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“Fossil corals, archaeocyaths and sponges” Proceedings of the 10th International Symposium on Fossil Cnidaria and Porifera, August 12–16, 2007, Saint-Petersburg, Russia

Preface

The 10th meeting of the “International Association for the Study of Fossil Cnidaria and Porifera” was held in Saint-Petersburg, Russia from August 12 to 16, 2007. Saint-Petersburg was elected to host the 10th International Symposium on Fossil Cnidaria and Porifera during the general assembly of the International Association in Graz, Austria in 2003. This 10th jubilee Symposium of the Fossil Cnidaria and Porifera Association was dedicated to the Academician of the Russian Academy of Science, Boris Sokolov, one of the ‘founding fathers’ of the Association and the President of the First Symposium in Novosibirsk in 1971.

A number of colleagues with the support of the Administration of The Karpinsky Research Geological Institute organized the scientific and social programme.

About 120 participants from 24 countries attended the meeting (Fig. 1).

During the 4 days of the meeting there were 78 oral and poster presentations, including a special thematic session dedicated to the memory of the late William Oliver. The subjects of the Symposium embraced the different aspects of fundamental and applied palaeontology, biostratigraphy, palaeoecology, and biogeography of various coral and poriferan groups. The general problems of palaeoclimatology, ecosystem evolution and patterns of reef and build-ups distribution were highlighted. The influx of new molecular and microstructural data on scleractinian corals require a tight cooperation between the specialists working on modern and fossil scleractinians in order to propose a new, reliable scheme of phylogeny and a framework of classification.

Four geological excursions were organized: two pre-Symposium and two post-Symposium.

During the first pre-Symposium excursion to the Lower Carboniferous deposits of the north-western part of the Moscow Syncline, the key section along the Msta River was examined. Additionally, we visited Uglovka Quarry to collect rugose corals. The Kozhim section was the object of the second pre-Symposium excursion to the Palaeozoic deposits of the Subpolar Urals. This key-section includes the stratigraphic interval from the Ordovician to Carboniferous. Travelling by landrovers and staying in field camps, the participants of the excursion studied more than 30 km of sedimentary succession.

Unique geological objectives were demonstrated during the first post-Symposium excursion to sections and reefs of the Palaeozoic of Bashkiria. The Famennian deposits yielding large numbers of stromatoporoids and the Devonian/Carboniferous boundary in the Sikaza River section were studied in the first day. Permian reef massifs represent part of the barrier reef and are traceable along the Urals from north to south for more than 2000 km. The second (post-Symposium) excursion was carried out in the Lower Palaeozoic deposits of Estonia. It evoked a great interest. Participants had the possibility to collect corals and enjoy the magnificent views of the Baltic Sea.

In this proceedings, 23 papers presented during the meeting are included. The arrangement of articles follows the two main sessions taking part in the meeting. First—the General Session, which includes papers on all types of fossil Cnidaria and Porifera (Young and Hagadorn, Gandin and Debrenne, Fedorowski, Stewart et al., Zaika, Ospanova, Deliya and Danshina, Ogar, Aretz and Herbig, Rodríguez and Somerville, Hecker, Webb and Yancey and Zlatarski). These articles are ordered according to the stratigraphical record. The Second Session and appropriate part of the volume is devoted to William Oliver. It is separated in the volume as the William Oliver Memorial Session and includes the following articles arranged in alphabetical order with the exception of the first special article about William Oliver: Sorauf and Fedorowski, Budd, Cuif, Elias, Fedorowski, Morycowa and Szulc, Poty, Rodríguez and Bamber, Roniewicz, Somerville and Rodríguez, and Sorauf. The topics embrace the corals and poriferan occurrences distributed worldwide.

Each manuscript submitted to the symposium committee for publication was sent for peer review to two or more specialists. We would like to take this opportunity to thank all colleagues for their intensive work:

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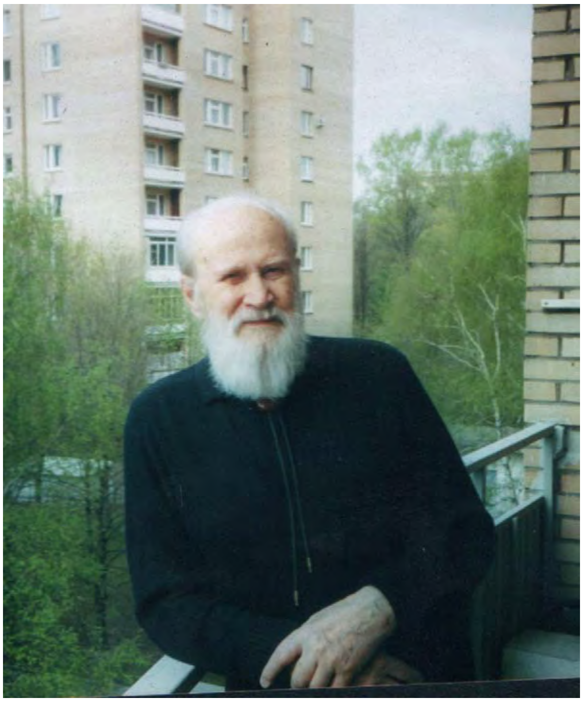
Fig. 1. Participants of the 10th International Symposium on Fossil Cnidaria and Porifera.

1. Bruno Mistiaen
2. Valentina Stolbova
3. Eddy Poty
4. Narima Ospanova
5. Bernard Lathuilière
6. Hideko Takayanagi
21. Jörn Geister
22. Wayne Bamber
23. Anna Gandin
24. Anthony Wright
25. Thomas Albert Stemann
26. Alberto Gómez Herguedas
41. Jarosław Stolarski
42. Bogusław Kołodziej
43. Rene Georg Meier
44. Robert Elias
45. Koichi Nagai
46. German Álvarez-Pérez
61. Tetsuo Sugiyama
62. Błażej Berkowski
63. ?
64. Alexander V. Kanygin
65. Marie Coen-Aubert
66. Vyara Idakieva

7. Michel Pichon
8. Jean-Pierre Cuif
9. Antonio Perejón
10. Benoit Hubert
11. Aleksei Kim
12. Wei-Hua Liao
13. Irina Soroka
14. Evgenia Antropova
15. Vladimir Lukin
16. Silvia Menendez Carrasco
17. Elena Moreno-Eiris
18. Ross McLean
19. Vladimir Ogar
20. Graham Young
27. Michaela Bernecker
28. Xiang-Dong Wang
29. Jerzy Fedorowski
30. Irina Bugrova
31. Yuki Tokuda
32. Gregory Webb
33. Higa Keiichiro
34. Carden Wallace
35. Erika Kido
36. Mikołaj Zapalski
37. Maria Hecker
38. Dieter Weyer
39. Marko Taviani
40. Nadezhda Danshina
47. Francesca Benzoni
48. Pere Busquets Buezo
49. Markus Aretz
50. Bernhard Hubmann
51. Agostina Vertino
52. Kyoko Sugiyama
53. Stephen Kershaw
54. Yoichi Ezaki
55. Anne Somerville
56. Ian Somerville
57. Lori Stewart
58. Boo-Young Bae
59. Dong-Jin Lee
60. John Pickett
67. Vassil Zlatarski
68. Klemens Oekentorp
69. Dimitri Kaljo
70. Galina Melnikova
71. Sergio Rodriguez
72. John Jell
73. Elzbieta Morycowa
74. Olga L. Kossovaya
75. James E. Sorauf
76. Paul Copper
77. George D. Stanley, Jr.
78. Françoise Debrenne
79. Makoto Kato
80. Isao Niikawa

Markus Aretz, Ann Budd, Paul Copper, Jean-Pierre Cuif, Robert Elias; Jerzy Fedorowski, Maria Hecker, Dimitri Kaljo, Steve Kershaw, Olga Kossovaya, Ross McLean, Elena Moreno-Eiris, Elzbieta Morycowa, Klemmens Oekentorp, Eddy Poty, Sergio Rodríguez, Ewa Roniewicz, Ian Somerville, Jim Sorauf, George Stanley, Gregg Webb, Dieter Weyer, and Graham Young.

The organizers are very grateful to the sponsors of the 10th International Symposium on Fossil Cnidaria and Porifera—the Ministry of Natural Resources, Russian Academy of Science, National Geological Committee of Russia, Saint-Petersburg State University, Institute of Geology of KOMI Scientific Center of RAS and Institute of Geology of the Bashkirian Scientific Centre of the Uralian Branch of RAS. The Estonian Technical University was an associated member of the Organizing Committee. The organization of the meeting was supported by a special grant of Russian Foundation for Basic Research 07-05-06041-g.



Boris S. Sokolov (born April 9, 1914), Academician of Russian Academy of Science (RAS), Professor, famous geologist and palaeontologist. Field works in Russian Platform, Central Asia, Western China, Siberia. Worked in Leningrad State University, All Russia Petroleum Research Exploration Institute (VNIGRI), Institute of Geology and Geophysics of the Siberian Branch RAS (Novosibirsk), Paleontological Institute RAS (Moscow). He is the President of the Russian Paleontological Society, Interdepartmental Stratigraphical Committee of Russia. Field of interest: tabulate corals, Chaetetidae, stratigraphy and palaeontology of Pre-Cambrian and Palaeozoic, general problems of palaeobiology and stratigraphy. The author of the more than 400 scientific publications. Boris S. Sokolov was awarded the Lenin Prize and the highest award of the Russian Academy of Science—Lomonosov Major Gold Medal.

Olga L. Kossovaya*
All-Russian Geological Research Institute (VSEGEI), Sredny pr. 74, Saint-Petersburg 199106, Russia

Ian D. Somerville
School of Geological Sciences, University College Dublin, Belfield, Dublin 4, Ireland

* Corresponding author.
E-mail address: Olga_Kossovaya@vsegei.ru (O.L. Kossovaya)

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Research paper

The fossil record of cnidarian medusae

Graham A. Young[a,b,*], James W. Hagadorn[c]

[a] The Manitoba Museum, 190 Rupert Avenue, Winnipeg, MB, R3B 0N2, Canada
[b] Department of Geological Sciences, University of Manitoba, Winnipeg, MB, R3T 2N2, Canada
[c] Department of Earth Sciences, Denver Museum of Nature and Science, Denver, CO 80205, USA

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Abstract

Fossils of cnidarian medusae are extremely rare, although reports of fossil "medusoids," most of which do not represent medusae, are rather common. Our previous inability to distinguish these fossils has hampered attempts to investigate patterns and processes within the medusozoan fossil record. Here we describe criteria for the recognition of *bona fide* fossil medusae and use them to assess the evolutionary, paleoenvironmental, and taphonomic history of the Medusozoa. Criteria include distinctive sedimentologic and taphonomic features that result from transport, stranding, and burial of hydrous clasts, as well as unequivocal body structures comparable to those of extant animals. Because the latter are uncommon, most fossil medusae remain in open nomenclature; many are assigned to stem-group scyphozoans.

The majority of described medusae are associated with coastal depositional environments (such as tidal flats or lagoons). They rarely occur in oxygen-poor deeper-water facies. All medusan groups have long geologic histories. Scyphozoa are known from the Cambrian, but more derived scyphomedusae were not demonstrably present until the Carboniferous; Mesozoic scyphozoans are rather diverse. Hydromedusae are known from the Ordovician but may extend back to the Cambrian. The record of cubozoans is shorter and sparser; the oldest definite cubozoan is Carboniferous in age.

Keywords: Medusae; Jellyfish; Scyphozoa; Hydrozoa; Cubozoa; *konservat-lagerstätten*

1. Introduction

In comparison with the modern world, the cnidarian fossil record is hugely biased toward biomineralized forms. Cnidarian medusae are abundant and widespread today, but only represented by rare and sporadic occurrences through the fossil record, mostly in *konservat-lagerstätten*. This study assesses the fossil records of the three major medusan groups: scyphozoan medusae, hydrozoan medusae, and cubozoans. Porpitid (chondrophorine) hydromedusae and conularids are not included because they possess tough or hard parts and have been the subject of recent reviews (e.g., Fryer and Stanley, 2004; Van Iten et al., 2006). Similarly, we do not present a comprehensive review of the many reported "medusoids" (i.e., medusa-like structures or fossils) that do not meet our criteria for recognition (Outlined in Section 2, below).

Fossil medusae usually tell us more about their preservational history than their palaeobiology (Schäfer, 1941, 1972). Nevertheless, in rare instances it is possible to identify unequivocal body structures comparable to those of extant organisms. More commonly, sedimentologic and taphonomic criteria are required to distinguish medusae from non-cnidarian medusoid structures. There is a long history of study of fossil medusoids (e.g., Haeckel, 1869; Walcott, 1898) and possible occurrences are spread through a great variety of literature. Most represent non-medusan fossils and trace fossils, or inorganic features such as fluid escape structures, microbial decomposition structures, and scratch circles. Only a few published medusoids represent unequivocal *medusae*, and we have been able to satisfactorily recognize only nine major medusa-bearing deposits (Table 1). Since these are in units spread across international and other mapping boundaries, there might appear to be more deposits than really exist: many occur in genetically related lithostratigraphic units. This is a shockingly small fossil record for groups with such importance in modern seas, but by considering them

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[*] Corresponding author at: The Manitoba Museum, 190 Rupert Avenue, Winnipeg, MB, R3B 0N2, Canada.

E-mail addresses: gyoung@cc.umanitoba.ca (G.A. Young), jwhagadorn@dmns.org (J.W. Hagadorn).

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Table 1
Recognized occurrences of bona fide fossil cnidarian medusae. Occurrences are clustered into nine genetically related depositional groups (A–I).

Lagerstätte group	Age/unit(s)	Location	Lithology; Dep. Environment	Mode of preservation	Taxa	# of Specimens; # of Horizons	Diameter (mm)	Previous interpretation	Revised interpretation	Key reference(s)
A	Middle Cambrian (Series 3); Burgess Shale	Mount Field, British Columbia, Canada	Shale; subtidal	Organic carbon, aluminosilicate film	–	>30; Unknown	40–120	Unknown	Scyphozoa?	Devereux (2001)
B	Middle Cambrian (Series 3); Marjum Formation	House Range, UT, USA	Mudstone; subtidal	Organic film – composition unknown	–	10; >3?	7–15	Scyphozoa? (Semaeostomeae?, Coronatae?), Hydrozoa? (Narcomedusae?), Cubozoa?	Scyphozoa? (Semaeostomeae?, Coronatae?), Hydrozoa? (Narcomedusae?), Cubozoa?	Cartwright et al. (2007)
C	Middle Cambrian (Series 3); Elk Mound Group	Mosinee, WI, USA	F- to m-grained quartz arenites; intertidal	3D, mouldic	–	>10,000; >19	50–950	Cnidarian medusae	Scyphozoa	Hagadorn et al. (2002), Tarhan (2008)
C	Middle Cambrian (Series 3); Potsdam Group	Ausable Chasm, New York, USA; Havelock, Quebec, Canada	F- to m-grained quartz arenites; intertidal	Mouldic	–	>1000; >6	70–660	Scyphozoa (Semaeostomeae?, Rhizostomeae?)	Scyphozoa (Semaeostomeae?, Rhizostomeae?)	Hagadorn and Belt (2008), Lacelle et al. (2008), Tarhan (2008)
D	Upper Ordovician; Stony Mountain Formation	William Lake, Manitoba, Canada	F-grained argillaceous dolomudstone; intertidal – lagoonal	3D, mouldic and replacement	–	>100; >4	20–65	Hydrozoa, Scyphozoa?	Hydrozoa (Anthomedusae?, Leptomedusae?), Scyphozoa?	Young et al. (2007)
E	Upper Carboniferous; Carbondale Formation	Essex and Astoria, IL, USA	Siderite concretions in siltstone; restricted marine – lagoonal	Impressions	*Anthracomedusa turnbulli*	>20	28–100	Cubozoa (Carybdeidae)	Cubozoa (Chirodropidae)	Johnson and Richardson (1968), Foster (1979), Sroka (1997), Gershwin (2003), Selden and Nudds (2004)
					Octomedusa pieckorum	∼15	3–21	Scyphozoa (Coronatae?)	Hydrozoa or Scyphozoa (Narcomedusae or Coronatae)	
					Essexella asherae	>35,000	6–90	Scyphozoa (Rhizostomeae?)	Scyphozoa or Hydrozoa (Trachymedusae)	
					Reticulomedusa greenei	∼3	45	Scyphozoa (Rhizostomeae?)	Scyphozoa	
					Lascoa mesostaurata	1; 1	40	Scyphozoa (Semaeostomeae)	Scyphozoa (Semaeostomeae)	
F	Upper Carboniferous; Cherryville Formation	Limekiln Hollow, IA, USA	Shale; subtidal	Carbon films; mouldic?	*Prothysanostoma eleanorae*	7	∼30–50	Scyphozoa (Rhizostomeae)	Scyphozoa (Rhizostomeae)	Ossian (1973)

Table 1 (*Continued*)

Lagerstätte group	Age/unit(s)	Location	Lithology; Dep. Environment	Mode of preservation	Taxa	# of Specimens; # of Horizons	Diameter (mm)	Previous interpretation	Revised interpretation	Key reference(s)
G	Lower Triassic; Grès à Voltzia Formation	Vilsberg and Arzviller, Vosges Septentrionales, France	Silt and clay laminites; delta plain ponds	$CaPO_4$ replacement	*Progonionemus vogesiacus*	10; Unknown	8–40	Hydrozoa (Limnomedusae)	Hydrozoa (Limnomedusae)	Grauvogel and Gall (1962), Gall (1990), Selden and Nudds (2004)
H	Upper Jurassic; Cerin Lithographic Limestone Formation	Cerin, Jura Mtns, France	Lithographic limestones; lagoon	Mouldic	*Bipedalia cerinensis*	14; 1	45–70	Cubozoa (Carybdeidae)	Cubozoa (Carybdeidae)	Gaillard et al. (2006)
					Paracarybdea lithographica	5; 1	50	Cubozoa, (Carybdeidae)	Cubozoa? (Carybdeidae?)	
					Paraurelia cerinensis	>1000; >6	15–105	Scyphozoa (Semaeostomeae)	Scyphozoa (Semaeostomeae)	
					Paraurelia sp. A	∼3; 2	120	Scyphozoa (Semaeostomeae)	Scyphozoa (Semaeostomeae?)	
I	Upper Jurassic; Solnhofen Formation	S. Franconian Alb, Bavaria, Germany	Laminated micritic limestones; lagoon	Mouldic	*Quadrimedusina quadrata*	1; 1	76	Cubozoa (Order Carybdeidae)	Cnidarian medusa, unknown affinities	Haeckel (1866, 1869, 1874), Walcott (1898), Maas (1906), Kuhn (1938), Kieslinger (1939), Kolb (1951), Harrington and Moore (1955, 1956a,b,c), Barthel et al. (1990), Selden and Nudds (2004)
					Epiphyllina distincta	Unknown	∼13	Scyphozoa (Coronatae)	Scyphozoa (Coronatae)	
					Cannostomites multicirratus	1; 1	∼200	Scyphozoa (Coronatae?)	Scyphozoa	
					Leptobrachites trigonobrachius	Rare; unknown	∼170	Scyphozoa (Rhizostomeae?)	Scyphozoa	
					Semaeostomites zitteli	1; 1	∼80	Scyphozoa (Semaeostomeae)	Scyphozoa (Semaeostomeae)	
					Eulithota fasciculata	1; 1	∼70	Scyphozoa (Semaeostomeae)	Scyphozoa	
					Rhizostomites sp.	Many; unknown	>500	Scyphozoa (Lithorhizostomatida)	Scyphozoa (Lithorhizostomatida)	
					Acalepha deperdita	>1; Unknown	∼70	Hydrozoa (Trachylinida?)	Cnidarian medusae, poss. Hydrozoa	
					Acraspedites antiquus	Unknown	∼140	Hydrozoa (Trachylinida?)	Cnidarian medusae, poss. Hydrozoa	
					Hydrocraspedota mayri	>1; Unknown	∼200	Hydrozoa (Trachylinida?)	Hydrozoa	

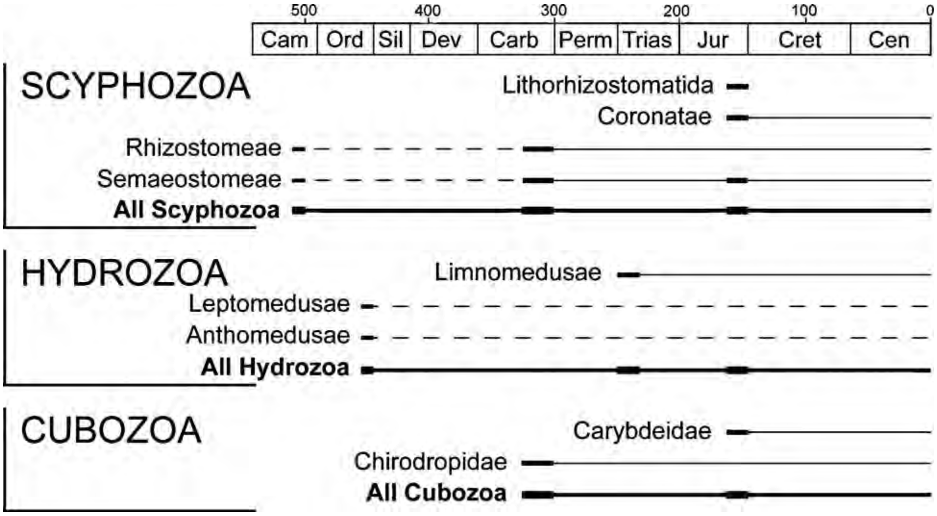

Fig. 1. Stratigraphic distribution of fossil medusae. Thick lines show intervals of known occurrence and thin lines show inferred occurrence. Dashed lines denote range extensions based on occurrences that have not yet been formally published.

together, we gain insights into the patterns of evolution and extinction among mobile cnidarians.

2. Fossilization of medusae and criteria for recognition

Medusae are relatively easy to study in modern intertidal to mid-water subtidal settings, and are commonly deposited *en masse* along coastlines. Studies of these stranded medusae, in combination with laboratory burial experiments and observations of premortem behaviour, have provided insights into medusan fossilization processes (Schäfer, 1941, 1972; Kornicker and Conover, 1960; Müller, 1984, 1985; Norris, 1989; Bruton, 1991). Together with our own studies of modern medusan taphonomy, these ecologic and taphonomic studies permit establishment of criteria for recognition of fossil medusae, which are summarized below.

Because they have nearly the same density as seawater and are difficult to bury, medusae are rare in sediments deposited below storm wave base, except where the latter are depleted of oxygen (Table 1A and B). Similarly, although mass strandings are common on sandy shorefaces, such settings often have too much scavenging, bioturbation, and hydraulic energy to preserve delicate carcasses. Preservation of medusae is best facilitated in low-energy tidal flats or lagoons (Schäfer, 1941, 1972). In such settings, most live stranded jellyfish will orient dorsal side up; these are commonly covered with sediment as wave energy wanes or tides ebb (Fig. 2A, B, and E). Medusae deposited after death are generally in hydrodynamically stable orientations, typically with dorsal side up or down (Fig. 2D). Most do not orient preferentially on their sides, with the exception of rhizostome scyphozoans (Schäfer, 1972).

Live medusae pump their bells in attempting to escape stranding; this can result in the ingestion of considerable amounts of sediment. As a result, fossil medusae commonly exhibit raised sediment mounds in the mouth area, moat-like depressions near the bell margins (Fig. 2H), and/or globular internal moulds (Schäfer, 1941, 1972; Müller, 1985; Bruton, 1991). Fossilization potential is enhanced by the cementation of sediment by decomposing fluids and bacteria, and by partial dehydration due to subaerial exposure. These processes favour the preservation of specimens deposited dorsal side up. Dehydration and shrinking of a medusa can result in the development of wrinkles or fissures and progressive loss of structure (Fig. 2I). Medusae buried by sediment may show a history of crumpling and slumping, and can collapse during decomposition to produce concave hemispheric structures (Fig. 2C).

Tentacles, an important feature of living jellyfish, are among the first features to disappear during decomposition. Fossil medusae rarely have recognizable tentacles (but see Fig. 2I), except members of groups that have particularly thick and tough tentacles in life (e.g., Cubozoa). Oral arms are often thicker, and may be preserved. Although impressions of radial canals may also be visible, tentacles and oral arms are never oriented in a perfectly radial pattern when medusae come to rest on or are entrained in sediment. Instead, they are usually dispersed or tangled like strands at the head of a mop.

Several authors have stated that medusae can only fossilize as moulds (Schäfer, 1972; Bruton, 1991; Fürsich and Kennedy, 1975) but outer or inner soft tissues can be preserved by authigenic mineralization (cf. Briggs, 2003; Fig. 2F; Table 1A, B, D, F, and G). With mouldic preservation, any one specimen will show some structures but not others, depending whether it represents a dorsal or ventral surface, or internal structure. This necessitates study of multiple specimens. The complexity of studying mouldic material is further increased by the varied processes of decay and transport. Effects of waves or currents include twisting, folding, tearing, and preservation in varied orientations (Fig. 2G).

It is thus possible to establish taphonomic criteria for the identification of fossil medusae. They are almost never perfectly radially symmetrical, nor are they always oriented parallel to, or on top of, a single bed surface. Sites at which medusae occur demonstrate paleoenvironmental and sedimentologic features consistent with the deposition and preservation of jellyfish; often they occur in conjunction with sedimentary structures or fossils characteristic of hypersaline, brackish, or emergent conditions.

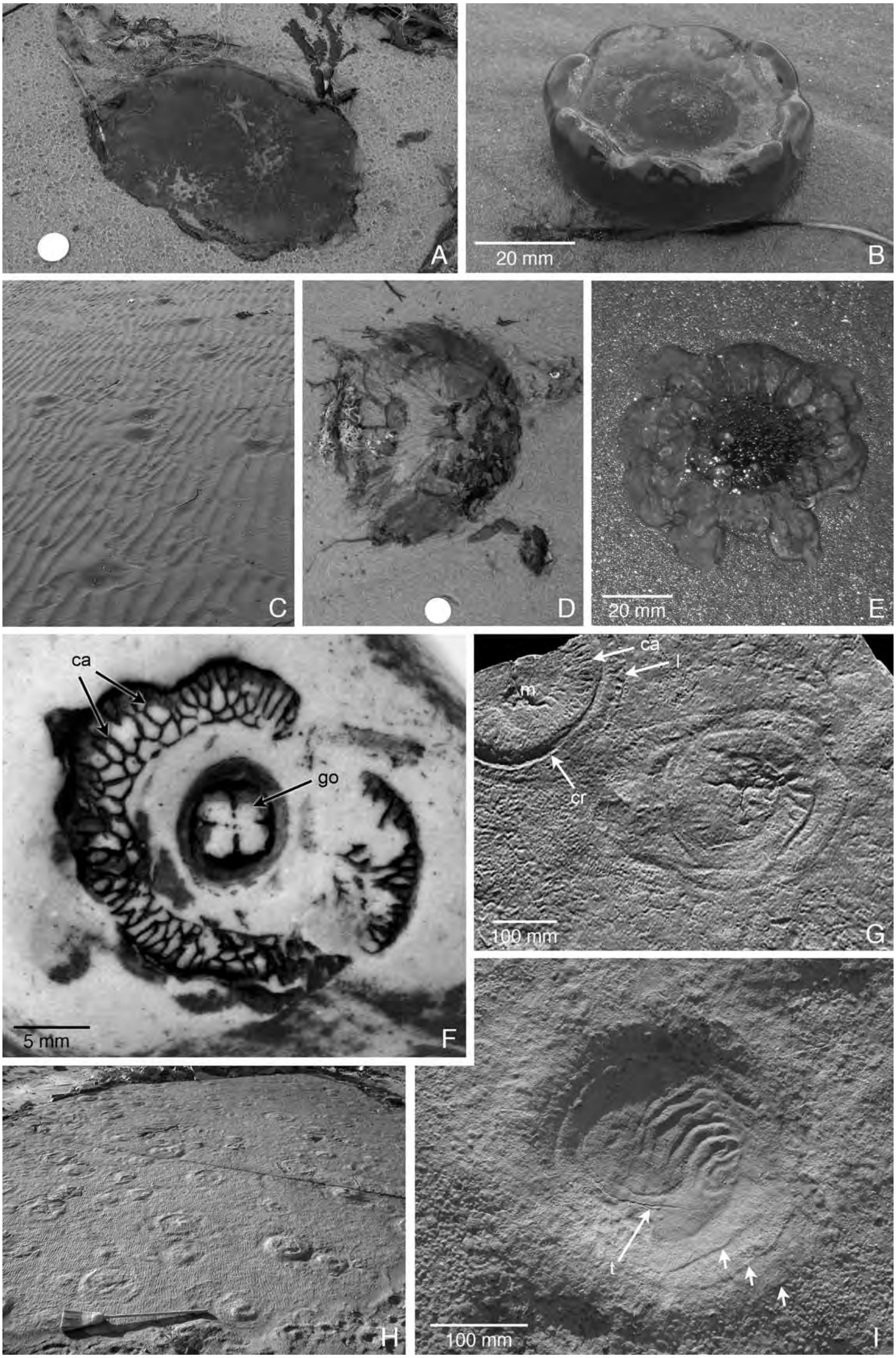

Fig. 2. Taphonomy of modern Scyphozoa, preservation of fossil medusae, and examples of Cambrian medusae. (A–E) Taphonomy of modern *Cyanea capillata* (Linnaeus) in shoreline environments, Prince Edward Island, Canada: (A) medusa with subumbrella down, note irregular outline and attached debris (coin diameter 24 mm); (B) medusa subumbrella down with muscles contracted; (C) pits resulting from decay of shallow-buried *Cyanea* (pits are about 50–200 mm wide); (D) medusa subumbrella up with attached debris and sediment (coin diameter 24 mm); (E) medusa with subumbrella down, bell margin damaged by birds and waves.

Bona fide medusae typically occur on many different horizons within a deposit, often with dozens to thousands of specimens on individual surfaces (Fig. 2H). Medusae occur in both clastic and carbonate rocks, representing a wide range of grain sizes; many of these rocks exhibit evidence of microbial binding and/or stagnation.

On the basis of this understanding of the fossilization of medusae, we have considered all documented occurrences of medusoids or medusae using several criteria: (1) evidence of original morphology consistent with cnidarian medusae; (2) evidence of preburial transport, deformation, tearing, and/or desiccation; (3) an appropriate paleoenvironment based on associated lithology, biota, and sedimentary structures; (4) number of individuals and horizons of occurrence; and (5) evidence that the medusoid(s) cannot be readily assigned to other phenomena, such as scratch circles, gas release structures, non-medusan body fossils, trace fossils, evaporite pseudomorphs, archaeological etchings, or inorganic concretions. Using these criteria, we divided all published medusoid and medusae occurrences into three categories: well documented fossil medusae (Table 1), possible medusae or those of uncertain affinities (many of which are based on single specimens), and non-medusae. With the exception of the Proterozoic medusoid record, only the *bona fide* medusae are treated here.

3. The Proterozoic record

Since their initial discovery (Sprigg, 1947), many Ediacaran fossils have been considered to be allied with cnidarian medusae. Their hypothesized medusozoan affinity stems from their discoidal shape, pliability, antiquity (and thus proximity to basal nodes on the metazoan tree), and unusual preservation in sandstones. No Ediacaran medusoids exhibit evidence of transport (e.g., Peterson et al., 2003) and most possess radial structures and rooting features indicating that they grew below the sediment-water interface as attachments for frond-like Ediacarans (e.g., Jenkins and Gehling, 1978; Seilacher, 1992; Steiner and Reitner, 2001). Moreover, tentacle-like structures on Ediacarans are always radial or quasi-radial; they are never tangled, twisted, draped across/under/around the “bell,” or enmeshed with adjacent specimens as one would expect from deposition of a mop-like jellyfish. Radial structures reported from Ediacarans often extend beyond the central disc and thus cannot be impressions of radial canals. Simple discoidal Ediacarans are still less plausible as cnidarians: they lack structures diagnostic of cnidarian morphology, including even the most basic radial patterns seen in anthozoan trace fossils such as *Bergaueria*, and do not show evidence of shearing or transport. Many Ediacaran medusoids exhibit margin-deformation features that suggest they grew in place next to one another, glued to or resting on the sediment surface. All Precambrian medusoids are Neoproterozoic in age, and most are Ediacaran. Cryogenian medusoids (e.g., *Bunyerichnus*) have been reinterpreted as inorganic scratch circles. Thus, there are no *bona fide* published Proterozoic medusae.

4. The Palaeozoic record

Nearly all Palaeozoic medusae belong to stem groups of the modern medusan classes (Table 1; Fig. 1), although medusae with derived features may have occurred as early as the Middle Cambrian. More complex forms appeared by the Late Carboniferous.

The oldest known medusae come from the Series 3 (i.e., middle) Cambrian. In the Burgess Shale, dozens of specimens are known, yet detailed taxonomic analysis of these medusae is lacking and at present they have only been broadly categorized as Scyphozoa (Devereux, 2001). Slightly younger occurrences from a Burgess-type deposit in Utah, USA (Cartwright et al., 2007) provide tantalizing hints that the major medusozoan clades diversified early. The Utah medusae are very small and few specimens are known, but they show remarkable preservation of features such as tentacles and muscles. Four informally recognized types show strong similarities to narcomedusan hydrozoans, semaeostome and coronate scyphozoans, and possibly cubozoans. The extreme rarity of medusae in these deeper-water *konservat-lagerstätten*, from which thousands of specimens of other groups are known, is consistent with the suggestion that the low density of medusae makes them unlikely to be deposited in such settings.

Abundant medusae also occur in Series 3 (middle) Cambrian coarser-grained clastic rocks deposited in intertidal settings at three sites in North America (Hagadorn et al., 2002; Hagadorn and Belt, 2008; Lacelle et al., 2008) (Fig. 2G–I). Their mouldic preservation is more similar to that of Ediacaran fossils than to preservation in younger Palaeozoic rocks; the Cambrian taphonomic regime permitted the preservation of carcasses that would presumably have been lost to bioturbation or decomposition later in the Palaeozoic. Despite their occurrence in fine- and medium-grained sands, part-counterpart molds and steinkerns of these fossils reveal radial canals, manubria, oral arms, coronal rings, and lappets. Most are likely semaeostome or rhizostome scyphozoans (Tarhan, 2008).

Numerous medusae occur in Upper Ordovician marginal marine dolostones at William Lake, central Canada (Young et al., 2007). The best-preserved specimens are three-dimensional. Tissues that are thick and tough in living medusae, such as

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(F) Semaeostome scyphozoan medusa similar to modern *Aurelia*, with canals (ca) and gonads (go) preserved as pyrite in chert nodule (pyrite has been weathered), probably of Ordovician age, Manitoba, Canada (Manitoba Museum specimen, MM I-2555). (G–I) Cambrian scyphozoan medusae from Wisconsin, USA: (G), two medusae on bed sole which have “double impressions”, having been shifted after first coming to rest subumbrella down on the sediment; note radial canals (ca), lappets (l), manubrium (m), and coronal ring (cr); (H) composite stranding surface bearing hundreds of large medusae that were buried in at least four successive depositional events (broom in foreground is 1.37 m long); (I) medusa on bed sole that exhibits post-depositional shrinkage of the bell (three successively smaller bell margin impressions are arrowed), and rippling of sand which was formerly encased in the stomach. Both events postdate initial excavation of a moat by the living jelly; also note pustular, possibly microbial, textures adjacent to carcass, radial lappet-like impressions at upper left, and diagonal strand across carcass that may be a sand-coated tentacle (t).

manubria, stomachs, and canals, have been replaced by calcareous and pyritic material (Fig. 3A–C). Bells and tentacle bases appear as colour variations in dolostone. The majority are hydromedusae, some showing affinities to the extant orders Anthomedusae and Leptomedusae. A few specimens are likely scyphozoans (Fig. 3D).

Unequivocal fossil medusae have not yet been discovered in Silurian or Devonian rocks, but the Carboniferous provides a rich assemblage of Palaeozoic medusae. Thousands of specimens occur in siderite concretions of the Mazon Creek *konservat-lagerstätte* of Illinois, USA (Fig. 3E–H). Some of these preserve external features such as bell margins and tentacles, but internal details are obscure. Mazon Creek medusae include the oldest definite cubozoan, a member of the still-extant family Chirodropidae (Johnson and Richardson, 1968; Gershwin, 2003; see Fig. 3E and F), and the oldest definite semaeostome scyphozoan (Foster, 1979). Other Mazon Creek medusae are more problematic; *Octomedusa pieckorum* Johnson and Richardson (1968; see Fig. 3H) may be a coronate scyphozoan (Foster, 1979) or a narcomedusan hydrozoan. *Essexella asherae* Foster (1979), by far the most abundant Mazon Creek medusan, is a blob-like form that could be either a scyphozoan or a hydromedusan.

The finest described Palaeozoic fossil medusae are the seven specimens of the Late Carboniferous *Prothysanostoma eleanorae* Ossian (1973) from Iowa, USA. These are preserved as carbon films in indurated black shale, showing remarkable details of the bell and oral arms; they are the oldest rhizostome scyphozoans.

5. The Mesozoic and Cenozoic record

The Mesozoic medusan record comprises some spectacularly preserved fossils, including forms that are distinctly more derived than their Palaeozoic precursors. Since all recognized medusae occur in just a few *konservat-lagerstätten*, all of them in Europe, it is possible that the Mesozoic record is even less complete than that for the Palaeozoic.

Progonionemus vogesiacus Grauvogel et Gall (1962) is the oldest known limnomedusan hydrozoan. In these specimens from the Lower Triassic Grès à Voltzia of France, soft tissues including gonads and tentacles occur, allowing direct comparison with the extant genus *Gonionemus.*

Upper Jurassic lithographic limestones in France contain mouldic medusae that bear tentacles and gonads. These medusae include the oldest definite carybdeid cubozoan and a semaeostome scyphozoan very similar to the widespread extant *Aurelia* (Gaillard et al., 2006).

The diverse medusae found in the Upper Jurassic lithographic limestones of the Solnhofen lagerstätte of Germany are probably the most famous fossil jellies (Haeckel, 1866, 1869, 1874). The most striking specimens are very large ($\geq$50 cm diameter) scyphozoans assigned to *Rhizostomites* (Fig. 3I), which have been placed in their own order, the Lithorhizostomatida (Harrington and Moore, 1956a). Other notable Solnhofen medusae include the oldest coronate scyphozoan and several hydrozoans (Maas, 1906). Unambiguous fossil medusae have not been described from post-Jurassic deposits. Most of the medusoids known from Cretaceous and Tertiary deposits have been demonstrated to represent other structures such as flysch trace fossils (e.g., Häntzschel, 1975).

6. Discussion

This preliminary analysis of the complete, screened fossil record of medusozoans affects our understanding of the evolutionary and phylogenetic history of the Cnidaria. For example, the general pattern of medusozoan diversification (Fig. 1) establishes an earliest known date for each group and provides a logical starting place for calibrating the timing of divergences predicted by molecular phylogenies (e.g., Collins, 2002). The major medusan groups were apparently established concomitant with or shortly after the Ediacaran-Cambrian metazoan diversification; more derived forms, including Cubozoa, appeared in the Late Palaeozoic and Mesozoic. The earliest published Scyphozoa are Middle Cambrian; at least two of the three major orders (Semaeostomeae and Rhizostomeae) may have been present at this time. Two orders of Hydromedusae (Anthomedusae and Leptomedusae) were probably present by the Late Ordovician; this group apparently diversified by the Mesozoic. Cubozoa resembling modern forms are known from the Late Carboniferous and Late Jurassic.

One striking feature for all three classes, even when considering Palaeozoic forms, is the general morphological similarity between fossil and living medusae; almost all well-preserved fossil medusae possess characters consistent with membership in extant groups. Although there has apparently been diversification through time, and convergence is difficult to assess without cnidarian biomarker or molecular data, it may be that medusozoan clades, once established, were unlikely to become extinct. Many jellyfish might thus be considered “living fossils”. This fits with the pattern recognized for other groups of plankton, which are notoriously conservative and long-lived (e.g., Rigby and Milsom, 2000). Huge numbers, wide geographic distribution, and limited interspecies competition may make extinction less likely.

Modern mass strandings of medusae are commonplace (e.g., Bruton, 1991). The huge numbers of fossil medusae in certain marginal marine deposits (e.g., Hagadorn et al., 2002; Table 1C) suggests similar mass strandings as early as the Cambrian. Modern mass strandings reflect the immense abundance of jellyfish and the ancient examples suggest that similar abundances existed but had low preservation potential. Thus, studies of large-scale patterns in marine trophic webs and guilds should presume the presence of medusae.

Evolutionary paleoecological changes may have influenced large-scale shifts in the taphonomic “windows” that foster medusan preservation. For example, there was relatively little pre-Silurian bioturbation in marginal marine environments (Buatois et al., 2005). Fossil medusae are only abundant in such facies prior to this increase in bioturbation. Further increases in bioturbation through the Mesozoic and early Cenozoic are paralleled by rarity and then disappearance of medusan fossils from such settings.

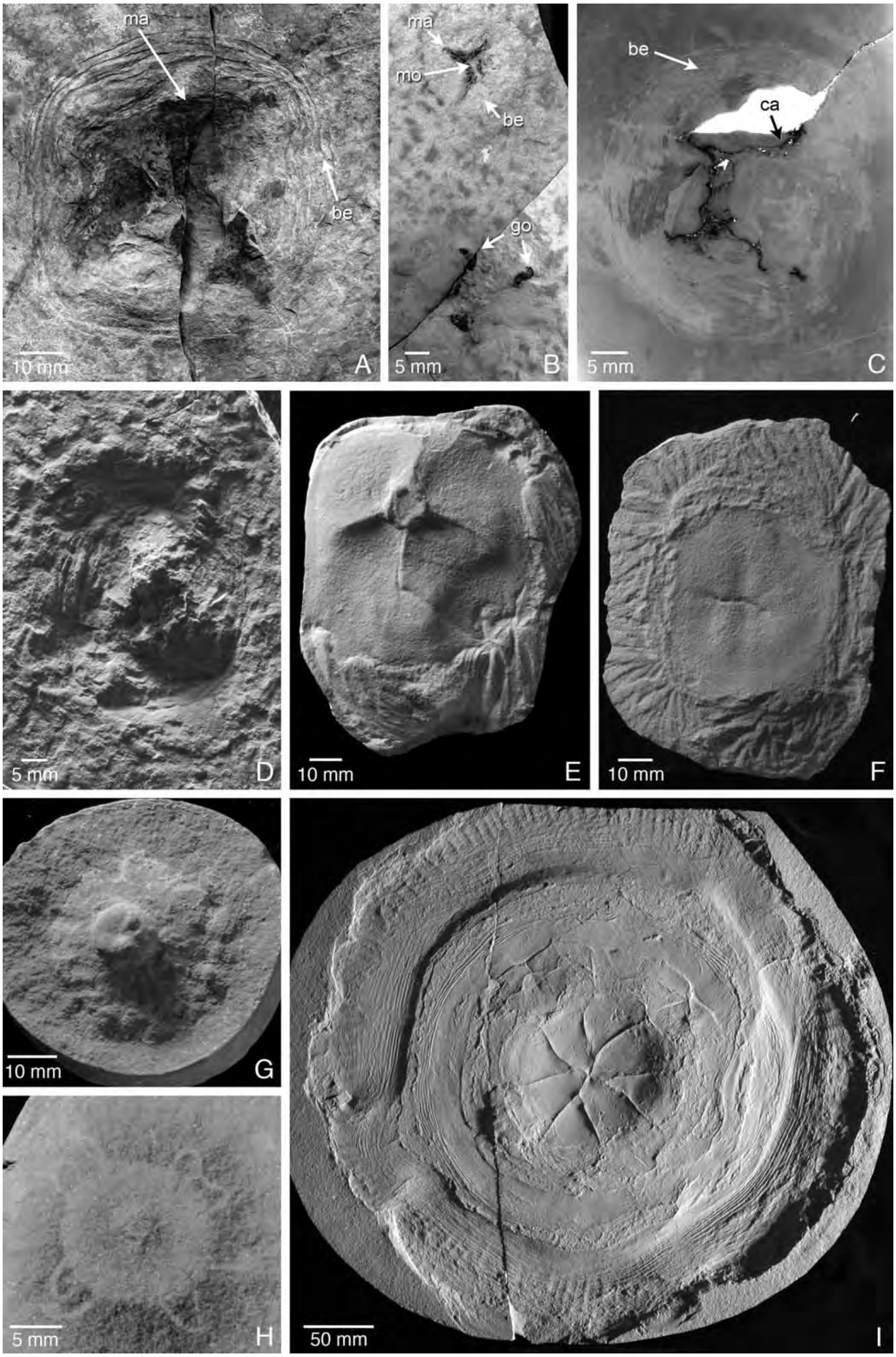

Fig. 3. Ordovician, Carboniferous, and Jurassic fossil medusae. A-D, Late Ordovician (Richmondian) medusae from the Williams Member, Stony Mountain Formation, at William Lake, Manitoba, Canada: (A) large medusa (Hydrozoa) on weathered surface, note quadrate manubrium (ma) and wrinkled bell (be) (MM I-4261); (B) Small anthomedusan (upper) and?leptomedusan hydrozoans on fresh bedding surface, with features including partly pyritized manubrium (ma), mouth (mo) bell (be), and probable gonads (go) (MM I-4058); (C) transverse thin section of a hydromedusan showing dark, partly pyritized canals (ca), and wrinkled bell (be) (MM I-4262B); (D), weathered medusa (?Scyphozoa) with dense axial structure and wrinkled bell (MM I-4055A). (E–H) Late Carboniferous (Westphalian) medusae from the “Mazon Creek” (Francis Creek Shale Member, Carbondale Formation), Illinois, USA: (E and F) two specimens of the cubozoan *Anthracomedusa turnbulli*, showing distinct axial structure and abundant tentacles (Royal Ontario Museum Invertebrate Palaeontology specimens, ROM 47980 and 53730); (G) the scyphozoan *Reticulomedusa greenei* (ROM 47991); (H) the problematic medusan *Octomedusa pieckorum*, showing distinct bell margin and tentacles (ROM 47540). (I) Late Jurassic (Tithonian) scyphozoan *Rhizostomites* sp. from the Solnhofen Formation, Franconian Alb, Bavaria, Germany, showing well-preserved bell and axis (ROM 18325).

Similarly, in the early Palaeozoic there are virtually no scavengers known to have operated at or above the strandline. By the late Palaeozoic there were many more potential shoreline scavengers of medusan carcasses (e.g., eurypterids, tetrapods), and this intensified in the late Mesozoic as birds and crabs colonized coastal settings. Moreover, early Palaeozoic coastal systems probably included immense tidal flats unlike anything in the modern world, because salt marsh, delta swamp, and mangrove communities were absent. The subsequent colonization of tidal flats by plants would have left far less area available for the deposition and preservation of medusae.

Given that the shifting of these medusae-rich taphonomic windows may be linked to large-scale evolutionary paleoecological changes in bioturbation, scavenging, microbial binding, and vegetation dispersal, there is a bright future for those of us with jellyfish on our minds. We can use this knowledge to search for new *konservat-lagerstätten* and enrich our understanding of the early evolutionary history of the Cnidaria.

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Research paper

Distribution of the archaeocyath-calcimicrobial bioconstructions on the Early Cambrian shelves

Anna Gandin[a,*], Françoise Debrenne[b]

[a] Dipartimento di Scienze della Terra, Via Laterina 8, 53100 Siena, Italy
[b] UMR 514, 13, rue du long foin, Sainte Geneviève des bois 91700, France

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Abstract

The differences and variety of structural, depositional, and compositional features observed in the Early Cambrian microbial-archaeocyath buildups preserved in the present-day continents, suggest a direct correlation between the physico-chemical factors of deposition and the structural architecture of the buildups. This can be explained in terms of their palaeogeographic collocation on the shelves (depth, energy), and hence of the areal distribution of epeiric basins and perioceanic/pericontinental platforms.

Data on the analysis of biohermal communities and their architectures indicate that the relative development of the main reef-building components, as well as their evolution within the reef communities, reflects the dominant physico-chemical factors, mainly temperature and nutrient availability, and the physiography of the primary depositional setting. The bioaccumulations show different reef building styles, defined by the types of associated facies and by the early diagenetic features. They are represented by (i) mud-supported simple (*Kalyptrae*) to compound mounds locally with stromatactis-like cavities; (ii) dendrolitic bioherms and crustose buildups with large shelter cavities and low synoptic relief; (iii) cement-supported skeletal reefs with wave resistant frameworks often associated with oolitic shoals, and (iv) bioclastic sands, developed at photic and shallow sub-photic depths on low-angle/low-energy ramps (i–ii) or on high-energy conditions on platforms distally rimmed (iii) or occasionally swept by storm currents (iv).

The results of the analysis provide information on the spatial conditions of the primary depositional settings of the first metazoan involved in reef building in the history of the Earth, and suggest that the architecture of the bioconstructions was controlled not only by the physiography of the depositional setting and global/astronomic climate but also by local climatic conditions constrained by the latitudinal distribution of the Early Cambrian continental blocks.

Keywords: Archaeocyaths; Calcimicrobes; Bioconstructions; Early Cambrian

1. Introduction

The differences in architecture and the variety of structural, depositional, and compositional features observed in the Early Cambrian microbial-archaeocyath buildups preserved in the present-day continents have been explained in terms of global climate and palaeogeographic collocation on the shelves (Courjault-Radé et al., 1992; Savarese et al., 1993; Rowland and Shapiro, 2002) whereas the influence of temperature and nutrient availability has been less considered (Wood et al., 1993; Riding and Zhuravlev, 1995).

The analysis of the different reef building styles, defined by the types of associated facies and by the early diagenetic features, can provide information on the latitudinal/climatic and spatial conditions of the primary depositional setting since the relative development of the main reef-building components and their evolution within the reef communities appear to reflect the dominant physico-chemical factors of the environment.

Cambrian bioaccumulations have been widely assumed in the past to represent reef communities and for comparison with Recent analogues, ascribed to tropical warm waters (Debrenne, 1959; James and Klappa, 1983; Rowland and Gangloff, 1988; Debrenne and Courjault-Radé, 1994; Debrenne and Zhuravlev, 1996; Zhuravlev, 2001). However, the temperatures of the water in a deep setting of the tropical zone may equate to the temperatures of shallow water in higher latitudes. Consequently,

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* Corresponding author.
E-mail address: gandin@unisi.it (A. Gandin).

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"cool-water" communities might have played an important role in the formation of Phanerozoic bioconstructions.

Early Cambrian world-wide bioaccumulations can be divided in two main categories:

(1) Mound-type buildups, dominated by lime-mud and/or calcimicrobes with accessory solitary regular or simple modular archaeocyaths, that lived on a soft substrate in mildly eutrophic or oligotrophic conditions, in deeper waters at low-latitude or in shallow, temperate/cool conditions at high-latitude. The normal-to-slightly saline waters were rich in nutrients, coming from the mainland or from upwelling currents along the west facing coasts of continents. This type of construction is commonly associated with bioclastic storm-generated floatstones. Non-skeletal allochems are conspicuously absent.

(2) Biohermal frameworks composed of complex, modular colonies of archaeocyaths having a real frame-building potential, associated with calcimicrobes and cements, which show the typical architecture of Recent, wave-resistant reefs. The modular archaeocyaths concurred with *Renalcis* to build wave-resistant, often cement-supported, sometimes ecologically zoned constructions. *Epiphyton*, coralomorphs, and radiocyaths were common accessories present in the community. This kind of consortium has been interpreted as living in a probable photosymbiotic regime (Rowland and Shapiro, 2002), also suggested by the observation (Camoin et al., 1989) of the presence of "putative bacteria" (Debrenne, 2007) within the skeletal elements of archaeocyaths, and therefore able to live in warm, nutrient-poor waters on low-latitude coasts.

    A variety of allochem sands, and in particular oolitic grainstone forming shoal complexes, are commonly associated with this type of construction.

The distribution in space and time of the archaeocyath-calcimicrobe buildups appears to reflect the evolution of the archaeocyaths with a peak in the Botoman Stage when most of the shelves were positioned in the tropical zone, and a drastic decrease in the Toyonian Stage when most of the continental masses began to drift towards the southern pole, except Antarctica which still located in low latitudes, harboured a few archaeocyath communities during Middle and even Late Cambrian. The remaining Middle Cambrian carbonate platforms were located in high latitudes and inhabited by photoautroph microbes, probably the only calcareous secreting organisms able to survive the Early/Middle Cambrian cooling crisis.

2. History of research

The international community of coral specialists, who before 1971 used to communicate their current researches through informal groups in USA, France, and the former URSS, were ready to follow the recommendation of the academician B.S. Sokolov during the first international meeting in Novosibirsk in August 1971, to establish an International Committee on Fossil Corals (and later some other coelenterates and Porifera) and related reefal structures, and to organize periodical meetings in different countries once in every four years. All specialists, the survivors of the 1st meeting (including the second author of this paper) as well as newcomers, met as a mark of their esteem and gratitude, in St Petersburg in August 2007 for the Xth Symposium to celebrate the 90th anniversary of the founder of the Association, Academician Boris Sergueievitch Sokolov. The impact of the numerous investigations on all fossil groups and related subjects and the progress obtained are unquestionably attested by the contributions presented in the successive Symposia and published in special volumes.

Concerning the Early Cambrian Archaeocyatha, two important unsettled problems were presented for the first time at different Symposia: their place in the living world and their role in the Cambrian bioconstructions.

Since their discovery in the mid-nineteenth century, on the basis of superficial similarities, archaeocyaths have been attributed to a variety of groups including corals, sponges, protists, and algae. In 1971, they were, almost generally, regarded as an independent phylum. At the IVth meeting (Washington 1983), Debrenne and Vacelet (1984) demonstrated that they belong to the phylum Porifera by scientific comparisons of the structural organisation of archaeocyaths with that of recent sponges having a massive calcareous skeleton, with or without spicules. This position was possible only after the discovery by scuba divers of sponges with massive calcareous skeleton, living in submarine caves of the Caribbean. At last, consensus was reached on considering Archaeocyatha as a Class among the Porifera (Debrenne et al., 2002b).

The term "reef" was used from the beginning to describe archaeocyath settings by geologists working in USA, Sardinia, Russia, and Australia. Archaeocyatha and associated "algal" organisms (now thought to be related to calcified microbes) were interpreted as responsible for constructions comparable with the Great Barrier Reef (Hyatt, 1885). Detailed investigations took place only after I.T. Zhuravleva's pioneer works (Zhuravleva and Zelenov, 1955). She was the first to propose several types of "bioherms" according to their biological components (Zhuravleva, 1960) and was followed by the Russian authors. At the 3rd meeting (Warsaw, 1979), Françoise Debrenne, in collaboration with the eminent specialist on carbonates Noël James, provided a synthesis of all data published in the USSR from 1955 to 1977 on archaeocyath-rich bioherms and their major components, allowing western specialists to have access to the Russian literature otherwise not readily available.

Noël James and collaborators (James and Kobluk, 1978; James and Debrenne, 1980; Debrenne and James, 1981; James and Gravestock, 1990; Kruse et al., 1995) proposed a method of quantification of the reef components, based on the detailed mapping of the different biological and abiotic domains (Figs. 1 and 2). This method adopted since 1980 by most of the scientists studying the bioconstructions throughout the Early Cambrian world (Table 1) has been recently applied to La Sentinella reef in Sardinia (Fig. 3): the different sedimentological and fossil components were located and quantified in grid squares measuring 30 × 30 cm (Gandin et al., 2007).

Table 1
Distribution of the Lower Cambrian archaeocyathan reefs.

Stratigraphic distribution	Locality	Authors	Reef types and components
Tommotian (*regularis*, *lenaicus-primigenius* zones)	Russia Siberian Platform	Kruse et al. (1995)	single; stacked, 1–3 m 1. archaeocyaths and mud 2. *Renalcis* dominant builders 3. archaeocyaths bowls, plates, shelter cavities and cements
Tommotian (*A. sunnaginicus* zone)	Russia Aldan River Ulakhan Sulugur	Riding and Zhuravlev (1995)	single, 1 m 68 × 1 m 12 builder dominant: archaeocyaths 5 successive stages of development
Tommotian (*D. regularis-D. lenaicus* zone)	Russia Lena River Titiriktek	Zhuravleva (1966, 1972)	isolated *Kalyptrae*, 0.5 m × 0.5–2 m several levels of stacked *Kalyptrae* 45 m high binders *Renalcis* and cement, archaeocyaths at top and flanks
Atdabanian Lower Botoman	Russia Lena River Kokulin-Oi-Muran		Kokulinsk kalyptrate reef archaeocyath dominant + *Renalcis*, ×10 km Oi-Muran kalyptrate complex reef 50 m × 1 km archaeocyath-*Renalcis-Epiphyton*
Bazaikh to Sanachtykgol-Obrutchev	Russia Altai-Sayan Tuva	Zadorozhnaya (1974)	calcimicrobial-archaeocyath single *Kalyptra* 5 m × 8 m and complex stacked *Kalyptrae* up to 80 m
Kameski-Sanachtykgol	Mongolia Western Mongolia	Voronin and Drozdova (1976), Drosdova (1980)	single *Kalyptrae* from 1 to 10 m complex reef with stacked *Kalyptrae* $h < 100$ m classical types: *Renalcis* dominant with associated calcimicrobes archaeocyath dominant, rare calcimicrobes *Renalcis-Epiphyton* + archaeocyaths regulares dominant in diversity
Mid-Atdabanian? Lower Botoman (Salaany-Gol Formation)	Mongolia Zuune Arts	Wood et al. (1993)	single complex 1. builders: dominant archaeocyaths-radiocyaths-calcimicrobes 2. calcimicrobes, rare archaeocyaths 3. *Cambrocyathellus*-calcimicrobes, moderate to high energy conditions to deep water
Mid-Atdabanian? Lower Botoman (Salaany-Gol Formation)	Mongolia Zavkhan Basin	Kruse et al. (1996)	Type 1. Gordonophyton-*Girvanella* crusts, cryptic community of cribricyaths, coralomorphs and archaeocyaths Type 2. radiocyath-archaeocyath bioherms, modular and encrusting forms as binders; minor calcimicrobes Type 3. calcimicrobial bioherms, archaeocyaths rare
Toyonian (Tianheban Formation)	China Yangtze Province	Debrenne et al. (1991)	isolated *Kalyptrae* 1. solitary archaeocyath with exocyathecal tissue, encrusted by *Renalcis*, *Epiphyton* and *Girvanella* 2. modular branching archaeocyaths linked by exocyathecal tissue smaller calcimicrobes
Botoman (Xiannüdong Formation)	China Shaanxi Province	Yuan et al. (2001)	10 levels of archaeocyath bioherms 2–3 m high, along a 30 km belt, *Renalcis* dominant and *Girvanella*
Atdabanian (Issendalenian)	Morocco N. Anti-Atlas	Debrenne et al. (1992), Debrenne and Debrenne (1995)	simple 1 m × 1–2 m *Renalcis* + rare Archaeocyaths-bafflestone with modular archaeocyaths = *Epiphyton-Renalcis* dominant + *Girvanella* + modular archaeocyaths and large cups sheltering cavities
Botoman (Banian 1–2)	Morocco N. Anti-Atlas	Debrenne et al. (1992), Debrenne and Debrenne (1995), Álvaro and Debrenne (2007)	giant reef 20 m × 100 m *Renalcis* dominant boundstone locally archaeocyath framework complex accumulation, H: 2 m × 2–3 m up to 200 m
Botoman (Banian 1–2)	Morocco S. Anti-Atlas	Debrenne (1975), Debrenne et al. (1992), Debrenne and Debrenne (1995)	simple 1 m × 1–2 m *Renalcis* + rare archaeocyaths-complex H: 200 m archaeocyaths = *Epiphyton-Renalcis* dominant + *Girvanella* + associate archaeocyaths
Botoman (Banian 3)	Morocco High Atlas	Debrenne et al. (1992), Debrenne and Debrenne (1995)	simple *Renalcis* dominant
Atdabanian	France Normandie	Debrenne (1958), Doré (1972)	*Kalyptra*: 0.25–0.50 m, dominant oligotypic assemblages modular-branching archaeocyaths, *Epiphyton*, *Girvanella* open shelf, low energy

Table 1 (*Continued*)

Stratigraphic distribution	Locality	Authors	Reef types and components
Botoman	France Montagne Noire	Debrenne et al. (2002a)	pioneer reefs, *Epiphyton*, *Girvanella*, scattered archaeocyaths low energy, subtidal mud-mounds with dominant *Epiphyton*, minor *Renalcis* and saucer-like *Anthomorpha* sheltering cavities and marine cement high energy
Atdabanian (Ovetian)	Spain Serra di Cordoba Zafra-Alconera Zone	Zamarreño and Debrenne (1977), Perejón (1986), Moreno-Eiris (1987), Perejón and Moreno-Eiris (1992, 2006), Perejón et al. (2001)	Cordoba: *Kalyptra* archaeocyath dominant + *Epiphyton* complex *Kalyptrae Renalcis* dominant, rare archaeocyaths Alconera reef (quarry) *Renalcis* and stromatactis, rare archaeocyaths
Atdabanian-Botoman (upper Ovetian)	Spain Central Iberic Zone Urda	Perejón and Moreno-Eiris (1978), Moreno-Eiris (1987), Perejón and Moreno-Eiris (2006)	oolitic, bioclastic, microbial limestone mounds with *Anthomorpha*
Atdabanian-Botoman (upper Ovetian)	Spain Catalonia	Perejón et al. (1994), Perejón and Moreno-Eiris (2006)	reef 23 × 50 m *Epiphyton* dominant, *Renalcis* and less *Girvanella*, archaeocyaths minor components above small *Kalyptrae* with large archaeocyaths encrusted by calcimicrobes
Toyonian (mid-upper Bilbilian)	Spain Cantabrian Mts.	Debrenne and Zamarreno (1975), Álvaro et al. (2000), Perejón and Moreno-Eiris (2003)	*Kalyptra* 0.8 × 1 m modular archaeocyath dominant, *Renalcis* and *Girvanella*
Botoman (lower Matoppa Formation)	Sardinia Matoppa Valley	Gandin and Debrenne (1984), Debrenne (2007)	discontinuous *Kalyptrae*, 0.5 × 2 m core = boundstone: branching or saucer-like archaeocyaths encrusted by *Renalcis*, *Girvanella* wave resistant pioneer reefs
Botoman (mid-Matoppa Formation)	Sardinia San Pietro area	Gandin and Debrenne (1984), Debrenne (2007)	calcimicrobial biostromes *Epiphyton* dominant minor *Renalcis* and *Tarthinia*, *archaeocyaths* at the periphery
Botoman (mid-Matoppa Formation)	Sardinia Gonnesa area (la Sentinella)	Gandin and Debrenne (1984), Gandin et al. (2007), Debrenne (2007)	reef complex: initial stage thrombolitic flat stacked microbial crusts arched microbial-crust system *Renalcis* cement boundstone open shelf, shallow marine increasing energy
Botoman (mid-upper Matoppa Formation)	Sardinia Rio Cannas	Debrenne et al. (1980), Gandin and Debrenne (1984), Debrenne (2007)	*Girvanella* lenticular buildups, massive reefs with cortex of nodular floatstone with archaeocyaths core: calcimicrobial boundstone *Renalcis* dominant, *Epiphyton*, isolated archaeocyaths periphery: *Girvanella* dominated boundstone with scattered archaeocyaths, skeletal debris
Botoman (lower Punta Manna Formation)	Sardinia Punta Manna	Debrenne et al. (1989a)	patch-reef and biostromes builder: *Girvanella* and low-diversity archaeocyath assemblages back shoal lagoons in oolitic complex
Atdabanian (Puerto Blanco Formation-1)	Mexico Sonora	Debrenne et al. (1989b)	Type 1: *Kalyptra*, wave resistant, framework dominated by branching archaeocyaths, strengthened by encrusting *Renalcis*, shelf margin
Botoman (Puerto Blanco Formation-2-3)	Mexico Sonora		Type 2: patch-reef and biostromes builder: *Girvanella* and low-diversity archaeocyath assemblages back shoal lagoons in oolitic complex
Botoman (Montenegro-Poleta Formation)	USA Nevada and California	Gangloff (1976), Rowland (1984), Rowland and Gangloff (1988)	complex reef $H = 65$ m archaeocyaths and algal boundstone, cavities with pendant *Renalcis* replacement sequence: bioclastic lime-mudstone (stabilization stage) low diversity archaeocyath fauna and thrombolitic fabric (colonization stage) archaeocyath fauna 13% in volume, *Renalcis* (diversification stage) oligotypic branching archaeocyath 38% in volume (domination stage)
Late Botoman (Scott Canyon Formation)	USA Nevada Lander County	Debrenne et al. (1990)	Galena Canyon: crusts of *Girvanella*, *Botomaella*, *Bija* + *Renalcis*, *Epiphyton*, *archaeocyaths*, diverse fauna – small cavities Iron Canyon: *Epiphyton*, calcimicrobial crusts dominant archaeocyaths in diverse proportion, cavities
Late Botoman (upper Harkless Formation)	USA Western Nevada	Savarese and Signor (1989)	complex lenticular, framework = domal Retilamina (archaeocyath dominant) sheltering cavities encrusted by *Renalcis* 4 archaeocyath genera

Table 1 (*Continued*)

Stratigraphic distribution	Locality	Authors	Reef types and components
Late Botoman (Shady Dolomite Formation)	USA Appalaches New Jersey and Virginia	McMenamin et al. (2000)	NJ: branching archaeocyaths with exothecal outgrowths, bafflestone, clotted fabric, micritic mud calm subtidal conditions VA: bafflestone of branching archaeocyaths associated with other archaeocyaths, calcimicrobes, coralomorphs and stromatactis cavities subtidal agitated environment
	Canada Yukon	Handfield (1971), Read (1980)	kalyptrate reef complex, $H = 90$ m *Renalcis* dominant, branching archaeocyaths
Botoman (Nevadella to Bonnia-Olenellus zones)	Canada NW Territories British Columbia	Handfield (1971), Stelck and Hedinger (1975), Voronova et al. (1987), Mansy et al. (1993)	archaeocyaths bioconstructions only in Eastern Rocky Mountains Trench, small cups bounded by *Renalcis* (builder) and some *Epiphyton* (Regulares dominant on Irregulares)
Late Botoman (Forteau Formation)	Canada Labrador	James and Kobluk (1978), Debrenne and James (1981)	single *Kalyptrae*, oligotypic modular archaeocyaths with binding exothecal structures dominant, *Renalcis*, *Epiphyton* = primary association variable within other *Kalyptrae* in complex reefs cavities – boring at top shallow near shore environment, low energy
Lower-Mid Botoman (Wilkawillina Formation)	Australia Flinders Ranges	Gravestock (1984), James and Gravestock (1990)	single, 1 m × 1 m; complex, 100 m × 100 m calcimicrobes dominant – interior platform archaeocyath dominant + spongiomorphes + rare *Renalcis* – open shelf *Renalcis* dominant, rare archaeocyaths – inner shelf-low energy *Epiphyton* dominant, cryptic archaeocyaths – high energy, shelf margin *Girvanella* dominant, *Renalcis*, *Epiphyton*, archaeocyaths – open shelf, high energy
Upper Botoman-Lower Toyonian (Wirrealpa Limestone)	Australia Flinders Ranges	Kruse (1991)	*Epiphyton* + low diversity archaeocyath assemblages radiocyath open shelf
Upper Botoman (Moorowie Formation)	Australia Flinders Ranges	Lafuste et al. (1991)	single, 3–4 m × 2 m archaeocyaths dominant + tabulate corals, *Girvanella* + less frequent *Renalcis* and *Epiphyton* shelf margin, high energy environment
Upper Atdabanian-Lower Botoman (Ross River Dolomite)	Australia Central Australia	Kruse and West (1980), Kennard (1991)	1–3 m × 1–2.5 m archaeocyath rich + calcimicrobes reef-shoal turbulent shallow water
Botoman (Cymbric Vale Formation)	Australia New South Wales Mt. Wright	Kruse (1982)	2 m × 2 m archaeocyaths dominant
Botoman (Shackleton Limestone)	Transantarctic Mts. Holyoake area	Rees et al. (1989)	0.5–3 m × 0.3–2 m single to complex three levels of bioherm complexes reefs with archaeocyath-*Epiphyton* dominated core associated with others dominated by calcimicrobes *Renalcis*, *Epiphyton*, *Girvanella* intraplatform open shelf

3. Anatomy of the Early Cambrian reefs

As data on Early Cambrian buildups increased, questions arose as to whether the relatively diversified, simple calcimicrobial-archaeocyathan communities could be equated with the more complex Recent/Present reefs.

Studies have been carried out to compare the structures of true reefs with those of the Cambrian bioconstructions (Rowland and Gangloff, 1988; Wood et al., 1993; Kruse et al., 1995; Wood, 1999; Zhuravlev, 2001; Rowland and Shapiro, 2002; Rowland and Hicks, 2004; Debrenne, 2007). All the authors involved in the study of calcimicrobial-archaeocyathan communities have agreed, except for some minor differences, on their effective contribution to form a framebuilding that has all the prerequisites of a reef and in comparison with Recent analogues, ascribed them to tropical warm waters (Debrenne and Courjault-Radé, 1994). Nonetheless, the results of analysis of Recent bioaccumulations show that even if the tropical setting is the privileged factory of carbonate deposits, cooler settings at higher latitudes may produce non-discernible quantities of carbonates exclusively derived from skeletal particles accumulation (James, 1997). Moreover, temperatures of the water in a deep setting of the tropical zone may equate to the temperatures of shallow water in higher latitudes. Consequently, the carbonate

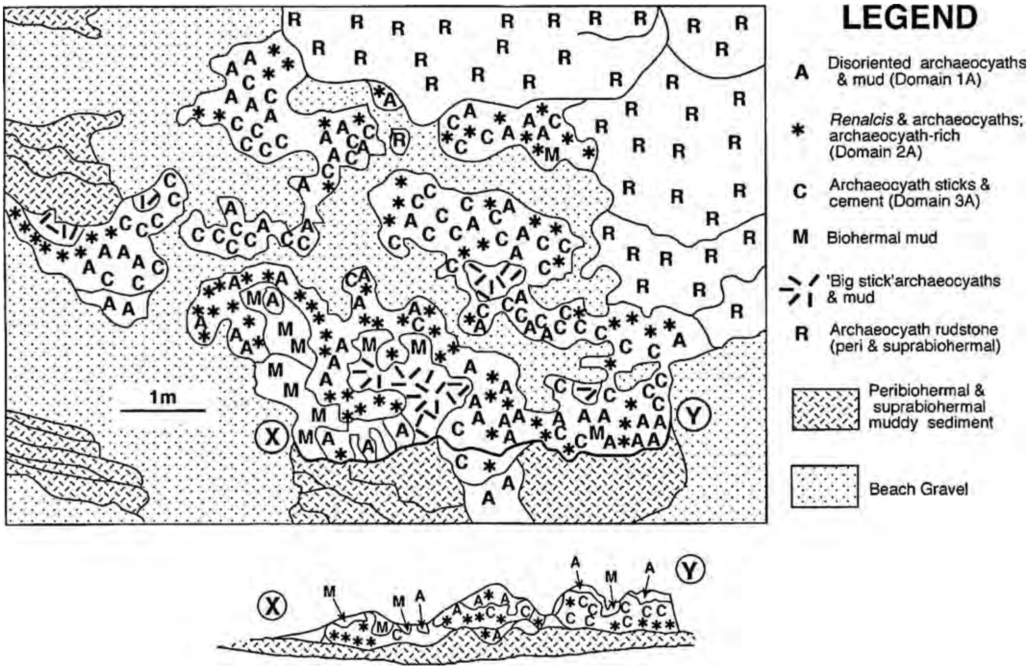

Fig. 1. Distribution (seen in map and in cross-section) of the different compositional domains of a multimound bioherm (Pestrotsvet Formation, Lena River, Siberia; modified after Kruse et al., 1995).

deposits formed in different latitudinal ranges may have a similar composition and may both fall in the field of the cool-water carbonates.

The Recent cool-water and warm-water benthic, skeletal communities are characterized by two biological assemblages (James, 1997):

- the warm-water Photozoan Assemblage dominated by *light dependent* organisms such as hermatypic corals and green algae/calcified phototrophs is commonly associated to non-skeletal allochems;
- the Heterozoan Assemblage dominated by *light independent* benthic organisms such as bryozoans, brachiopods, echinoderms, molluscs and sponges associated with coralline algae that are prolific in every marine environment where there is: (i) abundant nutrient supply, (ii) shallow cool water or (iii) deeper cooler water below the photic zone in the tropical latitudes, to prevent the development of the photozoan assemblages.

In the case of the Early Cambrian calcimicrobe-archaeocyathan communities, the problem arises concerning the palaeoecological behaviour of the dominant calcimicrobes,

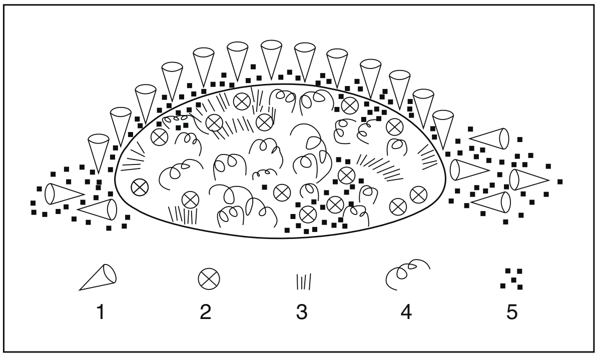

Fig. 2. Solitary or simple, modular archaeocyaths growing in loose, sandy sediment at the periphery of structured mounds (Pestrotsvet Formation, Lena River, Siberia; schematic illustration modified after Kruse et al., 1995, fig. 3 pars). Key: 1 – large stick archaeocyaths; 2 – stick and bowl archaeocyaths; 3 – cement; 4 – *Renalcis*; 5 – mud.

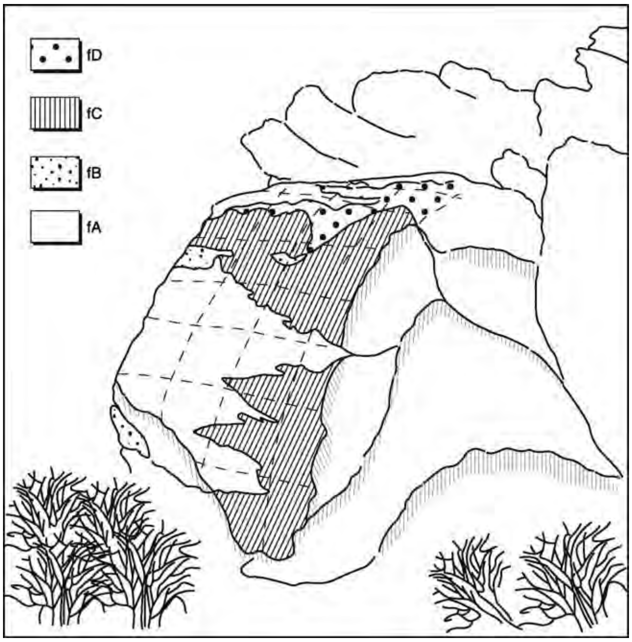

Fig. 3. An example of mapping on grid squares the different biological and abiotic domains identified on the reef surface (Matoppa Formation, la Sentinella reef, Sardinia, Italy; modified after Gandin et al., 2007). Key: fA – facies A: pink laminated limestone; fB – facies B: red marly limestone; fC – facies C: light grey massive limestone with shelter cavities; fD – facies D: light grey massive, crystalline limestone. Measure of the sides of the grid squares is 30 cm.

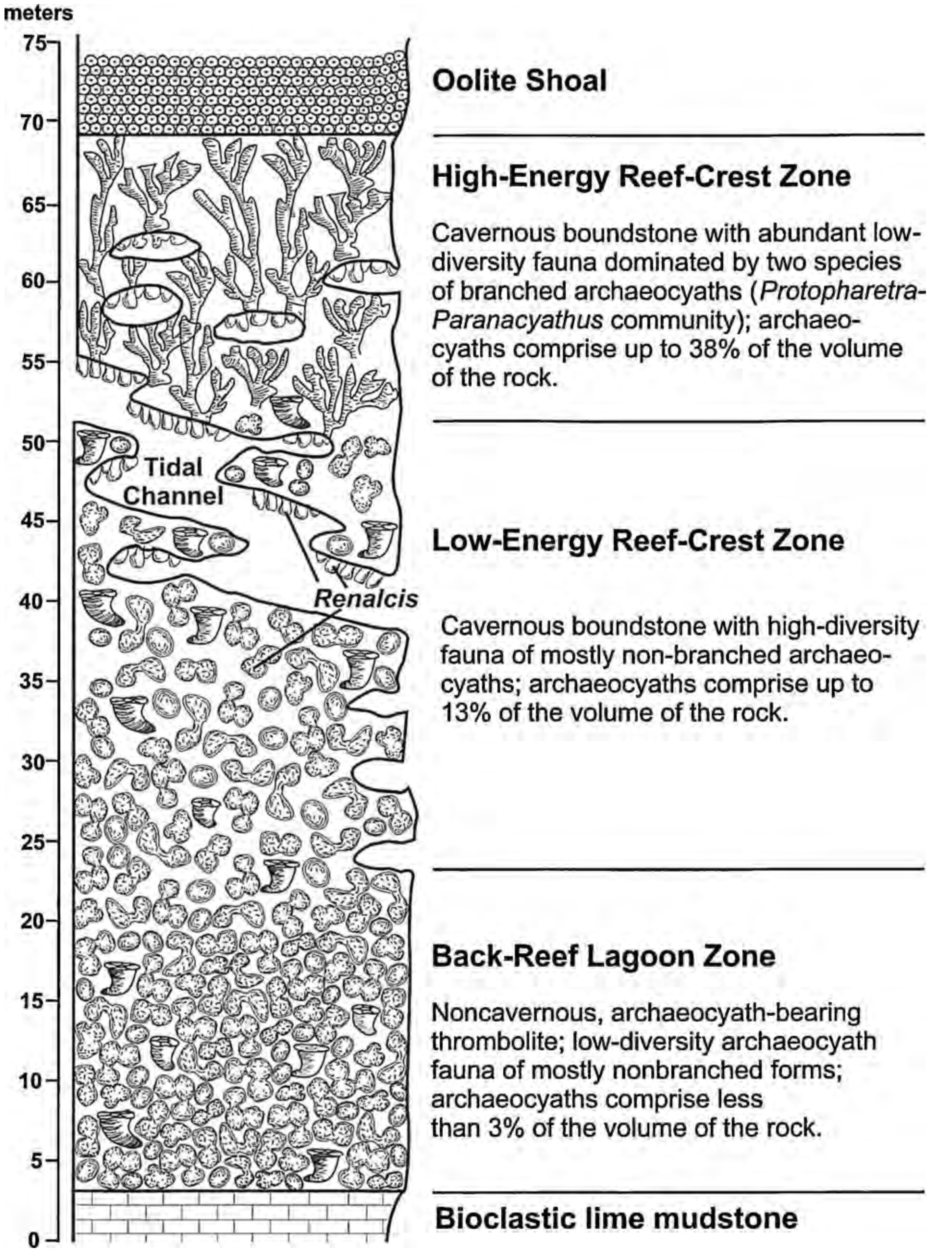

Fig. 4. Vertical ecological zonation of a reef complex (Poleta Formation, Nevada; modified after Rowland and Shapiro, 2002).

which we assume to correspond to the phototroph components of the bioconstructions (Figs. 4, 6 and 7), and of the accessory heterotroph association consisting of sponges/archaeocyaths (Figs. 5–7), and a few other taxa such as coralomorphs (Fig. 6E) that are passively involved in the framebuilding, or as chancelloriids, trilobites, hyolithids, molluscs, and brachiopods that appear to have acted commensally (Fig. 8A).

Actually, since the Early Cambrian bioherms were built by low diversity communities and all of the component biota were extinct before the appearance in Ordovician times, of climate sensible organisms such as bryozoans, green algae and many other biota, it is difficult, only on the basis of biological/ecological affinities, to recognize in the composition, distribution and architecture of buildups, a possible response to climatic/latitudinal variations.

However, the sedimentological analysis of the different reef building styles, defined by facies associations and early diagenetic features, and of their interrelationships with the surrounding sediments, can provide basic information (I) on the geomorphology of the primary depositional setting, since the relative development of the main reef-building components and their evolution within the reef communities appear to reflect the dominant physico-chemical factors (II) on the environment.

3.1. Reef building styles and composition

Considering the influence of the depositional setting, it is possible to go further in the study of the ecological properties of archaeocyaths within reefs. The previous studies have

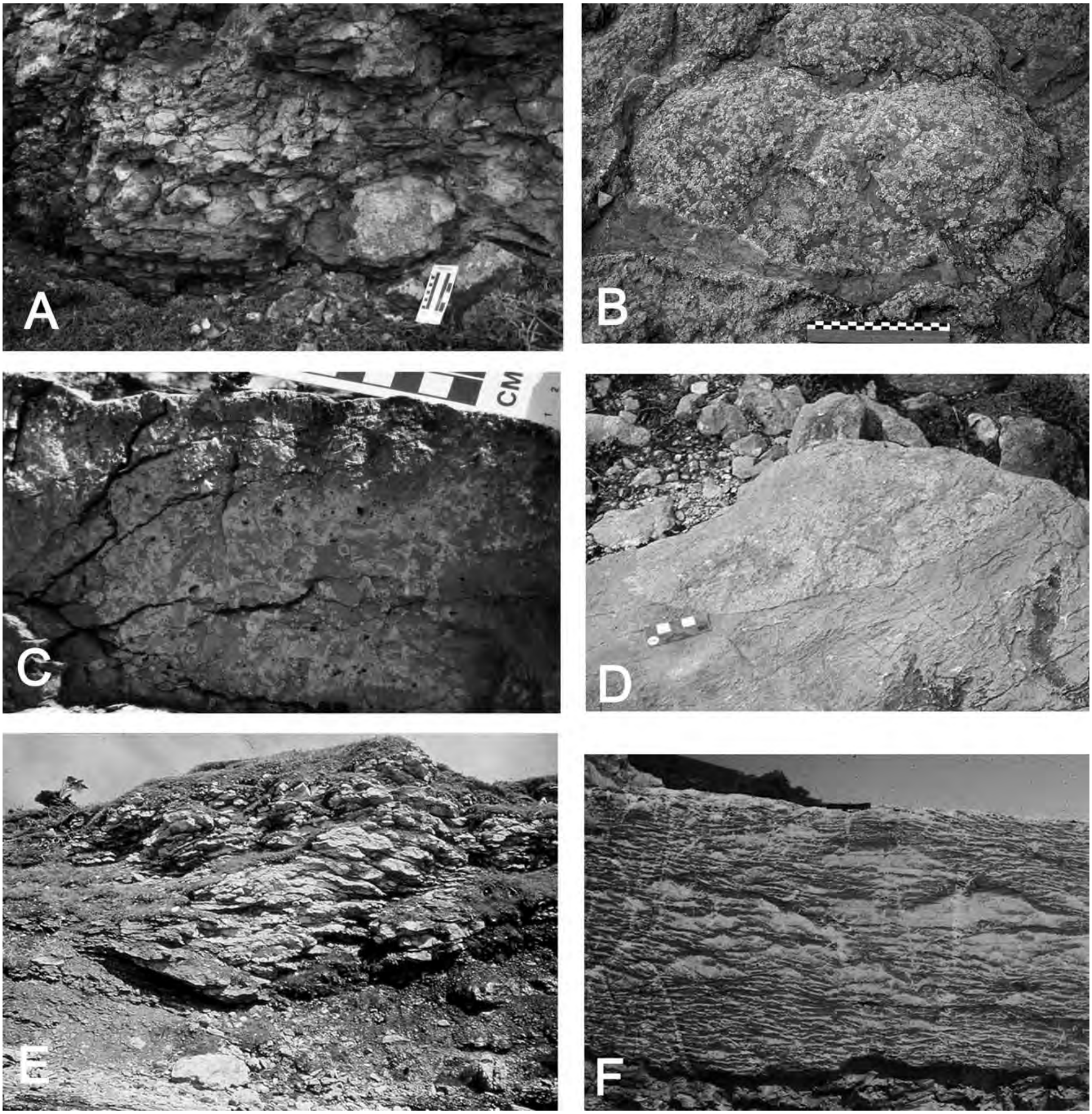

Fig. 5. (A) Small structured mound enclosed in well-bedded platform intermound mudstone (Pestrotsvet Formation, Dvortsy section, Aldan River, Siberia); (B) small pioneer kalyptrate mud mounds made of *Epiphyton* bushes, growing in tidal channels (Pestrotsvet Formation, Oi Muran section, Lena River, Siberia); (C) mud-supported fabric of an archaeocyath/calcimicrobial mound (Pestrotsvet Formation, Dvortsy section Aldan River, Siberia); (D) Framebuilt mound associated to intermound platform bioclastic facies (Aroona section Mount Scott Range, Australia); (E) Large composite buildup made of stacked lenticular bodies (*Kalyptrae*) (Forteau Formation, Fox Cove, Labrador); (F) large mud mound-bearing stromatactis-like cavities filled with white calcite (Matoppa Formation Funtana Calomba, Sardinia, Italy).

established that the calcimicrobes interpreted as photoautotroph organisms acted at the beginning of the Phanerozoic as the basic builders of the pioneer reefs and only in the Tommotian were joined in the framebuilding by archaeocyaths (Kruse et al., 1996), the first sessile heterotroph metazoan in the history of the Earth. Their association persisted throughout the Early Cambrian with only minor variations and when the archaeocyaths disappeared, the calcimicrobes resumed and persisted in their mainly solitary activity, eventually associated in the Early Ordovician with other organisms, mainly sponges.

The ecology of Archaeocyaths has been interpreted considering the environmental conditions of Recent counterparts. Archaeocyaths were thought to have harboured photosynthetic algal symbionts (Rowland and Savarese, 1990) although this interpretation is hard to support in the case of cryptic archaeocyaths (Kruse et al., 1995). Moreover, their solitary and low integration organization and inferred inter-

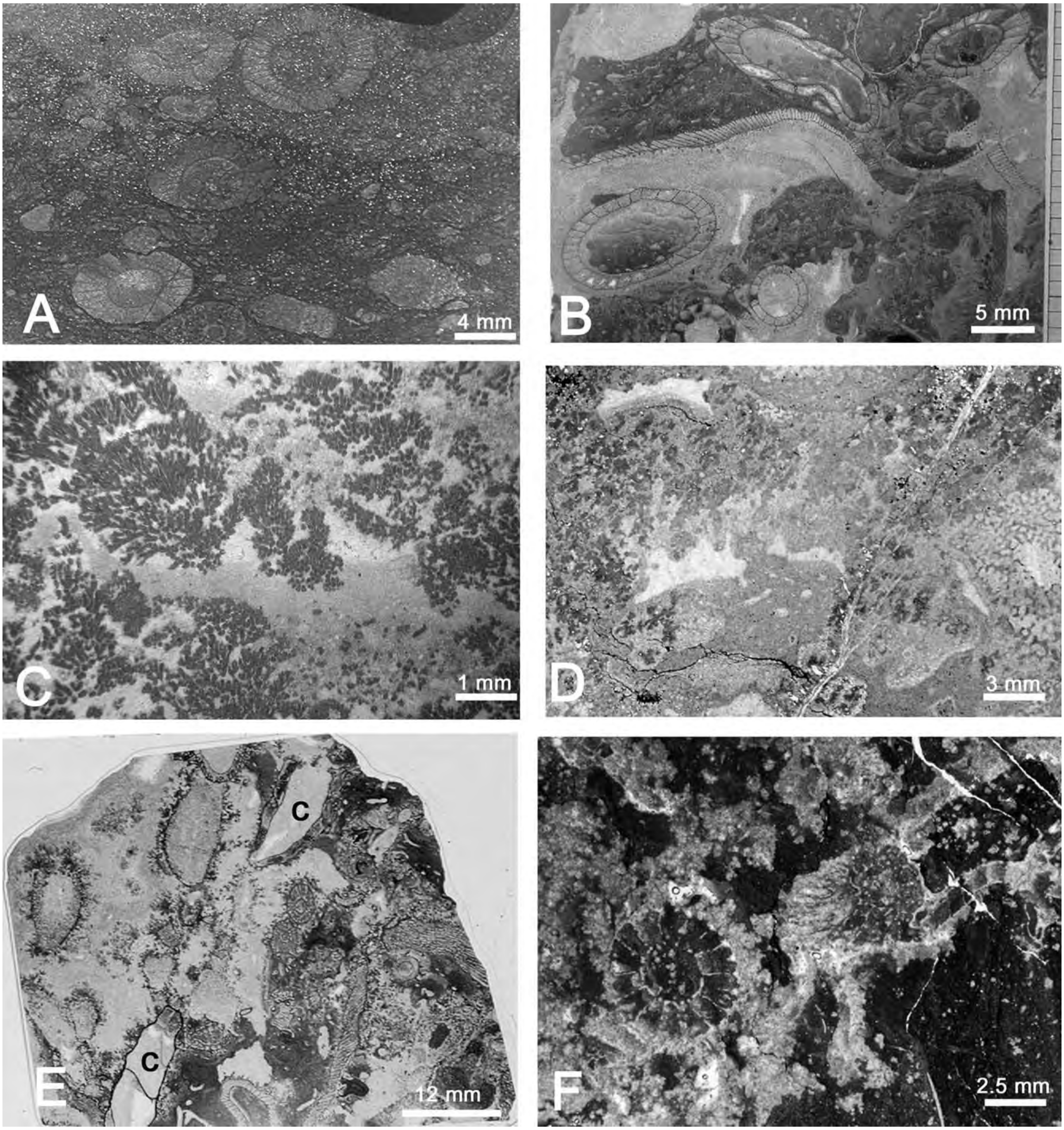

Fig. 6. (A) Assemblage of low diversity solitary archaeocyaths in silty lime mud matrix Punta Manna Formation, Punta Manna section, Sardinia, Italy); (B) large growth cavities in an archaeocyath framestone in-filled by geopetally laid lime mud and cement (Pestrotsvet Formation, Byd'yanga section, Lena River, Siberia); (C) *Epiphyton* dendrolitic framestone with geopetal infilling in the growth cavities (Pestrotsvet Formation, Achchangy-Kyyry-Taas section, Aldan River, Siberia); (D) Modular archaeocyath/dendrolitic *Renalcis* framestone with geopetal cavities (Puerto Blanco Formation, Cerro Rajón section Sonora, Mexico); (E) cement-supported framestone built by modular archaeocyaths and coralomorphs (c), Siberia; (F) solitary archaeocyath cups and associated *Epiphyton* bushes enclosed in red micritic matrix: microscopic view of Fig. 5C (Pestrotsvet Formation, Dvortsy section, Aldan River, Siberia).

nalized soft tissue suggest that they were not photo- or mixotrophs (Wood et al., 1993). Evidence from the palaeoecological analysis and sedimentary features suggest they could live indifferently on soft or hard substrates, preferring turbid waters high in nutrients and consequently mildly eutrophic or oligotrophic conditions (Wood et al., 1993; Riding and Zhuravlev, 1995; Zhuravlev, 2001), in low-latitude deeper waters or in high-latitude shallow, temperate/cool conditions, with normal-to-slightly saline waters (Gandin, 1987).

The construction style of world-wide Early Cambrian bioaccumulations can be subdivided into six categories according to the role played by the organism in response to environmental physico-chemical conditions.

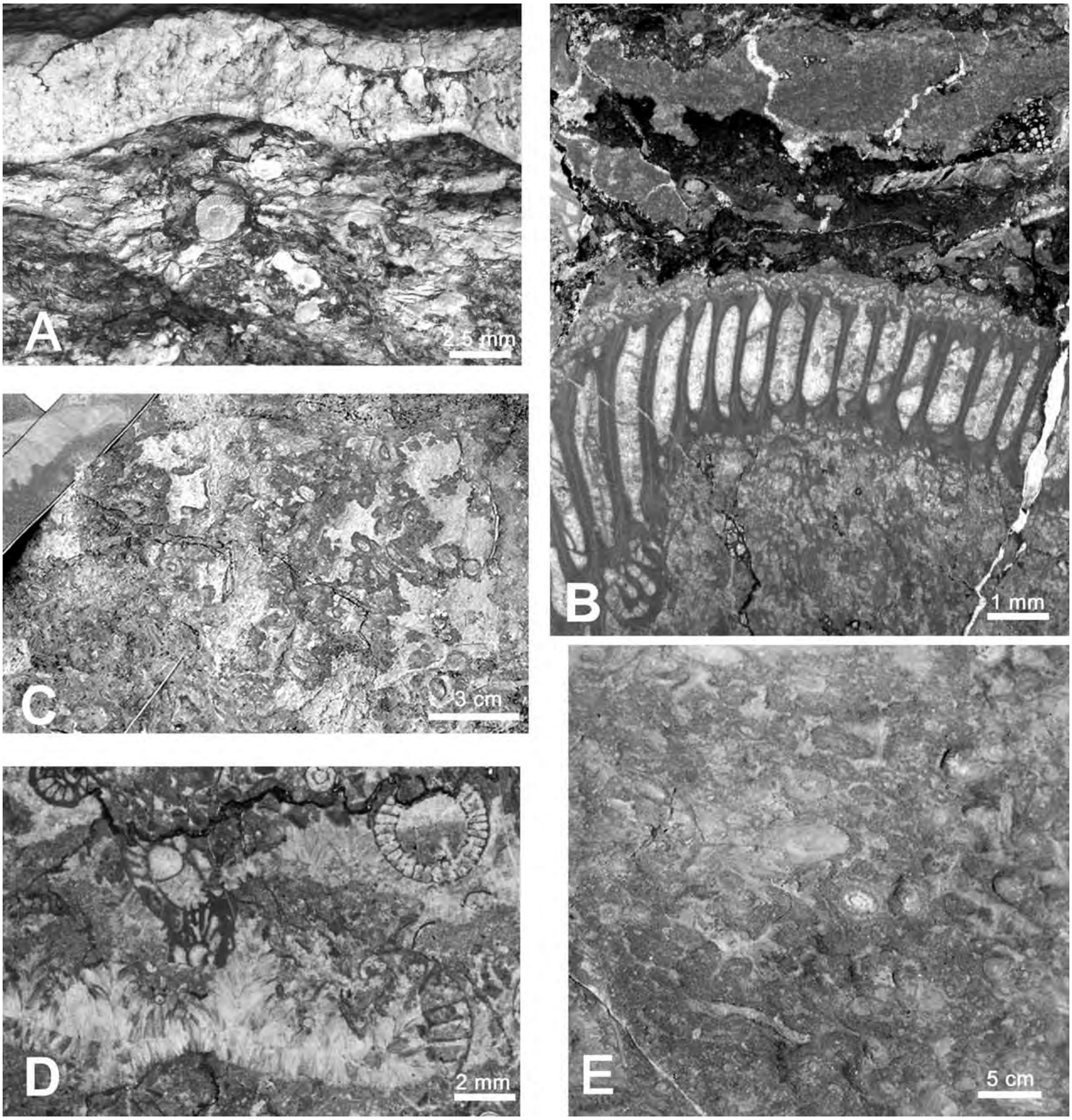

Fig. 7. (A) Bioclastic accumulation roofed by a large dish-like *Anthomorpha* cup whose upper wall has been overgrown by a calcimicrobial dendrolitic crust (Matoppa Formation, la Sentinella section, Sardinia; Italy); (B) Calcimicrobial cruststone, composed of superposed crusts of *Girvanella*, *Botomaella* or Razumovskia and cements, developed on top of a large *Anthomorpha* cup (Matoppa Formation, La Sentinella reef, Sardinia; Italy); (C) Archaeocyath/calcimicrobial framework with structural cavities filled by lime mud (Wilkawillina Limestone, Flinders Range, Australia); (D) cement-supported framestone with well-developed abiotic marine cements made of Mg calcite fibres precipitated within the structural cavities of the biological framework (Salany Gol Formation, Zavkhan Basin, western Mongolia); (E) archaeocyatha/calcimicrobial framestone with well-developed crusts of calcite cements (Asrir section, Anti Atlas Range, Morocco).

3.1.1. Type 1

Mud-supported calcimicrobial buildups represented by loaf- or pillow-shaped mounds (Figs. 2 and 5A–D) called *Kalyptrae* (Debrenne, 2007 and references therein) and dominated by abiotic syn-sedimentary components such as lime-mud and/or fine sand. Biotic components are represented by calcimicrobial dendrolitic frameworks, mostly made of *Epiphyton* (Figs. 5B, 6C and F) and less frequently of *Renalcis* and/or *Girvanella*, with or without accessory solitary regular archaeocyaths. The growth/shelter cavities are commonly occluded by micritic internal sediment sometimes associated with fibrous cements (Fig. 6C). Abundance of lime-mud/fine grained sediment reinforces the biotic framework (Figs. 6F and 7C). Muds settle in low-energy conditions and record deeper waters, below the fair-weather wave-base. Pioneer populations of solitary (Fig. 6A) or simple modular archaeocyaths could live in loose, sandy sediment at the immediate periphery of structured frame-mounds (Figs. 2 and 6A) (e.g., Pardail-

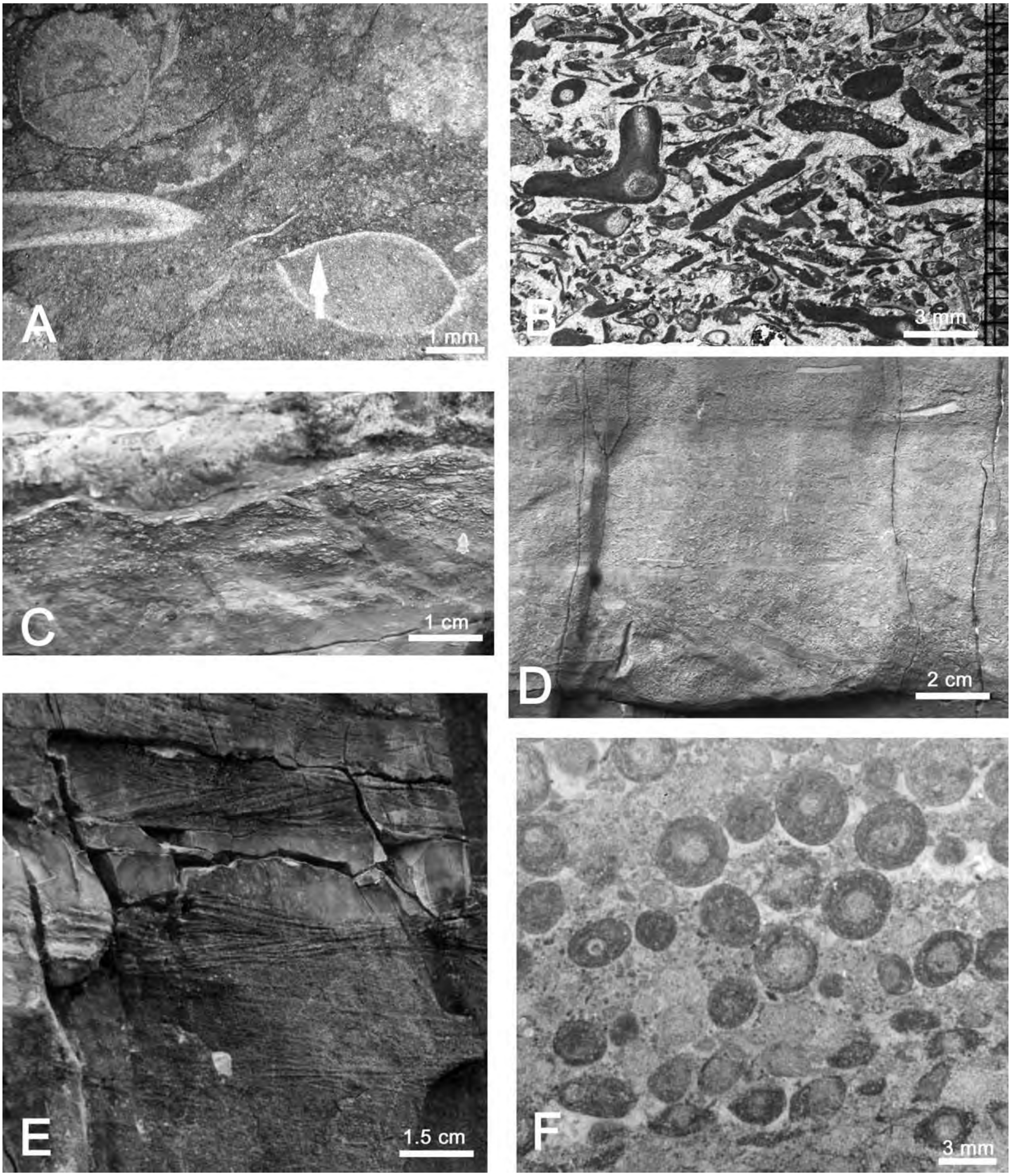

Fig. 8. (A) Assemblage of commensal biota (chancelloriids, trilobites, hyolithids, molluscs, brachiopods) in the matrix of the youngest, archaeocyath-bearing buildups (Pestrotsvet Formation, Dvortsy section, Aldan River, Siberia); (B) storm accumulation of skeletal particles preserved as unsorted grainstone (Pardailhan Formation, Montagne Noire, France); (C) rippled storm layer made of a mud-supported (packstone) bioclastic accumulation (Pestrotsvet Formation, Isit section, Lena River, Siberia); (D) unsorted accumulation of bioclastic debris in a storm layer (Pestrotsvet Formation, Dvortsy section, Aldan River, Siberia); (E) oolitic grainstone with herring-bone cross-lamination (Pestrotsvet Formation, Dvortsy section, Aldan River, Siberia); (F) microscopic view of the oolitic grainstone of E (Pestrotsvet Formation, Dvortsy section, Aldan River, Siberia).

han Formation, Montagne Noire, France: Debrenne et al., 2002a; lower Pestrotsvet Formation, Lena and Aldan Rivers, Siberia: Kruse et al., 1995; Matoppa Formation, Sardinia, Italy: Gandin, 1987; Wilkawillina Limestone, Flinders Ranges and Mount Scott Range, Australia: James and Gravestock, 1990).

3.1.2. *Type 2*

Calcimicrobial thrombolitic framestone composed mainly of dominant *Renalcis* meadows (Figs. 6D, 7B and C, lower part) associated with low diversity clusters of small regular (Fig. 6A) or modular (Fig. 6D) archaeocyaths. Most of the intraskeletal small cavities are occluded by lime mud or geopetal infilling

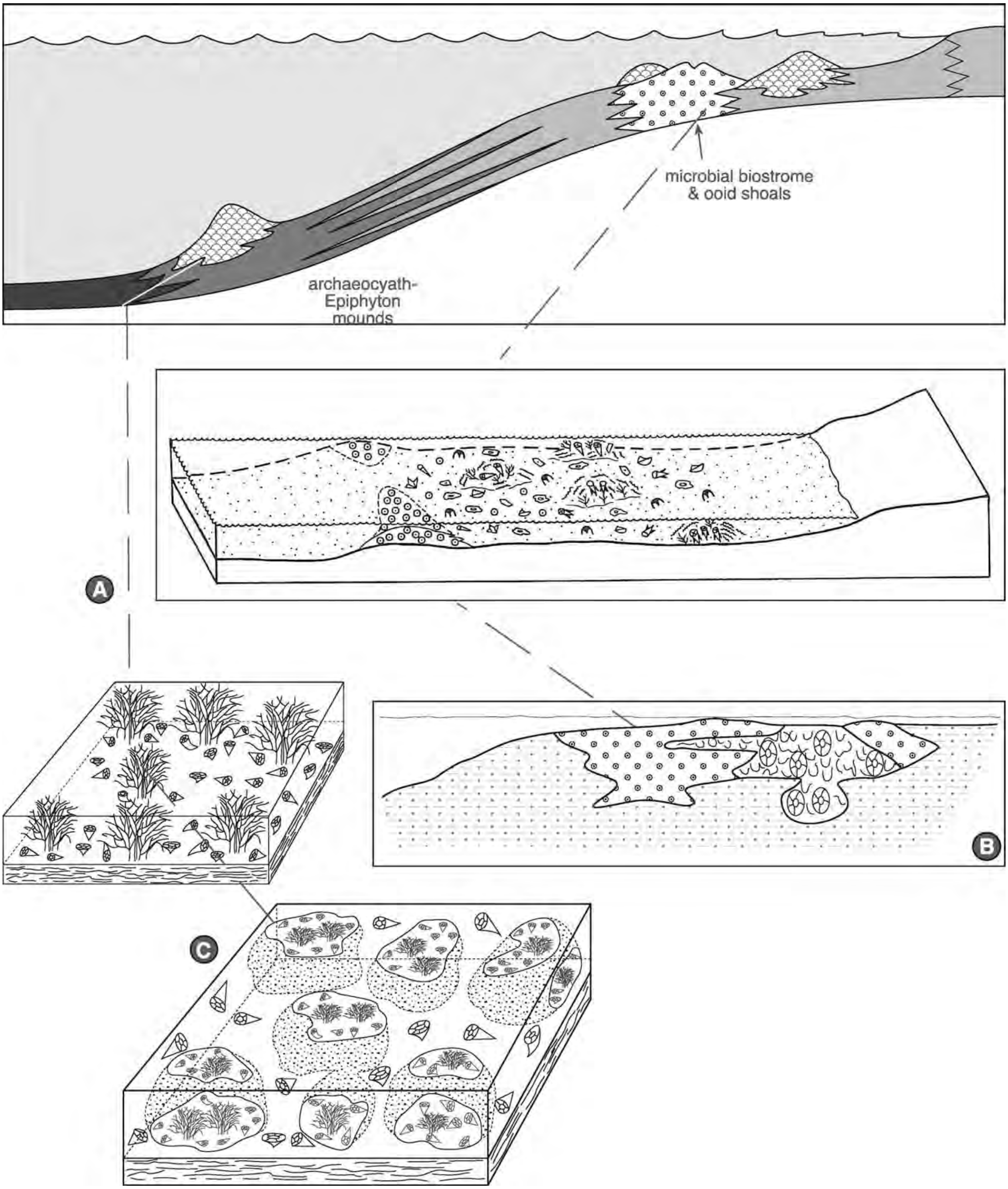

Fig. 9. Model of a homoclinal ramp. Early Cambrian buildups related to: the inner section of the ramp with a fringing ooid–shoal complex made of oolitic sands associated with biostromal thrombolitic bodies of calcimicrobial framestone and back shoal, low diversity communities of solitary archaeocyaths (A, Debrenne et al., 1991: Tianheban Formation, Yangtze, China, and B, modified after Debrenne et al., 1989b: Puerto Blanco Formation, Type 2, Sonora, Mexico); the outer, deeper part of the ramp with *Epiphyton*-dominated patch reefs and scattered solitary archaeocyaths, enclosed in well-bedded open platform lime-mudstone and wackestone (C, modified after Gandin, 1987: Matoppa Formation, Sardinia, Italy).

(Fig. 6D). The depositional setting of this assemblage, commonly associated with high-energy oolitic and skeletal/oolitic shoal complexes (Fig. 8E and F), has been interpreted to have formed as isolated patch reefs or laterally continuous biostromal bodies (Fig. 9B and C) in rather restricted back-shoal settings (e.g., Punta Manna Formation, Sardinia, Italy: Debrenne et al., 1989a; Puerto Blanco Formation, Type 2 buildups, Sonora, Mexico: Debrenne et al., 1989b; Yukon Territory, Northwestern

Canada: Read, 1980 and Rowland and Gangloff, 1988; Poleta Formation, Nevada, California: Rowland and Shapiro, 2002; Tianheban Formation, Yangtze River, China: Debrenne et al., 1991 and Gandin and Luchinina, 1993; Wilkawillina Limestone, Flinders Ranges, Australia: James and Gravestock, 1990; Shackleton Formation, Transantarctic Mountains, Antarctica: Rees et al., 1989).

3.1.3. Type 3

Calcimicrobial cruststone, composed of superposed crusts of *Girvanella*, *Botomaella* and/or *Razumovskia*, accessory *Renalcis*, *Epiphyton* and cements (Fig. 7B, upper part) with associated large, solitary regular, dish- or cup-like archaeocyaths, forms large shelter cavities (Figs. 7A and B, 10B–E) roofed by coelobionts and rim cements and infilled by geopetal muddy sediment, by calcimicrobial framestone or bioclastic packstone. Thus, the archaeocyaths and microbial crusts consortium gave rise, with the support of cement and mud infillings, to an unusual, rather resistant framework with a low synoptic relief probably consistent with medium energy levels (e.g., Matoppa Formation, La Sentinella section, Sardinia, Italy: Gandin et al., 2007; Puerto Blanco Formation, Sonora, Mexico: Debrenne et al., 1989b; Las Ermitas, Spain: Moreno-Eiris, 1994; Perejón and Moreno-Eiris, 2006).

3.1.4. Type 4

Archaeocyath cement-supported framestone composed of a complex intergrowth of modular archaeocyaths, microbes (mainly *Renalcis*) and abundant marine cements (Figs. 4, 6E, 7D and E) that concurred to build wave-resistant frameworks. These bioconstructions rarely display a discernible pattern of internal organization or evolution (Kruse et al., 1995; Zhuravlev, 2001). Incipient ecological zonation has been recognized in the Tommotian of the Siberian Platform (Kruse et al., 1995) while the only documented example of evident vertical zonation (Fig. 4) has been found in the bioconstructions growing on the Botoman shallow shelf rimming southwestern North America (Rowland and Gangloff, 1988; Rowland and Hicks, 2004). *Epiphyton*, coralomorphs (Fig. 6E), radiocyaths, and solitary archaeocyaths were common accessories of this community. The latter are found exclusively in cement-supported, dominantly microbial framestones. This kind of consortium has been interpreted as living in a photosymbiotic regime and therefore able to live in warm, nutrient-poor waters in low-latitude seas (Rowland and Shapiro, 2002). Abiotic marine cements made of well-developed fibres of Mg calcite (Figs. 6E, 7D and E) and/or aragonite prevail within the structural cavities of the biological framework. They record high energy and evaporation of the marine waters and hence depths of deposition above the fair-weather wave-base and warm climatic conditions. This framework can be equated to that of the wave-resistant modern reefs (e.g., Pestrotsvet Formation, Lena River, Siberian Platform: Kruse et al., 1995; Zavkhan Basin, Mongolia: Kruse et al., 1996; Scott Canyon Formation, Battle Mountain, Nevada, USA: Debrenne et al., 1990; Poleta Formation, Nevada, USA: Rowland and Gangloff, 1988; Puerto Blanco Formation, Type 2 buildups, Sonora, Mexico: Debrenne et al., 1989b; Wilkawillina Limestone, Flinders Ranges, Australia: James and Gravestock, 1990; Matoppa Formation, Matoppa-1 section, Sardinia, Italy: Gandin and Debrenne, 1984).

3.1.5. Type 5

Mud mounds with stromatactis-like, irregular spar-filled voids (Fig. 5F), sometimes roofed by archaeocyath walls or *Girvanella* crusts and floored with geopetal internal sediment, can be referred to low-energy, deeper water intrashelf settings by analogy with the better known Devonian/Carboniferous mud-dominated complexes assumed to have formed in deep marine environments (Krause et al., 2004 and references therein) (e.g., Wilkawillina Limestone, Flinders Ranges, Australia: James and Gravestock, 1990; Issafènes and Amagour sections, Morocco: unpublished personal observation; Matoppa Formation, Funtana Calomba section, Sardinia, Italy: Bechstädt et al., 1985; Shackleton Formation, Transantarctic Mountains: Rees et al., 1989; Mackenzie Mountains, Canada: Handfield, 1971).

3.1.6. Type 6

Granular accumulations are locally associated to the bioconstructions. They are composed of skeletal grainstones (Fig. 8A, C and D) derived from inequigranular sands formed by fragments of the skeletal components of the bioconstructions (Fig. 8B) and of the associated calcimicrobial tufts and crusts. The bioclasts were cemented by thin marine calcite rims and abundant freshwater equant calcite. This fabric suggests high-energy, wave-swept settings around biohermal frameworks that were partially or totally destroyed by storms (e.g., Scott Canyon Formation, Battle Mountain, Nevada, USA: Debrenne et al., 1990; Pardailhan Formation, Montagne Noire, France: Debrenne et al., 2002a; Wilkawillina Limestone, Flinders Ranges, Australia: James and Gravestock, 1990).

Oolitic grainstones and oncolitic rudstones, often containing a fair amount of skeletal particles mainly represented by echinoderm ossicles and cups of archaeocyaths, formed sand waves and shoals (Fig. 8C and E), which concurred to the establishment of relatively restricted backshoal environments suitable for the development of thrombolitic biostromes.

The Early Cambrian first consortium of metazoans and photoautotroph calcimicrobes, defined by the types of associated facies and by the early diagenetic features, was able to build reefs in a variety of shallow-marine settings, whose latitudinal range has been related to the tropical zone, inferred to be comprised like the present one, between 30°N and 30°S (Rowland and Shapiro, 2002). However, in the Recent bioaccumulations, different building communities and different building architectures have been observed to develop in different geographic settings: the *Phototroph assemblages* flourishing in the lower, tropical latitudes while the *Heterotroph assemblages* living at higher latitudes in the northern and southern hemispheres.

3.2. Physico-chemical factors of the reef environment

Besides the ecologic and physico-chemical factors controlling the carbonate sedimentation, the development of the bioconstructions is also a function of the morphology of the depositional setting, in turn symptomatic of specific geodynamic regimes. Thus, the architecture and structure of the bioconstructions reflect not only on temperature, energy and depth of the sea waters as described above, but also on the morphology of the shelf and its latitudinal position.

Phanerozoic shelves and carbonate platforms display variable morphologies, gradients, and consequently depths that are constrained by the geologic nature of the basin and its genesis.

The results of the analysis of the sedimentological and ecological features of most of the Early Cambrian bioaccumulations still preserved in the present-world continental blocks imply different physico-chemical depositional conditions suggestive of the specific morphologies of the carbonate platform. As a matter of fact, it appears, that as it happens today, also in the past, the reef architecture was controlled by the levels of energy and consequently by the morphology of the carbonate platforms.

The best preserved and studied, Early Cambrian carbonate successions are found in Siberia (Kruse et al., 1995), Southern Australia (James and Gravestock, 1990), and western and northeastern North America (James and Debrenne, 1980; Rowland and Gangloff, 1988; Debrenne et al., 1989b). In the other regions, tectonics affected the old Palaeozoic rocks so badly sometimes that sporadically good outcrops depend on fortuitous structural conditions and the reconstruction of the platform complex is somehow conjectural (e.g., Montagne Noire, Debrenne et al., 2002a; Sardinia, Gandin et al., 2007). Nevertheless, these successions represent wide and complex carbonate platforms where an array of different microenvironments resulted in a variety of bioconstructions, which developed simultaneously or evolved in time.

The first reefs, a consortium of calcimicrobes and metazoans dominated by archaeocyath porifera, appeared in Siberia during the Tommotian, as individual metre-scale mounds (*Kalyptra*, Fig. 5A, C and D), later stacked to form multi-mound bioherms (Fig. 5E). They spread in the adjacent continents during the Atdabanian and reached a maximum of diffusion during the Botoman, building much larger edifices sometimes showing a crude ecological zonation (Fig. 8), but still composed of the basic building *Kalyptra* blocks. At the end of the Early Cambrian, during the Toyonian, when the archaeocyaths were in full decline, the reefs reached the northeastern coasts of North America, their architecture still displaying the same basic structure of the Tommotian ones of Siberia.

The distribution in space and time of archaeocyath-calcimicrobe buildups reflects the evolution of the archaeocyaths with a peak in the Botoman Stage when wide shelves with uniform low-angle inclinations on the margins of very flat landmasses located in the tropical zone, apparently provided the optimal conditions of development. The drastic decrease of archaeocyath contribution to the buildups occurred during the Toyonian Stage when the beginning of the drifting towards the southern Pole and a consequent more abrupt morphology of the shelves should have led to adverse conditions of life. Nonetheless, new forms persisted during the Middle and even the Late Cambrian in Antarctica, the only continent set in low latitudes. During Middle Cambrian, the remaining carbonate platforms were located in high latitudes and inhabited by photoautotroph microbes. They were probably the only calcareous secreting organisms able to survive the Early/Middle Cambrian cooling crisis. This biogeographic evolution is also supported by the palaeogeographic and palaeomagnetic reconstruction of the relative position of continental blocks, epeiric basins, and perioceanic/pericontinental platforms, at the end of the Early Cambrian (Courjault-Radé et al., 1992; Rowland and Shapiro, 2002).

4. Models of carbonate platforms and related Early Cambrian bioaccumulations

Given the abiotic and biotic composition as well as the architecture of the Early Cambrian bioconstructions, it appears that carbonate sedimentation developed mostly on shelves with low-angle depositional profiles. The results of the analysis of the sedimentary architecture of the known models of carbonate platforms suggest that their different depositional profiles result mostly from the interaction of morphology/geodynamic regime, latitude/climate and biotic, and abiotic production of carbonate sediment, in turn controlled by genetic factors such as the hydraulic energy and the light requirements of the existing biota (Read, 1985; Barnaby and Read, 1990; James, 1997; Pomar, 2001). The dominance during Early Cambrian times of muddy carbonate sediments and of oligotrophic or photo-independent biota in all water depths supports the inference that most of the lime-mud rich bioaccumulations grew in deeper low-energy settings contributing to the development of homoclinal to distally steepened ramps and that only locally, cement-rich framestones developed on and built up rimmed shelves.

The combined effects of inherited topography, tectonic activity, and sea-level changes appear to control the development of the rim relief that can evolve into a barrier reef system when high-energy conditions support the growth of rigid framework-building biota (robust skeletons and encrusting organism) and abiotic calcite cements.

The Early Cambrian bioconstructions represented by small pioneer, calcimicrobial buildups (Kalyptrae) associated with biostromal and/or oolitic shoals complexes showing evidence of a general low level of energy, can be related to a fringing ooid–shoal complex (Read, 1985) in the shallower part of attached carbonate platforms, developed in intracratonic basins or oceanic shelves of very flat landmasses that can be equated with the very low-angle profile, without slope, of a homoclinal ramp. Both kalyptrate bodies and biostromal constructions consist of silty-mud to lime-mud supported dendrolitic frameworks dominated respectively by *Epiphyton* or *Renalcis* and associated with low diversity solitary archaeocyath assemblages. Pioneer Kalyptra buildups (Type 1, Figs. 9, 10 and 11) occur in the Great Basin, California (Rowland and Gangloff, 1988), Siberia (Kruse et al., 1995); Forteau Formation, Labrador (Debrenne and James, 1981), and Montagne Noire (Debrenne et al., 2002a). Larger, mud-dominated *Epiphyton*-built mounds occurring in Sardinia, Matoppa Formation (Gandin and Debrenne, 1984) and in the Flinders Ranges Shelf, Australia (James and Gravestock, 1990), can be ascribed to the deeper, outer part of the ramp (Fig. 9).

