ARCHAEORADIOLIITES, A NEW GENUS FROM THE UPPER APTIAN OF THE MEDITERRANEAN REGION AND THE ORIGIN OF THE RUDIST FAMILY RADiolITIDAE

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Abstract: Archaeoradiolites gen. nov. (Radiolitidae), mainly characterized by radially arranged branching walls structuring the outer shell layer, includes two species, Archaeoradiolites primitivus gen. et sp. nov. and Archaeoradiolites hispanicus gen. et sp. nov. (type species), the distinction of which is based on size, shell habit and development of the radially branching microstructure. Their geographical distribution is restricted to south-east Spain and south-west France, i.e. the Western European Tethyan margin, whereas data from the Black Sea coast of Turkey suggest a possible extension to the Eastern European Tethyan margin. Each species has a distinct biostratigraphic distribution within the Upper Aptian (mainly the Gargasian). Agriopleura is suggested to be the direct ancestor of Archaeoradiolites, which in turn is considered as the progenitor of Eoradiolites. The onset of the Radiolitidae is associated with global oceanic changes that favoured calcite as opposed to aragonite biomineralization. The acquisition of a porous shell microstructure appears, in many respects, biologically advantageous and may account for gaining a rapid (<1 myr) ecological ability for efficient colonization and occupation of space of the family in the earlier phase of its radiation.

Key words: rudist bivalves, Upper Aptian, new genus, biostratigraphy, evolution.

The Late Aptian–Albian marked the onset of the radiation of Radiolitidae, which followed the mid-Aptian crisis that affected shallow water, carbonate platform biotas, including rudists (Masse 1989; Masse and Gallo-Maresca 1997). This family is characterized by specific attributes regarding: (1) shell structure: the calcitic outer shell layer tends to exhibit a cellular microstructure, with various geometrical patterns; (2) myocardinal features: myophores of the left valve (LV) are represented by vertical, downward-projecting plates into the right valve (RV), teeth are nearly equal and also project deeply in sockets or gutters of the opposite valve.

The so-called cellular structure has been attributed by earlier workers (Palmer 1928; Bøggild 1930; Douville 1935; Milovanovic 1935; Masse and Philip 1972; Strum and Perkins 1975; Amico 1977) to the association of two distinct sets of laminae or plates: the funnel plates, here labelled plates, conforming with the overall conical outer shell habit, and the radial plates, muri or walls, that are orthogonal to the plates, here labelled walls. Walls represent salient infoldings of the plates. This organizational mode is found, for instance, in Eoradiolites davidsoni (Hill) and other, relatively advanced, forms of the genus Eoradiolites, and also in some species of Praeradiolites and Bourmonia, forms in which the resulting, cellular pattern is mainly quadrangular (Amico 1977). The polygonal cell geometry of the Sauvagesiinae relates to the same process (Milovanovic 1935) whereas this group has been considered as a division of the Radiolitidae (Douville 1902).

Cellular structures belonging to the foregoing categories are not observed in all Radiolitidae. For instance, a radial irregular pattern tends to characterize the genus Katzeria Sliskovic (Sliskovic 1966; Caffau et al. 1992; Pejovic 2002), while in Rajka Milovanovic walls are represented by minute columns (Grubic 2002). Moreover, some Radiolitidae lack any type of cellular porous...
microstructures, as in Gorjanovicia Polsak (Polsak 1967), which has a compact outer shell, similar to that of the Monopleuridae.

The objective of the present paper is to describe a new genus, Archaeoradiolites, found in the Upper Aptian of south-east Spain, characterized by a radially branching outer shell microstructure, which departs from that observed in other Radiolitidae, especially the subcontemporaneous Eoradiolites. The form here described has been formerly ascribed to Eoradiolites, essentially *Eoradiolites plicatus* (Hill) (Gallo-Maresca 1993; Masse 1995; Masse et al. 1998). Identical or closely related forms have also been reported from south-west France (Masse 1995) (Text-fig. 1A) and the western Black Sea region of Turkey (Masse et al. 2002). Because the new taxon is the oldest Radiolitidae documented until now and has potential to be the root of the family, we discuss its relationships with both the progenitor of the Radiolitidae, the genus Agriopleura Kühn, and the genus Eoradiolites Douville, formerly regarded as the origin of the family.

**STRATIGRAPHY OF THE RUDIST-BEARING BEDS FROM SOUTH-EAST SPAIN**

Radiolitidae have a significant record in the Late Aptian–Albian of south-east Spain where they have been reported from various localities distributed in the Alicante, Valencia, Albacete and Murcia provinces (Arias et al. 1989, 1993, 1996; Masse et al. 1992, 1998; Gallo-Maresca 1993, in press) (Text-fig. 1B). The following will focus on Late Aptian radiolitid-bearing beds where specimens of *Archaeoradiolites* have been collected, mainly the Almansa-Jumilla region, including the Carche (Masse et al. 1992), Sopalmo (Arias et al. 1996), Sierra Larga, La Oliva, Caroch series, where the stratigraphic distribution of rudists has been calibrated to benthic foraminifera, essentially Orbitolinidae, having potential for distinguishing the lower and upper part of the Gargasian, and the Clansayesian.

