

The fossil record of coastal coccolithophores

Paul R. Bown, Jeremy R. Young

Department of Earth Sciences, University College London, Gower Street, London WC1E 6BT, UK;
p.bown@ucl.ac.uk

Abstract

Modern coastal environments support low diversity communities of eurytopic coccolithophore species but also non-oceanic, coastal taxa, which are often small and weakly calcified. Our understanding of palaeo-coastal coccolithophores is limited by the infrequent study of shallow-water sediments, first, because they provide only stratigraphically-incomplete records and second, because they typically contain poorly-preserved fossils, sometimes reworked fossils, or none at all. The geological past, however, was characterized by higher sea-levels than present and so sediments from vast, non-analogue epicontinental seaways form the basis for a significant proportion of Mesozoic and Paleogene coccolithophores studies. These reveal clear distinctions between neritic and oceanic coccolithophorid assemblages, which is particularly evident in the distribution of large and highly distinctive braarudosphaerids and nannoconids, but also non-coccolith fossils such as *Lithostromation*, calcareous dinoflagellates (calcispheres) and ascidian spicules. Like modern coastal coccolithophorid assemblages, the ancient examples tend to be dominated by opportunistic or stenotypic species, the watznauerids in the Mesozoic and noelaerhabdids in the Cenozoic. Despite the relatively poor record of fossil coastal taxa it has, nevertheless, become apparent that they played a disproportionately significant role in the evolutionary history of the group, with several extant species among the handful which survived the Cretaceous-Paleogene mass extinction event and forming the basis for recolonization and diversification in the ocean realm.

Keywords coastal, neritic, coccolithophores, calcareous nannofossils

1. Introduction

Extant coccolithophores are widespread in all marine photic zone environments, with biogeographic variability controlled principally by the temperature and nutrient characteristics of water masses and oceanographic features, such as, divergence, upwelling, ocean gyres and seasonal mixing. Modern coastal and estuarine environments usually support lower diversity communities, comprising eurytopic species (e.g., *Emiliania* and *Gephyrocapsa*) but also non-

oceanic, neritic or coastal taxa, with many of the latter group being small and weakly calcified, and therefore with little or no fossil record, e.g., *Hymenomonas*, *Pleurochrysis* (Konno and Jordan, 2006). Our understanding of palaeo-coastal and near-shore coccolithophores is limited by lack of study of these environments, first, because they provide incomplete stratigraphic records and second, because coarser-grained, shallow-water sediments typically contain poorly-preserved fossils, sometimes reworked fossils, or none at all. The poor preservation or absence of fossils is often the result of high porosity which facilitates dissolution. Despite this lack of study of coastal palaeoenvironments, much of the geological past was characterized by higher sea-levels than present, and so sediments deposited in vast, non-analogue epicontinental shelf seas form the basis of a significant proportion of studies of Mesozoic and, to a lesser extent, Paleocene and Eocene coccolithophores. The clear distinction between neritic (i.e. shelf, including coastal habitats) and oceanic coccolithophorid assemblages was recognized early in Mesozoic and Paleogene studies, in particular because of the strongly neritic affinities of the large and highly distinctive braarudosphaerids and, additionally in the Cretaceous, the nannoconids (Bybell and Gartner, 1972; Thierstein, 1976; Roth and Krumbach, 1986; Applegate et al., 1989). Here, we review the fossil record of coastal coccolithophores, including observations on neritic vs oceanic distributions that are relatively well established for most geological time intervals.

2. Neritic and coastal fossil coccolithophores

Until the advent of ocean drilling, through the Deep Sea Drilling Project and subsequent Ocean Drilling programs, fossil coccolithophore study was focused predominantly on shelf sediments, ranging from inner to outer shelf and water depths of several metres to around 1500 m. The switch in emphasis to open-ocean deep-sea sediments was accompanied by the recognition of clear differences between the two oceanographic settings, most obviously apparent in the distribution of large and distinctive shelf nanoplankton, such as *Micrantholithus*, *Braarudosphaera* and *Nannoconus*, which appear to represent primary, biogeographic features (e.g., Bybell and Gartner, 1972; Thierstein, 1976; Roth and Bowdler, 1981) (Plate 1). Other coccolithophore taxa were also identified as having predominantly shelf distribution, most obviously holococcoliths and Paleogene rhabdoliths (*Blackites*) (Perch-Nielsen, 1985) (Plate 1), but in these cases the records are strongly affected by the taphonomic differences between shelf and ocean environments and their sediments, as both these groups have low preservation potential (Roth and Thierstein, 1972; Roth and Berger, 1975; Bown et al., 2008). This taphonomic bias operates because in older, deeply-buried sediments it is the clay-rich hemipelagic sediments of

shelf environments that provide more favourable preservation scenarios with higher diversities and greater numbers of small and fragile taxa (especially holococcoliths) conserved (Bown et al., 2008). In deep-sea oozes, but also shallow-water carbonates, the destructive effects of carbonate diagenesis are pervasive and these tend to destroy small and fragile coccoliths, while causing overgrowth on larger liths. This effect increases with burial depth and therefore sediment age. In addition, as depositional settings approach the calcite compensation depth and beyond, the destructive effects of dissolution also come into effect.

The most obvious difference between neritic and oceanic assemblages is shown by braarudosphaerids in the Lower Cretaceous (Berriasian-Aptian: *Micrantholithus*) and Paleogene (Paleocene-Eocene: *Braarudosphaera*, *Micrantholithus* and *Pemma*), when these taxa can be dominant assemblage components. In addition, in Lower Cretaceous sediments, the braarudosphaerids are often accompanied by abundant nannoconids, especially in the mid to low latitudes. The distribution of other important groups has also been linked to neritic environments, for example, holococcoliths (Mesozoic to Cenozoic) and, in the Paleogene, *Blackites*, *Helicosphaera*, *Pontosphaera* and *Scyphosphaera* (e.g., Perch-Nielsen, 1985), but in all of these cases the influence of preservation is probably the predominant factor (e.g., Bown, 2005a; Bown et al., 2008). By contrast, the occurrence of exclusively oceanic taxa is not particularly evident from the fossil record.

The explicit study of ancient near-shore and coastal settings is uncommon because coccolithophores are often absent or poorly preserved in the coarse-grained silty and sandy sediments or lithified carbonates that typify such environments. When near-shore or lagoonal sediments do contain nannofossils, they tend to be represented by low diversity assemblages dominated by taxa that are considered to be eurytopic or opportunistic, namely, Watznaueriaceae (e.g., *Watznaueria*) in the Mesozoic (e.g., Keupp, 1977; Tribovillard et al., 1992) and Noelaerhabdaceae (e.g., *Reticulofenestra*) in the Cenozoic (Bukry, 1974; Wade and Bown, 2006). In many cases, these taxa also tend to be the most robust and most likely to survive unfavourable taphonomic processes.

