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New Maastrichtian and Paleocene calcareous nannofossils from Africa, Denmark, the USA and the Atlantic, and some Paleocene lineages

By KATHARINA PERCH-NIELSEN¹)

ABSTRACT

Fourteen new calcareous nannofossil species from the Maastrichtian and Danian of Tunisia, the Danian of Denmark, South Africa and the Atlantic and from the uppermost Paleocene of Egypt and the USA are described: Biscutum ? ponticulatum B ? romeinii, Chiastozygus ultimus, Discoaster mahmoudii, Ericsonia sparsa, Neochiastozygus eosaepes, N. primitivus, Neocrepidolithus biskavae, N. bukryi, Nodosella ? elegans, N. ? franzii, Podorhabdus ? elkefensis, Prinsius africanus, Zygodiscus bramlettei. The Paleocene species of Biscutum, Neochiastozygus, Neocrepidolithus and Zygodiscus are discussed.

ZUSAMMENFASSUNG

Vierzehn neue kalkige Nannofossilarten aus dem Maastrichtien und dem Danien von Tunesien, dem Danien von Dänemark, Südafrika und dem Atlantik und aus dem obersten Paleozän von Ägypten und den USA werden beschrieben: Biscutum ? ponticulatum, B. ? romeinii, Chiastozygus ultimus, Discoaster mahmoudii, Ericsonia sparsa, Neochiastozygus eosaepes, N. primitivus, Neocrepidolithus biskayae, N. bukrvi, Nodosella ? elegans, N. ? franzii, Podorhabdus ? elkefensis, Prinsius africanus, Zygodiscus bramlettei. Paleozäne Arten der Gattungen Biscutum, Neochiastozygus, Neocrepidolithus und Zygodiscus werden diskutiert.

Introduction

During very detailed studies of various sets of samples from the Cretaceous-Tertiary boundary sections near El Kef, Tunisia, from Richards Bay, South Africa, from Deep Sea Drilling Project (DSDP) Leg 39 in the South Atlantic and from Denmark, several new calcareous nannofossils were found. This was rather surprising, since well preserved assemblages of both the Maastrichtian and the Danian have been illustrated and studied in detail by many authors: BRAMLETTE & MARTINI (1964); BUKRY (1969); GARTNER (1968); PERCH-NIELSEN (1967, 1969, 1977, 1979a); ROMEIN (1977, 1979); VERBEEK (1977) and WIND & WISE (1977). The explanation for the fact that they were not found (or described) before, is probably different for the different species. Some are very small and sparse and are therefore likely to be overlooked in an otherwise rich assemblage: Biscutum ? ponticulatum, Nodosella ? elegans and Nodosella ? franzii. Biscutum ? romeinii were found in sediment of an age rarely - if ever - recovered before: several samples between "typical" Maas-

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trichtian and "typical" Danian near El Kef, Tunisia. The large Maastrichtian form *Podorhabdus ? elkefensis* seems to be very sparse and the also relatively large *Ericsonia sparsa* looks like the very common *E. cava*. But at high magnification an extra cycle of elements around the central area can be distinguished in *E. sparsa*. *Prinsius africanus* is quite common but very small and *Discoaster mahmoudii* seems to have quite a short range in time. The new species of *Chiastozygus* and *Neochiastozygus* have all been illustrated before, but not enough observations were then available to define separate species. Thus they were listed as "Zygolithus crux", included in *Neochiastozygus saepes* or incorrectly assigned to *N. denticulatus*.

The new species of *Neocrepidolithus* and *Zygodiscus* are coccoliths which form part of evolutionary lineages which were presented at the meeting of the Paleonto-logical Association in Maastricht, The Netherlands, in 1978.

Samples

Atlantic (Deep Sea Drilling Project, DSDP Sites)

Details about the location of DSDP Site 356 on São Paulo Plateau, from which several Lower Danian specimens are illustrated, can be found in PERCH-NIELSEN (1977), where the complete coccolith assemblages of the samples are given. DSDP Site 119 on Cantabria Seamount in the Bay of Biscay has been described in PERCH-NIELSEN (1972).

Denmark

Samples 170/1 and 364/1 were collected from outcrops in Hvalløse and Legind, respectively (PERCH-NIELSEN 1979a). Cores from the borings at Hvalløse and Trælborg near Rold, both in Jylland and drilled for ERICO in 1971 (PERCH-NIELSEN 1979a) were the source of samples 347/43 (Hvalløse) and 352/78 and 352/80A (Trælborg). Sample 50 comes from Sundkrogen in Copenhagen and is of Selandian age (about NP5 of the Standard Zonation of MARTINI 1971, which is used throughout this paper; PERCH-NIELSEN 1979a).

Egypt

The samples from Egypt were provided by M. Mohamed (Paris & Assiut) and were collected at Gebel Taramsa near Qena in the Nile Valley. M. Mohamed is preparing a thesis on the micropaleontology of several Maastrichtian through Eocene sections from Egypt. The sample number is 640/36 and preliminary results are published in MOHAMED et al. (1980 and in press).

France

Two samples from France furnished specimens illustrated in this paper: Bellocq, from where MARTINI (1961) described Zygolithus concinnus and Gan 14, from where the same author described Discoaster nobilis. Both samples belong to the Discoaster multiradiatus Zone, NP9 of MARTINI (1971).

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South Africa

The samples from South Africa were provided in part by W.N. Orr (Eugene, Oregon) who collected them at Richards Bay in eastern South Africa. I also collected the same section after DSDP Leg 39 which ended in Capetown. ORR & CHAPMAN (1974) discussed the Danian marine rocks at Richards Bay and STAPLETON (1975) reported on planktic foraminifera and calcareous nannofossils from this locality. Sample 566 contains *Prinsius africanus* with *Braarudosphaera bigelowii*, *Chiasmolithus danicus* (early forms), *Cruciplacolithus primus*, *C. tenuis* s. ampl., *Ericsonia cava*, *E.* sp. cf. *E. subpertusa*, *Lanternithus duocavus*, *Markalius inversus* s. ampl., *Micrantholithus* sp., *Neochiastozygus primitivus*, *N.* sp. cf. *N. modestus*, *Thoracosphaera* and *Placozygus sigmoides*.