The synthetic stratigraphic section of the Sierra del Carche (Aptian–Albian) (Text-fig. 2) illustrates the stratigraphic distribution of the two species of *Archaeoradiolites* and also *Eoradiolites*, in the Gargasian–Clansayesian interval. The biostratigraphic interpretation that conforms to the Masse et al. (1992) former dating can be summarized as follows: (1) *Orbitolina* (Mesorbitolina) *pervia* Douglass and *Dictyoconus? pachymarginalis* Schroeder mark the Lower Gargasian; (2) *Orbitolinopsis? aquitanica* Schroeder and Poignant and *Orbitolinopsis reticulata* Moullade and Peybernes identify the Upper Gargasian; (3) *Pseudochofottella cuvillieri* Deloffre marks the Clansayesian.

The tripartite division of the Upper Aptian, based on specific micropalaeontological assemblages, is well documented on a regional scale (Arias et al. 1993, 1996) and is corroborated by sequence analysis. The Lower/Upper Gargasian boundary is marked by a major sedimentary discontinuity: a subaerial truncation surface followed by marginal marine or continental sands and sandstones (the so-called Montemayor sands), with a wide regional extent.

**TEXT-FIG. 1.** A, radiolitid-bearing locations in south-west France and south-east Spain. B, radiolitid sites in the Valencia-Albacete and Murcia provinces in south-east Spain (stars indicate fossil-bearing localities).
Aside from *Archaeoradiolites* these stratigraphic sections also document the FO (first occurrence) of *Eoradiolites* sp. *sensu stricto*. Associated rudists consist of *Pseudotoucasia santanderensis* (Douville), *Horiopleura* gr. *almerae* Paquier and *Polyconites verneuili* (Bayle).
The symbols used in the descriptions are as follows: LV, left valve; RV, right valve; D, dorsal side; V, ventral side; A, anterior side; P, posterior side; AVC, anteroventral carina; mp, anterior myophoral plate; pmv, posterior myophoral plate; mpv, myophoral plate; at, anterior tooth; pt, posterior tooth; as, anterior socket; et, central tooth; ps, posterior socket; L, ligament ridge; Ab, anterior band; Pb, posterior band; Ib, interband.

Size estimates include dDV, the dorsal-ventral diameter, and dAP, the antero-posterior diameter of the RV, the average diameter being (dDV + dAP)/2.

Order HIPPURITOIDA Newell, 1965
Superfamily HIPPURITOIDEA Gray, 1848
Family RADIOLITIDAE d’Orbigny, 1847

Genus ARCHAEORADIOLITES gen. novo.

Type species. Archaeoradiolites hispanicus gen. et sp. novo.

Derivation of name. From Hispania, the ancient Roman name of Spain.

Type locality. Sopalmo, south-east of the city of Jumilla, Province of Murcia (south-east Spain) (Text-fig. 1B); lat. 38°24’58”N, long. 1°14’48”E.

Holotype. In the two slabs from sample 12077 from Sopalmo (Text-figs 4–5), which contains 15 serial transverse sections of conjoined RVs; the holotype is labelled 12077-1; the slab and associated thin section are housed with other materials in the Centre de Sédimentologie-Paléontologie, Université de Provence, Marseille.

Paratypes. Sample 12077, adjacent individuals (labelled 12077-2–15) from the above-mentioned slab; samples 11666 from the Sierra del Carche, 12091 from Sierra Larga (an isolated specimen) and 12079 (eight isolated juvenile specimens) from Sopalmo.

Additional material. Sample 10920, a slab including 11 serial transverse sections from Almansa.

Diagnosis. Conical RV and flat LV. Outer shell microstructure consisting of radially arranged branching walls. Plates virtual, formed by adjoining inflated terminations of the radial walls. Anterior band flattened, moderately salient, interband depressed, posterior band rounded and salient. Ligament ridge present, myophoral organization conforming to the radiolitid type. LV with a laminated concentric structure.

Discussion. The definition of Archaeoradiolites gen. novo. focuses on two main attributes of the RV: radially arranged branching walls, and virtual plates. None of the Radiolitidae described until now possesses these two characteristics. Eoradiolites has a typical cellular quadrangular structure, which consists of the combination of walls and plates (Douville 1902, 1909; Amico 1977; Coogan 1977; Gallo-Maresca 1992). Praeradiolites and Sphaerulites also display a cellular structure (Douville 1902; Milovanovic 1935; Dechaseaux et al. 1969; Amico 1977). Katzeria is the only form having a radially arranged outer shell architecture (Sliskovic 1966; Caffau et al. 1992; Pejovic 2002), whereas in this genus the radial walls are very thick, branching appears irregular (pl. 2, fig. 1 in Caffau et al. 1992) and mainly restricted to the inner shell margin (pl. 4, figs 1, 3 in Pejovic 2002). Moreover Katzeria lacks a ligamental ridge and possesses pseudopillars (Sliskovic 1966). Radial structures are locally present (i.e. dorsal side) in Petkovicia verajana Sliskovic, figured by Steuber (1999) whereas the overall organization is cellular, i.e. built after walls and plates.

Additional material. Sample 10920, a slab including 11 serial transverse sections from Almansa.
where the orientation of the shell axis may be modified during growth in connection with the available space left by the coeval growth of neighbouring individuals. Transverse shell outline varies from subcircular (juvenile stage) to rhomboidal or quadrangular (adult stage) (Text-fig. 5). The ventral side is usually flattened and the dorsal side rounded or lobate with a longitudi-
TEXT-FIG. 4. Transverse section through a congregation of in situ Archaeoradiolites (slab cut parallel to bedding) showing the variability in shell outline, due to shell packing, cardinal features and the outer shell radial microstructure (RV); individuals are labelled from 1 to 15, 1 being the holotype; Sopamo, sample 12877; scale bar represents 1 cm.