3. The neritic distribution of *Nannoconus* and braarudosphaerids

Nannoconus is a nannolith group that appeared in the late Jurassic (Tithonian, ~148 Ma) and was a significant component of Tethyan early Cretaceous assemblages until a numerical decline in the

late Barremian-early Aptian (Erba, 1994). They are especially abundant in the marginal basins of the western Tethys, proto-Atlantic, and Caribbean, where they can be rock forming (Thierstein, 1976; Mutterlose, 1989, 1992; Street and Bown, 2000). By contrast, they are much less common in oceanic sediments and are virtually absent from the Pacific and Indian oceans, which represented around 80% of the Cretaceous marine ecosystem (Bown, 2005b). They are more frequently found in Atlantic Ocean sites, but this ocean was a narrow basin at the time and sediment transport from surrounding shelves was common, with nannoconids (and braarudosphaerids) associated with shelf-sourced turbidites (Applegate et al., 1989). Sporadic occurrences in the Pacific Ocean are also associated with transported material, sourced from shallow-water platforms and guyots (Thierstein, 1976; Bown, 2005b).

This distinct distribution pattern has led to a wide range of explanations concerning nannoconid biology and paleoecology, with focus on the link with low-latitude (tropical), sediment-starved, epicontinental basins and the close association with braarudosphaerids (Roth and Krumbach, 1986; Mutterlose, 1989; Street and Bown, 2000; Bown, 2005b). Busson and Noël (1991) suggested that nannoconids may have been meroplanktonic (i.e., having a benthic life-cycle stage) and excluded from deep and anoxic marine environments by water-depth constraints on cyst viability: they further suggested they might be dinoflagellates. There is little doubt that the paleoecology of nannoconids was in some way related to water depth and to some extent latitude (they are most common in the subtropics and tropics 30°N-30°S) and their distribution may have been limited by large ocean basins, such as the eastern Tethys, Indian and Pacific. Extra-Tethyan nannoconid occurrences most likely occurred along shallow-water migration routes *via* epicontinental basins or *via* island hopping with nannoconids living above and around certain Pacific atolls and guyots (Bown, 2005b). It is interesting to note that modern coastal species such as *Cruciplacolithus neohelis* and *Braarudosphaera bigelowii* also have global distribution, and so this coastal ecology is not a barrier to widespread dispersal (Fresnel, 1986; Takano et al., 2006; Hagino et al., 2015).

The distribution of nannoconids is closely associated with braarudosphaerids in the early Cretaceous, which suggests shared ecological strategy, and, alongside morphological and evolutionary considerations, may be evidence for a phylogenetic link between the two groups (Lees and Bown, 2016). Despite the braarudosphaerids being an extant group, their ecology remains something of a puzzle, but information gained from living braarudosphaerids may well be also directly applicable to the extinct nannoconids.

Extant *Braarudosphaera* has a modern distribution that is unusual for coccolithophores, being limited to neritic or coastal environments. It has been especially studied in the seas around Japan, where it is restricted to water depths of <70m and in places is found very close to shore (Tanaka, 1991; Hagino et al., 2013; 2015). Hagino et al. (2013) showed that *Braarudosphaera*-bearing cells are part of a life cycle that includes an organic-scale-bearing phase, formerly known as *Chrysochromulina parkeae*, which may be lightly calcified (Saez et al., 2004). The *Braarudosphaera* phase is only represented in the water column for very short periods of time (several weeks) during the year (Hagino et al., 2015). Some *Chrysochromulina*, and many other non-coccolithophorid prymnesiophytes, are coastal haptophytes with benthic resting stages. Such a life cycle suggests that the distribution of *Braarudosphaera* is probably constrained by the shallow water requirements in one stage of its life cycle. *Nannoconus* may well have had a similar constraint, as originally suggested by Busson and Noël (1991).

4. Lagoonal nannofossils

The best examples of ancient near-shore nannofossils come from lagoonal sediments, predominantly of Jurassic age. These include the well known Solnhofen lithographic limestone (also famous for the iconic bird-like dinosaur fossil *Archaeopteryx*), which was deposited in a shallow, lagoonal environment with marine influence (e.g., the ammonites and radiolarians are also present). The nannofossil assemblages are of low diversity and dominated by watznaueriaceans, and in particular *Watznaueria* and *Cyclagelosphaera* (e.g., Keupp, 1977) (Plate 1). *Watznaueria* is a ubiquitous Mesozoic coccolithophore with eurytopic and opportunistic ecology (Lees et al., 2006). *Cyclagelosphaera* appears to have been more specifically adapted to shelf environments and may have become more restricted in distribution through time, being rarely observed in the open ocean after the mid-Cretaceous. The abundance of *Cyclagelosphaera* in ancient coastal sediments is intriguing given this taxon has recently been rediscovered as a 'living fossil' (*Tergestiella adriatica*) in the near-shore waters of Japan, usually alongside *Braarudosphaera* (Hagino et al., 2015). There are other claims of relatively widespread Mesozoic lagoonal nannofossils but the images of these 'diagenetically-altered coccoliths', interpreted as being relict tube cycles, are questionable (Busson et al., 1993). Erba et al. (1995) also suggested that dwarfing of otherwise relatively normal diversity Cretaceous nannofossils may have been related to the lagoonal setting on a central Pacific guyot.

A number of Neogene examples of shallow water nanoplankton assemblages also exist, notably in Paratethys and in association with the drying of the Mediterranean during the late Miocene Messinian event. Sediments both underlying and overlying thick Messinian evaporitic deposits contain assemblages that are low diversity and dominated by reticulofenestrads (e.g., *R. antarctica*, *R. minuta*), *Umbilicosphaera jafari*, *Helicosphaera carteri*, *Pontosphaera japonica* but also, more unusually, with common to dominant sphenoliths (*Sphenolithus abies*) (Wade and Bown, 2006; Lozar et al., 2010). These taxa are widely distributed marine species, but evidently were also able to flourish in the pre- and post-Messinian rapidly-fluctuating environments, which included eutrophic, hypersaline and brackish conditions that excluded most other open-ocean taxa. This is consistent with our knowledge of modern lagoonal environments, which also feature noelaerhabdaceans (*Emiliana* and *Gephyrocapsa*), *Helicosphaera* and *Umbilicosphaera* (Konno and Jordan, 2006). The Paratethyan Basins, of modern day Eastern Europe became increasingly isolated from the open-ocean through the Miocene and assemblages within them are typically of low diversity and may contain abundant braarudosphaerids (e.g., Bartol et al., 2008) and even some distinctive endemic species, such as *Bekelithella echinata* and *Noelaerhabdus bozinovicae* (Young et al., Nannotax; Galovic and Young, 2012).

