## ORIGINAL ARTICLE

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## Coral zonation of an Oxfordian reef tract in the northern French Jura

Received: 2 June 2004 / Accepted: 13 October 2004 / Published online: 25 January 2005 © Springer-Verlag 2005

**Abstract** During the Middle Oxfordian, numerous coral reefs flourished on the northern margin of the Tethys Ocean. The outcrop of Bonnevaux-le-Prieuré (northern French Jura mountains) provides a rare opportunity to observe a nearly complete section allowing the installa-

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tion, evolution and demise of this global carbonate reef rich event to be studied. Quantitative data on coral assemblages together with sedimentological and palaeoecological observations lead to the reconstruction of a reef tract coral zonation. Starting from the outer slope, *Dimorpharaea*, *Microsolena*, *Dendraraea*, *Comoseris*, and *Stylina* ecozones are recognized. This new facies model implies a central position for an oolitic shoal in the highest energy zone, within the *Comoseris* ecozone. Applying this facies model to the sequence stratigraphic interpretation of the vertical succession results in recognising a third-order relative sea-level fluctuation, which can be correlated at least with Lorraine (France) and Switzerland.

**Keywords** Jurassic · Benthic communities · Palaeoenvironment · Corals · Reefs · Facies model · Carbonate platform

## Introduction

While the bionomic zonation of Recent reefs is commonly used as a powerful proxy to reconstruct Cenozoic fluctuations of sea-level (e.g. Geister 1983; Camoin et al. 1997; Perrin 2000), zonations of Jurassic reefs based on coral taxa are nearly non-existent. The morphology of reef bodies so clearly related to sea-level fluctuations (Neumann and Macintyre 1985) is much more difficult to reconstruct in Jurassic than in Cenozoic series. Consequently, reliable biological zonations are needed. The most advanced attempt in this direction is probably that made on Kimmeridgian ramps in Iberia (Werner et al. 1994; Nose 1995). For Oxfordian times, a conceptual depositional model has already been proposed (Insalaco et al. 1997) based on very diverse build-ups organised according to three environmental variables: light, hydrodynamism, and sedimentation. Compared to this first attempt, our contribution is based on the quantification of corals over a single outcrop in order to avoid palaeolatitudinal variability and to restrict as far as possible tem-

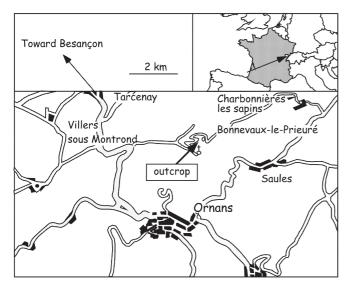


Fig. 1 Location of the section of Bonnevaux-le-Prieuré

poral variability with its unavoidable consequences in difficulties to separate biological evolutionary changes and short term environmental fluctuations effects.

This work is a contribution to a multidisciplinary project conducted by the Groupe Français d'étude du Jurassique (GFEJ), which is dedicated to the palaeoenvironmental comparison of several sections across a transect going from deep basinal settings toward emersive areas. The comparison is made within a biochronologically well-defined short time-span: the Middle Oxfordian interval. See Gaillard et al. (1996) and http:// www.gfej.fr.st/ for more details and the philosophy of the project. Within this transect, the outcrop of Bonnevauxle-Prieuré is the most complete section of reefal facies, providing the opportunity to understand (i) installation, life, and finally demise of a reefal environment in the Oxfordian, and (ii) how an Oxfordian corallian ramp/ platform might have been divided into bionomic zones, based on our quantitative data. The present paper provides the first palaeontological and sedimentological synthesis of this project based on this outstanding section; complementary data can be found in several previous papers dealing with foraminifera (Bouhamdi 2000; Bouhamdi et al. 2000, 2001) and corals (Habrant and Lathuilière 2000). A complementary work involving a more precise study of micro- and macrofauna is in progress.

## **Geological setting**

The section studied is located on the Ornans Plateau in the northern French Jura mountains along the road connecting Bonnevaux-dessous to Bonnevaux-le-Prieuré (Fig. 1). The considered lithologic succession belongs to the so-called "faciès franc-comtois" well exposed in the northern Jura and connected with similar facies in neighbouring areas: Burgundy, Lorraine, and Switzerland (Enay et al. 1984). As established earlier (Contini and Rollet 1971;

Contini 1972; Enay et al. 1988) the base of the section starts within the "Calcaires argileux de Bonnevaux Formation," dated Vertebrale Subzone, and ends within the "Calcaires de Clerval Formation," late Transversarium Zone. The "Marnes à *Creniceras renggeri* Formation," dated Early Oxfordian (Mariae Zone *p.p.* and Cordatum Zone *p.p.*) does not outcrop because it is covered by scree and dense vegetation. The zonal biostratigraphic framework refers to the synthesis by the Groupe Français d'Etude du Jurassique (1997).

Of the 86 m thick section, only a few metres are hidden from investigation. Bonnevaux-le-Prieuré is the southernmost outcrop of reefal facies at this time in the northern Jura. This is probably due to structural control of palaeotopography by normal faulting (Konate 1992). From a palaeogeographical viewpoint, the section was located on a vast platform, which extended south of the present-day Vosges Massif facing the open sea. It was part of a long reef belt along the northern margin of the Tethyan gulf, extending from Transcaucasian areas to Western European Peritethyan intracratonic platforms (Martin-Garin et al. 2002). Southward, the outer platform is made of Argovian deeper facies separated from slope and basinal facies by an algal-sponge bioherm belt (Gaillard 1983; Enay et al. 1988 for a Recent synthesis). The general organisation of sedimentary units is very close to the well-known frame proposed by Gygi and Persoz (1986) for Switzerland and recently debated by Allenbach (2002) and Gygi (2003).