...median depression where the ligamental groove is located. The transverse development of the anteroventral carina (arête V sensu Douville 1910) correlates to the overall dorsoventral shell compression (i.e. the elongation of the axis joining the carina to the posterior side) (Text-figs 4, 5, 6B). Shell compression of this band is found in dense aggregations where shell morphology is modified according to the available space. The conica RV is made of tiered, fitted funnels resulting in foliated morphology (Text-fig. 6A), usually consisting of 4–6 folia separated by constrictions, the diameter of which increases during successive growth steps; however, the last step in some specimens records some size reduction (Text-fig. 7). Tiering or foliation is mainly developed on the dorsal side (Text-figs 4, 5A, 6A) and tends to invade the anterior then posterior sides during growth, the ventral side being usually smooth except for large specimens at adult stage (e.g. holotype). The growth surface extending from the shell edge to the inner margin of the outer shell (i.e. where the junction with the former aragonitic inner shell layer was situated) slopes inward. Commissural transverse dimensions range from 12 to 25 mm (antero-posterior) and 13 to 31 mm (dorsoventral) (holotype 16–29 mm), whereas the shell height varies from 19 to 35 mm.

The anterior band is represented by a moderately salient, flat (slightly depressed in the middle), wide area (4–6 mm) followed by a depressed interband flanking a salient rounded posterior band located at the junction between the ventral and posterior sides (Text-figs 5, 8). The inner shell margin facing the bands is flattened. Radia bands are well defined in specimens with a compact ventral outer shell layer (Text-fig. 5A) or where radial walls are restricted to the bands (Text-fig. 8). Where the ventral side is totally invaded by the radial walls, bands are fused and consequently more difficult to define (Text-figs 3A, 5D).

LV flat, slightly depressed dorsally (Text-fig. 9A–B), the margin of which only partially covers the sloping inward outer shell margin at the opposite valve (Text-fig. 9C). Transverse (Text-fig. 9D) and longitudinal axial sections (Text-fig. 9E) show the laminated concentric structure, frequently obscured by microborings (Text-fig. 9D) or micritization (Text-fig. 9C).

Internal characters The cardinal apparatus of the right valve is convex inward and includes two sockets, the anterior larger than the posterior (Text-figs 3A, 4), the central tooth is lamellate and oblique to the dorsal shell margin (Text-fig. 10). Teeth of the left valve possess an elliptical transverse outline.
**TEXT-FIG. 5.** *Archaeoradiolites hispanicus*, holotype. Serial transverse sections of the RV showing the overall organization. Note that in A the ventral side has a compact outer shell structure whereas other sections cut in the adult shell portion show radially arranged walls; B displays the myophoral apparatus of the LV projecting into the RV. Scale bar represents 1 cm.

Myophoral plates protrude from the left valve down into the opposite valve with a bull-horn transverse outline; the posterior one is shorter and thicker than the anterior (Text-fig. 11). Ligament ridge with a triangular or trapezoidal transverse outline and a concave end (Text-figs 3A, 10E–C) flanked by a ligamenta cavity (Text-fig. 10B–C).
**TEXT-FIG. 6.** *Archaeoradiolites hispanicus*, isolated specimens (RV). A, posterior view showing the foliated habit; sample 12091, Sierra Larga, Gargasian. B–C, Sepalmo, sample 12079. B, anterior view. C, apical view showing the transverse outline. See text for explanation of abbreviations; scale bar represents 1 cm.

**TEXT-FIG. 7.** *Archaeoradiolites hispanicus*. A, longitudinal (near the dorsal side) section of a bivalve specimen showing the lamellar, foliated outer shell habit of the RV; size of foliae increases upward then abruptly decreases (arrow). B, longitudinal tangential proxima (right) and dista (left) sections of two specimens showing the foliated shell habit. Both thin sections from Sepalmo, sample 12077. Scale bars represent 1 cm.

Microstructure of the outer shell layer. The outer shell layer includes compact, banded, locally wavy parts (Text-figs 7, 12–13) and radially arranged walls the geometry of which is revealed by transverse and longitudinal (subaxial and tangential) sections (Text-fig. 13). In transverse section walls radiate from the cortical layer towards the body cavity; convex microbanding
Fig. 11. Archaeoradiolites hispanicus. A–B, transverse sections showing the organization of the radial bands; wide flattened anterior band (Ab) and salient rounded posterior band (Pb) separated by a depressed interband (Ib). AVc: anteroventral carina. Carche, sample 11666. Scale bar represents 1 cm.

