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Myths and models of rudist ecology

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ABSTRACT

Characterizing the ecology of rudist bivalves has long proved challenging, given their baroque shell shapes and the inconvenience of their extinction. Contrasting interpretations have taken hold in the literature via two different approaches. On the one hand, the appealing but simplistic hypothesis of 'rudist reefs' based on analogy with Recent tropical coral reefs has been uncritically accepted by many, ignoring both the contrasts between the organisms concerned and the differing effects on sedimentation of icehouse versus greenhouse patterns of sea-level change. Worse, untested speculations have been spun on this suspect foundation, including the hypotheses of widespread photosymbiosis in rudists and of their competitive displacement of corals. On the other hand, opposed to such myth-making is an approach that respects the primacy of evidence. Here, synthetic interpretative models of rudist formations are built up from all circumstantial considerations and iteratively tested for compliance with field and laboratory observations. This process involves collating evidence ranging from well-supported inferences concerning rudist and coral palaeobiology, and growth fabrics and sedimentological contexts, to larger scale reconstructions of facies anatomy. The picture that commonly emerges – in contrast to the classic actualistic barrier-reef model – is of opportunistic settlements of usually low relief on flat-topped, tabular-bedded platforms distally grading into flanking clinoforms, without distinct intervening reefal edifices. Opportunities to test such synthetic models are provided by exceptional outcrops that display the full panorama of facies relationships. The latter is one of many achievements of detailed field studies over many years by the 'Ramon Salas School' in the Maestrat Basin.

KEYWORDS **Rudist formations. Organic reefs. Synthetic ecological models. Greenhouse world.**

INTRODUCTION

Bizarre-looking extinct organisms have long been popular subjects for imaginative 'Just-So' stories. As late as the 1960s, for example, after reviewing the fossil record of dinosaurs a popular book of respected provenance concluded:

'Taken together, these facts mean that old and tried stocks (exhausted perhaps by evolutionary activity) and those like the Ceratopsia that were very specialized were suddenly faced with changing environmental conditions that demanded new efforts from them at the very time they were unable to give them. It is not surprising that the dinosaurs died out in the circumstances' (Swinton, 1962, p. 36)

Today, with improved understanding of evolution and extinction, misconceived ideas of 'racial senility', such as this, are no longer taken seriously (Benton, 1990; Brusatte *et al.*, 2015) and are dismissed as unscientific myths.

Yet other narratives, just as speculative but concerning less critically scrutinized groups, still pervade the scientific literature. For example, the extinct rudist bivalves –of famously baroque morphology (Skelton, 2018)– have often been portrayed as having displaced corals to become the principal 'reef builders' of the Cretaceous (Fig. 1; *e.g.* Cowen, 1988; Kauffman and Sohl, 1974; Kauffman and Johnson, 1988; Stanley and van de Schootbrugge, 2009; Stanley and Lipps, 2011). The key to this purported ecological take-over, according to those authors, was the acquisition of photosymbiosis by rudists, which conferred on them a capacity for rapid upward growth that enabled them to outcompete corals in constructing 'reef frameworks'.

Plausible though this scenario may sound, it relies entirely on speculatively connecting two uncontroversial but independent observations: first, that 'rudist (or 'coral-rudist') formations' (*sensu* Masse and Philip, 1981), which contain abundantly clustered rudist shells, with or without corals, and associated debris (Fig. 2A), formed in carbonate-dominated shallow marine habitats in low-latitudes (Philip, 1998, 2003; Simo *et al.*, 1993), as do tropical coral reefs today; and secondly, that exceptionally large shell sizes, similar to those attained by some rudists, are rapidly grown by certain living photosymbiotic bivalves, most notably of the genus *Tridacna* (Fig. 2B; Yonge, 1982).

Notwithstanding its still hypothetical status, this simplistic narrative of 'the rise of rudist reefs' persists as a sort of geological meme in textbooks, popular literature and social media. For example, the *Wikipedia* entry on 'Rudists' currently states 'During the Cretaceous, rudist reefs were so successful that they may have driven scleractinian corals out of many tropical environments, including shelves that are today the Caribbean and the Mediterranean', while the AI Bot '*ChatGPT 4o mini*', when asked 'Did rudists build reefs?' returned the answer 'Yes, rudists were important contributors to the formation of ancient reefs during the Late Jurassic to Late Cretaceous periods… Their unique shapes allowed them to anchor themselves to hard surfaces, such as rocks or other shells, and build complex structures that resembled modern-day coral reefs' (see also Johnson, 2002; Stanley, 1979, for example). As an earlier attempt to lay this myth to rest in a critical paper we wrote with our long-time colleague Jean-Pierre Masse 30 years ago (Gili *et al.*, 1995) has evidently met with only partial success, we feel the need to reprise its argument here in more detail.

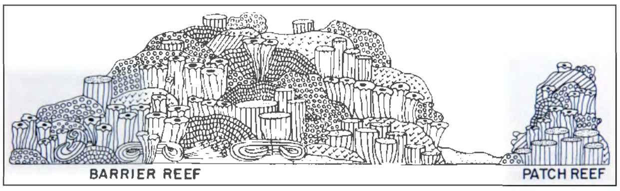

FIGURE 1. Schematic depiction of an inferred 'climax reef' composed of rudists and corals, based on 'Caribbean rudist frameworks' (reproduced with permission of the publisher from Kauffman and Sohl, 1974, top part of fig. 10).

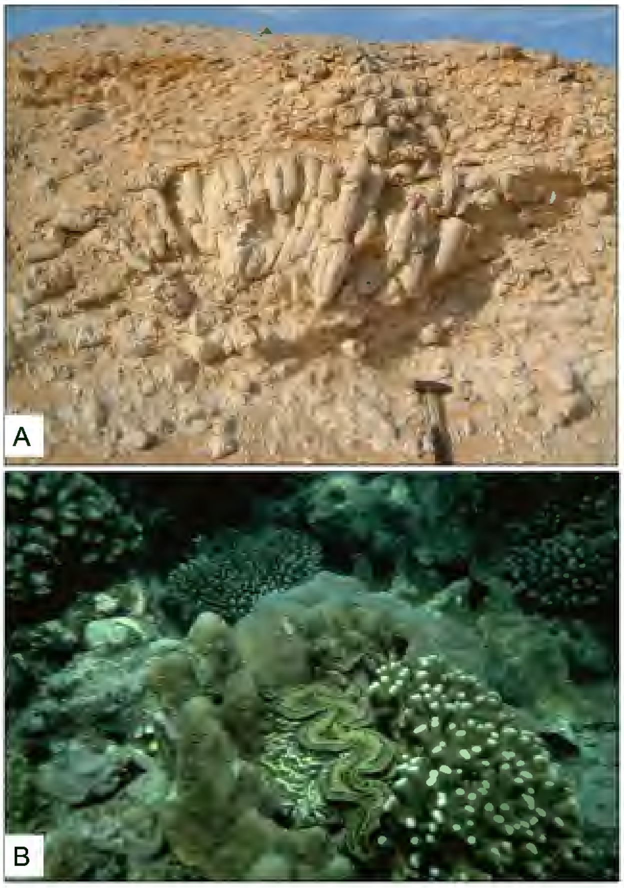

FIGURE 2. A) Rudist lithosome dominated by the large hippuritid *Vaccinites vesiculosus*, in the Campanian Samhan Formation of Saiwan, Haushi-Huqf massif, Central Oman (See Schumann, 2000, for locality details). Hammer is 35cm long. B) Live *Tridacna* sp. (lower centre) nestling amidst colonial corals, at about 3-4m depth, in patch reef, Chole Bay, Mafia Island, Tanzania. (Photos by Peter Skelton).

The reader may wonder why we offer this polemic in a volume dedicated to Ramon Salas. We do so not because the topic was one he has been particularly concerned with, but more in homage to his characteristic style of geological research. Through cautious and carefully questioning observation in the field and laboratory, he has always patiently allowed the rocks to 'tell their own story', rather than setting out to impose any preconceived explanatory model on them –a wise working approach that he has successfully passed on to his fortunate students, together with judiciously selected field areas for their investigations. We would all do well to emulate his style in our own studies.

THE PROBLEMS OF THE PALAEOECOLOGICAL MYTH

Attempts to characterize ancient communities from the fossil record are frequently based on superficially similar Recent (‘actualistic’) examples, by appeal to the principle of geological uniformitarianism –a ‘broad-brush’ approach that can prove misleading on closer analysis (Skelton, 1986).

There are two potential ‘Achilles’ heels’ to such simplistic comparisons (enough for them to fall over!): i), vague and/or inconsistent definitions, which defy objective verification of compared examples; and ii) differences in the longer-term historical contexts in which they developed.

The problem of definition

Borrowing vernacular terms for technical descriptions often gives rise to confusion through diverse and inconsistent usage, and the term ‘reef’ –derived from the Old Norse ‘*rif*’ (Heckel, 1974) for any shallow submarine ridge potentially hazardous to navigation– is no exception. We focus here on those examples in which skeletonized organisms have played a constructive role, termed ‘organic reefs’. Many different kinds of organic reef have been described in the literature (Wood, 1999), some Recent examples of which are described below to illustrate their variety, with their attributes summarised in Table 1:

Tropical coral/algal reefs (Fig. 3A, B) are largely associated with shallow carbonate-dominated settings. The robust outer crests of barrier-, and fringing-reefs, in particular, are built predominantly by colonial, calcified photozoan and photo-autotrophic biota (mainly corals and coralline algae, respectively), and are commonly noted to withstand normal wave-surge. Such reefs usually possess high species diversity, with numerous niches for accompanying biota provided by their complex surface structure. Hence both ‘wave resistance’ and diverse biotic composition are regarded as characteristic of such reefs. Furthermore, the need for high water clarity of their light-dependent framework-building biota largely confines their development to non-turbid, oligotrophic waters (Hallock, 1981).

