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Early Carboniferous Chinese and Australian „*Siphonodendron*" (Anthozoa, Rugosa): ecological and geographical influence on taxonomy

Wczesnokarbońscy przedstawiciele chińskich i australijskich „*Siphonodendron*" (Anthozoa, Rugosa): wpływ środowiska i rozprzestrzenienia geograficznego na taksonomię

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Abstract

Normal marine salinity is the main limiting factor for the Subclass Rugosa. Water depth and temperature are less critical. Individual characteristics of specimens and some characteristics of species are, however, excellent environmental indicators. Being distributed exclusively by larvae, Rugosa required free distribution by means of marine currents, as well as midway areas suitable for settlement and metamorphosis of the larvae. Not distance but rather geography and midway environments are therefore the limiting factors for their distribution, relationships and stratigraphic value.

Siphonodendron and *Siphonodendron*-like ("*Siphonodendron")* corals are discussed as examples of morphological similarity, but not necessarily representing a phylogenetic relationship. The known homeomorphy of European and western North American *Siphonodendron* taxa (Fedorowski & Bamber 2007) may be extended on the European, some southern Chinese and all south-eastern Australian *Siphonodendron*-like corals, but only the Chinese and SE Australian forms may be truly related. The latter relationship would extend the boundaries of the Early Carboniferous Australian rugose coral province. The Late Tournaisian age of the earliest Australian "siphonodendrons" indicates an ancestry of the coral fauna within the province (SE Australia and S China). A mechanism for north-westward migration of this fauna, from SE Australia to S China, is not clear.

Keywords: „*Siphonodendron*", Rugosa, Early Carboniferous, China, Australia

Streszczenie

Normalne zasolenie mórz stanowi główny czynnik ograniczający występowanie podgromady Rugosa. Głębokość i temperatura wody są mniej istotne. Tym niemniej, poszczególne cechy okazów i niektóre cechy gatunkowe są doskonałymi wskaźnikami środowiska. Rugosa rozprzestrzeniały się wyłącznie w stadium larwalnym. Kolonizacja nowych obszarów była zatem związana z istnieniem otwartej komunikacji morskiej, odpowiednio ukierunkowanych prądów, a w przypadku długich dystansów również z istnieniem pośrednich obszarów dogodnych dla osiadania i metamorfozy larw. Tak więc nie odległość jako taka, lecz układ lądów i mórz oraz warunki ekologiczne na obszarach pośrednich były czynnikami ograniczającymi dla rozprzestrzenienia, pokrewieństw i wartości stratygraficznej Rugosa.

Właściwy rodzaj *Siphonodendron* i koralowce podobne do tego rodzaju („sifonodendrony") zostały w tym artykule przedyskutowane jako przykład podobieństwa morfologicznego, ale niekoniecznie pokrewieństw filogenetycznych. Homeomorfia europejskich i północno-amerykańskich taksonów (Fedorowski & Bamber 2007) może zostać przeniesiona również na europejskie oraz niektóre chińskie i wszystkie australijskie „sifonodendrony". Tylko gatunki z ostatnich dwóch obszarów mogą być rzeczywiście spokrewnione. Pokrewieństwo to rozszerzyłoby granice wczesnokarbońskiej prowincji australijskiej (SE Australia i S Chiny). Późnoturnejski wiek najstarszych „sifonodendronów" australijskich wskazuje na ich pozycję wyjściową w obrębie prowincji. Mechanizm rozprzestrzeniania się tych faun ku północnemu zachodowi, z SE Australii do S Chin, pozostaje niejasny.

Słowa kluczowe: "*Siphonodendron*", Rugosa, wczesny karbon, Chiny, Australia

Introduction

Fasciculate Rugosa, most commonly identified as *Siphonodendron* McCoy 1849, much less frequently as *Lithostrotion* Fleming 1828, were among the most common components of the Viséan and Serpukhovian shallow water marine faunas. They occur in many sites of that and slightly older age (Late Tournaisian) on almost all continents. *Erismatolithus Madreporites affinis* Martin, 1793 was perhaps the first described member of *Siphonodendron*. Unfortunately, that British specimen was lost. However, Fleming (1828), Philips (1836), McCoy (1849) and other 19-th century British palaeontologists described numerous specimens undoubtedly belonging in that genus. Hill (1938–1941) revised Scottish representatives of *Siphonodendron*, proving its abundant occurrence in Britain. Poty (1975, 1981 and several subsequent papers) created the basis for the modern understanding of the European, i.e., typical *Siphonodendron*.

Siphonodendron and *Siphonodendron*-like ("*Siphonodendron*") corals were also described from several European and Asiatic countries, northern Africa, North America and Australia. Similar general morphology of specimens from all areas cited and a tendency to include in the European taxa the specimens found in those areas, resulted in their identification as *Siphonodendron, Lithostrotion* Fleming, 1828 and/or *Diphyphyllum* Lonsdale, 1845. Such an approach was common up to the second half of 20th century. Only Hill (1948) suspected that some Australian species do not belong in European genera. Fedorowski (1981) developed that idea and questioned an identification of Australian specimens as *Siphonodendron* McCoy, 1849 and *Orionastraea* Smith, 1917. That position was acknowledged by Webb (1990, 1994, 2000). North American *Siphonodendron*-like corals were included in that genus and/or in *Diphyphyllum* until very recently, when their taxonomic position was questioned by Fedorowski & Bamber (2007), who postulated that their lineage separated from the stratigraphically older European *Siphonodendron* proper. The *Siphonodendron*-like corals from other areas, distant from Europe, such as China and Japan, have not been revised yet in respect of their microstructure, blastogeny, morphology of pseudocolumella and tabularium. Thus, their relationships can only be suspected on the basis of incomplete data.

Chinese authors continue to include in *Siphonodendron* and/or *Diphyphyllum* the Early Carboniferous specimens similar to European representatives of those genera (e.g., Fan *et al.* 2003). In this paper the potential relationship of some Chinese fasciculate rugose corals, collected by myself in 2001, to Australian forms is proposed. Unfortunately, an Australian genus proper for those specimens does not exist, whereas introduction of a new genus based on the Chinese species seems unfair in the situation when corals of that morphology are common in Australia and are known from there for more than a Century. Thus, an introduction of the formal name is not proposed here for the specimens mentioned and is postponed until the new generic name is introduced for the Australian *Siphonodendron*-like corals similar to "*Lithostrotion*" *arundineum* Etheridge, 1900. Only a short description, restricted to main characteristics (see below) and illustrations (Figs. 2, 3) is included.

