Fabric transitions from shell accumulations to reefs: an introduction with Palaeozoic examples

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Abstract: One unresolved conceptual problem in some Palaeozoic sedimentary strata is the boundary between the concepts of 'shell concentration' and 'reef'. In fact, numerous bioclastic strata are transitional coquina–reef deposits, because either distinct frame-building skeletons are not commonly preserved in growth position, or skeletal remains are episodically encrusted by 'stabilizer' (reef-like) organisms, such as calcareous and problematic algae, encrusting microbes, bryozoans, foraminifers and sponges. The term 'parabiostrome', coined by Kershaw, can be used to describe some stratiform bioclastic deposits formed through the growth and destruction, by fair-weather wave and storm wave action, of meadows and carpets bearing frame-building (archaeocyaths, bryozoans, corals, stromatoporoids, etc.) and/or epibenthic, non-frame-building (e.g. pelmatozoan echinoderms, spiculate sponges and many brachiopods) organisms.

This paper documents six Palaeozoic examples of stabilized coquinas leading to (pseudo)reef frameworks. Some of them formed by storm processes (generating reef soles, aborted reefs or being part of mounds) on ramps and shelves and were consolidated by either encrusting organisms or early diagenesic processes, whereas others, bioclastic-dominated shoals in barrier shelves, were episodically stabilized by encrusting organisms, indicating distinct episodes in which shoals ceased their lateral migration.

A paramount quantity of information characterizes the formation and distribution of shell concentrations and reefs in modern and Cenozoic strata, but the knowledge of Phanerozoic shell concentrations and reefs is decreasing when increasing in age. The Palaeozoic is a key time span in the history of life owing to the wide occurrence of skeletonized metazoans (the so-called 'Cambrian explosion': Zhuravlev & Riding 2000) and the successive biodiversifications related to: (i) major extinctions, such as the end-Ordovician (Cooper 2004), the Frasnian–Famenian boundary (Buggisch 1991; Copper 2002; Racki & House 2002) and the end-Permian extinction (Wignall & Hallam 1992); and (ii) major community replacements, such as the Lower–Middle Cambrian transition (Debrenne 1991; Zhuravlev 1995), the Cambrian–Ordovician transition (Barnes *et al*. 1996) and the so-called 'Mid-Carboniferous extinction' (Tappan & Loeblich 1988; Raymond *et al*. 1990; Vachard & Maslo 1996).

Shell concentrations (also named bioaccumulations, coquinas or lumachelles) are defined as 'relative dense accumulations of biomineralized animal remains with various amounts of sedimentary matrix and cement, irrespective of taxa composition and degree of post-mortem modification' (Kidwell *et al*. 1986). By contrast, the concept of reef is more complex: reefs can form as a result of microbial growth, mixed microbial–skeletal growth, complex microbially devoid biomineralized metazoan assemblages, or the accumulation of reef-builder

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remains (Webb 1996). Following Wood's (1998) definition, reefs 'develop due to the aggregation of sessile epibenthic marine organisms, with the resultant higher rate of in-situ carbonate production than in surrounding sites'. Although the relative capacity of some gregarious epibenthic organisms bearing mineralized skeletons to be preserved in living position is a common characteristic of reef organisms, this character is also shared with other non-reef metazoans adapted to soft substrates and forming bundles-like clusters. One group of these organisms, named 'secondary soft-bottom dwellers' by Seilacher (1984), differs from mud stickers (e.g. non-encrusting pelmatozoans and sponges) in the heavy weight of their shells. These metazoans, mainly brachiopods and molluscs, develop common cup-, boulder- and fan-shaped convergent morphologies favouring recliner strategies (Seilacher 1984; Savazzi 1999).

Skeletal concentrations can be subdivided, according to their biostratinomic features, into biogenic, sedimentary, diagenetic and mixed concentrations (Kidwell *et al*. 1986). Biogenic concentrations can be intrinsic or extrinsic in character, the former generated by the organisms that produce the hard parts resulting from intrinsic gregarious behaviours of autochthonous and parautochthonous skeletal organisms (e.g. preferential colonization by larvae, and single colonization events of opportunistic species), and the latter produced by other organisms that interact with skeletonized organisms on their discarded hard parts leading to the formation of parautochthonous and allochthonous concentrations (e.g. hard-part-rich fecal masses and shell-filled pits). Sedimentary concentrations result from physical (usually hydraulic) processes of concentration, in which hard parts behave as sediment particles and non-bioclastic matrix is either reworked or fails to accumulate (e.g. shelly storm lags, aeolian beach pavements, channel lags in fluvial, intertidal and subtidal environments or shell-paved turbidities). Diagenetic concentrations form or are significantly enhanced by processes acting after burial, such as compaction or selective dissolution of matrix. And, finally, mixed concentrations form by the interplay of two or more kinds of the aforementioned processes, and can display both autochthonous, parautochthonous and allochthonous shell assemblages.

One unresolved conceptual problem in some of these mixed shell concentrations is the boundary between the concepts of 'shell accumulation' and 'reef'. Some of them are transitional coquina–reef deposits, because either distinct frame-building skeletons are not commonly preserved in growth position, or skeletal remains are episodically encrusted by 'stabilizer' (reef-like) organisms, such as calcareous and problematic algae, encrusting microbes, bryozoans, foraminifers and sponges. Some of these centimetre- to metre-thick, mixed shell assemblages are named biostromes, and are described as tabular or sheet-like, bioclastic beds. Biostromes are built up by alternating gregarious settlement and hydraulic reworking leading to multiple events of hard-part concentrations. Originally, the term biostrome was coined by Cumings (1932), who defined it as a stratiform bed composed 'mainly or exclusively of shell remains', so that it included the modern concepts of shell accumulation and reef. This was subsequently constrained by Kershaw's (1994) concept of 'parabiostrome', where the constructing organisms are less than 20% in place. Therefore, the (para)biostromes formed through the growth and destruction, by fair-weather wave and storm wave action, of meadows and carpets bearing frame-building (archaeocyaths, bryozoans, corals, stromatoporoids, etc.) and/or epibenthic, non-frame-building (e.g. pelmatozoan echinoderms, spiculate sponges, and many brachiopods) organisms.

Another mixed shell accumulation results from the colonization of shell accumulations by bottom-dwelling, substrate-dependent organisms. This process, named 'taphonomic feedback' by Kidwell & Jablonski (1983), allows a better understanding of the influence of hard parts on the ecological success of living benthos. The reworking of skeletal material by waves and storms commonly provides scattered hard shells in otherwise soft-bottom habitats. This can facilitate colonization and reproductive success by species that require or prefer hard substrates (mainly epibenthic suspension feeders), and at the same time inhibit earlier species that can tolerate only the initial soft-bottom conditions (Kidwell 1991; Kidwell & Bosence 1991). In some cases, preferential colonization by shelled benthos of isolated shells, on otherwise disadvantageously soft sea floor, is the first stage of development in many reefs: these mixed accumulations are usually interpreted as reef soles and reef pioneer communities (Lecompte 1954).