However, some organic buildups, formed in other settings and sometimes referred to as reefs, are so termed only on account of their physiographic prominence, regardless of depth and latitude. The best known examples are deep-water coral ‘reefs’ (Fig. 3C; Mortensen *et al*., 2001; Sowers *et al*., 2024, though referred to as ‘mounds’ by the latter authors). These are among the largest reef systems in today’s oceans, extending over hundreds of kilometres, mostly at depths of several hundred metres, though with some reaching two to three thousand metres’ depth. They create ‘forest-like structures on the sea floor, comparable to their warm-water cousins in size and complexity. These cold-water

TABLE 1. Characteristics of a selection of different types of Recent ‘reef’

Examples Features	Tropical coral/algal reefs	Deep-water coral reefs/mounds	Oyster reefs
Physiographic prominence	Barrier/fringing reefs have shallow, steeply fronted outer rims	Form prominent mounds down to considerable depths	Dense clusters usually of low-relief in marginal marine settings
Wave/current resistance	Robust rims damp incoming waves; sheltering deeper lagoons behind	Baffling allows *in situ* sediment accumulation	Can stabilize shoreline mud or sand by frictional drag on currents
Growth fabric (see discussion below)	Superstratal frameworks rise above surrounding seafloor	Superstratal growth and encrusting fauna stabilize mounds	Low superstratal, to constratal by multi-generational over-growth
Clonal vs., aclonal development	Colonial stony corals create main framework	Colonial stony and soft corals provide main framework	Aclonal, shell-on-shell encrustation
Trophic status of main constructional biota	Photosymbiotic ‘hermatypic’ corals and coralline algae predominate	Heterozoan ‘ahermatypic’ colonial corals predominate	Heterozoan, suspension-feeding bivalves
Biodiversity	Many species of colonial corals: complex surfaces host highly diverse associated biota	Few species of branching corals, with diverse associated fauna	Oysters usually monospecific, though may host diverse inter-shell crevice fauna

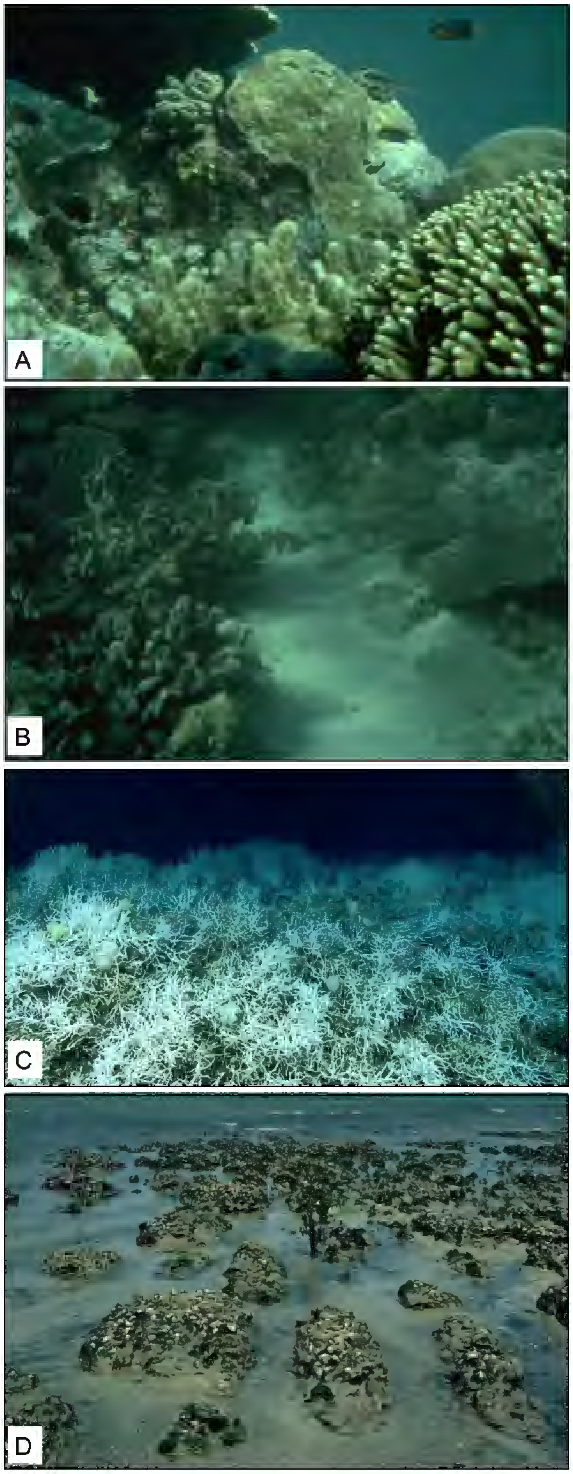

FIGURE 3. A, B) Coral reef in about 3-4m depth in patch reef, Chole Bay, Mafia Island, Tanzania, showing metre-scale superstratal growth (A) and bioclastic sand channel (B); C) Deep-water coral reef dominated by stony coral *Desmophyllum pertusum* between 754 and 826m depth, Blake Plateau Knolls, Southeast US Continental Margin (Location: Lat= 29.65001042°, Long= -78.46918893°). Photo from *Okeanos Explorer* expedition dive 04 off the coast of Florida, 2019; D) Oysters superficially encrusting channelled, partially cemented sand surface, Chole Bay, Mafia Island, Tanzania. (Photos A, B, D by Peter Skelton; C Image source: NOAA, 2019.

reefs and structures act like islands in the normally flat, featureless and muddy surroundings and harbour a distinct and rich ecosystem, providing niches and nursery grounds for a variety of species, including commercial fish species' (Freiwald *et al.*, 2004, p. 1).

Yet other, non-colonial sessile benthic metazoans may also congregate in dense clusters –such as 'oyster reefs' (Fig. 3D), which can build from small clusters attached to localized hard surfaces to extensive, low multigenerational mounds of mutually attached shells in intertidal to subtidal waters along muddy to sandy shorelines (Thurston *et al.*, 2024; see also the well-illustrated blog by Diaz De Villegas, 2010).

One further example that must be mentioned is that of the 'Great Pearl Bank Barrier' in the southern Arabian Gulf (Fig. 4; Hughes, 1997). Though described as a 'bank barrier complex' rather than as a reef, it is particularly relevant to the present discussion as it has been explicitly proposed as a suitable analogue for certain rudist formations. Lying at water depths of less than eight metres and extending for some 200km between the Qatar Peninsula and Abu Dhabi, this irregular submarine ridge, up to 50km wide, consists predominantly of molluscan debris. Much of this debris is derived from bivalves, notably including clusters of large, byssally attached pen shells (genus *Pinna*), which live partially embedded in the loose sediment with the posterior feeding margin of their shells exposed above its surface (Fig. 5 shows examples from Spain, associated with a sea-grass meadow). Clusters of the eponymous 'pearl oysters' (genus *Pinctada*) are especially concentrated lying prone in the more wave-swept areas of the bank.

Examples of apparently reef-like bodies from the geological record present the additional challenges to interpretation of unravelling the cumulative effects of deposition, erosion and biotic reworking, and diagenetic

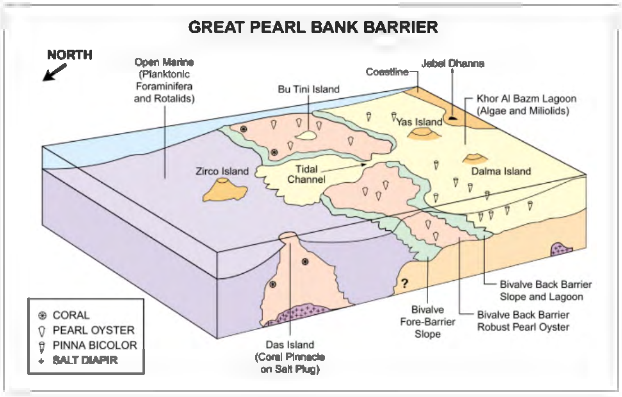

FIGURE 4. 'Great Pearl Bank Barrier' model (adapted from Hughes, 1997, fig.7, with permission of the author).

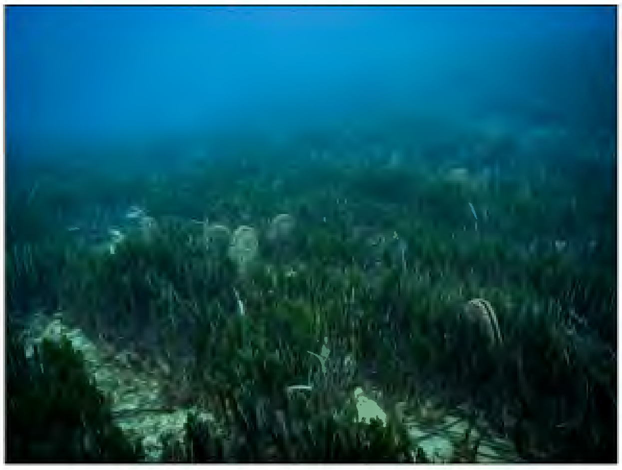

FIGURE 5. Endobyssate *Pinna nobilis* in life, partially implanted in sediment, in sea-grass (*Posidonia oceanica*) meadow, Calpe, Alicante Province, Spain (photo courtesy of Sebastián Hernandis).

modification or destruction of skeletal fabric. Such bodies have incorporated many different kinds of organisms at different times, for example, stromatolites, calcareous algae, sponges, stromatoporoids, benthic foraminifers, bryozoans, bivalves, vermetid gastropods, serpulids and others, besides corals (see Wood, 1999, for an extensive review).

There have been several attempts to distil general definitions of 'reefs' from such diverse examples. Some authors have sought to include 'wave resistance' as a diagnostic criterion, including Heckel (1974), who proposed that a reef be defined as:

> '…a buildup that displays i) evidence of a) potential wave resistance or b) growth in turbulent water which implies wave-resistance, and ii) evidence of control over the surrounding environment'. (Heckel, 1974, p. 96)

Sounding a more cautious note concerning this first criterion, Longman (1981) remarked:

> 'However, different facies must occur in ancient reefs that lacked rigid organic frameworks such as the Palaeozoic bryozoan and/or crinoid mounds, Late Paleozoic phylloid algal mounds, Cretaceous rudistid banks, and early Tertiary *Nummulites* banks.' (Longman, 1981, p. 9)

Recognizing the difficulties involved in establishing wave-resistance in fossil examples, Wood (1999, p. 4-5), proposed, more simply, 'a discrete carbonate structure formed by *in situ* or bound organic components that develops topographic relief upon the sea floor', while Riding (2002, p. 165) proposed, even more broadly, 'calcareous deposits created by essentially in place sessile organisms'.

Two definitional issues that stem from such discussions concern the meaning of 'framework', in relation to wave-resistance, and the question of spatial scale.

Framework, conceived as an organically grown self-supporting infrastructure (Insalaco, 1998), is the product of a dynamic interplay between benthic skeletal growth, binding and sedimentation.

Given the diversity of modes of skeletogenesis, of types of sedimentary infill (though carbonate sediments naturally predominate) and of kinds of binding (organic and/or cement), there is immense scope for variation in the resulting fabrics (Rosen, 1991). However, two end-member genetic categories –or 'growth fabrics'– can be distinguished (Gili *et al.*, 1995; Insalaco, 1998; Wood, 1999):

Superstratal growth fabrics (Fig. 6A) are produced where self-supporting skeletal structures grow so as to rise substantially (~metre-scale or more) above the contemporaneous surrounding and interstitial sedimentary surface. They necessarily involve truly self-supporting frameworks (*sensu* Insalaco, 1998) and indeed play an important role in generating the wave-resistant frontal crests of Recent tropical coral/algal barrier reefs.

Constratal growth fabrics (Fig. 6B), by contrast, are produced where surrounding and interstitial sediment accumulates more or less in tandem with skeletal growth, as a result of baffling, or sheltering from winnowing of *in situ* bio-eroded skeletal debris. Progressive sinking into soft substrata may also be involved (in mud-based oyster reefs, for example). Hence, skeletal projection of live individuals above the sediment surface remains limited (cm to decimetre-scale) –though sufficient at least for suspension feeding from the overlying water. The extent of projection naturally varies with ambient current activity. These partially embedded growth fabrics are thus essentially sediment-supported –lacking exposed, self-supporting framework. They are most commonly associated with the development of oyster reef-like bodies or sedimentary banks of bioclastic debris colonized by sessile shelly epifauna, as in the Great Pearl Bank Barrier (Fig. 4; Hughes, 1997).

