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ON THE RELATIONSHIP BETWEEN RUGOSA AND SCLERACTINIA (SUMMARY)

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Mesozoic-Cenozoic scleractinian corals were not derived by descent from late Paleozoic rugose corals. Rather, they probably originated from a group of Paleozoic sea anemones that survived into the Mesozoic after the extinction of the Rugosa at the end of the Paleozoic. This conclusion is based on three arguments: 1. all scleractinians have cyclic septal insertion in contrast to the serial insertion of rugosans; there are no intermediates; 2. scleractinians have aragonite skeletons; those of rugosans are calcite; 3. there are no Lower Triassic corals. It is unlikely that two important characters (points 1 and 2) would change so drastically during the only stage in the history of the corals in which no corals are known (point 3).

Key words: corals, Rugosa, Scleractinia, Permian-Triassic evolution.

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INTRODUCTION

Modern stony corals (hexacorals) belong to the Order Scleractinia which ranges from Middle Triassic to Holocene. The Paleozoic analog of the Scleractinia is the Order Rugosa (rugose or tetracorals) which ranges from the Middle Ordovician through the Permian. Two hypotheses of the relationship between these two groups of corals are current: 1) direct descent; the Scleractinia evolved directly from the Rugosa, either mono- or polyphyletically; and 2) independent origin; the Scleractinia evolved by the development of a skeleton in members of one of the soft-bodied anthozoan groups that probably existed throughout the Paleozoic.

Of the many lines of evidence that have been used to argue either for or against a direct descent relationship between rugose and scleractinian corals, only three seem fundamental. These are summarized here and discussed in the following sections.

I. Rugosan septal insertion is serial and bilateral for major septa, and probably so for minor septa; scleractinian insertion is cyclic and either bilateral or radial.

II. Rugose coral skeletons were apparently composed of calcite; scleractinian skeletons are, and most were, of aragonite.

III. The latest known rugose corals were latest Permian in age; the earliest known scleractinians were Middle Triassic. No Early Triassic (Scythian) corals are known.

Advocates of either hypothesis must make their arguments conform to the above lines of evidence.

Schindewolf (1942) summarized earlier discussions and set the stage for all later work. More recent analyses are those of Iljina (1965), Montanaro-Gallitelli (1975) and Cuif (1977).

I. SEPTAL INSERTION

The typical patterns of septal insertion in rugose and scleractinian corals are shown in figures 1 and 2. The fundamental difference between the two coral groups is that rugosan insertion is serial (producing the pinnate appearance in many forms) and that scleractinian insertion is cyclical. Comparison of figures 1 and 2 should make this difference clear.

All anthozoans are bilateral. All living polyps show this bilaterality in an elongate mouth and pharynx, in the arrangement of muscles, and in the arrangement and development (insertion) of their mesenteries. Rugosan skeletons are strikingly bilateral in their early stages but may appear either bilateral or radial when mature. Scleractinian skeletons more commonly appear radial, but obviously bilateral skeletons are known throughout the record of this group.

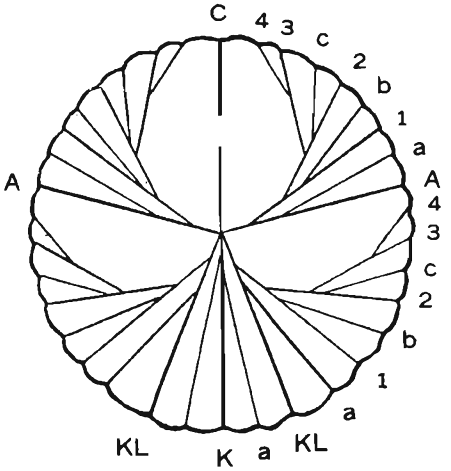

Fig. 1. Serial-bilateral insertion of septa in rugose corals (after Hill (1935)). Protosepta: *C*, cardinal septum; *A*, alar septa; *KL*, counter-lateral septa; *K*, counter septum. Metasepta: *1, 2, 3, 4* (in order of insertion in each sector). Minor septa: *a, b, c* (in order of insertion in each sector).