#### **Material and methods**

The stratigraphic column was collectively elaborated, sedimentary structures were observed and extensive sedimentological and palaeontological sampling was performed in order to define the depositional environment and describe the main faunal assemblages with special focus on corals. For these animals, specific random sampling was performed in every coral-bearing unit. As far as possible, at least 30 samples in each unit were collected and 21 units were sampled. Experience shows that some sampling bias may occur. The dimensions of the colonies probably introduces some bias: a large colony has more chance of being sampled than a small solitary coral. Diagenesis also is not equal for all coral genera. Corals whose size, structure, shape and porosity favour fluid circulation are potentially underevaluated because of their bad preservation and more or less complete dissolution. Moreover, it is often difficult to know the difference between two different colonies of the same genus and a single colony counted and collected twice. However, the bias seems rather weak and we are convinced that, imperfect as it is, a quantitative approach is an obvious step forward in biofacies description. All coral samples were cut in oriented sections and determined at the generic level, which is presently the most reliable category in coral taxonomy. Numerous coral genera have nevertheless unclear taxonomic status and need thorough revision, which is far beyond the scope of this paper. For this reason, several genera have been regrouped here. For instance, "Stylina" includes Heliocoenia. The genus name "Allocoenia" is used here for archaeocoeniid small cerioid forms commonly named Actinastrea, Stephanastrea, or Stephanocoenia (Lathuilière 1989). Here also, Cryptocoenia is grouped with Pseudocoenia and Adelocoenia. Dimorpharaea refers to D. koechlini Haime Microsolena refers to M. irregularis d'Orbigny (or to a senior synonym). These last genera were separated mainly on septal and trabecular density criteria rather than colonial structure (Habrant 1998).

Diversity was evaluated using the Shannon-Wiener index according to the following formula:

$$Shannon\,Wiener\,Index = -\sum_{i=1}^G P_i \log P$$

where G is the number of genera in the sample and P is the percentage of the genus in the assemblage.

Equitability was calculated according to the following formula:

$$Equitability = -\sum_{i=1}^{G} P_i \log P_i / \log G$$

It varies between 0 and 1. A value close to 1 means that all genera are almost equally represented in each sample. If one genus is strongly dominant, the value will be close to zero.

# Sedimentary succession, biofacies and related environments

The succession of lithostratigraphic units is described using Contini's (1989) nomenclature (Fig. 2).

## Calcaires argileux de Bonnevaux

#### Lithofacies

This formation is composed of a marl and limestone alternation. The dominant fine terrigenous input is greater in the lower part. The microfacies is a wackestone rich in reniform spicules of siliceous sponges (5–30%), in echinoderm fragments (3–20%), and in bivalve bioclasts. Small crusts of serpulids, bryozoans, and microbialite are abundant. In the upper part, siliceous sponges are progressively replaced by calcareous sponges. Peloids range between 3 and 20% (Fig. 3a, b). Sub-rounded quartz grains from 20 to 100  $\mu$ m in size are relatively abundant (1–5%). Dolomitization of the micritic matrix is intense and silicification of matrix and skeletons are pronounced.

#### **Biofacies**

No corals are found in this formation but the invertebrate fauna is fairly abundant and diverse.

#### Ammonites

They are not uncommon but badly preserved in beds B to N (beds 8 to 10 in Contini and Rollet 1971). Owing to better outcropping conditions at that time, the specimens in the Contini and Rollet collection are better preserved (now housed in Lyon University Collection). They are included in the following list:

Beds B-C (C8 in Contini and Rollet): Perisphinctes
 (Dichotomosphinctes) sp., P. (Arisphinctes) sp.

- Beds I-L (C9 upper part of Contini and Rollet): P.
   (Dich.) arkelli Glowniak [= P. (Dich.) rotoides Arkell non Ronchadzé], P. (Dich.) cf. buckmanni Arkell., P. (Dich.) sp., P. (Arisph.) sp., Passendorferia (Enayites) gr. birmendorfensis (Moesch).
- Beds M-R (C 10 of Contini and Rollet): P. (Dich.) arkelli, and cf. arkelli., P. (Dich.) sp., P. (Dich.) sp. or P. (Arisph.) sp. and P. (P.) gr. alatus-pumilus Enay in bed R.

Although perisphinctids are the only group, the assemblage is well known in the upper part of the Plicatilis Zone, Antecedens Subzone. *P.* (*Dich.*) *arkelli* was selected recently in Poland (Glowniak 2000; 2002) as the index species of the Arkelli Subzone, just below the Antecedens Subzone, which is questionably included in the Transversarium Zone.

Other macrofossils are terebratulid brachiopods, softbottom deep-burrowing bivalves, endobenthic irregular sea urchins, and *Thalassinoides*.

#### Palaeoenvironment

Bedding, petrography, microfacies, and fauna point to a calm depositional palaeoenvironment below the fairweather wave base. The absence of corals and the occurrence of ammonites and siliceous sponges progressively replaced by calcareous sponges suggest a circalittoral environment evolving to shallower conditions. A hardground occurs at the J2/K limit (Fig. 2); its significance is not yet clear from a sequence stratigraphic viewpoint.

## Calcaires siliceux de Dole

#### Lithofacies

These limestones are either wackestones with sponge spicules and peloids or boundstones (sheetstones according to the classification in Insalaco 1998) with a wackestone matrix. The most common bioclasts are reniform spicules (3–30%), probably responsible for chert genesis, calcareous sponges, and echinoderms (1–10%). Small crusts of serpulids, bryozoans and microbialites still occur. Dolosparite may replace original micrite in some places (Fig. 3c).

