# Reappraisal of three calcareous nannofossil species: *Coccolithus crassus, Toweius magnicrassus,* and *Toweius callosus*

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## ABSTRACT

Type material of calcareous nannofossil index species *Coccolithus crassus* and two geographically widespread species *Toweius magnicrassus* and *T. callosus* have been studied by both light and SEM microscopy and morphometric measurements were made. *Coccolithus crassus* resembles *Coccolithus pelagicus* but has a raised cycle of elements around the centre of the distal shield. It probably evolved from *C. pelagicus*. Both *T. magnicrassus* and *T. callosus* have three cycles of elements in distal view, which is a characteristic of *Toweius*. *Toweius magnicrassus* is larger than *T. callosus*. Differentiation of *T. magnicrassus* from *T. callosus* is possible and useful because there is generally a size gap between them in a given sample and they have different stratigraphic ranges. However, both *T. callosus* and *T. magnicrassus* appear to increase in size from high to low latitudes. *Toweius callosus* most probably evolved from *Toweius pertusus* in the latest Palaeocene and gave rise to *T. magnicrassus* in the early Eocene. *J. Micropalaeontol.,* 12 (1): 91-98, August 1993.

## INTRODUCTION

*Coccolithus crassus* was described by Bramlette and Sullivan (1961) from the Eocene Lodo Formation of California. The first occurrence of this species is a zonal marker for the CP10/CP11 zonal boundary in the widely used nannofossil zonation of Okada and Bukry (1980). This marker could be used for biostratigraphy by Bukry in virtually all lower Eocene DSDP cores that he examined (Fig. 1). However, most nannofossil workers cannot use this marker because of confusion about the species concept of *C. crassus.* For instance, Matter et al. (1974, pl. 4, fig. 8) mistook *C. crassus* for *Ericsonia ovalis* Black; Romein (1979) considered *C. crassus* a junior synonym of *Coccolithus eopelagicus* (Bramlette and Riedel) Bramlette and Sullivan; Perch-Nielsen (1985, p. 433, figs. 3.46 and 3.47, p. 504, figs. 58.12 and 58.13) figured *Toweius callosus* Perch-Nielsen as *C. crassus.* The problem of using this marker was echoed by Filewicz and Hill (1983, p. 51).

Associated with the *C. crassus* problem is the general confusion in the literature about the species

concepts of *Toweius magnicrassus* (Bukry) Romein and *Toweius callosus* Perch-Nielsen. Bukry (1971a) described *C. magnicrassus* from light microscope study and the holotype was illustrated beside *C. crassus* to show the different rim optics. The species name, chosen because of central area similarities, created a false impression that *T. magnicrassus* is a larger form of *C. crassus,* even though the original text
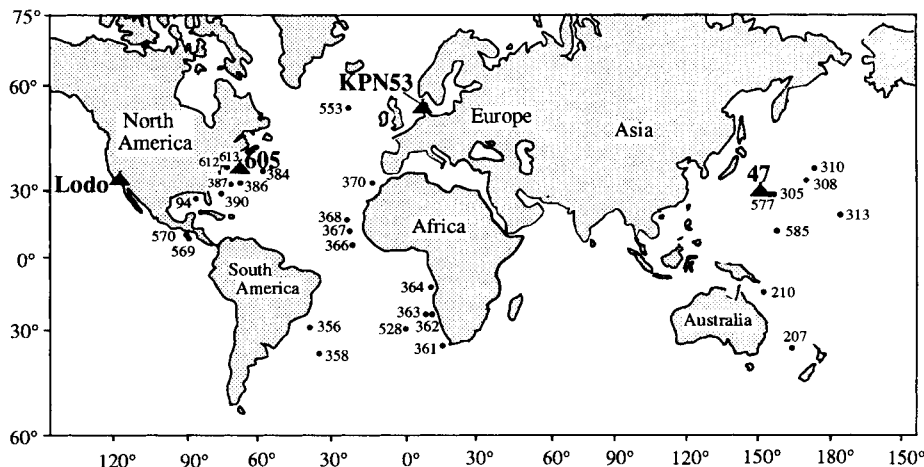


Fig. 1 DSDP sites at which *Coccolithus crassus* has been found useful for biostratigraphy (mostly by D. Bukry; refer to *DSDP Initial Reports* for details). Locations of sites investigated in this study are indicated by triangles.

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clearly distinguished the two by their upper rim optic differences. The original size range of *T. magnicrassus* as (16-20μm) was too large according to our new measurements.

*Toweius callosus* was described from the lower Eocene sediment of Denmark based on transmission electron micrographs (Perch-Nielsen, 1971). The only light micrographs (isotype) of this species (Perch-Nielsen, 1971, pl. 61, figs. 32 and 33) unfortunately were of *Reticulofenestra dictyoda* (*R. samodurovii* of some authors). Besides, the size range of this species was not described. Confusion of this species with *T. magnicrassus* and *C. crassus* thus arose frequently in the literature. For example, Romein (1979) illustrated *T. magnicrassus* as *T. callosus*; Gallagher (1989, p. 47) considered *T. callosus* as a junior synonym of *C. crassus*.