The development of these contrasting growth fabrics appears to be influenced by the reproductive biology of the main skeletal benthos involved. In particular, superstratal growth fabrics tend to be dominated by colonial clonal organisms –hermatypic corals being the prime example in the Recent. This is perhaps not surprising in so far as coloniality allows the indefinite and variable growth of branching and projecting structures that can stably overgrow their foundations, conferring competitive advantage in the occupation of localized hard substrata (Jackson and Coates,

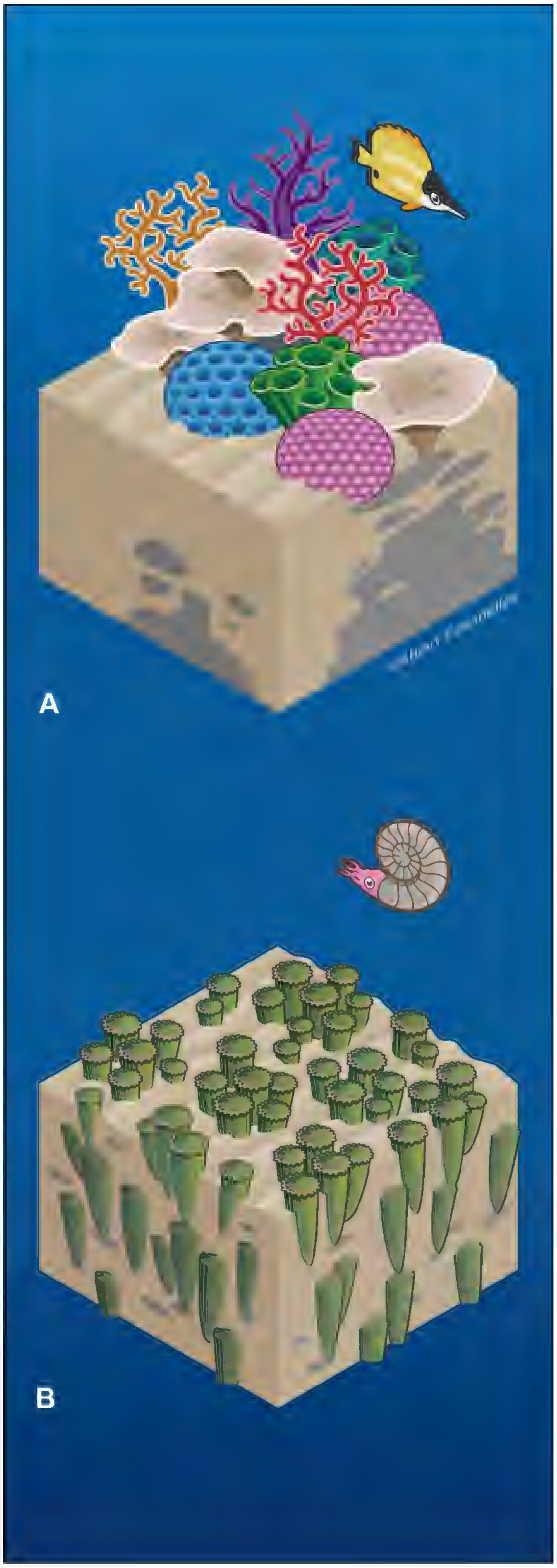

FIGURE 6. Growth fabrics of sessile shelly benthos: A) Superstratal; B) Constratal. (Artwork by Albert Casanelles; adapted from Gili *et al.*, 1995, fig. 15).

1986; Wood, 1995). Moreover, natural selection could be expected to favour cooperative interaction, including fusion, between genetically identical neighbouring projections or even previously divided colonies for mutual architectural benefit. By contrast, notwithstanding any advantages gained from clustering (resisting predation, for example), the potential for competition always remains in principle between closely clustered aclonal –hence genetically distinct– individuals. Such competition may inhibit the construction of highly integrated, hence robust free-standing frameworks.

Another issue, that of the relationship between photosymbiosis and reef development, is complex (Wood, 1999, Ch. 8), but it is worth noting here that whereas the majority of frame-building colonial scleractinian corals in Recent tropical coral/algal reefs are photosymbiotic (Campoy *et al.*, 2020), reef-associated photosymbiotic bivalves such as *Tridacna* and *Hippopus* mainly just nestle within coral frameworks (Fig. 2B), although they can form localised mounds (‘*mapikos*’), besides contributing abundant shell debris (Gilbert *et al.*, 2006; Neo *et al.*, 2015).

Spatial Scale bears on the origin of relief. On the metre- to decametre-scale of local communities, such as a patch reef, or of a single bioherm in a geological context, ‘prominence’ is usually regarded simply in terms of bioconstructional elevation above the local sedimentary surface. From a larger, platform-scale perspective, however, the prominence of a reef-tract relative to neighbouring environments, such as lagoons, may have been to a large extent inherited from antecedent topography, such as karst towers or fault-generated scarps (*e.g.* Fig. 7; Longman, 1981; Purdy and Winterer, 2001; Purdy and Gischler, 2005; Winterer, 1998). This introduces the consideration of longer temporal scales, to which we turn next.

Differences in longer-term depositional context

The eustatic cycles that provide accommodation for shallow marine sedimentation have not remained consistent

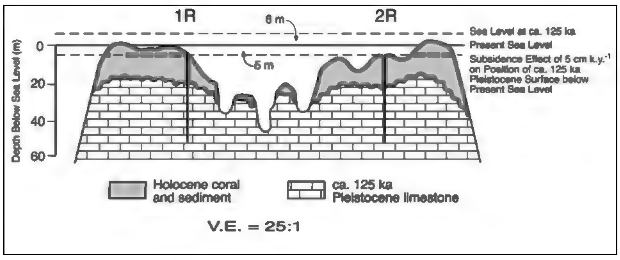

FIGURE 7. Pleistocene reef growth on antecedent karst promontories (adapted from Purdy and Winterer, 2001, fig. 14B, under GSA ‘Fair Use’ permission).

in amplitude, but have, rather, been modulated by long-term climatic changes. In particular, the amplitudes of 4th/5th order cycles (falling within time-frames of tens to hundreds of thousands of years) have varied widely between icehouse and greenhouse climatic periods. The corresponding thicknesses of depositional cycles typically reach many tens of metres during icehouse periods, due to the waxing and waning of polar continental icecaps, but only a few (mostly <10) metres during warm, greenhouse periods (Fig. 8; Tucker, 1993).

These variations in amplitude have in turn governed patterns of deposition, and particularly of reef development, on carbonate platforms. Whereas Recent tropical barrier reef rims have in many cases grown perched upon the inherited relief of karstic foundations, as noted above (Fig. 7; see especially Purdy and Winterer, 2001), Cretaceous carbonate platforms, for example, are typically composed of stacked tabular beds of wide extent, incorporating relatively thin rudist and/or coral lithosomes, each usually only a few metres thick, grading distally to inclined marginal platform-slope beds, without intervening rims (Bover-Arnal *et al.*, 2011; Carannante *et al.*, 2007; Simone *et al.*, 2003; Skelton, 2003; Skelton and Gili, 2012).

An additional point worth noting in this context is the effect of differential sedimentary compaction on the appearance of fossil reef-like bodies (‘stratigraphic reefs’ of Heckel, 1974), which may amplify original relief (Hunt *et al.*, 1996; Rusciadelli and Di Simone, 2007).

SO, WERE RUDISTS ‘REEF BUILDERS’?

A problematic corollary of attempts to gather so many very different examples, such as those cited earlier, under an all-purpose general heading of ‘reefs’ is the danger of implying that they all share some distinct but undefined essence of ‘reefiness’. Features that are regarded as typical of one kind of ‘reef’ may implicitly –though erroneously– be supposed to be shared by others. This is not merely a theoretical concern: for example, some studies of Urgonian platforms (of primarily sedimentological focus) casually refer to their rudist associations as being ‘photozoan’ (*e.g.* Bodin *et al.*, 2006; Föllmi and Godet, 2013) –hence, by implication, presumed to have been dominated by photosymbiotic taxa, by analogy with extant hermatypic coral reefs. That assumption is, however, at best untested and indeed controversial, as pointed out by Steuber *et al.* (2023) and Michel *et al.* (2023). Hence, acceptance of any generalized definition of reefs comes at the cost of an inability to reliably infer any shared characteristics other than those already cited in the definition.

As far as so-called ‘rudist reefs’ are concerned, however, it is analogy with Recent tropical coral/algal reefs that was explicitly postulated by the authors of the speculative narrative referred to in the Introduction. Hence, our critical discussion here is limited to that particular comparison. Whether or not rudist formations can otherwise be regarded as ‘reefs’ under more generalized definitions becomes merely a matter of arbitrary classification, unrevealing of any useful further insights into their character.

FROM MYTH TO OBJECTIVE SCIENTIFIC MODELS

To avoid the definitional and contextual confusions concerning fossil ‘reef-like’ bodies described above it is necessary to deconstruct given examples into discrete aspects of composition and history that can be objectively characterized from observable evidence. Thus, with respect to the history of rudist formations we can investigate four main aspects: i) rudist autecology, especially concerning reproductive strategies, modes and rates of shell growth and trophic ecology; ii) growth fabrics and biodiversity of rudist congregations; and iii) larger scale stratal relationships, reflecting the depositional contexts in which rudist formations developed.

From these three aspects, *synthetic* models of what rudist associations were like in life can be built descriptively ‘from the ground up’, so to speak, instead of being speculatively straightjacketed in the garb of today’s reef-building corals.

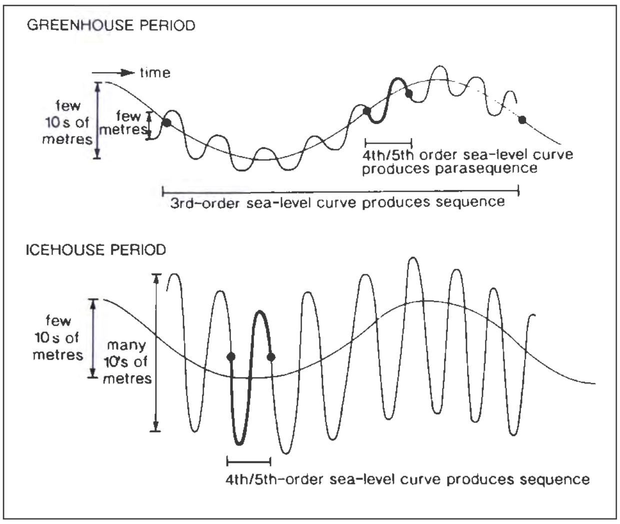

FIGURE 8. Schematic representation of greenhouse vs., icehouse eustatic cycles, showing contrast between small amplitude 4th/5th order oscillations in greenhouse periods and large amplitude oscillations caused by waxing and waning of continental glaciers during icehouse periods (adapted from Tucker, 1993, fig. 4.7, with permission of the author).