5. Ascidiaceans and calcareous dinoflagellates

Nannofossil assemblages from shallow water environments may also include calcareous fossils that originate from other biological groups, and, in particular, ascidiaceans and calcareous dinoflagellates can be conspicuous. In general, both groups produce structures that are larger than coccoliths and smaller than foraminifera, so they are often overlooked by micropalaeontologists. However, small representatives or abundant broken fragments of larger specimens may be conspicuous to dominant components in assemblages from shallow to coastal environments (Plate 1; see also Young et al., Nannotax - <http://www.mikrotax.org/Nannotax3/index.php?id=20219>).

Ascidiaceans are a class of extant benthic invertebrates belonging to the Phylum Chordata and certain taxa, especially the Family Didemnidae (didemnids), produce numerous aragonitic spicules, typically <0.1 mm in diameter (Brookfield, 1988; Varol and Houghton, 1996). They mostly live in warm, shallow-water environments, ranging from 0 to 50 m, especially carbonate-rich environments associated with reefs and carbonate banks. Certain species do live at greater depths and it is likely that spicules are also transported into deeper-water sediments. The spicules are often fibrous and form globular, stellate clusters but also includes a wide variety of other forms

(Plate 1). They can be common in nannofossil samples and may dominate smear slides especially from tropical, shallow water environments, which lack other nannofossils (Varol, 2006). They are not particularly well documented but reviews are provided by Varol and Houghton (1996) and Varol (2006).

Calcareous dinoflagellates are hollow, spherical to oblate calcitic tests formed by certain dinoflagellates and have a long fossil record stretching from the Triassic to Recent (Streng et al., 2004; Kohring et al., 2005; Zonneveld et al., 2005). They are relatively widely distributed but are more abundant in shelf to coastal settings and may be particularly associated with intervals of environmental perturbations, e.g., Cretaceous oceanic anoxic event 2, the Cretaceous-Paleogene (K-Pg) boundary mass extinction and the Paleocene-Eocene thermal maximum (Hildebrand-Habel et al., 1999). Shelf taxa, such as *Scrippsiella* have tests constructed from relatively large crystal units that are distinctive when disaggregated (Plate 1) and these have on occasion been identified as nannofossil species, e.g., *Anacanthaica mitra* (Varol, 1989; and see Bown 2005a, Pl.

26; <http://www.mikrotax.org/Nannotax3/index.php?id=20435>).

Lastly, a Cenozoic (Eocene-Pliocene) group of enigmatic, globular and stellate nannofossils, mainly classified within the genus *Lithostromation*, is also virtually restricted to near-shore and coastal environments, but they are usually rare (e.g., Perch-Nielsen, 1985) (Plate

1; <http://www.mikrotax.org/Nannotax3/index.php?id=820>).

6. The evolutionary significance of coastal and neritic coccolithophores

Although the geological study of coastal coccolithophores has not been widespread or systematic, the evolutionary significance of these taxa is beyond doubt and especially their role in survivorship and recovery, following the K-Pg mass extinction event. Only a handful of nanoplankton species escaped extinction during this event and several of the most conspicuous survivors, which displayed striking acmes in the immediate aftermath, are now known to be extant, obligate coastal coccolithophores, namely *Braarudosphaera bigelowii*, *Cyclagelosphaera/Tergestiella reinhardtii* and *Cruciplacolithus neohelis* (Bown, 2005c; Hagino et al., 2015). This suggests that the K-Pg extinctions were highly selective and eliminated the diverse oceanic coccolithophores, and that subsequent recolonization of the oceanic realm occurred from the surviving coastal nannoflora. Survivorship was likely the result of these coastal plankton being necessarily adapted to more variable environmental conditions and therefore less vulnerable to the environmental

shocks (cooling, darkness, thermal shock, acidification) that accompanied the bolide impact at the K-Pg boundary.

As well as their significance during the atypical post-K-Pg mass extinction interval, the geological record of coastal and neritic nannoplankton also reveals a contrast between intervals when they were common and periods when they were rare. Most obviously, the Early Cretaceous and early Paleogene were intervals of common occurrences, whereas during the Late Cretaceous and Oligocene to Recent they were less common. One possible explanation for this broad-scale trend might be the influence of sea-level, with periods of high sea-levels in the Early Cretaceous and early Paleogene creating shallow-shelf seaways where taxa with neritic adaptations flourished (e.g., braarudosphaerids). Even higher sea-levels in the Late Cretaceous appear to have created unusual, oceanic-like conditions across shelf areas, as evidenced by the widespread deposition of shelfal pelagic ooze sediments ('Chalk'), which resulted in lower abundances of neritic taxa. Falling sea-levels following the build-up of Antarctic ice sheets at the Eocene-Oligocene boundary resulted in less extensive shelf seas and relatively low abundances of distinctly neritic nannoplankton taxa from the Oligocene to Recent.

7. Summary

Although the infrequent study of ancient coastal sediments has resulted in little fossil evidence of obligate coastal coccolithophores, nevertheless, what information we do have is consistent with the modern observations that these environments tend to be dominated by widely distributed opportunistic or stenotypic species, watznauerids in the Mesozoic and noelaerhabdids in the Cenozoic. In one case, *Cyclagelosphaera (Tergestiella)* is demonstrably coastal and neritic in the Mesozoic and remains similarly adapted at the present day, though it has rarely been identified in the fossil record for much of post-Paleocene Cenozoic. Furthermore, the extant braarudosphaerids and extinct nannoconids, also display long term coastal-neritic adaptation, and were especially abundant in the Early Cretaceous (both groups) and Eocene (braarudosphaerids). The main controlling factor on the distribution of modern *Braarudosphaera* is still uncertain (and by association their extinct ancestors) but a life cycle stage requiring shallow water remains a strong possibility. Finally, other calcareous components are also characteristic of shallow water sediments, and the abundance of ascidian spicules and calcispheres is particularly diagnostic.

