NON RUDISTID BIVALVES FROM CRETACEOUS RUDIST FORMATIONS

A review of bivalve species associated with rudists in Cretaceous formations is presented and their geographical distribution and palaeoecological significance are discussed. Particular attention is paid to the faunas from "Urgonian", Albian, Cenomanian and varied "Senonian" formations, especially the genera Neithia (Pectinidae), the oyster homoeomorph Chondrodonis (Chondrodonitidae, ? Pectinacea) and to the poorly known Turkmenia (probably a pteriid genus).

Introduction

Reefs and reef-like structures throughout geological history always contain several faunal elements, but corals are probably the most common basic reef-element. Yet, bivalves have at least twice been the basic builder for reef-like frameworks: the Lithiotacea in the Lower Jurassic (Accorsi Benini & Broglio Loriga, 1977; Accorsi Benini, 1979; Chinzei, 1982) and the rudists in varied Cretaceous formations. Within such Cretaceous rudist frameworks, other essential elements of the biocenostuctures were algae and stromatoporoids. Between the structural "reef" elements and on the flanks of the frameworks lived many other molluscan species. Sometimes these species are unknown or rare in non-rudist environments.

In the present paper a survey has been made of the specific non-rudistid bivalve species associated with rudists in some Euro-American platform deposits.

Rudist associated Cretaceous bivalves

Rudist frameworks have often been compared to Recent coral reefs because they also existed in a marine, shallow and relatively warm environment. Such rudist "reefs" are especially common in the Urgonian facies (Barremian-Aptian), in the Albian, and in all Upper Cretaceous stages (Fréneix, 1960).

"Urgonian" (Barremian-Aptian)

Some discussion exists as to the interpretation of the term "Urgonian". Here, for practical reasons, it is understood as defined during the "Colloque sur le Crétacé inférieur" in Lyon (1963): "Calcaires à Toucasia et à ceux qui leur sont directement associés, du Barrémien et de l'Aptien" (Rat, 1965, p. 833).

In the Urgonian formations a rich non-rudist bivalve fauna existed. A few examples are cited hereafter. The fauna from the type locality, at Orgon (Vaucluse, SE France), was already included in the major works of Matheron (1843) and d'Orbigny (1843-1847), and was later described monographically by Cossmann (1918). Pictet & Campiche (1864-1871) discussed in their monograph the virtually coeval fauna from Châtillon-de-Michaille (Ain, E. France). Cossmann (in Pellat & Cossmann, 1907; in Brun et al., 1916) described another similar Urgonian fauna (with few rudists though) found at Brouzet-les-Alès (Gard, SE France).

Cossmann (1918), in his paper on the fauna from Orgon, already recognized a lithological subdivision of the outcropping strata. He described twenty-two bivalve species from the "Calcaire oolithique", and twenty-one of the overlying "Calcaire crayeux" [this last formation is interpreted here as being the "Calcaire crayeux à Rudistes" in Masse (1983, p. 6)]. From Brouzet-les-Alès, Cossmann (1908, 1916) described thirty-one non-rudist bivalve species, along with nerineids, Neritidae and other gastropods typical for rudist environments. From Châtillon-de-Michaille Pictet & Campiche (1864-1871) described eighteen non-rudist bivalve taxa.

These Urgonian bivalve faunas have a comparable composition: they include mainly pteriomorphs such as boring mytilids, limids, pectinids [among which Neithia deshayana (Matheron, 1843), named Janira eurytis in Pictet & Campiche, 1871] and heterodonts such as limbridi. Basically the bivalves in this assemblage are epifaunal. As already stated by Cossmann (in Brun et al., 1916), many "Urgonian" species seem characterised by strongly developed, heavy and thick shells.

