On the Cretaceous origin of the Order Syracosphaerales and the genus *Syracosphaera*

Paul R. Bown, Jeremy R. Young & Jacqueline A. Lees[*]

Department of Earth Sciences, University College London, Gower Street, London WC1E 6BT, UK
[*] Correspondence: j.lees@ucl.ac.uk

Abstract: New scanning electron microscope observations of unadulterated calcareous nannofossil assemblages on lamina surfaces of Cretaceous Tanzania Drilling Project sediments reveal high diversity in the <3 μm size-range and high abundances of small and frangible morphologies. These assemblages prompt comparison to modern assemblages, which show similar high diversity and abundance of very small and fragile taxa, although these assemblages are generally not preserved in the fossil record due to taphonomic filtering. Not only are there broad similarities between the general composition of modern assemblages and those of the Tanzanian *lagerstätte*, but also our discovery of several new Cretaceous taxa provides evidence for greatly extended fossil lineages of extant orders, with implications for both deep-time biodiversity divergence and survival through the end-Cretaceous mass extinction. Our findings include: new species that are the first-recorded Mesozoic representatives of the extant Syracosphaeraceae and Papposphaeraceae; potentially previously unrecorded diversity in the Mesozoic Calciosoleniaceae, another extant order, represented by extant species that have been described already; and new species and unusually high abundances of the Mesozoic Stephanolithiaceae. We also highlight the extended range of an *incertae sedis* Cenozoic genus, *Ellipsolithus*, into at least the Turonian.

   Here, we describe seven new miniscule to very small Cretaceous species: *Syracosphaera antiqua*, *S. repagula*, *Pocillithus macleodii*, *P. crucifer*, *Stradnerlithus wendleri*, *S.? haynesiae* and *Tortolithus foramen*.

Keywords: Syracosphaerales, Syracosphaeraceae, Rhabdosphaeraceae, Calciosoleniaceae, Stephanolithiaceae, Cretaceous, Turonian, Tanzania Drilling Project

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The second phase of the Tanzania Drilling Project (TDP, 2007 – 09) primarily targeted Cretaceous stratigraphy and recovered sediments that extend the Kilwa Group microfossil *lagerstätte* down through a Maastrichtian to Aptian succession. Analysis of the Paleogene Kilwa Group led to the surprising discovery of many extant coccolithophorid taxa that had little or no previous fossil record (e.g. *Gladiolithus*, *Syracosphaera*, *Algirosphaera*, *Acanthoica*, papposphaerids: Dunkley Jones *et al.* 2009). Using material from the Cretaceous TDP drilling, we have been looking to see if such taxa ranged into even older time intervals. This is of particular interest because the end-Cretaceous mass extinction event ostensibly saw the loss of the majority of Mesozoic coccolithophores, with most of the modern groups originating in the subsequent Paleocene radiation (e.g. Bown *et al.* 2004). One of our primary search targets was *Syracosphaera* and other syracosphaeralids, as this is the most diverse group of extant coccolithophores (Young *et al.* 2003), with deep (Early Jurassic) divergence times indicated by molecular phylogenies (Medlin *et al.* 2008; Young *et al.* 2014), but particularly poor preservation potential due to this group's small and fragile coccolith morphologies, as we explain below. We report here on our discovery of a diversity of miniscule to very small coccoliths from the Turonian of Tanzania, some of which closely resemble *Syracosphaera* coccoliths. The presence of these coccoliths, and another syracosphaeralid genus, *Calciosolenia*, confirms the Cretaceous record of this significant group.

The fossil record of calcareous nannoplankton indicates an origination of the group in the Late Triassic, with major diversification events in the Early Jurassic and Early Paleocene (Bown *et al.* 2004). The Paleocene radiation followed the almost complete elimination of the group at the Cretaceous/Paleogene (K/Pg) mass extinction, and the originations of most modern coccolithophore groups have been recorded from this time, including the Coccolithales, Isochrysidales

and Zygodiscales. These particular orders have relatively large and/or robust coccoliths and, consequently, provide long and consistent fossil records that allow evolutionary history reconstructions with strong stratophenetic support. A significant proportion of the modern coccolithophore diversity, however, is less well represented in the fossil record and so the timings of significant evolutionary innovations, such as the first appearance of the Syracosphaeraceae and origination of deep photic-zone taxa (e.g. *Gladiolithus*), has remained uncertain or unknown. The Tanzanian microfossil *lagerstätte* provides a unique preservational window, revealing previously unseen diversity of small and fragile coccoliths, and includes records of evolutionary lineages not previously found in the fossil record.

Nannofossils are commonly used as biostratigraphic markers and palaeoceanographic proxies, but despite this widespread use, our knowledge of their taphonomy is still incomplete. It is often assumed that assemblages in seafloor sediments and ancient sedimentary rocks relatively faithfully represent the living populations from which they derive. This assumption has been challenged through the comparison of plankton, sediment-trap and seafloor assemblages (e.g. Roth & Coulbourn 1982; Andruleit *et al.* 2004) and through advances in the documentation of living coccolithophore species, many of which produce small, fragile and/or weakly-calcified coccoliths that are not represented in modern seafloor sediments or the Holocene fossil record (Young *et al.* 2003, 2005; Andruleit *et al.* 2004). Findings show that, typically, coccoliths that are <3 μm in length are unlikely to enter the fossil record, but larger, fragile coccoliths are equally subject to destruction by mechanical and chemical taphonomic processes acting in the photic zone during export and within the sediment through lithification and diagenesis. This taphonomic bias applies to smaller coccoliths, in particular, because they are more likely to be destroyed during grazing, they

typically sink more slowly until incorporated in marine snow, and thus they are more susceptible to dissolution in the water column. If they *are* incorporated into seafloor sediments, they are then more liable to be obliterated by recrystallization, with synchronous dissolution of small crystals and overgrowth of large ones (Wise 1977). Post-sampling, smaller coccoliths are also more likely to be destroyed through preparation techniques, including the making of relatively low-impact smear or settling slides, and they are typically more difficult to observe in the light microscope (LM). Overall, a high degree of assemblage transformation occurs in the water column (e.g. Andruleit *et al.* 2004) and this is then amplified during post-depositional diagenesis (Wise 1977).

This taphonomic loss is mostly biased towards a small number of modern groups, but these include the most diverse order, the Syracosphaerales, plus a number of less diverse, but functionally significant, groups, such as deep photic-zone, coastal and high-latitude forms (e.g. *Gladiolithus*, *Pleurochrysis*, *Papposphaera*). Typically, one out of four extant orders and seven out of 17 extant families are poorly represented in the fossil record (Young *et al.* 2005). The poor fossil record of the Syracosphaerales is a particularly significant gap in our understanding of the Cenozoic evolutionary history of coccolithophores and we have not known whether the proliferation of syracosphaeralid coccolithophores, with small, lightly calcified coccoliths, was a relatively recent, Late Neogene phenomenon, or a much longer-lived, but unrecorded, Mesozoic or Early Cenozoic feature of the group.

It has been suggested that one other Mesozoic coccolith group, the small, delicate stephanolithids (Stephanolithiaceae), is a possible Syracosphaerales relative, based on morphological similarities, including multi-bar central-area structures and comparable, but not identical, rim morphology (Perch-Nielsen 1985; Bown & Young 1997). Coccolithophore molecular phylogenetics suggests that the Syracosphaerales had a deep divergence, possibly rooted in the Early Jurassic diversification (Medlin *et al.* 2008; Young *et al.* 2014). In order to address the question of the evolutionary roots of the Syracosphaerales, we need to study exceptionally-preserved assemblages, such as those sampled by the TDP.

Morphology and fossil record of the groups discussed

Syracosphaerales

The Order Syracosphaerales comprises the families Calciosoleniaceae, Rhabdosphaeraceae and Syracosphaeraceae. It is the most diverse living coccolithophore group, accounting for *c.* 25% of modern species (*c.* 75 out of 280 species: Young *et al.* 2003, 2005). These three families are united by possession of similar coccolith structure (Figs 1 and 2): the rim is typically narrow (Figs 1b and 2a, d) and shows regular crystallographically vertical/radial (V/R-) unit structure (Figs 1a, c and 2b, e), whilst the central-area is formed from a disjunct cycle of radial laths (Figs 1a, b, g–i and 2a, b, e, f) and often a central structure formed from additional elements (Figs 1b and 2a, d). The radial laths interdigitate with the rim units, and there is typically the same number of these laths as there are rim units, but the radial laths show tangential *c*-axis orientation (i.e. T-units: Young *et al.* 2003, 2004; Figs 1a, c and 2b, e). The central-area structures show highly variable morphology, especially in the Rhabdosphaeraceae (e.g. Young *et al.* 2003; Probert *et al.* 2007).

Syracosphaeraceae

The rim structure of *Syracosphaera pulchra* has been described in detail by Inouye & Pienaar (1988) and Young *et al.* (2004), who added crystallographic interpretations based on LM crystal form. The rim is composed of a lower cycle of V-units and an upper cycle of R-units, with a peg-like extension to the protococcolith ring locus, which is near the proximal surface (Fig. 1c and g). The central-area laths interdigitate with the rim units (Fig. 1c), but have tangential *c*-axis orientation. Other species of *Syracosphaera*, and the genera *Ophiaster*, *Calciopappus* and *Michaelsarsia*, have similar rim-structures, but with variable development of the V- and R-cycles; typically the R-unit forms most of the rim, as exemplified in Figure 1a by *Ophiaster*. In *Coronosphaera*, the structure is similar, but the R-units show strong anticlockwise imbrication.

