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Research paper

Morphological limits to diversification of the rugose and tabulate corals

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Abstract

At the family level, the evolution in the compound rugose corals is usually characterized by the progressive integration of corallites. This type of evolution corresponds to paedomorphic processes in the astogeny of colonies: the separation of the daughter polyp from the parent being progressively delayed as compared to the development of the other characters. At the end of the lineage, relations between mature polyps are similar to those existing in the first stages of the increase in the ancestor.

Tabulate corals are strictly colonial and usually have connections between polyp cavities. They can develop colonies similar to those known in the compound rugose corals (fasciculate or massive), but also other forms (such as cateniform, ramose and coenenchymal). However, a relative separation of growth habit exists between rugose and tabulate corals from their radiation during the Ordovician. Besides the differences in colony shapes, corallite diameters are generally larger in the Rugosa than in Tabulata.

Several crises affected Palaeozoic corals, and some of them caused the disappearance of major morphotypes. After these crises, neither the surviving tabulate nor the rugose corals gave rise to new taxa with these forms. The evolutionary processes in post-crisis coral recovery correspond mainly to heterochronic processes. These proceed within the limits of ontogenetic (or astogenetic) variability and do not allow innovations such as a type of colonial development that is not a usual type of increase within a taxon. Therefore, the replacement of extinct habits by an evolutionary convergence of taxa with other major habits does not occur in Palaeozoic corals. These evolutionary processes probably differ from those acting during an original evolutionary radiation.

Keywords: Evolution; Rugose coral; Tabulate coral; Heterochrony; Morphological variability; Recovery

1. Introduction

The disparity (i.e., the diversity at the level of the bodyplans and corallum forms) of the tabulate and rugose corals was at its highest level during the latest Ordovician and the earliest Silurian. Afterward, they suffered extinctions and lost major bodyplans and forms which were never replaced by evolution of the survivors. Consequently, after the late Frasnian extinctions, Tabulata lost their dominant position and only a few groups survived (Scrutton, 1997). Rugosa were not so highly affected and lost little of their disparity, but did not occupy the vacated tabulate morphologies. However, for other major groups of invertebrates or vertebrates, mass extinctions caused radiations, during which the survivors often assimilated the morphologies of extinct groups and reoccupied their niches. For example, bivalves replaced most brachiopods and the scleractinians the extinct tabulate and rugose corals after the Permian-Triassic crisis, and mammals replaced dinosaurs after the Cretaceous-Tertiary crisis. This paper is to address the question why Palaeozoic corals did not really recover after they suffered crises.

2. Comparisons between Tabulata and Rugosa

Tabulate and rugose corals were the dominant groups of corals during the Palaeozoic. They developed in the same environments and were associated. A comparison of their forms, corallite sizes, and morphological strategies is conducted here to see whether or not they occupied the same niches and thus were in competition.

2.1. Comparison of their main forms of coralla (Fig. 1A)

Tabulate corals had many forms of coralla and only a few were shared with rugose corals.

