

New data on the stratigraphic distribution of the nannofossil genus *Catinaster* and on evolutionary relationships among its species

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ABSTRACT – Examination of Upper Miocene–Lower Pliocene sediments at IODP Site U1338, in the Eastern Equatorial Pacific, provided new data on the distribution range of the calcareous nannofossil genus *Catinaster*. In addition to the well-known occurrence of *Catinaster coalitus* and *Catinaster calyculus* in the early Late Miocene, we document *Catinaster mexicanus* in both the mid-late Miocene and the Early Pliocene. We confirm its taxonomic validity, rejecting previous interpretations of Pliocene *C. mexicanus* specimens as the result of dissolution of *Discoaster altus*. Instead, the Pliocene appearance of *C. mexicanus* seems to originate from the *D. altus* lineage. The short interval of occurrence (*c.* 50ka) in the Late Miocene may document a preliminary evolutionary emergence of *C. mexicanus* that lacks any relationship with the other *Catinaster* species. Clear ancestor species to validate its independent origin from *Discoaster* are, however, missing. In the stratigraphic intervals where *Catinaster* species are found, their co-occurrence with *Discoaster* species bearing a prominent star-shaped boss on one side is noteworthy. This suggests that *Catinaster* and *Discoaster* at times developed a common morphological feature (a stellate structure, with or without hexaradial symmetry), possibly under recurrent changes in climatic/environmental conditions. The data presented on *C. mexicanus* suggest a wider geographical distribution than previously thought, extending from the tropical Pacific to the Gulf of Mexico, equatorial Atlantic and tropical Indian oceans. *J. Micropalaeontol.* 32(2): 197–205, July 2013.

KEYWORDS: calcareous nannofossils, *Catinaster*, Upper Miocene–Lower Pliocene, distribution range

INTRODUCTION

During a biostratigraphic study of Upper Miocene–Lower Pliocene sediment cores from IODP Site U1338 (Pälike *et al.*, 2010; Backman *et al.*, 2013), located in the Eastern Equatorial Pacific (Fig. 1), discontinuous occurrences of specimens belonging to the genus *Catinaster* were observed. This observation prompted investigation in more detail of the stratigraphic distribution of *Catinaster*. This genus comprises rather small (5–10 µm) forms taxonomically related to *Discoaster*, and both genera belong to the family Discoasteraceae (Tan, 1927), informally referred to as ‘discoasterids’. Two well-established species, *Catinaster coalitus* Martini & Bramlette, 1963 and *C. calyculus* Martini & Bramlette, 1963, characterize the calcareous nannofossil assemblages in deep-sea sediments during a *c.* 1 Ma time interval in the Late Miocene (from 10.79 Ma to 9.65 Ma; Backman *et al.*, 2012). Another species, *Catinaster mexicanus*, has been observed sporadically at various locations (Fig. 1) from different stratigraphic intervals. It was described by Bukry (1971) from Upper Miocene sediments (*c.* 8 Ma in age) from the Gulf of Mexico (DSDP Site 3) and was subsequently recorded in Lower Pliocene sediments (*c.* 4 Ma in age) (Müller, 1974; Pujos, 1985). On the basis of the documented stratigraphic and geographical occurrences, *C. mexicanus* is considered a species with uncertain evolutionary development (Peleo-Alampay *et al.*, 1998) despite its morphological similarity to the other *Catinaster* species. *C. mexicanus* has ‘a very limited geographic distribution and seems to prefer specific environments. It usually occurs in the late Miocene’ (Peleo-Alampay *et al.*, 1998, p. 82). Similar occurrences of *C. mexicanus* in Miocene and Pliocene intervals were observed in sediment cores from IODP Site U1338. This study is intended to document in detail the recurrent presence of *C. mexicanus* in the stratigraphic record and investigate its possible

evolutionary relationship with the other *Catinaster* species and/or with coeval *Discoaster* species.

MATERIAL AND METHODS

The intervals in the IODP Site U1338 sedimentary succession selected for this study correspond to the occurrences of *C. mexicanus* that were observed during on-board biostratigraphic analysis (IODP Expedition 320/321, Pälike *et al.*, 2010) and, subsequently, in the more detailed study of the succession (M. Ciummelli, unpublished PhD thesis; Backman *et al.*, 2013). For these studies, the complete Middle Miocene to Lower Pliocene section of Site U1338 was analysed and *C. mexicanus* specimens were observed in two short discrete intervals. The studied sediments are characterized by calcareous nannofossil ooze with varying concentrations of biosiliceous components, mostly diatoms, showing decimetric to metric lithological cycles. Across the two intervals with *C. mexicanus*, other samples were collected to improve sampling resolution. The average sampling resolution throughout the studied section (1 sample every 75 cm) was improved to 1 sample every 10 cm in selected portions (from 168.3 m to *c.* 83.5 m CCCSF-A, and from 69.1 m to *c.* 40.3 m CCCSF-A depth intervals). Following standard procedures, 180 smear slides were made from unprocessed sediment and analysed using a Zeiss Axioscope at 1250×. Semi-quantitative abundance evaluation of *Catinaster* species was obtained by counting the number of specimens in a prefixed area (Backman & Shackleton, 1983). The same methodology was used to evaluate the abundance of *Discoaster berggrenii* Bukry, 1971 and *Discoaster altus* (Müller, 1974) in the Upper Miocene and Lower Pliocene sections, respectively.