*Coccolithus crassus* is a marker species with one of the widest geographic distributions in the Cenozoic (Fig. 1) and *Toweius magnicrassus/T. callosus* are generally abundant from low through high latitudes (see, for example, Bukry [1971a], Wei and Wise [1989], Pospichal and Wise [1990]). It is thus important to clear up the confusion about the species concepts so that these species can be used widely and consistently in biostratigraphy and in palaeoecological studies. We have re-examined type material of these species and photographed the species both in a light microscope and scanning electron microscope (SEM). Morphometric measurements for the three species were made in the type samples and in samples from different stratigraphic levels and different latitudes.

## MATERIAL AND METHODS

Topotype material of *Coccolithus crassus* is from a split of Bramlette's original sample (Lodo #68, holotype was from Lodo #71, which was not available), the type material of *Toweius magnicrassus* (DSDP 47B-7-3, 104 cm) was obtained from the DSDP Core Repository at Scripps Institution of Oceanography, and the type material of *Toweius callosus* (KPN53) was kindly provided by K. von Salis Perch-Nielsen. Smear slides were made directly from unprocessed samples and examined with a light microscope at a magnification of about 1250X. For SEM study, samples were mounted on a cover glass glued to a specimen stub and coated with a thin film of gold-platinum alloy in a vacuum coater.

For morphometric studies, at least 30 (typically >50) specimens encountered along random traverses of each smear slide were measured with a ruler on a Panasonic monitor screen connected to a Panasonic video camera mounted on a Zeiss Photomicroscope III. The magnification we achieved in this study is 6600X, that is, one cm on the screen corresponds to about 1.5μm for a fossil specimen. This enables a size resolution better than 0.3μm, which is sufficient for this study.

## RESULTS AND DISCUSSION

Light and SEM micrographs of *Coccolithus crassus*, *Toweius magnicrassus*, and *Toweius callosus* are shown in Plate 1. The
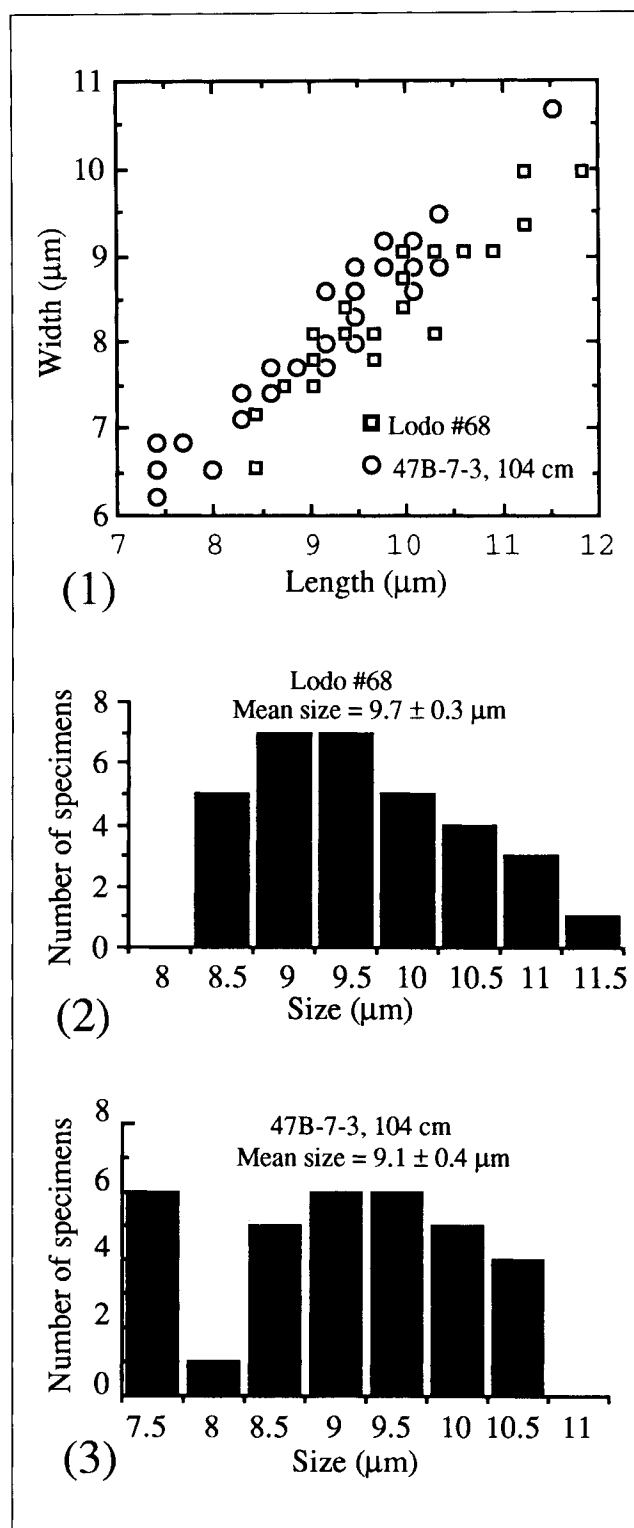


