

LOWER CRETACEOUS RUDIST BIOSTRATIGRAPHY OF SOUTHERN FRANCE—A REFERENCE FOR MESOGEAN CORRELATIONS

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ABSTRACT

The Lower Cretaceous rudist fauna of southern France consists of 61 species corresponding to 23 genera belonging to Diceratidae, Requiéniidae, Monopleuridae, Caprinidae, Polyconitidae and Radiolitidae. From southeastern France (Provence, Languedoc-Bas Vivarais, Subalpine, Jura and Paris basin margin regions) rudists are mainly recorded from the Berriasian-lower Aptian interval, whereas in southwestern France (Aquitaine, Pyrénées) they are essentially known from the Aptian-Albian. Regional distributions show a relatively well defined biostratigraphic zonation with particularly well marked mid-Valanginian and mid-Aptian breaks, though uppermost Hauterivian and uppermost Barremian faunal changes are also well expressed. Chronostratigraphical correlations are by reference to ammonite bearing beds complemented by micropaleontologic data from the rudist facies. Resolution is therefore provided at stage, substage or even ammonite zone levels. This specific zonal framework and the relatively high regional diversity, with many taxa common to adjacent regions, make the proposed biozonation a valuable reference for Mesogean correlations.

Key words: Biostratigraphy, rudists, Lower Cretaceous, southern France, Mesogea correlations, biozonation.

RESUMEN

La fauna de rudistas del Cretácico Inferior del sur de Francia consiste en 61 especies correspondientes a 23 géneros de las familias Diceratidae, Requiéniidae, Monopleuridae, Caprinidae, Polyconitidae y Radiolitidae. Del sureste de Francia (Provenza, Languedoc-Bas Vivarais, Subalpine, Jura y regiones del margen de la cuenca de París) los rudistas se encuentran principalmente en el intervalo Berriasiano-Aptiano inferior en tanto que en el suroeste de Francia (Aquitania, Pirineos) se encuentran esencialmente en el Aptiano-Albiano. La distribución regional muestra una zonificación estratigráfica relativamente bien definida, enfocada en los intervalos del Valanginiano medio y del Aptiano medio, aunque en la parte final tanto del Hauteriviano tardío como del Barremiano tardío también son manifiestos los cambios faunísticos. La correlación cronoestratigráfica de capas con amonites se complementa con datos micropaleontológicos de las facies de rudistas. Por lo tanto, una distribución cronológica incluye piso, subpiso, y aun niveles de zonas de amonites. Este marco zonal específico y la diversidad regional relativamente alta, con muchos taxa comunes en regiones adyacentes, posibilitan que la biozonación propuesta constituya una referencia valiosa en las correlaciones de la Mesogea.

Palabras clave: Bioestratigrafía, rudistas, Cretácico Inferior, sur de Francia, correlaciones de la Mesogea, biozonación.

INTRODUCTION

The Lower Cretaceous rudist faunas of southern France (Figure 1) were submitted to detailed paleontological investigations since the end of the last century, providing basic, and mainly still relevant, taxonomic and biostratigraphic data.

During the last few decades, there have been improvements in the micropaleontologic biozonations of carbonate platform series (based on benthic foraminifera and dasyclad algal distributions), referred to ammonite standard biozones. These have provided the opportunity to reappraise Lower Cretaceous regional rudist biostratigraphy in a precise, well documented biochronologic framework, at stage, substage or even at ammonite zone levels. In southeastern France—Provence, Languedoc-Bas Vivarais, Subalpine and Jura regions—the Berriasian-lower Aptian rudist-bearing carbonate sequences are interbedded with or grade laterally into hemipelagic sediments containing cephalopods, from which

the biostratigraphical ranges of rudists can be deduced. In southwestern France, a similar pattern is known for the Aptian-Albian interval from the Aquitaine and Pyrénées regions.

The objectives of this paper are to describe the vertical distribution of the main rudist species in the Berriasian p.p.-Albian p.p. (*pro-parte*) interval, in order to provide a reference biozonation useful for correlations, at the scale of the Mesogée (*sensu* Douvillé, 1900).

The ammonite zonation is compiled from the works of Casey (1961), Le Hegarat (1971), Busnardo and Moullade (1979), Busnardo (1984), Busnardo and Thieuloy (1989), Hoedemaker and Bulot (1990), and Bulot and coworkers (1993).

Rudist localities are presently located south of 47°N, reflecting the existence of a major E-W paleobiogeographic boundary corresponding to the Mesogée/Boreal boundary (Figure 1). This boundary is also documented from Switzerland and offshore Brittany (Pastouret *et al.*, 1974) with the same latitudinal position. From palinspastic reconstructions (Masse *et al.*, 1993) the corresponding paleolatitude is estimated from 27 to 31°N, during the early Aptian, that is a little bit north of the tropic.

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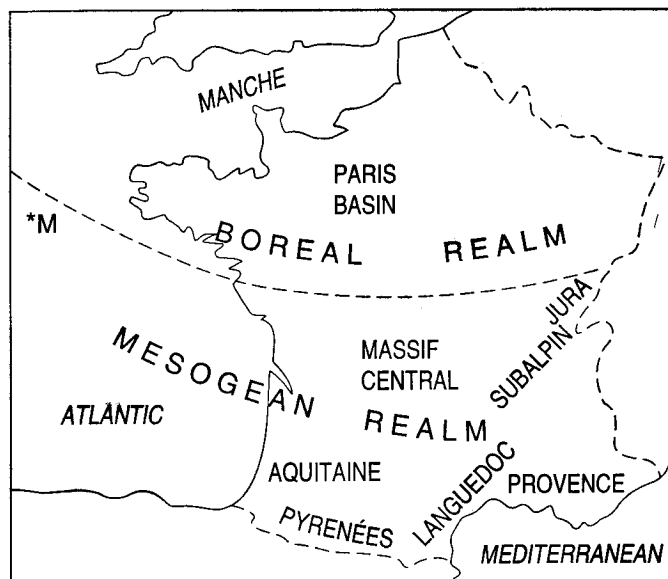


Figure 1. Geographical sketch map of France displaying the main rudist-bearing regions restricted to southern France, and the E-W paleobiogeographic boundary between the Boreal and Mesogean realms (M = Meriadzek Bank).

HISTORICAL BACKGROUND

SYSTEMATIC ASPECTS

The first investigations on Lower Cretaceous rudists from the south of France were reported by Matheron (1842, 1878), who described four genera and nearly 15 species of requienids and monopleurids mainly from the "Urgonian stage" of Provence. Some of them were subsequently split or modified by Munier-Chalmas (1873). Considering also the data provided by Gras (1852) and Pictet and Campiche (1867-1870) from western Switzerland, the information available at the end of the XIX century on the Lower Cretaceous rudists of SE France and some adjacent localities concerned 25 species, corresponding to eight genera, for the Valanginian-lower Aptian interval. Besides the works of Coquand (1865) and Munier-Chalmas (1882), data concerning southwestern France were of limited importance. From the northern subalpine region, at the turn of the century, Paquier (1900, 1903, 1905) first mentioned the presence of primitive caprinids in the Barremian-lower Aptian, leading to the description of three new genera. He also described new species of requienids. Significant advances obtained in southwestern France are due to Douvillé (1902, 1909) who described new taxa of "caprotinids"—the *Horiopleura-Polyconites* group—and demonstrated the existence of primitive radiolitids during the late Aptian-Albian. Douvillé (1914, 1918) also contributed to the revision of the genus *Petalodontia* in the Provence-Languedoc area. Further significant reports concern Albian faunas, from the Pyrénées, where Astre (1933) mentioned the genus *Agriopleura*, and the northern subalpine regions, where *Durania* was found (Moret, 1936). From the fifties till now, discoveries were mainly due to Mongin and Trouvé (1953) who described a primitive *Matheronia* in the Valanginian, while

Astre (1961) described a new *Pachytraga* from the Barremian; the corresponding type levels were subsequently ascribed to the Berriasian and the Hauterivian, respectively (Masse, 1976; Masse *et al.*, 1989). Recently, the present author proposed a new genus, *Lovetchenia*, that is a requienid restricted in this region to the Hauterivian (Masse, 1993b).

BIOSTRATIGRAPHIC ASPECTS

Rangé charts for the Lower Cretaceous rudists from the south of France (with some additional data from adjacent countries) were initially compiled by Paquier (1905), Toucas (1907), Hang (1907) and Kilian and Reboul (1915). Though providing more refined time scale distributions, recent attempts from Skelton (1976), Masse (1976) and Yanin (1989) were nevertheless mainly given at stage levels.

TAXONOMIC REMARKS

The recognized taxa consist of 23 genera and 61 species belonging to the families: Diceratidae Dall, Requiiniidae Douvillé, Monopleuridae Dechaseaux, Caprinidae d'Orbigny, Policontinidae MacGillavry and Radiolitidae Gray.

Among the Requiiniidae, some generic attributions herein depart from those of the previous literature (*e.g.*, Douvillé, 1918) and are based on a general revision of the internal characters; some of the results have recently been published (*e.g.*, Masse, 1993b). Some species with dubious status (*e.g.*, belonging to *Toucasia*) are not taken into account. Among the Monopleuridae, the tubular forms ascribed by Matheron (1842, 1978) to *Monopleura* and subsequently placed in the genus *Petalodontia* by Douvillé (1918), are maintained in the latter genus, even if this attribution is probably to be revised (Masse, in press). Similarly, the form described as *Monopleura Marcida* (White) by Douvillé (1918) cannot be ascribed to this taxon because it shows a myophoral arrangement close to that of "*Petalodontia*". The generic assignments of *Gyroleura kiliani* Paquier and *Agriopleura dardieri* (Astre) are also questionable. *Gyroleura kiliani* seems to lack the posterior myophoral plate on the posterior side of the right valve, whereas the upper valve of "*Agriopleura dardieri*" differs from those of *Agriopleura* species (Masse and Philip, 1974; Masse, in press). The internal characters of *Monopleura dumortieri* Matheron (horizontal myophoral plate on the free valve) show that this species belongs to *Horiopleura*. The genus *Pachytraga* is here considered a member of the Caprinidae as assumed by MacGillavry (1935), whereas it was classically ascribed to the Caprotinidae (*e.g.*, Dechaseaux and Perkins, 1969).

REGIONAL STRATIGRAPHIC DISTRIBUTIONS

SOUTHEAST FRANCE

This domain is characterized by the spreading of carbon-

ate platforms which prograded towards the Vocontian Basin, an extension of the Alpine Basin: the Jura-Subalpine platform lay to the north and the Provence platform to the south. This converging system was drowned close to the Bedoulian-Gargasian boundary (mid-Aptian event) (Figure 2).

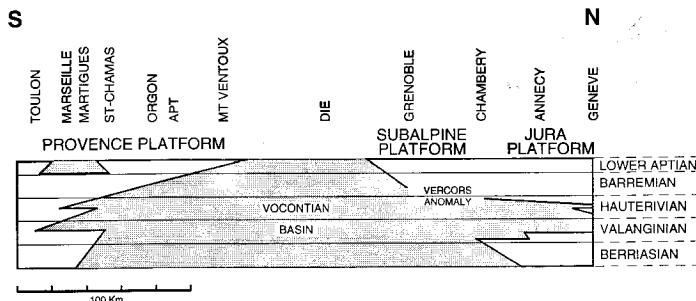


Figure 2. Stratigraphic organization of the SE French Lower Cretaceous carbonate platforms (white), showing the southward stepwise progradation of the Jura-Subalpine platform, and the northward progradation of the Provence platform, both converging toward the Vocontian basin (grey), and the middle Aptian drowning. Compiled after various sources.

Provence (Figures 3 and 4)

The so-called "Urgonian limestones of Provence" range from the Valanginian to lower Aptian and extend from the Mediterranean coast (Marseille-Toulon) to the Monts-de-Vaucluse-Ventoux region, where they pass laterally to the hemipelagic facies, then to the pelagic of the Vocontian Basin (Masse, 1976, 1993c).