Rhabdosphaeraceae

The structure of the Rhabdosphaeraceae has been described many times (e.g. Aubry 1988; Varol 1989; Kleijne 1992) and modern species of *Algirosphaera* and *Rhabdosphaera* have been described in particular detail (Probert *et al.* 2007; van de Locht *et al.* 2014). The rim consists of an upper/outer cycle with radial sutures and a lower/inner cycle with strongly oblique sutures (Figs 1h and 2b, c). A radial lath cycle typically interdigitates with the lower rim cycle units (Fig. 2b and c), although this cycle is absent in *Rhabdosphaera*, whilst in *Blackites* there are typically more laths per rim-unit. Observations of Rhabdosphaeraceae coccoliths are not easy in the LM, since the coccoliths are typically small and the rim cycles are closely appressed; however, the larger, upper/outer cycle appears to be formed of V-units and the lower/inner cycle formed of R-units (e.g. Bown 2005, pl. 26, figs 16–24; Fig. 2b).

Calciosoleniaceae

In the Calciosoleniaceae, the rim is again elevated to give a murolith form, with a well-developed lath cycle in the central-area (Figs 1i and 2d–f). These coccoliths have been described in detail by Manton & Oates (1985) and Malinverno (2004), but the rim structure and crystallography have not been well documented, so we briefly describe it here. In distal view, it is often clear that there are two layers or cycles to the wall (Malinverno 2004; Fig. 2e) and, by comparing specimens in various orientations, it can be seen that the inner cycle extends to the proximal surface and underlies the outer cycle (Figs 1i and 2f). In cross-polarized light, the inner cycle is strongly birefringent (Fig. 2h), with radial crystallographic orientation (R-units), whilst the outer cycle is weakly birefringent (Fig. 2g and i), implying subvertical orientation (V-units). The inner cycle is typically better developed in the coccoliths situated toward the ends of the coccosphere and so this part of the coccosphere shows the highest birefringence. This V/R structure is the reverse of that shown by the Syracosphaeraceae, i.e. V-units form the outer/upper rim cycle in *Calciosolenia*, but the lower/inner cycle in *Syracosphaera* (compare Fig. 1g and i). This difference justifies retaining the Calciosoleniaceae as a separate family, at least until molecular genetic data are available. It is also notable that the rim structure of *Calciosolenia* is very similar to that of the Mesozoic stephanolithids.

Occurrence of Syracosphaerales

To date, the only members of the Syracosphaerales for which molecular genetic data are available are *Syracosphaera pulchra*, *Coronosphaera mediterranea* and *Algirosphaera robusta*. These cluster together in most analyses, supporting the inference from traditional taxonomy that they are closely related (e.g. Sáez *et al.* 2004; Young *et al.* 2005, 2014).

In the fossil record, the Rhabdosphaeraceae can be unambiguously identified by their distinctive rim structure and formation of prominent spines and processes. Similarly, the Calciosoleniaceae are unambiguously identifiable by the combination of rhombic-murolith shape and radial laths, which also are typically offset along the median axis. Identification of the Syracosphaeraceae is more problematic, especially as most species are too small to reliably
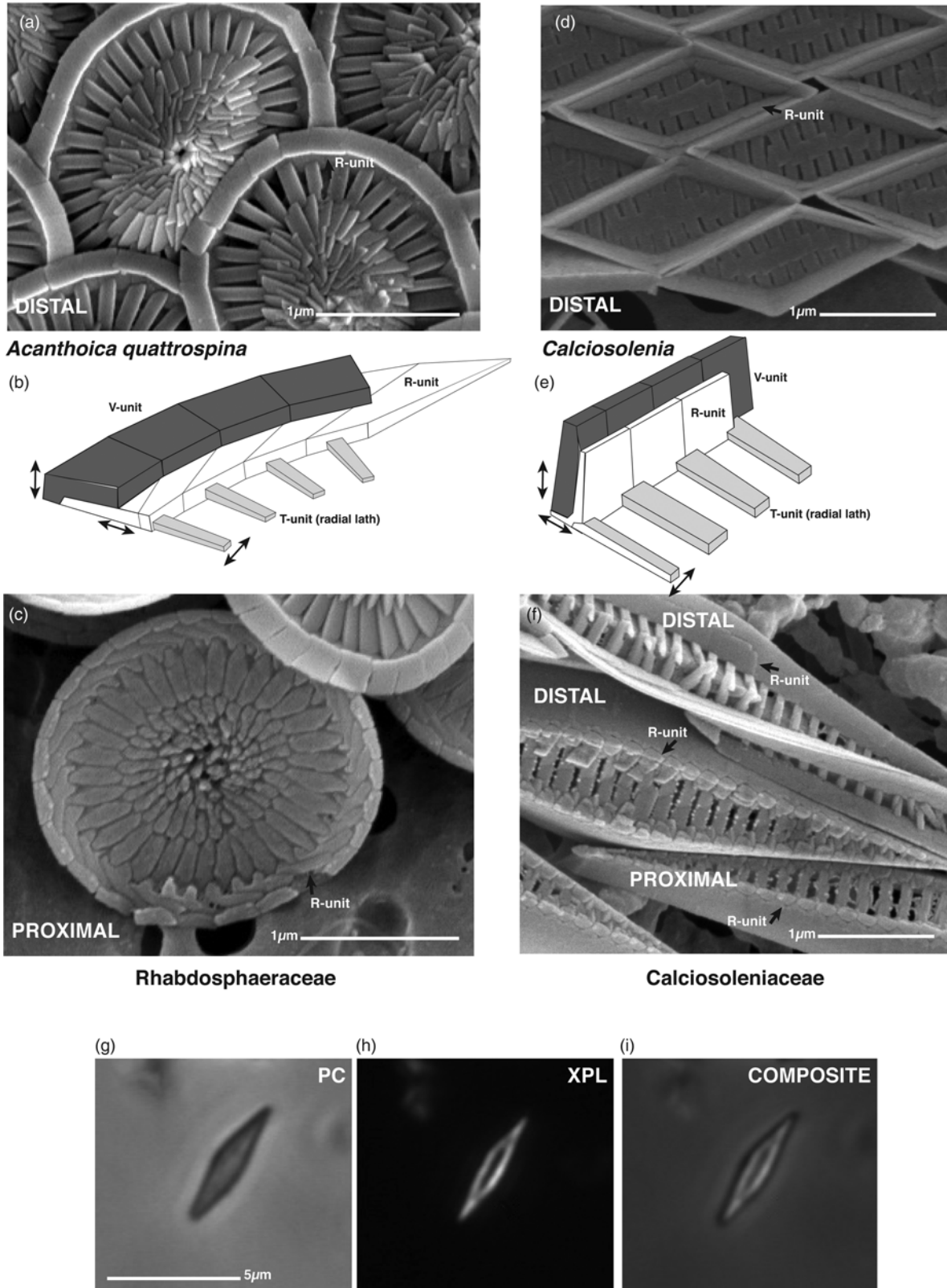
Syracosphaeraceae structure
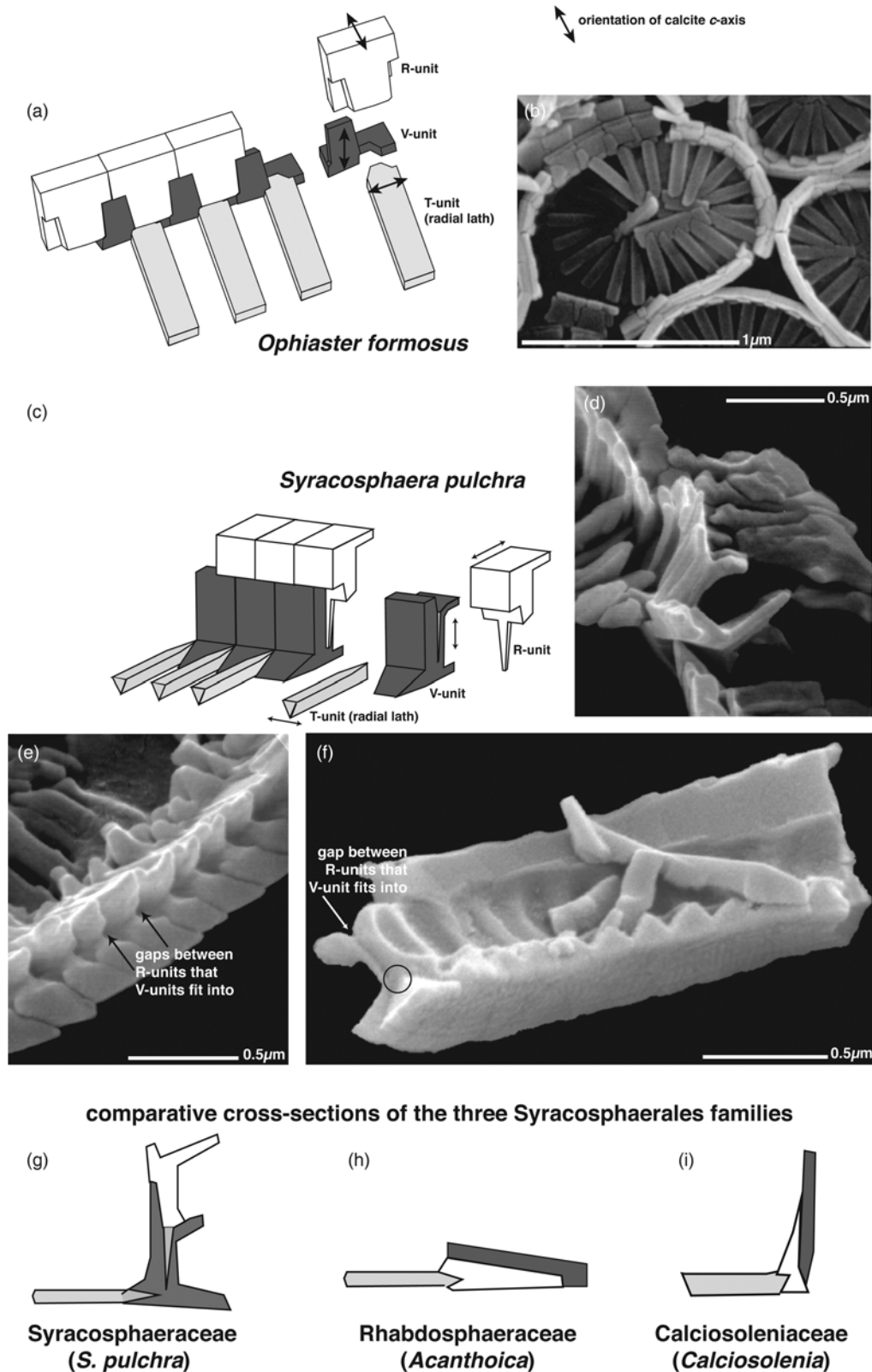
Fig. 1. Structure of the families of the Order Syracosphaerales – Syracosphaeraceae: (**a**) interpretative drawing of (**b**) SEM image of *Ophiaster formosus* coccoliths; (**c**) interpretative drawing of (**d–f**) SEM images of broken portions of *Syracosphaera pulchra* rim; (**g–i**) comparison of rim construction in Syracosphaeraceae, Rhabdosphaeraceae and Calciosoleniaceae rims (see Young *et al.* (2004) for extended explanation).

