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Editors' choice

A new coral with simplified morphology from the oldest known Hettangian (Early Jurassic) reef in southern France

MÉLANIE GRETZ, BERNARD LATHUILIÈRE, and ROSSANA MARTINI



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The family Zardinophyllidae (Pachythecaliina) represents one of the most enigmatic coral groups known from the beginning of Mesozoic record of stony corals. They share some features with Paleozoic rugosans (overall architecture of the corallite) but also modern-day scleractinians (aragonite mineralogy). Fossil record of zardinophyllids was up to now restricted to the Triassic. Here we describe a new coral genus *Cryptosepta* collected in the oldest known Jurassic (Hettangian) reef in the Ardèche department in southern France. *Cryptosepta* gen. nov. has poorly developed (cryptic) septa, which is a peculiarity that extends the boundaries used to distinguish post-Palaeozoic corals and an oversimplification that could support reinitialisation of the evolutionary clock during extinction events or that support an adaptation to specific environmental conditions. Occurrence of *Cryptosepta* gen. nov. in Jurassic suggests zardinophyllid survival through the Triassic–Jurassic boundary, and may represent (possibly with Sinemurian genus *Pachysmilia*) a missing link to Amphiastreidae.

Key words: Anthozoa, Pachythecaliina, T–J boundary crisis, survival, Jurassic, Hettangian, France, Ardèche.

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Introduction

The Triassic–Jurassic (T–J) boundary crisis is one of the five largest mass extinctions of the Phanerozoic. The end of the Triassic and Early Jurassic are periods with profound biotic and environmental changes (Tanner et al. 2004), and they are especially characterised by a dramatic decrease in marine fauna diversity. Reef communities, especially corals, suffered high extinction rates (Kiessling et al. 2007; Lathuilière and Marchal 2009). The Early Jurassic is traditionally defined as exhibiting a "reef gap", wherein genuine frameworks for colonial coral are scarce and concentrated in the western Tethys (Lathuilière and Marchal 2009 with references therein; Gretz et al. 2013).

The oldest known Hettangian reef is located in the Ardèche department (southern France) (Fig. 1) and was referred to as Elmi's reef (Kiessling et al. 2009). It was discovered by Elmi and Mouterde (1965), studied in a PhD thesis by Martin (1984) and mentioned in several papers (e.g., Elmi 1986a, b; 1990; Elmi et al. 1993; Elmi and Rulleau 1993; Dumont 1998). Kiessling et al. (2009) provided a modern detailed description of this reef in which the coral assemblage taxonomy comprises a short list of 4 genera, primarily branching corals. These genera are: *Chondrocoenia*, *Rhaetiastraea*, *Phacelophyllia*, and *Phacelostylophyllum*.

Our paper describes a new coral genus from the Elmi's reef. The new coral, classified as zardinophyllid (Pachythecaliina), was collected through three specimens that because of unusual, tube-like morphology of calices can be confused with serpulid tubes. The importance of this finding is in filling a stratigraphic gap between Triassic and Late Jurassic occurrences of pachythecaliine corals, whose origin and evolution is a matter of long-standing debate.

Institutional abbreviations.—MHNG, Natural History Museum of Geneva, Switzerland.

Geological setting, material and methods

Located in the Ardèche department (southern France) (Fig. 1), Elmi's reef grew during a very early interval of the Hettangian. No ammonites were found in the reef; nevertheless, the

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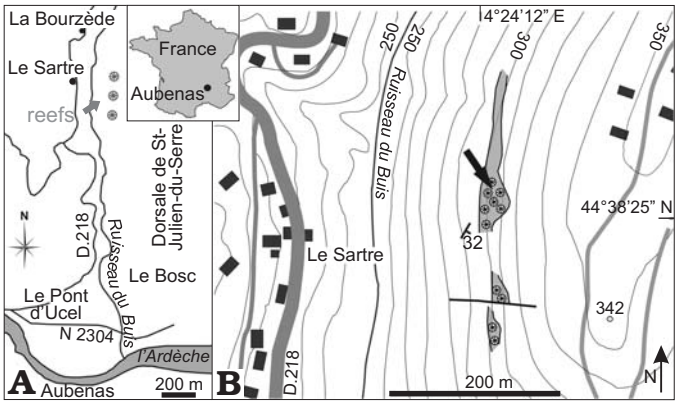


Fig. 1. Geographic location for Elmi's reef (**A**, modified from Elmi et al. 1993) and position of the locality near Ucel, Ardèche (**B**), samples corresponding to the new genus *Cryptosepta* indicated by black arrow (modified from Kiessling et al. 2009).

detailed work of Elmi and Mouterde (1965) permitted to constrain better its age. Indeed, 15 m below the reef structure they found the species *Psiloceras psilonotum*, *P. plicatulum* and *Caloceras* gr. *johnstoni* that suggest an early Hettangian age (*Psiloceras planorbis* Zone, *Psiloceras planorbis* and *Caloceras johnstoni* subzones) (Kiessling et al. 2009). Five meters above the reef structure, they found *Waehnoceras portlocki* indicating the *Alsatites liasicus* Zone, *Waehnoceras portlocki* Subzone of Hettangian (Kiessling et al. 2009). Regarding these elements, the reef grew certainly in the older part of the Hettangian (Kiessling et al. 2009).

It is a coral-microbial framestone reef, which developed below the fair-weather wave base but above the storm wave base in an inner-ramp setting (Kiessling et al. 2009). Most of the reef structure is strongly affected by diagenesis with coral skeletons recrystallised and replaced by blocky calcite, silica or, locally, by dolomite. Thus, the original structure of the corals is rarely preserved. The reef comprises three distinct patch reefs (Fig. 1). The largest reef includes massive reef limestone with corals that alternate with beds of coral floatstone and coquinas of crinoid ossicles as well as shell debris. Such interbedding with crinoidal limestone suggests growth in two or three distinct episodes. The newly observed coral colonies were in the largest patch reef and in a bed which corresponds to one of the growing episode of the reef. These corals are relatively rare in this reef. Three colonies were collected at the locality Ucel (Ardèche, France) (Fig. 1) and studied macroscopically. Using these samples, eight thin sections were prepared for microscopic analysis. Following Rittle and Stanley (1993) methodology, the optical petrography and cathodoluminescence microscopy (CL) were employed to detect possible preservation of the skeletal microstructures. The CL microscopy generally can account for a complete replacement of the original aragonite by a blocky calcite through a cementation process within the moldic porosity and no additional macro or microstructural features could be added to the natural light observations.

