BERRIASIAN TO EARLY APTIAN CALCAREOUS NANNOFOSSILS FROM THE VOCONTIAN TROUGH (SE FRANCE) AND DEEP SEA DRILLING SITE 534: NEW NANNOFOSSIL TAXA AND A SUMMARY OF LOW-LATITUDE BIOSTRATIGRAPHIC EVENTS

James A. Bergen, Amoco Production Company, Houston, Texas

Abstract: Recent investigation of 17 sections in the Mesozoic Vocontian Trough (southeastern France) spanning the Callovian to Cenomanian has shown great potential for improving Tethyan nannofossil biostratigraphic resolution. Both predefined zonal taxa and newly-recognized biostratigraphic events were calibrated to the Lower Cretaceous ammonite biostratigraphy. Coeval strata drilled at Deep Sea Drilling Program Site 534 offered the chance to test the viability of these new events and evaluate the calibration of the deep sea nannofossil biozonation. Reported here is a summary for the Berriasian to lower Aptian, with the most significant improvements being for the Valanginian and Hauterivian. Ten new species and two new combinations are introduced.

Introduction

The thick basinal sequence of the Mesozoic Vocontian Trough in southeastern France contains a fairly complete record of nannofossil evolution and now provides an excellent opportunity to calibrate the nannofossil record to the Tethyan ammonite biostratigraphy. The Vocontian Trough also contains several of the stage-stratotypes (Berriasian, Barremian, and Aptian; Valanginian hypostratotype) and has been the subject of recent sequence stratigraphic work. The first published Lower Cretaceous nannofossil biozonation by Thierstein (1971, 1973) also was founded on sections in this basin. Bralower, Monechi, and Thierstein (1989) improved biostratigraphic resolution for the Tithonian to Berriasian and were able to tie the nannofossil biostratigraphy to both the Tethyan ammonite biostratigraphy and palaeomagnetic record. Deep Sea Drilling Project Site 534 is an important reference section for M-sequence palaeomagnetic record. Roth (1983) published the original nannofossil biostratigraphy of this site, for which he assigned numbers his Lower Cretaceous zones (NC1-10). Sissingh (1977, 1978) published a numbered, zonal scheme for the Cretaceous (CC Zones); Applegate and Bergen (1988) further refined this zonal scheme based on Lower Cretaceous sections drilled on the Galicia Margin during O.D.P Leg 103.

This paper describes the new species found during study of the Lower Cretaceous sections in the Vocontian Trough and D.S.D.P Site 534. An outline of the sequence of nannofossil events in common between these two localities is provided and correlated to the ammonite biostratigraphy of the French sections. Comparisons also are made to the aforementioned nannofossil biozonations. The taxonomic problems encountered are beyond the scope of the current paper and, hopefully, will be addressed in a future publication on the entire Callovian-Cenomanian interval.

Methods

Research on the Vocontian Trough sections was completed during 1991 at Amoco Production Research in Tulsa, Oklahoma. Two factors had a significant impact on the results obtained during this study: centrifugation of samples and analysis time. These factors improved the continuity of stratigraphic ranges, especially for many of the rare taxa.

Abbreviations used in this paper include: LM for light microscope; SEM for scanning electron microscope; LO for lowest occurrence; HO for highest occurrence; TR for total range; Sa for samples; T for top; B for bottom; and SZ for Subzone. Two rough estimates for the biostratigraphy reliability of an individual species are cited: (1) percentage of samples in which the species was found throughout its entire documented stratigraphic range; or (2) the number of samples in which the species was found in either the top or bottom ten samples of its documented stratigraphic range.

Acknowledgments

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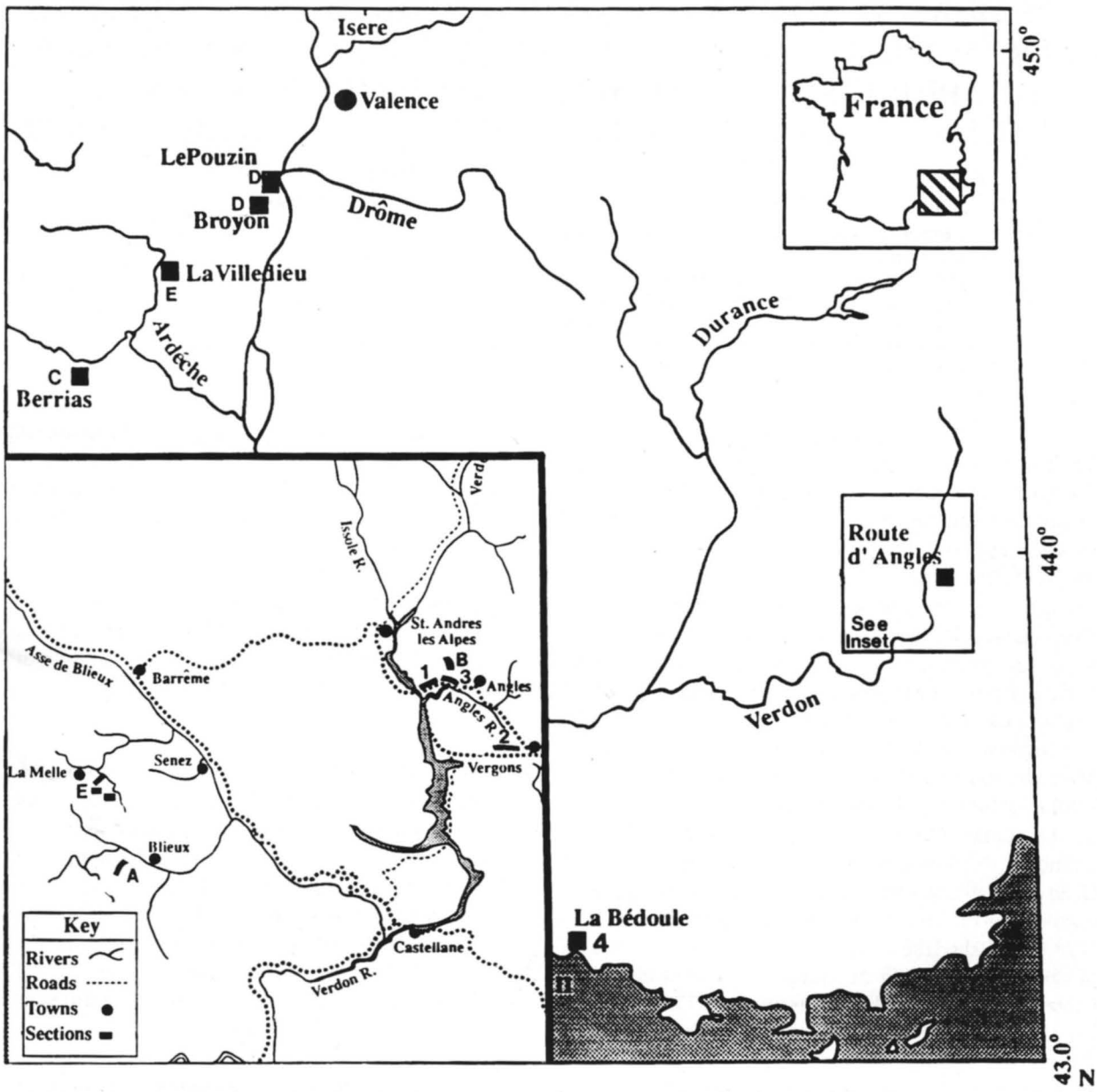
Sections Considered