determine crystallographic orientations from, but we regard the combination of murolith morphology with a central-area formed of disjunct, radial laths, interdigitating with the rim elements, as suggestive of the group.

Overall, the Order Syracosphaerales is poorly represented in the fossil record, although representatives of the Rhabdosphaeraceae are known from the Eocene, and a few Calciosoleniaceae species have been sporadically recorded from the Lower Cretaceous

Rhabdosphaeraceae and Calciosoleniaceae structure

Fig. 2. Structure of the families of the Order Syracosphaerales – Rhabdosphaeraceae and Calciosoleniaceae: (**a**) distal and (**c**) proximal SEM images of *Acanthoica quattrospina* coccoliths, with (**b**) interpretative drawing; (**d** and **f**) SEM images of distal and proximal views of *Calciosolenia* coccoliths, with (**e**) interpretative drawing; (**g–i**) LM images of a single *Calciosolenia* coccolith: (**g**) phase-contrast, V-unit dark; (**h**) crossed-polars, R-unit strongly birefringent; (**i**) Photoshop composite of (**g**) superimposed on (**h**) at 50% transparency, showing R-unit surrounded by V-unit (compare this with (**d**) and (**e**)).

(Valanginian, *c.* 136 Ma) to Holocene (Bown 1998*b*). It has been unclear whether this low palaeodiversity is the result of taphonomic biases (as described above), or actually a reasonable representation of an evolutionary history that has seen a very recent and dramatic diversification, especially in the family Syracosphaeraceae. Although the lack of continuous Neogene sections in Tanzania

does not allow us to fully address this question, in the Tanzanian Paleogene we have found anomalously high diversities in the Rhabdosphaeraceae (>40 species), including the oldest-yet, unequivocal representatives of the extant genera *Acanthoica*, *Algirosphaera* and *Rhabdosphaera*, and the oldest representatives of Syracosphaeraceae (*Syracosphaera* and *Coronosphaera*: e.g. Bown *et al.* 2009; Dunkley Jones *et al.* 2009). The presence of six out of 14 living syracosphaeralid genera in the Paleogene indicates that a significant proportion of modern Syracosphaerales diversity was established by at least the Eocene.

Prior to this study, there has been little evidence of a significant Mesozoic fossil record of the Syracosphaerales. This, in part, reflects the significance of the K/Pg boundary mass extinction event (66 Ma), which almost entirely extinguished oceanic coccolithophores and is strongly evidenced by the very different dominant nannofossil taxa seen either side of the boundary (e.g. Bown *et al.* 2004). Of the living Syracosphaerales, only *Calciosolenia* (sometimes called by its junior synonym, *Scapholithus*, in fossil studies) has been unequivocally recognized as having Mesozoic ancestral representatives.

Papposphaeraceae

This a relatively rare, but diverse, group of extant coccolithophores characterized by producing small coccospheres formed of numerous narrow-rimmed muroliths. The family traditionally included only *Papposphaera* and *Pappomonas*, but has been expanded by Andruleit & Young (2010) to include several other similar genera: *Kataspinifera*, *Picarola*, *Pseudowigwamma*, *Vexilarius* and *Wigwamma*. They are best known from Arctic waters, but also occur at lower latitudes, mostly in the middle photic zone (e.g. Cros & Fortuño 2002). The studied species typically have prominent haptonemata and lack chloroplasts, hence they are inferred to be heterotrophic, rather than autotrophic (Marchant & Thomsen 1994). The species-level taxonomy of the group is currently being revised (e.g. Thomsen & Ostergaard 2014) and it appears likely that the group contains at least 30 species. As noted by Andruleit & Young (2010), five morphological features characterize this group. (1) Rim shape – the coccoliths have simple, narrow murolith rims, i.e. they have a narrow, subvertical outer wall without flanges. In *Pappomonas* and *Papposphaera*, the rim has a serrated upper margin, whilst this is smooth in the other species. (2) Rim structure – typically, the majority of the rim is formed of a single cycle of directly abutting elements with subvertical sutures. In addition, a second cycle of elements occurs proximally, with one of these elements interposed between each of the larger elements. (3) Central-area structure – most species possess either an axial cross or an axial cross plus additional elements. (4) Spine structure – the different genera have distinctly different central processes, but in each case, these are hollow structures. (5) Coccolith size – all these genera are characterized by small coccosphere diameter (*c.* 5 μm, excluding spines) and miniscule coccoliths (coccolith length typically 1 – 2 μm).

Prior to the TDP, the group had no known fossil record, but a single species, *Pocillithus spinulifer*, was described from the Eocene of Tanzania by Dunkley Jones *et al.* (2009) and its assignment to the Papposphaeraceae was supported by Andruleit & Young (2010).

Stephanolithiaceae

This is a well-documented group of Mesozoic coccoliths. They are narrow-rimmed muroliths with vertical elements – V-units form most of the rim, R-units the lower/inner cycle. The central-area contains radial bars, typically formed of multiple elements, sometimes supporting a spine, usually showing low birefringence

in LM plan view (e.g. *Rhombolithion*, *Rotelapillus*, *Stephanolithion*, *Stradnerlithus geometricus*, *S. fragilis*, *Truncatoscaphus*), but some show moderately birefringent central structures (e.g. *Corollithion*, *Stoverius*). The number of (radial) bars varies greatly between taxa, but is typically regarded as constant within species, and there are much fewer bars than rim elements in most taxa. Taxa typically have polygonal or circular outlines. They are conventionally grouped together with the Parhabdolithaceae in the Stephanolithiales (Bown & Young 1997). The Parhabdolithaceae also have non-imbricate murolith rims, but are typically elliptical, with the central-area spanned by an axial cross or transverse bar.

Although numerous genera and species of Stephanolithiaceae have been described, most of them are infrequently reported, due to their being small, rare, fragile and inconspicuous in the LM. Notable exceptions are, for example, *Rotelapillus crenulatus*, *Corollithion signum* and *Stephanolithion bigotii*, which are relatively larger and more robust, and which are standard components of Mesozoic nannofossil assemblages. Many taxa, however, have only been recorded a very few times and then often from scanning electron microscope (SEM) studies of unusually well-preserved assemblages (e.g. Goy 1981; Lambert 1987).

The family ranges throughout the Mesozoic, from the Early Jurassic to the Late Maastrichtian, but appears to have gone extinct at the K/Pg boundary.