A comparative analysis was performed at ODP Site 926 (Ceara Rise, Western Equatorial Atlantic; Curry *et al.*, 1995) in

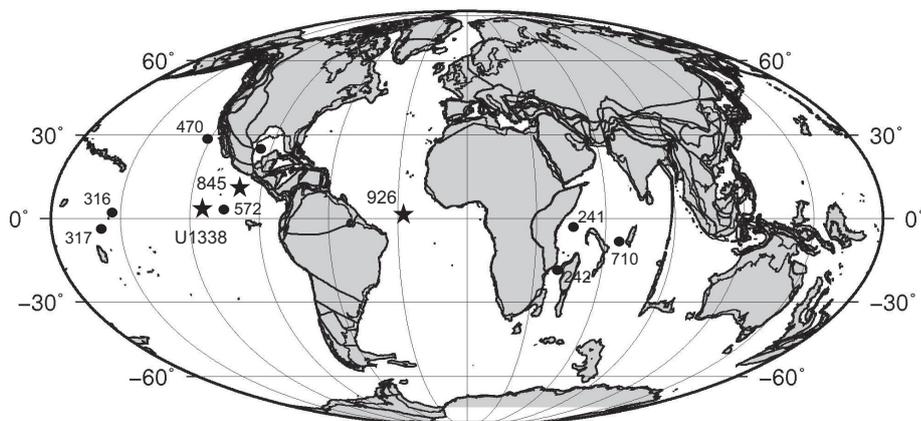


Fig. 1. Location of IODP/ODP sites (black stars) and DSDP/ODP sites (black circles) cited in the text on a palaeogeographical map at 4 Ma (modified from <http://www.odsn.de/odsn/services/paleomap/paleomap.html>).

which the same counting method was used in the same stratigraphic intervals as at Site U1338. Fifty-six samples from the Upper Miocene (214.47–198.33 mcd) and 143 samples from the Lower Pliocene (140.2–111.95 mcd) were analysed, taken from the set of samples used in a previous study on Miocene calcareous nanofossil biochronology (Backman & Raffi, 1997). The range of *C. mexicanus* in the Upper Miocene was reconstructed also at ODP Site 845, in 13 samples from *c.* 6 m of sediments of Hole 845A (core 12H, 108.7–103.2 m below sea floor (mbsf)).

All studied material is deposited in the Dipartimento di Ingegneria e Geologia (Ingeo) – CeRSGeo, Università ‘G. d’Annunzio’ di Chieti-Pescara.

TAXONOMIC AND STRATIGRAPHIC REMARKS

The characteristic morphology of *Catinaster* nanofossils is a basket-like shape with a variable outline in plan view, ranging from smooth sub-circular to hexagonal and/or denticulate forms (Plate 1). In this study, we considered the three described species of the genus, *C. coalitus*, *C. calyculus* and *C. mexicanus*. For simplicity, we did not adopt the taxonomic concepts proposed by Peleo-Alampay *et al.* (1998) to differentiate subspecies within *C. coalitus* and *C. calyculus*.

C. coalitus is the first *Catinaster* species that appears in the stratigraphic record, at 10.79 Ma (Backman *et al.*, 2012), and it is used as biostratigraphic marker for defining Zone CNM12 ‘*C. coalitus* BZ’ of Backman *et al.* (2012) (equivalent to Zone CN6 of Okada & Bukry, 1980, and Zone NN8 of Martini, 1971). *C. coalitus* evolved from the small *Discoaster micros* Theodoridis, 1984 (= *Discoaster transitus* Peleo-Alampay *et al.*, 1998; Raffi *et al.*, 1998), by reduction of the rays and expansion of the bifurcations that merge at the tips to form a basket.

Just above and after the first occurrence of *C. coalitus*, *C. calyculus* evolved from it through a gradual extension of the thin rays beyond the external central area profile (Peleo-Alampay *et al.*, 1998; Raffi *et al.*, 1998). The range of *C. calyculus* encompasses Zones CNM12 and CNM13 of Backman *et al.* (2012) (equivalent to Zones CN6 and CN7 of Okada & Bukry, 1980, and NN8 and NN9 of Martini, 1971). Both *C. coalitus* and *C. calyculus* become extinct close to the top of Zone CNM13.

C. mexicanus was described by Bukry (1971) from Upper Miocene sediments from the Gulf of Mexico (DSDP Site 3) and also recorded in that site by Ellis *et al.* (1972). It was also observed in this time interval from sediment cores in the Eastern Pacific Ocean (DSDP Site 470; Bukry, 1981), the northern Gulf of Mexico (Jiang & Watkins, 1992), and in two Eureka drill sites (E68-136 and E66-73) in the same area (Aubry, 1993), in the Eastern Equatorial Pacific Ocean (ODP Site 845; Peleo-Alampay *et al.*, 1998) and in the Indian Ocean (ODP Site 710; Peleo-Alampay *et al.*, 1998). These reported scattered occurrences within nanofossil assemblages of zones CN7–CN9a of Okada & Bukry (1980) indicate that *C. mexicanus* evolved later than the other *Catinaster* species. In addition, *C. mexicanus* was found in Lower Pliocene sediments from the Western Indian Ocean (DSDP Site 241; Müller, 1974) and the Equatorial Pacific (DSDP Sites 572 and 574; Pujos, 1985). However, this Pliocene occurrence, within Zones CN10 and CN11 of Okada & Bukry (1980) has been considered doubtful (Pujos, 1985; Peleo-Alampay *et al.*, 1998; see discussion below).

Discoaster altus was described by Müller (1974) from Pliocene sediments from the Western Indian Ocean (DSDP Site 242) within Zone CN11 of Okada & Bukry (1980). From the same sediment cores Bukry (1976) described the species *D. tristellifer* that he observed also in the equatorial Pacific (DSDP Sites 316 and 317). Although Bukry (1976) provided a more detailed documentation for *D. tristellifer* based on light microscopy, and retained the two species separated, *D. tristellifer* is commonly considered a synonym of *D. altus* (see Young, 1998) and we follow this taxonomic concept.