The aim of this paper is to outline the fabrics and geometries of Palaeozoic bioaccumulations and reefs, and to illustrate some transitions between both biosedimentary geometries. The role played by distinct encrusting organisms and early diagenetic cements, stabilizing the sea floor as a response to hydrodynamic fluctuations and palaeoecological relationships, is documented in detail.

Palaeozoic shell concentrations

Overlying the earliest occurrence of skeletonized microfossils in the Ediacaran and earliest Cambrian, shell concentrations are found in most Palaeozoic lithofacies, except in high-porosity sedimentary rocks (such as conglomerates and breccias) because of shell dissolution. Thickness, abundance, packing, internal fabric and fossil preservation are all affected by changes in sediment accumulation rate and vary locally (Kidwell 1991). The physical scale, frequency of occurrence and taphonomic attributes of shell beds in different sedimentary environments are controlled by intensity and frequency of storms, background current and wave agitation, and diagenetic processes (Aigner 1985; Brett & Baird 1986; Speyer & Brett 1988; Kidwell 1991; Speyer 1991)

Patterns of shell accumulation varied over Palaeozoic time because of changes in the diversity and environmental distribution of skeletonized organisms and those that interact with skeletal parts. Kidwell (1990) recognized two different modes of shell concentrations: archaic and modern modes. The archaic mode of shell concentration is represented in Palaeozoic and Triassic strata, and is characterized by relatively thin concentrations dominated by brachiopods and other epifaunal and semi-infaunal organisms (except for crinoidal calcarenites). In contrast, the modern mode is primarily Cretaceous–Quaternary in age, and contains thin pavements and full three-dimensional bioclastic concentrations dominated by molluscs and other epifaunal and fully infaunal organisms. Li & Droser (1992, 1997) further recognized distinct differences across the Cambrian shell beds, and between Cambrian and Ordovician shell beds. Cambrian shell beds are dominated by trilobites and occur as thin pavements, whereas Kidwell's (1990) archaic mode first really occurred during the Early Ordovician with the onset of the Ordovician biodiversification. After the Ordovician, the shell beds became more common, thicker and taxonomically diverse (Kidwell & Brenchely 1994). As a result, Li & Droser (1997) proposed to distinguish three types of shell concentrations, named Cambrian, post-Cambrian (but still Palaeozoic) and modern modes. In addition, although fluctuations in biodiversity of shell concentrations are primarily related to the appearance of new biomineralized clades, they are also controlled by the ecospace occupation: Cambrian faunas utilized relatively little ecospace, occupying mostly epifaunal guilds, and subsequently diversified during the rest of the Palaeozoic in association with a distinct diversification in infaunal and pelagic guilds (Bottjer *et al*. 1996).

Palaeozoic reef geometries and their nomenclatural problem

The variety and complexity that make reefs and mounds so interesting is also responsible for long-lasting problems with concepts and definitions. It is not the aim of this introduction to review reef classifications, but to give some working definitions of the most frequently used terms. Recent and extensive reviews by James & Bourque (1992), Bosence & Bridges (1995), Wood (1998, 2001), Kiessling *et al.* (2002), Riding (2002), and Schlager (2003), and give full access to nature and characteristics of reefs and mounds.

A major distinction between reefs (*sensu stricto*) and other kinds of buildups was highlighted by Lowenstam (1950): 'reefs and 'ecological reefs' of Dunham (1970) are organically produced wave-resistant topographic structures'. This concept was further developed by Heckel (1974), in which he proposed that reefs are buildups which display evidence of potential wave resistance or growth in turbulent water and of control over the surrounding environment. Although these characteristics may be relative and difficult to be established in ancient buildups, this definition satisfied a need to give a special status to reefs. Other buildups, usually lime-dominated, were grouped under the term 'mound' or 'mud mound'. This term was popularized by Wilson (1975), but attributed to so many different examples of buildups that it lost parts of its meaning. This probably led James (1978) to propose the term 'reef mound' for quiet-water buildups growing below the fair-weather wave base, rich in poorly sorted lime mud. Later, James & Bourque (1992) simplified matter by referring to 'mounds'. They also suggested that there are three end members of mounds that would grade into reefs in a tetragonal diagram (Fig. 1). These three mound types are microbial or cryptalgal mounds, skeletal mounds and mud mounds. Microbial or cryptalgal mounds are formed by stromatolites and/or thrombolites; skeletal mounds (such also correspond to the 'biodetrital mounds' of Bosence & Bridges 1995) are those with organisms baffling, trapping or stabilizing mud; and mud mounds are those resulting from piling of lime mud with minor amount of benthic biota.

Several case studies show that overlapping of this mound type is frequent as is vertical

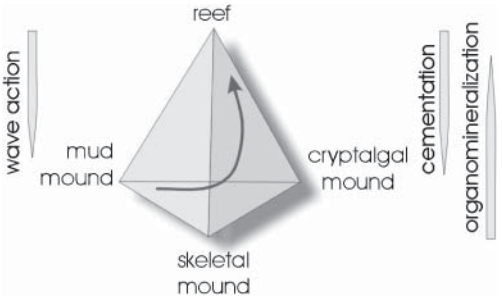

Fig. 1. Schematic classification of reef and mounds, together with variation of some basic parameters. The dark arrow represents an evolution from mud mound to reef via skeletal mound and, possibly, cryptalgal mound due to bathymetric decrease.

evolution from one type to another, or from mound to reef (Textoris 1966; Bourque & Gignac 1983; Boulvain 2001). This mound–reef transition is usually related to shallowing (Hoffman & Narkiewicz 1977; Boulvain 2001) rather than to ecological maturation (Walker & Alberstadt 1975). It is accompanied by textural evolution, community replacements (Fagerstrom 1991) and change in the dominant early diagenetic process, from organomineralization in mounds to cementation in reefs (Neuweiler *et al*. 1999; Schlager 2003).

The wide diversity of patterns preserved in reefs allow the application of Root's (1967) concept of community guilds, each consisting of several species competing for the same 'class of environmental resources'. These are called constructor, baffler, binder, destroyer (borers, raspers, etc.) and dweller (passive members). The three first guilds build the rigid framework of reefs at a rate of upwards accretion that exceeds the rate of deposition of the adjacent level-bottom sediments to give the reef positive topographic relief (Fagerstrom 1988).

If the vertical succession of different kinds of shell concentrations is commonly related to community replacements, which are directly controlled by changing external factors (Copper 1988), reef systems can display radial facies changes associated with intrinsic ecological successions. An ecological succession is 'an orderly, directional, and predictable, pioneer-to-climax process of community and species development' (Copper 1988). Ecological successions take place in environments where external physico-chemical constraints (responsible for the aforementioned community replacements) are not undergoing major changes. In addition, Copper (1988) distinguished a kind of incomplete ecological succession, the so-called 'arrested reef successions', in which full climax stages are not formally attained. These pioneering stages are typical in environments in which strong external control limits the potential of reefs to reach the climax stage.

Palaeozoic examples of coquina-to-reef transitions

This section documents six examples of stabilized coquinas. Some of them formed by storm processes (generating reef soles, aborted reefs or being part of mounds) on ramps and shelves and were consolidated by either encrusting organisms or early diagenesic processes, whereas others – bioclastic-dominated shoals in barrier shelves – were episodically stabilized by encrusting organisms, marking distinct episodes in which shoals ceased their lateral migration.

