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Autor: Kaenel, Eric de / Bergen, James A.
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New Early and Middle Jurassic coccolith taxa and biostratigraphy from the eastern proto-Atlantic (Morocco, Portugal and DSDP Site 547 B)

By ERIC de KAENEL ¹⁾ and JAMES A. BERGEN ²⁾

ABSTRACT

Lower to Middle Jurassic basinal marl/limestone sections in the Lusitanian Basin of Portugal and the High Atlas of Morocco contain nearly continuous successions of calcareous nannofossil assemblages. Many of the nannofossil bioevents identified in this paper have been calibrated to the ammonite biostratigraphy in these basins. The definition of precise species concepts is fundamental to recognizing these events and eliminating diachroneity apparent in the published stratigraphic ranges of previously-described taxa. The marine sediments in these basins also provide new information about the origin and early evolution of a major group of Mesozoic coccoliths, the Order Podorhabdales. Early developments within this order are related to changes in coccolith rim construction. This is reflected in significant taxonomic revisions of the two oldest families within this order of coccoliths, the Bussoniaceae and the Biscutaceae.

One new genus and nine new species are described: *Similiscutum*, *Similiscutum orbiculus*, *Similiscutum avitum*, *Similiscutum cruciulus*, *Similiscutum precarium*, *Similiscutum gephyrion*, *Biscutum profundum*, *Triscutum sullivanii*, *Triscutum tiziense*, and *Triscutum pricatillus*. Two families, four genera, and one species are emended. Five new combinations are proposed.

RÉSUMÉ

Une série de sections marneuses et calcaires du Jurassique inférieur et moyen des bassins de Lusitanie, Portugal, et du Haut Atlas, Maroc, contiennent une succession presque continue de nannofossiles calcaires. De nombreux bioévénements de nannofossiles identifiés dans ce travail, ont été calibré selon la biostratigraphie des ammonites de ces bassins. La définition de concepts taxonomiques précis est fondamentale pour reconnaître ces événements et pour résoudre l'apparente diachronéité des successions stratigraphiques des taxa précédemment décrits dans la littérature. De plus, les sédiments marins de ces bassins fournissent de nouvelles informations quant à l'origine et à l'évolution d'un groupe majeur de coccolithe du Mésozoïque, l'ordre des Podorhabdales. Le développement premier de cet ordre est lié aux changements de la construction de la marge des coccolithes. Ceci a amené des révisions taxonomiques significatives des deux plus anciennes familles de cet ordre, les Bussoniaceae et les Biscutaceae.

Un nouveau genre et neuf nouvelles espèces sont décrites: *Similiscutum*, *Similiscutum orbiculus*, *Similiscutum avitum*, *Similiscutum cruciulus*, *Similiscutum precarium*, *Similiscutum gephyrion*, *Biscutum profundum*, *Triscutum sullivanii*, *Triscutum tiziense*, et *Triscutum pricatillus*. Deux familles, quatre genres, et une espèce sont amendés. Cinq nouvelles combinaisons sont proposées.

1. Introduction

There has been renewed interest in the study of Jurassic calcareous nannofossils within the past six years. Bown (1987 b) proposed the first comprehensive classification

¹⁾ Department of Geology, Florida State University, Tallahassee, FL 32306, USA.

²⁾ Amoco Production Company, 501 WestLake Park Boulevard, Box Office 3092, Houston, TX 77253, USA.

of Liassic calcareous nannofossils. He identified the major taxonomic groups in the Jurassic and demonstrated the importance of rim ultrastructure in their classification and evolution. Some of these ideas on evolution built upon the landmark paper on Early Jurassic coccoliths published by Prins (1969).

Although the major taxonomic groups have now been identified and researchers are beginning to understand the evolution of this fossil group during the Jurassic, species concepts have not yet stabilized. Only a handful of speciation events have been identified as widespread biohorizons among the various researchers at the Workshop of the International Nannoplankton Association, London 1990, but this may be due largely to different taxonomic concepts among micropaleontologists. This stresses the need to fully document new species.

The small size of calcareous nannofossils is an advantage to the biostratigrapher because a very large number of specimens can be observed during each sample analysis. However, their size is a hindrance to taxonomic work because individual specimens cannot be reoriented (proximal and distal views) or their optical properties (light microscope) and ultrastructure (electron microscope) easily documented. The earliest taxonomic descriptions of Jurassic calcareous nannofossils were based on holotypes illustrated as hand-drawings (Deflandre & Dangeard 1938, Deflandre 1952, Deflandre & Fert 1954, Noël 1957, 1959, Stradner 1963), although Deflandre & Fert (1954) also published light photomicrographs with their newly described taxa. Such drawings often lack the necessary detail to identify specimens with the light microscope (LM) and cause obvious taxonomic problems. A resurgence in Jurassic calcareous nannofossil research during the late 1960's and 1970's was stimulated by widespread availability of the electron microscope. The publication of a number of important taxonomic papers (Noël 1965, 1973, Medd 1971, 1979, Rood, Hay & Barnard 1971, 1973, Rood & Barnard 1972, Grün, Prins & Zweili 1974, Grün & Zweili 1980, Goy 1981) coincided with the first attempts towards a general biostratigraphic zonation of the Jurassic. Many of these taxonomic studies relied either heavily or exclusively on the electron microscope. This has created some taxonomic problems because routine biostratigraphic work is based on light microscope observations. More recent publications have illustrated taxa in both techniques; however, this does not always eliminate all doubt in identifications. Specimen transfer techniques between the light microscope and electron microscope are sometimes needed to eliminate uncertainties. Unfortunately, such procedures consume time.

The current paper is an outgrowth of detailed investigations on the calcareous nannofossils in the Lusitanian Basin in Portugal (Bergen) and the High Atlas of Morocco (de Kaenel). Refined biozonations have been developed within these basins and many similarities exist between the assemblages recovered from these two basins. The new taxa common to these two studies are described herein.

2. Provenance of material

The Lusitanian Basin of northern Portugal and the High Atlas Region of Morocco (Figure 1) were both active, proto-Atlantic rift basins during the Jurassic. Initial Mesozoic rifting commenced in both basins during the late Triassic. Open marine conditions were established in the deep portions of these basins during late Sinemurian time, marked

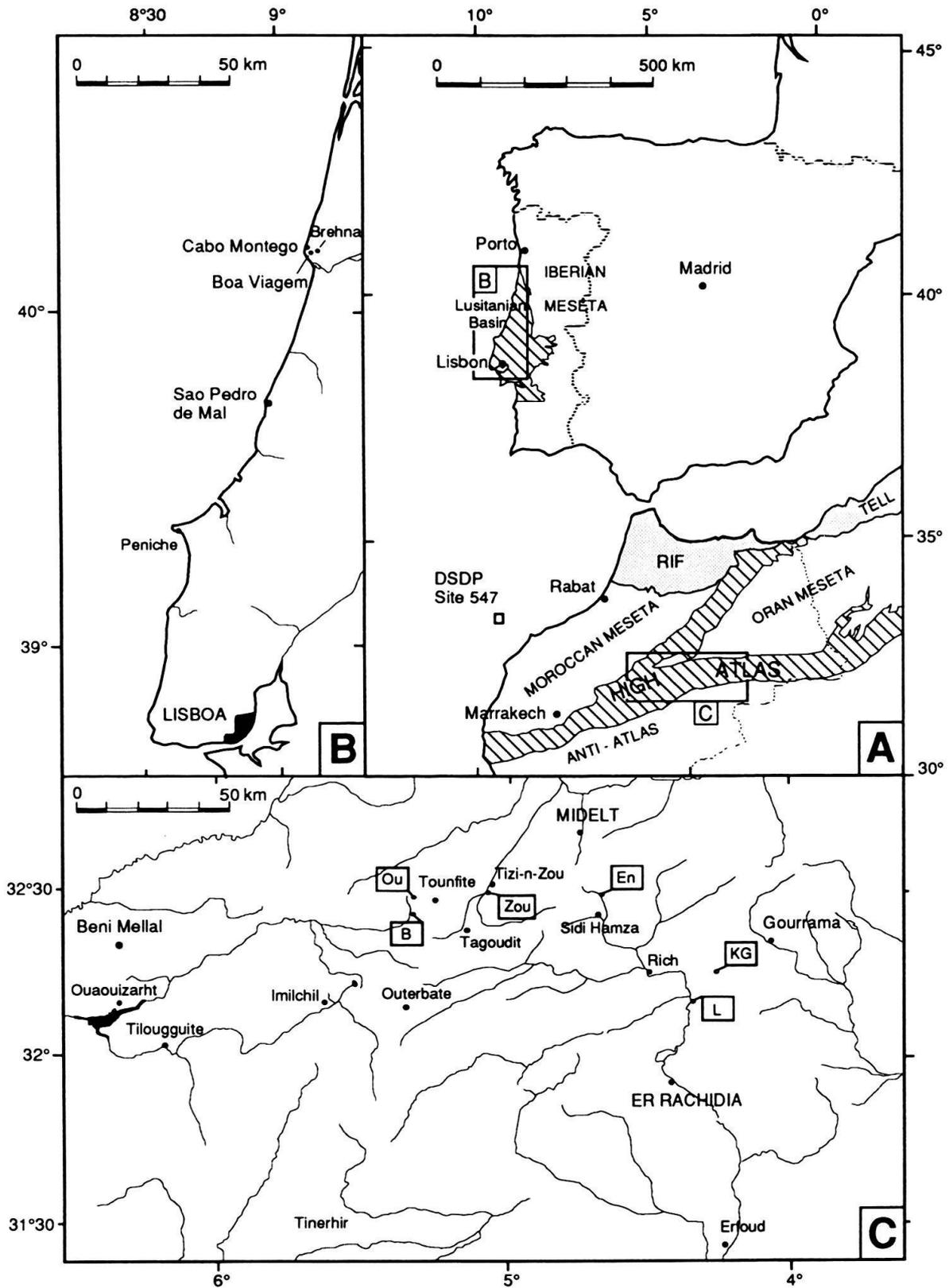


Figure 1. A: Location of Lusitanian and High Atlas basins. B and C: Enlargement of the studied area in Portugal (Lusitanian Basin) and in Morocco (Central High Atlas) showing the location of outcrops studied.

by the deposition of limestone/marl beds containing ammonites and calcareous nanofossils. Normal marine conditions persisted throughout the Early Jurassic and into the Middle Jurassic in both basins. A Middle Callovian/Upper Oxfordian unconformity truncates the succession in the Lusitanian Basin, whereas marine carbonates containing ammonites and calcareous nanofossils do not occur any higher than the upper Bajocian in the Central High Atlas Basin. One significant difference between the Lower-Middle Jurassic sections in these two basins are the much higher sedimentation rates in the High Atlas.

The ammonites provide a biostratigraphic framework for the calcareous nanofossil studies in both Portugal and Morocco (Figure 2). The ammonite fauna in the Moroccan Jurassic is Tethyan, whereas those from the Lusitanian Basin in Portugal have more Boreal components.

2.1 Portugal

The oldest Mesozoic sediments in the Lusitanian Basin are marginal marine to non-marine deposits, consisting of conglomerates, sandstones, shales, dolomites, and evaporites. Palynological analyses indicate these sediments are late Triassic-Hettangian in age (Doubinger et al. 1970). The Sinemurian Coimbra Beds, consisting of dolomites and limestones, were deposited basinwide upon this complex combination of facies. An open marine facies consisting of an alternating series of marls and limestones first developed in the western portion of the basin during the late Sinemurian. Ammonites became common throughout this portion of the basin during the latest Sinemurian (Wilson & Exton 1979), a time when the first calcareous nanofossils were deposited. The area of limestone-marl deposition expanded during the Pliensbachian. By the early Toarcian, this facies has reached its maximum extent (Wilson & Exton 1979). This trend was changed in the late Toarcian as sedimentation became progressively more calcareous; it continued until carbonate shelf deposits covered most of the basin by Bathonian time (Stam 1986). Two separate basins developed during the Callovian, each containing marine deposits with common ammonites. Salt diapirism and renewed movements across basement faults contributed to the formation of these two sub-basins and controlled facies distributions for the remainder of the Jurassic (Wilson & Exton 1979, Stam 1986).

Five Lower-Middle Jurassic sections were sampled in the Lusitanian Basin. Lower Jurassic section was sampled at three widely separate localities (Figures 1, 2). The Middle Jurassic was sampled at three localities along an east-west trending outcrop belt north of Figueira de Foz. Both the Lower and Middle Jurassic crop out along the road east of Brehna. The entire Middle Jurassic succession is exposed at Cape Mondego. Lithologic descriptions of these sections and their ammonite biostratigraphy are as follows: Peniche (Mouterde 1955), Sao Pedro de Mal (Mouterde 1967), Brehna Road (Schott & Stasche 1957, Ruget-Perrot 1961, Mouterde et al. 1980), Cape Mondego (Ruget-Perrot 1961, Rocha et al. 1981), and Boa Viagem-Quiaios (Ruget-Perrot 1961, Mouterde et al. 1978). Hamilton (1977, 1979) published biostratigraphic studies of the calcareous nanofossils from the Brehna Road, Cape Mondego, and Peniche sections prior to most of the detailed descriptions of the ammonite biostratigraphy.

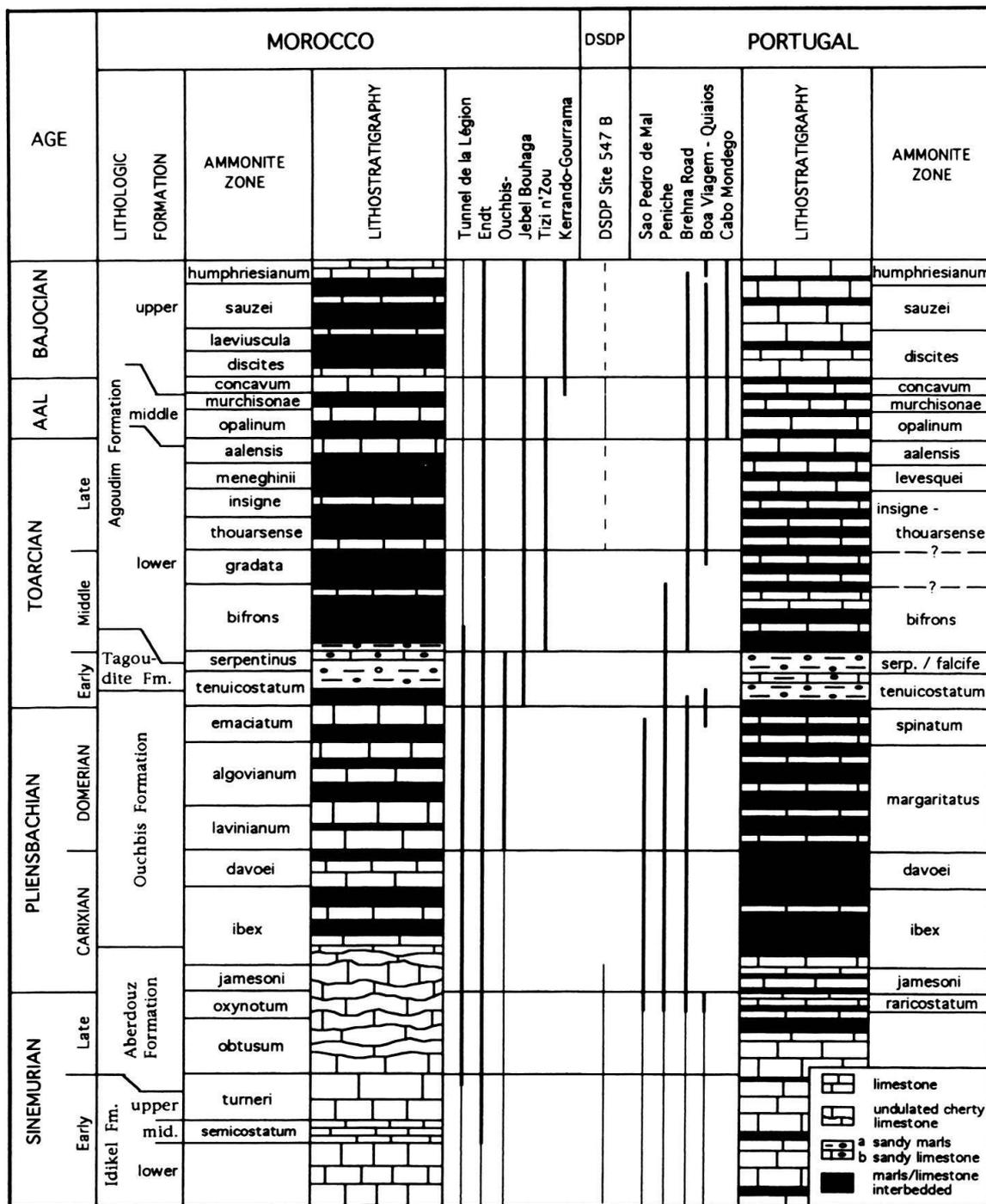


Figure 2. Stratigraphy and lithostratigraphy of Moroccan and Portuguese sections with ammonite zonation and corresponding stratigraphic interval of DSDP Hole 547 B. Correlation with the lithologic Formations of the Central High Atlas. (intervals without ammonite biostratigraphy are indicated by a thin line).

