Turkish Journal of Earth Sciences (Turkish J. Earth Sci.), Vol. 19, 2010, pp. 573–581. Copyright ©TÜBİTAK
doi:10.3906/yer-0904-10 First published online 22 October 2010

Debrunia occitanica nov. sp. (Monopleuridae) from the Early Aptian of SE France

MÜKERREM FENERCİ-MASSE & JEAN-PIERRE MASSE

Géosystèmes carbonatés, Université de Provence, 13331 Marseille cedex 3, France
(E-mail: mugemasse@hotmail.com)

Received 28 April 2009; revised typescript received 28 August 2009; accepted 14 September 2009

Abstract: *Debrunia occitanica* nov. sp., described from the early Aptian platform limestones of SE France, is characterized by: a moderately convex left valve, inconspicuous radial bands and a ligament groove in a depression flanked by two longitudinal rounded edges. *Debrunia occitanica* nov. sp. is considered as a chronospecies belonging to a single lineage rooted in the Barremian, and including *Debrunia bruni* and *Debrunia mutabilis*. Evolutionary trends in the three species include flattening of the left valve, development of the corresponding myophores, and reduction of the radial bands. This new species has the potential to be a stratigraphic marker for the early Aptian.

Key Words: Rudists, Monopleuridae, new species, Early Aptian, France

GD Fransa Geç Apsiyen'inde Bulunan *Debrunia occitanica* nov. sp. (Monopleuridae)

Özet: GD Fransa'nın erken Apsiyen yaşlı karbonat platformlarında bulunan *Debrunia occitanica* nov. sp., sol kavkısının hafifce dışbükey, ön ve arka bandlarının belirsiz ve ligamentinin derin bir çukur olmasıyla tanımlanır. *Debrunia occitanica* nov. sp., Barremiyen yaşlı *Debrunia bruni* ve *Debrunia mutabilis*'in erken Apsiyen'deki devamı, yani kronotürü olarak düşünülmektedir. Üç türün evrimsel gelişimi sol kavkının düzleşmesi, miyoforların buna bağlı olarak gelişmesi ve bandların belirsizleşmesini içerir. Bu yeni tür erken Apsiyen için stratigrafik tanımlayıcı olma özelliğine sahiptir.

Anahtar Sözcükler: Rudistler, Monopleuridae, yeni tür, Erken Apsiyen, Fransa

Introduction

The genus *Debrunia* Masse & Fenerci-Masse (2010) is a cylindro-conical rudist characterized by asymmetric, erect myophoral apophyses in the left valve: the posterior myophore is a plate and the anterior a crest. The myophore attachments in the right valve are on the shell wall. *Debrunia* conforms to the 'elevator' mode of growth (Skelton 1991; Skelton & Gili 2002), a key morphotype which was allowed by the invagination of the ligament with a potential for rapid upward growth and clustering to from dense aggregations of individuals. This genus, assigned to the petalodontid Monopleuridae, that is those with one or two myophoral plates in the left valve, was hitherto represented by two species *Debrunia mutabilis* (Matheron) and *Debrunia bruni* (Douvillé), from the Barremian of southern France (Matheron 1878; Douvillé 1918; Masse & Fenerci-Masse 2009).

The objective of the present paper is to describe a new species, *Debrunia occitanica,* restricted to the early Aptian and documented from various localities from southern France (Figure 1). Our description includes data on the stratigraphy and associated faunas from the *Debrunia occitanica* nov. sp. bearing sites. A comparison with the above mentioned Barremian species allows us to discuss the evolutionary implications of the discovery of our new species.

