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Cretaceous microporid cheilostome bryozoans from the Campanian historical stratotype of southwest France

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ABSTRACT

The Campanian of southwest France hosts rich and diverse bryozoan assemblages of global importance in tracing the faunal turnover from cyclostome to cheilostome dominance. Nevertheless, bryozoans from this historical stratotype region for the Campanian stage have been poorly studied, and most of the species erected by Alcide d'Orbigny in the 1850s remain unrevised. Here we focus on the four species of anascan-grade cheilostomes with opesiulate cryptocystal frontal walls, conventionally classified in the family Microporidae. One new genus and two new species are introduced: *Platelinella solea* n. gen. et n. sp. and *Micropora mikesmithi* n. sp. The enigmatic genus *Dimorphomicropora* Ducasse & Vigneaux, 1960 and the two species (*D. voigti* Ducasse & Vigneaux, 1960 and *D. crestulata* (Ducasse, 1958)) from southwest France are revised. Mandibulate polymorphs present in *D. voigti* resemble the B-zooids of *Steginoporella* but are unlikely to be homologous.

KEY WORDS
Cretaceous,
Campanian,
Aquitaine Basin,
lectotypification,
new genus,
new species,
new combinations.

RÉSUMÉ

Les Microporidés crétaqués, bryozoaires cheilostomes, du stratotype historique du Campanien dans le sud-ouest de la France.

Le Campanien du Sud-Ouest de la France héberge une abondante et riche faune de bryozoaires, importante à l'échelle globale pour suivre le changement progressif de dominance des Cyclostomes par les Cheilostomes. Cependant, les faunes de bryozoaires de la région stratotypique du Campanien restent peu étudiées et la plupart des espèces décrites par Alcide d'Orbigny dans les années 1850 n'ont toujours pas été révisées. Dans cet article, nous nous intéressons à quatre espèces de Cheilostomes classées par convention au sein de la famille des Microporidae et caractérisées par l'absence d'ascopore, un mur frontal formé par un cryptocyste étendu jusqu'à l'ouverture et laissant des orifices latéraux appelés opésiules. Un nouveau genre et deux nouvelles espèces sont décrits: *Platelinella solea* n. gen., n. sp. et *Micropora mikesmithi* n. sp. Le genre énigmatique *Dimorphomicropora* Ducasse & Vigneaux, 1960 est revu, et les deux espèces du Sud-Ouest de la France (*D. voigti* Ducasse & Vigneaux, 1960 et *D. crestulata* (Ducasse, 1958)) révisées. Des zoïdes mandibulés présents chez *D. voigti* ressemblent aux zoïdes de type B de *Steginoporella*, mais n'en sont probablement pas homologues.

MOTS CLÉS
Crétacé,
Campanien,
Bassin d'Aquitaine,
lectotypification,
genre nouveau,
espèces nouvelles,
combinaisons nouvelles.

INTRODUCTION

Bryozoans are a conspicuous element of the fossil assemblages found in the carbonates of the Campanian Stage historical stratotype region between Royan (Charente-Maritime) and Aubeterre-sur-Dronne (Charente) in south-west France. Not only are they extremely abundant in these shallow-water deposits, but they are also diverse, totalling more than 200 species. From an evolutionary standpoint, this bryozoan biota is particularly important because the Campanian was the time when the cyclostomes were first surpassed in diversity by cheilostomes (Lidgard *et al.* 1993), the bryozoan order that have dominated bryozoan biotas from that time until the present-day. The faunal turnover from cyclostome to cheilostome dominance is nowhere better documented than in southwest France where our collecting has shown that bryozoans can be found in all of the formations of the Campanian sequence. Nevertheless, remarkably little research has been published on the Campanian bryozoans of SW France. Indeed, the work of d'Orbigny (1851-1854) published over 150 years ago remains the main source for descriptions and illustrations of the species present. Apart from Canu (1900), Pergens (1889) and the thesis of Ducasse (1958), later papers have either consisted of faunal lists without supporting figures (e.g., Canu 1910; Gillard 1940a, b, 1942), or have concerned just a few species (e.g., Ducasse & Vigneaux 1960; Prudhomme 1961; Buge 1975; Voigt 1985). Crucially, none of these publications utilised scanning electron microscopy (SEM), now considered essential for the precise morphological characterization and accurate illustration of bryozoan species. Only a few publications (Voigt 1983; Voigt & Ernst 1985; Taylor 1994; Taylor *et al.* 2018) have included SEM images of bryozoans from the Campanian of south-west France.

Research in progress has focused on improving our knowledge on the species present in the Campanian of south-west France by recording the changing taxonomic composition of bryozoan assemblages through the sequence. Among the cheilostome bryozoans present are a small number of anascan-grade species with cryptocystal frontal shields pierced by opesiules. During life, these opesiules would have allowed the passage through the cryptocystal skeleton of the parietal muscles that depressed the frontal membrane to bring about protrusion of the lophophores. The species with opesiules are conventionally assigned to the extant family Microporidae Gray, 1848, although it must be noted that cheilostome classification is currently in a state of flux because of new findings from phylogenetic analysis based on molecular sequence data from extant taxa that is revealing significant issues with existing classifications (e.g., Orr *et al.* 2018).

The main aim of the current paper is to describe the four microporid species found in the Campanian of south-west France. Two are recognized as new taxa: *Micropora mikesmithi* n. sp. and *Platelinella solea* n. gen. et n. sp. In addition, the enigmatic genus *Dimorphomicropora* and its two species

from south-west France – *D. voighti* Ducasse & Vigneaux, 1960 and *D. crestulata* (Ducasse, 1958) – are redescribed.

GEOLOGICAL BACKGROUND

Upper Cretaceous deposits form a large slightly folded belt along the north of Aquitaine basin, cropping out for about 200 km, from the Atlantic coast in Charente-Maritime on the North-West to the Périgord noir, in Dordogne on the South-East. Three of the currently used stages of the Cretaceous were defined in the area, Coniacian, Santonian and Campanian (Séronie-Vivien 1972). One specificity of the area is the smooth landscape that offers limited sections for study. None of the stages can be described entirely from a single outcrop. The series of Campanian are by far the best developed with a thickness of more than 200 metres, and the stage definition initially considered several sections from the coastal cliffs of Charente-Maritime to the village of Aubeterre-sur-Drone in Charente (Coquand 1858). The difficulties in establishing a clear stratigraphical succession of sedimentary facies and of correlating across the scattered sections led to major inconsistencies in the definition of the Campanian stage, and in the placement of the Campanian-Maastrichtian boundary.

