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Proceedings of the XIth International Symposium on Fossil Cnidaria and Porifera, Liège, Belgium, August 19-29, 2011: Preface

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The XIth symposium of the "International Association for the Study of Fossil Cnidaria and Porifera" was held in Liège, Belgium, from August 19th to 29th, 2011. The choice of organizing the meeting in Belgium was made in 2007 during the General Assembly of the International Association for the Study of Fossil Cnidaria and Porifera in Saint-Peterbourg. The organizing committee composed of colleagues from the universities of Liège and Toulouse made tremendous effort to ensure both the scientific and social success of the meeting.

During the 5 days of the meeting, the University of Liège welcomed 103 participants from 27 countries. 101 abstracts associated with 65 oral presentations and 33 posters covering a wide range diversity of topics in time, space and subject were presented. The organizing committee had chosen to mix the session, alternating contributions of young scientists with those of established colleagues. The main discussed theme concerns the Rugosa (34 oral and poster contributions, Fig. 1), followed by the Scleractinia (30 contributions), reefs (11), general topics (10), the Stromatoporoids and Tabulata (both 6 contribution), and two devoted to the Archaeocyatha. In term of stratigraphic distribution, the Devonian and Carboniferous faunas were the most discussed (22 contributions for each), followed by the Cainozoic (13), the Holocene (9), the Cretaceous and Ordovician-Silurian (both 6 contributions), the Jurassic (4), the Cambrian (2) and one contribution for the Permian and Triassic faunas.

Thanks to a brilliant idea of J. Sorauf a special historical session was organized to remind the contribution of the great Fossil Cnidaria and Porifera researchers of the past and their heritage to the current science. It was a great success and ten talks were devoted respectively to Maria Różkowska, Masao Minato, Dorothée Le Maître, Genevieve Termier, James Alloiteau, Marius Lecompte, Jean-Gabriel Lafuste, Patrick Sutherland, William Sando and to Dorothy Hill. These tributes are combined in the paper by Sorauf et al. opening this volume of proceedings.

The organizing committee awarded in 2011 the first Henri Milne Edwards Medals to Françoise Debrenne (Muséum national d'Histoire naturelle de Paris, France) and John Jell (University of Queensland, Australia) for their major and long-lasting contributions to the study of corals and archaeocyaths. Both are deeply thanked for their work. This medal is offered as the gratitude mark to specialists of fossil Cnidaria and Porifera from the scientific community. The Best Poster Award was attributed by vote of the participants of the symposium. The 2011 laureate is Luke Nothdurft (Queensland University of Technology) for its poster entitled: Skeletal fusion of clonal fragments in *Acropora*. The figure illustrating the cover of this volume is extracted from this poster.

Three geological field trips were organized; two pre-symposium and one post-symposium. The first pre-symposium field-trip was devoted to the Givetian and Frasnian of Southern Belgium (Boulvain et al. 2011) and particularly to the type area of the two stages. Sections in the Meuse and Vesdre valleys showing the upper Frasnian succession were studied before moving south to observe the reefal facies of the Givetian in the Ourthe and Lesse valleys and along the type section in the Meuse Valley at Givet. The reefal successions of the Frasnian were examined in the Rochefort, Frasnes-les-Couvin and Philippeville areas.

During the second pre-symposium field-trip entitled "Classical Devonian and Carboniferous sites in the Ferques area, Boulonnais, Northern France" (Mistiaen et al. 2011), the participants examined outcrops of reefal Devonian facies near Ferques and well weathered fossiliferous blocks (Devonian and Carboniferous in age) along the sea shore. The Carboniferous formations were observed in Rinxent and near the Napoléon Quarry. Some classical outcrops of the Cretaceous chalk were observed at the Cap Blanc Nez.

The post-symposium field-trip presented renowned sections of the Uppermost Devonian and Lower Carboniferous strata of Southern Belgium (Poty et al. 2011). The first day was devoted to the Strunian coral-stromatoporoid biostromes, the Devonian-Carboniferous transition and the Tournaisian of the Vesdre, Ourthe and Hoyoux valleys. During the second day, the participant examined the Upper Viséan biostromes of the Hoyoux valley, the Tournaisian strata of the Meuse area, including the Waulsortian buildups, and middle Viséan biostromes and bioherms of the Namur area. The Tournaisian fauna of the type

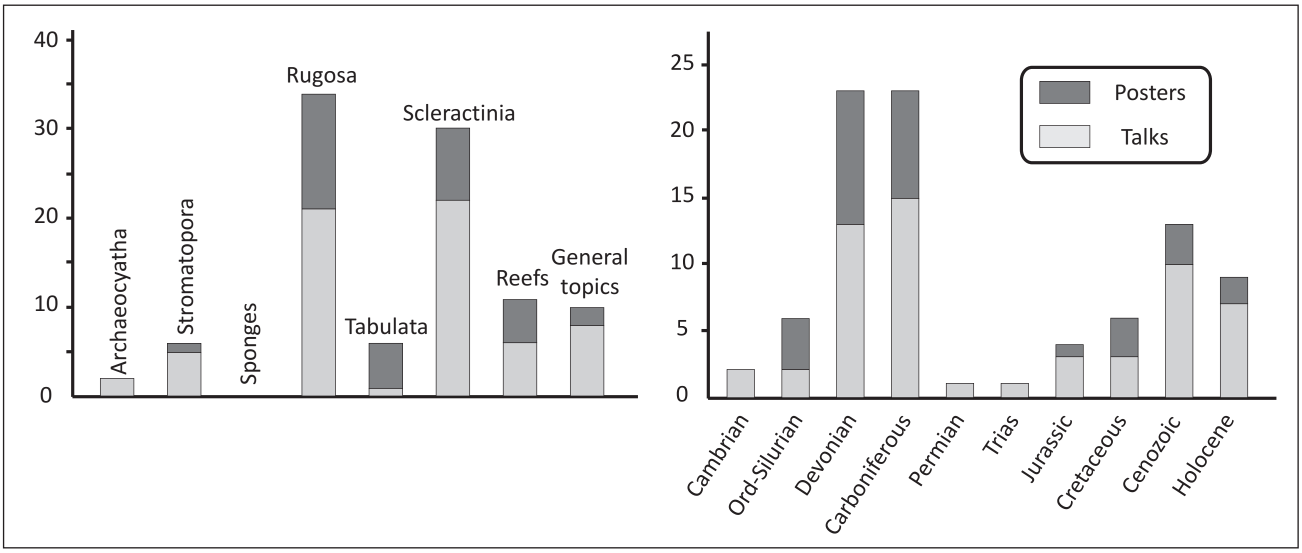

Figure 1. Thematic and time distribution of the contributions for the XIth Symposium on Fossil Cnidaria and Porifera.

area at Tournai was the focus of the third and last day. An atlas figuring the Uppermost Devonian and Lower Carboniferous rugose corals of Southern Belgium (Denayer et al., 2011) is associated to this field guide.

The field-trip guides are published as volume 20 of the Kölner Forum für Geologie und Paläontologie (Aretz & Poty, 2011), and the abstract volume of the symposium as volume 19 of the same journal (Aretz et al. 2011). The present volume of Geologica Belgica includes the 25 contributions accepted for the proceedings of the symposium after being peer reviewed by specialists. The scientific committee thanks all the colleagues for their intensive and quick work for the review of the manuscripts: Błażej Berkowski, Frédéric Boulvain, Marie Coen-Aubert, Keith Dewing, Owen Dixon, Maria Hecker, Hans-Georg Herbig, Bogusław Kolodziej, Olga Kossovaya, Peter Kruse, Jacob Leloux, Andreas May, Josef Michalik, Elena Moreno Eiris, Bernard Mottequin, Mari-Ann Motus, Ross McLean, Klemens Oekentorp, John Pickett, Sergio Rodríguez, Ian Somerville,

Figure 2. XIth International Symposium on Fossil Cnidaria and Porifera, 22-26 August 2011, Liège, Belgium. Picture of the congress participants. From back left to front right: 1: Valentin Fischer (Be); 2: Mari-Ann Motus (Ltu); 3: Tomas Suttner (Aut); 4: Erika Kido (Aut); 5: Paweł Wolniewicz (Pol); 6: Francis Baldwyns (Be); 7: Eric Bouchez (Be); 8: Christoph Iven (Ge); 9: Madhi Badpa (Ir); 10: Daniel Ungureanu (Rom); 11: Jacob Leloux (Nld); 12: Vassil Zlatarski (USA); 13: Peter Kruse (Aus); 14: Edwin Lord (USA); 15: Joel Stake (USA); 16: Kenneth Johnson (UK); 17: John Pickett (Aus); 18: Bernard Lathuillière (Fr); 19: Bruno Mistiaen (Fr); 20: Cyrille Prestianni (Be); 21: Sandrine Delculée (Be); 22: Asuka Sentoku (Jap); 23: Cristianno Ricci (It); 24: Jean-Claude Rohart (Fr); 25: Mélanie Gretz (CH); 26: Victor Ogar (Ukr); 27: Shaahin Zaman (Ir); 28: Sergio Rodríguez (Sp); 29: Ian Somerville (Ire); 30: Ismail Said (Sp); 31: Ross McLean (Can); 32: Brian Rosen (UK); 33: Paul Sartenaer (Be); 34: Agostina Vertino (It); 35: Nadhiezda Santodomingo (UK); 36: Michaela Bernecker (Oma); 37: George Stanley (USA); 38: Yves Plusquellec (Fr); 39: Fokko Van Hulten (Ndl); 40: Jill Darrel (UK); 41: Emilie Pinte (Fr); 42: ???; 43: Adeline Dutrieux (Be); 44: Lin Wei (Chi); 45: Bernard Hubmann (Aut); 46: Yoichi Ezaki (Jap); 47: Makoto Kato (Jap); 48: Luke Nothdurf (Aus); 49: Jaroslaw Stolarski (Pol); 50: Ann Bud (USA); 51: Francesca Bosselini (It); 52: Jerzy Fedorowski (Pol); 53: Adeline Kerner (Fr); 54: Maria Hecker (Rus); 55: Miss. Ospanova (Taj); 56: Narima Ospanova (Taj); 57: Dieter Weyer (Ge); 58: Yohan Cornet (Be); 59: Julien Denayer (Be); 60: Weihua Liao (Chi); 61: Xiaojuan Wang (Chi); 62: Xiangdong Wang (Chi); 63: Bogusław Kolodjziej (Pol); 64: Hannes Löser (Mex); 65: Hans-Georg Herbig (Ge); 66: Mrs Kato (Jap); 67: Katarzyna Janiszewska (Pol); 68: Błażej Berkowski (Pol); 69: Gregory Webb (Aus); 70: James Sorauf (USA); 71: Natsuko Adachi (Jap); 72: Isao Niikawa (Jap); 73: Carden Wallace (Aus); 74: ???; 75: Markus Aretz (Fr); 76: John Jell (Aus); 77: Satomi Ueda (Jap); 78: Firuza Salimova (Taj); 79: Firdaus Karimova (Taj); 80: Klemens Oekentorp (Ge); 81: Marie Coen-Aubert (Be); 82: Edouard Poty (Be); 83: Mrs. Niikawa (Jap); 84: Françoise Debrenne (Fr); 85: Ewa Roniewicz (Pol); 86: Galina Melnikova (Taj); 87: Elzbieta Morycowa (Pol); 88: Olga Kossovaya (Rus); 89: Antony Wright (Aus).

Figure 3. Some pictures of the symposium and the field trip. A: Field trip n°3 in the Uppermost Devonian and Carboniferous of Southern Belgium, the group in the Namur Citadelle (back: Julien Denayer, Sandrine Delculée, Valentin Fischer; mid: Lin Wei, James Sorauf, Fokko Van Hulten, Edouard Poty, Jerzy Fedorowski, Yoichi Ezaki, Dieter Weyer, Olga Kossovaya, Ian Somerville, Shaahin Zaman, Madhi Badpa; front: Markus Aretz, Jean-Claude Rohart, Błażej Berkowski, Victor Ogar). B: Luke Nothdurft, Best Poster Award laureate. C: Coffee break during the symposium. D: John Jell and Françoise Debrenne, both awarded with the Henri Milne Edwards Medal for their major contributions on the study of the fossil Cnidaria and Porifera. E: The Organizing Committee and the staff (from left to right: Edouard Poty, Markus Aretz, Julien Denayer, Florie Robert, Yohan Cornet, Marie Heren, Adeline Dutrieux, Valentin Fischer, Sandrine Delculée, Nicolas Lepers and Cyrille Prestianni). F: Closing Ceremony: "*So, it's finished*!".

James Sorauf, George Stanley, Gregory Webb, Dieter Weyer, Pawel Wolniewicz, Anthony Wright and Graham Young.

As stated above, the first contribution to this volume of proceedings is the paper on our "mentors" by Sorauf et al. reporting the great heritage of the past corals masters: James Alloiteau, Dorothy Hill, Marius Lecompte, Masao Minato and Maria Różkowska.

Kerner introduces the Archaeocyatha computer program used as a determination key for the identification of archaeocyathids.

Ospanova discusses the taxonomical rank of the Heliolitida as an order by comparing the morphology of several Ordovician genera and species from Central Asia.

Sorauf & Kissling report the presence of the solitary rugose coral *Streptelasma* sp. anchored within colonies of *Paleofavosites prolificus* from the Silurian of Ohio.

May & Rodríguez describe the stromatoporoids and rugose corals association from the Pragian reefal limestone of Zújar (S. Spain) and introduce one new species of *Martinophyllum*.

Wolniewicz compares seven stromatoporoid species from the Devonian of Poland and Belgium in order to show the taxonomic confusion leading to the wrong estimation of the palaeobiodiversity.

Berkowski & Weyer describe *Hamaraxonia*, a pseudocollumelate rugose coral genus from the middle Eifelian of Morocco based on the species *H. africana* and they discuss the terminology, morphology and origin of the columella and pseudocolumella.

Plusquellec et al. describe two new species of the solitary rugose coral *Angustiphyllum* from the Middle Devonian of Armorica and discuss their life strategy.

Coen-Aubert reviews the upper Frasnian massive rugose corals in Belgium and describes two new species of *Frechastraea*: *F. coeni* and *F. glabra*, two common taxa marking the base of the upper Frasnian in the Namur-Dinant Basin.

Denayer et al. describe the coral occurrences from the Lower and Middle Famennian strata of Belgium. They also expose the post-crisis context of these poorly diversified but morphologically highly variable association.

van Hulten presents new data for the reconstruction of the Devonian and Mississippian reef complex of the North Sea and the comparison with the contemporaneous reef complexes of Alberta (Canada) and Caspian area.

Hecker reviews several colonial rugose coral genera from the Viséan of the Urals and Donetz Basin that were described under different names but belonging all to the genera *Dorlodotia* and *Ceriodotia*.

Hecker describes the tabularium particularities (axial cones, biform tabulae) of *Lonsdaleia* and supposes that the genus forms the root of *Cystolonsdaleia* characterized by such a tabularium.

Somerville et al. provide an analysis of the rich and diverse late Viséan coral fauna from the Tabainout mud-mound complex in the Khenifra region of Central Morocco.

Denayer describes the corals of a microbial-sponge-bryozoan-coral bioherm in the Taurides (South Turkey) and discuss the palaeoecological context and the palaeobiogeographical affinity of this coral fauna.

Lin et al. provide an overview on the rugose coral fauna from the upper Viséan and Serpukhovian of the Yashui section (South China).

Ogar gives an overview of the Carboniferous reefs of the Donets Basin and highlights specific reef communities for individual time slices.

Fedorowski & Bamber discuss the paleobiogeographic significance of Bashkirian rugose corals from Arctic Canada, surprisingly composed of common Late Viséan to Serpukhovian taxa.

Rodríguez & Bamber review several genera belonging to the family Geyerophyllidae that were supposed to be colonial. These colonial corals being, in fact, composed of gregarious, solitary corals, true colonies are unknown in the Geyerophyllidae.

Kossovaya et al. introduce the new genus *Sloveniaxon* form the Permian of Slovenia as an homeomorph of *Cyathaxonia* and discuss its affinity with the Carboniferous and Permian *Cyathaxonia*-like corals.

Zlatarski & Stake present a summary of the last 3 centuries of researches on corals and explain the major steps that occurred in the study of this famous group.

Melnikova & Roniewicz describe the coral association from the Late Triassic and Early Jurassic of the Pamir Mountains (central Asia) and the figure the appearance pattern of taxa following the Triassic/Jurassic boundary.

Löser exposes statistical methods helping to species identification, based on measurements on Cretaceous plocoid coral genus *Stelidioseris*.

Wallace presents the diversity of living and fossils genera belonging to the Acroporidae in the Caribbean.

Nothdurft & Webb discuss the incorporation of coral macro-fragments in *Acropora* colonies and the relationship with the host colonies in case of living clonal fragments, living non clonal fragments and dead fragments.

The organizers of the XI^th^ Symposium on Fossil Cnidaria and Porifera thank the team who worked in front and behind the scene before, during and after the symposium, for the field-trips and for the edition of the proceedings volume (Figs 2-3). Financial and logistic support from Geologica Belgica, University of Liège, University of Köln, La Ville de Liège, Fond National pour la Recherche Scientifique (FNRS), Carmeuse s.a., and the International Association for the Study of Fossil Cnidaria and Porifera are greatly acknowledged.

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Mentors: the generation 1935-1985

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ABSTRACT. The lives and scientific contributions of five eminent academic geologists and paleontologists; James Alloiteau (Museum National d'Histoire Naturelle, Paris, France), Dorothy Hill (University of Queensland, Australia), Marius Lecompte (University of Louvain, Belgium), Masao Minato (Hokkaido University, Sapporo, Japan), and Maria Różkowska (Adam Mickiewicz University, Poland) are briefly summarized here. Each of these paleontologists made major contributions to the study of fossil corals and/or sponges, and each overcame considerable difficulties and disruptions in their lives to excel as mentors to us. All showed remarkable determination and love for paleontological research, and inspired their students and colleagues to understand details of structure and systematic positions of fossil corals and sponges. Each of these individual mentors was the subject of a presentation by a former student at the 11th International Symposium on Fossil Corals and Sponges in Liege, Belgium; thus, somewhat broader coverage of each is provided in the abstracts volume of the meeting.

KEYWORDS: Alloiteau, Hill, Lecompte, Minato, Różkowska.

1. Introduction

This paper summarizes portions of a group of papers presented at the 11th International Symposium on Fossil Cnidaria and Porifera in Liege, Belgium, during August 19 to 29, 2011. These contributions were each composed by one or more former students of a well-known and influential mentor in our chosen field, research on fossil corals and/or sponges. The presentations focused on the lives and accomplishments of these mentors and possible character traits that led them to their various degrees of pre-eminence in our area, but taken in total, are far beyond the present allowable space to allow presenting them here in full detail. What follows is a distillation of, and selections from, individual presentations. All of these were published as brief but extended abstracts in the *Kölner Forum für Geologie und Paläontologie* (Aretz et al., 2011). Biographic information on deceased coral specialists of this vintage can also be found in proceedings volumes for meetings of the International Association for Study of Fossil Cnidaria and Porifera; Maria Różkowska (Fedorowski, 1980), Jean-Pierre Chevalier (Coates, 1984), and William A. Oliver, Jr. (Sorauf & Fedorowski, 2010). Each of the five distinguished scientists treated here come from the generation that was studying and professionally active just before, during and after World War Two. Individuals are discussed by their former students below (with initials of contributing authors included) along with a brief summary of their lives and careers. These summaries focus on the major contributions of each and lead to a summing up of common characteristics that enabled them to excel as scientists, as role models for students and friends, and as mentors of the present generation of researchers on fossil corals and/or sponges.

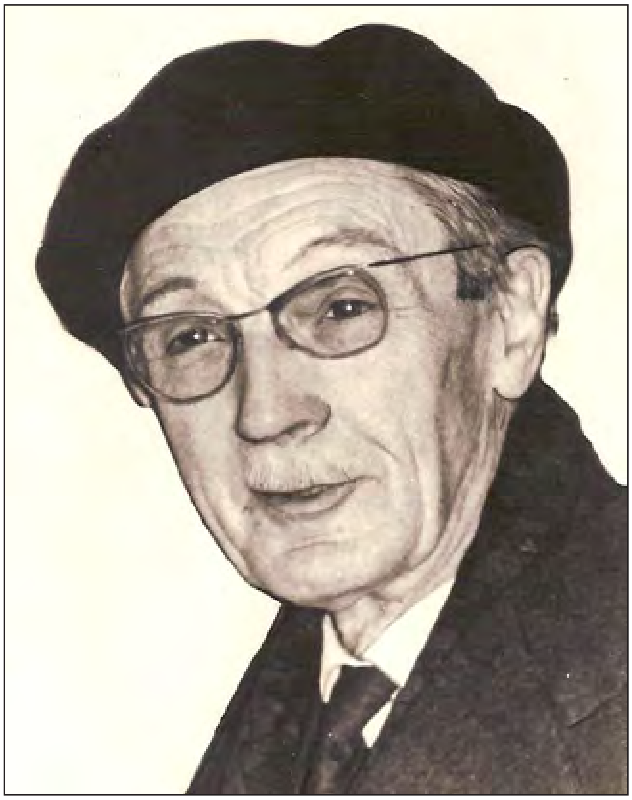

Figure 1. James Alloiteau, January 1966.

2. James Henri Alloiteau (*E. R. and E. M.*)

James Henri Alloiteau (Fig. 1) was born in Chartres, France, in 1890 into the family of a gardener; and died in early 1969. His early studies in Paris were interrupted by the First World War. After this, he studied at the Sorbonne, and in 1926 obtained a diploma in geology. In 1939, he began paleontological research in the *Centre National de Recherches Scientifiques,* and this too was interrupted by war. During the Second World War, he was a member of the resistance, was arrested in 1943, and suspended from his position at the university, but returned to his research again at war's end.

In 1952, he published his systematics of the Scleractinia in the *Traité de Paléontologie* (Jean Piveteau, ed.), predominantly based on microstructural criteria and above all, on septal microstructure and its external expression, septal ornamentation. This new approach to scleractinian systematics was based primarily on his own observations of living and fossil corals. His proposed scheme of coral systematics has, in large part, survived to the present, despite more than a half of century of research by many other specialists since its publication. He defended his doctoral thesis in 1955, and soon thereafter published his widely acclaimed book, *Contribution à la systématique des Madréporaires fossiles* (1957).

James Alloiteau awakened general interest in scleractinian microstructures, a direction of research neglected in the 20th century until the 1950s, although traditionally, it was prominent in publications of 19th century coral workers. Some of his new and increased understanding of coral microstructure has been used extensively in following systematic treatment of the Scleractinia, such as that of Vaughan and Wells, without modification. In the following generation, it was James Alloiteau who was most responsible for continuation of research on skeletal structures of corals and systematics based on them. Moreover, his "French school" also initiated new techniques for microstructural studies in ultra-thin sections. These have been united with scanning electron microscopy and molecular studies to further develop modern scleractinian taxonomy in accordance with skeletal structures. While at the Sorbonne, Alloiteau recruited young paleontologists for his team at the *Muséum Nationale d'Histoire Naturelle* in Paris. Each was a specialist in a different group at different stratigraphic levels: J.-P. Chevalier, Cenozoic scleractinians; M. and L. Beauvais, Cretaceous and Jurassic scleractinia; J. Lafuste, Tabulata; P. Semenoff-Tian-Chansky, rugosans, and F. Debrenne, archaeocyaths. Under the guidance of Alloiteau, each of these coral workers completed theses to become Doctorates of the State, along with J.-P. Cuif (Triassic Scleractinia) and S. Barta-Calmus (Tertiary Scleractinia). In addition, while in charge of this research group, he provided post-doctoral research positions at the museum for coral specialists from Israel, Poland, Bulgaria, Argentina, Belgium, and Germany.

James Alloiteau is the author or co-author of over 30 scientific papers, published in France as well as in international scientific journals. His special contribution to understanding corals was to focus on their microstructure (1952, 1957, 1958). The legacy of Alloiteau continued to influence coral studies for decades, as all the members of the "French Coral Group" use microstructure as a practical systematic criterion for supra-generic taxa. This is widely accepted as a fruitful method. Members of the Alloiteau group have thus contributed greatly to microstructural studies of the Scleractinia, with results confirmed by molecular studies. For his scientific achievements and contributions to society, James Alloiteau was awarded numerous titles, including *Chevalier de la Légion d'honneur* and *Officier d'Académie.*

3. Dorothy Hill (*J. S. J.*)

Dorothy Hill (Fig. 2) was born in Brisbane in 1907, the third eldest of seven children. Dorothy was raised in Brisbane, with a classical education that included Latin, French, Mathematics, and Science. She had a truly admirable career in addition to her contributions to coral and archaeocyathid paleontology. She was honored by her university, her province, and her country for academic and societal accomplishments; a list of honors too long to provide details here (see Campbell & Jell, 1999). She graduated from the University of Queensland with a gold medal, and earned her MSc in one year. She was awarded a scholarship to undertake studies at Cambridge University, where she earned the PhD in two years. Her dissertation on Carboniferous coral faunas of Queensland and Scotland was published in part as a Palaeontolographical Society Monograph (1938). After postdoctoral years at Cambridge and service in the Australian Navy, she joined the University of Queensland, where she taught and conducted research for the rest of her life. In addition to her coral studies, she was an extremely prominent professor on campus and was instrumental in the development of her department and the university during her tenure until her retirement in 1972. Dorothy was also deeply involved throughout her career with the scientific study of the Great Barrier Reef. As secretary of the Great Barrier Reef Committee (1945-1955), she arranged finances for the establishment of the research station on Heron Island. She was recognized as a lady of great intellect and energy, of the highest integrity and loyalty, and an advocate of equality for women.

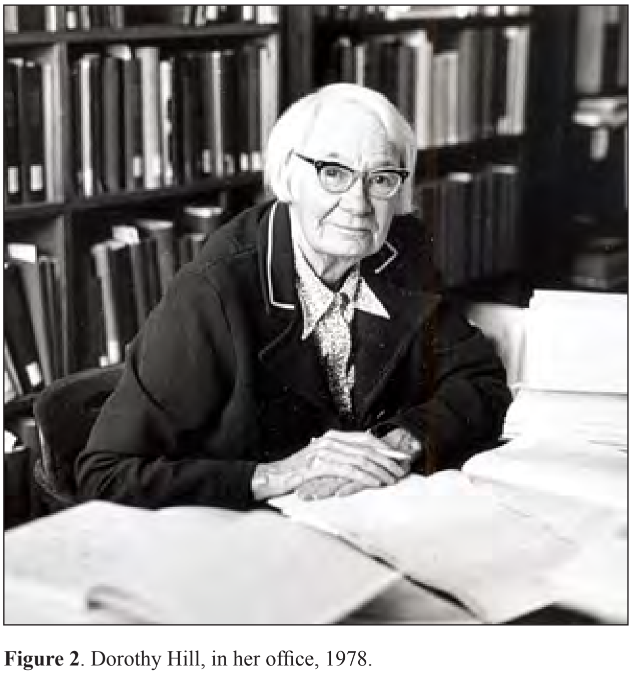

Figure 2. Dorothy Hill, in her office, 1978.

Her coral work at Cambridge was greatly influenced by Stanley Smith of Bristol University, who fostered her interest in skeletal structure and its relationship to soft tissue. At this time she published the *British terminology of rugose corals i*n 1935, her well-received paper on coral microstructure. *The British Silurian rugose corals with acanthine septa* (1936) followed soon after. Her seven years at Cambridge were a great influence both career-wise and personally.The stay provided her with all she needed for the study of fossil corals which in turn facilitated her understanding of the geological history of Australia. She resumed description of Australian coral faunas, emphasizing their stratigraphic usefulness. The quality of her work, her understanding of the coral skeleton and her knowledge of the world-wide stratigraphic distribution of Paleozoic corals were soon recognized, prompting overseas workers to send her collections for study. She published taxonomic papers on material from the following: the Devonian and Permian of New Zealand, Ordovician of Norway, Ordovician of USA, and the Ordovician of Canada. Additionally, she had introduced concepts of palaeobiogeography of coral faunas that are still prominent today. She contributed to the first Coelenterata volume of *The Treatise on Invertebrate Paleontology* (1956). After retirement, Dorothy was appointed Emeritus Professor and continued her work on the revision of the Tabulata and Rugosa *Treatise* (1981). She regarded this as the culmination of her life's work on corals. The two volumes are not just a compilation of past papers on Paleozoic corals but are the comprehensive and careful distillation of five decades of experience. They are the single most important reference on Paleozoic corals.

With discovery of large archaeocyathid faunas in Antarctica, Dorothy began to interpret the structure of their skeletons using thin sections, as she had for corals. She published several taxonomic papers and a major monograph on these Antarctic faunas, the latter based on fossils collected by a former student on the Trans-Antarctic Expedition. She then revised the treatise volume on the Archaeocyatha (1972).

Dorothy Hill was a pre-eminent Palaeozoic coral and archaeocyath specialist. She was an inspiring lecturer and a superb supervisor, producing several generations of students with the necessary tools to carry on the research she fostered throughout her career. She epitomized the twin virtues of humility and sincerity, and was a person of boundless energy, enormous intellect and great vision. Throughout her life she also showed exceptional organizational and administration skills in groups as small as field parties or as large as international scientific societies.

4. Marius Lecompte (*J. E. S.*)

Marius Lecompte (Fig. 3) died in 1970, at the age of 68. He was born in Morlanwelz, Belgium and upon graduation from school taught the natural sciences at a secondary school in Chimay (Ugbaghs, 1977). With money he saved from work as a mining geologist in Katanga, Belgian Congo (1927-1930), he supported himself as a doctoral student at the University of Louvain. In 1933, he began his career at the Royal Museum of Natural History in Brussels, where he rose to become head of

Figure 3. Marius Lecompte, in academic procession, 1950s.

Paleontology (1952). After World War Two, he began teaching at Louvain as an instructor (1945), and became Professor in 1949.

Beginning study of the Middle and Upper Devonian tabulate corals in the Dinant Basin, Lecompte first focused on species described by Goldfuss in the 19th century, widely quoted and utilized but until this time, never studied in thin section. His first paper was on tabulates described by Goldfuss, based entirely on thin sections of types and his research on them, wisely chosen as preparation for his studies on Devonian tabulates which resulted in his major monograph on tabulate faunas from the Dinant Basin (1939), in quarto-size. These were based, he noted, on study of five to six thousand thin sections.

After World War II (1951,1952), Lecompte published classic studies of Devonian stromatoporoids, two major monographs. He noted that the monographs were based on study of 9,000 to15,000 thin sections, and he presented lengthy discussions of skeletal structure and microstructure. Lecompte reviewed the systematics of 13 genera of Devonian stromatoporoids, three of which were newly proposed along with numerous species. Based on his understanding of the genera involved, he established family boundaries for the Paleozoic stromatoporoids very like those later utilized in the section he wrote for the Treatise on Invertebrate Paleontology (1956). The treatise contribution was built on his previously published summaries of stromatoporoids, tabulates and rugosans in the earlier *Traité de Paléontologie,* edited by Piveteau (1952).

His paper on the reef phenomenon and sedimentology of Devonian strata of the Ardennes (1954) was classic. His publications on the origin and ecological characteristics of Frasnian reefs of the Ardennes were major contributions to clarification of relationships of Middle and Upper Devonian strata and accompanying reefal carbonates of the Dinant Basin.

The contributions of Lecompte were multiple; first, his seminal systematic works on the Tabulata and Stromatoporida that culminated in the monographs of the Royal Museum of Natural History. These brought the study of tabulate corals and stromatoporoids into the twentieth century. Following publication of these monographs and sections of the (Piveteau) *Traité* and (Moore) *Treatise*, his attention focused more on unraveling facies relationships and stratigraphy of the Ardennes Devonian, begun on bicycle during World War II. He here developed and refined methods for correlation based on paleobathymetry of Devonian strata as reflected by their coral and stromatoporoid faunas and shapes of sponges and of coral colonies. He developed correlations between outcrops within the Dinant Basin and extended them to the Namur Basin to the north based on cycles of bathymetric change reflected in the development of reefal and peri-reefal carbonates.

His legacy was primarily that of publishing fundamental research that provides a sound systematic framework for Devonian stromatoporoids and tabulate corals, as well as basic concepts for paleoecological interpretation of Devonian strata and their coral and sponge faunas. His recognition of shallowing upward cycles on a faunal basis and correlation on the basis of them was an early precursor of present day techniques of event stratigraphy and sequence stratigraphy. Marius Lecompte was a totally dedicated scientist, with an indefatigable mind. He attained international recognition and renown as a student of tabulate corals and stromatoporoid sponges as well as reefal and peri-reefal carbonate rocks of Devonian age in Belgium.

5. Masao Minato (*M. K. and Y. E.*)

Masao Minato (Fig. 4) was born in Akita Prefecture, Japan in 1915. His family soon moved to Sapporo, Hokkaido, where he received his education, graduating from university in 1939. After wartime travel to China, Korea and Sumatra in a geological capacity, he was appointed Professor at Sapporo in 1950. In 1945, Minato married Chiyoko Asahina, and fathered three children. Masao Minato was widely known in Japanese geological circles. He was also a founding member of the International Association for the Study of Fossil Cnidaria and Porifera. He was president of the Geological Society of Japan (1972-1974), and founded *Pacific Geology* (1968).

Figure 4. Masao Minato, in his prime, 1960s.

Minato's research field was truly broad. He published no less than 360 scientific papers and books, primarily on geologic history. His paleontological studies dealt with corals, brachiopods, and echinoids, but the central theme of his research was the Paleozoic history of northern Japan. During 40 years of service at Hokkaido University, he trained no fewer than 160 undergraduates, 31 Masters, and 45 doctoral students. He directed research in paleomagnetism, micropaleontology, isotope geology, and engineering geology as well as paleontology. Professor Minato retired from Hokkaido University in 1979, as Emeritus Professor. In 1984, Minato was inspecting damage of his home's roof caused by heavy snow, which suddenly slipped from the roof and killed him at the age of 68.

One major research result was a monograph on Japanese Permian corals published in 1955, with 202 pages and 43 plates. Minato here established many new species, two new genera, *Taisyakuphyllum* and *Pseudodorlodotia*, a new family Geyerophyllidae and such descriptive terms as "septal grating" and "pseudoherringbone dissepiments." He treated all of the Japanese Carboniferous and Permian corals then known, and revised and classified them, and presented a scheme of coral zonation as well. Phylogeny of the Clisiophyllidae was shown in conjunction with the introduction of the Geyerophyllidae. Minato was visiting Professors in Stockholm during 1958-1959, and while there he completed ontogenetic studies of Silurian rugose corals from Gotland, notably the phaulactids (1962) based on serial peels.

Together with Kato, he published papers on the Waagenophyllidae (1965), and later on the Durhaminidae, Pseudopavonidae, and Geyerophyllidae from 1965 to1975. Each of these were prepared following the same scheme; each family was chosen as unit, all known forms were treated, and their morphology, ontogeny, geological and palaeogeography were dealt with, and phylogenies were established. Observation of fine skeletal features, ontogenetical changes in axial structures, and the nature of vertical tabular arrangement were particularly stressed in these papers. After retirement, Minato continued research on Strunian corals.

Minato had a keen interest in languages. In the late 1930's he learned Ainu. Later he learned Chinese, German, Malay, and English. After World War II, American troops were based in Sapphoro on the university campus, and he served as liaison officer between them and the university. Students remember his saying, "We should never forget that we owe much to society for what we are. We are fortunate to do things we enjoy doing, so we have to concentrate and work hard on what we do, because we are professionals." As a teacher, he was demanding and inspired by example. He was talkative and witty. He believed in democracy in theory, but admired a powerful leader in action. He was kind and thoughtful in general, but was short tempered at times. His personality was thus full of contradiction, in other words very human, but was so impressive that he is remembered by many, and in this way Minato still lives.

6. Maria Różkowska (*J. F.)*

Maria Różkowska (Fig. 5) was born Maria Dembińska, in 1899 in the village of Gorzewo, Poland. At that time, she was a German citizen of Polish nationality. Girls at that time only received a very basic education unless wealthy. However, Maria received a Prussia government fellowship and thus attended higher level schools, completing gymnasium well educated in professional subjects and fluent in German, English, and French just as the University of Poznań was founded by the newly formed Polish Government in 1919. Maria Dembińska attended the university and received her MSc degree in 1923. The same year she married Kazimierz Różkowski and combined study and maternity; as a mother of a small child she defended her PhD thesis in 1926, and she bore two more children in 1928 and 1931.

Her interest in corals surfaced in 1929 as a result of her visit to the British coral specialist Stanley Smith. She completed and published a monograph, *The Miocene corals of Poland* in 1932. Then she suddenly left the university, and was away from her studies for 13 years. This included the years of World War Two, when she and her children were banished from their home to eastern Poland. As a teacher and a trained nurse (another accomplishment before the war), she was able to treat local people and additionally, taught children above the fourth grade of elementary school (then forbidden for Poles beyond this level) and she served as a nurse in a guerilla group under the pseudonym "Kazimierz." At the end of the war, her husband returned seriously ill from a Polish officer's internment camp, never fully recovered, and died in 1947. Maria was alone in a ruined country and widowed with three small children. Despite these circumstances, she went back to the university in 1945 and published her first paper after the war, *The Silurian rugose corals from Podolia* (1946), based on studies conducted before the war.

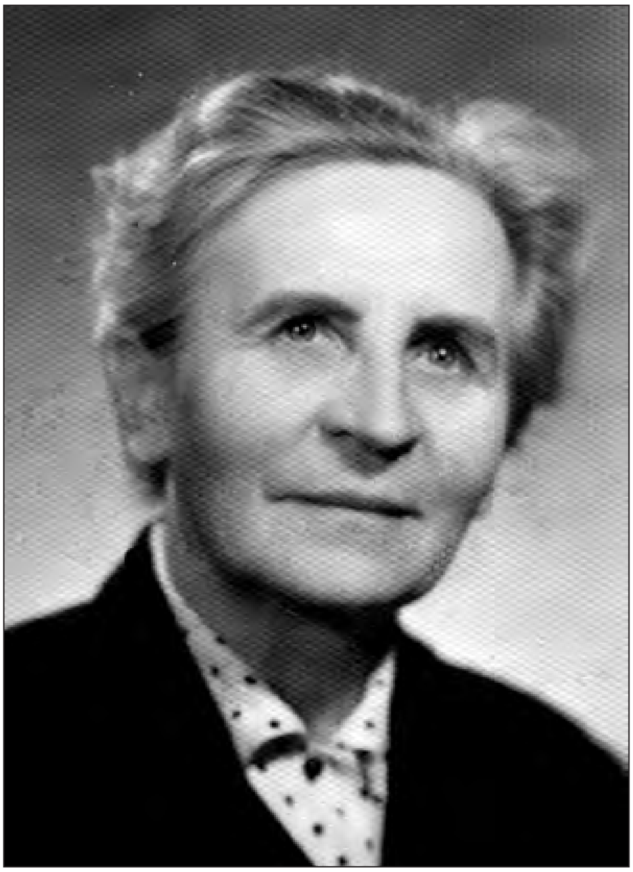

Figure 5. Maria Różkowska, at approximate age 50.

Maria Różkowska was the only paleontologist and one of very few geologists in Poznand during the early postwar years, thus, a laboratory was created for her to conduct research along with her university duties. She remained director of the laboratory until her retirement in 1970. She continued scientific activity until the very end of her life. She passed away in July 1979 after long and painful illness.

Coral research always came immediately after her family, and she was determined enough to combine those two priorities, family and corals. Her international recognition blossomed when she published her first monograph devoted to Devonian rugose corals (1953). Two things are pertinent; 1) She was the only coral specialist in Poland, so had nobody to consult with, and 2) this monograph was the first paper devoted to Devonian rugose corals ever published by a Polish author (although earlier work had been published by foreign authors). She then produced well received papers on the Phillipsastraeidae (1956) and on blastogeny (1960). This documented the taxonomic and phylogenetic value of coral development, necessary for a natural taxonomy of colonial Rugosa.

Maria Różkowska's work on Famennian corals of Poland (1969) was ground breaking. Famennian rugose corals are rare throughout the world and were very poorly known, while Heterocorallia of that age were totally unknown prior to this work. She here described more Famennian coral taxa than were known at that time in the entire world. The access to strata yielding these corals in Poland was generally difficult; in the quarry "Kadzielnia," she collected corals while hanging on a rope 20 meters above the ground (at an advanced age).

Professor Różkowska was a dedicated teacher and an excellent lecturer, but detested grading students. She was very busy, with both professional and family duties, but was never too busy to refuse advice to a graduate student. Her own research and writing never served as a reason to postpone help. This was sometimes restricted to a single sentence, but it would always be to the point. Her method was patiently listening rather than talking, and often depending on one to answer their question for themselves. She told students, "You will never solve all of the mysteries hidden in every fossil specimen, but you must be sure that you have dealt with all of those that you could with your present knowledge and the tools available." And she would add, "If there is nothing more you can do at that stage of your scientific development, publish your results and do not be ashamed if they are corrected later by you or somebody else."

7. Conclusions

Each of these academic paleontologists was an accomplished and eminent scientist and a successful human being as well, in addition to providing an inspiring example for students. It is also of interest to learn of the external conditions they had to deal with, in Europe primarily connected with war and occupation of their homelands.

How then to summarize the communal characteristics of these individuals? They all were tenacious in pursuing, and had a notable affection for, their chosen field of paleontology in spite of outside conditions and pressures, and all remained fruitful until the end of their lives. These were leaders who, as mature scientists freely offered valuable advice and free access for students and colleagues. They also recognized such basic research needs as having access to a good library and physical facilities, and it is of note that their research topics were chosen consciously and wisely. They were demanding and inspiring individuals, while at the same time retaining very human qualities.

Each of the above was international in the scope of their activity within restrictions of the times. Some made significant contributions to the immensely important volumes of the *Treatise on Invertebrate Paleontology.* Each of the five were prominent in national and international scientific societies, and some were better known internationally than locally. It can also be noted that each of these mentors accomplished major systematic work on corals and/or sponges, and that this is perhaps the most lasting of their contributions. So too did Chevalier and Oliver, other workers of the same generation memorialized by this society. This reinforces the idea that systematic study of fossil species is the best way for self-introduction to the literature concerning them. Thus, we collect details of morphology to arrive at a logical nomenclature for individuals.

Each of these mentors was eminent or pre-eminent, with huge accomplishments during their lives. Each succeeded through superior intelligence, hard work, tenacity, and devotion to their profession. All contributed greatly to our training and general knowledge of corals, and several of them received worldwide recognition. But we must also realize that it was not easy for any of them; they had to overcome humble beginnings, sexism, wartime devastation of their homelands, and/or national hatreds. Several fought for their freedom. Each of them was a remarkable human being and we are extremely fortunate to have had training and inspiration from them.

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Archaeocyatha, a computer-aided identification of genera

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ABSTRACT. An online service is proposed for recognition of the genera of a Cambrian fossil group, the Archaeocyatha, using Xper^2. It stores, edits and publishes the descriptive data compiled in the available documentation and provides a free access key. Why Archaeocyatha? They are well studied by an international cooperation, so avoiding most of the problems of an abundant and contradictory nomenclature as well as quarrels about the taxonomic rank of the taxa. Any geologist finding new Cambrian faunas may use this easy tool to help the identification of the collected material. The archaeocyath knowledge base comprises: 307 valid genera, their Cambrian stratigraphical and geographical distribution. Each genus is defined by figures of the type-specimen and 120 descriptors, each one comprising definition, pictures and character states. If an incomplete specimen cannot be identified at the genus level using traditional diagnosis, identification can be obtained with the free access key. Xper^2 offers tools to analyze geographic and systematic data of the knowledge base, to create lists of taxa for local faunal revisions, and to compare relationships between genera of the same taxonomic rank. The knowledge base is interactive and could be modified and improved at any moment. This work is permanently up to date and in progress.

KEYWORDS: Xper2, knowledge base, standardized characters, interactive identification key.

1. Foreword

Establishing a data base, generally extended to a knowledge base, is currently one of the necessary steps for systematic identification of recent or fossil specimens. It could be also applied to researches on biodiversity, ecology, and spatial and temporal distribution. Xper^2 is a management system for storage and editing descriptive data (knowledge base). Knowledge bases on various taxonomic groups are already available. Comparison of descriptions, export of data and interactive identification are operational (Ung et al., 2010). This system and associated tools is the software used for the present study devoted to the Archaeocyatha, a Cambrian fossil group. The resulting free interactive identification key offers specialists and non-specialists a tool that is easy to use (Kerner et al., 2011a, 2011b).

2. Why Archaeocyatha? Reasons for establishing a knowledge base on Archaeocyatha

2.1. First studies of a recently discovered group

The group seems an ideal candidate for establishing a knowledge base. Their range is limited in time, mainly early Cambrian to the end of late Cambrian (i.e. Cambrian stages two to nine according to the International Stratigraphic Chart), and in space, as components of reefs in inter-tropical zones (Debrenne & Courjault-Rade, 1994; Debrenne, 2007; Gandin & Debrenne, 2010). Archaeocyatha were discovered only in the mid-nineteenth century (Bayfield, 1845), whereas many other fossil groups were known for a longer period, in some cases since the eighteenth century, and consequently, were independently studied by numerous authors in different languages using their own descriptive terms, thus making further standardization very complex. On the contrary, the first studies on archaeocyaths concerned more their putative affinities with other known groups (corals, sponges, protozoans, even sphenophytes, Debrenne & Zhuravlev, 1992) than detailed descriptions of specimens. The first regional monograph was written by Bornemann on Sardinian fossils (Bornemann, 1884, 1886). He described and figured four new genera and 31 new species while only nine species were previously known from worldwide. He established a new subdivision “Archaeocyathinae” and named the group “Archaeocyatha” a class among Coelenterata. He was the first author to publish high-quality photographs rather than ink drawings. The second monograph, published by Taylor (1910), dealt with Australian faunas. He described 31 new species distributed among 12 genera (six of which were new). He established the first higher subdivision in archaeocyathan systematics by the allocation of the 15 known genera into five families, based on differences in intervallar structures. He was also the first to recognize their distinctiveness in considering Archaeocyatha as an independent group, intermediate between Porifera and Coelenterata and of the same taxonomic rank. Progressively, discoveries took place around the world (Debrenne & Zhuravlev, 1992). The real start of modern researches took place around 1930. Two schools were in competition, the Eastern school led by A.G. Vologdin and his team in Moscow, and the Western school led by V.J. Okulitch in Vancouver, and associated with the Bedfords in Australia. Okulitch’s systematics is based on ontogenetic stages (Okulitch, 1943). He proposed a new class of Porifera, the Pleospongea, divided into three subclasses according to the number of walls and the structure of the central cavity. This classification was not accepted by other specialists because parallel researches in the USSR by the Eastern school came to a more coherent pattern based on abundant and well preserved material. In the fifties about 400 species of archaeocyaths had been described, of which over 230 were due to the studies on material from the former USSR, (Siberian Platform, Altay-Sayan, Tuva, Urals, Kazakhstan) and Mongolia. For the Eastern school, archaeocyaths are divided into two classes Regularia and Irregularia on the basis of morphological differences of the secondary calcareous skeleton and ontogenetic stages, (Vologdin, 1937) and considered as an independent phylum, Archaeocyatha (Vologdin & Zhuravleva, 1947). Okulitch (1955) accepted the concept of an independent phylum and the name Archaeocyatha instead of Pleospongea (being too evocative of sponges), and slightly modified previous systematics by establishing seven orders including three classes (previously subclasses): (1) one wall, central cavity empty; (2) two walls; (3) central cavity full. He distinguished among others Metacyathida and Ajacicyathida equivalent to the Russian subdivisions.

2.2. Archaeocyatha: an international field of research

From the mid-1950s, I.T. Zhuravleva (Novosibirsk, USSR) began to exchange regular correspondence with F. Debrenne (Paris, France), despite the language barrier. From 1970 onwards, Debrenne was the guest of the All Soviet Union of Paleontologists periodic meetings and then became the link between the two research worlds even during this Cold War time. Since then, Russian and Western specialists have engaged in active cooperation that still continues today. Zhuravleva was at the origin of all modern researches. She proposed a firmer basis for the definition of Regulares and Irregulares, and emended the names Regularia and Irregularia to avoid confusion with the major subdivisions of Echinoidea and Cystoidea (Zhuravleva, 1955). She established the basis of modern systematics by applying the ontogenetic principle (Zhuravleva, 1960) (Fig. 1), studying the order of appearance and complication of skeletal structures. She

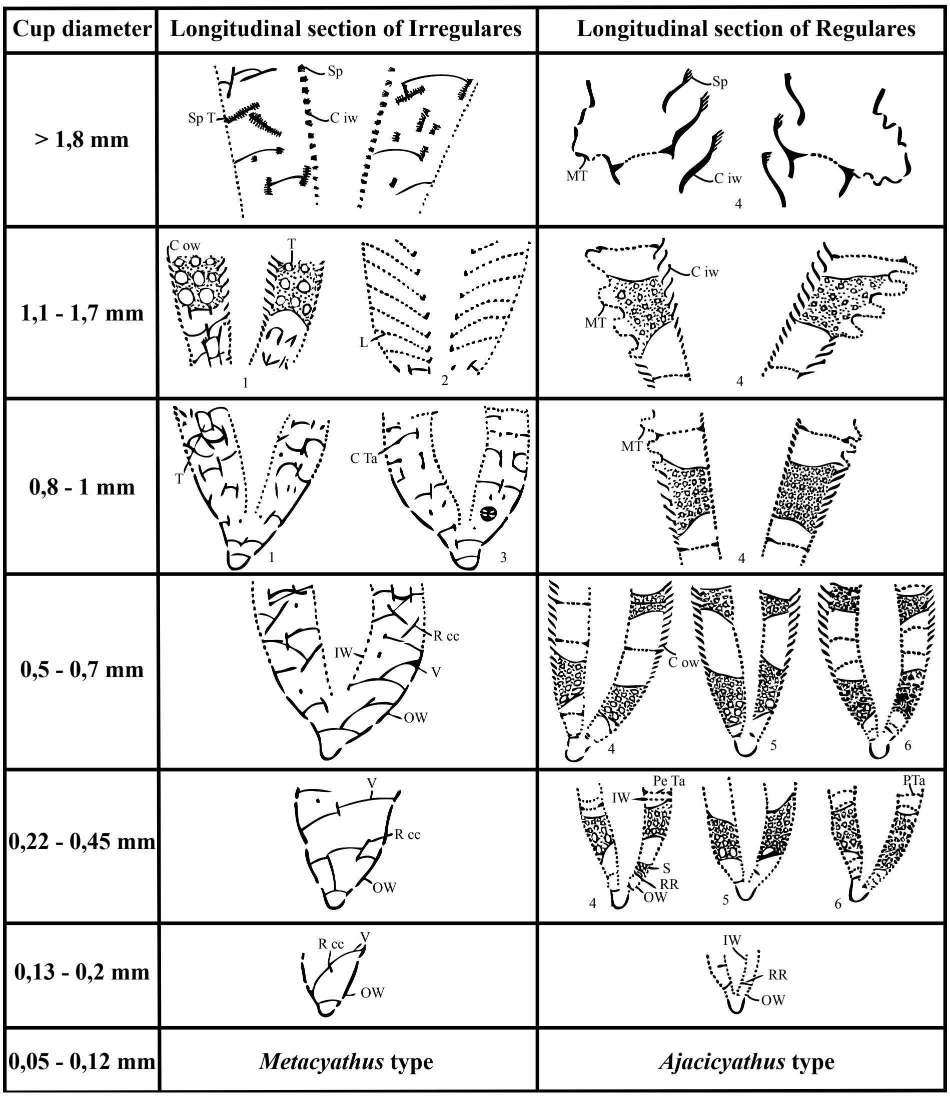
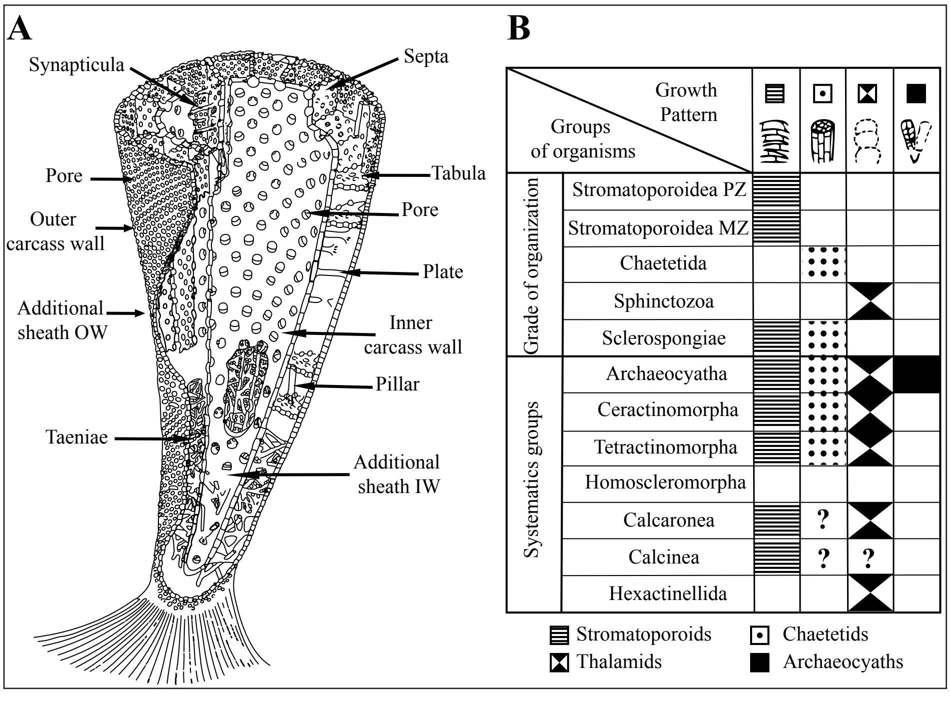


Figure 1. Ontogeny of archaeocyaths, stages of growth. 1: form with taeniae, 2: form with hexagonal radial tubes (syringes), 3: form with taeniae and tabulae, 4: form with pectinate tabulae, 5: form without tabulae, 6: form with tabulae. C iw: inner wall with canals, C ow: outer wall with canals, C Ta: convex tabulae, IW: inner wall, L: hexagonal loculi, MT: multiperforate tabulae, OW: outer wall, P Ta: porous tabulae, Pe Ta : pectinate tabulae, RR: radial rods, S: septa, Sp : spine, Sp T: spinose taeniae, T: taeniae, V: vesicular tissue. (Zhuravleva, 1960, modified).

demonstrated that the intervallar elements have hierarchic primacy over the outer wall structures, which in turn have primacy over the inner wall structures. Debrenne, working on North African-West European faunas (Debrenne, 1964), and Hill on Antarctic faunas (Hill, 1965, 1972) and in the new version of the Treatise on Invertebrate Paleontology, agreed with Zhuravleva's principle of classification. Nevertheless, they did not accept her view that Archaeocyatha were neither Metazoa nor Parazoa nor Protozoa but a superdivision of a new subkingdom, Archaeozoa (later emended to Archaeata). Debrenne, Hill and most other specialists,



	Groups of organisms / Growth Pattern	▤	⊡	⧗	■
Grade of organization	Stromatoporoidea PZ	▤			
	Stromatoporoidea MZ	▤			
	Chaetetida		⁙		
	Sphinctozoa			⧗	
	Sclerospongiae	▤	⁙		
Systematics groups	Archaeocyatha	▤	⁙	⧗	■
	Ceractinomorpha	▤	⁙	⧗	
	Tetractinomorpha	▤	⁙	⧗	
	Homoscleromorpha				
	Calcaronea	▤	?	⧗	
	Calcinea	▤	?	?	
	Hexactinellida			⧗	

▤ Stromatoporoids ⊡ Chaetetids
⧗ Thalamids ■ Archaeocyaths

Figure 2. Archaeocyath growth patterns. A: Archaeocyath skeleton (Debrenne, 1964, modified) B: Growth patterns in various groups of Porifera and allied organisms (Debrenne & Zhuravlev, 1994, modified).

except some prescient zoologists who persisted in including them in Porifera, estimated that Archaeocyatha were a type of primitive organism convergent to many groups without dominant affinities. The position of archaeocyaths was definitively settled by the discovery of Recent calcified sponges in submarine caves. In this environment, Vacelet found a chambered demosponge with a massive calcareous skeleton devoid of spicules, described as *Neocoelia* (now *Vaceletia) crypta* (Vacelet, 1977; Picket, 1982). The absence of spicules is no longer a necessary character to define a sponge. Debrenne and Vacelet, (1984) demonstrated that the sponge model is consistent with the structural organization of archaeocyaths, a proposal accepted by Pickett (1985) and Kruse (1990) (Fig. 2). Immune reactions, asexual reproduction, cells interpreted as crypt cells suggest probable affinities with demosponges (Debrenne & Zhuravlev, 1994). In Systema Porifera , a Guide to the Classification of Sponges (Hooper et al., 2002), Debrenne, Zhuravlev & Kruse (2002) updated the diagnoses of genera published by Debrenne et al. (1990) and Debrenne & Zhuravlev (1992): every valid genus is defined by a short synonymy, its type species, its holotype, its definition, age, and stratigraphic and geographic distribution. A hierarchical set of keys is provided, based on the principles established by Zhuravleva (1960). This work was used to establish the present knowledge base on Archaeocyatha.

2.3. Sources for the knowledge base

Since 1960s, the genus has become a taxonomic category whose definition has achieved general consensus among specialists. It is based on variations of skeletal elements, particularly within designated categories of wall construction, and presence or absence of supplementary elements. Rozanov (1973), applying Vavilov's Principle (repetition of the same limited set of features = homologous series in variation, Vavilov, 1922), found homological series at the genus level in Archaeocyatha, permitting the establishment of classification based on homological variability. This is one of the first attempts at an identification key. The increasing number of genera between 1975 and 1990 reflects regional discoveries worldwide. Unfortunately, the splitting of taxa based on minor variations of the same morphological element led to inflation, and subsequent intensive revision was necessary to determine the systematic value of skeletal variations, and to list invalid names corresponding to incomplete or poorly preserved specimens, or to lost types, when no topotypes could be found. The different skeletal structures have been typified and their variations carefully defined to result in a clear systematization and the recognition of junior synonyms. Consequently, the number of genera in the whole group was drastically reduced from 587 before 1989 to 298 in 1992. This simplification allowed a better knowledge of the group and better application to paleogeographic reconstructions, biostratigraphic zonations and correlations (Debrenne et al., 1990; Debrenne & Zhuravlev, 1992). Debrenne, Zhuravlev and Kruse completed the research on genera: every valid genus is defined by a short synonymy, its type species, its holotype, its definition, age, stratigraphic and geographic distribution. This work, together with unpublished documents compiled for the Treatise of Invertebrate Paleontology (in press), are the sources used for the present computerization of Archaeocyatha.

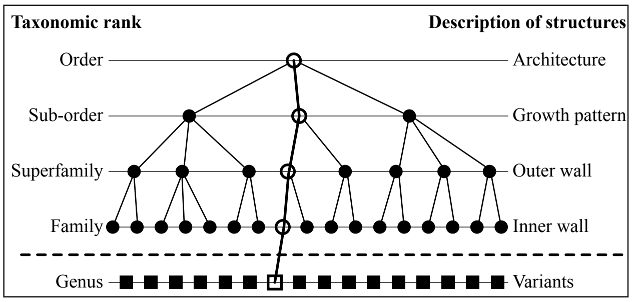


Figure 3. Archaeocyaths traditional key follow the classification: a natural identification keys.

3. Archaeocyatha, a free-access knowledge base: http://www.infosyslab.fr/archaeocyatha

When one opens this knowledge base for the first time the screens appear rather complex and inaccessible for the novice, but its use is more intuitive than it appears. We outline below how to work with and obtain an identification.

3.1. Identification tools

Traditionally, an identification paper key is used to identify a specimen. This type of key has a fixed sequence of questions. When the user has answered each question without doubt, an identification is obtained. In the case of archaeocyaths, the identification key is named a natural key, because the asked questions follow the classical systematic classification. In conventional determination, if one structure is missing, no complete identification can be obtained. In such cases a more flexible tool is required. The free access key offers several possibilities (Fig. 3 and Tab. 1). The archaeocyathan interactive key belongs to latter type. It is included in a three-part website: (1) introduction to Archaeocyatha, their role in the Cambrian system, their morphology and a list of references; (2) general remarks about the knowledge base and some exports: list of genera and their detail sheets, list of descriptors, list of groups of descriptors and knowledge base properties; (3) the interactive key and its tools: user guide, matching terminology and glossary.

3.2. Knowledge base construction

Standardization seems to be unnecessary after the important revisions quoted above. Nevertheless when definitions have been added to the knowledge base some difficulties appear. So a standardization step is required even for this group.

Firstly, terms already present in the base are examined and questioned: are they homogeneous and/or are they synonymous? A single term may correspond to different

Table 1. Comparison of two identification methods: natural key and free access key (Hagedorn et al., 2010, modified).

	Natural key (single access keys)	Free access key
Information reduction	High	None (complete information is optimal)
Identification speed	Depends on the creators of the key	Depends on user's background knowledge; may exceed average
Complex statements (and, or...)	Yes but not recommended for polytomous keys	No
Question-answer style	Possible for simple statements	Implicit in character state or value choice
Difficulty of choosing next decision	None	Often high for beginners
Doubt managment	Difficult: all alternative paths must be followed to the end	Easy
Incomplete specimens managment	Identification is possible but taxonomic rank is higher	Easy
Resources required for construction	Low for first draft. Good keys require high expertise	High investment until first version can be tested

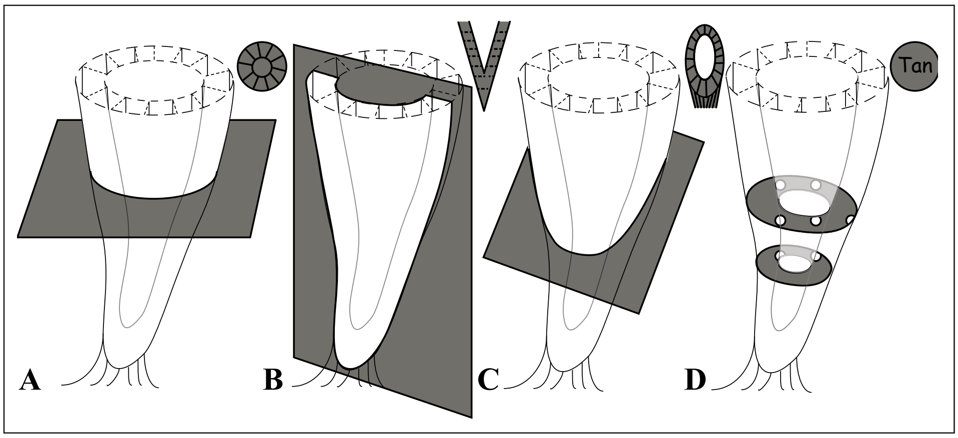


Figure 4. Different orientation of sections illustrated as in the knowledge base. A: Transverse section. B: Longitudinal section. C: Oblique section. D: Example of tangential section of tabulae.

structures, i.e. spine, a skeletal element close to bracts or tiny skeletal elements dividing pores to form an additional sheath. For a traditional determination there is no confusion but, for computer identification, the terms must be distinguished and standardized; the term *spine* is attributed to a structure equivalent to small bracts and protrusion leading to pore subdivision. Besides, some traditional terms included several concepts: *anthoid pore* contains information on pore shape and arrangement. Next, each character and its states have been reexamined and broken down into basic descriptors. Only terms corresponding to one concept are retained while similar concepts are regrouped. Only characters with taxonomic interest are present in previous diagnoses, but for computer-aided identification it is necessary to find other descriptive terms even without taxonomic importance, for instance external shape, solitary or colonial forms and so on. New terms are thus added.

Thin sections are absolutely necessary to study archaeocyathan skeletal structures. The resulting observations may correspond to primary morphological structures or to distorted observations because of the orientation of the sections. Descriptors have to be sorted by the type of section (Fig. 4).

3.3 Knowledge base conformation

When the standardization is complete, an adapted terminology is adopted. For specialists accustomed to the traditional terminology, a table explains the correspondence between ancient terms and computerized ones (Fig. 5). The taxonomic description module comprises 307 genera with systematics information and figures of type specimens. It is composed of 120 descriptors: 85 on morphology, 8 on stratigraphic and geographic distribution, 27 on traditional classification. Each descriptor has several states and descriptors and states are defined and illustrated (Fig. 6A).

4. User guide to the knowledge base

4.1. Successive steps of identification

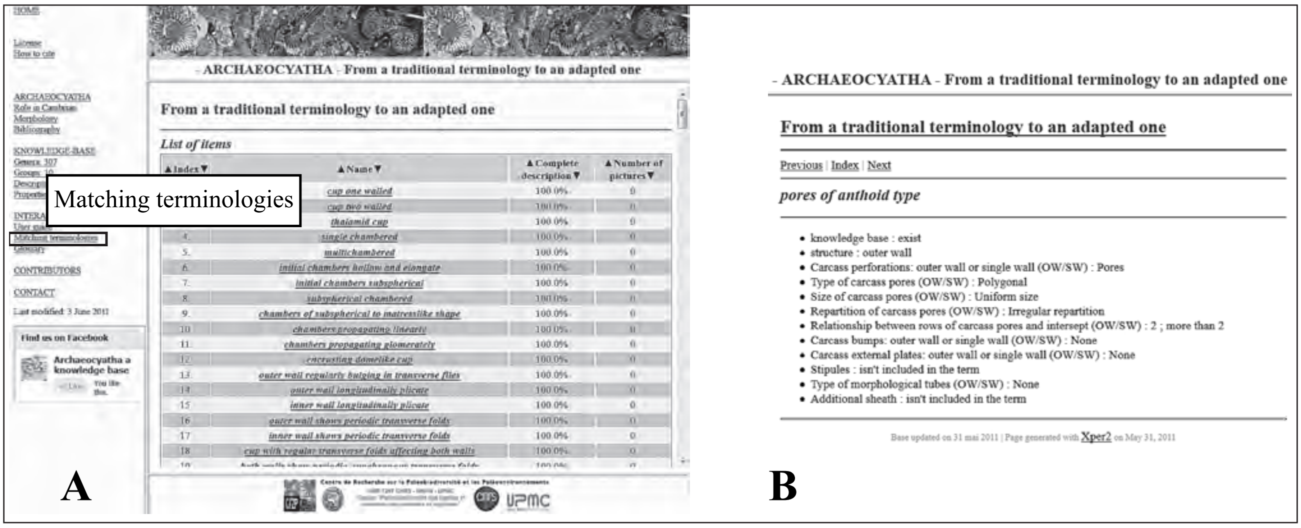
To identify a specimen, it is necessary to follow several steps. The first is the choice of an adequate descriptor; the second, the choice of the states; the third, the confirmation of your choice. When this part is completed, the description is submitted and the process is repeated until the identification is obtained (Fig. 6B). At any time, it is possible to know how many states are different between the described specimen and each discarded genus and to check the differences (in red) on the detailed sheet of the discarded genus. At the end a detailed sheet appears with information on the classification, the genus type species, with figure of the type specimen and the complete description of the identified genus.

4.2. Tools

Moreover, other tools may help in the choice of the different steps described above. For example, it is possible to sort descriptors in alphabetical order, to display or conceal miniature pictures of descriptors, states and genera and eventually to reset the button and begin a new identification.

Descriptors may be sorted by special tools: the filter and the discrimination power. The filters reduce the list of descriptors to one special domain, for instance, by type of skeletal structure (outer or inner wall, intervallum), by other information (stratigraphy, geography, classification) or by orientation of the sections (transverse, longitudinal, oblique…). The second possibility is sorting descriptors by discrimination power. There are three possible sorting methods: Xper original sorting, Sokal and Michener sorting and Jaccard sorting.

The descriptors that discriminate more genera are placed at the top of the list. This order has to be examined with a



- ARCHAEOCYATHA - From a traditional terminology to an adapted one

From a traditional terminology to an adapted one

List of items

▲Index▼	▲Name▼	▲Complete description▼	▲Number of pictures▼
	cup one walled	100.0%	0
	cup two walled	100.0%	0
	thalamid cup	100.0%	0
4.	*single chambered*	100.0%	0
5.	*multichambered*	100.0%	0
6.	*initial chambers hollow and elongate*	100.0%	0
7.	*initial chambers subspherical*	100.0%	0
8.	*subspherical chambered*	100.0%	0
9.	*chambers of subspherical to matresslike shape*	100.0%	0
10.	*chambers propagating linearly*	100.0%	0
11.	*chambers propagating glomerately*	100.0%	0
12.	*encrusting domelike cup*	100.0%	0
13.	*outer wall regularly bulging in transverse files*	100.0%	0
14.	*outer wall longitudinally plicate*	100.0%	0
15.	*inner wall longitudinally plicate*	100.0%	0
16.	*outer wall shows periodic transverse folds*	100.0%	0
17.	*inner wall shows periodic transverse folds*	100.0%	0
18.	*cup with regular transverse folds affecting both walls*	100.0%	0

- ARCHAEOCYATHA - From a traditional terminology to an adapted one

From a traditional terminology to an adapted one

Previous | Index | Next

pores of anthoid type

- knowledge base : exist
- structure : outer wall
- Carcass perforations: outer wall or single wall (OW/SW) : Pores
- Type of carcass pores (OW/SW) : Polygonal
- Size of carcass pores (OW/SW) : Uniform size
- Repartition of carcass pores (OW/SW) : Irregular repartition
- Relationship between rows of carcass pores and intersept (OW/SW) : 2 ; more than 2
- Carcass bumps: outer wall or single wall (OW/SW) : None
- Carcass external plates: outer wall or single wall (OW/SW) : None
- Stipules : isn't included in the term
- Type of morphological tubes (OW/SW) : None
- Additional sheath : isn't included in the term

Base updated on 31 mai 2011 | Page generated with Xper2 on May 31, 2011

Figure 5. Comparison tool between traditional and adapted terminology. A: List of traditional terms in matching terminologies webpage. B: "Anthoid pores" example of computerization.

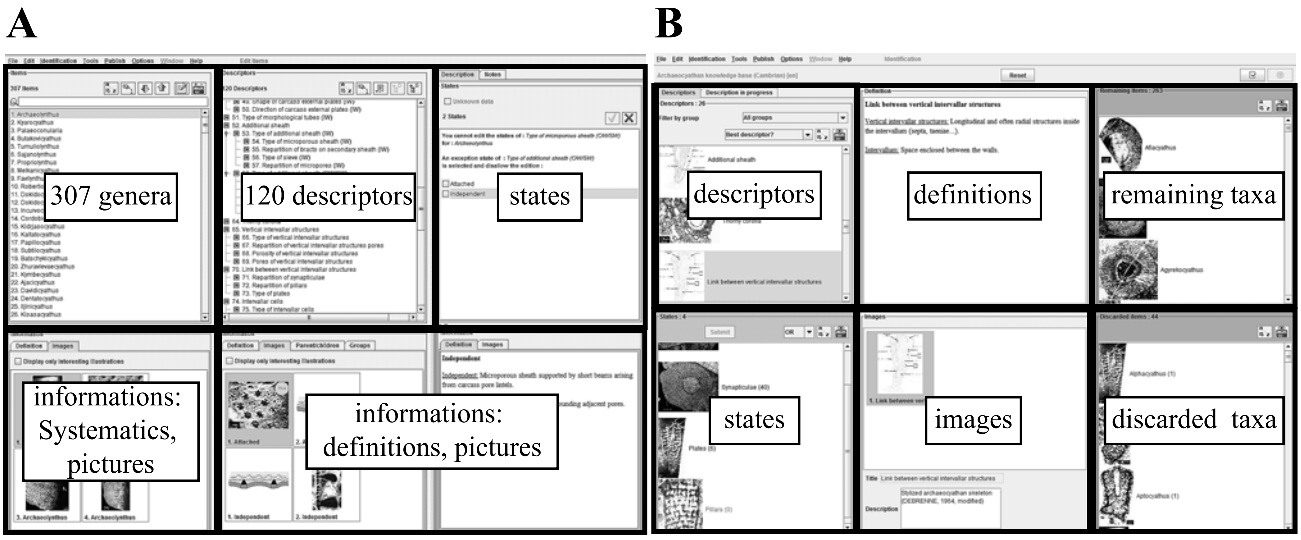


Figure 6. Knowledge base interfaces. A: Taxonomic description module with the 307 genera described with 120 descriptors. B: Interactive identification module: left: list of available descriptors and their states; middle: definitions above and images below, and right: list of remaining taxa above and list of discarded taxa below.

critical mind as the first descriptor could be difficult to define or might not be morphological data.

To be as precise as possible for the description of the studied specimen, logical operators (or, and, not, nor…) allow to improve the description or to raise doubt. For example, if external plates are observed they may be scales or annuli then OR is used (doubt); if these two structures are present in the same specimen then AND is used (qualification).

Several genera are compared by opening the window "comparison" on the data sheet. Descriptive data are represented in a table of taxa (row) and times descriptors (columns). This last tool permits to conclude an identification or to find the characteristics of different taxonomic ranks.

5. Conclusions

This knowledge base is either used as an identification genera key or as a special motor for different domains of archaeocyathan research, for instance, faunal geographic and stratigraphic distributions. The knowledge base is interactive and can be modified and sophisticated at any moment. This work is permanently up to date and in progress: a future stage is to include paleoecological data.

6. Acknowledgements

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Taxonomical problems of the Heliolitida

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ABSTRACT. Systematic position of group is accepted by the beginning scientist after the teacher or after the leader in the field of studying of this group of corals. But the lowest categories (species and genera) are established by him, first of all, on a regional material. Long-term study of heliolitids of Central Tajikistan and their comparison with heliolitids from other regions shows faunistical peculiarity of each region. Ambiguity of treatment of the same morphological features as a result takes place. The situation becomes complicated by parallelism of development between some taxa of the Heliolitida and wide variability of features of many species. Standardization of arrangement of coenenchyme because of parallelism of development results in occurrence of forms with a similar structure, but with a different genetic basis. So we can tell now that the main problem in definition of taxa of the Heliolitida is the heterogeneous genus *Heliolites*.

KEYWORDS: Paleozoic corals, Variability, Autotomy, Taxa definition, Middle Asia.

1. Introduction

Taxonomical problems of the Heliolitida include such aspects, as discussion about a rank of group and difficulty of an establishment of the taxa within the Heliolitida. At the hearth of these problems lies an interpretation ambiguity of the same morphological features by various researchers. Interpretation ambiguity of the same morphological features depends on individual point of view, material that every investigator has, and a degree of the study of group. The other trouble of the taxa definition in the Heliolitida is standardization of arrangement of coenenchyme due to parallelism of development. Also wide variability of features could take place among some taxa of the Heliolitida. Variability of the species *Propora speciosa* (Billings) will be considered below as an example.

2. The rank of Heliolitida

A question about the rank of Heliolitida is the question about its independence from the Tabulata or the others Coelenterata. Many investigators consider heliolitids as a part of Tabulata (Dixon, 1974; Lin Baoyu & Chow Xinghu, 1977; Hill, 1981; Noble &Young, 1984; Young & Noble, 1990; Scrutton, 1997; Chatterton et al., 2008). In means the rank of Heliolitida should be lower than the rank of Tabulata. It can be mentioned here that the rank of Heliolitida is interpreted differently - from the family to the subclass (Bondarenko, 1992; Ospanova, 2010). Sokolov (1955, 1962) analyzed relationship of the Heliolitida 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. He concluded that the Heliolitida is a separate taxon that is equal to the Tabulata and Rugosa in rank. Long-term study of heliolitids of Central Tajikistan confirms his point of view. The concept of the sum of common features has been used by me (Ospanova, 2010) for comparison of the Heliolitida with other groups of Paleozoic corals (Tabulata and Rugosa) and determination of its position within the common system of corals. The Tabulata, Heliolitida and Rugosa as a result included into one subclass Paleosclerocoralla (Ospanova, 2007a) as related orders. I support point of view of Ivanovsky (1990) about common classification system for ancient and modern corals. If we make common classification system for ancient and modern corals, the rank of such subdivisions as Tabulata, Heliolitida or Rugosa must be not higher than order. On the other hand, their rank cannot be lower than order owing to big capacity of these groups. Thus, it seems well proved that the rank of the Heliolitida is the order.

3. Individual point of view

Individual point of view depends on scientific school to which paleontologist belongs, and a private experience in group studying. Some Canadian researchers (for example, Dixon, 1974; Noble & Young, 1984) following Hill (Hill & Stumm, 1956) considered the Heliolitida as the family. And they come to consider this group of corals as the order (Dixon et al., 1986; Young & Noble, 1990; Dixon, 1998) after new Treatise of Hill (1981) or as suborder (Chatterton et al., 2008) according to Scrutton's classification (Scrutton, 1997). Many Russian and Chinese researchers (for example, Bondarenko, 1971; Mironova, 1974; Leleshus, 1975; Ospanova, 1978; Li & Lin, 1982; Kim & Salimova, 2007) following Sokolov (1962) consider heliolitids as the subclass. Sokolov (1971) has in the sequel proposed the subclass Tabulata (Tabulatomorpha) with three super-orders: Tabulata s. str., Heliolitoidea and ?Chaetetoidea. Bondarenko (1992) has used this rank in her "System of Heliolitoidea" following Sokolov (1971). However she considers that group of corals as the subclass at the present time (Bondarenko, 2003). As a rule, the beginning scientist holds the opinion of his teacher. Only private experience allows him to have another opinion.

Taxa	**Features**
Superorder **Heliolitoidea**	Polymorphism + fixing number of septa
Orders	Macrostructure of skeletal tissue of vertical elements; *variants of heteromorphous components*
Order **Coccoseridida:** superfamilies	Texture of skeletal tissue; arrangement of heteromorphous components; *degree of stereoplasmatic filling of corallites*
families	variant of texture + aureole; *presence of axial structures in corallites*
subfamilies	*arrangement of heteromorphous components*
tribes	*orientation of trabecula and bacula*
Order **Proporida:** families	Presence or absence of crowns, aureoles and diadems around the corallites
subfamilies	*combination of heteromorphous components*
Order **Khangailitida:** superfamilies	Constancy or inconstancy of structure of skeletal elements in a cyclomorphosis; shape of colonies + presence of crowns, aureoles and diadems around the corallites
families	variation of structure of skeletal tissue; arrangement of heteromorphous components; arrangement of corallites; presence or absence of aureoles and diadems
Order **Heliolitida:** families	Arrangement of central parts of corallites; presence or absence of crowns, aureoles and diadems
genera	Density of corallites disposition in coenenchyme; number and type of septa; variants of symmetry; axial structure; shape of tabula; appearance of new structures in the cyclomorphosis
species	Numerical diagnostics

Table 1. Taxonomical criteria used in the system of Bondarenko (1992). Characteristics used in system, but not listed Bondarenko in an anticipating part, are italicized.

Such investigators as Nicholson (1876), Sardeson (1896) and Bondarenko (1978, 1987b) considered the colonies of the Heliolitida as polymorphic. They supposed that coenenchyme is not lateral or sole enlargement of polyps but small true

Taxa	Features
Order **Heliolitida:**	Presence of coenenchyme, fixing number of septa, vertical or inclined-up orientation of septa
Suborders (**Coccoseridina, Proporina, Heliolitina**)	Type of coenenchyme and its development trend
families	Morphogenesis (asto-phylogenesis); mode of decrease of stereoplasma; arrangement of walls and septa; presence of aureole; arrangement of tabula as auxiliary feature
genera	Density of corallites disposition in coenenchyme; shape of corallites; septal apparatus; axial structure; shape of tabula; structure of walls; type of folding of corallites' cavities; aureole; texture; cyclomorphosis; arrangement of coenenchyme; branchy form of colonies
species	Density of corallites disposition in coenenchyme; numerical diagnostics; insignificant qualitative varieties

Table 2. Taxonomical criteria used for description of the heliolitids of Central Tajikistan.

polyps. Bondarenko uses a special terminology in order to show differences between coenenchyme and zooids' tissue. She calls that as *heteromorphous components* (1978, 1982) or *heterolites* (1987b). She distinguishes between them cystolites, eucystolites, and siphonolites (Bondarenko, 1978), and also protolites (Bondarenko, 1980), prosiphonolites, parasiphonolites (Bondarenko and Minzhin, 1980), and siphonotella (Bondarenko, 1982), and also paraprotolites (Bondarenko, 1987b). New system of the Heliolitoidea has been formulated by Bondarenko (1992) with the using new terminology. Two tables are given here as examples of the various individual points of view on definition of the taxa of the Heliolitida. The taxonomical criteria used in system of Bondarenko are summarized here in the Table 1. The taxonomical criteria used for the description of the heliolitids of Central Tajikistan are summarized in the Table 2.

It can be seen from the Table 2 that we consider coenenchyme only as connecting intermediate tissue between polyps. Most researchers held this opinion. Between them are Lindström (1899), Sokolov (1955) and Beklemishev (1964).

4. Taxonomical value of morphological characters depending on material

Comparison of heliolitids of Central Tajikistan with those of other regions (Baltic region, Ural, Kazakhstan, Mongolia, and others) shows that unique (specific) fauna is characteristic for every region (Ospanova, 2003). Complexes of species or degree of variability of cosmopolitan species can differ from each other. So each paleontologist establishes taxonomical value of characters, leaning against an own material. Two examples will be considered below.

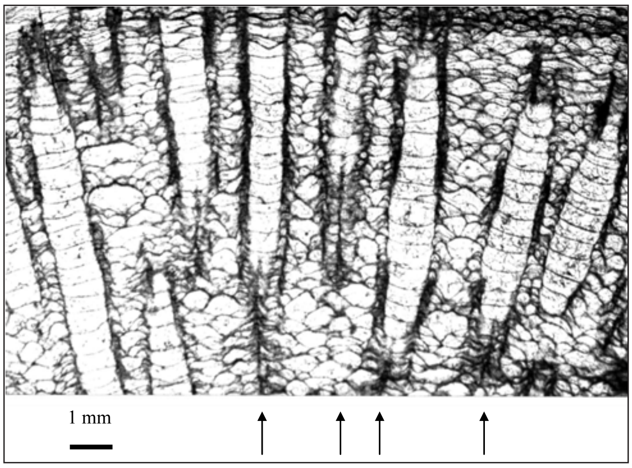

Figure 2. Autotomy of corallites in *Oskaria islamovi* Ospanova; autotomic seams are shown by arrows. Oblique section of the holotype IGEES 605-11 (Turkestan-Alaj mountain oblast, Nuratau mountains, south mountainside of Merishkor; Upper Silurian, Ludlovian, the Dal'an formation). Author's collection (1978).

Such feature as type of folding of corallites' cavities is mentioned in the Table 2. Study shows that for Ordovician and Silurian heliolitids of Central Tajikistan broad development of autotomy is characteristic. On the bases of that, the using of the term ***autotomy*** in relation to the Heliolitida has been defined more exactly by me. This term was firstly used by Bondarenko (1987a). She supposed that small part (or some parts) which disjoined from margin of parent corallite can grow and transform into new corallite ("metacorallite"). Parent corallite can also exist or transform into heterolites (i.e. coenenchyme). However, individuality is present in the other animals after autotomy. And also Lindström (1899) showed (in heliolitids with tubular coenenchyme) that such parts cannot change into mature corallites. So autotomy in the Heliolitida is such separation of small parts from the periphery of parent polyp when its individuality is present (Ospanova, 2007b). Study shows that these parts cannot transform into new corallites or tubules of coenenchyme, but they can form additional wall of corallite (Figs 1, 2). In Central Tajikistan autotomy occurs in representatives with vesicular coenenchyme. It can be added that

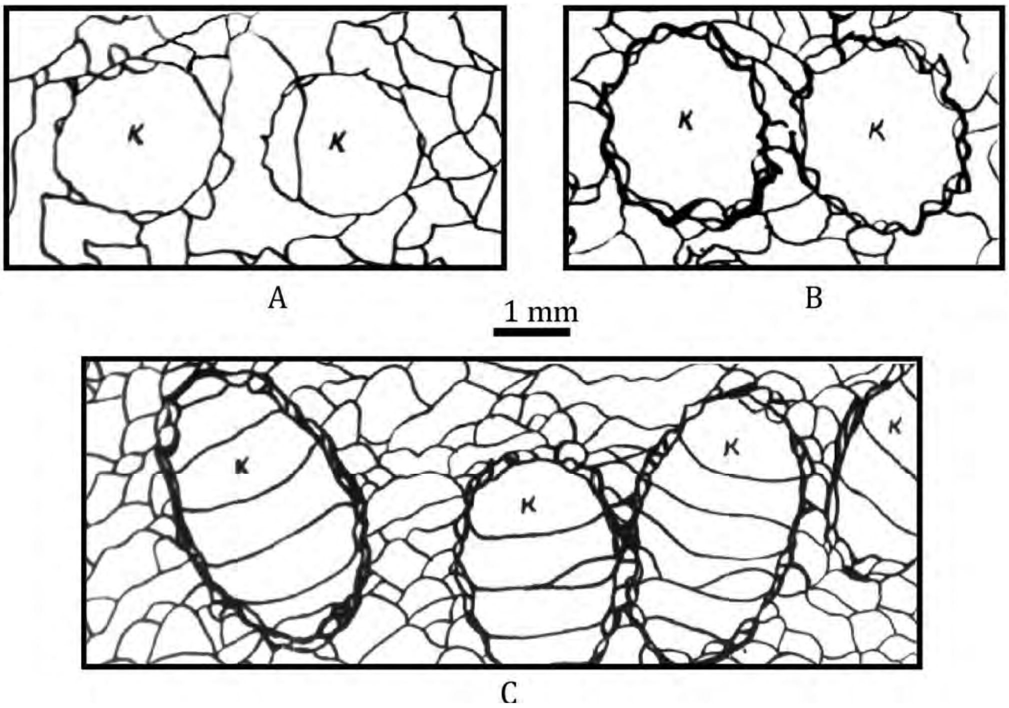

Figure 1. Autotomy of corallites in *Rotalites nuratensis* (Chekhovich). A: Initial stage of the astogenesis of colony; autotomy is no intensive, and cavities plicated slightly and irregularly (cross-section of a specimen IGEES 605-59). B, C: Later stages of the astogenesis of colonies; autotomy is more intensive and cavities plicated more intensively (B: Cross-section of the specimen IGEES 603-26. C: Oblique section of the specimen IGEES 605-63). Turkestan-Alaj mountain oblast, Nuratau mountains, south mountainside of Merishkor; Upper Silurian, Ludlovian, the Dal'an formation). Author's collection (1978).