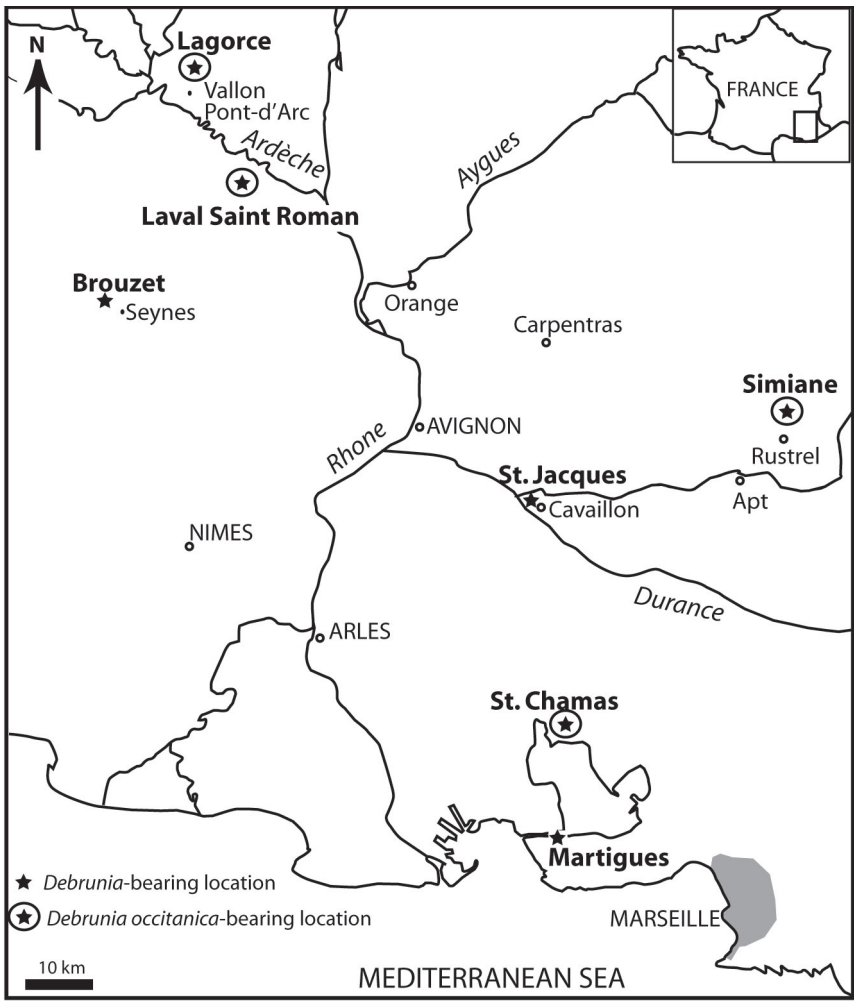

Figure 1. Geographic distribution of early Cretaceous *Debrunia* bearing localities in SE France, focusing on early Aptian *Debrunia occitanica* nov. sp. sites.

Systematic Palaeontology

Abbreviations: LV– left valve; RV– right valve; D– dorsal side; V– ventral side; A– anterior side; P– posterior side; BC– body cavity; am– anterior myophore; amc– anterior myophoral crest; pm– posterior myophore; pmp– posterior myophoral plate; at– anterior tooth; pt– posterior tooth; ct– central tooth; t– tooth; s– socket; as– anterior socket; ps– posterior socket; Lg– ligament groove; Lr– ligament ridge; AB– anterior band; PB– posterior band; cl– calcitic outer shell layer; al– formerly aragonitic inner shell layer; co– commissure.

Order Hippuritoida Newell 1965

Superfamily Hippuritoidea Gray 1848

Family Monopleuridae Munier-Chalmas 1873

Genus *Debrunia* Masse & Fenerci-Masse (2009)

Type Species. Monopleura mutabilis Matheron 1878

***Debrunia occitanica* nov. sp.**

Figures 3, 4 and 5

Generic Placement. The left valve (LV) bears a vertical, posterior, myophoral plate, protruding into the opposite valve and a thin lamellar, anterior commarginal crest; the myophores of the right valve (RV) are on the shell wall. The outer calcitic shell layer is compact-fibrous and its junction with the inner shell (formerly aragonitic) is not scalloped, by contrast with *Mathesia* Mainelli (Masse & Fenerci-Masse 2010). The myophoral organisation and shell structure conform to those of *Debrunia* Masse & Fenerci-Masse (2009).

Derivation of Name. From Occitania the southern, Latin, part of France, where 'langue d'Oc' instead of 'langue d'Oil' (i.e. French) was spoken up to the beginning of the XX century.

Type Locality. 'Ferme Michelet', Ibie valley, south of the village of Lagorce (Ardèche) (Figure 2) illustrated and described by Charollais *et al.* (1998). In this locality *Debrunia occitanica* nov. sp. forms a dense monospecific assemblage which consists of erect, closely packed, individuals. The corresponding lithosome underlies a major regional discontinuity, which marks the boundary between rudist-dominated limestones and overlying marly limestones with ammonites, corresponding with the regional Mid-Bedoulian break. Rudist beds contain: *Pachytraga paradoxa* (Pictet and Campiche), *Praecaprina* sp., *Horiopleura* sp. indicative of an Early Aptian age, a dating corroborated by the associated micropalaeontological assemblage, which includes *Palorbitolina lenticularis* (Blumenbach) and *Orbitolinopsis kiliani* (Prever). Ammonites found in the overlying beds include: *Deshayesites* sp., *Cheloniceras* sp. and *Tropaeum* sp., indicating a Late Bedoulian (*Deshayesites deshaysesi – Dufrenoya furcata* ammonite zones) age (Charollais *et al.* 1998).