The current understanding of the Campanian stage is grounded on combined geomorphological, lithological and micropaleontological studies undertaken in the type area during the years 1970-1990. Stratigraphical variations in rock hardness are reflected in the landscape. Smooth cuestas can be traced through the area and help with correlations (Platel 1977). The lithological units forming cuestas are used in all geological maps edited by BRGM for Northern Aquitaine. The Campanian series include 6 lithostratigraphical units (numbered Campanien 1 to Campanien 6). Platel (1999) transcribed the lithological/cartographical units into formal geological formations. From base to top, the Campanian series is divided into Gimeux, Segonzac, Biron, Barbezieux, Aubeterre, and Maurens formations. A Lower Campanian age is assigned to the Gimeux and Segonzac formations, and an Upper Campanian age for the others. Note that the Middle Campanian recognized by North American stratigraphers, would be equivalent to the Biron Formation (J.-P. Platel pers. comm. 2018).

A comprehensive micropaleontological survey considered benthic and planktonic foraminifera, calcareous nannofossils, dinoflagellates, and ostracods (Andreieff & Marionnaud 1973; Neumann *et al.* 1983). The finer stratigraphical resolution was obtained from benthic foraminifera, with 11 distinct zones distinguished in the Campanian stage (Platel 1999). However, comparisons of foraminiferan and nannofossil zonations suggest that the first appearance of the index foraminifera may not be coeval everywhere on the North Aquitaine margin, especially in the Upper Campanian (Platel 1996). Pending more refined time constraints, sections and records of fossil species are usually dated using the benthic foraminifera zones. All sampled

bryozoan faunas are dated to the formation level, and to the foraminifera zones where is information available.

The Lower Campanian levels are dominated by chalky limestones, containing some clay and glauconite. The environment is interpreted as an open marine shelf, with muddy bottoms (Platel 1996). Bryozoans occur mostly as colony fragments and are only abundant in levels rich in sponge debris. Sedimentary facies remain grossly the same in the Biron Formation, with chalky and marly glauconitic limestones, some levels being rich in sponges. Fossil remains are much more abundant and diverse in the Upper Campanian than in the Lower Campanian. Oysters (*Pycnodonte*, *Cerato-streon*), other bivalves, bryozoans and echinoderms are very common in Biron Formation. The Barbezieux and Aubeterre formations are characterized by coarse, muddy sediments (wackestone to packstone) and the abundance of large benthic foraminifera (*Orbitoides*). *Pycnodonte* forms thick shell beds and radiolitic rudists become common elements of the fossil assemblages. Bryozoan richness and diversity reach a maximum for the stage during this interval.

Microporid bryozoans were collected from Upper Campanian levels only (Biron, Barbezieux and Aubeterre formations). The facies succession of the Upper Campanian records a shallowing upward trend (Platel 1996). The uppermost Campanian Maurens Formation is characterized by shallow water limestones of packstone texture, rich in large benthic foraminifera and algal debris. Rudists and oyster shells are extremely common, with the rudists developing locally into large bioherms. The upper part of Maurens Formation changes to yellow tuffaceous limestones, just before the Campanian-Maastrichtian stage boundary (Platel 1999).

MATERIAL AND METHODS

Scanning electron microscopy (SEM) was conducted on uncoated specimens using a low-vacuum scanning electron microscope LEO VP-1455 at the NHMUK, and Hitachi TM 3000 at Sorbonne Université. Measurements of characters were made from SEM images. Mean values are given in brackets following observed ranges.

ABBREVIATIONS

The material used in this study is lodged in the following institutions:

MNH.N.F	Muséum national d'Histoire naturelle, Paris, collection de Paléontologie;
NHMUK	Natural History Museum, London;
SU	Sorbonne Université, Paris;
UB	Université de Bordeaux.

Other abbreviations

OL	orifice length;
OW	orifice width;
N	number;
SD	standard deviation;
ZL	zooid length;
ZW	zooid width.

SYSTEMATIC PALAEOLOGY

Family MICROPORIDAE Gray, 1848

Genus *Micropora* Gray, 1848

TYPE SPECIES. — *Flustra coriacea* Johnston, 1847 (*non* Esper, 1791), by monotypy; Recent, British Isles.

REMARKS

Gordon (1984) listed the key features of *Micropora* as its encrusting colony-form, raised lateral walls, granular cryptocyst that is minutely perforated and penetrated by opesiules close to the orifice, and basal pore chambers. Oral spines are rare, and ovicells are recumbent or immersed. In addition, the orifice is typically semielliptical in shape, and there is an avicularium located immediately distally of the orifice in most species.

Micropora is a speciose genus distributed pan-globally at the present-day. Bock (<http://www.bryozoa.net/cheilostomata/microporidae/micropora.html>, accessed 5/7/2020) listed a total of 70 species living and fossil, including 16 species from the Cretaceous. According to Voigt (1981: p. 450) the genus is recorded as far back as the Early or Middle Cenomanian but this needs to be confirmed. Putative Cretaceous species of *Micropora* have not been adequately described or illustrated, and at least some are probably not congeneric with the type species.

None of the multitude of French Cretaceous bryozoans described by Alcide d'Orbigny were assigned by him to *Micropora*. A species originally assigned to *Vincularia* by d'Orbigny (1851: 78, pl. 657, figs 7-9) was later transferred to *Micropora* by Voigt (1968) but this species, *M. transversa* from the Maastrichtian of Cotentin, Manche, has an erect colony-form with narrow branches and would fall outside the definition of *Micropora* given by Gordon (1984) who restricted the genus to species that have encrusting colonies. Although Voigt's illustrations (1968: pl. 7, figs 9-12) of this species comprise photographs of poorly preserved branches, there are clear similarities with *Dimorphomicropora crestulata* (Ducasse, 1958) described below. The lectotype of *M. transversa* (MNHN.F.R61499) is also poorly preserved but is consistent with possible synonymy between this species and *D. crestulata* (see below).