The primary sections for the current paper include D.S.D.P. Site 534 (Blake-Bahama Plateau, NW Atlantic) and four outcrops in SE France (see Text-Figure 1): (1) Berriasian to Valanginian at Angles; (2) Hauterivian at Vergons; (3) Barremian stratotype at Angles; and (4) the lower Aptian stratotype at La Bedoule. Also referenced are the Speeton section in Great Britain, the BGS Speeton Borehole, as well as other sections in SE France (see Text-Figure 1): (A) Albian near Blieux; (B) upper Aptian at Angles; (C) the Berriasian stratotype; (D) Tithonian to lower Berriasian sections at Broyon and Le Pouzin (Route de Grads & Carriere de Anges); and (E) Upper Jurassic sections in SE France at La Melle and Lavilledieu. Relevant nannofossil publications include: Thierstein (1971, 1973) on the Barremian stratotype, Berrias, and Broyon; Bralower et al. (1989) on Berrias, Broyon, and D.S.D.P. Site 534; Roth (1983) on D.S.D.P. Site 534; and the most recent paper on the Speeton section (Crux, 1989). The Berriasian-Barremian ammonite biostratigraphy is based on Bulot (1993 & 1994, pers. comm.) and the published framework of Hoedemaeker & Bulot (reporters) (1990) and Hoedemaeker & Company (1993). The lower Aptian



Text-figure 1: Location of Vocontian Trough sections in southeast France. See text (under Sections Considered) for numbering and lettering of sections.

ammonite zones were taken from Busnardo (1984) and a guide prepared for an Amoco field excursion (Busnardo *et al.*, 1987).

Biostratigraphic Summary

A sequence of nannofossil events observed in the composite Vocontian Trough section and their correlation to the ammonite biostratigraphy are summarized in the Text-Figure 2. Only four of these events, which were very distinct and reliable in the French sections, were observed out of sequence at D.S.D.P. Site 534. Sample density (~1Sa/5m) at Site 534 was a limiting factor (see Appendix for list of samples). The thicker Vocontian sequence was densely sampled (1 Sa/2 m); facies and sampling density were only problematic for the lower-middle Berriasian. The following nannofossil events supplemented ammonite correlations of the four primary Vocontian Trough sections (see Table in Appendix): (1) LO of *Hayesites irregularis* for the Barremian and lower Aptian stratotypes; (2) HO of *Lithraphidites bollii* for the Barremian stratotype and Vergons; (3) HO of *Eiffellithus windii* for Vergons and Angles (Berriasian-Valanginian section).

Systematics: New Species and New Combinations

Assipetra terebrodentarius (Applegate, Bralower, Covington & Wise, 1987) Rutledge & Bergen, new combination

Remarks: Small specimens transitional between this species and *Assipetra infracretacea* (Thierstein) occur in the upper Hauterivian.

Range: LO is uppermost Hauterivian in: (1) DSDP Site 534 (100% Sa), Core 51-1, 61-64cm; (2) SE France, Angles, Barremian stratotype, Bed 70, angulicostata Zone (76% Sa); (3) Speeton (approximate), Bed LB5.

Calcicalathina, species A
(Plate 1, figures 11a, b)

Remarks: This large (9-10 µm), elliptical murolith is a form transitional between *Rhagodiscus asper* (Stradner, 1963) Reinhardt, 1967 and *Calcicalathina oblongata* Thierstein, 1971. It differs from the former species by its large size and coarsely granular (more birefringent), elevated central area. It differs from the latter species by its wider rim (more optically distinct) and lower central area. In cross-polarized light, *Calcicalathina oblongata* displays an irregular longitudinal extinction line and its poles uniform, bright birefringence (see Thierstein, 1971, pl. 4, figs. 6-10 for comparison).

Range: earliest Berriasian to latest Aptian. DSDP Site 534: LO in 90-3, 21-22cm. SE France: LO in grandis SZ (Route de Grads, Bed 27), 0.5m below grandis SZ (Broyon, 19.5m); HO at Angles, Bed 77, upper Clansayesian.

Diloma, species A
(Plate 1, figures 12a, b)

Remarks: This medium-sized species of *Diloma* has a perforate central area spanned by an axial cross. Other *Diloma* species with axial central structures are differentiated by the presence of diagonal struts in the central area and/or inner rim margin. These accessory bars are restricted to the inner rim margin in *Diloma primitiva* (Worsley, 1971) and beautifully illustrated by Wind & Čepek (1979; pl. 8, figs. 2, 3). However, such structures are not mentioned in the original description of this species and only barely visible in one (Worsley, 1971, pl. 1, fig. 2) of the three photographs of the holotype. The original description of *Diloma primitiva* also mentions an imperforate central area.

Range: Cosmopolitan, early Valanginian to early Barremian. DSDP Site 534: Sa 76-6, 94-95cm; SE France: LO at Angles, Bed 289, campylotoxum Zone; HO at Vergons, Bed 146, ligatus Zone; Speeton (approximate), Beds D2 to LB5.

Diloma galiciense, new species
(Plate 1, figures 13a-c, 14a-c)

1988 *Vekshinella angusta* (Stover) Verbeek, 1977b. Applegate & Bergen, p. 318, pl. 8, figs. 5, 6, 8.

1991 *Chiastozygus* sp. Bralower, p. 430, fig. 6, nos. 31-32.

Derivation of name: after the Galicia Bank, off Portugal.

Diagnosis: Eiffelithid exhibiting a bicyclic rim extinction pattern (outer faint/inner bright) and having in its central area an off-axis central cross attached to a proximal plate of faint birefringence.

Description: Medium to large, elliptical murolith. The rim is bicyclic in distal view. The inner rim cycle is constructed of blocky elements and is brightly birefringent. The narrow outer rim cycle is faintly birefringent and its elements show strong dextral imbrication. A faintly birefringent proximal plate circumscribes the outer central area margin, giving the impression of a tricyclic rim extinction pattern. A central cross spans the central opening and its arms flare as they attach to the proximal plate. The central cross is oriented 10-30 degrees off the major ellipse axis and becomes brightly birefringent when the coccolith is oriented 45 degrees to the polarizing direction. A fibrous, distal projection is present at the centre of the cross. Size of measured specimens: 7.0-9.0 µm.

Remarks: *Diloma galiciense* is distinguished from other *Diloma* species by its diagonal central structure and from other Neocomian muroliths by its tricyclic rim extinction pattern.

Range: Cosmopolitan. DSDP Site 534 (58% Sa), lower to uppermost Hauterivian, 63-2, 66-69cm to 52-1, 82-85cm; SE France (Vergons, 25% Sa), Hauterivian, Bed 42 (radiatus Zone) to Bed 89 (sayni Zone). North Sea (Rutledge, written comm., 1994), lower Hauterivian to lower Barremian.

Holotype: Applegate & Bergen (1988), plate 8, figs. 5, 6, 8; ODP Site 638B-25R-4, 48-49cm; upper Hauterivian.

Grantarhabdus quadratus (Worsley, 1971)
new combination
(Plate 1, figure 10)

1971 *Watznaueria quadrata* - Worsley, p. 1315, pl. 2, figs. 20-22.

