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The Turonian–Campanian rudist bivalve succession in the Central Iberian Basin

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ABSTRACT

Four rudist assemblages: lower Turonian, upper Turonian, upper Coniacian, and Santonian–?Campanian, are distinguished in the shallow water carbonate platform successions of the Iberian Basin, nowadays Iberian Range, a Mesozoic intra-continental basin in the western margin of the Mediterranean Tethys. Because of the depositional evolution of the Iberian Basin, the occurrence, abundance, taxonomic diversity, diagenetic processes, and shell preservation, for each assemblage, is linked, both, to the shallow character of these carbonate platform successions, and the successive high and low frequency sea level falls. Twenty identified rudist taxa are described and figured: Hippuritidae, six species of two genera; Radiolitidae, ten species of six genera, one new, *Hoyosites tozoi* gen. et sp. nov; Requieniidae, one genus. The knowledge of the shell characters of some taxa has been improved and the taxonomic, biostratigraphic, and palaeobiogeographic significance of most of them increased. The precise positioning of the first three rudist assemblages in high-frequency depositional stacking pattern (parasequence sets) and their correlation and calibration with ammonite biozones provide biostratigraphic datums of great importance. This fact notably improves the chronostratigraphic framework of the Cretaceous sedimentary successions of the Iberian Basin, especially towards the coastal margins, and allows the accurate quantification of the hiatuses associated with the parasequence sets boundaries, so enabling their precise hierarchization.

1. Introduction

Reports of rudist occurrences in central areas of the Iberian Peninsula are relatively common in the results of regional geology research, mainly PhD thesis and geological mapping (references in 3.1. Localities). These rudists appear in shallow-water carbonate platform successions genetically linked to the Iberian Basin (nowadays, Iberian Range), a Mesozoic intra-continental basin in the western margin of the Mediterranean Tethys.

During Late Cretaceous, successive, essentially eustatic, depositional events overflowed the basin and flooded wide areas of its SW coastal margin, enabling the development of shallow-water carbonate platform environments, where rudists proliferated and resulted in one of the main carbonate producers.

The shallow character of these carbonate platform successions, together with the depositional interruptions linked to high and low frequency sea level falls, facilitated intense post-sedimentary processes, mainly dissolution and dolomitization, which caused poor preservation conditions for fossils, thus making their taxonomic identification difficult.

Nevertheless, as rudists are considered significant biostratigraphic markers in shallow-water carbonate platform successions of the Peri-Tethys continental areas, with a reasonably high resolution, it seems appropriate to carry out a revision of all these rudists, incorporating those recently discovered and not yet described.

The aim of this paper is, thus, to portray and describe in detail the Upper Cretaceous rudist fauna of Central Spain, within the Central Iberian Basin sequence stratigraphy framework, according to the most recent interpretations. Because of differences in preservation, some rudist assemblages could be investigated in more detail than others; those of the fourth assemblage could not even be identified. The knowledge of the shell characters of some taxa, and of their intraspecific variability has been improved. The

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positioning of the rudist assemblages within the depositional framework of high and low frequency, and the correlation with ammonite biozones, increased their taxonomic, biostratigraphic, and palaeobiogeographic significance.

2. Geological setting and stratigraphy

The Iberian Basin, nowadays Iberian Range, was a narrow and relatively shallow basin within the Iberian Microplate that, with a NW—SE trend, connected the Proto-Atlantic, at N and NW, with the Tethys, at SE, during the Mesozoic (Fig. 1). Following an Early Cretaceous rifting phase, a thermal subsidence phase took place for much of the Late Cretaceous (García et al., 2004). This phase of tectonic calm, together with the epi-continental character of the basin, its inter-tropical location (below 35° N latitude), and a global sea-level rise (Haq, 2014), favoured a predominantly eustatic pattern of basin in-filling, with development of successive carbonate platforms, open to the Tethys, to the Proto-Atlantic, or to both, depending on the Microplate swaying. Benthic communities flourished in these carbonate platforms, with rudists being one of the main carbonate producers, as it is common in most epi-continental areas of the Tethys Realm (Philip, 2003).

The sedimentary succession under study is reasonably well known. Formal lithostratigraphic units were defined by Floquet et al. (1982) and Vilas et al. (1982), and later revised by Gil et al. (2004). As are also, the depositional stacking pattern of low- and high-frequency eustatic sequences, and the stratigraphic architecture and lithostratigraphic framework of the main depositional episodes (Floquet, 1998; Segura et al., 2002; García et al., 2004; Gil et al., 2004, 2006; García-Hidalgo et al., 2007). For some intervals, high-frequency sequences of orbital origin, or astronomic-cycles in the sense of Strasser et al. (2006), have been identified (Gil et al., 2009a).

The rudist-bearing stratigraphic succession type here studied encompasses part of two, high amplitude eustatic megacycles of allocyclic origin (Fig. 2), globally recognized (Hardenbol et al., 1998; Haq, 2014; among others). The succession starts with outer platform facies composed of nodular marlstones rich in ammonites, echinoderms, bivalves, and gastropods (Picofrentes Formation in central areas of the basin, and its lateral equivalent Casa Medina Formation at southeastern end), which overlies inner carbonate platform facies (Villa de Ves Formation), showing a retrogradational trend that culminates with the eustatic maximum

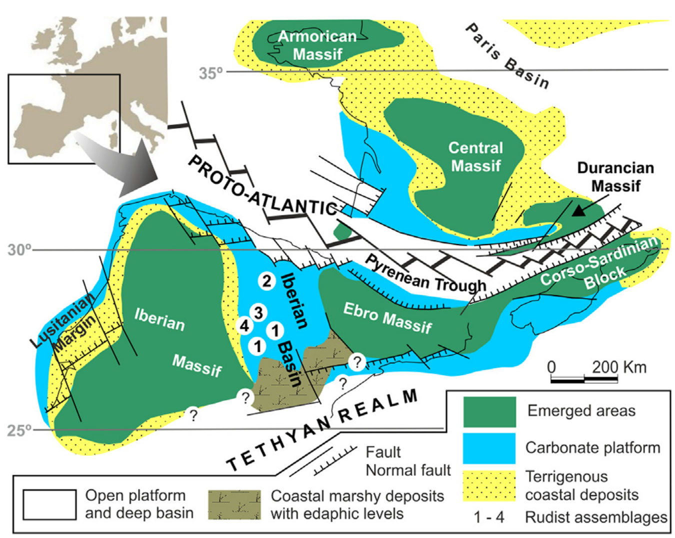

Fig. 1. Palaeogeographical scheme of the Iberian Plate during Late Cretaceous, showing the location of the recognized rudist assemblages. Based on Floquet and Hennuy (2001) and modified from García-Hidalgo et al. (2012).

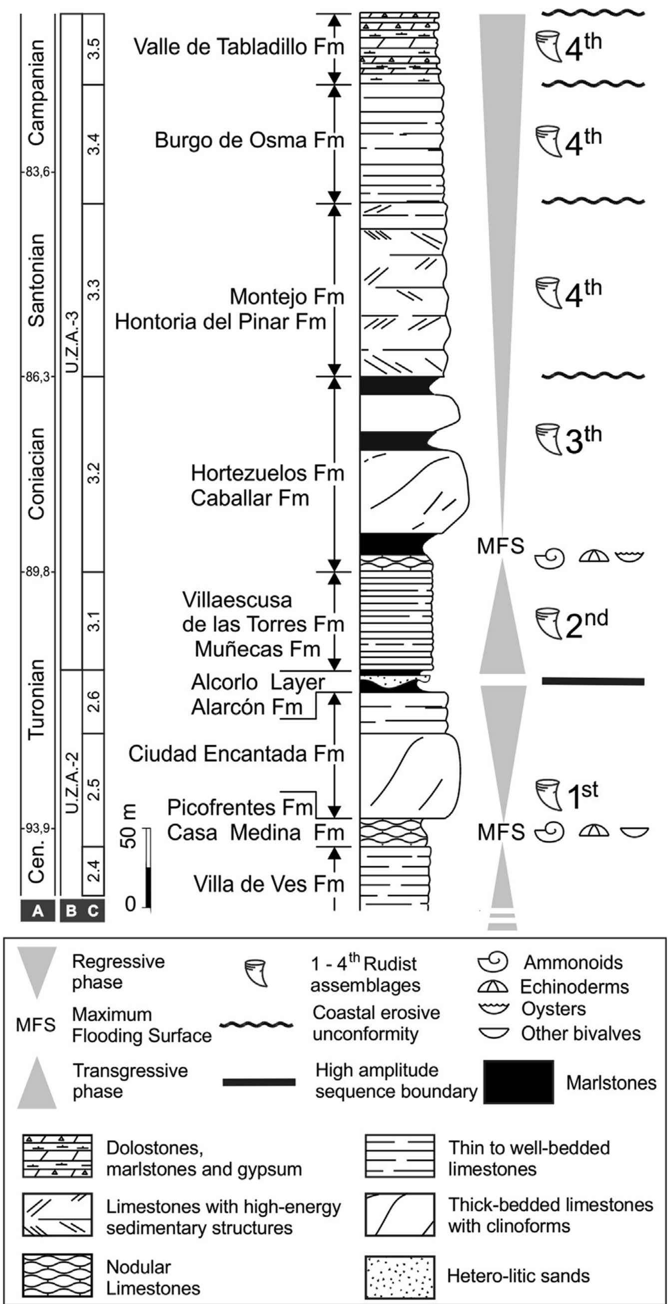

Fig. 2. Synthetic stratigraphical succession, lithostratigraphic framework, high amplitude depositional trends, and stratigraphic location of the recognized rudist assemblages. Chronostratigraphic and low frequency depositional framework is based on Gil et al. (2004); A) Stages; B) 2nd order depositional megasequences; C) 3rd order sequences. Age (Ma) is after Gradstein et al. (2020).

peak of the lower Turonian. The succession continues with a limestones and dolostones inner platform unit (Ciudad Encantada Formation), prograding North-westwards over the underlying marlstones and showing large clino-forms, shallowing-upwards trend, and culminating in a guide horizon of green marlstones of marshy environments with edaphic levels (Alcorlo Layer). This layer increases its thickness and diachrony South-eastwards (Alarcón Formation) while at NE shows discontinuous intercalations of hetero-lithic sandstones representing the progradation of the siliciclastic coastal facies belt towards the basin (Gil et al., 2004). This progradation indicates a relevant sedimentary break in the Upper Cretaceous succession at the central sector of the Iberian Basin that has been correlated with the globally recognized 2nd order minimum eustatic peak of the middle Turonian. Above, a successive inner carbonate platform (Villaescusa de las Torres and Muñecas formations), open to the Proto-Atlantic (NW), indicates the beginning of the second eustatic megacycle (2nd order), and reaching its maximum eustatic peak in the fossiliferous nodular marlstones of the Hortezuelos Formation. Its ammonite association allows the correlation of this marly lithosome with a second eustatic peak in the Coniacian (Segura et al., 2014). The regressive phase of this eustatic megacycle is composed of successive inner carbonate platforms, represented by the upper lithosome of the Hortezuelos Formation and the Hontoria del Pinar, Burgo de Osma and Valle de Tabladillo formations (Gil et al., 2004), showing a shallowing upwards trend. On top, the development of a thick detrital and evaporitic succession reflects the definitive installation of continental environments in the central sector of the Iberian Basin and the progradation of the coastline towards more northern areas of the basin (Floquet, 1998).

3. Material and methods

3.1. Localities

The rudists for this study have been collected at several fossil localities (Fig. 3, and Supplemental material 1). Some of these localities were discovered during field work for PhD thesis of regional character on the Upper Cretaceous successions of the Iberian Basin (Alonso, 1981; Fernández-Calvo, 1982; Segura, 1982; Floquet, 1991). Other, came across more recently during stratigraphical and sequential analysis research on the basin (Gil and García, 1996; Gil et al., 2010). Some of the recovered rudists have been the subject of special taxonomic publications (Gil et al., 2002, 2009b) or have been treated, together with other fossils, in the palaeontological section of papers on local stratigraphic successions (Berrocal-Casero et al., 2013; Barroso-Barcenilla et al., 2017) or on low frequency depositional events (García-Hidalgo et al., 2012).

3.2. Methods

The study of the fossils, around 760 rudist specimens preserved in the Palaeontological Collections of the *Universitat Autònoma de Barcelona* (PUAB), followed the standard method: cleaning and registering; sections, acetate peels, and thin sections; drawings and photographs, and, also, anaglyphs for stereoscopic view of selected specimens. Original type material was used for comparison, when available.

4. Rudist assemblages

Considering the geographic location of the outcrops and their stratigraphic position, four rudist assemblages may be differentiated (Fig. 3, Table 1).

4.1. First rudist assemblage

This rudist assemblage has been recognized in central areas of the Iberian Basin (Torremocha del Campo, Carabias, Santamera, Tamajón, Modamio), but also in its southern coastal margin (La Alberca de Záncara). The former in the lower middle part of the Picofrentes Formation, where rudists are soft matrix supported and may be recovered single. The latter in the Casa Medina Formation, the lateral (south-eastwards) equivalent of the Picofrentes Formation, where rudists form segment and cluster reefs, and are affected by advanced silicification processes (Fernández-Calvo, 1982). Rudists reported by Floquet (1991) in areas more towards NE (Abejar, Monterde, Peñalcázar; Segura de los Baños) and towards N (Peña Castro, Rebolledo de Traspeña) may be correlated with this assemblage.

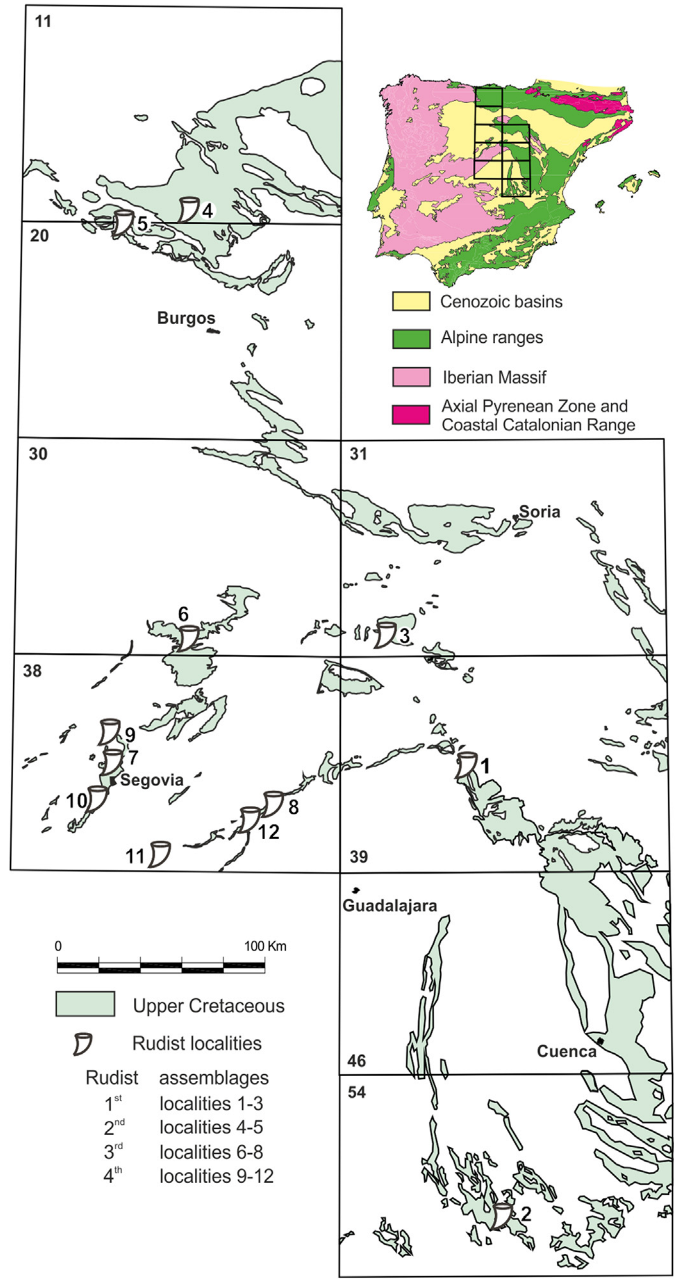

Fig. 3. Location of rudist sites and assemblages. Gridding corresponds to sheets of the 1:200,000 Spanish Geological Map: 1.- (41°04′39″N; 02°43′24″W), Torremocha del Campo, Carabias, Santamera, Tamajón, and Muriel; 2.- (39°30′04″N; 02°28′44″W), La Alberca de Záncara; 3.- (41°22′09″N; 02°59′01″W), Modamio; 4.- (42°49′08″N; 03°45′58″W), Quintanilla-Escalada; 5.- (42°40′45″N; 04°04′05″W), Humada-La Riba de Valdelucio, and Hoyos del Tozo; 6.- (41°23′47″N; 03°50′54″W), Castroserracín, Castrojimeno, Castro de Fuentidueña, Tejares, and Fuentidueña; 7.- La Lastrilla; 8.- (40°50′45″N; 03°31′43″W), Barranco de las Cuevas and Barranco del Mortero; 9.- (41°10′02″N; 03°51′11″W), Pajares de Pedraza and Lastras de Cuéllar; 10.- (40°56′17″N; 04°08′33″W), Valle de Tejadilla and Ituero y Lama; 11.- (40°44′36″N; 03°45′13″W), Soto del Real; 12.- (40°50′15″N; 03°32′27″W), Torrelaguna.

