Turkish Journal of Earth Sciences (Turkish J. Earth Sci.), Vol. 19, 2010, pp. 543–556. Copyright ©TÜBİTAK
doi:10.3906/yer-0901-11 First published online 22 October 2010

Mathesia Mainelli (Hippuritoidea, Monopleuridae) from the Late Aptian–Albian of the Mediterranean Region: A Revision

JEAN-PIERRE MASSE & MÜKERREM FENERCİ-MASSE

Laboratoire de géologie des systèmes et des réservoirs carbonatés, Université de Provence,
13331 Marseille Cedex 03, France (E–mail: Jean-Pierre.Masse@univ-provence.fr)

Received 1 April 2009; revised typescript received 18 June 2009; accepted 15 October 2009

Abstract: *Agria darderi* Astre and *Mathesia terticolloquiirudistarum* Mainelli represent a single taxonomic entity: *Mathesia darderi* (Astre). *Mathesia* is characterized by an erect posterior myophoral plate and an anterior myophoral crest in the LV, the RV myophores being on the shell wall. A peculiar shell structure is observed in the RV: the junction between the outer calcitic shell layer and the inner formerly aragonitic shell layer is scalloped or festooned and usually includes longitudinal tubes. The overall morphological traits and myocardinal organisation of *Mathesia* are similar to those of *Debrunia*, although the latter lacks the scalloped or tubular inner shell features of the former. *Debrunia* is regarded as the ancestor of *Mathesia*. The palaeobiogeographical distribution of *Mathesia darderi* includes the southern and northern margins of the Mediterranean Tethys, and its maximum geographical extent coincides with the late Aptian–Albian.

Key Words: Rudists, *Mathesia*, Aptian–Albian, palaeobiogeography, Mediterranean region

Akdeniz Bölgesi'ndeki Geç Apsiyen–Albiyen Yaşlı Mathesia Mainelli (Hippuritoidea, Monopleuridae)'nin Revizyonu

Özet: *Agria darderi* Astre ve *Mathesia terticolloquiirudistarum* Mainelli tek taksonomik birlik sunarlar: *Mathesia darderi* (Astre). *Mathesia* üst kavkısındaki arka miyoforun ince tabaka ve ön miyoforun ay şeklinde ve alt kavkı miyoforlarının kavkı duvarında olmasıyla karakterize edilir. Alt kavkı duvarında gözlenen özel yapı, dış kalsitik kavkı tabakasının ve önceden aragonit olan iç kavkı tabakasının birleşme çizgisinde yeralır, fistolu veya oymalıdır ve her zaman boyuna tüpler içerir. *Mathesia*'nın bütün dış özellikleri ve miyokardinal düzeni *Debrunia*'ninkilerle benzerlik gösterir, ancak *Debrunia* iç kavkısında oymalı yapı veya boyuna tüpler içermez. *Debrunia*, *Mathesia*'nın atası olarak kabul edilebilir. *Mathesia darderi* geç Apsiyen–Albiyen'de Akdeniz Tetisinin güney ve kuzey kıyılarında geniş bir palaeobiyocoğrafik dağılım gösterir.

Anahtar Sözcükler: Rudistler, *Mathesia*, Apsiyen–Albiyen, paleobiyocografya, Akdeniz bölgesi

Introduction

The genus *Mathesia*, with type species *Mathesia tertiicolloquiirudistarum*, was erected by Mainelli (1996), and ascribed to the «Caprinidae having some radiolitid features», and also compared with *Ichthyosarcolites* and *Agriopleura,* including *Agriopleura darderi* (Astre) (Astre 1933).

The objective of the present paper is to demonstrate the synonymy of *Mathesia tertiicolloquiirudistarum* and *Agriopleura darderi* and to discuss the implications for the generic position of *Agriopleura darderi,* which has been repeatedly regarded as erroneously placed in *Agriopleura* (Masse *et al.* 1992, 1998a; Masse 1996; Masse *et al.* 1998b; Steuber & Bachmann 2002). This revision involves a reinterpretation of many characters of *Mathesia sensu* Mainelli, and therefore the diagnosis of this genus. Our study includes the reappraisal of Mainelli's figures and is also based on new observations on specimens collected or illustrated

from the northern and southern margins of the Mediterranean Tethys. This systematic investigation is complemented by biostratigraphical and palaeobiogeographical data and a discussion on evolutionary aspects.

Historical Aspects: *Mathesia* as a Valid Genus Name for «*Agria*» *darderi* Astre

The description of *Agria darderi* (Astre 1933) was based on transverse sections cut in a collection of right valves (RV), the generic concept being founded on the cylindro-conical habit, radial bands, a circular outline in transverse section, the presence of a ligamentary crest and the outer shell ornamentation (fine and acute ribs) (Figure 1a), regarded as close to the characteristics of «*Agria*» *blumenbachi* (Studer). Unfortunately the placement of this form in the genus *Agria* Matheron (Matheron 1878) did not address the organisation of the left valve (LV), depressed and with protruding myophoral bulges (Figure 1b, c), which is highly critical for the definition of the genus in question, as shown by the earlier works of Paquier (1900), Toucas (1907) and Douvillé (1910, 1918). Subsequently the formal replacement of *Agria* by *Agriopleura,* proposed by Kühn (1932) did not modify the definition and characters of the former genus, moreover Astre (1954) still used *Agria* Matheron instead of *Agriopleura* in his description of *Agria darderi* var. *pyrenaica*. In a revision of the genus *Agriopleura* by Masse & Philip (1974) the formal modification of Kühn from *Agria* to *Agriopleura* was acknowledged and the assignment of *Agria darderi* to *Agriopleura* accepted. Because *Agria darderi* var. *pyrenaica* defined by Astre (1954) was described as «cellular», casting some doubt on the generic position of this form and suggesting a placement in the Radiolitidae, Masse & Philip (1974) reappraised the type and other specimens of the same group collected in Spain, in order to check for the presence of the cellular structure in question. Observations performed on this material revealed the presence of a very specific microstructure found at the junction between the inner (formerly aragonitic) and outer (calcitic) shell layer, which was described as consisting of «longitudinal tubes derived from the invagination of the inner margin of the calcitic layer». This structure is markedly different from that of the Radiolitidae, in particular from that of the Late Aptian–Albian coeval *Archaeoradiolites* which has a radially branching pattern, and *Eoradiolites* with a quadrangular regular network (Fenerci-Masse *et al*. 2006; Masse *et al*. 2007). Specimens with this diagnostic microstructure, subsequently found and described from the Late Aptian of Algeria (Chikhi-Aouimeur 1983) were also ascribed to *Agriopleura*, and those from Tunisia as well (Tlatli 1980; Masse 1984).

The discovery in SE Spain, namely at Sierra del Carche (SE Spain) (Masse *et al*. 1992) of a bivalve specimen of «*Agria*» *darderi* and sections of the same found at El Caroch, allow us to analyse the myophoral organisation of the LV, which consists of a posterior myophoral plate, slightly oblique, and an anterior crest, both protruding below the commissure (Figure 2).