Remarks: This species has a diagonal, sigmoid cross-structure, small central area, and a thick proximal shield. It is assigned to the genus *Grantarhabdus* based on its central structure orientation, although its rim construction is more typical of the genus *Helenea* (junior synonym: *Microstaurus*).

Range: Cosmopolitan, earliest Berriasian to late Hauterivian. DSDP Site 534 (88% Sa): 91-2, 145-146cm to 55-3, 75-78cm. SE France: LO at Le Pouzin, Bed 27, grandis SZ; LO at Broyon, 19.5m, 0.5 m below grandis SZ; HO at Vergons (87% Sa), Bed 119, ligatus Zone. Speeton (approximate): HO in Bed C8.

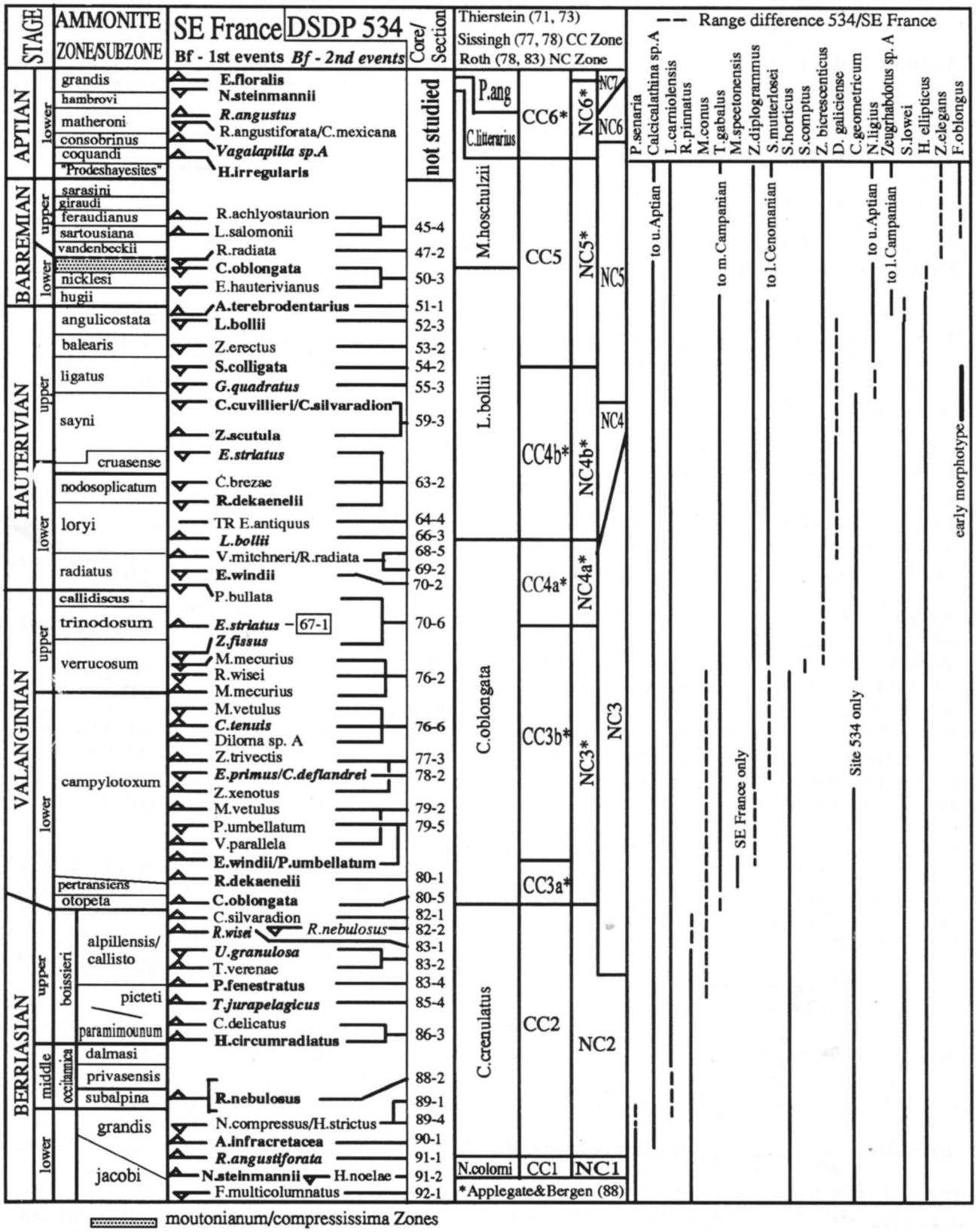
Hexalithus strictus, new species
(Plate 1, figures 1a-b, 2a-b)

Derivation of name: Latin. *strictus* = straight.

Diagnosis: A species of *Hexalithus* with triangular-shaped elements (*i.e.* their peripheries are straight).

Description (LM only): Medium-sized, nannolith constructed of six, triangular, non-imbricated elements separated by radial sutures. The individual element peripheries are straight, giving the nannolith a hexagonal, peripheral outline. Size of observed specimens: 4.8-6.0 µm.

Remarks: *Hexalithus noelae* Loeblich & Tappan, 1966 has elements with lobate peripheral margins. *Hexalithus strictus* has a younger appearance and extinction.



Text-Figure 2: Stages divisions and subdivisions and ammonite zones based on SE France; Berriasian to Barremian ammonite zones after Hoedemaeker & Bulot (1990) and Hoedemaeker & Company (1993) as communicated by Bulot (1993, 1994); Aptian ammonite zones after Busnardo (1984) and Busnardo *et al.* (1987). The third column summarizes the sequence of nannofossil events in SE France and correlation to ammonite zones; reliability indices (see **methods**) indicated are: (1) primary (1st), more than 90% Sa; and (2) secondary (2nd), more than 70% Sa. Correlation of nannofossil events to DSDP Site 534 is shown at the right side of column three and the Core-Sections are indicated in the fourth column. The nannofossil zones of Thierstein (1971, 1973), Sissingh (1977, 1978), Roth (1978, 1983), Applegate & Bergen (1988) are illustrated in the fifth column relative to the sequence of nannofossil events; the slanted NC3/NC4 Zone boundary is due to variance in the HO of *T. verenae*. The stratigraphic ranges of other important nannofossil species are shown on the right side of the figure (relative to sequence of nannofossil events); differences in their stratigraphic ranges between SE France and DSDP Site 534 are shown as dashed lines.

Range: earliest Berriasian; DSDP Site 534 (55% Sa): Cores 92-4, 147-148cm to 89-4, 35-36cm; SE France: Le Pouzin-Route de Grads, Bed 25 (jacobi SZ) and Bed 27 (grandis SZ); Broyon, 19.5m, (0.5m below grandis SZ).

Holotype: Plate 1, figs. 1a-b; DSDP Site 534, 91-4, 131-132cm; lower Berriasian.

Lucianorhabdus salomonii, new species
(Plate 1, figures 17a-b, 18a-b)

Derivation of name: named in honour of Ralph A. Salomon.

Diagnosis: A species of *Lucianorhabdus* with a massive, truncated distal stem which displays a bright, longitudinal band down its central portion.