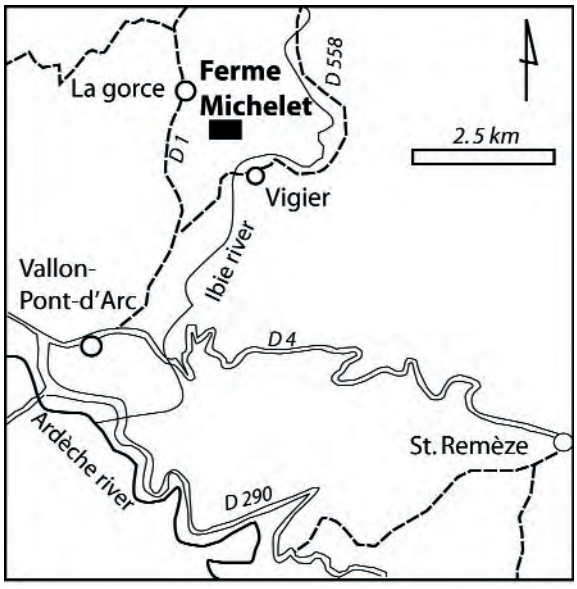

Figure 2. Geographic sketch of the type locality of *Debrunia occitanica* nov. sp. in the Ardèche region.

Material. From Ferme Michelet, one sample (JPMA14113); two tight limestone blocks including several tens of individuals, cut longitudinally and transversally in slabs, some partly silicified specimens displaying myophores in 3D, and the outer shell form of both LV and RV (sample numbers JPMA11413 -1 to 15); two partly silicified incomplete specimens from Laval -Saint -Roman; one bivalve specimen from the Lower Aptian chalky beds of Simiane (Monts-de-Vaucluse); and 3 specimens from Saint-Chamas, where *Debrunia occitanica* nov. sp. is associated with caprinid rudists including *Offneria rhodanica* Paquier, *Praecaprina varians* Paquier and *Pachytraga paradoxa* (stratigraphic context in Masse 1976; Masse *et al.* 1999). All this material has an early Bedoulian age. Specimens housed in Musée de Paléontologie, Université de Provence, Marseille (J.-P. Masse collection).

Holotype. Specimen JPMA14113-1 (Figure 3A, B) from Ferme Michelet, is housed with other materials in Musée de Paléontologie, Université de Provence, Marseille.

Paratypes. Block samples JPMA14113- 2 to 15, cut in slabs, including a set of 6 serial sections (15 slabs with transverse and longitudinal sections) from the same locality.

Diagnosis. Conico-cylindrical *Debrunia* with a moderately convex LV, flattened ventrally. RV

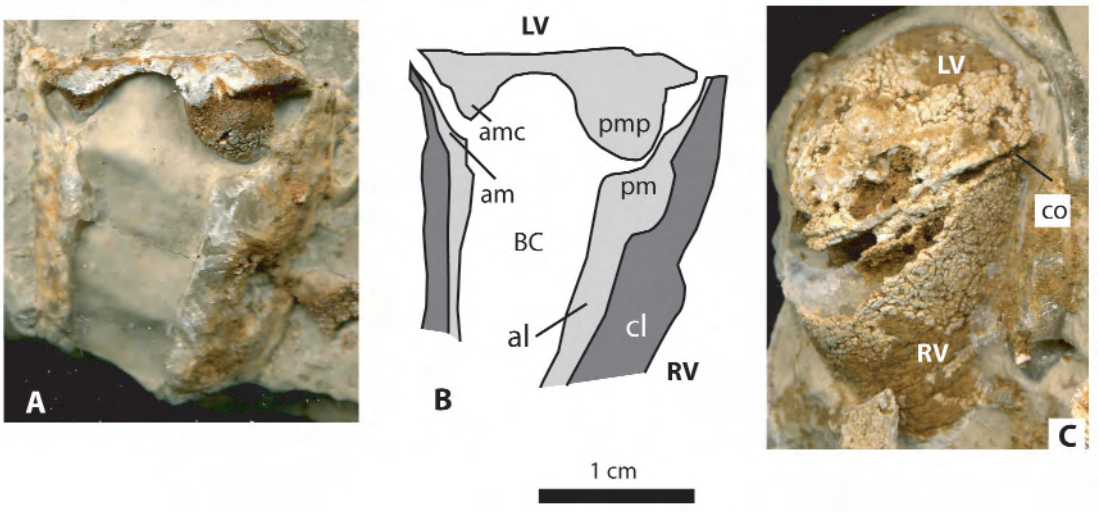

Figure 3. *Debrunia occitanica* nov. sp., holotype (sample JPMA 14113-1). **(A)** ventral view of a broken bivalve specimen showing the myophoral organisation, partly 3D. **(B)** interpretation, partly 3D. **(C)** Paratype, view of a silicified bivalve specimen to show the moderately convex dorsal side of the LV (JPMA14113-6).

ligament groove deep, flanked by salient rounded edges giving to the dorsal side a bilobate outline, radial bands poorly defined.