Micropora mikesmithi n. sp.
(Fig. 1)

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TYPE MATERIAL. — **Holotype**. NHMUK PI BZ 8809, Aubeterre Fm, Archiac, Charente-Maritime (France). — **Paratypes**. NHMUK PI BZ 8363, Aubeterre Fm, rock face behind car-park, Aubeterre-sur-Dronne, Charente (France); NHMUK PI BZ 8655, Aubeterre Fm, roadcutting at junction of D5 and C18, east of Saint-Privat-des-Prés, Dordogne (France); SU.2021.1.1.0, Aubeterre Fm, roadcutting along the freeway RN10, Pont-du-Noble, Reignac, Charente (France).

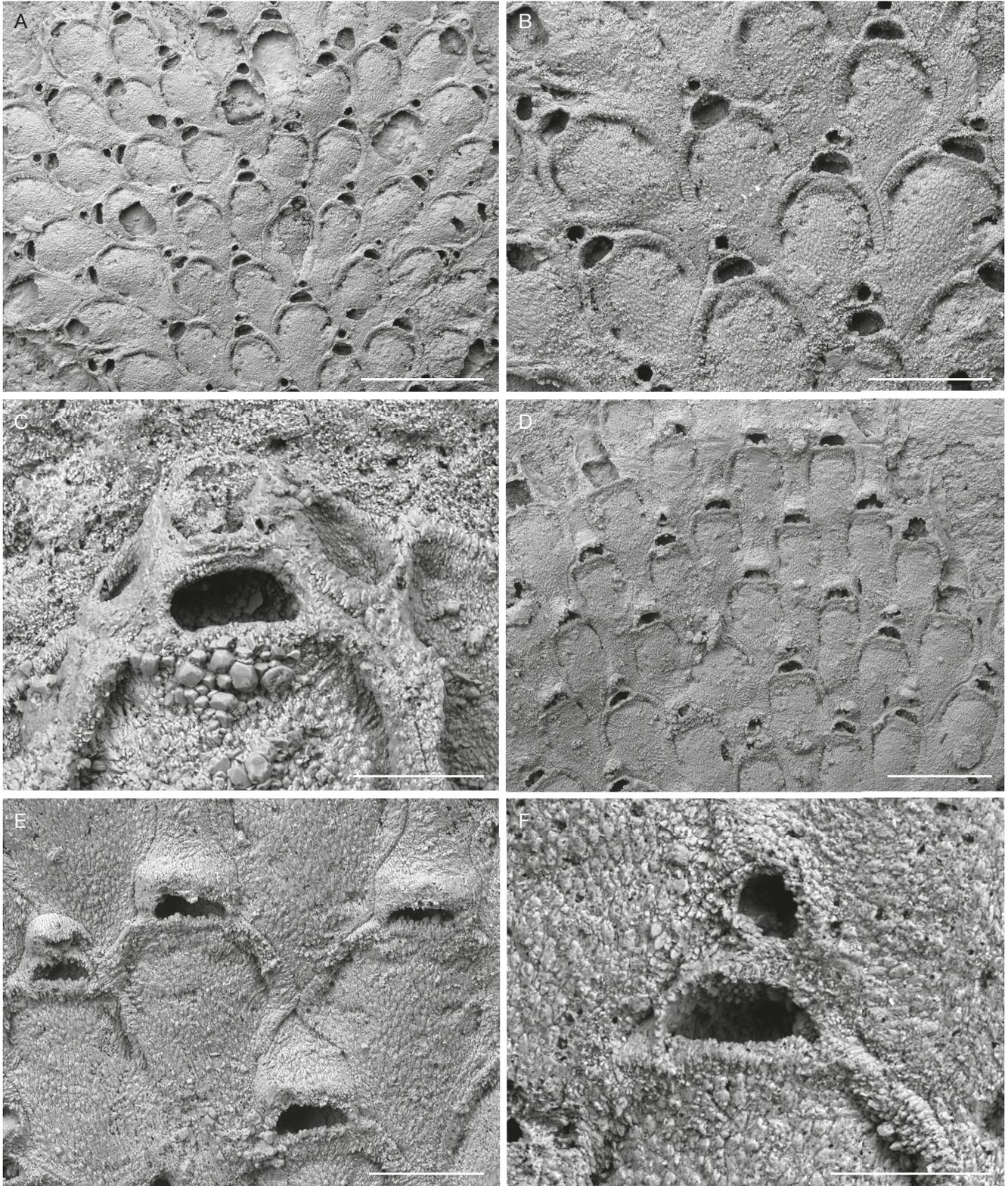


FIG. 1. — *Micropora mikesmithi* n. sp.: **A-C**, paratype, NHMUK PI BZ 8363, Aubeterre Fm, rock face behind car-park, Aubeterre-sur-Dronne, Charente: **A**, part of the colony; **B**, group of autozooids with avicularia distal of the orifices; **C**, autozooid at the growing edge; **D-E**, holotype, NHMUK PI BZ 8809, Aubeterre Fm, Archiac, Charente-Maritime: **D**, part of the colony; **E**, three ovicellate autozooids lacking an associated avicularium, and one infertile autozooid (**left**) with an avicularium; **F**, paratype, NHMUK PI BZ 8655, Aubeterre Fm, roadcutting at junction of D5 and C18, east of Saint-Privat-des-Prés, Dordogne, orifice and avicularium. Scale bars: A, D, 500 µm; B, E, 200 µm; C, F, 100 µm.

TYPE LOCALITY. — Aubeterre Fm, Archiac, Charente-Maritime (France).

ETYMOLOGY. — Named for Mike Smith, enthusiastic volunteer at the NHMUK, who helped during fieldwork in the Campanian of SW France.

OCCURRENCE. — Upper Campanian, Barbezieux and Aubeterre formations.

