J. Nannoplankton Res., **41**(1), 2023, pp. 15–25
ISSN 1210-8049 Printed by The Sheridan Press, USA

Some proposed changes to the systematics of Cenozoic and Mesozoic nannoplankton

Jeremy R. Young
Department of Earth Sciences, University College London, Gower Street, London WC1E 6BT, UK; jeremy.young@ucl.ac.uk

Manuscript received 10th December, 2021; revised manuscript accepted 17th December, 2021

Abstract A series of changes are proposed to the systematics of certain nannoplankton taxa in order to resolve various taxonomic inconsistencies and anomalies. One new Cenozoic species—*Calcidiscus thiersteinii*—and one new Mesozoic species—*Watznaueria leesiae*—are proposed, along with 32 new Cenozoic combinations—*Coccolithus floralis*, *Pletolithus hulliae*, *Reticulofenestra chriskingii*, *R. nicolasii*, *R. larae*, *R. artuziae*, *Gephyrocapsa maceria*, *Hornibrookina elegans*, *Syracosphaera franzii*, *S. isselii*, *S. magnaghii*, *Solisphaera miocaenica*, *Blackites mericii*, *B. perfectus*, *B. prolatus*, *B. elongatus*, *B. rothii*, *B. australensis*, *Ceratolithus vidalii*, *Craterolithus hirsutus*, *C. eolutetiensis*, *C. plenilutetiensis*, *Discoaster glenos*, *D. mexicanus*, *Lithostromation concavum*, *L. martinii*, *L. nodosum*, *L. hohnensis*, *L. pyramidale*, *Peritrachelina arenaria*, *P. minuta* and *Martiniaster menneri*.

Keywords Nannofossils, Cenozoic, systematics

1. Introduction

Several recent papers have reported a range of invaluable new taxonomic observations and recommendations. However, when incorporating these results in the *Nannotax* system, it is quite common to come across taxonomic problems that the authors had overlooked, arcane complications caused by the need to comply with the *International Code for Nomenclature of algae, fungi and plants* (*ICN*), or inconsistencies between the taxonomy of the authors and that in use on *Nannotax*. Several of these were deemed sufficiently significant to require resolving directly. However, it seemed inconsistent to produce formal solutions for some new problems whilst leaving similar long-standing problems unaddressed. So, I systematically went through the Cenozoic section of *Nannotax* looking for anomalies, such as species for which there was no formally proposed combination in the logically correct genus.

The paper is organised in a series of sections, taxon by taxon, with a short introduction explaining the issue in each case and the proposed solution, followed by the formal taxonomic proposal.

2. Changes proposed within the Order Coccolithales

2.1 *Coccolithus*

Wei and Wise (1992) described, as a subspecies of *Coccolithus pelagicus*, a form with a flaring collar on the distal side. Aubry and Bord (2009) proposed the combination *Ectalithus floralis*. Although it is agreed that it is sensible to treat the morphotype as a species, there is no compelling reason to remove it from the genus *Coccolithus*.

Coccolithus floralis (Wei & Wise, 1992) Young n. comb.

Basionym: *Coccolithus pelagicus* subsp. *floralis* Wei & Wise, 1992. *Proceedings of the ODP, Scientific Results*, **120**: 514–516, pl. 2, figs 5–8.

2.2 *Pletolithus*

Capelli et al. (2020) introduced the genus *Pletolithus* for a group of large Eocene Coccolithaceae species bearing a cross in the central area. This genus appears necessary because there is good evidence that these forms evolved from *Coccolithus* not from *Cruciplacolithus*. *Coccolithus hulliae* is a somewhat smaller (8–10 μm) member of the same lineage and so should also probably be included.

Pletolithus hulliae (Bown & Newsam, 2017) Young n. comb.

Basionym: *Coccolithus hulliae* Bown & Newsam, 2017. *Journal of Nannoplankton Research*, **37**: 34, pl. 4, figs 7–17.

2.3 *Calcidiscus*

It is well established that, in the modern ocean, *Calcidiscus* includes three morphotypes, distinguished on the basis of size, some other details of heterococcolith morphology,

holococcolith morphology and molecular genetics (e.g. Kleijne, 1993; Knappertsbusch et al., 1997; Quinn et al., 2003, 2004; Saez et al., 2003; Geisen et al., 2004). The two larger forms are formally distinguished as either subspecies—*Calcidiscus leptoporus* subsp. *quadriperforatus* and *C. leptoporus* subsp. *leptoporus*—or as species—*C. quadriperforatus* and *C. leptoporus*.

Whereas the larger forms overlap in size and can only be consistently separated by electron microscopy, the small form is consistently smaller than *C. leptoporus* subsp. *leptoporus* and is also distinguished from it by having fewer elements and by the elements showing more complex sutures (e.g. Kleijne, 1993). It seems sensible to separate this form as a discrete species.

However, this small form has never been formally named, having been simply referred to as *C. leptoporus* 'small'. It had been anticipated that a holococcolith phase of the life-cycle would be identified, and if this had been described, then this would have provided the name for the species. However, no such holococcolith phase has yet been observed, and the lack of a formal name has become increasingly anomalous, so a new name is proposed for it here.

Calcidiscus thiersteinii Young n. sp.
Pl. 1, fig. 1

Derivation of name: In honour of Prof. Hans Thierstein (ETH–Zurich), who pioneered culture studies of morphological variations in *Calcidiscus* and supervised extensive research on the genus. **Diagnosis**: Species of *Calcidiscus* with a coccosphere composed of circular coccoliths 3–5 μm in diameter. **Description**: Coccospheres subspherical, monomorphic, 6–10 μm in diameter, composed of 25–40 overlapping placolith coccoliths. Coccoliths circular, 3–5 μm in diameter, formed of 15–20 elements. Distal shield with narrow, conical depression in the central area, which does not normally extend to the proximal shield. Elements in the central area angular. Sutures on the distal surface straight near the central opening, with weak clockwise obliquity, then deflected anticlockwise and with a serrated margin, they may then extend to the margin or show a distinct anticlockwise kink. Proximal shield elements near radial, but often with intricately interlocking sutures. As with all *Calcidiscus* coccoliths, the distal shield is formed of V-units and shows very low birefringence in plan view, whilst the proximal shield is formed of R-units and shows high birefringence with a near radial pseudo-extinction cross. **Holotype**: Specimen imaged by Young et al. (2003, pl. 6, fig. 7; image no PM NF 4631 136-03). This image is reproduced here in Pl. 1, fig. 1. **Type sample**: M48-04 Stn. 20, 5m. Collected by Markus Geisen and Claudia Sprengel during research cruise M48-4 of the RV *Meteor* from the South Atlantic, west of Namibia, -20.87ºN, 6.25ºE, in October 2000. **Type depository**: Natural History Museum, London. **Occurrence**: Knappertsbusch (1997) showed that the species had a global distribution in surface sediments. In the plankton, it has most often been recorded from the South Atlantic. Knappertsbusch (2000, fig. 7) also showed that the morphotype was continuously present in the fossil record through the Pleistocene. Possible homoeomorphs also occur in the Early and Middle Miocene, but if it proves useful to distinguish these, a different name should be applied to them.

