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Paleoecology of Rudists

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PART N, VOLUME 1, CHAPTER 26B: PALEOECOLOGY OF RUDISTS

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INTRODUCTION

Rudist bivalves were variously adapted as level-bottom sediment dwellers, their diverse shell growth forms closely correlated with the nature of the substrate, allowing them to occupy a wide range of environments from areas with net sediment accumulation to areas where sediment bypassing predominated over accumulation (Skelton & Gili, 2002).

Most rudists were highly gregarious and formed vast congregations on the shallow tops and gently sloping flanks of carbonate platforms. In slightly deeper or more open settings, diverse assemblages of corals, stromatoporoids, calcareous sponges, and algae were often associated with rudist congregations within tabular bedded units, even forming dense associations (Scott, 1988).

In this section, we review the paleoecology of rudist bivalves, considering their autecological attributes and the depositional fabrics of rudist assemblages, including associated biota, with special attention to corals. Finally, we survey the general biofacies architecture of rudist-dominated carbonate platforms.

AUTECOLOGICAL ATTRIBUTES OF RUDISTS

PALEOECOLOGICAL MORPHOTYPES

The principal functional requirements of rudist shell growth included (1) optimal presentation of the feeding apparatus to feeding and respiratory water currents, and (2) stabilization of the shell so that the optimal feeding posture could be maintained. The paleoecological morphotypes resulting from these functional constraints were defined by Skelton and Gili (2002) as elevators, clingers, and recumbents (Fig. 1).

Elevators

In this morphotype, the entire commissure of the attached valve (AV) was involved in upward growth. The mean angle of elevation (E), based on the maximum (α) and minimum (β) inclination with respect to the horizontal of the AV outer rim, tended toward 90° in life (see Fig. 1). Shells that accidentally toppled and subsequently showed geniculate recovery growth, shells in which upward growth was obstructed, or those that had an initially inclined position might show lower values of E (Steuber, 1999b). Nevertheless, the limit for rudist elevators is arbitrarily defined as E>45°. Stabilization was passively achieved through implantation of the AV in accumulating sediment, sometimes reinforced by lateral attachment to neighbors. This morphotype is therefore most often associated with muddy (wackestone to packstone) substrates in areas of net positive sediment accumulation, perhaps only occasionally swept by storm traction currents. The regular, weakly conical to cylindrical shell forms typical of this morphotype were well suited for aggregative life (Fig. 2). However, some elevator taxa tended to be solitary (Fig. 3).
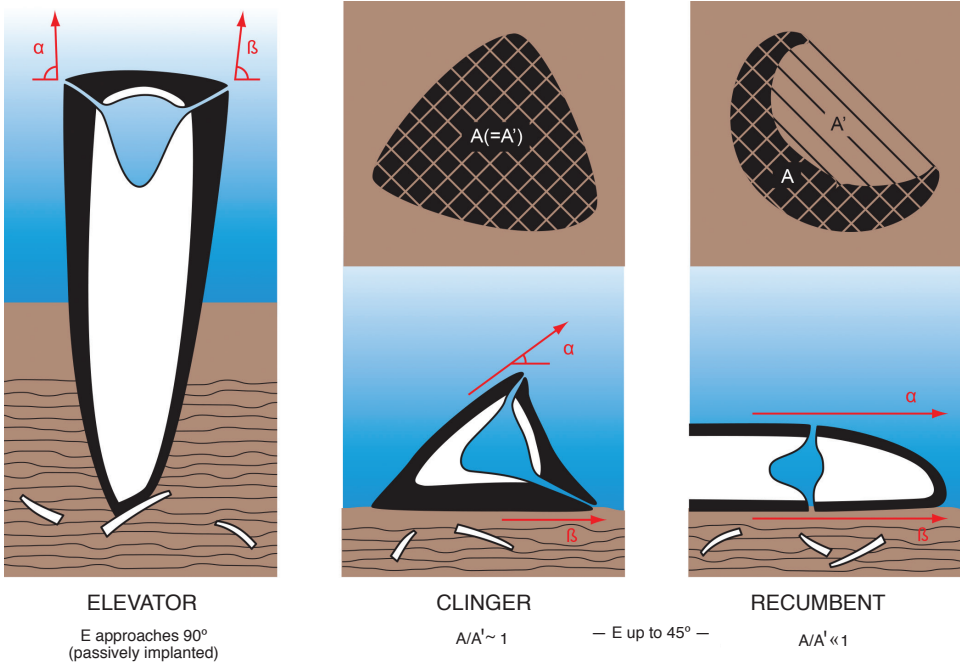
Fig. 1. Rudist ecological morphotypes. Shells are shown in vertical section and, for clinger and recumbent, in plan view. Double diagonal ornament, for recumbent, shows A (surface area of basal contact), and single diagonal ornament, A' (virtual area of support). In elevators, the mean angle of elevation (E) tended towards 90° (maximum [α] and minimum [β] inclination). In clingers and recumbents, E<45° (adapted from Skelton & Gili, 2002, fig. 5).

Clingers

In clingers, part or all of the AV margin overgrew the substrate, forming a broad basal area of frictional or adherent contact. The E angle was generally low (less than 45°) in life position, because the attached part of the shell wall was usually more or less horizontal (Fig. 1). This morphotype achieved stability on relatively firm or hard substrates by maximizing the basal area of direct contact (A) with the substrate. In consequence, A equals A' the virtual area of support, defined as the entire area of the convex polygon mapped onto the substrate by the shell's base. This growth mode required areas with stable sediment or hard surfaces (e.g., other shells, hardgrounds) with little or no sediment accumulation. Many clingers, however, tolerated sporadic influx of sediment (storm-driven sands) through upward-stepping growth of the basal surface. Interdigitation of foliaceous outgrowths from the AV

and the surrounding sediment can provide evidence of this ascending growth. Growth geometries of this morphotype are quite diverse. The more plesiomorphic rudists (diceratids, epidiceratids, and requieniids) were spiraling clingers (the basal area formed by the spirally grown anterior face) that lived either attached—perhaps to other shells (e.g., *Toucasia* Munier-Chalmas, 1873), or merely in frictional contact with the substrate (e.g., *Requienia* Matheron, 1842–1843), or even partially embedded in the sediment (e.g., *Diceras* Lamarck, 1805). Uncoiled rudists developed prone or expanded conical shells, depending on whether the AV margin overgrew the substrate laterally or radially. In the latter case, the entire outer margin of the AV spread out over the surrounding substratum all around (Fig. 4).

Recumbents

The recumbent mode of basal stabilization also involved part of the AV margin
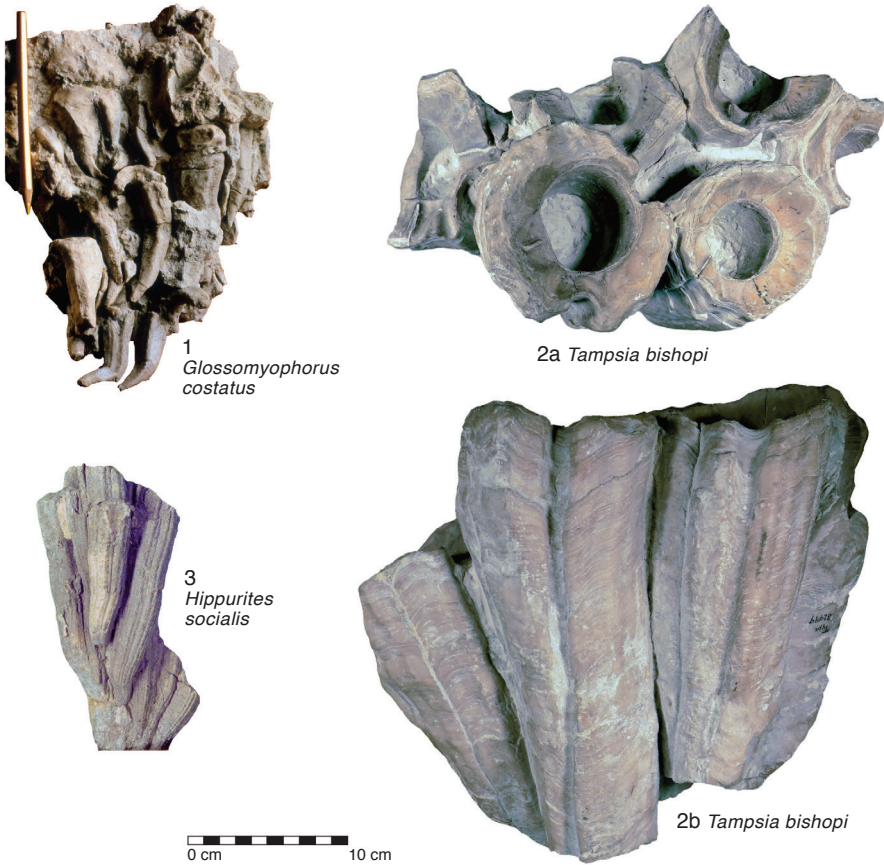
FIG. 2. Examples of clustered elevator rudists. *1, Glossomyophorus costatus* MASSE, SKELTON, & SLIŠKOVIĆ, 1984 (monopleurid, internal molds) from lowermost Aptian of Sarone, Friuli, northeastern Italy, with pencil for scale (Cestari & Sartorio, 1995; photo by Dario Sartorio); *2a–b,* tubular attached valves of the radiolitid *Tampsia bishopi* STEPHENSON, 1938, USNM 32499, from Upper Cretaceous of Mendez shale at Las Flores hacienda, State of Tamaulipas, Mexico; *2a,* view down into the cluster; *2b,* side view with radial bands (new; photos, Peter W. Skelton); *3,* bouquet of *Hippurites socialis* DOUVILLÉ, 1890 (hippuritid), PUAB 27836, from the Santonian Collades Member of Abella Formation, in the southern Central Pyrenees (Gili & Skelton, 1994).

in contact with the substrate throughout growth, with an E value of less than 45°. In contrast to clingers, however, such shells were not attached, and the area of contact with the substrate (A) played only a minor role in stabilization. Broadly arcuate forms produced an expanded virtual area of support (A') with broad effective diameters (Fig. 1). The ratio A/A' was therefore considerably lower than 1, and is defined as <0.75. Shells of this shape resisted overturning by currents, and they reduced the possibility of sediment washout and subsequent burial.