## Tanzania Drilling Project occurrences

Material and methods

TDP Phase II (2007 – 09) drilled 22 shallow boreholes, 18 of which provide an incomplete, yet extensive, stratigraphic coverage of the Upper Cretaceous (Cenomanian to Maastrichtian), with the others covering short intervals of the Aptian–Albian and Middle–Upper Paleocene. The entire recovered section spans the interval 120 – 60 Ma. Initial stratigraphic results, based on integrated lithological and micropalaeontological analyses (nannofossils, foraminifera) and stable isotope geochemistry are presented in Jiménez Berrocoso *et al.* (2010, 2012, 2015). The lithologies are predominantly dark claystones and siltstones, with occasional thin sandstone beds, which have never been deeply buried. Lithofacies and benthic palaeontological analyses indicate deposition in bathyal, outer shelf to upper slope environments at water depths of around 300 – 500 m (Jiménez Berrocoso *et al.* 2010, 2012, 2015). In the Late Cretaceous, the region was located at around 30°S palaeolatitude.

The results presented here are based on observation of broken rock surfaces using an SEM, following the method of Lees *et al.* (2004; see also Bown *et al.* 2008 and Lees & Bown 2016). The rock-surface method is particularly productive in these laminated, hemipelagic sediments, allowing the imaging of *in situ* nannofossil concentrations on bedding or lamination surfaces, which have remained undisturbed by primary metazoan bioturbation or secondary preparation processes. The method therefore facilitates the observation of exported (in marine snow and faecal pellets) coccolith concentrations, including collapsed coccospheres and small and fragile taxa (Fig. 3).

Results

Here, we predominantly report on SEM results from the Turonian of TDP Sites 31 and 36, which have been particularly productive for this type of study. At both sites, LM study (Lees 2007, work in progress; Lees & Bown 2016) has revealed high-diversity assemblages, and the abundant and diverse presence of preservation-sensitive taxa, such as holococcoliths and miniscule to very small heterococcoliths (<3 μm). Many samples also conserve frequent, unaltered coccolith concentrations, as observed in the SEM.
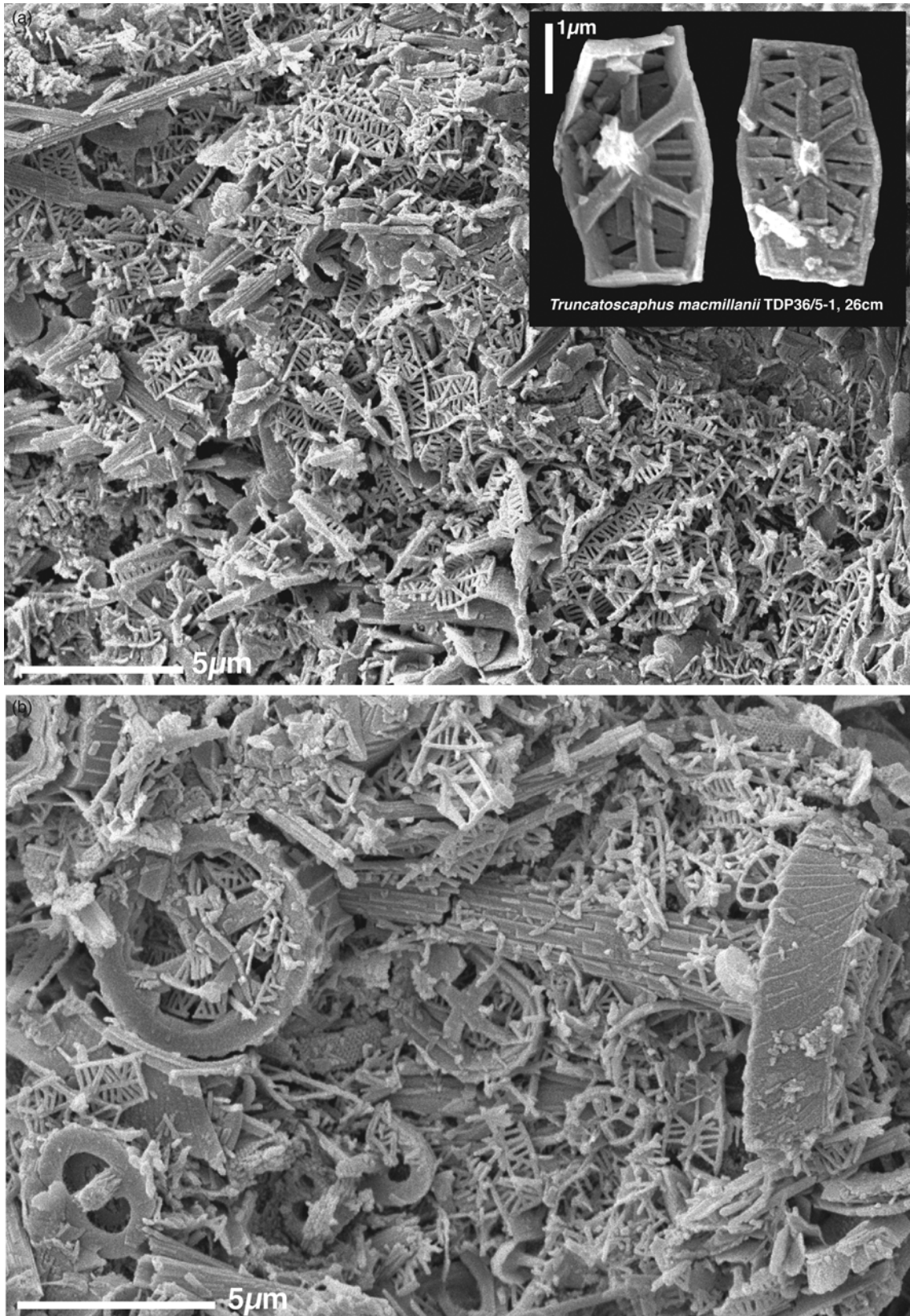
Fig. 3. SEM images of pristine Turonian sediment surfaces (TDP 36/5-1, 26 cm) showing (**a**) concentrations of coccoliths dominated by *Truncatoscaphus macmillanii* (shown in detail in inset), and (**b**) view with typical, small to medium-sized, robust Cretaceous coccoliths (*Eiffellithus*, *Rotelapillus*, *Corollithion*, *Zeugrhabdotus*) along with abundant, frangible *Truncatoscaphus* and *Stradnerlithus*.

Nannofossil assemblages in sediments with 'normal' preservation states are typically dominated by larger coccoliths (5 – 10 μm) and tend not to include <3 μm coccoliths or holococcoliths, or if they do, these occur inconsistently, in insignificant numbers and/or are overgrown and consequently made more robust and/or less

recognizable (e.g. Young *et al.* 2005). In Figure 4, we illustrate 24 Cretaceous coccoliths that are <3 μm long, alongside a medium-sized *Watznaueria* coccolith (*c.* 8 μm long), the latter being a form that typically dominates Jurassic and Cretaceous assemblages. Some of these <3 μm coccoliths are new/recently described taxa

(Lees 2007; Lees & Bown 2016; herein) and some are diminutive varieties of known genera (*Biscutum*, *Corollithion*, *Sollasites*). Such coccoliths are seen throughout the Tanzanian succession, and new taxa are discovered frequently, both in the LM and the SEM. Furthermore, a number of these minute and/or fragile taxa are seen frequently to abundantly and/or consistently in the majority of samples, in both the SEM and LM. For example, in the majority of Paleogene samples, *Gladiolithus* is common, and often dominant.

Calciosoleniaceae

Calciosolenia is relatively well represented in Tanzanian nanno-fossil assemblages (seen in the SEM and LM), and is consistently present throughout the Kilwa Group, but in relatively low abundances (<5%). Although new species have been described (*C. alternans* Bown & Dunkley Jones, 2006; *C. huberi* Lees, 2007), their diversity is modest and comparable to the modern diversity of just three living species, *C. corsellii*, *C. brasiliensis* and *C. murrayi*, the latter two of which we illustrate here from the Turonian (Fig. 4).

Syracosphaeraceae

We have found rare Cretaceous coccoliths in the SEM that have morphology that is virtually identical to modern and Paleogene *Syracosphaera*, and they represent the most convincing Mesozoic records yet of the Syracosphaeraceae (Figs 4–6). The coccoliths are very small (1.5 – 2.5 μm) and fragile, with overall morphology unlike other Mesozoic forms, but with the murolith rim-structure and typical central-area structure (one interdigitating lath-element per rim-element forming the central lath cycle) suggestive of

Cenozoic *Syracosphaera*. Their diminutive size and fragility suggests that taphonomic bias may well routinely remove any trace of these coccoliths from the deep-time fossil record, but also renders these coccoliths imperceptible, or virtually impossible to identify, using the LM. Although we have yet to find confirmed specimens of these forms in the LM, the SEM specimens are best described as new species of *Syracosphaera* (see below).

Papposphaeraceae

Other miniscule to very small coccoliths occur in our Mesozoic samples (Figs 4 and 7). From SEM observation, some of these appear very similar to the species *Pocillithus spinulifer*, recently described from Eocene TDP samples, and assigned to the Papposphaeraceae (Bown *et al.* 2008, 2009; Dunkley Jones *et al.* 2009; Fig. 7b). The new specimens are also muroliths with a high, narrow rim and a tall spine. Two species were observed that differ from each other and *P. spinulifer* in details of outline, central-area, spine cross-section and rim margin. Remarkably, one species, *P. macleodii*, has a serrated distal margin identical to that of modern *Pappomonas* and *Papposphaera*. Clearly, if *P. spinulifer* is accepted as an Eocene representative of the Papposphaeraceae, then it is reasonable to infer that these new species extend the range of the family into the Late Cretaceous.