4.2. Second rudist assemblage

This assemblage is formed by up to four rudist beds recognized in the northernmost part of the Iberian Basin (Humada-La Riba de Valdelucio, Hoyos del Tozo, Quintanilla-Escalada) within the

Table 1
Recognized rudist assemblages.

Rudist taxa identified in the Iberian Basin
First rudist assemblage
Radiolites lusitanicus (Bayle, 1857)
Durania arnaudi (Choffat, 1891)
Second rudist assemblage
Hippurites resectus Defrance, 1821
Hippurites vasseuri Douvillé, 1894
Vaccinites rousseli (Douvillé, 1894)
Radiolites lusitanicus (Bayle, 1857)
Radiolites radiosus d'Orbigny, 1847
Hoyosites tozoi gen. et sp. nov.
Third rudist assemblage
Hippurites incisus Douvillé, 1895
Vaccinites giganteus (d'Hombres-Firmas, 1838)
Vaccinites moulinsi (d'Hombres-Firmas, 1838)
Vaccinites rousseli (Douvillé, 1894)
"*Radiolites*" *douvillei* Toucas, 1908
Radiolites sauvagesi (d'Hombres-Firmas, 1838)
Biradiolites canaliculatus d'Orbigny, 1850
Bournonia gardonica (Toucas, 1907)
Praeradiolites ponsianus (d'Archiac, 1837)
Praeradiolites requieni (d'Hombres-Firmas, 1838)
Apricardia sp.
Fourth rudist assemblage
Hippurites? sp.
Radiolitidae indet.

Villaescusa de las Torres Formation, where rudists form close cluster reefs and segment reefs. Several rudist occurrences reported by Floquet (1991) in neighbouring areas may be attributed to this assemblage.

4.3. Third rudist assemblage

This assemblage has been widely recognized in the SW coastal margin areas of the Iberian Basin (Barranco de las Cuevas, Barranco del Mortero, Castroserracín and surrounding areas, Castrojimeno, Castro de Fuentidueña, Tejares, Fuentidueña) in the Hortezuelos Formation, and locally, in the Caballar Formation (La Lastrilla). A large taxonomical diversity of rudists is found, as single specimens in marlstones, or forming mono- to pauci-specific open cluster to close cluster/frame reefs in limestones. A detailed description of the rudist facies succession in the Hortezuelos Formation at Castrojimeno is given in Gil et al. (2009b).

4.4. Fourth rudist assemblage

Several rudist localities above the third rudist assemblage, most probably with different taxa and age, have been grouped as a fourth assemblage. This assemblage has been recognized in the SW coastal margin of the Iberian Basin (Pajares de Pedraza, Lastras de Cuéllar, Ituero y Lama, Valle de Tejadilla, Soto del Real, Torrelaguna) in different stratigraphic levels of the Montejo, Burgo de Osma, and Valle de Tabladillo formations. Because of intense diagenetic processes, the outer shell layer of the rudists was dissolved and only inner moulds are preserved. Thus, the taxonomic determination cannot go beyond than hippuritids (*Hippurites*?) and radiolitids with and without a ligament ridge (*Radiolites*? and *Biradiolites*?).

5. Systematic palaeontology

The rudist families recognised in Bouchet et al. (2010) and Carter et al. (2011) are the supra-generic taxa used. The synonymy list for each taxon only includes the original reference, the taxonomic emendations and/or discussions, those discussed in the text, and previous references in the study area. When appropriate, reference to taxonomic data bases or extensive monographs is also given. Several specimens of each species are figured to illustrate their intraspecific variability. Species of Hippuritidae are figured as drawings of the transverse cross section of right valves (detail of thin sections is included when necessary), and photos of left valves, or the external view of right valves when relevant. All transverse cross sections are figured in standard orientation, i.e., in adapical view and with the dorsal side up, unless indicated. In cross-sectional drawings, the outer shell layer is represented in black, the inner shell layer of the right valve in pale gray, and the inner shell layer of the left valve in dark gray. Species of Radiolitidae are figured as acetate peels of the transverse section of right valves or, a few, as scanner images (also detail of thin sections when convenient), and photos of the external view of both valves; anaglyphs for stereoscopic view of some species are provided as 'Supplemental material'. Riding (2002) structural categories of organic reefs are used to describe the mode of occurrence of rudists in the field. Abbreviations in figures: AD = antero-dorsal cavity; AM = anterior myophore; AT = anterior tooth; CT = central tooth; DC = dorsal cavity, LV = left valve; MC = main body cavity; PB = posterior radial band; PM = posterior myophore; PMP = posterior myophore plate; PT = posterior tooth; RV = right valve; VB = ventral radial band.

Family: Hippuritidae Gray, 1848

Genus *Hippurites* Lamarck, 1801
Type species: *Hippurites bioculata* Lamarck, 1801 from the upper Santonian/lower Campanian of Montagne des Cornes (Aude), France, by monotypy.

Hippurites incisus Douvillé, 1895
Fig. 4A-J

1895 *Hippurites resectus* var. *incisa*; Douvillé, p. 168, pl. 26, figs. 4, 4a, 5, 6, 6a, 7.
1903 *Orbignya incisa* (Douvillé); Toucas, p. 22, text-fig. 33.
2009b *Hippurites incisus* Douvillé; Gil et al., p. 533, figs. 4b, 5a,b, 6a,b, 7a.
2012 *Hippurites incisus* Douvillé; García-Hidalgo et al., p. 275, fig. 9G.
2015 *Hippurites incisus* Douvillé; Troya, p. 99, figs. 48-56. [with complete synonymy list and a taxonomic discussion]

Description. All the available specimens, mostly right valves, have been recovered from close cluster/frame reefs, monospecific or as minor components together with other rudists. The diameter of larger specimens measures 30 mm. The external surface bears fine rounded ribs, and the radial furrows corresponding to the three inner folds may be gently market. The transverse cross section shows the three inner folds: the ligament ridge, triangular, with a truncated point; the first pillar, quadrate to short rectangular; and the second pillar, long rectangular. The three inner folds occupy approximately 1/3 of the shell contour. The myocardinal apparatus has not been observed. The pores of the left valve are rounded or lineal, short, and irregular.
Remarks. First described by Douvillé (1895) as a variety of *H. resectus* from the Coniacian of Espluga de Serra (southern Pyrenees), was considered as a species by Toucas (1903). The specimens from Espluga de Serra have folded growth lamellae, producing acute ribs on the right valve surface, and pustules on the left valve.
Third rudist assemblage. Upper part of the Hortezuelos Formation, upper Coniacian, at Castrojimeno and Castroserracín, and Caballar Formation, upper Coniacian, at La Lastrilla.

Hippurites resectus Defrance, 1821
Fig. 4K-L

Fig. 4. A-J. *Hippurites incisus* Douvillé, 1895. A, B. Left valve and detail of the pores, respectively, PUAB 74430. C-J. Transverse sections of right valves from cluster reefs, PUAB 74433, PUAB 74432, PUAB 78574, PUAB 74431, PUAB 43739 (group of specimens), PUAB 78576, PUAB 78577, PUAB 78575, Castrojimeno (G), Castroserracín (A-F, H-J). Hortezuelos

1821 *Hippurites resecta*; Defrance, p. 196.
1892 *Hippurites resectus* Defrance; Douvillé, p. 54, text-figs. 37, 38; pl. 5, figs. 9-12.
1999 *Hippurites resectus* Defrance; Simonpietri, p. 113, pl. 30, figs. 1-24, pl. 36, figs. 1-9. [with complete synonymy list and a taxonomic discussion]
2015 *Hippurites resectus* Defrance; Troya, p. 88, figs. 42-47. [with complete synonymy list and a taxonomic discussion]

Description. Most of the available specimens, variably crashed right valves, have been recovered from a segment reef and have been studied on transverse sections. Few transverse sections of specimens were also observed and photographed, up section, as minor components on cluster reefs of other species. The estimated diameter measures 20–30 mm; the external surface bears fine rounded ribs, and the radial furrows corresponding to the three inner folds may be gently marked. The three inner folds occupy approximately 1/3 of the shell contour and are equidistant each other: the ligament ridge is triangular, with a wide base and a truncated tip; the first pillar is short and robust, wide triangular to quadrate; the second pillar is rectangular. The myo-cardinal apparatus has not been observed.
Remarks. This species was first described from the upper Turonian of St-Paul-Trois-Châteaux (Drôme), France, and has subsequently been widely reported from numerous other Turonian areas, although a few Coniacian reports are also registered (Steuber, 2002). Toucas (1903) considered this species as being the origin of two Coniacian species, *Hippurites socialis* Douvillé, 1890 and *H. incisus* Douvillé, 1895, each one representing a different successful evolutionary lineage, *H. organisans* and *H. canaliculatus* species groups, respectively, in Toucas (1903). The first group species loose the truncation of the ligament ridge in the Coniacian, while the second maintained this character as late as the Santonian.
Second rudist assemblage. First rudist bed, first parasequence set and, as minor component, also the fifth of the Villaescusa de las Torres Formation, upper Turonian at Hoyos del Tozo section.

Hippurites vasseuri Douvillé, 1894
Fig. 4M-Q

1894 *Hippurites Vasseuri* Douvillé, p. 120, pl. 18, fig. 5.
1991 *Hippurites vasseuri* Douvillé; Floquet, p. 784.
2015 *Hippurites vasseuri* Douvillé; Troya, p. 109, fig. 57.

Description. The specimens have been studied on transverse sections of right valves included in limestone, from a bed corresponding to a close cluster/frame reef (thicket of closely packed right valves, with shell walls attached each other and, locally, small space in between filled with matrix). The diameter measures 20–25 mm and specimens may be up to 800 mm long; the growth lamellae are deeply (more than 45°) inwards inclined and radially folded; as observed on isolated shells, the outer surface bears fine rounded ribs, interrupted by conspicuous frequent growth interruptions, and three furrows in correspondence with the three inner folds. These last occupy somewhat more than 1/3 of the shell contour and are approximately equidistant each other; the ligament ridge is short, triangular, with a wide base and a truncated tip; both first pillar and second pillar, are long and clearly pinched at their base. One of the sections shows the position of the myo-cardinal apparatus: the posterior myophore is embedded behind the first pillar; a small anterior-dorsal cavity is present.
Remarks. Douvillé (1894) created *Hippurites vasseuri* based on specimens from Martigues, France, appearing on beds below those containing the same rudist fauna previously described by d'Hombres-Firmas (1838) from Gatigues (*Vaccinites giganteus*, *Vacinites moulinsi*, *Radiolites sauvagesi*, and *Praeradiolites requieni*), considered Coniacian. Toucas (1903) included these specimens, together with those from Espluga de Serra, Spain, named *Hippurites resectus* var. *incisa* by Douvillé (1895), in *Orbignya incisa* (Douvillé). Consequently, many authors followed Toucas (1903) in considering *H. incisus* and *H. vasseuri* as synonyms, but noticing (Kühn, 1932) that the specific name *H. vasseuri* Douvillé, 1894 should have priority over *H. incisus* Douvillé, 1895, contrarily as considered by Toucas (1903). This created much confusion in taxonomy, not only because it is not easy to discern to which species are authors really referring in literature when using any of both names but mainly because *incisus* and *vasseuri* are clearly different species (see Troya, 2015), appearing in different stratigraphic horizons and, thus, being of different age.
Second rudist assemblage. Fifth parasequence set in the upper part of Villaescusa de las Torres Formation, upper Turonian, at Hoyos del Tozo section.

***Hippurites*?** sp.
Fig. 4R-V

Description. Several cylindrical inner moulds, unambiguously attributed to hippuritids due to the presence of three longitudinal furrows, one corresponding to a short triangular ligament ridge with a rounded tip, and the other two to sub-equal quadrate pillars, have been identified as *Hippurites*? sp. The three furrows occupy nearly one third of the circumference. *Hippurites matheroni* and *H. socialis* may be possible candidates.
Fourth rudist assemblage. Valle de Tejadilla and Ituero y Lama, Valle de Tabladillo Formation. Santonian–?Campanian.

Genus *Vaccinites* Fischer, 1887
Type species: *Hippurites cornuvaccinum* Bronn, 1832 from the Santonian–Campanian of Untersberg, Austria, by original designation.

Vaccinites giganteus (d'Hombres-Firmas, 1838)
Fig. 5A-I

1838 *Hippurites Gigantea*; d'Hombres-Firmas, p. 198, pl. 4, fig. 1.
1891 *Hippurites giganteus* d'Hombres-Firmas; Douvillé, p. 19, text-figs. 7-8, pl. 3, figs. 4-6.
1904 *Vaccinites giganteus* (d'Hombres-Firmas); Toucas, p. 93, text-figs. 102, 148-149, pl.13, fig.4.
1999 *Vaccinites giganteus* (d'Hombres Firmas); Simonpietri, p. 37, pl. 4, figs. 4-6; pl. 6, figs. 7-12; pl. 7, fig. 1-11; pl. 9, figs. 6, 12, 15. [with complete synonymy list and a taxonomic discussion]
2012 *Vaccinites giganteus* (d'Hombres Firmas); García-Hidalgo et al., p. 277, fig. 9I.
2015 *Pseudovaccinites giganteus* (d'Hombres Firmas); Troya, p. 158, figs. 83-91. [with complete synonymy list and a taxonomic discussion]

Description. All available specimens are single, from open cluster or segment reefs, several among them with the left valve reasonably well preserved. Diameter may attend 80–90 mm, and cylindrical shells up to 250 mm long are not rare. The outer surface of the right valve bears fine rounded ribs and furrows; the location of the ligament ridge is indicated by a wider furrow. The outer shell layer

Formation. Upper Coniacian. K, L. *Hippurites resectus* Defrance, 1821. Transverse section of right valves, PUAB 81332a, from a radiolitid close cluster/frame reef, Quintanilla-Escalada, PUAB 81423, crashed specimens from a segment reef, Hoyos del Tozo. Villaescusa de las Torres Formation. Upper Turonian. M-Q. *Hippurites vasseuri* Douvillé, 1894. Outer surface of a right valve and transverse sections of right valves from a close cluster reef, PUAB 79210, PUAB 81421, PUAB 81420, PUAB 81419, PUAB 81422, Hoyos del Tozo. Villaescusa de las Torres Formation. Upper Turonian. R-V. *Hippurites*? sp. Internal mould fragments, PUAB 79154, PUAB 79153, PUAB 79155, PUAB 79156, PUAB 79151, Valle de Tejadilla. Valle de Tabladillo Formation. Santonian–?Campanian. Scale bars measure 10 mm.

