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Research paper

Stability strategies and hydrodynamic behavior of liberosessile solitary rugose corals (Ordovician; Red River–Stony Mountain Province, North America)

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Abstract

In the Late Ordovician Red River–Stony Mountain Province of North America, four closely related genera of solitary rugose corals are represented exclusively by liberosessile species: *Salvadorea*, *Grewingkia*, *Deiracorallium*, and *Lobocorallium*. These rugosans benefitted from innovative and in some cases unique strategies involving corallum form, which improved stability with respect to the substrate and currents, and took advantage of water flow during life. Trochoid form was a compromise for ensuring adequate stabilization of the corallum by sediment, while keeping the calice rim sufficiently elevated above the substrate. In life orientation with the convex cardinal side of the corallum facing down, triangulate and trilobate cross-sectional shapes offered resistance to lateral tipping or rotation. Depressed coralla resisted gravity-induced subsidence or tilting. With the convex side facing downcurrent, the streamlined shape of compressed and triangulate forms improved stability by reducing drag. Trilobate form may have had a drag-reducing "splitter plate" effect. Strategies for drag reduction were especially beneficial for corals inhabiting relatively high-energy environments, but the greatest significance may have been in reducing fatalities due to dislodgement during storms. The hydrodynamic behavior of coralla in life position, especially if leaning downcurrent, resulted in beneficial water flow. Vortices ascending from the substrate on the downcurrent side provided the polyp with water drawn from both the mainstream and the substrate surface. Such circulation facilitated feeding, enhanced the quantity and variety of food, and delivered other necessary substances. Wastes and gametes could be effectively expelled from the polyp and removed downcurrent without entrainment into the food-bearing flow. Functional analysis of the fascinating range of corallum forms in the Red River–Stony Mountain Province provides insight into paleobiology and paleoecology, which is applicable to many Paleozoic solitary rugosans.

Keywords: Solitary corals; Corallum shape; Functional morphology; Paleobiology; Paleoecology

1. Introduction

The vast majority of Paleozoic solitary rugose corals can be considered liberosessile (Neuman, 1988; Scrutton, 1998). Although most, if not all, liberosessile individuals were initially attached to relatively small objects, either they became detached or the objects were insufficient to provide support throughout life. The corals consequently lived free on soft substrates, depending on sediment to support the corallum with its calice in an orientation that was suitable for the polyp. Sessile benthic organisms such as corals rely on water flow to bring food items and necessary substances, as well as to remove wastes and spread gametes, but they also risk being overturned or transported by hydrodynamic forces (Wainwright and Koehl, 1976). Liberosessile solitary rugosans are rarely preserved in life position; death is attributed mainly to overturning, transportation, and/or burial during high-energy storm events (Scrutton, 1998). These corals would have benefitted from strategies that improved stability with respect to the substrate and currents, and that took advantage of water flow during life.

The purpose of this paper is to examine some innovative strategies involving the corallum form of liberosessile solitary rugosans. External form and its variation in such corals have been considered mainly in the context of adaptation to the substrate and enhancement of stability, in some cases in response to current strength (Scrutton, 1998). The present study goes further, by also considering the hydrodynamic behavior of coralla

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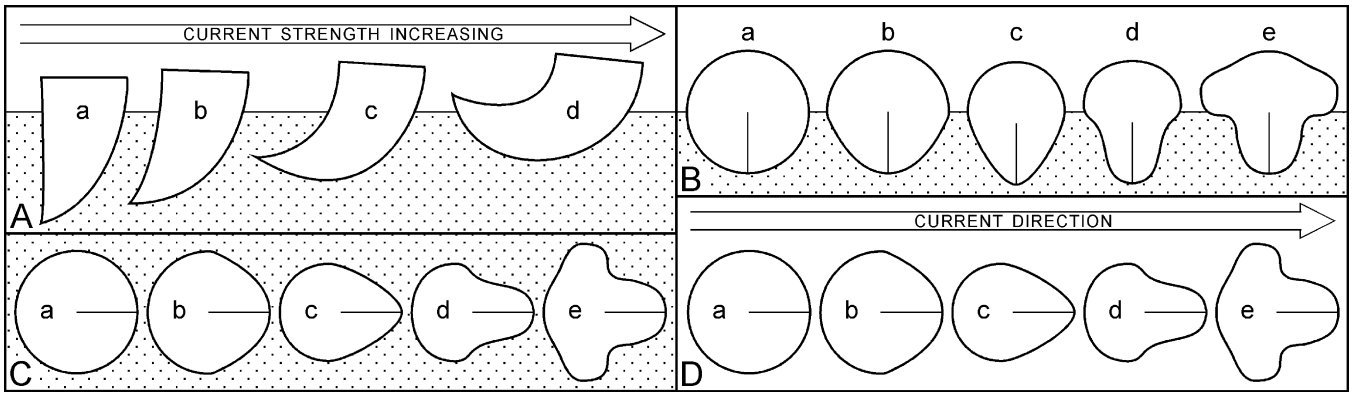