Finally, iv) to test the coral replacement hypothesis, the comparative stratigraphical records of rudist and coral associations must be considered.

The key methodological point is thus the primacy of identifying evidence relating to specific testable hypotheses, instead of random observations being cherry-picked to suit preconceived general hypotheses (‘confirmation bias’).

Rudist autecology

Reproduction. Clonal reproduction is exceedingly rare in living bivalves (Breton *et al.*, 2018), so we may assume by default that rudists were aclonal. Evidence is lacking for any rudists being strictly colonial, despite their frequently gregarious habits (Skelton, 1979) –unlike corals. While limited prodissoconch size data are consistent with either planktotrophy or brooding, evidence for wide dispersal of many rudist species suggest most were planktotrophic (Gili and Götz, 2018). Preferential aggregation of conspecific spat in some rudist taxa, at least, strongly hints at the deployment of biochemical attraction of recruits, as in living gregarious sessile bivalves such as mussels and oysters (Hennhöfer *et al.*, 2014).

Shell morphology. Despite the enormous morphological diversity of rudists, Skelton and Gili (2002) identified three broad categories of ‘ecological morphotype’, based on how the commissural growth margin of the attached valve was positioned relative to the substratum during growth –elevators, clingers and recumbents (Fig. 9; Gili *et al.*, 1995; Gili and Götz, 2018, the latter with extensive illustration of examples and discussion of their association with different carbonate platform facies). This tripartite scheme has been widely adopted in the rudist literature, testifying to recognition of its utility, though more detailed specific case studies could further improve its value. For example, facultative adoption of recumbent growth by some normally elevator rudist species (*e.g.* Skelton and Masse, 1998), points to a capacity for opportunistic switching of growth mode in response to changing sedimentation. Much scope also remains for recognizing subtler links between developmental variation and environmental differences (*e.g.* Gili *et al.*, 2023; Korbar, 2007). The elevator and recumbent morphotypes in effect represent different strategies for occupying unconsolidated sedimentary substrata, whereas clingers are more suited for exploiting firmer, or hard surfaces.

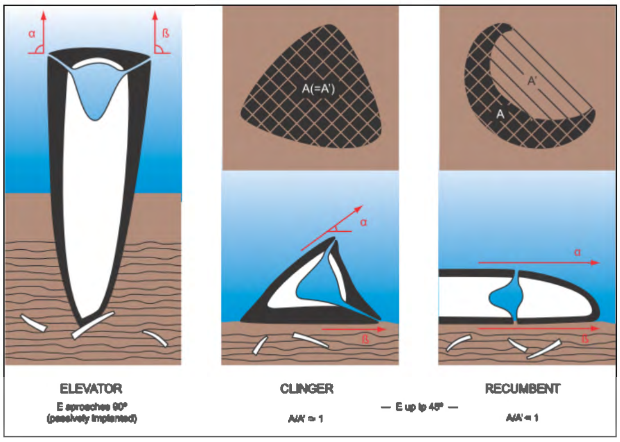

FIGURE 9. Ecological morphotypes of rudists. Shells shown in diagrammatic vertical section for all three types, together with plan views (above) of clinger and recumbent, with basal area of contact with substratum (A) indicated in each by cross-hatched ornament and virtual area of support (A’) by single diagonal ornament. Mean angle of elevation of attached valve rim, E, is mean value of maximum [α] and minimum [β] inclination of external valve margin (adapted from Gili and Götz, 2018, fig. 1).

Shell growth rates. Sclerochronological studies of cyclic isotopic variations preserved in the calcitic outer shell layer of rudists have been investigated by Steuber (2000), who found annual rates of shell accretion reaching up to 54mm/annum in some elevator rudists. It is likely that some giant recumbent rudists grew even more rapidly (Gili and Götz, 2018), though unfortunately the calcitic outer shell layer in these forms is too thin to allow reliable isotopic analysis.

Trophic ecology. As noted in the Introduction, the ‘rudist reef’ narrative relied in part upon the assumption that the exceptional size of (some) rudists was linked with possession of symbiotic zooxanthellae. However, although light-enhanced calcification is well documented in certain living zooxanthellate bivalves (including *Tridacna*), as well as in corals, not all photosymbiotic taxa habitually grow to large size (*e.g.* the Heart Cockle *Corculum*; Kirkendale and Paulay, 2017), nor are high rates of skeletal growth exclusive to zooxanthellate taxa (Steuber, 2000; Wood, 1999).

Demonstrating photosymbiosis in fossil metazoans, and particularly rudists, has in fact proved notoriously difficult. For example, Vogel (1975) compared the ‘needle-shaped’ prismatic microstructure he observed in the thin upper (left) valve of the radiolitid *Osculigera* to that seen in the posterior ‘windows’ of *Corculum*, which transmit light to internally housed symbiotic zooxanthellae (Kirkendale and Paulay, 2017). He thus accepted the possibility of *Osculigera* having been similarly adapted. Yet the microstructure described in the latter is no more than the typical fibrillar prismatic calcite of the outer shell layer seen in all rudists (Skelton, 2018). Lacking further specific modification to form lens-like structures similar to those in *Corculum* (Kirkendale *et al.*, 2021), *Osculigera* thus stands only as a tenuous candidate for photosymbiosis.

For rudists, the only well-substantiated case for photosymbiosis made to date is for the Late Cretaceous genus *Torreites*, based on ultra-high (sub-daily) resolution multi-proxy trace element and isotopic chemical records preserved in its calcitic outer shell layer (de Winter *et al.*, 2020). Indeed, this exceptionally modified hippuritid genus had already been singled out as a likely contender for photosymbiosis, because of the clear modification of its valve margins to expose mantle tissue, similarly to *Tridacna* (Skelton and Wright, 1987).

Otherwise, no such convincingly corroborated case for photosymbiosis has yet been made for any other rudist taxon. So, by default, most may be interpreted as having been heterotrophic –on present evidence at least (Skelton, 2018). Hippuritids, in particular, other than *Torreites*, possess pore-fed radial canals in the left (upper) valve that are most simply interpreted as a filter-feeding system (Schumann, 2010; Skelton, 1976). Further support for the latter view comes from flume-tank experiments showing that the preferentially downstream-oriented inclination of clustered hippuritid shells frequently observed in the field (Fig. 10A; *e.g.* Gili, 1992; Grosheny and Philip, 1989; Skelton *et al.*, 1995; Vilardell and Gili, 2003) would have had the effect of maximising the combined supply of particles carried in the main flow plus those re-suspended from the sea-floor by leeside eddies to the porous left valve feeding surfaces at the tops of the shells (Fig. 10B, C; Gili and LaBarbera, 1998). Hence, the frequently repeated suggestion that photosymbiosis was widespread among rudists (*e.g.* Cowen, 1983; Dubicka *et al.*, 2024; Kauffman and Johnson, 1988; Seilacher, 1998; Vermeij, 2013; and, with qualification, Kirkendale and Paulay, 2017) remains unsubstantiated.

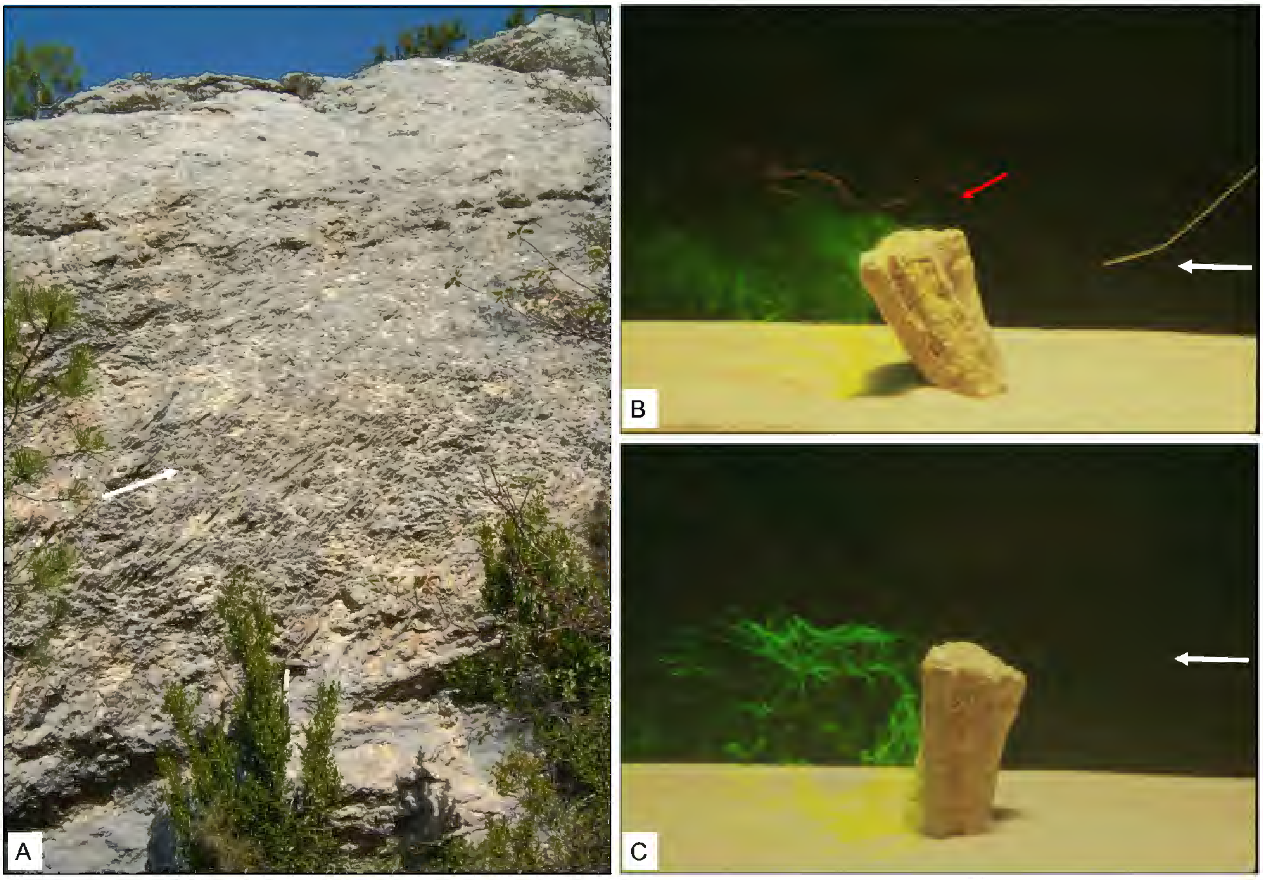

FIGURE 10. Inclined life orientation of hippuritid shells. A) Hippuritid lithosome in Santonian Sant Pere de Vilanoveta Member of Sant Corneli Formation in the southern Central Pyrenees (Skelton *et al.*, 2003; 'Bed 3' of Skelton *et al.*, 1995, fig. 4, S-T), tectonically tilted to north (left), showing hippuritid biostrome in N-S section, with rudists inclined towards south (to right), so facing away from incoming currents from basin (white arrow). B, C) Observations in a flow tank located in the Department of Geophysical Sciences of University of Chicago (USA). In both figures, flow is from right to left at a speed of about 10cm/s (white arrows). Diameter of the right (attached) valve is 3cm. B) Hippurites inclined downstream. The mainstream flow (red) separates from the top of the specimen at the leading edge (arrowed in red). The top of the specimen is covered by a separation bubble fed from the climbing vortex generated behind the specimen (green), supplying the upper (feeding) surface with a mixture of both re-suspended food particles and those incorporated from the mainstream flow. C) Hippurites in vertical orientation. Note that the helical vortex carrying fluid up the back of the specimen (green) here detaches from the downstream rim of the specimen, so does not bathe the top of the specimen (the same holds for specimens inclined upstream). (Photo in A by Peter Skelton; B and C from work of Gili and LaBarbera, 1998).