The diagnosis provided by Mainelli (1996) for the genus *Mathesia,* based on *Mathesia tertiicolloquiirudistarum,* is as follows: «Shell very inequivalve, attached valve conical, free valve capuliform. Shell wall of compact inner layer and outer layer ornamented with longitudinal angular ribs. Attached valve with a median layer of two rows of small round canals. In both valves, siphonal bands with one rib in the interband; ligament ridge without ligamental external groove; body cavity without tabulae». The associated description and figures (Figure 3) indicate:

(1) that myophores of the LV are represented by small apophyses somewhat comparable to those of *Agriopleura* (table 1, p. 208), those of the RV being on the shell wall, although this organisation was not illustated;

(2) the presence of a «cellulo-prismatic structure» of the outer shell layer.

For Mainelli, the existence of «canals» in the «median layer» is considered a diagnostic feature of the family Caprinidae to which he assigned *Mathesia*. Moreover shell morphology, ornamentation, radial bands and myophoral organisation are compared to those of the Radiolitidae and therefore *Mathesia*, he proposed, may belong to the so-called «informal group number

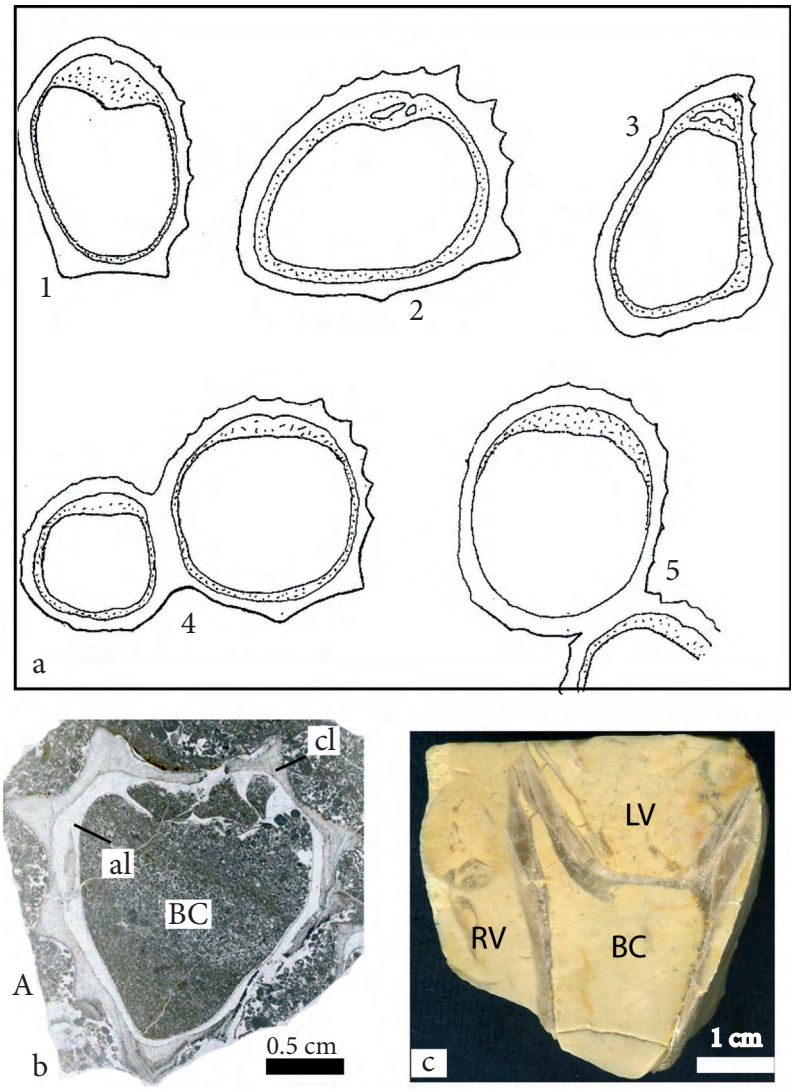

Figure 1. **(a)** *Agria darderi* Astre. Type figures referring to transverse sections of the RV; **(b, c)** *Agriopleura cf. marticensis* (d'Orbigny) (Barremian, Provence); **(b)** transverse section of the RV showing the cardinal apparatus and the strong ribs; **(c)** longitudinal section of a bivalve specimen showing the concave upward LV protruding into the RV. Abreviations: RV– right valve; LV– left valve; A– anterior; P– posterior; pmp– posterior myophoral plate; amb– anterior myophoral bulge; BC– body cavity; cl– calcitic outer shell layer; al– inner shell layer, formerly aragonitic.

3» of Dechaseaux *et al.* (1969) including «caprinids with radiolitid characters».

Careful observations of Mainelli's figures and the study of our own sample collection show that the foregoing diagnosis, description and systematic placement have to be modified.

(1) The so-called «canals» of the «median layer» are located at the inner margin of the outer

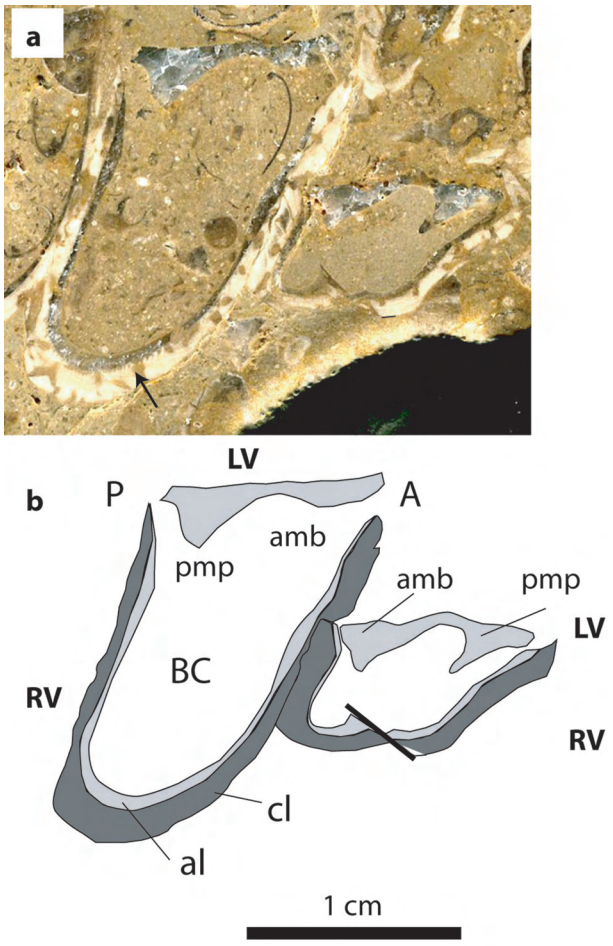

Figure 2. Myophoral features of the LV of '*Agria*' *darderi*. Albian from El Caroch (Almansa region, SE Spain). **(a)** slab showing longitudinal sections of two bivalve specimens; **(b)** interpretation focusing on the myophoral organisation. Arrow indicates the scalloped inner margin of the outer shell layer.

calcitic shell layer. In the Caprinidae and *Ichthyosarcolites*, by contrast, they develop within the inner, formerly aragonitic, shell layer (Skelton & Masse 1998), therefore *Mathesia* must be excluded from the Caprinidae and the Ichthyosarcolitidae. Mainelli pointed out the «double row of inner canals» as a generic attribute. This structure conforms to that of «*Agria*» *darderi* which possesses one or two rows of «canals» (Masse & Philip 1974; Masse *et al.* 1998a; Steuber & Bachmann 2002).

