

Anatomy of the Early Cambrian 'La Sentinella' reef complex, Serra Scoris, SW Sardinia, Italy

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Abstract: All bioherms from the Early Cambrian (Botoman) Matoppa Formation of the Nebida Group in SW Sardinia were previously thought to be dominated by *Epiphyton*. However, at 'La Sentinella' (Serra Scoris Hill), they are composed of *Girvanella*, *Razumovskia*, *Botomaella* and *Renalcis*, with *Epiphyton* and archaeocyaths as accessory components. This association forms two unusual types of crust boundstone, consisting of stacked flat or curved crusts and saucer-like archaeocyaths delimiting shelter cavities. Dendrolitic *Renalcis* archaeocyath-cement boundstone caps the bioherm. Analysis of the La Sentinella reef complex and comparison with similar constructions from Mongolia (Zuune Arts, Salaany Gol), Nevada (Stewart's Mill, Battle Mountain), Mexico (Sonora) and China (Tianheban Formation) suggest that episodic deposition of fine-grained siliciclastic or carbonate sediment followed by periods of non-deposition enabled the calcimicrobial rafts and crusts to colonize the substrate and then provide synoptic relief for the development of a dendrolitic *Renalcis*-cement framework. 'La Sentinella' is one of the rare examples of Cambrian reef complex displaying community replacement, from an initial stage of thrombolitic and/or flat-stacked microbial crusts on a muddy substrate to an arched microbial crust system, to a more resistant *Renalcis*-cement boundstone. Such bioherms reflect an open-shelf, shallow-marine environment of increasing energy.

The buildups already described in the Lower Cambrian (Early Botoman) Matoppa Formation, in SW Sardinia (Figs 1–3), consist of microbial reef complexes made of a massive core mainly built by *Epiphyton* with rare scattered archaeocyaths, that is commonly surrounded by pink-red, laminated flank facies, with laminae still built by *Epiphyton*, or by marly nodular beds, or by green and red shales containing carbonate lenses and floated archaeocyath cups. This complex in some localities rests on dark grey nodular, thrombolitic or oncolitic marly limestone mainly built by *Girvanella* (Debrenne *et al.* 1979, 1993; Gandin & Debrenne 1984b). So far, only one of the bioconstructions exposed in Matoppa Valley (labelled MT 1–2 in fig. 4 of Debrenne *et al.* 1993) results to be of different composition: branching archaeocyaths and *Renalcis* are the dominant framebuilders reinforced by abundant cement. However, the study of a new outcrop, which we call 'La Sentinella' (the Sentinel) because of its distinctive shape, revealed a completely different structure of the construction and a much more diverse calcimicrobial association, in which the main framebuilders are *Girvanella*, *Razumovskia*, *Botomaella*

and *Renalcis* while *Epiphyton* appears to represent only an accessory component.

The field investigations and the first draft of this paper were carried out in co-operation with the late David Gravestock, F. Debrenne's student on archaeocyaths and one of the most promising Australian Cambrian specialists. We miss him and his contribution to the completion of our common research.

Geological setting

'La Sentinella' is the most prominent of several limestone outcrops related to the upper carbonate horizon of the Matoppa Formation (Figs 2 & 3) situated on the southern side of Serra Scoris Hill near Gonnese (Iglesiente) in SW Sardinia (Figs 1, 2 & 4a). The Matoppa Formation is composed mainly of green, fine-grained sandstone, siltstone and shale with two interbedded carbonate horizons (Fig. 3). The upper calcareous horizon consists of massive white or pale grey reef kalyptrae (loaf-like or pillow-shaped mounds, according to Rowland & Gangloff 1988), laterally and vertically associated with red/pink, more or less marly limestones. Locally, the kalyptrae rest directly on the green sandstones or on dark

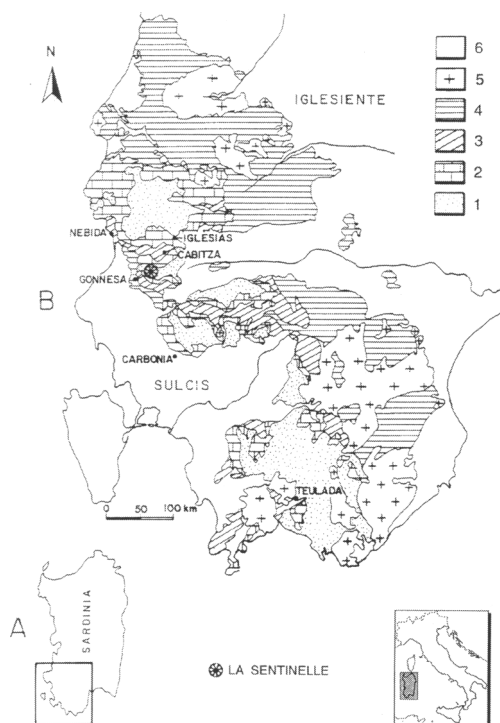


Fig. 1. Schematic geological map showing the outcrop pattern of Cambrian–Ordovician rocks in SW Sardinia. Legend of symbols: 1, Nebida Group (Lower Cambrian); 2, Gonnessa Group (Lower Cambrian); 3, Iglesias Group (Middle and Upper Cambrian); 4, Ordovician deposits; 5, Variscan granite; 6, post-Ordovician deposits (Palaeozoic, Mesozoic and Cenozoic). (After Debrenne *et al.* 1993, modified.)

grey, mostly thrombolitic or nodular, oncolitic, bioclastic limestone. The top of this carbonate interval is overlain by red and/or green shales, with archaeocyaths in carbonate nodules, or by fine-grained sandstone (Gandin 1987). ‘La Sentinella’ is one of the bowl-shaped outcrops described as an isolated buildup (Fig. 4a, b) by Gandin & Debrenne (1984b). However, investigations of the structural aspect of the Lower Cambrian rocks of Iglesias (Carmignani *et al.* 1986; Galassi & Gandin 1992; Regoli *et al.* 1995) suggest that most of the Matoppa calcareous outcrops correspond to emergence of the hinges of folds derived from the interference of multiple deformational phases linked to the Sardinian–Caledonian and Variscan tectonic events. According to this reconstruction, the present morphology of the calcareous bodies can be related to tectonic *boudinage* when the more competent parts of the originally continuous but

inhomogeneous carbonate bed were re-folded. ‘La Sentinella’, corresponding to the intersection between a subvertical morphological plane and the normal limb of the anticline that re-folds older folds with E–W axes, exposes a flat vertical surface 2.0 m high and 1.3 m wide (Fig. 4b, c). The layers dip gently about 10°–20° northward. The depositional structures and facies relationships are fairly well preserved, even though pressure-solution seams tend locally to conceal some of the boundaries.

‘La Sentinella’ reef complex

Field analysis shows that ‘La Sentinella’ is a composite bioconstruction consisting of different lithofacies that can be grouped in two units (Fig. 4a), the basal grey, locally dolomitized, limestone and the overlying light, pale grey–pink and rusty-red limestone. The lithological, sedimentological and faunistic composition of the upper unit, chosen for its good exposition and relatively low imprint of the tectonic deformation, has been studied first in the field and sampled with a saw (Fig. 4b). The composition of the basal grey limestone could not be determined in the field because strong folding and local extensive dolomitization make components difficult to evaluate.

Method

A 30 × 30 cm grid was traced on the flat, vertical surface of the Upper Bioherm (Fig. 4c), in which the different sedimentological and fossil components were located and quantified (Figs 5 & 6). Methodical field observations were carried out to evaluate the distribution of bioherm constructors and the relative proportions of sediments and cements within each square and through the vertical section of the outcrop (Fig. 5). In the laboratory, thin sections were cut in three perpendicular planes fixed by reference marks on sawn slabs collected in the field, in the unsuccessful tentative attempt at a three-dimensional reconstruction of the buildup. Sedimentological, palaeontological and palaeoecological studies aimed at determining the depositional conditions of one of the best preserved Matoppa bioconstructions were undertaken by the different authors according to their specialities.

The results of this detailed analysis disclose that ‘La Sentinella’ calcareous body corresponds to a complex mosaic of facies that can be regarded as a reef complex, resulting from the growth activity of sessile benthic organisms and exhibiting topographic relief in ‘La Sentinella’

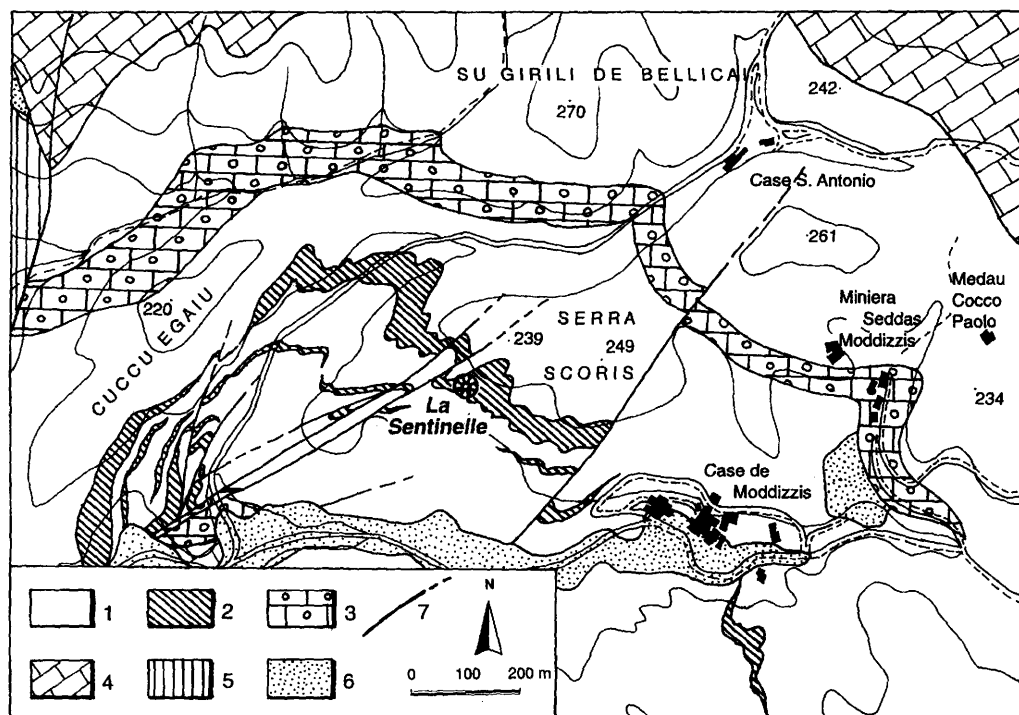


Fig. 2. Schematic geological map of the Serra Scoris area showing the upper carbonate layer of the Matoppa Formation deformed by interference folds derived from the superposition of Variscan and Caledonian tectonic phases. Legend of symbols: 1, Nebida Group sandstones and shales; 2, Matoppa Formation limestones; 3, Punta Manna Formation limestones; 4, Gonnese Group; 5, Ordovician 'Puddinga'; 6, alluvial deposits; 7, faults. (Unpublished map by R. Regoli.)

Hill. It can be divided into two units, representing geometrically well-defined bodies, the 'Lower Bioherm' and the 'Upper Bioherm' (Fig. 4a), formed by the superposition of smaller buildups (facies A, C, D and G), resulting from the intergrowths of diverse assemblages of metazoans and calcified microfossils. These compound biohermal bodies are laterally associated with muddy interbiohermal facies (facies B and facies G') with local coquinas of archaeocyaths.