RESULTS

The studied interval at IODP Site U1338 comprises the Upper Miocene–Lower Pliocene zones CNM12 through CNPL4 of Backman *et al.*’s (2012) zonation, corresponding to the time interval from *c.* 11 Ma to 3.2 Ma (Fig. 2). The biostratigraphic framework and chronology for Site U1338, and the data on the distribution of *C. coalitus* and *C. calyculus* (Fig. 2) are from Backman *et al.* (2013).

In the Upper Miocene, *C. coalitus*, *C. calyculus* and *C. mexicanus* show low abundances and fluctuating distribution patterns

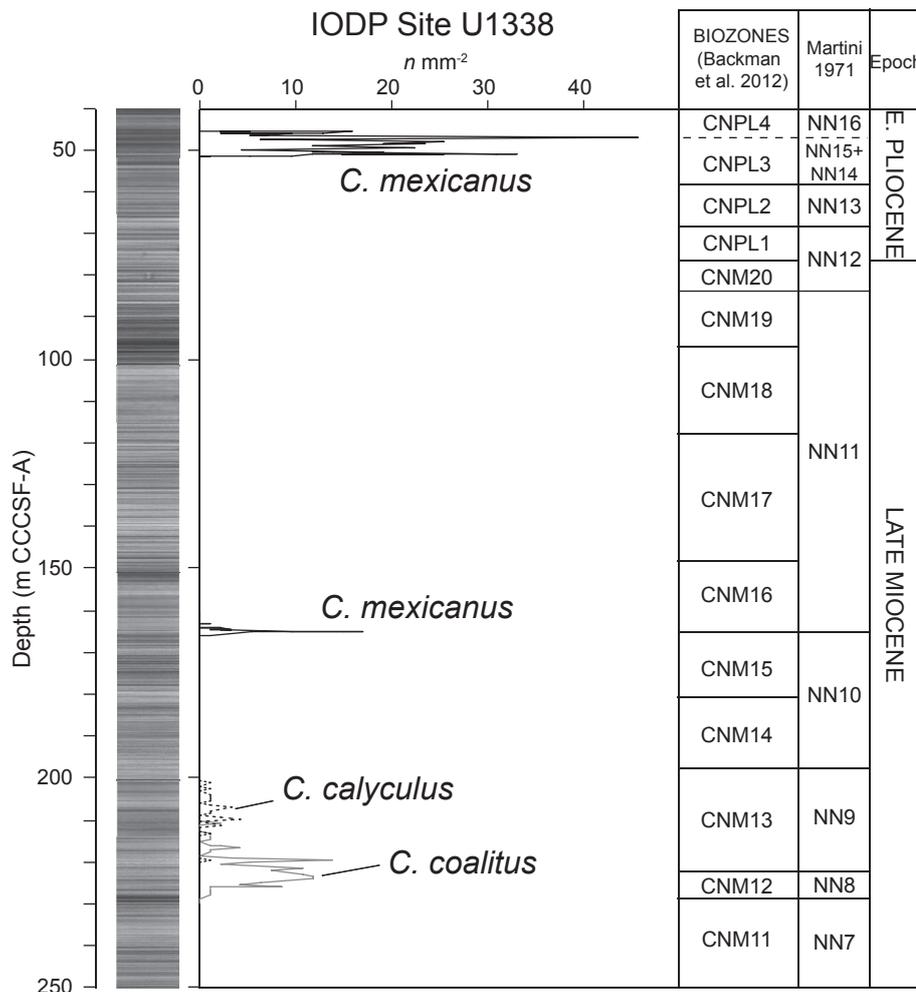


Fig. 2. Quantitative distribution ranges of *Catinaster* species and biostratigraphy (Backman *et al.* 2012; Martini, 1971), Upper Miocene–lower Pliocene interval, IODP Site U1338.

