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Discussion

Rugosa and Scleractinia – a commentary on some methods of phylogenetic reconstructions

JERZY FEDOROWSKI

The origin of the Rugosa and relationships between the Rugosa and Scleractinia are debated. In the present account I comment on some recently published phylogenetic reconstructions, which in my opinion, are based on inadequate data.

Cothonion as a rugose coral ancestor

Dzik (1993) made an attempt at the reconstruction of the earliest history of the Rugosa. He favored the early Middle Cambrian operculate *Cothonion* Jell & Jell, 1976, as ancestral for all of the Rugosa. He based his conclusions only on the original description of Jell & Jell (1976), who described (p. 186) the external wall of *Cothonion* as follows: 'Externally the corallites are covered by a thin sheath showing well developed concentric growth lines [...] Specimens with this outer sheath not evident exhibit fine, closely spaced longitudinal striation, extending from the apex to the calical rim...'. Identical striation was mentioned by Jell & Jell (1976) and illustrated (fig. 9C, E) on the opercula. No interpretation or further investigation of such a double external wall were given by them. The wall was not considered by Dzik (1993), although such microstructure is unknown among the Rugosa and should be thoroughly studied in any paper dealing with phylogeny of that group of animals.

The calices of *Cothonion* are very deep. However, transverse and longitudinal sections illustrated by Jell & Jell (1976: fig. 7A–C) and described (p. 186) as showing 'the lumen [...] filled with calcite fibres...' show either the external wall in a sense accepted for the Rugosa (fig. 7A, B) or, at most, a type of basal disc or attachment (fig. 7C), but not a lumen *sensu stricto*. Thus, true lumina are either absent from that genus (they are also absent from the oldest uncontested rugosans, the Palaeocyclidae Dybowski, 1873), or require additional study and re-definition.

Septa in *Cothonion* were described by Jell & Jell (1976) as inserted in three cycles appearing successively upward in the calices. However, the sequence and pattern of their appearance, crucial for any phylogenetic consideration, have not yet been established. The same is true for septa developed on the opercula. As stated by Jell & Jell (1976: p. 189): 'Usually 2, 5 or 7 of the first order septa are longer and more prominent than others [...] no septum appears in the fossula, but there is a long septum opposite the fossula'. The foregoing statement leaves no doubt that the authors were unable to establish protosepta. They succeeded only in establishing the length of some structures considered to be septa, but the information presented by Jell & Jell (1976) does not allow to compare the mode of septal insertion of *Cothonion* with that of Rugosa. Moreover, these structures are not necessarily 'septa' in the sense established for Coelenterata, although they may have been dividing structures called 'septa' in such taxa as the Annelida or the Archaeocyathida. Thus, the process of septal insertion, axiomatic for any phylogenetic considerations within Coelenterata, remains unknown in the calices and is totally different (on opercula) from that in the Rugosa.

The details described and illustrated by Jell & Jell (1976) were as precise as the material allowed, but are, nevertheless, inadequate for establishing the true taxonomic position of *Cothonion*. These authors placed their new family Cothoniidae in the Rugosa with a question mark. Hill (1981: p. F669) considered that genus and family as 'Taxa probably neither Rugosa nor Tabulata'.

Regardless of the facts presented above, Dzik (1993) simply considered that genus to be a rugosan coral, and made it ancestral for all of the Rugosa. He proposed his own reconstruction of *Cothonion sympomatum* Jell & Jell, 1976 (Dzik 1993: fig. 14a) which, contrary to his explanation for the illustration 'based on Jell & Jell (1976)' cannot be compared to any specimen illustrated by those authors. They did not show a calice with septa identical to Dzik's (1993) drawing, an operculum with septa arranged more or less in the rugosan manner, or the relationship between the calice and the operculum as drawn by him. Thus Dzik's (1993: fig. 14a) reconstruction is his subjective interpretation of various illustrations of Jell & Jell (1976). Dzik (1993: p. 372) stated: 'Adults of *Cothonion* are so similar to juveniles of *Calceola* that a convergent origin of such an organization in each of them seems hardly possible.' In this way he introduced the 'recapitulation theory' in its classic form, ignoring all gaps in the available data. Such an approach led him to ignore not only everything what could have happened, but is not preserved, in coelenterate evolution during 120 Ma that passed between the existence of *Cothonion* and *Calceola*, but also the sequence of appearance of individual morphotypes or taxa that have been documented.