Results

The Lower Bioherm is made of grey massive and nodular or oncolitic marly limestones, in places extensively affected by fabric-destructive dolomitization. The massive facies (facies G) has a thrombolitic fabric and contains scattered broken archaeocyath cups (Fig. 7a-d). The rare archaeocyaths are often found in the cores of oncolites or in the bioclastic facies surrounded by microbial overgrowths. The nodular facies

(facies G') is locally bioclastic and characterized by irregularly alternating lenses and nodules of packstone with oncolites and yellowish dolomitic bands (Fig. 7e, f). Irregular yellowish, dolomitized seams and patches are common.

The Upper Bioherm consists of pink laminated to light grey/white massive limestone surrounded by pink to red archaeocyath-rich marly lithofacies. The pink laminated limestone (facies A) contains interspersed archaeocyaths of various sizes (Figs 8 & 9a) and commonly grade to the massive facies C characterized by rather large growth and shelter cavities in some cases roofed by archaeocyath cups (Fig. 10a-c), lined by cement (Fig. 10c) or filled with internal sediment (Figs 10a & 13).

In the upper part, the massive facies D lacks large cavities and appears more homogeneous and crystalline. Contact with the underlying and overlying muddy interbiohermal sediments is abrupt. Judging by the irregular but smooth

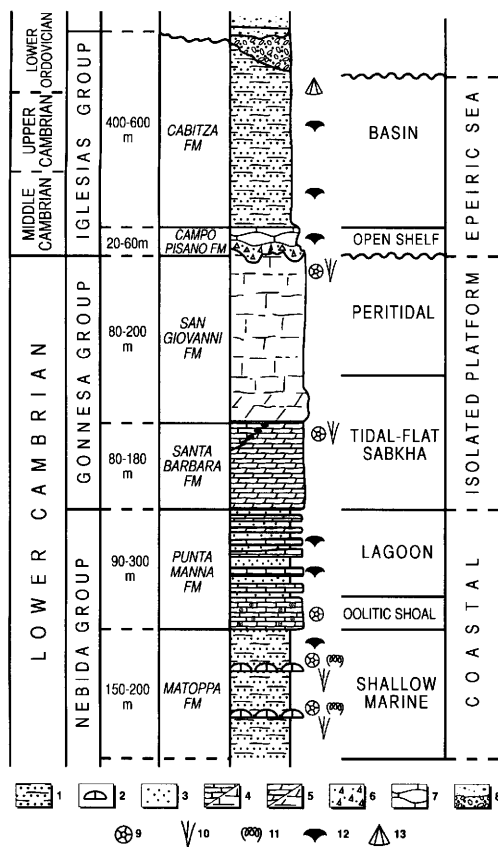


Fig. 3. Stratigraphic log of the Cambrian of Sardinia. The 'La Sentinella' reef complex occurs within the upper of the two carbonate horizons of the Matoppa Formation. Legend of symbols: 1, fine-grained sandstones and shales; 2, Matoppa limestones; 3, quartzarenites; 4, bedded and massive limestone; 5, laminated and massive dolostone; 6, calcareous breccia; 7, marly nodular limestone; 8, conglomerate ('Puddinga') and sandstone; 9, archaeocyath; 10, *Epiphyton*; 11, renalcids; 12, trilobites; 13, graptolites. (After Galassi & Gandin 1992, modified.)

shape of the upper surface of the buildup, synoptic relief at the upper contact was probably no more than 20–30 cm.

Lateral to the Upper Bioherm is a well-bedded homogeneous rusty-red muddy-marly limestone (facies B) with numerous small- to medium-sized cups and ribbon-like fragments of archaeocyaths (Fig. 9d, g). This red sediment passes transitionally into the pale pink–deeper rose laminated limestone (facies A) (Figs 8 & 9a). Although accumulations of archaeocyath cups in the mud-supported facies have a floatstone

texture, the skeletons are clearly in place or floated from the surrounding areas.

Fabric and components

Six microfacies were recognized from field observations and petrographic analysis. Two pertain to the dark grey lithofacies of the Lower Bioherm (facies G and G') and four to the pale grey Upper Bioherm and pink interbiohermal lithofacies (facies A–D).

Lower Bioherm

Thrombolitic–oncolitic lithofacies. Dark grey marly limestone (Fig. 7a, b) resting on the Matoppa green sandstones.

Facies G: spongy crust and raft boundstone (Fig. 7c, d). Facies G is a complex and irregular association of microbial communities and intervening irregular mud-filled cavities characteristic of the thrombolitic fabric. Superposed thick spongy masses of *Razumovskia* and/or *Girvanella* (Fig. 7d) include oncoid agglomerates, dense sheets of *Botomaella*, scattered *Epiphyton* bushes and, less frequently, corroded and/or encrusted cups of archaeocyaths. The oncoids commonly consist of *Girvanella* filaments with an occasional outer irregular coating of *Razumovskia* (Fig. 7e). Rather large growth cavities are filled with dense micrite containing small siliceous sponge spicules or large *Chancelloria* sclerites. Less common are fragments/intraclasts of *Epiphyton* bushes, trilobite sclerites, echinoderm ossicles and bivalve shells. Cups of *Protopharetra protea* (Fig. 11b, d), probably preserved in life position, *Anthomorpha margarita* (Fig. 7b), *Afiacyathus alloiteui* and encrusted fragmented remains of *Erismacoscinus*, *Coscinocyathus*, *Gandinocyathus* and *Ichnusocyathus* (Fig. 7d, f) are found entrapped in the microbial framework.

Grey nodular–bioclastic lithofacies. Dark grey dolomitized marly limestone.

Facies G': bioclastic wackestone–packstone–floatstone (Fig. 7f). This facies consists of calcareous nodules bounded by marly carbonate partings and interbeds, showing a high degree of dolomitization (Fig. 7b). The calcareous nodules mainly consist of bioclastic packstone–floatstone. Thick microbial crusts with interlaminar internal sediment are associated with oncoids, but given the nodular nature of the sediment it is not always clear if all of them represent depositional grains or interbedded pioneer bioconstructions rather than mechanically induced boudins. The packstone matrix is microsparitic, but relics of the micritic fabric are preserved in

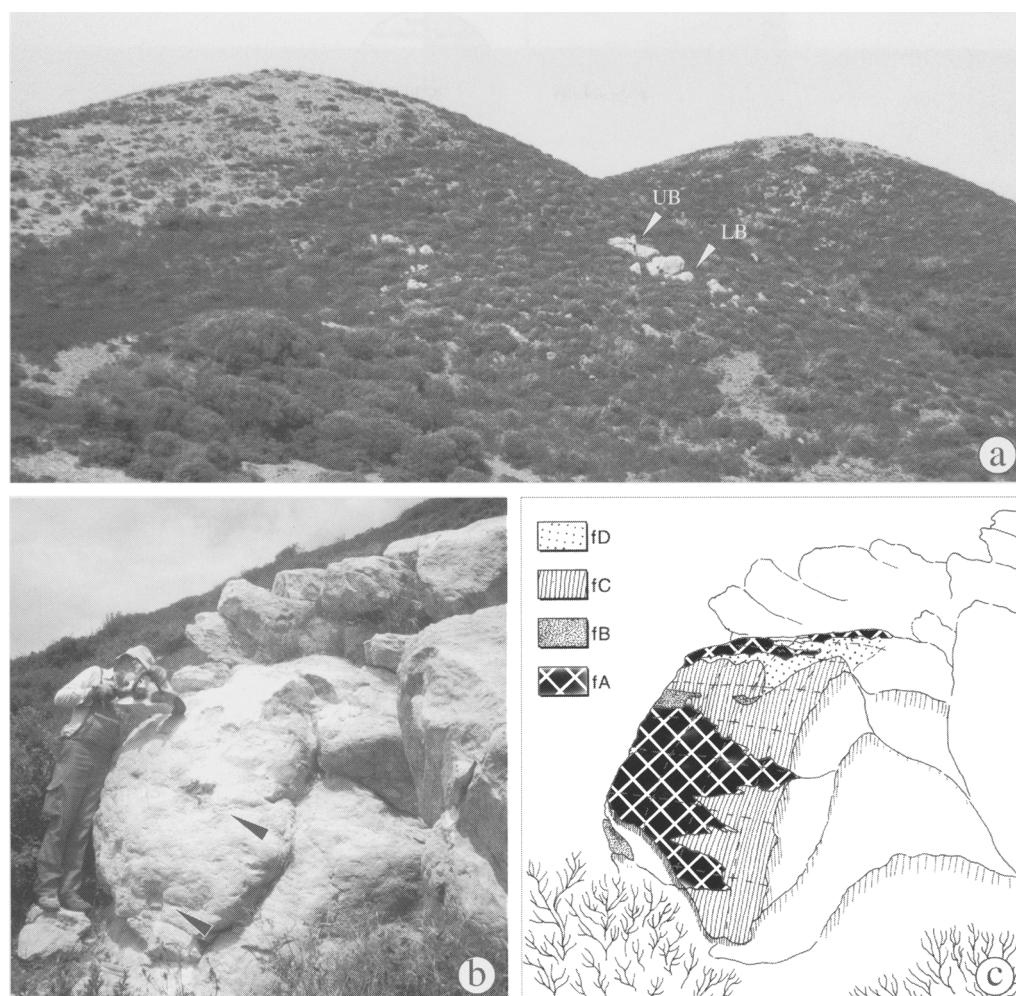


Fig. 4. Views of the 'La Sentinella' outcrop. (a) On the southern side of Serra Scorci Hill 'La Sentinella' is one of the exposed white blocks of the upper carbonate horizon of the Matoppa Formation, isolated by tectonic boudinage. The arrows mark the relative position of the Lower Bioherm (LB) and Upper Bioherm (UB). (b) The Upper Bioherm of the 'La Sentinella' outcrop has been sampled with a saw (black arrows on left side of photograph mark the sampling scars) on the normal limb of a second-phase anticline. The underlying Lower Bioherm is not visible. (c) Sketch of the outcrop showing the method of sampling: samples were extracted from the flat surface of the Upper Bioherm after the different facies were identified and mapped along a 30 × 30 cm grid (see Fig. 5). The lithofacies recognized are: pink laminated limestone—facies A; red marly limestone—facies B; light grey massive limestone with shelter cavities—facies C; and light grey massive, crystalline limestone—facies D.

some places. The often dolomitized/recrystallized nodular sediment (Fig. 7f) usually contains angular quartz-silt, mica and scattered recrystallized skeletal particles. The skeletal particles are well-sorted angular skeletal fragments of echinoderms, trilobites, phosphatic brachiopods, molluscs (?) and *Chancelloria*, together with oncoids and laminar fragments of *Girvanella* crusts

and *Razumovskia* rafts. Clasts of archaeocyaths include some apex portions of *Erismacoscinus* (Fig. 7c) and large *Coscinocyathus dianthus* (Fig. 7f) cups, with abraded and corroded outer walls. Most of the skeletal particles are rimmed by a more or less developed microbial micritic coating, in some cases obviously produced by *Girvanella* filaments. The original structure of the