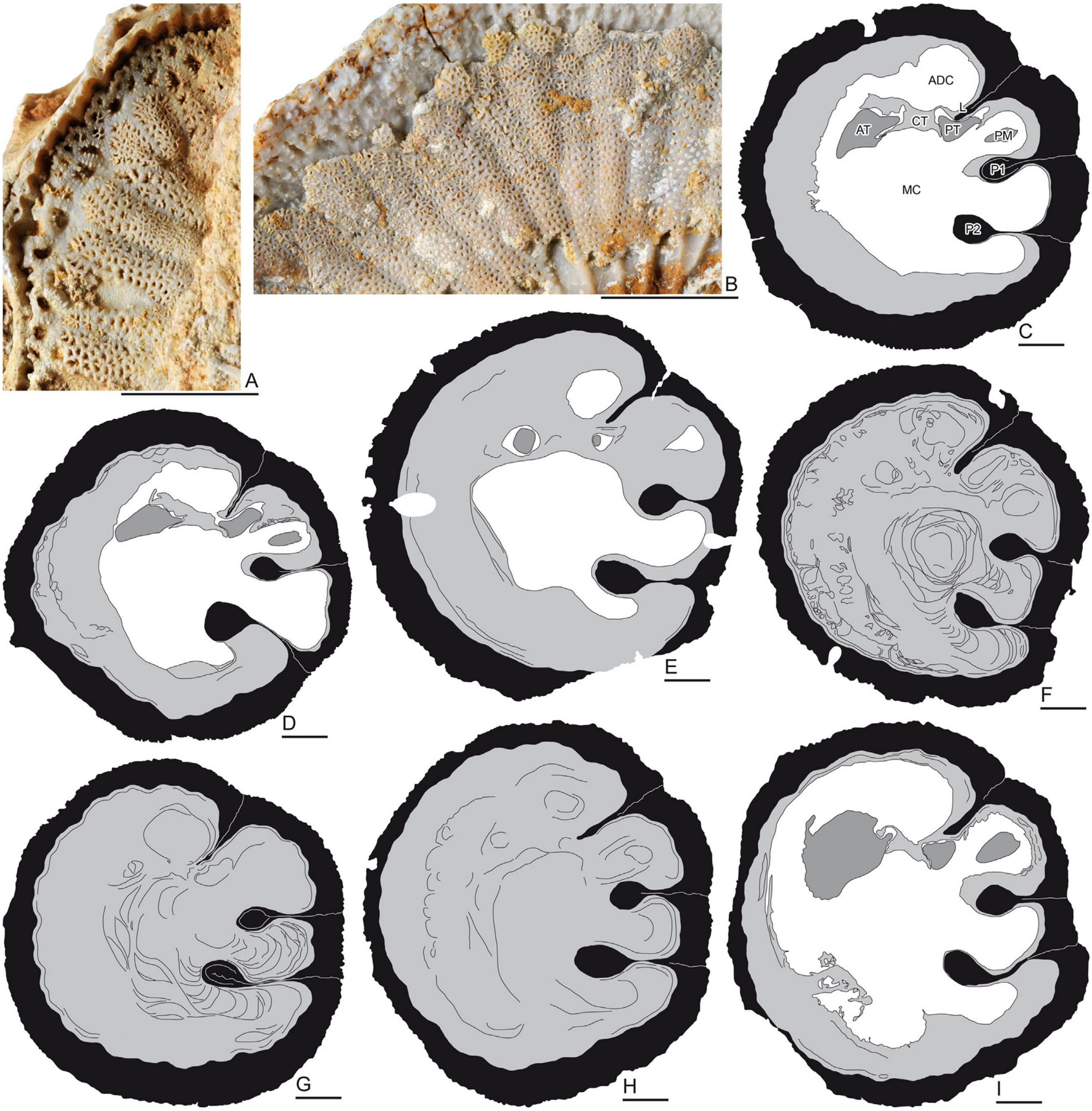

Fig. 5. *Vaccinites giganteus* (d'Hombres-Firmas, 1838). A, B. Details of left valve pores, PUAB 74412, PUAB 74410. C-I. Transverse sections of right valves, PUAB 74419, PUAB 74410, PUAB 74379, PUAB 44445, PUAB 74413, PUAB 44446, PUAB 74411. Castroserracín (A-D, G, I), Castrojimeno (E, F, H). Hortezuelos Formation. Upper Coniacian. Scale bars measure 10 mm.

measures around 5 mm in thickness and its inner margin is somewhat undulate. The three pillars occupy around 1/5 of the shell contour, the distance between the ligament ridge and the first pillar is wider than that between the first and second pillar. The ligament ridge is lamellar and has a triangular base and a clearly truncated distal end. The first pillar, long as the ligament ridge, is pinched in young specimens and clearly pedunculate in adults. The second pillar is the longest, has a rounded or elliptical head and a long fine peduncle. The angle between the ligament ridge and the myo-cardinal apparatus is comprised between 40 and 45°. The posterior myophore is robust, embedded between the ligament ridge and the first pillar, and triangular in section, with the base outwards and a vertex inward. The posterior tooth is located close to the distal end of the ligament ridge and the anterior tooth far anteriorly. The left valve is nearly flat, canals are 2–3 mm wide and the walls between them 1 mm thick. The pore layer is convex above each of the canals and the small pores are finely reticulate.

Remarks. This species has been reported previously from the Coniacian of Gatigues (Gard), its type locality, Noyères (Vaucluse), Nyons (Drôme), Martigues (Bouches du Rhône), Le Beausset (Var), and Bugarach (Aude) in France (Toucas, 1904), Espluga de Serra and other Pyrenean localities in Catalonia, Spain (Pons, 1982), and many other localities in the Adriatic area (see references in Steuber, 2002). The Coniacian age of the Gatigues rudist fauna, widely accepted since Toucas (1904, 1908), was confirmed by Sornay (1950) and Philip (1970).

Third rudist assemblage. Upper part of the Hortezuelos Formation, upper Coniacian, at Castrojimeno and Castroserracín.

Vaccinites moulinsi (d'Hombres-Firmas, 1838)
Fig. 6A-L

1838 *Hipp. Moulinsii* d'Hombres-Firmas, p. 199, pl. 4, fig. 6.
1891 *Hippurites Moulinsi* d'Hombres-Firmas; Douvillé, p. 17, pl. 3, figs. 1, 2 (non 3 = *V. beaussetensis*)
1895 *Hippurites praemoulinsi* Douvillé, p. 156, pl. 22, fig. 5 (non 6 = *V. beaussetensis*)
non 1895 *Hippurites Moulinsi* d'Hombres Firmas; Douvillé: 158, pl. 22, fig. 7 [= *V. beaussetensis*]
1999 *Vaccinites moulinsi* (d'Hombres Firmas); Simonpietri, p. 75, pl. 20, figs. 9-11; pl. 21, figs. 7-12; pl. 22, figs. 1-9. [with a taxonomic discussion]
2002 *Vaccinites moulinsi* (d'Hombres-Firmas); Steuber. [with complete synonymy list]
2012 *Vaccinites moulinsi* (d'Hombres-Firmas); García-Hidalgo et al., p. 277, fig. 9H.
2014 *Vaccinites moulinsi* (d'Hombres-Firmas); Pons et al., p. 69, fig. 22.1-6. [with a taxonomic discussion]

Description. All available specimens are single, from open/close cluster reefs, with both valves conjoined. Diameter measures around 60 mm, many specimens right valves are conical, while other continued growing cylindrically up to 150 mm long. The outer surface bears rounded ribs separated by thin furrows, disrupted by coarse transverse growth lines. Three manifest radial furrows indicate the location of the internal folds. The outer shell layer is around 7 mm thick, and its inner margin is smooth. The three pillars occupy almost 1/4 of the shell contour and are equidistant each other. The ligament ridge is triangular, with a wide base and a clearly truncated distal end. The first pillar is short, quadrangular to sub triangular. The second pillar, rectangular, is somewhat longer than the ligament ridge and may be slightly pinched at its base. The angle between the ligament ridge and the myo-cardinal apparatus measures 35°. The posterior myophore is embedded between the ligament ridge and the first pillar, closer to this last, and sub-elliptical in section. The posterior tooth is close to the distal part of the ligament ridge, and the anterior tooth far anteriorly, limiting the inner margin of the anterior-dorsal cavity. The left valve is nearly flat, canals are 2 mm wide and the walls between them 0.5 mm thick. The pores are small and fainty reticulated.

Remarks. This species was first reported from the Coniacian of Gatigues (Gard), France. Until now, it has only been reported from southern France and northern Spain. Some misinterpretation of the tip of the ligament ridge lead Douvillé (1895) to propose a new species, *H. praemoulinsi*, which was later considered invalid by Toucas (1904).

Third rudist assemblage. Upper part of the Hortezuelos Formation, upper Coniacian, at Castroserracín.

Vaccinites rousseli (Douvillé, 1894)
Fig. 7A-B

1894 *Hippurites Rousseli* Douvillé, p. 117, pl. 19, fig. 1, pl. 20, figs. 1-3.
1897 *Hippurites Rousseli* Douvillé; Douvillé, p. 206, pl. 34, fig. 6.
1904 *Hippurites Rousseli* Douvillé; Toucas, p. 78, text-figs. 118-120, pl. 10, figs. 1, 1a, 2.
1999 *Vaccinites rousseli* (d'Hombres Firmas); Simonpietri, p. 75, pl. 20, figs. 7, 9-11; pl. 21, figs. 7-12; pl. 22, figs. 1-9. [with a taxonomic discussion]
2002 *Hippurites rousseli* (Douvillé); Steuber. [with complete synonymy list]
2015 *Pseudovaccinites rousseli* (Douvillé); Troya, 173, figs. 93, 94. [with a taxonomic discussion]

Description. The few available specimens were recovered from radiolitid close cluster/frame reefs where they are minor components. The transverse section of two right valves, close below the commissure, have been observed, but also part of a poorly preserved left valve. Right valves are short conical, the diameter measures up to 45 mm, and the outer surface bears three radial furrows in correspondence with the three inner folds. These last, occupy about 1/4 of the shell contour. The ligament ridge is wide triangular with clearly truncated tip; the first pillar is short and wide, nearly triangular; the second pillar is rectangular, somewhat turned towards the ligament ridge. The angle between the ligament ridge and de myo-cardinal axis measures around 50°; the posterior tooth and myophore are embedded in the area between the ligament ridge and the first pillar; the anterior-dorsal cavity is quite large. No details may be observed from the left valve.

Remarks. This species was first reported from the upper Turonian of the Martigues at Bugarach (Aude), France and has been recognized in many other Turonian localities of the Mediterranean Tethys areas.

Second rudist assemblage. Fifth parasequence set in the upper part of Villaescusa de las Torres Formation, upper Turonian, at Hoyos del Tozo section.

Family: Radiolitidae d'Orbigny, 1847

Genus *Radiolites* Lamarck, 1801

Type species: *Radiolites angeiodes* Lamarck, 1801 from the upper Santonian of Rennes les Bains, Aude, France, by original designation.

"*Radiolites*" *douvillei* Toucas, 1908.
Fig. 8A-M (+ Supplemental material 2)

1908 *Radiolites Douvillei* Toucas, p. 62, text-fig. 30, pl. 11, fig. 12.
2002 *Radiolites douvillei* Toucas; Steuber. [with complete synonymy list]

Description. All available specimens are single shells, with different preservation, recovered from open cluster reefs. Maximal diameter is comprised between 80 and 100 mm and may reach up to 150 mm in length. Right valve's growth laminae, irregularly grouped in sets, are deeply inwards inclined and radially folded only at its margin, in most of the shell contour. At the outer surface, successive steps of growth laminae set, and irregularly spaced coarse rounded longitudinal ribs are developed. The outer shell layer structure is normal cellular. The radial structures correspond to two large down-and-outward radial folds, producing two strong ribs separated by a narrow inter-band, and two straight or slightly inwards protruding segments at the inner shell margin. The ligament ridge is long, normally with an expanded distal end. The myo-cardinal apparatus is robust and two large dorsal cavities are left between the teeth and the ligament ridge. The left valve is slightly convex with a subcentral apex at its central part and conforming the inclination of the right valve's growth laminae at its margin.

Remarks. Toucas (1908) first reported this species from the Coniacian beds with *Vaccinites moulinsi* and *Radiolites sauvagesi* at Piolenc, Noyères près Bollène (Vaucluse) and Bagnols (Gard), France. The type specimen, from Piolenc, is preserved in the

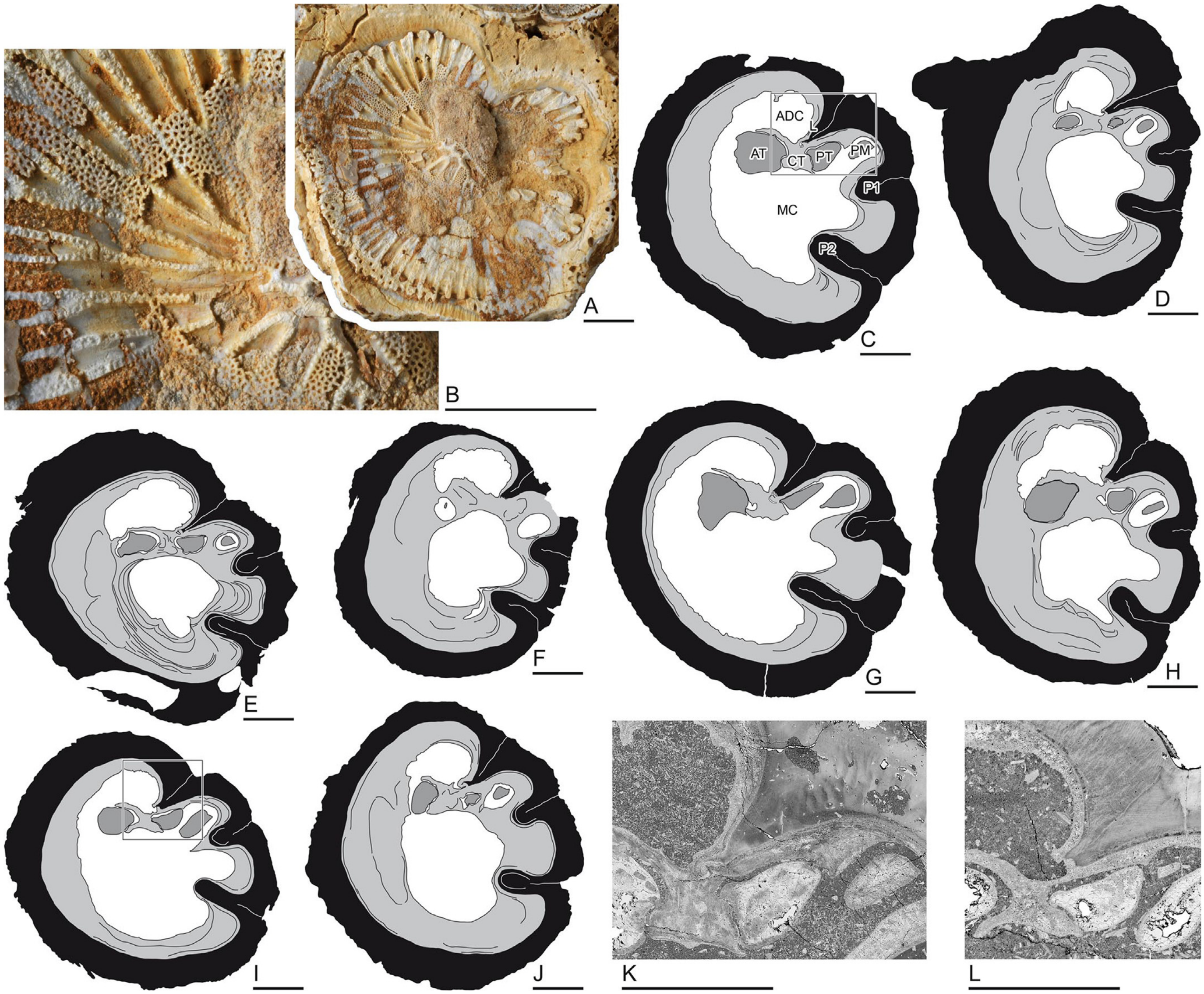

Fig. 6. *Vaccinites moulinsi* (d'Hombres-Firmas, 1838). A, B. Left valve and detail of canals and pores. PUAB 74423. C-J. Transverse sections of right valves, PUAB 74429, PUAB 78544, PUAB 78546, PUAB 74421, PUAB 74427, PUAB 74426, PUAB 74424, PUAB 78543. K, L. Details of ligament ridge as indicated by squares in C and I. Castroserracín. Hortezuelos Formation. Upper Coniacian. Scale bars measure 10 mm.

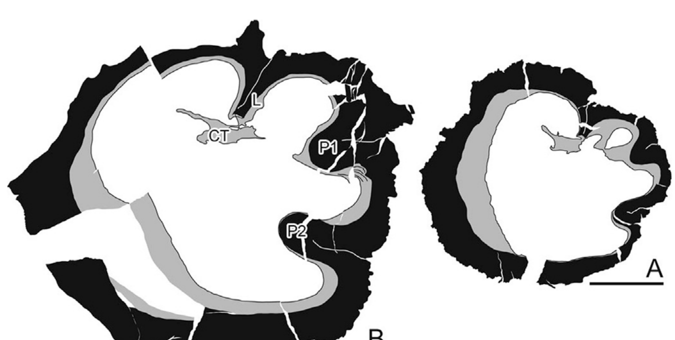

Fig. 7. *Vaccinites rousseli* (Douvillé, 1894). A, B. Transverse section of right valves from a radiolitid close cluster/frame reef, PUAB 79198, PUAB 79199. Hoyos del Tozo. Villaescusa de las Torres Formation. Upper Turonian. Scale bars measure 10 mm.