Genetic and protein electrophoretic studies of the Rugosa are impossible, making their true relationships difficult to establish. Moreover, several myths, such as an extreme endemism on one side and similarities in the macromorphology on the other, resulted in their mostly artificial taxonomy and their distrust as index fossils. Thus, some of those questions are discussed as an introduction to the discussion on some Chinese *Siphonodendron*-like corals.

Endemism of the Rugosa

Life habits

As with the majority (?) of Mesozoic and Recent Scleractinia, many Rugosa tolerated rather narrow ranges of environmental change. That in turn lead to their endemism, *a priori* extended by many scientists to nearly all taxa of both subclasses. Shallow, warm, well aerated and normally saline waters are commonly attributed to corals in handbooks and repeated by educated geologists afterwards. That trivialized opinion is correct exclusively to the last of the limits listed. Thus, strata yielding Rugosa *in situ* may be accepted as deposited in normally saline marine waters, and that is all. The expression "*in situ*" is not incidental. Many small and morphologically simple Rugosa occurred both in deep and/or calm, as well as in warm and shallow waters, including mud mounds in the Emsian and Givetian of Morocco (Berkowski 2004, 2006) and reefs in the Permian deposits of SW Texas (my unpublished data). The environment of such corals is rather easy to establish when they were not washed out and re-deposited. Thus, their *in situ* position is fundamental for reconstruction of their life habit. Not only small solitary corals, but also colonies more than 2.5 meters across may be re-deposited. Lack of recognition of their re-deposition may lead to their treatment as bioherms (Birkenmajer 1979), whereas they may be large bioclasts (Fedorowski 1982), indicative for the environment of their deposition, but not for their life habit. Thus, corals offer very little for reconstructions of the environment, if the lithologic context is not compared against recognition of the *in situ* position and specialized external and internal characteristics of particular coral specimens.

The examples cited apparently negate the indicative paleoecological value of corals, but they do not. Only a schematic approach to the corals is negated here. Although the relationship of the Rugosa to the Scleractinia is distant, only the latter remain to refer to as analogues when environmental requirements of the Rugosa are analyzed. To prove a symbiosis with intracellular microbes, such as *Zooxanthella,* is a precondition in the case of Scleractinia, because only hermatypic taxa may serve as complete environmental indicators. Investigation on Recent hermatypic taxa allow them to be accepted as inhabitants of permanently warm, shallow marine waters.

Unquestionable criteria allowing establishment of the hermatypic character of the Rugosa do not exist. Heavy, solid, non-porous skeletons of the great majority of them may rather be indicative of ahermatypic character. However, some colonial and few dissepimental solitary species may have been hermatypic. This can be suggested from both light skeletons and the lithological context, but cannot be considered conclusive. Light skeletons may be equally indicative of quiet environment. In spite of the probable ahermatypic character of most Rugosa, a careful analysis of their external and internal features may successfully serve for a precise reconstruction of the environment they had lived and/or were buried in. Unfortunately, descriptions of the lithologic context of the occurrence of Rugosa remain rather scarce (e.g., Fedorowski 1982; Neumann 1988; Scrutton 1998; Rodriguez 2004; Berkowski 2004, 2006), whereas the utilization of corals as the environmental indicators, irrespective of the context mentioned, are common.

The Rugosa were occupants of differentiated habitats. Thus, an environment typical for them did not exist. They cannot be considered indicative for paleoecology as a subclass or down to the genus level inclusively. In contrast to the taxonomically higher level units, many species are restricted in their habits, thus being important environmental markers. Particular ontogenetic traits of corallites and colonies are even more important in that respect than species, leading eventually to several morphological repetitions across the taxonomy. The unrelated taxa adopted themselves to the environment so closely that not only their external features, but also macro-architectural characteristics of their skeleton became misleadingly similar. That fact had led to negation of the Rugosa as index fossils for stratigraphy. The reason for that negation was simple: poor and artificial taxonomy of the Rugosa paradoxically resulted from their environmental plasticity. The genus *Amplexus* Sowerby, 1816 supplies one of the best examples. Described from the Early Carboniferous (*A. coralloides* Sowerby, 1816), the suspected representatives of that genus were afterwards found in the strata starting from the Upper Ordovician and ending in the Upper Permian. More or less detailed analysis allows already several new, much shorter existing amplexoid genera to be established (e.g. *Amplexizaphrentis* Vaughan, 1908; *Amplexocarinia* Soshkina, 1928; *Pentamplexus* Schindewolf, 1940; *Pleramplexus* Schindewolf, 1940; *Falsiamplexus* Fedorowski, 1987, etc.). Much more will perhaps be recognized when such "amplexuses" as those described by Fomichev (1953), de Groot (1963), Fan *et al*. (2003) and several other authors are studied in detail. Thus, detailed studies show that the Rugosa may serve as index fossils for stratigraphy and palaeogeography without losing their indicative value for paleoenvironmental reconstructions. This is discussed below in more detail. Corals discussed briefly in the present paper may serve as an example.

Palaeogeography

Sedentary life habit, an absence of medusa generations and the distribution exclusively by relatively short living larvae (few hours to several weeks), were important limits for the Rugosa in addition to the normal salinity they tolerated. Thus, direct marine communication between particular areas during the period studied and a suspected length of the larval stage must be considered when the relationship *vs.* endemism of individual lineages and/or taxa is studied. Temperature of water should also be taken into account when dealing with possibly hermatypic taxa. Environment in geographically intermediate areas, acceptable for larvae, mostly shallow sea floor, supplied with stable objects, allowing larvae to settle and metamorphose and proper directions of marine currents are next conditions to be taken into account. Un-metamorphosed larvae die. The limits listed above resulted eventually in the commonly mentioned endemism of the Rugosa.