Tunisia

The Tunisian samples were collected by P. Donze (Lyon) and A. Ben Salem (Tunis) during 1978 as a part of IGCP Project 145 on West African geological correlations and cover the uppermost Maastrichtian and lowermost Danian (PERCH-NIELSEN 1980 and in press, a, b). The locality near El Kef is described in SALAJ (1974) and the coccolith stratigraphy derived from an earlier sampling of the section by the author was given in PERCH-NIELSEN (1979b). Sample numbers are 630/LM and 553.

USA

Samples Lodo 6+1 and Lodo 31 were provided by the late M.N. Bramlette. They were collected from Lodo Canyon in California and BRAMLETTE & SULLIVAN (1961) described several species from these samples. Lodo 6+1 belongs to the Heliolithus riedelii Zone (NP7), Lodo 31 to the Discoaster multiradiatus Zone (NP9).

Systematic descriptions

The genera are treated in alphabetical order for easy reference, since general agreement has not yet been reached as to the assignment to families for all genera.

Biscutum BLACK 1959

Type species: Biscutum testudinarium BLACK 1959

Biscutum was defined by BLACK as a group of imperforate coccoliths composed of a closely appressed distal and proximal shield. Biscutum has since been restricted to elliptical forms and is one of the few genera to cross the Cretaceous-Tertiary boundary. The two species B. ? ponticulatum and B. ? romeinii are only tentatively assigned to Biscutum because their central area is not imperforate (B. ? romeinii) or is spanned by a bridge (B. ? ponticulatum) and thus they do not fit the original definition exactly. On the other hand, there seems to be no other genus available for the time being, to which one or both forms could be assigned.

Biscutum ? ponticulatum n.sp. Pl. 1, Fig. 6, 10

Holotype. - Plate 1, Figure 10 (Negative 6-3254/11, ETH SEM Archive, Hönggerberg, Zürich).

Type locality. - El Kef, Tunisia.

Type level. - Late Maastrichtian, Micula prinsii Zone.

Diagnosis. – Small, elliptical coccolith with a distal shield of elements extending into the central area, meeting along the long axis. A bridgelike structure is situated along the short axis.

Description. – The distal shield consists of about 20 to 30 closely appressed elements. Most of them extend into the lower lying central area and meet along the long axis. Along the short axis additional elements form a bridge, probably supporting a knob or short(?) spine. Its base also extends slightly along the long axis. No proximal view was found and no specimens were observed in the light microscope.

Remarks. – This small species is difficult to place into an existing genus. The rim could fit into *Podorhabdus* or *Biscutum*, but the closed central area with a bridge does not fit into either of these genera. Its tentative assignement to *Biscutum* is due to the lack of a more likely genus to assign it to.

Occurrence. – B? ponticulatum was only found in sample 630/LM9 of latest Maastrichtian age from El Kef, Tunisia.

Biscutum ? romeinii n.sp. Pl.2, Fig.7, 11-14

Holotype. – Plate 2, Figure 7 (Negative 6-3255/12, ETH SEM Archive, Hönggerberg, Zürich).

Type locality. - El Kef, Tunisia.

Type level. – Earliest Danian, Markalius inversus Zone, NP1 and B. romeinii Subzone of PERCH-NIELSEN (in press, a).

Diagnosis. – A small, elliptical coccolith with closely appressed shields and a row of small elements bordering the net-covered central area on the distal side.

Description. – The distal and the proximal shield consist of about 20 to 25 elements lying side by side or slightly interlocking as is often found in *Biscutum*. The elements of the distal shield continue into the central area to form a net, while the elements of the proximal shield extend to the distal side where they form a row of elements surrounding the central area.

Remarks. - B? romeinii is not a typical Biscutum because of its wide central area covered by a net. The new species seems similar in proximal view to a proximal view of a Biscutum assigned by WIND & WISE (1977) to their B. notaculum. The new species, however, has a wider central area and seems to have narrower elements in the shields. The holotype of B. notaculum is only figured between crossed nicols and shows a small, longe-elliptical form with a completely filled or covered center. While

the Maastrichtian form illustrated by WISE & WIND (1977, Pl.26, Fig.4) may be a Cretaceous ancestor to *B*? romeinii. *B*. ? parvulum ROMEIN 1979 from the lower Danian of Spain and Israel and also found in Tunisia (Pl.2, Fig.8-10), seems to have evolved from *B*? romeinii.

Occurrence. – B? romeinii is quite common in the lowermost Danian ("Eodanian"?) samples 630/LM 11 through 15 but was also found in lower numbers up to the first occurrence of Cruciplacolithus primus and down to the first sample containing coccoliths above an interval without any calcareous fossils. Its range overlapps with the range of *B. parvulum* (PERCH-NIELSEN, in press, a).

Chiastozygus GARTNER 1968

Type species: Zygodiscus? amphipons BRAMLETTE & MARTINI 1964

The elliptical "basal disc" is constructed of a single cycle of imbricate elements and an X-shaped structure spans the central area. In *Neochiastozygus*, the wall consists of two cycles of oppositely imbricated elements.

Chiastozygus ultimus n.sp.

Pl. 3, Fig. 1, 2, 4, 7; Pl. 5, Fig. 8

1979 Chiastozygus sp. 1, PERCH-NIELSEN, p. 126, Pl. 2, Fig. 8

Holotype. – Plate 5, Figure 8 (Negative 6-3038/3, ETH SEM Archive, Hönggerberg, Zürich).

Type locality. - Hvalløse boring, Jylland, Denmark.

Type level. - Danian, lower Chiasmolithus danicus Zone, NP3.

Diagnosis. – Small, elliptical coccolith with one wall of inclined elements and a central cross aligned with the axes or at a slight angle with them. The arms of the cross have two laths from which plate elements extend.

Description. – The wall consists of about 40 inclined elements. The central cross consists of two closely appressed laths from which plate elements, in the form of thinner laths, extend to form a grid covering part of the remaining space in the central area. In the specimens from the North Sea area, the arms seem "swollen" due to overgroth of the plate elements and the bars. The bars of the cross are aligned with the axis in early forms in Zones NP1 and NP2. Forms with an angle of up to about 30° between the axes and the central cross also already appear in NP1. A thin proximal rim is visible in proximal view.