In the coastal region, carbonate platform beds overlie the "Marnes vertes" Formation, a mixed shallow water, carbonate/marly unit of shallow water origin, containing the

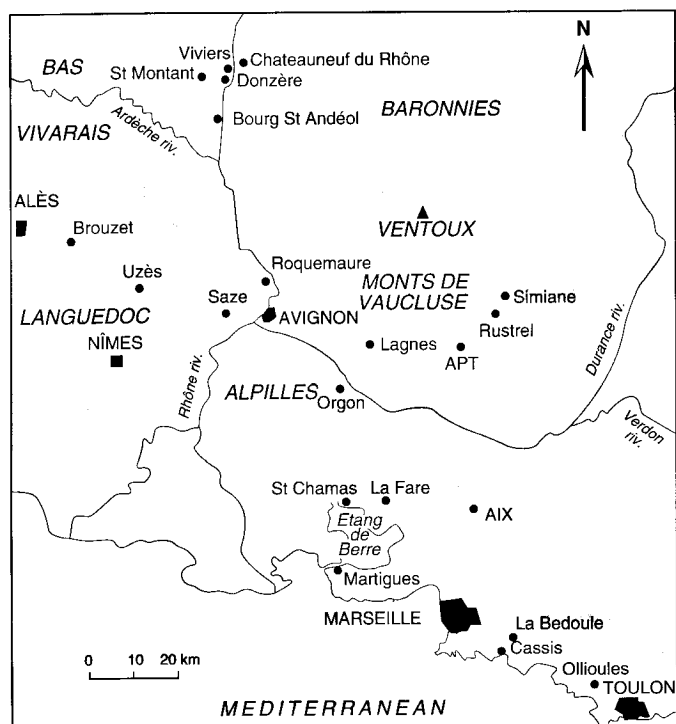


Figure 3. Geographical sketch map of Provence-Languedoc and Bas-Vivarais showing the main areas and localities with Lower Cretaceous rudist assemblages.

foraminifer *Danubiella gracilima* Neagu and the dasyclads *Zergabriella embergeri* (Bouroullec and Deloffre) and *Falsolikanelia campanensis* (Jaffrezo *et al.*); an association diagnostic of the *Boissieri* zone (upper Berriasian) (Masse, 1993c; Virgone and Masse, 1993). Rudists are scarce here and only represented by a single species, *Matheronia rougonensis* Mongin and Trouvé (Plate 1, figure 1). This taxon was also recorded at the same stratigraphic level in the Verdon Canyon area (type locality) (Mongin and Trouvé, 1953). The underlying "Calcaire blanc inférieur" Formation yields *Matheronia* sp. and a form tentatively ascribed to *Heterodicerias luci* (Defrance). The containing beds belong to the middle-lower Berriasian, based on the presence of *Pseudoclypeina neocomiensis* (Radoicic) and *Clypeina jurassica* Favre.

In the Marseille region, the "Marnes vertes" Formation (Babinot *et al.*, 1971) is capped by the "Calcaire blanc supérieur" (*sensu* Denizot, 1934), characterized by *Valdanchella miliani* (Schroeder), *Pseudotextulariella salevensis* Charollais and others, and *Pfenderina neocomiensis* (Pfender), ascribed to the lower Valanginian, an age corroborated by the ammonite association found in the overlying marls which belong to the *Verrucosum* Zone (basal zone of the upper Valanginian) (Masse, 1976). Rudists, frequent and locally abundant, are represented by *Monopleura* sp. 4 in Masse, 1976 (Plate 1, figure 2), *Matheronia* cf. *eurystoma* Pictet and Campiche, *Valletia* cf. *tombecki* Munier-Chalmas, *Heterodicerias*? sp. (Plate 1, figure 3), and a *Monopleura* close to the *M. valangiensis-valdensis* group of Pictet and Campiche (1867-1870) (Plate 1, figures 4 and 7).

The upper Valanginian and lowermost Hauterivian are represented by ammonite-bearing marls and cherty limestones, respectively. Rudists are recorded higher up, in the "Pachytraga limestones" (Figure 4) *sensu* Masse, 1976, which overlie beds with *Lyticoceras cryptoceras* (d'Orbigny), a typical member of the *Nodosoplicatum* Zone. The *Pachytraga* limestones are in turn overlain by "Toxaster marls" (Martigues) ascribed to the *Sayni* Zone (Masse, 1984). The "Pachytraga limestones" therefore belong to the *Nodosoplicatum* Zone. With *Pachytraga tubiconcha* Astre (Plate 1, figure 6), the cardinal taxon, are found *Matheronia* sp. (Plate 1, figure 8) and *Lovetchenia* sp. This association is also well represented near Toulon, in the lower part of the Ollioules canyon section.

In the Marseille area, the overlying beds are rudist-free biocalcarenes regarded as the lateral equivalent of the Martigues-La Fare "Toxaster marls" of late Hauterivian age. The age of the overlying "Cassis-Port-Miou Limestones" is mainly Barremian, whereas the basal part still belongs to the latest Hauterivian (*i.e.*, *Angulicostata* Zone), an attribution based on the presence of primitive representatives of the *Praedictyorbitolina-Dictyorbitolina* group, diagnostic forms of the uppermost Hauterivian-lowermost Barremian (Schroeder *et al.*, 1990). *Praedictyorbitolina-Dictyorbitolina* beds are marked by the onset of *Agriopleura blumenbachi* (Studer). The overlying Barremian p.p. sequence contains: *Toucasia* cf. *carinata*

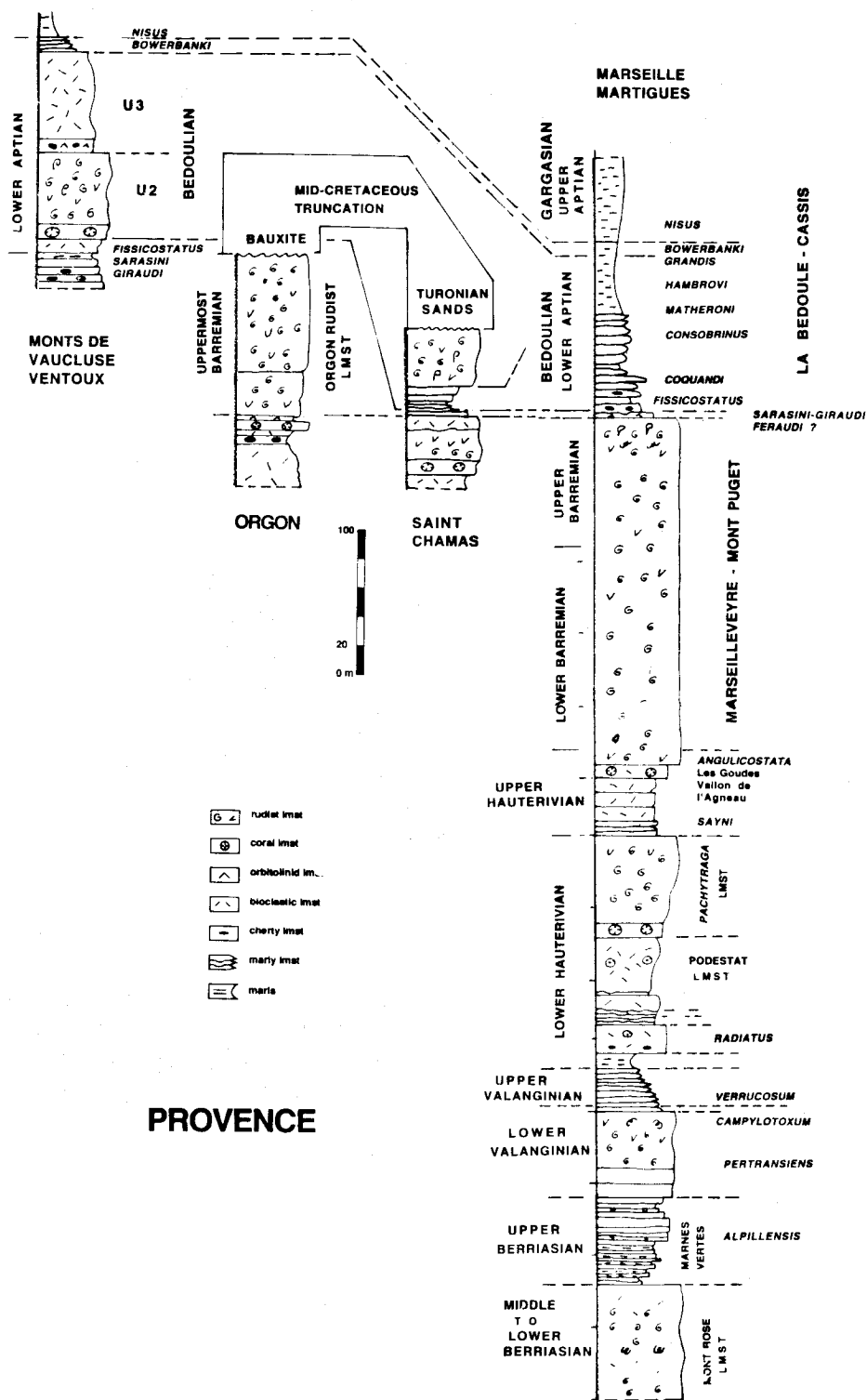


Figure 4. Stratigraphic reference sections for Lower Cretaceous rudist-bearing rock units from Provence.

Matheron, *Requienia ammonia* (Goldfuss), *Requienia migliorinii* Tavani (Plate 2, figure 4), *Agriopleura marticensis* (d'Orbigny) and *Petalodontia sulcata* (Matheron). The topmost part of the Barremian sequence corresponds with the "Heteroceras beds", which underlie at La Bédoule the lower Aptian stratotypic section. The "Heteroceras beds" are ascribed to the *Sarasini* and probably *Giraudi* Zones.

The Martigues chalky rudist limestones from where many requienid and monopleurid specimens were described by Matheron (1842, 1878), Paquier (1903, 1905) and Douvillé (1914, 1918), belong to the *Vandenheckei-Feraudi* zones. These beds, which are equivalent to those in the upper part of the Cassis-Port-Miou ones, are still present in the La Fare-Saint-Chamas region, with the same age. Their rudist fauna