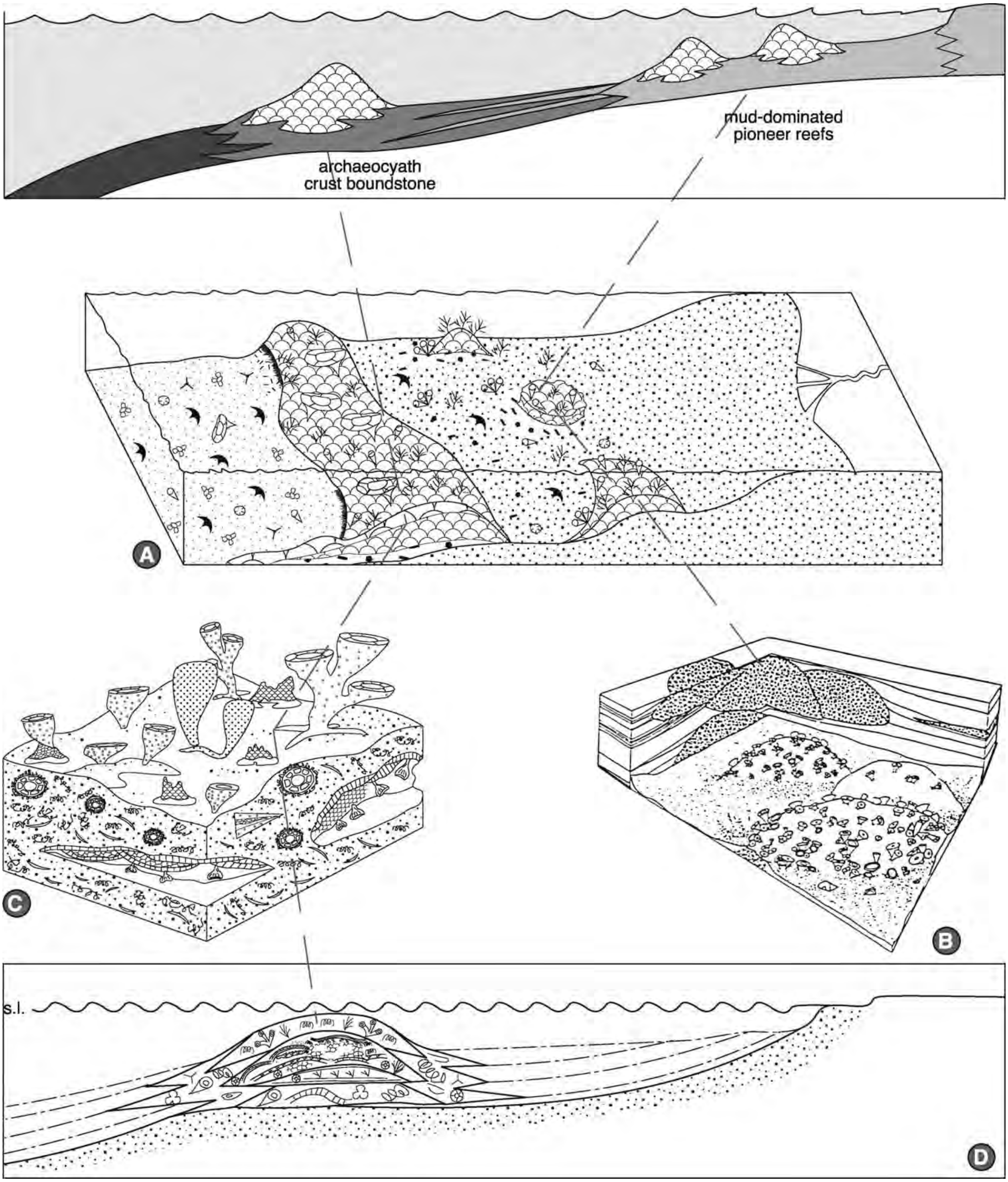

Fig. 10. Model of a distally steepened ramp. Early Cambrian buildups related to: the inner part of the ramp: small pioneer bodies (*Kalyptrae*) built up on a quartz-sand substrate, by dendrolitic *Epiphyton*/*Girvanella* frameworks in silty lime mud (A, after Debrenne et al., 2002a: Pardailhan Formation, Montagne Noire, France; B, after James and Kobluk, 1978); the steeper ramp margin: complex calcimicrobial cruststone bioherms with low synoptic relief and shelter cavities (C, modified after Perejón and Moreno-Eiris, 2006, Cerro de Las Ermitas section, and D, after Gandin et al., 2007, Matoppa Formation, la Sentinella reef, Sardinia, Italy).

Larger, oolitic-sheltered lagoonal complexes made of patch reefs or thrombolitic framestone and/or calcimicrobial biostromal bodies (Type 2, Fig. 9), which can be related to a barrier ooid–shoal complex on a ramp (Read, 1985), have been described in the Great Basin, California, and Nevada (Rowland and Gangloff, 1988; Rowland and Shapiro, 2002); Puerto Blanco Formation, Sonora, Type 2 buildups (Debrenne et al., 1989b); Punta Manna Formation, Sardinia (Debrenne et al., 1989a); Transantarctic Mountains (Rees et al., 1989); Tianheban Formation, Yangtze Platform, China (Debrenne et al., 1991) and

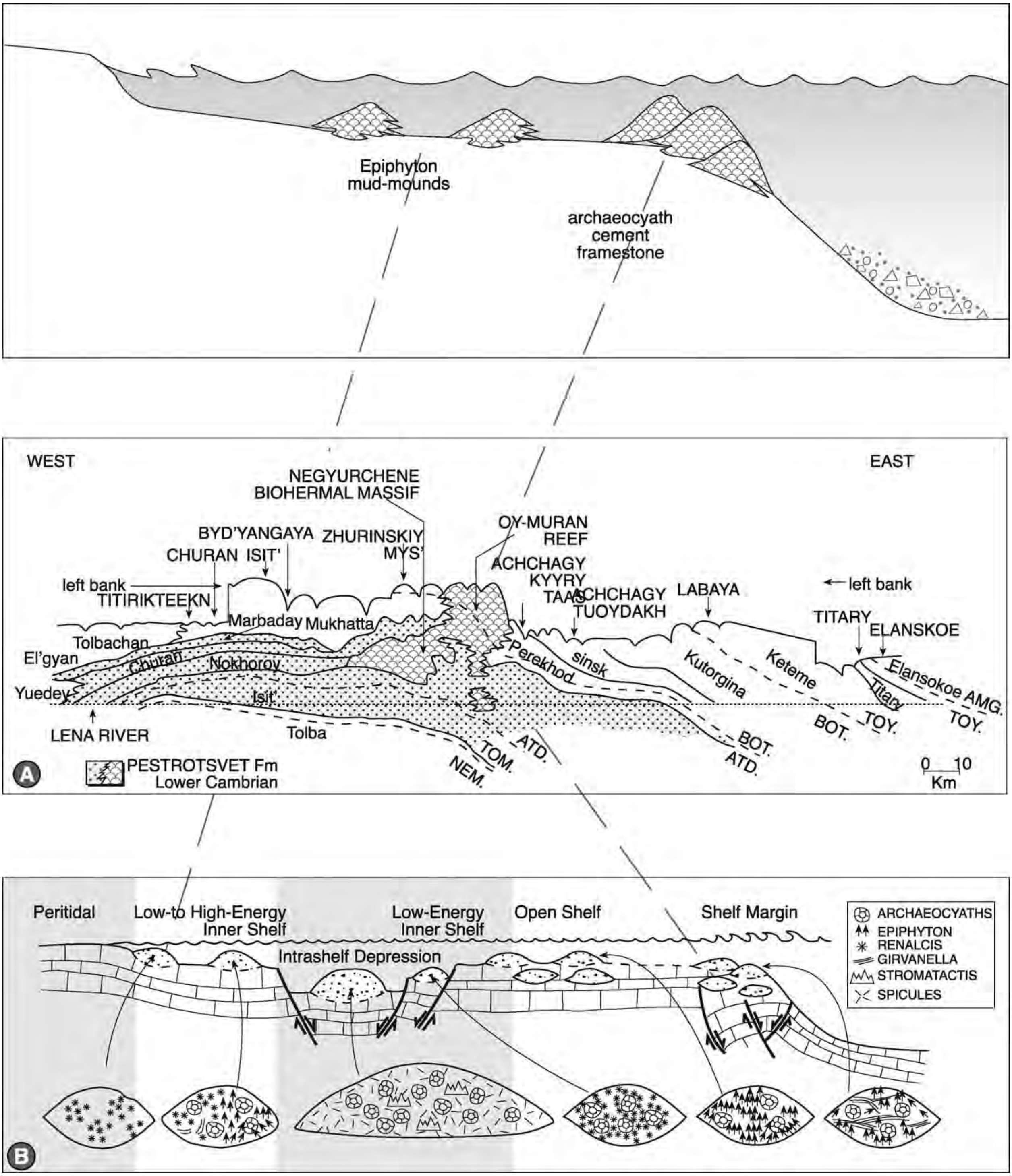

Fig. 11. Model of a distally rimmed platform. Early Cambrian buildups related to: multi-stored bioherms built on the shelf margin by calcimicrobial/*Epiphyton* bioherms and archaeocyath framestone supported by abundant marine fibrous cements: A, the "Great Siberian Barrier Complex" (modified after Kruse et al., 1996 and Rowland and Gangloff, 1988); B, the Flinders Ranges Shelf, Australia (modified after Rowland and Shapiro, 2002 and James and Gravestock, 1990).

in the Wirrealpa Limestone, Flinders Ranges Shelf, Australia (Kruse, 1991). Calcimicrobial cruststone bioherms (Type 3, Fig. 10) composed of superposed calcimicrobial crusts and large saucer-like solitary archaeocyaths have been recognized in La Sentinella reef, Matoppa Formation, Sardinia (Gandin et al., 2007), in the Puerto Blanco Formation, Type 2 buildups, Mexico (Debrenne et al., 1989b) and illustrated in Las Ermitas bioconstructions of Spain (Perejón and Moreno-Eiris, 2006). They show a low but conspicuous synoptic relief suggesting mild energy conditions of the depositional setting that can be related to the gentle marginal break of a distally steepened ramp.

Composite lenticular bodies, stacked to form multi-storied mound bioherms (Type 4, Fig. 11), concurred to form a

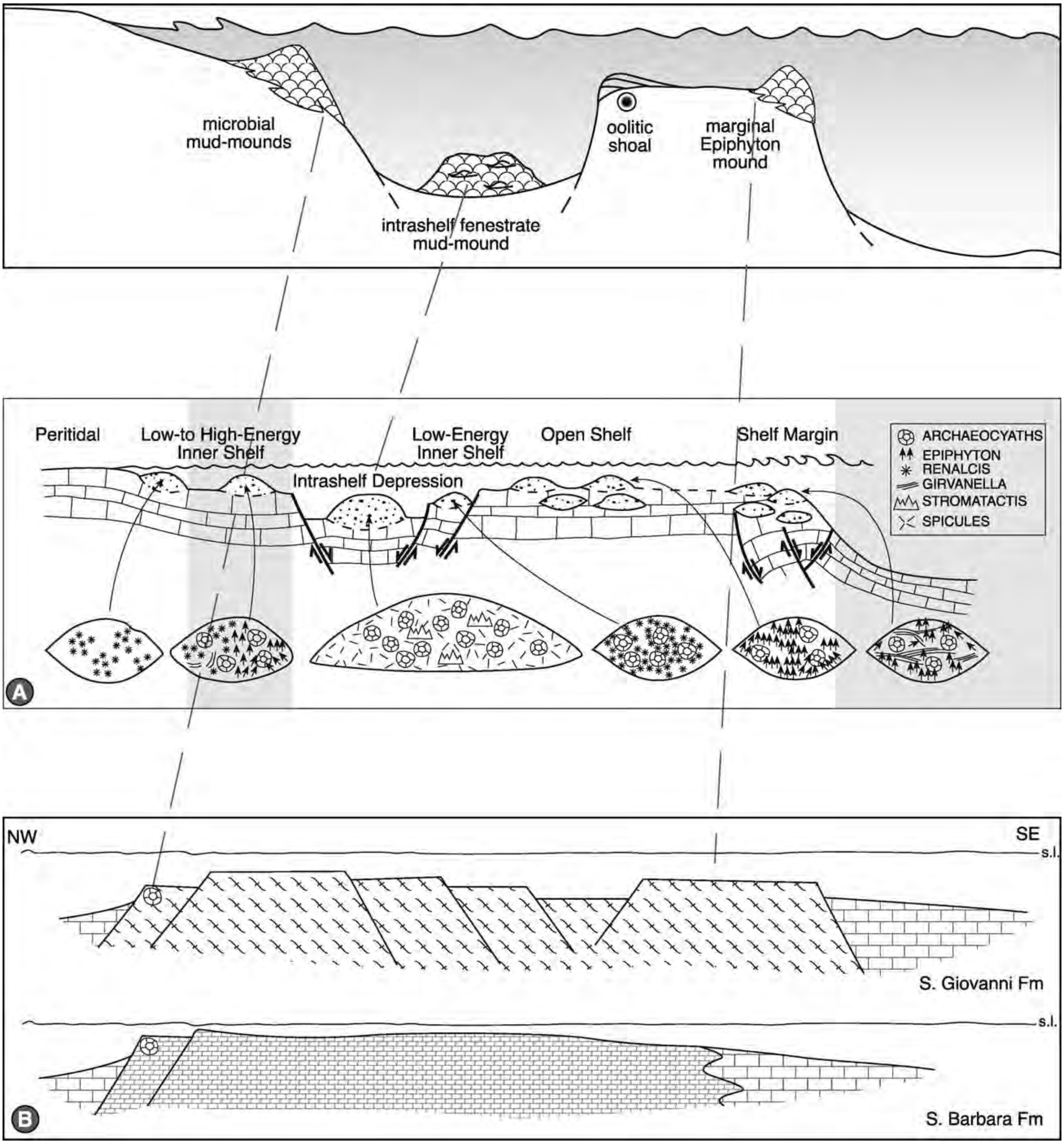

Fig. 12. Model of an isolated platform/intrashelf basin complex. Early Cambrian buildups related to: A, the intrashelf basin: stromatactis-bearing mud mounds (modified after Rowland and Shapiro, 2002 and James and Gravestock, 1990, Flinders Ranges Shelf, Australia); B, the Bahamian-type isolated platforms rimmed by calcimicrobial/*Epiphyton* bioherms on the seaward margin and by oolitic shoal on the landward side (modified after Gandin, 1987, Gonnesa Group, Sardinia, Italy).

barrier–reef complex, the first on the history of the Earth, called the "Great Siberian Barrier Complex" (Rowland and Gangloff, 1988; Kruse et al., 1995). It grew in warm climate latitudes, on the marginal part of a platform with steeper slope and prominent margins and higher energy gradients that over time developed into a distally rimmed platform. Microbially bound bioherms and associated modular/branched archaeocyaths provided a rigid framework supported by abundant marine fibrous cements that attests the high energy and well-oxygenated depositional conditions of the Tommotian/Atdabanian Siberian Platform. The patchy distribution of the bioconstruction did not restrict the free circulation of seawater so that open carbonate platforms developed in the wide interior shelf where lower energy conditions prevail, well-bedded mudstone/wackestone were occasionally affected by storm-induced, mass sediment/bioclastic reworking. Similar constructions are extensively represented in the Flinders Ranges Shelf, Australia (James and Gravestock, 1990); the Zavkhan Basin, Mongolia (Wood et al., 1993; Kruse et al., 1996); Forteau Formation, Labrador (Debrenne and James, 1981) where rubbles of the broken parts of the modular/branched builders were accumulated in unsorted breccias at the base of the slope.

The *Epiphyton*-dominated, calcimicrobial mounds, and oolitic accumulations described in the Toyonian of Sardinia (Gonnesa Formation) have been interpreted (Debrenne and Gandin, 1985; Cocozza and Gandin, 1990) as developed on the rifted passive margins of continental blocks resulting from a tensional tectonic regime that fostered the formation of Bahamian-type system of isolated platforms (Type 1, Fig. 12). They are characterized by a slope gradient higher than that of the homoclinal ramps and by high-energy margins where skeletal reefs grow on the seaward side of the platform, supported by a steady supply of nutrients provided by upwelling currents, while on the opposite side only oolitic shoals develop. Similar conditions are also reported from the Flinders Ranges Shelf, Australia (James and Gravestock, 1990) and probably from Buelna Formation in Mexico (Debrenne et al., 1989b).

Large mud mounds with flat-floored, stromatactis-like cavities occluded by several generations of marine and/or non-marine calcite cements (Type 5, Fig. 12) have been reported from the Flinders Ranges Shelf, Australia (James and Gravestock, 1990), from Morocco (Issafènes and Amagour red limestone, personal observations), and from Sardinia (Matoppa Formation, Funtana Calomba section, Bechstädt et al., 1985). They can be related to deeper conditions in intrashelf basins where the low-energy of the waters preserves and promotes the deposition of lime mud, the major component of the mounds.

Granular accumulations of skeletal sands/grainstone (Type 6), apparently unrelated to bioconstructions but evidently derived from rarely preserved calcimicrobial/archaeocyath mounds, have been observed in (i) Nevada olistoliths associated with Botoman-Toyonian reefs (Battle Mountains, Nevada, Debrenne et al., 1990); (ii) in the Toyonian deposits of Siberia (Elanka Section, Lena River, personal observations); and (iii) in the Montagne Noire, Pardailhan Formation, Debrenne et al., 2002a). Their occurrence suggests depositional conditions that can be related to high-energy ramps and/or open shelves swept by strong wave and current flows, and possibly to less warm/cooler marine waters.

5. Concluding remarks

The oldest bioconstructions on the Earth in which metazoans with a rigid mineralised skeleton are involved were built in Early Cambrian by photoautotroph organisms, mainly cyanobacteria, able to precipitate in the outer cellular wall a mineralised coating made of micritic calcite, and by archaeocyaths, suspension feeder, sessile heterozoan organisms representing an extinct class of Porifera.

The depositional features and the different styles of reef building appear to reflect the ecologic conditions of the microbial-archaeocyath communities and the highly diversified physico-chemical factors controlling the carbonate sedimentation. A direct correlation between the physico-chemical factors of deposition and the structural architecture of the buildups results from the analysis of most of the Early Cambrian bioaccumulations exposed in the present continental blocks.

Thus, the architecture and structure of the bioaccumulations can be related to the combined effects of energy and depth of the sea waters controlled by the morphology of the shelf, and of the temperature and nutrient availability controlled by their latitudinal collocation.

Consequently, different biohermal communities and architectures of the buildups reflect the physiography of the primary depositional setting. They all developed at photic and shallow sub-photic depths on low-angle ramps or distally rimmed platforms of pericontinental/epeiric basins:

- mud supported simple to compound mounds, locally with stromatactis-like cavities, developed in subtidal low-energy ramp/intraplatform settings;
- dendrolitic bioherms and crustose buildups with large shelter cavities and low synoptic relief grew on medium-energy ramp margins;
- cement-supported skeletal reefs with wave-resistant frameworks often associated to oolitic shoals were located on high-energy platform rims;
- bioclastic sands were accumulated by storm currents on the shelves.

Traditionally, all archaeocyath-bearing bioaccumulations have been generically considered of reefal origins and for comparison with recent analogues, ascribed to tropical warm waters. However, the architecture of the buildups varies with their spatial distribution, suggesting that their development was affected not only by the physiography of the depositional setting but also by local climatic conditions constrained by the latitudinal position of the continental blocks.

The cement/skeletal constructions corresponding to wave-resistant reefs developed in arid zones in tropical latitudes, forming barrier reef complexes. Dendrolitic and crustose buildups with large shelter cavities and low synoptic relief grew in medium energy conditions on ramp margins probably in intermediate warm/temperate latitudes. The mud-supported buildups, the stromatactis-like mounds typical of subtidal, low-energy cooler settings, and the bioclastic accumulations related to storm events were mainly established in higher latitudes. Thus, most of the Early Cambrian bioaccumulations can be considered as true bioconstructions, but only some of them can be related to wave-resistant reefs.

Moreover, reconstruction of the Early Cambrian palaeogeography based on palaeomagnetic data suggests a southern distribution of the continental masses and basins that during the Botoman, promoted the maximum diffusion of the archaeocyath communities and led to the development of a variety of reefs.

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Research paper

Remarks on rugose coral taxonomy

Jerzy Fedorowski *

Institute of Geology, Adam Mickiewicz University, Maków Polnych 16, Pl 61-606 Poznań, Poland

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Abstract

Precise taxonomy is possible only when specimens are thoroughly investigated and checked against well known types. This simple procedure is not always followed and as a result, credible data are often lacking.

Accuracy: To match his interpretation of calice morphology, Schindewolf (1942, pl. 33, fig. 2a–d, text-fig. 89a–d) inaccurately oriented transverse sections of *Pentamplexus simulator* Schindewolf, 1940. His errors were in part corrected by Weyer and Ilina (1979), but they also misidentified the counter protoseptum. Re-orientation of the original and two new thin sections allows that genus to be transferred to the family Polycoeliidae de Fromentel, 1860.

Manipulation: Schindewolf's (1942) manipulation of the data on *Pentaphyllum* De Koninck, 1872 and *Cryptophyllum* Carruthers, 1919 resulted in an incorrect diagnosis, which was followed by many students who introduced 49 species (Ilina, 1984). Despite its name and Schindewolf's (1942) description, the poorly preserved type of *Pentaphyllum* possesses six, instead of five, dominant septa in its calice.

Lack of attention to detail: Biform morphology in the tabularium is not always recognized and is commonly incorrectly described, despite its importance as a factor in water distribution within the gastro-vascular cavity and its diagnostic value for taxonomy. Failure to recognize that feature can lead to incorrect classification up to the family level.

Keywords: Taxonomy; Rugosa; Protosepta; Biform tabularium

1. Introduction

The value of precise taxonomy, which is needed for use in biostratigraphy, palaeogeography, palaeoecology, and phylogeny, is very seldom questioned. Taxonomic precision, however, is commonly lacking. Many old, non-revised names remain in use, even though knowledge of the supposed morphology of their types is not supported by the facts. Also, the complete early ontogeny of solitary forms and the blastogeny of colonial corals are seldom studied in spite of their fundamental value. The importance of blastogeny in the taxonomy of European *Siphonodendron* Fleming, 1828 and its North American counterpart may be taken as an example (Fedorowski and Bamber, 2007). The microstructure of septa is commonly not considered and diagenetic alterations often are either not recognized or are confused with the original microstructure. Finally, one can seldom find a recent paper based on a large collection of specimens that were studied in all the aspects listed plus intraspecific variability; instead, many papers are based on random sections of one or a few specimens. The present miserable status of rugose coral taxonomy is exaggerated by subjectivity in the evaluation of characters superimposed on all the other faults and omissions. This in turn has resulted in a disrespectful attitude of biostratigraphers to corals as index fossils, whereas there are examples of documenting regional (Sando and Bamber, 1985) and inter-regional (Fedorowski et al., 2007) correlations based on rugose corals that are at least comparable in precision to those based on fusulinids or conodonts.

Examples discussed in this paper show the necessity of comprehensive investigation of all aspects of corals, beginning with revision of the types, most of which were introduced without adequate documentation. This is understandable for very early papers, but unfortunately, there are numerous taxa introduced in the 20th Century for which the morphology was misinterpreted for various reasons. Two such misinterpretations by Schindewolf (1942) are investigated here because of his influence on rugose coral taxonomy.

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* Corresponding author.
E-mail address: jerzy@amu.edu.pl.

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2. *Pentamplexus simulator* Schindewolf, 1940 and recognition of its protosepta

Following Hudson (1936) and Fedorowski (1997), only the axial (if developed), the cardinal, and the counter septa are here considered as protosepta. In contrast to most Scleractinia, the proper orientation of transverse sections of coral skeletons is crucial for the identification of many Rugosa. The difference between *Plerophyllum* Hinde, 1890 and *Sochkineophyllum* Grabau, 1928 exemplifies this observation (Fig. 2I and J). This important problem of orientation may be difficult to deal with when the morphology of the immature skeleton differs considerably from that of the mature one, as in the holotype of *P. simulator* Schindewolf, 1940, but a solution must be found. Also, in various growth stages of particular rugose corals, the length and/or the arrangement of septa may be pathologically or diagenetically altered. Both of those obstacles are also met in the study of the holotype of *P. simulator*. Recognition of the protosepta requires special care in such instances.

The holotype of *P. simulator* can serve as an example of a mixture of true characters, secondary pathological changes, and diagenetic alterations. Such a combination of features led to the detailed investigation of this mysterious, single representative of the genus and species by Weyer and Ilina (1979), Fedorowski (2009a), and in this paper. In this specimen, the septal insertion, the size and septal content of the quadrants, and the position of the counter protoseptum changed during corallite growth from strongly irregular and asymmetrical in the earliest growth stage preserved to more regular in the mature growth stage and at the calice floor.

Selected drawings of Schindewolf (1942), Weyer and Ilina (1979) and Fedorowski (2009a) are re-illustrated here in Fig. 1A$_{301–5}$, B$_{1–3}$ and C$_{1–8}$ respectively for comparison. Those of Schindewolf (1942) and Weyer and Ilina (1979) are rotated 180° in order to orientate the true or suspected cardinal protoseptum downward, but the original orientations of those pictures are not changed otherwise. Thus, the picture of Schindewolf (1942, text-fig. 89d = Fig. 1A$_5$ in this paper) is in a mirror image position to his picture illustrated in the text-figure 89c (= Fig. 1A$_4$ in this paper). The numbers accompanying the capital letters A–C in the illustrations correspond to the same illustrations presented by individual authors. Thus, Fig. 1A$_3$ is absent from the series of pictures in Fig. 1, copied from Schindewolf (1942, text-fig. 89), who did not illustrate that section. The picture of Schindewolf (1942, text-fig. 89d = Fig. 1A$_5$), illustrating the calice floor, does not find its counterpart in the series from Fedorowski (2009a). It is replaced here by the photograph (Fig. 1C$_6$) from the latter paper. The true or suspected protosepta, as well as the alars and counter laterals in some figures, are marked either by dots or by triangles.

The following remarks begin with my own observations (Fedorowski, 2009a). In the earliest growth stage preserved, the irregularity and asymmetry in this specimen are demonstrated by a considerable reduction in volume of the left cardinal quadrant and in the asymmetrical position of the counter protoseptum, which is located not opposite to the cardinal protoseptum, but left of the symmetry plane (Fig. 1C$_1$). Such a position for that protoseptum was not recognized by earlier authors (Fig. 1A$_1$ and B$_1$). Accelerated insertion and growth of major septa in both left quadrants during the neanic growth stage (Fig. 1A$_2$, B$_{2,3}$ and C$_{2,3}$) forced the counter protoseptum to the right until it reached a position that was only slightly asymmetrical in the mature growth stage (Fig. 1A$_4$ and C$_4$) and in the calice (Fig. 1A$_5$ and C$_6$).

Schindewolf's (1942, fig. 89, pl. 33, fig. 2a–d and Fig. 1A$_{1,2,4,5}$ in this paper) original orientation of the calice floor and thin sections illustrates what "should be seen" in a pentaphylloid morphology, but not what occurs in the holotype of *P. simulator*. He did not recognize two major septa occurring in one of the quadrants, and identified that apparently single major septum as the counter protoseptum (Schindewolf, 1942, fig. 89a, upper and Fig. 1A$_1$, lower left in this paper). The next transverse section was again oriented by Schindewolf (1942, fig. 89b and Fig. 1A$_2$ in this paper) in accordance with that imaginative pattern, but not in a manner consistent with either the preceding one (Fig. 1A$_1$, B$_1$ and C$_1$) or the calice (Fig. 1A$_5$ and C$_6$). The septum that he designated as the counter protoseptum in his second figure is in fact the last inserted major septum of the right counter quadrant (compare Fig. 1B$_2$ and C$_2$). It seems reasonable to suggest that only such an orientation would allow his proposed agreement between the morphology in that early growth stage and the morphology of the calice, if one does not recognize and accept both the asymmetry in the arrangement of the major septa, suggested here, and the great length of the major septum that precedes the last short septum in the right counter quadrant. The question of the elongation of the counter protoseptum seen in the transverse section cut beneath the calice floor (Fig. 1A$_4$ and C$_4$) is discussed below.

Weyer and Ilina (1979) corrected Schindewolf's (1942) orientation of the thin sections relative to the calice and recognized the true cardinal protoseptum and alar septa (Fig. 1B$_{1,2}$). However, they followed him in considering the specimen to be plerophylloid. They arrived at that conclusion by identifying the long counter protoseptum in the calice as a counter-lateral septum. Following Schindewolf (1942, fig. 89c), they identified the inner margin of that septum in the transverse section as part of a tabula (Weyer and Ilina, 1979, figs. 5:5 and 5:4 respectively). Neither of those identifications is accepted here.

The counter protoseptum and counter-lateral septa indicated here in the illustrations of the immature growth stage differ from those proposed by both Schindewolf (1942) and Weyer and Ilina (1979). The shortened septum, marked by Weyer and Ilina (1979, figs. 5:1, 5:2 and Fig. 1B$_{1,2}$ in this paper) as the counter protoseptum is in fact the right counter-lateral septum, whereas the long, thick septum to the left of it, i.e., the left counter-lateral septum of those authors, is the asymmetrically located counter protoseptum (Fig. 1C$_{1,2}$). It constitutes a part of the axial protoseptum, best seen in the new thin section at a slightly more advanced growth stage (Fig. 1C$_3$). "Middle lines", interrupted by diagenesis in the thin sections of the early growth stage (Fig. 1A$_{1,2}$, B$_{1,2}$ and C$_{1,2}$) became united in that new thin section (Fig. 1C$_{3,7}$). Unfortunately, Weyer and Ilina (1979, fig. 5:3 and Fig. 1B$_3$), who based their drawing on a peel, were perhaps not able to recognize that detail, camouflaged by diagenetic alterations. Recognition

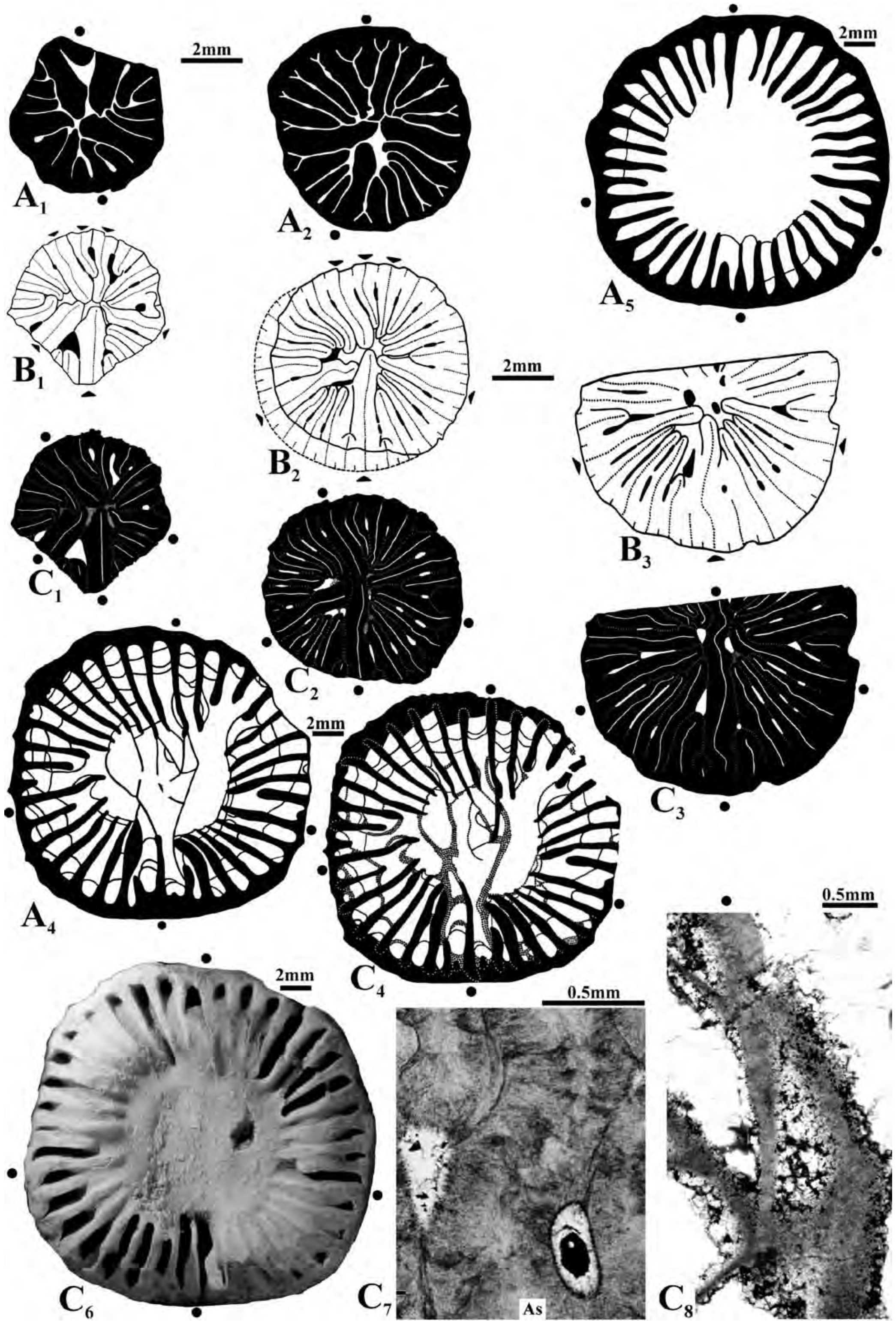

Fig. 1. (A–C) Comparison of the identification by Schindewolf (1942), Weyer and Ilina (1979), and Fedorowski (2009a) of the cardinal and counter protosepta and alar septa in *P. simulator* Schindewolf, 1940. Holotype No. 9182, Bitauni, Timor Island, Lower Permian. $A_{1,2,4,5}$ from Schindewolf (1942). B_{1-3} from Weyer and Ilina (1979). $C_{1-4,6,7}$ from Fedorowski (2009a). Corresponding drawings bear the equivalent numbers in sets A–C. Absence of a given figure in a series (A_3, C_5) means that the illustration was not present in the original paper. All figures are oriented with the cardinal protoseptum downward. Thus, those by Schindewolf (1942) and Weyer and Ilina (1979) were rotated 180°. The protosepta and alar septa are marked either by dots or by triangles. The latter marks also the counter laterals in the pictures copied from Weyer and Ilina (1979). ($A_{1,2}$, $B_{1,2}$, $C_{1,2}$) Neanic growth stage; (B_3, C_3) late neanic growth stage not illustrated by Schindewolf (1942), B_3 based on peel; C_3 based on new thin section; (A_4, C_4) thin section approximately 7.5 mm beneath calice floor; (A_5) camera lucida drawing, perhaps from calice floor; (C_6) calice floor; (C_7) axial protoseptum (As), corresponding to axial part of C_3; (C_8) relationship of elongated counter protoseptum to tabulae (compare Fig. 1C_4).

of the axial protoseptum is important for the identification of the family in which *Pentamplexus* should be included. That protoseptum does not occur in the Pentaphyllidae in the sense of Schindewolf (1942), but is well developed in the Polycoeliidae de Fromentel, 1860, to which that genus belongs.

Recognition of the permanent elongation of the counter protoseptum, as proposed in this paper, was a matter of deciphering the camouflaging role of diagenesis. Neither Schindewolf (1942, text-fig. 89c and Fig. 1A$_4$) nor Weyer and Ilina (1979) recognized that factor and interpreted the elongated inner fragment of the counter protoseptum as a section of the tabula. The elongation of the counter protoseptum is proven by both the continuity of its inner and peripheral sectors, seen at large magnification, and the differences between the effects of recrystallization on the septa and tabulae (Fig. 1C$_{4,8}$).

To sum up the preceding discussion, the following should be noted: (1) Not only must early ontogeny be studied, but the specimen must be properly oriented in all phases of its growth. (2) Diagenesis is a factor that must be kept in mind. It may camouflage the primary microstructure and morphology of septa to the extent of precluding the use of the peel method for taxonomic identification. (3) The incorrect orientation of thin sections by Schindewolf (1942) had substantial consequences in taxonomy.

3. *Pentaphyllum* De Koninck, 1872: an example of the manipulation and misuse of a generic name

Ilina (1984, pp. 80–82) proposed an enormous synonymy and species content of the seemingly long-lasting and apparently cosmopolitan genus *Pentaphyllum* De Koninck, 1872. It is questionable, however, whether or not all of the species listed by Ilina (1984) are truly related. The facts suggest that they are not.

De Koninck (1872) introduced two new species, *armatum* and *caryophyllatum*, assigning them to his new genus *Pentaphyllum*. Each of those species was based on a single specimen from Belgian Tournaisian deposits. Both specimens were illustrated by him with some degree of imagination (De Koninck, 1872, pl. 4, figs. 8, 9). Hinde (1890) selected the first of those species as the type for the genus, but did not examine either of the specimens. The same was true for nearly all coral workers applying the name *Pentaphyllum* up to the present, except for Schindewolf (1942, p. 173), who declared that he saw the specimens. Unfortunately, he failed to illustrate them and did not describe them in detail.

Hudson (1936) based his considerations on the illustrations of the lectotypes of both of De Koninck's (1872) species, but illustrated only the lectotype of *Pentaphyllum caryophyllatum*. A photograph of the lectotype of the type species of the genus, which serves as the family type (Hill, 1981, p. F330) and seemingly contains about 49 species included by Ilina (1984) in her list, is for the first time being shown by Fedorowski (2009b) and in this paper (Fig. 2C).

Hudson (1936, p. 8) correctly pointed out that the lectotype of *Pentaphyllum armatum* was poorly preserved. Not only is it broken, but also its entire internal skeleton is dissolved. Only its strongly silicified external shell is preserved (Fedorowski, 2009b). Thus, the only data available for the species and genus are from the calice, supplemented by external characters. Six leading septa are clearly seen in both the illustration by De Koninck (1872, pl. 4, fig. 8a) and the photograph of the calice (Fig. 2C). This was already pointed out by Hinde (1890, p. 195) as contradicting the name, but was ignored by the majority of subsequent authors, including myself (Fedorowski, 1973), who followed Schindewolf (1942).

Schindewolf (1942) began his revision by placing *P. caryophyllatum* in synonymy with *P. armatum*. Considering that synonymy proven, he then declared synonymy of the genus *Cryptophyllum* Carruthers, 1919 with *Pentaphyllum*. This allowed him to use an excellent ontogenetic study by Carruthers (1919, pl. 11, fig. 1a–j) as an illustration of the ontogeny in *Pentaphyllum* (Schindewolf, 1942, figs. 72, 73). The obvious similarity of *P. caryophyllatum* to *C. hibernicum* Carruthers, 1919 at maturity (Fig. 2D–G), already established by Hudson (1936, p. 10), and the lack of photographs of *P. armatum*, made the synonymy proposed by Schindewolf (1942) acceptable to subsequent coral workers. Only Flügel (1968, 1973) pointed out the flaw in Schindewolf's (1942) procedure and kept using the name *Cryptophyllum* for specimens with the permanently underdeveloped counter protoseptum.

Data derived from the lectotype of *P. armatum* (Fig. 2C) are insufficient for an explanation of the development and relationships of the genus *Pentaphyllum*. It certainly does not exhibit five leading septa, the most important character attributed to that genus by a great majority of Schindewolf's followers, including Hill (1981, p. F330); its counter protoseptum is not underdeveloped or reduced, but is at least as long in the calice as the counter-lateral septa. Thus, nearly all taxa included by Ilina (1984) in her list of *Pentaphyllum* species should be excluded from it. Only those possessing six leading septa should be included in that list, i.e., only those similar to or belonging to *Hexalasma* Soshkina, 1928 (Fig. 2A and B).

When six leading septa are present in the calice, however, it does not necessarily mean that the counter protoseptum is permanently elongated, although this is true for the Permian type of *Hexalasma*. The recognition by Soshkina (1928) of an axial protoseptum developed prior to the division into the cardinal and counter protosepta (Fig. 2A) was confirmed by Ilina (1984). Such development may not, however, be true for *Pentaphyllum*. That genus may theoretically have had a short counter protoseptum at the beginning of its septogenesis. This is observed in some lower Bashkirian specimens from the Donets Basin (Fedorowski, in preparation). Also, *Pentaphyllum* is not necessarily related to other taxa permanently possessing six leading septa. The long time span between their occurrences in the Late Silurian (Sutherland, 1965), Early Carboniferous (De Koninck, 1872), and Permian (Soshkina, 1928) makes the supposition of their relationship doubtful. Nevertheless, rugose coral taxa that have an underdeveloped counter protoseptum in the mature growth stage and were previously identified as *Pentaphyllum* should not be assigned to that genus.

Considering Schindewolf's restudy of De Koninck's (1872) originals proven, one can suspect a conscious manipulation from his side. His synonymization of *Cryptophyllum* Carruthers, 1919 with *Pentaphyllum* and his utilization of Carruthers's (1919)

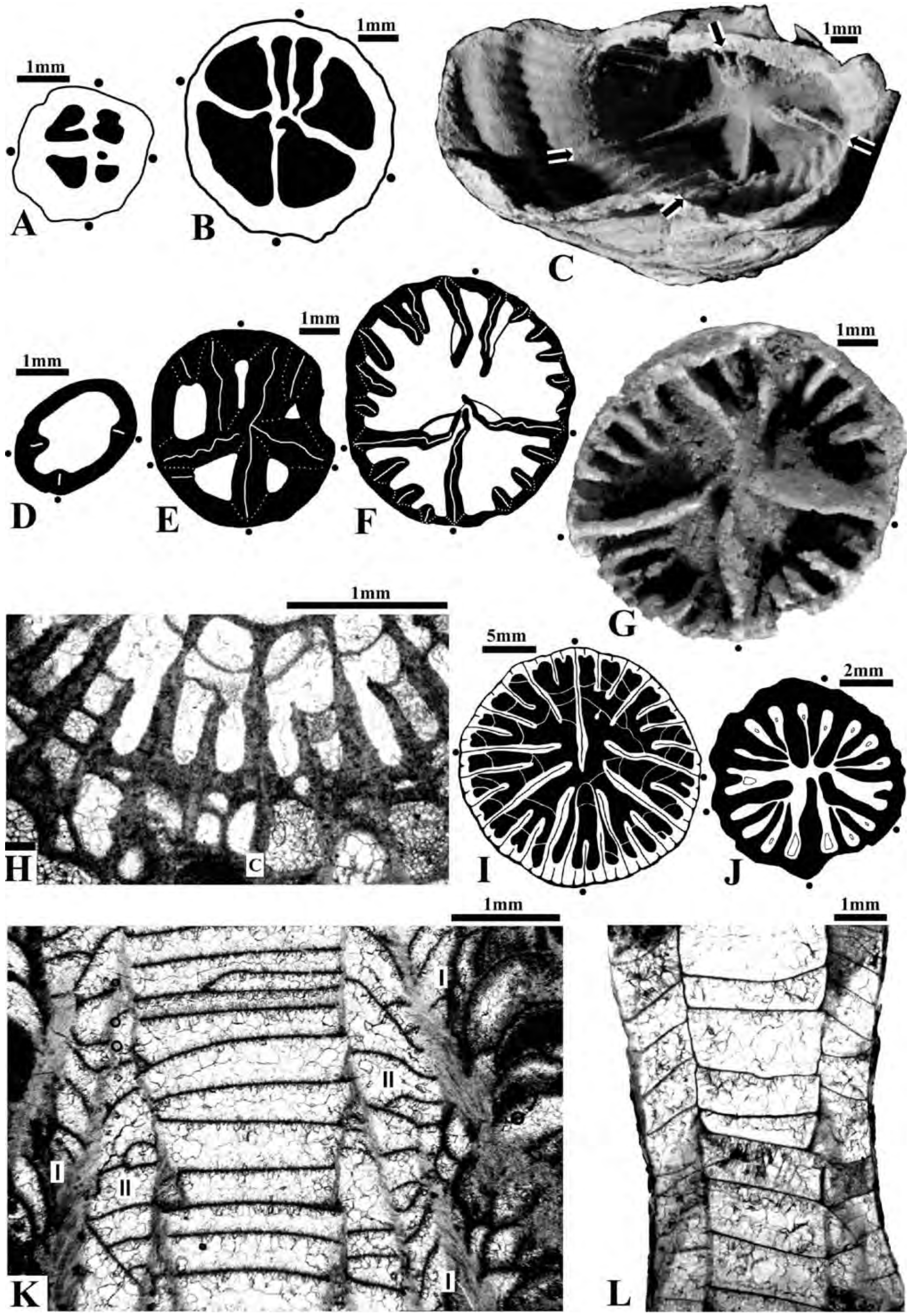

Fig. 2. (A and B) *Hexalasma primitivum* Soshkina, 1928. Holotype No. 146/498. Shchugor River, Northern Urals, Russia, Artinskian. (A) Neanic growth stage. (B) Mature growth stage. Both figures re-drawn from Soshkina (1928, text-fig. 11a, c respectively). (C) *Pentaphyllum armatum* De Koninck, 1872. Lectotype No. 257. Tournai, Belgium, Tournaisian. Calice. Arrows point to protosepta and alar septa. (D–F) *Cryptophyllum hibernicum* Carruthers, 1919. Lectotype Nos. 1090, 1091. Donegal Bay, Ireland, Bundoran Shale Formation, Arundian. (D) Early neanic growth stage; (E) late neanic growth stage; (F) mature growth stage. All figures re-drawn from Carruthers (1919, pl. 11, fig. 1b, h, j respectively). (G) *Pentaphyllum caryophyllatum* De Koninck, 1872. Lectotype No. 258. Tournai, Belgium, Tournaisian. Calice. (H) Genus et species novum. Specimen No. 16/92. Donets Basin, Ukraine, lower Bashkirian. Transverse section. Sections of peripheral parts of biform tabulae absent from septal loculi facing towards the cardinal protoseptum (c). (I) *Sochkineophyllum artiense* (Soshkina, 1925). Holotype No. 146/809. Central Urals, Lytva River area, Artinskian. Transverse section. Re-drawn from Soshkina (1925, pl. 2, fig. 12b). (J) *Plerophyllum australe* Hinde, 1890. Irvin River area, western Australia, Fossil Cliff limestone, Lower Permian. Transverse section. Re-drawn from Schindewolf (1942, fig. 41d). (K) ?*Solenodendron furcatum* (Smith, 1925). Specimen 1986/3. Bishop's Quarry, Great Ormes Head, Britain, Upper Viséan. Longitudinal section. Biform tabularium. I—Position I of Sutherland (1965), II—Position II of Sutherland (1965) (Specimen provided by Professor E. Poty, Liège, Belgium). (L) *Amplexocarinia muralis* Soshkina, 1928 of Różkowska, 1969. Specimen No. 1234. Kadzielnia Quarry, Holy Cross Mountains, Poland, lower Famennian. Longitudinal section. Differently arranged peripheral tabellae.

ontogenetic study for *Pentaphyllum* resulted in the erroneous identification of many species all over the World.

4. Recognition of a biform tabularium

Discussion on this topic may seem unnecessary since Weyer (1972) documented the occurrence of biform tabularia not only in the non-dissepimented horn corals with contratingent minor septa, as originally shown by Sutherland (1965), but also in several dissepimented taxa, both solitary and colonial. However, recognition of a biform tabularium is not always obvious from descriptions, even in more recent papers. The reasons for this are numerous. It may not be recognized, for instance, when a longitudinal section cuts a tabularium in position II of Sutherland (1965) exclusively.

Descriptions such as "tabularium variable in shape", or "peripheral tabellae either elevated or depressed towards the axis" may suggest the occurrence of a biform tabularium, but does not necessarily prove it. Besides, the difference in the position of individual parts of a tabula would remain unknown and its completeness would be negated in such a description by use of the word "tabellae". Thus, biform tabulae in specimens with non-contratingent minor septa are complete. They slope downward and upward on either side of given septa (Fig. 2K), but are uniform from the inner margin of a minor septum towards the axis. This means that the term "peripheral tabellae" is not applicable to biform tabulae. Whether it should be applied to species possessing contratingent minor septa is another question, not discussed in this paper. The name "tabulae" was originally applied to such species by Sutherland (1965).

Transverse sections of peripheral parts of tabulae may help to recognize a biform tabularium of specimens otherwise inadequate for a longitudinal section. Different numbers of intercepts of tabulae on either side of minor septa, larger towards the counter protoseptum (Fig. 2H), indicate the presence of a biform tabularium and, to some extent, differences in its depth at the periphery.

The morphology of the tabularium, i.e., the major part or entire calice floor, plays an important role in bringing water into the gastro-vascular cavity for the distribution of food and oxygen. Water distribution along a uniformly elevated calice floor must have been different from one that is biformly depressed at the periphery. The physiological control must remain in conjecture, but differences in the shape of the tabulae mentioned have been accepted as a family character in several instances. Being constant on the family level, the development of either biform or normal tabularium must have been genetically controlled and must possess taxonomic value. Consequently, omission of that character or its misinterpretation may result in incorrect taxonomic identifications, commonly with phylogenetic, palaeogeographic, stratigraphic, and palaeoecologic bearings. The distinction between the Waagenophyllidae Wang, 1950 and the Durhaminidae Minato et Kato, 1965 was not clear until biform tabulae, as opposed to clinotabellae, were recognized in the Durhaminidae (Fedorowski et al., 2007). As a result, it was established that those two families were clearly separated geographically with the Waagenophyllidae being restricted to the Palaeotethys Realm and the Durhaminidae to the Cordilleran-Arctic-Uralian Realm. The records of the Durhaminidae from Palaeotethyan sites appear to be incorrect when the morphology of the tabularia are checked, and the palaeogeographic reconstructions made by Minato and Kato (1965, 1970) on the basis of coral distribution thus cannot be confirmed.

Some Famennian specimens from Poland, included by Różkowska (1969) in *Amplexocarinia* Soshkina, 1928, serve as another example. Minor septa are absent from corallite lumens of those specimens, and they possess a true aulos that may be interrupted in some parts of their growth. Thus, their tabularia are mostly incomplete, consisting of inner and peripheral tabellae. The peripheral tabellae are positioned in different ways on either side of a given longitudinal section (Fig. 2L). Such tabularia are not biform in the classic sense, because the minor septa are absent from the corallite lumen, but they also are not uniform. Thus, they are here considered as a potentially distinct kind of the tabularium.

5. Conclusions

Only precise taxonomy, based on comprehensive ontogenetic and microstructural studies and supported by palaeogeographic studies, allows reasonable reconstructions of rugose coral phylogeny. Reconstructions proposed without such studies must be considered with caution.

The vast majority of old types require careful revision. Important characters of these types may have been either overlooked by early workers or were unknown to them.

Serious taxonomic errors may result if diagenetic alterations of skeletal structures are not recognized and biform tabularia are not detected.

In addition to inadvertent omissions and/or misinterpretations, examples of apparently purposeful manipulations exist. These cannot be recognized without modern revisions based on type specimens.

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Research paper

Stromatoporoids and colonial corals hosting borers and linguloid brachiopods, Ordovician of Manitoba, Canada

Lori A. Stewart[a], Robert J. Elias[a,*], Graham A. Young[a,b]

[a] Department of Geological Sciences, The University of Manitoba, Winnipeg, MB, R3T 2N2 Canada
[b] The Manitoba Museum, 190 Rupert Avenue, Winnipeg, MB, R3B 0N2 Canada

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Abstract

There have been very few published reports of stromatoporoids and colonial corals with borings that contain linguloid brachiopods; all are from the Ordovician and/or Silurian in just four areas of eastern Canada and northwestern Europe. Here, we report the discovery of an earlier Ordovician occurrence, in both stromatoporoids and corals, and expand the geographic range of such associations to central Canada. In the Upper Ordovician Selkirk Member of the Red River Formation, southern Manitoba, the stromatoporoid *Stratodictyon* and tabulate coral *Protrochiscolithus* commonly contain cylindrical macroborings representing the ichnogenus *Trypanites*, almost certainly produced by worms. In a few specimens, a small proportion of borings contain single linguloids. The linguloids occur predominantly in borings with relatively large diameters, but their occurrence with respect to boring length and their vertical location within borings are random. They are interpreted as nestlers that occupied vacant borings throughout life. Although some of the borings were covered over by subsequent growth of the host or recolonization of its surface, there is no evidence of embedment structures in stromatoporoids or corals that would indicate interaction of the host with either the borers or linguloids. This is comparable to occurrences in the Ordovician of Manitoulin and Anticosti islands in eastern Canada, in that the linguloids are found within *Trypanites* borings without associated embedment structures. In the Silurian of Anticosti, Gotland, and the Welsh Borderlands, however, some borings were further developed into embedment structures during upward growth of the hosts, indicating that these relationships involved some type of symbiosis.

Keywords: Stromatoporoids; Corals; Linguloid brachiopods; Nestlers; *Trypanites* borings

1. Introduction

Instances in the fossil record of one kind of organism consistently taking up residence within the skeleton or tissues of another kind of organism are important to our understanding of ancient ecosystems. In some cases, these fossils may show evidence of direct interaction between the organisms, providing information about physiology and relationships (Boucot, 1990). Other examples lacking evidence of direct interaction can still tell us about the behaviour and growth of one of the organisms (Taylor and Wilson, 2003).

Many stromatoporoids and corals hosted macroboring activity during life and/or after death (Darrell and Taylor, 1993; Scoffin and Bradshaw, 2000; Tapanila et al., 2004). There have, however, been very few reports of linguloid brachiopods within the borings. Such associations are known only from the Ordovician and Silurian, and have previously been found in just four areas: (1) in the sarcinulid tabulate coral *Columnopora* from the Upper Ordovician (Rawtheyan) of Manitoulin Island, Ontario, Canada (Tapanila and Holmer, 2006); (2) in the sarcinulid *Calapoecia* and the heliolitid tabulate *Propora* from the Upper Ordovician (Hirnantian), and in the clathrodictyid stromatoporoids *Clathrodictyon* and *Ecclimadictyon* and in *Propora*? from the Lower Silurian (Llandovery), of Anticosti Island, Québec, Canada (Tapanila and Holmer, 2006); (3) in the actinostromatid stromatoporoid *Densastroma* and in the heliolitid *Heliolites* from the Upper Silurian (Ludlow) of Gotland, Sweden (Richards and Dyson-Cobb, 1976); and (4) in *Heliolites* from

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[*] Corresponding author.
E-mail addresses: eliasrj@cc.umanitoba.ca (R.J. Elias), gyoung@cc.umanitoba.ca (G.A. Young).

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the Ludlow of the Welsh Borderlands, Great Britain (Newall, 1970). Here we report the discovery of an earlier Ordovician occurrence, in both stromatoporoids and corals, and expand the geographic range of such associations to Manitoba, Canada.

2. Geologic setting, material, and methods

The Upper Ordovician (Cincinnatian) Selkirk Member of the Red River Formation is exposed in quarries at Garson in southern Manitoba (for map and stratigraphic column, see Bae et al., 2008, fig. 1). This member is considered to be middle Maysvillian to early Richmondian in age (Elias, 1991). It consists of fossiliferous carbonate wackestone to packstone, with dolomitic mottles, and was deposited in a shallow subtidal, open marine environment with occasional storms (Kendall, 1977; Westrop and Ludvigsen, 1983). Quarries at Garson expose about 8 m of strata within the Selkirk Member and begin 6 m above the base of the member, which is locally about 50 m thick (Kendall, 1977, fig. 1).

The diverse fossil assemblage in the Selkirk Member includes various stromatoporoids and corals. Linguloid brachiopods have not previously been reported from this member, although many detailed palaeontological studies have been conducted. In the present study, they were found only within macroborings in stromatoporoids and colonial corals, not within the rock matrix.

This study is based on an examination of numerous stromatoporoids and colonial corals exposed in cut and broken quarry rubble. Fourteen specimens of the labechiid stromatoporoid *Stratodictyon* and four of the heliolitid tabulate *Protrochiscolithus* were discovered to have linguloid brachiopods within some cylindrical macroborings. Specimens are deposited in the Manitoba Museum, Winnipeg, Manitoba (MM I-4264 to I-4281). Observations were made on all cut and broken surfaces of these specimens. In some cases, acid etching was done and thin sections were prepared to further reveal the nature of borings and linguloids. A linguloid shell in one specimen (MM I-4278) was analyzed using the electron-dispersive X-ray detector system (EDS) of a scanning electron microscope (SEM), in order to determine the relative elemental composition. In addition, five of the specimens of *Stratodictyon* and one of *Protrochiscolithus* were selected for quantitative analysis as described below.

Of the selected specimens, four of *Stratodictyon* (MM I-4264, I-4265, I-4268, I-4277) and the specimen of *Protrochiscolithus* (MM I-4278) were cut transversely or obliquely (MM I-4264 only) and polished. Diameters of all borings were measured using a stereomicroscope with an ocular graticule. The minimum dimension was recorded in order to take into account any lack of circularity, due to borings that may be oblique rather than perpendicular to the cut surface. In addition, the type of infilling in each boring and presence or absence of linguloids at the level of the cut surface were recorded. The combined data from all five specimens were separated into two groups: (1) borings without linguloids, and (2) borings occupied by linguloids. For quantitative analysis, Jandel SigmaStat was employed to obtain descriptive statistics, to test for normality of the overall distribution with the Kolmogorov–Smirnov Normality Test (P value for significance = 0.05), and to compare between the groups with the Mann–Whitney Rank Sum Test (P value for significance = 0.05).

The fifth specimen of *Stratodictyon* (MM I-4276) was serially sectioned transversely into 10 slabs and the surfaces were polished. The slabs range in thickness from 3.1 to 5.3 mm (average 4.1 mm), and the missing intervals between slabs, removed by cutting, are 1.1–2.5 mm (average 1.7 mm). Using each of the 20 resulting surfaces, individual borings were tracked vertically through the specimen and the type of infilling and occurrences of linguloids were recorded. Borings that begin or end within a slab were considered to extend half way through that slab, and those that begin or end within an interval that is missing due to cutting were considered to extend half way between the slabs. Thus, the full lengths of borings that were completely contained within the specimen were estimated, and the vertical positions of linguloids within occupied borings were determined. Data on the length of borings were separated into two groups: (1) borings without linguloids, and (2) borings occupied by linguloids. For quantitative analysis, Jandel SigmaStat was employed to obtain descriptive statistics and to compare between the groups with the Mann–Whitney Rank Sum Test (P value for significance = 0.05).

3. Results and analyses

In the Selkirk Member at Garson, *Stratodictyon* and *Protrochiscolithus* commonly contain unlined, cylindrical macroborings with circular apertures and rounded bottoms (Fig. 1A). Such borings, which are also common in solitary rugose corals from the same locality, represent the ichnogenus *Trypanites* and are thought to have been produced by worms such as polychaete annelids (Elias, 1980). The host taxa that contain *Trypanites* borings are characterized by relatively dense skeletal structures, which made them suitable substrates for the borers.

The *Trypanites* borings in *Stratodictyon* and *Protrochiscolithus* penetrate downward into the host's skeleton from its growth surface (Fig. 1A). In some cases, borings are concealed within the skeleton due to subsequent growth of the host or later recolonization of the surface (Fig. 2B). A few specimens of *Stratodictyon* and *Protrochiscolithus* were found in which a small proportion of *Trypanites* borings contain single linguloids (Fig. 2A–C). Linguloids are otherwise unreported from the Selkirk Member, and were not observed in matrix surrounding the stromatoporoids and corals examined in the present study. Shells of other organisms were not observed within *Trypanites*, except as bioclastic particles where the borings were filled in with sediment.

The four specimens of *Stratodictyon* and one of *Protrochiscolithus* for which single polished surfaces were studied had areas ranging from 33.6 to 213.4 cm^2. The density of *Trypanites* borings on these five surfaces ranges from 0.3 to 0.8 borings/cm^2 (average 0.5 borings/cm^2). A total of 287 *Trypanites* borings were observed, 22 (8%) of which contain linguloids. For the serially sectioned specimen of *Stratodictyon*, linguloids were found in 14 (16%) of 88 borings. The greater frequency of borings in this case is to be expected, since multiple polished surfaces within each boring were examined. The proportion of

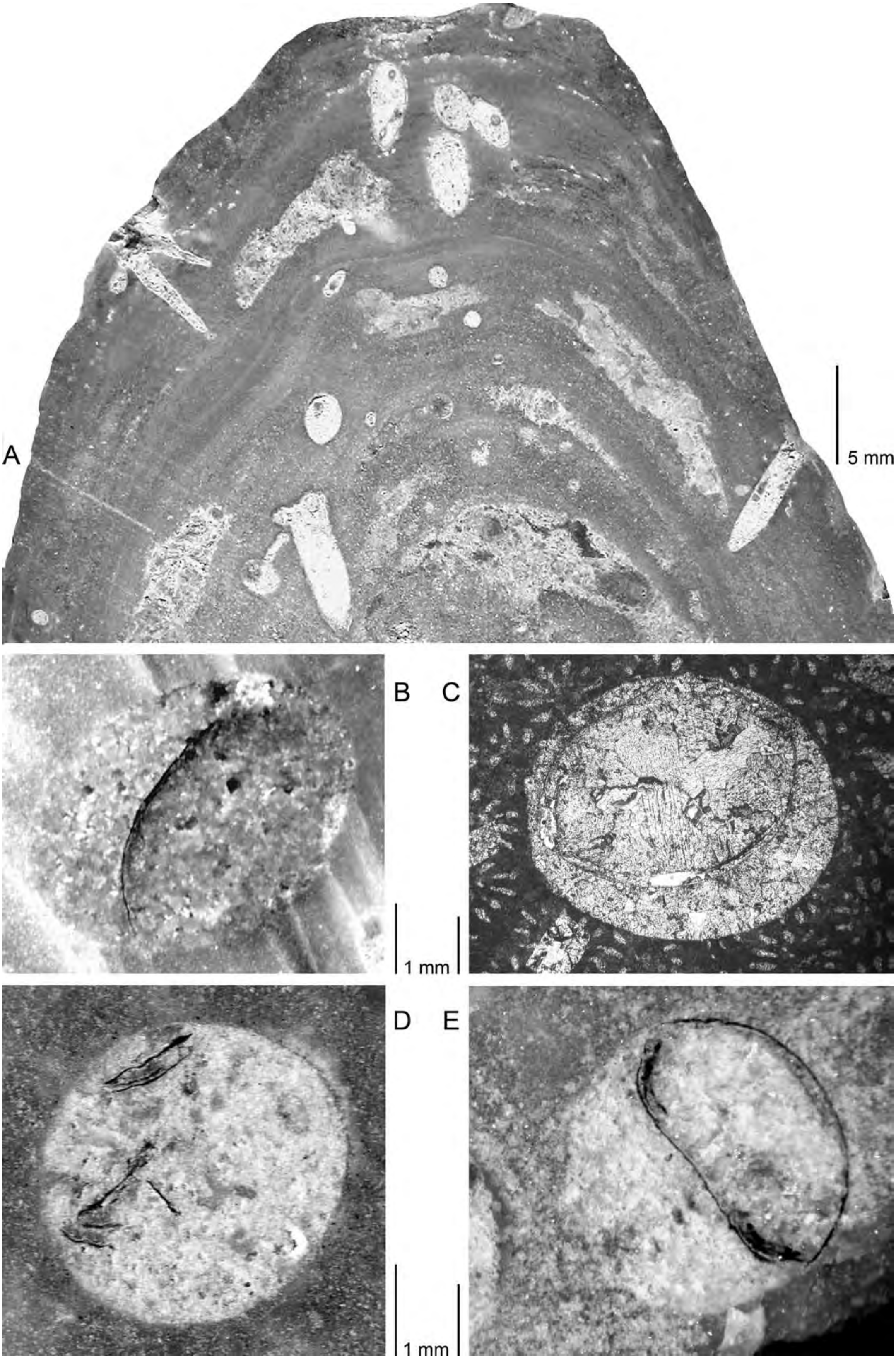

Fig. 1. *Stratodictyon* and *Protrochiscolithus* with *Trypanites* borings, some containing a linguloid; Selkirk Member, Red River Formation (Upper Ordovician), Garson, Manitoba. (A) *Stratodictyon* with *Trypanites*; oblique polished section, MM I-4264. (B) Single valve of linguloid within *Trypanites* in *Stratodictyon*; transverse polished section, MM I-4275. (C) Articulated valves of linguloid within *Trypanites* in *Protrochiscolithus*; transverse thin section, MM I-4278. (D) Fragmentary linguloid remains within *Trypanites* in *Stratodictyon*; transverse polished section, MM I-4276. (E) Articulated valves of linguloid within *Trypanites* in *Stratodictyon*; transverse polished section, MM I-4277.

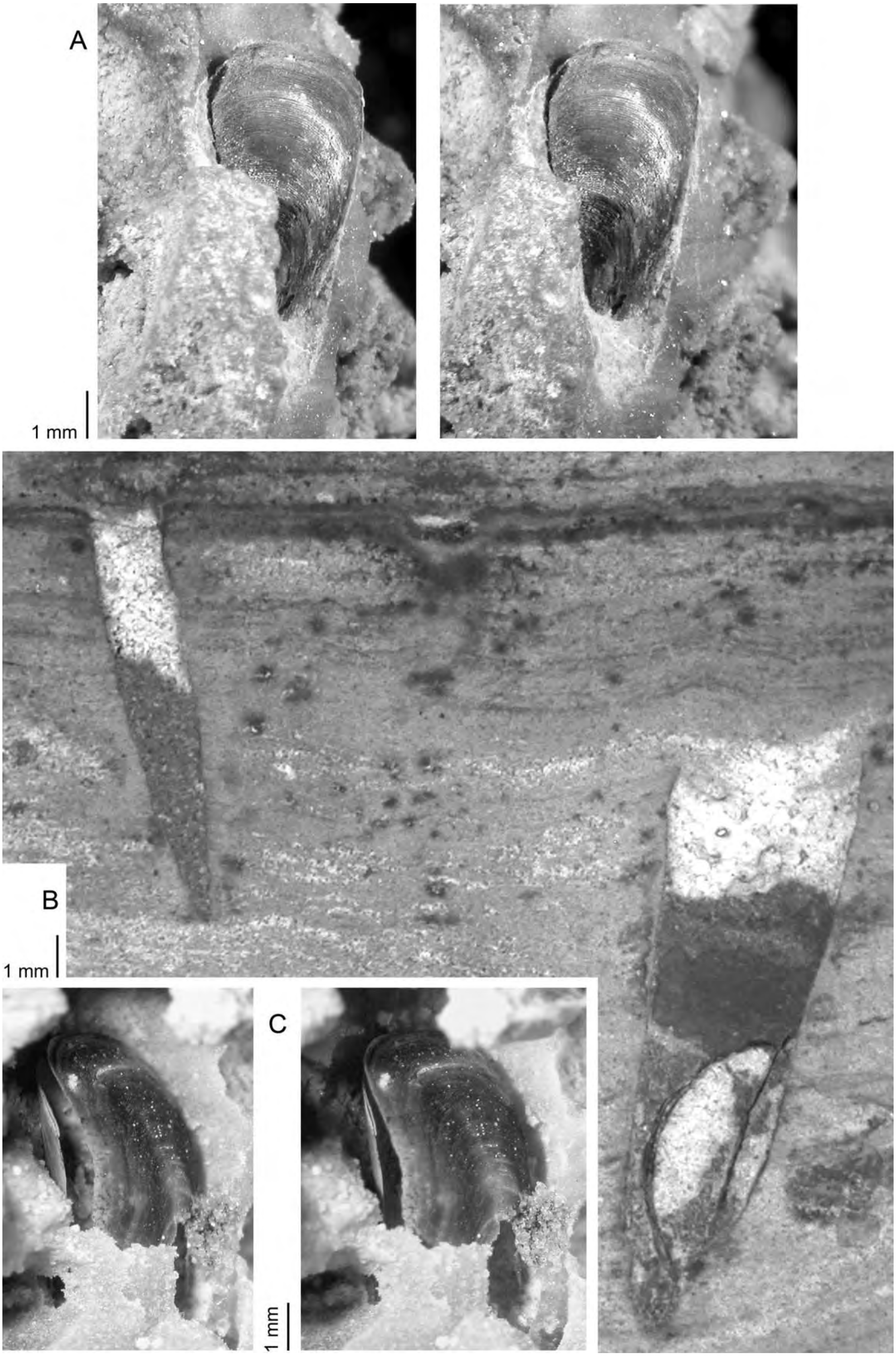

Fig. 2. Linguloids within *Trypanites* borings in *Stratodictyon*; Selkirk Member, Red River Formation (Upper Ordovician), Garson, Manitoba. (A) Articulated, upright valves of linguloid within *Trypanites*; etched longitudinal surface, stereo pair, MM I-4271. (B) Two *Trypanites*, one on right containing articulated valves of linguloid; longitudinal thin section, MM I-4277. (C) Articulated, upright valves of linguloid within *Trypanites*; etched longitudinal surface, stereo pair, MM I-4277.

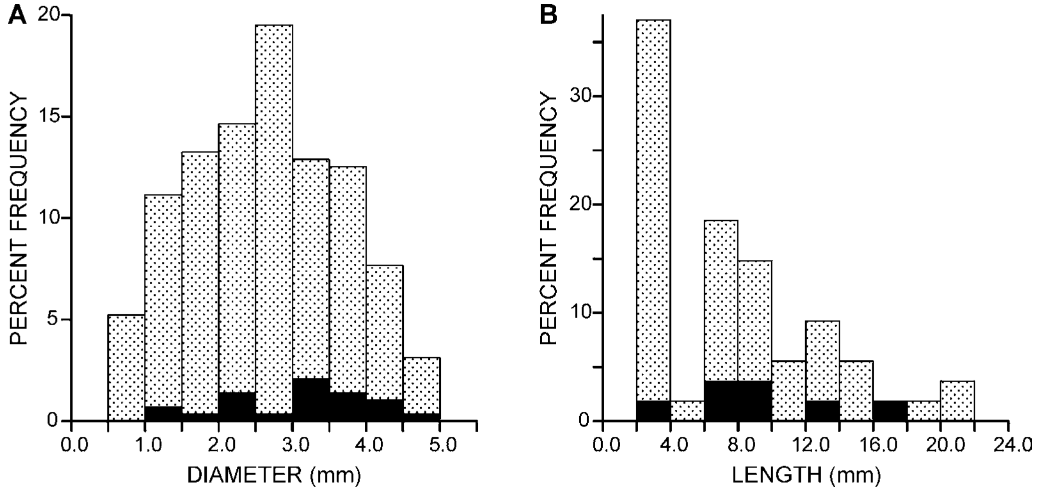

Fig. 3. Frequency distributions for *Trypanites* borings (solid = borings occupied by linguloids, stippled = unoccupied borings); Selkirk Member, Red River Formation (Upper Ordovician), Garson, Manitoba. (A) Diameter of *Trypanites* within *Stratodictyon* and *Protrochiscolithus* ($N = 287$ *Trypanites*; 265 unoccupied, 22 occupied). (B) Length of *Trypanites* within *Stratodictyon* ($N = 54$ *Trypanites*; 47 unoccupied, 7 occupied).

borings that actually contain linguloids in these specimens is undoubtedly even higher.

The *Trypanites* borings in *Stratodictyon* and *Protrochiscolithus* range in diameter from 0.6 to 5.0 mm (average 2.5 mm) (Fig. 3A). The data for diameters of all borings represent a normal distribution (Kolmogorov–Smirnov Normality Test; $P = 0.09$), suggesting that they may have been produced by a single species. The borings in *Stratodictyon* range in length from 2.1 to 20.3 mm (average 7.8 mm) (Fig. 3B). *Trypanites* borings in both *Stratodictyon* and *Protrochiscolithus* truncate the host skeleton through their entire length (Figs. 1C and 2B). Evidence of upward extension of borings as embedment structures produced by growth of the host in response to a symbiont has not been seen. Of 375 *Trypanites* borings observed on single and serial polished surfaces, 281 (76%) are filled with wackestone, 45 (12%) with sparry calcite cement, and 46 (12%) with a combination of both. This indicates that sediment washed into and filled or partially filled most borings (Fig. 2B).

The small, brown to bluish, phosphatic (confirmed by EDS), spatulate, convex shells within some borings are identified as linguloids on the basis of composition and general morphology (Fig. 2A and C). Of the 36 linguloid remains that were observed on all polished surfaces of *Stratodictyon* and *Protrochiscolithus*, 11 (31%) represent articulated valves (Fig. 1E), 12 (33%) are single valves (Fig. 1B), and 13 (36%) are fragmentary (Fig. 1D). Shell orientation and growth-line curvature of all linguloid remains observed on broken and etched surfaces indicate preservation in upright life orientation (Fig. 2A and C). We infer that linguloids lived in the borings and were not washed in from elsewhere because they occur exclusively within *Trypanites* borings in the Selkirk Member, are oriented upright, and the delicate shells are commonly preserved in articulated condition. Disarticulation and fragmentation of some shells is attributed to factors such as water circulation, sediment infilling, and compaction of matrix in the boring.

Statistical comparison of diameters of borings between the groups with and without linguloids (Fig. 3A) indicates a significant difference (Mann–Whitney Rank Sum Test; $P = 0.01$), implying a relation between the diameter of borings and linguloid occurrence. The average diameters of borings with and without linguloids are 3.0 and 2.5 mm, respectively, indicating that linguloids tend to occur in borings with relatively large diameters. Statistical comparison of lengths of borings between the groups of borings with and without linguloids (Fig. 3B) does not indicate a significant difference (Mann–Whitney Rank Sum Test; $P = 0.41$), implying that the occurrence of linguloids with respect to boring length is random. Linguloids were found to occur at various depths, from top to bottom, within *Trypanites* borings, suggesting that their vertical location is random (Fig. 4).

4. Discussion and conclusions

The linguloid brachiopods within *Trypanites* borings in the stromatoporoid *Stratodictyon* and tabulate coral *Protrochiscolithus* of the Selkirk Member at Garson, Manitoba, are interpreted as nestlers. Although the burrowing activity of linguloids is well known since the Cambrian (Zonneveld et al., 2007), there is no evidence that they are able to bore into hard substrates (Newall, 1970). We infer that a linguloid larva selected a vacant boring, preferably one with a relatively large diameter, which it then occupied throughout life. Although some of the borings were covered over by subsequent growth of the host or recolonization of its surface, there is no evidence of embedment structures in the stromatoporoids or corals that would indicate interaction with either the borers or brachiopods.

The linguloid occurrences in the Selkirk Member at Garson are comparable to those in the Ordovician of Manitoulin Island, Ontario, and Anticosti Island, Québec, in that the linguloids are present in *Trypanites* borings without associated embedment structures (Tapanila and Holmer, 2006). In the Silurian of Anticosti, the Welsh Borderlands of Great Britain, and the Swedish island of Gotland, linguloids also inhabited borings (Newall, 1970; Richards and Dyson-Cobb, 1976; Tapanila and Holmer, 2006). In these cases, however, some of the borings were further

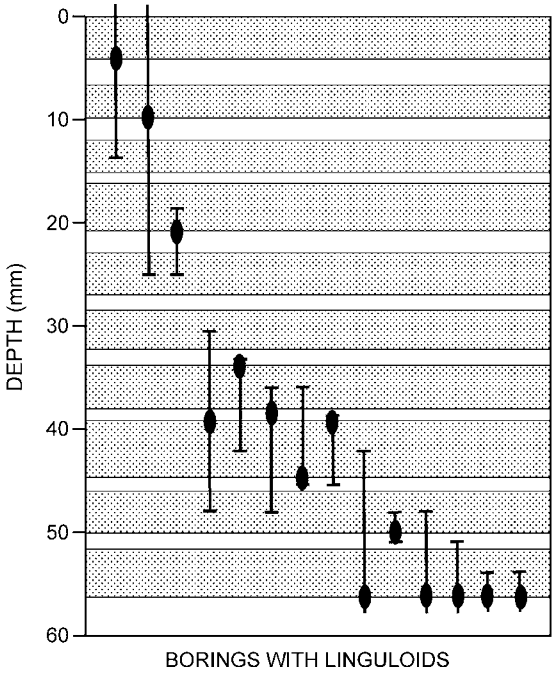

Fig. 4. Longitudinal diagram of *Stratodictyon* specimen that was serially sectioned transversely (depth measured from top of uppermost slab; stippled bar = transverse slab, white bar = interval lost due to cutting), showing positions of occupied *Trypanites* borings (vertical line = occurrence of *Trypanites*, horizontal line = estimated position of top or bottom) and locations of linguloids within them (solid ellipse = position of linguloid); Selkirk Member, Red River Formation (Upper Ordovician), Garson, Manitoba.

developed into embedment structures during upward growth of the hosts, indicating that these relationships involved some type of symbiosis.

In the Selkirk Member at Garson, linguloids occur predominantly within borings with relatively large diameters, but their occurrence with respect to boring length is random. In the Silurian of Gotland, however, both the diameter and length of boring/embedment structures containing linguloids are on average greater than those of unoccupied structures, although the differences are not statistically significant (Richards and Dyson-Cobb, 1976). The vertical locations of linguloids within the structures that contain them are random in the Selkirk Member and in the Silurian of the Welsh Borderlands (Newall, 1970).

The earliest previous report of a linguloid-coral association was from the uppermost Ordovician unit, the Kagawong Member (Rawtheyan; i.e., upper Richmondian) of the Georgian Bay Formation, on Manitoulin Island, Ontario (Tapanila and Holmer, 2006). The Selkirk Member of the Red River Formation in southern Manitoba is older (middle Maysvillian to early Richmondian; Elias, 1991), and is separated from the Ordovician–Silurian boundary, in ascending order, by the Fort Garry Member of the Red River Formation, the Stony Mountain Formation, and the lower Stonewall Formation (Bae et al., 2008, fig. 1). The earliest previous report of a linguloid-stromatoporoid association was from the Lower Silurian (Llandovery) of Anticosti Island, Québec. Thus, the Selkirk Member contains the earliest known occurrence of a linguloid-coral association and the only known linguloid-stromatoporoid association prior to the Silurian. This discovery expands the geographic range of such associations from Gotland and the Welsh Borderlands in northwestern Europe, and Québec and Ontario in eastern Canada, to Manitoba in central Canada.

Although the number of known cases is small, the occurrence of linguloids in association with borings in stromatoporoids and corals presents an interesting stratigraphic pattern. The new Late Ordovician examples from the Selkirk Member indicate that this type of association appeared quite early in the history of stromatoporoids and tabulate corals, which both originated in the Early Ordovician (Webby, 2004; Webby et al., 2004). It is notable that no such associations have been reported in Devonian stromatoporoids and corals, even though they have been studied intensively and contain a considerable diversity of other kinds of endosymbionts (Tapanila, 2005). Tapanila and Holmer (2006) suggested that the linguloid larvae might have been attracted to the borers themselves, either chemically or behaviourally. *Trypanites* borings appeared in the Cambrian and are common through the remainder of the Phanerozoic record. Their peak density, however, is in the Ordovician and Silurian (Wilson and Palmer, 2006), corresponding with the linguloid association.

Acknowledgements

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Research paper

Structure of the corallite wall of the Upper Ordovician and Silurian Favositidae (Tabulata) and its possible use in stratigraphic correlation

Yury Zaika

All-Russian Geological Research Institute (VSEGEI), Saint Petersburg, Russia

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Abstract

Based on an analysis of the significant collections of Favositidae (tabulate corals) from the Upper Ordovician–Lower Devonian of the Taimyr Peninsula, Western Slope of the North Urals and the Tchernychev Uplift, this paper focuses on the macro- and micro-structure of the corallite wall. Seven structural types of the corallite wall have been recognized; some of them seem to have a definite stratigraphic range. The results contribute to the long-time discussion on the applicability of skeletal structure for systematics of the Favositidae, its evolutionary implications, and stratigraphic correlation. It has been held that the skeletal structure of the fossilized remains of Favositidae is inapplicable for such purposes because diagenetically, it is secondary, being a product of mineral replacement of the primary structure. In contrast, an assumption is made here that the "secondary" skeletal macro- and micro-structure may reflect in some way the "primary" skeleton. As a result, it is proposed that some evidence of evolution of the Favositidae may be obtained by evaluating the stratigraphic range of favositid representatives possessing different types of structure of the corallite wall.

Keywords: Ordovician; Silurian; Arctic Region; Favositidae; Skeletal microstructure; Corallite wall

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1. Introduction

Beginning with the monographs of Milne-Edwards and Haime (1849, 1851), a considerable knowledge on the skeletal microstructure of the Favositidae corals has been compiled. Despite this, there is no consensus on the taxonomic value of the skeletal microstructure up to now and a wide range of different terminologies has been proposed. Numerous attempts have been undertaken to establish precise relationships between the skeletal microstructure, evolution, and systematics of the Favositidae corals but these seem to be speculative in the light of the diagenetic concept (Oekentorp, 2007).

Researchers of the Favositidae family (and the Favositida order) have established many varieties of microstructure, but little attention has been focused on their stratigraphic range. Only a few papers refer in some way to some differences between the Silurian and Devonian Favositida (e.g., Lafuste, 1958a, 1962; Smirnova, 1967; Mironova, 1971; Yanet, 1971).

Based on the study of Favositidae corals collected from Upper Ordovician–Lower Devonian marine carbonate successions in Taimyr Peninsula, Western Slope of the North Urals and Tchernychev Uplift (Fig. 1), the present paper considers the stratigraphic range of the established varieties of skeletal macro- and micro-structure, focusing mainly on the corallite wall.

2. Materials and methods

The term "macrostructure" is applied here to the macroscopic parts (or layers) composing the corallite wall of the Favositidae corals (Fig. 2). In well-preserved specimens, these macroscopic parts show differing microstructure. The study is focused on the uppermost microstructure, which has been examined and photographed in transmitted light both in transverse and longitudinal thin-sections using a petrographic microscope, with magnifications up to ×330. Only extremely well-preserved material has been suitable for the examination of the skeletal fine building; however, it does not allow concluding exactly how stable the revealed structural types are.

Spectral analysis of some of the macroscopic parts of the corallite wall has been carried out in an effort to find out if

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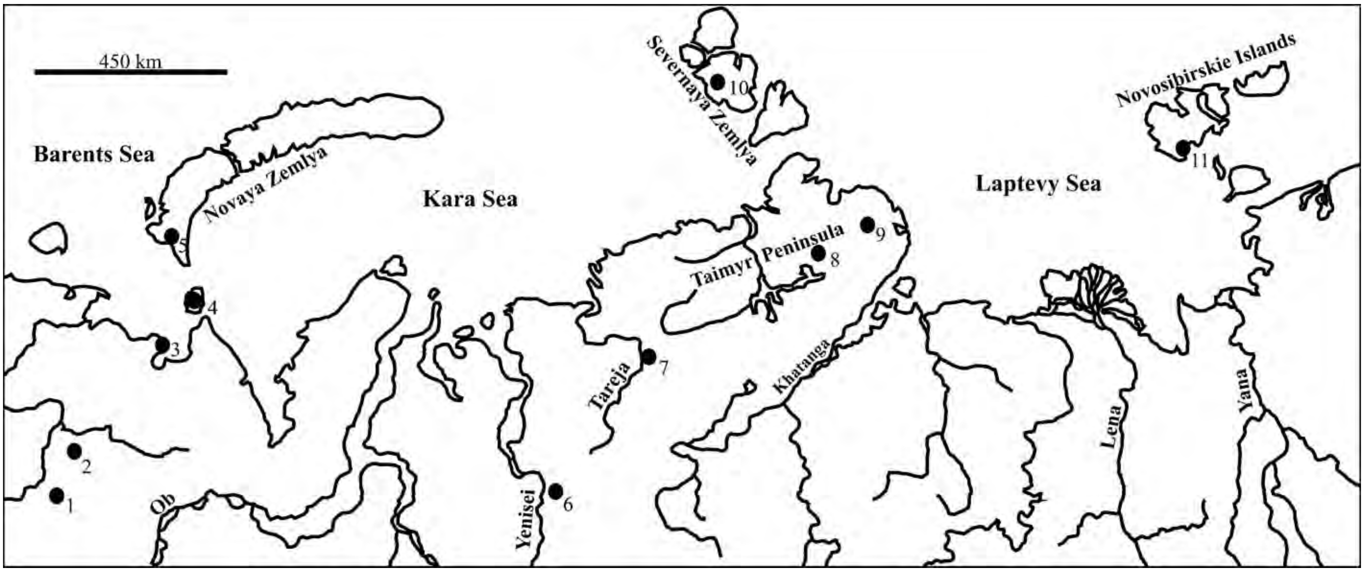


Fig. 1. A generalized map of locations of the Ordovician and Silurian corals in the Arctic Region. 1 – Western Slope of North Urals, 2 – Tchernychev Uplift, 3 – Dolgij Island, 4 – Vajgatch Island, 5 – Southern part of Novaya Zemlya, 6 – Noril'sk region, 7–9 – Southern region of Taimyr Peninsula: Central Taimyr (7), Eastern Taimyr (8, 9), 10 – Severnaya Zemlya, 11 – Kotel'ny Island.

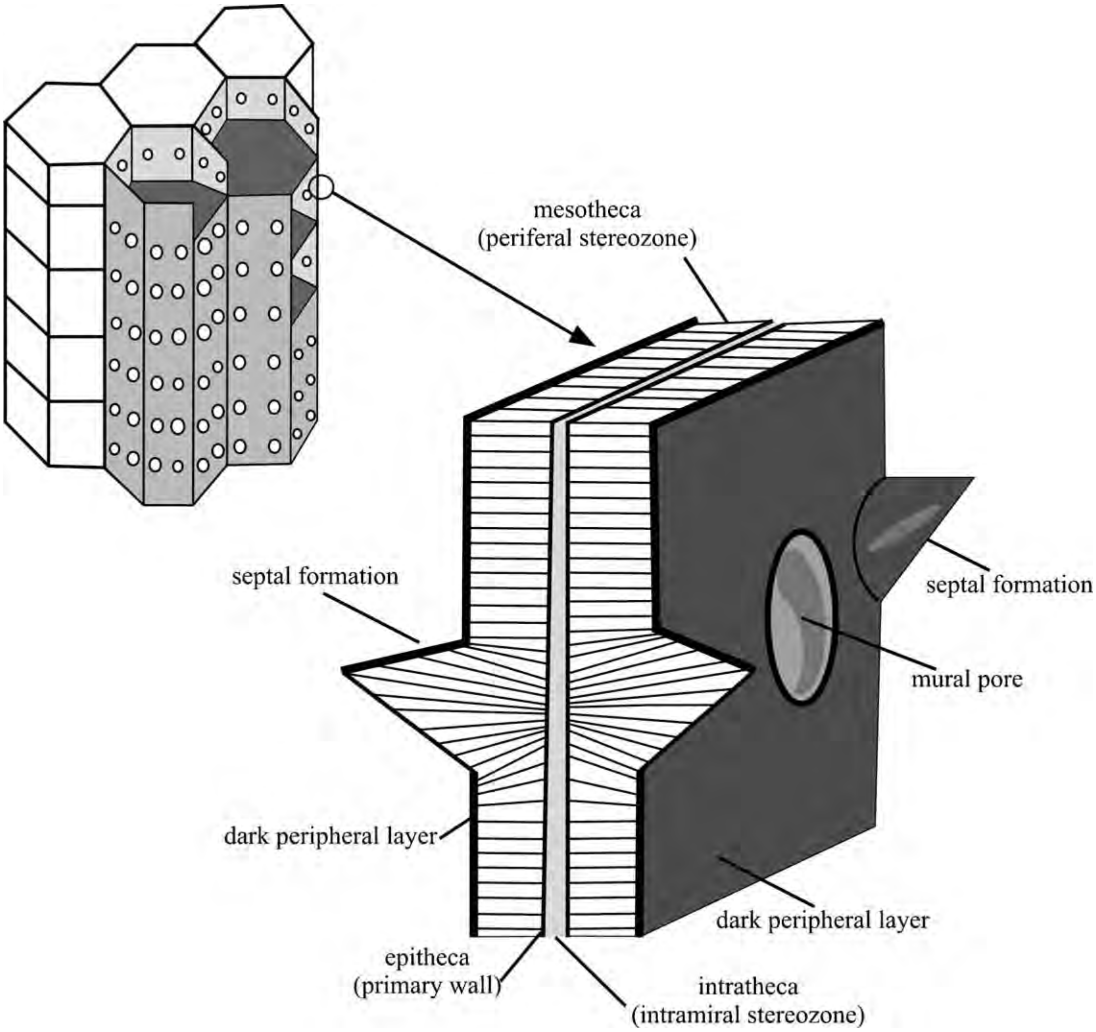


Fig. 2. Schematic diagram showing the macroscopic structure of corallite wall in the Favositidae. Terminology after Swann (1947) (in parentheses) and Mironova (1974), with some modifications.

there is any substantial difference between them, but it has shown the same chemical composition, denoting the calcite formula.

The studied material is reposited in the Department of Stratigraphy and Paleontology of VSEGEI (St. Petersburg, Russia).

3. Regional and stratigraphic setting

The Upper Ordovician to Lower Devonian regional successions in the Western Slope of North Urals, the Tchernychev Uplift and the Southern Region of the Taimyr Peninsula are represented with shallow marine and littoral sediments

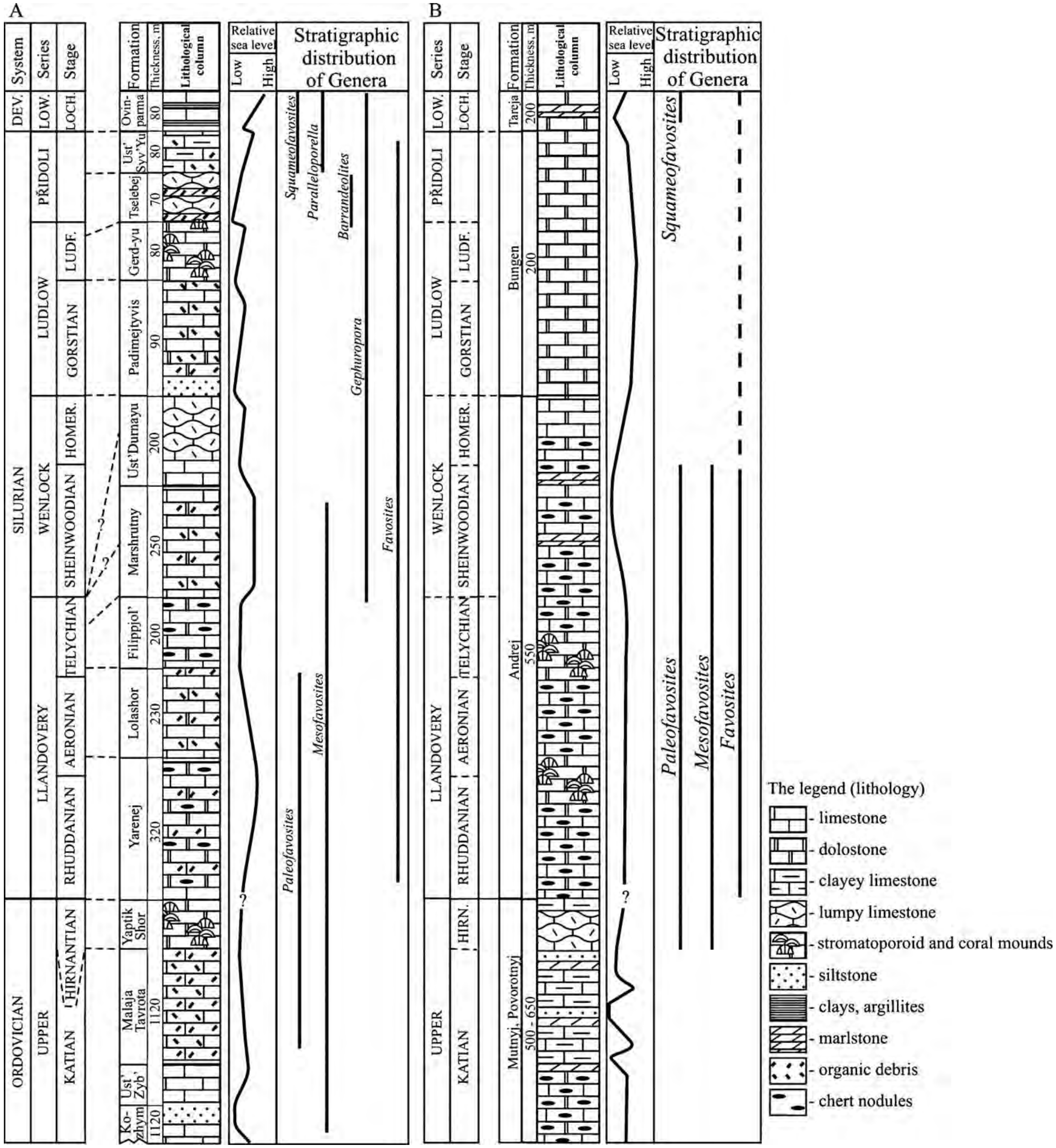


Fig. 3. Stratigraphic distribution of the Favositidae in the Ordovician–Lower Devonian of the North Urals (A) and Taimyr Peninsula (B). Regional stratigraphical charts after Antoshkina (2000) and Sobolevskaja (2003). HOMER. – Homerian; LUDF. – Ludfordian; LOCH. – Lockhovian; LOW. – Lower Devonian. Formation thicknesses are shown not in proportion.

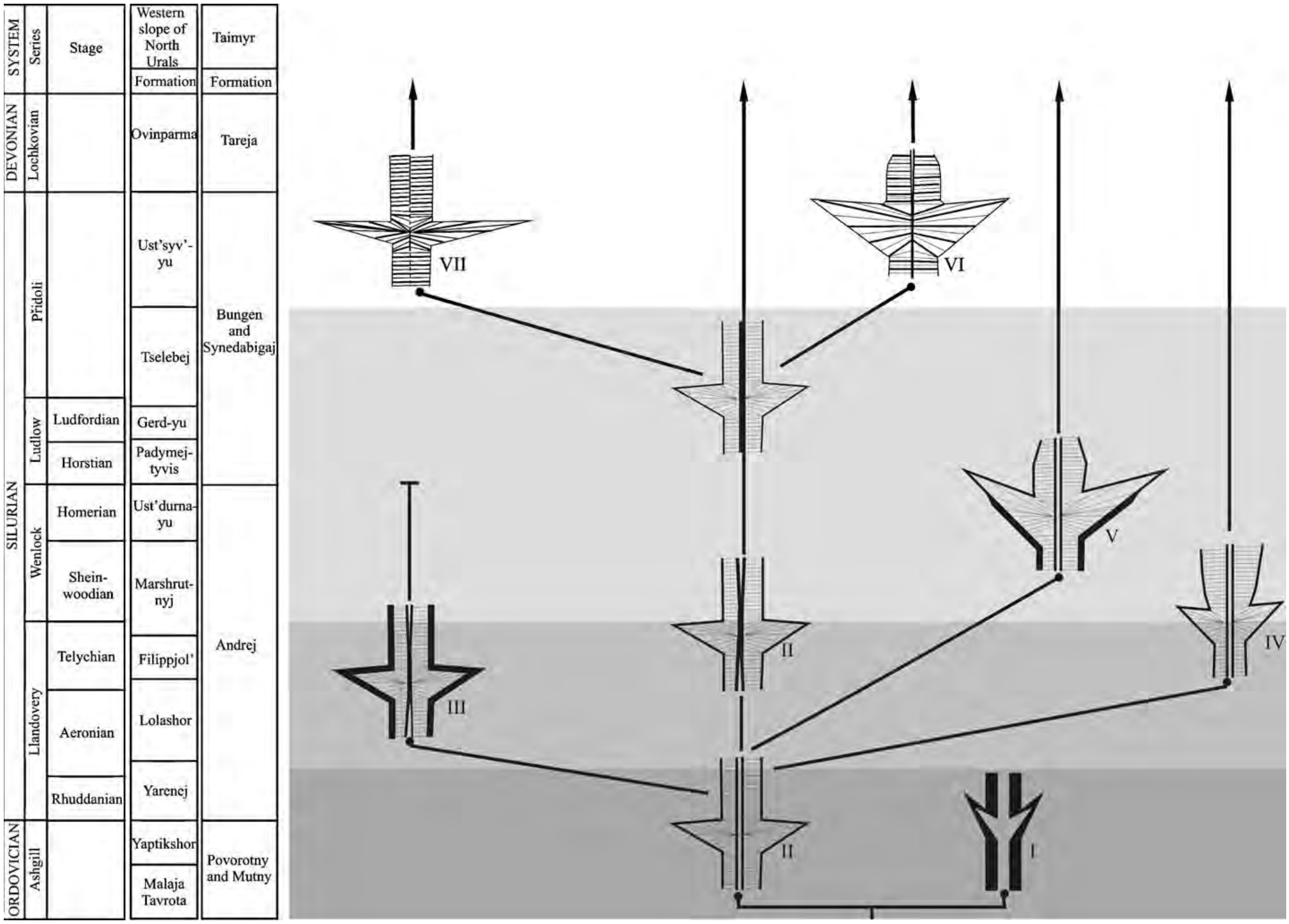


Fig. 4. Stratigraphic succession of structural types of corallite wall of the Favositidae in the Upper Ordovician–Lower Devonian of the Western Slope of North Urals and Taimyr Peninsula, and their possible evolutionary interrelations. Regional stratigraphical charts after Antoshkina (2000) and Sobolevskaja (2003). I–VII – structural types of corallite wall; ● – the first known record of a structural type; — the last known record of a structural type.

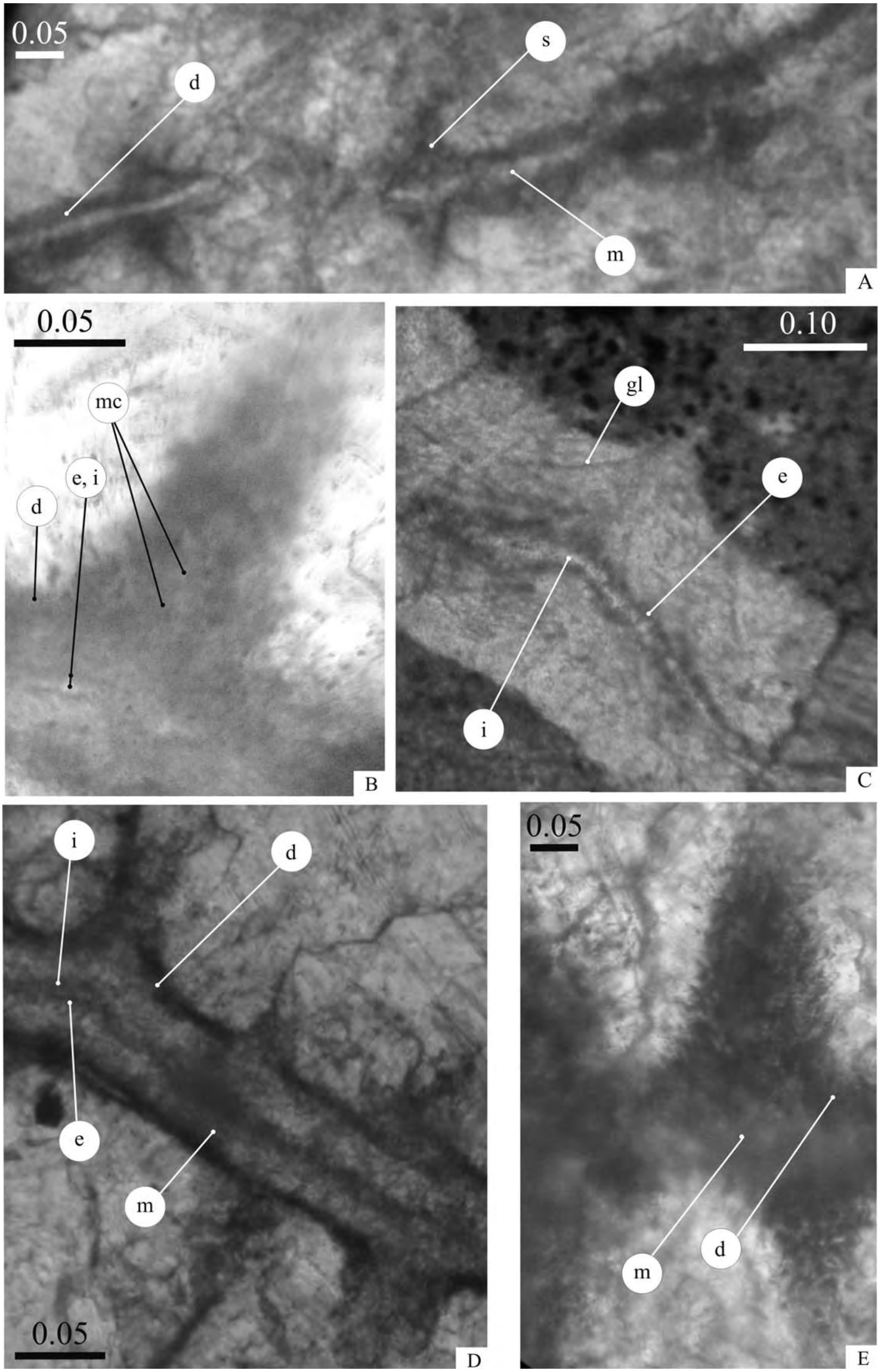
(Figs. 3 and 4), rich in fossil benthic associations, including numerous Favositidae corals of comparatively good preservation (Chekhovich, 1965; Antoshkina, 2000; Sobolevskaja, 2003; Zaika, 2006). The exception is the Ludlow and Přidoli Series in the Taimyr Peninsula, where the tabulate corals are so strongly recrystallized that they could not be included in the present research.

Based on several palaeogeographic and palaeotectonic reconstructions of the Late Ordovician and Silurian time (Torsvik et al., 1996; Dalziel, 1997; Torsvik, 1998; Cocks and Torsvik, 2005), the selected regions were shelf margins of two palaeocontinents: Palaeobaltica (which included the Western Slope of the North Urals and some adjacent regions) and Palaeosiberia (which included Taimyr Peninsula), separated by a comparatively deep-water basin, which at least partly prevented mixing of benthic faunas (Zaika, 2005).

4. Skeletal morphology and microstructure in the Favositidae corals

A biogenic primary skeleton of a living colony of corals is a biocrystalline build-up. Almost immediately after its death and internment in the sediment and during the subsequent lithification process, the skeletal microstructure undergoes diagenetic obliterations (Potthast, 1992). For this reason, a wide variety of different kinds of microstructure have been suspected to be not primary (biogenic) (Schouppé and Oekentorp, 1974; Oekentorp, 1974a,b, 1980, 2001, 2007; Brühl and Oekentorp, 1997; May, 2007). This casts doubt on the suitability of skeletal microstructure for taxonomic and evolutionary considerations, although many authors pay much attention to the microstructure as a taxonomic character (e.g., Nicholson, 1879; Struve, 1898; Kraicz, 1935, 1937; Lecompte, 1936, 1952; Swann, 1947; Sokolov, 1955, 1962; Lafuste, 1958a,b, 1959a,b, 1962, 1963; Chudinova, 1959; Chang, 1959; Flower, 1961; Plusquellec, 1965; Mironova, 1965, 1971, 1974; Yanet, 1965, 1971; Smirnova, 1967; Dubatolov, 1969, 1971; Plusquellec et al., 2007; Plusquellec and Fernández-Martínez, 2007; Nothdurft and Webb, 2007).

In a comparatively simple skeleton of the Favositidae corals, the corallite wall is the most distinguishable part. When examined with the petrographic light microscope, the corallite wall of the Favositidae is not homogeneous in either longitudinal or transverse sections and shows several parts (layers) having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dissimilar fine building. Mironova (1965, 1971) attempted to simplify the terminologies of the previous authors and proposed a formal nomenclature of parts of the corallite wall with no relation to their hypothetical genesis or biological significance. According to Mironova (1971), with some modifications, the following parts can be recognized in the most complicated corallite wall (Fig. 2): the dark peripheral layer, the mesotheca, the epitheca, and the intratheca.

The *dark peripheral layer* inlays the corallite lumen. Subject to its structure, there are several possible explanations of its nature.

1. In some samples the dark peripheral layer can be seen as an opaque and non- or crypto-crystalline layer 0.030–0.045 mm thick (or 30–45 μm) (Fig. 5D). Its distinct delineation and colouration marks it out clearly as a separate part of the wall. This may indicate its origin from some biogenic precursor. It is significant to note, however, that although spectral analysis of the dark peripheral layer has been carried out, the presence of any pigmenting agent has not been proved, so the dark colouration is supposedly a result of irregular arrangement of crystals. From these considerations, the term "*dark peripheral layer*" is used in the present paper instead of the "*peripheral pigmented layer*" of many Russian-language papers.
2. In some other samples, the inner dark peripheral cover of the corallite wall has a very fine but visible crystalline microstructure and is certainly almost the same as the "cement A" sensu Oekentorp (2001), most probably of diagenetic origin.
3. In several samples, the peripheral part of the mesotheca is coloured by the Iron-, Magnesium- or Manganese-containing compounds, giving the "false dark peripheral layer" appearance, which is distinguished by its blurred outlines.

The framework of the corallite wall is the *mesotheca*. This term is synonymous with some other frequently used terms: e.g., the "*peripheral stereozone*" (Swann, 1947), the "*wall*" or "*theca*" (Sokolov, 1955, 1962) or the "*bright middle line*" (Yanet, 1971). The microstructure of the mesotheca is usually cryptocrystalline, although in many specimens some trabeculae-like structures can be seen, being arranged perpendicularly to the growth direction of corallites. Based on the work of Schouppé and Oekentorp (1974), trabeculae are not characteristic of the Favositida. Their conclusion fits the present author's observations, which show crypto- or fine-crystalline but not trabecular microstructure. Trabeculae-like structures seem to be segregations or linear aggregates of juxtaposed fine crystals, arranged perpendicularly to the median plane of the wall (Fig. 6E, F, H). In the studied collection, they are especially characteristic of the Ludlovian, Přidolian, and Lochkovian Favositidae.

Probable growth lamination of the mesotheca is also to be mentioned, being an ordinary feature in many "thick-walled" Favositidae (Fig. 5C).

A significant feature of corallite walls with well-developed mesotheca is the "Y-shaped figure" (a new term introduced here): the three-radiate clefts, visible in transverse sections, radiating from corner points of contact of neighbouring corallites (Fig. 6E and G). The clefts usually cross the wall at an angle between 60° and 90°, whereas the angle between the clefts themselves is about 120°. Sometimes they may extend into the internal calcite filling of the corallite lumen.

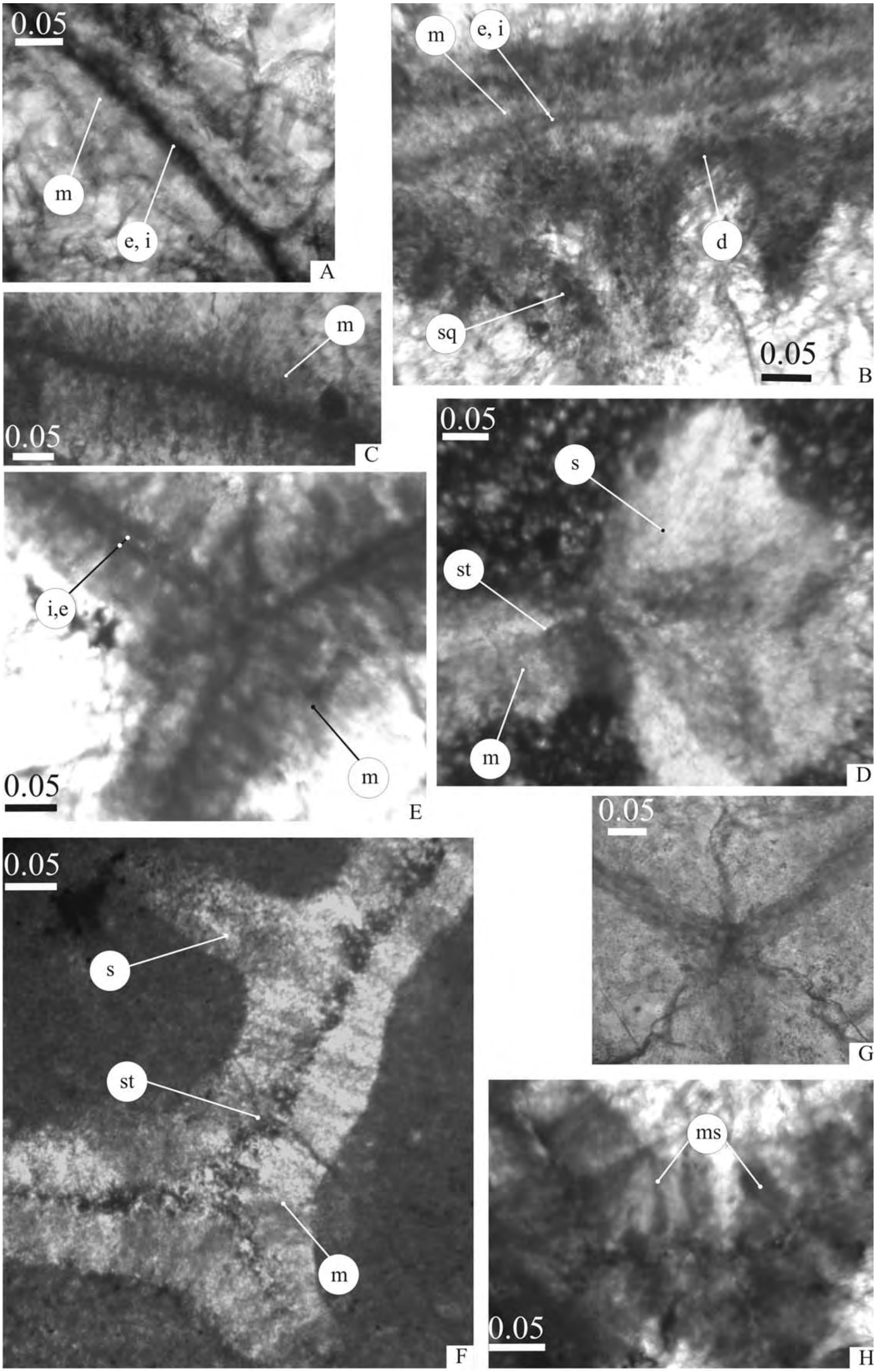
The following explanation of the "Y-shaped figures" arises from the assumption that the primary corallite wall had a fibrous microstructure and was aragonitic (Schouppé and Oekentorp, 1974). As fibres should have been arranged perpendicularly to the polyp ectoderm, they were not as much compacted in the corners of corallites as in their sides. Accordingly, the corner zones were presumably more susceptible to cracking due to compression of the surrounding rock during the lithification process. The diagenetic inversion of the aragonite into the calcite in the corallite wall could also have been important. The most likely direction of the clefts was that along skeletal fibres in the three available "starved spots" of the contacting corallite walls.

The "*epitheca*", as introduced by Milne-Edwards and Haime (1848), or the "*primordial wall*" (Nicholson and Lydekker, 1889), or the "*primary wall*" (Swann, 1947), is a thin opaque cryptocrystalline peel, overlying the mesotheca from the outer side of the corallite (Fig. 5C and D). According to Sokolov (1955), the epitheca is an outer cover of a solitary corallite. Tiny diametrical striations, possibly reflecting periods of corallite growth, can be seen in some cases with a naked eye on the surface of epitheca (see, e.g., Tchernychev, 1937 or Sokolov, 1955).

The *intratheca*, or the "*fissure axialle*" (Lecompte, 1936), or the "*intramural coenozone*" (Swann, 1947), or the "*intermural space*" (Ross, 1953), is located between the neighbouring layers of the epitheca (i.e., between the contacting walls). It consists of optically homogeneous calcite and can be up to 0.03 mm in thickness (Fig. 5C and D), separating walls of the adjoining corallites. Its nature remains unclear and the origin is most likely diagenetic.

Owing to their thinness, the intratheca and the epitheca may become dissolved, probably by diagenetic merging of their calcite with the calcite of adjoining parts of the wall. The term "*inter-wall suture*" may be applied for an intercorallite contact with no epi- and intra-theca. This term is a translation of the

Fig. 5. (A) The first (I) type of corallite wall. *Mesofavosites differens* Preobrazhenskij, No. 536-5a/4. Transverse section. Central Taimyr, Tareja River. Andrej Formation, lower part (Lower–Middle Llandovery). (B, E) Thin structure of septal spines. *Mesofavosites verus* Leleshus, No. 115-1. Western Slope of North Urals, Kozhym River. Lolashor Formation (Llandovery, Aeronian). (C) The second (II) type of corallite wall. *Mesofavosites dualis* Sokolov, No. 547-6/2. Transverse section. Central Taimyr, Tareja River. Mutninskaja Formation (Uppermost Ordovician) (D) The third (III) type of corallite wall. *Mesofavosites moyeroensis* (Sokolov et Tesakov), No. 121-2. Longitudinal section. Western Slope of North Urals, Kozhym River. Lolashor Formation (Llandovery, Aeronian) Scale bars in mm. Abbreviation: i – intratheca; e – epitheca; d – dark peripheral layer; m – mesotheca; st – inter-wall sutura; gl – growth lamination; mc – mesothecal core; ms – pseudotrabecular mesothecal segregations; sq – septal squamulae; s – septal spine.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Russian-language “mezhstennyj show” (Sokolov, 1955, 1962), used for the designation of all possible sorts of contact between corallites in cerioid colonies of the Tabulata. It should be noted that the inter-wall suture is especially typical of the Ludlovian, Přidolian, and Devonian Favositidae and is comparatively rare in the Upper Ordovician, Llandoverian, and Wenlockian representatives of the group.

5. The corallite wall microstructure and the stratigraphic record

The studied material allows distinguishing seven types (I–VII) of structural building of the corallite wall, differing both in microstructure and in combination of the above-described macroscopic parts (layers). Some intermediate forms also exist, which may be the result of inadequate preservation.

The simplest corallite wall (the first type (I)) consists of the bright cryptocrystalline mesotheca (about 0.05 mm thick) and the opaque cryptocrystalline dark peripheral layer (approx. 0.02 mm thick). The epitheca and the intratheca are absent and the contact between the neighbouring walls has no sign of the inter-wall suture, so the cryptocrystalline mesotheca in transverse section looks like a single innermost layer, which is common for the both adjoining corallites. The example is *Mesofavosites differens* Preobrazhenskij from the lowermost Llandovery of the Taimyr Peninsula. The species has been reported also from the Upper Ordovician of the North-East of Russia and Kolyma (Preobrazhenskij, 1968) (Fig. 5A). This type of corallite wall is uncommon among the Favositidae and shows definite similarity to several other Silurian Favositida genera, such as *Multisolenia*, *Mesosolenia* and *Subalveolites*.

The second type (II) is especially characteristic of the Upper Ordovician and Llandoverian Favositidae, although it can be found until the Devonian. In specimens of *Mesofavosites dualis* Sokolov from the uppermost Ordovician of Taimyr (Fig. 5C), the mesotheca, usually 0.060–0.075 mm thick, constitutes the main part of the wall. As seen in the figure, it has clearly marked growth laminae that pass laterally along the wall. The epitheca is represented by an opaque disrupted line up to 0.003 mm thick between the mesotheca and almost transparent cryptocrystalline intratheca (about 0.03 mm thick) from the other side.

The most complicated type of the wall is the third type (III), occurring in the Middle Llandovery (Aeronian)–Wenlock Series. It differs from the preceding by the pronounced dark peripheral layer (Fig. 5D), covering walls and septal spines.

A stereoscopic view of the tiny structure of a septal spine, enclosed in the highly transparent calcitic matrix, has been observed in a thin section of a comparatively well-preserved colony of *Mesofavosites verus* Leleshus from the Aeronian of the Western Slope of the North Urals (Fig. 5B and E). Inside a spine, there is an internal cryptocrystalline mesothecal core, covered with a thin-crystalline dark peripheral layer. Thin crystals of the peripheral layer are being combined into linear aggregates, which are exposed at an acute angle to the axis of a spine. The length of these aggregates is about 0.03 mm.

The crystalline microstructure of the dark peripheral layer may align it with the “cement A” sensu Oekentorp (2001). One may also conclude that, if examined in ultrathin sections, the “non- or crypto-crystalline” microstructure of the dark peripheral layer is in fact “thin-crystalline”. But, subject to the above-stated, it remains unclear why the dark peripheral layer has the specific stratigraphic range, being not usual or completely absent in many pre-Aeronian as well as in post-Ludlovian Favositidae. It may indirectly indicate that in some cases it is possibly a diagenetically transformed remainder of some biogenic part.

The corallite wall in elongated and ramose colonies of *Striatoporella* Rukhin has been referred to the fourth structural type (IV), quite similar to the second type (II), but differing by a gradual increase in the thickness of the mesotheca towards the outer zone of the colony, as in some other families (Pachyporidae, Theciidae, and Cleistoporidae). Being feebly marked in earlier species of *Striatoporella* (e.g., *Str. yermolaevi* (Therny-chev) from the Middle–Upper Llandovery of Taimyr), this feature is strongly expressed in the Přidolian and Lochkovian *Str. ramiferus* (Chekhovich), *Str. socialis* (Sokolov et Tesakov), and *Str. parastriatoporoides* (Dubatolov) from the North Urals and Tchernychev Uplift (Fig. 6C and D). In these species, the microstructure of the mesotheca transforms from the crypto- or thin crystalline in juvenile (internal) regions of colony to the pseudotrabecular in mature (peripheral) parts.

The fifth structural type (V) can be seen in the example of *Gephuropora* Etheridge, although also characteristic of some representatives of *Favosites* Lamarck (sensu lato). In the North Urals and Tchernychev Uplift, it ranges from the Upper Llandovery or the Lower Wenlock until the Lochkovian Series (Zaika, 2006). Its notable feature is the well expressed differentiation in thickness of the mesotheca in every single corallite, but, in contrast to *Striatoporella* Rukhin, the ontogeny is not relevant to this character. Thickened parts of the mesotheca are empha-

Fig. 6. (A and B) The fifth (V) type of corallite wall. *Gephuropora multispinosa* (Poulsen), No. 124-1. (A) A section of thin wall. Transverse section. (B) A section of thick wall bearing squamulae. Longitudinal section. Western Slope of North Urals, Kozhym River. Marshrutny Formation (? Upper Llandovery–Lower Wenlock). (C and D) The fourth (IV) type of corallite wall. *Striatoporella parastriatoporoides* (Dubatolov), No. 44-9. (C) A section of thin wall in axial (juvenile) part of colony. Transverse section. (D) A section of thick wall in peripheral (mature) part of colony. Longitudinal section. Tchernychev Uplift, Bolshaja Synja River. Ovinparma Formation (Lower Lochkovian). (E) The sixth (VI) type of corallite wall. *Squameofavosites thetidis* Chekhovich, No. 185-20. Transverse section in zone of corner contact of corallites with a “Y-shaped figure”. Tchernychev Uplift, Bolshaja Synja River. Ust’Syv’Yu Formation (Upper Přidolian). (F) The seventh (VII) type of corallite wall. *Paralleloporella favositiformis* (Holtedahl), No. 185-5. Transverse section. Tchernychev Uplift, Bolshaja Synja River. Ust’Syv’Yu Formation (Upper Přidolian). (G) A “Y-shaped figure”. *Mesofavosites versus* Leleshus, No. 115-1. Transverse section of corner zone of corallite contact. Western Slope of North Urals, Kozhym River. Lolashor Formation (Llandovery, Aeronian). (H) The fifth (V) type of corallite wall. *Favosites oculiporoides* Sokolov, No. 558-10/6. Transverse section. Central Taimyr, Tareja River. Upper part of the Andrej Formation (Llandovery–Wenlock boundary strata). Scale bars in mm. Abbreviation: i – intratheca; e – epitheca; d – dark peripheral layer; m – mesotheca; st – inter-wall sutura; gl – growth lamination; mc – mesothecal core; ms – pseudotrabecular mesothecal segregations; sq – septal squamulae; s – septal spine.

sized by well-developed squamulae or large cone-like spines, while thinned parts of the wall usually have ordinary septal spines (Fig. 6A and B). The fact that thick- and thin-walled corallites are being placed in close proximity within the same colony and on the same phase of its ontogeny indicates how irrelevant this character is to the *ante mortem* environmental conditions as well as diagenetic alterations.

The two following structural types are restricted to the uppermost Silurian and lowermost Devonian. The sixth type (VI), illustrated by *Squameofavosites* Tchernychev, is widely distributed in the Upper Přidolian and Lochkovian of the Western Slope of the North Urals and the adjoining regions. In contrast to all of the preceding types, its mesotheca shows a clearly visible transverse fibrous structure (Fig. 6E). This feature is combined with the well-developed septal squamules. The epitheca and the intratheca are present, sometimes being partly replaced with the inter-wall suture.

The type VII is characteristic of the genus *Paralleloporella* Holtedahl emend. Mironova, having almost the same geographic distribution and stratigraphic range as *Squameofavosites* Tchernychev. Its mesotheca has a strong transverse fibrous structure, but, unlike *Squameofavosites*, it is characterized by uniform thickness, determining the clear polygonal outline of the inner contour of the corallite, which is rounded in *Squameofavosites*. The epitheca, the intratheca, and the inter-wall suture seem to be reduced or poorly preserved. Septa are represented with long and straight spines, usually arranged almost perpendicularly to the wall median plane (Fig. 6F).