There is not an equivocal answer to the question of whether rugose coral endemism really existed or belongs to the legend category. An occurrence in the Early Permian (Cisuralian) of the same genera, sometimes species, along the enormous area along shelves of the northern and western Pangea and some accreted terranes, seems to contradict such an opinion (Fedorowski *et al*. 2007). It is worth restating that the area mentioned began in the Southern Urals and continued through the Timan Mountains, Novaya Zemlia, Svalbard Archipelago (including Bear Island), NE Greenland, Canadian Arctic Archipelago, western provinces of Canada, western United States, western part of Mexico to Bolivia and Peru. It would be impossible to consider such a rugose coral fauna endemic. The so called Old World Realm, existing during the Givetian and most of the Frasnian time (Oliver 1976) expanded even wider than the Cisuralian Cordillera-Arctic-Uralian Realm mentioned above. Several species and many genera were at that Devonian time common for western North America through Europe, North Africa and Asia to Australia. Only two remaining realms or kingdoms, distinguished by Oliver (1976), namely the New World Realm, restricted to the Appalachian region and the Malivino-Kafric Realm, both small in the area occupied, were isolated and truly endemic at that time.

During most of the time of the rugose coral's existence their endemism was more advanced than exemplified above. Also, the widespread occurrence of some related faunas does not

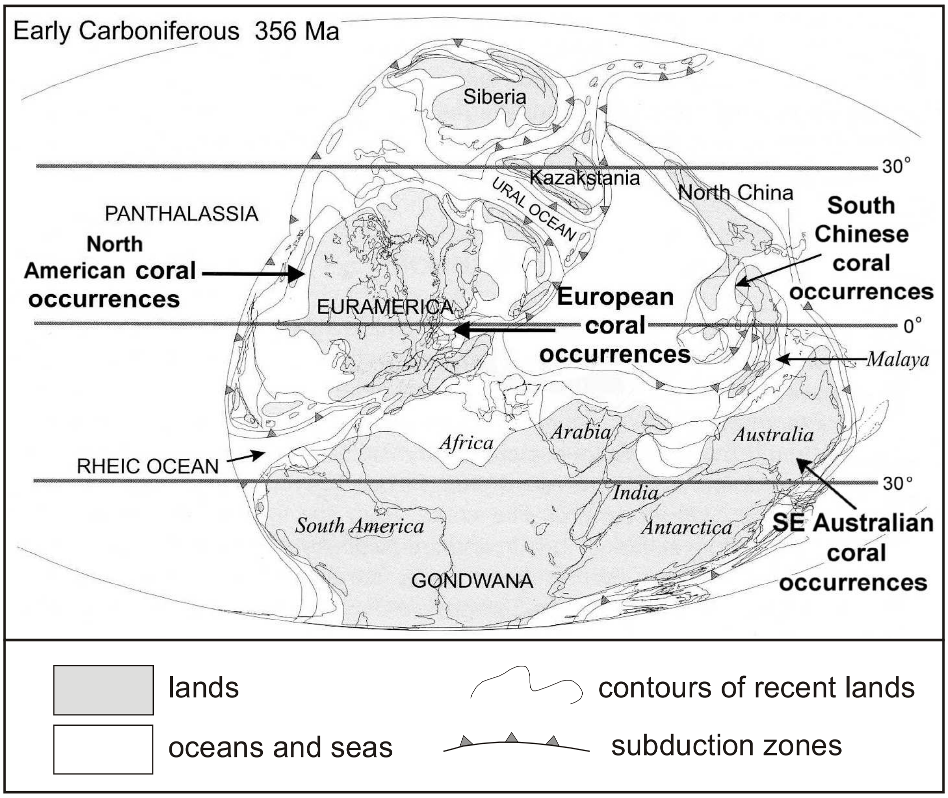


Fig. 1. Rugose coral occurrences within the main areas discussed in the present paper. Palaeogeography in Early Carboniferous after Scotese (2002, simplified)

Fig. 1. *Występowanie koralowców Rugosa na głównych obszarach omawianych w niniejszej pracy. Paleogeografia wczesnego karbonu wg Scotese'a (2002, uproszczone)*

contradict isolated occurrences for others. The New World and Malvino-Kafric Realms of the Devonian period may be supplemented by the isolation in the Late Tournaisian and Viséan of western North American rugose coral faunas from the European ones, and Australian faunas from most of the world. It first of all resulted from the absence of direct communication between individual areas inhabited by corals. Also, the marine communication between given areas may have existed, but their coral faunas differed greatly for reasons difficult to understand without sedimentological studies. Substantial differences between the Early Carboniferous European and North American rugose coral faunas may serve as an example of the latter. General palaeogegraphic maps of that time (Fig. 1) suggest an easy communication of those fauna along the Euramerica shelves. Only a detailed map, documenting sedimentary conditions, exposes a barrier impassable for rugose corals. Prevailing clastic deposition along those shelves (Ziegler 1988) points towards mostly ecological reasons for the difference. Although the kind of the sedimentation mentioned precluded the settlement of larvae, the long living larvae would had survived the transportation by marine currents from Europe to western North America or *vice versa*. Thus, it is suggested here that larvae of the overwhelming majority of the rugose coral species of both areas were short living.

The same example shows, however, that there may be some, mostly very rare, species bridging the generally different coral faunas. Taxa of that kind serve as key stones for establishing the phylogenetic connections between genera and families. *Dorlodotia* Salée, 1919 is such a key stone genus, bridging the European and North American *Siphonodendron* as possibly ancestral to both. Fedorowski & Bamber (2007) documented that relationship on the basis of the blastogenetic and microstructural studies. At the same time they established the distinction on a genus level between European *Siphonodendron* and/or *Diphyphyllum* and North American fascisulate Rugosa traditionally included in those genera. Survival of long transportation by larvae of *Dorlodotia* sp. nov. Fedorowski & Bamber 2007, too long for other larvae to stay alive, is the only possible theoretical explanation for that fact in the absence of direct data.

The above example was cited to point out that only detailed studies allow a distinction between relationships and homeomorphy with maximum probability offered by fossil taxa. Thus, only detailed microstructural and blastogenetic studies, but not the commonly applied method, whereby identifications are restricted to comparison of random thin sections, will allow confirmation or rejection of the occurrence of *Siphonodendron* along the enormous area, expanded from Britain and Spain in the northern hemisphere to SE Australia in the southern one. Although the Viséan and Serpukhovian geography differed considerably from the Recent one (Fig. 1), the distance between those two areas and their geographic positions were similar. Various obstacles may have occurred in such a large area, making transportation of larvae difficult or impossible. Thus, the Kuznetsk Basin *Siphonodendron* (Fomichev 1931; Dobrolyubova *et al*. 1966) may be only homeomorphic to the European type. Such a possibility is even more probable for the Chinese and Japanese *Siphonodendron*-like corals (see below). On the other hand, however, detailed studies mentioned may document relationships of at least some geographically distant taxa.