Description (LM only): Elliptical holococcolith having a tall, broad distal stem which fills the entire central area. The stem has a thin axial canal and a truncate distal extremity. Its vertical outline is somewhat variable, including: (1) slight or no distal taper; and (2) a straight or curved shape. In cross-polarized light, the stem displays a characteristic, bright longitudinal band down its central portion, whereas the remainder of stem is faintly birefringent. The rim elevation is normal to high (height ~1/2 the coccolith width) and its wall diverges in the distal direction. The narrow rim displays a first order white birefringence in both plan and lateral view. In plan view, isolated rims without distal projections have their imperforate central areas divided into four quadrants by diagonal extinction lines. Coccolith size: 4.5-6.0 µm; stem height about 10 µm.

Range: DSDP Site 534: Core 45-4, 10-13cm, upper Barremian; SE France (Angles): upper Barremian (Bed 161, sartousiana Zone) to basal upper Aptian, Angles, Bed 46.

Holotype: Plate 1, figs. 17a-b; Angles, upper Barremian, Bed 161 (top sartousiana Zone).

Markalius vetulus, new species
(Plate 1, figures 22a-b, 23a-b)

Derivation of name: Latin. *vetulus* (dim.) = somewhat old.

Diagnosis: A Neocomian *Markalius* species having a steep, brightly birefringent tube cycle and shields that exhibit a faint, smooth birefringence.

Description (LM only): Medium-sized, sub-circular to circular placolith constructed of two shields, which are both faintly birefringent and have indistinct sutures. The proximal shield size is about 3/4 that of the distal shield. Shield elements (~32 in number) are radial with slight curvature near the outer periphery. A steep tube cycle nearly encloses the central area (~1/3 coccolith diameter) and exhibits a bright, 1st order white birefringence. Sharp extinction lines cross the tube cycle, but do not extend onto the shields. A very small central perforation is present. Observed specimens: 6.0 to 7.5 µm.

Remarks: *Markalius inversus* (Maastrichtian-Palaeogene) is very similar. However, its birefringent tube cycle is not steep and its shield elements appear striated (i.e. individual elements are easily distinguished with the light microscope).

Range: late early Valanginian; DSDP Site 534 (57% Sa): Cores 79-2, 10-11cm to 76-6, 94-95cm; SE France (Angles, 80% Sa): Beds 278 to 302 (campylotoxum Zone).

Holotype: Plate 1, figs. 22a-b; Angles, Bed 278, upper lower Valanginian.

Percivalia bullata, new species
(Plate 1, figures 4a-b, 5a-b, 6a-b)

1979 *Parhabdolithus judithae* Black, 1972. Wind & Čepek, p. 231, pl. 11, figs. 5-7.

Derivation of name: Latin. *bullatus* = inflated.

Diagnosis: A species of *Percivalia* with a hollow, bulbous distal projection that fills the central area.

Description (LM only): Medium-sized, elliptical murolith exhibiting a bicyclic rim extinction pattern. The narrow outer rim is slightly less birefringent than the inner rim cycle, which grades into a finely granular central area of equal, 1st order white birefringence. Extinction lines extend from the juncture of the two rim cycles into the central area. A hollow, bulbous distal projection nearly fills the central area. The rim elevation is low; the stem height is about two times that of the rim. Size of observed specimens: 6.0-8.0 µm.

Remarks: Wind & Čepek (1979) illustrated a specimen from DSDP Hole 397A as *Parhabdolithus judithae* Black, 1972. However, the original specimens illustrated from the Albian Gault Clay by Black (1972; pl. 3, figs. 5, 6; pl. 4, fig. 4) have high rims and truncated distal projections.

Range: DSDP Site 534 (57% Sa): late Berriasian to earliest Hauterivian, Cores 83-4, 96-97cm to 70-6, 27-30cm (isolated specimen in 67-1, 80-83cm considered reworked); SE France (Angles, 35% Sa): lower Valanginian to basal Hauterivian, Bed 199 (base otopeta Zone) to Bed 386 (radiatus Zone).

Holotype: Plate 1, figs. 4a-b; Angles, Bed 334, upper Valanginian (verrucosum Zone).

Paratype: Plate 1, figs. 6a-b; Angles, Bed 352, (trinodosum Zone).

Pickelhaube umbellatum, new species
(Plate 1, figures 19a-c, 20a-b, 21a-b)

Derivation of name: Latin. *umbella* = parasol, sunshade.

Diagnosis: An irregular-shaped species of *Pickelhaube* with two faintly birefringent shields of low element number; the proximal shield elements are strongly curved.

Description: Medium to large placolith constructed of two faintly birefringent shields. The larger proximal shield is constructed of 13-19 elements with strongly curved sutures. The horizontal periphery is highly irregular, although the outline is basically sub-circular to circular. The small, narrow distal shield is about 1/3-1/4 the size of the proximal shield. A brightly birefringent central cross nearly fills the small central area and has arms that taper to points. A long, proximally-directed stem is present on some specimens and appears to have octoradiate symmetry. Size of observed specimens: 6.4-8.8 µm.

Remarks: *Pickelhaube furtiva* (Roth) has brightly birefringent shields, a smooth horizontal peripheral outline, and radial proximal shield elements.

Range: Rare, extremely short stratigraphic range within the middle lower Valanginian. DSDP Site 534: Sample 79-5, 120-123cm; SE France (Angles, 100% Sa): Bed 258 to 274 (lower campylotoxum Zone).

Holotype: Plate 1, figs. 19a-c; DSDP Site 534, Core 79-5, 120-123cm.

Reinhardtites scutula, new species
(Plate 1, figures 24a-c, 25a-b)

1989 *Zeugrhabdotus sisyphus* (Gartner, 1968) nov. comb. - Crux, p. 198, pl. 8.7, fig. 1, pl. 8.12, fig. 30.

(?) 1991 *Zeugrhabdotus sisyphus* (Gartner, 1968) Crux, 1989 - Mutterlose, p. 131, pl. 9, figs. 3, 5.

Derivation of name: Latin. *scutula* = diamond or lozenge-shaped figure.

Diagnosis: A species of *Reinhardtites* having a smooth, narrow rim and a central, transverse bar supporting a distal boss of equal width. A bright, elongated, diamond-shaped extinction figure is observed on the central portion of the faintly birefringent, transverse bar.

Description: Medium to large, normally to narrowly elliptical murolith. The distal shield is constructed of a single cycle of 32-40 elements with dextral imbrication. The central area is greater than 1/2 the coccolith width (0.53 to 0.67 relative width). An elevated, transverse bar spans the central area and is constructed of numerous fibrous elements oriented parallel the minor ellipse axis. A circular distal boss equal in width to the transverse bar is present at its centre. The rim extinction pattern is unicyclic and displays a first order grey birefringence; extinction lines spiral across the rim. The transverse bar exhibits same faint birefringence as the rim; when specimens are oriented 45 degrees to the polarizing direction, the bar is divided by a longitudinal extinction line. A brightly birefringent, elongate, diamond-shaped figure is observed on the central portion of the bar when specimens are oriented parallel to the polarizing direction. Measured specimens ranged from 6.5-8.5 µm in length and 1.3-1.6 in ellipticity.

Remarks: *Reinhardtites scutula* is the ancestral species of a lineage that has excellent biostratigraphic utility in the Upper Cretaceous. It is optically distinct from younger taxa within this lineage, which have broader rims (with a pitted or a serrate inner margin) and/or transverse bars that exhibit a diagonal, bright birefringence band (when parallel to the polarizing direction).