6. Discussion

The undertaken examination of the structure of the corallite wall, when related to the stratigraphic distribution of the Favositidae corals, suggests some structural differences between the stratigraphically older and younger representatives, as it has been shown on the material from the Upper Ordovician–Lower Devonian of the North Urals, the Taimyr Peninsula, and some other adjacent regions, that is, in the Palaeobaltic and Palaeosiberian shelf margins. As the Favositidae family is abundant in all the studied areas, it has been possible to compare collections from there and to find some similar traits in the stratigraphic range of several of the revealed types of corallite wall.

In particular, the stratigraphic range of the structural type I (three-layered) is restricted to the Uppermost Ordovician–Lower Silurian (Rhuddanian–?Lower Aeronian) (Fig. 4). The second type (II) (five-layered) is the most common among the Favositidae from the Uppermost Ordovician to Lower Devonian. The third type (III) (seven-layered) occurs in the Aeronian–Wenlockian Favositidae. The fourth type (IV) is rather rare in the Llandovery and Wenlock Favositidae and is common in the Upper Silurian to Lower Devonian Favositidae. The fifth type (V) (gephuroporoid) is characteristic of the Wenlockian–Lochkovian *Gephuropora* in the North Urals and archipelagos of the Barents Sea. Similar to this is *Favosites oculiporoides* Sokolov from Upper Llandovery–Wenlock Series of Taimyr (Fig. 6H). Types VI and VII are common in the Upper Přidolian and Lochkovian Favositidae (such as *Squameofavosites* and *Paralleloporella*) of North Urals, Chernychev Uplift, Bol'shezemel'skaja Tundra and some islands of Kara and Barents Seas (Chekhovich, 1965; Smirnova, 1970, 1981).

The main suggestion from the above-mentioned discussion is that the differences observed between the revealed structural types may at least partly have an evolutionary background (Fig. 4), reflecting primary structural peculiarities of the corallite wall.

The fact that most of these types have a uniform set of the principal parts with no sharp distinctions supports the belonging of the mentioned genera and species to the same family. At the same time, it should be noted that even among species of the same genus, different structural types have been distinguished. Particularly, types I, II, and III are characteristic of *Mesofavosites* Sokolov, types II, III, and V – of *Favosites* Lamarck. The possible explanation may be that some of these genera are formal but not natural (as has already been suggested: see, e.g., Powell and Scrutton, 1978).

The possible biological cause of the observed transformations is unclear. It may be supposed that in a living polyp, the secreting cells (calicoblasts) generated the corallite wall during some fixed phases of their cell cycle. In this case, the epitheca or the intratheca can be imagined as products of initial phases of secretion, followed by the other phases ("mesothecal" and "peripheral") in a cycle of calicoblast secretion. Every following cycle of secretion should be accompanied by (1) renovation of secreting cells, then (2) by the dislocation of the polyp upward, and (3) by the following secretion of the same set of parts of the wall. The presence of growth laminae in the mesotheca may show periodical hesitation and recommencement of the growth during the phase of mesothecal secretion. The assumption of periodical renovation of secreting cells corresponds well with the previous assumption on high regeneration capability of the Favositidae corals (Schouppé and Oekentorp, 1974; Dubatolov, 1974).

Hypothetically, the types of the wall structure, mentioned above, might have evolved as the sequence of phases of secretion, transforming through time. Primarily, during the Late Ordovician and Early Silurian (Llandovery and Wenlock), the process of secretion had become more complicated, involving up to five phases (Fig. 7). Subsequently, simplification of the secretion began, possibly coinciding with elimination of several phases. Its most advanced form is the corallite wall of some Přidolian and Lochkovian Favositidae, consisting almost only of the mesotheca. Along with that, prolongation of the mesothecal secretion and enlargement of mesothecal elements (or their biogenic predecessors) took place during the Silurian–Early Devonian time.

Any precise conclusions on the ways of biogenic formation, growth, and evolution of the corallite wall in the Favositidae seem to be problematic at the moment for two reasons. First, the diagenetic transformation of the primary microstructure is unquestionable. Second, there is a possible functional analogy between the Tabulata corals and the modern Anthozoa. Further studies are needed both on the fine structure of the wall and on stratigraphic distribution of its different types involving all the suitable material from all possible regions.

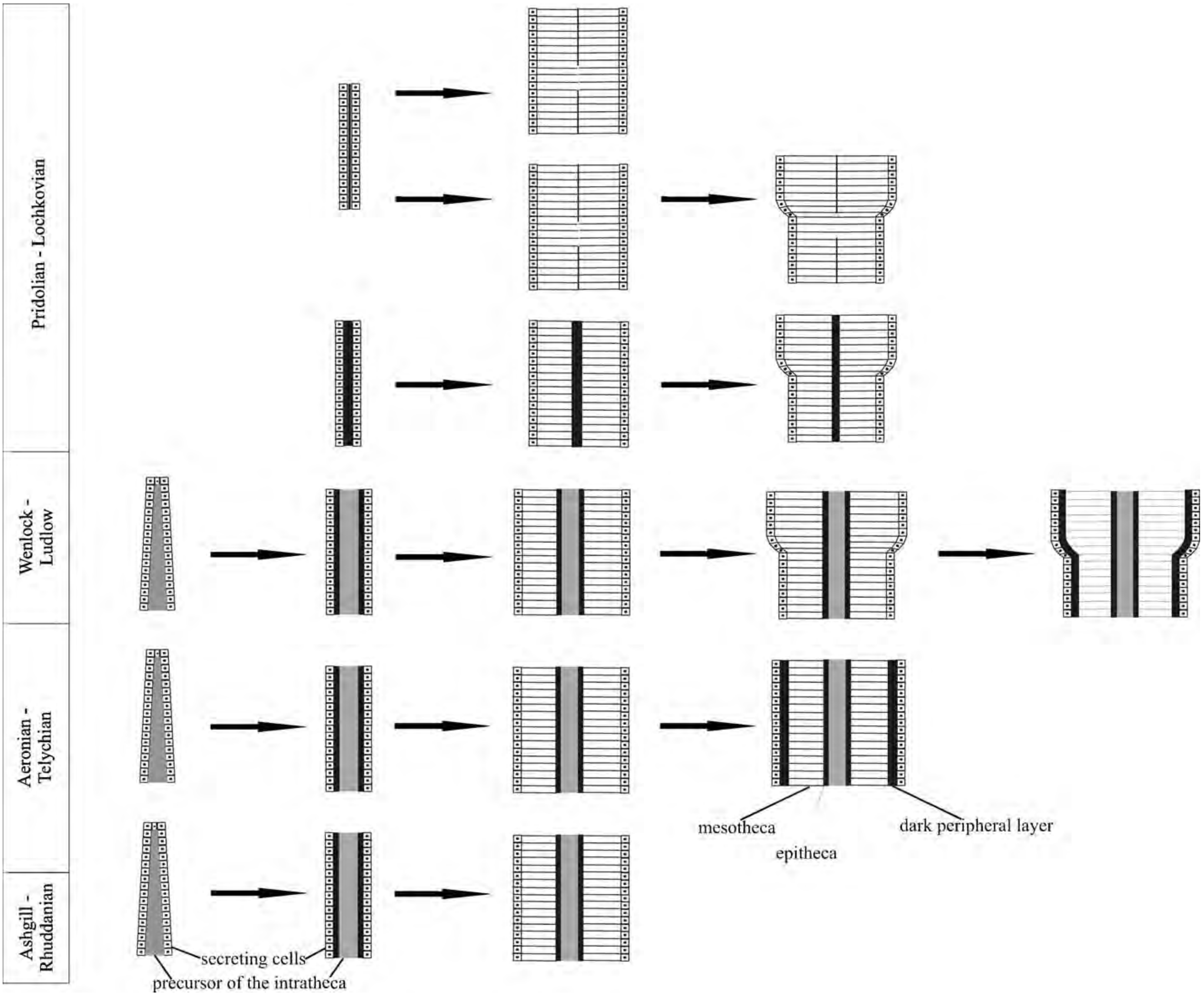

Fig. 7. Possible scheme of evolution of the corallite wall morphogenesis in Favositidae corals.

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Research paper

Remarks on the classification system of the Heliolitida

Narima K. Ospanova

Tajik Academy of Sciences, Institute of Geology, 267 Ayni str., 734063 Dushanbe, Tajikistan, Russian Federation

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Abstract

The concept of the sum of common features has been used in order to compare the Heliolitida with the Tabulata and Rugosa and determine the position of Heliolitida in the classification system of Palaeozoic corals. Such morphological characters as the number of septa, septa of the second order, epitheca, coenenchyme and multiplicity by four have been considered. Coenenchyme is present in many taxa and there are no more compelling reasons for the integration of Heliolitida and Halysitida than for the integration of Heliolitida with other taxa containing coenenchyme. The dynamics of some features shows that the differences between three main groups of Palaeozoic corals are within the limits of variation of relative organisms. A high degree of similarity testifies to the close relationship of the Heliolitida and the different qualitative and quantitative expression of similar features testifies to their early divergence from a common ancestor and subsequent independent evolution. Asto-phylogeny and morphological homogeny of all Heliolitida confirm their evolution as a separate, unitary group. Heliolitida is a monophyletic group of corals that is equal to the Tabulata and Rugosa in rank. A common origin requires that the orders should be united into one subclass Paleosclerocoralla of the class Anthozoa.

Keywords: Tabulate corals; Heliolitida; Classification; Coenenchyme; Phylogeny; Palaeozoic

1. Introduction

Sokolov (1955, 1962) examined the different views on the Heliolitida genesis and their relationship with other groups of Coelenterata (Tabulata, Hexacoralla, Rugosa, Alcyonaria, and Hydrozoa). He established the differences and independent development of that group of corals from other groups of Coelenterata and concluded that the Heliolitida is a separate taxon that is equal to the Tabulata and Rugosa in rank. His view has been supported by many Russian and Chinese, as well as some American, palaeontologists. For example, Oliver (1996) proposed that Heliolitida most likely had a tabulate ancestor; however, it can be considered as the separate taxon that is equal to the Tabulata and Rugosa in rank (Fautin et al., 2000). Another view is that the Heliolitida is a part of the Tabulata (Hill, 1981; Scrutton, 1997; Chatterton et al., 2008). Thus, there is no consensus on the systematic position of Heliolitida.

The study of the Heliolitida of Central Tajikistan has been carried out by the author for many years. This work has been done by comparing with the collections of Heliolitida and some Tabulata from other regions – Kazakhstan (Alma-Ata, 1979), Estonian (Tallinn, 1985; Leningrad, 1986), Russia, Ukraine (Leningrad, 1986), Uzbekistan (Kitab State Geological Reserve, 1986–1987; Tashkent, 2008), and Ural (Sverdlovsk, 1988, 1991). The results of these studies and a discussion of the systematic position and taxonomic level of the Heliolitida are presented below.

2. About the rationale

Only one character is usually taken as the basis for establishment of the relationship between different taxa of Palaeozoic corals and their systematic constructions. For example, the presence of coenenchyme unites the Halysitida (or the separate genus of them) and Heliolitida into one taxon. Klaamann (1975) assumed that the genus *Cystihalysites* could be considered as a katenimorph form of Proporida. Hill (1981) combined the suborders Halysitina and Heliolitina into one order, Heliolitida. Bondarenko (1992) included the tabulate genus *Spumeolites* in the superorder Heliolitoidea. Another example concerns spicules that have been found in some Silurian corals (Chatterton et al., 2008). Discovery of spicules in *Favosites* and *Heliolites* testifies to the close relationship of Favositina and Heliolitina.

E-mail address: ospanova2005@mail.ru.

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Table 1
Comparison of complexes of basic morphological features of the three main groups of Palaeozoic corals.

Features complexes	Taxa (subclasses, orders or superorders)		
	Heliolitida	Tabulata	Rugosa
Mode of growth	Only colonial	Colonial, as exclusion solitary	Colonial and solitary
Type of colony	Only massive	Massive, hemi-massive, fasciculate	Massive, hemi-massive, fasciculate
Corallites (in cross-section)	Rounded, stellar, polygonal	Rounded, oviform, polygonal, vermiform, semilunar, meandering	Rounded, polygonal, semilunar
Axial structure	Tubes, columns, plates, spines	Tubes, columns, plates, spines	Tubes, compound columns, plates
Tabulae	Horizontal, concave, swollen, incomplete, vesicular	Horizontal, concave, incomplete, funnelform	Complete, incomplete, compound, axial
Septa	Lamellae, spines, septal modification	Spines, rare ridges and lamellae	Lamellae, spines
Number of septa	12 (rare 6)	From 1 to 24 (32)	From 24 to 120
Septa of the second order	Absent	Absent	Present
Serial insertion of septa	Absent	Absent	Typical
Rolling of septa	Uncharacteristic	As an exclusion	Frequent
Fossula	Absent	Absent	Frequent
Walls of corallites in colony	One-layer	Two-layer and three-layer (more numbers of layers are due to pigmentation and secondary deposit of stereoplasma)	Two-layer and three-layer
Epitheca	Only at the base of colony	Around corallites or chains of corallites	Around corallites or colony
Mural pores	Absent	Frequent	As an exclusion
Coenenchyme	Present	Frequent	Rare
Asexual reproduction	Gemmation (coenenchymal)	Division, gemmation	Division, gemmation, fragmentation
Multiplicity by four	Almost always	Periodic	Almost always
Auloporoidity	Uncharacteristic	Present	Present

A separate similar feature can testify, with the same probability, both to the possibility of relationship and to casual similarity or convergence (common function). For example, similarities in spicule form between tabulate corals and the alcyonaceans may simply reflect common function rather than close ancestry (Chatterton et al., 2008). The higher probability of similarity suggests a higher probability of relationship. Thus, the concept of the sum of common features has been used in order to compare the Heliolitida with the Tabulata and Rugosa and to determine the position of Heliolitida in the classification system of Palaeozoic corals: closely related taxa of high level (subclasses, orders or superorders) must have the sum of common features. Similarities and differences between these three main groups of Palaeozoic corals are given in Table 1.

It is difficult to analyze all characters within a single article and thus only some of them are examined here.

3. Examination of some features

3.1. *The number of septa*

The presence of septa is an important characteristic of Palaeozoic corals. It is possible to see in Table 1 that the number of septa varies in different taxa. During a study of the dynamics of this feature, it can be observed that the number of septa depends on the diameter of the cavities of polyps.

As a rule, the number of septa in the Heliolitida and Tabulata colonies is higher in the darker mature zones than in the light ones. The number of septa in the Rugosa is less in rejuvenation zones where diameter of corallites decreases. Sometimes the septa can be observed only in the dark zones and there are no septa in light ones. For example, the diameter of corallites in *Laceripora uralica* in the axial area measures 0.4–0.8 mm and at the periphery makes 0.9–1.1 mm. There are no septa in the axial zone or they are developed in the number of 1–3, whereas the number of septa at the periphery increases up to 6 (Barskaja, 1965). The number of septa in colonies of *Palaeocorolites* increases in accordance with the growth of corallites' diameter at the periphery (Leleshus, 1965). The genus *Lecfedites* was established by Oliver (1975) due to presence of two types of corallites – large with septa, and small without them. The same variability is observed between different species and genera. For example, *Subalveolites elegans* has the smallest diameter of corallites compared to the other species of this genus and only one row of spines for each facet of the wall. The other species of this genus have larger corallites and several rows of spines for each facet of the wall (Chekhovich, 1971). Genera with small corallites (*Subcaliapora*, *Coenites*, *Tyrganolites*, and *Tuvaelites*) can have only one septal crest or one row of spines in corallites (Chekhovich, 1971). It is also known that the number of septa in some rugose corals with permanent growth increases during their whole life together with the diameter of corallites. The dependence of the number of septa on the diameter of corallites in Chaetetida was mentioned by Solovjeva (1980) who considered Chaetetida as probable Tabulata (Solovjeva, 1986).

The established dependence of the number of septa on the corallites' diameter can explain why the Rugosa have the highest number of septa. The heliolitids have the smallest diameter of corallites (not more than 6 mm); the number of their septa is usually not more than 12. The higher number of septa is connected with the multitrabecular structure of the wall (as in *Propora speciosa*) or secondary deposition of stereoplasma, i.e., it is not a characteristic feature for Heliolitida due to their rarity. The Tabulata can have larger diameter corallites and a higher number of septa (Table 1). Rugosan corals have the greatest diameter of corallites and highest number of septa. Based on these facts, it is not clear how the number of septa should correspond to the definite corallites' diameter, because many factors have influenced on the growth of each species – genetic and ecological. However, we can see a trend of development (the larger corallites have the higher number of septa) that is characteristic of all groups of Palaeozoic corals and explains the difference in number of septa in the Rugosa on the one hand, and the Tabulata and Heliolitida on the other hand. It seems that the largest rugose corals have been found in Middle Asia. In the section of Isfara (Pridoli, Central Tajikistan), I have observed solitary Rugosa (?*Mucophyllum*) with corallite diameters not less than 20–30 cm. Erina (2007) has described from the Chashman-Kalon and Shachriomon-2 sections (Upper Ordovician or Lower Silurian, Uzbekistan) the solitary rugose *Pseudophaulactis lycophylloides* Zaprudskaya and Ivanovsky with corallite diameters of 45 cm.

As the degree of development of septa reflects the degree of complication with the coelenteron of polyps, it is possible that divergence of these three groups of corals was connected with different food requirements that have allowed them live in the same or close biotopes (Ospanova, 2005).

3.2. *Septa of the second order*

I consider the development of septa of the second order in Rugosa as reduplication of septal apparatus that has taken place during formation of this group. It could be connected with the larger corallites compared with corallites of the Tabulata and Heliolitida, which have no septa of the second order (Table 1). An inverse relation could also exist: the appearance of septa of the second order has supported the increasing diameter of corallites. However, the basic cause of the largest sizes of the Rugosa polyps consists in their later maturing. As a rule, corallites of the Heliolitida become mature after growth of several parts of one millimeter. Corallites of the Tabulata become mature after about 1 mm growth, and corallites of the Rugosa (especially solitary) become mature after growth of one or several centimeters. Thus, it could be expected that the largest diameter corallites would be in the Rugosa. It is known that the final sizes among the relative organisms are larger in those which become mature later. In addition, palaeontological data corroborate this rule: displacement of the maturity on the earlier stages of development of organisms due to neoteny or paedomorphosis accompanied by a decrease of final sizes. The differential of corallites sizes among three main groups of Palaeozoic corals lies within the limits of variation of relative organisms. Thus, we should consider not only divergence on food requirements between them, but that formation of these groups of corals was connected also with the divergence on the rate of maturation among the different members of the ancestral group.

3.3. *Epitheca*

Epithecal rings exist around each corallite in cerioid and fasciculate colonies of Tabulata and Rugosa, corallites chains in hemi-massive colonies of some Tabulata, and the whole colony from the outside in the case of plocoid colonies of Rugosa. In cerioid and fasciculate colonies, the epitheca develops around a new corallite soon after its appearance and then the parent and daughter corallites grow independently of one another. "Hemi-massive" is a collective name for the colonies which are transitional between massive and fasciculate colonies. There are among them genera that have areas of massive and fasciculate structure in the same colony (such as *Eofletcheria* or *Duncanopora*), and also genera with partially connected and partially disconnected adjacent corallites (such as *Spumeolites* or *Hexismia*), and genera with single-row and multi-row chain structure of colonies (such as *Halysites*, *Catenipora* or *Tollina*). In some hemi-massive and plocoid colonies, the cavities of polyps have been connected directly when the epitheca has been reduced, so the epitheca can ring around the chains or groups of corallites from the outside. It shows that the epitheca in Palaeozoic corals was as individualization mean of polyps: if the epitheca was reduced, the theca could also be reduced so that the cavities of adjacent polyps were joined directly.

In the Heliolitida, epitheca can develop only at the base of the colony and never in the walls of corallites. It can be recovered in places of traumatism of the colony (e.g., Chatterton et al., 2008); in these cases, however, the epitheca is also common for corallites and coenenchyme. Absence of the epitheca between the different components of colony in all Heliolitida testifies to an early beginning of this feature in the evolution of this group. In fact, we can see the absence of the epitheca between corallites already in the oldest Heliolitida, which have entire trabecular–bacular structure. There is no distinct border between corallites and coenenchyme or between corallites in such forms. One of them is shown in Fig. 1.

In the Tabulata and Rugosa, the epitheca not only develops around new corallites of the colony but also remains between corallites in the case of transformation of a fasciculate colony into a massive colony, and as a result, two-layer or three-layer walls appear between the cavities of polyps. However, Heliolitida always only have single-layer walls due to the absence of the epitheca in the walls of corallites. It can testify that heliolitide corals had not arisen from the result of the joining of separate solitary corals, as supposed by Lindström (1899). Coloniality of the Heliolitida is an ancient character and is observed in all taxa. Hence, not only the permanent presence of coenenchyme is the characteristic of the Heliolitida, but also single-layer walls in corallites of the colony.

3.4. *Coenenchyme*

Coenenchyme is a connective tissue between polyps of the colony that also plays the role of general-colonial zone of growth and gemmation in case of its broader development (Beklemishev, 1964). Different types of intercorallite skeleton come under this definition, and thus the differ-

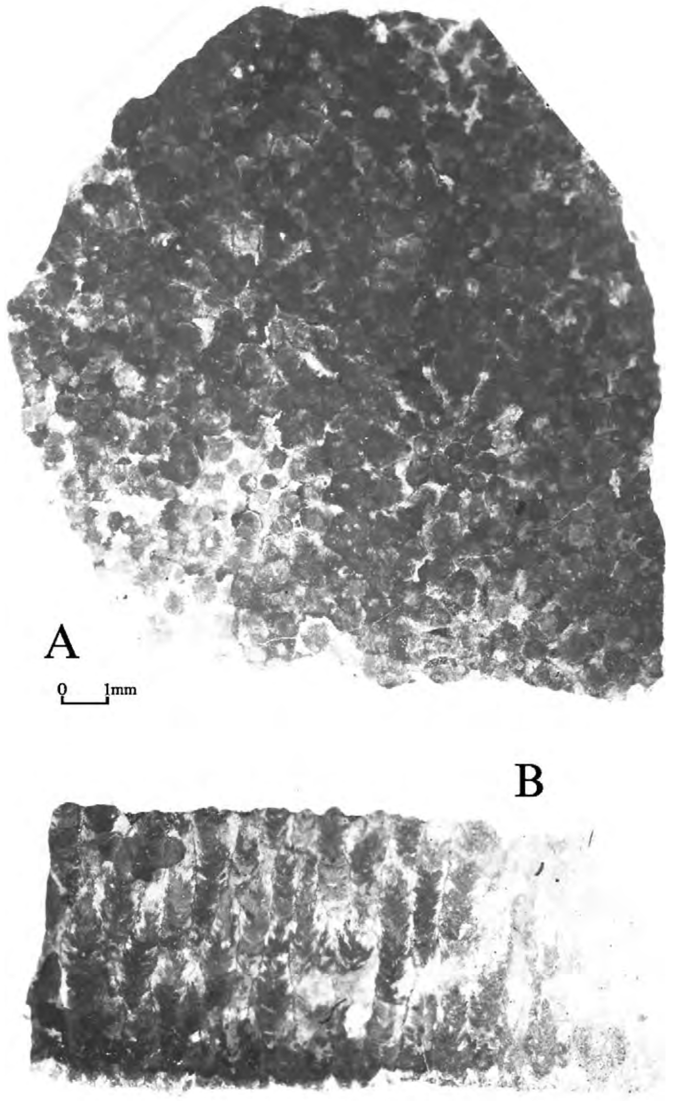

Fig. 1. *Coccoseris ungerni* Eichwald, 1855. (A) Transverse section, (B) longitudinal section; corallum 118/599, from the Vormsi Formation (Upper Ordovician, lower Ashgillian) of Estonian; the clear borders between corallites and between corallites and coenenchyme is absent. Collection by B.S. Sokolov N 599 (VNIGNI) in St.-Petersburg.

ent types of intercorallite connective tissue should also be considered as coenenchyme. Preobrazhensky (1982) suggested, for the Palaeozoic corals, tubular coenenchyme (suborder Syringoporina), lamellar coenenchyme (Sarcinulidae and Thecostegitidae), porous coenenchyme (*Lyopora favosa*, *Cleistopora*), and membranous coenenchyme (Heliolitida, *Halysites*, *Cystihalysites*, *Spumeolites*, *Hexismia*). To this can be added membranous coenenchyme in plocoid colonies of Rugosa and Cyrtophyllida. I summarize the first appearance of coenenchyme in different Palaeozoic corals briefly as follows.

3.4.1. Tubular coenenchyme of Syringoporina

Tubular coenenchyme of Syringoporina has a zooid nature (Ospanova, 1998). It is clear from its structural characteristics:

- outgrowths can increase in diameter and become normal buds, more often at the periphery of the colony where there is sufficient space;
- as a rule, the growth of tubes begins from one of the corallites, not necessarily from two corallites synchronously;
- development of "blind" outgrowths, i.e., without the achievement of a neighbor corallite;
- if the epitheca is preserved, outgrowth does not fuse with the other or with the neighbor corallite.

Zooid character of outgrowths is emphasized not only by their ability to transform into normal buds, when possible, but by more intensive development of connective tubes, often in the early stages of colony growth when there is the more intensive number of normal buds.

Modeling of the process of formation of syringoporoid habit of the colony suggested that the connective tubes arose in consequence of invalid budding, when the young buds stayed half-grown due to the compact growth of corallites (for more detailed discussion see Ospanova, 1998). They became the connecting peritheca in the process of establishing this feature as genetically fixed.

3.4.2. Lamellar coenenchyme of Thecostegitidae and Sarcinulidae

Thecostegitidae arose from the oldest Syringoporina, probably the genus *Tetraporella* (Chudinova, 1986). Decompaction of corallites and transformation of connective tubules into more extensive horizontal and slightly undulating offshoots led to the development of lamellae.

The probable ancestor of Sarcinulidae is *Lyopora* (Sokolov, 1955). It is characterized by having empty spaces (pores) between septal trabecules. Increase of soft tissue into empty spaces led to the appearance of lamellae. Preobrazhensky and Klaamann (1975) regarded the development line *Lyopora*–*Calapoecia*–*Sarcinula* as probable. The number of pores in *Lyopora* (24) coincides with the number of lamellae in *Calapoecia* and *Sarcinula*.

3.4.3. Porous coenenchyme of *Lyopora favosa* and *Cleistopora*

Lyopora favosa is characterized by the presence of pores in the form of a grate in the wall, and the narrow zones (no more than 0.5 mm) of the rounded corallites were considered coenenchyme (Preobrazhensky and Klaamann, 1975).

Cleistopora has very thick walls of corallites and a disorderly porosity. The pores change into the bent canals and cavities (Sokolov, 1955, 1962). Preobrazhensky (1982) regarded them as a special type of coenenchyme.

3.4.4. Membranous coenenchyme

Halysites, *Cystihalysites*, *Spumeolites*, *Hexismia*, Heliolitida: Preobrazhensky (1982) recognized a relationship between Halysitida and Heliolitida not only in the presence of coenenchyme but also in the coincidence of their geological time range. Distribution of forms without coenenchymal structures was confined by the geological time range of Billingsariidae

(Middle–Upper Ordovician), excluding the genus *Catenipora* (Upper Ordovician–Upper Silurian), but the time of appearance of forms with coenenchyme coincidences with the time of appearance of Heliolitida late in the Ordovician (Preobrazhensky, 1982).

Some facts argue against these estimates:

(1) The time of extinction of the forms with and without coenenchyme is the same, because *Quepora* (coenenchyme absent) and *Cystihalysites* (coenenchyme present) have been found in the Lower Devonian (Wright and Bourque, 1980; Wright and Byrnes, 1980). It appears from this that either Lichenariida became extinct in the Devonian or forms that Preobrazhensky referred to as Lichenariida (*Catenipora*, *Vacuopora*, *Tollina* and *Quepora*) are not Lichenariida.
(2) There are morphological transitions between tabulate forms with and without coenenchyme. Some areas with and without coenenchymal structures occur in the same colony (Buehler, 1955).
(3) The appearance of coenenchymal structures is fixed in different branches of corals connected with Lichenariida and not connected with Heliolitida directly. Many investigators pointed to the affinity of Halysitida to Lichenariida (Sokolov, 1955, 1962; Flower and Duncan, 1975; Preobrazhensky, 1979, 1982; Minzhin, 1981) and sometimes to Auloporida (Minzhin, 1981), for example, *Eocatenipora*. It is important that the relationship between Halysitida and Lichenariida is clearly established.

There are also differences between Halysitida and Heliolitida. (1) The number of septa of Heliolitida is fixed and equals 12, but Halysitida could have 16 septa or less than 12. (2) There were axial increases of corallites of Halysitida (Wright and Byrnes, 1980; Lee et al., 2007), which has never been recorded in Heliolitida. (3) The greatest peculiarity of Heliolitida is the vertical or inclined-up arrangement of septa. Halysitida have horizontal arrangement of septa like all the other Tabulata. (4) The appearance of lacunae or divergence (separation) of corallites from one another is characteristic for all of the Tabulata because of epithecal rings around each corallite in a colony. In Heliolitida, the epitheca occurs only at the base of a colony and never in the walls, so corallites of Heliolitida might not separate from a colony.

Preobrazhensky (1982) supposed that the genus *Halysites* arose from the genus *Heliolites* and the genera *Cystihalysites* and *Spumeolites* arose from the genera *Propora* or *Plasmoporella*. However, the presence of the epitheca only at the base of colonies of Heliolitida means that the soft body of Heliolitida was uninterrupted. Appearance of breaks in the entire soft body is a physiologically impossible trend. So, neither *Heliolites* nor *Propora* could be an ancestor of Halysitida (Ospanova, 1993). The beginning of coenenchyme can be observed just in the hemi-massive colonies of Tabulata (Figs. 2 and 3).

The same can be said about chain colonies: coenenchyme develops in the thick part of wall and does not exceed the total thickness of two adjoining corallites (Fig. 4).

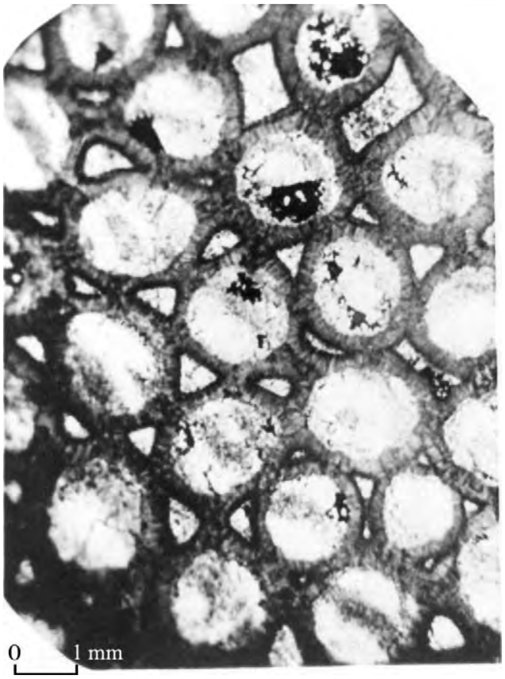

Fig. 2. The beginning of the development of coenenchyme in colonies of *Halysites compactus* Rominger with a hexismiid morphotype: the epitheca is reduced at the interfaces between corallites and preserved in the places of partial divergence (separation) of them, where there are lacunae. Transverse section; corallum 8543, Michigan, Manistiques River, near the basis Manistiques Formation (from Buehler, 1955).

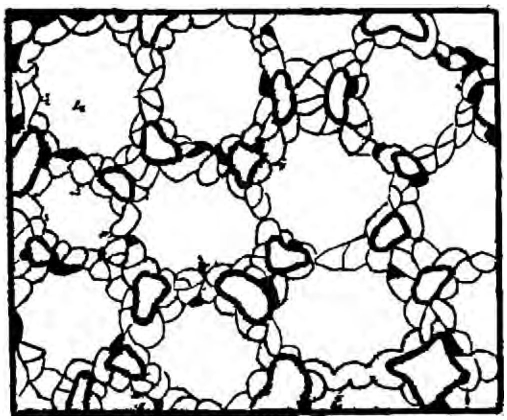

Fig. 3. The structure of *Spumeolites sokolovi* Zhizhina: the epitheca is present only in the places of partial divergence (separation) of corallites from one another and absent at the interfaces between them, where coenenchyme develops. Transverse section; holotype 345 b/1/8742, East Taimyr, Lower Taimyra River, Silurian, Llandovery (from Zhizhina, 1967).

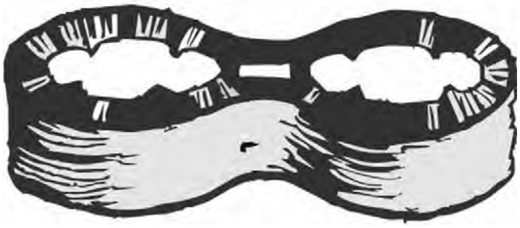

Fig. 4. Schematic sketch of a chain of two corallites of *Halysites*: coenenchyme develops at the interfaces between corallites where epitheca is absent, so its length does not exceed the total thickness of two adjoining corallites. Epitheca surrounds the chains on the outside.

Plocoid Rugosa: The appearance of plocoid colonies of Rugosa (e.g., Cystophoridae, Lonsdaleiastraeidae, *Taimyrophyllum*, *Billingsastraea*, *Phillipsastraea*, *Endophyllum*, etc.) was a consequent stage of the specialization of pleonophoran forms. The reduction of intercorallite walls led to the fusion of dissepimentariums and sometimes of the septa of adjacent corallites. Fused peripheral parts of corallites played a role of coenosarc because they were a zone of food distribution, connection between members of colony and gemmation. Plocoid Rugosa had the same morphotype of colonies as Heliolitida. The epitheca was present only on the outside of the colony.

Cyrtophyllidae: The position of Cyrtophyllida among Paleozoic corals is questionable. They are not Heliolitida (Ospanova, 1980). Fomin (1974) supposed they arose from forms similar to Lichenariida. Increase of distance between the compact corallites was accompanied by appearance of coenenchyme. There are the rests of intercorallite walls in the coenenchyme of Cyrtophyllida.

Thus, coenenchyme developed in the different groups of Palaeozoic corals (Tabulata, Heliolitida, and Rugosa). The different qualitative and quantitative expression was connected with the various ways of origin and a different genetic base of initial forms. However, there is a general similarity in its appearance: coenenchyme developed where the epitheca was reduced. The presence of coenenchyme in different taxa shows no compelling reasons for integration of Heliolitida and Halysitida than for integration with the other taxa containing coenenchyme.

3.5. Multiplicity by four

Multiplicity by four is widespread in all groups – Heliolitida, Tabulata, and Rugosa (Table 1). It is fixed in diverse representatives in different variants – in the number of septa or tentacles, quadrilateral forms of corallites, in the number of corallites' fold of the walls, etc. It has been considered briefly before (Ospanova, 2003). This integral peculiarity of Palaeozoic corals highlights the common ancestor for them.

4. Phylogenetic implications

Table 1 shows the three main groups of Palaeozoic corals (Tabulata, Heliolitida and Rugosa) with the sum of common features, and thus testifies to their close relationship. However, qualitative and quantitative expression of similar features is different in different groups, and that testifies to their early divergence from a common ancestor and subsequent independent evolution. Only some features (number of septa, septa of the second order, epitheca, coenenchyme, and multiplicity by four) have been considered above. In reality, the similarity is greater. All groups have the same types of septa (spines, lamellae), and also axial structures (plates, columns), and some identical types of microstructure (monacanths, rhabdacanths). If we move down to the ancient forms, similarity will increase. Sokolov (1955) and Ivanovsky (1965) showed that only the sizes distinguish the oldest Rugosa from the Tabulata in many cases.

Flower and Duncan (1975) regarded the genus *Lichenaria* as a probable ancestor of the rest of Palaeozoic corals. However, they did not explain how a huge morphological diversification of all corals can develop from such a simply arranged form as *Lichenaria*. For example, there are no intermediate forms between *Lichenaria* and Heliolitida. Obviously, their point of view is theoretically incorrect (Ospanova, 1991). Their scheme (Flower and Duncan, 1975, text-fig. 1) does not clarify what the Heliolitida represents. For example, they attributed the origin of part of the heliolitids to *Cyrtophyllum* that has no root in their scheme. They also took Coccoseridina out from *Lichenaria* through some tabulate genera (*Saffordophyllum*–*Trabeculites*–*Nyctopora*), assuming that the strengthening of trabecularity took place. In such a case, it should find forms with trabecular structure in younger deposits. However, forms with solid trabecular–bacular skeletons are the oldest among the heliolitide corals and disappeared in the Upper Ordovician. Many trends of the Heliolitida development testify to the decrease of trabecular–bacular complexes and replacement of solid skeleton by a skeleton with hollow structure – hollow corallites with septa and tabulae (Fig. 5), hollow coenenchymal tubes with diaphragms (e.g., genus *Acidolites* and others), and vesiculae. For example, representatives of the genus *Ellisites* with predominantly vesicular skeletons are more likely to have evolved from representatives of this genus with predominantly trabecular skeletons, and the genus *Ellisites* evolved from *Coccoseris* (Dixon et al., 1986). These investigations show a clear phylogenetic link between the Coccoseridicae and Proporicae (Dixon et al., 1986). Connection of Coccoseridina with the different Heliolitina has also been showed by Sokolov (1962) and Bondarenko (1982, 1983) earlier. Both asto-phylogeny and the complex of morphological features indicate a relationship of the suborder Coccoseridina with the two other derivative suborders of Heliolitida (Proporina and Heliolitina).

Thus, Flower and Duncan's scheme is not confirmed neither by phylogenetic nor chronostratigraphic data. Heliolitida is a monophyletic group. The morphological homogeny of all Heliolitida is as follows:

(1) Twelve-radial symmetry of corallites is outlined in Coccoseridina and preserved in the other Heliolitida.
(2) Vertical or inclined-up arrangement of septa in Coccoseridina makes conditional upon vertical or inclined-up arrangement of skeletal baculae and trabeculae that are normal to the soft body (Fig. 1B). Such orientation of septa is preserved in younger Heliolitida. Arrangement of septa is a significant feature for distinguishing different groups of Palaeozoic corals. Only Heliolitida among all other groups of Palaeozoic corals has vertical or inclined-up arrangement of septa.
(3) Absence of the epitheca in the walls of corallites in the colony.

Thus, not only 12-radial symmetry and the permanent presence of coenenchyme are distinguishing peculiarities of the Heliolitida as of the entire group, but also vertical or inclined-up arrangement of septa and the total absence of the epitheca in the walls of corallites. Such arrangement of septa is absolutely uncharacteristic for the Halysitida or the other Tabulata.

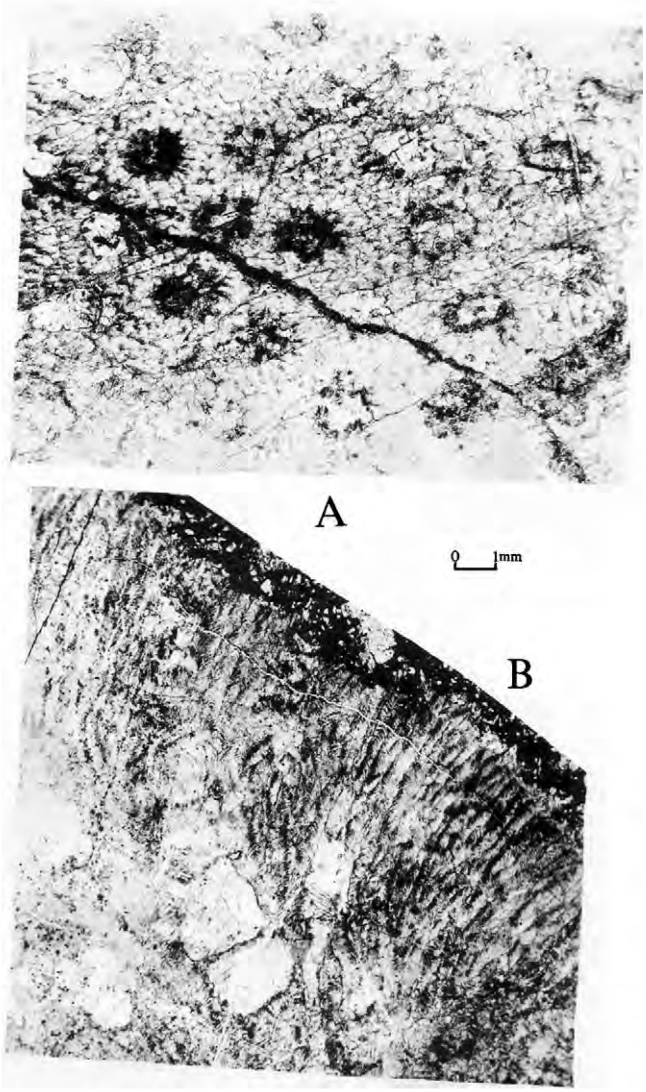

Fig. 5. *Starshininites pshanzensis* Ospanova n. gen. n. sp. with hollow corallites and solid coenenchyme; (A) transverse section, (B) longitudinal section; holotype No 11687-19, from Upper Ordovician (middle Ashgillian, Archalyk beds) of Zeravshan mountain, the upper reaches of the river Takphon, locality Pshanza. Sample was collected by V.I. Lavrusevich (1983).

Therefore, it can no longer be considered that Heliolitida is only a subdivision of Tabulata but rather as an independent group that is equal to the Tabulata and Rugosa in rank. The Heliolitida has evolved as a separate, unitary group.

Regarding the Tabulata, Heliolitida and Chaetetida as closely related taxa, Sokolov (1971) joined them in the subclass Tabulatomorpha Sokolov, 1971, or Tabulata. He did not include in this subclass the Rugosa. However, the Rugosa is closely related to the Tabulata and Heliolitida. The origin of the Heliolitida, Tabulata, and Rugosa from a common ancestor requires that these orders be united into one subclass. It cannot be the subclass Tabulata or Tabulatomorpha Sokolov due to another meaning of that subdivision by the author (Sokolov, 1971). Ivanovsky (1990) has proposed to divide Zoantharia s.l. into two subclasses – Zoantharia s. str. (without skeleton) and Sclerocorallia (corals with carbonate exoskeleton). He has also included in the last subdivision Scleractinia. However, scleractinian corals represent another (Mesozoic–Cenozoic) stage of evolution of corals. The name Paleosclerocoralla was proposed for the subclass that includes Tabulata, Heliolitida, and Rugosa (Ospanova, 2007). That name reflects such characteristic peculiarity as the presence of sclerosepta in all of them and its old age (Palaeozoic). It seems that only some Chaetetida can be included in this subdivision: Solovjeva (1986) pointed out the necessity of their revision.

5. About the rank of Heliolitida

The rank of Heliolitida is interpreted differently – from a family to subclass or superorder. It has been considered as a family by such investigators as Lindström (1873, 1899), Nicholson (1879), Kiaer (1899, 1904), Jones and Hill (1940), Hill and Stumm (1956), Dixon (1974), and Noble and Young (1984). Lecompte (1952) regarded it as a suborder. Heliolitida has been considered as an order by Wentzel (1895), Abel (1920), Hill (1981) and other investigators (Bondarenko, 1980, 1982; Dixon et al., 1986; Chatterton et al., 2008). Heliolitida has also been considered as a subclass (Bondarenko, 1958; Sokolov, 1962; Mironova, 1974; Lin and Chow, 1977; Li and Lin, 1982) or a superorder (Sokolov, 1971; Bondarenko, 1992).

This review shows that the taxonomic level of the Heliolitida has been considered differently not only by various investigators but it has been interpreted differently by the same investigators at different times. Most scientists accept the Rugosa at the rank of order. Regarding the Heliolitida as closely linked with the Tabulata and Rugosa, I suppose its rank to be order. Ivanovsky (1990) has also emphasized that if we make a common classification system for ancient and modern corals, the rank of such subdivisions as Tabulata, Heliolitida or Rugosa must be not higher than order.

6. Conclusions

The three main groups of Palaeozoic corals – Heliolitida, Tabulata, and Rugosa – have a large complex of common features. Thus, the concept of the sum of common features fit well for their comparison and determination of the Heliolitida position in the classification system of Palaeozoic corals. Study shows that these groups have a high degree of similarity and it is very probable that they are close relatives, i.e., they all had a common ancestor. However, qualitative and quantitative expression of similar features can be different. It testifies to their early divergence and subsequent independent evolution. The Heliolitida evolved as a unitary group that is evidenced both by asto-phylogeny and morphological homogeny of group. The rank of the Heliolitida is considered as variable – from the family to subclass or superorder. Given the Heliolitida as an equal taxon to Tabulata and Rugosa, it should therefore be order.

Differences between the Heliolitida, Tabulata, and Rugosa can be explained within the limits of variation of relative organisms. Study shows that the number of septa depends on the diameter of cavities of polyps. The larger corallites have the higher number of septa. Heliolitida has the smallest diameter of corallites and accordingly the fewest number of septa. Rugosa has the largest diameter of corallites and relatively highest number of septa; and Tabulata is intermediate between them. The different number of septa can point to different food requirements between Heliolitida, Tabulata, and Rugosa. The basic cause of the different sizes of polyps lies in the different rates of maturation. Formation of these groups of corals was connected with the differentiation on food requirements and the divergence on the rate of maturation among the different members of ancestral group. All morphological differences between Heliolitida, Tabulata, and Rugosa can be well explained from these aspects. For example, better development of septa of the Rugosa makes for the more complicated axial structure. Coenenchyme developed in many taxa of Palaeozoic corals and there are no compelling reasons for integration of Heliolitida with Halysitida than for integration with the other taxa with coenenchyme. In addition, the genetic affinity of the Halysitida with the other skeletal Tabulata prevents the integration of Halysitida and Heliolitida into one taxon. Different morphological appearance of coenenchyme makes conditional upon various ways of its origin from representatives with a different genetic base. However, there is a general similarity in its origin: coenenchyme developed where epitheca was reduced. Epitheca in Palaeozoic corals was as individualization mean of polyps: if the epitheca was reduced, the theca could also be reduced so that the cavities of adjacent polyps were joined directly.

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Appendix A.

A.1. Diagnosis of the subclass

Class ANTHOZOA Ehrenberg, 1834
Subclass PALEOSCLEROCORALLA Ospanova, 2007

Etymology: From the presence of true septa (sclerosepta) and geological age.

Diagnosis: Corals are solitary and colonial. Skeleton is composed of calcite and rarely aragonite.

Shape of solitary corals is from hornlike and cylinder-conic to discoid, rarely calceoloid and spool-like. Cross-section of calices is rounded, oval, semilunar and polygonal. Colonies are from fasciculate and hemi-massive to different massive (encrusting, lamellar, discoid, hemispheric, spherical, cylindrical, branching and tumor-like, sometimes with finger-shaped offshoots). Corallites are cylindrical, cylinder-conic and prismatic. Cross-section of calices is rounded, oval, semilunar, meandering, stellar and polygonal. Degree of isolation of corallites from each other in colonies is variable – from momentary during offsetting to the presence common distributive system (coenosarc).

Axial and peripheral zones are recognized in corallites. Axial cavities can be with and without complexes (present only as tabulae). Septa and tabulae form axial complexes. In other cases, axial complexes can be independent. Corals without tabulae are rare. Peripheral zones of corallites contain septa of different shape (spines, scales, solid ribs and lamellae) and direction (vertical, inclined up, horizontal and rarely inclined down). The number of septa is from 1 to 120. Septa are of either first or second orders (rarely more), absent sometimes.

Microstructure is lamellar, fibrous, trabecular, and trabecular–bacular.

There is sexual and asexual reproduction. Asexual reproduction is gemmation or fission. Epitheca can ring around each corallite, groups of corallites or at the base of a colony.

Composition and distribution: Three orders: Tabulata Milne-Edwards and Haime, 1850, Upper Cambrian or Lower Ordovician–Permian; Heliolitida Frech, 1897, Middle Ordovician–Middle Devonian; and Rugosa Milne-Edwards and Haime, 1850, Middle Ordovician–Permian.

A.2. Diagnosis of the genus

Order Heliolitida Frech, 1897
Suborder Coccoseridina Kiaer, 1899
Family? Pycnolithidae Lindström, 1899
Genus *Starshininites* Ospanova n. gen.

Etymology: In honour of geologist of Tajikistan D.A. Starshinin.

Type species: Starshininites pshansensis Ospanova n. gen. n. sp. (Fig. 5), Upper Ordovician, Middle Ashgillian, Archalyk beds, Middle Asia.

Diagnosis: Colony is hemispheric or cylindrical. Skeleton is from almost homogeneous trabeculae or baculae. Baculae are vertical or weakly bent. Corallites' cavities are solid stereoplasmatic or hollow. There are septal structures and rude tabulae in hollow corallites. Septa are ledges of baculae that can have spine form. The number of septa is uncertain and can be less than 12. From 2 to 5 rows, baculae are between hollow cavities of corallites.

Comparison: The genus *Starshininites* Ospanova n. gen. differs from the genus *Pycnolithus* Lindström, 1899 by the absence of the crowns and the walls in corallites. And there are also solid stereoplasmatic corallites that are similar to *Coccoseris* and absent in *Pycnolithus*.

Horizon and age: Archalyk beds, Middle Ashgillian, Upper Ordovician of Zeravshan Mountains.

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Research paper

A lithofacies model for the Upper Devonian Pamyatno-Sasovskoye reef (oilfield) (Volgagradskoe Povolzhye, Russia)

Sergey V. Deliya[a], Nadezhda V. Danshina[b,*]

[a] LLC LUKOIL-Nizhnevolzhskneft, Russia
[b] LLC LUKOIL-VolgogradNIPImorneft, Russia

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Abstract

Based on the exploratory drilling data provided by LLC LUKOIL-Nizhnevolzhskneft, we studied the structure, composition, and conditions of formation of the middle-upper Frasnian sections of the Pamyatno-Sasovskoye oilfield, Central Russia, which are related to a complex organogenic build-up. We also conducted a lithofacies section modeling based on the data derived from classification of secondary dolomitic limestones (as per Dunham's classification), palaeontological components (e.g., algae, stromatoporoids, crinoids, gastropods, protozoans), structural constructions, and logging data.

Keywords: Frasnian reefs; Stromatoporoids; Corals; Crinoids; Algae; Russia

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1. Introduction

Lithological and palaeontological data play a great role in analyzing the geological framework of organogenic fossil build-ups. The main instrument of lithofacies analysis is the identification of sedimentary rock characteristics, which indicate the conditions of formation of organogenic build-ups. Detection of genetically connected rock associations enables a more systematic and objective approach to lithofacies analysis. However, incompleteness of geological information may occur here as the core data were not taken from all well sections. Lack of a complete core was compensated for by cuttings and well logging data, as well as use of well sections from adjacent areas. Cores from 42 wells and logging data from 56 wells were used for modeling of a transverse lithofacies section of the Upper Devonian (Frasnian–Famennian) Pamyatno-Sasovskoye oilfield. A total of 62 wells were drilled in the oilfield, which were generally concentrated along the SW–NE structural axis.

The Pamyatno-Sasovskoye oilfield is associated with reefal deposits of the Evlanovian–Livnian Formation (upper Frasnian). The productive section of the whole oilfield is mostly covered by core material from four wells (Pamyatny-130 and -139, Sasovskaya-105, and Platovskaya-12). The areal extent of the massive reef is 0.6–1.2 × 15.7 km, and it is situated at a shallow water depth. Average top reservoir depth is 2659.4 m, and maximum oil column is 284.1 m (Platovskaya-11 well). Oil–water contact (OWC) is −2578 m below mean sea level.

The cap rock is represented by calcareous-marl-argillaceous sediments of the Zadonskian–Eletsian (lower Famennian) age. The Umetovsko-Linevian (basal Famennian) marly-argillaceous deposits act as lateral seals. The thickness of the cap rock ranges from 16 to 132 m.

2. Regional geology

Tectonically, the Pamyatno-Sasovskoye oilfield is located in the Pachelmsko-Saratov aulacogen, Central Russia. The oilfield lies in a zone of favorable barrier reefs development in the Umetovsko-Linevian depression (Novikov et al., 1998; Menning et al., 2006).

The Pamyatno-Sasovskaya organogenic build-up of the middle-upper Frasnian age lies in the Umetovsko-Linevian depression (Fig. 1). The Privolzhsky megaswell extends north-eastward from the build-up. The Pamyatno-Sasovskaya organogenic build-up of the Frasnian age is a complex intra-

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* Corresponding author.
E-mail address: OGuzhova@lukoilvmn.ru (N.V. Danshina).

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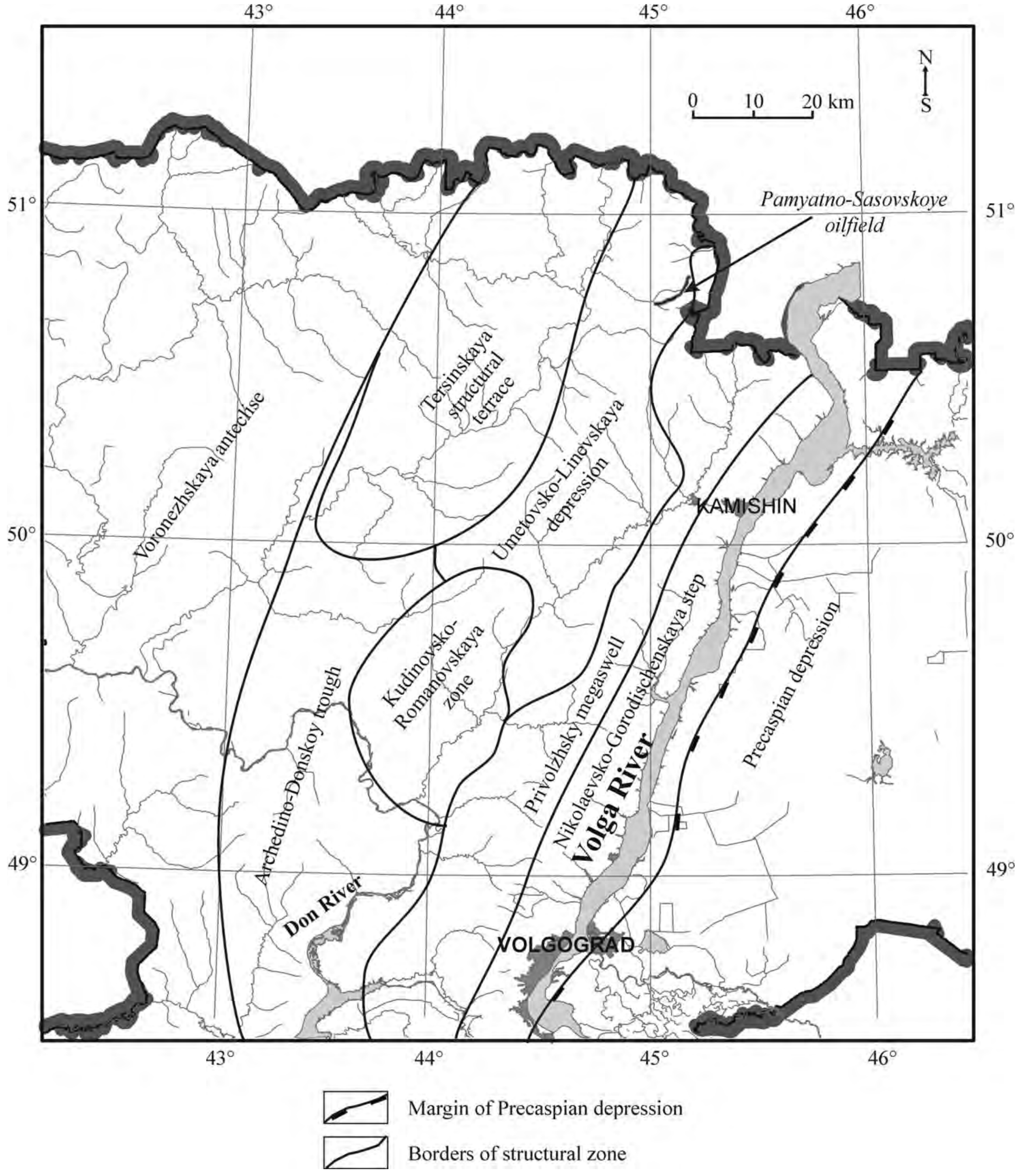

Fig. 1. Map showing regional tectonic units in Central Russia.

basin build-up extending from south-west to north-east. The Pamyatno-Sasovskoye reef field is distinguished by the complexity of its inner structure and by its deposition. The form and structure of the massive organogenic structure indicate a flat-topped, narrow, and extended reef (Fig. 2). The reef system is characterized by the presence of a steep (south-east) foreslope composed of relatively deep-water deposits and more gentle inner (north-west) slope represented by lagoonal deposits.

3. Palaeogeography and sedimentology

For the identification of oilfield forming conditions, a model of a lithofacies section (Fig. 3) from the top of the Timanian (lower Frasnian) to the top of the Zadonskian (lower Famennian) deposition was constructed.

In the Timanian time (area of Pamyatno-Sasovskaya-14 well) in the survey zone, finely-dispersed claystones of relatively deep-water basinal facies were accumulated.

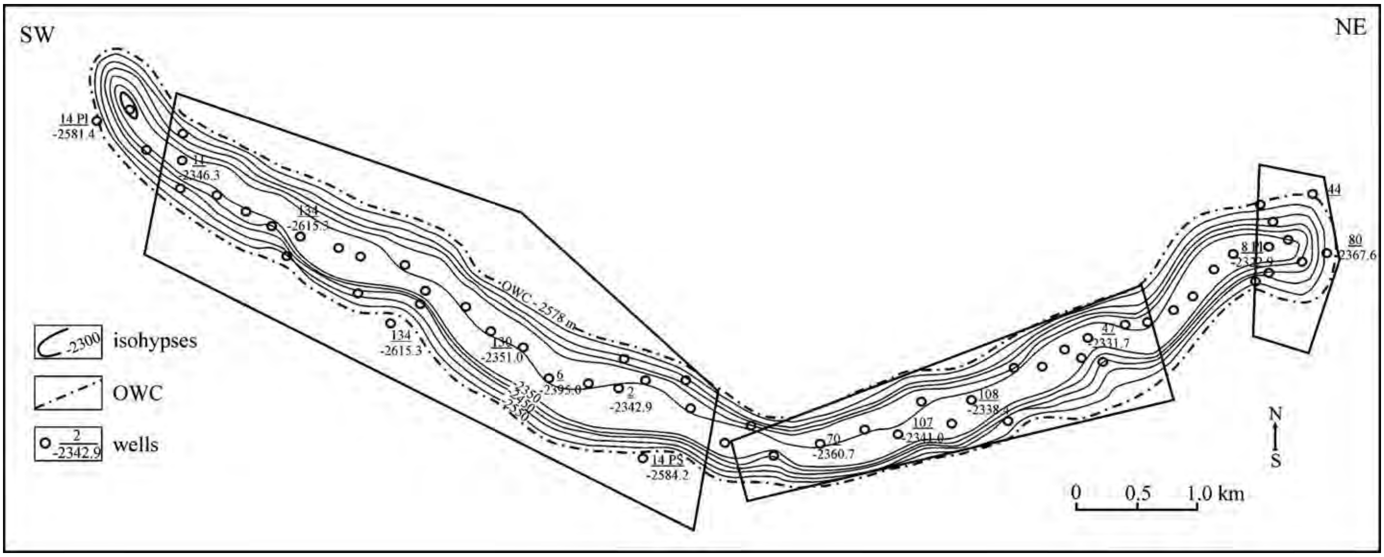

Fig. 2. Top structural map of the Pamyatno-Sasovskoye oilfield for the Evlanovian–Livnian (Frasnian) producing deposits. OWC: Oil–water contact.

The Sargaevian (middle Frasnian) interval was accompanied by accumulation of clayey-bituminous claystones, marls, and fine-grained mudstones with intercalations of spicule wackestones and packstones of varying thickness. Among the latter, accumulations of bottom *Coniconchia* detritus and balls of blue-green 'algae' can be traced.

In the early Semilukian (middle Frasnian) time, following the Sargaevian, basin stratified clayey-bituminous spicule wackestones, packstones, and marls were formed. The detrital components of stromatoporoids and corals also increased. The late Semilukian time in the explored area was a period of active growth of organogenic build-up with accumulation of algal–stromatoporoid boundstones, floatstones, rudstones, and wackstones in secondary dolomites. The growth of the Semilukian build-up was accompanied by a wide area of development as biostromes were identified at a significant distance (9 km) from it (Verkhne-Dobrinskaya-47 well) (Fig. 3). The top of the Semilukian organogenic build-up was evidently exposed to erosion processes. Here, secondary dolomitic floatstones as well as rudstones are leached, disaggregated, and sulphatized (Pamyatno-Sasovskaya-14 well). In the area of the Verkhne-Dobrinskaya-47 well, a back-reef-type section of the Semilukian deposition was exposed, where the dominant lithologies vary between claystones, marls, polydetrital wackestones, and packstones, with abundant subrounded crinoidal debris.

The Petinian (upper Frasnian) Regional Stage of the Pamyatno-Sasovskaya organogenic growth was accompanied by a decrease in the length and the width of the structure compared to the Semilukian. Thus, in the area of the Platovskaya-4 well located 1.5 km northeast of the Pamyatno-Sasovskoye oilfield, above Semilukian reef formations in the early Petinian, thin claystones, mudstones, and mud-detrital wackestones with sandy admixture were accumulated, though thin biostromal wedges formed by stromatoporoid boundstones also occurred. The early Petinian part of the section in the Pamyatno-Sasovskaya-14 well was composed of an alternation of floatstones, rudstones, wackestones, and boundstones, in which traces of secondary dolomites were found.

In most of the Pamyatno-Sasovskaya organogenic build-up, the late Petinian was represented by formation of alternating algal boundstones, floatstones, rudstones, and wackestones with secondary dolomites. In the fore-reef-type section (Pamyatno-Sasovskaya-14 well), at the end of late Petinian, stratified organogenic-detrital wackestones, packstones, and mudstones with claystone interlayers were accumulated, and in the back-reef-type section, additional lithologic types represented by thin alternation of claystones, marls, mudstones, and mud-detrital wackestones occur, together with the above-described lithologic sequence. The late Petinian is characterized by the presence of variably-sized fish remnants, especially in the back-reef-type section.

The Voronezhian Regional Stage (upper Frasnian) is connected along almost the whole area of the Pamyatno-Sasovskoye field facies with the expansion of the rigid, shallow-water carbonate platform inherited from the late Petinian and resulting from the increase of the role of stromatoporoids, corals, crinoids, calcareous algae (green and red), and cyanobacteria. Lithologic types are different, though the following ones are dominant: polydetrital, bioclastic floatstones, wackestones, packstones, and biohermal boundstones. Only in the fore-reef-type section (Platovskaya-14 well, Pamyatno-Sasovskaya-14 well), are mud-detrital wackestones, and packstones recorded together with the above-mentioned variety of limestone.

The back-reef-type section (Verkhne-Dobrinskaya-47 well) is characterized by mud-detrital wackestones, lumpy packstones with numerous tubular rhodophyaceae, and some mudstones and claystones. The Evlanovian–Livnian regional stages (upper Frasnian) of the Pamyatno-Sasovskoye oilfield are represented by the thickest sequence with a complex structure. The position inherited from the Semilukian–Voronezhian regional stages, with the tendency to narrowing of the reef width (see section model – Fig. 3), can be observed. In the fore-reef-type sec-

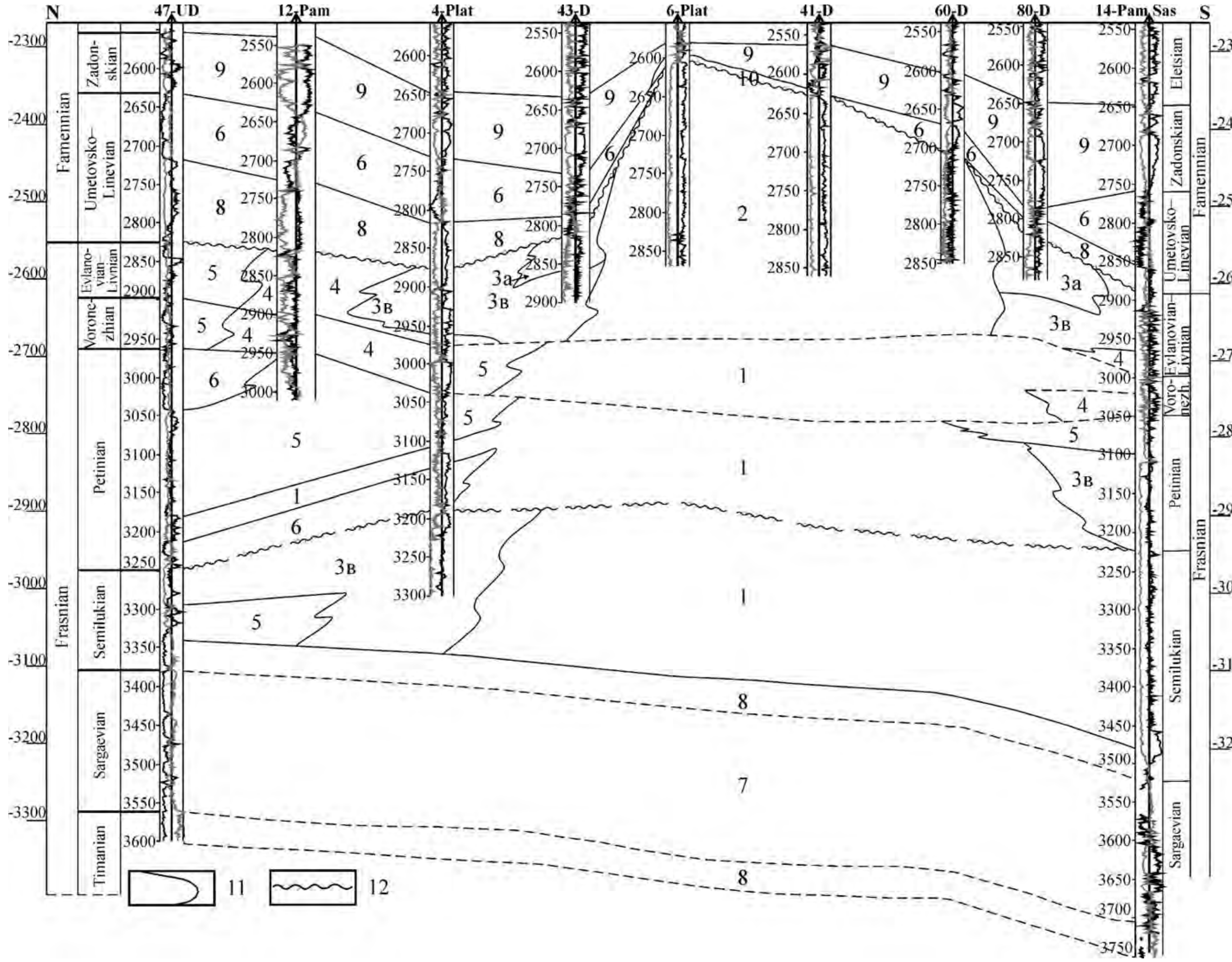

Fig. 3. Geological model of the Frasnian–Famennian carbonate complex in the Pamytno-Sasovskoye oilfield. Genetic types of carbonate depositions (1–10): (1) alternation of bioherm and organogenic-detrital secondary dolomites; (2) predominance of bioherm dolomites with organogenic-clastic dolomites lenses; (3) talus aprons from dolomites (3a), limestones (3b) organogenic-clastic with bioherm debris; (4) distal reef aprons (organogenic-clastic, organogenic-detrital, dolomitic with mudstones lenses limestones); (5) lagoonal laminated organogenic-detrital limestones, marls, mudstones; (6) slopes of basins from thinly laminated marls, mudstones, limestones with sand mixtures; (7) relatively deepwater facies (mudstones, marls, and spicule, irregularly bituminous limestones); (8) relatively deepwater basin clayey-bituminous mudstones, marls, micro-grain limestones; (9) shallow-shelf limnetics with mud-eaters tracks; (10) reef core overlapping basal nodular-algal limestones. Other symbols (11–12): (11) boundaries of lithofacies and stratigraphic complex; (12) washout.

tion – organogenic build-up slope, lower part (Platovskaya-14, Pamyatnaya-134, Pamyatno-Sasovskaya-14 wells) alternation of floatstones, rudstones, and wackestones is more common in secondary dolomites and less common in limestones. Organogenic build-up upper slope facies (Dobrinskaya-66, -80 wells) are composed of an alternation of breccias consisting of boundstones, floatstones, rudstones, and wackestones debris discovered in secondary dolomites.

The back-reef-type section (Platovskaya-4 well) on the slope of the organogenic build-up is characterized by alternation of *Amphipora* floatstones and bioclastic rudstones, with prevalence of biohermal debris and peloid wackestones, but mainly in limestones. Dolomitization in the back-reef type section is insignificant. At a 9 km distance from the organogenic build-up (Verkhne-Dobrinskaya-47 well), the following has been developed: organogenic-detrital, clotted-lumpy wackestones, packstones with plenty of locular foraminiferans, tubular rhodophyaceae and mudstones, with a small amount of claystones.

Central sections of the Pamyatno-Sasovskoye oilfield in the Evlanovian–Livnian stages are composed of secondary dolomites of light-grey to brown-grey in color, characterized by hydrocarbons saturation (Danshina and Fedorenko, 1995). According to the prevalence of dolomitic structural differences, they are divided into core facies and organogenic build-up apex facies (Danshina and Fedorenko, 1995). In the core of the organogenic build-up (Platovskaya-12 well), 60–75% are dolomites with biohermal structure (algal–stromatoporoids, stromatoporoid–algal boundstones), together with 25–40% organogenic-detrital and bioclastic dolomitic floatstones, rudstones, and wackestones are widespread. In the sections of the organogenic build-up cores, according to the

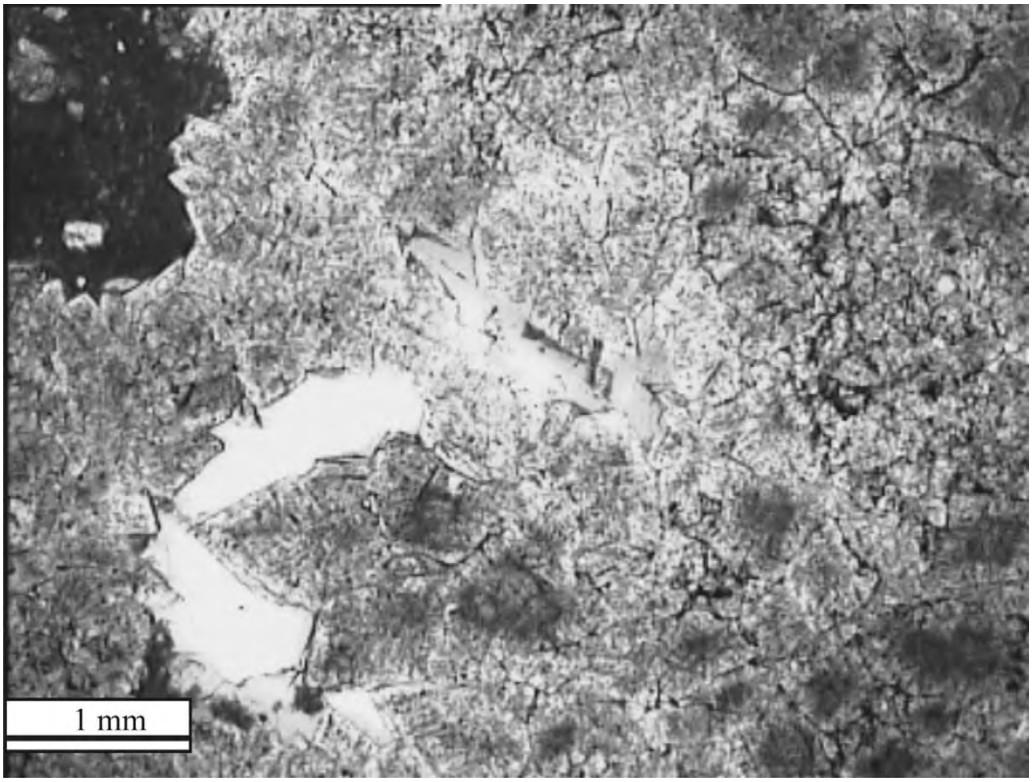

Fig. 4. Dolomitic relict algal facies, Platovskaya-6 well, depth 2672–2676 m, sample 183.

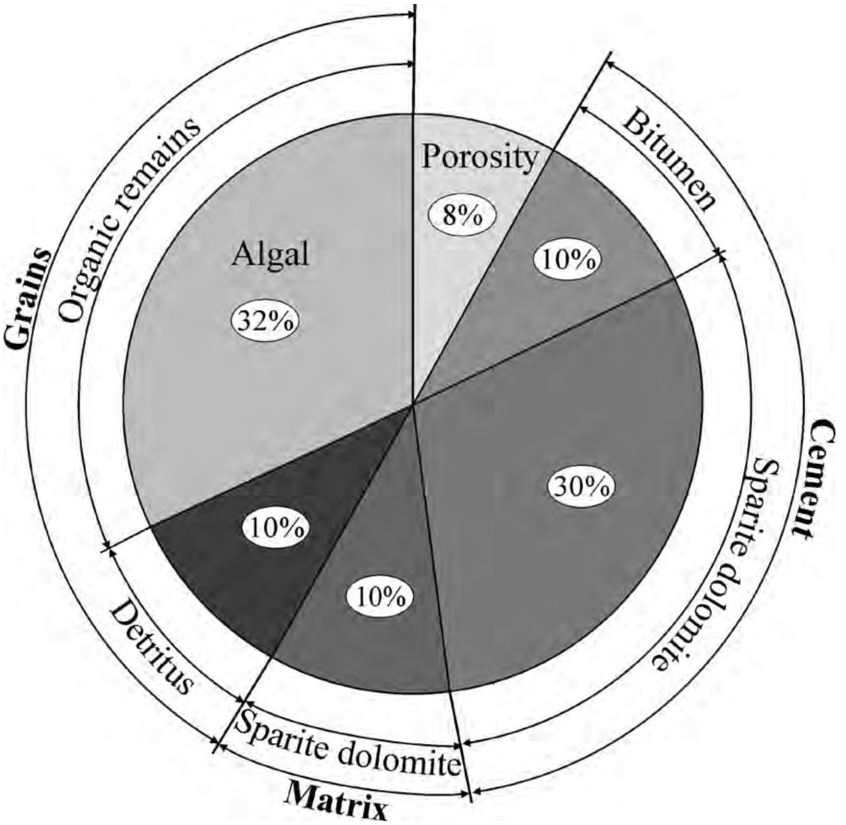

Fig. 5. Organogenic build-up apex (composition).

prevalence of palaeocoenosis, the following bands have been defined: algal–stromatoporoid, stromatoporoid–algal, algal, coral–stromatoporoid and crinoid–algal. According to core data, pocket-like substitutions of small columnar algal–stromatoporoid bioherms for organogenic-detrital, bioclastic floatstones, wackestones, and packstones can be distinctly traced here, thus indicating the proximity of a steep slope.

In the organogenic build-up apex facies, stromatoporoid–algal biohermal dolomites (Figs. 4 and 5) are most typical, with primary bedding at 40–60° angle to core axis (stratified boundstones), which make up 50–100% of the exposed section. Dolomitic (up to 50%) bioclastic and organogenic-detrital rudstones, wackestones, and floatstones are traced between small columnar algal bioherms, pointed subvertical intersecting sutural joints with pockets of 3.5 cm thickness. In the apex zone of well sections, the following bands with names as per prevailing representatives of biocoenosis: stromatoporoid–algal and crinoid-algal. Ubiquitous substitution of algal boundstones for bioclastic rudstones is timed to apex zones of the organogenic build-up; this is caused by the intensity of wave motion above reef crests, which contributed to their simultaneous break-up and generation of bioclastic deposits.

The steep slopes of the Evlanovian–Livnian reef deposits are overlain by thick formations of the Umetovsko-Linevian beds of the early Famennian age. Depending on which part of the organogenic build-up slope was exposed, the upper or the lower part, the thickness of the Umetovsko-Linevian deposits varies. In the first case (the upper part of the slope), the thickness decreases (60–80 m); in the second case (the lower part of the slope), the thickness increases (150–200 m). In the lower part of the Umetovsko-Linevian section, spicule wackestones of quiet water basin facies were accumulated. The upper part of the above-mentioned sequence is composed of thinly bedded rocks, represented by fine-grained mudstones, claystones with lenticular intercalations of bioclastic floatstones and wackestones. These intercalations are mostly observed in thinner (30–40 m) sections of the Umetovsko-Livenian sequence located near steep slopes of the organogenic build-up. In the most central sections above the Evlanovian–Livnian reef deposits, basal nodular-algal floatstones of the early Zadonskian (Famennian) age are deposited. They were accumulated in conditions of active shallow waters, which, due to the evidence of the Evlanovian–Livnian organogenic build-up, were developed in the sea bottom, probably in the form of an island (Danshina and Fedorenko, 1998). In the late Zadonskian, mudstones and wackestones with tracks of mud-eaters and lenticular intercalations of algal pillow-boundstones were deposited, which in a number of wells of the Pamyatno-Sasovskoe field (Platovskaya-8, -12 wells) were microporous and oil-saturated.

4. Conclusions

The lithofacies modeling carried out in this study showed the following trends in the Pamyatno-Sasovskoye oilfield:

1. In the Sargaevian interval appeared depth differences and biohermal shape of deposits formed as organogenic rock lenses on the basin bottom in the uplifted zones;
2. In the early Semilukian, the biohermal shape and depth differentiation were established and late Semilukian witnessed the active growth of an organogenic build-up with the key role of stromatoporoids and corals;
3. In the Petinian time, because of basin regression, reef-building areas narrowed; algae, stromatoporoids, and corals become equal parts of the organogenic build-up structure;
4. The Voronezhian time proceeded with formation of a rigid carbonate platform;
5. The Evlanovian–Livnian is connected with the most active growth of the organogenic build-up, as well as with its narrowing in width in comparison with the middle Frasnian period. Algae played the key role in reef structure, together with stromatoporoids;
6. Reservoir properties developed on the basis of palaeocoenosis by the formation of cavities in stromatoporoids and corals as well as fracturing in algal small bioherms;
7. In general, the Pamyatno-Sasovskaya organogenic build-up from the Semilukian to the Livnian was characterized by a transgressive-regressive type of development.

Acknowledgments

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Research paper

New data on the Carboniferous corals of the Donets Basin

Victor V. Ogar

Kyiv Taras Shevchenko University, Geological Department, 90 Vasilkivska str., 03022 Kyiv, Ukraine

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Abstract

Additional data are given here on the taxonomic diversity and distribution of the Carboniferous rugose and tabulate corals of the Donets Basin (Ukraine). *Keyserlingophyllum obliquum* (Keyserling, 1846) was recorded in the Tournaisian part of the section for the first time. *Rotiphyllum omaliusi* (Milne-Edwards et Haime, 1851) and *Dorlodotia pseudovermiculare* (McCoy, 1849) were found in Tournaisian-Viséan boundary deposits. *Zaphrentites parallelus* (Carruthers, 1910), together with *Sutherlandia* and *Cladochonus*, was discovered approximately in the mid-Viséan. The tabulate coral *Volnovakhipora* n. gen. from the Tournaisian and the rugose coral *Arctophyllum lugankaensis* n. sp. from the Gzhelian are established and described.

Keywords: Tabulata; Rugosa; Carboniferous; Donets Basin

1. Introduction

Carboniferous strata of the Donets Basin are thick, mostly continuous, and well-exposed; they have been relatively well studied. They contain a great variety of fossil groups such as foraminifers, conodonts, brachiopods, ostracods, ammonoids, bivalves, gastropods, crinoids, corals, and bryozoans (e.g., Aizenverg et al., 1963, 1975; Poletaev et al., 1989, 1990).

Carboniferous corals of the Donets Basin have been studied for more than one hundred years. Lissitsin (1925, 1929), Fomichev (1953), Vassilyuk (1960, 1964) carried out the most detailed studies. The basal Lower Carboniferous corals were described by Vassilyuk. Middle and Upper Carboniferous rugose corals were described by Fomichev (1953). Tabulates and chaetetid sponges of this age were described by Vassilyuk (1959, 1963). Other papers documenting corals include Zhizina (1956), Vassilyuk and Zhizina (1978, 1979), Polyakova (1983), Weyer and Polyakova (1995), and Fedorowski and Vassilyuk (2001). Lissitsin (1925, 1929) proposed the first brachiopod-coral biostratigraphy of the Lower Carboniferous. Fomichev established the coral zonation for the Middle and Upper Carboniferous. Vassilyuk (1975) proposed the detailed coral biostratigraphic scheme for the entire Donets Carboniferous succession.

Recently, a representative collection of the Carboniferous corals of Donets Basin was collected by the present author. The most important findings belong to several stratigraphic intervals: the Tournaisian, the Tournaisian-Viséan boundary deposits, mid-Viséan, and the lower Gzhelian. Though the collection is still undergoing review, new data on the composition and distribution of some corals through the Donets Carboniferous are presented in this paper.

2. Study area

The area of investigation embraces almost all of the Ukrainian part of the Donets Basin (Fig. 1). In the southernmost part of the basin (near the towns of Dokutchaevsk, Novotroitske, and the village of Styla), the carbonate strata of the Lower Carboniferous are exposed. The limestones and dolomites of the Devonian-Carboniferous transition deposits as well as the Tournaisian and Viséan ones crop out along the Mokra Volnovakha River and in numerous quarries.

To the southeast of Donetsk City, the upper Serpukhovian and lower Bashkirian terrigenous strata with thin limestone intercalations are exposed along the Kalmius River and near the Starobesheve Reservoir (Fig. 1).

In the central and north central parts of the studied area (near the Lutugine and Debaltseve towns), the terrigenous strata include not only the limestone interlayers, but also coal seams. Commercial coal seams are exploited in numerous coal mines.

E-mail address: ogar_victor@ukr.net.

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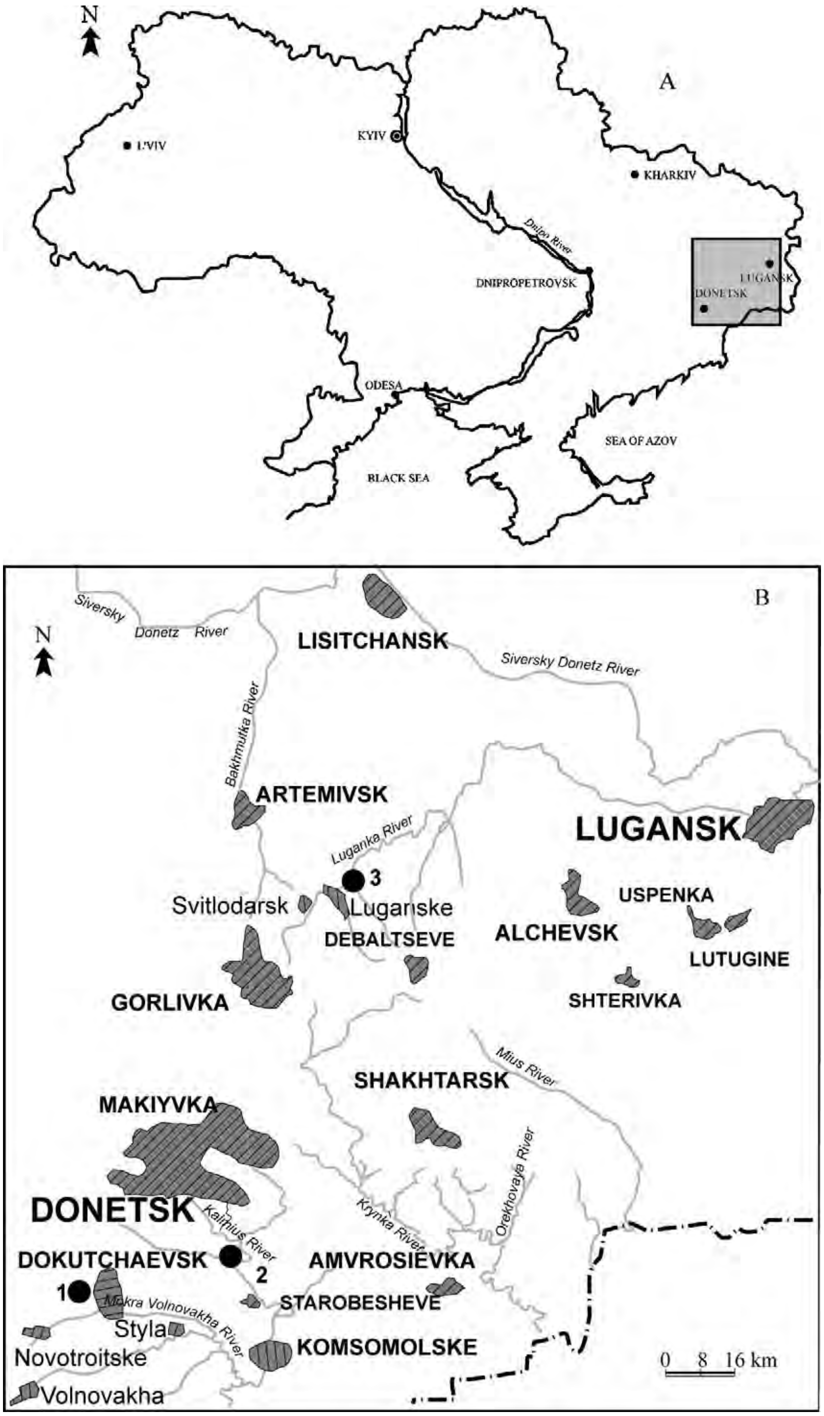

Fig. 1. Location map of the sections investigated. A – area of investigation; B – location of the sections: 1 – Central quarry, 2 – Starobesheve, 3 – Buchkov Yar.

In the north-western and northern part of the region, along the Luganka River near the towns of Svitlodarsk and Lisitchansk, the Upper Carboniferous terrigenous strata with limestone intercalations are exposed.

3. Materials and methods

Corals were sampled from the different levels of the Carboniferous succession of the Donets Basin, but only those from certain stratigraphic levels were studied and presented here. They include the corals from the Central quarry near the town of Dokutchaevsk (Fig. 1, Locality 1), an old quarry near the town of Svitlodarsk (Buchkov Yar section) (Fig. 1, Locality 3), and partly along the canal near Starobesheve town (Fig. 1, Locality 2). This new channel exposes limestone of a group E. In this limestone, the author detected uncommon dibunophyllid corals with frequent offsetting.

The large and small thin sections prepared from the collected corals were examined under the microscope. The studied collection is housed in the Paleontological

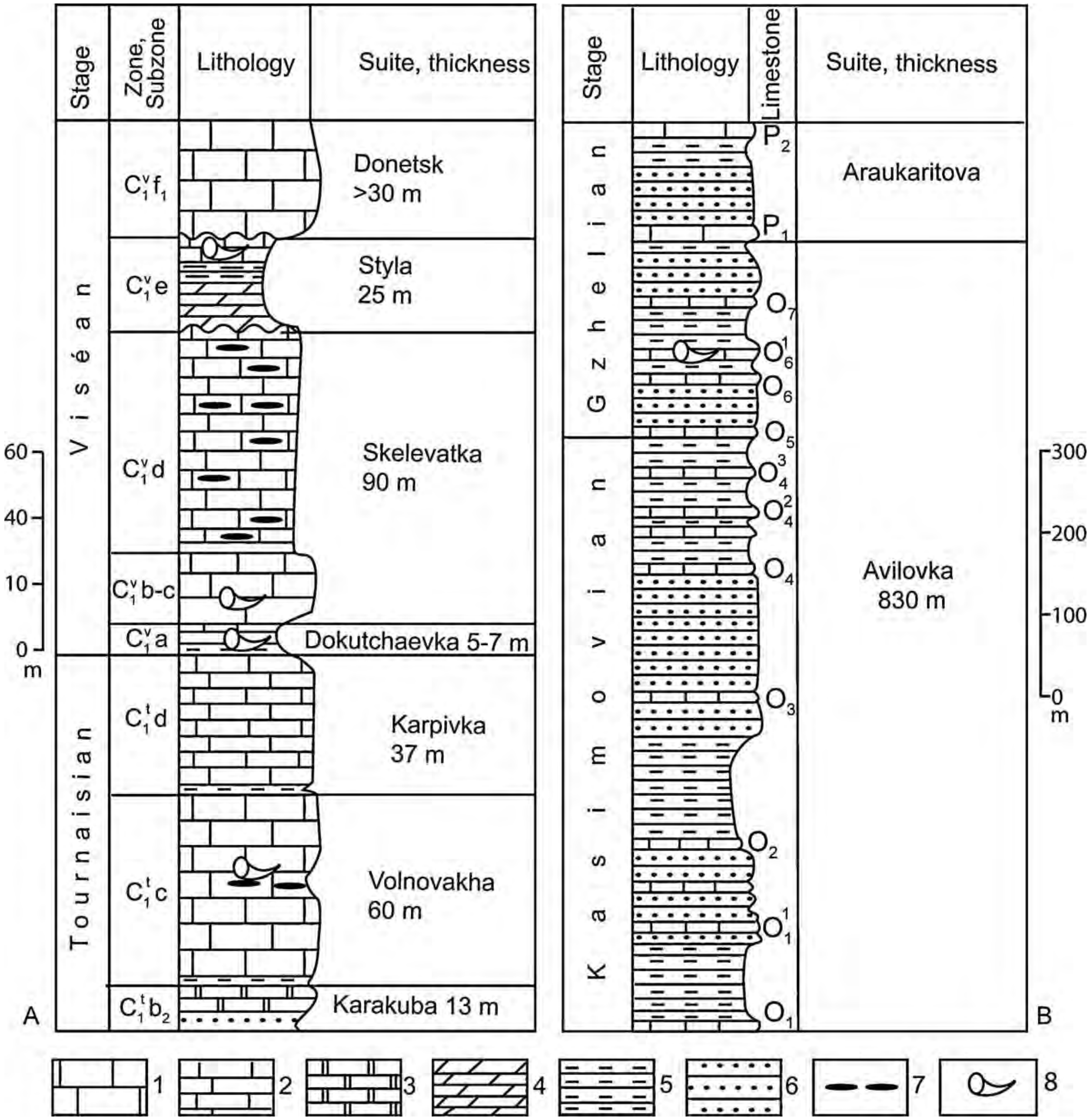

Fig. 2. Stratigraphic columns of the Lower Carboniferous deposits exposed in the Central quarry (A) and of the Upper Carboniferous deposits exposed along the Luganka River (B): 1 – Thick-bedded limestone; 2 – medium- and thin-bedded limestone; 3 – Dolomitic limestone; 4 – Marl; 5 – Shale; 6 – Sandstone; 7 – Cherts; 8 – The points with coral occurrences mentioned in the paper.

Museum of Kyiv Taras Shevchenko University, collection No. 2P264.

4. Corals

4.1. Tournaisian

In the lower part of the upper Volnovakha Suite ($C_1{}^t c$), *Keyserlingophyllum* Stuckenberg, 1895 was found for the first time (Fig. 6N–O) together with previously known *Cyathoclisia uralensis* (Sayutina, 1970), *Syringopora* Goldfuss, 1826, *Roemeripora* Kraicz, 1934, and *Michelinia de Koninck, 1841*. The Volnovakha Suite is composed of light grey massive bioclastic limestones (grainstones and packstones) (Fig. 2A). The limestones contain numerous brachiopods and corals. Large fragments of corals were discovered and identified as *Keyserlingophyllum obliquum* (von Keyserling, 1846). The genus *Keyserlingophyllum* was previously unknown from the Donets Basin. Only Fomichev (1953), referring to the list of corals from the manuscript of Gorsky, mentioned the uralinid corals there. The genus *Keyserlingophyllum* belongs to the family Uralinidae. In the same deposits ($C_1{}^t c$), new tabulate corals of unusual construction were found (see Section 6). The structure of these corals resembles early Palaeozoic Sarcinulacea Sokolov, 1955.

Among the known Carboniferous genera, *Groessensia* Termier et Termier, 1975 from the Belgian Tournaisian is very similar to our corals. Nevertheless, the above-mentioned corals of the Donets Basin differ to great extent from all known genera. Thus, I consider it possible to assign them to a new genus *Volnovakhipora* (family ?Neoroemeriidae Radugin, 1938).

4.2. Tournaisian–Viséan boundary deposits

The second stratigraphic level is exposed near the Tournaisian–Viséan boundary. Here, foraminifers of the phylogenetic lineges *Eoparastaffella simplex*–*E. rotunda* have been found (Vdovenko et al., 2005). In the Tournaisian part (the Dokutchaevka Suite $C_1{}^{v}a$), the small solitary rugose corals *Rotiphyllum omaliusi* (Milne Edwards et Haime, 1851) were found together with common, well-known *Calmiussiphyllum* Vassilyuk, 1960 and *Syringopora* Goldfuss, 1826. The Dokutchaevka Suite consists of dark grey shale and micritic limestones with abundant brachiopods and corals. The Viséan Skelevatka Suite ($C_1{}^{v}b$–d) overlies it conformably. This suite is composed of light grey bioclastic massive and thick-bedded limestones with gastropods, brachiopods, and corals. In the Skelevatka Suite, which is assigned to the Lower Viséan by foraminifers, *Dorlodotia pseudovermiculare* (McCoy, 1849) (Fig. 6P) was found together with fragments of ?*Siphonodendron*, *Koninckophyllum*, and *Sychnoelasma*. Vassilyuk cited *Dorlodotia pseudovermiculare* from the list of Gorsky and Zhizhina (unpublished report, 1940) from the Lower Viséan (Vassilyuk, 1960), but this species was never illustrated from the Donets Basin. The increase of taxonomic diversity in coral associations of the Skelevatka Suite might have been affected by the sea-level rise.

4.3. Viséan

Historically, there have been no studies before on the corals from the Styla Suite ($C_1{}^{v}e$). Vassilyuk (in Poletaev et al., 1990) included in coral zone C6 the corals only from the lower part of the overlying Donetsk Suite. Zone C6 was expanded down to the Styla Suite, but the present author did not find the zonal corals of the Zone C6 in the Styla Suite. Recently, they were found in the upper part of the Styla Suite ($C_1{}^{v}e$). This suite is represented by dark thin-bedded siliceous marls, muddy limestones, and shales with crinoids, brachiopods, bivalves, and bryozoans. At the base of the Styla Suite, thin bentonitic clay layers, ore-bearing interlayers, and karst were observed. At the top of the Styla Suite, a weathered surface indicates the regression and desiccation.

In the upper part of the Styla Suite, a great number of small solitary rugose corals were collected from the muddy limestones. In particular, *Zaphrentites parallelus* (Carruthers, 1910), *Amplexus*, *Bradyphyllum*, and others were found here. Some of small zaphrentid corals seem to represent a new species. They are tiny corals, sometimes with spines on the surface. Their inner structure is similar to "*Meniscophyllum*" *uralicum* from the South Urals described by Vojnovsky-Krieger (1934). A study of these corals has not been finished yet. Among the tabulate corals, *Cladochonus* and *Sutherlandia* are also common in these deposits.

4.4. Gzhelian

Abundant large solitary rugose corals were collected by the present author from the limestone $O_6{}^1$. This limestone is exposed in the Buchkov Yar section in the north-western part of the Donets Basin. A coral-bearing layer, 30 cm thick, belongs to the basal part of the Gzhelian Stage. It is represented by grey and dark grey bioclastic limestones with interlayers of dark grey shales (Fig. 2B).

Variability and good preservation of the coral fauna made it possible to understand the ontogenesis of several species. One of them is particularly abundant and was found in limestone $O_6{}^1$. This species was possibly described by Fomichev (1953) as *Caninia ruprechti* Stuckenberg var. *meridionalis* from the other localities, but as Fomichev did not have enough material to study different stages of its ontogenesis (like early growth stage), I am not sure whether it was the same species or not.

5. Conclusions

Two Lower Carboniferous stratigraphic levels correspond to considerable changes of sea level. The first is the level represented by dark limestones and shales of the Dokutchaevka Suite. The second level consists of siliceous marls and shales of the Styla Suite.

The study of the Donets Basin Carboniferous rugose and tabulate corals from several stratigraphic levels of the Donets Basin permitted to establish a new genus of Tournaisian tabulate coral *Volnovakhipora* and a new species of Gzhelian rugose coral *Arctophyllum lugankaensis*. *Keyserlingophyllum obliquum* was recorded from the middle Tournaisian (the Volnovakha Suite or $C_1{}^{t}c$) in the Donets Basin for the first time. This species was found in the upper Tournaisian of Russia (Hecker, 2001), as well as from Armenia (Papojan and Chudinova, 1974) and China (Poty and Xu, 1996). *Rotiphyllum omaliusi* (Milne-Edwards et Haime, 1851) registered in the Dokutchaevka Suite of Donbas is known in many regions of Eurasia including the Ivorian and Lower Moliniacian of France (Poty and Hannay, 1994). *Dorlototia pseudovermiculare* recovered from the Lower Viséan of Donbas before was illustrated for the first time. This species was found in the Chadian of England (Nudds, 1993) and in the lower Viséan of East Urals (Hecker, 2001). New occurrences of the above-mentioned coral fauna are potentially important for the correlation.

6. Systematic palaeontology

Class ANTHOZOA Ehrenberg, 1834
Subclass TABULATA Milne-Edwards et Haime, 1850
Family ?Neoroemeriidae Radugin, 1938
Genus *Volnovakhipora* n. gen.

Etymology. Named after its occurrence near the town of Volnovakha (Donets County).

Type species. *Volnovakhipora insignis* n. gen. n. sp.

Diagnosis. Cerioid-aphroid colonies with thin fragmental intercorallite walls and round tabularia. An inner wall is thick. Septal spines arranged in vertical rows on an inner wall. Tabularia

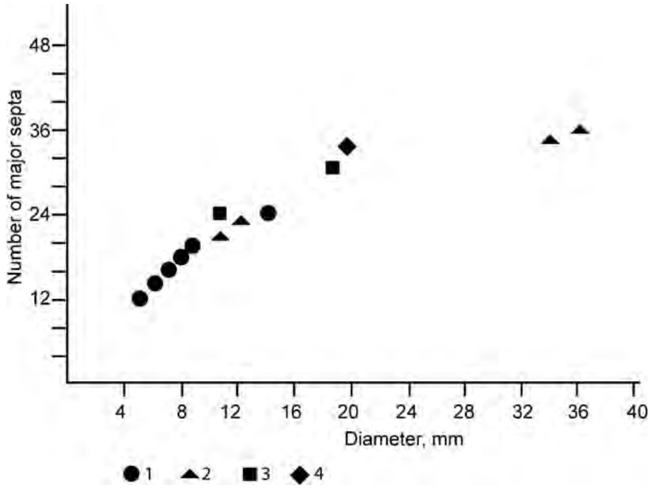

Fig. 3. Plot of corallite diameter against number of major septa in *Arctophyllum lugankaensis* n. sp.: 1 – specimen 2P264-O/11 (holotype); 2 – specimen 2P264-O/80; 3 – specimen 2P264-O/29; 4 – specimen 2P264-O/8.

intercommunicate by cylindrical connecting tubes. Tabulae are complete or partly incomplete, arched. They are pierced by thin needle-like subvertical visceral needles. Coenosteum is filled up with numerous thin and thickened irregular bent connection plates. Budding is interstitial.

Remarks. Among the Carboniferous tabulate corals the most similar genera were described by Termier and Termier (1975) from the Tournaisian (Tn^{1}b) of Belgium. Those authors included this genus in the family Syringoporidae de Fromentel, 1861, emend. Sokolov, 1950. Later, Tourneur and Lafuste (1988) studied in detail the type material. These researchers considered that *Groessensia* Termier et Termier could be included in the family *Roemeriidae* Počta. They also compared the corals of this genus with morphologically similar Palaeozoic tabulate corals. *Volnovakhipora* differs essentially from *Groessensia* by its complete or partly incomplete convex tabulae, the presence of a thick inner wall with needle-shaped components in the tabularia, which could be named “visceral needles”. These elements were not known before for tabulates. These considerable distinctions permit to establish a new genus – *Volnovakhipora*. Both genera seem to belong to the same family. It may be Neoroemeriidae Radugin, 1938, although we do not have yet enough evidence for that assignment.

Distribution of genus. As for the holotype.

Species assigned. Only one species *Volnovakhipora insignis* n. gen. n. sp.

Volnovakhipora insignis n. gen. n. sp.
(Figs. 4A, B and 5A–E)

Etymology. Named from Latin *insignis* – unusual, remarkable.

Holotype. Specimen 2P264-A/5 (Figs. 4A, B and 5A–E). Paleontological Museum of Kyiv Taras Shevchenko University; Tournaisian, Volnovakha Suite (C_1^tc), Donets Basin.

Type locality. Central quarry, Donets Basin, Ukraine.

Type stratum. Tournaisian, Volnovakha Suite (C_1^tc).

Material. Three colonies from Central quarry with three transverse and three longitudinal thin sections.

Diagnosis. Massive cerioid-aphroid colonies. In cerioid parts of the colonies, corallites are polygonal with thin fragmental intercorallite walls and round tabularia. In aphroid zones of colonies. Corallites are composed of tabularia and coenosteum. An inner wall is thick. Connecting tubes are frequent, cylindrical. Septal spines are triangular, arranged in vertical rows on an inner wall. Tabulae are complete or partly incomplete, arched. They are pierced by thin needle-like visceral needles. Coenosteum is filled up with thin and thickened irregular bent connection plates.

Description. Small massive hemispherical cerioid-aphroid colonies. Height of the holotype is 3 cm, length – about 5 cm. In cerioid zones corallites are polygonal with fragmental thin walls. Diameter of corallites – from 2 to 3 mm, on average 2.5–2.7 mm. In aphroid zones corallites consist of tabularia and coenosteum. The tabularia are wide rounded, limited by thick inner walls. Diameter of the tabularia is on average 1.7–2.0 mm. Connecting tubes are frequent cylindrical with diameter 0.2–0.25 mm. They allow adjoined corallites to intercommunicate. Intertabularia space (coenosteum) is filled with thin and thickened irregular bent plates as well as fragments of a corallites wall. Septal spines are long (0.15–0.25) and arranged in vertical ridges. Amount of septal spines in transverse sections is 20–24 at a diameter 2.0 mm. Distance between septal spines in vertical rows is 0.15 mm. Most tabulae are complete, arched, and partly incomplete. Tabulae are numerous, dense, disposed at a distance approximately 0.1 mm. They are penetrated by thin and long needle-like constituents. In transverse sections they point to the central zone. In longitudinal sections they traverse tabulae as thin vertical lines. Its thickness is 0.03–0.04 mm. They are located only in the tabularia zones, their number varies but increases with increasing diameter. The bud appears in the connecting tubes between the inner walls (Fig. 5A and B).

Subclass RUGOSA Milne-Edwards et Haime, 1850
Order STAURIIDA Verrill, 1865
Family Cyathopsidae Dybowski, 1873
Genus *Arctophyllum* Fedorowski, 1975

Arctophyllum lugankaensis n. sp.
(Fig. 6A–M)

? 1953 *Caninia ruprechti* Stuck. var *meridionalis* Fomichev, var. nov. – Fomichev, p. 231, pl. 10, figs. 12a–c; pl. 11, figs. 3a–b, 4, 5

Etymology. Named after occurrence near the Luganka River (Donets County).

Holotype. Specimen 2P264-O/11 (Fig. 6A–M), Paleontological Museum of Kyiv National University, Upper Carboniferous, lower Gzhelian, Avilovka Suite, Limestone O_6^1; Donets Basin, eastern outskirts of the Luganske village (Donets County).

Material. Besides the holotype (two transverse and one longitudinal thin section, along with early stages of ontogenesis, have already been studied in detail), there are 30 specimens of different degrees of preservations. The specimen 2P264-O/11 includes the early growth stages as well. The rest of specimens are represented by conical-cylindrical fragments.

Type locality. Buchkov Yar section, Luganske village, Donets Basin, Ukraine.

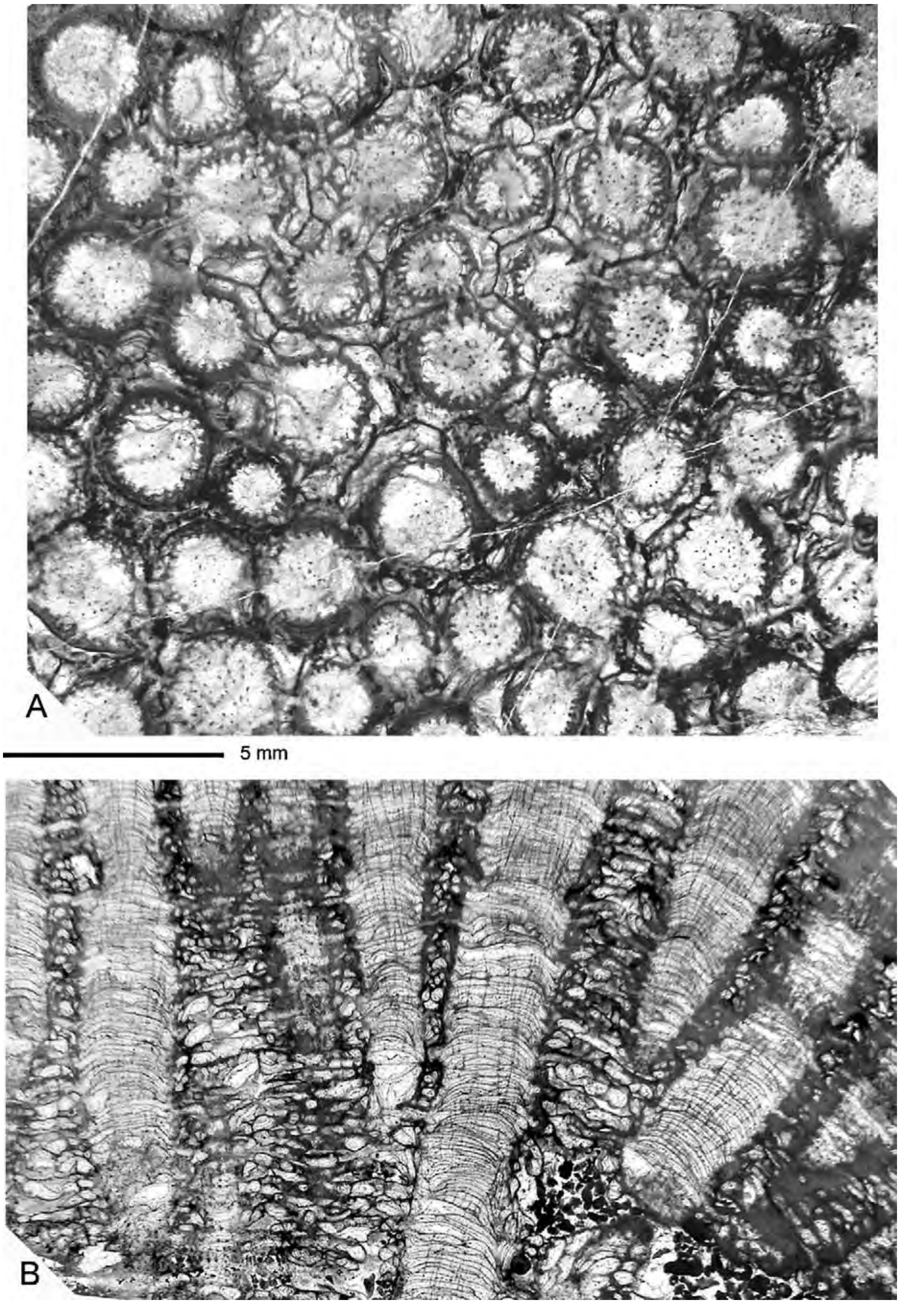

Fig. 4. (A and B) *Volnovakhipora insignis* n. gen. n. sp.; specimen 2P264-A/5 (holotype). Transverse and longitudinal sections respectively.

Type stratum. Upper Carboniferous, lower Gzhelian, Limestone $O_6{}^1$.

Diagnosis. *Arctophyllum* having (20–24) × 2 septa at a diameter of 10–15 cm with bipartite tabularia and thinned septa in early growth stage.

Description. Conical slightly curved corallites and conical-cylindrical fragments. Length of the holotype is about 5 cm. The length of other fragments amounts 6–6.5 cm. The greatest diameter in calice area attains 4.5 cm, and the reconstructed length of corals is 10 cm. The external corallite wall consists of fine growth lines. Calices are incomplete.

Transverse section. Major septa are short and do not reach the centre. In cardinal quadrants of mature growth stage, major septa are thickened, while in counter quadrants they are thin. The cardinal septum is shortened and located in open cardinal fossula. Counter septum shortens only at early growth stage. At mature growth stage, it does not differ in length from other septa of counter quadrants. The minor septa do not reach the inner dissepimentarium wall. The microstructure of sclerenchymal sheets of major septa of cardinal quadrants is fibronormal. A dissepimentarium consists of rectangular dissepiments. Its width increases as the diameter of the corallite increases. Fig. 3 shows a plot of the corallite diameter against the number of major septa.

Longitudinal section. Tabularia is divided into two parts. In the central zone, complete arched tabulae are located. In the

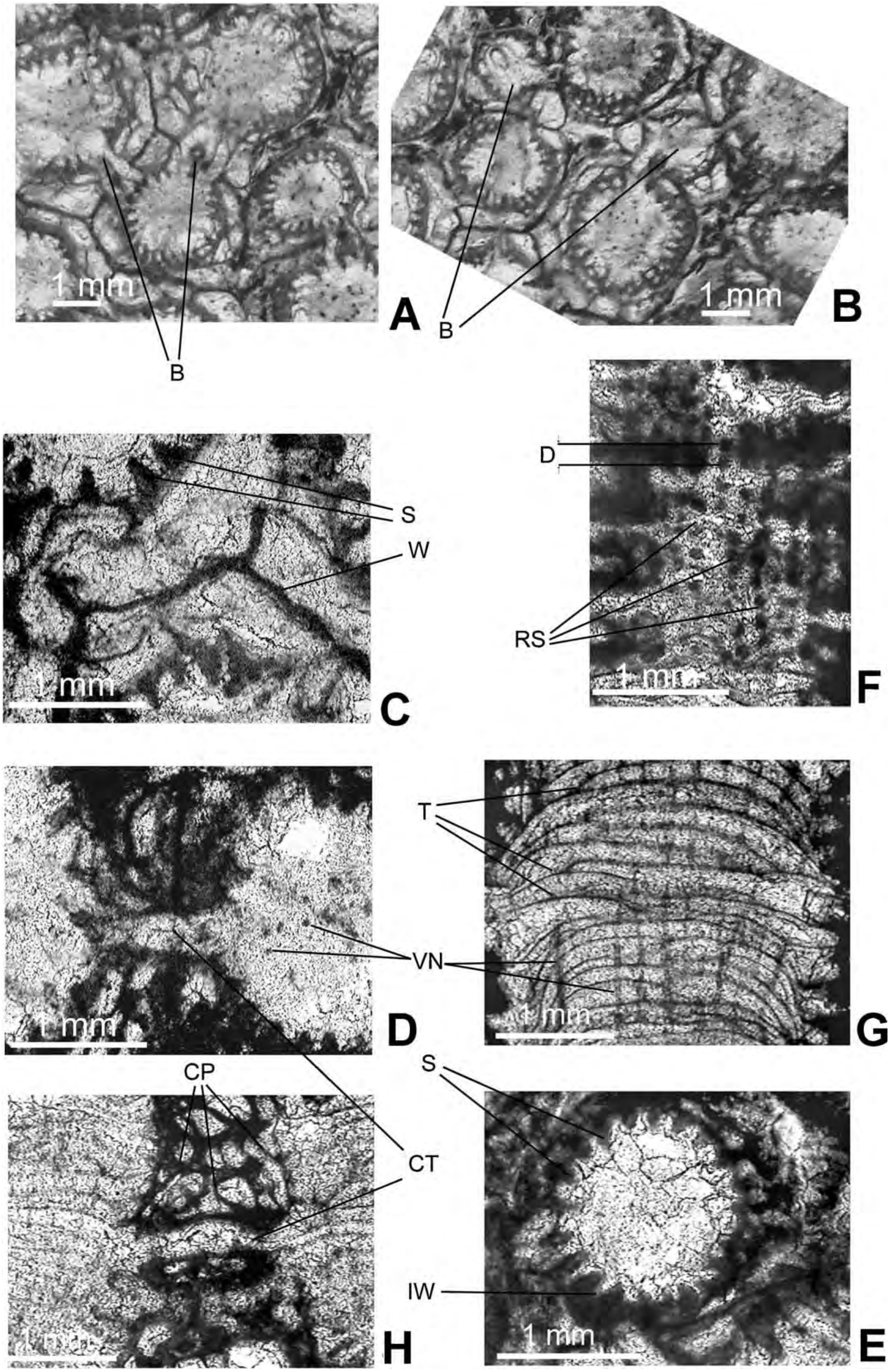

Fig. 5. *Volnovakhipora insignis* n. gen. n. sp., specimen 2P264-A/5 (holotype). Details of inner structure: A and B: Transverse thin sections showing appearance of the buds (B); C–E: Transverse thin sections showing intercorallite wall (W), inner wall (IW), septal spines (S), connecting tubes (CT), visceral needles (VN); F: Longitudinal section in peripheral part of the corallites showing septal spines in vertical rows (RS) and distance between septal spines in vertical rows (D); G–H: Longitudinal sections showing tabulae (T) connecting tubes (CT), visceral needles (VN) and connection plates (CP) of the coenosteum.

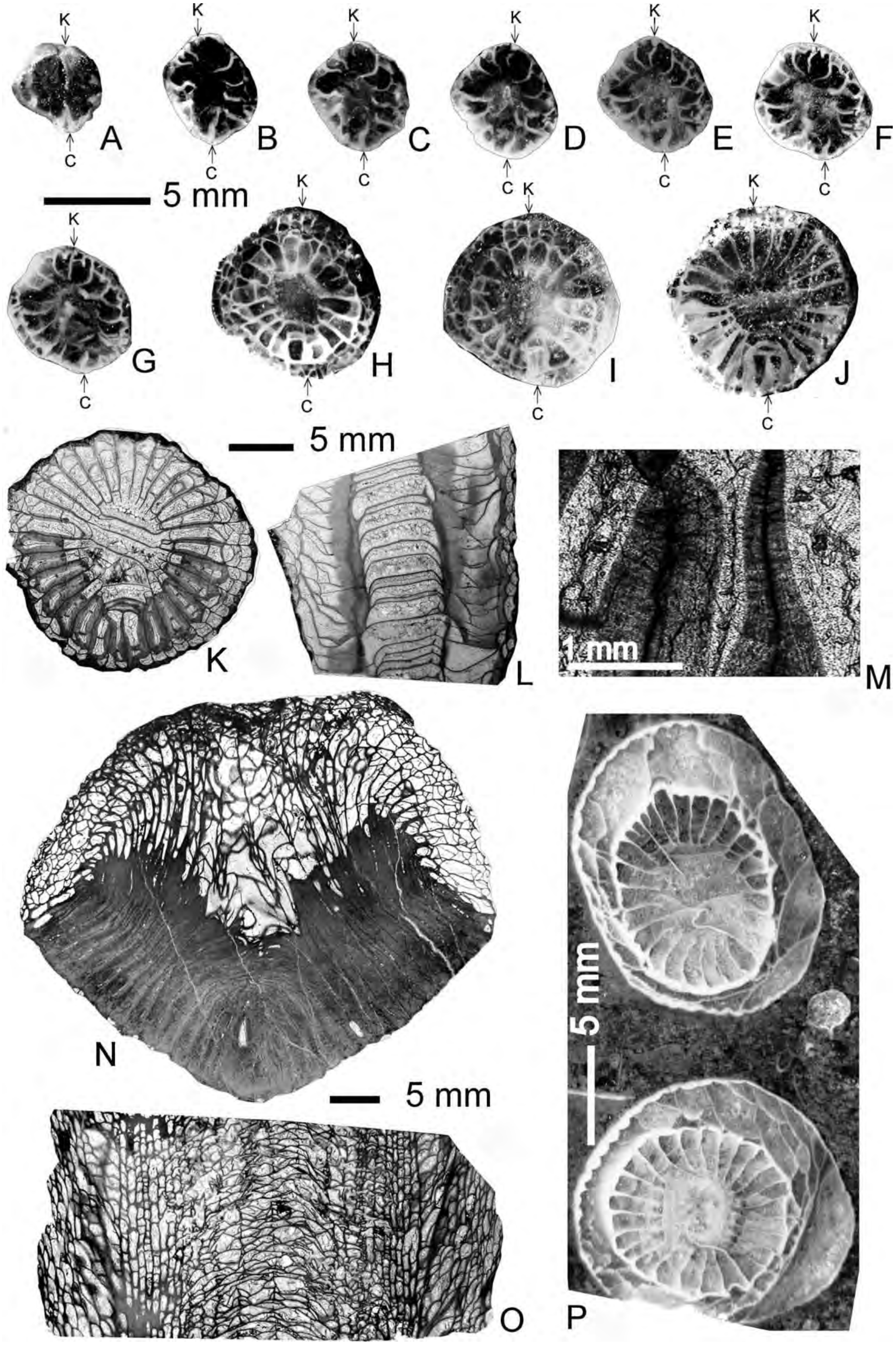

Fig. 6. Some Carboniferous rugose corals of the Donets Basin. A–M. *Arctophyllum lugankaensis* n. sp., specimen 2P264-O/11 (holotype); A–G: Transversal serial sections of early to late neanic growth stage; H and I: early mature growth stage; J and K: mature growth stage (c – cardinal septum, k – counter septum); L: longitudinal section of the mature growth stage; M: microstructure of sclerenchymal sheets of major septa. N, O. *Keyserlingophyllum obliquum* (Keyserling, 1846), specimen 2P264-A/62, Central quarry, Volnovakha Suite ($C_1{}^tc$), Tournaisian. Transverse and longitudinal sections respectively. P. *Dorlodotia pseudovermiculare* (McCoy, 1849), specimen 2P264-A/16, Central quarry, Volnovakha Suite ($C_1{}^tc$), Tournaisian. Transverse section of the fragment of colonies.

peripheral zone, incomplete tabellae with accessory plates bend downwards. A dissepimentarium is composed of vertical rows of convex equal dissepiments. An inner, thickened row forms an inner wall. The number of rows in mature growth stages reaches 8–10.

Ontogenesis. Ontogenetic stages were studied for the holotype. The early neanic growth stage shows elongated cardinal and counter septa (Fig. 6A). The late neanic growth stage demonstrates long cardinal, short counter septa, and first appearance of minor septa (Fig. 6B–G). Dissepiments appear at a diameter of 6.5 mm at first in the counter quadrants (Fig. 6E). Minor septa insert earlier than preceding the dissepimentarium. At the early mature growth stage, the septa of cardinal quadrants are thickened. Cardinal fossula is open with cardinal septum often longer then adjacent major septa. Septa of counter quadrants are thin, and counter septum does not differ from remaining septa in the length (Fig. 6H and I). At the mature growth stage, septa are progressively thinned and shortened. Dissepimentarium is 4.5–5 mm thick with the diameter of corallite 3.5 cm. Dissepimentarium is the greatest in counter quadrants.

Comparison. From *A. intermedium* (Toula, 1875), the type species of the genus *Arctophyllum* Fedorowski, 1975, which comes from the Upper Carboniferous of Bjørnøya and Spitsbergen, studied in detail by Fedorowski (1975) and known as well as from the Carboniferous of Novaya Zemlya and the Upper Carboniferous of the Moscow Basin, *A. lugankaensis* differs by having thin septa at the early growth stages and by the absence of an "amplexoid" developmental stage. The established species differs from *A. minima* Kossovaya (Kossovaya, 1986, 1997) from the Asselian of Samara Luka Area by the presence of bipartite tabularia and by less number of septa.