DESCRIPTION

Colony encrusting, multiserial, sheet-like, unilamellar. Autozooids longer than wide, ZL 354-597 μm (N colonies 4; N zooids 26; mean 446; SD 58 μm), ZW 231-355 μm (N colonies 4; N zooids 26; mean 288; SD 30 μm), the proximolateral margins typically concave and the distolateral margins convex with well-rounded distal ends. Frontal wall entirely lacking gymnocyst; cryptocyst forming most of the frontal surface, gently convex, depressed beneath the raised rims outlining the zooids, lacking paired tubercles at the distolateral corners, texture granular; cryptocystal pores not evident (quite possibly obscured by diagenetic neomorphism of the skeleton); opesiules located adjacent to the raised zooidal rim in the distal half of the zooid, long and narrow, curved, either a single pair or two pairs in which case the more proximal opesiules are shorter in length. Orifice semielliptical, wider than long, OL 44-52 μm (N colonies 2; N zooids 10; mean 47 μm ; SD 3 μm), OW 89-109 μm (N colonies 2; N zooids 10; mean 97 μm ; SD 7 μm), the proximal edge straight or slightly concave. Ovicells small, moderately raised, the oecium rounded rectangular, wider than long, 84-97 μm long by 168-181 μm wide, calcification continuous with the cryptocyst of the distal zooid; orifices of ovicellate zooids significantly wider than those of non-ovicellate zooids, about 90 μm long by 175 μm wide. Avicularia absent in ovicellate zooids but present in all non-ovicellate zooids, located immediately distal of the orifice, oriented transversely, small, about 100-104 μm long by 64-89 μm wide, the opesia round and the rostrum rounded triangular in shape; presence of condyles or a pivotal bar uncertain. Ancestrula and early astogenetic stages not observed.

REMARKS

As mentioned above, the lack of modern descriptions of species of putative *Micropora* from the Late Cretaceous makes comparisons with the new species difficult. However, the Maastrichtian species *Micropora biforis* (Marsson, 1887) from Germany and the Netherlands has a pair of rounded opesiules close to mid-length, whereas the opesiules of *M. mikesmithi* are more slit-shaped, located further distally and consist of two pairs. In both Marsson's species and *Micropora multicrescens* Brydone, 1936, there is no indication of the presence of avicularia distal to the autozooids. *Micropora mobli* (Hagenow, 1851) resembles the new species but the avicularia are directed almost distally in contrast to the transverse orientation seen in *M. mikesmithi*.

Colonies of *M. mikesmithi* encrust shells of the bivalve *Pycnodonte vesiculare* (Lamarck, 1806).

Genus *Platelinella* n. gen.

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TYPE SPECIES. — *Platelinella solea* n. sp.

DIAGNOSIS. — Microporid with encrusting colonies; autozooids with narrow marginal gymnocyst surrounding concave cryptocyst pierced by 8-10 opesiules distributed in a horseshoe-shaped crescent; orifice semielliptical with a thin opercular shelf; no spines or tubercles; ovicells and avicularia unknown.

ETYMOLOGY. — Named for Jean-Pierre Platel in honour of his seminal contributions to Campanian stratigraphy in SW France.

REMARKS

This new genus can be compared with *Metamicropora*, introduced by Arakawa (2016) for a Japanese Miocene-Recent species originally attributed to *Verminaria*, characterised by having opesiules with internal cribrate openings. Cribrate openings have not been observed in *Platelinella*, although this may possibly reflect preservational limitations. However, *Platelinella* lacks tubercles located at the distolateral corners of the autozooids, and avicularia have not been seen in the studied colonies all of which are moderately large. The radial elongation of the opesiules in *Platelinella* is another difference from *Metamicropora*.

Platelinella solea n. sp.

(Fig. 2)

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ETYMOLOGY. — “*solea*”, meaning horseshoe in Latin, refers to the opesiules arranged in a horseshoe shaped row.

TYPE MATERIAL. — **Holotype**. NHMUK PI BZ 8564, Biron Fm, Le Caillaud (north side of cliff), Talmont, Charente-Maritime (France). — **Paratype**. NHMUK PI BZ 8848, Biron Fm, top benthic foram zone CIVb, Le Caillaud (south side of cliff), Talmont, Charente-Maritime (France).

TYPE LOCALITY. — Biron Fm, Le Caillaud (north side of cliff), Talmont, Charente-Maritime (France).

OCCURRENCE. — Upper Campanian, Biron Formation.

DESCRIPTION

Colony encrusting, multiserial, sheet-like, unilamellar. Autozooids slightly longer than wide, ZL 435-611 μm (N colonies 2; N zooids 10; mean 484 μm ; SD 58 μm), ZW 353-412 μm (N colonies 2; N zooids 10; mean 388 μm ; SD 20 μm), well-rounded distally. Frontal wall with cryptocyst finely granular, forming most of the frontal surface, a narrow raised, convex gymnocystal rim surrounding an extensive flat to slightly concave central cryptocystal region; occasional cryptocystal pores; 8-10 opesiules distributed evenly in a horseshoe shaped row at the outer edge of the central part of the cryptocyst, decreasing in size proximally, not clearly paired, oval, elongated radially, countersunk. Orifice semielliptical, wider than long, OL 106-