(2) The alleged «radiolitid features», especially the shell morphology, ornamentation and radial bands, are found in other groups, namely the Monopleuridae and Caprotinidae; moreover myophores of the LV, as described by Mainelli, differ from those of the Radiolitidae, which are characterized by vertical plates protruding into the opposite valve. We regard the so called «cellulo-prismatic» peculiar structure illustrated on plate 3, figure 1b, without further comment in the text, as compact prismatic bound by funnel shape growth lines, a feature also found in «*Agria*» *darderi* (Masse & Philip 1974).

(3) Myophoral features of the LV are not well illustrated on Mainelli's plates which mainly refer to dorso-ventral sections and focus on teeth instead of myophores. Comparisons with «*Agria*» *darderi* are therefore difficult.

(4) The so-called accessory cavities mentioned on the RV include the ligament cavity and cavities which represent longitudinal invaginations of the sockets, in correspondence with longitudinally ribbed teeth, features also found in «*Agria*» *darderi.*

(5) Radial bands are slightly concave, in «*Agria*» *darderi* as well, a feature markedly different from that of *Agriopleura,* with salient bands.

The foregoing reappraisal of the characters of *Mathesia tertiicolloquiirudistarum* show no significant dissimilarities between this species and «*Agria*» *darderi* Astre, which implies that the two forms represent a single taxonomic entity. The existence of a simple or a double row of «longitudinal canals» has been observed in a single specimen (Steuber & Bachmann 2002) and cannot be used to distinguish *Mathesia terticolloquiirudistarum* from «*Agria*» *darderi*.

Characters of the LV: salient and with an asymmetric myophoral organisation are obviously distinct from those of *Agriopleura*. The genus *Mathesia* is therefore accepted as valid whereas the specific name attached to the former «*Agria*» *darderi* Astre, takes priority.

Figure 3. *Mathesia tertiicolloquiirudistarum* Mainelli. Type figures (1 to 13, 1a–b being the holotype) showing the overall morphology and some internal characters based on transverse or longitudinal sections (see text for comments).

Systematic Palaeontology

Order: Hippuritoida Newell 1965

Superfamily: Hippuritoidea Gray 1848

Family Monopleuridae Munier-Chalmas 1873

Mathesia Mainelli 1996 emend.

Type Species. *Mathesia tertiicolloquiirudistarum* Mainelli

Diagnosis. Cylindro-conical elongated RV, moderately salient (capuloid) LV. Outer shell layer with a scalloped or tubular inner margin. LV with an erect posterior myophoral plate, the anterior a crest; myophores of RV on shell wall. Ligamental ridge small, in a cavity; radial bands flat or concave.

Discussion. The peculiar structure of the shell wall of *Mathesia* , differs from that of *Agriopleura* and other Monopleuridae, and also departs from that of the Radiolitidae. The presence of an inner longitudinal structure tends to conform to the longitudinal striation usually observed in the RV of the Monopleuridae, a result of the orientation of the calcitic prisms.

Four basic microstructures having a strong bearing on the morphology of the inner margin of the outer shell layer of the RV, have been recognized (Figure 4): (1) radial fibrous, bilamellar, a feature commonly found in the Monopleuridae (Masse & Philip 1974), with a flat boundary with the inner shell layer; (2) semi-rounded bodies having a fan-like arrangement of prisms in transverse section, corresponding with a convex inward scalloped outline; usually there is a single row of semi-rounded bodies, flanked outward by radial prisms; (3) loosely packed convex inward protrusions, separated by sub-rounded or pyriform cavities, corresponding with the so-called 'tubular structure' described by Masse & Philip (1974), the invagination of the inner shell layer tends to produce deep festoons; (4) folded protrusions may result in the formation of two rows, or sometimes more, sub-rounded cavities, the orientation of which tend to be longitudinal to the shell axis (main tubes) or even oblique to the shell axis to form minute somewhat vermiform features.

The above microstructural types grade to each other, the common spatial sequence, of increasing complexity, being from (1) to (4).

We have observed the above peculiar microstructures on thin sections of specimens collected in late Aptian–Albian beds from Tunisia and various localities from Spain and Anatolia (Figure 5). The microstructural habit figured from specimens collected in Algeria (Chikhi-Aouimeur 1983), Italy (Cestari & Sartorio 1995; Mainelli 1996), and Egypt (Steuber & Bachmann 2002) conform to the above description.

The relative development of the four basic types of microstructures varies in correspondence with the size of the specimens and, in a given specimen, in correspondence with the different parts of the shell. For instance small individuals and/or apical sections tend to lack cavities which are therefore present only at adult stage. Moreover in small individuals the scalloped habit of the inner part of the outer shell layer has a limited extent relatively to the flat morphology which is a feature common to the Monopleuridae, e.g. *Monopleura*. At adult stage (Figure 6) the scalloped habit tends to be limited to the dorsal side and thinner parts of the ventral side of the shell, tubular cavities, especially the multiple rows, being present in thickened part of the shell, for instances near the ribs. These observations conform to those of Steuber & Bachmann (2002).

The peculiar stucture of the inner margin of the outer shell layer is expected to correspond with radial crenulations of the commissural surface, which are sometimes terminated by small tubercles found, for instance, in some forms of *Monopleura* (Skelton 1976). These aspects linked with the presence of radial muscles in the outer mantle lobe, allow deep withdrawal of the mantle margin, as in oysters (Skelton, personal communication). Testing this hypothesis will require specimens with a well-preserved commissural surface and allowing observation of the relationships between the scalloped inward outer shell layer and its morphological expression on the inner commissural margin; such specimens are presently lacking.