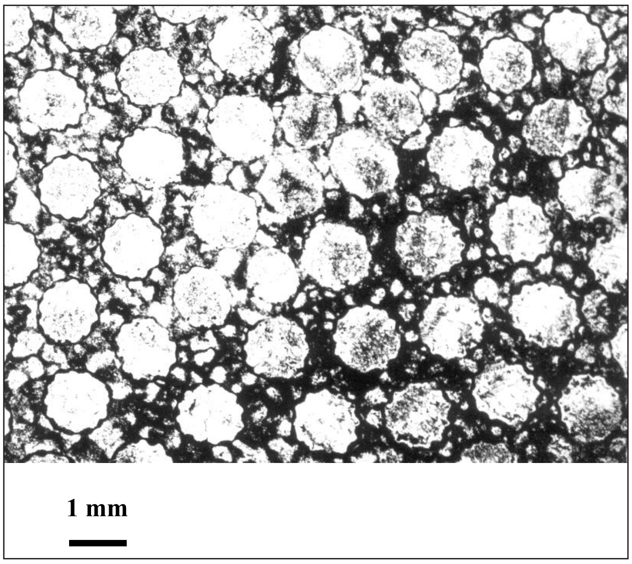

Figure 3. Undulatory type of plicated cavities of corallites in V*orupora exigua* (Billings). In dark zone are aureole-like structures. Cross-section of a specimen IGEES Sh-2-29 (west area of Zeravshan mountain, hole Shakhriomon, section Shakhriomon-2; Upper Ordovician, upper Ashgillian, Minkuchar beds). Author's collection (1986).

this feature has not been noticed by Leleshus at allocation of the genus *Rotalites* (Leleshus, 1974).

Partial or total transformation of corallite into coenenchyme was called as metatomy (Ospanova, 2007b). Autotomy in the Heliolitida can intensify folding of cavities of corallites (Fig. 1). Based on it, four types of longitudinal folding of cavities of corallites have been established by me (Ospanova, 2009): undulatory (Fig. 3), septate (Fig. 4), autotomic (Figs 1, 2) and coenenchyme-dependent (Fig. 5). They have been used as additional morphological feature for diagnostics of taxa of the Heliolitida of Central Tajikistan. It can be added here that longitudinal folding of cavities and walls of corallites studies in cross-sections and cross folding of cavities and walls of corallites studies in longitudinal cuts of coralla.

Scrutton (1993) has distinguished two species of *Propora* based on their different strategy of growth. Comparison of shape and internal structure of coralla from some localities allowed him to establish these species. Thus he used growth-form of colonies as additional taxonomical characteristic. This example demonstrates also that each researcher establishes taxonomical value of features, leaning, first of all, against a regional material.

Peculiarity of fauna of each region is connected with various environmental conditions in different parts of the basin. Repeated visiting of the same sections convinces us that eventually different parts of a biotope are exposed to erosion. They can contain various organic forms. So I have come to conclusion about necessity of repeated visiting of the same sections after some time (Ospanova, 2003).

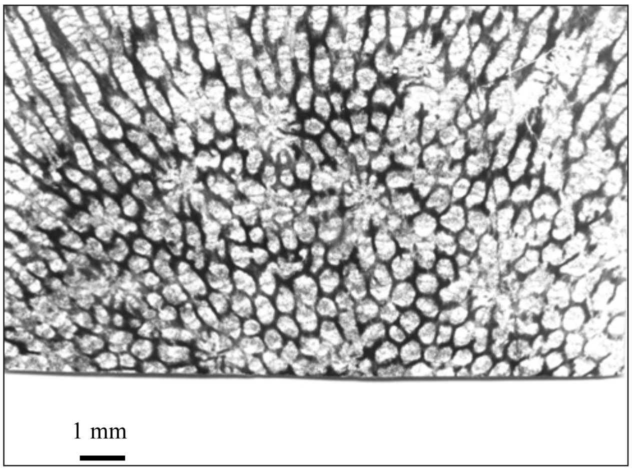

Figure 4. Septate type of folding of corallites' cavities in Bondarenkolites olgae Kim. Oblique section of a specimen IGEES 19-72 (Zeravshan mountain, Zinzinlban ravine; Lower Devonian, Emsian, the Khodzhakurgan Formation). Author's collection (1986).

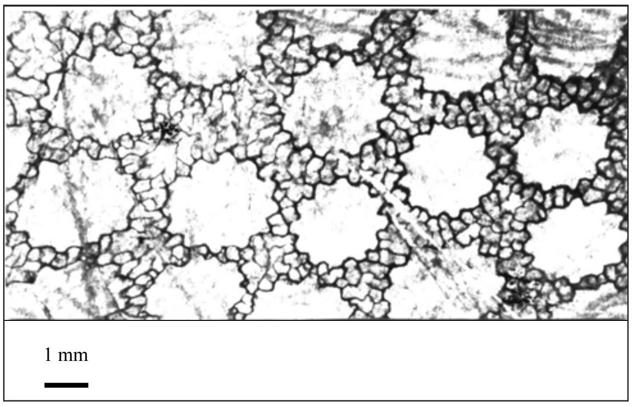

Figure 5. Coenenchyme-dependent type of folding of corallites' cavities in *Ducdonia interrupta* Leleshus. Cross-section of a specimen IGEES 18-85 (Zeravshan-Gissar mountain oblast, Obi-Hundy mountain, the Upper Kashka-Dar'a, left side of mouth Farab ravine, bed 18; Lower Silurian, upper Llandovery-lower Wenlock, stratigraphic analogues of beds H, I of Daurich mountain). Author's collection (1979).

5. Degree of the study of variability on an example of the species *Propora speciosa* (Billings)

Distribution and variability of the species *Propora speciosa* (Billings) have been studied by Bondarenko and Minzhin (1981). They showed that this species has global distribution. It occurs on Upper Ordovician of Canada, Central Mongolia, Scandinavia and Baltic region. Biozone of the species corresponds to Ashgillian (Members 2 and 6 of the Ellis Bay Formation, Anticosti Island, Canada; beds 5a and 5b of Norway; the Pirgu and Porkuni Stages of Estonia; upper strata of Middle Tsagandel and Upper Tsagandel beds of Mongolia). Colonies of *Propora speciosa* make two phylozones: lower and upper. Coralla with corallites' diameter of 1,3-2,2 mm make lower phylozone (lower part of the Ellis Bay Formation, Canada; the Pirgu Stage of Estonia; the Khangai Horizon of Central Mongolia, beds 6, 7). Coralla with corallites' diameter of 2,2-3,2 mm make upper phylozone (upper part of the Ellis Bay Formation, Canada; the Porkuni Stage of Estonia; beds 5b of Norway).

In Middle Asia the species *Propora speciosa* has been established by me (Ospanova, 1984). Representatives of this species have been defined before as *Propora* cf. *bacillifera* Lindström, *P. bacillifera* Lindström, *P.* aff. *magna* Sokolov (Leleshus, 1966; Muftiev et al., 1971; Lavrusevich, 1972; Lavrusevich et al., 1972) or as *Proporella rubanovi* Leleshus (Leleshus, 1975).

20 specimens of the species have been studied. Moreover some exemplars of *Propora speciosa* from the collection of Apekin (Kitab State Geological Reserve) were also examined. Therefore the ranges of corallites maximum sizes have been defined more exactly. Our coralla make four morphogroups and corallites' diameter varies from 1,8-2,2 mm to 4,0-4,5 mm. Some conclusions from this study are resulted more below (Ospanova, 2001):

1) One new region as Middle Asian (Tajikistan and Uzbekistan) of the distribution of *Propora speciosa* (Billings) is found.
2) Our researches confirm the data of Bondarenko and Minzhin (1981) about wide variability of the species *P. speciosa.* We can distinguish four morphogroups with different morphometric characteristics in our region.
3) Archalyk beds (we have found the first species in these beds) correspond to middle part of Ashgillian stage while Minkuchar beds correspond to upper part of Ashgillian stage. Archalyk beds can be stratigraphically compared with lower part of the Ellis Bay Formation of Canada, the Pirgu Stage of Estonia, and beds 5a of Norway and with beds 6, 7 of the Khangai Horizon of Central Mongolia. Minkuchar beds can be stratigraphically compared with upper part of the Ellis Bay Formation of Canada, the Porkuni Stage of Estonia, and beds 5b of Norway. Furthermore they can

be compared with the White Head Formation (Ordovician) of East Canada (peninsula Gaspe) after Bolton (1980).
4) Superior range of variability of the species *Propora speciosa* was determined. It is not equal with 3,2 mm as supported by Bondarenko and Minzhin (1981) but with 3,5-3,8 mm after Dixon (1974) and with 4,0-4,5 mm according to our data.
5) *Proporella rubanovi* Leleshus is younger synonym of *Propora speciosa* (Billings). So the genus *Proporella* is younger synonym of the genus *Propora*.

Thus, the cumulative data about morphology of the species *Propora speciosa* from different regions is a proof of the species high study level. Rather more through studies can help to confirm the allocation of the taxa of Heliolitida and to estimate the age of deposits precisely. Besides, the study of *P. speciosa* from our region shows its peculiarity: gigantism of skeletal elements is characteristic for some representatives of species.

6. Standardization of arrangement of coenenchyme due to parallelism of development

The main problem of the definition of taxa in Heliolitida is the genus *Heliolites*. The forms with *Heliolites*-like tubular coenenchyme could appear in next ways: (1) decrease of stereoplasma at some Coccoseridina with solid trabecular-bacular skeleton of colonies; (2) transformation of vesicular coenenchyme to tubular or vesicular-tubular one.
1) Sokolov (1962) supposed that some genera of Heliolitida descend from the Protaraeida (= Coccoseridina now). He considered well proved the relationship between these two groups. He has established following trend of development: *Protaraea* - *Estonia* - *Acidolites; Acidolites* - *Heliolites* ; *Heliolites* - *Stelliporella.*
2) Transformation of vesicular coenenchyme to tubular or vesicular-tubular one is characteristic for such families of heliolitids as Plasmoporidae Wentzel, 1895; Aviceniidae Ospanova, 1986; Ducdoniidae Ospanova, 1989; Khangailitidae Bondarenko, 1992; Hemiplasmoporidae Bondarenko, 1992; Helioplasmolitidae Ospanova, 1998; Wormsiporidae Ospanova, 1999. As a result, many forms have a similar structure but different genetic basis. It can be added that some heliolitids can take secondary similarity with the genus *Heliolites* (*Paraheliolites*). I have studied the variability of the species *Pachycanalicula opaca* Dubatolov, 1963 from Zinzilban-section, Lower Devonian, Emsian, the Khodzhakurgan Formation (Uzbekistan, Zeravshan-Gissar mountain oblast). 105 samples were examined. Study shows that thinning of skeletal elements led to occurrence of coralla with *Paraheliolites*-like arrangement. So we can see secondary similarity with the genus *Heliolites* (or *Paraheliolites*) in this case. I consider that mention on the genus *Paraheliolites* in Zinzilban section is erroneous.

The genus *Heliolites* includes at time 180-200 species (Bondarenko, 1992). Heterogeneous character of the genus *Heliolites* is obvious.

7. Conclusions

1) It seems well proved that the rank of the Heliolitida is the order.
2) Faunistical peculiarity of each region can cause interpretation ambiguity of the same morphological features of the Heliolitida. The study of variability of species can help to define the taxa more accurately and estimate the age of deposits precisely.
3) Transformation of vesicular coenenchyme to tubular or vesicular-tubular one is characteristic for many taxa of the heliolitids. Heliolitid morphotype could also appear owing to decrease of stereoplasma among some Coccoseridina with solid trabecular-bacular skeleton of colonies. As a result, many forms have *Heliolites*-like structure at a different genetic basis.
4) Heterogeneous character of the genus *Heliolites* is obvious. So researches must give more attention to the problem of the genus *Heliolites*.

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Rugosans immured in Silurian *Paleofavosites;* Brassfield Formation (Llandovery) of Ohio

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ABSTRACT. The occurrence of a solitary rugose coral, *Streptelasma* sp., anchored within colonial skeleton of the tabulate coral *Paleofavosites prolificus* is here reported. Numerous specimens of *Streptelasma* were found within three coralla of this tabulate species among 55 collected from the uppermost 30 cm of the Lower Silurian (Llandovery) Brassfield Formation at Fairborn, Ohio. These rugosans are largely immured in the favositid coralla, and, as bioclaustrations, reveal important information on the paleobiology of both species. However, the immuring of some *Streptelasma* within *Paleofavosites* coralla was not complete during the life of the rugosan, as calice openings of these are present at the corallum surface. Complete immuration (or total overgrowth) indicates that the rugosan no longer competed successfully for space; whether entombment occurred after the death of the rugosan or was the cause of its death is unknown. *Streptelasma,* in assuming an epibiotic lifestyle probably benefited from the secure attachment to the larger, stable colonial form of *Paleofavosites prolificus* and were able to exist within this particular Brassfield facies interpreted to have been a vigorous, current-swept environment. These high energy environments would have been inimical to the small, light-weight rugosans living as isolated corallites. The successful settling and growth of the rugosans on the tabulate colonies reflects their higher status in an aggression hierarchy. This interspecies interaction indicates an early Paleozoic development of an aggression hierarchy of corals belonging to the Rugosa and Tabulata (Phylum Cnidaria).

KEYWORDS: *Streptelasma*, bioclaustration, aggression hierarchy, Cnidaria, epibiont.

1. Introduction

We report the occurrence of rugose corals living during the Early Silurian as epizoans on massive colonies of tabulate corals, and becoming partially or totally immured within them. Close interspecies relationships of this sort between rugose and tabulate corals are of interest for several reasons, (1) they allow understanding the corals' position in the Brassfield ecosystem, and (2) they allow us to hypothesize biological relationships between organisms of different major Paleozoic taxa of the Cnidaria. We have found only one previous reference to the occurrence of rugose corals on, or within, coralla of massive tabulate corals; that of McLean (1974) who reported a species of *Streptelasma* occurring within a tabulate colony in Lower Silurian rocks of New South Wales, Australia*.* Kershaw (1978) also reported a species of the rugosan T*ryplasma* occurring as an endobiont within the stromatoporoid sponge *Clathrodictyon* in Middle Silurian strata of Gotland.

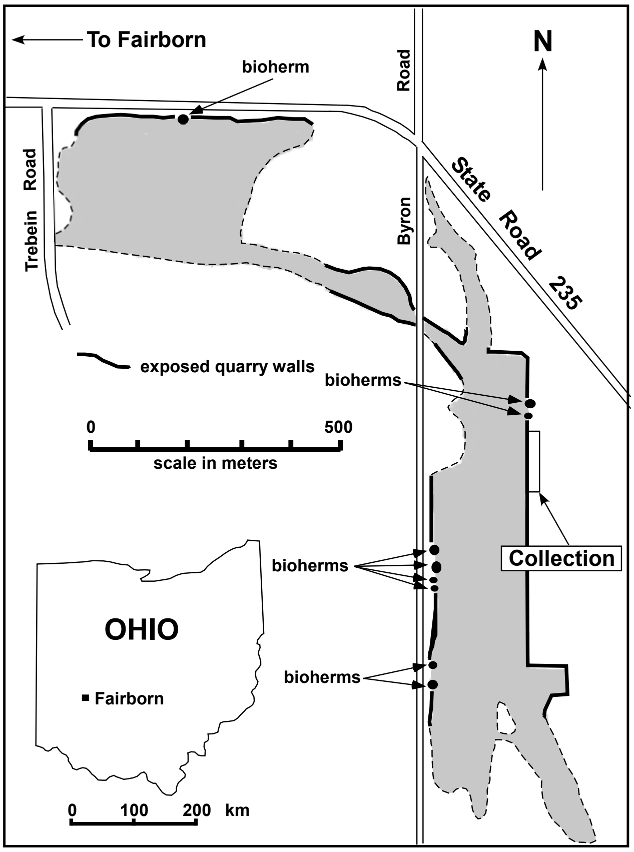

Figure 1. Map of the inactive Southwestern Portland Cement Company quarries at Fairborn, Ohio, as they existed during 1967-1975. Corals discussed in this paper came from the portion of the east quarry face labeled Collection on the map. This quarry also was Locality 7 of Laub (1979, p. 11), while newer quarrying to the south was his Locality 7a.

There is considerable potential for inferring various paleobiological aspects of the corals involved in this remarkable occurrence in Lower Silurian (Llandovery) Brassfield strata near Fairborn, Ohio (Fig. 1), where individuals of the solitary rugosan, *Streptelasma* sp., occur within colonies of the tabulate *Paleofavosites prolificus* (Fig. 2). Some interspecific relationships are described below, notably observations pertaining to the spatial and biological relationships between these rugosans and tabulates. Tapanila (2005, p. 89) noted that a faunal relationship where an endobiont occurs within a host skeleton is "particularly well-suited for studying animal interactions." He also added that this relationship can produce the special group of trace fossils called bioclaustrations (Palmer & Wilson 1988; Taylor 1990), as a result of immuring of epi- or endobionts by skeletal material of the host species. Although *Streptelasma* corallites are now found partially or wholly immured within the *Paleofavosites* coralla, their living tissues were confined to the most recently formed portion of the skeleton, and that lay *on* the contemporaneous surface of the host (Fig. 2); hence they were epibionts that became immured by later tabulate skeletal growth.

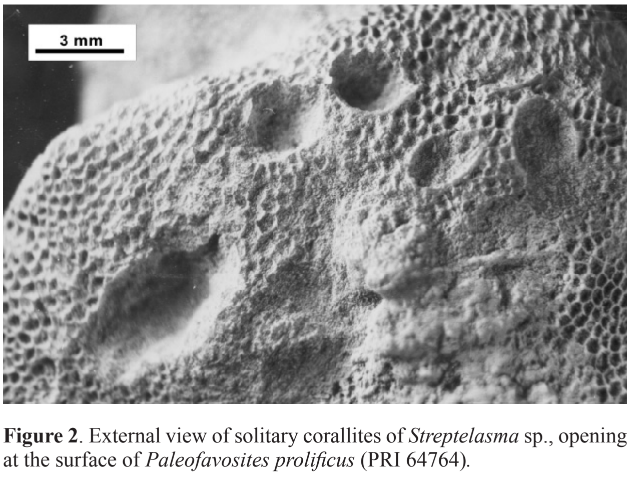

Figure 2. External view of solitary corallites of *Streptelasma* sp., opening at the surface of *Paleofavosites prolificus* (PRI 64764).

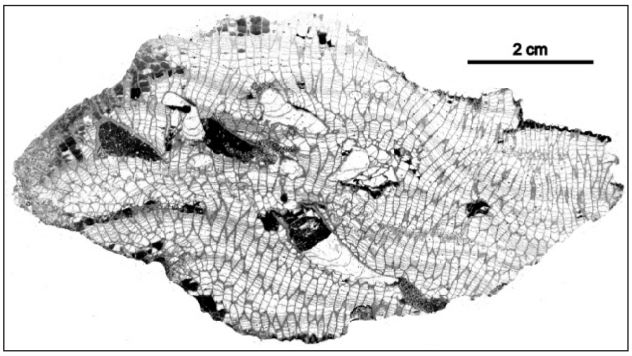

Figure 3. Transverse thin section of *Paleofavosites prolificus* containing numerous immured individual corallites of *Streptelasma* sp. (PRI 64764c). Section also shows placement of rugosans on and near zones of closely spaced tabulae in the favositid corallum. The two long *Streptelasma* corallites in the central part of this thin section are shown at greater magnification in Figures 7 and 8 below.

2. Bioimmuration, bioclaustration, and agression

A number of reports have focused on the bioimmuration of symbionts by their host organism, as here in the Brassfield where rugose corallites occur within colonies of *Paleofavosites prolificus*. Taylor (1990) surveyed paleontological occurrences of bioimmuration and suggested several types. Of these, the Brassfield occurrence is "epibiont bioimmuration," although several characteristics make this Lower Silurian occurrence somewhat special. Here there is not one organism overgrowing and encapsulating another, but rather, one organism living upon a colony of another and killing or displacing individuals of that colony to acquire living space. In addition, *Paleofavosites* does not here simply bend laterally and then overgrow the rugosan, but rather, after the rugose coral has occupied space on dead portions of its corallum (Fig. 3), with the rugosan dorsal skeletal wall intact, neighboring *Paleofavosites* polyps multiplied and overgrew the upper wall of the semi-recumbent rugosan corallite. That the rugosan deposited skeletal material, both an external wall and internal septa and tabulae makes it a special case in the spectrum of bioclaustrations reported by Palmer & Wilson (1988). The name was initially proposed for bioimmuration where an endobiont is a soft-bodied organism, one that would not otherwise have been preserved in the fossil record. Taylor later (1990, p. 4) modified the definition of the term to include skeletonized endobionts entombed by bioimmuration. It should be also emphasized that the living *Streptelasma* polyps only occupied the last formed portion of the rugosan corallite (perhaps 5 or 6 mm), so that there was not a living organism immured within the tabulate skeleton although the older portion of the *Streptelasma* corallite skeleton was surrounded and anchored within the *Paleofavosites* corallum.

Since the seminal work by Lang (1973), numerous authors have reported on mutual aggression between different coral species (Bak et al., 1982; Chornesky, 1983, etc.), especially reef-dwelling corals. These relationships have been summarized by Lang & Chornesky (1990) and further expanded by many authors since that date (summarized in Barnes & Hughes, 1999). Lang (1973) determined experimentally that each coral species attacked only certain other species, and each was itself only attacked by some others, providing a coral "aggression pecking order." She also determined that scleractinian corals extruded their mesentarial filaments both orally and through temporary openings in the polyp wall to digest the flesh of neighboring coral species externally (Lang, 1973). Among other authors, Chornesky (1983) observed that all modern coral polyps have such mesenterial filaments, but that additionally, some species develop sweeper tentacles. These are specialized tentacles that commonly appear on polyps adjacent to areas where mesenterial filaments are attacking adjacent coral soft tissues (Chornesky, 1983, p. 570), are larger than normal and more heavily armored than usual and extend farther into neighboring space (Bak, et al, 1983).

Evidence for this aggressive behavior between the Brassfield species of *Streptelasma* sp. on the tabulate species *Paleofavosites prolificus* is discussed below.

Materials and methods

Upper Brassfield strata in the inactive quarries of the Southwestern Portland Cement Company, east of Fairborn, Ohio (Fig. 1) were examined in detail and more than 2800 m of linear exposures were surveyed in the summers of 1967 and 1968. All *in situ* corals and stromatoporoids were either collected or identified in place and their locations, stratigraphic positions, axial dimensions, and burial orientations recorded. The Brassfield Limestone here is comprised of three distinct facies; (1) bioherms, (2) interbioherm strata, and (3) hardground (Kissling, 1977).

A specific collection of 203 corals from the uppermost 30 cm of the Brassfield from high-energy, current-deposited strata along 110 m of the east wall of the southern quarry extension (Fig. 1, labeled "Collection") includes three coralla of the tabulate species *Paleofavosites prolificus* that contain rugose corals. The total number of specimens and species of this limited 110 m collection includes the following: 19 *Paleofavosites prolificus*, 80 *Favosites favosus*, 8 *Halysites* sp., 7 *Heliolites* sp., and 89 solitary rugosans (Table 1). The total counts from seven collecting sites (six sites plus those noted above) of this uppermost zone in the south quarry (encompassing 354 m of quarry wall) are listed below and compared with the stromatoporoid sponge and coral fauna of both bioherms and contemporaneous interbioherm strata. Note that *Clathrodictyon vesiculosum,* although very abundant, is the sole stromatoporoid sponge taxon at this locality.

The three assemblages are distinct in terms of proportional representation of constituents. Of the total 274 *Paleofavosites prolificus* (Billings) colonies collected, slabbed, and examined throughout the quarry, only three coralla from the hardground high-energy facies exhibit infestation by rugosans. Nearly all *Paleofavosites prolificus* colonies collected from the bioherm and hardground facies (170 and 55 specimens, respectively) were sawn parallel to the vertical growth axis, polished, etched and reproduced as acetate peels to record annual growth increments and presumed ages of each to reconstruct age-frequency population structures for these distinct populations (Kissling, 1977). A series of 18 large thin sections

	Hardground	**Bioherms**	**Interbioherms**
Lateral coverage along quarry walls	354 m	149 m	2326 m
Taxon			
Clathrodictyon vesiculosum	124	59	45
Paleofavosites prolificus	55	173	46
Favosites favosus	137	588	96
Halysites	10	4	19
Heliolites	13	2	0
Alveolites	2	1	3
Solitary rugosans	140	106	25
Colonial rugosans	2	28	11

Table 1. Taxonomy and numbers of corals and stromatoporoids collected from the three facies of the Brassfield Formation studied on the east wall of the southern quarry at Fairborn, Ohio.

spaced approximately 10 mm apart and oriented in the plane of growth, were prepared from the largest of the three coralla, one which possessed a low domal, nearly tabular form. Similarly, four thin sections spaced 10 mm apart were prepared from a smaller, ellipsoidal corallum of *P. prolificus*. The third infested *Paleofavosites* corallum was not sectioned, but it does display six *Streptelasma* calices opening at its surface (Fig. 2). Detailed study of the small rugosans immured within the host *Paleofavosites* were carried out by microscopic examination of thin sections, which also furnished the photographic figures presented in this paper. All specimens are reposited in the Paleontological Research Institution collections at Ithaca, New York, USA, numbered PRI #64764a-64764n, 64765a-64765d, and 64766a-67466d respectively, for sections from the three colonies.

4. Geological setting

The Brassfield Formation of Late Llandovery Age (*Monograptus sedgwicki* Zone) represents basal Silurian limestone and dolomite throughout most of the western Cincinnati Arch region of Ohio, Indiana, Kentucky and Tennessee. Regionally the base and top of the formation are diachronous, the formation becoming older and thicker towards the east and southeast as it grades into the Tuscarora Sandstone in the Appalachian Basin.

At Fairborn, Ohio the Brassfield is unconformable on the Late Ordovician Elkhorn Formation, and measures 12 m thick. Local quarry workings were confined to the upper 4 m of the Brassfield which here contain numerous richly fossiliferous, argillaceous bioherms surrounded by thick-bedded coarse, crinoidal grainstones. Thin beds of crinoid grainstone interbedded with greenish gray, calcareous shale bearing abundant corals and stromatoporoids mark the uppermost part of the formation along the eastern wall of the southern quarry where this thin interval overlies a well marked discontinuity or hardground. In turn, this unit is overlain unconformably by the Dayton Limestone, locally dolomite, comprised of crinoid-brachiopod-bryozoan packstones. The uppermost Brassfield, with its crinoid grainstones, is interpreted to have represented wave-swept, high-energy, hardground environments that experienced episodes both of deposition and of erosion. This upper zone, a maximum 0.30 m thick, is marked by the presence of numerous lithic clasts, rotatory coralla of *Favosites favosus* (or circumrotatory, the term used by Kissling), well-abraded large, solitary rugosans, and some *F. favosus* coralla cemented to a lithified substratum (Kissling, 1973, p. 53). This thin unit, lying between erosional discontinuities at the top of the Brassfield Formation, was studied along a distance of 250 m along the eastern wall of the southern quarry, where all *in situ* fossils exposed were collected or recorded. It is absent where the two discontinuities merge. These observations serve to suggest that the numerous corals and stromatoporoids recovered *in situ* from the hardground facies had inhabited shallow, turbulent waters.

5. Discussion

5.1 The host

Paleofavosites prolificus. Of the many *Paleofavosites prolificus* coralla from the Brassfield that were sectioned and studied (274 coralla, 55 in the hardground facies above the recognizable lower disconformity), only three were infested by rugosans, each with multiple rugosans. These are numerous small, solitary streptelasmatid corals whose larvae settled on the tabulate colonies while the latter were still alive and secreting skeleton. Three-fourths of the 285 corals and stromatoporoids for which burial orientations could be established were seen to retain their original growth orientation; 80% of such specimens were encountered in bioherms, 75% in interbiohermal strata, and 67% on the hardground. This suggests that bioherms were the least turbulent and the hardground was the most turbulent of the habitats preserved in the upper Brassfield. Numerically, *Clathrodictyon vesiculosum* possessed the most stable form (as indicated by their having remained in growth position), while of corals present in these environments, *Paleofavosites prolificus* provided the most easily disoriented or overturned colony form. Only 58% of *Paleofavosites prolificus* colonies from all three habitats (as interpreted) were oriented in their growth position. Colony stability was dependent on their ability to adhere to the substratum or their capacity to adopt growth forms compatible with water turbulence. The premise that local environmental conditions influence the development of specific growth forms in organisms with accretionary skeletons is generally accepted.

The growth forms of large *P. prolificus* coralla are possibly the most indicative of habitat conditions. Shapes of 340 colonies were categorized as tabular (or low-mounded), hemispherical and columnar by measuring three perpendicular intercepts for each colony (one intercept coinciding with the growth axis), and transforming measurements to percentages. Columnar colonies are absent in the uppermost unit (hardground), whereas 95% of *P. prolificus* colonies have low-mounded, tabular forms in this facies, displayed by 75% of specimens from interbiohermal facies and by 70% of specimens from all bioherms.

All *P. prolificus* colonies exhibit well developed growth banding expressed as alternating zones of close-spaced tabulae and widely spaced tabulae; the couplet presumed to represent one year of skeletal secretion in which bands of close-spaced tabulae may signify seasonal conditions less conducive to skeletal growth than those of widely spaced tabulae (Kissling, 1977). Successful settling of the rugosan *Streptelasma* sp. and competition for space on the living surface of the host tabulate corals was most frequently accomplished either during the onset or within the midst of the "slow growth season." The poor growth conditions resulting in closely-spaced tabulae may also indicate that tabulate polyps were little able to fend off settling *Streptelasma* larvae at these times. Growth banding in *P. prolificus* does demonstrate that these widely differing corals grew simultaneously, but also that most of the individual rugosans were eventually outpaced in their upward growth and enveloped by host skeleton within several years after settlement. The presence of *Streptelasma* in the tabulate colonies was restricted to the uppermost, hardground facies.

Streptelasma sp. immured in *P. prolificus* skeletal tissue are bioclaustrations as described by Palmer & Wilson (1988), although here there is rugosan skeletal material present. These also vary from classic bioclaustrations in that there is no deflection of skeletal growth to surround the entombed species. Rather, in this case, mortality of *Paleofavosites* polyps occurred beneath the rugosans; later colonial skeletal growth overlapped and eventually covered the rugosan skeletons. The rugosan presence suggests that their polyps had a higher position in an aggression hierarchy (Lang, 1973, Bak et al, 1982, and others) than did the *Paleofavosites* polyps. By analogy to modern Scleractinia, cnidoblast-laden tentacles of smaller polyps (here of the tabulate) would have lacked the reach to dissuade the larger rugosans.

We consider encroachment onto the favositid surface by larvae of the epibiont rugosans and subsequent post-larval growth to result from rugosan requirements for living space on a hard

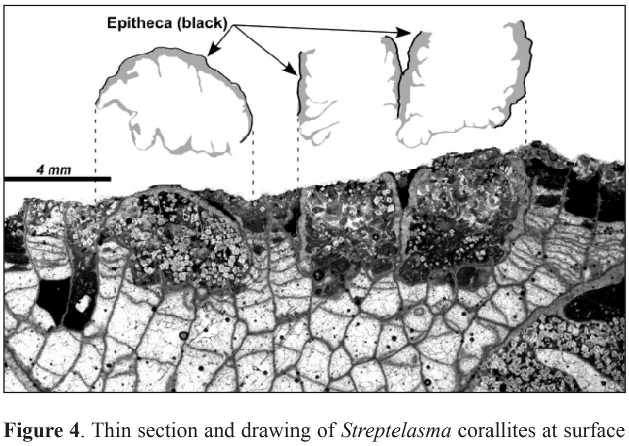

Figure 4. Thin section and drawing of *Streptelasma* corallites at surface of *Paleofavosites* (PRI 64764e). Note that growth orientation of the rugosans is here roughly parallel to the upper surface of the tabulate, and that their ventral wall is non-epithecate and incomplete. Note that the two corallites on the right side have been eroded, thus their epitheca and wall have been removed at the top of their sections.

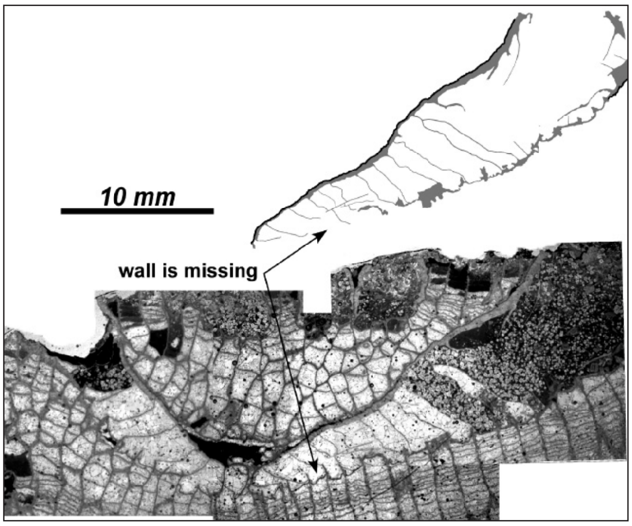

Figure 5. Corallites of *Streptelasma* sp. in longitudinal section immured within favositid (PRI64764d) along with drawing of corallite at right. Note that the dorsal wall of the right hand corallite is epithecate, but that the ventral wall is absent or composed of thin stereome only where the rugosan was in contact with the tabulate skeleton.

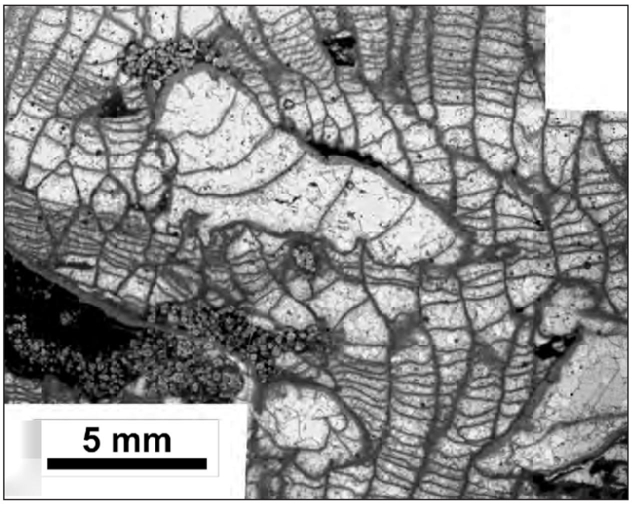

Figure 7. Corallites of *Streptelasma* sp. immured within *Paleofavosites prolificus* (PRI64764c). Note the occurrences within zones of varying growth as reflected by closely and widely spaced tabulae within the tabulate corallites. The large corallite at the upper central position here lacks wall between the rugosan and the tabulate skeleton. The apparent termination of the rugosan is apparently due to deflection of its growth direction out of the plane of the thin section.

substrate. It appears that individual polyps of *Paleofavosites* were killed due to their position in proximity to growing *Streptelasma* polyps. Colonial growth of *P. prolificus* corallites to encapsulate the rugosan skeletons was due to later corallite budding and corallum expansion over the individual corallites. Foremost of the needs of the rugosans was shelter from high-energy current action and improvement of feeding conditions. The survey by Tapanilla (2005) of bioclaustration taxa in a literature review, reported 43 bioclaustrations occurring in corals, and 38 of these occurred in Tabulata and Heliolitida. Surprisingly, of this group of 38, half are reported as occurring in the Favositidae, and 17 of these are reported to occur in either *Favosites* or *Paleofavosites*. Clearly, these were corals that provided a convenient place for settling organisms.

5.2 The epibiont

Streptelasma sp. - The solitary rugosan here reported as associated with *Paleofavosites prolificus* in the uppermost wave-swept hardground facies of the Brassfield is identified by us as *Streptelasma* sp. Laub (1979, p. 62) has reported a species of this genus, *S. scoleciforme* Laub, occurring in the upper unit of the Brassfield at its type locality in Kentucky (Laub, 1979, section 1). The individuals of *Streptelasma* sp. seen at Fairborn, here associated with *Paleofavosites*, cannot be identified with total confidence as *S. scoleciforme* Laub, as corallite morphologies differ, apparently due to incomplete development of skeleton here, with septa commonly lacking on the side adjacent to the tabulate colony, and wall either partially or totally absent where the rugosan lay directly on tabulate skeleton. The Laub species is the proper size and shape to be identical to the Fairborn species, but is characterized by often incomplete tabulae, while those in the latter are virtually all complete. This material from the Brassfield at Fairborn was previously misidentified as *Tryplasma* in a prior report (Sorauf & Kissling, 2011).

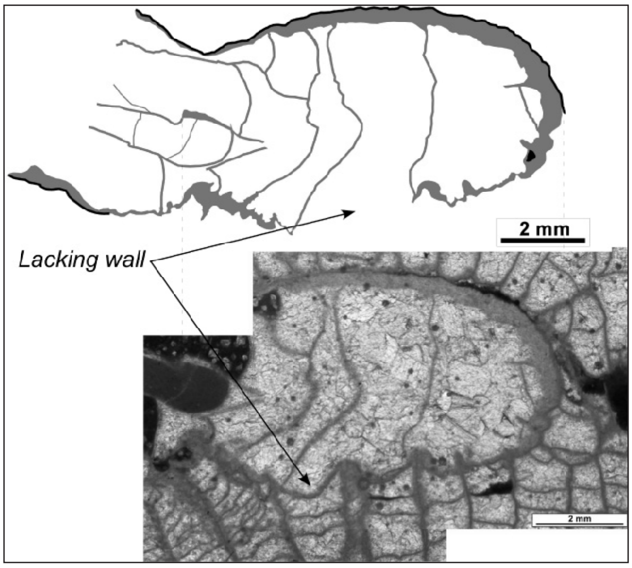

Figure 6. *Streptelasma* sp. with ventral wall lacking or very thin, with minor amounts of stereome deposited on tabulate skeleton (PRI64764e). The wall is thick and epithecate on the dorsal side where it presumably was exposed to sea water prior to being overgrown by the favositid.

Another species of *Streptelasma, S. recisum* McLean (1974, p. 41, pl. 1), has been reported as occurring embedded within a tabulate coral in Lower Silurian strata of New South Wales, Australia. McLean's species was found in the tabulate *Priscosolenia* and is fully developed in a rounded shape with a full complement of septa (26 – 30) and it has complete tabulae that are flat or somewhat sagging in the axial portion of the corallite. This Australian species is virtually identical in longitudinal section to the Fairborn material, except that the Ohio corals have an incomplete skeleton.

Because the Brassfield association is unique, normal taxonomy with respect to the rugosan is somewhat problematical. As shown in Figs 4-7, the Brassfield rugosan *Streptelasma* sp. here lacks some characteristics of the genus and, in fact, lacks some characters of rugosans in general, especially by lacking radial symmetry. Alteration of its morphology was apparently due to its having lived in a close relationship with, and being partially immured in *Paleofavosites*. As a result, the coral only developed the upper half of its semi-recumbent form, there retaining its normal, epithecate wall, with thin, sparse septa and complete tabulae. Dissepiments are totally lacking throughout the corallite (as in the genus). There is the appearance of sparse septal ridges in its calice, as expressed by those at the surface of the *Paleofavosites* colony (Fig. 2). It appears that modification of what would have been more typical rugosan morphology in the epibiont form is commonly expressed by, 1) a lack of septa in the lower half of the corallite, and 2) partial absence of the rugosan corallite wall in basal portions of it (ventral wall in a recumbent corallite). This lack of skeletal elements may have resulted simply from their position, lying on unoccupied tabulate corallites. It might also have had a more complex origin, a reflection of polypal skeleton modification resulting from continuing aggressive activity. Foremost of the needs of the rugosans was shelter from high-energy current action with its resulting improved feeding conditions. There was progressive

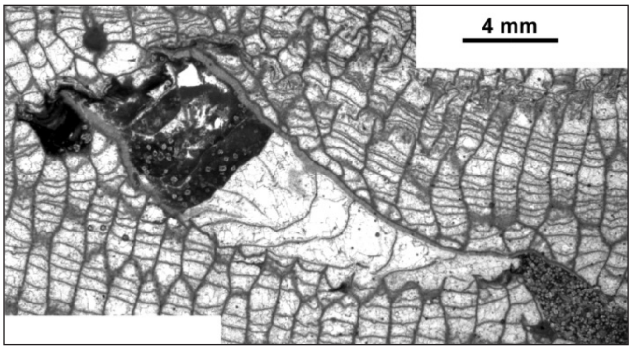

Figure 8. Immured individual of *Streptelasma* sp. lacking a ventral wall within corallum of *Paleofavosites prolificus* (PRI64764c). Note that the termination of growth of the rugosan appears to have preceded overgrowth of its calice, as the rugosan corallite was filled with sediment prior to being immured. Note also that some stereome of *Streptelasma* was deposited directly on the tabulate skeleton in the early stages of growth of the rugosan.

transgression by the growing rugosan along the tops of vacated tabulate corallites. The rugosan thus grew and secreted skeleton with sufficient rapidity to maintain the position of its polyp at the surface of the tabulate colony, avoiding for a time its complete immuration by skeletal growth of *Paleofavosites prolificus*.

The *Streptelasma* species, with its incomplete skeleton, most pronounced at its lower or ventral surface, may also reflect problems during growth of *Streptelasma* individuals with continuing contact with live tabulate polyps. One result may have been the internal rearrangement of *Streptelasma* mesenteries, with a resulting lack of septa and/or ventral wall on their undersurface. The incompleteness of the rugosan corallites also could be no more than conservation of energy, in that a wall (epithecal or not) was truly not needed on its ventral side because inert skeleton (of *P. prolificus*) was already there. Where the wall is absent however, some individuals did deposit a layer of stereome of varying thickness directly on tabulate skeletal elements (Figs 6, 8).

5.3 Symbiosis and Aggression

The relationship between the host colonies of *Paleofavosites* and the epibiont *Streptelasma* sp. was most likely not mutually beneficial. The only conceivable benefit the rugosan presence might have bestowed on the tabulate colonies would have been the presence of cnidarians with more potent cnidoblasts at the surface positions occupied. This is apparently negated by the vast majority of *Paleofavosites* colonies that existed in this facies without any symbionts being present (52 of 55 coralla).

The most obvious benefit to the rugosans would have been the anchoring of the fragile solitary corals in a high-energy environment where continuous currents could furnish an abundance of food. The hard-ground facies, apparently formed in shallow, turbulent environments late in the deposition of the Brassfield Formation, was likely subjected to episodic erosion and intermittent sediment accumulation. Being partially lodged within the tabulate colonial skeleton resulted in increased stability in currents afforded by the larger mass of the tabulate. The rugosans had to maintain growth rates sufficient to maintain their calices at the colony surface of the tabulate corallum, and those that were not able to maintain this position were simply overgrown and entombed, in most cases within a few years. Kershaw (1978, p. 379), noting the preference of *Tryplasma flexuosum* for *Clathrodictyon convictum* in the Middle Silurian Hemse Beds of Gotland, suggested that the preference here may have been largely due to selection of a stromatoporoid species with growth rates that were most comparable to the growth rate of the rugosan. His opinion also was that the *Tryplasma* individuals there chose stromatoporoids that adopted a relatively high profile, but inhabited high-energy environments that the solitary rugosan was too fragile to occupy otherwise.

It is uncertain whether there were other benefits to living as epibionts, in addition to the size and stability of the larger, stable, and broad-based tabulate colony in a high-energy and high-nutrient environment. The presence of the Brassfield species of *Streptelasma* as an epibiont clearly indicates that the rugosan was higher in the Paleozoic coral aggression hierarchy (Lang & Chornesky, 1990) than was *Paleofavosites prolificus*. It is unclear exactly what transpired to result in the lack of skeletal wall material of *Streptelasma* where the rugosan wall should have separated the soft tissues of the two disparate coral taxa.

The Brassfield rusosans apparently settled on and lived partially enveloped by tabulate skeleton; thus were anchored in low domal, hydrodynamically stable coralla of *Paleofavosites prolificus*. Thus they were able to inhabit high-energy, current-swept environments in Early Silurian time.

6. Conclusions

From this study, we are able to conclude the following:

1. The presence of the rugosan, *Streptelasma* sp., within coralla of *Paleofavosites proflificus* indicates that the rugosan occupied a higher position in the coral aggression hierarchy, presumably by possessing more powerful toxins and a superior means of delivering such toxins, perhaps analogous to those aggressive mechanisms (cnidoblasts, extrusion of digestive filaments) found among modern scleractinian corals, as described by Lang & Chornesky (1990).

2. The solitary corals, as indicated by their skeletons, were deformed where their lower surface was in contact with the *Paleofavosites* skeleton. The lower hemisphere of the roughly horizontal corallites generally shows a total lack of septa, and in places lacks walls, both epitheca and accompanying fibrous stereome, between the rugosan interior and the vacant tabulate skeleton. The lack of septa indicates a major reorganization of the rugosan polyp interior, a reflection of the mesenteries subdividing its gut. The lack of wall skeleton between the two greatly differing coral polyps suggests that the rugosans did not require additional protection from external forces in these locations, and also that *Paleofavosites* polyps were lacking beneath the rugosan polyps.

3. Partial bioclaustration or bioimmurration of the rugosans permitted these small, fragile, free-living corals to live anchored in a high-energy environment. This was due to the large size and hydrodynamically stable form of the tabulate colonies, as indicated by their abundance in the hardground portion of the upper Brassfield. This access to favorable feeding environments for the small, usually free-living corals provided a sufficient reward for their occurrence here as epibionts.

4. There appears to have been no particular benefit to the favositids, and they eventually overgrew and entombed the rugosans.

Favositid tabulate corals are common host organisms for epi- and endobionts as indicated by the occurrence of Paleozoic bioimmurrations. It appears clear that these small polyps were easily victimized by larger and more aggressive solitary rugosan polyps, and were situated lower on a Paleozoic coral aggression hierarchy. This occurrence in the Silurian Brassfield Formation provides us with the results of aggression of *Streptelasma* sp. on polyps of *Paleofavosites prolificus*, and is an expression of Silurian cnidarian behavior similar to that recognized in modern scleractinians.

7. Acknowledgments.

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Additionally, the final version of this report has benefited greatly from critical but positive reviews from B. Berkowski and A. May.

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Pragian (Lower Devonian) stromatoporoids and rugose corals from Zújar (Sierra Morena, southern Spain)

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ABSTRACT. The locality Zújar at the boundary between the Badajoz and Córdoba provinces belongs to the Obejo-Valsequillo-Puebla de la Reina Domain. Within the fossiliferous reefal carbonates of Pragian age cropping out in Zújar, 10 stromatoporoid species and 7 rugose coral species are identified. The new rugose coral species *Martinophyllum miriamae* n. sp. is described. *Hexagonaria soraufi* Rodríguez García, 1978 is a subspecies of *Martinophyllum ornatum* Jell & Pedder, 1969. The Pragian fauna of Zújar is a typical fauna of the Old World Realm with remarkably close relationships to Arctic Canada and Australia. Most species have been recorded for the first time from Spain. No significant relationships to the Eastern Americas Realm are visible. Remarkable is, that none of the stromatoporoid species of Zújar is known from the famous Pragian reef complex of Koněprusy in Bohemia, meanwhile the rugose coral fauna (e. g. *Joachimastraea barrandei* Galle, Hladil & May, 1999) shows some relations. Some of the species found are ancestors of important constructors of the Middle Devonian reef complexes, demonstrating that the roots of the Givetian-Frasnian reef complexes reach down to the Pragian.

KEYWORDS: Biogeography, reef, Anthozoa, Porifera, Devonian, Spain, Obejo-Valsequillo-Puebla de la Reina Domain, new species.

1. Introduction

Within the Middle Devonian and Lower Upper Devonian, reefs and biostromes made by stromatoporoids and corals are common world-wide (Burchette, 1981; Fagerstrom, 1987; Kiessling et al., 2003). Consequently, Middle and Upper Devonian stromatoporoids and corals are well investigated. Going down the Devonian timescale, the frequency of reefs and the knowledge on its constructors decrease, provoking several questions. (As a help for readers which are not familiar with the Devonian: the Lower Devonian is subdivided from lower to upper into Lochkovian, Pragian and Emsian.)

One obvious question is, how deep the roots of the Middle to Upper Devonian reef complexes reach: Is the fauna of corals and stromatoporoids in the Lower Devonian (e.g. Pragian) reefs completely different, or do we find the first ancestors of the constructors of the Middle to Upper Devonian reefs?

Other questions concern the biogeography: During the Pragian and Emsian, provincialism of the shallow marine benthos reached its maximum (Boucot, 1988: 211-212; Oliver & Pedder, 1994: 185; May, 1996, 1997). Up to now, concerning the biogeographic relations of the Southern Spanish Lower Devonian, only some data on Emsian stromatoporoids exist (May, 2006, 2007). The relations of the Pragian coral and stromatoporoid fauna were not known.

Another related topic involves the stromatoporoids of the Eastern Americas Realm: The Lochkovian and Emsian in the Eastern Americas Realm contain a distinct stromatoporoid fauna, characterized by the occurrence of *Habrostroma*. However, in the Eastern Americas Realm, there are virtually no stromatoporoids known from the Pragian (for details see Stock, 1997a; Stearn, 2001). Consequently, Stock (1994: 26) assumed that the Eastern Americas stromatoporoids survived in an unknown refuge in Bohemia, France, or Spain. Consequently, we try to answer in this paper the question: "Took the stromatoporoids of the Eastern Americas Realm during the Pragian refuge in the Sierra Morena?"

2. Investigated material

A first investigation of the Lower Devonian rugose corals in the Sierra Morena (Badajoz and Córdoba provinces, Southern Spain) was made by Rodríguez García (1978). Based on this study, since 2003 a group of palaeontologists from the universities of Valencia, León and Madrid is studying the main outcrops of Devonian reefal carbonates in the Sierra Morena (Research Projects BTE2003-2065 and GR-UCM/910231). All these localities belong to the Obejo-Valsequillo-Puebla de la Reina Domain.

First, we studied the locality Guadámez-2 (with Emsian reefal carbonates) in the Badajoz province and the locality Peñón Cortado in the Córdoba province (May, 2006, 2007; Valenzuela-Ríos et al., 2006; Rodríguez et al., 2010; see Fig. 1 and 2). Based on the stromatoporoid fauna, May (2006: 35) assumed an Emsian age for the reefal carbonates of the locality Peñón Cortado, which contain much *Hexagonaria soraufi* Rodríguez García, 1978. However, later investigations based on conodonts revealed a Pragian age for these reefal carbonates (Valenzuela-Ríos et al., 2006).

Later we extended our study to the locality Zújar at the boundary between the Badajoz and Córdoba provinces (38º29'30''N, 1º46'W). The locality Zújar is about 13.5 km north-easterly of Valsequillo, within the valley of the river Zújar (Fig. 2). Outcropping are siliciclastic sediments and limestones of Lochkovian, Pragian and Famennian age. Brachiopods and conodonts prove that the limestones with corals and stromatoporoids are Pragian in age (Pardo Alonso & Valenzuela-Ríos, 2006; Valenzuela-Ríos et al., 2006).

The Pragian limestones of Zújar are a 60-70 m thick sequence, which starts with about 10-15 m platy limestones, which may contain many brachiopods (Pardo Alonso & Valenzuela-

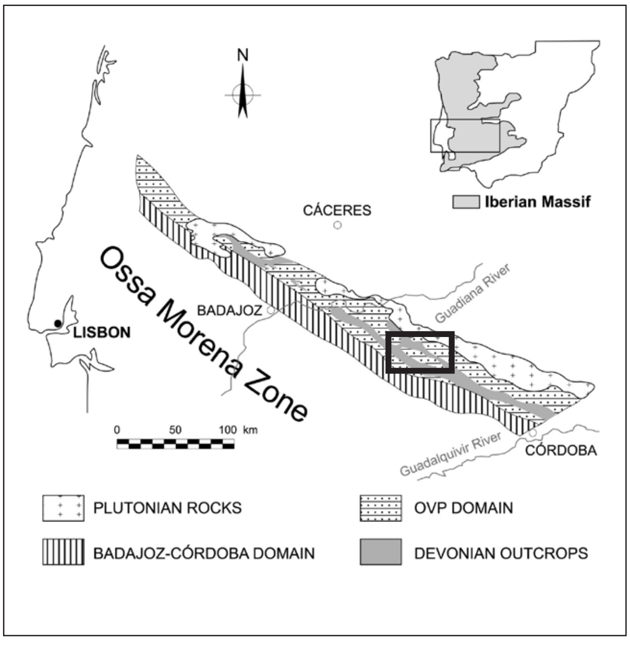

Figure 1. Structural map of the Ossa Morena Zone, showing the study area.

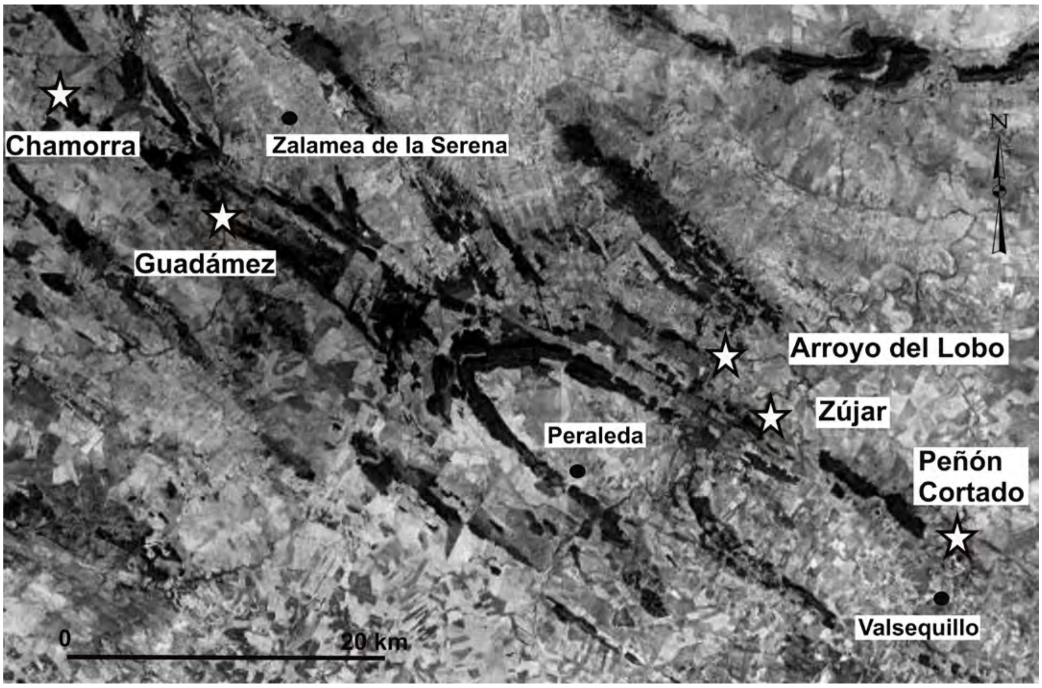

Figure 2. Location of studied outcrops. White asterisks mark the positions of the studied outcrops, meanwhile black dots mark the exact positions of three villages.

Ríos, 2006). In continuation follow about 17-32 m crinoidal limestones. Finally follow about 20-36 m bedded limestones with tabulate corals, stromatoporoids and rugose corals, which provided the fossils presented in this paper.

Furthermore we consulted material from other localities in the Sierra Morena (La Chamorra, Arroyo del Lobo, Peñón Cortado; see Fig. 2), especially the rugose corals described by Rodríguez García (1978) from the Pragian limestones of the locality Peñón Cortado. Further information on these localities is given by Rodríguez García (1978: 331-335) and May (2006: 31-32).

3. Systematic palaeontology

Up to now, in the Pragian limestones from Zújar, 10 stromatoporoid species and 7 rugose coral species have been identified.

Longitudinal and tangential (= transverse) thin sections have been taken from the stromatoporoid and rugose coral specimens collected. The methodology, terminology, and classification (including the genus definitions) follow those of Stearn (1993a), Stearn et al. (1999) and Hill (1981). The material is stored in the Departamento de Paleontología, Universidad Complutense, Madrid, under the numbers DPM-00276/Z1 to DPM-00276/ZE18.

3.1. Stromatoporoids

***Nexililamina dipcreekensis* Mallett, 1971**
(Plate 1 A-B)

Material. From Zújar: DPM-00276/Z4, Z13, Z18.

Description and discussion. Within the vertical sections, the commonly superposed pillars are spool-shaped or Y- or V-shaped. Their frequency is mostly 11-12 (min. 9, max. 15) pillars/2 mm. There are 9-11 laminae /2 mm. Horizontal dissepiments between the laminae are common. These horizontal dissepiments are more or less parallel to the laminae and connect neighbouring pillars.

The colonies fit well with the redescription of *Nexililamina dipcreekensis* Mallett, 1971 by Webby & Zhen (1997: 35-36, fig. 12 C-F). The only visible difference is, that the vertical sections of the Spanish material show slightly more pillars than the type material (mostly 9-11 pillars/2 mm). Up to now, *Nexililamina dipcreekensis* has only been found in the Emsian-Eifelian of Queensland (Webby & Zhen, 1997).

***Plectostroma altum* (Ripper, 1933)**
Plate 1 C-D

Material. From Zújar: DPM-00276/Z1, Z4, Z8, Z11, Z14, Z20, ZE9.

Description and discussion. The colonies fit well with the redescription of *Plectostroma altum* (Ripper, 1933) by Webby et al. (1993: 126-128, figs 7E-8D). Within the vertical sections, the density of pillars vary from 7-9 pillars/2 mm to 9-12 pillars/2 mm. The pillars have 0.03-0.06 mm thickness. There are 10-20 horizontal elements over a distance of 2 mm.

The type material of *Plectostroma altum* (Ripper, 1933) as well as the colonies from Zújar can be distinguished from *Plectostroma yunnanense* (Mansuy, 1914) and *Plectostroma salairicum* (Javorskij, 1930) by their shorter pillars and their more pronounced latilaminae (May, 2005: 152-154; Javorskij, 1930: 480, pl. 2; Prosh & Stearn, 1996: 15-16, pl. 1 figs 4-5). Furthermore, *Plectostroma salairicum* has a slightly higher density of pillars: 5-6 pillars/1 mm (Javorskij, 1930) or 6-8 pillars/1 mm (Prosh & Stearn, 1996).

Probably, the material from the Pragian limestones of Peñon Cortado, which May (2006: 32-34, fig. 3b; 2007: 142-143) assigned to *Plectostroma salairicum*, belongs to *Plectostroma altum*, too. *Plectostroma altum* was known up to now only from the Pragian of Victoria, Australia (Webby et al., 1993).

***Stictostroma gorriense* Stearn, 1995**
(Plate 1 E-F)

Material. From Zújar: DPM-00276/Z23.

Description and discussion. The colony fits well with the description of *Stictostroma gorriense* Stearn, 1995 by Stearn (1995: 26, figs 1-2) and Prosh & Stearn (1996: 24-25, pl. 8 figs1-5). Within the vertical sections, the density of skeletal elements is: 9-11 pillars/2 mm and 11-13 laminae /2 mm. *Stictostroma gorriense* occurs within the Lower and Upper Emsian of Arctic Canada and Ontario (Stearn, 1995; Prosh & Stearn, 1996).

***Stictostroma nunavutense* Prosh & Stearn, 1996**
(Plate 1 G-H)

Material. From Zújar: DPM-00276/ZE18.

Description and discussion. The colony fits well with the description of *Stictostroma nunavutense* Prosh & Stearn, 1996 by Prosh & Stearn (1996: 25-26, pl. 9 figs1-5). Within the vertical sections, the density of skeletal elements is: 4-6 pillars/2 mm and 7-8 laminae /2 mm. *Stictostroma nunavutense* was known up to now only from the Lower Emsian of Arctic Canada (Prosh & Stearn, 1996).

***Stromatopora* ex gr. *rarissima* Počta, 1894 - *polaris* (Stearn, 1983)**

Material. From Zújar: DPM-00276/Z8.

Description and discussion. This undoubted representative of *Stromatopora* is not very well preserved. It is very similar to the holotype of *Stromatopora rarissima* Počta, 1894 (see May, 2005: 194, pl. 40 fig. 2) and the described material of *Stromatopora polaris* (Stearn, 1983) (Stearn, 1983: 551–552, fig. 5; Stearn, 1990: 507, fig. 3.8; Prosh & Stearn, 1996: 31, pl. 14 fig. 5). *Stromatopora rarissima* and *Stromatopora polaris* are so similar, that they are possibly conspecific. May (2005: 194) was not able to define significative differences between them.

Stromatopora rarissima originates from the Wenlockian of Bohemia (May, 2005), meanwhile *Stromatopora polaris* occurs in the Upper Lochkovian to Upper Emsian of Arctic Canada (Stearn, 1983, 1990; Prosh & Stearn, 1996; Stearn, 2001: 14-15). Furthermore, similar forms are known from the Lower Emsian of Victoria (Webby et al., 1993:158–161, figs 5, 23, 24) and the Emsian of the Sierra Morena (May, 2006).

***Pseudotrupetostroma* cf. *pellucida* (Javorskij, 1955)**
(Plate 1 I-J)

Material. From Zújar: DPM-00276/Z3.

Description and discussion. The colony is not very well preserved. Nevertheless, it can be assigned to *Pseudotrupetostroma* Chalfina & Javorskij, 1971 because of its microstructure and its pillars, which are in many cases superposed over 2 to 4 interlaminar spaces. Within the vertical sections, the density of skeletal elements is: 6-9 pillars/2 mm and 7-8 laminae /2 mm. It can be distinguished easily from the only known Spanish *Pseudotrupetostroma* species, *P. anacontentoae* May, 2007. In *P. anacontentoae* May, 2007, the distances between the skeletal elements are much smaller. Furthermore, in the colony from Zújar, the astrorhizal canals are bigger, less frequent and and not oriented in the specific pattern of *P. anacontentoae* May, 2007 (May, 2007: 144-147, fig. 2).

Comparable to the colony from Zújar are two taxa: *Stromatopora pellucida artyschensis* Javorskij, 1955 and *Stromatopora pellucida pellucida* Javorskij, 1955. *Stromatopora pellucida artyschensis* Javorskij, 1955 from the Givetian of Siberia, the type species of *Pseudotrupetostroma*, has about 2 laminae per 1 mm (maximum 4 laminae per 1 mm) (Javorskij, 1955: 100–101). In *Stromatopora pellucida pellucida* Javorskij, 1955 from the Lower Devonian and the Givetian of Siberia, the laminae are spaced 8–9 per 2 mm and there are up to 6 pillars per 1 mm (Javorskij, 1955, p. 91–92).

The genus *Pseudotrupetostroma* Chalfina & Javorskij, 1971 is known from the Emsian to the Givetian in Australia, Asia, Canada, Spain and Central Europe (Stearn et al., 1999: 48; May, 2006, 2007; Salerno, 2008: 92-96). The material from the Pragian of Zújar is one of the oldest occurrences of the genus.

***Syringostromella zintchenkovi* (Chalfina, 1960)**
(Plate 1 K-L)

Material. From Zújar: DPM-00276/ZE2, ZE11, ZE16.

Description and discussion. The colonies ZE2 and ZE11 fit well with the descriptions of *Syringostromella zintchenkovi* (Chalfina, 1960) by Chalfina (1960: 327–328, pl. D-3 fig. 1), Webby et al. (1993: 163, figs 23-24) and Prosh & Stearn (1996: 34, pl. 15 figs 1-3). Within the vertical sections, the density of skeletal elements are: 3.5-6 (mostly 4-5) pillars/2 mm and 4-5 horizontal elements (mostly microlaminae) /2 mm. The pillars are 0.15-0.3 mm (mostly ca. 0.2 mm) thick.

The colony ZE16 resembles *Syringostromella labyrinthea* Stearn, 1990, because it has 4.5-6 pillars / 2 mm, slightly better developed coenostromes and a slightly more irregular growth. However, these differences do not justify separating ZE16 from *S. zintchenkovi*, because *S. labyrinthea* has 5-7 pillars /2 mm (Stearn, 1990: 507, figs 5, 7, 8).

Hitherto *Syringostromella zintchenkovi* has been found in the Upper Lochkovian of Russia (Chalfina, 1960), the Pragian of Victoria (Australia) (Webby et al., 1993), the Lower Emsian of Arctic Canada (Prosh & Stearn, 1996) and the Pragian and Emsian of the Sierra Morena (May 2006, 2007).

***Coenostroma* aff. *pustulifera* (Winchell, 1867)**
(Plate 2 C-D)

Material. From: a) Zújar: DPM-00276/Z27, Z33, ZE4. b) Arroyo del Lobo: DPM-00276/A12.

Description and discussion. The colonies are typical representatives of *Coenostroma*. Within the vertical sections, the dimensions of skeletal elements are: 4 coenostromes /2 mm, coenostromes are 0.2-0.5 mm thick, 7-14 pillars / 2mm, pillars are 0.08-0.22 mm thick. Among all species assigned to *Coenostroma* by Stearn (1993b), the colonies fit best with the redescription of *Stromatopora pustulifera* Winchell, 1867 from the Middle Devonian of Michigan by Galloway & Ehlers (1960: 54-56, pl. 2). However, *pustulifera* has 6 coenostromes /2 mm (Galloway & Ehlers, 1960).

***Habrostroma centrotum* (Girty, 1895)**
(Plate 2 A-B)

Material. From Zújar: DPM-00276/Z10, Z18.

Description and discussion. The colonies fit well with the descriptions of *Habrostroma centrotum* (Girty, 1895) by Stock (1988: 14-15, figs 4-5; 1991: 905-906, fig. 5; 1997b: 545, figs 4.1-2) and Stock & Burry-Stock (2001). Within the vertical sections, there are 6-7 coenostromes /2 mm and 4-8 coenosteles /2 mm. The horizontal skeletal elements dominate over the vertical elements and cystlike microlaminae are rare. *Habrostroma consimile* (Girty, 1895) is very similar to *Habrostroma centrotum*, but has much more cystlike microlaminae (Stock & Burry-Stock, 2001).

Habrostroma centrotum (Girty, 1895) is known from the Lochkovian of New York and Arctic Canada (Stock, 1997b; Stock & Burry-Stock, 2001, 2007) and the Pragian of northern Spain (Fernández-Martínez et al., 2010: 314-316, figs11 E-F).

***Amphipora* sp.**
(Plate 2 E-F)

Material. From Zújar: DPM-00276/ZE13.

Description and discussion. The material consists of branches with 1.1-1.9 mm diameter without a clearly visible axial canal. The cosmopolitan *Amphipora ramosa* (Phillips, 1841) as well as *Amphipora porrecta* (Webby, Stearn & Zhen, 1993) from the Pragian of Victoria have thicker branches with a better developed axial canal (Stearn, 1997: 845-849, figs 1-11; Webby, Stearn & Zhen, 1993: 177-179, fig. 30).

3.2. Rugose corals

***Loyolophyllum (Fasciloyolopyllum) qinlingensis* (Cao in Cao et al., 1983)**
(Plate 3 I-J)

Material. From Zújar: DPM-00276/Z16.

Description and discussion. The material consists of corallites of *Loyolophyllum (Fasciloyolopyllum)* Zhen, 2007 which are grown together with stromatoporoids. Sections of juvenile stages of corallites have 1.8 mm diameter and 8 x 2 septa. Adult stages of corallites with 4.7 mm diameter have 14-15 x 2 septa and a peripheral stereozone of 0.7-1.0 mm thickness with rare dissepiments. The material fits well with the description of *Battersbyia qinlingensis* Cao in Cao et al., 1983 from the Early Devonian of northwest China (Cao et al., 1983: 137, pl. 46 figs 7a–b). *Loyolophyllum (Fasciloyolophyllum) parallelum* (Etheridge, 1899) from the late Eifelian to early Givetian of New South Wales has 2.2 mm in average corallite diameter and a smaller peripheral stereozone (Zhen, 2007: 204-206, figs 2-3).

***Grypophyllum jenkinsi* (Strusz, 1966)**
(Plate 2 K-L)

Material. From Zújar: DPM-00276/ Z24, ZE18.

Description and discussion. Solitary coralla of *Grypophyllum* of 12-18 mm diameter with 56-62 septa and some lonsdaleoid dissepiments. Coralla without prominent rejuvenescence, septa not axially contorted. The material fits well with the descriptions of *Grypophyllum jenkinsi* (Strusz, 1966) by Strusz (1966: 562-563, pl. 87 figs 3-4) and Blake (2010: 90-92, fig. 55). Within the type material, usually the coralla have 15-20 mm diameter and 50-60 septa (Strusz, 1966: 562). The type material originates from the Garra Formation of New South Wales (Strusz, 1966) which is Lochkovian to Pragian in age (Trotter & Talent, 2005: 6). Blake (2010) found this species in the Givetian of Queensland.

***Chostophyllum* ex gr. *gregorii* (Etheridge in Jack & Etheridge 1892)**
(Plate 3 M-N)

Material. From Zújar: DPM-00276/Z18.

Description and discussion. Solitary corallum of 17 mm diameter with 62 peripherally dilated septa, which resembles several Givetian to Frasnian species assigned to the genera *Temnophyllum* Walther, 1929, *Pseudozaphrentis* Sun, 1958 and *Chostophyllum* Pedder, 1982 (for discussion of the genera see McLean, 1993a). The closest similarity exists with *Chostophyllum gregorii* (Etheridge in Jack & Etheridge 1892) from the Givetian of Queensland (Zhen & Jell 1996: 82-83, pl. 13 figs 7-10). Material which is conspecific or at least very similar to *Chostophyllum gregorii* is described by Blake (2010: 121-122, fig. 86) from the Emsian or Eifelian of Queensland and by Strusz (1965: 537, pl. 73 figs 4-5) from the Lochkovian to Pragian Garra Formation of New South Wales (Trotter & Talent, 2005: 6).

***Martinophyllum ornatum soraufi* (Rodríguez García, 1978)**
(Plate 3 A-B, 3 E-F)

Material. From: a) Zújar: DPM-00276/Z27, Z31, Z34. b) Pragian of Peñon Cortado: V24/7 (=holotype; Pl. 3 E-F), DPM-00276/P8. c) Arroyo del Lobo: DPM-00276/A18. d) La Chamorra: DPM-00276/C24.

Description and discussion. The cerioid coralla are typical representatives of *Martinophyllum* Jell & Pedder, 1969. Within the material from Zújar, the adult corallites have 3.6-4.8 mm diameter and 26-28 (sometimes up to 30) septa. They fit very well with the holotype of *Hexagonaria soraufi* Rodríguez García, 1978 from the Pragian limestones of the locality Peñón Cortado and the original description of this species by Rodríguez García (1978: 340-342, pl. 1 figs 7-9). They are very similar to *Martinophyllum ornatum* Jell & Pedder, 1969, the type species of *Martinophyllum*, which has slightly larger corallites, slightly more septa and a slightly broader dissepimentarium (Jell & Pedder, 1969: 736-737, pl. 95 figs 4, 6, 8) and is known in Queensland from beds of upper Lochkovian or lower Pragian age (Webby & Zhen, 1997: 5).

It should be noted, that the septa of *soraufi* are not as clearly fusiform as in *ornatum*. However, as well as in *ornatum* specimens with strongly fusiform septa coexist with specimens with weakly fusiform septa (compare Jell & Pedder, 1969: pl. 95 figs 6, 8), in *soraufi* specimens with weakly fusiform septa coexist with specimens with cuneiform septa (compare Plate 3 A, E). These differences justify treating *soraufi* as a subspecies of *ornatum*. Probably, *Martinophyllum ornatum soraufi* (Rodríguez García, 1978) could be used as index fossil for Pragian. However, it should be noted that Sorauf (1969: 185-186, pl. 36 figs 1-5) described from the Emsian of western France as *Hexagonaria* sp. cf. *longiseptata* material which belongs to *Martinophyllum ornatum soraufi*.

Coen-Aubert (2002: 33, pl. 4 figs 3-4) compares *soraufi* with *Argutastrea? pradoana* (Haime in De Verneuil & Barrande, 1855). It is true, that the transverse section of *pradoana* shows some similarities with *soraufi*. However, in *pradoana* the corallites have 4.3-6.7 mm diameter and 30-34 septa. Furthermore, the longitudinal section of *pradoana* is much more *Argutastrea*-like with steeply inclined dissepiments and preferentially concave tabulae and tabellae (Coen-Aubert, 2002: 33, pl. 4 figs 3-4).

***Martinophyllum miriamae* n. sp.**
(Plate 3 C-D, 3 G-H)

Derivation of name. The species is named in honour of Miriam May Contento, fourth daughter of Andreas May.

Type locality and horizon. Zújar, Pragian limestone.

Holotype. DPM-00276/ZE10, Pl. 3 C-D.

Paratype. DPM-00276/ZE6, Pl. 3 G-H.

Diagnosis. *Martinophyllum* species with 3.5-6.2 mm adult corallite diameter and more or less strongly reduced septa. Maximum are 32 septa.

Description. Cerioid corallum. In transverse section, adult stages have 3.5-6.2 mm (mostly 4.2-5.2 mm) corallite diameter and juvenile stages have 1.7-2.5 mm corallite diameter. If in adult stages the septa are more or less completely developed, 20-32 (mostly 28-30) septa are counted. Juvenile stages have up to 16 septa. As minimum 1-3 septa have been observed in juvenile as well as in adult stages. In transverse sections with very well developed septa, sometimes major and minor septa can be distinguished. In these cases, minor septa are somewhat shorter (about 65-80 percent of the length of the major septa) and may be slightly thinner. The major septa never reach completely to the centre, but always leave a central space of at least 1-2 mm diameter without any septa. In transverse sections with very well developed septa, all septa start at the outer wall, the septa are rarely interrupted and lonsdaleoid dissepiments do not occur. Frequently, the septa are slightly thickened within the peripheral part of the corallite. In transverse sections with very badly developed septa, only few, short, rudimentary septa are visible, which may start on lonsdaleoid dissepiments or on the outer wall. Between both extremes are continuous transitions.

The longitudinal section shows a clearly expressed periodicity between phases with well developed septa and badly developed septa. Within the phases with well developed septa, the longitudinal section resembles strongly *Martinophyllum ornatum ornatum* Jell & Pedder, 1969 and *Martinophyllum ornatum soraufi* (Rodríguez García, 1978), because the dissepimentarium is well developed, 0.4-1.2 mm broad and consists of 1-4 rows of globose to steeply inclined dissepiments, meanwhile the tabularium consists of densely spaced, arched tabulae and tabellae (14-17 horizontal elements per 5 mm distance). Within the phases with badly developed septa, the tabularium consists of widely spaced horizontal, inclined or arched tabulae and tabellae (4-6 horizontal elements per 5 mm distance) and the dissepimentarium is missing or consisting of remarkably larger dissepiments.

Discussion. At the first glimpse, someone might assign this peculiar species to *Carlinastraea* Merriam in Merriam, McKee & Huddle, 1976, *Utaratuia* Crickmay, 1960, or *Tawuphyllum* Pedder, 1980. However, each of these genera can be excluded easily: *Carlinastraea* Merriam in Merriam et al., 1976 has much thicker walls and completely different longitudinal sections (see Merriam et al., 1976: 32-34, pl. 6-7). *Utaratuia* Crickmay, 1960 can be easily distinguished by its longitudinal section as well as by the lack of transverse sections with well developed septa (see Jell & Hill 1970). Again, *Tawuphyllum* Pedder, 1980 can be easily distinguished by its longitudinal section. Furthermore, in *Tawuphyllum* the septa are well developed within the tabularium and suppressed within the dissepimentarium (see Pedder, 1980: 602-606, pl. 5), but in *Martinophyllum miriamae* n. sp. it is the contrary.

If there were only the phases with badly developed septa, no-one would assign this material to *Martinophyllum* Jell & Pedder, 1969. However, within the phases with well developed septa, the corallites strongly resemble *Martinophyllum ornatum ornatum* Jell & Pedder, 1969, the type species of *Martinophyllum*. In fact, corallite diameter and maximum number of septa are comparable to *Martinophyllum ornatum ornatum* Jell & Pedder, 1969 (p. 736-737, pl. 95 figs 4, 6, 8). Nevertheless, *Martinophyllum miriamae* n. sp. is distinguished from *Martinophyllum ornatum ornatum* and all other described species of *Martinophyllum* by the occurrence of corallites with strongly reduced septa. Furthermore, within *Martinophyllum ornatum ornatum* no such big central space without any septa exists. The other *Martinophyllum* species described by Jell & Pedder (1969) as well as *Martinophyllum daerdongense* Yu & Liao, 1982 from the Lower Devonian of Tibet (Yu & Liao, 1982: 106, pl. 2-3), *Martinophyllum altiaxis* Pedder, 1984 from the Lower Emsian of Canada (Pedder 1984: 320-322, figs 10-21) and *Martinophyllum planofundalis* Erina in Kim et al., 2007 from the Emsian of Uzbekistan (Kim et al., 2007: 193, pl. 55, figs 2-3) have larger corallites and more septa than *Martinophyllum miriamae* n. sp. *Martinophyllum ornatum soraufi* (Rodríguez García, 1978) has slightly smaller corallites and slightly less septa than *Martinophyllum miriamae* n. sp.

Important is the fact, that there are two coralla of *Martinophyllum miriamae* n. sp., which are distinguished from *Martinophyllum ornatum soraufi* (Rodríguez García, 1978) not only by their growth periodicity, but also by their skeletal dimensions. All coralla of *Martinophyllum ornatum soraufi* (Rodríguez García, 1978), which were found in Zújar, did not show any growth periodicity. From this observation it can be deduced, that the growth periodicity of *Martinophyllum miriamae* n. sp. was genetically induced. Nevertheless, we have not enough data to decide, if the growth periodicity was the response to extrinsic factors like sedimentation rate or length of the day or if it was an expression of intrinsic factors like periods of different intensity of reproduction.

Distribution. Not known outside the type locality.

***Joachimastraea barrandei* Galle, Hladil & May, 1999**
(Plate 2 H-J, 3 K-L)

Material. From Zújar: DPM-00276/Z35; from the Pragian of Peñon Cortado: PCR'-5, PCR-14; from La Chamorra: DPM-00276/C27.

Description and discussion. The well preserved material from Zújar has 4.0-5.5 mm corallite diameter and fits in all details (including the development of the dissepiments) very well with *Joachimastraea barrandei* Galle, Hladil & May, 1999, a genus and species which was known up to now only from the Pragian of Koněprusy (Bohemia) (Galle, Hladil & May, 1999: 182-184, pl. 1 figs 1-7, pl. 2 figs 1-5). The material from the Pragian limestones of Peñon Cortado and the material from La Chamorra are without any doubt conspecific.

***Rhizophyllum* ex gr. *bohemicum* Počta, 1902**
(Plate 3 O-P)

Material. From Zújar: DPM-00276/Z34.

Description and discussion. Coralla of *Rhizophyllum* with 13.2-17 mm diameter. Except of their much smaller size, the coralla are similar to *Rhizophyllum bohemicum* Počta, 1902 from the Pragian of Koněprusy (Bohemia) (Oliver & Galle, 1971: 84-85, pl. 2 fig 1-4, pl. 24 fig. 3).

4. Conclusions

4.1. Importance of the described fauna

That the described fauna is very important, is demonstrated by following comparison: Up to now, there were known from only three localities of Lower Devonian age of the Sierra Morena 11 stromatoporoid species (May, 2006, 2007) and 8 rugose coral species (Rodríguez García, 1978; concerning *Disphyllum pedrosense* Rodríguez García, 1978 see Rodríguez & Soto, 1979). In the Pragian limestones of Zújar, 10 stromatoporoid species and 7 rugose coral species were identified. This is almost as many as were known up to now in total from the Lower Devonian of the Sierra Morena.

Only one species from Zújar is completely new. However, most species collected in Zújar have been recorded for the first time from Spain. The exceptions are:

- 2 stromatoporoid species (*Stromatopora* ex gr. *rarissima – polaris*, *Syringostromella zintchenkovi*) and 1 rugose coral species (*Martinophyllum ornatum soraufi*) were known from other localities in the Sierra Morena.
- The stromatoporoid *Habrostroma centrotum* has recently been described from northern Spain (Fernández-Martínez et al., 2010).
- The stromatoporoid *Amphipora* is ubiquitous (May, 1993b; Stearn, 1997).

4.2. Biogeographic relations

The Pragian fauna of Zújar is a typical fauna of the Old World Realm with remarkably close relationships to Arctic Canada and Australia (New South Wales, Queensland, Victoria). No significant relationships to the Eastern Americas Realm are visible. *Habrostroma* is a characteristic stromatoporoid genus of the Eastern Americas Realm (Stock, 1990: 258; Stock, 1994; Stock, 1997a: 285; May, 2006: 36). However, *Habrostroma centrotum* is known to have immigrated into the Old World Realm (Stock & Burry-Stock, 2001, 2007; Fernández-Martínez et al., 2010). *Coenostroma pustulifera* is known from Michigan (Eastern Americas Realm) (Galloway & Ehlers, 1960), but the genus *Coenostroma* is widespread in the Old World Realm (Stearn et al., 1999: 53). Concluding, there is no hint, that the stromatoporoids of the Eastern Americas Realm during the Pragian took refuge in the Sierra Morena.

Remarkable is, that none of the stromatoporoid species of Zújar is known from the famous Pragian reef complex of Koněprusy (Bohemia) (compare May, 2005), meanwhile the rugose coral fauna shows similarities due to the occurrence of *Joachimastraea barrandei* Galle, Hladil & May, 1999 and *Rhizophyllum* ex gr. *bohemicum* Počta, 1902. Incidentally, these faunal relations between Koněprusy and Zújar are also demonstrated by the auloporid tabulate coral *Remesia koneprusiana* Galle, Hladil & May, 1999 (see Pl. 2G), which we found together with *Rhizophyllum* in DPM-00276/Z34.

Zújar has only *Habrostroma centrotum* in common with the Pragian fauna described by Fernández-Martínez et al. (2010) from Northern Spain.

4.3. Correlations with other localities in the Sierra Morena

The rugose corals described herein suggest a Pragian age for the limestones of the localities Arroyo del Lobo and La Chamorra (Fig. 2). For Arroyo del Lobo, no dating has been available up to now. Based on stromatoporoids, May (2006) suggested an Emsian age for La Chamorra. However, the dating based on rugose corals is more trustworthy.

4.4. Are there Pragian roots of the Middle Devonian reef complexes?

Among the stromatoporoid genera found in Zújar, the genera *Plectostroma*, *Stictostroma*, *Stromatopora*, *Pseudotrupetostroma*, *Habrostroma* and *Amphipora* are important constructors of the Middle Devonian reef complexes (e.g. Zukalová, 1971; Flügel, 1974; May, 1988, 1993b; Salerno, 2008). The rugose coral *Grypophyllum* is a characteristic member of the Middle Devonian reefs, too (e.g. Birenheide, 1978; Galle et al., 1988; May, 1993a; Wrzolek, 1993: 219; Schröder, 2005). In similar way, *Chostophyllum* is widespread in the Givetian and the closely related genus *Temnophyllum* is common in the Givetian to Frasnian reefs (Galle et al., 1988; McLean, 1993a; Wrzolek, 1993; Schröder, 2005).

From several places, especially in Australia, first occurrences of "typical" Givetian-Frasnian rugose coral genera and stromatoporoid genera are known from beds of Pragian or similar age (e.g. Strusz, 1965, 1966; Fedorowski & Gorianov, 1973: 29-30; McLean, 1993b: 58; Webby et al., 1993; Zhen, 1995; McLean, 2005: 29-30; May, 2005; Kim et al., 2007: 188). The same patterns can be shown also in tabulate corals. For example, *Scoliopora* is an important reef builder within the Givetian-Frasnian reef complexes (e.g. Galle et al., 1988; May, 1988: 184), but the oldest species of the genus are known from reefs of Pragian age (Hladil, 1989: 225-226; May & Pohler, 2009). Another example is *Syringopora praehanshanensis* May, 2005, the Pragian precursor of the Middle Devonian commensalic *Syringopora* species (for details see May, 2005: 221-226, 234-235).

Definitely, the roots of the Givetian-Frasnian reef complexes reach down to the Pragian.