Remarks. The mature growth stages of the new species are very similar to specimens described by Fomichev (1953) as *Caninia ruprechti* Stuckenberg var. *meridionalis* Fomichev. As Fomichev had incomplete material, he could not study the early growth stages. Thus, I am not sure that *A. lugankaensis* and the species described by Fomichev are the same species. Besides, a generic assignment to the species established as *Caninia ruprechti* Stuckenberg (1895), which comes from the Arkhangelsk area, is not clear because the holotype illustrated in pl. 16, fig. 9a, b (Stuckenberg, 1895) was lost. In turn, Iwanowski (1987) additionally studied typical material from the collection of Stuckenberg (the specimen 469/305, which was not illustrated by Stuckenberg). As a result, he came to the conclusion that one specimen belonged to the genus *Skolekophyllum* Fomichev, 1953 because this specimen had long major septa. Other researchers (Soshkina et al., 1941; Kossovaya, 1986) continued to consider this species belonging to the genus *Caninophyllum* Lewis, 1929. Soshkina, Dobrolyubova, and Porfiriev (Soshkina et al., 1941) proposed the specimen 472/505 from the Stuckenberg's collection as the holotype of *Caninophyllum ruprechti* (Stuckenberg). But this specimen is derived from a different area. It is found at the Belaya River in the South Urals. A cylindrical form of this specimen prevents us from studying the early growth stages. At present, the species *Caninophyllum ruprechti* is valid with some doubt.

Occurrence and age. Ukraine, the Donets Basin. The Upper Carboniferous, lower Gzhelian, the Avilovka Suite (limestone $O_6{}^1$).

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Research paper

Corals from the Upper Viséan of the southern Azrou-Khenifra Basin (Carboniferous, Central Moroccan Meseta)

Markus Aretz[a,b,c,*], Hans-Georg Herbig[d]

[a] *Université de Toulouse (UPS), LMTG (OMP), 14 Avenue Edouard Belin, F-31400 Toulouse, France*
[b] *CNRS, LMTG, F-31400 Toulouse, France*
[c] *IRD, LMTG, F-31400 Toulouse, France*
[d] *Institut für Geologie und Mineralogie, Universität zu Köln, Zülpicher Str. 49a, 50674 Köln, Germany*

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Abstract

This is the first taxonomic treatment of coral faunas from upper Viséan shallow-water limestones of the southern Azrou-Khenifra Basin (eastern central Morocco). Corals recovered during reconnaissance work represent 8 genera and 11 species of rugose corals, 1 heterocoral species, and 3 tabulate coral taxa. The fauna is tentatively attributed to the late Asbian. *Siphonodendron scaleberense* is described from Northern Africa for the first time. Facies differentiations clearly control the coral distribution in the stratotype of the Bou-Rifi Formation near Sidi-Lamine. In the Tabaïnout Ridge, the massive build-up facies is almost devoid of corals except for specialised forms such as ?*Sutherlandia*. Bioclastic and oncolitic limestone facies below and above the build-up facies contain coral faunas, which differ in their compositions. The fauna of the Azrou-Khenifra Basin is part of the West European-North African faunal province.

Keywords: Corals; Upper Viséan; Central Moroccan Meseta; Facies dependency; Build-up facies; West European–North African faunal province

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1. Introduction

Carboniferous corals have been scarcely studied in Morocco despite their almost ubiquitous distribution in shallow marine carbonate facies. In general, taxonomic information (Fig. 1A) is based on specimens that were collected during regional geological studies, resulting mostly in determinations like "*Dibunophyllum*", "*Caninia*" or "*Lithostrotion*". A notable exception is Izart et al. (1989), who described the new taxon *Caninophyllum skouraensae* Poty from the Skoura Massif, southern margin of the central High Atlas. Summaries of the knowledge were presented by Termier and Termier (1950) and Bensaid et al. (1985). Recent work (Said and Rodríguez, 2007; Said et al., 2007) in the Adarouch area in northeastern central Morocco (northeastern part of the Azrou-Khenifra Basin) demonstrated the presence of highly diverse coral assemblages. Similar diversities can be deduced from the fauna of the Jerada Massif in the Eastern Moroccan Meseta (Aretz, 2010) and the briefly described fauna of the eastern Anti-Atlas (Wendt et al., 2001) as well as from reefal facies in the western Jbilet (Permingeat, 1951; André, 1986). Therefore, diverse faunas are expected also elsewhere in Morocco in favourable facies.

From the southern part of the Azrou-Khenifra basin, only few data are available. Except for Termier (1936) and Termier et al. (1975), who listed Upper Viséan corals from various central Moroccan localities, only Chanton-Güvenç et al. (1971) discussed a coral faunule from the Jbel Hadid. They listed *Lithostrotion* aff. *arachnoideum* McCoy, 1849, *L.* aff. *martini* Milne-Edwards et Haime, 1851, *Clisiophyllum* aff. *ingletonense* Vaughan, 1911, *Siphonophyllia* sp. and an undetermined hapsiphyllid, and from unconformably overlying strata, "numerous fasciculate *Lithostrotion*", very close to *L. pauciradiale* (McCoy, 1844), *Dibunophyllum bipartitum* (McCoy, 1849), and *Siphonophyllia benburbensis* (Lewis, 1927) (=*S. samsonensis* Salée, 1913). Chanton-Güvenç and Morin (1973) noted the existence of corals from the Tabaïnout ridge and Verset (1988) from limestones of his Bou-Rifi Formation, which he equated with all the coral-bearing limestones mentioned above.

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[*] Corresponding author at: Université de Toulouse (UPS), LMTG (OMP), 14 Avenue Edouard Belin, F-31400 Toulouse, France.
E-mail address: markus.aretz@lmtg.obs-mip.fr (M. Aretz).

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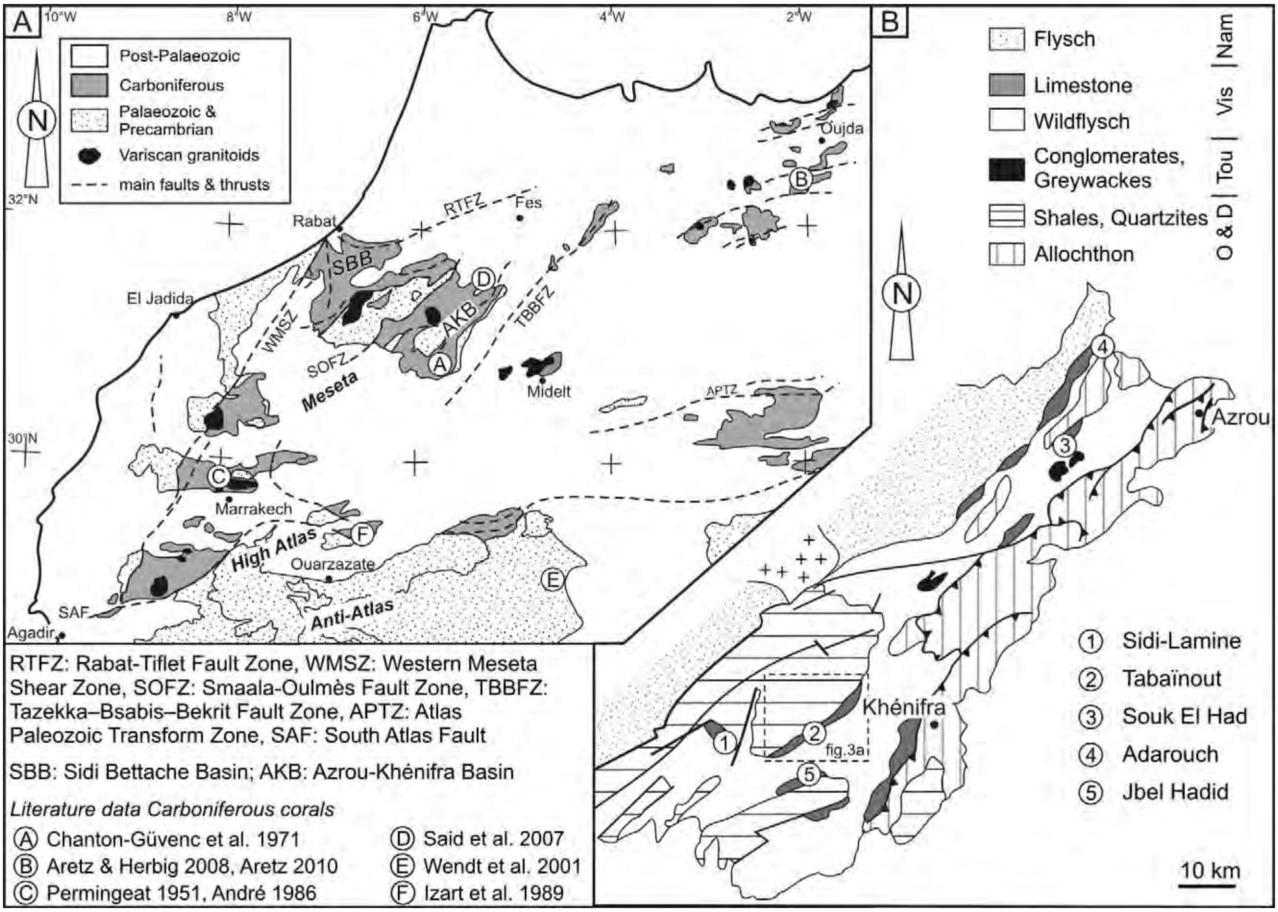

Fig. 1. (A) Overview of the major Palaeozoic structures of Morocco and important coral localities (map modified from Hoepffner et al., 2005). (B) Map of the Azrou-Khenifra Basin and localisation of the known coral occurrences. (1–3) Outcrops of this study; (4) Said et al. (2007); (5) Chanton-Güvenç et al. (1971) (after Bouabdelli and Piqué, 1996).

The corals described herein were collected during reconnaissance work by one of us (HGH) in September 1995 and were already discussed briefly by Aretz and Herbig (2004). Most are from the stratotype of the Bou-Rifi Formation and the Tabaïnout ridge in the southern Azrou-Khenifra Basin (Fig. 1B). They are complemented by a few specimens from a locality about 2 km south of Souk El Had in the northern part of the basin (Fig. 1B). The outcrops represent distinctive tectonically-controlled subunits in the Azrou-Khenifra Basin. Besides description of corals and hosting facies, stratigraphic and palaeobiogeographic implications are briefly discussed. Due to the preliminary sampling, coral diversity and intra-specific variability are probably not fully documented.

2. Geological setting, stratigraphic succession, and facies

The central Moroccan Meseta (Fig. 1A) belongs to the external Moroccan Variscides (e.g., Piqué et al., 1993; see also Hoepffner et al., 2005). Within that tectonically complex structural domain, two major Carboniferous basins are separated by the central Zaer-Oulmés Anticlinorium: the western Sidi Bettache Basin and the eastern Azrou-Khenifra Basin (Fig. 1B). During the Mississippian, the Azrou-Khenifra Basin was marked by important tectonic activity resulting in extensive gravitative redeposition within internal platform-basin topography. In general, a major unconformity separates Mississippian strata and lower to middle Palaeozoic basement (e.g., Beauchamp and Izart, 1987; Verset, 1988; Bouabdelli and Piqué, 1996; Huvelin and Mamet, 1997). In the eastern part of the basin, gravity-driven nappes consisting of Ordovician to Devonian strata were emplaced during the latest Viséan, whereas in its western part, flysch sedimentation continued into the Namurian and, in the northwestern part of the basin, into Westphalian times (Bouabdelli and Piqué, 1996).

The Mississippian succession within the southern Azrou-Khenifra Basin comprises at its base the deposits of the first Viséan transgression (Jbel Takkat and Bou-Iffouloussène formations) dated as middle/late Viséan by calcareous microbiota (probable Cf4δ–Cf5 of the Conil et al., 1980, 1991, foraminiferal zonation, Verset, 1988; for another proof of Middle Viséan age at Jbel Hadid see Huvelin and Mamet, 1997). The "Great Viséan transgression", known throughout Morocco, is recorded on top of another unconformity. Above a basal conglomerate, a mixed late Viséan carbonate-siliciclastic succession developed (Bou-Rifi Formation). Microfaunas of the Bou-Rifi Formation in general indicate Cf6γ–δ subzones (Verset, 1988). The Bou-Rifi Formation is topped by late Viséan black shales (Sidi-Lamine

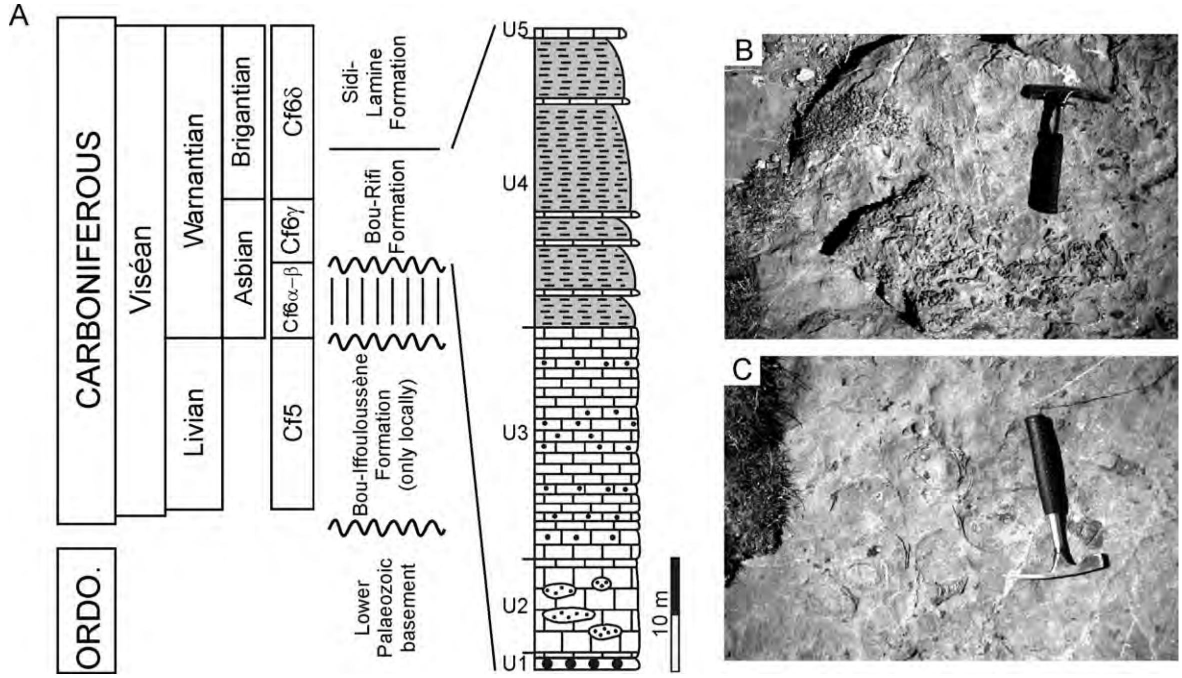

Fig. 2. (A) Stratigraphic overview of the stratotype of the Bou-Rifi Formation (only approximately to scale) (after Verset, 1988). (B) Almost intact *Siphonodendron* colony (upper left) and *Siphonodendron* debris (centre) from U3, Hammer is 20 cm long. (C) Limestone rich in productid brachiopods from U3, Hammer is 20 cm long.

Formation) followed by flysch and wildflysch deposits (Tiberkit Formation) of latest Viséan and Namurian age.

3. Studied outcrops

Stratotype of the Bou-Rifi Formation: It is situated east of Sidi-Lamine (Verset, 1988) directly south of the road to Khenifra (locality 1 in Fig. 1B), forming a low limestone ridge. Age determinations from the type locality are not available, but the formation is considered to be late Asbian-Brigantian (Conil et al., 1980, 1991, foraminiferal subzones Cf6γ–δ, Verset, 1988). The formation (Fig. 2) starts unconformably on top of the Bou-Iffouloussène Formation, with a 1 m-thick basal conglomerate grading into sandy limestone (unit 1). Unit 2 comprises conglomeratic limestone (8 m thick) with cross-stratified sandstone lenses. Unit 3 (20 m) is bluish limestones rich in coarse layers of fossil debris. Macroscopically they contain large fragments of *Siphonodendron* colonies, a few solitary corals, gigantoproductid brachiopods, fenestellid bryozoans, and echinoderm remains; crinoid stems of several cm long occur. The overlying 25 m rocks are dominated by dark shales with few intercalations of thin carbonate beds (unit 4). A 1 m-thick limestone horizon (unit 5) marks the top of the formation. Succeeding blackish shales belong to the Sidi-Lamine Formation. Hance and Verset (in Verset, 1988) differentiated 15 microfacies types for the carbonate rocks of the Bou-Rifi Formation. The corals were all collected from the 20 m-thick limestone interval of unit 3. They were almost completely restricted to some thick beds cropping out close to the top of the limestone ridge. They are encased in (1) sandy bioclastic wackestone with common bioturbation and (2) in bioclastic packstone and grainstone.

Tabaïnout **Ridge** (locality 2 in Fig. 1B): This is a prominent mountain ridge along the Khenifra–Sidi-Lamine road north of Sidi Amar (Fig. 3). Chanton-Güvenç and Morin (1973) studied the area (Fig. 3) and reported pinnacle reefs forming some of the peaks of that mountain ridge (e.g., “Cathédrale”). Dating of the Tabaïnout limestones by calcareous microbiota is slightly controversial. They were originally considered as upper V3c in age by Chanton-Güvenç and Morin (1973), then as V3bγ–V3c by Termier et al. (1975), and as the Moroccan foraminiferal zone Cfm6 (boundary interval V3bβ–V3bγ) by Vachard and Tahiri (1991). Finally, Huvelin and Mamet (1997) claimed the V3b for the first transgressive limestones and also for olistolites in the overlying strata; V3c was not mentioned. In short, an Asbian age is likely for the Tabaïnout limestones. The “reefs” remain unstudied and thus the term build-up is implied herein. Field observations and microfacies data indicate possible similarities to contemporaneous build-up facies from NE Morocco (Aretz and Herbig, 2008; Cózar et al., 2008).

Chanton-Güvenç and Morin (1973) divided the Upper Viséan limestones into (1) Lower Limestones below the build-ups, (2) Median Limestones, e.g., build-ups and surrounding facies, and (3) Upper Limestones above. These units represent each several tens of metres of thickness depending on the formation of build-ups; the maximum thickness is 250 m for the entire succession (Chanton-Güvenç and Morin, 1973). However, petrographical descriptions were not given, and as a result, our own field observations on the sediment encasing the studied corals are used to characterise the units.

The Lower Limestones comprise (a) fine-grained grainstone and packstone rich in foraminifers and calcareous algae and (b) poorly-sorted crinoidal packstone. In the field, rare bioclastic rudstone, productid-rich limestone and limestone breccia were

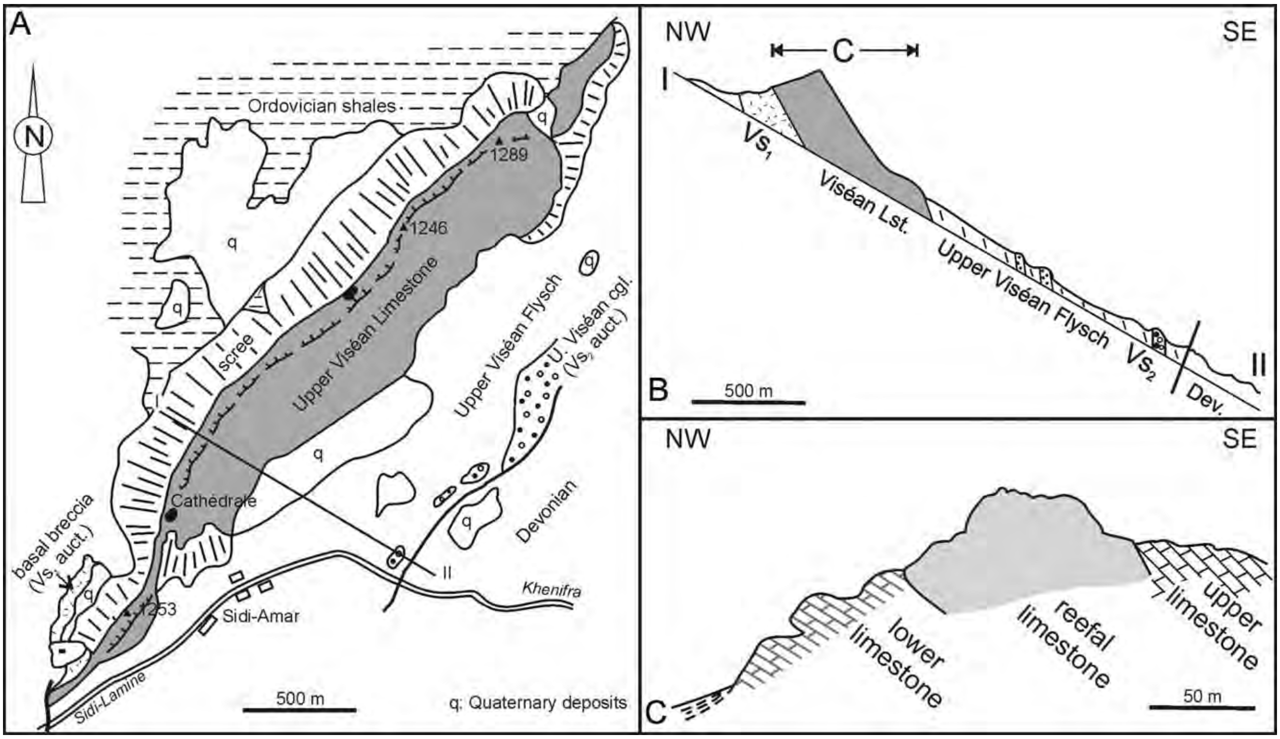

Fig. 3. (A) Geological map of the Tabaïnout Massif. (B) NW-SE orientated cross-section through the Massif. Note the important thickness of the flysch deposits. (C) Detail of B in the Cathédrale area showing the spatial relations of the three units of the upper Viséan limestone (all after Chanton-Güvenç and Morin, 1973).

also observed. The build-up facies, macroscopically a dense homogeneous limestone without macroscopically visible fossils (Chanton-Güvenç and Morin, 1973), is represented by peloidal boundstones rich in microbial incrustations, automicrites, and bryozoans. Primary porosity is filled with blocky spar-cement, but diagenetic overprint resulting in several cement generations partly obscures the original textures. The Upper Limestones comprise oncolitic rudstones, and fine-grained bioclastic grainstones with variable amount of foraminifers, calcareous algae, and crinoids. Corals remain scarce in the Lower limestone, large solitary corals and colonial corals have been derived from the Upper Limestones, and the build-up facies is almost devoid of corals.

Souk El Had: The outcrop (locality 3 in Fig. 1B) is a northeast-trending limestone ridge situated about 2 km south of Souk El Had along the road from Mrirt to Azrou. Bedded Viséan limestones yielded very few corals and coral fragments. Microfacies of the coral-bearing limestones consists of (1) coarse-grained oncolitic packstone in alternation with thin bioclastic grainstone layers and (2) bioclastic grainstone and rudstone with few coated grains.

4. Discussion of coral assemblages

4.1. Age

The Late Viséan age of the recovered specimens has already been indicated by the previously described macro- and microbiota. Additional taxa from the Jbel Hadid (southernmost Azrou-Khenifra basin) indicate the same stratigraphic interval (Chanton-Güvenç et al., 1971).

Coral taxa appearing in the late Asbian or in the Brigantian (Rodríguez and Somerville, 2007, table 1) are lacking so far from the southern part of the Azrou-Khenifra basin except for the report of *Dibunophyllum bipartitum* from the Jbel Hadid and the vague indication of few specimens that might belong to *Koninckophyllum interruptum* in our material, both appearing in the late Asbian. On the other hand, *Siphonodendron scaleberense* from the type section of the Bou-Rifi Formation was not yet reported from Brigantian strata and confirms the Asbian character of the fauna.

The hitherto known corals from the southern Azrou-Khenifra Basin share most taxa with the assemblages from the middle and basal upper member of the Tizra Formation in the northern part of the basin (Said et al., 2007). Diphymorph and small-sized lithostrotionid corals and the Brigantian marker *Palastraea regia* enter together above, but are absent in the south – note that Cózar et al. (2008) claimed the base of the Brigantian to coincide with the base of the upper member of the Tizra Formation. The missing taxa in the south might be related to insufficient sampling or to facies dependencies, e.g., generally thinner carbonate successions and more important siliciclastic influx. However, occurrence of *Siphonodendron scaleberense* and the absence of the Brigantian assemblage of the upper Tizra Formation indicate a late Asbian age of our fauna. This is supported by the fact that the basal part of the Bou-Rifi Formation was placed in the foraminiferal subzone Cf6γ and the Tabaïnout ridge contained foraminifers of V3b age (Huvelin and Mamet, 1997).

	Bou-Rifi Formation Bioclastic grain/rudstone	Bou-Rifi Formation Sandy bioclatic wackestone	Bou-Rifi Formation corals without matrix	Tabaïnout ridge Lower Limestones	Tabaïnout ridge Median Limestones	Tabaïnout ridge Upper Limestones	Souk el Had
Rugosa							
Palaeosmilia murchisoni				X			X
Koninckophyllum aff. *interruptum*		X					
Amygdalophyllum sp.						X	
?*Auloclisia* sp.			X				
?*Haplolasma* sp.			X				
Lithostrotion vorticale				X			
Siphonodendron pauciradiale		X				X	
Siphonodendron irregulare		X		X			?
Siphonodendron martini		X				X	
Siphonodendron scaleberense	X						
Axophyllum sp.						X	
Heterocorals							
Heterophyllia ornata	X			X			
Tabulata							
Syringopora sp. A.						X	
Syringopora sp. B						X	
?*Sutherlandia* sp.					X		
Auloporida indet.							X

Fig. 4. Facies distribution of the coral taxa in the studied outcrops.

4.2. *Distribution and facies*

Within the studied outcrops, facies controls the abundance of specific coral taxa (Fig. 4). In the stratotype of the Bou-Rifi Formation, three species of *Siphonodendron* occur in sandy bioclastic wackestone, whereas the species with the largest sized corallites (*S. scaleberense*) is found in pure bioclastic grainstone/packstone. In the Tabaïnout ridge, the Median Limestones of the build-up facies contained only ?*Sutherlandia.* The bedded facies of the Lower and Upper Limestones contain relatively diverse coral faunas, but compositional differences exist (Fig. 4). As already noted in the field, the abundance and diversity is higher in the Upper Limestones. Syringoporids were only found in the Upper Limestones of the Tabaïnout ridge. The collected corals are a typical shallow-water caniniid-clisiophyllid fauna (Hill, 1938), as also indicated by microfacies.

4.3. *Palaeobiogeography*

The recovered fauna shows strong similarities to late Viséan faunas of NW Europe and SW Spain (e.g., Poty, 1981; Rodríguez and Somerville, 2007). Thus, the Azrou-Khenifra Basin is part of the West European-North African faunal province. Contemporaneous coral faunas from southern France (e.g., Aretz, 2002a,b) and southern Spain (Betic Cordillera, Herbig, 1986) are clearly separated from this province by the occurrence of genera like *Kizilia* and *Gangamophyllum*. Also *Lonsdaleia*, which is common in southern France and southern Spain, is not recorded in the Azrou-Khenifra Basin.

5. Systematic descriptions

For the present preliminary study 29 samples had been available. Thus, intra-specific variabilities are mostly unknown. Short systematic descriptions are presented for all taxa; synonymy lists are reduced to a minimum in making references to more extensive lists [cum syn.] or to descriptions of regional relevance. It has been aimed to gain a maximum of transverse and longitudinal section of each specimen. Preservation of the individual specimens is often not good due to fragmentation, marginal erosion, and diagenesis. The material is housed in the collection of the "Institut für Geologie und Mineralogie, Universität zu Köln" under the numbers GIK 2241–2265.

Subclass RUGOSA Milne-Edwards et Haime, 1850
Family PALAEOSMILIIDAE Hill, 1940

Palaeosmilia murchisoni Milne-Edwards et Haime, 1848 (Fig. 5A)

*1848 *Palaeosmilia murchisoni* - Milne-Edwards et Haime, p. 261.
2005 *Palaeosmilia murchisoni* Milne-Edwards et Haime - Aretz and Nudds, p. 172, pl. 1, fig. 5 [cum syn.].

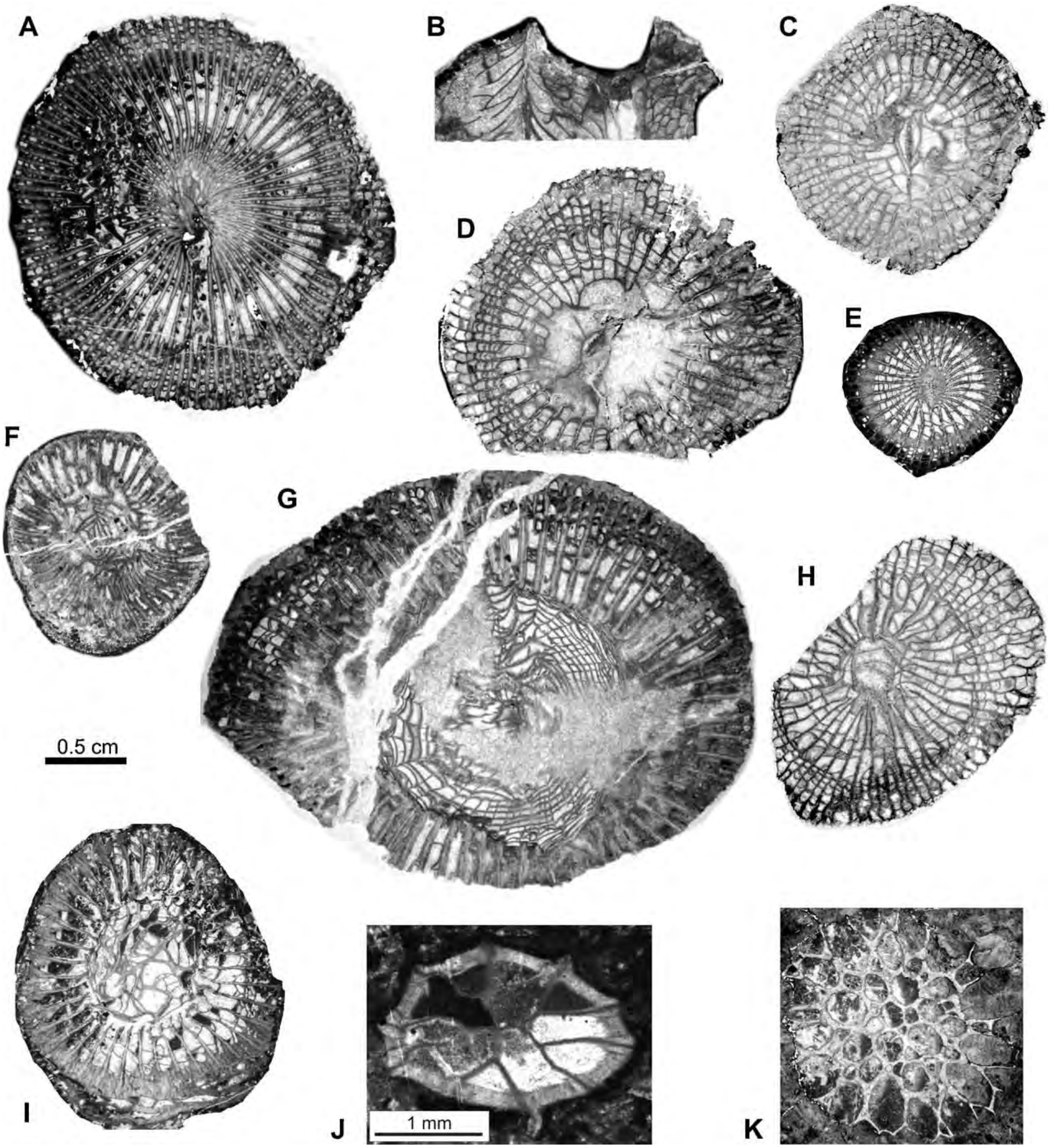

Fig. 5. (A) *Palaeosmilia murchisoni* Milne-Edwards et Haime, 1848; specimen GIK 2241, Tabaïnout ridge, Lower Limestones, transverse section. (B–D) *Koninckophyllum* aff. *interruptum* Thomson et Nicholson, 1876; specimen GIK 2243, type section of Bou-Rifi Formation. (B), longitudinal section, (C, D), transversal sections. (E) *Amygdalophyllum* sp.; specimen GIK 2247, Tabaïnout ridge, Upper Limestones, transverse section. (F, G) *Auloclisia*? sp.; type section of Bou-Rifi Formation, transverse sections. (F), juvenile stage (GIK 2248), (G), adult stage (specimen GIK 2249). (H) *Haplolasma*? sp.; specimen GIK 250, type section of Bou-Rifi Formation, transverse section. (I) *Axophyllum* sp.; specimen GIK 2260, Tabaïnout ridge, Upper Limestones, transverse section. (J) *Heterophyllia ornata* McCoy, 1849; specimen GIK 2261, Tabaïnout ridge, Lower Limestones, transverse section. (K) *Sutherlandia*? sp.; specimen GIK 2265, Tabaïnout ridge, Median Limestones (buildup facies), transverse section.

Material: Specimen GIK 2241: Tabaïnout Ridge, Lower Limestones; GIK 2242: Souk El Had, thin sections: 2 transverse.

Description: Two fragments, external wall and parts of dissepimentarium lacking; Maximum diameter up to 3.5 cm; Numbers of major septa 57 and 72 respectively; Deep cardinal fossula; Formation of an alar fossula in the larger specimen; Major septa always reach the axis; Septa thicker (av. 0.2 mm) in the dissepimentarium than in the tabularium (av. 0.1 mm); Minor septa reach a few mm into the tabularium; Septa straight to slightly sinuous in the dissepimentarium; Major septa in the tabularium strongly sinuous and may touch each other near the axis; Dissepimentarium only incompletely documented, inner parts consist of small, globose dissepiments

in regular concentric arrangement, outer parts become more irregular.
Discussion: Both fragments fit well into the variability of this species (Semenoff-Tian-Chansky, 1974).
Age and occurrence: This species is well known from the lower Viséan to Serpukhovian in Europe and North Africa (see, Semenoff-Tian-Chansky, 1974; Poty, 1981; Mitchell, 1989).

Family AULOPHYLLIDAE Dybowski, 1873

Koninckophyllum aff. *interruptum* Thomson et Nicholson, 1876
(Fig. 5B–D)
Material: Specimens GIK 2243 and GIK 2244: type section of Bou-Rifi Formation, thin sections: 5 transverse, 3 longitudinal.
Description: 2 ceratoid specimens, maximum diameter 1.8 and 2.0 cm; Thin wall rarely preserved; 37–40 septa in two series; Major septa long, sinuous, some fused with the simple axial structure, thickened at the base; Minor septa half as long as major septa; Irregular simple axial structure of a single axial plate which in transverse sections may be surrounded by one to several axial tabellae (?), however, the longitudinal sections only show incomplete tabulae inclined towards the axis; Regular concentric dissepimentarium, 0.3–0.4 mm thick, consisting of 6 rows of globose concentric dissepiments.
Discussion: The specimens are similar to smaller specimens of *K. interruptum*, but their axial structure is somewhat more complex and irregular, like in *K. variabile* Semenoff-Tian-Chansky, 1974 or *K. magnificum* Thomson et Nicholson, 1876.
Age and occurrence: *K. interruptum* is known from the late Viséan of Europe and North Africa.

Amygdalophyllum sp.
(Fig. 5E)
Material: 3 specimens (GIK 2245, GIK 2246, GIK 2247), Tabaïnout ridge, Upper Limestones, thin sections: 4 transverse, 1 longitudinal.
Description: Diameter of the corallites is 1.0–1–1 cm; Thin wall rarely preserved; 27–32 septa in two series; Carinate major septa long, sinuous, and thickened at the base; Minor septa very short; Well developed amygdalophyllid axial structure up to 2.8 mm long and 2.0 mm wide; 3–5 rows of regular concentric dissepiments; Stereoplasmatic thickening on the tabularium wall is present.
Discussion: The specimens share with *A. pachyphylloides* Semenoff-Tian-Chansky, 1974 septa/corallite diameter ratios, and the thickening of the septa. However, the Tabaïnout specimens differ in the thinning of the septa towards the axial structure, and the carinate septa. Thicker septa, carinate septa, and the short minor septa are different from younger stages of *A. etheridge* Dun et Benson, 1920, which have a comparable septa/corallite diameter ratio.

Auloclisia? sp.
(Fig. 5F, G)
Material: Two poorly preserved specimens (GIK 2248, GIK 2249), type section of Bou-Rifi Formation, thin sections: 3 transverse, 1 longitudinal.
Description: GIK 2248 only half of the adult corallite is preserved, GIK 2249 partly eroded at its wall; Coral diameters 3.3 (Fig. 5F) and 3.4 cm; Wall 0.2 mm thick; Two series of 66 septa in the complete specimen; Thick major septa attain axial structure; Minor septa variable in length, but generally relatively short (1/4–1/3 of major septa); Axial structure clisiophylloid with diameter of 1.5 cm consists of single axial plate, numerous septal lamellae and tabellae; 3–6 steeply declined rows of elongated dissepiments; Tabulae incomplete, densely spaced; In younger stages marked thickening of the major septa in the cardinal (?) quadrants (Fig. 5G), axial structure more open and fewer tabellae and lamellae.
Discussion: The transition from *Clisiophyllum* via *Auloclisia* to *Aulophyllum* (e.g., illustrated in Rodríguez et al., 2001) is gradual, and individual specimens may be problematic to place. Semenoff-Tian-Chansky (1974) reported an important intra-specific variability in *Clisiophyllum benziregense* Semenoff-Tian-Chansky, 1974 with representatives indicating the transition to the genus *Auloclisia* (his pl. 10, Fig. 6). The Khenifra specimen falls into this line, but its axial structure is larger than in typical *C. benziregense* and additionally, the dissepiments are elongated and larger. Based on its axial structure and the aulophyllid character of its septa, the specimens are provisionally placed into *Auloclisia*.

Haplolasma? sp.
(Fig. 5H)
Material: 1 specimen (GIK 2250), type section of Bou-Rifi Formation, thin sections: 3 transverse, 1 longitudinal.
Description: Single fragment of ceratoid coral; Approximately 3 cm long and 2.0–2.2 cm in diameter; Wall and outer parts of the dissepimentarium eroded; Two series of maximum 37 septa; Sinuous major septa always reach close to axis, in one thin section the septa are strongly curved in the corallite centre; Short cardinal septum and cardinal fossula developed; Minor septa project as septal spines into the tabularium; Dissepimentarium consists of 4–7 rows of globose dissepiments arranged in most parts in a regular concentric pattern, which becomes irregular in the outer parts; Complete tabulae slope down at their margins.
Discussion: The specimen shows typical characters of the genus *Haplolasma*, but due to the poor preservation of the outer parts of the dissepimentarium, the taxonomic affiliation is questionable.

Family LITHOSTROTIONIDAE d'Orbigny, 1852

Lithostrotion vorticale (Parkinson, 1808)
(Fig. 6A)

*1808	*Madrepora vorticalis* - Parkinson, p. 45, pl. 5, figs. 3 and 6.
2005	*Lithostrotion vorticale* (Parkinson) - Aretz and Nudds, p. 175, pl. 2, fig. 8 [cum syn.].

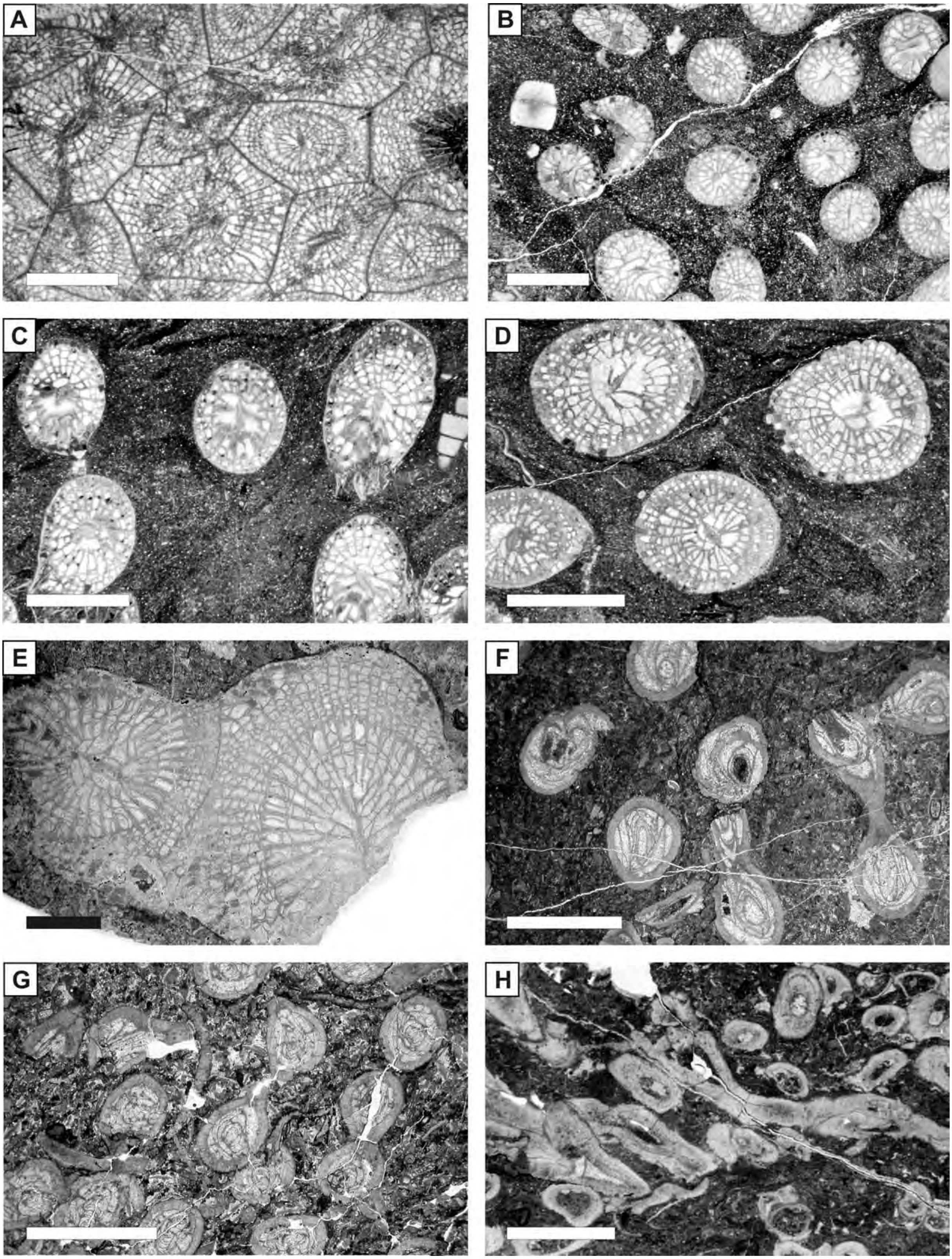

Fig. 6. (A) *Lithostrotion vorticale* (Parkinson, 1808); specimen GIK 2251, Tabaïnout ridge, Lower Limestones; transverse section. (B) *Siphonodendron pauciradiale* (McCoy, 1844); specimen GIK 2253, type section of Bou-Rifi Formation, transverse section. (C) *Siphonodendron irregulare* (Phillips, 1836); specimen GIK 2254, type section of Bou-Rifi Formation, transverse section. (D) *Siphonodendron martini* (Milne-Edwards et Haime, 1851); specimen GIK 2257, type section of Bou-Rifi Formation, transverse section. (E) *Siphonodendron scaleberense* Nudds et Somerville, 1987; specimen GIK 2259, type section of Bou-Rifi Formation, transverse section. Note cardinal fossula in the upper left of the left corallite. (F) *Syringopora* sp. A; specimen GIK 2263, Tabaïnout ridge, Upper Limestones, transverse section. (G) *Syringopora* sp. B; specimen GIK 2264, Tabaïnout ridge, Upper Limestones, transverse section. (H) Auloporidae indet.; specimen GIK 2256, limestone ridge 2 km south of Souk el Had, transverse section; all scale bars = 5 mm.

Material: 2 specimens (GIK 2251, GIK 2252), Tabaïnout ridge, Lower Limestones, thin sections: 2 transverse, 1 longitudinal.
Description: Cerioid corallum with polygonal shaped corallites; Thin wall; Two series of 22–24 septa; Cardinal and counter septum may be attached to styliform columella; Minor septa cross irregular dissepimentarium; Diameter of the tabularium 3.5–4.2 mm in width, incomplete tabulae increase towards axis; 23 tabulae/cm; 3–6 rows of globose to elongated dissepiments; lonsdaleoid dissepiments may occur.

Discussion: Both fragments show the typical morphological character of the species (Hill, 1940; Poty, 1981).
Age and occurrence: In Europe, the species extends from the Holkerian/Livian to the late Brigantian (Mitchell, 1989; Rodríguez et al., 2002). In North Africa, Semenoff-Tian-Chansky (1985) mentioned it from the upper Viséan of the Béchar Basin, and Said et al. (2007) reported it from the Brigantian of the Adarouch area.

Siphonodendron pauciradiale (McCoy, 1844)
(Fig. 6B)

*1844	*Lithodendron pauciradialis* - McCoy, p. 189, pl. 27, fig. 7.
2005	*Siphonodendron pauciradiale* (McCoy) - Aretz and Nudds, p. 176 [cum syn.].

Material: Specimen (GIK 2253), type section of Bou-Rifi Formation, thin sections: 1 transverse, 1 longitudinal.

Description: Fragment of fasciculate corallum; Corallite diameter 3.5–4 mm; Thin wall; Two series of 16–19 septa; Cardinal and counter septum may be attached to styliform columella; Short minor septa; Incomplete tabulae increase towards axis; 20–25 tabulae/cm; 1 row of globose dissepiments.

Discussion: The fragment of a colony shows the typical morphological character of the species (Poty, 1981).
Age and occurrence: In Europe, *S. pauciradiale* appears in the early Asbian (Fauna F, Mitchell, 1989) and persists into the Brigantian. In North Africa, Semenoff-Tian-Chansky (1985) mentioned it from the late Viséan of the Béchar Basin, and Said et al. (2007) reported it from the Brigantian of the Adarouch area.

Siphonodendron irregulare (Phillips, 1836)
(Fig. 6C)

*1836	*Lithodendron irregulare* - Phillips, p. 202, pl. 2, figs. 14 and 15.
2002a	*Siphonodendron irregulare* (Phillips) - Aretz, p. 112, pl. 1, fig. 8; pl. 5, fig. 4; pl. 10, fig. 4 [cum syn.].
2002	*Siphonodendron irregulare* (Phillips) - Rodríguez et al., p. 26, fig. 13a.
2005	*Siphonodendron* sp. - Aretz and Nudds, p. 178, pl. 3, fig. 1.

Material: 2 specimens (GIK 2254, GIK 2255), type section of Bou-Rifi Formation; 1 specimen (GIK 2262), Tabaïnout ridge, Lower Limestones, thin sections: 4 transverse, 3 longitudinal.

Description: Three fragments of fasciculate coralla with corallite diameters of 4.5–5.6 mm; thin wall; Two series of 20–24 septa; Major septa thin, straight or slightly sinuous, rarely attain columella, which is a simple axial plate; Minor septa cross dissepimentarium and end as septal spines in the tabularium, variable length up to 1/3 of the major septa; Dissepimentarium consists of two rows of globose to elongated dissepiments; Incomplete tabulae convex towards axial structure and curved peripherally downwards.
Discussion: Fragmented corallites in Souk el Had sample GIK 2256 resemble corallites of *S. irregulare* from the southern parts of the basin, but due to their poor preservation and scarcity, they have not been assigned to a specific affiliation. Aretz and Nudds (2005) discussed the main problems of the correct specific affiliation of *Siphonodendron* specimens between the two well-defined species *S. pauciradiale* and *S. martini*. In our study, *S. irregulare* Phillips (1836) is used as defined by Poty and Hannay (1994).

Age and occurrence: Due to the confusion of the correct specific affiliations, the occurrence of the species is somewhat uncertain. In Europe and North Africa, "*Siphonodendron irregulare*" has been used for specimens of middle and late Viséan age. It is probably the most often-cited species of *Siphonodendron* in Morocco.

Siphonodendron martini (Milne-Edwards et Haime, 1851)
(Fig. 6D)

*1851	*Lithostrotion martini* - Milne-Edwards and Haime, p. 436.
2005	*Siphonodendron martini* (Milne-Edwards et Haime) - Aretz and Nudds, p. 178, pl. 3, fig. 2 [cum. syn.].

Material: 1 specimen (GIK 2257), type section of Bou-Rifi Formation; 1 specimen (GIK 2258), Tabaïnout ridge, Upper Limestones, thin sections: 3 transverse, 2 longitudinal.
Description: Two colony fragments; Fasciculate corallum; Corallite diameter: 6–9 mm; Two series of 24–28 septa; Cardinal and counter septum almost always attached to styliform columella, other major septa occasionally; Short minor septa; Incomplete, tent-shaped tabulae; 2–4 rows of globose to elongated dissepiments.

Discussion: The two colony fragments show the typical morphological characters of the species (Semenoff-Tian-Chansky and Nudds, 1979; Poty, 1981).
Age and occurrence: In Europe, *S. martini* appears in the Holkerian/Livian and persists into the Brigantian. In North Africa, Semenoff-Tian-Chansky (1985) mentioned it from the upper Viséan of the Béchar Basin, and Said et al. (2007) reported it from the Brigantian of the Adarouch area.

Siphonodendron scaleberense Nudds et Somerville, 1987
(Fig. 6E)

*1987	*Siphonodendron scaleberense* - Nudds and Somerville, p. 295, figs. 2A-E, 5A, B.
2002	*Siphonodendron scaleberense* Nudds et Somerville - Rodriguez et al., p. 33, fig. 17.
2007	*Siphonodendron scaleberense* Nudds et Somerville - Rodriguez and Somerville, p. 303, pl. 1, figs. 6 and 7.

Material: Specimen GIK 2259, type section of Bou-Rifi Formation, thin sections: 1 transverse, 1 longitudinal.

Description: Single colony fragment of four large *Siphonodendron*-type corallites; Corallites partly in contact, fasciculate-subcerioid habit (Fig. 6E); Corallite diameters 15–18 mm; Tabularium diameter 10–13 mm; Thin wall; Two series of 30–32 septa; Septa mainly straight; Major septa reach towards the axis, but withdrawn; Counter septum attached to styliform columella; Cardinal fossula developed; Major septa thickened within tabularium; Minor septa half as long as major septa, end after 0.1–0.3 mm within the tabularium; Tabulae incomplete, tent-shaped in longitudinal section; Dissepimentarium of 4–6 rows of mainly globose, sometimes elongated dissepiments, becomes wider and more irregular and lonsdaleoid dissepiments develop in the areas of subcerioid habit.

Discussion: The specimen is considered to fall into the intraspecific variability of *S. scaleberense* although the major septa are rather long. Note that the same complex dissepimentarium is visible in a specimen figured by Rodríguez and Somerville (2007) and corresponds to corallites in contact to neighbours. The relatively close spacing and expanded contact of the corallites of the Tabaïnout specimen is somewhat unusual. Thickened major septa at the base of the tabularium have been also illustrated for other larger sized *Siphonodendron* (e.g., in Poty, 1981, *Siphonodendron* sp., his pl. 13, fig. 3).

Age and occurrence: *S. scaleberense* is known from the Holkerian and Asbian of the British Isles (Nudds and Somerville, 1987; Cózar et al., 2005) and from the Asbian of Spain (Rodríguez et al., 2002). It is the first record of the species in North Africa.

Family AXOPHYLLIDAE Milne-Edwards et Haime, 1851

Axophyllum sp.
(Fig. 5I)

Material: Specimen GIK 2260, Tabaïnout ridge, Upper Limestones, thin sections: 1 transverse.

Description: A single transverse section. Diameter 1.9 cm; Wall thin; 38 septa in two series; Major septa up to 6 mm in length, thin and sinuous, withdrawn from the axial structure, thick at their base; Minor septa short, 1/3 of major septa; Axophyllid axial structure with tendency to become gangamophyllid, 5 mm in diameter; Dissepimentarium contains lonsdaleoid dissepiments of first and second order, only a few mm thick and mostly abraded.

?Class HETEROCORALLIA Schindewolf, 1941

Family HETEROPHYLLIDAE Dybowski, 1873
Heterophyllia ornata McCoy, 1849
(Fig. 5J)

*1849	*Heterophyllia ornata* - McCoy, p. 127.
1981	*Heterophyllia ornata* McCoy - Poty, p. 72, fig. 62; pl. 34, figs. 5–13 [cum. syn.].
1995	*Heterophyllia ornata* McCoy - Sugiyama, p. 165, figs. 3–6, 8, 9.

Material: Specimen GIK 2259, type section of Bou-Rifi Formation, GIK 2261, GIK 2262, Tabaïnout ridge, Lower Limestones, thin sections: 3 transverse.

Description: Prismatic transverse sections; Diameter of the corallite up to 2.6 mm (longer axis), respectively up to 1.6 mm (shorter axis); Thickness of the yellowish wall 0.1–0.2 mm; 10–12 septa meet at or near the axis; Peripheral edges of septa thickened, cross the wall and form costae; Cardinal and counter cardinal septa easily distinguished; Only the two alar septa are separated.

Age and occurrence: The specimen fits well into the variability of the species (Poty, 1978, 1981), which is known from the Viséan and Serpukhovian in Eurasia.

Remarks: A single section of a heterocoral with six septa (diameter 0.4 mm) was found in the same thin section (GIK 2261) as one of the *Heterophyllia ornata* specimens. It either represents a juvenile of that species or belongs to *Hexaphyllia*.

Subclass TABULATA Milne-Edwards et Haime, 1850
Family SYRINGOPORIDAE de Fromentel, 1861

The two fragments described herein clearly belong to the genus *Syringopora*, but a specific attribution is so far not possible because of the lack of information on interspecific and intraspecific variations and the general poor knowledge of western European and North African syringoporid corals.

Syringopora sp. A
(Fig. 6F)

Material: Corallum fragment (GIK 2263), Tabaïnout ridge, Upper Limestones, thin sections: 1 transverse.

Description: Single fragment of fasciculate corallum; Corallite diameters 2.9–3.2 mm; Intercorallite spacing irregular, 2–5 mm; 3–5 corallites per cm^2; Lateral increase; Wall consists of outer 0.05 mm-thick dark layer (epitheca?) and inner zone (yellowish) of concentric laminae (up to 0.4 mm thick); Laminae interrupted by rows of short septal spines, less than 20 spines in transverse section; Tabulae infundibuliform, declined and irregular, in transverse sections concentric or subconcentric around axial syrinx of ~0.5 mm in diameter; Few syrinx in lateral positions; Stereoplasmatic thickening on tabulae.

Syringopora sp. B
(Fig. 6G)

Material: Corallum fragment (GIK 2264), Tabaïnout ridge, Upper Limestones, thin sections: 1 transverse.

Description: Single fragment of a fasciculate corallum; Corallite diameters 2.0–2.5 mm; Intercorallite spacing relatively irregular, 1–5 mm, 5–9 corallites per cm^2; Lateral increase; Wall consists of outer 0.05 mm-thick dark layer (epitheca?) and inner zone (yellowish) of concentric laminae (up to 0.35 mm thick); Laminae interrupted by rows of short septal spines, with 20–28 spines in transverse section, less than 30 spines/cm in individual vertical rows; Tabulae infundibuliform, declined and irregular, in transverse sections concentric or subconcentric around axial syrinx of ~0.3 mm in diameter; Few syrinx in lateral positions; Stereoplasmatic thickening on tabulae.

Remarks: *Syringopora* sp. B differs from *Syringopora* sp. A by smaller corallites, smaller syrinx, more corallites/cm^2, and more septal spines/cm.

Family FAVOSITIDAE Dana, 1846

Sutherlandia? sp.
(Fig. 5K)
Material: Specimen GIK 2265, Tabaïnout ridge, Median limestones (buildup facies), thin sections: 1 transverse.
Description: Poorly preserved sections of compound colony in petrographic thin section; Maximum diameter of corallum 1.4 cm; Polygonal corallites up to 2 mm in diameter; Much smaller corallites intercalated into the angles between larger ones; No squamulae and tabulae visible; Occasional septal spines; Few mural pores up to 0.2 mm in diameter.
Discussion: The specimen is placed into the genus with some doubt based on the absence of squamulae. However, the morphological characters fall into the variability of *Sutherlandia* cf. *parasitica* (Phillips, 1836) described from the upper Viséan of Portugal (Tourneur, 1998).

6. Conclusions

Corals recovered from the upper Viséan strata during reconnaissance work in the southern Azrou-Khenifra Basin are relatively diverse. They belong to 8 genera and 11 species of rugose corals, 1 heterocoral species, and 3 tabulate taxa. Some characteristic late Asbian-Brigantian taxa are lacking. The fauna is less diverse than in the northern part of the basin (Adarouch area). The lack of characteristic species could result from the low number of samples, but might be also attributed to facies differences. A late Asbian age is assigned to the studied assemblages on the basis of the occurrence of *Siphonodendron scaleberense* Nudds et Somerville, 1987, its first record in North Africa, data on foraminifers in literature, and the close match with the coral fauna of the middle and basal upper member of the Tizra Formation (Adarouch). The fauna of the entire basin belongs to the West European–North African faunal province. The distribution of the corals is facies-controlled. In the Bou-Rifi Formation, *Siphonodendron* is preferentially found in sandy wackestone; pure grainstone and packstone contain corals with larger diameters. Syringoporids are only known from the Upper Limestones above the Tabaïnout build-up.

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Research paper

Appearance of fasciculate rugose corals in the Viséan and Serpukhovian: A review

Sergio Rodríguez[a,*], Ian D. Somerville[b]

[a] Departamento y U.E.I. de Paleontología, Universidad Complutense de Madrid e Instituto de Geología Económica, 28040 Madrid, Spain
[b] UCD School of Geological Sciences, University College Dublin, Belfield, Dublin 4, Ireland

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Abstract

Appearances of new fasciculate rugose corals are especially abundant in the Viséan-Serpukhovian interval. Fasciculate corals may have two different origins. (1) Development of colonialism from solitary corals (e.g., *Corwenia* from *Dibunophyllum*); (2) morphological changes of the established fasciculate taxa that produce new species or genera. Most new fasciculates occur in shallow-water carbonate shelf environments, but the first occurrence is not always easy to identify from published data. One of the typical environments for their first occurrence during the Viséan was the top of microbial mud-mounds. The microbial mounds perhaps have provided isolated areas of shallower water above the sea bottom. These isolated elevated areas could have provided more favourable environments where pioneer coral colonies may have evolved.

All Viséan and Serpukhovian coral assemblages with new colonial corals are dominated by phaceloid species. Consequently, the explanation should be rejected that new colonial corals occur only in empty ecological “niches.” Most of these assemblages also contain solitary corals, including the ancestral “parent species”.

All these observations pose new questions concerning the origin of the fasciculate colonial forms in rugosans. There are evidences that single specimens develop colonial forms as a response to environmental factors. Development of colonialism is possible for single specimens of some solitary genera. However, the capacity for developing persistent colonial growth forms depends on multiple factors, including genetic and environmental ones.

Keywords: Fasciculate corals; Viséan; Serpukhovian; Microbial mounds; Environments; Evolution

1. Introduction

New genera and species of fasciculate rugose corals have appeared throughout the Palaeozoic, from the Upper Ordovician to the Permian. However, new occurrences are especially abundant in some periods, e.g., the Middle Devonian and the Viséan-Serpukhovian interval (see Hill, 1981). The aim of this paper is to analyse the environmental factors that may have increased the ratio of appearance of new fasciculate (mainly phaceloid) rugose corals and their consequences from an evolutionary and taxonomic point of view. Studies of Viséan rugose corals from Ireland, Great Britain, Spain, and Morocco have shown that colonial corals appear first, frequently, in very precise environmental settings. Consequently, we have searched the literature in order to compare the environments of as many genera as possible from the Viséan-Serpukhovian interval to help construct a general summary chart (Table 1).

The habit of corals is a feature that has been usually considered as useful for differentiating genera in rugose corals. This criterion has been increasingly used and some long established genera have been divided in several new genera on the basis of differences in the level of colonialism. Good examples of this are the separation of *Siphonodendron* from *Lithostrotion* (Poty, 1981) and the division of *Aulina* into several genera (Sando, 1976). But in some other cases, the differences are not clear and some genera are still considered to have different habits (e.g., *Aulokoninckophyllum*).

Both parricidal and non-parricidal increase are involved in colony formation in different species and genera of massive and fasciculate rugosans, but parricidal increase only accounts for about 10% of genera for which information is available. Moreover, of these, 85% is peripheral (Scrutton, 1998). In these cases,

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[*] Corresponding author.
E-mail address: ian.somerville@ucd.ie (S. Rodríguez).

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Table 1
Stratigraphic range, geographic distribution, environmental setting (where known), and possible origin of selected fasciculate rugose genera from the Mississippian (data obtained from many sources).

Genus	1st	Last	Environment	Locality 1st occurrence	Geographical distribution	Possible origin
Akiyoshiphyllum	V.	V.		Japan	Endemic	???
"*Aulokoninckophyllum*"	U.A.	U.A.	Shallow water, microbial	Spain	Endemic	*Aulokoninckophyllum*
Caninostrotion	Ch.	S.		USA	Broad?	*Siphonodendron*?
Chonaxis	L.C.	L.C.		Russia	Endemic	*Lonsdaleia*?
Cionodendron	V.	V.		Australia	Broad?	Amygdalophyllinid
Copia	U.V.	U.V.		Voronezh	Endemic	*Clisiophyllum*, *Dibunophyllum*?
Corwenia	U.V.	S.		???	Broad	*Dibunophyllum*
"*Corwenia*"	U.A.	U.A.	Shallow water, reefal	Spain	Endemic	*Clisiophyllum*
Cystoclisiophyllum	L.C.	L.C.		China	Endemic	*Amygdalophyllum*?
Dematophyllum	ST.	ST.		China	Endemic	*Stylostrotion*?, *Siphonodendron*?
Diphyphyllum	U.V.	S.		???	Broad	*Siphonodendron*
Dorlodotia	U.T.	V.		Belgium	Broad	*Axophyllum*
Espielia	L.B.	L.B.	Shallow water, microbial	Spain	Endemic	*Rylstonia*?
Flagelophyllum	V.	V.		China	Endemic	*Plerophyllum*?, *Carruthersella*
Guadiatia	S.	S.	Shallow water, microbial	Spain	Endemic	Amygdalophyllinid
"*Fomichevella*"	S.	P.	Moderate depth, muddy environment	Spain?	Broad	Cyathopsid
Howthia	T.	??	Waulsortian mound	Ireland	Endemic	*Axophyllum*
Huishiphyllum	C.	C.?		China	Endemic	*Clisiophyllum*, *Amygdalophyllum*?
"*Koninckophyllum*"	L.B.	L.B.	Shallow water, microbial	Ireland	Broad	*Koninckophyllum*
Koninckonaotum				Poland	Endemic	*Koninckophyllum*
Kusbassophyllum	V.	V.		Russia	Endemic	*Siphonophyllia*
Lonsdaleia	B.	S.	Shallow water	Europe	Broad	*Axophyllum*
Lublinophyllum	B.	B.		Poland	Broad	*Siphonophyllia*
Melanophyllidium	U.V.	S		Kyrgystan	Broad	*Kizilia*
Nagatophyllum	V.?	V.?		Japan	Endemic	Aulophyllid?
Nemistium	B.	S.		Britain	Broad	*Diphyphyllum*
Notaphrophyllum	V.	V.		Australia	Endemic	*Merlewoodia*
Palastraea	L.B.	S.		Europe	Broad	*Palaeosmilia*
Paralithostrotion	U.V.	S.		Russia	Broad	*Siphonodendron*
Protodurhamina	S.	B.		Russia	Endemic	*Siphonodendron*?, *Corwenia*?
Protolonsdaleia	L.V.	L.V.		Ukraine	Endemic	???
Pseudodorlodotia	U.V.	B.		Japan	Broad	*Dorlodotia*
Siphonodendron	U.T.	S.		Russia	Broad	???
Solenodendron	U.T.	B.	Moderate depth, muddy environment	Britain	Broad	???
Stylostrotion	L.V.	U.V.		China	Endemic	*Siphonodendron*
Tizraia	B.	B.	Shallow water, microbial	Morocco	Middle?	*Diphyphyllum*
Vesiculotubus	U.T.	U.T.		Russia	Endemic	???

Explanation of abbreviations: B. = Brigantian; C. = Carboniferous; Ch. = Chesterian; L.B. = Lower Brigantian; L.C. = Lower Carboniferous; L.V. = Lower Viséan; P. = Permian; S. = Serpukhovian; ST. = Strunian; T. = Tournaisian; U.A. = Upper Asbian; U.B. = Upper Brigantian; U.T. = Upper Tournaisian; U.V. = Upper Viséan; V. = Viséan. Geographical distributions are considered broad when they extend at least at a regional scale. Ancestor genera are tentative in most cases. First occurrence localities are tentative and further studies could change these statements. Localities of first occurrences are given in a broad sense.

new walls develop in the outer parts of the tabularium and extend into the dissepimentarium with an axial zone left devoid of axial structures. The number of offsets can range usually between 3 and 8 (Scrutton, 1998). Despite the variation in terminology of non-parricidal increase in fasciculate (phaceloid and dendroid) rugosans (Jull, 1965; Fedorowski, 1978; Scrutton, 1983, 1998), essentially all new offsets originate as lateral bulges in the epitheca involving only a small segment of the parental skeleton. The new corallite diverges rapidly from the parent with the initial dividing wall resulting from modified parental septa. Peripheral parricidal budding is the most common type of increase in protocolonial forms. They are solitary corals that develop some new individuals at the calice. Usually, these new polyps do not reach adult stages and no true colonies are formed. However, some

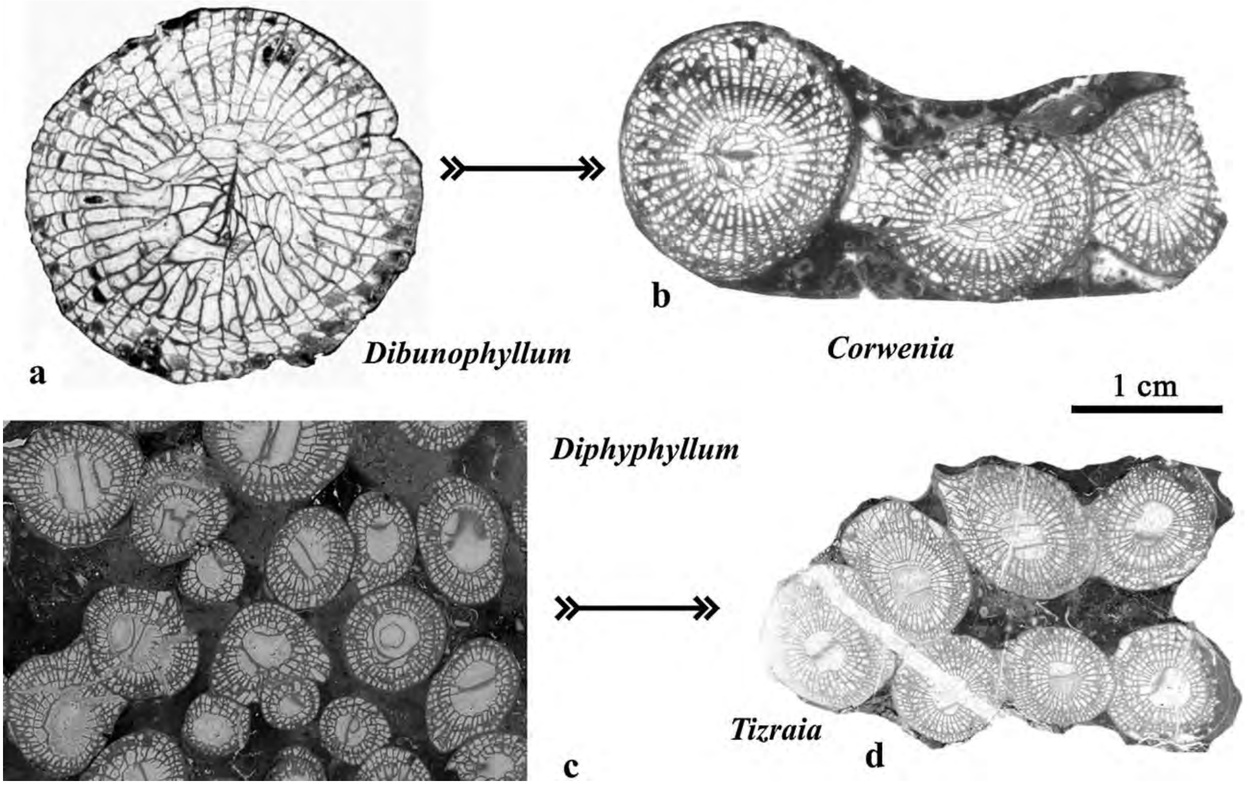

Fig. 1. Evolution of *Corwenia* (b) from *Dibunophyllum* (a) and *Tizraia* (d) from *Diphyphyllum* (c) illustrated with specimens from Morocco (*Tizraia* and *Diphyphyllum*), from Spain (*Dibunophyllum*) and Ireland (*Corwenia*).
Figures from Said and Rodríguez (2007) and Somerville (1997).

corals with this kind of budding readily develop adult polyps, and new individuals occur at their calices forming incipient colonies (*Guadiatia*, Gómez-Herguedas and Rodríguez, 2005). In other cases, the development of true colonies by direct lateral increase produces typical phaceloid colonies ("*Koninckophyllum*", Somerville, 1997).

2. Origin of new phaceloid genera

There are two main ways for the development of new phaceloid corals.

(a) development of colonialism by solitary corals, but still maintaining a similar morphology (e.g., *Corwenia* from *Dibunophyllum*, Fig. 1a and b).
(b) morphological changes that produce new species or genera (e.g., *Tizraia* from *Diphyphyllum*, Fig. 1c and d).

A third possibility is a reduction in the degree of colonialism from cerioid (or aphroid) to phaceloid. This is, however, only hypothetical, as there are no known examples from the published fossil record. The cerioid genus *Lithostrotion* can temporarily become partly phaceloid and resemble *Siphonodendron* when the environment is not favourable, but the coral reverts to a cerioid habit as soon as the environmental conditions become favourable again (Fig. 3). The reverse is also true, whereby phaceloid colonies of *Siphonodendron* can develop a partly cerioid habit (subcerioid), see Poty (1993, fig. 7.2). Transitions from phaceloid to massive colonies (Fig. 2) have been described in *Lonsdaleia* by Poty and Hecker (2003a).

3. Persistence of new colonial forms

Some fasciculate genera achieve a long stratigraphical range and broad geographical distribution, but many other taxa have a more localised geographical distribution (endemic) and/or much shorter stratigraphical range (see Table 1). These examples are numerous and may be regarded as failed evolutionary experiments. But even some of the genera with a broad geographical distribution and/or long stratigraphical range may represent several attempts at developing coloniality without establishing real evolutionary relations between the different species of such genera. Consequently, these genera would be regarded as polyphyletic and hence not valid. But, in this case, it is difficult to prove that different species of a genus have no evolutionary relationships.

If we consider the phaceloid genus *Corwenia*, according to the literature, some 50 species have been described from 70 citations of the genus, of which 25 species can be now reassigned to other Upper Carboniferous or Permian genera. Between 5 and 8 species of *Corwenia* are misinterpretations and belong to genera such as *Lonsdaleia*. The remaining 17–20 species of *Corwenia* may represent a triple case involving the following scenarios: (i) some species may be interrelated and constitute a real genus; (ii) some other species may be just failed experiments without continuation (they did not evolve into other species, nor

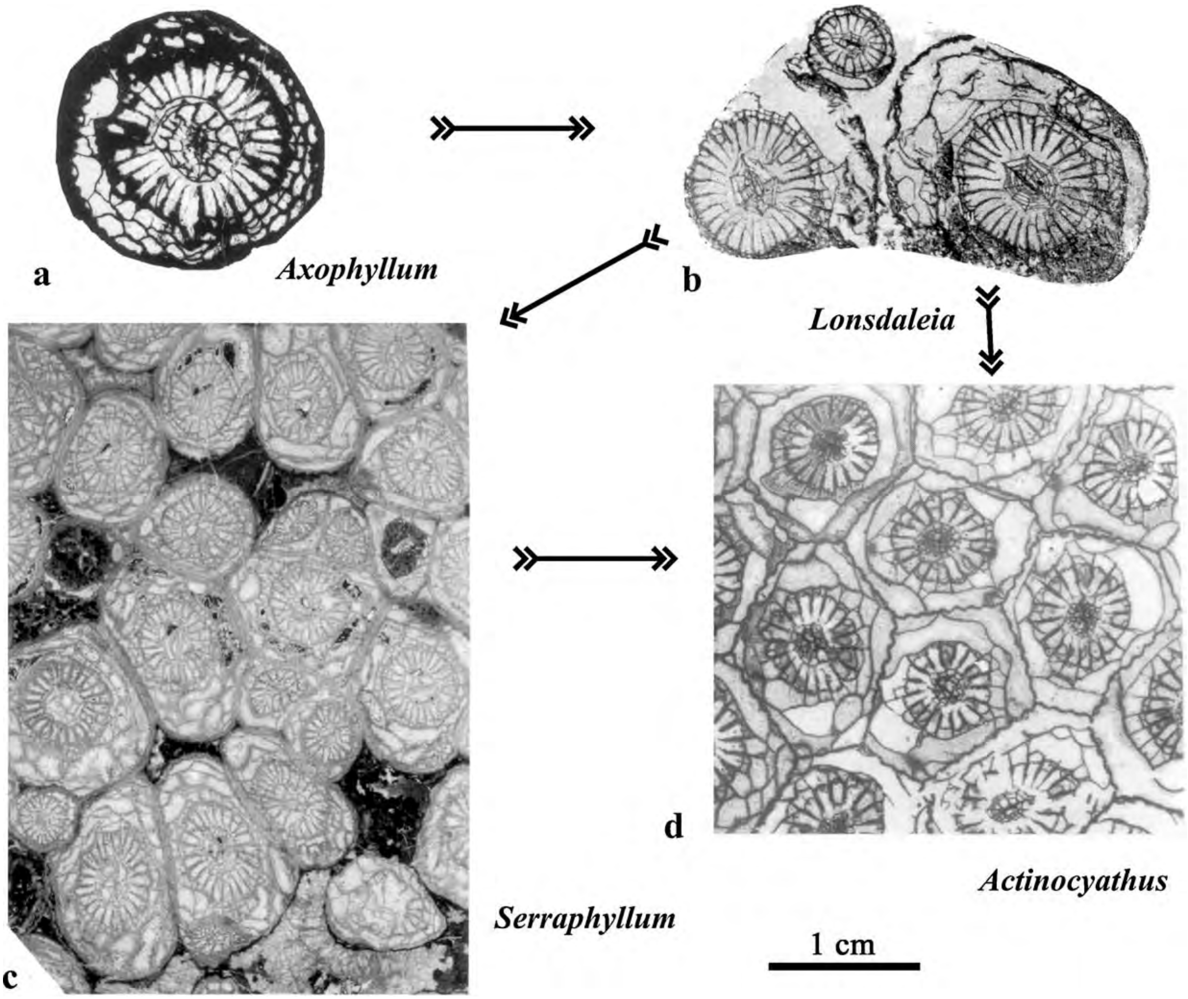

Fig. 2. Morphological variation from *Axophyllum* to *Actinocyathus* illustrated with specimens from Spain (*Axophyllum*) (a), France (*Serraphylum*) (c) and Russia (*Lonsdaleia* (b) and *Actinocyathus* (d)).
Figures from Rodríguez and Falces (1992), Dobrolyubova (1958) and Poty and Hecker (2003a).

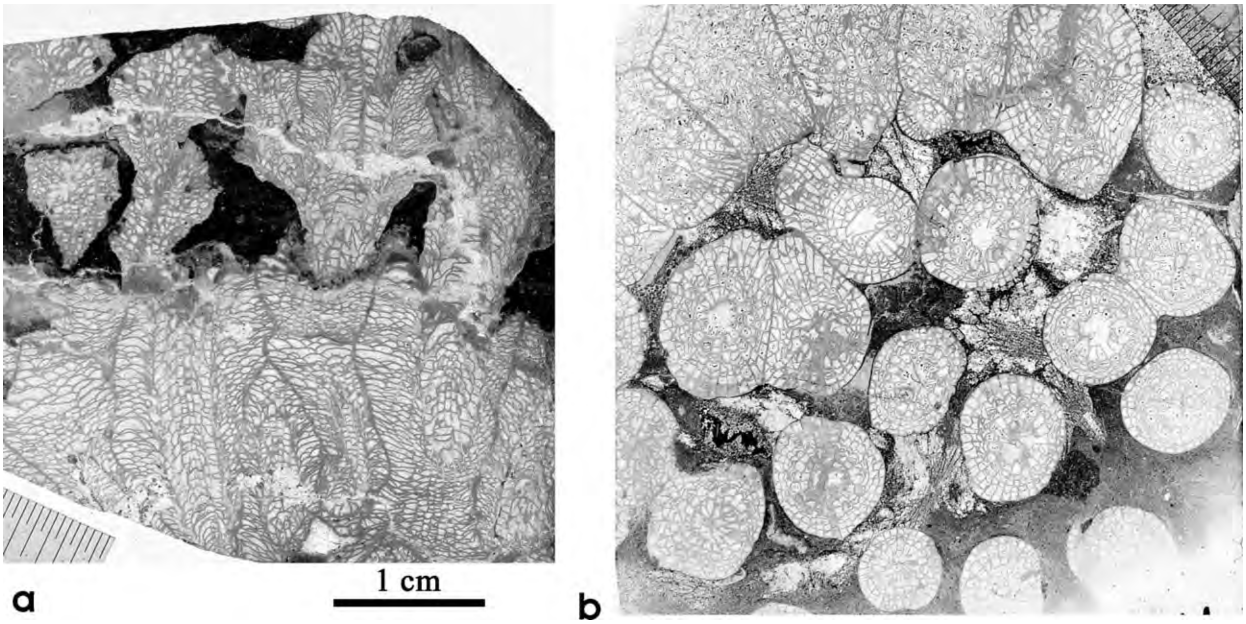

Fig. 3. Specimens of *Lithostrotion vorticale* (a) and (b) from Adarouch (Morocco) showing partly phaceloid habit related to changes in environment.

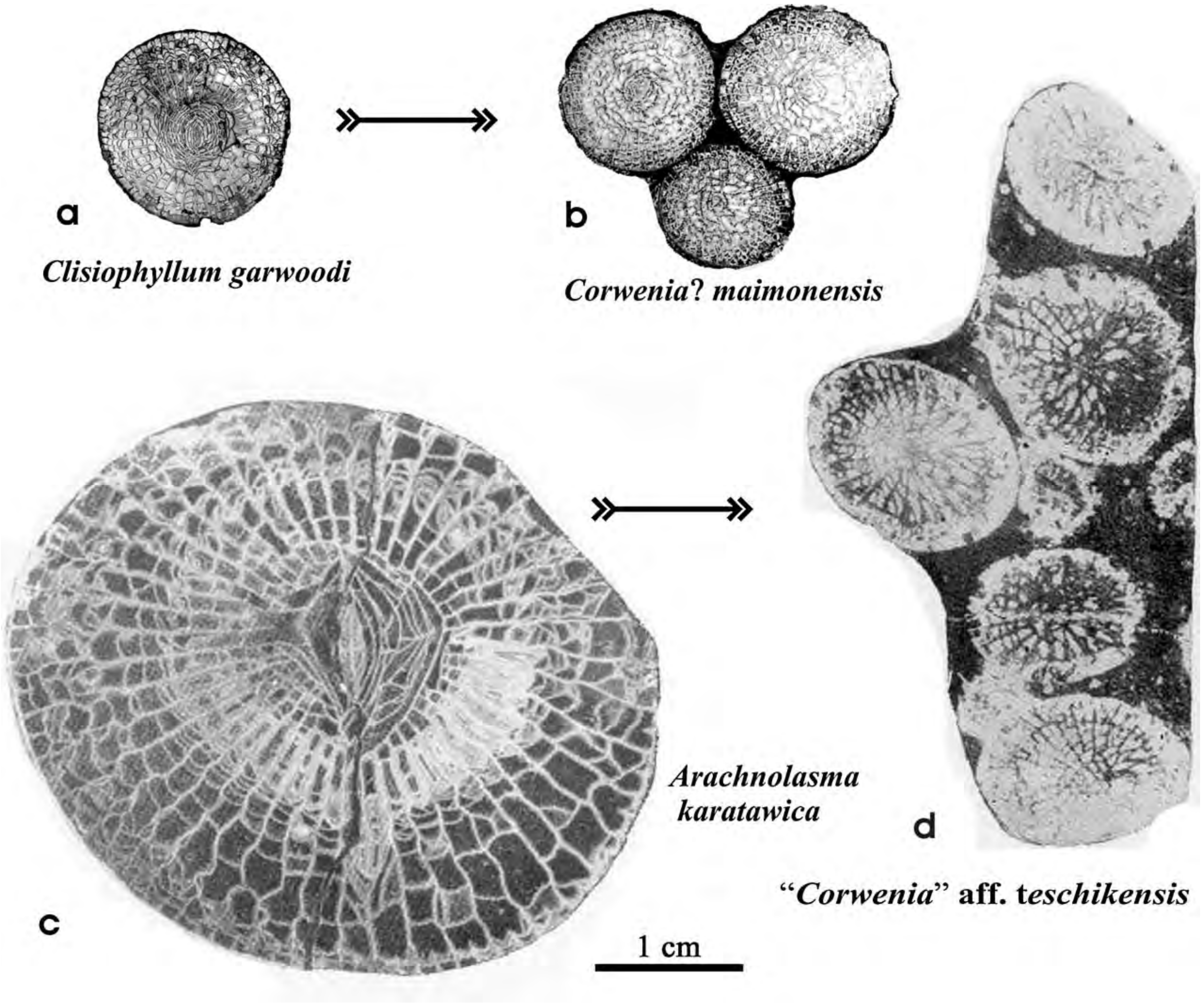

Fig. 4. Evolution of forms assigned to *Corwenia* from *Clisiophyllum* and *Arachnolasma*. *Clisiophyllum garwoodi* (a) and *Corwenia*? *maimonensis* (b) from SW Spain; *Arachnolasma karatavica* (c) and *Corwenia* aff. *teschikensis* (d) from Kasakhstan.
Figures from Rodríguez and Falces (1992), Rodríguez et al. (2001a) and Bykova (1966).

did they achieve a broad geographical dispersion or long time duration); and, finally (iii) some species may evolve from different but similar genera to *Dibunophyllum*. A good example of the third case is shown in the species of *Corwenia*? from Los Santos de Maimona (Rodríguez and Falces, 1992; Fig. 4a and b), and we suspect that some of the *Corwenia* species described by Bykova (1966) could have evolved from *Arachnolasma* (*C. densicolumellata* and *C.* aff. *teschikensis*) (Fig. 4c and d). Moreover, the species "*Corwenia*" *omiensis* from the Hina Limestone, Akiyoshi has been claimed by Ezaki et al. (2007, p. 411) to be related to the solitary aulophyllid *Echigophyllum*.

Siphonodendron is another special case. This genus attained a very broad geographical distribution (North America, Europe, North Africa, Asia, and Australia; Fedorowski, 1981) and relatively long duration (Late Tournaisian to Serpukhovian). But recent studies by Webb (1990, 1996, 2000) and by Fedorowski and Bamber (2007) seem to suggest that the "*Siphonodendron*" from Australia and from North America belong really to different genera. Also, Schindewolf (1927) proposed the subgenus *Cystidendron* for phaceloid lithostrotionid corals having a complex tabularium. The type species of this subgenus is *Cystidendron kleffense*, which has strikingly similar features to *Siphonodendron* aff. *martini*, recorded from Antolín, SW Spain (Rodríguez et al., 2002).

4. Environment

The main objective of the analysis is to identify the appropriate environment conducive to the emergence of phaceloid colonies arising from solitary rugosans in the Mississippian. The usual environments of the genera are not very important. In fact, most genera live typically in shallow water carbonate shelf environments (with the exception of *Solenodendron*, "*Fomichevella*", and perhaps *Melanophyllidium*, which appear to have frequented slightly deeper muddier shelf environments). The most important data are the environments of the first occurrences of each colonial coral. Unfortunately, most references to published taxa do not include data on the facies and lithology containing the corals. So, this analysis must be undertaken with our personal knowledge of the localities where phaceloid corals occur for the first time. When the coral is endemic and there are only a few or perhaps even a single locality, it is easy to identify (or at least to assume) the environment where the coral appeared for the first time. But in common corals that occur in many localities, this is almost impossible.

We have assumed that the localities where we found a coral once are the "first occurrences" and that when we have only a few localities to consider, the oldest (stratigraphic) locality is also the first occurrence. Based on these assumptions and published data, we have compiled the following data on new phaceloid taxa.

"*Aulokoninckophyllum*"

Aulokoninckophyllum is mainly a solitary genus, rarely fasciculate (Hill, 1981). Sando (1976) cited the existence of some pseudocolonial specimens, with some 'buddings' (off-sets), but they are not truly colonial. However, the specimen of "*Aulokoninckophyllum*" recorded in Sierra de la Estrella, SW Spain (Rodríguez et al., 2001a) is a true phaceloid colony, with poorly defined aulos and weakly carinate septa. It occurs in moderate to shallow water limestones of Upper Viséan (Asbian) age, some metres above a microbial mound and is related with other phaceloid corals (*Siphonodendron*, *Syringopora*). It is probably originated from *Aulokoninckophyllum*.

"*Corwenia*"

It occurs in very shallow water Asbian limestones (not very agitated water) associated with *Siphonodendron*, *Solenodendron*, *Clisiophyllum*, *Dibunophyllum*, *Siphonophyllia*, and syringoporoids (Fig. 4). No microbial limestones have been recorded in the succession in Los Santos de Maimona, SW Spain (Rodríguez and Falces, 1992). It is probably originated from *Clisiophyllum* (Fig. 4a and b).

Espielia

This endemic genus occurs in shallow quiet water limestones of Upper Viséan (Lower Brigantian) age in SW Spain, associated with other colonial genera such as *Siphonodendron* and *Palastraea* (Rodríguez and Hernando, 2005). The surrounding facies are rich in microbial limestones. It is probably originated from *Carruthersella* (Fig. 5c and d).

"*Fomichevella*"

The first colonial cyathopsids assigned to this genus occur in the Serpukhovian from the Cantabrian Mountains, NW Spain (Rodríguez, 1984). They are recorded from moderately deep wackestones and marly limestones near to, but apparently not related with, microbial mounds. It is probably originated from "*Caninia*"

Guadiatia

Guadiatia is a Serpukhovian endemic genus in SW Spain, occurring in a small microbial mound located in a very shallow water facies protected by oolitic bars. It is a protophaceloid coral that developed small sparse colonies with calicular budding (Gómez-Herguedas and Rodríguez, 2005). It is similar to a small *Amygdalophyllum*. It has been found in some other localities, but so far appears to be restricted to the Lower Serpukhovian (Pendleian) in the Guadiato Valley. It is probably originated from *Amygdalophyllum* (Fig. 5e and f).

Howthia

This is a small weakly fasciculate axophyllid genus from the late Tournaisian of Howth, Ireland, occurring in Waulsortian mud-mound facies. It is associated with protocolonial corals '*Fasciculophyllum*' and *Amplexocarinia* showing buddings (Somerville and Rodríguez, in press). It is probably originated from *Axophyllum*.

"*Koninckophyllum*"

It is located at the top of a large Brigantian-aged microbial mound at Kingscourt, NE Ireland (Somerville et al., 1996; Somerville, 1997; Rodríguez and Somerville, 2007). This genus is associated with other phaceloid corals (*Siphonodendron*, *Corwenia*) and solitary corals (*Axophyllum*, *Dibunophyllum* and *Koninckophyllum*) and is characteristic of Rugose Coral Assemblage RCA6 of Somerville and Rodríguez (2007). This colonial genus is geographically widespread, with occurrences in Alaska and Nova Scotia (Poty and Hecker, 2003b), Scotland (Hill, 1940) and Russia (Dobrolyubova, 1958). It is the phaceloid equivalent of *Koninckophyllum* (Fig. 5a and b). Recently, Poty and Hecker (2003b) proposed to assign this colonial koninckophyllid to the genus *Thysanophyllum* Nicholson et Thomson, 1876 even though the latter genus is cerioid.

Lublinophyllum

This colonial cyathopsid, first identified in the Upper Viséan of the Lublin Basin, Poland and Donbass (Khoa, 1977), has now been recorded in a broader area including Ireland (Cózar and Somerville, 2005; Rodríguez and Somerville, 2007). It probably is derived from *Siphonophyllia*.

Melanophyllidium

A supposed Upper Viséan colonial coral from Russia, but following recent stratigraphical studies by Hecker (2001; pers. comm.) it is probably Serpukhovian. It is recorded in moderately deep-water marly limestones in a similar environment to that of "*Fomichevella*". It is the phaceloid version of *Kizilia* (the type specimen of *Melanophyllum* is a *Siphonophyllia* and that generic name should not be used). These genera have been described from the Strunian (Poty and Onoprienko, 1984), but the stratigraphic gap between the Strunian and the upper Viséan is too large to indicate a close phylogenetic relationship. So, the species from the Strunian is not accepted here as congeneric with the Viséan-Serpukhovian species.

Nagatophyllum

Originally described as a Permian genus from Japan, it is most probably Upper Viséan based on recent studies (Ezaki et al., 2007). This large fasciculate genus, characterised by a compact axial structure and wide dissepimentarium with columns of naotic dissepiments, occurs in the Akiyoshi reef complex composed mainly of chaetetid sponges and algae. It is possibly derived from *Amygdalophyllum*.

Tizraia

Found in Brigantian shallow water limestones in Morocco (Said et al., 2007; Said and Rodríguez, 2007), its first occurrence is some metres above a large microbial mound, in a biostrome associated with colonial corals (*Diphyphyllum*, *Siphonodendron* and *Corwenia*). It is characterised by absence of an axial structure, mesa-shaped tabulae, lonsdaleoid dissepiments, and axial parricidal increase (Fig. 1d). The space between colonies is filled with micrite indicating a predominantly low-energy environment. It is typical of Rugose Coral Assemblage RCA6 of Somerville and Rodríguez (2007), containing a similar suite of

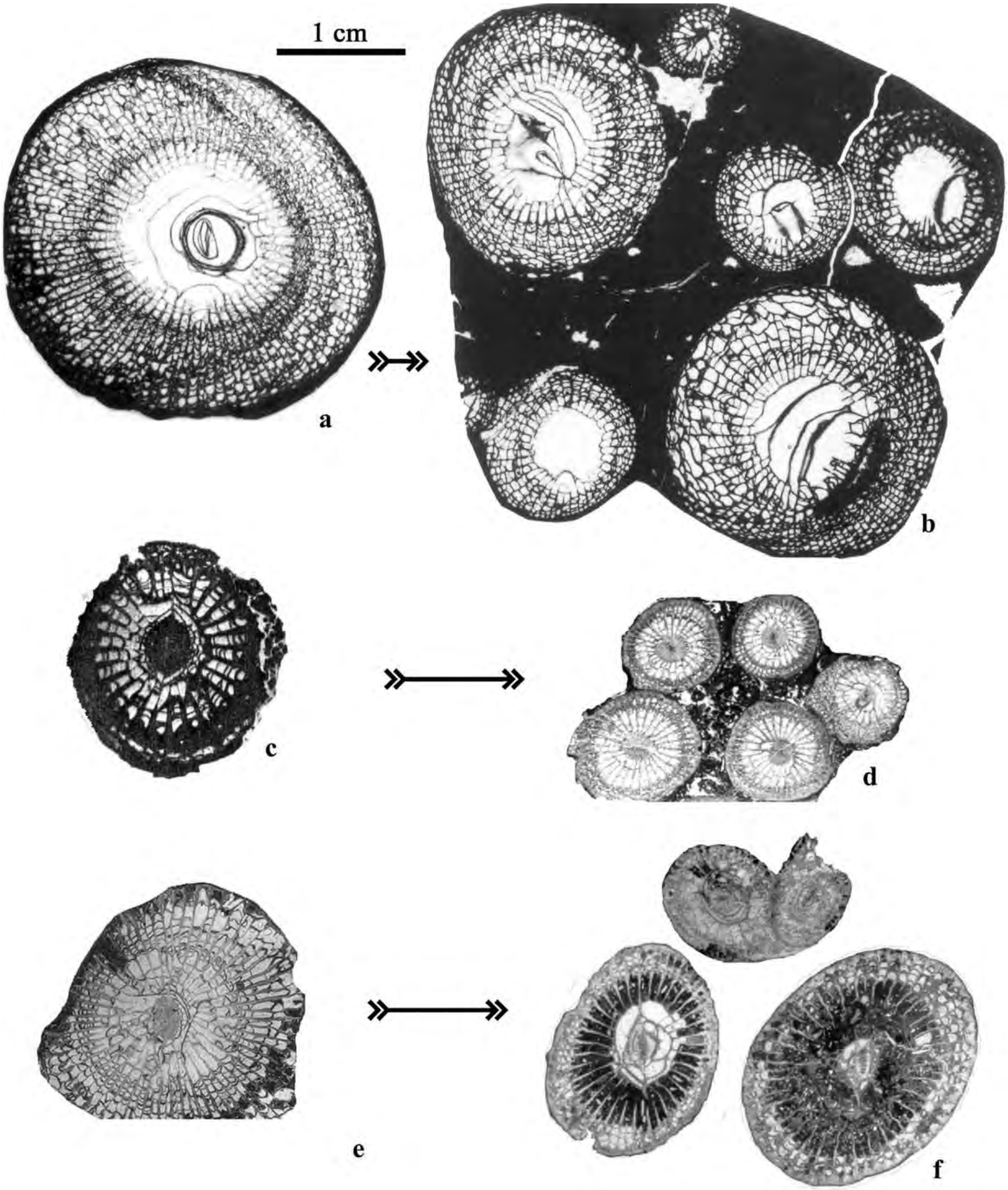

Fig. 5. Evolution of phaceloid from solitary corals in microbial environments. (a) *Koninckophyllum* (Ireland; Somerville, 1997). (b) "*Koninckophyllum*" (Ireland; Somerville, 1997). (c–d) *Espielia* (Spain; Rodríguez and Hernando, 2005). (e) *Amygdalophyllum* (Spain; Rodríguez et al., 2001b). (f) *Guadiatia* (Spain; Gómez-Herguedas and Rodríguez, 2005).

taxa as for "*Koninckophyllum*" in Ireland. This genus is probably endemic and it is originated from *Diphyphyllum* (Fig. 1c and d).

4.1. Environmental factors

The potential affinities of pioneer phaceloid corals and microbial mud-mounds and bioherms ('reefs') and adjacent facies may be somewhat controversial, particularly as most corals in Table 1 seem to have no strong relationships with microbial communities. Nevertheless, at least six new taxa are clearly affected in their growth by the sediments around them, which have typical imprints of microbial communities (Table 1, Fig. 5). In addition, some of them have their first occurrence on or above microbial mounds. The microbial mounds may perhaps have created topographic relief that provided isolated areas of shallower water above the deeper water sea bed, which was appropriate for the development of corals. These isolated elevated areas could be the best environment for evolutionary or ecological "experiments" where pioneer coral colonies may have evolved. This statement is based on the analysis of environmental factors at the top of those mounds (see also the depositional setting of *Howthia* in Somerville and Rodríguez, in press).

The first occurrence of most, if not all, phaceloid corals is related to shallow-water facies, but not always in an agitated environment. In contrast, most of the corals documented above occur in limestones containing a high percentage of micrite. However, many colonies are also associated with broken bioclasts, suggesting that the environment had an alternation of high energy and low energy depositional periods. This situation provided in the same place both, sufficient oxygenation and prolonged quiescent periods, for developing new offsets in stable conditions. Sometimes, though, a hard substrate that colonial corals need was provided by cemented oolitic rock, or by bioclasts. The relief of mounds also facilitated the possibility of upwelling from the bottom of the sea to the shallow waters above the mounds, providing moderate levels of nutrients. Thus, most environmental factors appropriate for the flourishing of colonial corals occur at the top of mounds.

4.2. Assemblages

All coral assemblages containing new colonial corals are dominated by phaceloid species. Thus, it is not surprising to find that the new colonial corals are also phaceloid. But it has two different implications. (1) As can be expected, the environment where the new corals appear is favourable for these kinds of corals. (2) Usually, it is suggested that the new taxa occur in environments where the ecologic "niches" for those taxa are empty, hence avoiding competition with similar older taxa. But this is not valid for our proposed scenario. The "niches" for the new phaceloid corals are not empty, but they are shared by several older taxa.

Most assemblages also contain solitary corals (and in some cases, this includes the "parent" species). Thus, the colonial corals did not appear because the environment was so much more favourable that the solitary corals developed only colonial forms. On the contrary, the environmental conditions are highly favourable for both colonial *and* solitary corals.

Additionally, it would appear that the best growth habit for pioneer colonies is fasciculate, as suggested by the analysis on growth rates of rugosans (Scrutton, 1998). In this study, the dendroid *Dorlodotia* had a calculated growth rate of >30 mm/year compared with typical massive cerioid forms, which recorded <10 mm/year. This might confer an evolutionary advantage to new taxa becoming established in specialised niches, such as the regions peripheral to or immediately above mud-mounds and bioherms.

5. Discussion

The two most conspicuous features derived from an analysis of the data in Table 1 are that production of new fasciculate genera is extremely high and that many of those genera (more marked if we consider species) have a reduced geographical and stratigraphical record. This could be an artefact of the fragmentary geological record, but we do not think that this is the main factor; thus, we should look for evolutionary or environmental causes for this phenomenon.

5.1. Evolutionary causes

A first hypothesis would be the possibility that rugose corals could hybridise, such as was suggested in Scleractinians by Veron (1995, 2007). This is a very controversial point (also in Scleractinians) and very difficult to evaluate in a group that has an exclusively fossil record. Then, the evolution of corals could have a "reticulate pattern". This kind of evolution was postulated by Russian authors for Archaeocyatha and has been supported by Gould (1985). Corals have a more advanced organisation than Porifera, but this could explain this kind of phenomena. In such a case, environmental causes would play an important role in the studied phenomenon.

A second hypothesis is that rugose corals suffered a high number of mutations during the Viséan and Serpukhovian, producing a high number of genotypic variations (point of diversification following the punctuated equilibrium theory). Evidences do not support this. A high number of mutations would produce also a high number of other variants in most structures if the cause is intrinsic; those mutations would affect too many other groups if the cause is extrinsic.

A third hypothesis would defend an extreme genetic "plasticity" in rugose corals; then, a genotype could develop different habits (morphotypes) in different environments. Rugose corals are quite simple from a genetic point of view. Thus, many of them probably could easily develop different morphologies in different environments. Some ecological factors could easily affect their growth and produce colonial or protocolonial habit in corals that are solitary in the majority (quasi-colonial or incipient colonial in the nomenclature of Fedorowski, 1978). Moreover, the form is the result of three factors, phylogenetic, functional, and fabricational (Gould, 1971). The growth in a special environment may produce special habits as demonstrated in other extant organisms. Perhaps, one of the effects of microbial communities on corals is the development of fasciculate habits. At least in one case, it is already proven, whereby colonies of *Lithostrotion vorticale* develop temporarily phaceloid habits in the presence of microbial communities in the Brigantian from Sierra Morena, SW Spain and Morocco (Fig. 3). Also, as in the first hypothesis, environmental causes would play an important role in the studied phenomenon.

A fourth hypothesis is that all these fasciculate corals are just ecological variations of solitary and/or colonial species/genera that adapted to a special environment. There are evidences that single specimens develop colonial forms as a response to environmental factors in many stages of the rugosans evolution. Development of colonialism is possible for single specimens of some solitary genera. The capacity of developing colonialism should be in this case a latent possibility, inserted in the genetic code of all individuals of a species or only in part of them. A good example of this is shown by specimens of *Palaeosmilia* developing peripheral offsets at the calices in the same bed where many other specimens did not develop offsets (Serpukhovian from Sierra Morena, Rodríguez, unpublished data).

5.2. *Environmental causes*

When a significant number of colonial specimens occur first in a precise stratigraphical level with a morphology that is not found outside that locality and/or in other stratigraphical units, the most reliable possibility is that a new species emerged in a favourable environment, but it had no later viability. An example of this might be *Siphonodendron multiradiale* Nudds et Somerville, 1987, which is known only from an Upper Viséan bioherm at Blue Pool, South Wales (Nudds and Somerville, 1987; Somerville and Rodríguez, 2007). The environmental factors that produced the new appearance could be diverse. We cited several of them above. They include:

- Shallow water environment isolated from areas where most niches are occupied.
- Integration in complex communities (other colonial corals, algae, microbial communities, etc.).
- Moderate levels of nutrients in areas of upwelling.

Finally, at least some phaceloid species seem to be local forms without relation to other similar forms in spite of their morphological similarities.

When checking some of the described species of *Corwenia*, we found that different species of *Dibunophyllum* could develop colonial forms. Some of them are endemic, occurring only in precise stratigraphic units, but not in a single level and even surrounded by different type of microfacies. It indicates that they were fertile colonial corals that produced several generations, but they could not disperse and did not achieve broad stratigraphic and geographic distributions. Consequently, some, if not most, fasciculate corals that show similar features to solitary corals are polyphyletic. Thus, an additional problem arises from this analysis. Our taxonomic system should be revised if we want to have a phylogenetic systematics, but it is not possible, because we do not have the means of discerning evolutionary relationships at this detailed level. Blastogenetic studies of all species could probably help to solve this problem, but many type specimens are not available for a general revision of genera, such as *Corwenia*.

6. Conclusions

- Appearance of new phaceloid corals is accelerated during the Viséan and Serpukhovian.
- The development of colonialism is favoured by special environmental factors (partial isolation, shallow water, changing environment (in terms of energy), integration in complex communities (other corals, microbial communities, algae, etc.), and high level of nutrients. One of the most favourable environments for new appearances of phaceloid corals is the top of microbial mounds where several of the above-mentioned factors occur.
- Most new species of phaceloid corals were endemic and they did not achieve broad stratigraphic and geographic distributions.
- Some solitary genera could produce the morphological appearance of new phaceloid species on several occasions, in different times, and with similar structures. Thus, some colonial genera are polyphyletic.

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Research paper

Some aspects of evolution in the *Lonsdaleia* (*Actinocyathus*) *crassiconus* species-group

Maria R. Hecker[a,b,*]

[a] *A.A. Borissiak Palaeontological Institute, Russian Academy of Sciences, 123, Profsouznaya, 117997, Moscow GSP-7, Moscow, Russia*
[b] *Department of Palaeontology, Royal Belgian Institute of Natural Sciences, Rue Vautier 1000, Brussels, Belgium*

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Abstract

The *Actinocyathus crassiconus* species-group represents a separate trend of evolution within the rugose subgenus *Lonsdaleia* (*Actinocyathus*) (d'Orbigny, 1849). It is distinguished by consistently developed minor septa and by regular axial structures. In the Moscow Basin, this species-group comprises seven species, *A. crassiconus* (McCoy, 1849), *A. lativesiculosus* (Dobrolyubova, 1958), *A. sarytschevae* (Dobrolyubova, 1958), *A. subtilis* (Dobrolyubova, 1958), *A. gorskyi* (Dobrolyubova, 1958), *Actinocyathus* sp. A, and *Actinocyathus* sp. B. It ranges from the Mikhailov horizon (Brigantian) to the Protva horizon (lower upper Serpukhovian), and is especially characteristic of the Tarusa horizon (lowermost Serpukhovian) in the north-western part of the basin. Evolution in the group took place at the beginning of Mikhailov time and in Tarusa time and showed three trends: (i) increase in corallite size and number of septa; (ii) increase in number of septa and tabularia diameter; and (iii) a wide range of variability in septal number without important changes in tabularia diameter. *Lonsdaleia ornata* Dobrolyubova, 1958, *L. heckeri* Dobrolyubova, 1958, and *L. longiseptata crassicolumellata* Dobrolyubova, 1958 are synonymised with *Actinocyathus subtilis*, and *Lonsdaleia subcrassiconus subcrassiconus* Dobrolyubova, 1958 is with *Actinocyathus gorskyi*.

Keywords: Rugosa; Evolution; Lower Serpukhovian; Moscow Basin

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1. Introduction

The rugose genus *Actinocyathus* d'Orbigny, 1849 was re-established by Hill (1981) to include typically cerioid species previously attributed to the genus *Lonsdaleia* McCoy, 1849. Poty and Hecker (2003) considered *Actinocyathus* as a subgenus of *Lonsdaleia*. This is suggested by the corallite morphology, by the presence of subcerioid and fasciculate zones in colonies of some *Actinocyathus* species, and by subcerioid zones in colonies of some *Lonsdaleia* species. This also agrees with the hypothesis of Smith (1916) on the origin of cerioid *Lonsdaleia floriformis* from fasciculate *L. duplicata*.

In the Moscow Basin, *Actinocyathus* has a long and uninterrupted range from the uppermost Visean (Brigantian) to the lower Upper Serpukhovian (Aleksin-Protva horizons). This subgenus does not represent a morphologically homogeneous unit; two species-groups, each originating from one of the species-migrants, *Actinocyathus floriformis* (Martin, 1809) and *A. crassiconus* (McCoy, 1849), may be distinguished (Hecker, 1997). They show clear differences in corallite morphology and ecological plasticity, and each of them represents a separate trend of evolution within the subgenus. Specific diversity, phyletic relations, and variability in the former species-group in the Moscow Basin have been discussed in detail (Hecker, 1992a,b; Poty and Hecker, 2003). The objectives of the present paper are: to discuss specific diversity, variability, and patterns of evolution in the *A. crassiconus* group in the same area. Short species descriptions and a comparative table of the species (Table 1) are provided. The synonymies are restricted to original citations for each species and basic references to regional publications. Regional subdivisions (horizons) adopted herein are not considered as formally defined regional sub-stages and therefore are spelled without the ending "-ian".

The study is based on the collection housed in the Palaeontological Institute, Russian Academy of Sciences, Moscow, as

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[*] Corresponding author at: A.A. Borissiak Palaeontological Institute, Russian Academy of Sciences, 123, Profsouznaya, 117997, Moscow GSP-7, Moscow, Russia.

E-mail addresses: hecker@paleo.ru, Maria.Hecker@skynet.be.

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Table 1
Comparative table of species of the *Lonsdaleia* (*Actinocyathus*) *crassiconus* species-group in the Moscow Basin.

Species	Septal number/tabularium diameter ratio	Corallite width (mm)	Corallite diagonal (mm)	Axial column: width; number of radial lamellae	Biform periaxial tabellae	Dissepimentarium width
A. crassiconus	$\frac{22-27}{4.75-6.5}$	8–12	15–20	1/2 tabularium diameter; 15–30	Locally present	1/5–1/4 corallite diagonal
A. lativesiculosus	$\frac{22-27}{6-8.5}$	15–20	18–30	1/3 tabularium diameter; 7–12	Not detected	1/3 corallite diagonal
A. sarytschevae	$\frac{34-40}{7.5-10.25}$	18–29	30–38	2/3 tabularium diameter; 10–30	Not detected	1/3 corallite diagonal
A. subtilis	$\frac{21-30}{4-6.25}$	7.5–12	12–20	1/3–1/2 tabularium diameter; 10–24	Locally present	1/3–1/2 corallite diagonal
A. gorskyi	$\frac{26-33}{5-7.5}$	8–12	15–20	1/2 tabularium diameter; 15–24	Locally present	1/6–1/4 corallite diagonal
Actinocyathus sp. A	$\frac{21-26}{4.75-6.5}$	13–14	20–25	1/3–1/2 tabularium diameter; 8–20	Locally present	1/4–1/3 corallite diagonal
Actinocyathus sp. B	$\frac{25-30}{7-9.5}$	16–25	20–28	1/3–1/2 tabularium diameter; 20–40	Not detected	1/3 corallite diagonal

part of the collections registered under No. PIN 703, 705 and 1562.

2. Taxonomy

Genus *Lonsdaleia* McCoy, 1849

Diagnosis: Fasciculate, subcerioid or cerioid. Increase lateral. Cardinal fossula indistinct to small. Minor septa indistinct to well developed. Axial column usually well-defined, more or less complex and thickened, comprising a medial plate connected to the cardinal and/or to the counter septum, radial lamellae, and axial tabellae, or sporadically reduced to a medial plate or absent. Periaxial tabellae concave, subhorizontal or variously declined, commonly complete. Dissepimentarium dominated by transeptal dissepiments.

Remarks: The genus comprises three subgenera: typically fasciculate *Lonsdaleia*, typically cerioid *Actinocyathus* d'Orbigny, 1849, and *Serraphyllum* Poty in Poty et Hecker, 2003, having both fasciculate and cerioid habitus.

Subgenus *Actinocyathus* d'Orbigny, 1849

Diagnosis: Typically cerioid. Cardinal and counter septa commonly indiscernible. Axial column typically dibunophylloid. Periaxial tabellae commonly complete, seldom divided. Biform morphology of tabularium locally expressed with tabellae in position I steeper abaxially declined than tabellae in position II. Dissepimentarium commonly wide, dissepiments thin except for locally slightly dilated, vertically inclined inner margins of innermost dissepiments.

Remarks: Two species-groups are distinguished. The *A. floriformis* group comprises species with short, commonly indistinct minor septa, and highly variably axial structures. Inconspicuous cardinal fossula is seldom present. Growth habit is typically cerioid, less commonly subcerioid. The *A. crassiconus* group is distinguished by its consistently developed, commonly long minor septa, and by less variable axial structures usually showing regularly conical, crowded axial tabellae. Cardinal fossula is typically indistinct. Growth habit is cerioid, less commonly subcerioid to fasciculate, seldom cerioid-astreoid.

Lonsdaleia (*Actinocyathus*) *crassiconus* species-group

Lonsdaleia (*Actinocyathus*) *crassiconus* (McCoy, 1849) (Fig. 1A–D)

*1849 *Lonsdaleia crassiconus* – McCoy, p. 12.
1851 *Lonsdaleia crassiconus* – McCoy, p. 104, pl. IIIb, figs. 5, 5a-b.
vp. 1958 *Lonsdaleia ossipovae* – Dobrolyubova, p. 98, text-fig. 21a-b, pl. XII, Fig. 2a-b.
vp. 1958 *Lonsdaleia subcrassiconus crassiconus* McCoy – Dobrolyubova, p. 106, text-fig. 23a-b, pl. XIII, Fig. 3a-b.

Type: Holotype, *Lonsdaleia crassiconus* McCoy, 1849. Specimen 47, Sedgwick Museum, Cambridge; lower Brigantian, uppermost Visean, Bristol area, Great Britain.

Description (based on the material from the Moscow Basin): Cerioid, rarely subcerioid. Corallites 8–12 mm wide, with diagonals 15–20 mm and tabularia diameters typically 4.75–5.75 mm, rarely up to 6.5 mm. Major and minor septa 22–27 in number. Major septa commonly penetrate dissepimentaria, locally reaching outer walls, commonly dilated in tabularia and in inner dissepimentaria. Their length in tabularium approximately half of its radius. Minor septa thin to dilated, attaining one-third to half length of major septa in tabularia, and developed in innermost parts of dissepimentaria, locally reaching outer walls. Axial structures attaining half of tabularium diameter in width. Medial plate straight, long, lens-shaped or thin, seldom irregular. Radial lamellae typically 15–30 in number, rarely up to 50. Axial tabellae regular, widely conical to steeply elevated, typically spaced 0.15–0.25 mm apart, locally become less crowded along

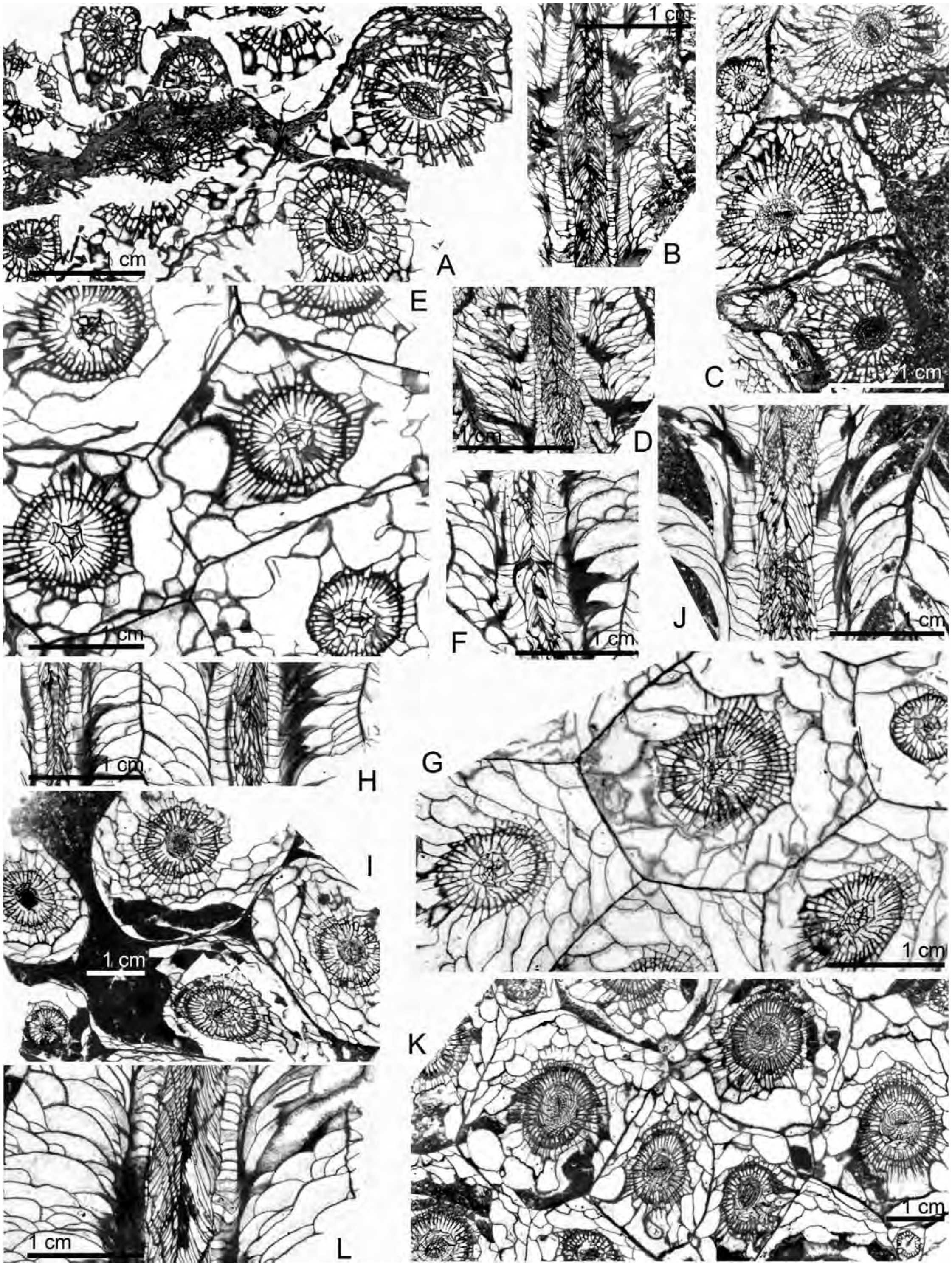

Fig. 1. (A–D) *Lonsdaleia* (*Actinocyathus*) *crassiconus* (McCoy, 1849). (A and B) Holotype of *Lonsdaleia ossipovae* Dobrolyubova, 1958; PIN 705/170: (A) transverse section, (B) longitudinal section. Lower Serpukhovian, Steshevo horizon, north-western part of the Moscow Basin, Tagazhma River, 20 km south of the town of Vytegra. (C and D) Type of *Lonsdaleia subcrassiconus crassiconus* Dobrolyubova, 1958; PIN 705/195: (C) transverse section, (D) longitudinal section. Lower Serpukhovian, Tarusa horizon, north-western part of the Moscow Basin, Andoma River. (E and F) Holotype of *Lonsdaleia* (*Actinocyathus*) *lativesiculosa* (Dobrolyubova, 1958); PIN 703/2733: (E) transverse section, (F) longitudinal section. Lower Serpukhovian, Tarusa horizon, southern part of the Moscow Basin, Kievka River near the city of Kaluga. (G and H) *Lonsdaleia* (*Actinocyathus*) sp. A.; PIN 703/5074: (G) transverse section, (H) longitudinal section. Lower Brigantian, Mikhailov horizon, southern part of the Moscow Basin, Vyssa River near the town of Venev. (I and J) *Lonsdaleia* (*Actinocyathus*) sp. B.; PIN 1562/14: (I) transverse section, (J) longitudinal section. Lower Serpukhovian, Tarusa horizon, southern part of the Moscow Basin, Gurievskiy Quarry, 10 km northwest of the town of Venev. (K and L) Holotype of *Lonsdaleia* (*Actinocyathus*) *sarytschevae* (Dobrolyubova, 1958); PIN 703/2732: (K) transverse section, (L) longitudinal section. Lower Serpukhovian, Tarusa horizon, southern part of the Moscow Basin, Kievka River near the city of Kaluga.

individual corallites. Periaxial tabellae complete, subhorizontal gently sagging to slightly abaxially declined, spaced 0.3–1 mm apart, locally biform. Tabellae in position I more crowded than tabellae in position II. Dissepimentaria one-fifth to one-fourth of corallite diagonals in width. Dissepiments transeptal of various sizes, locally regular interseptal in inner dissepimentaria, flat to moderately inflated, abaxially declined at angles of 40–70°.

Remarks: *Actinocyathus crassiconus* resembles *A. gorskyi* in corallite size, but shows lower number of septa and larger number of radial lamellae. Material on *A. crassiconus* includes the figured specimen attributed by Dobrolyubova (1958) to *Lonsdaleia subcrassiconus crassiconus* McCoy, 1849 (specimen PIN 705/195; Fig. 1C and D) and the holotype of *L. ossipovae* Dobrolyubova, 1958 (specimen PIN 705/170; Fig. 1A and B), which differ only in the aspect of dissepimentaria. Dissepimentaria in the holotype of *L. ossipovae* are dominated by first order transeptal dissepiments, whereas second order transeptal and regular interseptal dissepiments are developed in inner dissepimentaria of *L. subcrassiconus crassiconus*.

Material and occurrence: Eighteen specimens. Southern part of the basin. Brigantian, Mikhailov horizon, Gorenki Quarry (Venev area). North-western part of the basin. Lower Serpukhovian, Tarusa horizon: Andoma and Tagazhma rivers (Vytegra area), Pikalevo Quarry and Tutoka River (Tikhvin area), Patrovsky brook; Steshevo horizon: Tagazhma River (Vytegra area), Medveditsa River (Tikhvin area), Msta River (Borovichi area).

Lonsdaleia (*Actinocyathus*) *lativesiculosa* (Dobrolyubova, 1958)
(Fig. 1E and F)

vp.* 1958 *Lonsdaleia lativesiculosa* – Dobrolyubova, p. 108, text-fig. 24a-b, pl. XIV, Fig. 1a-c.

Type: Holotype, *Lonsdaleia lativesiculosa* Dobrolyubova, 1958. Specimen PIN 703/2733; basal Tarusa horizon, lower Serpukhovian, southern part of the Moscow Basin, quarry at the mouth of the Kievka River near the city of Kaluga.