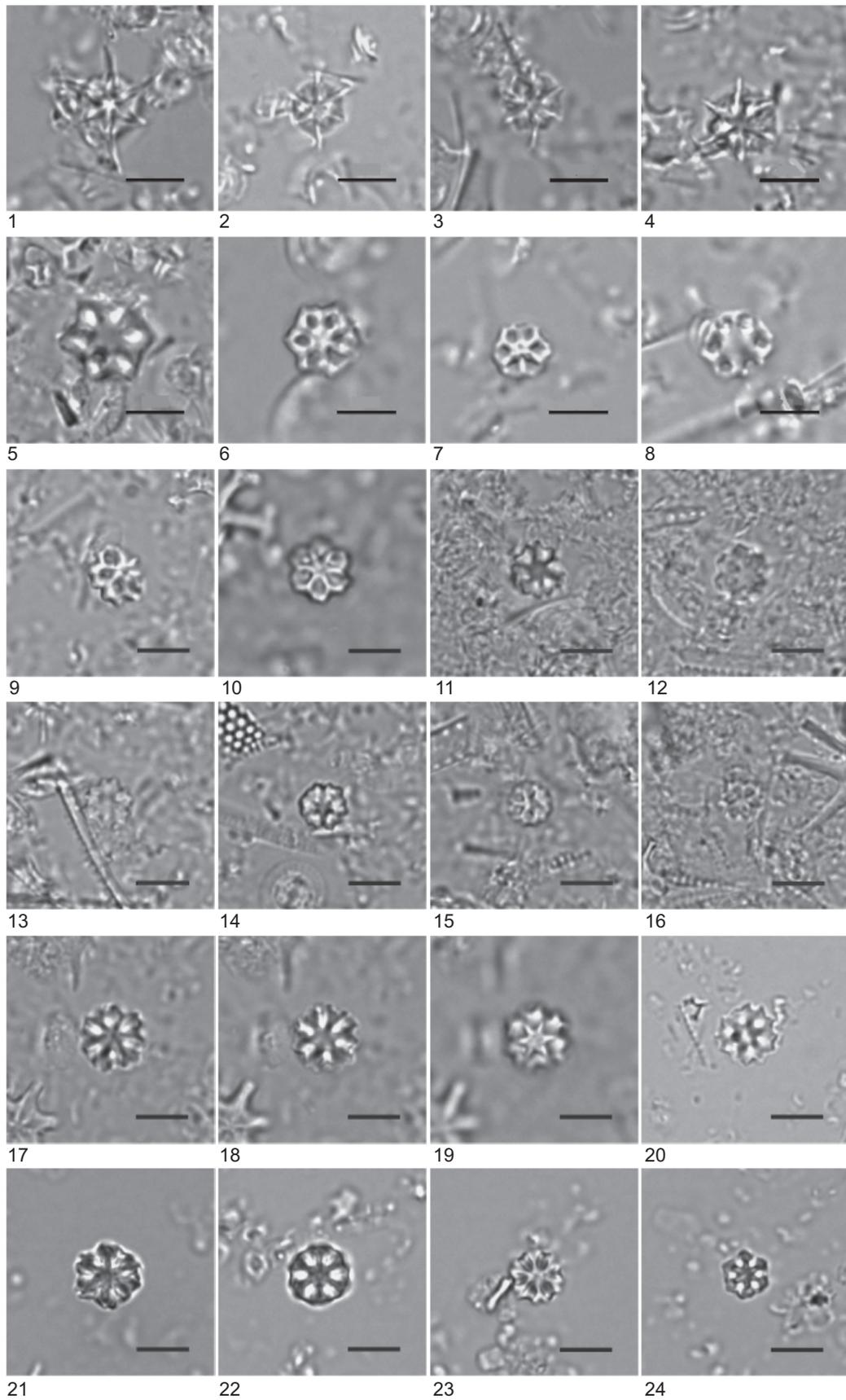
(Fig. 2). Specifically, *C. coalitus* and *C. calyculus* occur in the lower part of the Upper Miocene (228.46–201.37m CCSF-A) within zones CNM12 and CNM13, conformably with their known world-wide stratigraphic distribution. *C. calyculus* occurs shortly after *C. coalitus* and specimens with intermediate morphological features between the two species are present (Pl. 1, fig. 4).

The distribution range of *C. mexicanus* is restricted to a 1.4m thick sediment interval (165.13–164.21m CCSF-A; Fig. 2) in the mid-upper Miocene around 8Ma. This *C. mexicanus* occurrence corresponds to a short time interval (*c.* 0.05Ma) in the lower part of Zone CNM16 (equivalent to Zone CN9a of Okada & Bukry, 1980, and lower part of Zone NN11 of Martini, 1971). The short range is clearly disjunct from the *C. coalitus*–*C. calyculus* evolutionary sequence and is concomitant with the appearance of *Discoaster berggrenii* (Fig. 3). The same distribution for *C. mexicanus*, co-occurring with *D. berggrenii*, is observed in Upper Miocene sediments at Site 845 (Fig. 4), located in the Eastern Equatorial Pacific as Site U1338.

In the other succession considered in this study, ODP Site 926 (Curry *et al.*, 1995), previous biostratigraphic and biochronological analysis on a high resolution sampling set (Backman & Raffi,

1997) did not provide evidence of the presence of *C. mexicanus*. Nevertheless, we selected specific intervals to search for *C. mexicanus*, in stratigraphic positions time-correlative to the occurrences at Site U1338. As a reference, we considered the biostratigraphy and biochronology of Site 926 (Curry *et al.*, 1995; Shackleton & Crowhurst, 1997; Backman & Raffi, 1997). *C. mexicanus* was extremely rare in scattered samples, often as a single specimen, in a short interval of the Upper Miocene (208.425–210.66mcd; Fig. 5) that corresponds to a time interval of *c.* 0.05 Ma, according to the chronology of Site 926 (Shackleton & Crowhurst, 1997).

In the Lower Pliocene section of Site U1338, *C. mexicanus* and *D. altus* have consecutive distribution ranges within a stratigraphic interval of *c.* 30m that corresponds to a time interval of about 0.4Ma. The two species are continuously present and show variable but significant abundances within their ranges (Fig. 6). A clear abundance turnover occurs at 51.35m CCSF-A, with *C. mexicanus* sharply increasing in abundance when *D. altus* declines toward its disappearance. *D. altus* specimens with very short rays are common just below the Pliocene appearance of *C. mexicanus* (Fig. 6) and bear some resemblance to *C. mexicanus* specimens.



A Lower Pliocene occurrence of *C. mexicanus* was also found in samples from ODP Site 926 in a short interval from 129.86 mcd to 117.18 mcd (Fig. 5). The species has a scattered distribution and is extremely rare, showing the same pattern that was observed in the Upper Miocene. At this location only a few specimens of *D. altus* were found concomitantly with *C. mexicanus*. Although quantitatively irrelevant in comparison with the occurrences in the Pacific sites, the presence of *C. mexicanus* at Site 926 is significant because it provides evidence for a wider geographical distribution for the species and confirms its Pliocene occurrence.

