# Systematic palaeontology

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thae. However, the ranges of these species may also be extended from that cited in the literature. An example of this is the occurrence of *Stephanolithion speciosum* DEFLANDRE in the Oxfordian of the Gamlingay Borehole, whereas it had been considered previously to be confined to below the Callovian/Oxfordian boundary.

The extinction of the Upper Jurassic coccolith species may prove to be as stratigraphically valuable as their incomings (e.g. that of *Stephanolithion bigoti* DEFLANDRE in the Kimmeridgian), and this too is reflected in the proposed zonation.

## Systematic palaeontology

There is very little to add to the species descriptions given by NOEL (1965, 1973) and MEDD (1971). Only such information as supplements these descriptions is given below. Most of the additional data concerns the finding of new or rare species or additional stratigraphic information. The suprageneric arrangement has been altered from the previous papers and is based on taxonomic revisions of the Coccolithinae by ROOD, HAY & BARNARD (1971) and by BLACK (1972, 1973). This has necessitated some discussion; necessary species synonymies and other remarks are given below.

The classification is based on ICBN rules, and follows modern botanical work (BLACK 1972, p. 23), which places all coccolith groups into the Suborder Coccolithinae KAMPTNER. Many of the Mesozoic genera have structures similar to those of Tertiary forms, and by extrapolation these latter forms can be related to Recent taxa. From these analogies the proposed supra-generic classification is established.

One disadvantage of this, however, is that the major groups of coccoliths (e.g. Eiffellithales ROOD, HAY & BARNARD 1971) are restricted to the familial level, many of the defined families belonging to such groups are down-graded to subfamily status, subfamily groups now become tribe status.

Class Haptophyceae CHRISTENSEN 1962

## Suborder Coccolithinae KAMPTNER 1928

### Family Eiffellithaceae REINHARDT 1965

*Remarks.* - The classification is accepted here of all Upper Jurassic coccoliths that possess an eiffellithid rim that were placed in Eiffellithales new order by ROOD, HAY & BARNARD (1971, p. 248), but the grouping is here down-graded to family status.

The classification of these small Upper Jurassic coccoliths with such a rim and a variably developed central area is very tenuous, and no two publications are in agreement. One basis for such a classification is to consider the nature of their rim first and then to subdivide these groups on the arrangement of their central areas.

In most of the groups given below the arrangement of the crystallites of the rim is at a fairly uniform angle, with the elements of the outer ring either stacked almost vertically and so having little or no imbrication, or at an angle of 45-60 degrees with moderate imbrication. *Staurorhabdus* NOEL, considered by many workers to be the most primitive coccolith type, has the latter crystallite arrangement (at an angle of 60 degrees), constant throughout the Jurassic.

However, in the case of the zygoliths, the crystallite arrangement is very variable ranging from almost vertical to horizontal stacking with resulting little to extreme imbrication. There is also often found to be a complete gradation within a single species in many of the samples examined. The most variable development is seen in the genus Zeugrhabdotus REINHARDT, and to a lesser in the genus Actinozygus GARTNER, and these genera are grouped together with Mitrolithus DEFLANDRE, Parhabdolithus DEFLANDRE and Tubirhabdus PRINS into the Zygolithoideae new subfamily. These forms link with the Crepidolithaceae BLACK.

The most "primitive" group of genera are: Ahmuellerella REINHARDT, Discolithus HUXLEY, Staurorhabdus NOEL and Vekshinella LOEBLICH & TAPPAN. These are placed in the Ahmuellerelloideae new subfamily.

Those genera with nearly vertical stacked crystallites on the outer rim and with a complex central area are placed in the Eiffellithoideae new subfamily; these genera include Anfractus gen.n., Chiastozygus GARTNER, (Eiffellithus REINHARDT – whose Cretaceous forms have not yet been found in the Jurassic), and Neococcolithes SUJKOWSKI.

The final group comprises the subfamily Stephanolithioideae VEKSHINA, 1959 newly emended, for crystallites steeply stacked on the outer rim, and with a variable arrangement of rhomb shaped crystals in the central area, which may culminate in a central spine. There are two subgroups dependant on whether there are also outward projections from the rim or not. The early representatives of each subgroup: *Stephanolithion speciosum* DEFLANDRE and *Stradnerlithus asymmetricus* (ROOD, HAY & BARNARD) respectively, are found to merge into a single species plexus in the Bajocian material from a borehole in the English Channel, near to the Dorset coast (I.G.S. borehole number CSUS  $50/\overline{30}/329$ ).

Another example of the downhole merging of two species into a single plexus occurs in the uppermost Jurassic material of the DSDP Leg 11 Site 105 Borehole, when the characteristic Cretaceous *Cylindralithus laffittei* (NOEL) merges into the Jurassic *Rotelapillus radians* NOEL between cores 32-2 and 33-1.

The reverse of the two above cases of divergence of subgroups occurs in the Kimmeridgian of the DSDP Leg 36 Site 330 Borehole, when in cores 4-CC to 8-1 there is co-existence of *Corollithion helotatus* WIND & WISE and "Stephanolithion bigoti" DEFLANDRE. The only feature that separates these two species (and genera) are the small lateral projections in the forms assigned to Stephanolithion.

The genera without the projections are: *Diadorhombus* WORSLEY, *Rotelapillus* NOËL and *Stradnerlithus* BLACK and are grouped into the Stradnerlitheae new tribe; the genera with the projections are: *Stephanolithion* DEFLANDRE and *Cylindralithus* BRAMLETTE & MARTINI, and are grouped into the Stephanolithieae new tribe. It should be stressed that these two tribes are based on morphological differences, since the plexi mentioned above would merge them if accepted. However, the writer considers that such tribe discrimination is useful.

Rare oval forms are present in the *athleta* to *transversarium* zones samples of all three boreholes; they have been found also in samples of similar age from the Millbrook section. They are about  $4-8 \mu$  in length and usually consist of a single ring

of crystallites inclined at an angle of 60 degrees. When previously recorded (MEDD 1971, p. 826, but *non* Pl. iv, Fig. 1) they have been referred to the genus *Loxolithus* NOEL. Scanning electron micrographs and detailed optical micrographs have shown that some of the rings possess axial structures of sufficient variability as to place the specimens in different taxonomic groups, if the present classification is adopted. These forms therefore are the link between the various groups possessing an eiffellithid rim, and also perhaps the podorhabdids.

Specimens have been found which possess a central cruciform arrangement of very small rhomb-like platelets, following the principle axes of the oval rings. These are referred to the genus *Staurorhabdus* NOEL.

This cross, however, may be alligned obliquely to the principle axes of the oval ring; it may be diagonal or at some angle between this and the staurorhabdid forms. These forms are referred to the genus *Chiastozygus* GARTNER, as it is defined below. And so there is a link between the ahmuellerellids and the eiffellithids.

Another development found is to have the crystallites stacked (almost) vertically, but turned horizontally at the proximal margin to form a selvage edge. In addition, one or two rings of plates cover the distal surface. These forms are referred to the genus *Carinolithus* PRINS. Some specimens are very wide in cross-section and the central opening is also wide; these are separated here as the new genus *Proculithus*. The links between this group and *Diazomatolithus* NOEL are therefore considerable (e.g. NOEL 1965, Pl. vi, Fig. 10).

These specimens are closely related to the last group of structural variants so far found in the samples. This is also the most frequently found variant type in the samples. They possess one or two rings of plates at the distal margin, but there is no proximal selvage characteristic of the species of *Carinolithus* and *Proculithus*. These forms are referred to the new genus *Millbrookia*. The central distal structure is of interest in that it consists either of a reticulate network of small rhomb-like platelets, or of bar structures coalescing at the centre of the coccolith. These structures are analogous to those found in the podorhabdids: *Ethmorhabdus* NOEL and *Polypodorhabdus* NOEL respectively. This suggests either a taxonomic link between the podorhabdids and the eiffellithids or that such structures are polyphyletic in origin.

## Subfamily Ahmuellerelloideae subfam. n.

*Diagnosis.* - Eiffellithaceae with an outer rim comprising crystals at an angle of 45-60° and with a variably developed central structure.

## Genus Ahmuellerella REINHARDT 1964

Type species: by original designation: Ahmuellerella limbitenuis REINHARDT 1964 which is a junior synonym of Discolithus octoradiatus GORKA 1957; Upper Cretaceous, Poland.

*Remarks.* - NOEL (1970, p. 35; 1971, p. 880) has reviewed this genus and her comments are accepted here.

## Genus Staurorhabdus NOEL 1973

Type species: by original designation: *Discolithus quadriarcullus* NoEL 1965*a*, p. 4, Fig. 7; Oxfordian, France.

*Remarks.* - NOËL'S establishment of this genus in May 1973 is accepted here. The Cretaceous forms assigned to *Ahmuellerella* REINHARDT 1964 are sufficiently distinct as to warrant their generic separation. The writer agrees with NOËL (1973, p. 100) in regarding the earlier published, but invalid genus *Crucirhabdus* PRINS (PRINS 1969, p. 548) as congeneric with *Staurorhabdus* NOËL. The later work of ROOD, HAY & BARNARD of November 1973, validating *Crucirhabdus* was published too late to preclude this genus being the junior synonym of *Staurorhabdus*.

Thin oval rings of about  $4-8 \mu$  length have been found in the optical scanning of strew slides of many of the samples from all three boreholes and in other material from the *athleta* to *tenuiserratum* zones. They have a less imbricate and narrower crystallite arrangement than is here accepted as belonging to the genus *Loxolithus* NOEL and no other structures are usually seen. Their taxonomic position is therefore uncertain. However, forms have been found at several levels in this material, which possess central cruciform structures alligned with the principle axes of the oval ring. These forms are here referred to the new species *Staurorhabdus magnus*.

Two species were assigned by ROOD, HAY & BARNARD to the genus *Crucirhabdus* and they are here transferred to the genus *Staurorhabdus*:

- Crucirhabdus primulus ROOD, HAY & BARNARD 1973, p. 367 = Staurorhabdus primulus (ROOD, HAY & BARNARD).
- Crucirhabdus prinsi ROOD, HAY & BARNARD 1973, p. 368 = Staurorhabdus roodii nom.n. (as Staurorhabdus prinsi NOEL is a distinct species and has priority).

### Staurorhabdus magnus sp.n.

## Pl. 10, Fig. 6, 7, 10

Diagnosis. - A species of Staurorhabdus with a large oval rim (about 6  $\mu$  in length).

*Description.* - Coccoliths with a simple eiffellithid rim and with a central cruciform structure of small lath-like platelets alligned with the principle axes of the oval rim. The central cross projects distally and terminates in a large open pore.

*Differentiation.* - This species is separated from *S. quadriarcullus* (NOEL) by its larger size and closed nature of the central cross plate structure.

Holotype: SEM 76/12632 (Pl. 10, Fig. 10). Dimensions:  $6 \times 5 \mu$ . Type locality: Gamlingay Borehole, Cambridgeshire. Type level: Depth of 110 feet (33.53 m); Upper Oxford Clay.

Other material. - This form has been seen in the optical microscope studies of several Upper Oxford Clay samples of the Gamlingay Borehole. A similar form has been seen in English Bajocian and Bathonian samples.

Staurorhabdus quadriarcullus (NOEL 1965) NOEL 1973

Pl. 1, Fig. 5; Pl. 2, Fig. 4

1965a Discolithus quadriarcullus NOEL, p. 4, Fig. 7.

1971 Vekshinella stradneri: ROOD, HAY & BARNARD, p. 249, Pl. i, Fig. 2.

1971 Vekshinella quadriarculla: ROOD, HAY & BARNARD, p. 250, Pl. i, Fig. 1.

*Remarks. - Vekshinella stradneri* ROOD, HAY & BARNARD is here considered to by synonymous with *S. quadriarcullus* (NOEL). The type figures and descriptions of material as given by NOEL, MEDD and ROOD, HAY & BARNARD have been reexamined.

The author agrees with NOEL (1973) that the species should be included in her genus *Staurorhabdus*. The unreplicated specimen taken with the transmission electron-microscope, figured by MEDD (1971, p. 842), indicates the complex structure of the bars over the central area. The thickening of the arms adjacent to the rim, mentioned by ROOD, HAY & BARNARD (1971, p. 250), is not considered here, after an examination of the present material, to be of taxonomic significance. The paired plates, which bifurcate at the centre of the cross bars and form a composite open spine, are diagnostic (as seen in the holotype of NOEL 1965b, Pl. i, Fig. 15). The figure of ROOD, HAY & BARNARD (1971, Pl. i, Fig. 1) does not show the paired plates of the axial structure nor the inner set of tabular rim elements, but it may be poorly preserved or a poor electron micrograph.

Staurorhabdus quadriarcullus (NOEL) is differentiated from Ahmuellerella octoradiata (GORKA) by the simpler arrangement of the central area.

The species has been recovered from most samples of the Haddenham and Gamlingay boreholes. The species range is base of the Upper Oxford Clay to the Upper Kimmeridge Clay, with earlier developments in the Lias (ROOD, HAY & BARNARD 1973) and in the Bathonian (MEDD 1971).

### Staurorhabdus primulus (ROOD, HAY & BARNARD 1973) ex PRINS 1969

1969 Crucirhabdus primulus PRINS, p. 548, Pl. i, Fig. 1; Pl. ii, Fig. 1-3; Pl. iii, Fig. 1-3 (invalid).
1973 Crucirhabdus primulus: ROOD, HAY & BARNARD, p. 367, Pl. i, Fig. 1-2.

*Remarks.* - The specimen found in the Haddenham Borehole at 240 feet (73.15 m) agrees with the published descriptions. It may, however, be a reworked contaminant.

## Genus Vekshinella LOEBLICH & TAPPAN 1963

Type species: by original designation; *Ephippium acutiferrus* (sic) VEKSHINA 1959, p. 69; Upper Cretaceous, USSR.

Remarks. - Vekshinella LOEBLICH & TAPPAN was established to replace Ephippium VEKSHINA 1959, a homonym of the angiosperm Ephippium BLUME 1825; Ephippium BOLTEN 1798, quoted as the senior synonym (LOEBLICH & TAPPAN 1963, ROOD, HAY & BARNARD 1971), is a mollusc and so is not involved.

VEKSHINA figured and briefly described the type of *E. acutiferrum* as having a proximal projection and this feature must be considered as part of the generic diagnosis, until proved otherwise by re-examination of the type material. *Vekshinel-la* is therefore defined as possessing this feature.

Species previously assigned to Vekshinella LOEBLICH & TAPPAN, which do not show this character (e.g., as in GARTNER 1968) should be transferred to the genus Staurolithites CARATINI 1963. NOËL (1971, p. 33) has already commented on the genus Staurolithites, noting the similarity with "Vekshinella" s.l.; BUKRY (1969, p. 55) erected the genus Vagalapilla for these species, but Staurolithites has priority. The author does not agree with ROOD, HAY & BARNARD (1971, p. 249) in regarding Vagalapilla as a synonym of Vekshinella; but even if Vekshinella is eventually found to be established on the basis of an artefact, Staurolithites has priority for these species.

The forms Vekshinella imbricata GARTNER 1968, p. 30, and Vagalapilla imbricata (GARTNER) imbricata BUKRY 1969, p. 57, are not here considered to belong to Staurolithites, as the structure is much simpler than that for the type species. The author proposes to transfer this species and subspecies to the genus Ahmuellerella REINHARDT 1964, since, apart from the more complex central structure of the type species, A. octoradiata (GORKA), they are similar.

## Genus Discolithus HUXLEY 1868

Type species: by subsequent designation; *Discolithus latus* KAMPTNER 1948, p. 5, Pl. i, Fig. 7, ex DEFLANDRE 1952, Fig. 49; Miocene, Austria.