Growth fabrics and biodiversity

Most rudists were gregarious, especially so in the Late Cretaceous when many elongate conical to cylindrical elevator hippuritid and radiolitid congregations generated biostromes (Fig. 10A) that could spread across many square kilometres of platform tops (Fig. 11A). Densities of substrate coverage achieved within autochthonous clusters of rudist shells vary from loose (~50-60%; Fig. 11B) to dense (80-90%; Fig. 11C) (Gili and Götz, 2018). The clusters were stabilised during growth partly by mutual attachment of shells (Fig. 11D; Götz, 2007; Hennhöfer *et al.*, 2012, 2014) and partly through their progressive implantation in simultaneously accumulating sediment (Gili, 1992; Gili and Skelton, 2000; Grosheny and Philip, 1989; Philip, 1972; Skelton *et al.*, 1995; Vilardell and Gili, 2003).

Philip (1972) gives a vivid description of the multigenerational genesis of such a biostrome:

'...*d'abord les individus de la premiure gŭnŭration se fixent sur des dŭbris disponibles a la surface du sŭdiment, ensuite ceux des gŭnŭrations suivantes se fixent sur les coquilles dŭja en place … La colonie croot ainsi lentement en hauteur et sa stabilitŭ est assurŭe par l'enracinement des coquilles pionniures au sein du sŭdiment dans lequel elles sont peu a peu enfouies et qui jouent ainsi le rǿle de support*' (Philip, 1972, p. 214).

['…at first the individuals of the first generation attached to debris available on the sediment surface, then those of following generations attached to the shells already in place … the colony thus grew slowly in height and its stability was ensured by the rooting of the pioneer shells in the sediment in which they became buried little by little and which thereby provided support.']

In hippuritid congregations of relatively sheltered, shallow muddy embayments of the North-western Tethyan margin of France and Iberia, for example, much of the fine bioclastic matrix incorporated in the resulting biostromes was derived from *in situ* biodegradation of the rudist shells themselves, especially by boring clionid sponges (Fig. 12; Grosheny and Philip, 1989; Skelton *et al.*, 1995).

Evidence for the original sedimentary support of these hippuritid clusters is illustrated in Skelton *et al.* (1995), including domino-style toppling of shells following sedimentary wash-out (producing secondary 'dense horizontal fabric'), with some fallen individuals then showing curved recovery growth (Fig. 13 A-C), as well as partial projection of upright shells through lithological boundaries, indicating a minimum extent of burial achieved before the sedimentary change, as well as erosional decapitation of some upright shells, around the bases of which supporting matrix had evidently become cemented prior to the erosion. Elsewhere in the succession, bioclastic floatstones attest to sporadic storm-current transport of eroded shell debris from the rudist congregations (Fig. 13D). Notwithstanding variations in clustering density, these elevator rudist congregations were thus more or less constratal in character, creating only low but extensive banks upon the broadly flat-topped platforms and shelves they inhabited.

By contrast, on the more open central Tethyan platforms of Italy and Croatia, for example, displacement of shells and widespread re-distribution of coarse to fine bioclastic debris and sediment by wave and storm currents was more prevalent, especially in exposed, high-energy settings, though thin, tabular biostromes, mostly of radiolitids, but including some hippuritids, were more frequently preserved in inner shelf areas (Korbar, 2007; Moro *et al.*, 2002; Simone *et al.*, 2003; Stössel and Bernoulli, 2000).

However, in a description of the famously well-preserved rudist biostromes in the Campanian of Saiwan in southern Oman, Schumann (2000) argued in favour of a superstratal interpretation, because of the supposedly 'very resistant' mutual attachment of shells in the dense clusters (Fig. 2A). But this relatively dense clustering was, in any case, an inevitable geometrical consequence of the expansive growth of these large shells from shared attachment sites. It need not by itself imply significant (*i.e.* metre-scale) superstratal growth. As long as projection of the upper margins of host shells was sufficient for attachment of new settlers, growth of the congregation could continue (Götz, 2007).

Nevertheless, Schumann (2000) also expressed doubt that sediment accumulation could have kept pace with the growth of the rudists. He argued that the average sedimentation rate for the formation must have been about 1cm per 1000 years, based on a stratigraphic thickness of 40m deposited over 4-5 million years, falling far below that corresponding to the growth of a 40-50cm high shell of *Vaccinites* over 20-30 years, of 'approximately 13 meters in about 1000 years' (rate conventionally normalized to m/1000 years). But such a comparison is misleading as it ignores the systematic decrease in rates of sediment accumulation recorded for increasing time intervals, resulting from compounded stratigraphical incompleteness (Sadler, 1981). Thus, although a rate of 1cm per 1000 years for 'carbonate platform and reef environments' falls within the range of values recorded by Sadler (1981, fig. 3) for time-scales of a few million years, the values shown for time-scales of just tens of years (equivalent to the life-span of *Vaccinites*) are actually of the order of 10m per 1000 years – not so different from Schumann's (2000) 13m per 1000 years, after all. Nor should it be forgotten that the relatively dense

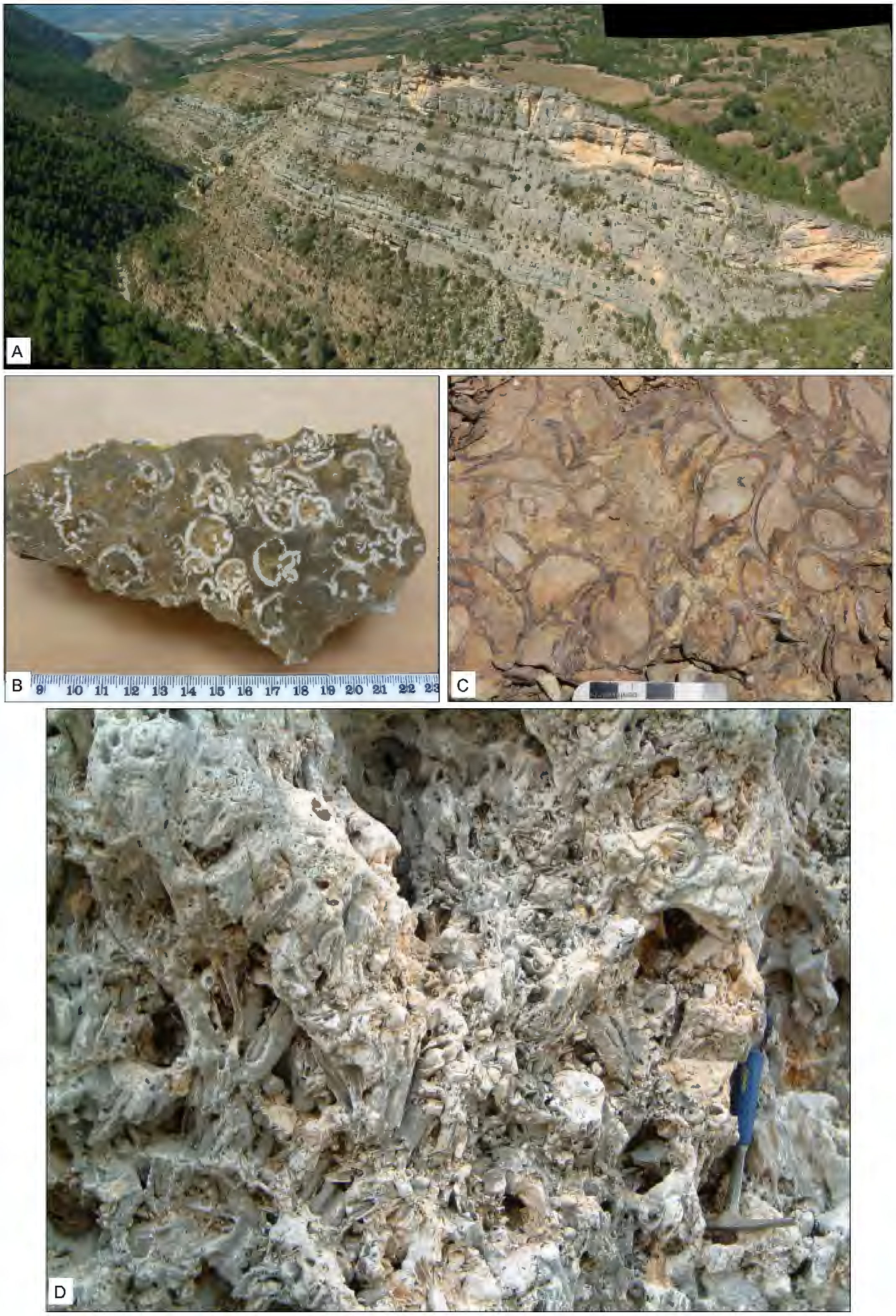

FIGURE 11. A) Tabular bedded limestones containing extensive hippuritid biostromes in Santonian Sant Pere de Vilanoveta Member of Sant Corneli Formation (blue-grey beds in upper half of main face) exposed on northern side of Riu Carreu gorge, southern Central Pyrenees (Skelton *et al.*, 2003). B, C, D) Elevator rudist cluster densities: B) relatively loose cluster of *Hippurites socialis*, Santonian of Piolenc, SE France (polished bed-parallel section, with cm scale); C) dense cluster of *Polyconites hadriani* with extensive mutual contact, uppermost lower Aptian of Las Mingachas, Maestrat Basin, eastern Iberia (Bover-Arnal *et al.*, 2011; Gili *et al.*, 2023; bed-top exposure, with cm scale); D) multiple bouquets of elevator caprinuloideids (*Coalcomana ramosa*) coalescing to form moderately dense cluster in natural vertical section, lower Glen Rose Formation (Lower Albian), Pipe Creek, 'Cycle 1' of Kerans (2005). (Photos by Peter Skelton).

clustering of the rudists would also have confined the space available for interstitial sediment, forcing yet more rapid vertical accumulation there.