Recumbents were especially associated with unstable, current-swept substrates, such as carbonate sands and loose shell gravels, where sediment bypassing predominated over accumulation. The size dependence of this growth strategy fostered the evolution of rapid early growth to large adult size, yielding some of the largest known bivalves (e.g., *Titanosarcolites* TRECHMANN, 1924) (Fig. 5).

Thus, these three morphotypes represent modes of growth appropriate for different kinds of substrates. However, combinations of growth forms are not uncommon

1 *Oedomyophorus shaybahensis*

2 *Sauvagesia? hilli*

3 *Vaccinites* sp.

4 *Vaccinites* sp.

Fig. 3. Examples of solitary elevator rudists, arranged as in life position. *1, Oedomyophorus shaybahensis* Skelton, 2004 (caprinuloideid, see Skelton, 2004, 2013), articulated shell, anterior aspect, paratype, NHM PI MB LL42058, from Lower Aptian Shu'aiba Formation of eastern Saudi Arabia (Skelton, 2004); *2, Sauvagesia? hilli* Stephenson, 1941 (radiolitid), postero-ventral flank of right, attached valve with radial bands, holotype USNM 76575 (note encrusting oysters); *3–4,* attached valves of large hippuritids (*Vaccinites* sp. Fischer, 1887) from the Santonian Collades Member of Abella Formation, in the southern Central Pyrenees, hammer shaft is 36 cm long, large cylindrical specimen (*3*) and geniculate specimen (*4*); centimeter scale at right for *1–2* (*2–4,* new, photos by Peter W. Skelton).

because short-term or localized differences in environmental conditions (e.g., protected habitats within a high-energy setting) allowed distinct morphotypes to settle in close temporal or lateral proximity. Morphotypes could also vary opportunistically within some species and during ontogeny. All juveniles formed a spirogyrally coiled encrusting AV on initial settlement, so were invariably attached clingers (Fig. 6). Clinging strategy was also used

by some elevators (e.g., large cylindrical forms such as *Vaccinites* Fischer, 1887) in their earlier, expanding adult growth stages (Fig. 7). Notwithstanding these complications, the determination of rudist life strategy is useful for identifying paleoenvironmental conditions.

Rudist Taphonomy

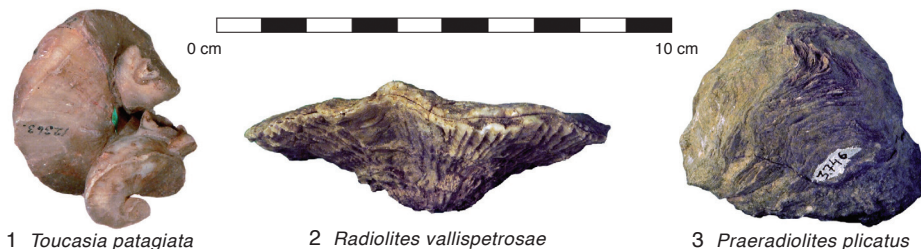Elevator rudists are commonly preserved in life position because of their original,

1 *Toucasia patagiata* 2 *Radiolites vallispetrosae* 3 *Praeradiolites plicatus*

Fig. 4. Examples of clinger rudists, arranged as in life position. *1,* spiraling clinger *Toucasia patagiata* (White, 1884) (requieniid), articulated shell showing basal anterior face of attached (left) valve, "cotype," USNMNH 12363; *2–3,* articulated shells of uncoiled clingers; *2, Radiolites vallispetrosae* Astre, 1954 (radiolitid), with radially expanded conical attached valve, PUAB 3959; *3, Praeradiolites plicatus* (Lajard, Négrel, & Toulouzan, 1821 in Lajard, Toulouzan, & Négrel, 1821) (radiolitid), note the broad base to the shell formed by the flattened anterior face of the attached valve, from the Santonian Collades Member of Abella Formation, southern Central Pyrenees (*1,* new, photo by Peter W. Skelton; *2–3,* personal archives).

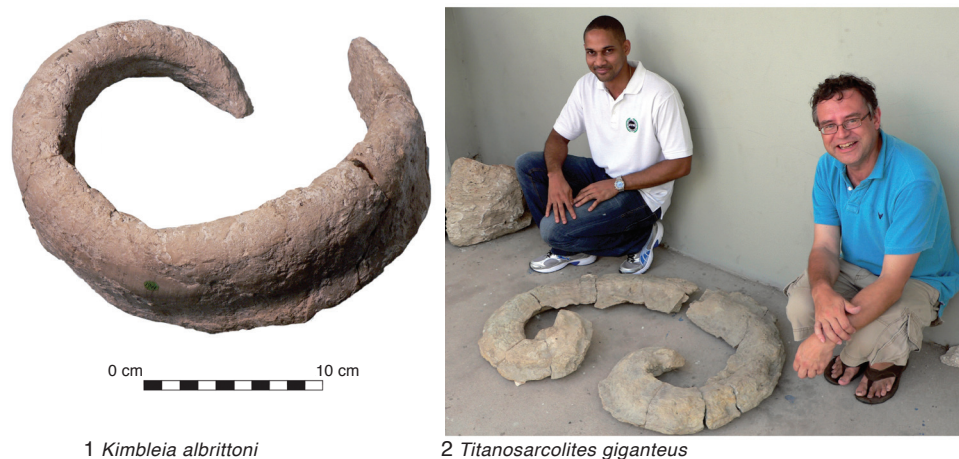1 *Kimbleia albrittoni* 2 *Titanosarcolites giganteus*

Fig. 5. Examples of recumbent rudists arranged as in life position—recumbents have an arcuate form and include caprinuloideids (*1*) and antillocaprinids (*2*). *1,* articulated shell of *Kimbleia albrittoni* (Perkins, 1960) from the Upper Albian of Texas, locality unknown (USNMNH Cretaceous Stratigraphy collection, no. CS2; field collection no. 1941); *2, Titanosarcolites giganteus* (Whitfield, 1897) from the Maastrichtian of Bruce Hall, Great River, Marchmont Inlier, Jamaica, articulated specimen (Department of Geography and Geology Museum, The University of the West Indies, Mona Campus, Kingston, Jamaica); scale, two members of the organization committee for the 9th International Congress on Rudists, held at UWI in 2011, left to right, Gavin Gunter and Simon Mitchell (new, photos, Peter W. Skelton).

more or less, embedded growth in relatively quiet environments. Recumbents and most clingers (e.g., diceratids, epidiceratids, and requieniids) are less frequently preserved in life position because their shells were more exposed, both in life and postmortem. Clinger-dominated examples are usually parautochthonous—that is, their shells are more or less locally displaced. Recumbents, because they frequently thrived in current-swept settings, are rarely found *in situ* and are more often associated with grainstone to packstone deposits (see Gili, Masse, & Skelton, 1995 for literature references).

FEEDING HABITS

Like most other bivalves, rudists were suspension feeders. However, most if not all uncoiled rudists probably used expanded mantle margins as well as their ctenidia

to capture food particles (SKELTON, 1976, 1979a). Rudists most likely fed on phytoplankton and other suspended particulate material (bacteria, organic detritus) filtered from feeding currents. Experimental evidence for elongated hippuritids suggested that individuals with inclined growth habits, in particular, could sample water from both the mainstream flow and the sediment-water interface (GILI & LABARBERA, 1998). Some field and laboratory studies suggest beneficial effects of sediment resuspension as a bivalve food supplement (e.g., GRANT, ENRIGHT, & GRISWOLD, 1990).

Vaccinites giganteus major

FIG. 7. Early adult stage of *Vaccinites giganteus major* TOUCAS, 1904, PUAB 28189, from the Santonian Collades Member of Abella Formation in the southern Central Pyrenees (Gili & Skelton, 1994).

The ability to form large shells from comparatively small bodies has led some authors to hypothesize that rudists possessed symbiotic zooxanthellae. This hypothesis, most explicitly advocated by KAUFFMAN and JOHNSON (1988), was critically examined by ROSS and SKELTON (1993) and GILI, MASSE, and SKELTON (1995). The latter authors considered the configuration of the expanded mantle margins to be a plausible indication of farming of zooxanthellae in certain rudist taxa, e.g., in *Torreites* PALMER, 1933, which had the mantle margins exposed (SKELTON & WRIGHT, 1987) and in *Osculigera* KÜHN, 1933 where they were only covered by a thin rim of the free valve (VOGEL, 1975). For most rudists, however,

there is no evidence for direct exposure of mantle tissue to the light. GILI, MASSE, and SKELTON (1995) further stated that "the frequently repeated claim that the right valve margin of *Durania* was freely exposed in life ... is an incorrect interpretation based upon incomplete specimens. In fact, the right valve rim was entirely covered by a thin flange of the outer (calcitic) shell layer of the left valve ...Whether or not the flange was sufficiently translucent to have allowed photosynthesis (as postulated by VOGEL, 1975, for *Osculigera*) remains to be demonstrated."

More recently, SEILACHER (1998) suggested that the pore and canal system of hippuritids was related to symbiosis with zooxanthellae.