References

- Applegate, J.L., Bergen, J.A., Covington, J.M. & Wise, S.W. 1989. Lower Cretaceous calcareous nanofossils from continental margin drill sites off North Carolina (DSDP Leg 93) and Portugal (ODP Leg 103): a comparison. *In* Crux, J.A. & Heck, S.E.v. (Eds), *Nannofossils and their applications*. British Micropalaeontological Society Series. Ellis Horwood, Chichester, pp. 212-222.
- Bartol, M., Pavsic, J., Dobnikar, M., Bernasconi, S.M. 2008. Unusual *Braarudosphaera bigelowii* and *Micrantholithus vesper* enrichment in the Early Miocene sediments from the Slovenian Corridor, a seaway linking the Central Paratethys and the Mediterranean. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **267**: 77-88.
- Bown, P.R., 2005a. Palaeogene calcareous nanofossils from the Kilwa and Lindi areas of coastal Tanzania (Tanzania Drilling Project 2003-4). *Journal of Nanoplankton Research*, **27**: 21-95.
- Bown, P.R. 2005b. Early to mid-Cretaceous calcareous nanoplankton from the northwest Pacific Ocean, Leg 198, Shatsky Rise. *Proceedings of the Ocean Drilling Program - Scientific Results 198*, 103. Online <http://www-odp.tamu.edu/publications/198_SR/103/103.
- Bown, P.R. 2005c. Selective calcareous nanoplankton survivorship at the Cretaceous-Tertiary boundary. *Geology* **33(8)**: 653-656
- 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.
- Brookfield, M.E. 1988. Where are all the fossil sea squirts? *Micropaleontology*, **34**: 277-283.
- Bukry, D. 1974. Coccoliths as paleosalinity indicators - evidence from Black Sea. *In* Degens, E.T. & Ross, D.A. (Eds), *The Black Sea - Geology, Chemistry and Biology*. AAPG Memoirs, **20**: 353-363.
- Busson, G. & Noël, D., 1991. Les nannoconidés indicateurs environnementaux des océans et mers épicontinentales du Jurassique terminal et du Crétacé inférieur. *Oceanol. Acta*, **14**: 333-356.
- Busson, G., Noël, D., Contini, D., Mangin, A.M., Cornee, A. & Hantzpergue, P. 1993. Omnipresence of coccoliths in middle-upper Jurassic lagoonal limestones in France. *Bulletin Des Centres De Recherches Exploration-Production Elf Aquitaine*, **17**: 291-301
- Bybell, L.M. & Gartner, S. 1972. Provincialism among mid-Eocene calcareous nanofossils. *Micropaleontology*, **18**: 319-336.
- Erba, E. 1994. Nanofossils and superplumes: The Early Aptian "nannoconid crisis". *Paleoceanography*, **9**: 483-501.

- Erba, E., Watkins, D. & Mutterlose, J. 1995. Campanian dwarf calcareous nannofossils from Wodejebato guyot. *Proceedings of the Ocean Drilling Program, Scientific Results*, **144**: 141-156.
- Fresnel, J. 1986. Nouvelles observations sur une Coccolithacée rare: *Cruciplacolithus neohelis* (McIntyre et Bé) Reinhardt (Prymnesiophyceae). *Protistologica*, **22**: 193-204.
- Galovic, I. & Young, J.R., 2012. Revised taxonomy of some Middle Miocene calcareous nannofossils of the Paratethys. *Micropaleontology*, **58**(4): 305-334.
- Hagino, K., Onuma, R., Kawachi, M. & Horiguchi, T. 2013. Discovery of an Endosymbiotic Nitrogen-Fixing Cyanobacterium UCYN-A in *Braarudosphaera bigelowii* (Prymnesiophyceae). *PLOS One*, **8** (12): e81749.
- Hagino, K., Young, J.R., Bown, P.R., Godrijan, J., Kulhanek, D.K., Kogame' K. & Horiguchi, T. 2015. Re-discovery of a "living fossil" coccolithophore from the coastal waters of Japan and Croatia. *Marine Micropaleontology*, **116**: 28-37.
- Hildebrand-Habel, T., Willems, H. & Versteegh, G.J.M. 1999. Variations in calcareous dinoflagellate associations from the Maastrichtian to Middle Eocene of the western South Atlantic Ocean (Sao Paulo Plateau, DSDP Leg 39, Site 356). *Review of Palaeobotany and Palynology*, **106**: 57-87.
- Keupp, H. 1977. Ultrafazies und Genese der Solnhofener Plattenkalke (Oberer Malm, Südliche Frankenalb). *Abhandlungen der Naturhistorischen Gesellschaft Nürnberg*, **37**: 128.
- Kohring, R., Gottschling, M. & Keupp, H. 2005. Examples for character traits and palaeoecological significance of calcareous dinoflagellates. *Paleontologische Zeitschrift*, **79**/1: 79-91.
- Konno, S. & Jordan, R.W. 2006. Lagoon coccolithophorids from the Republic of Palau, NW Equatorial Pacific. *Journal of Nanoplankton Research*, **28**: 95-100.
- Lees, J.A., Bown, P.R. & Young, J.R. 2006. Photic zone palaeoenvironments of the Kimmeridge Clay Formation (Upper Jurassic, UK) suggested by calcareous nanoplankton palaeoecology. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **235**: 110-134.
- Lees, J.A. & Bown, P.R. 2016. New and intriguing calcareous nannofossils from the Turonian (Upper Cretaceous) of Tanzania. *Journal of Nanoplankton Research*, **36**: 83-95.
- Lozar, F., Violantia, D., Pierrea, F.D., Bernardia, E., Cavagna, S., Claria, P., Iraceb, A., Martinettoa, E. & Trenkwald, S. 2010. Calcareous nannofossils and foraminifers herald the Messinian Salinity Crisis: The Pollenzo section (Alba, Cuneo; NW Italy). *Geobios*, **41**: 21-32.
- Mutterlose, J. 1989. Temperature-controlled migration of calcareous nannofossils in the north-west European Aptian. In Crux, J.A. & van Heck, S.E. (Eds), *Nannofossils and Their Applications*. Ellis Horwood, Chichester, pp. 122-142.
- Mutterlose, J. 1992. Biostratigraphy and palaeobiogeography of Early Cretaceous calcareous

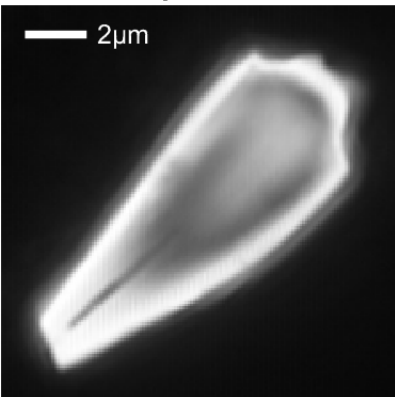
nannofossils. *Cretaceous Research*, **13**: 157–189.

