ORIGINAL ARTICLE

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Late Hauterivian coralline algae (Rhodophyta, Corallinales) from the Iberian Chain (E Spain). Taxonomy and the evolution of multisporangial reproductive structures

Abstract Upper Hauterivian reefal carbonates of the Llàcova Formation (Maestrat Basin, Iberian Chain, E Spain) contain *Sporolithon phylloideum* (Bucur and Dragastan) Tomás, Aguirre, Braga and Martín-Closas comb. nov. and *Sporolithon rude* (Lemoine) Ghosh and Maithy (1996). Moussavian et al. (1993) identified them as *Parakymalithon phylloideum* (Bucur and Dragastan) Moussavian 1987 and *Archaeolithothamnium rude* Lemoine 1925. The re-assessment of the type of *P. phylloideum* and additional material indicate that the diagnostic characters of the genus do not warrant separation from *Sporolithon* and the new combination *Sporolithon phylloideum* is proposed. The lectotype of *Sporolithon rude* presents sporangial cavities grouped in sori that can be merged originating a structure that resembles the multiporate tetrasporangial conceptacles of the Hapalidiaceae. We hypothesize that multiporate tetrasporangial conceptacles could have originated from the fusion of several sporangial cavities, suggesting a phylogenetic linkage between Sporolithaceae and Hapalidiaceae supported by other anatomical features, molecular phylogeny and the fossil record.

Keywords Hauterivian · Corallines · Rhodophyta · Maestrat Basin · Phylogeny · Taxonomy

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Introduction

Modern coralline red algae (Corallinales, Rhodophyta) have been significant constituents of benthic fossil assemblages in tropical to polar regions since the Early Cretaceous. They have an excellent fossil record owing to the presence of calcium carbonate impregnating their cell walls. The oldest feasible record of corallines is *Sporolithon rude* (Lemoine) Ghosh and Maithy (1996) from the Early Cretaceous (Early Hauterivian) sediments of the Sierra de la Oliva (Albacete, E Spain) (Arias et al. 1995). Despite references to corallines in older sediments, the assignment of these reported examples to this algal order and their age attribution are questionable (Aguirre et al. 2000, 2002).

Coralline algal assemblages and their taxonomy at the very beginning of the history of the group can be analysed in the Early Cretaceous (Late Hauterivian) reef carbonate deposits of the Llàcova Formation (Maestrat Basin, Iberian Chain, E Spain) (Moussavian et al. 1993; Götz et al. 2005). Moussavian et al. (1993) identified the species *Sporolithon rude* (as *Archaeolithothamnium rude* Lemoine 1925) and *Parakymalithon phylloideum* (Bucur and Dragastan) Moussavian 1987 among the corallines present in these deposits. Encrusting, laminar thalli of the peyssonneliacean *Polystrata alba* (Pfender) Denizot (1968) are occasionally associated with these corallines. Götz et al. (2005) have also reported the presence of *Kymalithon* sp. and *Iberopora bodeuri* Granier and Berthou (2002) (= "Krustenproblematikum" of Schmid 1996) but the nature of these taxa is uncertain.

Here we re-assess the taxonomic status of these early coralline algal species by examining the type material of the taxa, the original material studied by Moussavian et al. (1993) as well as of newly collected material. The analysis of the type material of *P. phylloideum* (*Archaeolithothamnium phylloideum* Bucur and Dragastan (1986) deposited at the Department of Geology, Babeş-Bolyai University, Cluj-Napoca, Romania) and that of specimens of this species collected from the type locality (Reşiţa-Moldova Nouă, SW Romania) have been crucial to clarify

the taxonomic status of the genus *Parakymalithon* created by Moussavian ([1987](#)). We have also examined the type collection of *S. rude*, housed at the Laboratoire de Cryptogamie, Muséum national d'Histoire naturelle (Paris), for comparison with the material studied herein. This taxonomic assessment provides further clues to understanding the early evolution of the group. The taxonomic study has been completed with additional data from material collected in Late Aptian reef deposits of Benicàssim (SE Maestrat Basin, Iberian Chain, E Spain), where *S. rude* also occurs.

In summary, the aims of this study are: (1) to re-assess the taxonomic status of the two aforementioned coralline species, *S. rude* and *P. phylloideum*; (2) to establish the possible affinities of *S. rude* with other Cretaceous taxa on the basis of the sporangial reproductive structures; and, (3) to analyse the implications of these coralline taxa in the early evolutionary history of the corallines and their possible phylogenetic relationships with other coralline groups. In this respect, it is worth highlighting the significance of the presence of isolated sporangial cavities merged together in *S. rude*, and other Cretaceous taxa, forming multiporate sporangial conceptacle-like structures of the family Hapalidiaceae. Based on anatomical features, molecular phylogeny and the first occurrences of taxa in the fossil record, it is proposed that conceptacles and sori are, respectively, derived and ancestral characters in the early evolution of the Corallinales.

Geological and stratigraphic setting

The studied Upper Hauterivian deposits crop out in Catí, about 72 km N of Castelló (E Spain), and the Aptian sediments are exposed near Benicàssim, about 13 km NE of Castelló (Fig. 1). All these rocks belong to the Maestrat Basin, an intraplate basin located in the southeastern part of the Iberian Chain (Fig. 1). The Iberian Chain was formed by inversion, during the Alpine orogeny, of the Mesozoic rift basins (Salas and Casas 1993; Salas et al. 2001; Mas and Salas 2002). The Maestrat Basin developed during the Late Jurassic–Early Cretaceous (Late Oxfordian–Middle Albian) rifting phase (Salas and Guimerà 1997; Salas et al. 2001). During this time interval, up to 4 km of shallow-marine carbonates together with siliciclastic terrigenous and non-marine carbonates accumulated in the basin (Salas and Guimerà 1997; Salas et al. 2001).

Shallow-marine carbonate deposits with associated estuarine transitional carbonates and siliciclastic sediments, up to 1,500 m thick, accumulated during the Early Cretaceous (Valanginian–Aptian). Locally, small patch reefs grew in shallow-marine settings (Salas 1995; Götz et al. 2005). This study is focused on Upper Hauterivian reefs exposed on the road from Catí to the shrine of l'Avellà (km 3.3–3.5); Catí section (Fig. 2). These reefs are included in the upper part of the Llàcova Formation, which transgressively overlies the sandstones of the Avellà Formation (Fig. 2). The Llàcova Fm. consists of platform carbonates with up to 25–30 m of high-angle cross bedded oolitic and bioclastic grainstones representing shoals (Fig. 2). Coralalgal reefs were intercalated in these shoals during periods of low sedimentation and steady conditions. The two studied reefs, 2–3 m in thickness and ~ 15 m in width (Fig. 3), are coralalgal bioherms with coralline and peyssonneliacean red algae, *Lithocodium-Bacinella* associations, and other skeletal encrusters. The co-existence of *Choffatella pyrenaica* (Peybernes and Rey 1975) and its phylogenetically derived species *Choffatella decipiens* Schlumberger 1905 in the Llàcova Formation indicates a Late Hauterivian age (R. Schroeder, pers. comm. 2006).

A second unit was studied in the Upper Aptian Benassal Formation. Coral-stromatolite patch-reefs of this unit were sampled in the Benicàssim area (SE Maestrat Basin) (Riding and Tomás 2006). They crop extensively out in the El Llom del Moltò hill, north of Benicàssim; Benicàssim section (Fig. 2). They consist of coral-stromatolite bioherms (Fig. 4) with coralline and peyssonneliacean red algae, *Lithocodium* and encrusting benthonic foraminifers. According to Neumann (1987), these reefs can be attributed to the Late Aptian due to the presence of *Orbitolina parva* Douglass (1960) and *Orbitolina* gr. *parva-minuta* Douglass (1960).

Methodology

A study of the material (86 ultra-thin sections) originally collected by Moussavian et al. (1993) in the Late Hauterivian reefs at Catí has been carried out. Moreover, a total of 92 new ultra-thin sections, about 10 μm thick, of different sizes (6.0 × 3.9 cm; 8.0 × 7.9 cm and 4.7 × 2.5 cm) were studied. Additional sampling in the Upper Aptian reef facies of the Benicàssim included 32 ultra-thin sections (7.0 × 4.9 cm). The studied samples are housed at the Departament de Geoquímica, Petrología i Prospecció Geològica, Universitat de Barcelona. The relative abundance of red algae in all these samples, estimated with the point-counting method of Perrin et al. (1995), is lower than 2%. The lectotype of *S. rude* and the ultra-thin section of the type material of *P. phylloideum* have been examined, as well as six additional ultra-thin sections from samples collected in the type locality of the latter species.

We follow the phyletic classification scheme of Harvey et al. (2003) for present-day corallines and the criteria for fossil corallines summarized by Braga (2003). In the taxonomic descriptions and algal-growth form terminology, we follow Woelkerling (1988) and Woelkerling et al. (1993).

Systematic palaeontology

Division Rhodophyta Wettstein (1901)
Class Rhodophyceae Rabenhorst (1863)
Order Corallinales Silva and Johansen (1986)
Family Sporolithaceae Verheij (1993)
Genus *Sporolithon* Heydrich (1897a)