When discussing the *Cothonion* problem, one should take into account the following data: (1) early Middle Cambrian *Cothonion* is morpholgically, ontogenetically and microstructurally dubious. The characteristics established to date are non-rugosan; (2) Rugosa-like and truly rugosan taxa have not been recorded in the time span between Middle Cambrian and Middle Ordovician; (3) Ordovician rugose coral taxa are rich and diversified; (4) they gave rise to several lineages or morphotypes that expanded into the Silurian and Devonian, except for the operculate morphotype; (5) operculate rugose coral taxa are restricted to a comparatively short time span: Silurian–Middle Devonian; (6) they developed a restricted number of morphotypes (taxa) but invented several types of opercula, mostly smooth; (7) most genera included in the Goniophyllidae (Calceolidae, according to Weyers' 1996 revision) are inadequately studied in terms of their early ontogeny, and, in particular insertion of first septa; (8) none of the Silurian–Devonian operculate taxa have septa in their calices similar to the septa in the *Cothonion*; (9) it is not true that 'linearly distributed attachments are the only signs of radial organization of the interior of the corallite' in *Calceola* (Dzik 1993: p. 374).

All of the above facts were either omitted or misinterpreted in Dzik's (1993) recapitulation of the early phylogeny of the Rugosa. He took the morphology and ontogeny of *Calceola sandalina* as the main basis for his reasoning and wrote (p. 374): 'As the opercular septa disappear later in ontogeny (while some incipient septa in the corallite develop at the same stage), there is hardly any reason to believe that they, as well as the operculum itself, are derived features.' and concluded: 'If so, the apparent morphocline ranging from rounded to angular in cross-section regular rugosan corallites (*Areopoma*), to corals with several internally smooth, irregular opercula (*Goniophyllum*), and finally to a brachiopod-like operculate form should perhaps be rooted at the end opposite to the traditionally assumed one.' My questions concerning that reasoning are: (1) Why is the disappearance of septa from the operculum late in the ontogeny conclusive for considering that structure (operculum) ancestral, if the intermediate taxa possess smooth opercula? Does this not contradict the recapitulation theory that seems to be the basis for the whole reasoning? (2) Why have taxa possessing four (*Areopoma*) and more (*Goniophyllum*) aseptate opercula been placed in the middle of a lineage that started and ended with taxa possessing single, septate opercula (i.e., *Cothonion* and *Calceola*)? (3) Why should operculate taxa be considered ancestral for all the Rugosa if they appeared after the main period of differentiation of the subclass?

The idea presented by Dzik (1993) of the underdevelopment or absence of nematocysts during the early evolution of the Cnidaria in combination with the development of opercula for protection against large arthropod predators looks attractive. I leave aside the problem of the Rugosa not being recorded from the time when those arthropods were supposed to be most active, i.e., Late Cambrian–Early Ordovician. Also, I will not bring up the problem of paucity of large arthropod predators in the fossil record. However, why is there practically no record of the early rugosan corals being wounded by those arthropod 'major predators on coelenterates' (Dzik 1993)? And, why are operculate rugose corals known to have occurred exclusively in the Silurian and Devonian, i.e., when the vertebrate and mollusc predators, suggested by Dzik (1993) to be promoting increased efficiency in the rugosan nematocysts, were already flourishing? I wish to remind the reader that rapid development of cephalopod predators early in the Ordovician is commonly considered to be the main reason for the abrupt decrease of trilobites.

The origin of Scleractinia

The origin of Scleractinia was recently debated by Wendt (1990) and Stolarski (1996). Below, I shall review critically the validity of some conlusions reached by those authors in the context of the current knowledge on morphology and evolution of Rugosa and Scleractinia.

Rugosa-Scleractinia similarities

The majority of morphological features of the Rugosa are similar or identical to those in the Scleractinia, both in their macro- as well as their microarchitecture. One can hardly find a structural element that is present in one and absent from the other taxon. Moreover, the microstructure of individual structural elements suggests a similar, if not an identical, development. The investigation by Barnes (1972) of the mutual relationship between soft and hard parts as well as the interpretation by Sorauf (1972) of biomineralization of the skeleton within the Scleractinia can be applied to the Rugosa.