Systematic palaeontology

Class Anthozoa Ehrenberg, 1831

Remarks.—Several observations lead to the conclusion that the fossil under study is a coral: (i), tubes are not preserved in original calcitic microstructure; (ii), even if septa are abortive they exist; (iii), the tubes are branching and provide a phaceloid colonial structure; (iv), tubes are conical rather than cylindrical; (v), walls are compact, not perforated. All these observations discard serpulid, scaphopod and sponge interpretations.

Order Hexanthiniaria Montanaro-Gallitelli, 1975

Suborder Pachythecaliina Eliášová, 1976

Family Zardinophyllidae Montanaro-Gallitelli, 1975

Remarks.—The suborder Pachythecaliina Eliášová, 1976 is known from the Late Triassic to Maastrichtian. The systematic position of Pachythecaliina is controversial in the literature (Kołodziej 2003; Kołodziej et al. 2012). Indeed, certain authors distinguish this suborder instead of the suborder Amphiastreina (e.g., Stolarski and Roniewicz 2001; Stolarski and Russo 2001; Kołodziej 2003; Roniewicz 2008; Melnikova and Roniewicz 2012; Morycowa 2012) as others still accept the priority of Amphiastreina (Kołodziej et al. 2012). According to Roniewicz and Stolarski (2001), the families Zardinophyllidae Montanaro-Gallitelli, 1975 (=junior synonym Pachythecalidae Cuif, 1975) and Amphiastreidae Ogilvie, 1987 represent the suborder Pachythecaliina sensu stricto (Stolarski and Russo 2001). Other post-Triassic groups of Mesozoic have been attributed to this suborder and they represent the Pachythecaliina sensu lato (Stolarski and Russo 2001). These groups have no typical pachythecal wall, which belongs to diagnostic features of this suborder (or the state of their preservation does not permit to recognise them) and thus their affinity with pachythecaliines was based on the combination of characters or by the absence of characters that permitted to link them with other Jurassic scleractinians (Stolarski and Russo 2001). These corals are: Heterocoeniidae Oppenheim, 1930, Carolastraeidae Eliášová, 1976, Intersmiliidae Melnikova and Roniewicz, 1976 and Donacosmiliidae Krasnov, 1970. It has to be noticed that the phylogenetic relationship of heterocoeniids is controversial because most authors classify them into the suborder Heterocoeniina Beauvais, 1977 (see Kołodziej 1995; Kołodziej et al. 2012). Intersmilids and carolastraeids are similar and their only significant difference is the corallite symmetry that is respectively radial and bilateral (Stolarski and Russo 2001). The principal characteristic that link these groups with pachythecaliines are the smooth septal faces that are rare among the coeval scleractinians (Stolarski and Russo 2001). Donacosmiliids have similarities with amphiastreids but differ from them by their quasi-radial symmetry and lateral budding (Stolarski and Russo 2001). The stratigraphic distribution of pachythe-

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cal corals for the Triassic–Jurassic interval inspired from Stolarski and Russo (2001) is presented in the Fig. 2.

Pachythecaliine sensu stricto occupy a special place among post-Paleozoic corals (Kołodziej 2003). Indeed, Eliášová (1978) included the suborder Pachythecaliina in the order Hexanthiniaria Montanaro-Gallitelli, 1975 that is in some aspects intermediate between Rugosa and Scleractinia. By their peculiar morphological characteristics, zardinophyllids, amphiastreids and related families were considered by various authors (e.g., Koby 1888; Montanaro-Gallitelli 1975; Cuif 1975, 1980; Eliášová 1978, Melnikova and Roniewicz 1976; Stolarski 1996) as descendants of Rugosa (Kołodziej 2003). Pachythecaliines sensu stricto, have some distinct morphological characters that are comparable to those of the Palaeozoic plerophylline rugosans (Roniewicz and Stolarski 2001; Stolarski and Russo 2001; Kołodziej et al. 2012). Theses aspects are an early ontogeny and a skeletal architecture composed of a pachythecal wall and septa arranged in a bilateral symmetry that are commonly deeply located in the calice. However, Pachythecaliines ssp. have an aragonitic skeletal mineralogy and ?quasi-cyclic septal development in the adult stage that attest their link with scleractinians (Roniewicz and Stolarski 2001; Stolarski and Russo 2001). Amphiastreids differ principally from the zardinophyllids by their mode of budding that is "Taschenknospung" (Stolarski and Russo 2001).

The Triassic–Jurassic family Zardinophyllidae is composed in addition to the new genus presented in this work, of five other genera that are *Pachydendron* Cuif, 1975, *Pachysolenia* Cuif, 1975, *Pachythecalis* Cuif, 1975, *Zardinophyllum* Montanaro-Galitelli, 1975, and *Pachysmilia*, Melnikova, 1989. The morphological characters of the genus *Zardinophyllum* would indicate that this genus could represent an "ideal transitional form" between rugosans and non scleractinian, hexanthiniarian post paleozoic corals (Stolarski 1999; Roniewicz and Stolarski 2001). The link between Paleozoic and post-Paleozoic corals has been controversial for a long time (e.g., Oliver 1980; Fedorowski 1997) especially because no Early Triassic skeletonised anthozoans were found. In this debate, *Zardinophyllum* was considered either as "an abezrrant scleractinian" (Oliver 1981) or a Hexanthiniaria (Montanaro-Gallitelli 1975). This question is now renewed by molecular approaches and the finding of Ordovician Kilbuchophyllida (Scrutton and Clarkson 1991) interpreted as the earliest fossil scleractinian coral record (Stolarski et al. 2011)