Septal insertion in Rugosa is invariably bilateral; in Scleractinia, it is commonly bilateral. I hypothesize that the insertion of major septa in rugosans is invariably serial, whereas Scleractinian insertion is invariably cyclic. Too many coral specialists

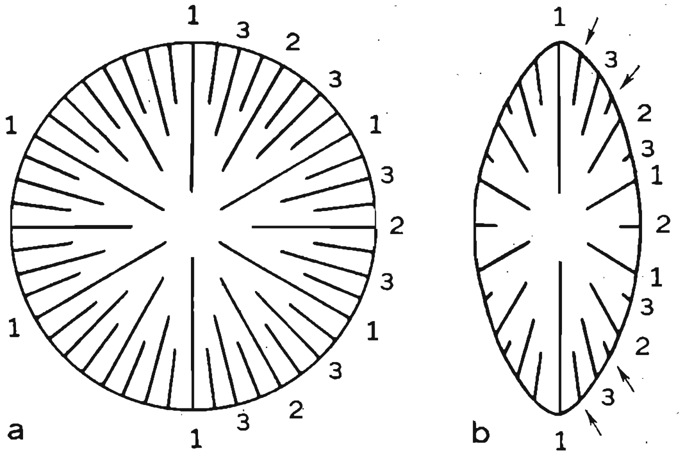

Fig. 2. Cyclical insertion of septa in scleractinian corals (after Wells 1956). a. Cyclical-radial insertion with four full cycles shown although the fourth cycle is not labeled. b. Cyclical-bilateral insertion with acceleration at both poles. Cycles one and two are complete; third cycle septa are complete in "polar" sectors, missing in lateral sectors; fourth cycle septa (arrows) present only in "polar" half-sectors. Key: *1*, protosepta; *2*, *3*, *(4)*, metaseptal cycles in order of insertion.

have emphasized bilaterality as a common character of rugose and scleractinian corals without noting that this is a basic feature of all Anthozoa.

Schindewolf's (1942) work on the late Paleozoic polycoeliids is basic to this part of the discussion. He emphasized that both rugose and scleractinian corals showed bilateral septal insertion, commonly manifested in the accelerated development of septa in two (or four) of the primary sectors.

Schindewolf did illustrate one Permian coral with apparent exceptional septal insertion. This was a specimen of *Pentaphyllum gracile* Schindewolf (1942: 203, 246; fig. 85*a*—*i*). Schindewolf had only a single specimen of this species and it seems most likely that it represents some kind of an accident and that the apparent deviations from the normal rugosan insertion plan were teratological and had no evolutionary significance.

Schindewolf's extensive study of the Polycoeliidae is of special importance, because this is the group of tetracorals that many workers have considered to be the specific ancestor of the scleractinians. He concluded that all Paleozoic rugose corals had serial-bilateral insertion (in spite of the noted "exception") and based his argument for direct descent on 1) the presence of six primary septa and sectors in both rugosans and scleractinians, 2) the existence of bilateral insertion (with accelerated sectors) in both, 3) the presence of cyclically inserted minor septa in all rugosans, and 4) the presence of a second cycle of minors ("tertiary septa") in some rugosans.

The most important discussion of late Paleozoic rugosans and their possible relationships since Schindewolf's, is that of Iljina (1965). Iljina followed Schindewolf in advocating direct descent after a study of late Paleozoic polycoeliids, although she disagreed with him in some details. She cited *Plerophyllum differentiatum* Iljina (1965: 52—56) as having features very similar to those of the hexacorals, including, in some individuals, major septa in the counter sectors, irregular insertion of major septa in other sectors, and the irregular presence of third-order septa (1965: 30, 52, 53—55). However, all of Iljina's illustrations can be interpreted as showing typical tetracorals, both in pattern of insertion and in lacking major septa in the counter-lateral sectors, and none of her septal formulae indicate the presence of major septa in the counter-lateral sectors. Iljina's work is of importance in elucidating the morphology of the latest tetracorals yet known, but she has not demonstrated a transition to the hexacorals.

Weyer (1972: 724—729) accounts for the apparent "out-of-order" insertion of septa in some of the polycoellids as due to the "loss" of major septa in the lower calice and subtabular parts of the coral wall because of wall thickening.

Positive identification of the protosepta and of the order of insertion of the metasepta requires that the very tip of the coral be available for study. The loss of 2 mm or less at the tip makes identification questionable and much of the controversy in the literature over insertion is because the preservation and study of the coral tip is so uncommon.

The insertion of major septa in the counter sectors in Paleozoic corals has not been demonstrated. Numerous contrary statements that have been made refer to corals of each period from Silurian to Permian but all such descriptions are probably based on erroneous interpretations.

Minor septa have been described as either serially or cyclically inserted, but they are cyclic in the sense that they are inserted in each interseptal space so that the number of minor septa commonly equals the number of major septa. Insertion is common bilateral beginning in the space next to the oldest metasepta (as shown in fig. 1). Insertion of minor septa and metasepta may take place together so that a regular alternation of major and minor septa exists throughout the further development of the coral. As new major septa are serially inserted, minor septa are also inserted in the new interseptal spaces. Weyer (1972) convincingly argued that this is the only mode of insertion, referring to it as the "serial and retro-alternate manner well-known from *Cyathaxonia*" (1972: 721—722, 729, 730). If Weyer is correct, then paired minor and metasepta are serially inserted in each of the four insertion positions and the minor septa *do not* form a cycle in the scleractinian sense.