Faunas with "Urgonian" (generally Barremian) elements have been described from Tethys deposits from SE France to Central Asia (USSR). The more northern occurrences are in Austria ("Schrattenkalk" facies which contains Neithia deshayana), in S. Ger-
many (Allgäu), in S. Poland, and in the Soviet Carpathians (Chernov & Yanin, 1979; Yanin, 1980). In Turkmenia (Central Asia, USSR) Barremian formations contain at least partially the same faunas as in SE France (Prozorovskii et al., 1961; Krimholz, 1962; Bogdanova, 1966). One element thought to be endemic in these Central Asian Barremian faunas is the genus *Turkmienia* Krimholz, 1936, described from the Barremian beds in Turkmenia with at least species *T. balkhanensis* Krimholz, 1936. However, from Orgon, Coissmann (1918, p. 397, pl. 13, figs. 1, 2) described the taxon *Chondrodonta barremica*, which is also characterised by commarginal plications especially near the umbo and seems to have a more or less smooth shell towards the ventral margin. Though we do not know the hinge of these specimens from Orgon, "*Chondrodonta* barremica" is considered here as also belonging to *Turkmienia* [after finding a specimen of the taxon at Orgon, Carrière du Cimetiére, and after having seen the Krimholz types (Leningrad State University), and the figured specimens of Bogdanova, 1966 (VSEGEI, All Union Geological Survey) in Leningrad].

Aptian (Bedoulian) rudist associations are known in SW Europe [i.e. S. France (Arnaud-Vanneau et al., 1979), Portugal (Rey, 1979)] but we did not have the opportunity to study their non-rudist bivalves.

**Albian**

Among the best known Albian rudist occurrences are those from the Edwards Limestone in Texas (USA, Lower Albian), which were mainly described in the last century. Though the non-rudist bivalve assemblage is not particularly diversified [only eleven species according to Adkins (1928)], it contains at least three species only known in rudist-assocations: the pelecypod *Neithia duplicicosta* (Roemer, 1852) and two oyster homoeomorphs, *Chondrodonta munsoni* (Hill, 1893) and *Ch. glabra* Stanton, 1901. Similar occurrences of rudists and *Ch. glabra* are also found in the Lower Albian of Arizona (R. Höfling, oral communication 1990).

In Europe comparable faunas are known from the Abian of Portugal (Choffat, 1902; Rey, 1979), with *Neithia stefanoi* (Choffat, 1902), and from the Zirc Limestone formation in Hungary with *Neithia stefanoi", "Chondrodonta cretacea* (Horváth, 1966)", *Ch. hantkenii* (Horváth, 1966)" (Czabaly, 1985).

**Cenomanian**

In the Tethys Cenomanian rudist associations are frequent. They are known of Early Cenomanian age and of Late Cenomanian age. Among the better known of such faunas, especially of the latter age, are those of Portugal [already described by Choffat (1886, 1902)], of the Ile Madame and of Angoulème, in SW France [known already to d’Orbigny (1843-1847) and Coquand (1860)], of Provence [especially from Cassis-la-Bedoulle, Bouches-du-Rhône, France, recently studied for the rudists by Philip (1978, 1983)], from several places in Italy such as Monti Prenestini, Latium (Carbone et al., 1971), the Materese Mounts, Molise (Accordi et al., 1990), Monti d’Ocre, Abruzzo (Parona et al., 1909), Apulia (Dainelli, 1901), and the classic locality Col dei Schiosi, Friuli (Piron, 1884; Futterer, 1898; Bohm, 1895; Parona 1908 a, b), from Istria, Dalmatia and other regions in Yugoslavia [Slovenian localities recently studied by Plenčar (1960, 1967), Croatian localities by Polšák (1965, 1967), Gušić & Jelaska (1990)], from Albania (Peza, 1989), and from Lebanon (Douville, 1910; Saint-Marc, 1970). It must be noted that localities with a fauna of "Schiosi age" in Yugoslavia (and Albania) have previously often been dated as being of Turonian age. However, Philip (1978) explained that this might be due to the following of erroneous age attributions for some rudists in Choffat, especially in the paper of 1902. Therefore we feel entitled to consider these faunas, containing virtually identical bivalve associations, as coeval with the Late Cenomanian faunas from NE Italy (see also Gušić & Jelaska, 1990).

All these Cenomanian rudist associations contain other bivalves and especially *Neithia fleuriauxiana* (d’Orbigny, 1847), *Chondrodonta delgadoi* (Choffat, 1886), *Ch. desori* (Coquand, 1869), *Ch. joannei* (Choffat, 1886) have been found in many of these localities (Frenex, 1960 and personal observations). Further occurrences of *Ch. joannei* have been documented i.e. in Lebanon and Syria (Pfender, 1938).