3. Changes proposed within the Order Isochrysidales

3.1 *Reticulofenestra*

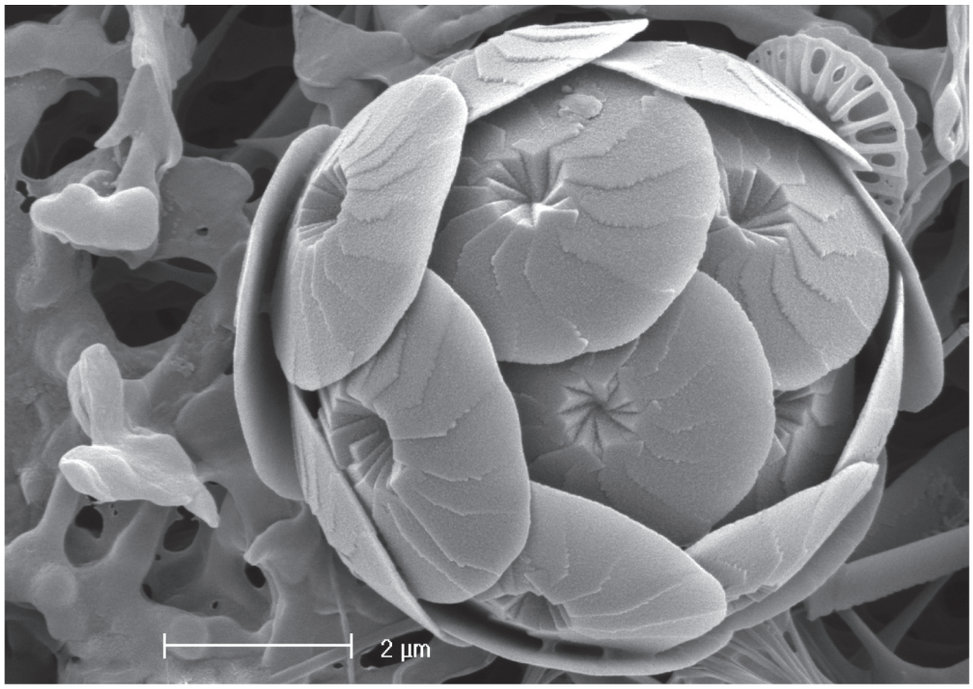
The reticulofenestrids are a large, abundant and taxonomically challenging group of coccoliths. There has been a tendency to reduce the number of genera used due to the likelihood that genera based on simple morphological criteria, such as a closed central area, are likely to be polyphyletic. This is followed on Nannotax, and so the consistent inclusion of various species requires new combinations to be proposed. In addition, two species recently described in *Hornibrookina* have been interpreted as instead belonging in *Reticulofenestra*.

Reticulofenestra chriskingii (Steurbaut, 2011) Young n. comb.

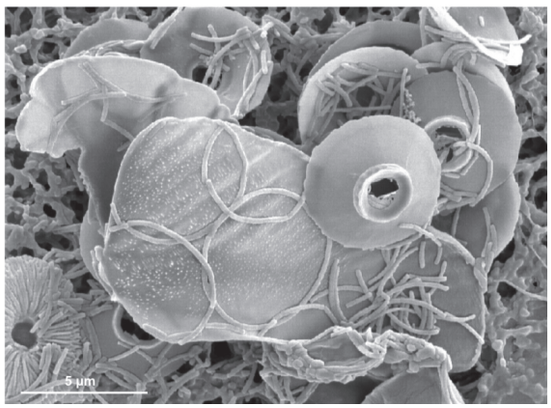
Basionym: *Dictyococcites chriskingii* Steurbaut, 2011. *Bulletin de l'Institut Royal des Sciences Naturelles de Belgique, Sciences de la Terre*, **81**: 260–261, pl. 1, figs 15–19, text-figs 13, 14.

Remarks: The group of species conventionally included in the genus *Dictyococcites* is polyphyletic, and so we prefer to include them all in *Reticulofenestra* on *Nannotax*. The species *D. chriskingii* appears to be useful, and thus the new combination, *R. chriskingii*, is warranted.

Plate 1

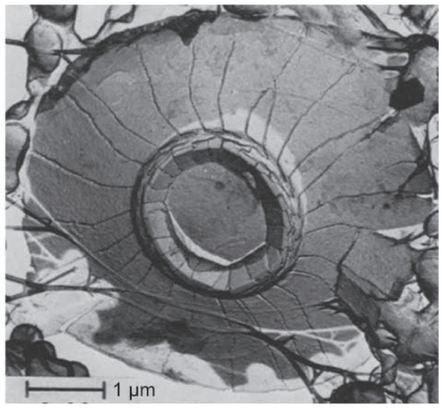


1. *Calcidiscus thiersteinii*, holotype (from Young et al., 2003, pl. 6, fig. 7)



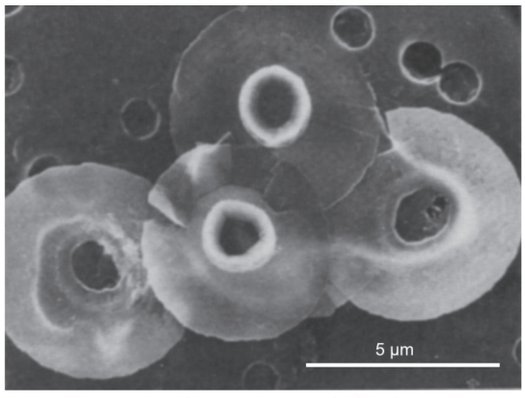
2. *Ceratolithus vidalii* combination coccosphere