Remarks. – C. ultimus is assigned to Chiastozygus since it only has one wall, while Neochiastozygus has two. The angle between the long bar and the short bar remains close to 90° also in specimens, where the long bar forms an angle of about 30° with the long axis. The Campanian Chiastozygus synquadriperforatus BUKRY (1969) also has a central cross which stands at an angle of 18° to 35° to the axis and plate elements which extend from the bars of the central cross. But the central cross also carries the base for a central process in form of a knob, a structural element never observed in C. ultimus. Both species measure about 5 microns.

Occurrence. – C. ultimus was found in samples from the Danian of Denmark. Tunisia and the South Atlantic DSDP Site 356.

Discoaster TAN 1927

Type species: Discoaster pentaradiatus TAN 1927

Discoaster mahmoudii n.sp.

Pl.4, Fig. 1-10

Holotype. – Plate 4, Figures 5, 7 (Negatives 6-3329/11 and 12, ETH SEM Archive, Hönggerberg, Zürich).

Type locality. - Gebel Taramsa, Nile Valley, Egypt.

Type level. - Late Paleocene; Discoaster multiradiatus Zone, NP9.

Diagnosis. – Asterolith with long arms, a prominent knob with a central depression on the proximal side and a flat, smaller starshaped knob on the distal side.

Description. - D. mahmoudii usually has five rays. In sample 640/36, from which the holotype is described, a count of 50 specimens of the new species furnished 6% 4rayed, 68% 5-rayed, 24% 6-rayed and 2% 7-rayed specimens. No counts were made in the other samples where the species was found since it is too sparse there. The rays are pointed at the end and usually straight. A slightly curved appearance seems to be due to dissolution and/or overgrowth rather than a primarily curved shape. The proximal knob is high and shows a central depression. From the knob a more or less radially oriented ridge leads to the area inbetween two rays. Between these ridges, quite deep depressions separate the central area from the base of the ray. Sixrayed specimens like the holotype thus have some similarities to the Middle Miocene species of *Catinaster*. The flatter structure on the distal side consists of the tangentially oriented extension of the rays towards the center. Distal views of fiverayed specimens thus resemble the Lower Eocene *Micrantholithus mirabilis* which, however, always has 5 rays and is much larger.

Remarks. – D. mahmoudii is considered to belong to Discoaster only due to the lack of a more appropriate genus. It does not fit easily into any of the previously suggested evolutionary lineages of asteroliths (i.e. PRINS 1971; ROMEIN 1979). Such long, detached arms only occur later in time in the previously known asteroliths, in forms like Discoaster lodoensis and young (Eocene) forms of D. binodosus. Discoaster falcatus has shorter detached rays which are curved towards the center. D. araneus also has quite long rays (7–10), but they are arranged irregularly and the central structures seem less elaborate than in D. mahmoudii.

Occurrence. – D. mahmoudii was found in several samples from the Taramsa section in the Nile Valley, Egypt. Romein (personal communication 1980) has observed it in the Upper Paleocene of the Caravaca section (Spain).

Ericsonia BLACK 1964

Type species: Ericsonia occidentalis BLACK 1964

Holotype. – Plate 4, Figure 12 (Negative 6-3044/6, ETH SEM Archive, Hönggerberg, Zürich).

Type locality. - Legind, Jylland, Denmark.

Type level. – Danian, Cruciplacolithus tenuis Zone, NP2 and Zone D4 of PERCH-NIELSEN (1979a).

Diagnosis. - Elliptical form of *Ericsonia* with an elliptical central opening surrounded by two cycles of elements in distal view.

Description. - The distal shield consists of about 40 to 50 elements (depending on the size of the coccolith). The central opening is surrounded by a cycle of slightly overlapping elements, which does not, as in most *Ericsonia*, lie directly on the distal shield, but which is separated from the latter by a cycle of small elements well visible on all three figures of the species. The proximal side is unknown and may not be distinguishable from the proximal view of *Ericsonia cava* and other species of *Ericsonia/Coccolithus*.

Remarks. – The extra cycle of elements distinguishes *E. sparsa* from the other species of this genus.

Occurrence. – E. sparsa is very rare in one sample from Legind, Denmark, and was also found in the sample from Richards Bay, South Africa (Danian). It is likely that this species has a wide distribution, but is usually overlooked and so lumped with *Ericsonia cava*.

Neochiastozygus PERCH-NIELSEN 1971

Type species: Neochiastozygus perfectus PERCH-NIELSEN 1971

Neochiastozygus has a wall which consists of two cycles of imbricated or vertical elements and an X or cross-shaped central structure. Current ideas about the early evolution in this genus and its ancestor, *Chiastozygus ultimus*, are discussed under "comments and discussion" later in this paper.

Neochiastozygus eosaepes n. sp. Pl. 5, Fig. 9-13

1979 Neochiastozygus saepes, early form, PERCH-NIELSEN, p. 126, Pl. 2, Fig. 1.

Holotype. – Plate 5, Figures 10, 13 (Negatives 6-3039/4, 5, ETH SEM Archive, Hönggerberg, Zürich).

Type locality. - Hvalløse, boring, Jylland, Denmark.

Type level. - Danian, Chiasmolithus danicus Zone, NP3.

Diagnosis. - Small, elliptical coccoliths with an outer wall of vertical elements, a poorly developed inner wall and an asymmetrical central X with a shorter and a longer bar.

Description. – The coccoliths are elliptical to long-elliptical. The outer wall consists of about 30 to 45 vertical elements with a tendency to irregular overgrowth. The inner wall is barely developed and consists of a low cycle of inclined elements. The central X is slightly asymmetrical, with a longer and a slightly shorter bar, each consisting of parallel laths. On the proximal side, a thin proximal rim is visible.

Remarks. – N. eosaepes is distinguished from other species of Neochiastozygus and namely from its descendant N. saepes by the form and orientation of the central X. Only few other Neochiastozygus have an outer wall consisting of vertical elements: N. saepes, N. imbrie. N. saepes is usually larger than N. eosaepes, 5.4 microns to more than 6 microns against less than 4-5.6 microns. N. eosaepes often shows a somewhat irregular outline but is usually less long-elliptical than the younger N. saepes.

Occurrence. – Danian, NP3/4, in Denmark and the North Sea area and in the Danian of the South Atlantic.

Neochiastozygus primitivus n.sp.

Pl. 5, Fig. 1-7

1979 Neochiastozygus modestus, early form, PERCH-NIELSEN, p. 126, Pl. 2, Fig. 7.

Holotype. – Plate 5, Figure 5 (Negative 6-3078/6, ETH SEM Archive, Hönggerberg, Zürich).

