length, width and central area width indicates similar varimorphism to that seen on modern *Calciosolenia* coccospheres (e.g., Malinverno, 2005).

Campylosphaera Kamptner, 1963 not figured

Remarks: Frequent as coccospheres.

Chiasmolithus Hay *et al.*, 1966

Remarks: Relatively frequent coccospheres.

Chiasmolithus bidens (Bramlette & Sullivan, 1961)

Hay & Mohler, 1967 Pl. 4, figs 12-14

Remarks: Relatively frequent coccospheres. Spherical to 'boxy' spheres with relatively low number of coccoliths.

Chiasmolithus expansus (Bramlette and Sullivan, 1961)

Gartner, 1970 Pl. 4, fig. 15

Chiasmolithus nitidus Perch-Nielsen, 1971

Pl. 4, figs 9-11

Remarks: Relatively frequent coccospheres. Spherical, monomorphic coccospheres, but wide range in coccolith and coccosphere sizes.

Clausicoccus Prins, 1979 not figured

Remarks: Relatively frequent coccospheres.

Coccolithus Schwartz 1894 Pl. 3

Remarks: Common coccospheres in LM and on rock surfaces.

Coccolithus eopelagicus (Bramlette & Riedel, 1954)

Bramlette & Sullivan, 1961 Pl. 3, fig. 11

Remarks: Rare. Spherical monomorphic coccospheres.

Coccolithus pelagicus (Wallich, 1877) Schiller, 1930

Pl. 3, fig. 10

Remarks: Common coccospheres in LM and on rock surfaces. Spherical, monomorphic coccospheres.

Coronocyclus Hay *et al.*, 1966

Coronocyclus nitescens (Kamptner 1963) Bramlette &

Wilcoxon 1967 Pl. 8, fig. 7

Remarks: Rare. Spherical, monomorphic coccospheres with relatively low number of coccoliths per cell.

Craticullithus Bown, 2010

Craticullithus cancellus Bown, 2010 Pl. 8, fig. 1

Remarks: Rare. Spherical, monomorphic coccospheres.

Cruciplacolithus Hay & Mohler in Hay *et al.* 1967

Remarks: Relatively frequent coccospheres.

Cruciplacolithus filigranus Mai, 2001 Pl. 8, fig. 3

Remarks: Not reported since its original description. Mai (2001) specimens show spherical monomorphic spheres with 16-20 coccoliths, but the younger specimen shown here is a larger coccosphere with >30 coccoliths.

Remarks: Rarely seen as coccospheres in LM and on rock surfaces.

Cruciplacolithus inaequalis Perch-Nielsen, 1969

Pl. 8, fig. 2

Remarks: Relatively frequent coccospheres seen in SEM but not LM. Spherical, monomorphic coccospheres, but variable morphologies are seen, including differing size and number of coccoliths on the spheres (e.g., compare Pl. 8, fig. 2 and Bown, 2010, Pl. 10, fig. 3).

Cruciplacolithus latipons Romein, 1979 Pl. 4, fig. 18

Remarks: Spherical, monomorphic coccospheres.

Cruciplacolithus primus Perch-Nielsen, 1977

Pl. 4, figs 19-20; Pl. 8, fig. 4

Remarks: Spherical, monomorphic coccospheres, but variable morphologies are seen, including differing size and number of coccoliths on the spheres (e.g., Pl. 4, fig. 21).

Cruciplacolithus tenuis (Stradner, 1961)

Hay and Mohler in Hay *et al.*, 1967 Pl. 4, fig. 17

Cyclagelosphaera Noël, 1965

Remarks: Relatively frequent coccospheres, which are spherical and monomorphic.

Cyclagelosphaera reinhardtii (Perch-Nielsen, 1968)

Romein, 1977 Pl. 4, figs 3-4

Remarks: Species that is conspicuous in the PETM interval. Sometimes difficult to reliably distinguish from *Cyclicargolithus luminis* coccoliths (*Cyclicargolithus parvus* of Shamrock and Watkins 2012).

Cyclicargolithus Bukry, 1971

Cyclicargolithus floridanus (Roth & Hay, in Hay *et al.*,

1967) Bukry, 1971 Pl. 6, fig. 9

Remarks: Spherical, monomorphic coccospheres. Occur more frequently as spheres than other reticulofenestrids, perhaps because they have wider shields (relative to total size) that more strongly interlock.

Discorhabdus Noël, 1965

Remarks: Relatively frequently seen as coccospheres.

Discorhabdus ignotus (Górka, 1957) Perch-Nielsen,

1968 Pl. 1, fig. 4

Remarks: Relatively frequently seen as spherical to ovoid, monomorphic coccospheres.

Gladiolithus Jordan and Chamberlain, 1993

Remarks: Collapsed coccospheres are common on Tanzanian Paleogene rock surfaces.

Gladiolithus flabellatus (Halldal & Markali, 1955)

Jordan & Chamberlain, 1993 Pl. 8, fig. 11

Remarks: Collapsed coccospheres are common on Tanzanian Paleogene rock surfaces (and rare in LM) but are rarely seen elsewhere. The dimorphism and lith number seen in the collapsed coccospheres is similar to that seen in modern specimens (e.g., Young & Poulton, this volume), indicating the long-lived (~60 million years) conservation of this morphology.

Helicosphaera Kamptner, 1954

Helicosphaera carteri (Wallich 1877) Kamptner, 1954

Pl. 4, figs 1-2

Remarks: Rarely seen in fossil material but ovoid spheres with spirally arranged coccoliths and apical openings is identical morphology to that seen in living representatives. The chiral morphology of *Helicosphaera* is an adaptation that facilitates neat interlocking of coccoliths on the coccosphere (Young, 1987). This feature has been conserved through the ~52 million year evolutionary history of the genus and has arguably been enhanced by stronger development of the wing (Young, pers. comm., 2014).

Kilwalithus Bown, 2010

Kilwalithus cribrum Bown, 2010 Pl. 10, figs 1-9.

Remarks: Coccospheres are frequently seen on Tanzanian Paleogene rock surfaces and LM slides. Very small coccoliths but relatively large spheres with high numbers of liths. Spherical coccospheres with varimorphic coccoliths, some having large, arched, processes and some without.

Markalius Bramlette and Martini, 1964

Remarks: Frequently seen as coccospheres, which are spherical and monomorphic, and composed of consistent numbers of coccoliths.

Markalius apertus Perch-Nielsen, 1979 Pl. 4, figs 7-8

Remarks: Spherical, monomorphic coccospheres.

Markalius inversus (Deflandre in Deflandre and Fert, 1954) Bramlette and Martini, 1964 Pl. 4, figs 5-6

Remarks: Spherical, monomorphic coccospheres with consistent number of coccoliths (12).

Neochiastozygus Perch-Nielsen, 1971

Neochiastozygus imbrii Haq & Lohmann, 1976 Pl. 8, fig. 10

Remarks: Collapsed coccospheres rarely seen on rock surfaces and typically show varimorphism

Pontosphaera Lohmann, 1902 Pl. 2, fig. 2

Prediscosphaera Vekshina, 1959

Remarks: Rarely seen as collapsing coccospheres on rock surfaces, suggesting relatively low preservation potential.

Prediscosphaera aff. *P. columnata* (Stover, 1966)

Perch-Nielsen, 1984 Pl. 1. Fig. 5

Remarks: Monomorphic collapsed coccosphere.

Reticulofenestra Hay *et al.*, 1966

Remarks: Spherical, monomorphic coccospheres with wide range of size (~3-40µm in diameter). Considering the abundance of disaggregated coccoliths and the typical placolith structure, they are relatively rarely seen, especially the larger forms.

Reticulofenestra bisecta (Hay *et al.*, 1966) Roth, 1970

Pl. 2, fig. 4; Pl. 6, fig. 12

Remarks: Spherical monomorphic coccospheres.

Reticulofenestra dictyoda (Deflandre in Deflandre &

Fert, 1954) Stradner in Stradner & Edwards, 1968

Pl. 2, fig. 4; Pl. 6, fig. 1, 2, 4, 5, 6, 8, 10, 11

Remarks: Spherical monomorphic coccospheres.

Reticulofenestra minuta Roth, 1970 Pl. 6, fig. 3

Remarks: Spherical, monomorphic coccospheres.

Reticulofenestra pseudoumbilicus (Gartner, 1967)

Gartner, 1969; Pl. 6, fig. 13

Remarks: Spherical, monomorphic coccospheres.