Description: Cerioid. Corallites 15–20 mm wide, with diagonals 18–30 mm and tabularia diameters 6–8.5 mm. Major and minor septa 22–27 in number. Major septa may penetrate dissepimentaria, locally reaching outer walls, commonly dilated in tabularia and in inner dissepimentaria. Their length in tabularium about half of its radius. Minor septa attain one-fourth to half length of major septa in tabularia, locally develop as ridges on inner wall, commonly penetrate dissepimentaria, dilated in tabularia and locally in dissepimentaria. Axial structures attaining one-third of tabularium diameter in width. Medial plate long, straight or sinuous, thin or slightly dilated. Radial lamellae 7–12 in number. Axial tabellae spaced 0.3–0.4 mm apart, regularly conical steeply elevated to irregularly conical. Periaxial tabellae complete or divided, subhorizontal gently sagging or convex, locally abaxially declined, spaced 0.5–1.5 mm apart. Dissepimentaria approach in width one-third of corallite diagonals. Dissepiments first order transeptal, locally second order transeptal in inner dissepimentaria, variously inflated, subhorizontal or abaxially declined at angles of 30–50°.

Remarks: *Actinocyathus lativesiculosus* is distinguished by relatively simple axial structure with few radial lamellae (up to 12).

Material and occurrence: Two specimens. Southern part of the basin. Lower Serpukhovian, Tarusa horizon: Kievka River (Kaluga area), Besputa River (Venev area).

Lonsdaleia (*Actinocyathus*) *sarytschevae* (Dobrolyubova, 1958)
(Fig. 1K and L)

v.* 1958 *Lonsdaleia sarytschevae* – Dobrolyubova, p. 111, text-fig. 25a-b, pl. XIV, Fig. 2a-c.

Type: Holotype, *Lonsdaleia sarytschevae* Dobrolyubova, 1958. Specimen PIN 703/2732; basal Tarusa horizon, lower Serpukhovian, southern part of the Moscow Basin, quarry at the mouth of the Kievka River near the city of Kaluga.

Description: Cerioid. Corallites 18–29 mm wide, with diagonals 30–38 mm and tabularia diameters 7–10.25 mm. Major and minor septa 34–40 in number. Major septa commonly penetrate dissepimentaria, dilated in tabularia and thin in dissepimentaria. Their length in tabularium one-fourth to one-third of its radius. Minor septa attain one-fourth to one-third length of major septa in tabularia, commonly penetrate innermost parts of dissepimentaria, dilated in tabularia. Axial structures approximate in width two-thirds of tabularium diameter. Medial plate long, straight or sinuous, thin, dilated, or short and lens-shaped. Radial lamellae 10–30 in number, commonly spiral, locally bifurcating. Axial tabellae steeply elevated, regularly to irregularly conical, spaced 0.3–0.5 mm apart. Periaxial tabellae complete, subhorizontal to abaxially declined, sagging to convex, spaced 0.5–1.7 mm apart. Dissepimentaria approximate one-third of corallite diagonals in width. Dissepiments first order transeptal, locally second order transeptal in inner dissepimentaria, variously inflated, subhorizontal or abaxially declined at angles of 30–60°.

Remarks: The species is distinguished by large size (up to 38 mm) and tabularium diameter (>10 mm), high number of major and minor septa (up to 40), and wide axial column (about 2/3 tabularium diameter).

Material and occurrence: The holotype.

Lonsdaleia (*Actinocyathus*) *subtilis* (Dobrolyubova, 1958)
(Fig. 2A–H)

v.* 1958 *Lonsdaleia subtilis* – Dobrolyubova, p. 87, text-fig. 19a-b, pl. XI, Fig. 1a-b.
vp. 1958 *Lonsdaleia longiseptata crassicolumellata* – Dobrolyubova, p. 90, pl. XI, Fig. 2a-b.
vp. 1958 *Lonsdaleia ornata* – Dobrolyubova, p. 93, text-fig. 20a-b, pl. XII, Fig. 1a-b.
v. 1958 *Lonsdaleia heckeri* – Dobrolyubova, p. 96, pl. XI, Fig. 3a-c.

Type: Holotype, *Lonsdaleia subtilis* Dobrolyubova, 1958. Specimen PIN 705/177; Tarusa horizon, lower Serpukhovian, north-western part of the Moscow Basin, Tutoka River, approximately 60 km northeast of the town of Boksitogorsk.

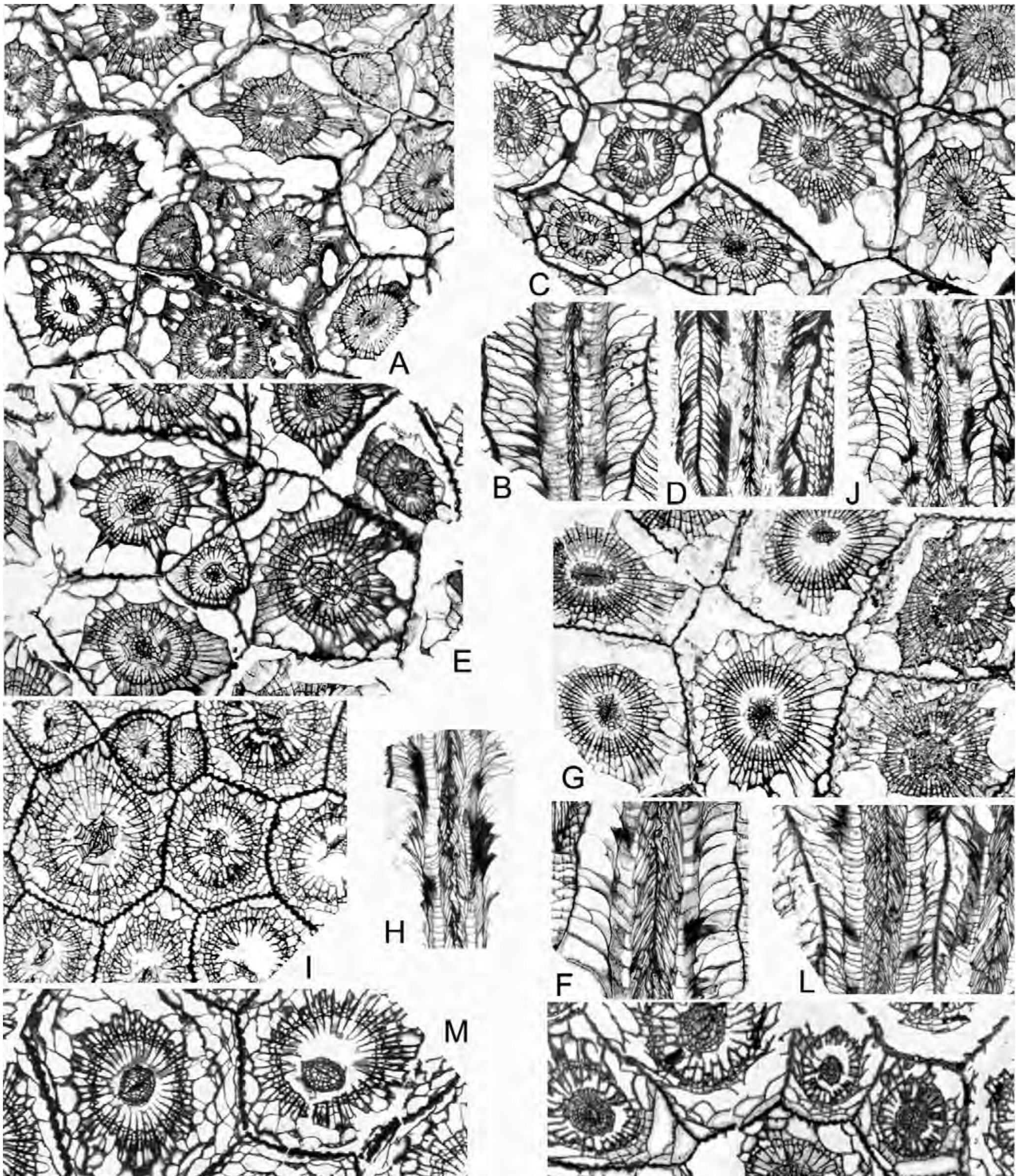

Fig. 2. (A–H) *Lonsdaleia* (*Actinocyathus*) *subtilis* (Dobrolyubova, 1958). (A and B) Holotype of *Lonsdaleia subtilis* Dobrolyubova, 1958; PIN 705/177: (A) transverse section, (B) longitudinal section. Lower Serpukhovian, Tarusa horizon, north-western part of the Moscow Basin, Tutoka River approximately 60 km northeast of the town of Boksitogorsk. (C and D) Holotype of *Lonsdaleia longiseptata crassicolumellata* Dobrolyubova, 1958; PIN 705/187: (C) transverse section, (D) longitudinal section. Lower Serpukhovian, Tarusa horizon, north-western part of the Moscow Basin, Tutoka River approximately 60 km northeast of the town of Boksitogorsk. (E and F) Holotype of *Lonsdaleia ornata* Dobrolyubova, 1958; PIN 705/182: (E) transverse section, (F) longitudinal section. Lower Serpukhovian, Tarusa horizon, north-western part of the Moscow Basin, Tutoka River approximately 60 km northeast of the town of Boksitogorsk. (G and H) Holotype of *Lonsdaleia heckeri* Dobrolyubova, 1958; PIN 705/653: (G) transverse section, (H) longitudinal section. Lower Serpukhovian, Tarusa horizon, north-western part of the Moscow Basin, Retesha River approximately 60 km northeast of the town of Boksitogorsk. (I–M) *Lonsdaleia* (*Actinocyathus*) *gorskyi* (Dobrolyubova, 1958). (I and J) Holotype of *Lonsdaleia gorskyi* Dobrolyubova, 1958; PIN 705/133: (I) transverse section, (J) longitudinal section. Lower Serpukhovian, Steshevo horizon, north-western part of the Moscow Basin, Sukhaya Poneretka Brook, 12 km southwest of the town of Borovichi. (K and L) Holotype of *Lonsdaleia subcrassiconus subcrassiconus* Dobrolyubova, 1958; PIN 705/119: (K) transverse section, (L) longitudinal section. Lower Serpukhovian, Steshevo horizon, north-western part of the Moscow Basin, unspecified locality on Msta River 12–20 km southwest of the town of Borovichi. (M) PIN 705/304: transverse section. Lower Serpukhovian, Tarusa horizon, north-western part of the Moscow Basin, Andoma River 36 km northeast of the town of Vytegra. (Figured as *Actinocyathus crassiconus* in Hecker, 1997, pl. 2, Fig. 1.)

Description: Cerioid. Corallites 7.5–12 mm wide, with diagonals 12–20 mm and tabularia diameters 4–6.25 mm. Major and minor septa 21–30 in number. Major septa may penetrate dissepimentaria, locally reaching outer walls, dilated in tabularia and locally in inner dissepimentaria. Their length in tabularium commonly one-third to half of its radius. Minor septa attain one-fourth to two-thirds length of major septa in tabularia, rarely approaching their length, may penetrate dissepimentaria, locally reaching outer walls, commonly dilated in tabularia and in dissepimentaria. Axial structures attaining one-third to half of tabularium diameter in width, varying in density due to variable number of radial lamellae and variable spacing of axial tabellae. Medial plate long, thin, dilated or lens-shaped, typically straight. Radial lamellae commonly 10–24 in number. Axial tabellae regularly widely conical to steeply elevated, spaced 0.25–0.5 mm apart, seldom irregularly conical. Periaxial cones seldom present. Periaxial tabellae complete, locally divided, subhorizontal, gently sagging to variously declined, spaced 0.4–1.5 mm apart, locally biform morphology. Width of dissepimentaria from one-fifth to two-thirds of corallite diagonals. typically one-third to half of diagonals. Dissepiments first order transeptal of various sizes, locally regular interseptal in inner dissepimentaria and second order transeptal in middle and outer dissepimentaria, variously inflated, abaxially declined at angles of 30–60°.

Remarks: *Actinocyathus subtilis* is mainly distinguished by great variability of septa. Material of this species includes the holotypes of *Lonsdaleia ornata* Dobrolyubova, 1958 (specimen PIN 705/182; Fig. 2E and F), *L. longiseptata crassicolumellata* Dobrolyubova, 1958 (specimen PIN 705/187; Fig. 2C and D), and *Lonsdaleia heckeri* Dobrolyubova, 1958 (specimen PIN 705/653; Fig. 2G and H). The holotypes of *Lonsdaleia subtilis* (Fig. 2A and B), *L. longiseptata crassicolumellata*, and *L. ornata*, all coming from the same locality, show corallites 8–12 mm wide with dissepimentaria dominated by first order transeptal dissepiments. The holotypes of *L. subtilis* and *L. longiseptata crassicolumellata* have 22–24 major and minor septa and tabularia 4–4.5 mm in diameter. They mainly differ in the aspect of axial columns, which are narrow and simple in *L. subtilis*, and dense and approximating in width one-third of tabularium diameter in *L. longiseptata crassicolumellata*. The holotype of *L. ornata* shows corallites with 23–28 major and minor septa, tabularia 5–5.75 mm in diameter, axial columns approximating in width half of tabularium diameter and varying in density depending on the number of radial plates. The holotype of *L. heckeri* resembles the holotype of *L. ornata* in number of septa, but tabularia are smaller (4.5–4.75 mm in diameter), axial columns narrow and dense, minor septa very long in tabularia, and both major and minor septa are well pronounced in dissepimentaria and locally reach outer walls.

Material and occurrence: Twenty seven specimens. North-western part of the basin. Lower Serpukhovian, Tarusa horizon: Pikalevo Quarry, Tutoka and Retesha rivers (Tikhvin area), Patrovsky brook; Steshevo horizon: Tutoka River and Poneretka brook (Borovichi area).

Lonsdaleia (*Actinocyathus*) *gorskyi* (Dobrolyubova, 1958) (Fig. 2I–M)

vp.* 1958 *Lonsdaleia gorskyi* – Dobrolyubova, p. 100, text-fig. 22a-d, pl. XIII, Fig. 1a-b.

vp. 1958 *Lonsdaleia subcrassiconus subcrassiconus* – Dobrolyubova, p. 104, pl. XIII, Fig. 2a-b.

Type: Holotype, *Lonsdaleia gorskyi* Dobrolyubova, 1958. Specimen PIN 705/133; Steshevo horizon, lower Serpukhovian, north-western part of the Moscow Basin, Sukhaya Poneretka Brook, 12 km southwest of the town of Borovichi.

Description: Cerioid, rarely subcerioid and cerioid-astreoid. Corallites 8–12 mm wide, with diagonals 15–20 mm and tabularia diameters 5–7.5 mm. Major and minor septa 26–33 in number. Counter septum locally longer than other major septa and connected to medial plate. Major septa commonly penetrate dissepimentaria, locally reaching outer walls, dilated in tabularia and locally in inner dissepimentaria. Their length in tabularium one-fourth to half of its radius. Minor septa thin, attain one-fifth to one-fourth length of major septa in tabularia or develop as ridges on inner wall, commonly develop in inner dissepimentaria, locally reaching outer walls. Axial structures attaining half of tabularium diameter. Medial plate long, thin, dilated or lens-shaped, typically straight, seldom irregular. Radial lamellae typically 15–24 in number, rarely 6–8, locally bifurcating. Axial tabellae widely conical to steeply elevated, regularly spaced 0.15–0.25 mm apart. Periaxial tabellae complete, locally divided, subhorizontal, gently sagging to variously declined, spaced 0.5–1.5 mm apart, locally biform. Tabellae in position I more crowded than tabellae in position II. Dissepimentaria attain one-sixth to one-fourth of corallite diagonals. Dissepiments transeptal of various sizes in outer dissepimentaria, regular interseptal in inner dissepimentaria, variously inflated, abaxially declined at angles of 20–70°.

Remarks: *Actinocyathus gorskyi* is distinguished by large variability of major septa, short minor septa, and relatively narrow dissepimentarium. It also differs from all other species of this group by the presence of astreoid zones in some colonies. Material of *A. gorskyi* includes the holotype of *Lonsdaleia subcrassiconus subcrassiconus* Dobrolyubova, 1958 (specimen PIN 705/119; Fig. 2K and L), showing corallites with 28–31 major septa, wide axial columns with regular crowded tabellae and dissepimentaria dominated by first order transeptal dissepiments.

Material and occurrence: Twenty specimens. North-western part of the basin. Lower Serpukhovian, Tarusa horizon: Andoma and Tagazhma rivers (Vytegra area); Steshevo horizon: Msta River and Poneretka brook (Borovichi area). Lower upper Serpukhovian, Protva horizon, Ragusha River (Tikhvin area).

Lonsdaleia (*Actinocyathus*) sp. A (Fig. 1G and H)

vp. 1958 *Lonsdaleia longiseptata crassicolumellata* – Dobrolyubova, p. 90 (non pl. XI, Fig. 2a-b = *Lonsdaleia* (*Actinocyathus*) *subtilis* (Dobrolyubova, 1958)).

vp. 1958 *Lonsdaleia subcrassiconus subcrassiconus* – Dobrolyubova, p. 104 (non pl. XIII, Fig. 2a-b = *Lonsdaleia* (*Actinocyathus*) *gorskyi* (Dobrolyubova, 1958)).

Type: Holotype, specimen PIN 703/5074; Mikhailov horizon, lower Brigantian, southern part of the Moscow Basin, Vyssa River near the town of Venev.

Description: Cerioid. Corallites 13–14 mm wide, with diagonals 20–25 mm and tabularia diameters 4.75–6.5 mm. Major and minor septa 21–26 in number. Major septa dilated in tabularia and penetrate dissepimentaria. Their length in tabularium one-third to half of its radius. Minor septa thin to dilated, attain one-fifth to one-third length of major septa in tabularia, locally develop as ridges on inner wall, and locally develop in innermost parts of dissepimentaria. Axial structures from one-third to half of tabularium diameter in width. Medial plate long, sinuous or lens-shaped. Radial lamellae 8–20 in number. Axial tabellae regular widely conical to steeply elevated, spaced 0.15–0.5 mm apart. Periaxial tabellae complete, seldom divided, subhorizontal gently sagging or convex, slightly declined abaxially or adaxially, spaced 0.5–1.5 mm apart, locally biform. Tabellae in position I more crowded than tabellae in position II. Dissepimentaria attain one-fourth to one-third of corallite diagonals. Dissepiments first order transeptal, locally second order transeptal and regular interseptal in inner dissepimentaria, variously inflated, subhorizontal or abaxially declined at angles of 50–75°.

Remarks: *Actinocyathus* sp. A is close to *A. crassiconus* in septal number and tabularium diameter, but has larger corallites with wider dissepimentaria. It also shows a close affinity to *A. lativesiculosus*, but has smaller tabularia and a larger number of radial lamellae.

Material and occurrence: Three specimens. Southern part of the basin. Brigantian, Mikhailov horizon, Vyssa River (Venev area). Lower Serpukhovian, Tarusa horizon, Gurievskiy Quarry (Venev area). North-westrn part of the basin. Brigantian, Venev horizon, Priksha River (Borovichi area).

Lonsdaleia (*Actinocyathus*) sp. B
(Fig. 1I and J)

vp. 1958 *Lonsdaleia subcrassiconus subcrassiconus*–Dobrolyubova, p. 104 (non pl. XIII, Fig. 2a-b = *Lonsdaleia* (*Actinocyathus*) *gorskyi* (Dobrolyubova, 1958)).

Type: Holotype, specimen PIN 1562/14; Tarusa horizon, lower Serpukhovian, southern part of the Moscow Basin, Gurievskiy Quarry, 10 km northwest of the town of Venev.

Description: Cerioid and subcerioid. Corallites 16–25 mm wide, with diagonals 20–28 mm and tabularia diameters 7–9.5 mm. Major and minor septa 25–30 in number. Major septa penetrate dissepimentaria, dilated in tabularia and locally in inner dissepimentaria. Their length in tabularium approximately half of its radius. Minor septa attain one-fifth to two-thirds length of major septa in tabularia, seldom approaching their length, locally develop as ridges on inner wall and penetrate innermost parts of dissepimentaria, commonly dilated in tabularia. Axial structures approximating in width half of tabularium diameter. Medial plate long and straight, thin or dilated to lens-shaped. Radial lamellae typically 20–40 in number, rarely up to 50. Axial tabellae elevated, regularly and irregularly conical. Their spacing changes along individual corallite from 0.20–0.25 to 0.40–0.50 mm apart. Periaxial tabellae complete, locally divided, subhorizontal to variously declined, sagging to convex, spaced 0.5–1.3 mm apart. Dissepimentaria approximate one-third of corallite diagonals in width or wider. Dissepiments first order transeptal, locally second order transeptal in inner dissepimentaria, variously inflated, abaxially declined at angles of 30–80°.

Remarks: *Actinocyathus* sp. B shows a close affinity to *Actinocyathus* sp. A, but has wider tabularia and a larger number of septa and radial lamellae. It is distinguished from other members of this species-group by a large number of radial lamellae (up to 50) and irregular spacing of axial tabellae.

Material and occurrence: Two specimens. Southern part of the basin. Lower Serpukhovian, Tarusa horizon, Gurievskiy Quarry (Venev area). Westrn part of the basin. Lower Serpukhovian, Steshevo horizon, Vazuza River (Rzhev area).

3. Evolution, phyletic relationships, and ecology

The *A. crassiconus* species-group ranges in the Moscow Basin from the lower Brigantian to the lower upper Serpukhovian (basal Mikhailov–Protva horizons). Since the very beginning of its evolution in the Moscow Basin, this group showed a clear preference to the habitats distinguished by active hydrodynamics, especially to the habitats in the zone of bottom currents in the north-western part of the basin. The earliest records of the group in the Moscow Basin are in its southern part (Mikhailov horizon). By that time the *A. floriformis* group had already colonized the most favourable habitats in the open sea zone in this part of the basin, and successfully evolved there and played the leading role in rugose communities. It was almost always numerically superior to the *A. crassiconus* group except during Tarusa time (earliest Serpukhovian) in the north-western part of the basin (Hecker, 1992a,b, 1997). This phenomenon may be explained by early migration of *A. crassiconus* to this part of the basin (Venev time, late Brigantian) and by consolidation of its position in a habitat similar to those occupied by the group in Tarusa time.

The specific diversity in this species-group resulted from a long-term existence of *A. crassiconus* in the basin (basal Mikhailov–Protva) and its successful evolution. Two stages of evolution and three trends may be discerned (Fig. 3). At the first stage (Mikhailov time), the group consolidated itself in the open sea zone of the southern part of the basin. The most important evolutionary changes – those giving substantial opportunities of colonization of new kind of habitats – took place at the very beginning of the Serpukhovian (Tarusa time).

The first trend of evolution was characteristic for the species typically restricted to the southern part of the basin. They evolved in the direction of increase in corallite size and number of septa. The first member of this lineage, *Actinocyathus* sp. A, appeared in the open sea zone in Mikhailov time. It differed from *A. crassiconus* mainly in dissepimentarium width. This species most probably gave rise to *A. lativesiculosus*, *A. sarytschevae*, and *Actinocyathus* sp. B at the beginning of Tarusa time. Increase in tabularia diameter and simplification of axial structures led to *A. lativesiculosus*, whereas increase in number

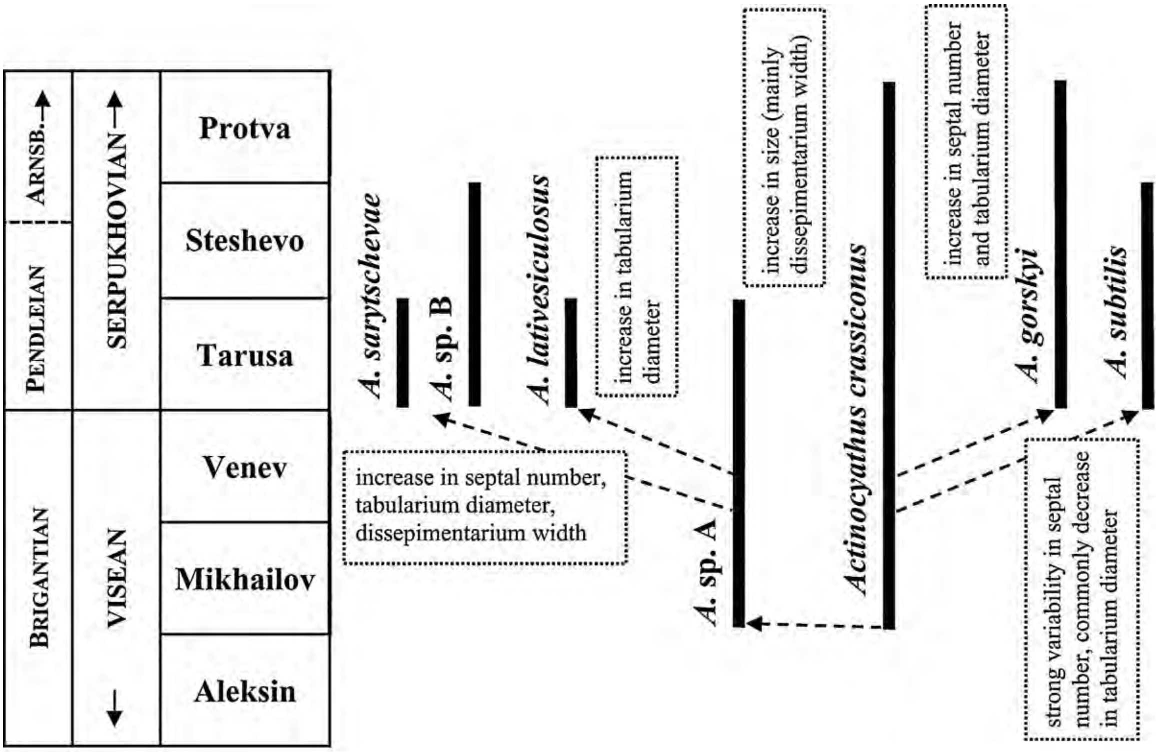

Fig. 3. Range and phyletic relationships of species of the *Lonsdaleia* (*Actinocyathus*) *crassiconus* species-group in the Moscow Basin during the latest Visean (Brigantian) and Serpukhovian.

and length of septa, increase in tabularia diameter and complication of axial structures led to *Actinocyathus* sp. B and *A. sarytschevae*. Both *A. lativesiculosus* and *A. sarytschevae* remained restricted to the southern part of the basin, where they inhabited the open sea and the near-shore shallow-water zone with active hydrodynamics. *Actinocyathus* sp. A and *Actinocyathus* sp. B also colonized the near-shore shallow-water zone with active hydrodynamics in the north-western part of the basin.

In the north-western part of the basin, *A. crassiconus* evolved at the beginning of the Serpukhovian following two trends. Increase in number of septa and tabularia diameter led to *A. gorskyi*, and a wide range of variability in septal number commonly associated with a decrease in tabularia diameter to *A. subtilis*. Both species dominated in the zone of bottom currents in Tarusa and Steshevo times, but occupied different habitats. In general, *A. subtilis* was mostly confined to the habitats affected by influence of the coast (terrigenous supply and recurrent increase of iron content), and *A. gorskyi* was abundant in the most favourable habitats, where it also survived in Protva time. *Actinocyathus subtilis* remained restricted to the north-western part of the basin, and *A. gorskyi* also colonized the zone of bottom currents in its western part in Tarusa time.

Compared to the other members of this group, *A. crassiconus* has low specialization. It is reported from the open sea zone in the south of the basin and from various habitats in the near-shore shallow-water zone and zone of bottom currents in its north-western part.

4. Variability

Variability, involving dissepimentarium width, length of minor septa, size of axial columns, and number of radial lamellae, was characteristic for the majority of species. Size of tabularia and the number of major septa were the most stable characters in all species except for *A. subtilis*.

Intracolonial variability was typical for all species, but is better pronounced in *A. subtilis* and *A. gorskyi*, the species altogether abundant and rather long-ranging. However, it was not constant during their existence in the basin, and reached a very high level in Tarusa time when both species became dominant in rugose communities of the zone of bottom currents in the north-western part of the basin. *Actinocyathus gorskyi* reached the peak of intracolonial variability in the most favourable habitats of this zone, and *A. subtilis*, in the habitats affected by the influence of the coast.

Variability within a biotope also became higher when the role of species increased in the communities. This kind of variability was extremely high in *A. subtilis* in Tarusa time and involved all structures including tabularium diameter and number of septa. The holotypes of *Lonsdaleia subtilis* (Fig. 2A and B), *L. longiseptata crassicolumellata* (Fig. 2C and D), *L. ornata* (Fig. 2E and F), and *L. heckeri* (Fig. 2G and H) represent various aspects of variability of this species in the habitats of the zone of bottom currents. Variability within a biotope was also characteristic for *Actinocyathus gorskyi* in Tarusa time in the most favourable habitats of the zone of bottom currents. Colonies mostly differed in width of dissepimentaria, density of axial columns and in growth habit (cerioid, subcerioid, and cerioid-astreoid).

Intraspecific variability was especially characteristic for *A. gorskyi*, an abundant and not too highly specialized species. Three groups may be discerned, mainly differentiated by composition and width of dissepimentarium length of septa, and, to less extent, by size and density of axial columns. The first group was restricted to the most favourable habitats in the zone of bottom currents in Tarusa time. It comprised cerioid, subcerioid, and cerioid-astreoid colonies, showing axial structure of medium size and dissepimentaria dominated by first order transeptal dissepiments of various sizes (Fig. 2M). The second group colonized the same type of habitats in Steshevo and Protva times. It includes the holotype of *Lonsdaleia subcrassiconus subcrassiconus* (Fig. 2K and L) and is distinguished by large and dense axial columns. Minor septa are not well pronounced in tabularia, and dissepimentaria are wide and dominated by large first order transeptal dissepiments. The third group was restricted to the near-shore shallow-water zone in Steshevo and Protva times. It includes the holotype of *Lonsdaleia gorskyi* (Fig. 2I and J) and is distinguished by narrow dissepimentaria composed of small transeptal and regular interseptal dissepiments. Minor septa are typically long in tabularia and well pronounced in dissepimentaria, locally reaching outer walls. Axial columns are commonly narrow and show few radial lamellae.

Intraspecific variability in *Actinocyathus crassiconus* is less striking and may be exemplified by length of minor septa, composition of dissepimentarium, and, to less extent, by the density of axial columns. In the north-western part of the basin, this species commonly occurred together with its descendants in various habitats and typically resembled them in aspect of dissepimentaria and axial columns, and in length of septa, differing mainly in corallites and tabularia size and in number of septa.

5. Conclusions

The *Actinocyathus crassiconus* species-group in the Moscow Basin comprised seven species, *A. crassiconus*, *A. lativesiculosus*, *A. sarytschevae*, *A. subtilis*, *A. gorskyi*, *Actinocyathus* sp. A, and *Actinocyathus* sp. B. It ranged from the lower Brigantian to the lower upper Serpukhovian and showed a clear preference to the habitats distinguished by active hydrodynamics, especially to the zone of bottom currents in the north-western part of the basin, where it dominated in rugose communities during the earliest Serpukhovian.

Two stages of evolution may be discerned in this group, in the early Mikhailov (*A. crassiconus–Actinocyathus* sp. A) and at the very beginning of the Serpukhovian, when all other species appeared. In the southern part of the basin, the group evolved in the direction of increase in corallite size and number of septa (*A. crassiconus–Actinocyathus* sp. A–*A. lativesiculosus–Actinocyathus* sp. B–*A. sarytschevae*). Evolution in the north-western part of the basin followed two trends: strong variability in septal number, common decrease in tabularium diameter (*A. crassiconus–A. subtilis*), and increase in septal number and tabularium diameter (*A. crassiconus–A. gorskyi*).

Intracolonial variability was typical for all of the species studied. Variability within a biotope was especially characteristic for the species altogether abundant and highly specialized, and intraspecific variability for the species rather abundant and not too highly specialized.

Lonsdaleia longiseptata crassicolumellata Dobrolyubova, 1958, *L. ornata* Dobrolyubova, 1958, and *L. heckeri* Dobrolyubova, 1958 are synonymous with Actinocyathus subtilis, Lonsdaleia subcrassiconus subcrassiconus Dobrolyubova, 1958 with Actinocyathus gorskyi, and Lonsdaleia ossipovae Dobrolyubova, 1958 is with Actinocyathus crassiconus.

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Research paper

Skeletal repair of extreme damage in rugose corals, Pella Formation (Mississippian, Iowa, USA)

Gregory E. Webb[a,*], Thomas E. Yancey[b]

[a] School of Natural Resource Sciences, Queensland University of Technology, GPO Box 2434, Brisbane, QLD 4001, Australia
[b] Department of Geology and Geophysics, Texas A&M University, College Station, TX 77843, USA

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Abstract

Little is known about predation on rugose corals or the repair of damage to rugose coral skeletons. Here we describe a population of the solitary rugose coral *Amplexizaphrentis spinulosa* (Milne-Edwards and Haime, 1851) from the Late Mississippian Pella Formation in Keokuk County, Iowa, USA wherein ~30% of 135 specimens experienced sublethal damage resulting from compression apparently inflicted by fish or other large predators. Many corals were able to repair severe damage and re-establish a relatively normal morphology despite the loss of parts of the wall. Healed damage includes: (1) chips to the edge of the calice, (2) punctures in the wall, (3) lost sections of wall, (4) re-cemented sections of wall, some at odd angles, (5) changes in growth direction, and (6) rejuvenescence. Multiple episodes of damage and repair occurred in 5% of samples. More severe damage on the cardinal side in almost one-half of damaged samples may reflect structural weakness at the cardinal fossula relative to the counter side, but septa were broken in all positions in many samples. The pattern of alignment and preservation of broken plates in the calice suggests that soft tissues were better attached to the skeleton in a band relatively far above the calice floor. Better musculature also may have occurred in the same band. Where parts of the wall were broken free from septa that remained fixed at their axial ends, new wall was deposited as stereoplasm against and enveloping the adaxial ends of the original septa. Lost lengths of septa were replaced by adaxial growth. New septa were commonly contorted, presumably owing to deformation of surviving soft tissues that had lost structural support. Broken septa were generally healed, commonly with poor alignment. The high survival rate, even following multiple attacks, suggests that the soft tissues of the coral polyps were robust. The rarity of changes in growth direction following attacks suggests that the corals may have been more capable of righting themselves and re-establishing an optimum growth orientation than has commonly been suggested for solitary Rugosa.

Keywords: Rugosa; Palaeobiology; Skeletal repair; Damage; Late Mississippian; Pella Formation

1. Introduction

Scleractinian corals fall prey to a variety of coralivores, including gastropods, polychaetes, fish, and echinoderms, such as *Acanthaster planci* (e.g., Goreau, 1964; Bak et al., 1977; Reese, 1977). However, many of those predators cause little damage to the coral skeleton, primarily removing soft tissue. Although responses of polyps to stresses and injuries are becoming better known, most studies focus on colony regeneration rather than skeletal damage repair within individual polyps (e.g., Oren et al., 2001; Henry and Hart, 2005; Titlyanov et al., 2005). Bak et al. (1977) showed that polyps of *Montastraea* extend septa into damaged areas of the corallum and Bak (1983) documented extension of new skeleton over dead regions in *Acropora palmata*. Tumour-like irregular coral growths have been described (e.g., Domart-Coulon et al., 2006 and sources cited therein), but they do not appear to represent repair of physical damage in coralla. Regeneration of broken solitary fungiid corals has been studied in terms of its role in vegetative reproduction (Yamashiro et al., 1989). However, most studies on regeneration following damage to scleractinian corals have focused on soft tissue regeneration.

Common responses to stress in Palaeozoic corals include rejuvenescence and growth irregularities resulting from substrate instability (e.g., Elias, 1984b; Neuman, 1988; Sorauf, 2001). Skeletal responses to parasites or commensal organisms have been documented in Palaeozoic corals by many authors (e.g., Oliver, 1983; Elias, 1986; Falces, 1997), but skeletal

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[*] Corresponding author.
E-mail address: ge.webb@qut.edu.au (G.E. Webb).

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repair in damaged corals has been documented only rarely. Elias (1984a) documented cases of skeletal damage in Ordovician rugose corals, wherein parts of the polyp withdrew from the wall and emplaced new inner walls, giving the impression of healed breakage to the original wall. Emplacement of new epitheca by contracted polyps and associated rejuvenation was a common response of *Heliophyllum* to encroaching sediment at the margin of the polyp (Sorauf, 2001). Falces (1997) documented a specimen of the solitary rugose coral *Ufimia* where the tip of a septum was broken free and covered over by stereoplasm. Falces (1997) also documented cavities within the wall of some specimens of *Rotiphyllum*, attributing them to an unknown pathology. A specimen of *Calceola sandalina* from the Devonian of Moravia had most of the alar quadrant of its skeleton removed, but the injury was healed within the calice (Galle and Mikuláš, 2003; Galle and Ficner, 2004). Those authors attributed the injury to a large, probably vertebrate, predator on the basis of the robust skeleton damaged and depressions that may represent teeth marks. Rodriguez (2004) illustrated two cases where broken skeletons were repaired in the rugose corals *Palaeosmilia* and *Axophyllum*. Despite those cases, documentation of damaged Palaeozoic corals has been sporadic, and repaired damage to such corals must be considered unusual.

In describing damage repair in Mississippian brachiopods from Utah, Alexander (1981) illustrated a specimen of *Triplophyllum spinulosum* with minor repaired damage. He attributed the damage to shark predation on the basis of puncture morphology. The purpose of this paper is to describe a population of *Amplexizaphrentis spinulosa*, possibly the same species as discussed by Alexander (1981), that includes a large proportion of damaged and repaired individuals that may reflect attempted predation by large vertebrates (i.e., fish). These corals are exceptional in that: (1) a large percentage (∼30%) of recovered samples shows evidence of having survived one or more attacks, and (2) repairs to skeletons of some samples are the most extreme so far documented. The corals are significant in that the pattern of repair provides new insight into the palaeobiology of the Rugosa. Specimens are reposited in the University of Iowa Paleontology Repository (SUI).

2. Setting and material

A collection of 135 corals was made from weathered shale on the north side of Taylor Quarry (NW ¼, SW ¼ section 13, T.74N, R13W) in Keokuk County, ∼45 miles southwest of Iowa City, Iowa, USA. The corals were obtained during a single visit to the site and all corals that appeared to be fairly complete were collected, including juveniles, but small fragments of specimens were not collected. The corals occur in a richly fossiliferous section in the upper part of the upper Mississippian (lower Chesterian) Pella Formation, ∼5–6 m above the base. The formation consists of intertidal deposits at the base passing upwards into shallow subtidal marine deposits making up part of a large cyclothem (Johnson and Vondra, 1969; Witzke et al., 1990). The shale represents a relatively low-energy environment, but the earliest tips of the coralla have been broken or abraded from some specimens, and some samples appear to have had some surface abrasion or possibly dissolution. Regardless, fossils are well preserved with little post-depositional compaction, even in inflated *Anthracospirifer* brachiopods. Corals from the Pella Formation were originally described as *Zaphrentis pellaensis* by Worthen (1890, p. 74), and similar samples were illustrated by Ulrich (1917), but Sando and Bamber (1985) considered *Z. pellaensis* to be a junior synonym of *A. spinulosa* (Milne-Edwards and Haime, 1851).

3. Observations

Approximately 30% of corals collected (i.e., the total collection: TC) have some type of healed skeletal damage, including the following six categories: (a) chips to calice rim (4.4% TC) (Fig. 1A); (b) compressions and punctures in wall (4.4% TC) (Fig. 1B and C); (c) loss of original fragments of wall (23% TC) (Fig. 1F); (d) re-cementation of fragments of wall into position (19% TC) (Fig. 1D and E) or out of position (6% TC) (Fig. 1G), rarely even at right angles to their original orientation (Fig. 1J–L); (e) rejuvenescence (6% TC) (Fig. 1H); and (f) change in growth axis (6% TC) (Fig. 1I). Many specimens show more than one type of damage, and multiple episodes of damage were survived by 5% of corals in the total collection (Fig. 1A and G) with one specimen showing three separate cycles of damage and repair. Damage occurred to all skeletal quadrants, but almost 50% of damaged samples had most damage (i.e., more lost skeletal fragments) directly adjacent to the cardinal fossula. In general, damage was also more intense in more mature portions of coralla.

Breakage of the wall varied in position and degree. The most severe damage involved loss of entire sections of wall (Fig. 2A). Where large sections of skeleton were lost, the new wall was thin (Fig. 2B) and some septa were abandoned at the axis. Dissepiment-like plates were emplaced in some cases, before new septa were formed. Although such areas of damage appear similar externally to rejuvenation, it is clear that part of the polyp was removed; it did not contract towards the axis. In some cases, the wall broke free of septa near their junction with it, leaving septa in place that were still attached at their axial ends. In other cases, lengths of septa were lost along with sections of wall. In the former case, a new wall was emplaced initially as layers of stereoplasm that enveloped the broken ends of septa. Ends of septa were extended a short way towards the new wall in some cases (Fig. 2C). New sections of wall were commonly thinner than the original wall (Fig. 2B), and new epitheca has growth lines that became continuous with those in undamaged areas within a short distance of distal extension. In some cases, damaged areas were repaired prior to continued growth around the undamaged edge of the calice. However, some of the replacement wall that cemented plates back into position in severely crushed specimens is smooth (Fig. 1G), apparently lacking growth lines. Even where a large amount of the original wall was lost, the corals do not contain trapped coarse detritus that penetrated through the damaged area.

Where lengths of septa were lost along with a section of wall, new septal growth was initiated from the remaining free end of the original broken septa and extended out towards the

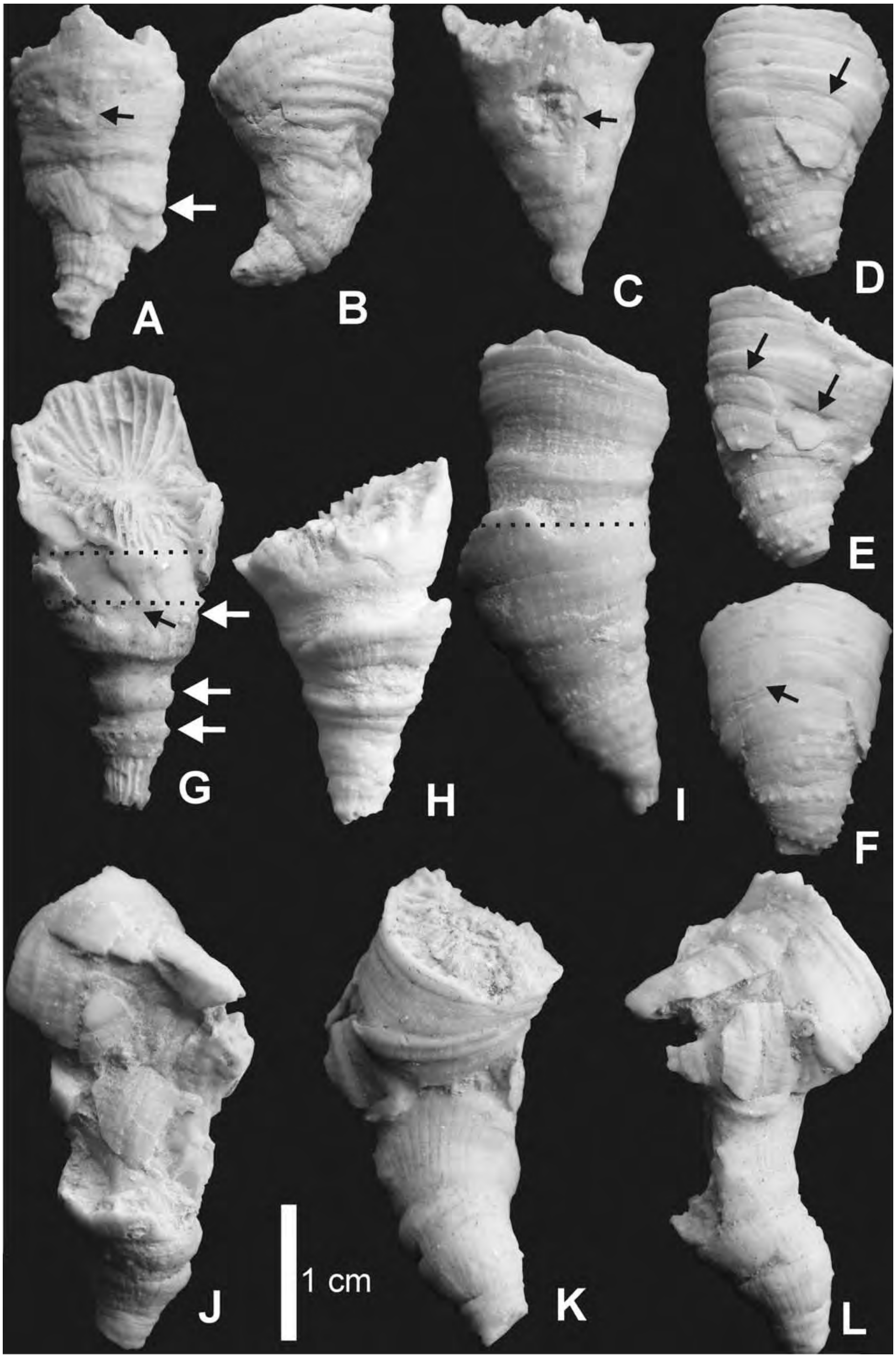

Fig. 1. (A–L) *Amplexizaphrentis spinulosa*, Mississippian, Iowa, USA, showing various degrees of sublethal damage and skeletal repair. Scale bar at base is for all specimens. (A) Lateral view of SUI-116718 showing repaired chip to edge of calice (black arrow) and lower damaged interval (white arrow) with wall fragments cemented back into position. (B) Lateral view of SUI-116719 showing compression and indentation on side of corallum. (C) Lateral view of SUI-116720 showing conical depression in corallum. (D–F) lateral views of SUI-116721; (D) and (E) showing wall fragments cemented into position with better alignment at their distal edges (black arrows). Note that the fragments project away from the coral at their proximal ends; (F) shows a replaced wall fragment (arrow). (G) Lateral view of a badly crushed SUI-116716 showing wall fragments irregularly cemented back into position. Black arrow shows position of smooth stereoplasm that replaced missing wall, and the three white arrows show the positions of three different damage events. Upper dotted line is level of thin section shown in Fig. 2D. Lower dotted line is level of thin section shown in Fig. 2F. (H) Lateral view of SUI-116722 showing rejuvenation. (I) Lateral view of SUI-116717 showing a change in growth axis at the level of skeletal damage. Dotted line is level of thin section shown in Fig. 2A. (J–L) Severely damaged specimen (SUI-116715) showing a change of growth orientation and irregularly re-cemented fragments of the wall.

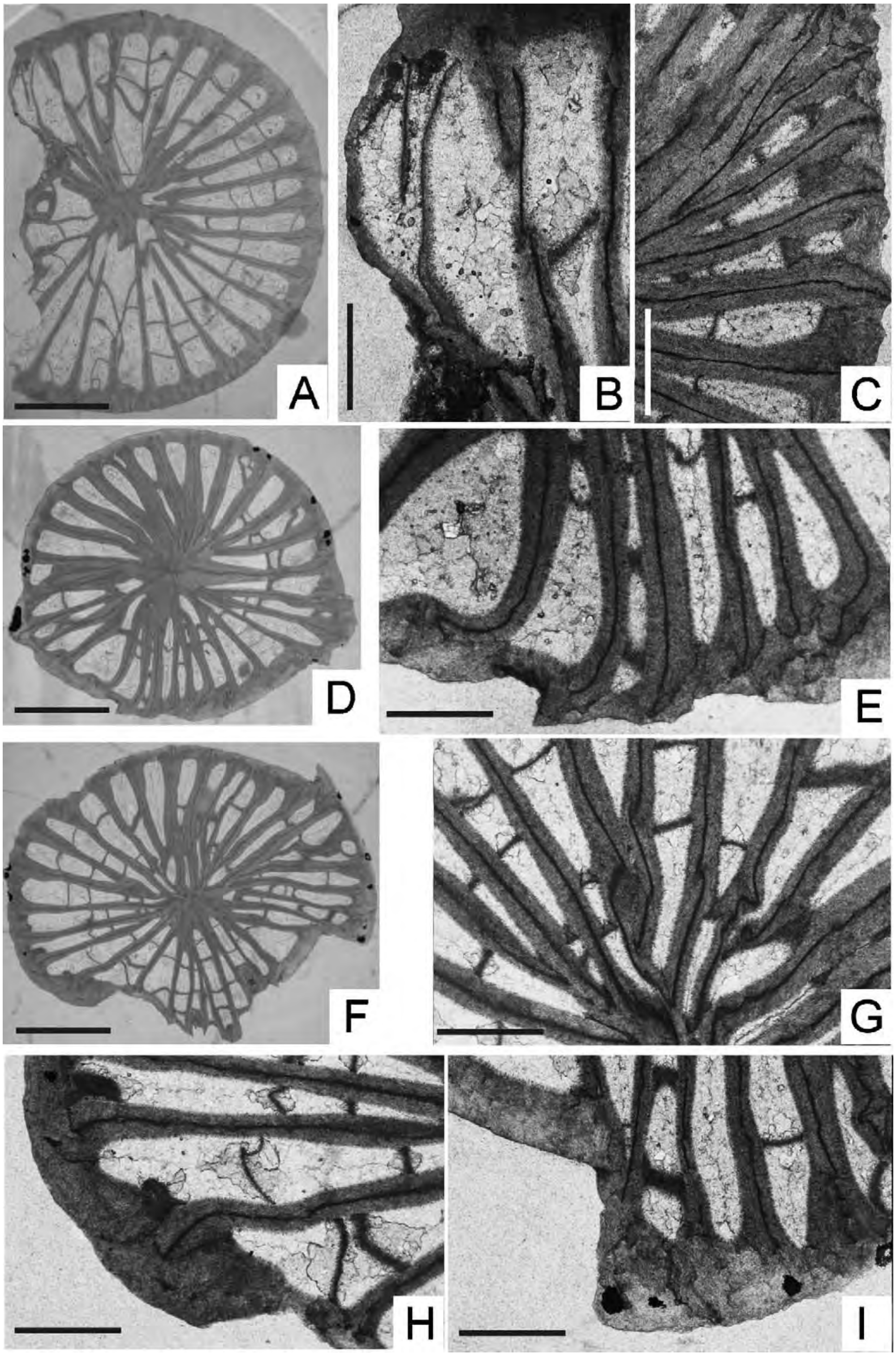

Fig. 2. (A–I) *Amplexizaphrentis spinulosa*, Mississippian, Iowa, USA, thin sections showing various degrees of sublethal damage and skeletal repair. Scale bars for A, D and F are 3 mm. Scale bars for B, C, E and G–I are 1 mm. (A) Transverse section of SUI-116717 wherein the left side of the corallum was lost along with soft tissues and replaced by a thin wall and thin new septa. (B) Enlargement of (A) showing the thin wall, thin new septa, and the thin replacement segment where a septum was broken. (C) Transverse section of SUI-116723 wherein the wall was lost near where it joined the septa and new wall was emplaced around the septa after minor adaxial growth. (D) Lower transverse section of a compressed specimen (SUI-116716) that lost a section of wall with portions of septa attached (lower side of specimen). (E) An enlargement of (D) showing that new septa grew adaxially within soft tissues that were warped to one side, thus becoming almost parallel to the new section of wall. (F) Upper transverse section of a compressed specimen (SUI-116716) with offsets in the walls and broken septa. (G) An enlargement of the axial areas of (F) showing broken and repaired septa near the axis. (H) An enlargement of (F) showing new sections of wall enveloping repaired septa. (I) An enlargement of (F) showing where a compressed segment of wall was healed back against the side of an undamaged septum.

position of the missing wall. In some cases, septa appear to have grown back before the new segment of wall was emplaced. However, the new portions of septa are commonly deformed, being deflected in one direction or another (Fig. 2D and E). In some cases, the resulting septa have outermost ends that curve until they almost parallel the newly emplaced section of wall.

In some cases, fragments of wall were healed back into place with resultant compression of the corallum. Where original wall fragments were not properly aligned in compressed areas, they abut the sides of septa on adjacent, non-compressed sections of coral (Fig. 2F and I). Individual fragments were set back into place by layers of stereoplasm, and even some very small pieces of original wall were retained. Retained plates were commonly better aligned at their distal-most ends (i.e., towards the edge of the calice) (Fig. 1D and E), but some plates were healed back into the corallum completely out of alignment and rotated more than 90°, suggesting the severe distortion of adjoining soft tissues. Where septa were broken, they were generally repaired as continuations of the original septa, but they are commonly out of alignment and have overlapping ends where significant compression occurred. No example was noted where the broken end of one septum was healed back to the opposing end of a different septum. Where part of a septum was lost between two broken ends, a new section was emplaced complete with new dark mid-line, but it was commonly thinner than the original septum (Fig. 2B). Replacement septa, where entire septa were lost, were thin, and some septa were highly contorted. Sections of broken septa that were free at both ends were rarely cemented into interseptal spaces with stereoplasm.

4. Interpretation

Increased damage on the cardinal side of the coral may result from that part of the skeleton being less structurally sound owing to the large fossula and septa that are commonly thinner on the cardinal side. The less dilated mature sections of coralla may also have been easier to damage, whereas juvenile parts of coralla are commonly more thickened by stereoplasm. However, increased damage around the fossulae could also reflect differences in the biology of the soft tissues in those regions (e.g., Elias, 1984a).

Rapid re-establishment of continuous growth lines on the epitheca suggests that the regular secretory margin of the coral was healed in damaged areas early during the repair phase. However, smooth epitheca in severely crushed zones suggests secretion of layers of stereoplasm by the normal calicoblastic layer that lines the calice. This tissue is responsible for secreting vertical elements like septa within invaginations in the polyp base, but also stereoplasmic thickening on the sides of walls and septa. Hence, it is possible that the soft tissues, including the intact calicoblastic layer, were not lost with sections of wall that came free, and thus, they retained their ability to secrete stereoplasm and heal damage to the skeleton. Elias (1984a) suggested that soft tissues of Ordovician corals could retract from the septa and still secrete smooth layers of stereoplasm, leaving an open gap in septal lamination. Further evidence that most soft tissue survived intact comes from the way in which septa healed. Coordinated curvature of adjacent new septa suggests that soft tissues remained intact where sections of skeleton were lost and that the lack of structural support led to distortion of the soft tissues, and thus, to distorted septal growth away from the axis. The length of the invaginations in which septa were secreted on the base of the soft tissue would have remained unchanged irrespective of warping or compression. Thus, new septa formed in those invaginations would be curved if the soft tissues were warped to one side. A similar process was inferred by Elias (1984a) for contortion of septa in Ordovician corals where soft tissues had contracted towards the axis. The lack of coarse detritus within the damaged areas of skeleton in the Pella corals is also consistent with retention of all or much of the original soft tissue.

5. Discussion

Pella corals represent the most extreme cases of damage repair so far documented in rugose corals. As with the repaired broken septum in *Rotiphyllum* (Falces, 1997), stereoplasm was used to heal over broken skeletal elements. However, in *Rotiphyllum* stereoplasm merely sealed over the break; there was no new extension of the septum itself. Thus, the repair did not replace the missing part of the septum as in the present material. A similar pattern may be shown in *Axophyllum* (Rodriguez, 2004), although breakage of the septa is less clear. The occurrence of thin vertical plates that are similar to dissepiments in some of the severely damaged Pella corals is similar to the 'vesicular tissue' that replaced abandoned septa in damaged *Palaeosmilia* (Rodriguez, 2004). Otherwise, few comparable cases of repaired damage have been documented.

The soft-part biology of rugose corals is poorly understood despite many detailed studies based on palaeoecology, functional morphology, and structural analogy with the Scleractinia (e.g., Flügel, 1975; Elias, 1984a; Fedorowski, 1997; Scrutton, 1999; Gudo, 2002). The pattern of recovery in the Pella corals suggests that their soft tissues commonly remained more or less intact, even where large parts of the skeleton were fractured, broken free and lost. The relationship between areas that easily lost skeletal sections and those that did not may provide information about the attachment of the soft tissues to the skeleton. Better retention and alignment of broken segments of wall at their distal edges (i.e., towards the calice rim) suggests that soft tissues were better attached to the skeleton in a band above the base, but below the edge of the calice. Breakage into the dead, abandoned part of the corallum would clearly have led to the loss of fragments, but even where all breakage occurred within the calice, there seems to have been a band below the top of the calice where skeletal fragments were more commonly retained by soft tissues. Better alignment of broken plates with the undamaged parts of the corallum in that band may also suggest the occurrence of well developed musculature in the band as compared to lower in the calice. Such a concentration of musculature might be consistent with better muscle development around the mouth of the polyp. Small chips that were lost from the edge of the calice in some specimens suggest that the band of more effective soft tissue attachment did not extend all the way to the edge of the calice. The distal edge of the calice may have been free of attachment so that the polyp could retract below the edge of the skeleton for protection. Thus, desmocytes, the cells that attach the calicoblastic epithelium to the skeleton (Muscatine et al., 1997; Goldberg, 2001), may have been concentrated in a band that allowed polyp retraction into the calice at the top, but they may have degenerated somewhat lower in the calice, possibly to aid the movement of the soft tissues upwards when new tabulae were emplaced (Wells, 1969). Desmocyte scars are well known in scleractinian corals (Wise, 1970; Sorauf and Podoff, 1978) and they have been described on the walls between septa in some rugose corals (Ilina, 1980; Fedorowski, 1985, 1989; Stolarski, 1993), but their relative abundance throughout the calice has not been documented and attachment structures may have been too small to leave visible scars in many rugose corals (Fedorowski, 1997).

Cases where solitary rugose coral polyps continued growing through rejuvenation and changes in growth axis after abandoning substantial parts of their calices as a result of toppling or sediment encroachment have been well illustrated by Sorauf (2001), but it is not clear if the soft tissues retracted from the abandoned skeleton intact or if tissues in those regions were killed. The degree to which rugose coral tissues may have been capable of purposeful detachment from the skeleton is controversial at two levels. Matthai (1914) suggested that new horizontal elements, such as dissepiments or tabulae, were emplaced within a horizontal infolding of the calice wall, thus isolating the lower part of soft tissues and leaving them to atrophy below the completed structure. Weyer (1972) agreed on the basis of embedments of trapped foreign bodies in the base of rugose coral calices. However, Wedekind (1937) suggested that tissues detached and were raised within the corallite by ‘blistering’ wherein hydraulic pressure held the pedal disk above the old calice floor. Subsequent authors have largely agreed with Wedekind’s interpretation (e.g., Wells, 1969; Sorauf, 1970; Fedorowski, 1997). The other area of controversy centres on the ability of coral tissues to intentionally pull free of the walls of cardinal and alar fossulae. Elias (1984a) suggested that the soft tissues of rugose corals could detach from the skeleton high within the calice and continue to secrete lamellar stereoplasm based on: (1) the withdrawal of tissues from the wall and subsequent emplacement of contorted septa; (2) the withdrawal of soft tissues from the sides of septa and subsequent secretion of discontinuous septal growth lamellae; and (3) embedment of foreign objects within interseptal spaces. Elias (1984a) considered that soft tissues located within the cardinal and alar fossulae were especially capable of expanding and contracting away from the skeleton in order to carry out feeding and or reproductive functions. The greater degree of loss of wall fragments on the cardinal side of the present corals may be consistent with that interpretation, but as mentioned previously, could also reflect structural weakness owing to the large open fossula. Fedorowski (1997) discussed the embedment of foreign bodies in Rugosa at length, and concluded that the polyp could not intentionally contract away from the inner wall of the calice. He suggested that foreign objects were inadvertently swallowed, became trapped within the gastric cavity, and then irritated the tissues until they were allowed to pass through to the floor of the calice where they were covered by stereoplasm. Regardless, the concentration of desmocytes could have varied in different parts of the calice, and they conceivably could have been less abundant in the fossulae to allow more flexibility in movement of tissues there.

Alexander (1981) noted that predation on late Mississippian (Chesterian) brachiopods and one coral in Utah did not appear to target specific species and that there was a high survival rate from attacks. Although the depressions in the present material are unlike depressions made by the shark in Alexander’s samples, and grasping invertebrates such as crabs cannot be discounted, the Pella predator also showed a low degree of specificity in targeting prey, picking up a wide variety of shells from the sea floor including both corals and *Composita* brachiopods. The apparent high survival rate in the present material suggests that the corals were not the targets of the predation and were dropped by the predator after being tested. However, attempted predation was common, because several of the corals were picked up, damaged, and dropped multiple times.

Changes in the growth axis in solitary rugose corals are generally attributed to dislocations on the substrate (e.g., Neuman, 1988; Sorauf, 2001). The low percentage of Pella specimens that changed growth direction following a non-lethal attack suggests that *A. spinulosa* may have been capable of righting itself on the sea floor following disturbance. It is unlikely that the severe crushing damage experienced by the corals could have been accomplished without affecting their orientation and position on the sea floor. When corals were released after being picked up and damaged, they could have landed in almost any orientation, and it is very unlikely that they would have landed in their original growth positions, presumably reclining on the convex side for curved individuals, or apex buried in the mud for straight conical examples. However, only 21% of damaged samples (6% TC) show any associated change in growth direction. Hence, many specimens must have re-established a consistent growth position in order to survive and continue growing. Of course it is possible that some percentage of samples that does not show healed damage represents specimens that were killed by an attack because they landed in the wrong orientation and could not right themselves or change their growth direction. It is not possible to determine the ultimate cause of death of corals in the collection, only to determine that some samples recovered from sublethal attacks. Hence, the present sample does not allow that hypothesis to be tested adequately, because the percentage of samples that was picked up by the predator cannot be clearly established, as they may or may not have been damaged or survived. In any case, the possibility of self-righting ability is at odds with the typical view of solitary rugose corals as being incapable of such movement. Elias (1984b) and Scrutton (1999) suggested that solitary rugose corals were generally killed if they were toppled or overturned on the sea floor, based primarily on the argument that only a low percentage of taxa appears to have been capable of changing growth direction following disturbance. The extreme geniculation shown by some *Heliophyllum halli* (Sorauf, 2001) is the exception rather than the rule.

As most *A. spinulosa* specimens are curved, they probably reposed on their convex sides with calices opening obliquely upward. The polyp may have been capable of re-establishing that relatively stable position (i.e., self-righting) by the use of tentacular motion and/or their ability to swell and contract. Hubbard and Pocock (1972) discussed the potential for scleractinian corals to manipulate both sediment and their own skeletons by using, for example, mucus production, tentacular motion, and retraction and distension of the polyp. They associated corals' abilities for self-righting with skeletal characteristics, such as light-weight skeletons, numerous, ornate septa and large calices. For the most part, *A. spinulosa* and most other solitary rugose corals lack such skeletal features. However, they do have deep, V-shaped calices, which Hubbard and Pocock (1972) considered to provide an efficient base for extension and retraction of soft tissues, and the cardinal fossula may have contained active tissues with the ability to expand and contract, possibly to promote circulation within the gastric cavity (Elias, 1984a; Fedorowski, 1997). Fedorowski (1997) also noted that, although there has never been proof of tentacles in the Rugosa, there have been no serious challenges to the concept either, and most workers accept that they were present based on analogy with other skeletal cnidarians. Owing to the low-energy, muddy setting that the corals inhabited, it is unlikely that *A. spinulosa* could have benefited from a passive righting capacity that depended on current activity, such as has been demonstrated in higher energy settings for the scleractinian coral *Manicina areolata* (Hubmann et al., 2002). In any case, *A. spinulosa* lacks the external morphology that would promote such passive righting. Regardless, many of the Pella Formation corals survived multiple disturbance events where they almost certainly became dislocated on the sea floor. Some ability for self-righting seems likely as the majority did not change growth direction. The types of robust soft tissues that are required for such movement are consistent with survival of intact soft tissues even where parts of the skeleton were lost during attempted predation and the lack of infiltrated sediment into the broken skeletons in the muddy environment is consistent with robust soft parts and production of abundant mucus by the injured polyp.

6. Summary

Skeletal breakage and repair patterns in *A. spinulosa* allow several inferences and speculations to be made about its soft part anatomy. The polyps may have had durable soft tissues with a band of well attached muscular tissue well above the calice floor, possibly at the level of the polyp's mouth. They may have been capable of sediment rejection by polyp expansion, tentacular motion and or production of mucus. Importantly, the low percentage of specimens having directional change in growth axis associated with healed damage suggests that the corals may have had some ability for self-righting, which would be consistent with the previously mentioned attributes, but is not expected in solitary rugose corals.

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Research paper

Palaeobiological perspectives on variability and taxonomy of scleractinian corals

Vassil N. Zlatarski *

131 Fales Rd., Bristol, RI 02809, USA

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Abstract

Scleractinians are well known for their exceptional variability and difficult taxonomy. Until the end of the nineteenth century, these corals were studied outside their natural habitat. In situ investigation brought to attention their variability and led to description of formae and attempts to depart from the typological taxonomy. Studies commenced in 1950s of extant scleractinians of Jamaica, the South Pacific, Madagascar, the Red Sea, Cuba, and Australia demonstrated instances of coralla unclassifiable in the described species because they possess intermediate characters, and sometimes one corallum exhibits the characteristics of more than one species. Since 1984, discoveries about scleractinian life history and molecular data further challenged the conventional taxonomy. The coral holobiont is now being studied as a totality of the coral animal, its endosymbiotic zooxanthellae, and its associated community of microorganisms. Molecular genetics and studies of life history combined with morphological variability and variability in geological time are needed for scleractinian taxonomy. The input of palaeontologists with temporal aspect as well as an enormous amount of morphological data is invaluable, as demonstrated by several examples based on detailed morphological observations later supported by molecular and life history information. Efforts to resolve the variability vs. taxonomy dilemma for fossil scleractinians would benefit from further actuopalaeontological work: studies at all levels of biological organization, including ancient DNA and evolutionary genetics, the rich fossil record, fractals and RLQ analysis, palaeopathological research, sclerochronology, the ecology and skeletogenesis of extant deep sea corals.

Keywords: Scleractinia; Variability; Taxonomy; Palaeobiology; Actuopalaeontology

1. Introduction

The aim of this article is two-fold: first, to review the development of the thorny problem of scleractinian variability and taxonomy and summarize its present state, with an emphasis on the role of palaeontologists in forging a solution; and second, to offer recommendations for future palaeobiological work.

Variability offers a real reflection of life production and constitutes an integral part of the evolutionary process. It is the fuel of the evolutionary machine. Like any engine without fuel, evolution without variation has nothing on which to work (Palumbi, 2001).

The term "plasticity" has sometimes been used in coral papers interchangeably with "variability". "Plasticity" may be morphologic, phenotypic or relate to areas of molecular genetics and life history, but it has the additional connotation of responsiveness and flexibility and implies "the ability o[f] an organism to react to an internal or external environmental input with a change in form, state, movement, or rate of activity" (West-Eberhard, 2003). Occasionally, plasticity is also used to hint at the elusive nature of corals. To describe plasticity is an important aim for investigators, but in the majority of cases, especially in fossil material, there are not enough data to clarify cause–effect relationships. Therefore, the term "plasticity" is not used in this article.

"Taxonomy" is used here to mean "the theory and practice of delimiting kinds of organisms and of classifying them" (Mayr, 1969, 1982). The evolutionary approach requires defining taxa as units corresponding to the different steps of the evolutionary process of organisms (Zlatarski and Martinez Estalella, 1982).

"Actuopalaeontology" was introduced as an application of the principle of uniformitarianism in the area of taphonomy (Efremov, 1940). Later, its usage was broadened to include

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* Corresponding author.
E-mail address: vzlatarski@yahoo.com.

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many aspects of living organisms of interest to palaeontologists. Scleractinians offer an especially useful perspective for actuopalaeontological studies because their skeletons closely reflect their biological activity and they build reefs, the largest organism constructions (Zlatarski and Martinez Estalella, 1982).

2. History

The following historical review is not by any means a full account of existing contributions about scleractinian variability and taxonomy, but rather merely marks several significant steps in their evolution.

2.1. First serious attention to variability/taxonomy

At the end of the nineteenth century, observations in the natural habitat brought attention to the rich variability in scleractinians and made it necessary to introduce formae as species subdivisions (Quelch, 1886; Vaughan, 1901, 1907). During the first half of the twentieth century, zoologists did not pay much attention to corals. Eminent palaeontologists synthesized all known information about Scleractinia (Vaughan and Wells, 1943; Wells, 1956).

2.2. Detailed skeletal investigations

In the late 1930s, Alloiteau launched revisions of fossil collections by describing considerably more morphological characters and focusing on the microarchitecture and histological structure (Alloiteau, 1952, 1957). Later, his disciples, the members of the Parisian school, did the most extensive skeletal descriptions ever produced, with data on coralla variability of scleractinians of all geological periods since the Triassic.

2.3. Field-geological and scuba-diving investigations

Extensive field research establishing the rich variability of Miocene scleractinians (Chevalier, 1961) led Alloiteau's successor to conduct extensive scuba studies in the natural coral habitats of the South Pacific (Chevalier, 1968, 1971, 1975). His posthumously published synthesis on scleractinians in Traité de Zoologie (Chevalier, 1987) made an important palaeontological contribution to the field. Chevalier's detailed description of the variability of morphological characters and microstructure remains unparalleled.

Analogically, the massive sampling in the late 1950s in Bulgaria demonstrated an exceptional variability, which posed taxonomic challenges and led to extensive actuopalaeontological study from 1970 to 1976 on Cuban Scleractinia. It became evident that a number of specimens did not "fit" within the published taxa. For example, some specimens showed intermediate characters between two species; others exhibited the characters of more than one species; and there were series of coralla that could not be discerned morphologically. Nearly six thousand coralla collected in depths to 70 m. and subsequent laboratory analysis demonstrated variability on various levels (Zlatarski and Martinez Estalella, 1982): structural element (ibid. pl. 114, figs. 3 and 4; 5 and 6), corallite, corallum, population, subspecies, species, genus, family, ontogeny, and pathology. This rich variability made species identification of many specimens difficult and raised serious challenges to the taxonomy of Caribbean scleractinians.

Meanwhile, researchers of extant corals in Jamaica, the South Pacific, Madagascar, the Red Sea, and Australia also established enormous morphological variability. The penetration into the natural habitat and the massive sampling revealed common problems on a planetary scale (Zlatarski, 2009).

At the same time, serious data on rich variability came from fossil corals and challenged the taxonomy. The investigations started in the 1960s by Tesakov on Tabulata radically changed their taxonomy by introducing various intraspecific categories (Tesakov, 1978). This was not a simple coincidence, but rather the result of applying a methodology of very detailed and massive field sampling and variability analysis. A series of studies was dedicated to the variability and taxonomy of fossil scleractinians (e.g., Triassic: Melnikova, 1992; Jurassic: Lathuilière, 1996; Pandey and Lathuilière, 1997; Cretaceous: Kuzmicheva, 1992; Oligocene: Pfister, 1977; Foster, 1985). The planetary spatio-temporal variability prompted re-evaluation of the scleractinian taxonomy. The Parisian school of detailed skeletal studies produced microstructural data for scleractinian megataxonomy (Roniewicz and Morycowa, 1993), demonstrating the importance of palaeontological information.

The puzzle of the existence of series of coralla demonstrating a gradual transition of characters or a lack of morphological discontinuity that could not be taxonomically discerned raised the question how these continuous variations could be explained in terms of discontinuous Mendelian genes. The answer came from the fact of multifactorial inheritance. Its essence is that several independent genes can control a single character of the phenotype. The effect of a multifactorial inheritance is to convert discontinuous variation of the genotype into continuous variation of the phenotype (Mayr, 1982). Additional explanations of the dilemma were possible as result of the occurrence of mosaic evolution and the process of species formation (Zlatarski and Martinez Estalella, 1982).

The search for explanations of variability did not bring an operational taxonomic resolution of the problem. Lang (1984) brought attention to the variability of non-skeletal scleractinian characters.

2.4. Molecular genetics and life history discoveries

Since the 1980s, a series of discoveries related to life history and molecular genetics shed new light on scleractinian biology: long generation times and frequent propagation fragmentation, simultaneous multispecific spawning, hybridization, reticulate concept for speciation, astonishing growth in aquaria, and intricate character of symbiosis (Zlatarski, 2007). After a very detailed in situ sampling of morpho-variability, Wolstenholme (2004) analyzed molecular, morphological, and reproductive criteria indicating that hybridization events occur in nature, but that these are rare.

Studies on coral health and the role microorganisms led to phage therapy (Rosenberg and Loya, 2004; Efrony et al., 2007). The concept of the coral holobiont as the totality of the coral animal, its endosymbiotic zooxanthellae, and its associated community of microorganisms means that coral cells possess a combined genome. This notion generated thoughts about possible biochemical negotiation between coral and algae. In such cases, the mutation has to be qualified as somewhat directed, which represents a serious departure from the concept of randomly generated genetic variation (Roughgarden, 2006). The question of the human impact on rapid evolutionary change ("the evolution explosion", Palumbi, 2001) of the coral holobiont remains open.

The summary of the coral taxonomy session of 10th International Coral Reef Symposium stated that "integration of molecular and morphological data is still in its infancy," "the fossil record remains a largely untapped resource for understanding evolutionary rates and patterns," and "rigorous assessments of homology have only just begun" (Knowlton et al., 2006).

The 2006 European Meeting of the International Society for Reef Studies in Bremen brought further news on variability. Comparison of *Pocillopora damicornis* from two different reef areas demonstrated genetic variability (Rosengren and Souter, 2006); the high intraspecific variability in *Platygyra daedalea* showed significant genetic difference between the two proposed morphotypes with no sharp discontinuity of skeletal variation between them and indicated shared ancestral polymorphism or current introgression (Souter and Mangubhai, 2006). The light acclimation of zooxanthellae in *Pocillopora damicornis* revealed intra-colonial variability (Ulstrup et al., 2006); zooxanthellae type can influence the physiological properties of corals, sometimes to a stunning degree (Mieog et al., 2006).

Separately, variations in the diel patterns of planula release displayed the existence of variable strategies of reproductive timing for brooding species (Fan et al., 2006).

A case study of *Diploastraea heliopora* observed that clones from colonies more than 10 km apart can be more closely related to each other than clones from the same polyp (Lam et al., 2006). The factors of coral stress (Grober-Dunsmore et al., 2006) and resilience (van Oppen and Gates, 2006), as well as the role of hybridization in the evolution of reef corals (Willis et al., 2006), were recently seriously considered. Molecular and morphological data contributed to the phylogenetic relationships of the genus *Psammocora* (Benzoni et al., 2007) and morphological, reproductive and genetic evidence resulted in the recognition of separate genera within *Acropora* (Wallace et al., 2007).

Since 1995, molecular genetics has opened a new venue for coral megataxonomy (Chen et al., 1995; Veron et al., 1996; Romano and Palumbi, 1996; Romano, 1996; Romano and Cairns, 2000; Stolarski and Roniewicz, 2001; Stolarski and Russo, 2002), which has led to an impasse in the use of conventional macromorphologic taxonomy. Most traditional supra-family taxa and some families and genera were evaluated not to be monophyletic units. Findings of homoplasious gross-morphology characters contradicted existing classifications. A comparison of molecular information with the skeletal microstructure data showed congruence. As result, the taxonomic importance of the traditional "septo-centric" scleractinian taxonomy was rediscovered (Roniewicz and Morycowa, 1993; Cuif et al., 2003; Fukami et al., 2004; Stolarski and Vertino, 2007).

The promise of Coral ID, an identification key to reef-building corals worldwide on CD-ROM, seems unrealistic. Release 2, intended to facilitate identifications of all taxa to the species level, was expected in 2004 but remains unavailable (www.aims.gov.au/coralid).

3. Importance of palaeontological and actuopalaeontological investigation

The history of scleractinian research demonstrates the importance of palaeontological contributions. It is no coincidence that the classifications were made by palaeontologists, because for a long time the research was focused on hard parts.

Before approaching any conclusion and recommendations, it is useful to consider some illustrative examples of the importance of palaeontological and actuopalaeontological investigations of variability and detailed skeletal characters. They demonstrate how taxonomic problems and their solutions were initially primarily detected and resolved only by studying the hard parts, and later interpreted or confirmed through new techniques offered by molecular genetics and life history study.

The actuopalaeontological study of the variability of Cuban corals cast doubts on the existing taxonomy of the Caribbean scleractinians (Zlatarski and Martinez Estalella, 1982) and introduced a palaeobiological dimension to Caribbean *Acropora* hybridization. For example:

- The acroporid species *prolifera* was described with doubt as *Acropora prolifera*? The reasons for this taxonomic decision were that it was extremely rare; it was found with neighbouring colonies of *A. cervicornis* and *A. palmata*; its corallum morphology presented a combination of the characters of both species; and it never showed gradual morphological transition with the two other *Acropora* species. Recently, two independent molecular studies (van Oppen et al., 2000; Vollmer and Palumbi, 2002; Miller and van Oppen, 2003; van Oppen and Gates, 2006; Willis et al., 2006) have shown that *prolifera* is a hybrid between *A. cervicornis* and *A. palmata* and its presence is to be recorded as *Acropora prolifera* = *A. cervicornis* + *A. palmata*. Furthermore, long-term observations on *prolifera* distribution between 1970 and 2001 (a period known as very bad for shallow water coral life in Caribbean, devastating for both parent species) revealed intriguing changes. First, from 1970 to 1973, *prolifera* was extremely rare in Cuba, only appearing as single colonies in clear water. Later, during a 1983 to 1984 investigation in the waters off the Yucatán Peninsula, SE Mexico (Zlatarski, 2008), colonies appeared to be single and in clusters at the margin of densely populated zones of the parent species *Acropora*. Finally, in observations again in Cuba in 2001 (Zlatarski, 2002; Zlatarski et al., 2004; and personal observations), *prolifera* was more frequently encountered, even in murky shallow water, sometimes far from the devastated *A. palmata* and *A. cervicornis* zones. At that time in the Archipiélago Jardines de la Reina, SE Cuba, the AGRRA survey established that 95% of the studied reef crest had more than 40% dead surface of *Acropora palmata*. In the protected places of the laguna, *prolifera* branches were accumulated in a way that provided with other benthonic organisms a base of peculiar build-ups on sandy bottom. These long-term observations coincide with recent joint conclusions of five leaders in the areas of coral genetics and reproduction (Willis et al., 2006) on the opportunistic character of hybridization in Caribbean *Acropora*. What is the scale and impact of this hybridization? It is defined, first, by the occurrence of *prolifera* throughout the entire Caribbean range of its parent species; second, by the capacity to colonize marginal habitats and adapt to environmental changes, as well as provide substratum on sandy bottom; and, third, by the long duration of the hybridization process (presence of fossil *prolifera* before the Pleistocene sensu Frost, 1977). In this way, the case of *prolifera* takes on greater importance. It also has a palaeobiological dimension with temporal and bioconstructive aspects.

- The variability in *Madracis* left open taxonomic questions and led to the usage of formae. Yet the explanation came from the evidence of a temporal absence of reproductive isolation in the genus (Diekmann et al., 2001; Vermeij et al., 2004; Vermeij and Sandin, 2006; van Oppen and Gates, 2006).
- Data on skeletal variability of *Porites porites* and *P. furcata* did not permit a separation of them in many cases. Molecular systematic studies indicated that they currently do not represent distinct lineages (Stake and Neigel, 2007).
- The existence of colonies showing interspecific characters in representatives of the genus *Siderastraea* in some instances made it difficult to identify species. This taxonomic difficulty is now considered to indicate a rate of concerted evolution that is faster than the rate of speciation (Forsman et al., 2006).
- The exceptional skeletal variability at the colony and intercolony level of *Favia fragum* revealed a very complex enigmatic morphoseries. A recent study of two morphotypes with opposing depth distributions added scleractinians to a few marine examples showing morphological and genetic divergence that follow the divergence-with-gene flow model of speciation, in which the initial phase of speciation is possible in the absence of spatial barriers (Carlon and Budd, 2002).
- The resemblance of the micromorphology of various Cuban scleractinians was later explained by the evolutionary distinctiveness of Atlantic corals (Fukami et al., 2004).

The above-mentioned cases mark only the beginning of a better understanding of the variability described on the basis of the Cuban material. The phenoids of many genera (including *Scolymia*, *Mussa*, *Isophyllia*, *Mycethophyllia*, *Agaricia*, *Helioseris*, *Dichocoenia*, *Meandrina*, and *Eusmilia*) indicative of a complicated dynamic in the Caribbean scleractinian speciation process are still awaiting the application of the new research methodologies. In the meantime, the conventional microtaxonomy is to be used as a *modus operandi.*

The taxonomic value of detailed skeletal observations is in evidence by the extant species *Porites colonensis*. Although this species is abundant in waters visited by researchers, it was published surprisingly late as a new Caribbean species. Its description was based on distinctive skeletal characters and the absence of morphological transitions with the other *Porites* (Zlatarski, 1990). Yet molecular studies proved it to be a monophyletic clade (Stake and Neigel, 2007) and also that it is not a geminate species to *P. panamensis*, supposedly separated by the closure of the Central American Seaway, 3.5–3.8 Ma (Forsman et al., 2006).

Gill (1981) demonstrated the importance of understanding the detailed skeletal characters. By studying the fulturae structure, he declared the erroneous systematic position of Fungiidae (Gill, 1981). It took 15 years and DNA study to confirm his discovery (Veron et al., 1996).

An investigation of the ontogenetic development of the thecal structure (Stolarski, 1995) was recognized eight years later as a new way of resolving the identification of scleractinian recruits from Indo-Pacific reefs (Babcock et al., 2003).

4. Conclusions

The past approach and the present state-of-the-art of the dilemma of scleractinian variability and taxonomy lead to the following conclusions:

- Scleractinian variability and taxonomy continue to be a Gordian knot and the role of palaeontologists in undoing it is indispensable.
- The solution presupposes joint efforts of biologists and palaeobiologists by using four independent lines of information (morphology, molecular biology, life history, and geological time) and considering them in concert.
- The multidisciplinary cooperation benefits from actuopalaeontological studies.
- Knowledge of histology and detailed morphology is helping to reconcile existing taxonomic contradiction between grossmorphology and genetics.
- The integration of molecular and detailed skeletal data is in its early stages.
- The comprehension of the established homology is far from satisfactory.
- Every step in the process of multidisciplinary research, starting from the methodology of sampling and field observations, is important.
- It is risky to announce taxonomic solutions in advance.

5. Recommendations

Joint collegial consideration is necessary in order to crystallize the best set of recommendations for future palaeobiological strategies for resolving the variability/taxonomy saga. Here are the author's suggestions for such a discussion:

- Promote better tapping of the information from the rich fossil record by means of revision of type specimens, massive sampling, extensive fieldwork, and detailed skeletal studies of variability on all levels.
- Focus on actuopalaeontological work, since taxonomic efforts dedicated to both fossil and extant scleractinians target the same classification. The genetic revelations that DNA also presents a reliable record of evolution (Carroll, 2006) strengthened the role of fossil material in shedding light upon the evolutionary process. This directs attention to the homoplasious characters as a possible consequence of the role of toolkit genes that oversee development.
- Direct attention to palaeopathology, partial mortality, and colony resheeting.
- Investigate ancient DNA.
- Prompt RLQ analysis on three separate ordinations: R – environmental variables, L – species composition and Q – species trait (Dolédec et al., 1996; Rachello-Dolmen and Cleary, 2007).
- Use fractals to characterize interspecific variability (Martin-Garin et al., 2007).
- Study sclerochronology to detect variability resulting from environmental and climatic change through space and time.
- Apply recent data concerning ecology and skeletogenesis of extant deep-sea corals for the interpretation of fossil material.
- Consider the evolutionary potential of deep-sea waters as genetic refugia in the geological past during intervals unfavourable to shallow-water coral life.

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Nomenclatorial Note

William A. Oliver, Jr. (1926–2005)

William A. Oliver, Jr. died on October 8, 2005, in the evening, shortly after being struck by an automobile while crossing a darkened street in Rockford, Illinois, where he was visiting the family of his deceased wife Jo. This was a shock to all who knew Bill, and his friends around the world are saddened by their loss, and continue to miss him, the paleontologist who was their colleague and friend.

Bill was born in 1926, in Columbus, Ohio, where his father taught in the Department of Civil Engineering at Ohio State University. He grew up in Champaign, Illinois, after his father moved the Oliver family to Illinois, where he taught in Civil Engineering at The University of Illinois. Bill was schooled at the University High School in Champaign, and served in the United States Navy at the end of World War II, where he was trained to be an air gunner; but, the war ended prior to his seeing combat. Bill attended the University of Illinois and received the Bachelor of Science in geology in 1949. Bill (and his wife Johanna, or Jo) moved to Ithaca, New York, where he became a graduate student in geology at Cornell University. Bill received the Master of Science degree in 1950, and Ph.D. in Geology in 1952. Both his MS thesis ("Middle Devonian coral beds of central New York", *American Journal of Science*, October, 1951, 23 pp.), and his Ph.D. dissertation were published (Stratigraphy of the Onondaga Limestone (Devonian) in central New York, *Bulletin of the Geological Society of America*, 1954, vol. 65, 31 pp. and, Stratigraphy of the Onondaga Limestone (Devonian) in eastern New York, *Bulletin of the Geological Society of America*, 1956, vol. 67, 33 pp.). Here at Cornell, Bill and Jo developed what was to be a life-long friendship with John and Pie Wells. John served as Bill's graduate advisor and truly inspired him to become a first-class student of fossil corals, haunter of antiquariat bookstores, annual visitor to London, and career-long researcher on the Devonian strata and faunas of New York, especially the rugose coral fauna.

Bill was Instructor and Assistant Professor at Brown University from 1952 to 1957, and continued New York research during summer months with the support of the New York State Geological Survey. He began his long association with the United States Geological Survey in 1957, and this association continued until (and after) his "retirement" in 1993 (see Bibliography), when he became Scientist Emeritus. He was a Research Associate in the Department of Paleobiology at the Smithsonian Institution from 1967 until his death.

Bill's career with the USGS was a rich one, and by no means restricted to work for the Geological Survey. While employed at the Paleontology and Stratigraphy Branch of the survey, Bill served the Paleontological Society as co-editor (with P. Kier) of the Journal of Paleontology (1964–1969). He was president of the Association of Earth Science Editors (1966–1968), president of the Paleontological Society (1974–1975), president of the American Geological Institute (1976–1977), editor (with J. Sorauf) of Fossil Cnidaria (1976–1980), president of the International Association for the Study of Fossil Cnidaria and Porifera (1983–1988), long time trustee of The Paleontological Research Institution (PRI) in Ithaca, and president of PRI (1984–1986), secretary-general of the International Palaeontological Association (1984–1989), and chairman of the Subcommission on Devonian Stratigraphy (of the International Stratigraphic Commission) (1984–1989) after serving on the subcommission for a number of years.

Additionally, Bill received other honors, including a National Science Foundation – National Academy of Science Award for Study and Research in Europe (1969–1970). He also received the Meritorious Service Award from the US Department of the Interior (1993), and the Gilbert Harris Award for Excellence in Systematic Paleontology from the Paleontological Research Institution (1994).

1. The person

Bill was extremely well-organized and single-minded. In order to avoid losing commuting time in traffic, he arose before 5 AM each day to drive to his office at the National Museum of Natural History, Washington. Visitors had to arise and be ready to eat breakfast and drive before daybreak to "beat the traffic". This was done six days a week at the beginning of his career, later the work week shortened to five days, and the trip was only modified by his finding numerous side streets to travel, thus shortening his trip. In the 1980s, when the "Metro" light rail and subway system was completed to Rockville, near Bill and Jo's home in Kensington, Maryland; Bill drove to the Metro station, parked his car, took one of the earliest trains and enjoyed reading a book or magazine in an empty compartment instead of driving his car.

At his office, Bill had a routine which he followed religiously throughout his nearly 50-year career with the Geological Survey.

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Bill unlocked his door, took off his coat and sport coat (he wore a coat and tie each day, liked having protection against drafts and/or air conditioning), put on a cardigan sweater, put water to heat for tea, and sat down at his desk and consulted his list of things to do on that day, which had been prepared the previous afternoon. This was invariable, and if Bill had a visitor, on his list were the things he wanted to discuss with the visitor, or research to be conducted with the visitor.

Bill was remarkably enthusiastic about having the opportunity to study corals on a full time basis, and extremely grateful to the USGS for providing him with a full time assistant, William P. Pinckney, Jr., a trained biologist, excellent thin section maker, photographer and extremely agreeable personality. He was also grateful for Survey funding of his travel and participation in numerous projects on a worldwide basis. Bill was one of those fortunate persons that are truly convinced that they were born at exactly the right time, and he felt that he had experienced opportunities in his life that young persons could almost never have today.

At the end of the work day, Bill jotted down what he wished to do the next morning, put on his coat, overcoat in inclement weather, as well as his flat cap and muffler. When he left his office, he left his research, unless he had a visitor who wished to discuss corals while driving or while having a cocktail in the Oliver living room. At home, Bill had a large number of magazines, ranging in content from the Atlantic Monthly to the Journal of Paleontology. He habitually perused each one every month.

Bill's interests ranged far from coral paleontology. He was very aware politically, and was a long time political and social liberal, having true empathy for unfortunate people in modern society. Having an office in the Natural History Building on Washington's Mall meant that he could (and did) visit every traveling exhibit that was shown at the National Gallery of Art, situated nearby on the Mall, and Bill was familiar with every exhibit within the entire Smithsonian agglomeration of museums. He was a true *aficionado* of classical music, and he and Jo, while she lived, were frequent visitors to the Kennedy Center for the Performing Arts in Washington, and made an annual trip for a week in New York City, with the timing of the trip coinciding with memorable (to him) performances at the Metropolitan Opera House. They also had a large collection of records of classical music and opera at their home in Maryland. His habit after returning home was as rigorously observed as that already described at his office. He said hello to Jo, and reviewed the day's happenings while he took off his coat, then settled the record player with the disk already selected for that particular afternoon, took one of two arm chairs (always that to the right of a traditional style lamp), and chatted with Jo while selecting a magazine for reading that evening. After the death of Johanna Oliver in 1991, Bill continued his routines as best he could, and continued his pilgrimages to the Metropolitan Opera with brother Tod and his wife.

Bill early became a bibliophile. He was an expert on the author Charles Dickens, and a buyer, having a large book collection which most prominently contained suitable representatives of numerous editions of the Dickens classic, "The Mystery of Edmund Drood". This was in addition to a house full of books on varied subjects, including numerous versions of other classics. Bill also had a very large collection of slides and photographs that he had taken on trips around the world, and had framed numerous favorites for hanging in his home.

Bill not only published on the systematic paleontology of corals, but also lived a life that was systematically organized in set ways. This worked beautifully for him, and this, plus the wisdom to write things down and prioritize, meant that Bill never forgot important things, and also that he could accurately foretell when he would have a particular task under way, and approximately when it would be completed. His devotion to his subject meant that he worked without losing focus for long hours, during consecutive days, and on through the years. He was as productive in his later years as he was in the earlier ones, at least until he had some health problems (shoulder damage and vertigo), and until he lost his wife Johanna. Jo provided a wonderful home environment for Bill, and took care of all business pertaining to their home, so that Bill was free to think about his Survey work and research on a full time basis.

2. Research legacy

Bill's research method was to be extremely thorough, painstakingly so, starting with field collecting and recording of each collection site on a detailed topographic map, so that he could return for more specimens should the need arise during the years of his career and for posterity. In the 1980s and 1990s, Sorauf and Oliver could easily reoccupy collecting localities where Bill had recorded certain species in the 1950s. He was very thorough in preparation of specimens, photography and placement on plates. He was quite disturbed in one project, when Sorauf had photomicrographs of solitary rugosans taken from a mixture of oral and apical orientations; this needed to be rectified, and it was.

Bill was famous for his extreme kindness and gentility to coral colleagues internationally and especially was he cordial and helpful to young paleontologists and stratigraphers around the world, and most especially in New York State and eastern North America. He saw his infrequent contact with students as the greatest lack in his position with the USGS, perhaps because of his great enjoyment of teaching while at Brown University. Bill's thoughtfulness also extended to paying for American paleontological journals for several of his friends in Europe at the time when their countries had non-exportable currencies. For example, Fedorowski profited from his kindness in exchanging Acta Palaeontologica Polonica for journals, the Journal of Paleontology and Paleobiology. Moreover, Bill's recommendation was a main factor for his receiving a year-long postdoctoral Smithsonian Institution award that opened the door for him (Fedorowski) to the "western" international community of coral students and many other paleontologists at a time of isolation for east European scientists. This is typical of the support that paleontologists could expect to receive from Bill.

On field trips and at symposia, Bill was always attentive, precisely dressed, tolerant of other's opinions and demanding

Fig. 1. Oliver Memorial (photo source in parenthesis). (A) Field trip group photo at Cayuga Lake, New York State – 1983 (Official). (B) Bill and Alan Pedder, Novosibirsk – 1971 (Oekentorp). (C) Bill and Ivo Chlupach, Klonk, Czech Republic – 1986 (Oekentorp). (D) Bill in his Washington office (Stolarski). (E) Klemens Oekentorp, Makoto Kato, Bill Oliver, Kei Nori and John Jell, Sendai – 1999 (Oekentorp). (F) Bill and Jerzy Fedorowski, Holy Cross Mts., Warsaw field trip – 1979 (Oekentorp). (G) Jerzy Fedorowski, Bill and Nancy Budd, Wine Evening, Graz – 2003 (Stolarski). (H) Bill with group of paleontological colleagues, Novosibirsk – 1971 (Official). (I) Bill in Wales with Subcommission for Devonian Stratigraphy – 1986 (Sorauf). (J) Bill and Pat Sutherland, Novosibirsk – 1971 (Oekentorp). (K) Bill explains to Ross McLean and Jim Sorauf, New York State field trip, 1983 (Oekentorp). (L) Klemens Oekentorp, Bill and John Jell, Sendai – 1999 (Oekentorp). (M) Bill identifies fossil for Tony Wright, New York State – 1983 (Oekentorp). (N) Bill in front row with Adriano Ferrari, Gustav Altevogt and Klemens Oekentorp; Jurgen Kullman, Colin Scrutton and Rudoph Bierenheide in the back row, Northern Spain – 1969 (Scrutton). (O) Des Strusz, Bob Jull, Pat Sutherland, Jim Sorauf and Bill at a sidewalk café, Paris – 1975 (Oekentorp). (P) Bill with Jim, Jo, and Bob Oliver, Northern Spain – 1969 (Oekentorp). (Q) Bill with Colin Scrutton, Alan Pedder and Boris Sokolov, Warsaw – 1979 (Oekentorp). (R) Bill and Jo Oliver having a picnic lunch in the Ardennes, field trip – 1975 (Oekentorp). (S) Group photo at Mte. Fromme, New South Wales, field trip. Front row, Bev Bolton, Bill Oliver, Barry Webby, Carl Stock and Jim Sorauf. Back row, Makoto Kato, Yves Plusquellec, Tom Bolton, Jo Oliver, Yoichi Ezaki, Des Strusz, John Pickett, Bob Elias, unknown, Ross McLean – 1988 (Wright). (T) With Ken Johnson and Charley Veron at wine night, Graz, Bill proposes a toast – 2003 (Stolarski).

of himself. Bill enjoyed talks about corals, irregardless of who gave them, and would always have any mention of corals circled in his abstract volume ahead of time when he attended national or international meetings, to ensure that he would not miss any (Fig. 1).

3. Publications in the International Symposia Proceedings volumes of the International Association for Study of Fossil Corals and Sponges

Bill Oliver was one of the founders of the international association and he attended each of the nine international symposia, beginning with the first one in Novosibirsk, USSR, and ending with his last, in Graz, Austria. He also published at least one paper in the proceedings volume for each symposium during his lifetime, with abstracts in Symposia I through IX, the only person to do so.

The papers are:

1975	(with C.W. Merriam and M. Churkin, Jr.) Ordovician, Silurian and Devonian Corals of Alaska. Ancient Cnidaria 2, 95–103, *and*,
1975	Endemism and evolution of Late Silurian to Middle Devonian rugose corals in eastern North America. Ancient Cnidaria 2, 148–160 (First International Symposium Proceedings Volumes, Novosibirsk, Russia, 1971).
1977	Devonian rugose coral assemblages in the United States. Mémoires du Bureau de Recherches Géologiques et Minières 89, 167–174 (Second International Symposium on Corals and Fossil Coral Reefs, Paris, 1975).
1980	On the relationship between Rugosa and Scleractinia (summary). Acta Palaeontologica Polonica 25, 395–402 (Proceedings Volume, Third International Symposium, Warsaw, 1979).
1984	*Conchopeltis*: its affinities and significance. Recent Advances in the Paleobiology and Geology of the Cnidaria. Palaeontographica Americana 54, 141–147 (and additional introductory contributions to this proceedings volume for the Fourth International Symposium, Washington, DC, 1983).
1989	Intraspecific variation in pre-Carboniferous rugose corals: a subjective review. Association of Australasian Palaeontologists, Memoir 8, 1–6, *and*,
1989	(with A.E.H. Pedder) Origins, migrations, and extinctions of Devonian Rugosa on the North American Plate. Association of Australasian Palaeontologists, Memoir 8, 231–237 (Proceedings Volume, Fifth International Symposium, Brisbane).
1993	Origins and relationships of Devonian Rugosa endemic to the Eastern Americas Realm. Courier Forschungsinstitut Senckenberg 164, 131–140 (Proceedings Volume for the Sixth International Symposium on Fossil Cnidaria and Porifera, Muenster, 1991).
1997	Origins and relationships of colonial *Heliophyllum* in the upper Middle Devonian (Givetian) of New York. Boletín de la Real Sociedad Espacola de Historia Natural (Secciyn Geolygica) 91, 53–60 (First of two proceedings volumes of the Seventh International Symposium on Fossil Cnidaria and Porifera, Madrid, 1995).
2001	The origin of "*Spongophylloides*" in eastern North America. Bulletin of the Tohoku University Museum 1, 77–85 (Proceedings volume, Eighth International Symposium on Fossil Cnidaria and Porifera, Sendai, 1999).
2003	The genus *Zaphrentis* and its relatives. Berichte des Institutes für Geologie und Paläontologie der Karl-Franzens Universität Graz/Austria. Volume 7, p. 78 (Abstracts, 9th International Symposium on Fossil Cnidaria and Porifera).

4. An appreciation of published research on fossil corals: William. A. Oliver, Jr.

Bill's publications (>85) stem from his lengthy professional career, here arbitrarily divided into four periods:

(1) During Bill's early days as a student at Cornell University, and as a young professor at Brown University (with summer research for the NY State Geological Survey), he focused on the Middle Devonian stratigraphy of New York and its fossils. This commenced with work on Onondaga Limestone stratigraphy and on Onondaga bioherms and biostromes. Additionally, this was the time when he began collecting and field study of Hamilton Group rugose corals, which kept him interested and engaged until his death. (A major paper on Hamilton solitary rugosa was published posthumously by PRI, 2007.) Bill defined the lower boundary of the Onondaga limestone and subdivided it into four well-established members. He carefully completed collections of all groups of fossils available from the rocks and the well-defined lithology of the members allowed him to make his stratigraphy and faunal lists useful for decades. His masters thesis, "Middle Devonian coral beds of Central New York" and the last paper in this early group, "Biostromes and bioherms of the Onondaga Limestone in Eastern New York" clearly established this as one of his main fields of interest, i.e. fossil corals and their geologic setting, their behavior and living conditions. Only slightly later, his "Rugose corals from reef limestone in the Lower Devonian of New York" was the first coral paper devoted to that fauna (with six new species and three new genera). It is a complete treatment of these corals, including (1) the intraspecific variability of individual species based on coral morphology, measurements and statistics; (2) the environmental significance of the corals; (3) their age and stratigraphic relationships; and (4) their systematics. This paper won the award given for the best paper of 1960 for the Journal of Paleontology.

(2) Early days at the USGS. These were times when Bill furnished numerous identifications for USGS field geologists throughout the US, including Alaska and the contiguous 48 states. He was assigned by the USGS to the "Lower Paleozoic corals", which meant the Ordovician, Silurian and Devonian faunas. During this time he became aware of the provinciality of Lower and Middle Devonian coral faunas, and this topic of biogeography of provincial coral faunas interested him for a number of years. This was the time of preparation of the monograph on the Onesquethaw corals, "Noncystimorph colonial rugose corals of the Onesquethaw and Lower Cazenovia stages (Lower and Middle Devonian) in New York and Adjacent areas" (1976). This work alone would be adequate for making Bill very important for future generations of coral students. This monograph involves nearly everything that concerns these corals, including, biostratigraphy, and palaeobiogeography, a thorough study of their morphology, intracolonial and intra-specific variation, blastogeny and modern systematics.

In 1968 Bill published very important papers, singly and as group contributions, summarizing knowledge of Devonian biostratigraphy of the Appalachian Basin and on the succession of Lower and Middle Devonian Rugosa in eastern North America. Both of these remain standard references for students of Devonian strata and faunas of North America. The first two were presented at the International Symposium on the Devonian System in Calgary.

In general, it can be said that this was the time when Bill got to know coral faunas that were the subject of systematic studies, and he also began to realize the provinciality of Eastern Americas faunas.

(3) Prime years at the USGS. Early in this period Bill received a Fulbright Award to spend a year in Czechoslovakia studying Middle Devonian corals (1968–1969), and he traveled widely collecting Devonian corals and familiarizing himself with European Devonian stratigraphy and European paleontologists. Two papers published in 1971 present results of Bill's stay in Czechoslovakia and complement each other. Both were written jointly with A. Galle and both deal with taxa from the Lower Devonian Koněprusy Limestone of the Barrandian area. These papers were based on previous collections by Počta (1902), supplemented by new material gathered by the authors. These new collections allowed much more precise determination of ages and ranges of individual species than was possible earlier. Recognition for the first time in Europe of such genera as the North American *Iowaphyllum* and Australian *Xystriophyllum* modified concepts of paleogeographic distribution for some Devonian taxa.

At this time Bill's interest in coloniality also was expressed in several papers, including, "Some aspects of colony development in corals" (1968). This is an important contribution in several ways, such as definition of individual parts of increase and form of colonies, but above all in recognizing intracolonial variability. This subject was studied by a very few people prior to his study, thus he was the first to draw attention to the fact that the number of septa in individual corallites is not solely a function of diameter. This has important taxonomic implications when small fragments of colonies are identified based on septal number and diameter is regarded as one of the most important distinguishing factors. More general observations on coloniality are contained in the paper written with A.G. Coates (1973), where a comprehensive discussion of the question of colony integration was a very important aspect of the paper.

"The relationship of the scleractinian corals to the rugose corals" (1980), which was read at the Third International Symposium on Fossil Corals and Sponges in Warsaw, but published in Paleobiology, is one of Bill's best papers in the opinion of many. His postulate that a direct relationship between the Scleractinia and the Rugosa is unlikely has been followed by numerous, but not all, coral paleontologists. Only time and acquisition of new data will prove the point, but Bill clearly documented his position that morphological similarity and some possible "intermediate forms" do not prove descent of the Scleractinia from the Rugosa.

This was also the time when Bill began to express his understanding of the paleobiogeography of North American Late Silurian and Devonian corals. His 1977 paper in Palaeogeography, Palaeoclimatology, Palaeoecology is a summary of earlier papers on that subject, largely supplemented by maps. Only some of those were used a year earlier in his presidential address to the Paleontological Society (1976). These papers were based on the newest paleomagnetic maps available at the time with all important literature data utilized. The difference of eastern North American corals from those of western part of North America and their endemism was shown by him to be the result of tectonism and isolation from both North Africa and Europe on one side and western North America on the other. The paper is widely cited in many papers dealing with the paleogeography, distribution and succession of Devonian faunas.

By this time, Bill also represented the Geological Survey with leadership positions in a number of professional organizations, including presidency of the International Association for Study of Fossil Corals and Sponges. This position involved organizing the Fourth International Symposium on Fossil Cnidaria, held in Washington, D.C., in August of 1983, and being the lead editor of the symposium proceedings volume, published in 1984 as Palaeontographica Americana Number 54.

(4) Later years at the USGS and as *emeritus*. This was the time of fruition of several long term studies, one with Sorauf on *Heliophyllum halli*, a common rugosan in the Hamilton Group of New York State, and of interest to Bill since his days at Cornell, working on his graduate research with John W. Wells, who had published a very influential paper on the species and its multiple solitary and colonial forms. During this time Bill also published (or had in press) monographic treatments on the other major groups of solitary corals in the Hamilton Group.

"Extinctions and migrations . . ." (1990) is similar to earlier paleogeographic studies, but also recognizes that the Givetian turnover was almost equal to the end-Frasnian and that migration was principally from western North America. In co-operation with Alan Pedder (1990), a large set of published data was analyzed and the occurrence of Devonian rugose coral faunas was tested against paleogeography proposed by Scotese. Although positions of most faunas agrees with paleomagnetic reconstructions, some do not, indicating that corals can be of use in geographic modeling despite their restricted environmental requirements.

The paper presented by Bill at the Münster Symposium, "Origins and relationships . . ." (1993), can be considered a summary of many of his papers dealing with the taxonomy, distribution, sequence and relationships of rugose corals from the Eastern North Americas (ENA) Realm. He analyzed the main characteristics of the Zaphrentidae, Craspedophyllidae and Siphonophrentidae in detail and proposed relationships within each family based on cladograms. In summary he proposed an evolutionary tree of six main families present in the ENA Realm and suggested the derivation of each of them.

"The genus *Heliophyllum* ..." (2002) is the last and most comprehensive chapter on the peculiar genus *Heliophyllum* in a series produced by Oliver and Sorauf. They summarized knowledge of the genus in all aspects: growth form, intraspecific variability, population or subspecies problems, microstructure, formation of carinae, ontogeny and astogeny, environment and paleoecology, biogeography and stratigraphic positions. Thus, students will find it difficult to find something new in that variable genus, after becoming acquainted with all papers dealing with it, in particular, the last, this monograph. An additional treatment of major coral genera (the Zaphrentidae) of the Hamilton Group from New York was published posthumously as a Bulletin of American Paleontology in 2007.

Bill left behind many published ideas on taxonomy, paleogeography, paleobiology, the relationship of the Rugosa to other Anthozoa, and on other fields, particularly Devonian stratigraphy. His scientific achievements are an inspiration, and his numerous meticulously produced publications and his work habits were exemplary. His published works thus comprise a legacy that will remain a source of inspiration for coral workers during many years and decades to come.

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James E. Sorauf*
Department of Geological Sciences, Binghamton University, Binghamton, NY 13902-6000, USA

Jerzy Fedorowski
Institute of Geology, Adam Mickiewicz University, Makow Polnych 16, Pl 61-606 Poznan, Poland

* Corresponding author.
E-mail addresses: jsorauf@binghamton.edu (J.E. Sorauf), jerzy@amu.edu.pl (J. Fedorowski)

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Research paper

Tracing the long-term evolution of a species complex: Examples from the *Montastraea* "*annularis*" complex

Ann F. Budd

Department of Geoscience, University of Iowa, Iowa City, IA, USA

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Abstract

Recent molecular work has revealed numerous species complexes of scleractinian reef corals. Although species within complexes are distinct through much of their distribution, hybridization has been discovered at species margins, and has been hypothesized as playing an important role in mediating responses to changing environments. In the present study, I examine the long-term evolution of the *Montastraea* "*annularis*" complex over the past 5 million years to determine when speciation, extinction, and hybridization took place over the past 6.5 million years, with the eventual aim of understanding how these events corresponded with environmental changes in the Caribbean region. The material consists of colonies collected in the Mio-Pliocene of the Dominican Republic and the Plio-Pleistocene of Costa Rica and Panama. Genetically characterized colonies from the Recent of Panama are included in the analyses for comparison. Species are distinguished in the fossil material using a landmark-based morphometric approach that focuses on the size and shape of architectural features within corallites in transverse thin sections. Evolutionary relationships among species are examined using phylogenetic analyses based on parsimony. Phylogenetic characters are derived from the results of multiple comparisons tests, which statistically evaluated differences among species using morphometric data.

The results show that the *Montastraea* "*annularis*" complex originated during late Miocene time, and consisted of >12 species during the Pliocene, with a maximum of 4–5 species co-occurring at any one time. The three modern species do not form a monophyletic group but belong to separate clades within the complex. The ranges of two of the three modern species may extend back to 2.9–3.5 Ma, indicating that they are survivors of the Plio-Pleistocene extinction event in which ~80% of Caribbean reef coral species became extinct. Morphologic differences among species (disparity) were higher during the Pliocene than they are today.

Keywords: Reef coral; Cenozoic; Caribbean; Morphometrics; Species; Evolution

1. Introduction

Recent molecular work has led to the discovery of numerous species complexes within scleractinian reef corals. Although species within complexes have distinct morphological and ecological characteristics through much of their geographic range, hybridization may occur at species margins, causing overlap among species. Such hybridization has been hypothesized as playing an important role in mediating responses to changing environments over evolutionary time scales (Budd and Pandolfi, 2004; Fukami et al., 2004a; Willis et al., 2006).

The research described in this paper is part of a larger project examining the genetic and morphologic structure of the *Montastraea* "*annularis*" species complex and tracing its long-term evolution through the fossil record. The overall objective of the project is to determine when speciation, extinction, and hybridization within the complex took place, and how these events corresponded with environmental changes across the Caribbean region. In the present paper, I review the species that have been recognized within the complex to date, and perform a preliminary phylogenetic analysis. Evolutionary patterns are interpreted within the context of the resulting phylogenetic tree.

2. The three modern species and their fossil record

My colleagues and I have focused on the *Montastraea* "*annularis*" complex, because it is an ecological dominant on Caribbean reefs (Goreau, 1959). Morphologically, the complex is distinguished from other members of the genus *Montastraea*

E-mail address: ann-budd@uiowa.edu.

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by having three septal cycles (i.e., 24 septa) and corallite diameters of 2–3.5 mm. The complex was long thought to consist of a single species that had high phenotypic plasticity in response to different light levels (Graus and Macintyre, 1982; but see Klaus et al., 2007). However, recent molecular work (Fukami et al., 2004a) has shown that it consists of at least three species that differ in overall colony shape. *M. annularis* s.s. forms regular-shaped columns, *M. faveolata* forms massive heads with skirt-like edges, and *M. franksi* forms bumpy, irregular mounds and plates.

Recent molecular work on the complex in Panama has found differences in AFLP markers, a noncoding region of the mitochondrial genome, and ITS sequences (Fukami et al., 2004a). For example, for the GGAG-1 locus, samples of *M. franksi* and *M. annularis* s.s. have a diagnostic 920 band; whereas samples of *M. faveolata* have a diagnostic 880 band. *M. franksi* and *M. annularis* s.s. exhibit differences in frequencies at two AFLP loci and the non-coding region. Although laboratory experiments indicate that the potential for hybridization exists, F1 hybrids have not been observed in the field. Moreover, differences in spawning timing and gamete incompatibility support the reproductive isolation of the three species (Levitan et al., 2004).

Although traditional morphologic measurements (corallite diameter, number of septa per corallite) reveal no differences between the three modern species in Panama, morphometric analyses performed on genetically characterized colonies using landmarks in two and three dimensions (Budd and Johnson, 1996; Budd and Klaus, 2001; Knowlton and Budd, 2001; Fukami et al., 2004a) reveal significant differences in the structure of the corallite wall, development of the costae, and calical shape (Fig. 1). In these analyses, the coordinates of 25 landmarks were digitized in two- and three-dimensions. Six corallites were digitized on colony tops and six on colony sides. Bookstein size and shape coordinates were calculated and served as variables in statistical analyses, which consist of a series of canonical discriminant analyses including cluster analyses performed using Mahalanobis distances among colonies (see Budd and Klaus, 2008, for details). The results show that calices of *M. franksi* have less relief; their costae are thick and well-developed; and their corallite walls are thick and septothecal (formed by coalesced septa). The septa of *M. faveolata* are highly exsert, and slope steeply toward the columella; the costae are short and thin; septal teeth are long and distinct; corallite walls are very thin and partially parathecal (formed by dissepiments). Calices of *M. annularis* s.s. have features intermediate between these two extremes, but are closer to *M. franksi*. Their costal development is highly regular, their primary septa are often prominent, and their corallite walls are thin but septothecal.

In contrast to Panama, the three modern species overlap both genetically and morphologically in the Bahamas (Fukami et al., 2004a). This overlap has been interpreted to be the result of an ancestral polymorphism that has been maintained in *M. annularis* s.s. but not in the other two species. It suggests that a north-to-south hybridization gradient may exist within the complex with introgression being strongest in the north. Despite this overlap and possible hybridization, Fukami et al. (2004a) conclude that the species complex (a syngameon) is composed of three species, which tolerate a degree of interspecific hybridization and gene exchange at the margins of their distributions.

Morphometric studies of fossil collections of the complex using 2D landmarks (Fig. 2) indicate that the three modern species were widely distributed across the Caribbean during the late Pleistocene, including Barbados (Pandolfi et al., 2001, 2002) and the Dominican Republic (Klaus and Budd, 2003), and that they co-occurred with other exclusively fossil species in the complex, including the organ-pipe coral *M. nancyi* (Pandolfi, 2007). However, the overlap observed today among species in the Bahamas has also been found during the late Pleistocene (Budd and Pandolfi, 2004), suggesting hybridization may have persisted in the Bahamas since the late Pleistocene and may have occurred in response to fluctuations in temperature and sea-level associated with northern hemisphere glaciation.

3. Plio-Pleistocene species in Costa Rica and Panama

To trace the evolution of the complex further back through geologic time, my colleagues and I have performed morphometric analyses of specimens that were collected in the Plio-Pleistocene of Costa Rica and Panama (Budd et al., 1999; McNeill et al., 2000; Budd and Klaus, 2001). The specimens (94 colonies) were collected within the context of the stratigraphic sections, which have been dated using high resolution methods, integrating data on microfossils, palaeomagnetics, and strontium isotopes (Coates, 1999; McNeill et al., 2000). The collections were made in four stratigraphic units: (1) two reef trends (Lomas del Mar, Empalme) in the Moín Formation near Límon, Costa Rica, dated at 2.9–1.5 Ma; (2) one reef trend (Buenos Aires) in the Quebrada Chocolate Formation near Límon, Costa Rica, dated at 3.5–2.9 Ma; (3) two reef trends along the northern coast Isla Bastimentos and at Swan Cay in the Bocas del Toro region of Panama, dated at 2.2–0.8 Ma; and (4) one reef trend on Isla Colón in the Bocas del Toro region of Panama, dated at 3.5–1.7 Ma. Using the same two-dimensional landmark methods as above, we performed a series of canonical discriminant analyses on each stratigraphic unit and found 10 morphotypes in the Costa Rica and Panama collections (Fig. 3). Discriminant analysis comparing the morphotypes in different units showed that each of the 10 morphotypes was distinct, and could be considered a separate morphospecies (Budd and Klaus, 2001). They are also distinct from the three modern species. Moreover, superimposing the cladogram (16 ingroup taxa, 8 characters, 29 states) on the stratigraphy indicated that the oldest occurrences of *M. franksi* and *M. faveolata* are early late Pliocene (2.9–3.5 Ma), and the oldest occurrence of *M. annularis* s.s. is late Pleistocene (0.5 Ma).

4. The Mio-Pliocene species in the Dominican Republic

My colleagues and I have also performed analyses of the Mio-Pliocene Caribbean species *M. limbata*, which is distinguished from modern *M.* "*annularis*" s.l. by having thick primary septa, paliform lobes, and widely spaced calices (Budd, 1991; Klaus and Budd, 2003; Budd and Klaus, 2008). Like the *M.* "*annularis*" s.l., *M. limbata* is highly variable, and has various morphotypes,

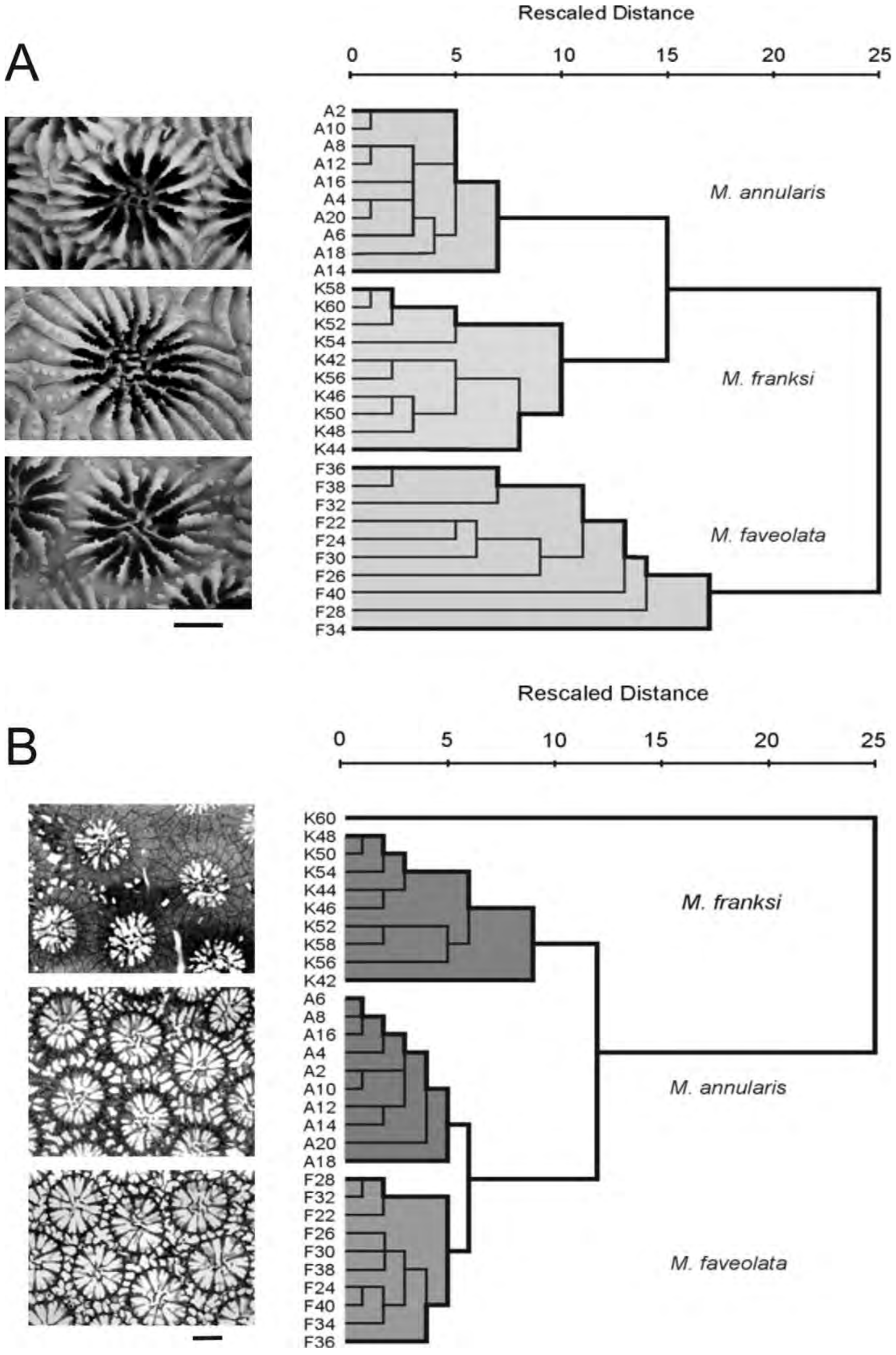

Fig. 1. Cluster analyses of landmark data collected on colonies of three modern, genetically characterized species of the *Montastraea* "*annularis*" complex from the San Blas Islands of Panama. The analyses were performed on Mahalanobis distances calculated using canonical discriminant analyses between colonies. Each branch of the dendrogram represents one colony. A's indicate colonies of *M. annularis* s.s., F's indicate colonies of *M. faveolata*, and K's indicate colonies of *M. franksi*. After Budd and Klaus (2001). Scale bars = 1 mm. A, Three-dimensional data. The most important variables are related to the elevation and length of the costae, the shape of the septal margin, and the length of the tertiary septa. B, Two-dimensional data. The most important variables are related to the thickness of the corallite wall and the length of the costae beyond the wall.