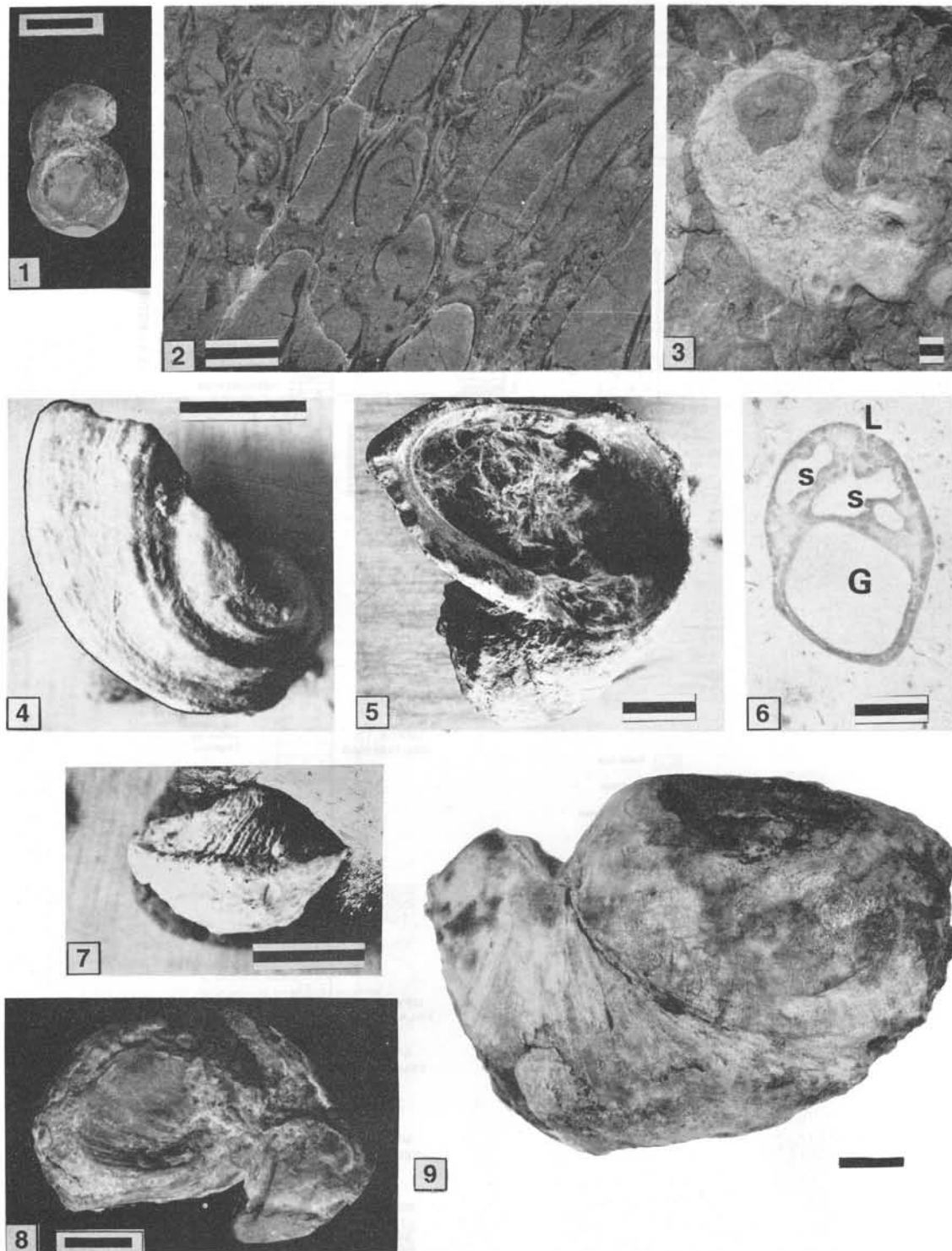


Plate 1. Berriasian, lower Valanginian and Hauterivian faunas. Figure 1—*Matheronia rougonensis* Mongin and Trouvé. Isolated bivalve specimen showing the short coiling of the lower valve and the rounded outline of the commissure. Upper Berriasian, Verdon Canyon (type locality). Provence. Figure 2—*Monopleura* sp. 4 (in Masse, 1976). Polished slab cut in a dense packed cluster of individuals showing the tubular shape of the lower valve. Lower Valanginian, Marseille region. Provence. Figure 3—*Heterodiceras?* sp. Section of lower valve (?) showing the thick (mainly sparry calcite) shell, slightly curved. Lower Valanginian, Marseille region. Provence. Figure 4—*Monopleura valangiensis* Pictet and Campiche. Posterior view of lower valve showing the coarse prominent radial bands. Type specimen from the Geneva Museum collection. Lower Valanginian, Arziers marls, Swiss Jura. Figure 5—*Matheronia eurystoma* Pictet and Campiche. Lower valve showing the elliptical outline of the commissure and the acute carina. Type specimen from the Geneva Museum collection. Lower Valanginian, Arziers marls, Swiss Jura. Figure 6—*Pachytraga tubiconcha* Aste. Transverse section of a lower valve showing the anterior and posterior tooth sockets (s), the body cavity (G) and the ligament groove (L). Lower Hauterivian, Marseille region. Provence. Figure 7—*Monopleura valdensis* Pictet and Campiche. Ventral view of a bivalve specimen. Radial bands are poorly developed, the upper valve is finely ribbed. Type material from the Geneva Museum collection. Lower Valanginian, Arziers marls, Swiss Jura. Figure 8—*Matheronia* sp. (in Masse, 1976). Isolated bivalve specimen showing the short coiling and subpolygonal outline of the commissure. Lower Hauterivian, Marseille area. Provence. Figure 9—*Lovetchenia* sp. Posterior view of a bivalve specimen showing the bulge shaped upper valve and the low coiling of the lower valve. Lower (?) Hauterivian, Saint-Claude-Le Ponthoux. French Jura. Scale bar is 1 cm.

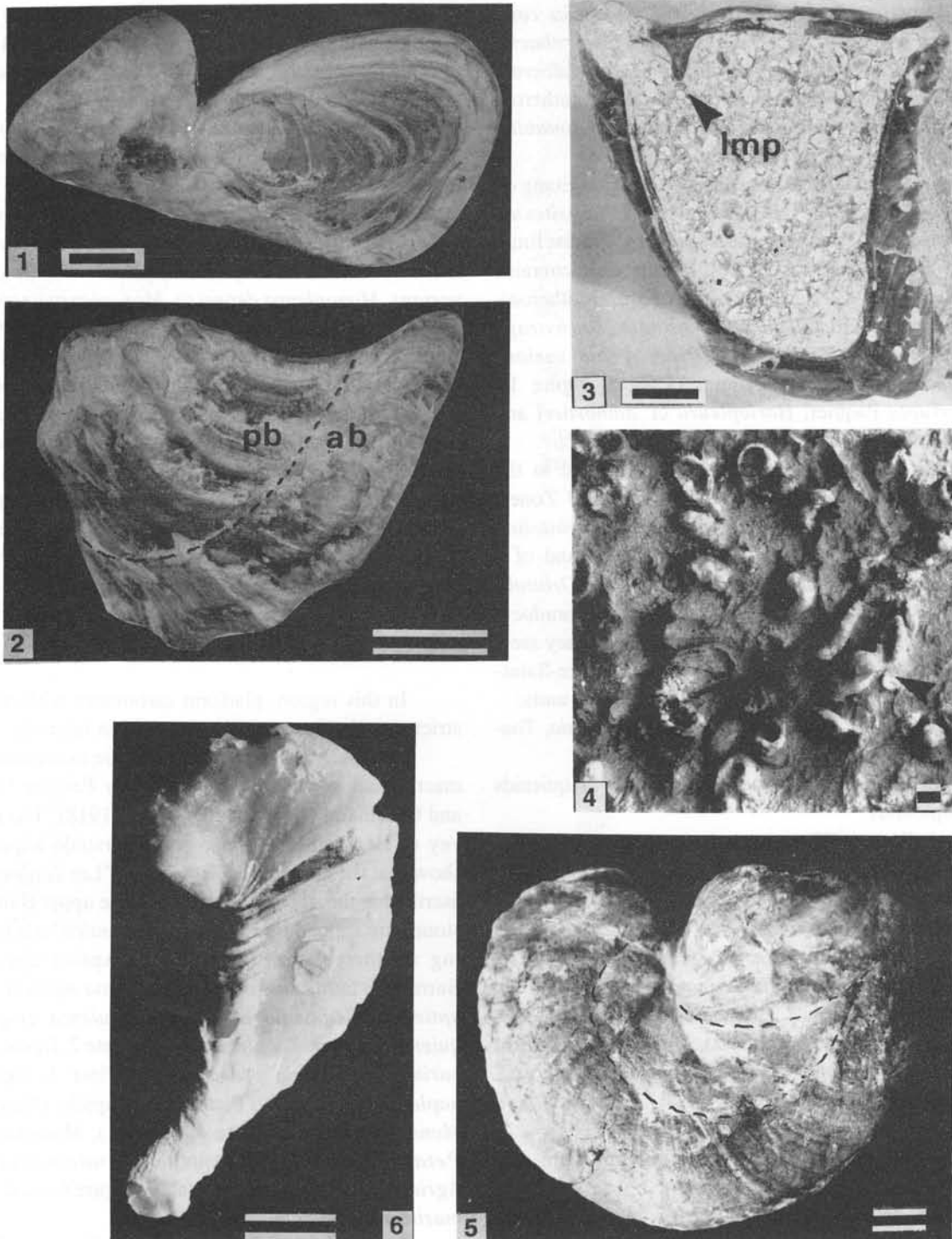


Plate 2. Barremian fauna. Figure 1—*Requieria gryphoides* Matheron. Isolated bivalve specimen showing the elliptical asymmetrical outline of the commissure and the low coiling of the lower valve. Barremian, Orgon. Provence. Figure 2—*Requieria pellati* Paquier. Ventral view of the lower valve of an isolated specimen showing the well delineated radial bands and the concave shape of the commissure. The anterior (ab) and posterior band (pb) are separated by a groove. Upper Barremian, Brouzet, Languedoc. Figure 3—*Requieria ammonia* (Goldfuss). Transverse section of a bivalve specimen showing the flat upper valve with the posterior myophoral plate (Imp). Upper Barremian, Orgon. Provence. Figure 4—*Requieria migliorinii* Tavani. Natural weathered sections (monospecific association) with randomly cut sections showing one or several whorls (arrow) of the lower valve. Barremian, Marseille region. Provence. Figure 5—*Toucasia carinata* Matheron. Posterior view of a bivalve specimen showing the rounded inclined upper valve and poorly defined external grooves (underlined) crossing at the commissure, and representing the trace of the internal posterior myophoral plate. Upper Barremian, Orgon. Provence. Figure 6—*Monopleura michailensis* Pictet and Campiche. Anterior view of a bivalve specimen showing the prominent upper valve and the conical shape of the lower valve. Upper Barremian, Brouzet, Languedoc. Scale bar is 1 cm.

consists of: *Matheronia munieri* Paquier, *Requienia gryphoides* Matheron, *Requienia ammonia*, *Toucasia carinata*, *Toucasia transversa* Paquier, *Agriopleura blumenbachi*, *Agriopleura marticensis*, *Monopleura imbricata* Matheron, *Monopleura varians* Matheron, *Monopleura affinis* Matheron, *Monopleura depressa* Matheron, *Petalodontia? mutabilis* (Matheron) and *Retha dubiosa* (Matheron).

Near Saint-Chamas, on the northern side of the Etang de Berre, the "Heteroceras beds" are overlain by *Deshayesites* sp. bearing marly limestones with cherts, capped by a rudist limestone of Bedoulian age (Masse, 1976). This unit contains *Requienia ammonia*, *Requienia semirugata* (Matheron), *Matheronia virginiae* Gras, *Toucasia carinata*, *Pachytraga paradoxa* (Pictet and Campiche), *Praeacprina varians* Paquier, *Praeacprina gaudryi* Paquier (Plate 5, figure 1), *Offneria interrupta* Paquier, *Horiopleura* cf. *dumortieri* and *Monopleura* sp. 2 in Masse (1976).

The Orgon rudist limestones are now ascribed to the uppermost Barremian, that is, the *Giraudi-Sarasini* Zones. This age assessment is based on the presence of *Palorbitolina lenticularis* (Blumenbach) in the underlying beds and of a micropaleontological assemblage characterized by *Orbitolinopsis buccifer* Arnaud-Vanneau and Thieuloy and *Pseudocyclamina allobrogica* Arnaud-Vanneau. Therefore they are a little bit younger than those from Martigues and La Fare-Saint-Chamas. These rudist limestones are divided in three units:

- A lower chalky unit (4 m) with *Requienia ammonia*, *Toucasia carinata* and *Agriopleura marticensis*.
- A dense, hard unit (20 m) with poorly preserved requienids and monopleurids.
- An upper chalky unit (80 m), extensively caved, representing the classical "Orgon Facies" with abundant macrofossils. The rudist fauna consists of *Requienia ammonia* (Plate 2, figure 3), *Requienia gryphoides* (Plate 2, figure 1), *Requienia semirugata*, *Matheronia aptiensis* Paquier (Plate 3, figure 3), *Matheronia munieri*, *Toucasia carinata* (Plate 2, figure 5), *Toucasia transversa* (Plate 3, figure 2), *Monopleura urgoniensis* Matheron (Plate 4, figure 2), *Monopleura depressa* (Plate 4, figure 7), *Monopleura varians* (Plate 4, figure 5), *Retha munieri* (Matheron) (Plate 4, figure 3) and *Horiopleura dumortieri* (Plate 3, figure 4).