2.2 Morocco

The Central High Atlas mountains of Morocco (Figure 1) include the site of Triassic to Middle Jurassic basins, oriented SW-NE, which contain marine to non-marine sediments. Above the shales and basalts of the Triassic (Infraliasic Formation) are lower

Liassic limestones, dolomites and shales, which are more than 1000 m in thickness (Idikel, Aberdouz and Ouchbis Formations; Figure 2). The lower Toarcian (Tagoudite Formation) is represented by interbedded shales and siltstones, with minor amounts of grainstones. A marine facies consisting of an alternating series of limestones, shales, marls and calcareous siltstones developed from the Middle Toarcian through the Middle Bajocian. This formation (Agoudim Formation) may attain considerable thickness along the axial portions of the basins and may be more than 8000 meters thick. The deep water deposits of the Agoudim Formation are capped by corals reefs and by conglomerates, sandstones, clays and evaporites (Anemzi and "Couches rouges" Formations) representing the infilling of the Central High Atlas Basins. This change in depositional regime occurred earlier in the northern and southern parts of each basin (late Aalenian-early Bajocian) and had progressed to their centers by middle Bajocian time.

Fifteen Lower-Middle Jurassic sections were sampled in the Central High Atlas Basin. Six of these are well correlated with ammonite Zones (Figures 1, 2) and are used to analyse calcareous nannofossil bioevents. The other sections have been used to correlate lithological formations between the northern and southern part of the High Atlas basin. Together, the four sections on the Figure 1 (L: Tunnel de la Légion-Timri; En: Endt; Ou-B: Ouchbis-Jebel Bouhaga) contain a continuous succession of nannofossil assemblages from the Lower to Middle Jurassic (*semicostatum* Zone to *humphriesianum* Zone). Ouchbis and Jebel Bouhaga sections form a continuous sections of about 3500 m from the Jebel Ouchbis Anticlinal to the Tounfite Synclinal. Two other short sections were used to study the Toarcian – Bajocian interval (Zou: Tizi n'Zou; KG: Kerrando-Gourrama). Detailed nannofossil study has concentrated on intervals indicated in Figure 2 where ammonite control was possible. Lithologic descriptions of these sections are found in the following: Tunnel de la Légion-Timri (Bernasconi 1983), Endt (Brechtbühler 1984), Ouchbis-Jebel Bouhaga (Studer 1980, 1987), Tizi-n'Zou (Dubar, 1938; Sadki, study in progress) and Kerrando-Gourrama (Sadki et al. 1987).

2.3 D.S.D.P. Site 547

Deep Sea Drilling Project Site 547 is located on the northwest African margin off the coast of Morocco (Figure 1). The Jurassic section penetrated at this site consists of syn-rift and post-rift marine sediments deposited prior to the opening of the Atlantic. The Jurassic carbonates recovered from the Hole 547 B were separated into three lithologic units by the shipboard scientists (Hinz, Winterer et al. 1984). The Upper Jurassic is composed of bioclastic wackestones, limestones, conglomerates, and interbeds of claystones. The Middle Jurassic is composed of nodular limestones with a few interbeds of alternating boundstones and laminated claystones. The Middle Jurassic unconformably overlies Lower Jurassic nodular limestones within a matrix of calcareous mudstones and claystones.

The first calcareous nannofossil study at this site was by Wiegand (1984) during DSDP Leg 79 and later by Bown (1987 b), and is currently being investigated by Gardin (in prep.).

The coccolith assemblages recovered from Upper Jurassic section at this site are much less diverse than those in basins in the Western High Atlas and Portugal. The Middle Jurassic assemblages show more affinities to the Portuguese than the Moroccan

sections, but again, are less diverse than both. The Lower Jurassic assemblages contain taxa present in both the Morocco and Portuguese sections. According to the paleogeographic reconstruction (Biju-Duval et al. 1977), the proto-Atlantic trench did not connect directly with the High Atlas basins. Its connection with the Mesogea must have been further north at an interconnecting rift of the Azores-Gibraltar lines (Du Dresnay 1988).

3. Morphologic developments

The initial appearance of the placolith rim construction during the late Sinemurian was a major development in the early evolution of coccoliths. The placoliths rapidly diversified during the Pliensbachian. By the close of the Early Jurassic, all the Jurassic placolith families had been established.

The Bussoniaceae Goy (1981) and Biscutaceae Black (1971) are the oldest known placolith families. The Biscutaceae, with their non-imbricate, two-shield construction, were once considered the ancestral placolith family. Early morphologic developments within this family have been discussed in several publications (Prins 1969, Bown 1987a, b, Crux 1987a, Cobianchi 1992). Bown (1987b) demonstrated that placoliths with a three-shield construction (Bussoniaceae) form a distinct lineage separate from and pre-dating the Biscutaceae. He also provided the first comprehensive classification for the genera with a three-shield (tiered) rim construction and outlined their evolutionary trends. New evidence from the proto-Atlantic sites included in this paper has advanced our understanding of the early morphologic developments for the Bussoniaceae and Biscutaceae. This has resulted in new taxonomic concepts of these two families and their incorporated genera and species.

Family Bussoniaceae

All three Jurassic placolith genera with a three-shield (tiered) rim construction (Figure 3) are retained within the family Bussoniaceae in this paper and are distinguished by fundamental differences in distal shield construction (see taxonomic descriptions). The family originated during the late Sinemurian and is not known from strata younger than Kimmeridgian (Bown 1987b, Bown et al. 1988, this paper). Although the stratigraphic record of the early evolution of this group is fragmentary, two new pieces of information from Deep Sea Drilling Site 547 B and Portugal have led to a revision of their classification and evolutionary trends.

(1) Deep Sea Drilling Site 547 B contains the oldest known record of early placolith evolution. Bown (1987b) described *Mazaganella pulla*, which has a non-imbricate, horizontal distal shield, as the oldest placolith in this section. He also illustrated the evolution of *Mazaganella pulla* to *Triscutum protensum* by the vertical extension of the distal shield and the development of a prominent inner rim wall. Also present at the base of this section with *Mazaganella pulla* are very small specimens of a three-shield placolith having a vertical distal shield. This new species, *Triscutum pricatillus*, lacks the prominent, birefringent inner wall of *Triscutum protensum*. Larger specimens of *Triscutum pricatillus* are also present in the uppermost Sinemurian in Portugal.

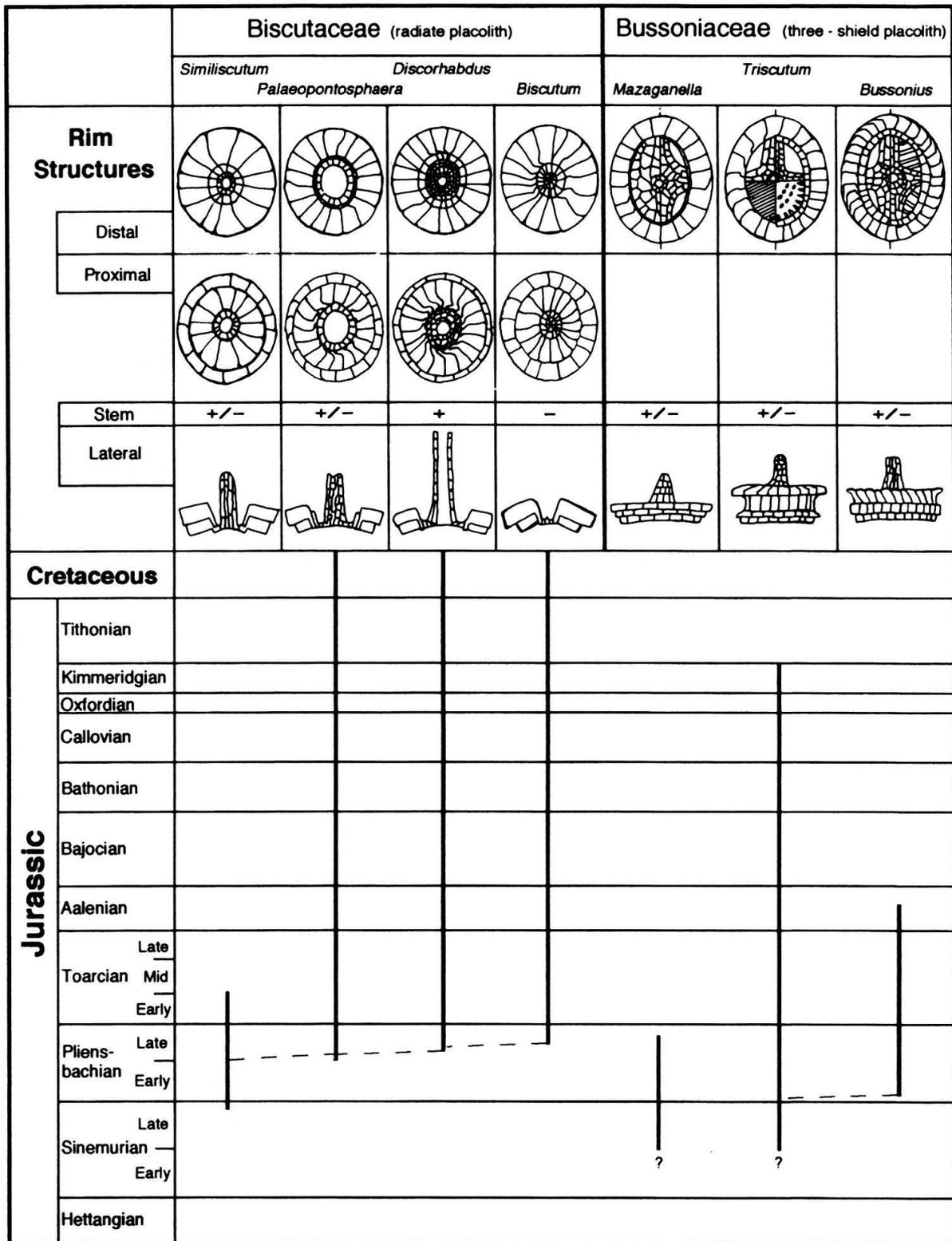


Figure 3. Overview of rim ultrastructure characteristics of genera in the Biscutaceae and Bussoniaceae, and their stratigraphic distribution.

2) Bown (1987b) considered *Bussonius* an evolutionary descendant of the imbricate placolith genus *Lotharingius*. He theorized that the protruding inner distal cycle of *Lotharingius barozii* expanded to form the discrete, distal shield with imbricate elements of *Bussonius prinsii*. Therefore, Bown (1987b) considered *Bussonius* unrelated to the tiered placoliths with non-imbricate distal shields, for which he erected the family Mazaganellaceae. This conclusion was based on the stratigraphic occurrence of *Lotharingius barozii* in older sediments than *Bussonius prinsii*. New stratigraphic evidence from Portugal (*Uptonia jamesoni* ammonite Zone) and DSDP Site 547B (Gardin 1991) demonstrates that *Bussonius prinsii* predates the first *Lotharingius*. *Bussonius prinsii* also shows close morphologic similarities to *Triscutum protensum*, differing only by its distal shield imbrication and presence of central lateral bars. Both species have now been reported from the lower Pliensbachian and older specimens of *Bussonius prinsii* are also characterized by a lower number of lateral bars.

The following conclusions are made:

(1) the oldest known placoliths have a non-imbricate, three-shield rim construction, no inner wall, and an axial cross-structure. We can no longer conclude whether the oldest species had either a horizontal or vertical distal shield;

(2) the development of an inner rim wall appears to be an important morphologic event. The inner wall is developed to various degrees in forms with non-imbricate distal shields and is characteristic of *Bussonius*, which has an imbricate distal shield;

(3) the development of an imbricate distal shield and central lateral bars characterizes the appearance of *Bussonius* during the earliest Pliensbachian. We believe *Bussonius* is related to the tiered placoliths with non-imbricate shields and is ancestral to the imbricate placolith genus *Lotharingius*; and

(4) all known Sinemurian-Pliensbachian Bussoniaceae have axial central structures.

Family Biscutaceae

The Biscutaceae are the oldest known placoliths with a two-shield rim construction that appeared near the end of the Sinemurian (Figure 3). These radiate placoliths rapidly diversified during the Pliensbachian and are present throughout the remainder of the Mesozoic. The Biscutaceae survived the end of Cretaceous mass extinction event, but are not known from strata younger than Paleocene.

The early evolution of this group during the Pliensbachian suggests a revised generic classification based on rim construction. The oldest Biscutaceae show considerable variations in coccolith outline and central area construction. However, all these early forms are characterized by a birefringent inner rim cycle that results from a proximally protruding inner rim cycle of the proximal shield (**collar**). A new genus, *Similiscutum*, is created for coccoliths with this rim construction. This genus is restricted to the late Sinemurian to early Toarcian. The three genera which evolved from *Similiscutum* during the Pliensbachian survived into the Cretaceous.

The development of an inner distal rim cycle (**wall**) during the early Pliensbachian is characterized by the genus *Palaeopontosphaera*. This genus displays a bicyclic rim extinction pattern similar to *Similiscutum*. The Jurassic *Palaeopontosphaera* have steep inner distal cycles; elliptical outlines, central cross structures and distal central projections are

CHARACTERISTIC FEATURES	Outline			Distal shield cycle		Proximal shield cycle			Central area						Rim extinction pattern				
	elliptical	broadly elliptical	circular	unicyclic	bicyclic inner cycle	unicyclic	collar	bicyclic	Open		closed / imperforate	element cycle	bar	cross	stem	unicyclic	bicyclic	rim cycle	
									wide	narrow								outer	collar
BISCUTACEAE																			
<i>Similiscutum</i>	+	+	+	+		+	+	+		+	+		+	+	+		+	faint	white
<i>S. avitum</i>	+	+		+		+	+	+		+									
<i>S. cruciulus</i>		+	+	+		+	+	+						+	+				
<i>S. finchii</i>	+			+		+	+			+			+						
<i>S. gephyrion</i>	+			+		+	+			+			+				base		
<i>S. orbiculus</i>		+	+	+		+	+			+									
<i>S. precarious</i>	+	+		+		+	+			+				+	+				
<i>Palaeopontosphaera</i>	+	+	+		+			+	+	+			+	+	+		+	weakly bare fr.	white
<i>P. dubia</i>	+	+			+			+		+				+	+				
<i>P. erismata</i>	+				+			+	+	+				+	+				
<i>Discorhabdus</i>	+	+	+	+		+				+					+			faint	
<i>D. novus</i>	+	+	+	+		+				+					+				
<i>Biscutum</i>	+	+	+	+		+				+	+				+			weakly bare fr.	
<i>B. profundum</i>		+	+	+		+				+	+								
<i>B. striatum</i>		+	+	+		+				+									
<i>B. criotum</i>		+	+	+		+				+	+								

Figure 4. Overview of characteristics of genera and species of Jurassic Biscutaceae.

typical. Circular outlines and imperforate central areas may have developed during the Late Jurassic.

The late Pliensbachian saw the introduction of the new rim construction represented by the genera *Discorhabdus* and *Biscutum*. These genera are constructed of two unicyclic shields which display a unicyclic rim extinction pattern. The *Discorhabdus* lineage is characterized by a delicate central distal projection. Although common in the Jurassic, rare occurrences of *Discorhabdus* are also known from the Lower Cretaceous. In contrast, *Biscutum* survived into the early Cenozoic. Both of these genera typically have circular to subcircular outlines while their early representatives have deep central areas.

Figure 4 gives an overview of the characteristics mentioned above for the four Biscutaceae genera discussed above and described below in this paper (*Similiscutum*, *Palaeopontosphaera*, *Discorhabdus*, and *Biscutum*).

Figure 5 gives a correlation of ammonite biostratigraphy with calcareous nannofossil events discussed below for sections in the Lusitanian Basin of Portugal and in the High Atlas of Morocco. More stratigraphic occurrence details on Biscutaceae and Bussoniaceae species are also indicated in the discussion of each taxa.