Description. Conico-cylindrical RV (dorso-ventral diameter 17 to 20 mm, antero-posterior diameter 19 to 24 mm, maximum length observed 70 mm), and moderately convex LV (5 to 6 mm height above the commissural plane) flattened ventrally (Figure 3A, B). RV ligament groove deep, flanked by salient rounded edges giving to the dorsal side a bilobate outline, well marked during early ontogenesis, with the anterior lobe more inflated than the posterior (Figure 4). Anterior and posterior sides flat or slightly convex outside, ventral side convex, smooth, radial bands inconspicuous. LV teeth relatively long, smooth (Figure 5A), the anterior with an elliptical transverse outline, larger than posterior (Figure 4A, B), with a proximal constriction followed by a distally inflated myophore (Figure 5G); posterior tooth with a subtriangular transverse outline (Figure

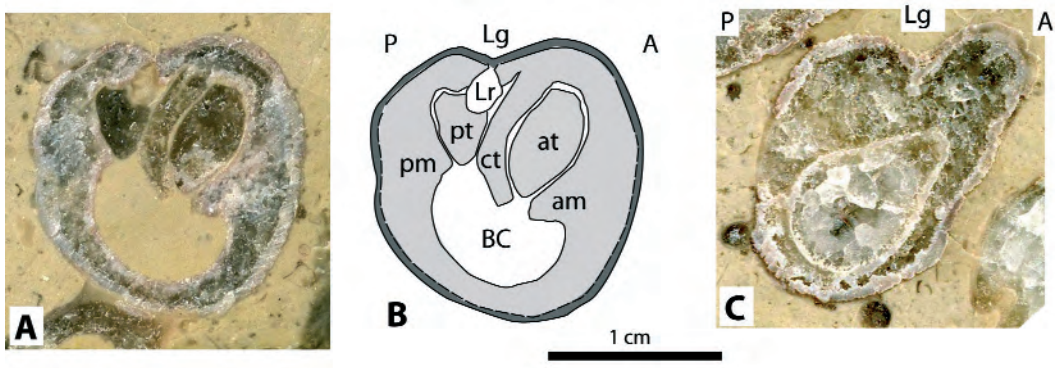

Figure 4. *Debrunia occitanica* nov. sp., transverse sections of paratypes. **(A)** section below the commissure showing cardinal elements and inflated ligament ridge of LV, and RV attributes. **(B)** interpretation (JPMA 14113-8). **(C)** oblique section of RV (silicified specimen) showing the ligament groove and the bilobate dorsal side (JPMA 14113-7a).