*Remarks.* - The validity of the genus *Discolithus* HUXLEY is open to debate. K. Perch-Nielsen (pers. commun.) suggests that the genus should lapse. However, the author agrees with NOEL (1970, p. 35), who states "Il en ressort que les structures d'une partie au moins des discolithes tertiaires sont nettement différentes de celles des discolithes mésozoïques," and so the Jurassic discoliths previously assigned to *Discolithus* are transferred below to other genera.

### Subfamily *Eiffellithoideae* subfam.n.

*Diagnosis.* - Eiffellithaceae with nearly vertically arranged crystallites on the outer rim and with a complex central area.

## Genus Anfractus gen.n.

Type species: by original designation; Anfractus harrisonii sp.n.; Upper Jurassic (Oxfordian), England.

*Diagnosis.* - Coccoliths with a compound eiffellithid rim and a stem supported by a reticulate network of prismatic elements, that also form one or more rings of pores.

*Remarks.* - In the optical microscope studies this group is similar to forms of *Ethmorhabdus* NOEL, but the structure as determined by the electron micrographs is completely different. NOEL (1973, p. 112) has described a Lias form, *Ethmorhabdus crucifer*, which also appears to have the compound rim, but which possesses a cruciform central process. The suprageneric classification is provisional.

### Anfractus harrisonii sp.n.

Pl. 1, Fig. 1-4

Diagnosis. - A species of Anfractus with two rings of pores.

*Description.* – The rim consists of two rings of small plates, with a zig-zag suture between them. The central area consists of a reticulate network of small tabular elements, which form two rings of pores: 4–8 in the inner ring, and 8–16 in the outer. The stem is also made up of small tabular elements.

*Differentiation.* - This species differs from forms of *Ethmorhabdus* NOËL in the optical microscope examination only by its smaller size and more irregular arrangement of the central axial platelets; in the electron microscope studies, however, the structure of this species is completely different.

*Remarks. - Ahmuellerella ? retiformis* REINHARDT (1965, p. 39, Pl. 3, Fig. 2) is similar to this species, but is poorly preserved. The position of the two sets of pores seen in his holotype suggest a third set may be present. If so, this species is differentiated from the two established in the present paper.

Holotype: SEM 72/3639 (Pl. 1, Fig. 1).

Dimensions:  $1.9 \times 1.2 \mu$ .

Type locality: Gamlingay Borehole, Cambridgeshire.

Type level: Depth of 70 feet (21.64 m), Upper Oxford Clay.

Other material. - SEM 72/: 3647, 3683, 3697, 3725, from various levels in the Gamlingay Borehole and 72/3828 from the Haddenham Borehole at 230 feet (70.10 m).

## Anfractus variabilis sp.n.

## Pl. 1, Fig. 6

Diagnosis. - A species of Anfractus with a single ring of 8-10 large pores in the central complex.

Description. - Elliptical coccoliths with an eiffellithid rim which consists of two rings of small plates with a zig-zag suture between them. The central area consists of a reticulate network of small tabular elements which also form a very broad shallow open stem. There is one ring of 8-10 large pores within the central area.

Differentiation. - This species differs from A. harrisonii sp.n. in the smaller number of larger pores arranged in one ring.

Holotype: SEM 73/4949 (Pl. 1, Fig. 6). Dimensions:  $1.8 \times 1.2 \mu$ . Type locality: Gamlingay Borehole, Cambridgeshire. Type level: Depth of 140 feet (42.67 m), Middle Oxford Clay.

## Genus Chiastozygus GARTNER 1968

Type species: by original designation; Zygodiscus? amphipons BRAMLETTE & MARTINI 1964; Upper Cretaceous (Maastrichtian), USA.

*Remarks.* – BLACK's annotated manuscript notes (1975, p. 117) suggested that Cretaceous forms with a cross asymmetrically disposed in relation to the axes of the ellipse should be referred to a new genus. However, species of *Eiffellithus* have arms of the central cross disposed at any angle to axis of the ellipse, and so the variation is considered to be of specific value only.

ROOD, HAY & BARNARD (1973, p. 370) have described a species *Chiastozygus* primitus (PRINS) ex ROOD, HAY & BARNARD from the Lower Jurassic of Dorset. The bars of this small species form an X-shaped central structure. The next published occurrence of the genus is from the Lower Cretaceous (Upper Barremian; THIER-STEIN 1971, p. 471).

Thin oval rings of about  $4-8 \mu$  in length have been found in the optical scanning of strew slides of many of the samples from all three boreholes and in other material from the *athleta* to *tenuiserratum* zones. Occasionally small crystals project from the inner wall of the ring into the central area, but do not coalesce to form any recognizable central structure. Exceptionally well-preserved material from the *lamberti* Zone of the Millbrook section near Ampthill has shown that some of these rings may possess an X-shaped bar with a short central spine. The structure, when present, may or may not be aligned with the axes of the ellipse of the rim. If it is then the forms are referred to the genus *Staurorhabdus* NOEL. If the structure is asymmetrical to the axes then the forms are referred to the genus *Chiastozygus* GARTNER, unless BLACK's proposal (1975, p. 117) for a new genus for such forms is accepted.

> *Chiastozygus asymmetricus* sp. n. Pl. 10, Fig. 4, 5

Diagnosis. - A species of Chiastozygus with slightly offset X-shaped central structure.

*Description.* – Elliptical coccoliths with an eiffellithid rim. The central area consists of an X-shaped structure of paired crystallites which meet in the centre to form a short spine. The bars are not parallel to the axes of the ellipse.

Differentiation. - This species differs from others assigned to this genus by its asymmetrical X-shaped central structure, and the fragile nature of the bars. Those forms with the cruciform structure alligned with the principle axes of the ring are referred to the genus *Staurorhabdus* NOEL. Other forms with a similar rim, but with a basal platform central complex of platelets are referred to the new genus *Millbrookia*.

*Holotype:* Number MPK 1173, lodged in the IGSMPK collection of types (Pl. 10, Fig. 4).

*Type locality:* Millbrook, near Ampthill, Bedfordshire. Sample SAB175 (IGS sample register).

Type level: Middle Oxford Clay, lamberti Zone. Dimensions:  $6 \times 5 \mu$ .

Other material. - Forms with a complete central cruciform structure have been seen in the optical examination of the strew slides from several levels in the Middle

and Upper Oxford Clay of the Gamlingay Borehole. Forms which may be referred to this species, but with the central structure only partially developed have been found in many samples from the three boreholes, and these samples range from the Middle Oxford Clay to the Ampthill Clay (*athleta* to *tenuiserratum* zones). Such forms have also been found in other samples from the English Oxford Clay.

## Genus Neococcolithes SUJKOWSKI 1931

Type species: by monotypy; *Neococcolithes lososnensis* SUJKOWSKI 1931; Upper Cretaceous, Poland.

Remarks. - The present concept of the genus has been established by BLACK (1967, p. 142). PERCH-NIELSEN (1968, p. 21) rejected this, but after a detailed study of the species (1971, p. 47) she has accepted his synonymy. NoëL stated (1970, p. 24), that Zygolithus KAMPTNER emend. NoëL should stand with Z. erectus DEFLANDRE as the type species, even though Z. dubius DEFLANDRE, the species first fixed as the type-species, is transferred to Neococcolithes SUJKOWSKI. This is not valid under the ICBN rules, and so Zygolithus KAMPTNER remains a synonym of Neococcolithes.

K. Perch-Nielsen (pers. commun.) does not accept that there are any Jurassic forms belonging to this genus, as she considers it to have evolved in the Paleocene/Eocene.

#### *Neococcolithes dubius* (DEFLANDRE 1952)

Pl. 2, Fig. 5, 6

1952 Neococcolithes (?) sec.: DEFLANDRE, Fig. 362 F-G.
1954 Zygolithus dubius: DEFLANDRE in DEFLANDRE & FERT, p. 149, Fig. 43, 44, 68.
1957 Zygolithus dubius: GORKA, p. 241, Pl. i, Fig. 6.
1964 Chiphragmalithus dubius: SULLIVAN, p. 179, Pl. i, Fig. 2.
1967 Neococcolithes dubius: BLACK, p. 143.

Remarks. - BLACK (1967) and PERCH-NIELSEN (1971) transferred Zygolithus dubius DEFLANDRE to the genus Neococcolithes SUJKOWSKI, and this is accepted here. The specimens identified with the aid of the optical microscope have a central area containing an open space bridged by four diagonal elements; the scanning electron micrographs confirm this (e.g. SEM 72/3646). The arrangement of the central bars closely corresponds with the figures of PERCH-NIELSEN (1971); certainly they are not broken Actinozygus geometricus (GORKA), since the phase-contrast optical images of these two species are different. Specimen number SEM 72/3684 is of interest in that the central area is also partially covered by a reticulate meshwork of small plates of the type also seen in the species of Anfractus gen.n.

K. Perch-Nielsen (pers. communic.) suggests that the figured forms may be holococcoliths; she does not accept that these Jurassic specimens belong to *Neococcolithes*. The present writer does not consider the holococcolith/heterococcolith question to be relevant to the taxonomic assignment of the forms. These coccoliths possess an axial structure analogous to the Tertiary specimens, although they are smaller. Using phase-contrast light microscopy, the thick axial bars are clearly seen to be offset at their centre. They are unlike anything else seen in the Jurassic.

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Certainly the bars are completely dissimilar to any of the Jurassic actinozygids or stradnerlithids.

*N. dubius* has been recovered from the Upper Oxfordian of the Haddenham Borehole; from the Upper Oxford Clay and the Elsworth Rock Series of the Gamlingay Borehole; and from the Upper Oxford Clay of the Ampthill Borehole. It has also been found in the Middle and Upper Oxford Clay of the Millbrook section, and in material from several surface exposures of Upper Oxfordian age (MEDD 1971).

## Subfamily Zygolithoideae subfam.n.

*Diagnosis.* – Eiffellithaceae with an outer rim comprising crystallites at a variable angle of stacking, ranging from vertical to almost horizontal in inclination, with resulting variably developed imbrication.

*Remarks.* - A widely differing angle of the coccolith plates in their outer rim in forms referred to *Zeugrhabdotus* REINHARDT together with a variable crystallite thickness, gives a superficially different overall shape to the coccoliths in this subfamily. However, this variation can be seen to be continuous in many samples and is accepted as being of intraspecific difference only. The coccolith width / pore width ratio is of specific difference, as is the number of plates in the outer rim.

The variable angle of the coccolith plates in the rim is also seen in the material referred to Actinozygus crux (DEFLANDRE & FERT), but to a lesser extent than in Zeugrhabdotus erectus (DEFLANDRE) specimens from the same beds. Actinozygus geometricus (GORKA) has been seen only with nearly vertically stacked crystallites. Actinozygus GARTNER is here considered to form a morphological link between the Ahmuellerelloideae and the Stradnerlitheae (see below). The fact that Actinozygus crux has a cruciform central crystal arrangement does not contravene GARTNER's generic diagnosis, and the thin walled specimens of Zeugrhabdotus erectus, Actinozy-gus crux and A. geometricus are identical in most respects except for the structure of their central areas, together with the possible increase in imbrication in some Z. erectus specimens.

The angle of the rim plates is fairly constant in *Mitrolithus, Parhabdolithus* and *Tubirhabdus*, but the central axial structure is very variable and provides the basis for their generic separation.

### Genus Actinozygus GARTNER 1968

Type species: by original designation; *Tremalithus regularis* GORKA 1957; Upper Cretaceous (Maastrichtian), Poland.

*Remarks.* - The validity of the genus as summarized by ROOD, HAY & BARNARD (1971, p. 254) is accepted here. There is little to be gained in discarding this distinctive genus, as proposed by LOEBLICH & TAPPAN (1969, p. 569).

Although *T. regularis* GORKA is figured very diagrammatically, examination of equivalent material indicates fairly clearly what she meant by this species. There is little to separate this, and other Cretaceous forms that possess six axial bars, from *A. geometricus* (GORKA) apart from the thickening of the rim elements and in being

twice the size of comparable Jurassic forms. These latter forms, therefore, are retained in the genus Actinozygus.

The relationship between forms assigned to *Actinozygus* and to *Corollithion* STRADNER 1961 is still not understood. However, the type species, *C. exiguum* STRADNER (1961, p. 83) has an angular rim with shallowly inclined elements, and so the genus is retained for these coccoliths.

### Actinozygus geometricus (GORKA 1957)

## Pl. 3, Fig. 1-3

- 1957 Discolithus geometricus GORKA, p. 259, 279, Pl. iv, Fig. 8.
- 1966 Discolithus geometricus: LOEBLICH & TAPPAN, p. 133.
- ? 1967 Corollithion derosus: LYUL'EVA, p. 97, Pl. iv, Fig. 42.

1968 Zygolithus geometricus: STRADNER, ADAMIKER & MARESCH, p. 40, Pl. xxxvi, Fig. 1; Pl. xxxvii, Fig. 1-4.

- 1969 Corollithion ellipticum: BUKRY, p. 40, Pl. xviii, Fig. 10-11.
- 1971 Zygolithus cf. geometricus: MEDD, p. 825, Pl. 1, Fig. 6; Pl. iii, Fig. 3-4.
- 1971 Actinozygus geometricus: ROOD, HAY & BARNARD, p. 254, Pl. 1, Fig. 6.
- 1971 Corollithion ellipticum: THIERSTEIN, p. 480, Pl. vii, Fig. 6.
- 1971 Corollithion geometricum: MANIVIT, p. 109, Pl. vi, Fig. 4-5.
- 1972 Actinozygus geometricus: ROOD & BARNARD, p. 333, Pl. ii, Fig. 8.
- 1973 Actinozygus geometricus: NoëL, p. 102, Pl. iii, Fig. 4.
- 1973 Corollithion ellipticum: BLACK, p. 93, Pl. xxx, Fig. 1.

*Remarks.* - This small but distinctive species has occasionally been recovered from material of the Oxford Clay, the Ampthill Clay and the Lower Kimmeridge Clay in the two boreholes.

An examination of unreplicated specimens with the transmission electron microscope (Pl. 3, Fig. 1) reveals the central perforation, and there is a complete gradation in the angles between the six rays comprising the axial structure; therefore there is no justification in the continued use of *Corollithion ellipticum* BUKRY (BLACK 1973, p. 94), which was defined on the basis of these angles.

### Actinozygus crux (DEFLANDRE & FERT 1952)

## Pl. 2, Fig. 3; Pl. 9, Fig. 11

1952	Discolithus crux Deflandre & Fert, p. 2101, Textfig. 8.
1954	Discolithus crux: DEFLANDRE in DEFLANDRE & FERT, p. 143, Pl. xiv, Fig. 4.
non 1961	Zygolithus crux: Bramlette & Sullivan, p. 149, Pl. vi, Fig. 8-10.
non 1962	Cyathosphaera crux: HAY & TOWE, p. 507, Pl. ii, Fig. 1.
? 1963	Zygolithus crux: STRADNER, p. 9, Pl. iv, Fig. 6-7.
1963	Staurolithites crux: CARATINI, p. 25.
? 1964	Zygolithus cf. Zygolithus crux: BRAMLETTE & MARTINI, p. 304, Pl. iv, Fig. 19-20.
? 1965	Zygolithus crux: MANIVIT, p. 191, Pl. ii, Fig. 13.
? 1967	Zygolithus crux: MOSHKOVITZ, p. 152, Pl. i, Fig. 1.
non 1967	Zygolithus crux: Reinhardt & Gorka, p. 250, Pl. xxxii, Fig. 13; Pl. xxxiii, Fig. 3.
1968	Zygolithus crux: STRADNER, ADAMIKER & MARESCH, p. 36, Pl. xxviii, Fig. 1 (non Pl. xxix,
	Fig. 1, nec Pl. xxx, Fig. 1-7).