DISCUSSION

The data obtained from the study of Site U1338 confirm that the origin of *C. mexicanus* is independent from the other catinasters, as inferred by Peleo-Alampay *et al.* (1998) on the basis of morphological observations. Those authors suggested that *C. mexicanus* could be a second derivation from *Discoaster*, but stratophentic evidence of a specific *Discoaster* species as a possible ancestor was never found. In the *Discoaster* assemblage coeval with the Upper Miocene occurrence of *C. mexicanus* there are no species that could be morphologically related to it and so could be considered the ancestor taxon, as *D. micros*/*D. transitus* was the ancestor of the first *Catinaster* species *C. coalitus* c. 2.8 Ma earlier. The alternative hypothesis that *C. mexicanus* could be a 'preservational fragment of a discoaster rather than a genuine species' (J. Young in Peleo-Alampay *et al.*, 1998, p. 77) is in conflict with the data presented here. Although *C. mexicanus* occurs in association with *D. berggrenii*, there is no morphological evidence indicating that *C. mexicanus* specimens could result from dissolution of *D. berggrenii* specimens, namely through corrosion of the rays. The star-shaped knob in the central area of *D. berggrenii*, with pentaradiate symmetry, differs in morphology and size from the hexaradiate symmetry of Miocene specimens of *C. mexicanus* (Fig. 3). This morphological difference is even more striking in the specimens observed at ODP Site 845 (Fig. 4) whose morphology would suggest the presence of an ancestral taxon similar to *D. micros* that, however, is not found in the assemblage.

The effect of preservation as responsible for 'origination' of *C. mexicanus* has been previously postulated by Pujos (1985) to explain the common but anomalous presence, in Pliocene sediments at DSDP Site 572, of *Catinaster* specimens, considered then as a typically, maybe exclusively, Miocene taxon. The author regarded the Pliocene *C. mexicanus* specimens as 'relicts' of dissolved specimens of *D. tristellifer* (syn. of *D. altus*) on the basis of the morphological affinity between *C. mexicanus* and the stellate (hexaradiate) knob in the central area of *D. altus*. On the other hand, Perch-Nielsen (pers. comm., in Aubry, 1984) suggested that *D. altus* could be considered an evolutionary link between *Discoaster* and *Catinaster*.

From analysis of Lower Pliocene sediments at Site U1338, it is clear that the possible 'preservational origin' for *C. mexicanus* is contradicted by the lack of signs of etching on the rest of the nannofossil assemblage. Therefore, it seems unlikely that the presence of *C. mexicanus* represents an 'artefact' of dissolution of *D. altus* specimens. Instead, it is an evolutionary appearance, and *D. altus* is representative of the evolutionary link between *Discoaster* and *Catinaster* in the Pliocene, in agreement with Perch-Nielsen's suggestion. The *C. mexicanus* specimens observed in the Upper Miocene are identical to the Lower Pliocene specimens (Plate 1, cf. figs 11 and 20), show the same morphological variability (except for a slightly larger average size in the Pliocene specimens) but do not seem morphologically related to any preceding or coeval *Discoaster* species. These data suggest that *C. mexicanus* could be an unrelated homeomorph of the catinasters that evolved from *Discoaster* at least twice in the Late Miocene and in the Early Pliocene, in agreement with the hypothesis of Young (in Peleo-Alampay *et al.*, 1998, p. 77; and pers. comm.), although the late Miocene emergence is not supported by the presence of an ancestor species.

The morphological similarity between *C. mexicanus* and *D. altus* pertains to the whole structure of the catinaster and massive central area of the discoasterid, both having hexaradiate symmetry. A similar morphological affinity associates, in the early Late Miocene, the earlier catinasters *C. coalitus* and *C. calyculus* with the coeval *Discoaster musicus* Stradner, 1959 and *D. sanmiguelensis* Bukry, 1981, bearing a stellate (hexaradiate) knob in the central area. The Upper Miocene *C. mexicanus* occurrence is also concomitant with discoasterids bearing a prominent stellate ornamentation in the central area (*D. berggrenii*), although with lack of other similarity. Therefore, it is noteworthy that discoasterids (*Catinaster* and *Discoaster*) at times developed a common morphological feature, namely a prominent stellate structure, with or without hexaradiate symmetry. These records could be interpreted as episodes of iterative evolution, possibly controlled by the influence of recurrent changes in climatic/environmental conditions, such as those existing in the Eastern Equatorial Pacific in the late Miocene–early Pliocene (Pälike *et al.*, 2010).

If future studies should confirm that *C. mexicanus* does not have any evolutionary relationship with the earlier catinasters, pointing to a polyphyletic character of the *Catinaster* lineage, then its taxonomy would need to be revised.

The presence of *C. mexicanus* at Site U1338 and Site 926 suggests a wider areal distribution for this species, that can be extended from 'semi-enclosed basins or in locations proximal to the continental borderland' (Peleo-Alampay *et al.*, 1998, p. 82) to the warm waters in an open-ocean realm. The significant abundance of *C. mexicanus* at Site U1338 could indicate that high nutrient conditions, prevailing at that site (Pälike *et al.*, 2010; Backman *et al.*, 2013), could have favourably affected its productivity in contrast to its suppressed abundance in more oligotrophic settings, such as Site 926.

Explanation of Plate 1. figs 1–3. *Catinaster calyculus*: 1, sample U1338B-23H-2, 70–71 cm; 2, sample U1338B-24H-3, 142–143 cm; 3, sample U1338B-24H-4, 72–73 cm. **fig. 4** *Catinaster coalitus*–*Catinaster calyculus* intermediate morphotype (sample U1338A-24H-4, 58–59 cm). **figs 5–7.** *Catinaster coalitus*: 5, sample U1338B-24H-5, 142–143 cm; 6, sample U1338B-24H-6, 72–73 cm; 7, sample U1338B-24H-4, 142–143 cm. **fig. 8.** *Discoaster micros*–*Catinaster coalitus* intermediate morphotype (sample U1338A-25H-4, 120–121 cm). **figs 9–16.** Upper Miocene *Catinaster mexicanus*: 9, 13, samples U1338B-18H-4, 50–51 cm; 10, 14, 15, 16, sample U1338B-18H-4, 60–61 cm; 11, 12, sample U1338B-18H-4, 70–71 cm. **figs 17–24.** Lower Pliocene *Catinaster mexicanus*: 17, 19, same specimen at different focus (sample U1338B-6H-5, 5–6 cm); 18, 20, sample U1338B-6H-5, 5–6 cm; 21, sample U1338B-6H-4, 45–46 cm; 22, 23, 24, sample U1338B-6H-4, 120–121 cm. Magnification 1250×. Scale bars 5 µm.