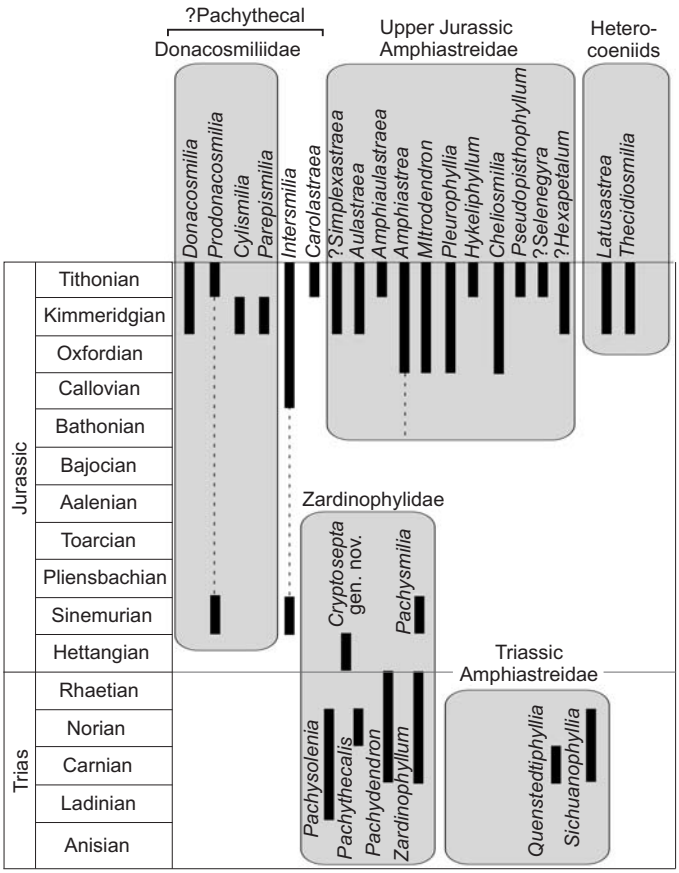


Fig. 2. Stratigraphic distribution of pachythecal corals and related genera inspired from Stolarski and Russo (2001) and modified. As an approximation, a vertical bar indicates a full stage when such corals were identified in the stage. When a single stage lacks such corals between two stages with such corals, the black bar was elongated. By approximation, Štramberk limestone was considered Tithonian. This figure shows only the Triassic–Jurassic range of Pachythecaliines but most of Jurassic genera occur also in the Cretaceous.

Genus *Cryptosepta* nov.

Type species: *Cryptosepta nuda* gen et. sp. nov.; monotypic; see below.

Etymology: From Greek *crypto*, hidden, for the cryptic septa.

Diagnosis.—As of the type species.

Cryptosepta nuda sp. nov.

Figs. 3, 4, 6.

Etymology: From Latin *nuda*, nude, because the septa are so short that the tube seems nude.

Type material: Holotype: MHNG 2013-34 to MHNG 2013-37 (Figs. 3A$_1$, A$_2$, B, D, 4B, C, E–G); sample S6. Rubble of a *Cryptosepta nuda* colony. Corallites can be observed on both faces of the sample. Paratypes: MHNG 2013-38 to MHNG 2013-41 (Figs. 3C, E, 4A, D); sample MG 156. Two rubbles containing each a *Cryptosepta nuda* colony.

Type locality: Ucel, Ardèche, France.

Type horizon: Lower Hettangian (in an interval that could extend from the upper *Psiloceras planorbis* ammonite Zone to the lower *Alsatites liasicus* Zone).

Material.—Type material only.

Diagnosis.—Phaceloid growth form. Corallites forming conical calices. Variable corallite wall thickness, which is proximally thick and distally thin. In transverse and longitudinal sections, the wall often has a corrugated aspect that produces an irregular corallite shape. The number of septa is low. In the more distal parts, the estimated number of septa ranges between 20 and 25. The septa are poorly developed as septal ridges along the inner side of the wall; they are irregular and randomly distributed but not distinct in the distal corallite parts. No visible symmetry. Budding lateral or possibly parricidal. No columella. Certain corallites display a distinct fine external epithecal layer separated from the massive thecal structure and