The following should be pointed out in summary: 1. Truly related rugose coral taxa may have colonized areas distant from each other only when their larvae were able to survive transportation between those areas being carried by properly directed marine currents. 2. Rugose coral faunas may have differed greatly on shelves of the same continent despite marine communication between them and location in latitudes excluding polar climate. Widely expanded clastic sedimentation may have formed a barrier impassable for most larvae. 3. Such barriers as distance to cross are difficult to establish when dealing with fossil taxa. Difference between the Recent coral faunas of the Caribbean area and western African shelves may serve as an example. 4. An opposite situation may have occurred in the Viséan time when the Palaeotethys and Rheic Oceans were connected directly and their circum-equatorial position theoretically supported an easy communication and long-distance transportation of larvae. Whether the rugose coral taxa, *Siphonodendron* in particular, were able to adopt themselves to that opportunity will be known when studied in detail.

Chinese Early Carboniferous *Siphonodendron*-like taxa

The Chinese coral faunas, including *Siphonodendron*-like corals, have been commonly treated without regard for the complex tectonic history of the area. This at least in part results from the inadequate knowledge of those corals. Not only the microstructure of septa and the blastogeny remain unknown, but also morphology of the tabularium (normal *vs*. biform), architecture of the pseudocolumella (monoseptal *vs*. incorporating septal lamellae) and derivation of the median lamella in the pseudocolumella (from axial, counter or cardinal protoseptum) have not been described. Such substantial differences as lateral *vs*. axial offsetting may also occur in that group of corals, making them distant on a genus level. Only very few of those details can be read from inadequately enlarged illustrations of Chinese papers, starting from first descriptions of the *Siphonodendron*-like corals by Yu (1933) and ending with the study by Fan *et al*. (2003).

Nevertheless, the overview of the Chinese taxa summarized in several Atlases (1974 to 1983, not cited in the references) allows us to establish some possible differences in the morphology of tabularia and the composition of pseudocolumellae. Some Chinese species already included in *Siphonodendron* resemble *Siphonodendron* proper (e.g. Fan *et al.* 2003, pl. 40, figs. 1–3), but may appear different when studied in detail. For the reasons listed above, it is impossible to establish whether several Chinese *Siphonodendron*-like taxa were related or homeomorphic among themselves and to taxa outside China. Thus, an attempt to make a general analysis of that fauna was not made. It should only be mentioned that axial offsetting does not occur in the Chinese fasciculate *Siphonodendron*-like taxa described so far. Thus, *Cionodendron* is absent from that country. However, several laterally offsetting, Chinese *Siphonodendron*-like taxa, including those illustrated in the present paper, resemble some Australian species. Thus, boundaries of the SE Australian Province suggested by Webb (2000) and Webb *in*: Jones *et al*. (2000) to be wider than those supposed by Fedorowski (1981) are likely.

The sequence of appearance of individual *Siphponodendron*-like Chinese species was impossible to establish. Thus, this question is omitted from the considerations. Also, derivation of most Chinese *Siphonodendron*-like species cannot be pointed out with adequate certainty. Judging from the Atlases mentioned and from such papers as Yu (1933), Wu (1964), Lin *et al*. (1995), Fan *et al*. (2003) and others, *Siphonodendron*-like corals were absent from the Chinese Tournaisian and, perhaps, from the Early Viséan strata. Thus, the Chinese *Siphonodendron*-like species are younger than those of the following areas:

1. Western European Coral Province. *Siphonodendron* proper is known from that area since the late Moliniacean, corresponding most probably to the very early Viséan (Fedorowski & Bamber 2007 based on letter communication by Professor E. Poty). Thus, if *Siphonodendron* proper occurs in China, its relationship to the European ancestor and derivation from the latter is possible. Such rugose coral taxa in common for both areas as *Clisiophyllum* Dana 1846, *Dibunophyllum* Thomson & Nicholson 1876, *Arachnolasma* Grabau 1922 and several other genera, support the thesis of an open communication between those remote areas (Fedorowski 1981), making the above supposition probable.

2. SE Australia. *Siphonodendron*-like corals occurred there since the Late Tournaisian (Hill 1934; Jull 1965, 1969, 1974a, b; Pickett 1967; Webb 1990, 1994, 2000) and some of them may have given rise to such Chinese species as those discussed in the present paper. Unfortunately, those relationships cannot be actually expanded to other Chinese species that must be studied in detail first.

3. Western North America. *Siphonodendron*-like corals occur there since the latest Tournaisian (Kelly 1942; Sando & Bamber 1985; Fedorowski & Bamber 2007). However, derivation of some Chinese *Siphonodendron*-like corals from the North American ones seems very unlikely. Width of the Panthalassa rather excluded migration of western North American *Siphonodendron*-like corals to any part of the Chinese territory.

Taking in mind all uncertainties mentioned, only specimens studied for the purpose of the present paper are considered in the discussion that follows.