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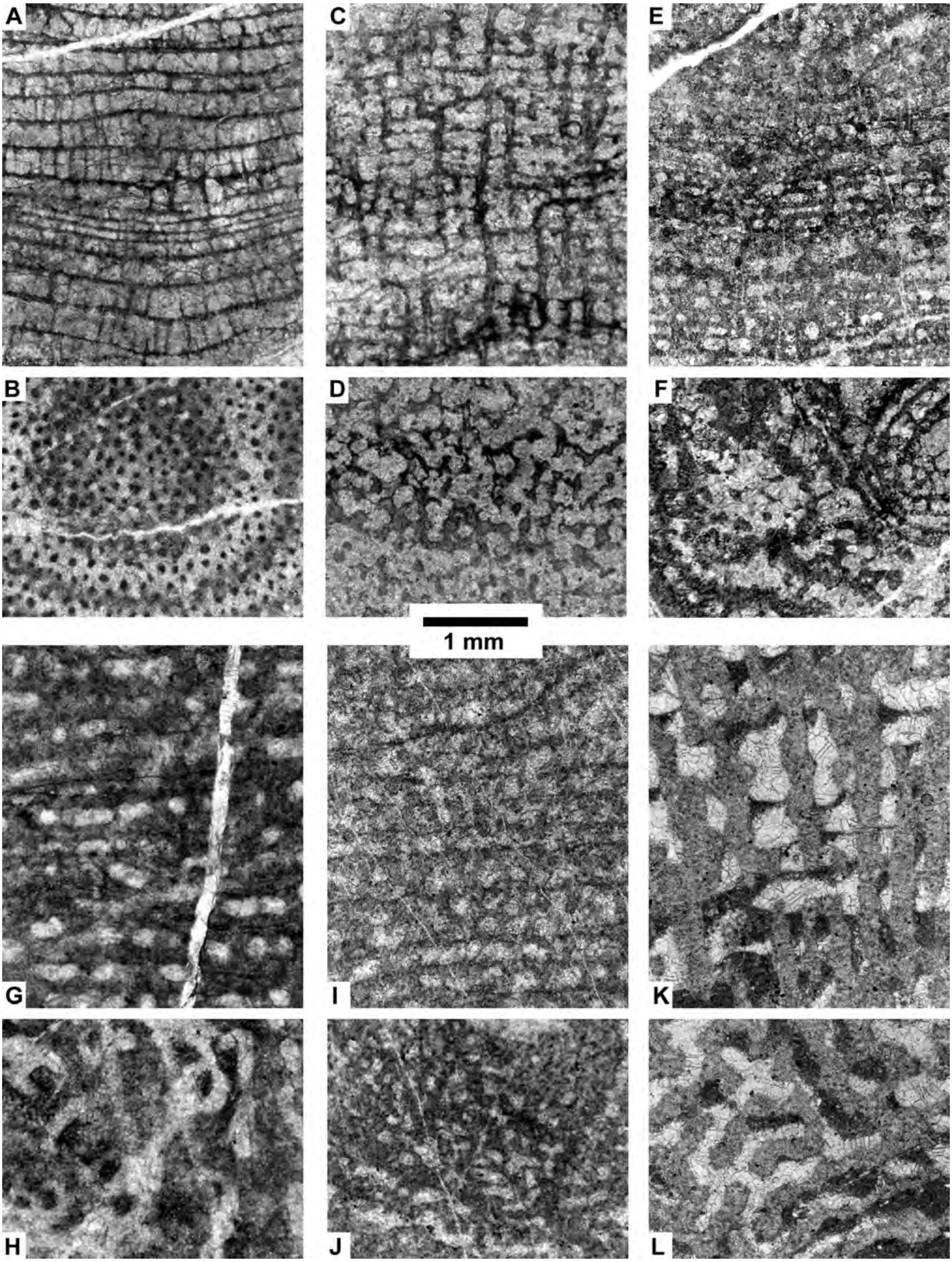

Plate 1. A-B: *Nexililamina dipcreekensis* Mallett, 1971, Pragian of Zújar, DPM-00276/Z18, (A) longitudinal section, (B) tangential section. C-D: *Plectostroma altum* (Ripper, 1933), Pragian of Zújar, DPM-00276/Z14, (C) longitudinal section, (D) tangential section. E-F: *Stictostroma gorriense* Stearn, 1995, Pragian of Zújar, DPM-00276/Z23, (E) longitudinal section, (F) tangential section. G-H: *Stictostroma nunavutense* Prosh & Stearn, 1996, Pragian of Zújar, DPM-00276/ZE18, (G) longitudinal section, (H) tangential section. I-J: *Pseudotrupetostroma* cf. *pellucida* (Javorskij, 1955), Pragian of Zújar, DPM-00276/Z3, (I) longitudinal section, (J) tangential section. K-L: *Syringostromella zintchenkovi* (Chalfina, 1960), Pragian of Zújar, DPM-00276/ZE11, (K) longitudinal section, (L) tangential section. Scale bar is 1 mm.

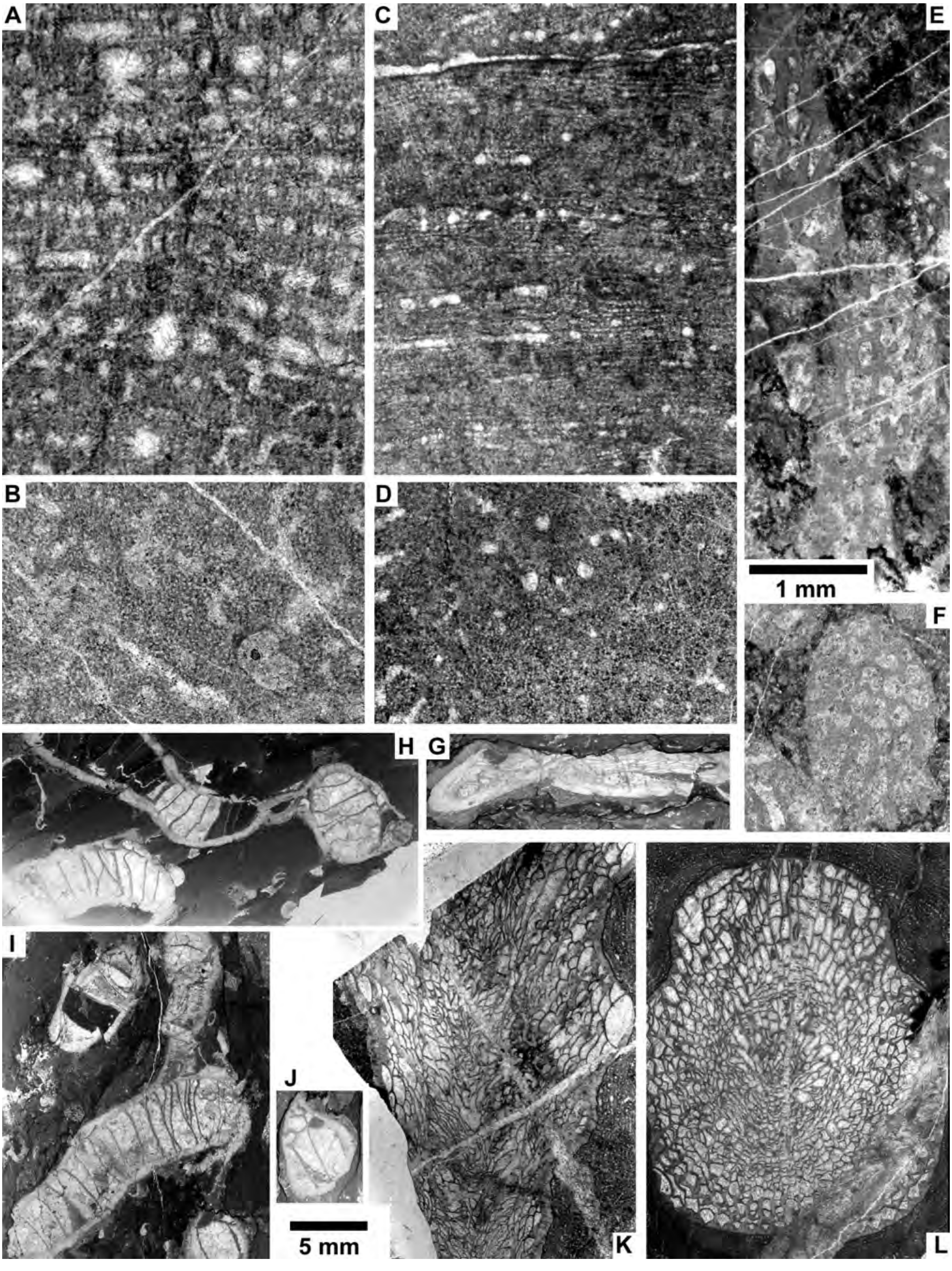

Plate 2. A-B: *Habrostroma centrotum* (Girty, 1895), Pragian of Zújar, DPM-00276/Z10, (A) longitudinal section, (B) tangential section. C-D: *Coenostroma* aff. *pustulifera* (Winchell, 1867), Pragian of Zújar, DPM-00276/Z33, (C) longitudinal section, (D) tangential section. E-F: *Amphipora* sp., Pragian of Zújar, DPM-00276/ZE13. G: Auloporid tabulate coral *Remesia koneprusiana* Galle, Hladil & May, 1999, Pragian of Zújar, longitudinal section, DPM-00276/Z34. H-J: *Joachimastraea barrandei* Galle, Hladil & May, 1999, Pragian of Zújar, DPM-00276/Z35, (H-I) longitudinal and transverse sections, (J) transverse section. K-L: *Grypophyllum jenkinsi* (Strusz, 1966), Pragian of Zújar, DPM-00276/Z24, (K) longitudinal section, (L) transverse section. Scale bar is 1 mm for A-F and 5 mm for G-L.

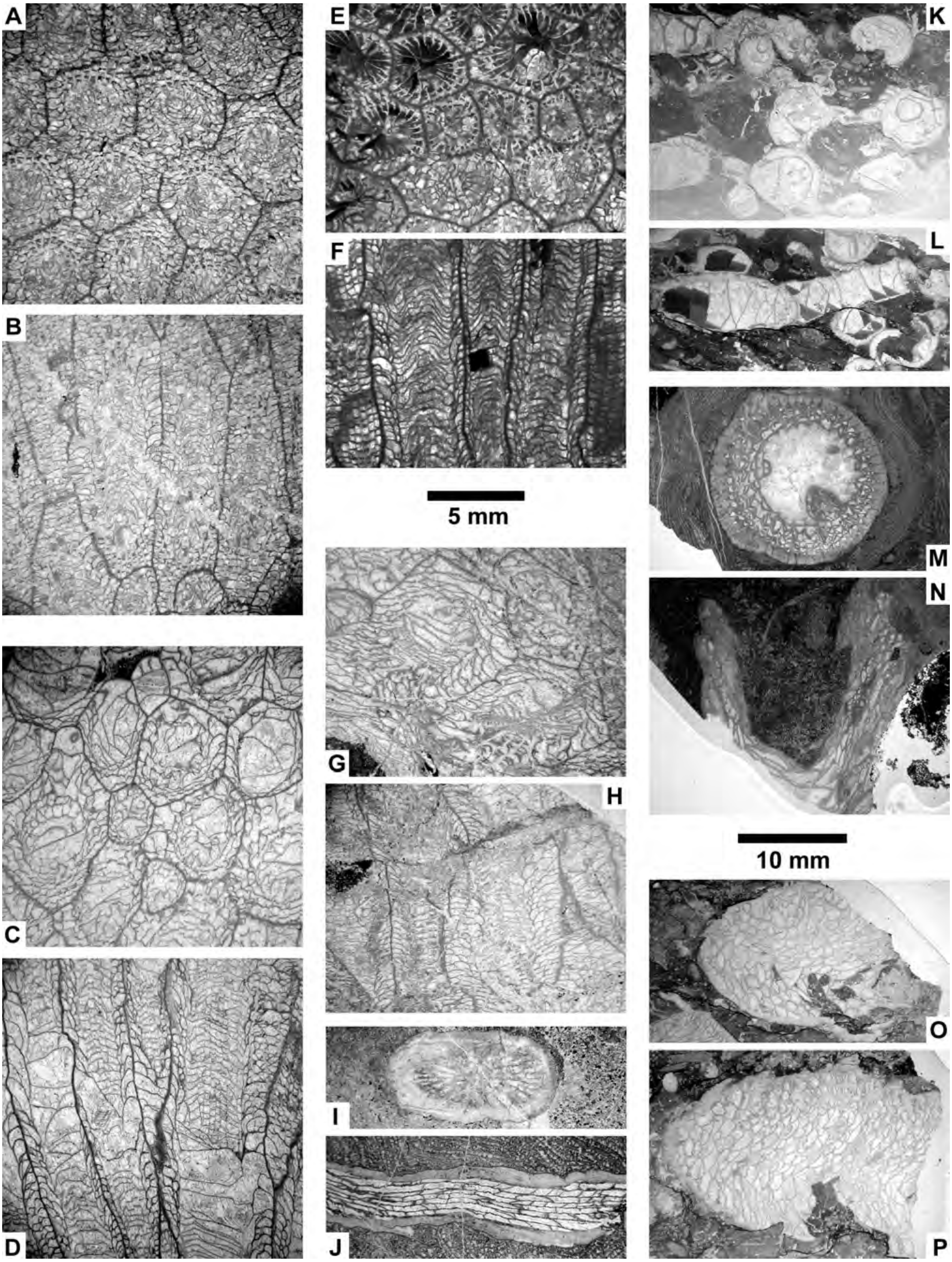

Plate 3. A-B: *Martinophyllum ornatum soraufi* (Rodríguez García, 1978), Pragian of Zújar, DPM-00276/Z31, (A) transverse section, (B) longitudinal section. C-D: *Martinophyllum miriamae* n. sp., holotype, Pragian of Zújar, DPM-00276/ZE10, (C) transverse section, (D) longitudinal section. E-F: *Martinophyllum ornatum soraufi* (Rodríguez García, 1978), holotype, Pragian of Peñon Cortado, V24/7, (E) transverse section, (F) longitudinal section. G-H: *Martinophyllum miriamae* n. sp., paratype, Pragian of Zújar, DPM-00276/ZE6, (G) transverse section, (H) longitudinal section. I-J: *Loyolophyllum (Fasciloyolopyllum) qinlingensis* (Cao in Cao et al., 1983), Pragian of Zújar, DPM-00276/Z16, (I) transverse section, (J) longitudinal section. K-L: *Joachimastraea barrandei* Galle, Hladil & May, 1999, Pragian of Peñon Cortado, PCR-14, (K) transverse sections, (L) longitudinal section. M-N: *Chostophyllum* ex gr. *gregorii* (Etheridge in Jack & Etheridge 1892), Pragian of Zújar, DPM-00276/Z18, (M) transverse section, (N) longitudinal section. O-P: *Rhizophyllum* ex gr. *bohemicum* Počta, 1902, Pragian of Zújar, DPM-00276/Z34, (O) transverse section, (P) longitudinal section. Scale bar is 5 mm for A-J and 10 mm for K-P.

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Same taxonomic name, different species: a threat to stromatoporoid biodiversity research

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ABSTRACT. Taxonomic inconsistencies between two published collections on Devonian stromatoporoids were examined. The studied collections contain stromatoporoids sampled from the Middle and Upper Devonian from the Ardennes (collection by Lecompte) and the Holy Cross Mountains (collection by Kaźmierczak). The study was limited to stromatoporoid species that were assigned to the order Stromatoporellida. At least eight species which were described from the Devonian of both the Ardennes and the Holy Cross Mountains should be revised: *F. ruedemanni*, *H. crassum*, *H. porosum*, *H. perseptatum*, *S. lensiforme*, *S. socialis*, *T. laceratum*, *T. pingue*. Specimens that were assigned to *C. damnoniensis*, *C. spissa*, *H. episcopale*, *H. schlueteri*, *P. cellulosum* and *S. huronense* do not need to be revised. The inconsistencies may severely influence the outcome of palaeogeographic and biodiversity studies, since the error in not distributed randomly among stratigraphic intervals and it affects classification at the genus-level.

KEYWORDS: stromatoporoids, Devonian, palaeobiodiversity, Stromatoporellida.

1. Introduction

Recently developed global palaeontological databases allow researchers to analyze biodiversity patterns, extinction rates and to generate diversity curves. The data compiled into these databases are also used for global palaeogeographic studies. Projects such as the Paleobiology Database (http://paleodb.org/) provide instant access to occurrence and taxonomic data. Paleomapping tools are also available, allowing for plotting the locality palaeocoordinates on the palaeogeographic maps. In addition, changes in taxonomic nomenclature of fossil organisms are much easier to follow.

Unfortunately, the improvement in the availability of palaeontological data is accompanied by the decline in taxonomic studies. This general tendency is also observed in the case of Palaeozoic stromatoporoids. Some collections have not been revised for a period of over forty years. This suggests that at least some species diagnoses require further examination and revision. Moreover, many collections were studied and described in detail in times when no scientific databases existed. The access to scientific works was thus limited and the availability of palaeontological data was hampered by the limitations of the traditional printed media. In addition, the scientific community of the former Soviet bloc was further isolated from research work done in other countries. As a result, some species received taxonomic names different from those used in other countries (Ruban, 2011). Thus, it is likely that some specimens described by many authors under the different names indeed belong to the same species; and, conversely, that different species or genera were conglomerated under the same taxonomic name. Such ambiguous identifications can severely affect the biodiversity studies and result in incorrect conclusions.

Taxonomic inconsistencies between two published studies (Lecompte 1951, 1952 and Kaźmierczak, 1971) are discussed. Both collections include the Middle and Upper Devonian stromatoporoids, which were sampled from the Ardennes and the Holy Cross Mountains. The collections have not been substantially revised since 1971. However, the taxonomic position of some species established by Lecompte (1951, 1952) was changed by subsequent workers (eg. Stearn, 1966; Kaźmierczak, 1971; Mistiaen, 1980, 1988; May, 2005; Salerno, 2008). At least seven species described by Lecompte and Kaźmierczak are represented in the Paleobiology Database.

2. Material

Specimens used in this study, taken from collections made by Lecompte (1951, 1952) and Kaźmierczak (1971), were supplemented by specimens collected by the author. Stromatoporoids described by Lecompte are from the Ardennes (Belgium), while others were sampled in the Holy Cross Mountains (Poland). All specimens are Devonian (Givetian and Frasnian) in age. The collections studied are respectively deposited in the Royal Belgian Institute of Natural Sciences, Brussels, Belgium and in the Institute of Paleobiology, Polish Academy of Sciences, Warsaw, Poland.

The present study is limited to stromatoporoid species assigned by Lecompte and/or Kaźmierczak to the genera belonging to the order Stromatoporellida, established as an independent order by Stearn (1980), nearly ten years after the study by Kaźmierczak was published. It is very likely that taxonomic inconsistencies arose in clades that were not precisely defined when the studied collections were assembled; the order Stromatoporellida was therefore used as a test group. In total, 133 specimens representing 20 species were personally investigated by the author.

3. Systematic Palaeontology

A short morphological comparison of specimens assigned to the same species by Lecompte and Kaźmierczak is summarized in Table 1. Each of at least eight species of Stromatoporellida which were described from the Devonian of both the Ardennes and the Holy Cross Mountains should be revised and split into two different taxa. Skeletal features that were considered by the previous authors (Stearn et al., 1999; Stearn, 2011) to be of taxonomic value vary significantly, suggesting that specimens described under the same taxonomic name indeed belong to different species or even genera. The morphological differences between specimens from the Ardennes and the Holy Cross Mountains, assigned to the same species, are discussed below. The taxa that do not need a revision (differences between specimens are insignificant) are omitted. The chronostratigraphic ranges for all species were estimated after Racki (1993) and Bultynck & Dejonghe (2001).

Order Stromatoporida Stearn, 1980
Family Ferestromatoporidae Khromych, 1969

Genus *Ferestromatopora* Yavorsky, 1955

Ferestromatopora ruedemanni (Lecompte, 1952)
(Plate 1 A-F)

1952 *Trupetostroma ruedemanni* Lecompte: 243-247, pl. 39, figs 4-5, pl. 40, fig. 3.
non 1952 *Trupetostroma ruedemanni* Lecompte: 243-247, pl. 40, figs 1-2.
non 1971 *Ferestromatopora talovensis* Yavorsky 1955; Kaźmierczak: 102-103, pl. 25, fig. 2.
non 1971 *Ferestromatopora krupiennikovi* Yavorsky 1955; Kaźmierczak: 103-104, pl. 25, fig. 3.

Material. Type specimens of *F. ruedemanni* (5281, 17120, 17173, 17184, 17274, 17462, 17687). Specimens not assigned to *F. ruedemanni*: type specimens 17092, 17318 and 17491 from the collection by Lecompte; specimens ST1 44 and 45, ST1 47, 48 and 49, ST1 141 and 142 from the collection by Kaźmierczak;

specimen UAM DEB 11 from the Givetian of Dębnik, southern Poland.

Emended diagnosis. Coenostromes densely spaced (2-4 per 1 mm); coenosteles coarsely cellular, straight or oblique, densely spaced (5 per 1 mm), 0.1-0.2 mm in diameter; astrorhizae present; astrorhizal canals between 0.4 and 0.5 mm in length; mamelons absent; intraskeletal variation significant.

Discussion. *F. ruedemanni* was moved by Galloway & St. Jean (1957) and Kaźmierczak (1971) to the order Stromatoporida. The structure dominated by coenostromes and coenosteles forming amalgamate network supports this conclusion. However, the presence of coarsely cellular pillars (Plate 1 A, lower part of the microphotograph) casts doubts on the assignment to the genus *Ferestromatopora*. According to Salerno (2008) *F. ruedemanni* should be moved to the genus *Pseudotrupetostroma*. Type specimens of *F. ruedemanni* differ significantly from one another suggesting that they belong to at least two species (Plate 1 A and C). The taxonomic decision of Kaźmierczak (1971), who splitted *F. ruedemanni* into three species (*F. ruedemanni*, *F. talovensis* and *F. krupiennikovi*), was therefore justified.

Specimens assigned by Kaźmierczak (1971) to the species *F. talovensis* and type specimens 17092, 17318 and 17491 show coarsely cellular coenosteles and/or microlaminae, diagnostic for the genus *Pseudotrupetostroma*. The structure is

Species under study	**Differences (S = significant, M = minor) between the specimens from collections by Lecompte (Ardennes) and Kaźmierczak (Poland)**		
	Ardennes	**Poland**	**Differ.**
Clathrocoilona damnoniensis (Nicholson, 1886) revised by Salerno (2008)	laminae thick (mean thickness 0.2 mm)	laminae of variable thickness	M
	foramina uncommon	foramina locally common	M
	autotubes present	autotubes absent	M
	intraskeletal variation low	intraskeletal variation significant	M
Clathrocoilona spissa (Lecompte, 1951) revised by Zukalová (1971)	in loose parts of the skeleton laminae thin, continuous	in loose parts of the skeleton laminae are reduced	M
	foramina absent	large foramina in places	M
	pillars thin, short, confined to a single interlaminar space	pillars thicker than laminae, short, confined to an interlaminar space or longer, intersecting 2-3 galleries	M
Ferestromatopora ruedemanni (Lecompte, 1952); synonymized by Kaźmierczak (1971) with *Ferestromatopora krupiennikovi* and *F. talovensis*	densely spaced paralaminae, reduced in places	densely spaced, continuous paralaminae	M
	coenosteles coarsely cellular, straight or oblique	coenosteles coarsely cellular, mostly straight	S
	structure dominated by coenosteles	structure dominated by paralaminae	S
	cassiculate networks build up of oblique structural elements in type specimen 17184 (supporting Kaźmierczak's synonymy)	cassiculate networks less prominent than in specimens from the Ardennes	S
	astrorhizae and astrorhizal canals present	astrorhizae rare or absent	S
	intraskeletal variation significant	intraskeletal variation medium to high (specimens from the Holy Cross Mountains belong to *Pseudotrupetostroma*)	M
Hermatoporella crassum (Lecompte, 1952)	microlaminae thin, continuous, locally replaced by dissepiments	microlaminae thicker, commonly reduced	S
	coenosteles thick, straight, superposed	coenosteles thinner than in specimen from the Ardennes, straight, superposed	S
	autotubes rare	autotubes numerous	S
Hermatoporella porosum (Lecompte, 1952); synonymized by Kaźmierczak (1971) with *Hermatoporella maillieuxi* (Lecompte, 1952) revised by May (2005)	microlaminae more prominent than in specimens from the Holy Cross Mountains	microlaminae locally reduced	S
	coenosteles straight, cellular in places	coenosteles coarsely cellular	S
	coenosteles intersected by microlaminae	coenosteles only locally intersected by microlaminae	S
	peripheral vacuoles apparent	peripheral vacuoles less apparent	S
	dissepiments present	dissepiments present, less common	M
	coenotubes common	coenotubes densely spaced, more prominent	S
	autotubes irregular, small	autotubes oval, large, more common than in specimen from the Ardennes (specimens from the Holy Cross Mountains belong to *Pseudotrupetostroma*)	S
Hermatostroma episcopale Nicholson, 1892	laminae continuous, reduced in places	laminae locally reduced	M
	dissepiments locally common	laminae pierced by foramina or replaced by dissepiments	M
	foramina present	foramina more common than in type specimen	M
Hermatostroma perseptatum Lecompte, 1952	laminae well developed	laminae reduced, replaced by dissepiments	S
	coenosteles straight, systematically superposed	coenosteles straight	M
	coenosteles forming a grid with the laminae	coenosteles irregular or oblique in longitudinal sections	S
	coenosteles oval or irregular in transverse thin section	coenosteles form amalgamated networks in transverse thin section	S
	peripheral membranes present	peripheral membranes well developed, more prominent	S
Hermatostroma schlueteri Nicholson, 1886	laminae prominent	laminae less prominent than in specimens from the Ardennes	M
	foramina absent	laminae locally pierced by foramina	M

Species under study	**Differences (S = significant, M = minor) between the specimens from collections by Lecompte (Ardennes) and Kaźmierczak (Poland)**		
	Ardennes	**Poland**	**Differ.**
Pseudotrupetostroma cellulosum (Lecompte, 1952) revised by Salerno (2008)	coarsely cellular structure of pillars	coarsely cellular structure of pillars less visible than in specimens from the Ardennes	M
Stictostroma lensiforme (Lecompte, 1951) revised by Galloway & St. Jean (1957)	laminae compact or cellular, darker than pillars, continuous, locally pierced by foramina, branching dichotomously, locally intersecting pillars	laminae cellular, usually not darker than pillars, foramina rare, dichotomous branchings absent	S
	pillars straight, short and superposed systematically	pillars short, confined to an interlaminar space, superposed	M
	pillars thicker than laminae	pillars of thickness comparable to laminae	S
	galleries angular or rounded, large (up to 0.4 mm in diameter)	galleries angular	M
	autotubes scattered within the skeleton	autotubes absent	S
Stictostroma socialis (Nicholson, 1892) Note: *Stictostroma socialis sensu* Kaźmierczak (1971) was synonimized by Salerno (2008) with *Stictostroma laminatum* (Bargatzky, 1881); the present study supports this concept	autotubes absent	autotubes present (as in *Stictostroma laminatum*)	S
	intraskeletal variation low	intraskeletal variation significant	M
Stromatoporella huronense (Parks, 1936); synonymized by Kaźmierczak (1971) with *Clathrocoilona saginata* (Lecompte, 1951) revised by Stearn et al. (1999)	laminae of variable thickness (> 0.1 mm), tripartite in places	laminae thin (< 0.1 mm), locally tripartite	M
	foramina rare	foramina common	M
Trupetostroma laceratum Lecompte, 1952; synonymized by Kaźmierczak (1971) with *T. tenuilamellatum* and *T. bassleri*	laminae continuous, reduced in places	laminae reduced, locally replaced by numerous dissepiments	S
	pillars short, superposed, forming a grid with the laminae	coarsely cellular pillars, straight or oblique, short, superposed	S
	autotubes common	autotubes numerous, more common than in specimen from the Ardennes	S
	dissepiments locally common	dissepiments common	M
	astrorhizae and astrorhizal canals present	astrorhizae rare or absent (specimen from the Holy Cross Mountains belongs to *Pseudotrupetostroma*)	M
Trupetostroma pingue Lecompte, 1952 Note: in places, type specimens show diagnostic features of the genus *Pseudotrupetostroma* (Stearn et al., 1999; Stearn, 2011).	laminae thin, continuous and compact or thick, pierced by foramina and tripartite, with lighter axial zone	laminae of variable thickness, darker than pillars, continuous, locally tripartite or coarsely cellular	S
	foramina common in dense parts of skeleton	foramina rare	M
	coenosteles compact, cellular or coarsely cellular, superposed systematically	coarsely cellular structure of coenosteles, diagnostic for genus *Pseudotrupetostroma*	S
	autotubes common, filled with dissepiments	autotubes absent	S
	dissepiments common	dissepiments absent	S
	astrorhizae and astrorhizal canals present in dense parts of skeleton	astrorhizae absent	S
	intraskeletal variation significant	intraskeletal variation low (specimens from the Holy Cross Mountains belong to *Pseudotrupetostroma*)	S

Table 1. Short morphological comparison of specimens assigned to the same species by Lecompte (1951, 1952) and Kaźmierczak (1971).

dominated by coenosteles (specimens from the Ardennes) or by paralaminae (specimens from the Holy Cross Mountains). The type specimens of *F. ruedemanni* differ significantly from *F. krupiennikovi*, showing densely spaced paralaminae (2-4 per 1 mm; Plate 1 C, upper part of the microphotograph). This suggests that specimens described by Kaźmierczak (1971) should not be synonymized with any species recognized by Lecompte (1951, 1952).

Distribution. Ardennes: middle to late Givetian, middle Frasnian.

Order Stromatoporellida Stearn, 1980
Family Stromatoporellidae Lecompte, 1951

Genus *Stictostroma* Parks, 1936

Stictostroma lensiforme (Lecompte, 1951)
(Plate 1 G-J)

1951 *Syringostroma lensiforme* Lecompte: 211-212, pl. 34, figs 5, pl. 35, fig. 1.
non 1971 *Stictostroma lensiforme* Lecompte 1951; Kaźmierczak: 85-86, pl. 17, fig. 1.

Material. Holotype and a paratype (4802 and 5134 from the collection by Lecompte). Specimens not assigned to *S. lensiforme*: 15 specimens from the collection by Kaźmierczak (ST1-145 to ST1-152, ST1-199 to ST1-205); specimens UAM ZEL 1 and UAM ZEL 7 from Zelejowa Góra (Holy Cross Mountains).

Emended diagnosis. Laminae thin (thickness < 0.1 mm), compact or cellular, continuous, locally pierced by foramina, branching dichotomously; pillars straight, thicker than laminae, short and superposed systematically, cellular; ring pillars absent; galleries angular or rounded; numerous large (up to 0.4 mm in diameter) autotubes scattered within the skeleton.

Discussion. Stromatoporoids assigned by Kaźmierczak to. *S. lensiformis* differ significantly from the type specimens (Table 1). Those specimens should be therefore moved to other species. Moreover, the differences presumably affect features that are of taxonomic value at the genus level. Specimens the Holy Cross Mountains reveal diagnostic characteristics of the genus *Stictostroma*, although pillars are superposed in some places (Plate 1 J). Specimens from the Ardennes need to be revised. Their relationship to the genus *Stictostroma* remains unclear since the microlaminae intersecting pillars are visible in places (Plate 1 G, upper part of the photo). It is likely that the inconsistencies noted above affect taxonomic assignments at the species and at the genus level.

Kaźmierczak (1971) synonymized *S. lensiforme* and *Habrostroma percanaliculata* (Lecompte, 1951). However, the type specimen of *H. percanaliculata* shows prominent coenostromes and coenosteles forming an irregular network in tangential thin section, confirming that these two species belong to different genera and orders.

Distribution. Ardennes: early Givetian to middle Frasnian.

Family Trupetostromatidae Germovsek, 1954

Genus *Hermatoporella* Khromych, 1969

Hermatoporella crassum (Lecompte, 1952)
(Plate 2 A-D)

1952 *Trupetostroma crassum* Lecompte: 239-240, pl. 43, fig. 4, pl. 44, fig. 1.
non 1971 *Hermatostroma crassum* Lecompte 1952; Kaźmierczak: 126-127, pl. 35, fig. 3.

Material. Holotype (5270). Specimens not assigned to *H. crassum*: four specimens from the collection by Kaźmierczak (ST1-115, ST1-116, ST1-117, ST1-130); specimens UAM STO 41-43 from Stokówka (Holy Cross Mountains).

Emended diagnosis. Thin (thickness < 0.05 mm) microlaminae, continuous, locally replaced by dissepiments, straight; coenosteles straight, superposed systematically, thick (thickness > 0.15 mm), peripheral vacuoles absent; autotubes rare, oval to irregular, visible in central parts of mamelons; dissepiments common; microstructure compact to cellular.

Discussion. Specimens described by Kaźmierczak (1971) differ significantly from the holotype. Microlaminae are commonly reduced. Coenotubes are numerous and highly variable in shape, ranging from oval to irregular and meandering (Plate 2 C, lower part of the photograph). The holotype of *H. crassum* reveals straight coenotubes, crossed by well developed microlaminae and dissepiments (Plate 2 A). The differences in features of taxonomic importance suggest that the specimens from the Holy Cross Mountains should not be assigned to *H. crassum*. Lecompte (1952) did not describe any specimens that resemble those studied by Kaźmierczak (1971). These specimens should be thus moved to other species within the genus *Hermatoporella*.

Distribution. Ardennes: early Givetian to middle Frasnian.

Hermatoporella porosum (Lecompte, 1952)
(Plate 2 E-F)

1952 *Trupetostroma porosum* Lecompte: 236-237, pl. 42, fig. 3, pl. 43, fig. 1.
non 1952 *Trupetostroma maillieuxi* Lecompte: 237-239, pl. 43, figs 2-3.
non 1971 *Hermatostroma porosum* Lecompte 1952; Kaźmierczak: 123-124, pl. 8, fig. 5, pl. 34, fig. 1.

Material. Type specimen of *H. porosum* (5179 from the collection by Lecompte). Specimens not assigned to *H. porosum*; type specimens of *H. maillieuxi* (5760 and 17444 from the collection by Lecompte); four specimens from the collection by Kaźmierczak (ST1-111, ST1-112, ST1-128, ST1-129).

Emended diagnosis. Thin (thickness < 0.1 mm) microlaminae straight, reduced, replaced by dissepiments; coenosteles straight or oblique, short, superposed, thick (thickness > 0.15 mm), peripheral vacuoles numerous; autotubes common, irregular, filled with dissepiments in places; microstructure cellular.

Discussion. Specimens described by Kaźmierczak (1971) only in places reveal the diagnostic characteristics of the genus *Hermatoporella*: microlaminae intersecting coenosteles and superposed coenosteles with peripheral vacuoles (Plate 2 E). Most vertical thin sections show coarsely cellular coenosteles (Kaźmierczak, 1971, pl. 8, fig. 5) with numerous vacuoles (Kaźmierczak, 1971, pl. 34, fig. 1) which are less common in the type specimen. The cellular structure of pillars and laminae reveals similarity to the genus *Pseudotrupetostroma*. In addition, laminae are reduced and replaced by numerous foramina. Large, up to 1.0 mm in diameter, oval galleries, interconnected through foramina are common in specimens from the Holy Cross Mountains; however, in the type specimen such voids are smaller (less than 0.6 mm in diameter). Specimens described by Kaźmierczak (1971) do not belong to genus *Hermatoporella*; they reveal the diagnostic features of *Pseudotrupetostroma*. Those specimens therefore should not be assigned to *H. porosum*.

Kaźmierczak (1971) synonymized *H. porosum* with *Hermatoporella maillieuxi* (Lecompte, 1952). Both species are similar, differing only in thickness and spacing of coenosteles. Peripheral vacuoles are better developed in *H. maillieuxi* than in *H. porosum*. Specimens from the Holy Cross Mountains do not resemble type specimen of *H. maillieuxi* since they show the diagnostic features of *Pseudotrupetostroma,* their microlaminae are more reduced, coenosteles are thinner (mean diameter 0.2 mm) and peripheral vacuoles are more prominent. These specimens should not be therefore included in the same species, although Salerno (2008) suggested that specimens from the collection by Kaźmierczak are closely related to *H. maillieuxi*.

Distribution. Ardennes: middle to late Givetian.

Genus *Hermatostroma* Nicholson, 1886

Hermatostroma perseptatum Lecompte, 1952
(Plate 2 G-H)

1952 *Hermatostroma perseptatum* Lecompte: 251, pl. 45, fig. 2.
non 1971 *Hermatostroma perseptatum* Lecompte 1952; Kaźmierczak: 124, pl. 8, fig. 6, pl. 34, fig. 2.

Material. Holotype 17175. Not assigned to *H. perseptatum*: two specimens from the collection by Kaźmierczak (ST1-131, ST1-138).

Emended diagnosis. Laminae well developed, regularly spaced (2-3 per 1 mm), variable in thickness; coenosteles straight, systematically superposed, forming a grid with the laminae, densely spaced (3-4 per 1 mm); peripheral membranes present; dissepiments common; astrorhizae and astrorhizal canals present.

Discussion. Specimens ST1-131 and ST1-138 differ from the holotype of *H. perseptatum* in having reduced laminae, commonly replaced by dissepiments. Coenosteles are long (up to 12 interlaminar spaces) and straight, but less regular than in the type specimen. Peripheral membranes are more prominent than in the holotype. Differences between specimens from the Ardennes and the Holy Cross Mountains are similar to those described for *Hermatoporella crassum*. The species of *Hermatostroma* and *Hermatoporella* from the Devonian of southern Poland reveal reduced laminae, irregular coenotubes and well developed peripheral vacuoles. Specimens described by Kaźmierczak (1971) clearly belong to the genus *Hermatostroma*. However, they should not be synonymized with any species described by Lecompte (1952).

Distribution. Ardennes: middle to late Givetian.

Genus *Trupetostroma* Parks, 1936

Trupetostroma laceratum Lecompte, 1952

(Plate 2 I-J)

1952 *Trupetostroma laceratum* Lecompte: 228-230, pl. 38, fig. 1.

non 1952 *Trupetostroma tenuilamellatum* Lecompte: 223-225, pl. 36, figs 1-5.

1952 *Trupetostroma bassleri* Lecompte: 227-228, pl. 37, fig. 3.

non 1971 *Trupetostroma laceratum* Lecompte 1952; Kaźmierczak: 113-114, pl. 30, fig. 1.

Material. Holotype of *T. laceratum* (5170). Specimens not assigned to *T. laceratum*: holotype of *T. bassleri* (7260); type specimens of *T. tenuilamellatum* (17277, 17021, 17026, 17077, 17147, 17439); specimen ST1-132 (Kaźmierczak, 1971) from the Holy Cross Mountains.

Emended diagnosis. Laminae continuous, reduced in places, straight or irregular, cellular, densely spaced (4-5 per 1 mm), thin (<0.15 mm); pillars short, systematically superposed, straight, cellular, forming a grid with the laminae, variable in thickness (0.1-0.25 mm), round, oval or irregular in tangential thin section; dissepiments common in places; astrorhizae and astrorhizal canals present.

Discussion. Specimen from the Holy Cross Mountains reveals thick (up to 0.3 mm in diameter), coarsely cellular pillars. Thus, it differs significantly from the type specimen of *T. laceratum* and shows the characteristic features of the genus *Pseudotrupetostroma*. Taxonomic inconsistencies affect not only species but also genera, although Salerno (2008) suggested that specimen described by Lecompte (1952) also belongs to the genus *Pseudostrupetostroma*.

Kaźmierczak (1971) synonymized *T. laceratum* with *T. tenuilamellatum* Lecompte, 1952 and *T. bassleri* Lecompte, 1952. However, the type specimens of *T. tenuilamellatum* show features that are diagnostic for the genus *Hermatoporella* (laminae intersecting coenosteles, coenosteles forming a labyrinthine network in tangential thin sections). The taxonomic position of *T. bassleri* is unclear; Salerno (2008) suggested moving it to the genus *Pseudotrupetostroma*.

Distribution. Ardennes: middle Givetian to middle Frasnian.

Trupetostroma pingue Lecompte, 1952

(Plate 3 A-D)

1952 *Trupetostroma pingue* Lecompte: 230-231, pl. 38, fig. 2, pl. 29, figs 1-3.

non 1971 *Trupetostroma pingue* Lecompte 1952; Kaźmierczak: 113, pl. 29, fig. 1, pl. 30, fig. 2.

Material. Type specimens 17199, 17020, 17187 and 17256. Specimens not assigned to *T. pingue*: specimen ST1-94 from the collection by Kaźmierczak; specimen UAM SOG 18 from Sowie Górki (the Holy Cross Mountains).

Emended diagnosis. Laminae thin, continuous and compact or thick, planar or undulated, densely spaced (4-6 per 1 mm), pierced by foramina and tripartite, with lighter axial zone; foramina common in dense parts of skeleton; autotubes common, filled with dissepiments; coenosteles compact or cellular, superposed systematically, oval or forming a labyrinthine network in tangential thin section, densely spaced (5-6 per 1 mm); astrorhizae present in dense parts of skeleton; astrorhizal canals well developed; intraskeletal variation significant.

Discussion. Specimen ST1-94, studied by Kaźmierczak (1971), shows coarsely cellular structure, diagnostic for genus *Pseudotrupetostroma*. However, the specimens from the collection by Lecompte also show cellular coenosteles in places (Plate 3 A, uppermost and lowermost parts of the microphotograph), which are forming a labyrinthine network in tangential thin sections (Plate 3 B). Thus the type specimens show in places diagnostic features of the genus *Pseudotrupetostroma* (Stearn et al., 1999; Stearn, 2011).

Distribution. Ardennes: middle to late Givetian, middle Frasnian.

4. General discussion

The inconsistencies observed in the present study affect mainly species that were established by Lecompte (1952). *Pseudotrupetostroma cellulosum* is an exception, however the dimensions of the skeletal elements vary between two studied collections (see Plate 3 E-H). Specimens that belong to species described earlier are strikingly similar to one another. The inconsistencies affect mainly species from the Givetian of the Holy Cross Mountains; species that were described both from the Frasnian of the Ardennes and the Holy Cross Mountains do not need to be revised, except for *Ferestromatopora ruedemanni*, *Hermatoporella crassum* and *Trupetostroma pingue*. Four out of eight taxa that reveal significant differences between the specimens from both studied collections (*Hermatoporella porosum*, *Hermatostroma perseptatum*, *Trupetostroma laceratum* and *Trupetostroma pingue*) were sampled by Kaźmierczak (1971) exclusively from the Early to Middle Givetian *Stringocephalus* Beds; three of them (*Hermatoporella porosum*, *Hermatostroma perseptatum*, *Trupetostroma laceratum*) were found at a single locality in Jurkowice-Budy quarry in the eastern part of the Holy Cross Mountains. The taxonomic inconsistencies are not therefore distributed randomly among stratigraphic intervals. A significant loss of the endemicity occurred at the end of the Givetian since only two Givetian representatives of the order Stromatoporellida are present in both studied collections. This supports earlier estimates of palaeobiodiversity at the global scale (Stock, 2005). In the Frasnian at least four stromatoporellid species appeared in both areas.

The present contribution shows that specimens assigned to the same species by different workers belong not only to different species, but also genera (*Stictostroma lensiforme*, *Hermatoporella porosum*, *Trupetostroma laceratum*). This can severely influence biodiversity, which is generally estimated at genus-level, considered as being more taxonomically robust (Alroy, 1996). Fortunately, if error is randomly distributed among genera and stratigraphic intervals, then the database, although rife with errors, can accurately estimate the large-scale patterns of biodiversity (eg. Adrain & Westrop, 2000). However, the present study shows that most of the species that should be revised were sampled from a single stratigraphic unit. Moreover, other studies indicate that even noisy data show periodicity that can affect biodiversity assessments (Patterson & Smith, 1987). Similar conclusions were reached by Stearn (1999), who noticed that 70% of invalid stromatoporoid genera were of Russian provenance. The taxonomic bias thus reveals clear geographical patterns. This also suggests that number of synonyms could have been increased due to limited scientific interchange between western and eastern palaeontologists.

5. Conclusions

The present study shows that at least eight stromatoporoid species described earlier from the Givetian and the Frasnian of both the Ardennes and the Holy Cross Mountains should be revised (*Ferestromatopora ruedemanni*, *Hermatoporella crassum*, *Hermatoporella porosum*, *Hermatostroma perseptatum*, *Stictostroma lensiforme*, *Stictostroma socialis*, *Trupetostroma laceratum* and *Trupetostroma pingue*). Specimens from the Holy Cross Mountains that were originally assigned to those species (Kaźmierczak, 1971) should not be synonymized with any species described by Lecompte (1951, 1952). *F. ruedemanni*, *H. porosum*, *T. laceratum* and *T. pingue* from the collection by Kaźmierczak (1971) are here assigned to the genus *Pseudotrupetostroma*. Specimens that belong to *Clathrocoilona damnoniensis*, *Clathrocoilona spissa*, *Hermatostroma episcopale*, *Hermatostroma schlueteri*, *Pseudotrupetostroma cellulosum* and *Stromatoporella huronense* do not need to be revised.

Some specimens described under the same taxonomic name indeed belong not only to different species, but also genera (*Stictostroma lensiforme*, *Hermatoporella porosum*, *Trupetostroma laceratum*). This may severely affect the outcome of palaeogeographical and palaeobiodiversity studies, which are commonly based upon supra-species level data.

The taxonomic inconsistencies are not distributed randomly among stratigraphical units. This may further affect potential biodiversity estimations. The present study and earlier observations by Stearn (1999) therefore indicate that at least some of the stromatoporoid species described from the Devonian of western and central Europe should be revised. This should be done before entering data into any global palaeontological database.

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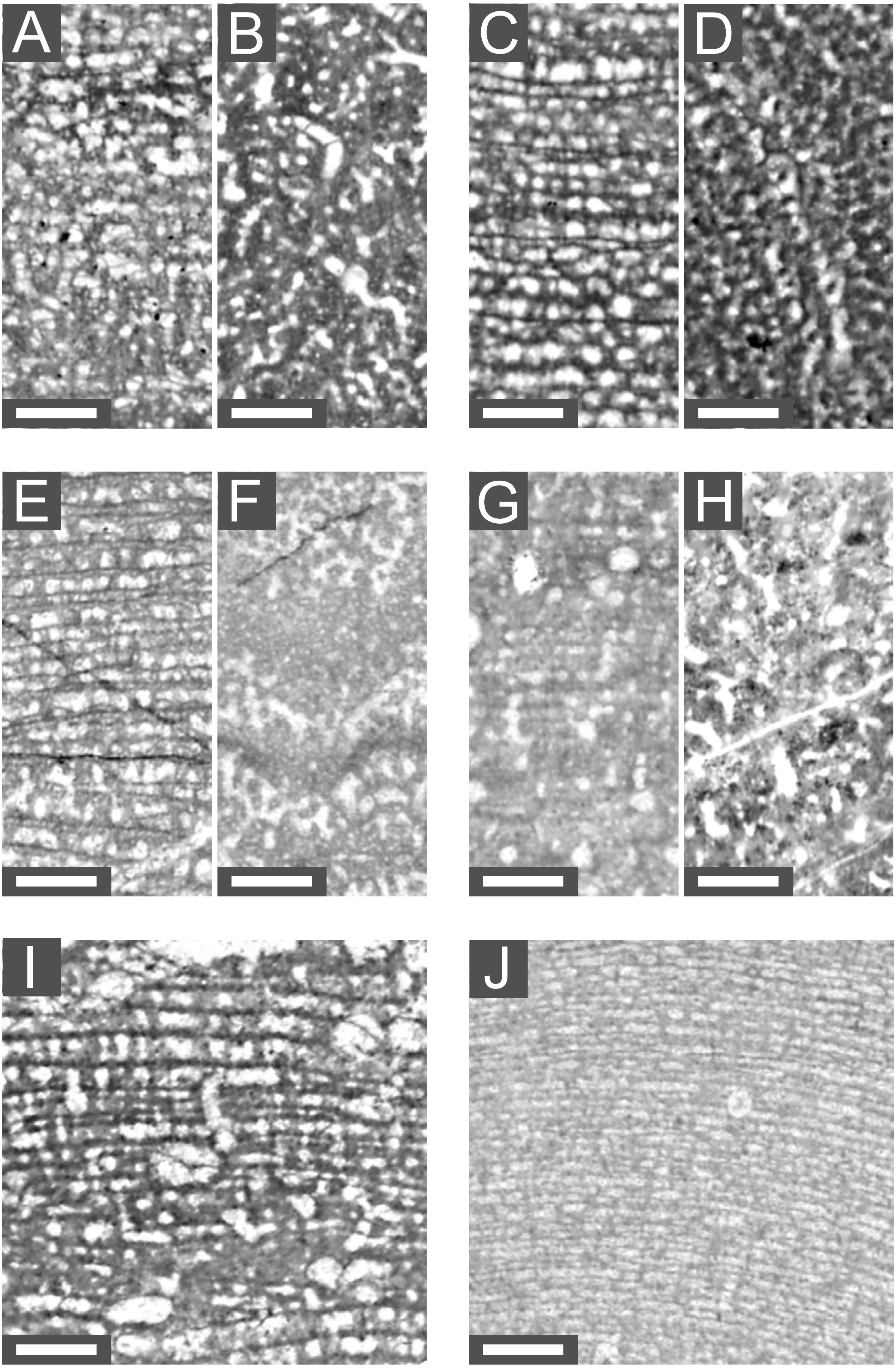

Plate 1. A-F: *Ferestromatopora ruedemanni*. G-J: *Stictostroma lensiforme*. A: Longitudinal section of the type specimen 17092 (Upper Givetian of the Ardennes), showing coarsely cellular coenosteles and microlaminae. B: Tangential section of the same specimen, with a closed network formed by coenosteles. C: Longitudinal thin section of the type specimen 17184 (Upper Givetian of the Ardennes), showing oblique skeletal elements and thin, continuous paralaminae. D: Tangential section of the same specimen. E: Specimen UAM DEB 11 from the Upper Givetian of the Dębnik Anticline, southern Poland, resembling *Ferestromatopora talovensis sensu* Kaźmierczak (1971); longitudinal thin section. F: Tangential thin section of the same specimen. G: Longitudinal thin section of the type specimen 5134. H: Tangential section of the same specimen. I: Longitudinal thin section of the same specimen, showing less dense part of the skeleton. J: Longitudinal thin section of specimen UAM ZEL 7 from Zelejowa Góra quarry, Early Frasnian of the Holy Cross Mountains. Scale bars: 1 mm.

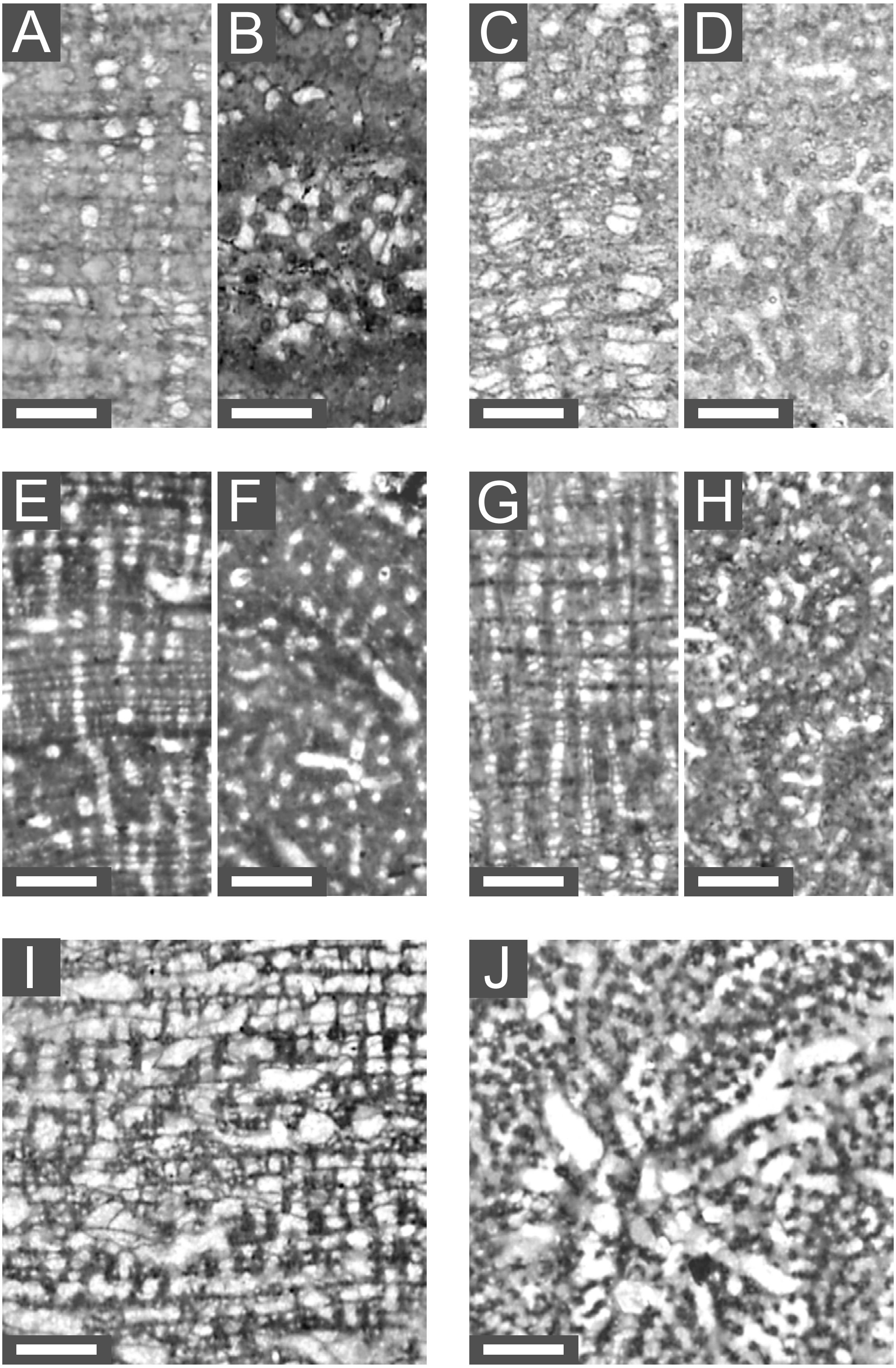

Plate 2. A-D: *Hermatoporella crassum*. E-F: *Hermatoporella porosum*. G-H: *Hermatostroma perseptatum*. I-J: *Trupetostroma laceratum*. A: Longitudinal thin section of the type specimen 5270. B: Tangential section of the same specimen. C: Longitudinal section of the specimen UAM STO 43 from Stokówka (Upper Givetian of the Holy Cross Mountains). D: Tangential thin section of the same specimen. E: Longitudinal thin section of the type specimen 5179. F: Tangential thin section of the same specimen. G: Longitudinal thin section of the type specimen 17175. H: Tangential thin section of the same specimen. I: Longitudinal thin section of the type specimen 5170. J: Tangential section of the same specimen. Scale bars: 1 mm.

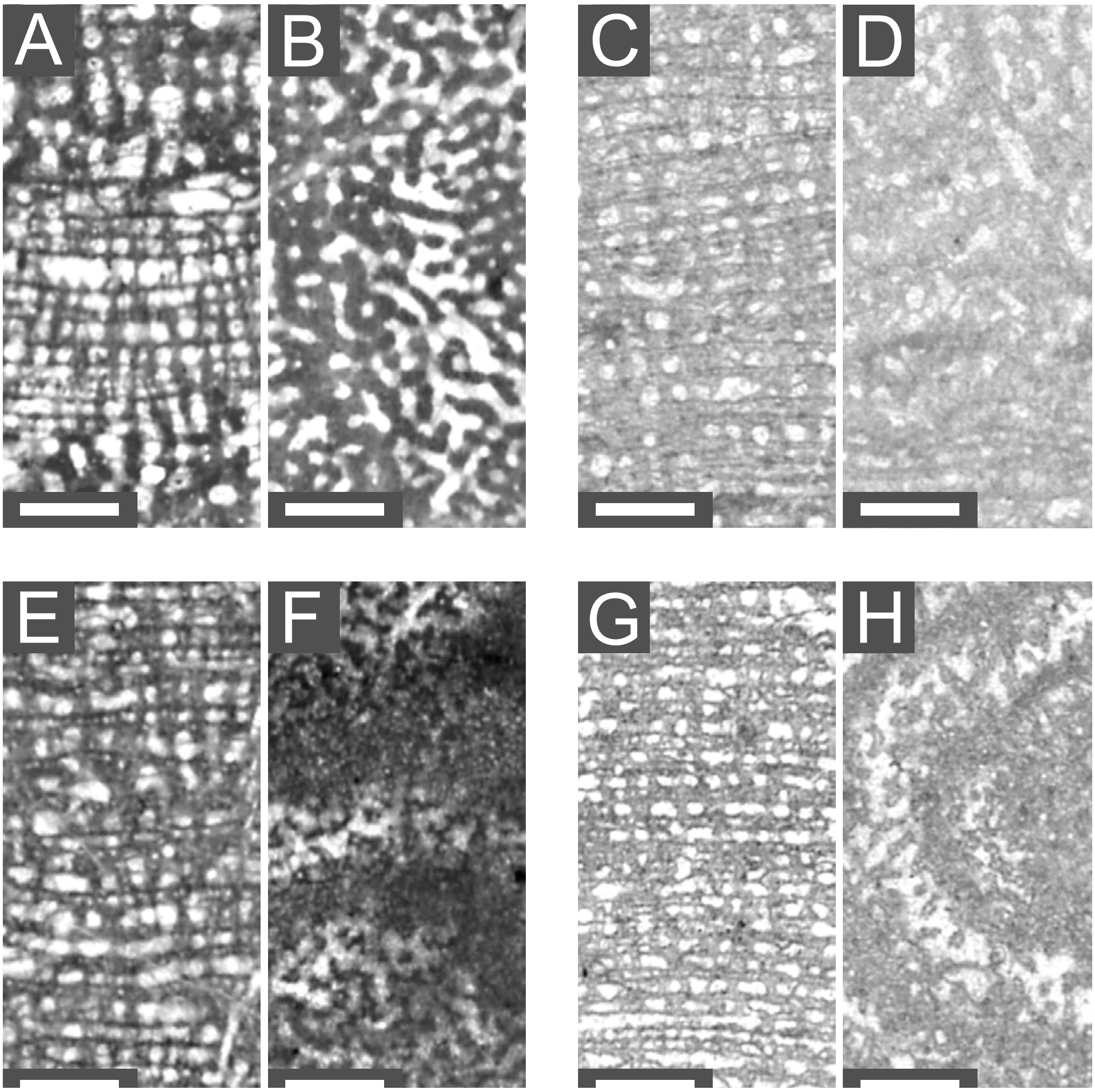

Plate 3. A-D: *Trupetostroma pingue*. E-H: *Pseudotrupetostroma cellulosum*. A: Longitudinal thin section of the paratype 17020. B: Tangential thin section of the same specimen. C: Longitudinal thin section of the specimen UAM SOG 18 from the Upper Givetian of Sowie Górki (Holy Cross Mountains). D: Tangential section of the same specimen. E: Longitudinal section of paratype 5136. F: Tangential thin section of the holotype (5267). G: Longitudinal section of the specimen UAM DEB 1; Upper Givetian of the Dębnik Anticline (southern Poland). H: Tangential section of the same specimen. Scale bars: 1 mm.

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Hamaraxonia, a new pseudocolumellate genus of Middle Devonian deep-water Rugosa (Anthozoa) from Morocco

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ABSTRACT. The monotypic genus *Hamaraxonia* gen. nov., with type species *Hamaraxonia africana* sp. nov., is described, based on only four specimens, from the middle Eifelian (top *Costapolygnathus costatus* Zone to basal *Tortodus australis* Zone) of the Hamar Laghdad, Anti-Atlas, SE-Morocco. In its prominent axial boss and dissepiments in maturity, the new genus is unique among pre-Carboniferous ahermatypic Rugosa. It is classified within the still polyphyletic subfamily Columnaxoninae Weyer, 1980 of the family Cyathaxoniidae Milne-Edwards & Haime, 1850 (suborder Cyathaxoniina Spasskiy, 1977). Possible ancestors will probably be found among the neighbouring subfamily Laccophyllinae Grabau, 1928. For the moment, a phylogenetic line: *Laccophyllum* Simpson, 1900 → *Hamarophyllum* Berkowski, 2004 → gen. nov. pro *Cyathaxonia hercynica* Roemer, 1855 (Weyer & Zagora, 1990) → *Hamaraxonia* gen. nov. may be proposed, pending further records from other regions and additional intermediate taxa. The commonly used term columella (aseptal origin) and the nearly forgotten term pseudocolumella (septal origin) are redefined in the already morphogenetic sense of their authors (Milne-Edwards & Haime 1848) by selecting morpho-terminological types: *Cyathaxonia cornu* Michelin, 1847 (late Tournaisian), and *Clisiophyllum keyserlingi* M'Coy, 1849 (middle/late Viséan).

KEYWORDS: Rugose corals, taxonomy, *Cyathaxonia* fauna, axial structure, Devonian.

1. Introduction

Long ago, small solitary Rugosa of the *Cyathaxonia* facies (sensu Hill, 1938) provided with an axial structure ("columella") were regarded as typical of Carboniferous and Permian coral communities. Hill (1956) classified them as three families of Cyathaxoniicae (suborder Streptelasmatina): Cyathaxoniidae, Lophophyllidiidae, Timorphyllidae. Hill (1981) accepted five families in two suborders for such taxa: Metriophyllina (Cyathaxoniidae, Metriophyllidae) and Plerophyllina (Lophophyllidae, Timorphyllidae, Verbeekiellidae). At present, further approaches towards a more natural phylogenetical taxonomy support the independent development of these "columellate" structures in ten Carboniferous-Permian family-level units:

suborder Cyathaxoniina Spasskiy, 1977
    Cyathaxoniinae Milne-Edwards & Haime, 1850
suborder Zaphrentoidina Schouppé & Stacul, 1959 (synonyms Metriophyllina Spasskiy, 1965; Stereolasmatina Hill, 1981; Hapsiphyllina Nudds in Nudds & Löser, 2001):
    Rylstoniinae Yü, Lin, Shi, Huang & Yu, 1983
    Lophophyllidae Grabau, 1928
    Variaxoninae Fedorowski, 2010
    Lophophyllidiidae Moore & Jeffords, 1945
    Timorphyllidae Soshkina in Soshkina, Dobrolyubova & Porfiriev, 1941
    Verbeekiellidae Schouppé & Stacul, 1955
    Wannerophyllidae Fedorowski, 1986
    Lophotichiidae Weyer, 1972
    Asserculiniinae Fedorowski, 1986

Radical changes in the stratigraphic aspect started with Różkowska (1969), who recorded *Cyathaxonia* Michelin, 1847 already in the Early and Late Famennian and its subgenus *Cyathocarinia* Soshkina, 1928 in the Late Famennian of Poland. Her species are now renamed *Cyathaxonia* (*Cyathaxonia*) *rozkowskae* Fedorowski, 2003 and *Cyathaxonia* (*Cyathocarinia*) *famenniana* Fedorowski, 2003. Similar collections occur in Germany (Weyer, 1984, 21, fig. 4/4-5) and in Morocco.

The next surprising discovery was *Columnaxon* Scrutton, 1971 from the Ludlowian of Venezuela. Then several Devonian "columellate" taxa were erected: *Famaxonia* Weyer, 1971 (Late Famennian, Germany), *Yishanophyllum* Wu & Liao, 1988 (Late Famennian, Guangxi province of China), *Cyathaxonia*? *hercynica* Roemer, 1855 = new genus (Weyer & Zagora, 1990, 27, fig. 3, Middle Givetian, Germany, meanwhile also found in France and Morocco), nov. gen. nov. sp. I (Weyer et al. 2003, 76, fig. 2D, Late Frasnian, Germany), *Cheilaxonia* Weyer 2004 (Early Famennian, Germany). In addition, there are further Devonian, unrevised species bearing an axial boss, as *Lophophyllum constrictum* Maurer, 1885 (Weyer 2005, 6, Middle Givetian, Germany) and *Lindstroemia stellata* Goryanov, 1967 (nomen nudum, mentioned in a faunal list of Goryanov & Klishevich (1968, 908), Pragian or Early Emsian, Kirgistan).

Actual systematics classified such pre-Carboniferous "columellate" genera into two subfamilies (Protozaphrentinae Ivanovskiy, 1959; Columnaxoninae Weyer, 1980) and as *incertae sedis*, probably all within the relatively deep-water representatives of the suborder Cyathaxoniina Spasskiy, 1977. Surely, this procedure is not reflecting real phylogenetic relationships and will be continuously emended according to urgently needed worldwide future studies of these "forgotten" rare corals in Silurian and Devonian times, and at the moment still completely unknown in the Ordovician (except for the stratigraphically curious genus *Protozaphrentis* Yü, 1957 from China).

Devonian Rugosa of the *Cyathaxonia* facies (ahermatypic, of dysphotic/aphotic and psychrospheric environments) are extremely poorly known in the Givetian (especially in its upper part after the Taghanic Event), in the complete Frasnian, and in the basal Famennian (time span of seven conodont zones, from Lower *Palmatolepis triangularis* to Uppermost *Palmatolepis crepida*). Perhaps, they are sometimes really rare (e.g. immediately after the Upper Kellwasser Event), but mainly they remained uncollected and unstudied. This explains the high number of Frasnian "silent taxa" (Wrzołek, 2002, including many "Lazarus taxa" and isolated "Elvis taxa"). Some of the few existing, mostly rather ancient literature data can be interpreted in the terms of actual biozonations only by stratigraphic insiders, and according to modern taxonomy only after intensive morphological revisions (e.g. Ludwig, 1865-1866; Weissermel, 1939).

Eight new Rugosa species of Ludwig (1865-1866) had been found in an iron ore horizon of the Rhenish Mountains (*Amplexus umbilicatus*, *Amplexus breviradiatus*, *Anorygmaphyllum obtusum*, *Zaphrentis ampla*, *Hexorygmaphyllum radiatum*, *Liocyathus loculatus*, *Ptychocyathus excelsus*, *Taeniocyathus trochiformis*). Their age is either Middle Givetian (*Maenioceras terebratum* Zone), Late Givetian (*Pharciceras Genozone*), or lower Frasnian. All these taxa are now invalidated (Opinion ICZN, 1971); none had ever been redescribed or could be identified using only the original illustrations, prepared before the introduction of thin sectioning techniques.

The six new taxa proposed in Weissermel (1939, based on badly preserved mould materials) are partly Late Frasnian (Hirtenrangen Formation – *Zaphrentis curvatissima*, *Metriophyllum volki*, *Amplexus liliiformis*), and partly Early Famennian (Plattenbruch Member of Bohlen Formation, *Cheiloceras* Genozone – *Syringaxon thuringiacum*,

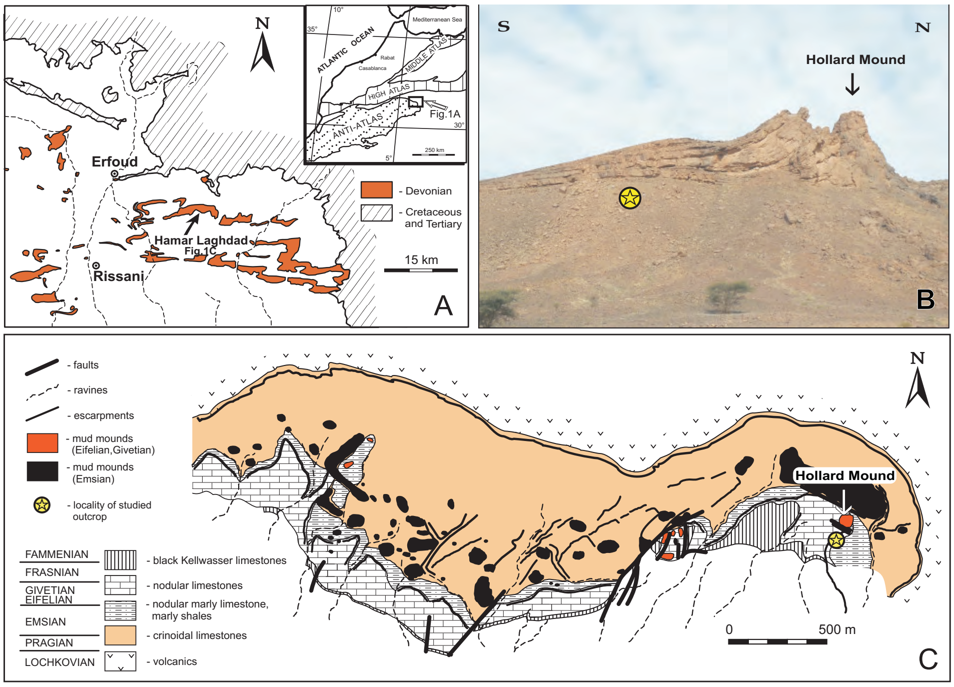

Figure 1. A: Simplified geologic map of northeastern Anti-Atlas, Devonian rocks and Hamar Laghdad are indicated; B: Outcrop marked by star in circle on southeastern slope of the "Hollard Mound" (view from the east). C: Detailed geological map of Hamar Laghdad with distribution of particular types of Devonian rocks. Star in circle indicates outcrop, where studied specimens were collected. Drawings A and C courtesy of Belka (1998 and unpublished) - updated.

Combophyllum asteriscus, *Lindstroemia*? *cornuhirci*). The author had noted the lithostratigraphical symbols (tob, toc) and bed numbers (in his plate explanations), indicated on the original labels of the collector Max Volk (1900-1969) and well explained in Volk (1939, with pelagic ostracod zonation). At present, most of these taxa seem to be undeterminable (especially in view of the probably lost type collection), excepting *Neaxon thuringiacus* (Weissermel, 1939) which is identical with *Amplexus pauciradiatus* Ludwig, 1865.

Here we describe the unexpected new pleonophorous genus *Hamaraxonia* from the Middle Eifelian of the famous mud mound area at the Hamar Laghdad, in continuation of the first monograph of Emsian deep water Rugosa in that region (Berkowski, 2008). This will be followed by the proposal of another "columellate" new genus, collected from Germany, France, and Morocco (Weyer & Berkowski, in preparation), rather strange in its mid-Eifelian to mid-Givetian occurrences and somewhat more reminiscent of the Permo-Carboniferous *Lophophyllidium* Grabau, 1928 (or its subgenus *Lophbillidium* Fedorowski, 1986).

2. Locality and Stratigraphy

The studied specimens were collected at the famous Moroccan locality Hamar Laghdad, in its eastern part called "Hollard Mound" (Fig. 1B). The Hamar Laghdad area is located approximately 18 km southeast from Erfoud city (Fig. 1A) in the easternmost part of the Anti-Atlas in southeastern Morocco. In this area, Devonian rocks dip gently southward and form an elongated W-E ramp where more than 50 conical buildups are perfectly exposed. The majority of the mounds are Emsian, but several of them cropping out in the most eastern side of Hamar Laghdad are either Eifelian or Givetian (Fig. 1C). Emsian mud mounds became the subject of extensive geological and palaeontological studies (e.g.: Roch, 1934; Massa et al., 1965; Hollard, 1974; Alberti, 1982; Brachert, et al., 1992; Wendt, 1993; Belka, 1998; Aitken et al., 2002; Berkowski, 2004, 2006, 2008, 2012; Belka & Berkowski, 2005; Cavalazzi et al., 2007; Berkowski & Klug, 2012). Belka (1998) and Mounji et al. (1998) related the formation of Hamar Laghdad mounds to hydrothermal venting activity. During the Early Devonian, submarine eruption formed an elevation on the sea floor, which subsequently became a site of extensive carbonate production. Conical mud mounds formed along synsedimentary faults that served as conduits for migration of hydrothermal fluids to the sea floor (Belka, 1998). Vents were episodically active during a time of approximately 30 Ma (from the Pragian until the early Frasnian). During the Eifelian and early Givetian, the subvolcanic activity persisted in the most eastern part of Hamar Laghdad ("Hollard Mound") where hydrothermal fluids contained thermogenic methane derived presumably from the underlying volcanic intrusion (Peckmann et al., 1999).

"Hollard Mound" is located in the easternmost part of Hamar Laghdad (Fig. 1B) close to the complex of the easternmost Emsian mounds. On the eastern side it is cut by a fault, so its internal structure is well exposed. According to Peckmann et al. (1999, 2005) the deposition of the "Hollard Mound" carbonates started at the beginning of the Eifelian and ended by the end of the Givetian. These data are partly confirmed by detailed conodont stratigraphy of Hamar Laghdad, in preparation by Belka (personal comm.). The so-called "core of Hollard Mound" (*sensu* Peckmann et al., 1999) forms a large zone of sediments that exhibit isotopic signatures of hydrocarbon venting. They are composed of dyke fillings, vent deposits and carbonates related to venting activity. Fauna in the "core facies" is very diversified. The most conspicuous are clusters of large chemosynthetic bivalves and vestimentiferan tubes, which are located on the northeastern slope of the "Hollard Mound" (Peckmann et al., 1999, 2005), and monospecific Rugosa assemblages of *Amplexus florescens* (see Berkowski, 2006). The well-bedded sediments surrounding "the core" from the south (Fig 1B) include other numerous invertebrate taxa: i.e. cephalopods, gastropods, crinoids, trilobites, brachiopods, tabulate and solitary rugose corals.

Rugose corals described in the present paper were found within the well bedded nodular limestone covering "Hollard Mound" on its southern side (Fig. 1B). The beds are middle Eifelian in age and represent boundary beds of upper *Costapolygnathus costatus* and lower *Tortodus australis* zones (detailed stratigraphic investigation is now under preparation by Z. Belka).

3. Note on columella and pseudocolumella

In principal, the morphological glossary follows Hill (1981), though there a clear distinction between morphographic and morphogenetic terms is sometimes missing. Several emendations are already proposed (aulos: Fedorowski, 2009; septa: Weyer, 2008), and here - in view of the "columellate" new genus *Hamaraxonia*, unexpected in the Devonian - it seems necessary to start a similar procedure for the "columella" type of axial structures or axial bosses.

Milne-Edwards & Haime (1848a, 78) introduced the term **columella** for all skeleton-bearing corals (Scleractinia, Rugosa, Tabulata), but not alone: it was paralleled by another new term **pseudocolumella**, which nearly had been forgotten (even in the glossary of Hill, 1981). The main difference was seen in the genesis – septal origin in a pseudocolumella, non-septal origin in a columella ("columella propria"). At present, it is appropriate to define such terms separately for Scleractinia and Rugosa, also using a "morpho-terminological type" genus/species (if possible, more or less in the sense of the original authors).

This is easy for **"pseudocolumella"**, as Milne-Edwards & Haime (1848a) had already named the genus *Clisiophyllum* Dana, 1846 as an example. Thus we propose its genotype, the Early Carboniferous (late Viséan) *Clisiophyllum keyserlingi* M'Coy, 1849 as the definitive morpho-terminological type of the term **pseudocolumella**, which was already used in the description of that species (Milne-Edwards & Haime, 1851, 412). Future studies should subdivide this term for septal axial bosses using attributes other than the special structure of its type, characterizing many Ordovician to Permian taxa: e.g. *Grewingkia* Dybowski, 1873, *Dinophyllum* Lindström, 1882, *Scenophyllum* Simpson, 1900, *Dibunophyllum* Thomson & Nicholson, 1876, *Ipciphyllum* Hudson, 1958). Special sub-terms (comparable to those of Milne-Edwards & Haime, 1848a: columella septalis, parietalis, styliformis, fascicularis) are indispensable for other septal axial structures (pseudocolumella in wider sense), e.g. the mainly/exclusively antiseptal everted prolongation (with or without additional septal lamellae and tabulae) as in the genera *Lophophyllidium* Grabau, 1928, *Rylstonia* Hudson & Platt, 1927, *Dorlodotia* Salée, 1920, or *Lithostrotion* Fleming, 1828.

The term **columella** is defined within the superorder Rugosa by its here proposed morpho-terminological type *Cyathaxonia cornu* Michelin, 1847 (Early Carboniferous, Late Tournaisian). Milne-Edwards & Haime (1848a, 79, pl.4/2a,1a) had mentioned only Scleractinian examples for their "columella propria" growing independently from septa, directly from the base of the skeleton: *Turbinolia sulcata* Lamarck, 1816 and *Turbinolia dixonii* Milne-Edwards & Haime, 1848 for a "columella propria styliformis", *Turbinolia obesa* Michelotti, 1838 (transferred by Milne-Edwards & Haime, 1848b to their new genus *Trochocyathus*) and *Cyathina* Ehrenberg, 1834 = *Caryophyllia* Lamarck, 1801, namely *Caryophyllia cyathus* (Ellis & Solander, 1786) for a "columella propria fascicularis". Later (Milne-Edwards & Haime, 1850, LXV, 1851, 163) ascribed a "columella styliformis" to *Cyathaxonia* Michelin, 1847; this justifies our morphological type choice. The columella of *Cyathaxonia* is a completely aseptal structure. Fedorowski & Vasilyuk (2011) described it as structure without any septal lamellae and developed tabulae-like sclerenchyme. Weyer (2001) simply interpreted this structure as an everted aulos, which shows only regular concentric growth lines in cross sections. By this redefinition, the axial boss of *Hamaraxonia* gen. nov. proposed here is a typical **pseudocolumella**.

4. Systematic Palaeontology

Abbreviations used: N = number of all septa, n = number of major septa (protosepta, metasepta), D = diameter, CS = cross/

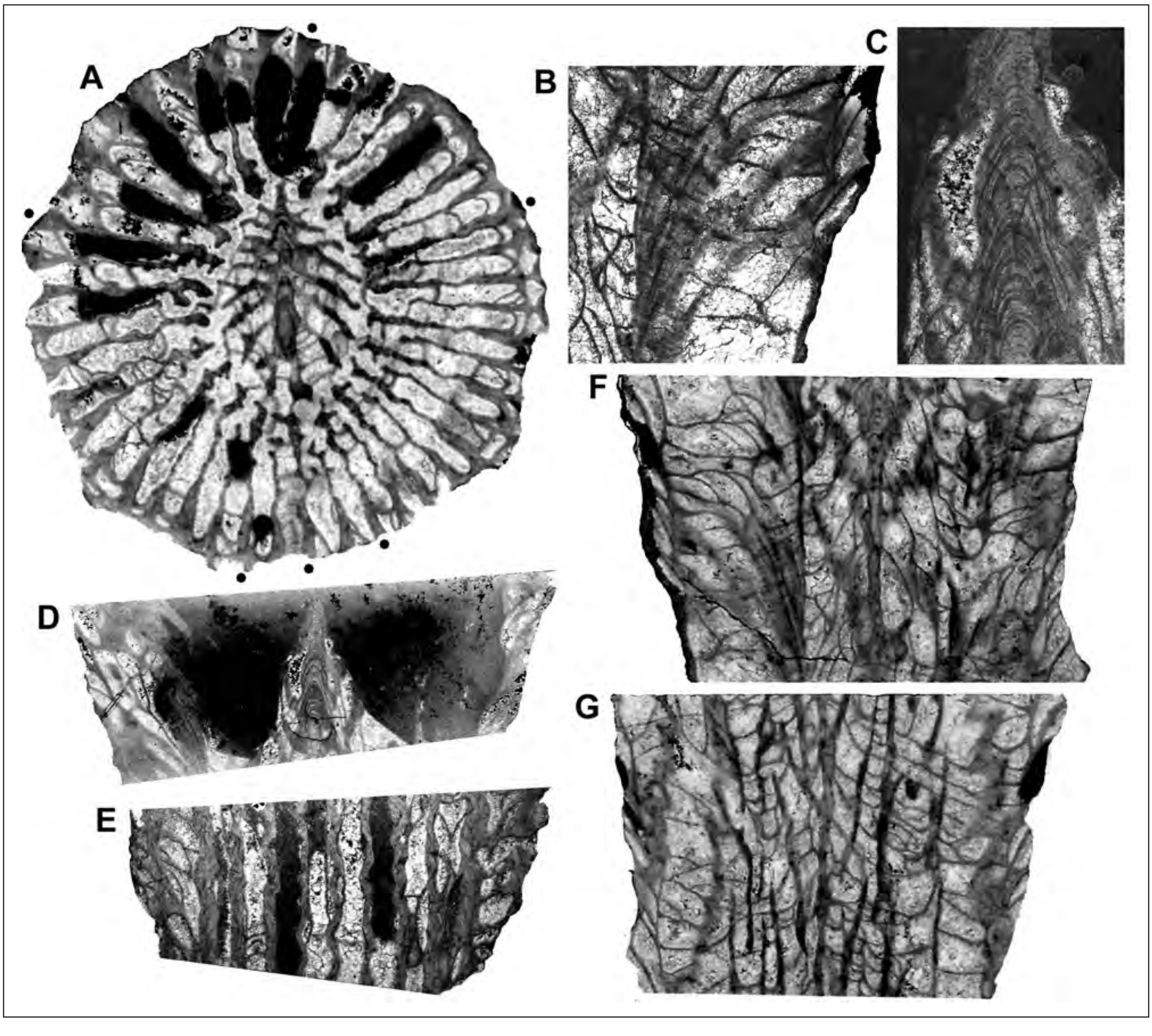

Figure 2. *Hamaraxonia africana* sp. nov., holotype no. HD/0/A/2-6, middle Eifelian, boundary beds of upper *Costapolygnathus costatus* and lower *Tortodus australis* zones, Hamar Laghdad Ridge (eastern slope of Hollard Mound) ESE of Erfoud (Tafilalt, Anti-Atlas), collection B. Berkowski 2001-2002 and 2010. A: CS13 at base of calice, x8, B: subtabular LS17, x12, with growth lines in a medially cut metaseptum, C: pseudocolumella of LS8, x18, D: calicular median LS4, x6, E: calicular tangential LS11, x8, F, G: subtabular median LS17, 20, x8, normal to cardinal-counter septal plane, with biform tabularium (inclination of tabulae adaxial in position I and abaxial in position II).

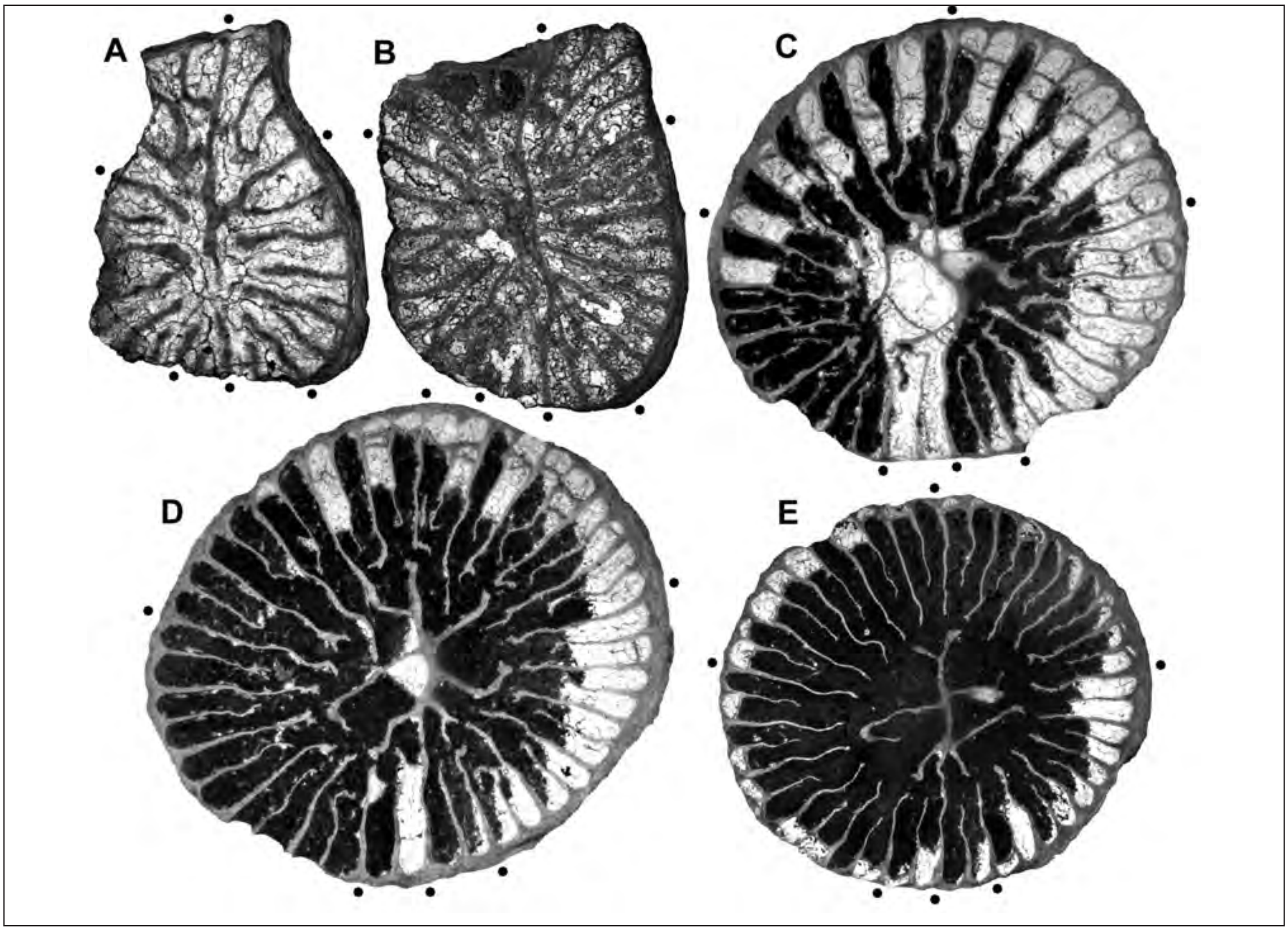

Figure 3. *Hamaraxonia africana* sp. nov., paratype no. HD/0/A/0-19, middle Eifelian, boundary beds of upper *Costapolygnathus costatus* and lower *Tortodus australis* zones, Hamar Laghdad Ridge (eastern slope of Hollard Mound) ESE of Erfoud (Tafilalt, Anti-Atlas), collection B. Berkowski 2001-2002 and 2010. Ontogenetic series of 2 subtabular and 3 calicular CS, with well developed biform tabularium and first isolated mature dissepiments; A: CS12, x20, B: CS9, x18, C: CS 5, x10, D: CS4, x10, E: CS3, x8.