FIG. 6. Rudist settlement. *1–2, Coralliochama* WHITE, 1885, from Upper Cretaceous Rosario Formation, Punta Banda Cap, Baja California, Mexico. *1a,* settling juvenile in section attached to a cobblestone; *1b,* magnification of the spirogyrally coiled apex of the attached valve; *2a,* attached valve of *Coralliochama; 2b,* magnification of the anterior face of the apex, showing the first spirogyrate growth phase; *3–4, Coralliochama gboehmi* BÖSE, 1906, from upper Maastrichtian Cardenas Formation in central Mexico; *3a–b,* different view of same sample; *3a,* posterior face of a young specimen attached to the attached valve of an adult, radiolitid (*R*), coral (*C*); *3b,* left to right, posterior face of another young specimen and attached valve of the young specimen in *3a; 4,* apex of a specimen attached to the underside of a projecting shell fragment, and then with growth proceeding away from the observer; *5,* young specimens of *Polyconites hadriani* SKELTON & others, 2010 (*P*) attached to a *Toucasia* MUNIER-CHALMAS, 1873 (*Touc*) fragment from uppermost Lower Aptian part of Villarroya de los Pinares Formation, western Maestrat Basin, eastern Spain; *6a–b,* thin section photomicrographs from an assemblage of *Hippuritella vasseuri* (DOUVILLÉ, 1894) from the Turonian–Coniacian of the Northern Alpine Gosau Group of Brandenberg, Austria, in horizontal view; *6a,* two juveniles attached to the shell wall of adult specimens, showing early ontogenetic hinge system; *6b,* settling juvenile attached to adult showing two weakly developed pillars and a barely developed ligamentary ridge, but with calcitic outer shell layer already well developed; *7a–d,* transversal (*7a–c*) and longitudinal (*7d*) thin sections from a *Alencasterites mooretownensis* (TRECHMANN, 1924) (=*Biradiolites mooretownensis* TRECHMANN, 1924; Hennhöfer, Götz, & Mitchell, 2012) assemblage from Rio Grande Limestone (*Titanosarcolites* Limestone, upper Campanian) in the Blue Mountain Inlier of Jamaica; *7a,* small settler attached to an adult shell, showing primary inner and outer shell material in the attached valve (*white lines* at the bottom); *7b,* settlers attached to adult specimens; *7c,* juveniles at an early ontogenetic stage previous to the addition of the calcitic outer shell layer; *7d,* juvenile settling and growing attached to the attached valve of an adult specimen (*white arrow*); scale bars are 1 cm where not specified (*1–5, 6a,* new, photos by Stefan Götz; *6b,* adapted from Götz, 2007, fig. 16,G; *7a–d,* Hennhöfer, Götz, & Mitchell, 2012, fig. 1,*C–D, F–G*).

He considered the possibility that the canals gave way for extensions of mantle tissue housing the algae. However, the system of pores and canals in hippuritid rudists has been demonstrated to have been well adapted for filtering (Skelton, 1976; Schumann, 2010). If correct, this makes additional speculation on the role of the pore and canal system redundant. Besides, hippuritids frequently grew in muddy deposits (Philip, 1970; Freytet, 1973; Floquet, 1982; Grosheny & Philip, 1989; Skelton & others, 1995; Steuber, Yilmaz, & Löser, 1998; Götz & Mitchell, 2009) associated with turbid, nutrient-rich water. These mesotrophic environmental conditions are generally not favored by photosymbiontic organisms (Hallock, 1981). Among recent bivalves, many thin-shelled taxa (e.g., *Corculum* Röding, 1798, *Fragum* Röding, 1798, *Clinocardium* Keen, 1936) bear symbiotic zooxanthellae (Kawaguti, 1950, 1983; Jones & Jacobs, 1992; Schneider, 1998) and some taxa with massive and rapidly growing shells (e.g., oysters) do not. Symbiosis with zooxanthellae is primarily related to nutrition (Muscatine & Porter, 1977). High shell-secretion rates should therefore not be taken *a priori* as evidence for endosymbiosis (Jones & Jacobs, 1992). Unfortunately, $\delta^{13}C$ isotope measurements of expected vital effects caused by photosynthesis are difficult to interpret in fossil mollusks (Jones, Williams, & Romanek, 1986; Romanek & Grossmann, 1989; McConnaughey & others, 1997) and have so far failed to answer this question, because isotopic signals are obscured by variable metabolic rates, kinetic effects, and diagenesis (Jones & Jacobs, 1992).

GROWTH RATES AND CARBONATE DEPOSITION

Inferred annual growth increments of rudists have been measured based on seasonality documented by oxygen-stable isotope sclerochronology (Steuber, 1996, 1999a, 2000; Steuber, Yilmaz, & Löser, 1998; Steuber & others, 2005) and based on tidal cycles preserved in growth micro-rhythms (Masse & Philip, 1972; Amico, 1978; Schumann, 1995; Regidor-Higuera, García-Garmilla, & Skelton, 2007). Indirect estimates have been drawn from the spacing of dark, organic-rich bands in the shell (e.g., Steuber & others, 2005, supplementary figure), the spacing of zones with thinned growth laminae (Schumann, 1995; Regidor-Higuera, García-Garmilla, & Skelton, 2007) or from the development of salient growth rugae in some radiolitids (Cestari & Pons, 2007). All such zones mark decelerated growth or even cessation, and may be the result of extreme temperatures during the warm or cold season (Steuber, 1996), or indicate annual periods of spawning that may be linked to a specific season, and may not always have occurred in summer (Fig. 8).

Depending on taxonomy and paleoenvironmental constraints, inferred annual rudist growth increments vary between 0.3 cm, e.g., in *Praeradiolites ciryi* Floquet, 1991 (Regidor-Higuera, García-Garmilla, & Skelton, 2007) and 7 cm, e.g., in *Toucasia carinata* (Matheron, 1842–1843) (Steuber & others, 2005). Most common values range between 1–2 cm. The fastest growth rates are reported from requieniids—7 cm in *Toucasia carinata* (Steuber & others, 2005) and hippuritids—4–6 cm in *Vaccinites ultimus* (Milovanović, 1935) (Steuber, Yilmaz, & Löser, 1998). Radiolitids show a broad range, between 0.3 and several centimeters (Regidor-Higuera, García-Garmilla, & Skelton, 2007). Reliable data on other rudist families are presently unavailable.

Vertical growth rates were not correlated with commissural diameter. Small taxa (around 1 cm commissural diameter), such as *Hippuritella* Douvillé, 1908 and *Biradiolites* d'Orbigny, 1850, also grew in this range—e.g., 1.6 cm in *Hippuritella vasseuri* (Douvillé, 1894) and 1.4 cm in *Alencasterites mooretownensis* (Trechmann, 1924) (=*Biradiolites mooretownensis* Trechmann, 1924; Hennhöfer, Götz, & Mitchell, 2012) (Hennhöfer, Götz, & Mitchell, 2012). This was true as well with large
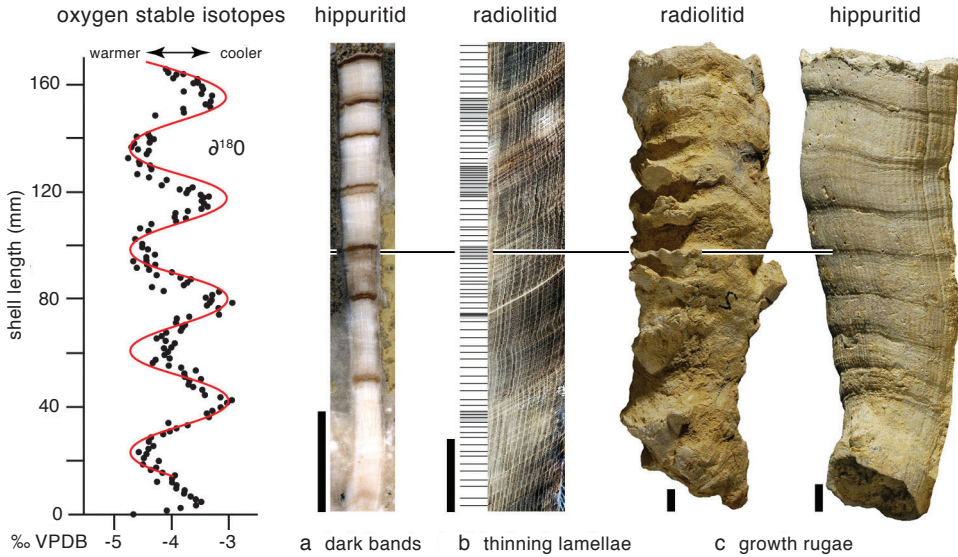
FIG. 8. Growth rates. The oxygen-isotope curve on the left of the figure is the result of uniform growth rates throughout the year. The photographs of longitudinal sections of rudist specimens shown on the right (*a–b*), show evidence of seasonal growth deceleration—dark, organic-rich bands in hippuritids (*a*), and thinned growth lamellae in radiolitids (*b*). Macroscopically, these zones are expressed by growth rugae in hippuritids and radiolitids (*c*); scale bars, 1 cm (oxygen-isotope curve adapted from Steuber, 1999a, fig. 10; *a–c*, new, photos by Stefan Götz).

taxa with more than 50 cm commissural diameter, for example, 1–4 cm in *Durania* DOUVILLÉ, 1908 (SCHUMANN, 1995).

Individual growth rates in rudists varied ontogenetically. Fastest shell deposition is observed during the first one or two years of growth (STEUBER, 1999a), often accompanied by salient ribs and rapid increase of the commissural diameter in hippuritids (GÖTZ, 2003b). Adult growth was slower by 10% to 50%, but unlike most other bivalves, growth rates in rudists remained stable throughout adult life (STEUBER, 1999a). Before natural death, individual growth rates decreased again to less than half of the adult rates; this was often accompanied by a reduction of ornamentation and a thinning of the outer shell layer (ZAPFE, 1937; GÖTZ, 2003b).