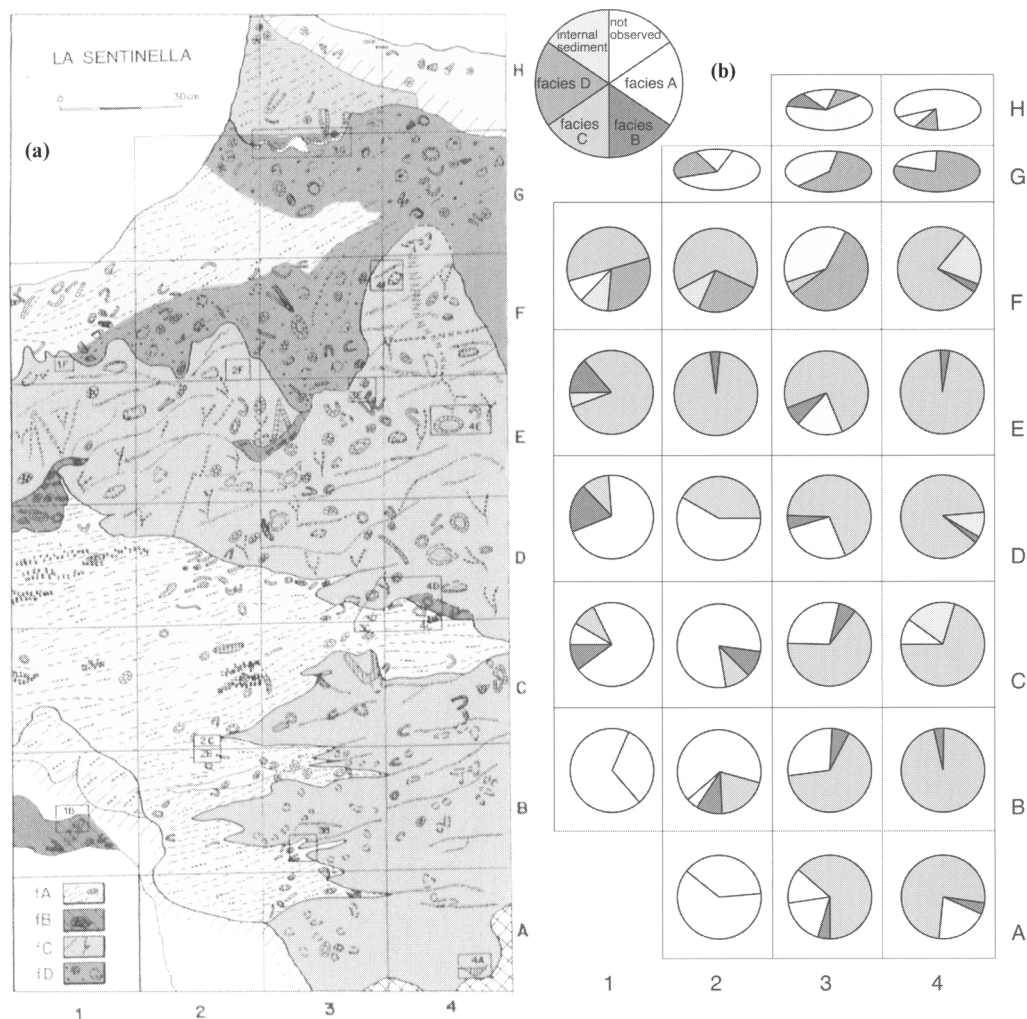


Fig. 5. Detailed facies map of the exposed surface of the Upper Bioherm. **(a)** Location of the samples and the spatial distribution and relationships of the facies A–D resulting from: **(b)** the quantification in every grid square, of the sedimentological features and the fossil components recognized in the field. Legend of symbols: facies A, laminar facies (cement $\leq$ matrix up to 50% of the construction); facies B, bioclastic floatstone/packstone; facies C, crust boundstone with large shelter cavities (matrix $\gg$ cement up to 50% of the construction); facies D, dendrolitic facies (cement $\gg$ matrix up to 30% of the construction).

skeletal particles has been replaced by equant calcite except for the echinoderm, trilobite and phosphatic brachiopod fragments.

Upper Bioherm

Laminar lithofacies. Laminated, microbial or micritic limestone (Figs. 8 & 9a).

Facies A: *Botomaella*–*Girvanella* microbial crust boundstone (Fig. 9b, c). It is formed by the superposition of nearly flat, thick sheets of

Botomaella (Fig. 9b, c, e), *Girvanella* (Fig. 9b, c) and, less frequently, *Razumovskia* (Fig. 9f); the sheets are commonly tightly stacked (Fig. 9b, c), in some cases are separated by narrow laminar cavities mainly filled by pink micritic sediment or by dark red marly residual mudstone–wackestone (Fig. 9c) or skeletal packstone–floatstone (Fig. 9f) similar to facies B. Cement is poorly represented and usually less developed than the interlaminar sediment. Small pendant clusters of *Renalcis* (Fig. 9b, c) and *Epiphyton*

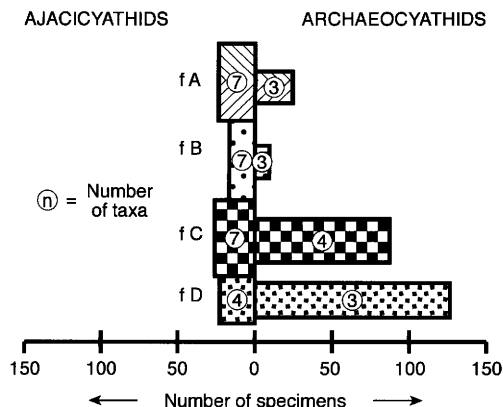


Fig. 6. Repartition of the archaeocyath taxa (see Table 1) recognized in the different facies of the 'La Sentinella' Upper Bioherm.

line the roofs of cavities beneath the microbial crusts and are always embedded in a thin irregular band of fine-grained marine cement. Archaeocyaths are not involved in the framework construction, but are frequently found as small floated cups or as fragments of the same size in the red muddy interlaminar facies. Ajacicyathids are represented by seven genera. Archaeocyathids are less diverse in terms of recognizable genera, as they are mostly represented by juveniles (Table 1), but they equal the ajacicyathids in number of specimens. Ajacicyathina, *Erismacoscinina* and *Coscincocyathina* are represented by genera recognized in other localities of the same horizon. *Tabulacyathus insperatus*, the only Tabulacyathida known in western Europe, is present but rare (Fig. 12a, right).

Red bioclastic marly lithofacies. Skeletal dark red marly mudstone (Fig. 9d).

Facies B: bioclastic wackestone, packstone–floatstone (Fig. 9g). The matrix consists of rusty-red-stained microbioclastic microsparite rich in residual clay minerals and iron oxides. Unsorted, sometimes large, skeletal particles (Figs 9a, d, g & 14a) are represented by echinoderm ossicles, trilobite sclerites and fragments, and/or apex portions of archaeocyathan cups generally larger than in facies A. Although accumulations of archaeocyath cups in the mud-supported facies have a floatstone fabric, the skeletons are clearly in place or floated from the surrounding areas. The ajacicyathids, with the same generic composition as in facies A, are more diverse and more numerous than the archaeocyathids.

Some large cups of *Afiacyathus alloiteaui* (Fig. 12b) and stick-like cups of *Tubicoscinus cupulosus* (Fig. 9g) are present. Laminar fragments of microbial crusts of *Botomaella*, *Girvanella* and *Razumovskia* can be interpreted as intraclasts or as fractured slivers probably resulting from tectonically induced pressure-solution disruption of formerly contiguous crust boundstone.

Massive lithofacies with large shelter/growth cavities. Microbial massive crust limestone with large shelter cavities in part also roofed by archaeocyaths and filled with pink lime-mudstone (Figs 10 & 13).

Facies C: crust boundstone with accessory archaeocyaths and Renalcis or Epiphyton dendrolitic clusters. Curved, relatively thick microbial crusts are associated with *Renalcis* clusters and small archaeocyath cups. Large growth cavities with geopetal infill have developed mostly beneath *Girvanella*–*Razumovskia* crusts (Fig. 13b, e) and, less frequently, beneath saucer-like *Anthomorpha* (Fig. 10c) or bowl-shaped *Coscincocyathus* (Fig. 10b). Cavity roofs and walls are lined by festoon-like microcrystalline cement rinds that commonly enclose cryptobionts such as *Renalcis* in pendant clusters (Figs 10b, c & 13b, c, e) and, less frequently, *Archaeopharetra* (Fig. 10b). Fine-grained, locally recrystallized cement partly fills the cavities. It commonly encloses *Renalcis* clusters and in places *Epiphyton* dendrolitic clusters (Fig. 13b) and floating *Razumovskia* rafts (Fig. 10b, e). The internal sediment consists of pink micrite characterized by scattered calcite-filled microborings (Figs 10c & 13b–e). On the floor of the cavities, rare accumulations of particles in the matrix consist of skeletal remains of trilobites, bivalve shells and small *Protopharetra* cups, calcareous microspheres (Fig. 13b, d) and fragments of the roof pendant-cement. *Botomaella* fans and *Epiphyton* clusters sometimes hang from the walls or fill the cavities (Fig. 13b). The outer wall of some *Protopharetra* cups is thickened, apparently in response to microbial encrustation (Fig. 10f). Delicate crusts of *Razumovskia* and some *Protopharetra* cups may support pendant *Renalcis* clusters (Fig. 10d, e).

Archaeocyaths are relatively abundant as isolated cups in the boundstone, with dominant tabulate conical forms of *Erismacoscinus elongatus* (Fig. 12c), *Erismacoscinus cancellatus* (Fig. 11a) and stick-like cups of *Tubicoscinus cupulosus*, *Gandincocyathus gravestockii* (Fig. 12c, d), and *Taylorcyathus vologdini* (Fig. 11b) together with solitary *Protopharetra protea* (Fig. 11b) and *Dictyocyathus tenerrimus*