Chalky limestones similar to those of Orgon are also present at Cavaillon with the same fauna.

Northward, the Urganian limestones with rudists are mainly restricted to the lower Aptian. Rudist-bearing beds known as the U2 Member after Leenhardt (1890) are frequently represented by chalky facies, such as at Lagnes, Rustrel, Simiane (Monts de Vaucluse) as well as the southwestern part of the Ventoux Massif.

The U2 rudist member overlies a bioclastic limestone (*i.e.*, the U1 biocalcarenes of Mont-Ventoux), the basal part of which contains *Martelites* and *Prodeshayesites* (Masse, in press) of the *Sarasini* (uppermost Barremian) and *Fissicostatus* (lowermost Bedoulian) Zones. The rudist unit is

capped by a bioclastic unit (*i.e.*, the U3 biocalcarenes of Mont-Ventoux) overlain by marls ascribed to the *Bowerbanki* Zone (Bedoulian) (Masse, 1976). The uppermost U2 member therefore probably belongs to the *Consobrinus-Matheroni* Zones (Masse, 1993c).

In all of these localities the rudist faunal composition is identical and consists of the following taxa: *Matheronia aptiensis*, *Matheronia virginiae* (Plate 5, figure 5), *Requienia ammonia*, *Requienia gryphoides*, *Requienia gryphus* (Douvill ), *Requienia semirugata*, *Toucasia carinata*, *Toucasia transversa*, *Toucasia praecarinata* Douvill , *Monopleura varians*, *Monopleura depressa*, *Monopleura urgoniensis*, *Monopleura affinis*, *Monopleura* sp. 2 in Masse (1976) (Plate 4, figure 6), *Petalodontia sulcata*, *Horiopleura* aff. *dumortieri* (Plate 4, figure 4), *Pachytraga paradoxa*, *Praeacprina varians* (Plate 5, figure 2), *Praeacprina gaudryi*, *Offneria intermedia* Paquier, *Offneria interrupta* (Plate 5, figure 3) and *Offneria rhodanica* Paquier.

In the Nesque river canyon, rudist-bearing limestones recorded underneath the *Sarasini* beds have recently proved the presence of this so called "lower Aptian assemblage" which therefore appears probably in the *Feraudi* zone.

Eastern Languedoc and Bas-Vivarais

In this region, platform carbonates with rudists are restricted to the Barremian-lower Aptian interval.

Near Al s, at Brouzet, rudists are associated with a rich macrofossil assemblage described by Paquier (1903), Pellat and Cossmann (1907) and Douvill  (1918). The regional survey of Hamdan (1977) and some personal unpublished data show that the classical rudist locality "Les Augustines" can be ascribed to the upper Barremian. These upper Barremian limestones are capped by *Palorbitolina lenticularis* beds supporting another rudist unit of early Aptian age. The upper Barremian fauna consists of *Matheronia munieri*, *Matheronia aptiensis*, *Requienia ammonia*, *Requienia gryphoides*, *Requienia gryphus*, *Requienia pellati* (Plate 2, figure 2), *Toucasia carinata*, *Toucasia praecarinata* (Plate 3, figure 1), *Monopleura michaillensis* Pictet and Campiche (Plate 2, figure 6), *Monopleura affinis* (Plate 4, figure 1), *Monopleura varians*, *Petalodontia? bruni* Douvill , *Petalodontia mutabilis*, *Agriopleura blumenbachi* (Plate 3, figure 6), and *Agriopleura marticensis* (Plate 3, figure 5).

In the Avignon region, between Saze and Roquemaure, the Urganian sequence is similar to the Ventoux Massif one, the U2 Member containing the same fauna, especially the *Offneria-Praeacprina-Pachytraga* association. These beds are also recorded in the Ardeche Canyon, near Bourg-Saint-And ol and in the Viviers-Donz re-Chateaufort-du-Rh ne area. These rudist-bearing localities, first described by Paquier (1903-1905), are also very similar to the Ventoux Massif ones, a similarity explained by their age identity and their palaeogeographical setting: they are situated on the outer platform

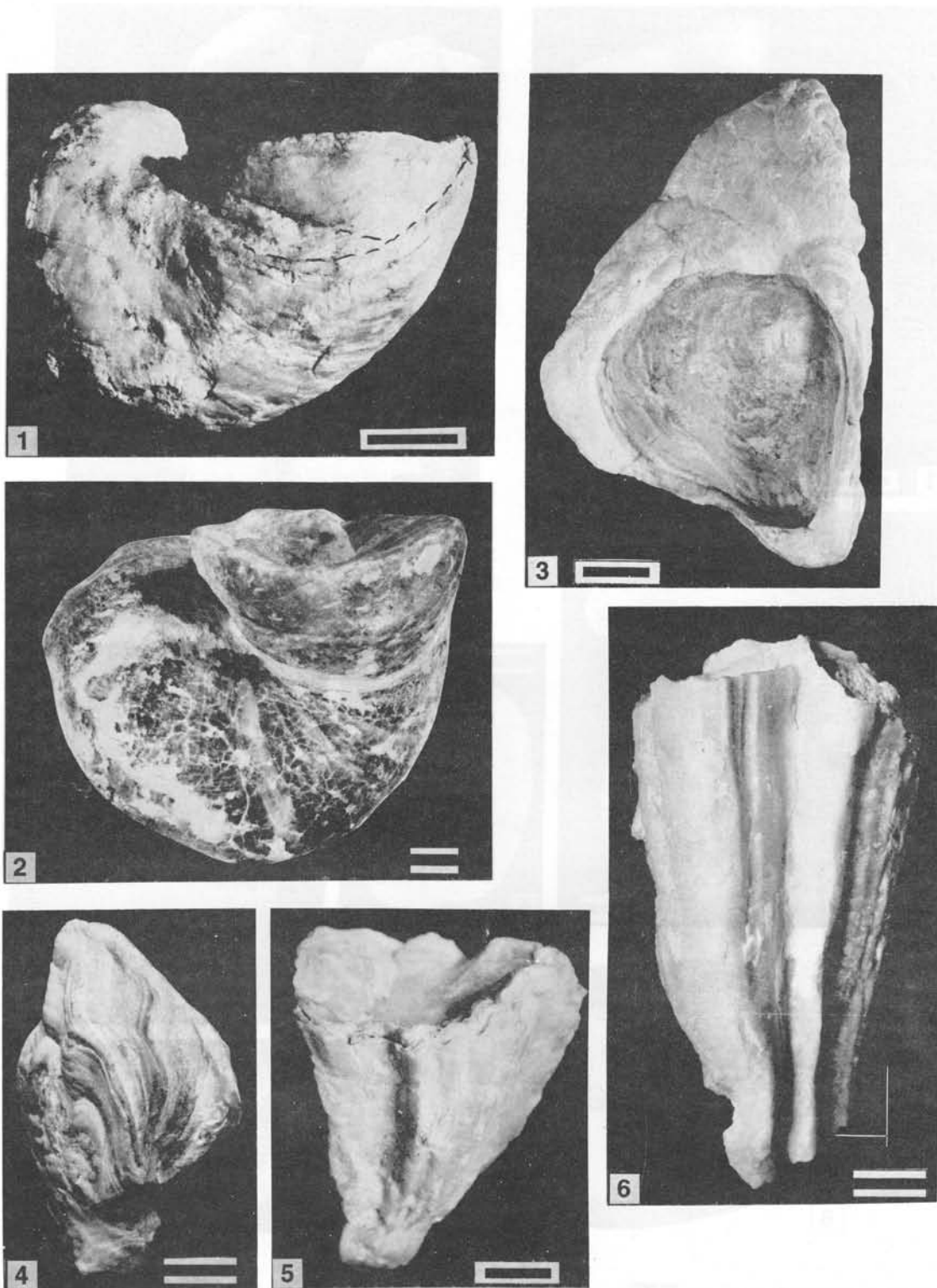


Plate 3. Barremian fauna. Figure 1—*Toucasia praecarinata* Douvillé. Posterior view of a bivalve specimen showing the low, flat upper valve and poorly visible external grooves. Upper Barremian, Brouzet. Languedoc. Figure 2—*Toucasia transversa* Paquier. Posterior view of a bivalve specimen showing the strongly coiled salient upper valve. Upper Barremian, Orgon. Provence. Figure 3—*Matheronia aptiensis* Matheron. Bivalve specimen showing a subtriangular general outline with a flat anterior side, angular posterior side and low coiling. Upper valve slightly depressed. Upper Barremian, Orgon. Provence. Figure 4—*Horiopleura dumortieri* (Matheron). Posterior view of a bivalve specimen showing the prominent upper valve and the undulose growth lines on both valves. Upper Barremian, Orgon (type locality). Provence. Figure 5—*Agriopleura marticensis* (d'Orbigny). Ventral view of a bivalve specimen showing the low conical shape of the lower valve with well-marked crenulated radial bands, the depressed upper valve. Upper Barremian, Brouzet. Languedoc. Figure 6—*Agriopleura blumenbachi* (Studer). Cluster of lower valves showing their tubular shape and longitudinal costulation. Upper Barremian, Brouzet. Languedoc. Scale bar is 1 cm.