1971 Zygolithus crux: PERCH-NIELSEN, p. 21.

*Remarks.* - This small but distinctive species has been recovered from most of samples examined. There is considerable doubt if all of the forms assigned by

previous authors to this species belong here or are even assignable to the genus *Actinozygus*. STRADNER (1963), STRADNER, ADAMIKER & MARESCH (1968), BRAM-LETTE & MARTINI (1964) and MOSHKOVITZ (1967) all illustrate simple zygoliths, but their length is in the range 4-7  $\mu$ , which is larger than the Jurassic specimens seen (1.5-3  $\mu$ ).

Forms illustrated by BRAMLETTE & SULLIVAN (1961), HAY & TOWE (1962), REINHARDT & GORKA (1967) and STRADNER, ADAMIKER & MARESCH (1968, Pl. xxix and xxx) have a complex axial structure together with an inner ring of tabular elements on the distal side of the rim, which is characteristic of *Vekshinella* LOEB-LICH & TAPPAN, and these forms are here transferred to that genus.

### Actinozygus fragilis ROOD & BARNARD 1972

Pl. 3, Fig. 6

## 1972 Actinozygus fragilis ROOD & BARNARD, p. 334, Pl. ii, Fig. 9.

*Remarks.* - This very small species has so far been seen only four times: two electron micrographs are of specimens from the *mariae* Zone from the Ampthill Borehole at 150 feet (45.72 m) and from the Gamlingay Borehole at 110 feet (33.53 m). This is at the same level as the type material. The third and fourth specimens extend the range of the species. The third specimen is from the Gamlingay Borehole at 68 feet (20.73 m) and belongs to the *bukowskii* Subzone of the *cordatum* Zone; the fourth specimen is from the *lamberti* Zone of the Millbrook section, near Ampthill, the type locality. The SEM photograph numbers are: 74/9142, 75/11345, 76/12392 and 76/12528 respectively.

## Genus Mitrolithus DEFLANDRE 1954

Type species: by original designation; *Mitrolithus elegans* DEFLANDRE in DEFLANDRE & FERT 1954; Upper Jurassic (Oxfordian), France.

*Remarks.* – Forms referred to this genus are distinguished by the very characteristic globose spine; also the birefringence pattern of the calcite plates is usually distinct, when the specimen is examined under  $\times$ -nicols in an optical microscope.

## Mitrolithus elegans DEFLANDRE 1954

*Remarks.* - Forms with the birefringence pattern of the calcite plates characteristic of this species have been found in several samples from the Oxford Clay of these boreholes. There is, however, a gradation in the birefringence pattern between this species and forms referred to *Tubirhabdus patulus* PRINS. All of the material seen has had the spine broken off and so the taxonomic position has been uncertain. Recently, the lateral view of a specimen has been seen in the sample from 110 feet (33.53 m) in the Gamlingay Borehole, which possesses the inflated spine and so these specimens are assigned to this species.

Although the type material of DEFLANDRE is from the Oxfordian of France, all other specimens of this species, with the exception of the material seen in this study, have been restricted to the Lias. PRINS (1969, p. 555) records the species from the Sinemurian and Pliensbachian stages and the English Lias material so far found is restricted to the Pliensbachian. There is therefore the possibility that the Oxfordian material has been reworked from the Lias, particularly as most of the specimens seen in the present study have been broken.

## Genus Parhabdolithus DEFLANDRE 1952

Type species: by original designation; *Parhabdolithus liasicus* DEFLANDRE 1952; Jurassic (Lias), France.

*Remarks.* - The summary of characters given by NOËL (1970, p. 887) as amended by BLACK (1972, p. 29) defines the genus. The two Upper Jurassic species continuing from the Lias are not common but do conform to this diagnosis. A new species is also proposed below.

## Parhabdolithus liasicus DEFLANDRE 1952

1952 Parhabdolithus liasicus DEFLANDRE, p. 466, Textfig. 362 J-M.

*Remarks.* - In addition to the example recovered by MEDD (1971), this species has been found in *mariae* Zone beds of the Gamlingay and Haddenham boreholes.

#### Parhabdolithus marthae DEFLANDRE 1954

### Pl. 1, Fig. 10

1954 Parhabdolithus marthae DEFLANDRE in DEFLANDRE & FERT, p. 163, Pl. xv, Fig. 22-23.

Stratigraphical Distribution. - The base of the Ampthill Clay to the base of the Kimmeridge Clay in the samples studied. Elsewhere the species ranges down into the Lias.

Parhabdolithus pseudobelgicus sp.n.

Pl. 9, Fig. 6-8

*Diagnosis.* - A species of *Parhabdolithus* with a stem having node-like rhombs ornamenting the surface.

*Description.* - The long parallel-sided stem has irregularly distributed node-like rhombs on the surface.

*Remarks.* - The species differs from all others in the ornamentation of the stem. When isolated from the disc, the stem has a superficial resemblance to *Microrhabdulus belgicus* HAY & TOWE 1963, to which these forms have previously been assigned (MEDD 1971, p. 824). Although rare in occurrence, the species is persistent in the *mariae* and *cordatum* Zone samples of these boreholes. If only secondary growth is invoked, then such overgrowth should be seen on the stems of other species in the samples; this is not the case.

Holotype: SEM 76/12274, 76/12277 (an oblique view) recovered from sample SAC 197 (I.G.S. sample register number) (Pl. 9, Fig. 6). Type locality: Gamlingay Borehole, Cambridgeshire. *Type level:* Depth of 64 feet (19.51 m); Upper Oxford Clay, *cordatum* Zone. *Type dimensions:*  $4.8 \times 2.4 \mu$ ; 14  $\mu$  stem.

Stratigraphical distribution. - Upper Oxford Clay, mariae and cordatum zones.

## Genus Tubirhabdus ROOD, HAY & BARNARD 1973 ex PRINS 1969

Type species (by subsequent designation): Tubirhabdus patulus ROOD, HAY & BARNARD 1973 ex PRINS 1969.

*Remarks.* - The genus was validated by ROOD, HAY & BARNARD (1973, p. 373) and placed in the Actinozygaceae ROOD, HAY & BARNARD. This is accepted in principle, but their family is emended to the Zygolithoideae new subfamily.

## Tubirhabdus patulus ROOD, HAY & BARNARD 1973 ex PRINS 1969 Pl. 9, Fig. 9.

1969 Tubirhabdus patulus PRINS, p. 549, Pl. i, Fig. 10 (invalid).
1973 Tubirhabdus patulus: ROOD, HAY & BARNARD, p. 373, Pl. ii, Fig. 3.

*Remarks.* - A specimen recovered from the Haddenham Borehole at 240 feet (73.15 m) agrees with the published descriptions of the species. It may, however, be a reworked contaminant, although the excellent preservation suggests it to be indigenous.

## Genus Zeugrhabdotus REINHARDT 1965

Type species: by original designation; Zygolithus erectus DEFLANDRE 1954; Jurassic (Oxfordian), France.

*Remarks.* – With the removal of *Zygolithus dubius* DEFLANDRE, the type species of *Zygolithus* KAMPTNER ex MATTHES 1956, to the genus *Neococcolithes* SUJKOWSKI 1931, there remain a number of species, formerly assigned to *Zygolithus*, which do not possess the diagnostic features of *Neococcolithes*, and which must be transferred to other genera. *Zeugrhabdotus* was established by REINHARDT (1965, p. 37) for forms with a double cycle of wall elements and a bar across the minor axis of the central area, surmounted by a central process, and *Zygolithus erectus* DEFLANDRE was designated as the type-species.

This has been accepted by most modern workers. The genus Zygodiscus BRAM-LETTE & SULLIVAN (1961, p. 148) is considered to be distinct from Zeugrhabdotus, in that it possesses a more complex axial structure. BLACK (1972, p. 21, footnote) has established a new genus Zygolithites for very similar forms found in the Cretaceous.

## Zeugrhabdotus bussoni (NOËL 1956)

## Pl. 2, Fig. 7, 8

- 1956 Zygolithus bussoni NOEL, p. 321, Pl. ii, Fig. 13-14.
- 1957 Zygolithus fibulus: GORKA, p. 242, 267, Pl. i, Fig. 4.
- 1959 Zygolithus repali: MANIVIT, p. 341, Pl. i, Fig. 2.
- 1961 Zygolithus sigmoides: BRAMLETTE & SULLIVAN, p. 149, Pl. iv, Fig. 11a-e.

1965a Zygolithus bussoni: NoëL, p. 3, Fig. 1a-c.

1966 Zygolithus ponticulus: MARESCH, p. 383, Pl. iii, Fig. 1.

*Remarks.* – This species has been recovered from most of the samples examined. There is nothing to add to the description of NOEL (1965b, p. 59) and the amendments given by MEDD (1971, p. 825).

Zeugrhabdotus erectus (DEFLANDRE 1954)

Pl. 2, Fig. 7, 8; Pl. 9, Fig. 10; Pl. 10, Fig. 1-3

1954 Zygolithus erectus DEFLANDRE in DEFLANDRE & FERT, p. 150, Pl. xv, Fig. 14-17; Textfig. 60, 61.

1971 Zeugrhabdotus noëlae: ROOD, HAY & BARNARD, p. 251, Pl. i, Fig. 4.

*Remarks.* - The type figures and the descriptions of Zygolithus erectus DEFLAN-DRE and Zeugrhabdotus noëlae ROOD, HAY & BARNARD have been re-examined, together with the descriptions mentioned in the synonymy. The author concludes that Z. noëlae ROOD, HAY & BARNARD is conspecific with Z. erectus DEFLANDRE. There is a complete gradation in size, number of elements constituting the shields and in the thickness of the shield. This is particularly well shown in the sample 50 M (MEDD 1971, p. 832), although the extreme members of the plexus Zeugrhabdotus erectus/bussoni possess considerable differences when viewed together, as in EM 1650 from locality 219 G (MEDD 1971, p. 837).

Z. erectus (DEFLANDRE) occurs in most of the samples examined, and usually comprises a significant element in the nannoflora.

## Zeugrhabdotus salillum (NOËL 1965)

Pl. 9, Fig. 12

- 1965 Discolithus salillum NOEL, p. 4, Textfig. 5-6.
- 1965b Discolithus salillum: NOEL, p. 72, Pl. i, Fig. 8-12.
- 1966 Discolithus salillum: LOEBLICH & TAPPAN, p. 137.
- 1971 Discolithus salillum: MEDD, p. 826.
- 1971 "Discolithus" salillum: WORSLEY, p. 1309.
- 1971 Zeugrhabdotus salillum: ROOD, HAY & BARNARD, p. 253, Pl. i, Fig. 5.

*Remarks.* - The species was transferred to the genus Zeugrhabdotus REINHARDT by ROOD, HAY & BARNARD, as the genus *Discolithus* HUXLEY, as defined above, is not available for such a taxon. The species has been recovered from the Oxford Clay and the Ampthill Clay samples of the boreholes.

## Subfamily Stephanolithioideae VEKSHINA 1959, emended here

Amended diagnosis. – Quoted from BLACK (1973, p. 92): "Hollow coccoliths with a cylindrical or polygonal wall, consisting of elements, which are not markedly imbricate and within the wall an open framework of rods arranged radially or otherwise."

Remarks. - The above diagnosis was given by BLACK for his family Stephanolithiaceae BLACK 1968, which is here downgraded to subfamily status.

## Tribe Stradnerlitheae trib.n.

*Diagnosis.* - Stephanolithioideae whose outer rim does not possess outwardly projecting crystallites; and whose central structure is made up of four or more bars, which are bilaterally asymmetrical about the major axis of the coccolith.

*Remarks.* - This new tribe is erected in place of the Diadozygeae trib.n., which would have replaced the Diadozygoideae ROOD, HAY & BARNARD (1971, p. 255), as the type genus *Diadozygus* ROOD, HAY & BARNARD (1971, p. 255) is a junior synonym of *Stradnerlithus* BLACK (1971, p. 414).

## Genus Stradnerlithus BLACK 1971

Type species: by original designation; *Stradnerlithus comptus* BLACK 1971; Upper Jurassic (Kimmeridgian), England.

*Emended diagnosis:* - Elliptical to rhomboidal coccoliths with a marginal wall on the distal side consisting of parallel upright elements, which are not markedly imbricate. The proximal side has either a solid bar or bar-like structure made up of small tabular elements, which runs along the maximum length of the coccolith and which may bifurcate at the ends, and lateral branches which join this bar to the outer wall. A slender spine may arise from the centre of the distal side.

Remarks. - Stradnerlithus was erected by BLACK in July 1971; Diadozygus was erected by ROOD, HAY & BARNARD in August 1971 for the same species group and so the latter taxon is a junior synonym, notwithstanding their subsequent remarks (ROOD, HAY & BARNARD 1973, p. 371). The author agrees with BLACK in recognizing the wall shape to be of specific importance only, and so *Truncatoscaphus* ROOD, HAY & BARNARD (1971, p. 257) is also a junior synonym.

## Stradnerlithus asymmetricus (ROOD, HAY & BARNARD 1971)

Pl. 3, Fig. 5

### 1971 Diadozygus asymmetricus ROOD, HAY & BARNARD, p. 255, Pl. i, Fig. 7.

Remarks. - The author agrees with ROOD, HAY & BARNARD in that the shape of this form warrants its separation from Stradnerlithus rhombicus (STRADNER & ADA-MIKER 1966) (pro Dictyolithus emendatus LYUL'EVA 1967, p. 96, Pl. iv, Fig. 41). The specimens so far recovered from the Gamlingay Borehole at a depth of 68 feet (20.73 m) are smaller than the holotype (SEM 72/3668 being  $2.0 \times 1.1 \mu$ ). Other specimens have been found in the three boreholes at many depths.

## Stradnerlithus rhombicus (STRADNER & ADAMIKER 1966)

Pl. 3, Fig. 10

1966	Zygolithus rhombicus Stradner & Adamiker, p. 339, Pl. ii, Fig. 1	ί.
1967	Dictyolithus emendatus: LYUL'EVA, p. 96, Pl. iv, Fig. 41.	

- 1969 *Corollithion rhombicum:* BUKRY, p. 41, Pl. xix, Fig. 2-4.
- 1972 Diadorhombus rhombiscus [sic]: ROOD & BARNARD, p. 338.
- 1972 Diadorhombus speetonensis: ROOD & BARNARD, Pl. ii, Fig. 7.
- 1973 Stradnerlithus rhombicus: NOËL, p. 106, Pl. iii, Fig. 6.

*Remarks.* – This characteristic Lower Cretaceous species has been found in the Upper Oxford Clay of the Gamlingay Borehole at 68 feet (20.73 m), SEM 76/12291, 76/12394.

## Stradnerlithus rotatus (ROOD, HAY & BARNARD 1971)

Pl. 3, Fig. 11, 12

1971 Diadozygus rotatus ROOD, HAY & BARNARD, p. 256, Pl. i, Fig. 9; Pl. ii, Fig. 1.

*Remarks.* - This rare species has been recorded from the Upper Oxford Clay of the Gamlingay Borehole at 68 feet (20.73 m), and in the Millbrook section.

## Stradnerlithus bifurcatus NOËL 1973

Pl. 3, Fig. 4

1973 Stradnerlithus bifurcatus NOËL, p. 105, Pl. ii, Fig. 7-8.

*Remarks.* – This form has been recovered from the Ampthill Clay *tenuiserratum* Zone of the Ampthill Borehole at a depth of 80 feet (24.38 m). The specimens found are smaller than the Kimmeridgian holotype, being  $1.6 \times 1.0 \mu$ .