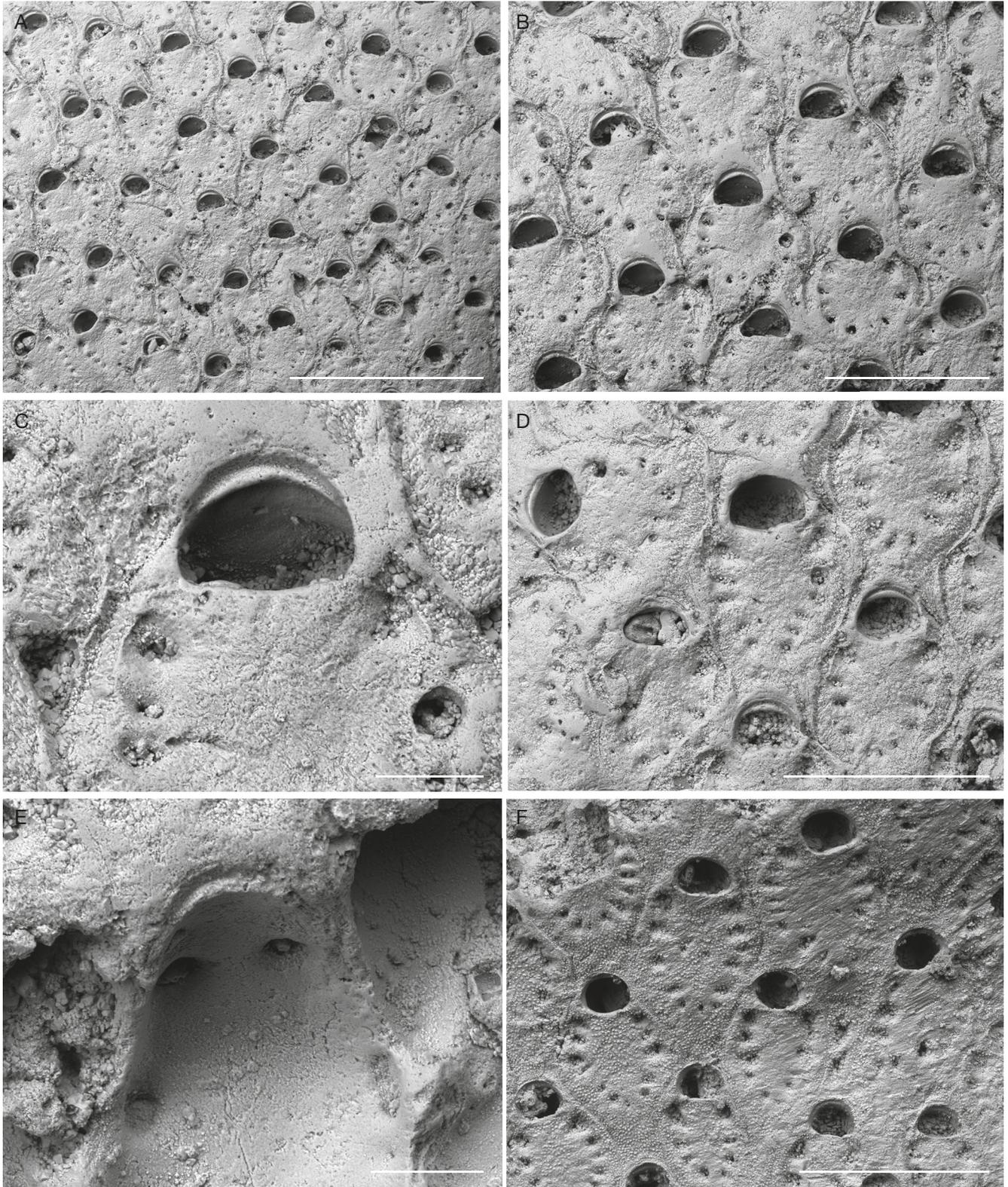


FIG. 2. — *Platelinella solea* n. gen. et n. sp.: **A-E**, holotype, NHMUK PI BZ 8564, Biron Fm, Caillaud (north side), Talmont, Charente-Maritime: **A**, part of the colony; **B**, group of zooids; **C**, zooid with narrow distal opercular shelf; **D**, group of zooids, one with a slightly enlarged orifice (upper centre); **E**, broken zooid revealing two distal and two distolateral septular pores; **F**, paratype, NHMUK PI BZ 8848, Biron Fm, Caillaud (south side), Talmont, Charente-Maritime, group of zooids. Scale bars: A, 1 mm; B, D, F, 500 µm; C, E 100 µm.

118 μm (N colonies 2; N zooids 10; mean 109 μm ; SD 10 μm), OW 118–153 μm (N colonies 2; N zooids 10; mean 136 μm ; SD 11 μm), the proximal edge gently convex, a narrow opercular shelf around the distal edge. Ovicells not observed; occasional zooids with slightly larger orifices (OL 115 μm , OW 170 μm) may perhaps have been brooding zooids. Avicularia absent. Ancestrula and early astogenetic stages not observed. Pore chambers lacking; a pair of septular pores visible in the distal vertical walls and a pair in the distolateral vertical walls.

REMARKS

Compared with the type and only previously described species of the most similar genus, *Metamicropora*, *P. solea* has radially rather than longitudinally elongate opesiules, which number 10–12 (12–18 in *M. areolae*), autozooids bordered by a narrow gymnocyst rather than the granular raised edge of the cryptocyst, and an opercular shelf along the distal edge of the orifice. It is readily distinguished from other microporid species recorded in the Campanian of SW France by the large number of opesiules which are distributed all around the lateral and proximal margins of the cryptocyst.

Genus *Dimorphomicropora* Ducasse & Vigneaux, 1960

TYPE SPECIES. — *Dimorphomicropora voighti* Ducasse & Vigneaux, 1960, by original designation.

OTHER SPECIES. — *Dimorphomicropora cretulata* (Ducasse, 1958) (described below); *Dimorphomicropora rugica* (Marsson, 1887), Lower Maastrichtian, Rügen, Germany, and Upper Maastrichtian of Maastricht, Netherlands (Voigt 1975); *Dimorphomicropora transversa* (d'Orbigny, 1851), Lower Maastrichtian, Néhou, Contentin, France.

REVISED DIAGNOSIS. — Microporid with erect colonies, narrow cylindrical branches lacking complete bifurcations, colonies probably articulated; autozooids lacking a gymnocyst, cryptocyst depressed centrally, pierced by 2 large opesiules; orifice subcircular to dummy shaped with a raised rim; no spines or tubercles; ovicells clustered resulting in branch dilation, oecia helmet-shaped, continuous with cryptocysts of the distal zooids, orifices of fertile zooids enlarged; mandibulate polymorphs in some species, infrequent, larger than autozooids but with similar frontal wall and opesiules, orifice semi-elliptical, longer than wide.

REMARKS

The name *Dimorphomicropora* refers to the zooidal dimorphism evident in the type species of this genus. In addition to normal autozooids (“Cellules A” of Ducasse & Vigneaux 1960), there are occasional polymorphic zooids (“Cellules B” of Ducasse & Vigneaux 1960) with an enlarged orifice and presumably an enlarged operculum or mandible. These mandibulate polymorphs resemble the B-zooids found in *Steginoporella*. Like the B-zooids of *Steginoporella*, it seems possible that they had the capacity to feed.

The existence of mandibulate polymorphs in *Dimorphomicropora* has led to the suggestion that this Cretaceous genus belongs to the Cenozoic family Steginoporellidae. However, Ostrovsky (2013: 329) believed *Dimorphomicropora* to be probably an unrelated homeomorph of *Steginoporella* and excluded

it from his superorder Thalamoporellina to which *Steginoporella* is assigned. Ducasse & Vigneaux (1960) hypothesised that *D. voighti* might be an evolutionary link between *Micropora rugica* [since assigned to *Dimorphomicropora* by Voigt 1975] and Steginoporellidae. At the time of their publication, this was consistent with the stratigraphy because the type locality (Meschers, Charente-Maritime) of *D. voighti* was considered to be of middle Maastrichtian age, whereas *D. rugica* was known only from the early Maastrichtian. However, the re-dating of Meschers as Campanian makes the order of occurrence of these two species incongruent with this evolutionary hypothesis.