The presence of microbial mats (commonly called stromatolites and thrombolites) is conspicuous, coating numerous erosive discontinuities where the crusts commonly fossilize substrate irregularities enhanced by skeletal fabrics. Where these erosive discontinuities are repeated vertically the episodic growth of microbial mats can be used as a time record of when they interrupted background-sedimentation patterns, which are characterized by the amalgamation of high-energy events that involved repeated shell accumulations. The biological response of microbial communities to coat stratigraphic discontinuities can be considered as an integral part of dynamic stratigraphy, as they enhance the preservation and identification potential of interruptions in the background sedimentation on substrates devoid of burrowing activity. A semantic problem is related to the use of apparent synonym words related to microbial fabrics, such as 'thrombolite', 'thromboid' or 'clotted fabric'. Kennard (1994) followed the general terminology proposed by Kennard & James (1986), except for the replacement of 'mesoclots' with 'thromboids' (Shapiro 2000, p. 168): 'I recommend that the term 'thromboid' should not be used because 'mesoclot' is a suitable word for meaning the mesostructural elements, and the similarity of 'thromboid' with 'stromatoid' (macrostructural form of a stromatolite in the revision of Grey, 1989) will be misleading' (Shapiro 2000, p. 169). As explained in this work and those included within this Special Publication, this nomenclatural problem is still open to discussion according to the experience of each research worker.

Cambrian shell concentrations stabilized by microbial mats

One example of successive shell accumulation–microbial crust alternations is illustrated by the amalgamation of: (i) millimetre- to centimetre-scale, high-energy sedimentary events, characterized by deposition of broken to disarticulated shells; (ii) interrupted by episodes with extremely low sedimentation rates that led to development of centimetre- to decimetre-thick, microbial reefs (Fig. 2a). The case study reported here is taken from the *Micmacca* Breccia, a member of the lowermost Middle Cambrian Jbel Wawrmast Formation from the Moroccan Atlas that deposited on temperate-water substrates. The member consists of reddish–brownish, volcanoclastic-bearing, bioclastic limestones that alternate with shale or sandstone strata. Each limestone, up to 1.2 m thick, is composed of amalgamated units (up to 0.4 m thick), separated by erosive surfaces, which show a vertical modification of textures: the lenses that directly cover the scour surfaces show chaotic lithoclast orientations, passing upwards into packstones and local grainstones and brecciated volcanoclast-dominated levels (Fig. 2b), in some cases forming low-angle laminae. The shell accumulations display a wide diversity of trilobite debris, echinoderm ossicles, and subordinate heteractinid and hexactinellid sponge spicules, chancelloriid sclerites, brachiopods and helcionellids (Álvaro & Clausen 2006). The aforementioned limestone units are separated by stromatolitic crusts, which are up to 8 cm thick, and vary from wrinkled to domal and columnar in shape (Fig. 2c). The stromatolites grew perpendicularly to substrate surfaces, and generally followed their irregularities.

Although the stromatolitic microfabric was largely the consequence of *in situ* calcite precipitation, there is evidence of litho- and bioclastic incorporation into the structures, in a manner analogous to many modern microbial mats generating agglutinated stromatolites (Riding 1999).

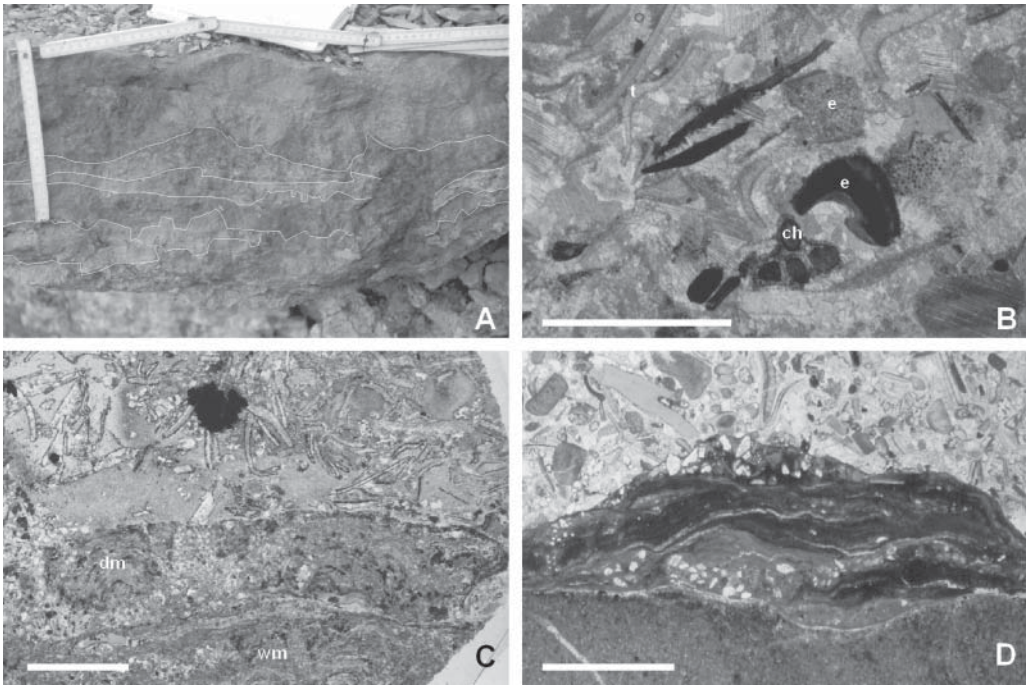

Fig. 2. (**a**) Field aspect of the *Micmacca* Breccia limestones with marked intrabed erosive discontinuities covered by packstone-dominated shell concentrations capped by microbial mats, Tarhoucht, Anti-Atlas. (**b**) Photomicrograph of a packstone with polyphase bioclasts replaced by iron oxides: e, echinoderm ossicle; ch, chancelloriid sclerite; t, trilobite sclerite, Lemdad valley, High Atlas; scale = 250 μm. (**c**) Wrinkled (wm) to domal (dm) stromatolites encrusting a shell concentration and topped by a wacke-packstone; Tarhoucht, Anti-Atlas; scale = 1 mm. (**d**) Trapping of bioclasts and volcanoclasts within a microbial mat, subsequently covered by a packstone, Lemdad valley, High Atlas; scales = 1 mm.

Sediment consisting of quartz, feldspar, corroded micas, volcanoclastic sand- and silt-sized grains, and skeletons was episodically trapped and bound into the surface, increasing upwards in some crusts from 10 to 60% in volume (Fig. 2d). No evidence of grazing and boring organisms was found.

The limestones of the *Micmacca* Breccia represent low-relief shoals that recorded abrupt changes in hydrodynamic patterns. These are indicated by the presence of centimetre- to decimetre-thick, microbial (stromatolitic) reefs that reflect successive interruptions of the background sedimentation, represented by the aforementioned high-energy coquinas.