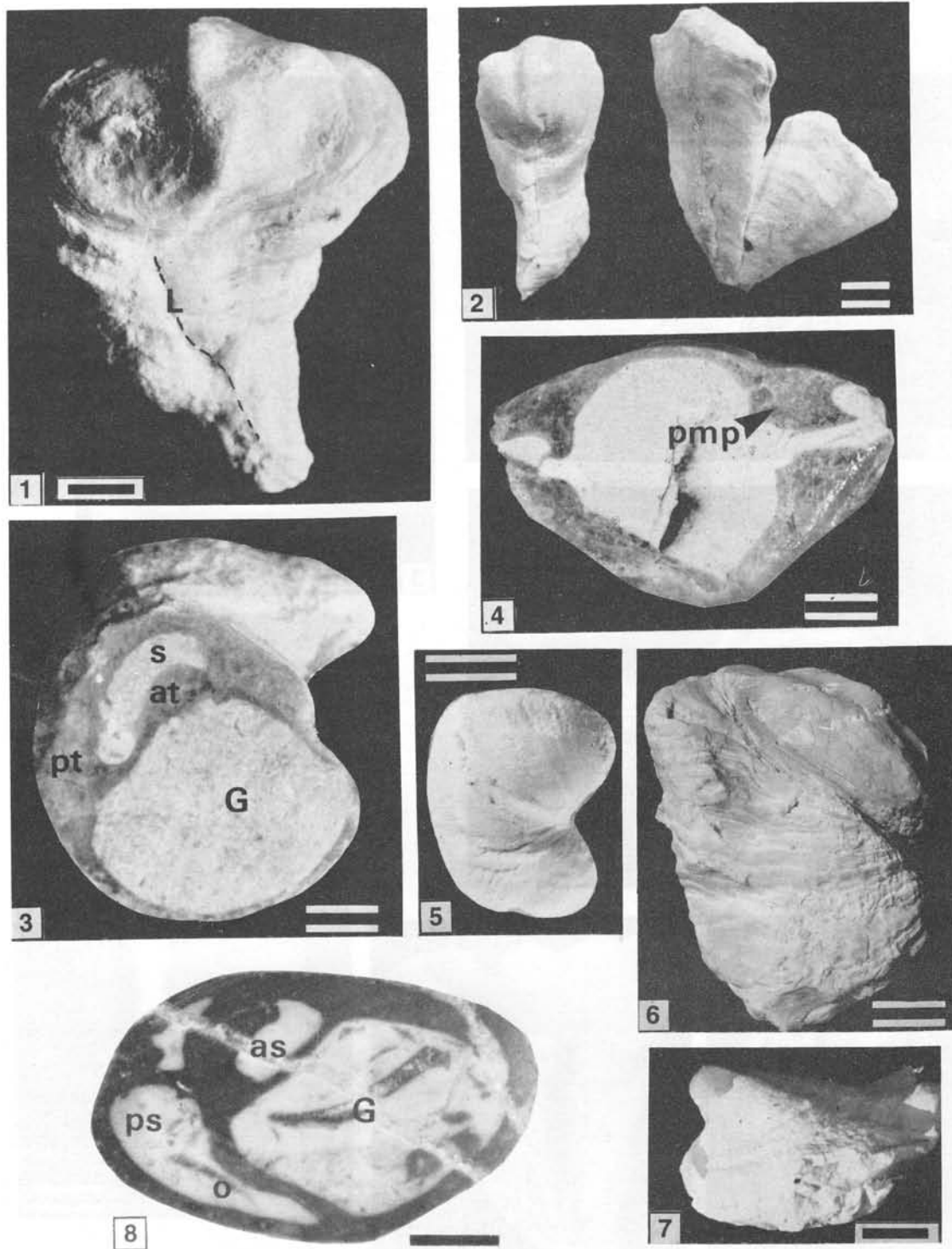


Plate 4, Barremian and lower Aptian fauna. Figure 1—*Monopleura affinis* Matheron. Dorsal view of a bivalve specimen showing the conical lower valve and trilobate elliptic upper valve (L, ligament groove). Upper Barremian, Brouzet, Languedoc. Figure 2—*Monopleura urgoniensis* Matheron. Bivalve specimens; single specimen viewed from its dorsal side, twins viewed from their ventral side. Discrete but well-expressed trilobation. Upper Barremian, Orgon, Provence. Figure 3—*Retha munieri* (Matheron). Transverse section of the upper valve; G, body cavity; at, anterior tooth; pt, posterior tooth; s, central socket. Upper Barremian, Cavaillon, Provence. Figure 4—*Horiopleura* aff. *dumortieri* (Matheron). Longitudinal section of a bivalve specimen showing the myophoral attributes. pmp, posterior pedunculate myophore of the upper valve. Lower Aptian, Lagnes, Monts-de-Vaucluse, Provence. Figure 5—*Monopleura varians* Matheron. Bivalve juvenile viewed from its posterior side. Upper Barremian, Orgon, Provence. Figure 6—*Monopleura* sp. 2 (in Masse, 1976). Bivalve specimen viewed from its posterior side showing trilobation and the fine lamellar growth lines of the lower valve. Lower Aptian, Rustrel, Monts-de-Vaucluse, Provence. Figure 7—*Monopleura depressa* Matheron. Anterior view of a bivalve specimen showing the low "compressed" shell habit with a flat convex downward lower valve and inverted conical upper valve. Upper Barremian, Orgon, Provence. Figure 8—*Pachytraga paradoxa* (Pictet and Campiche). Transverse section of the lower valve showing the body cavity (G), anterior (as) and posterior (ps) sockets and accessory cavity (o). Lower Aptian, La Clape Massif region, Eastern Pyrénées-Languedoc. Scale bar is 1 cm.

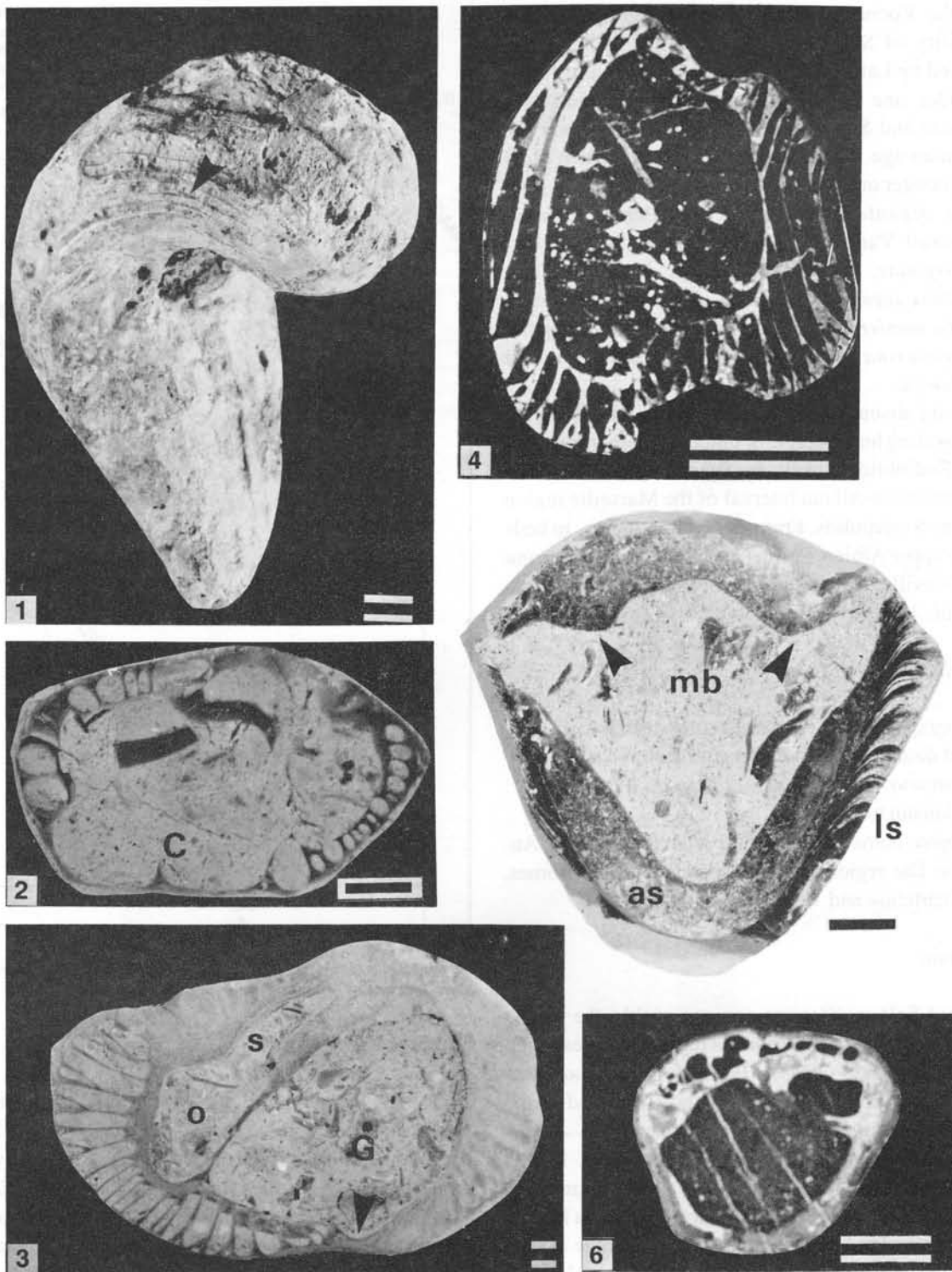


Plate 5. Lower Aptian fauna. Figure 1—*Praeacprina gaudryi* Paquier. Isolated specimen showing the conical lower valve and coiled upper valve with radial (arrow) plates intersecting the shell surface. Lower Aptian, Saint-Chamas. Provence. Figure 2—*Praeacprina varians* Paquier. Transverse section of the upper valve showing the simple subrectangular pallial canals, lacking on the ventral side and the inner ventral crest (c). Lower Aptian, Lagnes, Monts-de-Vaucluse. Provence. Figure 3—*Offneria interrupta* Paquier. Transverse section of the upper valve. Mainly radial (bifurcated) plates developed throughout the shell except on a short ventral inner depression (arrow). Central socket (s) and adjacent accessory cavity (p). Lower Aptian, Rustrel. Provence. Figure 4—*Caprina parvula* Douvillé. Tangential section of the upper valve showing the well developed canal system with multiple bifurcations on the antero-ventral and postero-ventral sides and the depressed ventral side. Lower Aptian, Aude Canyon, Pays-de-Sault. Eastern Pyrénées. Figure 5—*Matheronia virginiae* Gras. Transverse section of a bivalve specimen showing the lamellar outer (primary calcitic) shell of the lower valve (ls), the thick inner (primary aragonitic) inner valve (as) and the myophoral bulges (mb) of the upper valve. Lower Aptian, Lagnes, Monts-de-Vaucluse. Provence. Figure 6—*Caprina douvillei* Paquier. Transverse section of the upper valve showing the pyriform canals (no bifurcating plates) on the ventral and posterior sides. Lower Aptian, Meriadzek Bank (off Brittany). Scale bar is 1 cm, except for figures 4 and 6 where it is 5 mm.

edge facing the Vocontian Basin. The stratigraphy of the classical locality of Saint-Montant (Paquier, 1900, 1905) recently revised by Lafarge (1978) contains two main rudist units. The older one with *Palaeodictyoconus actinostoma* Arnaud-Vanneau and Schroeder and *Orbitolinopsis buccifer* of late Barremian age is characterized by *Agriopleura marticensis*. The younger one with *Palorbitolina lenticularis*, *Rectodictyoconus giganteus* Schroeder and *Paracoskinolina arcuatus* Arnaud-Vanneau of early Aptian age yields: *Matheronia virginiae*, *Matheronia munieri*, *Matheronia aptiensis*, *Requienia ammonia*, *Toucasia carinata*, *Monopleura depressa*, *Retha munieri*, *Pachytraga paradoxa*, *Praeacprina varians*, *Praeacprina gaudryi*, *Offneria intermedia* and *Offneria rhodanica*.

Rudists are absent of the upper Aptian and Albian sequences representing hemipelagic or outer shelf environments. The so-called Radiolitidae specimens figured by Masse (1988) from the Clansayesian-Albian interval of the Marseille region probably belong to serpulids. From the Toulon region, in beds ascribed to the upper Albian, Philip (1970) mentioned *Caprina* aff. *choffati* Douvillé. These beds are now dated as Cenomanian (Machhour, 1988).

Subalpine Northern Region

This geographic entity (Figure 5) consists of two distinctive geological domains (*i.e.*, defined after tectonic and paleogeographic features):

- The Jura domain to the NW.
- The Subalpine domain to the SE, extending from near Annecy to the Die region and corresponding to the Bornes, Bauges, Chartreuse and Vercors massifs.

The Jura Domain

The Mont-Salève (Geneva region) yields the oldest Lower Cretaceous rudist fauna from this region, first described by Joukowsky and Favre (1913). "L'Assise à *Heterodicerias luci*" (*in* Joukowsky and Favre, *op. cit.*) now ascribed to the "Pierre Chatel Formation" is of middle Berriasian age—*Occitanica* Zone—(Clavel *et al.*, 1987b; Deville, 1990). In this area, the transition between the Chambotte and Calcaire Roux Formations is considered as equivalent to the "Arziers Marls" from nearby Switzerland, where Pictet and Campiche (1867-1870) described the following fauna: *Monopleura valdensis*, *Monopleura valangiensis* (Plate 1, figures 4 and 7), *Matheronia eurystoma* (Plate 1, figure 5) and *Matheronia jaccardi* (Pictet and Campiche). These beds are presently considered lower Valanginian and referred to the *Pertransiens* Zone (Deville, 1990). From Yzieux (near La Tour-du-Pin), the author collected *Monopleura* sp. 5 (*in* Masse, 1976) in beds ascribed to the lower Valanginian. The rudist fauna found in the upper Barremian-lower Aptian Urgonian limestones is poorly documented.