(from Sprengel &Young, 2000, pl. 1, fig. A)



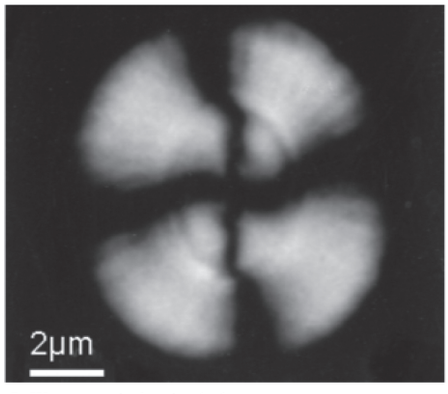
3. *C. vidalii* holotype

(from McIntyre & Bé, 1967, pl. 5, fig. b)



4. *Neosphaera placolithomorpha* var. *nishidae* holotype

(from Kleijne, 1993, pl. 3, fig. 4)



5. *Watznaueria leesiae* holotype

(from Burnett et al., 1998, pl. 6.7, fig. 27)

Reticulofenestra nicolasii (Perez Panera *in* Perez Panera & Ronchi, 2021) Young n. comb.

Basionym: *Hornibrookina nicolasii* Perez Panera *in* Perez Panera & Ronchi, 2021. *Journal of Nannoplankton Research*, **39**: 6–7, pl. 3, figs 1–9; pl. 4, figs 1–30.
Remarks: This is an unusual Eocene species with a robust central grille and slits in the distal shield. It was very well illustrated and described in Perez Panera & Ronchi (2021), but its assignment to *Hornibrookina* is not supported because the entire coccolith is formed of R-units. Thus, it is reassigned here to *Reticulofenestra*.

Reticulofenestra larae (Perez Panera *in* Perez Panera & Ronchi, 2021) Young n. comb.

Basionym: *Hornibrookina larae* Perez Panera *in* Perez Panera & Ronchi, 2021. *Journal of Nannoplankton Research*, **39**: 5–6, pl. 1, figs 1–9; pl. 2, figs 1–16.
Remarks: As with the previous species, this is almost certainly a *Reticulofenestra* not a *Hornibrookina*.

Reticulofenestra artuziae (Varol, 1989) Young n. comb.

Basionym: *Cyclicargolithus artuziae* Varol, 1989. *Revista Española de Micropaleontología*, **21**: 293, pl. 2, figs 19, 20; pl.4, figs 32–34.
Remarks: As with *Dictyococcites*, there is good reason to regard *Cyclicargolithus* and *Cribrocentrum* as polyphyletic genera. Consequently, on *Nannotax*, we prefer to place the relevant species in *Reticulofenestra*.

Reticulofenestra maceria and ***Gephyrocapsa maceria***

There are currently two *Reticulofenestra maceria* species––*R. maceria* (Okada & McIntyre, 1977) Young *in* Young et al., 2003, an extant species originally described as *Umbilicosphaera maceria* Okada & McIntyre, 1977, and *R. maceria* Shafik, 1989, a Late Eocene species. It was previously suggested, on *Nannotax*, that this meant a new name should be proposed for the Eocene species. However, recent molecular genetic work (Bendif et al., 2016, 2019; Filatov et al., 2021) has shown that the very small extant reticulofenestrid formerly known as *Reticulofenestra parvula* is very closely related to *Gephyrocapsa ericsonii* and so only indirectly related to true *Reticulofenestra*. Consequently, the species has been recombined as *Gephyrocapsa parvula* (Okada & McIntyre, 1977) Bendif et al., 2016. The extant *R. maceria* is similarly small and is probably a variant of *G. parvula*, rather than being a discrete species. To remove the nomenclatural ambiguity, the combination *Gephyrocapsa maceria* is formally proposed here. This means the Eocene form is no longer a junior homonym, and so there is no need for a replacement name.

Gephyrocapsa maceria (Okada & McIntyre, 1977) Young n. comb.

Basionym: *Umbilicosphaera maceria* Okada & McIntyre, 1977. *Micropaleontology*, **23**: 12–13, pl. 1, fig. 8.

3.2 *Hornibrookina*

The following species is clearly similar to described fossil species of *Hornibrookina*, and so it seems logical to recombine it in that genus. This also removes the anomaly of having a Paleocene species included in a genus (*Nodosella*) that was based on an Early Jurassic species, and which is now regarded as a junior synonym of *Stradnerlithus*. The only other described species of *Nodosella* is recombined below in *Syracosphaera*.

Hornibrookina elegans (Perch-Nielsen, 1981) Young n. comb.

Basionym: *Nodosella elegans* Perch-Nielsen, 1981. *Eclogae Geologicae Helvetiae*, **74**: 840–841, pl. 2, figs 1–5.

4. Changes proposed within the Order Syracosphaerales

4.1 *Syracosphaera*

The following fossil species is very similar to both modern *Syracosphaera* and fossil species, such as *S. croatica*, and so it should be recombined in that genus.

Syracosphaera franzii (Perch-Nielsen, 1981) Young n. comb.

Basionym: *Nodosella franzii* Perch-Nielsen, 1981. *Eclogae Geologicae Helvetiae*, **74**: 840, pl. 1, figs 4, 5, 7–9.

The following two species, which are only known from the holococcolith phase, have previously been assigned to the genus *Poricalyptra*. However, the other two members of the genus—*P. gaarderae* and the type species *P. aurisinae*—have now been shown to be alternate life-cycle phases of closely related *Syracosphaera* species (Keuter et al., 2019, 2021). Thomsen et al. (1991) and Archontikis et al. (2020) argued, in the analogous cases of holococcoliths formerly assigned to *Turrisphaera* and *Anthosphaera*, that it was reasonable to assume the remaining species would also prove to have similar life-cycle associations, and so should be reassigned to the same heterococcolith genus. This principle is equally applicable here, so the species have been reassigned to *Syracosphaera*.

Syracosphaera isselii (Borsetti & Cati, 1976) Young n. comb.

Basionym: *Helladosphaera isselii* Borsetti & Cati, 1976. *Giornale di Geologia*, **40**: 220, pl. 16, figs 1–3.
Synonym: *Poricalyptra isselii* (Borsetti & Cati. 1976) Kleijne, 1991.