Type locality. - Trælborg near Rold, boring, Jylland, Denmark.

Type level. - Danian, Chiasmolithus danicus Zone, NP3.

Diagnosis. - Small, elliptical coccoliths with a well-developed outer wall of inclined elements and an inner wall of inclined elements. The central cross is not aligned with the axes and contains a longer and a shorter bar.

Description. - The outer wall is fully developed and contains about 40 inclined elements. The elements of the partly (like in the holotype) or fully developed inner wall are inclined in the opposite direction than those of the outer wall. The central cross consists of a long bar and a short bar. The long bar forms an angle of a few degrees to about 40° with the long axis. Plate elements extend from the bars towards the open space between the bars. In the specimens from the North Sea area the central structure appears bulky due to overgrowth. In specimens from the South Atlantic, the long bar is straight or slightly curved and the plate elements extending from it are very well preserved. A thin proximal rim is visible on the proximal side.

Remarks. – *N. primitivus* is probably the oldest Tertiary representative of the genus *Neochiastozygus:* the inner wall evolves during Zone NP2, possibly already earlier from a form with only one wall described as *Chiastozygus ultimus* in this paper. *N. primitivus* can be distinguished from *N. modestus* by the form of the central cross, which is built by bars of nearly equal or equal length in *N. modestus. N. primitivus* can be distinguished from *C. ultimus* by the presence of two walls, which both show up in cross-polarized light. *N. primitivus* is about 5 microns long.

Occurrence. - N. primitivus was found in the Danian (Zones NP1?, NP2 and NP3) of Denmark, Tunisia and the South Atlantic.

Neocrepidolithus Romein 1979

Type species: Crepidolithus neocrassus PERCH-NIELSEN 1968

Neocrepidolithus biskayae n.sp. Pl.6, Fig. 2, 3

Holotype. - Plate 6, Figure 2 (Negative 6106, KPN personal negative collection).

Type locality. – DSDP Site 119, Bay of Biscay, Cantabria Seamount (sample 30-6, 60 cm).

Type level. - Late Paleocene, Discoaster gemmeus Zone of MARTINI 1971 (NP7).

Diagnosis. – *Neocrepidolithus* with a very thin outer rim, a prominent inner rim and a small, distal central area; radial elements form the proximal cycle of elements.

Description. – The outer rim consists of about 100 very thin, inclined elements, the inner rim of fewer, about 60, elements which are inclined inverse in respect to those of the outer rim. The distal central area is occupied by a few blocky elements. The proximal central area is not distinctive for the species and is covered by radially oriented elements.

Remarks. – *N. biskayae* differs from the other species of *Neocrepidolithus* by having a very thin outer rim only and a central area filled with blocky elements. Similar thin outer rims occur in several Paleocene/Eocene genera: *Lophodolithus, Neochiastozygus, Pontosphaera, Transversopontis* and *Zygodiscus.* Of these, only *Pontosphaera* does not have a central bridge or a central cross. In *Pontosphaera* the distal side is completely covered with concentrically oriented elements.

Occurrence. - Late Paleocene of Gan (France) and the Bay of Biscay (Zones NP7, 8, 9?).

Neocrepidolithus bukryi n.sp. Pl.6, Fig.4–6

Holotype. - Plate 6, Figure 6 (Negative 5450, KPN personal negative collection).

Type locality. – DSDP Site 119, Bay of Biscay, Cantabria Seamount (sample 25-2, 38 cm).

Type level. – Late Paleocene, Discoaster multiradiatus Zone (NP9 of MARTINI 1971).

Diagnosis. – *Neocrepidolithus* with a thin outer rim, a broad inner rim and a third, rim consisting of more or less concentrically arranged elements, and a very small central area; proximally, radial elements form the "floor".

Description. – The outer rim consists of about 100 thin, inclined elements, the inner rim of about 60 to 80 inversely oriented elements. The central area is divided in an outer part (or third rim) still closely related to the inner rim and consisting of more or less concentrically arranged elements that do not reach out to the elements of the outer rim. The small inner part of the central area is occupied by blocky elements. The proximal side consists of radial elements.

Remarks. – N. *bukryi* differs from the other species of *Neocrepidolithus* by having a third rim. The second rim has usually more elements than in *N*. *biskayae* and generally increases in younger forms.

Occurrence. – Paleocene of Gan (France) and DSDP Site 119 in the Bay of Biscay (Zones NP8 and NP9).

Nodosella Prins ex Rood et al. 1973

Type species: Nodosella clatriata PRINS ex ROOD et al. 1973.

Nodosella was described from the Upper Lias and thus is a Jurassic genus. Its diagnosis is met quite well by the Danian forms described below and assigned to *Nodosella* despite the fact that this genus is only known from the Lower Jurassic sofar.

Nodosella ? franzii n. sp. Pl. 1, Fig. 4, 5, 7-9

Holotype. - Plate 1, Figure 8 (Negative 6-3503/6, ETH SEM Archive, Hönggerberg, Zürich).

Type locality. - El Kef, Tunisia.

Type level. - Danian, Cruciplacolithus edwardsii Subzone of PERCH-NIELSEN (in press, a).

Diagnosis. – Elliptical coccolith with a wall of slightly inclined elements, a ring of proximal elements connected to the elongated central island by about 16 subradial bars.

Description. – The wall is relatively narrow and consists of about 20 to 30 slightly inclined and internally overlapping elements. The proximal ring of elements consists of an equal number of wedge-shaped to rectangular, small elements. The elongate central plate – called an island by ROOD et al. (1973) – is connected with the proximal ring by about 16 bars which are oriented subradially and consist of one or more elements.

Remarks. – The assignment of this species to *Nodosella* is problematical, because *Nodosella* is a Jurassic genus not so far found in the Cretaceous. Also, the elements of the wall are vertically oriented in the type species, while they are slightly imbricated and internally overlapping in *N. ? franzii.* This latter fact also is the main distinguishing characteristic of the new species from *N. clatriata* and similar forms of other, similar Jurassic and Cretaceous genera.

Occurrence. - N. ? franzii was found in only two Danian samples from El Kef. Tunisia (630/LM 29 and LM 31).

Nodosella? elegans n.sp.