**Discussion.** The shells might have been covered by a conchiolin sheet (periostracum), known to offer some defence against predation by boring (Harper 1994). In a given growth band, quantitative estimates of micro-rhythms formed by the alternation of micritic and fibrous laminae (doublet fundamental sensu Massé and Philip 1972) (Text-fig. 13B, D) document between 20 and 30 alternations. The assumption that a given doublet represents 15 days of growth (Amico 1977; Regidor-Higuera et al. 2002) suggests that one folia may have been produced during one year; therefore, an individual with 4–6 foliae may have been 4–6 years old. This life duration does not depart significantly from those reported for Upper Cretaceous Radiolitidae, notwithstanding their larger size (Amico 1977; Steuber 1996). Peeling off the cortical layer for producing lamellar bioclasts appears a typical property of the Radiolitidae (Philip et al. 1977; Sanders 1999). Archaeoradiolites hispanicus gen. et sp. nov. documents an unusual mode of shell alteration; the radial walls tended to disintegrate into silt-size particles that transferred to the surrounding sediment (Text-fig. 14). The process of disintegration, which needs further investi-
**TEXT-FIG. 9.** *Archaeoradiolites hispanicus.* A–B, longitudinal (nearly anteroposterior) section of a bivalve specimen showing the flat LV and the downward projecting myophora plates. C, close-up of B showing the interruption of the (former) inner aragonitic shell layer at the inner slope of the inner shell margin and corrugations (arrow) indicative of a lamellar porous inner structure (due to peeling of the outer shell surface). D, transverse tangential section showing concentric arrangement of the laminations (somewhat obscured by microboring). E, longitudinal section showing the porous lamellar structure (arrow points to the commissure). All from Sepamu, sample 12077.

...gation, might be due to microdissolution, as suggested by Text-figure 14B.

**Distribution of the radial structure in the shell.** The study of the slabs including 14 specimens (Text-fig. 4) shows that the radial pattern is always present on the dorsal side and may invade the anterior and posterior sides whereas the ventral side is usually compact. Only one specimen (i.e. holotype) has an overall radial structure. Image analysis performed on transverse sections (*n* = 3) indicated that the septate structure represents 44–100 per cent of the outer shell surface (see above). The carina found at
Fig. 10. Archaeoradiolites hispanicus. A, transverse section showing the cardinal apparatus; note the lamellar central tooth (RV), the posterior gutter and the anterior tooth in the corresponding socket; Carche, sample 11666. B-C, close-up of the ligament ridge and the adjacent ligament cavity; Sepalm, sample 12077.

Fig. 11. Archaeoradiolites hispanicus, myophora apparatus. A-B, transverse sections at the same scale showing the bull-horn shape transverse outline of the myophora plates; Sepalm, slab 12077. Scale bar represents 0.5 cm.

The junction between the ventral and the anterior shell portions appears to be a critical site for the distribution of the radial structure. Radial walls tend to converge towards the plane of symmetry of the carina, the ventral portion being usually compact or with a limited radially arranged structure, whereas the anterior portion is typic-
ally septate (Text-fig. 15). The radial structure characterizes thickened parts of the shell whereas thin parts tend to be compact. This distribution of the radial structure is identical to those of the cellular one in Eoradiolites, for instance *E. plicatus* (Conrad) (Douville 1913; Chikhi-Aouimeur 1983) (Text-fig. 3B). The relative extent of radial vs. compact structure tends to increase with increasing shell diameter. Some relatively large sections possess a limited septate portion (restricted to the dorsal side) because the section appears to be cut between two consecutive foliae. Because the radial structure is essentially developed within the foliae, the foliated structure is mainly found on the dorsal side, extending to the anterior and posterior sides.

**Ontogenetic development of the radial structure.** The stepwise growth mode of the shell is not only recorded by the tiered fitted funnels but also within the corresponding foliae. Foliae from the initial growth stages show a compact structure (juvenile stage analogous to adult stage of *Archaeoradiolites primitivus*; see Text-fig. 16A), whereas the succeeding ones record an increasing intraskeletal porosity linked to increasing development of the radial walls. Four successive growth stages are illustrated on Text-figure 16C-F, each represented by a close-up of the microstructure showing that the number of radial walls tends to increase as their thickness decreases at each growth step. This trend is documented by a quantitative estimate of the intraskeletal voids measured (using image analysis) for successive foliae and within distinctive parts of each folia. The corresponding curve shows that the onset of each step is marked by a compact structure (i.e. cortical layer) followed by radial walls, but each step records a reduction of the compact structure relative to the radial one, the last having the highest value for intraskeletal voids. The terminal folia marks a size retreat coupled with a relative reduction of the porous structure.

**Archaeoradiolites primitivus sp. nov.**

Text-figures 17-19

1993 *Eoradiolites plicatus* (Conrad); Gallo-Maresca, p. 56, pl. 7, fig. 3.

**Derivation of name.** After the primitive characters of the species.

**Type locality.** Sierra del Carche, south-east of the city of Jumilla, Province of Murcia, south-east Spain (Text-fig. 1B); lat. 38°26'16"N, long. 1°09'58"E.

**Holotype.** Four thin sections and slabs from sample 10769 from Sierra del Carche housed with other materials in the Centre de Sedimentologie-Paleontologie, Université de Provence, Marseille.

**Paratype.** Five thin sections and slabs from sample 15206 from Sierra del Carche (underlying beds to the type level).

**Additional material.** Five thin sections from sample 5886 from Arudy.

**Specific diagnosis.** Small (max dDV 18 mm, dAP = 18 mm; average diameter (dDV + dAP)/2 = 13 mm), conical, somewhat foliated *Archaeoradiolites*. Radial branching structure restricted to the anterior side, somewhat extending to the dorsal side. Radial bands compact, the anterior wide and flat, fused to the posterior (interband inconspicuous), salient at the posteroventral articulation. Ligament ridge with a low trapezoidal transverse outline, termination concave. LV flat or slightly upward with a porous, laminated structure.