Reticulofenestra umbilicus (Levin, 1965) Martini & Ritzkowski, 1968 Pl. 2, fig. 1; Pl. 6, fig. 7

Remarks: Very large, spherical, monomorphic coccospheres. Very rarely seen on rock surfaces.

Rhabdophidites Manivit, 1971 emend. Lambert, 1987

Rhabdophidites parallelus (Wind and Cepek, 1979)

Lambert, 1987 Pl. 2, fig. 3

Remarks: Collapsed coccospheres rarely seen on rock surfaces and suggest monomorphic coccospheres.

Towieus Hay & Mohler, 1967 Pl. 5

Remarks: Common coccospheres.

Towieus eminens (Bramlette & Sullivan, 1961)

Perch-Nielsen, 1971 Pl. 5, fig. 7

Towieus pertusus (Sullivan, 1965) Romein, 1979

Pl. 5, figs 2, 5, 6, 7-15

Remarks: Common coccospheres that have consistent morphology comprising cubiform spheres often made up of around 6-8 coccoliths.

Towieus serotinus Bybell & Self-Trail, 1995 Pl. 5, fig. 18

Towieus sp. Pl. 5, figs 16-17

Tranolithus orionatus (Reinhardt, 1966a) Reinhardt, 1966b Pl. 1, fig. 9

Tranolithus Stover, 1966

Umbilicosphaera Lohmann, 1902

Umbilicosphaera bramlettei (Hay & Towe, 1962)

Bown *et al.*, 2006 Pl. 4, figs 22-25

Remarks: Spherical to cubiform, monomorphic coccospheres with relatively low number of coccoliths per cell (6-8).

Watznaueria Reinhardt, 1964

Remarks: Common coccospheres, which are spherical and monomorphic.

Watznaueria barnesiae (Black, 1959) Perch-Nielsen, 1968 Pl. 1, fig. 3

Remarks: Common coccospheres, which are spherical and monomorphic.

Watznaueria fossacincta (Black, 1971a) Bown in Bown and Cooper, 1989 Pl. 2, fig. 4

Remarks: Common coccospheres, which are spherical and monomorphic.

Zeugrhabdotus Reinhardt, 1965

Remarks: Common Mesozoic coccoliths relatively frequently found as collapsed coccosphere on rock surfaces.

Zeugrhabdotus sp. Pl. 1, fig. 6 and possibly fig. 7.

Remarks: Collapsed spheres show relatively consistent coccolith size but some suggestion of varimorphism in spine length.

Acknowledgements

The discovery of many of these geological materials that contain exceptional nannofossil preservation has often resulted from the pioneering work of Paul Pearson and Bridget Wade, who have sought out these sections in their search for the best preserved planktonic foraminifera. They have been very generous in sharing their sample material and providing fruitful collaborations, more generally, and we gratefully acknowledge their generosity. We also acknowledge the provision of sample material that has come from Ocean Drilling Program and the Tanzania Drilling Program, and also for the funding of parts of this research by the Royal Society, NERC and the UK Ocean Acidification Programme. Thanks to Jeremy Young and Jorijntje Henderiks for their positive and constructive reviews, which improved the manuscript.

References

- Andruleit, H., Rogalla, U. & Stäger, S. 2004. From living communities to fossil assemblages: origin and fate of coccolithophorids in the northern Arabian Sea. *Micro-paleontology*, **50** (supl. 1): 5-21.
- Bown, P.R. 2010. Calcareous nannofossils from the Paleocene/Eocene Thermal Maximum interval of southern Tanzania (TDP Site 14). *Journal of Nannoplankton Research*, **36**: 11-38.
- Bown, P.R. & Young, J.R. 1998. Techniques. In: Bown, P.R. (Ed.), *Calcareous Nannofossil Biostratigraphy*. Kluwer Academic, London: 16-28.
- Bown, P.R., Dunkley-Jones, T., Lees, J.A., Randell, R.D., Mizzi, J.A., Pearson, P.N., Coxall, H.K., Young, J.R., Nicholas, C.J., Karega, A., Singano, J. & Wade, B.S. 2008. A Paleogene Calcareous microfossil Konservat-Lagerstätte from the Kilwa Group of coastal Tanzania. *GSA Bulletin*, **120**: 3-12.
- Bown, P. R., Dunkley Jones, T., Young, J.A. & Randell, R. 2009. A Palaeogene record of extant lower photic zone calcareous nannoplankton. *Palaeontology*, **52**: 457-469.
- Bralower, T.J. 2002. Evidence of surface water oligotrophy during the Paleocene-Eocene Thermal Maximum: Nannofossil assemblage data from Ocean Drilling Program Site 690: Maud Rise, Weddell Sea. *Paleoceanography*, **17**: 1-13.
- Covington, J.M. 1985. New morphologic information on Cretaceous nannofossils from the Niobrara Formation (Upper Cretaceous) of Kansas. *Geology*, **13**: 683-686.
- Dunkley Jones, T., Bown, P.R. & Pearson, P.N. 2009. Exceptionally well preserved upper Eocene to lower Oligocene calcareous nannofossils (Prymnesiophycidae) from the Pande Formation (Kilwa Group), Tanzania. *Journal of Systematic Palaeontology*, **7**: 359-411.
- Gibbs, S.J., Bown, P.R., Sessa, J.A., Bralower, T.J. & Wilson, P.A. 2006. Nannoplankton origination and extinction across the Paleocene-Eocene Thermal Maximum. *Science*, **314**: 1770-1773.
- Gibbs, S.J., Poulton, A.J., Bown, P.R., Daniels, C., Hopkins, J., Young, J.R., O'Dea, S.A., and Newsam, C. 2013. A cellular perspective on plankton sensitivity to past global climate change. *Nature Geoscience*, **6**: 218-222.
- Hagino, K., Takano, Y. & Horiguchi, T. 2009. Pseudocryptic speciation in *Braarudosphaera bigelowii* (Gran and Braarud) Deflandre. *Marine Micropaleontology*, **72**: 210-221.
- Henderiks, J. 2008. Coccolithophore size rules - Reconstructing ancient cell geometry and cellular calcite quota from fossil coccoliths. *Marine Micropaleontology*, **67**: 143-154.
- Henderiks, J. & Pagani, M. 2007. Refining ancient carbon dioxide estimates: Significance of coccolithophore cell size for alkenone-based pCO₂ records. *Paleoceanography*, **22**: PA3202, doi:10.1029/2006PA001399.
- Honjo, S. 1976. Coccoliths: production, transportation and sedimentation. *Marine Micropaleontology*, **1**: 65-79.
- Kleijne, A. 1992. Extant Rhabdosphaeraceae (coccolithophorids, class Prymnesiophyceae) from the Indian Ocean, Red Sea, Mediterranean Sea and North Atlantic Ocean. *Scripta Geologica*, **100**: 1-63.
- Lambert, B. 1987. Nannofossiles calcaires de l'Albien supérieur et du Vraconnien du Cameroun méridional. *Cahiers de micropaleontology*, **2**: 33-60.
- Mai, H., von Salis Perch-Nielsen, K., Willems, H. & Romein, A.J.T. 1997. Fossil coccospheres from the K/T boundary section from Geulhemmerberg, The Netherlands. *Micropaleontology*, **43**: 281-302.
- Mai, H. 2001. New Coccolithophorid Taxa from Geulhemmerberg Airshaft, Lower Paleocene, the Netherlands. *Micropaleontology*, **47**: 144-154.
- Malinverno, E. 2004. Morphological variability within the genus *Calciosolenia* (coccolithophorids) from the eastern Mediterranean Sea. *Micropaleontology*, **50** (supl. 1): 81-91.
- Perch-Nielsen, K., 1985. Cenozoic calcareous nannofossils. In: H.M. Bolli, J.B. Saunders & K. Perch-Nielsen (Eds), *Plankton Stratigraphy*. Cambridge University Press, Cambridge: 427-554.
- Shamrock, J.L. & Watkins, D.K. 2012. Eocene calcareous nannofossil biostratigraphy and community structure from Exmouth Plateau, Eastern Indian Ocean (ODP-Site 762). *Stratigraphy*, **9**: 1-54.
- Wise, S.W. 1977. Chalk formation: early diagenesis. In N.R. Anderson & A. Malahoff (Eds), *The fate of fossil fuel CO₂ in the oceans*. New York, Plenum Publishing Corp.: 717-739.
- Young, J.R. 1987. Possible functional interpretations of coccolith morphology. *Abhandlungen der Geologischen Bundesanstalt*, **39**: 305-313.
- Young, J.R., Bergen, J.A., Bown, P.R., Burnett, J.A., Fiorentino, A., Jordan, R.W., Kleijne, A., van Niel, B.E., Romein, A.J.T. & Salis, K.v. 1997. Guidelines for coccolith and calcareous nannofossil terminology. *Palaeontology*, **40**: 875-912.
- Young, J.R. & Bown, P.R. 1991. An ontogenetic sequence of coccoliths from the Late Jurassic Kimmeridge Clay of England. *Palaeontology*, **34**: 843-850.
- Young, J.R., Geisen, M., Cros, L., Kleijne, A., Sprengel, C., Probert, I. & Ostergaard, J. 2003. A guide to extant coccolithophore taxonomy. *Journal of Nannoplankton Research Special Issue* **1**.
- Young, J.R., Geisen, M., & Probert, I. 2005. A review of selected aspects of coccolithophore biology with implications for paleodiversity estimates. *Micropaleontology*, **51**: 267-288.
- Young, J.R., Bown, P.R. & Lees, J.A. 2014. Nannotax3: <http://ina.tmsoc.org/Nannotax3>.
- Young, J.R. & Poulton, A.J. this volume. *Gladiolithus adeyi* a new deep photic coccolithophore species. *Journal of Nannoplankton Research*.