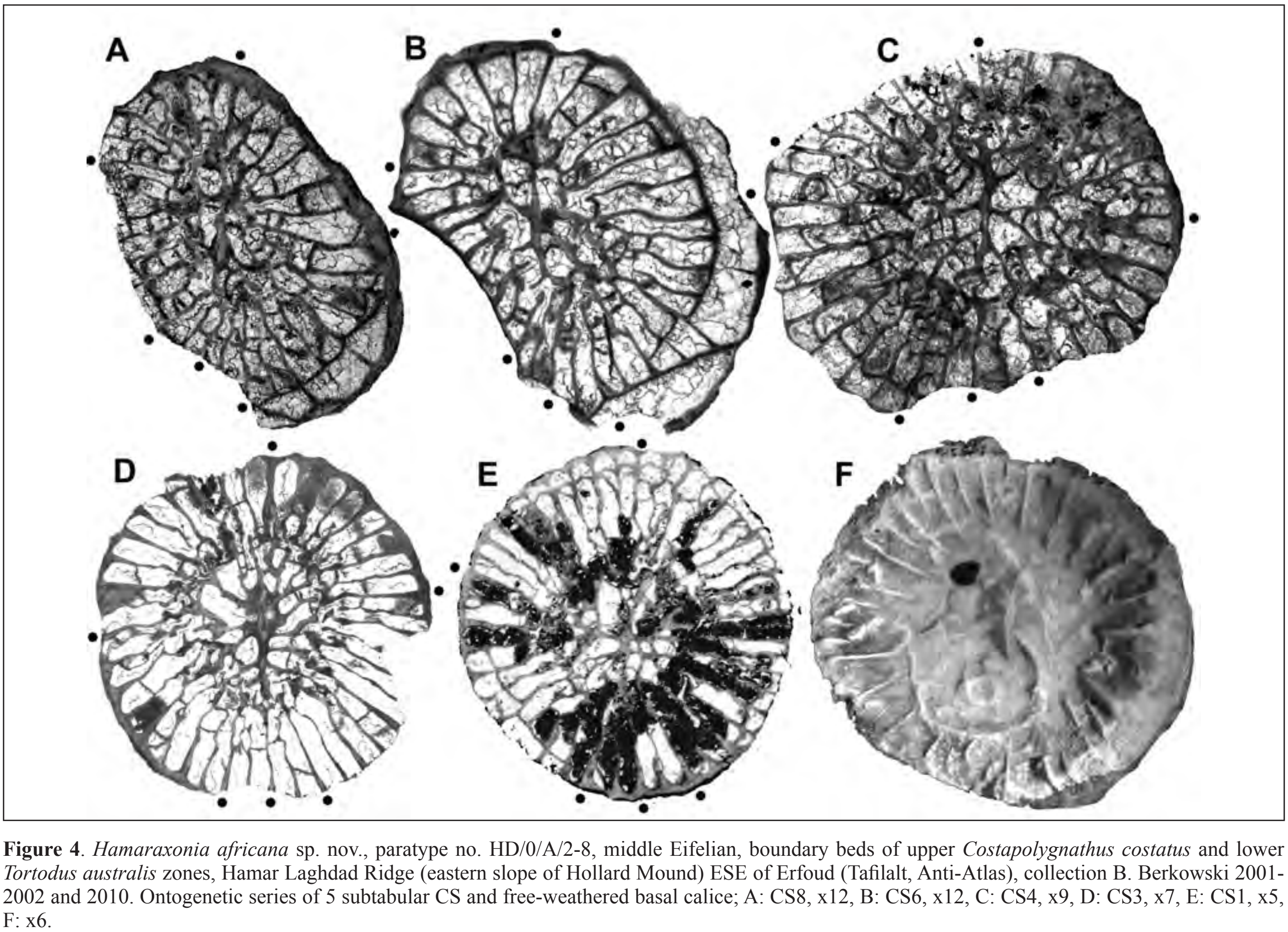

Figure 4. *Hamaraxonia africana* sp. nov., paratype no. HD/0/A/2-8, middle Eifelian, boundary beds of upper *Costapolygnathus costatus* and lower *Tortodus australis* zones, Hamar Laghdad Ridge (eastern slope of Hollard Mound) ESE of Erfoud (Tafilalt, Anti-Atlas), collection B. Berkowski 2001-2002 and 2010. Ontogenetic series of 5 subtabular CS and free-weathered basal calice; A: CS8, x12, B: CS6, x12, C: CS4, x9, D: CS3, x7, E: CS1, x5, F: x6.

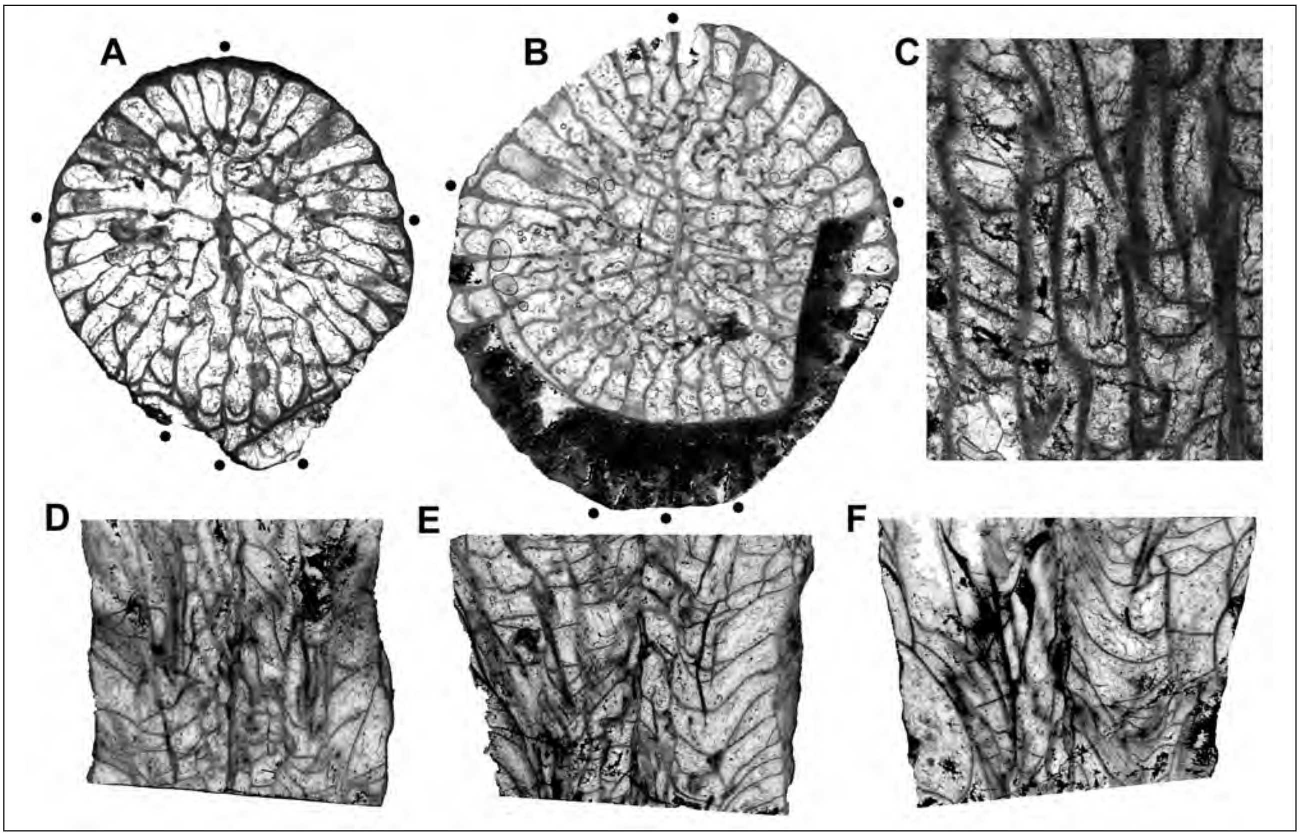

Figure 5. *Hamaraxonia africana* sp. nov., paratype no. HD/0/A/0-25, middle Eifelian, boundary beds of upper *Costapolygnathus costatus* and lower *Tortodus australis* zones, Hamar Laghdad Ridge (eastern slope of Hollard Mound) ESE of Erfoud (Tafilalt, Anti-Atlas), collection B. Berkowski 2001-2002 and 2010. A: subtabular CS26, x7, B: CS5, x6, older upper calice with again subtabular stage after rejuvenescense, C: slightly tangential LS9, x15, normal to cardinal-counter septal plane, with *Metriophyllum*-like carinae, D, E, F: median LS18, 11, 8, x5, oblique (D) and normal (E, F) to cardinal-counter septal plane, with opposite inclined tabulae of a strongly biform tabularium.

transverse section, LS = longitudinal section, TH = thin section, P = Peel, R = remaining part of corallum. Traditionally, six septa were marked; the cardinal septum is situated upside. All cross sections are presented in calicular view (from above); their orientation in an ontogenetic series is always equilateral (never reversed).

The studied corals are deposed in the collections of the Institute of Geology, Adam Mickiewicz University, Poznań (Poland), abbreviated UAM Tc/B HD/0/A/xx.

Suborder Cyathaxoniina Spasskiy, 1977
Superfamily Cyathaxonioidea Milne-Edwards & Haime, 1850
Family Cyathaxoniidae Milne-Edwards & Haime, 1850
Subfamily Columnaxoninae Weyer, 1980

1980 Columnaxoninae nov. subfam.; Weyer, p. 1214.
2005 Columnaxoninae; Weyer, p. 7.

Genera included. *Columnaxon* Scrutton, 1971 (Ludlowian), *Antilacca* Weyer, 2005 (Late Emsian), nov. gen. nov. sp. I, Weyer et al., 2003 (Late Frasnian), nov. gen. pro *Cyathaxonia*? *hercynica* Roemer, 1855, Weyer & Zagora, 1990 (Middle Eifelian—Middle Givetian). Surely, these taxa constitute an at least partly polyphyletic assemblage to be reclassified (at subfamily level) after better understanding their true relationships. The source is mainly among the ancient family members, the Laccophyllinae Grabau, 1928.

Genus *Hamaraxonia* gen. nov.

Derivation of name. From the name of the North African locality Hamar Laghdad (Morocco) and presence of an axial structure.

Type species. *Hamaraxonia africana* sp. nov.

Diagnosis. Small long-conical pleonophorous corallum with a deep calice bearing a high pseudocolumella, which starts with a primary cardinal-counter lamella and finally has many additional septal lamellae (only a little less than the number of long major septa) with many steep tabulae. The long, radially arranged major septa, all (including the cardinal septum) of equal length, join the pseudocolumella a few times in juvenile phases; during middle growth stages their axial ends become free and slightly thickened, later at maturity often with irregular bifurcations or even trifurcations. The rather long minor septa are contraclined, never contratingent. Septal flanks with flanges parallel to the distal margin of septa, sometimes with few metriophylloid carinae. There is only an extremely weak stereoplasmatic thickening of the complete septal apparatus; interseptal spaces are always much wider than the thin septa. Tabularium strongly biform, with contrary inclined tabulae in position I (centripetally) and position II (steeply centrifugally). A normal concentric dissepimentarium (1-3, maximally 5 rows) arises in adult stages; very rare lonsdaleioid dissepiments are perhaps related to rejuvenescence.

Relationships. The peculiar combination of diagnostic features is unique among Rugosa. At present, the only probable ancestor will be a still not described other new genus, already mentioned by Weyer & Zagora (1990), based on a hitherto unrevised Middle Givetian ancient species from the German Harz Mountains, *Cyathaxonia hercynica* Roemer, 1855. We are now preparing the revision (based on a rich topotype collection) of this taxon (with a massive pseudocolumella, without dissepiments), which also occurs at the same level of the German Rhenish Mountains, in the Lower Givetian of the Montagne Noire (France), and in the Middle Eifelian—Middle Givetian of the Hamar Laghdad (Anti-Atlas, Morocco). A possible phylogenetic line *Laccophyllum* Simpson, 1900 → *Hamarophyllum* Berkowski, 2004 → gen. nov. (pro *Cyathaxonia hercynica* Roemer, 1855) → *Hamaraxonia* gen. nov. is proposed, indicating a doubtless origin from the subfamily Laccophyllinae Grabau, 1928, and waiting for future emendations after the discovery of additional, still unknown intermediate generic taxa.

Occurrence. At present, monotypic in the Middle Eifelian of Morocco.

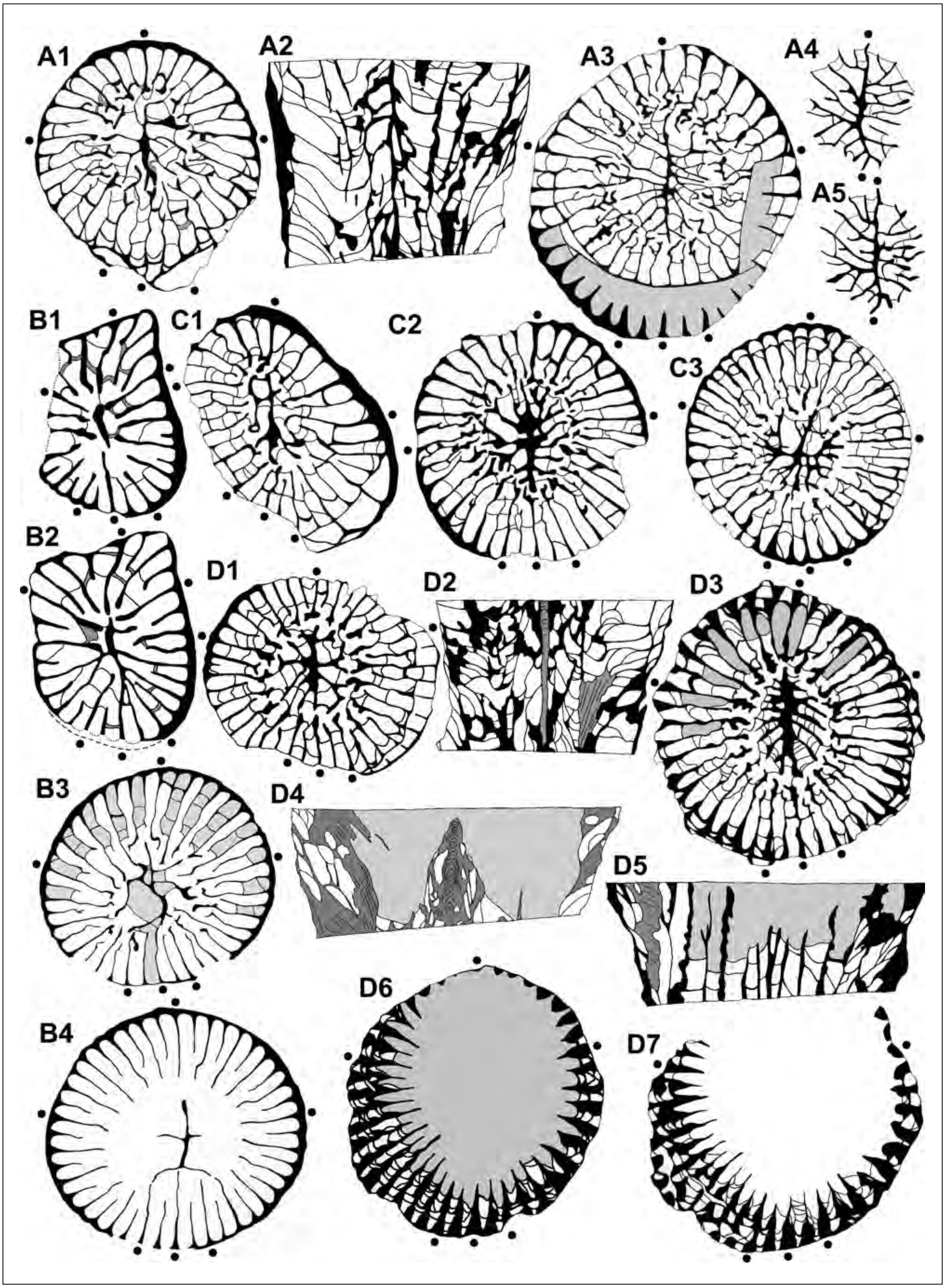

Figure 6. *Hamaraxonia africana* sp. nov., middle Eifelian, boundary beds of upper *Costapolygnathus costatus* and lower *Tortodus australis* zones; Hamar Laghdad Ridge (eastern slope of Hollard Mound) ESE of Erfoud (Tafilalt, Anti-Atlas); collection B. Berkowski 2001-2002 and 2010. A: paratype no. HD/0/A/0-25; A: subtabular LS26, x6, with an early rejuvenescense near counter septum, A2: subtabular median LS 11, x5, normal to cardinal-counter septal plane, A3: mature CS5, x5 (supratabular areas light grey), A4, A5: septal lamellae and tabulae of the pseudocolumella in CS2, CS1, x5. Photos see Fig. 5A-F. B: paratype no. HD/0/A/0-19; juvenile subtabular (B1, B2, x12) and adult calicular (B3, B4, x6) ontogenetic series of CS (no. 10, 9, 5, 1); light grey regions in B3 are subtabular. Photos see Fig. 3A-E. C: paratype no. HD/0/8/2-8; successive subtabular CS (no. 8, 3, 1), x10, x6 and x5. Photos see Fig. 4A-F. D: holotype no. HD/0/8/2-6; D: subtabular CS22 of middle growth stage, x6, D2: subtabular LS17, x5, normal to cardinal-counter septal plane, D3: CS13 at base of calice, x5 (light grey areas are calicular), D4, D5: lower calicular median and tangential LS (no. 8, 7), x5, normal to cardinal-counter septal plane, D6, D7: upper calicular CS (no. 2, 1), x4. Photos see Fig. 2.

Hamaraxonia africana **sp. nov.**
(Figs 2-6)

Derivation of name. After the African locality where the type species was found.

Holotype. Specimen no. HD/0/A/2-6. =10CS(4TS,6P),16LS(9TS,7P),1R. (1 duplicate peel (cross section no.12) in Berlin (Museum of Natural History, no. MB.K.7939.)) - Figs 2A-G, 6D1-7.

Type locality. Hamar Laghdad Ridge ESE of Erfoud, eastern slope of Hollard Mound (Tafilalt, Anti-Atlas, Morocco).

Type horizon. Middle Eifelian, boundary beds of upper part of *Costapolygnathus costatus* Zone, and lower *Tortodus australis* Zone.

Paratypes. 3 specimens, all – as the holotype – collection B. Berkowski 2001-2002 and 2010.
1. no. HD/0/A/0-19.=12CS(6TS,6P),2R.
Figs 3A-E, 6B1-4.
2. no. HD/0/A/0-25.=14CS(6TS,8P),12LS(7TS,5P),1R.
Figs 5A-F, 6A1-5.
3. no. HD/0/A/2-8. =8CS(5TS,3P),3R.
Figs 4A-F, 6C1-3.

Diagnosis. For the moment, identical with that of the still monotypic genus.

Description. The small long-conical corallum is straight and/or irregularly cornute (length 20-25 mm, calicular D 9-14 mm). The normally damaged proximal tip (minimal observed D 2.5 mm) was fixed by a tiny talon (Fig. 6B1); in addition, once a root-like outgrowth was present just above the talon. In the case of curvature (Fig. 3), the cardinal septum is situated on the convex side. Weak rejuvenescense may occur sometimes (Figs 4, 5). The archaeotheca bears fine growth rugae and distinct weak longitudinal septal furrows (Fig. 6C3) of protosepta, metasepta, and catasepta, but not of hyposepta; interseptal ribs are narrow and rounded to nearly sharp.

Mature calices with a slightly thickened wall have a prominent pseudocolumella occupying about one third of D. A primary, hardly ever thicker cardinal-counter septal lamella (Figs 2C, D, F) is connected with thin, occasionally bifurcating septal lamellae, more or less corresponding to the number of major septa (Fig. 6A3-5), but sometimes excepting the last one in a quadrant, which usually appears like a minor septum (Figs 6C2, 6D3). A section near the top of the pseudocolumella (Fig. 6B4) shows only 6 septal lamellae of the protosepta. The structure becomes delimited by steeply (up to vertical) inclined tabellae (Fig. 6D4), passing over to the normal tabularium. During juvenile stages (Fig. 6B1-2), only the cardinal-counter septal lamella is present; then in middle growth phases those of further major septa appear slowly.

The adult septal apparatus consists of 40-44 thin, radial arranged septa:

<table>
<tr><td><u>4|4</u> n 24, N 40</td><td><u>5|5</u> n 26, N 44</td><td><u>4|4</u> n 26, N 44</td></tr>
<tr><td>6|6 D 11 mm</td><td>6|6 D 8-8.8 mm</td><td>7|7 D 10.4 mm</td></tr>
<tr><td>Fig. 6A3</td><td>Figs 6B4, 6C3</td><td>Fig. 6D3</td></tr>
</table>

They start at the calicular rim with a broadly rounded base (Fig. 6D6) that later becomes (for the greater part) incorporated into the somewhat thickened wall. After growth in the calice (growth lines visible in Figs 2B, 6D4), the major septa nearly reach the pseudocolumella, but retain their free axial ends – some few connections are visible only in the extreme youth (Fig, 6B2). All major septa (except the last one of every quadrant) have the same length; also the cardinal septum is never shortened. The slightly thinner, rather long minor septa reach about 75 % of the major septal length; they are never contratingent, but always contraclined (seen by the biform tabularium, not in any inclination towards the antiseptal/counter side). Stereoplasmatic thickening of all septa is always minimal; interseptal lumina are much wider (except the broad dissepiment zone in Fig. 6D6-7 after a rejuvenescense). Septal flanks bear a weak "ornament" of flanges (parallel to the distal margin) and rare metriophylloid carinae (Figs 5C, 6A3, 6D5). A strange mature specialisation occurs in most major septa: their thickened, sometimes nearly rhopaloid axial ends show irregular bifurcations or even trifurcations in cross sections; a conceivable explanation as pali-like structures, initially suggested by locally everted tabellae in Fig. 6D2 (upper right tabularium), could not be verified. The septal microstructure is lamellar (term of Schindewolf, 1942; a synonym is "fibronormal" of Kato, 1963); the distal septal margins are smooth (Figs 2B, 6D6) and do not bear trabecular spines.

The tabularium is strongly biform, with different inclination and type, in position I (*sensu* Sutherland 1965) centripetally, dominant tabellae; in position II centrifugally, dominant simple tabulae). This is well seen in subtabular sections, both LS (Figs 5E, 6A2) and CS (curvature of tabular intersections convex towards the wall in position I, concave in position II). The calicular base (Figs 3C, 6D3) demonstrates this by the regular different filling of the interseptal spaces, alternately either with sparite or with detritus. The height difference between the uppermost tabulae in position I and II can be estimated in Fig. 6D4.

A narrow dissepimentarium of normally 1 to 2, rarely 3 rows of vesicles arises at maturity. The first appearance in Fig. 6C2 (D 7 mm, left antiquadrant/counterquadrant) is recognizable by the curvature of the intersection in position II (convex towards the wall); later (Fig. 6C3) there exists one regular row of concentric vesicles between most major and minor septa. The broader dissepimental zone in Figs 6D6-7 (up to 5 rows) is an exception restricted to a rejuvenescence zone, which also caused some few lonsdaleioid vesicles (Figs 4B, 6A1, 6D7).

Discussion. The smallest paratype (Fig. 3) differs from the other specimens in the distinctly weaker development of the pseudocolumella and dissepimentarium. This is interpreted as intraspecific variation, though we can not exclude another decision in view of the restricted available material of only four specimens (but known from one locality in two directly neighbouring beds). The occurrence of the genus/species in other regions (especially Europe), where such small Rugosa of the cold and deep-water facies often remained unstudied, might be expected.

5. Acknowledgements.

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New data on *Angustiphyllum* Altevogt, 1965, an automobile free-living rugose coral from the Eifelian of the Western Armorican Massif (France)

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ABSTRACT. The genus *Angustiphyllum* is recorded for the first time in the Armorican Massif (Rade de Brest) and two new species are erected: *A. stylophorum* and *A. vidalae*. The well preserved material shows the indisputable presence of costae on the exterior side of the corallum, which, besides the wedge-like morphology of the corallum, constitutes the main diagnostic feature of the genus. *Angustiphyllum* seems to be a good index for the Upper Eifelian of the Ibero-Armorican Domain.

KEYWORDS: Hadrophyllidae, new species, Rade de Brest, Upper Eifelian, Ibero-armorican Domain.

1. Introduction

The discovery by one of us (P.-A. J.) of numerous, well preserved specimens of *Angustiphyllum* at Saint-Fiacre in the Saint-Fiacre Formation, Rade de Brest, Western Brittany, allows the description of two new species and the presentation of new data on the structure and the morphology of the genus.

The genus *Angustiphyllum* was erected by Altevogt (1965) for wedge-like or cuneiform (sphenoid sensu Hill 1981) solitary corals from the Eifelian of the Cantabrian Zone (North Spain). Later, Soto (1986) working on new material from the same area suggested that the axial crest was "formed by synapticulae arranged perpendicularly to the cardinal-counter plane" and described the fibrolamellar microstructure of the septa. Lastly, Plusquellec (2006) noticed the presence of costae on the proximal side of the coral and, taking into account the septal pattern, indicated affinities, not with *Combophyllum*, but with *Hadrophyllum*.

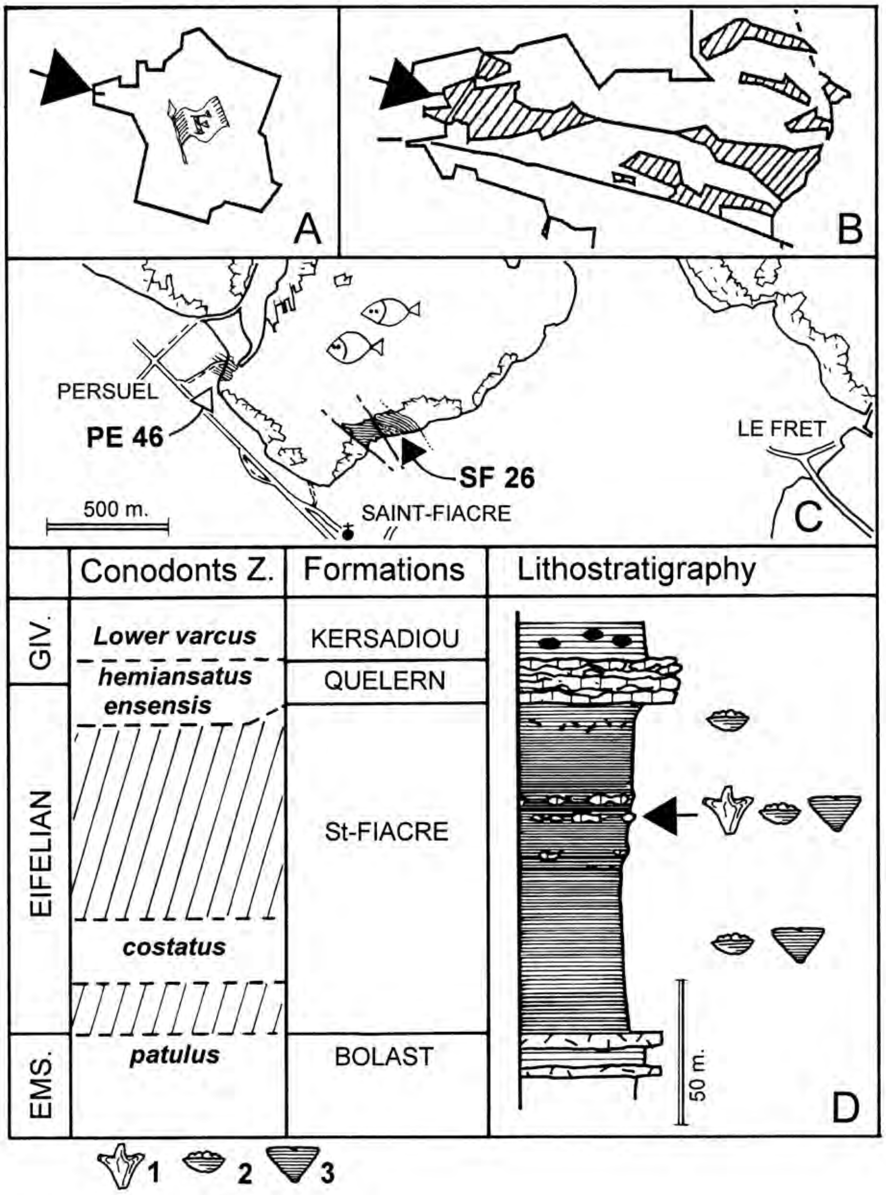

Figure 1. Saint-Fiacre, type locality of the Saint-Fiacre Formation, geographic and stratigraphic data. A-B: Location of the Palaeozoic outcrops. C: The Saint-Fiacre area with the location of the Saint-Fiacre Formation. D: The *Angustiphyllum*-bearing level in its stratigraphical context. 1: *Angustiphyllum*, 2: "*Convexocyclus*", 3: *Calceola*.

2. Lithostratigraphic, biostratigraphic and geographic data

In the Western part of the Massif Armoricain the Devonian of the Châteaulin synclinorium is well exposed in the sea cliffs and on sea strands of the Rade de Brest along the southern coasts of the Plougastel Peninsula, the northern coasts of the Crozon Peninsula and on both sides of the Le Faou River.

The Palaeozoic of this area belongs to the Central-North Armorican Domain, and the Upper Emsian-Famennian time interval was carefully studied and mapped by Morzadec (1983). He recognized above the Reun ar C'hrank Formation a set of 13 lithostratigraphic units constituting the Troaon Group. Within this Group the Saint-Fiacre Formation represents the main part of the Eifelian (Fig. 1).

Outcrops of the Saint-Fiacre Formation are recorded in numerous sections along the sea side and in some places in the country in the western part of the Châteaulin synclinorium, and the level is known for yielding *Calceola sandalina* since the first report (Collin 1929). The Saint-Fiacre Formation chiefly consists of brown to dark shales with some levels of calcareous concretions and/or nodular limestones. A sedimentological/ sequential study of the Lochkovian to Famennian formations of the Rade de Brest (Guillocheau 1991) shows that the maximum flooding surface occurs in the Eifelian during the deposition of the Saint-Fiacre Formation. The environment varies from lower offshore to distal upper offshore.

Two sections are of special interest. The first one is the type section exposed on the sea strand north of the little village of Saint-Fiacre, district of Crozon (see a detailed map in Morzadec 1983, fig.14) which has yielded numerous specimens of *Angustiphyllum* and the only ones preserved in calcite. The second one is the section of Goasquellou, district of l'Hopital-Camfrout, in the eastern part of the Rade de Brest (Morzadec 1983, fig. 23), where conodonts of the *costatus costatus* Zone were recorded in the lower part of the formation (Morzadec & Weyant 1982; locality GO10 in Morzadec 1983, fig. 23), giving a "lower" Eifelian age to this level.

In the type locality of the formation, the *Angustiphyllum*-bearing level (locality SF 26 in Morzadec 1983, fig. 14) is situated in the middle part of the formation and thus a little higher in the succession than level GO10, which has provided conodonts of the *costatus costatus* Zone (Fig. 1). Unfortunately the conodonts provided by the calcareous lenses in locality SF26 are without precise biostratigraphic significance and the *partitus*, *australis* and *kockelianus* Zones are not recorded within the Saint-Fiacre Formation.

Nevertheless, the presence in the middle part of the formation (GO12, SF25-26) of *Asteropyge cantarmorica* (Morzadec and Arbizu,1978, formerly described as *Kayserops*? *cantarmoric*a in the Saint-Fiacre Formation and in the Huergas Formation, Cantabrian Mountains) and of *Subanarcestes macrocephalus* Schindewolf, 1933, which is characteristic of the Upper Eifelian in Morocco (Ebbighausen et al., 2011) allow, according to Morzadec (pers. comm.), assignment of the middle and upper part of the Saint-Fiacre Formation to the Upper Eifelian, the Eifelian/Givetian boundary being placed within the overlying Quelern Formation (*ensensis-hemiansatus* Zone).

2.1. Additional data on the coral macrofauna

At Saint-Fiacre, another species of Hadrophyllidae has been collected in the formation, probably a new genus showing affinities with *Crassicyclus* Soto, 1978, *Microcyclus* Meek & Worthen, 1868 and "new genus P" Plusquellec, 2006, but having a very well marked convex proximal side and in some cases a problematic scar at its apex. It is provisionally called *Convexocyclus* nom. nud.; the species is new. In addition, *Calceola sandalina* occurs in at least two levels of the formation at Saint-Fiacre, in its lower part in the yellow facies and in its middle part in the *Angustiphyllum* beds (Fig. 1).

Some tabulate corals are recorded in the Saint-Fiacre Formation, such as *Granulidictyum* e.g. *granuliferum* (Schlüter, 1889) in the middle part of the formation, in the section of Goasquellou (locality GO12 in Morzadec 1983) and *Kerforneidictyum kerfornei* (Collin, 1912) in its upper part (in association with *Calceola sandalina* and *Convexocyclus*) on the strand of Goasquellou (locality GO27) and in the cliff SW of Squiffiec, district of Plougastel-Daoulas (locality SQ12 in Morzadec 1983, fig. 17).

Beside the corals it is interesting to note that the oldest tetrameral grapnels of *Ancyrocrinus*, *A. crozonensis* Le Menn & Jaouen, 2003 are described at Saint-Fiacre from the *Angustiphyllum*-bearing level and that pelagic elements, such as dacryoconarids, goniatites and orthoconic nautiloids, are abundant.

3. Systematic palaeontology

The material studied in this paper is housed at the Université de Bretagne Occidentale, Brest (France), Laboratoire de Paléontologie, catalogue number LPB 15 347-15 406 (Armorican material) and LPB 15 407-150413 (plastercasts from Cantabrian material). In addition, some specimens belonging to the Geologisch-Paläontologischen Institut und Museum der Universität Münster are figured (catalogue number GIM B2).

Subclass Rugosa Milne-Edwards & Haime, 1850
Order Stauriida Verill, 1865
Family Hadrophyllidae Nicholson, 1889
Subfamily Hadrophyllinae Nicholson, 1889 emend Plusquellec, 2006

Genus *Angustiphyllum* Altevogt, 1965

Type species. *Angustiphyllum cuneiforme* Altevogt, 1965

Comments on the diagnosis. Taking into account the succinct diagnosis of Altevogt (1965), the main features of the genus are as follows: small wedge-like solitary coral with ellipsoidal transverse section, only order I septa (= major septa) meeting along axial plane of wedge, tiny sparse tabulae, dissepiments lacking. Hill (1981) followed Altevogt but indicated "no epitheca preserved", "minor septa stunted to ?absent", "no coarse septal trabeculae observed". Soto (1986) gave nearly the same diagnosis but he added some interesting data in his description on the subject of costation "murallas…, las cuales presentan una costación grosera exértil bastante marcada".

The well preserved specimens collected in the type locality of the Saint-Fiacre Formation show that one of the main diagnostic feature of the genus has either not been seen by the previous authors, or not well understood. The septal apparatus clearly shows extensions of the septa beyond the wall: the costae. Thus the radial septal structures are costosepta and the "lack of preservation" of the so-called epitheca is not due to abrasion, weathering or corrosion, but this morphological feature is basically lacking. Moreover, the presence of minor septal structures is indisputable and they are often mainly formed by their costal part. In addition, and as stated by Soto (1986), the microstructure of the septal apparatus is fibrolamellar, or mainly of this type.

It is thus necessary to add these new data in the diagnosis of the genus.

***Angustiphyllum stylophorum* n. sp.**

(Figs 2-10; Plate 1, figs A-M)

2011 *Angustiphyllum* n. sp. 1. Plusquellec et al., p. 128, fig. 1-7.

Derivation of name. From stylus, to indicate the presence of a columella-like structure.

Holotype. Specimen LPB 15 347

Type locality and horizon. Saint-Fiacre, district of Crozon, Finistère (France), Saint-Fiacre Formation, Upper Eifelian.

Material. About 25 specimens with calcitic skeleton and 10 as natural casts; 5 thin sections, 4 acetate peels. All the specimens with their skeleton preserved come from the type locality (LPB

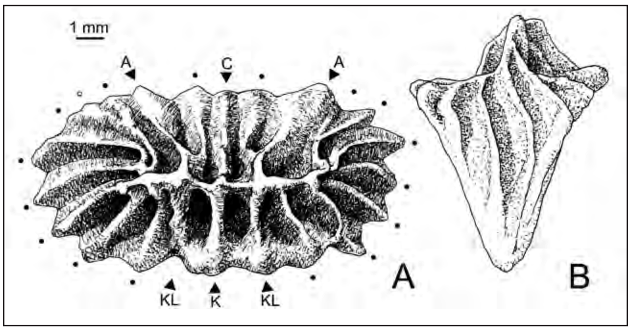

Figure 2. *Angustiphyllum stylophorum*, LPB 15 347, holotype. A: Calicinal view. B: Side view of narrow side of wedge, cardinal septum on left side. Black triangles indicates protosepta (C= cardinal [always in "North" position in calicinal view or transverse sections], K= counter, KL= counter-lateral); black circles and/or solid lines indicate major costo-septa; open circles and/or dotted lines indicate minor costo-septa; hatched lines show fossulae; broken line shows the interseptal crest (the same symbols apply for the following figures).

15 347-15 348, LPB 15 351-15 370, LPB 15 395-15 396); those in casts from 1) Le Caro, along the road between the harbour and Lannéguel, district of Plougastel-Daoulas, Finistère (LPB 15 397-15 401), 2) northern side of Le Caro cove (LPB 15 402), 3) unnamed locality along the "voie express", near Le Faou, Finistère (LPB 15 403-15 406).

Diagnosis. Large species of *Angustiphyllum* with a flat prominent columella-like structure rising in the axial part of the transversal crest and a strongly convex calicinal outline on broad side of wedge. Sides of the corallum flat to concave, commonly with a wide-mouthed outline seen from narrow side of wedge. Apical angle up to 60°-70° in large specimens. Maximum corallite diameter mainly between 6.5-14 mm and generally situated below half height. Usual number of major septa about 17-24; number of costae generally less than twice the number of septa.

Description. *Form of corallum*. The corallum is wedge shaped, and thus, two different outlines appear in lateral view of the exterior side. Normal to the plane of flattening (broad side of wedge) the outline shows a strongly curved calicinal margin; parallel to this

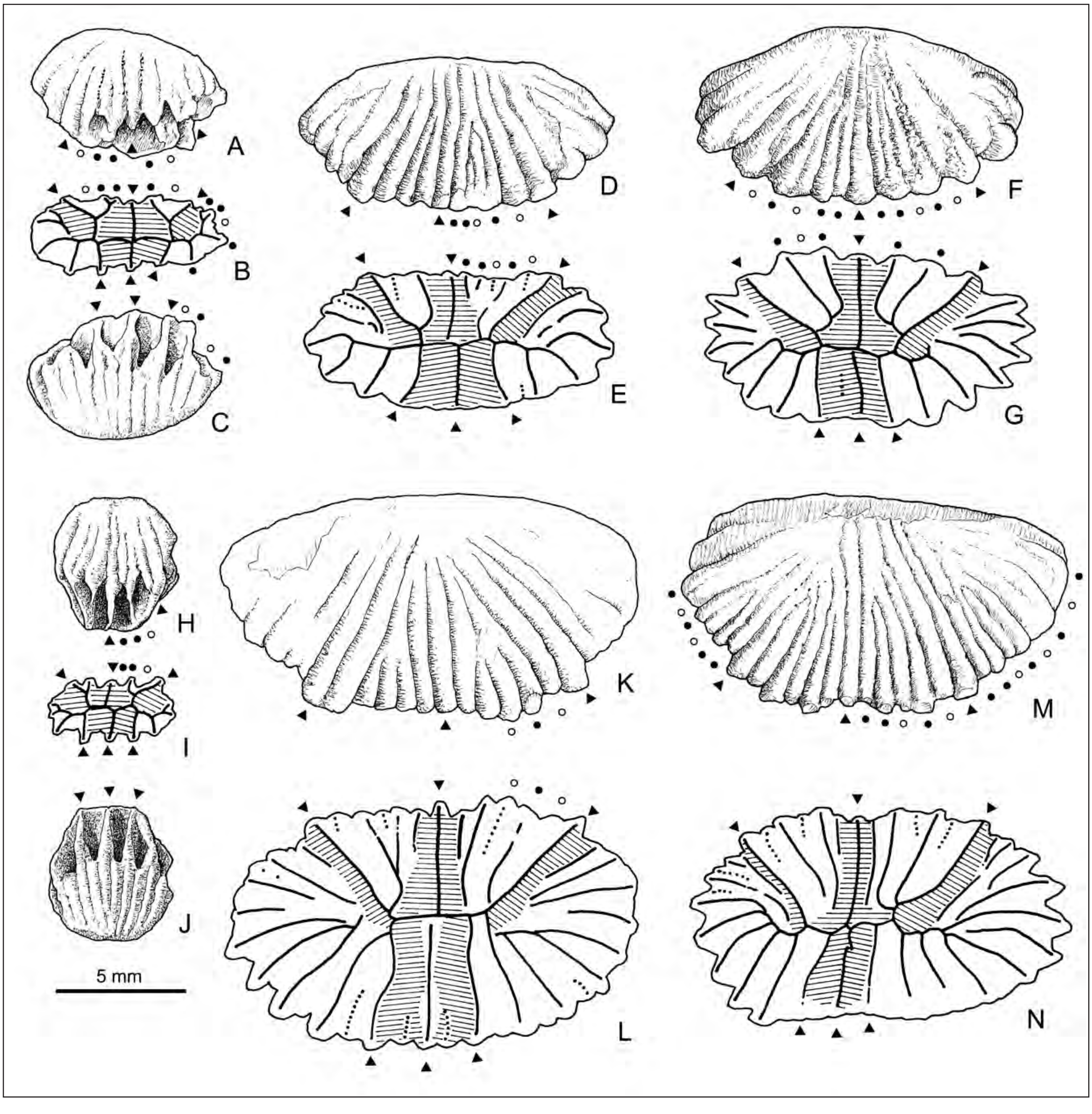

Figure 3. *Angustiphyllum stylophorum*, morphology with its interpretation. Note: for large specimens the columella is not visible on exterior views because the views are not normal to the axial plane of the corallum but to the plane of the broad side of wedge. A-C: LPB 15 368. D-E: LPB 15 361. F-G: LPB 15 360. H-J: LPB 15 348. K-L: LPB 15 358. M-N: LPB 15 355.

plane (narrow side of wedge) the sides of the corallum are flat or gently concave, and commonly in large specimens, the outline of the wedge is wide-mouthed. The maximum corallum diameter is generally situated below one-half of its height (see Table 1, h3/h4 ≤ 1). In calicular view, the outline is ellipsoidal, serrated, the long axis normal to the counter/cardinal plane.

External morphology (Figs 2-3). This exterior shows costae corresponding to major and minor septa. They are wide, smooth and separated by a narrow intercostal furrow, in some cases bearing a line of small pits. Major and minor costae generally have the same morphology; nevertheless, in some specimens the minor costae are less cambered and wider than the major ones. In young specimens the minor costae are shorter than the major ones and their distal ends are indented. In addition, the cardinal costa may be lower than the metacostae. On the counter side the costae are regularly arranged and the protocostae (K and KL) cannot be morphologically distinguished from the metacostae. On the other hand, on the cardinal side, patterns of splitting or insertion of costae are exposed in some cases, especially in large specimens. They occur on the counter side of the alar costae and on both sides of the cardinal one; these patterns are rather irregular. Following the Vollbrecht and/or the Weyer model of appearance of septa, with which we agree (Plusquellec & Semenoff-Tian-Chansky 1972; Hill 1981) it is assumed - in some cases despite appearances - that the last costoseptum arising on the counter side of each alar septum and on both sides of the cardinal one is necessarily a major costoseptum. However, whatever the model of septal insertion, the total number of costae is the same (see chapter measurements).

Specimen	Septal formula		Nbr of major septa	Total nbr of costo-septa	∅L	∅l	Apical angle (d°)	h1	h2	h3	h4	h3/h4	h4/∅L	h3/h2
LPB 15 347	1 7	1 7	22	39	12,8	6,5	51	7,6	9,3	5,2	4,1	1,27	0,32	0,56
LPB 15 348	1 3	1 3	14	23	4,9	2,6	35	3,4	5,4	2,7	2,7	1,00	0,55	0,50
LPB 15 353	1 4	1 5	17	36	9,2	4,3	56	4,8	6,2	2,9	3,3	0,88	0,36	0,47
LPB 15 354	3 6	2 7	24	41	13,2	9,2	67	7,0	7,6	3,7	3,9	0,95	0,30	0,49
LPB 15 355	3 8	3 10	30	52	14,7	8,4	65	6,5						
LPB 15 356	3 7	3 7	26	45	16,7	12,2	72	8,0	9,3	4,2	5,1	0,82	0,31	0,45
LPB 15 357	2 7	2 7	24	42	14,8	10,0	81	6,5	7,6	3,0	4,6	0,65	0,31	0,39
LPB 15 358	3 8	3 8	28	48	15,5	9,5	67	7,6	8,8	3,2	5,6	0,57	0,36	0,36
LPB 15 359	2 7	2 7	24	42	11,7	8,0	70	6,3	6,9	2,5	4,4	0,57	0,38	0,36
LPB 15 360	2 6	2 6	22	44	12,3	6,6	62	6,0	6,8	3,3	3,5	0,94	0,28	0,49
LPB 15 361	1 5	3 5	20	36	11,7	5,3	55	5,7	6,7	3,1	3,6	0,86	0,31	0,46
LPB 15 362	2 6	1 6	21	38	13,8	8,0	57	7,6	6,7	4,1	2,6	1,58	0,19	0,61
LPB 15 363					15,9	10,2	67	7,9	9,3	3,5	5,8	0,60	0,36	0,38
LPB 15 367	1 5	1 5	18	34	7,1	2,9	37	4,6	5,6	2,9	2,7	1,07	0,38	0,52
LPB 15 368	2 4	1 4	17	27	7,6	2,8	32	4,0	5,0	2,3	2,7	0,85	0,36	0,46
LPB 15 369	1 2	1 2	12	18	4,3	1,6	35	2,2	3,6	2,2	1,4	1,57	0,33	0,61
LPB 15 370	1 1	1 1	10	16	3,4	1,5	25	2,1	2,9	1,9	1,0	1,90	0,29	0,66
Mean			20,6	36,3	11,2	6,4	54,9	5,8	6,7	3,2	3,6	1,01	0,34	0,49
Median			21,5	38,5	12,3	6,6	57,0	6,3	6,8	3,1	3,6	0,91	0,32	0,48
Standard deviation			5,6	10,4	4,3	3,4	16,5	1,9	1,9	0,8	1,4	0,39	0,07	0,09

Table 1. Biometric data for *Angustiphyllum stylophorum*.

Calicinal morphology. The calice margin is slightly concave at the short axis of the wedge (not taking into account the columella-like structure) and convex at its long axis. The major septa exhibit a well marked bilateral symmetry and a clear pinnatepattern. The cardinal septum, opposite to the counter septum, is in middle of broad side of the wedge. The proximal parts of the six protosepta remain attached during all stages of development (Fig. 3 B young specimen and Fig. 3 L adult specimen) and thus the fossulae are closed. The cardinal fossula, with its low cardinal septum, is inverted T-shaped in adult specimens; the alar fossulae exhibit a rhopaloid outline; the counter fossula is more or less rectangular and not differentiated from adjacent interseptal loculi. The presence of retrocontratingent major septa is rather usual and gives rise to inconspicuous fossuloidae described for the first time in *Hadrophyllum orbignyi* Milne- Edwards & Haime, 1850 by Plusquellec (2006, fig. 9). The proximal part of the protosepta, and generally the one of the two first metasepta of the counter-lateral/alar quadrants, meet at long axial plane of wedge to form a more or less straight transverse crest. This pattern, diagnostic of *Angustiphyllum*, is in fact very similar to the one shown by the central area of some specimens of *H. orbignyi* figured by Plusquellec (2006, fig.7C-D). A prominent flat columella-like structure showing, when not worn, a protuberance at each extremity, rises from the axial part of the transverse crest of *A. stylophorum*. Remark that, following Milne-Edwards & Haime 1848, the true columella is not of septal origin, the reason why the axial boss is here called columella-like structure. The axis of the corallum (= meeting point of protosepta) is slightly eccentric, invariably towards the counter side. The metasepta are not numerous, especially in the alar/cardinal "quadrants"; see for example the holotype with only one metaseptum in this area, see also the septal formulae of other specimens (Table 1). It should be noted that the septal part (septum sensu stricto) corresponding to the most recent radial structure may be lacking in the calice while its costal part is already exposed on the exterior side. This pattern also has been mentioned in *H. orbignyi* (see Plusquellec 2006, comment of fig. 10). In at least one specimen, the two youngest metasepta in the cardinal fossula show an anomalous contratingent pattern; the adaxial ends of these septa are attached to the protoseptum. The margin of the major septa is generally sharp but in some cases the counter and counter-lateral protosepta show a slightly spatulate morphology with a depressed axis (Plate 1, fig. E). This feature is reminiscent of diplosepta (Weyer 1997). The minor septa are generally not exposed in the calice, but rarely some of them are quite obvious. In specimen LPB 15 353, two narrow ridges bounding the cardinal fossula and showing their ends curved towards the protoseptum are interpreted as minor septa taking into account the unusual morphology of the exterior side of this area (Plate 1, fig. G).

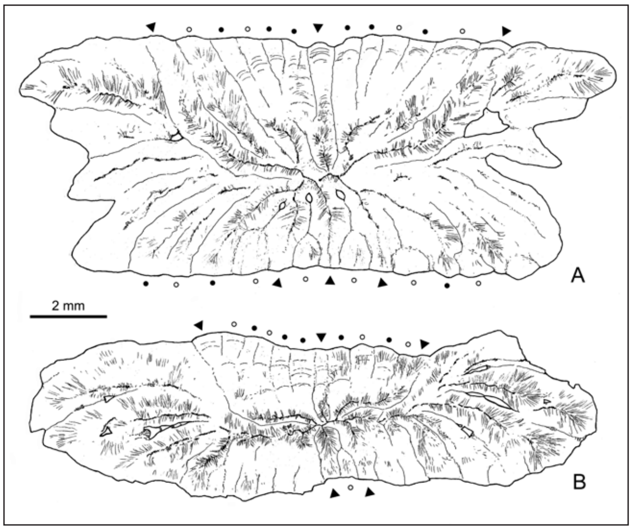

Figure 4. *Angustiphyllum stylophorum*, transverse sections of LPB 15 352, showing the structure and microstructure of the corallum. A: Rather distal section, note the small interseptal loculi between K and KL. B: More proximal section, note the lack of median line in the alar/cardinal quadrant, the interseptal loculi and tabellae at extremities of wedge.

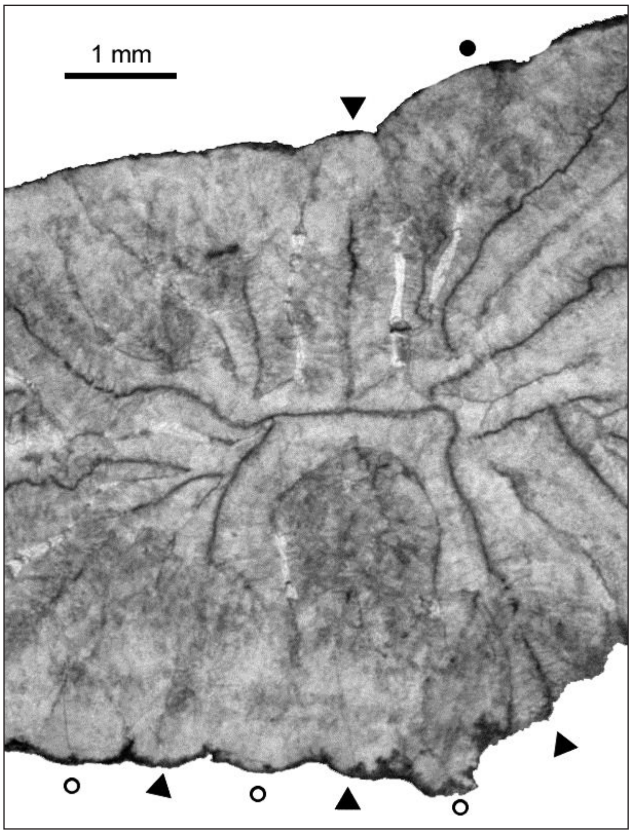

Figure 5. *Angustiphyllum stylophorum*, transverse sections in LPB 15 395, showing the development of interseptal loculi and tabellae.

Internal structure. Transverse sections have been made in four specimens and show more or less the same features. The costo-septa are almost completely contiguous, especially in the medio distal part of the corallum. However, in the proximal part of the corallum narrow interseptal loculi develop mainly in the counter-lateral/alar quadrants (Figs 4B and 5). They show sections of tabulae, or more likely tabellae, probably interstitial tabellae sensu Poty (2002); unfortunately vertical sections of these structures are not available. The area between the peripheral ends of the interseptal loculi and the costal furrows corresponds to the wall: it is of the septothecal type. In the central area of the proximal and medio-distal sections made in specimen LPB 15 352 (Fig. 4A) the protosepta and the first inserted metasepta exhibit an obvious median dark line and a contratingent pattern. The cardinal and the counter septa are not exactly opposite. In the alar/cardinal quadrants of the proximal transverse section the median line of the metasepta does not appear, and only the slightly divergence of the fibers and the concentric growth lines allow their identification (Fig. 4B). In the counter-lateral/alar "quadrants" the median line of the metasepta is better exposed and they appear contratingent or contraclined. In the alar/cardinal "quadrants" of the distal transverse section it is to be noted 1) that the dark line of the first pair of major metasepta is well developed and that they are inserted by splitting of the median line of the protoseptum and 2) that the first pair of minor septa seems to be inserted not by splitting of the median line, but by appearing in fact in the fork made by the two major septa like an interpolated sheet. In the two sections, the minor costo-septa are longer in the alar/cardinal quadrants than in the counter-lateral/alar ones, and they are difficult to recognize in the extremities of wedge. In the counter/counter-lateral and the "older" part of the counter/alar quadrants the minor structures are very short and probably mainly represented by their costal part. The features described in LPB 15 352 can be recognized in the transverse sections of other specimens. The transverse sections as well as the longitudinal one do not show any structures that could be called synapticulae. In our opinion, their presence in *Angustiphyllum* as stated by Soto (1986) cannot be supported and is the result of a misinterpretation of the transverse crest.

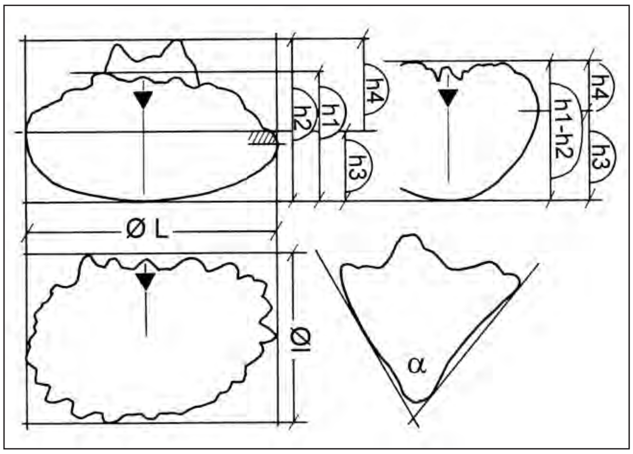

Figure 6. *Angustiphyllum*. Method of measurements. In specimens devoid of columella (*A. vidalae*, *A. cuneiforme*) h1 and h2 are amalgamated.

Microstructure. In the transverse sections of *A. stylophorum* the median dark line of the septa is continuous in the axial part of the corallum, and somewhat discontinuous, even dotted, in its periphery (Fig. 4). On both sides of the midplane of the septum the fibers are slightly outwardly divergent. Thus these features show some similarities with those figured by Plusquellec & Semenoff-Tian-Chansky (1972, fig. 8-10) in *Combophyllum osismorum* where a trabecular microstructure has been recognized. However, in longitudinal sections the fibers appear to be directed at right angles to the growth lamellae and no trabecular pattern is exposed. Thus, the costo-septa belong - mainly at least - to the fibrolamellar type. A transverse section (ultra thin section) in the columella-like structure shows a microlamellar thickening and a granular nature of the median line.

Measurements. Some comments and pecise details about the measurements (see Fig. 6) and the caption of Table 1 are given below.

- septal formula: the 6 protosepta are diagrammatically illustrated and the number of major metasepta indicated in each quadrant.
- number of major septa includes the 6 protosepta.
- the total number of costo-septa is counted on the exterior side of the corallum and includes all the costae corresponding to the protosepta, major metasepta and minor septa.
- the maximum diameter of the corallum at long axial plane of wedge is here called ØL, normal to this measurement is the minimum diameter Øl.
- the apical angle (narrow side of wedge) and height of the corallum are taken as shown on Figure 6.
- for each measurement the mean, the median, the standard deviation are given in the table.

In addition to Table 1, some diagrams (Figs 7-8) and box plots (Fig. 9) are provided.

Discussion. Apart from *A. stylophorum* n. sp. only two species of *Angustiphyllum* are described: the type-species *A. cuneiforme*

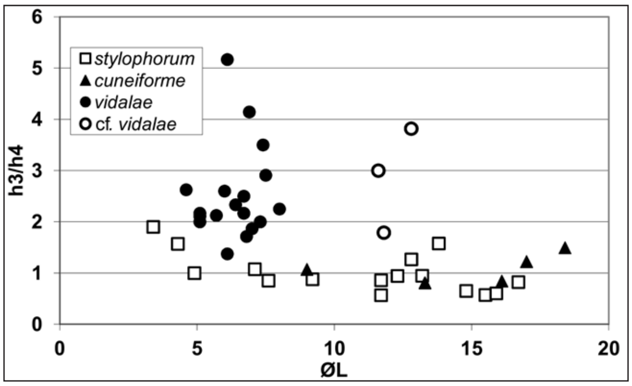

Figure 7. Diagram showing the relationships between the length of the corallum (ØL) and its height and relative curvature, represented by the ratio h3/h4 (see Fig. 6) for 3 species of *Angustiphyllum*.

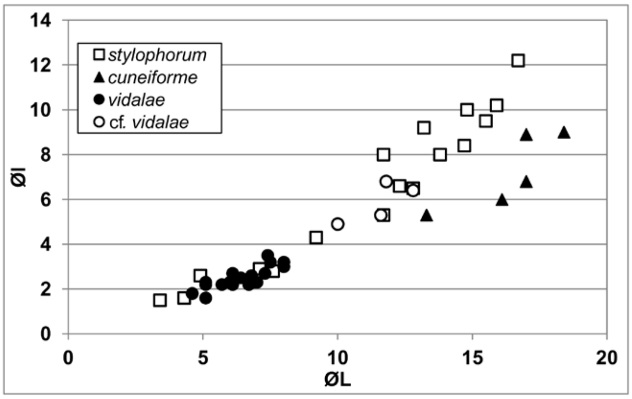

Figure 8. Relationships between length (ØL) and width (Øl) of the corallum for 3 species of *Angustiphyllum*.

Altevogt and *A. vidalae* n. sp. (this paper).

A. stylophorum clearly differs from these species by the presence of a flat columella-like structure, the usually wide-mouthed outline of the narrow side of wedge and by some biometric data such as the size of the corallum, the apical angle, the number of septa and the structure of the septal formula (see Tables 1-4).

In addition, the transverse crest of *A. cuneiforme* is much straighter than that of *A. stylophorum* (Figs 10A and 11A, D-E) and its wedge is flatter, with a transverse proximal section showing a slight median narrowing.

Our new species differs from *Angustiphyllum*? sp. A Soto, 1986 by its more flattened transverse outline and the shallower intercostal furrows. The interseptal loculi shown by Soto - figura 2A - are in fact opened towards the margin, especially in the counter part of figure, and thus are intercostal furrows.

***Angustiphyllum vidalae* n. sp.**
(Figs 12-13; Plate 1, figs N-W)

2011 *Angustiphyllum* n. sp. 2. Plusquellec et al., p. 128, fig. 8-13.

Derivation of name. The species is named after Dr. Muriel Vidal (UBO, Brest).

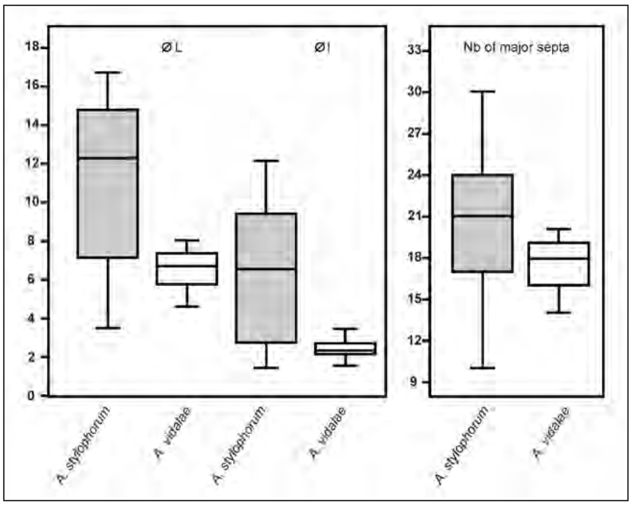

Figure 9. Boxplot representing biometric data for *Angustiphyllum stylophorum* and *Angustiphyllum vidalae*. ØL and Øl respectively length and width of the corallum.

Holotype. Specimen LPB 15 349.

Type locality and horizon. Saint-Fiacre, district of Crozon, Finistère (France), Saint-Fiacre Formation, Upper Eifelian.

Material. 25 specimens with calcitic skeleton from the type locality (LPB 15 349-15 350, LPB 15 371-15 391), of which 2 thin sections, 2 acetate peels.

Diagnosis. Small species of *Angustiphyllum* with flat to gently convex calicinal outline on broad side of wedge. Sides of the corallum flat to slightly convex on the narrow side of wedge. Apical angle mainly circa 35°. Maximum corallite diameter usually between 5.5-7.5 mm and markedly situated above half of its height. Number of major septa about 16-20; number of costae generally less than twice the number of septa.

Description. *Form of corallum*. On broad side of wedge, the

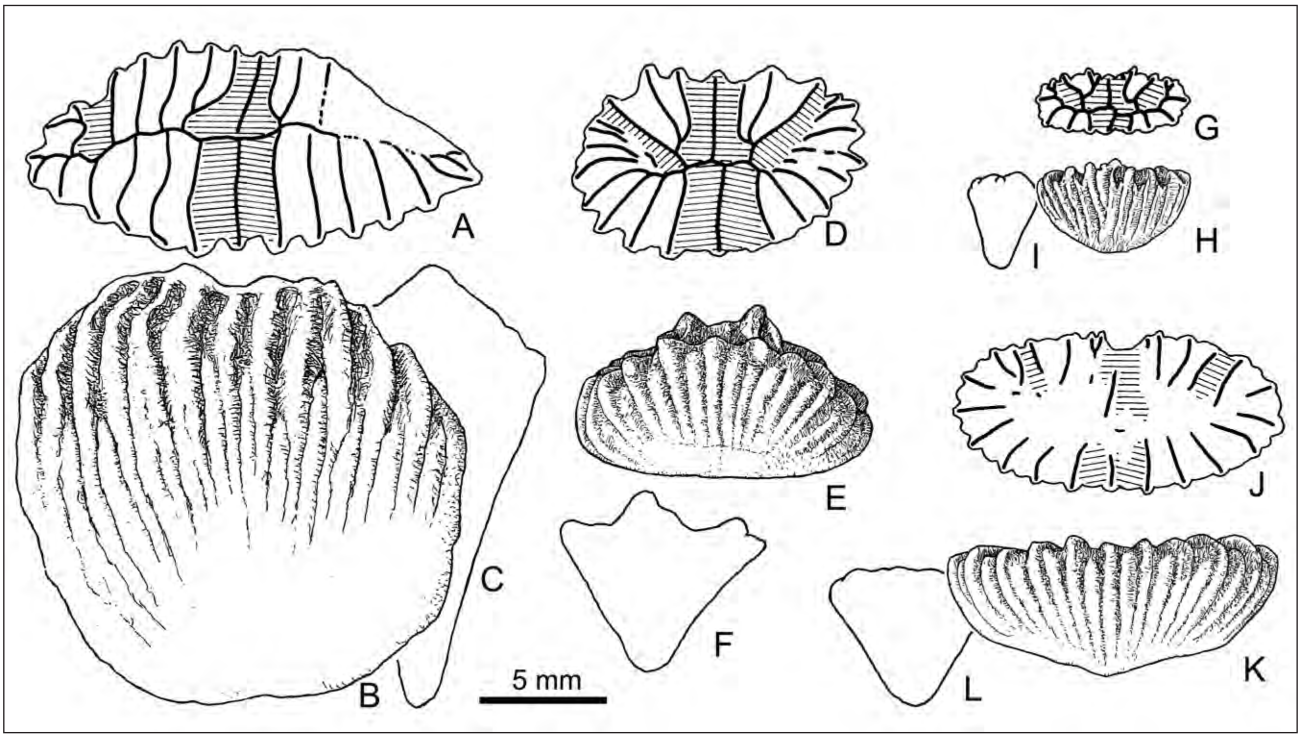

Figure 10. For comparison, the species of *Angustiphyllum* at similar magnification. Calicinal views, exterior (counter side) from broad side of wedge and outline of narrow side of wedge. A-C: *A. cuneiforme*, GIM B2. 21. 45. D-F: *A. stylophorum*, LPB 15 359. G-I: *A. vidalae*, LPB 15 380. J-L: *A.* cf. *vidalae*, LPB 15 392.

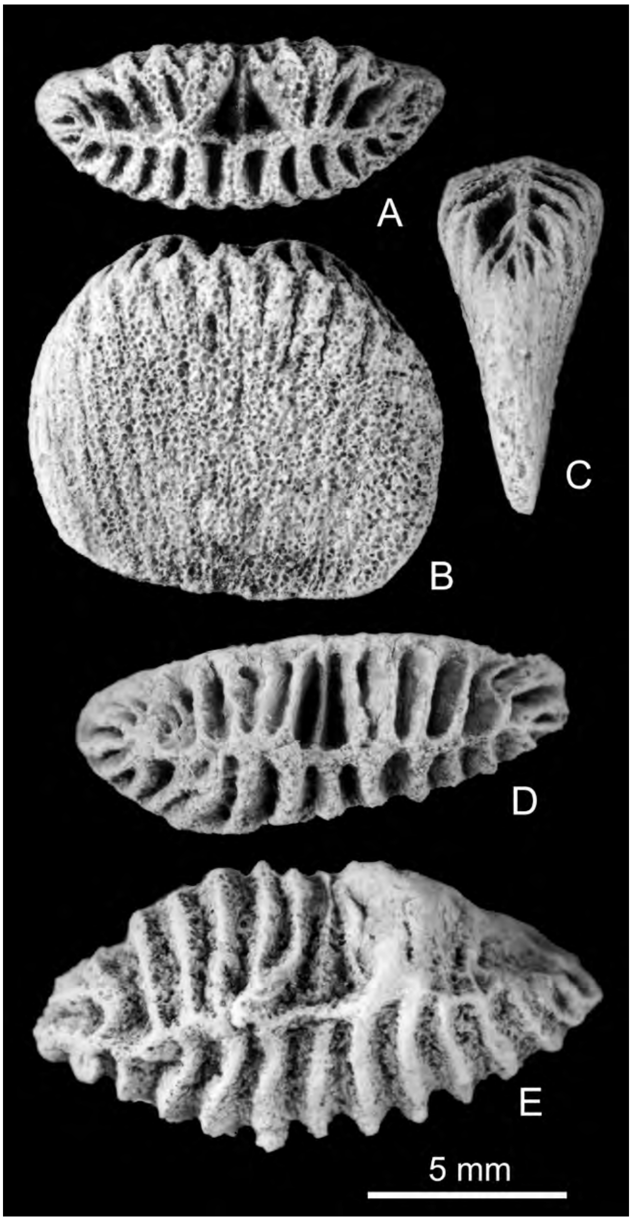

Figure 11. *Angustiphyllum cuneiforme*. A-C, GIM B2. 21. 44. A: Calicinal view. B: Side view of broad side of wedge. C: Side view of narrow side of wedge. D: DPO 11 478, calicinal view. E: GIM B2.21.45, calicinal view.

calicinal part of the outline is flat to gently convex, while its proximal part is regularly rounded (Fig. 12A, C) to wide U-shaped (Fig. 12K). The maximum corallum diameter is clearly situated above one-half height (see Table 2, h3/h4 mainly circa 2.50). On the narrow side of wedge view, the sides of the corallum are flat to slightly convex and the apical angle rather acute. In calicinal view, the broad sides of the wedge appear more flattened than in *A. stylophorum* and thus the calice of *A. vidalae* is proportionally more elongated; the indentations corresponding to the minor costae are well marked but the costae themselves are generally not very obvious.

External morphology. The costae corresponding to both major and minor septa are well marked and particularly well exposed on the broad side of the wedge. The minor costae are generally wider than the major ones and their distal part shows a strong notch (Fig. 12F and Pl. 1, fig. P). In some specimens, a row of small pits emphasizes the intercostal furrows (Fig. 12G).

Calicinal morphology. Roughly speaking, the pattern of proto- and metasepta and of fossulae is very close to that of *A. stylophorum* and, in fact, characterizes the genus *Angustiphyllum*. Nevertheless, the major septa are generally thicker and less numerous in *A. vidalae*. The presence of smooth dentations on the margin of some septa (Pl. 1, fig. T) reflects its underlying structure. This morphology is usual in corals having the septa composed of simple trabeculae such as *Combophyllum osismorum* (Plusquellec & Semenoff-Tian-Chansky 1972); see below comments about the microstructure.

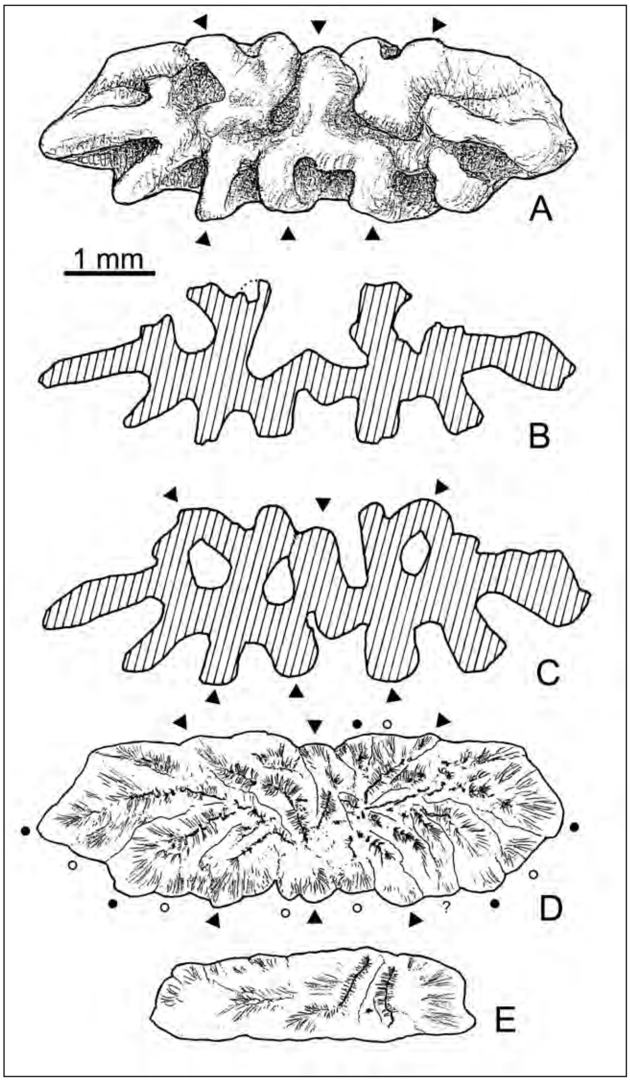

Figure 13. *Angustiphyllum vidalae*, LPB 15 350. Calicinal view of the corallum (A) and serial transverse sections, from distal part of the corallum (B) to proximal (E). B-C: Acetate peels showing the "decorative" outline of the very distal sections, but the microstructure is not visible. D: Note that the costo-septa are contiguous in the whole section; thin section Bb 964. E: See text; thin section Bb 965.

Internal structure. Two transverse sections have been made from a single specimen. In the proximal section the septa are impossible to identify, most of them being devoid of median line (Fig. 13E); in the distal section the septal units are clearly individualized but their contratingent pattern is less well expressed than in *A. stylophorum* (Fig. 13D). The fibrous microstructure of the septa and costae is indisputable but in some parts of the median plane of septa, the dotted pattern of the "dark" line is reminiscent of trabeculae. Unfortunately no longitudinal section is available.

Measurements. The biometric data are provided in Table 2 (see comments of Table 1 for captions) and diagrams (Figs 7-9).

Discussion. Apart from its small size, *A. vidalae* differs from both *A. cuneiforme* and *A. stylophorum* by its flat calicinal outline on the broad side of the wedge, by the flat to slightly convex outline of its exterior sides on the narrow side of the wedge, and by the distal position of the maximum diameter; from *A. stylophorum* by the lack of columellar structure.

Angustiphyllum cf. *vidalae*

(Figs 10J-L, 14)

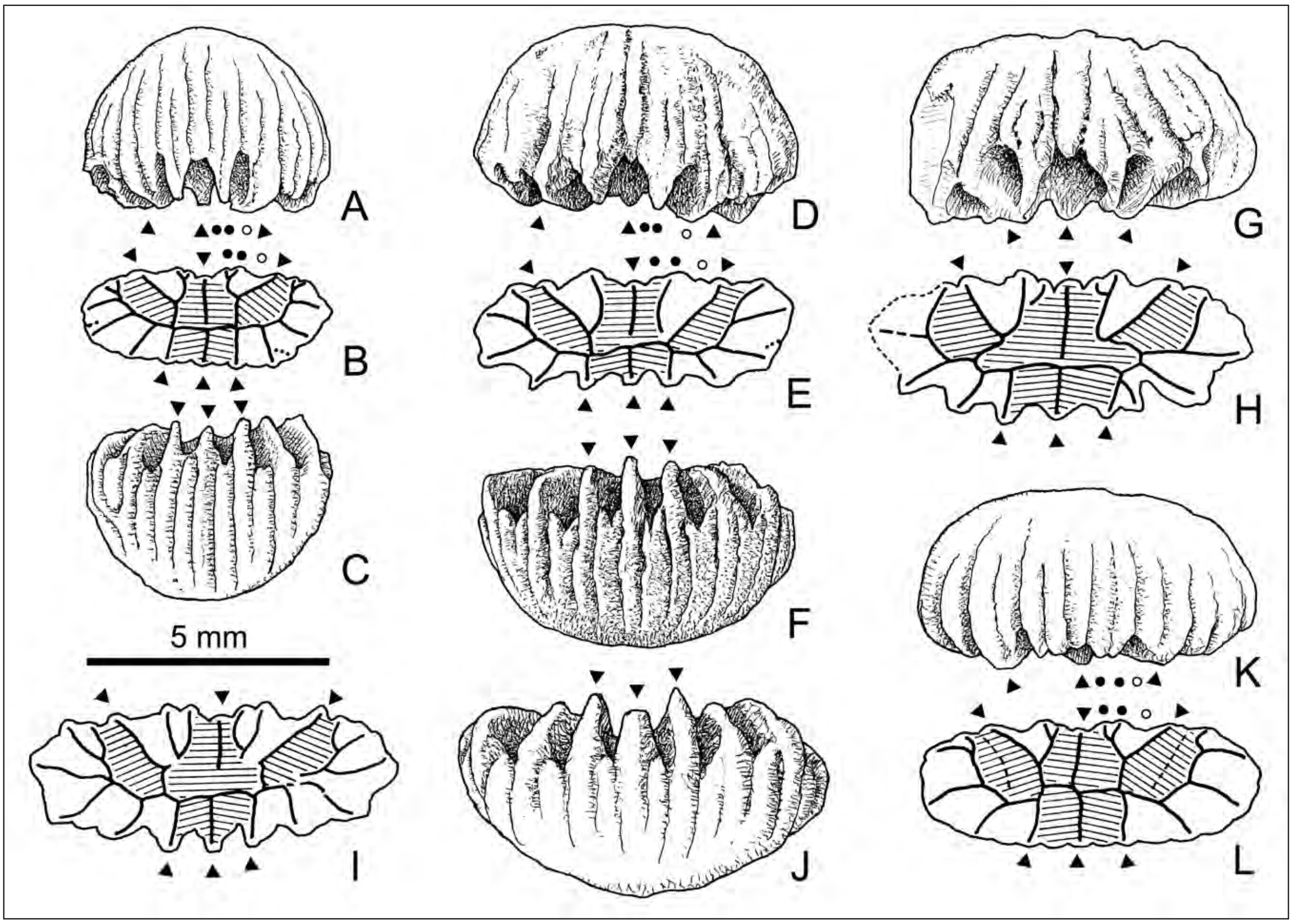

Figure 12. *Angustiphyllum vidalae*, morphology. A-C: LPB 15 388. D-F: LPB 15 349, holotype. G-H: LPB 15 374. I-J: LPB 15 391. K-L: LPB 15 375, note the presence of an interseptal crest in the alar fossulae, described for the first time in *Hadrophyllum orbignyi* by Plusquellec (2006).

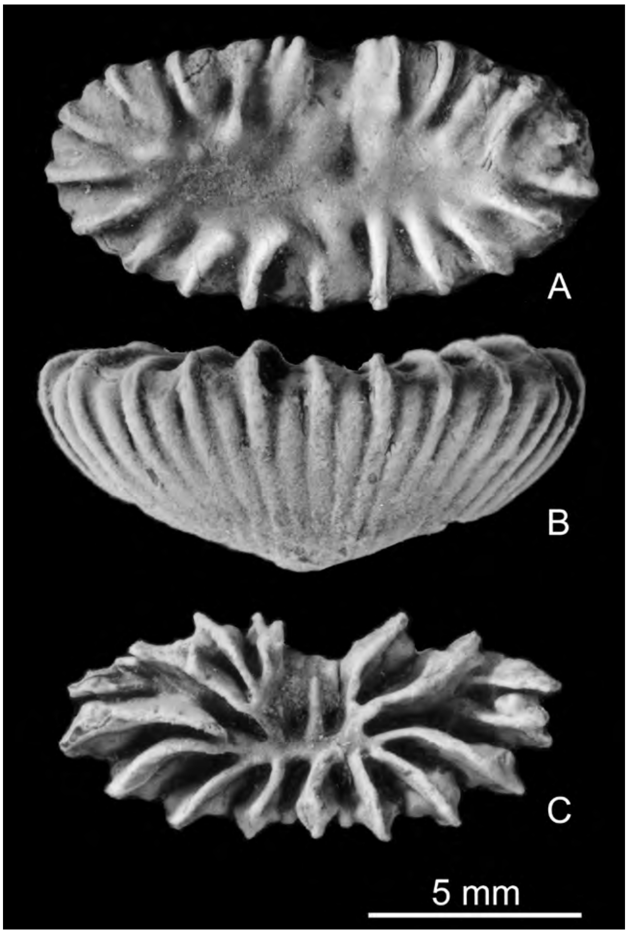

Figure 14. *Angustiphyllum* cf. *vidalae*. A-B, LPB 15 392. A: Calicinal view. B: Side view of broad side of wedge. C: LPB 15 394, calicinal view.

Material. 3 specimens with calcitic skeleton from Saint-Fiacre, district of Crozon, Finistère (France), Saint-Fiacre Formation, Upper Eifelian, same level as *A. stylophorum* and *A. vidalae*, LPB 15 392-15 394; 3 specimens in natural cast from 1) Le Caro, along the road between the harbour and Lannéguel, district of Plougastel-Daoulas, Finistère, LPB 15 414-15 415, 2) Persuel, district of Crozon, locality PE 46 in Morzadec 1983, fig. 14, LPB 15 416, Saint-Fiacre Formation, (probably Upper) Eifelian. In the localities of Le Caro and Persuel, *Angustiphyllum* is found together with *Asteropyge cantarmorica* (Morzadec, pers. comm.).

Description. Form of corallum. On the broad side of the wedge, the calicinal outline is flat and that of the proximal part more or less rounded or like a widely opened V (Fig. 14B). The height of the corallum is proportionally small and the ratio between height and maximum diameter is 1:2.2 - 3.2; the maximum diameter of the corallum is situated in its distal part as in *A. vidalae*. On the narrow side of wedge, the sides of the corallum are slightly convex and the apical angle rather significant (65°-99°), i.e. markedly greater than that of *A. vidalae*. In calicinal view, the outline shows indentations corresponding to major and minor costae. The major ones exhibit a clear-cut profile, the minor ones are distinctly less marked.

External morphology. The major and minor costae are roughly of the same size in LPB 15 392, 15 393 and LPB 15 414, the minor costae clearly wider and notched in their distal part in LPB 15 594.

Calicinal morphology. In one of the specimens (LPB 15 394) the pattern of major septa and fossulae is close to that of *A. stylophorum*, in the other specimens the septa seem to be embedded in a kind of calicinal platform, the pinnate pattern is poorly or not exposed and the fossulae are not closed. The cardinal septum is invariably low as is usual in *A. vidalae*.

Measurements. The specimens are larger than those of *A. vidalae* but close to *A. stylophorum* (see Table 3).

Specimen	Septal formula	Nbr of major septa	Total nbr of costo-septa	∅L	∅l	Apical angle (d°)	h1-h2	h3	h4	h3/h4	h4/∅L	h3/h2
LPB 15 349	1 1 4 5	17	32	6,4	2,5	35	4,0	2,8	1,2	2,33	0,19	0,70
LPB 15 350	1 1 3 3	14	26	7,4	3,5	37	4,5	3,5	1,0	3,50	0,14	0,78
LPB 15 371	2 1 5 5	19	32	6,7	2,2	29	3,5	2,5	1,0	2,50	0,15	0,71
LPB 15 372				8,0	3,0		3,6					
LPB 15 373	2 2 4 4	16	28	7,3	2,7	39	4,5	3,0	1,5	2,00	0,21	0,67
LPB 15 374	2 2 4 4	18	30	8,0	3,2	57	3,9	2,7	1,2	2,25	0,15	0,69
LPB 15 375	2 2 4 4	18	28	6,8	2,6	28	3,8	2,4	1,4	1,71	0,21	0,63
LPB 15 376	1 1 4 4	16	28	7,0	2,3	31	4,3	2,8	1,5	1,87	0,21	0,65
LPB 15 377	2 2 4 4	18	28	6,7	2,3	25	3,8	2,6	1,2	2,17	0,18	0,68
LPB 15 379	2 2 4 4	17	27	5,1	2,3	33	3,6	2,4	1,2	2,00	0,24	0,67
LPB 15 380	2 2 5 5	20	32	6,1	2,7	40	3,7	3,1	0,6	5,17	0,10	0,84
LPB 15 382	2 2 4 4	18	32	6,1	2,2	28	3,8	2,2	1,6	1,38	0,26	0,58
LPB 15 384	1 1 4 4	16	28	4,6	1,8	32	2,9	2,1	0,8	2,63	0,17	0,72
LPB 15 386	2 1 5 3	15	25	5,1	1,6	39	2,8	1,9	0,9	2,11	0,18	0,68
LPB 15 387	2 2 5 5	20	32	6,0	2,3	32	3,6	2,6	1,0	2,60	0,17	0,72
LPB 15 388	2 2 5 5	20	32	5,1	2,2	25	3,8	2,6	1,2	2,17	0,24	0,68
LPB 15 389		17		5,7	2,2	44	2,5	1,7	0,8	2,13	0,14	0,68
LPB 15 390	1 1 4 4	16	30	6,9	2,3	39	3,6	2,9	0,7	4,14	0,10	0,81
LPB 15 391	2 2 5 5	20	32	7,5	3,2	45	4,3	3,2	1,1	2,91	0,15	0,74
Mean		17,5	29,5	6,4	2,5	35,4	3,7	2,6	1,1	2,53	0,18	0,70
Median		17,5	30,0	6,7	2,3	34,0	3,8	2,6	1,2	2,21	0,18	0,69
Standard deviation		1,8	2,4	1,0	0,5	8,1	0,5	0,5	0,3	0,92	0,05	0,06

Table 2. Biometric data for *Angustiphyllum vidalae*.

Discussion. The specimens share some morphological, and above all some biometric characteristics with *A. stylophorum* but the outline of broad side of wedge and especially the morphology of the calice (which is devoid of columella) show strong affinities with *A. vidalae*.

In our opinion these specimens could be gerontic forms of this species. Moreover, it should be noted that in the Cantabrian Mountains as well as in the Armorican Massif, beside the standard species there are rare specimens showing unusual morphology: *A*.? sp. A Soto, 1986 and A. cf. *vidalae*, this paper.

4. Discussions

4.1. Fossil record

The genus *Angustiphyllum* is recorded for the first time in the Armorican Massif where at least two species lived together in the same environment during Upper Eifelian time.

Owing to the number of specimens collected the representatives of this genus are not scarce and thus could be a good index for the Upper Eifelian and useful for mapping, especially in the Armorican Massif.

Specimen	Septal formula	Nbr of major septa	Total nbr of costo-septa	∅L	∅l	Apical angle (d°)	h1-h2	h3	h4	h3/h4	h4/∅L	h3/h2
LPB 15 392	3 3 7 6	25	43	12,8	6,4	65	5,3	4,2	1,1	3,82	0,09	0,79
LPB 15 393	2 2 5 5	20	40	11,8	6,8	77	5,3	3,4	1,9	1,79	0,16	0,64
LPB 15 394	3 1 5 5	20	35	11,6	5,3	99	3,6	2,7	0,9	3,00	0,08	0,75
LPB 15 414	3 3 5 4	21		10,0	4,9		4,5					
Mean		21,5	39,5	11,6	5,9	80,3	4,7	3,4	1,3	2,87	0,11	0,73
Median		20,5	40,0	11,7	5,9	77,0	4,9	3,4	1,1	3,00	0,09	0,75
Standard deviation		2,4	4,0	1,2	0,9	17,2	0,8	0,8	0,5	1,02	0,05	0,08

Table 3. Biometric data for *Angustiphyllum* cf. *vidalae*.