## Stradnerlithus sattinii sp.n.

### Pl. 4, Fig. 4

*Diagnosis.* - Elliptical species of *Stradnerlithus* with twelve bars, arranged symmetrically from the long central axis.

*Description.* – The twelve bars are arranged so that the ellipse is bilaterally symmetrical. The bars fuse at the centre to a long elliptical boss.

*Remarks.* - The species differs from all others in having twelve bars. It has been seen so far only with optical equipment.

Holotype: Number MPK 1175. Lodged in the MPK Collection of types at the Institute of Geological Sciences, Leeds, England (Pl. 4, Fig. 4).

Type locality: Ampthill Borehole, Bedfordshire.

Type level: Depth of 60 feet (18.29 m); Lower Ampthill Clay, tenuiserratum Zone. Type dimensions: About  $2.0 \times 1.5 \mu$ .

Stratigraphical distribution. - This species has also been found in the Ampthill Borehole at 80 feet (24.38 m), 90 feet (27.43 m) and 150 feet (45.72 m) and so ranges down into the Upper Oxford Clay, *mariae* Zone.

## Stradnerlithus escovillensis (ROOD & BARNARD 1972)

1972 Diadozygus escovillensis ROOD & BARNARD, p. 335, Pl. ii, Fig. 4.

*Remarks.* - This form has been recovered from the Ampthill Borehole at a depth of 150 feet (45.71 m), and so extends the range into the Upper Oxford Clay, *praecordatum* Subzone, *mariae* Zone, another specimen has been found in the Gamlingay Borehole at a depth of 124 feet (37.80 m) also from the Upper Oxford Clay, *mariae* Zone.

#### Upper Jurassic coccoliths (Cambridgeshire)

### Stradnerlithus comptus BLACK 1971

### Pl. 3, Fig. 7, 8

- 1971 Stradnerlithus comptus BLACK, p. 415, Pl. xxxi, Fig. 10.
- 1971 Diadozygus dorsetense: ROOD, HAY & BARNARD, p. 257, Pl. ii, Fig. 2-3.

1972 Diadozygus dorsetense: ROOD & BARNARD, p. 336, Pl. ii, Fig. 5.

1973 Stradnerlithus comptus: NOEL, p. 105, Pl. iii, Fig. 5.

*Remarks.* - This form has been recovered from the Upper Oxford Clay samples in the three boreholes. It has also been recorded from the Kimmeridge Clay (by BLACK) and the Upper Oxford Clay (by ROOD, HAY & BARNARD) of Dorset.

The specimens recovered from the boreholes are smaller than the previously described material, being 1.7 to 2.5  $\mu$  in length.

### Stradnerlithus octoradiatus sp.n.

Pl. 4, Fig. 2, 3

*Diagnosis.* - A species of *Stradnerlithus* with eight bars in the axial structure, four of which dissect the longer sides of the rim at  $\frac{1}{3}$  of the distance from its corners.

*Description.* – The eight bars are arranged so that the oblong-shaped coccolith is bilaterally symmetrical. The bars fuse at the centre in an elliptical boss. There are 28 to 30 tabular elements to the rim.

*Remarks.* - The species differs from the other eight rayed members of this eiffellithid group, *Stradnerlithus emendatus* (LYUL'EVA) and *S. asymmetricus* (ROOD, HAY & BARNARD), in having an oblong, and not a rhomboidal or elliptical, shaped rim.

*Holotype:* SEM 72/3570 recovered from sample SAC 22 (I.G.S. sample register number) (Pl. 4, Fig. 2).

Type locality: Haddenham Borehole, Cambridgeshire.

*Type level:* Depth of 80 feet (24.38 m); Lower Kimmeridge Clay, *mutabilis* Zone. *Type dimensions:*  $1.9 \times 1.2 \mu$ .

Stratigraphical distribution. - Upper Oxford Clay to the Lower Kimmeridge Clay.

#### Stradnerlithus pauciramosus BLACK 1973

### Pl. 3, Fig. 9

non 1966	Zygolithus delftensis:	STRADNER &	Adamiker,	p. 338,	Pl. ii, Fig. 3.	
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non 1968 Zygolithus delftensis: STRADNER, ADAMIKER & MARESCH, p. 41, Pl. xxxix, Fig. 1-5.

- 1971 Stradnerlithus delftensis: BLACK, p. 415, Pl. xxxi, Fig. 11.
- 1971 Truncatoscaphus delftensis: ROOD, HAY & BARNARD, p. 257, Pl. ii, Fig. 4-5.

1972 Truncatoscaphus delftensis: ROOD & BARNARD, p. 338, Textfig. 2.

non 1973 Truncatoscaphus delftensis: NoEL, p. 108, Pl. iv, Fig. 4-6.

1973 Stradnerlithus pauciramosus BLACK, p. 98, Textfig. 47.

Remarks. - This very small form has been recovered from the Upper Oxford Clay and from the base of the Ampthill Clay in the Ampthill, Haddenham and Gamlingay boreholes. The writer agrees with BLACK (1973, p. 98) in separating this species from *Stradnerlithus delfensis* (STRADNER & ADAMIKER) by its fewer elements

in the centre. NOËL, however, has found specimens from the Upper Kimmeridgian with the more numerous elements which must be referred to *S. delftensis*.

## Genus Diadorhombus WORSLEY 1971

Type species: by monotypy; *Diadorhombus rectus* WORSLEY 1971; Upper Jurassic / Lower Cretaceous; Joides Borehole 5A, Leg 1, Caribbean Sea.

Remarks. - WORSLEY (1971, p. 1307) established this genus for forms with a "rhomboid to square rim and an open centre spanned by cross bars aligned with the sides of the rim". The species Zygolithus scutulatus MEDD is assigned below to this genus. There is some similarity in the otuline of Stradnerlithus rotatus (ROOD, HAY & BARNARD) comb.nov. (ex Diadozygus rotatus ROOD, HAY & BARNARD 1971, p. 256) with the species of Diadorhombus, although the axial bars of S. rotatus are more complex and show a greater affinity with Stradnerlithus BLACK. Stradnerlithus octoradiatus sp.n. is another development in the morphological series, with eight axial bars and a quadrangular outline; the extreme form of the series so far seen is Stradnerlithus delftensis (STRADNER, ADAMIKER & MARESCH) with its thicker rim and ten axial bars.

### Diadorhombus scutulatus (MEDD 1971)

Pl. 4, Fig. 1

1971 Zygolithus scutulatus MEDD, p. 826, Pl. iii, Fig. 1-2.

1971 Diadorhombus minutus: ROOD, HAY & BARNARD, p. 258, Pl. ii, Fig. 6.

1972 Diadorhombus minutus: ROOD & BARNARD, p. 337, Pl. ii, Fig. 10.

*Remarks.* – This species differs from *Diadorhombus rectus* WORSLEY in being much smaller, 2.1–1.5  $\mu$  instead of 6  $\mu$  in length, and in being more rhombic in shape. *Diadorhombus minutus* ROOD, HAY & BARNARD is a junior synonym.

The species has been recovered from various levels in the Haddenham Borehole and at 70 feet (21.34 m) in depth in the Gamlingay Borehole. The range is now considered to be from the Upper Oxford Clay to the Lower Kimmeridge Clay.

## Tribe Stephanolithieae trib.n.

Diagnosis. - Stephanolithioideae whose rim possesses outwardly projecting crystallites.

### Genus Stephanolithion DEFLANDRE 1939

Type species: by original designation; *Stephanolithion bigoti* DEFLANDRE 1939; Jurassic (Oxfordian), France.

### Stephanolithion bigoti DEFLANDRE 1939 bigoti ssp. n.

### Pl. 4, Fig. 5

1939 Stephanolithion bigoti DEFLANDRE, p. 1332, Textfig. 1-14 (pars).

*Remarks.* - DEFLANDRE (1939, p. 1332) mentioned that the average size with the spines was  $3.0-4.5 \times 2.6-4.0 \ \mu$ . The largest specimens to be seen were  $5.0-9.5 \ \mu$ ,

"cette dernière n'étant atteinte, dans ce qui j'ai vu, que très exceptionellement". The measurements given by NOËL (1965b, p. 82) fall into separate groups, those based on electron micrographs, giving a maximum measurement of  $4.3 \times 3.5 \mu$ , and all based on material from the "Oxfordien supérieur de Niort", and those based on the optical microscope investigation with a maximum measurement of  $10.0 \times 9.0 \mu$ , based on material from the "Oxfordien, Weymouth".

The author concludes that, from a detailed re-examination of the Oxfordian material, this species has two distinct size ranges and that very few specimens have an overall length of between  $4.5-6.0 \mu$ . It is therefore proposed to separate these two types as distinct subspecies, with the smaller size as representative of *Stephanolithion bigoti* DEFLANDRE *bigoti* ssp.n. A new subspecies, described below, represents the larger material.

Stephanolithion bigoti DEFLANDRE bigoti ssp. n. has been recovered in most of the samples examined and ranges from the base of the Lower Oxford Clay to the Lower Kimmeridge Clay. NOËL (1973, p. 109) has recorded the species from the Upper Kimmeridgian of France. This extends the stratigraphical range assigned to the species by ROOD & BARNARD (1972, p. 331).

## Stephanolithion bigoti DEFLANDRE 1939 maximum ssp.n.

Pl. 4, Fig. 5, 6

- 1956 Stephanolithion bigoti: NOEL, p. 317, Pl. ii, Fig. 1-2.
- 1963 Stephanolithion bigoti: STRADNER, p. 13, Pl. iv, Fig. 2.
- 1968 Stephanolithion bigoti: BLACK, p. 808, Pl. ii, Fig. 1.
- 1970 Stephanolithion bigoti: REINHARDT, p. 27, Textfig. 18-19.
- 1971 Stephanolithion bigoti: ROOD, HAY & BARNARD, p. 260, Pl. ii, Fig. 8.
- 1972 Stephanolithion bigoti: ROOD & BARNARD, p. 329, Pl. i, Fig. 5, 11.
- 1973 Stephanolithion bigoti: NoëL, p. 109, Pl. v, Fig. 1-4.
- 1973 Stephanolithion bigoti: BLACK, p. 92, Textfig. 44.

Diagnosis. – A subspecies of Stephanolithion bigoti DEFLANDRE 1939 with overall measurements exceeding  $6.0 \times 3.0 \mu$ .

*Description.* - Coccoliths with a rim comprising two cycles of simple tabular elements and lateral projections extending outwards from the rim. There is an axial structure consisting of four rows of small tabular elements projecting inward from the rim and meeting at a large central boss, which may be developed as a spine.

Differentiation. - This species differs from Stephanolithion bigoti DEFLANDRE bigoti ssp. n. by its large size. It differs from Stephanolithion speciosum DEFLANDRE by its slightly larger length and by its simpler axial structure.

Holotype: SEM 72/3695 (Pl. 4, Fig. 6). Dimensions:  $7.0 \times 6.2 \mu$ . Type locality: Gamlingay Borehole, Cambridgeshire. Type level: Depth of 64 feet (19.51 m), Upper Oxford Clay.

Stratigraphical distribution. - Restricted to the cordatum and the mariae zones of the Oxfordian.

## Stephanolithion speciosum DEFLANDRE (in DEFLANDRE & FERT 1954) speciosum ssp.n.

1954	Stephanolithion speciosum DEFLANDRE in DEFLANDRE & FERT, p. 146, Pl. xv, Fig. 7-8.
1956	Stephanolithion speciosum: NOEL, p. 318, Pl. ii, Fig. 3-4.
1965b	Stephanolithion speciosum: NOEL, p. 107.
1966	Stephanolithion speciosum: LOEBLICH & TAPPAN, p. 166.
1968	Stephanolithion speciosum: LEZAUD, p. 16, Pl. i, Fig. 4.
1968	Stephanolithion speciosum: BLACK, p. 808.
1970	Stephanolithion speciosum: REINHARDT, p. 28, Textfig. 22.
1971	Stephanolithion speciosum: MEDD, p. 827.
1972	Stephanolithion speciosum: ROOD & BARNARD, p. 330, Pl. i, Fig. 1, 7.
1973	Stephanolithion speciosum: ROOD, HAY & BARNARD, p. 376.

Diagnosis. - A subspecies of Stephanolithion speciosum DEFLANDRE in DEFLAN-DRE & FERT 1954 with the characters typical for the species.

Remarks. – This subspecies is retained for those larger Stephanolithion forms with a complex central area and is found in all three boreholes. The author does not accept the suggestion of NoëL (1956, p. 318) that Stephanolithion laffittei NoëL is intermediate between Stephanolithion bigoti DEFLANDRE and S. speciosum. S. laffittei has a more complex rim and central structure, and is considered to belong to Cylindralithus BRAMLETTE & MARTINI. Measurements for S. speciosum given by DEFLANDRE are  $5.8 \times 4.0 \mu$ ; specimens of the subspecies seen by the author agree with this.

ROOD & BARNARD (1972, p. 330) have separated out a smaller form as a new variety *S. speciosum octum*, which possesses longer spines, but giving the same overall measurements as the species. This variety is here upgraded to species rank: *S. octum*.

## Stephanolithion speciosum DEFLANDRE 1954 elongatum ssp.n.

Pl. 4, Fig. 9

Diagnosis. - A subspecies of Stephanolithion speciosum DEFLANDRE in DEFLAN-DRE & FERT 1954 with an overall length/width ratio equal to or greater than 2:1.

*Description.* - Coccoliths with a rim comprising two cycles of simple tabular elements and lateral projections extending outwards from the rim. There is an axial structure consisting of eight rows of small tabular elements projecting inwards from the rim and meeting at a small central boss, which may be developed as a spine.

Differentiation. - This species differs from Stephanolithion speciosum DEFLANDRE speciosum ssp. n. by its very narrow elongate appearance.

*Remarks.* - This species is included in this paper only to validate its use in the proposed Jurassic zonal chart; it has been seen only with optical equipment.

Holotype: Number MPK 1902. Lodged in the MPK collection of types at the Institute of Geological Sciences, Leeds, England (Pl. 4, Fig. 9).

*Dimensions:* About  $4.5 \times 2.2 \mu$ .

Type locality: Horsecombe Vale Borehole no. 15 [NGR ST 7555 6225].

Type level: Depth of 105 feet 3 in (32.00 m); Middle Jurassic, Upper Fullers Earth retrocostatum Zone (Bathonian).

Stratigraphical distribution. - This species is restricted to the *retrocostatum* Zone of the Bathonian and is considered to be the nannofossil zonal equivalent of part of this macrofossil zone.

## Stephanolithion carinatum sp. n. Pl. 4, Fig. 7, 8, 10, 11

*Diagnosis.* - A species of *Stephanolithion* with seven or eight axial bars supporting a central stem.

*Description.* - Coccoliths with a polygonal rim consisting of two cycles of elements with numerous short lateral projections extending outwards from the rim. The central area is occupied by seven or eight bars which support a short open stem.

Differentiation. - This species is distinguished from Stephanolithion bigoti DEFLANDRE bigoti ssp.n. by the more complex central area, and more numerous shorter projections; from S. speciosum DEFLANDRE by the smaller size; from S. bigoti maximum ssp.n. by the smaller size and the more complex central area; and from Stephanolithion hexum ROOD & BARNARD (1972, p. 329) by the greater number of axial bars and by the smaller size.

Holotype: SEM 72/3659 (Pl. 4, Fig. 8). Dimensions:  $3.3 \times 2.5 \mu$ . Type locality: Gamlingay Borehole, Cambridgeshire. Type level: Depth of 68 feet (20.73 m), from the Upper Oxford Clay.

Other material. SEM 72/3631, 72/3665, 72/3680.