Community carbonate deposition rates depended on annual growth incrementation, shell thickness, shell density, and animal congregation density (STEUBER, 2000). In dense congregations where rudists covered the substrate 80% to 90% (GÖTZ & STINNESBECK, 2003; GÖTZ, 2007), maximum carbonate-deposition rates ranged between 10 kg and 30 kg per square meter per year. These are exceptionally high values compared to recent carbonate-producing ecosystems. Coral reefs produce between 1 kg (REES & others, 2005) and 4 kg $CaCO_3$ per square meter per year (KINSEY, 1983), but in most settings, production is less than 2 kg (HEISS, 1995). In *Crassostrea virginica* (GMELIN, 1791) congregations, annual carbonate production has been estimated to reach 0.5 kg per square meter (DAME, 1976). However, when carbonate production by rudists is averaged over stratigraphical time scales, calculated net vertical accumulation rates drop by orders of magnitude (19–50 kg per square meter per 1,000 years) (MASSE & FENERCI-MASSE, 2006). This reduction is the result of limited accommodation in shallow settings. Reworking of rudists by storms usually redistributed much of the shell carbonate to neighboring environments (as bioclastic sediment) and resulted in rudist congregations as laterally extended but relatively thin (meter scale) lenticular
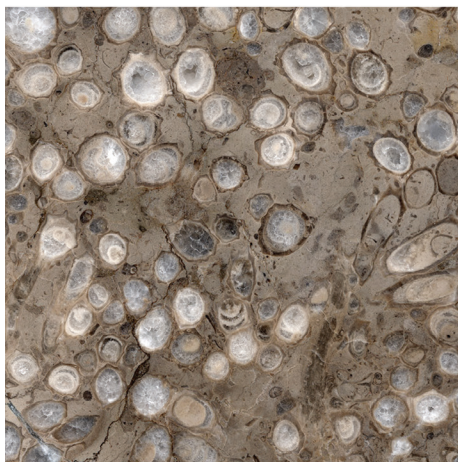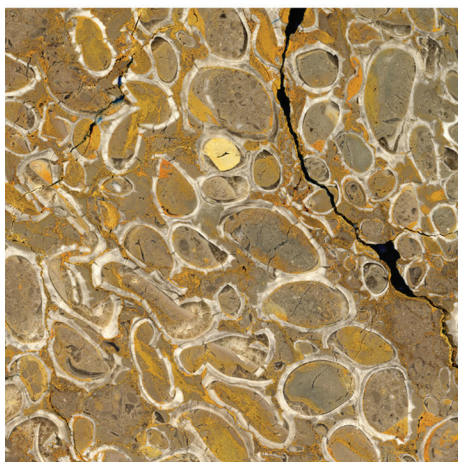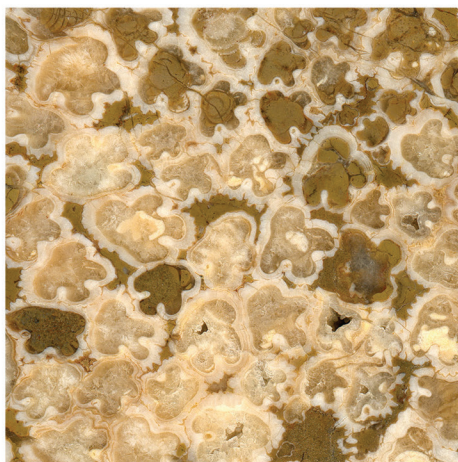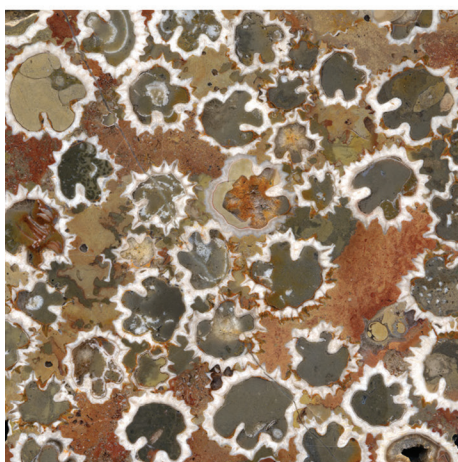
1 *Alencasterites mooretownensis*

2 *Biradiolites lombricalis*

3 *Mathesia darderi*

4 *Hippuritella vasseuri*

5 *Vaccinites sulcatus*

6 *Durania cornupastoris*

Fig. 9. *For explanation, see facing page.*

bodies separated by truncation surfaces or barren intervals.

PALEOBIOLOGY OF DENSE RUDIST CONGREGATIONS

Serial sectioning through *in situ* elevator rudist congregations has provided insights on their internal growth dynamics (GILI & SKELTON, 2000; GÖTZ & STINNESBECK, 2003; VILARDELL & GILI, 2003; KORBAR, 2007). High-resolution grinding tomography datasets have added further information on both reproduction and mortality patterns and population dynamics (GÖTZ, 2007; HENNHÖFER, GÖTZ, & MITCHELL, 2012; HENNHÖFER & others, 2014).

Dense, monospecific rudist associations growing under favorable ecological conditions are characterized by stable optimum coverage (up to 80% to 90%) of available space through time and a continuous overturn of generations. These high-coverage values appear in different families (Fig. 9) and can be observed in *Monopleura* MATHERON, 1842–1943, *Mathesia* MAINELLI, 1996, *Biradiolites, Durania, Hippurites* LAMARCK, 1801, *Vaccinites, Hippuritella,* and *Coralliochama* WHITE, 1885 associations. Other paucispecific congregations reached maximum coverage rates of only 50% to 60%, e.g., in *Hippurites praecessor* DOUVILLÉ, 1895 (VILARDELL & GILI, 2003) and in *Alencasterites mooretownensis* (HENNHÖFER, GÖTZ, & MITCHELL, 2012), suggesting either taxonomic variability or environmental control. Stable coverage rates throughout lithosome development and continuous overturn of generations are also evident in these congregations (GILI & SKELTON, 2000;

VILARDELL & GILI, 2003). Whether this was controlled genetically or by the environment (e.g., through high-particle resuspension rates) remains to be tested.

Decrease of rudist coverage was accompanied by increased spat/early juvenile mortality and/or reduction of new recruits.

Rudist reproduction in some dense associations had an annual cyclic pattern. This is marked by equidistant peaks of larval recruitment, as observed in bouquets of *Hippuritella vasseuri* (GÖTZ & STINNESBECK, 2003; GÖTZ, 2007), *Alencasterites mooretownensis*, and *Biradiolites lombricalis* (HENNHÖFER, GÖTZ, & MITCHELL, 2012).

Inside dense congregations, rudist spat settled almost exclusively on attached adult shells near the commissural plane and only occasionally on shell debris (GILI & SKELTON, 2000; GÖTZ, 2003b; HENNHÖFER, GÖTZ, & MITCHELL, 2012; HENNHÖFER & others, 2014). The maximum spat density observed is 8 per square decimeter (giving an extrapolated density of 800/m^2), comparable to recent spat densities in oyster beds (MAC-KENZIE, 1981). Most new settlers, however, died early, and less than 30% of juveniles reached adulthood (GÖTZ & STINNESBECK, 2003; GÖTZ, 2007; HENNHÖFER, GÖTZ, & MITCHELL, 2012) (Fig. 10).

The mortality of juveniles in these dense rudist lithosomes seems to have been controlled by the amount of coeval competitors (GÖTZ & STINNESBECK, 2003; GÖTZ, 2007) and by the space available for settling and its subsequent change during juvenile growth. This pattern is even visible in less densely packed congregations (GILI & SKELTON, 2000; KORBAR, 2007). Hippuritids

FIG. 9. Cross-section views (*1–5*) of various elevator rudist congregations to show examples of different coverage in dense paucispecific associations. *1, Alencasterites mooretownensis* (TRECHMANN, 1924) (=*Biradiolites mooretownensis* TRECHMANN, 1924; Hennhöfer, Götz, & Mitchell, 2012), from Rio Grande Limestone (*Titanosarcolites* Limestone, upper Campanian) in the Blue Mountain Inlier of Jamaica (see Hennhöfer, Götz, & Mitchell, 2012 for details); *2, Biradiolites lombricalis* (d'ORBIGNY, 1842) (=?*Radiolites* sp. in Götz, 2007), from the Santonian of Punta Mrlera, southern Istria, Croatia (see Götz, 2007 for details); *3, Mathesia darderi* (ASTRE, 1933) from the Upper Aptian in the Basque-Cantabrian Basin, northern Spain; *4, Hippuritella vasseuri* (DOUVILLÉ, 1894) from the Turonian–Coniacian of the Northern Alpine Gosau Group of Brandenberg, Austria (see Götz & Stinnesbeck, 2003 for details); *5, Vaccinites sulcatus* (DEFRANCE, 1821) from the Turonian–Coniacian of the southern Central Pyrenees; *6, Durania cornupastoris* (DES MOULINS, 1826), USNM 442109, general view of bouquet, with attached valves in adapical view, from the Turonian Greenhorn Limestone in Colorado (see Cobban, Skelton, & Kennedy, 1991 for details); scale bars, 1 cm (*1,* new, photo by Dominik Hennhöfer; *2–5,* new, photos by Stefan Götz; *6,* new, photo by Peter W. Skelton).
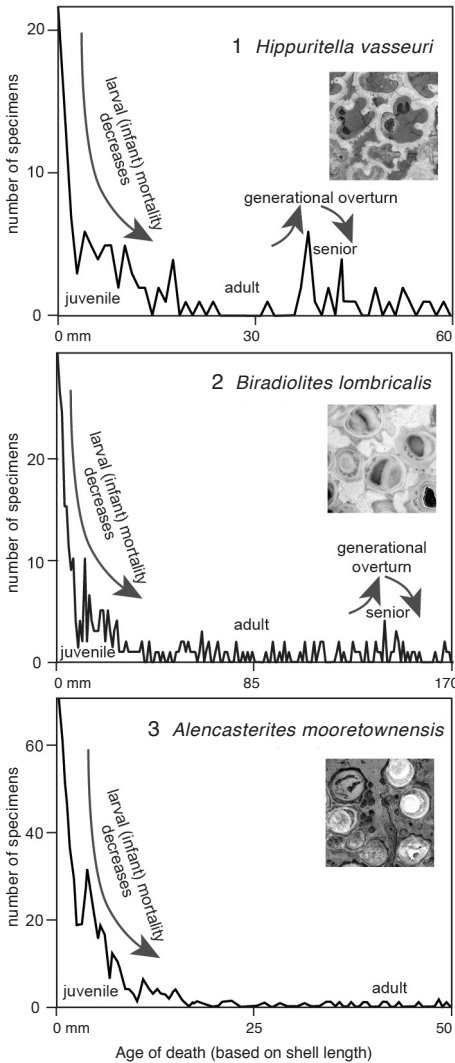
FIG. 10. Population dynamics of *Hippuritella vasseuri* (DOUVILLÉ, 1894), *Biradiolites lombricalis* (D'ORBIGNY, 1842) (= ?*Radiolites* sp. in Götz, 2007), and *Alencasterites mooretownensis* (TRECHMANN, 1924) (=*Biradiolites mooretownensis* TRECHMANN, 1924; Hennhöfer, Götz, & Mitchell, 2012). Number of specimens plotted against their shell height (proxy for relative age) in mm. The majority of spat died shortly after settlement, and less than 30% of juveniles reached adult sizes (chart new, adapted from: *1,* Götz & Stinnesbeck, 2003, fig. 5; *2,* Götz, 2007, fig. 9; *3,* Hennhöfer, Götz, & Mitchell, 2012, fig. 6).