Syracosphaera magnaghii (Borsetti & Cati, 1976) Young n. comb.

Basionym: *Helladosphaera magnaghii* Borsetti & Cati, 1976. *Giornale di Geologia*, **40**: 221, pl. 16, figs 4-6.
Synonym: *Poricalyptra magnaghii* (Borsetti & Cati, 1976) Kleijne, 1991.

***Syracosphaera* and *Calyptrosphaera* synonymy**

Calyptrosphaera Lohmann, 1902 was described with two species—*C. globosa* and *C. oblonga*. The type species is generally cited as *C. globosa*, following, for example, Loeblich and Tappan (1966), but this does not seem to have been formalised. The nature of *C. globosa* has, however, never been clear. Lohmann (1902) described it as differentiated from *C. oblonga* primarily on coccolith size, with *C. oblonga* coccoliths being 1.7–2.0 μm long versus 2–3 μm in *C. globosa* coccoliths. The forms currently assigned to *oblonga* also span this size range, and Lohmann's illustrations of *C. globosa* could easily be specimens of *oblonga*, as currently understood. So, it is sensible to regard *C. globosa* as a synonym of *C. oblonga*. Given this, *Calyptrosphaera* Lohmann, 1902 and *Syracosphaera* Lohmann, 1902 are unambiguously synonyms. Under *ICN* Art. 11.5, in situations where a "choice is possible between legitimate names of equal priority at the corresponding rank, or between available final epithets of names of equal priority at the corresponding rank, the first such choice to be effectively published establishes the priority of the chosen name". In this case, the synonymy was recognised by Cros et al. (2000), and they recommended using the name *Syracosphaera*. Hence, *Syracosphaera* probably now has priority over *Calyptrosphaera*. The process for effective publication of such choices is not, however, clear in the *ICN*. So, in case there is any doubt as to the effectiveness of the choice of Cros et al. (2000), it is repeated here. The genera *Syracosphaera* Lohmann, 1902 and *Calyptrosphaera* Lohmann, 1902 are synonyms and, of these names, *Syracosphaera* is selected as the chosen name.

This leaves six species currently placed in *Calyptrosphaera* that are 'orphaned' as a result of *Calyptrosphaera* being a synonym of *Syracosphaera*—*C. sphaeroidea* Schiller, 1913, *C. radiata* Sym & Kawachi, 2000, *C. cialdii* Borsetti & Cati, 1976, *C. dentata* Kleijne, 1991, *C. heimdaliae* Norris, 1985 and *C. lluisae* Keuter et al., 2021. Two of these species—*C. heimdaliae* and *C. lluisae*—are under review as part of a revision of related holococcoliths (Archontikis, pers. comm., 2021). Two others—*C. sphaeroidea* and *C. radiata*—are probably related and are under separate review (Probert, pers. comm., 2021). For the others, it would be appropriate to place them in *Holococcolithophora*, as recommended by Jordan et al. (2004); that is, to use the combinations *Holococcolithophora dentata* (Kleijne, 1991) Jordan et al., 2004 and *H. cialdii* (Borsetti & Cati, 1976) Jordan et al., 2004.

4.2 *Solisphaera*

The following fossil species, although described in *Calyptrosphaera*, is clearly a heterococcolith, being very similar to modern *Solisphaera*. Thus, it should be recombined in that genus.

Solisphaera miocaenica (Müller, 1974) Young n. comb.

Basionym: *Calyptrosphaera miocaenica* Müller, 1974. *Senckenbergiana Lethaea*, **55**: 390, pl. 2, figs 16, 17.

4.3 *Blackites*

Bown (2005) adopted a broad concept for the genus *Blackites*, including numerous species previously placed in other genera, rather than using multiple genera based on differences in ultrastructure that are difficult to determine without electron microscopy. This is a pragmatic solution, which has been followed on *Nannotax*. However, several additional species have been left out of *Blackites* because they were not found in the material studied. Those species are here recombined into *Blackites*. *NB* The gender of the name *Blackites* is not immediately obvious, but it has always been treated as masculine, having been created in honour of Maurice Black (who was male), so this convention is followed in the combination proposed.

Blackites mericii (Varol, 1989) Young n. comb.

Basionym: *Cruxia mericii* Varol, 1989. *Revista Española de Micropaleontología*, **21**: 293, pl. 2, fig. 2; pl. 4, figs 1–4.

Blackites perfectus (Shafik, 1989) Young n. comb.

Basionym: *Amitha perfecta* Shafik, 1989. *Alcheringa*, **13**: 72–74, fig. 3A–J.

Blackites prolatus (Shafik, 1989) Young n. comb.

Basionym: *Amitha prolata* Shafik, 1989. *Alcheringa*, **13**: 74–76, fig. 4A, B.

Blackites elongatus (Roth, 1970) Young n. comb.

Basionym: *Cepekiella elongata* Roth, 1970. *Eclogae Geologicae Helvetiae*, **63**: 864, pl. 11, figs 1, 2.

Blackites rothii (Shafik, 1989) Young n. comb.

Basionym: *Notiocyrtolithus rothii* Shafik, 1989. *Alcheringa*, **13**: 77, fig. 5A–H.

Blackites australiensis (Shafik, 1989) Young n. comb.

Basionym: *Ommatolithus australiensis* Shafik, 1989. *Alcheringa*, **13**: 79, fig. 6A–H.

5. Changes proposed within various genera of nannoliths, holococcoliths and heterococcoliths *incertae sedis*

5.1 *Ceratolithus*

The genus *Ceratolithus* is best known for producing horseshoe-shaped nannoliths—ceratoliths—but extant species also produce hoop-shaped coccoliths and, in a separate life-cycle phase, circular planolith heterococcoliths (e.g. Young et al., 2003). Archontikis and Young (2020) showed that there were two persistent associations of ceratolith and heterococcolith types, concluding that these should be regarded as separate species—*Ceratolithus cristatus* and *Ceratolithus nishidae*. Unfortunately, however, the species *Craspedolithus vidalii* Bukry, 1975 has been overlooked, which, like *Neosphaera coccolithomorpha* var. *nishidae* Kleijne, 1993, had been based on the heterococcolith phase, and specifically on forms with a narrow central area. This is a validly described species based on extant material, and so it is a senior synonym of *Ceratolithus nishidae*. Indeed, the holotype of *C. vidalii* designated by Bukry (1975) was a specimen from McIntyre and Bé (1967), and this specimen was also included by Kleijne (1993) in her synonymy of *Neosphaera coccolithomorpha* var. *nishidae*. Thus, it is necessary to use this name and to propose the combination *Ceratolithus vidalii* and to use this instead of *Ceratolithus nishidae*. To clarify this, the holotype images of both *vidalii* and *nishidae* are given on Plate 1, together with an image of a combination coccosphere with planolith coccoliths, hoop coccoliths and an ornate ceratolith.