**Fig. 2.** Size measurements of *Coccolithus crassus* from topotype sample Lodo #68 and DSDP Sample 47B-7-3, 104 cm, from which Bukry (1971, pl. 2, fig. 2, right specimen) illustrated *C. crassus*. (1) length vs. width; (2) size distribution in Lodo #68; (3) size distribution in DSDP Sample 47B-7-3, 104 cm.

most distinctive feature of *C. crassus* is a raised cycle of elements around the centre of the distal shield (Pl. 1, fig. 1; see also Wei [in press]). This cycle can also be seen easily in a light microscope by focusing up and down through the specimen. Although the elements of the raised cycle appear to be slightly irregular, they are not likely to be the product of overgrowth since they are consistently present in the topotype material, which contains generally well-preserved nannofossils, and in age-equivalent material from DSDP Sites 47 (Pl. 1, fig. 1) and 528. Without the raised cycle, the species would look very similar to *Coccolithus pelagicus* (Wallich) Schiller. On the other hand, *C. crassus* differs significantly from species of *Toweius* in that it shows only two cycles of elements in distal view whereas *Toweius* shows three cycles of elements. *C. crassus* thus should not be transferred to the genus *Toweius* as proposed by Perch-Nielsen (1984) but should remain in the genus *Coccolithus*. The reasons for the use of *Coccolithus* rather than *Ericsonia* have been discussed by Wise (1983).

*Coccolithus crassus* can be differentiated from *C. pelagicus* by the following features: (1) in phase-contrast light, the distal shield of *C. crassus* is less dark than that of *C. pelagicus*; (2) the area around the central opening is very bright; (3) the distal and central margins of *C. crassus* show slight irregularities mimicking overgrowth; (4) in polarized light, an orange line is present close to the central opening of *C. crassus*, and virtually the entire placolith appears to be birefringent (see Pl. 1. fig. 7).

Measurements on *C. crassus* (Fig. 2) show that the length/width ratio (mean=1:0.83) is relatively constant for specimens of different sizes and the species is elliptical. The size range is commonly 8-12 µm. This size range is in good agreement with the holotype size (9.5µm), although Bramlette and Sullivan (1961) gave a size range of 10-13µm for the species.

*Toweius magnicrassus* was described by Bukry (1971a) from the lower Eocene of DSDP Site 47 in the northwestern Pacific. Both holotype and isotypes are light micrographs. Published SEM micrographs of *Toweius magnicrassus* are rare, the two in Wei (1992, pl. 1, figs. 1 and 2) are probably the only ones available. Here we present SEM and light micrographs of *T. magnicrassus* from the type material (Pl. 1, figs. 4, 5, and 8-11). Romein (1979) transferred *Coccolithus magnicrassus* to the genus *Toweius*. However, as pointed out by Perch-Nielsen (1985, p. 505), the two specimens he illustrated as *T. magnicrassus* (pl. 4, figs. 2 and 3) are 6.5µm and 7.2µm long, respectively, and therefore too small to be *T. magnicrassus*. They are actually specimens of *T. callosus*. Thus it was not clear whether *C. magnicrassus* belonged to *Toweius* and Perch-Nielsen (1985) attached a question mark to Romein's new combination. It is now clear that the question mark should be removed because *T. magnicrassus* clearly shows three cycles of elements in distal view (see Pl. 1, figs. 4 and 5), which is characteristic of the genus *Toweius*. It is also clear that *T. magnicrassus* is not a larger form of *C. crassus* because the two species do not even belong to the same genus.
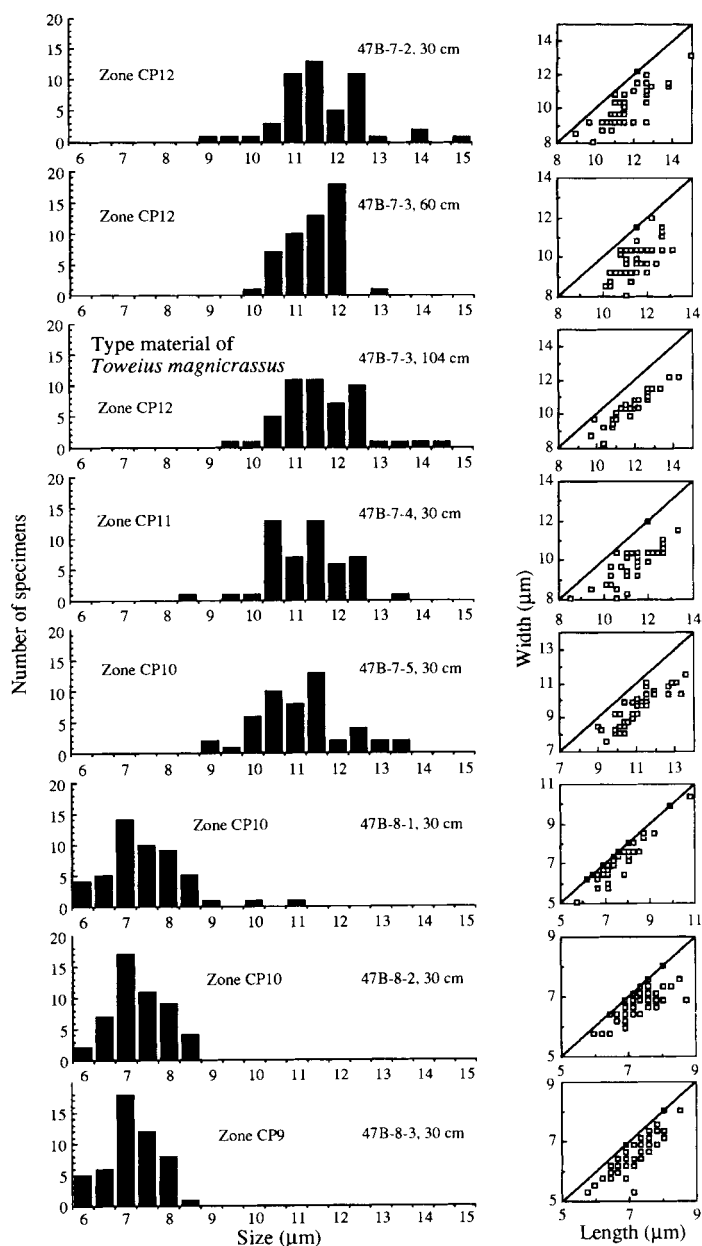