Pl. 2, Fig. 1-5

1979a Toweius ? sp. 3, PERCH-NIELSEN, Pl. 4, Fig. 22, 23.

Holotype. – Plate 2, Figure 3 (Negative 6-3436/4, ETH SEM Archive, Hönggerberg, Zürich).

Type locality. - Richards Bay, South Africa.

Type level. - Danian, Chiasmolithus danicus Zone, NP3.

Diagnosis. – A small, elongate-elliptical coccolith with a narrow distal "shield" or wall in the form of a steep, narrow band of elements surrounding the large central area, which is covered by more or less radially oriented elements. The proximal "shield" is smaller than the distal one.

Description. – The distal "shield" consists of about 20 to 30 elements forming a steep, narrow band surrounding the central area. The latter is covered by more or less radially oriented elements often showing overgrowth, and meeting along the long axis without forming a prominent bar. No whole proximal view was found, but it can be seen from Plate 2, Figures 1 and 5, that the proximal "shield" must be smaller than the distal one. No light microscope observations could be made.

Remarks. – *N.*? *elegans* is not easily assigned to an existing genus. The forms illustrated in PERCH-NIELSEN (1979a, Pl.4, Fig.21-23) as *Toweius*? sp. 3 were tentatively called *Toweius* mainly due to the lack of any more likely genus to which the forms could be assigned. The situation has changed a little since then, as a better preserved specimen has been found (the holotype) and seems to be related to the Jurassic genus *Nodosella* (see also *N.*? *franzii*).

Another possibility for a generic assignment seemed *Hornibrookina*. But, as the illustration of a member of this genus (Pl.2, Fig.6) shows, this genus has a well developed distal shield, a structural element differing in N. ? elegans.

Occurrence. – N. ? elegans was found in a Danian sample from Tunisia (630/LM 22), in sample 352–80A from the boring through the Danian near Rold, Denmark, and in sample 566 from the Danian of South Africa.

Podorhabdus NOEL 1965

Type species: Podorhabdus grassei NOEL 1965

Podorhabdus ? elkefensis n. sp. Pl. 1, Fig. 1-3

Holotype. – Plate 1, Figures 1, 2 (Negatives 6-3331/7, 8, ETH SEM Archive, Hönggerberg, Zürich).

Type locality. - El Kef, Tunisia.

Type level. - Late Maastrichtian; Micula prinsii Zone.

Diagnosis. – A large elliptical coccolith with a high rim (remainder of a shield?) consisting of numerous elements. The central area is spanned by a domeshaped structure consisting of very small elements and pierced by two perforations situated at opposite ends of the central area along the long axis.

Description. – The high rim consists of about 50 to 60 vertically oriented elements forming a conical base. The central area is covered by a domeshaped structure with a nearly round outline and consisting of very small, randomly(?) oriented elements. The two perforations are each bordered by a ring of elements and lie in the ends of the central area not occupied by the domeshaped structure. No proximal views or light microscope observations are available.

Remarks. - P? elkefensis seems a unique form and probably does not belong to Podorhabdus or any other known genus. It was tentatively assigned to this genus because of the two perforations (see definition of Podorhabdus in WISE & WIND 1977, p. 305) in the central area. One also can argue that the domeshaped structure replaces the usual central process of Podorhabdus. The rim, however, does not resemble the typical podorhabdid rim (two closely appressed single cycle shields constructed of nonimbricate or slightly imbricated elements). The rim has some resemblance to the two-level rim of Teichorhabdus, a genus twice the size of our form and with a similar number of rim elements but with more than 12 perforations and a granular stem.

Occurrence. – P? elkefensis was so far only found in the upper Maastrichtian samples LM9 and 553 from El Kef, Tunisia.

Prinsius HAY & MOHLER 1967

Type species: Coccolithus bisulcus STRADNER 1963

P. bisulcus, on which the genus *Prinsius* is based, was described by STRADNER (1963) to have irregularly placed pores in the central area and showing two furrows along the ends of the long axis of the central area. This suggests that the pores were on the proximal side and that the distal side was covered by more or less radially oriented elements. ROMEIN (1979) has given a good overview of the optical characteristics of this genus.

Prinsius africanus n. sp. Pl. 3, Fig. 3, 5, 6, 8, 9

Holotype. - Plate 3, Figure 3 (Negative 6-1444/9, ETH SEM Archive, Hönggerberg, Zürich).

Type locality. - Richards Bay, South Africa.

Type level. - Danian, Chiasmolithus danicus Zone, NP3.

Diagnosis. – Round to broadly-elliptical, small coccolith with a distal and a proximal shield and a crown of elements around a central area covered by a net-like structure.

Description. - The distal shield consists of 9 to 16 partly interlocking elements and has a round to broad-elliptical outline. A crown of tangentially oriented elements surrounds the central area. In well-preserved specimens, the crown is higher than the distal shield. The net-like structure covering the central area is also easily visible in distal view. The proximal shield is slightly smaller than the distal shield and consists of two cycles. The central net-like structure seems to have 2 or 3 to over 10 perforations. In cross-polarized light, the central area stays quite dark, the crown shows very high birefringence, and the distal and proximal shields remain almost invisible, but the proximal shield shows very slight birefringence. Remarks. – P. africanus was assigned to Prinsius despite the central net-like structure, which is not usually a feature of species assigned to this genus, but of *Toweius*. In *Toweius*, on the other hand, there are usually two cycles of elements around the open or net covered central area. The partly interlocking elements of the distal shield are not found in younger forms of *Prinsius* and *Toweius* but in most species of *Biscutum*. *P. africanus* may be related to *Prinsius petalosus*, in which the crown is extremely high, and its tangential elements oriented the other way round than in the new species. Also, *P. petalosus* has an elliptical outline and only a single proximal shield. In other small Danian coccoliths as *Prinsius dimorphosus* and *Prinsius tenuiculum* (OKADA & THIERSTEIN) n. comb. (Basionym *Biscutum ? tenuiculum* OKADA & THIERSTEIN 1979, p. 521, 522, Pl.9, Fig. 5) the central area is either closed. i.e. covered or completely open, and both species do not have a crown. *Biscutum ? romeinii* also has a central net-like structure, but is elliptical to elongate-elliptical and has no crown. The coccospheres of the new species are spherical and contain about 20-40 coccoliths which measure about 1.5-3.5 microns.