Fig. 1 Geological map of the Maestrat Basin, in the southeastern part of the Iberian Chain (NE Spain). *Asterisks* indicate the location of the studied outcrops; the Late Hauterivian reefs of Catí (in the north of the basin) and the Late Aptian reefs of Benicàssim (in the south of the basin)
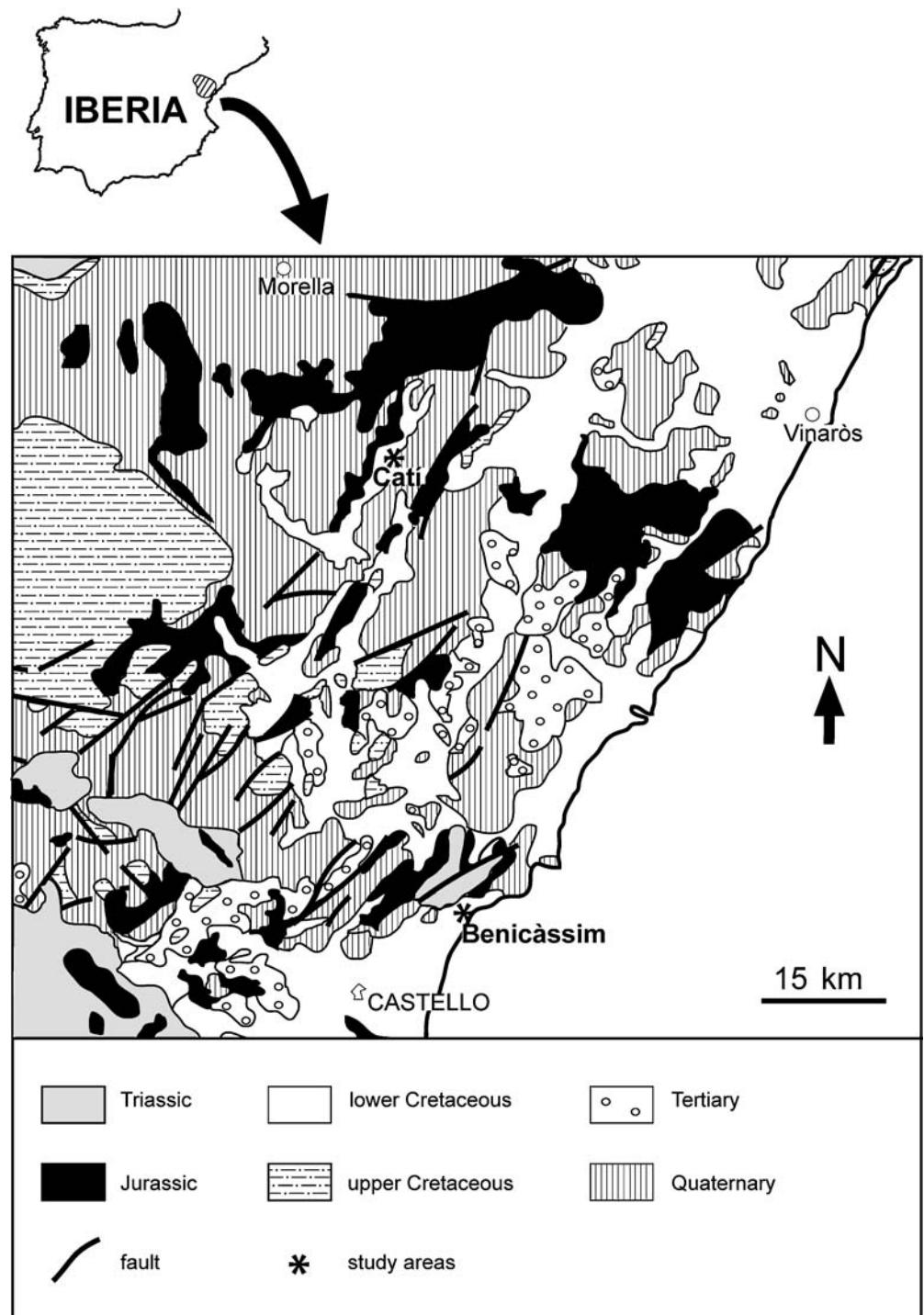
Type species *Sporolithon ptychoides* Heydrich (1897a)

Sporolithon phylloideum (Bucur and Dragastan) Tomás, Aguirre, Braga and Martín-Closas comb. nov.

Basionym: Archaeolithothamnium phylloideum Bucur and Dragastan (Revue de Micropaléontologie, 1986, vol 28, issue 4, pp 228–232, Plate 1, Figs. 1–9).
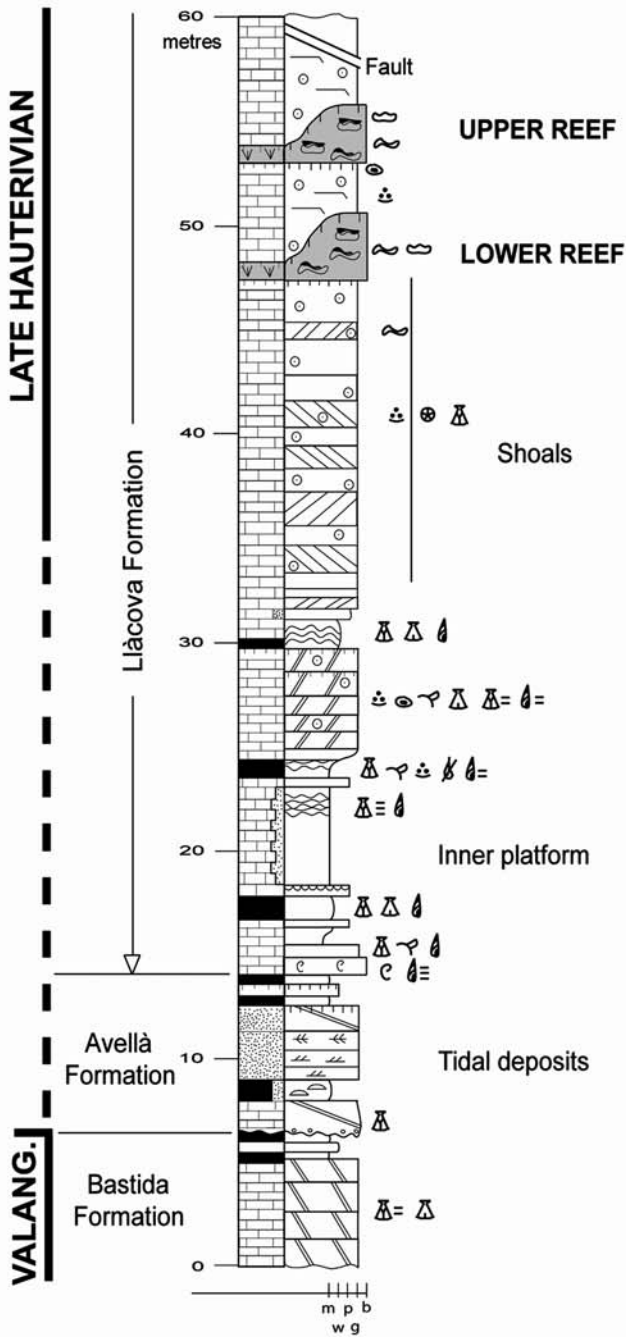
Type material: Bucur and Dragastan (1986) designated the specimen in the thin section 33A, no 1101, illustrated in

Figs. 1 and 2 of the Plate 1 as the holotype. The rest of the specimens illustrated by the authors in Plate 1 (Figs. 3–9) were designated as syntypes. All the specimens are housed at the Department of Geology, Babeş-Bolyai University, Cluj-Napoca (Romania).
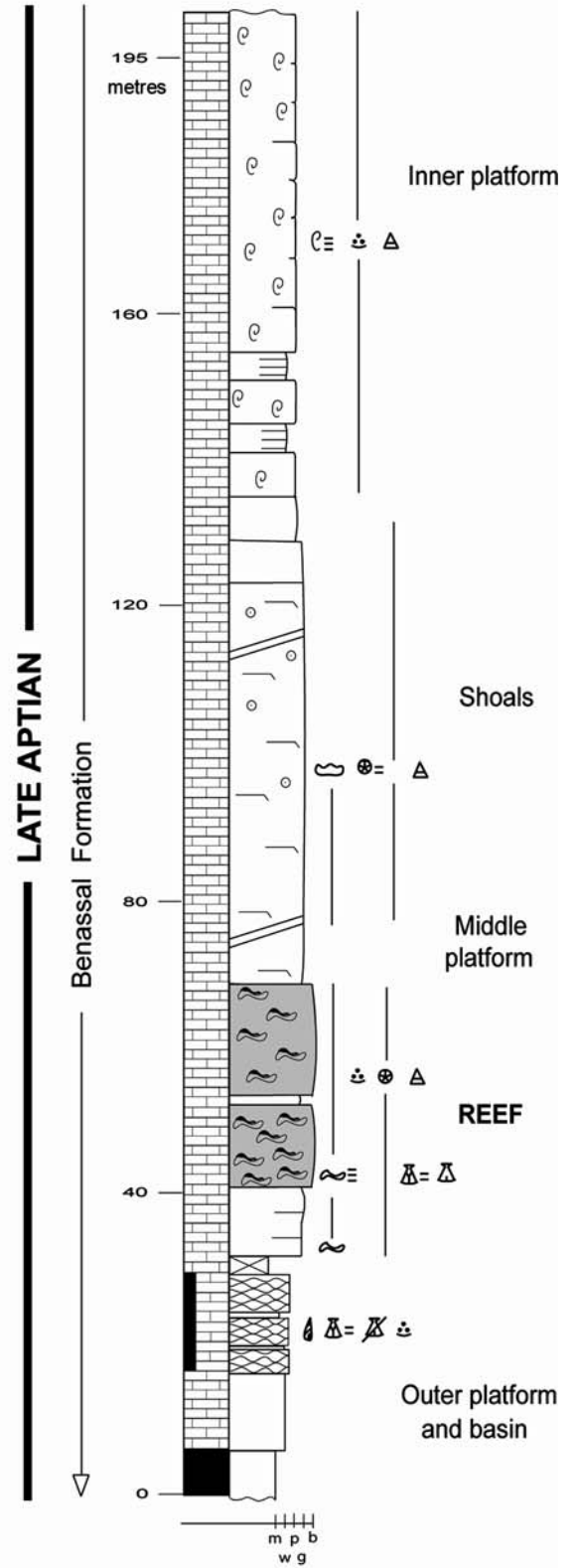
Type locality: 1 km south of Doman, on the right side of the road from Reşiţa to Caraşova (Late Aptian).

Synonym: Parakymalithon phylloideum Moussavian (1987), Plate 36, Figs. 1–5.

CATI SECTION

BENICASSIM SECTION

LATE HAUTERIVIAN

VALANG.

Llàcova Formation

Avellà Formation

Bastida Formation

60 metres

Fault

UPPER REEF

50

LOWER REEF

Shoals

40

30

Inner platform

20

10 Tidal deposits

0

m p b
w g

LATE APTIAN

Benassal Formation

195 metres

Inner platform

160

120

Shoals

Middle platform

80

REEF

40

Outer platform and basin

0

m p b
w g

	low angle cross bedding		linsen structure		serpulids
	high angle cross bedding		oolites		benthic foraminifers
	nodular bedding		gastropods		orbitolinids
	undulous bedding		echinoids		rudistids
	discontinuous bedding		echinoid spines		platy corals
	current cross lamination		oysters		massive corals
	herringbone lamination		lamellibranchs		stromatolite-algae crusts

Vegetative anatomy. The thallus is non-geniculate and monomerous with a dorsiventral organization (Fig. 5A). *S. phylloideum* generally occurs as unattached laminar thalli, locally encrusting fragments of corals or other bioclasts.

Thallus thickness ranges from 225 μm (rarely 135–150 μm) to 570 μm and can undergo considerable changes owing to local adaptations of the plant to uneven substrates forming irregular zones in the thallus (Fig. 5A). The thickness of the zones is 175–200 μm.

The thallus organization is very characteristic. Half of the thallus corresponds to the ventral core, 120–220 μm (mean 150 μm) in thickness (Table 1). Cell filaments in the core are generally "fountain-like" arranged, diverging upwards and downwards from the core centre (Fig. 5B). The cell filaments in the central part of the core are parallel to the ventral surface of the thallus and curve upwards, giving way to the dorsal peripheral region of the thallus, and downwards becoming oblique to the base of the thallus. Sometimes, this arrangement coexists with a plumose core in the same thallus (Fig. 5B). In this case, filaments run approximately parallel to the base of the thallus and curve upwards to the peripheral region and the cells are thin and slightly sinuous.

Cells in the core are elongated and narrow measuring 10–31.2 μm (21.8 ± 5.7 μm; mean ± standard deviation) in length and 3–11.2 μm (6.8 ± 2.4 μm) in diameter (Table 1). The cell size along a filament in the core decreases from the centre to the periphery.