Voigt (1975) misunderstood the nature of the dimorphism described in *Dimorphomicropora* by Ducasse & Vigneaux (1960), interpreting it to refer to the contrast between non-brooding and brooding ovicellate autozooids. However, the original description of *Dimorphomicropora* makes no mention of brooding zooids or ovicells. The type specimen of *D. crustulenta* (Ducasse, 1958) is ovicellate (Fig. 4A), as is a poorly preserved specimen of *D. voighti* (Fig. 3H).

Dimorphomicropora voighti Ducasse & Vigneaux, 1960 (Fig. 3)

MATERIAL. — **Lectotype.** UB C.B.993 (Ducasse & Vigneaux 1960: fig. 1), probably Aubeterre Fm, Meschers, Charente-Maritime (France). — **Paralectotype.** UB C.B.994 (Ducasse & Vigneaux 1960: fig. 2), probably Aubeterre Fm, Meschers, Charente-Maritime (France). — Other material: NHMUK PI BZ 8767, 8768, 8769, Aubeterre Fm, Pointe de Suzac, Meschers, Charente-Maritime (France).

OCCURRENCE. — Upper Campanian, Aubeterre Formation.

DESCRIPTION

Colony erect, consisting of cylindrical branches, complete bifurcations not observed, probably articulated during life. Branches 8- to 10-serial, up to 2 mm in preserved length, normally 0.61–0.66 mm wide increasing to about 1 mm in diameter where fertile zooids are present. Colony base unknown. Autozooids longer than wide, ZL 444–489 μm (N colonies 1; N zooids 5; mean 458 μm ; SD 20 μm), ZW 178–200 μm (N colonies 1; N zooids 5; mean 182 μm ; SD 20 μm), elongate hexagonal. Frontal wall cryptocystal, margins raised, centre depressed, smooth textured; cryptocystal pores lacking; single pair of opesiules located proximolaterally of orifice within depressed central part of cryptocyst, longitudinally elliptical. Orifice dummy shaped, longer than wide, OL 118–141 μm (N colonies 2; N zooids 8; mean 132 μm ; SD 8 μm), OW 70–94 μm (N colonies 2; N zooids 8; mean 87 μm ; SD 10 μm), divided into a broad, rounded quadrate distal part and a narrow, long, tongue-like proximal prolongation, each with a salient rim. Fertile autozooids clustered, oecia helmet shaped, slightly wider than long, about 200–220 μm long by 240–300 μm wide, calcification smooth, continuous with the cryptocyst of the distal zooid, orifice of ovicellate zooids round, larger than those of non-ovicellate zooids, about 200 μm in diameter. Mandibulate polymorphs sporadically distributed, larger