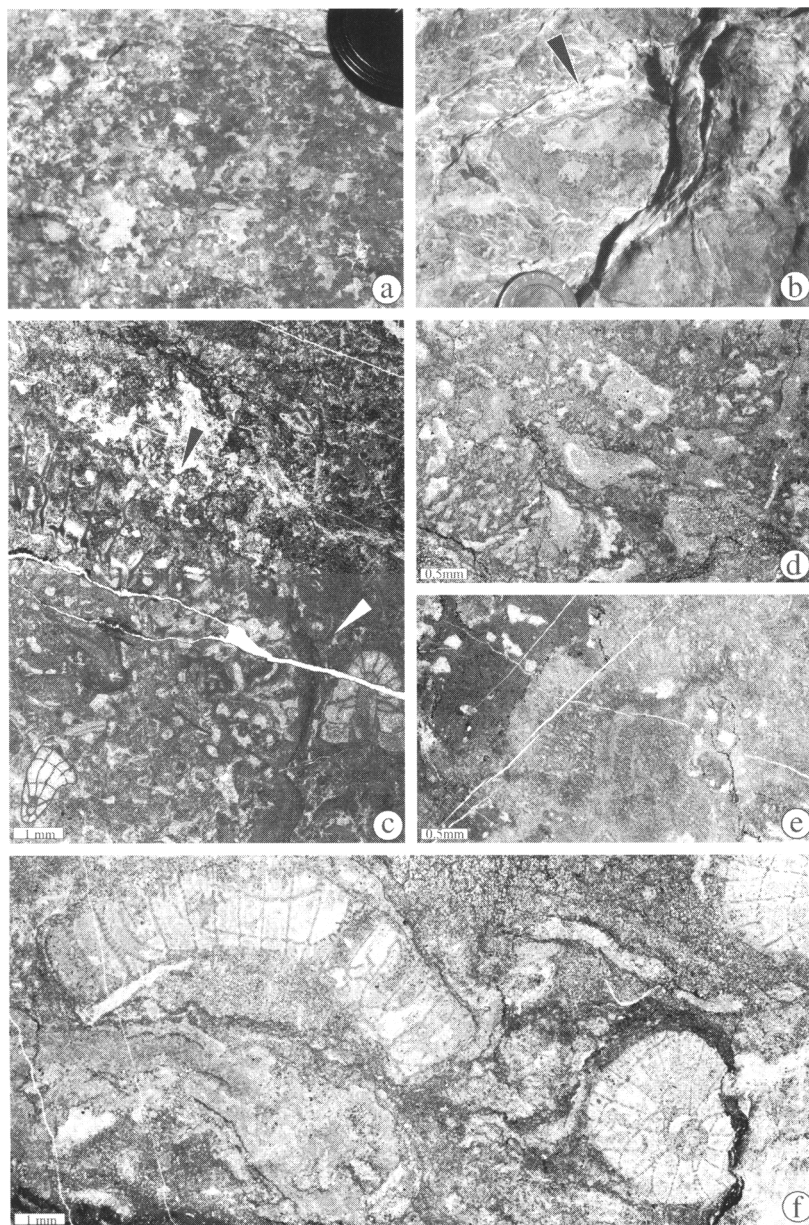


Fig. 7. Macro- and microfacies of the Lower Bioherm, consisting of dark grey thrombolitic–oncolitic limestone (facies G) and bioclastic–nodular wackestone–packstone–floatstone (facies G'). (a) Thrombolitic fabric of the dark grey limestone. (b) Thrombolitic–nodular facies with a mud-filled shelter cavity (arrow) roofed by a large saucer-like cup of *Anthomorpha margarita* Born. (c) microbial corrosion and encrustation (arrow) of the outer wall of a fragmented *Ichnusocyathus* cup entrapped in the thrombolitic framework (facies G). In the central cavity skeletal sediment with small cups of *Erismacoscinina* (facies G'). [SCS G3 II © – M84492.] (d) Thrombolitic fabric of the *Girvanella*–*Razumovskia* boundstone. Irregular growth cavities filled with microsparitic matrix and recrystallized cement. [SCS 95Sent1.] (e) Micritic sediment with calcite-filled microborings embedding an oncoïd composed of dense filamentous microbial layers (?*Girvanella* and *Botomaella*?). [SCS G2B.] (f) Recrystallized–dolomitized marly floatstone (facies G'). Matrix contains silt-sized quartz and small skeletal fragments; outer walls of *Coscinocyathus dianthus* Born. corroded or locally encrusted. [SCS G3II.] [SCS numbers correspond to field sampling, M84xxx numbers to the collection of figured archaeocyaths housed in the Muséum National d'Histoire Naturelle, Paris.]



Fig. 8. The unusual pink and white laminated limestone built by flat microbial crusts (facies A), passes upwards to the more massive crust boundstone buildup containing large saucer-like archaeocyath cups (facies C) that bound shelter cavities filled by pink mudstone.

(Fig. 11c). Rare pseudo-modular specimens of *Archaeopharetra ertashkaense* are recognized here for the first time in the bioherm (Fig. 10b).

Biohermal lithofacies. White, massive crystalline limestone.

Facies D: cement-supported *Renalcis dendrolitic* boundstone with archaeocyaths (Fig. 14a–d). *Renalcis* is the main frame-builder (Fig. 14b–e), frequently associated with numerous budding cylindrical cups of branching *Archaeopharetra* (Fig. 14c, d). *Epiphyton* bushes (Fig. 14c) and *Botomaella* fans are occasional components. Stick-like cups of *Erismacoscinus*, *Porocoscinus*, *Tubicoscinus* and *Coscinoxyathus*, solitary *Dicthyocyathus*, apices of *Anthomorpha* with exothecal roots (Fig. 14f) and large bowl-shaped cups of *Porocoscinus flexibilis* (Fig. 14b) are sporadically present.

Pore spaces and some of the infrequent small growth cavities are commonly occluded by yellowish, fine-grained marine cement (Fig. 14b–f) while late diagenetic, clear prismatic/equant cements mainly infill the intraskeletal pores of archaeocyath cups (Fig. 14c–f). Less frequently the cavities are infilled by marine multilayered fibrous cements or by silt-sized internal sediment (Fig. 14d), coarser than that found in facies C. Microbial crusts are characteristically absent.

Bioherm components

Fauna

The faunal composition of the biohermal complex is dominated by archaeocyaths, while various other organisms are associated in the peri-biohermal deposits.

Archaeocyath assemblages are more diversified in the crust boundstone facies C and peri-biohermal mudstone facies B. All the species previously recorded in the Matoppa Formation (Debrenne *et al.* 1993) were also found at ‘La Sentinella’ (Table 1); their distribution depends on the different depositional facies (Figs 6 & 15).

In the interbiohermal wackestone–floatstone deposits of the Lower and Upper Bioherms the archaeocyaths are accumulated as transported skeletal particles. The faunal composition of the pink–rusty red facies B is diverse and similar to that of facies A, with a slight dominance of ajacicyathids over archaeocyathids, while only rare floated cups of small *Erismacoscina* (Fig. 7c) and of skeletal fragments of *Coscinoxyathus dianthus* (Fig. 7f) occur in the dark grey basal facies (facies G’). Archaeocyath remains are rare in the basal thrombotic boundstone (facies G): only corroded and encrusted fragments of *Ichneocyathus* (Fig. 8c) cups have been found entrapped in the *Girvanella*–*Razumovskia* microbial framework.

In the pink laminated microbial boundstone (facies A) the archaeocyath assemblage consists of small cups or fragments of larger cups. It shows a well-balanced distribution (Table 1) between diversified solitary ajacicyathids (formerly ‘Regular’) and archaeocyathids (formerly ‘Irregular’).

In the *Renalcis*-crust boundstone (facies C), the ajacicyathids display greater generic diversification than the archaeocyathids, but the latter are much more diversified at the specific level and are occasional builders owing to the presence of modular budding *Protopharetra* and *Archaeopharetra*.

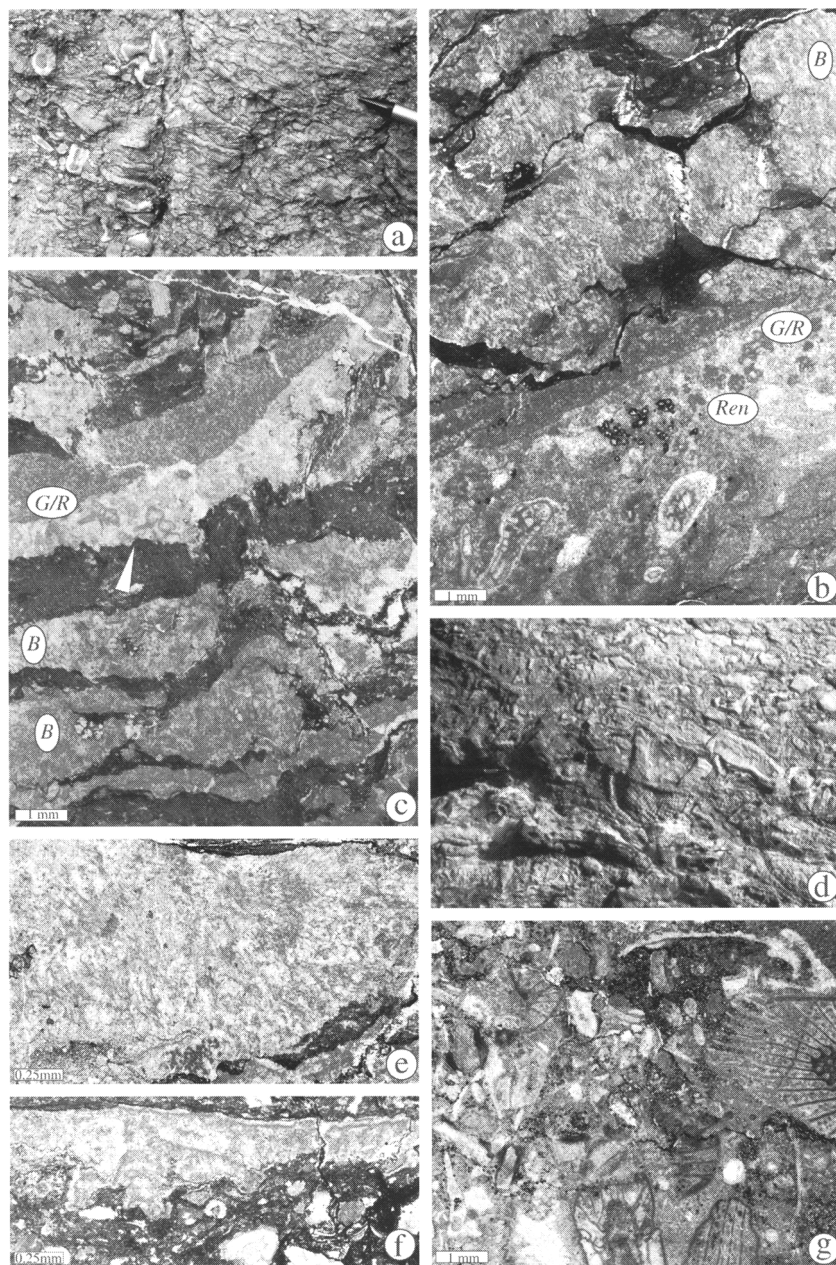


Fig. 9. Macro and microfacies of the microbial-crust boundstone (facies A) and rusty-red wackestone–packstone–floatstone (facies B). (a) Pink laminated limestone (facies A) with small scattered archaeocyath cups. (b) & (c) Microbial crust boundstone (facies A) composed of superposed plane laminae built by *Botomaella*, *Girvanella* and *Razumovskia*. Interlaminar sheet-like open spaces partially filled by muddy sediment (facies B), with roof lined by cement, pendant renaloids (c, arrow) and small archaeocyath cups (c). [SCS2B $\perp$ + SCS4C.DG.] (d) Disoriented archaeocyath cups enclosed in microbial crusts. (e) Detail of *Botomaella* tuft of filaments. [SCS1B 1a.] (f) Detail of a *Razumovskia* crust embedded in skeletal wackestone. [SCS1B 1a.] (g) Skeletal packstone–floatstone (facies B) produced by the accumulation of small cups of *Tubicoscinus cupulosus* Debr. and fragments of archaeocyaths, echinoderms, trilobites, sponge spicules and chancelloriid sclerites. [SCS R6 bas/M84485.] [SCS numbers correspond to field sampling, M84xxx to the collection of figured archaeocyaths housed in the Muséum National d'Histoire Naturelle, Paris.]