Plate 1

Examples of placolith coccospheres and murolith coccospheres

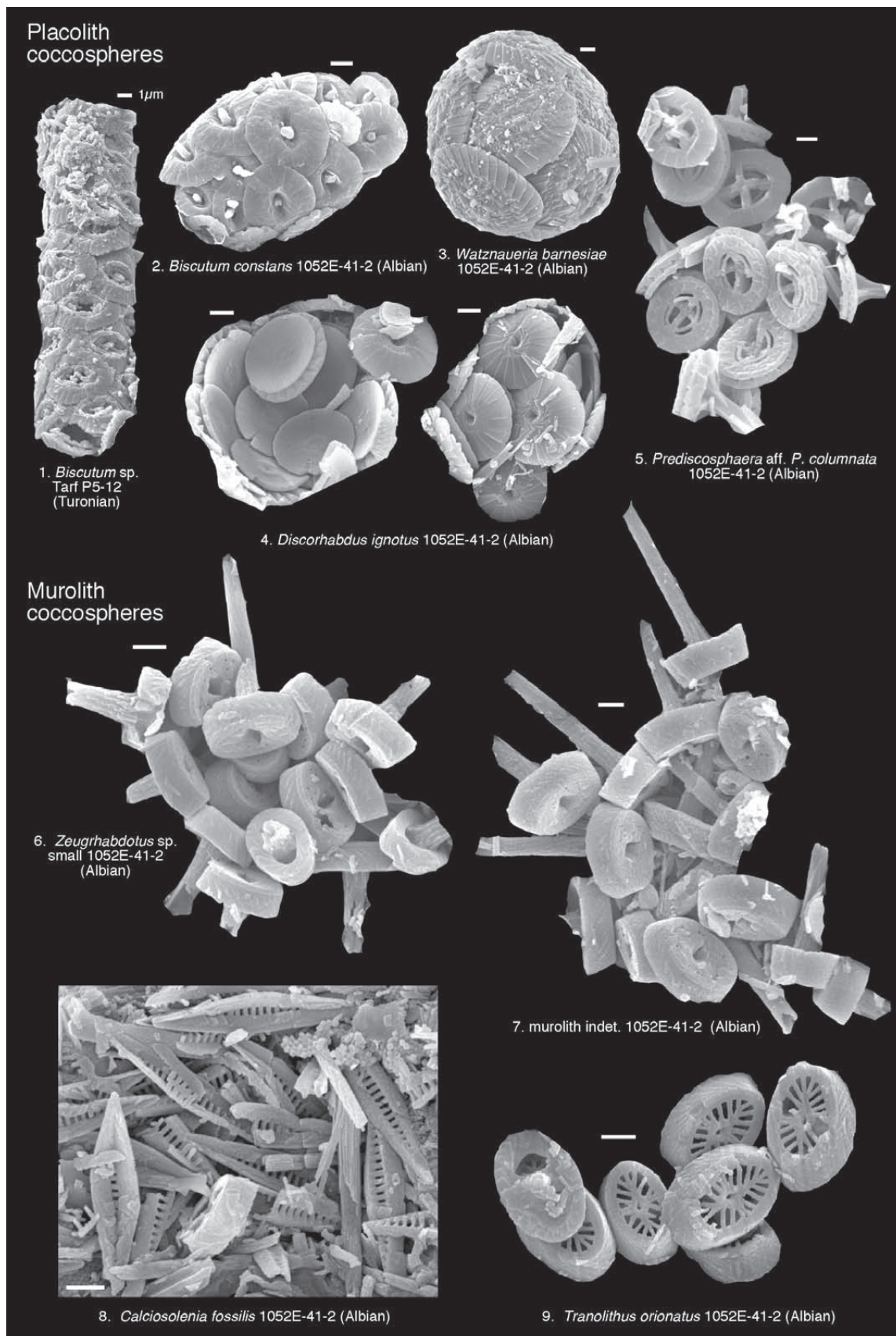
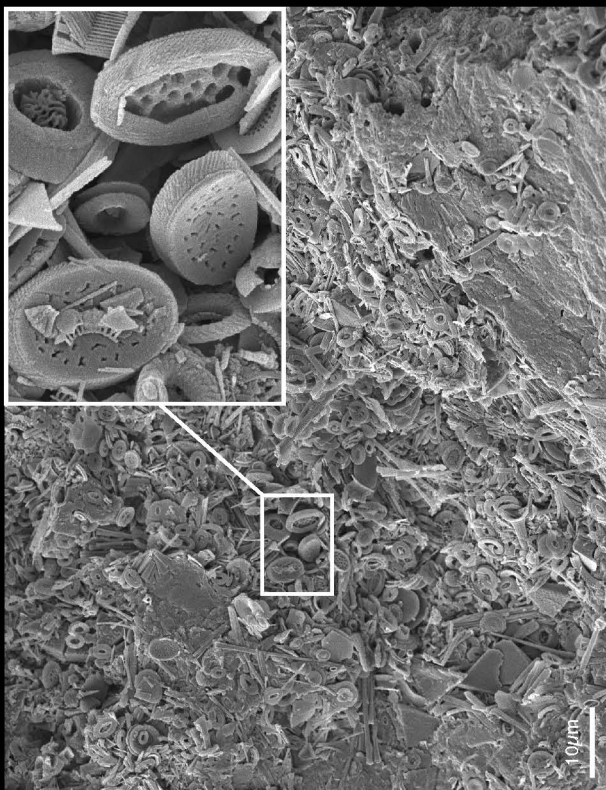
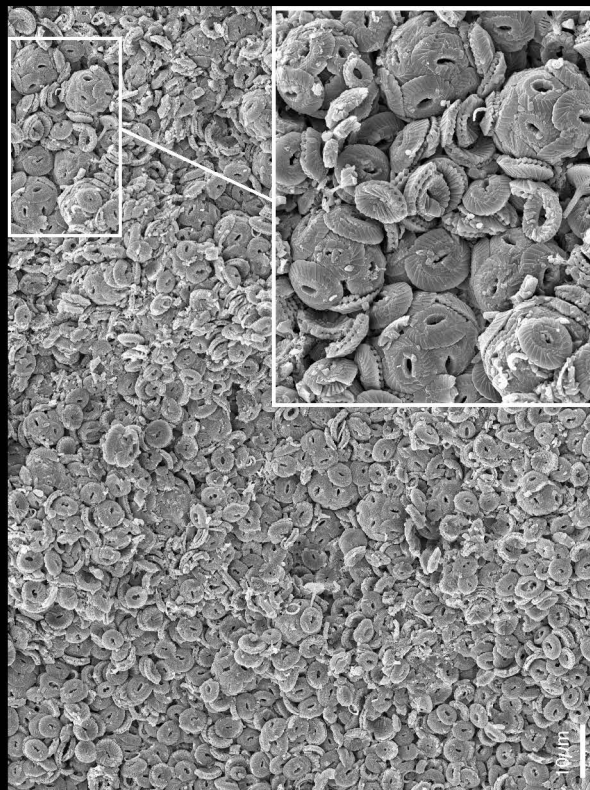