Range: Cosmopolitan; mid-Hauterivian to Santonian. Its LO in the following sections: (1) DSDP Site 534, 59-3, 76-79cm (B 9/10 Sa); (2) SE France (Vergons, B 9/10 Sa), Bed 92, sayni Zone; (3) Speeton (approximate), Bed C8.

Holotype: Plate 1, figs. 24a-c; Speeton Borehole, 11.01m.

Rhagodiscus dekaenelii, new species
(Plate 1, figures 7a-c, 8a-d, 9a-b)

1979 *Parhabdolithus swinnertonii* (Black, 1971) Wind & Čepek, p. 231, pl. 11, figs. 8-16.

Derivation of name: named in honour of Eric de Kaenel.

Diagnosis: A species of *Rhagodiscus* with a brightly birefringent, solid distal stem; the stem tapers distally and its horizontal periphery extends to, or outside, the central area margin.

Description: Medium-sized, elliptical murolith. The distal shield is constructed of lath-shaped, dextrally-imbricated elements with radial distal sutures. The proximal shield is narrow and thin. The thick, imperforate central area is composed of granular elements. A solid, tapered distal projection nearly fills the central area and occupies 1/2 to 2/3 of the coccolith width (reaching to or extending beyond the central margin). Its height is equal to, or is slightly less, than the height of the rim. The stem has a serrate horizontal periphery and is constructed of two element cycles. The large, outer cycle is non-imbricate (10 or more elements); a small central cycle can be observed on some specimens. The stem is brightly birefringent and is divided into quadrants by the extinction lines. Size of observed specimens: 4.8-6.4 µm.

Remarks: The holotype of *Rhagodiscus swinnertonii* (Black) Applegate *et al.*, 1987 was recovered from the Aptian Sutterby Marl; its stem does not extend to the central area margin and is constructed of numerous elements showing strong laevogyre curvature. Both the appearance and extinction of *Rhagodiscus dekaenelii* are excellent biostratigraphic datums in low-latitude and deep-sea sections.

Range: early Valanginian to early Hauterivian. DSDP Site 534 (100% Sa): 80-1, 0-3cm to 63-2, 66-69cm. SE France (90% Sa): base campylotoxum Zone (Angles, Bed 250) to base nodosoplicatum Zone (Vergons, Bed 57). Also reported from DSDP Site 397A (Wind & Čepek, 1979) and Site 603 (Covington & Wise, 1987), ODP Sites 638-641 (Applegate & Bergen, 1988).

Holotype: Plate 1, figures 8a-d, DSDP Site 534, 71-1, 63-66cm, upper Valanginian.

Rucinolithus pinnatus, new species
(Plate 1, figures 3a-b)

1989 *Rucinolithus terebrodentarius* Applegate *et al.*, 1987. Bralower, Monechi, & Thierstein (partim), p. 223, pl. 7, figs. 4-6 (non pl. 7, figs. 1-3).

Derivation of name: Latin. *pinnatus* = feathered, plumed.

Diagnosis: A species of *Rucinolithus* possessing eight elements that broaden outwards along the sutures between adjoining elements and then taper to points once the elements become separate.

Description: Medium-sized, robust nannolith constructed of eight, imbricated elements with curved sutures. The elements are broadest at their outer peripheral contact and then taper outwards to form pointed terminations. A small element cycle surrounds a small central perforation or boss. Size of holotype: 6.9µm.

Remarks: Bralower *et al.* (1989) reported the range of *Rucinolithus terebrodentarius* as upper Hauterivian to Turonian, but one of their illustrated specimens was recovered from Berrasian section (other illustrated specimens from the same sample include *Diadorhombus rectus, Umbria granulosa* ssp. *granulosa*, and *Rhagodiscus nebulosus*) and serves as the holotype for *Rucinolithus pinnatus*. *Nannoconus ligius* is another robust Neocomian nannolith with a petaloid form and eight-fold symmetry. It is possible that *Rucinolithus pinnatus* is an isolated distal calyx; this was demonstrated for another nannolith with eight-fold symmetry, *Retecapsa radiata* (Worsley) Applegate & Bergen. *R. pinnatus* is distinguished from *Kokia* spp. by the strong imbrication of the elements.

Range: Very rare, composite range of mid-Tithonian to latest Berriasian. DSDP Site 534 (34% samples): Cores 96-3, 9-12cm to 83-1, 18-19cm; SE France, Angles (55% Sa), upper Berriasian, Bed 158 to Bed 180.

Holotype: Bralower, Monechi, & Thierstein (1989), plate 7, figures 4-6; DSDP Site 100, 1-1, 13cm, Berriasian.

Vagalapilla, species A
(Plate 1, figures 28a-b)

1966 *Coccolithus matalosus* Stover, p. 139, pl. 2, fig. 2 (non pl. 2, fig. 1, pl. 8, fig. 10).

Remarks: The holotype of *Vagalapilla matalosa* (Stover, 1966) Thierstein, 1973 (see Stover, 1966, pl. 2, fig. 1) is a placolith belonging to the genus *Broinsonia* Bukry, 1969; its lowest occurrence in the Vocontian Trough sections is lowermost Albian. The other photographed specimen in Stover (1966) is a murolith, which has a diamond-shaped central opening. Very rare specimens having elliptical central openings were recovered from the upper Hauterivian.

Range: early Aptian to early Cenomanian. SE France: LO at La Bedoule (92% Sa), Bed 86.

GENUS *Zeugrhabdotus* Reinhardt, 1965

Remarks: The large number of Cretaceous muroliths having transverse central bars show a great range in optical properties and ultrastructure. Four species cited and/or described herein have been retained within the Mesozoic genus *Zeugrhabdotus*, whereas four others are left within the Palaeogene genus *Zygodiscus* (see list under **Other Species Considered**). The proper classification of such forms cannot be made until the ultrastructure and evolution of this entire murolith family is better understood, especially their transitions across the Cretaceous/Tertiary boundary.

Zeugrhabdotus trivectis, new species
(Plate 1, figures 26a-b, 27a-c)

Derivation of name: Latin. *trinus* = three. *vectis* = bar, lever.

Diagnosis: A species of *Zeugrhabdotus* exhibiting a bicyclic rim extinction pattern of contrasting birefringence (inner cycle is bright); optically, the transverse bar gives the impression of three element bundles arranged at slightly oblique angles to each other.

Description: Medium-sized, normally elliptical murolith. The distal shield is constructed of a single cycle of 28-32 elements with strong dextral imbrication. A thin, narrow, basal inner cycle observed in distal view may represent the inner portion of the proximal shield. The central area is spanned by a transverse bar constructed of fibrous elements. The bar broadens slightly near the juncture with the inner rim margin. A circular distal projection, which is narrower than the bar, is present at the centre of the coccolith. Specimens exhibit a bicyclic rim extinction pattern. The inner cycle displays a 1st order white birefringence and the outer cycle is faintly birefringent. The transverse bar displays the same bright birefringence as the inner rim cycle when specimens are oriented parallel to the polarizing direction. The bar elements are optically grouped into three bundles oriented at slightly oblique angles to each other. Measured specimens: length 4.7-6.0 µm; ellipticity 1.3-1.5; relative central area size 0.50-0.57.

Remarks: As with most *Zeugrhabdotus* species, the optical properties of *Zeugrhabdotus trivectis* are more distinct than its ultrastructure.