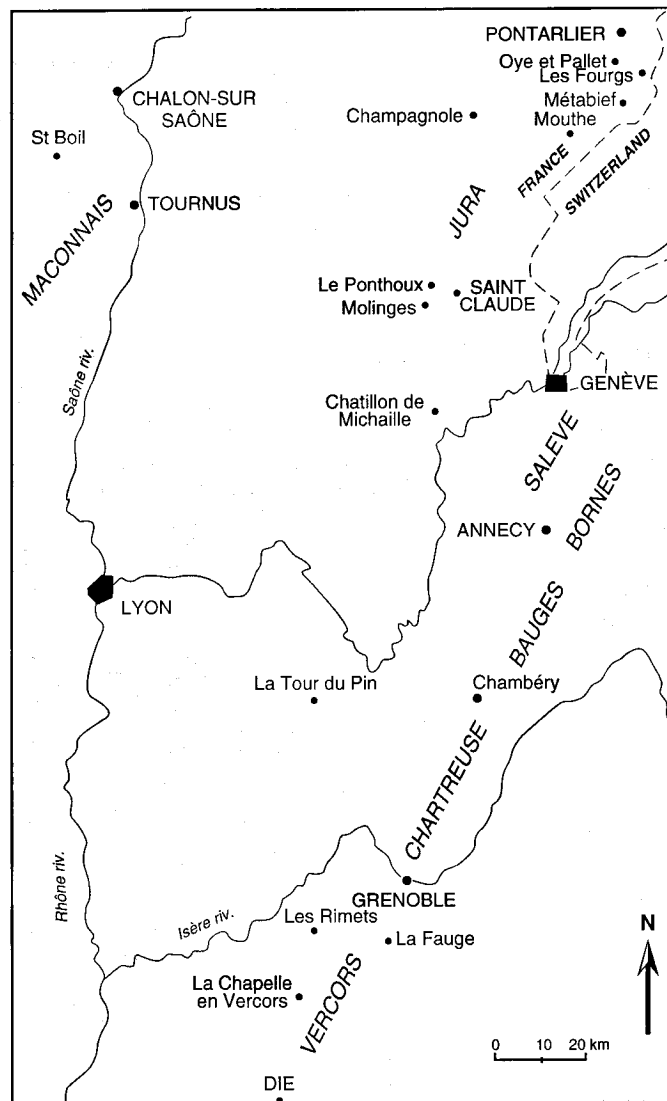


Figure 5. Geographical sketch map of Subalpine-Jura and southeast Paris Basin showing Lower Cretaceous rudist-bearing localities.

The Subalpine Domain

Pre-Barremian rudists are restricted to the northwestern margin of this region, in the so-called presubalpine zone, between Annecy and Chambéry. Near Chambéry—Le Corbelet—the Valanginian limestones yield *Valletia tombecki* (Munier-Chalmas, 1882). Recent investigations by Boisseau (1987) suggest that these beds are lowermost Valanginian. In the Annecy region, the lowermost part of the Urgonian limestones formerly ascribed to the Barremian (Paquier, 1903), then to the lower Barremian (Conrad, 1969), are now placed in the upper Hauterivian (*Balearis-Angulicostata* Zones) (Clavel *et al.*, 1987a). In these beds was found *Lovetchenia* sp., formerly described as *Matheronia lovetchensis* var. *drinovi* Zlatarski, by Paquier (1903). Lower Barremian rudists are poorly known from here. This could be related to the absence of the corresponding beds, as postulated by Arnaud and Arnaud-Vanneau (1991). Whereas Clavel and others (1987b) and

Schroeder and others (1990) have documented the existence of lower Barremian limestones in these regions, one can explain the paucity of rudist occurrences either because of paleoecologically unsuitable conditions—oobioclastic facies seem to dominate—and/or inadequate sampling.

Therefore, rudist-bearing beds are mainly represented in the upper Barremian and lower Aptian Urgonian limestones from the Vercors and Chartreuse near Grenoble. They have been mainly documented by Gras (1852) and Paquier (1900, 1903, 1905), while the biostratigraphy has been extensively revised by Arnaud-Vanneau (1980), Arnaud (1981), Clavel and others (1987a) and Arnaud and Arnaud-Vanneau (1991). From the foregoing, Barremian rudist occurrences mainly belong to the *Giraudi* and *Sarasini* Zones and are known from the southern Vercors, near Archiane onto the Vercors Plateau and its western edge. The rudist fauna consists of: *Requienia gryphoides*, *Toucasia carinata*, *Requienia ammonia*, *Requienia semirugata*, *Monopleura trilobata*, *Agriopleura blumenbachi* and *Agriopleura marticensis*. *Praecaprina varians* is present in the topmost Barremian (unpublished data from Arnaud-Vanneau and the present author). Lower Aptian occurrences are mainly documented from the Vercors Plateau where *Matheronia virginiae*, *Matheronia aptiensis*, *Requienia ammonia*, *Monopleura trilobata*, *Pachytraga paradoxa*, *Praecarina varians* and *Offneria interrupta* were described (Paquier, 1900, 1903, 1905).

Rudist-bearing beds are well exposed in the topmost part of the lower Aptian sequence of central Vercors near Le Rimet (Paquier, 1900, 1905; Arnaud and Arnaud-Vanneau, 1991) where they are capped by *Palorbitolina* marls belonging to the *Bowerbanki* Zone. Immediately below these latter marls, *Matheronia virginiae* (type locality), *Caprina douvillei* Paquier, *Praecaprina varians*, *Offneria sp.* and *Toucasia carinata* are known. *Gyropleuria kiliani* was described from these marls (type locality).

From the Vercors Plateau, near La Fauge, Moret (1936) described *Durania delphinensis* found with *Stoliczkaia dispar* (d'Orbigny), a characteristic ammonite of the Vraconian (upper Albian).

Jura

Lower Cretaceous platform carbonates of this region were extensively studied in the 19th century, especially by Pictet and Campiche (1867-1870) and revised during the last decades by Guillaume (1966), Bronnimann and Conrad (1966), Charollais and others (1966), Conrad (1969), Vieban (1983), Darsac (1983). Rudists were mainly considered by Pictet and Campiche (1867-1870), Astre (1961), Guillaume (1966) and Masse and others (1989).

The oldest occurrences are known from Champagnole-Metabief, where Pictet and Campiche (1867-1870) mentioned *Valletia germari* (Pictet and Campiche) in beds of probable Valanginian age (Guillaume, 1966). Hauterivian rudist-bearing

limestones known as the "Calcaire à *Pachytraga tubiconcha*" (Masse *et al.*, 1989) run along the French-Swiss border zone, between Oye and Palet—near Pontarlier—through Rochejean and Molinges—near Saint-Claude. With the cardinal taxon *Pachytraga tubiconcha*, first described by Astre (1961), poorly defined representatives of *Requienia*, *Monopleura* and the genus *Lovetchenia* (Plate 1, figure 9) are found (Masse, 1993b). The Hauterivian age is derived from those of the micropaleontological assemblage: *Dissocladella hauteriviana* Masse, *Suppiluliumaella sp.*, *Salpingoporella genevensis* (Conrad), *Angioporella neocomiensis* Conrad and Masse, *Urgonina alpillensis* Foury, the *Dictyorbitolina-Praedictyorbitolina* group and *Pseudolituonella gavonensis* Foury (Masse *et al.*, 1989).

The so-called "Urgonien blanc" or "upper Urgonian" with rudists contains poorly defined requienids and monopleurids. In the Val-de-Travers (Switzerland), the corresponding beds are ascribed to the upper Hauterivian-lowermost Barremian (Arnaud-Vanneau and Masse, 1989). From this level was described *Requienia renevieri* Paquier. This species was also mentioned from the southern Jura, at Chatillon-de-Michaille (Paquier, 1903), where it is associated with *Monopleura michaillensis* (type locality). The corresponding micropaleontological assemblage *Heteroporella? paucicalcareia* Conrad, *Likanella? danilovae* Radoicic and *Urgonina cf. alpillensis* (Foury), suggests here an early Barremian age, whereas the latest Hauterivian cannot be excluded.

Southeastern Paris Basin

Between Châlon-sur-Saône and Tournus, at the northern edge of the Monts du Maconnais, from the locality of Saint-Boil, *Valletia* bearing beds of Valanginian age have been recorded (Munier-Chalmas, 1882). *Valletia* is associated with *Monopleura valangiensis* and a micropaleontological assemblage with *Pseudoclypeina? neocomiensis*, *Trocholina alpina* Leupold and *Trocholina delphinensis* Arnaud-Vanneau and Darsac, suggesting an early Valanginian age.

SOUTHWESTERN FRANCE: AQUITAINE-PYRÉNÉES (Figures 6, 7)

Platform carbonates developed throughout the Berriasian-Albian time span, interrupted by several breaks, corresponding to ammonite marls, during the Aptian-Albian. Rudists are essentially identified in the Aptian-Albian interval.

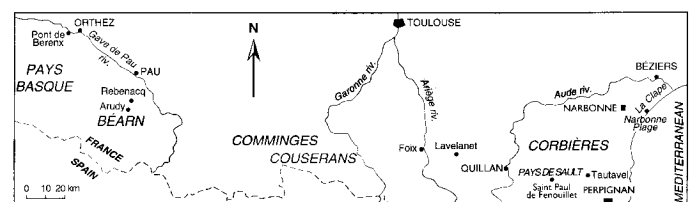


Figure 6. Geographical sketch map of southwestern France: Aquitaine-Pyrénées, showing the main areas and localities with Lower Cretaceous rudist assemblages.

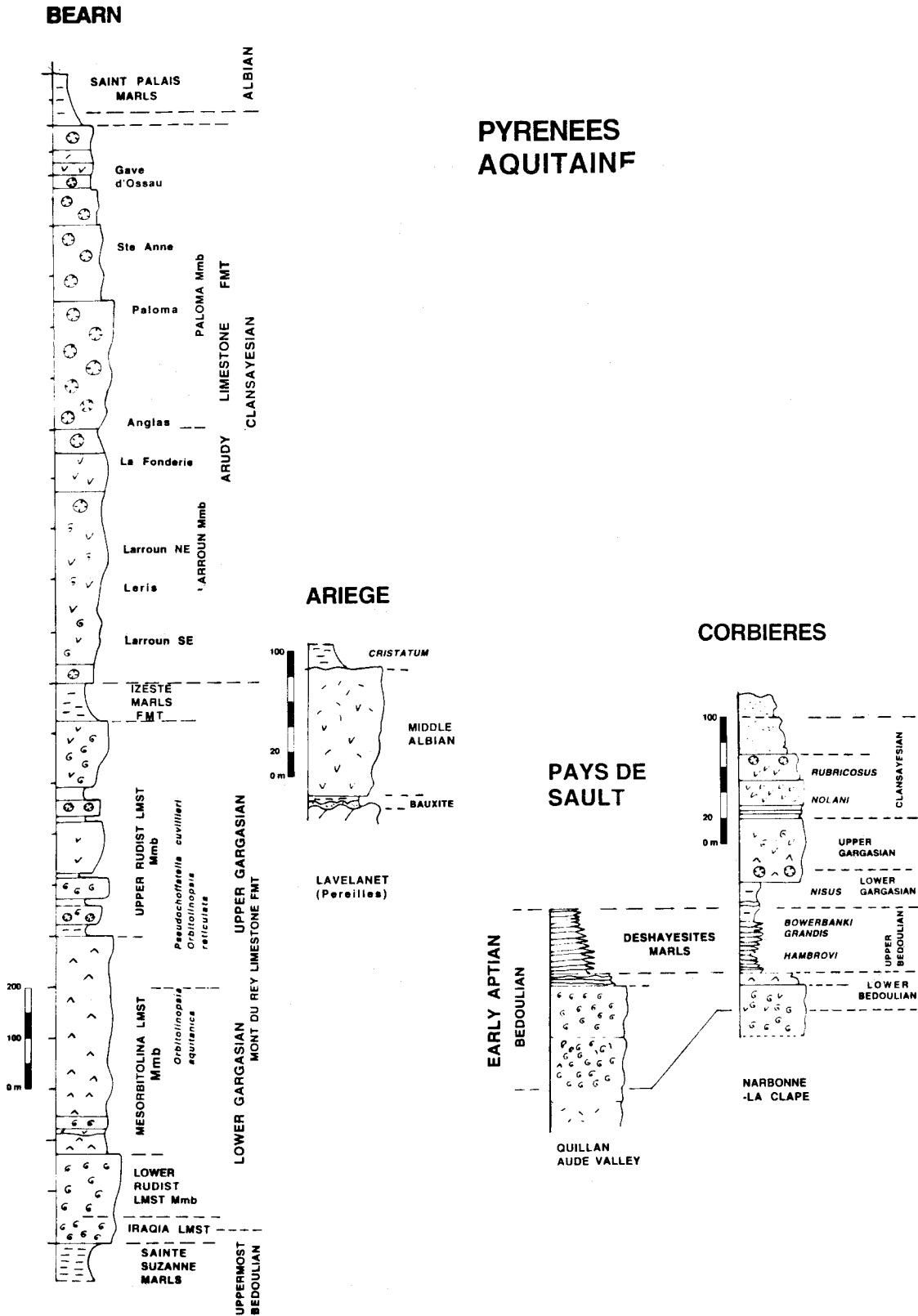


Figure 7. Stratigraphic reference sections for Lower Cretaceous rudist-bearing rock units from Aquitaine-Pyrénées.