Plate 2

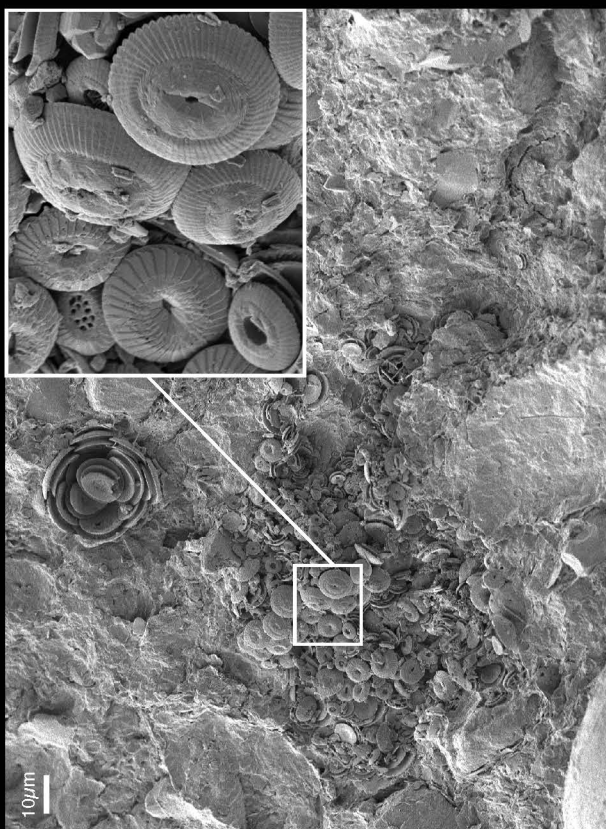
Examples of rock surfaces with coccospheres



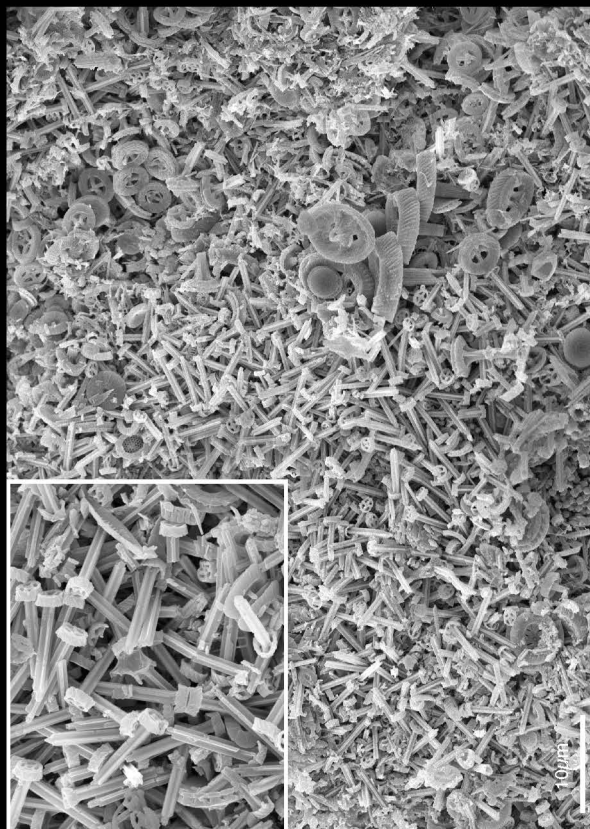
2. *Pontosphaera*, etc. TDP Site 12, Tanzania (U. Eocene)



4. *Watznaueria fossilis* Kimmeridge White Stone Band, UK (U. Jurassic)



1. *Reticulofenestrula*, etc. TDP Site 12, Tanzania (U. Eocene)



3. *Rhabdophidites parallelus* ODP Site 1052, N. Atlantic (Albian, L. Cretaceous)