Range: Cosmopolitan, early Valanginian to middle Cenomanian. LO in the following sections: (1) DSDP Site 534 (28% Sa), Core 77-3, 43-44cm; (2) SE France (Angles, 70% Sa), Bed 284, campylotoxum Zone.

Holotype: Plate 1, figure 27a-c, BGS Speeton Borehole, 14.07m.

Zeugrhabdotus species A
(Plate 1, figure 16a-b)

Description (LM only): Medium-sized, normally elliptical murolith. The rim exhibits a uniform 1st order grey birefringence. An oblong, transverse bar spans the central area and has pointed terminations that extend into the rim.

The transverse bar displays a 1st order white birefringence that strongly contrasts with the birefringence of the rim. A central, circular distal projection is non-birefringent, interrupting the continuity of the birefringent transverse bar. Longitudinal extinction lines further subdivide the transverse bar. Size of observed specimens 4.8-5.8 µm.

Remarks: Specimens must be transferred from the LM to the SEM before this taxon can be recognized either as a valid or new species. It is closely related to *Zeugrhabdotus erectus*, from which it is distinguished by the optical properties of its central structure (see Plate 1).

SPECIES	DSDP 534 (Core-Section, cm)			SE France (Section, Bed #)		
	Freq.	LO	HO	Freq.	LO	HO
C. oblongata	95%	80-5, 121	50-3, 71	99%	Angles 1, 199	Angles 2, 116
C. tenuis	68%	76-6, 94	---	74%	Angles 1, 275	---
C. mexicana	---	---	---	80%	---	La Bedoule, 114
C. geometricum	T9	---	56-1, 49	---	absent	absent
C. silvaradion	B3/T9	82-1, 132	59-3,76	B3/T2	Angles 1, 170	Vergons, 110
C. delicatus	B7	86-3, 40	---	30B	Angles, 126	---
C. cuvillieri	95%	91-2, 145	59-3, 76	100%	---	Vergons, 110
C. brezae	80%	95-3, 64	63-2, 66	B8/T4	Route de Grads, 1	Vergons, 68
C. deflandrei	T9	---	78-2, 85	T5	---	Angles 1, 278
D. rectus	B4	85-3, 108	---	B6	Angles 1, 164	---
D. primitiva	24%	67-1, 80	51-1, 61	2Sa	Angles 1, 299	Angles 1, 306b
E. primus	T2	---	78-2, 85	T8	---	Angles 1, 278
E. striatus	43%	67-1, 80	63-2, 66	98%	Angles 1, 354	Vergons, 78
E. windii	77%	79-5, 120	70-2, 50	96%	Angles 1, 258	Angles 1, 397; Vergons, 19
E. antiquus	1Sa	64-4, 25	64-4, 25	1Sa	Vergons, 51	Vergons, 51
E. floralis	---	---	---	100%	La Bedoule, 169	---
E. hauterivianus	T5	---	50-3, 70	T2	---	Angles 2, 94
F. multicolumnatus	62%	106-1, 54	92-1, 79	---	*bimammatum* Zone	Route de Grads, 25
F. oblongus	1Sa	44-4, 11	---	43%	Angles 2, 147	---
H. circumradiatus	100%	86-3, 40	---	98%	Angles 1, 102	---
H. ellipticus	67%	104-1	49-2, 70	---	Route de Grads, 25	Angles 2, 90
H. irregularis	---	---	---	B7	Angles 2, 199 La Bedoule, 59	Blieux, u. Albian
H. noelae	---	96-3, 9	91-2, 145	---	*fallauxi* Zone	Route de Grads, 25
L. bollii	64%	66-3, 60	52-3, 72	95%	Vergons, 48	Vergons, 196 Angles 2, 52
L.carniolensis	92%	88-4, 141	---	---	Angles 1, 77 (?)	---
M. mecurius	1Sa	76-2, 61	76-2, 61	60%	Angles 1, 305	Angles 328
M. speetonensis	---	---	---	80	Angles 1, 250	Angles 2, 261
M. conus	70%	85-4, 126	75-2, 49	2Sa	Angles 1, 258	Angles 1, 264
N. compressus	---	97-1, 19	89-1, 26	---	*fallauxi* Zone	Route de Grads, 27
N. ligius	75%	56-1, 49	---	B9	Vergons, 141	Angles, u. Aptian
N. steinmannii	---	91-2, 45	---	---	Angles 1, 79	La Bedoule, 161
P. fenestrata	100%	83-4, 96	---	100%	Angles 1, 132	---
P. senaria	57%	93-2, 41	89-4, 35	---	---	Route de Grads, 27
R. angustiforata	96%	91-1, 80	---	B8/T9	Angles, 79	La Bedoule, 114
R. radiata	33%	69-2, 95	47-2, 80	B2/T9	Vergons, 40	Angles 2, 134
R. achlyostaurion	---	45-4, 10	---	B5	Angles 2, 165	---
R. angustus	---	---	---	85%	la Bedoule, 129	---
R. nebulosus	100%	88-2, 17	82-2, 49	---	Route de Grads, 27?	Angles 1, 158
R. wisei	B10	83-1, 18	76-2, 61	B8/T3	Angles 1, 167	Angles 1, 306a
S. lowei	---	---	52-3, 72	---	---	Angles 2, 79
S. colligata	94%	91-1, 80	54-2, 57	T10	Route de Grads, 27	Vergons, 141
S. mutterlosei	43%	78-2, 85	---	13%	Angles 1, 321	lower Cenomanian
S. comptus	1Sa	71-1, 63	71-1, 63	2Sa	Angles 1, 306b	Angles 1, 309
T. gabalus	16%	80-5, 129	---	9%	Angles 1, 180	---
T. jurapelagicus	B9	85-4, 126	---	B8	Angles 1, 131a	lower Turonian
T. verenae	B9	83-2, 92	67-1, 80	B6/T6	Angles 1, 139	Vergons, 96
U. granulosa	T10	96-3, 9	83-2, 92	T7	---	Angles 1, 147
V. mitcheneri	57%	68-5, 1	49-3, 60	19	Vergons, 32	Vergons, 123
V. parallela	B3	79-2, 10	---	B5	Angles 1, 264	Blieux, Albian
Z. erectus	T8	---	53-2, 60	T5	---	Vergons, 160
Z. fissus	T8	116-1	70-6, 27	T6	la Melle, Oxfordian	Angles 1, 324
Z. bicrescenticus	B5	70-2, 50	---	B6	Angles 1, 311	---
Z. diplogrammus	B8	78-3, 49	---	B9	Angles 1, 258	---
Z. elegans	---	48-2, 110	---	---	Angles, u. Aptian	---
Z. xenotus	B6	77-3, 111	---	B7	Angles 1, 278	middle Cenomanian

Table 1: Biostratigraphic Summary (excluding species described or recombined here). Freq. refers to either: (1) the percentage of samples containing species within its stratigraphic range (*e.g.* 70%); or (2) the number of samples in which a species was observed either in the top (T) or bottom (B) ten samples of its stratigraphic range (*e.g.* T3 means specimens observed in 3 of 10 samples at the top of its stratigraphic range). Angles 1 refers to the Berriasian-Valanginian section and Angles 2 to the Barremian stratotype along Route d' Angles.

Range: latest Hauterivian to early Campanian. Its LO in the following sections: (1) DSDP Site 534, 52-1, 82-85cm; (2) SE France, Angles, Barremian stratotype, Bed 60, angulicostata Zone; (3) Speeton (approximate), upper Hauterivian, Bed C2, marginatus Zone.