Cells in the peripheral region are rectangular in longitudinal section, 10–23.7 μm (15.9 ± 3.7 μm) long and 4–11.2 μm (7.7 ± 1.6 μm) in diameter (Table 1). Cells are laterally well aligned in 2 to 14 rows. This, together with the virtual absence of cell fusions, results in a grid-like and regularly organized thallus (Fig. 5C).

Epithelial cells were not recognized.

Reproductive structures. Asexual reproductive structures of *S. phylloideum* are individual sporangial chambers grouped in sori. In section, each sorus consists of 4 to 8 sporangial compartments. Sori slightly protrude on the thallus surface (Fig. 5B) measuring 450–580 μm in diameter and 90–120 μm in height. A distinct basal layer of larger cells at the base of each sporangial compartment is observed (Fig. 5D). No stalk cells were recognized.

Individual sporangial chambers are fusiform or oval in shape, 90–120 μm (100 ± 10.3 μm) high and 40–70 μm (55.6 ± 9.3 μm) in diameter. They are separated by 2–4 filaments of calcified cells (paraphyses), which occasionally disappeared, producing local contacts between contiguous cavities (Fig. 5D).

No sexual reproductive structures were recognized.

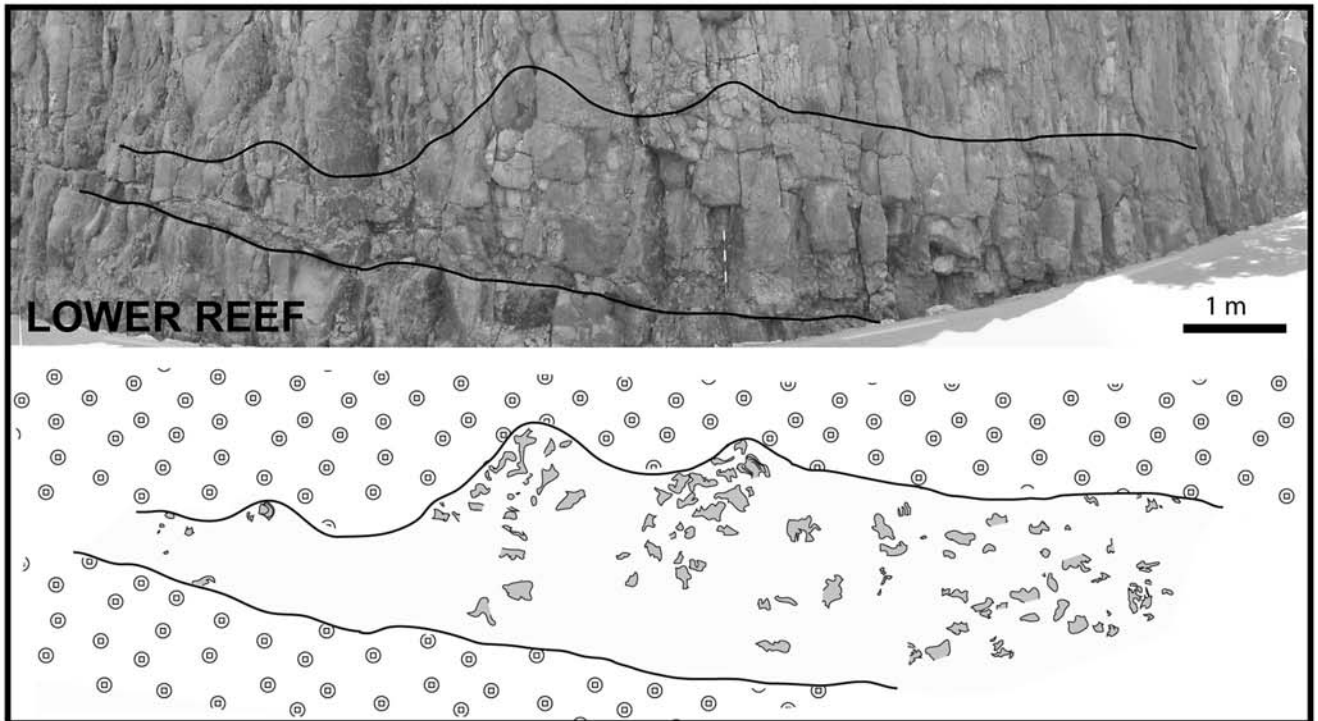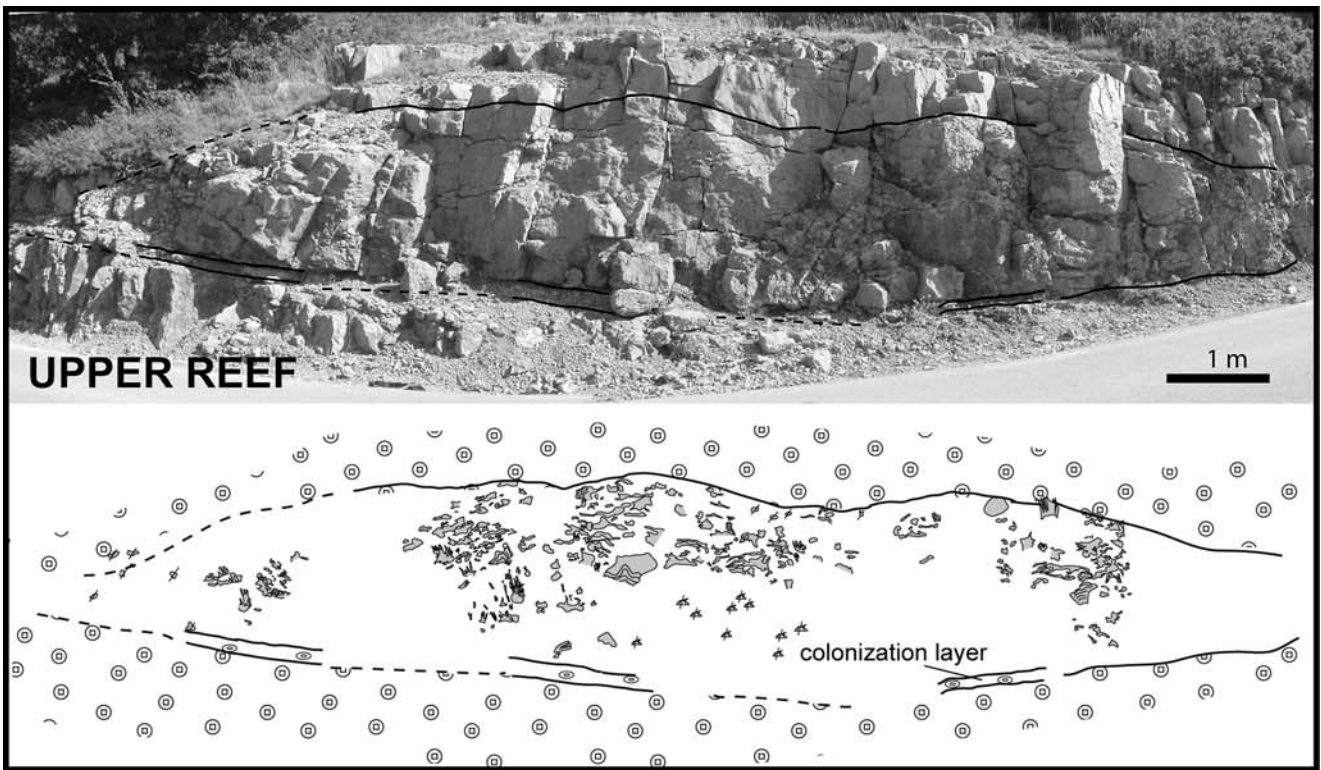*Remarks*. Bucur and Dragastan (1986) defined the species *Archaeolithothamnium phylloideum* from the Upper Ap-

◀ **Fig. 2** Stratigraphy of the two studied sections. The Late Hauterivian coralalgal reefs of the Catí section are included in the upper part of the Llàcova Formation. Section modified from Salas and Martín-Closas (1991). The Late Aptian coral-stromatolite patch-reefs of the Benicàssim section are in the lower part of the Benassal Formation

tian carbonates of the Reşiţa-Moldova Nouă zone (Banat, SW Romania) to designate a coralline alga with: (1) an encrusting thin thallus; (2) a very characteristic fountain-like basal region; (3) a peripheral region with a few cell rows locally forming zonation; and (4) sporangial compartments arranged in sori formed by 3–4 alternating rows of oval-to-fusiform isolated cavities. The presence of sori buried in the thallus justified the generic assignment. All these anatomical and reproductive features were considered by Bucur and Dragastan (1986) in order to separate this species from *Sporolithon rude*, another common species of Lower Cretaceous sediments.

A reassessment of the type material of *A. phylloideum* by Moussavian (1987) prompted this author to propose the new coralline genus *Parakymalithon* in order to include the only species *P. phylloideum*. The name of the new genus refers to its similarities with the vegetative anatomy of *Kymalithon* Lemoine. One of the diagnostic characters defining *Parakymalithon* would be the occurrence of alternating rows of sporangial compartments arranged in protuberant structures similar to nemathecia, not to sori (Moussavian 1987). According to Moussavian (1987), *P. phylloideum* differs from *Kymalithon belgicum* (Foslie) Lemoine in having a thinner peripheral region with larger cells.

The examination of the type material of this species and additional material collected from the type locality as well as the material collected in the Hauterivian coral reefs of the Llàcova Formation of the Maestrat Basin leads us to conclude that the features of its type species do not necessitate the separation of *Parakymalithon* as an independent genus. In the description of the genus, Moussavian (1987) stressed as diagnostic characters a) the occurrence of sporangial compartments in "nemathecia" protruding on the thallus surface, not in sori; and b) the presence of rows of alternating sporangial chambers. Nevertheless, the sori of some present-day species of *Sporolithon*, such as the type species *S. ptychoides* Heydrich (1897a) as well as *S. durum* (Foslie) Townsend et al. (1995) (in Townsend et al. 1995) and S. *episporum* (Howe) Dawson (1960), are raised on the thallus surface (Keats and Chamberlain 1993; Townsed et al. 1995; Harvey et al. 2002). Moreover, the type material, the samples from the type locality and the specimens from the Llàcova Formation (Fig. 5D) show that the sporangial cavities are aligned in rows in real longitudinal sections (Bucur and Dragastan 1986; Figs. 3–5), whereas in oblique sections, they may occur as two or more alternating rows (Bucur and Dragastan 1986; Pl. 1, Figs. 1, 2 and 6). Therefore, the second diagnostic character of Moussavian (1987) appears to be the result of viewing oblique sections.

Taking into account all these aspects, we propose to return to the original interpretation of Bucur and Dragastan (1986) but using the new combination *Sporolithon phylloideum* (Bucur and Dragastan) Tomás, Aguirre, Braga and Martín-Closas, since *Sporolithon* Heydrich is the valid generic name for this and other species formerly attributed to *Archaeolithothamnium* Rothpletz (Woelkerling 1988; Moussavian and Kuss 1990).