Plate 3

Coccolithus pelagicus

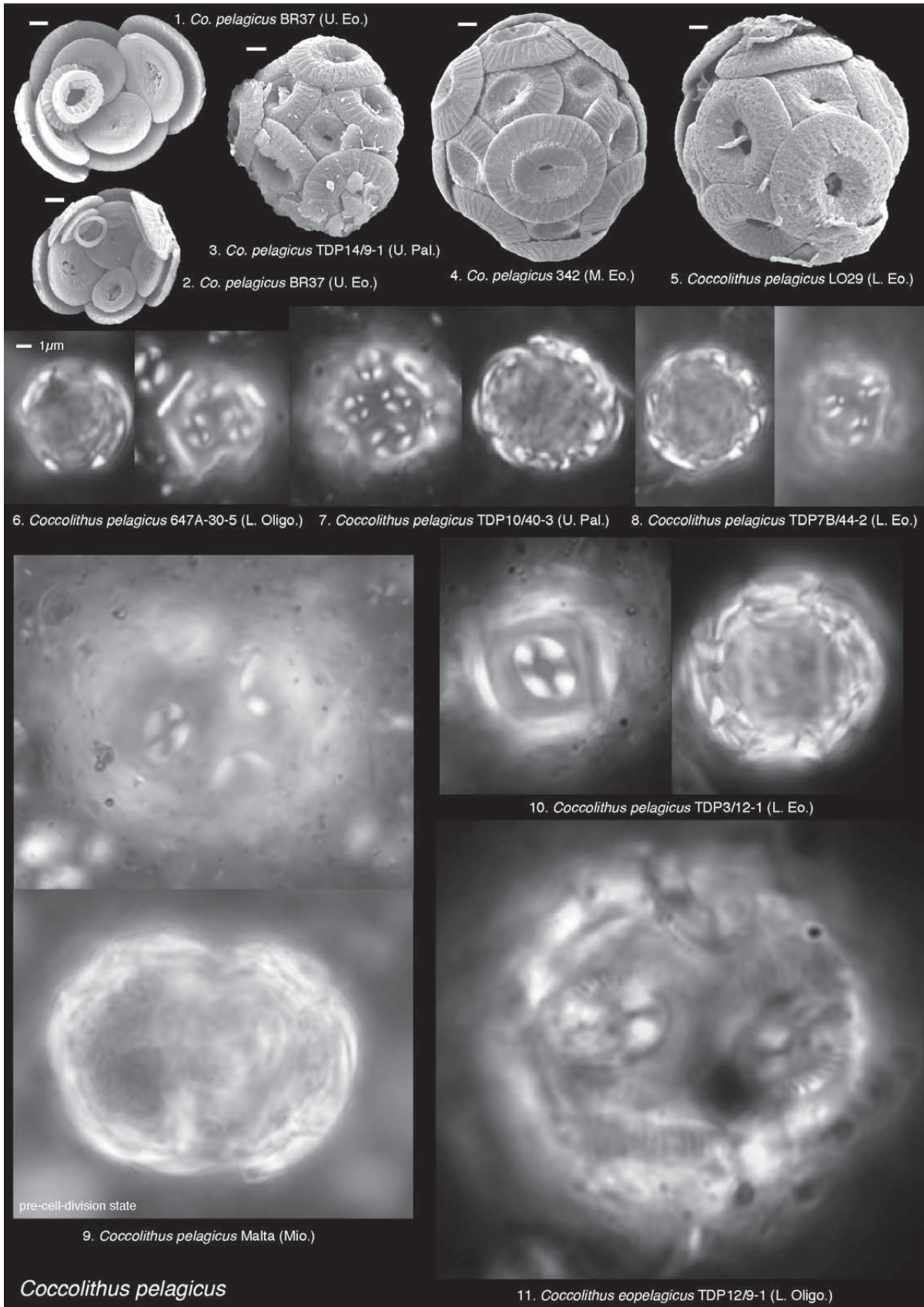


Plate 4

Helicosphaeraceae, Coccolithaceae and Calcidiscaceae

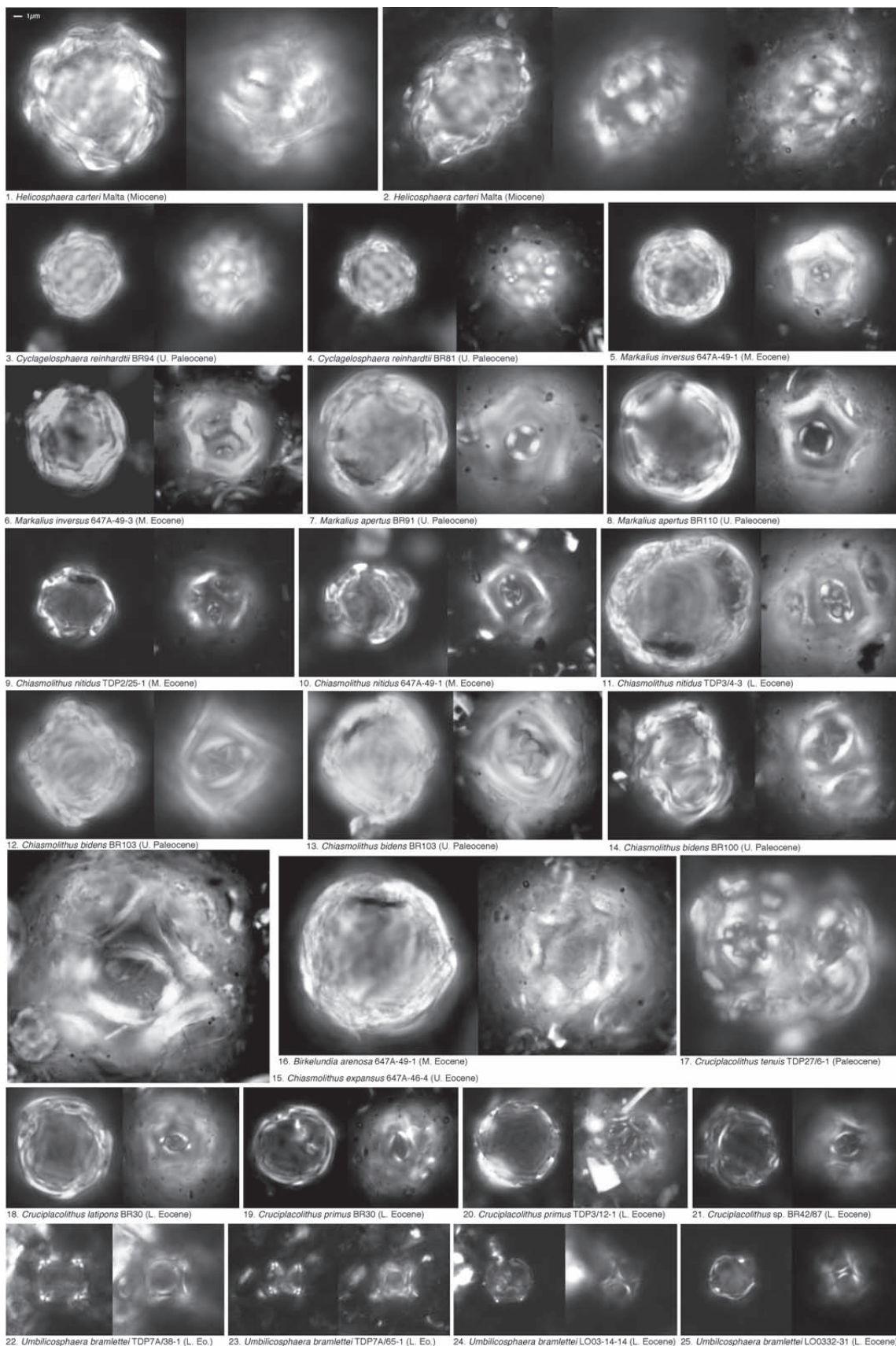


Plate 5

Prinsiaceae