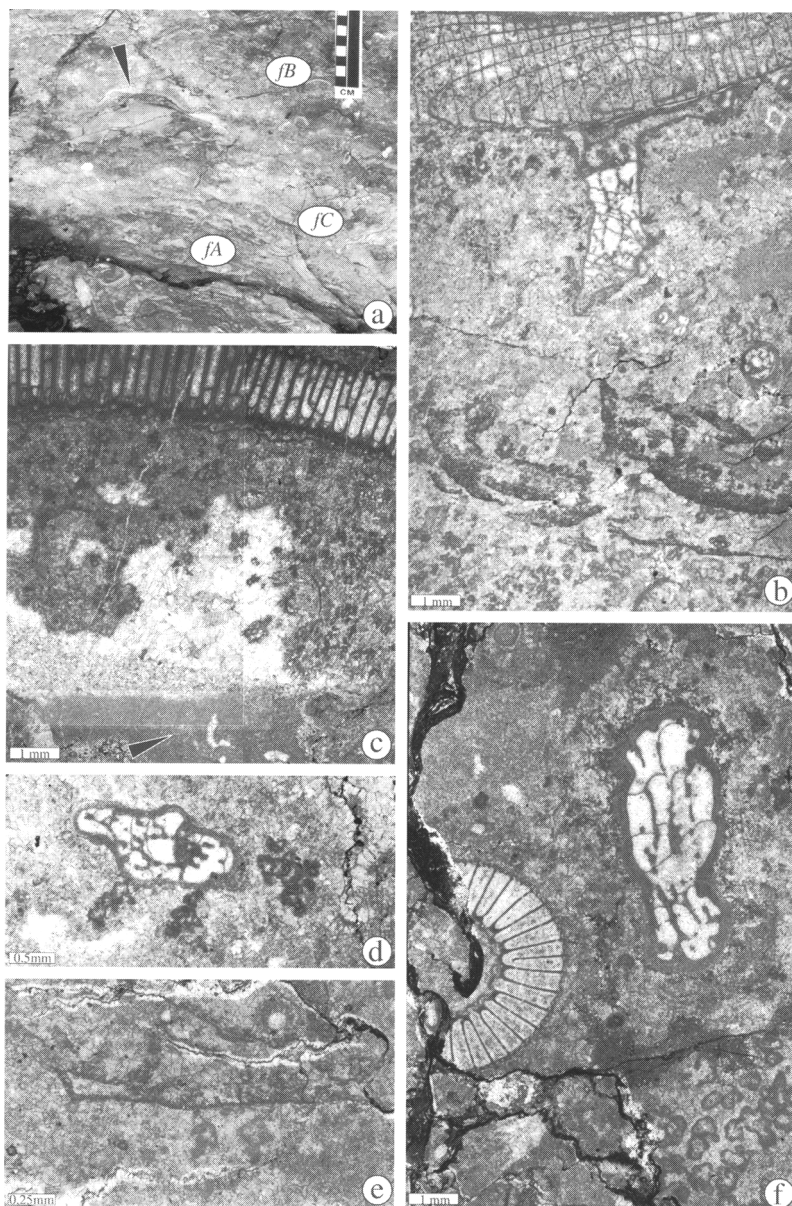


Fig. 10. Macro and micro-facies of large shelter cavities roofed by archaeocyath saucer-shaped cups (facies C). (a) Macroscopic view of the relationships among facies A, B and C: a large saucer-like cup of archaeocyath (arrow) forms a shelter cavity filled by pink micrite, resting on the pink laminated facies A, which support the light grey massive facies C; both are in lateral contact with the rusty-red interbiohermal facies fB. (b) Large growth cavity roofed by a bowl-cup of *Coscinocyathus dianthus* Born. supporting cryptobionts: *Archaeophatretra ertashkaense* Vol. and pendant *Renalcis*. Cement infills most of the cavity, enclosing arcuate rafts of *Razumovskia*, *Renalcis* clusters and small cups of *A. ertashkaense* Vol. [SCS 5 R.L.] (c) Shelter cavity roofed by a saucer-like cup of *Anthomorpha margarita* Born. A festooned irregular band of finely crystalline marine cement encases pendant renalcids and drapes the inner wall of the archaeocyath cup. Microboring (arrow) in micritic internal sediment. [SCS 3G II ⊙.] (d) & (e) *Protopharetra* (d) and a delicate *Razumovskia* crust (e) supporting pendant *Renalcis* clusters. [SCS 4D II; SCS 4A I ⊥.] (f) Cups of *Tubicoscinus* (left) and *Protopharetra* (right) associated with *Renalcis* boundstone surrounding a mud-filled cavity. *Protopharetra* outer wall thickened in response to microbial encrusting. [SCS 4D II.] [SCS numbers correspond to field sampling, M84xxx numbers to the collection of figured archaeocyaths housed in the Muséum National d'Histoire Naturelle, Paris.]

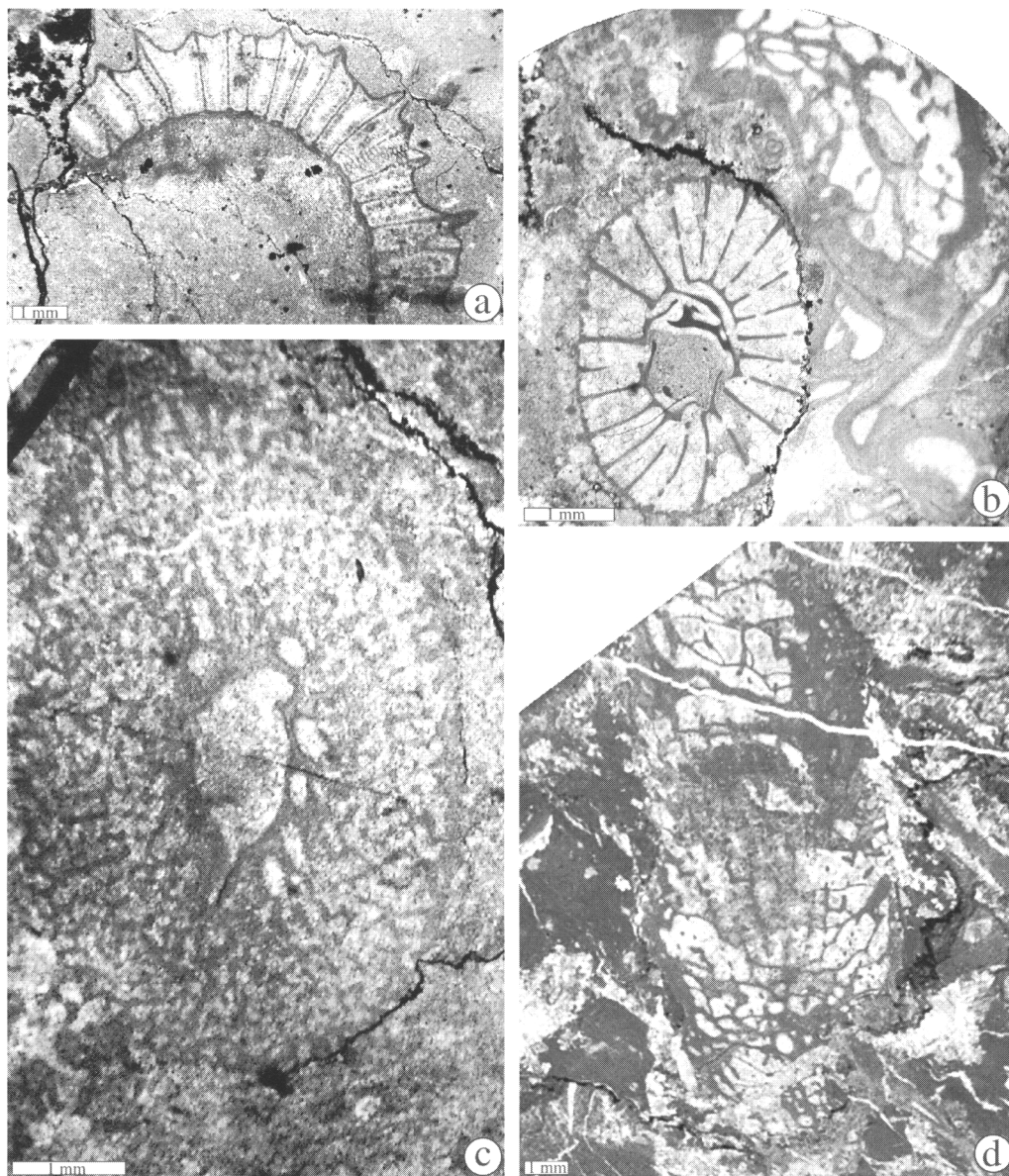


Fig. 11. (a) *Erismascosinus cancellatus* (Born.), fragment of a crenulate transverse section of the cup. [SCS R5○/MNHN 84479.] (b) *Taylorcyathus vologdini* Debr. (centre) [SCS 3GIII/MNHN 84481], *Protopharetra protea* (Born.) (top left). [SCS 3GIII/MNHN 84482.] (c) *Dictyocyathus tenerrimus* (Born.), oblique transverse section. [SCS 3G/IV, 1/MNHN 84483.] (d) *Protopharetra protea* (Born.), longitudinal section through the intervallum. [SCS G1/MNHN 84484.] [SCS numbers correspond to field sampling, M84xxx numbers to the collection of figured archaeocyaths housed in the Muséum National d'Histoire Naturelle, Paris.]

Cement-supported *Renalcis* boundstone (facies D) shows lower diversity and a decreasing number of ajacicyathid genera, represented only by tabulate forms. Clustered *Archaeopharetra* budding-cups contribute to the bioconstruction

(Fig. 14c, d), while large bowls of *Anthomorpha* form shelter cavities (Fig. 14a, b).

Among the other faunal components, rare sponge spicules, replaced by equant calcite mosaics, occur exclusively in the micritic infilling of

Table 1. Facies distribution of the archaeocyath taxa

ARCHAEOCYATHA	Interbiohermal facies B + G'	Lower Bioherm facies G	A	Upper Bioherm facies C	D
'Regulares'					
<i>Inessocyathus spatiosus</i> (Born.)				●	●
<i>Afiacyathus alloiteaui</i> Debr.	●		●		
<i>Taylorcyathus vologdini</i> Debr.	●		●	●	
<i>Gandinocyathus gravestocki</i> Debr.*		●		●	
<i>Erismacoscinus elongatus</i> (Born.)	●		●	●	
<i>Erismacoscinus calathus</i> (Born.)	●	●	●	●	●
<i>Erismacoscinus cancellatus</i> (Born.)				●	
<i>Porocoscinus flexibilis</i> Debr.	●			●	●
<i>Tubicoscinus cupulosus</i> Debr.	●			●	●
<i>Tabulacyathus insperatus</i> Debr.			●		
<i>Coscincyathus dianthus</i> Born.	●	●	●	●	●
<i>Coscincyathus fornicatus</i> Debr.	●		●	●	
'Irregulares'					
<i>Anthomorpha margarita</i> Born.			●	●	
<i>Dictyocyathus tenerrimus</i> Born.	●		●	●	●
<i>Archaeopharetra ertashkaense</i> Vol.	●	●		●	●
<i>Protopharetra protea</i> (Born.)			●	●	

Gandinocyathus DEBRENNE F&M; [**G. gravestocki*, OD; holotype (Debrenne *et al.*, 1993, plate 3, Fig. 1), M84234 MNHN, Paris]. Outer wall with horizontal to upwardly projecting straight canals, bearing supplementary bracts externally (imparting overall inverted V-shaped appearance to outer wall); inner wall with one row of pores per intersept, bearing upwardly projecting cupped bracts; septa completely porous. Lower Cambrian (Bot.), Europe (Sardinia).

the shelter cavities of facies C and G, whereas in the interbiohermal facies G' they are mostly siliceous and smaller. Rare *Chancelloria* sclerites, also replaced by equant calcite, are found in the micritic infilling of facies C cavities. They appear more frequently in facies G', where they are sometimes corroded and filled with dense micrite. Rare sclerites are also entrapped in the *Renalcis* boundstone of facies C and D.

Echinoderm ossicles, trilobite sclerites and disarticulated bivalve shells are the main components of the bioclastic packstones (facies B and G'). In the biohermal facies only fragments of trilobites occur, while echinoderm ossicles are notably absent.

Microbial assemblages

Calciemicrobes are the primary constructors of the buildups. They form different framework morphologies according to their living requirements. The dominant forms in the 'La Sentinella' buildups are *Girvanella-Razumovskia* and *Botomaella*, which often form crusts or rafts up to 15 mm long, and *Renalcis*, which usually produces dense dendrolitic frameworks. *Epiphyton* bushes are frequently associated.

Girvanella-Razumovskia act as builders in facies A and C, commonly forming thick and dense sheets which delimit planar (Figs 9c, d & 13c, e) or curved (Fig. 13b) shelter cavities or irregular spongy frameworks characteristic of the thrombolitic facies G (Fig. 7). The fabric of the dense sheets results from the subparallel arrangement of the filaments, while the thrombolitic spongy fabric consists of a nest-like arrangement of fine (*Girvanella-Razumovskia*) or coarse (*Cladogirvanella?*) filaments. They outline rounded or irregularly shaped cavities filled by micritic mud and/or calcite spar. *Girvanella* also acts as an encrusting organism, coating most of the skeletal particles (facies B and G'), and as a builder of oncoids (Fig. 7e).

Razumovskia also forms thin arcuate rafts (Figs 9f & 10e), commonly scattered in the cement (Fig. 10b) or in the micritic infilling of the cavities.