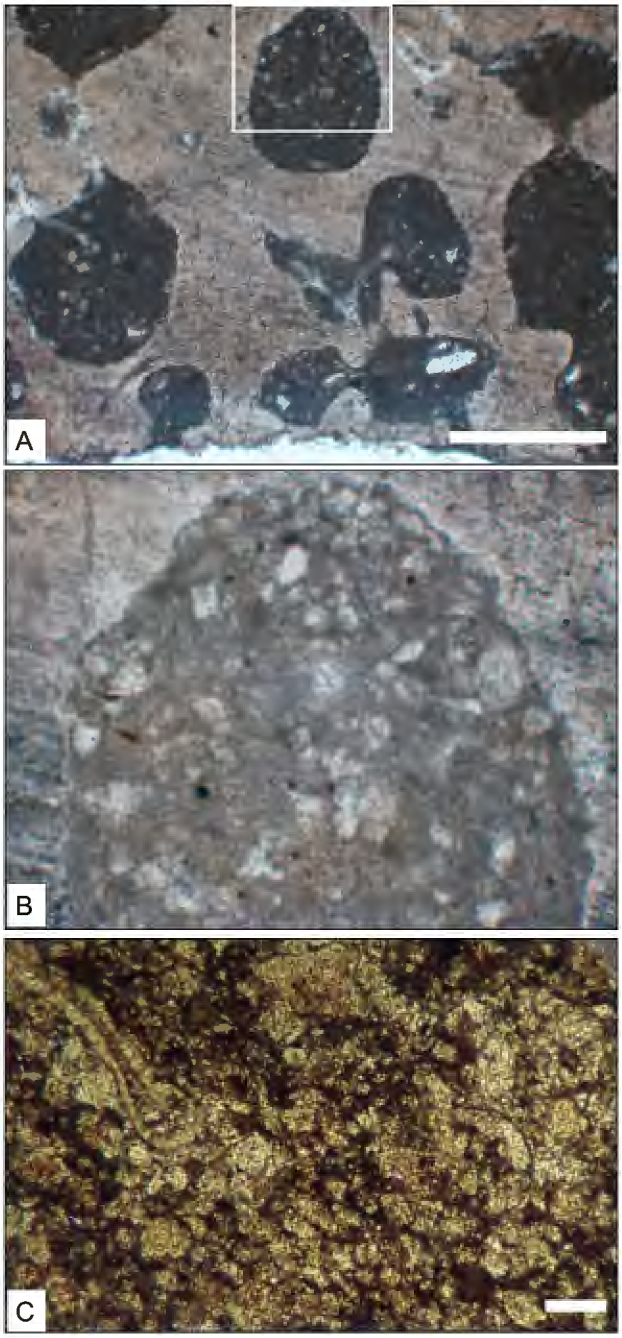

FIGURE 12. Photomicrographs of microperforations in hippuritid shells, with scalloped margins and derived rudist shell micrograins, Santonian Sant Pere de Vilanoveta Member of Sant Corneli Formation (Fig. 11A): A) Perforations in fibrillar prismatic calcite outer shell layer of *Vaccinites galloprovincialis*, scale bar, 1mm; B) Detail from white rectangle in A, showing scalloped margins typical of clinoid borings; C) Matrix of hippuritid biostrome, with abundant silt-, to very fine sand-grade rudist micrograins, scale bar, 0.1mm. (Photomicrographs by Peter Skelton).

Schumann (2000, p. 152) did acknowledge, though, that '…in spite of superstratal growth the Saiwan associations did not develop a significant relief'. Indeed, Van Steenwinkel (2018) records that 'Mapping of the facies geometries in these magnificent outcrops shows rudist factories as thin, extensive layers, rather than laterally restricted vertical mounds.' She found that two, consistent, *in situ Vaccinites* layers 0.5–2m thick could be traced over the entire outcropping area of 5 by 20km.

In the southern Pyrenees another Campanian rudist lithosome likewise dominated by a large-sized hippuritid species –in this case *Hippurites radiosus*– has nevertheless been interpreted by Boix *et al.* (2023) as resulting from progradation of a rigid reef-crest framework. They interpret the vertical succession of facies seen here as passing upwards from i), 'proximal reef slope' deposits, via ii) 'close-cluster reef' and iii), 'frame/close cluster-reef', to iv, v) back-reef 'spaced cluster reef' and 'very spaced cluster reef' fabrics (Fig. 14A shows facies units 1-3). The inferred direction of progradation to yield this succession was regarded as having been towards the SE, as shown in their figure 5C, with SE-sloping clinoforms duly indicated. However, these clinoforms are not visible in the field and were described during a field visit to the site in 2014 as being 'speculative' (verbal *pers. comm.*, Enric Vicens and Oriol Oms, 22/06/2014). Hence the relief, as well as the direction of migration of the rudist bank suggested by these interpolated clinoforms are themselves only conjectural. Figure 4 of Boix *et al.* (2023), meanwhile, includes stereoplots of the rudist orientations that indicate 'a general S/SE leaning of rudists specimens' in their Interval 3. This apparent inclination of the rudists *towards* the supposed direction of 'progradation' is surprising as it runs counter to our experience, in numerous other examples, of the tendency for such elevators to be inclined in the opposite direction, away from the open sea (*cf.* Fig. 10A, for example). So, this outcrop might alternatively be interpreted as showing the *retrogradational* spread of the lee-side flank of a hippuritid bank towards the platform interior –similarly to the model illustrated in Skelton *et al.* (1995, fig. 6). The relatively larger cumulative thickness of the lithosome at l'Espà could be attributed simply to greater accommodation being provided by more rapid, tectonic subsidence in the Campanian.

Given the tectonic isolation of the thrust sheet that contains this outcrop, Boix *et al.* (2023, p. 5) admit that 'Unfortunately, hardly any sedimentological or paleoecological data exist on the paleogeography affecting the rocks that build the Intermediate Unit, whose best locality for the study of rudists is l'Espà'. Indeed, they contradict both their own rudist orientation data and interpreted progradation, mentioned above, in their Discussion (Boix *et al.*, 2023, p. 11), where they say 'the

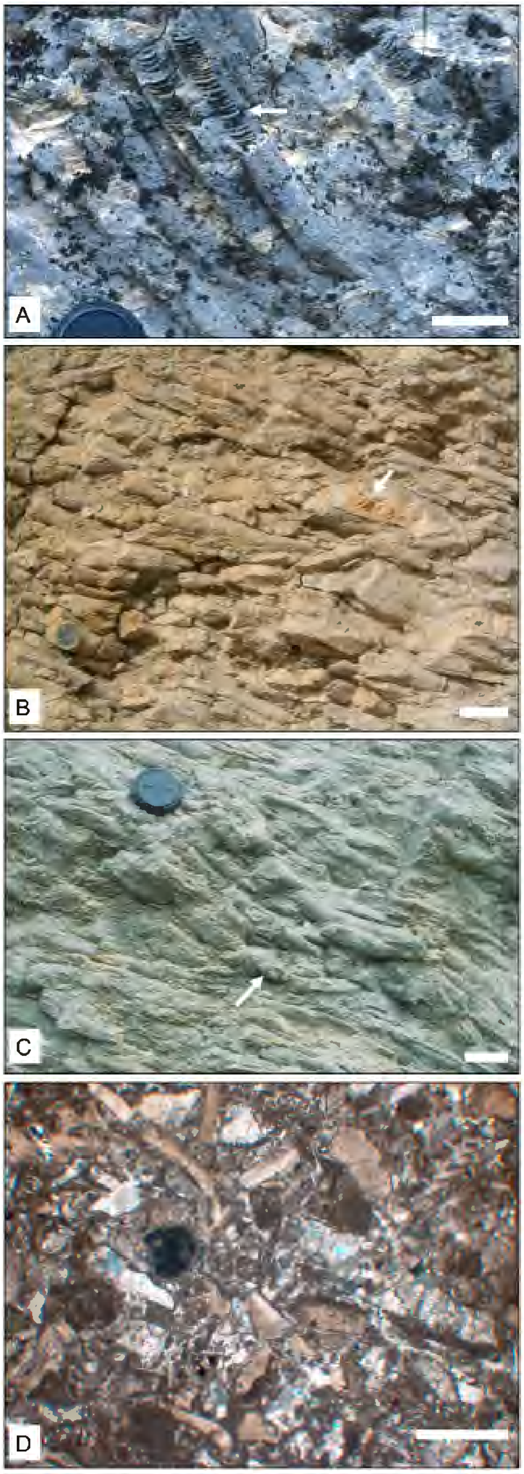

FIGURE 13. A-C) Evidence for original sedimentary support of slender hippuritid congregations in Santonian Sant Pere de Vilanoveta Member of Sant Corneli Formation (scale bars all 5cm): A) Loose cluster preserved in inclined life position (note horizontal tabulae, arrowed), with some upward curvature from slight initial toppling prior to stabilization; B) 'Dense horizontal fabric' caused by domino-like toppling of shells following washout of fine interstitial sediment (note tilted tabulae, arrowed); C) Curved recovery growth of some toppled individuals (arrowed). D) Photomicrograph of rudist floatstone (with secondary thrombolitic cementation of bioclasts); Scale bar= 1mm. (Photos by Peter Skelton).

seaward plunging of rudists towards NW (as seen in interval 3), indicates that this was also the direction of progradation'. Finally, the assertion by Boix *et al.* (2023, p. 11) 'that the reef had a rigid framework' seems again to be based only on the relatively close packing of the clustered rudists (Fig. 14B; *cf.* Schumann, 2000), as no corroborative evidence is provided for any significant superstratal growth.

Until such contradictory statements and unsupported assertions are resolved, it is not currently possible to critically evaluate the interpretation of Boix *et al.* (2023), which appears to be primarily aimed at fitting their observations to a preconceived actualistic coral barrier reef model, rather than objectively characterizing the structure of the lithosome. Hence, the claim of Boix *et al.* (2023, p. 12) that 'The obtained hippuritid reef model has a strong similarity with most coral reefs' remains questionable.

Certain Early Cretaceous rudist bioherms, especially those of the Aptian and Albian of the Caribbean Province, however, do show some significant contrasts with the Late Cretaceous examples cited above. A classic case is that of the bioherms of closely packed elevator caprinuloideids (*Coalcomana ramosa*) exposed in remarkable outcrops of the lower Albian Glen Rose Limestone in Central Texas (Fig. 11D; Perkins, 1974; Petta, 1977). In this case, the mounded form of the lithosomes is clearly visible in the outcrop, justly qualifying them as 'stratigraphic reefs' *sensu* Heckel (1974), though as Perkins (1974, p. 140) noted they incorporate some composite stacking of 'multiple organic reefs 5 to 25 feet thick and generally a few tens of yards in diameter', as revealed by internal disconformities. The main 'Wonder Hole' complex there, where the densest packing of rudists can be observed (Fig. 11D), reaches some 4m total thickness, in a mound core of 20m diameter, flanked by a broad (>100m) apron of coarse rudist rudstone, dipping away downdip on the shelf, at up to 15° in places (Kerans, 2005). This coupling of facies indeed testifies to mound growth into the zone of normal wave action.