External wall. — Although most of the Scleractinia develop a complex, mainly trabecular external wall, and most of the Rugosa restrict themselves to a primitive epitheca, there are examples showing the opposite in both taxa. Stolarski (1996) described an epitheca in extant *Gardineria* and discussed the modes of development of the more complex external wall in some other scleractinians. Early information on the microstructure and formation of individual structural elements in the Rugosa, was given by Kato (1963). This has since been furthered by several authors in great detail. The external wall in solitary Rugosa show an epithecal structure. Also, most colonial Rugosa possess external walls which are non-trabecular, although not necessarily identical in origin. Fedorowski (1965) investigated the formation of two types of non-trabecular walls – both primitive fibro-normal, but one comparable to fibro-normal septa, and the other to typical epitheca. There are some Wentzelellinae of the Tethys Realm that possess walls with complex microstructures. Minato & Kato (1965) utilized that character as a subgeneric and generic taxonomic indicator, and were followed by other students. However, it can hardly be compared, if at all, with the trabecular walls in the Scleractinia, being at most composed of septa common to neighboring corallites. Thus, a better comparison could be drawn between the rather simple, epithecal walls of ahermatypic scleractinians, and those of the Rugosa, than between the complex rugosan external walls and the trabecular walls in the Scleractinia.

Calice rim. — The Scleractinia may generally be characterized as possessing an edge zone, whereas the calice rim in most of the Rugosa forms the outermost part of their skeletons. However, exceptions are present in both taxa. The Devonian family Phillipsastreidae Roemer, 1883 is the best known example and the Carboniferous/Permian family Sestrophyllidae Fomichev, 1953 is another. Stratigraphically advanced (i.e. Early Permian) representatives of the latter family from SW Texas not only developed an advanced edge zone, but also reduced their external walls to isolated rings (Fedorowski in preparation). These taxa exhibit edge zones strikingly similar to those commonly occurring in the Scleractinia. The question concerning similarities or differences in mechanisms of skeletogenesis in both subclasses remains open, because external walls in rugosan taxa developing an edge zone are never trabecular; or at least, trabeculae have not yet been found in such walls.

Septa. — In spite of their origin (sequential rather than cyclic) and mineralogy (calcitic rather than aragonitic), the microstructure of septa in the Rugosa is strikingly similar to that in the Scleractinia. Again, a rather simple fibro-normal microstructure prevails in the Rugosa, whereas it is almost entirely restricted to rare ahermatypic taxa among Scleractinia. However, trabecular septa are known to have occurred throughout the history of the Rugosa including the Late Permian, Dzhulfian (= Wuchapingian) taxa from Transcaucasia (Ilina 1965).

Dissepiments and tabulae. — Although students of scleractinian corals prefer to use the term dissepiments, rather than tabulae, both structures are present in sleractinians and both are closely comparable to those in the Rugosa. There is, perhaps, no structure in the Scleractinia comparable to the type of tabulae occurring in the ampleximorphs or forming an aulos in the rugose corals, but such small details should not be considered in a general comparison. Thus, there is no contradiction in extending Wells' (1969) reconstruction of the development of dissepiments in the Scleractinia to the formation of dissepiments and tabulae in the Rugosa. Also, the interpretation of the origin and mutual relationship of primary and secondary skeletal structures, first proposed in a broad sense for the Rugosa by Schouppe & Stacul (1955), can well be applied to the Scleractinia.

In this discussion I have omitted such morphological structures as synapticulae, various types of columella and/or axial structures, attachment processes and/or rhizoids, spines, caps, etc., present in one or both subclasses. These structures are not crucial for the present discussion. However, I believe that most morphological features discussed above seem to be similar in the two groups (analogous), rather than truly related (homologous). The incomplete external walls and calice edge zones present in some Rugosa can well be explained as traits which evolved independently from each other and were restricted to short and separated periods of time in Devonian and Late Carboniferous–Early Permian. The similar microstructure of radial and basal morphological structures in both subclasses derived from secretion by either flat or folded epidermis of various parts of polyps. Thus, they developed in such a manner, because the primitive level of development of the Anthozoa offers restricted possibilities for morphological and microstructural variation.