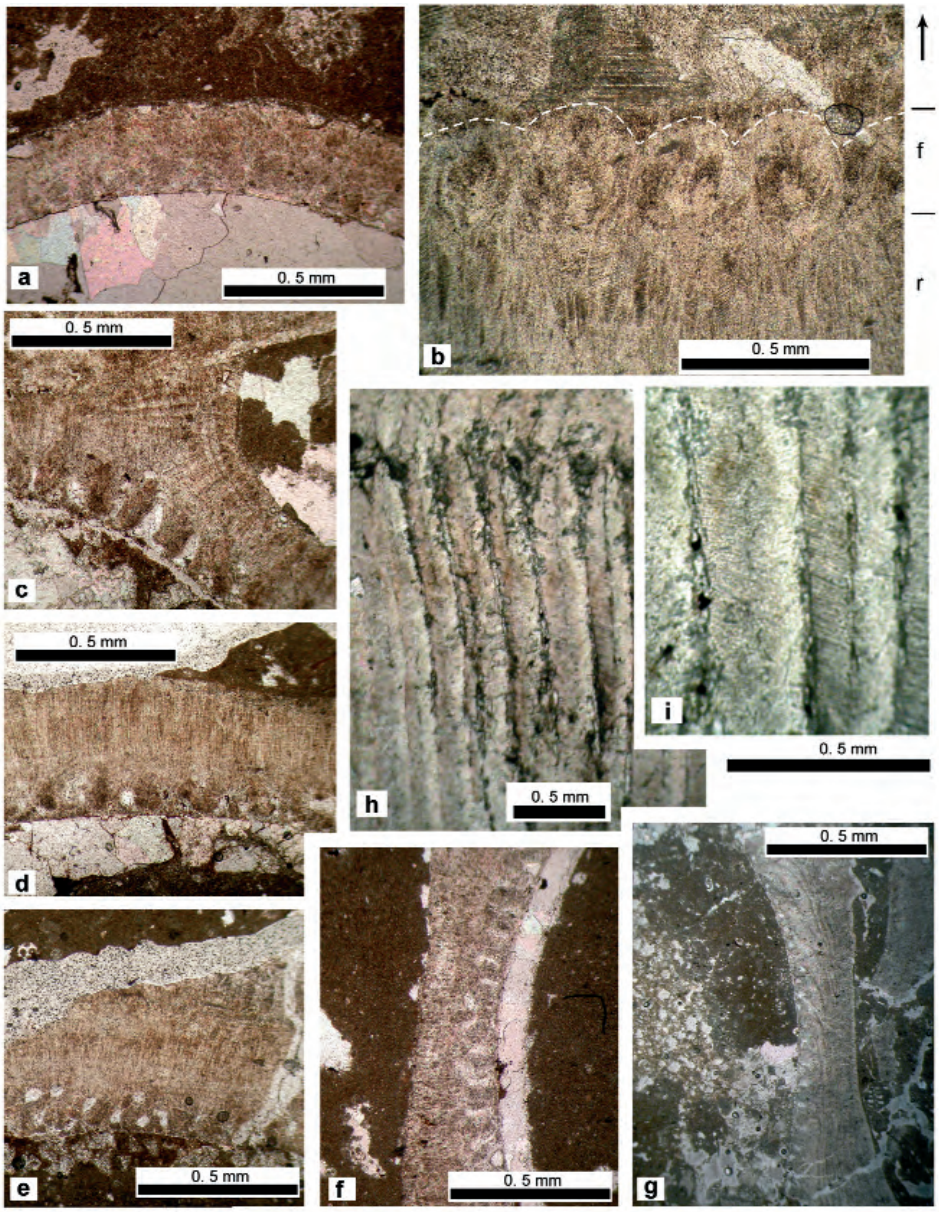

Figure 4. Types of microstructures of the inner margin of the outer shell layer (transverse habit) of *Mathesia darderi*. **(a)** bilamellar structure, notice the flat boundary with the inner shell layer; **(b)** tightly linked adjacent sub-rounded bodies with a fan like fibrous structure responsible for the scalloped aspect of the boundary between the outer and inner shell layer (f), flanked outward by radial fibers (r) (polarized light), arrow points to body cavity; **(c)** deeply scalloped (festoons) inner margin; **(d)** ibidem with minute tubes; **(e)** double row of minute tubes; **(f)** ibidem to show the radial orientation of tubes; **(g)** longitudinal oblique section showing the connection between the inner, tubular, and outer, compact, portions of the outer shell layer; **(h)** longitudinal, tangential, section of the inner scalloped portion of the outer shell layer showing the elongated structures with a feather-like microstructure, distal (commissural) terminations acute; **(i)** close up of (h) showing diverging fibres from a median dark line. Figures (a, c, d, e, f, g) are from specimens of El Carche (SE Spain), figures (b, h, i) are from specimens from the Karaburun Peninsula (Western Turkey).

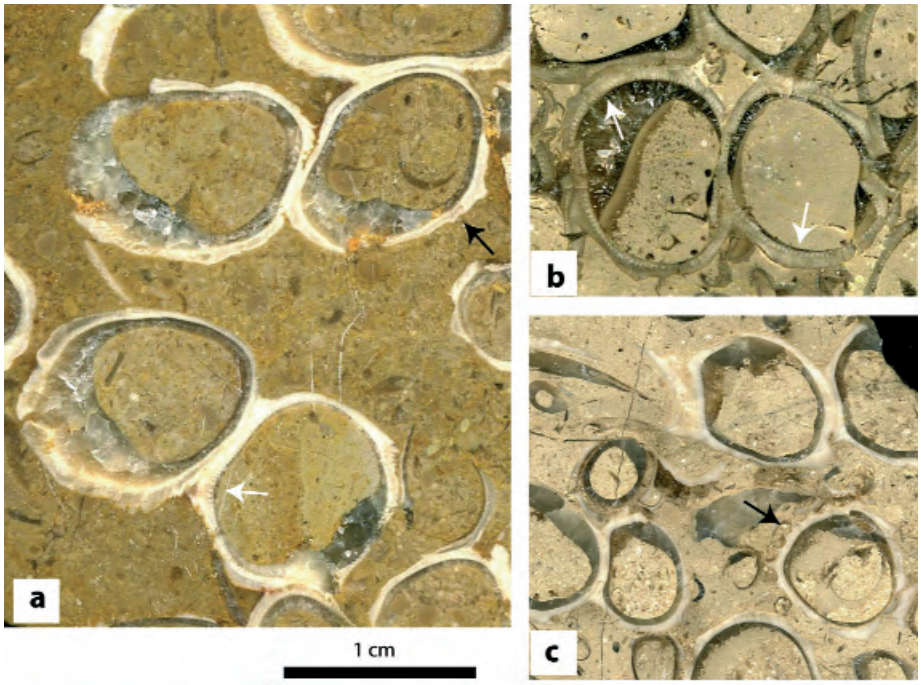

Figure 5. Shell habit (RV) and structure of *Mathesia darderi*: the scalloped and striated inner margin of the outer shell layer is indicated by white arrows, black arrows showing longitudinal ribs of the dorsal side. **(a)** Albian from El Carche, SE Spain (15808); **(b)** late Aptian of Jebel Serdj, Tunisia (15809); **(c)** late Aptian from Gata, SE Spain, type region of '*Agria' darderi* described by Astre, 1933 (15795).