Stephanolithiaceae

Whilst *Rotelapillus* and *Cylindralithus* coccoliths are relatively large and robustly constructed, and thus consistently recorded from the Cretaceous in general, and from the TDP LM samples in
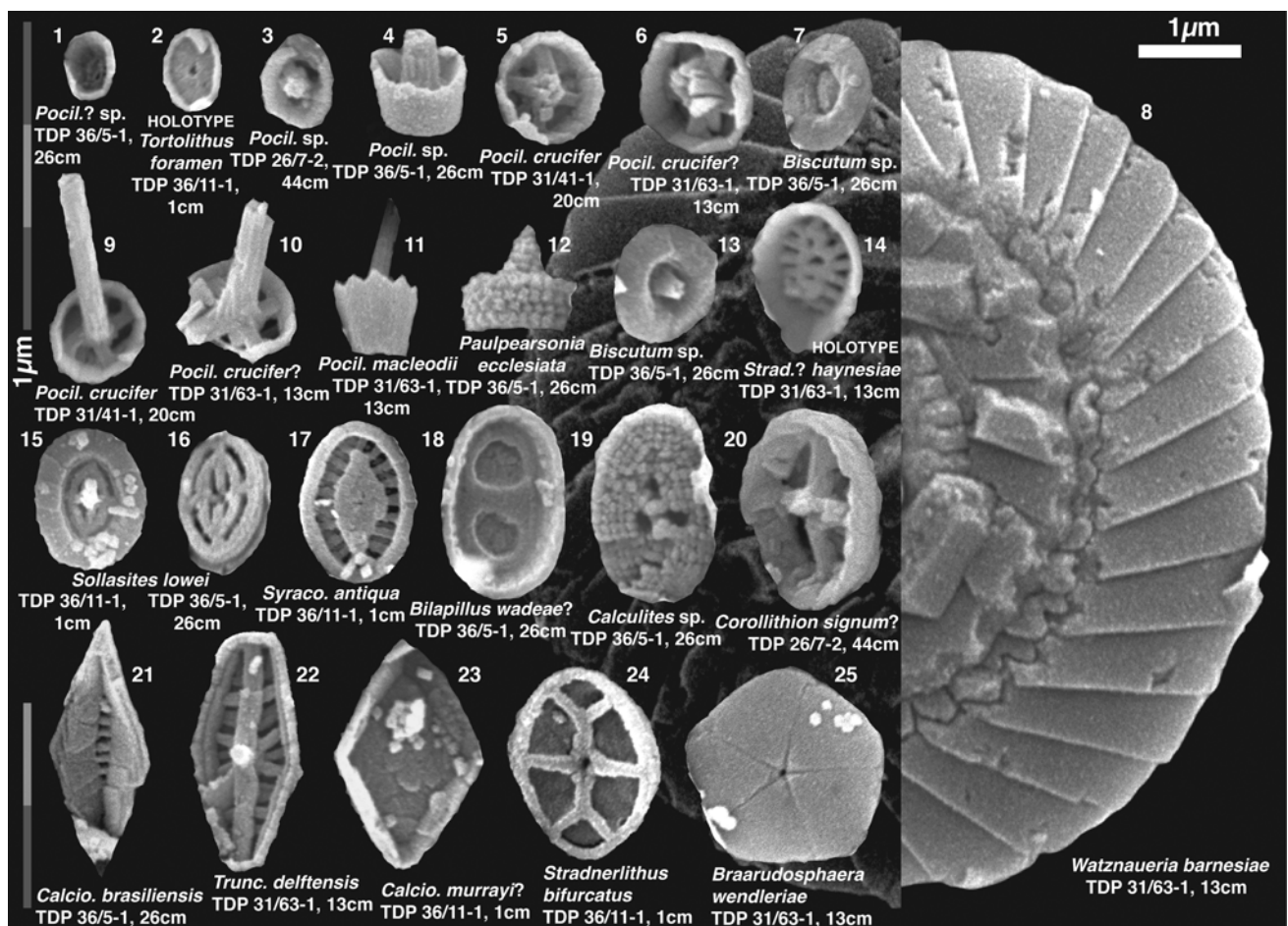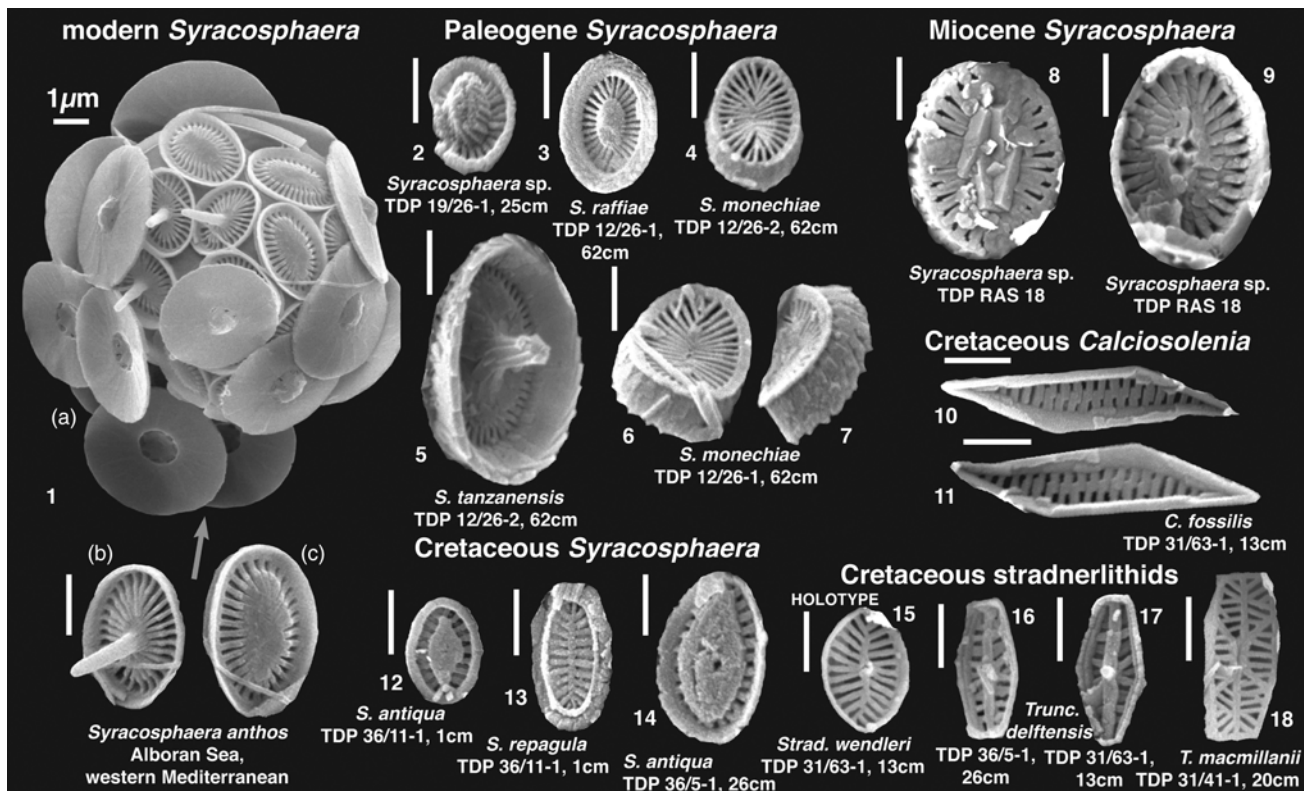

Fig. 4. SEM images of some miniscule to very small (all <3 μm long) Turonian coccoliths (TDP Sites 26, 31 and 36). The medium-sized *Watznaueria barnesiae* (*c.* 8 μm long) demonstrates the contrast in size in these assemblages (all at same magnification).

Fig. 5. SEM images of *Syracosphaera*, *Calciosolenia* and stradnerlithids (*Stradnerlithus* and *Truncatoscaphus*). The *Syracosphaera*s include modern *S. anthos* (left) and Tanzanian specimens from the Early Miocene (TDP RAS outcrop sample), Late Eocene (TDP Site 12), Late Paleocene (TDP Site 19) and Turonian (TDP Site 36). *Calciosolenia* specimens are from the Turonian (TDP Site 31). Stradnerlithid specimens are from the Turonian (TDP Sites 31 and 36).

particular (Lees, work in progress), the family Stephanolithiaceae is otherwise poorly represented in the Cretaceous fossil record. In the Tanzanian Turonian SEM samples, however, they are abundant, sometimes dominant, and consistently present (Figs 3–5). They include abundant *Truncatoscaphus* (usually *macmillanii*, with subordinate *delftensis*), and frequent *Rhombolithion* (usually *rhombicum*, some *rotatum*) and *Stradnerlithus* (*bifurcatus*, *wendleri*) specimens. This *Truncatoscaphus* dominance is surprising, in much the same way as is the dominance of *Gladiolithus* in the Paleogene samples (Bown *et al.* 2008, 2009). Both *Calciosolenia* and *Truncatoscaphus* are relatively small, but the latter have very low birefringence, and so can be rather inconspicuous in the LM, and this may partly explain their rare documentation. In the Cretaceous TDP LM study, *Calciosolenia* is a fairly consistent, but rare, assemblage component, whilst *Truncatoscaphus*, *Rhombolithion* and *Stradnerlithus* are only rarely and sporadically recorded (Lees, work in progress). Undoubtedly, the main factor influencing the general record of these stephanolithids is preservation quality, which strongly biases the record of small and frangible coccoliths, as discussed above, but in addition, such taxa seem to be easily lost during even the most gentle preparation of LM slides. Two new species of *Stradnerlithus*, so far found only in the SEM study, are described below.