## Stephanolithion hexum ROOD & BARNARD 1972

1972 Stephanolithion hexum ROOD & BARNARD, p. 329, Pl. i, Fig. 3, 4, 9, 10.
1973 Stephanolithion hexum: ROOD, HAY & BARNARD, p. 376.

*Remarks.* - This small species of *Stephanolithion* has been found in the Gamlingay and Ampthill boreholes at depths of 66 feet (20.12 m) and 203 feet (61.87 m) respectively, the *bukowskii* Subzone of the *cordatum* Zone and the *scarburgense* Subzone of the *mariae* Zone, Upper Oxford Clay. It has also been recorded from the lower part of the *athleta* Zone of the Normans Cross Pit, Peterborough [NGRTL 171915].

## Family Crepidolithaceae BLACK 1971

*Remarks.* - The nature of the thick outer ring of coccolith and distal axial structure is sufficiently distinct from the eiffellithids to warrant familial separation. BLACK (1971, p. 392) would include *Parhabdolithus* DEFLANDRE in this family but the writer prefers to regard it primarily as an eiffellithid. The Lower Lias (Jurassic) forms of *Crepidolithus* and *Parhabdolithus* are very distinct. The writer agrees with BLACK (1972, p. 28) in separating these forms from the NoëL (1965) family Discolithaceae.

### Genus Crepidolithus NOËL 1965

Type species: by original description; *Discolithus crassus* DEFLANDRE in DEFLANDRE & FERT 1954; Jurassic (Oxfordian), France.

*Remarks.* - The proximal cycle of tabular elements noted for the type species by ROOD, HAY & BARNARD (1971, p. 259) is rarely seen and may only be occasionally present in the material.

## Crepidolithus crassus (DEFLANDRE 1954)

## Pl. 1, Fig. 7-8

1954 Discolithus crassus DEFLANDRE in DEFLANDRE & FERT, p. 144, Pl. xv, Fig. 12-13.
1965b Crepidolithus crassus: Noël, p. 85, Pl. ii, Fig. 3-7; Pl. iii, Fig. 1-5.

*Remarks.* – This species has been recovered from the Oxford Clay of the Haddenham and Gamlingay boreholes. NOËL (1965) and PRINS (1969) have also found it in the Lias.

Material. - Includes a proximal view SEM 72/3650.

## Genus Proculithus gen.n.

Type species: by original designation; *Carinolithus fistulatus* sp.n. (ex PRINS 1969, nom. nud.); Lower Jurassic (Toarcian), England.

*Diagnosis.* – Coccoliths with one shield that comprises two or three cycles of plates with a wide central opening and a short bundle of axial rod-like plates that extend from the shield and diverge into a wide distal selvage margin.

*Remarks.* – The genus *Carinolithus* and the species *C. fistulatus* were introduced invalidly by PRINS in 1969 (p. 549); the genus was subsequently validated by PRINS in GRÜN, PRINS & ZWEILI (1974, p. 313), but in the revised synonymy *C. fistulatus* was excluded from the genus; no further comment or assignation was given for this species. The writer agrees with them in placing species with a wide central opening and a short bundle of axial rods elsewhere. These forms are considered to be intermediate between *Carinolithus* PRINS and *Diazomatolithus* NoëL.

In addition to *C. fistulatus* two further species are diagnosed below as belonging to the new genus *Proculithus*. Alhough *Calyculus* NOËL possesses some of the external features of *Proculithus*, it also possesses a central area covered by a reticulate meshwork of small calcite rhombs.

# Proculithus fistulatus sp. n. (ex PRINS 1969, nom. nud.)

Pl. 10, Fig. 8, 9

1969 Carinolithus fistulatus PRINS, p. 549, Pl. i, Fig. 6 (nom.nud.).

*Diagnosis.* – A species of *Proculithus* with axial rods that diverge distally and are inclined at an angle of about  $60^{\circ}$  to the horizontal; the height of the coccoliths is usually greater than the width.

Description. - Coccoliths with a thin proximal shield comprising about 12 plates. From this shield a bundle of rod-like plates extend distally and terminate in a wide distal selvage margin. The rods also diverge distally at an angle of about 60°, giving rise to the characteristic "flower-pot" shape.

*Differentiation.* - The species has not yet been examined using electron optical equipment and so the description is based on light microscope studies only. The characteristic external shape differentiates this species from the others in the genus.

*Holotype:* Slice number MPK 1174; lodged in the MPK collection of types at the Institute of Geological Sciences, Leeds, England (Pl. 10, Fig. 8; the specimen marked \* in Textfig. 3).

Dimensions: About 6  $\mu$  in both width and height.

*Type locality:* Hill Lane Borehole, Brent Knoll, Somerset, England [NGRST 33465156] at 13 m depth.

Type level: Lower Jurassic (Toarcian). falciferum Zone, exaratum Subzone.

Remarks. - The species of PRINS (1969, p. 549) is here validated.



Fig. 3. Range of variation in Proculithus fistulatus sp.n.

All of the specimens are from the Lias of the Hill Lane Borehole at a depth of 13 m (IGS sample number SAC 2452), except for the specimen marked\*\*, which is a reproduction of PRINS' figure. The specimen marked\* is the Holotype.

Proculithus charlotteii sp.n.

Pl. 10, Fig. 11; Pl. 11, Fig. 9

*Diagnosis.* - A species of *Proculithus* with parallel sided vertically inclined axial rods; the height and width of the coccoliths are approximately the same.

*Description.* - The proximal shield comprises two thin cycles of about 16 plates. From this shield a bundle of 14 axial rod-like plates extend distally and terminate in a wide distal selvage. These plates do not diverge distally and are at right angles to the proximal shield.

Differentiation. - The species is separated from the others by its parallel sides and in having equal height/width measurements. Plate 10, Figure 12 illustrates a lateral view of *Diazomatolithus lehmani* NOËL for comparison, note that the proximal shields are much broader than those of *Proculithus* species.

Holotype: SEM 76/12547 (Pl. 11, Fig. 9).

Dimensions: Overall diameter 4  $\mu$ ; diameter of the stem and the height 3  $\mu$ .

Type locality: Millbrook section, near Ampthill, Bedfordshire.

*Type level:* 73 feet (22.25 m) below ground surface; Upper Oxford Clay, *mariae* Zone, *scarburgense* Subzone.

Other material. - SEM 76/12634 is a broken interior of this species. This specimen is from the Gamlingay Borehole at 110 feet (33, 53 m); horizon the same as the

holotype: it has also been found in the *cordatum* Zone beds of this borehole (at 68-70 feet).

## Proculithus expansus sp.n.

Pl. 11, Fig. 1, 5, 6

*Diagnosis.* - A species of *Proculithus* with parallel-sided or slightly distally diverging bundles of axial rod-like plates, which are inclined at an angle of about  $60-75^{\circ}$  to the proximal shield; the shield comprises two or three cycles of about 40 plates; the height of the coccolith is less than half of its width.

Description. - Coccoliths with a proximal shield comprising two or three cycles of plates; the proximal cycle is very fragile and not usually seen but there may be a vestige of a central area covered by rhomb-shaped elements (Pl. 11, Fig. 1) the central opening is half or more of the width of the shield. A short bundle of rod-like plates extend distally and at an angle of about  $60-75^{\circ}$  to the proximal shield and diverge slightly distally; at the distal margin they turn abruptly outwards to form a wide selvage.

*Differentiation.* - This species is separated from the others in this genus by its much greater width/height ratio.

Holotype: SEM 76/12545 (Pl. 11, Fig. 1).

Dimensions: Overall width of the coccolith is 4  $\mu$ ; height approximately 1.5  $\mu$ .

Type locality: Millbrook section, near Ampthill, Bedfordshire.

*Type level:* 73 feet (22.25 m) below ground surface; Upper Oxford Clay, *mariae* Zone, *scarburgense* Subzone.

Other material. - This is the most frequently found species of Proculithus and occurs in several Oxford Clay samples of the Gamlingay and Haddenham boreholes. It has also been found in the Lower Jurassic (Toarcian) beds of Dorset (SEM 76/12593).

Genus Millbrookia gen.n.

Type species: by original designation; *Millbrookia perforata* sp.n.; Upper Jurassic (Oxfordian), England.

*Diagnosis.* – Elliptical coccoliths with a simple wide eiffellithid rim and a central area covered by a complex of small rhomb-shaped crystallites that extend from the proximal shield to form a regular pattern.

*Remarks.* – This group is found in the optical microscope examination to possess the basic character of a high optical relief using plane polarised light. Also a central area of small plates is occasionally inferred but this area is either broken or more usually covered by clay minerals. Electron microscope studies clearly show the nature of this area and results in the two species so far differentiated.

Millbrookia is distinct from Proculithus gen.n. in having an eiffellithid rim and without the characteristic distal selvage margin of the latter. It is distinct from Calyculus NOEL in that there is no distal selvage and that there is only one ring of proximal plates. GRÜN, PRINS & ZWEILI (1974, p. 311) do not consider their spe-

cimens, which have bar structures covering the central area, to be specifically distinct from the type of NoëL (*Calyculus cribrum* NoëL 1973, p. 116). The writer would place these two types in different species of *Calyculus*.

## Millbrookia perforata sp. n. Pl. 11, Fig. 2, 3, 4

*Diagnosis.* - As for the genus; the small plates in the central area form a reticulate meshwork pattern.

*Description.* - Coccoliths with a proximal shield comprising one thin ring of small rhomb like plates. A series of very small lath-like plates extend into the central area; these may be elongate at the margins, but become equidistant inwards and give rise to small circular perforations over the central area. The distal shield comprises a single cycle of broad lath-shaped crystallites that are inclined at an angle of about 60° and thus gives an imbricate distal margin.

*Differentiation.* - This species is differentiated by its reticulate pattern of small rhomb plates covering the central area. As mentioned earlier (page 34), there is a superficial similarity to forms assigned to *Ethmorhabdus* NOEL. However in the light microscope the rim of *Millbrookia* is completely different being eiffellithid rather than podorhabdid, and the elements are much thinner and with a different crystal pattern.

Holotype: SEM 76/12535 (Pl. 11, Fig. 2).

Dimensions:  $4 \times 3 \mu$ .

Type locality: Millbrook section, near Ampthill, Bedfordshire, England. Type level: 99 feet (30.17 m) below ground surface; Middle Oxford Clay, lamberti Zone.

Other material. - This form has been seen in many samples from the three boreholes; but it is confined to the *athleta* to *tenuiserratum* zones; and it is only rarely found in the Haddenham Borehole.

## Millbrookia virgata sp.n.

Pl. 11, Fig. 7, 8

*Diagnosis.* – As for the genus; the small plates in the central area form a pattern of bar structures that coalesce in the centre.

*Description.* - Coccoliths with a proximal shield comprising one thin ring of small rhomb-like plates. About 20 lath-like plates extend from the inner wall into the central area and coalesce in the middle (the central part is covered by clay minerals in all of the specimens so far seen). The distal shield comprises a single cycle of broad lath-shaped crystallites that are inclined at an angle of about 60° and so gives rise to an imbricate margin.

Differentiation. - This species is differentiated by its inwardly radiating pattern of bar-like crystals. Corollithion silvaradion FILEWICZ, WIND & WISE is a similar form, but the arrangement of the bar-like crystal radiating inwardly to a central

spire with jointing where the bars intersect the central platform. *M. virgata* has a much simpler arrangement, without a central spire.

Holotype: SEM 76/12531 (Pl. 11, Fig. 7). Dimensions:  $2 \times 1.5 \mu$ . Type locality: Millbrook section, near Ampthill, Bedfordshire, England. Type level: 99 feet (30.17 m) below ground surface; Middle Oxford Clay, lamberti Zone.

Other material. - This species is confined to the mariae and cordatum zones samples of the three boreholes; it has also been found in the mariae Zone samples of the Millbrook section.

## Genus Diazomatolithus NOËL 1965

Type species: by monotypy; *Diazomatolithus lehmani* NOËL 1965; Jurassic (Oxfordian), France.

*Remarks.* - The placing of this genus in the family Crepidolithaceae BLACK is provisional; NOEL (1973, p. 114) would place the genus in her newly established family Lotharingiaceae.

Diazomatolithus lehmani Noël 1965

Pl. 10, Fig. 12

1965a Diazomatolithus lehmani NOEL, p. 5, Textfig. 25-27.

*Remarks.* - Specimens have been recovered from most of the samples examined from the Gamlingay Borehole; rarely seen in the Haddenham Borehole.

## Genus Rhabdolithus KAMPTNER ex DEFLANDRE 1952

Type species: by monotypy; *Rhabdolithus perlongus* DEFLANDRE in GRASSE, 1952; Eocene, France.

*Remarks.* - KAMPTNER (1949, p. 78) proposed the genus *Rhabdolithus*, but gave no type species. DEFLANDRE (1952, p. 466) gave a brief description of the genus and also the type species, which validated the genus. The Jurassic material provisionally assigned to this genus in MEDD (1971) has now been placed elsewhere as the writer's understanding of the discorhabdids has matured.

## Genus Carinolithus PRINS 1974

Type species: by original designation; Rhabdolithus superbus DEFLANDRE 1954.

## 1969 Carinolithus PRINS (partim), p. 549, Pl. i, Fig. 7, 8, non 6 (nom.nud.).

*Remarks.* - This genus was validated by PRINS in GRÜN, PRINS & ZWEILI (1974, p. 313). *Carinolithus fistulatus* PRINS (nom.nud., Pl. i, Fig. 6) was excluded from his revised generic concept, but no further comment was made.

The writer accepts his separation of this species after studying specimen of *C. clavatus* (DEFLANDRE) with intact proximal margins. They compare well with the figures of GRÜN, PRINS & ZWEILI of the species *C. superbus* (DEFLANDRE), and this margin is found to be distinct from that of the *C. fistulatus* type. Specimens of this latter type are here transferred to the new genus *Proculithus*.

The major parameters for specific discrimination within the genus *Carinolithus* are: the length and the angle of the bundle of axial rods between the distal and selvage margin.

*Rhabdolithus clavatus* DEFLANDRE is transferred here to the genus *Carinolithus*. Although the proximal margin rarely ends in a selvage, this has been seen in a few scanning electron micrographs (Pl. 1, Fig. 12), and where present is usually much smaller than that of *C. superbus* (Pl. 2, Fig. 1). The axial rods do not diverge distally.

*Rhabdolithus sceptrum* DEFLANDRE is also here transferred to *Carinolithus*. The length of the axial rods is less than that of *C. superbus* or *C. clavatus*, but the distal selvage margin is pronounced. The axial rods diverge slightly distally, but not so much as is seen in *C. superbus*.

### Carinolithus clavatus (DEFLANDRE 1954)

### Pl. 1, Fig. 11, 12

1954 Rhabdolithus clavatus DEFLANDRE, in DEFLANDRE & FERT, p. 160, Pl. xv, Fig. 36-39.

*Remarks.* – This species has been found in the Gamlingay Borehole at depths of 68 feet (20.73 m) and 110 feet (33.53 m), and the Haddenham Borehole at 240 feet (73.15 m).

## Carinolithus sceptrum (DEFLANDRE) in DEFLANDRE & FERT 1954 Pl. 2, Fig. 2

1954 Rhabdolithus sceptrum DEFLANDRE in DEFLANDRE & FERT, p. 159, Pl. xv, Fig. 34-35.

*Remarks.* - Recovered from only three samples in addition to those given by MEDD (1971) from the Ampthill Borehole, one from the base of the Ampthill Clay in the Gamlingay Borehole, the other two from the Upper Oxford Clay of the Gamlingay and Haddenham boreholes.