**Description of material from south-east Spain**

**External characters.** Owing to the absence of isolated specimens the following data derive from the observation of variously oriented sections.

RV conical, from low to high angle, with moderate foliated habit (Text-fig. 18A-B). Transverse outline subrounded at juvenile stage (Text-fig. 17A), elliptical and somewhat lobate dorsally, and anteriorly carinate at adult stage, the carina located at the anteroventral junction (Text-fig. 17B-C). Radial bands with a compact structure, the anterior band flattened and wide, the posterior band salient and corresponding with the posteroventral
TEXT-FIG. 13. Archaeoradiolites hispanicus; microstructure of the outer shell layer. A–C, transverse sections showing the radially arranged microbanded branching walls. Note the evolution in B from compact to branching habit and the increase of micritic laminae against (wide) fibrous laminae; vp, virtual plates formed by the distally thickened adjoining radial walls. D, longitudinal radial section showing the discontinuous porous nature of the radial walls. E, tangential folia termination showing the absence of carbonate material covering the radial walls. F, tangential section of the radial walls. Arrows point to growth direction; scale bars represent 0.5 mm.

articulation; interband inconspicuous or hardly depressed (Text-fig. 17). Growth surface, extending from the shell edge to the inner margin of the outer shell, slopes inward, so the LV is located in a depression relative to the shell edge. Commissural dimensions fluctuate from 8 to 18 mm (dAP) (average 13 mm) and 9 to 18 mm (dDV) (average 13 mm). LV is flat or slightly concave upward (Text-fig. 18A, C).

Internal characters. The cardinal apparatus of the RV includes two sockets changing upward, near the commissure, to gutters and a lamellar central tooth (Text-fig. 17B–C). Myophora elements of the LV were not observed, except at juvenile stages, showing short asymmetric myophoral plates. Ligament ridge is short, with a trapezoida to triangular transverse outline.

Microstructure of the outer shell layer. Radially orientated branching wall found on the anterior side of the RV tends to bifurcate towards the body cavity (Text-fig. 19A–B). Dista thickening resulting in virtual plates is also observed. Besides the thin elongated and branching walls, short thick and columnar walls are also present, which are interbedded with the compact structure (Text-fig. 19C). Image analysis performed on transverse sections (n = 3) indicates that the septate structure represents 0–42 per
TEXT-FIG. 14. Archaeoradiolites hispanicus, shell alteration. A, evidence for in situ disintegration of radial walls. B, disintegration of radial walls probably due to early dissolution (fitted polygonal elements). C, silt-size elements derived from shell disintegration, within the muddy matrix surrounding a congregation of Archaeoradiolites hispanicus. Scale bars represent 0.5 mm.

TEXT-FIG. 15. Archaeoradiolites hispanicus. A-B, microstructure of the anteroventral carina showing the convergence of radial walls towards the plane of symmetry and the distinctive radial habit of the anterior and ventral side of the carina. A, Carché, sample 11666. B, Sopalma, sample 12077. Scale bars represent 0.5 mm.

Transverse sections of juvenile specimens and longitudinal sections of adult specimens mainly display a compact outer shell structure. The LV shows corrugations suggesting a septate structure analogous to those of A. hispanicus.

Comparison Archaeoradiolites primitivus is similar to A. hispanicus but some characters are significantly different: (1) slightly smaller in size, a property that fits with 'Cope's rule' (Cope 1887), predicting that primitive forms are expected to be smaller than their descendants; (2) the foliation of the RV is less pronounced; (3) the radial branching microstructure is restricted to the anterior and the dorsal sides, with the result that the ventral radial bands are always compact; (4) the radial bands tend to be fused, due to the inconspicuous interband; (5) the ligament ridge is smaller.

Owing to the above differences, most of which are related to the more primitive evolutionary state of A. primitivus compared with A. hispanicus, and their distinctive stratigraphic position (see discussion below),
**TEXT-FIG. 16.** A, *Archaeoradiolites hispanicus* at juvenile stage. B, *ontogenetic variation of the radial structure*, longitudinal section; *Sopamo*, sample 12877. C–F, close-up of B; *folia* represent successive growth steps with shell structure changing from *compact* (C), *porosity 0 per cent*, to highly *porous* (58 per cent) (F). Each *folia* records the same trend whereas the *porous* structure increases with *folia* size.
the two species are regarded as phylogenetically related chronospecies.

EVOLUTIONARY ORIGIN OF ARCHAEORadiolites

Archaeoradiolites primitivus is the oldest and most primitive representative of the Radiolitidae yet recognized. Considering Agriopleura to be the ancestor (Douvillé 1910; Masse and Philip 1974) or even the origin of Radiolitidae (Paquier 1900; Toucas 1907; Dechaseaux et al. 1969) necessitates a discussion of the relationships between A. primitivus and the youngest representatives of Agriopleura. The attributes of this genus (type species Agria marticiensis d'Orbigny) include a depressed LV, a compact outer shell layer and the presence on the LV of myophoral bulges (distinct from true plates) flanking elongated...
TEXT-FIG. 18. Archaeoradiolites primitivus. A, longitudinal section showing the conical shell habit of the RV and the flat LV. B, specimen with larger apical angle; note the moderate foliated outer shell surface in both. C, slightly concave LV showing the porous and laminar structure (arrow). All from Sierra del Carche, sample 10769. Scale bars represent 0.5 cm.