Fig. 3 Field photographs and interpretative schemes of the lower and upper coralalgal reefs of the Catí section (Late Hauterivian). Both reefs are mound-shaped bioherms
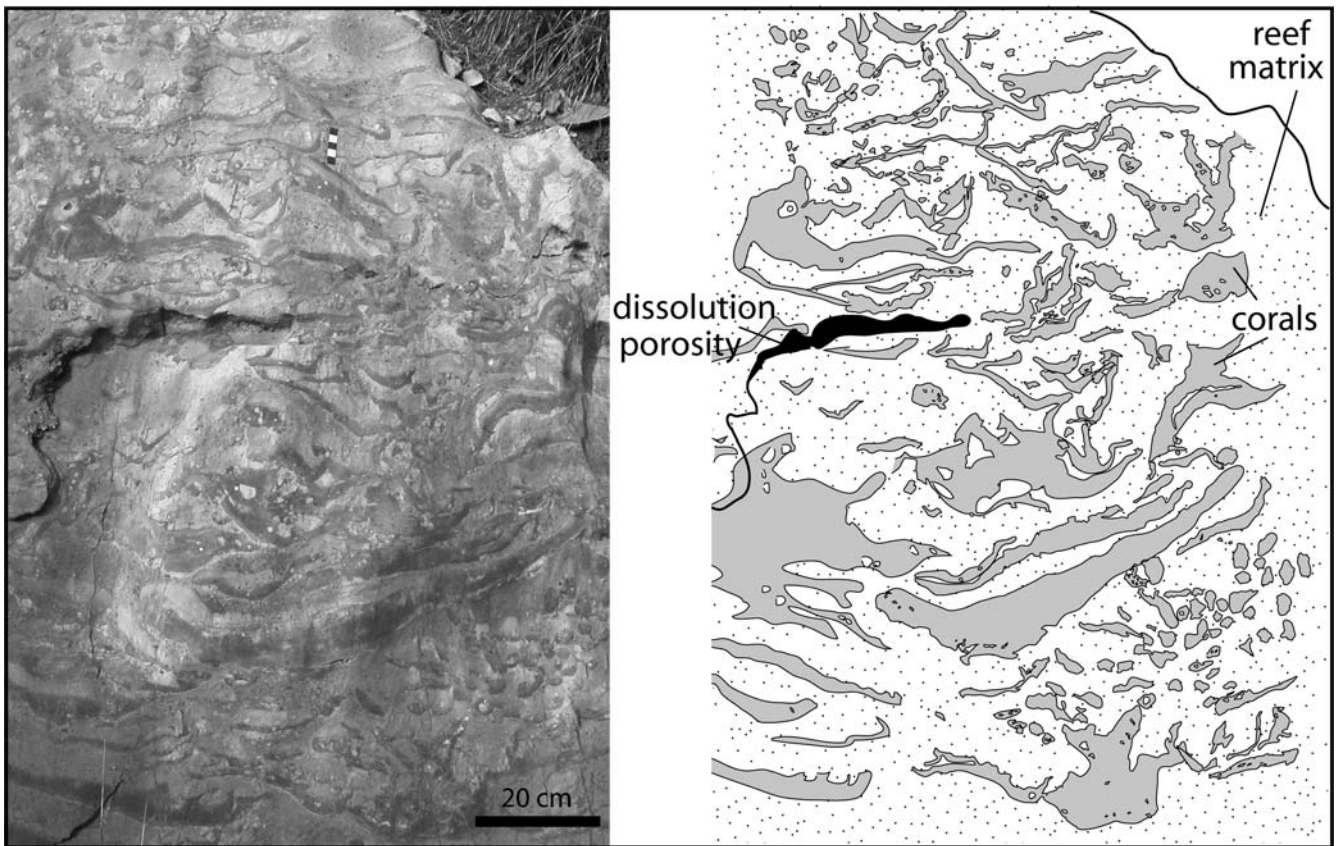
Fig. 4 Close-up view of the Benicàssim patch-reef and an interpretative scheme

Sporolithon rude (Lemoine) Ghosh and Maithy

Type material: Lemoine (1925; p 3, Plate 1, Figs. 1–2) referred to a lumpy-fruticose rhodolith collected by H. Douvillé from Aptian deposits of the Vimport (SW France) as the "*principal échantillon*". In the protologue, she also mentioned another rock sample from Albian deposits belonging to a different collection (with no illustration): "*Un autre échantillon recueilli dans l'Albien paraît appartenir à la meme espèce à un état plus jeune….*" (Lemoine 1925, p 4).

Woelkerling (1998, p 286) considered the Aptian rhodolith illustrated by Lemoine (1925, Plate 1, Figs. 1–2) and three thin sections, one labelled by Lemoine as Aptian (Woelkerling et al. 1998; Fig. 121 lower right) and the other two labelled by Lemoine as Albian material (Woelkerling et al. 1998; Fig. 121 lower left), as the holotype. All these samples are housed at the Laboratoire de Cryptogamie, Muséum national d'Histoire naturelle, Paris (PC) (Woelkerling 1998; Woelkerling et al. 1998).

However, Lemoine (1925) did not explicitly designate a type in the protologue, and based the species on two different collections that were incorrectly referred to as the holotype by Woelkerling (1998) and Woelkerling et al. (1998). Therefore, we designate the Aptian rhodolith illustrated by Lemoine (1925, Plate 1, Figs. 1–2) and the Aptian thin section depicted by Woelkerling et al. (1998, Fig. 121, lower right) as the lectotype.

Type locality: Vimport, Landes (SW France).

Synonyms

1925 *Archaeolithothamnium rude* Lemoine, Fig. 1; Plate 1, Figs. 1–2.
1926 *Archaeolithothamnium rude* Pfender, Plate 5, Fig. 3; Plate 8, Fig. 3.
1928 *Archaeolithothamnium rude* Lemoine, p 93.
1970 *Archaeolithothamnium rude* Lemoine, Plate II, Fig. 1; Plate VIII, Fig. 1; Plate XV, Fig. 2.
1997 *Sporolithon ? rudae* Bucur, Plate 19, Figs. 18.
2001 *Sporolithon ? rude* Bucur, Plate 4, Figs. 2–5.
2002 *"Archaeolithothamnium rude"* Bucur and Baltres, Plate 6, Figs. 2, 3, 5.

Vegetative anatomy. The thallus is non-geniculate and monomerous with dorsiventral organization. Plants are encrusting and warty, and occur attached, unattached or forming rhodoliths. The thalli are generally thin, 50–120 µm thick (Fig. 6A), although thicker crusts of 180–1,200 µm may occasionally occur (Fig. 6B). The thickness of the thallus is usually laterally constant. Protuberances are 700–1,050 µm in diameter and 780–1,675 µm in length (Table 1).

The ventral core of the thallus is plumose, with cell filaments running almost parallel to the ventral side and subsequently curving upwards, giving way to the peripheral
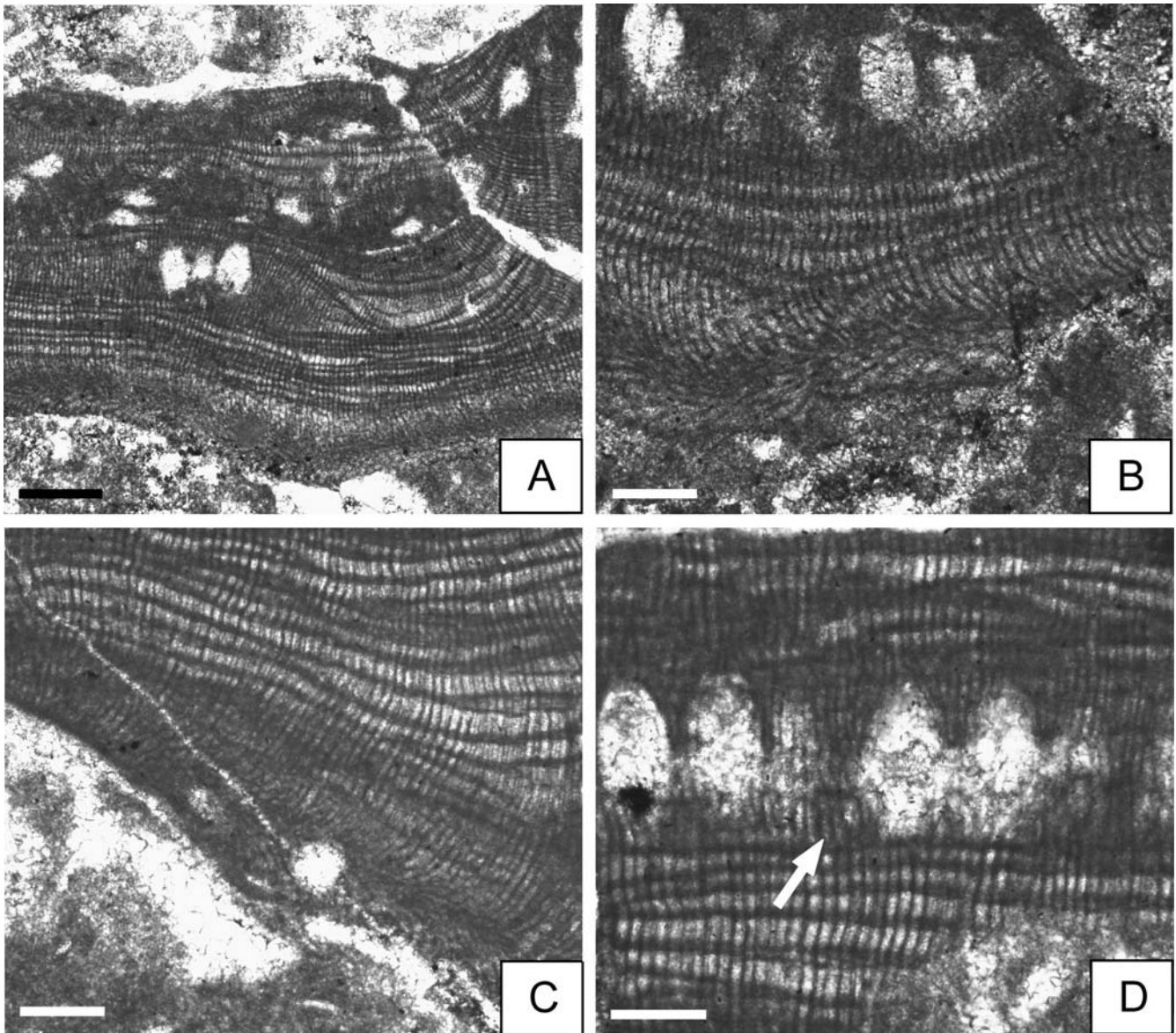
Fig. 5 **A–D** *Sporolithon phylloideum* (Bucur et Dragastan) Tomás, Aguirre, Braga et Martín-Closas comb. nov. from Late Hauterivian reef deposits of the Llàcova Formation (Maestrat Basin, NE Spain). **A** General view of an encrusting thallus with irregular zones developed locally. A protruding sorus with three sporangial cavities is present in the central part of the picture. Sample AV-B-5, Moussavian's collection. *Scale bar* 250 μm. **B** Close-up view of the ventral region of the thallus. Cell filaments diverge both upwards and downwards from the central part of the ventral region, giving way to the characteristic "fountain-like" arrangement. Laterally, to the left of the picture, this cell arrangement changes to a plumose organization in the same thallus. Some isolated sporangial cavities of a protruding sorus can be observed in the upper part of the photograph. Sample AV-B-5, Moussavian's collection. *Scale bar* 100 μm. **C** Ventral core of a thallus with a plumose organization giving way upwards to filaments of the peripheral region. Cells of adjacent filaments in the peripheral region are laterally well aligned. Cells in the peripheral region change from rectangular to quadrangular. Note, also, the interfingering of new rows of cells, laterally wedging out, that gives rise to the irregular zones in the thallus. Sample AV, Moussavian's collection. *Scale bar* 100 μm. **D** Close-up view of ellipsoidal sporangial chambers of a sorus. Sorus is developed on a row of cells larger (*arrow*) than the surrounding cells of the peripheral region. Sample AV, Moussavian's collection. *Scale bar* 70 μm

region (Fig. 6C). Core thickness ranges from 15 to 50 μm (Table 1), and represents about the third of the thallus. In those exceptions of thick crusts, core thickness ranges from 60 to 300 μm. Cells of the core are rectangular in section (Fig. 6C), measuring 13–36 μm (21.4 ± 6.7 μm) in length and 3–10 μm (7.5 ± 1.6 μm) in height.