In the above conclusions I do not wish to discredit the taxonomic value of the characters discussed, especially that of the microstructure of septa. I only try to draw attention to the fact that identical macro- and micro-structures, for instance edge zones and trabeculae, may well appear independently within the Rugosa and the Scleractinia.

Rugosa – Scleractinia differences

Mineralogy. — The skeletons of the Rugosa are generally calcitic and of the Scleractinia generally aragonitic. Excellent preservation of many thousands of rugosan specimens collected from the Middle Ordovician through Permian. and investigated during many decades, has made it clear that we are mostly dealing with original mineralogy. Secondary changes such as dolomitization, silification, recrystallization, etc., are known. The summary by Sorauf (1993: p. 68): '[...] Paleozoic corals, both rugosans and tabulates, had a calcitic skeleton with considerable magnesium present, although probably not high-magnesium calcite...' allows me to omit discussion of Wendt's (1990) considerations in this matter. Sorauf (1993) did not exclude the possibility of aragonitic mineralogy of *Numidiaphyllum gillianum* Flügel, 1976, which may be correct, but the evidence given by Wendt (1990), for both elemental content and crystallography are not convincing. However, the problem of the skeletal mineralogy of *N. gillianum* loses its critical role for phylogeny when one considers the stratigraphic position of that species, established by Flügel (1976) as the *Yabeina* Biozone. In modern stratigraphy this biozone belongs to the middle, not to the 'uppermost Permian' as Wendt (1990) stated.

I will not discuss here whether or not the data presented by Wendt (1990) are adequate for concluding that the original mineralogy of *Numidiaphyllum gillianum* was aragonitic. However, what would such a single occurrence have meant for the Rugosa/Scleractinia relationship? Very little, if anything, when based on recent knowledge of that taxon (see Ezaki 1997). Furthermore, why should a single discovery of aragonitic mineralogy (if proven) be evaluated more highly than the edge zone in Devonian Phillipsastreidae and Permo–Carboniferous Sestrophyllidae or the Scleractinia-like arrangement of septa in the Ordovician *Kilbuchophyllia*? Simply because *Numidiaphyllum* appeared in Permian? Therefore, I do not accept the indicative role of *Numidiaphyllum gillianum* emphasized by both Wendt (1990) and Stolarski (1996), and would rather classify its apparent aragonitic mineralogy as an incidental phenomenon similar to other phenomena parallelling those in Scleractinia. They may indicate possibilities of scleractinian solutions present within the Rugosa, but do not prove a direct relationship between these two groups.

In contrast to the known, calcitic skeleton of the Rugosa, that of the Sleractinia is considered to be aragonitic. The discovery of some well preserved Triassic (e.g., Cuiff 1975, 1980; Roniewicz 1989) and younger (e.g., Morycowa 1964; Stolarski 1991) specimens allowed reconstruction of their original microarchitecture and the establishment of some phylogenetic lineages (Roniewicz & Morycowa 1993). However, there are suggestions of calcitic nuclei in skeletons in some Scleractinia (e.g., Bøggild 1930; Constantz & Meike 1990; Wendt 1990). Again, its occurrence means no more than a unique appearance, parallel to the normal mineralogy of the Rugosa. Rather than such incidental occurrences, a direct linkage between particular uppermost Permian rugose and Triassic scleractinian taxa must be established in order to demonstrate a direct relationship between these two subclasses. The family Numidiaphyllidae Flügel, 1976 was only tentatively included by its author in the Rugosa, because of its peculiar morphology and incomplete data. This position was also adopted by Hill (1981: p. F427) who placed it within 'subclass uncertain'. Wendt (1990) published a series of drawings (fig. 2: 1–8) which are either badly oriented and inaccurate or show non-rugosan septal increase. This is especially well shown in his figs 2: 4 and 6, in which new metasepta(?) were drawn in the area between the counter and counter-lateral septa. None of Wendt's (1990) illustrations proves that *Numidiaphyllum gillianum* should be transferred to the Polycoeliidae Roemer, 1883. Therefore, Wendt's (1990) paper does not contribute conclusive data to the question of the Rugosa/Scleractinia relationship. The most Recent proposition by Ezaki (1997) to consider *Numidiaphyllum gillianum* as a Permian scleractinian coral is reviewed by me in a separate review as unsupported.