Botomaella builds thick stacked sheets with narrow intralaminar cavities (facies A) (Fig. 9b, c, e). It can also occur as isolated fans or in dense irregular masses intergrowing with other calciemicrobes.

Renalcis builds dense dendrolitic aggregates in facies D (Fig. 14b-d), while in facies A and C

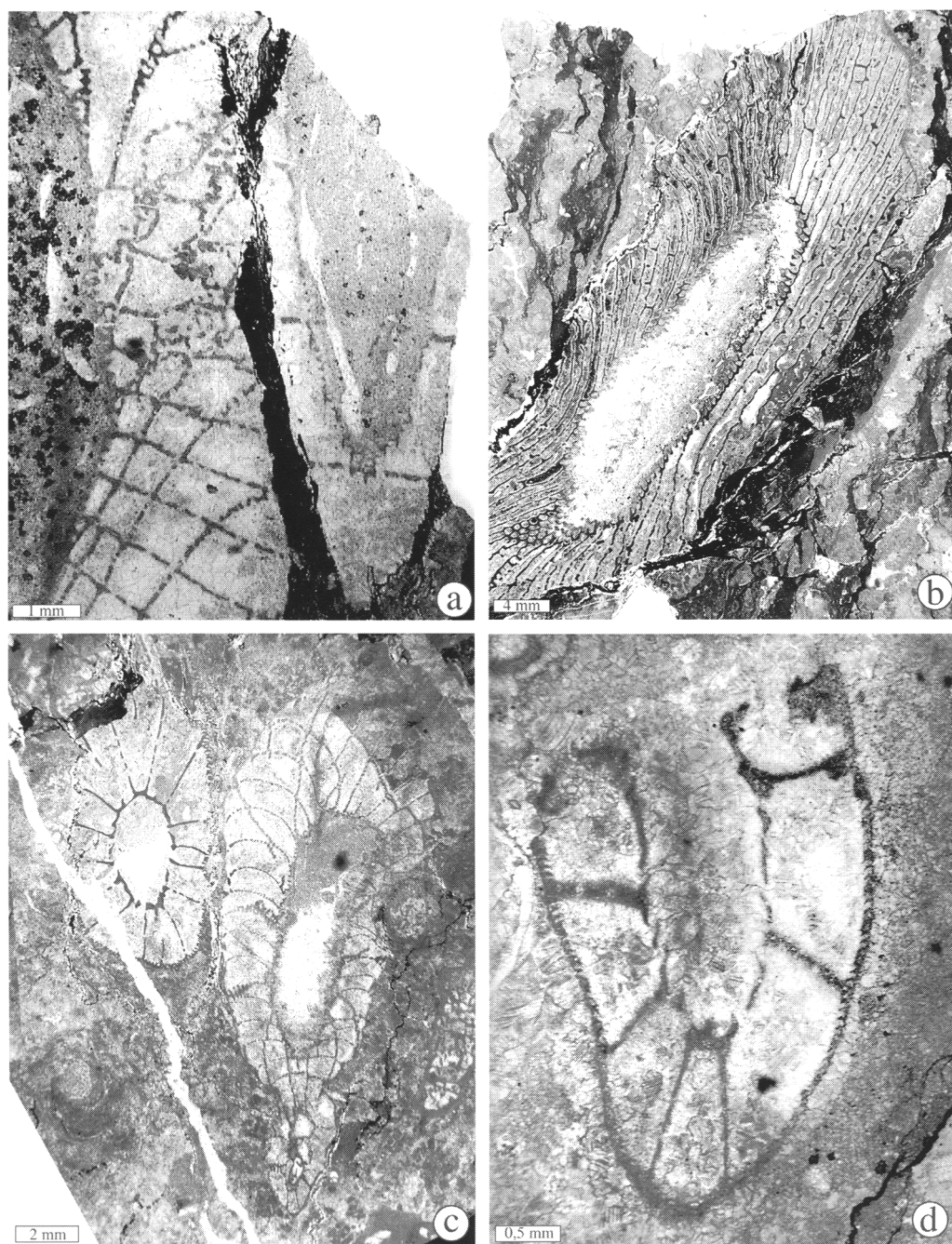


Fig. 12. (a) *Tabulacyathus insperatus* Debr., longitudinal section (right) and *Coscinocyathus dianthus* Born. (left). [SCS1BII (a)/MNHN 84475.] (b) *Afiacyathus alloiteaui* Debr., oblique longitudinal section. [SCS1BIa/MNHN 84476.] (c) *Gandinocyathus gravestockii* Debr., oblique transverse section (left), [SCS2F/MNHN 84477]; *Erismascosinus elongatus* (Born.), oblique longitudinal section (right). [SCS2F/MNHN 84478.] (d) *Gandinocyathus gravestockii* Debr., longitudinal section showing the upward bracts of the inner wall and inverted V-shaped canals of the outer wall. [SCS R5 /MNHN84480.] [SCS numbers correspond to field sampling, M84xxx numbers to the collection of figured archaeocyaths housed in the Muséum National d'Histoire Naturelle, Paris.]

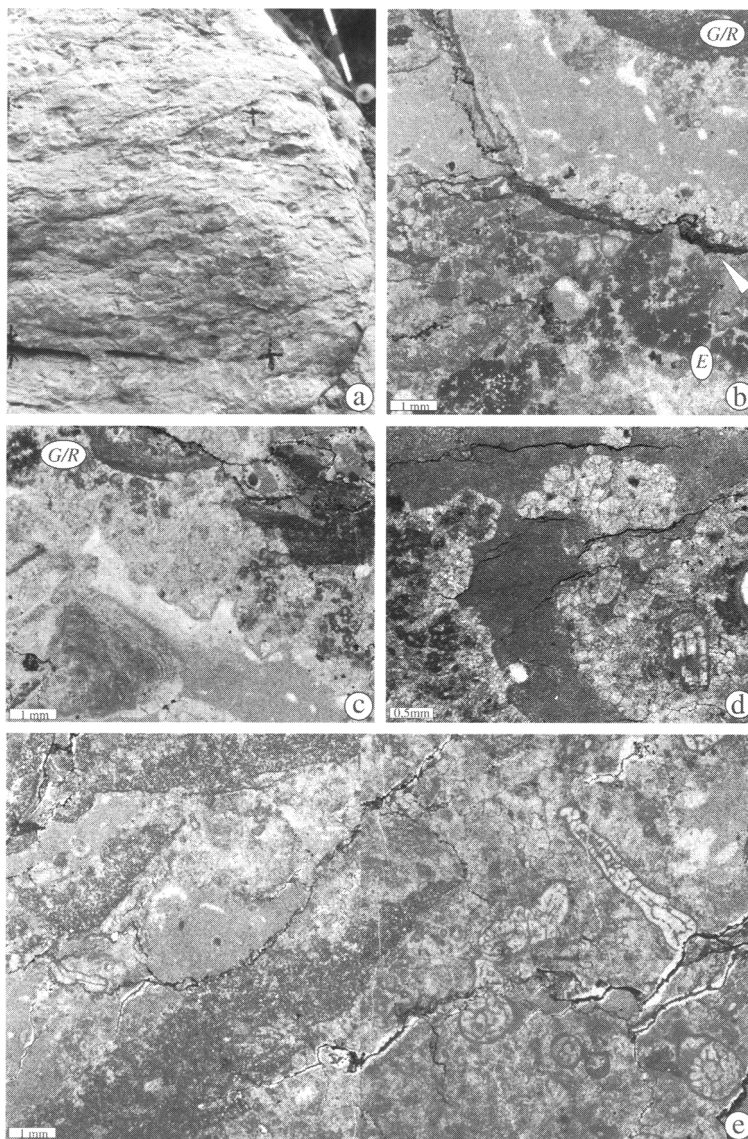


Fig. 13. Macro and microfacies of the microbial-crust boundstone with large shelter cavities (facies C). (a) A square of the sampling grid on the pale-grey massive limestone (facies C). (b) Superposed shelter cavities roofed by *Girvanella-Razumovskia* crusts with different infills. The lower cavity houses thick clusters of *Renalcis* and *Epiphyton* cemented by finely crystalline marine calcite followed by late equant calcite; the roof has been partially destroyed by pressure-solution processes, which spared some remains of the microbial sheet (arrow). The upper cavity is infilled with bioturbated mud-matrix and concentration of spherulites with a micritic core (the enigmatic alga *Acanthina*?); its roof is delimited by a thick *Girvanella-Razumovskia* crust, downwards draped by a festoon-shaped band of microcrystalline cement encasing pendant *Renalcis* clusters. [SCS 4AI.] (c) Large geopetal cavity roofed by a microbial crust partially destroyed by pressure solution, and draped by a festoon-shaped band of microcrystalline cement encasing pendant *Renalcis* clusters; bottom and lateral walls are lined by a rind of stubby blades and locally by multilayered cement. Micritic internal sediment with microboring, filled with late equant calcite. [SCS 4AIL.] (d) Growth cavity lined by a monolayered rind of stubby fibres and blades encasing neighbouring archaeocyath cups and *Renalcis* clusters. Spherulites with a micritic core (*Acanthina* alga?), apparently float in the homogeneous micritic matrix. [SCS R5.] (e) Open growth spaces outlined by thick sheets of *Razumovskia* and clusters of *Archaeopharetra ertashkaense* Vol. is filled by micritic matrix with scattered microborings. [SCS 1F1.] [SCS numbers correspond to field sampling, M84xxx numbers to the collection of figured archaeocyaths housed in the Muséum National d'Histoire Naturelle, Paris.]