In addition, Agriopleura possesses well-defined radial bands and a ligament ridge associated with a ligamental cavity. Agriopleura belonging to the Agriopleura blumenbachii (Studer) and Agriopleura marticensis (d'Orbigny) group are well documented from the Barremian of France and Switzerland (Toucas 1907); they disappeared from the European Tethyan margin in the latest Barremian (Masse 1995). The early Aptian Agriopleura species found in Italy (Masse 1992), Lebanon (Douville 1913) and the Middle East (Hughes 2003) represent a distinct taxonomic entity (see discussion in Masse 1992). The reference material of Agriopleura used for comparison with Archaeoradiolites comes from the Shuaiba Formation (Upper Bedoulian) (J.-P. Masse, work in progress) of Saudi Arabia and Oman (Skelton and Masse 2000). Two morphotypes are present: conical and cylindro-conical (Hughes 2003), both with a depressed asymmetric LV having grooves running from the commissural margin and converging towards the dorsal side, i.e. to the centre of the valve depression. The ventral bands correspond to a flat, relatively wide anterior band and a salient posterior band forming the posteroventral carina (Text-fig. 21) whereas in the European forms each band possesses a longitudinal depression bound by two fine ridges (Douville 1910, 1913). The organization of the radial bands of Archaeoradiolites hispanicus is nearly identical to the late Bedoulian representatives of Agriopleura from the Middle East. Differences between the latter and Archaeoradiolites include the following: (1) in Agriopleura the edges of the RV and LV are conjoined (Text-fig. 21), whereas the LV of Archaeoradiolites is located within the depression formed by the sloping inward outer shell margin (Text-fig. 9); (2) whereas the size of Arabian forms of Agriopleura depends on the morphotypes (the conical ones tend to be smaller than the cylindro-conical ones) the average size is greater than that of Archaeoradiolites species; (3) myophoral plates are present in Arabian forms of Agriopleura (Text-fig. 21), a character by which
they differ from their European homologues, whereas their dorsoventral extent is more limited than those of *Archaeoradiolites* (i.e. *A. hispanicus*); and (4) the outer shell structure of *Agriopleura* is compact throughout its development.

Comparison between *Archaeoradiolites* and the late Bedoulian representatives of *Agriopleura* (instead of those of Barremian age) provides additional evidence for the close similarity of the latter genus with primitive Radiolitidae, noted mainly as *Eoradiolites* by many authors (Toucas 1987; Dechaseaux et al. 1969 among others).

To conclude, notwithstanding generic-level differences between Arabian forms of *Agriopleura* and *Archaeoradiolites*, similarities between the two genera suggest derivation of the latter from the former in accordance with earlier hypotheses regarding *Agriopleura* as the root for Radiolitidae. Size reduction associated with the onset of *Archaeoradiolites* and the absence of septate microstructures in the juveniles of *A. primitivus* suggest derivation from *Agriopleura* through paedomorphosis, a process documented in some rudist lineages (Gourrat et al. 2003).

**EVOLUTIONARY RELATIONSHIPS WITH EORADIOLITES**

The erection of *Archaeoradiolites* necessitates a discussion of the relationships between this genus and *Eoradiolites*, which up to now was considered the progenitor of the...
Radiolitidae (see discussion above). Stratigraphic evidence documents the coexistence of Archaeoradiolites and the first representatives of Eoradiolites in the Upper Gargasian of Sierra del Carche (Text-fig. 2); the two genera are still coeval in the Clansayesian from south-east Spain and southern France. The definition of Eoradiolites must combine the organization of the radial bands (to follow Douville's view) and the presence of the quadrangular cellular habit of the outer shell layer, built of walls and plates s.s. (instead of virtual plates).

We have identified specimens found in the uppermost Gargasian of the Sierra del Carche, with a cellular organization as Eoradiolites sp. (Text-fig. 22). The cellular fabric consists of: (1) radially branching walls with a distal inflation and a pronounced microbanding, associated with micritic or relatively thick banded plates; (2) thin, elongated, usually unbranching walls interrupted by micritic plates. The radial branching habit closely resembles that of Archaeoradiolites, whereas virtual plates are replaced by plates s.s. This type of microstructure is found, for instance, on the dorsal side of Eoradiolites plicatus (Text-fig. 3B).

Likewise we assign to Eoradiolites sp. a form formerly placed in Eoradiolites plicatus by Masse et al. (2002) (see
TEXT-FIG. 21. *Agriopleura* sp., Upper Bedoulian Shuiba Formation, Shayba field, Saudi Arabia. A, ventral view showing the configuration of the radial bands. B, longitudinal section of the same specimen showing the myophoral plates. Scale bars represent 1 cm.

TEXT-FIG. 22. *Eoradiolites* sp., Upper Gargasian, Sierra del Carche, sample 11672. A, transverse section showing the overall organization. B, close-up of the anterodorsal area showing radial branching structures (a) and quadrangular cells (b), both with plates.

fig. 8, p. 531) (Text-fig. 23) found in the Upper Aptian of the Zonguldak region (western Black Sea, Turkey). In this form the cellular structure is limited to the dorsal side and consists of radial branching walls with an inward distal thickening plus micritic walls, locally somewhat incomplete. Although this form appears to be identical to
Archaeoradiolites, the presence of plates warrants its placement in Eoradiolites.