The peripheral region generally consists of filaments with 4 to 15 cells. Cells of the peripheral region are rectangular to equidimensional in section with curved walls. They are 10–24 μm (18.1 ± 3.9 μm) long and 4–14 μm (10.3 ± 2.5 μm) in diameter. Locally, the peripheral region shows a diffuse zonation. Cells of contiguous filaments are not well aligned and cell fusions are common (Fig. 6D).

A single row of cells trapezoidal in section is present on the dorsal side of some plants (Fig. 6E and F). The cells are interpreted as the remains of flared epithelial cells. They

Table 1 Growth form, dimensions of cells and reproductive structures and other relevant characters found in both *S. phylloideum* and *S. rude*; *n* number of measures; *s.d.* standard deviation. All measurements are in µm

Characters	Sporolithon phylloideum	Sporolithon rude
Growth form	encrusting	encrusting to warty (rarely fruticose)
Thallus thickness	225–570 (rarely 135–150)	50–120 (occasionally 180–1,200)
Protuberances-branches	absent	
length range		780–1,675
diameter range		700–1,050
Core region		
thickness	120–220	15–50 (occasionally 60–300)
cells	*n* = 41	*n* = 39
length range	10–31.2	13–36
mean ± s.d.	21.8 ± 5.7	21.4 ± 6.7
diameter range	3–11.2	3–10
mean ± s.d.	6.8 ± 2.4	7.5 ± 1.6
Peripheral region		
cells	*n* = 39	*n* = 39
length range	10–23.7	10–24
mean ± s.d.	15.9 ± 3.7	18.1 ± 3.9
diameter range	4–11.2	4–14
mean ± s.d.	7.7 ± 1.6	10.3 ± 2.5
Epithallial cells	not observable	
cells		*n* = 6
length range		12.4–17.4
mean ± s.d.		14.4 ± 1.9
diameter range		8.1–10.4
mean ± s.d.		9.2 ± 0.7
Tetrasporangial sori		
sori diameter	450–580	430–1,000
sori height	90–120	140–175
no. of sporangial chambers	4–8	up to 10
sporangial chambers	*n* = 13	*n* = 22
diameter range	40–70	56–110
mean ± s.d.	55.6 ± 9.3	80.6 ± 14.6
height range	90–120	130–170
mean ± s.d.	100 ± 10.3	147.2 ± 12.6
stalk cells	not observable	present 40 wide—45 long
larger cells at the base of sori	yes (*n* = 9)	no
length range (mean ± s.d.)	39.8–43.4 (41.6 ± 1.49)	
diameter range (mean ± s.d.)	0.8–1.2 (0.96 ± 0.15)	
no. of cells filaments among chambers	2–4	1–5
Mature sexual conceptacles	not observable	*n* = 2
diameter range		150–240
height range		125–150
Others		
lateral cell alignment	well alignment	poor-absent
banding-zones in the peripheral region	irregular zones (zone thickness 175–200)	weakly zonated
cell fusions	not observable	frequent
cell arrangement in the ventral core	plumose and "fountain-like" with cell filaments diverging upwards and downwards	plumose

are 12.4–17.4 µm (14.4 ± 1.9 µm) long and 8.1–10.4 µm (9.2 ± 0.7 µm) in diameter.

Reproductive structures. These are sporangial compartments grouped in sori protruding slightly on the thallus surface, which become buried in the peripheral region as the plant grows (Fig. 7A). Up to 10 sporangial cavities occur in sorus sections that measure 430–1,000 µm in diameter and 140–175 µm in height.

Individual ellipsoidal/oval-shaped sporangial cavities can be recognized. They are 56–110 µm (80.6 ± 14.6 µm) in diameter and 130 to 170 µm (147.2 ± 12.6 µm) in height.

One to five filaments of vegetative cells (paraphyses) are interspersed among sporangial chambers. However, a number of cavities often merged due to the loss of the filaments separating them, giving the sporangial structure the appearance of a multiporate conceptacle (Fig. 7C). Some of the cavities show trapezoidal stalk cells, 40 μm wide and 45 μm long, at their base (Fig. 7B). In some cases, ovoidal structures with sharp walls can be seen inside the cavities (Fig. 7D). These features can be interpreted as the remains of the walls of individual sporangial compartments. All these characters indicate that the spore formation in *S. rude* took place in sporangial compartments instead of conceptacles.

Two uniporate protruding conceptacles with conical pore canals are present in one specimen. Both conceptacle chambers are trapezoidal in section, and the cell filaments curve around them, adapting themselves to the cavity (Fig. 7E). These two conceptacles measure 150×125 μm and 240×150 μm in diameter and height, respectively. They recall the mature sexual conceptacles of extant species of the genus *Sporolithon* because of their size and shape (see, for example, the mature male and female-carposporangial conceptacles of *S. durum*, Townsed et al. 1995; Table 1; Woelkerling 1996a; Figs. 6C and D).

Bucur (1981; Plate II, Fig. 6) and Bucur and Urian (1989; Plate II, Fig. 5) figured uniporate conceptacles of *S. rude* (as *Archaeolithothamnium rude*) that are comparable both in size and shape to those observed in the studied material. Bucur (1981) interpreted the structures as the sexual conceptacles of the species.

A smaller uniporate conceptacle (52 μm in diameter and 23 μm in height) has been recognized in one specimen (Fig. 7F). It is triangular in shape with a short conical pore canal on the roof. This reproductive structure resembles the immature states of spermatangial conceptacles of extant *Sporolithon* (i.e., Verheij 1992; Fig. 8; Townsed et al. 1995; Figs. 12B and 13A).

Remarks

Lemoine (1925) described the species *Archaeolithothamnium rude* based on material collected by Douvillé from Aptian-Albian rocks of the Vimport (SW France). She did not identify sporangial reproductive structures in that material and the attribution to the genus was exclusively based on the growth morphology and the vegetative features: encrusting thalli with a thin basal region and a peripheral region consisting of rectangular cells. Lemoine (1925) only mentioned the presence of gametangial reproductive structures but in a specimen belonging to a different collection from Albian deposits.

Pfender (1926), studying Cretaceous material from Cassis (Provence, S France), and samples from the collection of E. Munier-Chalmas, identified some thalli of coralline algae as *Archaeolithothamnium rude* Lemoine describing reproductive structures as sporangia aligned in the thallus. Although she recognized that sporangial reproductive structures were not previously observed in the studied material by Lemoine (1925), she assigned the fossil plants to this species based on the vegetative structure and cell sizes.

Studying the material collected by J.R. Bataller in Early Cretaceous rocks from Catalonia and Valencia (NE and E Spain, respectively), Lemoine (1928) raised some doubts about the co-specificity of the samples identified as *A. rude* by Pfender (1926) and the species type. Nevertheless, Lemoine (1939; Fig-text. 2, p 49) recognized this species in Cretaceous deposits of Algeria and identified numerous sporangial reproductive structures as isolated chambers merged due to the destruction of the vegetative filaments separating them, akin to those described and illustrated by Pfender (1926; Pl. V, Fig. 3). Subsequently, in a paper summarising the Cretaceous flora of southern France, Lemoine (1970) showed some corallines identified as *Archaeolithothamnium rude* with sporangial reproductive structures formed by isolated sporangial compartments grouped in sori that usually fused together because of the disappearance of the cell filaments between cavities. She also pointed out that these organs resemble the ones described and illustrated by Pfender (1926). Therefore, although the species *A. rude* was validly published and described by Lemoine (1925), the diagnostic characters she used were ambiguous and with no taxonomic significance for a generic placement. Pfender (1926), interpreting different samples from the original type material, used appropriate characters for a generic assignment and her interpretation was subsequently accepted by Lemoine (1939, 1970).

Sporangial cavities fused together are clearly observed in one broken branch (upper left branch in the Fig. 121 of Woelkerling et al. 1998) of the lectotype of the species (J.A. and J.C.B. personal observations). Thus, we confirm that the distinctive sporangial reproductive structures of *A. rude* as described and illustrated by Pfender (1926) do occur in the type material.

In the studied material from the Llàcova Formation and the Benicàssim reef, a number of isolated sporangial compartments, some of whose limiting walls are clearly visible,