Fig. 1. Various views of liberosessile solitary rugosan coralla in life position. (A) Lateral views (cardinal side convex) showing orientation with respect to substrate-water interface (sediment stippled) and current direction (arrow), and relation between current strength (see arrow) and curvature of corallum (a, very weak; b, weak; c, moderate; d, strong). (B) Cross-sectional views (vertical orientation) of recumbent coralla (line is cardinal septum), showing orientation with respect to substrate-water interface (sediment stippled) and various cross-sectional shapes (a, circular equidimensional; b, triangulate equidimensional; c, triangulate compressed; d, trilobate compressed; e, trilobate depressed). (C) Cross-sectional views (horizontal orientation just below substrate-water interface; sediment stippled) of upright coralla (line is cardinal septum; cross-sectional shapes a–e as in B). (D) Plan views of calice rims (above substrate-water interface; line is cardinal septum; cross-sectional shapes a–e as in B), showing orientation with respect to current direction (arrow).

in life orientation and its possible benefits to the polyps. The findings of this functional analysis expand our understanding of the paleobiology and paleoecology of these extinct corals.

This paper focuses on particular liberosessile solitary rugosans in the Late Ordovician (Cincinnatian) Red River–Stony Mountain Province of North America. This biogeographic province occupied a vast area of predominantly carbonate deposition in the epicontinental sea and on the adjacent continental shelf (Webby et al., 2004). Among the characteristic solitary rugose corals are four closely related genera that are represented exclusively by liberosessile species: *Salvadorea*, *Grewingkia*, *Deiracorallium*, and *Lobocorallium*. This group exhibits a fascinating range of corallum forms; the trilobate cross-sectional shapes of *Lobocorallium* and some representatives of *Grewingkia* are unique among corals in general. Major publications in which these taxa are described and illustrated include Nelson (1963, 1981), Elias (1981, 1982a, 1983, 1985), and Buttler et al. (1988).

2. Corallum form and variability

As seen from the side and in cross-section, corallum form varies within and among *Salvadorea*, *Grewingkia*, *Deiracorallium*, and *Lobocorallium* in the Red River–Stony Mountain Province. The shape in lateral view is generally trochoid, but curvature is variable (Fig. 1A) as follows: *Salvadorea* (very weak to strong, usually weak), *Grewingkia* (weak to strong, usually moderate), *Deiracorallium* (very weak to moderate, usually weak to moderate), and *Lobocorallium* (weak to strong, usually weak to moderate). Coralla are smoothly curved in the cardinal-counter plane, with the cardinal septum on the convex side and the calice rim perpendicular to the direction of growth. The ranges of maximum corallum length attained by species of these genera are as follows: *Salvadorea* (50–75 mm, exceptionally 120 mm), *Grewingkia* (75–180 mm), *Deiracorallium* (22–88 mm), and *Lobocorallium* (125–150 mm).

In addition to the circular cross-sectional shape that is typical of solitary rugose corals in general (Fig. 1Ba), this group of genera exhibits a range from triangulate (V-shaped convex side; Fig. 1Bb, c) to trilobate (lobate convex and lateral sides; Fig. 1Bd, e). The degree of triangulation or trilobation in individual coralla commonly increases and then decreases progressively during ontogeny. With respect to cross-sectional dimensions in the cardinal-counter and lateral directions, coralla may be equidimensional (typical of solitary rugosans in general; Fig. 1Ba, b), compressed (laterally narrow; Fig. 1Bc, d), or depressed (laterally broad; Fig. 1Be). Cross-sectional variability of coralla is as follows: *Salvadorea* (generally circular, slightly triangulate in some; equidimensional), *Grewingkia* (usually triangulate, some circular or trilobate; generally equidimensional to compressed, some depressed), *Deiracorallium* (commonly triangulate; compressed), and *Lobocorallium* (trilobate; compressed to depressed).

3. Orientation during life

Virtually all liberosessile solitary rugose corals in the Red River–Stony Mountain Province are preserved in orientations that are consistent with deposition following transportation (Elias et al., 1988). Their life orientations were initially reconstructed using various lines of indirect evidence: location of associated boring and epizoic organisms inferred to be symbionts, location of bioclastic material partially embedded in the corallum wall during growth, location and orientation of the initial attachment site, and functional considerations (Elias, 1984). Verification was provided by the discovery of two specimens preserved incontrovertibly in life position beneath large colonial corals, which shielded them from high-energy events that transported other individuals (Elias and Buttler, 1986). Subsequently, in situ coralla were documented from a unique deposit that accumulated under relatively low-energy conditions (Elias et al., 1988).

During life, the cardinal-counter plane of the corallum was vertical, the convex side was down, and the calice rim was horizontal or nearly so (Fig. 1A). There was gradation from very