Ordovician shell concentrations stabilized by encrusting bryozoans

Late Caradocian–early Ashgillian echinoderm–bryozoan thickets and bundles characterize temperate-water substrates located on the northern margin of Gondwana. The Ashgillian, high-latitude, mixed substrates of the Lower-Ktaoua Formation, in the Alnif area (eastern Anti-Atlas, Morocco), have recorded three distinct carbonate factories, displaying some examples of coquina–reef transition, primarily controlled by accommodation space, distance from source areas and subsequent siliciclastic input, and benthic-community replacements (Álvaro *et al.* 2006).

The first benthic community is preserved on the foresets of siliciclastic shoal complexes. It is volumetrically dominated by brachiopods and non-pelmatozoan echinoderms, whereas robust bryozoans and phosphate-shelled brachiopods are secondary (Fig. 3a, b). The brachiopods are dominated by heterorthids and drabovids, which are epibenthic, fixosessile and plenipedunculate, and rafinesquinids interpreted as ambitopic, liberosessile juvenile brachiopods capable to change into quasi-endobenthic adult stages. This brachiopod assemblage was apparently adapted to sandy substrates, where heterorthids and drabovids with highly developed diductor muscles were able to prevent the sharp closure of their valves in turbulent waters, and

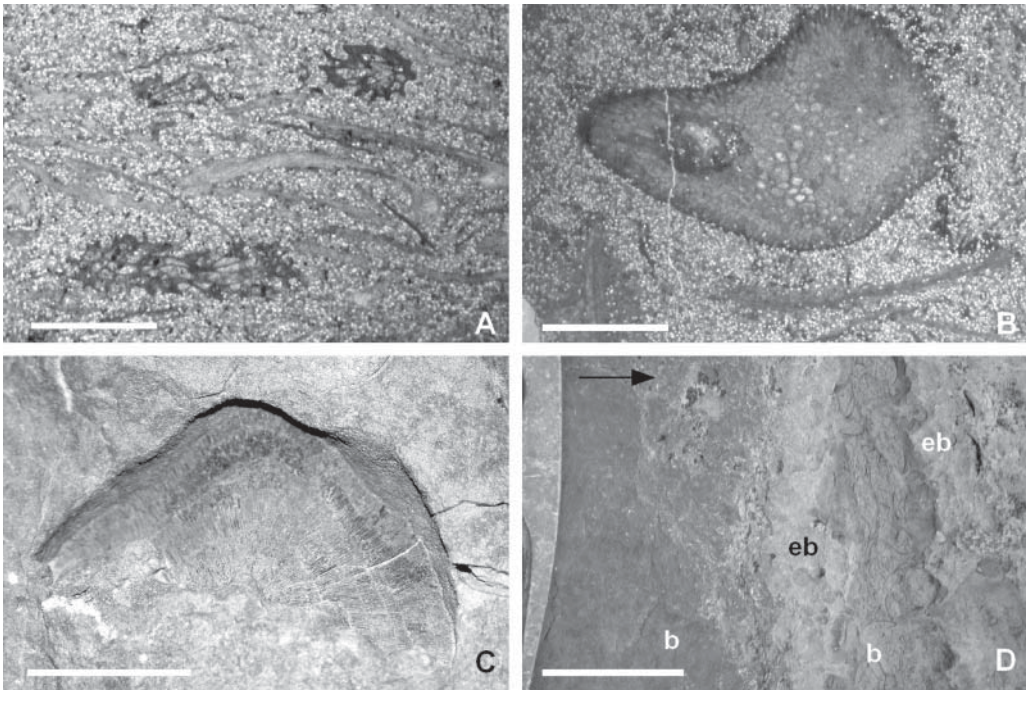

Fig. 3. (**a**) Carbonaceous siltstone of the Lower-Ktaoua Formation rich in calcite-walled brachiopods and fragile-ramified bryozoans paralleling the inclined foreset of a shoal; scale = 2 mm. (**b**) A robust-ramified bryozoan inclined to the foreset plane; scale = 2 mm. (**c**) Non-pelmatozoan echinoderm with flat base parallel to the foreset plane; scale = 2 cm. (**d**) Distal phosphatic limestone (top arrowed) with alternation of encrusting bryozoans (eb) and brachiopod-dominated tempestites (b); scale = 5 cm.

rafinesquinids would have been able to change their position on unstable substrates. Sphaeronitid and aristocystitid echinoderms are also abundant (Fig. 3c). Despite their lack of encrusting strategies, they display their flat bases parallel to the foreset laminae, indicating episodic quiescent episodes in the shoal migration. As a result, this brachiopod–echinoderm benthic community marks episodes of decreased energy in prograding sandy shoals.

The second benthic community, preserved in distal phosphatic limestones, is dominated by disarticulated to fragmented bryozoans and brachiopods (Fig. 3d). Common growth forms of bryozoans are robust and delicate branching, and multilaminar and unilaminar encrusting (nomenclature after Nelson *et al.* 1988). Carbonate- and phosphate-shelled brachiopods, trilobites, bivalves, ostracodes, ortoconic nautiloids and conulariids are locally abundant. The widespread variety of bryozoans indicates the establishment of bryozoan thickets that helped to stabilize episodically the substrate but without trapping significant amounts of mud.

Finally, the top of the Lower-Ktaoua Formation is recognizable as a phosphatized coquina, which contains the peak in biodiversity patterns of the whole studied succession. It includes trilobites, brachiopods, bivalves, conulariids, orthoconic nautiloids, disarticulated pelmatozoan stems and scattered encrusting bryozoans. Brachiopods consist of fixosessile, plenipedunculate heterorthids and rhynchonellids, as well as the liberosessile ambitopic, quasi-infaunal xenambonitid *Aegiromena aquila aquila*. The condensed level also contains abundant trilobite debris derived from calymenids, dalmanitids, cheirurids and illaenids. Other taxa are sinuitid, eotomariid and holopeid gastropods, and hyolithids. This phosphatized coquina indicates development of condensation associated with marine depositional hiatuses, which allowed repeated early diagenetic phosphate cementation and encrustation made up by bryozoans.

Silurian shell concentrations stabilized during early diagenesis

The strata of Gotland (Sweden) represents an extraordinary well-preserved example of tropical carbonate platform development during Silurian times (late Llandovery–late Ludlow), and reflects a series of stacked carbonate platforms (Calner *et al.* 2004). On Gotland, a huge variety of carbonate facies is developed, from extremely shallow-water deposits mostly on the eastern part of the island to open-marine shelf deposits dominating the western part (Samtleben *et al.* 1996, 2000). Accordingly, the variety of different shell accumulations is very remarkable. However, a common characteristic of most of these deposits is that cementation occurred early in diagenetic history. Except for some crinoidal limestones, most coarse-grained limestones on Gotland do not show any fitted fabrics (Fig. 4b, c). This indicates that the original pore space was filled by calcite spar prior to mechanical compaction (cf. Bathurst 1995). Stylolites, which according to Bathurst (1991) are defined as 'serrated interface between two masses of rock', are common, and represent structures developed during late diagenesis. However, stylolites form only on sediment that has been lithified before. An early diagenetic lithification is also typically observed in fine-grained limestones from Gotland, where undeformed trace fossils and organic-walled microfossils document an early stabilization (=cementation) of the original carbonate mud (Munnecke & Samtleben 1996; Westphal & Munnecke 1997). These observations point to one of the fundamental questions in carbonate petrology (Bathurst 1970): how to cement a carbonate sediment while it is still largely uncompacted. Where was the source of such an enormous quantity of $CaCO_3$?