#### **Biofacies**

### Corals

The dominating morphology is lamellar and thamnasterioid. It seems that in the more argillaceous beds, colonies exhibit a low-angled V-shaped morphology. These corals are not encrusting but their lower surface is encrusted by a fauna of serpulids, thecideans, bryozoans, and calcareous

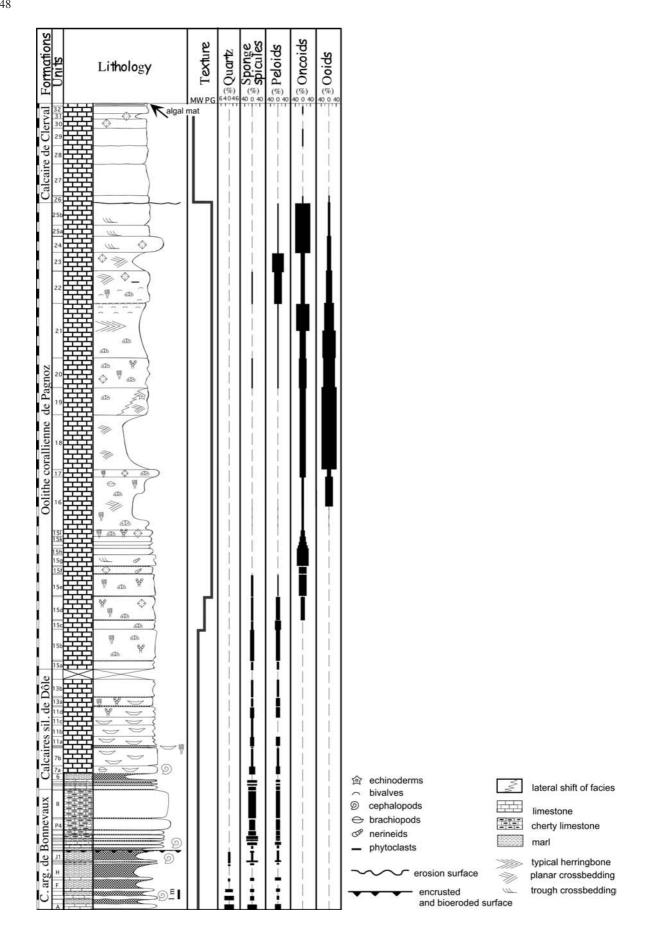
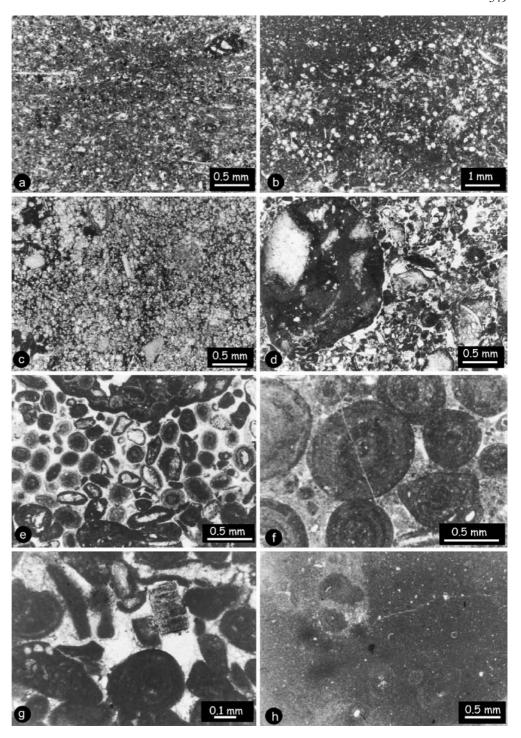


Fig. 3 Microfacies;  $\mathbf{a}$  – Wackestone with reniform spicules and quartz grains, Calcaire argileux de Bonnevaux Formation, bed I3, BLP I-3; **b** – Wackestone with spicules and peloïds, Calcaire argileux de Bonnevaux Formation, bed 1, BLP L; c - Locally dolomitized matrix within a boundstone, Calcaire siliceux de Dole Formation, bed 11c, BLP 11c; **d** – Grainstone with peloids, intraclasts and bioclasts, Oolithe de Pagnoz Formation, bed 15d, BLP 15d1; e – Grainstone with radial ooids, Oolithe de Pagnoz Formation, bed 19, BLP 19; **f** – Grainstone with micritic ooids, Oolithe de Pagnoz Formation, bed 15h, BLP 15h; **g** – Grainstone with micritic ooids and isopachous drusy cements, Oolithe de Pagnoz Formation, bed 25, BLP 25; **h** – Lagoonal mudstone, Calcaire de Clerval Formation, bed 26, BLP 26



sponges, while the upper surface is commonly postmortem colonised by serpulids and encrusting bivalves. Coral diversity is low but higher in beds 7b and 11a than in beds 11b to 13a; equitability is low everywhere (Ta-

**Fig. 2** Lithology, lithostratigraphy and significant components along the section of Bonnevaux-le-Prieuré. Width of black sticks are semiquantitave estimates. M = mudstone, W = wackestones, P = packstones, G = grainstones. In boundstones, only the texture of the matrix is given. Symbols related to corals and numbers corresponding to thin units can be found on Fig. 5

ble 1). The most common genera belong to the microsolenids (*Comoseris*, *Dimorpharaea*, *Microsolena*). *Dimorpharaea* (Fig. 4a) is the most abundant.

#### Ammonites

Contini and Rollet (1971) collected the only ammonite known in the formation, in bed D 12, probably bed 7a in Fig. 2. The specimen (now housed in the Lyon University

Table 1 Quantitative parameters of coral distribution. No bed refers to units in Fig. 2. Numbers below genera names are