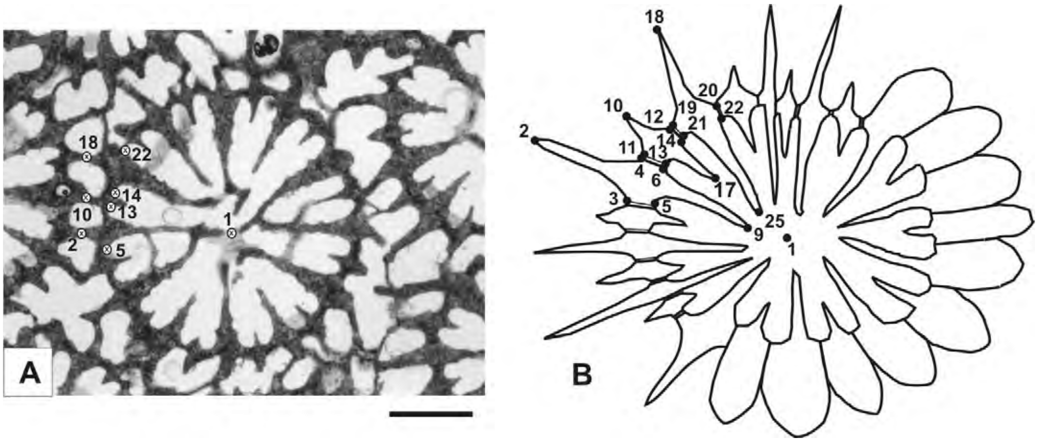

Fig. 2. Two-dimensional Cartesian coordinates collected for 25 landmarks on transverse thin-sections of corallites. Eight of the 25 landmarks are indicated on the thin-sections on the left. Landmarks were selected to characterize the structure of the corallite wall and costal extensions beyond the wall. Scale bar = 1 mm. After Budd and Klaus (2008).

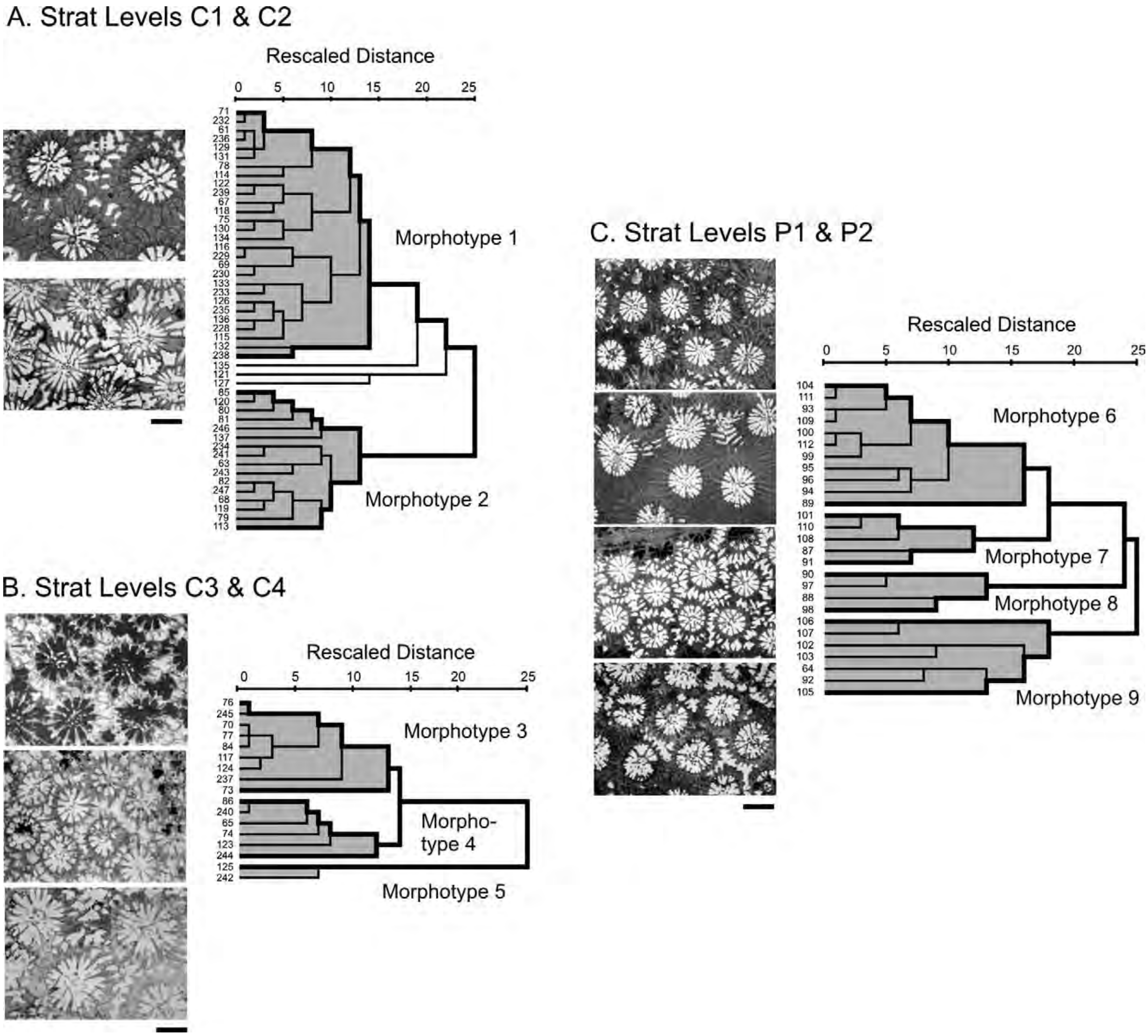

Fig. 3. Cluster analyses of three of the four stratigraphic units in Costa Rica and Panama. The analyses were performed on Mahalanobis distances calculated using canonical discriminant analyses between colonies. Each branch of the dendrogram represents one colony. Nine morphotypes were recognized in the three units. A tenth morphotype was recognized in the fourth unit. Scale bars = 2 mm. After Budd and Klaus (2001).

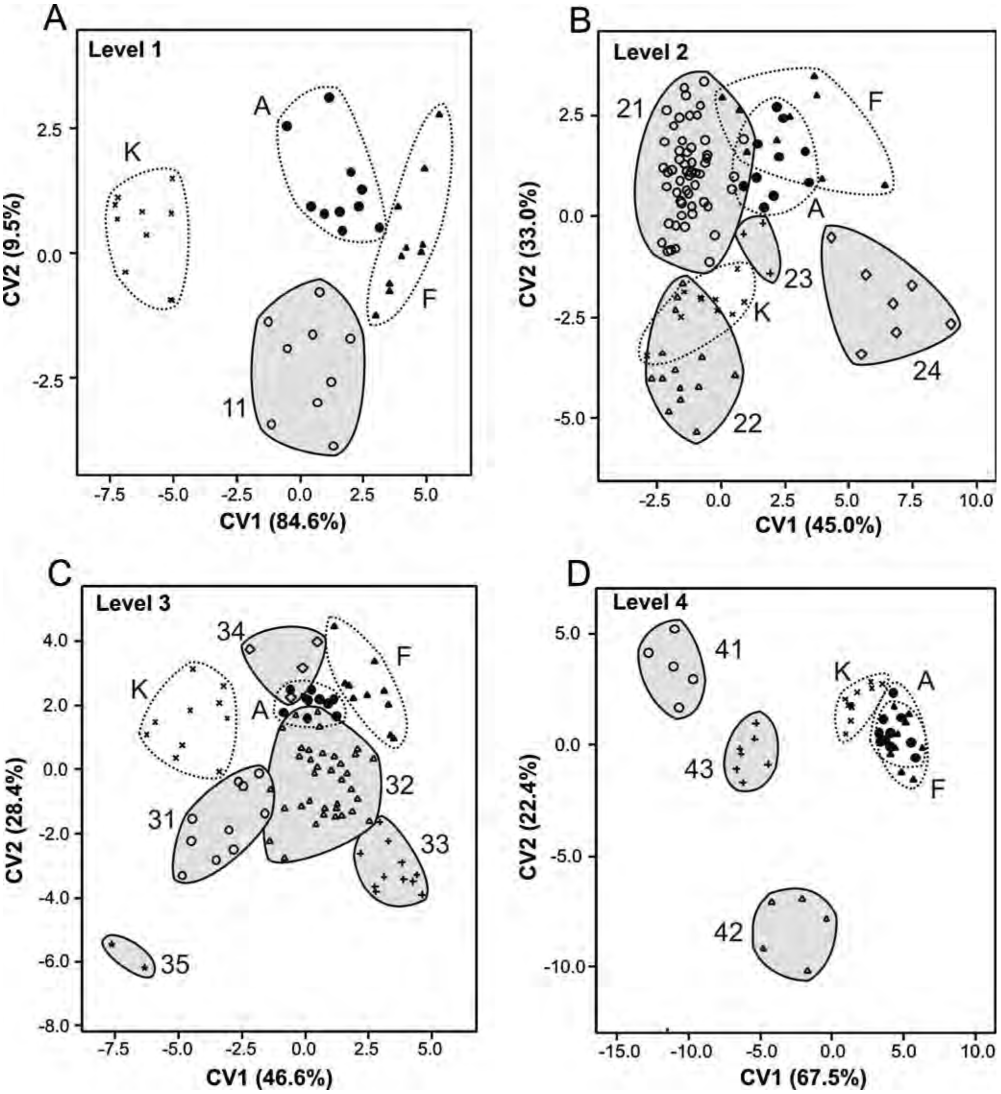

Fig. 4. Plots of scores on canonical discriminant analyses comparing morphotypes in the four stratigraphic units in the Dominican Republic. Each point on the plot represents one colony. Solid polygons enclose the fossil morphotypes; dotted polygons enclose the three modern species, which were included in the analyses for comparison. Subsequent analyses comparing the 13 fossil morphotypes indicate that DR43 = DR35; DR42 = DR32 = DR21; DR34 = DR23. After Budd and Klaus (2008).

which has suggested that it too may be a complex consisting of numerous species. Specimens (166 colonies) were collected within the context of stratigraphic sections that were constructed by Saunders et al. (1986); high-resolution age dates have recently been determined for the sequence by McNeill et al. (2008). The collections were made in four stratigraphic units along Río Gurabo and Río Cana (including Arroyo Bellaco and Cañada de Zamba): (1) Baitoa Formation, early to middle Miocene, ~13.1–17.3 Ma; (2) Cercado Formation, late Miocene, ~6.5–5.6 Ma; (3) Gurabo Formation, late Miocene to early Pliocene, ~5.6–4.5 Ma; (4) Mao Formation, early to late Pliocene, ~4.5–3.4 Ma. Using the same two-dimensional landmark methods as above, we performed a series of canonical discriminant analyses on each stratigraphic unit and found 13 morphotypes in the Dominican Republic collections (Fig. 4). Discriminant analysis comparing the morphotypes in different units showed that 4 morphotypes were the same as morphotypes occurring in other units (i.e., DR43 = DR35; DR42 = DR21; DR32 = DR21; DR34 = DR23), making a total of nine morphospecies [eight belonging to what has traditionally been called *M. limbata*, and one belonging to what has traditionally been called *M. trinitatis* (see Budd and Klaus, 2008)].

Although diversity is roughly the same (3–5 morphospecies) in all of the fossil units analyzed except the oldest level in the Dominican Republic, morphologic comparisons among and within species through geologic time show: (1) no directional change occurred in the overall morphology of the complex through time, (2) morphologic disparity (distances among morphospecies) was higher in the Mio-Pliocene than it is today, and (3) analysis of one relatively long-ranging morphospecies within the complex revealed directional change in some, but not all, species diagnostic morphologic features (Budd and Klaus, 2008). The lower disparity in the late Pleistocene to Recent may be the result of more frequent hybridization.

Table 1
Characters used in the phylogenetic analysis.

	Morphologic feature	Measurement	Tukey's HSD multiple comparisons test ($p < 0.05$)	Number of states
1	Number of septa	ns = count of septa	6 subsets	4
2	Tertiary costa width	tcw = (13,14)	11 subsets	5
3	Corallite diameter	cd = ((1,14) + (1,22) + (1,13) + (1,5))/4	9 subsets	5
4	Columella size	clwrat = (((1,9) + (1,25))/2)/cd	6 subsets	4
5	Tertiary septum length	tslrat = (1,17)/cd	8 subsets	3
6	Wall thickness	wt = ((11,13) + (3,5) + (12,14) + (20,22))/4	7 subsets	5
7	Dissepiment thickness	para = ((4,11) + (12,19) + (6,13) + (14,21))/4	6 subsets	4
8	Tertiary costa shape	tcwrat = (11,12)/(13,14)	10 subsets	5
9	Primary costa shape	pcwrat = (3,4)/(5,6)	10 subsets	4
10	Prim. vs. sec. costa width	p scwrat = (5,6)/(21,22)	8 subsets	4
11	Prim. vs. tert. costa width	p tcwrat = (5,6)/(13,14)	4 subsets	4
12	Primary costa length	pcl = ((3,2) + (4,2))/2	8 subsets	4
13	Prim. vs. sec. costa length	p sclrat = pcl/scl	6 subsets	3
14	Prim. vs. tert. costa length	p tclrat = pcl/tcl	8 subsets	5

5. Phylogenetic analysis

A preliminary phylogenetic analysis was performed using 22 taxa, consisting of: the 3 modern species in the *Montastraea* "*annularis*" complex, the 10 morphospecies in the *M.* "*annularis*" complex from the Plio-Pleistocene of Costa Rica and Panama, the 8 morphospecies in the *M.* "*limbata*" complex from the Mio-Pliocene of the Dominican Republic, and the stratigraphically oldest Dominican Republic species, *M. trinitatis* (=DR11, Fig. 4A), which was designated as the outgroup.

The characters consisted of 14 traditional measures (counts, linear distances, ratios; Table 1) calculated using the 25 2D landmarks shown in Fig. 2. All of the characters are continuous variables. As explained in Budd and Klaus (2008), I used traditional measures instead of Bookstein size and shape coordinates, because traditional measures encompass a greater range of skeletal features, including all of characters that have been recognized in past and present research as species diagnostic. Moreover, each measure has a unique pattern of variation among species. To determine states for each character, I performed multiple comparisons statistical tests (Tukey's HSD) for each of the 14 characters using the 22 taxa, and based the definitions of each state on subsets of taxa with little or no overlap (see Budd and Klaus, 2001). The final character matrix (Table 2) consisted of 59 states for the 14 characters. All characters were treated as ordered, and equal in weight.

A maximum parsimony analysis was performed using PAUP* (Swofford, 2002) and a heuristic search consisting of 150

Table 2
Character matrix. Character numbers ("Ch #") refer to characters defined in Table 1. Morphospecies refer to taxa shown in Figs. 1, 3 and 4. DR11 (*M. trinitatis*) was designated as the outgroup.

Morpho-species	Number of colonies	Ch #1	Ch #2	Ch #3	Ch #4	Ch #5	Ch #6	Ch #7	Ch #8	Ch #9	Ch #10	Ch #11	Ch #12	Ch #13	Ch #14
CP01	31	2	5	4	2	2	5	1	4	2	3	2	3	3	1
CP02	16	2	3	3	2	2	2	2	2	2	3	2	2	2	2
CP03	9	2	4	3	3	2	2	3	1	2	3	2	3	3	3
CP04	5	2	2	2	3	3	2	2	2	1	2	2	1	2	3
CP05	2	2	5	5	3	1	3	2	3	2	2	1	2	2	1
CP06	11	3	2	2	2	3	4	1	4	3	3	3	1	3	1
CP07	3	3	2	2	2	2	4	1	5	3	3	4	1	1	1
CP08	4	2	1	1	1	3	1	1	2	2	3	2	1	3	2
CP09	7	2	3	2	2	2	3	1	4	2	2	2	2	3	2
CP10	3	1	4	3	3	2	2	2	2	1	3	2	2	2	1
DR11	9	3	4	4	1	2	3	2	2	1	4	2	2	3	2
DR21	96	2	3	2	3	3	3	2	3	2	2	2	2	2	3
DR22	14	3	5	5	3	2	5	1	4	2	2	2	3	3	2
DR23	7	2	5	4	2	2	2	3	1	2	2	1	4	2	4
DR24	7	2	3	3	1	2	1	4	1	1	2	2	4	3	5
DR31	10	2	3	3	1	2	4	2	4	3	1	2	2	2	2
DR33	11	2	1	3	4	3	2	4	1	2	1	2	3	2	5
DR34	9	3	2	2	2	3	5	2	4	4	2	2	2	2	3
DR41	5	4	2	4	3	3	5	2	4	3	3	2	2	2	4
annularis	10	2	2	2	1	2	2	3	2	2	3	2	2	2	3
faveolata	10	2	3	3	2	3	1	3	1	2	3	2	2	3	4
franksi	10	2	4	3	2	2	4	2	4	2	4	2	2	2	1

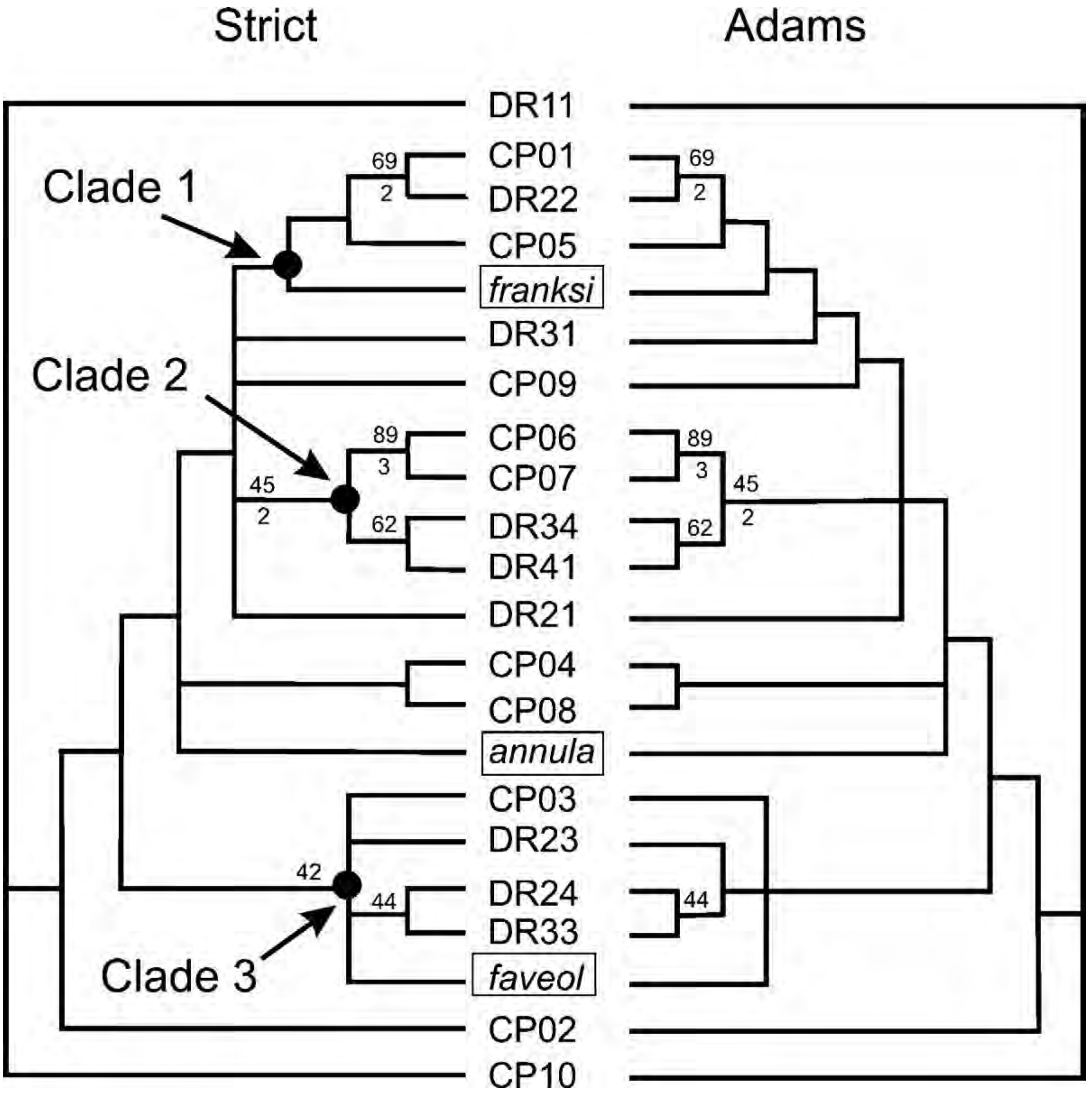

Fig. 5. Strict consensus and Adams consensus trees for extant and fossil species within the *Montastraea* “*annularis*” complex based on maximum parsimony. Numbers above and below nodes are bootstrap values and Bremer support values >1, respectively. Twelve most parsimonious trees (MPTs) of length 116 were recovered. “CP”, Costa Rica and Panama morphospecies; “DR”, Dominican Republic morphospecies. The names of the three modern species are abbreviated and in italics.

random addition sequence replicates. TBR was utilized as the branch swapping algorithm for the heuristic search. Support for the resulting most parsimonious trees (MPTs) was evaluated by a bootstrap analysis of 100 replicates with 10 random addition sequence replicates for each bootstrap replicate. Bremer support values were calculated using TreeRot.v.3 (Sorenson and Franzosa, 2007).

Twelve most parsimonious trees (MPTs) of length 116 were recovered (Fig. 5). The consistency and retention indices for the MPTs were 0.388 and 0.567, respectively. The topologies of the Strict and Adams consensus of the MPTs were identical except for two branches (DR31, DR23). As in previous phylogenetic analyses of the complex (Budd and Klaus, 2001; Pandolfi et al., 2002), bootstrap support is extremely low for most nodes. Two smaller clades (i.e., monophyletic groups containing three or more species) have bootstrap values that are >40%: (1) Clade #2 = CP06 + CP07 + DR34 + DR41, (2) Clade #3 = CP03 + DR23 + DR24 + DR33 + *faveolata*. Although bootstrap support is low, a third smaller clade (Clade #1 = CP01 + DR22 + CP05 + *franksi*) contains the same taxa as found in previous analyses performed using different taxa, outgroups, and characters (Budd and Klaus, 2001; Pandolfi et al., 2002).

Examination of the consensus trees shows that the three modern species are not members of the same clade, but are widely scattered across each tree, belonging to two or more clades. Moreover, each of the three distinguishable clades (Fig. 5) contains a mix of morphospecies from the Dominican Republic and from Costa Rica and Panama, indicating that each clade has a long fossil record that dates back to the Mio-Pliocene of the Dominican Republic. Species of the *M.* “*annularis*” complex and *M.* “*limbata*” complex do not form separate clades, but are intermixed, indicating that the two complexes are the same. Only two of the three clades (#1, 3) contain modern species, and exist today; the third clade (#2) is extinct. The topology of the cladogram suggests that two modern species, *M. franksi* and *M. faveolata*, have long-range extensions, extending back to the early late Pliocene (2.9–3.5 Ma).

Future work will focus on adding additional characters and alternative outgroups to the character matrix, as well as using stratigraphic information to evaluate equally parsimonious trees. The additional characters will include a variety of non-landmark measures that describe colony growth and form (including budding angles, frequencies, and twist) and expansion rates of individual corallites after budding (e.g., Kaandorp and Kübler, 2001). Contrary to scleractinian classification, recent molecular work has shown that *M. annularis* s.s. and *M. cavernosa* belong to different families and are distantly related (Fukami et al., 2004b), calling into question the use of *M. cavernosa*-like corals as outgroups in analyses of the *M.* "*annularis*" complex (as in Budd and Klaus, 2001). Alternative outgroups based on the new molecular trees will need to be considered. Finally, stratigraphic data will be used to assess equally parsimonious trees (see Huelsenbeck and Rannala, 2000). Adding occurrences at additional sites may further help to minimize stratigraphic range extensions (e.g., as in the three modern species).

6. Conclusions

The present study has shown that species within the *Montastraea* "*annularis*" species complex can be recognized using morphologic data and their evolutionary histories can be traced through geologic time. Results to date have shown that:

1. The *Montastraea* "*annularis*" complex has a long evolutionary history, dating back more than 6 million years.
2. Since its origination, the complex has consisted of 3–5 species living together at the same time. The mean morphology of the complex has not changed through time, but morphologic disparity is lower today than in the geologic past.
3. The three modern species do not form a monophyletic unit, but belong to different clades within the complex. These clades originated early during the evolution of the complex.
4. Maximum diversity occurred within the complex during the Plio-Pleistocene in association with faunal turnover on Caribbean reefs. Two of the three modern species appear to be survivors of turnover.

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Research paper

The converging results of microstructural analysis and molecular phylogeny: Consequence for the overall evolutionary scheme of post-Paleozoic corals and the concept of Scleractinia

Jean-Pierre Cuif

UMR 8148 IDES, Geology Bât 504, Faculty of Sciences, 91405 Orsay, France

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Abstract

During the last three decades, a series of paleontological and biological results have brought considerable changes to the long-standing question of a possible relationship between the Paleozoic and modern corals. Microstructural descriptions of samples from the alpine outcrops (Salzkammergut and Dolomites) along with new specimens from Turkey have shown first that the classical Wells' scheme have to be re-examined. Accordingly, several investigations based on molecular phylogeny have repeatedly led to the conclusion that, at the family level, the taxonomy inherited from Vaughan and Wells cannot be maintained. From an overall evolutionary viewpoint, agreement also exists between microstructural analysis and molecular phylogeny. A recently discovered Triassic family, the Pachythecalids, exhibits highly unexpected skeletal features and microstructures in both septa and walls. Additionally, structural relationships between walls and septa demonstrate a particular mode of growth, with ontogenic priority to the theca. Comparison of the corallite microstructures suggests that most of the Triassic fauna can be derived from this unique family by an evolutionary process during which the septal system became progressively prevalent upon the wall. This monophyly of the modern corals is also well supported by molecular phylogeny.

The present concept of Scleractinia has to be re-examined because it cannot include neither Pachythecalids, probably related to the Late Permian Polycoelids, nor some other post-Paleozoic corals, including extant Guyniidae, with long recognized specific structural patterns.

Keywords: Coral phylogeny; Skeleton microstructure; Pachythecalids; Taxonomy; Evolution; Scleractinia

1. Introduction

Current ideas about the overall evolution of corals are still based on Haeckel's scheme (1896). In this model, the "bilateral and serial" mode of septal insertion, first described by Kunth (1869), is opposed to the "axial and cyclic" insertion of septa in the living species *Caryophyllia cyathus* that has been previously described by Milne-Edwards and Haime (1848). Generalized to the corals of the Paleozoic era and post-Paleozoic times, respectively, Haeckel's hypothesis became classic as the "diphyletic theory" of coral evolution, which postulate no phyletic relationship between Late Permian corals and the Scleractinia known from the Middle Triassic.

Two independent circumstances have lent additional support to this view.

i) Knowledge of Triassic faunas long relied on two major studies done at the end of the 19th century. In 1890, F. Frech described the corals from the "Juvavischen Triasprovinz" (essentially the Salzkammergut district, Austria) including the very rich Rhaetian site of Fischerwiese, whereas Volz (1986) greatly improved the knowledge of the Ladino-Carnian faunas of the South-Tyrol (now the Dolomites) exemplified by the famous faunas of the Richthofen reef (Sett Sass). At that time, the Milne-Edward's "Histoire Naturelle des Coralliaires" (1857–1860) was very influential among taxonomists. Most of the generic terms used to describe the Triassic faunas were borrowed from this authoritative synthesis, creating a taxonomic framework directly linked to the modern corals.
ii) More recently, the mineralogy of coral skeletons is also contributed to the diphyletic theory. Microscopic analyses of skeletal structures have made clear a sharp contrast between the diagenetic behavior of Paleozoic and post-Paleozoic

E-mail address: jean-pierre.cuif@u-psud.fr.

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coral skeletons. Paleozoic corals have corallites in which the fine-scale organization of the skeletal tissue is frequently preserved. This supports the hypothesis that calcite was the initial mineral of fibers. In contrast, the structural components of recent corals are aragonitic and when transformation to calcite occurs (exceptions to this process are very rare), the aragonite/calcite inversion is highly destructive with respect to the three-dimensional arrangement of the aragonite fibers. This led to the concept of an essential difference in the biomineralization process between the Paleozoic and post-Paleozoic corals, and a confirmation of the diphyletic theory.

1.1. *The comparison between skeleton-based and molecular phylogenies*

Over the past 30 years, two different approaches suggest the necessity for a re-examination of the Haeckel's scheme. In 1973, *Zardinophyllum zardinii* Montanaro-Gallitelli, an isolated species with "primitive characters", was discovered in the Dolomites classical outcrops, and a series of other species with very comparable features (Cuif, 1975) was described from lower Norian outcrops recently discovered in Southern Anatolia (Lycian Taurus, Alakir Cay Valley). Fortunately, in these new coral faunas, the aragonitic mineralogy is preserved (Cuif, 1972) allowing precise descriptions of skeletal architectures and growth processes. A series of species with very unusual microstructural characters was thus recognized, leading to the formation of a new coral family (Pachythecalidae Cuif, 1975). Members of this family exhibit microstructural organization and septal/wall relationships that very closely resemble that known from some Late Permian corals. Additionally, extensive microstructural descriptions suggested that the various microstructural schemes observed in the Triassic coral faunas (including those of the Alps of western European) could be derived from Pachythecalid corals through a double evolutionary trend: (i) reduction of the wall and progressive prevalence of the septal system; (ii) development of fibrous axes replacing the fibro-normal arrangement of fibers on both sides of the septum. These two concomitant processes result in the hypothesis of a microstructural monophyly of the Triassic corals derived from a "rugosa-looking" family (Cuif, 1977, 1980).

On the other hand, several attempts have been made during the last decades that aim to establish taxonomic schemes based on non-skeletal characters of Scleractinia. Application of the molecular method based on the 16S mitochondrial gene by Romano (1996) has shown that a much different arrangement of scleractinian families could be proposed. A test of the taxonomic consistency of the Scleractinia families compared to their microstructural features was carried out using more than 40 species, most of which are type species of major genera (Cuif et al., 2003a). Some of these families were shown to be valid, particularly those presenting well-established architectural/microstructural patterns, whereas most of the major families (i.e., Faviidae) had to be dismantled. In the latest and most extensive study (Fukami et al., 2008), molecular positions of 128 species were compared by using mitochrondrial and nuclear genes simultaneously. Not only have comparable results been obtained at the family level, i.e., 11 of 16 Scleractinian families shown to be polyphyletic, but monophyly of the whole taxon Scleractinia itself has been demonstrated.

Thus, two distinct approaches, one dealing with the organization of fibrous skeleton of the corallites and the other based on criteria from living tissues, produce converging conclusions. Recent investigations have also further completed our information about biological signals included within the skeleton in the Scleractinia. In situ biochemical characterization of the corallites of Pachythecalid and derived families has made it clear that a photosymbiotic metabolism was already operating in these rugosan-like corals (Muscatine et al., 2005). On the other hand, the extant family Guyniidae has revealed an atypical overall architecture compared to the general Scleractinian scheme, suggesting possible remnants of Paleozoic characters (Stolarski, 2000). These various results have to be analyzed together with information collected during the last decades concerning the leading role of organic components that determine the properties of calcareous skeletons among invertebrates (including corals), and the nanoscale organization of their skeletons (Cuif et al., 2003a; Stolarski, 2003). Additionally, recent data about changes in Earth conditions through the Permo-Triassic times must be taken into account. They provide us with a new basis to discuss the long-standing question of the Rugosa/Scleractinia relationships and what might have occurred during the 10-million-year gap in the history of corals, during which data are completely lacking.

2. Materials and methods

Corals used in this study were collected in lower Norian outcrops of the Lycian Taurus (close to Gödene, Alakir Cay Valley, Antalya province). Experimental data reported here focus on recent results concerning their biomineralization and growth mode with possible evolutionary implications.

Physical characterization of remaining organic matrix has been done by thermo-gravimetric analysis coupled with absorption of selected infrared wavelengths (1508 and 2363 cm^{-1}) corresponding to water and CO_2 emission, respectively.

In situ characterization of sulphated polysaccharides was obtained at the Synchrotron Radiation Facility (ESRF) at Grenoble (France) by using the X-ray absorption near edge structure (XANES) method. The ID-21 beam line microscope also enables determining a precise distribution of these mineralizing matrices. Carefully polished surfaces (without any coating) are submitted to an X-ray beam at the selected wavelength (2.3450 keV), focused at a sub-micrometer spot size (0.2 μm) by specially designed lenses. Piezoelectric driven devices or stepping motors allow a stepping displacement of the sample depending on the surface analyzed. Owing to the high brilliance of the X-ray synchrotron beam, dwell times of about 0.5/0.8 s allow mapping of 100/100 square micrometers (at highest resolution) up to a few square millimeters to be obtained overnight.

The exceptional thickness of the wall in *Pachythecalis major*, the type species of the family, has made possible the extraction and chemical characterization of organic matrices remaining within the skeletons of the corals. After checked

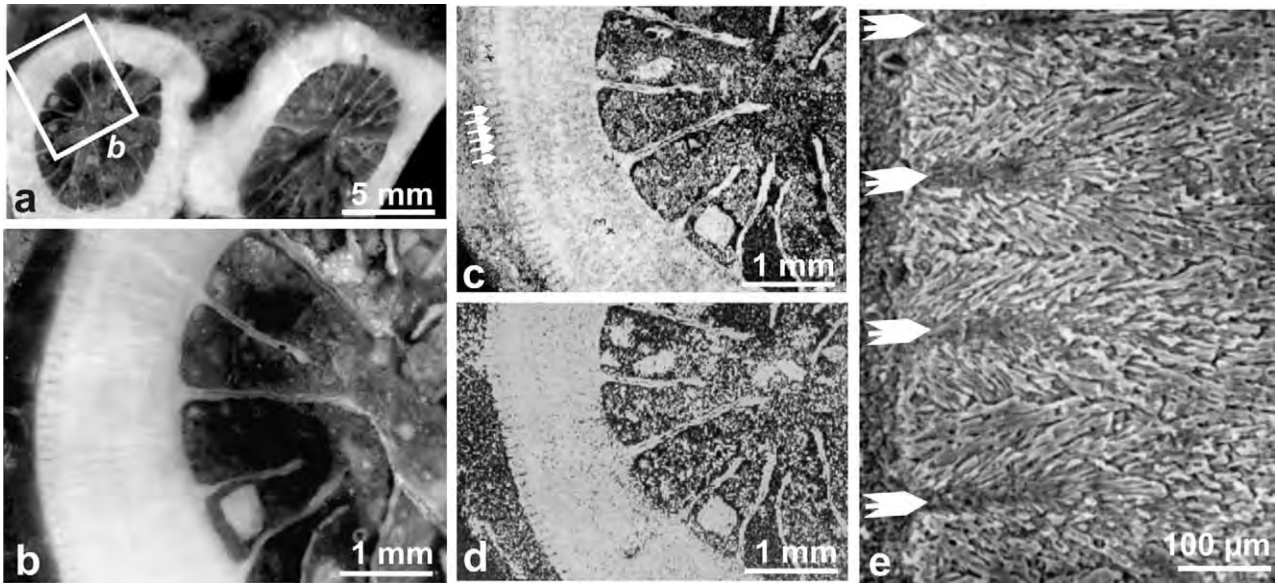

Fig. 1. Main skeletal features of *Solenocoelia cylindrica* (lower Norian, Lycian Taurus, Turkey): (a and b) thick walls in the dendroïd corallites; (c and d) distribution of strontium (c) and sulfur (d)—note the absence of strontium and sulfur in the zones of early mineralization of the fibrous bundles, due to diagenesis of these easily dissolved parts of the coral skeletons; (e) external part of the wall: the early mineralization zones are well shown (arrows) as well as the beginning of the radiating aragonite fibers.

to insure the absence of endolithic borers within the compact fibrous fascicles forming the wall, the skeleton was crushed (calibrated powder 40 µm) and dissolved in progressively acidified water using a pH controlled device (low limit of the pH fixed to 4, to avoid the possible degradation of organic molecules). After centrifugation and lyophilization, the remaining matrix was subjected to biochemical or isotopic characterizations.

3. Results: skeletogenetic process in the most primitive of the Triassic corals: micro- and nano-structual status of skeletal units; biochemical and isotopic properties of skeletal organic matrices

Corallites of the Norian species *Solenocoelia cylindrica* (Fig. 1) are good examples of two of the main properties of the pachythecalid corals. Walls are always the main component of the corallites (Fig. 1a and b), and they are built by inward growing bundles of fibers. The origins of bundles are located at the periphery of the wall (see arrows in Fig. 1c–e, for example). A SEM view (Fig. 1e) clearly shows the basis of these parallel and densely associated bundles, which built a perfectly compact thick wall.

Distributions of sulfur (0.4% weight) and strontium (0.7% weight) illustrate the exceptional preservation of these skeletons. Aragonite fibers have preserved minor element concentrations close to those measured in skeletons of extant corals. The early mineralization zones of the fiber bundles in the walls and the median plan of the septa are practically dissolved and recrystallized, however.

Pachythecalis major exhibits comparable skeletal features with a considerable hypertrophy of the wall structure. The concentric pigmented zones visible on polished sections of the wall (Fig. 2c), demonstrate the well-coordinated growth of parallel (in fact, weakly radiating) fiber bundles (Fig. 2d). When cut obliquely, the fiber bundles show a rather regular alternation of the fibrous fascicles, a feature accentuated by observation with polarized light (Fig. 2f). The septa are built by fiber fascicles inserted perpendicular to the median plane (Fig. 2e), which is usually dissolved in spite of the excellent preservation of aragonite in these outcrops. Noticeably, the septa are inserted at and on the internal surface of the wall. They do not participate in the wall structure in any way (Fig. 2c and e). This particular feature begins right at the early beginnings of skeletal development (compare Figs. 2g and 5a).

Because of the extremely thick wall of this species, extraction of the skeletal matrices from the massive aragonite structure was possible: no significant contamination by sediment has occurred as shown by the pure blocky calcite infilling of the internal cavities of corallites.

Thermo-gravimetric analyses (TGA) reveal that organic compounds are still present within the thick wall of *Pachythecalis* at significant levels (compared to modern corals, Fig. 3a). Water is still associated with the organic compounds, as indicated by the intense and short IR absorption peak correlated to the first decay of organic material during heating, at about 300 °C (Fig. 3b). First analyses of the remaining organic matrices confirm the high degree of preservation of skeletal tissues. As in recent corals, aspartic and glutamic amino acids are still present in large amounts (Gautret and Marin, 1993), suggesting their role in the biomineralization process. Recently, measurements of the δ^{15}N ratio within these matrices (Fig. 3c) make possible a definite statement on the symbiotic metabolism of Pachythecalids (Muscatine et al., 2005). Additionally, synchrotron radiation mapping carried out at 2.4825 keV, with XANES peak typical for organic sulfates (Cuif et al., 2003b) showed that not only proteins but also sulfated polysaccharides are preserved in these Triassic skeletons (Fig. 3d).

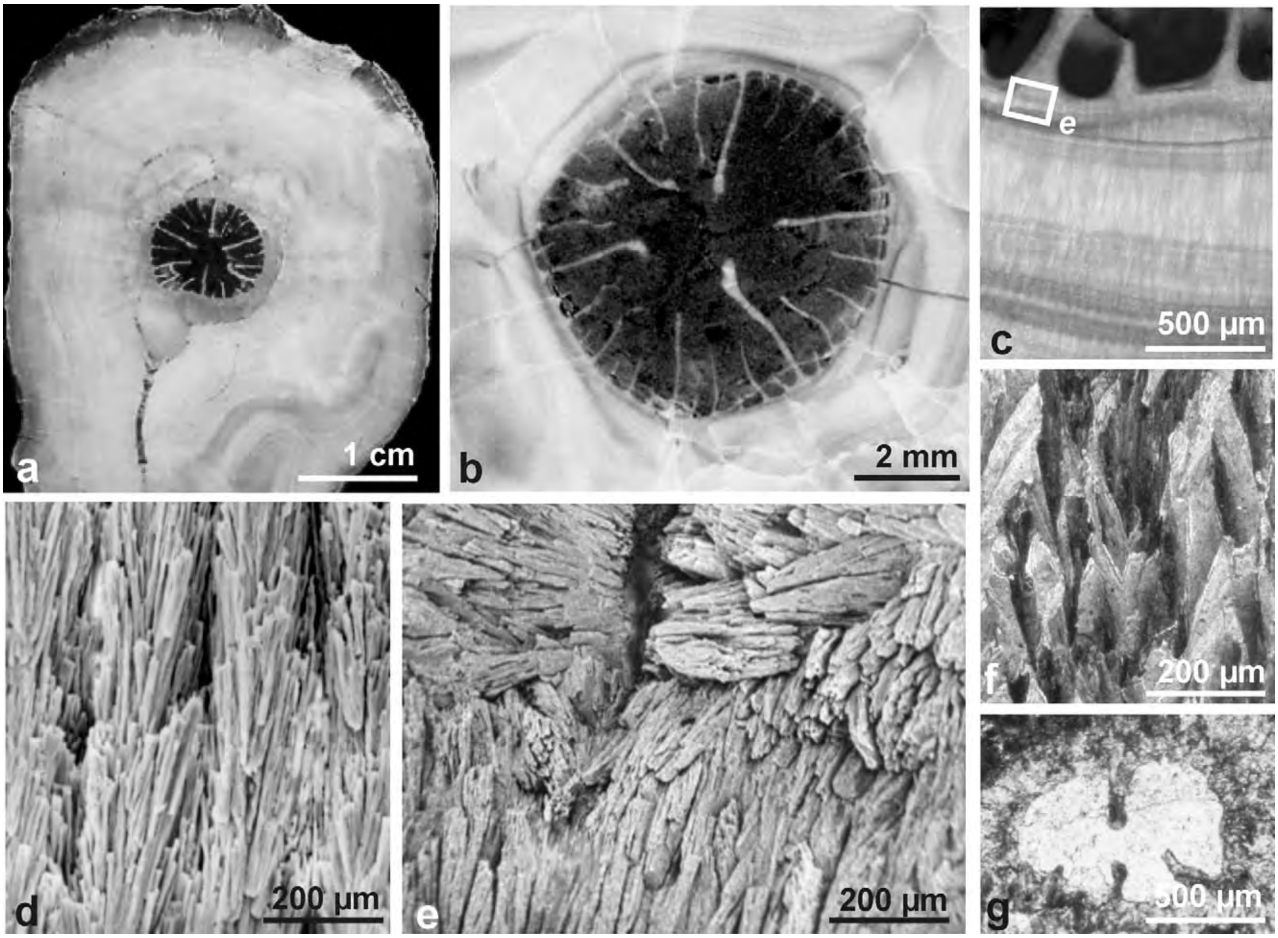

Fig. 2. Main features of the genus *Pachythecalis*: (a and b) section perpendicular to the growth axis of the calyx; (c and d) pigmented traces of regular growth steps within the wall, perpendicular to the parallel fiber bundles; (e) contact between septa and wall (see c). The inner ends of the fiber bundles of the wall (lower part of the picture) are nearly perpendicular to the most external fiber fascicles of septa. Note the empty median plan of the septa; (f) the "zigzag" pattern of the wall fibers is due to the neighboring of the closely packed inward growing fiber bundles. In each of them, fibers diverge from the axis, producing angular pattern between the fibers of neighbor bundles; (g) the lowest section obtained in a *Pachythecalis* corallite. Between this early section and the latest (b, this figure), no evidence of a purely serial or cyclic septal insertion is visible.

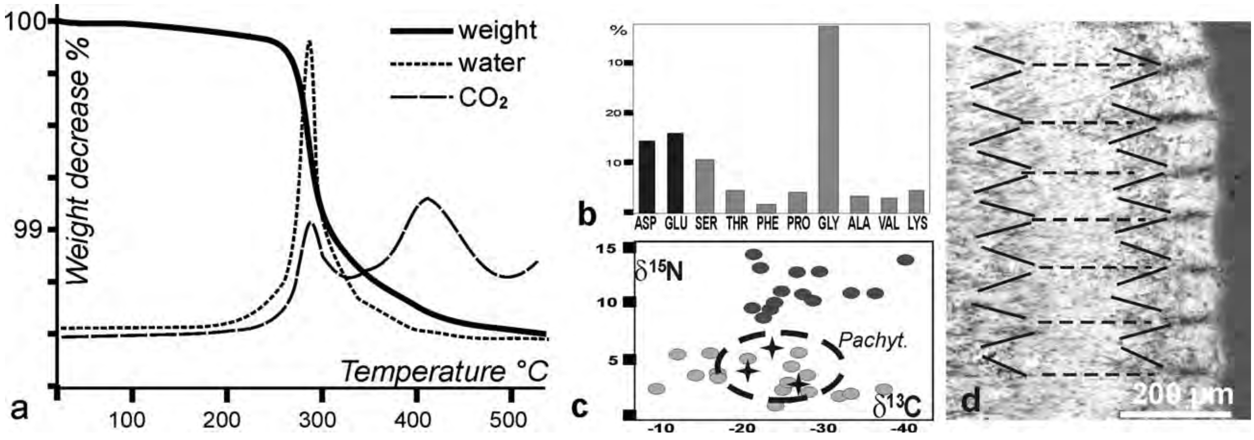

Fig. 3. Biochemical features of the skeletons in the Pachythecalidae. (a) TGA analysis of skeletal wall of *Pachythecalis major*. Weight loss, water and CO_2 emissions during heating are quite comparable to what is measured in recent corals, but with a reduced amplitude of about half. (b) Graph of amino acid proportions in isolated matrix from *Pachythecalis*: in black, aspartic and glutamic aminoacids. (c) Measurements of $\delta^{15}N$ in the matrix obtained from *Pachythecalis*. Stars indicate the position of *Pachythecalis* among photosymbiotic corals. (d) Distribution of sulphated polysaccharides (white surfaces) indicates that organic sulphates are still present within the aragonitic fibers.

4. Discussion: the status of Pachythecalid corals: wall/septa relationships as a major evolutionary process—the concept of Scleractinia in the light of recent data

4.1. Microstructural similarities between Pachythecalids and Permian Polycoelids

The most striking feature of the Pachythecalid corallites is the structure of the wall and the mode of septal insertion. Throughout growth, the thick inward-growing wall is formed before appearance of the septa, as shown by the relationships between the inner end of fiber bundles of the wall and the external part of the septa. Therefore, despite the position of the wall, which seems to rely upon the outer margin of the septa, the wall of Pachythecalids cannot be characterized as epithecal. Actually, epitheca is deposited by the basal ectoderm of the polyp on the external side of septa, and this obviously implies that the septa were previously built. No arrangement equivalent to Pachythelid wall/septa status has been described among the post-Triassic corals, except for the very atypical Guyniidae recently re-described by Stolarski (2000).

In contrast, several Permian corals of the family Polycoelidae demonstrate the closest similarity to the Pachythecalids as exemplified by microstructures in *Polycoelia angusta* and *P. clausa* (Fig. 4) from the Permian outcrops of Basleo, Timor (collection of the Münster Geologisch-Paleontologisches Institute). In both examples, the inward growing fiber fascicles constructed the wall before the beginning of septa formation, resulting in the insertion of the septa against the internal surface of the wall. Clearly, as in Pachythecalids, the septa are here produced by the polyp *after* completion of the wall. At times, when early mineralization zones of the septa begin to be formed, the fiber bundles of the septa continue to grow for a short time. As the septal fibers develop on both sides of the early mineralization zone, growth of the wall fibers stops progressively, leading to a V-shaped insertion of the septa (Fig. 4d and e: arrows; compare to Fig. 2e *Pachythecalis* and Fig. 5a–e, other Pachythecalids).

Also typical for the Polycoelids is the growth mode of septa. In sections perpendicular to growth direction, they appear to be formed by a small number of superposed growth stages (up to 3–4 in the longest septum). Each growth stage consists of fibers growing perpendicularly to the median plane, without any radiating arrangement, except at the beginning and the end of each growth stage. After completion of a stage, the next one is simply superposed on the previous one (Fig. 4d: sequence gs1–gs2–gs3). Such septal morphology and growth mode is similar in the Pachythecalidae (Fig. 5a–c). The overall aspect of walls and septa in *Zardinophyllum zardinii* (Montanaro-Gallitelli, 1973) suggests an analogous organization of the skeletal fibers, supported by the arrangement observed in *Gallitellia* from the Dolomite outcrops (Fig. 5b).

Thus, not only overall morphology but also fine-scale arrangements of the skeleton components in both wall and septa reveal a similar control on the skeletogenetic activity of the

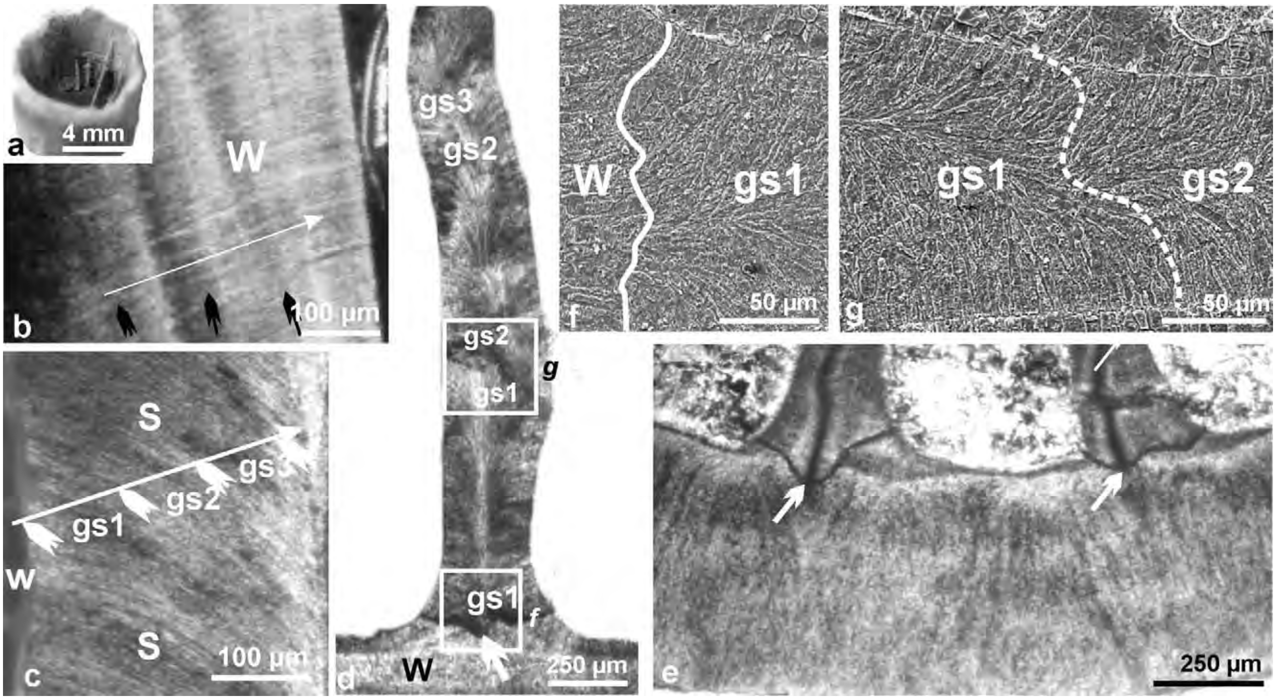

Fig. 4. Wall/septa relationships in the light of microstructure analysis of Permian Polycoelid corals: (a) calicinal view of *Polycoelia angusta*; (b) inward/upward growing fibers in the wall (W) of *P. angusta*. Note the large gray growth zonation (black arrows); (c) growth sectors (gs1, gs2, gs3) in the septum of *P. parva*. Arrows show the contact between growth sectors. Equivalent views are visible on the transversal section (d) and two of them detailed in (f) and (g); (d and e) overall view of a wall/septum contact in *P. angusta* (d) and closer view of this contact (e) to be compared to Fig. 2e, an equivalent area in the *Pachythecalis*; (f and g) detail of two successive growth sectors of the septum. The wall septum contact W-gs1 (f), and contact between the growth sectors gs1 and gs reveal the absence of microstructural differentiation within the fibrous skeletal material, to be compared to Fig. 5a and b, microstructure of Triassic Pachythecalid corals.

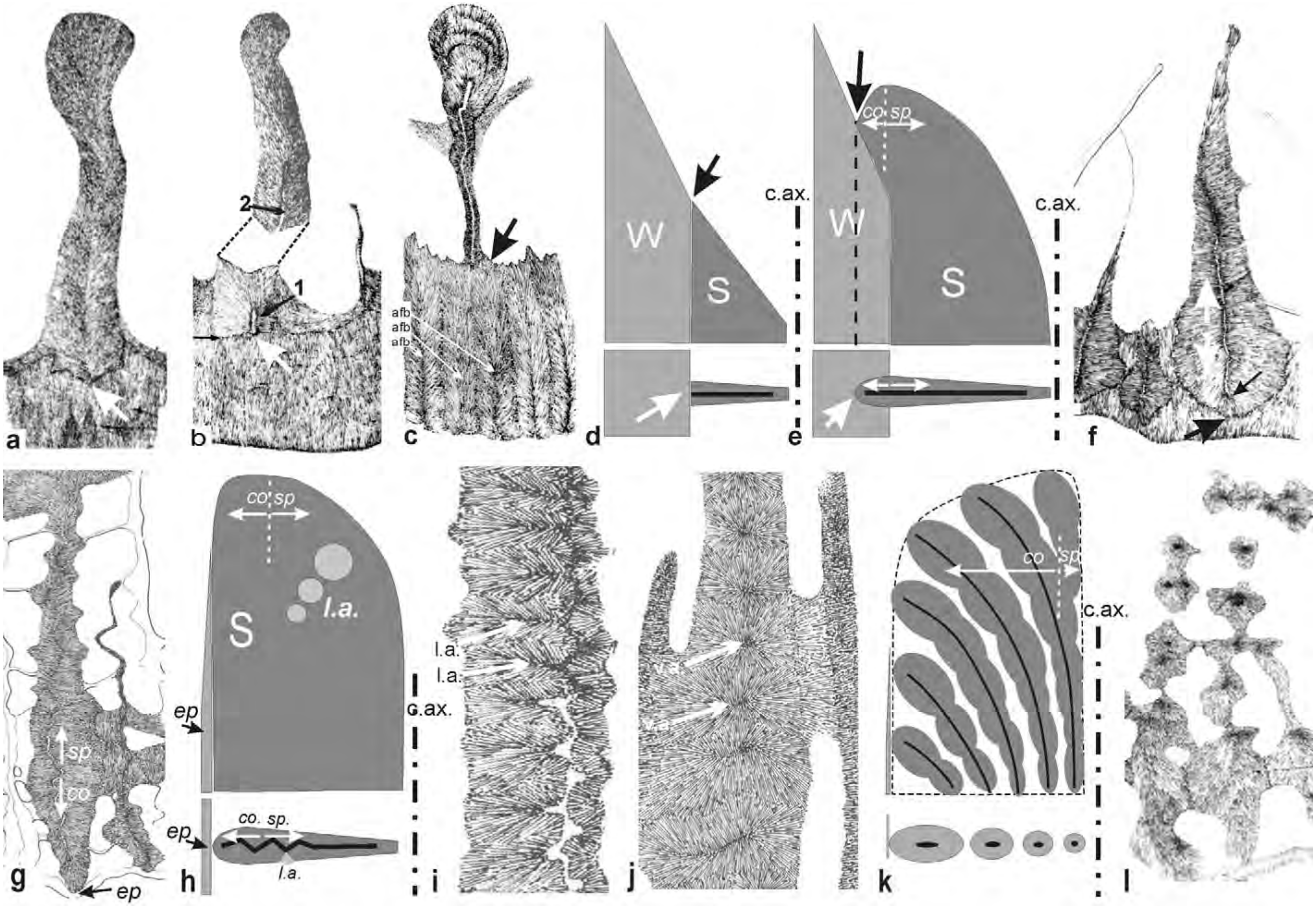

Fig. 5. Scheme of evolutionary changes in the wall/septum relationships and differentiation of septal microstructures among the Triassic corals: (a and b) microstructures of septa in *Gallitellia*, a Pachythecalid from the Dolomites (a: young and b: adult stages); (c) *Pachydendron*, a pachythecalid; with characteristic microstructure made of parallel and closely packed axial fiber bundles (afb) producing the typical zigzag pattern; (d) wall/septal scheme for Pachythecalids (c.ax.: corallite axis, w: wall, s: septum); (e and f) wall/septal scheme for Volzeid corals (note the origin of the costal part at the top of the septa (co), still small compared to the septal part (sp); (g and h) retiophyllid corals. The costal part of septa is now well developed and a true epitheca exists (ep), lying onto the outer part of the septa; (i) microstructure of a *Distychophyllia* coral. Formation of laterally growing fibrous axes (l.a.) inserted onto the zigzag median plan (partly dissolved in this figure) is now a regular feature in this group; (j) section of a septa in a truly trabecular coral (*Craspedophyllia*). The median plan is not longer continuous, but separated into distinct vertical axes (v.a.). Note that lateral axes continue to be produced; (k and l) septal scheme (k) and microstructure (l) in *Araiophyllum* showing the porous septal structure and the trabecular axes bending outwards.

basal ectoderm in the Pachythecalidae and the Polycoelidae, as described by Schindewolf (1942) in the Late Permian corals. Attention must be drawn on the term "zigzag" structures, used by Schindewolf. These patterns are influenced by diagenetic process and seems to be linked to recrystallization in environments with high magnesium contents (see for instance Webb and Sorauf, 2002). However, in aragonitic walls of Pachythecalids, contacts between the adjacent V-shaped fiber bundles produce closely comparable patterns (see Fig. 3d) in absence of recrystallization as attested by minor element concentrations and biochemical characterizations.

From an evolutionary viewpoint it seems unlikely that during the basal Triassic Period, the commonly hypothesized "newly calcifying anemones" starting a new calcification process *de novo* might have developed a skeleton so obviously similar to what was produced, about 10 million years earlier, by corals of the Late Permian lineages after several tens of million years of evolution.

During recent years, several molecular studies led to the conclusion that the origin of the modern corals is much older than Middle Triassic (Romano and Cairns, 2000). Remarkably, the proposed dates converge towards the early part of the late Paleozoic (Late Devonian to Early Carboniferous). For instance, Medina et al. (2006) indicate a possible origin "at least 300 million years" BP. All these studies conclude that from these middle Paleozoic times up to the Middle Triassic, ancestors of the Scleractinia were "naked anemones". Comparative microstructural studies of the fossil support another equally consistent hypothesis. The first Polycoelids are reported from the Late Devonian-Early Carboniferous times (Hill in Wells, 1956). Thus, if as suggested by microstructural data, some Polycoelids are ancestors of the Triassic Pachythecalids and modern corals derive from this family, molecular information regarding the date of origin of modern corals is in close agreement with paleontological studies. In this view, corals as "naked anemones" may have existed only during the almost general gap of fossil data, in the lower Triassic. Disappearance of Polycoelids in the Late Permian due to a gradual decrease in mineralization related to a change in sea water chemical composition is a much more probable hypothesis. With additional negative consequences on the fossilization process, this led to the decrease of documentation during the Early Triassic. It has been shown that a lowering of sea water pH by only 0.1–0.2 points (by increasing the pCO_2 in controlled aquaria) results in a very visible reduction of the calcification process (Marubini et al., 2002). More importantly, Scleractinia has shown a remarkable capacity to survive even when environmental conditions led to a complete suppression of skeletogenesis (Fine and Tchernov, 2007). Such experimental data thus support the conclusion that an interruption of the skeletogenetic process during the Early Triassic may be the actual cause of the gap in coral's evolutionary documentation during this period.

4.2. The rapid radiation of the Triassic corals: from a primitive "rugosan" scheme to fully perforate septal architecture

Triassic corals exhibit a remarkable microstructural diversity. Extensive analyses (Cuif, 1965, 1968, 1972, 1975, 1977, 1980; Roniewicz, 1974, 1989; Roniewicz and Moricowa, 1993; Roniewicz and Stolarski, 2001; Melnikova, 1968, 2001) have shown that the full range of microstructural organizations is already present in the Lower Norian fauna, from the archaic architectures of the Pachythecalids to advanced corallites with fully perforate septa. Comparative study of the wall/septa relationship suggests a possible pathway followed by this rapid evolutionary radiation. Considering the respective importance of wall and septa among the Lower Norian corals, we can hypothesize an evolutionary process marked by a stepping regression of the walls and simultaneously a progressive prevalence of the septal systems. Actually, between the archaic Pachythecalids and the fully perforate *Araiophyllum*, the main steps in this wall decreasing *versus* septa increasing process, leading to a complete inversion of the architectural role of wall and septa, can be very well documented by the Triassic fauna.

Whatever the diversity of the corals gathered in the Pachythecalidae (Fig. 5a–c), the overall architectural scheme (including that of *Zardinophyllum*) can be summarized by Fig. 5d. The fibrous inward-growing wall is fully formed before occurrence of septae. Closely related corals are gathered in the family Volzeidae (Fig. 5e and f). The septa (at least the major ones) have started a rapid upward development that allows their fibrous skeletons to be produced before the full completion of the wall. In this free-growing part of the septa, not located against the wall (in contrast to typical Pachythecalids), the septal fibers can grow outwards (Fig. 5f: big arrows). This results in the "closure" of the outer part of the septal median line (Fig. 5f: small arrow). In reality, this is the origin of the costal part of the septa (Fig. 5e: *co*). However, in these Volzeid corals, the wall is still a thick inward-growing structure, basically similar to the Pachythecalid wall in spite of a reduced thickness.

In the next main step of this process of architectural/microstructural evolution (Fig. 5g and h), the costal part of the septa becomes of significant importance compared to the septal part. The costal part of septa increases (compared to the Volzeid corals) and, at this stage of the structural evolution of corallites, the true epithecal wall appears, a thin skeletal structure lying on the outermost part of the septum costae (Fig. 5g and h: *ep*). In the basal ectoderm of the polyp, the cellular areas constructing the septal system are now largely prevalent compared to the surface of the cellular areas responsible for construction of the wall. This can be exemplified as the Retiophyllid level (from the *Retiophyllia fenestrata* Frech, 1890). Additionally, the early mineralization line of the septa, which was perfectly rectilinear in Pachythecalid and Volzeid corals (as it was in Permian corals), begins to assume more or less accentuated zigzag patterns. Consequently, the fibrous fascicles are no longer oriented perpendicular to the overall septal plan. True fibrous axes appear, not yet vertical, but laterally oriented, towards the interseptal spaces. Such an organization is well shown by the *Distychophyllum* (Fig. 5i). Then, organization of fibrous axes variously oriented becomes a very common process, leading to the formation of the typical "trabeculae": vertical fibrous axes (Fig. 5j).

The concept of "trabecula" has been included in the reexamination of Scleractinian microstructures by several authors during the last decades, e.g., Alloiteau (1952), Sorauf (1972, 1980, 1983, 1999), Roniewicz and Moricowa (1993), and Stolarski and Roniewicz (2001). Those authors recognized the major value of microstructural features for coral taxonomy, although various opinions exist in interpreting this diversity of structures with more or less typical "trabecular" characters. A microstructure-based classification has been shown to be valuable by comparing microstructural patterns and molecular phylogeny in more than forty type-species of extant corals (Cuif et al., 2003a). But, in contrast to the classical description of septal micro-structures (i.e., Wells, 1956), the various spatial arrangements of fibers in the Scleractinia from the Triassic suggest that the "typical trabeculae" are not the basic (i.e., initial) components of the Scleractinia skeletons. Conversely, they result from an evolutionary process, whose reconstruction may be suggested as a reliable way to approaching a "natural" classification of corals.

The final step in architectural/microstructural evolution of Triassic Scleractinia is illustrated by Lower Norian *Araiophyllum* Cuif, 1975. In these species, the septa are built by distinctly separate fibrous axes ("trabeculae") resulting in a perforate structure. Vertical in the central part of the corallite, these axes bend outwards: septa are then built only by the costae, the septal part being limited to the vertical axes in the corallite center (Fig. 5k and l). Such architecture demonstrates that already in the Lower Norian, the process of radiation had produced the whole type or wall/septa relationships, which were probably repeated throughout the Mesozoic and Tertiary times, with variations that have yet to be deciphered.

4.3. Adjusting the concept of Scleractinia to the present knowledge of fossil data and recent results of molecular phylogeny

Investigations during the last three decades indicate that the Triassic coral fauna is undoubtedly more complex than that sug-

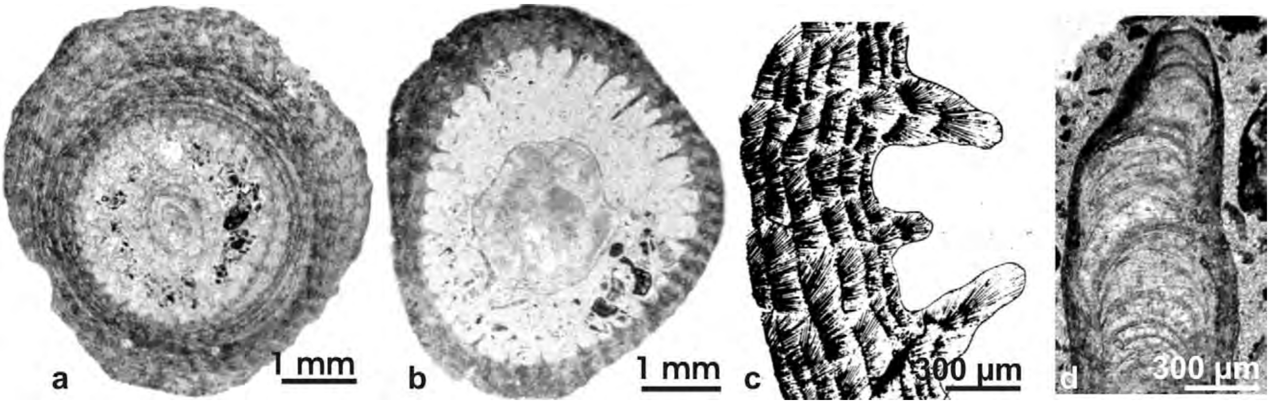

Fig. 6. Skeletal feature of the *Gigantostylis epigonus* Frech, 1890: (a) section of the thick layered inward growing wall; (b and c) septal system composed of very small and undifferentiated septa; (d) longitudinal section of the layered styliform columella.

gested by the diphyletic scheme. The family Pachythecalidae is at present the better known and much consistent group with a well established microstructural affinity to Permian corals. There is little doubt that the isolated species from Western Europe (*Zardinophyllum*, *Gallitellia*) belongs to the same group. Probably other species with such archaic characters exist, as exemplified by *Gigantostylis epigonus* Frech, 1890 from the Rhaetian outcrops at Fischerwiese (Fig. 6). The thick inward-growing wall (Cuif, 1965), the reduced septa, and the large styliform columella led Frech to emphasize these surprising structural characters of this species compared to the numerous modern architectural types.

Others enigmatic types (i.e., Stylophyllids) are present in the Triassic fauna and their possible role in further evolution of corals have been discussed (Stolarski and Russo, 2002). Therefore, we can reasonably admit that several isolated remnants or even groups of corals descending from Late Permian corals were present among the Triassic fauna. Remarkably, Frech, in discussing the position of *Gigantostylis*, emphasized its "rugosan" affinities.

What we see now is that not only surprising exceptions were present among the Triassic corals, but so were significant groups with understandable evolutionary relationships to the other members. Compared to the classical figure by Wells (1956, Treatise part F), a very different picture appears. Triassic faunas were based on remnants from the Paleozoic that seem to have survived at least up to the end of Triassic. We can even ask the question of possible survival of Paleozoic remnants within the extant corals forming the Guyniidae, which have been considered as such by early investigators (Pourtales, 1868). Careful recent studies including microstructural observations (Stolarski, 2000) suggest that this may be the case.

Thus, we are now facing a surprising situation. Clearly the term Scleractinia cannot be applied to the whole of the Triassic fauna, but only to the main part that results from the rapid evolutionary process probably rooted in the family Pachythecalidae. Consistency of the results of molecular phylogeny of modern corals and microstructural analyses of the Triassic corals derived from Pachythecalidae suggests monophyly for this group, supporting its designation by using the term Scleractinia. Besides these Scleractinia *sensu stricto*, the group of the "Paleozoic remnants" cannot definitely be included in Scleractinia. From these two main components of the Triassic fauna, we are not able to evaluate how many have survived the Late Triassic crisis, whose strength has long been underestimated. Very probably, most of the Triassic "rugosa-like" corals have definitely disappeared (except perhaps the Guyniidae).

Conclusively, from both the origin and the Mesozoic history of corals, the lineages described by the Wells' picture have to be re-examined. In addition to a better knowledge of the relationships between lineages throughout this long term history, two major questions remain to be explored to understand the evolution of corals during the Permo-Triassic transition—the mineralogical change in skeleton biomineralization and the long standing problem of septal insertion.

4.4. The question of skeleton mineralogy

Numerous evidences indicate that Paleozoic corals were producing calcitic skeletons. Well-preserved corals presently known from the Triassic outcrops have aragonitic skeletons, thus supporting the concept of a clear-cut difference between Paleozoic and modern corals. However, recent discoveries (Ezaki, 1997, 2000; Wendt, 1977, 1990) demonstrate that the Permian period was marked by occurrence of aragonite in coral skeletons. Biological control of skeletal mineralogy is thus a crucial point in our representation of coral phylogeny.

Investigations throughout the last three decades have revealed the complexity of the biomineralization process. In molluscan species that are simultaneously producing calcite and aragonite (such as the Pteriomorphid bivalve *Pinctada*), recent researches are not able yet to determine the leading factor responsible for selecting the Ca-carbonate polymorph: calcite in the outer layer, aragonite in the inner one. Among the several tenths of proteins that are involved in shell formation (Duplat, 2007), only a few have been isolated from the mineralizing cells of the mantle and their amino acid sequenced. Significantly, the two sequenced proteins were recently shown to be simultaneously present in both calcite and aragonite. Consistently, very informative results have been obtained from pearl cultivation sites, in which grafting operations are carried out all along the year. Very frequently, the small epithelium fragments cut in the mollusk mantle and used as

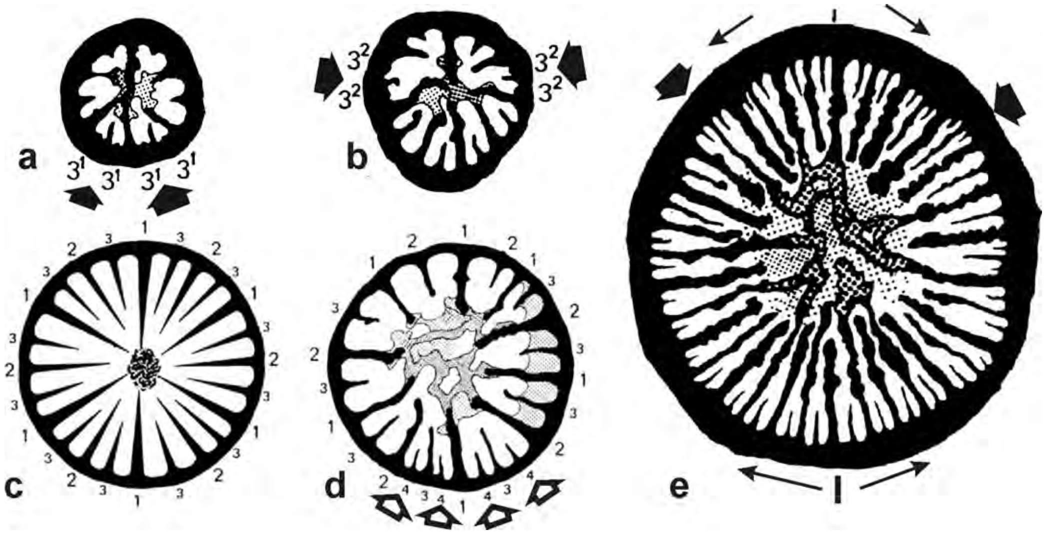

Fig. 7. Septal insertion in *Caryophyllia cyathus*: (a and b) place of appearance of the first (a) and second (b) pairs of third order septa; (c and d) comparison between the original figure from Milne-Edwards and Haime (1848, pl. 4, fig. 1c) here reproduced in (c) and (d) the equivalent serial section whose interpretation is based on previous stages. Note the paired symmetrical appearance of new septa, heterochronic (accelerated) development of which creates the radial aspect of the calices; (e) throughout the whole development of the corallites, the symmetrically paired insertion of the septa is the rule, based on the presence of the two opposite poles. At the skeletal level, this process exactly corresponds to the symmetrical development of the polyp.

a graft to produce the nacreous layer of a new pearl is producing calcite instead of nacre. Additionally, a given graft is able to produce calcite first and then aragonite (Cuif et al., 2008).

In extant corals, biochemical and in situ physical characterization of organic compounds associated with the skeletal fibers at a submicron level has shown the major role of acidic sulphated polysaccharides (Dauphin and Cuif, 1997; Cuif et al., 2003a,b; Cuif and Dauphin, 2005) associated with acidic amino acids (Mitterer, 1978). This is a very common compositional pattern among invertebrates and no clear-cut correlation can be made with production of either calcite or aragonite in the skeletons or shells. Among Cnidaria, calcite is almost constant among Octocorals, except in the aragonitic *Heliopora coerulaea*, showing that the genetic potential of Cnidaria would enable them to produce either calcite or aragonite. What is known about mineralizing matrices in *Corallium rubrum*, for instance (Dauphin, 2006; Allemand, 1993), does not suggest biochemical differences that could be significantly correlated to calcitic mineralogy. Interestingly, a recent mineralogical and microstructural study by Stolarski et al. (2007) has convincingly established that calcitic microstructures (including organic remnants) can be found in perfectly preserved coral skeletons from the Cretaceous.

Clearly, skeletal mineralogy is not able to provide us with reliable phylogenetic criteria.

4.5. *Coral phylogeny and septal insertion*

Haeckel's scheme suggests that during more than 400 million years of the coral evolutionary history, only two types of septal insertions have been used: the serial symmetric during the Paleozoic and the radial cyclic from the Triassic to Recent. Shortly after the publication of Milne-Edwards' classical observations on septal development of *Caryophyllia cyathus*, the radial + cyclic scheme was already criticized. Milne-Edwards never did true ontogenetic analysis but, using a large collection of *Caryophyllia cyathus*, he simply arranged the calicinal faces following the growing number of septa. Biologists dealing with coral embryology (i.e., Lacaze-Duthiers, 1872) have shown that post-larval development is purely bilateral (see Chevalier, 1987 for review). Moreover, a true serial section study was carried out on specimens from the Museum National d'Histoire Naturelle in Paris, from the Milne-Edwards collection, communicated by Dr. Ranson (Laboratoire de Biologie des Invertébrés marins). This study has shown that the septal insertion follows the overall bilateral plan and is not directed by a cyclic scheme: septa appear on a bilateral paired mode (Cuif, 1968). The regular organization visible at the calicinal faces is clearly due to differences in growth rhythm between the successive septal pairs (Fig. 7). To summarize, the living corals seems to be neither radial nor cyclic. Additionally, concerning fossil Scleractinia, note must be made that no serial section is known allowing assessment the "radial-cyclic developmental pattern". In addition to evidence provided by investigations on living corals, this absence of data for a crucial period in the theory is obviously an essential point missing to validation of the Haeckel's diphyletic scheme. Already by Milne-Edwards' time, investigators had observed innumerable exceptions to his "developmental law" and the resulting scheme was rapidly considered obsolete. Concerning the Paleozoic corals, this essential question was marked by some famous controversies focusing on particular examples (Gordon and Duerden, then later between Schindewolf and Yakovlev). Compared to the great diversity of coral faunas throughout the Paleozoic era, homogeneity of septal insertion among the various families is simply postulated and still far from being established on the basis of serial sections. Presently, no one is able to assess the taxonomic efficiency of the ancient schemes whose universality is very doubtful. Suffice to look at the introductive part to Rugosa in the Treatise (Hill, 1956, pp. F234–F256) to see that, after a short recall of the formal dogma, the practical subdivisions are based on other skeletal patterns. No use is made, for instance, of the remarkable investigation carried out by Wang (1950) on microstructures in the Rugosa corals, just a few years before Hill's synthesis. It is truly regrettable that, due to our lack of reliable information, an in-depth knowledge of septal developments cannot be associated with the microstructural patterns, which also reflects the mineralizing activity of the basal ectoderm. As shown by recent progresses in the long-standing question of coral evolutionary history during the Permian-Triassic periods, close association of the molecular results from recent coral studies and ontogenic + microstructural analyses of fossil faunas results in a consistent method allowing improved definitions of the coral major lineages to be established. From this viewpoint, note must be made of the conclusion drawn by Ogilvie (1895), who was the first to demonstrate the impact of a careful analysis of the skeletal microstructures on coral taxonomy. Among the conclusive statements of her pioneering work, she wrote (p. 16): "The author's results bear inevitably to the conclusion that the suborder Madreporaria Rugosa erected by Edwards and Haime draws an entirely artificial barrier between the Paleozoic Madreporaria and the younger suborders". Converging results from very distinct methods bring some support to this statement.

5. Conclusions

1. The Late Triassic coral fauna includes a series of species exhibiting architectural patterns and skeletal microstructures closely similar to some Late Permian corals. Members of the family Pachythecalidae that includes most of these corals were photosymbiotic and produced an aragonitic skeleton.
2. Skeletal organization of most of the Triassic coral families seems to be derived from the skeletal patterns of these Pachythecalids.
3. These Rugosa-like Triassic corals make the traditional concept of Scleractinia ambiguous. A more acceptable position for Pachythecalids (and some other post-paleozoic corals) implies an evolutionary tree involving corals from the upper part of the Paleozoic.
4. Conclusions based on molecular phylogeny supporting both monophyly of the modern corals and their origin in the upper Paleozoic are in agreement with the results of microstructural studies.

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Research paper

Stability strategies and hydrodynamic behavior of liberosessile solitary rugose corals (Ordovician; Red River–Stony Mountain Province, North America)

Robert J. Elias

Department of Geological Sciences, University of Manitoba, Winnipeg, MB, R3T 2N2, Canada

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Abstract

In the Late Ordovician Red River–Stony Mountain Province of North America, four closely related genera of solitary rugose corals are represented exclusively by liberosessile species: *Salvadorea*, *Grewingkia*, *Deiracorallium*, and *Lobocorallium*. These rugosans benefitted from innovative and in some cases unique strategies involving corallum form, which improved stability with respect to the substrate and currents, and took advantage of water flow during life. Trochoid form was a compromise for ensuring adequate stabilization of the corallum by sediment, while keeping the calice rim sufficiently elevated above the substrate. In life orientation with the convex cardinal side of the corallum facing down, triangulate and trilobate cross-sectional shapes offered resistance to lateral tipping or rotation. Depressed coralla resisted gravity-induced subsidence or tilting. With the convex side facing downcurrent, the streamlined shape of compressed and triangulate forms improved stability by reducing drag. Trilobate form may have had a drag-reducing "splitter plate" effect. Strategies for drag reduction were especially beneficial for corals inhabiting relatively high-energy environments, but the greatest significance may have been in reducing fatalities due to dislodgement during storms. The hydrodynamic behavior of coralla in life position, especially if leaning downcurrent, resulted in beneficial water flow. Vortices ascending from the substrate on the downcurrent side provided the polyp with water drawn from both the mainstream and the substrate surface. Such circulation facilitated feeding, enhanced the quantity and variety of food, and delivered other necessary substances. Wastes and gametes could be effectively expelled from the polyp and removed downcurrent without entrainment into the food-bearing flow. Functional analysis of the fascinating range of corallum forms in the Red River–Stony Mountain Province provides insight into paleobiology and paleoecology, which is applicable to many Paleozoic solitary rugosans.

Keywords: Solitary corals; Corallum shape; Functional morphology; Paleobiology; Paleoecology

1. Introduction

The vast majority of Paleozoic solitary rugose corals can be considered liberosessile (Neuman, 1988; Scrutton, 1998). Although most, if not all, liberosessile individuals were initially attached to relatively small objects, either they became detached or the objects were insufficient to provide support throughout life. The corals consequently lived free on soft substrates, depending on sediment to support the corallum with its calice in an orientation that was suitable for the polyp. Sessile benthic organisms such as corals rely on water flow to bring food items and necessary substances, as well as to remove wastes and spread gametes, but they also risk being overturned or transported by hydrodynamic forces (Wainwright and Koehl, 1976). Liberosessile solitary rugosans are rarely preserved in life position; death is attributed mainly to overturning, transportation, and/or burial during high-energy storm events (Scrutton, 1998). These corals would have benefitted from strategies that improved stability with respect to the substrate and currents, and that took advantage of water flow during life.

The purpose of this paper is to examine some innovative strategies involving the corallum form of liberosessile solitary rugosans. External form and its variation in such corals have been considered mainly in the context of adaptation to the substrate and enhancement of stability, in some cases in response to current strength (Scrutton, 1998). The present study goes further, by also considering the hydrodynamic behavior of coralla

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E-mail address: eliasrj@cc.umanitoba.ca.

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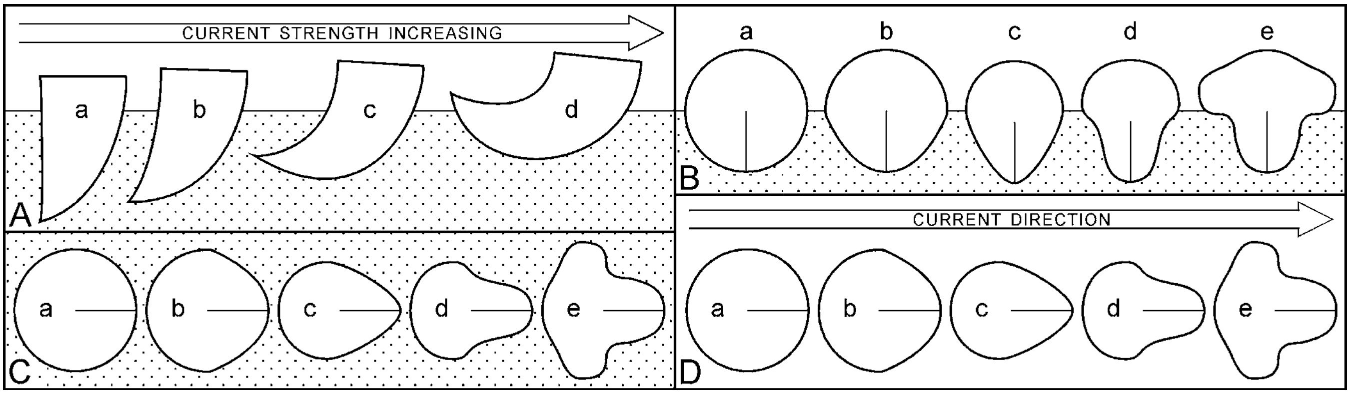

Fig. 1. Various views of liberosessile solitary rugosan coralla in life position. (A) Lateral views (cardinal side convex) showing orientation with respect to substrate-water interface (sediment stippled) and current direction (arrow), and relation between current strength (see arrow) and curvature of corallum (a, very weak; b, weak; c, moderate; d, strong). (B) Cross-sectional views (vertical orientation) of recumbent coralla (line is cardinal septum), showing orientation with respect to substrate-water interface (sediment stippled) and various cross-sectional shapes (a, circular equidimensional; b, triangulate equidimensional; c, triangulate compressed; d, trilobate compressed; e, trilobate depressed). (C) Cross-sectional views (horizontal orientation just below substrate-water interface; sediment stippled) of upright coralla (line is cardinal septum; cross-sectional shapes a–e as in B). (D) Plan views of calice rims (above substrate-water interface; line is cardinal septum; cross-sectional shapes a–e as in B), showing orientation with respect to current direction (arrow).

in life orientation and its possible benefits to the polyps. The findings of this functional analysis expand our understanding of the paleobiology and paleoecology of these extinct corals.

This paper focuses on particular liberosessile solitary rugosans in the Late Ordovician (Cincinnatian) Red River–Stony Mountain Province of North America. This biogeographic province occupied a vast area of predominantly carbonate deposition in the epicontinental sea and on the adjacent continental shelf (Webby et al., 2004). Among the characteristic solitary rugose corals are four closely related genera that are represented exclusively by liberosessile species: *Salvadorea*, *Grewingkia*, *Deiracorallium*, and *Lobocorallium*. This group exhibits a fascinating range of corallum forms; the trilobate cross-sectional shapes of *Lobocorallium* and some representatives of *Grewingkia* are unique among corals in general. Major publications in which these taxa are described and illustrated include Nelson (1963, 1981), Elias (1981, 1982a, 1983, 1985), and Buttler et al. (1988).

2. Corallum form and variability

As seen from the side and in cross-section, corallum form varies within and among *Salvadorea*, *Grewingkia*, *Deiracorallium*, and *Lobocorallium* in the Red River–Stony Mountain Province. The shape in lateral view is generally trochoid, but curvature is variable (Fig. 1A) as follows: *Salvadorea* (very weak to strong, usually weak), *Grewingkia* (weak to strong, usually moderate), *Deiracorallium* (very weak to moderate, usually weak to moderate), and *Lobocorallium* (weak to strong, usually weak to moderate). Coralla are smoothly curved in the cardinal-counter plane, with the cardinal septum on the convex side and the calice rim perpendicular to the direction of growth. The ranges of maximum corallum length attained by species of these genera are as follows: *Salvadorea* (50–75 mm, exceptionally 120 mm), *Grewingkia* (75–180 mm), *Deiracorallium* (22–88 mm), and *Lobocorallium* (125–150 mm).

In addition to the circular cross-sectional shape that is typical of solitary rugose corals in general (Fig. 1Ba), this group of genera exhibits a range from triangulate (V-shaped convex side; Fig. 1Bb, c) to trilobate (lobate convex and lateral sides; Fig. 1Bd, e). The degree of triangulation or trilobation in individual coralla commonly increases and then decreases progressively during ontogeny. With respect to cross-sectional dimensions in the cardinal-counter and lateral directions, coralla may be equidimensional (typical of solitary rugosans in general; Fig. 1Ba, b), compressed (laterally narrow; Fig. 1Bc, d), or depressed (laterally broad; Fig. 1Be). Cross-sectional variability of coralla is as follows: *Salvadorea* (generally circular, slightly triangulate in some; equidimensional), *Grewingkia* (usually triangulate, some circular or trilobate; generally equidimensional to compressed, some depressed), *Deiracorallium* (commonly triangulate; compressed), and *Lobocorallium* (trilobate; compressed to depressed).

3. Orientation during life

Virtually all liberosessile solitary rugose corals in the Red River–Stony Mountain Province are preserved in orientations that are consistent with deposition following transportation (Elias et al., 1988). Their life orientations were initially reconstructed using various lines of indirect evidence: location of associated boring and epizoic organisms inferred to be symbionts, location of bioclastic material partially embedded in the corallum wall during growth, location and orientation of the initial attachment site, and functional considerations (Elias, 1984). Verification was provided by the discovery of two specimens preserved incontrovertibly in life position beneath large colonial corals, which shielded them from high-energy events that transported other individuals (Elias and Buttler, 1986). Subsequently, in situ coralla were documented from a unique deposit that accumulated under relatively low-energy conditions (Elias et al., 1988).

During life, the cardinal-counter plane of the corallum was vertical, the convex side was down, and the calice rim was horizontal or nearly so (Fig. 1A). There was gradation from very weakly curved coralla positioned upright with the apical portion buried in sediment (Fig. 1Aa), to weakly and moderately curved coralla partially buried in increasingly tilted positions (Fig. 1Ab, c), to strongly curved coralla recumbent on the substrate (Fig. 1Ad). The upper portion of the corallum generally rose above the substrate so that all sides of it were exposed to the water column (Elias et al., 1988). In some cases, mainly involving small coralla, the calice rim was near or at the substrate surface on the convex side (Elias, 1982b). This may indicate that the calice rim was inclined slightly downward on the convex side and/or that sediment was scoured from the concave side and deposited to a higher level on the convex side of the corallum. For large, strongly curved forms that were recumbent on the substrate, the calice rim was situated a considerable distance above the substrate surface (about 4 cm in the case of a specimen preserved in life position; Elias and Buttler, 1986, fig. 2a).

A positive relation between the degree of corallum curvature and current strength (Fig. 1A) has been inferred from examinations of the intensity of abrasion of corallum exteriors (Elias and Buttler, 1986). Evidence of preferential orientation of the cardinal-counter plane with respect to unidirectional currents was provided by a unique occurrence that includes coralla preserved in life position, coralla that are in situ but tilted to a more prone position, and transported coralla in horizontal depositional positions (Elias et al., 1988). The convex cardinal side was downcurrent during life (Fig. 1A), according to the paleocurrent direction indicated by the tilted and transported coralla.

All solitary rugosans in the Red River–Stony Mountain Province lived above storm wave-base, and the liberosessile forms were especially susceptible to overturning and transportation during high-energy events (Elias et al., 1988). Such incidents were fatal because these corals lacked the ability to grow upward from the resulting depositional orientations, as indicated by the absence of high-angle bends during growth (Elias, 1984).

4. Stability strategies with respect to substrate

Adaptations for maintaining a suitable, stable orientation with respect to the substrate-water interface are of fundamental importance to sessile benthic organisms facing the problems associated with life on soft sediment (Thayer, 1975). “Iceberg” strategies that provide buoyancy and stability by partial submergence in the sediment, and “snowshoe” strategies that increase the bearing area on the substrate, have been identified in numerous modern and ancient taxa (Thayer, 1975). In the case of liberosessile solitary rugose corals, such strategies can be recognized in various accounts of adaptation to the substrate and enhancement of stability involving corallum form (Elias, 1984; Neuman, 1988; Scrutton, 1998; Sorauf, 2001).

For *Salvadorea*, *Grewingkia*, *Deiracorallium*, and *Lobocorallium* in the Red River–Stony Mountain Province, corallum shape seems to have been important in maintaining stability with respect to the substrate. The moderately expanding trochoid shape that is typical of these corals (Fig. 1A) may have been an effective compromise for ensuring that an appropriate proportion of the corallum was buried within or rested upon the sediment, while the calice rim remained sufficiently elevated to keep the polyp a suitable distance above the substrate. A trochoid shape would have provided greater resistance to subsidence than a narrowly expanding ceratoid shape, and a greater vertical component of growth than a broadly expanding turbinate shape.

Compared with coralla having a circular cross-sectional shape (Fig. 1Ba, Ca), the triangulate and trilobate forms (Fig. 1Bb–e, Cb–e), especially if compressed (Fig. 1Bc, d, Cc, d), would have offered greater resistance to lateral tipping or rotation from life position on unstable substrates (Elias, 1984). In particular, the lobe on the convex side of a trilobate corallum likely served as a stabilizing keel in the sediment (Fig. 1Bd, e, Cd, e). The lateral lobes of such a corallum would have resisted gravity-induced subsidence or tilting (Elias and Buttler, 1986). Depressed coralla (Fig. 1Be, Ce) would have provided a broader base of support than forms with equidimensional or compressed cross-sectional shapes.

5. Stability strategies with respect to currents

Many benthic marine organisms are subjected to unidirectional currents or to bidirectional flow related to tides and waves (Wainwright and Koehl, 1976; Koehl et al., 2001). Drag, the hydrodynamic force that pushes an object downcurrent, can result in dislodgement (Koehl, 1984, 1996). As sessile organisms grow larger and rise higher above the substrate into the velocity gradient of the benthic boundary zone, they are subjected to increasing drag (Wainwright and Koehl, 1976; Koehl et al., 2001). Therefore, drag-reducing shapes and orientations become increasingly important. A shape and orientation that places most of the object’s surface area parallel to flow will reduce the size of the downcurrent wake and therefore decrease drag (Koehl, 1984; Koehl et al., 2001). A streamlined shape, with the blunt end upcurrent and the elongated, tapered end downcurrent, minimizes drag in unidirectional currents (Koehl, 1977; Vogel, 1994; Koehl et al., 2001). Such a shape is also somewhat beneficial if the flow direction is reversed (Vogel, 1994).

Strategies with drag-reducing potential are apparent in the case of the Red River–Stony Mountain solitary rugosans. Compared with coralla of *Salvadorea*, which are equidimensional in cross-section (Fig. 1Da, b), the compressed forms that characterize *Deiracorallium* and are common in *Grewingkia* and *Lobocorallium* would have decreased drag when oriented with the cardinal-counter plane parallel to flow (Fig. 1Dc, d). In addition, triangulation is characteristic of *Deiracorallium* and common in compressed coralla of *Grewingkia* (Fig. 1Dc). The streamlined shape of such corals, oriented with the elongated, V-shaped cardinal side downcurrent, may have minimized drag and thereby enhanced stability. Interestingly, paleoecologic and taphonomic studies suggest that *Salvadorea* preferred lower energy conditions than *Grewingkia*, *Deiracorallium*, and *Lobocorallium* (Elias, 1991).

Depressed coralla, oriented with the broad counter side upcurrent, would have maximized drag and seemingly been disadvantageous in terms of stability with respect to currents (Fig. 1De). It is noteworthy that depression is far less common than compression, and is most pronounced in some coralla of *Lobocorallium*, which are characteristically trilobate, and in some trilobate coralla of *Grewingkia.* The lateral lobes of such corals would have provided resistance to downcurrent tilting in the substrate (Fig. 1Be, Ce), possibly compensating for the increased drag due to their depressed form.

There may also be another reason for the association between depression and trilobation. A flat “splitter plate” or similar structure extending along the downcurrent side of an object restricts circulation in the wake and reduces vortex size, thereby decreasing drag (Chamberlain, 1976). In the case of a cylindrical object having a circular cross-section, drag is minimal when the length of the plate in cross-section equals the diameter of the cylinder (Apelt et al., 1973; Anderson and Szewczyk, 1997). Perhaps trilobate form in *Lobocorallium* and some coralla of *Grewingkia* resulted in drag reduction, due to the cardinal lobe protruding downcurrent from the broader counter side of the corallum (Fig. 1Dd, e). In cross-section, the ratio of length of the cardinal lobe to width of the corallum tends to increase from depressed forms (Fig. 1De) to compressed forms (Fig. 1Dd), approaching 1:1 and possibly enhancing the “splitter plate” effect.

Presumably, drag-reducing shapes and orientations were especially advantageous for corals inhabiting relatively high-energy environments. Regardless of the normal energy level, however, the greatest significance of such strategies may have been in reducing fatalities due to overturning or dislodgement during all but the most intense storms. Adaptation for extreme, rather than normal, flow conditions seems to be most important to organisms (Vogel, 1981; Koehl, 1996).

6. Hydrodynamic behavior and beneficial water flow

In addition to strategies for minimizing the effects of water flow (see Section 5), maximization of flow in suitable ways has been recognized in studies of modern cnidarians (Wainwright and Koehl, 1976; Koehl, 1977). Corals are mainly passive suspension feeders, depending primarily on ambient water movement to bring food items to their tentacles (Wainwright and Koehl, 1976; Vogel, 1981; Koehl et al., 2001). The effect of the coral’s morphology on flow is therefore important. Coralla of *Salvadorea*, *Grewingkia*, *Deiracorallium*, and *Lobocorallium* in the Red River–Stony Mountain Province can be thought of as conical to cylindrical objects that rose from the substrate into the water column, with the cardinal side downcurrent during life (Fig. 1A). The degree to which they were tilted in a downcurrent direction seems to have been related positively to the general current strength of the environment. The polyp in the calice faced directly upward or slightly downcurrent. Presumably, the polyp had two rings of tentacles (corresponding to the major and minor septa) for feeding, an axially located mouth for ingestion of food, and possibly a slit above the fossular structure on the cardinal side, for expulsion of wastes and gametes (see Fedorowski, 1997).

A cylindrical object rising from the substrate into a velocity gradient has a significant effect on water flow (Friedrichs, 2004). Of particular importance is the pattern of circulation on the downcurrent side, which is enhanced if the object is tilted downcurrent (Vogel, 1994). A pair of vortices rotating in opposite directions ascends from the substrate to the top of the object (Vogel, 1994, fig. 10.7). This circulation pattern does not depend strongly on flow regime, current velocity, object shape, or height to which the object rises above the substrate (Carey, 1983; Gili and LaBarbera, 1998). Flume studies of a modern annelid and phoronid show that feeding, by the tentacular structure or lophophore atop the cylindrical body, occurs on the downcurrent side where particle abundance and capture efficiency are maximized (Carey, 1983; Johnson, 1988). Gili and LaBarbera (1998) conducted flume experiments on cylindrical models and conical to cylindrical fossils of Cretaceous hippuritid rudist bivalves. A downcurrent inclination was found to provide the greatest hydrodynamic advantage. In such an orientation, the top of the object was bathed with water drawn from the wake. The strong helical vortices rising on the downcurrent side provided water from both the mainstream flow and the substrate surface, which would have enhanced the quantity and variety of food available to the animal.

It is reasonable to conclude that the hydrodynamic behavior of coralla belonging to *Salvadorea*, *Grewingkia*, *Deiracorallium*, and *Lobocorallium* was comparable to that of other conical to cylindrical objects. In life orientation, the resulting water flow was likely of benefit to the polyp, by facilitating feeding and supplying food and necessary substances from various levels in the water column as well as from the substrate surface. Modern scleractinian corals consume a variety of material including zooplankton, bacteria, particulate organic matter, and sediment (Ferrier-Pagès et al., 2003), and utilization of multiple food types may be a necessity (Palardy et al., 2006).

The cross-sectional shapes of coralla also affected water flow and may have influenced feeding behavior and the sources of food, whether from the mainstream or wake. Compared with a circular cross-section, streamlining moves the point of flow separation toward the downcurrent end of an object, thereby reducing wake size (Chamberlain, 1976, fig. 1b, c; Koehl, 1977). Thus, the proportion of a polyp’s perimeter and number of tentacles that were directly exposed to water from the wake may have been greater for a coral having circular shape (Fig. 1Da) rather than a compressed, triangulate shape (Fig. 1Dc). If a “splitter plate” is present on the downcurrent side of an object, it separates the two vortices of flow (Chamberlain, 1976, fig. 8). Perhaps trilobate coralla oriented with the cardinal lobe downcurrent had a similar effect (Fig. 1Dd, e). If vortices rose in the indentations between the lateral lobes and cardinal lobe, they would have circulated past a significant proportion of the polyp’s periphery, where food items could have been extracted by the tentacles.

In flume studies using models of hippuritids, excurrent flow was simulated from a pair of openings situated near the periphery of the top surface (Gili and LaBarbera, 1998). The excurrent flow passed through and did not mix with the water that was drawn over the top of the object. In the case of *Salvadorea*, *Grewingkia*, *Deiracorallium*, and *Lobocorallium*, it is reasonable to infer that wastes and gametes could have been effectively expelled from the polyp via a slit above the cardinal fossular structure, and removed downcurrent without entrainment into the food-bearing flow.

7. Summary and conclusions

In the Late Ordovician Red River–Stony Mountain Province of North America, the liberosessile solitary rugose corals *Salvadorea*, *Grewingkia*, *Deiracorallium*, and *Lobocorallium* benefitted from innovative and in some cases unique strategies involving corallum form. These strategies improved stability with respect to the substrate and currents, and took advantage of water flow during life. The trochoid shape of these corals may have been a compromise for ensuring that an appropriate proportion of the corallum was stabilized by sediment, while the calice rim remained sufficiently elevated to keep the polyp a suitable distance above the substrate. Triangulate and trilobate corallum forms, especially if compressed, offered resistance to lateral tipping or rotation from life position. Depressed coralla would have resisted gravity-induced subsidence or tilting.

Compressed coralla would have experienced a reduction in drag when oriented in life position with the cardinal-counter plane vertical and parallel to water flow. With the convex side of the corallum downcurrent, the streamlined shape of triangulate forms may have minimized drag and thereby enhanced stability. Perhaps trilobate form, with the cardinal lobe protruding downcurrent from the broader counter side of the corallum, resulted in drag reduction due to the “splitter plate” effect. Drag-reducing strategies would have been especially beneficial for corals inhabiting relatively high-energy environments, but the greatest significance may have been in reducing fatalities due to overturning or dislodgement during storm events.

In life position, a corallum rising as a conical to cylindrical object from the substrate into the velocity gradient of the water column would have significantly affected flow on its downcurrent side, especially if it was tilted downcurrent. A pair of helical vortices ascending from the substrate would have provided the polyp with water drawn from both the mainstream flow and the substrate surface. Such circulation likely facilitated feeding, enhanced the quantity and variety of food, and delivered other necessary substances. Cross-sectional shape of the corallum also affected water flow on the downcurrent side and may have influenced feeding behavior and the sources of food. Streamlining would have reduced the size of the wake, and trilobation may have separated and localized the circulation cells. In all of these corals, wastes and gametes could have been effectively expelled from the polyp and removed downcurrent without entrainment into the food-bearing flow.

Throughout their range in the Paleozoic, liberosessile solitary rugose corals were rarely preserved in life position, so reconstructions of their growth orientation have been largely speculative and have seldom been confirmed. There is general agreement that straight coralla having the calice rim perpendicular to the direction of growth were positioned upright, whereas smoothly curved forms were oriented in tilted to recumbent positions with the plane of curvature vertical and the convex side down (Scrutton, 1998, fig. 14). Various authors have suggested that solitary rugosans were preferentially oriented during life in the presence of prevailing currents, but there is uncertainty as to whether liberosessile curved forms leaned toward the flow with the convex side upcurrent (Scrutton, 1998) or leaned away with the convex side downcurrent (Elias et al., 1988).

The possibility that curved solitary rugosans leaned away from prevailing currents, with the convex side downcurrent, is supported by the present study. Hydrodynamic behavior would have been most beneficial for feeding with the corallum leaning away from the flow, and corallum forms with drag-reducing potential would have been most effective with the convex side downcurrent. Compression of coralla accompanied by triangulation of the convex side occurred in some Ordovician species and later, for example in a few Mississippian species (Easton, 1951, figs. 2, 3, 7–9). It is noteworthy that the cardinal septum is on the convex side in the Ordovician cases, but is on the concave side in the Mississippian ones. Thus, even though the orientations of the polyps were reversed, coralla having the same streamlined external form were produced. Confirmatory evidence that curved liberosessile solitary rugosans leaned away from water flow with the convex side downcurrent is provided by a unique Ordovician occurrence that includes coralla preserved in situ (Elias et al., 1988). Functional analysis of the fascinating range of corallum forms in the Red River–Stony Mountain Province provides insight into paleobiology and paleoecology, which is applicable to many Paleozoic solitary rugose corals.

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Research paper

Does similarity in rugosan characters and their functions indicate taxonomic relationship?

Jerzy Fedorowski *

Institute of Geology, Adam Mickiewicz University, Maków Polnych 16, Pl 61-606 Poznań, Poland

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Abstract

Functional analysis of changes in shape and arrangement of septa in the genera *Zaphrentites*, *Caninia*, and *Ufimia* allows one to move slightly beyond the usual boundaries of description and to ask why the arrangement in *Zaphrentites* is permanent, but becomes radial in *Caninia* and bilateral in *Ufimia*? This may be explained in terms of changing function and biological role of major septa in the ontogeny.

The creation of open space to accommodate strongly developed mesenteries is proposed as an explanation for the shortening and radial arrangement of axially free septa in mature *Caninia*, whereas the development of a slit on an oral disc, increasing water flow through the gastro-vascular cavity, is postulated for *Ufimia*. Both solutions point towards increased effectiveness of feeding and oxygenation, necessary for the growing organism. Such a conclusion negates the simple application of a given arrangement of septa as an indicator of taxonomic relationship.

Keywords: Rugosa; Functional analysis; Arrangements of septa

1. Introduction

Plotnick and Baumiller (2000) summarized a long-lasting debate concerning the credibility of functional analysis in palaeobiology. They distinguished the following aspects of the analysis:

1. *Feature*: any aspect of an organism, including morphological, behavioural, and physiological attributes.
2. *Form*: the appearance, configuration, composition, shape, etc. of a feature.
3. *Function*: what a feature does or how it works. A given feature can have multiple functions.
4. *Faculty*: the combination of a given form and a particular function. It is defined as "what the feature is capable of doing in the life of the organism".
5. *Biological role*: how the organism uses the faculty during its lifetime, in the context of its environment.

Some features, such as septa and tabulae are so common that their analysis in terms of function, faculty, and biological role seems unnecessary. When we describe facts, such as "tabulae domed" or "major septa amplexoid", we attempt to find similarly characterized specimens in the existing literature to either identify our specimens as belonging to a known fossil taxon or to create a new one. Thus, we stop our investigation on the level of the most obvious details of a feature and its form. The function of that feature has already been omitted because of the absence of the simple question "why?" Moreover, why "domed" or "amplexoid" in some combination of accompanying characters is in a given part of growth, but not in another part of the same specimen? What does that change in the course of growth mean for the polyp in terms of the faculty and biological role? Our answers to such questions would perhaps change our taxonomic decisions if we asked them, but we commonly do not ask.

Functional analysis of all rugose coral features in all their lineages would be a lifetime task for dozens of scientists. Thus, this paper is restricted to some aspects of the most common features of the Rugosa, i.e., their septa. Occurring in the greatest majority or all of these corals, septa are so general that their presence in unrelated lineages is axiomatic. Thus, their value for taxonomy and phylogeny depends on their pattern, shape,

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* Corresponding author.
E-mail address: jerzy@amu.edu.pl.

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number, etc. That recognition had been accepted previously by the early and middle 19th Century coral workers and is valid up to the present.

The question concerning function, faculty, and biological role of septa may be reduced to: "Are they absolutely necessary for the functioning of a coral?" The answer is "No, they are not". Absence of septa from very early growth stages was documented by Różkowska (1956), Ilina (1984), Fedorowski (1986, 1987), Stolarski (1993), and some others. Also, septa may by reduced, to a large extent, from the mature growth stage of some taxa, or perhaps completely, as in some Cystiphyllidae Milne-Edwards et Haime, 1850. If septa are unnecessary, what about mesenteries? We are accustomed to think about them as accompanying septa. Does the lack of septa mean the absence of mesenteries? Birenheide (1965) questioned the occurrence of mesenteries in the Rugosa, but a critique by Schindewolf (1967) of his position leaves no doubts in that matter. Desmocyte scars documented in very well preserved calices, discussed by Fedorowski (1997), further prove the occurrence of mesenteries.

2. The zaphrentoid morphotype and general considerations

The succession of different septal arrangements in ontogeny, i.e., transformation in form of that feature, suggests that its function, faculty, and biological role were transformed as well. Three common genera: *Caninia* Michelin 1840 (in Gervais, 1840), *Ufimia* Stuckenberg, 1895, and *Zaphrentites* Hudson, 1941 were selected to illustrate that question.

The functions of septa for the support of the polyp's body, strengthening of the calice and division of the gastro-vascular cavity into narrow, centripetally opened chambers are most obvious. Such functions illustrate, in part, the faculty and pose the question: what is the feature capable of doing in the life of the organism? The answer may be that it increases effective oxygenation and food capturing and safety of the polyp, thus increasing the efficiency of the animal in its functioning. However, the question remains unanswered as to how the organism uses the faculty during its lifetime, i.e., the biological role in regards to the arrangement, shape, and strength of septa.

The so-called zaphrentoid arrangement of septa illustrates one of the simplest examples of how it does. That arrangement (Fig. 1B) functioned during the entire life of specimens in *Zaphrentites*, *Rotiphyllum* Hudson, 1942, *Saleelasma* Weyer, 1970, and several other Devonian to Permian genera. Also, it was very common among other Rugosa in their early growth stages, i.e., when they were small (e.g., Figs. 1F and 2A–D). This pattern seems perfect for the three functions mentioned. The centripetal arrangement and axial connection of septa made the skeleton resistant and its supportive function stable, acting similarly to spokes in the bicycle wheels. Large parts of the polyp's basal discs were elevated by septa, facilitating oxygenation, which was further increased by enlarging the polyp's surface within septal loculi. The pinnate arrangement of loculi allowed the easy distribution of water inside the gastro-vascular cavity. Thus, incoming water oxygenated the entire endoderm and brought food to all cells capable of catching food particles. Water that was depleted of food and oxygen, but enriched with waste products, was then directed into the cardinal fossula and released through the slit in the oral disc (see Fedorowski, 1997 for details). Thus, the question arises, why did so many Rugosa change that apparently perfect arrangement and develop differentiated structures at different growth stages? Some examples of those changes are shown in Figs. 1A, C–E and 2F.

The absence of living representatives of the Rugosa requires us to refer to the Scleractinia when looking for functional and behavioural analogies. Unfortunately, the Scleractinia differ in the insertion of septa. Thus, the interpretation of reasons for changes in the arrangement of septa during ontogeny of the Rugosa remains speculative. Nevertheless, repeated sequential changes suggest a genetic control on them. That genetic control does not mean that all specimens of a given morphotype were related. On the contrary, it is suggested here that various lineages, comprising truly related taxa, evolved in parallel towards reaching a common or similar morphology.

Modifications may appear at every growth stage. Thus, particular growth stages should be analyzed separately and compared exclusively to corresponding growth stages of other specimens or species. This obvious requirement is seldom observed in rugose coral studies, leading to all sorts of misunderstandings.

Water bringing food and oxygen is always the most important factor for marine sessile organisms. They must adapt their morphology for the most effective use of that supply. Thus, that factor is here considered as mostly responsible for the morphological trends in the ontogeny of various rugose corals. The position of the organism on the sea floor, its attached or floating habit, shape and strength of the body and skeleton, and other genetically controlled modifications are all dependent on that priority.

Having in mind the possibility of an independent achievement in various lineages of a given morphotype, the microstructure of septa must be considered the fundamental character for the recognition of their origin. Unfortunately, that kind of study remains very unsatisfactory among the Rugosa, whereas convergences in the occurrence of particular skeletal constructions should be predicted to be common among such primitive organisms. Being unable to conduct molecular and genetic studies on the Rugosa, we should go into as much detail in our studies on the skeletons as we can, i.e., we must establish the microstructure of septa prior to looking at their arrangement and their changes during the lifetime of the organism. Besides, the difference between the microstructure of the primary septa and their secondary, sclerenchymal cover and the diagenetic alterations of both must be made clear before any analysis begins. Only the original microstructure of the primary septa is important. An analogy to a plastered building wall is quite instructive in this case (Fig. 1L): a wall built from wood, bricks, stones or clay look the same until the plaster is removed and its inner structure is studied. Thus, identical arrangement of septa should be neglected as indicating a close relationship of animals until a close similarity in the original microstructure and its diagenetic alterations are established. It must be kept in mind that the advanced diagenesis may change the microstructure of septa completely (Fig. 1M).

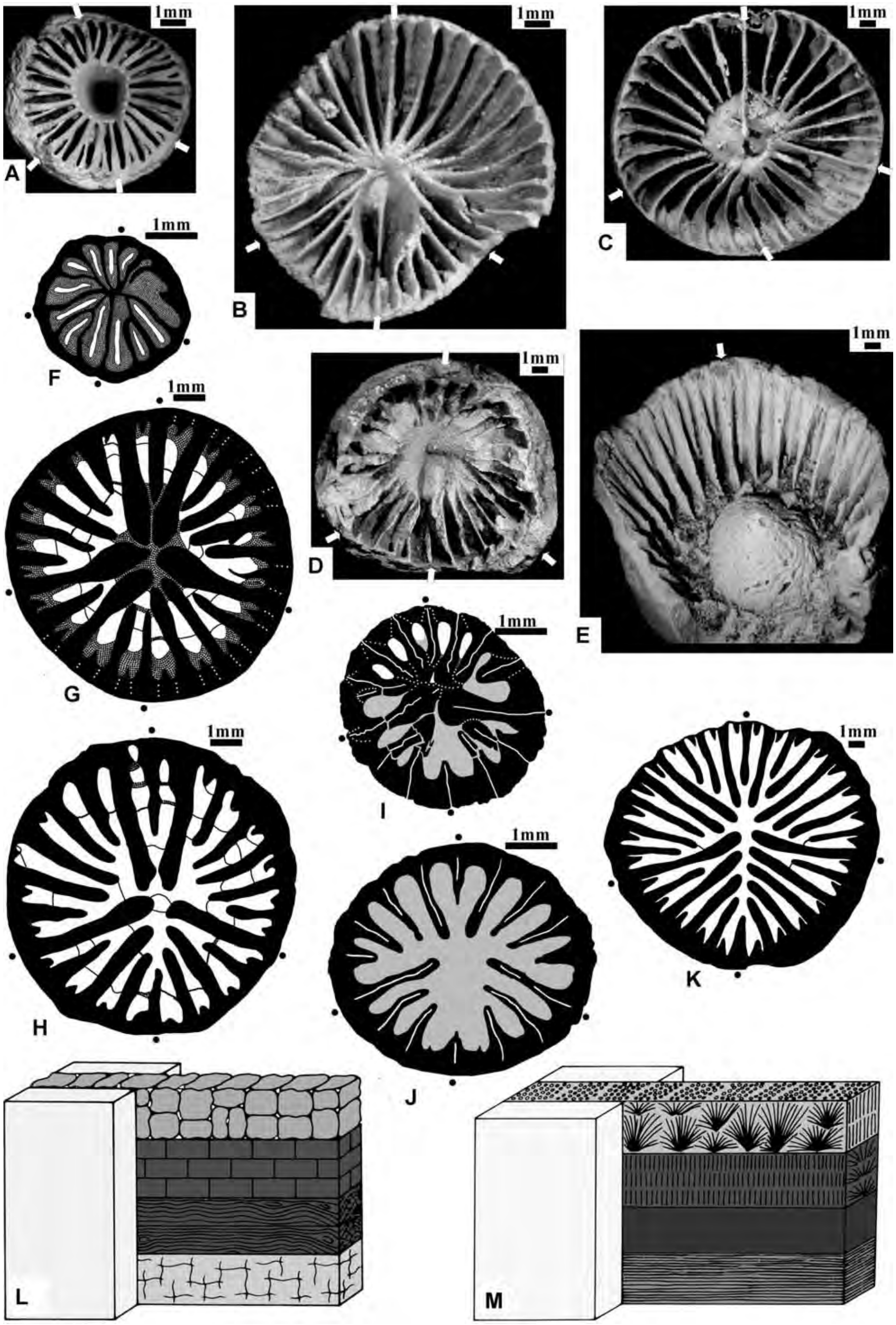

Fig. 1. Protosepta and alar septa marked by dots in transverse sections and by arrows in calices whenever possible. (A) ?*Syringaxon* sp. Specimen UAM.Tc/Sim/1. Middle Devonian, Holy Cross Mountains, Poland. Calice with very deep aulos-like structure. (B) ?*Muensteraia* sp. Specimen UAM.Tc-Sim/2. Upper Tournaisian. Tournai, Belgium. Zaphrentoid arrangement of septa in calice. (Specimen provided by Professor E. Poty, Liège, Belgium.) (C) *Wannerophyllum* sp. Specimen UAM.Tc/Sim/3. Middle Permian, SW Texas, USA. Loose axial structure in calice, based on elongated counter protoseptum. (D) *Caninia cornucopiae* Michelin, 1840. Specimen UAM.Tc/Sim/4. Upper Tournaisian. Tournai, Belgium. Calice with deep cardinal fossula and flat floor. (Specimen provided by Professor E. Poty, Liège, Belgium.) (E) *Verbeekiella* sp. Specimen UAM.Tc/Sim/5. Strong axial structure in the calice. Middle Permian strata of Basleo, Timor Island. (F and G) *Ufimia carbonaria* Stuckenberg, 1895. Specimen 23/45 (most probably part of the lectotype). Ufa River area, Russia. Lower Permian (Artinskian). Transverse sections. (F) Zaphrentoid neanic growth stage. (G) Early mature growth stage. (H) *Ufimia carbonaria* Stuckenberg, 1895. Specimen 21/45. Lectotype. Locality as above. Transverse section; mature growth stage just beneath the calice floor. (I and J) *Ufimia*-like new genus. Specimen B-1056. Ostrava area, Czech Republik, Lower Carboniferous (Serpukhovian, Arnsbergian). Transverse sections. (I) Partly above (shadowed), partly beneath calice floor. (J) Middle part of calice. (K) *Ufimia persymmetrica* Schindewolf, 1942. Holotype. Bitauni, Timor Island, Lower Permian. Transverse section (re-drawn from Schindewolf, 1942, text-fig. 48i). (L and M) Diagrams illustrating various constructions of a wall, not seen when plastered: analogy to primary septa and sclerenchymal cover of septa in corals. (L) Original. (M) Altered by diagenesis.

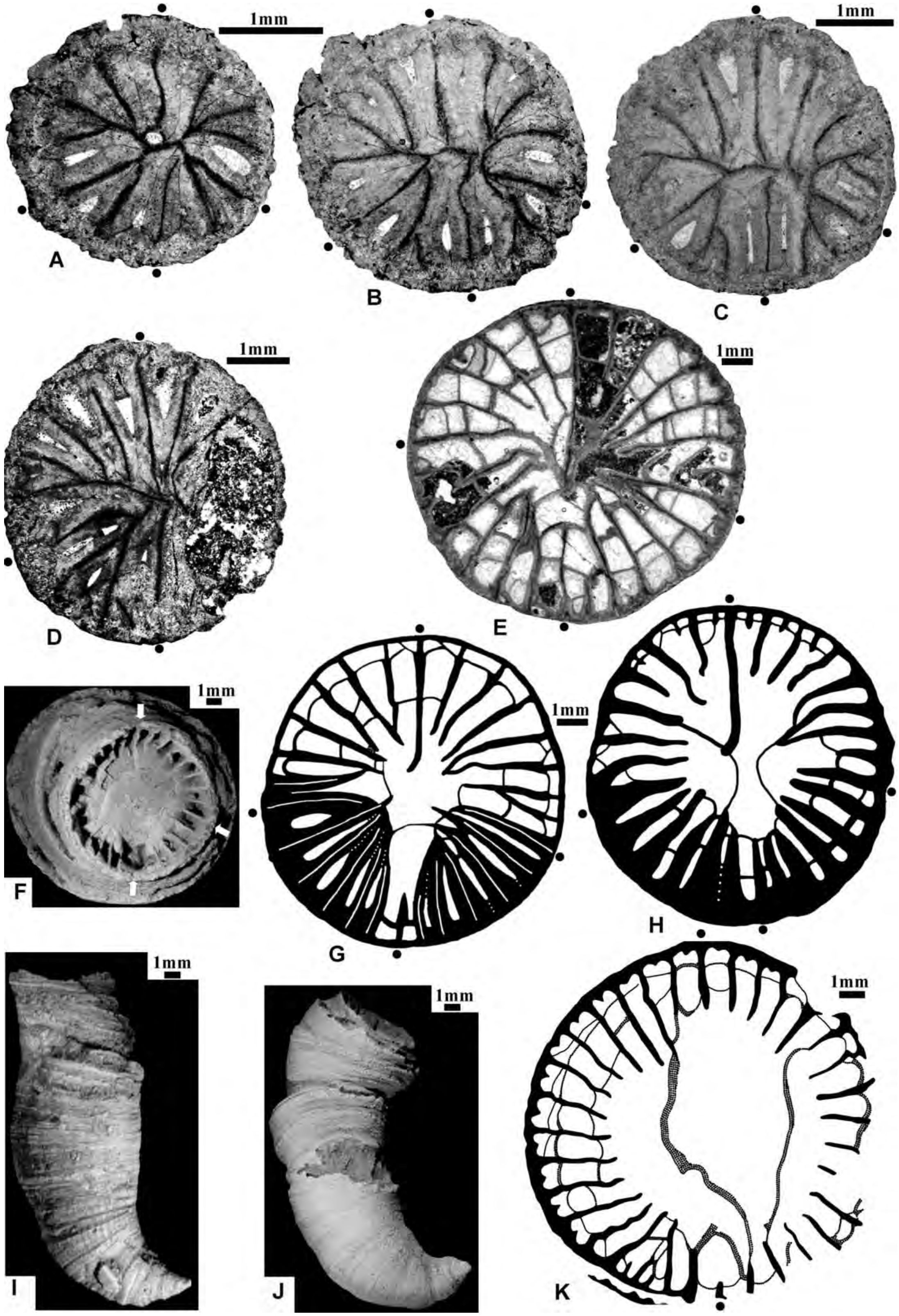

Fig. 2. Protosepta and alar septa marked by dots in transverse sections and by arrows in calices whenever possible. *Caninia cornucopiae* Michelin, 1840. (A–E and I) Specimen UAM.Tc/Sim/7. Tournai, Belgium. "Tournaisian Limestone". Upper Tournaisian. (A–E) Transverse sections. (A–D) Zaphrentoid neanic growth stage. (E) Mature growth stage; counter protoseptum elongated. (I) Side view. (Specimen provided by Professor E. Poty, Liège, Belgium.) (F and J) Specimen UAM.Tc/Sim/6. Locality and age as above. (F) Calice with wide, flat floor and strongly shortened major septa. (J) Side view showing two re-juvenations. (Specimen provided by Professor E. Poty, Liège, Belgium.) (G, H and K) Specimen RC 331. Tournai, Belgium. Upper Tournaisian. Transverse sections (re-drawn from Carruthers, 1908, pl. 6, fig. 1d, e, j respectively).