Early skeleto- and septogenesis. — The occurrence of sequential versus cyclic insertion of the first septa, continuing into subsequent growth stages, is traditionally listed among the most important characters distinguishing the Rugosa and the Scleractinia. Differences between these two groups during the earliest skeletogenesis are poorly known. Stolarski (1996), following Jell (1980), pointed at the very early appearance of the first septa in extant *Porites lutea*. They are secreted by the larva shortly after secretion of its granular basal disc. Stolarski (1996) correctly contrasted such an early septogenesis with the aseptal, early ontogeny in some Rugosa (Różkowska 1956; Fedorowski 1987; Stolarski 1993). It seems acceptable that taxa possessing calices typical for the Rugosa, and lacking septal furrows early in the ontogeny, should have built their external walls first and their septa later. Unfortunately, as there are no uncontested data to fully confirm this idea, we may regard this character only as potentially crucial for distinguishing the Rugosa and Scleractinia.

Only those Rugosa that form an edge zone may perhaps be expected to secrete their incipient septal apparatus first and their external wall afterwards, i.e. in a manner similar to that in the Scleractinia. However, the complete earliest skeletogenesis of such taxa remains unknown. The Rugosa possessing an edge zone, mentioned above as possible exceptions within that subclass, have their counterpart in the Carnian solitary genus *Zardinophyllum* Montanaro-Gallitelli, 1975, which is exceptional among the Scleractinia. The broken corallites, briefly discussed by Montanaro-Gallitelli (1974) as *Protoheterastraea leonhardi* (Volz), are certainly not typical for the Scleractinia; they possess a variable number and arrangement of septa, suggesting insertion in series – i.e., in the rugosan manner. However, this phenomenon was observed only in isolated instances in different specimens and the earliest skeletogenesis has not been investigated. In describing these specimens, Montanaro-Gallitelli (1974: p. 15) used rugosan terms, such as 'cardinal septum', which she considered 'constantly shorter' etc. Stolarski (1996: fig. 10A–C) illustrated a broken, juvenile part of *Zardinophyllum zardinii* Montanaro-Gallitelli, 1975, and interpreted its septa as being inserted in sequence and in quadrants. At first glance, the specimen is striking for the rugose coral student. I would have been mislead if I had discovered this small fragment associated with Paleozoic Rugosa, and had not studied its complete ontogeny, the morphology of its surface, or the mineralogy of the skeleton. I know from personal information from Stolarski that this specimen was incomplete, and only the illustrated fragment was available. However, Stolarski wrote (1996: p. 359): 'The corallum of *Z. zardinii* illustrated here has its metasepta inserted in quadrants, as in the Rugosa (Fig. 10).'

With regard to this statement I would like to point out that: (1) the ontogenetically younger and older morphology of the illustrated corallite is not known. Both growth phases could well be typically scleractinian. Thus, considering insertion of metasepta in quadrants is at least premature. Several complete specimens must be studied in detail prior to making such an observation valid; (2) small septa, interpreted by Stolarski (1996) as 'Km' may be metasepta of the second scleractinian cycle inserted with some delay; (3) increase of metasepta is not the only important factor for distinguishing between the rugosan and the scleractinian septogenesis. Appearance of the first six septa is equally important. Irrespective of how many of these septa are considered protosepta in the Rugosa (2, 4 or all 6), the first six septa were never inserted simultaneously in any well documented specimen of that subclass, whereas simultaneous insertion of the first six septa is the rule in the Scleractinia – even in such a simple and primitive genus as *Gardineria* (see Stolarski 1996: p. 348). When well documented, *Zardinophyllum zardinii* may be an exception to that rule. However, the late appearance of *Zardinophyllum zardinii* in the stratigraphic column and the earlier existance of typically developing Scleractinia must be considered as well.