**Fig. 3.** Size distribution and length vs. width for *Toweius magnicrassus* and *Toweius callosus*, DSDP Site 47. Data points on the diagonal lines indicate circular specimens.

SEM and light micrographs of *Toweius callosus* from the type material (KPN53) are also shown (Pl. 1, figs. 2, 3, 12, and 13). As *T. magnicrassus*, *T. callosus* clearly shows three cycles of elements in distal view, and in fact, the structure of *T. callosus* is virtually the same as that of *T. magnicrassus*. However, there is generally a size gap between the two species and they have different stratigraphic ranges. It is thus useful to distinguish the two species. Perch-Nielsen (1985, p. 505) remarked that "*T. callosus* is difficult to distinguish from Neogene species of *Reticulofenestra* or from

early forms of *R. dictyoda* with the LM" (light microscope). It is now clear that the birefringence pattern of *Toweius callosus* is very different from that of *Reticulofenestra* because the outer rim of *T. callosus* birefringes very weakly (Pl. 1, figs. 12 and 13) whereas the entire placolith of *Reticulofenestra* birefringes strongly.

In order to investigate the size patterns of *T. magnicrassus-T. callosus* through time, we made morphometric measurements on eight samples from different stratigraphic levels at DSDP Site 47 (Fig. 3). Previous nannofossil biostratigraphy for this site was provided by Bukry (1971b). Here we redated this interval using the nannofossil zonation of Okada and Bukry (1980) to achieve higher biostratigraphic resolution. Samples 47B-7-2, 30 cm through 47B-7-3, 104 cm contain *Discoaster sublodoensis, Discoaster kuepperi,* and *Coccolithus crassus* among other Eocene species but no *Nannotetrina fulgens,* and can be assigned to Zone CP12. *Discoaster sublodoensis* and *Tribrachiatus orthostylus* are not present in Sample 47B-4, 30 cm whereas *Discoaster lodoensis, Discoaster kuepperi* and *C. crassus* are abundant, and this sample is placed in Zone CP11. Samples 47B-7-5, 30 through 47B-8-2, 30 cm yielded both *D. lodoensis* and *T. orthostylus* but no *C. crassus* and this interval is dated as Zone CP10. Sample 47B-8-3, 30 cm contains *Discoaster diastypus* but no *Discoaster lodoensis* and can be assigned to Zone CP9.

Samples 47B-7-2, 30 cm through 47B-7-5, 30 cm contain *T. magnicrassus* but no *T. callosus* (Fig. 3). It is clear from these samples, including the type sample of *T. magnicrassus* (Sample 47B-7-3, 104 cm), that the size of *T. magnicrassus* generally ranges from 9 to 15μm. The 16-20μm size range for this species in the original description of Bukry (1971a) thus should be revised. Measurement of the holotype (Bukry, 1971a, pl. 2, figs. 1 and 2) using the magnification stated results in a size of 15μm. The length vs. width diagrams (Fig. 3) show that there is a relatively large range in the length vs. width ratio (mean=1:0.75) and that a few specimens are circular whereas most specimens are elliptical to subelliptical.

*Toweius callosus* is abundant in Samples 47B-8-1, 30 cm through 47B-8-3, 30 cm (Fig. 3). A few specimens of *T. magnicrassus* have been recorded in Sample 47B-8-1, 30 cm, which are ≥9 μm in size. It is noticeable from Figure 3 that there are generally more circular or virtually circular specimens in *T. callosus* than in *T. magnicrassus.* In fact, the holotype of *T. callosus* is close to circular.