seem to have been unaffected by settling space at the time of larval attachment but reacted sensitively to subsequent decreases. In dense radiolitid associations, however, the initial space seems to have been crucial for survival, but subsequent decrease after settling caused no additional mortality. This probably reflects a phase of vulnerability during the spirogyrate, earliest growth stages, but also a higher ecophenotypic flexibility of radiolitids compared to hippuritids (GÖTZ, 2007; HENNHÖFER, GÖTZ, & MITCHELL, 2012).

RUDIST REPRODUCTION STRATEGIES

Most bivalves, whether planktotrophic or brooding, reproduce in a cyclic pattern with reproduction frequency varying according to taxonomy and environmental factors (GIESE & PEARSE, 1974). The earliest, larval aragonitic growth stages of *Hippuritella* and *Biradiolites* are about 300 μm in maximum dimension (GÖTZ, 2003b; HENNHÖFER, GÖTZ, & MITCHELL, 2012). This is comparable with the larger size of partly or completely lecithotrophic bivalves with only a short (if any) planktic stage (KASYANOV, 2001), but these are only maximum estimates based on already attached spat. Most *Hippuritella* species, such as *Hl. vasseuri, Hl. resecta* (DEFRANCE, 1821), and *Hl. lapeirousei* (GOLDFUSS, 1840), show a preference for gregarious growth in spatially constricted bouquets, compared to other hippuritid lithosomes (PHILIP, 1972; SKELTON, 1979b; VICENS, 1994; GÖTZ, 2001; GÖTZ & STINNESBECK, 2003), suggesting genetic rather than environmental control. Regarding radiolitids, BRETON (1996) reported a cluster of juveniles in the pallial chamber of *Durania blayaci* (TOUCAS, 1909) and interpreted this as evidence for brooding. However, the wide paleogeographic distribution of many species of *Durania* in the Boreal realm (RÖMER, 1865; KÜHN, 1949; REITNER, 1991) is best explained by long distance drift of planktotrophic larvae.

Nevertheless, there is circumstantial evidence for planktotrophic reproduction among hippuritids in the form of the stratigraphically synchronous pan-Tethyan dispersion of the first hippuritids at the start of the Turonian (e.g., PHILIP, 1978;

PHILIP, BORGOMANO, & AL-MASKIRY, 1995; AGUILERA-FRANCO, 2003), and probable east-west migration across the Pacific suggested for *Torreites* (see SKELTON & WRIGHT, 1987).

DEPOSITIONAL FABRICS OF RUDIST ASSEMBLAGES

Cretaceous carbonate platforms are characterized by the presence of extensive lithological units dominated by rudist bivalves with or without associated corals. In this review, these are termed rudist lithosomes, or coral-rudist lithosomes. The term lithosome is a generic epithet with no compositional, size, or shape connotations. It carries no interpretative implications and is not connected to any particular type of deposition; as its etymology suggests, it simply means "rock body."

RUDIST LITHOSOMES

Three kinds of general rudist lithosomes can be identified based on the predominant rudist morphotype.

Elevator Rudist Lithosomes

Elevator rudists, especially hippuritids and radiolitids, formed the most prominent members of elevator rudist lithosomes. Their elongate, conical to cylindrical shapes, and growth habits were well suited for clustering with mutual contact. Paleoecological and sedimentological analyses of hippuritid and radiolitid lithosomes are numerous (e.g., PHILIP, 1972; FREYTET, 1973; BEIN, 1976; HÖFLING, 1985; GROSHENY & PHILIP, 1989; GILI, 1992; CARANNANTE, CHERCHI, & SIMONE, 1995; SKELTON & others, 1995; MORO, 1997; STEUBER, YILMAZ, & LÖSER, 1998; SCHUMANN, 2000; STÖSSEL & BERNOULLI, 2000; and SIMONE & others, 2003). Less numerous are analyses of elevator caprinid, monopleurid, and other rudist congregations, though some examples have been described in detail (e.g., PERKINS, 1974; MASSE, 1976; SCOTT, 1981, 1990; HARTS-HORNE, 1989; and HUGHES, 2000).

The aggregative habit of elevator rudists is manifested to different degrees: from

FIG. 11. Plan view of an elevator rudist lithosome in Santonian Sant Pere de Vilanoveta Member of Sant Corneli Formation in the southern Central Pyrenees, showing hippuritid shells in mutually attached clusters; scale, 2 euro coin, 25 mm diameter; see Skelton & others, 1995 for details (new, photo by Peter W. Skelton).
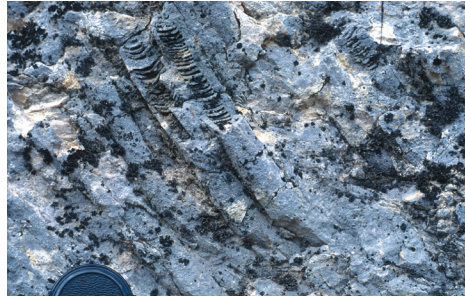

FIG. 12. Vertical section of an inclined cluster of hippuritids in Santonian Sant Pere de Vilanoveta Member of Sant Corneli Formation in the southern Central Pyrenees, showing bed-parallel tabulae; lens cap (at bottom of photo) is 5.5 cm across; see Skelton & others, 1995 for details (new, photo by Peter W. Skelton).

two or three individuals attached together and forming a small bouquet, to millions of clustered shells forming laterally extensive congregations, where individuals were closely packed or formed a dispersed fabric with individuals rarely entering into point contact. Most commonly, however, elevator rudists were in close proximity with no more than three or four individuals attached together (Fig. 11). Neighboring elevators grew implanted in the sediment that accumulated around and between them, forming upright to somewhat-inclined growth fabrics. The bulk of the congregation was thus
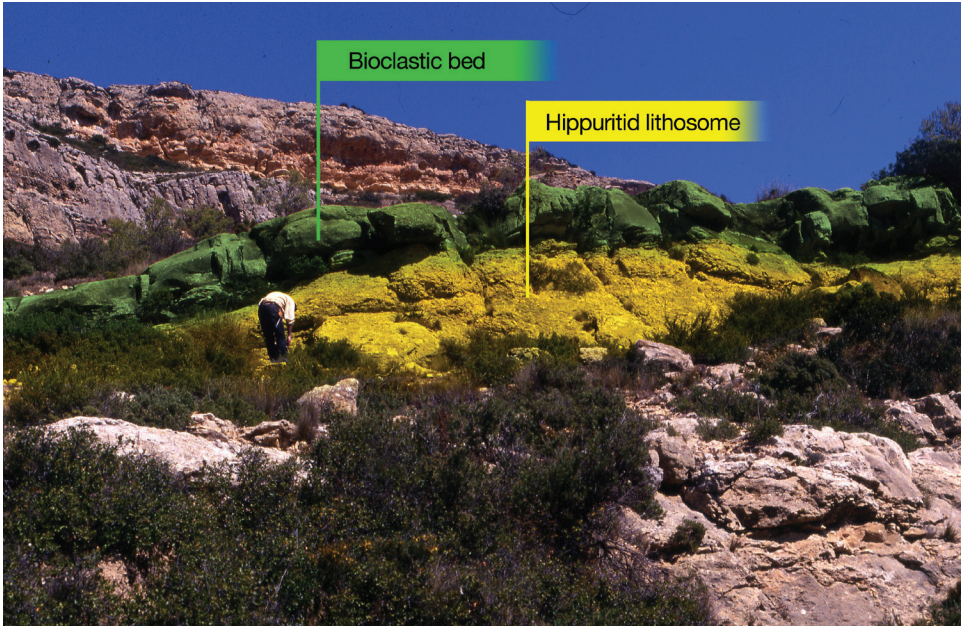
Fig. 13. View of an elevator hippuritid lithosome in Santonian Sant Pere de Vilanoveta Member of Sant Corneli Formation in the southern Central Pyrenees; overlying the hippuritid lithosome is a massive bioclastic bed, with geologist nearby for scale (for details see Vilardell & Gili, 2003; adapted from Vilardell & Gili, 2003, fig. 3).

more or less embedded in the sediment, with the growing ends of the slender shells projecting only centimeters (about 10 cm for large *Vaccinites* shells; SKELTON & others, 1995) from the sea floor. Occasionally, young individuals attached to the older shells. The upward growth of the rudist congregation was probably related to sediment accumulation, since the sediment matrix was largely produced *in situ* by postmortem disintegration of shells, previously weakened by bioeroders, and supplemented by faeces and pseudofaeces. This mode of growth was described as constratal by GILI, MASSE, and SKELTON (1995), in contrast to the superstratral growth exhibited by frameworks projecting significantly (at meter scale) above the sediment surface (e.g., modern coral-algal reefs).