## Carinolithus superbus (DEFLANDRE) in DEFLANDRE & FERT 1954 Pl. 2, Fig. 1

1954 Rhabdolithus superbus DEFLANDRE in DEFLANDRE & FERT, p. 160, Pl. xv, Fig. 24, 25.

*Remarks.* – This species has not been recovered from Upper Jurassic material so far. It is included here for comparative purposes.

## Genus Tremalithus KAMPTNER 1952

Type species: by monotypy; *Tremalithus placomorphus* KAMPTNER 1952; Miocene, Austria.

*Remarks.* - Many simple tremaliths have been seen in the optical microscope investigation of most of the samples from the Haddenham and the Gamlingay boreholes. Scanning electron microscope studies indicate that there are too few characters available for the writer to establish a satisfactory species or generic grouping. The genus *Tremalithus* is therefore used as a "provisional resting place" until further work is done. This does not signify that the writer accepts the validity of *Tremalithus*.

## Family Podorhabdaceae NOEL 1965

## Subfamily Podorhabdoideae REINHARDT 1967

*Remarks.* – Genera have been recorded from the Upper Jurassic material examined, which possess none to twelve arms supporting the central perforate spire. Species of *Podorhabdus* NOEL are the most commonly found members of the group. The family has been revised by BLACK (1972, p. 31). A twelve-armed form in a single cycle is also found in the Upper Cretaceous: *Dodekapodorhabdus noëlae* PERCH-NIELSEN 1968 (p. 46) and a twelve-pored form in two cycles has been recovered from the North Wootton Borehole (NGRTF 64392457) in the Kimmeridgian.

## Genus Podorhabdus NOEL 1965

Type species: by original designation; *Podorhabdus grassei* NOEL 1965; Jurassic (Oxfordian), France.

Remarks. - LOEBLICH & TAPPAN (1966, p. 157) consider this genus to be invalid under ICBN Articles 38 and 43, as the type species is invalid. However, the genus was validated when a fully figured description of the type species was given by NOËL (1965b, p. 100).

BLACK (1972, p. 32) has altered the emphasis of the species diagnoses from the nature of the spine to the structure of the basal shield. The Jurassic forms, however, are here still defined primarily on the spine structure.

## Podorhabdus grassei NOEL 1965

Pl. 4, Fig. 12

1965a Podorhabdus grassei NOEL, p. 6 (invalid under ICBN Articles 38 and 43).
1965b Podorhabdus grassei: NOEL, p. 103, Pl. ix, Fig. 1-2.

*Remarks.* - This species has been recovered from the Gamlingay Borehole at a depth of 90 feet (27.43 m).

Podorhabdus cylindratus NOEL 1965

## Pl. 5, Fig. 1, 2

1965a Podorhabdus cylindratus NOEL, p. 6, Textfig. 30.

*Remarks.* – This species has been recovered from most of the samples examined from the boreholes from the Lower Oxford Clay to the top part of the Lower Kimmeridge Clay.

Material. - Includes a proximal view, SEM 72/3615.

## Podorhabdus rahla NOEL 1965

Pl. 4, Fig. 13; Pl. 5, Fig. 10, 11

?1954 Rhabdolithus annulatus: DEFLANDRE in DEFLANDRE & FERT, p. 162, Pl. xv, Fig. 32-33.
non 1958 Rhabdolithus annulatus: NOEL, p. 167, Pl. ii, Fig. 13.
1965b Podorhabdus rahla NOEL, p. 105, Pl. ix, Fig. 8.

*Remarks.* – This distinctive species has now been recovered from many more samples than previously recorded. In the present boreholes it has been found to be common in the *mariae* Zone, its total range is from the lower part of the *cordatum* Zone to the upper part of the *athleta* Zone. Rotation of specimens during a scanning electron microscope examination to investigate the joining of the spire to the shield indicates that a fourfold buttress arrangement is usual. The "alae" are usually only slightly developed, much less so than in the type, but one specimen has been found, whose alae are nearly as wide as the shields (SEM 72/3634).

### Podorhabdus sp.

*Remarks.* - In many of the samples examined optically there are specimens which appear to be identical with *Podorhabdus cylindratus* NOEL, but that are considerably smaller. The size of these specimens is approximately  $3.0 \times 2.5 \mu$ . These have been referred to on the range charts as *Podorhabdus* sp. (small).

## Genus Cleistorhabdus BLACK 1972

Type species: by original designation; *Cleistorhabdus williamsii* BLACK 1972; Cretaceous (Upper Gault), England.

*Remarks.* – This genus, established by BLACK (1972, p. 36) for Cretaceous forms, is also found in the Upper Jurassic. The Jurassic species is very similar in an optical examination to the type species, but electron micrographs indicate them to be two distinct forms. This genus forms a link with *Discorhabdus* NOEL.

### Cleistorhabdus moorei sp.n.

Pl. 5, Fig. 3

*Diagnosis.* - A species of *Cleistorhabdus* with a recessed central area, and a central open stem supported by flat tabular elements.

Description. - Elliptical podorhabdid coccoliths with a rim consisting of 32 keystone elements and a central area markedly recessed proximally, of tabular elements which coalesce at the centre to a hollow spine base, which is 0.5  $\mu$  in diameter. The spine is absent in the specimens seen.

Differentiation. - This species differs from Cleistorhabdus williamsi BLACK in the more pronounced boundary between the rim and the central area, and in the smaller size.

Holotype: SEM 72/3702 (Pl. 5, Fig. 3). Dimensions:  $3.3 \times 2.8 \mu$ ; central area  $2.0 \times 1.6 \mu$ ; pore diameter  $0.5 \mu$ . *Type locality:* Gamlingay Borehole, Cambridgeshire. *Type level:* Depth of 66 feet (20.12 m), Upper Oxford Clay.

### Genus Hemipodorhabdus BLACK 1971

Type species: by original designation; *Hemipodorhabdus latiforatus* BLACK 1971; Lower Cretaceous (Hauterivian), England.

Remarks. - BLACK (1972, p. 37) separates this genus from Bipodorhabdus NOEL as the latter genus has a "solid boss at the centre of the bridge instead of a hollow spine". Several specimens of *H. conjugatus* sp.n. have been found with the wider rim, more characteristic of Discorhabdus NOEL. ROOD, HAY & BARNARD (1973, p. 381) erected a new species *D. biperforatus* which is intermediate between the two genera.

## Hemipodorhabdus conjugatus sp. n.

Pl. 5, Fig. 4, 8, 9, 12

Diagnosis. - A species of Hemipodorhabdus with a central stem supported by two bars.

*Description.* – Elliptical podorhabdid coccoliths with two wide bars, made up of numerous small elements coalescing high over the central opening to form a large open stem. The two bars cover about half of the area of the central opening when viewed from above.

Differentiation. - This species differs from Bipodorhabdus tesselatus NOEL in the more massive nature of the bars and in the larger open stem; it differs from B. cf. granulatus (REINHARDT) in the different arrangement of the calcite elements comprising the bars and in having the large open stem. The species differs from H. latiforatus BLACK and H. biforatus BLACK in the different nature of the proximal shield, and from Discorhabdus biperforatus ROOD, HAY & BARNARD by its smaller size.

Holotype: SEM 72/3632 (Pl. 5, Fig. 12). Dimensions:  $3.7 \times 2.7 \mu$ . Type locality: Gamlingay Borehole, Cambridgeshire. Type level: Depth of 70 feet (21.34 m), Upper Oxford Clay.

## Genus Tetrapodorhabdus BLACK 1971

Type species: by original designation; Tetrapodorhabdus coptensis BLACK 1971.

*Remarks.* - Forms agreeing with the generic diagnosis of BLACK have been found at several levels in the Jurassic, including one in the Gamlingay Borehole. The species is common in the Fullers Earth (Bathonian, *retrocostatum* Zone) of southern England and has also been found in clays from the Bajocian (*parkinsoni* and *garantiana* zones).

## Tetrapodorhabdus shawensis sp. n. Pl. 6, Fig. 9-12

*Diagnosis.* - A species of *Tetrapodorhabdus* with a very thin cycle of inner ring elements from which the buttresses emerge.

Description. - The buttresses, which are steeply inclined, merge to the open pore characteristic of the genus. The outer ring of elements is typically podorhabdid with simple sutures directed radially. The inner ring is made up of small rhomb-shaped elements, that are clearly seen in the proximal view. The proximal shield is nearly as large as the distal, with the suture gently inclined in an anticlockwise direction.

*Remarks.* - The species is smaller than *T. coptensis* and has a narrower inner ring of elements.

*Holotype:* SEM 76/12399, distal view recovered from sample SAC 2874 (reticulation is an artefact) (Pl. 6, Fig. 11).

Type locality: Burton Bradstock Cliff, near Bridport, Dorset (NGR SY 4840, 8920). Type level: Sponge bed 80 cm below top of zig-zag Bed. Bajocian, P. parkinsoni

Zone; Upper Inferior Oolite.

*Type dimensions:*  $3.4 \times 2.8 \mu$ .

Paratype: SEM 76/12396, proximal view from sample SAC 199 Gamlingay Borehole at 68 feet (20.73 m).

Stratigraphical distribution. - Bajocian: garantiana and parkinsoni zones; Bathonian: retrocostatum Zone; Oxfordian: cordatum Zone.



Fig. 4. Sketches of rarely occurring coccoliths, based on optical micrographs. The optical micrographs are included in the plates, but these are poor photographs and no SEM photograph has been obtained.

- a) Stradnerlithus sattinii sp. n.: Holotype.
- b) Stephanolithion speciosum DEFLANDRE elongatum ssp.n.: Holotype.
- c) Tetrapodorhabdus shawensis sp.n.: Distal view.
- d) Chiastozygus asymmetricus sp.n.: Holotype.
- e) Staurorhabdus magnus sp.n.: Distal view.

## Genus Hexapodorhabdus NOEL 1965

Type species: by monotypy; *Hexapodorhabdus cuvillieri* NOEL 1965; Upper Jurassic (Oxfordian), France.

### Hexapodorhabdus cuvillieri NOEL 1965

## 1965b Hexapodorhabdus cuvillieri NOEL, p. 105, Pl. ix, Fig. 4-6.

*Remarks.* - This form has been recovered intermittently from samples of the two boreholes at all levels. The specimen figured as this species by MEDD (1971, Pl. i, Fig. 4) is considered to be *Octopodorhabdus decussatus* (MANIVIT).

## Genus Octopodorhabdus NOEL 1965

Type species: by original designation; Octopodorhabdus praevisus NOEL 1965; Upper Jurassic (Oxfordian), France.

Remarks. - BLACK (1972, p. 38) established the genus Octocyclus for forms with four principal buttresses, which lie along the principal axes of the ellipse, and this differs from Octopodorhabdus, in which the type species has windows in this position. Examination of the Jurassic material indicates the extremely variable nature of the central axial structure of this group of genera, and so these two genera are here united. The Cretaceous species include Octopodorhabdus magnus (BLACK) comb.n. (pro Octocyclus magnus BLACK 1971, p. 38).

## Octopodorhabdus decussatus (MANIVIT 1961)

Pl. 5, Fig. 5-7; Pl. 6, Fig. 1

1961	Discolithus decussatus MANIVIT, Pl. 14; Pl. i, Fig. 7.
non 1963	Rhabdolithus decussatus: STRADNER, p. 9, Pl. v, Fig. 8.
1966	Discolithus cryptochondrus: STOVER, p. 142, Pl. ii, Fig. 8-9; Pl. viii, Fig. 13.
1968	Cretarhabdus decussatus: STRADNER, ADAMIKER & MARESCH, p. 29, Pl. xiii, Fig. 1-2; Pl. xiv,
	Fig. 1-6.
1971	Hexapodorhabdus cuvillieri: MEDD, p. 828, Pl. i, Fig. 4 (non Fig. 3).
1971	Octopodorhabdus decussatus: ROOD, HAY & BARNARD, p. 262, Pl. iii, Fig. 4.
1971	Octopodarhabdus [sic] decussatus: MANIVIT, p. 98, Pl. iv, Fig. 10-14.

Remarks. – The average dimensions of the distal shield is  $7 \times 5 \mu$ , made up of about 36 tabular elements. This species has been recovered from many samples of the Upper Oxford Clay of the Haddenham and the Gamlingay boreholes, material from the mariae Zone of the Warboys Brick Pit, Huntingdonshire (sample 35cM of MEDD 1971, p. 837), and cordatum Zone material from the same locality (sample number 33M). It has also been found in the Ampthill Clay of the Ampthill Borehole. One specimen found (SEM 72/3824) has seven bars, and is intermediate between this species and Hexapodorhabdus cuvillieri NOËL.

BLACK (1972, p. 38) has separated out the large members of this group as the species O. magnus.

### Genus Dekapodorhabdus gen.n.

Type species: by monotypy; *Dekapodorhabdus typicus* sp.n.; Upper Jurassic (Oxfordian), England.

*Diagnosis.* - Elliptical coccoliths with a podorhabdid rim and a stem supported by ten arms.

Dekapodorhabdus typicus sp.n.

Pl. 6, Fig. 2

*Diagnosis.* - An elliptical species of *Dekapodorhabdus* with two symmetrically arranged arms that lie in the major (bifurcated) and the minor axes of the ellipse, and also along the diagonals.

*Description.* - The central structure consists of ten arms, which coalesce to a central open spire. There are about 44-48 tabular elements to the elliptical rim.

*Remarks.* – This is the only member of the Podorhabdaceae NOEL with ten arms. The specimens are very rare. It has also been found in the Ampthill Borehole at 150 feet (45.72 m).

Holotype: SEM 72/3691 (Pl. 6, Fig. 2). Dimensions:  $2.8 \times 2.1 \mu$ . Type locality: Gamlingay Borehole, Cambridgeshire. Type level: Depth of 64 feet (19.51 m); Upper Oxford Clay.

Genus Polypodorhabdus NOEL 1965

Type species: by original designation; *Polypodorhabdus escaigi* NOEL 1965; Upper Jurassic (Oxfordian), France.

Remarks. - REINHARDT (1967, p. 171; 1970, p. 47) places this genus with Cretarhabdus BRAMLETTE & MARTINI 1964. However, comparison of the type of Polypodorhabdus with that of Cretarhabdus (Cretarhabdus conicus BRAMLETTE & MARTINI) indicates that the two genera are distinct and the author agrees with PERCH-NIELSEN (1968, p. 48) in separating them. BLACK (1972, p. 40) has emended the generic diagnosis. BLACK (1971, p. 408) differentiates various species on the number of "windows" or "grid bars" within the axial complex; this is accepted here and the two Jurassic forms are retained with one new species added. However, such differentiation is usually only possible on examination with the electron microscope and Polypodorhabdus escaigi NOEL has been retained for those forms which have been identified with the optical microscope, or that possess the larger number of bars mentioned by BLACK as being characteristic of this species.

Polypodorhabdus escaigi NOEL 1965

### Pl. 6, Fig. 3

1965a Polypodorhabdus escaigi NOEL, p. 6, Textfig. 32.

Remarks. - REINHARDT (1967, p. 171) considers that this species is a synonym of Cretarhabdus surirellus (DEFLANDRE in DEFLANDRE & FERT). Examination of the

Fichier electron micrographs Nos. 4920, 5369 (DEFLANDRE & DEFLANDRE-RIGAUD 1970) indicates that the Cretaceous species has a different axial structure, is coarser, and the plates coalesce at the central boss in a different manner.

### Polypodorhabdus madingleyensis BLACK 1968

### Pl. 6, Fig. 4, 5

#### 1968 Polypodorhabdus madingleyensis BLACK, p. 806, Pl. cl, Fig. 2.

Remarks. - The four strong fibrous buttresses, mentioned by BLACK (1971, p. 619) as being characteristic of this species are seen in the electron micrographs of the present investigation to be very variably developed, and forms assigned to Polypodorhabdus escaigi NOEL may also possess this feature; however, the number of "grid-bars" of the two species is completely distinct and the two species are retained.