4. Taxonomic descriptions

The descriptive and taxonomic nomenclature used in this paper is largely based on the terminology proposed by Bown (1987 a, b) and Young (in prep.). The main differ-

AGE	AMMONITE ZONE MOROCCO	NANNOFOSSIL EVENTS			AMMONITE ZONE PORTUGAL
		LAST OCCURRENCE FIRST OCCURRENCE	EXACT FIRST OR LAST OCCURRENCES UNCERTAIN	PRESENT	
BAJOCIAN	EARLY	humphriesianum			humphriesianum
		sauzei		<i>Triscutum sullivanii</i>	sauzei
		laeviuscula	<i>Biscutum profundum</i>	<i>Triscutum tiziense</i> <i>Biscutum profundum</i> / <i>Triscutum pricatillus</i>	discites
		discites	<i>Triscutum tiziense</i> <i>Triscutum sullivanii</i>		
AALENIAN		concovum			concovum
		murchisonae	<i>Triscutum sullivanii</i>	<i>Triscutum sullivanii</i>	murchisonae
		opalinum	<i>Triscutum tiziense</i>	<i>Triscutum tiziense</i>	opalinum
TOARCIAN	LATE	aalensis			aalensis
		meneghinii			levesquei
		insigne			insigne - thouarsense
		thouarsense			— ? —
	MIDDLE	gradata			— ? —
		bifrons			bifrons
	EARLY	serpentinus	<i>Similiscutum finchii</i>	<i>Biscutum striatum</i> <i>Similiscutum finchii</i>	serp. / falc.
		tenuicostatum	<i>Biscutum striatum</i> <i>Similiscutum orbiculus</i> / <i>Similiscutum avitum</i> <i>Similiscutum cruciulus</i>	<i>Similiscutum cruciulus</i>	tenuicostatum
DOMERIAN	emaciatum	<i>Similiscutum gephyrion</i>	<i>Similiscutum precarium</i>	spinatum	
	algovianum	<i>Biscutum profundum</i>	<i>Similiscutum avitum</i> / <i>Similiscutum gephyrion</i> <i>Biscutum profundum</i>	margaritatus	
	lavinianum	<i>Discorhabdus novus</i> <i>Palaeopontosphaera dubia</i> <i>Similiscutum finchii</i>	<i>Discorhabdus novus</i> <i>Palaeopontosphaera dubia</i>		
	davoei	<i>Similiscutum orbiculus</i> (> 4.3 µm)	<i>Lotharingius</i> spp. <i>Similiscutum finchii</i>	davoei	
CARIXIAN	ibex	<i>Similiscutum avitum</i> / <i>Similiscutum cruciulus</i>	<i>Similiscutum orbiculus</i> <i>Bussonius prinsii</i> <i>Similiscutum cruciulus</i>	ibex	
	jamesoni	<i>Similiscutum orbiculus</i>	<i>Similiscutum precarium</i>	jamesoni	
			<i>Triscutum pricatillus</i>	raricostatum	
SINEMURIAN	LATE	oxynotum			
		obtusum		<i>Mazaganella pulla</i> / <i>Triscutum pricatillus</i>	DSDP 547B
	EARLY	turneri			

Figure 5. Correlation of ammonite biostratigraphy with Late Sinemurian to Early Bajocian calcareous nannofossil events from Morocco and Portugal. Two important nannofossil occurrences from Site 547 B are also included at the base of the Lusitanian events.

ences in the nomenclature used in this paper concern the rim structures and the corresponding rim extinction patterns. The rim extinction pattern can be unicyclic or bicyclic. A bicyclic rim extinction pattern is observed when a second inner distal rim cycle (**wall**) is present or when a **collar** is developed on the proximal shield. A collar corresponds to a narrow inner rim cycle in the birefringence pattern which encircles the central area. A collar is a small structure of the proximal shield related to the proximally development of the shield elements near the inner edge of the proximal shield. In some cases, this protrusion may form a distinct inner proximal cycle. The birefringence pattern of the collar is due to a different crystallographic orientation of the protruding crystals.

Size refers to coccolith length unless otherwise specified. General descriptive terms for size are given by Young (in prep.): Very small coccoliths correspond to specimens < 3.0 μm , small (3.0 to < 5.0 μm), medium (5.0 to < 8.0 μm), large (8.0 to 12.0 μm) and very large (> 12.0 μm). Species descriptions include both the optical properties (LM) and the ultrastructure (SEM) of the coccoliths. Abbreviations are used for the lowest occurrence (LO) and for the highest occurrence (HO).

Light microscopic slides and scanning electron microscope photographic negatives are deposited at the Florida State University (USA) in the collections of the nannofossil laboratory of the department of Geology. Negative numbers (films and frames) are used as types.

Class **Prymnesiophyceae** HIBBERD 1976

Order **Podorhabdales** ROOD, HAY & BARNARD 1971 emend. Bown 1987b

Family **Biscutaceae** BLACK 1971 emend. Bown 1987b

Diagnosis. – “Radiating placolith coccoliths (i.e. composed of non-imbricating, radially arranged rim elements), with broad shields and a small central area which may be imperforate, vacant or spanned by a variety of central structures.” (Bown 1987b, p. 40).

Discussion. – The family Biscutaceae was emended to include all the Mesozoic radiate placoliths (non-imbricate) with low, broad shields (see Bown 1987b). Such non-imbricate rim constructions are faint in cross-polarized light and appear dark blue in phase contrast illumination. Another significant optical characteristic of the Biscutaceae rim is the presence or absence of a brightly birefringent (1st order white) central collar (Figure 4). In *Palaeopontosphaera* NOËL (1965) and *Sollasites* BLACK (1967) this birefringent collar results from an inner distal cycle of elements (i.e. two rim cycles can be seen in distal view). This birefringent collar is not observed in the genera *Discorhabdus* NOËL (1965), and *Biscutum* BLACK (in Black & Barnes 1959) new emendation. These genera have unicyclic distal shields. A third structural group has been identified among the Jurassic Biscutaceae, including circular to elliptical forms. This new genus, *Similiscutum*, displays a bicyclic rim extinction pattern similar to *Palaeopontosphaera* or to *Biscutum criotum*. However, its birefringent inner rim cycle results from its unique proximal shield construction. *Similiscutum* is the oldest known genus of Biscutaceae.

Genus *Similiscutum* gen. nov.

Figure 3

Derivation of name. – From Latin *similis*, like, resembling and *scutum*, shield.

Type species. – *Similiscutum cruciulus* sp. nov.

Diagnosis. – Circular to elliptical Biscutaceae having a proximal shield constructed of elements that have a light proximal extension near the inner rim margin and may form a separate inner proximal cycle. The resulting rim extinction pattern is bicyclic with a bright, narrow inner rim cycle and a broad, faint outer rim cycle. The distal shield is unicyclic and the proximal shield is often visible at the base of the central area. The small central area may be imperforate, open or spanned by a variety of central structures.

Description. – Circular to elliptical placolith coccoliths constructed of two, broad, subhorizontal shields which are closely appressed. The shield elements are lath-shaped and non-imbricate. The proximal shield elements bend proximally to form a protruding inner rim margin or a separate, narrow inner proximal cycle of blocky elements. In distal view, the inner proximal shield margin is visible below the base of the distal shield. The distal shield is constructed of a single cycle of lath-shaped elements, which may have radial or slightly kinked sutures. The inner rim margin is relatively steep, forming a central distal depression. 12 to 18 rim elements were observed.

The small central area may be open, imperforate or spanned by a variety of cross-structures. Central structures, when present, are on the level of the proximal surface. A short distal spine may be present.

In the LM, species from this genus exhibit a bicyclic rim extinction pattern formed by a broad faint outer cycle and a narrow bright collar. This white collar, produced by a protruding cycle of elements, is optically distinct in cross-polarized light.

Differentiation. – *Similiscutum* differs from *Palaeopontosphaera* and *Sollasites* by its unicyclic distal shield construction (the proximal shield does not extend above the base of the distal shield). In the latter two genera, a distally-extended inner cycle of elements lines the central area (i.e. two cycles are visible in distal view). *Similiscutum* exhibits a rim extinction pattern similar to these two genera, although its inner rim cycle may be slightly less birefringent. *Discorhabdus* and *Biscutum* are distinguished from *Similiscutum* by their unicyclic rim extinction patterns and flat, unicyclic shields, which show no proximal or distal extension.

Discussion. – The forms described within this new Biscutaceae genus were first illustrated among *Palaeopontosphaera* by Prins (1969). *Similiscutum* is named for this ancestral group of Liassic Biscutaceae. Five new species are described and one new combination is introduced herein.

Occurrence. – *Similiscutum* is the oldest known placolith genus constructed of two shields, ranging from the late Sinemurian to early Toarcian. The genus is present at DSDP Site 547B and sections in Morocco, Portugal, Italy, France, Switzerland, and northwest Europe.

Similiscutum orbiculus sp. nov.

Plate 1, Figures 1–11

1969 *Palaeopontosphaera repleta* PRINS, pl. 2, fig. 11 (nomen nudum).

1986 *Biscutum* sp. YOUNG et al., p. 124; plate, fig. F.

Derivation of name. – From Latin *orbiculus*, small circle.

Diagnosis. – A very small to small, subcircular to circular species of *Similiscutum* with a small central perforation.

Description. – Subcircular to circular placoliths composed of two subhorizontal, closely adpressed, broad shields. The distal shield is larger than the proximal shield. Shield elements are non-imbricate and have radial sutures. The proximal shield contains one cycle of elements. The proximal shield elements extend proximally at the inner rim margin, forming a narrow collar around the small central opening. It is visible at the base of the central area in distal view where it is joined to the base of the distal shield. The inner rim margin is relatively steep, forming a central distal depression.

In the LM, the rim extinction pattern is bicyclic. It consists of a narrow, birefringent (low 1st order white) inner rim cycle and a faint, broad outer rim cycle. Both shields can be easily distinguished when focusing up and down upon specimens. The individual rim elements can also be distinguished, giving both shields a striated appearance. In phase contrast, the rim appears dark gray, as is characteristic for the genus.

Length or diameter. – 2.7 to 4.7 μm .

Discussion. – Specimens observed have between 12 to 17 rim elements. Smaller specimens have fewer rim elements (12–15) and an early stratigraphic occurrence (down into the upper Sinemurian). Specimens 4.3 μm or larger first occur in the early Pliensbachian (*davoei* Zone). The central pore is less than one-fifth of the coccolith size.

Differentiation. – *Similiscutum orbiculus* differs from *Similiscutum cruciulus* by having no cross structure and from *Similiscutum avitum* by its subcircular to circular outline. *Similiscutum orbiculus* may also be confused with the oldest species of *Discorhabdus* and *Biscutum*, which did not appear until the late Pliensbachian. *Discorhabdus novus* (GOY 1979) n. comb., and *Biscutum striatum* (MOSHKOVITZ & EHRLICH 1976) n. comb. lack the proximally extended collar of *Similiscutum* and therefore have unicyclic rim extinction patterns. *Discorhabdus novus* is further distinguished by its distal spine.

Occurrence.

- Northwest Europe (Prins 1969). LO: *spinatum* Zone. HO: *tenuicostatum* Zone.
- Switzerland (de Kaenel). LO: base *ibex* Zone. HO: *tenuicostatum* Zone.
- Morocco (de Kaenel). LO: *jamesoni* Zone. HO: *tenuicostatum* Zone.
- Portugal (Bergen). present; stratigraphic range not yet determined.

Holotype. Plate 1, Figures 11 a, b (same specimen: FSU-F7-D29, FSU-F7-D27).

Type level. Sample L 34, *algovianum* Zone.

Type locality. Tunnel de la Légion, Morocco.

Similiscutum avitum sp. nov.

Plate 1, Figures 12–14; Plate 2, Figures 1–4

1977 *Calculus cribrum* (NOËL 1973); Hamilton, p 586; pl 1, fig. 9.

1990 *Biscutum novum* (GOY 1979) BOWN 1987 a; Cobianchi, p. 134; fig. 4 b.

1992 *Biscutum novum* (GOY 1979) BOWN 1987 a; Cobianchi (partim), p. 92–93; fig. 19b (non figs. 19c, d).

Derivation of name. – From Latin *avitus*, ancestral.

Diagnosis. – A small, normally to broadly elliptical species of *Similiscutum* with an open central area.

Description. – Elliptical placoliths composed of two subhorizontal, broad shields. The distal shield is larger than the proximal shield. Shield elements are non-imbricate and have radial sutures. The proximal shield contains two elements cycles. The narrow inner cycle extends below the base of the broad outer cycle and is connected to the base of the

inner margin of the distal shield (visible at the base of the central area in distal view). A central perforation is present.

In the LM, the rim extinction pattern is bicyclic, consisting of a thin, birefringent (1st order white) inner rim cycle and a faint, broad outer rim cycle.

Length. – 3.3 to 5.0 μm .

Discussion. – Specimens observed have between 13 to 17 rim elements. The length of the central pore is less than one-fourth of the coccolith length.

Differentiation. – *Similiscutum avitum* is distinguished from *Similiscutum orbiculus* by its elliptical shape and from *Similiscutum cruciulus* by its elliptical shape and lack of the central structure. *Similiscutum precarium* is elliptical, but has a central cross structure. Other elliptical Biscutaceae which occur in the Pliensbachian belong to the genus *Palaeopontosphaera*, and have brightly birefringent inner distal cycles and central cross structures.

Occurrence.

- Switzerland (de Kaenel). LO: base *ibex* Zone. HO: top *spinatum* Zone.
- Morocco (de Kaenel). LO: base *ibex* Zone. HO: top *emaciatum* Zone.
- Portugal (Bergen). *margaritatus* Zone (incomplete stratigraphic range).

Holotype. Plate 1, Figure 13 (APR-1370).

Type level. Sample SP 33, upper Pliensbachian (*margaritatus* Zone).

Type locality. Sao Pedro de Mal, Portugal.

Similiscutum cruciulus sp. nov.

Plate 2, Figures 5–11

1987b *Biscutum dubium* (NOËL 1965) GRÜN in Grün et al. 1974; Crux p. 89; pl. 2, figs. 4–7.

1990 *Biscutum* aff. *novum* (GOY 1979) BOWN, 1987a; Cobianchi, p. 134, 136; fig. 4c.

1992 *Biscutum* aff. *B. novum* (GOY 1979) BOWN, 1987a; Cobianchi (partim), p. 93; fig. 19e (non fig. 18).

Derivation of name. – From Latin *crux*, cross.

Diagnosis. A small to medium-sized, subcircular species of *Similiscutum* with a small central opening spanned by a cross, which may support a distal projection.

Description. – Subcircular placoliths composed of two subhorizontal, broad shields. Shield elements are non-imbricate and have radial sutures. The proximal shield is bicyclic; the narrow inner rim cycle is separated from the broad outer cycle by a distinct suture. The inner margin of the unicyclic distal shield is steep and inward sloping. A small central opening is spanned by a delicate cross structure. The elements of the cross structure are built up at the center, forming a hollow distal node.

In the LM, the rim extinction pattern is bicyclic. It consists of a faint, broad outer rim cycle and a narrow birefringent (low 1st order white) inner rim cycle. The delicate central structure is faintly birefringent. The individual rim elements can be distinguished, giving the rim striated appearance. In phase contrast, the rim appears dark gray, as is characteristic for the genus.

Length or diameter. – 3.8 to 5.5 μm .

Discussion. – *Similiscutum cruciulus* and *Similiscutum precarium* both have central cross structures. The latter species is distinguished by its elliptical outline. *Similiscutum orbiculus* and *Similiscutum avitum* is further distinguished from *Similiscutum cruciulus* by its elliptical outline.

Discorhabdus novum and *Biscutum striatum* are other circular to subcircular Biscutaceae. These species display unicyclic rim extinction patterns, have no central cross structures and did not appear until the late Pliensbachian.

Occurrence.

- Morocco (de Kaenel). LO: base *ibex* Zone. HO: top *emaciatum* Zone.
- Portugal (Bergen). LO: *jamesoni* Zone. HO: lower Toarcian.
- DSDP Site 547B. LO: core 15, section 1, 45–47 cm (upper Sinemurian?).
- Italy (Cobianchi 1990). LO: upper Carixian. HO: lower Toarcian.
- Italy (Cobianchi 1992). LO: upper Carixian. HO: lower Toarcian (*serpentinus* Zone).

Holotype. Plate 2, Figure 9 (FSU-EM-336).

Type level. Sample SP 26, lower Pliensbachian (*ibex* Zone).

Type locality. Sao Pedro de Mal, Portugal.

Similiscutum precarium sp. nov.

Plate 2, Figures 12–15

- 1965 *Palaeopontosphaera dubia* NOËL (partim), p. 76–78; pl. 7, figs. 11–13 (non pl. 7, figs. 1–10; textfig. 8).
 1969 *Palaeopontosphaera veterna* PRINS, p. 554; pl. 2, fig. 9 (nomen nudum).
 non 1969 *Palaeopontosphaera veterna* PRINS ex Rood, Hay & Barnard 1973, p. 378–379; pl. 3, figs. 2–3.
 1973 *Palaeopontosphaera dubia* NOËL 1965; Rood, Hay & Barnard, p. 378; pl. 3, fig. 1.
 1974 *Palaeopontosphaera dubia* NOËL 1965; Barnard & Hay, pl. 2, fig. 2.

Derivation of name. – From Latin *precarius*, precarious.

Diagnosis. – A small to medium sized, normally to broadly elliptical species of *Similiscutum* with an axial central cross which may support a stem.

Description. – Elliptical placoliths composed of two subhorizontal, broad shields. The unicyclic distal shield is larger than the proximal shield. Shield elements are non-imbricate and have radial sutures. The inner margin of the distal shield is steep. An axial cross structure spans the small central area. A hollow distal spine base is present at its center.

In the LM, the rim extinction pattern is bicyclic. The narrow inner rim cycle is brightly birefringent. The broad outer rim cycle and the central structure are faintly birefringent.

Length. – 4.0 to 5.6 μm .

Differentiation. – *Similiscutum precarium* differs from *Palaeopontosphaera* by its unicyclic distal shield construction. However, its rim extinction pattern is similar to *Palaeopontosphaera*. *Palaeopontosphaera erismata* WIND & WISE (1977) appeared later in the early Pliensbachian than *Similiscutum precarium*. In the LM, this species is distinguished from *Similiscutum precarium* by its smaller size and brightly birefringent central structure. Other *Palaeopontosphaera* species which are also known to occur in the Pliensbachian are much larger than *Similiscutum precarium* (Bergen, in prep.).

Similiscutum precarium differs from *Similiscutum avitum* by having a central cross structure and from *Similiscutum orbiculus* by its elliptical outline and central cross structure. *Similiscutum cruciulus* also has a central cross structure, but has a circular to subcircular outline.

Occurrence.

- Northwest Europe (Prins 1969). LO: base of *jamesoni* Zone. HO: *spinatum* Zone.

- Portugal (Bergen). LO: *raricostatum* Zone. HO: *spinatum* Zone.
Holotype. Plate 2, Figures 15a, b (FSU-LM-08-15, FSU-LM-08-17).
Type level. Sample SP 28, lower Pliensbachian (*davoei* Zone).
Type locality. Sao Pedro de Mal, Portugal.