Ceratolithus vidalii (Bukry, 1975) Young & Archontikis n. comb.

Basionym: *Craspedolithus vidalii* Bukry, 1975. *Initial Reports of the Deep Sea Drilling Project*, **32**: 689. Holotype: pl. 5, fig. B of McIntyre & Bé, 1967. *Deep Sea Research*.
Synonyms: *Ceratolithus nishidae* (Kleijne, 1993) Archontikis & Young, 2020; *Neosphaera coccolithomorpha* var. *nishidae* Kleijne, 1993; *Ceratolithus cristatus* forma *rostratus* Borsetti & Cati, 1976 (invalid).

5.2 *Craterolithus*

Steurbaut and Nolf (2021) proposed a new genus—*Luminocanthus*—with four species—*L. hirsutus* (Müller), *L. hoerstgensis* (Müller), *L. eolutetiensis* and *L. plenilute-*

tiensis. However, one of these species—*L. hoerstgensis*—had already been proposed as the holotype of another genus—*Craterolithus* Firth, 1989. While it is agreed that this is a discrete, if rare, genus, because the name *Craterolithus* has priority, new combinations are necessary. Conversely, the scanning electron microscope (SEM) study of Firth (1989) showed that *C. hoerstgensis* has a very distinctive and unusual morphology, so it is possible that the other species would be better classified in a separate genus. However, this would require SEM imagery, which is not currently available. The genus *Luminocanthus* was included in the Calcidiscaceae by Steurbaut and Nolf (2021), and this is certainly possible, although more data is needed to confirm this. Consequently, this will be left as a genus *incertae sedis*.

Craterolithus hirsutus (Müller, 1970) Young n. comb.

Basionym: *Cyclococcolithus hirsutus* Müller, 1970. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen*, 135: 93, pl. 9, figs 1–4.
Synonym: *Luminocanthus hirsutus* (Müller, 1970) Steurbaut & Nolf, 2021.

Craterolithus eolutetiensis (Steurbaut & Nolf, 2021) Young n. comb.

Basionym: *Luminocanthus eolutetiensis* Steurbaut & Nolf, 2021. *Geodiversitas*, **43**: 344, fig. 19B, C.

Craterolithus plenilutetiensis (Steurbaut & Nolf, 2021) Young n. comb.

Basionym: *Luminocanthus plenilutetiensis* Steurbaut & Nolf, 2021. *Geodiversitas*, **43**: 344–345, fig. 19G–J.

5.3 *Discoaster*

Several mid-Miocene discoasterids apparently transitional to *Catinaster* have been described, including *Discoaster micros* (Theodoridis, 1984), *D. virginianus* (Self-Trail, 2014), *D. catinatus* de Kaenel & Bergen, 2017, *D. transitus* Peleo-Alampay et al., 1998 and *Catinaster glenos* de Kaenel & Bergen, 2017. At present, *C. glenos* is anomalous within this group in being placed in *Catinaster*, so the alternative combination *Discoaster glenos* is proposed.

In addition, the species *Catinaster mexicanus* Bukry, 1971 differs from the true *Catinaster* species in having stubby rays without bifurcations, and so lacking deep inter-ray areas (see discussion in Peleo-Alampay et al., 1998). It is almost certainly not directly related to *Catinaster* and so should be recombined in *Discoaster*.

Discoaster glenos (de Kaenel & Bergen *in* de Kaenel et al., 2017) Young n. comb.

Basionym: *Catinaster glenos* de Kaenel & Bergen *in* de Kaenel et al., 2017. *Journal of Nannoplankton Research*, **37**(2–3): 233–234, pl. 6, figs 11–16.

Discoaster mexicanus (Bukry, 1971) Young n. comb.

Basionym: *Catinaster mexicanus* Bukry, 1971. *Micropaleontology*, **17**: 50, pl. 3, figs 7–9.

5.4 *Lithostromation*

Steurbaut and Nolf (2021) described new species in the genera *Trochoaster* and *Trochastrites*. However, Bybell (1975) had synonymised *Trochoaster* and *Lithostromation* on the grounds that they show multiple similarities and are hard to consistently separate. Similarly, the type species of the genus *Trochastrites* is *Discoaster bramlettei* Martini, 1958, which is regarded as a synonym of *Lithostromation simplex*. Consequently, *Trochastrites* is a synonym of *Lithostromation*. Here, new combinations in *Lithostromation* are proposed for both the new species in Steurbaut and Nolf (2021) and a couple of other species that may prove useful, but which have not yet been included in *Lithostromation*. *NB* The gender of *Lithostromation* is not immediately obvious, but it has always been treated as neuter, and so this convention is followed in the combinations proposed.

Lithostromation concavum (Bona, 1964) Young n. comb.

Basionym: *Trochoaster concavus* Bona, 1964. *Földtani Közlöny—Bulletin of the Hungarian Geological Society*, **94**: 128–130, pl. 14, figs 8, 9, text-fig. 3.

Lithostromation martinii (Best & Müller, 1972) Young n. comb.

Basionym: *Trochoaster martinii* Best & Müller, 1972. *Senckenbergiana Lethaea*, **53**: 108, pl. 2, figs 8, 9; pl. 3, figs 18–21.

Lithostromation nodosum (Steurbaut & Nolf, 2021) Young n. comb.

Basionym: *Trochoaster nodosus* Steurbaut & Nolf, 2021. *Geodiversitas*, **43**: 347, fig. 18W–Y.

Lithostromation hohnensis (Martini, 1958) Young n. comb.

Basionym: *Discoaster hohnensis* Martini, 1958. *Senckenbergiana Lethaea*, **39**: 358, pl. 2, fig, 10a, b.
Synonym: *Trochastrites hohnensis* (Martini, 1958) Bouché, 1962.