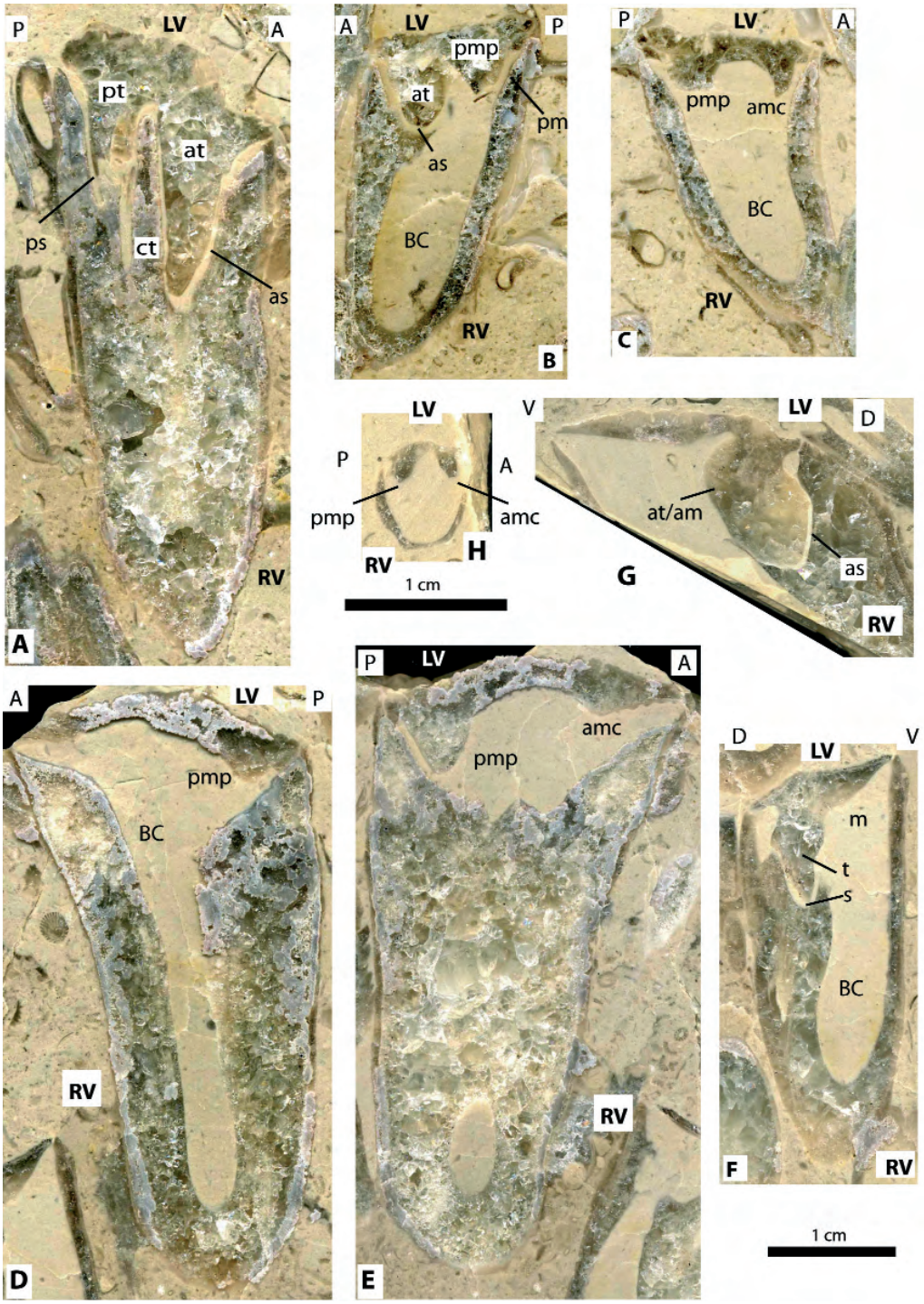

Figure 5. *Debrunia occitanica* nov. sp., longitudinal sections of paratypes showing the myocardinal organisation (serial sections JPMA 14113-7a, b, c, e). **(A)** antero-posterior dorsal section of a bivalve specimen showing the teeth. **(B, C)** pair of antero-posterior slightly oblique sections, showing dorso-ventral changes of the myocardinal elements, notice the acute anterior myophore. **(D, E)** same, pair of sections cut more ventrally, showing the ventral extent of the posterior myophoral plate. **(F)** dorso-ventral section showing myocardinal elements. **(G)** dorso-ventral section showing the proximal constriction tooth - myophore junction and and distally inflated myophore of LV. **(H)** antero-posterior section of a juvenile showing the myophores of LV, nearly equal.

4A, B); central tooth on RV erect (Figure 5A) with an arcuate transverse outline (Figure 4A, B). Ligament ridge small, subtriangular in transverse section. Myophoral anterior crest with a limited ventral extent, compared to the posterior myophoral plate (Figure 5C–E). Shell relatively thick, body cavity of RV relatively small compared to shell diameter (Figure 4A–C).

Comparisons with the Other *Debrunia* Species and Evolutionary Significance of *Debrunia occitanica* nov. sp.

External Characters. In *Debrunia bruni* the LV is spirogyrate and salient, in *D. mutabilis* this valve is usually non spirogyrate but somewhat salient and asymmetric with a pronounced dorsal inflation, by contrast (Figure 6), in *D. occitanica* nov. sp. the LV is not spirogyrate and relatively flattened. Radial bands are depressed and well marked on both valves of *D. bruni,* flattened on the LV of *D. mutabilis,* by contrast they are poorly marked in *D. occitanica* nov. sp. Contrasting features are also observed regarding the morphology of the ligament area between *D. mutabilis* in which the ligament groove is flanked by a ridge and growth lines are strongly deflected on both sides of the corresponding groove (features not found in *D. bruni*), and *D. occitanica* nov. sp. in which the ligament groove is in a depression with rounded salient edges, giving to transverse sections a dorsal bilobate outline. To conclude, the development of radial bands, the shape of LV, and the morphology and features observed on the dorsal side of RV, appear to be reliable external features to distinguish: *D. bruni; D. mutabilis* and *D. occitanica* nov. sp.