- Noel, D., Busson, G. & Cornee, A. 1993. Importance and significance of coccolithophorids in Lower Oligocene (Stampian-Rupelian) lagoonal deposits from France. *Revue de Micropalaeontologie*, **36**: 29-43.
- Perch-Nielsen, K. 1985. Cenozoic calcareous nannofossils. *In*: H.M. Bolli, J.B. Saunders & K. Perch-Nielsen (Eds.). *Plankton Stratigraphy*. Cambridge University Press, Cambridge, pp. 427–554.
- Roth, P.H. & Berger, W.H. 1975. Distribution and dissolution of coccoliths in the south and central Pacific. *Cushman Foundation for Foraminiferal Research, Special Publication*, **13**: 87-113.
- Roth, P.H. & Krumbach, K.R. 1986. Middle Cretaceous calcareous nannofossil biogeography and preservation in the Atlantic and Indian oceans: implications for palaeoceanography. *Marine Micropaleontology*, **10**: 235-266.
- Roth, P.H. & Bowdler, J.L. 1981. Middle Cretaceous calcareous nannoplankton biogeography and oceanography of the Atlantic ocean. *SEPM Special Publication*, **32**: 517-546.
- Roth, P.H. & Thierstein, H., 1972, Calcareous nannoplankton: Leg 14 of the Deep Sea Drilling Project. *Initial Reports of the DSDP*, **14**: 421-485.
- Sáez, A.G., Probert, I., Young, J.R., Edvardsen, B., Wenche, E. & Medlin, L.K. 2004. A review of the phylogeny of the Haptophyta. *In*: Thierstein, H.R. and Young, J.R. (Editors), *Coccolithophores - from molecular processes to global impact*. Springer, pp. 251-270.
- Street, C. & Bown, P. 2000. Palaeobiogeography of Early Cretaceous (Berriasian-Barremian) calcareous nannoplankton. *Marine Micropaleontology*, **39**: 265-291.
- Streng, M., Hildebrand-Habel, T. & Willems, H. 2004. A proposed classification of archeopyle types in calcareous dinoflagellate cysts. *Journal of Paleontology*, **78**: 456-483.
- Takano, Y., Hagino, K., Tanaka, Y., Horiguchi, T. & Okada, H. 2006. Phylogenetic affinities of an enigmatic nannoplankton, *Braarudosphaera bigelowii* based on the SSU rDNA sequences. *Marine Micropaleontology*, **60**: 145-156.
- Tanaka, Y., 1991. Calcareous nannoplankton thanatocoenoses in surface sediments from seas around Japan. *Sci. Rep. Tohoku Univ., Second Ser. (Geol.)*. Tohoku Univ., Sendai, Japan, pp. 127-198.
- Thierstein, H.R. 1976. Mesozoic calcareous nannoplankton biostratigraphy of marine sediments. *Marine Micropaleontology*, **1**: 325-362.
- Tribovillard, N.-P., Gorin, G.E., Belin, S., Hopfgartner, G. & Pichon, R. 1992. Organic-rich biolaminated facies from a Kimmeridgian lagoonal environment in the French Southern Jura

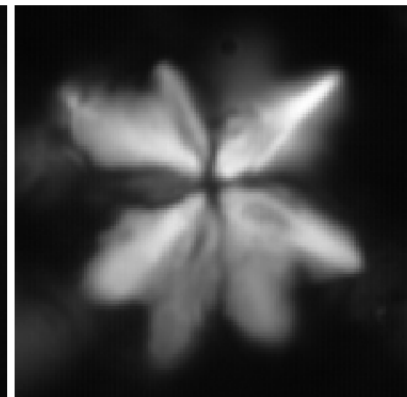
- Mountains - a way of estimating accumulation rate variations. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **99**: 163-177.
- Varol, O. 1989. Eocene calcareous nannofossils from Sile (northwest Turkey). *Revista Espanola de Micropaleontología*, **21**: 273–320.
- Varol, O. 2006. Didemnid ascidian spicules from the Arabian Peninsula. *Journal of Nannoplankton Research*, **28**(1): 35-56.
- Varol, O. & Houghton, S.D. 1996. A review and classification of fossil didemnid ascidian spicules. *Journal of Micropalaeontology*, **15**: 135-149.
- Wade, B.S. & Bown, P.R. 2006. Calcareous nannofossils in extreme environments: The Messinian Salinity Crisis, Polemi Basin, Cyprus. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **233**: 271-286.
- Young, J.R., Bown P.R., Lees J.A. (eds). *Scrippsiella; Bekelithella; Noelaerhabdus*; Calcareous dinoflagellates; Ascidian spicules. Nannotax3 website. International Nannoplankton Association. URL: <http://www.mikrotax.org/Nannotax3/>
- Zonneveld, K.A.F., Meier, K.J.S., Esper, O., Siggelkow, D., Wendler, I. & Willems, H. 2005. The (palaeo-)environmental significance of modern calcareous dinoflagellate cysts: a review. *Paläontologische Zeitschrift*, **79**: 61-77.

Plate 1

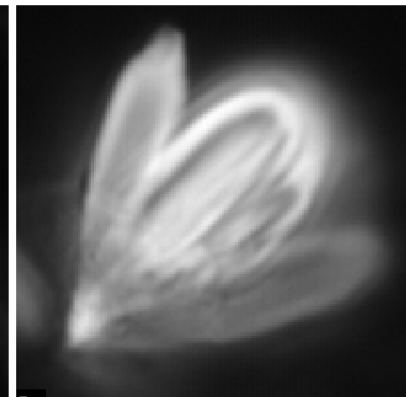
Selected examples of coastal and neritic nannoplankton from the fossil record. Abbreviations as follows: L. – lower, M. – middle, U. – upper, Oxf. – Oxfordian (U. Jurassic), Berr. – Berriasian (L. Cretaceous), Alb. - Albian (L. Cretaceous), Pal. – Paleocene, Eo. – Eocene, Oligo. – Oligocene, Atl. Oc. – Atlantic Ocean, Aust. – Australia, Tanz. – Tanzania.

Ascidian spicules

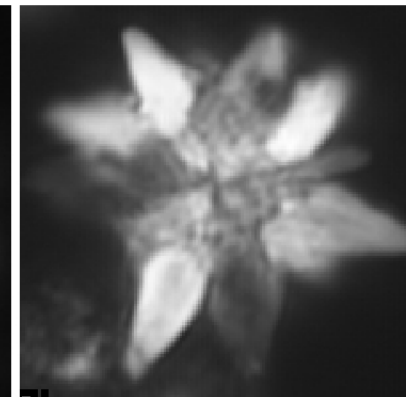
ascidian spicule U. Pal., Tanz



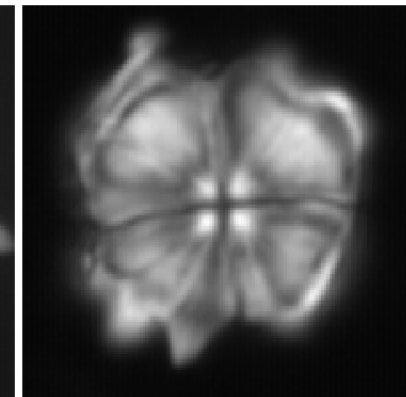
ascidian U. Eo., Aust.