Lithostromation pyramidale (Steurbaut & Nolf, 2021) Young n. comb.

Basionym: *Trochastrites pyramidalis* Steurbaut & Nolf, 2021. *Geodiversitas*, **43**: 347–348, fig. 20T–W.

5.5 *Peritrachelina* and *Clathrolithus*

Bown (2005, p. 42) synonymised *Peritrachelina ornata* and *Clathrolithus ellipticus* on the grounds that they "represent two different views of the same, rather strangely constructed, holococcolith". This opinion was supported by extensive illustration and has not been disputed. However, Bown (2005) incorrectly stated that the two species were described in the same publication—Deflandre and Fert (1954). In fact, *P. ornata* had been described in a previous publication—Deflandre (1952). Hence, *P. ornata* is the senior synonym of *C. ellipticus*. This also affects the genera, with *P. ornata* being the type species of *Peritrachelina* Deflandre, 1952, whereas *C. ellipticus* is the type species of *Clathrolithus* Deflandre, 1954. So, *Peritrachelina* is the senior synonym of *Clathrolithus*. This leads to some further combinations being needed.

Peritrachelina arenaria (Stradner, 1962) Young n. comb.

Basionym: *Corannulus arenarius* Stradner, 1962. *Verhandlungen der Geologischen Bundesanstalt* (*Wien*), **2**: 366, pl. 1, figs 14–20.

Synonym: *Clathrolithus arenarius* (Stradner, 1962) Bown, 2005.

Peritrachelina minuta (Bramlette & Sullivan, 1961) Young n. comb.

Basionym: *Clathrolithus minutus* Bramlette & Sullivan, 1961. *Micropaleontology*, **7**(2): 157, pl. 10, fig. 18.

5.6 *Martiniaster*

There are currently two genera in use for circular, discoidal Lithostromationaceae with multiple radial ridges—*Lacunolithus* Lyul'eva, 1989 and *Martiniaster* Loeblich & Tappan, 1963. This is unnecessary, so a recombination of the species *L. menneri* in *Martiniaster* is required.

Martiniaster menneri (Lyul'eva, 1989) Young n. comb.

Basionym: *Lacunolithus menneri* Lyul'eva, 1989. Dopovidi Akademii Nauk Ukrains'koi RSR, Seriya B: Geologichni, Khimichni ta Biologichni Nauki, 1: 11, figs e–k.

6. Change proposed within the Mesozoic genus *Watznaueria*

Watznaueria coccoliths show rather limited size variation (Gollain et al., 2019), predominantly falling in the range of 4–8 μm. Larger specimens do, however, occur sometimes in the geological record, notably at the end of the Jurassic and in the lowermost Cretaceous. These large forms have frequently been identified as *W. manivitiae* Bukry, 1973. However, as noted by Varol and Bowman (2019), this identification is not tenable because *W. manivitiae* is an objective junior synonym of *Cyclagelosphaera deflandrei* (i.e. the two names have the same holotype). Varol and Bowman (2019) consequently proposed the new name *W. moshkovitzii* for this form.

Large (≥9 μm) specimens of *Watznaueria* in the Late Cretaceous have also been assigned to *W. manivitiae* Bukry, 1973 by Burnett et al. (1998) and some subsequent workers. These forms are not as large as the older *W. moshkovitzii* and there is a long stratigraphic gap between their occurrences, so the Late Cretaceous specimens should not be assigned to that species and another name is thus needed. None of the generally accepted junior synonyms of *Watznaueria barnesiae* are based on holotypes larger than 8 μm, so it seems there is no available name for

this taxon/species concept. Hence, one is proposed here.

Watznaueria leesiae n. sp.

Derivation of name: In honour of Dr Jacqueline Lees (formerly Burnett) who illustrated the type specimen. **Diagnosis**: *Watznaueria* coccoliths >9 μm long, but otherwise similar to *W. barnesiae*. **Holotype**: Specimen imaged in Burnett et al. (1998), pl. 6.7, fig. 27. This image is reproduced here as Pl. 1, fig. 5. **Type location**: The Warren, Folkestone, Kent, UK, 51.09ºN, 1.21ºE. **Type level**: Cenomanian.

Acknowledgements

David Bord and Richard Howe are thanked for their constructive comments on a previous draft of this manuscript.

References

Archontikis, O. & Young, J.R. 2020. Extant *Ceratolithus cristatus* life-cycle observations and taxonomic simplification. *Journal of Nannoplankton Research*, **30**(1): 27–39.

Archontikis, O.A., Young, J.R. & Cros, L. 2020. Taxonomic revision and classification of extant holococcolithophores previously placed in the genus *Anthosphaera* Kamptner emend. Kleijne, 1991. *Acta Protozoologica*, **59**: 121–139.

Aubry, M.-P. & Bord, D. 2009. Reshuffling the cards in the photic zone at the Eocene/Oligocene boundary. In: C. Koeberl & A. Montanari (Eds). *The Late Eocene Earth—Hothouse, Icehouse, and Impacts*. *Geological Society of America, Special Papers*, **452**: 279–301.

Bendif, E. M., Probert, I., Diaz-Rosas, F., Thamas, D., van den Engh, G., Young, J. R. & Dassow, P. v. (2016). Recent Reticulate Evolution in the Ecologically Dominant Lineage of Coccolithophores. Frontiers in Microbiology. 7: 1-15.

Bendif, E., Nevado, B., Wong, E.L.Y, Hagino, K., Probert, I., Young, J.R., Rickaby, R.E.M. & Filatov, D.A. 2019. Repeated species radiations in the recent evolution of the key marine phytoplankton lineage *Gephyrocapsa*. *Nature Communications*, **10**(2): 1–9.

Best, G. & Müller, C. 1972. Nannoplankton-Lagen im Unter-Miozan von Frankfurt am Main. *Senckenbergiana Lethaea*, **53**(1–2): 103–117.

Bona, J. 1964. Coccolithophorida-vizsgalatok a meceski retegekben (Coccolithophoriden-Untersuchungen in der neogenen Schichtenfolge des Mecsekgebirges). *Földtani Közlöny—Bulletin of the Hungarian Geological Society*, **94**: 121–131.