Collection of the *École supérieure des Mines de Paris*, now in Villeurbanne (Lyon). Although the description of the external aspect of the shell, as well as its comparison with that of *Radiolites lusitanicus*, is accurate, Toucas failed with the identification of the radial structures. These correspond to down-and-outward radial folds (externally ribs) instead of up-and-inward folds (externally furrows) as is considered characteristic of genera *Radiolites* and *Praeradiolites*. The species reminds those of genera *Bournonia* and *Eoradiolites* by the radial structures, but differs in the outer shell layer structure, ligament, and myo-cardinal apparatus. These last characters are more similar with those of genus *Praeradiolites*. Pons et al. (2011) proposed the genus *Paronaites* for the Cenomanian Parona's (1921) species *Radiolites zuffardi*. In this last, the growth laminae are regularly radially folded, the radial structures are two very narrow down-and-outward folds separated by a wide interband with similar ribs as in the rest of the contour, the ligament ridge is small, and the inner marginal groove is much developed,

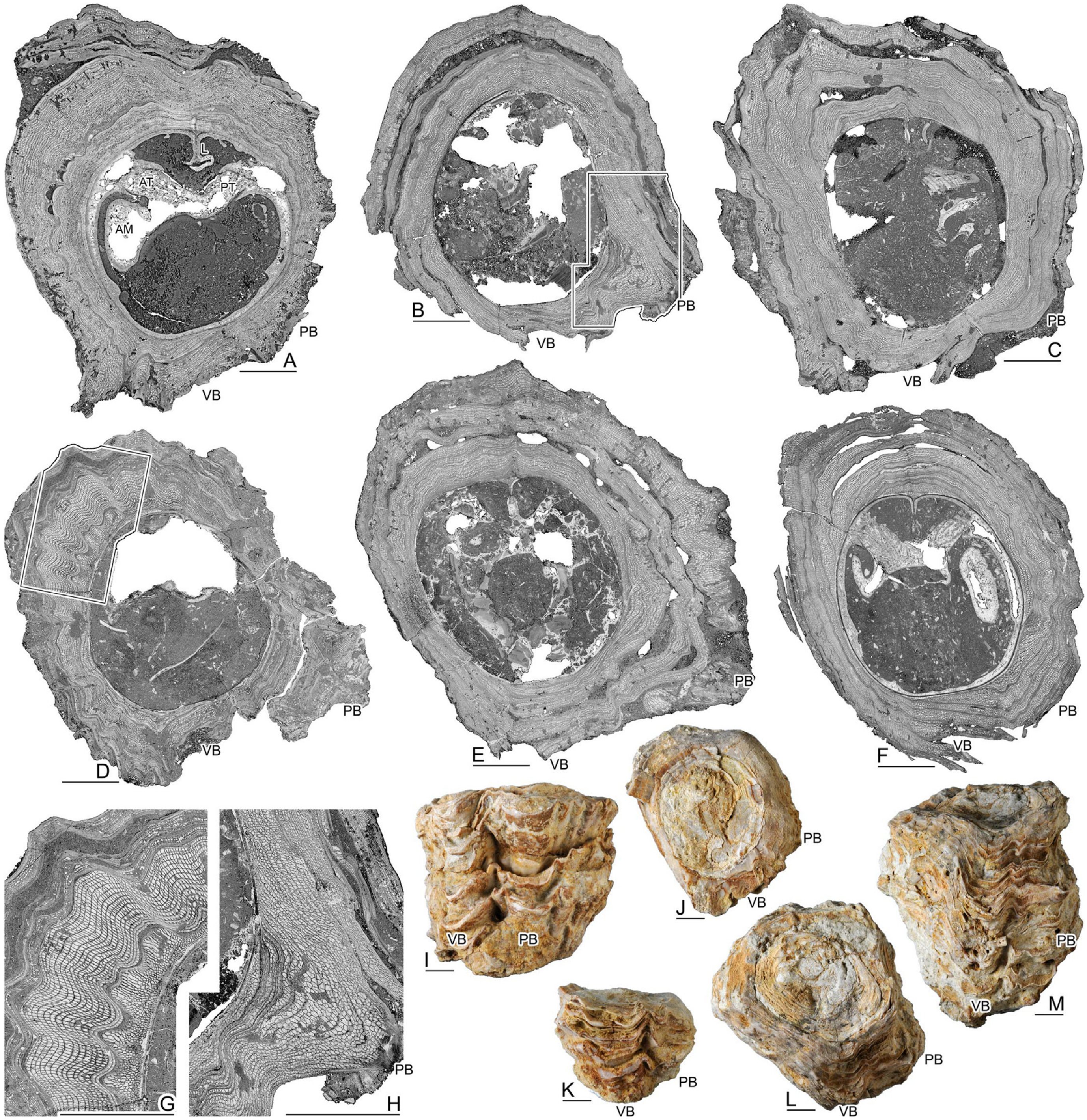

Fig. 8. "*Radiolites*" *douvillei* Toucas, 1908. A-F. Transverse section, acetate peel, close below the commissure of right valves. A. PUAB 74446. B. PUAB 78601. C. PUAB 74448. D. PUAB 78580. E. PUAB 78591. F. PUAB 78585. G, H. Details indicated, respectively, in D and B. I-M. External views (upper and lateral) of bivalve specimens. I. PUAB 74449. J, K. PUAB 78605. L, M. PUAB 78592. Castroserracín. Hortezuelos Formation. Upper Coniacian. Scale bars measure 10 mm.

particularly in coincidence with the radial structures. Similarly, a new genus for "*Radiolites*" *douvillei* would be necessary.

Third rudist assemblage. Upper part of the Hortezuelos Formation, upper Coniacian, at Castroserracín.

Radiolites lusitanicus (Bayle, 1857)
Fig. 9A-G

1857 *Sphaerulites lusitanicus* Bayle, p. 692.
1886 *Sphaerulites lusitanicus* Bayle; Choffat, p. 32, pl. 4, figs. 2-8.
1902 *Sphaerulites lusitanicus* Bayle; Choffat, p. 144, pls. 10, 11.
1908 *Radiolites lusitanicus* (Bayle); Toucas, p. 62, pl. 11, figs. 10, 11, 11a.
1999 *Radiolites lusitanicus* (Bayle); Steuber, p. 95, pl. 15, figs. 1-6, pl. 16, figs. 1-5. [with a taxonomic discussion]
2002 *Radiolites lusitanicus* (Bayle); Steuber. [with complete synonymy list]

Description. Available specimens are single or groups of 2 to 4–5 shells attached each other, extracted from open/close cluster reefs.

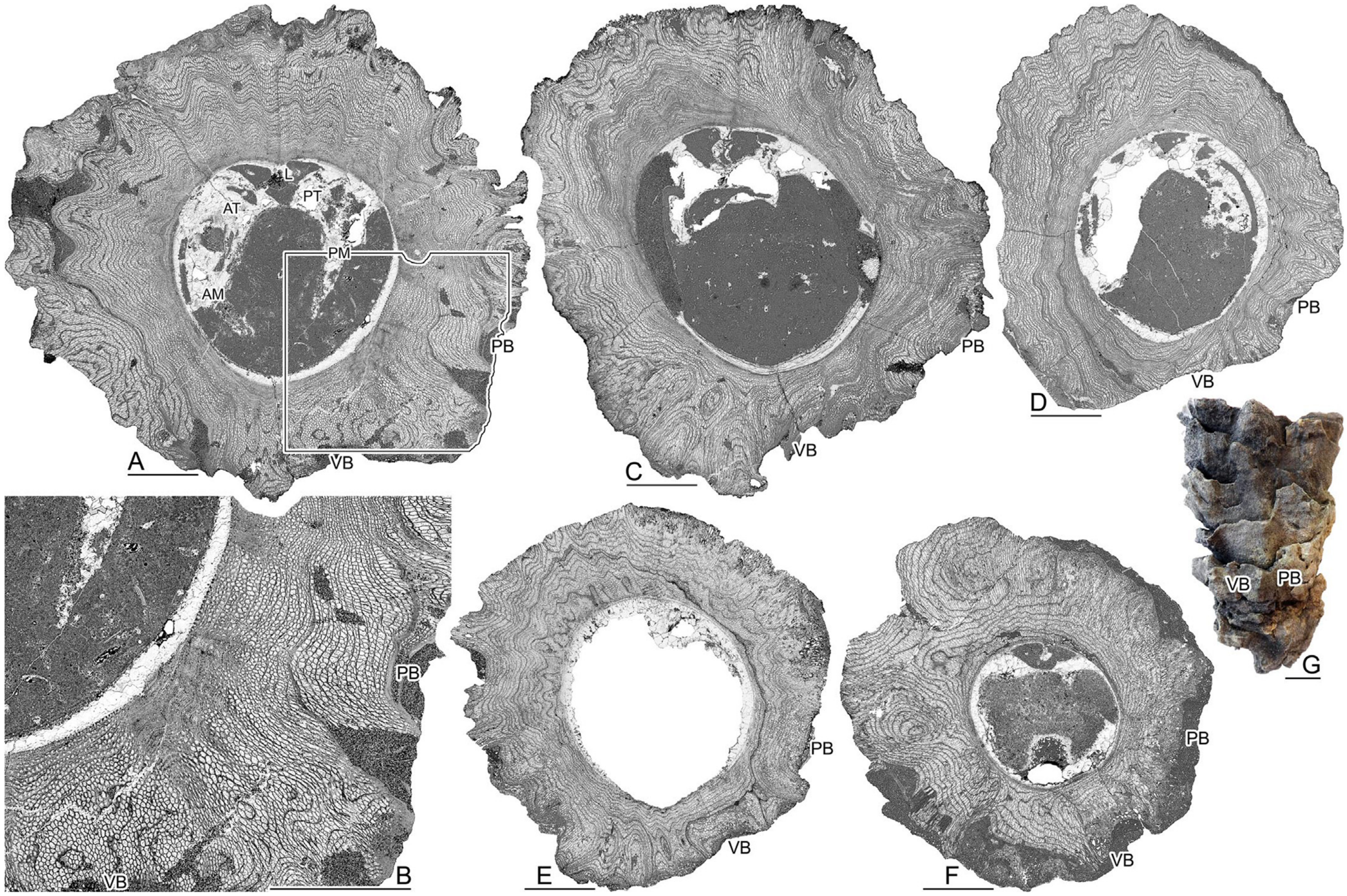

Fig. 9. *Radiolites lusitanicus* (Bayle, 1857). A-F. Transverse section, acetate peel, of right valves and detail as indicated. PUAB 44432, PUAB 44430, PUAB 44442, PUAB 44240, PUAB 44242. G. External view of right valve. PUAB 79192. Humada-La Riba de Valdelucio (A-D, G). Villaescusa de las Torres Formation. Upper Turonian. La Alberca de Záncara (E, F). Casa Medina Formation. Lower Turonian. Scale bars measure 10 mm.

Maximal diameter is comprised between 50 and 80 mm and may reach up to 150 mm in length. Growth laminae are deeply inwards inclined, irregularly grouped in sets, and radially folded at its margin. Thus, the outer shell surface bears irregularly spaced longitudinal ribs. Two wider subequal radial upfolds of the growth laminae form the two radial sinuses, which are separated by a narrower downfold. This last may be subdivided in the adult part of larger shells. A short lamellar ligament ridge, relatively small dorsal cavities at each side, a dorsally located myo-cardinal apparatus, the normal cellular structure of the outer shell layer, the radial folds of the growth lamellae at the margin, and the radial structures are clearly observable in the transverse section of right valves cut close below the commissure. The left valve is slightly convex with a subcentral apex.

Remarks. This species was first described from Alcantara, Portugal, locality attributed either to the Turonian (Toucas, 1908) or to the Cenomanian (Berthou, 1973), and has been widely reported from many other Cenomanian and Turonian localities of the Mediterranean Tethys.

First and second rudist assemblages. Alberca de Záncara, Casa Medina Formation, lower Turonian; Humada-La Riba de Valdelucio, Villaescusa de las Torres Formation, upper Turonian.

Radiolites radiosus **d'Orbigny, 1847**
Fig. 10A-B

1842 *Radiolites radiosus* d'Orbigny, p. 183.
1847 *Radiolites radiosus* d'Orbigny; d'Orbigny, p. 212, pl. 554, figs. 1-3. [non 4-7]
1908 *Radiolites radiosus* d'Orbigny; Toucas, p. 70, text-figs. 41-43, pl. 13, figs. 5-7.
2002 *Radiolites radiosus* d'Orbigny; Steuber. [with complete synonymy list]

Description. An incomplete right valve, minor component from a cluster reef of another radiolitid, allowed observing its transverse cross section and a short interval of the external surface. The growth laminae are horizontal, widely extended, radially folded, and developing two wide subequal up-and-inwards folds separated by a single, also wide, down-and-outwards fold. These folds depict two wide furrows limited by a wide rib, at the outer surface, and two straight segments at the inner margin of the outer shell layer. The outer shell structure is normal cellular. The ligament ridge is long, lamellar, somewhat posteriorly turned, and developing a very wide distal end. The myo-cardinal elements are quite asymmetrically developed, anterior tooth and myophore are larger than posterior ones, as are also the dorsal cavities.

Remarks. This species was established by d'Orbigny on specimens from the Turonian of Pons (Charente-Maritime), Angoulême (Charente), and Le Beausset (Var), France, and has subsequently been reported from many other Turonian Mediterranean Tethys localities. Macé-Bordy (2007, p. 91) proposed the specimen R63774, from Pons, as lectotype, and B17070, R09210, and R08810, from the same locality, as paralectotypes.

Second rudist assemblage. Fifth parasequence set in the upper part of Villaescusa de las Torres Formation, upper Turonian, at Hoyos del Tozo section.

Fig. 10. A, B. *Radiolites radiosus* d'Orbigny, 1847. Transverse section, acetate peel, of right valve and detail as indicated. PUAB 79200, Hoyos del Tozo. Villaescusa de las Torres Formation. Upper Turonian. C-L. *Radiolites sauvagesi* (d'Hombres-Firmas, 1838). C-G. Transverse section, acetate peel, of right valve and details as indicated. C, D. PUAB 74355, Castrojimeno. E. PUAB 78587, Castroserracín. F, G. PUAB 74337, Castrojimeno. H-L. External view of right valves., PUAB 43748, Castrojimeno. Hortezuelos Formation. Upper Coniacian. Scale bars measure 10 mm.

Radiolites sauvagesi (d'Hombres-Firmas, 1838)
Fig. 10C-L

1838 *Hipp. Sauvagesii* d'Hombres Firmas, p. 193, pl. 3, figs. 1-8.
1850 *Radiolites sauvagesi* (d'Hombres Firmas); d'Orbigny, p. 211.
1908 *Radiolites sauvagesi* (d'Hombres Firmas); Toucas, p. 65, text-figs. 34-36, pl. 12, figs. 9-11.
2002 *Radiolites sauvagesi* (d'Hombres Firmas); Steuber. [with complete synonymy list]
2009b *Radiolites sauvagesi* (d'Hombres Firmas); Gil et al., p. 532, fig. 6a,b.
2012 *Radiolites sauvagesi* (d'Hombres Firmas); García-Hidalgo et al., p. 277, fig. 9F.

Description. Available specimens are single, or groups of shells attached each other together with other species, extracted from open/close cluster reefs the former, or frame reefs the latter. Maximal diameter is comprised between 50 and 100 mm and may reach up to 170 mm in length. The growth laminae are deeply inwards inclined and radially folded. The outer shell layer structure is normal cellular. Radial ribbing ranges from acute and narrow to rounded and broad. Spacing of growth lamellae is highly variable. The radial structures are two up-and-inwards radial folds, producing, at the shell surface, two furrows slightly wider than those in the rest of the contour. The inter-band is an out-and-outwards fold, that may be subdivided in the adult part of larger specimens. The ligament ridge is long and frequently with an expanded tip, in some specimens it is partly broken, or not completely preserved, because of dissolution of the inner shell layer and/or the infilling; two dorsal cavities are developed between the ligament ridge and the two teeth.