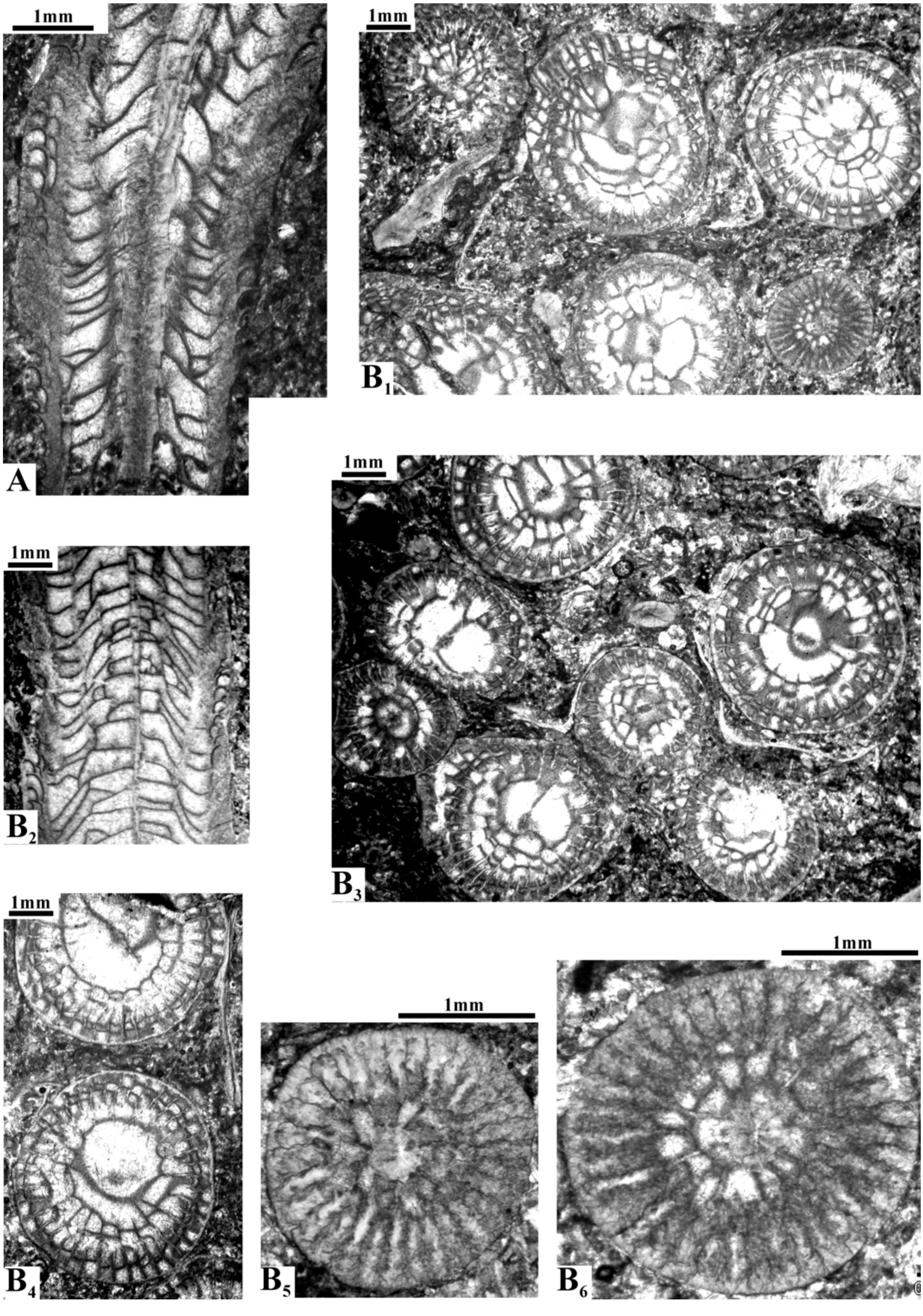
Chinese specimens *vs.* *"Lithostrotion" arundineum* Etheridge, 1900

The specimens illustrated in the present paper were collected from the vicinity of the Kapu village, Dushan County, Guizhou Province, south China. The stratigraphic position of the section is uncertain. Yu & Wang (1987) considered it Lower Bashkirian. However, several specimens closely resembling *Dibunophyllum bipartitum konincki* Milne, Edwards & Haime, 1851 found there by us in 2001 indicate the Late Viséan or the Serpukhovian age. More precise dating is not yet possible. All corals were redeposited. Thus, only fragments of several colonies were found.

Main characteristics of these colonies are:

1. Lateral offsetting. Some immature corallites (e.g. Fig. 2:$B_{5,6}$) found unattached (Fig. 2:B_1) to mature specimens may be post-larval skeletons, i.e., potential protocorallites that died prior to reaching maturity. Their morphologically more advanced growth stages were not found.

2. Tabularium biform. However, this feature is weakly expressed, being recognizable only in fragments of longitudinal sections (Fig. 2:A, upper right; Fig. 2:B_2, lower left; Fig. 3:D_3, upper left). The tabularium may be partly incomplete with short series of linked tabellae (term introduced by Fedorowski *et al*. 2007, p. 44) in the axial area (Fig. 3:D_3).


1mm
A
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B1
B2
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1mm
B3
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B4
1mm
B5
1mm
B6

3. Major septa differentiated in length. Commonly meet the pseudocolumella in the immature corallites, and mostly free in mature growth stage (Fig. 2:$B_{1,\,4–6}$; Fig. 3:$A_{1,2}$; B, C_1; $D_{1,2}$; E). Minor septa invariably well developed; enter the tabularium.

4. Pseudocolumella derived from axial protoseptum and is supplemented by septal lamellae. Its thin median lamella may remain connected to the counter protoseptum. Septal lamellae are laterally contiguous (Fig. 3:$C_{2–4}$) in most corallites, but the pseudocolumella may be reduced to an irregular body in some (Fig. 3:A_4). It may look like an axial column in the eccentric longitudinal section (Fig. 2:A, upper).

5. The microstructure of septa is coarsely trabecular (Fig. 3:A_3) and different from finely trabecular microstructure in the European *Siphonodendron s.s.* Unfortunately, nearly all specimens are diagenetically altered to an extent making recognition of their microstructure impossible.