On Gotland, most of the section is developed as alternation of limestones and marls, which exhibit a wide morphological variety from nodular marl-dominated alternations to well-bedded limestone-dominated alternations. According to Munnecke & Samtleben (1996), lithification of the limestones in these alternations took place just below the sea floor in the shallow-marine burial realm. The source of the carbonate cement lithifying the micritic limestones is a selective dissolution of aragonitic constituents in the intercalated marl layers. Consequently, the marls are not cemented and represent a residual sediment depleted in aragonite. Owing to ongoing sedimentation, the marl layers were more and more compacted. But, what about coarse-grained shell accumulations? Where is the source for their carbonate cement? Bathurst (1995) pointed out that 'the style of pressure dissolution in pure limestones, fitted-fabric or stylolite, depends strongly on the availability of aragonite in the original sediment'. This, however, was questioned by Railsback (1996). But how can we prove the former existence of aragonite as source for the carbonate cement when it is dissolved during diagenesis? And when – that is, in which diagenetic environment – does aragonite dissolution occur?

Cherns & Wright (2000), who compared early silicified faunas from Gotland with non-silicified faunas, show that aragonite dissolution must

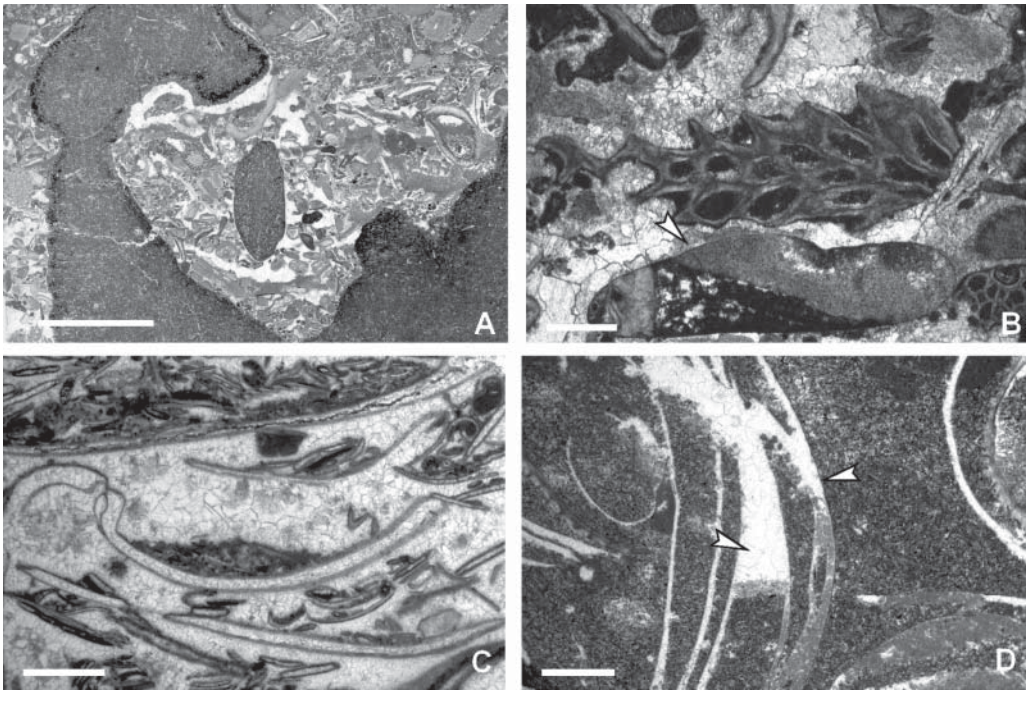

Fig. 4. All thin sections come from the Silurian of Gotland, Sweden. (**a**) Irregular hard ground with thin pyrite-enriched layer, and reworked intraclast in the overlying sediment (Slite Group, Wenlock, proximal shelf facies, locality Haganäs 1) ; scale = 1 cm. (**b**) Reworked intraclast (arrow) with sharply eroded bryozoan (left) and crinoid (right) debris. The fact that matrix as well as biogenic components are sharply truncated indicate that the reworked layer was already completely lithified prior to erosion (?Högklint Formation, locality Gutevägen); scale = 1 mm. (**c**) Shell accumulation dominated by bivalve shells, partly with geopetal fillings. All components show micritic envelopes, which is a common feature in shallow, warm water. The bivalve shells are completely recrystallized to clear, blocky calcite spar (Halla Formation, marginal marine to lagoonal facies, locality near Gothemhammar 1); scale = 2 mm. (**d**) Vertically stacked bivalve and brachiopod shells embedded in a fine peloidal–grainstone matrix. The sharp boundaries of the bivalve shells indicate that dissolution of the aragonitic shells occurred after cementation of the matrix. Interestingly, the bivalve shells are partly filled with fine-grained sediment. This indicates that after the aragonite dissolution fine-grained material was flushed into the pore network filling primary (left arrow) and secondary pores (the dissolved shells). Sometimes the shells are filled geopetally (right arrow) (Halla Formation, marginal marine–lagoonal facies, locality near Gothemshammar 1); scale = 2 mm.

have happened very early in diagenetic history. Their finding is confirmed by our results: Figure 4d illustrates that aragonite dissolution in the limestones of Gotland must have occurred very early, but after cementation. The sharp boundaries of the former aragonitic bivalve shells indicate that the first step in diagenesis was the lithification of the matrix. Later, the shells were dissolved and partly refilled with fine-grained sediment. This must have taken place where soft mud was still available, i.e. close to the former seafloor. The bivalve shells themselves, however, cannot be the source for the cementation of the matrix because: (a) the limestone was cemented prior to dissolution of the aragonite shells; and (b) the amount of $CaCO_3$ provided by this process would be far too low. So, a source outside the limestone bed has to be considered (see above).

An early cementation of the Silurian rocks on Gotland is also documented by the occurrence of abundant hard grounds and reworked intraclasts, mainly in proximal environments (Fig. 4a, b) (Samtleben *et al*. 2000). Hard grounds are sedimentary surfaces that have existed as hardened sea floor prior to the overlying sediment (Flügel 2004). In general, hard-ground formation can be explained in two different ways:

(i) by an interruption in sedimentation resulting in cement precipitation directly from sea water; and (ii) by an exhumation of a limestone bed that was lithified close to the surface, i.e. a few decimetres or metres below the sea floor. Such sedimentary depth is assumed for the cementation of the limestones in limestone–marl alternations (Munnecke & Samtleben 1996). Changes in the local hydrodynamic regime can easily result in erosion of the topmost part of the sediment, which consists of soft, unlithified mud, and thus resulting in an excavation of the early cemented limestone layer. As long as the water energy is high enough to prevent accumulation of new carbonate sediment this layer represents a hardened sea floor, and might be either encrusted by hard-bottom communities, or corroded or bored by chemical processes or biological activities (bioerosion). As the internal character of hardground beds is indistinguishable from 'normal' limestone layers on Gotland, and no traces of early marine cements have been found (Fig. 4a), this second process is assumed to be the common process in hard-ground formation (Munnecke 1997). A similar process is proposed for the formation of so-called 'hiatus concretions' (Voigt 1968).