The morphometric measurements of the *T. magnicrassus/T. callosus* group in the type material of *T. callosus* (KPN53) are shown in Fig. 4. *T. callosus* is very abundant in this sample whereas *T. magnicrassus* is more than an order of magnitude less abundant, so we measured these two species separately to reveal the size distribution of both species. Separation of the two species based on size is possible because there seems to be a size gap between them, with 6.5-7.5μm sized specimens being absent. *T. callosus* is 4 to 6μm long and *T. magnicrassus* 8 to 11μm (Fig. 4). This is consistent with most
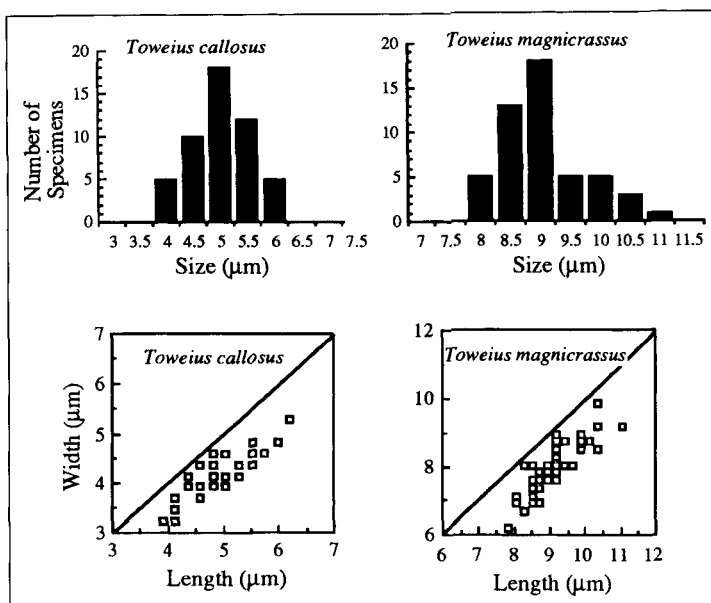


**Fig. 4.** Size distribution and length vs. width for *Toweius callosus* and *Toweius magnicrassus,* type sample of *Toweius callosus* (KPN53).

of the illustrations of Perch-Nielsen (1971), where the holotype of *T. callosus* is 5.4μm long (Perch-Nielsen, 1971, pl. 17, fig. 5), and the isotypes are 5.1μm (Perch-Nielsen, 1971, pl. 17, figs. 3 and 5). However, one of her isotypes of *T. callosus* (Perch-Nielsen, 1971, pl. 18, fig. 5) is not *T. callosus* because that specimen is about 8.0μm long and it belongs to *T. magnicrassus.*

*T. magnicrassus* and *T. callosus* are both smaller in high-latitude (56°N) Sample KPN53 than in low-latitude samples from DSDP Site 47 (DSDP Site 47 lay in low latitudes in the early Eocene [Prince et al., 1980]). In order to better examine latitudinal variation in *T. magnicrassus/T. callosus,* we also measured the size of *T. magnicrassus* and *T. callosus* in two samples from mid-latitude Site 605 (39°N). These results are compared with those from the high and low latitudes in Fig. 5. There appears to be a size increase for both *T. callosus* and *T. magnicrassus* from high to low latitudes. The upper size limit of *T. callosus* in the low-latitude samples overlaps with the lower size limit of *T. magnicrassus* in the high-latitude sample, although these two species generally do not overlap in size at individual sites. Consequently, the definition of the size range of the two species should take into account this size shift through latitude. This size-latitude relationship may have significant implications in palaeoecologic studies. However, a detailed investigation of this is beyond the scope of the present paper.

The evolution of the three species investigated is either not clear or incorrectly stated in the literature, partly because of the confusion of the species concepts. For instance, Romein (1979, p. 72, fig. 38) suggested that *T. magnicrassus* evolved directly from *Toweius pertusus.* He did not discuss the evolution of *T. callosus* or *C. crassus.* Gallagher (1989, p. 49, fig. 3.4) indicated that *T. pertusus* evolved to *T. crassus* (his *T. callosus,* [Gallagher, 1989, p. 47]),
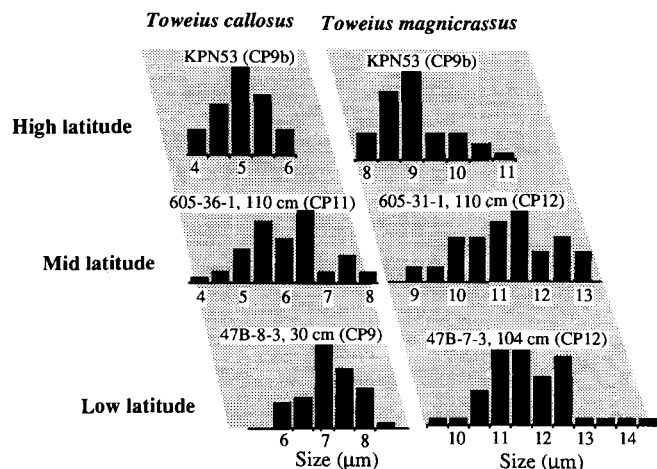
Fig. 5. Size distribution of *Toweius callosus* and *Toweius magnicrassus* at different latitudes. Note the general size increase for both species from high to low latitudes as indicated by the shaded patterns.