In the Turonian samples, we have found *Truncatoscaphus* and *Stradnerlithus* in all samples observed in the SEM, with *Truncatoscaphus* dominating in many of them (Fig. 3); in the LM, taxa such as *Calciosolenia*, *Corollithion*, *Bilapillus* (Figs 3 and 4) and diverse holococcoliths (see Lees 2007) are frequently and fairly consistently present throughout the entire Upper Cretaceous. *Truncatoscaphus* species have been described from widely-spaced Jurassic and Cretaceous horizons, but they are generally rarely documented and so their consistent and abundant occurrence here is very interesting. These coccoliths are *c.* 3 μm long, but are clearly delicate and frangible (see Fig. 3).

Discussion

One inference from our observations is that the small, delicate stephanolithids (primarily *Truncatoscaphus* and *Stradnerlithus*) may well have been among the most abundant Mesozoic coccoliths, but are essentially un- or under-represented in the deep-time fossil record, due to a pervasive taphonomic filter on fragile coccoliths. This observation is further supported by previous accounts of exceptional Mesozoic preservation (predominantly in clay-rich, organic-rich and/ or laminated lithologies), which consistently show abundant *Truncatoscaphus* and/or *Stradnerlithus* since at least the Early Jurassic (e.g. Early Jurassic – Goy 1981; Late Jurassic – Gallois & Medd 1979; Bown *in* Bown & Cooper 1998a; Lees *et al.* 2004; Early Cretaceous – Thomsen 1989; mid-Cretaceous – Lambert 1987, 1992). Notably, the Jurassic taxonomic literature includes the description of around 20 species of *Stradnerlithus* and *Truncatoscaphus*, a figure that represents around 20% of the total known Jurassic diversity (*c.* 85 coccolith species, plus 20 small, delicate stephanolithids: Bown & Cooper 1998) and this albeit fragmentary record further suggests that they may have been significant assemblage components, in terms of both abundance *and* diversity.

The Tanzanian microfossil *lagerstätte* has also revealed the presence of representatives of extant coccolithophore groups that are typically unrepresented in the fossil record, or have rare, sporadic and strongly preservation-mediated records. These TDP records provide new minimum estimates of divergence times for these groups and, in the case of the Syracosphaeraceae and Papposphaeraceae, these are *major* range extensions (71 and 93 Ma, respectively: Fig. 8). Such large range extensions may seem rather surprising for such a well-studied group as the coccolithophorids, with its generally abundant fossil record, but, as discussed above, there are many factors that limit the fidelity of the regular fossil record. Indeed, similar range extensions have recently been proposed for several other coccolithophores: for
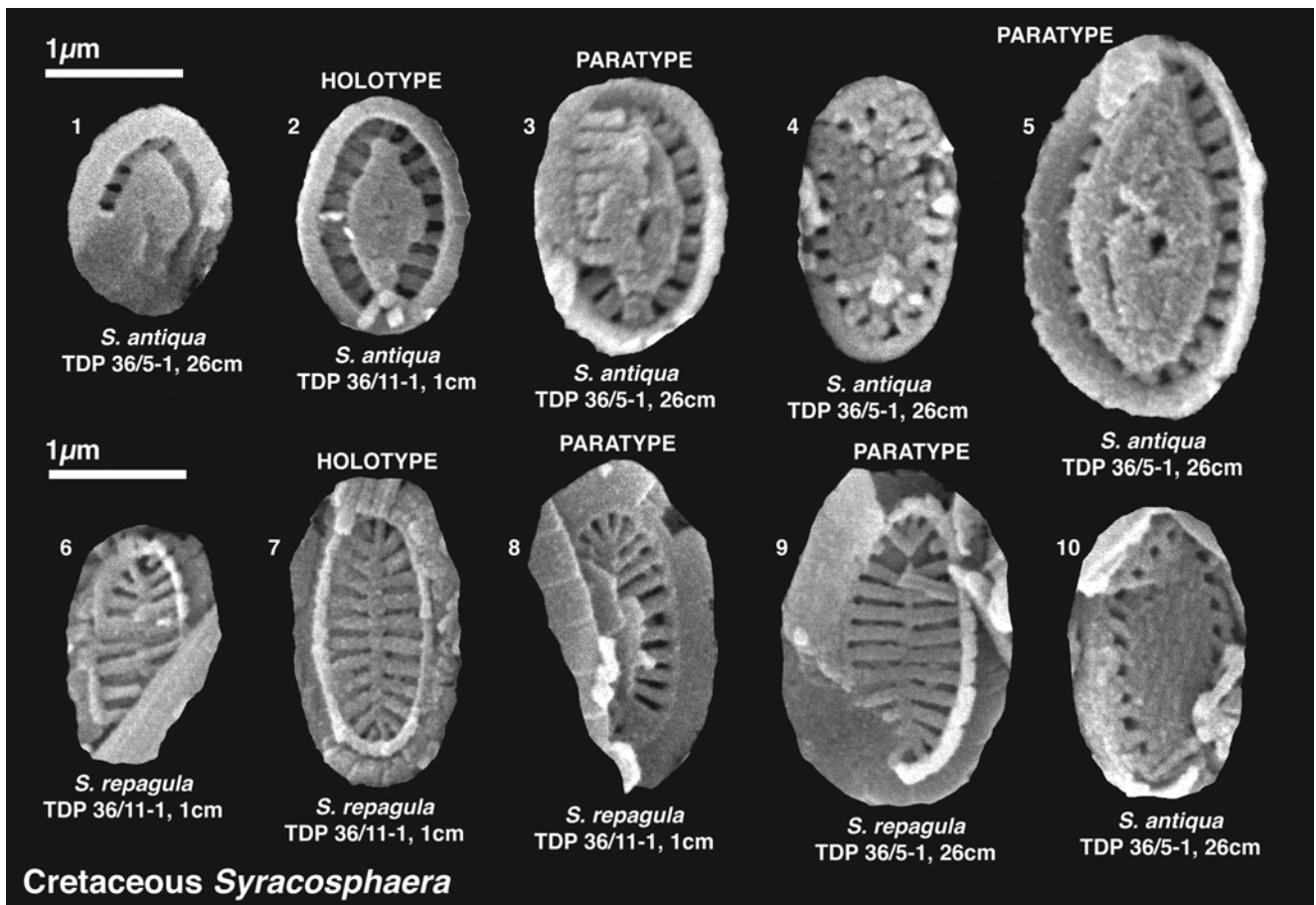
Fig. 6. Cretaceous *Syracosphaera*.

example, Hagino *et al.* (2015) described living-fossil evidence that the Watznaueriaceae did not go extinct in the Early Paleogene, but are still extant; Bown *et al.* (2009) used exceptionally well-preserved samples from the Paleogene of Tanzania to extend the range of *Gladiolithus* from the Recent to the Paleocene; and Lees & Bown (2016) have similarly extended the range of *Ellipsolithus*, from the Paleocene to the Cenomanian (Fig. 8).

It may be that, of the modern taxa, Syracosphaeraceae is the group that suffers the strongest taphonomic bias because it is represented by especially small and fragile coccoliths, perhaps combined with rare and patchy ecological distributions, which is also a feature of many of the modern *Syracosphaera* species. The phylogenetic link with the Cretaceous small, delicate stephanolithids is intriguing, but tentative, although based on shared morphological characteristics. We are confident, however, in the evidence provided by the Cretaceous coccoliths identified here as *Syracosphaera antiqua* and *S. repagula*, but like the Paleogene records, these *Syracosphaera* taxa are rare and low in diversity. If the small, delicate stephanolithid group *is* a deep-time representative of the Syracosphaerales, however, it might suggest that this group has *always* been a significant component of coccolithophore diversity, and potentially played a significant ecological role, even though it is under-represented in 'normal' nannofossil records.

These new observations bring into focus the likely phylogenetic relationships of classic Mesozoic and Cenozoic groups and, consequently, their classification. Bown (1987) argued that *rim structure* could be used to classify Jurassic coccoliths into a limited number of phylogenetic groups, including protolith coccoliths, which had non-imbricate murolith rims, classified in the families Parhabdolithaceae and Stephanolithiaceae. This grouping has been followed since then, and was separated out as the Order

Stephanolithiales by Bown & Young (1997). Based on rim structure alone, the Calciosoleniaceae, and indeed the Papposphaeraceae, could both be included in the Stephanolithiales. Conversely, the Syracosphaerales is essentially defined on the basis of shared *central-area* structure, i.e. possession of a disjunct cycle of radial laths with tangential *c*-axis orientations. Our observations show that these two groups overlap in geological range and some taxa show characteristics of both groups. Most obviously, this applies to *Calciosolenia*, but also to some *Syracosphaera* and *Stradnerlithus* species (e.g. *S. wendleri*). So it may be reasonable to predict that the various families discussed here form a single clade, which would suggest that they should all be included in the Order Syracosphaerales. Following on from this, we would predict that molecular genetics will place the Papposphaeraceae within, or sister to, the conventional Syracosphaerales clade. It is also noteworthy that holococcolith stages are widely known within the Syracosphaeraceae, Rhabdosphaeraceae and Papposphaeraceae, so it would be reasonable to infer that the ancestral Stephanolithiaceae, and possibly the Parhabdolithaceae, also produced holococcoliths.