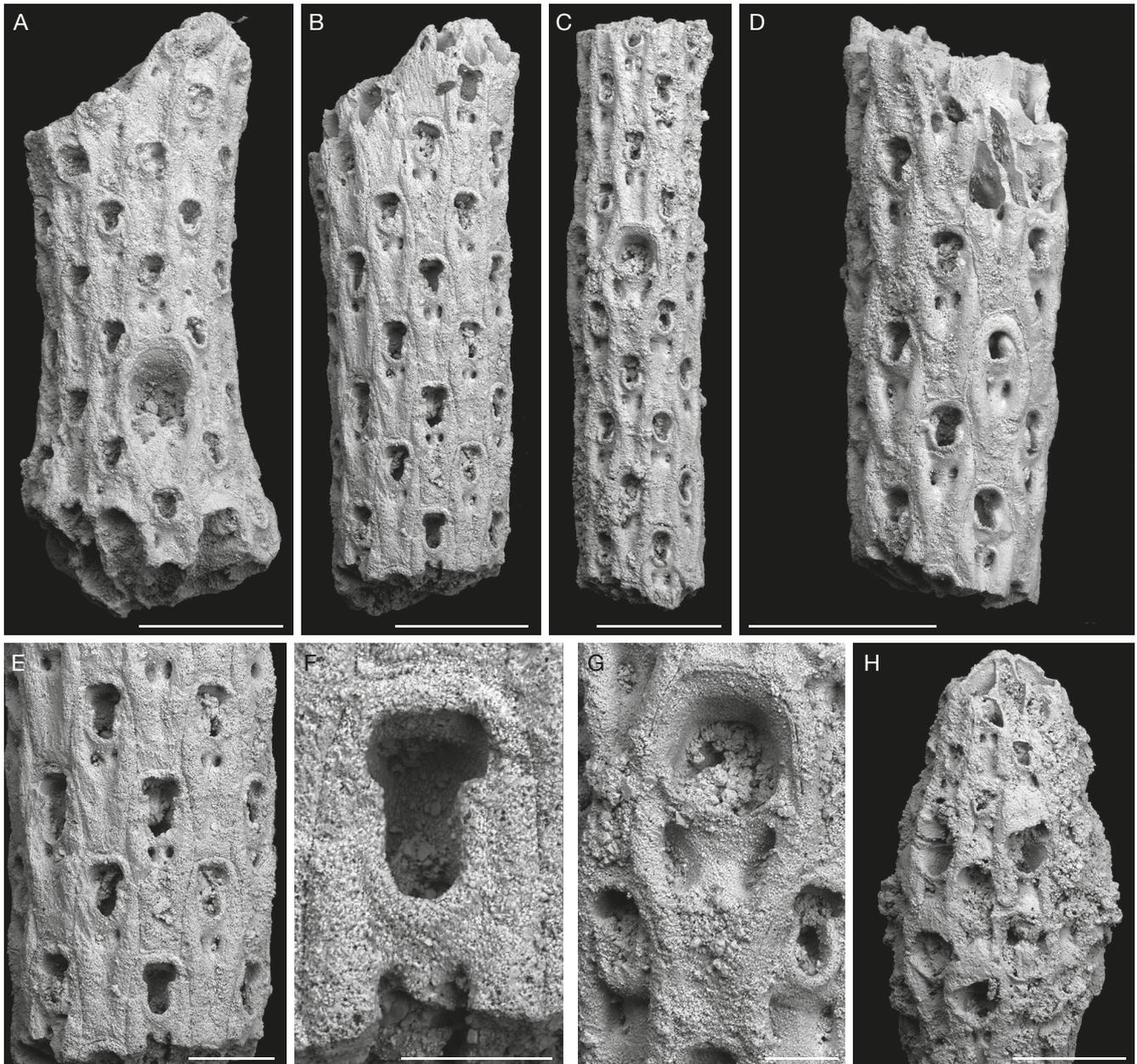


FIG. 3. — *Dimorphomicropora voighti* Ducasse & Vigneaux, 1960: **A**, lectotype, UB C.B.993 (Ducasse & Vigneaux 1960: fig. 1), probably Aubeterre Fm, Meschers, Charente-Maritime, branch with large polymorphic zoid near base; **B**, **E**, **F**, NHMUK PI BZ 8767, Aubeterre Fm, Pointe de Suzac, Meschers; **B**, branch; **E**, autozooids near base of branch; **F**, detail of an orifice; **C**, **G**, NHMUK PI BZ 8768, Aubeterre Fm, Pointe de Suzac, Meschers; **C**, branch with a large polymorphic zoid near the centre; **G**, detail of polymorph; **D**, paralectotype, UB C.B.994 (Ducasse & Vigneaux 1960: fig. 2), probably Aubeterre Fm, Meschers, Charente-Maritime; **H**, NHMUK PI BZ 8769, Aubeterre Fm, Pointe de Suzac, Meschers, Charente-Maritime, dilated branch with a cluster of ovicellate zooids. Scale bars: A, B, C, D, H, 500 µm; E, 200 µm; F, G, 100 µm.

than autozooids, 550-590 µm long by 260-290 µm wide, frontal wall and opesiules similar to those of the autozooids, orifice semielliptical with a slight proximal lip, longer than wide, about 290 µm long by 210-240 µm wide.

REMARKS

The presence of mandibulate polymorphs and the dummy shaped orifices serve to distinguish *D. voighti* from *D. crestulata* (described below) and also from the Maastrichtian species *D. rugica*.

Dimorphomicropora crestulata (Ducasse, 1958) (Fig. 4)

MATERIAL. — Holotype: UB C.B.917, Ducasse Collection (Ducasse 1958: pl. 7, fig. 3), probably Barbezieux Fm (foram biozone CVI), RN 730, close to police station, Mirambeau, Charente-Maritime. Other material: NHMUK PI BZ 8271, 8272, Aubeterre Fm, cliff north of town, Meschers, Charente-Maritime.

OCCURRENCE. — Upper Campanian, Barbezieux and Aubeterre formations.

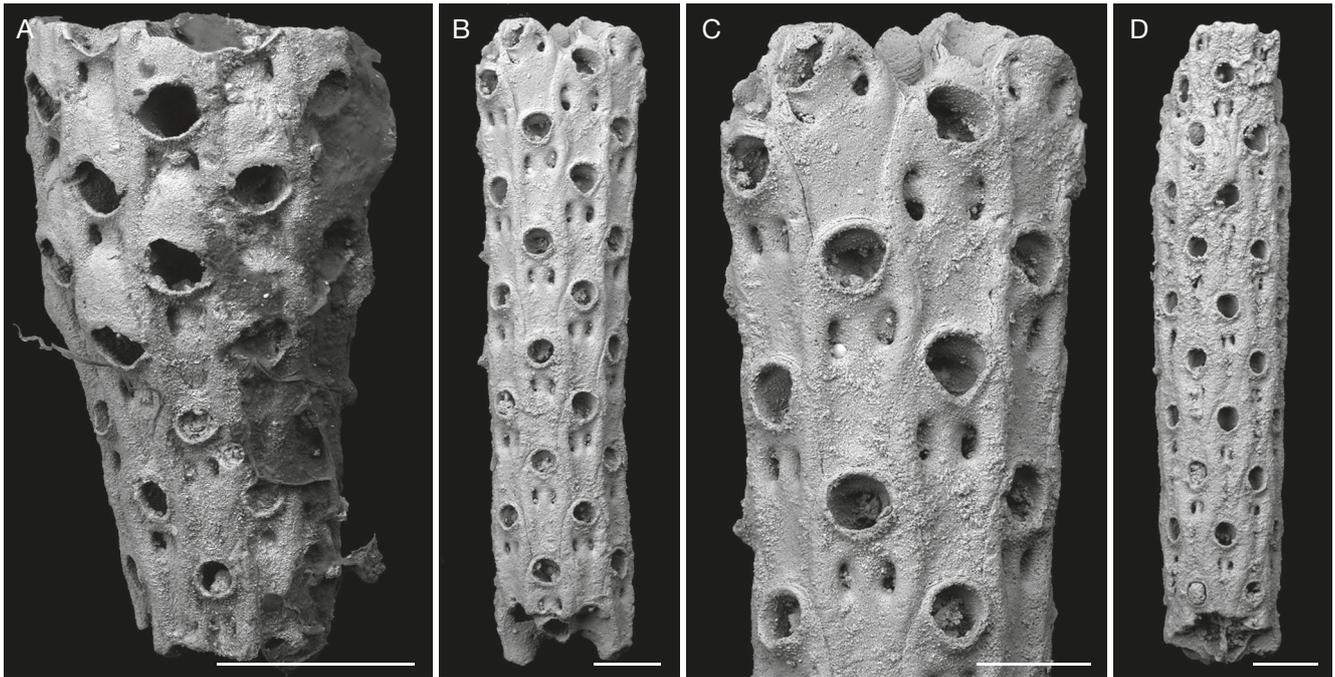


FIG. 4. — *Dimorphomicropora crestulata* (Ducasse, 1958): **A**, holotype (Ducasse 1958: pl. 7, fig. 3), UB C.B.917 Ducasse Collection, probably Barbezieux Fm (foram biozone CVI), RN 730, close to police station, Mirambeau, Charente-Maritime, dilated branch with ovicellate zooids; **B**, **C**, NHMUK PI BZ 8271, Aubeterre Fm, cliff north of town, Meschers, Charente-Maritime; **B**, well-preserved branch; **C**, detail of autozooids; **D**, NHMUK PI BZ 8272, Aubeterre Fm, cliff north of town, Meschers, branch. Scale bars: A, 500 μ m; B, C, D, 200 μ m.