Some corals have been described as lacking minor septa but this may be only apparent as minor septal grooves may be present on the outer wall even though the septa cannot be seen as inward projections from the wall (see discussion in Weyer, 1972: 715—724).

Third order septa have been described or noted in rugose corals of Silurian, Devonian, Carboniferous and Permian age. Occurrences were reviewed and some good Devonian examples were illustrated by Sayutina (1965). Fourth and fifth order septa have also been reported. In described examples, the third and higher orders of septa are commonly incomplete although examples of complete or virtually complete third orders, are known. The insertion pattern or mode of third and higher order septa is not known, but it is difficult to attach any evolutionary significance to them because they show no consistent or general pattern.

The argument over the number of protosepta in rugosans is largely sterile and neither strengthens nor weakens arguments for or against direct descent. Certainly a six-septa stage exists and I have labeled these six septa as protosepta in figure 1. However, I have done this to avoid reducing or diluting my emphasis on serial insertion in four sectors. Flügel (1975: 418—419) pointed out that in all respects the counter-lateral septa behave as though they were the first pair of metasepta in the alar sectors (quadrants if this interpretation is correct); this includes their relationship to the single minor septum in each counter sector. If Weyer's statement regarding the insertion of minor septa is correct then the recognition of six protosepta and six sectors in the Rugosa is not logical.

The typical insertion pattern for scleractinian corals (hexacorals) is cyclic and radial in appearance (but probably not in reality). This pattern is simple to diagram (fig. 2a) and is well known to all coral specialists. Protosepta may be inserted two at a time so that stages having two, four, or six protosepta exist in many (or most?) scleractinians. Insertion of later septa in the six sectors is commonly bilateral also (see Schindewolf 1942: 232—243; and Cuif, 1977: 30—32, fig. 6). The bilateral insertion of septa reflects the bilateral insertion of mesenteries and the basic bilateral symmetry of all known anthozoans.

Schindewolf (1942: 236—239) described and illustrated several Triassic corals as intermediates between tetracorals and scleractinians, but this interpretation was totally based on bilateral insertion (as was stated), and all examples are cyclic and have insertion in six sectors.

Schindewolf diagrammed his concept of rugosan-scleractinian evolution in a series of figures (1942: figs 123—128, repeated in figs. 139*a*—*f*). The key element in Schindewolf's scheme is a hypothetical missing link (his figs. 126 and 139*d*) which has not been shown to exist.

Iljina (1965) discussed and illustrated several scleractinians as possible intermediate forms. However, as in Schindewolf's examples, all scleractinians discussed have cyclic insertion in six sectors.

Montanaro-Gallitelli (1975) discussed the ontogeny and septal insertion in some "primitive" Triassic corals (Carnian; Italian Alps). In *Zardinophyllum zardinii*, protosepta are inserted bilaterally, two at a time, as earlier noted by Schindewolf (1942). Only 20% of the specimens studied have "more or less developed" metasepta, but these were said to be inserted at random, and neither a serial nor a cyclic plan could be recognized. It seems most likely that *Zardinophyllum* is an aberrant scleractinian because the principal differences between rugosan and scleractinian septal insertion are seen after the protoseptal stage, and *Zardinophyllum* does not develop to a stage where its affinities might be recognized.

Cuif (1977) gave the most extensive modern discussion of rugosan-scleractinian relations by a scleractinian specialist. Cuif favored direct descent and based his argument on several lines of evidence. In discussing septal insertion, he emphasized bilaterality ("polarity gradient") in the Scleractinia and illustrated numerous examples (see Cuif, 1977, especially fig. 6 and pls. 9—10). All the forms that he illustrated have cyclic septal insertion and Cuif added nothing to the arguments of previous workers in this respect. He did show clearly that scleractinian septal cycles can be bilaterally introduced from either or both poles. However, this is not the serial bilaterality of Paleozoic corals.

II. SKELETAL MINERALOGY

There is direct evidence that some rugosan skeletons were originally calcitic, and indirect evidence suggests that most or all were calcitic. In contrast, all living scleractinians have aragonitic skeletons. In addition, there is direct evidence that some fossil scleractinians were aragonitic and indirect evidence that most were.