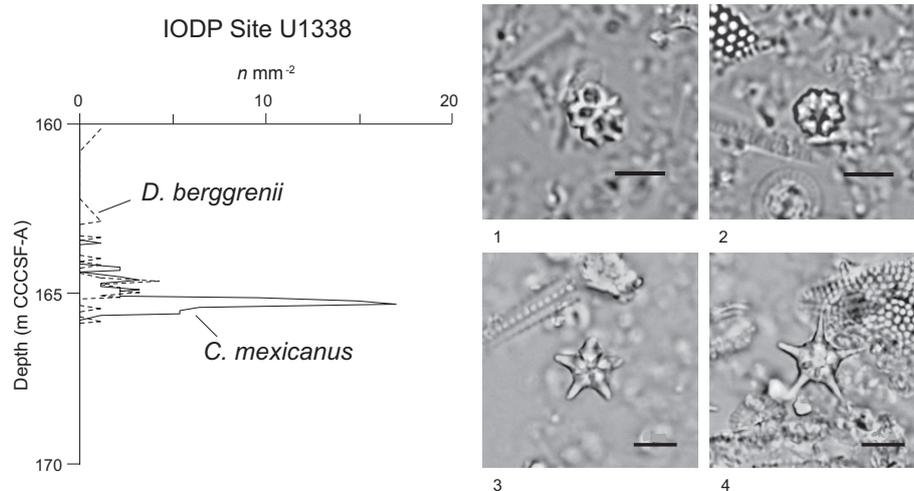


Fig. 3. Abundance of *Catinaster mexicanus* and *Discoaster berggrenii* in the Upper Miocene at IODP Site U1338. 1, 2. *Catinaster mexicanus*: 1, sample U1338B-18H-4, 50–51 cm; 2, sample U1338B-18H-4, 60–61 cm. 3, 4. *Discoaster berggrenii*: 3, sample U1338B-13H-2, 120–121 cm; 4, sample U1338B-13H-3, 45–46 cm. Magnification 1250 \times . Scale bars 5 μ m.

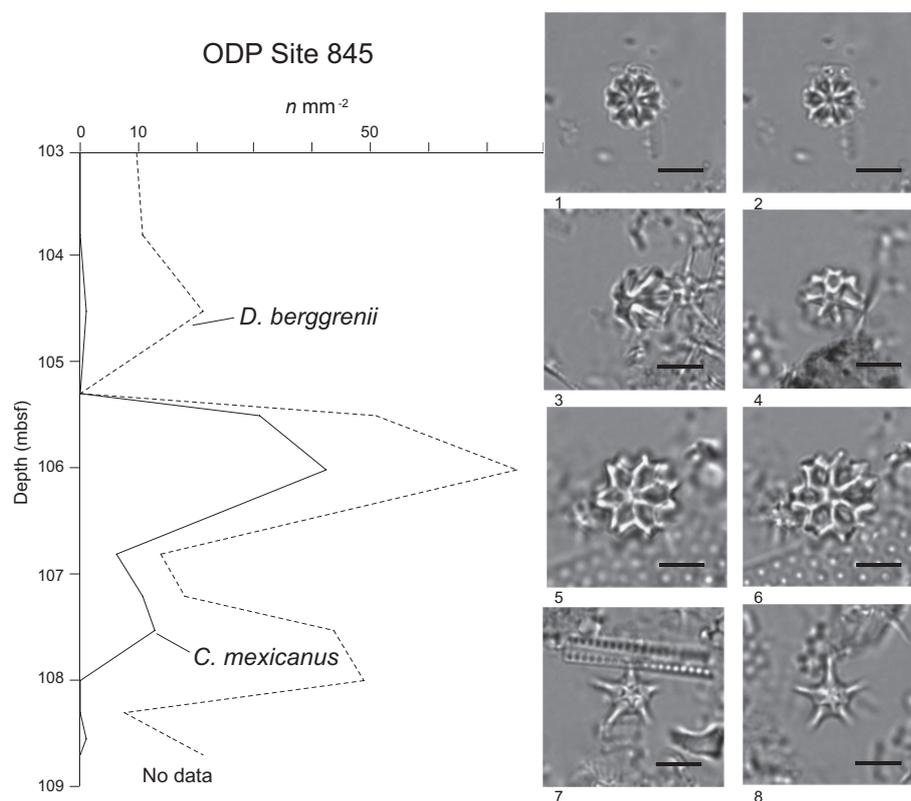


Fig. 4. Abundance of *Catinaster mexicanus* and *Discoaster berggrenii* in the Upper Miocene at ODP Site 845. 1–6. *Catinaster mexicanus*: 1, 2, same specimen at different focus (sample 845A-12H-2, 141–142 cm); 3, 4, sample 845A-12H-3, 42–43 cm; 5, 6, same specimen at different focus (sample 845A-12H-3, 42–43 cm). 7, 8. *Discoaster berggrenii* (sample 845A-12H-3, 42–43 cm). Magnification 1250 \times . Scale bars 5 μ m.

SYSTEMATIC PALAEOONTOLOGY

Family **Discoasteraceae** Tan, 1927

Genus *Catinaster* Martini & Bramlette, 1963

Catinaster mexicanus Bukry, 1971

(Pl. 1, figs 9–24)

1971 *Catinaster mexicanus* Bukry: p. 50, pl. 3, 7–9.

1972 *Catinaster mexicanus* Bukry; Ellis *et al.*: p. 37, pl. 10, fig. 1.