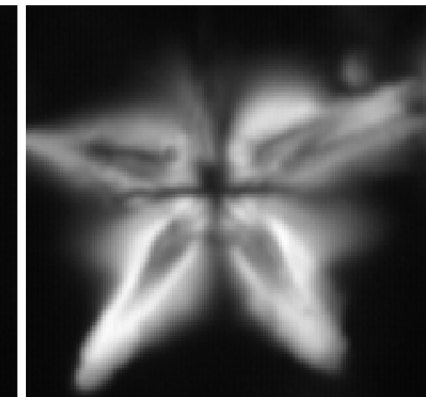
ascidian spicule L. Eo, Tanz.



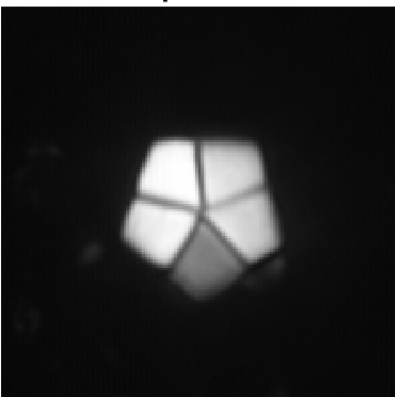
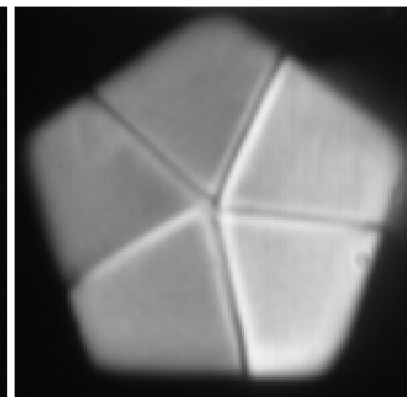
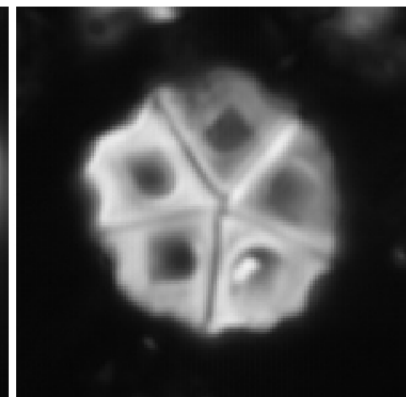
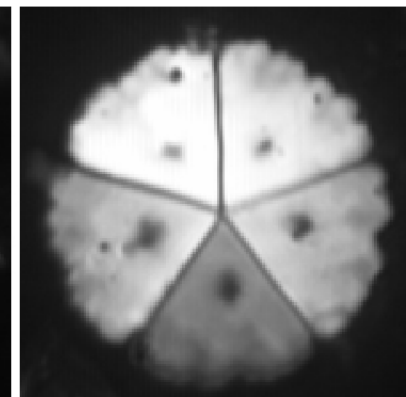
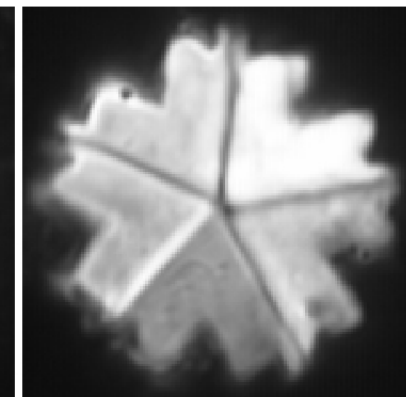
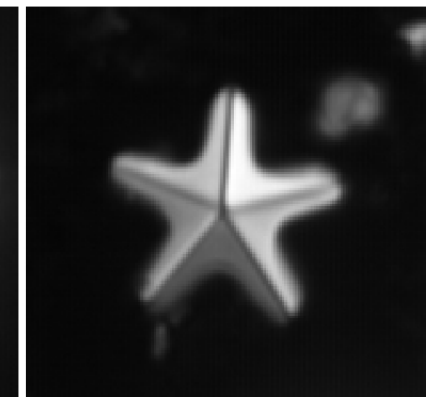
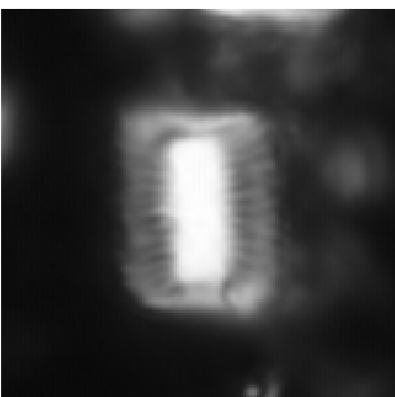
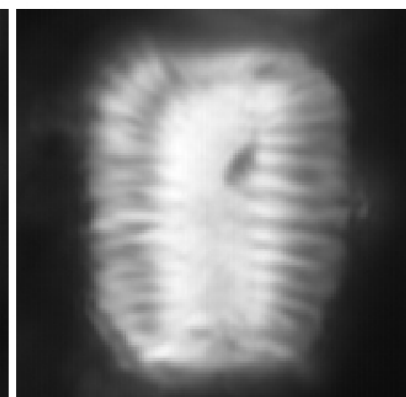
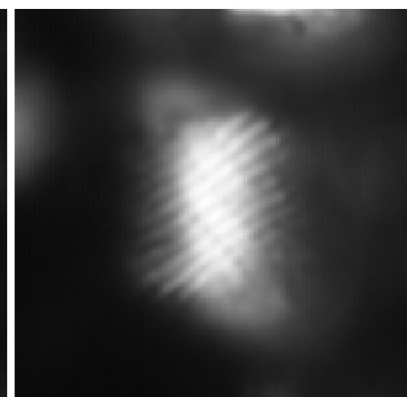
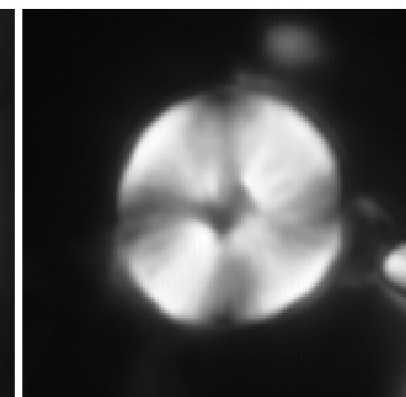
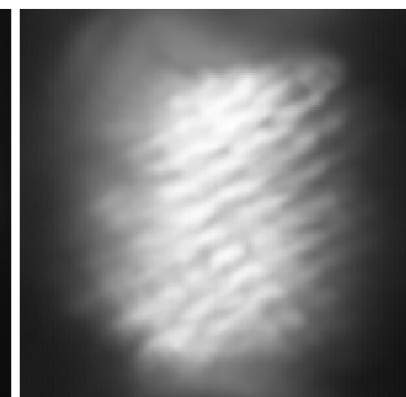
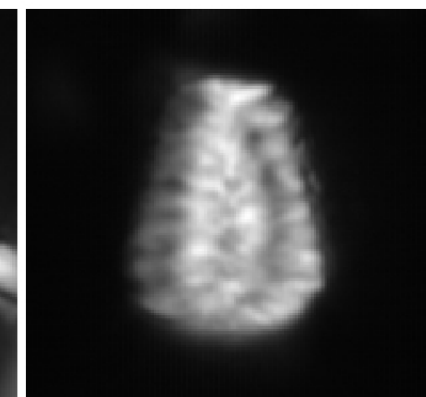
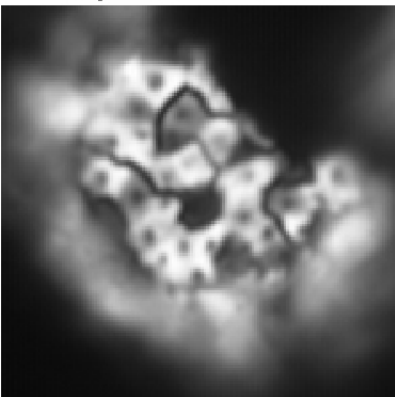
ascidian spicule Oligo., Tanz.