ONSET OF THE RADIOLITIDAE IN THE EARLY GARGASIAN: BIOLOGICAL AND PALEOENVIRONMENTAL SIGNIFICANCE

The onset of the Radiolitidae is associated with major global changes responsible for the mid-Aptian biological crisis (Masse and Philip 1986; Masse 1989; Skelton 2003) marked by the extinction of 42 per cent of the generic biodiversity and 57 per cent of the specific diversity of the cardinal benthic forms (foraminifera, dasycladalean algae and rudists) thriving on shallow carbonate platforms. Aside from the reduction in the spatial distribution of carbonate platforms, changes in chemical properties of the ocean (Masse 1989) coupled with a rise in CO₂, an increase in productivity and changes in seawater saturation with respect to aragonite (Bergen 1998; Weissert et al. 1998) have been suggested. The drop in biodiversity started in mid Bedoulian times and continued across the Bedoulian/Gargasian boundary (Masse 2003). The anoxic event OAE 1a (Arthur et al. 1990), which occurred in the Hambrovi Subzone of the Deshayesi Zone (Upper Bedoulian) and pre-dates the extinction peak (the Furcata/Töbleri boundary event), was not
responsible for the biological crisis for that reason, but was involved in the biodiversity decline preceding the extinction peak.

Lowering of the Mg/Ca ratio is a good candidate to account for a change from an 'aragonite regime' to a 'calcite regime' (Sandberg 1983; Stanley and Hardie 1998), expressed by dasycladalean algae, aragonitic foraminifera and caprinid rudists. Linking the evolution of bivalves and the modification of seawater chemistry has been documented by Harper et al. (1997), who stressed the difficulty of maintaining aragonite shells in 'highly corrosive' calcite seas. By contrast with the 'Hardie model' (Hardie 1996; Steuber 2002), which predicts that a modification from an aragonite to a calcite regime occurs over time periods of the order of 10 myr, data from the mid-Aptian suggest a rapid change (<0.5 myr). Similar short-term changes were also proposed by Pomar et al. (2004) for the Miocene. For Stanley and Hardie (1998) the development of the Radiolitidae was not a direct consequence of the mid-Cretaceous shift from aragonite to calcite seas. They suggested that the decline of the aragonitic corals, resulting from a decrease in the Mg/Ca ratio of seawater, opened the way for rudists in the highly competitive reef environments. However, as shown earlier (Scott et al. 1990; Gili et al. 1995), rudists and corals were thriving in distinctive environments so that competition between the two groups must be ruled out. Therefore, the development of the Radiolitidae in the Late Aptian appears to have been independent of the evolution of scleractinian corals, but has much to do with: (1) the vacant space left by the extinct Early Aptian Caprinidae; and (2) the onset of a calcite regime, which was also advantageous for other coeval rudists: Polycoenitidae (Polyconites, Horiopleura), Capronitidae (Caprotonia) and Menopneuridae ('Agriopleura darderi', 'Petalodontia'), all with a thick outer calcitic shell layer by comparison with the inner aragonitic shell layer (Masse et al. 1998).

The development of a porous, septate, structure in the calcitic outer shell layer of the Radiolitidae might be compared with the development of the canalicate structure observed in the originally aragonitic, inner shell layer of the Caprinidae. In both groups the strategy appears likely to have minimized the cost of metabolic energy used for shell production (Douville 1904; Palmer 1983) and may have facilitated quick growth. As shown in modern oysters (Chinzei 1995) vesicular shells allow soft-bottom bivalves to float on muddy bottoms, an advantage for solitary individuals. This hypothesis looks likely for Late Aptian Radiolitidae, which are essentially associated with wackstones (or very fine packstones). Another advantage of septate structures is the potential to resist shell breakage (Skelton 1976). A striking feature of Archaeoradiolites species is the high density of sponge (Cliona type) borings, which are restricted to shell portions with a compact microstructure, i.e. portions with radially arranged walls are free of borings (Text-fig. 7). Data from the Recent show that clionid sponges tend to infest various living or dead carbonate substrates, either compact or porous, but avoid parts with a large pore size (Schönberg 2002). The distribution of clionid borings in Archaeoradiolites may only reflect this biological need; nevertheless, it is necessary to be aware of the global context of the coeval high seawater productivity (see above). High productivity is known to promote an increase in sponge biomass and therefore an increase in infestation of carbonate substrates (Rose and Risk 1985). From the foregoing it is suggested that the acquisition of a septate structure by Archaeoradiolites might have been advantageous for avoiding detrimental strong infestations by clionid sponges. This strategy has already been discussed by Skelton (1976) for caprinid rudists. An alternative strategy, used by accompanying rudists, appears to have been an increase in shell thickness (e.g. Pseudotoucasia, Horiopleura) or the development of tubular structures at the interface between the outer and inner shell layer as, for instance, in 'Agriopleura' darderi (Masse and Philip 1974).

The development of Archaeoradiolites communities, which started with Archaeoradiolites primitivus in the Lower Gargasian, was studied at the Sierra del Carche. This study was based on quantitative estimates of the following ecological attributes (Fenerci-Masse et al. 2004): packing density (number of individuals in a 100-cm² vertical surface); packing-index (number of individuals in lateral contiguity, expressed in per cent); coverage (per cent of cumulative surface covered by individuals on a given bedding plane); and skeletal contribution (ratio of shell material vs. sediment in per cent).

