ORIGIN AND PALEOBIOLOGY OF WALL-BASED CORALS

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Plerophyllum (Permian)

Pachythecalis (Triassic)

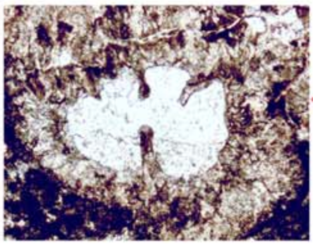
Gardineria (Recent)

Two basic structures of the coral skeleton - wall and septa - contribute in different degree to the formation of the corallum. In most species the septa appear predominant, and the remarkable diversity of their morphology and microstructural organizations have dominated attention since the beginning of coral studies. Clearly, the great evolutionary potential of septal microstructures, as well as the direct relationship of the septal system with the internal organization of the polyp, offered a wide perspective on the evolution of Scleractinia.

Shallow-water, zooxanthellate *Siderastrea* (Recent)

Deep-water, azooxanthellate *Letepsammia* (Recent)

In *Pachythecalis* (Triassic) the wall is a predominant skeletal element. Longitudinal section (left) with strong ring-like wall foldings (arrow), and transverse section (right).

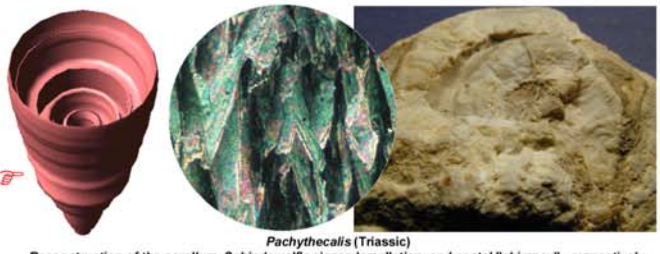


Pachythecalis (Triassic) - initial septal insertion pattern is identical to that in some Late Permian Plerophyllina.

In some cases, however, the wall becomes so strongly predominant that questions arise about the origin of this unusual skeletal structure as well as its possible biological significance. Among Recent corals, *Guynia* and *Gardineria* are examples of such predominately wall-based genera, but looking back to the Triassic origin of Scleractinia, corals attributed to Zardinophyllidae probably exhibited the highest degree of wall-dominated organization.

Extreme examples of "wall-based" coral architectures

In Zardinophyllidae (5 solitary and phaceloid fossil genera), the wall is developed in advance of the septa, forming a long conical or pipe-like calice, whereas relatively few septa are later developed, being hidden deeply in the calice. *Pachythecalis*, one of the largest Triassic solitary corals, builds a conical wall, thickened centripetally by aragonite fibers arranged in penicillate units, which if diagenetically altered may display Schindewolf's zigzag lamellation. Rhopaloid septa are smooth, and their calcification centers are not separated. Striking features of the *Pachythecalis* are its strong ring-like wall foldings, and the reduction of the septal part to a small "chimney".



Pachythecalis (Triassic)
Reconstruction of the corallum, Schindewolf's zigzag lamellation, and septal "chimney" - respectively.

Extant *Guynia* and *Gardineria* have an almost identical general skeletal architecture as early Mesozoic Scleractinia. Both genera have entirely epithecal walls, thickened centripetally by aragonite fibers. *Guynia* especially resembles solitary zardinophyllids in having a long, pipe-like epithecal calice, and a reduced number of smooth septa with non-separated calcification centers, but differs from them in septal insertion pattern, having specialized thecal pores, and dwarf size. In *Gardineria*, although septa are much better developed than in *Guynia*, the thick epithecal wall remains the main structural unit. In both genera, as well as in various other corals, formation of the epithecal wall, and not septa, appears to be most resistant to unfavorable environmental conditions ("rejuvenescence").

Zardinophyllum (Triassic)

Pachydendron (Triassic)

Gardineria (Recent) - skeletal architecture (left) and distal view of the calice (right)

Guynia (Recent) - skeletal architecture (left) and istal view of the calice (right)

Origin of the wall-based corals

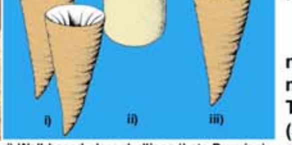
Ontogenetic and microstructural relationships between wall and septa, as well as the initial septal insertion pattern, in wall-based Triassic Zardinophyllidae are also identical to that in some Late Permian Plerophyllina, contributing to the following hypothesis of their evolutionary relationships. In the presumed scenario of pleurophylline -› zardinophyllid transition we distinguished three successive steps:

i) a progressive change of biogeochemical conditions in the Late Permian caused severe stress among the coral fauna. Among survivors are some pleurophylliines, a number of them demonstrating the "wall-based" architecture especially in early growth stages;

ii) increase of the chemical stress led to an hiatus in biomineralization of Anthozoa (and perhaps astrosclerid sponges), reflected by the lack of their fossil remains (ca. 10-15 Ma);

iii) recovery of an effective biomineralization could be associated with a minor change in biochemical composition of mineralizing matrices, driving mineralogical change between these corals - calcite vs. aragonite skeletal fibers. Today, similar minor changes in microstructural units occur in some cnidarians (stylasterids), and a calcitic/aragonitic sequence of microstructural units is very frequent in shells of bivalves for instance.

In *Hoplangia* (Recent) as well as various other corals, formation of the epithecal wall, and not septa, appears to be most resistant to unfavorable environmental conditions ("rejuvenescence").



i) Wall-based plerophyllines (Late Permian)
ii) Hiatus in biomineralization (Early Triassic)
iii) Wall-based zardinophyllides (Middle Triassic)