Eastern Pyrénées (Corbières, Pays de Sault)

In the Corbières, the Puech de Labade limestones from La Clape Massif, near Narbonne and the Montpeyrus lime-

stones near Tautavel, are ascribed to the Barremian-lowermost Aptian (Peybernès, 1976, 1979; Jaffrezo, 1980). The early Bedoulian age of the upper part of these carbonates is based on the presence of *Orbitolinopsis kiliani* (Prever), *Palorbi-*

tolina lenticularis and *Orbitolinopsis buccifer* (La Clape) and the presence in the overlying "Deshayesites marls" of ammonites belonging to the uppermost Bedoulian: *Dufrenoyia furcata* (Sow.), *Dufrenoyia discoidalis* (Casey), *Cheloniceras cornuelli* (d'Orbigny), and *Deshayesites deshayesi*, an association referred to the *Deshayesi-Bowerbanki* Zones of southern England or *Hambrovi-Grandis-Bowerbanki* ones of La Bedoule.

At La Clape, rudists are represented by *Toucasia* sp., *Horiopleura* aff. *dumortieri*, *Pachytraga paradoxa* (Plate 4, figure 8), *Offneria interrupta* and *Praecaprina* sp. In the Pays de Sault, near Quillan, carbonates equivalent to the Puech de Labade-Montpeyrus limestones—with their overlying *Deshayesites* marls—are recorded, with a similar early Bedoulian age. In the Aude river canyon are identified *Pachytraga paradoxa*, *Offneria* cf. *interrupta*, *Caprina parvula* Douvillé (Plate 5, figure 4), *Praecaprina* sp. and *Toucasia* sp.

In the Corbières, upper Aptian platform carbonates with rudists are well developed and correspond with the following units:

Plan de Roques and Tuffarel limestones (Peybernès, 1976) from La Clape Massif, ascribed to the upper Gargasian and Clansayesian p. p. (*Nolani* and *Rubricosus* Zones), an age based on the presence in the underlying marls of *Aconeceras nisus* (d'Orbigny) and *Melchiorites melchioris* (Raspail) (*Nisus-Martinioides* Zone) and the presence of *Mesorbitolina minuta* Douglass, *Mesorbitolina parva* (Henson) (Plan de Roques) and *Simplorbitolina* cf. *chauvei* Fourcade (Tuffarel). Near Tautavel, the Plan de Roques unit is known as the Château d'Opoul limestones, while the Tuffarel limestones grade to hemipelagic marls. In these two units are recorded *Toucasia* sp., *Horiopleura lamberti* (Munier-Chalmas), *Polyconites* cf. *verneuili* Bayle, *Eoradiolites plicatus* (Conrad) and *Agriopleura?* *darderi* (Plate 6, figure 5).

In the Pays de Sault, the *Deshayesites* marls are overlain by the "*Mesorbitolina parva* limestones" here ascribed to the early Gargasian, an age based on the presence in the overlying marls of *Cheloniceras subnodosocostatum* Sinz (Peybernès, 1976). In the Aude river canyon this unit contains *Polyconites* cf. *verneuili*, *Horiopleura* cf. *lamberti* and *Toucasia* sp.

Upper Clansayesian and Albian rudist limestones are unknown in the eastern Pyrénées; the corresponding interval is represented by deep-water sediments.

Central and Western Pyrénées

In this region, rudist facies are essentially known in the upper Aptian-Albian. In the Ariège valley, the Foix-Lavelanet region displays Albian rudist limestones (e. g., at Pereilles). After Peybernès (1976), they contain *Simplorbitolina conulus* (Douvillé) and *Coskinolinella daguini* Delmas and Deloffre, indicative of a middle Albian age (*Tardefurcata-Mammillatum* Zones) and are overlain by marls belonging to the *Cristatum* Zone (lowermost upper Albian). Astre (1954) mentioned the

presence of *Agriopleura darderi* var. *pyrenaica* (Astre), *Eoradiolites rousseli* (Toucas) (Plate 6, figure 3); additional observations from Peybernès (*op. cit.*) show the presence of *Horiopleura lamberti*, *Polyconites* sp. and *Toucasia* sp. Middle Albian rudist limestones are also reported from the Comminges-Couserans regions (Peybernès, 1976), but their faunal composition is still poorly documented.

Westward, in the Bearn-Pays-Basque regions, rudist limestones are represented by two main units: the Mont du Rey Limestone and Arudy Limestone Formations (N'da Loukou, 1984).

The Mont du Rey Limestone overlies the "Sainte Suzanne marls", a lateral equivalent of the eastern Pyrénées "*Deshayesites* marls", whereas the topmost part of the marls is significantly diachronous. The "Sainte-Suzanne marls" lack any Gargasian taxa, and are characterized in their upper part by *Dufrenoyia discoidalis*, an index of the *Bowerbanki* Zone. The basal part of the overlying Mont du Rey Limestone displays *Iruqia rubiensis* (Bassoullet and Moullade), an orbitolinid also reported from the *Bowerbanki* Zone. The corresponding rudist limestone is characterized by *Caprina parvula* (the type-locality of which is Rebenacq). The rudist association is nevertheless dominated by *Toucasia*.

This unit is overlain by the *Mesorbitolina parva* marls and limestones, also containing *Orbitolinopsis aquitanica* Schroeder and Poignant, and *Pseudochoffatella cuvillieri* Deloffre, diagnostic taxa of the upper Gargasian. The Mont du Rey limestone contains *Toucasia* sp., *Pseudotoucasia* cf. *santanderensis* (Douvillé) and *Eoradiolites* aff. *katzeri* Sliskovic. The Mont du Rey Limestone is capped by the marls of the Izeste Formation, overlain by the Arudy Formation limestone, ascribed to the Clansayesian (with *Mesorbitolina texana* [Roemer]) and consists of a rudist member (Larroun limestones) overlain by a coral member (Arudy limestones s.s.). The rudist unit is characterized by *Pseudotoucasia* cf. *santanderensis*, *Eoradiolites plicatus* (Plate 6, figure 4), *Polyconites verneuili* and *Horiopleura lamberti*. This fauna is recorded in small quarries surrounding Arudy—Leris, La Fonderie, Anglas—while the Paloma-Sainte Anne quarries are dominated by corals.

Northward, near Orthez, the Pont de Berenx locality, from which Douvillé (1889) described *Praeradiolites cantabricus* (Douvillé), is situated in these Arudy limestones, placed in the Clansayesian, although the above mentioned author cited an Albian age. Tercis, the type locality for *Horiopleura lamberti* (Plate 6, figure 1) initially ascribed to the Albian (see Seunes, 1890; Poignant, 1964) is presently considered Clansayesian. The Arudy limestones also yield *Horiopleura baylei* Coquand, *Horiopleura almerae* Paquier and *Toucasia seunesi* Douvillé.

In its type locality, at Arudy, the Arudy Formation limestone is capped by the Saint-Palais marls ascribed to the topmost Clansayesian and/or lower Albian (N'da Loukou, 1984), a situation assumed for all the Bearn localities.

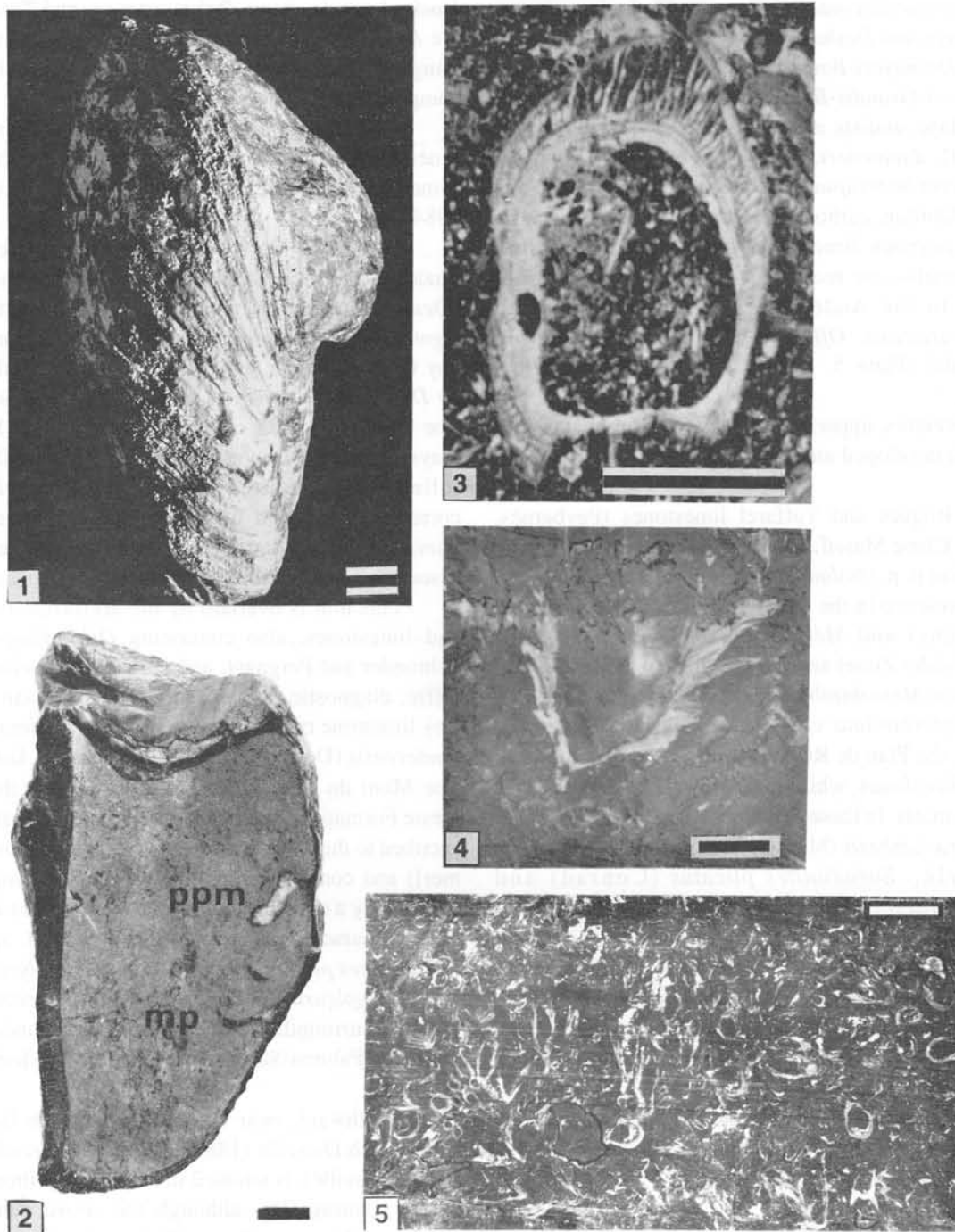


Plate 6. Upper Aptian and Albian faunas. Figure 1—*Horiopleura lamberti* (Munier-Chalmas). Bivalve specimen viewed from its posterior side showing the prominent upper valve and the conical lower valve. Clansayesian. Paleontological collection of the Toulouse University; locality Tercis, Landes, Aquitaine. Figure 2—*Pseudotoucasia santanderensis* (Douvillé). Transverse section showing the pedunculate posterior myophore of the upper valve (ppm) and the simple inclined myophore plate of the lower valve (mp). Commissure indicated by an arrow (posterior side). Clansayesian (Albian?), Santander region, Spain. Figure 3—*Eoradiolites rousseli* (Toucas). Transverse section of the lower valve (thin section) showing the well developed radial meandriform "cellular" structure on the thick parts of the shell (less developed or nearly absent in thinner parts) especially on the dorsal part and on the radial ventral bands. Middle Albian, Pereilles, Central Pyrénées. Figure 4—*Eoradiolites plicatus* (Conrad). Longitudinal section (slab) showing the lateral growth expansions mainly consisting of a compact shell structure. Clansayesian, Arudy, Western Pyrénées. Figure 5—*Agriopleura? darderi* Astre. Transverse section of a lower valve showing the characteristic structure of the inner part of the calcitic layer (arrow). Upper Gargasian, La Clape. Scale bar is 1 cm.