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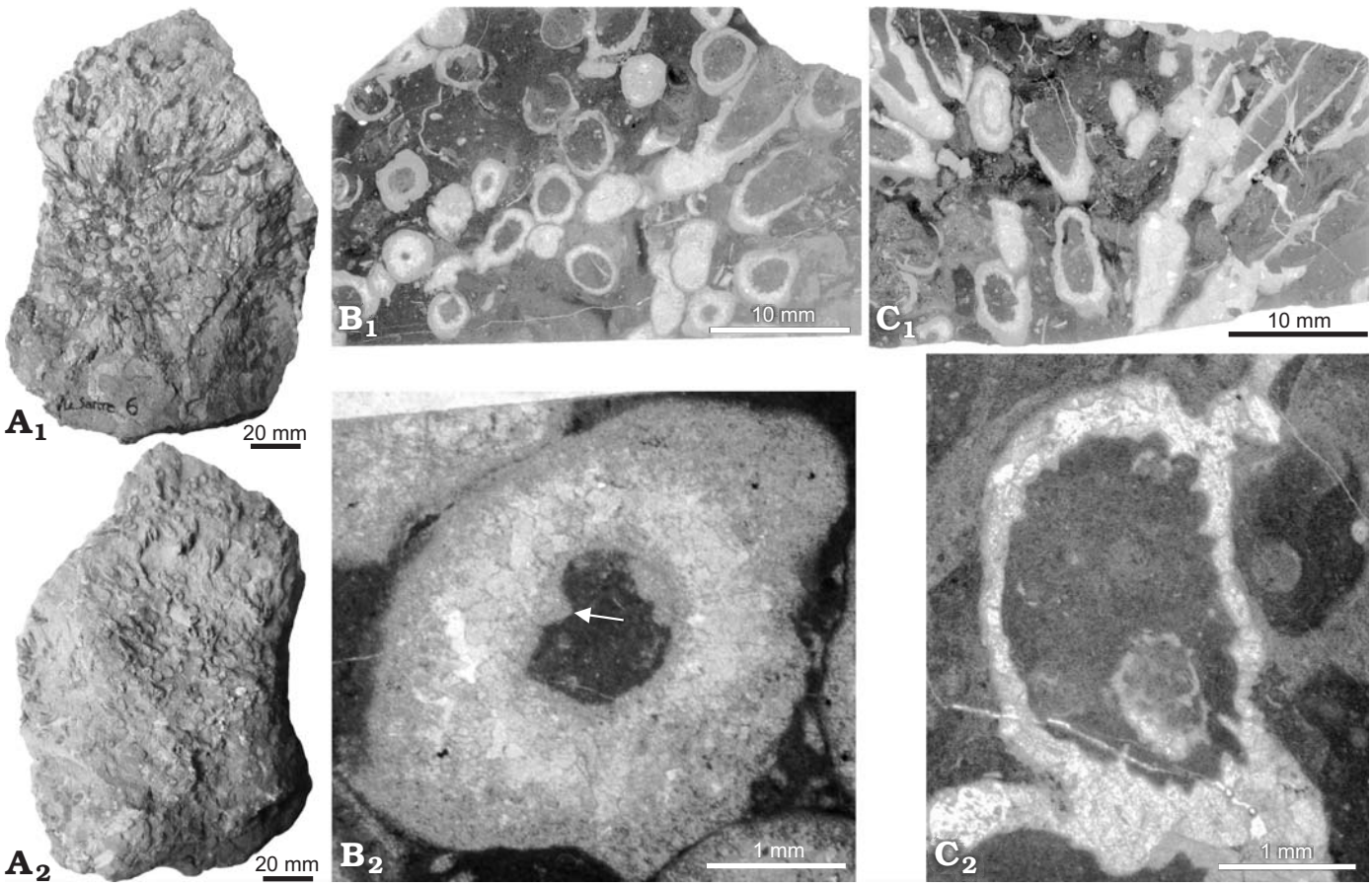


Fig. 3. Hettangian (Early Jurassic) zardinophyllid coral *Cryptosepta* gen. nov. from Ucel, Ardèche, France. **A**. Holotype (sample S6; MHNG 2013-34), global view of the colony. Corallites can be observed on both faces of the sample (A_1, A_2). **B**. Holotype (sample S6c; MHNG 2013-37), transverse and longitudinal corallite sections (B_1); transverse section, juvenile stage (B_2), characterised by a thick wall and only one septum (white arrow). **C**. Corallite (sample MG156c; MHNG 2013-40), transverse and longitudinal sections (C_1); transverse section, adult stage (C_2), characterised by a fine wall and relatively high number of septa. The septa are long and fine as well as short and thick.

occasionally a fine layer that covers the internal theca. Rare endothecal structures represented by large horizontal tabulae. They separate the corallite into distinct portions. A new septal apparatus grows at the upper surface of these tabulae.

Dimensions.—The different measured parameters of the holotype are shown in Fig. 5, and their values are in Table 1. The holotype size is 18 cm length × 12.5 cm width.

Description.—Phaceloid growth form. The corallites are formed by thick walls that become thinner distally. The walls are irregular, thick and often have a corrugated aspect that produces in an irregular corallite shape. The original structure of the corallite walls are difficult to identify and the cathodoluminescence analyses did not permit to reveal the original microstructure. Nevertheless, in some cases, in natural light observations, fine fibre-like structures are visible (Fig. 6), and the diagenesis likely affected in a different manner the distinct structures that originally formed the theca. For example, some corallites have a distinct fine external epithecal layer separated from the massive thecal structure and occasionally a fine layer that covers the internal theca.

Rejuvenescence phases are visible in longitudinal sections and induced more or less important calicinal aperture retractions. The radial elements are poorly developed and deeply hidden in the calices. Thus, the distal corallite portion has no septa and, in transverse sections, it appears as empty tubes. The septa develop on the pre-existent wall and are gradually inserted. In the proximal part, the number of septa is low, and in the more distal part, the estimated number of septa ranges between 20 and 25. In the transverse section, the septa are short, and the majority is thick. Thinner and longer septa were also observed, occasionally curved and rarely somewhat rhopaloid.

Budding is dominantly lateral; the new bud grows centrifugally at a wide angle from the outer side of the parental corallite wall, and it rapidly becomes quasi parallel to the mother corallite. Additionally, a case of possible parricidal budding could be considered (Fig. 3E). Nevertheless, it is difficult to distinguish it from rejuvenation. It is worth to note that in this case, two septa are elongated and are more or less involved in the budding process similar to as it is known in *Intersmilia* (Melnikova and Roniewicz 1976). In the longitudinal section, endothecal structures are rare, and they comprise large horizontal tabulae that separate the corallite into distinct portions. A new septal apparatus grows at

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Table 1. Values for the different measured parameters in *Cryptosepta nuda* gen. et sp. nov. from St Julien du Serre (Ardèche, France); Hettangian.