4.2. Palaeobiogeography

The genus *Angustiphyllum* is known in the (Upper) Eifelian of the Cantabrian Mountains and in the western part of the Armorican Massif, the two areas forming the Ibero-Armorican Domain situated on the north-western margin of Gondwana on the shelf of the Rheic Ocean (Fig. 15).

4.3. Mode of life

According to the morphology of the corallum, the genus *Angustiphyllum* shares numerous characteristics with 1) the Emsian Rugosa *Combophyllum* Milne-Edwards & Haime, 1850; 2) the Eocene-Recent Scleractinia *Shenotrochus* Milne-Edwards & Haime, 1848; and 3) despite the lack of costae, the Eocene-Recent *Flabellum* Lesson, 1831; thus its mode of life could be similar.

The presence of costae and consequently the lack of the so-called epitheca indicate that the polyp was fully covered with living tissue. Thus, *Angustiphyllum* belongs to the automobile free living coral group and was probably able to move (lateral migration) on the soft bottom of the Saint-Fiacre sea, or was at least capable of vertical movement to right or exhume itself (Plusquellec et al., 1999).

The presence of *Angustiphyllum* species in the rather deep environment of the Saint-Fiacre Formation (the *Angustiphyllum*-bearing level is mainly in the distal upper offshore) provides interesting data on the bathymetric distribution of the genus. Nevertheless, it would be hazardous to correlate its presence with a given depth. For example, if we refer to extant Scleractinia, the cuneiform *Sphenotrochus andrewianus* Milne-

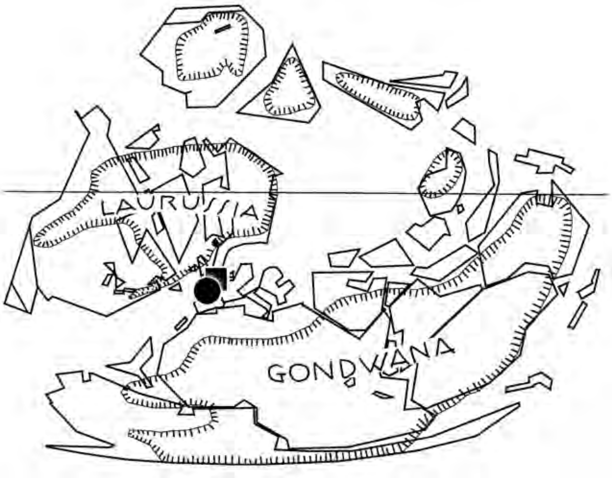

Figure 15. Paleogeographic distribution of *Angustiphyllum*. Black square for *A. stylophorum*, *A. vidalae* and *A*. cf. *vidalae*; black circle for *A. cuneiforme*.

Specimen	Septal formula	Nbr of major septa	∅L	∅l	Apical angle (d°)	h1-h2	h3	h4	h3/h4	h4/∅L	h3/h2
Holotype		27	17,0	8,9		14,0	7,7	6,3	1,22	0,37	0,55
Fig. 11 Altev.			9,0			8,7	4,5	4,2	1,07	0,47	0,52
Fig. 8 Altev.					35						
DPO 11 478	3 3 10 9	31	16,1	6,0	27	14,0	6,4	7,6	0,84	0,47	0,46
DPO 11 479	3 3 13 10	35	17,0	6,8	34	12,0					
GIMB2,21,45	4 8		18,4	9,0	33	18,7	11,2	7,5	1,49	0,41	0,60
GIMB2,21,44	3 3 7 8	26	13,3	5,3	28	11,4	5,1	6,3	0,81	0,47	0,45
Mean		29,8	15,1	7,2	31,4	13,1	7,0	6,4	1,09	0,44	0,51
Median		29,0	16,6	6,8	33,0	13,0	6,4	6,3	1,07	0,47	0,52
Standard deviation		4,1	3,5	1,7	3,6	3,4	2,7	1,4	0,28	0,05	0,06

Table 4. Biometric data for *Angustiphyllum cuneiforme*.

Edwards & Haime, 1850 (which morphology is very similar to that of *Angustiphyllum*) lives between 15 to 105 m depending of the localities (Zibrowius, 1980).

5. Acknowledgments

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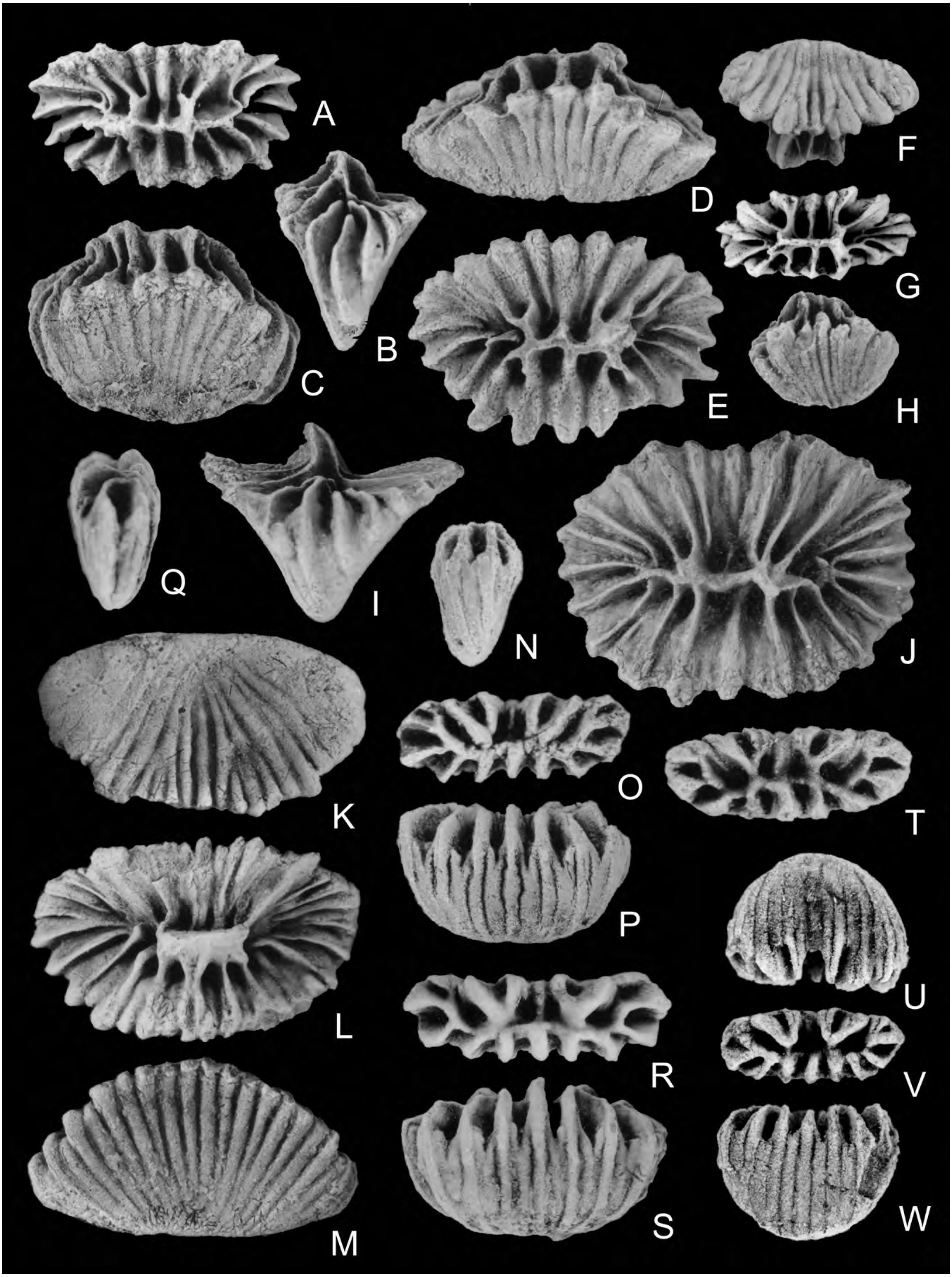

Plate 1. Morphology of *Angustiphyllum stylophorum* (A-M) and *A. vidalae* (N-W). A, G, J, L, O, R, T calicinal views, C, D, F, K, M, P, S, U, W views of broad side of wedge, B, Q, N views of narrow side of wedge. A-C: LPB 15 347, holotype, D-E: LPB 15 357, F-G: 15 353, H: LPB 15 367, I-J: LPB 15 356, K-M: LPB 15 358, N-P: LPB 15 349, holotype, Q-S: LPB 15 376, T: LPB 15 375, U-W: LPB 15 388.
Magnification: *A. stylophorum* x4; *A. vidalae* x7.

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New species of *Frechastraea* Scrutton, 1968 at the base of the Late Frasnian in Belgium

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ABSTRACT. *Frechastraea coeni* n. sp. is widely distributed at the base of the Late Frasnian from the Philippeville Massif, the north side of the Dinant Synclinorium, the south side of the Namur Synclinorium and the Vesdre Massif. It occurs within the Early *Palmatolepis rhenana* conodont Zone and is locally associated with *F. glabra* n. sp. and *F. phillipsastraeiformis* (Moenke, 1954). However, *F. phillipsastraeiformis*, which is also described in this paper, may be already present at the top of the Middle Frasnian from the Philippeville Massif and the south side of the Dinant Synclinorium.

KEYWORDS: Rugose corals, taxonomy, stratigraphy, Namur-Dinant Basin, Frasnian.

1. Introduction

This paper is devoted to the taxonomic description of *Frechastraea* species present at the base of the Late Frasnian of Belgium. These species are *Frechastraea phillipsastraeiformis* (Moenke, 1954), *F. coeni* n. sp. and *F. glabra* n. sp. They occur in the Neuville Formation from the Philippeville Massif and the north-western part of the Dinant Synclinorium as well as at the base of the Aisemont Formation from the north side of the Dinant Synclinorium, the south side of the Namur Synclinorium and the Vesdre Massif. These lithostratigraphic units have been described in detail by Boulvain et al. (1999) and Bultynck & Dejonghe (2002). As for the base of the Late Frasnian, it has been fixed recently by the Subcommission on Devonian Stratigraphy (Newsletter N° 26 of the Subcommission on Devonian Stratigraphy printed in March 2011, p. 11), at the entry of the conodont *Palmatolepis semichatovae*. According to Sandberg et al. (1992), the entry of *P. semichatovae* is observed within the Early *Palmatolepis rhenana* Zone, together with the first occurrence of *Ancyrognathus triangularis*, in bed 150 lying 2.6 m above the base of the Neuville Formation as it is exposed along the southern access road to the Lion quarry at Frasnes, on the south side of the Dinant Synclinorium.

The main part of the material described herein was collected by the author *in situ* during geological surveys made bed by bed in different localities from the southern part of Belgium (Fig. 1). This sampling is supplemented by a few older thin sections referred in this paper to the "Old collection from the Institut royal des Sciences naturelles de Belgique".

2. Geological and stratigraphical setting

The Late Frasnian of the Philippeville Massif in the southwest central part of the Dinant Synclinorium is noteworthy due to the occurrence of bioherms of red limestone belonging to the Petit-Mont Member. These bioherms start their development in the Neuville Formation and continue to grow up more or less high in the overlying Les Valisettes Formation (Fig. 2). The base of the Late Frasnian can be identified in Neuville about 6 m above the base of the Neuville Formation, at the first occurrence of *Ancyrognathus triangularis*. This locality has been studied among others by Coen (1978).

At the very base of the Neuville Formation, massive rugose corals are represented by *Hexagonaria davidsoni* (Milne-Edwards & Haime, 1851), *H. mae* Tsien, 1978 and *Scruttonia bowerbanki* (Milne-Edwards & Haime, 1851). *Frechastraea phillipsastraeiformis*, the first representative of the genus *Frechastraea* Scrutton, 1968 appears in association with the last specimens of *Hexagonaria davidsoni*. It is still present at the base of the Late Frasnian where it is accompanied by numerous colonies of *F. coeni*. The latter taxon occurs also in the lower part of the Petit-Mont Member together with *F. glabra* and sometimes *F. limitata* (Milne-Edwards & Haime,1851). *F. micrastraea* (Penecke, 1904) appears in the upper part of the small lens of Les Bulants quarry at Neuville and is associated with *Phillipsastrea ananas* (Goldfuss, 1826) in the upper part of the larger bioherms of Petit-Mont quarry at Vodelée and Beauchâteau quarry at Senzeille. *Ancyrognathus asymmetricus* indicating the Late *Palmatolepis rhenana* Zone has been identified by Coen et al. (1977) in the first two outcrops together with *Frechastraea micrastraea* and *Phillipsastrea ananas*.

The Neuville Formation is also exposed in all the north-western part of the Dinant Synclinorium. In localities such as Barbençon (Dumoulin, 2001), Laneffe and Gourdinne (Dumoulin & Marion, 1997) and Gerpinnes, *Frechastraea coeni* is abundant at the base of the lithostratigraphic unit and is associated with

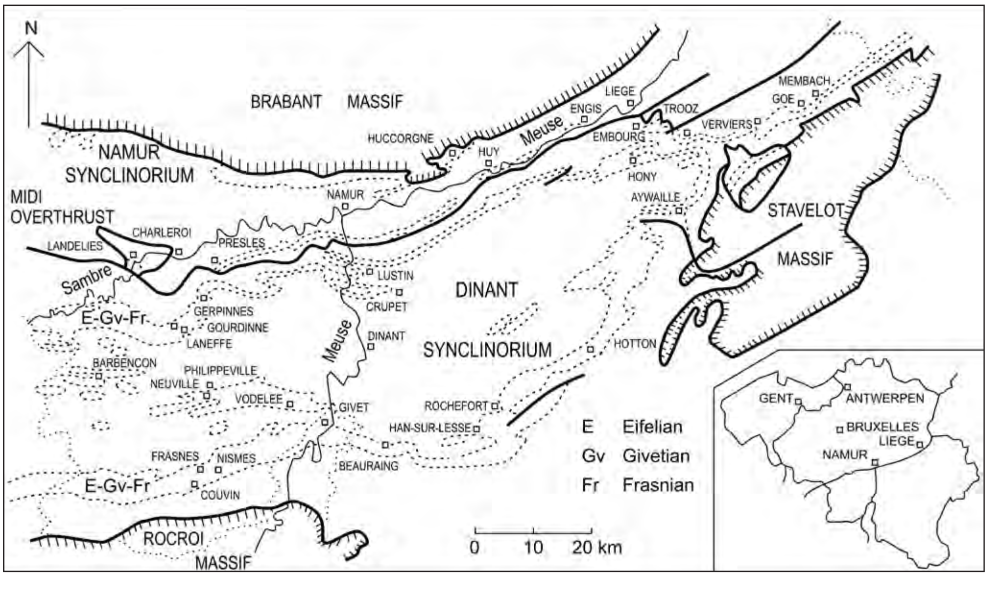

Figure 1. Geological setting and locality map in the southern part of Belgium.

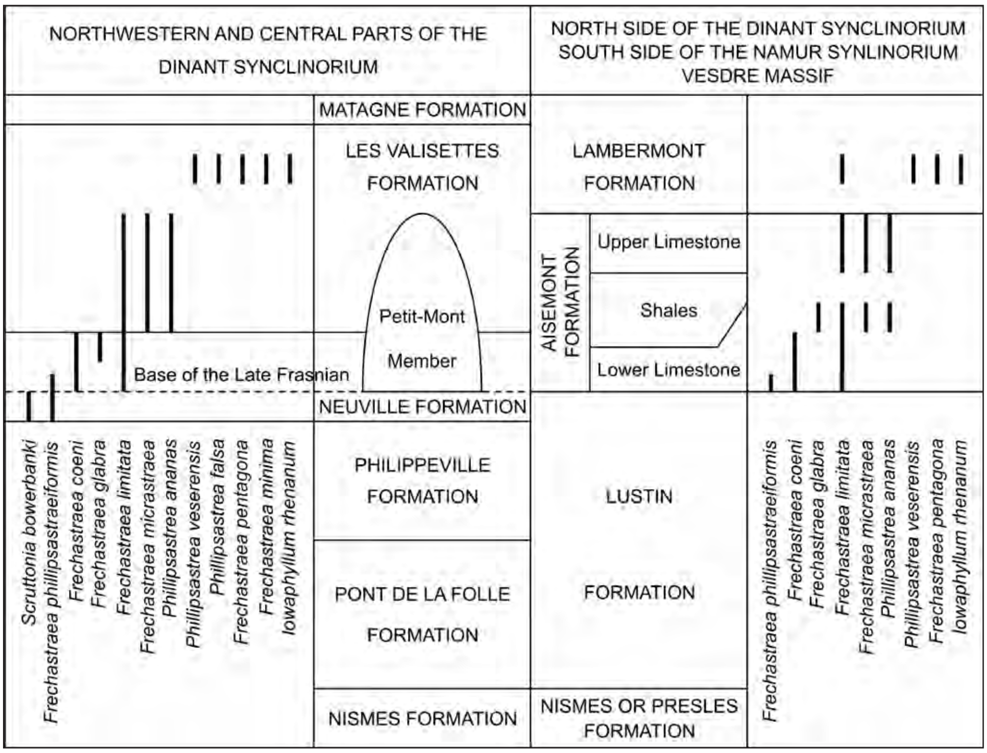

Figure 2. Stratigraphic distribution of massive rugose corals in the Late Frasnian from the northwestern and central parts of the Dinant Synclinorium as well as from the north side of the same structural area, the south side of the Namur Synclinorium and the Vesdre Massif.

a few specimens of *F. phillipsastraeiformis* and *F. limitata*. However, *Hexagonaria davidsoni* is still present at Barbençon, about one metre before the first *Frechastraea*.

To the east of the Meuse valley, the Neuville Formation passes laterally into the Aisemont Formation which is characterized by two levels of limestone separated by shales. This lithostratigraphic unit occurs on the north side of the Dinant Synclinorium from Lustin to Hony (Coen-Aubert & Coen, 1975) and also at Aywaille and Comblain-la-Tour along its north-eastern border (Coen, 1974), in the Vesdre Massif and the Theux Window (Coen-Aubert, 1974a, 1974b), in the Landelies outlier (Coen, 1976), along the south side of the Namur Synclinorium from Presles to Engis (Coen-Aubert & Lacroix, 1979) and at Huccorgne on the north side of the Namur Synclinorium (Coen-Aubert & Lacroix, 1985). In this broad geographical area, the lower limestone level of the Aisemont Formation normally has its thickness reduced to a few metres and it is characterized by rather argillaceous limestones, that is to say more or less nodular limestones with shaly intercalations, containing brachiopods and some colonies of *Frechastraea*, especially at the base. Most of these massive rugose corals belong to *F. coeni*, although they are accompanied locally by *F. phillipsastraeiformis* and *F. limitata*. One colony of *Hexagonaria davidsoni* comes from the very base of the Aisemont Formation at Lustin, in contact with the underlying Lustin Formation.

In the more northern sections from the Vesdre Massif and the south side of the Namur Synclinorium such as at Embourg, Chaudfontaine, Streupas and Engis, the first level of limestone of the Aisemont Formation is much thicker and developed as a typical biostrome with numerous platy colonies of *Frechastraea* and *Alveolites*. This biostrome has been described recently by Poty & Chevalier (2007). *F. coeni* is common in the main part of this biostrome, once more associated with a few specimens of *F. phillipsastraeiformis* and *F. limitata*. But in its upper part appear *F. micrastraea* and *Phillipsastrea ananas*, just as is the case in the upper part of the Petit-Mont Member from the Philippeville Massif. At Engis, I have found also *F. glabra* at the top of the biostrome occurring in the lower part of the Aisemont Formation. As for the upper limestone level of this lithostratigraphic unit, it contains only *F. micrastraea*, *F. limitata* and *Phillipsastrea ananas*.

At first glance, it seems that there are many differences between the facies of the Philippeville Massif where the bioherms of the Petit-Mont Member are observed and the northern facies characterized by the three subdivisions of the Aisemont Formation. Additionally, it can be noted that a bioherm of red limestone has been intersected by several boreholes in Chaudfontaine at the northwestern end of the Vesdre Massif. These boreholes have been investigated by Graulich (1967) and Graulich et al. (1980). Correlations between the deep bioherm of Chaudfontaine and the surface outcrops of the Aisemont Formation at the same locality have been proposed by Coen-Aubert (1974b). In fact, the biostrome corresponding to the lower limestone level of the Aisemont Formation serves as basement for the bioherm whereas the overlying shales and upper limestone level are lateral facies to this reefal lens.

3. Systematic Palaeontology

The types of the new species and figured specimens are also stored in the collections of the Institut royal des Sciences naturelles de Belgique (IRScNB).

Family Phillipsastreidae Roemer, 1883

Genus *Frechastraea* Scrutton, 1968

Type species. By original designation, *Cyathophyllum pentagonum* Goldfuss, 1826.

Diagnosis. Massive rugose corals, pseudocerioid to astreoid at times with small corallites. Septa of two orders, carinate or non-carinate, dilated in the dissepimentarium and occasionally thicker at its inner border, thin in the tabularium. Major septa extending nearly to the axis of the corallites or restricted to the dissepimentarium. Dissepimentarium composed of several rows of small globose dissepiments arranged in horizontal layers with a possible occurrence of a few horseshoe dissepiments at the border of the tabularium. Tabulae complete or incomplete.

Remark. The term pseudocerioid has been introduced independently and defined in precisely the same way by Sorauf (1967, p. 15) and Scrutton (1968, pp. 192 and 280; fig. 4b). It refers to a strong, straight or zigzagged pseudotheca of septal origin. In astreoid colonies, the pseudotheca is much thinner without reduction of septa which usually alternate in neighbouring corallites. Since its introduction, the term pseudocerioid has been widely used, among others by Tsien (1978), Wrzołek (1993), Sorauf (1994, pl. 4D and pl. 5), McLean (1994, 2010) and Brownlaw & Jell (2008).

***Frechastraea coeni* n. sp.**
(Pl. 1A-G)

p. 1967 *Phillipsastraea pentagona* (Goldfuss); Sorauf: 29, figs. 13, 1c-d (non figs. 13, 1a-b, 1e-f).
v 1974a *Phillipsastrea pentagona carinata* (Scrutton, 1968); Coen-Aubert: 14, pl. 2, figs. 4-5.
v 1977 *Frechastraea pentagona carinata* Scrutton, 1968; Coen et al.: 325.
v p. 1978 *Phillipsastrea goldfussi* (de Verneuil et Haime, 1850); Tsien: 203, pl. 1, figs. 4-5 (non fig. 4, pl. 1, fig. 6).
v 1994 *Frechastraea carinata* Scrutton, 1968; Coen-Aubert: 30.
v 1994 *Frechastraea goldfussi*; Sorauf: pl. 5.
v 2000 *Frechastraea carinata* Scrutton, 1968; Coen-Aubert: 744.
v 2011 *Frechastraea* n. sp. A; Coen-Aubert: 28.

Derivation of name. The species is dedicated to my husband Michel Coen (1943-2006), a distinguished field geologist and specialist of Devonian as well as Carboniferous ostracods and conodonts.

Holotype. IRScNB a12819 (= Pl. 1A-C). Specimen Beaumont MC-1979-9-G35 collected by M. Coen in 1998, 6 m above the base of the Neuville Formation.

Type locality and horizon. Active quarry 1300 m to the west of Barbençon, described and located by Dumoulin (2001, fig. 3). Map sheet Beaumont 52/6, Lambert coordinates: x= 142.425 and y = 100.75, western part of the Dinant Synclinorium. Base of the Neuville Formation, base of the Late Frasnian.

Material. With the exception of Embourg H92, all the colonies mentioned by Coen-Aubert (1974a, p. 14). In addition to this material, 70 specimens with 111 thin sections. Personal sampling with that of M. Coen, E. Groessens and D. Lacroix: Braives MC-1979-3-X67; Fontaine l'Evêque MC-1974-135-L2, L3 and L4; Tamines MC-1975-1-2, 3 and 4; Gesves MC-1978-2-U96; Huy MC-1977-8-U55; Saint-Georges MC-1978-5-V3, V4, V6, V7, V82, V9, V10, V11, V12, V13, V23, V25, V26 and V27; Naninne MC-1974-115-4.2; Malonnes MC-1975-9-719; Nalinnes MC-1975-2-1, 2 and 4; Walcourt MC-1974-131-P85, P86, P87, P89, P90 and P92; Walcourt MC-1976-5-U21, U22, U23, U24 and U25; Walcourt MC-1976-6-U29; Walcourt MC-1976-7-746, 747 and 748; Beaumont MC-1979-9-G1, G2, G3, G4, G5, G11, G14, G15, G19, G21, G26, G32, G33, G34 and G35; Senzeille MC-1974-106-T80 and T82; Senzeille MC-1976-4-LB1 and LB6; Surice MC-1974-133-V11. Old collection from the Institut royal des Sciences naturelles de Belgique: Beaumont 6306-F2i-14745; Beaumont 6306a-F2i-14757 and 14762; Saint-Georges 7010 (= Saint-Georges MC-1978-5)-F2IIIc-16746 and 16787; Sautour 6802-F2i-15567: Senzeille 31a (= Senzeille MC-1974-106)-F2i-20805.

Diagnosis. A pseudocerioid species of *Frechastraea* with 18 to 24 septa at tabularial diameters of 0.9 mm to 1.7 mm. Septa variably but typically carinate and restricted to the dissepimentarium.

Description. The material consists of laminar, tabular, nodular and discoidal colonies which are complete or fragmentary. Their height varies between 1 cm and 7 cm whereas the largest piece has a diameter of 20 cm. Some specimens are composed of several sheets; this may be due to the input of sediments or to a local disruption of colonial growth followed by rejuvenescence. The holotheca is sometimes preserved. At the upper surface of some samples are observed calices excavated and bordered by flat platforms. The corallites usually polygonal in shape are separated by a zigzagged or straight pseudotheca. In a few specimens, the outer zigzagged wall is weaker and locally absent so that colonies are more or less astreoid. There are only rare lateral and pericalicinal offsets.

The septa of both orders are dilated and generally restricted to the dissepimentarium. They bear frequent knobbly carinae which are occasionally yardarm or spinose. However, this carination is less developed in some specimens. An inner thickening of the septa is rather uncommon at the boundary of the tabularium. It may happen that a few major septa become thinner and are extending into the tabularium, normally without reaching the axis of the corallites. It is rare that the minor septa do not traverse the entire dissepimentarium.

The dissepimentarium consists of 3 to 9 or even 2 to 11 rows of globose dissepiments which are arranged in horizontal layers. In a few colonies occur occasionally at the border of the tabularium small specialized dissepiments close to the shape of horseshoes or one row of inclined dissepiments. The tabulae are concave, horizontal or incomplete and intersecting laterally without any trace of septa disrupting them.

There are 16 to 28 septa per corallite. The width of the tabularium ranges from 0.7 mm to 2 mm. The diameter of the corallites varies commonly between 2.5 mm and 5.5 mm and more generally between 2.1 mm and 7 mm.

Discussion. *Frechastraea coeni* shows some variability mainly concerning carinae, which are more or less strong and numerous, and to a lesser extent the outer wall which is usually typically pseudocerioid. The material assigned herein to *F. coeni* has been identified formerly by Coen-Aubert (1974a) as *F. carinata* Scrutton, 1968. In fact, it resembles the paratype illustrated by Scrutton (1968, pl. 9, fig. 2) where major septa are slightly shorter and do not reach systematically the axis of the corallites as it is the case in the holotype. Moreover, the tabularia of *F. carinata* are narrower than those of *F. coeni*. The new Belgian taxon has been confused by Sorauf (1967, 1994) and Tsien (1978) with *F. pentagona* (Goldfuss, 1826), which is the genotype of *Frechastraea* Scrutton, 1968 and *F. goldfussi* (De Verneuil & Haime, 1850). As mentioned by Scrutton (1968, p. 253) and Coen-Aubert (1974a, p. 19; 1994, p. 38), these two pseudocerioid species are very similar and characterized by non-carinate septa extending close to the centre of the tabularium. The lectotype of *F. pentagona* coming from the Frasnian of Limbourg, probably close to Verviers in Belgium, has been illustrated in thin sections by Pickett (1967) whereas the holotype of *F. goldfussi* also from the Goldfuss collection in Bonn, Germany and collected in the Frasnian from the vicinity of Namur in Belgium is lost. Therefore it is impossible to know what the species *F. goldfussi* is in actuality.

By its pseudotheca being zigzag to straight and by its septa being carinate and restricted to the dissepimentarium, *F. coeni* has some affinities with *F. regularis* (Chen, 1959) from the Frasnian of Guizhou Province in China. However, the latter taxon differs from the former by slightly greater septal number and diameters of the tabularia and corallites. The Chinese species has been introduced by Chen (1959, p. 308) as *Prismatophyllum pentagonum regulare* and has been referred by Kong & Huang (1978, p. 88) to the genus *Mixogonaria* Kong, 1978 whose type species is *M. sanduensis* Kong, 1978 also from the Frasnian of Guizhou. Pedder (2006, p. 52) considers that *M. sanduensis* and *M. regularis* are cerioid whereas *Mixogonaria* and *Frechastraea* are two related genera according to Liao & Birenheide (1985, p. 281) and Birenheide (1986, p. 13).

Distribution. The species is only known at the base of the Late Frasnian in different areas from Belgium. The material collected by the author, M. Coen, E. Groessens and D. Lacroix comes from:

- the base of the Aisemont Formation at Huccorgne on the north side of the Namur Synclinorium, at Presles, Strud, Huy and Engis on the south side of the same structural unit, at Landelies and Streupas in the La Tombe and Streupas outliers, at Embourg, Colonstère, Chaudfontaine, Prayon, Trooz, Goffontaine, Pepinster and Les Surdents close to Verviers in the Vesdre Massif, at La Reid in the Theux Window, at Lustin, Lesves and Crupet on the north side of the Dinant Synclinorium and at Comblain-la-Tour on the east side from the same structural unit;
- the base of the Neuville Formation at Gerpinnes, Gourdinne, Laneffe, Barbençon and Neuville in the northwestern and central parts of the Dinant Synclinorium;
- the lower part of the bioherms from the Petit-Mont Member at Neuville and Vodelée in the Philippeville Massif.

Frechastraea glabra n. sp.
(Pl. 2A-D)

v 1979 *Frechastraea carinata* subsp.; Coen-Aubert & Lacroix: 275.
v 2011 *Frechastraea* cf. *borealis* McLean, 1994; Coen-Aubert: 28.

Derivation of name. From *glaber, bra, brum* (latin)= smooth, referring to the lack of carinae in the new species.

Holotype. IRScNB a12823 (= Pl. 2A-B). Specimen Senzeille MC-1976-4-LB4 collected by M. Coen in 1976, 7 m above the base of the red marble bioherm from Les Bulants quarry at Neuville.

Type locality and horizon. Disused Les Bulants quarry lying about 1 km to the west of Neuville, described and located among others by Boulvain et al. (1999, point 4 of fig. PHV1, pp. 72 and 74). Map sheet Senzeille 57/4, Lambert coordinates: x= 159,975 and y= 95,625, Philippeville Massif. Lower part of the Petit-Mont Member, Neuville Formation, Late Frasnian.

Material. 11 specimens with 19 thin sections. Personal sampling with that of M. Coen: Saint-Georges MC-1978-5-V14, V16 and V19; Senzeille MC-1976-4-LB4 and LB11; Surice MC-1974-133-V10, V13, V29, V32 and A521. Old collection from the Institut royal des Sciences naturelles de Belgique: Sautour 6802-F2i-15568.

Diagnosis. An astreoid species of *Frechastraea* with 18 to 24 septa at tabularial diameters of 1 mm to 1.6 mm. Septa non-carinate and restricted to the dissepimentarium.

Description. The material consists of platy and sheet-like colonies which are complete or fragmentary. Their height varies between 1 cm and 6 cm whereas the largest piece has an area of 17 cm x 9 cm. The corallites are separated by a zigzagged or rarely straight pseudotheca which is often weak and not very well delimited. Therefore, the shape of the corallites is not regularly polygonal. In a few specimens, the septa are occasionally confluent or forked at the periphery. In longitudinal sections, it can be seen that the growth of some colonies is locally disrupted and followed by rejuvenescence; this is sometimes due to the input of sediments. A few lateral offsets have also been observed.

The septa are normally non-carinate; however, a few poorly developed, spinose and knobbly carinae occur in some corallites. The septa of both orders are dilated and usually restricted to the dissepimentarium; sometimes, they show a spindle-shaped thickening at the boundary with the tabularium, but without forming an inner wall. In some specimens, a few major septa become thinner and are extending into the tabularium; they may even reach the axis of the corallites where there are possibly pseudofossulae.

The dissepimentarium consists of 3 to 7 or even 9 rows of globose dissepiments which are arranged in flat layers. In one colony, there are occasionally at the border of the tabularium small specialized dissepiments close to the shape of horseshoes. The tabulae are horizontal, concave or incomplete and intersecting laterally without any trace of septa disrupting them; sometimes, they are convex.

There are 18 to 26 septa per corallite. The width of the tabularium ranges from 0.9 mm to 1.8 mm. The diameter of the corallites varies commonly between 3 mm and 5.5 mm and more generally between 2.5 mm and 6.4 mm.

Discussion. *Frechastraea glabra* is similar to *F. coeni* in its quantitative data and the length of septa which are mostly restricted to the dissepimentarium. The former species is distinguished from the latter by a much weaker astreoid pseudotheca and by the scarcity to the complete absence of carinae. Subsidiarily, the septa of *F. glabra* may be affected by some thickening at the inner border of the dissepimentarium whereas a few major septa may extend into the tabularium; these two features are rarely present in *F. coeni*.

F. glabra has been identified as *F.* cf. *borealis* McLean, 1994 by Coen-Aubert (2011). This taxon introduced by McLean (1994, p. 86) in the Late Frasnian from the Northwest Territories in Canada is different in having a rather thamnasterioid aspect as well as slightly greater septal number and diameter of the tabularium. The tabularia are still wider in *F. whittakeri* (Smith, 1945) from the late Frasnian of the same area. However, one typically astreoid colony figured and assigned by McLean (1994, pl. 7, figs. 5-6) to *F. whittakeri* resembles more *F. glabra*. It may be discussed whether *F. borealis* and *F. whittakeri* should be better referred to the thamnasterioid genus *Scruttonia* Tcherepnina, 1974 rather than to the genus *Frechastraea* which is normally pseudocerioid.

F. kaisini (Tsien, 1978) is another species from the Late Frasnian of Belgium which is astreoid with all the septa restricted to the dissepimentarium. But it is easily separated from *F. glabra* by the occurrence of an inner wall and by much smaller tabularia.

Distribution. The species is only known from the base of the Late Frasnian in Belgium. The colonies from Engis on the south side of the Namur Synclinorium come from the top of the lower limestone level belonging to the Aisemont Formation. The material of Neuville and Vodelée in the Philippeville Massif has been collected in the lower part of the bioherms from the Petit-Mont Member.

Frechastraea phillipsastraeiformis (Moenke, 1954)
(Pl. 2E-F)

* 1954 *Hexagonaria phillipsastraeiformis* n. sp.; Moenke: 476, pl. 1, figs. 7-8.
v p. 1967 *Phillipsastraea goldfussi* (de Verneuil & Haime); Sorauf: 27, figs. 11, 1a-b (non fig. 10)
v 1994 *Frechastraea phillipsastraeiformis* (Moenke, 1954); Coen-Aubert: 38, pl. 4, figs. 5-8, pl. 5, figs. 12-13.
2003 ?*Phillipsastrea phillipsastreiformis* (Moenke, 1954); Fedorowski: 104, pl. 50, figs. 3, ?4.

Holotype. Specimen Tc 8/2 stored in the Department of Geology from the University of Poznan, Poland. Point 11 of the Psie Gorki quarry at Kielce, Holly Cross Mountains, Poland. Middle to Late Frasnian. Pl. 1, figs. 7-8 in Moenke (1954) and pl. 50, fig. 3 in Fedorowski (2003).

*Material***.** In addition to the 9 colonies listed by Coen-Aubert (1994), 11 specimens with 20 thin sections. Personal sampling with that of M. Coen: Huy MC-1977-8-U53; Saint-Georges MC-1978-5-V2; Chênée MC-1974-77-L15; Nalinnes MC-1975-2-3; Walcourt MC-1974-131-P88; Walcourt MC-1976-6-U28; Surice MC-1974-134-V1. Old collection from the Institut royal des Sciences naturelles de Belgique: Beaumont 6306-F2i-14742; Beaumont 6306a-F2i-14771; Sautour 8302-F2i-15563 and 15566.

Diagnosis. A pseudocerioid species of *Frechastraea* with 22 to 30 septa at tabularial diameter of 1.3 mm to 2.5 mm. Septa weakly carinate and spindle-shaped dilated at the inner border of the dissepimentarium. Major septa extending into the tabularium.

Description. This description completes that given by Coen-Aubert (1994). Like the two preceding species, these laminar and tabular colonies nay be composed of two sheets or show a local disruption in their growth followed by rejuvenescence. The corallites polygonal in shape are separated by a zigzagged or sometimes straight pseudotheca.

The septa bear some weak spinose and knobbly carinae and they are dilated in the dissepimentarium. Mostly the major ones are affected by a spindle-shaped thickening which is normally restricted to the boundary with the tabularium, but which is slightly wider in some specimens. The major septa become thin in the tabularium. They are extending to the axis of the corallites or they are leaving a more or less extensive open space in the centre of the tabularium. The minor septa traverse the entire dissepimentarium.

The dissepimentarium consists of 3 to 8 or even 2 to 10 rows of globose dissepiments which are arranged in horizontal layers. In a few colonies, some specialized or inclined dissepiments occur locally at the border of the tabularium. Some symmetrical tight fans of septal trabeculae have been observed at the inner margin of the dissepimentarium. The tabulae are incomplete and intersecting laterally; occasionally, they are concave or they are characterized by a flat-topped axial part.

There are 20 to 28 septa and even 30 to 32 septa per corallite. The width of the tabularium ranges from 1.1 mm to 2.6 mm with frequent values between 1.3 mm and 2.1 mm. The diameter of the corallites varies commonly between 3.5 mm and 7 mm and more generally between 2.9 mm and 8.5 mm.

Discussion. The Belgian material is very similar to the holotype of *Frechastraea phillipsastraeiformis* which has been figured by Moenke (1954) and Fedorowski (2003) and which is characterized by tabularia and corallites of slightly greater sizes. The other specimen assigned to the species by Fedorowski (2003, pl. 50, fig. 4) is somewhat different as its septa are uniformly and more strongly dilated throughout the dissepimentarium. At the generic level, *F. phillipsastraeiformis* is without doubt pseudocerioid as was already mentioned by Wrzołek (1993, p. 244) and Coen-Aubert (1994). However, it was assigned by McLean (2010, p. 80) to *Kuangxiastraea* Yu & Kuang, 1982 whose type species is *K. elegans* Yu & Kuang, 1982 from the Late Givetian of Guangxi in China. According to Yu (1997), Coen-Aubert (2002) and Brownlaw & Jell (2008, p. 113), this genus is represented by thamnasterioid to astreoid colonies with rather large corallites and septa typically carinate.

Frechastraea phillipsastraeiformis has been identified by Sorauf (1967) as *F. goldfussi* which is considered to be related to *F. pentagona*. There are certainly some affinities between this species and *F. phillipsastraeiformis*. But *F. pentagona* is distinguished by slightly smaller septal number and diameters of the tabularia and corallites, by non-carinate septa and by a short bulbous thickening of the septa which is restricted to the border of the tabularium with possibly the formation of an inner wall.

Distribution. In Belgium, the species occurs at the transition between the Middle and the Late Frasnian. Indeed, the material collected by the author and M. Coen comes from:

- the base of he Aisemont Formation at Huy and Engis on the south side of the Namur Synclinorium and at Chaudfontaine in the Vesdre Massif;
- the base of the Neuville Formation at Gerpinnes, Gourdinne and Laneffe in the north-western part of the Dinant Synclinorium, at Neuville, Vodelée and Merlemont in the Philippeville Massif and at Frasnes and Boussu-en-Fagne on the south side of the Dinant Synclinorium.

Outside Belgium, *Frechastraea phillipsastraeiformis* is only known in the Middle to Late Frasnian (*Palmatolepis jamieae* to *P. rhenana* conodont Zones) from the Holy Cross Mountains in Poland.

4. Conclusion

As noted by Coen-Aubert (2011), *Frechastraea coeni* is an excellent marker for the base of the Late Frasnian in Belgium. In some localities, it is associated with *F. glabra* and *F. phillipsastraeiformis*. However, the latter species may be already present at the top of the Middle Frasnian from the Philippeville Massif and the south side of the Dinant Synclinorium, in some of the outcrops described by Coen-Aubert (1994).

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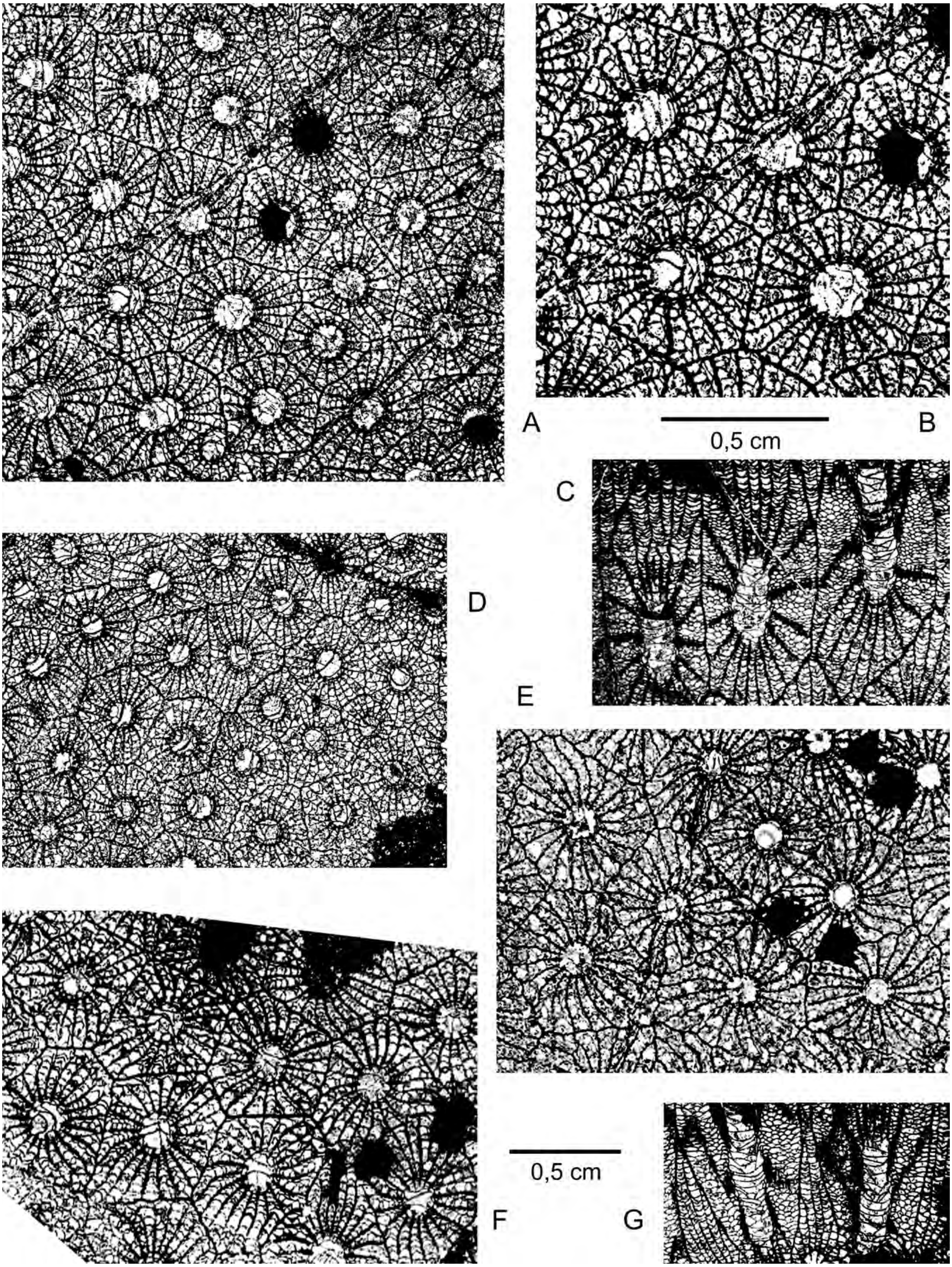

Plate 1. A-G: *Frechastraea coeni* n. sp. A-C: Holotype, IRScNB a12819, Beaumont MC-1979-9-G35; transverse sections and longitudinal section. D: Paratype, IRScNB a12820, Beaumont MC-1979-9-G11; transverse section. E: Paratype, IRScNB a12821, Senzeille MC-1974-106-9; transverse section. F-G: Paratype, IRScNB a12822, Beaumont MC-1979-9-G34; transverse and longitudinal sections. Magnification x 4 except figure B x 6.

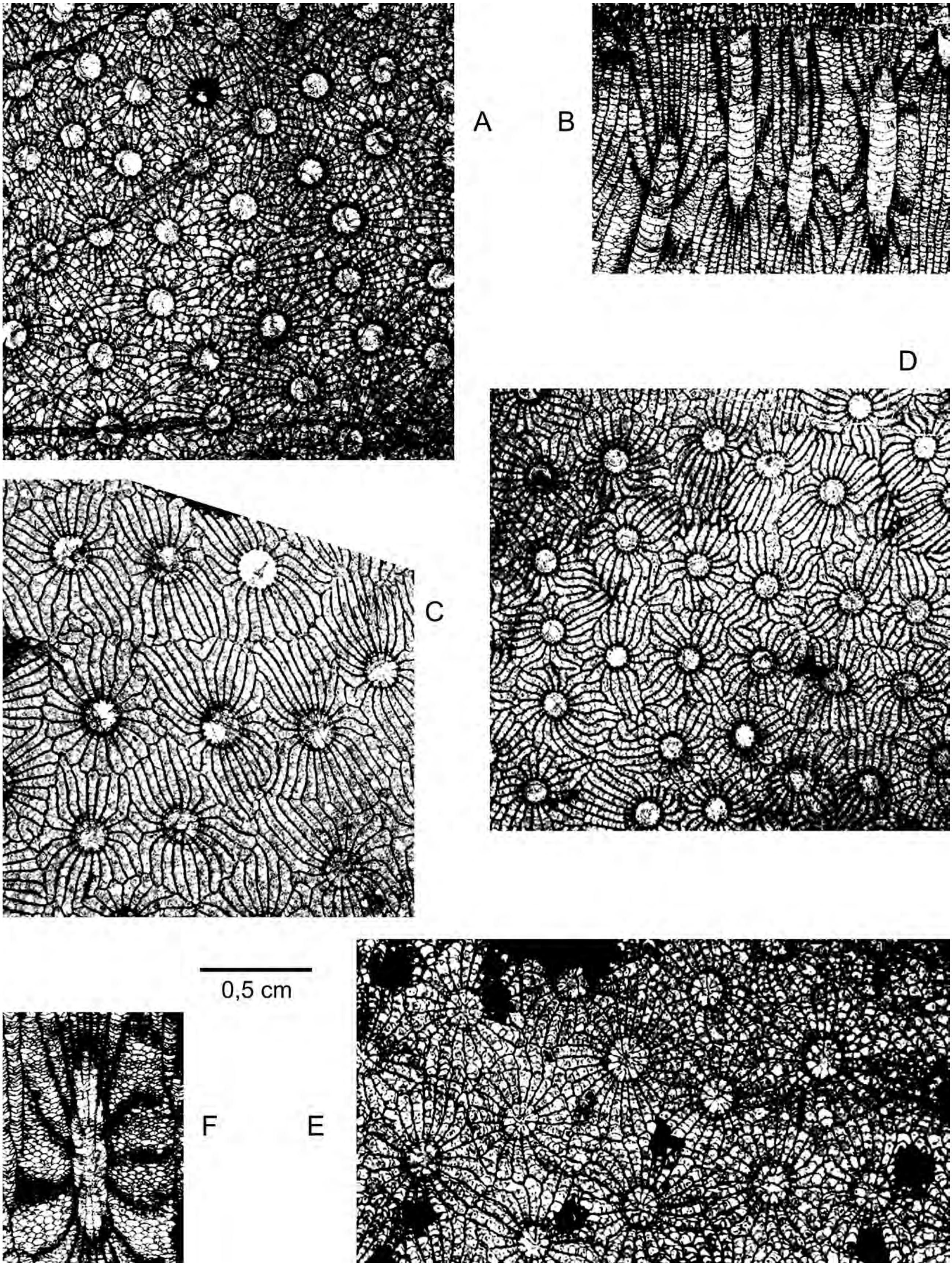

Plate 2. A-D, *Frechastraea glabra* n. sp. A-B: Holotype, IRScNB a12823, Senzeille MC-1976-4-LB4; transverse and longitudinal sections. C: Paratype, IRScNB a12824, Surice MC-1974-133-V32; transverse section. D: Paratype, IRScNB a12825, Saint-Georges MC-1978-5-V19; transverse section. E-F: *Frechastraea phillipsastraeiformis* (Moenke, 1954), IRScNB a12826, Nalinnes MC-1975-2-3; transverse and longitudinal sections. Magnification x 4.

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Lower and Middle Famennian (Upper Devonian) rugose corals from southern Belgium and northern France

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ABSTRACT. After the late Frasnian extinctions, the rugose corals slowly recovered during the Lower and Middle Famennian (*crepida* to *marginifera* conodont zones) in southern Belgium and northern France (Avesnois) (Namur–Dinant Basin). Six genera represented by seven species are recognized and described here; one species (*Breviphrentis superstes*) is new. The rugose coral fauna described herein includes small solitary forms belonging to the so-called *Cyathaxonia* fauna and is similar or very close to those previously described within the same stratigraphic interval in Australia, China and Germany. It also contains a large species belonging to the genus *Breviphrentis* which was considered as extinct since the end of the Givetian (Middle Devonian) (“Lazarus taxon”). The tabulate corals from the Lower and Middle Famennian of this area, mainly represented by auloporids, are also briefly discussed. Rugosa only constituted a minor part of the fauna after the end-Frasnian crisis in the Namur–Dinant Basin contrary to the brachiopods, which were abundant and relatively diversified, and no rugose corals have been recovered from the early Lower Famennian (*triangularis* Zone). The first important Famennian coral radiation only took place during the Latest Famennian (Strunian).

KEYWORDS: Rugosa, Tabulata, *Breviphrentis*, *Cyathaxonia* fauna, post-extinction diversification.

1. Introduction

On a worldwide scale, the Lower and Middle Famennian (Upper Devonian; *triangularis–marginifera* conodont zones) is almost devoid of corals. This is one of the numerous consequences of the Late Frasnian mass extinction that drastically affected the rugose and tabulate corals (e.g. Sorauf & Pedder, 1986; Poty, 1999; Copper, 2002). Their decline was a progressive phenomenon (Poty & Chevalier, 2007; Poty et al., 2011), as was the case for the brachiopods (Mottequin & Poty, 2007, 2008). It started in the Lower *rhenana* conodont Subzone, before the Lower Kellwasser Event, and was practically completed in the Upper *rhenana* Subzone, before the Upper Kellwasser Event that took place during the *linguiformis* Zone.

Very few coral associations were described in Lower Famennian strata (Germany: Weyer 1991, 2004; China: Soto & Liao, 2002; Australia: Hill & Jell, 1971). They usually correspond to the *Cyathaxonia* Fauna constituted of small solitary non-dissepimented corals. These associations are rarely diversified and the corals are usually not abundant, witnessing unsuitable environments.

This paper is the first comprehensive systematic study of the Lower and Middle Famennian rugose corals from southern Belgium and northern France (Fig. 1) which have been considerably less investigated than those of Frasnian age. Until the recent attempts to precise their diversity (Poty, 1986, 1999; Mottequin et al., 2011), they were only known by lists of species devoid of illustrations, which dated back to the second half of the 19th century and which erroneously included species from the shaly formations of Upper Frasnian age (Dewalque, 1868; Gosselet, 1879, 1887, 1888; Mourlon, 1881). On the contrary, due to their greater abundance, their counterparts of the uppermost part of the Famennian (Strunian) have received much more attention (e.g. Haime in Hébert, 1855, Gosselet, 1880; Salée, 1913; Dehée, 1929; Poty, 1986, 1999; Denayer et al., 2011).

2. Geological setting

The studied material is from nine localities belonging to the Namur and Dinant synclinoria, the Vesdre Area and the Theux Window (Fig. 1; see also Appendix 1). These Variscan structural elements constituted the Namur–Dinant Basin, which developed along the southeastern margin of Laurussia during the Devonian and the Carboniferous. The material is from three formations that are briefly described below.

The Famennian (Fig. 2) is particularly well-developed and exposed in the Dinant Synclinorium, from its south-western part in the Avesnes area (northern France) to its north-eastern extension in the East of Belgium. It is mainly composed of predominantly siliciclastic sediments with some calcareous intercalations. The depositional setting approximately corresponds to a ramp with an accentuation of the marine influence and a deepening southwards (Thorez et al., 2006). Therefore, the northern proximal facies, which frequently show a continental influence, are dominantly sandy, silty and shaly, whereas the southern distal facies are dominantly shaly with some calcareous intercalations.

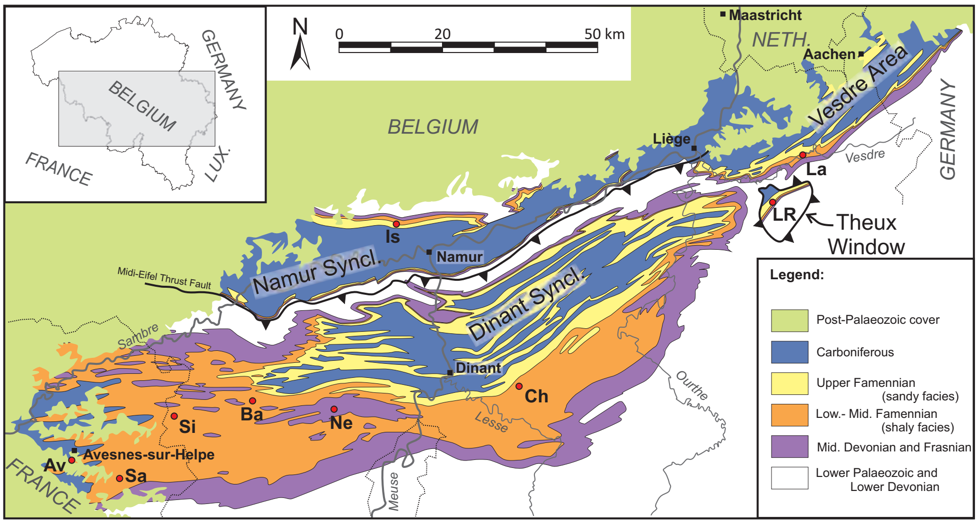

Figure 1. Simplified geological map of southern Belgium and surrounding areas, including the Avesnois (northern France). The red points localize the sampled localities. Legend; Av: Avesnelles and Avesnes-sur-Helpe; Ba: Badon; Ch: Chevetogne; Is: Isnes-les-Dames (Les Isnes); La: Lambermont; LR: La Reid; Ne: Neuville; Sa: Sains-du-Nord; Si: Sivry.; ; NETH.: The Netherlands.

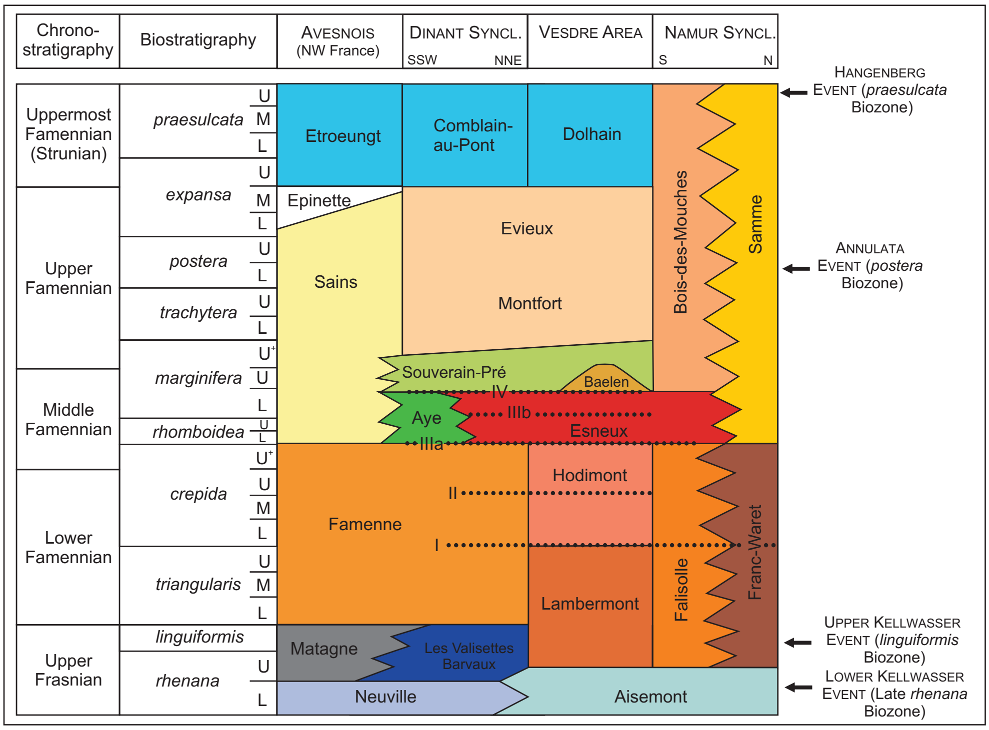

Figure 2. Simplified lithostratigraphical scheme of the Famennian in different tectonic units of southern Belgium, incorporating the Avesnois (northern France) (modified from Thorez et al. (2006) and Delcambre & Pingot (2000, 2008)). Black dotted lines correspond to oolitic ironstone levels (see Dreesen 1982). Syncl.: Synclinorium.

In the Belgian part of the Dinant Synclinorium, deposits of the Lower and of the lower part of the Middle Famennian are almost exclusively argillaceous and are included in the Famenne Group. From the base of the middle part of the Middle Famennian, they pass to the siltstones and sandstones of the Esneux Formation, except in the southern part of the synclinorium where the shales remain predominant and correspond to the Aye Formation (Fig. 2). From the base of the upper part of the Middle Famennian, both formations, which are devoid of corals due to unfavourable facies, pass to the nodular shaly and silty limestones of the Souverain-Pré Formation. The transition between the Aye–Esneux formations and the Souverain-Pré Formation is clearly diachronous, the latter is younger northwards and where it is very weakly developed or even missing.

In the most south-western part of the Dinant Synclinorium, e.g. the southern part of the Avesnes area, which corresponds to the most distal facies, the deposits remain argillaceous (Famenne Group and Sains Formation), but an unit of calcareous shale and shaly limestone beds occurs within the Sains Formation, and laterally correspond to the Souverain-Pré Formation.

The carbonated levels of the Souverain-Pré (Bouckaert & Dreesen, 1977; Poty, 1999; Marion & Barchy, 2004) and of the Sains formations (Poty, 1999; Thorez et al., 2006), that yielded corals, belong to the Upper *marginifera* Subzone (late Middle Famennian). However, the Sains Formation extends from the Lower *rhomboidea* Subzone (middle part of the Middle Famennian) to the Lower–Middle *expansa* subzones (upper part of the Upper Famennian) according to Thorez et al. (2006), and its levels rich in corals were previously assigned to these subzones by Poty (1999).

In the Vesdre Area and the Theux Window, the lowermost part of the silty and shaly Hodimont Formation yielded small solitary non-dissepimented rugose corals, which were collected from the carbonate and shaly beds immediately above an oolitic ironstone level (Dreesen's level I, 1982). The latter corresponds to a condensation horizon comprising at least the Upper *triangularis* and the Lower *crepida* subzones (Dreesen, 1982). Only very uncommon, small and poorly preserved rugose corals were found in the rest of the Hodimont Formation.

On the southern flank of the Namur Synclinorium, rugose corals are known from an oolitic ironstone marker bed that occurs within the Lower Famennian part of the shaly Franc-Waret Formation.

The geological and geographical data of the sampled localities (Fig. 2) are placed in the Appendix 1.

3. Systematic palaeontology

Except two corals coming from the old collection of the University of Liège, all the material investigated was collected by the authors and is deposited in the collections of the Palaeontology Unit of the Liège University (PAULg). The material is listed by locality in Appendix 2. Abbreviations used in the text are as follows: l.s., longitudinal section; t.s., transverse section.

Family Breviphyllidae Taylor, 1951

Genus *Breviphrentis* Stumm, 1949

Type species. *Amplexus invaginatus* Stumm, 1937, Nevada Limestone, Emsian, Atrypa Peak near Eureka, Nevada.

Diagnosis. See Hill (1981), Oliver (1998), and Pedder (2002).

Discussion. As stated by Stumm (1949), Hill (1981), Oliver (1992) and Pedder (2002; see this author for the synonymies and the species assigned to *Breviphrentis*), the genera *Breviphrentis* Stumm, 1949 and *Breviphyllum* Stumm, 1949 are closely related, and *Breviphyllum* would differ from *Breviphrentis* by the presence of dissepiments and the lack of calicinal expansions (Pedder, 2002). *Breviphrentis* is a relatively well-known genus, which was revised by Oliver (1992, 1998) and Pedder (2002) but *Breviphyllum* remains relatively enigmatic and badly needs a revision as suggested by both authors. Oliver (1998) and Pedder (2002) considered that the presence of septa composed of coarse monacanthine trabeculae and calicinal expansions are characteristic of *Breviphrentis*, which mainly includes species from the Emsian of Western North America. Oliver (1998) established the genus *Contophrentis* for Givetian species from Eastern America previously assigned to *Breviphrentis* but devoid of these characters; its type species is *Zaphrentis halli* Milne-Edwards & Haime, 1851 (*Breviphrentis halli* (Milne-Edwards & Haime) in Oliver, 1993) from the Middle Devonian of the Skaneateles Lake, New York.

Our Famennian specimens have calicinal expansions linked to constriction–rejuvenescence cycles, a character considered as diagnostic for *Breviphrentis* in the literature, but which is typically due to ecological variations and therefore without any taxonomic value. They have lonsdaleoid dissepiments, a character diagnostic for *Breviphyllum*, *Breviphrentis* having not. Nevertheless, these dissepiments are only developed in the calice during the constrictions, but not during the rejuvenescences, and they do not form a vertically continuous dissepimentarium. Similar development of the dissepimentarium related to constriction and rejuvenescence was described in *Catactotoechus instabilis* (Berkowski, 2012). Their septal microstructure is relatively variable, partly because of their diagenesis, showing well-defined (coarse?) monacanthine trabeculae or not, the presence of coarse monacanthine trabeculae being another character of *Breviphrentis*. Therefore, and although we consider that the relations and differences between

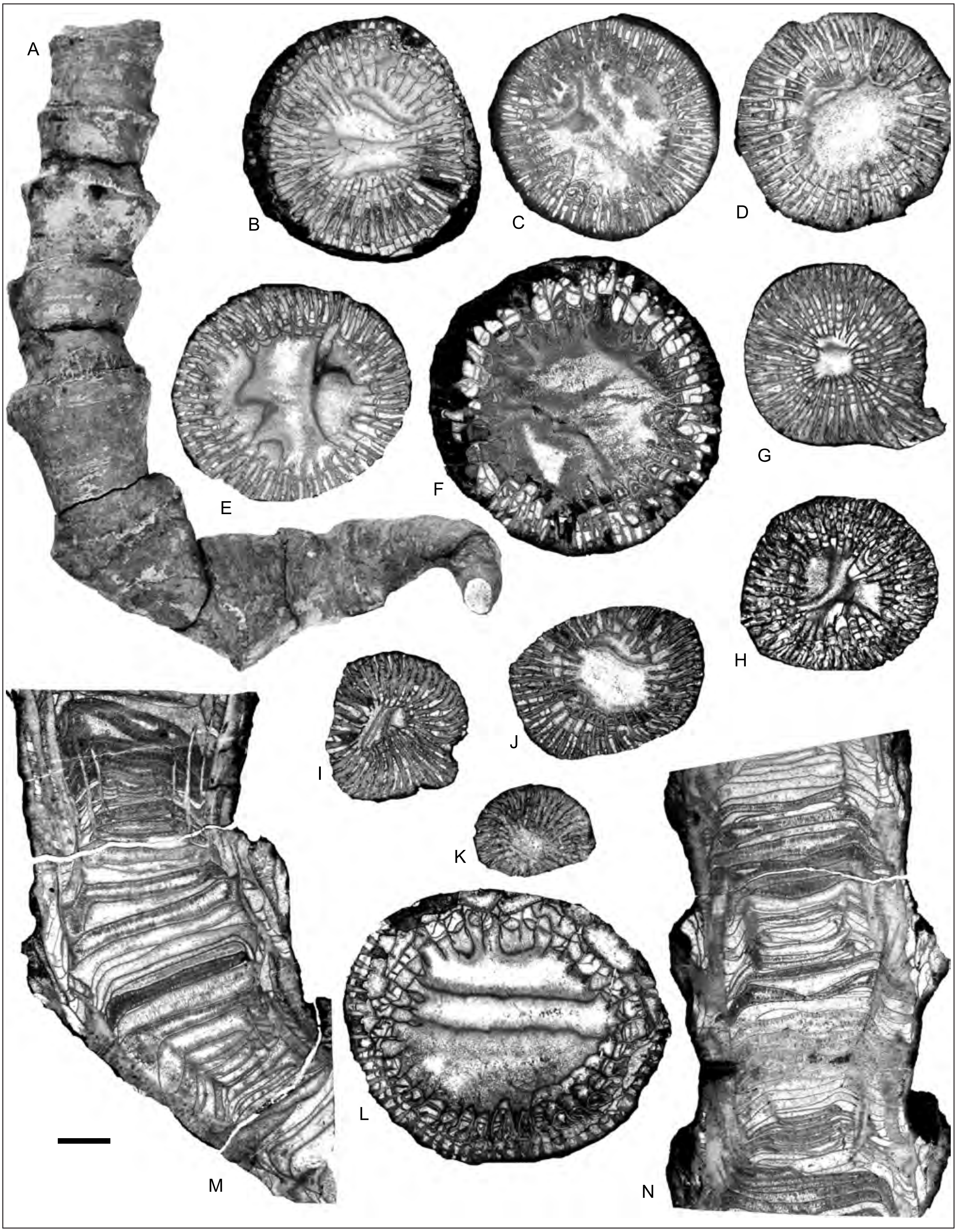

Figure 3. Holotype of *Breviphrentis superstes* sp. nov. Poty & Denayer. Specimen PAULg-S-d-N/6 from the lower part of the Sains Formation, probably Upper *marginifera* conodont Subzone, Sains-du-Nord, Avesnois, North France; sections a to o, successive sections from the top to the base of the coral. A: View of the specimen showing a scolecoid habitus and strong constrictions and rejuvenescences. B: Transverse section 6a. C: Transverse section 6b. D: Transverse section 6d. E: Transverse section 6i. F: Transverse section 6e. G: Transverse section 6j. H: Transverse section 6k. I: Transverse section 6n. J: transverse section 6m. K: transverse section 6o. L: Transverse section showing lonsdaleoid dissepiments due to a constriction phase. 6h. M: Longitudinal section 6g'. N: Longitudinal section 6c showing constrictions and rejuvenescences. A: x1, scale bare: 10 mm. B-N: x2, scale bar : 5 mm.

Breviphrentis, *Breviphyllum*, and *Contophrentis* remain unclear, the Famennian specimens are assigned here to *Breviphrentis*.

Breviphrentis superstes **sp. nov. Poty & Denayer**
(Figs 3, 5)

Derivation of name. Superstes - to survive - by reference to the reappearance of the genus which was not recorded at least from the Givetian, but indeed survived the Taghanic and the Late Frasnian crises.

Holotype. PAULg-S-d-N/6 (15 t.s., 3 l.s.).

Type locality and horizon. Railway cutting north of the Sains-du-Nord station, Avesnois (northern France) (see Appendix 1); lower part of the Sains Formation, probably Upper *marginifera* conodont Subzone.

Material. Besides the holotype, 24 additional specimens from the same level and area (see Appendix 2).

Diagnosis. Breviphrentis with a mature stage varying between 17–38 mm in diameter and having 31 to 53 major septa (Fig. 4). Major septa sometimes split longitudinally and usually prolonged by a septal lamella. Minor septa relatively long, contratingent or contraclinent. Lonsdaleoid dissepiments present in constricted parts of the coral.

Description. The corallum is usually ceratoid, sometimes trochoid, in the young stages, and becomes cylindrical in mature stages, sometimes scolecoid after toppling over. It has regular periodic constrictions giving up calicinal expansions and rejuvenescences (Figs 3A, 5A, 5O). Each constriction–rejuvenescence cycle is between 15 and 35 mm long. The longest corallum observed reaches a length of 18 cm and shows 8 cycles (Fig. 3A). All our specimens died during constrictions. Three parricidal buds are present in one specimen.

In transversal sections, the youngest stages observed (17 to 23 major septa and 4.3 to 7.5 mm in diameter; Figs 5M, 5P), show irregularly pinnately connected septa reaching 0.5-0.7 mm in thickness, the cardinal fossula is not well-marked, some very short minor septa can be present. From sections with 21 to 23 major septa and 6.5 to 7.0 mm in diameter (Figs 5H, 5I), the major septa lost their connection and withdraw from the axis, and minor septa are well-developed.

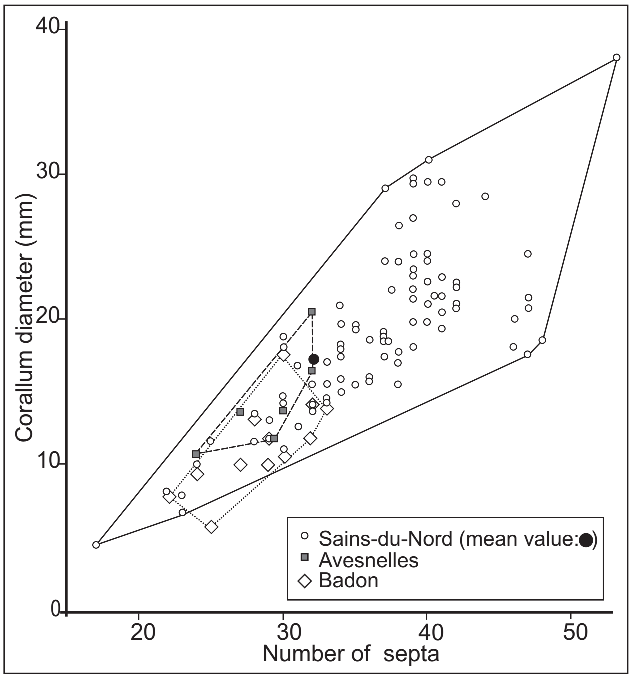

Figure 4. Plot of number of septa versus corallum diameter for *Breviphrentis superstes* sp. nov. Poty & Denayer (specimens from Sains-du-Nord and Avesnelles) and *B*. cf. *superstes*. (specimens from Badon).

The cylindrical parts of the corals have diameters varying from 17–20 mm to 30–38 mm and 30 to 53 major septa The number of septa does not decrease during constrictions. The major septa extend for 1/4 to 4/5 of the radius and they never reach the axis. They are short to long, straight to sinuous, sometimes split by the development of lateral vesicules or terminated by a inner fork. They can be slightly rhopaloid, and their thickness varies from 0.4–0.7 mm at their base to 0.1–0.3 mm in their medium part and to 0.3–0.4 mm at their inner end which are often prolonged by a whip-like septal lamella. The minor septa are relatively long with regard to the major ones, reaching 1/3 to 4/5 of their length (1/4–1/3 of the radius). They are contraclinant and sometimes contratingent, their thickness can reach 0.8 mm. The septa can be a little more thickened in the cardinal quadrants than in the counter ones. A cardinal fossula is inconspicuous to well-marked, with a short cardinal septum. The counter septum is not well differentiated from the others. Lonsdaleoid dissepiments are present in some transverse sections. The outer wall is usually not well-preserved and its thickness varies from 0.5 to 1.5 mm.

In longitudinal sections (Figs 3M, 3N, 5R), tabulae are complete to slightly divided; they are flat to moderately concave and decline outwards to form a peripheral, sometimes deep, gut. The width of the axial elevated part of the tabulae decreases during constrictions and enlarges during rejuvenescences. The space between tabulae in the axial part varies between 0.1 to 2 mm. Dissepiments are formed during each constriction of the corallum, diminishing the internal diameter of the calice. They do not form a continuous dissepimentarium and do not develop during rejuvenescences.

Discussion. Due to wide variations in morphology and size, some specimens of *B. superstes* sp. nov. resemble to species known from the Lower and Middle Devonian:

B. invaginata, the type species of *Breviphrentis* from the Emsian of Nevada (see its revision by Oliver, 1992) is 18–22 mm in diameter with 37–46 major septa, but its major septa are usually longer, more dilated at periphery than in *B. superstes*, and forming a septotheca.

Contophrentis halli (Milne-Edwards & Haime, 1851), from the Givetian, Staghorn Point coral bed, New York (40 to 63 major septa in sections having diameters of 30 to 50 mm) is close to *B. superstes*, but its septa are a little longer and thicker that in our specimens.

Contophrentis cista Oliver, 1992, Givetian, Staghorn Point coral bed, New York, has a size similar to that of our specimens (20–40 mm, reaching 50 mm and 40 to 58 major septa in sections having diameters of 25 to 50 mm), but differs by its shorter minor septa, its tabulae thickened and widely spaced with their axial part strongly concave.

Contophrentis pumilla Oliver, 1992, Givetian, Centerfield Member, Ludlowville Formation, Hamilton Group, western New York, is smaller, 13–18 mm in diameter, with 24–32 major septa.

Moreover, the new species can be easily distinguished by its major septa affected by splitting and their inner end prolonged by septal lamellae which are not known in other species of this group.

Distribution. B. superstes sp. nov. (= *B.* sp. B in Poty, 1999) is only known from the lower part of the Sains Formation in the Avesnes area. Note that Gosselet (1880, p. 547) reported corals in the same stratigraphic levels in the railway cutting north of the Sains-du-Nord station, that he assigned to *Clisiophyllum omaliusi* Haime (*in* Hébert, 1855). Haime's species was never observed below the Uppermost Famennian (Strunian) and Gosselet (1880) probably mistook it with our new species.

Breviphrentis **cf.** ***superstes*** **sp. nov.**
(Fig. 6)

Material. Six specimens from Badon and four from Sivry (see Appendix 2).

Description. The corals are small and cylindrical, with a diameter of 10 to 17 mm and 25 to 30 major septa in mature stages. They can

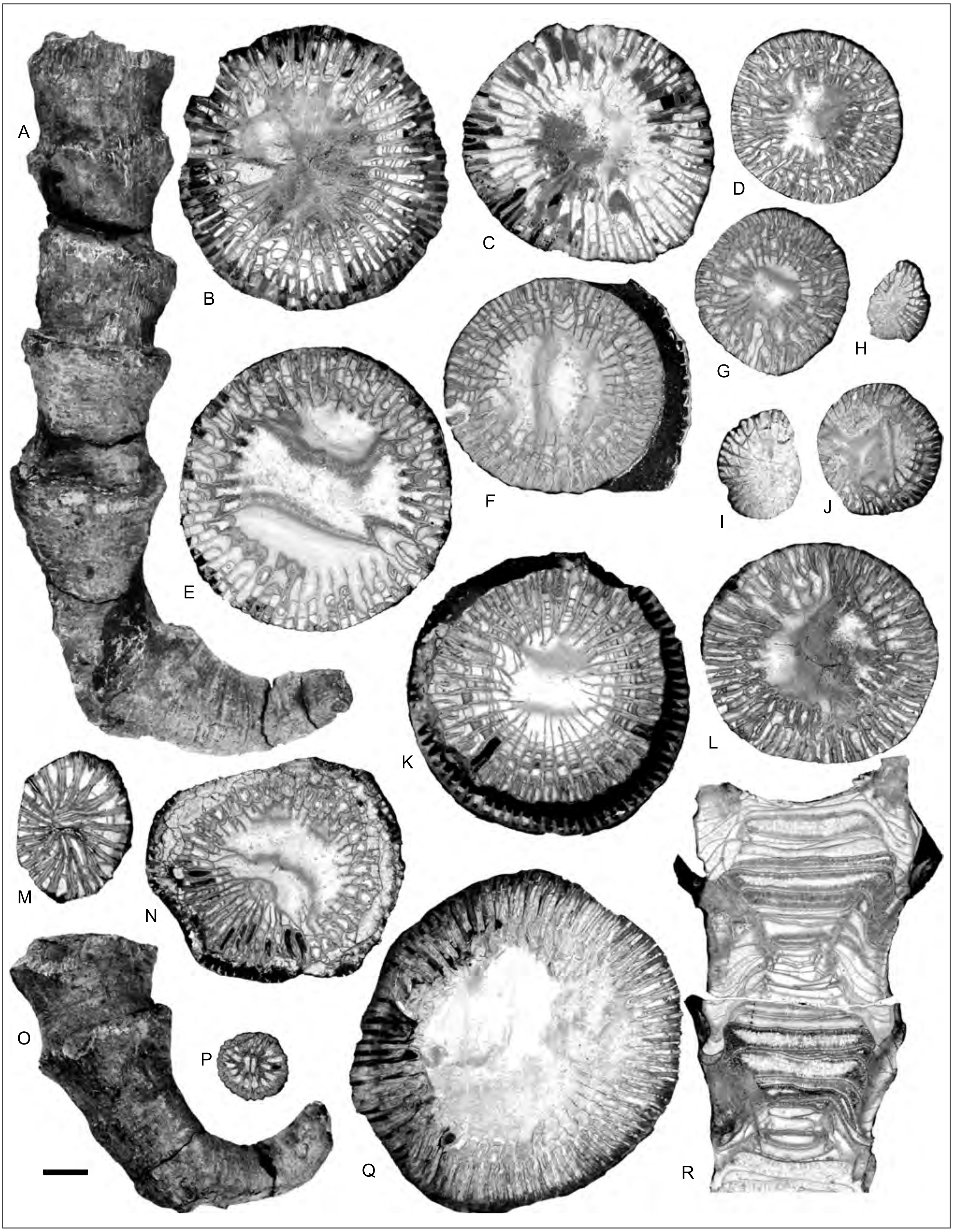

Figure 5. *Breviphrentis superstes* sp. nov. Poty & Denayer. A-J, L: Specimen PAULg-S-d-N/14 from the lower part of the Sains Formation, probably Upper *marginifera* conodont Subzone, Sains-du-Nord, Avesnois, North France. A: View of the specimen showing a toppling over, strong constrictions and rejuvenescences. B: Transverse section 14a. C: transverse section 14b. D: Transverse section 14h. E: Transverse section 14g. F: Transverse section 14f. G: Transverse section 14o. H: Transverse section 14n. I: Transverse section 14q. J: Transverse section 14p. L: Transverse section 14m. K: Specimen PAULg-S-d-N/17 from the lower part of the Sains Formation, Sains-du-Nord. K: Transverse section 17d showing calicinal a expansion due to a constriction phase. M: Specimen PAULg-S-d-N/9 from the lower part of the Sains Formation, Sains-du-Nord, transverse section 9d in a young stage showing pinnately connected septa. N: Specimen PAULg-S-d-N/15 from the lower part of the Sains Formation, Sains-du-Nord, transverse section 15b showing lonsdaleoid dissepiments formed during a constriction phase. O: Specimen PAULg-S-d-N/9 from the lower part of the Sains Formation, Sains-du-Nord, transverse section 9d. P: Specimen PAULg-Avesnes-VII-2 from the lower part of the Sains Formation, Avesnes-sur-Helpe, Avesnois, North France, transverse section IIg in a young stage showing pinnately connected septa. Q: Specimen PAULg-S-d-N/5 from the lower part of the Sains Formation, Sains-du-Nord, transverse section 5a. R: Specimen PAULg-S-d-N/10 from the lower part of the Sains Formation, Sains-du-Nord, longitudinal section 10b showing strong constrictions and rejuvenescences. A, O: x1; B-L, N, Q-R: x2, scale bar : 5 mm, except A, N: 10 mm and M, P: 2.5 mm.

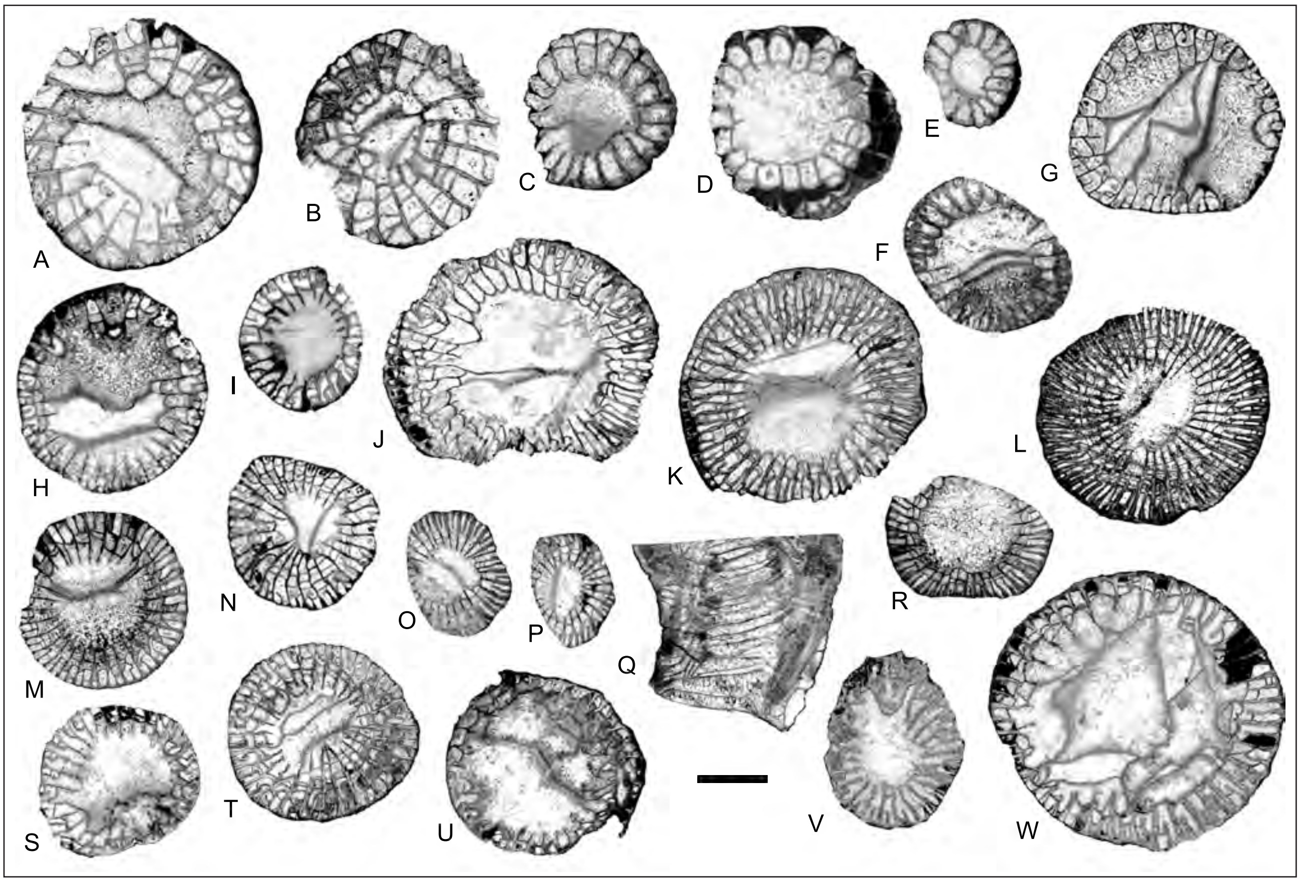

Figure 6. A-B, F-W: *Breviphrentis* cf. *superstes* sp. nov. Poty & Denayer. A: specimen PAULg-Sivry 66B/II from the Souverain-Pré Formation, Sivry, Belgium, transverse section IIa. B: Specimen PAULg-Sivry 66B/IV, transverse section IVa. F: Specimen PAULg-Badon/2 from the Souverain-Pré Formation, Badon, Belgium, transverse section 2b. G-H, N: Specimen PAULg-Badon/9, G: Transverse section 9c. H: Transverse section 9b. N: Transverse section 9e. I: Specimen PAULg-Badon/5, transverse section 5a. J-M, O-R: Specimen PAULg-Avesnes 50/75 from the Sains Formation, Avesnes-sur-Helpe, Avesnois, North France. J: Transverse section b. K: Transverse section c. L: Transverse section d. M: Transverse section f. O: Transverse section h. P: Transverse section i. Q: Longitudinal section e. R: Transverse section g. S-W: Specimen PAULg-Avesnes 57/50 from the Sains Formation, Avesnes-sur-Helpe, Avesnois, North France. S: Transverse section e. T: Transverse section d. U: Transverse section f. V: Transverse section g. W: Transverse section b. C-E: *Catactotoechus* sp. from the Souverain-Pré Formation (Upper *marginifera* Subzone), specimen PAULg-Chev.1993/1/I from, Chevetogne, Belgium. C: Transverse section Ic. D: Transverse section Ib. E: Transverse section Id. A-F: x4, scale bar : 2.5 mm, G-W: x2, scale bar: 5 mm.

show constrictions and rejuvenescences. The longest specimen is 5 cm long. The major septa are thin to thick, and extend for 1/4 to 2/3 of the radius. The minor septa are short, sometimes contraclinant or contratingent. The tabulae are complete to slightly divided, flat to moderately concave, and decline outward to form a peripheral gut. The width of the axial elevated part of the tabulae decreases during constrictions and enlarges during rejuvenescences. There are no dissepiments. Juvenile stages were not observed.