Fig. 6 **A–F** Vegetative characters of *Sporolithon rude* (Lemoine) ▶ Ghosh et Maithy. **A** Thin encrusting thallus of *S. rude* attached to a fragment of coral from the Benassal Formation, Late Aptian (Benicàssim). Sample 7.9–b. *Scale bar* 1 mm. **B** Thicker encrusting thallus of *S. rude* with a sorus in the central part of the thallus. Specimen from the Llàcova Formation, Late Hauterivian (Catí). Sample AV-B-2, Moussavian's collection. *Scale bar* 500 μm. **C** Plumose arrangement of cell filaments in the ventral part of the thallus. Cell filaments bend upwards passing to the filaments of the peripheral region. Specimen from the Benassal Formation, Late Aptian (Benicàssim). Sample 7.9–b. *Scale bar* 50 μm. **D** Close-up view of the peripheral region showing an irregular organization of the cells due to the lack of lateral alignment and presence of numerous cell fusions (*arrows*). Specimen from the Llàcova Formation, Late Hauterivian (Catí). Sample AV-B-2, Moussavian's collection. *Scale bar* 50 μm. **E** Lighter row of trapezoidal cells in the surface of a thallus that are interpreted as the remains of flared epithelial cells (*arrow*). Specimen from the Llàcova Formation, Late Hauterivian (Catí). Sample AV-A-1, Moussavian's collection. *Scale bar* 100 μm. **F** Close-up view of the epithelial cells showing their morphology. Specimen from the Llàcova Formation, Late Hauterivian (Catí). Sample AV-A-1, Moussavian's collection. *Scale bar* 40 μm
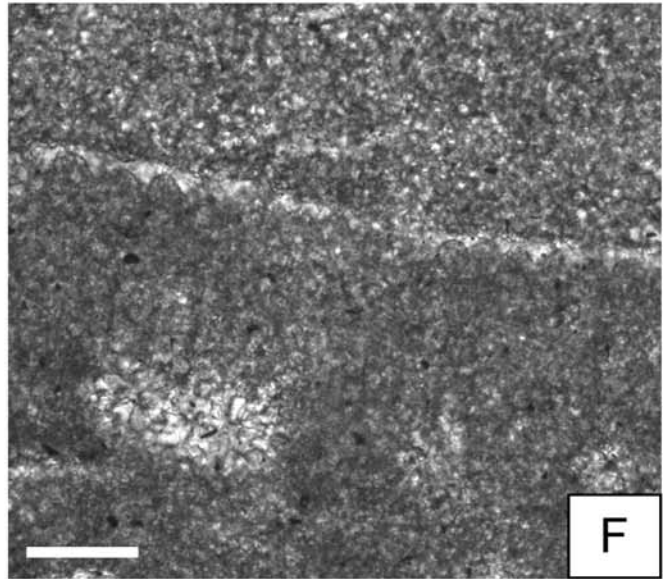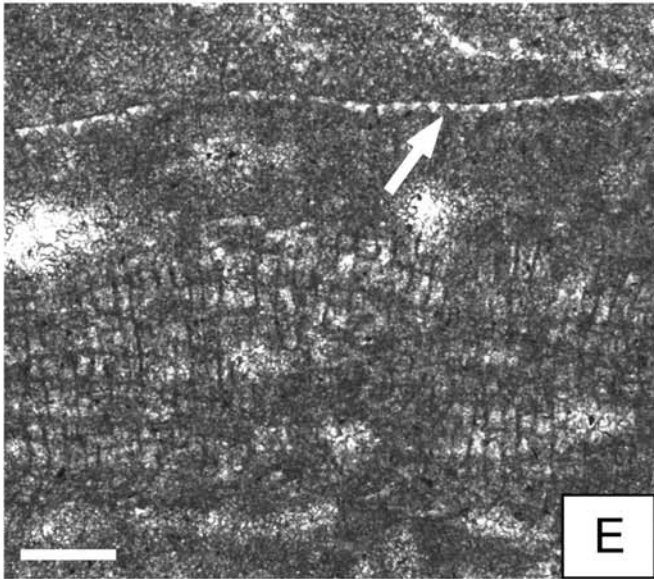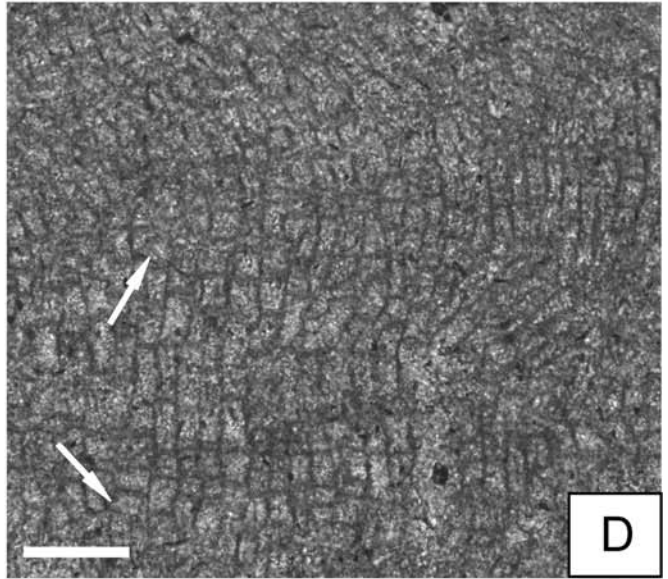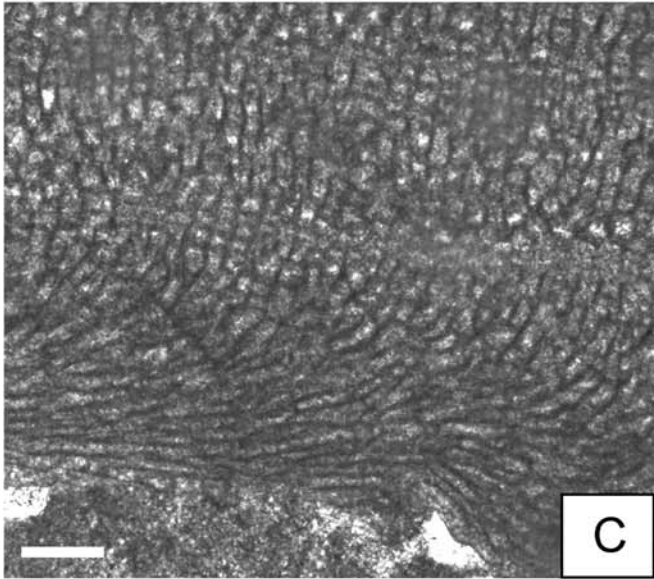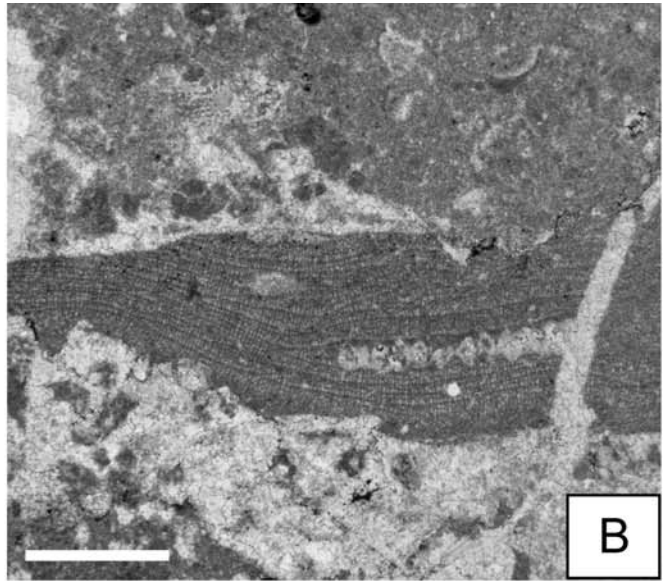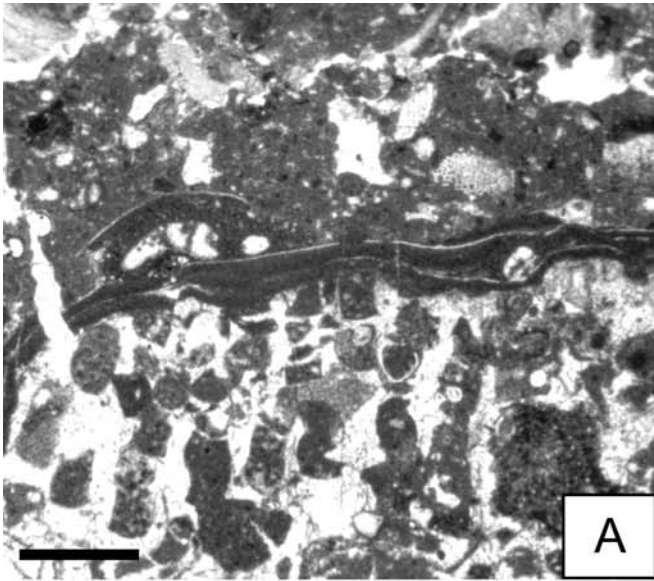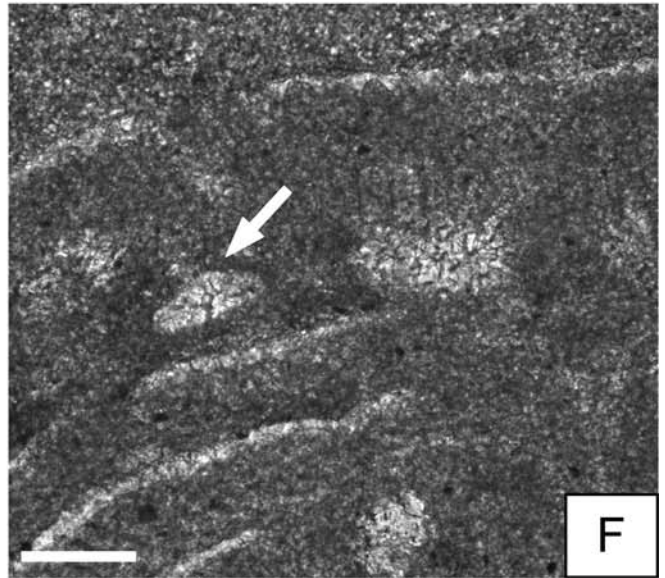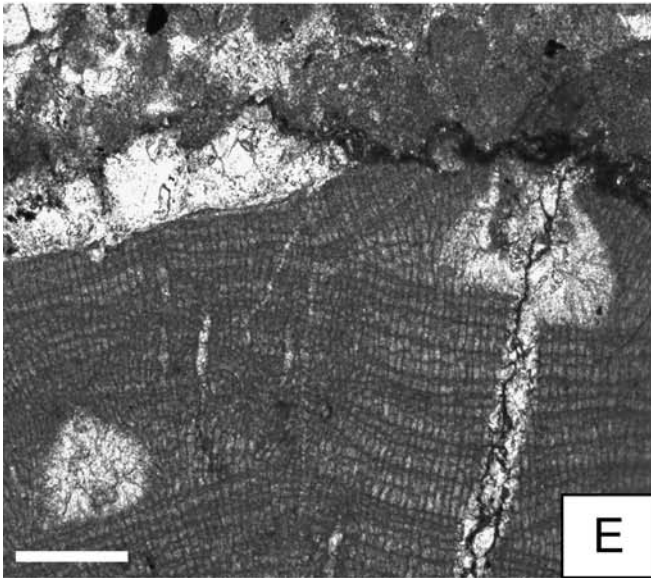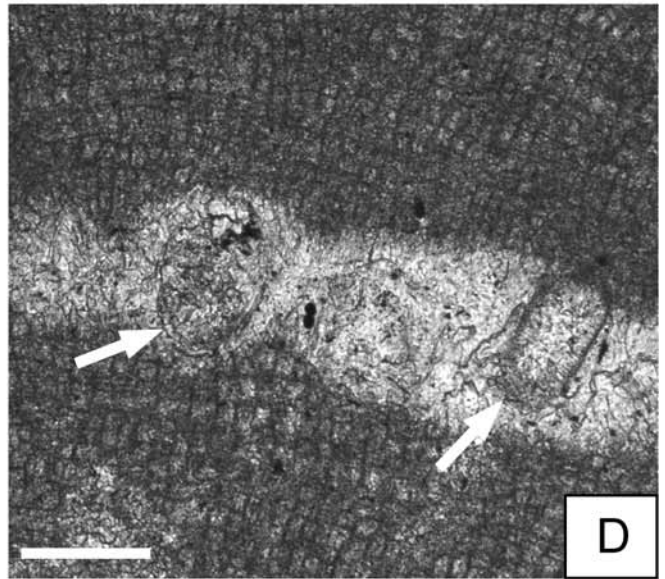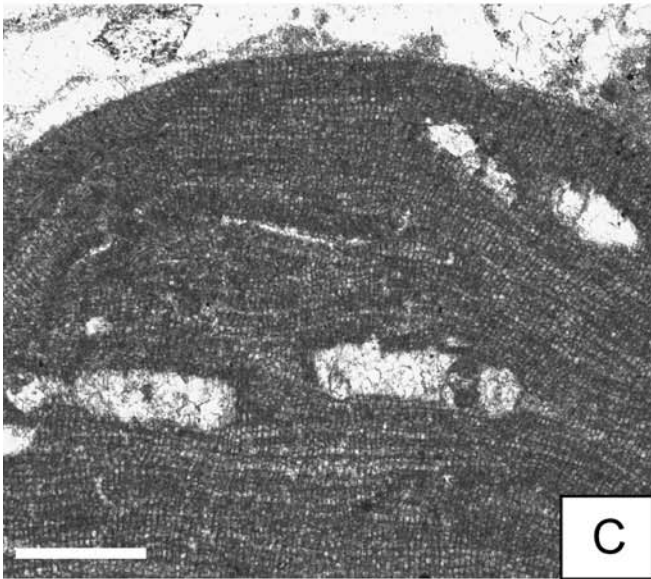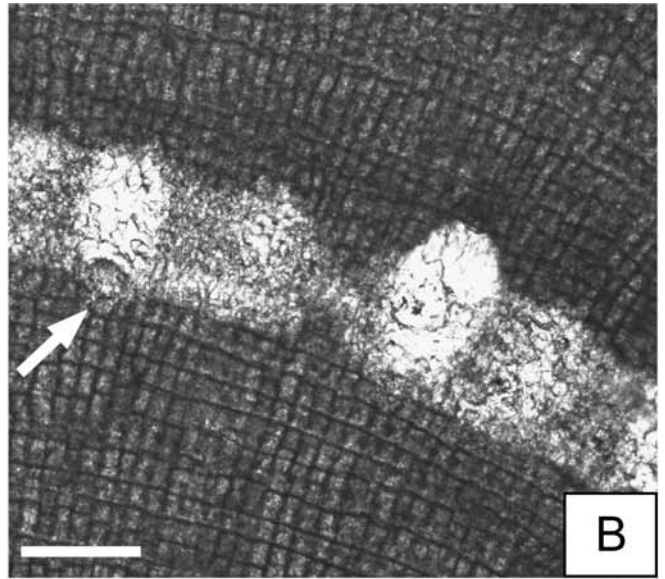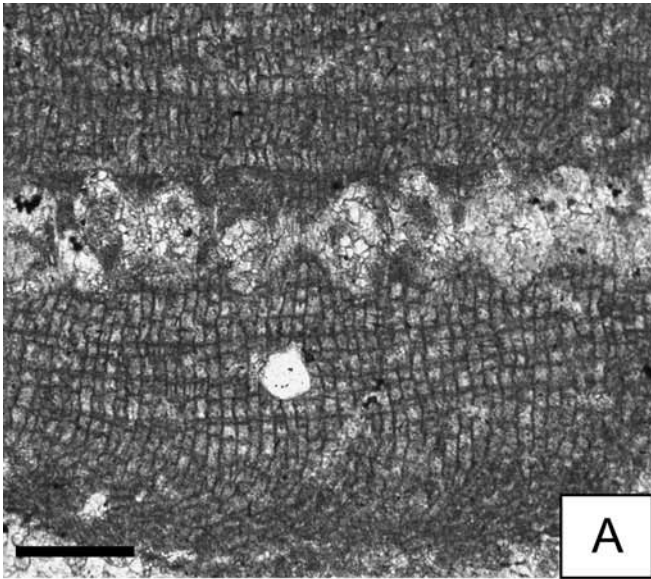
were observed. At least in two cases, the sporangial cavities have trapezoidal stalk cells at their bases. These anatomical traits indicate that the species should be considered as a member of the family Sporolithaceae. The similarity of these sporangial reproductive structures to the conceptacles is due to the loss of the vegetative tissue that separates the sporangial compartments. This tissue was probably not calcified or only weakly calcified. Therefore, the species should be referred to as *Sporolithon rude* as proposed by Ghosh and Maithy (1996).