	Thecos- milia		18.6	35.5	19.3	13.9	33.3		13.9		2.1								20
	Tham- nasteria	18.5 12.5	7.0		8.1	13.9	2.4		8.3										
	Stylos- milia	3.7	2.3	6.7	6.4												100		
	Stylina	17.3 12.5	11.6	3.2	6.4	1.5.4			2.8	2.7									
	Soleno- coenia		2.3																
	Crypto- coenia	7.4	4.6	3.2			2.4		2.8										
	Micro- solena				3.2	2.8	4.8		22.2		2.1	4.5	5.4						
	Micro- phyllia	4.9																	
	Mean- draraea	3.7																	
)	Latias- traea	2.5																	
	Isastrea	37.5	7.0	6.4	11.3		9.5		5.6										
	Fungias- traea	2.5	7.0		6.4	8.3			2.8										
•	Enall- helia			3.2															
	Dimor- pharaea		2.3	3.2	1.6	7. [	4.8	100	25.0	91.9	81.2	81.2	89.2	73.5	84.2			56.2	20
	Den- draraea		2.3		ו	27.8	23.8		2.8	2.7	6.2		2.7	5.9				15.6	
	Como- seris	27.2 37.5	23.2	32.2	19.3	22.2	7.1		8.3		2.1			5.9					
	Clausa- strea		2.3		8.8		2.4		2.8										
	Calam- ophyl- liopsis	2.5	2.3		8.1		2.4		2.8										
	Aplos- milia		2.3		1.6														
	Allo- coenia	6.6					7.1												
	Acti- naraea		4.6	3.2	3.2					2.7	6.2	13.6	2.7	14.7	15.8	100		28.1	
	Equi- tability	0.89	0.00	0.77	0.90	0.73	0.82	0.00	98.0	0.27	0.42	0.53	0.33	0.61	0.63	0.00	0.00	0.88	1.00
	Shannon- Wiener Index	3.07	3.50 0.00	2.43	3.34	2.58	2.82	0.00	3.07	0.53	1.09	0.84	99.0	1.21	0.63	0.00	0.00	1.4	1.00
,	Nb colonies	818	43 6	31	62	36	42	1	36	37	48	22	37	34	19	_	_	32	2
	Nb genera	11 4	15	6	13	o 1-	Ξ	_	12	4	9	33	4	4	2	_	-	33	7
	N° bed	22 21	19 20	17	16	15e	15d	15c	15b	13a	11d	11c	11b	11a	2 =	10	6	7P	7a

Collection) is confirmed here as *Perisphinctes* (*Perisphinctes*) *parandieri* de Loriol, the index species of the Parandieri Subzone of the Transversarium Zone.

The other most common macrofossils are bivalves (*Chlamys*, *Actinostreon*, *Opis*), brachiopods (mainly *Galliennithyris*), serpulids, and cidarids.

#### Palaeoenvironment

The depositional environment is still below the fairweather wave base. The palaeogeographic frame is in agreement with an offshore setting, opened toward the south. The habitat of the corals was poorly lit. The new interpretation of microsolenid structure and function suggests a dominant suspension feeding habit, which is coherent with a lower infralittoral mesotrophic situation (Lathuilière and Gill 1995; Morycowa and Roniewicz 1995; Leinfelder et al. 1996; Insalaco 1996; Gill et al. 2004). Epibenthos now strongly dominates endobenthos.

## Oolithe corallienne de Pagnoz

In this calcareous formation, the microfacies is highly variable. For this reason the description is subdivided into thinner informal units 15a to 25b.

## Lithofacies

Units 15a–15b display a matrix similar to that of the "Calcaires siliceux de Dôle," units 15c–15d are made of a peloidal bioclastic packstone with echinoderm debris (3–5%), corals, bivalves (10%) gastropods, brachiopods, and reniform spicules (3–5%); bioclasts are large. Peloids represent 10–15%. Elements are often encrusted.

Units 15e–15f are packstones-grainstones with oncoids/ooids and bioclasts. Ooids and oncoids, sometimes including nubecularians, represent respectively 1 and 25%. Bioclasts are echinoderm debris, bivalves, corals, sponges, gastropods and brachiopods (Fig. 3d).

Units 15j-25b are oolitic grainstones with sedimentary structures that indicate tidal influence (oblique bedding with tangential base and herringbone patterns). They include some reefal units of mixstone with an oolitic grainstone matrix. Within these units, the dominant type of ooid varies from radial to micritic (Fig. 3e–g). Oncoids represent 10–20%. Some lumps occur, bioclasts are less numerous (5–15%): echinoderms, brachiopods, bivalves, gastropods, and bryozoans. The earlier cement is isopachous and has a phreatic marine origin; it is followed by a later blocky sparry calcite rather indicative of a fresh water history which is not dated.

#### Ammonites

Corals

This formation corresponds to the maximum development of coral associations and build-ups.

At the base, unit 15b is characterised by a microsolenid association in which *Microsolena* (Fig. 4b) is as abundant as *Dimorpharaea*. *Thecosmilia* is also numerous but is found only as broken branches. Diversity and equitability are high (Table 1).

In unit 15d, morphologies are mostly phaceloid and ramose. Diversity and equitability are lower than in 15b. *Thecosmilia* (Fig. 4c) and *Dendraraea* (Fig. 4d) dominate together. Colonies are encrusted and bored.

In unit 15e, morphologies are mostly massive-meandroid and ramose-thamnasterioid. Colonies are small, diversity and equitability are higher than in 15d. *Dendraraea* and *Comoseris* are encrusted and bored, and locally display partial necrosis.

Phaceloid morphology is well represented in unit 151; diversity and equitability have decreased. The number of colonies found in this bed is low (n=13). The most abundant genus, *Thecosmilia*, occurs as broken branches; coral fragments are encrusted by microbialites.

In units 16–17, dominant morphologies are phaceloid and massive meandroid. The diversity is higher in bed 16 than in bed 17. Among phaceloid genera, *Thecosmilia* is the most abundant, other genera with smaller corallites are reworked. Among massive meandroid colonies, *Comoseris* (Fig. 4g) is dominant. Borings are numerous, generally post-mortem.

Unit 19 has yielded only 6 colonies of *Isastrea* (Fig. 4h). Encrusting serpulids and borings are frequent.

Unit 20 is a true build-up; massive meandroid and phaceloid colonies are numerous. Diversity and equitability have increased. *Comoseris* is abundant and shows high upward growth; many colonies exhibit signs of partial necrosis. Borings are common, microbialite crusts commonly coat coral surfaces.

In unit 21, dominant morphologies are massive meandroid and cerioid, diversity has decreased. Conversely, equitability is higher. *Isastrea* and *Comoseris* are less common and share a comparable abundance. Colonies are few, small, bored, and encrusted by bryozoans and serpulids.

Dominant morphologies of unit 22 are massive, meandroid or thamnasterioid (*Comoseris* and *Thamnasteria*). Diversity and equitability are high. Colonies can reach great sizes (60 cm in diameter). "*Allocoenia*" mainly occurs in this assemblage. "*Stylina*" (Fig. 4f) is also well represented here compared to other assemblages. From this unit comes also a microatoll-like colony, the first emersive colony ever found in the Jurassic (Habrant and Lathuilière 2000). The corals are at least partly reworked. Borings and crusts (notably solenoporaceans) are common.