Stolarski (1996: p. 359) paid special attention to the so-called 'aberrant' or 'teratological' specimens occurring within both the Rugosa and the Scleractinia, 'known from the fossil record just around the critical moment of the evolution for both groups'. I would like to note that the 'critical moment' comprises Changhsingian and the whole of the Scythian i.e., approximately 15Ma. Besides, one cannot expect to find a classic septal increase succession of Kunth (1869) or Carruthers (1906) in all the Rugosa. Their early septogenesis may vary (e.g., insertion of the lateral septa prior to the cardinal and counter septa in *Verbeekiella*). However, insertion of septa is invariably sequential within quadrants in every variant investigated so far. The so-called 'teratological Rugosa' (Stolarski 1996: p. 359), exhibit this character as well (Oliver 1980). Some differences in the sequence of appearance of septa in the Late Permian (Wuchapingian) *Pentaphyllum gracile*, postulated by Schindewolf (1942: fig. 85) and re-interpreted by Oliver (1980: fig. 4), has been observed only in the corallite lumen and not checked against insertion of septal furrows, which is truly important. Furrows of the delayed septa always appear in a regular sequence, whereas their blades may not be manifested at all, or may appear later in the ontogeny. Such a delay in the appearance of septa in the corallite lumen was not unique for *P. gracile* in the Rugosa. For instance it is normal for the counter septum in *Cryptophyllum* or *Tachylasma* and common for minor septa. Besides, a single specimen, even a truly teratological one, cannot be used for a phylogenetic comparison between subclasses; especially when not showing intermediate characteristics.

Mineralogy should be again recalled in the context of the relationship of *Z. zardinii* to the Rugosa. All Permian rugose corals investigated so far, except *Numidiaphyllum gillianum* (accepting its aragonitic mineralogy as proven), are calcitic. Thus, the question arises: Which taxon should be considered ancestral for that Late Triassic genus and/or for the ancestors of the 'living fossil *Gardineria*'? Two possible candidates for this taxon are the fairly old (*Yabeina* Biozone, Middle Permian), colonial, and morphologically different but aragonitic(?) species *Numidiaphyllum gillianum*; or the solitary genus *Soshkineophyllum*, which is morphologically similar to the single section illustrated by Stolarski (1996), but is calcitic and even older (Strunian–Kazanian). Both these variants require enormous changes in the skeletogenesis.

Finally, various trends in the arrangement and diversification in the length of major septa within the suborder Plerophyllina can easily be opposed to one constant character – the increase in septa – permanently sequential and in quadrants, since the appearance of the first representatives of that suborder in the Silurian and continuing until their termination near the end of Permian. More than 160 Ma of stability in this character, irrespective of all genetic and somatic changes in other features reflected in the morphology of skeletons, predicted physiology, response to extrinsic factors, etc., legitimizes two questions: is it rational to assume that such a stable character changed at the very end of the existence of such a long-lived taxon? Is it rational to predict that such a revolutionary event took place after the disappearance of the Rugosa from the fossil record and somewhere in their unknown theoretical refuge?

Stratigraphy

There is a widely recognized Early Triassic gap in the occurrence of corals. Reports of the occurrence of the Rugosa in Early Triassic deposits are either erroneous and are result of incorrect identifications of orthofossils (e.g., Ilina 1965), or the specimens are worn and redeposited (e.g., Flügel 1973). There is not a single reported occurrence of a rugose coral *in situ* either above the Permian–Triassic boundary or at the boundary itself. As the dividing line between two eras, that boundary is of a special interest and has been thoroughly studied in many regions of the world. The Changhsing section in South China has been accepted by the International Geological Congress (August 1996, Beijing) as the most complete and the best documented boundary section (see Sheng Jin-zhang & Jin Yu-gan 1994 for summary). The Changhsingian stratotype succession is based on a variety of thoroughly studied fossils. Rugose and tabulate corals are absent not only from the beds near the boundary but also for approximately 15 m below.

Rugosa are also absent from the fossil record of the youngest existing Permian strata in the Himalayas, Salt Range, Tibet and Kashmir. The Japanese, Afghanistan, Iran, Iraq and Armenia sections are incomplete at the very top. Again, rugose corals are absent from the uppermost beds of these sections, being mainly restricted to the equivalents of Wuchapingian. In the Changhsingian, they are present in older beds and only as random and restricted occurrences (e.g., Ilina 1965; Ezaki 1991).

I have restricted this discussion to the Tethys Realm because extinction of the rugose corals from the Cordillera-Arctic-Uralian Realm took place not less than 5 Ma before the P-T boundary. The global extinction of the Rugosa, which was diachronous (Fedorowski 1989), eliminated the possibility for corals of that Realm to survive. Thus, in view of the lack of corals in the most complete sections in the Tethys Realm and the diachrony mentioned above, I do not accept the possibility noted by Stolarski (1996: p. 361) that 'Rugosans [...] could however survive the P/T boundary in small refuges, which hitherto have not been discovered'.