Discussion. The transverse sections of these small corals are identical to those of young stages of *Breviprentis superstes* sp. nov. having the same diameter. Their longitudinal sections share similarities with those of *B. superstes*. These specimens may probably correspond to dwarf specimens of the latter and probably lived in ecological conditions not so favourable than those prevailing in the environment where *B. superstes* occurred, as the material from Sivry and Badon is from the Souverain-Pré Formation, which is represented mainly by sandy and argillaceous packstones and wackestones.

Distribution. Breviphrentis cf. *superstes* sp. nov. (= *B.* sp. A in Poty (1999) is known from the Souverain-Pré Formation in the southwestern part of the Dinant Synclinorium (Badon and Sivry sections). In Sivry, it is associated to spire-bearer (spiriferids and athyridids), orthid and rhynchonellid (*Centrorhynchus letiensis* group) brachiopods.

Family Laccophyllidae Grabau, 1928

Genus *Catactotoechus* Hill, 1954

Type species. Catactotoechus irregularis Hill, 1954, Famennian, *Spinulicosta proteus* Zone, Fairfield Formation, Oscar Hill, Canning Basin, NE Australia.

Discussion. The genus *Hillaxon* Różkowska 1969, from the Famennian of Poland is possibly a junior synonym.

***Catactotoechus* sp.**
(Fig. 6 C-E)

Material. two specimens from Chevetogne, Souverain-Pré Formation, upper *marginifera* Subzone.

Description. Small solitary subcylindrical coral 6.2 to 8.0 mm in diameter with 20 to 25 major septa. The major septa extend for 1/3 to 3/5 of the radius and are more or less sinuous. There are no minor septa. The cardinal fossula is inconspicuous. An aulos is present in sections of 3.5 and 4.0 mm in diameter with 16 major septa and disappears from sections of 6.2–6.5 mm in diameter with 20–24 major septa. Its diameter is above 0.4 of the diameter of the coral. Some single dissepiments develop from a section of 6.5 mm in diameter and form three incomplete series in the wider section observed (8.0 mm in diameter). The outer wall is 0.1–0.2 mm thick. Characters in longitudinal section were not observed.

Discussion. Both specimens clearly belong to the genus *Catactotoechus*, but until larger collections, it is advisable to leave them unnamed.

Distribution. *Catactotoechus* sp. is only known from the Souverain-Pré Formation (Upper *marginifera* Subzone) in the

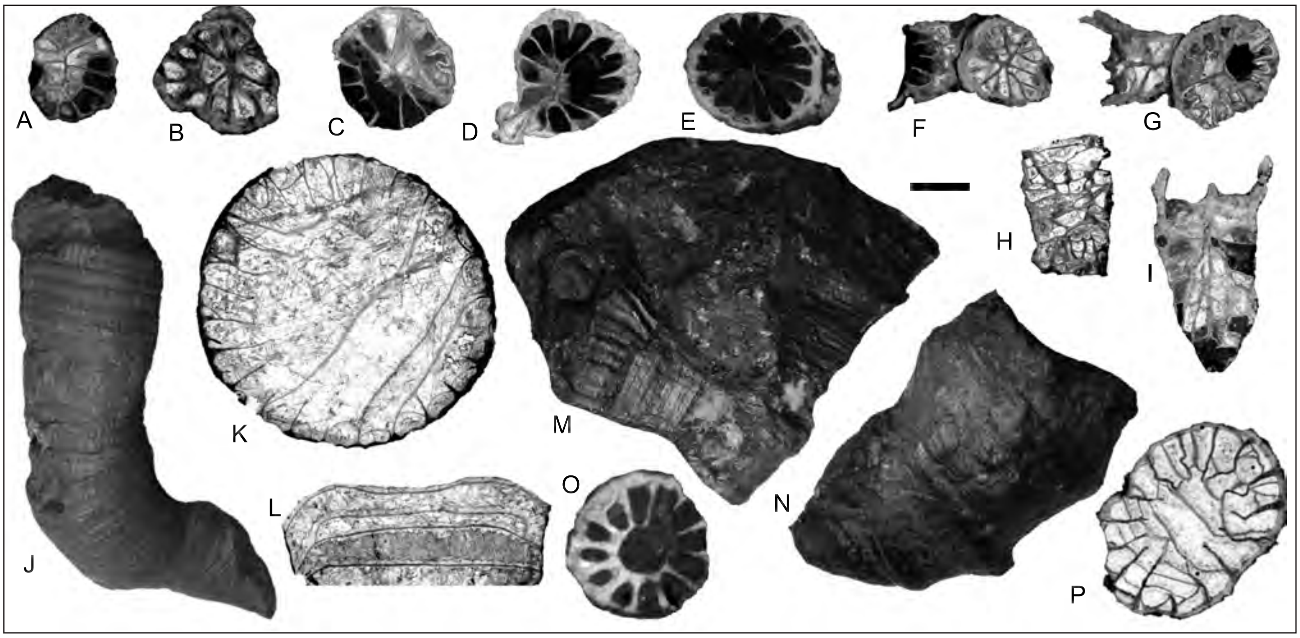

Figure 7. A-I: *Cheilaxonia* cf. *hofmanni* Weyer, 2004, from the base of the Hodimont Formation (Lower *crepida* Subzone), Lambermont section, Belgium. A: Specimen PAULg-Lamb.17/XXXVIII, transverse section. B: Specimen PAULg-Lamb.18/LV, transverse section. C: Specimen PAULg-Lamb.13/XI, transverse section. D: Specimen PAULg-Lamb.13/XII, transverse section. E: Specimen PAULg-Lamb.11/IV, transverse section. F: Specimen PAULg-Lamb.17/XXXIX., transverse section. G: Specimen PAULg-Lamb.15/XXVIII, transverse section. H: Specimen PAULg-Lamb.12/III, longitudinal section. I: Specimen PAULg-Lamb.11/I, longitudinal section. J-L: *Amplexus* sp., specimen PAULg-Isnes/dec.2011/I from the oolitic ironstone level I of the Franc-Waret Formation (Lower *crepida* Subzone) from the Isnes-les-Dames iron mine. J: View of the specimen showing a scolecoid habitus and growth ridges. K: Transverse section Ic. L: Longitudinal section Id. M-N: *Tabulophyllum* ? sp. specimen PAULg-Isnes/dec.2011/II from the oolitic ironstone level I of the Franc-Waret Formation (Lower *crepida* Subzone) from the Isnes-les-Dames iron mine. M: View of the sample showing 2 gregarious (?) specimens. N: View of the specimen showing growth ridges. O: *Neaxon* sp., specimen PAULG-Lamb.12/I form the base of the Hodimont Formation (Lower *crepida* Subzone), Lambermont section, Belgium, transverse section. P: Gen. et sp. unknown, specimen PAULg-Neuville 2012/VI/1 from the limestone level forming the base of the Matagne Formation (*linguiformis* Zone, Upper Frasnian), Neuville railway section, Belgium. J and M-N: x2, scale bar: 4 mm. A-I, K-L and P: x4, scale bar: 2 mm. O: x8, scale bar: 1 mm.

Chevetogne section (see Appendix 1). The genus is also known in the Famennian of Australia (Hill & Jell, 1971), in the Frasnian of northern France (Rohart, 1988) and from the Emsian of Morocco (Berkowski, 2008).

Family Protozaphrentidae Ivanovskiy, 1959

Genus *Cheilaxonia* Weyer, 2004

Type species. *Cheilaxonia hofmanni* Weyer, 2004, Lower Famennian (Middle–Upper *crepida* subzones), Thüringisches Schiefergebirge, Germany.

Cheilaxonia cf. *hofmanni* Weyer, 2004

(Fig. 7A-I)

Material. Sixty-five specimens badly preserved, crushed, bored and abraded from the base of the Hodimont Formation (Lower *crepida* Subzone) Lambermont section and several uncut specimens from the "Heid de Fer" section near La Reid (see Appendix 1).

Description. Our specimens are often found attached on each other by short outgrowth, proving a gregarious way of live. Consequently, their skeletal elements are deformed, and are often oval in section. The diameter varies from 2.5 to 7 mm. There are 12 to 16 (max. 18) septa, commonly curved and fusing in clusters of 2–4 before joining the axis. They form a weak axial structure in which cardinal and counter septa are almost always implied with several other major septa. The latter are not thickened, except near the wall. The cardinal and counter septa are slightly thicker where implied in the axial structure. The minor septa are absent in sections smaller than 4 mm and remain short in larger calicular sections. All the septa tend to withdrawn from the axis in the calice. Some rare simple dissepiments are present in the larger calicular sections. The wall is thick (0.1–0.3 mm) and undulating or festooned. The tabulae are flat in the axial zone and slightly declined outwards.

Discussion. The weak axial structure formed by the axial ends of the septa and the septa arranged in clusters near the axis of the corallite are the diagnostic character of the genus *Cheilaxonia* Weyer, 2004. The morphology of the Belgian material is close to the small undissepimented coral *Metriophyllum* Milne-Edwards & Haime, 1850, but the latter commonly shows small septal spines. Our corals show many common points with *Petraiella reichsteini* described by Weyer (1991) from the Lower Famennian limestone capping the Devonian Iberg Reef in the Harz Mountains. Dimensions and number of septa are comparable, as well as the curved septa but the axial structure is more developed in the Belgian corals. Nonetheless, our material displays the same characters and size than the type material of *C. hofmanni* from the Lower Famennian strata of Thuringia illustrated by Weyer (2004). However, the poor state of preservation precludes the definite specific identification.

Distribution. The small solitary undissepimented rugose corals identified as *Cheilaxonia* cf. *hofmanni* are known from the base of the Lower Famennian Hodimont Formation (Lower *crepida* Subzone) in the Vesdre Area (Lambermont) and the Theux Window (La Reid) (eastern part of Southern Belgium). In the Lambermont section (Vesdre Area), the bulk of the specimens was collected in a single bed of green to red argillaceous limestone overlying the oolitic hematite horizon (level I of Dreesen, 1982), which is characteristic of the base of the Hodimont Formation. In this section, additional specimens were also recovered from the base of a shaly bed, which caps the limestone bed described below, and were associated to several specimens of an unidentified species of rhynchonellid brachiopod (Fig. 8). The latter are small-sized and smooth (except the presence of a median furrow on the fold and a low median rib in the sulcus of some shells). However, the lack of knowledge about their internal morphology, because of a lack of material suitable for serial sectioning, prevents an accurate identification.

Family Petraiidae De Koninck, 1872

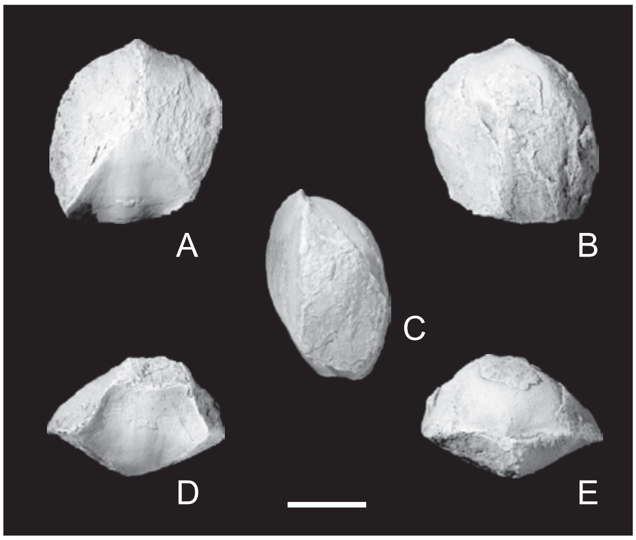

Figure 8. Undetermined rhynchonellid brachiopod (PAULg 2011-11-6) associated with *Cheilaxonia* cf. *hofmanni* Weyer, 2004 and *Neaxon* sp. in the lowermost part of the Hodimont Formation (Lower *crepida* Subzone), Lambermont section, Belgium. A: Ventral view. B: Dorsal view. C: Lateral view. D: Anterior view. E: Posterior view. A-E: x2, scale bar: 5 mm.

Genus *Neaxon* Kullman, 1965

Type species. *Neaxon regularis* Kullman, 1965, Upper Emsian, East of Muda, North Spain.

***Neaxon* sp.**
(Fig. 7 O)

Material. Two incomplete specimens from the Lambermont section (see Appendix 1).

Description. Our specimens are 3 and 4 mm in diameter and show 12 and 16 septa, respectively. The aulos is 0.5 to 0.8 mm in diameter. Wall and septa are at the maximum 0.25 mm-thick. No dissepiments were observed. Neither the external characters nor the longitudinal section are known. The bad preservation of the specimens does not allow further description.

Discussion. The absence of dissepiments excludes our specimen from genera such as *Amplexocarinia* Soskina, 1941 and *Czarnockia* Różkowska, 1969. Furthermore, the absence of contratingent minor septa excludes the attribution to *Syringaxon* Lindström, 1882. Nevertheless, the lack of knowledge about the location of the section through the corallite precludes an accurate specific identification, based on the size and number of septa. *Neaxon regularis*, the type species, is Emsian (Kullmann, 1965), whereas *N. regulus* Weyer, 1971*, N. bartzschi* Weyer, 1978 and *N. muensteri* Weyer, 1989 are Upper Famennian (Weyer, 1971, 1978, 1989). These three species are larger (>10 mm) than the Belgian one. *N. cheilos* Weyer, 1984 is the only species of *Neaxon* described from the Lower Famennian strata (Weyer, 1984). Our specimens could belong to this last species but the material is not sufficiently good to allow a specific attribution.

Distribution. *Neaxon* sp. is only known from the lowermost part of the Hodimont Formation in the Lambermont section, where it is associated to *Cheilaxonia* cf. *hofmanni*.

Family Amplexidae Chapman, 1893

Genus *Amplexus* Sowerby, 1814

Type species. *Amplexus coralloides* Sowerby, 1814, Lower Carboniferous, Limerick, Ireland.

***Amplexus* sp.**
(Fig. 7 J-L)

Material. One single specimen from Isnes-les-Dames iron mine (Les Isnes), housed in the old collection of the Liège university (Dewalque's collection). The specimen is hematitized but some parts of the original carbonated skeleton are preserved.

Description. This specimen is a 4-cm long scolecoid coral, showing two changes in growth direction, partly included in the hematitic rock. Small septal furrows and growth lines are visible on the external wall. The larger cylindrical part of the corallite is 11 mm in diameter and has 25 septa. The septa are very short (0.6–1 mm) and amplexoid. The minor septa are reduced to septal crest on the wall. The wall is 0.1 mm thick and undulating. In the longitudinal section, the tabulae are complete, flat and mesa-shaped, lately plunging towards the periphery. They are regularly spaced and there are 5 tabulae in a section of 5 mm high.

Discussion. Both the external and the internal characters are typical of the genus *Amplexus*. This specimen could be compared to *A*. sp. C from the Lower Famennian of Rübeland figured by Weyer (1991), but the latter specimen is 3 mm-large and shows almost no septa. Our specimen enters in the very large range of variability of the Carboniferous species *A. coralloides* Sowerby, 1814, and could be assigned to this species, but further specimens are needed to support this specific identification.

Distribution. *Amplexus* sp. is from the oolithic hematite horizon which occurs within the Lower Famennian part of the Franc-Waret Formation. This level was intensively mined for iron ores from 1830 to 1940, north of the Meuse Valley between Namur and Liège. This exploitation being hand-made, fossils were from time to time collected and then housed in the Liège University.

Family Endophyllidae Torley, 1933

Genus *Tabulophyllum* Fenton & Fenton, 1924

Type species. *Tabulophyllum rectum* Fenton & Fenton, 1924, Upper Devonian, Iowa.

***Tabulophyllum* ? sp.**
(Fig. 7 M-N)

Material. One sample with six (?) gregarious specimens, hematitized and poorly preserved, from the Isnes-les-Dames iron mine (Les Isnes), housed in the old collection of the Liège University (Dewalque's collection).

Description. This sample is made of three specimens included in the rock, plus at least, three other individuals known by their imprints on the same sample. These six corals seem to have formed a pseudo-colony. The larger specimen is 25 mm high and 16 mm in diameter. Shallow septal furrows and tight growth lines are visible on the external surface of the wall, on all the individuals. The internal structures are almost not preserved from the mineralization, except some fragments of septa and wall in one specimen. Therefore the description is very limited. The estimated number of septa is 28 for a diameter of 10 mm. The septa are sinuous and withdrawn from the axis, leaving a free (?) zone in the centre of the corallite. No minor septa are observed. Several lonsdaleoid dissepiments, arranged in a single (?) row, are visible.

Discussion. The present material is inadequate for a precise identification due to its poor preservation. However, the presence of lonsdaleoid dissepiments suggests the genus *Tabulophyllum*, which is common in the Upper Frasnian and also present occasionally in the Uppermost Famennian (Poty, 1999).

Distribution. Same as for *Amplexus* sp.

4. Stratigraphy and diversity

The stratigraphic range of the rugose corals genera for the considered biostratigraphic interval (*triangularis* Zone to *marginifera* Zone) across the Namur-Dinant Basin is presented in

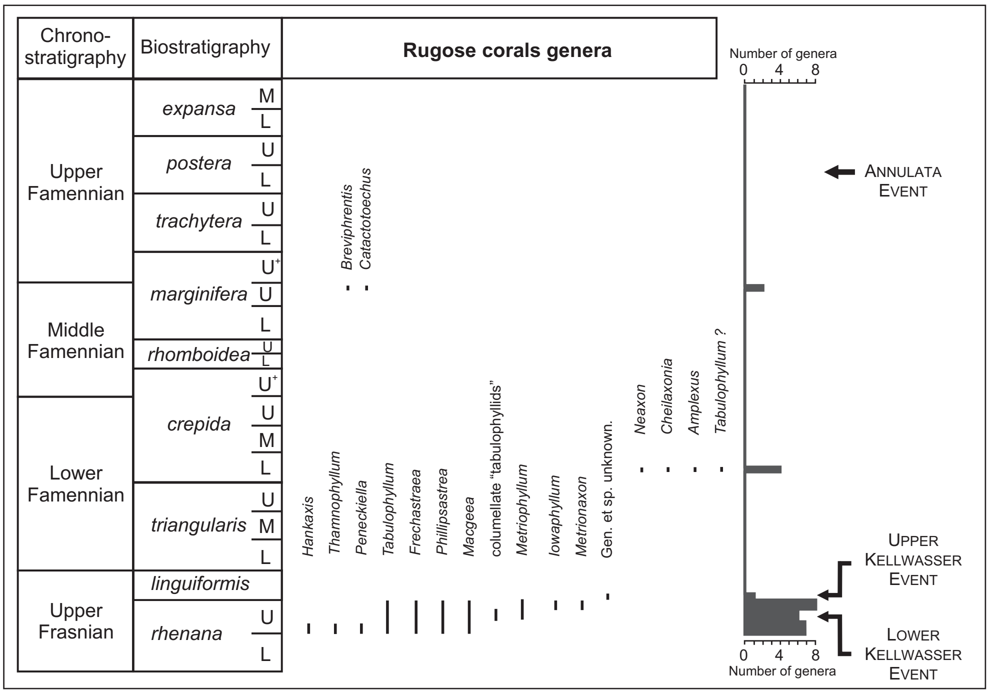

Figure 9. Stratigraphical distribution of the Upper Frasnian and Lower to Middle Famennian rugose corals from southern Belgium and northern France. The diversity curve, in the right part of the figure, clearly shows the extinction preceding the Frasnian/ Famennian boundary. Data from Paquay (2002), Denayer & Poty (2010), Poty & Chevalier (2007), Coen-Aubert (1974, 1982, 2011).

Fig. 9. The Belgian Lower and Middle Famennian rugose corals are only known from two levels as described in the introduction and in the following paragraph.

The diversity curve clearly shows the slow decrease in number of rugose coral genera during the Upper Frasnian and their complete extinction before the Upper Kellwasser Event (Fig. 9). The youngest Frasnian rugose corals of Belgium are very simple small solitary forms, of unknown affinity (Fig. 7 P), found at the top of the Les Valisettes Formation (*linguiformis* Zone (Bultynck et al., 1998)), in the Philippeville Anticlinorium (Neuville new railway section), just below the Upper Kellwasser black shales (Matagne Formation). The diversity of the lower Famennian strata is relatively high with regard to the upper strata (four genera, two of them being represented by single specimens), but there is an artefact due to a more intense exploration of this interval. The Middle Famennian, represented by the Souverain-Pré and Sains formations, yielded abundant but very poorly diversified material including two genera represented by three species. This poor diversity of corals clearly indicates that their post-extinction recovery was not facilitated by unfavourable environments during the Lower and Middle Famennian, long before the Strunian radiation (Uppermost Famennian), the Upper Famennian strata being devoid of corals in Belgium (Poty, 1986).

5. Discussion and conclusions

The rugose coral fauna from the Lower and Middle Famennian of the Namur–Dinant Basin comprises small solitary forms that belong to the so-called *Cyathaxonia* fauna of Hill (1981). This fauna is similar, or closely related, to those described from the Lower-Middle Famennian of China (Soto & Liao, 2002), Australia (Hill & Jell, 1971), Germany (Weyer, 1991, 2004), and the Omolon region in North-East Siberia (Poty, 1986). However, the Siberian fauna was considered as Upper Famennian by Shilo et al. (1984) but could be possibly older (Poty, 1999).

The coral fauna described by Różkowska (1969) in the Famennian of Poland also comprises small solitary corals without dissepiments, close to those described here, and dissepimented solitary and colonial ones. Nonetheless, the Polish coral fauna is difficult to compare with others as some corals were probably reworked from pre-Famennian deposits, and others were misidentified (Poty, 1986, 1999).

The Middle Famennian coral fauna of the Namur-Dinant Basin also includes large solitary rugosa which are assigned to the new species *Breviphrentis superstes* sp. nov. and *B*. cf. *superstes*. The genus *Breviphrentis* was considered as extinct for at least the end of the Givetian, and its brief reappearance during the Famennian qualifies it as a "Lazarus taxon". These corals may have migrated to deep-water-like environments (probably not true deep-water environments where anoxic conditions dominated and had to prevent their development) that permit them to survive at the late Frasnian crisis. They latter reappeared in shallow-water environments during Lower and Middle Famennian but probably became extinct (or migrated again) because of unsuitable conditions during the Upper Famennian times.

As described in the systematic paragraph, the morphology of *Breviphrentis superstes* and *B*. cf. *superstes* is unstable. The inter-individual and ontogenetic variations are very wide and witness the very plastic morphology of these taxa. This plasticity is most probably linked to the very low natural selection pressure conducted by ecological conditions through the mixed siliciclastic-carbonated deposition environment, as signalized for Strunian campophyllids (Poty, 2010). The corals were able to react rapidly to changes of environmental conditions (as shown by the constriction–rejuvenescence cycles) and adapt their morphology in consequence (Scrutton, 1998).

Most of these Lower and Middle Famennian rugose corals became extinct before the first Uppermost Famennian (Strunian) coral radiation which took place in the Upper *expansa* Subzone (Poty, 1999).

Tabulate corals are known from the Lower and Middle Famennian of the Namur–Dinant Basin but are only represented by species belonging to the primitive and long-ranging taxa *Aulopora* and *Cladochonus*. Auloporids were reported in the Lower Famennian Famenne Group by Gosselet (1877, 1888) and illustrated by Mottequin (2008, figs 10.3 and 10.13); *Cladochonus* only occurs in the Souverain-Pré Formation (Chevetogne section). Maillieux (1930) cited syringoporids in the Lower Famennian of southern Belgium, but micheliniids and syringoporids are not known before the Strunian. Note that stromatoporoids, which disappeared at the end of the Frasnian in the studied area, only reoccur during the Strunian, before their total extinction at the end of the Famennian (Hangenberg Event).

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Appendix 1. Geological and geographical data of the sampled localities

- Avesnes. Cemetery street section, (50° 06’ 42” N, 3° 57’ 25” E) (Conil, unpublished data), Avesnois, North France; Sains Formation.
- Avesnelles. Railway cutting, (50° 06’ 47” N, 3° 57’ 30” E) (Conil, unpublished data), Avesnois, North France; Sains Formation.
- Badon. Trench of the road Charleroi-Couvin (N5) (50°11’39.59” N; 4°22’46.79”) (e.g. Bouckaert & Dreesen, 1977; Dreesen, 1978; Poty, 1999); Souverain-Pré Formation.
- Chevetogne. Access road to the provincial domain of Chevetogne (N 50°13’28.38”; E 5°08’29.46”) (Poty, 1999); Souverain-Pré Formation.
- Isnes-les-Dames. Most probably form the old iron mine of Isnes-les-Dames (N50°30’21.73”; E4°43’42.58”), housed of the former palaeontological collections of the University of Liège (Dewalque’s collection) ; lower part of the Franc-Waret Formation.
- Neuville. Neuville, south-west of the village, on the eastern side of a trench dug for the Couvin-Charleroi railway (N50°10’00” ; E4°29’53.50”) (e.g. Bultynck et al., 1998; Azmy et al., 2012); top of the Les Valisettes Formation.
- Lambermont. Western access road to the highway Verviers-Prüm (N 50°35’40.36”; E 5°50’33.86”) (e.g. Dreesen, 1982; Laloux et al., 1996); base of the Hodimont Formation.
- La Reid. Foothpath linking the village of La Reid to the Becco hamlet (“Heid de Fer”) (N 50°29’47.28”; E 5°47’23.80”); base of the Hodimont Formation.
- Sains-du-Nord. Railway cutting (50° 05’ 34-36” N, 3° 59’ 57” E) (Conil, unpublished data), Avesnois, North France; Sains Formation (coral material from the lower part of the formation).
- Sivry. Along the Là-Haut street, north of the village of Sivry (N 50°10’11.68”; E 4°10’51.38”) (Marion & Barchy, 2004); Souverain-Pré Formation.

Appendix 2. List of specimens

Breviphrentis superstes Poty & Denayer:
- Sains-du-Nord: S-d-N/1 (1 t.s.), S-d-N/2 (6 t.s.), S-d-N/3 (11 t.s. & 1 l.s.), S-d-N/4 (2 t.s. & 1 l.s.),S-d-N/5 (6 t.s. & 1 l.s.), S-d-N/7 (7 t.s.), S-d-N/8 (4 t.s.), S-d-N/9 (3 t.s. & 1 l.s.), S-d-N/10 (3 t.s. & 1 l.s.), S-d-N/11 (4 t.s.), S-d-N/12 (8 t.s. & 1 l.s.), S-d-N/13 (9 t.s. & 1 l.s.), S-d-N/14 (17 l.s. & 1 l.s.), S-d-N/15 (7 t.s. & 1 l.s.), S-d-N/16 (4 t.s.), S-d-N/17 (13 t.s.), S-d-N/18 (5 t.s. & 2 l.s.), S-d-N/19 (8 t.s.), S-d-N/20 (4 t.s.), S-d-N/21 (2 t.s.), S-d-N/22 (2 t.s. & 1 l.s.), S-d-N/23 (2 t.s. & 1 l.s.), S-d-N/24 (1 t.s. & 1 l.s.), S-d-N/25 (6 t.s. & 1 l.s.).
- Avesnes: A.VII/1 (5 t.s.), A.VII/4 (3 t.s.), A.VII/5 (2 t.s. & 2 l.s.), A.VII/7 (1 t.s. & 1 l.s.).
- Avesnelles: A.50/57 (6 t.s. & 1 l.s.), A.50/74 (4 t.s. & 1 l.s.), A.50/75 (8 t.s. & 1 l.s.), A.50/79 (4 t.s. & 1 l.s.), A.50/94 (4 t.s. & 1 l.s.), all specimens from bed 50.

Breviphrentis cf. *superstes*:
- Sivry: S-66B-I (1 t.s. & 1 l.s.), S-66B-II (1 l.s.), S-66B-III (1 t.s. & 1 l.s.), S-66B-IV (2 t.s.).
- Badon: B-1 (1 t.s. & 1 l.s.), B-2 (1 t.s. & 1 l.s.) , B-4 (1 t.s.), B-5 (2 t.s.), B-7 (1 t.s.), B-9 (5 t.s. & 1 l.s.).

Catactotoechus sp.:
- Chevetogne: Chev. 1993/1-I (2 t.s.), Chev. 1993/1-II (2 t.s.).

Cheilaxonia cf. *hofmanni*:
- Lambermont: Lambermont/2011/11/I to V, 2011/12/I to VI, 2011/13/VII to XV, 2011/14/XVI to XXIV, 2011/15/XXV to XXIX, 2011/16/XXX to XXXVII, 2011/17/XXXVIII to LIII, 2011/18/LV to LX (60 t.s. , 5 l.s.).

Neaxon sp.:
- Lambermont: Lambermont 2011/12/I’ (1 t.s.), 2011/15/XXVI (1 t.s.).

Amplexus sp.:
- Isnes-les-Dames/dec.2011/I (4 t.s., 1 l.s.).

Tabulophyllum ? sp.:
- Isnes-les-Dames/dec.2011/II (6 t.s.).

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Devono-carboniferous carbonate platform systems of the Netherlands

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ABSTRACT. Large Palaeozoic carbonate build-ups, globally important for hydrocarbon exploitation, are generally not associated with the Netherlands or with the larger Southern North Sea region. The last ten years, information of new wells and seismic imaging have changed this perception. Recent seismic interpretations have indicated massive reef like carbonate platforms far below conventional petroleum exploration targets in the Netherlands. Some of the platforms are very sizeable and comparison with dimensions of Mississippian build-ups in the Caspian region or Devonian reefs of Canada can be made. New well information, released the last two years, dates the upper part of the platform as Mississippian. Based on seismic interpretation, some platforms most likely contain a Devonian core. UK petroleum exploration on the Mid North Sea High also provides new insights into Devonian carbonate build-ups. Due to the great depth of the Devono-Carboniferous strata in most areas, it is unclear if these carbonate platform reservoirs are a new petroleum exploration frontier or are situated below the economic basement. For many years the same palaeogeographic map could be used for North Western Europe for the Devonian and Mississippian time interval. The new data requires a revised palaeogeography. The following summary provides an overview.

KEYWORDS: North West Europe, Caledonian orogeny, Palaeo-trade winds, Luttelgeest-01, Uithuizermeeden-02, Groningen carbonate platform, Mid North Sea High, Tengiz, Canada.

1. Introduction

The Netherlands is a major hydrocarbon province in western Europe. With more than 5000 oil and gas wells and good seismic coverage, the first two to three kilometres of its subsurface is studied in detail (Wong et al. 2007). Relatively few geological studies were performed of horizons below the Permian Upper Rotliegend (Fig. 1), the major petroleum target in the country. Owing to its coal layers and gas reservoir potential, only the coal bearing Upper Carboniferous Limburg Group, directly below the Base Permian Unconformity, was studied in some detail (Wong et al. 2007). Of the more than 1300 exploration wells in the country, only 22 boreholes were drilled into the Mississippian Zeeland or Devonian Banjaard Group (Figs 1, 2, 3). Due to their depth, generally exceeding 4,000 m, the Devonian or Mississippian age formations are rarely considered a target for hydrocarbon exploration in the Netherlands or in the surrounding countries that share the same basin setting. The few wells drilled to these targets are further concentrated in specific areas. Therefore the geological evolution during the Devono-Mississippian can only be described in general terms. A few geological overviews are available (Glennie, 1998; Wong et al., 2007; Doornenbal & Stevenson, 2010). The new data changes the established palaeogeography. The aim of the study is to provide an overview with the incorporation of all the new information. The few isolated oil and gas finds in Mississippian or Devonian reservoirs in the United Kingdom (UK), like the Mississippian Hardstoft oil field (1919), do not suggest there is a regional Devono-Carboniferous petroleum play for North West Europe (Fraser & Gawthorpe, 1990; Glennie, 1998), however the new insights into the Palaeozoic carbonate platform development in the Netherlands are largely not reflected in these summaries and may change this perception.

2. Geological setting during Devonian and Mississippian (general setting of NW Europe)

After the Caledonian orogeny in the general Southern North Sea region, including the Dutch onshore area, sedimentation started during the Mid and Late Devonian. From that time until recently, sediments can be found in almost every period in the Dutch stratigraphic record (Van Adrichem Boogaert & Kouwe, 1997; Wong et al., 2007). Information from surrounding countries, make it clear that the sedimentary basement is formed during the Silurian as part of a Caledonian triple continental plate collision (Figs 4, 5 and 6). After these Caledonian orogenic events, intracratonic basin-fill is deposited in the vicinity of the Iapetus suture situated at the north west fringes of the presentday Western Europe. To the south east, basins belonging to the continental margin of the Rheic Ocean (Fig. 5), which is in existence till the Pennsylvanian, are characterized by marine deposits.

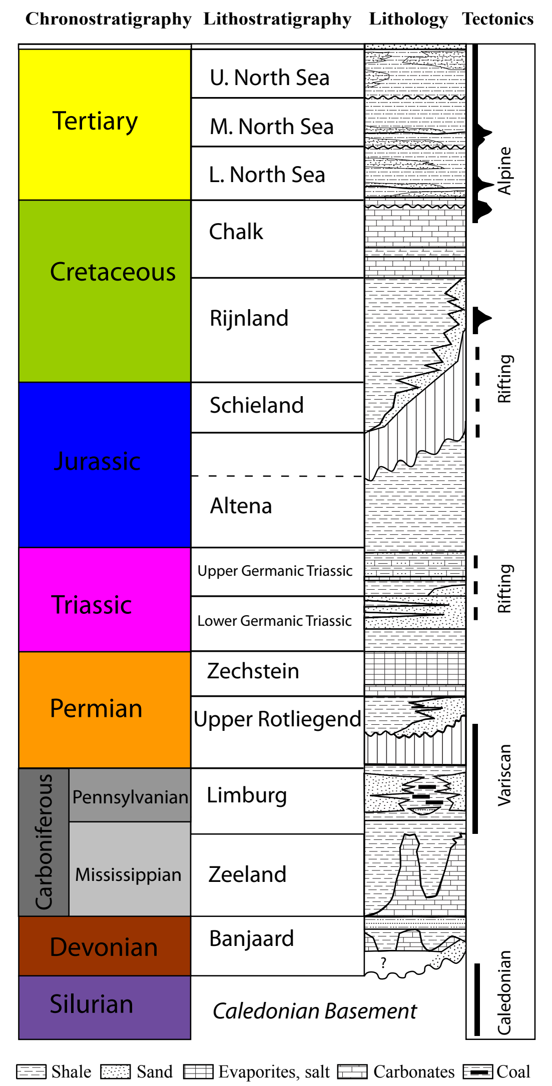

Figure 1. Stratigraphic table for the Netherlands showing the major lithological units on Group level. The Permian Upper Rotliegend (Slochteren Formation) is the major petroleum target in the country. The more shallow (Germanic) Triassic, informally known as Bunter sandstone, is the second most important exploration target. The nomenclature of the Devono-Carboniferous period is based on very few boreholes (see Fig. 3). The Devonian Banjaard Group includes carbonates in the southern part of the country (Wong et al., 2007). They include the Kyle type of limestone, known from the UK to the north of the Dutch offshore. For the Mississippian limestone it is customary to use Zeeland Formation. For the time equivalent basinal shale facies, no formal term has been proposed.

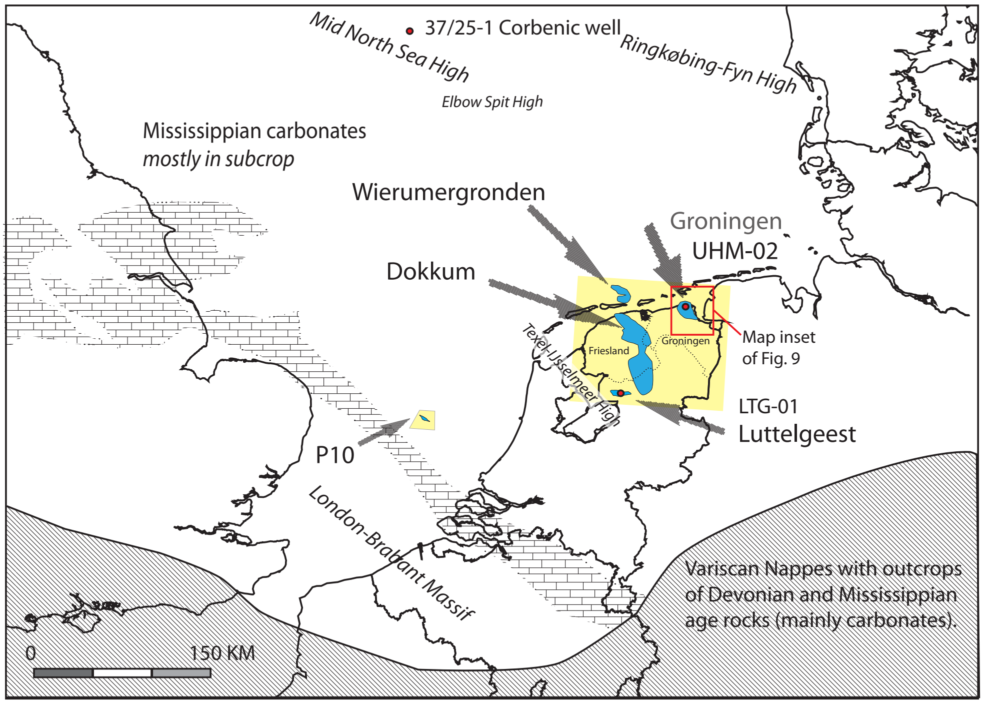

Figure 2. Index map shows recently discovered Devono-Carboniferous reefs and new wells drilled the last ten years. The well-known north west trending Mississippian carbonate (subcrop) trend, which fringes the north side of the London-Brabant Massif, is indicated. Devonian or Mississippian age rock is not present in Dutch outcrops, in contrast to neighbouring countries where these rocks can be studied in many exposures.

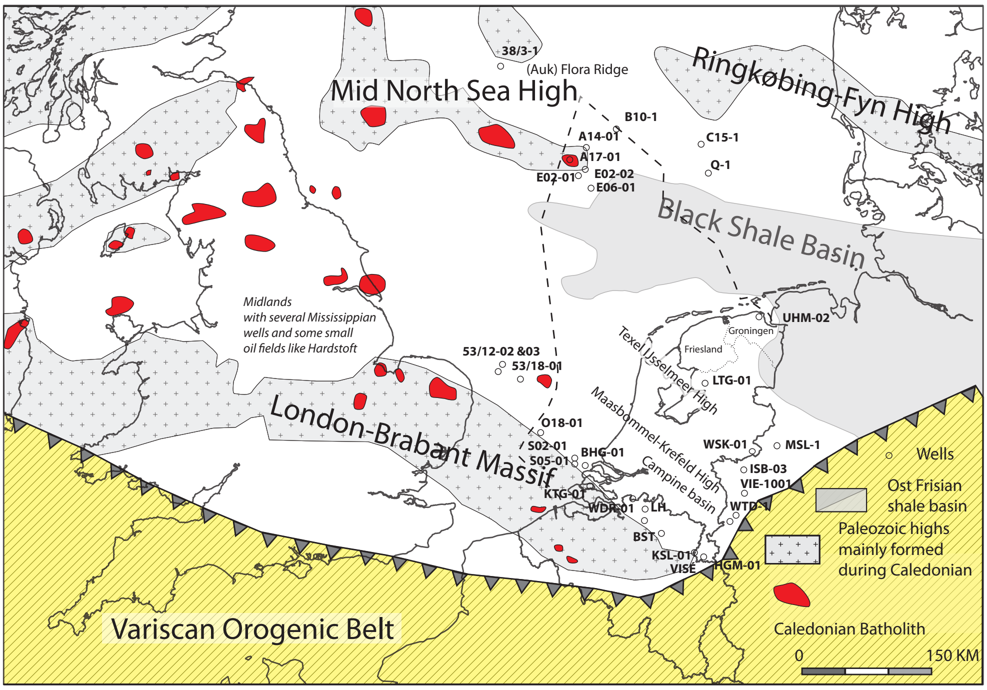

Figure 3. The most important wells, drilled into the Devonian or Mississippian, of the Netherlands and the direct vicinity. The map shows the major highs and batholiths of the Southern North Sea area based on Glennie (2005). The general outline of the (Ost Frisian) black shale basin (in dark for the deepest parts and light grey for shallower parts), based on Van Hulten & Poty (2008). The wells on this map are drilled at least into the Mississippian Zeeland Formation. The well UHM-02 and LTG-01 were the first wells drilled away from the basin fringes. To the south, the Variscan thrust and orogenetic belt has been indicated. This is an area with extensive outcrop information on Devono-Carboniferous carbonates, however also complex because of thrusting and telescoping.

In the Netherlands only few data points are available of wells which reach the pre Devonian basement (Wong et al., 2007). With regional information of the surrounding countries, a generalized depositional framework can be constructed for the earliest infill of the post Caledonian basin. Infill of the Southern North Sea region probably started during the Eifelian or even earlier, comparable to the outcrops in the allochtonous Variscan nappes of southern Belgium (Doornenbal & Stevenson, 2010). The oldest known sediments in the area north of the London-Brabant Massif are of Givetian age (Glennie, 1998; Evans et al., 2003; Wong et al., 2007). This study concerns mainly the carbonate sedimentation, which is dominant during the Devonian ages Givetian and Frasnian and during the Mississippian ages Tournaisian and Viséan. The youngest Devono-Carboniferous carbonates are of Warnantian age in the Netherlands, comparable to the termination of the reef growth in Belgium and the UK. Organic rich shales of Serpukhovian age can be found in the lows between the platforms or even cover the carbonates (Van Hulten & Poty, 2008; Doornenbal & Stevenson, 2010). A detailed discussion of these organic rich shale deposits is outside the scope of this study. The general stratigraphic term Devono-

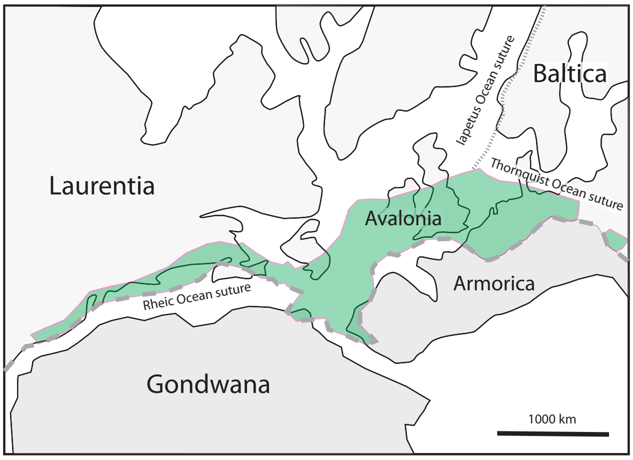

Figure 4. The basement in the Southern North Sea Area is formed during the Silurian as part of a Caledonian triple continental plate collision. Only parts of Avalonia are visible after the Variscian collision. The final Pangea assemblage after the Rheic closure in the late Carboniferous is shown as one sees it today.

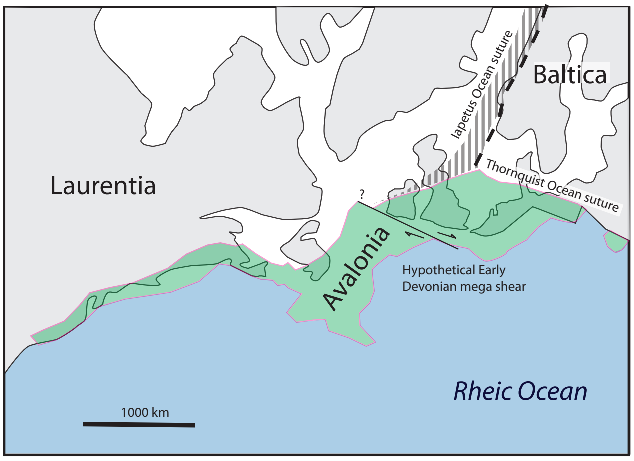

Figure 5. The basement in the Southern North Sea Area is formed during the Silurian as part of a Caledonian triple continental plate collision. The Variscian as shown in Fig. 4 is removed. This illustrates the position of the Netherlands at the continental margin of Laurussia, near the Rheic Ocean during the Devono-Carboniferous. Avalonian mega shear, caused by the early Devonian collision of the South American part of Gondwana with Avalonia (Fig. 12), may explain the extensional tectonics on the northern part of the Avalonia micro craton.

Carboniferous carbonates in this paper is used for carbonate deposits from the Givetian until Serpukhovian age.

3. New focus on Devono-Carboniferous

A number of world class hydrocarbon discoveries were made in Mississippian carbonate reservoirs of the Caspian Sea area and got lots of attention in the 1990's (Weber et al., 2003). As soon as their potential was realized, interest in age equivalent horizons outside that region was stimulated as well. More important were developments in geophysics ten years ago in the Netherlands. New and better quality seismic processing and acquisition made it possible to see deep horizons below the km thick Pennsylvanian section, which before were hidden on older seismic lines. The kilometre size build-ups mapped underneath the northern part of the onshore area of the Netherlands (Kombrink, 2008; Kombrink, 2009; Van Hulten & Poty, 2009; Kombrink et al., 2010) are reminiscent to Devono-Carboniferous bioherms at the eastern margin of the Russian platform like Astrakhan, Zhambay, Karachaganak (Kerogly), Kashagan (Sharburbali) and Tengiz (Weber et al., 2003).

The new seismic interpretations require well data to gain more certainty on the nature of these reefal build-ups. The Devono-Carboniferous depositional model is poorly constrained in the Netherlands, because only few wells, if any, have reached the Mississippian or Devonian formations in basin areas. Most wells were drilled in the southern part of the country at the basin margins (Wong et al., 2007; Van Hulten & Poty, 2008). On seismic, Devonian or Mississippian age formations are therefore rarely interpreted away from the Campine Basin near the London-Brabant Massif in the south of the Netherlands (Figs 2-3) or the Elbow Spit High, part of the larger Mid North Sea High in the northern offshore (Figs 2, 3). Only in the south of the country and the far northern offshore, these formations can be found at a relative shallow depth. Devonian or Mississippian age rock is not present in outcrops of the country, in contrast to neighbouring countries. This implies that the sedimentological setting is generally deduced from detailed information from these countries, like the UK and particularly Belgium (Boulvain, 2007; Boulvain & Wood, 2007; Poty et al., 2002; Paproth et al., 1983). In Belgium these Palaeozoic sections are especially well studied, partly due to the presence of a few classical stratotypes (Coen-Aubert & Boulvain, 2006; Thorez et al., 2006; Hance et al., 2006a, 2006b). Recently important insights were gained in the depositional setting of the Devono-Carboniferous platform carbonates of the Southern North Sea region, when two new exploration wells, Uithuizermeeden-02 (UHM-02) between November 2001 and June 2002 and Luttelgeest-01(LTG-01) between May and October 2004 (Figs 2 and 3), were drilled. The wells proved the existence of two Mississippian carbonate platforms and reached the top of the Devonian (Van Hulten & Poty, 2009; Abbink et al., 2009).

3.1. New seismic data

In the Southern North Sea region, seismic interpretation of Devonian or Mississippian markers is not customary. This is partly because of the strong emphasis on the much shallower Permian Rotliegend Slochteren gas play in the general Southern North Sea area (Glennie, 1998), which requires interpretation of much shallower horizons. It is also due to the poor imaging of these deeper Devono-Carboniferous horizons on conventional seismic. This is often caused by the complexity and disturbance of the seismic signal in the overburden, in particular the Permian Zechstein evaporites, present in the subsurface over large areas of the Netherlands. Multiples of strong reflectors, like the Permian Basal Zechstein Anhydrite horizon, can make interpretation of deeper levels like those of Mississippian or Devonian age carbonates very uncertain (Wong et al., 2007). It is therefore not

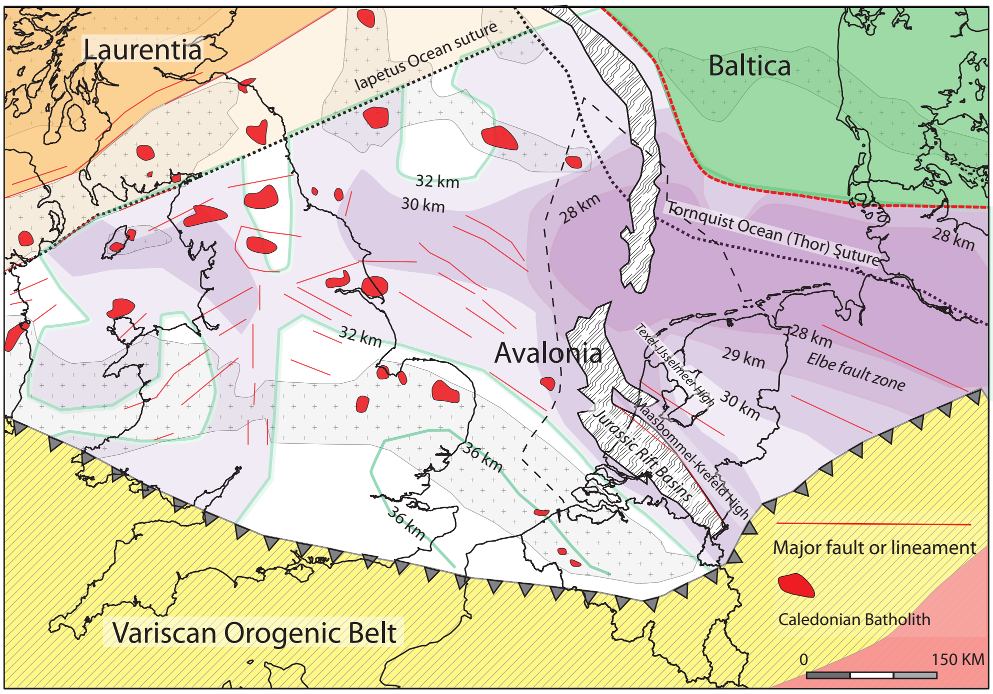

Figure 6. The depositional basement is formed during the Silurian as part of a Caledonian triple continental plate collision. Tectonic elements of the Southern North Sea area are based on very deep (15 seconds) seismic. In green the Baltica terrane, in orange the Laurentian terrane is shown. Structural elements with major faults and lineaments and the crustal terranes are indicated. The depth of the Moho is deduced from a few deep seismic lines only. Based on Moho depth it is suggested that the Avalonian plate can be subdivided in three parts. This is after a correction has been made for the Jurassic rift basins, indicated on the map.

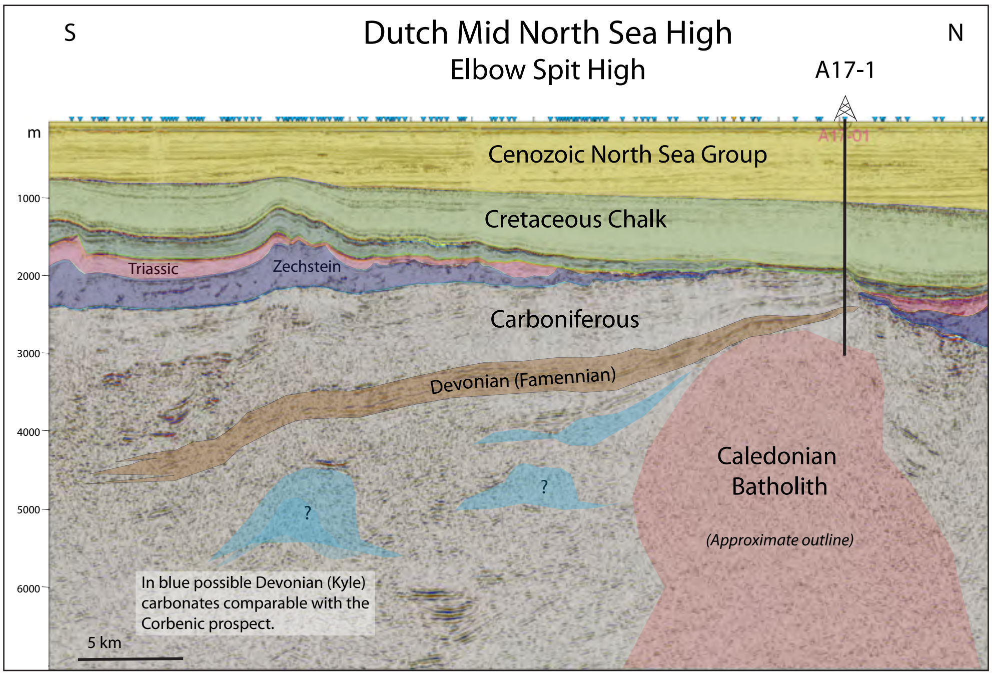

Figure 7. Seismic section of the Mid North Sea High. Note well A17-01. The interpretation shows hypothetical Kyle carbonates underneath Upper Old Red clastics, comparable to the interpretation of the UK Corbenic prospect target of the recent well 37/25-1.

uncommon that lower parts of a commercial seismic line are cut off, because it is perceived to contain mainly noise. The only areas where interpretations of Palaeozoic markers were published are in the Campine Basin, close to the Belgian border, and of the northern parts of the Dutch offshore, at the Mid North Sea High (Figs 2-3).

Interest in deeper horizons increased when in 2003 and 2004 the two, approximately five kilometres deep, exploration wells were drilled. It stimulated the publication of a map of the build-ups in the northern onshore provinces of about 100 km^2, which includes the locations where the two new deep wells are drilled (Kombrink et al., 2008; Kombrink, 2008). Visualization is shown of the Groningen carbonate platform, drilled by UHM-02 and a number of undrilled platforms are described in the Friesland province (Kombrink, 2008).

For most other onshore and offshore areas no interpretation is available of seismic horizons of Mississippian age or older. A few lines are published that give some insight in the geology of the Devono-Carboniferous horizons. De Jager in Wong et al. (2007) shows a deep seismic line which illustrates the thickening of the Carboniferous towards the east into the Lower Saxony Basin with extensive faulting of the basement. Van Hulten & Poty (2008) present a Dinantian structure in the block P10 (Fig. 2). Older seismic and well control in the southern part of the Netherlands (Van Adrichem Boogaert & Kouwe, 1997), cover large parts of the north flank of the London-Brabant Massif in the Campine Basin area. Abbink et al. (2007) show a seismic line with Devono-Carboniferous interpretation over the Campine Basin, which suggests a monotonous Mississippian age carbonate platform development. This seems to contradict the reef like development of that age in Loenhout-Heibaart and other small build-ups as described by Laenen et al. (2004) slightly farther to the east.

In the far north of the Dutch offshore the Mid North Sea High is shown on a few published seismic lines. Quirk (1993) shows a regional N-S line where Late Devonian clastics can be traced from the A17 granite far into the basin territory to the south. De Jager in Wong et al. (2007) and Abbink et al. (2007) also shows a comparable geology with Mississippian and Devonian horizons in more detail, albeit the carbonates underneath the Buchan Formation (Upper Old Red Group of Famennian age) clastics are not visible on their line. In the UK Central North Sea near the Auk and Argyll oil fields, Mid Devonian Kyle carbonates can be clearly seen on seismic (Milton-Worssell et al., 2010). A higher resolution line is shown in Fig. 7, which suggests a hypothetical undrilled Givetian-Frasnian age Kyle carbonates underneath the 'Upper' Old Red clastics, comparable to the Corbenic prospect (Fig. 2) drilled by Exxon in the well 37/25-1 (DECC, 2009).

Very deep (15 seconds) seismic is of importance for the understanding of the structure of the upper crust (Doornenbal & Stevenson, 2010; Abramovitz & Thybo, 2000). The few lines that are (partly) shot over the Netherlands give a better understanding of exceptional crustal conditions underneath the shale basin just north of the Groningen and Friesland platforms (Fig. 6). In the northern offshore part of Germany, adjacent to the Netherlands, the basement in this basin is estimated to be at 12-18 km depth (Ziegler & Louwerens, 1979). This means that the total Devonian may be of substantial thickness there and it supports the conclusion that during the Devono-Mississippian the ocean reached a depth of several kilometers.

3.2. New well data

In the Netherlands about a dozen wells penetrate the Devonian and about 20 reach the Mississippian. When a few wells near the Dutch border in Belgium, Germany, and the UK are added, the total well database hardly exceeds 30 wells (Fig. 3). At the UK side in the North Sea the penetration of Devonian strata has commonly been taken as reason to terminate an exploration well (Glennie, 1998). In the basin area between the major highs, only three or four wells have reached the Devonian in the Netherlands (Wong et al. 2007). In the known wells, no indications of hydrocarbons are described and good reservoir is rare. Because of the scarcity of data, the two new exploration wells were important new data points. Only part of the data has been released, because the UHM-02 well is still confidential until 2013. A zonation based on foraminifera and palynology was published of this borehole (Abbink et al., 2009). This confirmed the Mississippian age of the top part of the platform. The well reached the top of Devonian clastics. This is comparable to the bioherm of LTG-01 (Van Hulten & Poty, 2009). Physical well logs of the two wells are compared in Fig. 8. In both wells the drilling was terminated in the Famennian age clastics.

4. Structural framework

The Devono-Carboniferous palaeogeography of the Southern North Sea region cannot be constructed without general understanding of the Late Palaeozoic structural framework of this part of the Eurasian continental plate. Recent regional updates of the structural development in North West Europe during this period, can be found in Glennie (1998), Bayer et al. (2002), Glennie (2005), Wong et al. (2007), Doornenbal & Stevenson (2010).

The reef building in the Devonian and Mississippian takes place 20-30 Ma after the Caledonian orogeny, which ended during the last part of the Silurian or early Devonian. Substantial

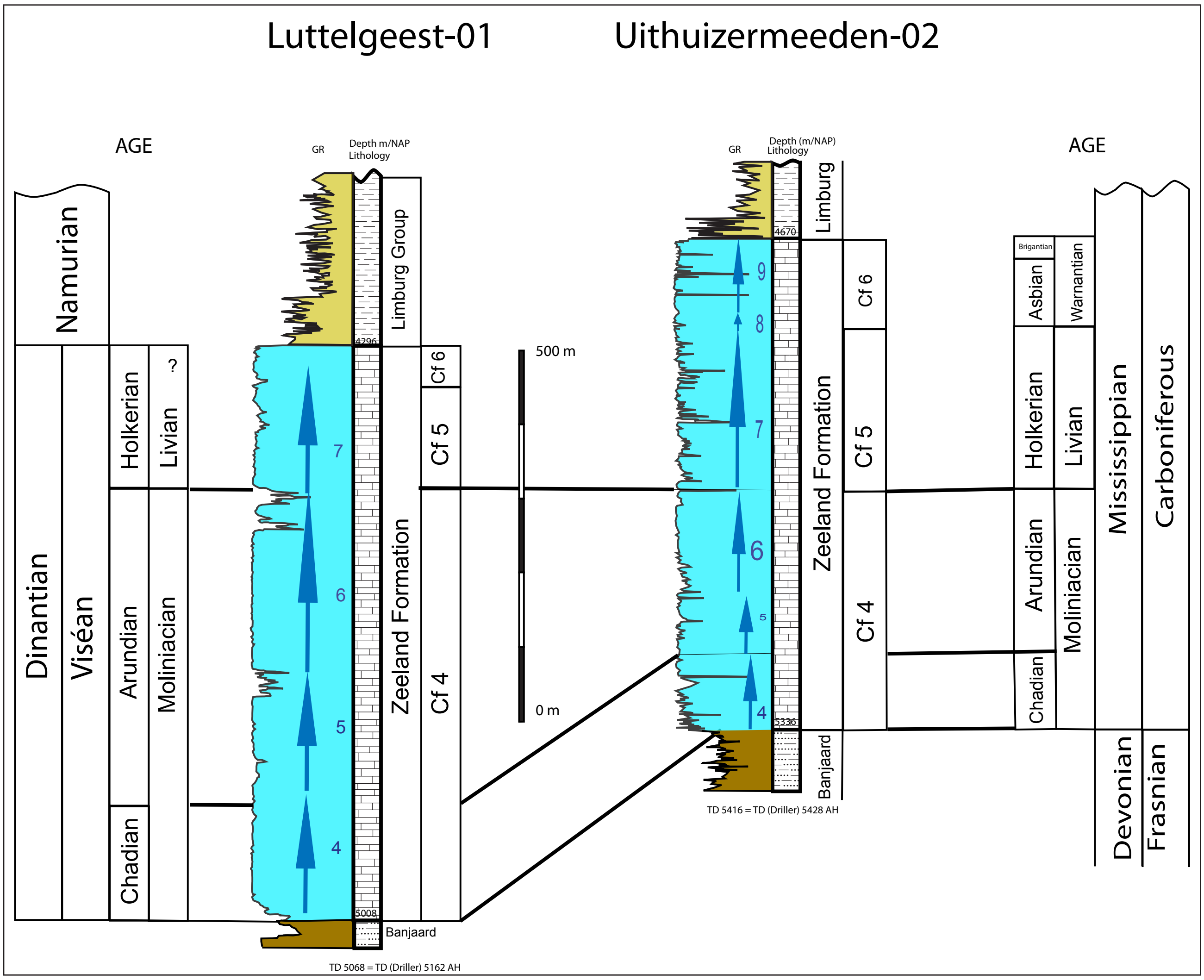

Figure 8. Cross section showing a stratigraphic comparison between the LTG-01 and UHM-02 wells. The Gamma Ray (GR) log of both wells is shown for comparison. Both wells reached TD (Total Depth) in the top of the Famennian clastics. The arrows shows widely recognized 3rd order sequences (Poty et al., 2002). The age interpretation is based on foraminifera (Cf zones). Contrary to the UHM-02 well , the reefgrowth in LTG-01 was terminated before the end of the Viséan.

erosion must have been taking place since the collision. Morphological hard to erode elements like granite landforms can become nuclei for reef growth later. Some aspects of this orogeny are helpful to understand the location of these granite intrusions. In addition, the origins of regional highs and shale basins can be explained.

The Netherlands are a part of the present day Eurasian continental plate. Before the orogeny, its deeper crust belonged to the micro-plate called Avalonia. It became part of the European plate in the Silurian (Torsvik & Cocks, 2004). The collision took place during an early phase of the Caledonian orogeny and resulted in the fusion of the Baltica plate (Scandinavia, Russia) with the Avalonia terrane (Figs 5 and 6). Shortly after this, the Laurentia continental plate (Greenland, North America) joined this fused plate. The Caledonian orogeny can therefore be described as a collision of Laurentia and the Baltica Craton, complicated by the merging with Avalonia (Glennie, 2005). Parts of Avalonia, in particular directly to the south and east of the Netherlands, are obscured by the overthrusting during the Variscan orogeny (Fig. 6) which took place at the end of the Carboniferous approximately 20 Ma later than the carbonate deposition discussed here.

Directly outside the country to the north-northeast, magnetic anomaly maps highlight the Thornquist (Thor) suture. This is indicated by the contrast between the highly magnetic ancient crust of Baltica and the less magnetic Avalonian younger crust SW of the suture (Abramovitz & Thybo, 2000; Williamson et al., 2002; Lyngsie & Thybo, 2007). It is suggested that the Tornquist Ocean between Avalonia and Baltica was closed by oblique convergence (Glennie, 1998). This soft docking is an explanation for the minor structuration along the suture. The major structuration in the Netherlands, which has a NW-SE strike, more or less parallels this suture. It is not quite clear if there is a causal relationship. The NW-SE strike can be found in the westerly part of the UK as well, contrary to the east of the Midlands craton where the strike is SW-NE (Glennie, 1998, 2005). Extensional tectonics provide the mechanism for these large scale structural trends. It is important because it is the mechanism that can explain the half grabens, so dominant in the palaeogeography of that period. Kombrink et al. (2010) list a number of mega-tectonic hypotheses as an explanation for the extensional stress, like back-arc extension or escape tectonics. However Avalonian mega shear (Fig. 5), caused by the early Devonian collision of the South American part of Gondwana with Avalonia (Simancas et al., 2005), instead of Arctic mega shear, may explain the extensional tectonics on the northern part of the Avalonia micro-craton. The Early Devonian timing of the Avalonia collision is more or less coinciding with the Brabantian phase (Verniers et al., 2002).

Differences of properties of the Dutch deep crust can subdivide the Avalonian plate there in three parts (Fig. 6). These three areas react differently to the Early Devonian extensional stress. The three areas display a different structural style, which is reflected in the palaeogeography. From south to north the three parts can be subdivided based on depth of the Moho (Doornenbal & Stevenson, 2010), this is after a correction has been made for the Jurassic and Tertiary rift grabens (Wong et al., 2007).

The most southern part, the London-Brabant Massif, is a Caledonian inversion structure (De Vos et al., 1993; Debacker et al. 2005). The depth of the Mohorovičić discontinuity (Moho) is at 36-38 km (Rijkers et al., 1993). This area is generally a positive geographical feature in the geological history, with mostly shallow water deposits or aerially exposed during the Devono-Mississippian period. This is different from the zone farther to the north were the depth of the Moho decreases to 29-30 km with the exception of the Texel-IJsselmeer High with a 31 km thick crust (Rijkers & Duin, 1994). This zone between the London-Brabant Massif and the zone in the northern part of the country shows a middle and lower crust, in total 10-15 km thick (Doornenbal & Stevenson, 2010). The structural style during the Devono-Mississippian period is characterized by a number of half grabens. This is very comparable to adjacent regions in the UK directly to the west (Fraser & Gawthorpe, 1990).

The third deep crustal zone differs significantly in its properties. In Germany the boundary of the two zones, coincide with a lineament called the Elbe fault zone (Scheck et al., 2002) (Fig. 6). In this last deep crustal zone, the crust is thinner with a Moho at 28 km depth and the crust is two layered. It misses the middle crustal part. The two layered zone has been interpreted as a part of an oceanic plate belonging to Avalonia (Scheck et al., 2002; Scheck-Wenderoth & Lamarche, 2005). The more oceanic crustal properties of this deep crustal zone, which is present in the Dutch northern North Sea and adjacent German basin regions, explain why this constantly “sinking crust” creates an important Palaeozoic depocenter. During the Devono-Mississippian period this area is a deep basin, assumingly partly filled with shale deposits.

Many large granite intrusions can be found in the larger Southern North Sea area, probably subduction related (Glennie, 1998). Most of these plutons are known from the UK close to the Iapetus suture and are explained by the Laurentian plate subducting underneath Avalonia. Some other granite intrusions are linked to local tectonic processes like in the London-Brabant Massif of Belgium (Debacker et al., 2005). The Mid North Sea High shows a number of very large plutons like the Dogger Granite (Glennie, 1998). In the Netherlands, one biotite monzo-granite has been drilled in the well A17-1 (Wong et al., 2007). It is likely that there are more plutons in the Netherlands; however magnetic anomalies are not very strong. The Groningen platform may have an intrusive as nucleus, because a magnetic anomaly was noticed (Kettel, 1983).

5. Devonian and Mississippian bioherms

Based on seismic and well control of both the Groningen and Luttelgeest carbonate build-ups, it is likely that both Devonian and Mississippian age carbonate platforms are present in the Netherlands. Seismic interpretation (Fig. 9) suggests that a very thick undrilled Givetian-Frasnian section is present at deeper levels below the Mississippian build-up. This differs from the interpretation of Kombrink et al. (2010) that terminates the build-up of the bioherm on a pre-Carboniferous basement. Their interpretation can be explained by low quality of the seismic lines available for their study. On the section of Groningen (Herber & De Jager, 2010) and to a lesser degree on the Luttelgeest seismic (Van Hulten & Poty, 2009), much more detail can be seen, which makes the presence of Devonian reefal build-ups very plausible. On this additional seismic section of the Groningen carbonate platform, it is almost certain that below the drilled Mississippian part of the platform, a possibly even thicker Devonian build-up is present. The dimensions of the reefs (Figs 10 and 11), can be compared with internationally known examples. Below the Famennian clastics that were logged in the wells and can be seen as a mappable horizon on the seismic, there is most likely a carbonate build-up, probably Givetian-Frasnian in age. The thickness in Groningen of the Devonian part of the build-up seems at least comparable in thickness to the 800 m of the Mississippian top part of the platform.

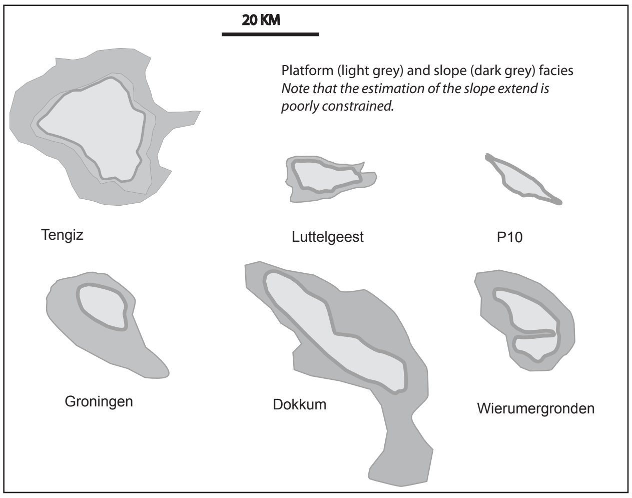

Figure 10. Comparison of the horizontal dimensions of the reefs of the Netherlands and Tengiz (Caspian Sea region). Most of the dimensions have been derived from Kombrink (2008).

Bioherms of Devonian age are very common worldwide. The West Canadian Basin in Alberta, Canada, one of the best-known Palaeozoic reef provinces in the world can be used as example (Figs 12-14). Very close to the Netherlands,

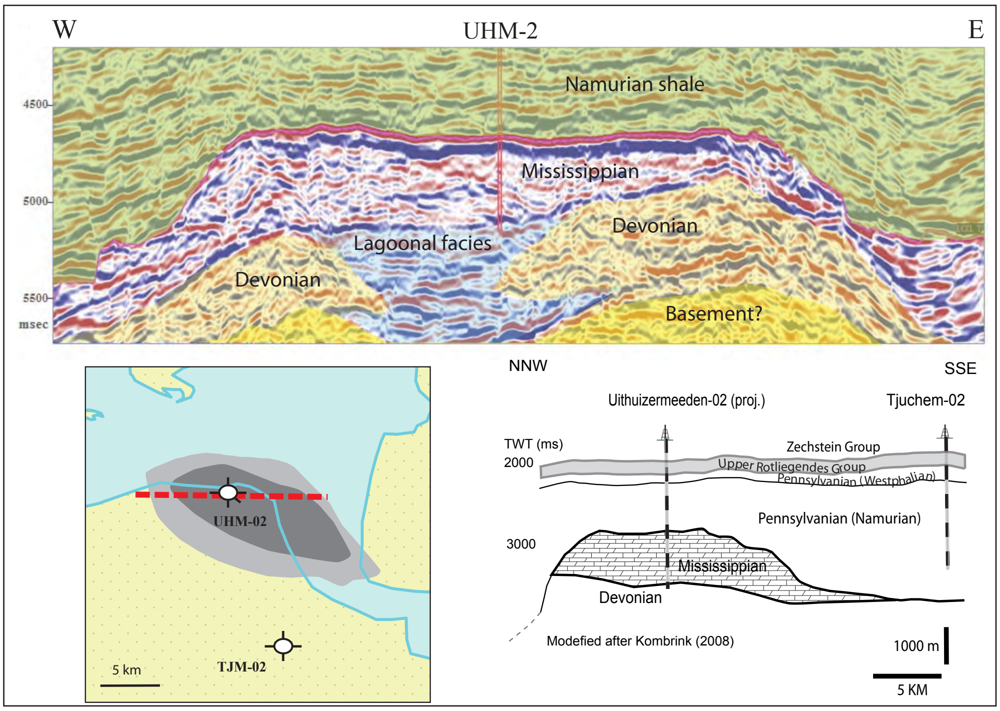

Figure 9. E-W cross section of the Groningen platform. A different interpretation based on a dominant wind direction from the west is published in Herber & De Jager (2010). Here the interpretation suggests a hypothetical presence of a Devonian reef underneath the drilled Mississippian carbonates as well. The well was drilled in the back reef (Menkema) facies. It is possible that better reservoir can be encountered closer to the edge with more grainstone (Meima facies).

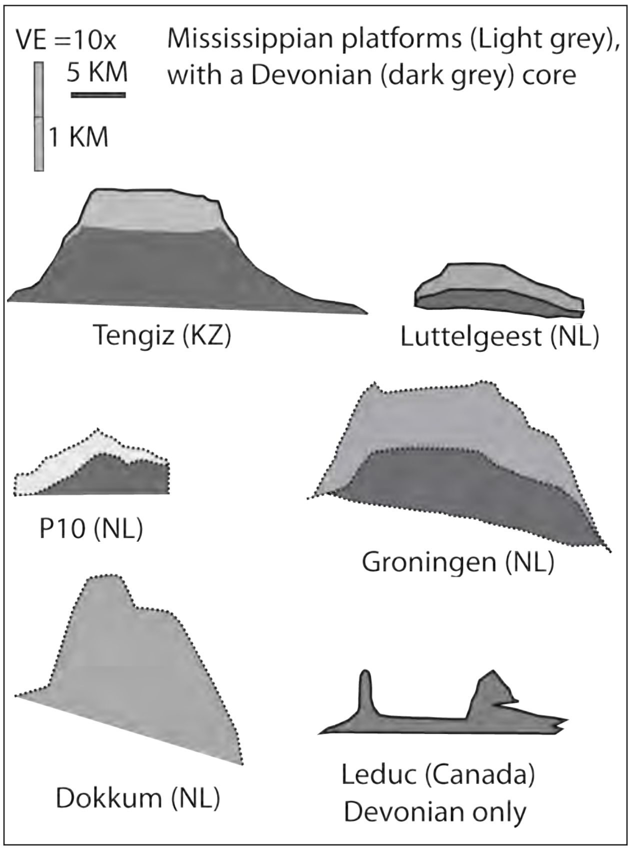

Figure 11. Vertical dimensions of the known reefs in the Netherlands and Tengiz (Caspian Sea region. Most of the Dutch dimensions have been derived from Kombrink (2008).

well-studied Devonian reefs in Belgium can be seen in outcrops (Tsien 1971, 1975; 1977; Boulvain, 2007). Globally the reef development is arrested at the end of the Frasnian (Copper, 2002). In Belgium and Canada it terminates before the end of that stage (Fig. 14). The transition of the mid Devonian build-ups to the Carboniferous carbonate reefs is more than a temporary halt of the sedimentation pattern. The nature of the reef building changes profoundly. Latest Devonian through mid-Carboniferous time (Famennian - Bashkirian) represents an interval of change in the style and extend of carbonate build-ups and in the composition of build-up communities (Webb, 2002). Globally shallow-water bioherms and reef mounds were still widely distributed during the Famennian despite the Late Frasnian Kellwasser extinction events. They become scarce by the end of the stage (Webb, 2002). The extinction of important reef builders like corals and stromatoporoids at the end of the Frasnian is often cited as the factor which stops reef growth. However, during the Famennian, the dominance of clastic sediment in the North Sea area, explained by rapid eustatic changes, brings carbonate build-up almost to a halt as well in the Netherlands. Reef building and diversity increased again in the Lower Carboniferous and peaked in the late Viséan. Albeit that the global late Viséan diversification trend is not well represented in nearby Belgium (Aretz & Chevalier, 2007).

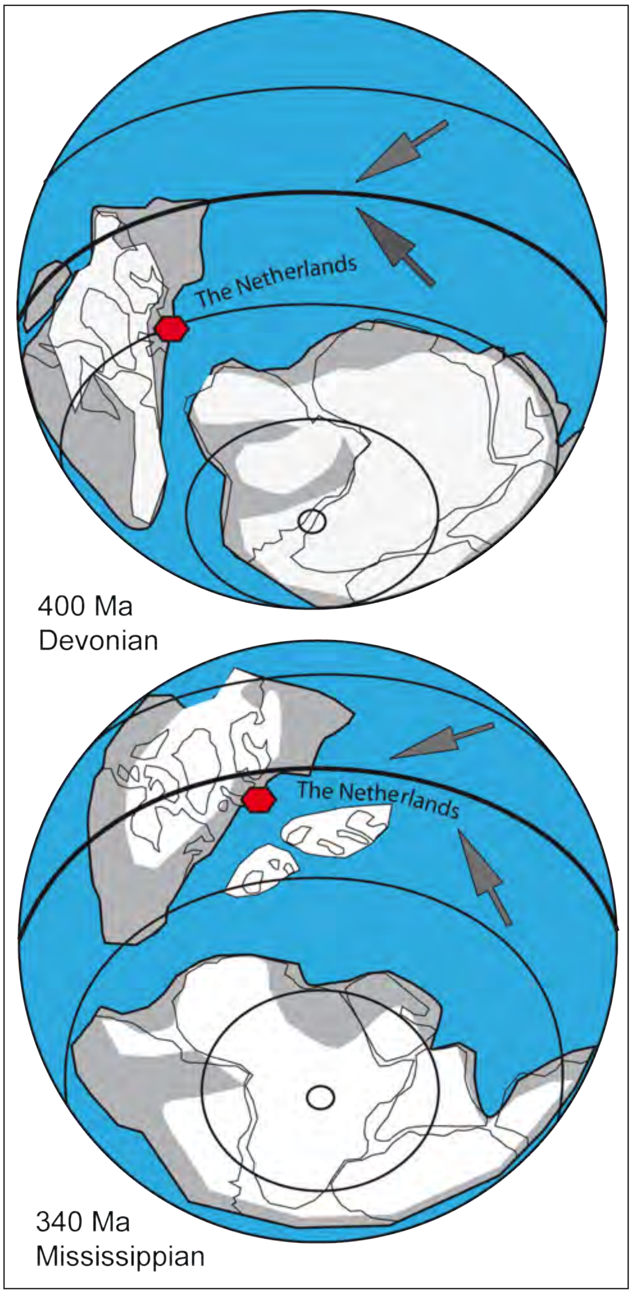

Figure 12. Continental plate position during the Devonian and the Mississippian (Torsvic & Cocks, 2004). Dominant palaeo trade wind directions are very important for the understanding of the reef development. It is likely that the dominant direction is from the south during the Devonian and shifts towards the east during the Mississippian.

At the Groningen platform, a resumption of the reef growth, on top of the older presumably Devonian platform, is seen in the Viséan. The platforms in the Groningen and Friesland provinces are quite different from the Belgian or Canadian Tournaisian and Viséan age shelf carbonates. They can be compared in size (Fig. 10 and 11) to the build-ups of the Caspian Sea area (Weber et al. 2003). Very thick carbonate microbialite platforms develop. In the Caspian platforms grainstone shoal deposits display good reservoir potential in the isolated platforms where primary porosity is mainly controlled by intergranular porosity and mud-lean packstone lithofacies. The limited well control in the Dutch carbonate platforms has not shown this kind of porosity. The seismic cross section of Figure 9 clearly shows that different facies types can be distinguished, comparable to the Tengiz platform (Weber et al., 2003) . Based on the seismic it is possible that the Uithuizermeeden-02 well was drilled in back-reef (Menkema) facies (Fig. 9). It is possible that closer to the reef edge grainstones (Meima) facies will be present. Particularly the Devonian section of this seismic line suggests a clear distinction between the reef edge and the lagoonal facies.

In Belgium (Boulvain, 2007) as well as in the Canadian Devonian reef sections (Fig. 14), a number of third order cycles can be distinguished, characterized by periodically arrested reef growth. In the Mississippian age sequences, comparable to Belgian sections, also third order sequences can be distinguished (Fig. 8). Karstification linked to sea-level low stands has been noted at a few intervals in LTG-01 (Van Hulten & Poty, 2009).

The continuation of the carbonate platform development in the Netherlands after the Devonian provides new insights how the bioherms developed during the Mississippian. Because most reef development in the early Mississippian was subdued, it is surprising that carbonate platforms could be so big in the Caspian area. Comparison of the Tengiz bioherm shows that the reefs in the Netherlands are comparable in size. Some Mississippian

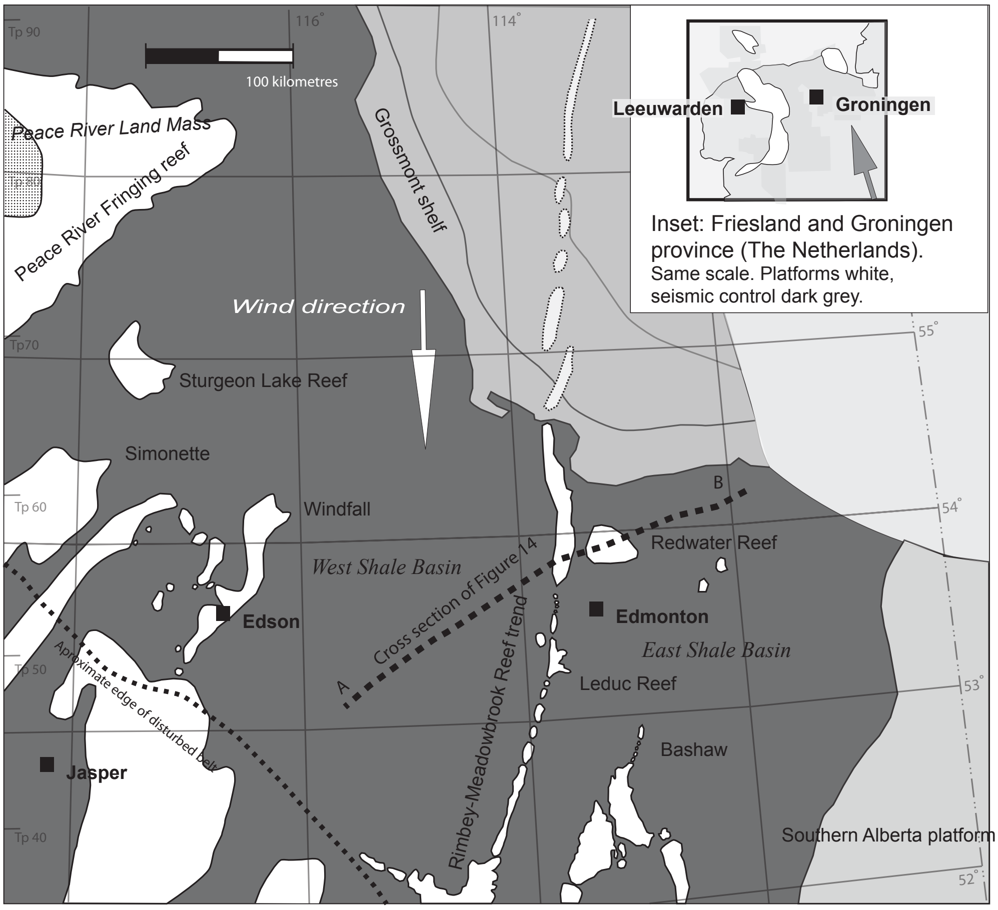

Figure 13. Comparison of the horizontal dimension of the West Canadian Devonian reefs (Mossop & Shetsen, 1994) with the reefs in the Friesland and Groningen province of the Netherlands.

age biohermal development was known in Belgium (Aretz & Chevalier, 2007) and in the UK (Gawthorpe et al., 1989), however the dimensions of those build-ups are significantly smaller.

The large platform complexes are only known from the limited mapping that has been performed in the northern onshore provinces of the Netherlands. The mapped area covers approximately 100 km^{2,} however it is large enough to make some general observations on the distribution of the carbonate platforms during the Devonian and the Mississippian. The lateral extend of the Belgian build-ups is often difficult to estimate, because of complex Variscan structuration (Tsien, 1975). Therefore, parts of the well-studied Devonian reefs of Alberta (Mossop & Shetsen, 1994), have been compared to the carbonate platforms of the Netherlands (Fig. 13).

Important for reef development is the dominance of the wind direction. For an individual Mississippian platform this is described for the Tengiz build-up (Weber et al., 2003). For a regional effect of the wind direction on larger scale carbonate platform development the Devonian Alberta reefs (Mossop & Shetsen, 1994), can be studied.

For the Mississippian in the Netherlands, a case can be made for a dominant wind direction from the east to north-east (Van Hulten & Poty, 2008), this is comparable to the wind direction in the Caspian during that time (Weber et al., 2003). It is in agreement with the general ramp setting of well-studied Belgian Mississippian (Poty et al., 2002). It explains also why no Lower Carboniferous reefs are developed at the Mid North Sea High.