As an example of a Late Cenomanian (Sartorio, 1989) rudist-associated bivalve fauna, the list of the species from Col dei Schiosi [western Friulian Prealps, NE Italy], recently studied by Dhondt & Dieni (in preparation), follows:

*Botuloides intermedius* (d’Orbigny, 1845)  
*Limaria elongata* (J. de C. Sowerby, 1827)  
*Plagiostoma asperum* (Mantell, 1822)  
*Lyroichiama ternata* (Münster in Goldfuss, 1833)  
*Neithia aequicostata* (Lamarck, 1819)  
*Neithia fleuriauxiana* (d’Orbigny, 1847)  
*Neithia zitelli* (Piron, 1884)  
*Chondrodonta delgadoi* (Choffat, 1886)  
*Chondrodonta joannei* (Choffat, 1886)  
*Perotrigonia scabra* (Lamarck, 1819)  
*Ludbrookia cattalina* (d’Orbigny, 1844)  
*Icanotia impar* (Zittel, 1865)

Four species of this fauna are only known from rudist associations: *Neithia fleuriauxiana*, *N. zitelli*, *Chondrodonta joannei*, *Ch. delgadoi*. *Neithia fleuriauxiana* has been recorded from Portugal to
Yugoslavia, *N. zittelii* has a more restricted distribution, limited to NE Italy and NW Yugoslavia. *Chondrodonta joannae* has been recorded from Portugal to Somalia, and the closely related *Ch. delgadoi* from Portugal to possibly W. Pakistan (Dhondt & Dini, in preparation).

By far the most common non-rudist bivalve in Col dei Schiosi is *Neithia zittelii* (Fig. 1). It is characterised by an uncommonly heavy shell and by a very incurved umbo, associated with larger hinge "teeth" than those found on any other *Neithia* species. *N. zittelii* can be interpreted as having lived in a high energy environment, in which the ratio weight/volume insured a relative stability. Similarly, the *Chondrodonta* species, especially *Ch. joannae*, developed very heavy umbalon areas in the Col dei Schiosi area. Thus their attachment to the substrate was stronger there than in other localities, probably for the same reason as suggested for *Neithia zittelii*. Yet, this may not have been a totally successful strategy, since the number of chondrodonts is relatively low in the Schiosi fauna.
However, in other Friulian localities chondrodonts were extremely common, as can be seen in Pradis, Pordenone (Fig. 2 shows part of a slab, housed in the Museo Friulano di Storia Naturale of Udine, on which more than fifty well preserved specimens are visible on a surface of about 2 m²). Presumably Chondrodonta species thrived generally in a back-reef environment (see also Freneix & Lefèvre, 1968, p. 772), whereas Neithia zitieli was able to live successfully also in a fore-reef environment. Sometimes Ch. joannae definitely lived in the rudist framework and some rudists even grew on Ch. joannae specimens (Fig. 3).

**Turonian-Santonian**

The faunas from the Lago di S. Croce area (localities Calloneghede and Pinei, province of Belluno, Eastern Venetian Prealps, NE Italy) were previously considered as Turonian, but more recent research has shown them to be of ages varying from Turonian to Santonian.

Only few rudist assemblages of undoubted Turonian age have been recently described. One is in the “Massif du Subeyran” near Marseille, SE France (Philip, 1980, 1983). It contains virtually no non-rudist bivalves. Another is “Assemblage Tu” from the Serra del Montsec, NE Spain (Pons, 1977; Pascual et al., 1989). Also for this Spanish locality we do not have precise information on the rudist-associated bivalves.

Rudists of Coniacian age are not uncommon. They have been recorded f.i. from several localities in the “Gosau” of Austria (Herm et al., 1979; Summesberger, 1985), and from NE Spain (Pons, 1977; Pascual et al., 1989).

The rich rudist associations from the Lago di S. Croce area (Belluno, Eastern Venetian Prealps, NE Italy), studied by Catullo (1834), Futterer (1892) and Boehm (1895), are now being dated as being mainly Coniacian-Santonian (J.M. Pons, oral comm., August 1990). The non-rudist bivalve faunas (Dhondt & Dieni, in preparation) contain so far twenty-five species, listed below:

- Lithophaga sp.
- Arca n. sp.
- Cucullaea matheroniana (d’Orbigny, 1845)
- Phelopteria cf. caudigera (Zittel, 1866)
- Cordiceramus muelleri (Petrascheck, 1906)
- Ctenoides tectus (Goldfuss, 1835)
- Limaria echinata (Etheridge, 1881)
- Limatula sp.
- Limea granulata (Nilsson, 1827)
- Plagiostoma hoernesi (Zittel, 1866)
- Camponectes virgatus (Nilsson, 1827)
- Mimachelanys n. sp.
- Neithia dutruei (Coquand, 1862)
- Neithia quinquecostata (J. Sowerby, 1814)
- Neithia sexangularis (d’Orbigny, 1847)
- Neithia sexcostata (Woodward, 1833)
- Neithia striatocostata (Goldfuss, 1833) n. ssp.
- Spondylus arcuatus (Catullo, 1834)
- Spondylus requienianus Matheron, 1843
- Fimbria alpaghina (Catullo, 1827)
- Myoconcha dilatata Zittel, 1865
- Cyclocardia cf. otonis (Geinitz, 1843)
- Crassatella macrodonta (J. de C. Sowerby, 1832)
- Granocardiun productum (J. de C. Sowerby, 1832)
- Pachymya frequens (Zittel, 1865).

None of these species are definitely restricted to rudist assemblages, but Neithia striatocostata n. ssp., Spondylus arcuatus are only known from the Lago di
S. Croce area and *Fimbria alpaghina* is only recorded associated with rudists from Lago di S. Croce and from the Trieste area. Thus these three species could be limited to rudist faunas. Further, several species from Lago di S. Croce have developed exceptionally heavy shells: *Cucullaea matheroniana*, *Neithia striatocostata* n. ssp., *Spondylus arcautus*, *Fimbria alpaghina* and *Granocardium productum*.

No chondrodont has been found at Lago di S. Croce, but *Spondylus arcautus* has evolved a morphology which is, on some specimens, surprising close to the external ornamentation and shape of *Chondrodonta joannae*.

Among the twenty-five taxa recognised at Lago di S. Croce, six are placed in open nomenclature. Of the nineteen others, twelve have also been found in the Gosau s.s., mainly in localities of Coniacian and Santonian age. Further, if we compare the fauna of the Lago di S. Croce area with those of probable Santonian age described by Freneix (in Freneix & Viaud, 1985) from rudist associated faunas of the Vendée (W. France), it becomes obvious that similar faunal elements (excluding the oysters which are found in the Vendée) are present in the two areas. Freneix (op. cit.) considers the Vendée faunas as representing a back reef environment (largely demonstrated by the presence of a strong proportion of oysters), and stresses the predominance of epifauna over endofauna. This last aspect is certainly also true at Lago di S. Croce (and at Col dei Schiosi) and undoubtedly has to do with the coarse bioclastic nature of the substrate.

Santonian rudist formations have been found f.i. in the “Gosau”, Austria (Herm et al., 1979), NE Spain (Pons, 1977; Pascual et al., 1989), Provence (Philip, 1980, 1983), and possibly in Turkey (Freneix & Lefèvre, 1968). However, except for the Turkish deposits, they do not seem to contain typical rudist-associated bivalves, but rather a fauna simply indicating a fairly shallow, warm environment.

An example of such a warm water, rudist-associated fauna is the assemblage from La Cadière (Var, SE France) of which a tentative, probably incomplete list follows, based on the specimens from the Musée Longchamp in Marseille, re-identified by Dhondt:

*Arca* sp.
*Brachidontes divaricatus* (d’Orbigny, 1845)
*Botuloides* sp.
*Chalmasia turonensis* (Dujardin, 1837)
*Limaria* cf. *ovata* (Nilsson, 1827)
*Neithia sexcostata* (Woodward, 1833)
*Neithia striatocostata* (Goldfuss, 1833)
*Spondylus truncatus* (Lamarck, 1819)
*Ceratostreon pliciferum* (Dujardin, 1837)
*Hyotissa semiplana* (J. de C. Sowerby, 1832)

**Crassatella macrodonta** (J. de C. Sowerby, 1832)
**Icainothia cf. impar** (Zittel, 1865)

This Santonian fauna from a rudist-reef environment is very close to coeval faunas from the Vendée described by Freneix (in Freneix & Viaud, 1985), and possibly is from a similar back-reef environment. It shows fewer similarities with Lago di S. Croce faunas.

The assemblage described by Freneix & Lefèvre (1968) from Turkey contains the youngest known *Chondrodonta* species, *Ch. elmaliensis* Freneix & Lefèvre, 1968, and a wide *Neithia* species, somewhat similar to *N. fleurisiana*, named *N. rotundata* Freneix & Lefèvre, 1968. These species, which are accompanied by rudists but not by other bivalves and have relatively heavy shells, were probably really living in the framework itself, and not in the back-reef area.