Similiscutum finchii (CRUX 1984) comb. nov.

Plate 3, Figures 11–13

- 1969 *Palaeopontosphaera binodosa* PRINS, pl., fig. (nomen nudum).
 1984 *Biscutum finchii* CRUX, p. 168; fig. 9, nos. 3 (?), 4; fig. 13, no. 5 (?).
 1987a *Biscutum finchii* CRUX 1984; BOWN, p. 44; pl. 2, figs. 3, 4, 10, 11.
 1987b *Biscutum finchii* CRUX 1984; emend. BOWN, p. 42–43; pl. 5, fig. 18; pl. 6, figs. 1–3; pl. 13, figs. 21, 22; textfig. 11.
 non 1990 *Biscutum finchii* (CRUX 1984) BOWN 1987c; COBIANCHI, p. 134; fig. 4d.
 1992 *Biscutum finchii* (CRUX 1984) BOWN, 1987a; COBIANCHI (partim), p. 92; fig. 18; fig. 19g (non figs. 19f, h).

Diagnosis. – ‘A large normally elliptical species of *Biscutum* with a modified radiating placolith structure. The distal shield is composed of non-imbricating elements with a gentle outer slope forming the shield and a steep inner edge producing a deep central area. The sutures are sharply kinked at the point from which the elements slope and they also have a slight anticlockwise precession due to the kinking. The proximal shield is only slightly smaller than the distal shield; its elements are non-imbricating with sutures only slightly deviating from the radial pattern. The central area is filled with granular elements’ (BOWN 1987b, p. 42, 44).

Discussion. – The proximal shield elements of this species bend at the inner rim margin, but do not form a separate cycle of elements (pl. 3, fig. 13; the holotype in Crux 1984, fig. 9, no. 4). The distal shield is unicyclic.

In the LM, *Similiscutum finchii* exhibits a bicyclic rim extinction pattern: the narrow, inner rim cycle is brightly birefringent and the broad outer rim cycle is faintly birefringent. These features are diagnostic of *Similiscutum*.

The central area is small and occupies less than 1/4 of the total surface of the coccolith. In cross-polarized light, a bright transverse bar is often observed when specimens are oriented 45 degrees to the polarizing direction. This optical feature results from a thickening of the central plate elements (e.g. BOWN 1987a, pl. 2, fig. 3).

Specimens recovered from the Portuguese Jurassic ranged from 5.5 to 8.0 µm in length; those recovered from the Moroccan Jurassic were as small as 5.0 µm. The holotype is 5.8 µm in length and BOWN (1987b) reported its length as 5.8–8.5 µm.

Differentiation. – This broadly elliptical species is characterized by its large size, granular central plate and kinked distal sutures. *Similiscutum finchii* is the largest known species of *Similiscutum*. *Palaeopontosphaera grande* (BOWN 1987b) n. comb. is another large Liassic Biscutaceae species, but features a bicyclic distal shield construction. *Similiscutum finchii* is distinguished from that species even by the LM by its small central area and imperforate granular plate. The central area elements which lie in the transverse axis are thick and brightly birefringent. *Palaeopontosphaera grande* has a perforate central area spanned by a faintly birefringent, transverse bar. Other elliptical species of *Similiscutum* are smaller than *Similiscutum finchii* and have radial distal sutures and different central area constructions.

Palaeopontosphaera binodosa (nomen nudum) PRINS (1969) is considered synonymous with *Similiscutum finchii*, but was not validly published.

Stratigraphic distribution. – The lowest occurrence of *Similiscutum finchii* is diachronous, ranging from early Pliensbachian (*davoei* Zone) to late Pliensbachian (*spinatum* Zone).

The extinction of *Similiscutum finchii* may define a synchronous biostratigraphic horizon of wide geographic extent. Detailed investigation of the lower Toarcian is needed to determine its precise relationship to other calcareous nannofossil events, egs. HO *Calxivascularis jansae* and FAD *Carinolitus superbus*. This sequence of events may then help to correlate between the Tethyan and Boreal realms.

Reported occurrence.

- Portugal (Bergen). LO: *davoei* Zone at all 3 sections. HO: *serpentinus* Zone at Brehna; *falciferum* Zone at Peniche.
- Morocco (de Kaenel). LO: *lavinianum* Zone. HO: *serpentinus* Zone.
- Switzerland (de Kaenel). LO: *margaritatus* Zone. HO: *serpentinus* Zone.
- Germany (Crux 1984). LO: *spinatum* Zone. HO: *falciferum* Zone.
- NW Europe (Bown et al. 1988). LO: *spinatum* Zone. HO: *falciferum* Zone.
- Italy (Cobianchi 1992). Specimen illustrated: *serpentinus* Zone.

Similiscutum gephyrion sp. nov.

Plate 3, Figures 14–15

Derivation of name. – From Greek *gephyrion*, little bridge.

Diagnosis. – A medium-sized, elliptical species of *Similiscutum* with a small central area spanned by a transverse bar which forms a distal spine base in its center.

Description. – Elliptical placoliths composed of two broad, subhorizontal shields. The unicyclic distal shield is larger than the proximal shield. The distal shield elements are non-imbricate and have radial sutures, but appear to be kinked at the inner rim margin. The inner margin of the distal shield is steep. The central area is small, occupying about one-tenth of the coccolith width. A short transverse bar spans the small central area and supports a short, circular distal spine base.

In the LM, the rim extinction pattern is bicyclic. The narrow inner rim cycle is brightly birefringent; the broad outer rim cycle is faintly birefringent. The brightly birefringent transverse bar appears to extend into the inner rim cycle. The distal spine is non-birefringent at its center.

Length. – 5.5 to 7.0 μm .

Discussion. – The illustration of *Palaeopontosphaera binodosa* PRINS (1969) (nomen nudum) has the same optical properties of the species described herein. However, the central area of Prins's specimen (pl. 2, fig. 12) is larger than that of *Similiscutum gephyrion* and has a brighter, larger inner rim cycle; it may be conspecific with *Palaeopontosphaera grande*.

Differentiation. – *Palaeopontosphaera grande* (BOWN 1987b) n.comb. also has a transverse central bar and a spine base. This species differs from *Similiscutum gephyrion* by its larger central area and bicyclic distal shield. *Similiscutum finchii* has a central plate and no distal spine base. The central area of this species is slightly larger than the central

area of *Similiscutum gephyrion*. The central area of specimens of *Similiscutum finchii* illustrated by Bown (1987a, plate 2, figure 11; Bown 1987b, plate 13, figure 21) show a diffuse central cross, whereas *Similiscutum gephyrion* displays a distinct transverse bar in cross polarized-light.

Known stratigraphic occurrence.

- Northwest Europe (Prins 1969). *Palaeopontosphaera binodosa* (synonymous?). upper Pliensbachian: *margaritatus* to *spinatum* Zone (?).
- Portugal (Bergen). upper Pliensbachian: *margaritatus* Zone.
- Morocco (de Kaenel). upper Pliensbachian: *emaciatum* Zone.

Holotype. Plate 3, Figure 15 (FSU-LEM-39-o).

Type level. Sample SP 33, upper Pliensbachian (*margaritatus* Zone).

Type locality. Sao Pedro de Mal, Portugal.

Genus *Palaeopontosphaera* NOËL 1965 emend.

Figure 3

Type species. – *Palaeopontosphaera dubia* NOËL 1965.

Previous emended diagnoses. – 'Elliptical coccoliths, formed of two closely appressed discs; central disc (slightly larger than the proximal disc) sloped in its center to allow the passage of a stem penetrated by an axial canal'(Noël 1973, p. 117).

'Elliptical coccoliths, composed of two closely appressed discs. The central area is very reduced with a stem attached at all points to the margin or well attached to the latter by buttresses'(Goy in Goy et al. 1979, p. 42).

Emended diagnosis. – Circular to elliptical Biscutaceae possessing an inner wall constructed of non-imbricate elements. The central area is imperforate, vacant, or spanned by a simple structure (cross or bar).

Description. – Circular to elliptical placoliths constructed of two broad shields; shield elements are non-imbricated and have radial sutures. An inner distal cycle (wall) constructed of non-imbricated elements is present. The resulting birefringence pattern is bicyclic: the thin inner cycle is brightly birefringent and the broad outer cycle displays little or no birefringence. The central area may be imperforate, vacant, or spanned by a simple cross or transverse bar (no accessory bars are present). A distal stem or spine base may be present.

Discussion. – The holotype of the type species is a badly etched coccosphere. Its coccoliths are elliptical, non-imbricate placoliths with high inner rim margins, but their central areas and inner rim structures (inner rim cycles) were not preserved. Subsequent descriptions and emendations of *Palaeopontosphaera dubia* (Noël 1973, Grün & Zweili 1980, Bown 1987b) characterized the species as an elliptical coccolith constructed of two shields with radial elements and a small, closed granular central area with a distal spine. Goy et al. (1979; Goy 1981) demonstrated that the stem was supported on the proximal surface by an axial cross which nearly filled the central area (the small openings are not visible from the distal surface), but illustrated specimens with more open central areas that belong to an undescribed species similar to *Palaeopontosphaera erismata* WIND & WISE (1977). Bown (1987b) first described the inner distal cycle of *Palaeopontosphaera dubia*, which is evident in numerous electron photomicrographs of the species. We consider this feature diagnostic of the genus *Palaeopontosphaera*. The emended diagnosis

presented herein also allows for variation in coccolith outline and central area construction.

The original generic diagnosis misinterpreted its rim construction (classified as a discolith), but mentioned its elliptical outline and vertical rim elements. Noël (1973) recognized its elliptical, two shield rim construction when she emended the generic diagnosis, but also emphasized the presence of a distal stem. Goy (in Goy et al. 1979) further restricted the generic diagnosis to include a small central area occupied by a distal stem, which was supported from beneath. Comparisons between the two species placed in *Palaeopontosphaera* by Goy (Goy et al. 1979; Goy 1981) demonstrate which morphologic features he considered diagnostic of the genus. His *Palaeopontosphaera dubia* and *Palaeopontosphaera nova* are both non-imbricate placoliths with two broad shields, small central areas, and distal stems. However, the two species illustrated in Goy (1981) differ in outline, central area construction, and rim ultrastructure.

Other authors have recognized *Palaeopontosphaera* as a junior synonym of *Biscutum* BLACK (in Black & Barnes 1959). However, the holotype of the type species of *Biscutum* is nearly circular ($3.7 \times 3.6 \mu\text{m}$) and has a different rim construction than *Palaeopontosphaera* (see discussion under *Biscutum*). The concept of *Biscutum* which has evolved in published studies of the Cretaceous is that of an elliptical genus. This more closely approximates *Biscutum castrorum* BLACK (in Black & Barnes 1959), which was described in the same publication as *Biscutum testudinarium*. Its holotype has 22 rim elements and it appears that its proximal shield elements extend into and close the central area; a distinct separate central cycle of elements is not evident in this specimen. Other electron photomicrographs of elliptical Biscutaceae recovered from the Upper Cretaceous (egs. Perch-Nielsen 1968, Bukry 1969) do not show any central cross structure or distal process, but do indicate the presence of an inner distal rim cycle as in *Palaeopontosphaera*. Specimens recovered from the Lower Cretaceous (egs. Black 1972, pl. 2; Grün & Allemann 1975, pl. 1, figs. 5–7) illustrate the transition from Jurassic forms with a central spine to the elliptical Upper Cretaceous Biscutaceae which do not have this central area feature. Grün & Allemann (1975) simply placed the large number of small elliptical Biscutaceae into synonymy as single species and assigned priority to *Biscutum* BLACK (in Black & Barnes 1959). Grün & Zweili (1980) later emended *Palaeopontosphaera dubia*. They distinguished it from the Cretaceous species *Biscutum ellipticum* (= *Biscutum testudinarium*) and *Biscutum castrorum* by its central spine, but still recognized *Biscutum* as a senior synonym of *Palaeopontosphaera*. However, *Palaeopontosphaera* should be retained as a separate genus from *Biscutum*, since the holotypes of their type species are unrelated; the elliptical Cretaceous Biscutaceae probably evolved from *Palaeopontosphaera dubia* and should be placed in that genus.

Differentiation. – *Palaeopontosphaera* and *Similiscutum* both display bicyclic rim extinction patterns. The bright inner rim cycle *Palaeopontosphaera* results from its inner distal rim cycle, whereas that of *Similiscutum* results from its proximally extended inner margin (which may be a separate rim cycle).

Sollasites BLACK (1967) has a rim construction and extinction pattern similar to *Palaeopontosphaera*, but is distinguished by its complex central area construction. The oldest documented specimens of *Sollasites* are early Toarcian (older specimens with identical central area constructions have a *Calyculus* rim construction) and lack a well developed inner distal rim cycle.

Biscutum displays a unicyclic rim extinction pattern and lacks an inner distal rim cycle (wall).

Crucibiscutum JAKUBOWSKI (1986) was described for Lower Cretaceous placoliths with a distinct axial cross, but an imbricate rim. The similarities in rim construction, coccolith outline, and central structures indicate that these forms may be closely related to *Palaeopontosphaera*.

Palaeopontosphaera has a rim construction similar to a family of Mesozoic placoliths (Family Podorhabdaceae NOËL 1965 of most authors), which are distinguished by their narrow rims. Specimens with rim dimensions transitional between *Palaeopontosphaera* and the 'podorhabdids' do exist (see discussion of *Palaeopontosphaera intermedia*). In this case, the two groups can be distinguished by their rim birefringence patterns. *Palaeopontosphaera* displays a distinctly bicyclic rim extinction pattern with a smooth, bright inner rim cycle, whereas the 'podorhabdids' display less birefringence contrast across their rim cycles and have a distinctly beaded inner rim cycle.

Palaeopontosphaera dubia NOËL 1965 emend.

Plate 1, Figure 15

- 1965 *Palaeopontosphaera dubia* NOËL (partim), p. 76–78; pl. 7, figs. 1, 2 (?), 5, 7–10 (non pl. 7, figs. 3, 4, 6, 11–13).
- 1971 *Palaeopontosphaera dubia* NOËL 1965; Medd (partim), p. 826; pl. 4, fig. 5 (non pl. 4, fig. 6).
- 1971 *Palaeopontosphaera dubia* NOËL 1965; Rood, Hay & Barnard, p. 265; pl. 4, fig. 9.
- 1973 *Palaeopontosphaera dubia* NOËL 1965; Noël (partim), p. 117; pl. 13, figs. 1, 2, 4, 5 (non pl. 13, fig. 3).
- non 1973 *Palaeopontosphaera dubia* NOËL 1965; Rood, Hay & Barnard, p. 378; pl. 3, fig. 3.
- non 1974 *Biscutum dubium* (NOËL 1965) GRÜN in Grün et al., p. 297; pl. 14, figs. 1–3.
- non 1974 *Palaeopontosphaera dubia* NOËL 1965; Barnard & Hay, pl. 2, fig. 2; pl. 5, fig. 1.
- 1975 *Biscutum ellipticum* (GORKA 1957) GRÜN in Grün & Allemann, p. 154–156; pl. 1, figs. 5, 6 (?), 7 (?).
- 1980 *Biscutum dubium* (NOËL 1965) GRÜN 1974; Grün & Zweili, p. 245; pl. 1, figs. 1–2; textfig. 4.
- 1981 *Palaeopontosphaera dubia* NOËL 1965; Goy (partim), p. 50–51; pl. 19, figs. 1–2; textfig. 11 (non pl. 18, figs. 7–8; pl. 19, figs. 3–4).
- non 1984 *Biscutum dubium* (NOËL 1965) GRÜN 1974; Crux p. 168; fig. 9, no. 5–6; fig. 13, no. 6.
- 1987 *Biscutum* sp.; COVINGTON & WISE, pl. 4, figs. 1, 3 (non pl. 4, fig. 2).
- 1987b *Biscutum dubium* (NOËL 1965) GRÜN 1974; Bown (partim), p. 45; pl. 14, figs. 3–4; textfig. 13 (non pl. 6, figs. 13–15).
- non 1987b *Biscutum dubium* (NOËL 1965) GRÜN in Grün et al.; Crux p. 89; pl. 2, figs. 4–7.

Previous diagnosis. – 'A species of the genus as emended herein with small buttresses in the ellipse axes, converging against a central stem' (Goy in Goy et al. 1979, p. 42).

Emended Diagnosis. – A small subelliptical to elliptical species of *Palaeopontosphaera* having a small central area nearly filled by a distal projection, which is supported beneath by an axial cross structure.

Discussion. – Bown (1987b) provided a detailed description of the species, but mentioned that it has a relatively open central area. The holotype is a badly etched coccosphere recovered from the Portlandian, whose coccoliths are lacking their distal spines and most of their inner rim walls. This gives the impression of a large central area. Other specimens illustrated by Noël (1965) from the Upper Jurassic (pl. 7, figs. 7–10) and the Lower Cretaceous (pl. 7, fig. 5) are broadly elliptical coccoliths with small central areas, an inner distal wall, and small distal spines. Lower Pliensbachian specimens (Noël 1965, pl. 7, fig. 11–13) with more open central areas placed in synonymy by Bown (1987b) do not have this inner distal cycle and represent Biscutaceae (*Similiscutum*) which appeared

before *Palaeopontosphaera dubia*. All small Jurassic *Palaeopontosphaera* are characterized by a well developed inner distal wall and have a distal spine.