Devonian build-ups are developed in Belgium south of the London-Brabant Massif and at the Mid North Sea High. This suggests a different dominant wind direction. For the Devonian the palaeo position of the Netherlands is south of the equator (Fig. 12). This makes a trade wind direction from the South or Southeast more likely. The nature of the Devonian build-ups in southern Belgium (Boulvain et al., 2005), does not contradict

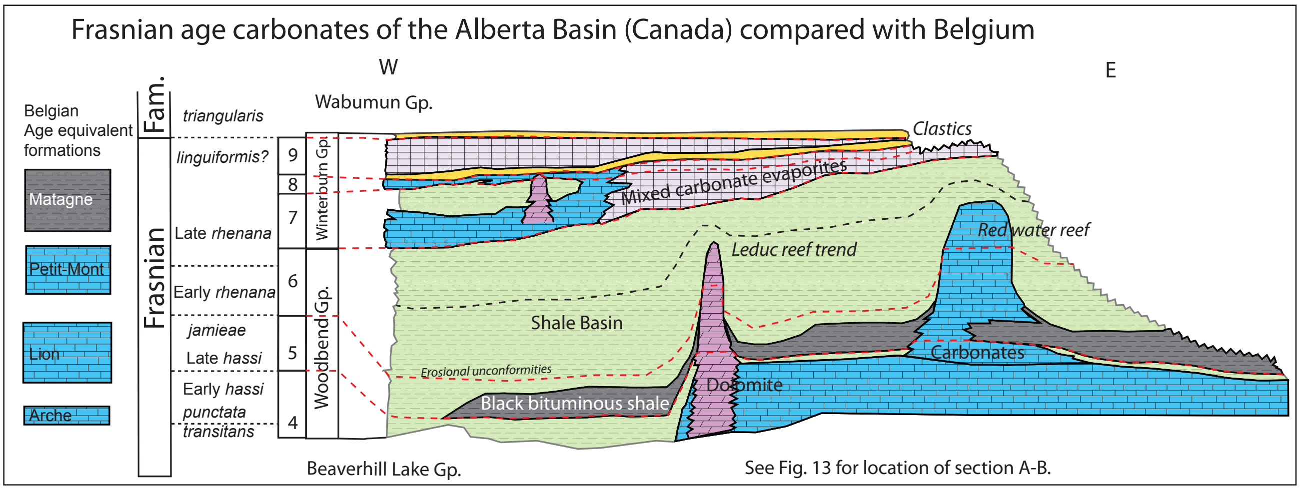

Figure 14. Comparison of the vertical dimensions and the dating of the West Canadian Devonian reef development (Potma et al. 2001; Mossop & Shetsen, 1994,) with the Devonian reefs in Belgium (Bultynck & Dejonghe, 2002). The Frasnian Canadian reefs can reach a thickness of 250 m. The Leduc reef trend terminates in the *rhenana* Conodont zone.

such southern wind direction. The large Dokkum reef trend in Friesland (Fig. 2) may also be Mississippian platform on top of an older Devonian fringe reef. Reminiscing to Canadian Givetian-Frasnian build-ups (Mossop & Shetsen, 1994), the huge Dokkum platform may be originally developed by oblique trade winds from the south comparable to the Devonian reefs in Canada, albeit that the wind in Alberta during the Devonian probably comes from the present day north, north-east (Mossop & Shetsen, 1994). Wells and better quality seismic than used by Kombrink (2008), is required to gain more certainty on this hypothesis.

6. Palaeogeography

From the new data a new palaeogeography for the Devono-Mississippian can be proposed for the larger Southern North Sea area. With the limited data available it is not possible to sketch a detailed palaeogeography, however it is possible to make general maps on Epoch level for the Givetian-Frasnian and Tournaisian-Viséan periods. It should be realized that not too long ago only the most southern part of the country could be mapped with confidence (see for example Bless et al., 1976; 1980). Of importance are cored limestones in the UK like in the well 38/3-1 (Glennie, 1998), close to the Mid North Sea High (Fig. 3). The fossiliferous lime mudstones, wackestones, packstones and grainstones in this well are proof of a marine connection of the Mid North Sea High region with the postulated Devonian Rheic Ocean in the South East (Ziegler, 1990). They give confidence to the idea that carbonate platforms develop during the Givetian-Frasnian on local topographical highs at the Mid North Sea High also in areas now covered with thick Late Devonian and Mississippian Yoredale type clastics (Milton-Worssell et al., 2009). Marine Givetian limestones are described in the German well Q/1 and in the German well Münsterland-1, not too far from the German Dutch border are in agreement with the idea of carbonate sedimentation during the Givetian and Frasnian. In the few wells that penetrate the Devonian in the Netherlands mostly clastic sediments are found. These wells were clustered in the south west part of the country. Frasnian marine shales in some wells like S05-01, make it certain that a coast line covered part of the Netherlands during the Middle Devonian. Not all areas near the London-Brabant Massif display clastic facies. More to the east some biostromal limestones in South Limburg have been found.

The new Devonian and the Mississippian maps share a number of geographical elements like highs and basin areas. The most important shared basin area is the East Frisian Black Shale Basin (Hoffmann et al., 2005; Van Hulten & Poty, 2008), which extends far to the east into northern Germany and connects further to the east to the Rheic Ocean. There is no reason to assume that a deep shale basin, as is postulated for the Mississippian (Van Hulten & Poty, 2008), is not present earlier during the Givetian-Frasnian. Successful magnetotelluric experiments which rely on conductive shales between the deep well Münsterland-1 and the Ringkøbing Fyn High make it more likely that a shale basin was already present in an early stage. The measured conductive shales can be of Devonian or Carboniferous age.

The highs which border the deep shale basin area are nuclei for reef development, provided that there is not too much clastic input. The map of the Devonian and the Mississippian differ. This can be explained because the carbonae platform architecture changes with the shifting dominant (trade) wind direction in time. The high sea level stand during the Givetian-Frasnian and Mississippian halts clastic input. During the periodic low stands of the Famennian there is a dominance of clastic sedimentation.

The prevailing wind direction (Fig. 12) is very important for the development of the reefs, however the Mississippian carbonate platform development can not be studied in isolation without taking into account the Devonian morphology of the previously existing bioherm. When during the Viséan, after a long hiatus, the carbonate build-up development resumes, in Groningen as well as in Luttelgeest, it builds on a massive Devonian platform. The sheer height of approximately 1000 m of the Devonian part of the build-up in the deeper water area makes it almost impossible to build new platforms outside the existing Devonian reefs. In the shallower parts, Mississippian platforms could develop as well. Also in areas with no or limited carbonate sedimentation during the Devonian, like the Campine Basin, platform carbonates are deposited.

6.1 Devonian Palaeogeography

The Devonian palaeogeography in Western Europe (Fig. 15), is often associated with the Old Red sedimentation. The peri-oceanic setting of the Netherlands makes it an unlikely candidate for the continental deposits so well exposed in the UK. With rising sea levels during the Givetian, the influence of the sea probably was present all over the Netherlands. The marine (Kyle) carbonates in the UK Auk and Argyll fields in the Central North Sea made it clear that the Mid Devonian Sea extended far to the north (Ziegler,

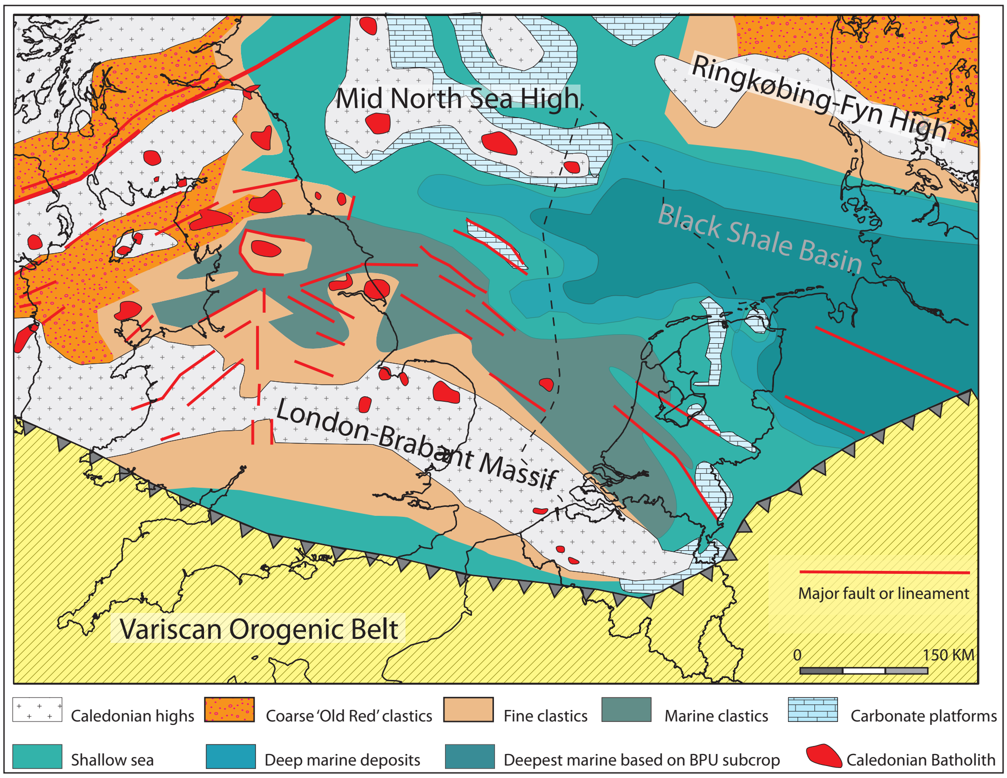

Figure 15. Palaeogeography during the Devonian (Givetian-Frasnian). Reefal limestone are present south of the London-Brabant Massif and at the Mid North High. A few large reefs may have developed in the northern part of the Netherlands. Carbonate platform development is consistent with a dominant wind direction from the south.

1990, Glennie, 1998, Evans et al., 2003). The carbonates have been traced as far north as the (Auk) Flora ridge (Milton-Worssell et al., 2009). During Mid Devonian times palaeogeography of the southern North Sea region is characterized by a deep sea fringed by carbonate platforms and reefs (Fig. 15), with local marine clastic sedimentation in the area just north of the London-Brabant Massif probably in a back reef setting. Towards the west, no marine passage way is known, as exists during the Mississippian. The Devonian sea in this area differs from the situation during the Mississippian where it is a strait, which is connected to present-day North America.

The sea level rise which started in the Eifelian and caused widespread carbonate deposition in the Givetian south of the London-Brabant Massif, affected also the Southern North Sea region north of the Massif. Based on prevailing trade winds it is plausible that platforms developed on batholiths of the Mid North Sea High. Kyle type of carbonates are witness that reef growth is possible in the area, however a sizable carbonate platform development has to be proven. It is likely that reef development has taken place on the other side of the Ost Frisian Shale Basin, in the Dutch Friesland and Groningen onshore provinces, directly north of the Texel-IJsselmeer High (Fig. 3).

The clastic sedimentation in the south western part of the Netherlands, is in agreement with a lee side of the London-Brabant Massif. Because of the relatively good well control in this area, the clastic nature of the Devonian is probably overstated and its deposition is restricted to a smaller sub-basin area. It is unclear if Devonian carbonates are developed on the Maasbommel-Krefeld High (Figs 3, 6).

6.2 Famennian clastics

A major change occurs during the Famennian which is difficult to capture on palaeogeographical maps because many different facies develop. The carbonate deposition of the Devonian and Mississippian halted in the onshore area and at the Mid North Sea High as well. Reef growth terminated there with the clastic influx of the Upper Old Red sandstones (Evans et al., 2003). On the Mid North Sea High most wells have been ended in these clastic facies. On seismic the transition from shale to coarse clastics of the 'Upper Old Red' is clearly traceable (Fig. 7).

The termination comes probably at the same time as in the south. Belgian outcrops provide a good insight in the kind of deposits which can be expected from this period. It ranges from shallow water to deep marine facies (Thorez et al., 2006). Well information in the southern area indicates thick clastic deposits. Even the big carbonate platforms of Groningen and Luttelgeest have a clastic interval. This is remarkable, because there seems no clear explanation how clastics can be deposited on top of a several hundred meter thick and isolated build-up.

6.3 Mississippian Palaeogeography

The geographical position of the Mississippian carbonate platforms (Fig. 16) is not the same as in the Devonian. In the southern part of the Netherlands, carbonate platforms are dominant, where clastic deposition was prevailing during the Devonian. In the Mid North Sea High area, clastic deposition is dominant after the Frasnian. During the Mississippian, this high is dominated by clastic deposits varying from shallow water deltaic to deep marine (Maynard & Dunay, 1999; Van Adrichem Boogaert & Kouwe, 1997).

In the Groningen and Friesland provinces, a continuation of the Devonian platform growth is seen during the Mississippian. In both the Groningen and the Luttelgeest platform area, carbonate sedimentation resumes again during the Viséan. Carbonate sedimentation starts earlier in the southern part of the country during the Tournaisian (Van Adrichem Boogaert and Kouwe 1997). In a number of Dutch wells, at the northern flank of the London-Brabant Massif, 900-1400 m thick light grey, brown carbonates have been encountered. Generally, it consists of a tight limestone ranging in age from Tournaisian to latest Viséan. A well in this area is the type locality for the Zeeland Formation (Van Adrichem Boogaert and Kouwe 1997; Fig. 1). These carbonates are very similar to platform carbonates described in the UK southern North Sea and onshore Midlands (Cameron and Ziegler 1997). The outcrops in the UK, supported by borehole and seismic information, make it likely, that these early Carboniferous carbonates do not consist of one single uniform shelf platform carbonate, but different facies belts exist related to the forming of half grabens (Fraser & Gawthorpe, 1990; Fraser et al., 1990). Towards the west there is a marine passage way towards Ireland. It is likely that there are more areas with carbonate platform development in the Netherlands. The Texel-IJsselmeer High and the Maasbommel-Krefeld High may be comparable to half grabens in the UK with platform carbonates developed on the highs (Fraser & Gawthorpe, 1990; Van Hulten & Poty, 2008). There are no wells that are drilled into the basinal facies. It is assumed, that a large area of the present North Sea area north of the Frisian Islands was a (black) shale basin during

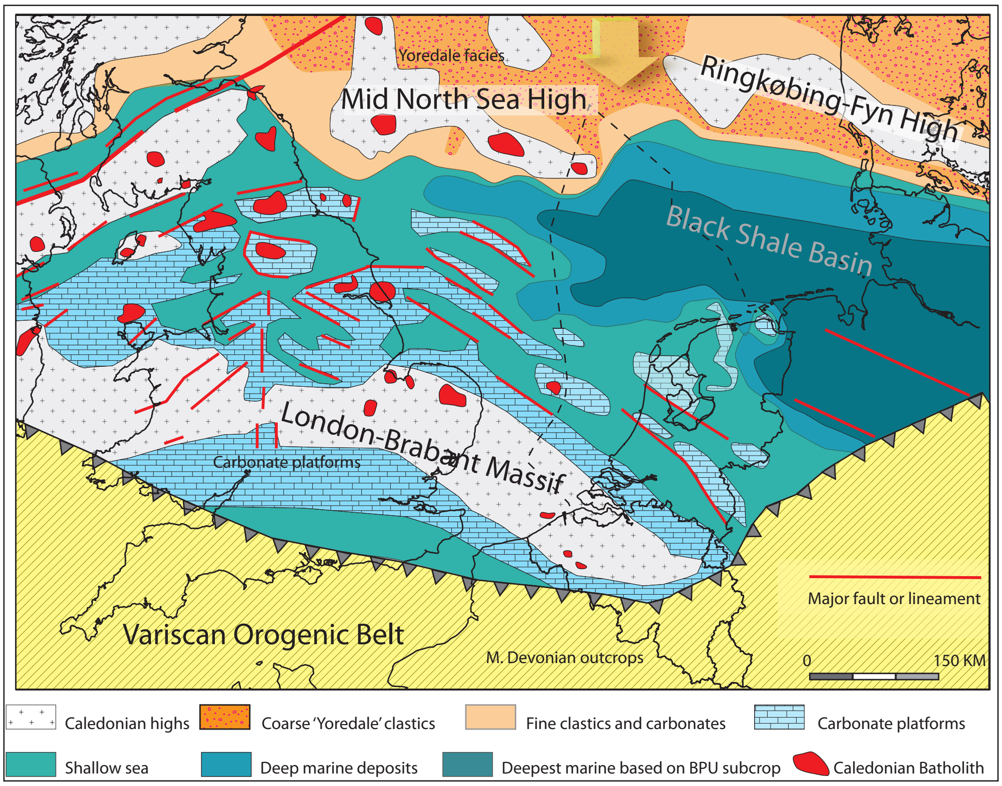

Figure 16. Palaeogeography during the Mississippian. It is very likely that the dominant wind direction during this period is from the North East or East based on the depositional characteristics. Bioherms can develop in the northern part of the Netherlands because the exposure to high energy wave action. There is an open water connection with North America, north of the London-Brabant Massif.

the Mississippian comparable to the Devonian period opening towards the Rheic Ocean in the east.

7. Hydrocarbon exploration

The relevance of the new palaeogeography may be important for oil and gas exploration. It is not the first time that Palaeozoic plays have been discussed (Krebs, 1975, 1978; Fraser & Gawthorpe, 1990; Fraser et al., 1990; Bénard & Bouché, 1991; Gérard, et al., 1993). Van Hulten & Poty (2008) list the major play elements for Mississippian carbonate platforms as trap, that are largely valid for Devonian build-ups as well, with the Pennsylvanian (Namurian) shales as seal and late Mississippian Geverik shales as source. Major risks are the presence of reservoir and the lack of charge because of depth of over 6000 m. A case can be made that the two new exploration wells were drilled in tight (Menkema) facies and that better reservoir quality can be found in grainstone (Meima) facies. Devonian may be better than Mississippian reservoirs, because a higher chance of dolomitisation. Intra Devonian top seal appears to be hardly present in North West Europe, if compared to the Albertan Devonian (Fig. 14), but this is not tested. Because of the very high cost of drilling, these Palaeozoic targets can be considered as a frontier play. With the improvements in seismic acquisition and processing, it is foreseen that more insights are gained in other areas of the Netherlands and more wells will be drilled.

8. Conclusions

In North West Europe, the Devono-Carboniferous section has received new attention, after the drilling in 2001 and 2004 of two deep wells, to very thick Mississippian carbonate build-ups in the Netherlands. The seismic and the well results of the UHM-02 well reveal the existence of a Mississippian carbonate platform that can be compared in size to build-ups in the Caspian region from that same period. Underneath this platform, a undrilled Devonian build-up is likely to be present. At the end of the Viséan carbonate deposition stops in Groningen. The other very deep hole LTG-01 reconfirms the presence of very thick Mississippian carbonates in the northern Netherlands. Carbonate sedimentation of this build-up was arrested much earlier. Based on the findings in these wells, several more than 10 km long reef trends can be mapped with confidence. They extend over large parts of the northern provinces of the Netherlands. Based on the information of the drilled wells and seismic, it is very likely that they have a Devonian carbonate core. The newly discovered carbonate build-ups most likely fringe the southern margin of a deep basin. On the northern margin of this basin at the Mid North Sea High, Givetian-Frasnian carbonates are probably more frequently present than previously thought, despite the failure to find carbonates in the recent UK 37/25-1 (Corbenic) exploration well. There are marked differences between the Devonian and the Mississippian age carbonate deposits. They share a similar depositional setting close to deep water in a transition to very shallow water. A number of depositional elements are well known from classical palaeogeographical maps of the larger North Sea region like highlands in the north west or north in Scotland and Norway. Important variation between these epochs is caused by differences of clastic influx from these highlands. In the classical palaeogeographical view, the more clastic deposition during the Devonian (Old Red) was often contrasted with the more carbonate setting during the Lower Carboniferous. This study showed that in both periods a mixed carbonate clastic system is present. Something which has received less attention, but is important for carbonate platform development, is the northward drift of the Laurussian continent. This probably gradually changed the prevailing tradewind direction, which is very important for reef or carbonate platform development.

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Dorlodotia Salée, 1920 (Rugosa), related and morphologically similar taxa in the Lower Carboniferous of Russia Ukraine

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ABSTRACT. Records of *Dorlodotia* Salée, 1920 in Russia and Ukraine include *Thysanophyllum vermiculare* Degtjarev, 1973 from the Moliniacian (?)-Livian of the Central Urals, *Dorlodotia briarti* Salée, 1920 and *D. fomitschevi* Zhizhina, 1978, possibly synonymous with it, both from the Moliniacian of the Donets Basin, *Pseudodorlodotia subkakimii* Vassilyuk, 1978 from the Warnantian of the same area and *Lonsdaleia sokolovi* Dobrolyubova, 1958 from the Brigantian of the Moscow Basin. *Protolonsdaleia tenuis* Zhizhina, 1978 from the Moliniacian of the Donets Basin, *Eolithostrotionella grechovkae* Degtjarev, 1973 from the upper Livian (?)-lower Warnantian of the South Urals, as well as *E. utkae* Degtjarev, 1973 and *Thysanophyllum druzhininae* Degtjarev, 1973 from the upper Moliniacian (?)-Livian of the Central Urals belong with *Ceriodotia* Denayer (2011). *Dorlodotia* and *Ceriodotia* are related genera and most probably belong to the family Axophyllidae Milne Edwards & Haime, 1851. *Eolithostrotionella* Zhizhina, 1956 is restricted to the Moliniacian of the Donets Basin and probably related to *Axoclisia* Semenoff-Tian-Chansky, 1974. *Eolithostrotionella cystosa* Zhizhina, 1960, *E. rotai* Zhizhina, 1960 and *E. lissitzini* Zhizhina, 1960 reported from higher intervals of the Donets Lower Carboniferous succession, are morphologically similar to *Ceriodotia*, but probably belong to a separate genus. Validity of the genera *Protolonsdaleia* Lissitzin, 1925 and *Sublonsdaleia* Lissitzin, 1925 should be discussed.

KEYWORDS: *Dorlodotia*, *Ceriodotia*, *Eolithostrotionella Protolonsdaleia*, *Sublonsdaleia* Dinantian, Russia, Ukraine.

1. Introduction

Fasciculate genus *Dorlodotia* Salée, 1920 is widely distributed in the Lower Carboniferous of Europe and Asia, comprises about forty species, most of them attributed to different genera, and is especially characteristic for the Moliniacian and Livian (Viséan). *Dorlodotia* is distinguished by typically fasciculate growth habit, major septa commonly dilated in tabularium, minor septa indistinct to poorly developed, inner wall commonly dilated, tabulae complete, conical to flat, dissepimentarium dominated by first order transeptal dissepiments. Axial structure is longitudinally discontinuous or lacking, typically represented by lath-like axial plate, sporadically by poorly defined primitive dibunophylloid axial column.

Cerioid genus *Ceriodotia* Denayer (2011) with the type species *C. bartinensis*, established on the material from the Livian of Northwestern Turkey, closely resembles *Dorlodotia* in having indistinct minor septa, major septa dilated in tabularium, dilated inner wall, complete, conical, tent-shaped or flat tabulae, dissepimentarium dominated by first order transeptal dissepiments, and axial structure typically represented by an axial plate, longitudinally discontinuous or lacking. Establishment of this genus allows clarifying the systematic position of few species from the Viséan of the Donets Basin and Urals, formerly attributed to the genera *Thysanophyllum* Nicholson & Thomson, 1876, *Protolonsdaleia* Lissitzyn, 1925 and *Eolithostrotionella* Zhizhina, 1956 (Degtyarev, 1973; Vasilyuk & Zhizhina, 1978).

The objectives of the present paper are: to specify occurrences of *Dorlodotia* and *Ceriodotia* in the Moscow Basin, Donets Basin and in the Urals; to discuss systematic position, range and evolution of *Dorlodotia*, as well as systematic position of *Eolithostrotionella* Zhizhina, 1956; and to describe a *Dorlodotia* species from the upper Warnantian (Brigantian) of the Moscow Basin attributed to the genus *Lonsdaleia* McCoy, 1849 by Dobrolyubova (1958).

Correlation of the Viséan-lowermost Serpukhovian of the Moscow and Donets Basins and selected areas of the Urals is summarized in the Tables 1 and 2. Regional subdivisions adopted herein are not considered as formally defined regional sub-stages and therefore are spelled without the ending "-ian".

2. Occurrences of *Dorlodotia* and *Ceriodotia* in the Lower Carboniferous of the Donets Basin, Moscow Basin and Urals

2.1. Occurrences of Dorlodotia

In the Donets Basin, *Dorlodotia* is reported from the Glubokaya

	Conil et al. (1990)			Poty et al. (2006)				Hecker (2001)	Moscow Basin Subdivisions after Makhlina et al. (1993)		Donets Basin Subdivisions after Poletaev et al. (1989)		
SERP. ↑	Pendleian	Cf7			↑ MFZ 16	RC9 →		↑ IX	Protva ↑		Prokhorovka	Sc	
									Steshevo			Sb	
									Tarusa		Samara	Sa	
VISEAN	Warnantian	Cf6	δ	Warnantian	MFZ 15	RC8		VIII	Venev		Mezha	Vg	
									Mikhailov				
									Aleksin		Donets	Vf	f₂
			γ₂		MFZ 14	RC7	β	VII	Tula	upper			f₁
			γ₁				α			middle	Styla	Ve	e₂
			β		MFZ 13			VI		lower			
			α										
	Livian	Cf5		Livian	MFZ 12	RC6			*hiatus*				e₁
						RC5			Bobriki		*hiatus*		
	Moliniacian	Cf4	γ-δ	Moliniacian	MFZ 11			V			Sukhaya	Vd	d₂
											Glubokaya		d₁
						RC4	β2		*hiatus*			Vc	
			β		MFZ 10				upper Radaevka			Vb	
			α₂		MFZ 9			IV					
	↓		α₁ ↓	Ivorian ↓	MFZ 8		← β1	III ↓	*hiatus* ↓		Dokuchaevsk	Va	

Table 1. Correlation of the Viséan and lowermost Serpukhovian of the Moscow and Donets Basins. Modified from Hecker (2001, 2002, 2009).

	Conil et al. (1990)			Poty et al. (2006)				Hecker (2001)	Urals Subdivisions modified from Antsygin et al. (1993)	
									Central Urals, western flank	South Urals, eastern flank
SERP. ↑	Pendleian	Cf7			↑ MFZ 16	RC9 →		↑ IX	Brazhka ↑	Khudolaz ↑
									Nizhnyaya Gubakha (Lenevka)	
										Suntur
										Bogdanovich Averino
									Ladeynaya	
VISEAN	Warnantian	Cf6	δ	Warnantian	MFZ 15	RC8		VIII		
									Gubashka	Kamensk-Ural’skiy
									Ust’ilim	
			γ2		MFZ 14	RC7	β	VII	Druzhinino	Uzunzyal
			γ1				α		Ilych	
			β		MFZ 13			VI		Ust’gre-khovka
			α							
	Livian	Cf5		Livian	MFZ 12	RC6				
									Pester’ki	
						RC5				Burlya
										Obruchevka
	Moliniacian	Cf4	γ-δ	Moliniacian	MFZ 11			V		
										Kos’va
			β			RC4	β2			
					MFZ 10					
			α2		MFZ 9			IV		
									hiatus	
			α1	Ivorian	MFZ 8		β1 ↓	III ↓	Kos’va	
	↓		↓	↓					Kizel ↓	*Kizel* ↓

Table 2. Correlation of the Viséan and lowermost Serpukhovian of selected areas of the Urals. Modified from Hecker (2001, 2002).

and Donets Formations (Vasilyuk, 1960; Vasilyuk & Zhizhina, 1978; Ogar, 2010) correlating with the Cf4α_2-γ, MFZ9-lower MFZ11 Foraminifera zones (Moliniacian) and Cf4 γ_2-lower Cf6δ, upper MFZ14-lower MFZ15 Foraminifera zones (Warnantian), respectively (Table 1). Records from the Glubokaya formation include *D. fomitschevi* Zhizhina *in* Vasilyuk & Zhizhina, 1978 (p. 27, pl. 1, figs 1a-c) (Vb Zone) and *D. pseudovermiculare* (McCoy, 1855) in the sense of Ogar (2010, fig. 6P) (Vb-Vc Zones), both species either synonymous with *D. briarti* or belonging to a morphologically similar species. From the Donets Formation is reported *Pseudodorlodotia subkakimii* Vasilyuk in Vasilyuk & Zhizhina, 1978 (p. 29, pl. 1, figs 1a-c) with corallites about 8 mm in diameter having 18-19 major septa, poorly developed minor septa, tabularium diameter 5-6 mm, longitudinally discontinuous axial plate connected to the counter septum, up to three locally developed radial lamellae, complete loosely packed tabulae, and dissepimentarium approaching in width one-third of corallite diameter, commonly composed of one row of large first order transeptal dissepiments.

Records of *Dorlodotia* in the Moscow Basin are from the Brigantian (Mikhailov horizon) and restricted to one species, *Lonsdaleia sokolovi* Dobrolyubova, 1958 (see chapter 4).

Dorlodotia also includes *Thysanophyllum vermiculare* Degtjarev, 1973 (p. 195, pl. 2, figs 2a-b) from the western flank of the Central Urals, which is restricted to the upper Pester’ki horizon correlating with the upper Moliniacian (?)-Livian (Table 2) and strongly resembles *Dorlodotia briarti*. The genus possibly also includes one species from the Serpukhovian (*Cravenoceras* Zone) of the Novaya Zemlya, *Thysanophyllum concavum* Gorsky, 1951, resembling *Pseudodorlodotia subkakimii*; *T. pseudovermiculare* in the sense of Gorsky (1951) most probably belongs to the same species.

2.2. Occurrences of *Ceriodotia*

Records of *Ceriodotia* in the Donets Basin are from the Vc-Vd Zones (Glubokaya-Sukhaya Formations) approximating to the Cf4β-δ, MFZ9-MFZ11 Foraminifera zones, Moliniacian (Table 1) and restricted to one species, *Protolonsdaleia tenuis* Zhizhina *in* Vasilyuk & Zhizhina, 1978, having corallites with diagonals 12-16 mm, 18-20 major septa, indistinct minor septa, tabularium 5-6 mm in diameter, longitudinally discontinuous axial structure represented by medial plate, few radial lamellae and locally developed irregular axial tabellae, abaxially declined tightly packed tabulae and wide dissepimentarium dominated by first order transeptal dissepiments (Vasilyuk & Zhizhina, 1978, p. 30, pl. 2, figs 1a-b).

In the Urals, records of the species belonging to *Ceriodotia* are by Degtjarev (1973) from the Zapadny Ural horizon. These are: *Eolithostrotionella grechovkae* Degtjarev, 1973 from the interval of the Viséan succession of the eastern flank of the South Urals now attributed to the upper part of the Ust’grekhovka horizon and correlating with the upper Livian (?)-Warnantian (Table 2), and *E. utkae* Degtjarev, 1973, *Thysanophyllum druzhininae* Degtjarev, 1973 and *T.* cf. *minus* Thomson, 1880 from the interval of the Viséan succession of the western flank of the Central Urals now attributed to the upper Pester’ki horizon correlating with the upper Moliniacian (?)-Livian (Table 2). Garan’ et al. (1966), based on identifications of Degtjarev, also reported *Thysanophyllum* cf. *minus* near the lower limit of the Moliniacian (lower part of the Pester’ki horizon).

Eolithostrotionella grechovkae (Degtjarev, 1973, p. 193, pl. 1, fig. 2, pl. 2, figs 1a-b) shows close affinity to *Protolonsdaleia tenuis*, including in septal number (18-20) and tabularium diameter (5.5-7 mm), but has smaller corallites (diagonals 10-12 mm) with narrower dissepimentaria. Its axial structures are represented by thin to dilated medial plates with few discontinuous radial lamellae and locally developed irregular axial tabellae. *Eolithostrotionella utkae* (Degtjarev, 1973, p. 192, pl. 1, figs 1a-b) shows corallites with diagonals 10-15 mm, 22-25 major septa dilated in tabularium, indistinct minor septa, tabularium diameter 5.5-8 mm, dilated inner wall, and relatively narrow dissepimentarium attaining one-sixth to one-fifth of corallite diagonals and dominated by second order transeptal dissepiments. In longitudinal section, *E. utkae* resembles *Dorlodotia euxinensis* Denayer (2011) in having crowded tent-shaped steeply elevated tabulae and axial structure represented by thick axial plate with few radial lamellae. *Thysanophyllum druzhininae* (Degtjarev, 1973, p. 196, pl. 3, figs 1a-b, 2) has larger corallites with diagonals 15-20 mm, 22-25 thin major septa and indistinct minor septa, and wider tabularia (7-10 mm in diameter). Dissepimentaria, similarly to *Eolithostrotionella utkae*, are relatively narrow and dominated by first order transeptal dissepiments; axial structure is represented by thin axial lamella connected to the counter (?) septum; tabulae are subhorizontal to slightly sagging, irregularly spaced 0.3-2 mm apart. *Thysanophyllum* cf. *minus* in the sense of Degtjarev (1973, pl. 5, fig. 5) is probably synonymous with *T. druzhininae*.

In the aspect of axial structure and tabulae, *Eolithostrotionella utkae* resembles the very variable type species of the genus *Acrocyathus* d’Orbigny, 1849, *A. floriformis* d’Orbigny, 1849, characteristic of the St. Louis Limestone and correlative formations of the North American Mid-continent, which corresponds to the 13-14 Mamet Foraminifera Zones (Mamet, 1974), thus approximating to the Livian. Sando (1983) placed *Eolithostrotionella utkae* into *Acrocyathus* and attributed *Eolithostrotionella grechovkae*, although with a query, to the same genus. Hecker (2001) followed Sando in attributing these taxa to *Acrocyathus*. It is noteworthy, that variability pattern of *Ceriodotia* from the Urals involving axial structure, length of septa and dissepimentarium strongly resembles that of *C. petalaxoides* Denayer (2011).

3. Discussion

3.1. Eolithostrotionella Zhizhina, 1956, Protolonsdaleia Lissitzin, 1925 and Sublonsdaleia Lissitzin, 1925

The cerioid genus *Eolithostrotionella* Zhizhina, 1956 with the type species *Lonsdaleia longisepta* Lissitzin, 1925 was established on the material from the Moliniacian of the Donets Basin. Four more species from the Lower Carboniferous of this area were attributed to *Eolithostrotionella* by Zhizhina (1960) and Vasilyuk (1960). These are: *E. zhizhinae* Vasilyuk, 1960 from the Moliniacian, as well as *E. cystosa* Zhizhina, 1960, *E. rotai* Zhizhina, 1960 and *E. lissitzini* Zhizhina, 1960 from higher levels of the Donets Lower Carboniferous succession.

Lonsdaleia longisepta Lissitzin, 1925 is restricted to the Vb-Vd Zones and distinguished by cerioid colonies with corallites having diagonals 15-20 mm, 24-32 thin septa of both orders, tabularium diameter 5-9 mm, and wide dissepimentarium dominated by transeptal dissepiments of various sizes in outer dissepimentarium and by regular interseptal dissepiments in inner dissepimentarium. Axial structures vary from longitudinally discontinuous thin axial plate commonly connected to the cardinal and counter septa, and few radial lamellae to poorly defined narrow axial column represented by slightly dilated medial plate connected to the cardinal and counter septa, 8-12 radial lamellae and locally developed irregular axial tabellae. Tabulae are abaxially declined, varying from complete tent-shaped to incomplete inflated; when axial tabellae present, periaxial tabellae abaxially declined, inflated (Zhizhina, 1956, p. 40, pl. 9, figs 1a-b; Vasilyuk, 1960, p. 112, pl. 30, figs 2, 2a).

Eolithostrotionella zhizhinae (Vasilyuk, 1960, p. 95, pl. 25, figs 1, 1a) is restricted to the Vc-Vd Zones. This species cannot be distinguished from *Protolonsdaleia mariupolensis* Lissitzin, 1925 as interpreted by Vasilyuk (1960, p. 107, pl. 25, figs 2, 2a-b) in corallite size, septal number, tabularium diameter, aspect of tabulae and other important diagnostic features. Both the holotype of *Eolithostrotionella zhizhinae* and the only described specimen attributed by Vasilyuk to *Protolonsdaleia mariupolensis* come from the same locality in the Vd Zone and show corallites with diagonals about 15 mm, 24-26 septa of both orders, minor septa reaching in tabularium one-fourth to one-third length of major septa, tabularium diameter 7-7.5 mm, longitudinally discontinuous axial plate, loosely spaced tabulae, tent-shaped when axial plate is present, and dissepimentarium reaching one-fourth corallite diagonal and dominated by first order transeptal dissepiments. The holotype of *Eolithostrotionella zhizhinae* shows locally contratingent minor septa, and the specimen of *Protolonsdaleia mariupolensis* sensu Vasilyuk shows few sporadically present radial lamellae.

To *Eolithostrotionella* also belongs *Protolonsdaleia intermedia* as interpreted by Vasilyuk & Zhizhina (1978, p. 30, pl. 2, figs 2a-b) (Vb-Vc Zones of the Donets Basin) [? = *Sublonsdaleia intermedia* Lissitzin, 1925]. It is distinguished by corallites having diagonals 11-17 mm, 19-24 septa of both orders, tabularia 5-6 mm in diameter, locally incomplete tent-shaped tabulae, axial structures varying from axial plate to poorly defined simple axial column composed of medial plate, few radial lamellae and longitudinally discontinuous irregular axial tabellae, and by dissepimentaria dominated by first order transeptal dissepiments.

Eolithostrotionella cystosa Zhizhina, 1960 (p. 250, pl. 61, figs 1a-b) and *E. rotai* Zhizhina, 1960 (p. 251, pl. 61, figs 2a-b), both from the Donets Formation (Warnantian), as well as *E. lissitzini* Zhizhina, 1960 (p.252, pl. 61, figs 3a-b) found in the Donets Formation and in the upper Serpukhovian (Arnsbergian, upper Zapal-Tyube and Voznesenka horizons) should be excluded from this genus. They resemble *Ceriodotia* in having major septa dilated in tabularium, minor septa indistinct to poorly developed, and dissepimentarium dominated by first order transeptal dissepiments. They differ from *Ceriodotia* in having incomplete tabulae; also, axial structure is less variable and represented by longitudinally continuous lath-like axial plate and locally developed radial plates.

Eolithostrotionella was considered as a subgenus of *Lithostrotion* Fleming, 1828 by Fomichev (1955), as a junior synonym of *Stelechophyllum* Tolmachev, 1933 by Dobrolyubova et al. (1966), Minato & Kato (1974), Hill (1981), and also by Sando (1983), who attributed the type species of *Eolithostrotionella* to the *Stelechophyllum microstylum* (White, 1880) species-group. The type species of *Eolithostrotionella*, however, shows close affinity to the solitary genus *Axoclisia* Semenoff-Tian-Chansky, 1974, established on material from the Lower Viséan of the Algerian Sahara in the aspect of septa, tabulae, dissepimentaria and axial structure, when fully developed. At least two *Axoclisia* species are present in the Moliniacian of the Donets Basin, *A. lissitzini* (Vasilyuk, 1960) in the Vb-Vd Zones and *A. brazhnikovae* (Vasilyuk, 1960) in the Vc Zone. *Eolithostrotionella* is most probably restricted to the Moliniacian of the Donets Basin, comprises three species, *E. longisepta, E. zhizhinae* and *Protolonsdaleia intermedia* as interpreted by Vasilyuk & Zhizhina (1978), and is most probably related to *Axoclisia*.

Both the genus *Protolonsdaleia* comprising three species, *P. carcinophyllosa, P. mariupolenis* and *P. ramulosa*, and the monospecific genus *Sublonsdaleia* were established by Lissitzin (1925) on the material from the Mariupol' Stage of the Donets Basin corresponding to the Vc-Vd Zones (Moliniacian). Lissitzin interpreted *Sublonsdaleia* as a genus close to *Thysanophyllum* (this generic name he applied to *Dorlodotia*), and defined it as a primitive lonsdaleoid genus lacking true axial column and possessing axial plate only. He considered *Protolonsdaleia*, distinguished by primitive axial column consisting of few irregular plates, as the genus transitional between *Sublonsdaleia* and *Lonsdaleia*. Vasilyuk (1960) accepted the genus *Protolonsdaleia*, and Vasilyuk & Zhizhina (1978) put *Sublonsdaleia* into the synonymy of *Protolonsdaleia*. Hill (1981) put *Protolonsdaleia* into the synonymy of *Actinocyathus* d'Orbigny, 1849; *Sublonsdaleia*, with a query, she put into the synonymy of *Thysanophyllum*. Sando (1983) considered both genera as possible junior synonyms of *Actinocyathus*. The original descriptions of the genera and illustrations are not adequate, the type species of *Protolonsdaleia* was not designated, and the figured types of both genera were never redescribed and are lost. Therefore, it is advisable to envisage submitting the case to the International Commission on Zoological Nomenclature.

3.2. Systematic position, range and evolution of Dorlodotia

Dorlodotia appeared during the "Avins event" (Latest Tournaisian, MFZ8 Foraminifera Zone, RC4β1 Rugose coral Biozone) (Poty, 2007) and, as indicated by the records of this genus in the Donets and Moscow Basins, ranged into the Warnantian.

Poty (2007) suggested that *Dorlodotia* evolved from a solitary caninoid coral that produced buds and developed a columella, and Denayer & Poty (2011) assumed that it evolved from *Corphalia* that could have originated from a solitary caninoid coral. Furthermore, they divided the genus *Dorlodotia* into two groups named "columellate *Dorlodotia*" and "acolumellate *Dorlodotia*", the former including *D. briarti* and evolving into *Ceriodotia*, and the other including *D. pseudovermiculare* and giving rise to *Dorlodotia* species from China lacking columella and distinguished by "the various development of lonsdaleoid dissepiments" (Denayer & Poty, 2011, p. 37).

Separation of *Dorlodotia* into two groups, depending on the development of a columella, each of them probably having different origin, does not agree with the data of Garwood (1912) and Smith (1916) on the presence of transitional forms between *Thysanophyllum pseudovermiculare* [= *Dorlodotia pseudovermiculare*] lacking axial structure and *Lonsdaleia praenuntia* Smith, 1916 distinguished by primitive and variable axial structure. Both species and transitional forms were recorded in NW England near the lower limit of the Viséan in the Upper C1-Lower C2 Zones correlating with the $Cf4\alpha_2$ Foraminifera zone (Riley, 1993), thus approximating to the RC4β2 Biozone of Poty et al. (2006). *Lonsdaleia praenuntia* showing close affinity to *Dorlodotia pseudovermiculare* in having short major septa, indistinct minor septa and dissepimentarium dominated by first order transeptal dissepiments, differs from it only in presence of longitudinally discontinuous loosely constructed poorly defined primitive dibunophylloid axial column composed of irregular medial lamella, few radial lamellae and conical axial tabellae. Presence of longitudinally discontinuous radial lamellae in *D. briarti* and *D. subkakimii* (Poty, 1975, 1981; Vasilyuk & Zhizhina, 1978), presence of longitudinally discontinuous radial lamellae and locally developed axial tabellae in *D. euxinensis* (Denayer, 2011) and, especially, high variability of axial structure detected in *Dorlodotia sokolovi* from the Moscow Basin (see chapter 4) suggest that *Lonsdaleia praenuntia* is also a *Dorlodotia* species distinguished by high variability of axial structure, possibly synonymous with *Dorlodotia pseudovermiculare*. Occasional presence in *Dorlodotia* of axial structure composed of medial plate, radial lamellae and axial tabellae, including at the early stage of evolution of the genus, could indicate that this genus belongs to the family Axophyllidae Milne Edwards & Haime, 1851.

As correctly suggested by Denayer (2011), *Ceriodotia* most probably evolved from *Dorlodotia*. It is noteworthy, that *Ceriodotia*, first reported from the Livian of Northwestern Turkey, shows earlier occurrence in the Donets Basin (Vc-Vd Zones). The Moliniacian age of this interval is confirmed by Foraminifera. *Eoparastaffella simplex* entering at the base of the Vb Zone defines the base of the Viséan, records of *Eoendothyranopsis donica* in the Vb-Vc Zones indicate the upper MFZ9 Zone, records of *Globoendothyra numerabilis* in the Vd_1 Subzone, records of *Uralodiscus rotundus* and of *Paraarchaediscus* in the Vd_2 Subzone indicate the13 Mamet Foraminifera Zone and the MFZ11 Zone, respectively (Hecker, 2002, 2009). The range of *Ceriodotia* on the western flank of the central Urals seems to be the closest to its range in Northwestern Turkey, whereas on the eastern flank of the South Urals this genus ranges into the lower Warnantian.

Near the limit of the early and late Warnantian in the Donets Basin, *Dorlodotia* could have evolved into a cerioid genus morphologically close to *Ceriodotia* and comprising *"Eolithostrotionella" cystosa, "E". rotai* and *"E". lissitzini*.

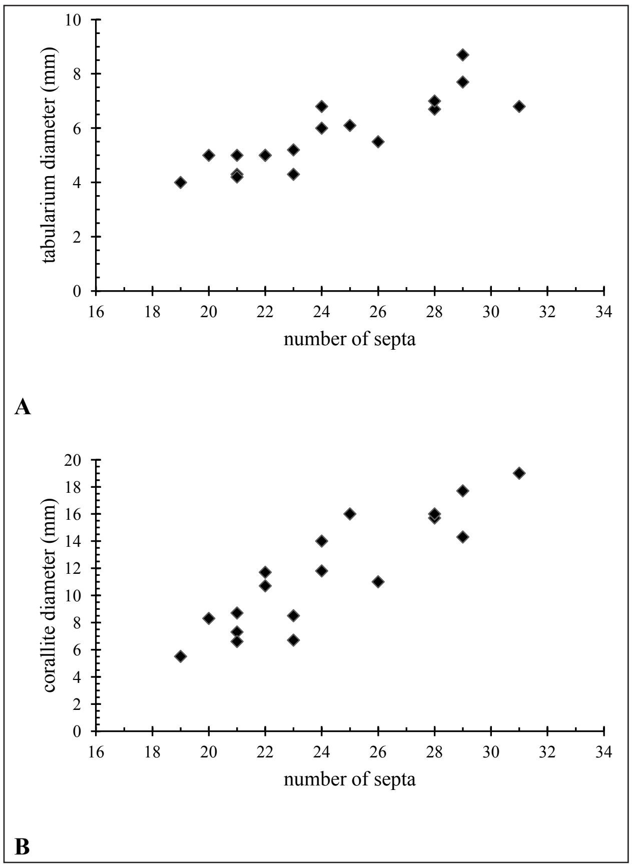

Figure 1. Statistical data of *Dorlodotia sokolovi*, specimen PIN 705/161, holotype. A: Ratio of the tabularium diameter to the number of major septa. B: Ratio of the corallite diameter to the number of major septa.

4. Systematic palaeontology

? Family Axophyllidae Milne Edwards & Haime, 1851

Genus *Dorlodotia* Salée, 1920

***Dorlodotia briarti* Salée, 1920 (p. 190, figs 5-6)**

Diagnosis. Fasciculate, with lateral increase; offsets arise in the outer dissepimentarium. Major septa typically withdrawn from the axis, commonly dilated in tabularium. Minor septa indistinct to poorly developed, commonly discontinuous longitudinally. Axial structure longitudinally discontinuous or lacking, typically a thickened axial plate, sporadically a simple dibunophylloid axial column comprising a medial plate, a few radial lamellae and irregularly conical axial tabellae. Tabulae typically complete, conical to flat. Dissepimentarium dominated by first order transeptal dissepiments, innermost series of interseptal dissepiments commonly dilated forming an inner wall (after Hill, 1981, emended).

Remarks. *Pseudodorlodotia* as originally defined (Minato, 1955) is considered herein as a junior synonym of *Dorlodotia*.

***Dorlodotia sokolovi* (Dobrolyubova, 1958)**
(Fig. 1, Pl. 1)

1958 *Lonsdaleia sokolovi* Dobrolyubova: p. 29, fig. 1, pl. 1, figs 1a-c.

Holotype. *Lonsdaleia sokolovi* Dobrolyubova, 1958. Specimen PIN 705/161, Borissiak Paleontological Institute, Russian Academy of Sciences, Moscow.

Type locality and horizon. Upper Mikhailov horizon, Brigantian, northwestern part of the Moscow Basin, Priksha River, 50-60 km N. of the town of Borovichi.

Material. Only the holotype.

Description. Corallites 7-18 mm in diameter, tabularia diameters 5-7.5 mm. Major septa 21-29 in number, dilated in tabularia, locally develop and thin in innermost dissepimentaria; their length in tabularium from half to two-thirds of its radius. Minor septa locally develop as ridges on inner wall. Axial structures lacking or varying from axial plate, thin to slightly dilated, to poorly defined axial column approximating one-fourth of tabularium diameter in width and composed of long, slightly to moderately dilated, straight to curved medial plate, one-two radial lamellae, irregularly conical steeply elevated axial tabellae spaced 0.4-0.6 mm apart. Periaxial tabellae subhorizontal, sagging or abaxially declined at angles of 10°-50°, spaced 0.25-1.55 mm apart. Periaxial cones composed of fused periaxial and axial tabellae may locally develop. Complete subhorizontal tabulae spaced 0.15-0.30 mm apart develop when axial structure is lacking. Width of dissepimentaria from one-fifth to one-third of corallite diameter. Dissepiments first order transeptal, locally second order transeptal in inner dissepimentaria, variously inflated, abaxially declined at angles of 30°-70°. Inner margins of innermost dissepiments vertically inclined and dilated forming thickened inner wall. Outer wall festooned, up to 0.4 mm thick.

Discussion. *Dorlodotia sokolovi* shows close affinity to *Dorlodotia subkakimii* in tabularium diameter, in aspect of dissepimentarium dominated by large first order transeptal dissepiments and in locally developed radial lamellae, but has bigger corallites with wider tabularia and a larger number of septa. The species is distinguished by high intracolonial variability involving axial structures and resembles in this aspect "*Lonsdaleia" praenuntia*, as it was emphasized by Dobrolyubova (1958).

Distribution. Only known by its holotype being from the upper Mikhailov horizon, Brigantian, north-western part of the Moscow Basin.

5. Conclusions

Fasciculate genus *Dorlodotia* is present in the Moliniacian (Glubokaya Formation) and Warnantian (Donets Formation) of the Donets Basin, in the upper Moliniacian (?)-Livian (upper Pester'ki horizon) of the western flank of the Central Urals and in the upper Warnantian (Brigantian, Mikhailov horizon) of the northwestern part of the Moscow Basin. *Lonsdaleia praenuntia* Smith, 1916 (lower Viséan, NW England) is also most probably a *Dorlodotia*. Cerioid genus *Ceriodotia* first reported from the Livian of Northwestern Turkey (Denayer, 2011) is present in the Moliniacian (Glubokaya Formation) of the Donets Basin, upper Moliniacian (?)-Livian (Pester'ki horizon) of the western flank of the Central Urals and in the upper Livian (?)-lower Warnantian (Ust'grekhovka horizon) of the eastern flank of the South Urals. Both genera probably belong to the family Axophyllidae.

Cerioid genus *Eolithostrotionella* is restricted to the Moliniacian (Glubokaya Formation) of the Donets Basin and is probably related to the solitary genus *Axoclisia*.

Eolithostrotionella cystosa Zhizhina, 1960 and *E. rotai* Zhizhina, 1960 (Warnantian, Donets Formation) of the Donets Basin, and *E. lissitzini* Zhizhina, 1960 (Warnantian, Donets Formation, Arnsbergian, upper Zapal-Tyube-Voznesenka horizons) are morphologically similar to *Ceriodotia,* but could belong to a separate genus ranging into the Serpukhovian.

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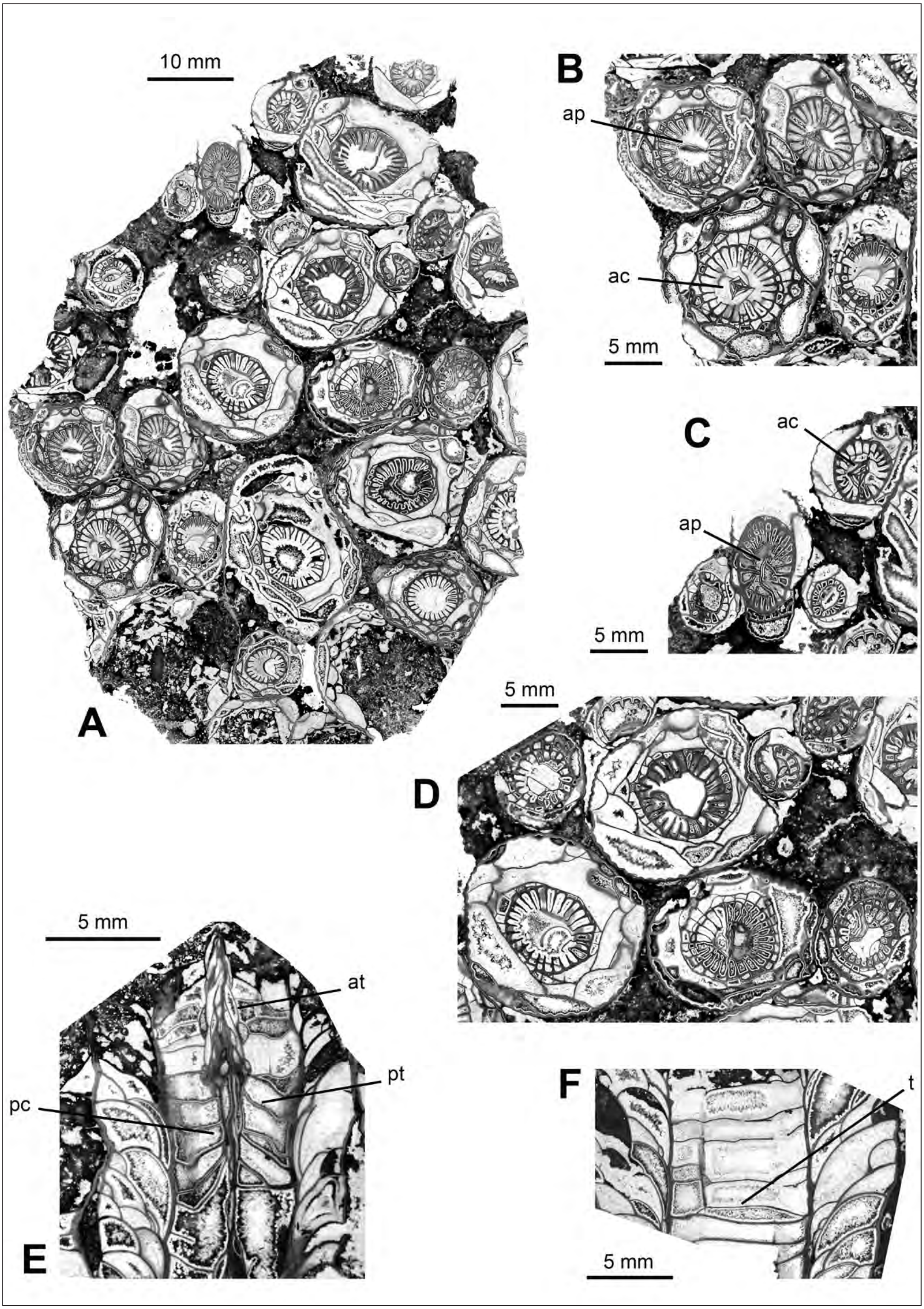

Plate 1. *Dorlodotia sokolovi* (Dobrolyubova, 1958), specimen PIN 705/161, holotype. A: Transverse section of the colony. B-D: Enlarged parts of the transverse section showing variability of axial structures. E: Longitudinal section of the corallite showing poorly defined axial column and periaxial cone on left side of column. F: Longitudinal section of the corallite lacking axial structure and showing subhorizontal tabulae; Dinantian, Brigantian, Mikhailov horizon, north-western part of the Moscow Basin, 50-60 km N. of the town of Borovichi. Legend: ac: axial column; ap: axial plate; at: axial tabella; pc: periaxial cone; pt: periaxial tabella; t: tabula.

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Biform tabularia and periaxial cones in *Lonsdaleia* McCoy, 1849 (Rugosa)

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ABSTRACT. Biform tabularia in rugose corals show different orientations of peripheral parts of tabulae situated on opposite sides of minor septa. Periaxial cones form irregular conical structures partly enclosing other structural elements of axial column and represent combination of steeply elevated, vertically extended axial parts of tabulae or periaxial tabellae with elongated axial tabellae. Both structures are characteristic of cerioid genus *Cystolonsdaleia* Fomichev, 1953, but also develop within the limits of variability in *Lonsdaleia* McCoy, 1849, including in some cerioid *Lonsdaleia (Actinocyathus)* d'Orbigny, 1849 species, thus suggesting that *Cystolonsdaleia* could have evolved from *Actinocyathus*. Among *Lonsdaleia* species from the uppermost Viséan-lower Serpukhovian of the Moscow Basin, biform tabularia are documented in *L. (Actinocyathus) crassiconus* (McCoy, 1849), *L. (A.) lativesiculosa* (Dobrolyubova, 1958), and *L. (Actinocyathus)* sp. A; periaxial cones in *L. (A.) bronni* (Milne Edwards et Haime, 1851) and *L. (A.) rossicus* (Stuckenberg, 1904); both biform tabularia and periaxial cones are documented in *L. (A.) floriformis* (Martin, 1809), *L. (A.) borealis* (Dobrolyubova, 1958), *L. (A.) subtilis* (Dobrolyubova, 1958), *L. (A.) gorskyi* (Dobrolyubova, 1958), *L. (A.) sarytschevae* (Dobrolyubova, 1958), *L. (Actinocyathus)* sp. A, and *L. (Lonsdaleia) duplicata* (Martin, 1809).

KEYWORDS: *Lonsdaleia*, morphology, uppermost Viséan-Serpukhovian, Moscow Basin, *Cystolonsdaleia*.

1. Introduction

The term *biform tabularium* was introduced by Weyer (1972) for different orientations, or *positions* in the sense of Sutherland (1965), of peripheral parts of tabulae in rugose corals situated on opposite sides of minor septa, those declined adaxially on one side of a given minor septum (*Position I*) and elevated on the other (*Position II*). First discovered in solitary genus *Ditoecholasma* Simpson, 1900 from the Upper Silurian of Oklahoma by Sutherland (1965), different orientations of peripheral part of tabulae were soon documented by Weyer (1972) in fourteen solitary genera and in one cerioid Upper Ordovician genus, *Crenulites* Flower, 1961, later in Upper Carboniferous *Cystolonsdaleia* Fomichev, 1953 and *Petalaxis* Milne Edwards & Haime, 1852 by Bamber & Fedorowski (1998) (Figs 1B, 1C), in fourteen Lower Permian colonial genera by Fedorowski et al. (2007), and in Lower Carboniferous *Actinocyathus* d'Orbigny, 1849 from the uppermost Viséan (Brigantian)-Serpukhovian of the Moscow Basin by Hecker (2010).

The term *periaxial cones* was introduced by Bamber & Fedorowski (1998) for components of axial structure in the genus *Cystolonsdaleia* representing combination of steeply elevated, vertically extended axial parts of tabulae with elongated axial tabellae. In this genus, periaxial cones form irregular, incomplete conical structures partly enclosing other structural elements of discontinuous and variable axial column (median lamella, radial and lateral lamellae, and discontinuous series of axial tabellae, Fig. 1E). Periaxial cones were also documented in few

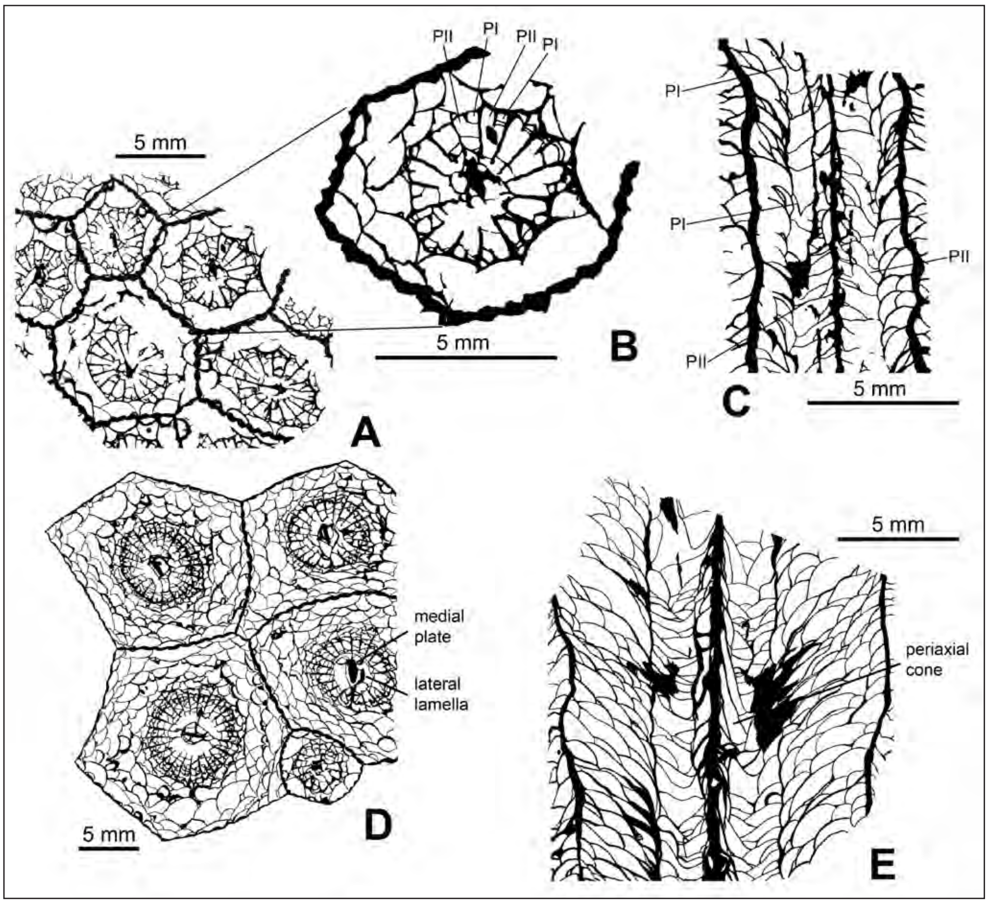

Figure 1. A-C: *Petalaxis maccoyanus* (Milne Edwards et Haime, 1851). A: Transverse section. B: Transverse section showing biform morphology of tabularium. C: Longitudinal section showing biform morphology of tabularium. D-E: *Cystolonsdaleia lutugini* Fomichev, 1953. D: Transverse section. C: Longitudinal section showing periaxial cones on right side of axial column. Legend: PI, tabellae or peripheral parts of tabulae in Position I; PII, tabellae or peripheral parts of tabulae in Position II. (After Bamber & Fedorowski, 1998).

Actinocyathus species from the Moscow Basin (Hecker, 2010).

The objectives of the present paper are: to confirm presence of biform tabularia and periaxial cones in the genus *Lonsdaleia*, and to discuss systematic value of these characters.

The study is based on the collection housed in the Borissiak Paleontological Institute, Russian Academy of Sciences, Moscow, as part of the collections registered under No. PIN 703, 705 and 1562.

2. Material

The genus *Lonsdaleia* McCoy, 1849 belongs to the family Axophyllidae Milne Edwards & Haime, 1851 and is distinguished by well-defined continuous axial column of dibunophylloid type comprising a median lamella, septal lamellae and typically regularly conical axial tabellae (Pl. 2D). The other diagnostic characters include indistinct to small cardinal fossula, indistinct to well-developed minor septa, concave, subhorizontal or variously declined, commonly complete periaxial tabellae and dissepimentarium dominated by transeptal dissepiments. Increase is typically lateral.

The genus comprises three subgenera: typically fasciculate *Lonsdaleia* and typically cerioid *Actinocyathus* d'Orbigny, 1849, both widely distributed in the uppermost Viséan (Brigantian) of Europe and Asia, and *Serraphyllum* Poty in Poty & Hecker, 2003 having both fasciculate and cerioid habitus, and reported so far from the Serpukhovian of Montagne Noire, South France only (see Poty & Hecker, 2003 for details).

In the subgenus *Actinocyathus*, two species-groups, each representing a separate trend of evolution within the subgenus, are distinguished (Hecker, 1997). The *A. floriformis* (Martin, 1809) group is characterized by its consistently short, commonly indistinct minor septa, and by its highly variable axial structures, whereas the *A. crassiconus* (McCoy, 1849) species-group is distinguished by its consistently developed, commonly long minor septa, and by less variable axial structures, usually showing regularly conical, crowded axial tabellae.

		biform tabularia	**periaxial cones**
	Lonsdaleia (Lonsdaleia) duplicata	present	present
***A. floriformis* species-group**	***L. (Actinocyathus) floriformis***	present	present
	L. (A.) bronni	not detected	present
	L. (A.) borealis	present	present
	L. (A.) rossica	not detected	present
***A. crassiconus* species-group**	***L. (A.) crassiconus***	present	not detected
	L. (A.) gorskyi	present	present
	L. (A.) subtilis	present	present
	L. (A.) lativesiculosa	present	not detected
	L. (A.) sarytschevae	present	present
	***L. (A.)* sp. A** *in* Hecker (2010)	present	present
	***L. (A.)* sp. B** *in* Hecker (2010)	present	not detected

Table 1. Biform tabularia and periaxial cones in *Lonsdaleia* species from the Moscow Basin.

Among *Lonsdaleia* from the Moscow Basin, biform tabularia are locally developed in *Lonsdaleia duplicata* (Martin, 1809) (Pl. 3A) and in *Actinocyathus* species belonging to both species-groups, *A. floriformis*, *A. borealis* (Dobrolyubova, 1958) (Pl. 1B), *A. crassiconus*, *A. subtilis* (Dobrolyubova, 1958) (Pl. 2B, 2C), *A. gorskyi* (Dobrolyubova, 1958) (Pl. 2H), *A. sarytschevae* (Dobrolyubova, 1958) (Pl. 3E, 3F), *A. lativesiculosus* (Dobrolyubova, 1958), *Actinocyathus* sp. A and *Actinocyathus* sp. B in the sense of Hecker (2010). When biform morphology of tabularium is expressed, periaxial tabellae in Position I are commonly steeper abaxially declined than tabellae in Position II (Pl. 1C). Biform tabularia are especially characteristic for the species comprising the *A. crassiconus* species-group distinguished by minor septa consistently penetrating tabularia (Pl. 2A, 2H, 3D). Biform tabularia are not detected in the two species characterized by systematically indistinct minor septa belonging to the *A. floriformis* species-group, *A. rossicus* (Stuckenberg, 1904) (Pl. 1E) and *A. bronni* (Milne Edwards et Haime, 1851) (Tab. 1).

Periaxial cones in *Lonsdaleia* are composed of fused periaxial and axial tabellae. They are locally developed in *Lonsdaleia duplicata* (Pl. 3B, 3C), *Actinocyathus floriformis*, *A. bronni*, *A. borealis* (Pl. 1C, 1D), *A. rossicus* (Pl. 1F, 1G), *A. subtilis* (Pl. 2E, 2F), *A. gorskyi* (Pl. 2I), A. *sarytschevae* (Pl. 3F) and *Actinocyathus* sp. A. Periaxial tabellae in *Lonsdaleia* typically extend from the dissepimentarium to the outer margin of the axial column and terminate adaxially against an axial tabella, whereas periaxial tabellae forming periaxial cones are steeply elevated near the axial column and merge with elongated axial tabellae joining the median lamella. It is possible to observe a transition from the state when elevated periaxial tabella terminates against an elongated axial tabella to the state when these structures merge to form a periaxial cone (Pl. 1C, 1D, 1F, 1G, 2E, 3B).

Periaxial cones are detected in the majority of the *Actinocyathus* species from the Moscow Basin (Tab. 1), except for *A. crassiconus*, *A. lativesiculosus* and *Actinocyathus* sp. A. *Actinocyathus crassiconus* is characterized by the most regular and well-defined axial column with densely spaced conical axial tabellae. *Actinocyathus lativesiculosus* and *Actinocyathus* sp. A showing marked intracolonial variability involving shape and spacing of axial tabellae and periaxial tabellae (see Hecker, 2010 for details) are represented by scanty material.

3. Discussion

Some published figures of *Lonsdaleia* from the Moscow Basin confirm presence of biform tabularia in *Actinocyathus subtilis* (Dobrolyubova, 1958, pl. 11, figs 1a, 2a, 3a, pl. 12, fig. 1a), *A. sarytschevae* (Dobrolyubova, 1958, pl. 14, fig. 2c), *A. borealis* (Poty & Hecker, 2003, pl. 5, figs 5-6), *A. crassiconus* (Hecker, 2010, fig. 1B) and *Actinocyathus* sp. A (Hecker, 2010, fig. 1H), presence of periaxial cones in *Lonsdaleia duplicata* (Dobrolyubova, 1958, pl. 2, fig. 4b) and *Actinocyathus crassiconus* (Hecker, 2010, fig. 1A), and presence of both biform tabularia and periaxial cones in *A. bronni* (Dobrolyubova, 1958, pl. 6, fig. 3) and *A. gorskyi* (Dobrolyubova, 1958, pl. 13, figs 1a, 1b, 2a, 2b).

Periaxial cones can be easily observed on the published figures of the longitudinal sections of the holotype of cerioid *Lonsdaleia floriformis laticlavia* Smith, 1916 (pl. 19, fig. 11) from the basal Pendleian of Northumberland, North England and "*Lonsdaleia floriformis laticlavia*, but convergent with *crassiconus*" (Smith, 1916, pl. 19, fig. 7) from the Brigantian of Derbyshire.

Bamber & Fedorowski (1998) considered biform tabularium and periaxial cones as the main characters distinguishing *Cystolonsdaleia* from similar cerioid taxa with complex axial structures and transeptal dissepiments, including *Lonsdaleia (Actinocyathus)*.

Biform tabularia, however, are expressed in many rugose species with minor septa long enough to penetrate tabularium as it was demonstrated by Weyer (1972) and Fedorowski et al. (2007). Among the *Actinocyathus* species from the Moscow Basin, biform tabularia were detected even in *A. floriformis* and *A. borealis* with typically short minor septa seldom penetrating tabularium.

Periaxial cones are far less common. In *Actinocyathus*, these structures occasionally develop within the limits of variability of some species. Periaxial cones are best expressed in *A. subtilis*, especially in the colonies form the northwestern part of the Moscow Basin (Pl. 2E, 2F), most probably because this was the area where the species reached the peak of its abundance and showed the highest variability in the Tarusa time (earliest Serpukhovian) (Hecker, 2010), including in the shape of periaxial tabellae locally becoming strongly concave (Pl. 2G).

Actinocyathus shows close affinity to *Cystolonsdaleia* and differs from it mainly by its typically well-defined continuous axial column composed of medial plate, radial lamellae and axial tabellae. In *Cystolonsdaleia*, axial structure ranges from axial plate to axial column, which, when fully developed, consists of medial plate, radial lamellae, lateral lamellae, discontinuous series of axial tabellae and periaxial cones (Fig. 1E) (Bamber & Fedorowski, 1998). Lateral lamellae, characteristic of *Cystolonsdaleia*, are lacking in *Actinocyathus*.

As suggested by presence of periaxial cones in both taxa, *Cystolonsdaleia* could have evolved from *Actinocyathus*, and evolution went in the direction of axial column becoming discontinuous and less regular, and lateral lamellae developing. Periaxial cones, developed within the limits of variability of the ancestral taxon, *Actinocyathus*, became characteristic structures in *Cystolonsdaleia* due to stabilizing selection.

Actinocyathus ranges in age from the uppermost Viséan (Brigantian) through the Serpukhovian, and *Cystolonsdaleia* from the Lower Pennsylvanian (Bashkirian) through the Lower Permian (Asselian). *Cystolonsdaleia* was originally described from the Moscovian (Pennsylvanian) of the Donets Basin, Ukraine (Fomichev, 1953). The earliest firmly dated occurrence of this genus is from the Bashkirian of the Voronezh area, Russia (Kozyreva, 1978); its presence in the Serpukhovian is not confirmed. *Cystolonsdaleia* has been found in the Pennsylvanian of Spain, Canada, USA and China; see Bamber & Fedorowski (1998) and Fedorowski et al., (2007) for details.

Six cerioid species from the Mississippian of the Western Interior Province, all showing periaxial cones, *Litostrotionella girtyi* Hayasaka, 1936 (Middle-Upper Viséan, Utah), *Lithostrotion pennsylvanicum* Shimer, 1926 (Middle Viséan, Alberta, British Columbia), *Lonsdaleia shimeri* Crickmay, 1955 (Middle-Upper Viséan, Alberta, British Columbia, Alaska, Arizona), *Lithostrotion (Lithostrotionella) berthiaumi* Merriam, 1942 (?Upper Viséan-Serpukhovian, Oregon), *Lithostrotionella peratrovichensis* Armstrong, 1970 (Upper Viséan, Alaska), *L. stelcki* Nelson, 1960 (uppermost Viséan-Serpukhovian, Alberta, British Columbia, Utah, Idaho, Wyoming), were assigned to *Cystolonsdaleia* by Bamber & Fedorowski (1998). All these species, however, most probably do not belong to *Cystolonsdaleia*, since they are lacking lateral lamellae and therefore do not completely fit the diagnosis of the genus given by Bamber & Fedorowski (1998) and Fedorowski et al. (2007).

4. Conclusions

Biform tabularia are expressed in many rugose species with minor septa long enough to penetrate tabularium; periaxial cones representing irregular, incomplete conical structures partly enclosing other structural elements of axial column develop less often. In *Lonsdaleia*, periaxial cones are composed of fused periaxial and axial tabellae. Biform tabularia are locally developed in ten species from the Brigantian-Serpukhovian (Mississippian) of the Moscow Basin, and periaxial cones in nine species.

Presence of biform tabularia and especially of periaxial cones in *Lonsdaleia* confirms and puts in evidence its close morphological similarity to *Cystolonsdaleia*. Periaxial cones, occasionally developed in *Lonsdaleia* within the limits of variability, became characteristic structures in *Cystolonsdaleia*. *Cystolonsdaleia* could have evolved from cerioid *Lonsdaleia* (*Actinocyathus*), and the evolution went in the direction of axial column becoming discontinuous and less regular with lateral lamellae and periaxial cones typically developed.

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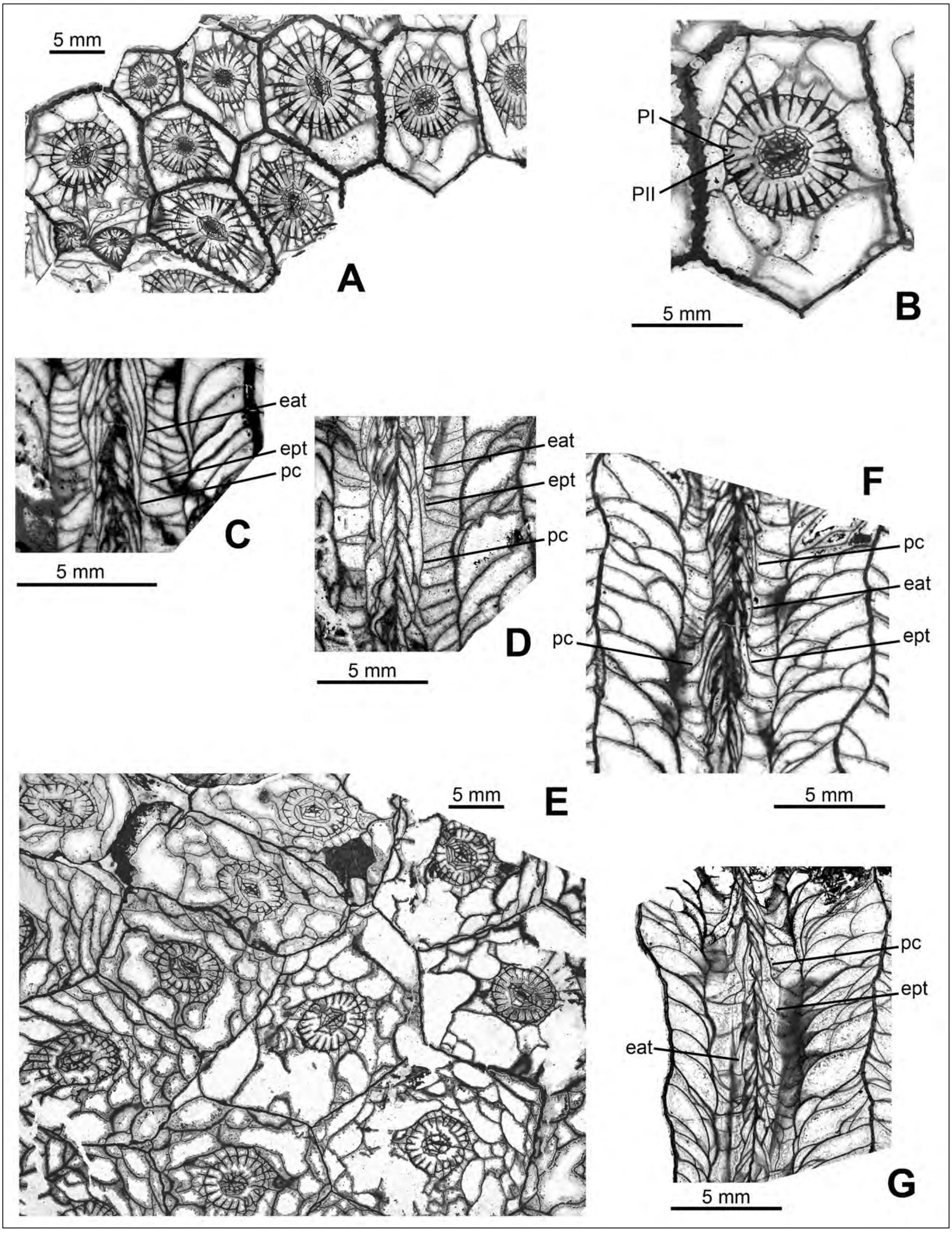

Plate 1. A-D: *Lonsdaleia (Actinocyathus) borealis* (Dobrolyubova, 1958). A-C: Specimen PIN 1562/2514. A: Transverse section. B: Transverse section showing biform morphology of tabularium. C: Longitudinal section showing axial column with elongated axial tabellae and periaxial cone on right side of axial column; Lower Serpukhovian, Steshevo horizon, north-western part of the Moscow Basin, village of Podbor'e, 7 km NW of the town of Borovichi. D: Specimen PIN 705/644, longitudinal section showing variously spaced and declined periaxial tabellae, axial column with elongated axial tabellae and periaxial cone on right side of axial column, x4; Lower Serpukhovian, Steshevo horizon, north-western part of the Moscow Basin, Sukhaya Poneretka Brook, 12 km SW of the town of Borovichi. E-G: *Lonsdaleia (Actinocyathus) rossicus* (Stuckenberg, 1904). E-F: Specimen PIN 703/33. E: Transverse section. F: Longitudinal section showing variously spaced and declined periaxial tabellae, axial column with irregular axial tabellae and periaxial cones on both sides of axial column; Lower Serpukhovian, Steshevo horizon, southern part of the Moscow Basin, left bank of the Oka River at the village of Luzhki, 12 km SE of the town of Serpukhov. G: Specimen PIN 703/40, longitudinal section showing irregularly spaced and variously declined periaxial tabellae, axial column with irregular loosely spaced axial tabellae and periaxial cones on both sides of axial column; Lower Serpukhovian, Steshevo horizon, southern part of the Moscow Basin, left bank of the Oka River at the village of Luzhki, 12 km SE of the town of Serpukhov. Legend: PI: periaxial tabella in Position I; PII: periaxial tabella in Position II; eat: elongated axial tabella; ept: elevated periaxial tabella; pc: periaxial cone; cpt : concave periaxial tabella.

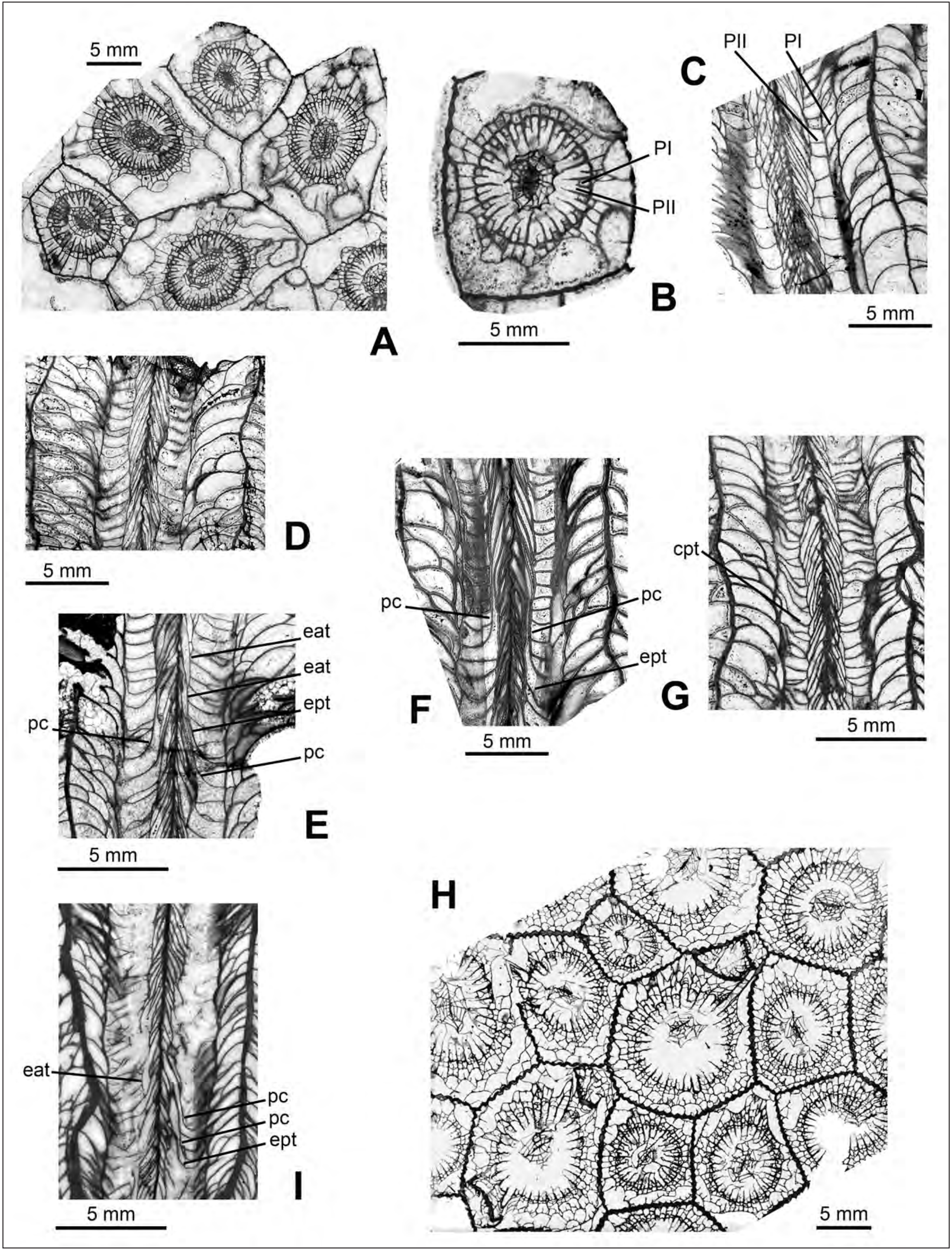

Plate 2. A-G: *Lonsdaleia (Actinocyathus) subtilis* (Dobrolyubova, 1958). A-C: Specimen PIN 705/646. A: Transverse section. B: Transverse section showing biform morphology of tabularium. C: Longitudinal section showing biform morphology of tabularium; Lower Serpukhovian, Tarusa horizon, north-western part of the Moscow Basin, Retesha River 60 km NE of the town of Boksitogorsk. D-E: Specimen PIN 705/184. D: Longitudinal section showing axial column with regularly conical steeply elevated axial tabellae. E: Longitudinal section showing axial column with variable axial tabellae and periaxial cones on both sides of axial column; Lower Serpukhovian, Tarusa horizon, north-western part of the Moscow Basin, Tutoka River 60 km NE of the town of Boksitogorsk. F: Specimen PIN 707/332A, longitudinal section showing axial column with regularly conical axial tabellae and long periaxial cones on both sides of axial column; Lower Serpukhovian, Tarusa horizon, north-western part of the Moscow Basin, Tutoka River 60 km NE of the town of Boksitogorsk. G: Specimen PIN 705/187, longitudinal section showing variously declined, including deeply concave, periaxial tabellae; Lower Serpukhovian, Tarusa horizon, north-western part of the Moscow Basin, Tutoka River 60 km NE of the town of Boksitogorsk. H-I: *Lonsdaleia (Actinocyathus) gorskyi* (Dobrolyubova, 1958); specimen PIN 705/133, holotype. H: Transverse section. I: Longitudinal section showing axial column with variable axial tabellae and periaxial cones on both sides of axial column; Lower Serpukhovian, Steshevo horizon, north-western part of the Moscow Basin, Sukhaya Poneretka Brook, 12 km SW of the town of Borovichi. Legend: see Plate 1.