Many specimens retaining zaphrentoid arrangement of septa in maturity were given the generic name *Zaphrentites* Hudson, 1941. Started from the Early Devonian *Zaphrentites* of Kullmann (1965) and ended with the Permian *Zaphrentites permicus* Xu in Jia et al., 1977, a seemingly continuous chain of zaphrentoid taxa can be established. Therefore, one might suggest survival of the Early Devonian taxa into Permian time. However, there exists no concrete evidence in the literature for the relationship of all those representatives of "*Zaphrentites*", except for the zaphrentoid arrangement of septa. Thus, we are trying to prove the idea with the idea itself. This is almost like including all flying insects in one genus pointing to their possession of wings. The absence of fundamental data allowing distinction between bearers of zaphrentoid arrangement of septa in maturity lead me to the idea that unrelated taxa adopted a similar form for the function, faculty, and biological role of that feature.

The above suggestion seems to question one of our fundamental premises in the taxonomy of the rugose corals, i.e., the role of early ontogeny in establishing relationships of taxa, but it does not. It only indicates that our ideas of relationships based on a single character—the arrangement of septa in this case—may not be correct and must be expanded to include other characteristics, the microstructure being the most important, in order to approach the truth. Palaeogeography is another factor to be considered when the relationship of taxa is reconstructed.

The influence of the land/sea configuration, probable directions of ancient currents, or simply width of an ocean lacking islands offering a possibility for larvae to metamorphose, are factors commonly underestimated in our taxonomic studies. The Permian, with its supercontinent Pangea and superocean Panthalassa, is perhaps the best to exemplify the value of that factor. Species on the eastern and western shelves of Pangea, i.e., in the Palaeotethys and the Cordillera-Arctic-Uralian Realms, cannot be related on the genus level, if their diagnostic generic characters appeared as late as in the Early Permian, i.e., when passages through the Uralian and Rheic Oceans were closed. This obvious restriction is generally abandoned on the cost of similarities in the morphology.

Euryphyllum Hill, 1938 first established from the Australian Permian and restricted to that period in the Palaeotethys Realm, described subsequently from the Upper Carboniferous of SW Texas (Fedorowski, 1987) and the Guadalupian of the Canadian Arctic (Fedorowski and Bamber, 2001), may serve as an example of the geographic isolation and of parallel evolution. The closing of the Rheic Ocean passage made it simply impossible for a true relationship of the Australian and North American taxa. This example is also important for functional analysis and its bearing on taxonomy. All of Plotnick and Baumiller's (2000) parameters of analysis in Australian and North American species included in that genus are apparently similar. Thus, there is no reason to question the faculty and biological role of the europhylloid morphology, but only the Palaeotethys species have the right to be included in *Euryphyllum* if the monophyletic rule is followed. Thus, the functional analysis, although generally very important, may also be misleading if not crosschecked with other factors, such as the palaeogeography in the example discussed above.

3. Mature morphology of caninomorphs and ufimiids

3.1. Caninomorphs (Figs. 1 and 2D)

The supportive role of the septal apparatus in most of the mature *Caninia*-like corals was obviously reduced to a minimum: short, thin septa, restricted to the peripheral part of the calice, supporting only the narrow girdle of the oral disc (Fig. 2F and K). Major septa may be slightly elongated in the mature growth stage of some specimens (Fig. 1D), but not to the extent making the supportive role of those septa truly important. Thus, the faculty and biological role of septa were not only changed during the transition period from the neanic to mature growth stage, but they were also greatly reduced in their main functions, i.e., support for the body, its elevation and strengthening of the calice. An almost equal length of major septa, with only the cardinal protoseptum shortened and located in a cardinal fossula, suggests water circulation inside the gastro-vascular cavity as proposed earlier (Fedorowski, 1997).

From the paper cited above, two factors were omitted: (1) the long-lasting or permanent elongation of the counter protoseptum (Fig. 2E, G and H) in *Caninia cornucopiae* Michelin, 1840, i.e., the type species for the genus. This important character was known to earlier workers (e.g., Carruthers, 1908), but was almost abandoned since and is elevated only recently by Professor Edouard Poty (oral communication, 2007). Some camera lucida drawings by Carruthers (1908), re-drawn here for comparison (Fig. 2G and H), illustrated that question well. (2) A strong development of mesenteries as a reason for shortening and reduction of the biological role of major septa was not suggested. However, the great success of the caninoid morphotype, developed in the various lineages on one hand and a very important role of mesenteries in the functioning of a coral on the other, implies that suggestion. Most polyps of modern Scleractinia expand their bodies when feeding. Such behaviour was even more likely in the Rugosa, the bodies of which were sheltered in deep calices. Room available for simple mesenteries between septa was sufficient for small, young polyps to feed and oxygenate. Thus, the inherited zaphrentoid arrangement of septa (Fig. 2A–D) was sufficient as well. However, mesenteries in the caninoid morphotype must have become more complex with enlargement of the polyp's body (Fig. 2I–K) to fulfill the increasing requirement for food and oxygen. This was especially important in the restricted environment "which is reflected in the lithofacies" as Professor I. Somerville suggested in his comments to my paper. He further points "to stressed low-energy lagoonal type (or mid-shelf) environments (wackestones and lime mudstones) where cylindrical caniniids can be found in situ in erect growth orientation" (see also Somerville, 1997, p. 372).

The strongly developed mesenteries, expanded during the feeding periods, must have been sheltered somewhere within the calice when contracted at times of rest. Thus, it is here proposed that the transition from the zaphrentoid early growth into mature morphology of *Caninia*-like corals was the result of the enlargement of the mesenteries that reduced the form, faculty and biological role of major septa, to increase room for their storage. It seems proper to suggest that the transition from the zaphrentoid to the caninoid morphotype, possible for taxa with an appropriate genetic potential, resulted from their living in an environment restricted in food and oxygen where large and complex mesenteries instead of a strong skeleton were necessary for survival. The above statement does not mean that any specimen dropped into an environment proper for the caninomorphs will achieve the *Caninia*-like morphology. It only suggests that unrelated taxa, armed with a proper genetic potential, would have reached such morphology.

Thus, the process should not be evaluated as random. On the other hand, however, the *Caninia*-like morphology was achieved either directly from the zaphrentoid arrangement, as the *Caninia* proper did (Fig. 2A–E) or from various morphologies appeared as intermediate between the zaphrentoid and caninoid morphotype. Genera such as *Koninckophyllum* Thomson et Nicholson, 1876; *Gshelia* Stuckenberg, 1888; *Bothrophyllum* Trautschold, 1879; *Haplolasma* Semenoff-Tian-Chansky, 1974 or *Arctophyllum* and *Siedleckia*, both of Fedorowski, 1975 may serve as examples. Consequently, achievement of the caninoid morphology is taxonomically important only within individual phylogenetic lineages, not across or between them.

3.2. Ufimiids

The genus *Ufimia* was introduced by Stuckenberg (1895) for specimens from the Artinskian (Lower Permian) deposits of the Ufa area (Russia) (Fig. 1F–H). Fedorowski (1973) reinvestigated the type specimen and documented its zaphrentoid ontogeny. However, that generic name has been applied to many taxa from the Early Devonian through Permian almost worldwide. Also, its relation to or synonymy with *Tachylasma* Grabau, 1922 was understood differently by various authors (e.g., Schindewolf, 1942; Fedorowski, 1973; Ilina, 1984; Fedorowski and Bamber, 2001).

In contrast to the caninomorphs, which tended to achieve a constant radial symmetry of septa with only the cardinal protoseptum shortened and counter protoseptum elongated in some, most species of *Ufimia* or *Ufimia*-like corals only have slightly modified the inherited zaphrentoid morphology. They accomplished the bilateral arrangement of major septa by disconnecting from their inner margins. In this way, the cardinal fossula became a part of the irregular tract along the symmetry axis (Fig. 1H, J and K). The lengths of the alar and counter-lateral septa, commonly longest in quadrants of *Zaphrentites*, were also inherited by *Ufimia*. They were strengthened in that genus, becoming the dominant major septa. Two characters were new for *Ufimia*: (1) shortening of the counter protoseptum, and (2) differentiation in length and thickness of major septa, the longest of which bounded compartments containing shorter major septa. All those compartments are open towards the middle tract.

The mature morphology of *Ufimia* proper, or *sensu lato*, implies a strategy of feeding and oxygenation different from those invented by caninomorphs, but similar to *Zaphrentites* in a sense that polyps may have expanded only slightly during the feeding periods. Strong, rhopaloid major septa (Fig. 1G–I), commonly persisting well above the calice floor, suggest their important supportive role for the body. Also, the comparatively great length of most of the septa indicates a large surface of the endoderm eligible for oxygenation and intracellular metabolism. Both of those characters, which allowed the mesenteries to remain simple, resemble *Zaphrentites*. This means that the main faculty and biological role of septa in *Ufimia* did not change much during the transition from the neanic to the mature morphology.

A strong and permanent shortening of the counter protoseptum, noticeable up to the calice margin, forms a distinct termination of the middle tract constituted by the inner margins of major septa. The cardinal fossula and a strongly shortened cardinal protoseptum terminate that tract on the opposite side. The commonly recognizable alar pseudofossulae can be treated as auxiliary tracts, inherited from *Zaphrentites*. Thus, all "ufimiids" developing the typical skeleton applied a solution different from that in the caninomorphs. They all probably intensified water flow through their gastro-vascular cavity instead of developing complex mesenteries. The large surface of strongly folded endoderm, located on the rhopaloid major septa, played the same role during the feeding period as the large surface of the mesenteries in the caninomorphs. It is suggested here that the water stream was directed by tentacles and cilia into the mouth and then downwards through all septal loculi. Food and oxygen were removed from the water when flowing down over the endoderm. When reaching the calice floor, the water stream was directed to the medial tract. Long alar and counter-lateral septa prevented the re-circulation of the depleted water, helping to direct its flow into two main slits in the oral disc, i.e., those located above the cardinal and counter protosepta, and into the auxiliary slits above the alar pseudofossulae. It is suggested here that all four slits were located behind the circle of tentacles in order to separate the stream of used water from the stream of clean food-bearing water. In this way, the demand for food and oxygen was achieved without weakening the skeleton, a condition important in a high-energy regime.

Shortening of major septa observed in some ufimiamorphs (e.g., "*Zaphrentites*" *shunnerensis* Hudson, 1944) resulted in widening of a free axial area capable of storing the enlarged and complex mesenteries, as was suggested above for the caninoid morphotype. Although such taxa retained the most characteristic ufimiid features, a behavioural solution similar to that in the caninomorphs can also be interpreted for them. That solution may have appeared as a response to the inadequate effectiveness of the typical ufimiid solution in given extrinsic conditions, i.e., a reduced requirement for strong skeletal support and the increased demand for supplies of food and oxygen.

The random appearance of "ufimiids" with short septa, scattered stratigraphically and geographically, precludes their evolutionary relationship, i.e., grouping into a single genus or subgenus. Thus, they are morphotypes rather than indicating a direct relationship. That means that in *Ufimia* sensu lato, convergence rather than relationship seems more probable. It is enough to look at the synonymy proposed by Ilina (1984, pp. 101–103) and compare the geographic and stratigraphic occurrences of individual taxa to conclude that monophyletic relationship of many of them is very unlikely in spite of the similar arrangement of septa. However, the above suggestions must be verified by study of the microstructure of septa of all *Ufimia*-like species. The peculiar microstructure described in the Middle Permian *Ufimia arctica* Fedorowski et Bamber, 2001 may now be treated only as one of the possibilities. This question is further elaborated by Fedorowski (in preparation).

4. Diagenesis

The role of diagenesis in the micro- and meso-structures of the rugose coral skeletons is only mentioned here as a factor commonly biasing our conclusions. It has been the subject of many notes and papers. Only a few are listed here as examples. Oekentorp (e.g., 1980, 1984, 2001) strongly supported the idea of common diagenetic alterations in the rugose coral skeletons, and Sorauf and Cuif (2001) demonstrated some very early diagenetic alterations occurring in skeletons of recent Scleractinia. Fedorowski (2003) briefly discussed some doubts concerning the original microstructures of rugose coral skeletons and some obvious diagenetic alterations. Recognition of diagenesis for a proper interpretation of the microstructure of septa and, consequently, for the recognition of the most probable relationships of taxa or their taxonomic position, seems indisputable. Difficulty in those studies is at the same time exemplified by different interpretations of the microstructure vs. diagenesis in septa of the same taxa from the same beds (Oekentorp, 1984; Sorauf, 1984). Thus, all of our higher-level taxonomic conclusions may be wrong if our interpretation of elements from which the skeleton was built is incorrect. Diagrams (Fig. 1L and M), although exaggerating some alterations, point to the fact that diagenetic alterations may be interpreted as the primary microstructure. This question is introduced here to indicate that there is a danger of an incorrect interpretation of either the morphology of the skeletons or the original microstructure if diagenetic alteration have occurred, but was not recognized. Alteration has nothing to do with faculty and the biological role of characters, thus being useless for functional analysis, taxonomy, phylogeny, palaeoecology, and palaeogeography, but having potential for an incorrect solution in all those areas.

5. Conclusions

(1) Every feature responds to both an animal's needs and restrictions of its surroundings. Thus, its form, function, faculty, and biological role may change during its ontogeny. Examples of taxa discussed above attempted to emphasize the different biological role of septa during ontogeny of a given individual and its bearing on taxonomy.

(2) The faculty and biological role of mesenteries in individual morphotypes can be interpreted on the basis of the arrangement, morphology, and length of the major septa. Their interpreted reconstruction helps in understanding the functioning of the organism, and its relationship to other taxa.

(3) Identical arrangement of septa early in the ontogeny does not prove a direct relationship by itself. Microstructural studies and comparisons to similar morphotypes are necessary prior to reaching a conclusion.

(4) Similarity in the mature characteristics of major septa means only a similar faculty and biological role. Thus, such characteristics cannot be employed for taxonomic and phylogenetic considerations until checked against other features.

(5) Skeletons of fossil corals preserve various features indicating the structure of the living tissues, but all features of those skeletons must be analyzed with care because all may had been altered diagenetically.

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Research paper

Environmental controls on growth of early scleractinian patch reefs (Middle Triassic; Silesia; Poland)

Elzbieta Morycowa*, Joachim Szulc

Institute of Geological Sciences, Jagiellonian University ul. Oleandry 2a, 30-063 Krakow, Poland

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Abstract

Anisian scleractinian corals are known from the Lower and Middle Muschelkalk of the Cracow-Silesian region, but in bioherms they occur only in the western part, i.e., in the Upper Silesian area, in the higher part of the Lower Muschelkalk (Karchowice Beds). Silesian reefs of Anisian (middle Pelsonian-early Illyrian) age are, so far, the oldest *in situ* coral reefs following the Permian/Triassic extinction. In Anisian time, Silesian corals formed a Tethys marginal reefal rim, separating offshore Tethyan open marine waters from the backreef area (Germanic Basin). The shallow-water coral-bearing facies capped sponge buildups, following a general shallowing trend in the basin. Final emersion in the early Illyrian halted coral reef growth. Anisian scleractinian corals appear to have been zooxanthellate, as suggested in Morycowa, 1988.

Keywords: Patch reefs; Scleractinian corals; Middle Triassic; Peri-Tethys; Upper Silesia; Poland

1. Introduction

Scleractinian corals are long known from the Lower and Middle Muschelkalk of the Cracow-Silesian region (e.g., Beyrich, 1852; Eck, 1865; Weissermel, 1926; Schmidt, 1928; Assmann, 1937; Morycowa, 1974, 1988, 1990; Morycowa and Szulc, 2007), but as reef components they occur only in the Upper Silesian area (Fig. 1), in the higher part of the Lower Muschelkalk, i.e., Karchowice Beds (Karchowice Formation after Bodzioch, 1997b).

The age of the Karchowice Beds, established by conodonts (e.g., Zawidzka, 1975; Narkiewicz and Szulc, 2004) and magnetostratigraphy (Nawrocki and Szulc, 2000), is Anisian, and more precisely, the interval from middle Pelsonian to early Illyrian time.

Coral reefs occurring in these sediments vary in dimension, morphology, and abundance (Fig. 2A and E). The most frequent scleractinians and reef constructors were branching *Volzeia szulci* Morycowa, lamellar *Pamiroseris silesiaca* (Beyrich) and *Eckastraea prisca* (Weissermel). Associated fauna are typically sponges, bivalves, gastropods, polychaetes, brachiopods, echinoderms (mainly crinoids), and ostracods (see Bodzioch, 1997a). Foraminiferids and microorganisms (*incertae sedis*) occasionally occur.

In the stratigraphically older Lower Muschelkalk, Gorazdze Beds (Weissermel, 1926; Assmann, 1937; Niedzwiedzki, personal com.) as well as in the Diplopora Dolomite (Middle Muschelkalk; e.g., Weissermel, 1926; Morycowa, 1988), scleractinians have been found only sporadically, as dispersed coralla or only their casts.

We provide more information on these oldest scleractinian reefs and present two examples of reefs, one from Tarnow Opolski (Fig. 2A and B) and the other from Kamien Slaski (Fig. 2E) as representative forms of Silesian reefs.

2. Materials and methods

The specimens and thin sections are housed in the Geological Museum of Institute of Geological Sciences, Jagiellonian University (coll.: UJ 34P). Only the thin sections of "*Coelocoenia* (?) *assmanni* Weisermel" (=here *Koilocoenia assmanni*) belong to the Weissermel collection, X 10136, BGR, Berlin).

We investigated macroscopic and microscopic samples of coral-bearing sediments in outcrop, as well as thin sections. Mineralogical analyses of coral skeletons were carried out

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* Corresponding author.
E-mail addresses: elzbieta.moryc@uj.edu.pl, elam@mpoczta.net (E. Morycowa), joachim.szulc@uj.edu.pl (J. Szulc).

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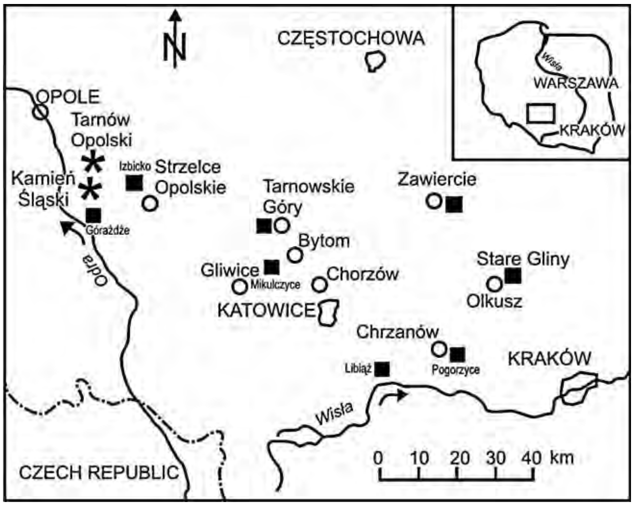

Fig. 1. Upper Silesian region. Location of scleractinian coral-bearing carbonates; limestones with corals shown by black squares; reefal limestones with corals shown by stars.

at the Institute of Geological Sciences, Jagiellonian University.

3. Palaeogeographic setting of the Cracow-Silesian region in the Northern Peri-Tethys

During Middle Triassic, the Cracow-Silesian region was situated in the SE part of the Germanic Basin (=Central European Basin). This basin, on the northern periphery of the western Tethys Ocean, was closed in the north, and open to the south (Senkowiczowa, 1962; Szulc, 2000) by tectonically controlled gates and thresholds. The threshold was dissected by deep grabens providing communication between the Tethys and the Germanic Basin.

The semi-enclosed nature of the basin resulted in distinctive environments. Open marine environments developed within the Silesian part of the basin, which we regard as an integral part of the Tethys Ocean, rather than an epicontinental sea. North and west of the Silesian domain, environments became more restricted. As indicated by faunal diversity, facies variability, and geochemical properties of the sediments during almost all of Anisian time, the eastern part (southern Polish basin) was dominated by open marine sedimentation, whereas the western part (mostly German) displayed restricted circulation, typical of the semi-enclosed, evaporitic basin.

Because the region was situated within the margins of the tropical zone (ca. 22–24° north palaeolatitude; Nawrocki and Szulc, 2000), its climate was hot and arid, favouring extensive carbonate and evaporite sedimentation. The region suffered severe subtropical storm activities, as evidenced by numerous tempestite deposits. After Ladinian time, the climate became more humid and milder, the probable result of vigorous volcanic activities within the Tethys spreading belt (Szulc, 2000).

Evolution of the southern parts of the Germanic Basin (Silesia, Holy Cross Mts., SW Germany) was influenced directly by Tethys rifting. As suggested by the timing between principal tectonic events and palaeontological evidence, the Cracow-Silesian Basin shows similarities to the Southern Alps (Szulc, 2000). Crustal motion was transmitted from the Tethys rifts onto its northern margin by reactivated Hercynian master faults. It seems very likely that the Silesian Gate and the southern Alpine Basin were influenced by the same master fault system.

4. Lithofacies succession and basin evolution of the Cracow-Silesian area in Scythian-Carnian times

The Cracow-Silesian Triassic displays a characteristic tripartition, reflecting the principal transgressive-regressive cycle. This cycle began with the Buntsandstein continental clastics, followed by marine carbonates of the Muschelkalk, and ended with continental Keuper evaporites and clastics. Conodont stratigraphy has enabled a relatively precise correlation of the Muschelkalk sequence with the alpine Middle Triassic (Zawidzka, 1975). Recently, the chronostratigraphic framework of the Silesian Triassic has been corroborated using magnetostratigraphic studies of Nawrocki and Szulc (2000). Based on integrated biostratigraphic dating and magnetostratigraphic data, the lower boundary of the Muschelkalk in the Cracow-Silesian Basin is assumed to be coincidental with the beginning of the Anisian Stage. Szulc (2000) has distinguished several third-order depositional sequences within the Muschelkalk succession, suggesting that the main Triassic transgressive phase took place in the Pelsonian interval. During this time, the Tethys margin reached as far north as Upper Silesia, where a tectonically controlled threshold separated the open ocean from the back ramp basin of the Muschelkalk Sea.

The marginal position of the Silesian threshold provided favourable environmental conditions for sponge-coral reef development. The Silesian reefs of Pelsonian-Illyrian age are the oldest known in situ coral reefs after the Permian/Triassic extinction.

With basin shallowing, the reefs of the Karchowice Beds were replaced by oncolites, dasycladacean grainstones, and finally by oolitic bars of the Diplopora Beds, representing the Middle Muschelkalk. The oolitic carbonates underwent a subsequent ephemeral emersion, giving rise to palaeosol formation, dolomitisation, karstic pavements, as well as playa clastics and evaporites. The Silesian-Moravian Gate became restricted in the uppermost Muschelkalk, while open communication persisted through the East Carpathian Gate. Shallowing trends and clastic sedimentation in the Polish Basin took place by intensive crustal uplift that occurred in the eastern basin by the end of Fassanian (=early Ladinian) (Szulc, 2000) (Fig. 3).

5. Characteristics of Silesian reefs

Anisian scleractinian reef corals were recorded from the Karchowice Beds, mainly from quarries still in operation at Tarnow Opolski (Figs. 1 and 2A and B) and from one of the old, no longer active, quarries in Kamien Slaski (Figs. 1 and 2E). The thickness of these beds in the Opole area reaches several metres (Dzulynski and Kubicz, 1971). The coral reefs occurring in these sediments vary in dimension, morphology and to a small extent in quantity of biotic components. Some of these

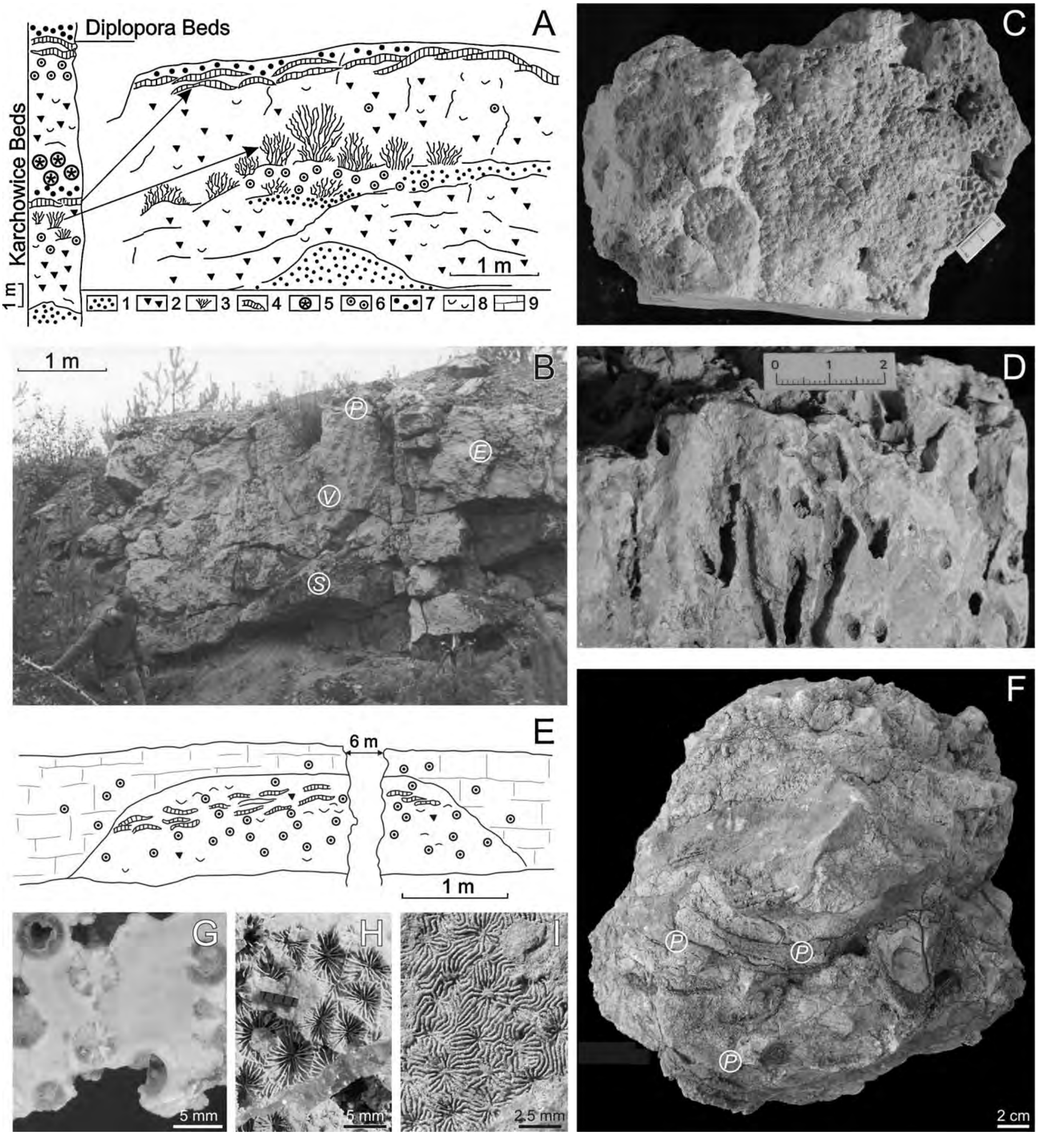

Fig. 2. (A and B) Coral-sponge reef from the Karchowice Beds at Tarnow Opolski quarry. In the middle part, the large branching-phaceloid coral *Volzeia szulci* occurs in situ above the sponge zone, and in the upper part, thin-lamellar colonies *Pamiroseris silesiaca* form dense, monospecific assemblages. Below the *Pamiroseris* level, *Eckastraea prisca* occur. On the left side of the drawing (A), there is a simplified log of the coral-bearing succession (explanations of symbols below). (C) Multistorey colony of *Eckastraea prisca* (UJ 34P/50). (D) Lateral broken surface of a branching coral of *Volzeia szulci* (UJ 34P/2). (E) Kamien Slaski quarry. Coral-crinoid reef within poorly bedded Karchowice limestones (explanation in A). Monospecific *Pamiroseris silesiaca* layer occurs in the upper part. (F) Fragment (UJ 34P/55) of *Pamiroseris silesiaca*-bearing limestone from the same site. (G–I) Tarnow Opolski quarry. (G), fragment of polished limestone with *Volzeia szulci* (UJ 34P/2); (H), calicular surface of *Eckastraea prisca* (UJ 34P/51); (I), *Pamiroseris silesiaca* (UJ 34 P/46). Explanation of the symbols of the log in (A): 1 – bioclastic sands, 2 – sponges, 3 – branching, phaceloid corals *Volzeia szulci*, 4 – lamellar corals *Pamiroseris silesiaca*, 5 – Cidaris calcarenites, 6 – crinoids, 7 – *Girvanella* oncoids, 8 –, pelecypod and brachiopod shells, 9 – poorly bedded limestones (see E). Other symbols: S – sponges; *V – Volzeia szulci*; *P – Pamiroseris silesiaca*; *E – Eckastraea prisca*.

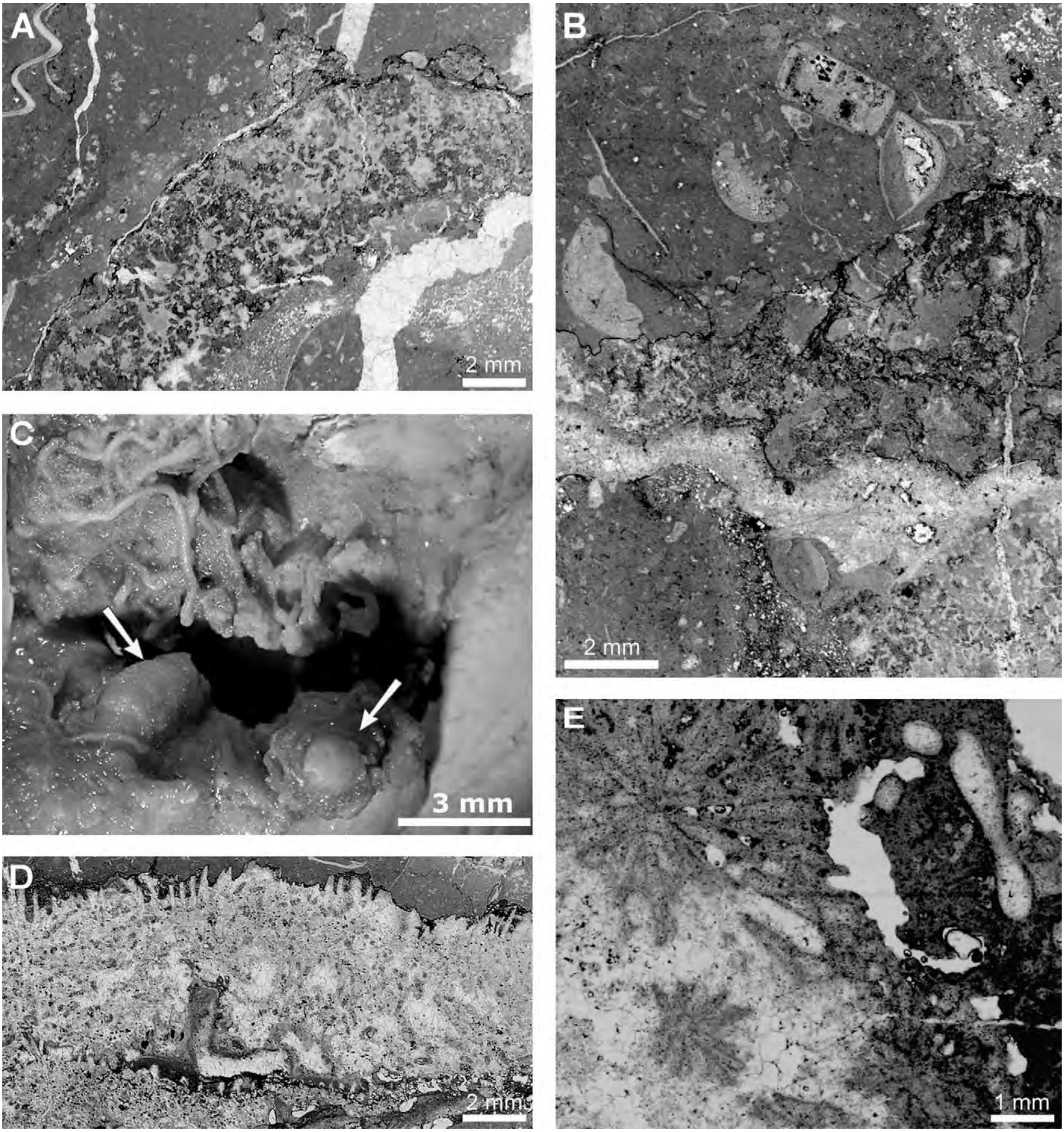

Fig. 3. Coral-crinoid patch reef at Kamien Slaski. Associated and boring organisms: (A) Sponge and fragment of brachiopod shell (thin section 7/7III). (B) Crinoid automicrite succeeding sponge facies (thin section 7/7e). (C). Bioherm from Tarnow Opolski. Polychaetes on basal and lateral surfaces of solitary corals (UJ 34P/56) (arrowed) occurring together with *Eckastraea* (below *Pamiroseris silesiaca* layer). (D and E) Coral-crinoid reef at Kamien Slaski. Traces of damage especially boring done to the coral skeletons by other organisms: (D) in *Silesiastraea weissermeli* (thin section: 7/34d); (E) in *Koilocoenia assmanni* (thin section: X 10135).

patch reefs may be classified as coral-crinoid, others as coral-sponge, or coral-sponge-crinoid. They formed domal structures and rarely elongated forms. Their diameters range from a few tens of centimetres to 10 m and their height ranges from a few tens of centimetres to about 2 m. About 20, mainly endemic, scleractinian species are present, but generally they played a subordinate role as components of these build-ups, except for one or two species forming monospecific assemblages. Such corals are dendroid-phaceloid *Volzeia szulci*, restricted to the lower part of the patch reefs, and platy, lamellar (sensu Rosen et al., 2000), thamnasterioid *Pamiroseris silesiaca*, forming dense, monospecific layers in the highest part of the reefs.

The corals are accompanied by rich invertebrate faunas of sponges, bivalves, gastropods, polychaetes, bryozoans,

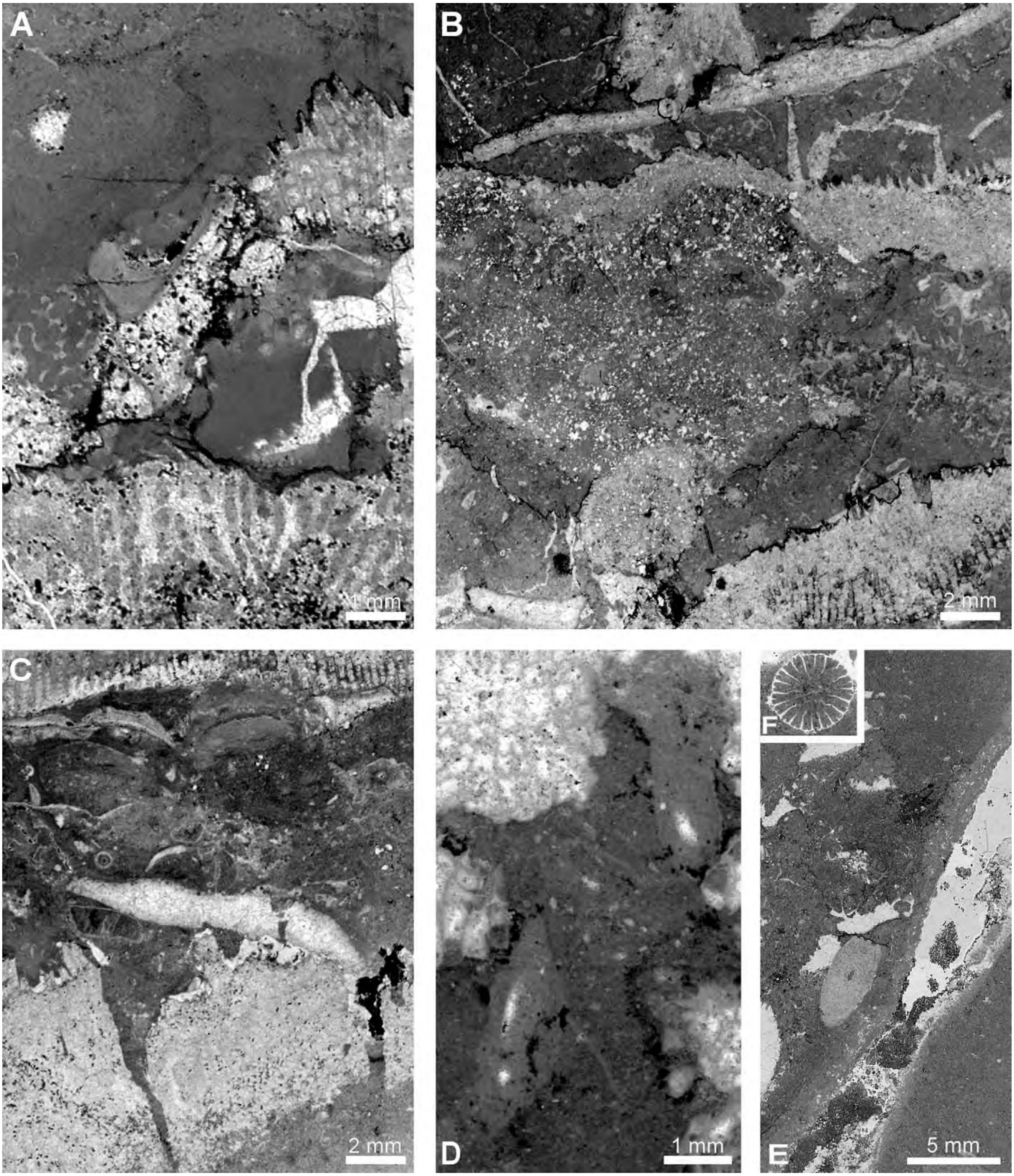

Fig. 4. Kamien Slaski. Coral-sponge overgrowths. (A) Part of the sponge body preserved as automicrite (thin section 7/34c). (B) Detrital sediments between two thin-lamellar colonies of *Pamiroseris silesiaca* (thin section 7/7e). (C) Break-up of *Pamiroseris* colonies, related most probably to synsedimentary earthquake event. (D) Among the *Koilocoenia* corallites (thin section X10136 are *Crescentiella* (="*Tubiphytes*") and biomicrite coated coral skeletons. (E and F) Tarnow Opolski. (E), fragment of *Volzeia szulci* skeleton almost totally altered and recrystallized, and partly filled by sparitic calcite (UJ 34P/2); (F), enlarged transverse section of exceptionally well-preserved corallite of *V. szulci* (thin section UJ 34P/2a). Diameter of corallite = 3.5 mm.

brachiopods, echinoderms, and ostracods as well as microorganisms (*incertae sedis*) and rare dasycladacean algae.

One of the coral-sponge reefs (Fig. 2A and B) is present in the Tarnow Opolski quarry. The most frequent constructors are branching and lamellar scleractinian corals: *Volzeia szulci* Morycowa, *Eckastraea prisca* (Weissermel), and *Pamiroseris silesiaca* (Beyrich). Delicate, large, phaceloid-dendroid corals such as *Volzeia szulci* (up to 1 m in height) occur in the lower part of the coral bioherm, above the sponge facies (Fig. 2A, B, D, G). The coral skeletons are not well preserved. The original aragonitic coral skeletons, as shown by mineralogical analyses, are calcitized, altered by secondary meteoric dissolution, and partly filled by sparry calcite (Fig. 4E). Only faint relics of the primary septal micro-architecture are still recognizable (Fig. 4F). The thin sections made from *Volzeia*-bearing limestone show automicrite (mostly of sponge origin) between corallites and a mainly pure micritic matrix.

In the higher part of the coral patch reefs (Fig. 2A and B), there is a layer with lamellar (occasionally encrusting) colonies, mainly *Pamiroseris silesiaca* (Fig. 2A and B). The coral skeletons are calcitized, but the calicular surfaces of colonies (Fig. 2I) are often well preserved (Morycowa and Szulc, 2007). The corals are accompanied by a rich invertebrate fauna of molluscs, polychaetes, brachiopods, and echinoderms.

A slightly different type of reef, coral-crinoid bioherm, occurs in the Kamien Slaski quarry (Fig. 2E). Small coral patch reefs are confined within the upper part of the Karchowice Beds. One of these (Morycowa, 1974, 1988) reveals lamellar (Fig. 2F) and rarely multistoried coral colonies, mainly *Pamiroseris silesiaca*, grouped in a layer 30–40 cm thick, situated in the upper part (Fig. 2E). From this reef are recorded *Eckastraea prisca* (Weissermel), *Silesiastraea weissermeli* Morycowa, *Morycastraea opoliensis* Morycowa, *Stylophylliopsis* sp., and rare solitary corals. The coralla are recrystallized and well preserved only on their calicular surfaces. Encrusting and boring fabrics (Fig. 3A–E) are common, mainly in the lower part of the coral. Among the corallites of *Koilocoenia assmanni* (Weissermel) from the Kamien Slaski quarry (=Gross Stein; Weissermel collection, X 10136, BGR, Berlin), *Crescentiella* Senowbari-Daryan et al., 2008 (=“*Tubiphytes*”) and biomicrite-coated coral skeletons may be also observed. The corals are accompanied by rich invertebrate faunas, e.g., crinoids, sponges, polychaetes, brachiopods (*Decurtella decurtata* (Girard)), bryozoans, and microbial structures. Foraminiferids and dasycladacean algae sporadically occur.

6. Palaeoecology

Middle Triassic coral build-ups generally developed in outer littoral environments, gradual shallowing upward, intermittently influenced by strong storm wave action and high sedimentation rates (Szulc, 2000). Additional data on reef growth forms and type of the environment are also provided by the corals themselves, their diameter, growth forms, and their distribution in these reefs.

The dominance of large branching, unbroken coral skeletons of *Volzeia szulci*, along with common sponges, occurring in the basal part of the reef (directly over the sponge facies) and the mainly pure micritic matrix, suggests a slightly deeper shelf palaeomilieu, with rather rapid sedimentation, keeping pace with growth of corals.

In contrast to the branching *Volzeia* level, the environment of platy, lamellar coral growth forms (*Pamiroseris silesiaca*) in the higher part of the reef must have been very shallow, periodically influenced by turbulent high-energy events, leading to mud in suspension, and a strong influx of sediments (Fig. 4B) that interrupted coral growth (Fig. 4A and C).

The final emergence during the early Illyrian resulted in cessation of the coral reefs.

7. Conclusions

1. Anisian (middle Pelsonian-early Illyrian) Upper Silesian coral patch reefs formed in the marginal part of the shelf of the northern Tethys Ocean (Peri-Tethys).
2. These patch reefs developed in a littoral, gradually shallowing-upward environment. Reefs vary in size, morphology, and faunal composition.
3. About 20 scleractinian species, mostly endemic, occur in these coral-bearing limestones, but generally they played a subordinate role as components of these build-ups, except for one or two species that formed monospecific layers, e.g., *Volzeia szulci* Morycowa – dendroid-phaceloid corals, restricted to the lower part of the coral reefs, and *Pamiroseris silesiaca* (Beyrich), platy, lamellar (sensu Rosen et al., 2000), thamnasterioid colonies, forming dense monospecific layers in the highest part of the reef structure.
4. Final emergence during the early Illyrian halted coral growth.
5. It seems likely that *Pamiroseris silesiaca* (Beyrich), one of the Anisian species having a wide palaeogeographic range in the Peri-Tethys: Poland, Germany; Tethys: Alps (Schauroth, 1859; see Weissermel, 1926); southern China (Qi, 1984; Deng and Kong, 1984), may be considered a good marker for Anisian time.
6. Anisian scleractinian corals appear to have been zooxanthellate (see Morycowa, 1988; Bodzioch, 1997a; Szulc, 2000; Morycowa and Szulc, 2007) and similar to the slightly younger scleractinian corals (Late Triassic), described by Rosen et al. (2000).

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Research paper

Morphological limits to diversification of the rugose and tabulate corals

Edouard Poty

Service de paléontologie animale et humaine, Département de géologie, Université de Liège, Bât. B18, Allée du 6 Août, 4000 Liège, Belgium

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Abstract

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

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

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

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

1. Introduction

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

2. Comparisons between Tabulata and Rugosa

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

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

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

E-mail address: e.poty@ulg.ac.be.

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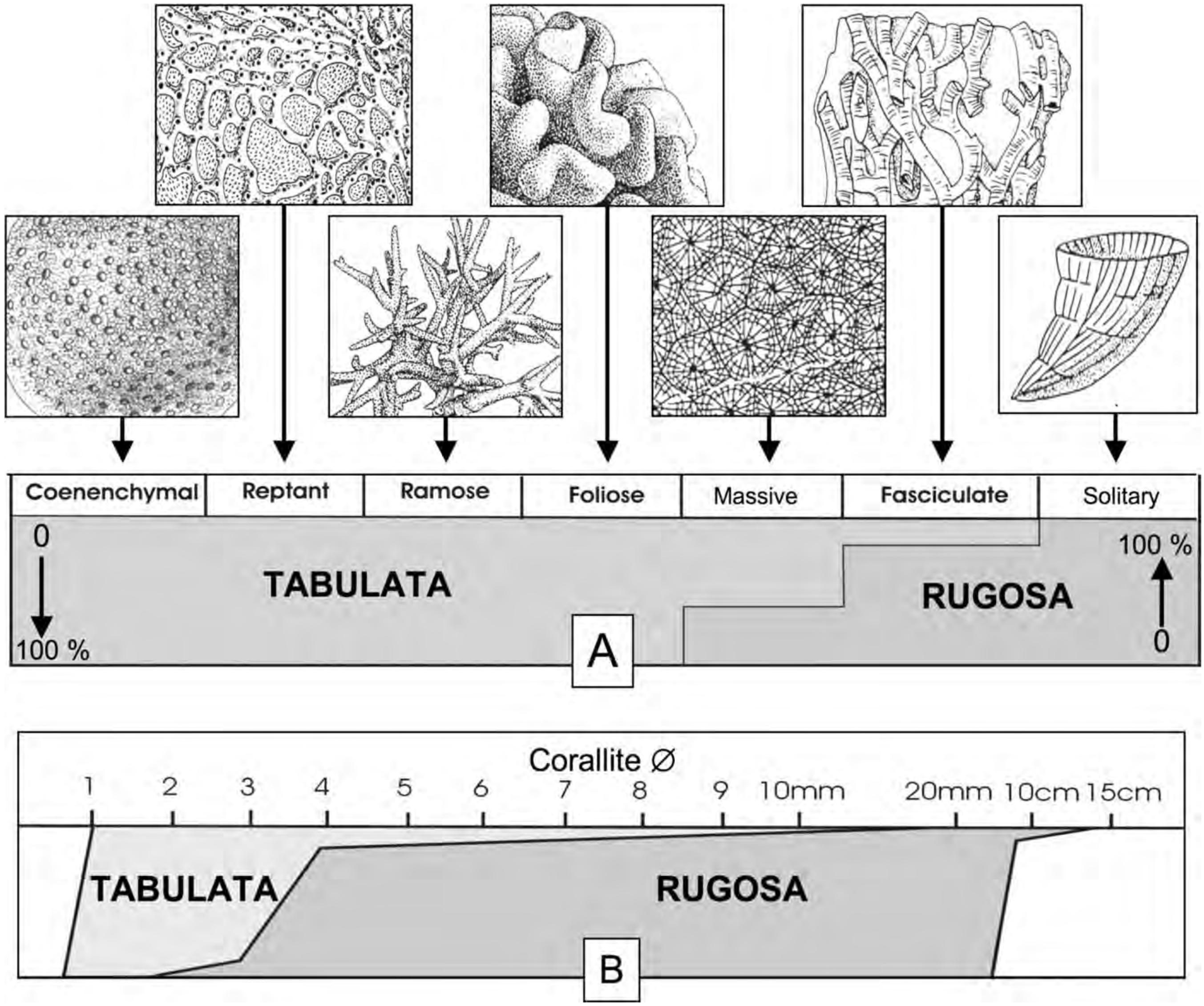

Fig. 1. (A) Comparison of the main forms of coralla in tabulate and rugose corals. (B) Comparison of the corallite diameters in Tabulata and Rugosa. Most Tabulata have diameters varying between 1 and 3 mm, whereas most Rugosa have diameters varying between 4 and 60 mm.

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

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

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

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

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

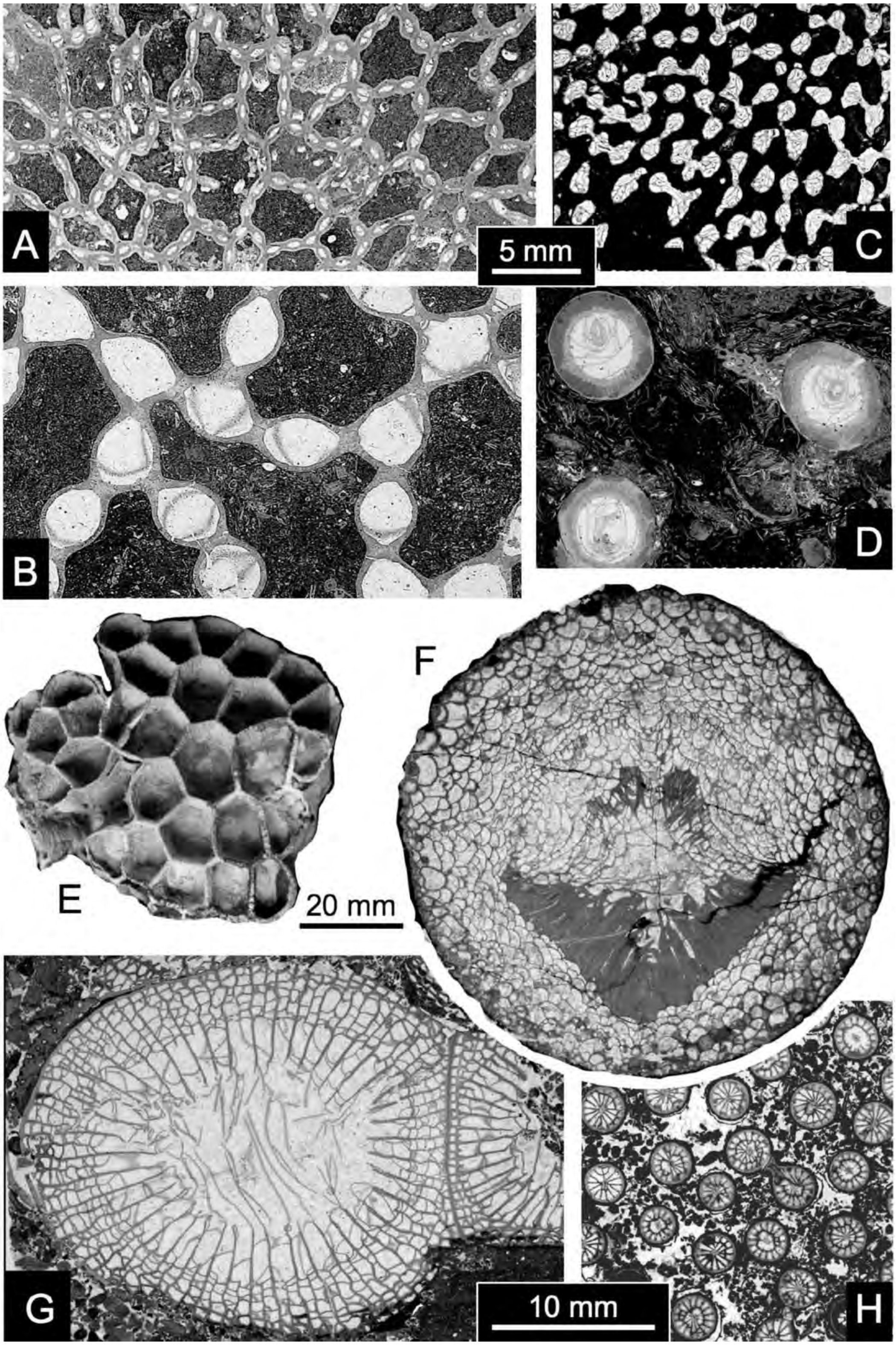

Fig. 2. (A–E) Some examples of corallite sizes in tabulate and rugose corals; A–D are at the same magnification to allow comparisons. (A) *Catenipora* sp. (Llandovery, Estonia), a cateniform coral with very narrow corallites. (B) *Catenipora maxima* (same locality). (C) A very narrow syringoporid (Lower Carboniferous of Hunan, China). (D) *Adaverina* sp. (Llandovery, Estonia), a wide syringoporid. (E) *Michelinia* sp. (upper Tournaisian, Omolon region, Russia); it is one of the largest tabulate corals (in the figured colony, mature corallites are between 10 and 15 mm wide). (F–H) Some examples of corallite sizes in rugose corals; G and H are at the same magnification. (F) *Uralinia* cf. *gigantea* (upper Tournaisian, Omolon region, Russia), one of the largest solitary rugose corals (the section figured here is 90 mm wide, but other specimens from the same locality can reach 120 mm wide), it is at the same magnification as in the *Michelinia*. (G) *Siphonodendron scaleberense* (base of upper Viséan, Belgium), the largest species of the genus. (H) *Siphonodendron junceum* (upper Viséan, Belgium), one of the smallest fasciculate rugose corals.

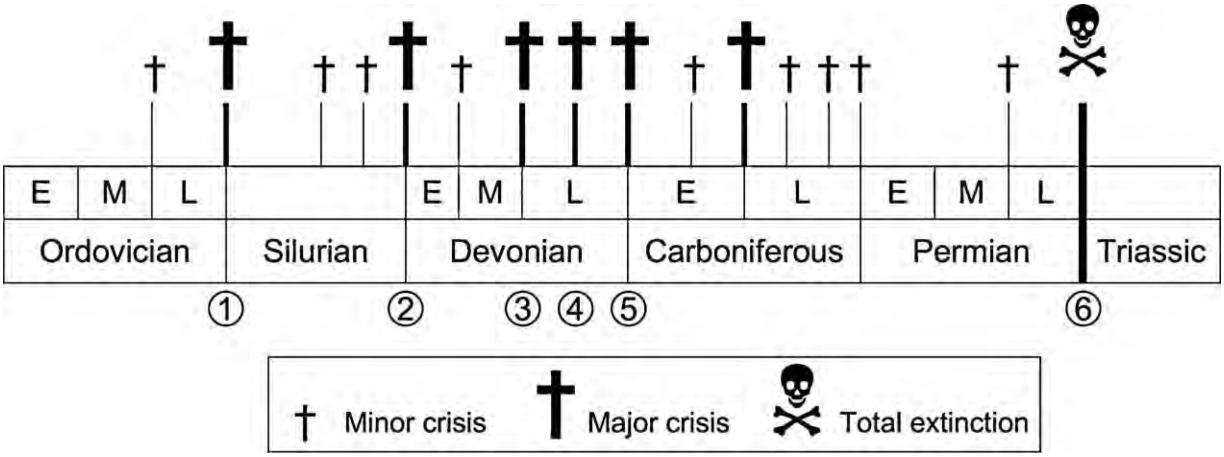

Fig. 3. Crises affecting tabulate and rugose corals. Among these, the Late Ordovician (1), Late Silurian (2), Late Givetian (3) and Late Frasnian (4) crises were particularly major for the tabulates, the Late Famennian crisis (5) was heavy for rugose corals (and fatal for the Palaeozoic stromatoporids), the Late Permian crisis (6) being fatal for both groups.
modified from Scrutton (1997).

of the Belgian Namur-Dinant Basin, *Siphonodendron junceum* (the illustrated example of small-sized colonial rugose corals in Fig. 2H) was abundant and contributed to construction of biostromes in environments devoid of syringoporids. Whereas syringoporids occurred together with *Siphonodendron pauciradiale* in levels more diversified in coral species (Aretz, 2001), but they are rarely associated with *S. junceum*. There was no real competition between syringoporids and *S. junceum* as it is suggested by their similar shape and size, because the more diverse *Siphonodendron* biostromes with *Syringopora* tend to occur in relatively shallow-water depths, whereas *S. junceum* biostromes are often in deeper water shelf settings (Aretz and Herbig, 2003; Somerville and Rodríguez, 2007).

The large-sized cerioid micheliniids were relatively common in the Tournaisian and in the early Viséan of Western Europe, which is devoid of cerioid Rugose corals (the cerioid genus *Lithostrotion* does not appear until the middle Viséan). This also suggests that they developed and occupied cerioid rugose coral niches in environments or basins where *Lithostrotion* was absent. A competition possibly occurred secondarily by migrations.

Therefore, Tabulata and Rugosa have not only different bodyplans but also, with a few exceptions, different forms of coralla and corallite sizes. These indicate that they occupied different niches and there was no real competition between them. This situation was probably established from the origin of the two groups and was definitively established from the earliest Silurian.

3. Coral extinctions

There are about 16 recorded crises affecting Palaeozoic corals (Fig. 3). Among these, some were responsible for the demise of major types of tabulate coralla (Scrutton, 1988, 1997):

- the end Ordovician crisis (Fig. 3, no. 1), with the demise of the coenenchymal perforate coralla;
- the end Silurian crisis (Fig. 3, no. 2), with the demise of the cateniform coralla (Halysitina);
- the end Givetian crisis (Fig. 3, no. 3), with the end of the coenenchymal imperforate colonies (Heliolitina) and the Favositidae;
- the late Frasnian crisis (Fig. 3, no. 4), with the extinction of the foliose and ramose types of colonies (Alveolitina, most of Pachyporicae).

Tabulate corals, which were dominant compared with the rugose corals, never recovered from this late Frasnian crisis. Afterwards their main representatives belong to the Auloporida (among which Syringoporidae were particularly common) and the Micheliniidae.

Rugose corals suffered also during these crises (Oliver and Pedder, 1994; Scrutton, 1988, 1997; Poty, 1999), but only the operculate type (Goniophyllidae) completely disappeared at the end of the Givetian.

4. Attempts to recover extinct forms

4.1. Recovering extinct morphologies at a low level (without major morphological evolution)

At the specific or generic level, evolutionary convergences allow to recover extinct morphotypes. The recovery of the "*Palaeosmilia* morphotype"—i.e., a large coral with numerous septa extending near or at the axis and numerous small tabellae forming a flattened dome with upturned edges and axially sagging—during the latest Tournaisian after the extinction of the Strunian "*Palaeosmilia*" *aquisgranensis* is an example of such an evolutionary convergence (Fig. 4A–D).

"*Palaeosmilia*" *aquisgranensis* (Fig. 4A and B) is common in the uppermost Famennian (Strunian substage, RC0β Coral Zone) of the Namur-Dinant basin, from the Avesnois in northern France to the Aachen area in western Germany. The species

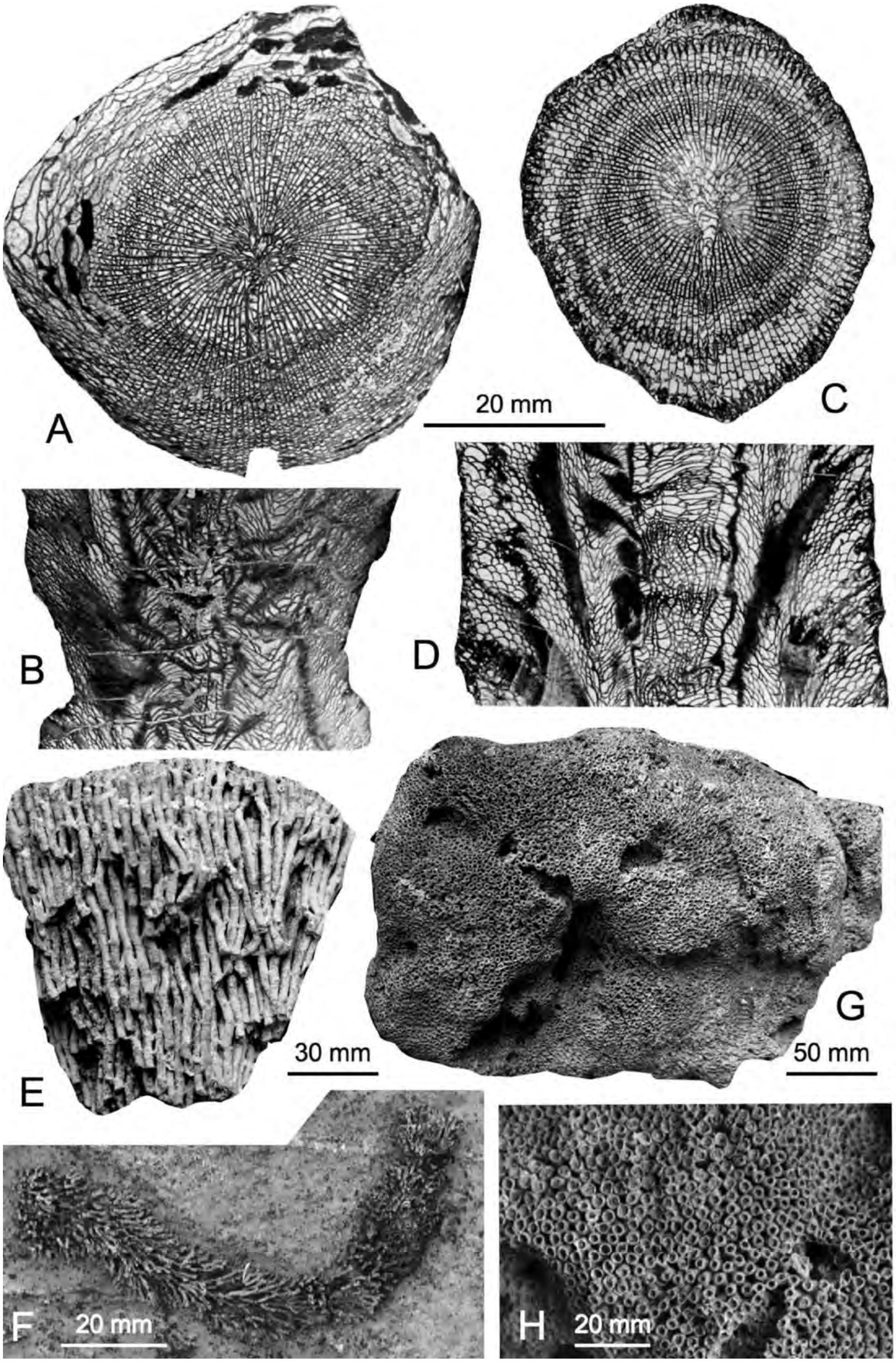

Fig. 4. (A–D) Morphological convergence between *Palaeosmilia murchisoni* (C and D) and the older "*Palaeosmilia*" *aquisgranensis* (A and B); same magnification. (A) "*Palaeosmilia*" *aquisgranensis*, Strunian (uppermost Famennian), Stolberg, Germany, transversal section. (B) "*Palaeosmilia*" *aquisgranensis*, same specimen, longitudinal section. (C) *Palaeosmilia murchisoni*, upper Viséan, Visé area, Belgium, transversal section. (D) *Palaeosmilia murchisoni*, same specimen, longitudinal section. (E–H) Variation in the corallum form in syringoporids. (E) *Syringopora ramulosa* (fasciculate), upper Tournaisian, Belgium. (F) Subramose undetermined syringoporid, lowermost Viséan, Guangxi, China. (G) *Roemeripora* sp. (subcerioid), upper Viséan, Royseux, Belgium. (H) A close-up of the former showing the densely packed corallites.

showed a large variability, from cylindrical, relatively thin corallites 2–3 cm in diameter, living in shallow-water environments with argillaceous inputs, to large (up to 7 cm in diameter) sometimes with lonsdaleoid dissepiments living in shallow-water stromatoporoid biostromes. The septal microstructure of "*P.*" *aquisgranensis* is different from the one known in *P. murchisoni*, the Viséan type species of the genus (Fig. 4C and D): a mesoplasm and a thick stereoplam for the former, only one fibrous layer for the latter. That allows to consider the Strunian one as belonging to a distinct genus, not yet formally named, and probably closely related to the genus *Campophyllum* from which it could have evolved. This relationship is suggested by some fossils with a tabularium not so highly divided and similar to that in *Campophyllum* sp. of Poty (1984a, pl. 2, Fig. 4). The species disappeared with the Hangenberg event (the major crisis at the end of the Famennian; no. 5 in Fig. 3).

The oldest *Palaeosmilia* s. str. is known from the uppermost Tournaisian. It shows similar characters with *Aulokoninckophyllum* (known from the lower part of the upper Tournaisian) from which it could arise, which include carinate septa, a divided tabularium that sometimes developed a poorly defined aulos (such as in some *Aulokoninckophyllum*). From the Viséan, *Palaeosmilia murchisoni* resembled the Strunian "*Palaeosmilia*" and lived in comparable shallow-water environments in which it developed similar ecotypes. *Palaeosmilia*-like corals are not restricted to the Strunian and the Carboniferous, but are also common in the Silurian and in the Lower-Middle Devonian.

4.2. *Recovering extinct morphologies at a higher level*

Because of their particular body plan, it is understandable that corals such as Heliolitids were not replaced through a convergent evolution from other groups of surviving tabulate corals. Foliose, ramose or cerioid tabulate corals with small-sized corallites were also never replaced by either, other tabulates, or rugose corals. However, there were some failed attempts to recover these forms. For example, during the Early Carboniferous, syringoporids (Fig. 4F) were relatively common and widespread and some of them attempted to recover extinct cerioid alveolitid-favositid-like coralla by developing domal to bulbous subcerioid colonies. This trend probably occurred sometimes, giving rise, for example, to the subcerioid *Roemeripora* in the Carboniferous (Fig. 4H and I), but seldom to a true cerioid taxon. Others attempted to recover extinct ramose coralla by developing subcolumnar to slightly subramose colonies (Fig. 4G). However, they failed to give rise to true ramose coralla.

Similarly, some Carboniferous micheliniids developed relatively small-sized corallites, but they never reach the corallite size and the form of the extinct favositids.

After the extinction of the tabulate and rugose corals at the end of the Permian, the diphyletic Scleractinia took up almost all the growth forms known in the former groups, even those that had disappeared a long time ago and were not replaced, such as the ramose, foliose or coenenchymal colonial forms.

5. Variability: the breeding ground for speciation

Rugose corals presented a high rate of morphological and size variability at different levels: in solitary corals, between specimens belonging to the same population of a species (intrapopulational variability), between populations living in different environments (ecotypic variability), and between populations developing in different areas (geographic variability).

Similar variabilities occurred also in compound coralla which showed an additional variability between corallites of the same colony (intracolonial variability) or during the life of a single corallite due to environmental changes or stresses, whether seasonal or not.

Intracolonial or intraspecific variabilities in the morphological characters can be as high as, or higher than, those usually considered to recognize different species and sometimes different genera. For example in the Viséan, cerioid rugose corals described by Sutherland (1989) show alternations of *Stelechophyllum*-like and *Sciophyllum*-like patterns. In *Stelechophyllum*, septa usually extend across tabularium to the columella and are absent in the lonsdaleoid dissepimentarium, whereas in *Sciophyllum* the columella is absent and septa absent or greatly reduced.

Some environmental factors of these variabilities have been enhanced. For example, Javaux (1994) compared similar lower Viséan coral assemblages in different environments; Poty (1981) showed that the development of connecting processes, the strengthening of the columella and the twisting of corallites in *Siphonodendron* were under the influence of currents.

Variability affects corals not only at the mature stage but also during their ontogeny or their astogeny. During the ontogeny, it can give rise to populations in which young corallites are sometimes relatively different from each other. For example, this can be observed in the ontogenies of *Siphonophyllia cylindrica*, *S. rivagensis* and *Conilophyllum priscum* described by Boland (1997), or in the variability of *Campophyllum flexuosum* (Uppermost Famennian) at different growth stages (Fig. 5).

During the astogeny, the variability can affect the form of coralla. For example, in *Phillipsastrea lacunosa* from the Upper Frasnian of Poland, the corallum varied from phaceloid to pseudocerioid (Wrzolek, 1993), in *Lonsdaleia* (*Serraphyllum*) *serraensis* and *L.* (*S.*) *vineensis* from the Serpukhovian of South France, the colonies may have fasciculate, subcerioid, and cerioid parts (Poty and Hecker, 2003), and in the fasciculate *Siphonodendron ondulosum*, turbulence can initiate a subcerioid habitus (Poty, 1993).

The variability in tabulate corals was also high, but affected mainly the growth-form and the corallum because their morphological characters are very simple and not as complex as those of the rugose corals. Examples of variability have been described in favositids (Young and Elias, 1993) and heliolitids (Scrutton, 1993; Young and Elias, 1993).

If the importance of the intraspecific variation of tabulate and rugose corals constitutes a serious problem for coral systematics and for the reconstruction of phylogenies, as pointed out by Oliver (1989) and Webb (1996), it is also the breeding ground

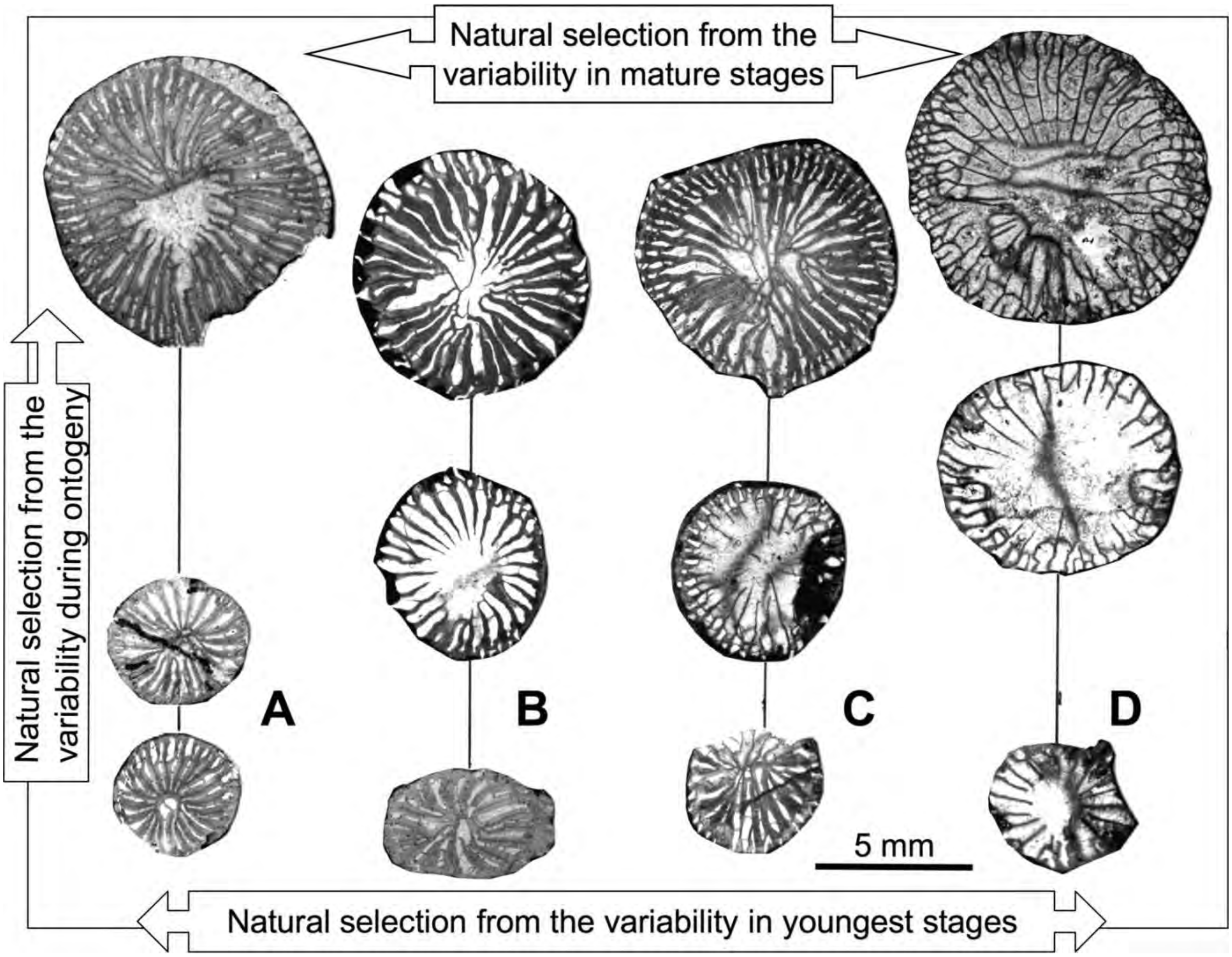

Fig. 5. Morphological variability in four specimens of *Campophyllum flexuosum* (Strunian, uppermost Famennian, Vesdre-Aachen area, eastern Belgium-western Germany) at three stages of their growth. (A) Specimen showing well-developed thick septa all along the growth, with septa connected to the sides of the fossula in the youngest (juvenile) stage; (B and C) in these specimens septa are withdrawn from the axis in the medium (neanic) stages, but not so much in the mature stages; (D) specimen with thin septa withdrawn from the axis in all three stages. That variability is linked to environmental influences and is the basis for the natural selection.

on which the natural selection process acted and gave rise to new taxa.

6. Processes of evolution in rugose corals

The processes of evolution in rugose corals have been addressed in several papers. I will take here as an example the evolution of western European Lithostrotionidae at the specific and generic levels.

6.1. The evolution of the western European lithostrotionids at the specific level

The timing and processes of evolution at the specific level in *Siphonodendron*, *Lithostrotion* and *Diphyphyllum* were described and considered as corresponding to heterochronic processes (Poty, 1984b, 1993). The lineage *Siphonodendron ondulosum* – *S. martini* – *S.* aff. *intermedium* – *S. irregulare* – *S. pauciradiale* – *S. junceum*, as well as the lineages *Lithostrotion araneum* – *L. vorticale* – *L. decipiens* – *L. maccoyanum* and *Diphyphyllum furcatum* – *D. fasciculatum* – *D. gracile* were characterized by a decrease of the corallite sizes. They corresponded to paedomorphic processes (in which the descendant species at the mature stage is similar to the ancestor at the young stage). In the opposite way, the lineages *Siphonodendron ondulosum* (or possibly *martini*) – *S. sociale* – *S. scaleberense*, and *Diphyphyllum furcatum* – *D. lateseptatum* – *D. maximum* were characterized by an increase of the corallite sizes. They corresponded to peramorphic processes (in which the descendant species at the young stage is similar to the ancestor at the mature stage). These lineages can be described successively as paedomorphoclines and peramorphoclines sensu McNamara (1982).

These processes of evolution affect the ontogeny but may not give rise to new species having no characters already corresponding to the ontogenetic and the phenotypic variability of the ancestor.

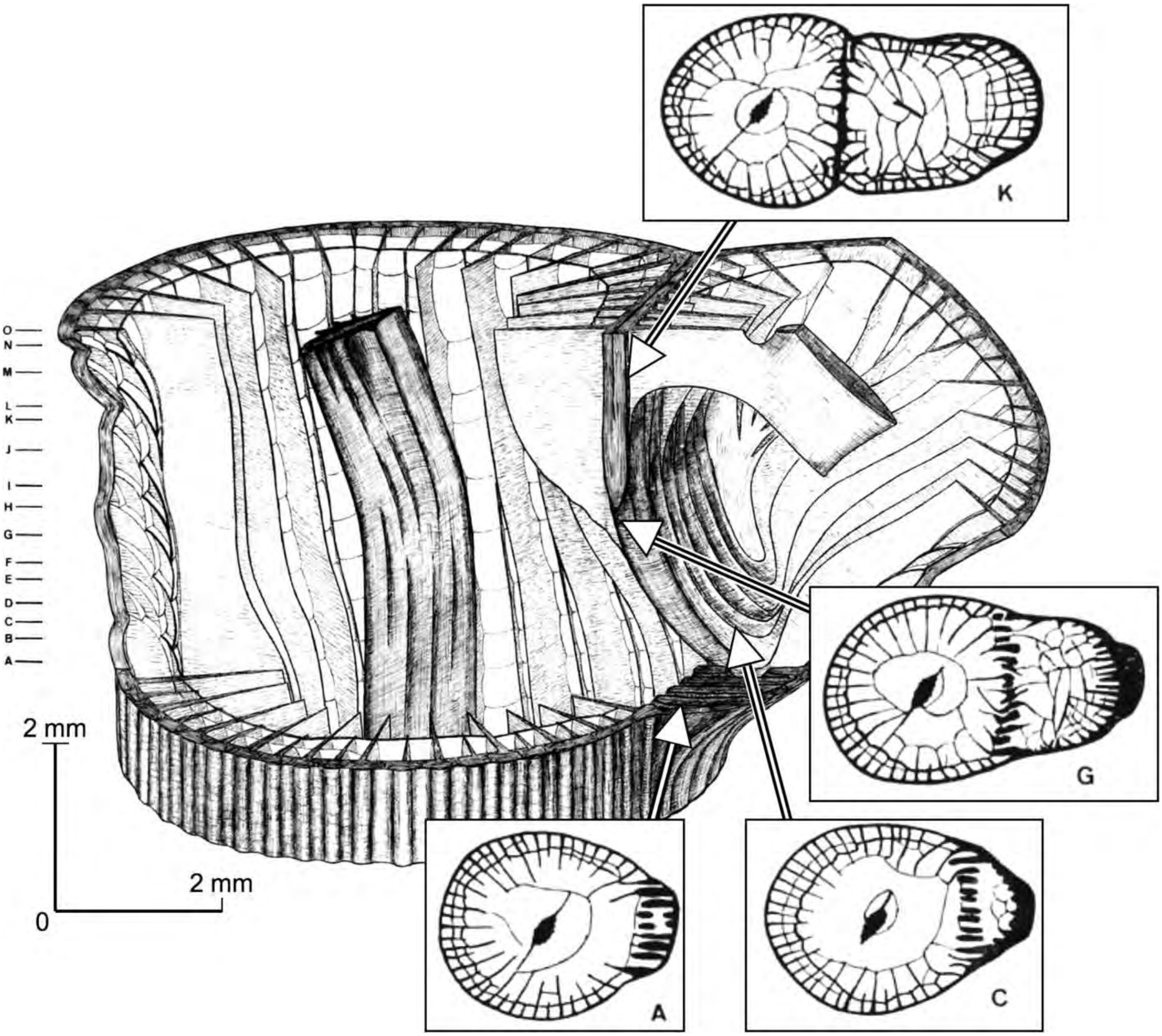

Fig. 6. Lateral increase in *Siphonodendron martini* (from Poty, 1975) with the successive astogenic stages corresponding to the mature stages characterizing the genera *Orionastraea* (C and G) and *Lithostrotion* (K). In the young stage corresponding to (A), the swelling of the septa is extending laterally, whereas the first swelled septa begin to divide and a bulge is developing outward. Tabulae are not represented in the reconstruction.

6.2. *The variability in the astogeny as the driving force for the evolution in the lithostrotionids at the generic level*

6.2.1. *Increase in Siphonodendron, Lithostrotion, and Orionastraea*

The increase in the fasciculate European dissepimented *Siphonodendron* was of the lateral type and has been precisely described in *S. martini* by Jull (1965) (*S.* cf. *martini* for the author) and Poty (1975) (*S. fraiponti* for the author). In summary (Fig. 6), the lateral increase started with the swelling of some septa (both majors and minors) in the periphery of the parent corallite, with no regard to the position of the parent symmetry. Then, the swelling was extended laterally to other septa whereas a bulge developed outward (Fig. 6A). The first swelled septa were divided, giving rise to an area free of septa and initiating the daughter calyx (Fig. 6A and C). Some new septa developed between the original ones. Afterwards, a wall developed progressively, separating the parent and the daughter corallites and indicating that they lost their gastrovascular and tissular connection (Fig. 6G and K). Finally, the daughter corallites are separated from the parent's.

Four stages of relationships between the parent and the daughter corallites, similar to four types of corallite relationships in compound coralla, can be recognized in that astogeny (Figs. 6 and 7):

1. A "thamnasterioid stage" (Fig. 6C), in which the sharing of some septa between the two corallites and the lack of skeletal separation (wall) suggest that the polyps remain integrated and keep connections between their gastrovascular cavities.

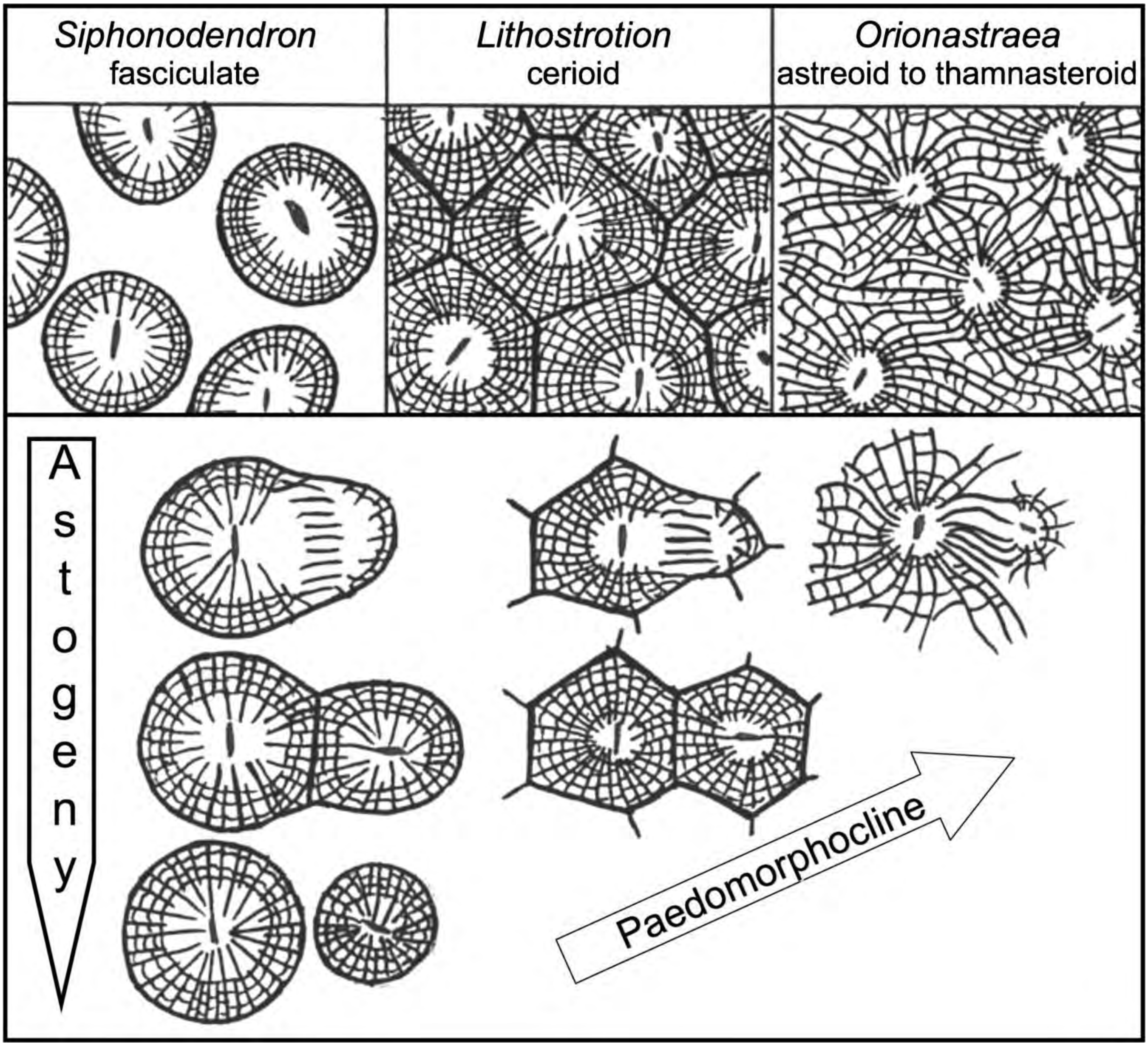

Fig. 7. Paedomorphic evolution in the *Siphonodendron* – *Lithostrotion* – *Orionastraea* lineage.

2. An "astreoid stage" (Fig. 6G), corresponding to the progressive development of a wall reducing the connections.
3. A "cerioid stage" (Fig. 6K), when the wall separates completely the two corallites remain united.
4. A "fasciculate stage", corresponding to the separation of the parent and daughter corallites.

The increase in the cerioid genus *Lithostrotion* was similar as in *Siphonodendron martini*, as stated by Jull (1965) who described it in *Lithostrotion* cf. *portlocki* (=*L. maccoyanum* Milne-Edwards et Haime) and *L. minus* (probably *L. vorticale* (Parkinson)) from the Viséan of Great Britain. But the increase ended before the separation of the corallites. Jull also described increases in Australian "*Siphonodendron*" ("*S.*" *stanvellense*) and "*Lithostrotion*" ("*L.*" *columnare*) and pointed out some differences with those in British species. This supports the idea that the Australian "lithostrotionids" resulted from parallel evolution as suggested by Webb (1994). Scrutton (1983) recognized, in three species of *Lithostrotion*, the presence of ducts (tubular structures) extended from the base of offsets through the dissepiments of the parent corallite. They served to prolong communication between parent and daughter polyps following budding and their function persisted some time after the wall separating parent and offset was developed. He did not find these structures in *Siphonodendron*.

In *Orionastraea*, the beginning of the increase resembles the type described in the dissepimented *Siphonodendron*, but here ended at the astreoid or thamnasterioid stages.

6.2.2. The Siphonodendron – Lithostrotion – Orionastraea lineage

The stratigraphical distributions and the phylogenetic relationships established in the lithostrotionids by Hudson (1930), Nudds (1979), and Poty (1984b, 1993) led to the recognition of a *Siphonodendron* – *Lithostrotion* – *Orionastraea* lineage. However, Nudds (ibid.) considered that each main species of the fasciculate lithostrotionids (*Siphonodendron*) gave rise to cerioid species (*Lithostrotion* s. str.) through subcerioid intermediates. Consequently, *Lithostrotion* would be considered a polyphyletic genus.

My own observations of the variability in the species of *Siphonodendron* and *Lithostrotion*, and of their stratigraphic distributions led me to consider (Poty, ibid.) that *Lithostrotion* was monophyletic: *Lithostrotion araneum*, the oldest middle Viséan cerioid species, evolving from the lower Viséan *Siphonodendron ondulosum*, through subcerioid ecotypes developed in turbulent environments.

That evolution corresponded to a paedomorphic process affecting the astogeny of *S. ondulosum*, giving rise to subcerioid ecotypes, which later on have given rise to the cerioid *L. araneum*, in which corallites remain in connection but separated by a wall ("cerioid stage" in the astogeny of *Siphonodendron*).

Following the same paedomorphocline (sensu McNamara, 1982), *Lithostrotion* had given rise to astreoid *Orionastraea* (astogenic "astreoid stage"), through *L. decipiens* and *O. ensifer* (Nudds, 1979), then to thamnasterioid *Orionastraea* (astogenic "thamnasterioid stage"). Afterwards, the trend continued to more integrated types of colonies (aphroid and indivisoid; Nudds, 1979).

Therefore, the separation of the daughter polyp from the parent's was progressively delayed as compared to the development of the other characters (Fig. 7).

Two species characterized by their large corallite size and high number of septa and referred to *Orionastraea* (*O. ensifer matura* and *O. magna*) are considered by Nudds (1999) to have evolved from another species of *Lithostrotion* (*L. vorticale*), by following a parallel evolutionary trend. Consequently, he referred them to another genus (*Pleionastraea* Nudds).

A comparable trend to more integrated types of colonies was also recognized in the Petalaxidae through the Bashkirian and Moscovian by Kossovaya (1998).

6.3. The development of coloniality from solitary rugose corals

Morphological and stratigraphic considerations lead to the consideration that colonial rugose corals evolved from solitary corals. For example, in the Mississippian:

- Corallites of the colonial *Lonsdaleia* are very similar to corallites of the simple *Axophyllum*. *Axophyllum lonsdaleiforme* (Salée) resembles corallites of *Lonsdaleia duplicata* (Martin) and could be a potential ancestor to *L. duplicata*. *A. lonsdaleiforme* is common in the upper Viséan RC7β Coral Zone, whereas the appearance of the genus *Lonsdaleia* is typical for the RC8 Coral Zone. However, a polyphyletic origin for *Lonsdaleia* from different species of *Axophyllum* has not been rejected.
- During the late Viséan, *Palaeosmilia murchisoni* gave rise to the colonial *Palastraea*. The transition between the two genera is well illustrated by transitional forms showing a limited, but not a true, colonial increase. Such specimens of *Palaeosmilia* with limited increase are known at the base of the upper Warnantian (equivalent to the base of the Brigantian) in Belgium. True colonial corals (*Palastraea*) are known close to the base and are characteristic of the upper Warnantian. Specimens of *Palaeosmilia* with limited increase are also known as low as the upper part of the lower Viséan (RC5 Coral Zone), suggesting that this trend occurred some time before giving rise effectively to a colonial coral.
- The origin of *Siphonodendron* is more difficult to determine. There are at least three stocks of "*Siphonodendron*" showing parallel evolution (Webb, 1994; Fedorowski and Bamber, 2007; Fedorowski, 2008): (1) an European, and partly Asiatic, stock (*Siphonodendron* s. str.), (2) a North American stock, mainly characterized by species with short or amplexoid septa and a weak columella, and (3) an Australian stock, mainly characterized by species with major septa connected to a robust columella, and axial tabellae. The oldest species of *Siphonodendron* s. str. are known in the lower Viséan of the Omolon region (north-eastern Siberia; Conil et al., 1982), and of Europe (Poty et al., 2006). *Siphonodendron* s. str. possibly arises from a solitary columnate coral, closely resembling the Tournaisian *Eostrotion tortuosum* as suggested by Vaughan (1917).

Breviphrentis is a Lazarus genus reappearing in the Famennian of the Belgian-French Namur-Dinant Basin after its "extinction" in the late Givetian (Poty, 1999). Two different species were recognized: *Breviphrentis* sp. A and *Breviphrentis* sp. B (Poty, ibid.); the latter being very common at the level of the Sains shale Formation in the Etroeungt area (northern France). Their stratigraphic ranges in the Famennian are very limited: the Uppermost *marginifera* conodont Zone for the former and the *expansa* Zone for the latter. *Breviphrentis* sp. B presents constrictions and rejuvenescences which were probably due to seasonal variations in the environment because of their regular distribution. Together with constriction stages, axial divisions of the corallite sometimes developed. They can be considered as a response to the same environmental stresses provoking the constriction of the polyp. Indeed, the division of the polyp increased its possibilities to survive as many as the number of resulting divided polyps, and a lower amount of nutrients being requested by each individual.

Therefore, the basic advantage to becoming colonial could be to increase the possibilities of surviving during hard environmental conditions, all the polyps of the colony having the same genotype. Afterwards, other advantages conferred include the possibility of other adaptations and colonization of new niches. Rodríguez and Somerville (this volume) have reviewed the appearance of fasciculates rugose corals in the Mississippian and discuss their possible evolutionary and environmental causes. They consider that one of the most favourable environments for development of colonialism was the top of microbial mud-mounds.

7. Conclusions

The major body plans and corallum forms of the Tabulata and Rugosa developed shortly after their first appearance in the Ordovician. These body plans and corallum forms are shared between the two groups and there are very few overlaps, i.e., competitions. Their diversifications corresponded mainly to heterochronic processes during the ontogeny or the astogeny, and were limited by the degree of morphological variability and constrained by the inherited body plan and the mode of growth. Consequently, that did not allow true innovations, such as a type of colonial development that is not a usual type of increase within a taxon. At a lower level, the limits of the variability in corallite diameters allowed by the polyp morphology could have also prevented the appearance of some types of shapes in rugose corals, such as ramose coralla in which corallites are usually very thin. Thus, the diversification of the tabulate and rugose corals after major extinctions remained limited and did not allow recovering morphologies of extinct groups by parallel evolution.

These evolutionary processes were probably different from those acting during their original evolutionary radiation. After the extinction of the tabulate and rugose corals at the end of the Permian, the diphyletic Scleractinia took up almost all the growth forms known in the former groups, even those that had disappeared a long time ago and were not replaced, such as the ramose, foliose or coenenchymal colonial forms.

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Research paper

Unusual offsetting in Serpukhovian (Lower Carboniferous) representatives of the rugose coral genus *Schoenophyllum* Simpson, 1900

Sergio Rodríguez[a,*], E. Wayne Bamber[b]

[a] *Departamento y U.E.I. de Paleontologia, Universidad Complutense y C.S.I.C., Madrid, Spain*
[b] *Geological Survey of Canada, Calgary, Canada*

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Abstract

Schoenophyllum has been described as a columellate, fasciculate genus in which the corallites bear slender lateral processes regarded as supporting structures or as tubules connecting adjacent corallites. Recent investigation of Serpukhovian specimens from the Etherington Formation and its lateral equivalents in western Canada has shown these lateral processes to be sub-horizontal to moderately elevated tubule-like structures forming the initial stages of new offsets and commonly containing tabulae. They locally reach and may interfere with the walls of neighbouring corallites, but remain structurally distinct from them and do not allow communication between parent and adjacent corallites. The initial, tubule-like stage is followed by a steeply elevated to vertical, sparsely septate stage in which the axial structure is developed as a prolongation of the cardinal septum. The origin and nature of the axial structure suggests assignment of *Schoenophyllum* to the family Petalaxidae.

Keywords: *Schoenophyllum*; Canada; Serpukhovian; Offsetting; Palaeobiology; Blastogeny

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1. Introduction

1.1. *Occurrence and age of the genus*

The genus *Schoenophyllum* Simpson, 1900 is known from the Upper Viséan and Serpukhovian of the mid-continent region of the USA and from widely separated areas in the North American Cordillera. In the mid-continent region, it occurs in the Ste. Genevieve Limestone of Kentucky, Indiana, and Tennessee (Easton, 1957; Sando and Bamber, 1985). In the northern Cordillera, it occurs in the Alapah Formation of the eastern Brooks Range of northeastern Alaska (Armstrong, 1972) and the British Mountains of northern Yukon (undescribed). Farther south, it is common in the Etherington Formation in the southern Canadian Rocky Mountains of southwestern Alberta and southeastern British Columbia (Nelson, 1960, 1961; Sando and Bamber, 1985). It also occurs in the northwestern USA, in the Great Blue Limestone and the Scott Peak Formation of Idaho, and the Monroe Canyon Limestone of Utah (Sando and Bamber, 1985) (Fig. 1).

Most of the specimens studied for this paper were collected from middle ramp carbonates in the lower Etherington Formation of the Lizard Range near Fernie, southeastern British Columbia. They occur consistently in the informally named Cyclamen Member of that formation (Scott, 1964) where they form part of a diverse coral fauna associated with lower Serpukhovian microfossils of Foraminiferal Zone 17 (Mamet and Skipp, 1970) in the lower part of Coral Zone V of Sando and Bamber (1985) (= *Lithostrotion genevievensis* Zone of Nelson, 1960, 1961). Supplementary morphological information was also obtained from other specimens collected in the southern Canadian Rocky Mountains and the British Mountains of northern Yukon. Coral specimens illustrated in this paper (hypotypes GSC 124274–124279) are kept in the type collection of the Geological Survey of Canada, Ottawa.

1.2. *Previous descriptions and taxonomic assignments*

In his original description of the genus *Schoenophyllum*, Simpson (1900) designated *S. aggregatum* as the type species, noting that the axial structure is formed by elongation and

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* Corresponding author.
E-mail addresses: sergrodr@geo.ucm.es (S. Rodríguez), wabamber@nrcan.gc.ca (E.W. Bamber).

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Fig. 1. Occurrence of *Schoenophyllum* Simpson, 1900 in North America. 1 – northeastern Alaska, Brooks Range; 2 – northern Yukon, British Mountains; 3 – southwestern Alberta and southeastern British Columbia, southern Canadian Rocky Mountains; 4 – Custer and Lemhi counties, Rocky Mountains of east-central Idaho, USA; 5 – Kentucky, Indiana and Tennessee, USA.

enlargement of the cardinal septum, that the tabulae are broad, commonly ascending to the axis, and that minor septa are inconspicuous. He also reported the presence in the type specimens of slender, lateral processes 3–4 mm in length, which he described as regularly diminishing in size toward their extremities and ascending to the adjacent "corallum" (= corallite?). He regarded these processes as supporting structures. An ascending process is shown in the interpretive drawing of a longitudinal section presented by Simpson (1900). According to the orientation of the dissepiments, however, this drawing represents an inverted corallite (also noted by Easton, 1957) with a descending, rather than an ascending, process.

Despite the establishment of the genus name *Schoenophyllum*, many geologists continued for decades to use the name *Lithostrotion harmodites* Milne-Edwards et Haime, 1851 for specimens of *Schoenophyllum* from the Ste. Genevieve Limestone and correlative formations in several states of the USA (e.g., Miller, 1919; Weller, 1920; Butts, 1922; Weller, 1923). Easton (1957), in his review of Simpson's type material and related corals, presented a more complete list of publications referring to *L. harmodites* and argued that the type material for that species belongs to a Silurian species of the genus *Synaptophyllum* Simpson, 1900. From his study of a Carboniferous specimen that he considered to be conspecific with *Schoenophyllum aggregatum*, Easton (1957) concluded that the long septum joining the axial structure is the counter septum, not the cardinal septum as was maintained by Simpson (1900). He mentioned the presence of lateral processes, but apparently assigned them little taxonomic value. He re-described the type material of *S. aggregatum* and re-assigned the species to the genus *Siphonodendron* McCoy, 1849. To avoid using the pre-occupied name *Siphonodendron aggregatum* McCoy, 1851, he proposed the name *Lithostrotion* (*Siphonodendron*) *genevievensis* for Simpson's species, thereby highlighting its widespread occurrence in the Ste. Genevieve Limestone.

Following Easton's (1957) study, illustrations of this species, without descriptions, were published under the names *L. genevievensis* by Nelson (1960, 1961) and *Lithostrotion* (*Siphonodendron*) *genevievensis* by Bamber and Copeland (1970). A new Serpukhovian species, probably belonging to the genus *Schoenophyllum*, was described by Armstrong (1972) as *Siphonodendron ignekensis* from the Alapah Limestone of northeastern Alaska. He did not mention processes in his description.

Hill (1981) suggested that *Paralithostrotion* Gorsky, 1938 may be a junior synonym of *Schoenophyllum* and stated that the corallites in *Schoenophyllum* are "anchored laterally to one another by slender, ascending processes". She also indicated that *Schoenophyllum* may belong in the Petalaxidae, but stated that the counter septum is long, with its inner margin enlarged to form the axial structure. Sando and Bamber (1985) followed Easton (1957) in identifying the septum connected to the axial structure as the counter septum. They stated, however, that the manner of formation of the axial structure, the presence of almost horizontal tabulae, and the development of processes are sufficient for separating *Schoenophyllum* from *Siphonodendron*, and therefore they reinstated the name *S. aggregatum*. They regarded the lateral processes not as supporting structures but as connecting tubules, based on the fact that they commonly reach and contact neighbouring corallites. Most recently, Webb (1990) described *S. dalmaensis* from Australia and indicated the presence of rare connecting tubules, suggesting that one of them may represent an offset.

2. Morphology

As noted above, the lateral processes in *Schoenophyllum* have been interpreted as supporting structures (Simpson, 1900; Hill, 1981) and connecting tubules (Sando and Bamber, 1985; Webb, 1990). These possibilities are discussed below, followed by a new interpretation based on our investigation of Canadian specimens, from which we conclude that the lateral processes are the very early stages in the development of offsets.

2.1. Supporting structures

Supporting structures are rare in adult stages of colonial rugose corals (Scrutton, 1998). They are common in the solitary genera of some families, such as the Axophyllidae, but are unknown in the colonial representatives of those families. Supporting structures formed by lateral outgrowth of the walls of adjacent corallites have been described in some Devonian colonial rugose corals (*Synaptophyllum*, *Acinophyllum*, *Eridophyllum*; see Oliver, 1976). The supporting system in colonial rugose corals normally consists of a strong basal attachment. Support for new corallites is achieved by attachment to, or direct contact with, parent corallites and in some instances by contact with the underlying sediment. Also, supporting processes (rootlets, talons or lateral expansions; see Rodríguez, 2004) are mostly directed downward or are horizontal.

In contrast to the features described above, we have observed that the lateral processes in our specimens of *Schoenophyllum* are almost entirely sub-horizontal to moderately elevated (Fig. 2B and C) and only rarely depressed, as in the longitudinal section of the type species figured by Easton (1957). Contrary to what would be expected if they were normal supporting structures, the lateral processes in our specimens have not been observed on the external surfaces of colonies, in contact with solid skeletal elements, such as brachiopod, mollusc or echinoderm fragments. Furthermore, contact between lateral processes and neighbouring corallites is most common in crowded colonies in which the corallites are closely spaced and already well supported, but less common in loosely packed colonies with widely spaced corallites, which presumably would require greater support.

2.2. *Connecting tubules*

Interpretation of the lateral processes in *Schoenophyllum* as connecting tubules (Sando and Bamber, 1985; Webb, 1990) implies an important departure in the palaeobiology of these corals. Development of connecting tubules implies a high level of communication between corallites, which is quite rare in fasciculate rugose corals. Among other Carboniferous colonial rugose corals, such tubules have been described only in *Tschernowiphyllum* Dobrolyubova, 1958 and *Paralithostrotion* Gorsky, 1938, which were placed in synonymy by Rakshin (1965) and Hill (1981). In the Permian fasciculate rugose coral genera *Sandolasma* Fedorowski, Bamber et Stevens, 2007 and *Waagenophyllum* Hayasaka, 1924, adjacent corallites are joined by connecting channels, but no tubules are present (Fedorowski, 1980; Fedorowski et al., 2007). “Connecting tubules” were illustrated in longitudinal section by Sando and Bamber (1985, pl. 8, fig. 1) but their figure is not conclusive. It shows several short, lateral “tubules” and a larger, ascending “tubule” reaching a neighbouring corallite and apparently penetrating it. The wall and internal structures of the latter corallite have been partly destroyed, however, and the nature of its contact with the “tubule” is not clear.

From our study of Canadian representatives of *Schoenophyllum*, based on observations from 60 transverse and 35 longitudinal thin sections from more than 40 specimens, we have concluded that the interpretation of the lateral processes as open tubules connecting adjacent corallites must be rejected for the following reasons: (1) The lateral processes open into the corallite from which they originate, but are consistently closed by a continuous wall at their distal ends. Where they reach neighbouring corallites, this complete, distal wall is maintained, allowing no exchange of material or common activity between the two corallites (Fig. 2D and E). (2) Many of the neighbouring corallites were clearly disturbed where they were contacted by lateral processes, commonly showing notable alterations in transverse outline and internal structure (Fig. 2E). Crowding of corallites during colony growth could have been the main cause of corallite deformation (e.g., curved and flattened walls, oval transverse sections), but fragmentation of walls and internal structures must have occurred during subsequent compaction, with the smaller, structurally stronger lateral processes penetrating the relatively thin walls of neighbouring, mature corallites. (3) Many lateral processes extend various distances from the parent corallite without reaching neighbouring corallites (Fig. 2A and D).

2.3. *Offsetting corallites*

Having rejected the possibilities that the lateral processes in *Schoenophyllum* are normal supporting structures or connecting tubules, we are left with the conclusion that they are simply the initial stages of offsetting corallites. All offsets passed through this early, aseptate, tubule-like growth stage and most of them developed into complete corallites. Some, however, terminated in early growth stages (Fig. 2B and F) to become lost structures (Fedorowski, 1978). Features indicating unusual offsetting were described in the original type material of the genus by Simpson (1900), who noted that the offsets originate from the margin of the calice but that, after further growth, the young corallites have the “appearance of proceeding from the side of the parent corallum at a great distance from the calyx”. A considerable degree of separation of young from mature corallites is also evident in the Canadian specimens, but the amount of separation varies. Such spacing of corallites is known in other rugose coral taxa (e.g., those that form gregaria; Fedorowski, 1980), but is rare in phaceloid colonies.

The initial, aseptate parts of the offsets in our specimens show several notable features:

(i) where they emerge from the originating corallite, they are commonly directed laterally and slightly upward, after which their orientation changes and they are directed upward at various angles (Figs. 2B, C, F and 3A);
(ii) contrary to the observation by Simpson (1900) that the “lateral processes” in the type material regularly become smaller toward their extremities, the early, aseptate stages in many of the Canadian specimens reach their maximum width at their distal ends, where they commonly have a circular or polygonal outline in transverse section (Fig. 3B and C). A distal decrease in size is shown by offsets that terminated without reaching another corallite (lost structures, Fig. 3B and C) or producing the septate stage of a new corallite (Fig. 3B, upper left);
(iii) the initial, tubule-like parts of some offsets show a small number of tabulae, most commonly near their junction with the parent corallite (Figs. 2B, 3B and C), but they never contain septa or any other internal structure;
(iv) all observed offsets were formed from mature corallites and several may develop at approximately the same level in a parent corallite (Fig. 3C).

Colonies with a large number of early, aseptate offsets also show a large number of young corallites, usually well separated from adult corallites. Some of the young corallites are in such an early growth stage that they show only one septum (Fig. 3D),

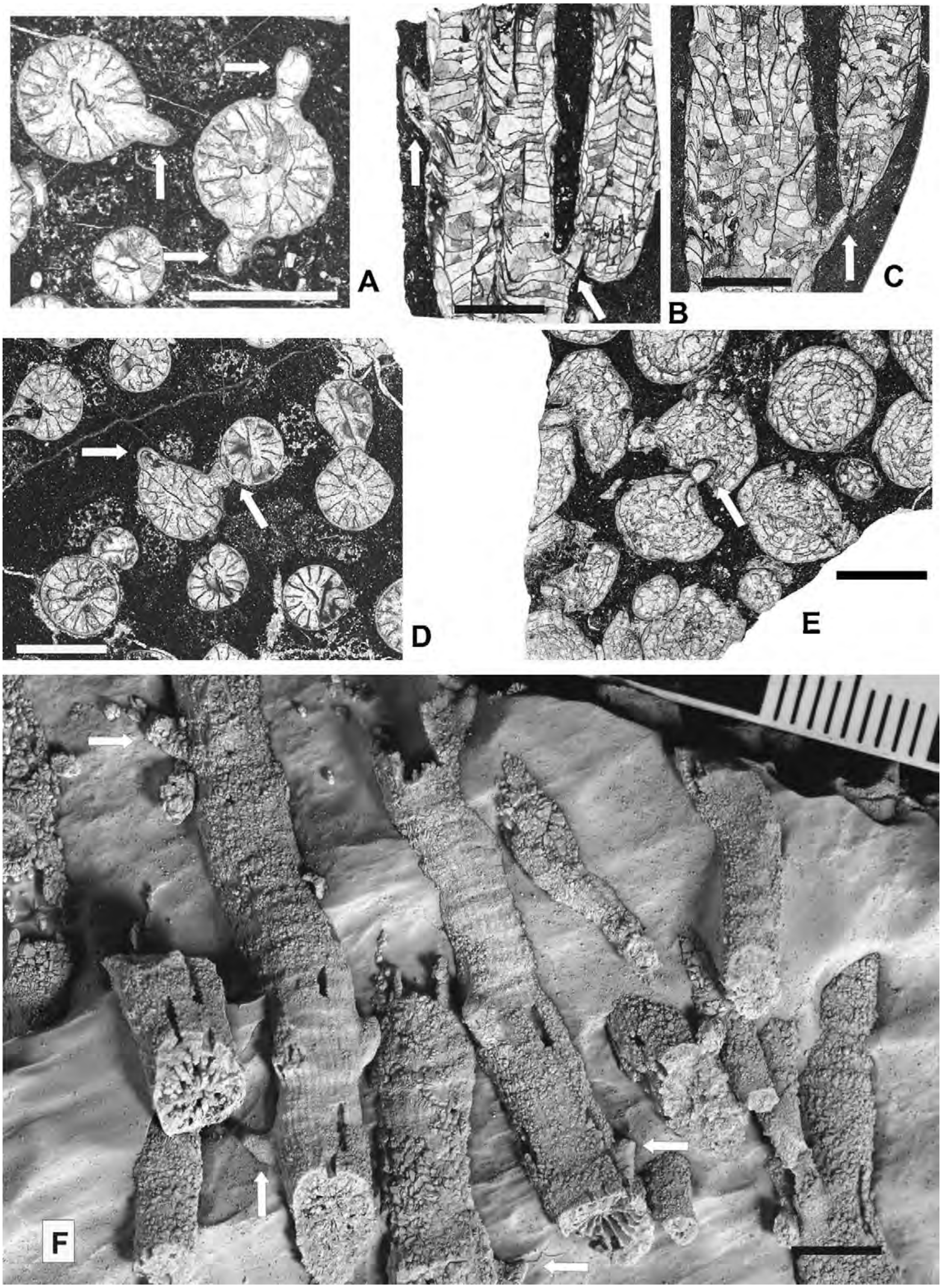

Fig. 2. (A) *Schoenophyllum* sp. Transverse thin section showing sub-horizontal initial stages of offsets containing tabulae and terminating in matrix (arrows). Hypotype GSC 124274, from GSC locality O-53422, southwestern Alberta, Early Serpukhovian. (B) *Schoenophyllum* sp. Longitudinal axial section showing offsets (arrows). Hypotype GSC 124275 from GSC locality O-66177, southwestern Alberta, Early Serpukhovian. (C) *Schoenophyllum* sp. Longitudinal acetate peel showing initial, non-septate stage originating from parent corallite and leading to septate stage of offset (arrow). Hypotype GSC 124275, from GSC locality O-66177, southwestern Alberta, Early Serpukhovian. (D) *Schoenophyllum* sp. Transverse thin section showing initial stage of offsets with open proximal and closed distal ends (arrows). Hypotype GSC 124276, from GSC locality C-193610, southeastern British Columbia, Early Serpukhovian. (E) *Schoenophyllum* sp. Transverse thin section showing initial stage of offset penetrating and disrupting neighbouring corallite (arrow); distortion and fragmentation of corallites caused, at least in part, by compaction. Hypotype GSC 124277 from GSC locality C-161245, northern Yukon, Early Serpukhovian. (F) *Schoenophyllum* sp. External view showing offsets extending laterally and terminating without reaching neighbouring corallites (arrows). Hypotype GSC 124278, from GSC locality C-11823, northern Yukon, Early Serpukhovian. Scale bar = 5 mm.

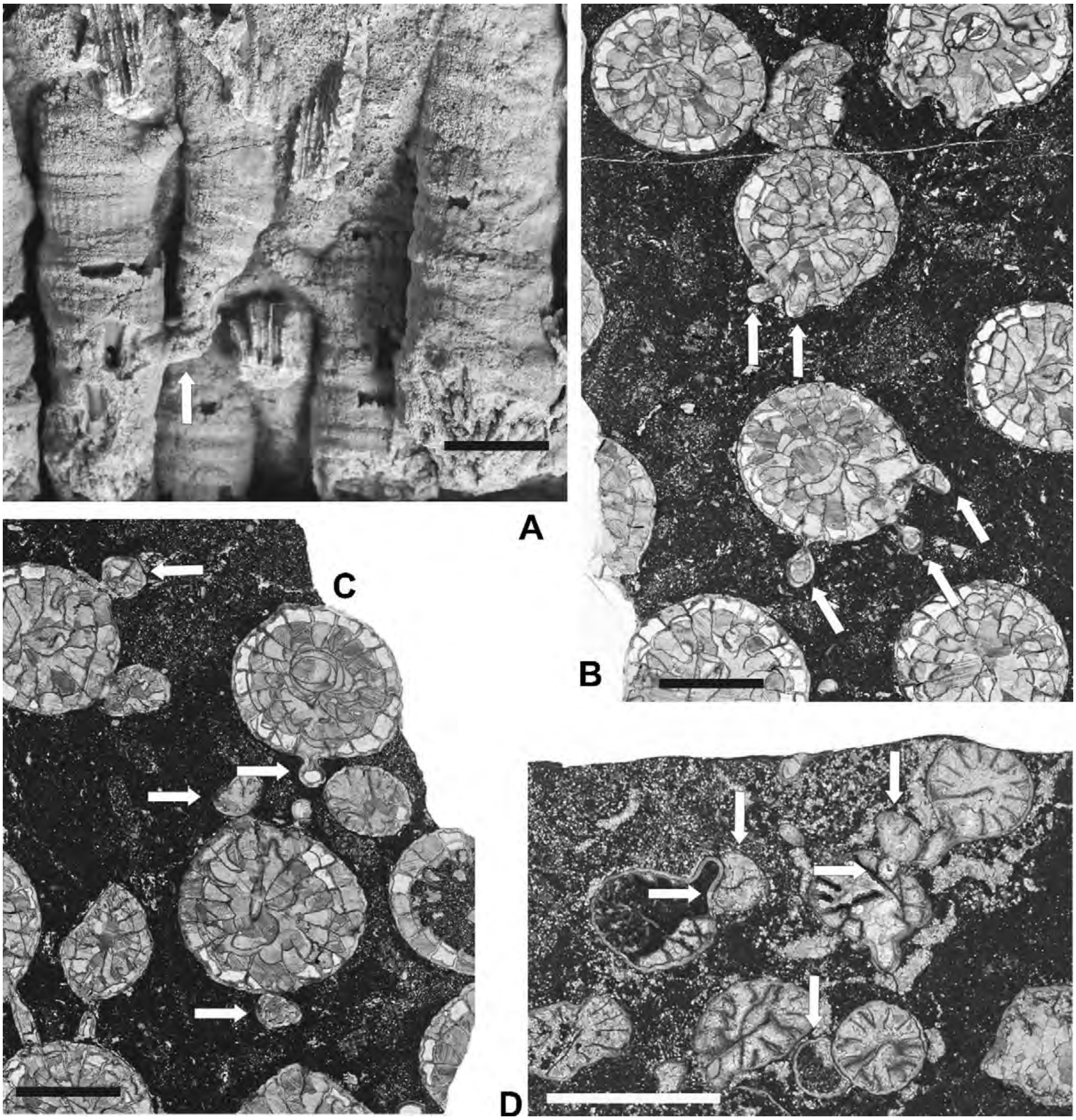

Fig. 3. (A) *Schoenophyllum* sp. External view showing initial, sub-horizontal stage of offset originating from parent corallite and leading to new corallite (arrow). Hypotype GSC 124279, from GSC locality O-55233, northern Yukon, Early Serpukhovian. (B) *Schoenophyllum* sp. Transverse thin section showing enlarged distal ends of immature offsets (arrows). Hypotype GSC 124275, from GSC locality O-66177, southwestern Alberta, Early Serpukhovian. (C) *Schoenophyllum* sp. Transverse thin section showing several offsets formed from parent corallites at approximately the same level (arrows). Hypotype GSC 124275, from GSC locality O-66177, southwestern Alberta, Early Serpukhovian. (D) *Schoenophyllum* sp. Transverse thin section showing deformation of neighbouring corallite walls (horizontal arrows) and early stages of offsets with only one septum developed (vertical arrows). Hypotype GSC 124276, from GSC locality C-193610, southeastern British Columbia, Early Serpukhovian. Scale bar = 5 mm.

but in a given transverse section none of them appears to be connected with aseptate offsets. To clarify this relationship, several series of transverse acetate peels and one series of longitudinal peels were prepared from specimens showing numerous young corallites (Figs. 4 and 5; see Section 2.4). These peels show that the enlarged distal ends of the initial, aseptate stages give rise to steeply elevated to vertical, sparsely septate young corallites. Thus, the offsets comprise an initial, aseptate, horizontal to moderately elevated stage, supporting a second, vertical stage of development comprising young corallites which subsequently develop internal structures normal for the genus. The offsets do not begin to develop new structures (septa, initially) until the beginning of the vertical growth stage (Figs. 2B, C, 3B, 4 and 5), and therefore, at or near their attachment to the parent, they always appear in transverse section as simple “tubules”. To our knowledge, this type of offsetting has not been previously described, but it is regularly developed in all colonies of several species of *Schoenophyllum* studied for this paper. Consequently, it must be regarded as an important diagnostic feature of the genus.

The need for physical support of new corallites may have been a factor affecting colony development in *Schoenophyllum*.

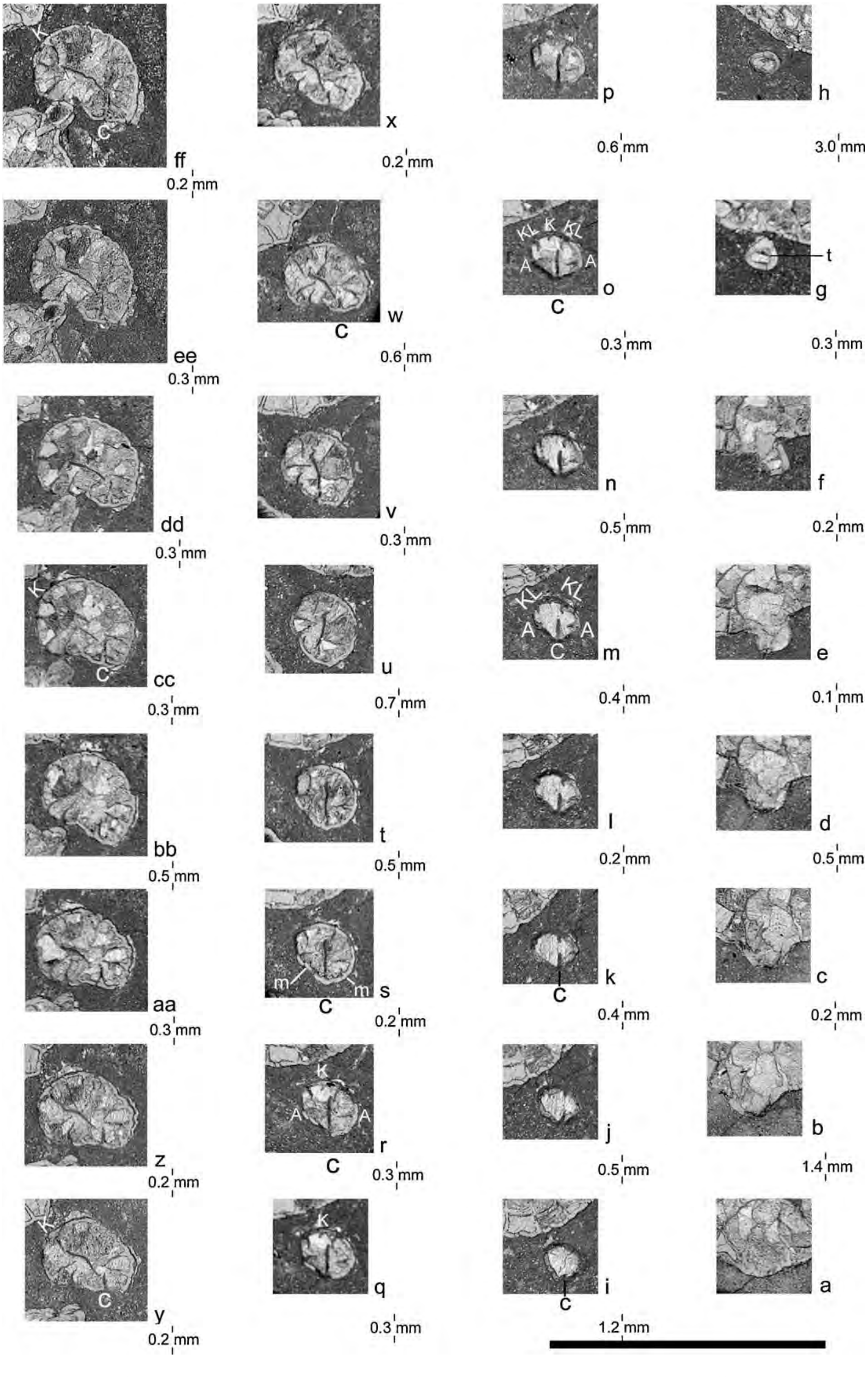

Fig. 4. *Schoenophyllum* sp. Series of closely spaced, transverse acetate peels illustrating early skeletal morphology of offset from well-preserved specimen. C – cardinal septum, K – counter septum, A – alar septa, KL – counter lateral septa, t – tabula, m – newly inserted major septa. Note deformation (bb–ff) of new corallite where contacted by offset from neighbouring corallite. Hypotype GSC 124275, from GSC locality O-66177, southwestern Alberta, Early Serpukhovian. Scale bar = 5 mm.