## Polypodorhabdus beckii sp.n.

Pl. 6, Fig. 6

1971 Polypodorhabdus escaigi: MEDD, p. 328, Pl. i, Fig. 5.

Diagnosis. - A species of Polypodorhabdus with 4-8 "grid-bars" only between the four fibrous buttresses.

Description. - An elliptical coccolith made up of about 34 tabular elements and supporting four strong fibrous buttresses, which follow the axes of the ellipse and which coalesce to a central hollow spine. There are 4-8 "grid-bars" between them.

Remarks. - This species is differentiated from other Polypodorhabdus species by the fewer number of "grid-bars" in the central area.

## Holotype: EM 381 (MEDD 1971, Pl. i, Fig. 5).

Dimensions:  $4.5 \times 3.0 \mu$ .

Type locality: Warboys brick pit, Huntingdonshire. Locality number 33M (MEDD 1971, p. 832).

Type level: Upper Oxford Clay, cordatum Zone.

Other material. - SEM 74/8783, Ampthill Borehole at a depth of 80 feet (24.38 m), Ampthill Clay, tenuiserratum Zone; Haddenham Borehole at a depth of 180 feet (54.86 m), also Ampthill Clay, tenuiserratum Zone.

## Subfamily Ethmorhabdoideae ROOD, HAY & BARNARD 1971

## Genus Ethmorhabdus NOËL 1965

Type species: by monotypy; Ethmorhabdus gallicus NOEL 1965; Upper Jurassic (Oxfordian), France.

Ethmorhabdus gallicus NOEL 1965

## Pl. 6, Fig. 7, 8

Ethmorhabdus gallicus NOEL, p. 6, Textfig. 33-34.

1965a

#### Upper Jurassic coccoliths (Cambridgeshire)

*Remarks.* - This species has been recovered from most of the samples examined from the boreholes. It differs in the optical microscope examination from *Anfractus harrisonii* sp. n. by its larger size and more precise arrangement of the crystallites in the central area, but the electron microscope examination shows that the two are structurally different. The scanning electron micrographs clearly indicate that the central spire of *E. gallicus* is a thin tube and not a rod as previously supposed (MEDD 1971, p. 829).

## Ethmorhabdus cf. anglicus ROOD, HAY & BARNARD 1971

1971 Ethmorhabdus anglicus ROOD, HAY & BARNARD, p. 263, Pl. iii, Fig. 8.

*Remarks.* – In many of the samples examined optically there are specimens which appear to be identical with *Ethmorhabdus anglicus* ROOD, HAY & BARNARD, but that are considerably smaller. The size being approximately  $3.5 \times 2.5 \mu$ .

## Subfamily Sollasitesoideae ROOD, HAY & BARNARD 1971

## Genus Sollasites BLACK 1967

Type species: by monotypy; Sollasites barringtonensis BLACK 1967; Upper Cretaceous (Cenomanian), England.

*Remarks.* - Several species of *Sollasites* have now been recovered from the Upper Jurassic material examined. The specimens are very rare; a five hour scanning electron microscope examination of a coccolith strew slide usually yields only one or two specimens. However, the samples are not considered to be contaminated with Cretaceous debris; the specimens are regarded as *in situ* Jurassic fossils.

### Sollasites horticus (STRADNER, ADAMIKER & MARESCH 1966)

Pl. 9, Fig. 1

1966Coccolithus horticus STRADNER, ADAMIKER & MARESCH, p. 337, Pl. ii, Fig. 4.non 1968Sollasites horticus: BLACK, p. 798, Pl. cxliv, Fig. 1-2.non 1969Costacentrum horticum: BUKRY, p. 44, Pl. xxi, Fig. 12; Pl. xxii, Fig. 1-4.

*Remarks.* - The separation of the larger forms of this species group by BLACK (1971, p. 412; 1973, p. 64) as *Sollasites barringtonensis* BLACK is accepted here, as no intermediate forms either in size or number of elements have been found (ROOD, HAY & BARNARD 1973, p. 381).

*Material.* - SEM 72/3705 has 26 elements to the distal shield, is  $1.7 \times 1.2 \mu$ , and was recovered from the Haddenham Borehole at a depth of 230 feet (70.10 m); 72/3738 has 24 elements, is  $2.4 \times 1.5 \mu$ , and was recovered from the Gamlingay Borehole at a depth of 140 feet (42.67 m). These are both from the Oxford Clay.

Sollasites lowei (BUKRY 1969)

Pl. 9, Fig. 2-5

1969	Costacentrum	lowei BUKRY, p.	. 44,	Pl. xxii	, Fig. 5	-6.
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1971 Sollasites lowei: ROOD, HAY & BARNARD, p. 264, Pl. iv, Fig. 1.

*Remarks.* - This species has been recovered from several samples of the Upper Oxford Clay of the Ampthill. Haddenham and Gamlingay boreholes. The forms found agree fully with the type from the Upper Cretaceous. SEM 72/3706 has the central area raised, and this difference from the type with its flat central plate complex may warrant specific separation.

*Material.* - SEM 72/3610 has 28 elements to the distal shield and is 4  $\mu$  long; 72/3698 has 24 elements and is  $2.0 \times 1.5 \mu$ , 72/3706 has 32 elements and is  $3.3 \times 2.4 \mu$ , 72/3733 has 30 elements and is  $2.0 \times 1.6 \mu$ .

## Sollasites bipolaris ROOD, HAY & BARNARD 1971 Pl. 7, Fig. 1

1971 Sollasites bipolaris ROOD, HAY & BARNARD, p. 265, Pl. iv, Fig. 3.

*Remarks.* – One specimen (SEM 72/3690) of this very small form  $(1.7 \times 1.0 \ \mu)$  has been recovered from the Upper Oxford Clay of the Gamlingay Borehole at a depth of 64 feet (19.51 m). Apart from the smaller measurements, the other characters for the specimen found agree with those given by ROOD, HAY & BARNARD.

### Subfamily Palaeopontosphaeroideae ROOD, HAY & BARNARD 1971

### Genus Palaeopontosphaera NOEL 1965

Type species: by monotypy; *Palaeopontosphaera dubia* NOËL 1965; Jurassic (Portlandian), Algeria.

*Remarks.* – GRÜN, PRINS & ZWEILI (1974, p. 297) consider this genus to be a junior synonym of *Biscutum* BLACK 1959. This is not accepted here as the arrangement and shape of the plate cycles are sufficiently different to warrant retention of both genera.

Palaeopontosphaera dubia NOEL 1965

Pl. 7, Fig. 2, 3

1965a Palaeopontosphaera dubia NOEL, p. 4, Textfig. 8.
1974 Biscutum dubium: GRÜN, PRINS & ZWEILI, p. 297, Pl. xiv, Fig. 1-3.

*Remarks.* - This species has been recovered from most of the samples examined. NOEL (1969, p. 486) has recorded the species from the Hauterivian, France. Coccospheres have been found in several of the samples.

### Family Prediscosphaeraceae ROOD, HAY & BARNARD 1971

## Subfamily Discorhabdoideae NOEL 1965

Remarks. - BLACK (1972, p. 24) has commented on the similarity between some forms of *Bidiscus* BUKRY (1969) and *Discorhabdus* NOEL (1965b) and he placed the first genus with the family Biscutaceae BLACK (1971).

### Genus Discorhabdus NOEL 1965

Type species: by original designation; *Rhabdolithus patulus* DEFLANDRE 1954; Upper Jurassic (Oxfordian), France.

## Discorhabdus patulus (DEFLANDRE) in DEFLANDRE & FERT 1954 Pl. 7, Fig. 4, 5

1954 Rhabdolithus patulus DEFLANDRE in DEFLANDRE & FERT, p. 162, Pl. xv, Fig. 40-45.

1971 Discorhabdus jungi NOËL: ROOD, HAY & BARNARD, p. 267, Pl. iv, Fig. 5, 6.

1975 Discorhabdus jungi: BARNARD & HAY, p. 576, Pl. iii, Fig. 5; Pl. v, Fig. 5.

*Remarks.* – This species has been found in most of the material examined. It is a very large and distinctive form when a strew sample is examined with a scanning electron microscope. The distal "flare" of the open central tube is very characteristic of the species. The specimens referred to *D. jungi* NOËL by ROOD, HAY & BARNARD and by BARNARD & HAY are referred to this species.

## Discorhabdus tubus Noël 1965

Pl. 1, Fig. 9

? 1954	Rhabdolithus inconspicuous: DEFLANDRE in DEFLANDRE & FERT, p. 160, Pl. xv, Fig. 49.
? 1965b	Rhabdolithus inconspicuous: NOEL, p. 83.
1965Ъ	Discorhabdus tubus NOEL, p. 145, Pl. xxi, Fig. 4, 15.
1965Ъ	Discorhabdus gibbosus NOEL, p. 146, Pl. xxii, Fig. 3.
? 1966	Rhabdolithus inconspicuous: LOEBLICH & TAPPAN, p. 161.
? 1968	Rhabdolithus inconspicuous: DEFLANDRE, p. 57, 62, 64.
? 1971	Stephanolithion bigoti: REINHARDT, p. 27.
1971	Rhabdolithus inconspicuous: MEDD, p. 827.
non 1971	Discorhabdus tubus: ROOD, HAY & BARNARD, p. 267, Pl. iv, Fig. 7.
? non 1974	Discorhabdus tubus: BARNARD & HAY, p. 573.
Darren	"Is There are many small discorphilide about 2.2 usin length and wi

Remarks. - There are many small discorhabdids about 2-3  $\mu$  in length and width in the Middle and Upper Jurassic, which have simple stems and flat or slightly concave discs. DEFLANDRE (1954, p. 160) described and figured such forms from the Oxfordian of Villers-sur-Mer, Normandy. However, NOËL (1965b, p. 83) considered that this species may be nothing more than the broken fragments of *Stephanolithion bigoti* DEFLANDRE; DEFLANDRE himself (1968) also agreed with this. It is proposed that *Rhabdolithus inconspicuous* DEFLANDRE be considered a *nomen dubium* until the type material has been re-examined and described. The small discorhabdids are here referred to the species *Discorhabdus tubus* NOËL. *Discorhabdus gibbosus* NOËL is very similar and the differences in the stem structure and disc concavity are not of sufficient importance as to warrant continued separation of the two species.

Discorhabdus tubus NOËL has described by ROOD, HAY & BARNARD (1971, p. 267) is a much larger form (9.5  $\mu$  across the disc) and possesses a thin, tapering stem. This form must be transferred elsewhere. By analogy the form referred to as Discorhabdus tubus NOËL in BARNARD & HAY (1975, p. 573-579) also belongs elsewhere.

### Discorhabdus jungi NOEL 1965

1965bDiscorhabdus jungi NOEL, p. 144, Pl. xxii, Fig. 5.non 1971Discorhabdus jungi: ROOD, HAY & BARNARD, p. 267, Pl. iv, Fig. 5, 6.non 1975Discorhabdus jungi: BARNARD & HAY, p. 576, Pl. iii, Fig. 5; Pl. v, Fig. 5.

*Remarks.* - This rare form has been recovered from a surface sample from the Warboys Brick Pit, Huntingdonshire; sample number 35dM (MEDD 1971, p. 837), and from the Ampthill Borehole at a depth of 170 feet (51.82 m; SEM 74/ 8915, 8917). Although this rarely occurring species is similar to *Podorhabdus grassei* NOEL, the shields are discorhabdid and not podorhabdid. The forms referred to this species by ROOD, HAY & BARNARD and BARNARD & HAY are transferred here to the species *D. patulus* (DEFLANDRE).

### Discorhabdus sp. 1

1971 Discorhabdus sp. 1 MEDD, p. 830.

Remarks. - This form has been recovered from several of the samples examined.

### Discorhabdus sp. 2

1971 Discorhabdus sp. 2 MEDD, p. 830.

*Remarks.* - This species has been recovered occasionally from the samples examined. Typical scanning electron micrographs of this species are: SEM 72/3574 (proximal view), 72/3682 (distal view), 72/3660 (distal view with spine developed).

### Discorhabdus longicornis sp. n.

Pl. 7, Fig. 9, 10

*Diagnosis.* - A species of *Discorhabdus* with a long thin median tube, which is slightly flared at the distal end.

Description. - A circular coccolith made up of 20 tabular elements, with a long central hollow tube, flared at the distal end, which is made of small lath-like elements.

*Remarks.* – This discorhabdid is very small (about 1.5  $\mu$  in diameter) and has been recovered in few samples from the material examined.

Holotype: SEM 72/3692 (Pl. 7, Fig. 9). Dimensions: Basal disc  $1.4 \mu$  in diameter, stem  $2.9 \mu$  long. Type locality: Gamlingay Borehole, Cambridgeshire. Type level: Depth of 64 feet (19.51 m); Upper Oxford Clay.

Stratigraphical distribution. - Praecordatum Subzone, mariae Zone to tenuiserratum Zone.

## Family Ellipsagelosphaeraceae NOEL 1965

Remarks. - ROOD, HAY & BARNARD (1971, p. 268) proposed the new family Watznaueriaceae as a substitute for the earlier designated Ellipsagelosphaeraceae as they considered the type genera to be synonymous. The author does not agree with this and the two genera are regarded as being distinct (see also BLACK 1973, p. 68).

## Genus Ellipsagelosphaera NOEL 1965

Type species: by original designation; Coccolithus britannicus STRADNER 1963, senior synonym of Ellipsagelosphaera frequens NOEL 1965 and of Watznaueria communis REINHARDT 1964. Upper Jurassic (Oxfordian), England.

Remarks. - The distinction between Ellipsagelosphaera NOEL and Watznaueria REINHARDT - the presence in forms of the first genus of a median tube connecting the two shields - as given by NOEL (1965b, p. 124; 1971, p. 894; 1973, p. 118) and PERCH-NIELSEN (1968, p. 68), with the resulting different aspect of the proximal side (BLACK 1973, p. 69, 82), is accepted here as being of generic importance, and the two genera are retained. This conclusion is based on a scanning electron microscope examination of Upper Jurassic and Upper Cretaceous material. Also in the first genus a bar across the central opening may or may not be present, in Watznaueria it is always absent.

PERCH-NIELSEN (1968, p. 69) cited Watznaueria angustoralis REINHARDT 1964, the type species of Watznaueria REINHARDT, as being the junior synonym of Tremalithus barnesae BLACK 1959, and so Watznaueria barnesae (BLACK) is the type-species of Watznaueria.

The placing of this species therefore into the genus *Tergestiella* KAMPTNER by REINHARDT (1964, p. 753) is not valid. The author does not follow BUKRY (1968, p. 31), however, in regarding *E.frequens* NOËL as a synonym of *W. barnesae* (BLACK).

Examination of the electron micrographs of material processed and from the literature indicates that there are three species at least of *Ellipsagelopshaera* in the Upper Jurassic; these are mentioned below.