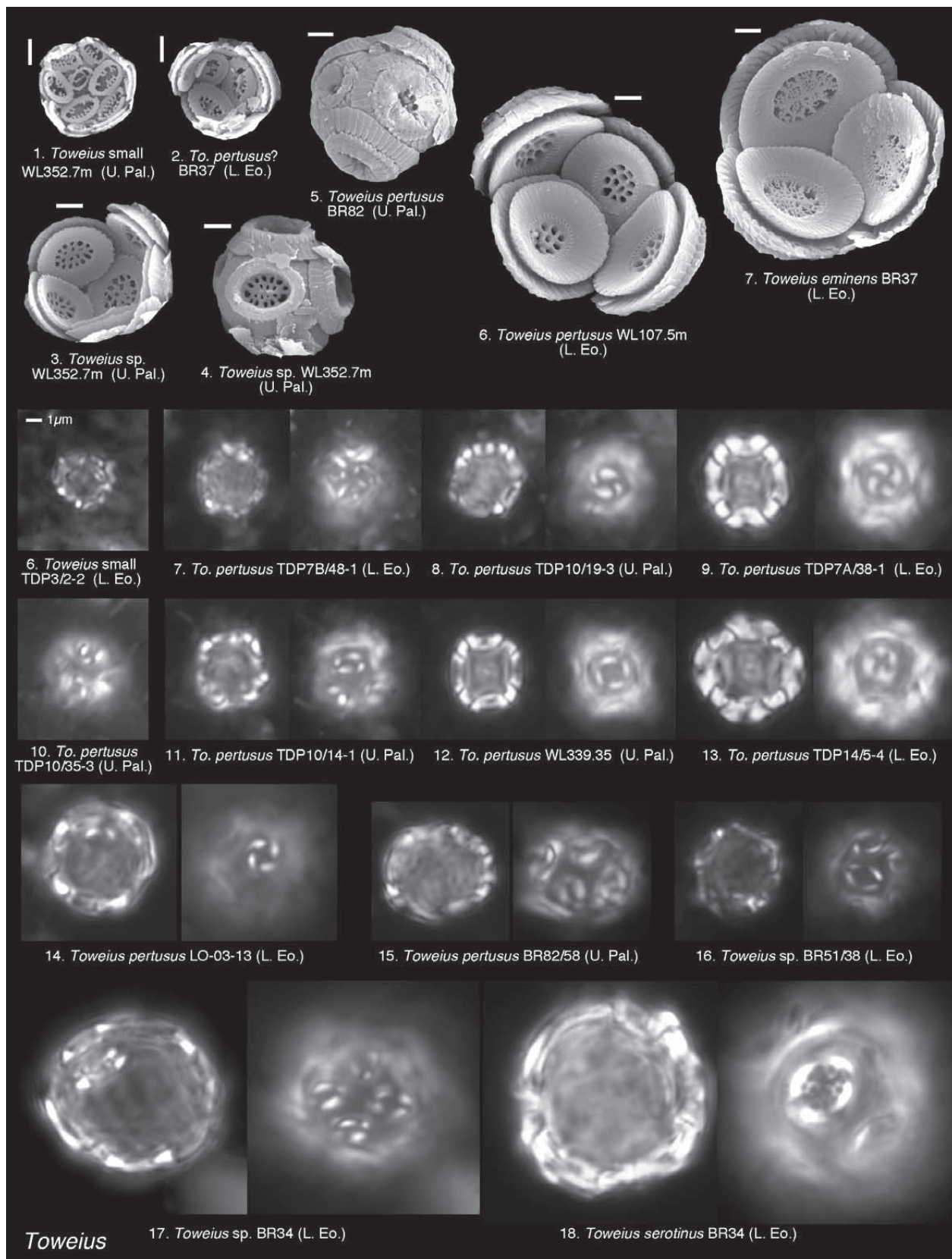


Plate 6

Reticulofenestra

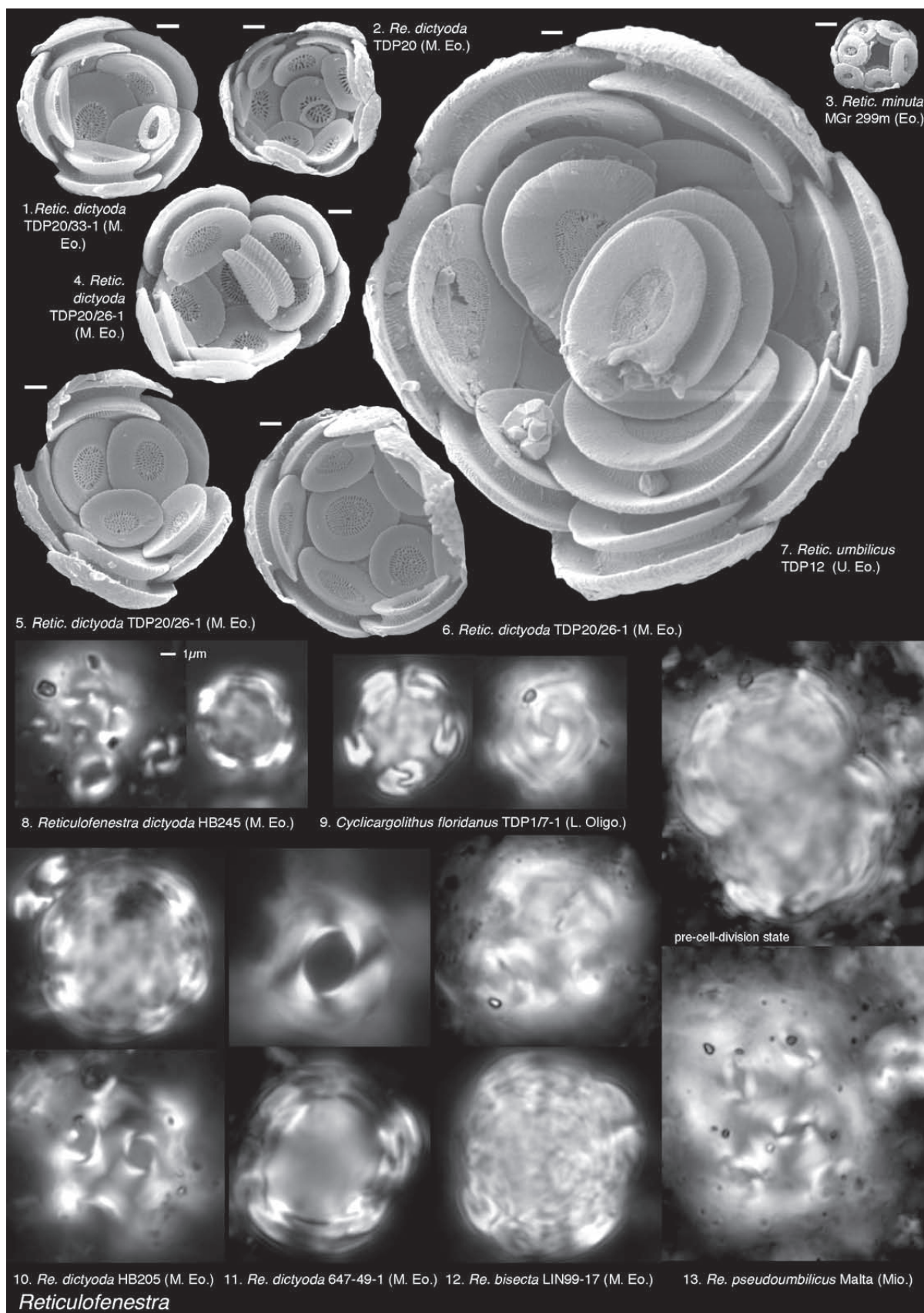


Plate 7

Braarudosphaera and *Biantholithus*

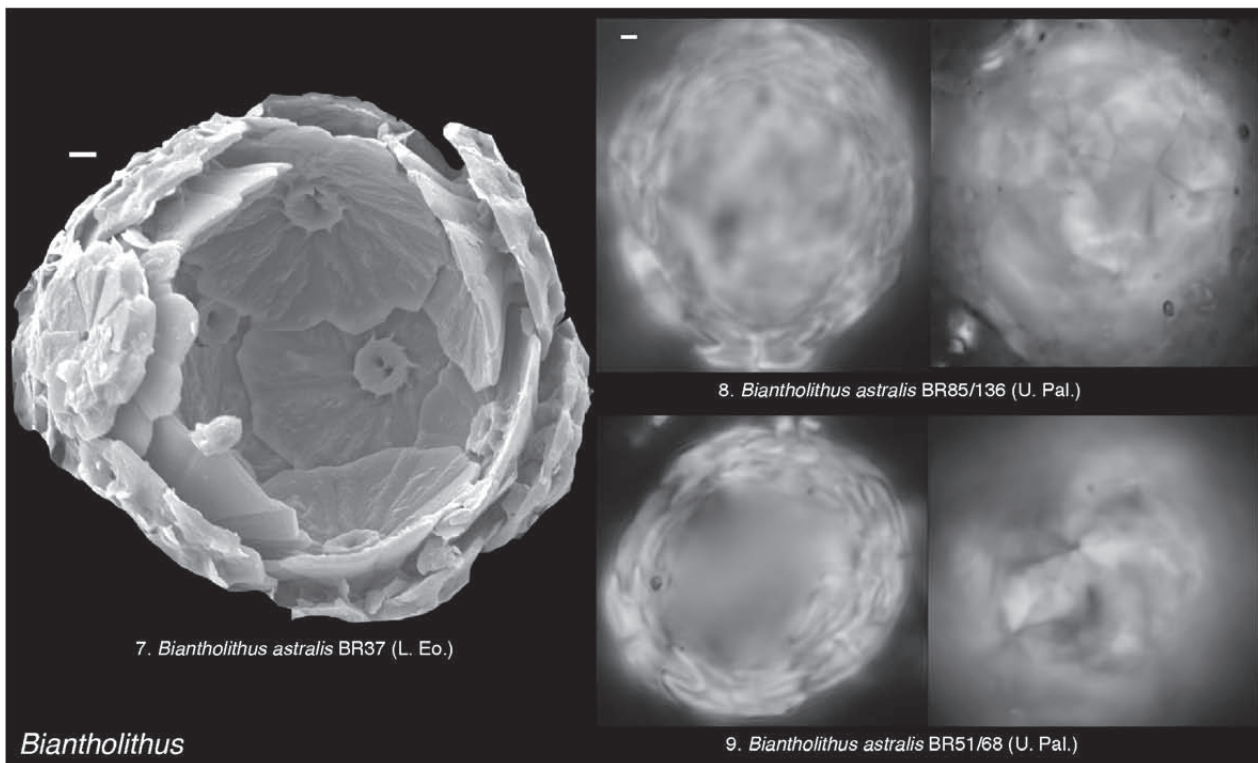
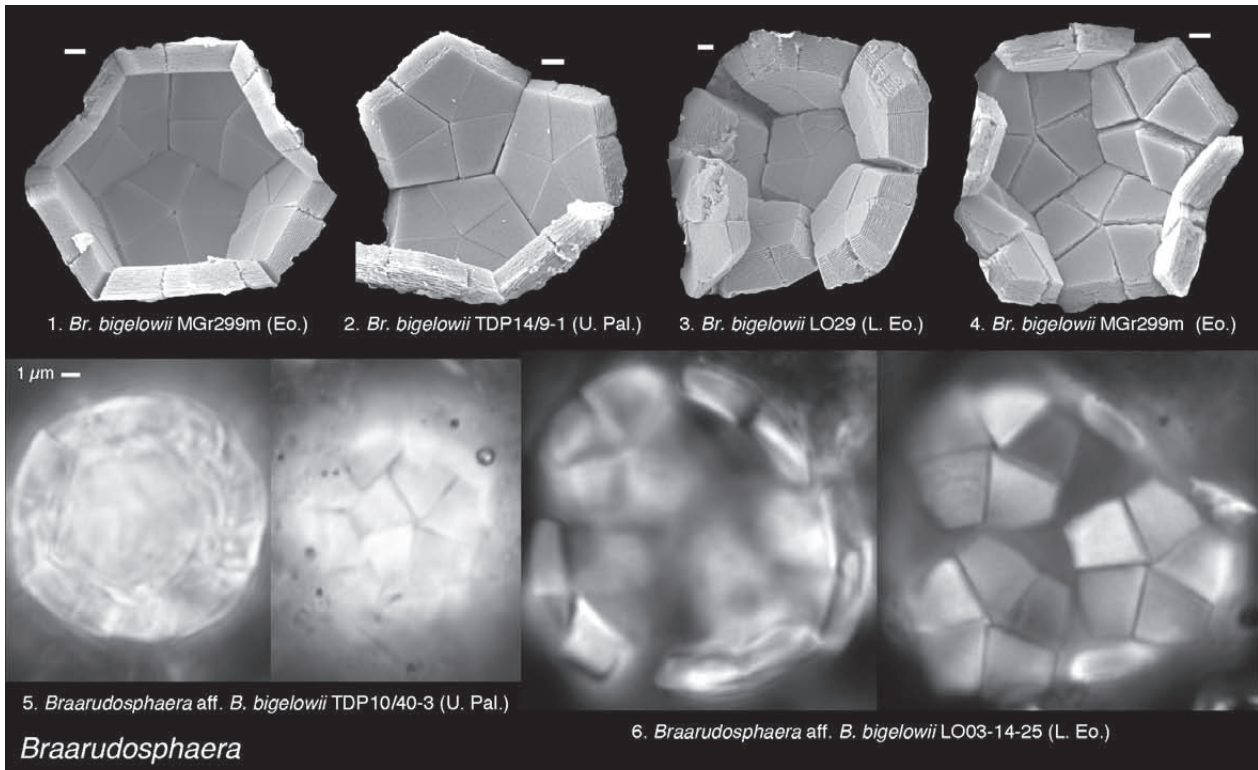