Occurrence. - P. africanus was only found in sample 566, from Richards Bay, South Africa, where it is common.

Zygodiscus BRAMLETTE & SULLIVAN 1961

Type species: Zygodiscus adamas BRAMLETTE & SULLIVAN 1961

ROMEIN (1979) has recently discussed the characteristic structure of this genus.

Zygodiscus bramlettei n.sp.

Pl. 7, Fig. 6

1979a Transversopontis? sp. 1, PERCH-NIELSEN, Pl. 4, Fig. 24

Holotype. - Plate 7, Figure 6 (Negative 6703, KPN personal negative collection).

Type locality. - Lodo 6 + 1, California (BRAMLETTE & SULLIVAN 1961).

Type level. - Late Paleocene, Heliolithus riedelii Zone (NP7 of MARTINI 1971).

Diagnosis. – Zygodiscus with an outer rim of inclined elements, an inner rim of inclined elements and blocky elements surrounding the two central openings. The central bridge consists of these blocky elements and thin elements.

Description. – The outer rim is thin and consists of about an equally high number of elements as the inner rim. The two central openings are surrounded by a ring of blocky elements leaving only little space for the bridge, which consists of elongated elements arranged more or less parallel to the bridge itself.

Remarks. – An early form of this species was found in the Selandian of Denmark (correlatable about to Zone NP5) and has fewer rim elements in the single(?) rim. *Z. bramlettei* differs from *Placozygus sigmoides* in lacking a central process and in having a double rim. In proximal view, the two species are hardly distinguishable. *Z. adamas* (Pl. 7, Fig. 7), the type species of the genus, has thinner and higher rims, a

thinner floor and much wider openings than the new species. It is suggested, that Z. adamas evolved from Z. bramlettei during the Late Paleocene. In Z. herlynii (Pl. 7, Fig. 1, 2) the rims are lower, less distinct than in Z. bramlettei, but not yet so low as practically to form part of the central area that takes over the whole coccolith in Z. plectopons (Pl. 7, Fig. 4). Both Z. herlyni and Z. plectopons, which were assumed to be synonymous by ROMEIN (1979), have a diamond-shaped to rectangular bridge consisting of elements lying more or less parallel to the bridge itself. This type of bridge could have evolved from the corresponding elements in the bridge of Z. bramlettei. Z. clausus (?Pl. 7, Fig. 5), finally, has a closed, elliptical plate which is somewhat thickened marginally, and a wide, bar-like central structure (no SEM available with the original description by ROMEIN 1979). From the form illustrated on Plate 7, Figure 5, with a small central structure in a otherwise closed central area, we seem not far from Pontosphaera plana (Pl. 7, Fig. 2) and thus an evolutionary lineage leading from Zygodiscus to Pontosphaera, one of the possibilities discussed in PERCH-NIELSEN (in press, b).

Occurrence. – Typical Z. bramlettei was found from NP7 through NP9 in the Lodo section, California, and in the Bay of Biscay. An early, probably related form, was found in the Selandian (correlatable to about Zone NP5) of Denmark.

Comments and discussion

ROMEIN (1979) and PERCH-NIELSEN (in press, b) have recently shown evolutionary lineages of several Paleocene and early Eocene genera. PERCH-NIELSEN (1979c) has done the same for some of the more common and well-known Cretaceous families. Neither the Cretaceous nor most Tertiary forms described here enter easily into these schemes.

Biscutum

PERCH-NIELSEN (1979c) did not discuss Biscutum, an originally Cretaceous genus. WISE & WIND (1977) described several new Maastrichtian species of Biscutum, but did not discuss their relationship with other species of the genus. ROMEIN (1979) also described a new species of Biscutum, the very small Danian form B. parvulum, but did not elaborate on its relation to other species of the genus. It seems that large as well as small forms of Biscutum survived the Cretaceous-Tertiary boundary event(s) unharmed. The large Maastrichtian form B. castrorum can not be distinguished from the large Danian B. castrorum. The proximal view of a small Biscutum from the Maastrichtian of the Falkland Plateau (WISE & WIND 1977, Pl. 26, Fig. 4) seems very close to proximal views of the new B? romeinii and could be assumed to be its ancestor. It is worth noting, that Biscutum disappears during the Danian, while several other genera surviving from the Cretaceous into the Tertiary disappear at the end of the Paleocene and some still live today (PERCH-NIELSEN, in press, b). GRÜN & ZWEILI (1980) have recently included the Jurassic genus Paleopontosphaera in Biscutum. This indicates that yet another Cretaceous-Tertiary boundary survivor has "proven roots" in the Jurassic. Others are Cyclagelosphaera, Neocrepidolithus/Crepidolithus, Nodosella and Placozygus.

Neochiastozygus

My current ideas about the early evolution in the genus Neochiastozygus are shown in Figure 1. At the base of the Danian only C. ultimus, with a cross aligned with the axes, is found. In slightly younger samples, still in the early Danian Markalius inversus Zone NP1, the cross becomes rotated to form an angle to the axes. Later, an inner wall cycle appears, first only low, later as high as the outer wall cycle, in N. primitivus. The central cross is usually at an angle to the axes, but, as in C. ultimus, plate elements extend from the bars of the central structure. In the Chiasmolithus danicus Zone NP3, the first forms with arms of almost equal length appear in N. primitivus. The angle between the bars is still nearly 90° while it becomes a narrower cross in N. modestus, which evolved from N. primitivus in Zone NP3. N. perfectus evolved from N. modestus probably in the later part of the Ellipsolithus macellus Zone NP4, by further narrowing of the central cross and by an increase in size from about 4-5 microns to 6-8 microns. Also in N. perfectus, plate elements extend from the central cross. A further narrowing of the wall and the central cross lead to N. cearae in Zone NP7. Following a general trend also observable in *Neocrepidolithus* and *Zygodiscus*, the outer rim becomes very thin and more



Fig. 1. Paleocene species of *Chiastozygus*, *Neochiastozygus* and *Neococcolithes* and their relationships (tentative!).

and smaller elements form the distal plate in the late Paleocene N.junctus, thought to have evolved from N.cearae. While we observe an increase in the size of the two major openings from N.modestus over N.perfectus to N.cearae, the size of the central area is generally decreasing from N.modestus over N.concinnus to N.distentus, where also the central cross becomes very small but often heavily overgrown.