Remarks. This species was first described from the Coniacian of Gatigues (Gard) in southeast France and has been frequently reported from deposits of the same age all along the Mediterranean Tethys margins. As d'Hombres-Firmas' original specimens are lost, Macé-Bordy (2007, p. 90) proposed the specimen B17419 of the d'Orbigny collection, from the same locality, as neotype. An undivided inter-band fold was considered a primitive feature by Toucas (1908) justifying the erection of the species *R. praesauvagesi*, but a divided or undivided inter-band appears to be related to growth constraints and ecological factors.

Third rudist assemblage. Upper part of the Hortezuelos Formation, upper Coniacian, at Castroserracín and Castrojimeno.

Genus *Biradiolites* d'Orbigny, 1850

Type species: *Biradiolites canaliculatus* d'Orbigny from the Coniacian of Martigues (Bouches-du-Rhône), France, by subsequent designation in Toucas (1909).

Biradiolites canaliculatus d'Orbigny, 1850

Fig. 11A-G (+ Supplemental material 3)

1850 *Biradiolites canaliculata*; d'Orbigny, p. 230, pl. 572, figs. 1-4.

1887 *Biradiolites canaliculatus* d'Orbigny; Fischer, p. 1066, fig. 828 [copy of d'Orbigny, pl 572, fig. 4].

1909 *Biradiolites canaliculatus* d'Orbigny; Toucas, p. 112, pl.22, figs. 1-3.

2002 *Biradiolites canaliculatus* d'Orbigny; Steuber (with complete synonymy list).

2007 *Biradiolites canaliculatus* d'Orbigny; Macé-Bordy, p. 95, text-fig. 8A.

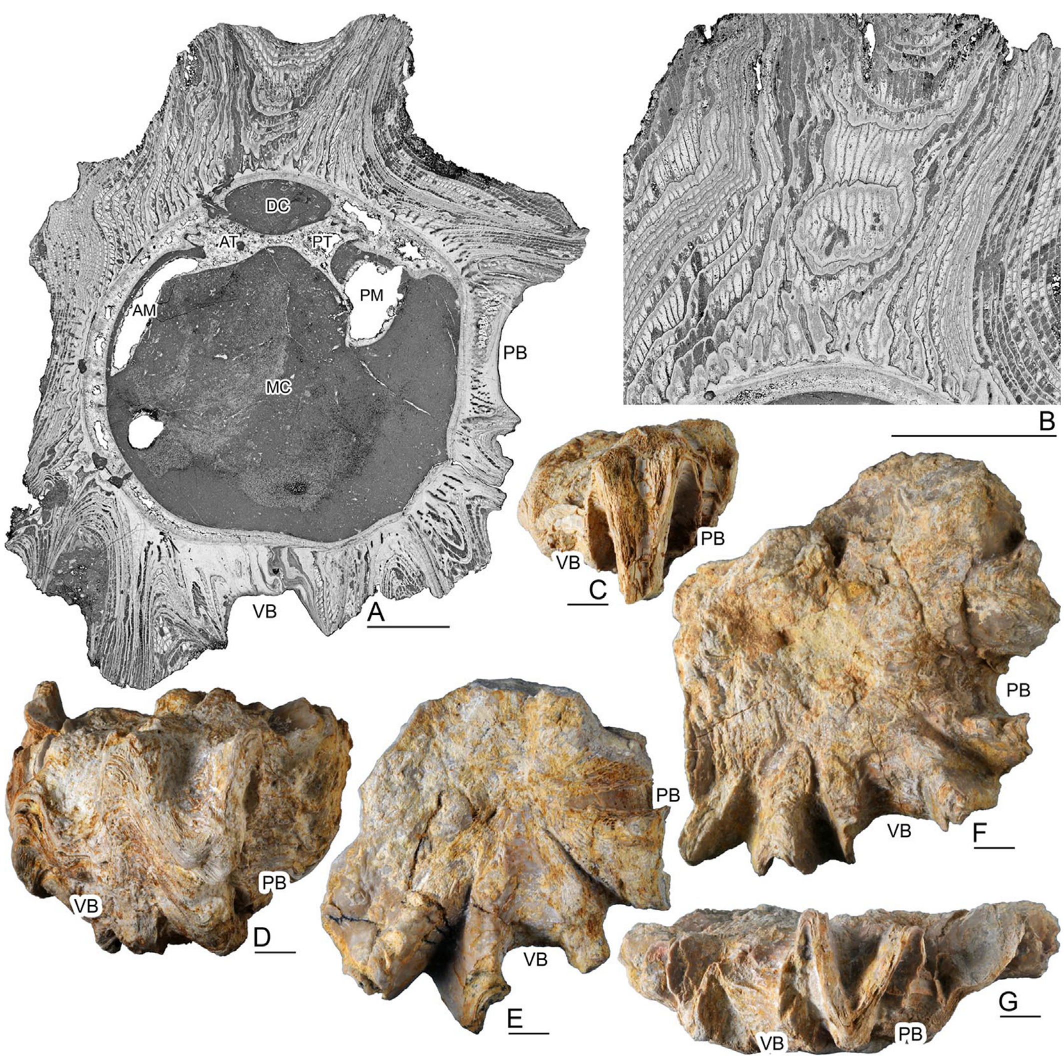

Fig. 11. *Biradiolites canaliculatus* d'Orbigny, 1850. A, B. Transverse section, acetate peel, of right valve close below the commissure, complete and detail of a lower section, PUAB 78638. C-G. External view of bivalve specimens. C. PUAB 74455. D. PUAB 78639. E. PUAB 78635. F. G. PUAB 74465. Castroserracín. Hortezuelos Formation. Upper Coniacian. Scale bars measure 10 mm.

2012 *Biradiolites canaliculatus* d'Orbigny; García-Hidalgo et al., p. 275, fig. 9D (non 9E = *Bournonia gardonica*).
2015 *Biradiolites canaliculatus* d'Orbigny; Troya, p. 328, figs. 188-200. [with complete synonymy list and a taxonomic discussion]

Description. Some of the available specimens have been recovered from frame reefs, attached to shells of other species, and could only be studied from polished cross sections of right valves. Other, recovered from open cluster reefs, are excellent single specimens preserved with both valves conjoined. The right valves of the former are long, narrow, and sub-cylindrical, while the latter are flat and very wide, with the characteristic inter-band fold as much developed downwards, as to reach or even surpassing the apex of the right valve. The growth laminae are smooth, downwards inclined at the dorsal side and developing three out-and-downwards radial folds at the opposite side, the middle one being the more developed, and the two smooth radial bands occupying the space between them. The radial bands are slightly protruding and may thus develop a rib and a furrow between them and the middle fold in very large flat specimens. The outer shell layer structure is non-compact, with radial ridges. The left valve has the same outer shell layer structure and is nearly flat, although following the folds and bands of the right valve.
Remarks. This species was first reported from the Coniacian of Martigues (Bouches du Rhône), Beausset (Var), Gatigues and Bagnols (Gard), all in South-east France, and has been sporadically reported from other localities including the southern Pyrenees, such as Montsec (Pascual et al., 1989). The species has traditionally been described as long conical, but it shows an extreme intra-specific diversity, from long to short wide flat shells, or with a flat anterior-dorsal side. This is probably the cause of some misidentifications in literature.
Third rudist assemblage. Upper part of the Hortezuelos Formation, upper Coniacian, at Castroserracín and Castrojimeno.

Genus *Bournonia* Fischer, 1887
Type species: *Sphaerulites Bournonii* Des Moulins, 1826, from the Maastrichtian of St. Mametz (Dordogne), France, by original designation.

Bournonia gardonica (Toucas, 1907)
Fig. 12A-O (+ Supplemental material 4)

?1869 *Radiolites fascicularis* Pirona, p. 30, pl. 8, figs. 6-12.
1907 *Agria gardonica* Toucas, p. 25, pl. 2, figs. 6-10.
1907 *Agria fascicularis* (Pirona); Toucas, p. 21, pl. 1, figs. 13, 14.
2009b *Biradiolites angulosus* d'Orbigny; Gil et al., p. 532, text-figs. 6A-C.
1910 *Bournonia gardonica* (Toucas); Douvillé, p. 49.
1926 *Bournonia gardonica* (Toucas); Parona, p. 34.
2002 *Bournonia gardonica* (Toucas); Steuber. [with complete synonymy list]
2002 *Bournonia gardonica* (Toucas); Gil et al., p. 252, fig. 3e-g, figs. 4a-e, 5a-e, 6a-d. [with complete description and figures of the outer shell layer structure]
2012 *Bournonia gardonica* (Toucas); García-Hidalgo et al., p. 273, fig. 9A.
2012 *Bournonia fascicularis* (Pirona); García-Hidalgo et al., p. 273, fig. 9B.
2012 *Biradiolites canaliculatus*; García-Hidalgo et al., p. 275, fig. 9E.
2018 *Bournonia fascicularis* (Pirona); Özer et al., p. 75, fig. 7E-I.
2018 *Bournonia gardonica* (Toucas); Özer et al., p. 75, fig. 7J-M.

Description. The numerous specimens available for study come from different localities with different depositional settings, thus, they display a wide spectrum of external morphologies. Right valves are conical, from narrow to wide, but mostly cylindrical shells also occur. These last, occurring in monospecific close cluster reefs, shells 100 mm high measure 10–30 mm in diameter, while conical specimens with the same high, occurring in other settings, may measure up to 60 mm in diameter. The growth laminae are deeply inwards inclined, and the outer shell surface is predominantly smooth, without evidence of growth lines (except in the radial bands) and, only sometimes and locally, showing weak spaced ribs. Radial structures are two out- and down flat, or slightly concave, folds of the growth laminae, producing two flat protruding bands at the outer shell surface. The different development of the radial bands is responsible for the wide spectrum of external shell morphologies observed. The ventral band is always wider than the posterior one, concave or even subdivided, and displays much variation. The initially flat out- and dawn folds of the radial structures, sometimes more or less concave, may subdivide with shell growth, or even become a wide flat in-and up fold limited by two very narrow out- and dawn folds. Thus, the flat protruding bands may become concave, or even bottom-flat limited by two acute narrow ribs. The inter-band varies from a depressed flat surface to a deep narrow furrow, depending on the radial band development. The transverse section of the right valve close below the commissure shows that the ligament ridge is absent and the barely observable myo-cardinal apparatus very weak. The outer shell layer is partly compact and with radial ridges structure in both valves (see detailed description in Gil et al., 2002). Left valves are deeply concave, conforming to the deeply inwards inclined growth laminae of the right valve and its folds.
Remarks. Pirona (1869) proposed *Radiolites fascicularis* for a few small specimens from the Coniacian of Colle di Medea in Friuli, Italy. The original description is based on some, taxonomically irrelevant, external shell characters and the figures are drawings (acknowledged to Prof. Torquato Taramelli). The original specimens, deposited in the museum of the *Istituto Technico di Udine*, are lost, because the building was destroyed by fire. Nevertheless, the figures remind some of the characters of *Bournonia gardonica* Toucas (1907). In fact, Toucas (1907) reported as *Agria fascicularis* (Pirona) some small specimen occurring in Gatigues, together with his new species *A. gardonica*, and García-Hidalgo et al. (2012) and Özer et al. (2018), as well, reported specimens of *Bournonia fascicularis* occurring together with abundant specimens of *B. gardonica*. In our opinion, although *B. fascicularis* (Pirona) and *B. gardonica* (Toucas) could possibly be synonymous, the former, being the senior, is insufficiently characterized and the types are lost, while the last may be uncontestably recognized and the types and abundant specimens, of the type locality and other, are preserved in the collections of the *École supérieure des Mines de Paris*, now in Lyon (Villeurbanne), and Toucas in the Sorbone, now in the *Museum national d'Histoire Naturelle* in Paris. Thus, we propose *B. gardonica* (Toucas, 1907) being recognized, instead of *B. fascicularis* (Pirona, 1869).
Third rudist assemblage. Upper part of the Hortezuelos Formation, upper Coniacian, at Castroserracín and Castrojimeno.

Genus *Durania* Douvillé, 1908
Type species: *Hippurites cornupastoris* Des Moulins, 1826, from the upper Turonian of les Pyles, Dordogne, France, by original designation.

Durania arnaudi (Choffat, 1891)
Fig. 13A-G

1891 *Biradiolites Arnaudi* Choffat, p. 203, 210, 211.
1902 *Biradiolites Arnaudi*; Choffat, p. 138, pls. 6, 7, 8, figs. 1-12.
1909 *Sauvagesia arnaudi* (Choffat); Toucas, p. 93, text-fig. 60, pl. 18, figs. 3-7.
1910 *Durania Arnaudi* (Choffat); Douvillé, p. 50, pl. 3, fig. 1.
2002 *Durania arnaudi* (Choffat); Steuber. [with complete synonymy list]

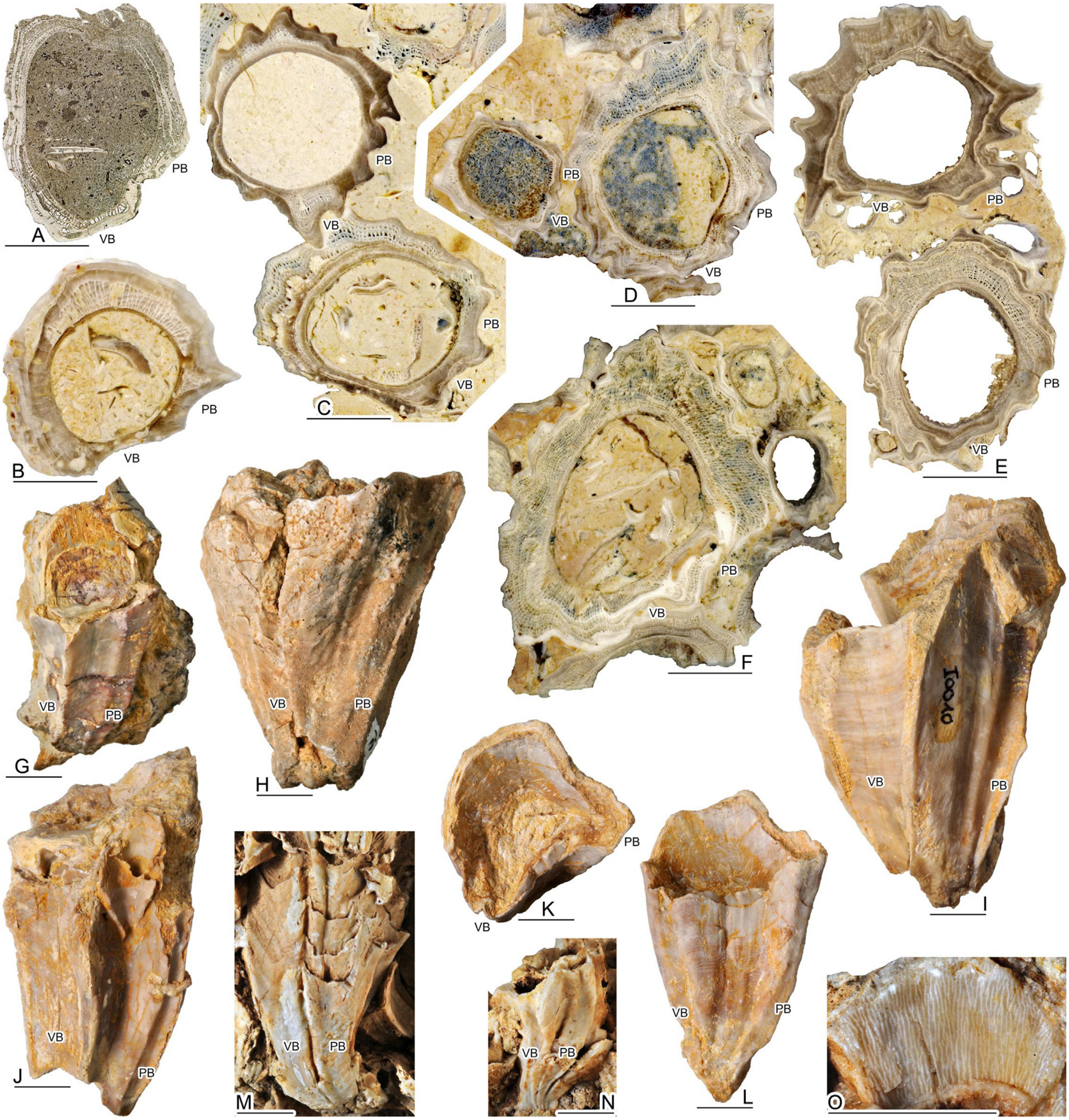

Fig. 12. *Bournonia gardonica* (Toucas, 1907). A-F. Transverse section, thin section (A) and scanner images (B-F), of right valve. A. PUAB 43933, Barranco de las Cuevas. B. PUAB 81340, Castroserracín. C. PUAB 43735. D. PUAB 81786_3. E. PUAB 43726. F. PUAB 82786_1. Castrojimeno. G-N. External view of bivalved specimens. G. PUAB 81763. H. PUAB 75900. I. PUAB 78519. J. PUAB 78510. K, L. PUAB 78515, Castroserracín, M. PUAB 43748_1, N. PUAB 43748_2. O. Detail of the outer shell structure. PUAB 43748, Castrojimeno. Hortezuelos Formation. Upper Coniacian. Scale bars measure 10 mm.