Borsetti, A.M. & Cati, F. 1976. Il Nannoplancton calcareo vivente nel Tirreno Centro-meridionale. Parte II. *Giornale di Geologia*, **40**(1): 209–240.

Bouché, P.M. 1962. Nannofossiles calcaires de Lutétien du Bassin de Paris. *Revue de Micropaléontologie*, **5**: 75–103.

Bown, P.R. 2005. Palaeogene calcareous nannofossils from the Kilwa and Lindi areas of coastal Tanzania (Tanzania Drilling Project 2003–4). *Journal of Nannoplankton Research*, **27**(1): 21–95.

Bown, P.R. & Newsam, C. 2017. Calcareous nannofossils from the Eocene North Atlantic Ocean (IODP Expedition 342 Sites U1403–1411). *Journal of Nannoplankton Research*, **37**(1): 25–60.

Bramlette, M.N. & Sullivan, F.R. 1961. Coccolithophorids and related nannoplankton of the Early Tertiary in California. *Micropaleontology*, **7**(2): 129–188.

Bukry, D. 1971. *Discoaster* evolutionary trends. *Micropaleontology*, **17**: 43–52.

Bukry, D. 1973. Phytoplankton stratigraphy, Central Pacific Ocean, Deep Sea Drilling Project Leg 17. *Initial Reports of the DSDP*, **17**: 871–889.

Bukry, D. 1975. Coccolith and silicoflagellate stratigraphy, northwestern Pacific Ocean, Deep Sea Drilling Project Leg 32. *Initial Reports of the DSDP*, **32**: 677–701.

Burnett, J.A., Gallagher, L.T. & Hampton, M. 1998. Upper Cretaceous. *In*: P.R. Bown (Ed.). *Calcareous nannofossil biostratigraphy*. British Micropalaeontological Society Publication Series, Kluwer Academic, London: 132–199.

Bybell, L. 1975. Middle Eocene calcareous nannofossils at Little Stave Creek, Alabama. *Tulane Studies in Geology and Paleontology*, **11**(4): 177–247.

Cappelli, C., Bown, P.R., Riu, M.D. & Agnini, C. 2020. Middle Eocene large coccolithaceans: Biostratigraphic implications and paleoclimatic clues. *Marine Micropaleontology*, **154**: 1–17.

Cros, L., Kleijne, A., Zeltner, A., Billard, C. & Young, J.R. 2000. New examples of holococcolith–heterococcolith combination coccospheres and their implications for coccolithophorid biology. *In*: J.R. Young, H.R. Thierstein & A. Winter (Eds). Nannoplankton ecology and palaeocology. Proceedings of the INA7 conference, Puerto Rico, February 2002. *Marine Micropaleontology*, **39**(1–4): 1–34.

Deflandre, G. 1952. Classe des Coccolithophoridés (Coccolithophoridae Lohmann, 1902). *In*: P.P. Grassé (Ed.). *Traité de Zoologie, Masson, Paris*: 439–470.

Deflandre, G. & Fert, C. 1954. Observations sur les coccolitho-

phoridés actuels et fossiles en microscopie ordinaire et électronique. *Annales de Paléontologie*, **40**: 115–176.

de Kaenel, E., Bergen, J.A., Browning, E., Blair, S.A. & Boesiger, T.M. 2017. Uppermost Oligocene to Middle Miocene *Discoaster* and *Catinaster* taxonomy and stratigraphy in the circum North Atlantic Basin: Gulf of Mexico and ODP Leg 154. *Journal of Nannoplankton Research*, **37**(2–3): 215–244.

Filatov, D.A., Bendif, E.M., Archontikis, O.A., Hagino, K. & Rickaby, R.E.M. 2021. The mode of speciation during a recent radiation in open-ocean phytoplankton. *Current Biology*, **31**: 1–11.

Firth, J.V. 1988. *Craterolithus*; a new calcareous nannofossil genus from the Oligocene of the Labrador Sea. *Journal of Paleontology*, **62**(6): 853–854.

Geisen, M. et al. 2004. Species level variation in coccolithophores. In: H.R. Thierstein & J.R. Young (Eds). *Coccolithophores—From molecular processes to global impact*. Springer, Berlin: 327–366.

Gollain, B., Mattioli, E., Kenjo, S., Bartolini, A. & Reboulet, S. 2019. Size patterns of the coccolith *Watznaueria barnesiae* in the Lower Cretaceous: Biotic versus abiotic forcing. *Marine Micropaleontology*, 152: 1–11.

Keuter, S., Young, J.R. & Frada, M.J. 2019. Life cycle association of the coccolithophore *Syracosphaera gaarderae* comb. nov. (ex *Alveosphaera bimurata*): Taxonomy, ecology and evolutionary implications. *Marine Micropaleontology*, **148**: 58–64.

Keuter, S., Young, J.R., Koplovitz, G., Zingone, A. & Frada, M.J. 2021. Novel heterococcolithophores, holococcolithophores and life cycle combinations from the families *Syracosphaeraceae* and *Papposphaeraceae* and the genus *Florisphaera*. *Journal of Micropalaeontology*, **40**: 75–99.

Kleijne, A. 1991. Holococcolithophorids from the Indian Ocean, Red Sea, Mediterranean Sea and North Atlantic Ocean. *Marine Micropaleontology*, **17**: 1–76.

Kleijne, A. 1993. *Morphology, taxonomy and distribution of extant coccolithophorids (calcareous nannoplankton)*. Drukkerij FEBO B.V., Katwijk: 1–321.

Knappertsbusch, M. 2000. Morphological evolution of the coccolithophorid *Calcidiscus leptoporus* from the Early Miocene to Recent. *Journal of Paleontology*, **74**(4): 712–730.

Knappertsbusch, M., Cortes, M.Y. & Thierstein, H.R. 1997. Morphologic variability of the coccolithophorid *Calcidiscus leptoporus* in the plankton, surface sediments and from the Early Pleistocene. *Marine Micropaleontology*, **30**: 293–317.

Loeblich, A.R. & Tappan, H. 1963. Type fixation and validation of certain calcareous nannoplankton genera. *Proceedings of the Biological Society of Washington*, **76**: 191-198.

Loeblich, A.R. & Tappan, H. 1966. Annotated index and bibliography of the calcareous nannoplankton. *Phycologia*, **5**: 81–216.