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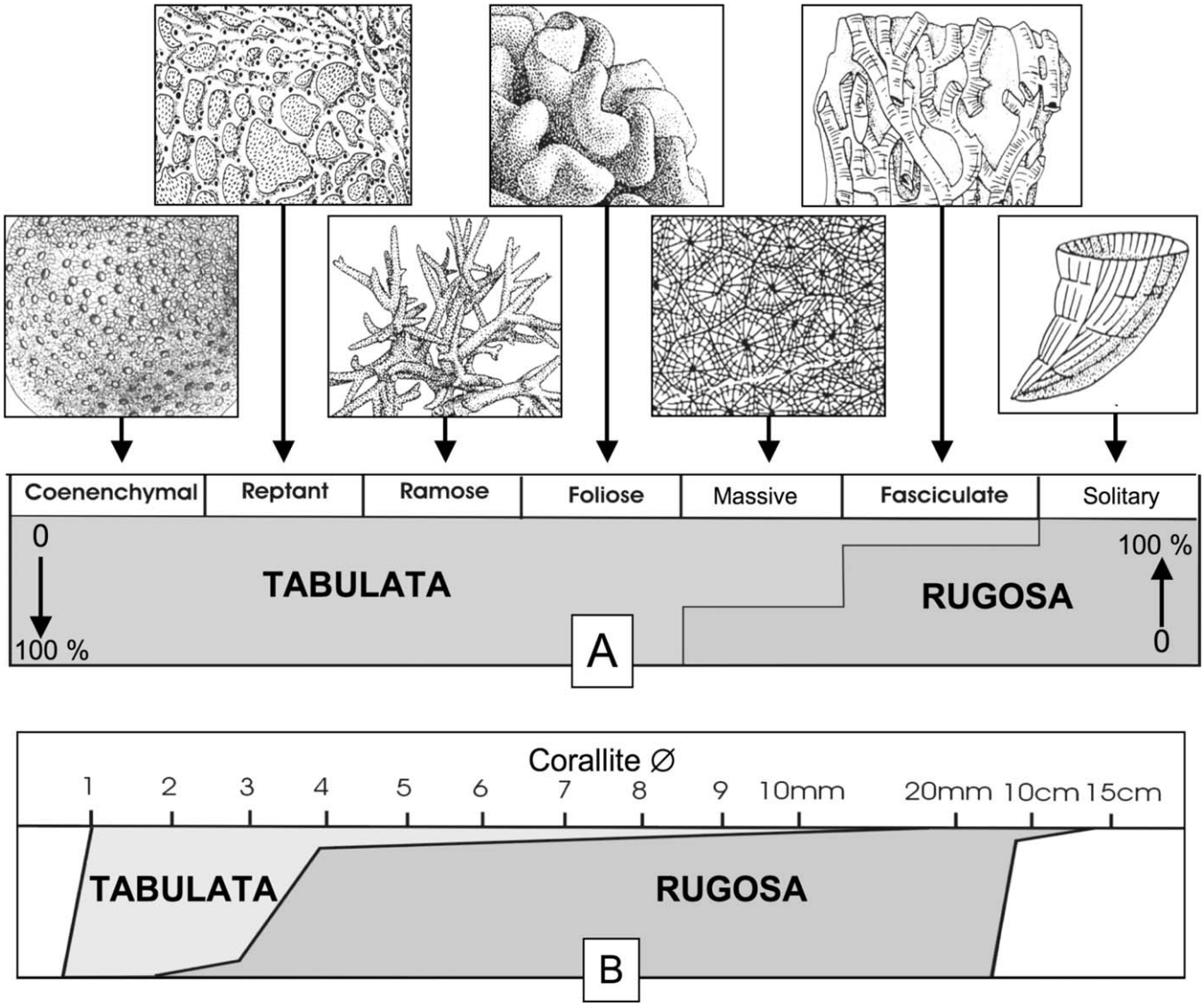

Fig. 1. (A) Comparison of the main forms of coralla in tabulate and rugose corals. (B) Comparison of the corallite diameters in Tabulata and Rugosa. Most Tabulata have diameters varying between 1 and 3 mm, whereas most Rugosa have diameters varying between 4 and 60 mm.

Coenenchymal (perforate and imperforate), cateniform, reptant, ramose and foliose coralla were restricted to tabulate corals. Cerioid and fasciculate forms were shared by tabulate and rugose corals, but the former is more common in tabulate (before the end of the Middle Devonian), and the latter is more in rugose corals. Only Rugosa had solitary forms. Moreover, integration between polyps (i.e., tissular or gastrovascular communications) is common in the tabulate corals but uncommon in the Rugosa.

2.2. *Comparison of their sizes (Fig. 1B)*

Tabulate corallites are narrow and their diameters are usually between 1 and 3 mm, but some genera can be narrower or wider. For example in cateniform coralla, the width (small axis) of the corallites can be as small as 0.8 mm in *Catenipora* sp. (Fig. 2A) and as large as 3.5 mm in *Catenipora maxima* (Fig. 2B), from the same Estonian locality of Llandoverian age. In fasciculate corallites, they can be as small as 0.6–1 mm in some Mississippian syringoporids (Fig. 2C), and as large as 6 mm in *Adaverina* sp. from the Llandovery (Fig. 2D). The larger sizes are known in michelinids up to 15 mm (Fig. 2E) or more, e.g., *Michelinia megastoma*.

In Rugosa, corallite diameters are larger than in Tabulata, varying usually from 4 to 20 mm in compound coralla and from 10 to 40 mm in solitary coralla. But in compound corals, corallites can be as small as 1.5 mm, for example, in *Siphonodendron junceum* from the Upper Viséan (Fig. 2H), whereas the largest species of the genus *S. scaleberense* also from the Upper Viséan can reach over 20 mm (Fig. 2G). In solitary corals, corallite diameter can be up to 120 mm and sometimes more, for example, in *Uralinia* cf. *gigantea* from the Upper Tournaisian (Fig. 2F).

There is almost no overlap of corallite diameters between Tabulata and Rugosa. Moreover, it seems that species sharing the range-size (and the form of corallum) characteristic of the other group occur mainly when the latter is absent or poorly developed in some environments. Thus, in the Upper Viséan