Plate 8

Miscellaneous

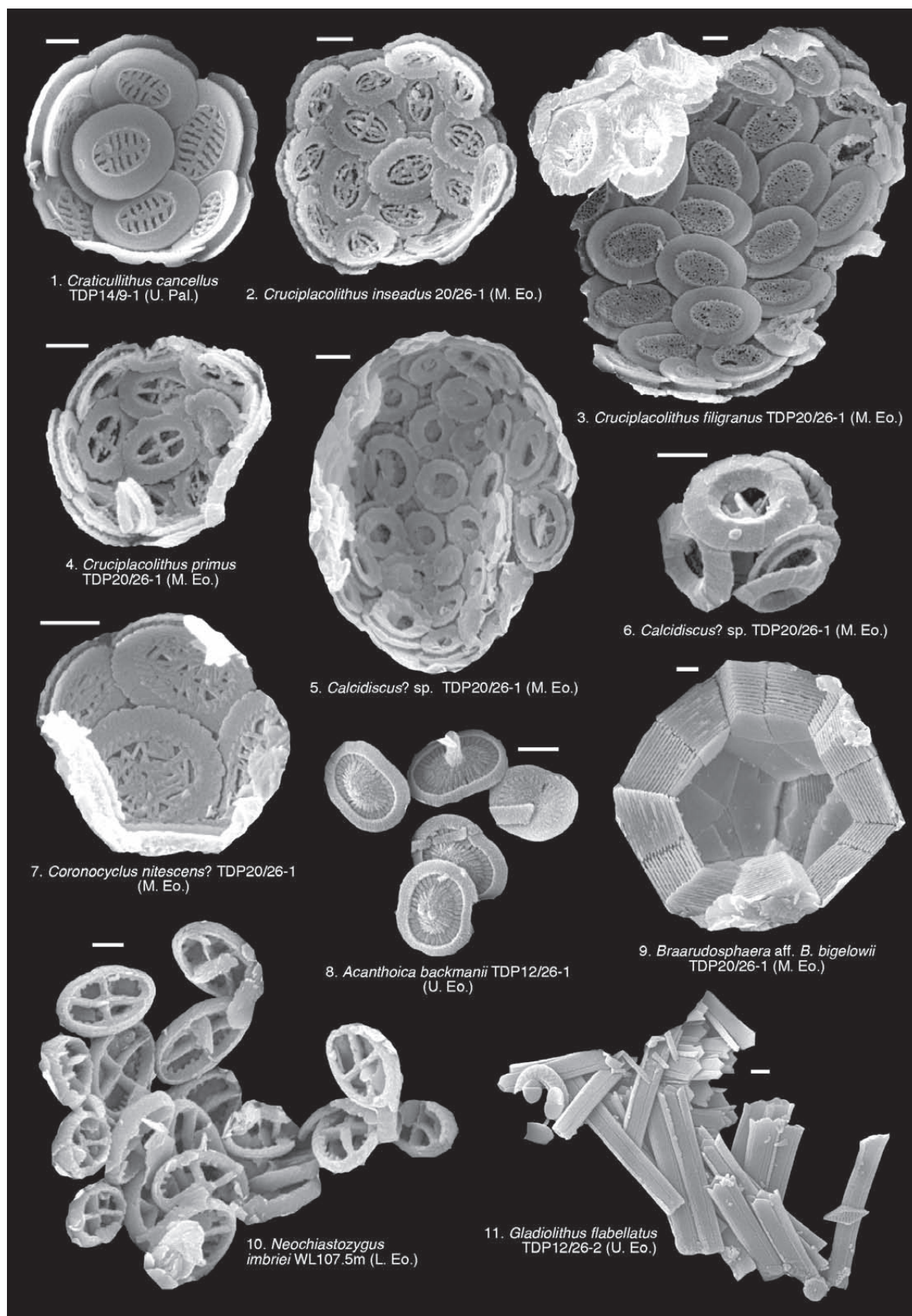
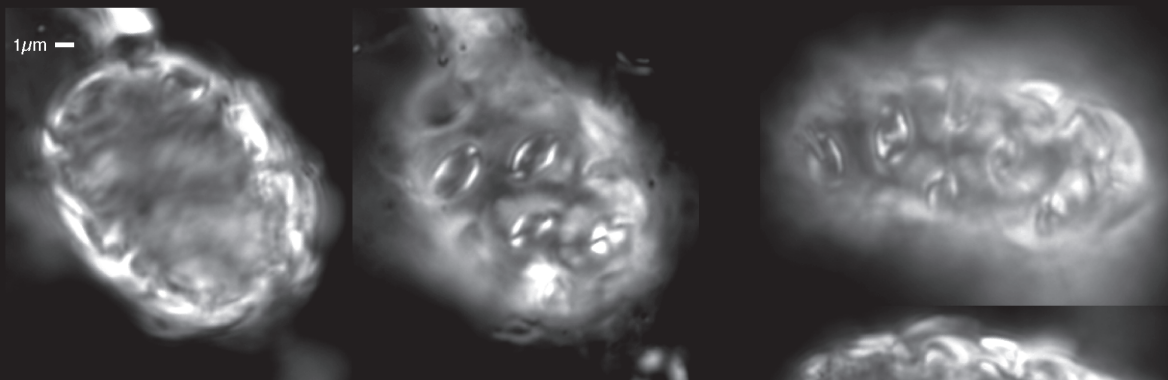
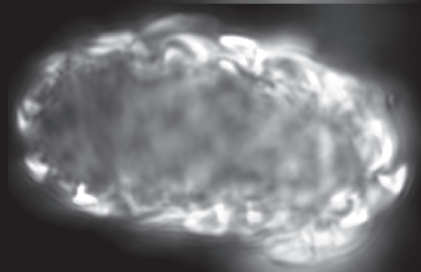


Plate 9

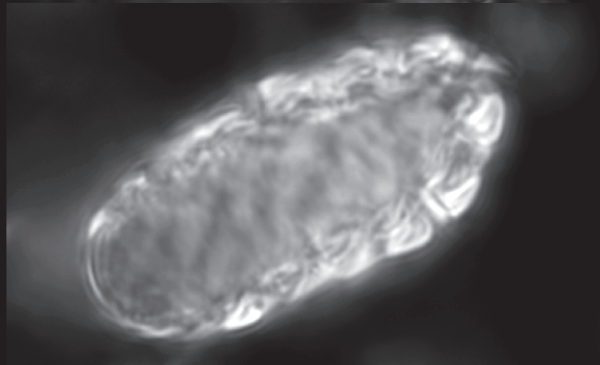
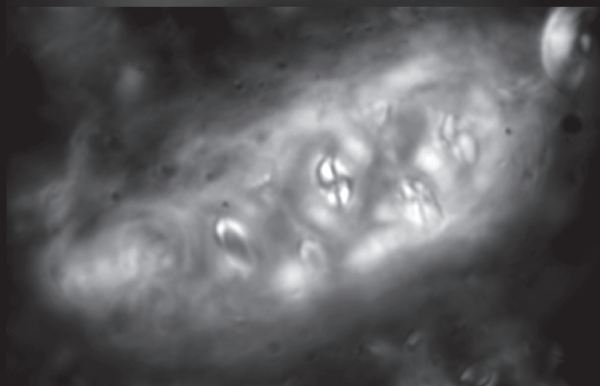
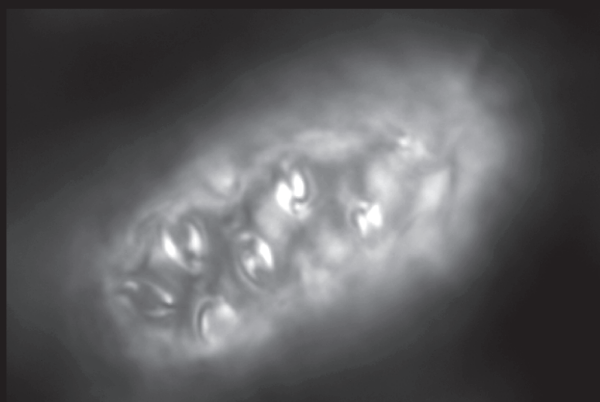
Biscutum braloweri