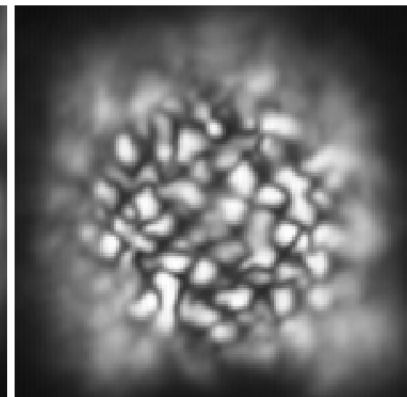
ascidian U. Eo., Aust.



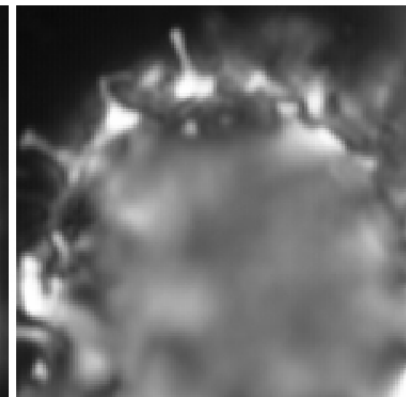
ascidian U. Eo., Aust.

Braarudosphaerids*Braarudo bigelowii* U. Pal., Tanz.*Braarudo perampla* U. Eo., Aust.*Pemma basquensis* U. Eo., Aust.*Pemma basquensis* M. Eo, Tanz.*Micranth. crenulatus* M. Eo, Tanz.*Micranth. astrum* Oligo, Aust.**Nannoconids***Nannoconus truittii* Alb., ODP 1052, Atl. Oc.*Nannoconus truittii* Alb., ODP 1052, Atl. Oc.*Nanno. truittii* Alb., ODP 1052*Nann. steinmannii* Berr., Pacific**Calcspheres**

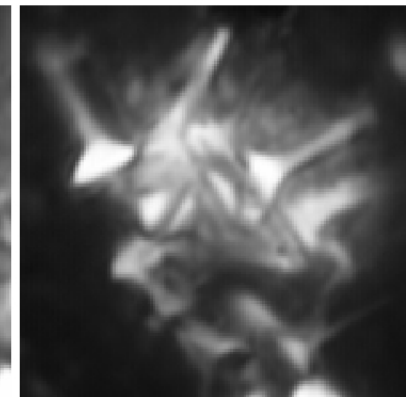
calcsphere L. Eo, Tanz.



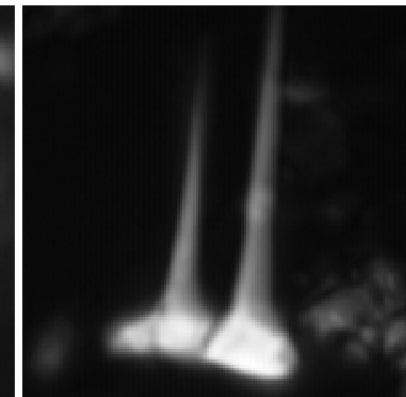
calcsphere U. Pal, Tanz.