Mathesia belongs to the sub-grouping of Monopleuridae having a myophoral plate on the LV (the informal petalodontid group sensu Masse & Fenerci-Masse 2009) including: *Petalodontia* Pocta (1889), *Pseudopetalodontia* Masse *et al.* (2007), *Debrunia* Masse & Fenerci-Masse (2009), and advanced species of the genus *Agriopleura* (Fenerci-Masse *et al.* 2006) (Figure 7). Notwithstanding its morphological similarities with *Agriopleura,* namely *A. blumenbachi* (Studer), concerning the RV, *Mathesia* contrasts with the former genus by the morphology and myophoral organisation of the LV, characterized by: a salient instead of depressed morphology, whereas myophores are strongly asymmetric. Additional differences include the presence of a ligament groove on the RV and depressed radial bands. *Mathesia* also differs from *Petalodontia* Pocta with a single, anterior, myophoral plate on the LV, and from *Pseudopetalodontia* Masse et al. with radiolitid type myophores (Masse *et al.* 2007). The myophoral organisation is close to that of *Debrunia* Masse & Fenerci-Masse (2009); this genus has a posterior myophoral plate and an anterior myophoral crest on the LV, myophores of the RV being on the shell wall. In *Debrunia* radial bands are also concave but the shell lacks the complex microstucture found in the calcitic layer of the RV.

The absence of a myophoral cavity on both valves warrant placement in the Monopleuridae.

Mathesia darderi (Astre)

1933- *Agria darderi* Astre, p. 103, text-figures 1–5

1954- *Agria darderi* var. *pyrenaica* Astre, plate V, figure 1, text-figure 19

1974- *Agriopleura darderi* (Astre), Masse and Philip, figures 2, 3.

1983- *Agriopleura darderi* (Astre), Chikhi-Aouimeur, p. 43, plate 2, figure 6.

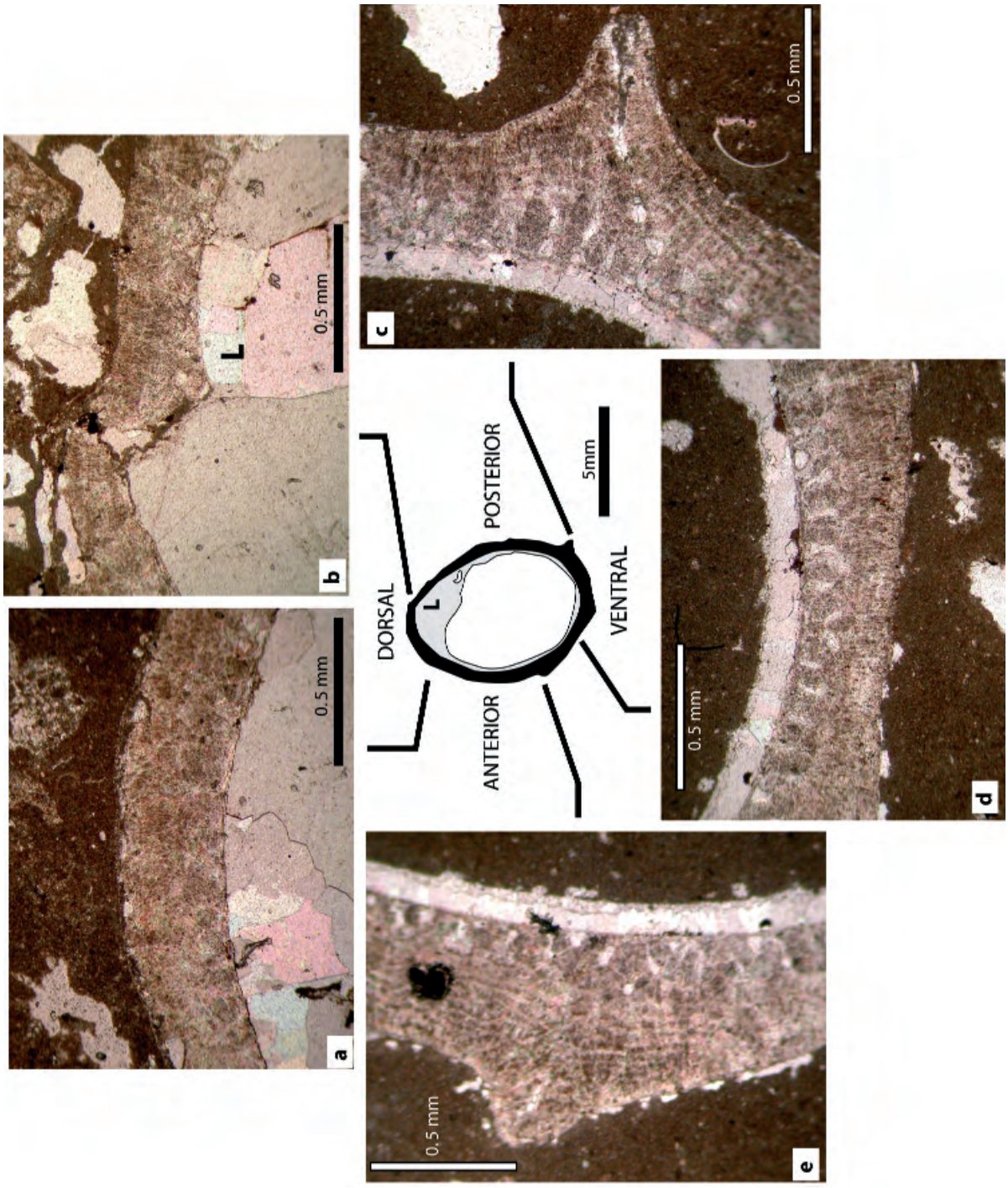

Figure 6. Variations in microstructure (see basic types on Figure 4) of the inner part of the outer shell layer of *Mathesia darderi*, in correspondence with the different parts of the RV. Specimen from El Carche (SE Spain).