Within Zone NP3, the first *Neochiastozygus* with a cycle of vertical elements are found. In *N. eosaepes*, the outline of the coccolith is elliptical to elongate-elliptical and the central cross slightly asymmetrical. Around the Zone NP3/4 boundary, those forms increase in size and the outline becomes more elongate-elliptical and pointed at the ends and the central cross narrows and becomes symmetrical in *N. saepes*. *N. imbriei* was found in Zones NP3 and NP4 and is thought to have evolved in Zone NP3 from early forms of *N. eosaepes*. *N. eosaepes* itself could have derived from *N. primitivus*, or, perhaps more likely, directly from *C. ultimus*.

N. digitosus and *N. denticulatus* are both species in which the plate elements extend from the rim and not from the central structure as in *N. primitivus*, *N. perfectus* and other species. Both species are known from the upper part of Zone NP4 or the lower part of Zone NP5 on upwards. *N. digitosus* is thought to have evolved from late forms of *N. primitivus* and later have given raise to the late Paleocene *N. chiastus*. *N. denticulatus* also could have evolved from *N. primitivus* but a derivation from *C. ultimus* seems as likely. No intermediate forms to either source have yet been observed.

Neococcolithes protenus also is first found around the Zone NP3/4 boundary and thought to have evolved from *C. ultimus*. Both forms have single cycle rims, as has *Neochiastozygus* sp. in which the inclination of the rim elements is the same as in the inner cycle of rim elements in the typical forms of *Neochiastozygus*.

Neocrepidolithus

ROMEIN (1979) introduced the genus *Neocrepidolithus* for elliptical coccoliths composed of a margin with slightly to strongly clockwise imbricating elements (rim) and a relatively thin basal cycle of elements (wall). In the Jurassic genus *Crepidolithus* the rim elements are usually vertical, but specimens with slightly imbricated rim elements have been illustrated recently by GRÜN & ZWEILI (1980, Pl. 13, Fig. 3, 5) from the Jurassic of Switzerland. The two genera thus seem, if not identical, so closely related and there seems little doubt, that the Late Cretaceous and Early Tertiary *Neocrepidolithus* derived from the Jurassic *Crepidolithus* at some point.

At least three new species of *Neocrepidolithus* evolved during the earliest Danian from *N. neocrassus* and *N. cohenii*, the two species already present in the Maastrichtian (Fig. 2): *N. fossus*, *N. dirimosus* and *N. cruciatus*. They are all relatively small, about 4-7 microns long. A fourth, larger form (about 9-15 microns long) has not yet been described but was illustrated in PERCH-NIELSEN (1979a) and in Figure 2. It has fewer rim elements and was found also from Zones NP1 on up to NP3. Two more new species, *N. biskayae* and *N. bukryi*, appear during the Late Paleocene and may or may not count as ancestors of *Pontosphaera*, for which role *Zygodiscus* could also be considered (see below and PERCH-NIELSEN in press, b).



Fig. 2. Paleocene species of *Placozygus*, *Zygodiscus* and *Neocrepidolithus* and their relationships with the genera *Lophodolithus*, *Transversopontis* and *Pontosphaera* (tentative!).

Zygodiscus

The evolution in the genus Zygodiscus is also shown in Figure 2. Placozygus sigmoides is here assumed to be the ancestor of Z. bramlettei, the earliest species of Zygodiscus, which appears in the Middle Paleocene (Zone NP5, probably). The "doubling" of the rim must have occurred during the Danian. From Z. bramlettei, Z. herlyni evolved in Zone NP7, itself giving rise to Z. plectopons in Zone NP8. From Z. bramlettei to Z. herlynii and Z. plectopons, the central bridge and the size of the openings generally decreases and the plate area increases in importance until, in Z. clausus, only a very small bridge and hardly any openings are left. It seems possible, that the bridge subsequently disappeared completely and thus Pontosphaera could be a descendant of Zygodiscus (see also Neocrepidolithus, above).

The link (Fig. 2) from Z. herlynii to Transversopontis, where the central bridge is part of the plate and not a separate structural element as in Zygodiscus, seems less obvious than most other links suggested in Figure 2. Like those, it should be studied in detail in suitable sections.

Z. adamas evolved from Z. bramlettei within Zones NP8 or NP9 through an increase in size of the openings, a narrowing of the bridge and through the development of a higher rim, which becomes very thin. Lophodolithus evolved from Z. adamas still in Zone NP9.

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Trends

A doubling of the rim can be observed in several genera during the Danian: (Crepidolithus) – Neocrepidolithus, from Placozygus to Zygodiscus, from Chiastozygus to Neochiastozygus. In Prinsius, the proximal shield develops two cycles in the early Danian. At the same time, the long-living form Watznaueria barnesae with a single cycle of elements in the proximal shield is replaced by Ericsonia cava with two cycles of elements in the proximal shield. Several specimens or forms of W. barnesae and Markalius inversus with a two-cycle proximal shield were found just below and just above the Cretaceous-Tertiary boundary (PERCH-NIELSEN 1979a). For yet unknown reasons, it seems to have been an advantage to produce two-cycle rims/ two-cycle proximal shields and even double central plates as in Ericsonia sparsa, Prinsius and Toweius during the Early Tertiary.

Another parallel trend in the development of the genera in the Paleocene can be observed in the arrangement of the elements of the distal side of the central plate. In early forms the inner rim consists of one layer of inclined elements (*Neocrepidolithus biskayae*, Zygodiscus bramlettei, Neochiastozygus perfectus, N. concinnus), while in the latest Paleocene forms, the distal central area tends to be covered by a layer of concentrically to tangentially arranged elements (*N. bukryi*, *Z. herlynii*, *Z. plectopons* and *Z. clausus* and *N. distentus*) in one or several species of Neocrepidolithus, Zygodiscus and Neochiastozygus.

Nonelliptical, slightly asymmetrical genera also develop during the latest Paleocene, roughly at the same time: *Helicosphaera* and *Lophodolithus*, both deriving from *Zygodiscus*.