Systematic palaeontology

Holotype images are curated in the Department of Earth Sciences at UCL.

Order **Syracosphaerales** Hay, 1977

Remarks: At present, the Order Syracosphaerales comprises three families of living and Cenozoic coccolithophores: the Syracosphaeraceae, Rhabdosphaeraceae and Calciosoleniaceae. These families are characterized by having complex central-areas, disjunct from the rim, and usually with a cycle of radial laths that
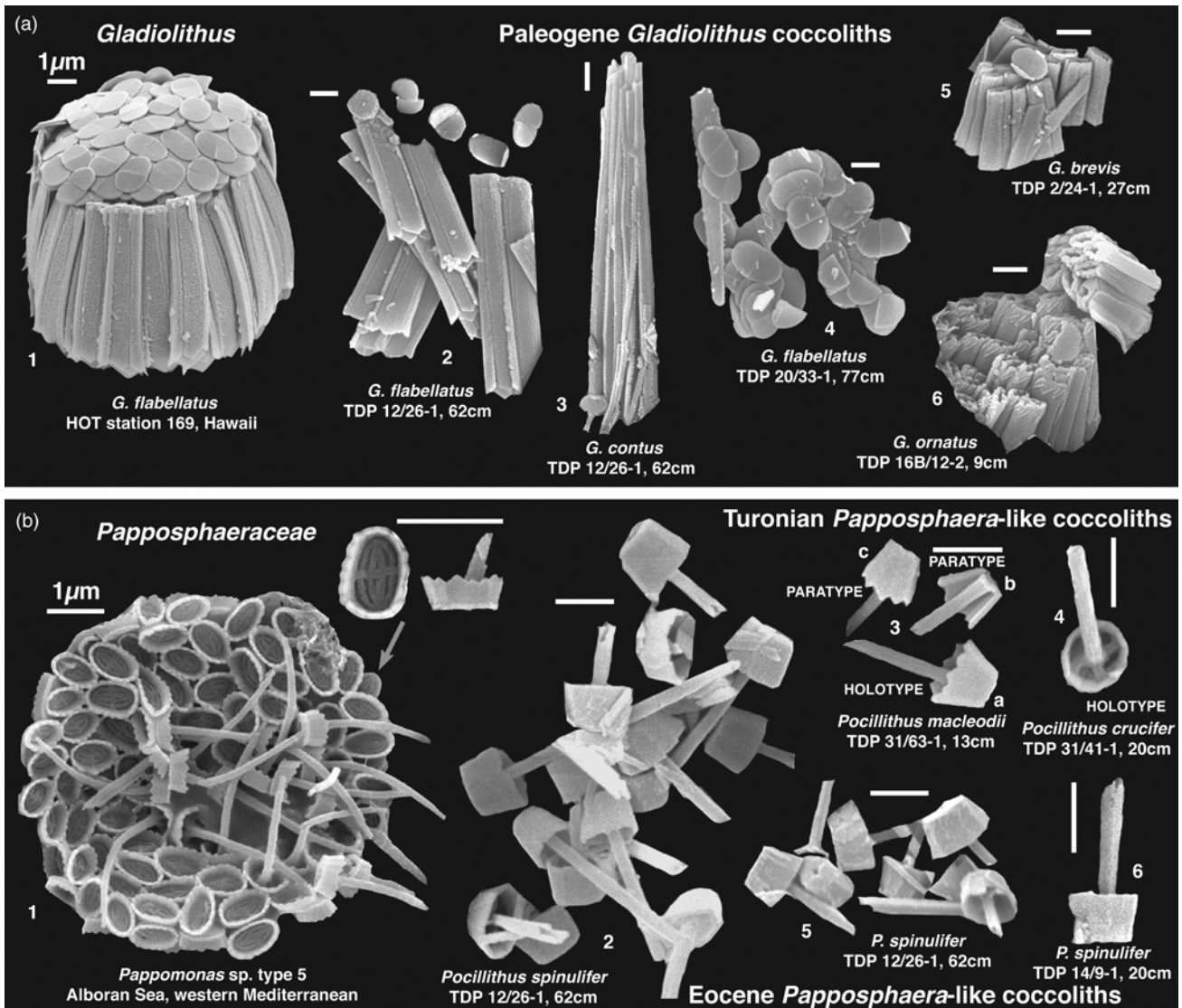
Fig. 7. SEM images of (**a**) *Gladiolithus*, showing modern specimens (left) compared to Tanzanian specimens from the Late Eocene (TDP Site 12), Middle Eocene (TDP Sites 2, 20) and Late Paleocene (TDP Site 16); (**b**) *Pappomonas* and related forms, showing modern specimens (*Pappomonas* sp. type 5 of Cros & Fortuño 2002, left) and Tanzanian specimens (*Pocillithus*) from the Late Eocene (TDP Site 12), Late Paleocene (TDP Site 14) and Turonian (TDP Site 31).

interdigitate with the rim units, but are discrete from them, and show tangential *c*-axis orientation (Figs 1 and 2; Young *et al.* 2003, 2004). The Order Syracosphaerales has not generally been used in the Mesozoic; however, the Calciosoleniaceae occur in the Cretaceous, where it shows affinities with the families Stephanolithiaceae and Parhabdolithaceae, which have been classified in the Order Stephanolithiales Bown & Young, 1997. The *Calciosolenia* specimens seen in the Mesozoic are identical to those in the Cenozoic, and they have a continuous record across the K/Pg boundary, so are clearly the same taxon and need to be classified in the same higher taxonomic group. Therefore, the Syracosphaerales already *does* occur in the Mesozoic and it appears increasingly likely that it evolved from the Stephanolithiaceae. This leaves the question of whether there is strong enough evidence to transfer the families Stephanolithiaceae and Parhabdolithaceae into the Syracosphaerales, which would make the Order Stephanolithiales redundant. Whilst we think the balance of probabilities is that the Syracosphaerales evolved from the Stephanolithiaceae, we do not have a problem with using paraphyletic taxa, and we are strongly aware both of the value of stability in nomenclature and of the likelihood of new evidence from molecular genetics and/or study of exceptionally-preserved coccoliths from other time intervals. As a general rule, we believe that taxonomic reorganization should be based on conclusive evidence and we feel it is sensible to follow this principle here. So we retain the traditional classification.

Family **Syracosphaeraceae** Lemmermann, 1908

Genus *Syracosphaera* Lohmann, 1902

Syracosphaera antiqua sp. nov. Bown, Lees & Young
(Figs. 4:17; 5:12, 5:14; 6:1 – 5, 6:10)

Derivation of name. From the Latin *antiquus*, meaning 'coming before', referring to the Cretaceous age of this *Syracosphaera* species.
Diagnosis. SEM – very small, elliptical, murolith coccoliths with narrow rims and wide central-areas spanned by numerous, short, broad, flat, regularly-spaced, radial laths that surround a broad, granular, rhomboidal central plate.
Holotype. Figure 6:2.
Paratypes. Figure 6:3, 6:5.
Type locality. TDP Site 36, west of main road, SW of Lindi, coastal Tanzania.
Type level. TDP36/11-1, 1 cm, Subzone UC6b, Lower Turonian.
Dimensions. Length = 1.7 µm, width = 1.3 µm.
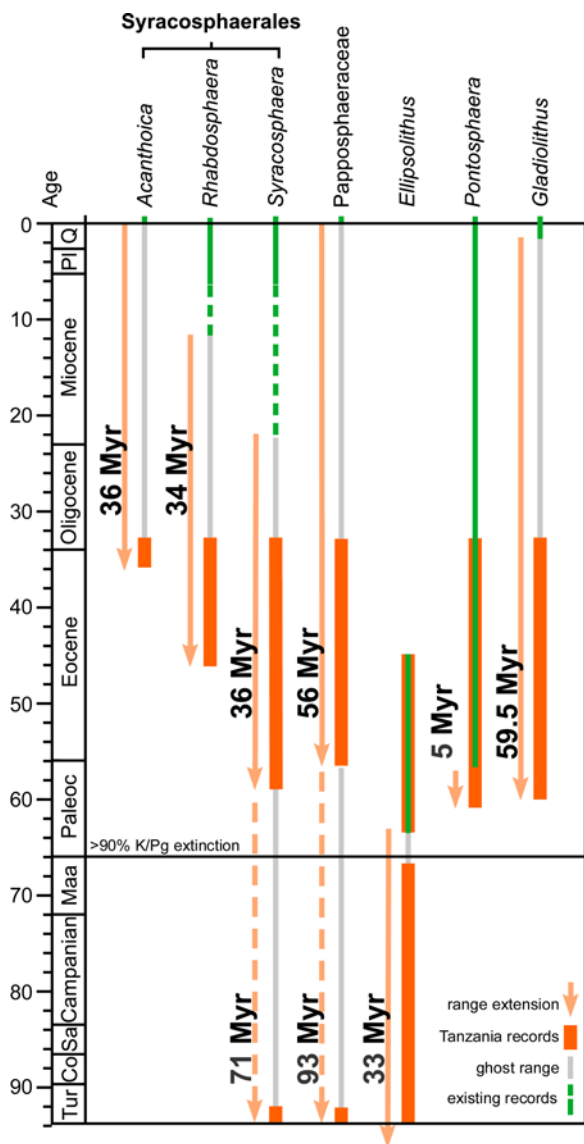**Occurrence.** TDP Site 36; Lower Turonian; UC6b.