Well-preserved calcitic rugosans, found associated with molluscs in which original aragonite is preserved, provide direct evidence that the original skeletal mineralogy of these rugosans was calcitic (Sorauf 1977, and included references). In addition, $MgCO_3$ content and Sr/Ca ratios in rugosans provide further evidence that the existing calcite was not converted from an original aragonite (Lowenstam 1964; Sorauf 1977). Furthermore, there is no direct evidence that any rugosans had aragonitic skeletons.

Indirect evidence for original calcite in rugosans can be simply stated: so many calcitic rugosans have such well preserved microstructure that it is unlikely that these could have been originally aragonitic; conversion from aragonite to calcite produces drastically different, much coarser textures.

All living scleractinians have aragonitic skeletons, and well-preserved aragonitic fossils of this group are known from rocks of Triassic and later age (Montanaro-Gallitelli 1975 and included references; Cuif 1977). Commonly, fossil scleractinians are very poorly preserved either as molds or composed of coarse calcite or dolomite; this poor preservation suggests that most scleractinians were originally aragonitic.

There is good evidence indicating that conversion from aragonite to calcite destroys or distorts skeletal microstructure and produces new coarse textures that cannot be mistaken for the original structure. This view has been supported by many carbonate petrologists and paleontologists (see review by Sandberg, 1975: 511—532).

Coral specialists have observed that Paleozoic rugosans commonly show microstructure whereas Mesozoic-Cenozoic scleractinians commonly do not. It is very unlikely that similar skeletal structures would be so differently preserved if their original mineralogy were the same.

The meaning of mineralogic difference in skeletons is uncertain. Extrinsic (environmental) factors might be important if there had been a change in oceanic chemistry through Phanerozoic time, but it is more likely that intrinsic biological differences were responsible for the mineralogical change.

Lowenstam (1964) noted that given independent origin of the two groups of corals, "the mineralogic differences... are related to physiologic differences of genetically distinct stocks that acquired carbonate metabolism at different times". On the other hand, if descent were direct, the mineralogic differences would be related to biochemical changes in a single evolving stock. The first alternative seems much more likely because it does not involve any sharp or sudden change in an evolving stock.

III. NO LOWER TRIASSIC CORALS

No corals are known from Lower Triassic rocks (Wells 1956; Krasnov 1970). Iljina (1965) described probably the youngest known Rugosa as Lower Triassic, but later revisions of Permo-Triassic zones and stages have placed these in the Permian (see Kummel and Teichert 1973, and numerous other papers in the same Permian-Triassic boundary symposium). The important point is the existence of a significant time gap between the last rugosans and the first scleractinians.

Kummel (1973) reviewed the fossil record of the Scythian Stage (Lower Triassic), and noted that all facies except true reefs are known in Scythian rocks. He concluded that the absence of a particular group of animals could not be blamed on the lack of a "correct" facies. Scythian limestones and shales are common, especially in the Tethys region (Kummel 1973: 560).

CONCLUSIONS

Three lines of evidence bearing on the possible relationships between the Rugosa and Scleractinia have been examined: 1) septal insertion, 2) skeletal mineralogy, and 3) the Lower Triassic gap. I conclude that: 1) bilateral symmetry is fundamental in anthozoans but that all rugosans have serial insertion (and are Paleozoic) and all scleractinians have cyclic insertion (and are Mesozoic-Cenozoic, and there are no morphologic intermediates; 2) the evidence indicates that rugosan skeletons were calcitic and that skeletons of Mesozoic scleractinians were aragonitic; the nature or meaning of the change from one to the other is not clear but the difference would seem to be fundamental; and 3) no corals are known from the Lower Triassic although many other groups of marine animals are known and appropriate facies are present.

Point 1, septal insertion, seems most clear and fundamental and is independent of the other points. Point 2, skeletal mineralogy, is also important even if we do not understand the processes involved, because the change is so complete. Point 3, the Lower Triassic gap, becomes very important in combination with 1 and 2: for two unrelated major changes to take place at the same time is coincidence, but for the changes to take place during the only stage in the history of the corals in which corals are totally lacking, defies acceptance.

Proof of the independent-origin hypothesis does not (and may not ever) exist, but separate origins of the two groups is much easier to explain than direct descent. The Rugosa probably became extinct at or near the end of the Paleozoic (as did many other groups of animals at all taxonomic levels). This vacated a niche that had been successfully occupied for 250 million years. As soon as any existing group of sea anemones "experimented" with secreting a skeleton, the way was open for the niche to be occupied by a new group of corals. In the Middle Triassic the Scleractinia developed in this way, possibly polyphyletically, and met with increasing success in succeeding periods.

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