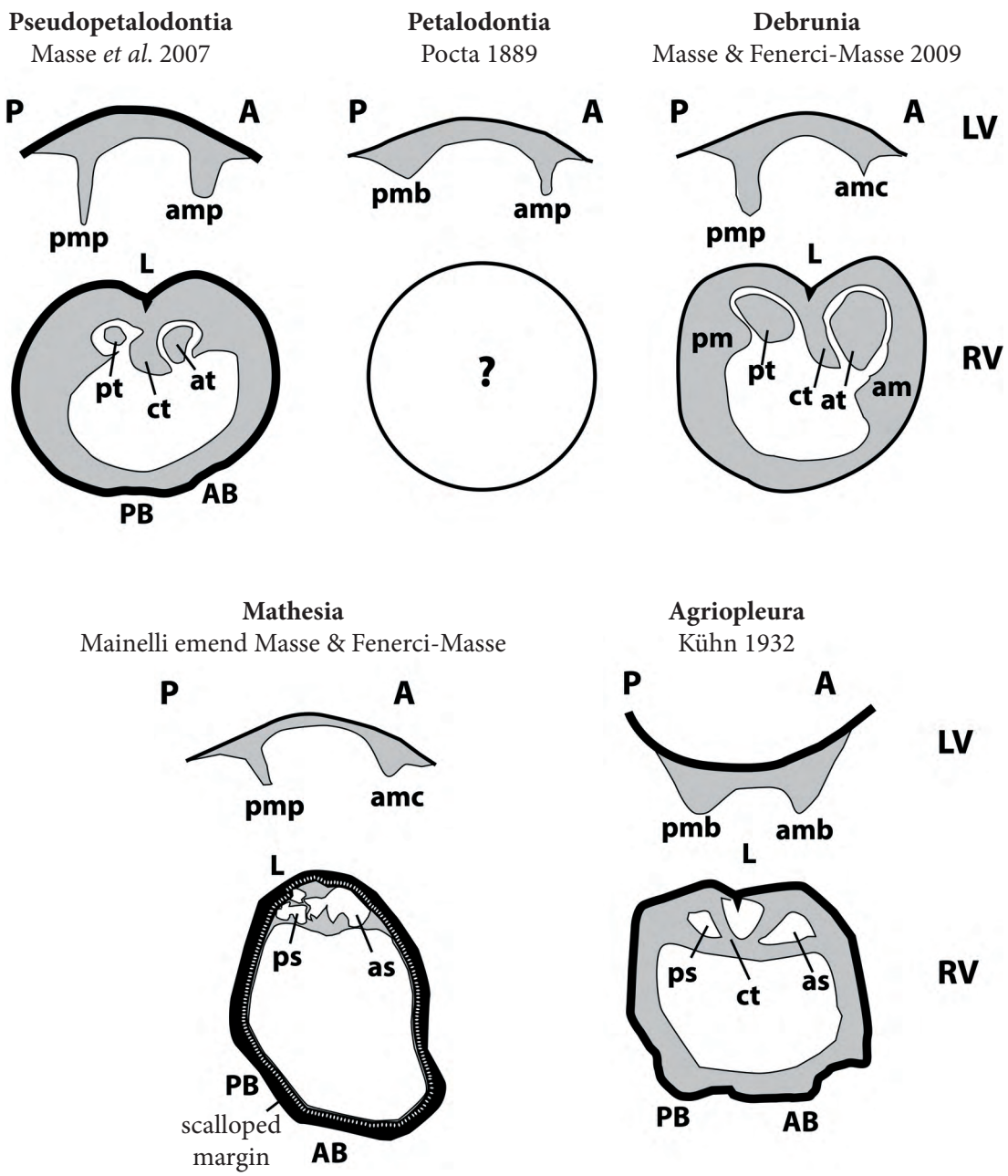

Figure 7. Synoptic view of the Monopleuridae with one or two myophoral plates on the LV (petalodontids); (based on transverse and longitudinal sections) to show the organisation of *Mathesia* compared with those of adjacent genera. Calcitic outer shell layer in black, formely aragonitic inner layer in grey.

1992- *Agriopleura* ? *darderi* (Astre), Masse *et al.*, p. 206, plate 4, figure 6

1995- *Agriopleura,* Cestari and Sartorio, p. 95, 97, text-figures

1996- *Mathesia tertiicolloquiirudistarum* Mainelli, p. 201–209, plate 1, figures 1–13; plate 2, figures 1–10; figure 4; plate 3, figures 1–4.

1998- *Agriopleura* ? *darderi* (Astre), Masse *et al.*, p. 201, figure 10-1

2002- *Agriopleura* ? *darderi* (Astre), Steuber and Bachmann, p. 736–738, text-figure 7E, F, plate 1, figure 1.

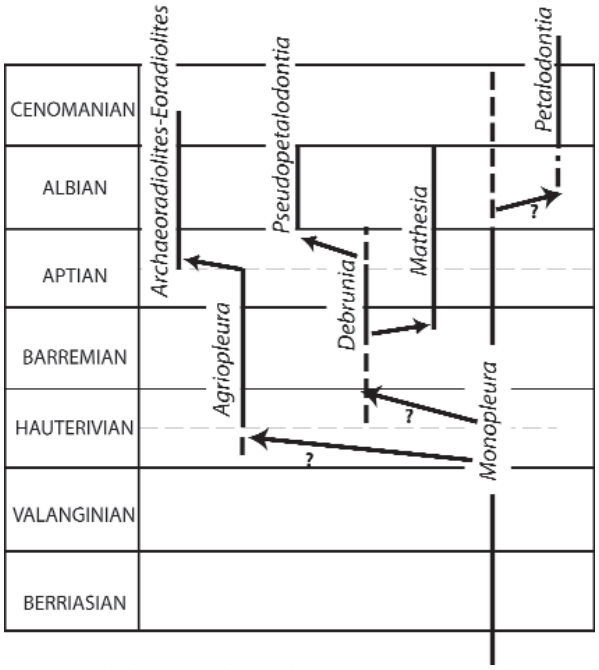

Figure 8. Phyletic model and stratigraphic distribution of petalodontid Monopleuridae showing the relationships of *Mathesia* with adjacent genera.

Diagnosis. *Mathesia* with RV subcylindrical, subcircular to elliptical (dorso-ventral diameter larger than antero-posterior) in transverse section, diameter 1 to 3 cm, usually 4 to 10 longitudinal ribs, more developed on the antero-dorsal side, but sometimes absent. Radial bands smooth, flat or slightly depressed, bounded by ribs, the antero-ventral commonly with a double keel, interband marked by a rib, ligament ridge subtriangular, in a cavity, ligament groove inconspicuous or weak, calcitic outer shell layer relatively thin, and having usually four types of microstructures within the inner shell layer, essentially the scalloped and deep festoon types, simply fibrous and multi-row types being subordinate. LV capuloid more or less flattened, especially ventrally.

Description and Variability. Transverse sections of the subcylindrical RV have been currently illustrated in the literature and their diagnostic microstrucure as well. Variability includes size, that is commissural diameter and length of RV, and the density of longitudinal ribs. The dorso-ventral diameter tends to be slightly higher than the antero-posterior one. Specimens with a relatively large size (dorso-ventral diameter higher than 20 mm and up to 30 mm) are uncommon, 12–16 mm being usual, therefore *Mathesia darderi* var. *pyrenaica* Astre, the diameter of which is 10–15 mm (Astre 1954), falls in the size range of the species and the validity of this variety must be rejected. In a given population specimens with well expressed longitudinal ribs are coeval with specimens with few or no costae, and we did not observe any clear relationships between size and ornamentation.

Evolutionary Aspects and Palaeoenvironmental Context

Similarities between *Debrunia* and the late Aptian–Albian *Mathesia* suggest a derivation of the latter from the former, *Mathesia* being a '*Debrunia*' with a peculiar microstructure of the inner margin of the outer shell layer, but retaining the overall morphology and myophoral organisation of its ancestor (Figure 8). As shown earlier, *Debrunia* is also the root for *Pseudopetalodontia*. Dissimilarities with *Agriopleura* rules out a phyletic derivation of *Mathesia* from the latter, notwithstanding microstructural similarities pointed out by Masse & Philip (1974).