Internal Characters. The most significant contrasts between the three species concern the relative development of the myophores in the LV. In *D. bruni* the posterior myophoral plate is small and the anterior crest poorly developed, in *D. mutabilis* the anterior crest is well defined and the posterior plate more developed (Figure 6). Increasing development and protrusion of the LV myophores into the opposite valve, associated with shell flattening, are observed in *D. occitanica* nov. sp.

The foregoing discussion shows that two Barremian species possess relatively convex LV and well-defined radial bands; by contrast, in the early Aptian *D. occitanica* nov. sp., the LV is relatively flattened, the radial bands tend to be inconspicuous and the ligament groove lies in between rounded longitudinal edges on the dorsal side of the RV.

Left valve flattening, which is an expression of increasing valve asymmetry associated with the evolution of rudists in general, especially in the 'elevator' group (Skelton 1991), is a common evolutionary feature in the Monopleuridae. For instance the transition from *Monopleura* to *Agriopleura* (Masse & Philip 1974) is associated with a change from convex to flat and /or depressed LV. This modification is coupled with drastic changes in myophoral organisation: myophores of the LV which were represented by shell thickenings in *Monopleura* modified in *Agriopleura* into protruding downward bulges (Douvillé 1918) or even plates (Fenerci-Masse *et al*. 2006). In the Polyconitidae, assuming that the onset of *Horiopleura* predates that of *Polyconites* (Masse 1996; Skelton *et al*. 2008) the transition from *Horiopleura* to *Polyconites* is also associated with LV flattening. In the two families, and in the Radiolitidae as well, the development of the LV myophores is associated with LV flattening and leads to the migration of the myophoral apparatus below the plane of the commissure. For Douvillé (1918) this constructional pattern was due to limited growth rates of the LV compared to that of the RV, assuming that muscles in bivalves must be relatively short, the only way to meet this requirement is an elongation of the myophores. A possible alternative whereas non exclusive hypothesis derives from Skelton (1976) views regarding the role of centralisation and lowering of the centre of gravity as a way for ensuring stability of the shell, which gives a clue for understanding the relationships between the elongation of the RV and the flattening of the LV in elevator morphotypes.

Given the stratigraphical and regional distribution of the three species of *Debrunia* we assume that they represent chronospecies from a single species lineage. The stratigraphic position of *Debrunia bruni* and *D. mutabilis* in the early late Barremian (see discussion in Masse & Fenerci-Masse