which in turn evolved to *Reticulofenestra dictyoda*. He did not mention the evolution of *C. crassus*. Based on ultrastructure and stratigraphical distribution, we propose a new evolution chart for *C. crassus*, *T. magnicrassus*, and *T. callosus* (Fig. 6). *Coccolithus crassus* is believed to have developed from *C. pelagicus* because it most resembles the latter species. *Coccolithus crassus* became extinct in the latest early Eocene in Subzone CP12a without a clear descendant. *Toweius callosus* is assumed to have evolved from *Toweius pertusus* by reducing the number of the central pores to one. *Toweius callosus* gave rise to *T. magnicrassus* by increase in size and in the number of elements. The transition of *Toweius callosus* to *Reticulofenestra dictyoda/R. samodurovii* in the lower Eocene has not been well documented. The change may have been accomplished by the loss of the middle cycle of elements and by change in crystal c-axis orientation in the rim elements of *T. callosus*. Alternatively, the distal shield elements of *Toweius* may have been reduced to virtually nothing whilst the middle cycle of elements expanded to become the distal shield of *Reticulofenestra* (Young et al., 1992).

## CONCLUSIONS

*Coccolithus crassus* resembles *Coccolithus pelagicus* but differs from the latter in that it has a raised cycle of elements around the centre of the distal shield. It does not belong to the genus *Toweius* as has been suggested and should remain in the genus *Coccolithus*. This species most probably evolved from *C. pelagicus* in the lower Eocene. *Toweius magnicrassus* is not a larger form of *C. crassus* as its name might suggest. Instead, it is a larger species derived from *T. callosus*. Both *T. magnicrassus* and *T. callosus* have three cycles of elements in distal view, which is distinctive of *Toweius*. The differentiation of *T. magnicrassus* from *T. callosus* is possible and useful because there is generally a size gap between these two species in a given sample and their stratigraphic
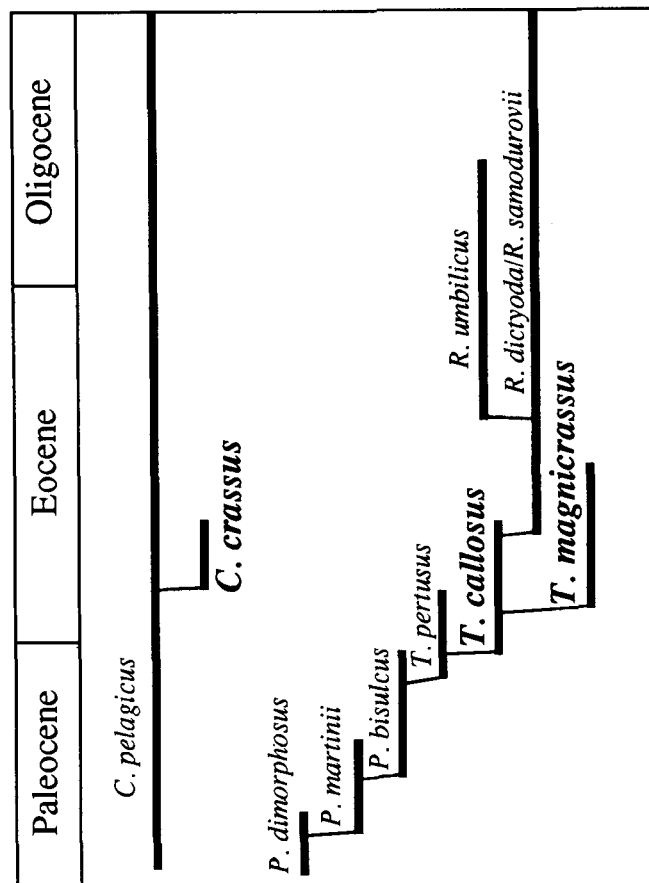


Fig. 6. Likely phylogenetic relationships of *Coccolithus crassus*, *Toweius callosus*, *Toweius magnicrassus* and other nannofossil species.

ranges are different. There is, however, a general size increase for both *T. callosus* and *T. magnicrassus* from high to low latitudes. *Toweius callosus* is usually 4 to 6μm long at high latitudes, 4 to 8μm at mid latitudes, and 6 to 8.5μm at low latitudes. *Toweius magnicrassus* is generally 8 to 11μm long at high latitudes, 9 to 13 mm at mid latitudes, and 9.5 to 14.5μm at low latitudes. *Toweius callosus* most probably evolved from *Toweius pertusus* in the latest Palaeocene (Zone CP8) and gave rise to *T. magnicrassus* in the early Eocene.