**Campanian-Maastrichtian**

Numerous rudist build-ups have been described of Campanian and Maastrichtian age. In the rudist formations from southern Europe not much attention has been given to rudist-associated bivalves. This may be due to several causes, such as?

— the hardness of the rock in which the rudists are preserved, making collecting of other bivalves extremely difficult;

— the very compact rudist framework not allowing sufficient space for other macro-organisms;

— the real absence or extreme rareness of other bivalves because of rudists living in a restricted environment.

According to the locality, one or more than one of these suggested explanations can apply.

Occasionally rudists of Campanian age have been found in marls, with a variety of other organisms such as ahermatypic corals, gastropods etc., but without other bivalves. In between these marls proper rudist-frameworks almost too hard to extract fossils from and not visibly containing other organisms, occur. An example of such an association is seen in the Campanian “Marnes de Saint-Cirac”, in the Ariège, S. France (Bilotte, 1990).

An example of a restricted environment containing rudists is seen in the Haute-Garonne, S. France, in the Maastrichtian “Marnes à faune d’Auzas”, where rudists are associated with “*Cyrena* garamnica” Leymerie, 1877 and gastropods known to be stenohaline (Bilotte, 1990).

The description of the Campanian-Maastrichtian formation “Calcare di Caranna” at the Strada dei Colli, Ostuni, Brindisi (S. Italy) by Guarneri et al. (1990) shows calcarenites and calcirudites containing corals, rudists, ostreids (small *Pycnodonte* specimens) and gastropods overlain by mainly hippocrite banks.
Kauffman & Sohl (1974) indicated epibionts of individual rudist-specimens from the Campanian-Maastrichtian of the West-Indies. Among these epibionts they list f.i. hermatypic and ahermatypic corals, bryozoans, lithophagid bivalves, oysters (including Pycnodonte), other rudists. Specific descriptions of these epibionts are not given. Other bivalves occurring together with the rudists are not mentioned. Yet, an alternation of a.o. rudist levels and “diverse” molluscan assemblages is shown to have taken place frequently in the Caribbean (Kauffman & Sohl, op. cit.).

Also Vicens (1984) noticed such alternate successions in Santonian-Campanian rudist formations of the Spanish Pre-Pyrenees. It is therefore not impossible that excluding the epibionts, rudist frameworks s.s. of Campanian-Maastrichtian age did not contain other bivalves.

Conclusions

Non-rudist bivalves from and near rudist frameworks lived in a shallow environment.

In many areas extensive faunas have been found which represent the back-reef fauna, having lived in the lagoon behind the rudist build-ups such as f.i. in the Vendée, W. France, and at La Cadière, SE France. A few taxa lived in the “reef” itself or sometimes even in the fore-reef and were adjusted to a high energy environment:

— Neithaea deshayana and probably Turkmenia spp. in the “Urgonian” of S. Europe and W. Asia;

— Neithaea duplicicosta, Chondrodonta munsoni and Ch. glabra in the Edwards Limestone of Texas (Lower Albian);

— Neithaea fleurussia, N. zitteli, Chondrodonta delgadoi, Ch. desoti, and Ch. joanneae from the Campanian, mainly of S. Europe;

— Neithaea rotundata and Chondrodonta elmaliensis from the Santonian (?) of Turkey.

Species living in the “reef” or in the fore-reef environments developed a very heavy shell. This is especially seen in assemblages from Col dei Schiosi and from the Lago di S. Croce area (NE Italy): especially Neithaea zitteli and Chondrodonta joanneae at Col dei Schiosi, and Neithaea striatocostata n. ssp., Spondylus arcuatus, Fimbria alpagnhina and Grano-

cardium productum at Lago di S. Croce.

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RIASSUNTO

Viene presentata una rassegna dei principali bivalvi associati alle rudiste durante il Cretaceo e di essi vengono discusso il significato paleoecologico nonché la distribuzione geografica. Particolare attenzione viene rivolta alle faune dell’“Urgonian”, dell’Albiano, del Cenomaniano e a quelle delle varie formazioni a rudiste del Senoniano, mettendo in evidenza il ruolo giocato dai generi Neithaea (Pectinidae), Chondrodonta (Chondrodontidae), ? Pectina-
cea), omeomorfo delle ostree, e dal poco noto Turkmenia (probabile pteride). Viene infine riportato un elenco ag-


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