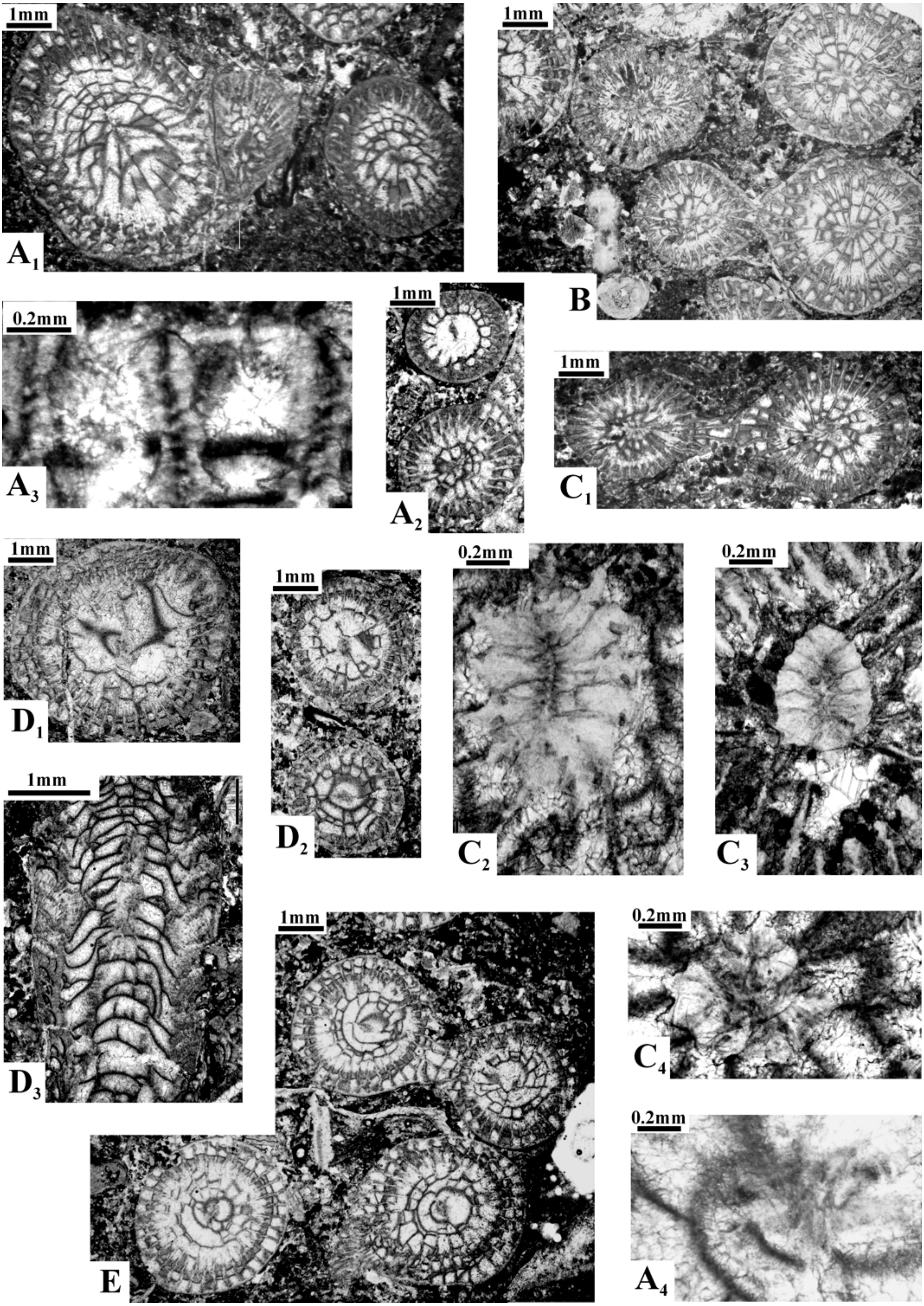
Several of the characters listed above resemble those of the Australian *"Lithostrotion" arundineum* group of corals. Diameters of the Chinese corallites (3–4, maximum 5 mm in one corallite) are only slightly smaller from those given by Webb (1990, p. 93) for *"L." arundineum* (4–5 mm). Also, their number of septa (most commonly16–20) closely approach 20 major septa established by Pickett (1967, p. 12) for topotypes of *"L." arundineum* and 20–22 major septa in specimens of that species described by Webb (1990, p. 93). Most corallites from Australia and China possess pseudocolumellae similar in morphology, varying in size from the largest approaching those in *Cionodendron columen* and the smallest or thinnest considerably reduced in size and thickness. Major and minor septa in specimens from both areas are commonly thicker in the dissepimentarium than in the tabularium. Unfortunately, the microstructure of septa in *"L." arundineum* remains unknown. Its offsetting is lateral as documented by Jull (1965, text-fig. 2:2).

The characteristics of Chinese *Siphonodendron*-like corals listed above and their similarity to some Australian species suggests the relationship of these taxa. The relationship is postulated here in spite of the difficulty in pointing out ways of migration in the southern hemisphere from south-west towards north-east first and towards the west afterwards. The concept of Webb (2000) solved the question only in part. He suggested development of carbonate platforms in the Late Devonian and the Early Tournaisian to the north-east of SE Australia. Faunas of these platforms may had constituted the common source for the Late Tournaisian corals of SE Australia and the Middle Viséan corals of the Akiyoshi Terrane in Japan, with the latter forming the midway settlement area for coral larvae migrating to southern China. Some doubts must be clarified before this concept is accepted.

At first, the occurrence of the *Siphonodendron*-like corals in the Akiyoshi Terrane, closely comparable to the discussed Chinese species, must be documented. Such corals were not described yet. *"Siphonodendron" hinense* Yamagiwa, Suzuki & Okimura, 2000 is the only species of the Akioshi Terrane that can be taken in mind as closely resembling one Australian species of *"Siphonodendron"* and exposing some features of the here described Chinese specimens. This opinion opposes that of Ezaki *et al.* (2007, p. 411), who maintain the position that it is related

Fig. 2. *"Siphonodendron"* sp. nov. A. **A** – specimen KP-02/16. Longitudinal section; thick, compound pseudocolumella. **B** – specimen KP-02/12. $B_{1,\,3–6}$ – transverse sections, $B_{1,3,4}$ – fragments of the colony, $B_{5,6}$ – early growth stages, B_2 – longitudinal section; pseudocolumella very thin, monoseptal (?).
Both specimens from Kapu village, Dushan County, Guizhou Province, south China. Upper Viséan or Serpukhovian

Fig. 2. *"Siphonodendron" sp. nov. A.* ***A*** *– okaz KP-02/16. Przekrój podłużny; kolumella masywna, złożona.* ***B*** *– okaz KP- 02/12.* $B_{1,\,3–6}$ *– przekroje poprzeczne,* $B_{1,3,4}$ *– fragmenty kolonii,* $B_{5,6}$ *– wczesne stadia rozwojowe,* B_2 *– przekrój podłużny; pseudokolumella bardzo cienka, monoseptalna (?).*
Obydwa okazy z okolic wsi Kapu, hrabstwo Duszan, prowincja Guizhou, Chiny południowe. Górny wizen lub sierpuchow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to the European *Siphonodendron s.s.* rather than to Australian *Siphonodendron*-like corals. Their opinion, based on the shallow embaying of septal bases into the external wall in the Japanese species, *versus* wedge-shaped septa in the Australian species (compare Webb 1990, fig. 51), is here considered inadequate for such a conclusion. The axial offsetting, linked axial tabelle and complex pseudocolumella, present in *"S." hinense*, occur in the Australian *"Lithostrotion" consanguineum* Pickett 1967, but not in the type species of the European *Siphonodendron*. First two features of *"S." hinense* listed above correspond to these of the European, North African and North American *Nemistium* Smith 1928, but its relationship to that genus is behind the scope of the present paper.