## SYSTEMATIC DESCRIPTIONS

Family Coccolithaceae Poche 1913
Genus *Coccolithus* Schwarz, 1894
*Coccolithus crassus* Bramlette and Sullivan, 1961
(Pl. 1, figs 1, 6, and 7)

1961 *Coccolithus crassus* Bramlette and Sullivan: 139, pl. 1, figs 4a-d
1963 *Coccolithus crassus* Bramlette and Sullivan; Stradner: 178, pl. 1, fig. 5.
1971 *Coccolithus crassus* Bramlette and Sullivan; Bukry: 311, pl. 2, fig. 2, right specimen.
1974 *Ericsonia ovalis* Black; Matter et al.: 914, pl. 4, fig. 8.

1984 Non *Coccolithus crassus* Bramlette and Sullivan; Steinmetz and Stradner: 741, pl. 42, figs 1 and 2.

1985 Non *Coccolithus crassus* Bramlette and Sullivan; Perch-Nielsen: 433, figs 3.46 and 3.47; 504, figs 58.12 and 58.13.

1989 Non *Coccolithus crassus* Bramlette and Sullivan; Varol: 302, pl. 4, figs 37 and 38.

1990 Non *Coccolithus crassus* Bramlette and Sullivan; Pospichal and Wise: 638, pl. 6, fig. 1.

**Remarks.** *Coccolithus crassus* resembles *C. pelagicus* but differs from the latter in that it has a prominent cycle of elements around the centre of the distal shield and virtually the entire placolith appears to be birefringent under cross nicols.

**Size.** Commonly 8-12µm long.

**Occurrence.** *Coccolithus crassus* has been reported from Zones CP11-CP12a of Okada and Bukry (1980) from low through high latitudes. It ranges from geomagnetic Subchrons C23N to C22N (54 to 52 Ma in the time scale of Berggren et al., 1985) based on magnetobiostratigraphic correlation at DSDP Site 522 in the South Atlantic (W. Wei, unpubl. data) and Site 577 in the Northwest Pacific (Monechi, 1985; Monechi et al., 1985).

Family Prinsiaceae Hay and Mohler 1967
Genus *Toweius* Hay and Mohler, 1967
*Toweius callosus* Perch-Nielsen 1971
(Pl. 1, figs 2, 3, 12, and 13)

1971 *Toweius callosus* Perch-Nielsen: pl. 17, figs 3, 5, and 6.

1971 Non *Toweius callosus* Perch-Nielsen: pl. 18, fig. 5; pl. 61, figs 32 and 33.

1972 Non *Toweius callosus* Perch-Nielsen; Perch-Nielsen: 1038, pl. 7, fig. 6.

1975 *Toweius callosus* Perch-Nielsen; Edwards and Perch-Nielsen: 510, pl. 7, fig. 8.

1975 Non *Toweius callosus* Perch-Nielsen; Edwards and Perch-Nielsen: 508, p;. 6, fig. 9.

1979 *Toweius magnicrassus* (Bukry) Romein; Romein: 216, pl. 4, figs 2 and 3.

1989 *Toweius callosus* Perch-Nielsen; Wei and Wise: 123, pl. 1, figs 3 and 6.

1990 *Toweius callosus* Perch-Nielsen; Pospichal and Wise: 637, pl. 5, figs 9a-9c.

1990 *Toweius callosus* Perch-Nielsen; Wei and Thierstein: 493, pl. 6, figs 9 and 10.

**Remarks.** This is a small species of *Toweius* with only one central opening. The area around the central opening is bright in polarized light and the outer rim birefringes weakly.

**Size.** Generally 4 to 6µm long at high latitudes, 4 to 8µm at mid latitudes, and 6 to 8.5µm at low latitudes.

**Occurrence.** Generally abundant from low through high latitudes and ranges from the latest Palaeocene to the early Eocene.

*Toweius magnicrassus* (Bukry) Romein, 1979
(Pl. 1, figs 4, 5, and 8-11)

1971 *Coccolithus magnicrassus* Bukry: 310, pl. 2, figs 1-5.

1971 *Toweius callosus* Perch-Nielsen: pl. 18, fig. 5.

1972 *Toweius callosus* Perch-Nielsen; Perch-Nielsen: 1038, pl. 7, fig. 6.

1975 *Toweius callosus* Perch-Nielsen; Edwards and Perch-Nielsen: 508, pl. 6, fig. 9.

1979 Non *Toweius magnicrassus* (Bukry) Romein; Romein: 216, pl. 4, figs 2 and 3.

1990 *Toweius? crassus* (Bramlette and Sullivan) Perch-Nielsen; Pospichal and Wise: 638, pl. 6, fig. 1.

1990 *Toweius mignicrassus* Perch-Nielsen; Pospichal and Wise: 638, pl. 6, fig. 2.

1990 *Toweius magnicrassus* (Bukry) Romein; Wei and Thierstein: 493, pl. 6, figs 11 and 12.

1992 Non *Toweius magnicrassus* (Bukry) Romein; Young et al.: 517, figs 2c and 2d.

1992 *Toweius magnicrassus* (Bukry) Romein; Wei: 1102, pl. 1, figs 1, 2, and 13.