Frequently, hippuritids in the elevator congregations show a persistent inclined posture, with their porous upper valves facing toward the inferred main downstream direction (GILI, 1992; SKELTON & others, 1995; VILARDELL & GILI, 2003). This orientation seems to be primary and the result of

active growth, since the tabulae observed in the attached valves are consistently parallel to the bed (Fig. 12), unlike those in clearly toppled shells. An experimental study on the hydrodynamic behaviour of hippuritid shells by GILI and LABARBERA (1998) led to the conclusion that individuals in an inclined downstream position would have filtered a mixture of water from both the main stream flow and that eddying up from the sediment-water interface. The latter would probably have been enriched with bacteria and detrital organic particles derived from the sediment. These findings suggest that the downstream-inclined posture could have been advantageous under conditions of reduced or fluctuating nutrient levels.

Elevator rudist congregations are typically paucispecific (sometimes almost monospecific), and associated benthic biota are very rare. The low diversity and species dominance of these rudist assemblages suggest marginal conditions for potential competitors (GILI & others, 1995). Rapid growth of rudist populations led to situations in which

most available space was occupied (Gili & Skelton, 2000).

Lithosomes of elevator congregations are characteristically thin and lenticular, or effectively tabular in those cases in which the lateral spreading of congregations and their debris was sustained, showing little or no evidence of original topographic relief (Fig. 13), although some examples of dominantly micritic mounds with a relief of a few meters have been reported (Perkins, 1974; Camoin, Bernet-Rollande, & Philip, 1988). Elevator lithosomes usually developed in areas of the carbonate platform protected from strong waves and traction currents.

Clinger Rudist Lithosomes

Clinger rudist lithosomes were constituted by congregations of clinger rudists, especially requieniids (e.g., Perkins, 1974; Masse, 1976; Scott, 1981; Malchus, Pons,

Fig. 14. Autochthonous cluster of clinger requieniids (*Toucasia* Munier-Chalmas, 1873), viewed from above, with loose specimen at right turned over to show basal anterior face of attached (left) valve (with centimeter ruler for scale), in uppermost Lower Aptian part of Villarroya de los Pinares Formation, western Maestrat Basin, eastern Spain (Skelton & Gili, 2012, fig. 8,*C*).

Fig. 15. *In situ* autochthonous clinger requieniids (*Toucasia* Munier-Chalmas, 1873) cemented to a hardground surface, viewed obliquely from above, in the Lower Aptian of Sao Juliao coastal section near Ericeira, southern Lusitanian Basin, Portugal; hammer head is 15 cm (new, photo by Peter W. Skelton).

Fig. 16. Recumbent caprinuloideid *Kimbleia albrittoni* (Perkins, 1960) lithosome viewed from above, showing autochthonous curved valves in longitudinal section, from the Upper Albian Georgetown Formation in Painted Canyon, Pecos River, western Texas; ruler in photo is 9 cm (new, photo by Peter W. Skelton).

& Salas, 1996; Fenerci-Masse, Masse, & Pernarcic, 2005; Gili & others, 2016). In general, these lithosomes comprise a variable mixture of rudist shells and muddy (packstone to wackestone) sediment. Individuals grew directly on the sediment surface (Fig. 14), were attached to other shells, or less frequently, cemented to hardground surfaces (Fig. 15). After death, shells often remained in place, but not necessarily in life position. Most commonly observed biofabrics consist of closely spaced to densely packed parautochthonous to autochthonous shells. Individuals rarely formed interlocking fabrics. Only occasionally, small clusters show several shells locally cemented together. Clinger congregations prospered in quiet to moderately agitated water, with low net sediment accumulation rate.

Rudist species diversity was very low and associated macrofauna was usually rare.

Clinger congregations, like elevator congregations, probably thrived in environmentally marginal settings in which other invertebrate species were excluded. Good examples of requieniid congregations extending well into inner platform settings have been described in the Albian of Texas, Arizona, and Mexico (Scott, 1990), and in the Aptian of Spain (Gili & others, 2016).

Clinger rudist lithosomes are the product of successive episodes of rudists growing on the sedimentary substrate. They usually have tabular shapes with meter-scale thicknesses and variable lateral extensions. They can be found in platform top areas where accommodation was limited.

Recumbent Rudist Lithosomes

Unlike lithosomes formed by elevators and clingers, recumbent rudist lithosomes with well-preserved shells are rare. The

recumbents lived mostly exposed on the sea floor as a consequence of their prone (horizontal) growth habit and tendency to thrive in current-swept settings. Consequently, they were infrequently preserved in life position, and more or less transported shell associations are more common. Some examples of preserved life positions have been documented in the literature (e.g., KAUFFMAN & SOHL, 1974; COLLINS, 1988; CESTARI & SIRNA, 1989; SKELTON, NOLAN, & SCOTT, 1990; LAVIANO & SKELTON, 1992; SKELTON & MASSE, 1998; MITCHELL, 2002; BAUER & others, 2004).

Recumbent rudist lithosomes usually consist of accumulations of parautochthonous to allochthonous shells and shell fragments in a sandy to muddy matrix. Complete specimens of recumbents in life position may also be found in marls, forming moderately dense congregations, but not in contact with each other (GILI, MASSE, & SKELTON, 1995). In these cases, as in the clinger lithosomes, the rudist shells float in the sediment, and no biogenic frameworks have been observed (Fig. 16).

Lithosomes consisting of coarse rudist rubble have been observed in intrashelf and platform margin settings exposed to strong waves and traction currents (KORBAR & others, 2001), whereas *in situ* recumbent rudist lithosomes are found in less extreme areas of the platform top (HUGHES, SIDDIQUI, & SADLER, 2003).

CORAL-RUDIST LITHOSOMES

Coral-rudist lithosomes include a variety of mixed associations of corals and rudists, with an abundance of corals. Detailed descriptions of coral-rudist lithosomes include MASSE and PHILIP (1981); CAMOIN, BERNET-ROLLANDE, and PHILIP (1988); GILI and others (1995); SANDERS and BARON-SZABO (1997); SKELTON and others (1997); IMMENHAUSER and others (2001); GÖTZ (2003a); SCHAFHAUSER and others (2003); BOVER-ARNAL and others (2012, 2015); and MORO and others (2016). These articles document the diversity of these associations

as well as their similarities. We presently focus only on their similarities.

The number of described Lower Cretaceous coral-rudist lithosomes is very limited, but a fine example is documented from the Albian of Arizona, where recumbent caprinids sit between corals at the margin of the platform (SCOTT, 1981). Similarly, MASSE and PHILIP (1981) mentioned that, in the Cenomanian of France, caprinids and corals occur together on the outer part of the platform.

In post-Cenomanian examples, the dominant organisms in coral-rudist lithosomes are colonial, platy to domal corals and hippuritids (Fig. 17. 1–2). Among the hippuritids, *Vaccinites* and/or *Pironaea* MENEGHINI, 1868 in PIRONA (with contribution by MENEGHINI), 1868 are the most conspicuous and recurrent genera, but other more slender hippuritids, either solitary or forming small bouquets or clusters, may be locally important. Less frequent are radiolitid, plagioptychid, small hippuritid, and requieniid rudists. Other colonial (flabello-meandroid, columnar, branching) and solitary corals may add to the coral assemblage. Associated macrofaunal elements also include occasional encrusting and rare branching chaetetid sponges, brachiopods, echinoids, gastropods, non-rudist bivalves, calcareous algae, and benthic foraminifers. The sediment matrix is variable, ranging from fine bioclastic wackestones to medium-grained bioclastic packstones.