Parameters	Min. value	Max. value	Mean	Standard deviation
Proximal external diameter of the corallite (4 measurements in mm)	3.58	5.02	4.16	0.63
Distal external diameter of the corallite (4 measurements in mm)	3.13	5.58	3.97	1.11
Proximal lumen diameter (4 measurements in mm)	0.38	1.46	1.15	0.52
Distal lumen diameter (4 measurements in mm)	2.02	4.28	2.93	0.96
Proximal wall thickness (4 measurements in mm)	1.08	1.37	1.27	0.13
Distal wall thickness (4 measurements in mm)	0.32	0.55	0.41	0.10
Height of the calice (4 measurements in mm)	4.19	8.45	5.93	1.91
Angle between neighbouring corallite axes (2 measurements)	37°	43°	40°	
Number of distinct septa (2 measurements)	20	22	21	
Septal density/2 mm (where septa are regularly present) (2 measurements)	4	6	5	
Calicular angle (3 measurements)	29	32	30.5	

their upper surface. Such tabulae are geometrically related to rejuvenation stages.

Remarks.—*Cryptosepta* gen. nov. exhibits plesiomorphic characters such as thick corallite wall developed before cryptic poorly developed septa. Though the wall microstructure is not well-preserved, such thickness is associated with poor septal development and suggests a pachythecalid wall (see Kołodziej et al. 2012 for a recent review on pachythecal corals), which is the predominant skeletal characteristic of Zardinophyllidae (=junior synonym Pachythecalidae Cuif, 1975). This family comprises additional colonial genera with phaceloid morphologies, including *Pachydendron* Cuif, 1975, *Pachysolenia* Cuif, 1975 and *Pachysmilia* (Melnikova, 1989). Additionally, it comprises the solitary forms *Pachythecalis* Cuif, 1975 and *Zardinophyllum* Montanaro-Galitelli, 1975. Among these genera, *Cryptosepta* is remarkable in its poorly developed septa (Table 2).

Compared with Jurassic or Triassic pachythecal Amphiastreidae as redefined by Stolarski and Russo (2001), *Cryptosepta* does not comprise the two zonal endotheca (no marginarium). The corallite illustrated in Fig. 4C suggests that a pocket may open within the wall. However, we could not characterise the typical mode of growth in the Amphiastreidae "Taschenknospung" (pocket budding) as it is defined by Roniewicz and Stolarski (2001).

Compared with Intersmiliidae, *Cryptosepta* has a much thicker wall, which suggests that it is more related to Zardinophyllidae than Intersmiliidae. The rhythmic growth of tabulae in *Intersmilia* is also a significantly discriminating characteristic.

Zardinophyllids have a pachythecalid type wall that is comprised of radially oriented, equal-sized fibre fascicles and exhibits full microstructural independence between theca and septa. However, the observed specimens show strong recrystallisation, and the original structure of the corallite wall is difficult to identify. The distinct fine external epithecal layer separated from the massive thecal structure that is observed around certain corallites of *Cryptosepta nuda* (Fig. 4F) is similar to those described by Cuif (1975: 169, fig. 6b), Melnikova and Roniewicz (1976: 99, pl. 24: 2, 3) and in particular to those presented by Kołodziej et al. (2012: 315, fig. 17).

In their initial and juvenile stages, zardinophyllids typically exhibit strong bilateral symmetry with an enlarged

Table 2. Comparison of zardinophyllid genera with the main characteristics that allow their distinction.

Zardinopyllid genera	Colonial or solitary	Radial elements	Symmetry	Endotheca
Zardinophyllum	solitary	thick, irregular septa; six primary septa, metasepta short, unfrequent, discontinuous	septal symmetry radio-bilateral	occasional tabulae
Pachysolenia	colonial, phaceloid	numerous, long, uniformly thin and septa subequal in thickness	radial-bilateral built of septa of three size orders	rare tabuloid elements
Pachydendron	colonial, phaceloid	very simple septal apparatus; generally twelve septa with two cardinal septa that are prominent by their length and strongly rhopaloid at their inner end; the other septa are shorter and slightly rophaloid	clear bilateral symmetry underlined by elongated one, or two opposite septa	rare, tabular elements
Pachythecalis	solitary	six thick primary septa, the succeeding septa numerous, thinner and shorter, differentiated into 3–4 size orders	radial-bilateral formed by the septa of the first order	rare tabuloid elements
Cryptosepta	colonial, phaceloid	extremely poorly developed, thick, irregular	not observed	rare large horizontal tabulae
Pachysmilia	colonial, phaceloid	thin, rather straight, slightly enlarged at the inner border, differentiated in length into 2–3 incomplete size orders; in some cases, two opposite septa can meet in the center of the corallite	hexameral symmetry, with occasional bilateral symmetry produced by one or two septa	horizontal, complete tabulae