Noël (1973) emended the species description as a placolith with a hollow central spine, acknowledging her previous misinterpretation of a discolith rim construction. Goy (in Goy et al. 1979; Goy 1981) later emended the species diagnosis, recognizing that it possesses small axial buttresses which attach the spine to the rim margin. These supports are only visible on the proximal surface of specimens and nearly close the central area (four very small openings can be seen). Goy (1981) also placed more narrowly elliptical specimens with larger central areas and a distinct axial cross (four perforations visible in both proximal and distal views) within *Palaeopontosphaera dubia* (pl. 18, figs. 7, 8). We believe that these specimens represent a separate species of *Palaeopontosphaera* which occurs in the Lower Jurassic. The proportions of its rim are similar to *Palaeopontosphaera erismata* WIND & WISE (1977), which was described from the Upper Jurassic. However, *Palaeopontosphaera erismata* differs from these Lower Jurassic specimens by also possessing an imperforate central plate. We believe the development of such a central plate took place during the late Aalenian. An imperforate plate also occurred within the more broadly elliptical forms possessing reduced central areas represented by *Palaeopontosphaera dubia*. By Early Cretaceous time, this group had clearly developed an imperforate central plate (e. g. . Grün & Allemann 1975, pl. 1, figs. 6, 7).

Occurrence.

- Morocco (de Kaenel). LO: middle *lavinianum* Zone.
- Portugal (Bergen). LO: lower *margaritatus* Zone at all three sections sampled. HO: lower Oxfordian (youngest section sampled).
- Switzerland (de Kaenel). LO: lower *margaritatus* Zone. HO: middle Oxfordian (youngest section sampled).

Palaeopontosphaera grande (BOWN 1987b) comb. nov.

1987b *Biscutum grandis* BOWN, p. 44; pl. 6, figs. 4–6; pl. 13, figs 23–25; textfig. 11.

Diagnosis. – ‘A large, normal to narrowly elliptical species of *Biscutum* possessing a bicyclic distal shield and a relatively large central area spanned by a thin bar bearing a central spine base’ (Bown 1987b, p. 44).

Discussion. – We place this species within *Palaeopontosphaera* because of its bicyclic distal shield. The presence of an inner distal cycle (wall) is considered as a diagnostic feature of the genus *Palaeopontosphaera* as emended above. The rim extinction pattern is bicyclic. *Biscutum* species are differentiated from *Palaeopontosphaera* species by having two unicyclic shields, which display a unicyclic rim extinction pattern.

Differentiation. – *Palaeopontosphaera grande* is the only known species of *Palaeopontosphaera* with a transvers central bar. This species differs from *Similiscutum gephyrion*, another medium-sized, elliptical Biscutaceae with a central transverse bar, by its bicyclic distal shield. In the LM, *Palaeopontosphaera grande* has a larger central area and a wider, more birefringent inner rim cycle.

Genus *Discorhabdus* NOËL 1965 emend.

Figure 3

Type species. – *Discorhabdus patulus* (DEFLANDRE 1954) Noël 1965.

Junior synonym. – *Podorhabdus* NOËL 1965.

Original diagnosis. – 'Circular base composed of two simple discs, joined firmly, perforated in the center to allow the passage of a variably developed and diversified spine. The upper disc is constructed from a single series of calcite lamellae which are radially disposed, joined all along their length giving the disc a nearly continuous surface, without festoons. The lower disc, generally smaller than or at most equal to the upper disc, is formed from the same number of calcite plates, flat, often thinner, also joined and radially disposed. This lower disc, slightly convex, forms a solid base pierced only at its center at the root of the spine (fig. 56, pl. 21, figs. 5–12, pl. 22, fig. 1).

The axial spine, of a more or less large diameter, and of variable length and morphology, is made up of crystals of calcite, almost cubic, or elongated rhombohedra, arranged around a central canal (pl. 21, fig. 7). The outer edge of the spine is closely contacted to the inner edge of the perforations of the upper and lower discs' (Noël 1965, p. 138).

Emended diagnosis. – Elliptical to circular placoliths composed of two, broad, unicyclic shields constructed of non-imbricate to slightly overlapping, radially-arranged elements. Proximal shield sutures are often slightly curved or kinked near the inner rim margin. A distal projection fills the central area. It extends above the distal shield and is attached at the proximal surface. The shape and outline of the distal projection are highly variable; the width of its central axial canal is also highly variable. Perforations may be present near the base of the distal projection. The distal projection can be very delicate and is frequently not preserved intact.

Discussion. – *Podorhabdus* NOËL (1965, p. 100) was described for non-imbricate placoliths with a narrow shield and a large central area spanned by four bars aligned with the major axes of the coccolith. The original diagnosis of this genus also mentioned that the bars support a thick, hollow stem of variable shape. Wind & Wise (in Wise & Wind 1977) recognized that the type species of *Podorhabdus*, *Podorhabdus grassei* NOËL (1965) is based on a holotype with two large central perforations. Because of this contradiction, they erected the genus *Axopodorhabdus* for forms with four central perforations and bars aligned with the major ellipse axes, and emended *Podorhabdus* for species with two large pillars separated by an arch. The concept of the family Podorhabdaceae NOËL (1965, p. 100) which has developed in published literature includes a group of non-imbricate, elliptical placoliths with a thin rim and large central area. Species classified within this family are also characterized by an inner rim wall (clearly evident as a second inner distal cycle), which gives the inner rim margin a 'beaded' appearance in cross-polarized and phase contrast light. *Podorhabdus grassei* does not have this rim construction, but is instead composed of two circular, unicyclic shields. Such a rim construction is instead typical of the genus *Discorhabdus*. It is further related to members of this genus by its broadly flaring stem, in contrast to the tapered stems of the elliptical placoliths which have been placed in the family Podorhabdaceae NOËL (1965). The holotype of *Podorhabdus grassei* is an electron photomicrograph, which has two distinct, large perforations near the base of the stem. The holotype of *Discorhabdus patulus* (DEFLANDRE 1954) Noël (1965), which is the type species of *Discorhabdus*, is illustrated as two light photomicro-

graphs (cross-polarized and transmitted light). Perforations are not clearly visible on the holotype. However, the outline of the distal stems of the two holotypes are identical and both were recovered from the Oxfordian of the Paris Basin. From examination of the original samples from which both holotypes were recovered and detailed investigations of the Moroccan and Portuguese Jurassic, we have observed that two perforations are always present near the base of stems with this outline. Therefore, we consider *Podorhabdus grassei* to be a junior synonym of *Discorhabdus patulus* and herein assign priority to the genus *Discorhabdus* NOËL (1965, p. 138). The original diagnosis of *Discorhabdus* included only circular forms with a single perforation at their centers (an axial canal). *Discorhabdus* is emended herein to allow for variation in coccolith outline and the presence of perforations near the base of the distal projection.

Differentiation. – Both *Discorhabdus* and *Biscutum* are constructed of two non-imbricate, unicyclic shields. *Discorhabdus* differs from *Biscutum* by having a distal projection. *Similiscutum* is distinguished from both these genera by its unique proximal shield construction, which extends proximally at the inner rim margin and may form a second proximal cycle of elements. The resulting bicyclic rim extinction pattern distinguishes *Similiscutum* from both *Discorhabdus* and *Biscutum* in cross-polarized light. *Palaeopontosphaera* has a bicyclic distal shield and also displays a bicyclic rim extinction pattern.

Distribution. – The lowest occurrence of *Discorhabdus* is near the base of the upper Pliensbachian in Portugal (*margaritatus* Zone), Switzerland (*margaritatus* Zone), and Morocco (*lavinianum* Zone). Thus, this event may be a useful datum for correlation between Mesogean (Morocco), northern Tethyan (Switzerland), and marginal Boreal (Portugal) provinces.

Discorhabdus novus (GOY 1979) comb. nov.

Plate 3, Figures 1–5

- 1965 *Palaeopontosphaera dubia* NOËL (partim), p. 76–78; pl. 7, fig. 3 (non pl. 7, figs. 1, 2, 4–13; textfig. 8).
 1973 *Palaeopontosphaera dubia* NOËL; Noël (partim), p. 117; pl. 13, fig. 3 (non pl. 13, figs. 1, 2, 4, 5).
 1974 *Biscutum dubium* (NOËL 1965); Grün in Grün et al., p. 297–298; pl. 14, figs. 1–3.
 1977 *Biscutum ellipticum* (GORKA 1957); Grün & Allemann 1975; Hamilton, p. 586; pl. 1, fig. 7.
 1979 *Palaeopontosphaera nova* GOY, in Goy et al., p. 42; pl. 4, fig. 5.
 1981 *Palaeopontosphaera nova* GOY; Goy, p. 52–53; pl. 19, figs. 4–7; pl. 20, figs. 1, 2; textfig. 12.
 1984 *Biscutum dubium* (NOËL 1965); Grün in Grün et al., 1974; Crux p. 168; fig. 9, no. 5–6; fig. 13, no. 6.
 1987a *Biscutum dubium* (NOËL 1965); Grün in Grün et al., 1974; Crux p. 53; pl. 1, figs. 1, 2 (?).
 1987a *Biscutum novum* (GOY 1979) comb. nov.; Bown (partim), pl. 2, fig. 2 (non pl. 2, fig. 1).
 1987b *Biscutum novum* (GOY 1979) BOWN 1987a; Bown (partim), p. 41–42; pl. 5, figs. 15, 17 (?); pl. 13, figs. 19–20; textfig. 11 (non pl. 5, figs. 13, 14, 16).
 1988 *Biscutum novum* (GOY 1979) BOWN 1987; Bown et al., pl. 1, figs. 8–9.
 1990 *Biscutum novum* (GOY 1979) BOWN 1987; Cobianchi (partim); p. 134; fig. 19c (non fig. 18; figs. 19b, d).
 1990 *Biscutum* aff. *finchii* (CRUX 1984) BOWN 1987c; Cobianchi, p. 134, fig. 4e.
 1992 *Biscutum* aff. *B. finchii* (CRUX 1984) BOWN 1987a; Cobianchi, p. 92; fig. 19i.

Diagnosis. – ‘A species of the genus *Discorhabdus* with an imperforate central area, the central spine is attached at all points to the marginal rim. Presence of a characteristic furrow on the proximal face’ (Goy, in Goy et al. 1979, p. 42).

Discussion. – The original diagnosis and description of the species emphasized the following morphologic features: 1) an elliptical-circular outline; 2) an imperforate central area; 3) a stem with a relatively large diameter; 4) a proximal furrow between the

inner rim margin and the central area; and 5) an average of twenty rim elements. Bown (1987b) later provided a detailed description of the species, but restricted it to specimens with 16–18 rim elements. However, he also illustrated two specimens (pl. 5, figs. 15, 17) with more than twenty rim elements. Based on specimens we have observed and those illustrated in published literature (see above synonym), we have concluded that the species has 18–24 rim elements and ranges from 3.6–5.2 μm in length. All measured Toarcian specimens have 20–24 rim elements. Upper Pliensbachian specimens have a minimum of 18 rim elements. Another consistent morphologic feature we have observed is the separation between the inner rim wall and the distal projection.

Differentiation. – *Discorhabdus novus* is the only known species of *Discorhabdus* with a subcircular to elliptical outline. Its slender stem is nearly cylindrical, but is hollow and flares slightly at both the distal and proximal extremities. It shares these morphologic features with *Discorhabdus patulus* and other related species that have much broader stems with large axial canals and more exaggerated proximal and distal flaring. *Discorhabdus novus* is further distinguished from such species by the separation between the inner rim wall and the stem. Another group of *Discorhabdus* species (e.g. *Discorhabdus tubus* NOËL 1965) has slender stems similar in outline to that of *Discorhabdus novus*. However, this group is distinguished from *Discorhabdus novus* by having nearly solid (a very thin axial canal is present), cylindrical (a slight distal flare may be present) stems which are constructed of rod-shaped elements. In contrast, the stem elements of *Discorhabdus novus* are plate-shaped.

In the LM, *Discorhabdus novus* is distinguished from *Similiscutum* species by its unicyclic rim extinction pattern (no bright collar). *Biscutum* also displays an unicyclic rim extinction pattern, but *Discorhabdus novus* is distinguished from this species by having a stem. When the stem is not preserved fully intact, *Discorhabdus novus* can be identified by the proximal stem base and the small central perforation remnants (and resulting central perforation for the hollow central stem), which are optically distinct.

Other *Discorhabdus* species are also commonly observed as isolated bases with little or no portion of the stem preserved intact. *Discorhabdus novus* is distinguished from such specimens by its non-circular outline and smaller central area.

Occurrence.

- Portugal (Bergen). LO: lower *margaritatus* Zone at all 3 sections.
- Morocco (de Kaenel). LO: *lavinianum* Zone.
- Switzerland (de Kaenel). LO: lower *margaritatus* Zone.
- France (Goy 1981). Specimens illustrated from the lower Toarcian.
- Germany. Specimens illustrated from the *spinatum* Zone and the *levesquei* Zone (Crux 1984, 1987a) and the lower Toarcian (Grün et al. 1974).
- England (Bown 1987b, Bown et al. 1988). Specimens illustrated from the lower and upper Toarcia.
- Italy (Cobianchi 1990, 1992). LO: upper Domerian. HO: upper Aalenian.

Genus *Biscutum* BLACK 1959 emend.

Figure 3

Type species. – *Biscutum testudinarium* BLACK in Black & Barnes 1959.

Taxonomic synonym. – *Bidiscus* BUKRY 1969.

Original diagnosis. – ‘Two circular, different sized concavo-convex discs standing upon each another. They surround a central hole, whose base is closed by a septum of granules’ (Reinhardt 1966, p. 30).

Emended diagnosis. – Circular to elliptical Biscutaceae constructed of two unicyclic shields, which display a unicyclic rim extinction pattern. A central cycle of elements is sometime present in the central area. A distal stem is not present.

Description. – Circular to elliptical placoliths composed of two, broad, unicyclic shields which are constructed of non-imbricate elements. Shield elements have radial sutures which may be straight or kinked. The slope of the inner rim margin varies. The imperforate (typically small) central area can be closed or surmounted by a cycle of elements separates from the rim. A distal stem is not present. In cross-polarized light, the shields are faintly birefringent and the rim extinction pattern is unicyclic. Specimens may become slightly more birefringent towards the inner margin where the shield thickness may increase.

Discussion. – The original description of the genus (Black in Black & Barnes 1959, p. 325) is too general, including all imperforate coccoliths with more than one shield, all of which are closely moulded onto each other. Reinhardt (1966) provided the first diagnosis for *Biscutum* (see above), which essentially conformed with the nearly circular holotype (1.03 eccentricity) of its type species. However, Black (1972; p. 26) later provided his diagnosis for the genus, restricting the genus to Biscutaceae with broadly elliptical to nearly circular outlines and bilateral symmetry. Although this diagnosis distinguished *Biscutum* from two other Biscutaceae genera originally defined as having circular outlines (*Bidiscus* BUKRY 1969 and *Palaeopontosphaera* NOËL 1965), it is artificial and excludes the vast majority of forms which are truly circular or elliptical. We have instead placed emphasis on the rim ultrastructure because it is the key to understanding the early evolution of coccoliths (see Bown 1987b). For example, the holotypes of *Biscutum* and *Bidiscus* have identical rim constructions and similar central area structures, but can only be distinguished by the very slight difference in their outlines. The holotype of the type species of *Biscutum* is a proximal view of an incomplete specimen recovered from the upper Cenomanian. This specimen is nearly circular ($3.7 \times 3.6 \mu\text{m}$) and is constructed of two, broad unicyclic shields, each possessing sixteen, non-imbricated elements with radial sutures. A separate horizontal cycle of eight (two are missing?) elements fill its small central area. The holotype of the type species of *Bidiscus* (*Bidiscus cruciatus* BUKRY 1969) is a distal view of a complete specimen recovered from the lower Santonian. This specimen is circular ($3.4 \mu\text{m}$) and is constructed of two, broad unicyclic shields, each possessing fifteen, non-imbricated elements with radial sutures. A separate horizontal cycle of four perpendicular elements surmounts its small central area. *Bidiscus* BUKRY (1969, p. 26) was described as having two unicyclic shields of radial elements and a small central area with varied ornamentation. The slight difference in coccolith outline between the circular shields described for *Bidiscus* and the slightly subcircular holotype of *Biscutum testudinarium* is not considered significant enough to warrant generic separation. Thus, *Bidiscus* is a taxonomic junior synonym of *Biscutum*.

The diagnosis of *Biscutum* is emended herein to define its rim construction and allow for variation in coccolith outline and central area structures. For example, a variety of central area structures are observed in circular Biscutaceae species illustrated from the Upper Cretaceous (Reinhardt 1965, pl. 1, fig. 3; Bukry 1969, pl. 6, figs. 10–12; pl. 7,

figs. 1–9) and the Albian (Black 1972, pl. 1, figs. 1–9). Most *Biscutum* species have circular to subcircular outlines, whereas elliptical outlines are rare (Bukry 1969, pl. 7, figs. 10–11; Perch-Nielsen 1973, pl. 1, figs. 4, 5). The same variation in outline exists within *Discorhabdus*, which is distinguished from *Biscutum* by its distal projection. Elliptical species previously classified within *Biscutum* that possess an inner distal cycle of elements are now considered to belong to *Palaeopontosphaera*. Numerous authors have considered *Palaeopontosphaera* to be a junior synonym of *Biscutum* (see discussion under *Palaeopontosphaera*). However, we believe that there is an important difference in their rim ultrastructures, representing two separate lineages within the Family Biscutaceae.