Fig. 8. Significant stratigraphic range extensions for several taxa, revealed by the Tanzanian *lagerstätte* succession. Range data from Dunkley Jones *et al.* (2009), Bown (2010, 2016), Lees & Bown (2016), Lees (work in progress) and herein.

Syracosphaera repagula sp. nov. Bown, Lees & Young
(Figs 5:13; 6:6 – 9)

Derivation of name. From the Latin *repagula*, meaning 'bars', referring to the multiple central-area bars that distinguish this species.
Diagnosis. SEM – very small, elongated, elliptical coccoliths with narrow rims, comprising a broader outer cycle and thin inner cycle (possibly an extended V-unit), and wide, elongated central-areas spanned by numerous short, regularly-spaced, radial laths that meet at a central longitudinal bar.
Holotype. Figure 6:7.
Paratypes. Figure 6:8, 6:9.
Type locality. TDP Site 36, west of main road, SW of Lindi, coastal Tanzania.
Type level. TDP36/11-1, 1 cm, Subzone UC6b, Lower Turonian.
Dimensions. Length = 2.2 µm, width = 1.3 µm.
Occurrence. TDP Site 36; Lower Turonian; UC6b.

Order **Stephanolithiales** Bown & Young, 1997
Family **Stephanolithiaceae** Black, 1968

Genus *Stradnerlithus* Black, 1971

Stradnerlithus? *haynesiae* sp. nov. Lees, Bown & Young
(Fig. 4:14)

Derivation of name. After Dr Shannon Haynes, TDP geochemist.
Diagnosis. SEM – very small, elliptical *Stradnerlithus*-like, murolith coccolith with a relatively high, narrow, flaring murolith rim and an open central-area spanned by a distinctive arrangement of lateral bars that abut against a central, irregular ring of elements that is itself spanned by bars.
Holotype. Figure 4:14.
Type locality. TDP Site 31, WNW of main road, SW of Lindi, coastal Tanzania.
Type level. TDP31/63-1, 13 cm, Subzone UC6b, Lower Turonian.
Dimensions. Length = 1.2 µm, width = 0.9 µm.
Occurrence: TDP Site 31; Lower Turonian; UC6b.
Remarks. Species of *Stradnerlithus* more typically have low rims, whereas the rim in this species is relatively moderately high.

Stradnerlithus wendleri sp. nov. Lees, Bown & Young
(Fig. 5:15)

Derivation of name. After Dr Jens Wendler, TDP calcareous dinoflagellate expert and geochemist.
Diagnosis. SEM – a very small, broadly elliptical *Stradnerlithus* distinguished by having multiple lateral bars (12 each side in this specimen) extending from the rim and meeting at a longitudinal bar that extends for most of the length of the coccolith. Beyond the extent of the longitudinal bar, at the ends of the ellipse axis, the last three lateral bars abut one another, creating an 'F' pattern. This species bears a short spine.
Holotype. Figure 5:15.
Type locality. TDP Site 31, WNW of main road, SW of Lindi, coastal Tanzania.
Type level. TDP31/63-1, 13 cm, Subzone UC6b, Lower Turonian.
Dimensions. Length = 2.1 µm, width = 1.5 µm.
Occurrence. TDP Site 31; Lower Turonian; UC6b.

HETEROCOCCOLITHS *INCERTAE SEDIS*
Family **Papposphaeraceae** Jordan & Young, 1990

Genus *Pocillithus* Dunkley Jones *et al.*, 2009

Pocillithus macleodii sp. nov. Lees, Bown & Young
(Figs 4:11; 7b:3a–c)

Derivation of name. After Prof Ken MacLeod, TDP co-chief and geochemist.
Diagnosis. SEM – miniscule to very small, *Pocillithus* protolith muroliths with subcircular, high, narrow, flaring, crenulate rims, and central-areas spanned by a proximal plate(?) supporting a tall, narrow, lathy, hollow spine.
Differentiation. *Pocillithus crucifer* has a central cross supporting the circular-cross-sectioned spine; *P. spinulifer* has a central cross that forms a square spine-base, and the spine is square in cross-section.
Holotype. Figure 7b:3a.
Paratypes. Figure 7b:3b, c.
Type locality. TDP Site 31, WNW of main road, SW of Lindi, coastal Tanzania.
Type level. TDP31/63-1, 13 cm, Subzone UC6b, Lower Turonian.
Dimensions. Diameter (distal) = 1.0 µm, coccolith height = 0.8 µm.
Occurrence. TDP Site 31; Lower Turonian; Subzone UC6b.

Pocillithus crucifer sp. nov. Lees, Bown & Young
(Figs 4:5, 4:6?, 4:9, 4:10?; 7b:4)

Derivation of name. From the Latin *crucifer*, meaning 'cross-bearing', referring to the central cross structure.
Diagnosis. SEM – miniscule to very small *Pocillithus* protolith muroliths with high, narrow, slightly-flaring rims, and central-areas

spanned by a proximal plate(?) supporting a right-angled cross that bears a tall, narrow, lathy, hollow spine.

Differentiation. *Pocillithus spinulifer* has a central cross that forms a square spine-base, and the spine is square in cross-section; *P. macleodii* has a proximal plate that supports the spine, and no cross.

Holotype. Figure 7b:4.

Paratype. Figure 4:5.

Type locality. TDP Site 31, WNW of main road, SW of Lindi, coastal Tanzania.

Type level. TDP31/41-1, 20 cm, Subzone UC6b-7, Lower Turonian.

Dimensions. Diameter = 1.0 μm.

Occurrence. TDP Site 31; Lower Turonian; Subzone UC6b-UC7.

Remarks. Figure 4:6 and 4:10 may belong to the same species, but have squarish outlines.

MUROLITHS *INCERTAE SEDIS*

Genus *Tortolithus* Crux *in* Crux *et al.*, 1982

Tortolithus foramen sp. nov. Lees, Bown & Young
(Fig. 4:2)

Derivation of name. From the Latin *foramen*, meaning 'hole', referring to the central perforation.

Diagnosis. SEM – miniscule, elliptical *Tortolithus*-like muroliths with low, narrow rims, and central-areas filled by overlapping plates surrounding a central perforation.

Differentiation. No other species of *Tortolithus* is perforate.

Holotype. Figure 4:2.

Type locality. TDP Site 31, WNW of main road, SW of Lindi, coastal Tanzania.

Type locality. TDP Site 36, west of main road, SW of Lindi, coastal Tanzania.

Type level. TDP36/11-1, 1 cm, Subzone UC6b, Lower Turonian.

Dimensions. Length = 0.8 μm, width = 0.5 μm.

Occurrence. TDP Site 36; Lower Turonian; Subzone UC6b.

Conclusions

SEM study of the TDP *lagerstätte* highlights the fact that taphonomic filtering has a substantial effect on 'normally-preserved' fossil coccolithophorid assemblages, particularly affecting the <3 μm size-range and fragile taxa. It also provides a rare opportunity for us to broadly compare extant with fossil assemblages, as broadly morphologically similar taxa are consistently, and sometimes abundantly, present in TDP sediments. Through such comparison, our observation that the extant Syracosphaerales – the most abundant and diverse living coccolithophorid group – bear a resemblance, in terms of morphology, size, abundance and diversity, to the small, delicate Cretaceous stephanolithids is intriguing. Furthermore, our documentation of Cretaceous *Syracosphaera* species *does* support a deep divergence time for the Syracosphaerales, which had previously been hinted at only by the sporadic occurrence of *Calciosolenia* in the Cretaceous.

In terms of classification, our observations highlight shared morphological features of the Stephanolithiaceae (Mesozoic) and the Calciosoleniaceae and Papposphaeraceae (based on rim structure), which would allow them all to be grouped into the Stephanolithiales. *Stradnerlithus* and the Calciosoleniaceae share central-area morphologies with the Syracosphaerales, and so could also be classified in that order. Clearly, there is an argument for phylogenetic contiguity of these disparate groups through the K/Pg boundary, hitherto obfuscated by the mass extinction event.

Here, through description of several new species, we have documented substantially extended ranges for the Order Syracosphaerales (by up to 71 Myr) and the family Papposphaeraceae (by 93 Myr), adding to recent observations extending the ranges of the *incertae sedis* genera *Ellipsolithus* (by 33 Myr), *Pontosphaera* (by 5 Myr) and *Gladiolithus* (by 59.5 Myr). This provides evidence for deeper-time evolutionary divergence in all of these groups, and also throws up implications for survival of the K/Pg boundary mass extinction and post-extinction recovery.

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