2013 *Durania arnaudi* (Choffat); Berrocal-Casero et al., p. 94, fig. 6.3a-c.

2017 *Durania arnaudi*; Barroso-Barcenilla et al., fig. 5C.

Description. The specimens from the Casa Medina Formation are larger, commonly weathered, and some preserved only as shell fragments; maximal diameter may attain 90 mm. Those few specimens, only sporadically found, from the Picofrentes Formation are smaller, single, and well-preserved; maximal diameter measures 60 mm and length 100 mm. The outer surface of the right valve bears regularly spaced longitudinal ribs interrupted by the growth lines. The two finely ribbed subequal radial bands are slightly concave and separated by a narrow and protruding interband bearing similar radial ribs as in the rest of the contour. The

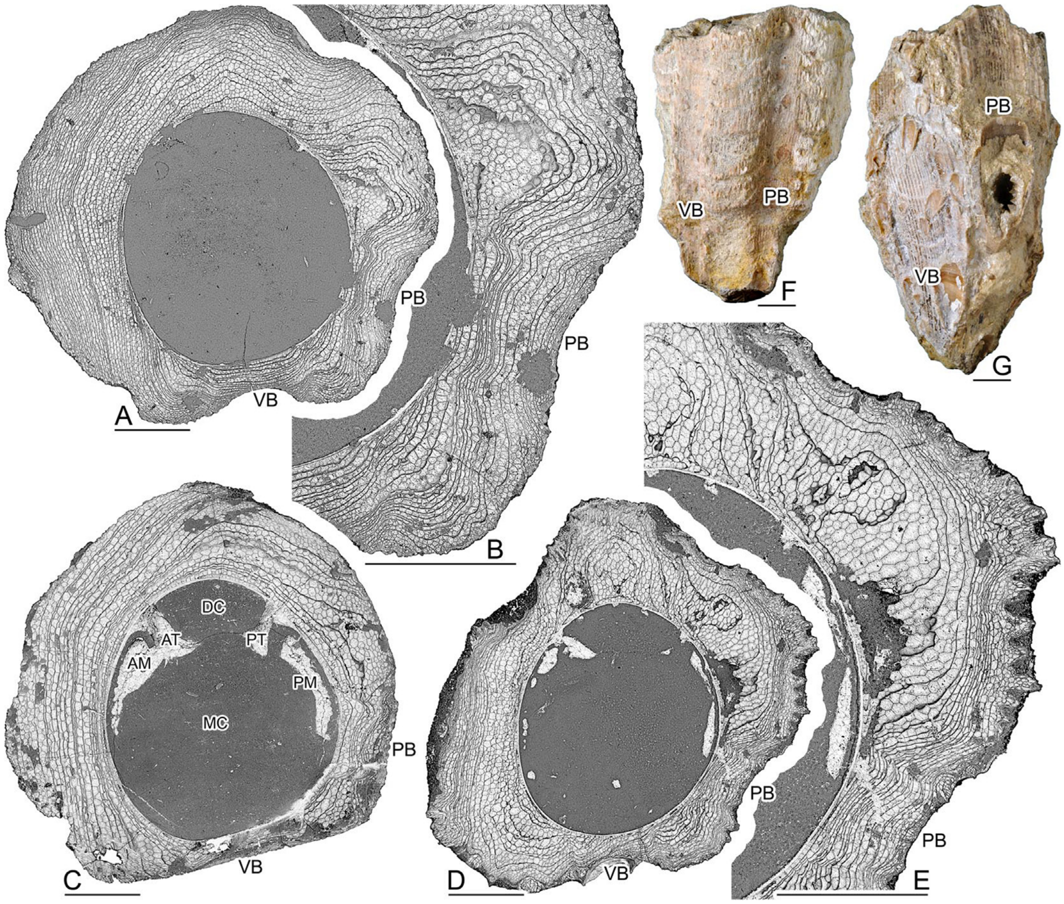

Fig. 13. *Durania arnaudi* (Choffat, 1891). A-E. Transverse section, acetate peel, of right valve and details. F, G. External view of right valve. A, B, F. PUAB 78534, Santamera. C. PUAB 81759, Carabias. D, E. PUAB 78535, Tamajón. G. PUAB 81757, Modamio. Picofrentes Formation, lower Turonian. Scale bars measure 10 mm.

growth laminae are sub-horizontal, with radial folds only at the margin, and have normal cellular structure. The left valve is flat, slightly convex at its centre, and has compact structure. As observed in transverse cross section close below the commissure, the ligament ridge is absent, and the myo-cardinal apparatus is very weak: teeth are very narrow, far each other, and glide into subtle furrows in the thin inner shell layer of the right valve; myophores are thin and much extended ventrally, close to the inner shell margin.

Remarks. The species was first reported from Runa, Portugal, locality attributed either to the Turonian (Toucas, 1909) or to the Cenomanian (Berthou, 1973) and has been subsequently identified in other Cenomanian and Turonian localities of the Mediterranean Tethys.

First rudist assemblage. Casa Medina Formation, lower Turonian, at La Alberca de Záncara; Picofrentes Formation, lower Turonian, at Modamio, Carabias, Torremocha del Campo, Tamajón, and Santamera.

Genus *Hoyosites*, gen. nov.
Type species: *Hoyosites tozoi*, gen. et sp. nov.

Origin of name. From the type locality, Hoyos del Tozo, with the suffix -ites, as used in some ancient generic names of rudists.

Type locality and age. Upper part of the Villaescusa de las Torres Formation, fifth parasequence set, upper Turonian, at Hoyos del Tozo, Burgos.

Diagnosis. Radiolitidae with the right valve's growth laminae gently inwards inclined and radially folded, forming numerous rounded ribs at the outer surface; radial structures are two flat down-and-outwards radial folds, forming two slightly protruding, concave and smooth radial bands, ventral one wider than posterior one, separated by a narrow furrow, the inter-band; outer shell layer structure predominantly compact, although may be non-compact punctually; no ligament ridge; left valve with concave margin, following the inclination of the laminae of the right valve; elements of the myocardinal apparatus robust.

Description. As the new species, the only one known until now.

Remarks. The new genus differs from genus *Milovanovicia* Polšak, 1967 by the numerous, regular, and short gentle ribs instead of few and long, and the radial bands being smooth instead of ribbed. No other radiolitid genera, with compact outer shell layer structure and without a ligament ridge are known.

Hoyosites tozoi, gen. et sp. nov.
Fig. 14A-L.

Diagnosis. As the genus.

Type specimens. Holotype PUAB 81424; Paratype PUAB 79195.

Origin of name. From El Tozo, the area of Burgos province where the type locality is situated.

Type locality and age. As the genus.

Description. Specimens were recovered from close cluster/frame reefs, being extremely difficult to obtain isolate specimens. Larger ones measure up to 45 mm in diameter and 150 mm in length. Young shells are conical, becoming cylindrical with growth. The outer surface of the right valve bears numerous (4–5 per 10 mm) rounded ribs alternating with narrow furrows, produced by radial

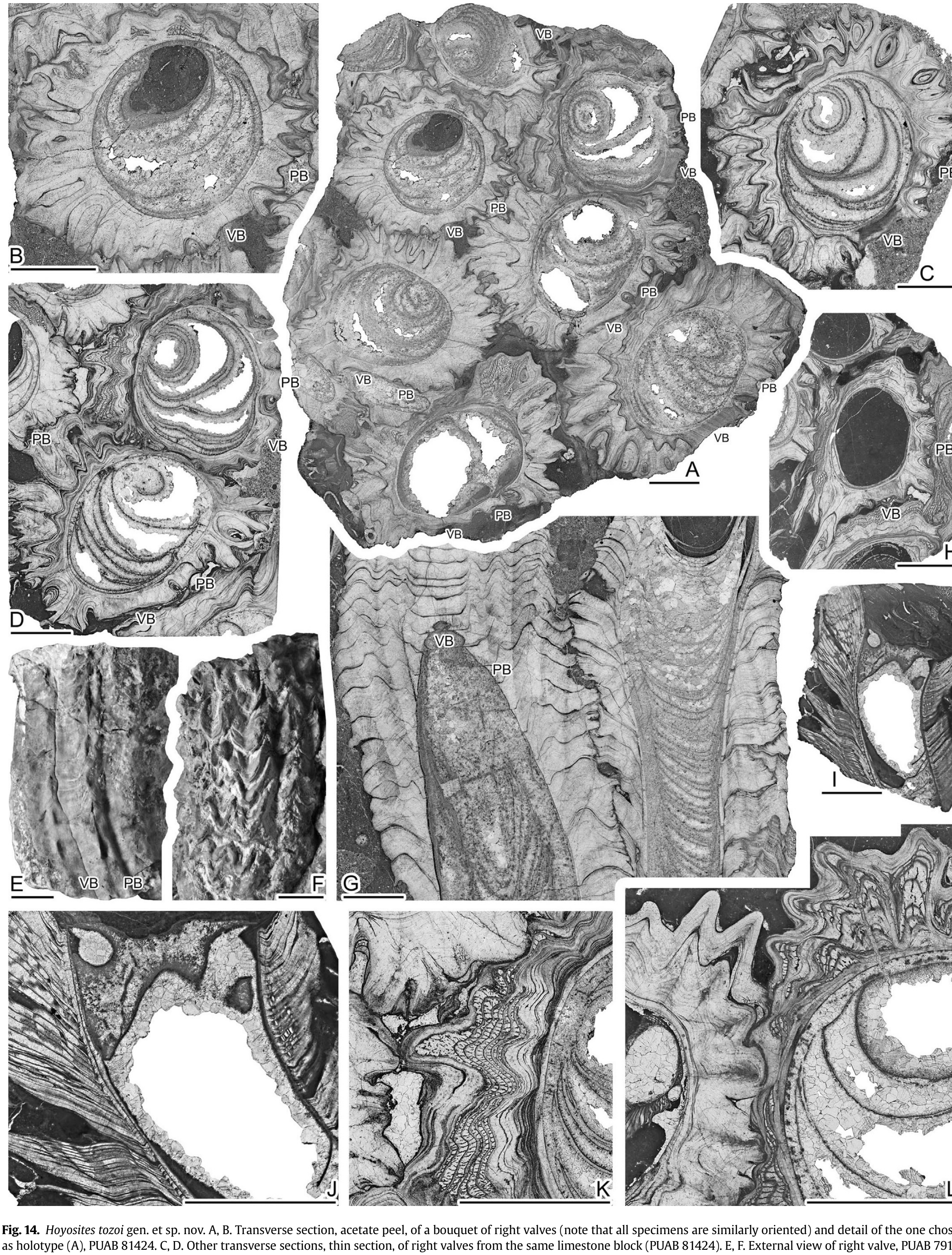

Fig. 14. *Hoyosites tozoi* gen. et sp. nov. A, B. Transverse section, acetate peel, of a bouquet of right valves (note that all specimens are similarly oriented) and detail of the one chosen as holotype (A), PUAB 81424. C, D. Other transverse sections, thin section, of right valves from the same limestone block (PUAB 81424). E, F. External view of right valve, PUAB 79195

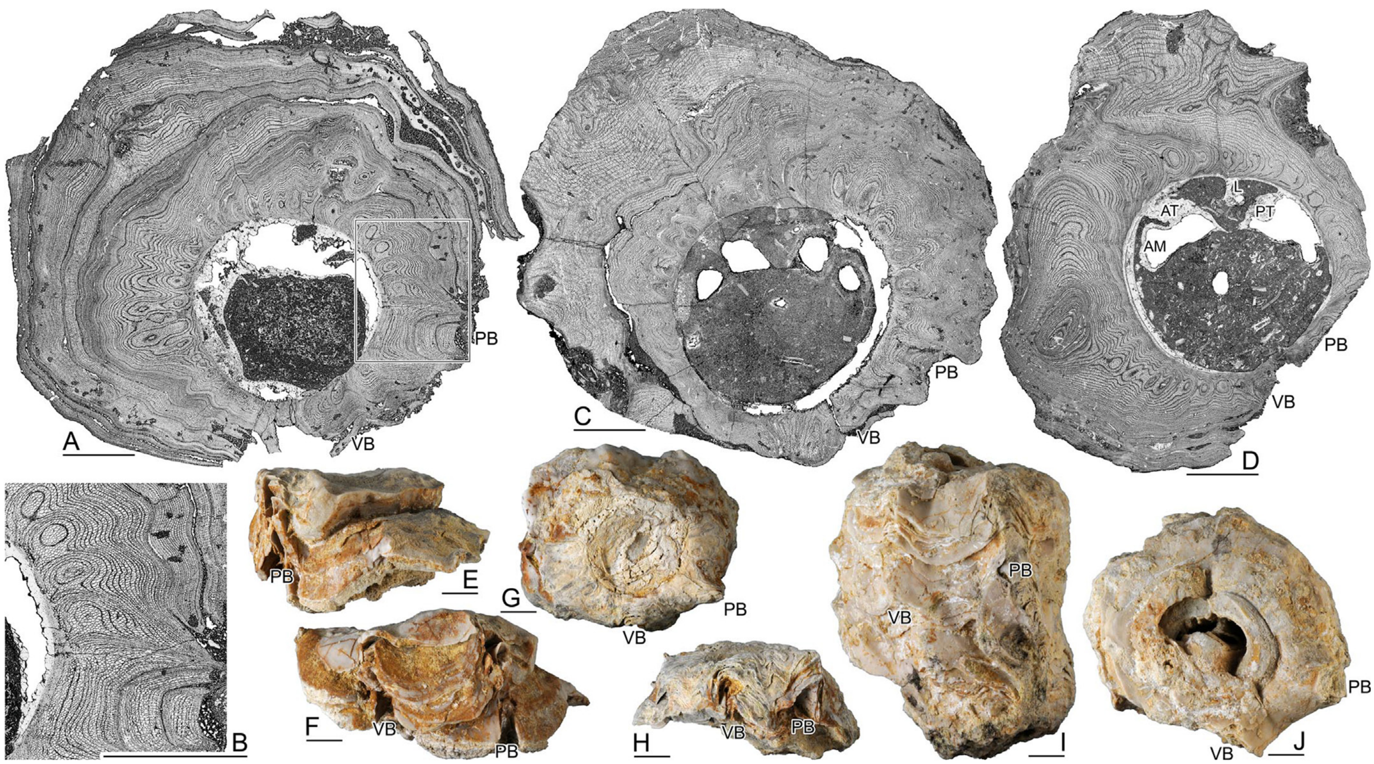

Fig. 15. *Praeradiolites ponsianus* (d'Archiac, 1837). A-D. Transverse section, acetate peel, of right valves and detail as indicated, A, B. PUAB 78622. C. PUAB 78619. D. PUAB 78623. E-J. External view of bivalved specimens. E, F. PUAB 78616. G, H. PUAB 78624. I, J. PUAB 78614. Castroserracín. Hortezuelos Formation. Upper Coniacian. Scale bars measure 10 mm.

folds of the growth laminae; ribs and furrows are interrupted in successive growth cycles. The ventral radial band, somewhat depressed, is smooth and slightly concave; the posterior radial band is similar, although narrower and less depressed; the interband is a narrow furrow. The growth laminae are inwards inclined and radially folded. Concave tabulae are developed in the inner shell layer, below the body cavity. The outer shell layer structure is compact; nevertheless, sporadically during shell growth and in reduced parts of the laminae, non-compact structure may develop which may present more or less irregular radial ridges. Growth laminae are more inwards inclined, and non-compact structure occurs more often, in young shells than in adult ones where it is very rare. There is no ligament ridge. The inner shell layer develops thick protuberances at the dorsal side, where the upper valve tooth glide. The upper valve has been observed in longitudinal section of shells with both valves conjoined, its outer margin is concave following the deeply inwards inclination of the right valve's growth laminae; the myocardinal apparatus is robust.