Based on the occurrence of *Perisphinctes* (*P*.) cf. *stru-matus* (Buckmann) in their oolitic unit E, Contini and Rollet (1971) dated the formation Bifurcatus zone. The fossil was re-examined by Enay; it is a fragment with a cast of the ventral part of inner whorls of a large *Perisphinctes* (*P*) sp., which cannot be identified at the specific level; consequently, the age proposed by Contini and Rollet (1971) is abandoned.

Other macrofossils are represented by diverse ecological types of suspension-feeding bivalves (parautochthonous assemblage), occasional terebratulid brachiopods and echinids, rare small chaetetid sponges and algae, among which solenoporacean algae are the most obvious.

#### Palaeoenvironment

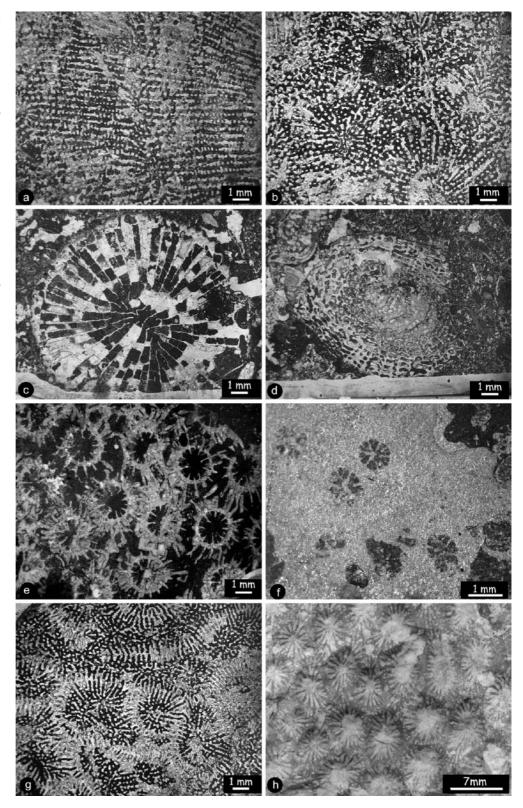
The environment is now much more variable than in the previous formations, due to decreasing bathymetry. Hydrodynamism significantly and progressively changes from 15a (packstones) to 15g (oolitic grainstones) to culminate in oolitic shoal environments dominated by tidal dynamics (herringbones). When hydrodynamism is too high, the instability of the oolitic sediment is dissuasive for the settlement of corals (e.g. unit 18). The corals indicate very well-lit water. In the coral meadows, closer to oolitic shoals, hydrodynamism and sedimentation rates appear as limiting factors, as it is deducible from the morphology of colonies and the development of encrusters and bioeroders. Unit 15d-e seems to be characterised by high sedimentary input inducing dominance of branching corals and sediment-adapted colonial structures, and low encrusting and bioeroding activity. Unit 20 shows a lower sedimentation rate allowing a true framework but with temporary acceleration inducing skullcap morphologies. The general trend of increasing oncoids and correlative decreasing ooids suggests a lagoonal position for units 18 to 25. The corals also support such a view with the occurrence of an emersive microatoll-like colony of *Comoseris* (Habrant and Lathuilière 2000) and the stronger development of plocoid structures ("Stylina," "Cryptocoenia") in unit 22.

#### Calcaire de Clerval

## Lithofacies

The Calcaires de Clerval are mudstones with only 2–5% of bioclasts from ostracods, bivalves, echinoderms, sponges, corals, and gastropods (Fig. 3h). Some oncoids occur together with pink gravel probably derived from thin algal mats. In unit 33, laminites probably of microbial origin are clearly visible.

Fig. 4 Main coral taxa involved in reefs of Bonnevaux-le-Prieuré; **a** – *Dimorpharaea* koechlini transverse thin section. Bonnevaux-le-Prieuré, Middle Oxfordian BLP 11c-3; **b** – *Microsolena* sp. transverse thin section. Bonnevaux-le-Prieuré, Middle Oxfordian BLP 15b-19; **c** – *Thecosmilia* sp. transverse thin section. Bonnevaux-le-Prieuré, Middle Oxfordian BLP 17c; d - Dendraraea racemosa transverse thin section of a branch. Bonnevaux-le-Prieuré, Middle Oxfordian BLP 15D; e - Cryptocoenia sp. transverse thin section. Bonnevaux-le-Prieuré, Middle Oxfordian BLP 20-36; f – Stylina echinulata transverse thin section. Bonnevaux-le-Prieuré, Middle Oxfordian BLP 22-20; **g** – *Comoseris* sp. transverse thin section. Bonnevaux-le-Prieuré, Middle Oxfordian BLP 16–30; **h** – *Isastrea* sp. upper view of an etched calicular surface. Bonnevauxle-Prieuré, Middle Oxfordian BLP 20-33



#### **Biofacies**

No more corals occur except as very small bioclasts. Other invertebrates are represented only by ostracods.

#### Palaeoenvironment

The lithology of pure fine carbonate, associated with laminites, ostracods and rivulariaceans, suggests a fairly restricted lagoonal tidal-flat environment.

## Reef zonation and facies model

The vertical succession and auteological features (Fig. 5) suggest a virtual zonation of the Oxfordian reef tract described above (Fig. 6).

The Dimorpharaea ecozone, the lower ecozone of this facies model, is dominated by Dimorpharaea koechlini. The position of this ecozone and its interpretation is now well documented in several other areas at the same time (Middle Oxfordian of Switzerland, Lorraine) or a little later (Upper Oxfordian of Burgundy) by autecological data as well as by the sedimentological context (Geister and Lathuilière 1991; Insalaco 1996; Insalaco et al. 1997; Chevalier et al. 2001; Gill et al. 2004). An indicative depth is suggested by analogy with Recent coral communities with nearly exclusive platelike paucispecific non-incrusting assemblages known from 30 to 70 m.