**Remarks.** This is species of *Toweius* with only one central opening. It is a larger species derived from *T. callosus* with more elements (commonly 60-70 in *T. magnicrassus* vs. 30-50 in *T. callosus*).

**Size.** Generally 8 to 11µm at high latitudes, 9 to 13µm at mid latitudes, and 9.5 to 14.5µm at low latitudes.

**Occurrence.** It occurs from lower to middle Eocene sediments from low through high latitudes. A precise age range has yet to be determined.

**REFERENCES**

**Explanation of Plate 1.**
**Figs 1, 6, and 7.** *Coccolithus crassus* Bramlette and Sullivan. (1) DSDP Sample 47B-7-3, 104 cm, 7,000x; (6) and (7) Sample Lodo #68. Figs 2, 3, 12, and 13. *Toweius callosus* Perch-Nielsen, Sample KPN53. (2) and (3), 8,000x. Figs 4, 5, and 8-11. *Toweius magnicrassus* (Bukry) Romein. (4) DSDP Sample 47B-3, 104 cm, 6,000x; (5) ODP Sample 690B-15-2, 130 cm, 6,000x; (8) and (9) DSDP Sample 47B-7-3, 104 cm; (10) and (11) Sample KPN53. All light micrographs have the same magnification (2,400x).
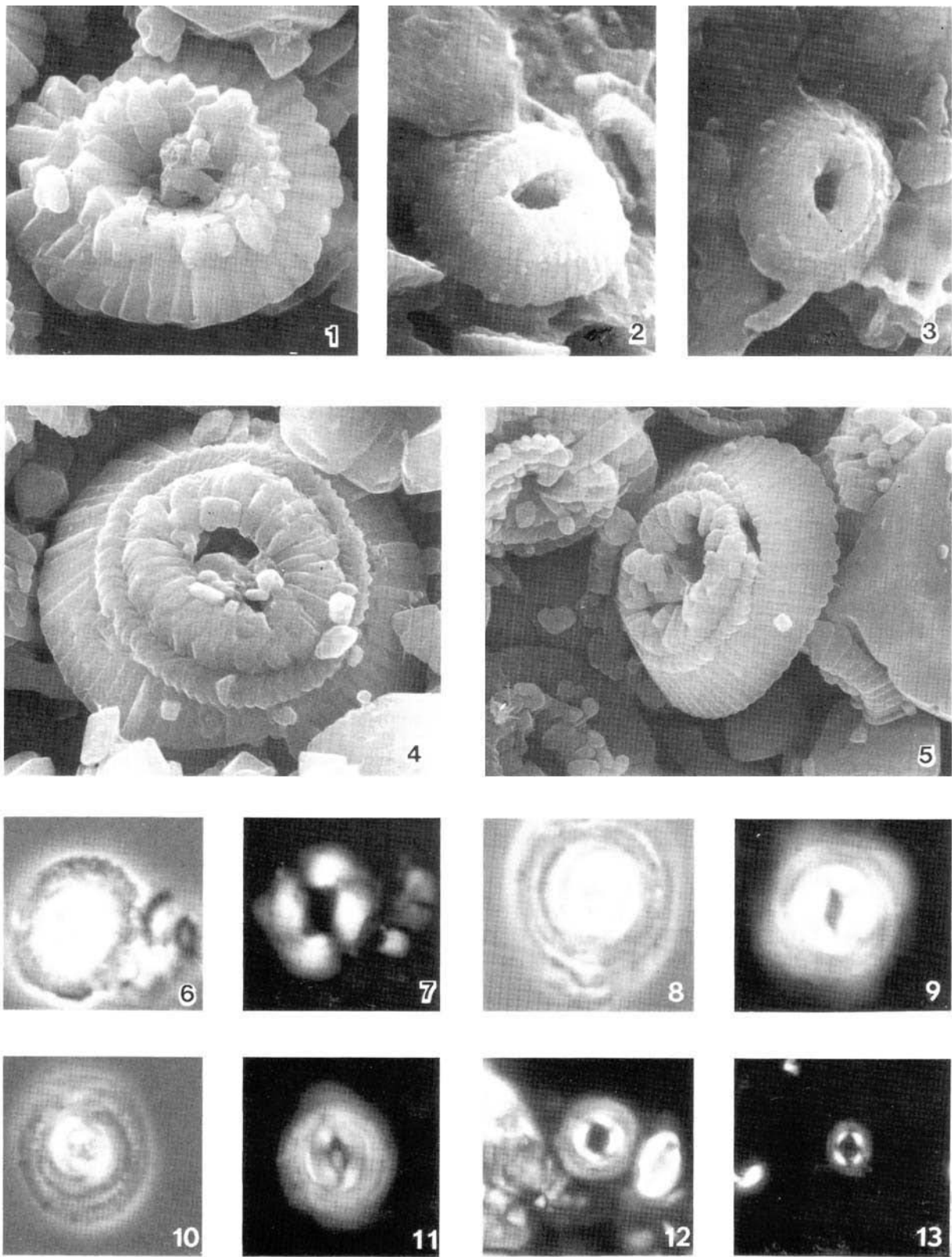
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