Biscutum profundum sp. nov.

Plate 3, Figures 6, 7, 9, 10

- ? 1969 *Striatococcus opacus* PRINS, pl. 2, fig. 15 (nomen nudum).
 1977 *Discorhabdus ignotus* (GORKA 1957) PERCH-NIELSEN 1968; Hamilton (partim), p. 586; pl. 2, fig. 10 (non pl. 2, figs. 1–9, 11).
 1987b *Discorhabdus ignotus* (GORKA 1957) PERCH-NIELSEN 1968; Bown (partim), p. 48–49; pl. 7, fig. 1 (non pl. 7, fig. 2–5; pl. 14, figs. 7–8; textfig. 11).
 1990 *Biscutum finchii* (CRUX 1984) BOWN 1987b; Cobianchi, p. 134, fig. 4d.
 1992 *Biscutum finchii* (CRUX 1984) BOWN 1987a; Cobianchi (partim), p. 92; fig. 19f (non figs. 18, 19g).
 1992 *Discorhabdus striatus* MOSHKOVITZ & EHRLICH 1976; Cobianchi, p. 93–94; fig. 20a.
 1992 *Discorhabdus* aff. *D. striatus* MOSHKOVITZ & EHRLICH 1976; Cobianchi (partim), p. 94; fig. 20d (non figs. 20b–c).

Derivation of name. – From Latin *profundum*, deep.

Diagnosis. – A small subcircular species of *Biscutum* with a small, deep central depression, a low number of rim elements and a thick proximal shield.

Description. A small, subcircular placolith constructed of two subhorizontal, unicyclic shields. The shields are constructed of 13 to 17, non-imbricate elements with radial sutures. The shields are relatively thick for a small placolith. Thus, the smaller proximal shield (about 7/10 to 9/10 the width of the distal shield) is optically distinct. Both the proximal and the distal elements form a relatively high inner margin around the central depression. The central area is imperforate and reduced. Its dimension is about 1/4 to 1/5 that of the rim. A small proximal central cycle of elements, that is not part of the rim, may be present in the central area.

In the LM, the rim extinction pattern is unicyclic. The distal shield exhibits a slight birefringence and the thick proximal shield is slightly more birefringent. The proximal central cycle of elements is weakly birefringent and may be resolved with the LM by focusing on the center of the coccolith.

Length. – 4.0–5.2 μm .

Discussion. – *Biscutum profundum* is the oldest known *Biscutum* species. The appearance of this small species during the late Pliensbachian is a distinct biostratigraphic event in both the Moroccan and Portuguese sections. *Biscutum striatum* evolved from *Biscutum profundum* during the early Toarcian.

Differentiation. – *Biscutum criotum* is another small species with a central depression on both the proximal and distal surfaces. It is distinguished from *Biscutum profundum* by its birefringent, central element cycle and kinked distal rim sutures. *Biscutum profundum*

and *Biscutum striatum* both have central distal depressions and small, imperforate central areas. *Biscutum profundum* also has a relatively thick proximal shield which surrounds a proximal central depression. *Biscutum profundum* is further distinguished from *Biscutum striatum* by its smaller size (up to 5.2 μm), fewer rim elements, relatively larger central area and, a deeper, central distal depression.

Biscutum profundum and *Discorhabdus novus* have similar rim constructions, outlines, and central area dimensions. Both species appeared during the late Pliensbachian. *Discorhabdus novus* has a distal projection, the base of which is seen as a small circular opening on isolated rims. *Biscutum profundum* has an imperforate central area and no distal projection. It is further distinguished by its thick proximal shield.

Similiscutum orbiculus and *Similiscutum cruciulus* are other small rounded Biscutaceae which occur in late Pliensbachian to early Toarcian assemblages with *Biscutum profundum*. These two *Similiscutum* species exhibit a bicyclic rim extinction pattern. *Biscutum profundum* is distinguished from these species by its rim construction and corresponding unicyclic rim extinction pattern.

Striatococcus opacus PRINS (1969) is illegitimate, but the illustration provided by Prins (1969, p. 550) has many similarities to *Biscutum profundum*. However, it differs by having more rim elements (24) and a slightly birefringent inner rim cycle.

Occurrence.

- (?) – Northwest Europe (Prins 1969). LO: *spinatum* Zone.
- Morocco (de Kaenel). LO: *algovianum* Zone. HO: *concauum* Zone (or lower Bajocian ?).
- Portugal (Bergen). LO: *margaritatus* Zone at all three sections sampled. HO: lower Bajocian (?).
- Italy (Cobianchi 1992). illustrated specimens are lower Toarcian, middle Aalenian, lower Bajocian (?).

Holotype. Plate 3, Figure 10 (IGN-F51-27).

Isotype. Plate 3, Figure 9 (IGN-F25-28).

Type level. Sample Ou 30, middle Toarcian (*thouarsensae* Zone).

Type locality. Ouchbis, Morocco.

Biscutum criotum (BOWN 1987b) comb. nov.

1977 *Discorhabdus ignotus* (GORKA 1957) PERCH-NIELSEN 1968; Hamilton (partim), p. 586; pl. 2, fig. 2 (non pl. 2, figs. 1, 3–11).

1987b *Discorhabdus criotus* BOWN, p. 49–50; pl. 7, figs. 6–9; textfig. 11.

1992 *Discorhabdus criotus* BOWN 1987b; Cobianchi (partim), p. 93; fig. 19 l (non figs. 19 m–n).

Discussion. – Bown (1987b) placed this species within *Discorhabdus* because of its circular outline, although he remarked that some specimens may have a subcircular outline. We have also observed the same variation in coccolith outline and believe that this is not a diagnostic generic character. The rim construction of *Discorhabdus criotus* BOWN (1987b) instead conforms to our emended diagnosis of *Biscutum*. The species is distinguished by its central area element cycle and sutures which kink near the outer rim margin. It is related to the other Jurassic *Biscutum* species presented herein by its rim construction, variation in outline, and central depression.

Bown (1987b) described the species as having 11 to 13 rim elements and being 3.6 to 5.6 μm in diameter. Specimen documented from the Moroccan Jurassic are as small as 3.1 μm and have up to 14 rim elements.

Biscutum striatum (MOSHKOVITZ & EHRLICH 1976) comb. nov.

Plate 3, Figure 8

1969 *Striatococcus nebulosus* PRINS, pl. 2, fig. 16 (nomen nudum).

1976 *Discorhabdus striatus* MOSHKOVITZ & EHRLICH, p. 14; pl. 7, figs. 1–5.

1987b *Discorhabdus ignotus* (GORKA 1957) PERCH-NIELSEN 1968; Bown (partim), p. 48–49; pl. 7, figs. 2–3; pl. 14, figs. 7–8; textfig. 11 (non pl. 7, figs. 1, 4–5).

1988 *Discorhabdus striatus* MOSHKOVITZ & EHRLICH 1976; Bown, Cooper & Lord, p. 113; pl. 1, figs. 17–18.

Diagnosis. – A medium-sized, subcircular to circular species of *Biscutum* with a small imperforate central area, shallow central depression and a moderate number (18 or more) of rim elements.

Maximum diameter. – 5.3–9.5 μm .

Discussion. – Moshkovitz & Ehrlich (1976) described this species for circular coccoliths with two unicyclic shields and a very small opening. The description also mentioned 20 to 24 radial elements and a distal diameter of 5.5 to 7.0 μm . The holotype (Moshkovitz & Ehrlich 1976, pl. 7, figs. 3–4) measures 7.5 μm and has 24 rim elements. Two other specimens illustrated as this species by Moshkovitz & Ehrlich (1976) measure 5.3 μm with 18 rim elements (pl. 7, figs. 1–2) and 8.1 μm with 24 rim elements (pl. 7, fig. 5). Our examination of original material shows specimens with 18 to 24 rim elements, but up to 9.5 μm in size. Some specimens in this sample and others illustrated in published literature also have a subcircular outline. Moshkovitz & Ehrlich (1976) did not provide a diagnosis with their description of the species. The diagnosis provided herein accounts for the aforementioned morphological variations and distinguishes it from other species which conform to our emended diagnosis of *Biscutum*.

Differentiation. – *Biscutum striatum* and *Biscutum criotum* are both subcircular to circular species with a central distal depression. In the LM, *Biscutum criotum* is distinguished by its birefringent central element cycle, kinked sutures near the outer distal rim margin, fewer rim elements, and generally smaller size.

The differences between *Biscutum striatum* and its ancestor, *Biscutum profundum*, are discussed under the latter species.

Occurrence.

- Morocco (de Kaenel). LO: middle *tenuicostatum* Zone. HO: Bathonian (top of section).
- Portugal (Bergen). LO: early Toarcian. Highest common occurrence: *subfurcatum* Zone; HO: Oxfordian/Kimmeridgian boundary (top of sections).
- Switzerland (de Kaenel). LO: *serpentinus* Zone. HO: middle Oxfordian.
- Northwest Europe (Bown, Cooper & Lord 1988). LO: *falciferum* Zone. HO: middle Oxfordian (*densiplicatum* Zone).
- Italy (Cobianchi 1992). LO: early Aalenian. HO: Oxfordian.

Family Bussoniaceae GOY 1981 emend.

Taxonomic junior synonym. – Mazaganellaceae BOWN 1987b.

Original diagnosis. – ‘Elliptical coccolith whose margin is made up of three superimposed series of elements. The constituent elements of the distal series are inclined and overlapping’ (Goy 1981, p. 32).

Emended diagnosis. – Placoliths constructed of three shields. The proximal and intermediate shields are subhorizontal. The height, morphology, and orientation of the distal shield elements are variable. An inner rim wall may be present.

Discussion. – Goy (1981) described the family Bussoniaceae for elliptical, three-shield coccoliths having an imbricate distal shield. Bown (1987b) later erected the family Mazaganellaceae for elliptical coccoliths with a rim consisting of three shields, each possessing elements showing little or no imbrication. Bown (1987b) placed *Bussonius* within the imbricate placolith family Watznaueriaceae based on its imbricate distal shield construction and because he believed that *Bussonius* descended from the genus *Lotharingius*. However, new stratigraphic evidence from DSDP Site 547 B (Gardin 1991) and Portugal demonstrates that the appearance of *Bussonius* predates all reported first occurrences of *Lotharingius*. *Bussonius* is also closely related to early Liassic forms placed within the family Mazaganellaceae by Bown (1987b). This includes the genera *Mazaganella* and *Triscutum*. Thus the classification of *Bussonius* becomes somewhat problematic. We see no reason to retain Bussoniaceae as a monotypic family. *Bussonius* should either be classified among the other three-shield placoliths or within the family Watznaueriaceae. When examining published electron micrographs of three-shield Jurassic placoliths and those taken of Moroccan and Portuguese specimens, we concluded that distal-shield imbrication is not a singular, distinct morphologic feature within this group. Although *Bussonius* essentially has an imbricate distal shield and *Mazaganella* and *Triscutum* non-imbricate distal shields, we always observed specimens within these three genera with slightly imbricate distal shields. Even on the same specimen, different portions of the distal shield often show this variation. Therefore, we have classified all the three-shield Jurassic placoliths within the same family and subsequently, assigned priority to the family Bussoniaceae. The distinction between *Bussonius* and *Lotharingius* is more obvious (a distal shield versus a median distal cycle).

A second morphological feature of the rim is the presence and the development of an inner wall. This wall is prominent in *Bussonius*, which has an imbricate distal shield, represented by the type species of *Mazaganella*. For the forms having a vertical distal shield (*Triscutum*), the wall may either be absent or show variable development. These same variations in rim construction (imbrication and inner wall development) are observed in the early Jurassic muroliths (family Crepidolithaceae).

Genus *Mazaganella* BOWN 1987b emend.

Figure 3

Type species. – *Mazaganella pulla* BOWN 1987b.

Original diagnosis. – ‘Elliptical coccoliths with a rim consisting of three shields, each possessing elements showing little or no imbrication and joined along radial or nearly radial sutures; the large, open central area may be filled with a composite plate or cross, usually supporting a central spine’ (Bown 1987b, p. 38).

Emended diagnosis. – Elliptical placoliths with a rim consisting of three, horizontal shields, each possessing elements showing little or no imbrication.

Discussion. – Bown (1987b) published the description of *Mazaganella* six months after *Triscutum* Dockerill (1987). He differentiated *Triscutum* from *Mazaganella* by its greater distal extension, broader ellipticity, and complex central grills. These morphologic features represent general differences between the Liassic *Mazaganella* and the *Triscutum* species documented from younger Jurassic strata, but the basic difference mentioned by Bown (1987b) was the type of central structure. Using the central structure to differentiate the two genera can cause difficulties when encountering specimens with neither of these two central area constructions. This would then involve the description of additional genera based on central area construction.

The most significant difference between the type species of these two genera is the orientation of the distal shield elements. *Triscutum beaminsterense* has an upright distal shield constructed of L-shaped elements and *Mazaganella pulla* has an horizontal distal shield constructed of planar elements.

Genus *Triscutum* DOCKERILL 1987

Figure 3

Type species. – *Triscutum beaminsterense* DOCKERILL 1987

Diagnosis. – ‘Elliptical placoliths with three shields in which the distal shield extends vertically to form a high collar, the elements of which diverge distally to form a wide distal margin. The two proximal shields are closely adjacent to one another’ (Dockerill 1987, p. 127).

Discussion. – The description and diagnosis of *Triscutum* mentioned only the rim ultrastructure. Although the type species has a central grill, the generic description allows for all forms with three shields and a vertically extended distal shield to be placed within *Triscutum*. Such a concept is practical because their delicate central structures are not often preserved. Secondary overgrowth is also a problem because it can obscure the shape of the L-shaped distal elements.

The morphology of the distal shield and its corresponding optical characteristics clearly define biostratigraphically useful taxa.

Differentiation. – *Triscutum* and *Calyculus* have identical distal rim constructions, but the former is distinguished by having an additional shield. The morphologic similarities between the two genera might be some basis for including *Triscutum* within the Calyculaceae. However, current understanding of the evolution of the two genera suggests they are unrelated. *Calyculus* evolved from the radiate placoliths, the Biscutaceae, during the Pliensbachian through extension of the distal shield (Crux 1987a, Bown 1987b). This trend continued into the Toarcian, marked by the entry of *Carinolithus*. The Bussoniaceae (*Triscutum*) originated in the early/late Sinemurian from a murolith ancestor.

Triscutum protensum (BOWN 1987b) comb. nov.

1987b *Mazaganella protensa* BOWN, p. 39; pl. 9, figs. 1–5; pl. 14, figs. 24, 25; textfig. 8.

Discussion. – *Triscutum protensum* shares morphologic features with the type species of *Mazaganella*, *Bussonius*, and *Triscutum*. It is transferred into the latter genus herein

based on its rim construction. The original diagnosis of *Triscutum* emphasizes a vertical distal shield and no particular central area construction. The description of this genus also mentions the presence of an inner wall, which surrounds the central area to the height of the intermediate shield. *Triscutum protensum* has the same rim construction. It differs from the type species, *Triscutum beaminsterense*, by its central structure and less extended distal shield.

Triscutum protensum and *Mazaganella pulla* (type species) both have a central axial cross and a non-imbricate, three-shield construction. Bown (1987b) indicated that *Triscutum protensum* evolved from *Mazaganella pulla* and placed both species into the genus *Mazaganella*. However, *Mazaganella pulla* has significant differences in its rim construction (it lacks a well developed inner rim wall and has a horizontal distal shield).

Triscutum protensum also shows many similarities to *Bussonius prinsii* (type species). Most significantly, both species have prominent inner rim walls, a feature not seen in *Mazaganella pulla*. The significant differences between *Bussonius prinsii* and *Triscutum protensum* are the imbrication of the distal shield elements and the presence of lateral bars in the central area of *Bussonius prinsii*. However, specimens of *Bussonius* with very few or no lateral bars have been observed in both the Portuguese and Moroccan early Jurassic.

Triscutum tiziense sp. nov.

Plate 4, Figures 1–8

Derivation of name. – From the locality Tizi n’Zou (High Atlas, Morocco).

Diagnosis. – A large, normally to broadly elliptical *Triscutum* species with a wide rim formed of three, relatively broad shields of different widths. The upright distal shield forms a thick, brightly birefringent distal shelf.

Description. – A large, normally to broadly elliptical placolith having a broad, three-shield rim construction. The shields are of different widths; each shield is constructed of non-imbricate elements with radial sutures. The distal shield elements are vertical and extend laterally in their distal portion to form a broad, thick, shelved margin. The relatively broad proximal and intermediate shields are composed of subhorizontal, tabular elements. The central area is relatively small, occupying between 1/2 to 1/3 of the total width. A very thin, delicate central grill fills the central area, but is rarely preserved intact.

In the LM and in plan view, the outer peripheries of the proximal and intermediate shields divide the rim into three cycles. In cross-polarized light, the distinct inner rim cycle appears smooth, is highly birefringent, and displays spiralled extinction lines. The radial sutures of the rim are very distinct in the outer two rim cycles.

Length. – 9.0–12.0 μm .