Discussion

Taxonomic comparison of *Sporolithon rude* with other Cretaceous coralline taxa

The presence of merged sporangial cavities is not exclusive to *Sporolithon rude*. Other Cretaceous taxa exhibit fusion of the sporangial compartments: *Kymalithon belgicum* (Foslie) Lemoine and Emberger (1967), *Paraphyllum amphiroaeforme* (Rothpletz) Lemoine (1970) and *Agardhiellopsis cretacea* Lemoine (1964). We refer to some of their features and discuss their generic assignment taking into consideration the original diagnoses and figurations. We show that these genera can be hardly distinguished from *Sporolithon*. However, whether or not their anatomical characters warrant separation from these taxa as independent genera depends on an appropriate taxonomic re-assessment of the type species, an objective beyond the scope of this paper.

Kymalithon was proposed by Lemoine and Emberger (1967) based on the species *Lithophyllum? belgicum* Foslie, which was originally attributed to *Lithophyllum* with

◄ **Fig. 7** **A–F** Reproductive structures of *Sporolithon rude* (Lemoine) Ghosh et Maithy. **A** Sorus formed by elliptical isolated sporangial cavities. Adjacent cavities can be partially fused together due to the loss of the cell filaments between the sporangial chambers (paraphyses). Specimen from the Llàcova Formation, Late Hauterivian (Catí). Sample AV-B-2, Moussavian's collection. *Scale bar* 100 µm. **B** Trapezoidal stalk cell at the base of an isolated sporangial chamber (*arrow*). Specimen from the Benassal Formation, Late Aptian (Benicàssim). Sample 7.9–b. *Scale bar* 100 µm. **C** Completely fused sporangial cavities of two sori (central part of the plant), originating multiporate tetra/bisporangial conceptacles similar to those present in members of the family Hapalidiaceae. Specimens from the Llàcova Formation, Late Hauterivian (Catí). Sample AV-A-6, Moussavian's collection. *Scale bar* 200 µm. **D** Remains of the calcified walls (*arrows*) of isolated sporangial cavities within a void sporangial conceptacle-like structure. Specimen from the Llàcova Formation, Late Hauterivian (Catí). Sample AV-A-6, Moussavian's collection. *Scale bar* 100 µm. **E** Trapezoidal uniporate conceptacles protruding on the thallus surface. The presence of a single pore canal on the roof, the shape and the size of these structures recall the spermatangial or carposporangial conceptacles of some extant species of *Sporolithon*. Specimen from the Llàcova Formation, Late Hauterivian (Catí). Sample R-AV-119, Moussavian's collection. *Scale bar* 150 µm. **F** Uniporate conceptacle, smaller than those of **E** interpreted as immature spermatangial conceptacle. Note, also, flared epithelial cells at the dorsal part of the plant. Specimen from the Llàcova Formation, Late Hauterivian (Catí). Sample AV-A-1, Moussavian's collection. *Scale bar* 50 µm
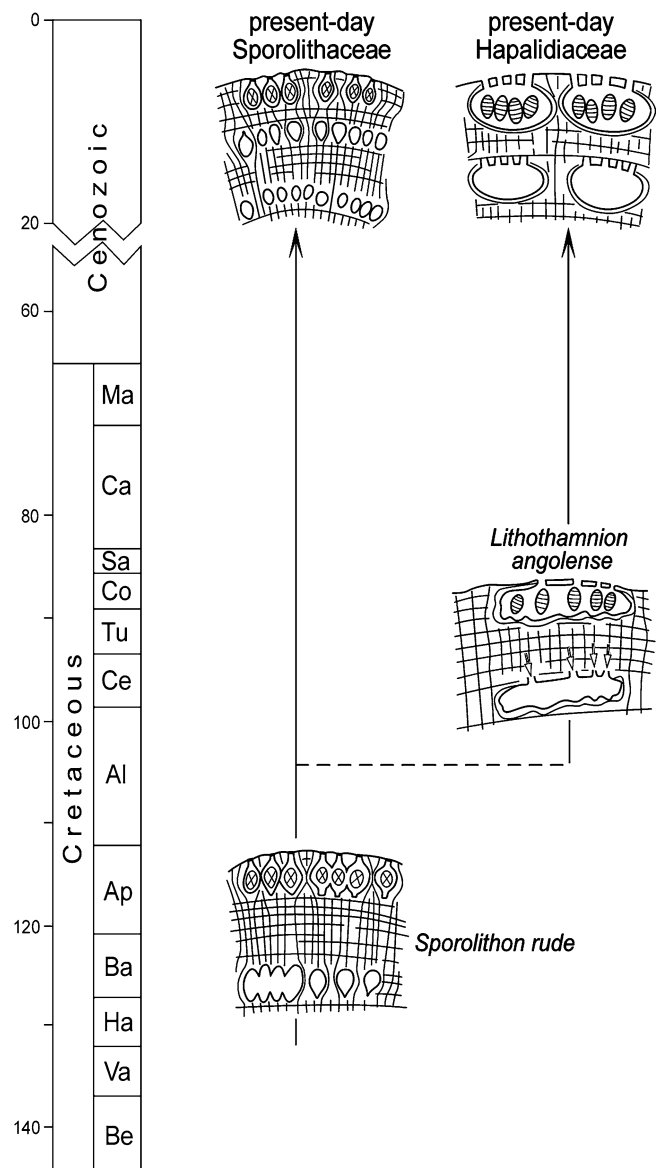
Fig. 8 Inferred evolutionary-phylogenetic relationship between the families Sporolithaceae and Hapalidiaceae. *S. rude* is at the base of the evolution of the sporolithaceans and could be the ancestor of hapalidiaceans. *Lithothamnion angolense* is the first feasible record of a member of the family Hapalidiaceae, appearing in Albian deposits (scheme of *Lth. angolense* is based on the original publication by Romanes (1916). White arrows point to several pore canals at the top of the conceptacle)

question mark by Foslie (1909) because of the lack of the reproductive structures. Lemoine and Emberger (1967) identified this species in the Early Cretaceous (Late Aptian) deposits from the southern Aquitanian Basin. They described sporangial reproductive structures formed by five to six sporangial cavities grouped in sori and pointed out the existence of several cavities fused together, giving way to larger tetra/bisporangial conceptacle-like structures. Within some of these conceptacle-like structures the original walls of the isolated sporangial cavities were preserved. Pfender (1926) and Andrusov (1938) referred to the species as *Archaeolithothamnium belgicum* due to the presence of

the sporangial cavities arranged in sori. However, Lemoine and Emberger (1967) proposed the new genus *Kymalithon*, basing the diagnosis almost exclusively on vegetative features, such as the arrangement of cells, both in the basal core (hypothallium) and in the peripheral region (perithallium).

Two species have been included in the genus *Paraphyllum*, the type species *P. amphiroaeforme* (Rothpletz) Lemoine and *P. primaevum* Lemoine (1970). The type species was initially assigned to *Lithothamnion* by Rothpletz (1891, as *Lithothamnium amphiroaeformis*) and then transferred to the genus *Lithophyllum* by Foslie (1909). Unfortunately, the type material studied by Rothpletz has no reproductive structures. Pfender (1926), analysing Turonian samples from Cadière (the type locality; in the Beausset Basin, SE France), Aptian rocks from Orthez and Vimport (SW France) and thin sections of the collection of E. Munier-Chalmas attributed the species to the genus *Archaeolithothamnium* (*A. amphiroaeforme*), due to the presence of isolated sporangial cavities grouped in sori. Subsequently, Lemoine (1970), after analysing new material collected from many areas of southern France and northern Spain, proposed for the species the new genus *Paraphyllum*. Although Lemoine described sporangial cavities grouped in sori, which were distributed in the outer part of the thallus and could be merged locally (Lemoine 1970; Plate VIII, Fig. 2), she based the diagnosis of the genus on vegetative characters.