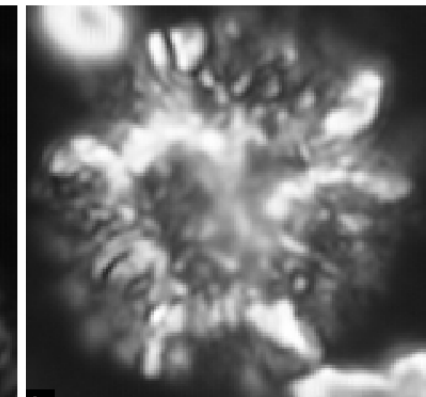
calcsphere ODP1052-41-2



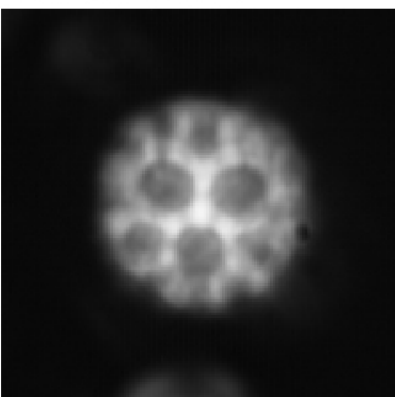
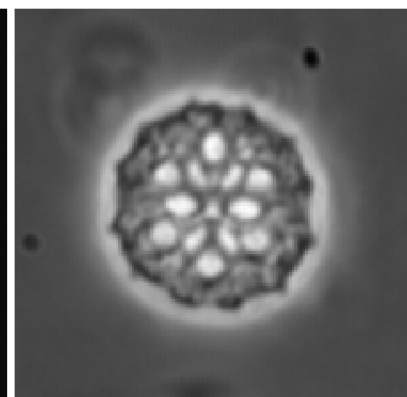
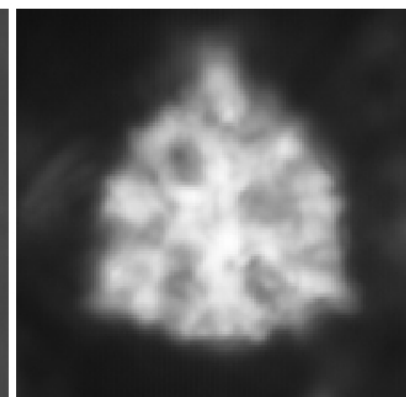
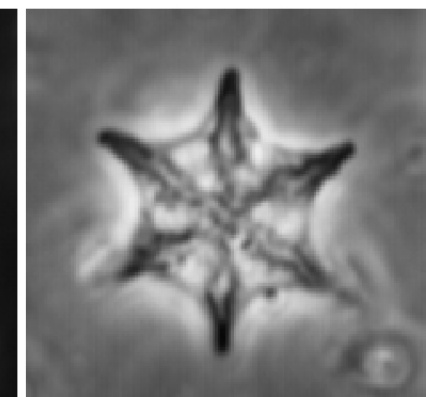
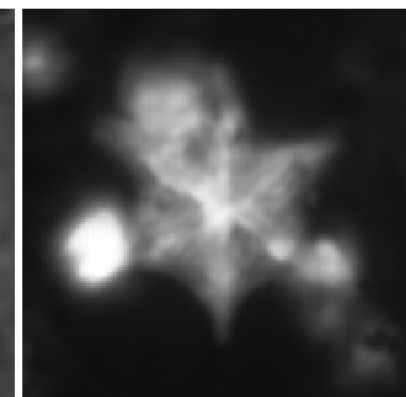
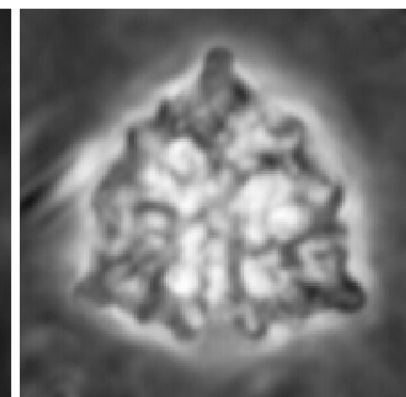
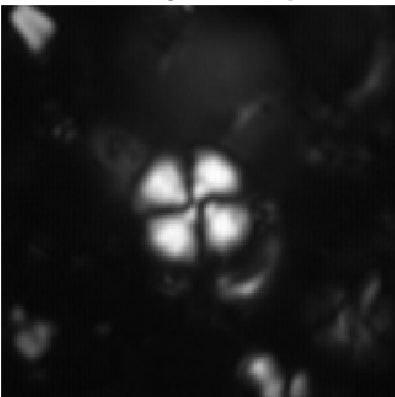
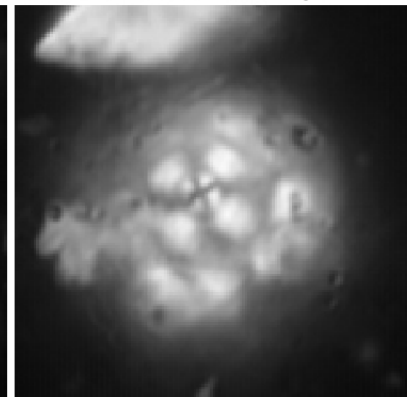
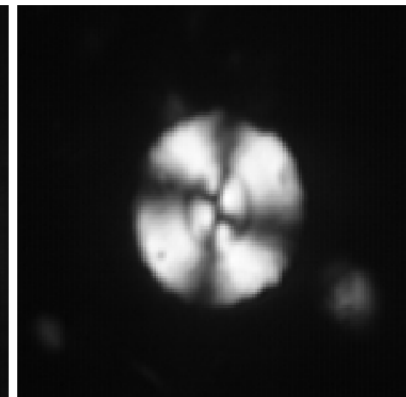
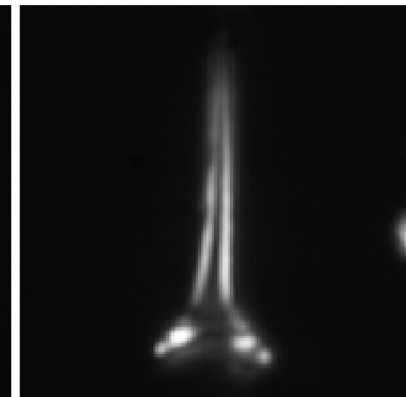
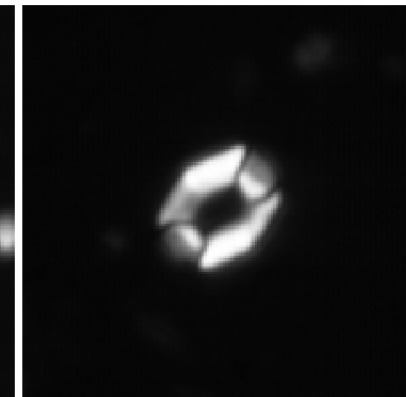
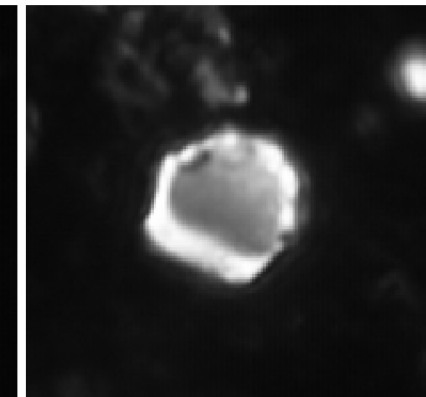
calcsphere U. Eo., Tanz.



calcsphere fragment U. Eo., Aust.



calcsphere M. Eo, Tanz.

Lithostromation*Lithostromation operosum* U. Eo., Aust.*Lithostromation perdurum* U. Eo., Gulf Coast, USA*Lithostromation stellaris* U. Eo., Gulf Coast, USA**Coccolithophores (hetero- and holococcoliths)***Cyclagelo. margerelii* Oxf., UK*Cyclagelo. margerelii* Oxf., UK*Watznaueria barnesiae* Oxf., UK*Bl. cf. Bl. spinosus* U. Eo., Aust.*Lanternithus minutus* Oligo, Aust.*Daktylethra unitatis* M. Eo., Tanz.