Differentiation. – *Triscutum tiziense* is distinguished from most other *Triscutum* species by its large size. *Triscutum sullivanii* is another large species. *Triscutum tiziense* is distinguished from that species by its larger size, more broadly elliptical outline, broader rim, and more highly birefringent distal shield. *Triscutum tiziense* appeared earlier in Morocco than in Portugal and Switzerland. The extinction of this species is consistent among all the sections examined.

Occurrence.

- Morocco (de Kaenel). LO: lower Aalenian (*opalinum* Zone). HO: lower Bajocian (top *discites* Zone).
 - Portugal (Bergen). lower Aalenian (upper *opalinum* Zone) – lower Bajocian (top *discites* Zone).
 - Switzerland (de Kaenel). lower Aalenian (upper *opalinum* Zone) – lower Bajocian
- Holotype.* Plate 4, Figures 7a–c (same specimen: FSU-LEM-40-22, FSU-LEM-40-N, FSU-LEM-40-23).
- Type level.* Sample BR 80, middle Aalenian (*murchisonae* Zone).
- Type locality.* Brehna, Portugal.

Triscutum sullivanii sp. nov.

Plate 5, Figures 1–7

1987b *Triscutum* sp. 1 BOWN, p. 40; pl. 9, figs. 6–9; pl. 12, figs. 26–27.

Derivation of name. – Named in honor of Dr. Frank Sullivan.

Diagnosis. – A relatively large, normally elliptical species of *Triscutum* with a large central area filled by a granular plate. The lateral extension of the distal shield forms about 1/2 the total rim width.

Description. – A medium to large, normally elliptical placolith composed of three shields connected by an inner wall. Each of the shields are constructed of 25–40, non-imbricate to slightly imbricated elements with radial sutures. The proximal and intermediate shields are composed of subhorizontal, tabular elements. The distal shield is composed of upright elements that extend laterally at their distal extremity to form a narrow distal shelf (about 1/2 the narrow rim width). The inner wall is visible as an inner cycle on the proximal shield and extends upwards to the lower portion of the distal shield. The central area is relatively wide, being greater than 1/2 the rim width. A very thin, granular central plate fills the central area, but is rarely preserved intact.

In the LM, the species exhibits a bicyclic rim extinction pattern. The thin, bright, inner rim cycle corresponds to the area occupied by the inner rim wall. This cycle also exhibits spiralled extinction lines and appears smooth in cross-polarized light. The remainder of the rim displays a faint, first order white birefringence and radial sutures. The central plate, when present, is barely visible and nearly extinct in cross-polarized light.

Length. – 7.4–9.2 μm .

Discussion. – Several different specimens were used to obtain a complete description of this species. The holotype is documented with both electron and light photomicrographs, confirming the optical properties and ultrastructure of the rim. The construction of the inner wall is best illustrated by the specimens in Bown (1987b; pl. 9, figs. 6–9), but is also visible as inner proximal rim cycle on the holotype. Two specimens (Pl. 5, Figs. 1, 2) were preserved with their central structures fully intact.

Differentiation. – *Triscutum tiziense* is distinguished from *Triscutum sullivanii* by its: (1) more massive and brightly birefringent distal shield; (2) largely unequal proximal and intermediate shields; (3) relatively smaller central opening; and (4) larger size. *Triscutum beaminsterense* is more broadly elliptical and has a relatively wide and more uniformly birefringent rim. The individual rim elements of *Triscutum beaminsterense* are optically more distinct than those of *Triscutum sullivanii*, giving its rim a striated appearance.

Occurrence.

- Portugal (Bergen). LO: middle Aalenian (base *murchisonae* Zone). HO: lower Bajocian (*sauzei* Zone).
- Morocco (de Kaenel). LO: middle Aalenian (*murchisonae* Zone). HO: lower Bajocian (*discites* Zone).
- Switzerland (de Kaenel). LO: upper Toarcian (*aalensis* Zone). HO: lower Bajocian (*sauzei* Zone). Weiach, North Switzerland.

Holotype. Plate 5, Figures 7a, b, c (same specimen FSU-LEM-40-7, FSU-LEM-40-5a, FSU-LEM-40-5b).

Paratype. Plate 5, Figures 1a, b (same specimen FSU-FO10-D13, FSU-FO10-D14).

Type level. Sample BR 107, lower Bajocian (*sauzei* Zone).

Type area. Brehna, Portugal.

Triscutum pricatillus sp. nov.

Plate 5, Figures 8–9

Derivation of name. – From Latin *prior*, first and *catillus*, small dish.

Diagnosis. – A small to medium-sized, elliptical species of *Triscutum* with a small central area nearly filled by an axial cross structure. The rim is uniformly birefringent (an inner wall is not recognizable).

Description. – A small to medium-sized, narrowly to normally elliptical placolith constructed of three shields. Each shield is formed by a single cycle of non-imbricate elements with radial sutures. The relatively low distal shield is constructed of upright elements which extend laterally in their distal portion to form a flat distal shelf (L-shaped elements). The horizontal proximal and intermediate shields are constructed of tabular elements and are of different widths (the proximal one being much smaller). The small central area is nearly filled by a thin axial cross structure that is attached to the proximal surface. A small opening is present in the center of the cross.

In the LM, the rim displays a faint, uniform birefringence. The outer peripheries of the unequal-sized shields are distinct in cross-polarized light. The axial cross structure is faintly birefringent, but is not frequently preserved intact.

Discussion. – The figured specimens of *Triscutum pricatillus*, which were recovered from the Pliensbachian, are 5.8 and 7.3 μm in length. However, smaller specimens down to 3 μm have been observed in the Sinemurian section at the base of DSDP Site 547 B. *Mazaganella* is also present at the base of this section. Thus both of these taxa represent the oldest known placolith species.

Differentiation. – *Triscutum pricatillus* and *Triscutum protensum* have similar central area constructions and rim morphologies. *Triscutum protensum* is distinguished by its prominent inner rim wall, which appears as a highly birefringent, wide inner rim cycle. *Triscutum pricatillus* is distinguished from *Mazaganella pulla* by its vertically extended distal shield and the unequal widths of its three shields. *Triscutum pricatillus* differs from *Triscutum sullivanii* and *Triscutum tiziense* by its axial cross structure, smaller size and absence of a birefringent inner rim cycle.

Occurrence.

- Normandy, France. Specimen illustrated is lower Pliensbachian.
- Portugal (Bergen). LO: upper Sinemurian (*raricostatum* Zone). HO: lower Bajocian.

– DSDP Site 547B. LO: Sinemurian (base of section).

Holotype. Plate 5, Figures 9a, b (same specimen: FSU-LEM-38-Ja, FSU-LEM-38-Jb).

Type level. Sample SP 28, lower Pliensbachian (*davoei* Zone).

Type locality. Sao Pedro de Mal, Portugal.

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Plate explanations

XP: cross-polarized light; Tr: transmitted light; Ph: phase contrast; LM: light microscope; SEM: scanning electron microscope; LEM: same specimen in both light and scanning electron microscopes. All light micrographs, $\times 2500$. Scanning electron micrographs as indicated. Holotype specimen micrographs are marked by a small asterisk.

Plate 1

Scale bar = 1 μm

Figs. 1–11. *Similiscutum orbiculus* sp. nov.

Figs. 1 a–b. Tunnel de la Légion, L 32-l (*lavinianum* Zone); 1 a-XP, FSU-FO15-D41; 1 b-Ph, FSU-FO15-D42.

Figs. 2 a–b. Endt, En 22 (*algovianum* Zone); 2 a-XP, FSU-FO13-D10; 2 b-Ph, FSU-FO13-D11.

Figs. 3 a–b. Tunnel de la Légion, L 32-l (*lavinianum* Zone); 3 a-XP, FSU-FO15-D33; 3 b-Ph, FSU-FO15-D34.

Figs. 4 a–b. Tunnel de la Légion, L 32-l (*lavinianum* Zone); 4 a-XP, FSU-FO13-D27; 4 b-Ph, FSU-FO13-D28.

Fig. 5. Lateral view, Ouchbis, Ou 11 (*emaciatum* Zone), IGN-F51-D14, $\times 10\,400$ (2.7 μm).

Fig. 6. Proximal view, Sao Pedro de Mal, SP 20 (*ibex* Zone), APR-1371, $\times 10\,000$ (3.3 μm).

Fig. 7. Distal view, Tunnel de la Légion, L 34 (*lavinianum* Zone), FSU-F7-D20, $\times 6\,000$ (4.1 μm).

Fig. 8. Distal view, Tunnel de la Légion, L 34 (*lavinianum* Zone), FSU-F8-D9, $\times 6\,000$ (4.8 μm).

Fig. 9. Distal view, Tunnel de la Légion, L 36 (*algovianum* Zone), FSU-F6-D2, $\times 6\,000$ (4.4 μm).

Fig. 10. Distal view, Endt, En 8C (*ibex* Zone), IGN-F52-D44, $\times 7\,000$ (3.5 μm).

Figs. 11 a–b. Holotype, proximal view, Tunnel de la Légion, L 34 (*lavinianum* Zone); 11 a FSU-F7-D29, $\times 6\,000$; 11 b: FSU-F7-D27, $\times 10\,000$ (4.2 μm).

Figs. 12–14. *Similiscutum avitum* sp. nov.

Fig. 12. Distal view, Ouchbis, Ou 11 (*emaciatum* Zone), IGN-F50-D12, $\times 6\,000$ (4.4 μm).

Fig. 13. Holotype, proximal view, Sao Pedro de Mal, SP 33 (*margaritatus* Zone), APR-1370, $\times 10\,000$ (3.3 μm).

Fig. 14. Distal view, Ouchbis, Ou 11 (*emaciatum* Zone), IGN-F51-D19, $\times 7\,000$ (4.7 μm).

Fig. 15. *Palaeopontosphaera dubia* Noel 1965. Distal view, primitive form with low inner distal cycle, Brehna, BR 27, APR-1369 (*margaritatus* Zone), $\times 10\,000$ (2.4 μm).

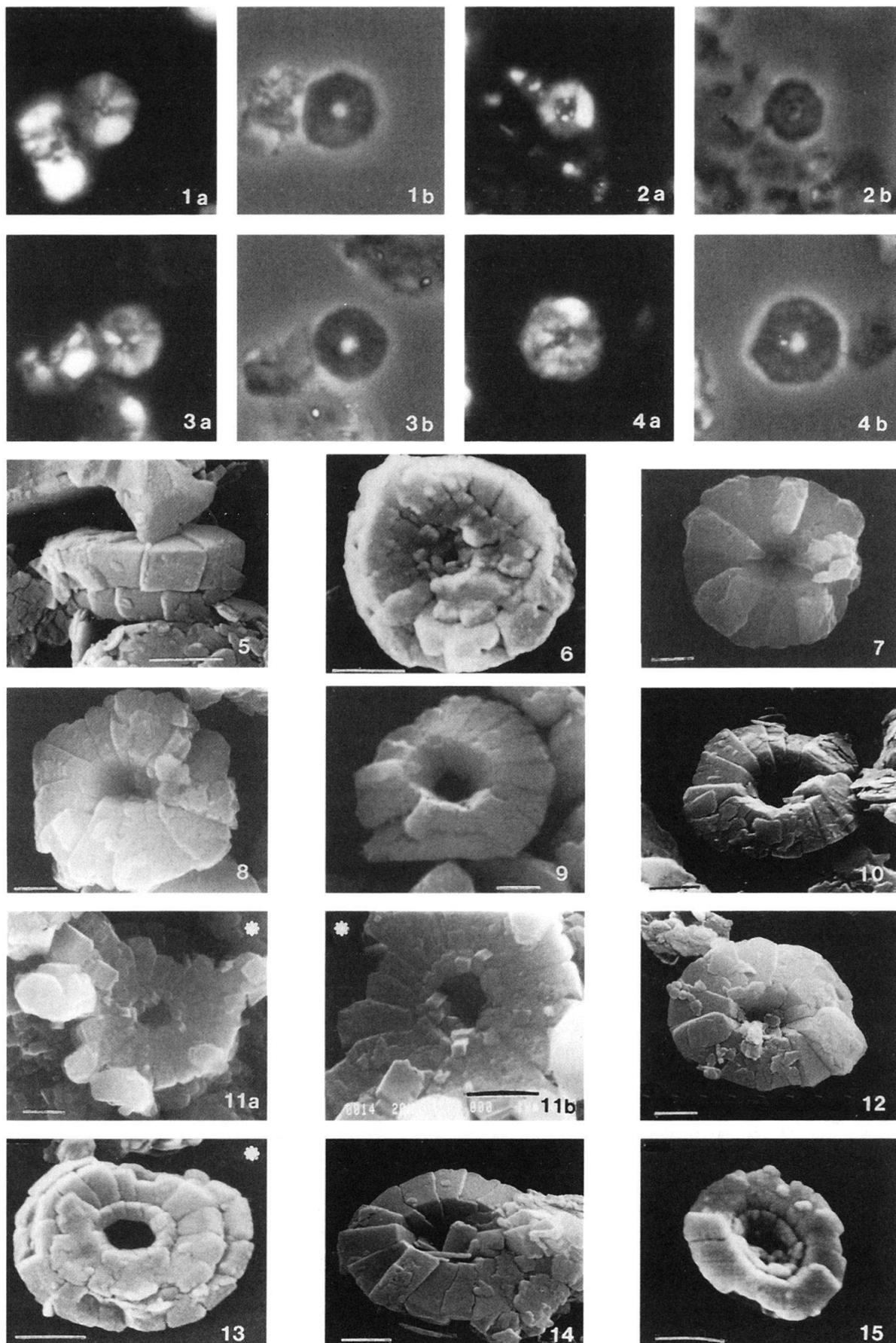


Plate 2Scale bar = 1 μm Figs. 1–4. *Similiscutum avitum* sp. nov.Figs. 1 a–b. Endt, En 8-l (*ibex* Zone); 1 a-XP, FSU-FO14-D3; 1 b-Ph, FSU-FO14-D5.Figs. 2 a–b. Tunnel de la Légion, L 32 (*lavinianum* Zone); 2 a-XP, FSU-FO12-D6; 2 b-Ph, FSU-FO12-D7.Figs. 3 a–b. Endt, En 22 (*algovianum* Zone); 3 a-XP, FSU-FO13-D21; 3 b-Ph, FSU-FO13-D22.Figs. 4 a–b. Endt, En 22 (*algovianum* Zone); 4 a-XP, FSU-FO13-D14; 4 b-Ph, FSU-FO13-D15.Figs. 5–11. *Similiscutum cruciulus* sp. nov.Figs. 5 a–b. Brehna, Br 28 (*margaritatus* Zone); 5 a-XP, FSU-LM-08-22; 5 b-Tr, FSU-LM-08-23.Figs. 6 a–b. Brehna, Br 28 (*margaritatus* Zone); 6 a-XP, FSU-LEM-34-02; 6 b-Tr, FSU-LEM-34-01.Figs. 7 a–b. Tunnel de la Légion, L 32 (*lavinianum* Zone); 7 a-XP, FSU-FO12-D8; 7 b-Ph, FSU-FO12-D9.Figs. 8 a–b. Tunnel de la Légion, L 32-l (*lavinianum* Zone); 8 a-XP, FSU-FO15-D18; 8 b-Ph, FSU-FO15-D19.Fig. 9. Holotype, proximal view, Sao Pedro de Mal, SP 26 (*ibex* Zone), FSU-EM-336, $\times 6000$ (3.9 μm).Fig. 10. Distal view, Sao Pedro de Mal, SP 26 (*ibex* Zone), FSU-EM-335, $\times 6000$ (3.9 μm).Fig. 11. Distal view, Sao Pedro de Mal, SP 34 (*margaritatus* Zone), APR-1367, $\times 6000$ (4.0 μm).Figs. 12–15. *Similiscutum precarium* sp. nov.Fig. 12. Distal view, Sao Pedro de Mal, SP 9 (*raricostatum* Zone), APR-1366, $\times 6000$ (4.1 μm).Fig. 13. Distal view, Sao Pedro de Mal, SP 20 (*ibex* Zone), APR-1368, $\times 6000$ (4.6 μm).Fig. 14. Distal view, Sao Pedro de Mal, SP 20 (*ibex* Zone), FSU-EM-351, $\times 8400$ (4.7 μm).Figs. 15 a–b. Holotype, Sao Pedro de Mal, SP 28 (*davoei* Zone); 15 a-XP, FSU-LM-08-15; 15 b-Tr, FSU-LM-08-17, (5.4 μm).