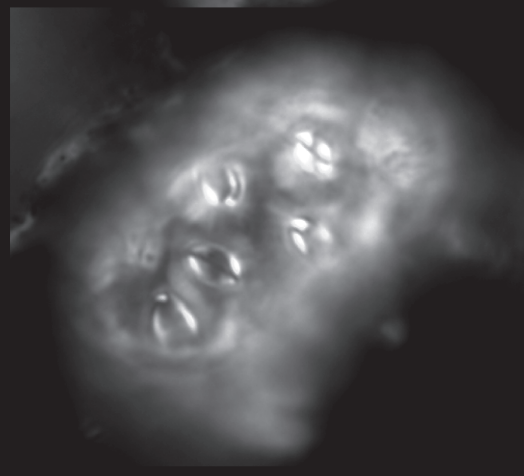
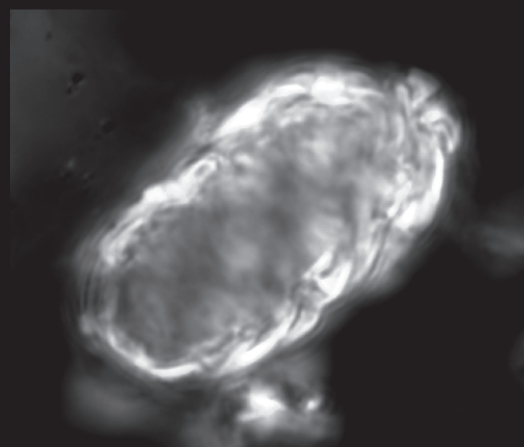
1. *Biscutum braloweri* BR100 (U. Pal.)



2. *Biscutum braloweri* BR100 (U. Pal.)



3. *Biscutum braloweri* BR85 (U. Pal.)



4. *Biscutum braloweri* BR100 (U. Pal.)

Biscutum braloweri sp. nov.

Plate 10

Kilwalithus cribrum

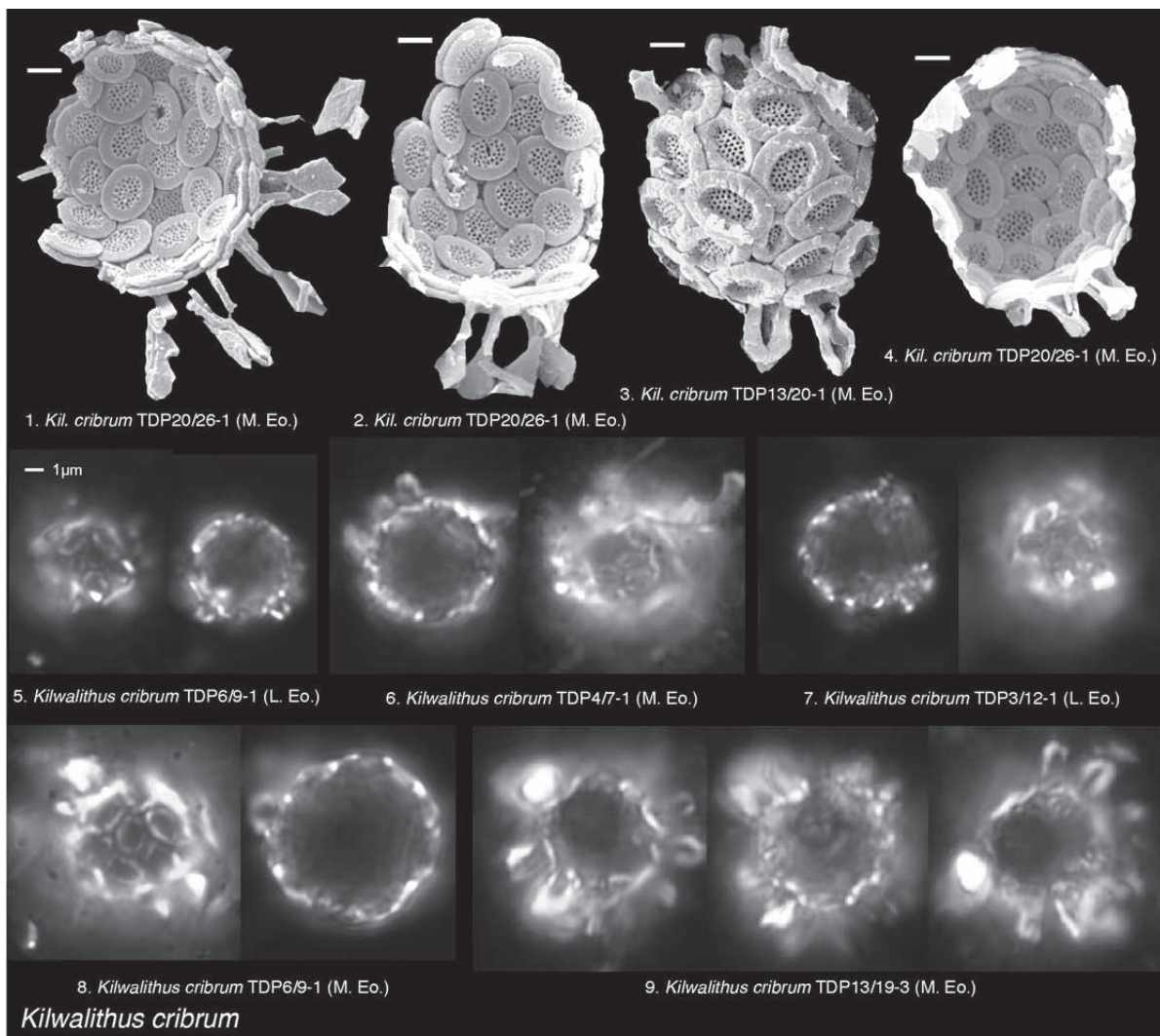
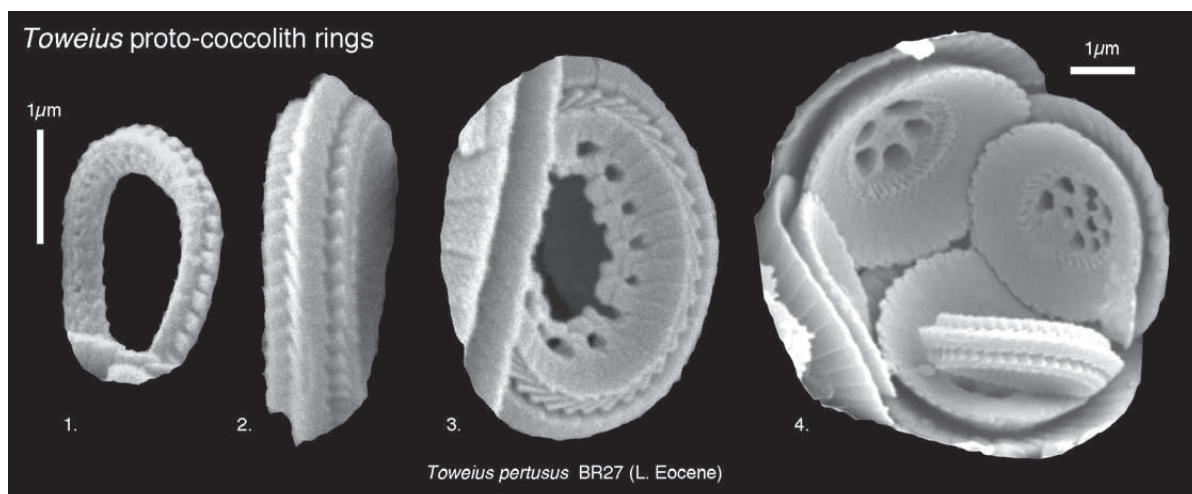


Plate 11

Toweius protococcolith rings



PDF vs. Published copy

In the published version of this paper the images on plate 9 were mislabelled, this has been corrected in this PDF version. In addition plate 2 has been rotated. No other changes have been made.

JRY Nov. 2014