VALANGINIAN

Matheronia jaccardi, *Matheronia eurystoma* (and other possibly allied requienids), *Monopleura valdensis*, *Monopleura valangiensis*, *Monopleura* sp. 4, *Valletia tombecki* (and possible thick shelled monopleurids) are characteristic members of the lower Valanginian. A problematic *Heterodicerias* also belongs to this association. Rudist formations are nearly absent in southern France during the late Valanginian, a situation linked to a drastic spatial reduction of carbonate platforms during the corresponding time span (Masse and Lesbros, 1987).

HAUTERIVIAN

Rudists are nearly unknown in the lowermost Hauterivian, whereas the *Loryi-Nodosoplicatum* zones yield *Pachytraga tubiconcha*, *Lovetchenia* sp. and *Matheronia* sp., still present in the upper Hauterivian. *Requienia renevieri* is recorded from the upper part of the stage (*Balearis-Angulicostata* Zones), while *Agriopleura* appears in the *Angulicostata* Zone. Monopleurids are weakly documented; they are represented by tubular forms, whose taxonomic description needs to be achieved.

BARREMIAN

The lower Barremian records *Agriopleura blumenbachi*, *Requienia ammonia*, *Requienia renevieri*, *Requienia migliorinii*, *Monopleura michaillensis* and *Toucasia carinata*. Except for *Requienia renevieri*, all these species are still present in the upper Barremian with *Requienia semirugata*, *Requienia pelati*, *Requienia gryphus*, *Requienia gryphoides*, *Monopleura varians*, *Monopleura depressa*, *Monopleura affinis*, *Monopleura urgoniensis*, *Monopleura imbricata*, *Petalodontia? mutabilis*, *Petalodontia bruni*, *Matheronia munieri* and *Matheronia aptiensis*. The upper part of the Barremian (*Feraudi-Giraudi* Zones) is marked by the presence of *Retha dubiosa*, *Retha munieri*, *Toucasia praecarinata*, *Toucasia transversa* and *Horiopleura dumortieri*. *Pachytraga paradoxa*, *Matheronia virginiae*, *Praecaprina varians*, *Praecaprina gaudryi*, *Offneria rhodanica* and *Offneria interrupta* are documented from the *Giraudi* p. p. *Sarasini* Zones.

APTIAN

Lower Aptian (Bedoulian)

The majority of Barremian species is still present with some exceptions like *Monopleura michaillensis*, *Monopleura imbricata* and *Petalodontia bruni*. This stage recorded the development of *Praecaprina varians*, *Praecaprina gaudryi*, *Offneria rhodanica*, *Offneria interrupta*, *Offneria intermedia* and *Monopleura* sp. 2. During the late Bedoulian, *Matheronia*

munieri and *Toucasia praecarinata* seem to disappear. The *Hambrovi-Grandis* and *Bowerbanki* Zones are marked by the occurrence of *Caprina douvillei*, *Gyroleura? kiliani* and *Caprina parvula*. The *Bowerbanki* Zone is marked by the disappearance of nearly all of the Barremian-Bedoulian species, except *Toucasia carinata*.

Upper Aptian (Gargasian-Clansayesian)

Gargasian

The drastic specific and generic turnover known at the lower-upper Aptian boundary (Masse, 1989) led to a drop in diversity connected with the extinction of the Caprinidae and of a large number of Requieniidae and Monopleuridae, not balanced by the evolution of the Polyconitidae and Radiolitiidae. The lower Gargasian recorded *Toucasia carinata*, *Horiopleura almerae*, *Horiopleura baylei* and *Polyconites verneuli*. During the late Gargasian is found the same assemblage, with *Eoradiolites* aff. *katzeri*, *Eoradiolites plicatus*, *Horiopleura lamberti*, *Toucasia seunesi* and *Pseudotoucasia santanderensis*.

Clansayesian

This interval displays the same association as those from the upper Gargasian but also shows the appearance of *Praeradiolites cantabricus* and possibly *Agriopleura? darderi*.

ALBIAN

Lower Albian rudist localities are not clearly documented. The middle Albian rudist fauna still contains some upper Aptian elements: *Polyconites verneuli*, *Horiopleura lamberti* and *Pseudotoucasia santanderensis*. *Agriopleura? darderi* and *Eoradiolites rousseli* are typical members of this interval.

Upper Albian rudist formations are nearly absent in connection with the drastic spatial reduction of carbonate platforms. Rudists are only known as isolated specimens from outer-shelf settings, exemplified by *Durania delphinensis* from the Vraconian.

DISCUSSION

Berriasian-Valanginian rudist faunas from southern France are by far the best known at a global scale. Data from the Caucasus (Yanin, 1989) concerning the same stratigraphic interval, deal with a smaller number of taxa showing some endemism. Other occurrences are very limited. Hauterivian faunas also appear as the best documented in the world even if rudist assemblages from Portugal, Spain and Sardinia are similar (Masse, 1993b and unpublished personal observations). The Barremian fauna is the richest one at generic and specific levels; Barremian rudists from Italy are far less diverse

(Mainelli, 1975; Masse, 1992). The lower Aptian fauna is also highly diverse in comparison with those from the Mediterranean area (Masse, 1985), especially from Spain (Masse *et al.*, 1992) and Italy (Masse, 1992) and the Caribbean (Harris and Hodson, 1922; Masse and Rossi, 1987; Mac Gillavry, 1935; Rojas *et al.*, 1993). This interval is also marked by a high degree of provincialism. Thus, the southern France fauna is clearly identified with the southwestern European province (Masse, 1985). The upper Aptian fauna is similarly one of the richest known so far at a global scale (Gallo-Maresca and Masse, 1992), though North-African assemblages also show a high faunal diversity (Chikhi-Aouimeur, 1982). Albian assemblages display a relatively limited faunal richness but close to those from coeval faunas from Spain (Masse *et al.*, 1992) or Portugal (Douvillé, 1898), that is to say less than that of Apulia (Di Stefano, 1889; Masse and Philip, 1986). Mediterranean diversity is far less than those of the Caribbean (Coogan, 1973; Palmer, 1928; Alencáster, 1987; Johnson, in press). Provinciality seems relatively limited during the late Aptian and increases significantly in the Albian. This phenomenon is well expressed between the Mediterranean and Caribbean regions but also within the Mediterranean region, between the Apulian (*i.e.*, African) and European areas, during the Albian.

Low diversity records from the Berriasian-Hauterivian are considered to reflect low original values compared to those from the Barremian-lower Aptian. Nevertheless, it must be kept in mind some geological and paleontological contingencies. The chalky limestones from which well preserved specimens can be obtained and clearly identified have probably enhanced our ability to produce complete inventories, a common situation for the Barremian-lower Aptian beds. On the contrary, hard limestones do not permit such refined studies, a common situation for the Berriasian-Hauterivian beds. Such contingencies are probably more limited for the upper Aptian-Albian beds (where no chalky facies exist) containing marly intercalations allowing to obtain well preserved sample collections. These contingencies are also probably enhanced by purely paleontological ones, that is to say, advanced rudists, *e.g.*, Caprinidae, Polyconitidae and Radiolitidae can be identified from hard rocks at a specific level, by means of oriented sections; an approach more difficult to achieve for primitive forms of Requiieniidae and Monopleuridae. That could explain the specific uncertainties concerning Berriasian-Hauterivian forms pertaining to these families and even the possibility of their total diversity being underemphasized.

The foregoing stratigraphic distribution documents the stepwise onset of basic morphostructural types for the Dextrodonts, Requiieniidae and Senestrodonts Monopleuridae, Caprinidae, Polyconitidae and Radiolitidae (Skelton, 1985, 1991). The gradual increase in taxonomic diversity through time was interrupted in mid-Valanginian and mid-Aptian times, which represented significant mass extinctions (Masse, 1989, 1993a). The mid-Valanginian break was typified by the extinction of the last Jurassic remnants (Diceratidae) and fol-

lowed by the appearance of primitive Caprinidae (*Pachytraga*) and an evolutionary pulse in the Requiieniidae during the Hauterivian. The Barremian-early Aptian time span had the highest diversity peak with a burst of caprinids. The mid-Aptian break corresponds to the near extinction of the Caprinidae and the radiation of the Polyconitidae, two groups originated earlier but which showed opposite kinds of behaviour, phenomena coeval with the onset of the Radiolitidae.

The mid-Valanginian and mid-Aptian biological crises are clearly connected with palaeogeographic regional changes: carbonate platforms are significantly or drastically spatially reduced. Nevertheless, because these biological events are also recorded outside the studied region and because they also affected other taxonomic groups from both shallow water and deep-water settings, global oceanologic factors are probably more significant than the regional paleogeographic ones (Masse, 1989, 1993a).

CONCLUSIONS

The southern French Cretaceous stratigraphic sequences are composed of carbonate formations with rudists, close to, or interbedded with hemipelagic deposits containing ammonites, in the vicinity of many stage stratotypic areas. Rudists are distributed throughout the Berriasian-Albian interval. Because geological, historical contingencies, upper Valanginian and Albian faunas are poorly represented. The southeastern French—Provence, Languedoc-Bas Vivarais, Subalpine and Jura—regions display well documented Berriasian-lower Aptian faunas. In southwestern France, rudists are mainly represented in the Aptian-Albian. Sixty one species have been recorded, corresponding to 23 genera. The vertical ranges of these species are provided at stage, substage and frequently even to specific ammonite key zones. Very few species are known to occur for durations exceeding two stages. The appearances and disappearances rarely coincide precisely with stage boundaries, but in many cases the species ranges fall within those of a stage or a substage. The main biostratigraphic boundaries correspond with the middle Valanginian and middle Aptian (*i. e.*, Bedoulian-Gargasian boundary). The Hauterivian-Barremian transition (*i. e.*, the *Angulicostata* Zone), and the uppermost Barremian (*Giraudi* and *Sarasini* Zones) are also considered levels of significant faunal changes with biostratigraphic implications. Such limited time ranges give to species a good biostratigraphical potential. Considering the wide palaeo-biogeographical distribution of the majority of taxa, their potential as chronologic markers, useful for large scale correlations, is also high. The Lower Cretaceous rudist faunal stratigraphical distribution of southern France therefore appears as a valuable reference for Mesogean correlations.

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