## Ellipsagelosphaera britannica (STRADNER 1963)

### Pl. 8, Fig. 1, 2

- 1963 Coccolithus britannicus STRADNER, p. 176, Pl. i, Fig. 7.
- 1964 Watznaueria britannica: REINHARDT, p. 753, Pl. ii, Fig. 3.
- 1964 Watznaueria communis: REINHARDT, p. 756, Pl. ii, Fig. 5.
- 1965a Ellipsagelosphaera frequens: NOEL, p. 8, Textfig. 35-39.
- 1965b Ellipsagelosphaera frequens: NOEL, p. 119, Pl. xi, Fig. 7-10; Pl. xii, Fig. 1-10; Pl. xiii, Fig. 1-10.
- 1965b Ellipsagelosphaera lucasi: NOEL (pars), p. 126, Pl. xi, Fig. 2 (only).
- 1966 Ellipsagelosphaera frequens: LOEBLICH & TAPPAN, p. 139.
- 1966 Watznaueria britannica: LOEBLICH & TAPPAN, p. 176.
- 1966 Watznaueria communis: LOEBLICH & TAPPAN, p. 176.
- 1966 Watznaueria communis: REINHARDT, p. 17, Pl. iv, Fig. 3, 5-6; Pl. xxiii, Fig. 5.
- 1966 Watznaueria britannica: REINHARDT, p. 17, Pl. iv, Fig. 7.
- 1968 Ellipsagelosphaera frequens: LEZAUD, p. 16, Pl. i, Fig. 12.
- 1968 Ellipsagelosphaera communis: PERCH-NIELSEN, p. 71, Textfig. 33 c-d.
- 1968 Ellipsagelosphaera britannica: PERCH-NIELSEN, p. 71.
- 1969 Watznaueria barnesae: BUKRY (pars), p. 31.
- 1969 Watznaueria ovata: BUKRY, p. 33, Pl. xi, Fig. 11-12.
- 1971 Watznaueria britannica: REINHARDT, p. 33, Textfig. 34-36.

1971	Watznaueria communis: REINHARDT, p. 33, Textfig. 38.
1971	Ellipsagelosphaera frequens: BLACK, p. 621, Pl. xlv. i, Fig. 8-9.
1971	Ellipsagelosphaera frequens: MEDD, p. 829, Pl. iv, Fig. 2.
1971	Watznaueria communis: ROOD, HAY & BARNARD, p. 268, Pl. v,
non 1971	Watznaueria britannica: ROOD, HAY & BARNARD, p. 269, Pl. v.
1973	Ellipsagelosphaera britannica: NOEL, p. 119, Pl. iv, Fig. 6, 7.
1973	Ellipsagelosphaera communis: NOEL, p. 119, Pl. xiv, Fig. 1-5.

Remarks. - The commonest of the Upper Jurassic forms is Ellipsagelosphaera britannica (STRADNER). This is conspecific with E.frequens NOEL, Watznaueria communis REINHARDT and part of E. lucasi NOEL. Examination of the electron micrographs of the types of these three species shows that they all possess the same features and measurements apart from the fact that the bar across the central opening is not always present; it may be absent or replaced by small tabular plates infilling part or the whole of the opening. This conflicts with the specification of GRÜN & ALLEMANN (1975) and HAMILTON (1977), who would separate out forms without a central bar as E. keftalrempti GRÜN & ALLEMANN (1975, p. 161). There are three size ranges, as already noted by MEDD (1971, p. 829), but this variation, however, has no taxonomic or stratigraphic value.

A.W. Medd

Fig. 1-4. Fig. 5.

Statistical analysis of all of the material shows that there are some specimens which have a wider central opening than is considered "typical" for *E. britannica* (STRADNER), and the lectotype of *E. lucasi* NOEL is within this size range. And so, this species is retained for those forms with an opening width / total width ratio of 0.32-0.44. There are, however, a few specimens which have an even greater ratio (greater than 0.44), and also the thin central bar bifurcates laterally. These forms are transferred to the species *Ellipsagelosphaera reinhardtii* ROOD, HAY & BARNARD.

### Ellipsagelosphaera lucasi NOEL 1965

1965a	Ellipsagelosphaera	lucasi NOËL, p.	8.	Textfig. 40, 41
1965a	Ellipsagelosphaera	lucasi NOEL, p.	ð,	, 1 exting. 40, 41

- 1965b Ellipsagelosphaera lucasi: NOEL, p. 126, Pl. xi, Fig. 1, 3, 5, 6 (non Fig. 2, nec Fig. 4).
- 1966 Ellipsagelosphaera lucasi: LOEBLICH & TAPPAN, p. 199.
- 1971 Ellipsagelosphaera lucasi: MEDD, p. 829.
- 1971 Ellipsagelosphaera lucasi: WORSLEY, p. 1309.
- 1971 Ellipsagelosphaera lucasi: BLACK, p. 621, Pl. xlv. i, Fig. 10.
- 1971 Watznaueria britannica: ROOD, HAY & BARNARD, p. 269, Pl. v, Fig. 5.

*Remarks.* – This species is retained for those forms which have a percentage pore width of 32-44%. The separation of these forms from the "typical" *Ellipsagelosphaera britannica* (STRADNER) appears to be valid for the Jurassic of North Western Europe; however, it is an arbitrary distinction and further analysis may indicate their conspecific nature.

# Ellipsagelosphaera reinhardtii (ROOD, HAY & BARNARD 1971)

Pl. 8, Fig. 7, 8

1965b	Ellipsagelosphaera lucasi: NOEL (pars), p. 126, Pl. xi, Fig. 4 (only).

1971 Watznaueria reinhardti ROOD, HAY & BARNARD, p. 269, Pl. v, Fig. 6.

1973 Ellipsagelosphaera reinhardti: NOEL, p. 120, Pl. xiv, Fig. 8.

*Remarks.* - This species retained for those forms of *Ellipsagelosphaera* which have a percentage pore width per total width of more than 44%.

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*Material.* – The author has only found this species in the Haddenham Borehole at a depth of 80 feet (24.38 m; SEM 72/3551, 72/3564), the Gamlingay Borehole at a depth of 64 feet (19.51 m; SEM 76/12273), and from the Lower Kimmeridge Clay at the Great Ouse River Board Pit at Ely (Sample No. 40M; MEDD 1971, p. 832).

## "Ellipsagelosphaera" crucicentralis MEDD 1971 Pl. 8, Fig. 9-12

## 1971 Ellipsagelosphaera crucicentralis MEDD, p. 829, Pl. i, Fig. 1-2.

Remarks. - A similar form to this species is Podorhabdus quadriperforatus BUKRY (1969, p. 38, Pl. xvi, Fig. 8-11) from the Upper Cretaceous of the U.S.A. E. crucicentralis differs from that species by having a large number of elements in the distal shield and different ratios for the rings of elements in the shield. These two species, however, are very similar and P. quadriperforatus BUKRY (1969, p. 38) is here transferred to the genus Ellipsagelosphaera NOEL.

GRÜN, PRINS & ZWEILI (1974) have revised the coccolith forms initially figured by PRINS (1969) with complex axial structures. They have referred those forms similar to the genus Ellipsagelosphaera NOEL, but with an axial cruciform structure to the genus Lotharingius NOEL. They have also included (1974, p. 304) Ellipsagelosphaera crucicentralis MEDD as a synonym of Lotharingius sigillatus (STRADNER). The writer, from an examination of STRADNER's figures (1961, Textfig. 14, 15) would keep these two species distinct, unless GRÜN, PRINS & ZWEILI have re-examined STRADNER'S specimens and consider his figure to be erroneous; this is not made clear in their paper. Examination of all the figured material referred by GRÜN, PRINS & ZWEILI to Lotharingius suggests that there are two groups. One group with E. crucicentalis having the outer cycle of plates only shallowly inclined forms are much nearer to the writer's generic concept of Ellipsagelosphaera NOEL than to Lotharingius NOEL and E. crucicentralis MEDD is here retained in that genus. However a specimen recently found in the Gamlingay borehole at 20.73 m (SEM 76/12391, Pl. 8, Fig. 12), which possessing the shallowly inclined plate structure characteristic of Ellipsagelosphaera, has a central axial structure much more akin to the Lias Lotharingius forms of GRÜN, PRINS & ZWEILI. The problem as to the generic grouping of these forms is therefore not yet resolved.

## Genus Cyclagelosphaera NOEL 1965

Type species: by monotypy; Cyclagelosphaera margereli NOEL 1965; Jurassic (Oxfordian), France.

## Cyclagelosphaera margereli NOËL 1965

Pl. 8, Fig. 5

1965a	Cyclagelosphaera margereli NOEL, p. 8, Textfig. 45, 46, 48.
1965Ъ	Cyclagelosphaera margereli: NOEL, p. 130, Pl. xvii, Fig. 4-9; Pl. xviii, Fig. 1-2; Pl. xx,
	Fig. 2–4.
1965	Coccolithus sp.: BLACK, p. 132, Textfig. 7.

Remarks. - This species has been recovered from most of the samples examined.

## Cyclagelosphaera sp.

*Remarks.* – In the slides prepared from the Gamlingay Borehole sample at 44 feet (13.41 m) depth there are rare forms of *Cyclagelosphaera* NOEL, which are considerably larger than *C. margereli* NOEL, being approximately  $9.0 \times 6.0 \mu$  in size. These specimens have been referred to on the range charts as *Cyclagelosphaera* sp. (large).

### Genus Calolithus NOEL 1965

Type species: by monotypy; Calolithus martelae NOEL 1965; Jurassic (Oxfordian), France.

Remarks. - REINHARDT (1971, p. 32) and ROOD, HAY & BARNARD (1971, p. 268) consider Calolithus NOEL to be a junior subjective synonym of Watznaueria REIN-HARDT, the type material of the former genus being fragmentary. Neither author gives any further synonymy or assignation of the type species Calolithus martelae NOEL. However, Calolithus martelae has one less inner ring of plates on the distal shield than species of Watzaueria REINHARDT and the two genera are here regarded as distinct. NOEL (1965b, Pl. xv, Fig. 2-4, 6) has figured coccoliths with a fully developed central area, but still distinctive of Calolithus. Coccospheres have also been found by the writer (EM433, EM3236, SEM 76/12548), which are not fragmentary; furthermore, resorption of calcium carbonate in the living cyst would have disarticulated the coccoliths and post-mortem weathering would not have given the state of preservation seen in most of the specimens. BLACK (1973, p. 72) also considers Calolithus to be a valid genus.

BLACK (1971, p. 617) places *Calolithus* in the Actinosphaeroideae NOEL 1965 "in which two shields are united at the inner border of the distal shield, without the development of a tubular connecting structure ... In *Calolithus* NOEL there is a zone in which the proximal rays are contracted so as to form a ring of slots or pits, concentric with the large central opening."

#### Calolithus martelae NOËL 1965

Pl. 8, Fig. 6

1965a	Calolithus martelae NOEL, p. 9, Textfig. 50-52.
1968	Coccolithus perforatus: HAG, p. 23, Pl. vi, Fig. 1-3.
1968	Coccolithus coronatus: GARTNER, p. 17, Pl. xxiii, Fig. 27.
1969	Watznaueria martelae: BUKRY, p. 32, Pl. xi, Fig. 3-5.

*Remarks.* - This species has been recovered only from the top of the Ampthill Clay and the Lower Kimmeridge Clay in the borehole material examined. It has also been found in a few surface samples from localities in the Oxford Clay (MEDD 1971), and BUKRY (1969) has recorded the species from the Campanian of the USA and Germany.

## Genus Actinosphaera NOEL 1965

Type species: by monotypy; Actinosphaera deflandrei NOEL 1965b; Upper Jurassic, Algeria.

## Actinosphaera deflandrei NOEL 1965 Pl. 8, Fig. 3-4

1965b Actinosphaera deflandrei NOEL, p. 133, Pl. xviii, Fig. 4-8; Pl. xix, Fig. 2, 6-8.

*Remarks.* – Rare specimens of this species have been seen in some samples from the Haddenham and Gamlingay boreholes.

## Family Thoracosphaeraceae DEFLANDRE 1952

### Genus Thoracosphaera KAMPTNER 1927

Type species: by original designation; *Thoracosphaera pelagica* KAMPTNER 1927; Recent, Cosmopolitan.

## Thoracosphaera deflandrei KAMPTNER 1956 Pl. 7, Fig. 11

1956 Thoracosphaera deflandrei KAMPTNER, p. 448, Textfig. 1-4.

*Remarks.* – This species has been recovered from many of the borehole samples examined, as is shown in the distribution charts.

### Thoracosphaera saxea STRADNER 1961

1961 Thoracosphaera saxea STRADNER, p. 84, Textfig. 71.

*Remarks.* – This form has been seen in the Haddenham Borehole sample from a depth of 240 feet (73.15 m). The crystallites are much larger than those of *T. deflandrei*.

Genus Schizosphaerella Deflandre & Dangeard 1938

Type species: by original designation; Schizosphaerella punctulata DEFLANDRE & DANGEARD 1938; Jurassic, France.

Schizosphaerella punctulata DEFLANDRE & DANGEARD 1938 Pl. 7, Fig. 12

1938 Schizosphaerella punctulata DEFLANDRE & DANGEARD, p. 115, Textfig. 1-6.
 1961 Nannopatina grandaeva STRADNER, p. 78, Textfig. 1-10.

*Remarks.* - This species has been recovered from the top of the Oxford Clay in the Haddenham and the Gamlingay boreholes. There is a possibility of these specimens being reworked from older beds.

### Incertae sedis

## Genus Loxolithus Noël 1965

Type species: by monotypy; Cyclolithus armilla BLACK & BARNES 1959; Upper Cretaceous, England.

### Loxolithus sp.

1965a	Loxolithus sp. NOEL, p. 3.
1965b	Loxolithus sp.: NOEL, p. 66.
1971	Loxolithus sp.: MEDD, p. 826, Pl. iv, Fig. 1.

*Remarks.* – This rare form has been seen in the optical microscope investigation of material from the Upper Oxford Clay of the Gamlingay Borehole at 60 feet (18.29 m). The generic assignation is provisional only.

## Genus Tetralithus GARDET 1955

Type species: by monotypy; *Tetralithus pyramidus* GARDET 1955; Miocene, Algeria.

**Remarks.** – PARKE (1971, p. 929) discusses the life histories of several haptophycean coccolithophorids and concludes that "calcareous elements, sometimes identical with the fossil genus *Tetralithus* are deposited in the mucilaginous matrix surrounding the benthic phase in the majority of the genera".

### Tetralithus gothicus DEFLANDRE 1959

1959 Tetralithus gothicus DEFLANDRE, p. 138, Pl. iii, Fig. 25.

*Remarks.* - This species has been recovered from most of the borehole samples examined. STRADNER & PAPP (1961) have also recorded it from the Palaeocene. K. Perch-Nielsen (pers. commun.) does not accept that these Jurassic forms should be assigned to *T. gothicus*, as this species should evolve in the Upper Cretaceous. However, the forms do consist of four hemi-scalenohedral crystals interlocking to a common centre with "peg-like" dovetailing (see MEDD 1971, Pl. ii, Fig. 3), and the writer considers that *T. gothicus* is available for these coccoliths.

## **Biostratigraphy and conclusions**

The Jurassic zonal schemes published by BARNARD & HAY (1975) and THIER-STEIN (1976) need revising since many of the index species found in the three boreholes have biostratigraphical ranges outside of their zonal limits. Revised zonations of the Middle and Upper Jurassic strata and of the Jurassic/Cretaceous boundary, together with analysis of this previous work, are the subjects of separate future papers.

A comparison of the species occurrences (as given in Tables 2-4) with the total known ranges (given in the Appendix) provides some indication as to the usefulness of those species cited by the above two authors.

A summary of that part of the coccolith biostratigraphy for the interval covered by the three boreholes, which will be published in the future paper, gives the Callovian/Oxfordian boundary coinciding with the coccolith *Podorhabdus rahla / Stephanolithion bigoti maximum* zones boundary. This latter zone continues up to the ammonite *tenuiserratum* Zone of the Oxfordian, when it, in turn, is replaced by the coccolith *Actinozygus geometricus* Zone. This latter zone continues to the top of the three boreholes studied (Kimmeridgian, ammonite *eudoxus* Zone). A further