In the core, the pattern of initial settlement and growth of the rudists appears remarkably similar to that in the hippuritid biostromes described by Philip (1972), cited earlier, with multiple bouquets springing up from scattered shell fragments (Fig. 11D) and coalescing with subsequent recruitment. Moreover, much of the fine interstitial sediment was likewise derived from clionid boring of the shells, as demonstrated by the detailed petrographic study of Petta (1977). The chief difference between the two cases appears to reflect a contrast in their respective diagenetic fates. Whereas the caprinuloideid buildup was subject to pervasive early marine cementation during growth (Petta, 1977; Kerans, 2005), the interstitial sediment accumulating in the hippuritid biostromes evidently remained loose for longer periods, hence was susceptible to occasional

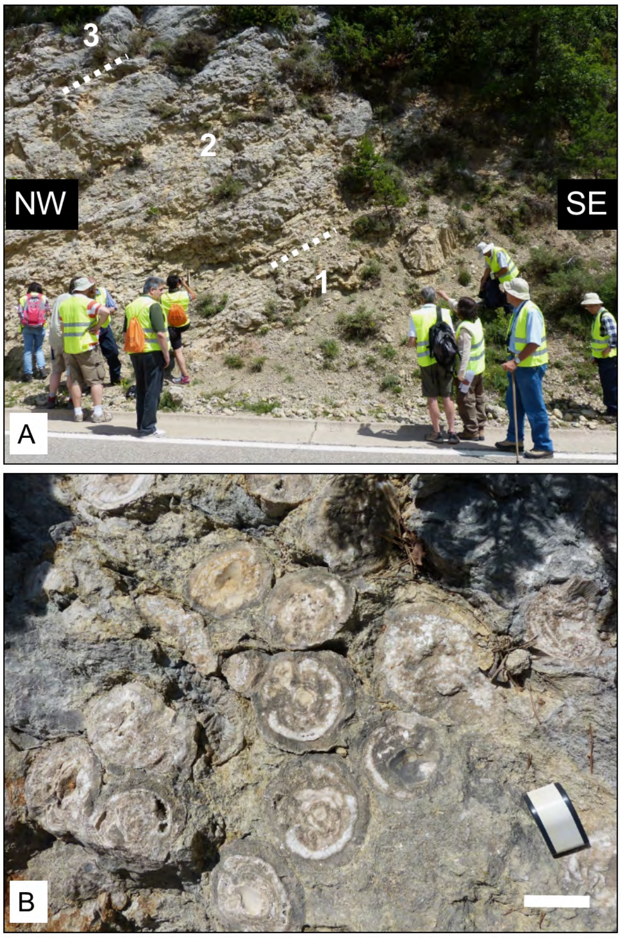

FIGURE 14. A) Road section of hippuritid lithosome at l'Espà (Campanian, southern Pyrenees), tectonically tilted to NW, with intervals 1 to 3 of Boix *et al.* (2023) indicated (1: 'proximal reef slope'; 2: 'close-cluster reef; 3: 'frame/close cluster-reef'); B) Packing density of large hippuritids in interval 3, viewed from above, scale bar= 5cm. (Photos by Peter Skelton).

washout and collapse of the rudists (Fig. 13). The former example thus soon acquired a cemented framework, while the latter did not, or at least not to the same degree. The extent of superstratal projection of the caprinuloideid framework during growth nevertheless remains unclear at present, though it seems unlikely that it could have approached the metre-plus scale achieved by living colonial reef corals by virtue of the limited apical attachment of new rudist settlers alone, without some sedimentary support.

Why such a contrast between these respective elevator congregations might have arisen –whether owing to the rudists concerned or to broader environmental reasons– is uncertain. One point worth noting, though, is that the original caprinuloidinid shells were largely aragonitic, with only a thin, skin-like calcitic outer shell layer, whereas the latter in the hippuritids was significantly thicker (Skelton, 2018). This compositional difference would in turn have affected the relative susceptibility of the bio-eroded debris derived from each to early diagenetic re-processing (dissolution and re-precipitation). Considerable scope remains for detailed petrographic investigation of this question.

In a broader context, Scott *et al.* (2007) point out that the Lower Glen Rose buildups developed some 50km landward of the early Aptian Sligo Formation shelf margin, which Kerans (2005) likened to the scale of the back-stepping in the initiation of the Shu'aiba platform margin from the preceding Thamama shelf margin in Arabia –illustrating the classic greenhouse pattern of wide lateral shifts in the layout of shallow carbonate platforms on the flooded passive continental margins of the time, in response to modest eustatic oscillations.

With regard to relative biotic diversity, that of rudist associations in general is usually relatively low, at least as revealed by autochthonous samples –certainly by comparison with Recent tropical coral reefs– and especially in the more internal platform-top biostromes of hippuritids and radiolitids. Most of the latter biostromes, as many authors have noted, are dominated by a few, or even a single rudist species (*e.g.* Fig. 15; Gili and Götz, 2018). Either their exposed surface structure was less inviting to diverse secondary settlement –or was usually only transiently available for such settlement because of the more or less constratal growth of the rudist congregations.

Larger scale stratal relationships

Large, well exposed and relatively little disturbed outcrop sections that clearly reveal carbonate platform architecture are uncommon but enormously valuable for assessing the contribution of rudist and coral lithosomes to their development (Michel *et al.*, 2023). As noted earlier, many Cretaceous examples show a proximal-distal depositional profile of a broad platform built up from stacked, metre- to decametre-thick tabular beds that steepen distally to grade into slope clinoforms, with no intervening salient rim (Fig. 16; see also Bover-Arnal *et al.*, 2012, 2015; Gili *et al.*, 2016; Martínez-Rodríguez *et al.*, 2024; Ross and Skelton, 1993; Skelton *et al.*, 2019; Tišlar *et al.*, 1998). Lenticular biostromes or low profile bioherms are most commonly developed in the outer platform-top beds, but may extend far back into the inner platform, most commonly as thin, sheet-like biostromes (Fig. 15). In some cases, however, this architecture was secondarily modified by faulting, gravitational collapse or submarine erosion at the platform margin, or through erosional incision during exceptional eustatic lowstands (*e.g.* Borgomano and Philip, 1987; Bover-Arnal *et al.*, 2024; Droste, 2010; Ferry and Grosheny, 2019; Stössel and Bernoulli, 2000).

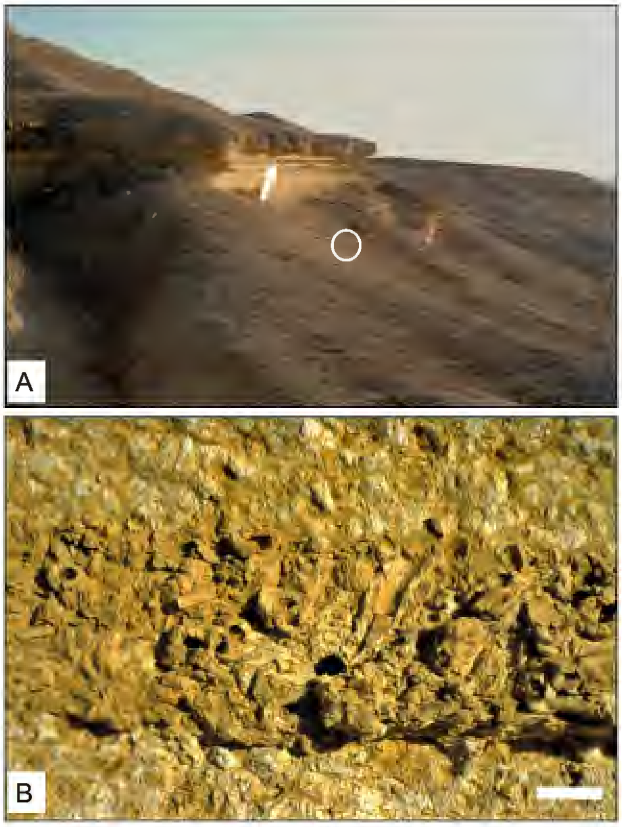

FIGURE 15. Monospecific (far-)inner platform radiolitid biostrome at top of Khanasir Limestone Member of Aruma Formation., in Wadi Itq, El Aramah Plateau, Central Saudi Arabia, ~100km NNW of Riyadh, of probable Maastrichtian age (Philip *et al.*, 2002; Skelton and El Asa'ad, 1992): A) White arrow indicates biostrome (thin dark unit, just below unconformity with resistant base of Hajajah Limestone Member), which persists for >90km along strike, person below ringed for scale; B) Close-up of biostrome in A, here composed entirely of *Durania* sp., with nodular marly limestones above and below, scale bar is 10cm. (Photos by Peter Skelton).

The key to the characteristic Cretaceous platform architecture described above was the combination of relatively ephemeral, opportunistic rudist settlement on sedimentary substrata and the lateral redistribution of shelly debris from them (*e.g.* Fig. 13D), especially on the more exposed outer parts of the platform tops (Stossel and Bernoulli, 2000). The latter effect reflects both the common lack of protective salient rims (Gili *et al.*, 2016; Martínez-Rodríguez *et al.*, 2024) and the confined bathymetric accommodation made available on the platform tops by low amplitude greenhouse eustatic oscillations (Fig. 8). Herein lies the main architectural contrast with the sustained aggradational growth of robust reefal rims shielding bucket-like back-reef lagoons, associated with the relatively larger amplitude eustatic cycles of the Recent icehouse world (Purdy and Winterer, 2001).

Besides the ephemeral nature of many rudist congregations, the lateral redistribution of shell material from them may account for much of the stark contrast found between estimated short-term rates of their *in situ* carbonate production and the longer-term calculated net rates of platform aggradation. Building on his sclerochronological analyses of individual rudist shells, Steuber (2000) estimated annual community carbonate production rates ranging from 4.6 to 28.5kg/m^2, comparing favourably with those estimated from modern coral reefs (1 to 35kg/m^2). By contrast, the longer-term maximum net accumulation rate calculated by Masse and Fenerci-Masse (2006) for the rudist communities on the Late Barremian platforms of Provence, for example, was 50kg/m^2 per 1000 years. Notwithstanding the differences in age and composition of the rudist communities concerned (Late Cretaceous in the first case and Barremian in the second), the massive three orders of magnitude difference between these two differently measured rates implies that much of the shell carbonate produced over short time intervals (~10s of years) must have been cumulatively redistributed elsewhere over multiple millennia, by, for example, sporadic storm currents or, over longer time intervals, highstand-related erosive episodes. (The cumulative effect of 'stratigraphic incompleteness' (Sadler, 1981) is again pertinent here.) The 'elsewhere', in this context, could mean on, or off the platform top – resulting in what might be termed 'sediment smearing' (once graphically described by Jean Borgomano as 'comme tartiner les sandwiches' ['like spreading the sandwiches']; pers. comm., 2001). The vast expanse of the platform-top carbonate factories together with the limited provision of accommodation space on the platforms also resulted in frequent highstand shedding of large quantities of bioclastic debris onto broad, low-angle distal bioclastic ramps skirting them (Enos, 1977; Michel *et al.*, 2023; Simone *et al.*, 2003).