It is more and more accepted that aragonite dissolution and early cementation is a very important process in early marine carbonate diagenesis, even in non-tropical carbonates (Munnecke & Samtleben 1996; Cherns & Wright 2000; Melim *et al*. 2002; James *et al*. 2005; Munnecke & Westphal 2005; Dix & Nelson 2006). However, there is an ongoing discussion as to whether the bulk of the carbonate cement is provided by dissolution of mud-sized aragonite derived from shallow carbonate platforms or by dissolution of benthic molluscs (Cherns & Wright 2000; Wright & Cherns 2004; see discussion in Munnecke & Westphal 2005).

Nebuloids: gel-stabilized shell concentrations in Devonian carbonate mounds

Late Frasnian Petit-Mont Member mounds occur in the southern part of the Dinant Synclinorium and in the Philippeville Anticline (SW Belgium). These mounds are 30–80 m thick and 100–250 m in diameter. They are embedded in shale, nodular shale and argillaceous limestone. Mound growth typically initiated from below the photic and storm wave base zones and continued into shallow-water environments. Above an argillaceous limestone substrate, the first mound facies consists of spiculitic wackestone with stromatactis, which becomes progressively enriched in crinoids and corals, then in peloids, stromatoporoids and cyanobacteria (named Pm3 in Boulvain 2001). The shallower facies consists of algal–coral–peloid wackestone and packstone with green algae and thick algal coatings. A core of algal and microbial bindstone sporadically occurs within large mounds (Boulvain 2001).

Of particular interest is the pink limestone with corals, crinoids, stromatactis, fenestrae and lamellar stromatoporoids (Pm3): this facies marks the entrance of the mounds into the storm wave zone. Corals are generally tabular (*Alveolites*, *Phillipsastrea*, *Thecostegites*), branching (*Thamnopora*, *Senceliaepora*) or fasciculate (*Thamnophyllum*); solitary rugose corals are also present. *Receptaculites* is locally abundant. Cyanobacteria form partial coatings around particles, and peloids are common and irregular. This muddy facies includes enigmatic structures consisting of decimetre-scale pockets or decimetre-thick beds of dark grey fibrous cement containing sorted brachiopods and crinoids (Fig. 5b, c). These particular structures (called 'nebuloids' by Boulvain 2001) may pass laterally, by reduction in the proportion of spar, into a network of centimetre-scale stromatactis or fenestrae. In some mounds, the nebuloids are laterally uninterrupted over tens of metres and show a rhythmic pattern consisting of decimetre-thick spar networks separated by layers of pink limestone (Fig. 5a). In these large-scale structures the fossil content changes laterally: brachiopods are prominent in the central part of the mounds, although crinoids are more abundant close to the flanks. This reflects the usual lateral zonation of the mounds at this growth stage.

In thin section, the fibrous cement corresponds to isopachous crusts of radiaxial calcite, with micron-sized inclusions of dolomite, and are very rich in organic matter (Fig. 5d). Internal sediment is very rare, although it is common in other types of fenestrae.

Sorting of bioclasts, rhythmic pattern, local hummocky cross-stratification and position of this facies in the shallowing-upwards mound-development sequence indicate that these nebuloid structures are formed by storms. Periodic increasing of water agitation was responsible for lime mud erosion and the concentration of bioclasts in beds or pockets. After deposition, fossils were cemented by early fibrous cement. It is, however, difficult to date the precipitation of the fibrous spar. Was it truly synsedimentary, before settling of the muddy interlayers, or did it postdate mud accumulation? Several lines of

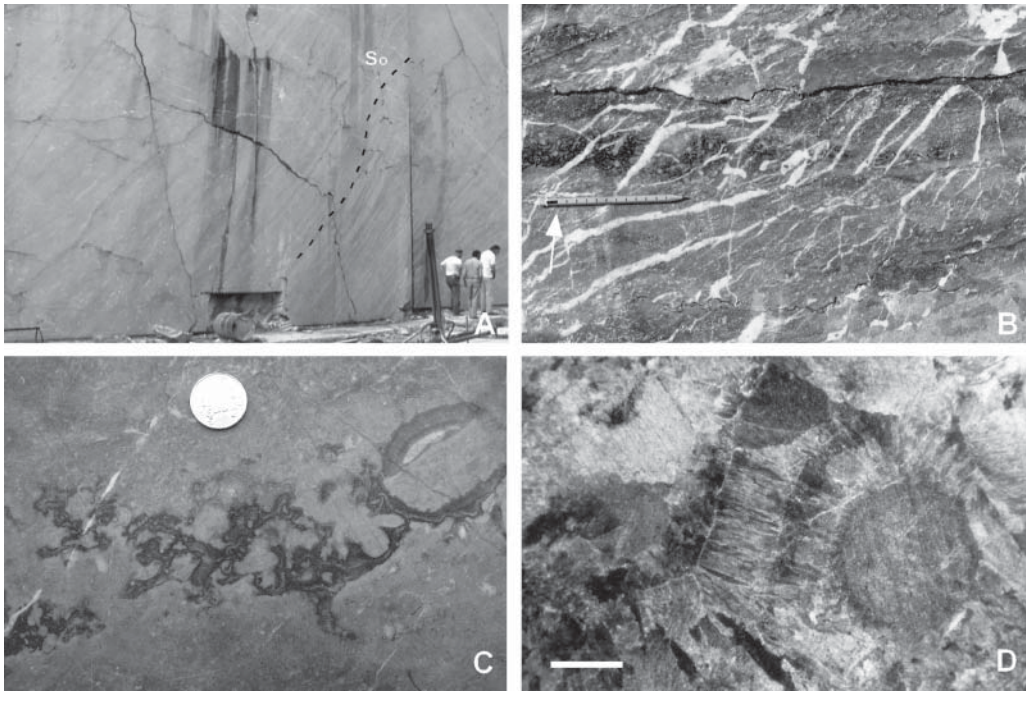

Fig. 5. All pictures come from the Late Frasnian Petit-Mont Member mounds, Philippeville Anticlinorium, Belgium. (**a**) Rhythmic succession of nebuloids in the middle part of the Tapoumont mound; So = bedding. (**b**) Nebuloid structures (grey) in reddish limestone; pencil (arrowed) for scale; Les Bulants mound. (**c**) Close-up of a nebuloid, cemented by dark organic matter-rich radiaxial spar; a *Receptaculites neptuni* is included in the spar to the right of the picture; coin (50 eurocents) for scale. (**d**) Thin section in a nebuloid, showing dark organic matter inclusions (arrowed) and crinoid ossicles; crossed nicols, Tapoumont quarry; scale = 2 mm.

evidence suggest that cement was precipitated into a gel-like microbial mat stabilizing the storm layer: first, the unusual richness of the radiaxial cement in organic matter; and, second, the lateral transition of the nebuloids into mud with stromatactoid fenestrae. This could be explained by progressive lateral reduction of the mat, allowing mud to settle between the bioclasts. Unusual absence of internal sediment could also be explained by the presence of an organic gel.