Agardhiellopsis Lemoine is a problematic Early Cretaceous red alga described in the Aptian-Albian deposits of southern France and Navarre (northern Spain) by Lemoine (1964). She included this genus within the Gigartinales, a paraphyletic group of rhodophytes (Garbary and Gabrielson 1995; van den Hoeck et al. 1995) and compared it with the present-day genus *Agardhiella* (Agardh) Schmitz. The diagnostic characters of *Agardhiellopsis* are the growth morphology, the cell arrangement in the thallus, and the reproductive structures (Lemoine 1964). *Agardhiellopsis* occurs as isolated branches and the cells are arranged in three different zones: a) a dark medullar zone made up of very thin cells; b) a white central zone of bigger cells; and c) a dark external zone ("perithallium") formed by rectangular cells. The sporangial reproductive structures occur in the external zone and consist of sporangial cavities grouped in sori-like structures. Each cavity shows a wall but the cell filaments separating them can be locally lost. One of the cavities illustrated by Lemoine (1964; Plate 1, Figs. 2–3) is filled by rounded structures that she interpreted as spores before releasing. According to Lemoine (1964), the presence of these structures within the sporangial cavities and the division of the thallus into three zones exclude *Agardhiellopsis* from the Corallinales. However, these structures, which were interpreted as spores in a fertile sporangial cavity, seem to be adventitious cells that filled the sporangium. This has been observed in present-day species of *Sporolithon*, such as *S. molle* (Heydrich) Heydrich (1897b) (Verheij (1993); Figs. 1–3) and *S. ptychoides* (Woelkerling 1988; Fig. 248) as well as in other members of the family Hapalidiaceae, such as *Mesophyllum* (i.e., Woelkerling 1988; Fig. 225). Moreover, trapezoidal stalk cells can

be observed at the base of some sporangial chambers (see Plate 1, Fig. 3 in Lemoine 1964). Similarly, Bucur and Duşa (1986; Plate II, Figs. 1–2) showed sporangial reproductive structures of *Agardhiellopsis cretacea* from Sîrbi-Vlâdeşti (Mureş Mountains, Romania) as cavities grouped in sori with distinct trapezoidal stalk cells at the base of some sporangial compartments. The presence of isolated sporangial chambers grouped in sori and the presence of spores rising from one stalk cell are characteristics of the present-day genus *Sporolithon* (Verheij 1993; Townsed et al. 1995; Harvey et al. 2005).

Phylogenetic significance of the fused sporangial cavities in the early evolution of Corallinales

One of the most characteristic features of *Sporolithon rude* shared by other Cretaceous species is the presence of merged sporangial cavities originating multiporate conceptacle-like structures. This suggests an evolutionary linkage between members of the family Sporolithaceae (presence of isolated calcified sporangial cavities) and members of the family Hapalidiaceae (characterized by multiporate tetra/bisporangial conceptacles). Anatomical and phylogenetical evidence together with the sequence of appearances in the fossil record confirm this relationship.

As regards the anatomy, *Sporolithon* (family Sporolithaceae) and *Lithothamnion* (subfamily Melobesioideae, family Hapalidiaceae) are the only two genera within Corallinales with flared epithelial cells. However, they differ in the presence of secondary pit connections in *Sporolithon* and in the sporangial reproductive structures (Woelkerling 1988). Sporolithaceans produce spores in isolated and calcified sporangial cavities grouped in irregular and indefinite sori (Townsed et al. 1995; Harvey et al. 2005). Each sporangial chamber has an apical pore canal for spore release and is separated from its neighbours by cell filaments (paraphyses). These vegetative cells among sporangial cavities may have been weakly calcified, and therefore taphonomically destroyed, resulting in a structure very similar to the multiporate conceptacles of the hapalidiaceans. This has been observed in the present-day species *Sporolithon durum* (Townsed et al. 1995).

Sporangial plants of hapalidiaceans produce spores enclosed within chambers (conceptacles) with many pores in the roof that have limited sizes and regular shapes (Harvey et al. 2005; Townsed et al. 1995). No vegetative filaments are usually preserved within the conceptacle separating the spores. However, paraphyses may sporadically remain after spore development and releasing, for example in *Lithothamnion muelleri* Lenormand ex Rosanoff (1866) (Woelkerling 1996b; Fig. 76E), *Lithothamnion indicum* Foslie (1907) (Woelkerling 1996b; Fig. 75E) or *Phymatolithon masonianum* Wilks and Woelkerling (1994) (Woelkerling 1996b; Fig. 79D). Conceptacles with preserved paraphyses recall the sporangial cavities of the sporolithaceans. This similarity between the sporangial structures together with the characteristic flared epithelial

cells exclusively shared by *Sporolithon* and *Lithothamnion* points to a possible evolutionary-phylogenetic relationship between both taxa.

Molecular phylogeny (Harvey et al. 2003) in combination with the fossil record of corallines (Aguirre and Braga 2005) supports the hypothesized evolutionary relationship that could help us to find out which sporangial reproductive structure is derived and which is ancestral. Harvey et al. (2003) have proposed a molecular phylogeny of many extant coralline taxa using the 18S rDNA and morphological/anatomical traits. According to these authors, the order Corallinales is divided into three families: the possibly monophyletic Sporolithaceae and the two undoubtedly monophyletic Hapalidiaceae (composed of the subfamilies Choreonematoideae and Melobesioideae) and Corallinaceae (including the subfamilies Mastophoroideae, Metagoniolithoideae, Lithophylloideae and Corallinoideae). The maximum-likelihood phylogeny of Harvey et al. (2003) suggests that Sporolithaceae includes a number of species of the stem-line of the coralline crown group (Hapalidiaceae and Corallinaceae).

The fossil record confirms that Sporolithaceae is the oldest group with a fossil record extending back to the Early Hauterivian (Arias et al. 1995). The studied corallines of the Llàcova Formation (Late Hauterivian), represented exclusively by the sporolithaceans *S. phylloideum* and *S. rude*, constitute further evidence of this long record of the family. Lukeneder and Schlagintweit (2005) also report the presence of *S. phylloideum* in Upper Hauterivian deposits from Kaltenleutgeben (Northern Calcareous Alps).

A comprehensive survey of the published papers concerning different aspects of corallines shows that the family Hapalidiaceae is the next group to appear in the fossil record, represented by the melobesioid *Lithothamnion* (Aguirre and Braga 2005). The first confidently identified representative of this subfamily is *Lth. angolense* Romanes (1916) from the Albian (latemost Early Cretaceous) of Angola. This is consistent with the polarity observed in the phylogeny proposed by Harvey et al. (2003).

This sequence of appearances supports the hypothesis that the sporangial conceptacle of the hapalidiaceans is a derived character. Furthermore, it could be confidently argued that the multiporate sporangial conceptacles could originate due to the fusion of several sporangial cavities of sori. The extant representatives of sporolithaceans and hapalidiaceans bear the two distinctive sporangial reproductive structures. However, *S. rude* is a sporolithacean with fused sporangial cavities giving way to multiporate conceptacle-like structures. In cross section, these structures are formed regularly by four to six sporangial chambers with a regular shape and a limited size within the range of the conceptacles of hapalidiaceans. This suggests that *S. rude* is at the base of the evolution of the family Sporolithaceae and could also be the ancestor of Hapalidiaceae. A corollary of this hypothesis is that conceptacles and sori are not only morphologically distinctive structures (Townsed et al. 1995), but they also seem to represent, respectively, derived and ancestral characters in the early evolution of the Corallinales. The evolutionary splitting of

the hapalidiaceans can be confidently dated to have taken place between the Hauterivian and the Albian, i.e., between the appearance of *S. rude* and the other taxa with fused sporangial cavities and the first feasibly recorded occurrence of *Lithothamnion* (Fig. 8). This evolutionary relationship is consistent with the phylogeny proposed by Harvey et al. (2003).

A similar tendency has also been reported in the evolution of gametangia in the Dasycladales. According to the recent molecular phylogenies of Zechman (2003), the derived family Acetabulariaceae bears gametophores fused in an umbrella-shaped structure (umbrellospores) containing a number of cysts with abundant gametes, whereas the basal group of this family bears the gametophores separated either terminally or laterally at the end of ramules (choristospores).

Conclusions

Coralline red algae occur in the Upper Hauterivian reef deposits in the Maestrat Basin (Iberian Chain, NE Spain). These coralline records confirm the possible origin of the group in reef habitats in the central Tethys and offer the opportunity of studying coralline algal assemblages at the beginning of the evolution of the group.

The taxonomic re-assessment of the Upper Hauterivian coralline algae of the Maestrat Basin indicates that none of the characters of *Parakymalithon* warrant its separation from *Sporolithon*. The sporangial reproductive structures protruding on the thallus surface of type species of *Parakymalithon* are indistinguishable from protruding sori present in some extant species of the genus *Sporolithon*. Hence, the new combination *Sporolithon phylloideum* (Bucur and Dragastan) Tomás, Aguirre, Braga and Martín-Closas is proposed.

Sporolithon rude (Lemoine) Ghosh and Maithy (1996) was formerly described as *Archaeolithothamnium rude* by Lemoine (1925). This species is characterised by the merging of several sporangial chambers as a consequence of the taphonomic loss of the cell filaments among cavities (paraphyses) since these were probably not or weakly calcified. The fusion of sporangial cavities produces tetra/bisporangial multiporate conceptacle-like reproductive structures. Nonetheless, the presence of 1) isolated sporangial chambers together with fused cavities in the same thallus, 2) stalk cells at the base of some of the sporangial chambers, and 3) the calcified walls of individual sporangial chambers within the fused structures confirms that the species should be included in *Sporolithon*.

Sporolithon is the oldest member of the Corallinales appearing in the fossil record. This agrees with the molecular phylogeny of corallines proposed by Harvey et al. (2003), in which the family Sporolithaceae is the ancestral group of the Corallinales. The merged sporangial chambers of *Sporolithon rude* are similar to the tetra/bisporangial multiporate conceptacles in members of the family Hapalidiaceae. From a vegetative anatomical point of view, *Sporolithon* shares an exclusive vegetative character (flared

epithelial cells) with the hapalidiacean genus *Lithotham-nion*, which is the first representative of the hapalidiaceans and the second member of the Corallinales occurring in the fossil record. This confirms the phylogenetical relationship between the two families and the polarity of appearance of taxa shown by the molecular phylogeny of Harvey et al. (2003). In this regard, the structures formed by the fusion of several sporangial cavities found in *S. rude* could be the precursor of the tetra/bisporangial multiporate conceptacles of *Lithothamnion* and the other hapalidiaceans.

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