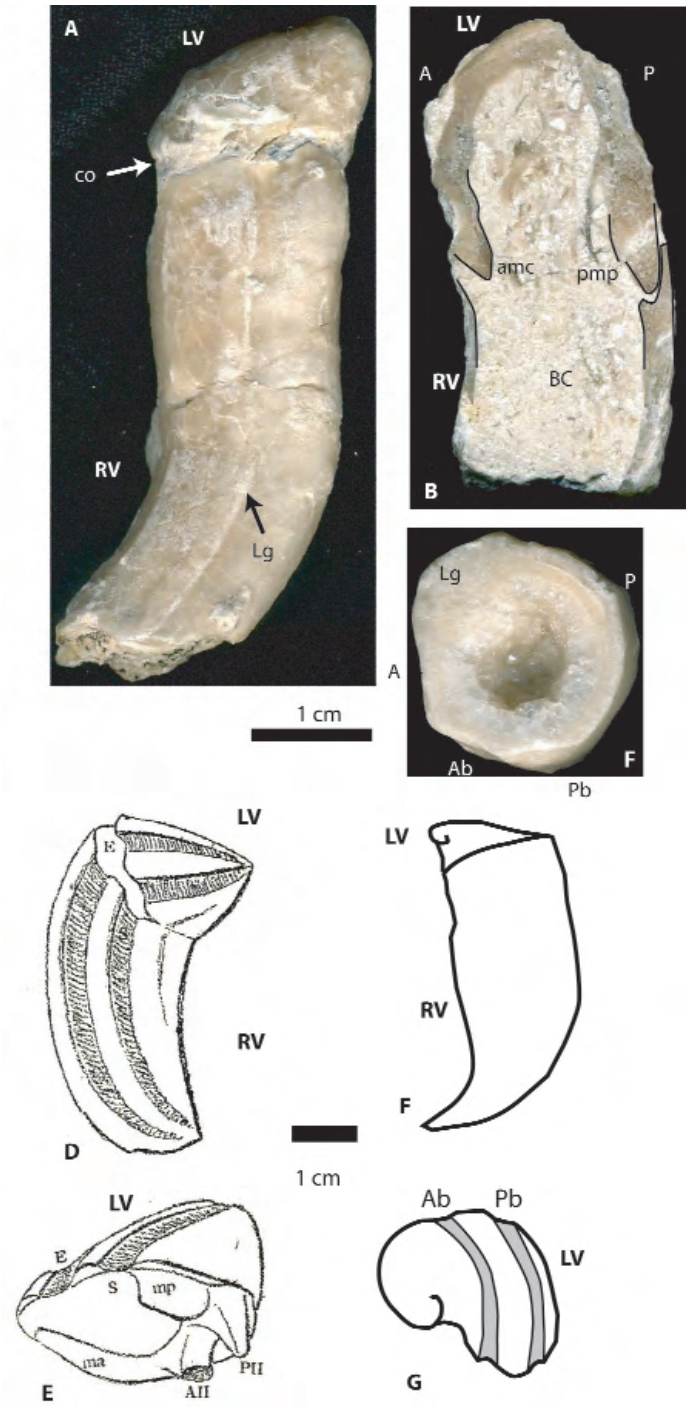

Figure 6. *Debrunia mutabilis* (Matheron), Cavaillon. **(A)** dorsal view of a bivalve specimen showing the main internal attributes of the species (JPMA 15795-1). **(B)** longitudinal, antero-posterior section of a bivalve specimen showing the myophores (JPMA 15795-2). **(C)** section of right valve showing the subrounded polygonal transverse outline and radial bands (JPMA 15795-8). *Debrunia bruni* (Douvillé). **(D, E)** original type figures in Douvillé (1918). **(D)** ventro-posterior view of a bivalve specimen. **(E)** posterior view of the left valve showing the cardinal organisation. **(F, G)** drawings based on the observation of the type material from Douvillé (centre des collections, Lyon). **(F)** dorso-anterior view of the specimen illustrated in D. **(F)** dorso-anterior view of the left valve showing the spirogyrate habit.

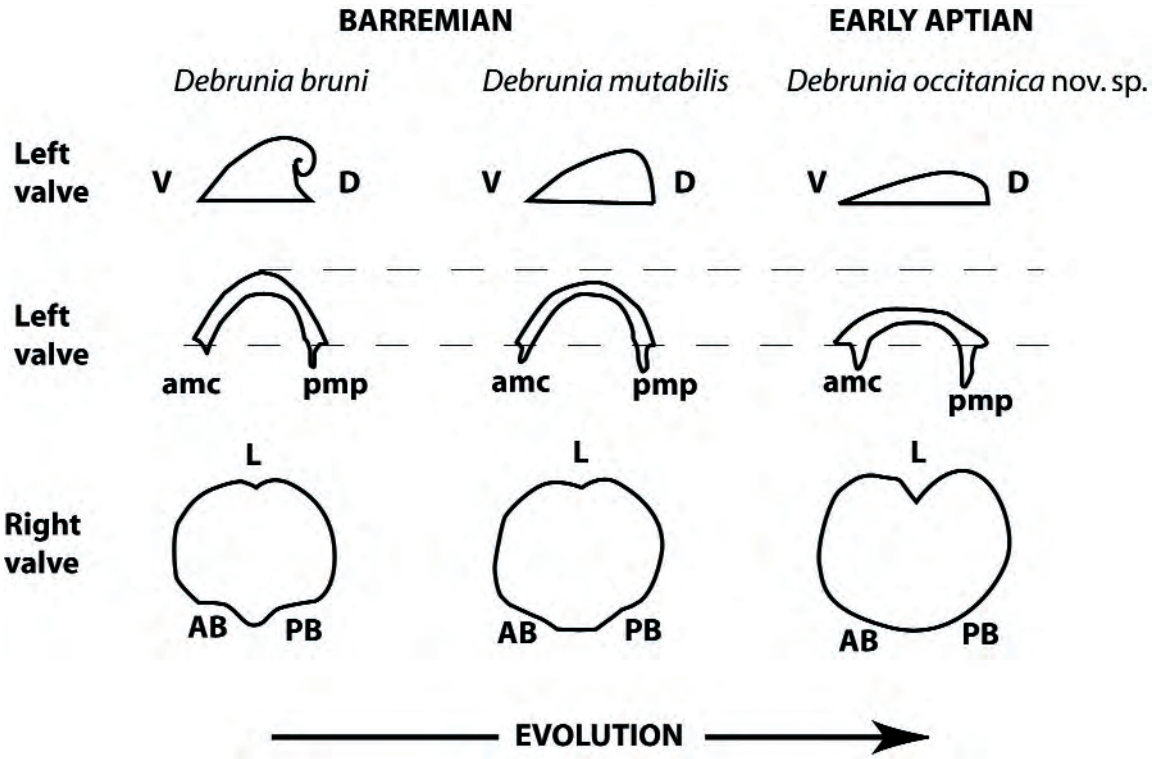

Figure 7. Evolutionary model for Barremian–early Aptian *Debrunia* species.