Lohmann, H. 1902. Die Coccolithophoridae, eine Monographie der Coccolithen bildenden Flagellaten, zugleich ein Beitrag zur Kenntnis des Mittelmeerauftriebs. *Archiv für Protistenkunde*, **1**: 89–165.

Lyul'eva, S.A. 1989. New Miocene and Pliocene calcareous nannofossils of the Ukraine. *Dopovidi Akademii Nauk Ukrains'koi RSR Seriia B–Geologichni Khimichni ta Biologichni Nauki*, **1**: 10–14.

Martini, E. 1958. Discoasteriden und verwandte Formen im NW-deutschen Eozän (Coccolithophorida). 1. Taxonomische Untersuchungen. *Senckenbergiana Lethaea*, **39**: 353–388.

McIntyre, A. & Bé, A.W.H. 1967. Modern Coccolithophoridae of the Atlantic Ocean—I. Placoliths and cyrtholiths. *Deep-Sea Research and Oceanographic Abstracts*, **14**: 561–597.

Müller, C. 1970. Nannoplankton aus dem Mittel-Oligozän von Norddeutschland und Belgien. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen*, **135**: 82–101.

Müller, C. 1974. Nannoplankton aus dem Mittel-Miozän von Walbersdorf (Burgenland). *Senckenbergiana Lethaea*, **55**: 389–405.

Norris, R.E. 1985. Indian Ocean nannoplankton. II. Holococcolithophorids (Calyptrosphaeraceae, Prymnesiophyceae) with a review of extant genera. *Journal of Phycology*, **21**: 619–641.

Okada, H. & McIntyre, A. 1977. Modern coccolithophores of the Pacific and North Atlantic Oceans. *Micropaleontology*, **23**(1): 1–55.

Peleo-Alampay, A., Bukry, D., Liu, L. & Young, J.R. 1998. Late Miocene calcareous nannofossil genus *Catinaster*: Taxonomy, evolution and magnetobiostratigraphy. *Journal of Micropalaeontology*, **17**(1): 71–85.

Perch-Nielsen, K. 1981. New Maastrichtian and Paleocene calcareous nannofossils from Africa, Denmark, the USA and the Atlantic, and some Paleocene lineages. *Eclogae Geologicae Helvetiae*, **74**(3): 831–863.

Pérez Panera, J.P. & Ronchi, D.I. 2021. Two new species of *Hornibrookina* Edwards, 1973 from the Austral Basin, Patagonia: Biostratigraphical and palaeoecological implications. *Journal of Nannoplankton Research*, **39**(1): 3–13.

Quinn, P., Thierstein, H.R., Brand, L.E. & Winter, A. 2003. Experimental evidence for the species character of *Calcidiscus*

leptoporus morphotypes. *Journal of Paleontology*, **77**(5): 825–830.

Quinn, P., Sáez, A.G., Baumann, K.-H., Steel, B.A., Sprengel, C. & Medlin, L.K. 2004. Coccolithophorid biodiversity: Evidence from the cosmopolitan species *Calcidiscus leptoporus*. *In*: H.R. Theirstein & J.R. Young (Eds). *Coccolithophores—From molecular processes to global impact*. Springer, Berlin: 299–326.

Roth, P.H. 1970. Oligocene calcareous nannoplankton biostratigraphy. *Eclogae Geologicae Helvetiae*, **63**: 799–881.

Sáez, A.G., Probert, I., Geisen, M., Quinn, P., Young, J.R. & Medlin, L.K. 2003. Pseudo-cryptic speciation in coccolithophores. *Proceedings of the National Academy of Sciences, USA*, **100**(12): 7163–7168.

Self-Trail, J. 2014. *Catinaster virginianus* sp. nov.: A new species of *Catinaster* from the Middle Miocene mid-Atlantic coastal plain. *Journal of Nannoplankton Research*, **33**(1): 49–57.

Shafik, S. 1989. Some new calcareous nannofossils from Upper Eocene and Lower Oligocene sediments in the Otway Basin, southeastern Australia. *Alcheringa*, **13**: 69–83.

Sprengel, C. & Young, J.R. 2000. First direct documentation of associations of *Ceratolithus cristatus* ceratoliths, hoop-coccoliths and *Neosphaera coccolithomorpha* planoliths. *In*: J.R. Young, H.R. Thierstein & A. Winter (Eds). Nannoplankton ecology and palaeocology. Proceedings of the INA7 conference, Puerto Rico, February 2005. *Marine Micropaleontology*, **39**(1–4): 39–41.

Steurbaut, E. 2011. New calcareous nannofossil taxa from the Ypresian (Early Eocene) of the North Sea Basin and the Turan Platform in west Kazakhstan. *Bulletin de l'Institut Royal des Sciences Naturelles de Belgique, Sciences de la Terre*, **81**: 247–277.

Steurbaut, E. & Nolf, D. 2021. The Mont-des-Récollets section (N France): A key site for the Ypresian–Lutetian transition at mid-latitudes—Reassessment of the boundary criterion for the base-Lutetian GSSP. *Geodiversitas*, **43**(11): 311–363.

Stradner, H. 1962. Über neue und wenig bekannte Nannofossilien aus Kreide und Alttertiär. *Verhandlungen der Geologischen Bundesanstalt* (*Wien*), **2**: 363–377.

Theodoridis, S. 1984. Calcareous nannofossil biostratigraphy of the Miocene and revision of the helicoliths and discoasters. *Utrecht Micropaleontological Bulletin*, **32**: 1–271.

Varol, O. 1989. Eocene calcareous nannofossils from Sile (northwest Turkey). *Revista Española de Micropaleontología*, **21**: 273–320.

Varol, O. & Bowman, A.R. 2019. Taxonomic revision of selected Late Jurassic (Tithonian) calcareous nannofossils and the application of mobile mounting. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen*, **291**: 65–87.

Wei, W. & Wise, S.W. 1992. Oligocene–Pleistocene calcareous nannofossils from Southern Ocean Sites 747, 748, and 751. *Proceedings of the ODP, Scientific Results*, **120**: 509–521.

Young, J.R., Geisen, M., Cros, L., Kleijne, A., Probert, I. & Ostergaard, J.B. 2003. A guide to extant coccolithophore taxonomy. *Journal of Nannoplankton Research*, *Special Issue*, **1**: 1–132.