Secondly, the age of Akiyoshi *Siphonodendron*-like corals, older than the Chinese ones, must be proven. Recent data support that supposition, but the occurrence in China of the *Siphonodendron*-like species older than the Late Viséan cannot be excluded.

Thirdly, the common Tournaisian ancestor for the Australian and Japanese *Siphonodendron*-like corals does not mean the direct relationship of the Chinese and Australian representatives of these groups. Lineages of both groups were perhaps isolated from each other until the Late Viséan. This isolation may had resulted in rather distant relationship of the Chinese and Australian species of that age. Thus, a close morphological similarity of the described here Chinese specimens to typical Australian *"Siphonodendron"*-like corals is not equal with their close relationship. A possibility of direct migration of larvae from SE Australia to southern China should be found in order to prove this suspected relationship.

Endemism of the Early Carboniferous Rugosa of SE Australia

On the basis of first papers dealing with the Early Carboniferous Australian corals (Etheridge 1900; Smith 1920; Benson & Smith 1923) and her own study (Hill 1934), Hill (1948) drew attention to the distinction of the Early Carboniferous rugose coral faunas from SE Australia. Those early studies and the coral papers published after Hill's (1948) summary (Jull 1965, 1969, 1974a,b; Pickett 1967) allowed Fedorowski (1981) to suggest an almost total isolation of that fauna from the remaining Early Carboniferous rugose coral provinces. He also questioned an inclusion of some Australian colonial Rugosa into the European genera *Lithostrotion, Orionastraea* and *Siphonodendron*, making an idea of isolation and endemic character of the Australian Early Carboniferous coral faunas better supported. Neither more than ¼ century ago nor now can a barrier other than a stretch of the ocean and an absence of properly directed sea currents, isolating SE Australian coral faunas, be suggested.

Fig. 3. "*Siphonodendron*" sp. nov. A. Transverse sections, except when stated. **A** – specimen KP-02/7. $A_{1,2}$ – fragments of colony, A_3 – trabecular microstructure of septa, A_4 – disintegrated lamellae in pseudocolumella. **B** – specimen KP-02/11. Fragment of colony. **C** – specimen KP-02/16. C_1 – parent corallite and mature offset remain in touch, C_{2-4} – differentiated micro-architecture of complex pseudocolumellae. **D** – specimen KP-02/5. D_1 – largest corallite found, D_2 – two short-septal corallites, D_3 – longitudinal section out of center; several linked tabellae. **E** – specimen KP-02/6. Fragment of colony.
All specimens from Kapu village, Dushan County, Guizhou Province, south China. Upper Viséan or Serpukhovian

Fig. 3. *"Siphonodendron" sp. nov. A. Przekroje podłużne za wyjątkiem wskazanych.* ***A*** *– okaz KP-02/7.* $A_{1,2}$ *– fragment kolonii,* A_3 *– trabekularna mikrostruktura septów,* A_4 *– luźne lamelle w pseudokolumelli.* ***B*** *– okaz KP-02/11. Fragment kolonii.* ***C*** *– okaz KP-02/16.* C_1 *– osobnik macierzysty i dorosły osobnik pochodny pozostają w kontakcie,* C_{2-4} *– zróżnicowana mikroarchitektura złożonych pseudokolumelli.* ***D*** *– okaz KP-02/5.* D_1 *– największy koralit w kolekcji,* D_2 *– przekrój podłużny poza osią koralita; łańcuch tabel osiowych.* ***E*** *– okaz KP-02/6. Fragment kolonii.*
Wszystkie okazy z okolic wsi Kapu, hrabstwo Dushan, prowincja Guizhou, Chiny południowe. Górny wizen lub sierpuchow

Webb (1990, 1994, 2000) supported Fedorowski's (1981) ideas and discussed the difference between European *Siphonodendron* and *Orionastraea* and SE Australian species included in those genera. Also, he analyzed all species of the apparent lithostrotionids, described outside Australia, but resembling the latter (Webb 2000, pp. 95, 96). Areas treated by him in that review include the accreted terranes of Japan, south China, Thailand, Sumatra and Fergana (former USSR, now mostly in Kazakhstan). Webb's (2000) suggestion of the relationship of species analyzed by him to the Australian rather than to European genera can be supported with some restrictions, mostly connected to the inadequate study of corals analyzed.

Uncertainties mentioned are well demonstrated by the paper of Kropacheva (1966). She described two specimens from southern Fergana as a new subspecies *Cionodendron columen ferganensis*. Poor illustrations restricted to two thin sections showing parts of colonies in low magnification and the laconic description have made impossible a close comparison to the Australian type species *Cionodendron columen* Benson & Smith, 1923. Nothing is known about the blastogeny and the microstructure of the Fergana specimens. Besides, they seem to develop an axial structure rather than the pseudocolumella, characteristic of *C. columen*. Thus, a new genus should perhaps be created for the specimens discussed, also including *Lithostrotion cionodendroides* Kropachova, 1966. Both those species have nothing in common with European lithostrotionids, but may be related to the Australian ones.

Cionodendron? mahaiense Lin & Rodriguez, 1993 from the Upper Viséan or Serpukhovian of NW China does not exhibit the main diagnostic characteristics of *Cionodendron*, but resembles corals illustrated in the present paper (Figs. 2, 3). Also, it may well be related to the Australian "*Siphonodendron*" as suggested by Webb (2000). The latter author excluded *Cionodendron? primitivum* Ivanovsky, 1967 from the genus *Cionodendron*. I fully agree with that suggestion.

Fasciculate rugose coral colonies are common in the Upper Tournaisian and Lower Viséan deposits of SE Australia, with some reaching up to 2 meters in diameter (Webb 1990, p. 93). Several species, identified as *Siphonodendron, Lithostrotion* and *Cionodendron* have been introduced (Etheridge 1900; Benson & Smith 1923; Hill 1934; Campbell 1957; Jull 1965, 1969, 1974a,b; Pickett 1967; Webb 1990). Variation in the morphology of these species, with some features qualitative, suggests a possibility of creation of new genera. None of these potential new taxa points towards the European *Siphonodendron*.