In the Microsolena ecozone, the coral fauna is more diverse. Microsolena (Fig. 4b) is not dominant but reaches its maximum of abundance and coral cover in this zone (Fig. 6). A similar transition between the Dimorpharaea zone and the Microsolena zone has also been observed in Lorraine (Geister and Lathuilière 1991). Insalaco et al. (1997) consider this transition as driven only by changes in sedimentary input. The Dimorpharaea ecozone is associated with more argillaceous sediments. This view is not easy to reconcile with the systematic position of these units in the sedimentary sequence. It is no easier to consider the sedimentation balance as everywhere higher for marls than for limestones, whatever the proximity of emerged lands. We are consequently more inclined to think that the deeper position of the Dimorpharaea ecozone also explains the difference in carbonate production, in proportion to clay. A more convincing explanation would involve light and/or depth zonation of water in nutrients and microorganisms. Since Hallock and Schlager (1986), it has been admitted that an excess in nutrients stimulates the primary production of autotrophic organisms but can lead to the demise of coral reef ecosystems. Algal blooms contribute to decrease water transparency but also deeply influence the structure of the ecosystem. Dupraz and Strasser (2002) have shown how heterotrophic pennular coral could flourish in mesotrophic waters of a mixed siliciclastic-carbonate protected Oxfordian platform. An increase of nutrients with depth is coherent with observed measurements in

Recent seas (Copin-Montégut 1996) and provides a satisfying explanation for the subsuperficial distribution of phytoplankton maxima (Bougis 1974; Jacques and Tréguer 1986). Consequently, such a depth-related gradient of nutrients could also explain benthic communities dominated by pennular corals, in extant as well as in Oxfordian reefs. Furthermore, we have observed in a few cases (bed 10) that, in more clayey layers, Dimorpharaea probably copes with sedimentation by producing a more acute conical funnel shape, which is not the standard situation. An alternative or rather complementary explanation is to consider that climatic warming has affected the northern margin of Tethys (Haug 1911; Martin-Garin et al. 2002; Dromart et al. 2003) and the Dimorpharaea ecozone represents a first pioneering reefal mesotrophic step toward the warm oligotrophic period of the Transversarium zone, which corresponds to the maximum of reef occurrence in the North of Europe (Martin-Garin et al. 2002). Microfacies data provide evidence of increasing hydrodynamism related to a shallowing-upward trend. Therefore, an explanation by climate alone must be rejected.

The Dendraraea ecozone is strongly marked by the increase in proportion of branching colonies, mainly Dendraraea and Thecosmilia (Fig. 4c, d). The position of this ecozone adopted in Figs. 6 and 7 is difficult to situate by content alone, because there is no discriminating bathymetric criterion between this assemblage and the following *Comoseris* ecozone assemblage. It is quite possible that the main controls are hydrodynamism and sedimentation balance rather than bathymetry. The growth of these branching forms is certainly quicker than that of massive forms, and they have better resistance in biotopes marked by high sedimentation and sediment transit. Here they are placed in the continuity of the Microsolena ecozone, as it is chronologically observed. This option places the maximum development of branching forms between the maximum of platy forms and maximum of dome-shaped forms. This scheme is comparable to Recent reefs (Chappell 1980; James 1984; James and Bourque 1992) and a little unexpected, because Recent branching forms are very fast-growing ramose colonies capable of keep-up behaviour near sea-level, whereas Jurassic branching colonies are comparatively slowgrowing phaceloid organisms (Lathuilière 2000: 177). We therefore believe that the most important factor is probably the branching morphology, which is better adapted to cope with sedimentary particles and has, both in the Jurassic and the Recent, faster growth than massive forms (dome-shaped or platy).

The Comoseris ecozone represents optimum coral growth, a highly diverse assemblage where Comoseris (Fig. 4g) is not dominant but significantly present among many other genera. This assemblage can be in a foreshoal or back-shoal situation (Fig. 7). Within this ecozone, the growth of "Stylina" would be favoured in the lagoon. The indicative depth is around 5–20 m, which is the average depth for optimum diversity in Recent reefs.

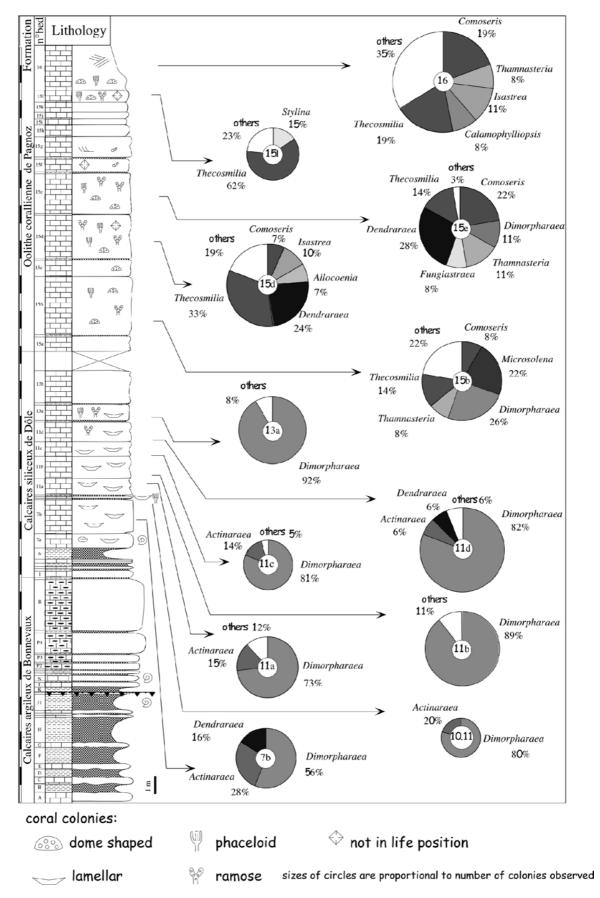


Fig. 5 Distribution of coral assemblages in the section of Bonnevaux-le-Prieuré. The category "others" represent less abundant genera, which can be identified in Table 1