DESCRIPTION

Colony erect, consisting of cylindrical branches, complete bifurcations not observed, probably articulated during life. Branches 8- to 10-serial, longest observed branch 2.4 mm, branch width 0.42–0.61 mm wide increasing to about 1 mm when fertile zooids are present. Colony base unknown. Autozooids longer than wide, ZL 395–526 μ m (N colonies 2; N zooids 8; mean 439 μ m; SD 43 μ m), ZW 184–211 μ m (N colonies 2; N zooids 8; mean 194 μ m; SD 14 μ m), elongate hexagonal. Frontal wall cryptocystal, margins raised, centre depressed, smooth textured; cryptocystal pores lacking; single pair of opesiules located proximolaterally of orifice within depressed central part of cryptocyst, longitudinally elliptical, some with a transverse bar subdividing the opening internally. Orifice subcircular, 94–118 μ m in diameter, sometimes with a slight proximal embayment, rim salient. Fertile autozooids clustered, oecia helmet shaped, about 220 μ m long by 200–240 μ m wide, calcification smooth, continuous with the cryptocyst of the distal zooid, orifice of ovicellate zooids round, slightly larger than those of non-ovicellate zooids, about 120–150 μ m long by 140–160 μ m wide. Mandibulate polymorphs unknown.

REMARKS

This species was introduced by Ducasse (1958) in her thesis as *Micropora crestulata*. Although it is clearly congeneric with *Dimorphomicropora*, it was not mentioned in the publication of Ducasse & Vigneaux (1960) when introducing this genus. Most specimens of *D. crestulata* come from the Aubeterre Formation in coastal localities south of Royan

where *D. voighti* also occurs. However, the type specimen is slightly older having been collected by Ducasse (1958) from an inland site at Mirambeau which exposes the Barbezieux Formation.

The subcircular orifice of *D. crestulata* allows this species to be distinguished from *D. voighti*. Scanning electron micrographs of *D. rugica* kindly provided by Oliver Kesselhut (Aachen) show similarities with *D. crestulata*; however, this Maastrichtian species sometimes has a lip extending over the proximal edge of the orifice, a feature not seen in *D. crustulenta*. The poorly preserved lectotype of *Micropora transversa* (d'Orbigny, 1851) from the Upper Maastrichtian of Contentin is possibly a senior synonym of either *D. crestulata* or *D. rugica*, but better material of *M. transversa* is needed before either of these synonymies can be accepted.

DISCUSSION

Campanian carbonates outcropping in the region between Royan and Aubeterre-sur-Dronne contain a wealth of bryozoans belonging to the orders Cyclostomata and Cheilostomata. Perhaps the commonest of the anascan-grade cheilostomes are species with cryptocystal frontal walls occupying most of the zooidal surface. The great majority of these belong to the Onychocellidae in which the frontal walls are generally imperforate; indeed, none of the onychocellids from the Campanian historical stratotype have cryptocysts perforated by opesiules for the passage of the muscles that depress the frontal membrane overlying

the cryptocyst during hydrostatic tentacle crown protrusion. A few species belonging to other families do possess opesiules. Most of these are traditionally assigned to the family Microporidae. The four opesiulate species recognised in the Campanian of southwest France and described here are *Micropora mikesmithi* n. sp., *Platelinella solea* n. gen. et n. sp., *Dimorphomicropora voighti* Ducasse & Vigneaux, 1960 and *D. crestulata* Ducasse, 1958.

Micropora mikesmithi is an encrusting species with a morphology closely similar to that of the type and other species of the extant genus *Micropora*. Unlike most other Cretaceous species historically assigned to *Micropora*, the placement of *M. mikesmithi* in this genus is unequivocal. Many of the supposed Cretaceous encrusting species of *Micropora* have been reassigned to *Stichomicropora* Voigt, 1949, a genus with spinose ovicells which is better placed in Monoporellidae. Others are erect and belong to such genera as *Dimorphomicropora* Ducasse & Vigneaux, 1960 (see below). After removal of encrusting species now assigned to *Stichomicropora*, *M. mikesmithi* becomes the oldest known species of *Micropora*.

The family level attributions of both *Platelinella solea* and, more particularly, the two species of *Dimorphomicropora*, are less clear-cut. Both genera have cryptocystal frontal walls containing holes that can be interpreted as opesiules, as in Microporidae. However, opesiules are not unique to this family and evidently evolved several times in cheilostome history. They are also found in Monoporellidae and Thalamoporellidae, as well as some genera of Onychocellidae (Taylor *et al.* 2018) and Pyrisinellidae (Di Martino & Taylor 2012; Matsuyama *et al.* 2017). Unfortunately, the lack of ovicells and avicularia limits the number of characters available to test the family assignment of *Platelinella solea* but it shows a greater overall similarity to Microporidae than to any of the other families containing opesiulate genera.

Dimorphomicropora was hypothesized by Ducasse & Vigneaux (1960) to be a possible ancestor of the Eocene-Recent genus *Steginoporella* on account of the presence of morphologically similar polymorphic zooids with enlarged opesia/orifices in both genera. These mandibulate polymorphs are known as B-zooids in *Steginoporella*, and have a functionally feeding lophophore (Winston 2010). Whereas opesiules and ovicells are lacking in *Steginoporella*, both structures are present in the related thalamoporelloidean genus *Thalamoporella*. However, the ovicells of *Thalamoporella* differ markedly from those of *Dimorphomicropora* in their bivalved construction (e.g., Ostrovsky 2013). Furthermore, a feature lacking in *Dimorphomicropora* but characteristic of thalamoporelloideans is the polypide tube, which was not evident when a specimen of *D. voighti* was sectioned. The weight of evidence supports the contention of Ostrovsky (2013) that *Dimorphomicropora* is not closely related to *Steginoporella*, implying independent origins of the mandibulate polymorphs in *D. voighti* and *Steginoporella*. Discovery of the colony base may be helpful in furnishing additional characters to provide a better insight into the family-level affinity of *Dimorphomicropora*.

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