2009) does not provide a clear evidence for significant contrasting ages of these two species. Nevertheless, by considering the evolutionary patterns discussed above, we may propose an evolutionary model (Figure 7) which postulates that *D. bruni* might be more primitive than *D. mutabilis,* and that *D. occitanica* is the more advanced species. This model links morphological changes including: LV convexity, development of radial bands and geometry of the ligament groove area, in a specific sequence of possibly related biological events.

Conclusions

Debrunia occitanica nov. sp., described from the early Aptian platform limestones of SE France, is associated with caprinid rudists (*Offneria rhodanica*, *Pachytraga paradoxa*) and an orbitolinid-dasycladale association which marks the Lower Bedoulian. This new species is characterized by: a moderately convex left valve, inconspicuous radial bands and a ligament groove in a depression flanked by two longitudinal rounded edges giving to the transverse sections a bilobate outline. *Debrunia occitanica* nov. sp. is considered as a chronospecies belonging to a single lineage rooted in the Barremian, and including *Debrunia bruni* (the most primitive) and *Debrunia mutabilis*. Evolutionary trends in the three species include the flattening of LV, development of the corresponding myophores, and reduction of the radial bands. The type locality of *D. occitanica* is in eastern Languedoc but the species is also present is several sites from Provence. This new species has a potential to be a stratigraphic marker of the early Aptian.

Acknowledgments

We thank S.F. Mitchell (Kingston, Jamaica) and P.W. Skelton (Milton-Keynes, UK) for their valuable constructive criticisms on our initial submission. We are grateful to J. Charollais, B. Clavel and R. Busnardo for their contribution in the discovery of the fossil location of *Debrunia occitanica* nov. sp. at Ferme Michelet.

References

Charollais, J., Clavel, B., Schroeder, R., Busnardo, R. & Masse, J.-P. 1998. La plate-forme urgonienne. Un exemple de plate-forme carbonatée: biostratigraphie, stratigraphie séquentielle, sédimentologie, études régionales. *Publications du département de Géologie et Paléontologie, Université de Genève. Série Guide Géologique* **8**.

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.

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

Masse, J.-P. 1976. *Les calcaires urgoniens de Provence. Stratigraphie Paléontologie, les paléoenvironnements et leur évolution*. PhD Thesis, Universite Aix Marseille II [unpublished].

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., Elalbani, A. & Erlenkeuser, H. 1999. Stratigraphie isotopique (d13C) de l'Aptien inférieur de Provence (S.E. de la France). Applications aux corrélations plate-forme/bassin. *Eclogae geologiae Helvetiae* **92**, 259–263.

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. 2010. *Mathesia* Mainelli (Hippuritacea**,** Monopleuridae**)** from the late Aptian–Albian of the Mediterranean region, a revision**.** *Turkish Journal of Earth Sciences* **19**, 543–556.

Masse, J.-P. & Philip, J., 1974. Définition, position systématique et répartition stratigraphique du genre *Agriopleura* Kühn (Rudiste). *Géologie Méditerranéenne* **2**, 53–62.

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

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.

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

Skelton, P.W. 1991. Morphogenetic versus environmental cues for adaptative radiations. *In*: Schmidt-Kittler, N. & Vogel, K. (eds), *Constructional Morphology and Evolution*. Springer-VerlagBerlin Heidelberg, 375–388.

Skelton, P.W. & Gili, E. 1991. Palaeoecological classification of rudist morphotypes. *Proceedings of the 1st Conference on Rudists (Beograd, 1988)*. Serbian Geological Society, Special Publication **2**, Beograd, 265–287 [preprint issued for unpublished volume].

Skelton, P.W., Gili, E., Bover-Arnal, T., Salas R. & Moreno-Bedmar, J. 2008. A new species of *Polyconites* from the uppermost Lower Aptian of Spain. *Eight International Congress on Rudists, 23–25 June 2008, İzmir, Turkey, Dokuz Eylül University, Abstracts*, p. 53.