Other Species Considered (by Generic Epithet)

Assipetra infracretacea (Thierstein, 1971) Roth, 1973.
Calcicalathina oblongata (Worsley, 1971) Thierstein, 1971.
Chiastozygus tenuis Black, 1971.
Corollithion geometricum (Górka, 1957) Manivit, 1971.
Corollithion silvaradion (Filewicz *et al.*, 1987) Perch-Nielsen, 1984.
Conusphaera mexicana Trejo, 1969.
Cretarhabdus delicatus Applegate, Covington, and Wise, 1987.
Cruciellipsis cuvillieri (Manivit, 1966) Thierstein, 1971.
Cyclagelosphaera brezae Applegate & Bergen, 1988.
Cyclagelosphaera deflandrei Manivit, 1966.
Diadorhombus rectus Worsley, 1971.
Diloma primitiva (Worsley, 1971) Wind & Čepek, 1979.
Eiffellithus primus Applegate & Bergen, 1988.
Eiffellithus striatus (Black, 1971) Applegate & Bergen, 1988.
Eiffellithus windii Applegate & Bergen, 1988.
Eprolithus antiquus Perch-Nielsen, 1979.
Eprolithus floralis (Stradner, 1963) Stover, 1966.
Ethmorhabdus hauterivianus (Black, 1971) Applegate *et al.*, 1987 in Covington & Wise, 1987.
Faviconus multicolumnatus Bralower, 1989.
Flabellites oblongus (Bukry, 1969) Crux, 1982.
Haqius circumradiatus (Stover, 1966) Roth, 1978.
Haqius ellipticus (Grün, 1975) Bown, 1992.
Hayesites irregularis (Thierstein, 1971) Applegate *et al.*, 1987 in Covington & Wise, 1987.
Hexalithus noelae Loeblich & Tappan, 1966.
Lithraphidites bollii (Thierstein, 1971) Thierstein, 1973.
Lithraphidites carniolensis Deflandre, 1963.
Metadoga mecurius Wind & Čepek, 1979.
Micrantholithus speetonensis Perch-Nielsen, 1979.
Microstaurus conus Wind & Čepek, 1979.
Nannoconus compressus Bralower & Thierstein, 1989.
Nannoconus ligius Applegate & Bergen, 1988.
Nannoconus steinmannii Kamptner, 1931
Percivalia fenestrata (Worsley, 1971) Wise, 1983.
Polycostella senaria Thierstein, 1971.
Retecapsa angustiforata Black, 1971.
Retecapsa radiata (Worsley, 1971) Applegate & Bergen, 1988.
Rhagodiscus achlyostaurion (Hill, 1976) Doeven 1983.
Rhagodiscus angustus (Stradner, 1963) Reinhardt, 1971.
Rhagodiscus nebulosus Bralower, 1989.
Rucinolithus wisei Thierstein, 1971.
Sollasites horticus (Stradner *et al.*, 1966) Čepek & Hay, 1969.
Sollasites lowei (Bukry, 1969) Roth, 1970.
Speetonia colligata Black, 1971.
Staurolithites mutterlosei Crux, 1989.
Stradnerlithus comptus Black, 1971.
Tranolithus gabalus Stover, 1966.
Tubodiscus jurapelagicus (Worsley, 1971) Roth, 1973.
Tubodiscus verenae Thierstein, 1973.
Umbria granulosa Bralower & Thierstein, 1989.
Vekshinella mitcheneri Applegate & Bergen, 1988.
Vekshinella parallela (Wind & Čepek, 1979) Applegate & Bergen, 1988.
Zeugrhabdotus erectus (Deflandre, 1954) Manivit, 1971.
Zeugrhabdotus fissus Grün & Zweili, 1980.
Zygodiscus bicrescenticus (Stover, 1966) Wind & Wise, 1976.
Zygodiscus diplogrammus (Deflandre, 1954) Gartner, 1968.
Zygodiscus elegans Gartner, 1968.
Zygodiscus xenotus (Stover, 1966) Hill, 1976.

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APPENDIX

D.S.D.P. Site 534 samples examined: 44-4, 11-14cm; 45-4, 10-13cm; 46-1, 99-102cm; 47-2, 80-83cm; 48-2, 110-113cm; 49-2, 70-73cm; 49-3, 60-63cm; 49-4, 61-64cm; 50-1, 68-71cm; 50-3, 71-74cm; 51-1, 61-64cm; 52-1, 82-85cm; 52-3, 72-75cm;

53-2, 60-63cm; 54-2, 57-60cm; 55-3, 75-78cm; 56-1, 49-52cm; 58-1, 42-45cm; 59-3, 76-79cm; 60-3, 52-55cm; 61-2, 80-83cm; 63-2, 66-69cm; 64-2, 78-81cm; 64-4, 25-28cm; 65-3, 102-105cm; 65-6, 69-72cm; 66-3, 60-63cm; 67-1, 80-83cm; 68-5, 1-4cm; 69-2, 95-98cm; 70-2, 50-53cm; 70-6, 27-30cm; 71-1, 63-66cm; 72-4, 12-15cm; 73-1, 125-128cm; 74-6, 73-76cm; 75-2, 49-52cm; 75-6, 103-107cm; 76-2, 61-64cm; 76-6, 94-95cm; 77-3, 43-44cm; 77-3, 111-114cm; 78-2, 85-86cm; 78-3, 49-52cm; 78-5, 7-8cm; 79-2, 10-11cm; 79-5, 120-123cm; 80-1, 0-3cm; 80-2, 80-82cm; 80-5, 129-130cm; 81-3, 57-58cm; 81-4, 48-51cm; 82-1, 132-133cm; 82-2, 49-52cm; 83-1, 16-18cm; 83-2, 92-95cm; 83-4, 96-97cm; 84-1, 89-90cm; 84-2, 129-132cm; 84-3, 113-114cm; 84-4, 41-42cm; 84-5, 86-87cm; 85-2, 51-54cm; 85-3, 108-109cm; 85-4, 126-127cm; 86-1, 122-125cm; 86-3, 40-41cm; 86-5, 36-37cm; 87-2, 64-67cm; 87-4, 40-41cm; 87-5, 122-123cm; 88-2, 17-20cm; 88-4, 141-142cm; 89-1, 26-27cm; 89-4, 35-36cm; 90-1, 123-124cm; 90-3, 21-23cm; 91-1, 80-81cm; 91-2, 45-46cm; 91-4, 131-132cm; 91-5, 134-135cm; 91-6, 1-2cm; 92-1, 79-80cm; 92-2, 131-132cm; 92-3, 109-110; 92-4, 147-148cm; 92-5, 69-72cm; 92-5, 86-87; 92-6, 48-49cm; 93-1, 105-106cm; 93-2, 41-44cm, 93-2, 100-103cm; 93-3, 122-125cm; 94-1, 93-94cm; 94-2, 89-92cm; 94-3, 89-92cm; 94-4, 3-4cm.

PLATE 1

All LM 2500X. XP - cross polarized light; Ph - Phase contrast illumination; Tr - transmitted light.

1-2: *Hexalithus strictus*, n. sp.; (1) holotype, DSDP 534, 91-4, 131-132cm, (a) XP, (b) Tr; (2) DSDP 534, 89-4, 35-36cm, (a) XP, (b) Tr.