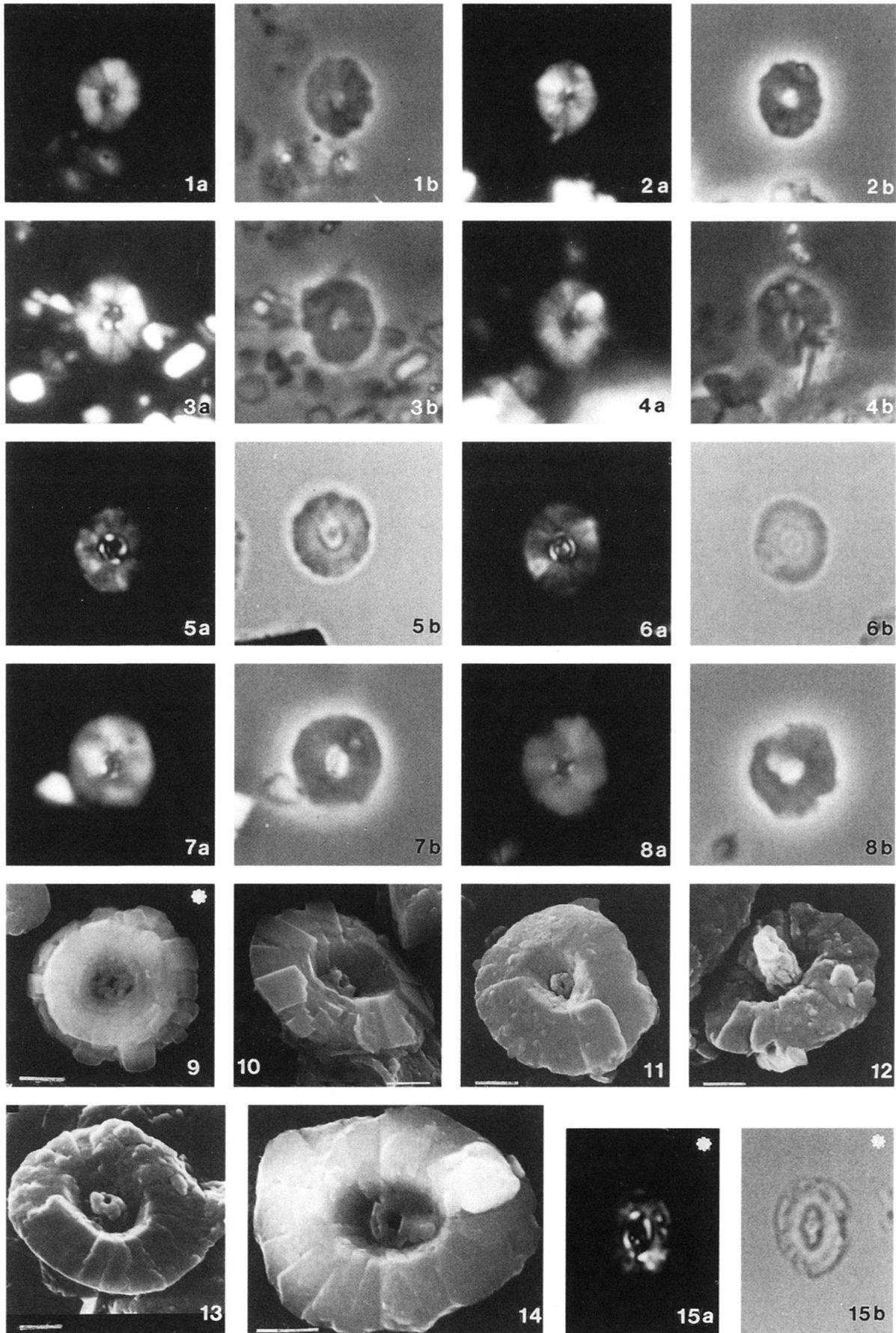


Plate 3Scale bar = 1 μ m

- Figs. 1–5. *Discorhabdus novus* (Goy 1979) *comb. nov.*
 Figs. 1 a–b. Peniche, Pen 26 (*spinatum* Zone); 1 a-XP, FSU-LM-07-20; 1 b-Tr, FSU-LM-07-21.
 Figs. 2 a–b. Tunnel de la Légion, L32-l (*lavinianum* Zone); 2 a-XP, FSU-FO15-D39; 2 b-Ph, FSU-FO15-D40.
 Figs. 3 a–b. Wittnau, We 33 (*aalensis* Zone); 3 a-XP, FSU-FO19-D26; 3 b-Ph, FSU-FO19-D28.
 Fig. 4. Distal view, Mont Terri TC 85 (*variabilis* Zone); IGN-F64-D37, \times 6000 (4.15 μ m).
 Fig. 5. Proximal view, Mont Terri, TC 85 (*variabilis* Zone); IGN-F66-D39, \times 6000 (4.6 μ m).
 Figs. 6, 7. *Biscutum profundum sp. nov.*
 Figs. 6 a–b. Peniche, Pen 19 (*margaritatus* Zone); 5 a-XP, FSU-LM-07-29; 5 b-Ph, FSU-LM-07-31.
 Figs. 7 a–b. Tunnel de la Légion, L32-l (*lavinianum* Zone); 6 a-XP, FSU-FO14-D8; 6 b-Ph, FSU-FO12-D5.
 Fig. 8. *Biscutum striatum* (Moshkovitz & Ehrlich 1976) *comb. nov.*
 Figs. 8 a–b. Gebel Maghara, N-133 (lover Bajocian); 8 a-XP, APR-LM-407-D27; 8 b-Tr, APR-LM-407-D28.
 Figs. 9–10. *Biscutum profundum sp. nov.*
 Fig. 9. Isotype, distal view, Tizi n'Zou, Zou 4 (*thouarsensae* Zone); IGN-F25-28, \times 6000 (5.2 μ m).
 Fig. 10. Holotype, proximal view, Ouchbis, Ou 30 (*bifrons* Zone); IGN-F51-D27, \times 6000 (4.2 μ m).
 Figs. 11–13. *Similiscutum finchii* (Crux 1984) *comb. nov.*
 Figs. 11 a–b. Sao Pedro de Mal, SP 33 (*margaritatus* Zone); 9 a-XP, FSU-LM-08-09; 9 b-Ph, FSU-LM-08-11.
 Fig. 12. Distal view, Tunnel de la Légion, L 34 (*lavinianum* Zone); FSU-F7-D21, \times 6000 (7.0 μ m).
 Fig. 13. Proximal view, Endt, En 13 (*lavinianum* Zone); FSU-F8-D4, \times 6000 (7.1 μ m).
 Figs. 14–15. *Similiscutum gephyrion sp. nov.*
 Figs. 14 a–b. Sao Pedro de Mal, SP 33 (*margaritatus* Zone); 12 a-XP, FSU-LM-08-06; 12 b-Tr, FSU-LM-08-07.
 Fig. 15. Holotype, distal view, Sao Pedro de Mal, SP 33 (*margaritatus* Zone); FSU-LEM-39-o, \times 6000 (6.2 μ m).

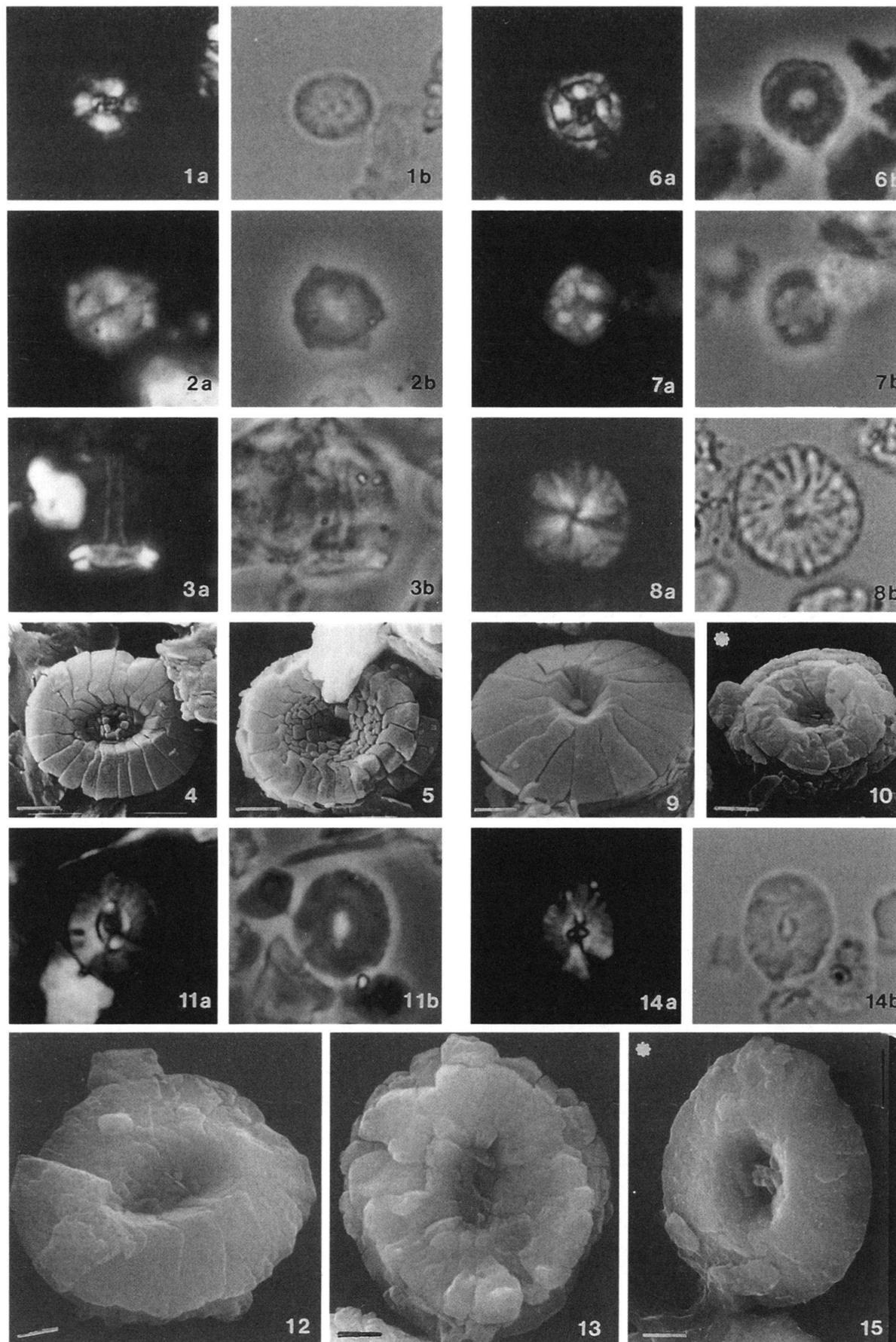


Plate 4

Scale bar = 1 μ m

Figs. 1–8. *Triscutum tiziense* sp. nov.

Figs. 1a–c. Brehna, Br 83 (*concauum* Zone); 1a-XP, FSU-LM-20-8; 1b-Ph, FSU-LM-20-10; 1c-Tr, FSU-LM-20-9.

Figs. 2a–c. Bao Viagem, BV 24 (*concauum* Zone); 2a-XP, FSU-LM-20-5; 2b-Ph, FSU-LM-20-7; 2c-Tr, FSU-LM-20-6.

Figs. 3a–b. Tizi n'Zou, Zou 31 (*concauum* Zone); 3a-XP, FSU-FO13-D8; 3b-Ph, FSU-FO13-D9.

Figs. 4a–b. DSDP Site 547B, Core 8-2, 118–119 cm (lower Bajocian); 4a-XP, FSU-FO14-D6; 4b-Ph, FSU-FO14-D7.

Figs. 5a–b. Brehna, Br 80 (*murchisonae* Zone); 5a-XP, FSU-FO13-D43; 5b-Ph, FSU-FO13-D1.

Figs. 6a–b. Brehna, Br 83 (*concauum* Zone); 6a, oblique proximal view, same specimen as fig. 6b, FSU-F2-D29, $\times 2300$ (12.8 μ m).

Figs. 7a–c. Holotype, Brehna, Br 80 (*murchisonae* Zone); 7a, proximal view, same specimen as figs. 7b–7c, $\times 4000$, FSU-LEM-40-22; 7b-XP, FSU-LEM-40-N; 7c-Tr, FSU-LEM-40-23 (11.2 μ m).

Figs. 8a–b. Brehna, Br 80 (*murchisonae* Zone); 8a, lateral view, same specimen as fig. 8b, FSU-LEM-40-Xb; 8b, distal view, FSU-LEM-40-Xa, $\times 3000$ (10.8 μ m).

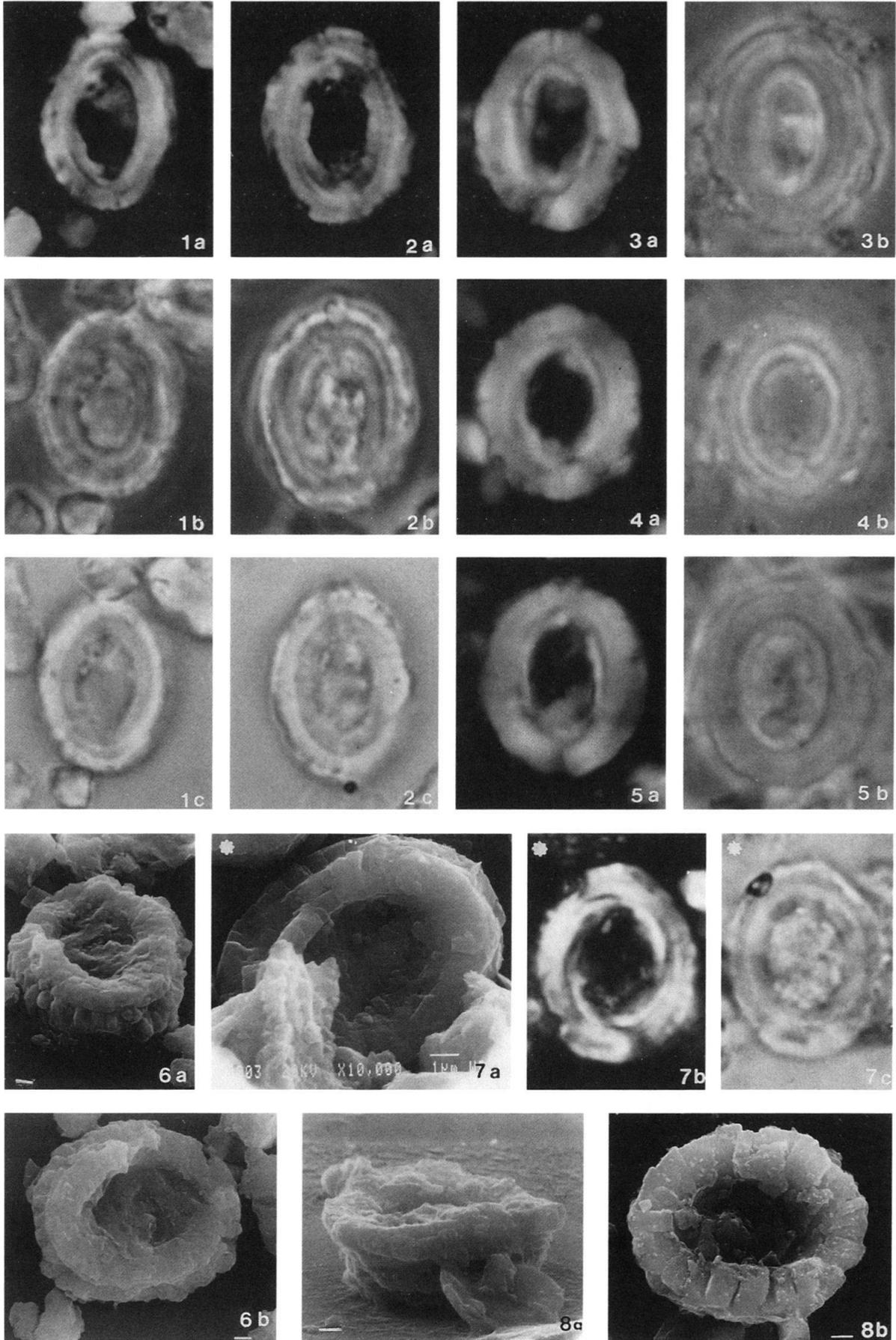


Plate 5

Scale bar = 1 μ m

Figs. 1–7. *Triscutum sullivanii* sp. nov.

Figs. 1a–b. Paratype, Weiach, We 666.96 m (*aalensis* Zone); 1a-XP, FSU-FO10-D13; 1b-Ph, FSU-FO10-D14.

Figs. 2a–b. Bouhaga, B 19 (*concauum* Zone); 2a-XP, FSU-FO12-D18; 2b-Ph, FSU-FO12-D19.

Figs. 3a–b. DSDP Site 547B, Core 8-2, 118–119 cm (lower Bajocian); 3a-XP, FSU-FO14-D18; 3b-Ph, FSU-FO14-D20.

Figs. 4a–b. Kerrando-Gourrama, KG 73 (*concauum* Zone); 4a-XP, FSU-FO13-D5; 4b-Ph, FSU-FO13-D6.

Figs. 5a–b. Brehna, Br 80 (*murchisonae* Zone); 5a-XP, FSU-FO13-D41; 5b-Ph, FSU-FO13-D42.

Figs. 6a–c. Brehna, Br 82 (*murchisonae* Zone); 6a-XP, FSU-LM-20-11; 6b-Ph, FSU-LM-20-14; 6c-Tr, FSU-LM-20-13.

Figs. 7a–c. Holotype, Brehna, Br 107 (*sauzei* Zone); 7a-XP, same specimen as figs. 7b–7c, FSU-LEM-40-7; 7b, proximal view, FSU-LEM-40-5a, $\times 4000$; 7c, oblique proximal view, FSU-LEM-40-5b, $\times 4000$ (8.8 μ m).

Figs. 8–9. *Triscutum pricatillus* sp. nov.

Figs. 8a–b. Annéot, DN5 (Noël, 1965), Charmouthian (Pliensbachian); 8a-XP, APR-LM-407-35; 8b-Tr, APR-LM-407-36.

Figs. 9a–b. Holotype, Sao Pedro de Mal, SP 28 (*davoei* Zone); 9a, proximal view, same specimen as Fig. 9b, FSU-LEM-38-Ja, $\times 4800$; 9b, oblique proximal view, FSU-LEM-38-Jb, $\times 4800$ (7.3 μ m).