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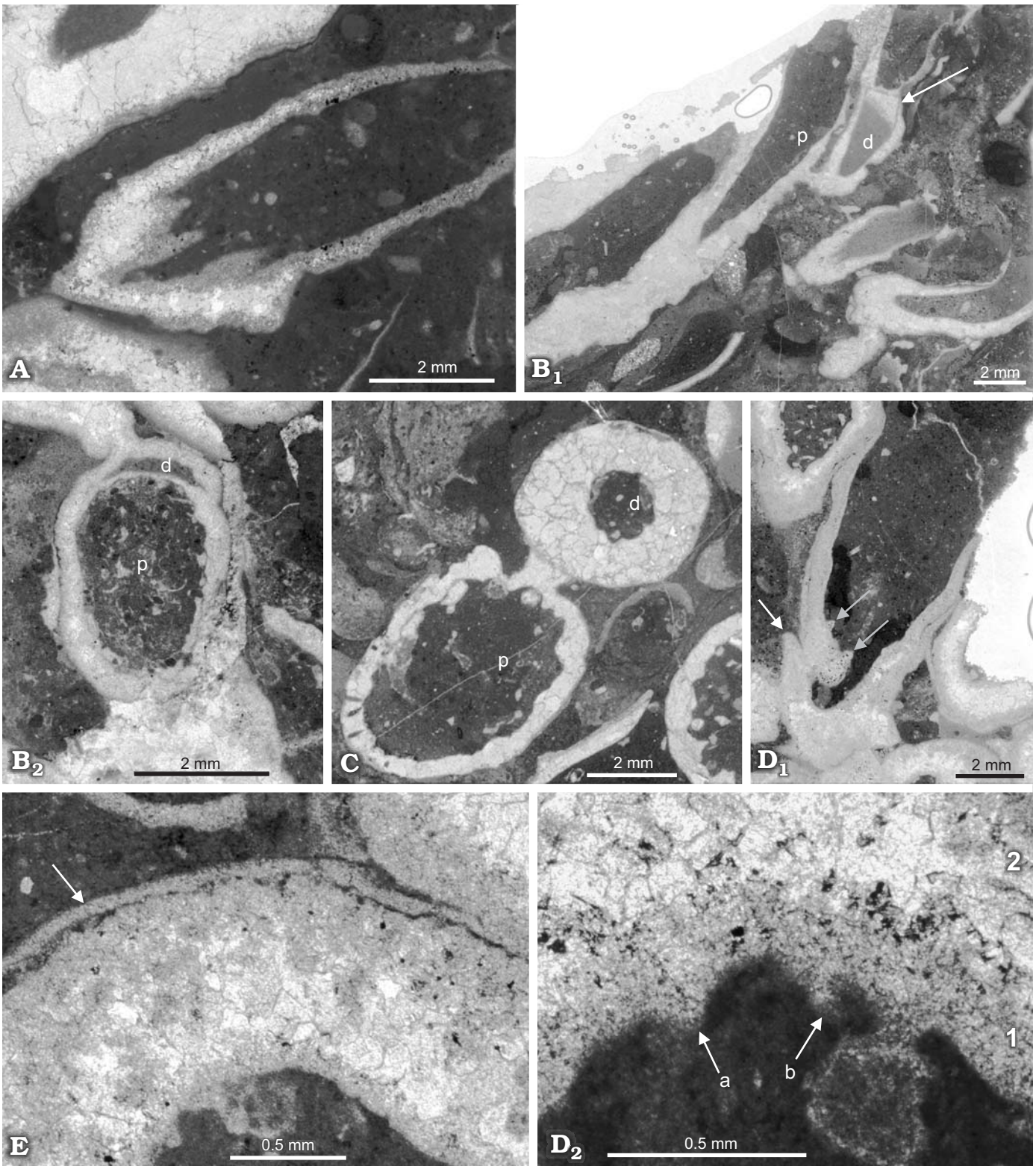


Fig. 4. Hettangian (Early Jurassic) zardinophyllid coral *Cryptosepta* gen. nov. from Ucel, Ardèche, France. **A**. Corallite (sample MG156b; MHNG 2013-39), longitudinal section showing the septa deeply hidden in the corallite. **B**. Holotype (sample S6b; MHNG 2013-36), longitudinal section (B_1), showing lateral budding with the parental (p) and daughter corallite (d), tabula (arrow) with septa developed on its upper surface; transverse section (B_2), young stage of lateral budding with the parental (p) and daughter corallite (d). **C**. Corallite (sample MG156d; MHNG 2013-41), transverse section, advanced lateral budding stage with the parental (p) and daughter corallite (d). **D**. Holotype (sample S6a; MHNG 2013-35), longitudinal section (D_1), rejuvenescence indicated through calicinal aperture retraction (white arrow), which facilitated new septa (grey arrows); transverse section in detail (D_2), septa morphologies: short and thick, which form a "tooth" shape (a) or thinner and curved (b), fine layer (fi) covering the internal part of the theca (ip). **E**. Holotype (sample S6c; MHNG 2013-37), transverse section in detail, fine external epithecal layer (arrow) separated from the massive thecal structure.

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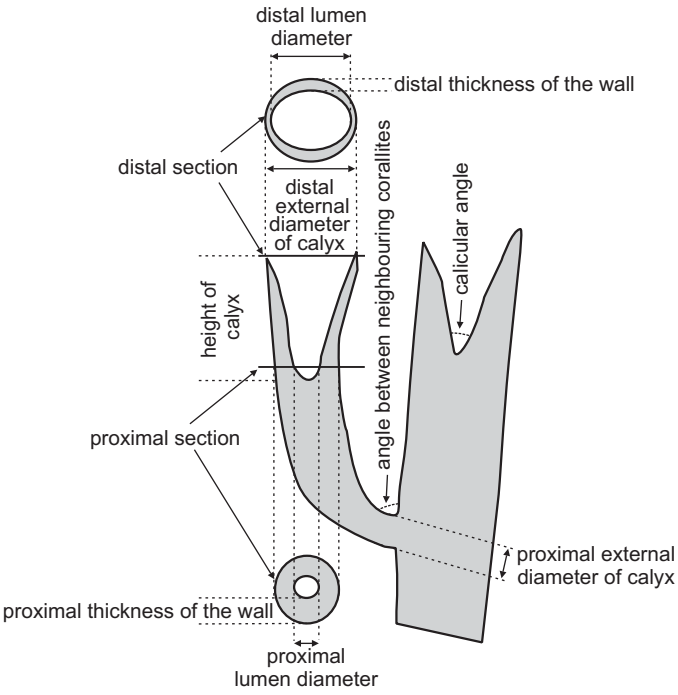


Fig. 5. Scheme illustrating the diagnostic parameters that characterise *Cryptosepta nuda* gen. et sp. nov.

primary septum; the adult stages often have quasi-radial symmetry. However, in *Cryptosepta*, the septa are often not clearly visible, and it was difficult to count the septa in the corallites. Therefore, it is also difficult to discern information about the symmetry.

Compared with the other Liassic genus *Pachysmilia* Melnikova, 1989, *Cryptosepta* has shorter and thicker septa. Nevertheless, *Pachysmilia* and the Triassic solitary corals *Pachythecalis* Cuif, 1975 and *Zardinophyllum* Montanaro-Galitelli, 1975 all display the same distinctive lamellar layer observed in *Cryptosepta*, which covers the internal theca and septa base. The colonial Triassic coral *Pachydendron* Cuif, 1975 also has more developed septa.