The stratigraphically oldest known „*Lithostrotion*" *williamsi* Pickett, 1967 with its rudimentary minor septa and lonsdaleoid dissepiments differs from the remaining Australian species to the extent that allowed Pickett (1967, p. 15) to express the possibility of its exclusion from the genus *Lithostrotion* (in his meaning = *Siphonodendron* in accordance to the taxonomic concept accepted in this paper). That species, as well as "*L.*" *hallense* Pickett, 1967 and "*Siphonodendron*" *fasciculiseptatum* Webb, 1990, also developing the lonsdaleoid dissepiments, described by Webb (1990, p. 100) as "major septa discontinuous in dissepimentaria of some corallites" and possessing the minor septa underdeveloped or discontinuous, may constitute one group of species (perhaps a new genus). „*Schoenophyllum*" *dalmaensis* Webb, 1990, very similar to "*L.*" *williamsi*, but definitely different from *Schoenophyllum aggregatum* Simpson, 1900, may either belong to that group or should be grouped separately. Revision of *S. aggregatum* by Rodriguez and Bamber (Dr. E. W. Bamber, e-mail message, 2007) shows a peculiar offsetting and other features proving an independent and, perhaps, endemic position of *Schoenophyllum*.

The first established and most commonly described Australian fasciculate species, "*Lithostrotion*" *arundineum* Etheridge, 1900 and most species included by Webb (1990) in the column „lateral increase" of his figure 49 (except for those mentioned above and "*Lithostrotion*" *stanvellense* Etheridge, 1900), may constitute the next group or genus. "*L.*" *stanvellense* differs from the remaining Australian „siphonodendrons" in morphology of the tabularium and in offsetting. The axially offsetting species (*Cionodendron columen* Benson & Smith, 1923 and "*Lithostrotion*" *consanguineum* Pickett, 1967) constitute the group that possesses its generic name *Cionodendron*. Despite Pickett's (1967, p. 21) opinion that *C. columen* is an aberrant form of *Lithostrotion*, the generic distinction of that coral is well documented by its axial offsetting. That character, rare among the Rugosa, is generally accepted adequate for distinguishing *Diphyphyllum* Lonsdale, 1845 and *Nemistium* Smith, 1928. Thus, it is also adequate for distinguishing the genus *Cionodendron*.

"Lithostrotion" tareense Pickett, 1967 with its contratingent minor septa may either represent a distinct genus or forms the most advanced representative of the *"L." arundineum* group of species. Webb (1990, p. 93) mentioned rare contratingent minor septa in the diagnosis of this species. Also Pickett (1967, fig. 4c) drew such septa in his specimen identified as *L. arundineum.*

Large morphological variability of the Early Carboniferous Australian "siphonodendrons" is obvious. However, the intraspecific variability cannot cross borders established for individual species and, what is most important, cannot include qualitative features. Those general rules apply to the Australian "*Siphonodendron*". Difficulties in the latter case may concern the following: 1) Is a given feature truly qualitative? 2) Is it constant? 3) On which phylogenetic level it appeared as constant? 4) Does it prove the relationship or should it be classified as homeomorphic? The brief overview of characters (see the preceding paragraph) shows that conditions „1" and „2" are followed. The condition „3" is not clear. Nevertheless, from options in the point „4" the relationship of some Australian species and the southern Chinese specimens illustrated in the present paper may be suggested, whereas both Australian species and Chinese specimens discussed here are homeomorphic to European *Siphonodendron*.

Grouping of the Australian "siphonodendrons" proposed here disagrees with Webb's (2000, p. 96) phylogenetic concept of those Australian taxa, but this question is beyond the scope of the present paper. My concept is informal and was introduced for two reasons: to support the suggestion of the relationship mentioned and to exclude North American *Siphonodendron*-like species from the consideration. The stratigraphically oldest among them are latest Tournaisian (Kelly 1942; Sando & Bamber 1985; Fedorowski & Bamber 2007) and thus can theoretically be taken in mind as ancestral for the Chinese "siphonodendrons".

Conclusions

1. Most ecological limits attributed to the Rugosa concern species and specimens. Normal marine salinity is the only limit that can be extended to higher taxonomic levels.

2. Being primitive organisms, restricted in variety of solutions of the skeletal architecture on one side and morphologically plastic on the other, the Rugosa produced many homeomorphs that are possible to establish only on the basis of careful specialized studies.

3. The Rugosa were dispersed exclusively by larvae. Thus, their migration, colonization of new territories and relationships relied on easy marine connections, proper directions of marine currents and an occurrence of midway areas available for larvae to settle and metamorphose into a polyp eligible for sexual reproduction. Lack of one or more of those conditions made the coral fauna endemic, whereas their occurrence allows the almost worldwide distribution of species.

4. *Siphonodendron s.l.* is common in the Upper Viséan and Serpukhovian Chinese strata, but was most probably absent from older deposits in that country. The occurrence mentioned, the morphological variability and the similarity of some variants of the Chinese corals to the European *Siphonodendron s.s.,* and the other to the Australian *Siphonodendron*-like corals suggest the possibility of a dual derivation and relationships of particular Chinese "*Siphonodendron*" species. Lineages in both Australia and Europe started with taxa older than the Chinese ones, supporting such a suggestion. The North American lineage is excluded as a possible ancestor of some Chinese "siphonodendrons" in spite of starting from the stratigraphically earliest *Siphonodendron*-like species studied so far. The Panthalassa was an ocean too wide for larvae to cross.

5. Specimens of *Siphonodendron*-like Chinese corals illustrated and briefly described in this paper, closely resemble the Late Viséan Austra-

lian species, *"L." arundineum*. Thus, the relationship of these two is proposed here. The literature data are inadequate for a detailed analysis of the other Chinese species.

6. The relationship postulated as well as the occurrence in small parts of the Japanese accreted terranes of species similar to the Australian *Siphonodendron*-like corals support such a possibility. Already Webb (1990) drew attention to the morphological similarity of the Japanese *„Siphonodendron" niikawai* Minato & Kato, 1957 to Australian species. *Siphonodendron* from the Hina Limestone (Yamagiwa *et al.* 2000) belongs most probably to that group of corals as well.

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