Description. *Catinaster mexicanus* is a small and thick nannolith with six short and bifurcated rays that merge at the tips creating a broadly circular and crenate margin with hexaradiate symmetry. A star-shaped knob is present in the centre.

Occurrence. *C. mexicanus* is present in Upper Miocene zones CN8–CN9 (of Okada & Bukry, 1980) and NN10–NN11 (of Martini, 1971) at DSDP Site 3 (Gulf of Mexico; Bukry, 1971; Ellis *et al.*,

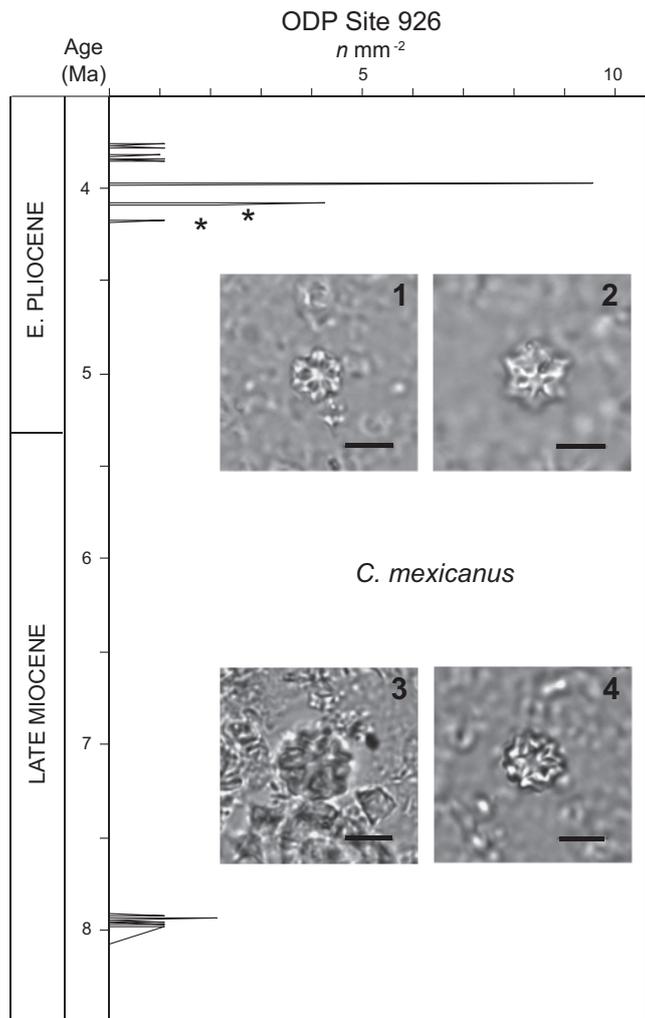


Fig. 5. Abundance of *Catinaster mexicanus* in the Upper Miocene–Lower Pliocene interval at ODP Site 926. Chronology from Shackleton & Crowhurst (1997) and Backman & Raffi (1997). 1, 2. *Catinaster mexicanus* (Lower Pliocene) (sample 926C-12H-5, 7–9 cm). 3, 4. *Catinaster mexicanus* (Upper Miocene) (sample 926B-20H-6, 64–65 cm). Asterisks indicate the presence of *Discoaster altus*. Magnification 1250 \times . Scale bars 5 μ m.

1972), at DSDP Site 470, ODP Site 845 and IODP Site U1338 (Eastern Pacific Ocean; Bukry, 1981; Peleo-Alampay *et al.*, 1998; this study), at ODP Site 710 (Indian Ocean; Peleo-Alampay *et al.*, 1998), at ODP Site 926 (Equatorial Atlantic Ocean; this study), and in the northern Gulf of Mexico (Jiang and Watkins, 1992; Aubry, 1993). In the Lower Pliocene, *C. mexicanus* is present in sediments of zones CN 11 (of Okada & Bukry, 1980) and NN15 (of Martini, 1971) at DSDP Site 241 (Western Indian Ocean; Müller, 1974), and at DSDP Sites 572 and 574 (Equatorial Pacific Ocean; Pujos, 1985). It is present in the interval between subzones CN11b to lower CN12a (NN15–lower NN16) at IODP Site U1338 (Eastern Equatorial Pacific Ocean) and ODP Site 926 (Equatorial Atlantic) (this study), corresponding to the interval uppermost Zone CNPL3–lowermost Zone CNPL4 (of Backman *et al.*, 2012).

Remarks. *C. mexicanus* is similar to *C. coalitus* (Pl. 1, cf. figs 6–7 with figs 10–11), has a somewhat more elaborate external

profile, derived from the merging of six short and bifurcated rays, and a star-shaped structure in the central area that is evident through a light microscope focal series. *C. mexicanus* is similar to *D. altus* specimens with very short rays. The central area of *D. altus* differs from *C. mexicanus* in having a large star-shaped knob on the proximal side and a smaller one on the distal side.

Family **Discoasteraceae** Tan, 1927

Genus *Discoaster* Tan, 1927

Discoaster altus Müller, 1974

1974 *Discoaster altus* Müller: p. 592, pl. 9, figs 1–3.

1976 *Discoaster tristellifer* Bukry: p. 499, pl. 1, figs 1–17.

Description. A valid description of *D. altus* was made by Bukry (1976, p. 499), describing the species *Discoaster tristellifer*, considered to be a junior synonym by Young (1998),

(*D. tristellifer*) is typically six rayed and is characterized by star-shaped knobs of different diameter on opposite sides of the central area. The main rays are long and taper from simple points or slightly indented tips toward the central area. The larger of the two central knobs fills most of the central area and has its six points aligned with the discoaster rays. The smaller knob, projecting from the center of the discoaster on the opposite side, has its points aligned between the discoaster rays.