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Fig. 1-3	Podorhabdus ? elkefensis n.sp.
	Distal views. Holotype: Figures 1, 2 (turned specimen). 630/LM9 and 553; \times 10,000 (Fig. 1) and \times 5000.
Fig. 4, 5, 7–9	Nodosella ? franzii n.sp.
	Proximal views (Fig. 5, 8, 9) and distal views (Fig. 4, 7, turned specimen). $630/LM29$ (Fig. 4, 7, 9), $630/LM31$ (Fig. 5, 8); $\times 22,500$ (Fig. 5, 8) and $\times 15,000$ (Fig. 4, 7, 9). Holotype: Figure 8.
Fig. 6, 10	Biscutum? ponticulatum n.sp.
	Distal views. Holotype: Figure 10. 630/LM 9; \times 15,000.

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Fig. 1–5	Nodosella ? elegans n.sp.
	Distal views. Holotype: Figure 3. 352/80A (Fig. 1, 2), 566 (Fig. 3), 630/LM 22 (Fig. 4, 5); ×10,000 (Fig. 1, 5), ×9000 (Fig. 2), ×20,000 (Fig. 3), ×15,000 (Fig. 4).
Fig. 6	Hornibrookina sp. cf. H. teuriensis EDWARDS
	Distal view of small specimen with partly covered central area. $630/LM29$; $\times 15,000$.
Fig. 7, 11–14	Biscutum? romeinii n.sp.
	Proximal view (Fig. 7) and distal views (Fig. 11-14). Holotype: Figure 7. $630/LM12$ (Fig. 7, 12, 13), $630/LM11$ (Fig. 11) and $630/LM13$ (Fig. 14); $\times 15,000$.
Fig. 8-10	Biscutum parvulum ROMEIN
	Coccosphere, proximal and distal view. 630/LM 15 (Fig. 8, 9) and 630/LM 13 (Fig. 10): \times 12,000 (Fig. 8) and \times 15,000 (Fig. 9, 10).

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Fig. 1, 2, 4, 7 Chiastozygus ultimus n.sp. Distal views. DSDP 356-29-2,30 cm (Fig. 1), 352/78 (Fig. 2), 170/1 (Fig. 4, 7); ×10,000 (Fig. 1, 2, 7) and ×9000 (Fig. 4).

Fig. 3, 5, 6, 8, 9 *Prinsius africanus* n.sp. Coccospheres (Fig. 3, 6, 9) and proximal views (Fig. 5, 8). Holotype: Figure 3. 566; ×14,000 (Fig. 3), ×15,000 (Fig. 5, 8), ×5000 (Fig. 6) and ×10,000 (Fig. 9).

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Fig. 1–10	Discoaster mahmoudii n.sp.
	Distal views (Fig. 1-3, 5, 7, 9, 10) and proximal views (Fig. 4, 6, 8). Holotype: Figures 5, 7 (turned specimen). $640/36$; $\times 2000$ (Fig. 1-3), $\times 5000$ (Fig. 4), $\times 3000$ (Fig. 5-7), $\times 2500$ (Fig. 8) and $\times 3500$ (Fig. 9, 10).
Fig. 11–13	Ericsonia sparsa n.sp.
	Distal views. Holotype: Figure 12, 364/1 (Fig. 11, 12) and 566; × 7500.

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Fig. 1-7	Neochiastozygus primitivus n.sp.
	Proximal views (Fig. 1, 3, 4, 6, 7) and distal views (Fig. 2, 5). Holotype: Figure 5. DSDP 356-29-2, 30 cm (Fig. 1, 3, 4), DSDP 356-29-1, 90 cm (Fig. 2), 352/80A (Fig. 5-7); \times 9500 (Fig. 1-4), \times 10,000 (Fig. 5-7).
Fig. 8	Chiastozygus ultimus n.sp. Distal view. Holotype. 347/43; ×9000.
Fig. 9-13	Neochiastozygus eosaepes n.sp. Proximal view (Fig. 9) and distal views (Fig. 10-13). Holotype: Figures 10, 13 (turned specimen). 347/43; ×9000 (Fig. 9, 11, 13) and ×8000 (Fig. 10, 12).

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K. PERCH-NIELSEN: Maastrichtian and Paleocene calcareous nannofossils PLATE 5



Fig. 1	Neocrepidolithus dirimosus (PERCH-NIELSEN) n. comb.
	(Basionym: Crepidolithus dirimosus n.sp. in PERCH-NIELSEN 1979a, Pl.2, Fig. 16-18. 23, 24; p. 124). Distal view showing the heavy outer and also heavy inner rim. Sample 50, Copenhagen, Paleocene; $\times 15,000$.
Fig. 2, 3	Neocrepidolithus biskayae n.sp.
	Distal views. Holotype: Figure 2. DSDP 119-30-6, 60 cm (Fig. 2) and DSDP 119-29-1, 86 cm; \times 18,000 and \times 12,000.
Fig. 4-6	Neocrepidolithus bukryi n.sp.
	Distal views. Holotype: Figure 6. DSDP 119-25-2, 38 cm (Fig.6), Gan 14, France (Fig.4), and DSDP 119-26-1, 73 cm (Fig.5); \times 11,000 (Fig.4), \times 9300 (Fig.5) and \times 10,000 (Fig.6).
Fig.7	Neocrepidolithus sp.
	Proximal view (can not be determined to species level). Gan 14, France; $\times 8500$.

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Zygodiscus herlynii SULLIVAN
Distal view of a specimen from Bellocq, D. multiradiatus Zone in southwestern France (Fig. 1) and a specimen from the sample, from which Z. aff. Z. plectopons was described by BRAMLETTE & SULLIVAN (Lodo $6+1$, Heliolithus riedelii Zone, NP7); $\times 10,000, \times 9800$.
Pontosphaera plana (BRAMLETTE & SULLIVAN) HAQ
Distal view, note rim of inclined elements and concentrically arranged elements in the central area. DSDP 119-28-2, 105 cm; \times 9800.
Zygodiscus plectopons BRAMLETTE & SULLIVAN
Distal view of a specimen from the material from which the species was described (Lodo 31); note the larger openings and smaller bridge than in Z. herlynii; $\times 11,200$.
?Zygodiscus clausus Romein
Distal view of a specimen from Gan 14, Discoaster multiradiatus Zone, France; \times 9800.
Zygodiscus bramlettei n.sp.
Distal view of a specimen from Lodo $6+1$ (BRAMLETTE & SULLIVAN 1961), California; $\times 10,300$.
Zygodiscus adamas BRAMLETTE & SULLIVAN
Distal view of a specimen from Gan 14, Discoaster multiradiatus Zone, France; $\times 8300$.

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