Three steps were recognized in the evolution of radiolitid assemblages of Archaeoradiolites primitivus: (1) isolated specimens found with a requieniid-dominated community (Pseudotoucasia) in the lowermost Gargasian (the paucity of individuals did not permit quantitative estimates); (2) low-density assemblages, the quantitative attributes of which (including packing-index, packing density and coverage) fluctuate between 0 and 0.3, associated with Requieniidae, in the upper part of the Lower Gargasian; (3) a radiolitid community with a relatively high packing-index and packing density (18.5% and 16 individuals, respectively), moderate coverage (35%) and macro-skeletal contribution (16%), Archaeoradiolites primitivus being the only member of this community (Bed 10769).

In assemblages of Archaeoradiolites hispanicus from the uppermost Lower Gargasian of Sopalmo (type level) (see slab 12077) and Almansa (bed 10920), packing density ranges from 10 to 40, packing-index from 26 to 46 per cent, and coverage between 55 and 70 percent, the skeletal
contribution being about 50 per cent. These high values indicate that this species played a significant role in carbonate production and possessed a constructional potential somewhat higher than that of hippuritid-dominated lithosomes of the Late Cretaceous, which have lower packing density and coverage (Vilardell and Gili 2003). As for the hippuritid lithosomes, Gargasian radiolites, locally, build rigid frameworks. tidal-dominated beds lack relief, and their average bed thickness is reduced (less than 1 m), but they may, at least locally, build rigid frameworks.

STRATIGRAPHIC AND GEOGRAPHICAL DISTRIBUTION OF ARCHAEORADIOLITES

Archaeoradiolites primitivus has been recorded from the upper part of the Dictyococmus pachymarginalis interval (Lower Gargasian) below the Montemayer Sands at Sepalme, whereas it is present in beds overlying these sands in the Orbitolinopsis reticulata/O.? aquitanica interval (Upper Gargasian) from the same locality and surrounding sites of the Jumilla area. One small specimen comes from the lower part of the Gargasian beds of Sierra del Carche. This species was also found in the Caroch area and at Almansa in Upper Gargasian beds. In south-west France Archaeoradiolites primitivus was found in the Gargasian, probably the lower part, of the Arudy area, near Pau.

Archaeoradiolites hispanicus has been recorded in Upper Gargasian beds from south-east Spain: Sierra del Carche, Sepalme, Almansa and Caroch. In the Sierra del Carche this species is still present in the Clansayesian Pseudochofiella cuvillieri-beari beds.

To conclude, the stratigraphic distribution of the two species of Archaeoradiolites may be summarized as follows: (1) Archaeoradiolites primitivus is found alone in the Lower Gargasian and together with Archaeoradiolites hispanicus in the uppermost Lower Gargasian and the lowermost Upper Gargasian; (2) Archaeoradiolites hispanicus is found with primitive representatives of Eoradiolites in the Upper Gargasian, then co-occurs with advanced Eoradiolites [the so-called Eoradiolites cantabricus (Douville)] group in the Clansayesian (Masse et al. in press).

Our data indicate that Archaeoradiolites appears to be restricted to south-west France and south-east Spain, i.e. the western part of the European Tethyan margin. Nevertheless, primitive Eoradiolites from the western Black Sea coast of Turkey, close to Archaeoradiolites, suggests a direct derivation of the former from the latter and therefore possibly the existence of Archaeoradiolites in the East European Tethyan margin, known to possess strong palaeobiogeographical affinities with the West European domain during the Barremian–Aptian (Masse et al. 2002).

CONCLUSIONS

A new genus, Archaeoradiolites, is described from the Upper Aptian of south-east Spain and south-west France, characterized by the microstructure of the outer shell layer of the RV, which consists of radial branching walls and virtual plates formed by adjoined, inflated terminations of the radial walls. The LV is flat and possesses a laminated concentric microstructure. The other organizational attributes, myophoral organs, radial bands and ligament ridge, are identical to those of Eoradiolites. Archaeoradiolites includes two species, A. hispanicus (type species) and A. primitivus, distinguished by the relative development of the radial branching walls in the outer shell layer microstructure, mainly restricted to the anterior side in A. primitivus and extending to the anterior, dorsal and posterior sides in A. hispanicus. In A. hispanicus the RV is strongly foliated, owing to the tiering of fotted funnels, and shows pronounced ontogenetic variations regarding the microstructure of the outer shell layer. In A. primitivus the foliation of the RV is less pronounced and there are also ontogenetic variations: the juveniles are essentially compact.

A. primitivus is found in the Lower Gargasian and the lowermost Upper Gargasian; A. hispanicus is present in the uppermost Lower Gargasian and extends to the Clansayesian. This distribution gives to the two species of Archaeoradiolites potential for characterizing and subdividing the Upper Aptian.

Archaeoradiolites appears to be the direct descendant of Agriopleura, probably through paedomorphosis. It was the progenitor of Eoradiolites, the cellular, quadrangular microstructure of which departs from that of Archaeoradiolites.

The onset of the Radiolitidae is associated with major global changes and a strong biological crisis in mid-Aptian times. The acquisition of an outer shell layer of porous, septate microstructure may relate to strategies combining the minimizing of metabolic energy for shell production, the provision of some ability to float on muddy bottoms, and an increase in resistance to shell breakage and in ensuring protection against sponge boring. This may account for the ability of Archaeoradiolites to form densely packed communities with a significant bioconstructional character, acquired during the earlier phase of the radiation of the family Radiolitidae in less than 1 myr after the mid-Aptian extinction event.

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