Stratigraphic and geographic range.—Type locality and horizon only.

Discussion

Pachythecal corals and the T–J boundary.—In their review on pachythecal coral phylogeny, Stolarski and Russo (2001: fig. 6) synthesized the extension of zardinophyllid genera (except *Pachysmilia*) and the stratigraphic range of the family that they suggested was exclusively Triassic (even if the ideal scope of the family progressed through the T–J boundary under a gradualistic interpretation). The *Cryptosepta* gen. nov. and the poorly known *Pachysmilia*, discovered by Melnikova (1989) in the Hettangian?–Sinemurian reefal facies of the south-eastern Pamir Mountains, change our notions on the pachythecal fossil record (Fig. 2).

Between the Late Triassic zardinophyllids and the Late Jurassic amphiastreids a large gap is present in the fossil record. This is especially true if we consider Middle Jurassic *Amphiastrea* (e.g., Gregory 1900; Pandey and Fürsich 1993) as a questionable identification for *Connectastrea piriformis* (Koby 1904–05; Beauvais 1966). Previously, this stratigraphic gap was only filled by intersmiliids (more precisely *Intersmilia djartyrabatica* and *I. kunteica* from the Callovian of Pamir described by Melnikova and Roniewicz 1976). Now this gap is finally filled by the Liassic zardinophyllids *Pachysmilia* and *Cryptosepta*.

These genera comprise corals that appeared after the T–J boundary crisis and support the notion that zardinophyllids survived this crisis. They are also the earliest known zardinophyllids as no younger corals from this family were indentyfied from subsequent strata. On the other hand, the simple

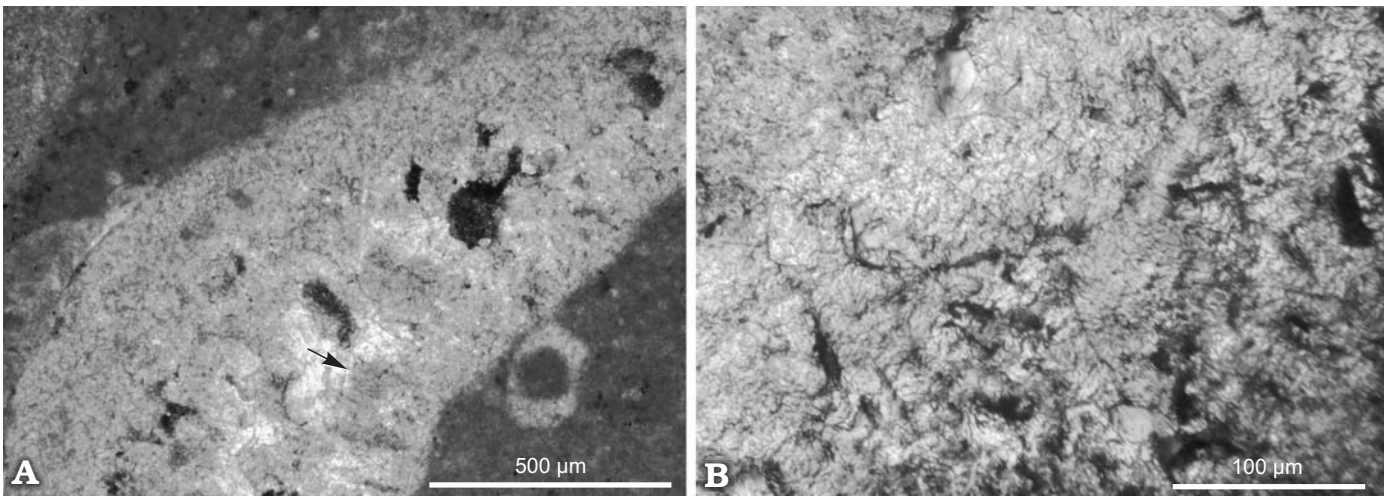


Fig. 6. Pachythecal structure of the walls of the Hettangian (Early Jurassic) zardinophyllid corallite *Cryptosepta* gen. nov. (sample S6a; MHNG 2013-35) from Ucel, Ardèche, France. **A**. A relatively well-preserved wall that reveals structures in some places (arrow) that may correspond to the original fibre-like structures. **B**. The fibre-like structures in detail.

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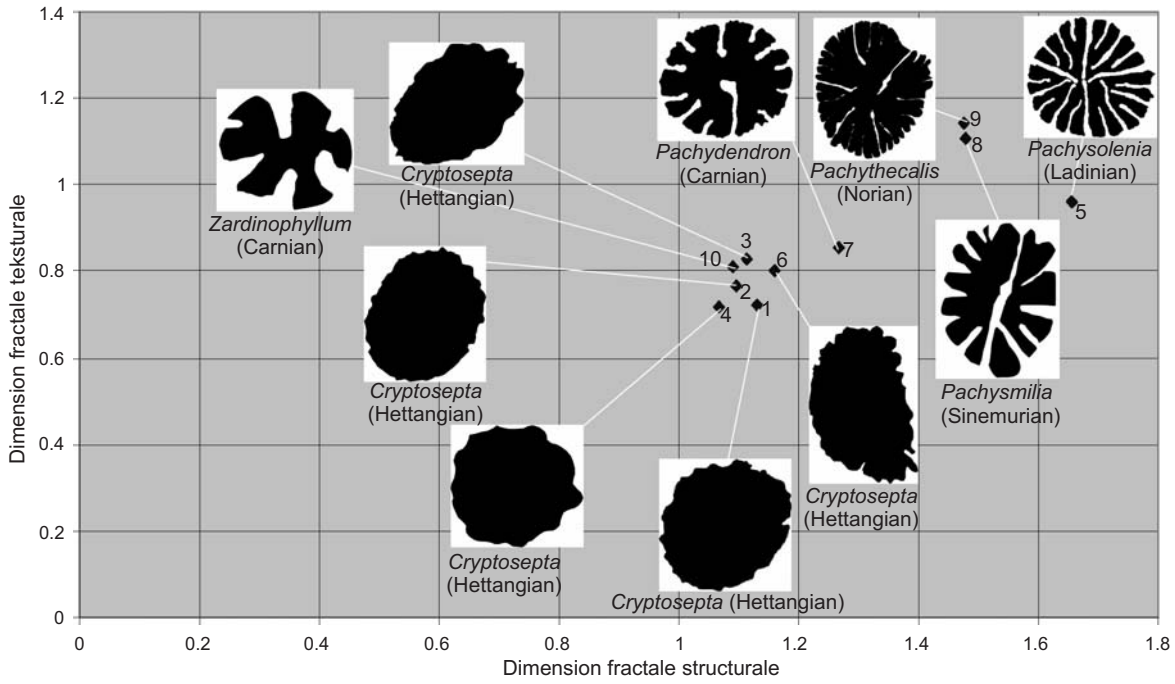