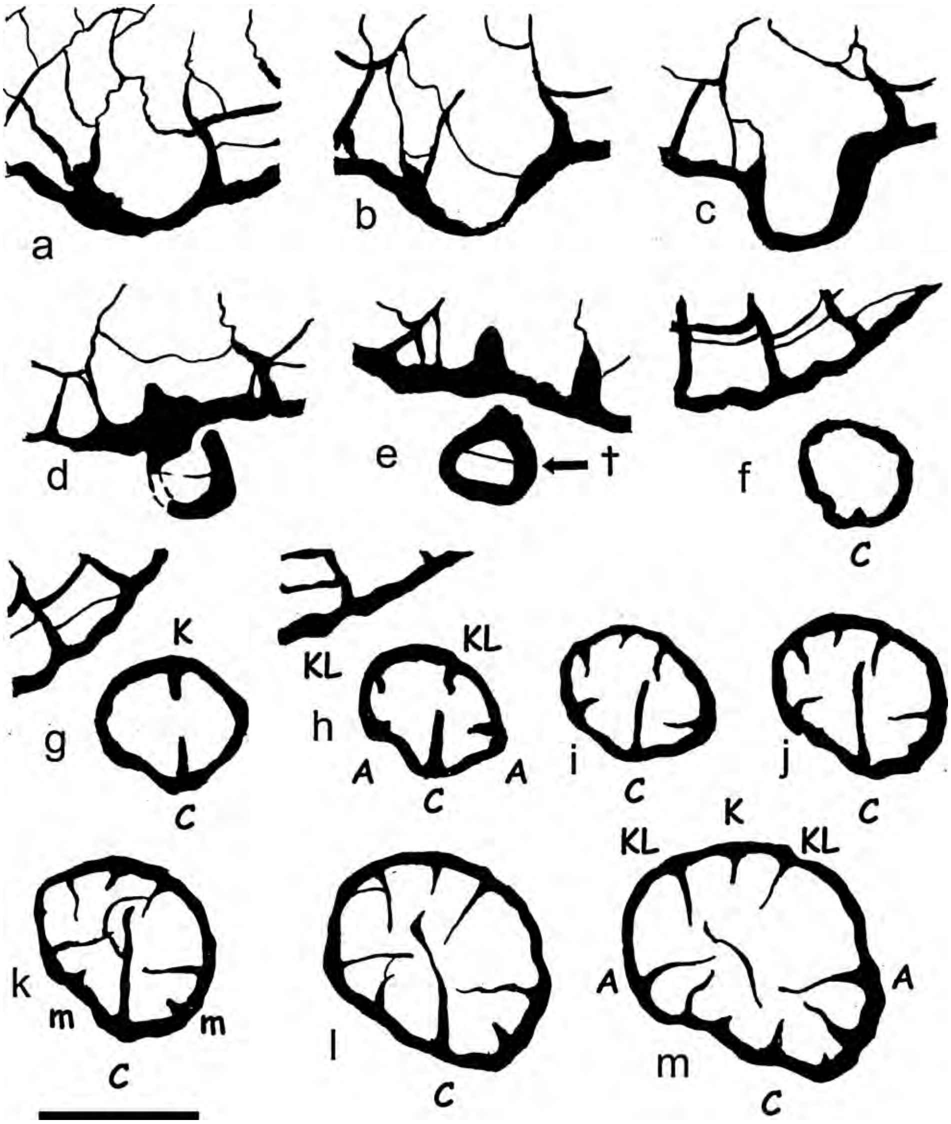

Fig. 5. (a–m) Drawings showing details of the main blastogeny features shown in Fig. 4. C – cardinal septum, K – counter septum, A – alar septa, KL – counter lateral septa, t – tabula, m – newly inserted major septa. Same specimen, scale bar = 2 mm.

In the type of offsetting described above, the connection between the offsets and the parent corallites was relatively weak, compared to that in corallites originating directly from the wall of the parent or from the surface of the calice. In both of the latter types of budding, the parent corallite provided strong support for the weight of the new corallite, whereas in *Schoenophyllum* the weight was initially born only by the early, narrowly attached, less stable aseptate stage. Lack of adequate support may account for the rare instances in which this growth stage is directed downward (e.g., Easton, 1957, pl. 71, fig. 12; Sando and Bamber, 1985, pl. 8, fig. 1, lower right). Normally, however, additional support for many new corallites was achieved very early in their development by lateral extension and attachment of their sub-horizontal to moderately elevated, aseptate stages to the walls of neighbouring corallites (Fig. 3D). The initial part of the subsequent, vertical, early septate stage commonly remains in contact with the mature corallite, with one or both corallites showing deformation in the area of contact (Figs. 2D and 3A). There are also young corallites that have no lateral contact with mature corallites, other than the parent (Fig. 3A–C).

2.4. Blastogeny

In the Canadian specimens of *Schoenophyllum*, new corallites originated from all quadrants of the parent corallite but most commonly developed from the cardinal quadrants. They commonly occur singly, but several may be attached to the parent at approximately the same level (Fig. 3C). The following observations on the earliest skeletal morphology were made mainly from a series of closely spaced acetate peels taken over a vertical interval of 19 mm through a single offset from a well-preserved specimen belonging to a new species (Figs. 4 and 5). Additional information was obtained from thin sections and less detailed peel series through this and other specimens.

During the development of an offset, the row of dissepiments in the parent corallite is interrupted and one or more major septa, which commonly curve laterally to leave an open area adjacent to the wall where the offset develops. Initially, the parent wall shows a slight outward curvature, which develops into a small protuberance and may be separated from the tabularium of the parent by one or more small plates (Figs. 4a–d and 5a–c). This protuberance elongates to form a distinct, slim (1 mm diameter) sub-horizontal "tubule", containing a single tabula and becoming slightly elevated over a vertical distance of 0.6 mm. (Figs. 4d–g and 5d, e). Above this, through an interval of 4.2 mm (Fig. 4h and i), the initial structure becomes more steeply elevated but develops no new internal elements. It expands over this interval to reach its maximum diameter (1.5 mm) at its distal end, where it is separated by 0.4 mm from the parent wall. At this level, the young corallite passes from its initial, aseptate stage to a nearly vertical, septate stage that approximately parallels the parent corallite. The cardinal septum is the first to appear, on the side of the offset facing away from the parent (Figs. 4i and 5f). Over the next 1.5 mm, the corallite expands to a diameter of 1.8 mm and the cardinal septum is followed by the alar septa and the two counter laterals, for a total of five septa (Figs. 4i–m and 5g, h). No further septa appear over the succeeding interval of 1.4 mm. The cardinal septum then becomes slightly thicker and longer than the others, extending beyond the corallite axis (Figs. 4n–q and 5h–j). Within the latter interval the counter septum appears between the counter lateral septa, beginning with a low crest on the corallite wall, which develops into a very short septum (Figs. 4o–q and 5h, i). This is followed by the appearance of several major septa in the cardinal quadrants (Figs. 4s–v and 5k–m), accompanied by shortening of the cardinal septum to leave an axial structure consisting of a long, curved, isolated lamella (Figs. 4w and 5m). Through the remaining interval covered by the peel series (Fig. 4x–ff), septal insertion is markedly accelerated in the right cardinal quadrant, with few septa appearing in other quadrants. The counter septum lengthens only slightly without joining either the elongated cardinal septum or the axial structure. Several peels at the top of the series (Fig. 4bb–ff) show distortion in the left quadrants of the new corallite, caused by interference from the aseptate stage of another offset from an adjacent corallite. Horizontal skeletal elements intersected by this peel series include the early tabula referred to above Figs. 4g and 5d, e and two curved plates (dissepiments?), one on either side of the cardinal septum (Fig. 4cc–ff). In longitudinal peels through another corallite in the same specimen (hypotype GSC 124275, Fig. 3), tabulae are present approximately 1.5 mm above the base of the vertical, septate stage, followed by dissepiments 2.5 mm higher in the section.

3. Taxonomic relationships

A full discussion of the taxonomic position of the genus *Schoenophyllum* is beyond the scope of this paper, but several possible relationships are worth mentioning. The derivation of the axial structure from the cardinal septum, described above (also, see Simpson, 1900, pp. 214, 215), removes the genus from the family Lithostrotionidae d'Orbigny, 1852 and suggests an assignment to the Petalaxidae Fomichev, 1953. This possibility was noted by Hill (1981, p. F381) and is supported by the appearance of septal lamellae and rare lateral lamellae in the mature axial structures of our specimens. Such a family assignment would further suggest that *Schoenophyllum* may be related to fasciculate petalaxid genera, such as *Paralithostrotion* Gorsky, 1938, which also has "lateral processes" (see Hill, 1981, p. F406), or *Lytvophyllum* Dobrolyubova in Soshkina, Dobrolyubova et Porfiriev, 1941.

4. Conclusions

The sub-horizontal to moderately elevated lateral processes in *Schoenophyllum* are neither supporting structures within colonies nor open tubules connecting adjacent, mature corallites, as previously supposed. Instead, they form an initial, aseptate growth stage, leading to a vertical, septate stage in the development of new corallites. The derivation of the axial structure from the cardinal septum in these offsets suggests assignment of *Schoenophyllum* to the Petalaxidae and indicates a relationship between that genus and the fasciculate petalaxid genera *Paralithostrotion* and *Lytvophyllum*.

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Appendix A.

Field locality register

Geological Survey of Canada (GSC) locality O-53422 – southwestern Alberta, west slope of Opal Range, east side of Kananaskis-Coleman Highway, 50°43′N, 115°05′W, lower Etherington Formation (Sando and Bamber, 1985, p. 52).

GSC locality O-55233 – northern Yukon, northeastern Old Crow Basin, 68°10′N, 138°58′W, Alapah Formation, isolated outcrop.

GSC locality O-66177 – southwestern Alberta, Elbow Lake, 0.8 km east of Kananaskis Highway, 50°38′N, 115°00′W, 33.6-33.9 m above base of Etherington Formation.

GSC locality C-11823 – northern Yukon, eastern Old Crow Basin, 68°01′N, 138°00′W (location approximate), Alapah Formation, isolated outcrop.

GSC locality C-161245 – northern Yukon, British Mountains, headwaters of Trail River, 68°48′36″N, 140°00′W, 658.8 m above base of Alapah Formation.

GSC locality C-193610 – southeastern British Columbia, northeastern slope of Lizard Range, 49°27′40″N, 115°07′05″W, 103.0 m above base of Etherington Formation.

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Research paper

Uniform habit spectrum vs. taxonomic discrepancy between two succeeding Triassic coral faunas: A proof of the intra-Norian faunal turnover

Ewa Roniewicz

Institute of Paleobiology, Polish Academy of Sciences, ul. Twarda 51/55, 00-818 Warszwa, Poland

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Abstract

Triassic coral fauna from the Tethys Ocean contains, besides colonial cerioid, meandroid and thamnasterioid corals, a high percentage of solitary and pseudocolonial, phaceloid corals with exclusively epithecal walls, about one-fifth of the genera with micromorphology of septa having pennules or menianes. These features are significant indications of moderate depth environments of low energy level and reduced illumination. Despite a uniform spectrum of growth forms, microstructural criteria allow discriminating a middle Anisian-early Norian (A2-N1) fauna from the middle/late Norian-Rhaetian (N2/3-R) one. Taxonomy of the two faunas shows meaningful differences: of four families that dominated in A2-N1 fauna, Volzeiidae, Conophylliidae, and Tropiastraeidae are absent from the N2/3-R fauna and Margarophylliidae are present in a considerably reduced volume. As a consequence of reduction of the earlier corals, particular morphologies were eliminated. In the N2/3-R fauna, five families are abundant: the solitary and phaceloid Reimaniphyllidae and Stylophyllidae, along with colonial Cuifastraeidae, Pamiroseriidae and Astraeomorphidae, all known as rare and rudimentary elements in the earlier fauna.

This change in faunal content in the Tethys during the Norian was controlled by environmental factor(s) hardly identifiable by simple observation, as this is not connected with any obvious facies or change in coral growth form.

Keywords: Scleractinian corals; Late Triassic; Intra-Norian faunal turnover

1. Introduction

Corals fossil assemblages inspire environmental interpretations. Coral morphology is a promising object for study. Commonly, fossil coral occurrences are compared to Recent reefs in their bathymetric situation and environmental requirements. However, the first morphological analysis of growth form and integration level of colonies of Phanerozoic corals published by Coates and Oliver (1973) indicated that such interpretations went too far. This analysis called my attention to the spectrum of coral habits that differ in Triassic and Jurassic corals from those characteristic of Recent scleractinians.

Late Triassic corals, similarly diverse morphologically, show an intriguing lack of taxonomic continuity between faunas of the early Norian and the middle/late Norian. The analysis presented here aims to characterize the phenomenon and point to morphological and micromorphological skeletal features that enable us to revise commonly encountered opinions on adaptations of Triassic corals to dynamic reef environments. These considerations focus on the Triassic, the most interesting period in the Mesozoic history of corals, which is subdivided into three phases of coral faunal recovery after the Permian/Triassic crisis: (i) the Anisian phase, (ii) the Ladinain-early Norian phase, and (iii) the late Norian-Rhaetian phase (Roniewicz and Morycowa, 1989).

This paper serves as a modest supplement to the comprehensive summary on Triassic coral constructions provided by Flügel (2002).

2. Growth form as an indicator of coral environmental requirements

Coates' and Oliver's (1973) analysis of Rugosa and fossil Scleractinia encompasses taxa contained in the Treatise of Paleontology (Hill, 1956; Wells, 1956). The analysis indicated that the majority of rugose taxa are solitary forms or phaceloid epithecal non-integrated forms, as well as colonial cerioid forms, the so-called incommunicate forms (with intercorallite epitheca)

E-mail address: eron@twarda.pan.pl.

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having a very low colony integration level. As such, the fauna was adapted to the environments below wave base. Coates and Oliver (1973) found significant numbers of taxa with these morphologies in the pre-Cretaceous Mesozoic (at least 52 genera, Coates and Oliver, 1973, figs. 1 and 4), comparable to the number of well integrated colonial corals such as co-occurring coenosteoid, meandroid and astraeoid taxa (47 genera, Coates and Oliver, 1973, figs. 1 and 4). The literature concerning the Triassic corals suggests the dominance of solitary and phaceloid corals in the Late Triassic, a group as a whole having epithecal walls.

In analyzing the structure and significance of the epithecal wall, a feature typical of nearly all Mesozoic solitary and phaceloid corals, Roniewicz and Stolarski (1999) pointed to their being unprotected against harm to their skeleton because of a lack of edge-zone. This is one of the arguments against their living in agitated water. Insalaco (1998) pointed to constratal growth fabrics of Mesozoic coral build-ups. Fine-grained sediments (limy mud and/or organodetrital and peloidal lime mud or silt) commonly associated with those build-ups also suggest their development in environments with low hydrodynamics.

The aim of the next morphological analysis made by Coates and Jackson (1987) was to determine, in Recent coral assemblages, whether there is a correlation of such morphological characters as coral growth form (five types distinguished), corallite size, integration state (six categories), and median corallite diameter, with the occurrence of zooxanthellae, and to test fossil corals with the same morphological criteria. This could indicate whether and when, in the past, corals obtained this adaptation, enabling them to populate shallow, agitated water to form reefs. The following set of features was typical in Recent zooxanthellate reef-building corals: multiserial growth form, median corallite size of 1.8–3.3 mm, and a high degree of colony integration (coenosteal colonies and colonies lacking walls between corallites), or medium degree of integration (cerioid with perforate walls).

The fossil coral assemblages of the Palaeozoic, Mesozoic, and Paleogene, when tested with the indices above, showed diverse frequency distributions of each of these morphological characters. Rugosans, as Coates' and Oliver's (1973) analysis shows, neither correspond with their morphology to modern shallow-water reef fauna, nor do they show the skeletal characters of zooxanthellate corals. In the scleractinians, the morphological features of diverse assemblages from the Late Jurassic on are compatible with those of Recent zooxanthellate corals. In the case of the Late Triassic coral assemblage from the Zlambach beds of Austria, indications are ambiguous. Geochemical data, however, from similar Triassic coral skeletons from the Alps and Taurus Mts. indicate carbon and oxygen isotopic compositions corresponding to those of Recent zooxanthellate corals (Stanley and Swart, 1995); similar indications come from the isotopic composition of carbon and nitrogen extracted from organic matter contained in skeletal biocrystals of Triassic pachythecalid coral from the Taurus Mts. (Muscatine et al., 2005). These are direct proofs of photoadaptations acquired by Triassic scleractinians, and help explain their ability to thrive in diverse environments of the photic zone. Another tool, micromorphology of septa, adds even more precision to the discussion of coral biology and environments.

3. Micromorphology of coral septa as an indicator of specific coral-feeding ability

The detailed examination of septal micromorphology published by Gill (1967, 1993 with references) pointed out that balcony-like structures developed on septal flanks, which he named pennules or menianes (if coalesced), are common in Jurassic and other Mesozoic corals. Due to an increased knowledge of Recent coral structure and biology, the reliability of interpretations concerning biology of those fossil corals is still improving. As it turns out, zoological observations were crucial for the functional interpretation of these structures (Schlichter, 1992). These concerned phenomena in the Recent agariciid, *Leptoseris fragilis.* This zooxanthellate coral lacks tentacles, and lives below 100 m water depth. In this dysphotic environment, its elaborate system of feeding is based on heterotrophy and phototrophy. Autofluorescence by its pigment cells keeps zooxanthellae alive and active. The usual manner of taking food with tentacles and directing it toward the polypal pharynx and then to the coelenteron divided by mesenteries has been transformed into true filtering in this coral. This is aided by rebuilding of the coelenteron into a system of canals. The water current with food particles is directed from the pharynx into the canals that lie on balcony-like structures (menianes) parallel to the septal distal border, and are extruded by microscopic pores (1–2 μm) that open on the oral disc. The agariciids, usually inhabiting deep slopes of reefs, are provided with menianes (Chevalier, 1987) and all display autofluorescence (Schlichter et al., 1993). Of course, fossil corals, although similar in the micromorphology of their septa, might differ from Recent ones in their adaptations in anatomy and for feeding. However, their micromorphology and skeletal structure are significant for ecological consideration for indicating life conditions alternative to the shallow-water modern reef model (compare Morycowa and Roniewicz, 1995; Roniewicz and Stolarski, 1999; Rosen et al., 2002). Actually, the most common Jurassic-Early Cretaceous genera of the suborder Microsolenina and a large percentage of Triassic corals (exceeding one-fifth of the total number of Triassic genera) show septal micromorphology analogous to that from the depth just described. I concur with Insalaco (1996) and of Rosen et al. (2002) on that these corals lived like their extant analogues in environments with low hydrodynamics and solar radiation reduced by depth or turbidity. Here, we observe a meaningful shift of opinion on the requirements of fossil scleractinian corals towards conditions at depths far below the surf zone.

4. Identification of an intra-Norian faunal turnover

Microscopic observations on fossil coral skeletal material preserved as aragonite lead to conclusions that go beyond palaeoecology. These observations enable us to avoid a trap, i.e., the homeomorphy, which is an especially bothersome obstacle in much macroscopic determination of fossil taxa. The Triassic fauna here is an instructive example. Observations presented herein are based especially on collections of Carnian corals from the Southern Alps and on the literature covering the vast region of Triassic Tethys.

The Triassic coral fauna from the Tethys Ocean and European epicontinental seas can be differentiated into more than 110 genera and 330 species, showing the following three distinctive morphological features that can be observed from the Anisian onward:

(1) the most spectacular is the high number of solitary, subcylindrical corals, and pseudocolonial phaceloid forms;
(2) an exclusively epithecal wall in solitary and phaceloid corals; and,
(3) a high frequency of corals with pennular and meniane-bearing septa, mostly with thamnasterioid and cerioid-meandroid colonial form.

The highly uniform habit spectrum and skeletal structural details of the most common Triassic corals noted above are not paralleled by any similar uniformity in taxonomy, if they are placed systematically by their skeleton microstructure and septal micromorphology, characters used to define familial and higher level taxa. Such research enables the discrimination of two groups of fauna that differ taxonomically.

The earlier, middle Anisian-early Norian fauna (A2-N1) is highly diversified, but awaits taxonomic revision. A large number of papers report on this early faunal diversity (Schauroth, 1859; Tornquist, 1899, 1900; Bechstädt and Brandner, 1970; Deng and Kong, 1984; Pfeiffer, 1988; Morycowa, 1989 with references; Qi and Stanley, 1989; Senowbari-Daryan et al., 1993; Morycowa and Szulc, 2006 with references), although rarely presenting taxonomical analyses. Our primary knowledge of the Carnian corals (Volz, 1896) was greatly augmented in the last decades of the 20th Century (Cuif, 1977 with references; Turnšek and Senowbari-Daryan, 1994; Turnšek, 1997 with references; Melnikova, 2001; Roniewicz and Michalik, 2002; Roniewicz et al., 2005; Melnikova and Roniewicz, 2007). A surprisingly close relationship between Carnian and early Norian faunas has been shown in a series of papers by Cuif (1975, 1977 with references), and later by other authors (Turnšek, 1997 with references; Roniewicz et al., 2007). At present, the number of formal genera and species, as well as informal taxa discriminated in collections, reaches more than 90 genera and 190 species in this fauna, with the most abundant ones of Carnian age.

The later, well-known faunas of the middle/late Norian and Rhaetian (N2/3-R) comprises 45 genera (of this number, 20 are common with A2-N1 fauna) with more than 140 species (Frech, 1890; Roniewicz, 1989 with references; Roniewicz, 1996; Turnšek, 1997 with references; Roniewicz and Michalik, 1998 with references; Melnikova, 2001). The earlier fauna contains 54% solitary and phaceloid genera of that age, and the later one has 42%; remaining corals are colonial of various types.

Having such a large quantity of solitary and phaceloid (thus, non-colonial and pseudocolonial) corals, all with epithecal walls, both faunas represent specific and, generally, similar environments. A large percentage of pennular and meniane-bearing corals reaches up to 22% of genera in each fauna. These specific feeding adaptations strengthen the similarity.

These two faunas became morphologically diverse in similar ways, and reveal meaningful differences in familial content. From the four families that dominated in the A2-N1 fauna, i.e., the Volzeiidae, Conophylliidae, Tropiastraeidae, and Margarophylliidae, that contain prevalent solitary and phaceloid taxa, three of the families are absent from the late Norian-Rhaetian fauna, and only Margarophylliidae are present but reduced to only two genera (*Margarosmilia*, *Distichomeandra*). As a consequence of this reduction, some particular morphology disappeared, as follows:

(1) multiseptal calices with a floor elevated at the calicular rim (typical of the Conophyllidae and of several species until now placed in the genus *Myriophyllum*),
(2) a styliform, monotrabecular collumella (typical of the Conophyllidae and Tropiastraeidae, and of the genus *Craspedophyllia*), and,
(3) multiple, crowded thin septa that are connected by synapticulae (corals determined as *Myriophyllum*). These features undoubtedly have biological significance.

In total, of the 25 families known in the A2-N1 fauna, only 13 are seen in the N2/3-R fauna. The N2/3-R fauna is not only poor in numbers but also with its diversity reduced to 17 families. From the families originating and known as rare and rudimentary in the A2-N1 phase, the Reimaniphyllidae and Stylophyllidae, most with solitary and phaceloid species, and three other colonial families, i.e., the Cuifastraeidae, Pamiroseriidae, and Astraeomorphidae are frequent and diversified taxonomically in the late Norian-Rhaetian fauna.

5. Conclusions

The early Norian change in coral fauna corresponds to the turnovers observed in various terrestrial and marine organisms during short periods (compare Benton, 1986; Hallam, 1995) preceding the end-Triassic extinction event.

The faunal turnover that took place early in the Norian was caused by environmental factor(s) that are barely identifiable by simple observation, as neither sedimentary facies nor coral growth forms changed in obvious ways. Carnian and Norian/Rhaetian marly facies and limestones contain zooxanthellate corals with the habit and micromorphology characteristic of corals in environments with low hydrodynamics, presumably at depth even below storm wave-base.

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Research paper

A new genus and species of colonial rugose coral from late Tournaisian (Waulsortian) mud-mounds in Ireland: Its ecological associations and depositional setting

Ian D. Somerville[a,*], Sergio Rodríguez[b]

[a] *School of Geological Sciences, University College Dublin, Belfield, Dublin 4, Ireland*
[b] *Departamento y U.E.I. de Paleontología, Facultad de Ciencias Geológicas e Instituto de Geología Económica, Ciudad Universitaria, 28040 Madrid, Spain*

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Abstract

A new genus and species of fasciculate rugose coral, *Howthia suttonensis* Somerville and Rodríguez, has been recorded from Howth peninsula, County Dublin, Ireland, in Waulsortian mud-mound limestones of upper Tournaisian age. The new colonial genus is characterized by having an axophyllid axial structure, steeply inclined tabellae, and presence of interseptal and lonsdaleoid dissepiments. It evolved probably from a solitary *Axophyllum* by the development of peripheral offsets. This new taxon may have been an ecological pioneer adapting to a specialised niche near the top of a large Waulsortian mud-mound in shallower water than most Waulsortian settings and, as such, may have provided a novel evolutionary opportunity. *Howthia suttonensis* is associated with *Amplexocarinia* and an unusual form of '*Fasciculophyllum*', both of which display budding and protocoloniality, as well as the fasciculate tabulate coral *Syringopora*.

Keywords: Rugose colonial corals; Mississippian; Systematics; Ecology; Mud-mounds; Ireland

1. Introduction

It has long been recognized that Mississippian mud-mounds are generally poor in rugose corals and normally contain sparse, small, solitary undissepimented taxa, such as *Amplexus*, *Cyathaxonia*, and zaphrentids. They are associated with tabulate corals represented by occasional *Syringopora* and *Michelina* colonies (Hudson et al., 1966; Ramsbottom in McKerrow, 1978; Mundy, 1980, 1994; Somerville et al., 1992a; Somerville, 2003). The Mississippian mud-mounds are characterized also by having fine-grained peloidal mudstone/wackestone lithofacies with complex cavity systems containing internal geopetal sediments and radiaxial fibrous marine cements, often referred to as stromatactis cavities (Lees and Miller, 1985, 1995; Somerville et al., 1992a,b; Mundy, 1994; Pickard, 1996; Somerville, 2003). The mud-mounds have demonstrable topographic relief and often can be differentiated into a massive core and bedded flank and cap facies (Lees and Miller, 1985, 1995; Somerville et al., 1992a,b; Mundy, 1994; Lees, 1997; Somerville, 2003). The mounds may be initiated on crinoidal-rich wackestone or bioclastic rudite facies. The mud-mound geometry is variable, ranging from isolated domes to clusters of stacked or coalesced mounds, or forming laterally extensive tabular banks and sheets (Lees and Miller, 1995; Somerville, 2003). Many of the mud-mounds, especially in the Tournaisian, developed on the distal parts of ramps, in relatively deep water, low energy, quiet water environments without dasyclad algae (Lees and Miller, 1985, 1995; Somerville et al., 1992b; Jeffery and Stanton, 1996). Waulsortian mud-mounds are known to extend from New Mexico to Western Europe and possibly South China. In the Viséan, many mud-mounds tend to develop at the margins of shelves adjacent to deep-water basins or within shallow-water shelf settings, but Waulsortian-type mud-mounds persist still in deeper shelf and basinal settings (Kelly and Somerville, 1992; Somerville et al., 1992a; Mundy, 1994; Somerville, 2003). In the shallower water Viséan mounds, colonial rugose colonies

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[*] Corresponding author.
E-mail address: ian.somerville@ucd.ie (I.D. Somerville).

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can form rich concentrations at or near the top of mounds, especially in the Asbian and Brigantian, where locally they can form frameworks (Mundy, 1994; Somerville et al., 1996; Somerville, 1997, 2003; Rodríguez and Somerville, 2007, in this volume). An unusually rich and diverse assemblage of rugose corals, both solitary and colonial (fasciculate and cerioid) forms, was recorded at the top of the >90 m-thick Brigantian mud-mound at Ardagh Quarry, Kingscourt, Ireland, where occur large colonies, up to 2 m in diameter, of *Siphonodendron*, *Corwenia* and '*Koninckophyllum*' (Somerville et al., 1996; Rodríguez and Somerville, 2007, in this volume). This suite of fasciculate and solitary rugosans is characteristic of Rugose Coral Assemblage RCA6 of Somerville and Rodríguez (2007). A similar suite of taxa including *Diphyphyllum* and *Tizraia* has been recently recorded from the top of Upper Viséan mounds in Morocco (Said et al., 2007; Said and Rodríguez, 2007).

Investigations in older Tournaisian mud-mounds in the Dublin Basin, Ireland has yielded local pockets of solitary rugose corals, such as the fauna collected from the well-known Feltrim Quarry (Hudson et al., 1966) and from boreholes in the basin (Somerville et al., 1992b). However, until recently, no colonial rugose corals have ever been recorded from Waulsortian mounds. But a recent discovery from a small patch of mostly dolomitized Waulsortian facies at Sutton on the Howth penin-

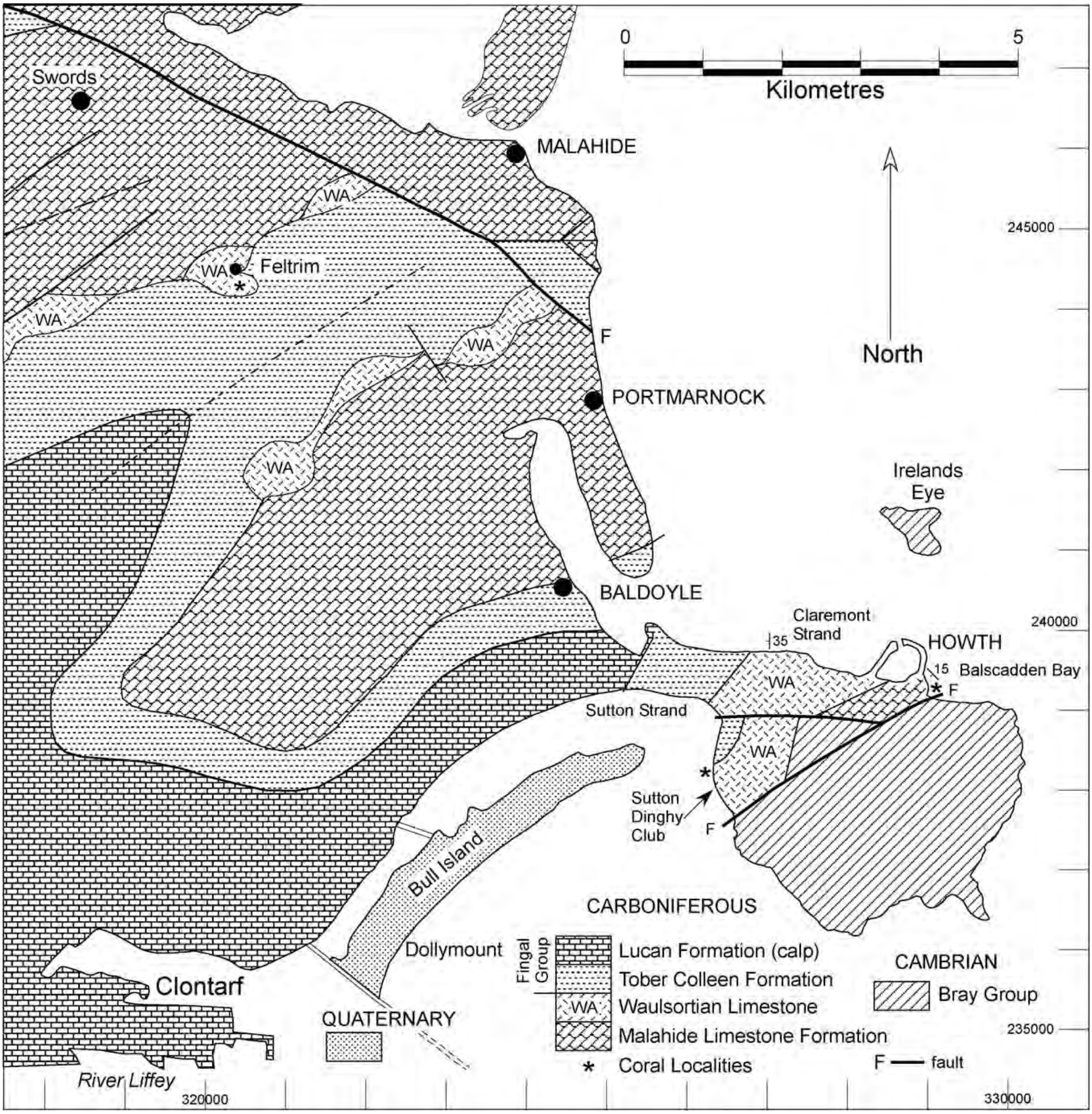

Fig. 1. Location map of north County Dublin area of the Dublin Basin (from 1:100 000 GSI Sheet 13 (McConnell et al., 2001) and Sheet 16 (McConnell and Philcox, 1994).

sula, about 10 km northeast of Dublin (Fig. 1), has uncovered a rich collection of rugosans, including one new colonial genus and several taxa showing protocoloniality. The description of these corals is the subject of this paper and their ecological associations and depositional setting will be assessed. Brief comparisons will also be made with coral faunas from other Mississippian and older mud-mounds.

2. Geological setting of upper Tournaisian rocks in the Dublin Basin and their coral faunas

The Early Carboniferous (Tournaisian) sequence of the Dublin region (East Central Ireland) is best known from continuous sections in inland boreholes in the Swords area, west of Malahide (Jones et al., 1988; Strogen et al., 1996) where Carboniferous basal siliciclastics ('Lower Limestone Shale') rest unconformably on Lower Palaeozoic rocks (Fig. 1). The succeeding bedded limestones (Malahide Limestone Formation) are well exposed in coastal sections at Malahide and on the north side of the Howth peninsula at Balscadden Bay (Figs. 1 and 2). The youngest Tournaisian strata in the Dublin Basin are pale grey massive mud-mound limestones (Feltrim Limestone Formation – informally referred to as the Waulsortian facies), which signify a marked deepening of sedimentation, especially in the centre of the basin (Somerville et al., 1992b; Somerville, 2003). These mud-mounds were later buried by a blanket of mud (Tober Colleen Formation), whose type section is at Rush, north of Malahide, which initiated the beginning of the deep-water basinal facies (Lucan Formation of the Fingal Group) of the Dublin Basin that was maintained throughout the Viséan (Nolan, 1989; Strogen et al., 1990, 1996; Fig. 2). However, in north county Dublin around Lane, shallow-water siliciclastics and limestones (McGuinness and Lane formations) equivalent to the Waulsortian deep-water mud-mounds are known from the Lane Borehole and from coastal exposures (Nolan, 1989; Somerville et al., 1992a; Strogen et al., 1996). The Lane Formation has yielded shallow-water solitary rugose corals (Matley and Vaughan, 1906; Somerville, 1994) of latest Tournaisian to

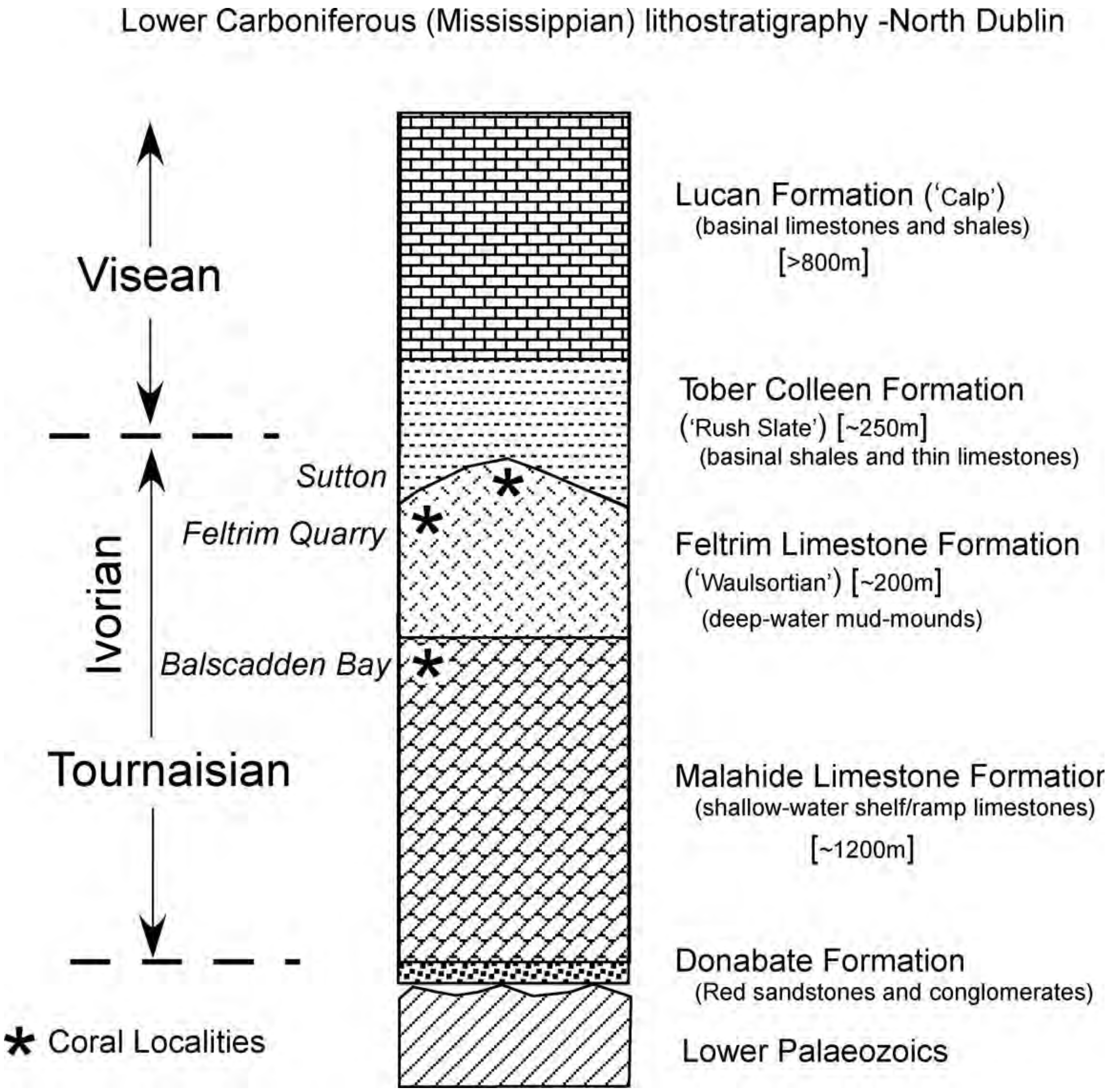

Fig. 2. Generalized stratigraphical log of the Mississippian succession in the north Dublin Basin region with the approximate horizons of rugose coral assemblages. N.B. The Sutton locality represents the top of the mud-mound where the new colonial rugose coral was collected.

early Viséan age (Rugose Coral Zone RC4 of Poty, 1989; Poty et al., 2006 and RC4ß Subzone of Poty, 2007).

2.1. Macrofaunal and microfaunal biostratigraphy

Rich rugose coral assemblages have been collected for over a century from Mississippian coastal outcrops in County Dublin, particularly in the Malahide area (Smyth, 1915, 1920), and between Rush and Skerries (Matley and Vaughan, 1906, 1908; Somerville, 1994). Also, from the north side of the Howth peninsula at Balscadden Bay (Fig. 1), Dingwall (1926) obtained a diverse solitary rugose coral assemblage.

Micropalaeontological data has established that the Malahide Limestone Formation is of late Tournaisian age, containing conodonts of the *Polygnathus mehli* Zone (Jones et al., 1988) and foraminiferans of the Cf2-Cf3 Foraminiferal zones (Marchant, 1974; Jones et al., 1988) (=MFZ 4–6 of Poty et al., 2006). The overlying Feltrim Limestone Formation has yielded very sparse foraminiferans of Cf3 (MFZ6) Zone age (Somerville et al., 1992b). Conodonts are very rare in Waulsortian facies in the Dublin Basin, with recently collected samples from Sutton, on the Howth peninsula, proving to be barren. However, *Polygnathus bischoffi* of latest Tournaisian (Ivorian) age has been recorded from boreholes in this facies (Jones et al., 1988; Somerville et al., 1992b), and *Scaliognathus anchoralis*, elsewhere in the basin (Sevastopulo, 1982; Sevastopulo and Wyse Jackson, 2001). The basal Viséan foraminiferal marker *Eoparastaffella simplex* of the Cf4α2 Subzone (=MFZ9 of Poty et al., 2006) has been recorded from near the top of the overlying Tober Colleen Formation, along with the important early Viséan conodont *Gnathodus homopunctatus* (Somerville et al., 1992b).

Coral assemblages recorded from the Malahide Limestone Formation at Malahide are dominated by solitary, mostly non-dissepimented taxa (Smyth, 1920; Mitchell and Somerville, 1988; Somerville, 1994), e.g., *Caninia*, *Cyathaxonia*, *Fasciculophyllum*, *Sychnoelasma*, *Zaphrentites*, and with rare *Caninophyllum* and *Rylstonia*. Tabulate corals are also common, with *Syringopora*, *Michelinia*, and *Palaeacis*. Younger beds in the Formation are exposed at Balscadden Bay (Figs. 1 and 2), where Dingwall (1926) recorded common large solitary dissepimented corals (*Cyathoclisia tabernaculum* (=*C. modavensis* (Salée, 1913) and *Caninophyllum patulum* (Michelin, 1846)). The latter taxa are well known from upper Tournaisian and lower Viséan bedded limestones in assemblages from Western Europe, Russia, and China (Poty, 1981, 1989, 2007; Fedorowski, 1981; Mitchell, 1989; Somerville, 1994). These assemblages correspond to Rugose Coral Zones RC3 and RC4 of Poty (1989) and Poty et al. (2006).

The Feltrim Limestone Formation is well known for its richness and diversity of molluscan, brachiopod, and bryozoan faunas, but corals are particularly rare, especially in the massive ‘core’ facies of the Waulsortian mud-mounds, although slightly richer in the inter-mound shales (Hudson et al., 1966). They include small, solitary, mostly non-dissepimented rugosans (*Amplexus*, *Amplexocarinia*, *Caninia*, *Cyathaxonia*, *Fasciculophyllum*, *Zaphrentites*) and rare tabulates. According to Hudson et al. (1966, p. 258) the majority of these taxa are absent from the ‘reef’ limestones (except *Amplexus coralloides* Sowerby, 1814). However, occasionally, large solitary dissepimented rugosans (e.g., *Siphonophyllia cylindrica* Scouler, 1844) have been reported from the Waulsortian facies at Feltrim and in boreholes within the Dublin Basin (Somerville et al., 1992b). The bedded dark grey pyritic argillaceous crinoidal limestones and shales of the Tober Colleen Formation above the massive Waulsortian limestones in Feltrim Quarry have a slightly more diverse coral fauna, with solitary rugosans and tabulate corals.

2.2. Waulsortian mud-mound facies at Howth peninsula

Waulsortian limestones are well exposed on the north side of Howth peninsula at Claremont strand (west of Howth harbour), where they are bedded and dip 30° to the west towards Sutton (Fig. 1). They also crop out on the west side of the peninsula around Sutton Dinghy club. However, most of the Waulsortian limestones in the Sutton area are extensively dolomitized, with only small patches of undolomitized limestone surviving. In the latter, typical stromatactoid cavities with laminated geopetal sediments, fenestellid bryozoan fronds and crinoids are present, but corals have not been reported previously.

Specimens of the new colonial genus were collected from the northern-most exposure on the Sutton foreshore, close to the seawall below Strand Road, 100 m north of Sutton Dinghy Club (Irish Grid Reference O 3262 2382), where the massive, pale grey, fine-grained peloidal lime mudstones and skeletal wackestones with cavities are mostly undolomitized. The corals occur in two small clusters, about 25 cm in diameter and about 50 cm apart, in exposures close to the seawall that are covered at high tide. The density of individual corallites in the clusters is ca. 30/10 cm^2, with the majority in situ and in growth position. These coral-bearing strata locally contain large crinoid stems and accumulations of ossicles, as well as concentrations ‘nests’ of ostracods, sponge spicules, occasional bryozoans and rare goniatites. Despite the very limited exposure at Sutton, the overall regional northwesterly dip of the Tournaisian rocks on Howth peninsula would suggest that these rocks might represent the youngest Waulsortian rocks exposed. In fact, the Geological Survey of Ireland 1:100 000 scale geological map for Sheet 16 (McConnell and Philcox, 1994) has inferred an unexposed conformable contact between the Waulsortian limestones and the overlying mudstones of the Tober Colleen Formation immediately north of this locality, similar to that exposed in Feltrim Quarry (Fig. 1). It is possible, therefore, that this facies at Sutton may have developed near the top of a large microbial mud-mound complex which is characteristic of the Waulsortian in the Dublin Basin area, with individual mounds reaching tens of metres in thickness and hundreds of metres in width (Lees and Miller, 1985, 1995; Somerville, 2003). The presence of colonial rugose corals in the late Tournaisian Waulsortian mud-mounds is unprecedented for the region or for the facies anywhere in Ireland. It is worth noting that colonial rugose corals are often encountered in younger Viséan mud-mounds in Ireland, but usually on the flanks or near the tops of mounds (Kelly and Somerville, 1992; Somerville et al., 1996; Somerville, 2003).

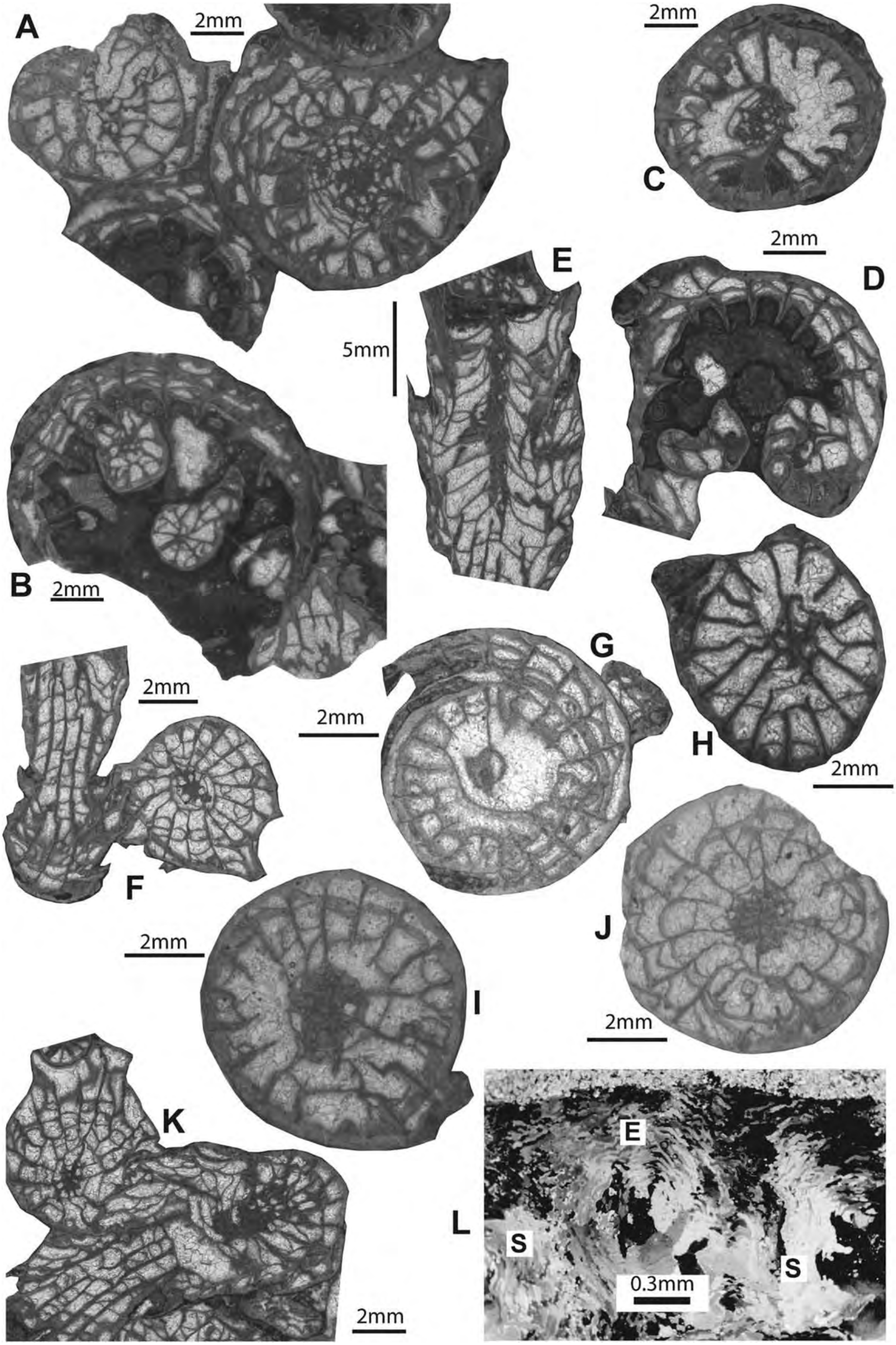

Fig. 3. Late Tournaisian Rugose corals from Howth. (A–L) *Howthia suttonensis* n. gen. n. sp.; Waulsortian limestone, Sutton Strand, Howth peninsula, County Dublin, late Tournaisian. (A) Holotype; transverse section showing 4 corallites with sub-cerioid growth, and well developed axophyllid axial structure in largest corallite. Specimen HW104; thin section UCD5416. (B) Holotype; Transverse section of calyx of corallite (cf. largest corallite in A) showing 2 off-sets. The one on the left shows clear septal connections with the mature corallite. Specimen HW104A; thin section UCD5417. (C) Transverse section of mature corallite with long

Other corals recorded with *Howthia suttonensis* n. gen. n. sp. (Figs. 3A–L and 4A–H, K–M) are the fasciculate tabulate genus *Syringopora*, and the small solitary? non-dissepimented rugosans '*Fasciculophyllum*' (Fig. 4I, J) and *Amplexocarinia* sp. (Fig. 4N, O). Interestingly, both of these genera show evidence of budding (protocoloniality of Fedorowski, 1978; see Rodríguez and Somerville, in this volume). This coral assemblage is characteristic of the deep-water *Cyathaxonia* phase fauna of Hill (1938) and typical of Rugose Coral Association RCA8 of Somerville and Rodríguez (2007), which is normally interpreted as representing deep-water slope and mud-mound environments on the margins of basins. The absence of dasyclad green algae in the mud-mound would also support this probable sub-photic setting. On the other hand, the high diversity of rugose corals and other skeletal invertebrates at Sutton, and the rarity of fenestellid bryozoans would indicate a position near the top of a mud-mound in a slightly shallower water depth (Fig. 2).

3. Comparisons with other mud-mound coral faunas

3.1. Mississippian mud-mounds

In Mississippian mud-mounds of northern England, Mundy (1980, 1994) has documented the presence of local pockets of non-dissepimented rugose corals dominated by *Cyathaxonia*. The corals from the lower slopes of the Upper Viséan mound at Sebden, near Settle, are associated with bryozoans, crinoids, and molluscs (see Ramsbottom in McKerrow, 1978, fig. 18). The crest of these mounds has a framework with *Siphonodendron* colonies. However, further south in the Craven Basin near Clitheroe, older Waulsortian mounds of late Tournaisian – early Viséan age (Lees and Miller, 1995) have yielded *Amplexocarinia cravenensis* (Smith, 1955), very similar to the species recorded at Sutton.

Recent studies in the Adarouch area of NE Central Morocco (Said et al., 2007; Said and Rodríguez, 2007; Cózar et al., 2008) have recognized the presence of large domal mud mounds and banks amid mostly Upper Viséan (Brigantian) shallow-water platform limestones, similar to those in Kingscourt, Ireland (Somerville et al., 1996; Somerville, 1997). These massive fine-grained mud-mounds with sponges are generally devoid of rugose corals in the core, but on the flanks locally abundant non-dissepimented solitary corals are present. However, towards the top of the mounds and in the immediately overlying bedded limestones, fasciculate rugose coral colonies occur. The most abundant genus is *Siphonodendron*, but *Diphyphyllum*, *Corwenia* and a new genus *Tizraia*, closely related to *Diphyphyllum* (see Said and Rodríguez, 2007; Rodríguez and Somerville, in this volume) is recorded.

Similar Upper Viséan mud mounds containing sponges are present in Sierra de la Estrella in SW Spain (Cózar et al., 2003; Rodríguez-Martínez et al., 2003), only there the colonial rugose corals are much rarer in the microbial mounds, with occasional *Siphonodendron* colonies near the top of mounds.

The Upper Viséan coral patch reefs in Montagne Noire, southern France are noteworthy, especially that from Castelsec quarry section, as it contains horizons dominated by the small solitary corals *Clisiophyllum* and *Axophyllum nanum* Poty, 1981, which are encrusted by microbial organisms (Aretz and Herbig, 2003). The latter species has many morphological similarities to *Howthia* (see Section 4) and may have occupied a similar ecological niche. *A. nanum* can be locally abundant at Castelsec, and frequently shows budding and protocoloniality (=pseudocoloniality of some authors) (E. Poty, pers. comm.).

3.2. Devonian mud-mounds

Recently, rugose corals have been described from Devonian build-ups in the Anti-Atlas Mountains of southern Morocco (Berkowski, 2004, 2006) and have been interpreted as thermophilic corals in an ancient hydrothermal vent community (Belka and Berkowski, 2005). These solitary deep-water corals usually occur as monospecific assemblages dominated by amplexoid corals ("*Amplexus*" *florescens*) lacking dissepiments. They occur in two sizes, large forms (0.5–1.5 cm) and small forms (<0.5 cm) with scolecoid cylindrical habit. What makes these corals unusual is that they are endemic forms very much localized to the region, occurring in dense pockets (clusters) with concentrations of 20–40 specimens/100 cm^2, arranged in life position, similar to those at Sutton. However, the corals from the Middle Devonian (Givetian) mound at Hamar Laghdad show unique calice-in-calice recolonization by settlement of juvenile specimens in the calyx of the dead adult individuals (Berkowski, 2006). This highly specialised niche is related to proximity to venting chimneys and hydrothermal circulation patterns. Small solitary rugose corals have also been recorded from Lower Devonian (Emsian) mud-mounds of southern Morocco associated with tabulate corals (Brachert et al., 1992), which have also been related to hydrothermal vents (Belka, 1994, 1998; Aitken et al., 2002). Although the location of Tournaisian Waulsortian mud-mounds have been suggested as being linked possibly to hydrothermal circulation along faults (Deeny, 1984), especially in relation to sulphide deposits, no supporting evidence has as yet been established.

counter septum joined to axial structure. Note also thick wall. Specimen HW69; thin section UCD5356. (D) Transverse section of calyx of corallite showing 2 off-sets. Specimen HW67D4; thin section UCD5464. (E) Longitudinal section of corallite with a well-developed axial column. Specimen HW67C; thin section UCD5354. (F) Transverse and oblique section of two corallites with joined skeletal tissue. Specimen HW67D3; thin section UCD5463. (G) Transverse section of mature corallite with several rows of broadly concentric dissepiments, rare outer lonsdaleoid dissepiments, long thin counter septum and major septa withdrawn from axis. Attached bud to wall. Specimen BQ2; thin section UCD5427. (H) Transverse section of immature corallite with rare lonsdaleoid dissepiments. Specimen HW41A; thin section UCD5304/1. (I) Transverse section of mature corallite with very short cardinal septum and prominent median plate in axial structure. Specimen HW98; thin section UCD5407/2. (J) Transverse section of mature corallite with well-developed axophyllid axial structure and angulo-concentric dissepiments. Specimen HW41A; thin section UCD 5304/1. (K) Transverse and oblique section of two corallites with joined skeletal tissue. Specimen HW67D2; thin section UCD5462. (L) Ultrathin section showing laminar epithecal wall (E) and laminar septa (S). Specimen HW66D; thin section UCD5465.

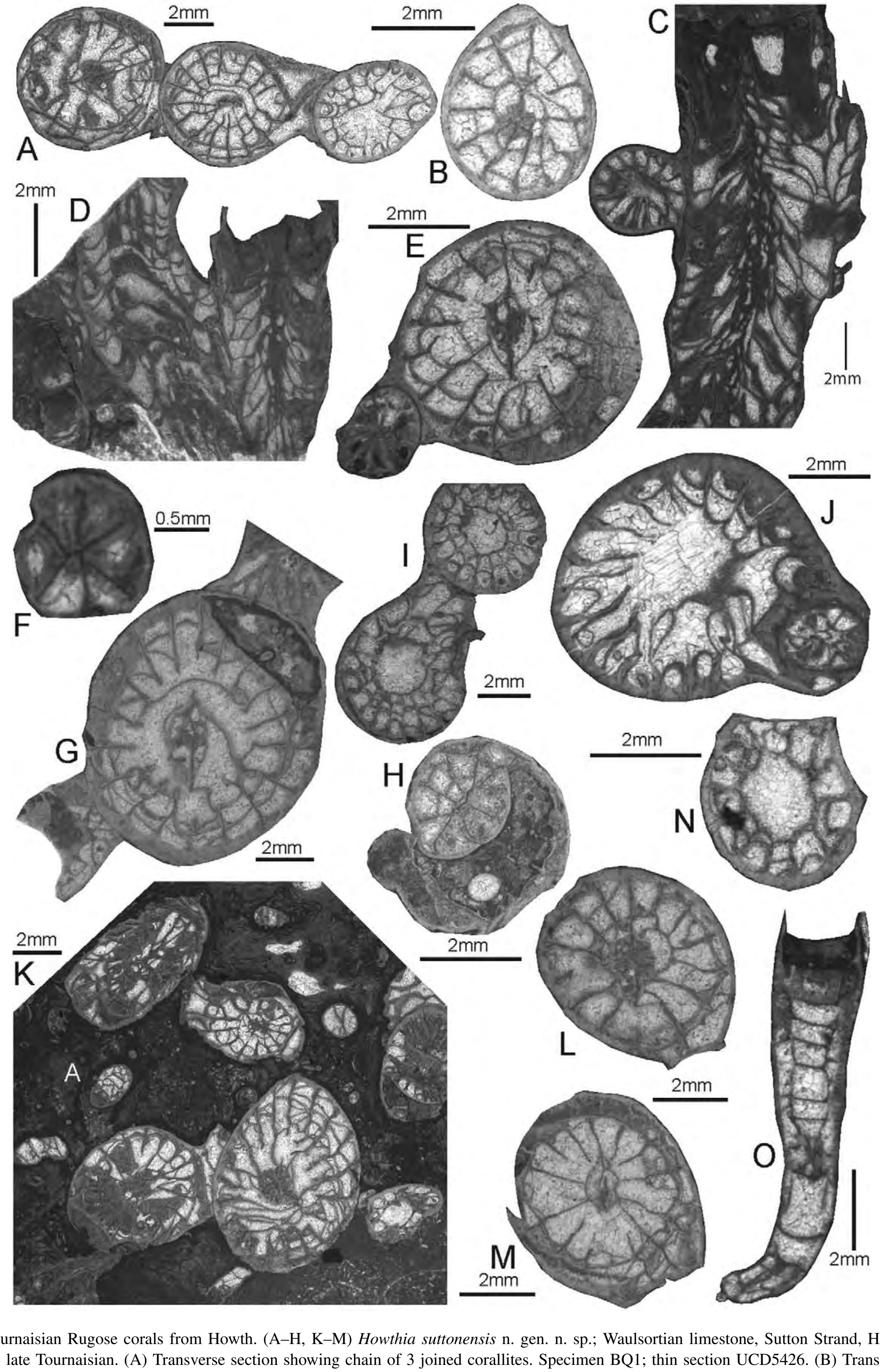

Fig. 4. Late Tournaisian Rugose corals from Howth. (A–H, K–M) *Howthia suttonensis* n. gen. n. sp.; Waulsortian limestone, Sutton Strand, Howth peninsula, County Dublin, late Tournaisian. (A) Transverse section showing chain of 3 joined corallites. Specimen BQ1; thin section UCD5426. (B) Transverse section of juvenile. Specimen BQ1; thin section UCD5426. (C) Longitudinal section of corallite showing continuous axial structure and attached bud ('*Fasciculophyllum*'?) to wall. Specimen HW68; thin section UCD5355. (D) Paratype. Longitudinal section of two corallites with a well developed axial structure in the corallite on the right

4. Systematic descriptions

We follow basically the classification and macrostructural terminology proposed by Hill (1981). The microstructural terminology is that proposed by Semenoff-Tian-Chansky (1974). All specimens are housed in the School of Geological Sciences, University College Dublin and are assigned numbers with the prefix UCD.

Subclass RUGOSA Milne-Edwards et Haime, 1850

Order STAURIIDA Verrill, 1865

Suborder LONSDALEIINA Spasskiy, 1974

Family AXOPHYLLIDAE Milne-Edwards et Haime, 1851

Subfamily AXOPHYLLINAE Milne-Edwards et Haime, 1851

Genus *Howthia* Somerville et Rodríguez n. gen.

Type species: *Howthia suttonensis* Somerville et Rodríguez.

Derivatio nominis: The genus name is derived from Howth, a peninsula in north County Dublin, eastern Ireland, where the type specimens come from.

Type locality and formation: Upper Tournaisian Waulsortian mud-bank limestones (Feltrim Limestone Formation) from the west side of the Howth peninsula, Sutton, County Dublin, Ireland.

Diagnosis: Small solitary to weakly fasciculate corallites with axophyllid axial structure, interseptal and large second-order lonsdaleoid (transeptal) dissepiments, absence of minor septa, steeply inclined tabellae forming pillar.

Remarks: This new colonial genus shows similar features to *Axophyllum* Milne-Edwards et Haime, 1850 in transverse section. However, many differences are observable when studied in detail. Most importantly, the development of lateral budding (offsets) in the periphery of the calyx (=peripheral increase of Jull, 1965) in *Howthia* is diagnostic, and the presence of connected corallites forming a weakly fasciculate colony distinguishes it from the solitary genus *Axophyllum*. The major septa are not as strongly thickened in the tabularium of *Howthia* compared to *Axophyllum*, particularly in the outer tabularium at the contact with the dissepimentarium. Also, *Howthia* lacks minor septa. The lonsdaleoid dissepiments that are characteristic of *Axophyllum* are not well-developed in *Howthia*, occurring mainly in the late stages of development. However, this feature is common in many species of *Axophyllum* (cf. Garwood, 1913; Ryder, 1930; Hill, 1940; Semenoff-Tian-Chansky, 1974; Poty, 1981).

Howthia has some similarities with *Dorlodotia* (Family Lithostrotionidae, Subfamily Thysanophyllinae): a fasciculate coral without minor septa, presence of lonsdaleoid dissepiments, and an axial structure connected to the counter septum. However, in *Howthia*, the axial structure, although variable, is generally more complex, with septal lamellae and tabellae around a median plate, whereas in *Dorlodotia*, the axial structure is represented by a simple columella. Interestingly, though, both genera have axial structures which may be longitudinally discontinuous, and young stages of *Howthia* corallites often only possess a median plate/columella, and hence can resemble *Dorlodotia*. Also, in the latter, the boundary wall between the tabularium and dissepimentarium is much thicker and more prominent. On the other hand, in contrast to *Howthia*, the fasciculate genus *Lonsdaleia* (Family Axophyllidae) has a much more advanced axial structure, i.e., a well-developed spider's web structure. Also, the dissepimentarium in the latter is much wider, with large lonsdaleoid dissepiments not crossed by the major septa.

The fasciculate genus *Nemistium* with weak axial structure (columella with a few septal lamellae and tabellae) can be compared with young stages of *Howthia*. However, in the former, the dissepimentarium with well-defined concentric rings of dissepiments without lonsdaleoid second-order type, and the presence of minor septa help distinguish it, and establish its characteristics as being typical of a different family (Lithostrotionidae).

The new genus *Howthia* may have important biostratigraphic value, as it represents a much earlier first occurrence than any other colonial genus belonging to the family Axophyllidae or Lithostrotionidae referred to above, which according to Hill (1940), Poty (1981), and Mitchell (1989) characterize the Viséan in Western Europe (*Dorlodotia* in the early Viséan – Chadian and Arundian; *Lonsdaleia* and *Nemistium* in the late Viséan – late Asbian and Brigantian). The probable latest Tournaisian to earliest Viséan age for the Waulsortian rocks at Sutton containing *Howthia* might also be significant as hosting the earliest colonial representative of the Axophyllidae, coeval with the earliest solitary form *Axophyllum simplex* (Garwood, 1913) that has been recorded in the Waulsortian facies in the Dublin Basin (Somerville et al., 1992b; Somerville, 1994; see remarks below), and in shallow-water platform rocks in Britain (Mitchell, 1989), Belgium, and Poland (Poty, 1985, 2007). Thus, we propose here that *A. simplex* is the probable ancestor of *Howthia*.

and weak impersistent wall between neighbouring corallites. Specimen HW98A; thin section UCD5407/1. (E) Transverse section of mature corallite with juvenile growing closely together. Specimen HW38/2; thin section UCD5301/2. (F) Transverse section of juvenile corallite from within a calyx. Specimen HW67D3; thin section UCD5463. (G) Transverse section of a mature corallite with 2 corallites growing close together. Specimen HWF; thin section UCD 5272/1. (H) Transverse section of immature corallite within a calyx. Specimen BQ3; thin section UCD5428. (K) Transverse section of fasciculate colony with several loosely connected corallites. The very small corallites are *Amplexocarinia* (A). Specimen HW66E; thin section UCD5350/1. (L) Transverse section of mature corallite with rare lonsdaleoid dissepiments. Specimen BQ6; thin section UCD5430. (M) Transverse section of mature corallite with lonsdaleoid dissepiments. Specimen BQ6; thin section UCD5430. (I–J) '*Fasciculophyllum*' sp. (Waulsortian limestone, Sutton Strand, Howth peninsula, County Dublin, late Tournaisian). (I) Transverse section of 2 joined corallites. Specimen HW17; thin section UCD5280/1. (J) Transverse section of mature corallite with lateral bud. Specimen HW22; thin section UCD5285/1. (N–O) *Amplexocarinia* sp. (Waulsortian limestone, Sutton Strand, Howth peninsula, County Dublin, late Tournaisian). (N) Transverse section with aulos. Specimen BQ4; thin section UCD5445. (O) Longitudinal section showing horizontal tabulae and aulos. Specimen HW20; thin section UCD5283/1.

Howthia suttonensis Somerville et Rodríguez n. sp.

(Figs. 3A–L and 4A–H, K–M)

Types: Holotype, specimen HW104/104A; thin sections UCD5416 and 5417, Waulsortian mud-mound facies at Sutton on the Howth Peninsula. Paratype, specimen HW98A; thin section UCD5407/1.

Derivatio nominis: The species name comes from the locality of Sutton on the west side of the Howth Peninsula, County Dublin. *Diagnosis*: Solitary to weakly fasciculate corallites showing peripheral offsets in the calyx. Corallites with axophyllid axial structure comprising irregular septal lamellae and tabellae. Dissepimentarium composed of interseptal and large second-order lonsdaleoid (transeptal) dissepiments in variable degrees of development. Gently to steeply inclined tabellae and stout axial pillar. Major septa range of 12–20 for alar diameter of 4–12 mm. Absence of minor septa.

Material: Over 120 cut and polished samples containing corals collected from the Waulsortian limestone at Howth have been examined including 21 thin sections (of which 12 are large, 7 cm × 5 cm); 17 transverse sections, 4 longitudinal sections. Measurements have been carried out on over 200 individual corallites (>190 T.S.; 12 L.S.).

Description:

External features: Small weakly fasciculate phaceloid corallites with some individuals showing irregular growth trajectories and adult corallites showing a broad range of diameters (Fig. 4K). The corallites are generally loosely packed in the colony (gregarious), and several individuals can be joined together in a chain (Fig. 4A). Some close packing of connected corallites in specimens can create a sub-cerioid character (Fig. 3A) and have vertically joined epithecal walls (Fig. 4D).

Internal features:

Transverse section: The range of the septal number within the colony varies from 12 to 20 with a mean of 16; the alar diameter varies from 4 to 12 mm and the tabularium diameter varies from 3.25 to 10 mm.

The individual corallite walls are generally thin (0.20–0.40 mm thick), but can be thicker (0.60 mm) due to the presence of a peripheral stereozone (Fig. 3C). They are smooth to slightly undulose (Fig. 3B–C, G–J).

The major septa show an approximately radial pattern; their length is highly variable, reaching 1/3 to 3/4 of the corallite radius. They are typically thin, but in some cases show thickening that may occur along the whole length of the septum but is more common in the outer tabularium, especially in mature corallites (Fig. 3A, C, I). The major septa are straight to slightly sinuous. Sinuosity is mainly developed in the axial ends and it is more conspicuous in thin septa (Fig. 3A, I, J). Major septa are often withdrawn from the axis in mature corallites (Figs. 3C, G and 4G). Alar septa can be conspicuously shorter than adjacent septa (Figs. 3G, I–J and 4E, G).

Six protosepta are present in juveniles at a diameter of 1.25 mm (Fig. 4F). In immature corallites with 12 septa, at a diameter of 4 mm, the counter and cardinal septa are joined and dissepiments (either concentric or lonsdaleoid types) start to appear irregularly (Fig. 4B). The cardinal septum is usually identifiable by being shorter than most septa in mature stages, and may be flanked by two adjacent shorter septa (Figs. 3H–J and 4E, M); the short cardinal septum is located in an inconspicuous cardinal fossula. The counter septum is usually longer than adjacent septa and often continuous with the median plate of the axial complex (Figs. 3G–J and 4E, L). It can be thinner than other septa (Fig. 3G). Minor septa are absent at all stages of growth.

The axial structure is very variable, but in many corallites is axophyllid, comprising a median plate with septal lamellae and tabellae (Fig. 3A, J). The number of septal lamellae ranges from 2 to 18 and they are irregular, sometimes branching or anastomosing, but can be radially disposed (Fig. 3A, J). They may be confluent with septa (Fig. 3F, J), but in some corallites are separated (Fig. 4E). The median plate is short and joined to the counter septum. In juveniles the median plate is represented by the conjoined cardinal and counter septa. Tabellae are usually few in number, 1–2 (Fig. 3J), but in larger mature corallites often develop late, with up to 5 rows (Fig. 3A). The axial structure in the holotype is relatively wide (2/5 corallite diameter), but is typically 1/4 corallite diameter, ranging from 1 to 4 mm in width in adult stages. It can be ovoid, circular or blade-like and can be fused with poorly developed septal lamellae and tabellae (Fig. 3I).

The dissepimentarium is typically composed of 1–2 rows of dissepiments, but can reach up to 4 rows (Fig. 3A, G). The dissepiments are mainly interseptal in the inner part of the dissepimentarium, but lonsdaleoid (transeptal) dissepiments can occur in the outer zone (Figs. 3A, G, J and 4A, G). Interseptal dissepiments are distributed in 1–3 rows and they are weakly concentric (Fig. 3G), but can be occasionally angulo-concentric (Fig. 3J). In some cases dissepiment rows are developed unevenly, occurring mainly on one side only (Fig. 3H–I). The transeptal dissepiments may be long and flat or globose and strongly curved (Fig. 4G). The inner row of dissepiments is sometimes thickened to form a discontinuous inner wall particularly in mature corallites (Fig. 3A, J).

Longitudinal section: 1–2 rows of dissepiments are typically observable in vertical section (Figs. 3E and 4C–D). They are small and vary from globose to elongated, moderately steeply inclined, ca. 50–60° declined towards the axis. The boundary with the tabularium is not sharp but in some cases may show discontinuous thickenings.

The tabularium is composed of 10–12 periaxial tabellae per cm, relatively regularly spaced at 1 mm, which vary from mostly complete to incomplete, and gently to moderately declined; axial tabellae are steeply declined to sub-vertical (Figs. 3E and 4C–D). The axial tabellae join a continuous axial pillar, which can form a prominent stout boss in the calyx (Fig. 3E).

Single corallites in thin section are mostly cylindrical, slightly curved, and over 27 mm long.

Increase: Increase is peripheral (sensu Jull, 1965). The new individuals develop in the periphery of the calyx of the parent corallite and are non-parricidal; the offsets can be clearly identified as having septa continuous with septa in the parent (Figs. 3B, D and 4H), with two to three new corallites recorded. In other cases, coloniality can be demonstrated by connecting skeletal elements of neighbouring corallites (Fig. 3F, K). In addition, clusters of corallites can be observed bound together by an outer envelope of dark microbial fabrics.

Microstructure: The septa are lamellar, as well as the walls and septal stereoplasm (Fig. 3L). A lamellar microstructure is typical of most axophyllids (see Semenoff-Tian-Chansky, 1974; Rodríguez and Falces, 1992).

Remarks: The different specimens of *Howthia suttonensis* show a diverse intracolonial variability, with major variations in the development of the lonsdaleoid (transeptal) dissepiments, diameter of the axial zone and alar diameter. Adult corallites can show an almost total absence of transeptal dissepiments (Fig. 3G–I) together with adult corallites showing a partially complete ring of them (Fig. 3A). In addition, the diameter of corallites showing adult features varies from 5 to 12 mm. The difference in the total number of septa between neighbouring corallites may reach 4, and the development of an axial structure is variable, from weak to well-developed. We regard these differences as either related to different developments of maturity or ecologically controlled factors. The variability in the colony with both crowded and widely spaced corallites is similar to that shown in *Heritschioides* n. sp. from the Lower Permian of Texas (Fedorowski, 1978). Furthermore, *Howthia suttonensis*, like *Heritschioides* n. sp., appears to be an unusual type of colonial species, which possessed only a weak ability to produce offsets.

Howthia suttonensis has some interesting similarities with *Axophyllum simplex* (Garwood, 1913) despite the obvious smaller size of the corallites (*A. simplex* has a maximum corallite diameter of 20 mm). According to Garwood (1913, p. 556), in the young stage of growth before the axial complex has developed, *A. simplex* has a ‘columella’ composed of a number of thick irregularly twisted vertical lamellae (septal lamellae), the majority of which are continuous with the major septa. A similar feature is present in the young stage of *H. suttonensis* (Fig. 3H). Likewise, in the mature (adult) stage of growth in *A. simplex* the majority of septa are discontinuous with the septal lamellae, but the central columella (median plate) remains attached to the counter septum in all ages, just as mostly is the case in *H. suttonensis* (Fig. 3G). Also distinctive of *A. simplex* is the late appearance of large lonsdaleoid dissepiments, only present in large specimens in calicular sections and characteristic of all species of *Axophyllum* in the Viséan. The same feature is generally typical of *H. suttonensis*. Important differences though in *A. simplex* are the greater number of septa (28 majors at diameter of 17 mm) which are thicker at the base (zaphrentid type) and the presence of minor septa which reach 1/4 length of majors. Interestingly, *A. simplex* has been recorded from Waulsortian limestones in the Dublin Basin from the Roselawn Borehole, 30 km WSW of Howth (Somerville, 1994). Also, *A.* cf. *simplex* has been recorded from the same facies in Belgium, together with *Amplexus coralloides* and *Carruthersella* cf. *compacta* (Demanet, 1923; Poty, 1981). In the corresponding shallow water oolitic limestones of the Avins Member in Belgium, *A. simplex* has been recorded from the RC4ß Subzone of uppermost Tournaisian to early Viséan age (Poty, 1989, 2007) and from equivalent strata in SW England (Rugose Assemblage A of Mitchell, 1989) and the lower Czerna Formation in the Krakow area of Poland (Poty, 2007). *Howthia suttonensis* has some similarities with *Axophyllum nanum* Poty, 1981 in its generally small size, with a range of corallite diameters (7.8–12 mm) overlapping the upper limit of *H. suttonensis*, but it does not overlap the range of septa (22–27). On the other hand, *A. nanum* does have minor septa and a relatively wider axial structure (1/3 to 2/5 corallite diameter), and the latter matched only in the holotype of *H. suttonensis*. Moreover, the axial structure in *A. nanum* is more complex with bifurcating and anastomosing septal lamellae, and has a well-defined outer ring of tabellae, seen only in the holotype of *A. nanum*. The dissepimentarium in *A. nanum* though is similar, with 1–2 rows of simple concentric dissepiments and sparse large transeptal second-order dissepiments.

5. Conclusions

A new, monotypic, weakly fasciculate colonial rugose genus, *Howthia*, is described from the Waulsortian mud-mound limestones in County Dublin, eastern Ireland. The type species, *Howthia suttonensis*, occurs on the west side of the Howth peninsula at Sutton. The stratigraphic horizon of this new genus is restricted to the uppermost Tournaisian to possible earliest Viséan? It is comparable morphologically with the coeval solitary genus and species *Axophyllum simplex* from which it is considered probably to have evolved. It also has similarities with *Axophyllum nanum* from the Upper Viséan. *Howthia suttonensis* may have been an ecological pioneer adapting to a specialised niche in microbial-dominated facies near the top of a large Waulsortian mud-mound, in shallower water than most Waulsortian settings and, as such, may have provided a novel evolutionary opportunity. Its co-occurrence with ‘protocolonial forms’ of *Amplexocarinia* and ‘*Fasciulophyllum*’ suggests an unusual stimulus for buddings in the mound.

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Research paper

Colonial form, free-living corals, and macroborers from the Pleistocene of South Florida

James E. Sorauf

Department of Geological Sciences, Binghamton University, Binghamton, New York 13902-6000, USA

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Abstract

Study of corallum shape in free-living colonies of *Manicina*, *Siderastrea* and *Solenastraea* collected from the Pleistocene Bermont formation in southern Florida indicates that they were mobile, either self-righting (*Manicina*), or rotatory (*Siderastrea* and *Solenastraea*), with colony forms that are the result of movement during growth. In rotatory corals, growth of a radial and centrifugal nature away from the corallum center indicates that rolling was frequent enough to maintain the health of individual corallites along the skeleton's entire spherical surface, as postulated previously by several authors. Post-mortem sponge boring and boring of sipunculid worms and the bivalves *Lithophaga* and *Gastrochaena* during the life of these colonies were common. Colonization by barnacles during the life of some colonies also occurred, but they were generally overgrown. Boring of rotatory coralla decreased the mass of the skeleton and probably increased the ease and frequency of rolling of round colonies. The presence of these rotatory coralla strongly suggests that the lower Bermont sediments accumulated on and around shallow banks populated by numerous free-living corals and some fixed corals such as branching *Porites*, along with a diverse molluscan assemblage indicative of a *Thalassia* (turtle grass) community.

The Pleistocene Bermont formation also contains numerous well-preserved colonies of *Manicina areolata*, indicative of deposition in shallow subtidal environments with abundant sea grass. This species was well-suited to life in this environment, and to overturning by current action, as it has the capacity to right itself after overturning, either biologically or hydrodynamically or both. The Bermont specimens of *Manicina* all (100%) possess a flat or slightly concave base, typical of self-righting forms. Colonies collected in the Bermont formation show several types of macroborers, sponges, sipunculid worms, but above all, the bivalve genera *Lithophaga* and *Gastrochaena* as well as epibionts, bryozoans and serpulid worms. *Manicina* is associated stratigraphically with rotatory colonies of *Siderastrea radians*, but the two have not been found within the same lamina. However, the two, taken together, provide strong indications of depositional environments on banks populated by sea grasses and associated fauna.

Keywords: Free-living; Pleistocene; Scleractinia; *Manicina*; *Siderastrea*; *Solenastraea*

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1. Introduction

The form and shape of their colonial skeleton, or corallum, is largely dependent on environmental conditions affecting the coral polyps that constructed it. Shapes and other characteristics of coralla thus accurately reflect these conditions and additionally, reveal much of the natural history of individual colonies. The Neogene free-living coral genera *Manicina*, *Siderastrea*, and *Solenastraea* can occur as rather uniquely shaped coral colonies that are highly characteristic of certain environments in the modern marine realm. These colony forms occur within modern and Neogene sediments and strata as old as Miocene. Late Neogene and Pleistocene environments can be interpreted with certainty to determine life conditions. In addition, the majority of Paleozoic corals, both Tabulata and Rugosa, were free-living; thus, it is of considerable interest to understand growth forms of younger, free-living scleractinian corals in order to interpret these extinct groups accurately. The present paper is a summary of extensive research on free-living massive corals that is being published as a series dealing with the corals, their shapes, their epibiont and macroborer communities, and environmental interpretations of them (Sorauf and Harries, 2009, in progress).

E-mail address: jsorauf@binghamton.edu.

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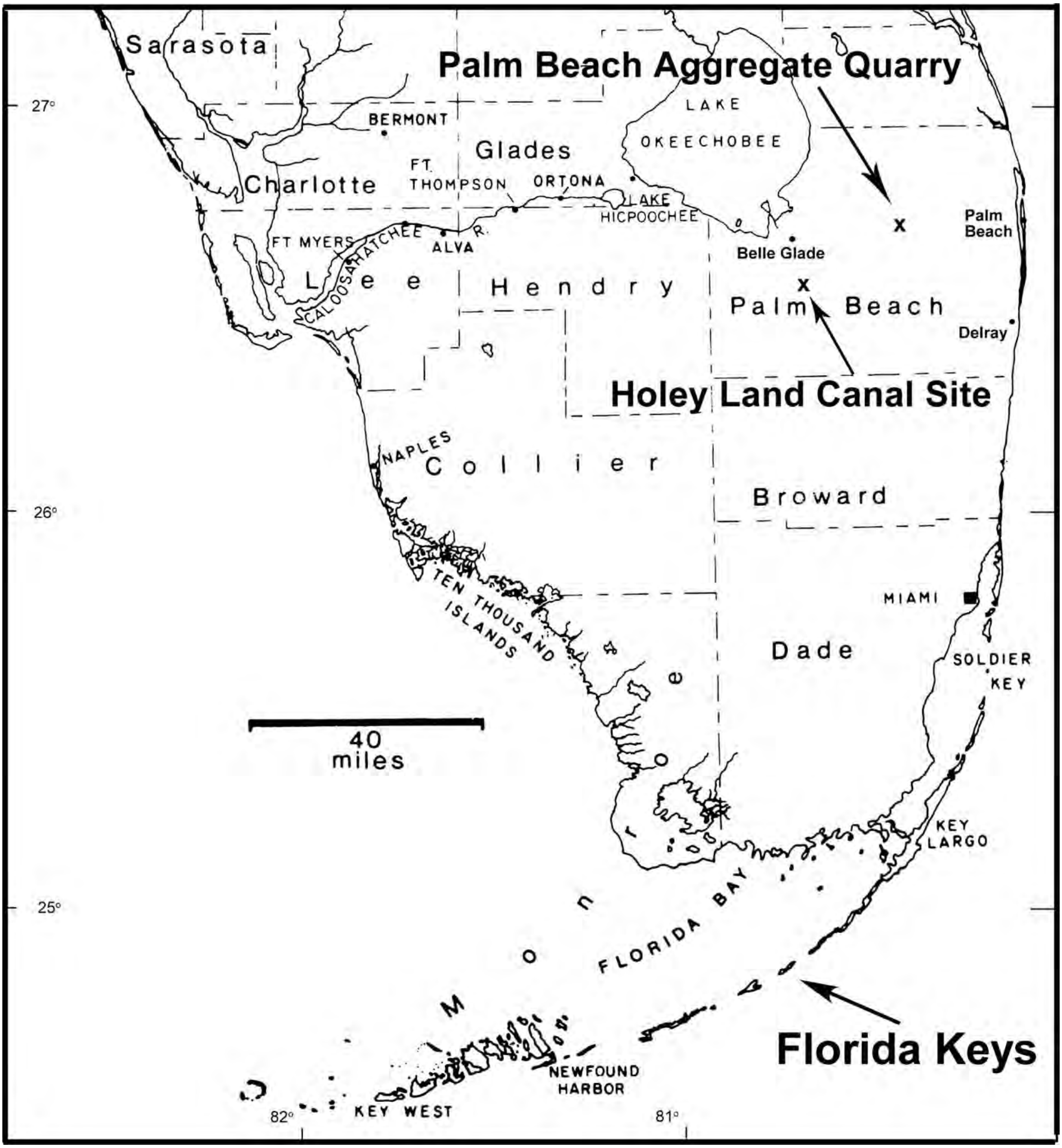

Fig. 1. Index map of South Florida. The arrows point to the two localities where Pleistocene Bermont faunas were studied and reported in this paper, as well as an arrow to point to the Florida Keys, modern rotatory *Siderastrea* was studied. The distance from the Palm Beach Aggregates Quarry to the Everglades (Holey Land) Canal is approximately 50 km.

1.1. Two colonial forms in free-living Bermont corals (Pleistocene)

In Pleistocene sediments of southern Florida (Fig. 1), *Siderastrea* and *Solenastraea* are found with rotatory growth forms, while *Manicina* occurs along with these in colony forms that indicate that they, just as their modern analogues, were corals able to right themselves when overturned, using differential inflation of their polyps (Fabricius, 1964).

1.1.1. Rotatory corals

The colony form here noted as "rotatory" has radiating growth of corallites in all directions; thus, these colonies have no base or top. Modern rotatory corals have been studied extensively

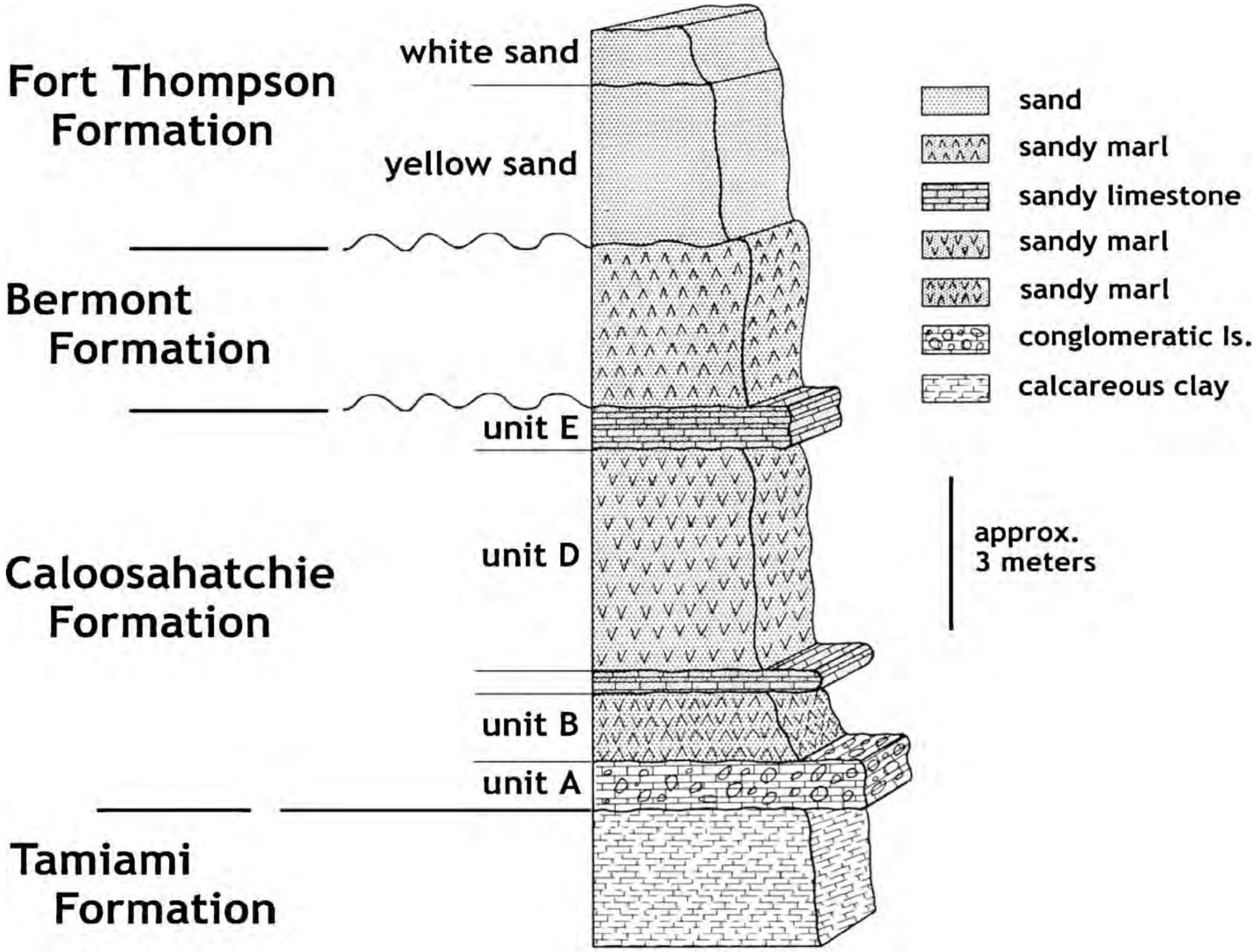

Fig. 2. Type locality of the informal unit proposed as the Bermont formation, in western Florida (modified from Dubar, 1962).

(Yonge, 1935b; Squires, 1958; Scoffin et al., 1985; Lewis, 1989), but for this study, by far the most useful research on modern *Siderastrea radians* is that by Kissling (1973) on *S. radians* at Rodriguez Key, one of the Florida Keys (Fig. 1).

Rotatory coralla of *S. radians*, along with those of *Solenastraea hyades* and *S. bournoni*, are abundant in Pleistocene strata of western Palm Beach County, southern Florida (Fig. 1). Rounded rotatory coralla of all three species are found here in the Bermont formation (Fig. 2), each with radial growth of component corallites. This growth is in general approximately equal in all directions and is the result of the coral colonies having been continuously rolled during life by physical processes. Rotation occurs often enough for the survival of coral polyps beneath the corallum until subsequent motion once again lifts them into the water column. The form was named “circumrotatory” (Kissling, 1973) and colonies were called “coralliths” (Glynn, 1974). Markedly different hypotheses have been advanced to explain their origin. The ideas of Kissling and others (Squires, 1958; Zlatarski and Estalella, 1982) are accepted; i.e., that the general cause of rotation of corals in shoal areas is to be found in the currents generated by breaking waves or tides, rather than biological activity by feeding fish. The resulting round colonies are here referred to as rotatory.

1.1.2. Self-righting colonies of Manicina

Coralla of free-living *M. areolata* are common in the lower Bermont formation of western Palm Beach County, Florida, and these invariably have flat bases. These were found to be typical of sea grass environments near modern day Bimini (Bahamas) by Squires (1958) and Fabricius (1964), in Belize and Panama (Johnson, 1988, 1992), and on reef flats of Cuba by Zlatarski and Estalella (1982).

The seminal paper by Squires (1958) on scleractinian corals near Bimini contains several important ecological observations on the free-living coral, *Manicina areolata*. Squires (1958) recognized *M. areolata* as free-living, and noted that it is one of the “more important lagoonal forms” (p. 255). Throughout, he noted that the sea grass *Thalassia* is generally present in areas where *M. areolata* is abundant, and in particular, that there are a number of overturned colonies in channels; he also recognized that coralla were apparently uninjured by overturning. His comment was that “It may be that through inflation of the tissues the species is able to right itself." Fabricius (1964) proved that this is what happens. Squires also noted that "cuneiform" colonies are present in a soft lime mud seafloor south of Bimini, and stated that this form is "developed in response to the sinking of the corallum in the mud" (since its tip extends into the soft bottom). Fabricius (1964) also recognized this aspect of colony form in *Manicina*. More recently, Hubmann et al. (2002) showed passive righting of cuneiform colonies on soft, sandy substrates by hydrodynamic positioning, which results in the re-orientation and righting of such colonies.

1.1.3. The Bermont formation

Dubar (1974, p. 221) proposed the Bermont formation (Fig. 2) as an informal stratigraphic unit to include a highly fossiliferous sequence that had formerly been regarded as the uppermost part of the Plio-Pleistocene Caloosahatchee Formation of southern Florida. The sequence is well developed in terms of thickness and coral-rich facies in the eastern half of the Florida Peninsula, where it attains a maximum thickness of approximately 9 m (Skinner, 1966) in western Palm Beach County (Fig. 2). Here, the Bermont contains an abundant coral fauna that is, however, not diverse, consisting in large part of free-living coral species such as rotatory colonies of *Siderastrea* and *Solenastraea*. These occur with non-rotated colonies of the same genera and with the free-living species *Manicina areolata* as well as the locally abundant branching coral, *Porites porites*.

2. Materials

The specimens reported here were collected from the Palm Beach Aggregates Quarry, GPS location, W 080.22.036′, N 26.54.508′, western Palm Beach Co., Florida, and from the Everglades (Holey Land) Canal, adjacent to Pump Station G203, GPS location, W 080.39.873′, N 26.23.788′, westernmost Palm Beach Co., Florida (Fig. 1). Prior to cutting with a rock saw, specimens were washed and photographed from various angles. Rather than photographing sawed slabs, these were placed in a flat-bed scanner to generate a digital image that was computer-modified to improve brightness and contrast to provide images of high quality. All specimens used in this study are deposited in the Florida Museum of Natural History in Gainesville, Florida (FLMNH), and illustrated specimens are cataloged under the numbers noted here in the explanations of Figs. 3 and 6.

3. Rotatory coralla: *Siderastrea radians*, *Solenastraea bournoni*, *S. hyades*

S. radians is abundant in the lower Bermont formation in its free-living, rotatory form, and it is present at multiple localities. Some coralla, such as the one shown in Fig. 3A, viewed from three sides, are almost perfectly round, and are rotatory, frequently rotated during the life of the coral polyps, often enough that no polyps were killed. This was noted in living *S. radians* by Yonge (1935a) and studied by Kissling (1973). Less symmetrical, ovoid coralla (Fig. 3B) of *S. radians* result from larvae having settled on a hard, biogenic substrate, such as the elongate piece of shell shown in the right hand image of the sliced corallum. This colony also has a rather prominent wall between corallites, as compared with modern specimens, perhaps in part due to diagenetic reinforcement of the wall. The graph in Fig. 4 indicates that coralla of *S. radians* tend towards being equidimensional as their size increases, thus approaching perfect sphericity as well as being very well-rounded. This is also true for both species of *Solenastraea*, although collecting bias shows in these graphs, due to the coralla shown being targeted for their rotatory nature. A specimen that ceased rotation has a barnacle that settled on top (Fig. 3C). It is characterized by sponge and fungal borings on its underside where polyps were smothered by encroaching sediment. In this cut section, the specimen was continuously rolled until the deposition of the barnacle, hence the very symmetrical growth increments clearly shown in Fig. 3C.

Many *S. radians* coralla are bored by lithophagid or gastrochaenid bivalves, some extensively (Fig. 3E and F). Much of this boring was apparently carried out during the life of the coral colony, as indicated by lithophagid bivalves that secreted a carbonate sleeve to line their borehole to form a tube to allow egress of their siphon. As shown in Fig. 3F, these borings may remove much of the skeleton in the rotatory coralla, which apparently decreased colony mass and increased the likelihood of its frequent rotation. Large rotatory *S. radians* commonly also has attached barnacles, which infested some colonies, but these generally were easily overgrown by healthy coral polyps depositing skeleton.

S. bournoni is also common in the lower Bermont formation and also forms rotatory colonies; here one is figured (Fig. 3D) with a round, symmetrical corallum having a grooved exterior. The grooves are regarded as most likely due to coral polyps having rested against a linear object on the sea floor during its latest period of growth. These are not bite marks, as the surface is intact, except where bored. *S. hyades*, with somewhat larger corallites than *S. bournoni*, also occurs as rotatory colonies in this Pleistocene fauna.

4. *Manicina areolata*

The following section separates the described occurrences of *M. areolata* in the two extensively studied localities. Regardless, the colony shapes in both localities are similar, in both cases flat or slightly concave, and maximum colony sizes are likewise approximately similar (maxima of 25–32 cm). This overall sameness is enhanced by the common presence of the bivalve *Chione congregata*, which provided support for settling larva and youthful coralla on the sedimentary substrate. Where the post-larval portion of the coral skeleton is preserved, especially in the Everglades Canal locality, there is no indication of a broken base to suggest that the individuals went through an attached phase in their youth, prior to assuming a free-living phase (Yonge, 1935a).

The graph in Fig. 5 illustrates the steady increase in volume with size in colonies collected (with increasing height in the largest). Smaller colonies of *Manicina*, with a slightly elongate, base tapered to a point in the early post-larval stage, are common, suggesting that these colonies spent their early life where larvae

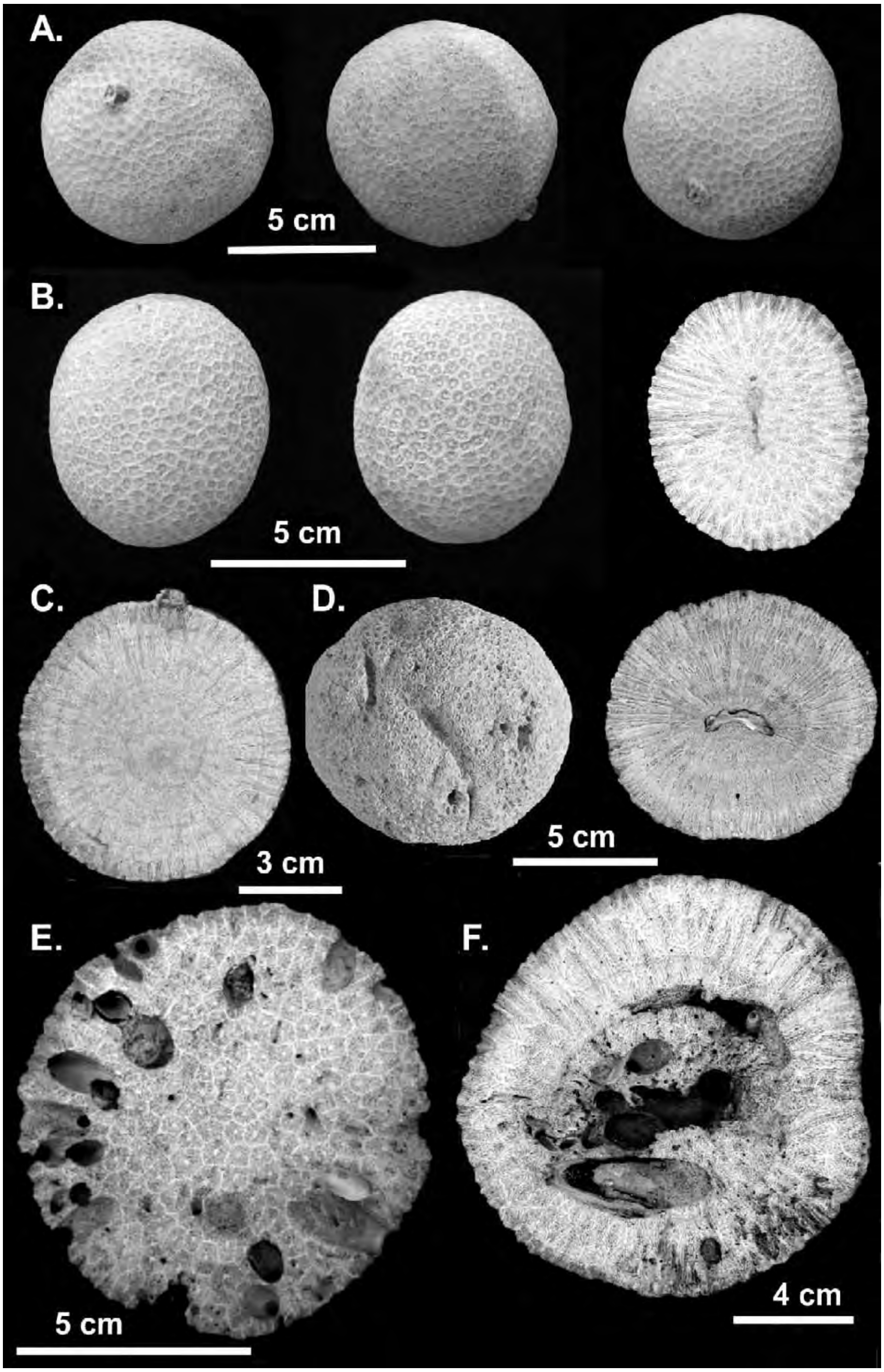

Fig. 3. A, B, C, E and F are of *Siderastrea radians* from the Pleistocene Bermont formation; D is of *Solenastraea bournoni*. All specimens collected in localities in south Florida noted in Fig. 1. (A) The specimen (FLMNH # 115137) seen from three sides, almost perfectly round, is a rotatory colony, which has been frequently rotated during the life of the coral polyps, often enough that no polyps were killed. This form also occurs in modern *S. radians* that are rolled on a consistent basis during life. The cross section of the specimen shown in the slide clearly illustrates the result of frequent rotation during growth. The rounded nature of the coral is reflected by symmetrical growth lines, with late or post-mortem settling of a barnacle seen at the top of the slice. (B) An egg-shaped *Siderastrea radians* (FLMNH # 115103), its larva having settled on a hard, organic substrate, here an elongate piece of shell. This specimen (as does A) has a rather prominent wall between corallites, as compared with modern specimens, perhaps due in part to diagenetic exaggeration of the wall. (C) The cross section of the specimen (FLMNH # 115137) shown in the slide clearly illustrates the result of frequent rotation during growth. The rounded nature of the coral is reflected by symmetrical growth lines, with late or post-mortem settling of a barnacle seen at the top of the slice. (D) *Solenastraea bournoni* (FLMNH # 115112) is present in the lower Bermont and also forms rotatory colonies, here one with a grooved exterior most likely due to having rested against a linear object on the sea floor during its latest growth period. These are not bite marks, as the surface is here intact. (E) Some of the rotatory *Siderastrea* are extensively bored. Much of this boring is apparently after the death of the colony (FLMNH # 115111). This was a large and round corallum, but now is quite lightweight as a result of boring. (F) (FLMNH # 115106) Many *Siderastrea* are bored by lithophagid bivalves (lower center); here one sees *Lithophaga*, probably *L. bisulcata*, as well as a thoroughly bored core to the corallum.

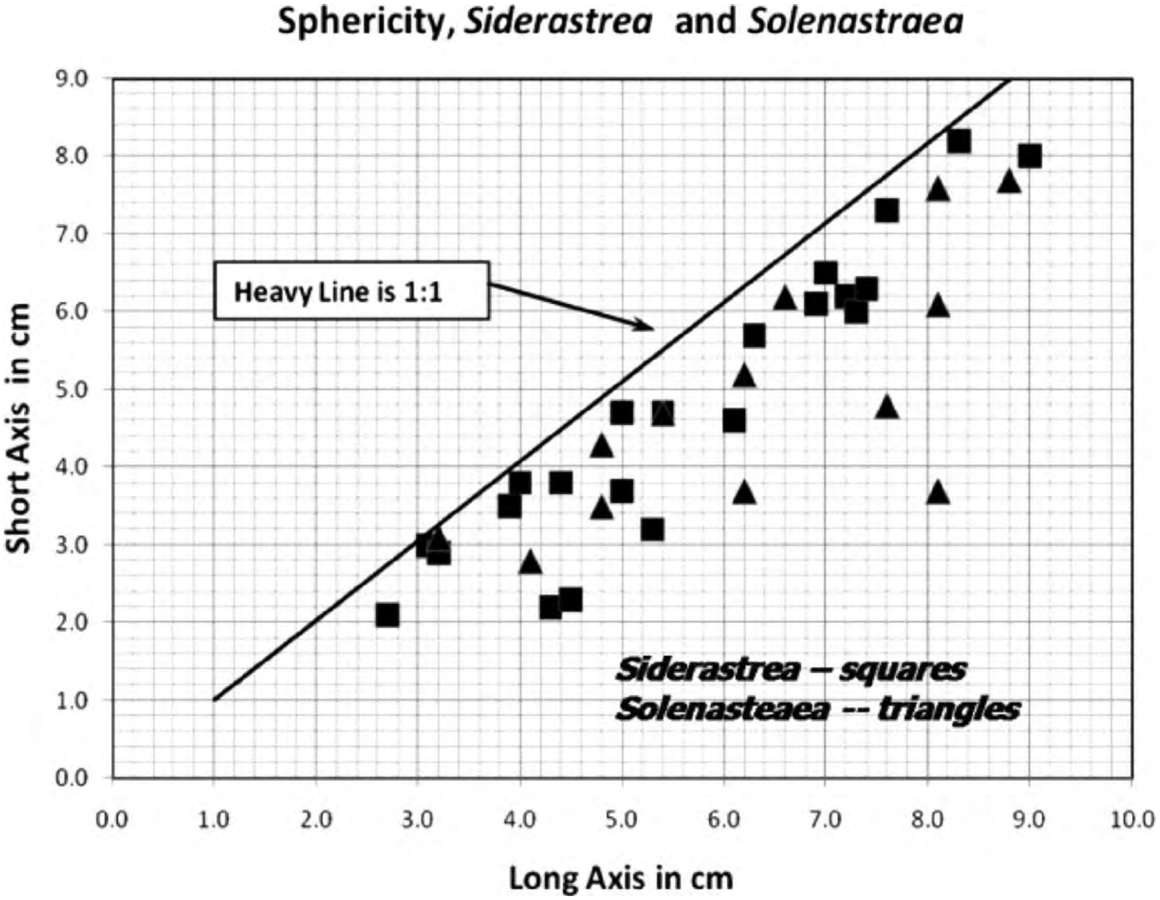

Fig. 4. Sphericity of Pleistocene *Siderastrea* and *Solenastraea*, here calculated on the basis of the ratio of shortest diameter: longest diameter = 1 representing perfect sphericity. In addition, all specimens in this sample are well-rounded.

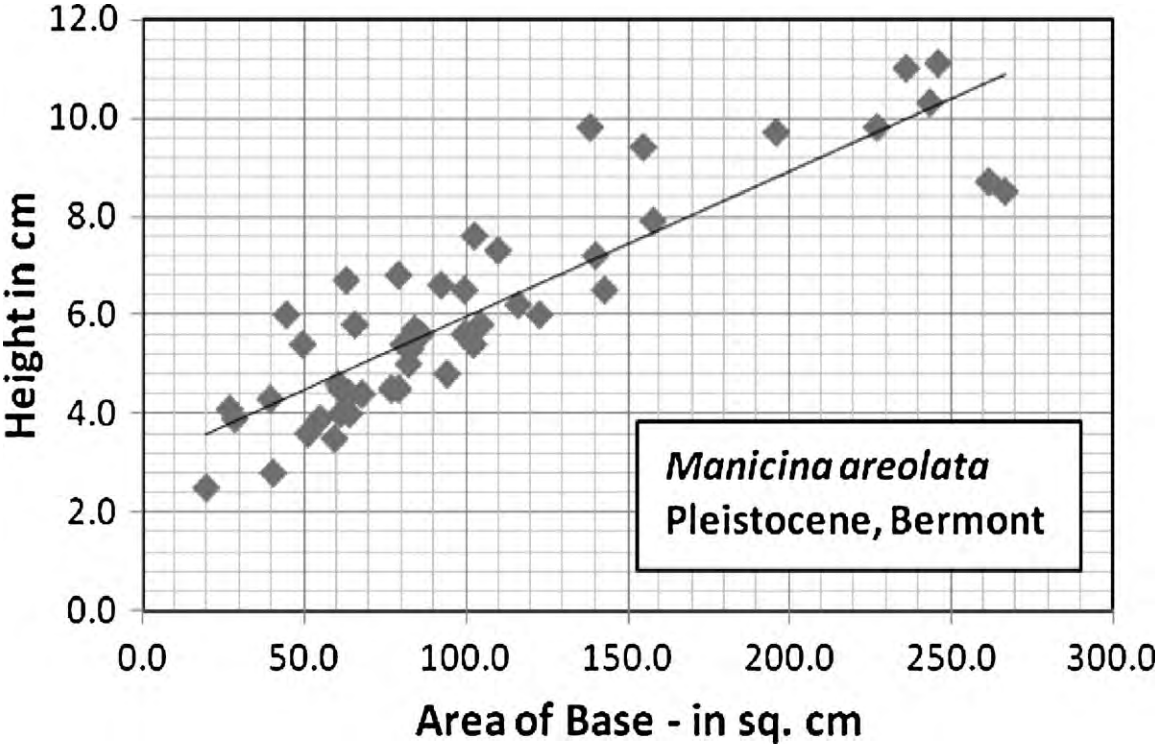

Fig. 5. A plot of area vs. height for Pleistocene specimens of *Manicina areolata* from the Palm Beach Aggregates Quarry and the Holey Land Canal localities. The area of the base was calculated as that of an ellipse, utilizing long and short diameters for each colony.

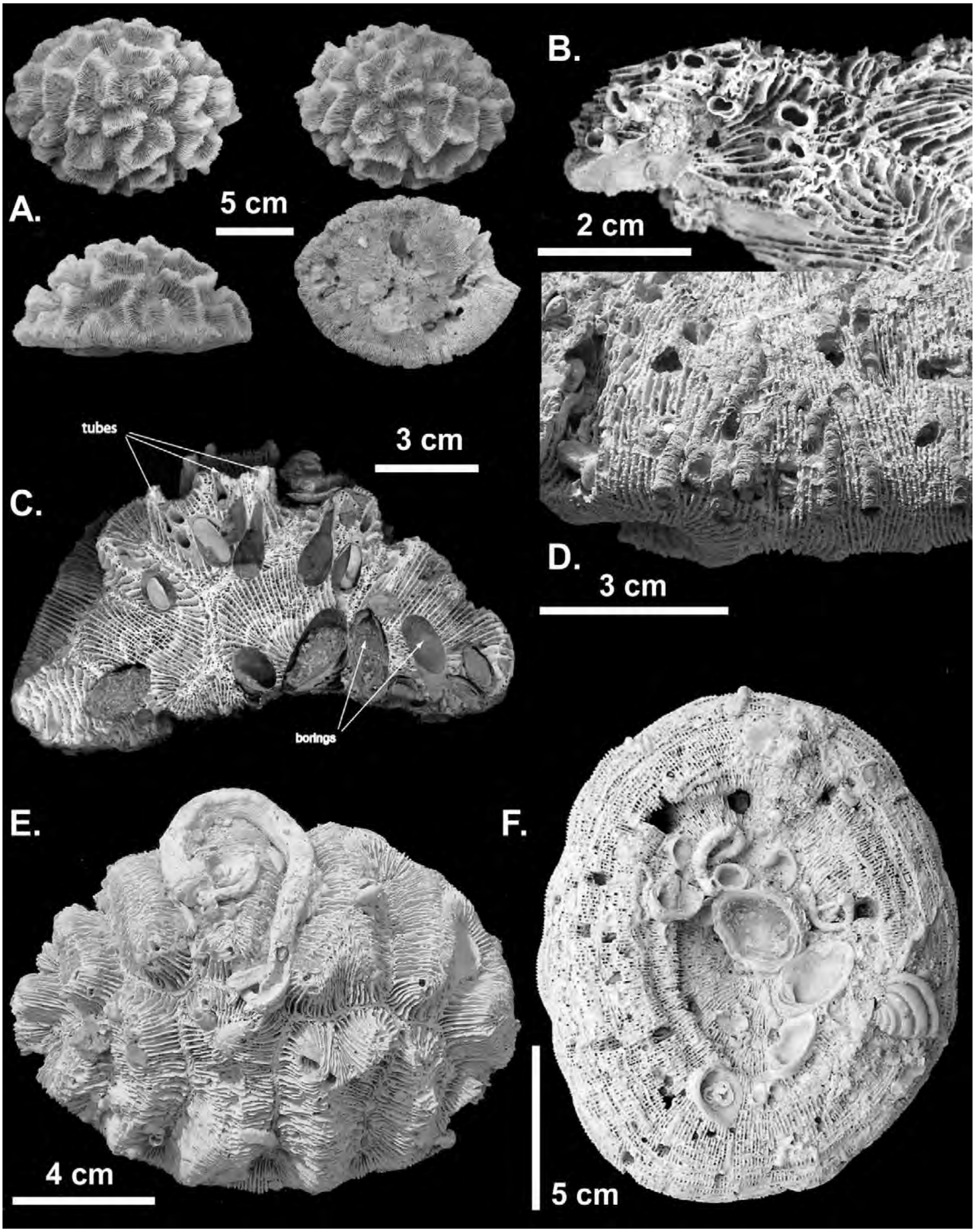

Fig. 6. All figures are of *Manicina areolata* from the Pleistocene Bermont formation of south Florida. (A) This is a very characteristic corallum of *Manicina areolata* from the Bermont at the Palm Beach Aggregates Quarry (FLMNH # 115184), elongate, low-arched, and flat-bottomed. This small colony shows little boring of its upper surface, but considerable lithophagid boring on the undersurface. (B) (FLMNH # 156747) Openings of bifid carbonate sleeves lining the access tube of the boring bivalve *Gastrochaena* hyans, which bores between polyps and resides there while the colony continues to grow, maintaining contact to the surface of the corallum with their remarkable tube. (C) Sawed section (FLMNH # 115142) showing borings by *Gastrochaena* in the upper portion of the corallum (along with forming a bifid tube as the corallum grew), and by *Lithophaga bisulcata*, which has bored into the lower surface of the corallum. (D) This upside-down photo illustrates lithophagids found beneath a very large (long D of 32 cm), low corallum (FLMNH # 115142), here forming elongate tubes that extended to the lateral margin of the coral skeleton, demonstrably during the life of the coral colony, presumably to get their siphons to the water column. (E) The upper surface of another corallum (FLMNH # 115143) from the PBA quarry shows typical bifid tube openings formed by gastrochaenid bivalves, as well as post-mortem cementation of a large serpulid test with its cap. (F) A typical corallum (FLMNH # 115172) from the Canal locality, with a relatively flat base, several species of serpulids, and *Chama congregate*, with sipunculid borings at the left. This locality is characterized by the rarity of boring bivalves, either lithophagid or gastrochaenid.

settled. Cryptic habitats present under flat or concave corolla are commonly home to bryozoans and/or serpulid worms. The presence of these filter feeders indicates that the substrate was firm, with reduced sinking of the corallum into sediment, thus maintaining protected open space beneath the corallum.

4.1. Palm Beach Aggregates Quarry

A typical *M. areolata* corallum from the Palm Beach Aggregates (PBA) Quarry in western Palm Beach County, Florida, has a low-arcuate upper surface and a flat or slightly concave lower surface, as shown in Fig. 6A. Boring is common, both by gastrochaenid and lithophagid bivalves. As shown in Fig. 6B, gastrochaenid borings are characterized by elongate bifid tubes that reach to the surface of the corallum. The bivalves settled between polyps, and bored into the skeleton, remaining while polyps continued to make additional skeleton. Thus, a tube was constructed by the bivalves to keep up with coral skeletogenesis and allow their siphon to reach the water column (Scott, 1988). Fig. 6C illustrates a sawed section through a colony from the PBA locality, characterized by borings of the upper, growing surface by *Gastrochaena* (Carter, 1978), and boring into the undersurface by *Lithophaga*. Tubes seen on the upper surface of the corallum are identical to those figured in Fig. 6B, formed by *Gastrochaena* in order to keep up with coral skeletogenesis to allow feeding from the water column. Fig. 6D illustrates part of the base of a very large colony of *M. areolata* (having a long dimension of 32 cm), which may be close to the maximum size attainable in this environment. This corallum has a flat to slightly concave base, and shows extensive boring of the undersurface by the bivalve *Lithophaga bisulcata*. The lithophagids normally bore into the base of coralla, but here formed elongate tubes that extended to the lateral margin of the corallum, demonstrably during the life of the coral colony. Presumably, this was to get their siphon into the water column for feeding. The upper surface of this colony shows little boring, and the size of the corallum probably exceeds the maximum size for overturned self-righting to occur. Additionally, the colony has a low-arched upper surface, making it even more difficult to self-right if overturned. It was too large to right itself, but its center of gravity was low enough and its mass great enough that it was not overturned.

The upper surface of the corallum shown in Fig. 6E, from the PBA quarry, exhibits the typical bifid tubes (arrows) formed by *Gastrochaena*, the characteristic borehole of *Gastrochaena*, the carbonate sleeves lining the access to the surface of the corallum. Additionally, there is the post-mortem attachment of a large serpulid test with its cap, to the corallum upper surface.

In general, *M. areolata*, as it occurs in the PBA locality, has gradations from small to large bases (Fig. 5), with younger and smaller coralla having a higher upper surface than at the canal locality, and all coralla have a flat base, except for very immature forms. Fig. 6A illustrates four views of a relatively small colony showing few signs of boring on its flat underside. Commonly, shells of the bivalve *Chama congregata* formed hard substrate for settling larvae. Serpulids and bryozoans are commonly present on undersides. It is characteristic of large colonies to display abundant and large borings by lithophagid bivalves, some of which (not the majority) is post-mortem. As noted above, the one extremely large and flat colony collected was characterized by the development of lithophagid tubes on its undersurface. Commonly, smaller boreholes that resemble sipunculid worm borings in size are also present on undersurfaces.

4.2. Holey Land Canal Locality

This locality is approximately 50 km south-southwest of the Palm Beach Aggregates (PBA) Quarry (Fig. 1) and, as judged by the differences in corallum form of *M. areolata*, had somewhat different bottom conditions than those interpreted for the PBA site. There is a very regular increase in size (as measured by the area of the base, Fig. 5) of specimens of *M. areolata* from this locality (Everglades Canal in the Holey Land). These are all colonies with flat or slightly concave bases, with few or no macroborers. This is presumed to be both a reflection of less-firm substrate and constancy of currents (with resulting frequent overturning and self-righting), and these samples differ somewhat from those collected at the PBA Quarry to the north-northeast. Typically, coralla from this locality exhibit an early, post-larval conical form as their early development. It was after this early development that the base is flat or slightly concave. The presence of abundant serpulid worms is also typical of the canal locality (Fig. 6F), and sipunculid worm borings are commonly present as well. The last figure illustrates the base of a typical form for this locality, thought to reflect conditions of a somewhat barren and fine-grained seafloor, with rather soft sediment. This locality is noteworthy for the rarity of bivalve boring, either by lithophagid or gastrochaenid bivalves, either during corallum life, thought due to the soft, fine-grained nature of the sea floor or due to post-mortem infestation.

5. Conclusions

5.1. Shape

It is basic, but it can be repeated that corallum shape, whether round or flattened, provides major insights into the life history of free-living coral colonies. Adaptations such as described here are important for the understanding of living conditions, both physical and biological. The shape of the base in free-living colonies apparently reflects sediment conditions and life habits rather clearly (for other shapes and other environments, see Squires, 1958, Fabricius, 1964, and Hubmann et al., 2002). Specialized forms such as the rotatory colonies provide exact information regarding current conditions and adaptability of coral species.

5.2. Macroborers

Their history is preserved in coralla, and indicates corallum history. Recognition of gastrochaenid or lithophagid types of macroboring provides rather exact indications of sediment and current conditions. Development of tubes for bivalve siphons provides an indication of their life style. They may also indicate a decrease in frequency of overturning in flat-bottomed coralla as size reaches near maximum.

5.3. Epibionts

Serpulid worms and bryozoans live cryptically, and provide information on firmness of sea floor underlying coral colonies, as firm sediment is a requirement for maintaining void spaces beneath coralla bases.

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Inset figure on cover: *Guiyu oneiros* from Late Ludlow, Silurian, Kuanti Formation, Qujing, Yunnan Province, China. Courtesy of Zhu Min.