Carboniferous shell concentrations stabilized by microbial communities

Shell accumulations are common features of many Carboniferous carbonate platforms. Some of these concentrations display important lateral extension, and thus are of stratigraphic importance; for example, the Upper Viséan *Orionastrea* bed of England (Cossey *et al.* 2003). The composition of shell beds varies significantly in time and space. 'Encrinites', which are limestones of various textures dominated by crinoid debris, are ubiquitously distributed (e.g. in the so-called 'Petit-Granit' in Belgium). Many Mississippian shell beds are macroscopically composed of brachiopods and/or corals. The compositional complexity of Pennsylvanian shell beds is similar to that of the older counterparts, but chaetetid sponges and calcareous algae play a more prominent role.

The case studies described herein are Mississippian in age, and it is our aim to provide examples of the involvement of microbial communities into the hydrodynamic context of these shell beds. The first example is taken from the Middle Viséan Lives Formation of the Namur Syncline (Belgium). The formation consists of a set of shallowing-upwards parasequences (Chevalier & Aretz 2005). An ideal parasequence starts with subtidal marine bioclastic packstones–grainstones, passing upwards into stromatolitic boundstones or peloidal mudstones of intertidal–supratidal environments, finally

capped by palaeosols. In one of the parasequences, a decimetre-thick bed rich in brachiopods, conventionally named the *Composita* bed, marks the transition from bioclastic limestone to lime mudstone. Without record of major macroscopical changes, the bed can easily be laterally traced over several kilometres. However, a microfacies analysis reveals a very heterogeneous composition of the bed: texture and allochem composition differ over short distances, with most of the bed grading between bioclastic grainstone (Fig. 6a) and oncoidal packstone (Fig. 6b). Microbial coating, resulting in advanced stages in oncolite formation, is ubiquitous in the bed, although increasing vertically in abundance and thickness. However, although reworking seems to be an important process in the shell bed formation, this trend may be partly obscured. The microbial coatings are important for the stabilization of the mobile substratum in which the shell bed formed. The development of proper boundstone fabrics is not observed. The transitional character of the shell bed fabric is further expressed by the formation of small patch reefs, which initiated upon this bed (Chevalier & Aretz 2005). However, the reef fabrics show fundamental compositional and structural differences compared to the shell bed facies.

The second example is taken from the Upper Viséan of the Montagne Noire (southern France). In the quarry of Castelsec, a small coral patch reef is topped by three well-bedded units, which are composed of partly argillaceous bioclastic limestones (Aretz & Herbig 2003). The lowest of these units is 2.8 m thick and comprises abundant small clisiophyllid and axophyllid rugose corals. Associated with the small corals are productid brachiopods, and larger and/or colonial rugose corals. All small rugose corals are coated with microbial crusts, which are differentiated into two crust morphotypes: (i) crusts forming through incrustation of coral skeletons, thus resulting in a more circular geometry; and (ii) crusts of more aligned habits, which do not necessarily encircle corals, but seem to bound a number of previously encrusted (?) corals

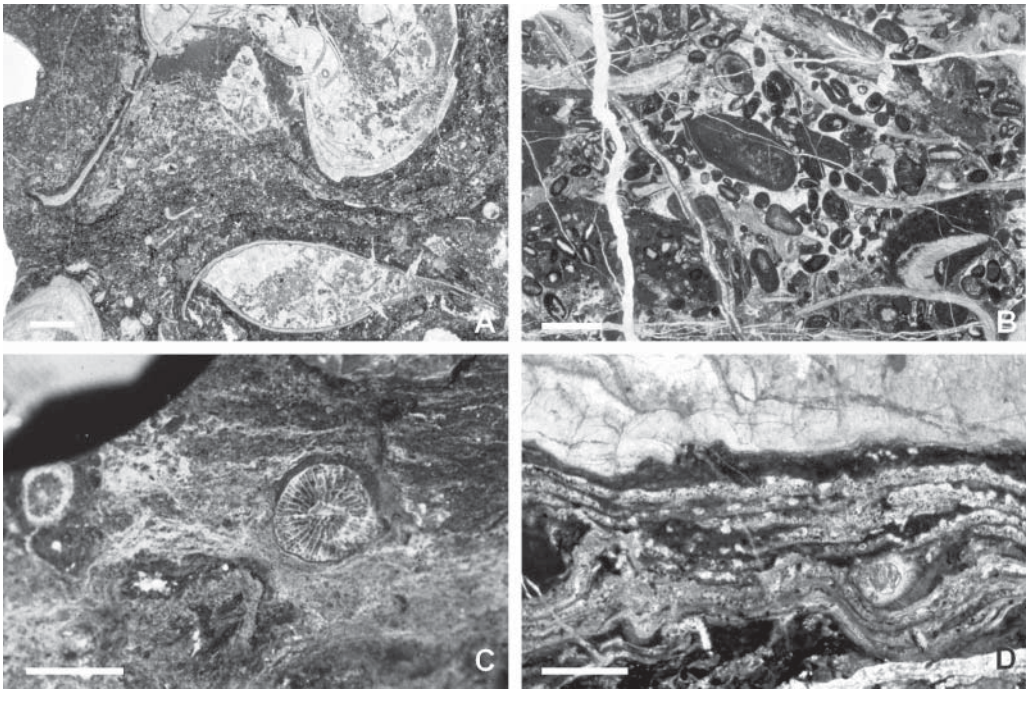

Fig. 6. (**a**) Bioclastic-dominated part of the *Composita* bed; larger bioclasts are mainly brachiopods and gastropods; note the presence of thin microbial coatings surrounding some clasts; *Composita* bed (Middle Viséan), Engihoul Quarry ; scale = 2 mm. (**b**) Oncoidal grainstone; note the high diversity of encrusted bioclasts; *Composita* bed (Middle Viséan), Engihoul Quarry; scale = 2 mm. (**c**) Inner circular crust (morphotype 1) around a small solitary rugose surrounded by more aligned crusts (morphotype 2); outcrop picture, Castelsec Quarry, Montagne Noire; scale = 5 mm. (**d**) Complex microbial-dominated crust on coral skeleton; note the incorporation of grains; thin section from below the shell bed, Castelsec Quarry, Montagne Noire; scale = 1 mm.

together. Both morphotypes are well preserved on weathered surfaces (Fig. 6c), but crusts of the first morphotype seem more abundant, as parts of the unit tend to develop a nodular appearance. The composition of these microbial crusts is complex, and involves dark micritic layers, calcimicrobes, trapped carbonate particles and sparry cement layers. The importance of the microbial crusts for shell bed formation is their bounding activity, which results in a well-preserved coral rubble, and the homogenous appearance of the shell bed. However, the relative smallness of the corals indicates an originally somewhat unfavourable environment for corals. The abundance and composition of microbial crusts in this shell bed is very similar to other deposits in the Montagne Noire (Fig. 6d), but the failure to develop a substantial reef development, as seen in other outcrops (Aretz & Herbig 2003), remains enigmatic.