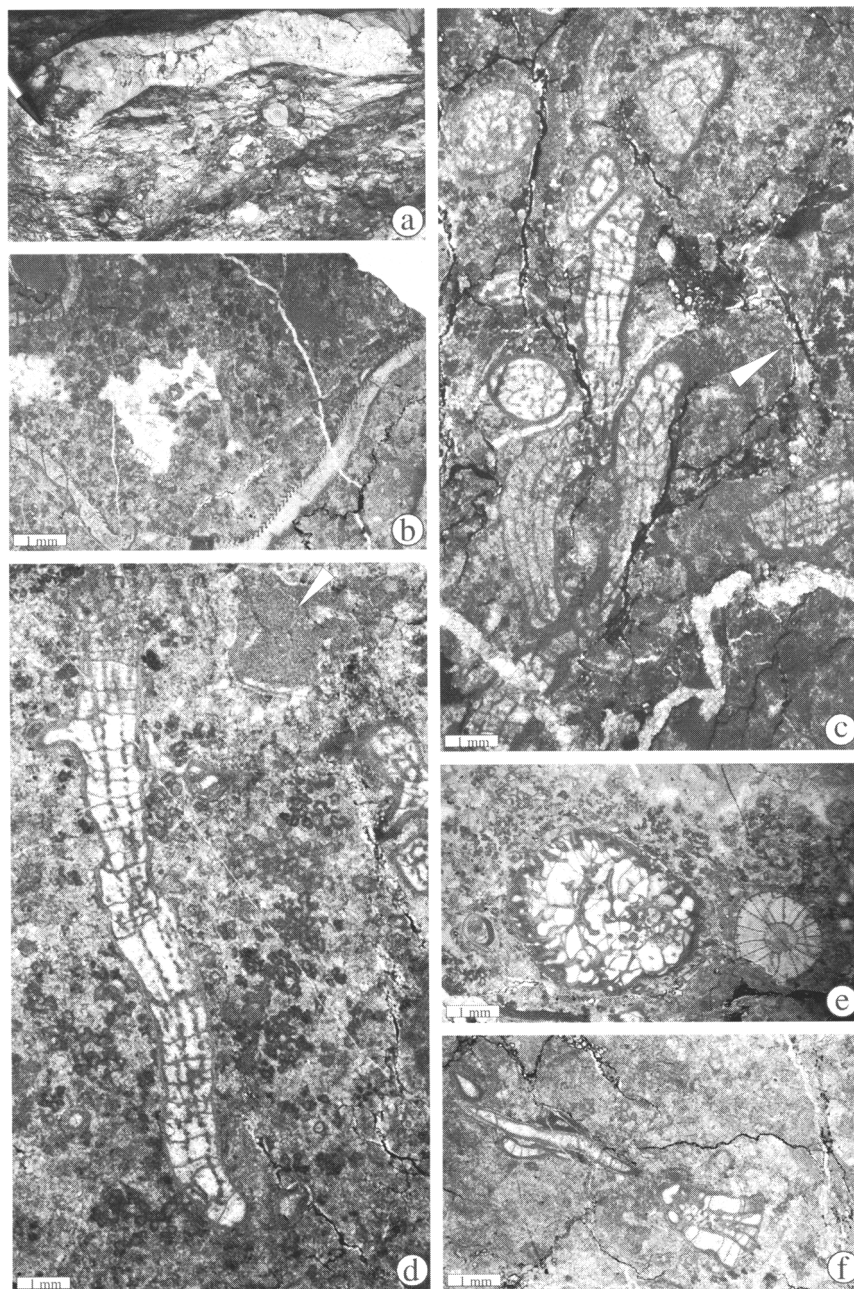


Fig. 14. Macro and micro-facies of cement-supported *Renalcis* boundstone with modular archaeocyath clusters (facies D). (a) *Anthomorpha* cup supporting the *Renalcis*-cement boundstone (facies D) shelters floated skeletal material in rusty-red matrix (facies B). (b)–(e) *Renalcis* dendrolitic boundstone with small growth cavities filled with fine-grained cement. (b) Large saucer-like cup of *Porocoscinus flexibilis* Debr. [SCS 4E II©/M84491.] (c) Cluster of branching *Archaeopharetra ertashkaense* Vol. with small bushes of *Epiphyton* (arrow). [SCS 2F)/M 84489.] (d) Budding *Archaeopharetra ertashkaense* Vol. with irregular growth cavities filled by dense microsparitic internal sediment (arrow). [SCS 5R/M 84490.] (e) *Erismaoscincus cancellatus* (Born.) (right) and *Protopharetra protea* Born. (left). [SCS 3B base.] (f) Apex of *Anthomorpha* cup with exothecal roots enclosed in bladed cement and encrusted by *Renalcis*. [3G II©.] [SCS numbers correspond to field sampling, M84xxx numbers to the collection of figured archaeocyaths housed in the Muséum National d'Histoire Naturelle, Paris.]

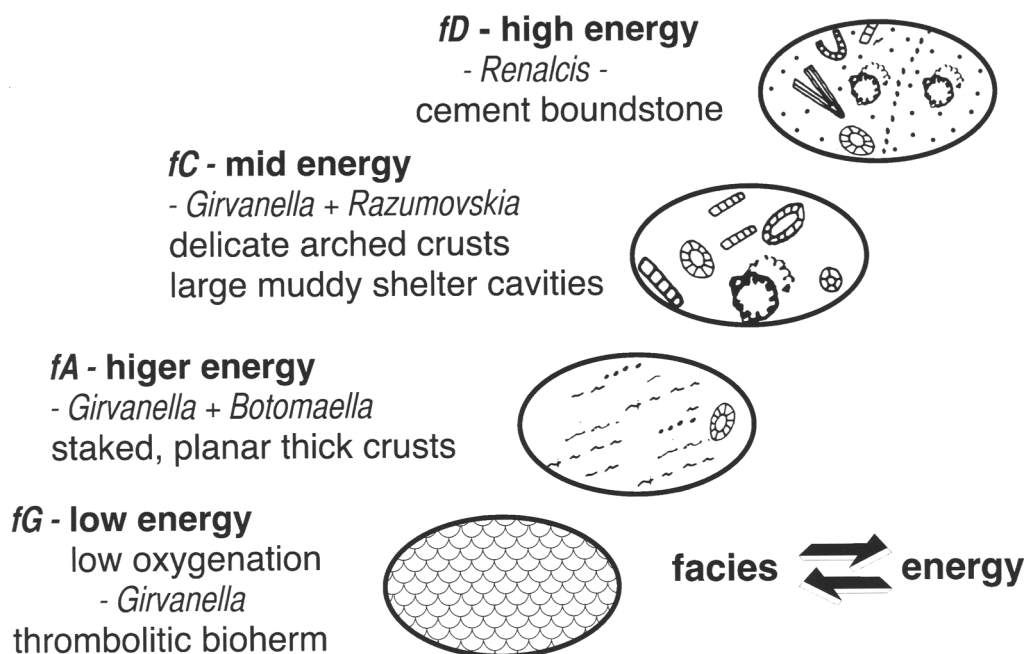


Fig. 15. Evolution of the depositional conditions of the 'La Sentinella' reef complex. As a response to a slow increase of energy and simultaneous decrease of siliciclastic input on the marginal zone of a shallow-marine setting, pioneer microbial communities and archaeocyaths gradually built up structures characterized by increasing synoptic relief: facies G, pioneer thrombolitic build-ups; facies A, planar microbial crusts, colonize the surrounding interbiohermal lime-muds and skeletal debris (facies G' and B); facies C, establishment of a relative relief built by superposed, arched microbial crusts and large saucer-shaped archaeocyaths, forming mud-filled sheltering cavities and supporting cryptobiont communities; facies D, growth to the maximum synoptic relief of 30 cm, of luxuriant *Renalcis* dendrolitic framework supported by thickets of modular archaeocyaths and early interskeletal marine cement.

it forms pendant clusters of small specimens attached to cavity roofs (Figs 9b, c, 10b, c & 13b-d); only occasionally is *Renalcis* found attached to hard substrates such as archaeocyath cups (Fig. 10d) or microbial crusts (Fig. 10e).

Epiphyton is represented by scarce but commonly large clusters, often interwoven with *Renalcis* (facies C and D) or *Botomaella* (facies G).

Circular-subcircular spherulites, consisting of micritic cores surrounded by elongated fibres of calcite, may represent the enigmatic alga *Acanthina* (Mankiewicz 1992). They are found 'floating' within the matrix (Fig. 13d) or concentrated at the bottom of large mud-filled cavities (Fig. 13b).

Matrix

The matrix made of pink or grey homogeneous micrite, only partially fills the central cavities of

archaeocyaths or the elongate or irregular framework cavities in the crust boundstone (facies C) and thrombolitic facies G to form geopetal structures. It corresponds to a mudstone with rare skeletal remains and spherulites, often found concentrated at the bottom of the cavity (Fig. 13b, d). It contains small elongate or irregular vugs filled by equant calcite (Figs 10c & 13b, c, e) that can be interpreted as being produced by soft-bodied burrowers and, more rarely, incipient stromatactis structures with geopetal infill. In some cases, this matrix, more than an original muddy internal sediment, can better be interpreted as normal shelf sediment that periodically interrupted the growth of the microbial crusts. On the other hand, the homogeneous matrix found in the small cavities of facies D, consisting of pink coarse microsparite, can be considered the product of diagenetic recrystallization.

The matrix of the interbiohermal marly sediment, occurring only in the bioclastic facies B and G', is composed of microsparite formed by

silt-sized skeletal particles associated with silt-sized quartz, clay minerals and iron oxides. The iron oxides, locally concentrated by pressure-solution processes, impart to the sediment a characteristic rusty-red colour.

Cements

Primary marine cements, which often are well preserved, are characterized by a distinctive yellowish colour. This feature can be related to the possible presence of microdolomite inclusions, which suggests an original high-Mg calcite composition for the cements (James & Klappa 1983). Limpid, equant calcite, interpreted as a late diagenetic cement of meteoric derivation owing to its blocky shape and lack of inclusions (Folk 1974), fills either residual syndiagenetic voids of geopetal cavities or syntectonic veins. The prismatic/blocky crystals are always deeply twinned as the result of intense tectonic stresses.

The marine cements are variably developed in the different facies and in general display a small size of the component crystals. In facies C, stubby cone-shaped crystals or blades (type 2 of James & Klappa 1983) form thin monolayered rinds around calcimicrobial crusts and clusters (*Renalcis*–*Epiphyton*), or infill part of the geopetal/shelter cavity (Fig. 13d). Less commonly, multilayered crystalline coatings line the inner part of cavity walls (Fig. 13c) and locally encrust isolated archaeocyaths or envelope the micritic core of spherulites (Fig. 13b, d).

Microcrystalline inequigranular mosaic cements form thick festoon-like rinds hanging from shelter cavity roofs (Figs 10b, c & 13b, c) and encase small *Renalcis* clusters (Figs 10b, c & 13b, c).

Fine-grained inequigranular mosaic cements are dominant in facies D, infilling the skeletal pores of *Renalcis* dendrolites (Fig. 14c–f). The intraskeletal open spaces of archaeocyaths (Fig. 14c–f) and the small angular framework cavities, later occluded by coarse microsparite (Fig. 14d), are often lined by rinds of cone-shaped blades.

Facies relationships

The depositional setting and evolution of the 'La Sentinella' reef complex results from detailed analyses of the microfacies, their relationships and spatial distribution. The basal part of both the Lower and the Upper Bioherm, consisting of marly lime-muds composed of skeletal mudstone to wackestone to floatstone (facies B and G'), indicates a shallow-marine setting that in the

beginning appears to have been rather restricted (facies G'). This low-energy setting hosted a diverse association of archaeocyaths, dominated by small solitary forms. The marly sedimentation (facies G') also documents the start of the carbonate deposition that can be connected with the decrease of the siliciclastic input consequent to the onset of more arid climatic conditions, on the shallow siliciclastic shelf of the Matoppa green sandstones.

On the restricted mudstones (facies G'), a pioneer construction was built by a *Girvanella*–*Razumovskia*–*Botomaella* association that formed a thrombolitic framework. Fragments and cups of archaeocyaths with corroded or encrusted outer walls appear to have been floated from the interbiohermal muddy bottom and entrapped within the microbial framework. These features, as well as the poor development of cements and the black colour of the rock, suggest a persistent restricted environment and general low-energy conditions (Fig. 15) that, however, may have been occasionally interrupted by storms of moderate energy.

Pioneer bioconstruction, built by stacked thick, flat crusts of *Botomaella* and *Girvanella*–*Razumovskia* (facies A), grew in well-oxygenated conditions trying to stabilize the loose sediment of the bottom (facies B). Archaeocyaths are relatively rare and isolated. The microbial colonization, at least in the beginning, was repeatedly interrupted by the sedimentation of marly lime-muds. The growth and increased thickness of the microbial crusts was enhanced by the disappearance of the clay input from the continent. The depositional conditions of this peculiar type of bioconstruction can be referred to a slight increase of the ambient energy due to steady bottom currents (Fig. 15).

The presence of a hard substrate promoted the growth of the microbial crusts, which gradually evolved into arcuate thin crusts and rafts (facies C). The crust and the rare but large saucer-like archaeocyaths delimit large growth cavities, lined on the ceiling by thick festoon-like rinds of microcrystalline cement (Figs 10c & 13b) enclosing small clusters of pendant *Renalcis* and small cryptic archaeocyaths (Fig. 10b). The origin of this peculiar festoon-like microcrystalline cement is uncertain: it may have been produced by some other 'non-skeletal' microbial organism or may have resulted from precipitation of calcite on the EPS (extracellular polymeric substance) mucilages enveloping the renalcid clusters. The growth cavities can be filled with associations of *Renalcis*–*Epiphyton* dendrolites associated with fans of *Botomaella*,

but more frequently are filled with pink homogeneous mudstone containing rare skeletal remains and spherulites that are often concentrated at the bottom. Small scattered irregular voids filled with equant calcite probably originated from bioturbation. Archaeocyaths are relatively rare and isolated. The depositional features of this delicate type of buildup appear to reflect a well-oxygenated setting (Fig. 15) with slow circulation of waters that deposited poorly developed cement rinds of short stubby blades on the walls of large cavities mainly supported by microbial crusts.