Second rudist assemblage. Upper part of the Villaescusa de las Torres Formation, fifth parasequence set, upper Turonian, at Hoyos del Tozo and Quintanilla-Escalada, Burgos.

Genus *Praeradiolites* Douvillé, 1902.

Type species: *Sphaerulites ponsiana* d'Archiac, 1837 from the Turonian of Pons (Charente-Maritime), France, by subsequent designation in Pons and Vicens (2011): Opinion 2314 (Case 3546), ICZN (2013) in substitution of *Radiolites fleuriaui* d'Orbigny, 1842, originally designed by Douvillé (1902, p. 469).

Praeradiolites ponsianus (d'Archiac, 1837)
Fig. 15A-J (+Supplemental material 5)

1837 *Sphaerulites Ponsiana* d'Archiac, p. 182, pl. 11, fig. 6.
1907 *Praeradiolites ponsi* (d'Archiac); Toucas, p. 30, pl. 3, figs. 3-5.
2002 *Praeradiolites ponsianus* (d'Archiac); Steuber. [with complete synonymy list]

Description. Available material are single specimens, many preserved with both valves conjoined, recovered from open cluster reefs. Maximal diameter measures 80 mm and height 100 mm, although shorter specimens, 40 mm tall, are common. Externally, the right valve growth laminae are smooth, much expanded, and turned downwards, thus overlapping each other. Two very narrow up-and-inward radial folds of the laminae form the two narrow radial sinuses, separated by a wide down-and-outward fold forming the inter-band. The left valve is convex, at its central part, and accommodates to the downward turned laminae of the right valve, at its wide marginal part; two protuberances, nearly oscula-like, may form in coincidence with the radial sinuses of the right valve. The transverse cross section of the right valve reveals that the growth laminae are radially folded at its inner part, although smooth and downturned at its outer margin; the ligament ridge is long, with an expanded tip; two large dorsal cavities are developed between the ligament ridge and the two teeth; the two myophores are robust. The outer shell layer structure is non compact, finely normal cellular.

Remarks. The species was first described from the upper Turonian of Pons (Charente), France, and has been widely reported from other Turonian and Coniacian Mediterranean Tethys localities.

(paratype). G. longitudinal/oblique section of right valves, PUAB 81424. Hoyos del Tozo. Villaescusa de las Torres Formation. Upper Turonian. H-J. Transverse, radial, and detail section, thin section, of right valves, PUAB 81333, Quintanilla-Escalada. Villaescusa de las Torres Formation. Upper Turonian. K, L. Detail of one of the specimens in D and of two other specimens of the same limestone block (PUAB 81424), respectively. Scale bars measure 10 mm.

Third rudist assemblage. Upper part of the Hortezuelos Formation, upper Coniacian, at Castroserracín.

Praeradiolites requieni (d'Hombres-Firmas, 1838)
Fig. 16A-N (+ Supplemental material 5)

1838 *Sphaerulite* d'Hombres-Firmas, p. 175, pl. 2, figs. 1, 2.
1839 *Spherulites requieni*; d'Hombres-Firmas, p. 242, pl. 6, fig. 3.
1907 *Praeradiolites requieni* (d'Hombres-Firmas); Toucas, p. 40, pl. 6, figs. 3, 4.
2002 *Praeradiolites requieni* (d'Hombres-Firmas); Steuber. [with complete synonymy list]
2009b *Praeradiolites requieni* (d'Hombres-Firmas); Gil et al., p. 532, fig. 7C.
2012 *Praeradiolites requieni*; García-Hidalgo et al., p. 275, fig. 9C.
2015 *Praeradiolites requieni* (d'Hombres-Firmas); Troya, p. 388, figs. 225-232. [with taxonomic discussion]

Description. Available material are single specimens, most preserved with both valves conjoined, recovered from open cluster reefs. Some specimens are conical (120 mm high and 70 mm wide), but others are remarkably flat (40 mm high and 80 mm wide) lying reclined on their flat dorsal margin. The right valve has a remarkably foliaceous external aspect, with the growth laminae extended and downturned at the dorsal side while forming two strong up-and-inward folds limited by three also strong down-and-outward folds [aligned] at the [flat] opposite side. The left valve is convex with the apex located dorsally, also foliaceous, and conforming with the folds of the right valve. The outer shell layer structure is non-compact, normal cellular.
Remarks. The species was first reported from the Coniacian of Gatigues (Gard), France, and has been successively reported from other Coniacian southern France and northern Spain localities.
Third rudist assemblage. Upper part of the Hortezuelos Formation, upper Coniacian, at Castrojimeno and Castroserracín.

Radiolitidae indet.

Description. Several cylindrical inner moulds, with very scarce thin rests of outer shell layer, some with a longitudinal furrow corresponding to the inner ligament ridge, and other without it, could

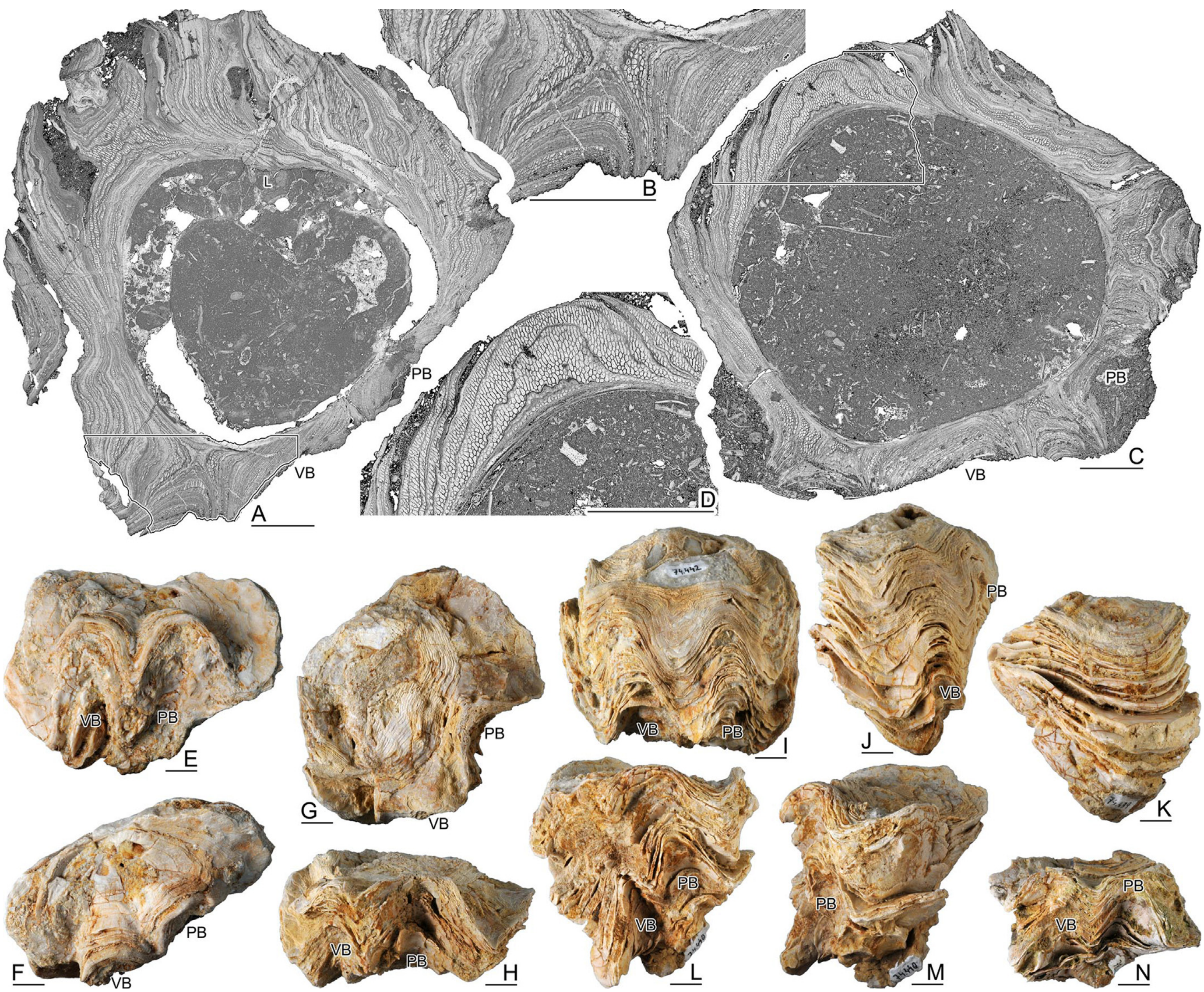

Fig. 16. *Praeradiolites requieni* (d'Hombres-Firmas, 1838). A-D. Transverse section, acetate peel, of right valves and detail as indicated. A, B. PUAB 78625. C, D. PUAB 78627. E-N. External view of bivalved specimens. E, F. PUAB 75916. G, H. PUAB 74441. I. PUAB 74442. J, K. PUAB 74439. L, M. PUAB 74440. N. PUAB 78631. Castroserracín. Hortezuelos Formation. Upper Coniacian. Scale bars measure 10 mm.

not be identified beyond indeterminate radiolitids, probably *Radiolites*? and *Biradiolites*?, respectively. Several specimens, cut close to the commissural margin, allow to distinguish the presence of the inner shell layer, including the myocardinal apparatus, and the infilling of the body cavity.
Fourth rudist assemblage. Valle de Tejadilla and Ituero y Lama, Valle de Tabladillo Formation. Santonian–?Campanian.

Family: Requieniidae Kutassy, 1934

Genus *Apricardia* Guéranger, 1853
Type species: *Apricardia carinata* Guéranger from the Département de la Sarthe, France, by original designation.

Apricardia sp.
Fig. 17A-D

2012 *Apricardia* sp.; García-Hidalgo et al., p. 277, fig. 9J.

Description. Available material is composed of internal moulds of single bivalve specimens. Small fragments of shell, composed of calcite with normal prismatic structure, are preserved on some of them. Both valves are very similar in coiling and transverse section, although the left one is slightly larger and has a flat anterior side. The section is triangular, higher than wide, and carinate ventrally. The furrow corresponding to the posterior myophore plate is evident at the outer surface in the internal mould of both valves. When observed in transverse section, both myophore plates are concave, appear curved dorsally.
Third rudist assemblage. Upper part of the Hortezuelos Formation, upper Coniacian, at Castroserracín.

6. Discussion

6.1. Sequential stratigraphy context

The low frequency depositional stacking scheme of the Iberian Basin Upper Cretaceous is reasonably well-known (García et al., 1996, 2004; Floquet, 1998; Segura et al., 2002, 2006; Gil et al., 2004, 2010). Recent research focuses in stablishing a more detailed scheme, based on high frequency sequences or sedimentary cycles in the sense of Strasser et al. (2006). These high frequency cycles are currently interpreted as the result of sea-level fluctuation caused by global climatic changes within the band of Milankovitch frequencies (Schwarzacher, 2000; Batenburg et al., 2012; Wu et al., 2013; among others). Nevertheless, the stratigraphic control of these sequences is difficult to establish in the Iberian Basin due to the lack of acceptable biomarkers, or because their preservation is not allowing a precise taxonomic determination. This is a consequence of the shallow character of the sedimentary setting where these successions were formed and, also, of the early diagenesis (eogenesis) during the sedimentary interruptions related to sequence boundaries, by being close to the coast margin (see 6.4. Preservation). This is particularly significant in the fourth rudist assemblage, where diagenetic processes caused the impossibility of any taxonomic precision, thus losing all its biostratigraphic potential (see 6.2.4. Age of the fourth assemblage).

Outer platform facies and fossils, allowing good biostratigraphic control through ammonite biozones, only occur in two depositional episodes: latest Cenomanian–early Turonian and Coniacian sequences (Segura et al., 1993, 2014; García-Hidalgo et al., 2012).

The rest of depositional sequences have been dated necessarily by correlation with global eustatic charts (Haq et al., 1988; Hardenbol et al., 1998; Haq, 2014). The presence of some of these rudist assemblages in different depositional sequences allows establishing a biostratigraphic datum of great importance in these Iberian Basin successions. These data both confirm or precise previous correlations for some of these sequences and allow calibration between ammonite and rudist occurrences in the depositional episodes where they co-occur. This calibration helps undoubtedly to precise the chronostratigraphic control of the high frequency sequences (4th order) currently being recognized and to determinate the temporal amplitude of their limiting hiatuses, as well as their variation towards the coastal margins of the basin.

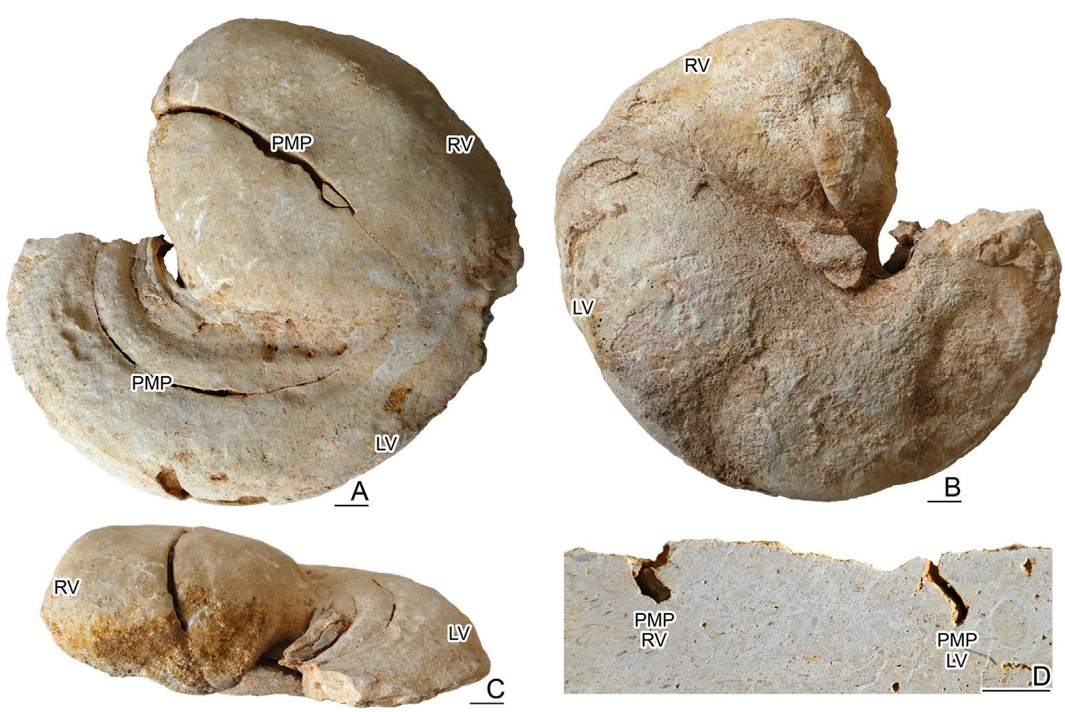

Fig. 17. *Apricardia* sp. A-C. Posterior, anterior, and apical view of both valves, PUAB 74463. D. Transverse section of the internal mould, cutting the posterior myophore plate (PMP) at both valves, PUAB 74462, Castroserracín. Hortezuelos Formation. Upper Coniacian. Scale bars measure 10 mm.