It is important to remark that microbial communities played a key role in the formation and preservation of many Mississippian shell beds, although they seem to be absent in others. Therefore, the functional role of microbial communities, which is mainly stabilization through binding, either remains open or is fulfilled by other encrusting organisms, such as bryozoans and chaetetid sponges. However, shell beds with an important microbial community commonly tend to be more compact and massive than other shell beds.

Permian shell concentrations stabilized by richthofenid brachiopds, calcisponges and bryozoans

In the Mixteco Terrane (SW Mexico), diverse Permian strata onlap the Acatlán metamorphic substrate as a result of a Devonian (probably Ligerian) suture. The Middle–Upper Permian Olinalá Formation (Guerrero state, Mexico) consists of three (lithostratigraphically unnamed) successions of, in ascending order, siliciclastic, carbonate and siliciclastic character (Flores de Dios & Buitrón 1982; Vachard *et al.* 2004). The lower siliciclastic succession is Wordian in age, and is composed of a lower massive conglomerate, a middle black shale bearing middle-Wordian goniatites (Vachard *et al.* 2004), and an upper palaeodelta complex with terrestrial plants and brachiopods (Buitrón *et al.* 2005). The overlying carbonate-dominated succession can also be subdivided into three levels: a lower stromatolitic level (Flores de Dios *et al.* 2000), probably early Capitanian in age, a middle part rich in channelized accumulations of giant fusulinids (e.g. *Polydiexodina capitanensis*) and an upper part containing mud mounds, dated as late Guadalupian based on the presence of the fusulinid *Codonofusiella extensa* (Vachard *et al.* 1993); its genus is commonly Lopingian (= Late Permian) in the other parts of the world. The third siliciclastic succession consists of shales with scattered indeterminate, but apparently Permian, ammonoids (Flores de Dios & Buitrón 1982).

If the mud mounds of the Olinalá Formation are late Capitanian in age, and grew up into the Lopingian, they would represent the youngest Permian evidences of North American reefs. As in the Lopingian reefs of South China (e.g. Rigby *et al.* 1989; Weidlich 2002), the Olinalá mud mounds are built in particular by calcisponges and richthofeniid brachiopods. These deposits are first composed of crinoid rudstones with rare *Polydiexodina* fusulinids, the whole fabric recording current structures and channel fillings. The richthofeniid and encrusting productid brachiopds occur directly attached to the surface of these encrinites (Fig. 7a, b). The space between the richthofenids is filled with micrite and/or crinoidal wackestone with thin carbonate cements (Fig. 7a, b). This benthic assemblage is subsequently replaced by sphinctozoan calcisponges (Fig. 7c) and encrusting bryozoans, in association with the aforementioned richthofeniids. At the top of the mud mounds, some stromatolites cap the buildups (Fig. 7d), which were finally drowned and buried by ammonoid-bearing shales. In summary, the Olinalá mud mounds display a vertical evolution that started by an accumulation of crinoidal ossicles, subsequently stabilized by richthofeniid brachiopods, secondarily replaced by sphinctozoan calcisponges and bryozoans, and finally capped by microbial mats.

Concluding remarks

The occurrence of new biomineralized metazoans during the Palaeozoic, and their synecological relationships with microbial communities, have greatly increased the concepts and nomenclature necessary to understand the evolution of benthic communities through this key time span. Although the concepts of reef and shell accumulation are clear, numerous transitional coquina–reef deposits reflect fluctuations in hydrodynamic conditions and palaeoecological relations leading, in some cases, to the episodic stabilization of epibenthic non-framebuilding meadows and carpets, and reef communities. Some of these skeletal-rich geometries

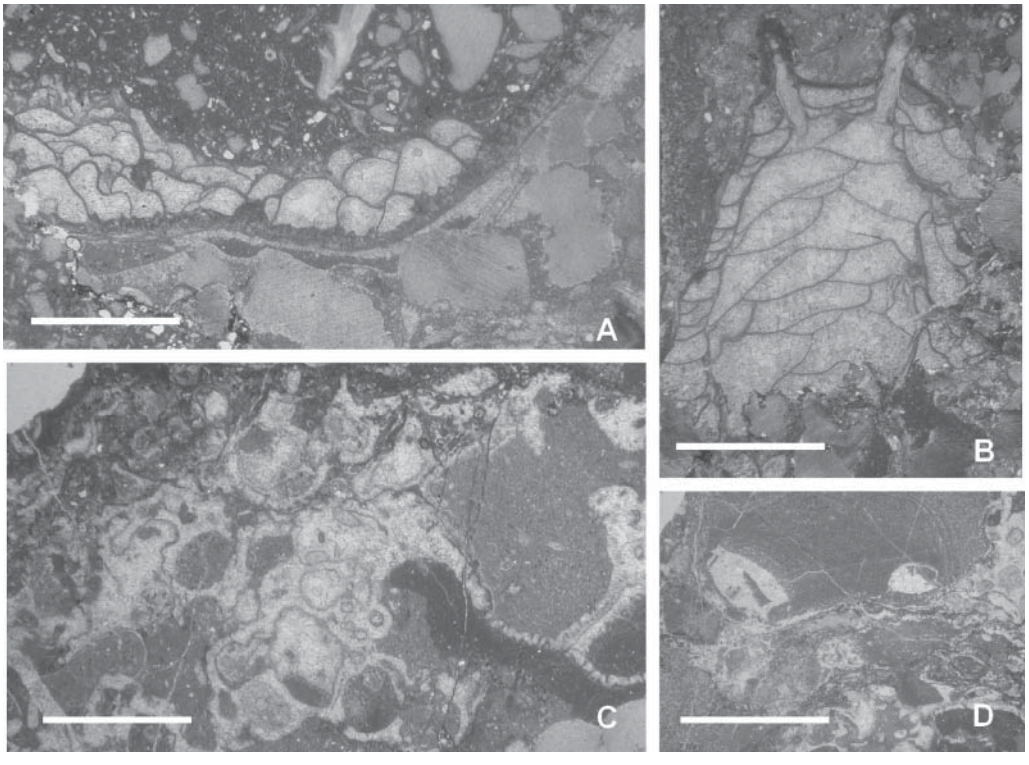

Fig. 7. (**a**) Two ventral richthofeniid valves, probably *Cyclacantharia* sp., directly attached to an encrinitic or bioclastic, slightly sandy, wackestone; note the numerous vesicles; Late Capitanian. (**b**) Another contact, although slightly modified by a small stylolite, of an encrinitic substrate of well-sorted ossicles and richthofenids; Late Capitanian. (**c**) Sphinctozoan calcisponges and encrusting bryozoa, associated with richthofeniids. (**d**) Stromatolites (top right) participating in the constructions with calcisponges (bottom). All samples from the Olinalá section, Guerrero, Mexico; Late Capitanian.

can be described using Kershaw's concept of 'parabiostrome', which takes into account the percentage of constructing organisms preserved in living position.

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