Occurrence. *D. altus* was observed in Lower Pliocene sediments within Zone CN11 (of Okada & Bukry, 1980) and NN13 (of Martini, 1971) at DSDP Site 242 (Western Indian Ocean; Müller, 1974; Bukry, 1976), at DSDP Sites 316 and 317 and IODP Site U1338 (Equatorial Pacific Ocean; Bukry, 1976; this study) and at ODP Site 926 (Atlantic Ocean; this study).

Remarks. Specimens with very short rays show morphological similarities with specimens of the genus *Catinaster*, specifically *Catinaster mexicanus* (Fig. 6).

CONCLUSIONS

The documented stratigraphic occurrence of *C. mexicanus* in specific time intervals indicates that its evolutionary relationship with other discoasterids (other species of genera *Catinaster* and *Discoaster*) is not straightforward. *C. mexicanus* entered the stratigraphic record in the Late Miocene and occurred for a short time interval of *c.* 50 ka, with scarce but typical specimens. This finding confirms the absence of an evolutionary relationship of *C. mexicanus* with the earlier *C. coalitus* and *C. calyculus* species, and indicates that *C. mexicanus* could have had an independent origin as a second derivation from *Discoaster*, despite the absence of a recognizable ancestor species at present. The second *C. mexicanus* occurrence, after *c.* 4 Ma in the early Pliocene, is linked to the extinction of *D. altus*. The two species share morphological similarity, evident in the thick hexaradiate structure of the catinaster and the thick stellate central area of the discoaster. Also, the Upper Miocene specimens of *C. mexicanus* co-occur with discoasters bearing a prominent star-shaped knob in the central area (*D. berggrenii*), but the two species lack other morphological similarity. These data suggest that discoasterids (*Catinaster* and *Discoaster*) at times developed a common morphological feature, the prominent star-shaped structure, and

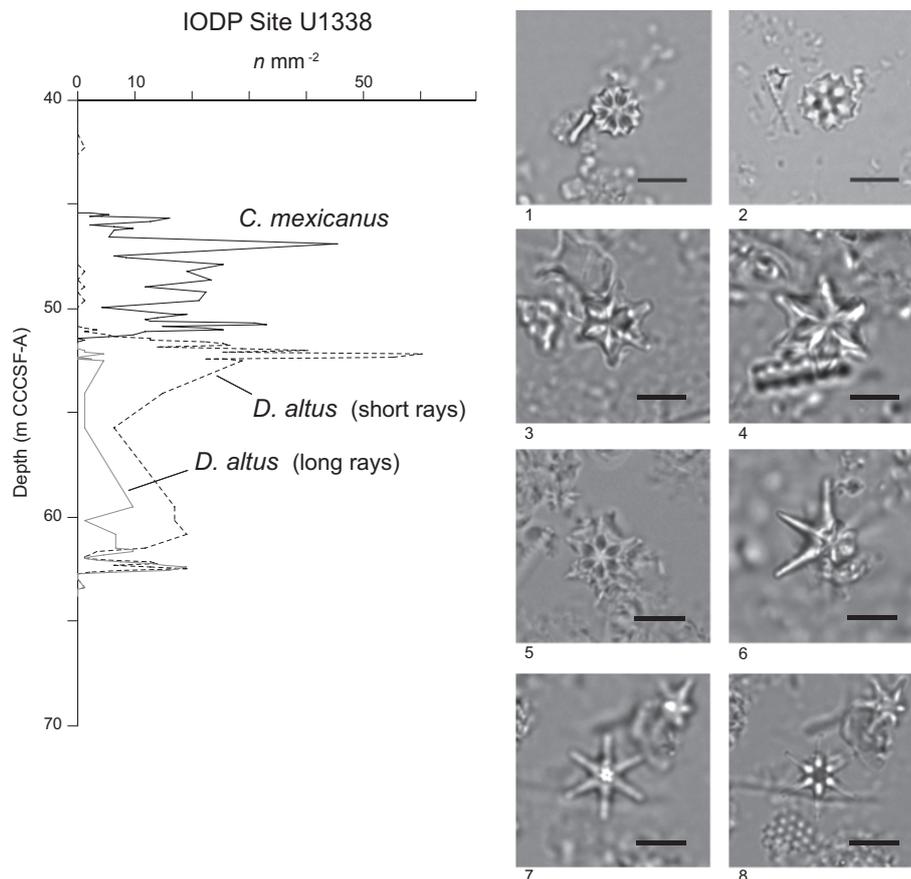


Fig. 6. Abundance of *Catinaster mexicanus* and *Discoaster altus* in the Lower Pliocene at IODP Site U1338. 1, 2. *Catinaster mexicanus*: 1, sample U1338B-6H-4, 120–121 cm; 2, sample U1338B-6H-5, 5–6 cm. 3–5. *Discoaster altus* with short rays: 3, sample U1338B-6H-5, 110–111 cm; 4, sample U1338B-6H-5, 90–91 cm; 5, sample U1338A-7H-6, 120–121 cm. 6–8. *Discoaster altus* with long rays: 6, sample U1338B-7H-5, 45–46 cm; 7, 8, same specimen at different focal levels (sample U1338B-7H-6, 70–71 cm). Magnification $\times 1250$. Scale bar $5\ \mu\text{m}$.

this resulted in the repeated occurrence of similar taxa. These occurrences could be interpreted as episodes of iterative evolution within Discoasteraceae and the recurring taxa would need taxonomic revision, when and if further studies confirm this evolutionary pattern.

The low abundance of *C. mexicanus* at Site 926, in comparison with its common occurrence at Sites U1338 and 845, could be explained by the different environmental conditions between the two oceanic areas, namely the oligotrophic waters of the Equatorial Atlantic (Site 926) and the high nutrient conditions in the Eastern Equatorial Pacific (Sites U1338 and 845).

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