The outbreak of *Mathesia darderi* in the late Gargasian coincides with the emergence of the Radiolitidae, coupled with the appearance of some representatives of the Requieniidae (*Pseudotoucasia)* and the outbreak of the Polyconitidae (Fenerci-Masse *et al*. 2006). This radiation is associated with the recovery following the Mid-Aptian extinction event (Masse & Philip 1986; Masse 1989; Skelton 2003).

Biogeographical and Biostratigraphical Distribution

As mentioned above, in the systematic section, *Mathesia darderi* has been identified from Spain (Catalonia, Murcia Province), Italy, Tunisia, Algeria,

France (Ariège), Turkey and Egypt, and was therefore present on the northern (European) and southern (African) margins of the Mediterranean Tethys (Figure 9). Recent data from Spain and Bulgaria (Fenerci-Masse *et al.* 2010) document the presence of *Mathesia darderi* in the Barremian–Bedoulian of these regions.

Late Aptian occurrences include the late Gargasian from eastern Algeria (Chikhi-Aouimeur 1983), the late Gargasian–Clansayesian from Tunisia (Tlatli 1980; Masse 1984), and the Clansayesian of Matese (Masse *et al*. 1993). Albian occurrences include SE Spain (Masse *et al*. 1992), northern Spain (Masse & Philip 1974; Mongin *et al*. 1983), SW France (Masse 1996), Italy (Cestari & Sartorio 1995; Mainelli 1996), Egypt (Steuber & Bachmann 2002) and Turkey (Masse *et al*. 2010).

Conclusions

Agria darderi Astre, subsequently transfered to *Agriopleura*, and *Mathesia terticolloquiirudistarum* Mainelli represent a single taxonomic entity: *Mathesia darderi* (Astre). *Mathesia* is characterized by an erect posterior myophoral plate and an anterior myophoral crest on the LV, the RV myophores being on the shell wall. A peculiar shell structure is observed on the RV: the junction between the outer calcitic shell layer and the inner formerly aragonitic shell layer is scalloped or festooned, usually with one to three rows of longitudinal tubes, a feature linked to the presence of convex inward protrusions of the calcitic shell layer. Longitudinal ridges found at the inner margin of the calcitic layer, in correspondence with the above microstructures, may be linked with muscles of the outer mantle lobe. The overall microstructure, in conjunction with myophoral characters warrants a placement of the genus in the Monopleuridae and precludes a placement in the Caprinidae or «caprinids with radiolitid features». Differences with *Agriopleura* concern the shape of the RV and corresponding myophores, radial bands and the inner shell structure. The overall morphological traits and myocardinal organisation of *Mathesia* are similar to those of *Debrunia*, although the latter lacks

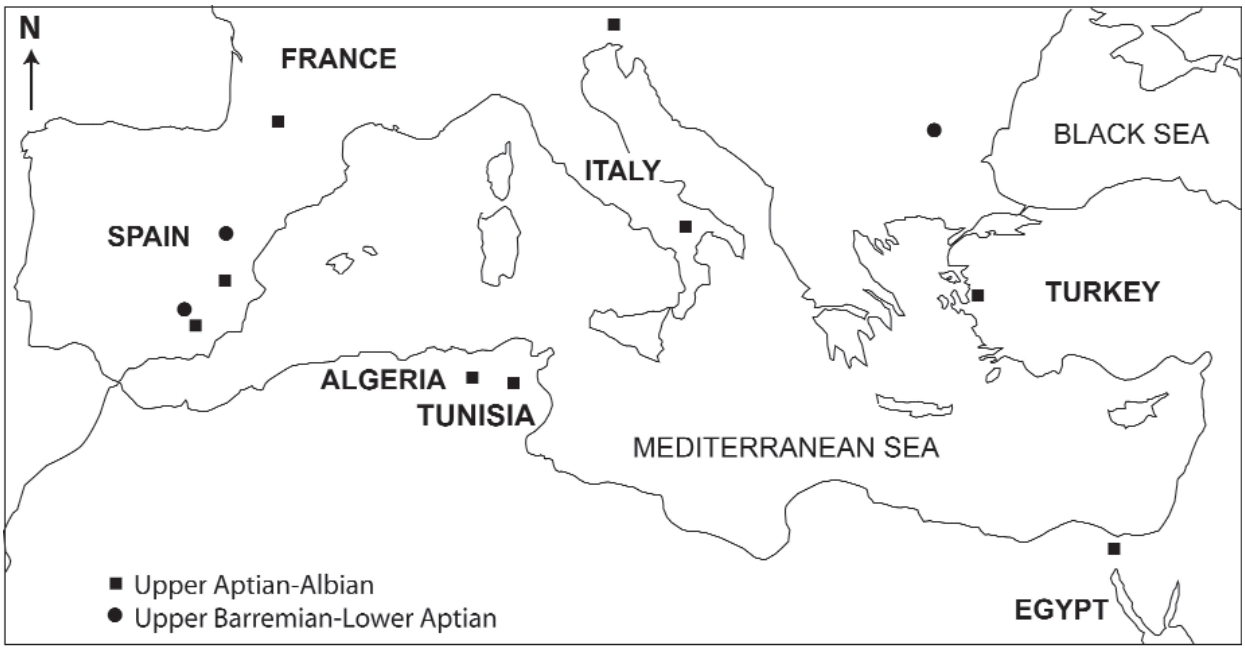

Figure 9. Geographic distribution of *Mathesia darderi*.

the scalloped or tubular inner shell features of the former. *Debrunia,* a Barremian– early Aptian form, is regarded the ancestor of *Mathesia*. The palaeobiogeographical distribution of *Mathesia darderi* includes the southern and northern margins of the Mediterranean Tethys, its stratigraphic acme range is the late Aptian–Albian, whereas its presence in the late Barremian–Bedoulian has been recently verified.

Acknowledgements

We thank F. Chikhi-Aouimeur (Alger) and P.W. Skelton (Milton-Keynes) for their useful review of a preliminary version of this paper. We are grateful to C. Arias-Ordas and L. Vilas (University Complutense, Madrid) for providing samples of early Aptian representatives of *Mathesia darderi* from SE Spain.

References

Astre, G. 1933. Sur les petits Agria tubuleux de l'Urgo-Aptien. *Bulletin de la Société géologique de France* **5**, 99–105.

Astre, G. 1954. *Radiolitidés nord pyrénéens*. Mémoire de la Société géologique de France **33**, 3–4, 71.

Cestari, R. & Sartorio, D. 1995. *Rudists and facies of the periadriatic domain*. AGIP, S. Donato Milanese.

Chikhi-Aouimeur, F. 1983. Etude paléontologique de quelques rudistes de l'Aptien supérieur du Djebel Ouenza (Algérie, NE). *Géologie Méditerranéenne* **10**, 33–48.

Dechaseaux,C., Coogan, A.H., Cox, L.R. & Perkins, B.F. 1969. Hippuritacea: systematic descriptions. *In:* Moore, R.C. (ed), *Treatise on Invertebrate Palaeontology*. University of Kansas, and Geological Society of America, Lawrence, Kansas, Part N, Mollusca 6 (Bivalvia) **2**, N776–817.