Most macrofaunal components are preserved in life position, though displaced and broken specimens are occasionally present. Some shells show thin algal crusts and microborings. The organisms may be sparsely dispersed or relatively densely packed. In some places, corals and rudists clump together in mutual overgrowth. However, *in vivo* contacts between corals and rudists are rarely observed. This was probably due to the different life spans of corals and rudists and different morphologies that made *in vivo* contact rare (GÖTZ, 2003a). Even in dense associations, coral-rudist
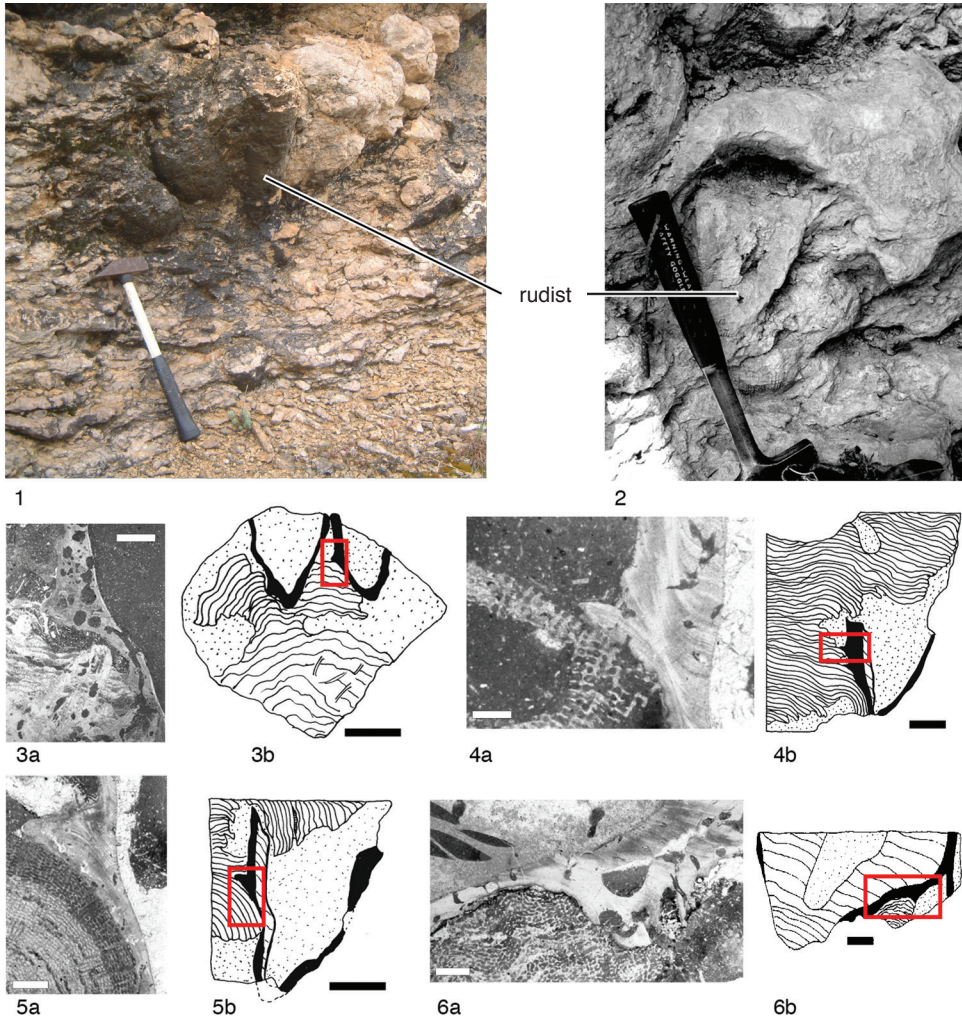
Fig. 17. Coral-rudist lithosomes. *1,* View of coral-rudist lithosome in Santonian Sant Pere de Vilanoveta Member of Sant Corneli Formation in the southern Central Pyrenees, hammer shaft is 36 cm long; *2–6,* photographic views and accompanying drawings from a coral-rudist lithosome in the Campanian of the Sierra de la Murta near Tabernes de Valldigna, in southeastern Spain; *2,* detail of the coral-rudist lithosome, *Pironaea milovanovici* Kühn, 1935 covered by the coral *Actinacis* sp. d'Orbigny, 1849, with hammer for scale; *3a, 4a, 5a, 6a,* photomicrographs of coral-rudist contact areas (longitudinal sections), note changed angle of growth-lamellae towards the coral surfaces; *3a, Vaccinites* sp. Fischer, 1887 (right side) in contact with the coral *Agathelia asperella* Reuss, 1854 (left side) (*red rectangle* in *3b*), note the balcony-like thickening of the outer shell layer, produced through an elongation of the growth laminae, *Vaccinites* suffered strong bioerosion and leaching, especially of the aragonitic shell layers; *4a, Hippurites* sp. Lamarck, 1801 (right side) in contact with the coral *Microsolena* sp. Lamouroux, 1821(left side) (*red rectangle* in *4b*), smaller balcony was produced; *5a, Hippurites* sp. (right side) in contact with *Microsolena* sp. (left side) (*red rectangle* in *5b*), note that a similar defense balcony is present; *6a, P. milovanovici* (upper part) in contact with the coral *Actinacis martiniana* d'Orbigny, 1850 (*red rectangle* in *6b*), the balcony was partially bioeroded by a clionid sponge; *3b, 4b, 5b, 6b,* drawings of the specimens, *dotted,* sediment; *black,* calcitic outer layer of rudist shells; *thick laminae,* original aragonitic inner layer (now recrystallized) of rudist shells (mostly leached); *thin laminae,* growth stages of corals; photos (*3a–6a*), scale bars, 1 mm, drawings (*3b–6b*), scale bars,1 cm; see Götz, 2003a for details of *2–6* (*1,* new, photo by Peter W. Skelton; *2,* adapted from Götz, 2003a, pl. 2,*1;* photos *3a–6a,* adapted from Götz, 2003a, pl.3,*1–3, 5;* drawings (*3b–6b*) adapted from Götz, 2003a, fig. 4).
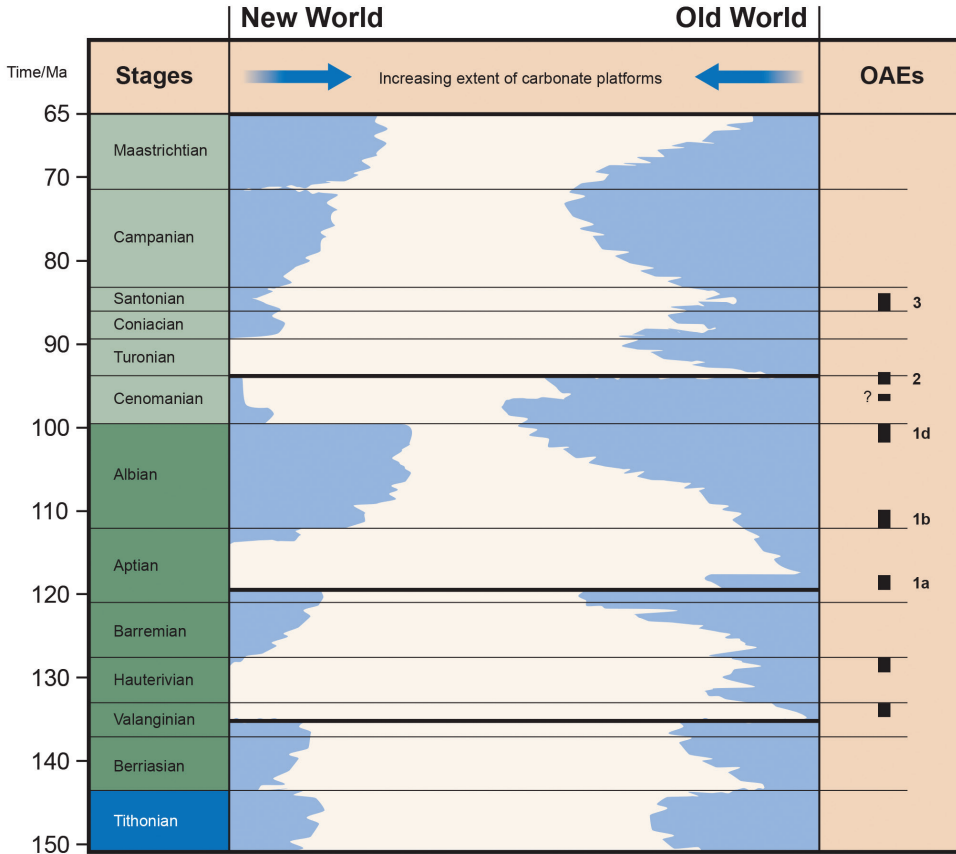
FIG. 18. Summary history of Tithonian and Cretaceous carbonate platform development in the New World and the Old World, with timings of major crises in the growth of platforms (*bold horizontal lines*) and oceanic anoxic events (OAEs) (Skelton & Gili, 2012, adapted from Skelton, 2003, fig. 5,*1*).

contact must have been short term and then expressed by localized shell thickening of rudists (GÖTZ, 2003a) (Fig 17. 3–6). Most rudists in coral-dominated lithosomes reached adult ages. This suggests mutual benefit through stabilization (encrustation) of rudist elevators in low sedimentation areas and increased availability of coral settlement area on living or dead rudist shells.

High diversities of corals and rudists, the variety of accompanying biota, and usual preservation in growth orientation are indicative of relatively quiet settings with good water circulation. Most studies on coral and rudist lithosomes associate them with platform margin environments more downslope than rudist-dominated associations (e.g., MASSE & PHILIP, 1981; CAMOIN, BERNET-ROLLANDE, & PHILIP, 1988; SKELTON & others, 1997).

RUDIST CARBONATE PLATFORMS

Carbonate platforms in which rudists formed a major, if not dominant, biotic component developed over vast shallow areas at low latitudes in the Tethyan/Atlantic oceanic realm. Their development during the Cretaceous was episodic, with long periods of widespread platform growth punctuated by global demises. The first

Fig. 19. Santonian carbonate platform succession forming part of Sant Corneli Formation in the southern Central Pyrenees, showing repeated minor shallowing units (predominantly <10 m thick) of remarkably tabular form, characteristic of such Cretaceous successions; see Skelton and Gili, 2005 for details (new, photo by Peter W. Skelton).

three major crises (mid-Valanginian, mid-early- to middle-Aptian, and at the end of the Cenomanian) coincided with oceanic anoxic events (Simo, Scott, & Masse, 1993; Skelton, 2003; Skelton & Gili, 2012) (Fig 18). No major oceanographic perturbations prior to the Cretaceous-Paleogene boundary (K/Pg) event accompanied the Maastrichtian decline, though climatic cooling may then have caused some contraction of platforms (Gale, 2000). However, lowering of temperature was apparently associated with the catastrophic impact recorded at the K/Pg boundary (Steuber, 2002; Steuber & others, 2002).

During the Cretaceous, prolific sediment production by rapidly growing, short-lived, benthic shelly biota caused rapid growth and expansion of platforms. The most abundant contributors were rudists, especially in the Late Cretaceous. Other contributors included calcareous algae, benthic foraminifers (some centimeter-scale), highly gregarious non-rudist bivalves, such as chondrodontids, gastropods (e.g., nerineids, acteonids), corals, and sponges.