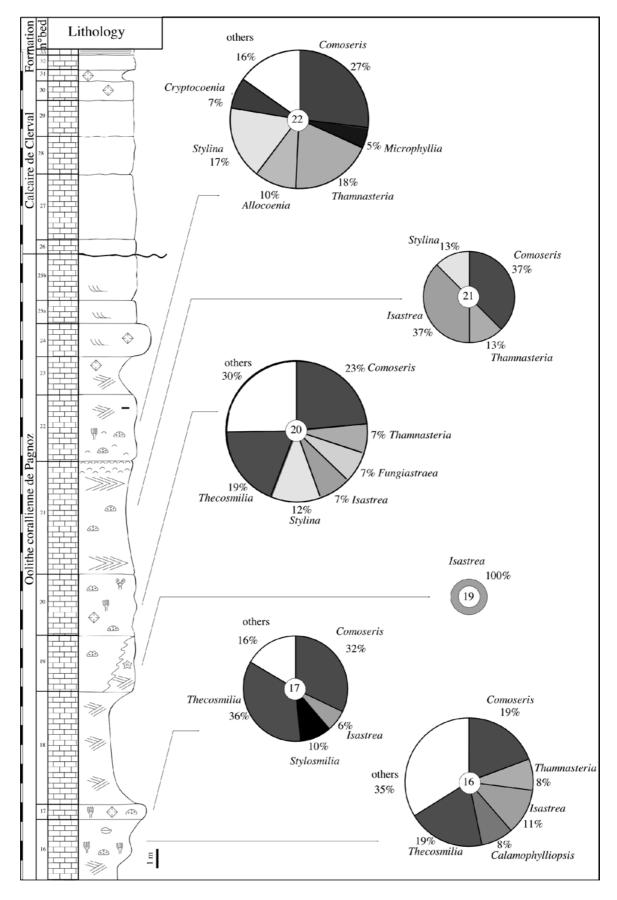
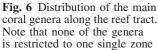
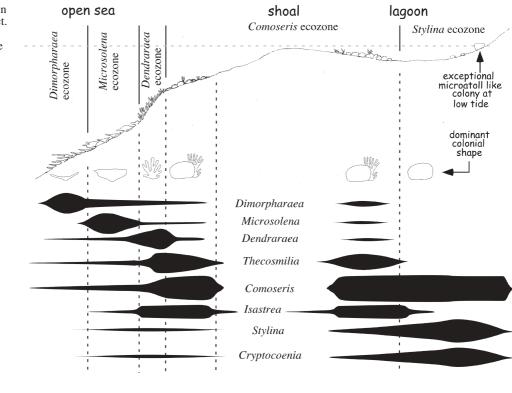


Fig. 5 (continued)





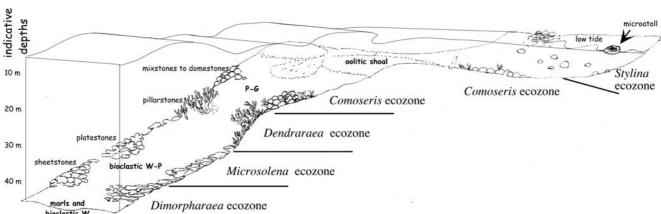


Fig. 7 Bionomic zonation of the corallian platform of Bonnevaux-le-Prieuré. Note the patchy reefal frameworks, their growth fabric, and their relation with textures of juxtaposed sediments (W = wackestones, P = packstones, G = grainstones)

The oolitic shoal (Fig. 7) is placed in the central position of the zonation. It appears that these Oxfordian reefs are not quite comparable to a large set of Recent reefs composed of a solid framestone, with a reef crest that faces the most aggressive place of the reef environment, where strong waves threaten to break the skeletons. In the present Oxfordian example, the crest of the hydrodynamic barrier is composed of oolitic grainstones. When the crest is not too high, symmetry may exist between back reef and fore reef. This has been demonstrated for Recent reefs in the Caribbean, where the most exposed reef crest is occupied by red algae (Geister 1980a, b). Here we suggest that it is possible to find at least the *Comoseris* ecozone on both sides of the oolitic shoals. This hypothesis requires a fairly open lagoon.

The Stylina ecozone is not really a reefal assemblage but rather a death assemblage derived from a diverse coral carpet, which is differentiated from the Comoseris zone mainly by the higher proportion of plocoid forms such as "Stylina" (Fig. 4f) or "Cryptocoenia" (Fig. 4e), and meandroid forms, which together point to the probable fairly turbid water on the lagoonal side of the shoal. This ecozone also corresponds to the maximum abundance of Allocoenia-like corals.

This zonation is parallel to a zonation of growth fabrics from open sea toward the hydrodynamic barrier (Fig. 7): sheetstones, platestones, pillarstones, mixstones and domestones. It is also parallel to a zonation of depositional textures observed in juxtaposed sediments,

which fit the standard hydrodynamic interpretation of the Dunham classification (Fig. 7).

A common exercise is to compare ancient to Recent reefs. This is obviously a risky enterprise because of the great variability of Recent coral reefs. Nor can we consider that the zonation proposed here is a world-wide representation of Middle Oxfordian coral reefs. We simply underline some specific characteristics of these Oxfordian reefs, for which we clearly reach a limit of the actualistic approach. Such close proximity of oolitic facies and reefs is not common in Recent seas. For Oxfordian times, the outcrop of Bonnevaux-le-Prieuré provides evidences that true lateral transitions occur between reefs and oolitic sediments (unit 20 is a good example). Other examples of such a contemporaneity can be found elsewhere in coeval or nearly coeval sediments (e.g. Chateauvieux-les-Fossés in Dupraz 1999). For Recent environments, Bahamas and Abu Dhabi provide interesting rare examples of contemporary active reefs and active oolite sand shoals (Purser 1983). For instance, in Bahamas, reefs are generally deeper and at a distance of oolitic shoals under the threat of their progradation (e.g. Hine and Neumann 1977). Luxuriant reefs are characteristic of seaward of islands, facing the ocean. The opposite western margins show only few occurrences of reefs because water from the platform interiors, warmer and saltier than normal, moves westward (Ginsburg and Shinn 1964). It seems that ooids develop rather in areas of slow carbonate skeletal grain production (Milliman 1969). In that sense, it is paradoxical to see an oolitic shoal in the centre of the zonation. At this place, near the scleractinian corals today, we rather find hydrozoans and/or red algae. Solenoporaceans, which represent red algae in Oxfordian reefs, are rather anecdotic secondary frame-builders and never constitute the primary structure of the build-up. We must also remember that when maximum annual growth of a Jurassic coral branch is around 1 cm (calculation based on measurement of growth bands), Recent Acropora can reach 23 cm. There are great differences: (1) in the capacity to adopt a keep-up or catch-up response to a sea-level rise; (2) in the capacity of regeneration in the reef crest, which is the hydrodynamically most aggressive part of the reef; (3) in the capability to produce skeletal grains.