3: *Rucinolithus pinnatus*, n. sp., Angles, Bed 164, (a) XP, (b) Tr.

4-6: *Percivalia bullata*, n. sp., Angles, (4) holotype, Bed 334, verrucosum Zone, (a) XP, (b) Tr; (5) Bed 364, trinodosum Zone, (a) XP, (b) Tr; (6) paratype, lateral view, Bed 352, trinodosum Zone, (a) XP, (b) Tr.

7-9: *Rhagodiscus dekaenelii*, n. sp.; (7) DSDP Site 534, 71-1, 63-66cm, u. Valanginian, (a) XP, (b) Tr, (c) proximal view; (8) holotype, DSDP Site 534, 71-1, 63-66cm, u. Valanginian, (a) lateral view, (b) distal view, (c) XP, (d) Ph; (9) Angles, Bed 357, trinodosum Zone, (a) XP, (b) Tr.

10: *Grantarhabdus quadratus* (Worsley) n. comb., Speeton, Bed C11A, regale Zone.

11: *Calcicalathina* sp. A, Angles, Bed 245, u. Berriasian, (a) XP, (b) Tr.

12: *Diloma* sp. A, Speeton, Bed LB5, lo. Barremian, (a) XP, (b) Tr.

13-14: *Diloma galiciense*, n. sp. (13) DSDP 534, 59-3, 76-79cm, u. Hauterivian, (a) XP, 45°, (b) XP, 0°, (c) Tr; (14) DSDP 534, 52-1, 82-85cm, u. Hauterivian, (a) XP, 45°, (b) XP, 0°, (c) Tr.

15: *Zeugrhabdotus erectus* (Deflandre), Speeton, Bed C11A, regale Zone, (a) XP, (b) Tr.

16: *Zeugrhabdotus* sp. A, Angles, upper Aptian, (a) XP, (b) Tr.

17-18: *Lucianorhabdus salomonii*, n. sp. (17) holotype, lateral view, Angles, Barremian, Bed 161, sartousiana Zone, (a) XP, (b) Tr; (18) plan view, rim, La Bedoule, Bed 157, (a) XP, (b) Tr.

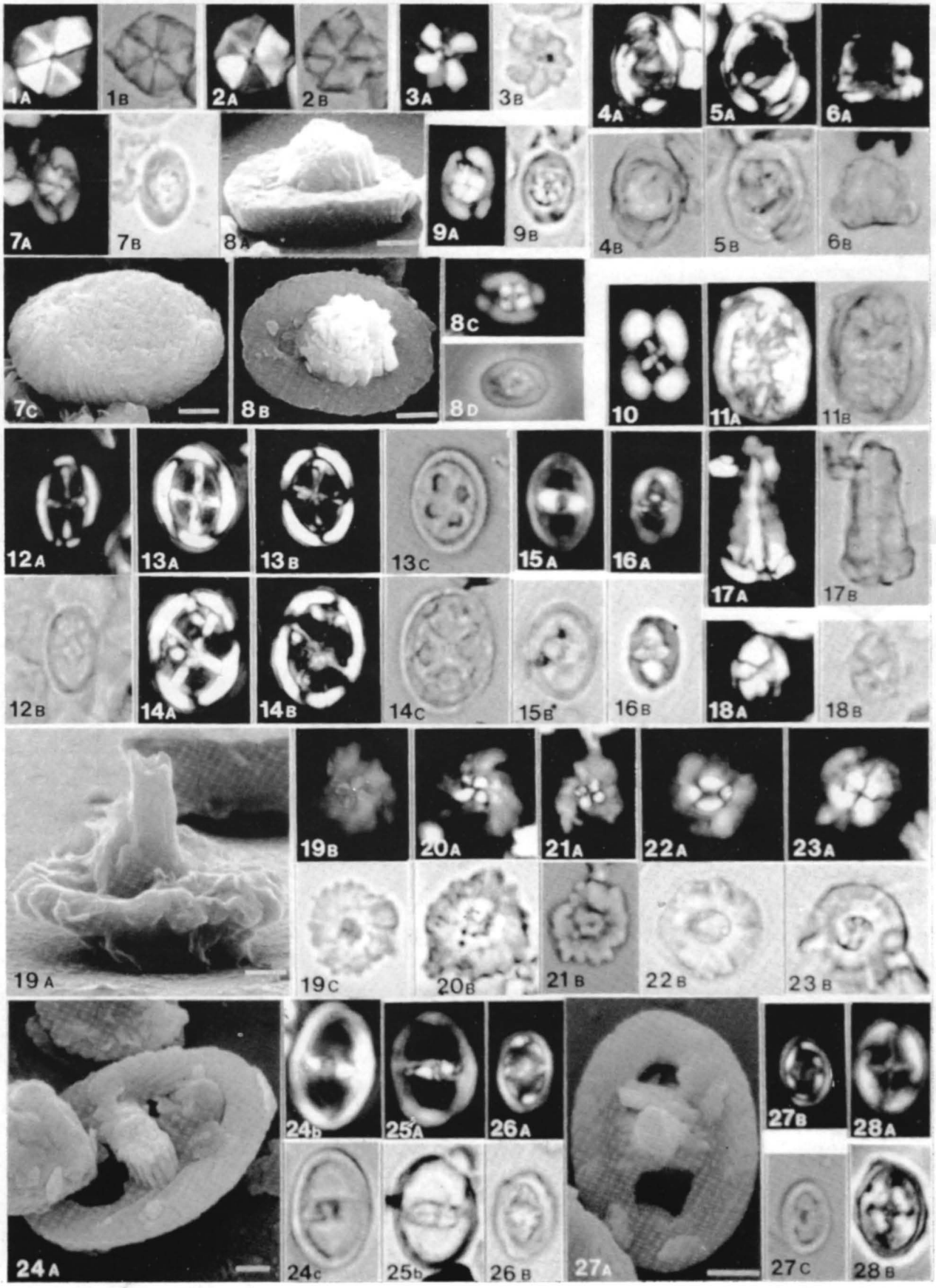
19-21: *Pickelhaube umbellatum*, n. sp., lo. Valanginian; (19) holotype, DSDP 79-5, 120-123cm, (a) lateral view, (b) XP, (c) Tr; (20) Angles, Bed 274, campylotoxum Zone, (a) XP, (b) Tr; (21) DSDP 534, 79-5, 120-123cm, (a) XP, (b) Tr.

22-23: *Markalius vetulus*, n. sp., Angles, campylotoxum Zone; (22) holotype, Bed 278, (a) XP, (b) Tr; (23) Bed 302, (a) XP, (b) Tr.

24-25: *Reinhardtites scutula*, n. sp. (24) holotype, Speeton borehole, 11.01m, (a) distal view, (b) XP, (c) Tr ; (25) Speeton, Bed LB5, lo. Barremian, (a) XP, (b) Tr.

26-27: *Zeugrhabdotus trivectis*, n. sp. (26) Angles,Bed 361, trinodosum Zone, (a) XP, (b) Tr; (27) holotype, Speeton borehole, 14.07m, (a) distal view, (b) XP, (c) Tr.

28: *Vagalapilla*, sp. A, La Bedoule, Bed 153, (a) XP, (b) Ph.


1A
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24C
25B
26B
27C
28B