This is the constantly dynamic sedimentary context in which Gili *et al.* (1995) recognized rudists as having evolved as essentially 'sediment-dwelling' organisms. Their aclonal production of widely dispersed, genetically varied planktonic larvae and the aggregative recruitment of conspecific spat by many suited them well to rapid opportunistic colonization of transiently stable surfaces on the shifting mosaic of sediments carpeting the platform tops. And their diverse repertoire of ecological morphotypes allowed them to establish broad shelly 'meadows' in varied sedimentary (and trophic) contexts, leading to the growth of low sedimentary banks, rather than superstratal reef-frameworks built up on localized hard foundations as in the preferred manner of today's hermatypic corals. Even the geometry –and the ultimate preservation– of rudist lithosomes was tightly accommodation-dependent (Stössel and Bernoulli, 2000). This biostratinomic perspective is of more than academic interest, incidentally, having important implications for the understanding and modelling of rudist-associated reservoirs. For example, Van Steenwinkel (2018)

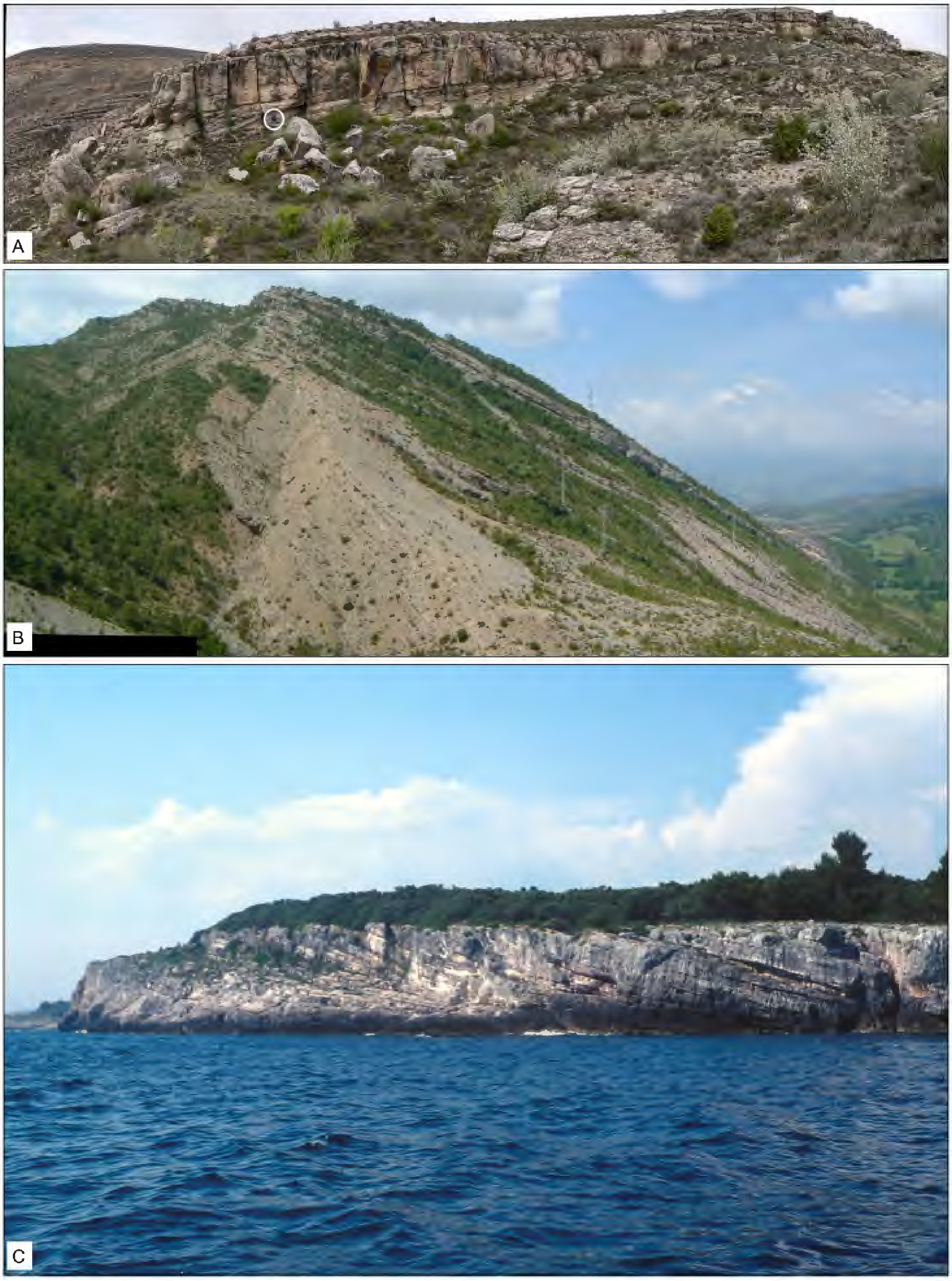

FIGURE 16. Examples of well exposed profiles of unrimmed, rudist-bearing carbonate platform to slope transitions: A) Uppermost lower Aptian Villarroya de los Pinares Formation, 'Depositional Sequence B' lowstand, SW-prograding platform to slope transition at Las Mingachas, western Maestrat Basin, eastern Iberia (Bover-Arnal *et al.*, 2011), with person for scale circled, beneath cliff at left; B) Eastern end of northern limb of Sant Corneli Anticline, in the Central southern Pyrenees, with Santonian Sant Pere de Vilanoveta Member beds (as in Fig. 11A) exposed in low cliffs at crest of hill on right, where rudist and coral lithosomes pinch out north-eastwards into slope deposits that crop out further East, across a fault situated to the right of this image (Skelton *et al.*, 2003, fig. 4A); C) Lower-middle Cenomanian prograding rudist bioclastic clinostratified body ('Facies Unit 5') exposed along a coastal cliff on Fraškulin Island, southern Istria, Croatia (Tišlar *et al.*, 1998). (Photos by Peter Skelton).

noted that 'Thick rudist units from subsurface data in North Oman previously interpreted as reefs, are most probably rather stacked cyclic layers, separated by thin, muddy intervals, as seen in cores. So, besides the huge difference in lateral continuity, the reservoir Kv/Kh is likely to be considerably lower than in a framework reef model' (see also discussion of compound mounds in Droste, 2010).

Cretaceous stratigraphic record of rudists and corals

The hypothesis of competitive displacement of reef-building corals by rudists through the Cretaceous has been criticized on both stratigraphical and palaeoecological grounds (Götz, 2003; Ross and Skelton, 1993; Scott *et al.*, 1990; Skelton *et al.*, 1997). In fact, corals remained abundant and diverse throughout the Cretaceous (Scott *et al.*, 1990), though they and rudists mostly occupied separate biotopes, with corals tending to favour deeper, more open settings, while rudists thrived on the shallow platform tops (Bover-Arnal *et al.*, 2012, 2015; Masse, 1979; Rosen *et al.*, 2002; Scott, 1988; Skelton *et al.*, 1997; Tomás *et al.*, 2008). 'Platy' corals, especially, occurred widely throughout the Cretaceous and indeed on into the Cenozoic (Rosen *et al.*, 2002). Furthermore, a close investigation of intimate growth interactions between corals and rudists in a mixed association of Campanian age, by Götz (2003), concluded that both groups benefited from their co-existence. Hence, the hypothesis of rudists 'replacing' corals still lacks any supporting evidence, so remaining entirely speculative and indeed improbable.

CONCLUSIONS

In all the respects reviewed here, rudist formations are shown to have had little in common with recent tropical coral reefs, either in terms of ecology or of the eustatic context governing their respective histories of development. The autecologies of rudists and living hermatypic corals are different (aclonal, versus clonal/colonial; and predominantly heterotrophic versus photosymbiotic). So, too, are their usual growth fabrics (constratal versus superstratal). More suitable analogues for rudist congregations might be 'oyster reefs' or carbonate banks colonized by endobyssate bivalves such as *Pinna*, although the latter lack the extreme autecological attributes of rudists.

More broadly, rudists were thus essentially sediment-dwelling forms, spreading widely across unrimmed platforms to form relatively thin tabular, lenticular or low mounded lithosomes, in contrast to recent barrier-forming reef corals, which build up narrow wave-resistant frameworks on localized hard foundations such as antecedent karstic rims –physiographic differences that have in turn profoundly influenced the respective sedimentary dynamics of the platforms themselves. Nor is there any evidence for the hypothesized competitive displacement of corals by rudists. Rather, both rudists and the corals that lived alongside them throughout the Cretaceous, along with their associated benthic biota, were adapted in their different ways for opportunistic occupation of the vast carbonate platforms that characterized the greenhouse world in which they lived– and to the development of which their own prolific carbonate production in turn contributed.

Hence the 'rudist reef' narrative, which explicitly draws a parallel with recent tropical coral reefs, turns out to be an unsupported and indeed unenlightening myth, after all. Although rudist lithosomes may still qualify as fossil 'reefs' under much more generalized definitions, little is gained from the latter beyond a mere label that is, moreover, potentially misleading (for those who uncritically pigeon-hole them as having all been 'photozoan communities', for example). To avoid the risk of such interpretative mistakes, the term 'rudist banks', used by Masse and Philip (1981) is preferable. In this regard, it is worth quoting in full a statement in the Introduction to one of the seminal discussions of 'rudist reefs' (Kauffman and Sohl, 1974, p. 401):

> 'Our collective observations reveal *no* development of true reefs –in the sense of coral reefs today– among Cretaceous rudists. The principal difference observed between them is an almost total lack of effective cementation of individual rudists by organisms which normally bind fossil and recent coral reefs into a solid, wave-resistant structure, even though binding organisms are commonly part of the rudist framework assemblage. Additional important differences are the open fabric of many rudist frameworks, with individual shells not extensively in contact' … 'and the fact that they are usually low, relatively thin lenticular structures which are comprised of one or a few generations and were never greatly elevated above the sea floor.'

Ironically, then, it seems that even one of this duo of authors was not, after all, persuaded by the other's imaginative graphic vision of a rudist 'climax reef' (Kauffman and Sohl, 1974, Textfig. 10, reproduced here as Fig. 1)!

More generally, the highly complex ecosystems that have come to occupy broad environmental settings –such as shallow marine carbonate platforms– are bound to have developed in more or less different ways through successive geological ages, given long-term changes both in the ecological characteristics of their constituent biotas and in the varying patterns of climatic and sea-level change to which they were subject. So it is naïve to expect close similarities between those of different times, especially for such different worlds as those of the Cretaceous and of today, and it is through discovering the differences between them that we will reach a better understanding of what they were really like.

In short, we therefore recommend the following research approach:

Don't uncritically impose actualistic models, 'top-down', on fossil examples, just 'cherry-picking' observations that are merely not inconsistent in support, as such attempts are likely only to result in unenlightening, even misleading myths;

Instead, build up synthetic interpretative models for fossil examples 'from the ground up', so to speak, based on multiple hypotheses concerning specific aspects and testing each in turn against field and laboratory evidence. Such a deconstructive analytical approach is more likely to yield a robust theory, *sui generis*, for each case.

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