## From palaeoenvironments to stratigraphic cycles

The general trend of the sedimentary succession is obviously shallowing upward. This is demonstrated by a large set of indicators including hydrodynamic markers as well as light-level markers. The section begins below the fair weather wave base, and evolves toward tidal-dominated deposits, to end with sheltered lagoonal mudstones. It begins without light-dependant organisms, and evolves toward microsolenid pioneering assemblages, adapted to water depth with poor light conditions, to end with very well-lit coral and algal assemblages. The succession from the "Calcaires argileux de Bonnevaux" to the "Oolithe

corallienne de Pagnoz" is also the story of increasing carbonate production. This is clearly demonstrated through the growth rates of corals. Slow growing corals appear first (lamellar microsolenid corals of "Calcaires siliceux de Dôle"), dome-shaped and branching fast-growing corals appear later ("Oolithe corallienne de Pagnoz").

The installation of the carbonate factory is accompanied by the decreasing amount of siliciclastic components. It appears that the open sea environment of the beginning has finally ended with a protected lagoon. Thus reef development had a key geo-morphological role in generating a rimmed platform starting from a ramp or amplifying a modest existing structural relief. An interesting actualistic comparison can be made with the last post-glacial stage of the catch-up phase of the coral reef barrier in New Caledonia (Montaggioni et al. 2002). This geomorphological reorganisation and its ecological consequences lead us to wonder to what extent we can apply Walther's facies rule, which considers that stratigraphic evolution in lithologic successions reflects the lateral shifts of environments through time. Are the first two coral ecozones dominated by platy microsolenids only the mesotrophic pioneering stage of an Oxfordian reef, or is it possible to find them contemporaneously to the oligotrophic Comoseris ecozone at the climax stage? We have no direct transition between these communities in Bonnevaux-le-Prieuré; therefore, the answer to this question should be sought in other outcrops. Recent qualitative observations of reefs in Burgundy (Lathuilière, pers. observations from Rochers du Saussoy) seem to support the contemporaneity of Microsolena and Comoseris ecozones.

It is beyond the scope of this paper to propose a detailed sequence stratigraphic frame or a correlation chart, but one prominent question arises from the stacking pattern of facies, which interferes with the facies model proposed here. We especially observe the recurrence of oncolitic and coral facies (units 15 to 21). This could be interpreted as autocycles induced by the displacement of an offshore oolitic bar leading to the opening of a sheltered area (Habrant 1998). The comparison with neighbouring areas at the same Oxfordian time interval leads us to consider this doubled succession rather as resulting from an allocyclic constraint. In fact, it is more parsimonious to consider the top of bed 15 as a good candidate for a sequence boundary. It is to be noted that the deposits of unit 15 of the "Oolithe corallienne de Pagnoz" are marked by decreasing bed thickness, maximum abundance of nerineids and a notable proportion of "Stylina" and oncoids, which are a set of lagoonal indicators. Based on the very close similarity of facies as well as iterative successions of coral communities, we consider that such a boundary would correspond to the Ox4 sequence boundary of Gygi et al. (1998) in the Swiss Jura. Nevertheless, the biostratigraphic calibration must be shifted upward because of the occurrence of P. parandieri in the "Calcaire siliceux de Dôle." This sequence only suggested in Lathuilière et al. (1994) is now more documented in

Lorraine (Lathuilière et al. 2003; Carpentier 2004). In both cases, they affect similar coral microsolenid and oncolitic facies. Sedimentological features of this sequence boundary surface are clearly demonstrated in Lorraine (Carpentier 2004), they are much more difficult to diagnose here (no clear evidence of emersion) and it is precisely worth noting that the application of the coral zonation model leads to a more harmonious sequence correlation. The similarity of Middle Oxfordian successions over the northern European Tethys margin becomes ever more apparent.

## **Conclusion**

- The outcrop of Bonnevaux-le-Prieuré displays a general shallowing-upward trend from circalittoral open sea to lagoonal environments. This trend is complicated by a eustatic event allowing correlation with the Ox4 of Gygi et al. (1998) in Switzerland.
- This Oxfordian reef complex now appears to be zoned and a detailed bionomic scleractinian-based zonation is proposed here for the first time (Figs. 6 and 7). The deeper ecozone is dominated by *Dimorpharaea* koechlini. In the following Microsolena ecozone, taxonomically more diverse, Microsolena is not dominant but reaches its maximum of abundance. In the Dendraraea ecozone the proportion of branching corals such as Thecosmilia and Dendraraea increase. The next Comoseris ecozone represents optimum coral growth, a highly diverse assemblage where the index genus is not dominant but significantly present among many other genera. Finally, the Stylina ecozone represents a coral carpet mostly differentiated from the previous ecozone by the higher proportion of plocoid and meandroid forms.
- The model displays a good parallelism with the zonations of growth fabrics (Insalaco's classification) or of textures of juxtaposed sediments (Dunham's classification)
- The scleractinian-based zonation is proposed together with a depositional model that involves a central position for an oolitic shoal in the reefal complex.

**Acknowledgements** We are grateful to Daniel Contini for helping us in the field and to Carmela Chateau for proof-reading the English text. The authors express their gratitude to Richard Höfling and Andreas Strasser for their fair and constructive criticism

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