The Cretaceous platforms typically show a tabular stratal architecture, with minor shoaling cycles (parasequences) predominating (Fig. 19) (see Gili, 1993; Hunt & Tucker, 1993; Skelton & others, 1995; Buchem & others, 1996; Ruberti, 1997; Sanders & Pons, 1999; Stössel & Bernoulli, 2000; Pomar & others, 2005; Bover-Arnal & others, 2010; Gili & others, 2016; among many others). Usually, meter-scale, low-energy platform top deposits grade laterally into thicker, platform margin cycles, including high-energy deposits (Fig. 20). Distally, the platform margin deposits

UPPER SLOPE   MARGIN   Outer ◄ PLATFORM TOP ► Inner
                               Cycles (up to 10 m thick)   Cycles (*c.* 1 m thick)

KEY

⌒ Recumbent rudists

⫰ Elevator rudists

⬬ Corals

▤ Algal laminites

10s to 100s m
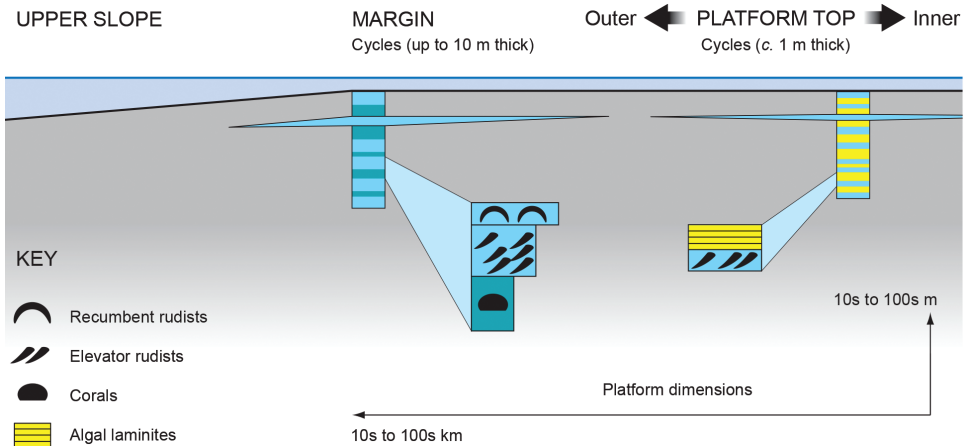
Platform dimensions

10s to 100s km

FIG. 20. Generalized transect model of Cretaceous carbonate platform showing typical cyclic deposits containing rudist lithosomes from outer platform margin and inner platform top, respectively. Expanded logs show idealized cycles. Clinger rudists may be found variously in all parts (Skelton & Gili, 2012, adapted from Skelton, 2003, fig. 5,*4*).

may grade into low-angle slope deposits, although tectonically induced steepening sometimes produced a sharper transition.

The platform top areas were often characterized by very active rudist growth, and usually consisted of lenticular to tabular lithosomes of pauci- to monospecific rudist congregations and their debris. Rarely more than a few meters thick, these lithosomes often extended laterally for hundreds of meters, even kilometers. In the early Cretaceous, these lithosomes were largely comprised of requieniid clingers, sometimes accompanied by clusters of primitive elevators (e.g., monopleurids and slender caprinids) (see Clinger Rudist Lithosomes, p. 15). In late Cretaceous platforms, such lithosomes were produced by vast congregations of elevators, mainly radiolitids and (in post-Cenomanian examples) hippuritids (see Elevator Rudist Lithosomes, p. 13). The latter lithosomes are frequently capped by floatstones generated by the destruction of the last congregation and/or blankets of bioclastic packstone to grainstone swept in from neighboring and usually more open marine areas (e.g., SKELTON & others, 1995) (Fig. 21).

Extensive paucispecific lithosomes formed in platform tops were often replaced seaward by mixed associations of corals and rudists accompanied by open marine biota (see Coral-Rudist Lithosomes, p. 17). These coral and rudist lithosomes evidently developed in relatively deep, open marine waters, although they may be absent in platforms that formed in enclosed basins, such as the Aptian Shu'aiba Formation of the Bab Basin in Abu Dhabi (HUGHES, 1997). Occasionally, associations of laminar to tabular corals with rare rudists also carpeted the seafloor in slightly deeper, poorly illuminated zones (SKELTON & others, 1997). Hence, corals and rudists largely occupied different biotopes during the Cretaceous (SKELTON & others, 1997), with little or no competition between them. Even in mixed assemblages, there is no evidence for competition between neighbors. This is contrary to the suggestion by KAUFFMAN and JOHNSON (1988) that rudists outcompeted hermatypic corals. An alternative view to explain the dominance of rudist congregations over coral reefs in Cretaceous carbonate platforms, is that the various (sediment-dwelling) rudist and coral associations were optimally adapted to the characteristic profiles and geometries of greenhouse platforms, in contrast to the predominance of superstratal reef growth on antecedent promontories typical of icehouse conditions (GILI, MASSE, & SKELTON,1995).
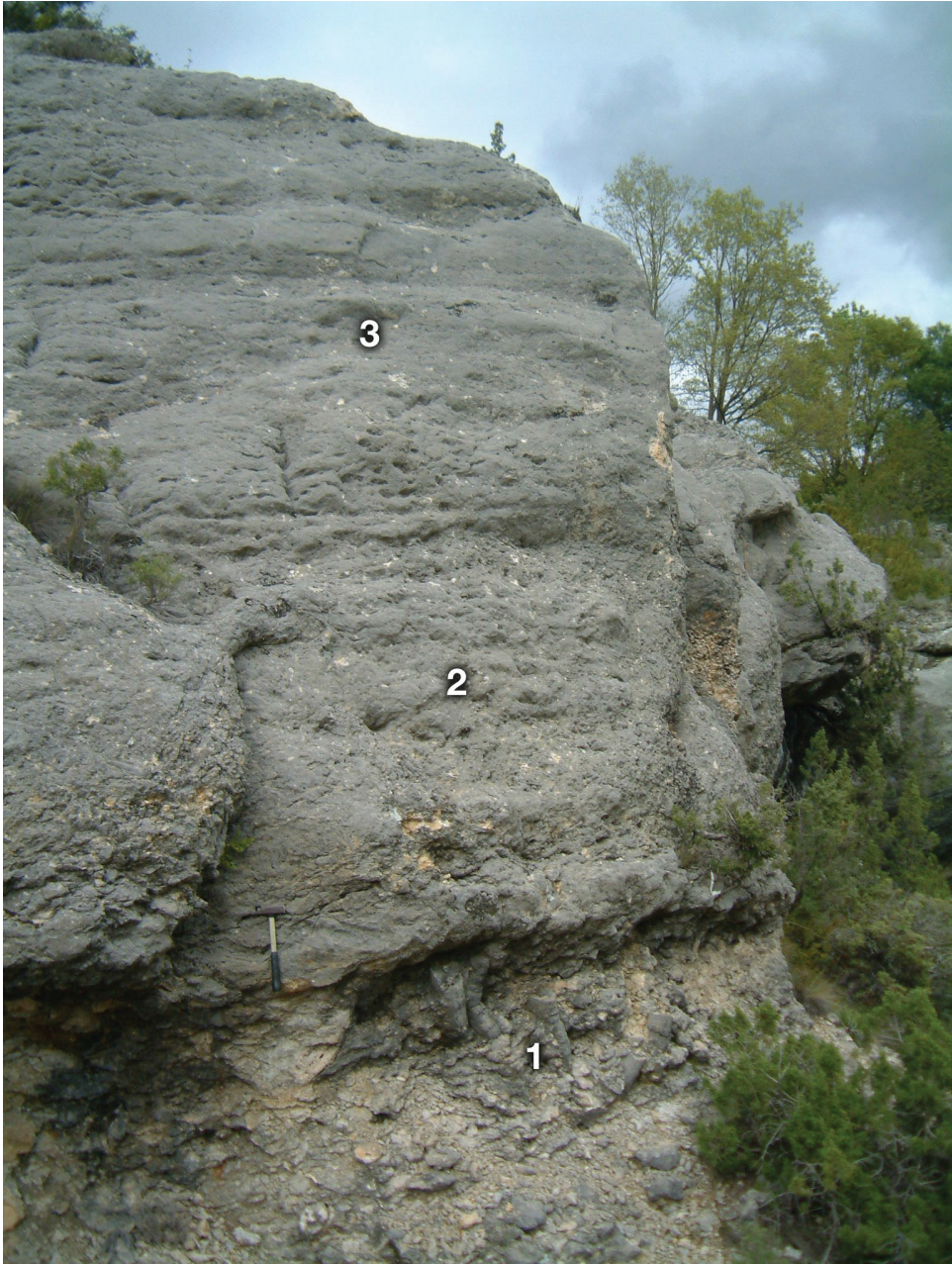
FIG. 21. View of a shallowing cycle from a platform top sequence in Santonian Sant Pere de Vilanoveta Member of Sant Corneli Formation in the southern Central Pyrenees, showing mixed coral and large elevator rudist (*Vaccinites* FISCHER, 1887) lithosome at the base (*1*), followed by a lithosome of clustered slender hippuritids in the middle (*2*), and bioclastic deposits in its upper part (*3*); with hammer for scale (shaft is 36 cm long); see Gili & others, 1995 for details (photo by Peter W. Skelton).

Fig. 22. Lower Aptian El Morrón platform, part of Villarroya de los Pinares Formation in western Maestrat Basin, eastern Spain, showing flat-topped, non-rimmed depositional profile and slope prograding clinoforms; see Bover-Arnal & others, 2009 for details (adapted from Gili & others, 2016, fig 3).

Episodically, diverse recumbent rudists occupied high-energy platform margins, lying prone in relatively current-swept areas with predominant sediment bypassing. Though their broken shells and debris were usually washed into neighboring areas, autochthonous shells may be found over the tops of bioclastic banks, capping outer platform cycles (see Recumbent Rudist Lithosomes, p. 16).

The depositional geometry of Cretaceous carbonate platforms reflects the nature of Cretaceous climate, as Simo, Scott, and Masse (1993) and Skelton (2003) have pointed out. They suggested that the small increments of accommodation typical of Cretaceous greenhouse-type oscillations of sea level, combined with high rates of carbonate production, promoted rapid shoaling, with overproduction and extensive lateral redistribution of bioclastic sediment during times of continuously decreasing accommodation. Drowning and backstepping occurred during times of increasing accommodation. Consequently, platforms usually assumed flat-topped profiles (Fig. 22) with broad outer zones. Bioclastic debris was swept both inwards across the platform top and down the flanking clinoforms.

ACKNOWLEDGEMENTS

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