6.2. Age of the rudist assemblages (Fig. 18)

6.2.1. Age of the first assemblage

Rudists of the first assemblage have been sampled in different and distant localities, although most of them within the third parasequence set of the five recognized by Segura et al. (1993) within the uppermost Cenomanian–lower Turonian low frequency depositional episode (Fig. 18). It is the first prograding parasequence set within the mentioned episode (Segura et al., 1993), with two rudist levels being identified: a) matrix supported isolated rudists, included in outer platform marls, in the lower half of the parasequence; and b) segment and cluster reefs, in the inner platform carbonate bars characterizing the upper part (fig. 2 in Segura and Wiedmann, 1982). According to the ammonite biozonation established for the Iberian Range (Barroso-Barcenilla et al., 2009), both rudist levels are within the *Spathites (Ingridella) malladae* Zone, and maybe reaching the top of the *Choffaticeras (Choffaticeras) quaasi* Zone. This local biozonation is correlated with the upper part of the *Watinoceras devonense* Zone (lower Turonian) in the Southern Europe standard ammonite zonation (Hardenbol et al., 1998). Although neither the poor record nor its difficult observation do not allow enough stratigraphic precision, considering that the silicified specimens from the southern coastal margin (La Alberca de Záncara, 2 in Fig. 3) could correspond to the landward wedge of the fourth parasequence set should not be disregarded. Upper Cenomanian foraminifera (Giménez, 1989; Caus et al., 2009; Consorti et al., 2016) and rudists (Martín-Chivelet and Giménez, 1993) have been reported from Casa Medina and/or Ciudad Encantada formations in the southern end of the basin (Valencian sector and Prebetic). This indicates that both reports correspond to parasequence I and II (lower part) in Segura et al. (1993). In fact, Alonso et al. (1993) replicate a progradational model similar to that in Segura et al. (1993), by defining a DS-5 sequence with rudists in the Valencian sector, upper Cenomanian, which could be easily correlated with parasequences I and II of Segura et al. (1993); and a sequence DS-6, lower-middle Turonian, prograding northwards on the previous one, where the localities of our first rudist assemblage are found, which would encompass the three upper parasequences of Segura et al. (1993).

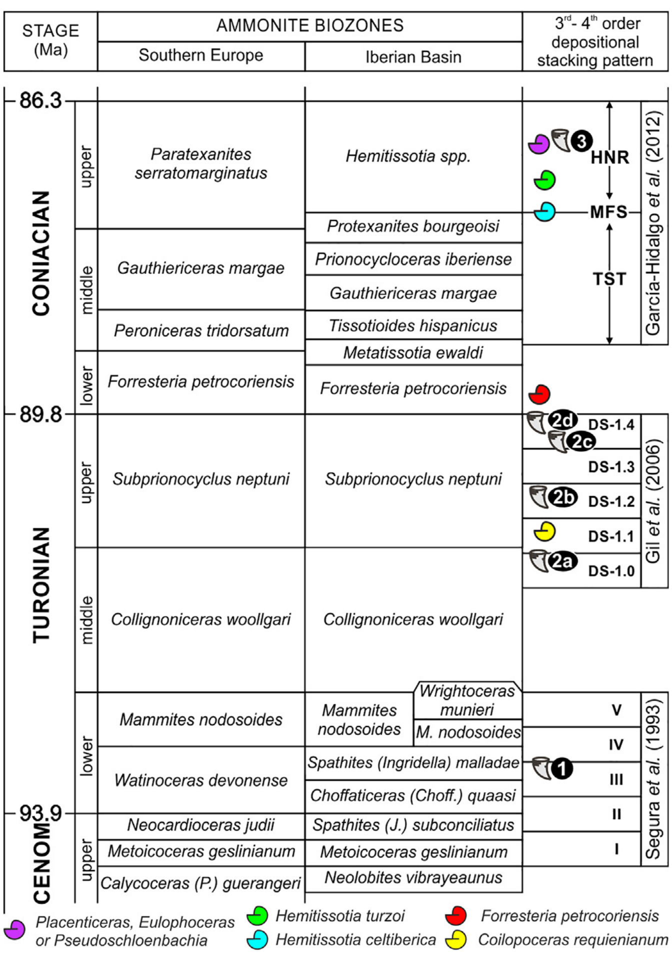

Fig. 18. Chronostratigraphic framework showing the correlation of the first three rudist assemblages and levels with the standard ammonite biozonation and the high and low frequency depositional stacking pattern recognized by previous authors. Southern Europe ammonite zones are after Hardenbol et al. (1998) and Ogg et al. (2004). Iberian Basin zones and subzones are after Gallemí et al. (2007) for the Coniacian, and Barroso-Barcenilla et al. (2009) for the upper Cenomanian–lower Turonian. Age (Ma) is after Gradstein et al. (2020). (*J.*) = (*Jeanrogericeras*). (*P.*) = (*Proeucalycoceras*).

6.2.2. Age of the second assemblage

The second rudist assemblage occurs at the northern margin of the Iberian basin, now southern margin of the Vasco-Cantabrian Range (4 in Fig. 3). Rudists appear in four differentiated levels in three of the five parasequence sets identified by Gil et al. (2006) within the upper Turonian low frequency depositional episode. The lower level (2a in Fig. 18) is a *Hippurites resectus* monospecific segment reef included in a carbonate bed, marking the top of the first parasequence set and correlating with the upper part of the *woollgari* Zone (middle Turonian). Above, in the second parasequence set, an ammonite level with *Coilopoceras requienianum* occurs (Floquet 1991; Gil et al., 2006; Barroso-Barcenilla et al., 2013), indicating the lower part of the *Subprionocyclus neptuni* Zone (Kennedy, 1984; Hancock, 1991; Hardenbol et al., 1998).

The second rudist level (2b in Fig. 18), in the third parasequence set, is a monospecific close cluster/frame reef composed exclusively of *Radiolites lusitanicus*. The other two rudist levels (2c and 2d in Fig. 18) are localized in the fifth parasequence set: a close cluster/frame reef of *Hippurites vasseuri*; and a frame reef of predominantly *Hoyosites tozoi*, with scarce specimens of hippuritids and another radiolitid. This upper group of parasequences ends with a significant hardground, also defining the end of the late Turonian low frequency depositional episode (Gil et al., 2006) and of the *Subprionocyclus neptuni* Zone record, as far as the presence of *Forresteria petrocoriensis* Zone immediately above (Berrocal-Casero et al., 2020; Berrocal-Casero, 2021) indicates the base of the Coniacian.

6.2.3. Age of the third assemblage

The third rudist assemblage (3 in Fig. 18) is identified in the upper carbonate lithosome of the Hortezuelos Formation (García-Hidalgo et al., 2012) characterizing the highstand normal regression of the Upper Cretaceous second more extensive depositional episode in the Iberian Basin (Gil et al., 2002, 2009b). This lithosome represents the progradation of an inner carbonate platform (including reef front and lagoon facies) where rudist occur in several successive levels (Gil et al., 2002; 2009b) above an intermediate lithosome of very fossiliferous outer platform facies (García-Hidalgo et al., 2012). The ammonite association reported from the upper and intermediate lithosomes (García-Hidalgo et al., 2012; Segura et al., 2014), suggests that the rudists, in the upper lithosome (3 in Fig. 18) correspond to the Iberian Basin *Hemitissotia* Zone, which correlates with the *Paratexanites serratomarginatus* Zone (upper Coniacian) in the Southern Europe standard ammonite zonation (Hardenbol et al., 1998).

6.2.4. Age of the fourth assemblage

The rudist specimens of this assemblage were sampled at different stratigraphic levels of the Montejo, Burgo de Osma and Valle de Tabladillo formations from different locations on the SW coastal margin of the Iberian Basin. These coastal margin successions suffered intense diagenetic processes which caused a strong dolomitization of sediments and the complete dissolution of shells (Gil et al., 2010), preventing any accurate taxonomic determination of rudists or any other group of fossils. So, the age of this fourth assemblage can only be inferred by sequential correlation with more internal successions of the Basin, being considered Santonian in a broad sense (Martín-Chivelet et al., 2019), or even lower-middle Campanian (García et al., 2004; Gil et al., 2004).

6.3. Palaeobiogeographic implications

The distribution of rudist assemblages within the Iberian Basin is consistent with the tecto-eustatic evolution of the Iberian Plate during Late Cretaceous. The north-westwards tilting of the microplate at the end of the Cenomanian (Segura et al., 2002; García et al., 2004), together with the globally recognized Late Cretaceous significant sea level rise (Haq, 2014, among others), determined the eustatic character and the Atlantic origin of the Iberian Basin marine depositional episodes. The amplitude of these depositional eustatic events governed the rudist assemblages setting within the Iberian Basin (Fig. 19).

An uppermost Cenomanian—lower Turonian high amplitude depositional event allowed open platform facies (Picofrentes Formation) to reach central and south-eastern areas (Casas Medina Formation) of the Iberian Basin. An inner carbonate platform (Ciudad Encantada Formation) developed above, prograding towards North and North-west (Segura et al., 2002; García et al., 2004). The first rudist assemblage settled on this depositional event, being the south-easternmost location of rudists in the Iberian Basin (1—3 in Fig. 3).

A mid Turonian high amplitude sea level fall caused a significant progradation of the facies belt North-westwards, the input of continental siliciclastics in central areas of the basin, and the partial exposure of the previous platform (Gil et al., 2004). A subsequent upper Turonian depositional event, less extensive than previous one, allowed the development of a new carbonate platform opened to the Atlantic (Villaescusa de las Torres and Muñecas formations). The second rudist assemblage settled on this platform, being the northernmost location of rudists in the Iberian Basin (4, 5 in Fig. 3). Finally, successive Coniacian to mid Campanian depositional events, each progressively more extensive than previous one, caused the south-eastwards retrogradation of carbonate platform environments flooding wide areas of the south-western continental margin, where the third and fourth rudist assemblages settled (6—12 in Fig. 3), pointing out a revealing displacement of shallow platform facies belts towards the W with respect to the axis of the basin, which is synchronous with the beginning of evaporite sedimentation in central areas of the basin (Serranía de Cuenca region) (Meléndez et al., 1975; García et al., 2004).

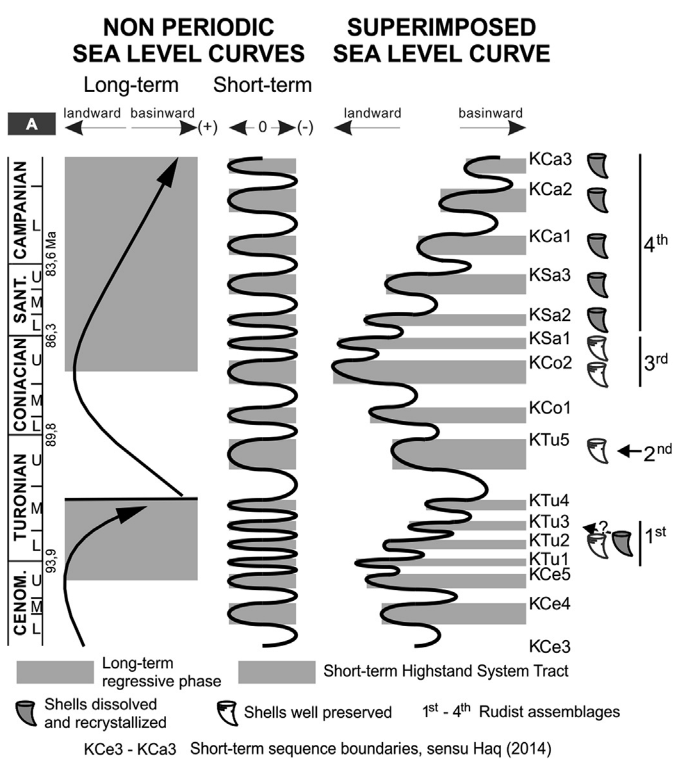

Fig. 19. Stratigraphic setting of the rudist assemblages on the Short-Term Cenomanian to Campanian Eustatic Cycle Chart of Haq (2014), showing its preservation degree related to superimposed see level curve. A) Chronostratigraphic scale. Age (Ma) is after Gradstein et al. (2020).

6.4. Preservation

Rudists mostly occur at the late highstand systems tract (LHST) of both low-order depositional sequences and parasequence sets, relatively close to the upper sequence boundary (Fig. 19).

This location, together with the superposition of sea-level cycles (sequences) of different order, mainly control the preservation degree of rudist shells because, in very shallow and inner platform environments, the early vadose diagenesis processes related to sea-level falls at sequence boundaries cause major shell dissolution and recrystallization, thus precluding their taxonomic identification. This is the case in the occurrence of the first and fourth rudist assemblages, coincident with long-term global sea-level fall trends after the global maximum eustatic peaks at lower Turonian and Coniacian, respectively. Second and third rudist assemblages, however, are better preserved although being also related to shallow inner platform environments. Early dissolution and dolomitization processes affected less such sequences because they were deposited in coincidence with the Coniacian long term global sea-level rise, or even the global maximum eustatic peak. Additionally, the hiatuses time gap associated to their sequence boundaries were shorter and the sea-level falls amplitude were lower and, consequently, the input of meteoric waters to induce early diagenesis was also smaller.

In addition to the previously exposed, the Iberian Basin Upper Cretaceous sedimentary record also influenced on the better or worse fossil record preservation during the subsequent normal diagenesis. The presence of marly lithosomes, either as outer platform or as restricted margin-littoral (lagoon and/or palustric) facies, intercalated between the carbonate bars of the successive platforms, played a significant control on diagenesis, in some cases inhibiting the entrance of diagenetic fluids, so protecting the underlaying materials, and in other, as source of the chemical elements necessary for the diagenetic recrystallisation processes (dolomitization, micritization, silicification).

Within this context, the presence of a very continuous mid Turonian marly lithosome, of palustric environment with intense subaerial paleoalteration (Alarcón Formation, Martín-Chivelet and Giménez, 1993) has been related with the continental fresh-water input mixed with the interstitial sea-water of the underlying carbonate sediments, thus generating the dolomitization, dedolomitization, and silicification processes (shallow phreatic eogenesis) affecting the first rudist assemblage materials (Fernández-Calvo, 1982).

Also, the presence of a thick evaporitic-dolomitic succession at the final part of the Cretaceous succession in the central part of the basin (Segura et al., 2006) is considered responsible for the intense dolomitization, dissolution, and recrystallization affecting the fourth rudist assemblage materials, inhibiting any taxonomic precision in the identification of their fossil record. In front of this situation, the search of new fossil localities in more northern successions of the basin (now Basque-Cantabrian Range), where the mentioned end-Cretaceous evaporitic-dolomitic succession is thinner or was not deposited, should focus subsequent field seasons.

7. Conclusions

Twenty rudist taxa occurring in the shallow water carbonate platform successions of the Iberian Basin (nowadays Iberian Range) are identified, described, and figured. The knowledge of the shell characters of some taxa, and of their intraspecific variability, has been improved. The positioning of the rudist assemblages within the depositional framework of high and low frequency, and the correlation with ammonite biozones, increased their taxonomic, biostratigraphic, and palaeobiogeographic significance. Seven taxa are described for the first time from the area, one of them a new species of a new genus. The controversial issue *Hippurites incisus* versus *Hippurites vasseuri* is elucidated: they are different species with different age, respectively, Coniacian and Turonian. The identification of the radial structures in *Radiolites douvillei* questions its adscription to genus *Radiolites*. The description of intraspecific variability in radiolitid species helped to resolve some taxonomic issues: *Bournonia gardonica* and *Bournonia fascicularis* synonymy; previous misidentifications of *Biradiolites canaliculatus*.

Four rudist assemblages are distinguished: lower Turonian, upper Turonian, upper Coniacian, and Santonian—?Campanian. The rudist abundance, taxonomic diversity, and shell preservation in each of them, is controlled by the depositional evolution (a succession of shallow water carbonate platforms affected by successive high and low frequency sea level falls) of the Iberian Basin.

The first three assemblages have been positioned within the Upper Cretaceous Central Iberian Basin sequence stratigraphy framework (high-frequency depositional stacking pattern, in the first two), and calibrated with ammonite biozones. This also provides biostratigraphic datums which help improving the chronostratigraphic framework of the Cretaceous sedimentary successions of the Iberian Basin, especially towards the coastal margins.

Both, the consistent coherence between the distribution of rudist assemblages and the tecto-eustatic evolution of the Iberian Plate during the Late Cretaceous, and the westwards displacement of the shallow water platform facies belts with respect to the axis of the basin, as it is for the 3rd and 4th rudist assemblages, suggest that more favourable localities of the fourth rudist assemblage (or more recent ones not identified in the Iberian Range) may be expected in areas situated further NW of the Iberian Massif margin (León and Palencia provinces). There, the thick end-Cretaceous evaporitic-dolomitic succession, responsible for the intense dolomitization, dissolution, and recrystallization affecting the preservation of rudists in the Iberian Range, is thinner or was not deposited.

Author statement

Javier Gil: Conceptualization, Investigation, Resources, Visualization, Writing-Original Draft. **Jose Maria Pons**: Conceptualization, Investigation, Resources, Data Curation, Writing-Original Draft, Writing-Review & Editing, Supervision. **Enric Vicens**: Methodology, Investigation, Visualization. **José García Hidalgo**: Investigation, Resources. **Manuel Segura**: Investigation, Resources.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.cretres.2023.105815.