Douvillé, H. 1910. Etudes sur les rudistes. Rudistes de Sicile, d'Algérie, d'Egypte, du Liban et de la Perse. *Bulletin de la Société géologique de France*, *Paléontologie* **41**, 1–83.

Douvillé, H. 1918. Le Barrémien supérieur de Brouzet. Partie III: les rudistes. *Mémoires, Bulletin de la Société géologique de France, Paléontologie* **52**, 1–28.

Fenercİ-Masse, M., Masse, J.-P., Arias, C. & Vilas, L. 2006. *Archaeoradiolites* a new genus from the late Aptian of the Mediterranean region and the origin of the rudist family Radiolitidae. *Palaeontology* **49**, 769–794.

Fenercİ-Masse, M., Masse, J.-P., Kolodziej, B., Ivanov,M., Idakieva, V. 2010. *Mathesia darderi* (Bivalvia, Hippuritoidea, Monopleuridae) morphological, biogeographical and ecological changes in the Mediterranean domain during the late Barremian–Albian. *Cretaceous Research* [in press].

Gray, J.E. 1848. On the arrangement of the Brachiopoda. *Annals and Magazine of Natural History* **2**, 435–440.

Kühn, O. 1932. *Fossilium Catalogus*. Pars 54, Rudistae.

Mainelli, M. 1996. The rudist *Mathesia tertiicolloquiirudistarum* n. gen. n. sp. in the upper Aptian of Serra Sbregavitelli, Matese, south Apennines, Italy. *Revista Mexicana de Ciencias Geologicas* **12**, 201–210.

Masse, J.-P. 1984. Données nouvelles sur la stratigraphie de l'Aptien carbonaté de Tunisie centrale, conséquences paléogéographiques. *Bulletin de la Société géologique de France* **7**, 1077–1086.

Masse, J.-P. 1989. Relations entre modifications biologiques et phénomènes géologiques sur les plates-formes carbonatées du domaine périméditerranéen au passage Bédoulien–Gargasien. *Géobios, Mémoire spécial* **11**, 279–294.

Masse, J.-P. 1996. Lower Cretaceous rudist biostratigraphy of southern France – a reference for Mesogean correlations. *In:* Alencáster, G. & Buitrón-Sánchez, B.E. (eds), *Number devoted to the Third International Conference on Rudists*. *Revista Mexicana de Ciencias Geológicas* **12** (for 1995), 236–256.

Masse, J.-P., Arias, C. & Vilas, L. 1992. Stratigraphy and biozonation of a reference Aptian–Albian p.p. Tethyan carbonate platform succession: The Sierra del Carche Series (oriental Prebetic zone – Murcia, Spain). *In*: Kollmann, H.A. & Zapfe, H. (eds), *New Aspects on Tethyan Cretaceous Fossil Assemblages*. Österreichische Akademie der Wissenschaften, Schriftenreihe der erdwissenschaftlichen Kommissionen **9**, 201-222.

Masse, J.-P., Arias, C. & Vilas, L. 1998a. Lower Cretaceous rudist faunas of southeast Spain: an overview. *Géobios, Mémoire Spécial* **22**, 193–210.

Masse, J.-P., Beltramo, J., Martinez-Reyes, J. & Arnaud-Vanneau, A. 2007. Revision of Albian polyconitid and monopleurid rudist bivalves from the New World. *In*: *Cretaceous Rudists and Carbonate Platforms: Environmental Feedback*. SEPM Special Publication **87**, 221–230.

Masse, J.-P. & Fenercİ-Masse, M. 2009. *Debrunia* nov. gen. a new Barremian-Aptian petalodontid Monopleuridae (Bivalvia, Hippuritacea) from the Mediterranean region. *Palaeontology* **52**, 1363–1372.

Masse, J.-P., Fenercİ-Masse, M., Işintek, İ. & Gungör, T. 2010. Albian rudist faunas from the Karaburun peninsula, İzmir region, Western Turkey. *Turkish Journal of Earth Sciences* **19**, 671–683.

MASSE, J.-P., GALLO-MARESCA, M. & LUPERTO-SINNI, E. 1998b. Albian rudist faunas from southern Italy: taxonomic, biostratigraphic and palaeobiogeographic aspects. *Géobios* **31**, 47–59.

MASSE, J.-P. & PHILIP, J. 1974. Définition, position systématique, répartition stratigraphique et évolution du genre *Agriopleura* Kühn (Rudiste). *Géologie Méditerranéenne* **1**, 53–62.

MASSE, J.-P. & PHILIP, J. 1986. L'évolution des rudistes au regard des principaux évènements géologiques du Crétacé. *Bulletin des Centres de Recherche Exploration-Production Elf-Aquitaine* **10**, 437–456.

MATHERON, P. 1878. *Recherches paléontologiques dans le midi de la France*. Livre 1–2.

MONGIN, D., PEYBERNES, B., SOUQUET, P., THOMEL, G. 1983. Le gisement vraconnien (Albien supérieur) de la Selva de Bonansa (Pyrénées espagnoles): intérêt stratigraphique, paléoécologique et paléobiogeographique. *Palaeogeography, Palaeoclimatology, Palaeoecology* **41**, 45–63.

MUNIER-CHALMAS, H. 1873. Prodrome d'une classification des rudistes. *Journal de Conchyologie* **3**, 71–75.

NEWELL, N.D. 1965. Classification of the Bivalvia. *American Museum Novitates* **2006**, 1–25

PAQUIER, V. 1900. *Recherches géologiques dans le Diois et les Baronnies orientales*. Grenoble.

SKELTON, P.W. 1976. *Investigations into the Palaeobiology of Rudists*. PHD Thesis, Oxford University [unpublished].

SKELTON, P.W. 2003. Rudist evolution and extinction. A North African perspective. *In:* GILI, E., NEGRA, M.H. & SKELTON, P.W. (eds), *North African Carbonate Platform Systems*. Kluwer Academic Publishers, Dordrecht, 215–227.

SKELTON, P.W. & MASSE, J.P. 1998. Revision of the Lower Cretaceous rudist genera *Pachytraga* Paquier and *Retha* Cox (Bivalvia: Hippuritacea), and the origins of the Caprinidae. *Géobios, Mémoire spécial* **22,** 331–370.

STEUBER, T. & BACHMANN, M. 2002. Upper Aptian–Albian rudist bivalves from northern Sinai, Egypt. *Palaeontology* **45**, 725–749.

TLATLI, M. 1980. *Etude des calcaires de l'Albo-Aptien des Djebels Serdj et Bellouta (Tunisie centrale)*. Thèse 3° cycle, Université d'Aix-Marseille I.

TOUCAS, A. 1907. Etudes sur la classification et l'évolution des radiolitidés: *Agria* et *Praeradiolites*. *Mémoires, Bulletin de la Société géologique de France, Paléontologie* **36**, 1–46.