Fig. 7. Plot for the fractal dimensions analysis applied to the different zardinophyllid genera.

morphology of the oldest known Jurassic zardinophyllid and the possible mosaic nature of its character states (especially the different modes of growth) suggest that *Cryptosepta* may be a possible candidate for amphiastreid ancestor. This speculative hypothesis is an alternative to the hypothesis that Amphiastreidae emerged at the end of the Triassic with the genera *Sichuanophyllia* and *Quenstedtiphyllia* (Stolarski and Russo 2001). Obviously, if *Cryptosepta* is an ancestor of Amphiastreidae, the Triassic amphiastreid phylogeny should be reinterpreted. Are they ancestors or dead branches on the phyletic tree? How labile are the two-zonal endotheca characteristics, which are present in Donacosmiliidae? Is the separation between amphiastreids and zardinophyllids justified? Currently, it is difficult to answer such questions.

Another Hettangian sample from the Defrance collection (housed in University of Caen; Normandy) was initially referred to as *Favosites valoniensis* by Defrance (1820) and subsequently classified in the genus *Amphiastrea* by Alloiteau in 1950. This coral could be misidentified because it does not include marginarium and most likely represents *Heterastraea*.

Post-extinction morphology of *Cryptosepta*.—As suggested by the genus name, *Cryptosepta* gen. nov. has cryptic septa; this coral extends the boundaries of post-Palaeozoic coral disparity and could represent a textbook example of the unpredictable evolutionary pathways and possible resulting shapes. We knew pachythecalid corals with absent or poorly developed septa in the distal parts, such as *Pseudopisthophyllum eliasovae* (Kołodziej 2003) *Latusastrea* or *Zardinophyllum*, but such a weak development of the septal apparatus in a post-Palaeozoic coral is something we believe to be new for science. This near absence of septa, is interpreted in terms of complexity; the quasi-suppression of the septa is a clear shape simplification process. A comparable simplification was reported by Guex (2006) in the post-extinction fossil records for certain cephalopod and silicoflagellate lineages, which is related to an evolutionary response to environmental stress. *Cryptosepta* gen. nov. is a new example of the Guex's (2006) concept of reinitialization of the evolutionary clocks. At the T–J boundary in corals this reinitialization produced an oversimplified and paedomorphic shape in the pachythecal coral lineage. An additional more radical way to simplify the coral skeleton shape is to entirely suppress the skeleton, which is "naked Lazarus effect", currently an attractive assumption for speculations (Stanley 2003; 2011).

Complexity as an aspect of evolution has long been a matter of debate for evolution since Lamarck (1809) in part at least because it is challenging even to define complexity (Adami 2002; Waldrop et al. 2008). Thus, a fractal dimensions analysis was used as a proxy to compare and quantify the corallite shape of different zardinophyllids genera. We followed the protocol was detailed by Martin-Garin et al. (2007) which resulted in a plot presented in Fig. 7. As expected, *Cryptosepta* is clearly less complex than almost all the other zardinophyllid genera. However, the genus *Zardinophyllum* is an exception because it has similar fractal dimension values. Thus, this coral is the least complex Triassic zardinophyllid. Despite a report of an Anisian *Zardinophyllum* by Senowbari-Daryan (1993), later reiterated by Lathuilière and Marchal (2009), we rather consider this as a misidentification (Jarosław Stolarski, personal communication 2013). Then we cannot ascertain that the simple shape of Zardinophyllum results from its post extinction Permian–Triassic origin.

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Analogously, the Recent zooxanthellate species *Guynia annulata* Duncan, 1872 has an aseptal early initial stage in ontogeny and also septa that are located deeply inside the calice (Stolarski 2000). Molecular analyses suggest that this coral is not particularly ancient and the earliest fossil forms were recorded from the Miocene (Cairns and Wells 1987; Stolarski 2000). The depth interval in which this species is found varies from 3 to 653 m (Cairns 1989; Stolarski 2000) but in the shallower settings *G. annulata* develop in cryptic environments (Zibrowius 1980; Stolarski 2000). It is maybe these specific environmental conditions that induced the specific morphology of *G. annulata*. This example suggests that an oversimplified morphology is not necessarily indicative of reinitialization of the evolutionary clocks after an important mass extinction event and that the morphology of *Cryptosepta* was perhaps a response to the specific environmental conditions.

Obviously the way in which simple shapes, their record, the potential stress initiators and the mass extinction are related need more documented examples.

Conclusions

We report a new genus of coral identified in the Hettangian of Ardèche department (southern France). Given its poorly developed septa, it is referred to as *Cryptosepta* gen. nov. *Cryptosepta* is a pachythecal coral classified in the family Zardinophyllidae. Its Hettangian age and its relevance to zardinophyllid corals support the notion that this family survived the T–J boundary crisis. *Cryptosepta* is considered a potential ancestor for Late Jurassic amphiastreids. By its oversimplified morphology with cryptic septa, this genus is the first plausible example of post-crisis reinitialisation of the evolutionary clock in corals.

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