Gardineria evolutionary lineage (Stolarski 1996)

Sheldon (1990: p. 107) wrote: 'The ideal recipe for establishing evolutionary patterns includes some ingredients that are very difficult to obtain: many complete specimens from successive, small stratigraphic intervals whose relative age is unequivocal; a framework of well-constrained absolute ages; samples spanning the entire geographical and temporal range of all closely-related lineages; as many ontogenetic stages as possible (in order to recognize heterochronic relationships) and statistical data on all available characters. To avoid generating artificial patterns, fossils should only be assigned to named species late in these procedures'. Although the 'ideal recipe' quoted above concerns species and was said to be 'very difficult to obtain', no one should feel free to side-step those difficulties and to compare randomly occurring fossils only because they are morphologically similar or can be interpreted as such.

Stolarski (1996) reconstructed the '*Gardineria* evolutionary lineage' on the basis of two or three genera that are widely isolated in time and space, poorly preserved, inadequately represented, and in which the earliest ontogeny and several microstructural features are unknown or only assumed. Moreover, the starting point of the lineage was placed by Stolarski (1996: fig. 11) somewhere on the supposed evolutionary line between the families Protoheterastreidae and Volzeiidae. One can assume from the discussion (Stolarski 1996: p. 357) that the divergence toward the Gardineriidae took place during the Ladinian–Carnian in the Alpine part of the Tethys. He did not indicate any particular taxon (species or genus) as ancestral – simply because there is none – but instead discussed protoheterastraeids and other simple Triassic representatives of various families. His discussion was, in a way, accompanied by a discussion on the roots of the 'Bauplan' (his terminology) of *Gardineria* (pp. 258–261). He attempted to show a direct connection between the Rugosa and the Scleractinia *via Zardinophyllum*, which surprisingly enough, was afterwards separated by a question mark (fig. 11) from the suborder Caryophyllina, in which he included *Gardineria*. As a result, we have two families divided by a question mark, discussed as ancestral for the third family, the true representatives of which are absent from the critical Ladinian–Carnian stratigraphic level. Moreover, in spite of all of the doubts and obstacles briefly discussed above, after questioning the direct connection between the two families that he knows from personal study, he linked one of them without doubt to the Late Permian Rugosa.

This lineage was reconstructed as a solid line (Stolarski 1996: fig. 11) extending upwards in time, passing through two intermediate(?) genera – one in the Pliensbachian of Morroco (approximately 195 Ma) and the second in the Albian of Texas (approximately 107 Ma). The lineage ends with the Recent *Gardineria* – a 'living fossil' with no record available for more then one hundred million years. Only two Eocene genera from New Caledonia were discussed as having some morphological similarities with the gardineriids. How were those few taxa, included by Stolarski (1996) in his new family Gardineriidae, connected to form a lineage? What happened during the dozens of millions of years that divided individual occurrences of the genera included by Stolarski (1996) in the Gardineriidae? On which basis then, can we assume that just those two presently known taxa are the intermediate forms? The time represented by the Carnian–Holocene stratigraphic gaps listed above offered many more opportunities for the appearance of truly intermediate taxa that disappeared from the fossil record or have not yet been found. Such considerations could be multiplied, but it seems enough to question the reality of a phylogenetic reconstruction such as that proposed by Stolarski (1996).

Instead of a summary

I have asked many questions throughout this critique because I wish to show that problems concerning the origin and early evolution of the Rugosa, and the origin of the Scleractinia, cannot be solved on the basis of current knowledge of these groups of animals. The evolution of the Anthozoa is full of gaps and misunderstandings, resulting from incomplete investigations opening doors to too many hypothetical syntheses. Dzik (1993) attempted to present roots for the group which in turn was rootlessly considered ancestral for the Scleractinia (Stolarški 1996). In this way, a chain of baseless predictions and interpretations begins to circulate as facts.

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Jerzy Fedorowski [jerzy@hum.amu.edu.pl], Instytut Geologii, Uniwersytet A. Mickiewicza, ul. Maków Polnych 16, PL-61-606 Poznań.