Towards the top of the bioherm the microbial crusts (facies C) gradually decrease in number and size, and are replaced by cement-rich boundstone (facies D) containing a few small growth cavities that sometimes are lined by a rind of short stubby blade calcite and filled by rusty-red coarse microsparite. *Renalcis* and modular archaeocyaths become the main framebuilders, associated with large clusters of *Epiphyton*. The microbial dendrolitic framework is sustained by the microcrystalline cement formed within the small interskeletal growth cavities (Fig. 14c–f). These features indicate a rather resistant framework that formed in response to the higher energy level (Fig. 15) reached by the 'La Sentinella' reefal environment.

Comparison with other Lower Cambrian bioconstructions

In the basal part of the 'La Sentinella' reef complex, the Lower Bioherm, made up of dark grey limestone, rests directly on the green sandstone of the Matoppa siliciclastic shelf. The pioneer *Girvanella* and *Razumovskia* communities form a spongy fabric disrupted and disconnected by soft-bodied burrowers (facies G), which often contains corroded and encrusted cups of stranded archaeocyaths. The features of this construction (Fig. 7), which can be referred to a thrombolite (Kennard & James 1986; Kennard *et al.* 1989), and those of the associated skeletal-oncoidal mudstones (facies G') can be compared to similar encrusting communities living in a muddy environment associated to oncoidal deposits, described in the Early Cambrian Tianheban Formation of China (Debrenne *et al.* 1991; Gandin & Luchinina 1993). Both units rest directly on marine sandstones and record the beginning of the carbonate deposition on a siliciclastic shelf. They represent the pioneer stage of the reef development in a restricted, low-energy shallow subtidal environment still polluted by land-derived input of fine-grained

detrital material. The lower part of the Upper Bioherm represents unusual facies in which crusts and rafts of *Girvanella*–*Razumovskia*–*Botomaella* are the major framework builders, with accessory dendrolitic *Renalcis* and *Epiphyton* (facies A and C). We apply the term 'crust boundstone' buildup to bioconstructions of this type. Similar crust fabrics, often built by different microbial communities and usually found as isolated occurrences enclosed in different frameworks, have been described in blocks of the Cow Head Breccia in Newfoundland (James 1981), and of the Shady Dolomite in Virginia (Read & Pfeil 1983), in Nevada from the Poleta Formation (Rowland & Gangloff 1988) and Battle Mountain (Debrenne *et al.* 1990), in Mexico from the Puerto Blanco Formation (type 2 build-ups: Debrenne *et al.* 1989), in Mongolia at Zuune Arts (Wood *et al.* 1993) and Zavkhan Basin (Kruse *et al.* 1996).

The crust boundstone buildup (facies A, Figs 8 & 9a–c) has a layered fabric that, according to Wood *et al.* (1993), represents a substrate surface that was alternately colonized by calcimicrobial crusts and then covered by sediments which temporarily stifled growth. This structure does not build synoptic relief but provides a hard substrate for the successive stage of development of the bioherm (facies C). It corresponds to the stabilization stage of the reef.

The crust boundstone buildup (facies C, Figs 10 & 13) is characterized by superposition of shelter cavities, delimited by arched crusts of *Girvanella*–*Razumovskia* and saucer-like archaeocyaths supporting *Epiphyton*, *Renalcis* and *Archaeopharetra* as cryptic dendrolitic components. However, in each documented case cited above, there is an obligate microbial component with erect dendrolitic growth habit, represented by *Tarthinia*, *Epiphyton* and *Gordonophyton* in Mongolia, and by *Epiphyton* and *Renalcis* in Mexico. In the Sardinian 'La Sentinella', this component is represented by *Renalcis* or *Epiphyton*. The resulting construction grown in shallow, moderately turbulent waters, reached a very low relief of about 30 cm.

The upper part of the Upper Bioherm (facies D, Fig. 14) is a typical Early Cambrian *Renalcis*-cement buildup with subordinated archaeocyaths, characteristic of low- to moderate-energy, open-shelf environments. Such buildups range from the Tommotian to the Toyonian in Siberia (James *et al.* 1990; Kruse *et al.* 1995) and are widely documented from Antarctica (Rees *et al.* 1989), Mexico (Debrenne *et al.* 1989) and Australia (James & Gravestock 1990). They may be kalyptate, composite or

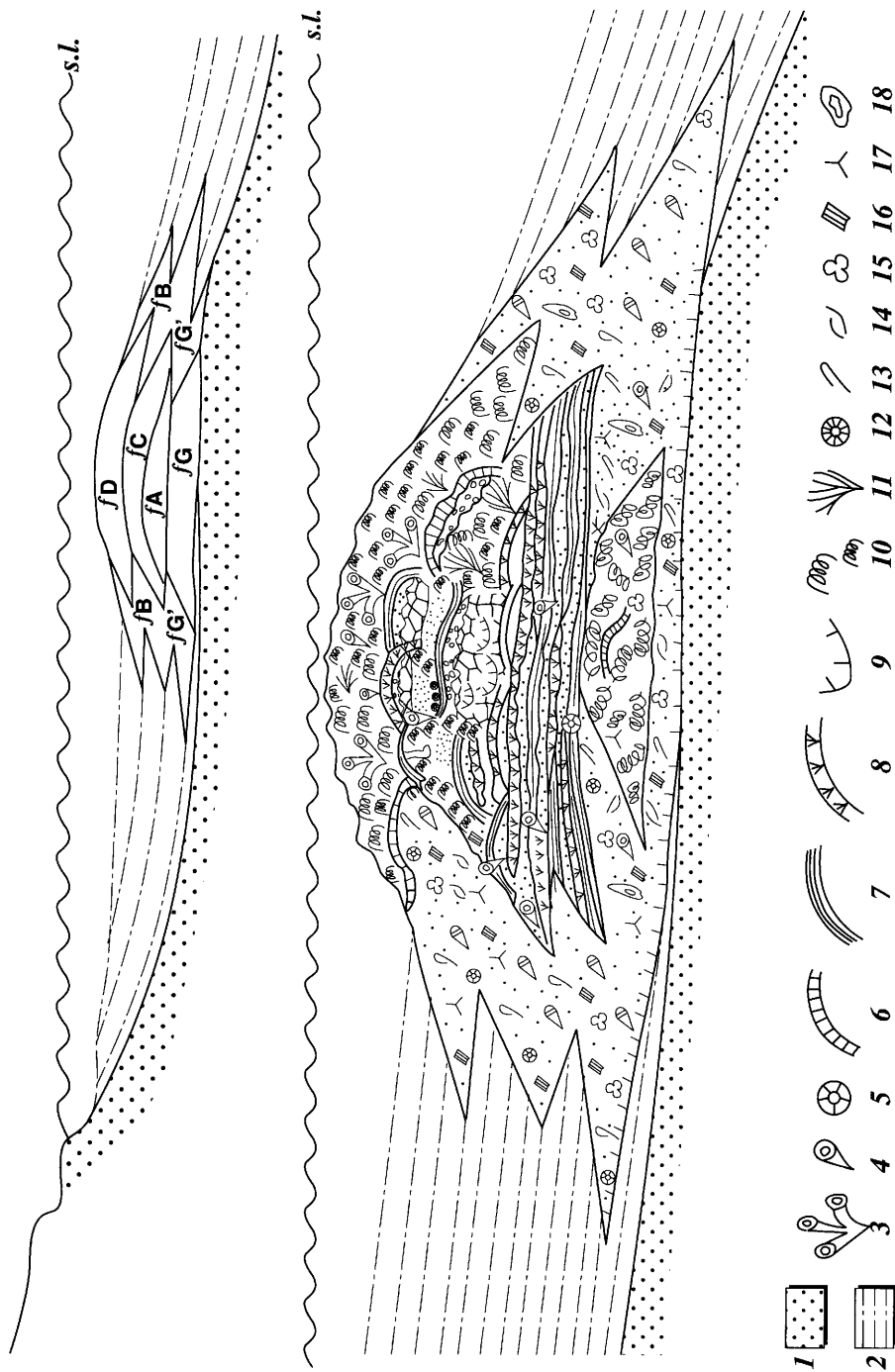


Fig. 16. Ecological evolution of the 'La Sentinella' reef complex on the Matoppa siliciclastic shelf. The growth of the superposed buildups (facies G, A, C and D) and associated flank facies (G' and B) was apparently driven by a moderate increase of aridity of climate and energy of the environment. Legend of symbols: 1, basal green sandstone; 2, shelf green and red shales; 3, branching archaeocyath; 4, solitary archaeocyath; 5, skeletal fragment of archaeocyath; 6, saucer-shaped archaeocyath; 7, *Girvanella* crust; 8, *Botomella* crust; 9, *Razumovskia* raft; 10, renalcids; 11, *Epiphyton*; 12, trilobite sclerite; 13, echinoderm ossicle; 14, cancellorid; 15, sponge spicule; 16, bivalve; 17, *Acanthina*? sphaerulite; 18, oncolite.

massive, as determined by the relative proportions of *Renalcis*, archaeocyaths and cement, as well as by the growth habit of *Renalcis* (encrusting v. dendrolitic). The depositional conditions of the Upper Bioherm seem to have become progressively more energetic. In the last phase of evolution of the 'La Sentinella' reef complex (facies D), the increase in the water energy is one of the factors that can explain the development of the building activity of dendrolitic *Renalcis* and archaeocyaths, the disappearance of mud and microbial crusts, and the contemporaneous development of calcite cements.

Thus, the complex intergrowth of calcimicrobes, archaeocyaths and cements, the builders of the superposed units of the 'La Sentinella' reef complex (Figs 15 & 16), appears to reflect a probable slight variation towards more arid climatic conditions, and a relative increase in energy from moderate in the Lower Bioherm to higher in the Upper Bioherm, within the marginal zone of an open shelf.

We suggest that two conditions were necessary for the genesis of the flat- and arched-crust boundstones. The first was an obligate calcimicrobe with erect growth in sufficient quantity to provide synoptic relief. The second was an episodic supply of fine-grained calcareous sediment followed by periods of non-deposition to enable calcimicrobial crusts to re-cover the substrate. These conditions appear to be satisfied by the calcimicrobial boundstones of Zuune Arts bioherms, which grew up to 2 m in diameter (Wood *et al.* 1993). The Upper Bioherm at 'La Sentinella' also satisfies these requirements. This bioherm is up to 1 m thick with synoptic relief up to 30 cm, but, as a result of folding, the lateral dimensions are unknown. The Zuune Arts crust boundstone buildups are at the base of a succession interpreted to represent upwards-deepening conditions. Thus, the buildups grew in agitated, shallow subtidal conditions (Wood *et al.* 1993). The Mexican crust boundstone biostromes are interpreted to have developed in a lagoonal setting protected by an oolitic shoal complex (Debrenne *et al.* 1989). The peculiar types of crust buildups (facies A and facies C) found in the 'La Sentinella' reef complex have never before been recorded in the Lower Cambrian of Sardinia or, as far as we know, in other regions of the world. They represent the second stage of evolution in the ecological succession of the 'La Sentinella' reef complex, which developed on the Matoppa shelf during a temporal interruption of the siliciclastic deposition.

In memory of David Gravestock and of Max Debrenne. 54 years of everyday life and scientific collaboration ended with Max's sudden death. He was closely

involved with Françoise's work. Cambrian research workers will miss him.

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