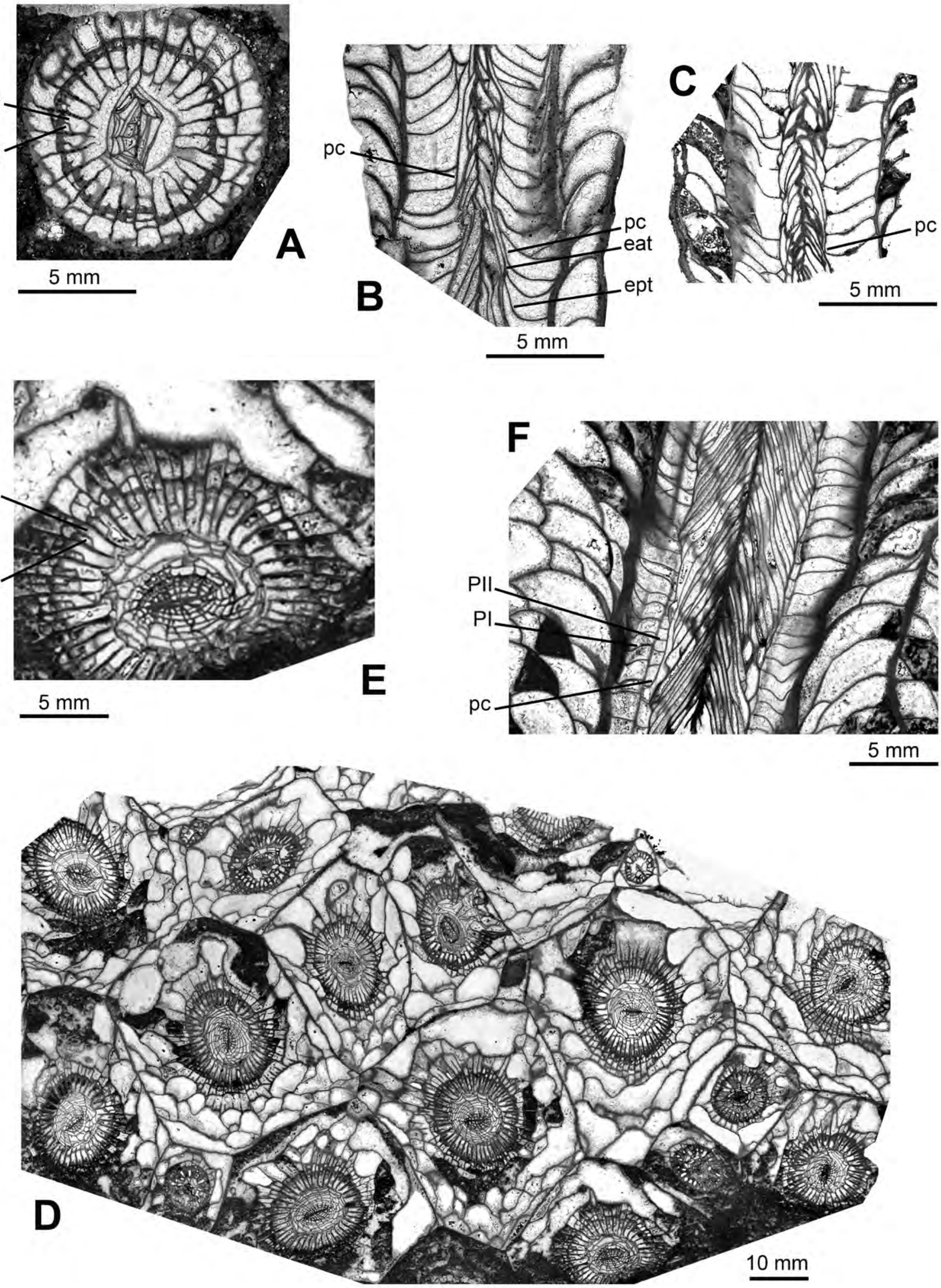

Plate 3. A-C: *Lonsdaleia (Lonsdaleia) duplicata* (Martin, 1809). A-B: Specimen PIN 705/200. A: Transverse section showing biform morphology of tabularium. B: Longitudinal section showing axial column with irregular axial tabellae and periaxial cones on both sides of axial column; Upper Serpukhovian, Protva horizon, north-western part of the Moscow Basin, 25 km SE of the town of Borovichi. C: Specimen PIN 703/2675, longitudinal section showing axial column with regular axial tabellae and periaxial cone on right side of axial column; Upper Viséan, Brigantian, Mikhailov horizon, southern part of the Moscow Basin, Kumova Gora Quarry, 8 km SW of the town of Mikhailov. D-F: *Lonsdaleia* (*Actinocyathus*) *sarytschevae* (Dobrolyubova, 1958); specimen PIN 703/2732, holotype. D: Transverse section. E: Transverse section showing biform morphology of tabularium. F: Longitudinal section showing axial column with regularly conical crowded axial tabellae and periaxial cone on left side of axial column; Lower Serpukhovian, Tarusa horizon, southern part of the Moscow Basin, Kievka River near the city of Kaluga. Legend: see Plate 1.

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Mississippian coral assemblages from Tabainout mud-mound complex, Khenifra area, Central Morocco

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ABSTRACT. Analysis of Mississippian coral assemblages from the Khenifra region of Central Morocco has demonstrated the presence of a rich and diverse coral fauna. Rugose coral assemblages from the Tabainout mud-mound complex comprise abundant colonial and solitary taxa, particularly in the basal bedded limestones, as well as the upper bedded flank and coquina capping beds. The massive core facies with stromatactoid cavities in contrast has rare solitary corals. The overlying shales, marls and limestone bands which buried the mud-mound are dominated by small non-dissepimented solitary rugosans. The age of the Tabainout mound based on foraminifers is established as upper Viséan (late Asbian-late Brigantian). The coral assemblage strengthens correlations with the Adarouch area in the northern part of the Azrou-Khenifra Basin where similar mud mounds occur. These assemblages also show similarity with coeval coral faunas from the Jerada mud-mounds (buildups) of NE Morocco and together represent part of the same palaeobiogeographic province (Western European Coral Province).

KEYWORDS: Morocco, Azrou-Khenifra Basin, Mississippian, upper Viséan, mud-mounds, rugose coral assemblages, palaeoecology, palaeobiogeography.

1. Introduction

In North Africa, especially Morocco and Algeria, coral-bearing mud-mounds and bioherms are not all that well known from the Carboniferous. The exceptions are the upper Viséan mud-mounds of the Erfoud region, eastern Morocco (Wendt et al., 2001) and bioherms from the Béchar Basin, W. Algeria (Pareyn, 1959, 1961; Semenoff-Tian-Chansky, 1974, 1985; Bourque et al., 1995). Recently, mud-mounds (buildups) containing rugose corals have been described from the Jerada Basin (NE Morocco) (Aretz & Herbig, 2008; Aretz, 2010), as well as corals from mud-mounds and platform limestones in the Adarouch area of north central Morocco in the northern part of the Azrou-Khenifra Basin (Said, 2005; Said & Rodríguez, 2007; Said et al., 2007, 2010, 2011; Cózar et al., 2008) (Fig. 1A). A brief summary of corals recorded from platform limestones and mud-mounds from the Azrou-Khenifra Basin (Central Morocco) have been recently noted (Aretz & Herbig, 2010).

Previous coral collecting from Carboniferous rocks in Morocco has been very limited, with occasional samples collected as part of reconnaissance mapping by the Moroccan Geological Survey (Termier, 1936; Owodenko, 1946; Termier & Termier, 1950). The dating of the Mississippian limestone successions in the Khenifra area of Central Morocco was established subsequently as upper Viséan, based on microfaunal and microfloral studies (Chanton-Güvenç et al., 1971; Chanton-Güvenç & Morin, 1973; Verset, 1988; Huvelin & Mamet, 1997). In 1995, a suite of coral specimens were collected from the Khenifra region (Aretz & Herbig, 2010), but these authors acknowledged that the results of this reconnaissance sampling probably under-represented the coral diversity present in the region.

In this study, we present a detailed description of coral faunas obtained from upper Viséan (Mississippian) limestones in the Khenifra area of central Morocco (Fig. 1B), which lies 70 km SSW of the Adarouch area. The aim of the paper is to document the coral assemblages from the Tabainout mud-mound complex near Khenifra, and compare them to the coral faunas from the Adarouch region and to relate any differences to local changes in facies and palaeoecology. Comparisons will be made also with corals recovered from upper Viséan mud-mounds (buildups) in the Jerada Basin of NE Morocco (Fig. 1A).

2. Geological setting of coral sections at Tabainout

The Palaeozoic Meseta of north central Morocco is divisible into three regions: in the west, near Rabat, the mostly Carboniferous siliciclastic rocks of the Sidi Bettache Basin; a central belt of mainly pre-Carboniferous rocks; and in the east, the Azrou-Khenifra Basin, extending from Azrou in the north to Jebel Hadid in the south (see Aretz & Herbig, 2010, fig. 1). This latter basin comprises Carboniferous siliciclastic and carbonate rocks resting unconformably on, and in thrust contact with, Ordovician and Devonian rocks, all affected by the later Variscan Orogeny (Allary et al., 1976; Hollard, 1978; Piqué, 1983; Hoepffner, 1987; Beauchamp & Izart, 1987; Bouabdelli & Piqué, 1996; Hoepffner et al., 2005).

The Tabainout complex, 20 km west of Khenifra (Figs. 1B-1D), represents an isolated exposure of Mississippian limestones bordered to the west and north by Ordovician siliciclastics and to the south and west by Mississippian shales. The Tournaisian and lower-middle Viséan rocks (where present) are composed mainly of sandstones and conglomerates, with the oldest limestones dated as late Viséan age, associated with a widespread transgression throughout the region (Chanton-Güvenç et al., 1971; Chanton-Güvenç & Morin, 1973; Verset, 1988; Huvelin & Mamet, 1997).

The Khenifra area formed part of a larger basin, the Azrou-Khenifra Basin, which is elongated NE-SW for c. 100 km and is c. 40 km wide (Aretz & Herbig, 2010). This basin has been affected by Variscan tectonics, in particular thrusting, on the eastern side. The Adarouch area lies some 40 km NW of Azrou at the northern end of the basin, where it is surrounded by younger Mesozoic and Cenozoic rocks (Berkhli, 1999; Berkhli & Vachard, 2001, 2002; Berkhli et al., 2001; Cózar et al., 2008).

3. Tabainout complex: lithofacies and microfacies

The Tabainout complex (N32°56’59”-W5°50’35”) forms a prominent NNE-SSW trending ridge, approximately parallel to the Khenifra - Sidi-Lamine road, composed mainly of massive mud-mound facies (Fig. 1C-1D), and extends c. 5 km to the northeast. The base of the Carboniferous sequence is exposed north of a track cutting E-W through the mud-mound complex, and comprises 2 m of well-bedded, slightly nodular, fine-grained bioclastic wackestone and packstone with thin interbedded shales occurring below the massive mud-mound facies. These beds rest unconformably on Ordovician shales and sandstones (Figs 1D, 2). The bedded limestones are relatively rich in corals, both solitary and colonial. At the SW end of the ridge, below the mound, are massive and brecciated micritic limestones with occasional solitary corals. The base of the succession here comprises 2 m

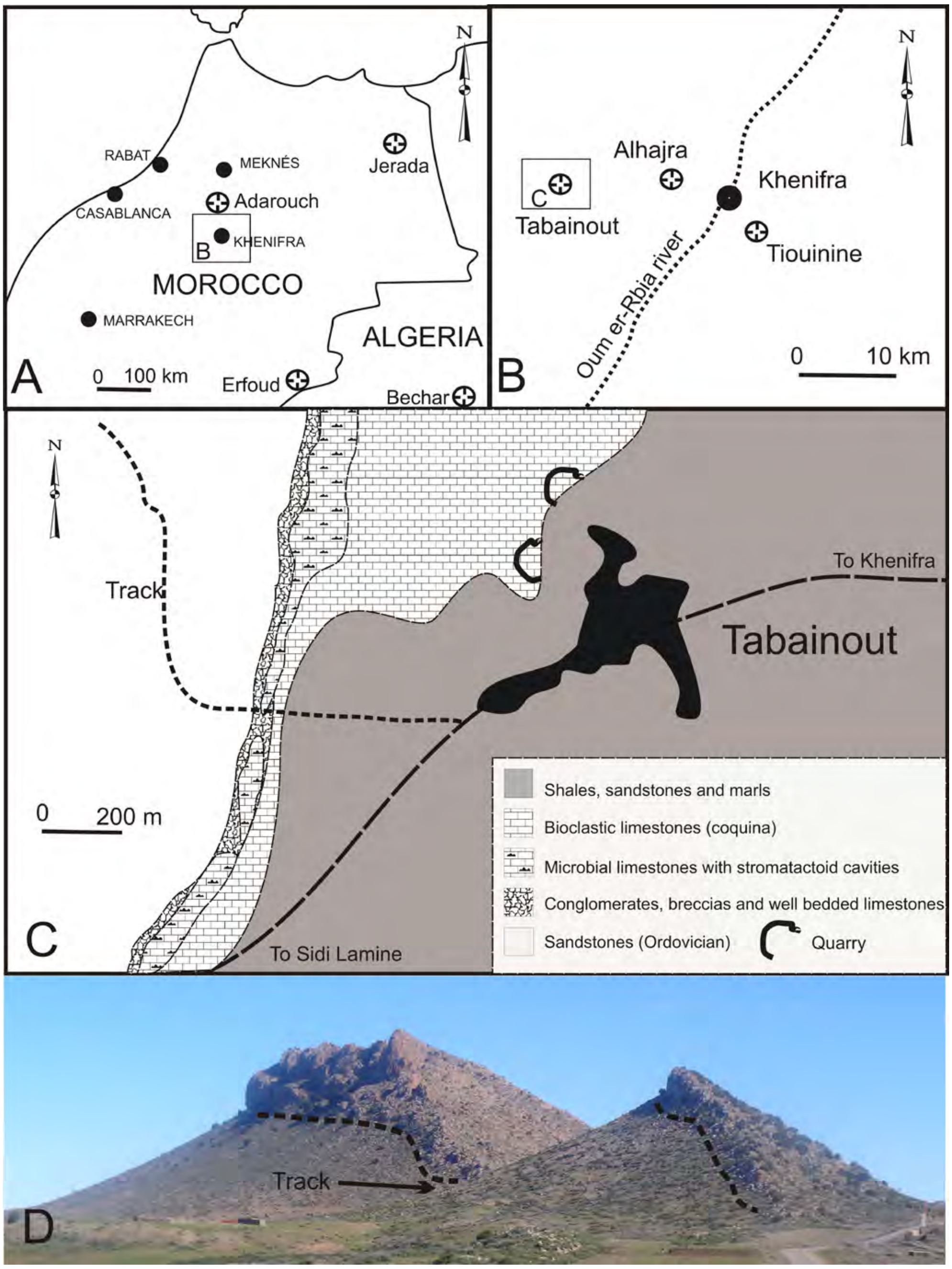

Figure 1. Sketch map with location of coral localities. A: Map of Northern and Central Morocco, with location of Khenifra area and other localities cited in the text. B: Location of Tabainout. C: facies distribution in the Tabainout area. D: General view looking northeast towards the Carboniferous mud-mound complex forming the ridge at Tabainout. The slopes to the west are underlain by Ordovician sandstones and the approximate position of the unconformity is indicated by the dashed black line.

of conglomerate, which thickens to >8 m southwestwards (Figs. 1D, 2), infilling the palaeotopography and is overlain by 1 metre of sandstone. These siliciclastic rocks are not developed below the large mound. The lowest limestone bed here contains angular sandstone clasts. The basal beds of the mud-mound are massive and bioclastic, with micritic facies containing stromatactoid cavities first appearing c. 8 m above the base. The measured thickness of the mound is c. 100 m, however, there are individual smaller mounds separated by thin intervals of bioclastic brecciated micrites and shales with solitary corals (intermound beds) The upper 20-25 m of the mound complex is bedded (cap beds) and locally rich in coquinas (shell bands encrusted with radiaxial fibrous calcite cements) (Fig. 2). These contain rich horizons of brachiopods (including gigantoproductids, and productids), bivalves, goniatites, orthocone nautiloids, crinoids and, locally, concentrations of mostly solitary corals on the flanks north of the track (Figs 1C, 2). These coquinas are interbedded with massive mudstones devoid of fauna and dip 40^0 to SE towards the village of Tabainout, succeeded by supramound shales and marls. Further north of the village the highest beds in the mound have recently been quarried (Fig. 1C). They expose the thick-bedded, shelly coquinas, as well as coarse-grained massive crinoidal grainstones which are laterally equivalent to the coquinas.

The bedded limestones at the base of the section are mostly medium-grained wackestone/packstone with extensive micritisation of bioclasts. Calcareous algae and Algospongia are locally very common with kamaenids, *Koninckopora, Borladella*, *Praedonezella cespeformis, Fasciella, Ungdarella uralica, Sparaphralysia tacanica* and *Draffania.* Foraminifers are relatively abundant with *Tetrataxis, Endotaxis, Vissariotaxis, Howchinia* and archaediscids at *angulatus* stage. The heterocoral *Hexaphyllia* is also recorded. The bulk of the Tabainout complex is composed of massive limestones, which in thin section are predominantly lime mudstone and sparse wackestone, with peloidal microbial fabrics and stromatactis cavity networks with geopetal sediment (Fig. 2). Fenestellid bryozoans and encrusting bryozoans can be conspicuous elements, but foraminifers are virtually absent, apart from very rare *Tetrataxis* and endothyrids. The top of the mound is more crinoid-rich with intraclasts, rare algae and foraminifers. The latter include *Neoarchaediscus parvus, N. ovoides, Endostaffella, Archaediscus karreri grandis, A.* at *angulatus* stage with *tenuis* sutures*, Praeplectostaffella, Euxinita efremovi, E. pendleiensis*?, *Pseudocornuspira, Asteroarchaediscus pustulus, Biseriella parva, Endothyranopsis compressa*?*/plana*?, and *Planospirodiscus taimyricus***.** Dasyclad algae include *Windsoporella* and *Koninckopora.*

In a stream section south of the main mound yellow and greenish shales, marls and thin interbedded bioclastic limestone

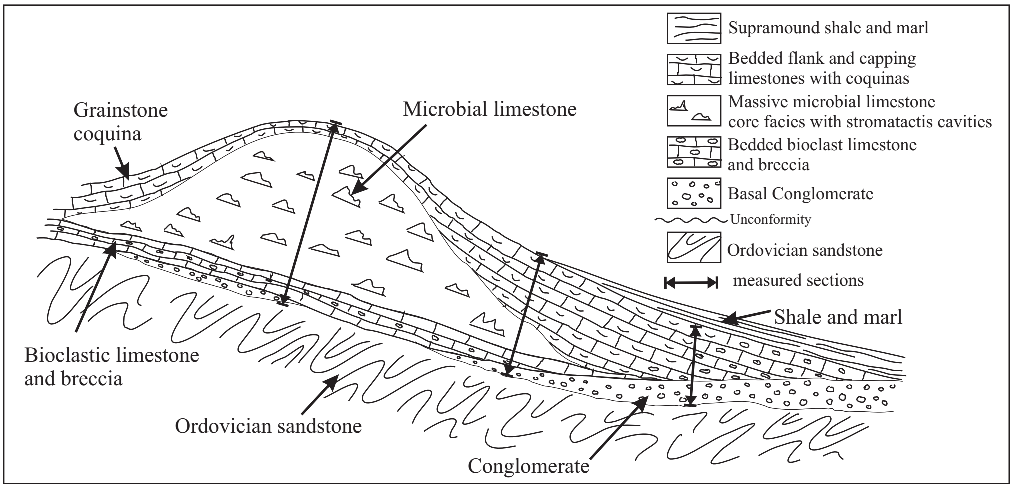

Figure 2. Model of the facies distribution in Tabainout mud-mound (not to scale) with approximate position of measured sections.

bands and nodules contain a rich assemblage of zaphrentid-type solitary corals, together with crinoids and goniatites. This sequence lies stratigraphically above, but also lateral to, the mud-mound, occupying a topographic low position (Figs. 1C, 2).

4. Age of the Tabainout mud-mound complex

Most of the foraminifers and algae at the base of the complex from the bedded limestones below the massive mud-mound facies are typical of late Asbian assemblages, and are comparable with the lower part of the Tizra Formation at Adarouch (Cózar et al., 2008). This is also supported by the presence of the rugose corals *Dibunophyllum bipartitum, Clisiophyllum keyserlingi, Siphonodendron intermedium* and *S. pauciradiale* (See Poty, 1981; Rodríguez & Somerville, 2007). The massive core facies is poor in corals and virtually devoid of foraminifers. The upper part of the mound in the bedded coquina grainstones and flank beds (capping beds), have a locally rich and diagnostic rugose coral assemblage, including *Kizilia* sp.*, Diphyphyllum furcatum, D. lateseptatum* and '*Pseudozaphrentoides' juddi*, establishing a Brigantian age (Rodríguez & Somerville, 2007). Moreover, rare samples have a diagnostic foraminiferal assemblage including: *Asteroarchaediscus pustulus, Biseriella parva* and *Planospirodiscus taimyricus* which indicate a late Brigantian age for the uppermost capping beds in the mound. Thus, the age of the limestones in the Tabainout complex ranges from late Asbian to late Brigantian (Cf6γ-Cf6δ, Foraminiferal zones and subzones of Conil et al., 1991). This differs from previous studies, which claimed an entirely Asbian age for the Tabainout mound (Huvelin & Mamet, 1997; Aretz & Herbig, 2010). A similar late Brigantian foraminiferal assemblage has been recorded from the upper part of the Tizra Formation at Adarouch (Cózar et al., 2008, 2011).

Cephalopods collected from coquina float are dominated by *Goniatites crenistria* of latest Asbian-earliest Brigantian age (P1a Zone) (Dieter Korn, pers. com.). Goniatites were also recovered in situ from the marls and limestones in the stream section. They include *Arnsbergites* sp. and *Hibernicoceras hibernicum*? which establish an early-mid Brigantian age (P1b-P1c zones; Riley, 1993) for the lower part of the supramound cover mudstones (Dieter Korn, pers. com.).

The implication is therefore, that continued upward growth of the mound complex was maintained during the Brigantian, when relief of tens of metres was developed. This led to shallower-water carbonates forming on the crest and upper flanks of the mound, whereas on the lower flanks and adjacent to the mound only marls accumulated in deeper water.

5. Description of the coral faunas

A total of c. 270 coral specimens was collected from the Tabainout complex and all of the material is reposited in the Departamento de Paleontología, Facultad de Ciencias Geológicas, Universidad Compultense de Madrid (Spain).

Corals are recorded at several distinct stratigraphic levels within the Tabainout complex. Below the massive mounds in thickly-bedded bioclastic limestones (Table 1, col. 1) was recorded a relatively rich assemblage of solitary and colonial rugose corals: *Amplexizaphrentis* sp., '*Amplexocarinia'* sp., *Arachnolasma cylindricum* Yu, 1934 (Fig. 3E), *Clisiophyllum keyserlingi* M'Coy, 1849, *Dibunophyllum bipartitum* (M'Coy,

		Tabainout complex					Adarouch	Jerada
	Genus & species	1	2	3	4	5		
Rugosa	*Amplexus* sp.	X	X		X	X		
	Kizilia sp.			X		X		
	'Amplexocarinia' sp.	X		X		X		
	Cyathaxonia cornu				X	X		
	Amplexizaphrentis sp.	X				X	X	
	Claviphyllum sp.				X	X		
	Rotiphyllum sp.	X		X	X	X	X	
	Bradyphyllum sp.				X	X		
	Ufimia sp.						X	
	'Pseudozaphrentoides' juddi	sp.		X		X		
	Siphonophyllia samsonensis	X				X	X	X
	Siphonophyllia siblyi						X	
	Clisiophyllum keyserlingi	X				X		
	Clisiophyllum garwoodi						X	
	Clisiophyllum sp.						X	
	?Axoclisia sp.						X	X
	Dibunophyllum bipartitum	X				X	X	X
	Corwenia spp.						X	
	Arachnolasma cylindricum	X		X		X	sp.	
	Haplolasma densum						X	
	Haplolasma sp.			X		X	X	
	Koninckophyllum sp.						X	
	*Palaeosmilia murchisoni**	X		X		X	X	X
	Palastraea regia						X	
	Lithostrotion araneum	X		X		X	X	
	Lithostrotion maccoyanum							X
	*Lithostrotion vorticale**	X		X		X	X	X
	Siphonodendron intermedium	X				X	X	
	Siphonodendron irregulare	X		X		X	X	X
	Siphonodendron junceum							X
	Siphonodendron martini	X		X		X	X	X
	Siphonodendron pauciradiale	X		X		X		X
	Siphonodendron sociale	X		X		X		
	Diphyphyllum furcatum			X		X	X	
	Diphyphyllum lateseptatum			X		X	X	
	Tizraia berkhlii						X	X
	Tizraia sp.						X	
	Aulokoninckophyllum carinatum						X	
	Axophyllum densum						X	
	Axophyllum aff. *pseudokirsopianum**	sp.	X	X		X	X	X
	Pareynia splendens							X
	Total number of rugose species	18	2	16	5	26	28	13
	Total number of rugose genera	13	2	11	5	19	19	9
Tabulata	*Michelinia* spp.	X	X	X	X	X	X	
	Syringopora sp.			X	X	X	X	
Hetero corals	*Hexaphyllia* sp.*	X				X		

*Taxa illustrated in Aretz & Herbig (2010)

Table 1. Comparison of coral taxa recorded from the Tabainout complex (columns 1-5) with Adarouch in the northern part of the Azrou-Khenifra Basin and Jerada (NE Morocco). The coral data from Adarouch is from the Tizra Fm (Said et al., 2007; Said & Rodríguez, 2007; Cózar et al., 2008). The coral data from Jerada is from the youngest Viséan Koudiat Es-Senn Fm containing mud-mounds (Aretz, 2010). The corals recorded from the Tabainout complex are: col. 1 = lowest bedded limestones and strata below the massive core facies, col. 2 = massive core facies, col. 3 = upper strata in the mounds (bedded coquina horizons and flanking beds), col. 4 = supramound shales, col. 5= combined data for columns 1-4. N.B.: The listing of genera follows the order in Hill (1981).

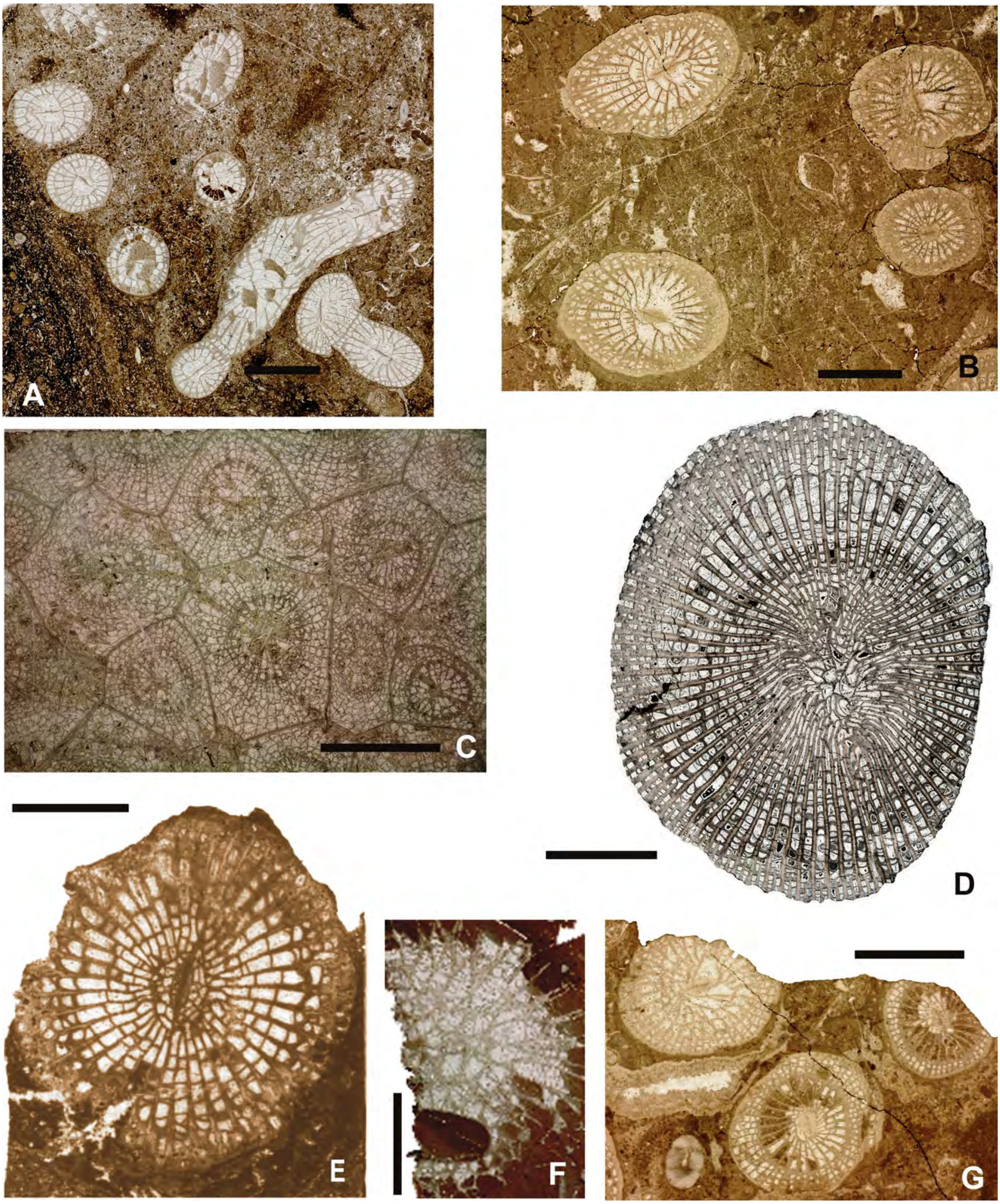

Figure 3. Corals from basal beds at Tabainout. A: *Siphonodendron pauciradiale* TAB/1-35. B: *Siphonodendron martini* TAB/2-5. C: *Lithostrotion vorticale* TAB/1-42a. D: *Palaeosmilia murchisoni* TAB/1-14. E: *Arachnolasma cylindrica* TAB/1-32. F: *Michelinia* sp. TAB/1-109a. G: *Siphonodendron sociale* TAB/1-2. Scale bars equal 5 mm.

1849), *Lithostrotion vorticale* (Parkinson, 1808) (Fig. 3C), *Palaeosmilia murchisoni* Milne-Edwards & Haime, 1851(Fig. 3D), *'Pseudozaphrentoides'* sp., *Rotiphyllum* sp., *Siphonodendron irregulare* (Phillips, 1836), *S. martini* (Milne-Edwards & Haime, 1848) (Fig. 3B), *S. intermedium* Poty, 1981, *S. pauciradiale* (M'Coy, 1844) (Fig. 3A), *S. sociale* (Phillips, 1836) (Fig. 3G), and *Siphonophyllia samsonensis* (Salée, 1913).

In the lower part of the massive limestones, particularly in the brecciated micritic facies that is interbedded with thickly-bedded bioclastic limestones, occur solitary corals, notably *Amplexus* sp., *Axophyllum* sp., *Rotiphyllum* and *Palaeosmilia*, with the tabulate *Michelinia* (Fig. 3F), and rare fragments of colonies of *Lithostrotion araneum* (M'Coy, 1844), *L. vorticale, Siphonodendron martini* and *S. sociale.* In addition, was recovered the heterocoral (*Hexaphyllia* sp.) (Table 1, col. 1).

In the main massive mud-mound facies characterised by the presence of stromatactid cavities were recorded rare *Amplexus* sp. (Fig. 4F), *Axophyllum* aff. *pseudokirsopianum* Semenoff-Tian-Chansky, 1974 and *Michelinia* (Table 1, col. 2).

In the upper part of the mud-mound which shows layers of bivalve/brachiopod and goniatite-rich coquinas interbedded with microbial limestones with stromatactoid cavities, are locally, rich pockets of rugose corals including *Diphyphyllum furcatum* (Hill, 1940) (Fig. 4B), *Lithostrotion araneum, Palaeosmilia* *murchisoni, Siphonodendron irregulare, S. martini, S. pauciradiale, S. sociale,* and a rare gregarious form of *Axophyllum* with budding (Fig. 4A). In the mound flank on the northern side close to the E-W track, similar capping bed facies are locally rich in large solitary corals, especially ‘*Pseudozaphrentoides’ juddi* (Thomson, 1893) (Fig. 4J) and *Palaeosmilia murchisoni*. In addition, were recorded ‘*Amplexocarinia’* sp. (a gregarious form showing microbialite encrustation) (Fig. 4G)*, Arachnolasma cylindricum*, *Diphyphyllum lateseptatum* (M’Coy, 1849) (Fig. 4C), *Kizilia* sp. (Fig. 4D), *Lithostrotion verticale*, *Haplolasma* sp.*, Rotiphyllum* sp., *Siphonodendron martini, S. pauciradiale,* as well as the tabulates *Michelinia* spp. (two species; one with a large diameter corallite and the other with a smaller diameter corallite) and *Syringopora* sp. (Table 1, col. 3).

In the stream section above the mud-mound within the shales, marls and interbedded limestone bands were recorded mostly non-dissepimented solitary rugose corals including ‘*Amplexus’, Bradyphyllum* (Fig. 4H), *Claviphyllum*? sp. (Fig. 4I), *Cyathaxonia cornu* Michelin, 1846 and *Rotiphyllum* sp. (Fig. 4E). Occasional tabulate corals recorded include *Michelinia* sp.*,* and *Syringopora* sp. (Table 1, Col. 4).

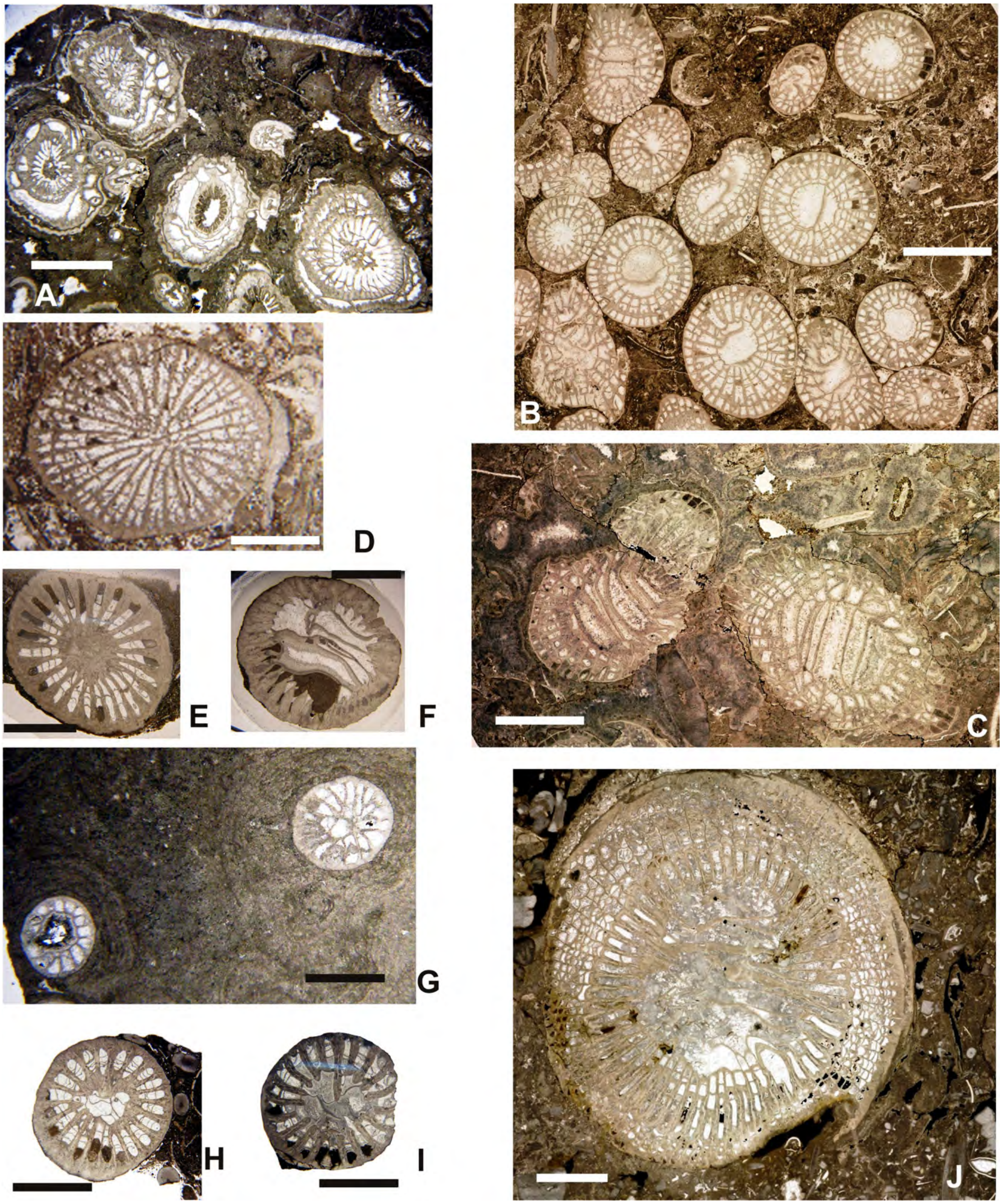

Figure 4. Corals from the mound and the surrounding shales. A: gregarious *Axophyllum* with budding exhibited in far left specimen TAB/1-27. B: *Diphyphyllum furcatum* TAB/1-3. C: *Diphyphyllum lateseptatum* TAB/1-25. D: *Kizilia* sp. TAB/1-81. E: *Rotiphyllum* sp. TAB/2-73, F: *Amplexus coralloides* TAB/2-31. G: *‘Amplexocarinia’* sp. with microbialite encrustation TAB/1-42b, H: *Bradyphyllum* sp. TAB/2-6. I: *Claviphyllum*? sp. TAB/22-28. J: ‘*Pseudozaphrentoides’ juddi* TAB/1-68. Scale bars equal 5 mm.

6. Analysis of Tabainout coral faunas

6.1. Comparison with previous coral studies in the region

In Tabainout there is a marked difference in the coral records presented here and in Aretz & Herbig (2010). The latter authors did not record any rugose corals from the massive mound core ('reefal limestone') and only three taxa below the 'reef' (*Lithostrotion vorticale*, *Siphonodendron irregulare* and *Palaeosmilia murchisoni*) in their 'bedded lower limestone'. They also recorded *Siphonodendron martini, S. pauciradiale, Axophyllum* sp. and *Amygdalophyllum* sp. in the 'bedded upper limestones'. Our recent sampling of the mud-mound complex has recorded 13 genera and 18 species of rugose corals from beds below the massive core facies of the mound, 2 rugosan genera and species from the massive core facies, and 11 genera and 16 species of rugosans from the flank beds and coquinas (capping beds) in the upper part of the mud-mound complex (Table 1). In addition, the shales, marls and limestones above the mound have yielded 5 genera and 5 species of solitary rugosans, and 2 genera and species of tabulate corals. Thus in total, 19 rugose genera and 26 species have been collected from the Tabainout complex, as well as 2 tabulate genera and 3 species (Table 1, col.5).

6.2. Variations in coral diversity in the Tabainout complex and palaeoecological interpretations

The studied outcrops in the Tabainout complex show a high variation in coral diversity, as each section shows different palaeoecological settings and environmental conditions (water depth, substrate, turbidity, turbulence and light levels), providing different possibilities for adaptation and settling of colonial and solitary corals. The Tabainout complex exhibits large mud-mounds with clear differentiation of basal bedded limestones, massive microbial mound core facies, bedded coquina grainstones and flank beds in the upper part of the mound (capping beds) and supramound shaly facies (Fig. 2). The bedded limestones below the massive part of the mound contain a rich and diverse assemblage of both solitary and colonial rugosans. In particular, *Siphonodendron* and *Lithostrotion* colonies are abundant, as well as large dissepimented solitary taxa (*Dibunophyllum, 'Pseudozaphrentoides'*, *Siphonophyllia*, *Clisiophyllum* and *Palaeosmilia*). These bedded limestones which are dominated by solitary rugosans are typical of Rugose Coral Association (RCA) 5 of Somerville & Rodríguez (2007). These packstones are also characterised by the presence of abundant dasycladacean algae, foraminifers, heterocorals and micritised grains, indicative of shallow water, moderately turbulent, euphotic conditions.

In contrast, the massive core facies has very rare corals, comprising small axophyllids and *Amplexus*. The absence of calcareous algae and foraminifers in the fine microbial lime mud sediment and the lack of allochems obviously inhibited coral attachment, and only specialist corals could adapt to the presumed deeper and quieter water conditions associated with the transgression.

The upper part of the mud-mound shows a significant increase in coral diversity, and locally, corals are very abundant in the coquina horizons, along with productid brachiopods, bivalves and goniatites. Large solitary corals can be locally conspicuous in these beds (*Palaeosmilia, 'Pseudozaphrentoides'*). In the flank beds colonial corals are present (*Diphyphyllum, Lithostrotion* and *Siphonodendron*). Interestingly, a gregarious form of *Axophyllum* with buddings is recorded from the upper part of the mound, which is distinguished from *Lonsdaleia* by its simpler axophyllid axial structure and dissepimentarium, and from *Howthia* by its larger size, more prominent axial structure and wider lonsdaleoid dissepimentarium. This taxon, together with gregarious '*Amplexocarinia'*, suggests that potential evolutionary opportunities were present in a shallower-water phase of later mound growth (cf. Rodríguez & Somerville, 2010; Somerville & Rodríguez, 2010). Interestingly, Mundy (1994) recorded abundant *Amplexocarinia* and *Cyathaxonia* in the upper part of the late Viséan Stebden Hill buildup in N. England. These solitary rugosans, that were encrusted in microbialite, were interpreted as forming a framework in a shallow-water niche.

The upper part of the mud-mound facies with its high diversity and abundance of rugose corals (11 genera and 16 species) is typical of RCA6. (Somerville & Rodríguez, 2007), and is characteristic of large upper Viséan (late Asbian-Brigantian) mud-mounds (c. 100 m thick) which grew up into shallower water, where colonial corals in particular could flourish (see Somerville et al., 1996; Somerville, 1997; Rodríguez & Somerville, 2007; Denayer and Aretz, 2011). A shallower-water setting for the upper part of the mound is also suggested by the presence of dasycladacean green algae.

The solitary corals of the supramound shales are typical of the RCA8 of Somerville & Rodríguez (2007), and characterised by small, undissepimented taxa (the *Cyathaxonia* fauna). They are representative of the basinal or flysch-type sediments that buried the mounds, particularly on their lower flanks and introduced much deeper water conditions into the Tabainout area, where colonial corals, apart from tabulates, are absent, and goniatites and crinoids are the only other distinctive faunal elements. A similar assemblage dominated by solitary corals was identified by Sando (1980) as having a very low indication of a shallow-water habitat.

7. Comparison with other Moroccan areas

7.1. Adarouch

Carboniferous rugose corals have been previously studied in detail in the Adarouch region (northern Azrou-Khenifra Basin), in particular, in the age-equivalent (late Asbian-Brigantian) Tizra Formation (Said, 2005; Said et al., 2007; Cózar et al. 2008; Said et al., 2011), which contains a development of large mud-mounds, similar to those at Tabainout. The basal bedded limestone facies of the mounds and mound core facies show similar features in both localities and, consequently, the coral assemblages have many taxa in common, notably large solitary cyathopsids, aulophyllids, colonial lithostrotionids, and axophyllids in the mound core facies (11 species, Table 1). Also, the flank beds in both regions can be locally dominated by small solitary corals and *Michelinia*. The main differences are related with the facies developed in the upper part of the mounds and above them. Spectacular coquinas containing large solitary and some colonial corals are developed as flank beds in Tabainout. On the other hand, biostromal beds dominated by fasciculate corals (e.g. *Siphonodendron*, *Diphyphyllum* and *Tizraia*) occur some metres above the mounds in Tizra (Said et al., 2011). Two of these genera are known from Tabainout, but *Tizraia*, an endemic genus to Morocco (Said & Rodríguez, 2007; Aretz, 2010), is absent. However, it is recorded at Tiouinine, southeast of Khenifra (Fig. 1B, Said et al., in press). Thus, in general, there are many close similarities of the rugose coral assemblages between Adarouch and Tabainout, not only at species level, but also in the distribution of corals within and adjacent to the mud-mound complexes (Table 1).

7.2. Jerada Basin

The Jerada Basin is located in northeastern Morocco, 375 km NE of Khenifra (Fig. 1A), and shows similar lithological features to the Tabainout complex, particularly in the development of large mounds in the youngest upper Viséan rocks (Koudiat Es-Senn Fm), of probable late Asbian-Brigantian age (Vachard & Berkhli, 2002; Aretz, 2010). Consequently, the coral assemblages are comparable in general, but show some differences in detail (Table 1). Fasciculate corals are dominant in Jerada, and the same genera present in Tabainout are recorded (except *Tizraia*). However, *Siphonodendron junceum* is present in Jerada but absent in Tabainout. On the other hand, larger species such as *S. sociale* are absent in Jerada. Aulophyllidae, Cyathopsidae and Axophyllidae are the most common solitary corals in Jerada (as well as in Tabainout), with at least 4 species in common (*Dibunophyllum bipartitum, Palaeosmilia murchisoni, Siphonophyllia samsonensis* and *Axophyllum* aff. *pseudokirsopianum*) (Table 1). In total, 8 rugose coral genera and species (>60% of the taxa) are common to Jerada and Tabainout, demonstrating that both areas belong to the same palaeobiogeographical province (see below). However, the presence of *Pareynia splendens* Semenoff-Tian-Chansky, 1974 in Jerada, which is absent in Tabainout, demonstrates some affinity with the fauna of the central Saharan basins to the south in Algeria e.g., Béchar Basin (Fig. 1A; Semenoff-Tian-Chansky, 1974; Aretz, 2010, 2011a).

7.3. Tafilalt Basin

In the eastern Anti-Atlas Mountains Wendt et al. (2001) described Viséan mud-mounds from the Zrigat Formation in the southeastern part of the Tafilalt Basin near Erfoud, eastern Morocco, 350 km SE of Khenifra (Fig. 1A). In the upper part of the formation the mounds are of late Viséan age (late Asbian to Brigantian) based on limited conodont and goniatite data. A sparse coral fauna was recorded from the mound and intermound facies with rare *Lithostrotion* (= *Siphonodendron*) colonies present in the massive core facies and in the intermound facies, as well as isolated specimens of undetermined solitary rugosans. The tabulate coral *Michelinia* was recorded in the intermound facies. Interestingly, below the mounds in the shaly facies, Wendt et al. (2001) recorded *Cyathaxonia*, lophophyllids, caniniids, hapsiphyllids, as well as *Dibunophyllum*. Unfortunately, because of the limited identification of coral taxa from these mounds, it is not easy to make a direct comparison with the coral fauna from the Tabainout complex. However, it would appear that although some taxa are present in both areas, the overall diversity and abundance is much lower in the Tafilalt area.

7.4. Discussion

The Tabainout mud-mound complex, as a whole, shows a much higher coral diversity compared to most other examples in Morocco (and Europe). However, the mound core facies ("microbial mound" facies) is particularly poor in corals, with only the occasional amplexid or axophyllid solitary rugosan, except where there are thin developments of intermound crinoidal limestone and shale. The remarkable features of this mud-mound that are not present in other mud-mounds (e.g.,Tizra, Jerada in Morocco and in Sierra Morena, SW Spain, see Cózar et al., 2003; Rodríguez-Martínez et al., 2003) are bedded flank facies and coquinas that contain a rich rugose coral assemblage. It is not comparable to the biostromes at the top of the Tizra mounds, because they lie above the mound, whereas in Tabainout, the corals occur interbedded with horizons showing stromatactid cavities and thus can be regarded as part of the mud-mound complex. At Tizra the mud-mounds are surrounded by marly limestones containing solitary corals and tabulates, but do not have the cemented coquinas alternating with beds having microbial textures. The total coral assemblage from the Tabainout mud-mound complex comprises 21 genera and 28 species. It represents an unusually high diversity for a mound, resulting from the presence of a diverse suite of environments of variable water depths hosting the rugose and tabulate corals.

8. Palaeobiogeography

The upper Viséan Tabainout assemblages contain many rugose genera and species that are also relatively common throughout Western Europe (SW Spain, Belgium, France, British Isles), e.g., *Siphonodendron pauciradiale, S. martini, S. sociale, Lithostrotion vorticale, L. decipiens, Diphyphyllum furcatum, D. lateseptatum, Siphonophyllia samsonensis*, and *Dibunophyllum bipartitum,* as well as rare taxa including *Kizilia* sp.. Moreover, assemblages corresponding to similar environments in Europe are dominated by the same species (cf. the standard upper Viséan assemblages of Somerville & Rodríguez, 2007). Consequently, the Tabainout upper Viséan coral assemblages indicate that the Azrou-Khenifra Basin should be considered as part of the Western European Coral Province (Fedorowski, 1981, fig. 2; Hill, 1981; Sando, 1990; Aretz & Herbig, 2010) and Western Palaeotethyan fauna (Hill, 1981). Thus, much of North Africa, north of the Atlas Transform Fault, including Tabainout, Adarouch and Jerada, can be included in this same palaeobiogeographic realm. Aretz (2011b) has recently grouped together these Moroccan basins, based on a statistical study of the rugose coral faunas , and referred to them as the 'Moroccan Meseta Province'.

9. Conclusions

Carboniferous (Mississippian) rocks from Tabainout in the southern part of the Azrou-Khenifra Basin contain rich coral assemblages. Detailed analysis of the coral faunas from the mud-mound complex has established that they are richer and more diverse than those recorded in previous studies, especially in the bedded limestones at the base and in the upper flank beds and coquinas (cap beds).

Comparison of the upper Viséan (late Asbian-Brigantian) coral assemblages at Tabainout with those previously recorded at Adarouch, in the northern part of the Azrou-Khenifra Basin, has recognised many similarities in the composition of the rugose taxa between both areas. Moreover, similar association are recorded from different facies in the mud-mounds from Tabainout and Tizra.

Further comparison of the Azrou-Khenifra Basin assemblages with coral assemblages in other parts of the Western Palaeotethys shows recognition of close similarities with assemblages from the Jerada Basin (NE Morocco), and south-western Spain (Sierra-Morena), where mud-mounds are recorded, establishing the location of all these areas within the same palaeobiogeographic province (Western European Coral Province).

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Corals of the Upper Viséan microbial-sponge-bryozoan-coral bioherm and related strata of Kongul Yayla (Taurides, South Turkey)

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ABSTRACT. The microbial-sponge-bryozoan-coral bioherm of Kongul Yayla in the Central Taurides (South Turkey) contains a rich and diversified fauna. Sponges and rugose corals are of particular interest. The most common taxa are *Siphonodendron irregulare, S. pauciradiale, S.* cf. *intermedium, Lithostrotion araneum, L. decipiens, L. maccoyanum, Axophyllum* aff. *pseudokirsopianum, Palaeosmilia multiseptata, P. murchisoni, Clisiophyllum* aff. *keyserlingi, Amygdalophyllum* sp., *Rotiphyllum* cf. *densum, Amplexocarinia* aff. *cravenensis, Soshkineophyllum*? sp. and *Espielia tauridensis* sp. nov. newly described here. The tabulate corals are mostly micheliniids, syringoporids, cladochonids and auloporids. Heterocorals and chaetetids are also present. *Siphonodendron pauciradiale* and *Lithostrotion maccoyanum* are the guide taxa for the RC7β biozone and indicate an late Asbian age for the bioherm. Facies and coral assemblage argue for a South-European affinity of the Kongul Yayla reef and probably for the whole Anatolian terrane.

KEYWORDS: Mississippian, Viséan, Asbian, rugose corals, tabulate corals, bioherm, Turkey, Taurides.

1. Introduction

The Anatolian sub-continent is made of several continental fragments (terranes) juxtaposed during the Alpine orogeny (Middle Triassic-Late Eocene, Şengör, 1984) and separated by complex suture zones. From North to South, these terranes are named Rhodope-Strandja Zone, Istanbul Zone, Sakarya Zone, Kirşehir Block, Menderes Massif, Anatolide-Tauride Block and the Arabian Platform (Fig. 1A, Okay & Tüysüz, 1999). There is no consensus about the denomination and classification of these units (see Robertson, 2000; Moix et al., 2008). Many controversies persist concerning boundaries of the continental terranes and oceanic zones, despite years of researches on tectonics, stratigraphy and palaeogeography of the Turkish geology (see Görür & Tüysüz, 2001).

The southern part of Turkey corresponds mainly to the Anatolide-Tauride Block (Özgül, 1984) - also named Anatolide-Tauride Platform (Şengör & Yilmaz, 1981) - which corresponds to juxtaposed tectono-stratigraphic units, bounded by major faults (Fig. 1A). Recent studies (see Moix et al., 2008) on Turkish tectono-stratigraphic units show the affinities of the Anatolian terranes with Eurasia and the affinities of the Taurus Terrane (the "Cimmerian blocks" of Şengör, 1984) with Gondwana.

In the Western Taurides, Mississippian sedimentary rocks are present in two allochtonous tectonostratigraphic units: the Aladağ unit and the Bolkar Dağı unit. In the Hadim region between the towns of Konya and Alanya, Turan (2000, 2001) described in the latter unit the Zindancık Formation composed of a thick siltstone succession, in which large limestone blocks are interpreted as olistoliths included in Triassic flysch.

Three limestone bodies are exposed along the section of the Kongul Yayla sheep barn (Fig. 2). Each body is an olistolith and forms a small hill, separated from each other by depressions corresponding to the siltty fysch (Fig. 1B). The northern limestone unit olistolith (NLU, Fig. 2 & 3) is composed of 120 m of well bedded limestone including 60 m of variegated shallow-water limestone (level KY.10 on Fig. 3), 10 m of dark bioclastic limestone with corals, brachiopods and crinoids, 3 m of limestone with abundant productid brachiopods, 10 m of light oolitic grainstone with corals and brachiopods (KY.11), an 0.5 m-thick bed with many large *Lithostrotion araneum* colonies, 25 m of limestone facies poor in macrofossils (KY.12). The contact with the surrounding siltstones (KY.13-16) is sharp and oblique to the bedding. The second unit, called biohermal limestone unit olistolith (BLU, Fig. 3), is approximately 50 m thick. Its reefal character was already recognized by Özgül (1984, 1997). Its base is made up of 15 m of thin-bedded coarse crinoidal limestone with numerous bioclasts and fragments of corals, brachiopods, gastropods, bivalves, etc. including a 0.4 cm-thick bed constructed by large colonies of *Siphonodendron pauciradiale* (KY.1). The bioherm *sensu stricto* begins above the *Siphonodendron* bed with a 25 m-thick massive pale limestone rich in macrofossils (KY.2-3). The diversified fauna includes productid and spiriferid brachiopods, gastropods, stemmed echinoderms, foraminifers attached to various skeletal grains, abundant lithistid and

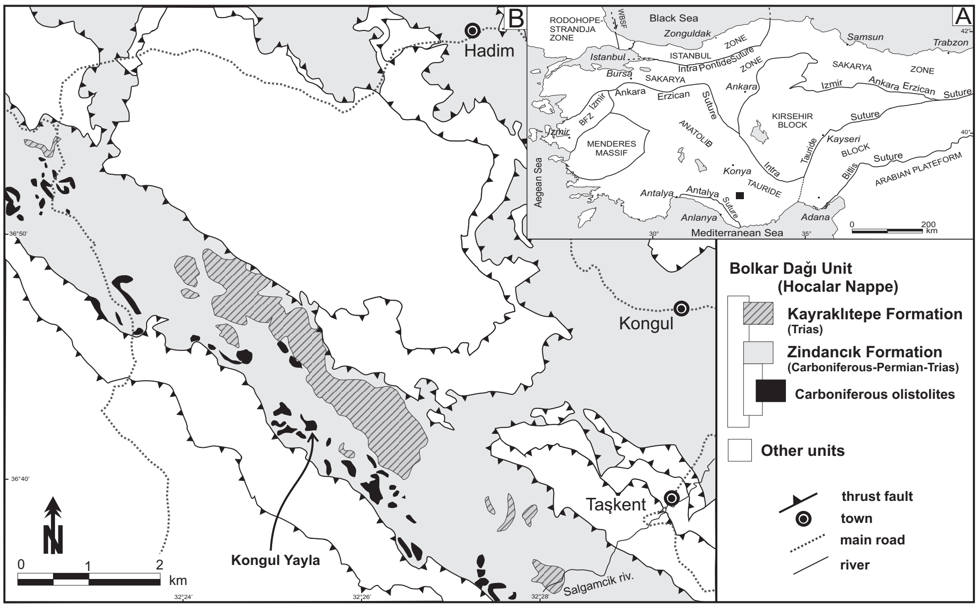

Figure 1. A: General structural map of Turkey, redrawn and modified after Okay & Tüysüz (1999) and Şengör (1984). The Anatolide-Tauride Block is presented in grey. B: Simplified tectonic map of the Hadım area (black square in Fig. 1A), redrawn after Turan (2000) showing the tectonostratigraphic units (nappes). The formations are detailled only for the Hocalar Nappe.

Figure 2. General view of the section with the three limestone units and the siltstone units. Abbreviations: NLU: northern limestone unit olistolith (part), BLU: biohermal limestone unit olistolith, SLU: southern limestone unit olistolith.

calcareous sponges, abundant massive stenoporids (*Tabulipora* sp.), massive encrusting fistuliporids (*Fistulipora* sp.), ramose rhabdomesid, reticulate fenestrate fenestellids bryozoans, tabulate corals (micheliniids, syringoporids, cladochonids, auloporids) and rugose corals. Most of the corals described here were collected in this facies. The bioherm is toped and flanked by a 5 m-thick coarse bioclastic limestone unit (KY.4). It is overlain by a 25-30 m-thick package of dark shale containing bioclasts (crinoids, corals and brachiopods), which is progressively silty and sandy up-section (KY.5-6). The southern limestone unit olistolith (SLU, Fig. 2 & 3) is a 20-25 m-thick, limestone block, mainly of bioclastic limestone with rare solitary rugose corals (KY.7), overlain by siltstone and sandstone beds (KY.8-9).

The facies analysis and discussions of the sedimentary

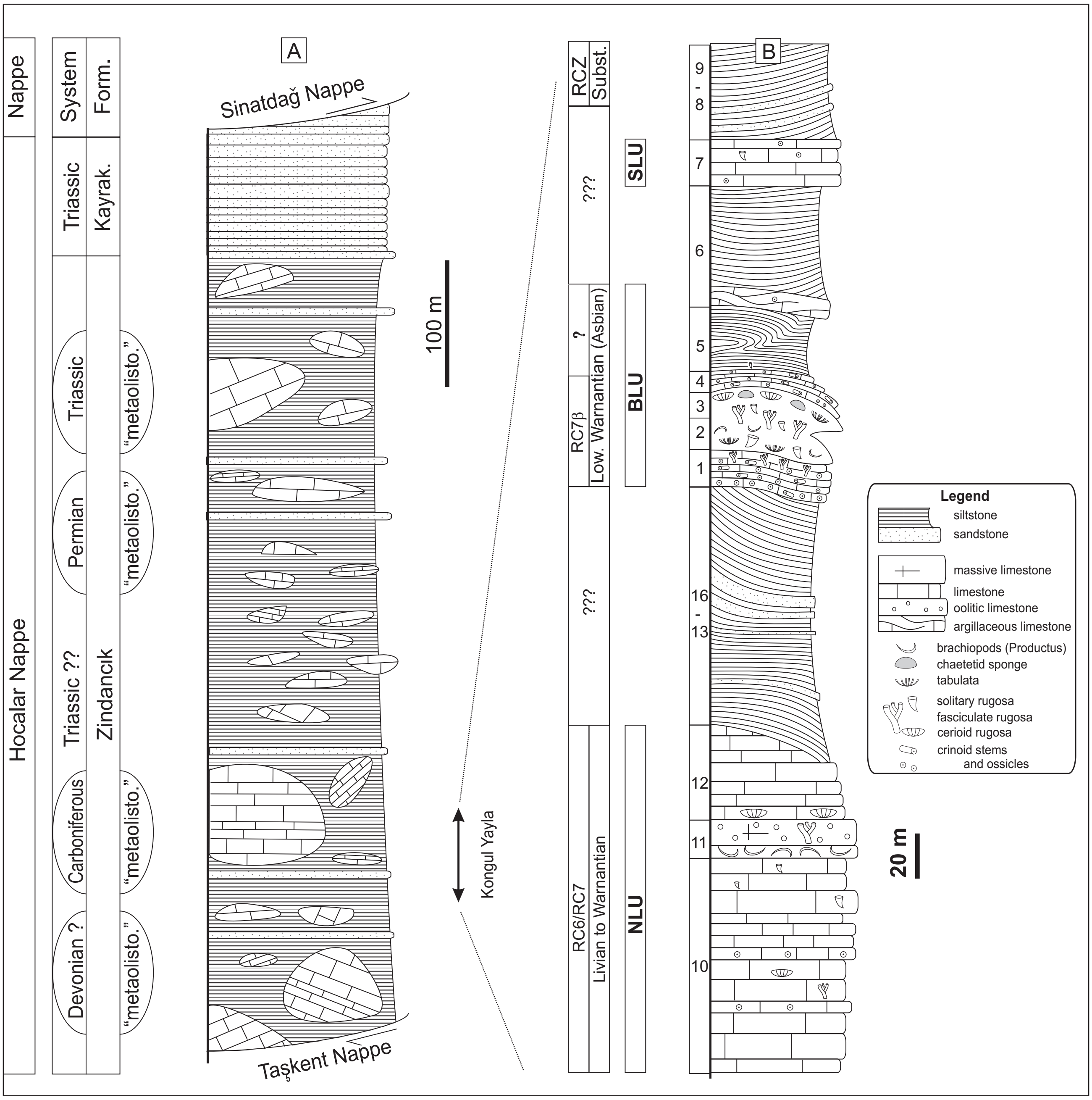

Figure 3. A: Lithostratigraphy of the Zindancık Formation with Carboniferous olistholites in siltstone-sandstone matrix, after Turan (2000). B: Schematic log of the Kongul Yayla section. SLU: southern limestone unit olistolith, BLU: biohermal limestone unit olistolith, NLU: northern limestone unitv. KY1 to KY16 corresponds to lithological units, KY1 to KY4 being the lithofacies of the bioherm. Legend: Kayrak.: Kayraklıtepe Formation; "metaolisto.": "metaolistostomu"(= olistoliths) of Turan (2000); RCZ: Rugose coral zones after Poty et al. (2006); Subst.: Viséan sub-stages (Belgium-British Isles).

and tectonic context are described and discussed in Denayer & Aretz (2011).

2. Systematic Palaeontology

The Mississippian corals of Turkey are very poorly known, especially in the Taurides where only few data are available. The main contribution is Ünsalaner-Kiraglı (1958) describing and figuring some corals, among which *Axophyllum vaughani*, *Clisiophyllum keyserlingi*, *Hexaphyllia* sp. and *Palaeosmilia* sp. coming from the Salahattin-Hadım area. The other taxa described in this paper come from the Eastern Taurides and North-Western Turkey (Zonguldak and Bartın area). The other contributions are very sparse: Frech (1895) described some small solitary undissepimented corals from the Eastern Taurides and Kato described a Viséan caninomorphic coral from the Eastern Taurides.

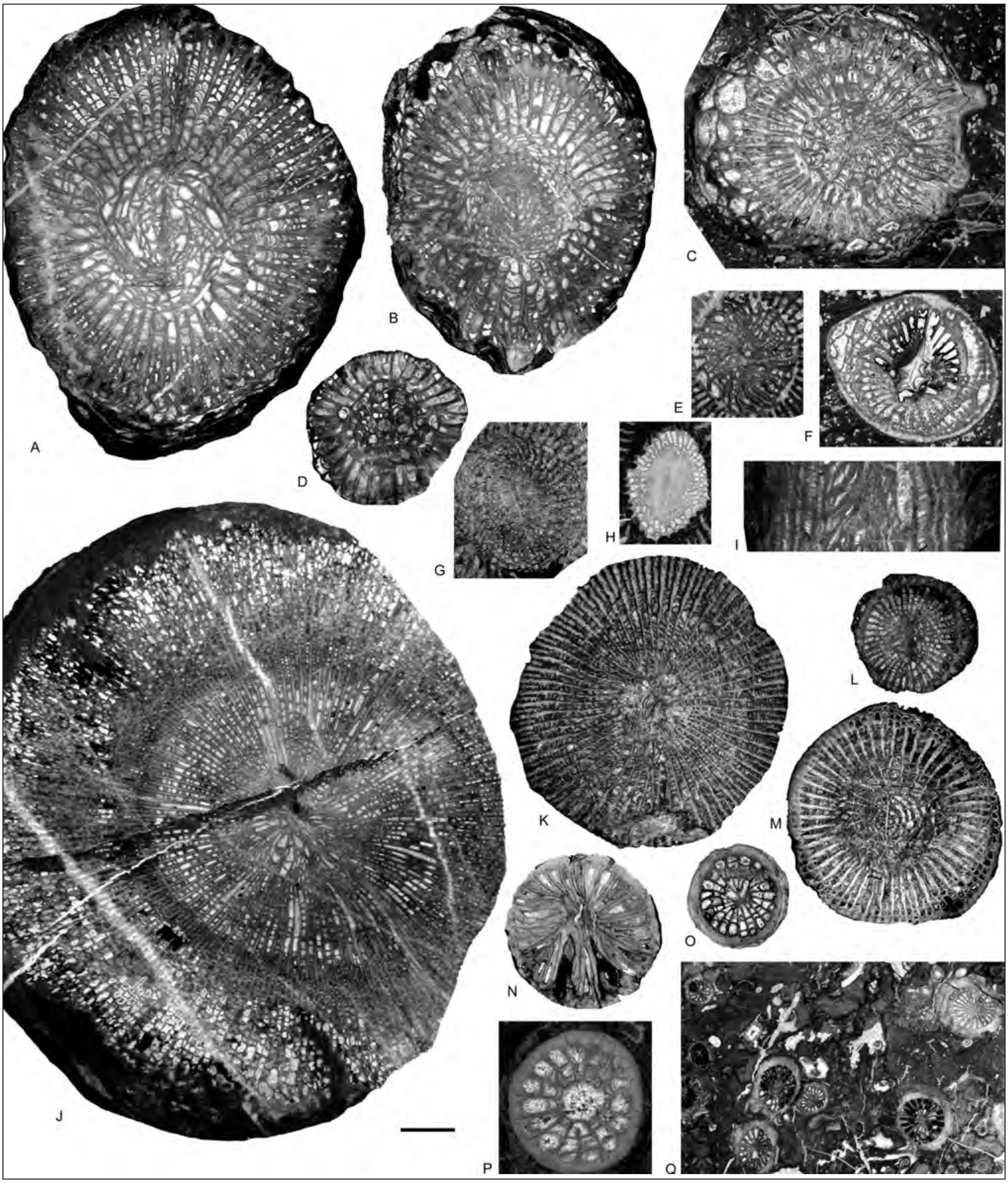

Figure 4. Solitary rugose corals from Kongul Yayla. a-i: *Axophyllum* aff. *pseudokirsopianum.* A-B, D: Successive transverse sections (specimen KY.2.3, x2); C: Mature stage (specimen KY.11.1, transverse section, x2); E: Spiral axial structure (specimen KY.2.10.b, transverse section, x2); F: Juvenile stage (specimen KY.10.2.e, transverse section, x2); G: Dense spiral axial structure (specimen TR.2.2.a, transverse section, x2); H: Dense amygdalophylloid-like axial structure (specimen KY.2.7.b, transverse section, x2); I: (specimen KY.2.3, longitudinal section, x2); J: *Palaeosmilia multiseptata* (specimen KY.2.2.d, transverse section, x2); K: *Palaeosmilia murchisoni* (specimen TR.1.1.I, transverse section, x2); L: *Amygdalophyllum* sp. (specimen TR.3.3, transverse section, x2); M: *Clisiophyllum* aff. *keyserlingi* (specimen KY.8.3, transverse section, x2); N: *Soshkineophyllum* ? sp. (specimen KY.5.1, transverse section, x2); O: *Rotiphyllum densum* (specimen KY.3.12, transverse section, x4); P: *Amplexocarinia* cf. *cravenensis* (specimen KY.8.2, transverse section, x4); Q: Microbial boundstone with gregarious *Rotiphyllum densum* (thin section KY.3.9, x2); Scale bar: 5 mm for all, except P and Q: 2.5 mm, cardinal fossula toward the bottom of the pictures.

The material presented here was collected during summer 2009 in the Taurus Mountains in order to give a preliminary description of the Mississippian coral fauna of Turkey. Many species are represented only by few specimen and the preservation is often very bad (tectonized and fractured rocks). The material is housed in the collections of the Service de Paléontologie animale et humaine of the Université de Liège (Belgium) and are labelled "Taurus 2009 - Kongul Yayla - KY.1.1" to "KY.13.2" and "Taurus 2009 -Tokluca -TR.1.1" to "TR.3.3". The classification follows Hill (1981).

Subclass Rugosa Milne-Edwards & Haime, 1850
Order Stauriida Verrill, 1865
Family Axophyllidae Milne-Edwards & Haime, 1851

Genus *Axophyllum* Milne-Edwards & Haime, 1850

Axophyllum aff. _pseudokirsopianum_ Semenoff-Tian-Chansky, 1974
(Fig. 4 A-I)

*Material.*13 specimens (KY.1.5, KY.2.1, KY.2.3, KY.2.7, KY.2.10, KY.3.11, KY.7.3, KY.10.1, KY.10.2, KY.11.1, KY.11.2, TR.2.2, TR.3.2).

Description. Medium to large solitary coral, conical or turbinate with common rhizoid process. The section of the calice is often elliptical. The mean diameter is 24 mm but usually up to 40 mm, the tabularium diameter varying between 10 and 22 mm. There are 39 major septa in average (max. 54). The major septa are long and thick, their axial ends are sharp or rounded. The minor septa are short to long (up to half the length of the major) and slightly thinner than the major. They enter the tabularium but never more than 1 mm. Major and minor septa are thickened, their maximum thickness is situated in the inner part of the dissepimentarium. The thickening is irregular and gives often a ragged aspect to the septa. Some specimens show a fibrous deposit continuous through the whole interseptal space. The dissepimentarium is made of 3-10 rows of interseptal dissepiments (simple concentric, V-shaped, herringbone, arched and irregular) and 2-5 rows of first and second order transeptal dissepiments. One or two rows (usually the innermost, Fig. 4a) are strongly thickened, continuous with the thickening of the septa. The outermost are long but narrow, except in juvenile stages where the dissepiments are irregular in shape and width. Some specimens show inconstant naotic dissepiments. The axial structure is complex (see below and discussion), always connected to the counter septum and often to the axial ends of other major septa. The axial structure varies in width (2/5 to 1/3 of the diameter of the coral) in shape and in thickening. The number and length of radial lamellae also varies, even in the ontogeny of the specimen. Many axial tabellae are involved in the axial structure, several being thickened. The tabulae are incomplete, axially depressed. There are in average 20 tabulae in 1 cm. The axial tabellae are strongly upturned toward the axis and form with the radial lamellae a strong axial column. In longitudinal section, the dissepiments are large and dip with an angle varying between 40 and 80°.

Discussion. These corals have all the generic features of the genus *Axophyllum* but resembles in some aspects *Gangamophyllum*. They have a very high morphological variability involving all the skeletal elements. For example, the shape of the axial structure, irregular in the juvenile stage, can change to a spiral with a distinct axial lamellae or a symmetrical clisiophyllid axial structure (Fig. 4A-B) or a very thick amygdallophyllid axial structure (Fig. 4G-H) or even to a irregular whorled gangamophyllid axial structure (Fig. 4C-E). The local disappearance of the axial plate is not sufficient to attribute our specimen to *Gangamophyllum* (as wrongly considered by Denayer & Aretz, 2011). Our corals cover the intraspecific variability of *A. pseudokirsopianum*, *A. kirsopianum* and *Axophyllum* sp. A (Semenoff-Tian-Chansky, 1974), but also the interspecific variability between them. The three species considered as distinct by previous authors seem to be the extreme poles of a highly variable group of taxa.

Distribution. *A. pseudokirsopianum* and close species are common in the upper Viséan, particularly in the reefal facies. It is known in Belgium (Poty, 1981), S Spain (Herbig & Mamet, 1985; Herbig, 1986; Gómez-Herguedas & Rodríguez, 2005) and N Africa (Said et al., 2007; Aretz, 2010a). In the Taurides, *A.* aff. *pseudokirsopianum* is known in the Kongul Yayla outcrop (both in the bioherm unit and the southern limestone unit olistolith). Ünsalaner-Kiraglı (1958) reported *A. vaughani* form the Taurides but the figured specimen is close to a juvenile stage of *A.* aff. *pseudokirsopianum*.

Family Palaeosmiliidae Hill, 1940

Genus *Palaeosmilia* Milne-Edwards & Haime, 1848

***Palaeosmilia murchisoni* Milne-Edwards et Haime, 1848**
(Fig. 4K)

See Semenoff-Tian-Chansky (1974), Poty (1981) and Aretz (2010a) for complete synonymy

Diagnosis. Small turbinate to cylindrical *Palaeosmilia* reaching 10 cm in diameter with usually 60-65 major septa (exceptionally up to 90). Many major septa reaching the axis. Narrow cardinal fossula widened toward the axis. Minor septa reaching 2/3 of the radius of the corallite but usually shorter. Incomplete tabulae forming an axial dome depressed in periphery.

Material. One unique badly preserved specimen (TR.1.1).

Description. Solitary corallite, 27 mm large with a tabularium diameter of 21 mm and 60 major septa. The major septa are long but do not reach the axis, creating a zone free of septa in the center, 5 mm wide. The cardinal major septum is shorter, withdrawn in a large fossula. The minor septa are long and enter slightly the tabularium. Minor and major septa are thick in the dissepimentarium, undulating and carinated. The fossula is narrow, open toward the free axial zone. The dissepimentarium shows 5-7 incomplete rows of small concentric dissepiments. Neither the outer part of the dissepimentarium, nor the wall is preserved.

Discussion. This specimen is clearly *Palaeosmilia*. Its dimensions and number of septa corresponds to *P. murchisoni* or to *P. ressoti*. It shares with the latter a large axial zone free of septa. Semenoff-Tian-Chansky (1974) distinguished *P. ressoti* on the base of this zone and on the narrow dissepimentarium. Because our specimen lacks a complete dissepimentarium, it is impossible to estimate its width. Moreover *P. murchisoni* shows occasionally this type of free axial zone (see Poty, 1981). For these reasons we consider our specimen as a small (juvenile?) form of *P. murchisoni*.

Distribution. P. murchisoni is a worldwide common species in the Viséan, particularly in the upper Viséan. In the Taurides, it is known the Kongul Yayla outcrop and reported from the same area by Ünsalaner-Kiraglı (1958).

***Palaeosmilia multiseptata* Semenoff-Tian-Chansky, 1974**
(Fig. 4J)

See Semenoff-Tian-Chansky (1974) for synonymy.

Diagnosis. Large *Palaeosmilia* (up to 50 mm in diameter) with many septa (more than 100 major septa). Minor septa half as long as the major and thinner. Both type of septa thickened, particularly in the inner edge of the dissepimentarium. Fossula large and almost reaching the axis. Axial zone occupied by the axial ends of the septa and upturned tabulae, producing a loose axial structure.

Material. 2 specimens (KY.2.2, KY.1.4).

Description. Large solitary corallite, 72 mm in diameter with a mean tabularium diameter of 30 mm and 110 major septa. The major septa are long and thickened in their median part. Their axial ends grouped into bundles of 5-7 before fusing in the center, creating a weak axial structure in which upturned axial tabulae take part. The cardinal major septum is shorter, withdrawn in a long and narrow fossula. The minor septa are long and enter slightly the tabularium. The outer parts of the septa are carinated and zig-zag-like. The dissepimentarium is composed of 10-15 rows of small simple concentric dissepiments and 10-15 rows of irregular arched and second order transeptal dissepiments. Some naotic dissepiments are also presents.

Discussion. The large dimensions and high number of septa (and thus the low ratio of number of septa/diameter), as well as the weak axial structure created by the axial ends of the septa are characteristic of *P. multiseptata* as defined by Semenoff-Tian-Chansky (1974). It is close to the largest *P. murchisoni* in which a weak axial structure can also appear but the high number of septa is a distinguishing feature.

Distribution. *P. multiseptata* is common in the upper Viséan and lower Namurian of the Béchar Basin (Semenoff-Tian-Chansky, 1974). In the Kongul Yayla, *P. multiseptata* was collected in the reefal facies of the bioherm. Moreover, *P. multiseptata* seems to be characterized, and perhaps restricted to reefal facies (I. Somerville, personal communication, 2012).

Family Aulophyllidae Dybowski, 1873

Genus *Clisiophyllum* Dana, 1846

***Clisiophyllum* aff. *keyserlingi* McCoy, 1849**
(Fig. 4M)

Material. One specimen (KY.8.3) and one fragment (KY.3.6).

Description. Solitary corallite, 22 mm large with a tabularium diameter of 17 mm. There are 45 major septa. Major septa short (no more than 1/4 of the diameter), straight and thickened. Maximum thickness (0.5 mm) reached near the inner edge of the dissepimentarium. Cardinal major septa shorter and counter one longer. Minor septa short (half length of major), thin and undulating. Axial structure typically clisiophyllid-like, with a long axial plate connected to the counter septum and bearing thin undulating radial lamellae connected to the axial ends of the major septa. Upturned axial tabulae taking part to the axial structure. Width of the axial structure reaching 10 mm in diameter. Dissepimentarium composed of 1-3 incomplete rows of small concentric dissepiments, the inner row being slightly thickened. Wall thick (up to 1.5 mm). Tabulae incomplete, laterally depressed in periphery and upturned toward the axis in the central part of the tabularium. There are 10-12 tabulae in 1 cm. Dissepiments small and almost vertical.

Discussion. This specimen belongs to the *C. keyserlingi* group of species although it is quite smaller. Moreover it seems to present some other juvenile characters as the narrowness of the dissepimentarium and the simplicity of the axial structure. In that points, it resembles in some aspect to *C. garwoodi*.

Distribution. *Clisiophyllum keyserlingi* (and related species) is common in the upper Viséan in Belgium (Denayer et al., 2011) S Spain (Rodríguez et al., 2005; Rodríguez and Somerville, 2007), N Africa (Semenoff-Tian-Chansky, 1974; Aretz & Herbig, 2010), Poland (Fedorowski, 1971), S China (Wu, 1964) and NW Turkey (Denayer, 2011). Ünsalaner-Kiraglı (1958) reported *C. keyserlingi* from a locality near Kayseri in the Eastern Taurides. In Kongul Yayla, it was collected in the SLU and BLU limestone unit olistoliths of the Kongul Yayla outcrop.

Genus *Amygdalophyllum* Dun & Benson, 1920

***Amygdalophyllum* sp.**
(Fig. 4L)

Material. One eroded specimen from an isolated block of non reefal facies (TR.3.3).

Description. The specimen is eroded and a large part of the dissepimentarium is missing. The corallite diameter is 12 mm, the diameter of the tabularium is 10 mm and 40 major septa have been counted. The cardinal and counter septa are connected to the axial structure. The other major septa extend almost to the axis but are intercepted by upturned tabulae. The minor septa do not reach the tabularium and thus, very few are preserved. The axial structure is composed of a axial plate, highly thickened, from which extend densely packed radial lamellae toward the axial ends of the septa. Thickened upturned tabulae are also included in the axial structure. Only three rows of simple dissepiments are preserved, the inner one is highly thickened (up to 1 mm).

Discussion. This specimen is very badly preserved and its outer margin is completely eroded at least to the inner part of the dissepimentarium. After the width of the tabularium, the number of septa and the shape of the axial structure, our specimen could be compared to *A.* aff. *nexile* figured by Rodríguez et al. (2001) or to juvenile stage of *A. etheridgei*. It is also very similar to *A.* sp. of Aretz & Herbig (2010) and *A. pachyphylloides* of Semenoff-Tian-Chansky (1974).

Distribution. *Amygdalophyllum* is represented by several species in the upper Viséan in Belgium (Denayer et al., 2011), S Spain (Rodríguez et al., 2005), N Africa (Aretz & Herbig, 2010; Semenoff-Tian-Chansky, 1974), Australia (Pickett, 1966) and Japan (Kato, 1990). In the Taurides, it is only known from a fallen block found in the Kongul Yayla outcrop.

Genus *Espielia* Rodríguez & Hernando, 2005

***Espielia tauridensis* sp. nov.**
(Fig. 5A-E)

Derivation of name. The new specific name refers to the Taurides where the material was found.

Holotype. Colony KY.3.10 (4 thin sections, 1 peel and 1 polish slab).

Paratype. Colony KY.3.7 (7 thin sections).

Type locality and horizon. Kongul Yayla bioherm, near the Kongul Yayla sheep barn, 7 km south of Hadım town, south of Konya, South Turkey. *E. tauridensis* was collected in the microbial facies of the bioherm (upper part, levels KY2-KY3), together with *Palaeosmilia multiseptata* and *Axophyllum* aff. *pseudokirsopianum.* Zindancık Formation, Bolkar Dağı tectonostratigraphic unit, Rugose coral biozone RC7β of Poty et al. (2006), Asbian (lower Warnantian, upper Viséan, Mississipian).

Diagnosis. Small *Espielia* with a mean diameter of 3.9 mm (max. 4.5 mm) and 18 major septa in average (16 to 20).

Description. The large colonies (up to 1 m in diameter, Fig. 5A) are phacelloid with long cylindrical corallites growing parallel to each other. The increase is lateral and non-parricidal. The corallites have a mean diameter of 3.8 mm (3.1 mm for the tabularium) for an average of 18 major septa (max. 20, see Fig. 6). The major septa are long and reach the axis where they are connected to the columella. The minor septa are short (1/2 length of the major) and restricted to the dissepimentarium. Major and minor septa are undulating and thickened in the dissepimentarium, their thickness is maximum near the outer wall. The columella is extremely thickened and sub-circular (0.3-1 mm in diameter) in transverse section. It is always connected to the counter septum and usually to the cardinal one. The other septa join the columella or are connected to it by radial lamellae. There is one (rarely a second) row of simple concentric dissepiments always thickened (0.2 mm), except in juvenile corallites. The wall is thick (0.2-0.4 mm) and straight. The tabulae are incomplete and arranged in two rows: bell-shaped tabulae occupying the axial half part of the tabularium, and depressed horizontal tabulae forming a peripheral gutter. There are 20-24 tabulae in 1 cm. The dissepiments are small (0.5 mm in height and length) and steeply declined (75°-

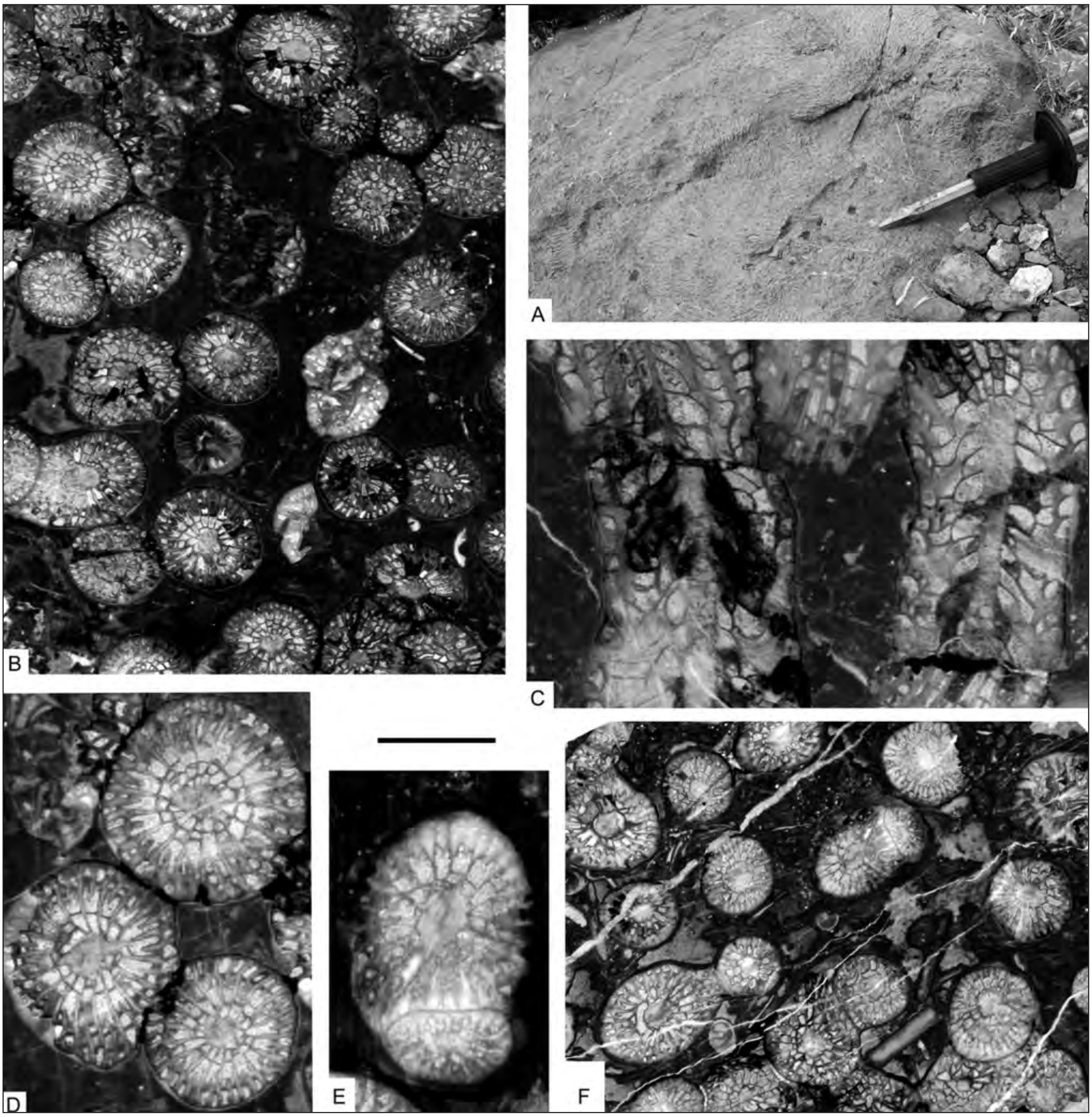

Figure 5. *Espielia tauridensis* sp. nov. from Kongul Yayla. A: Holotype (specimen KY.3.10.a, transverse section, x3); B: Large colonies of *Espielia tauridensis* sp. nov. (view from the field, the chisel is 30 cm long); C: Holotype (specimen KY.3.10, longitudinal section, x3); D: Closer view of the corallites (holotype, specimen KY.3.10.a, transverse section, x6); E: Offset in the holotype (specimen KY.3.10.c, transverse section, x6); E: Paratype (specimen KY.3.7, transverse section, x3). Scale bar: 5 mm for all, except D and E: 2.5 mm.

80°) toward the tabularium. There are 22-24 dissepiments in 1 cm. The variability of the species is not wide and affects mainly the thickening of the septa and dissepiments, and the width of the axial structure. Some corallites are diphymorphic and may develop very rare transeptal dissepiments.

Comparison. These corals belongs to the genus *Espielia* and share its generic features: the circular thick columella, the double rows of tabulae, the thickened septa and the lateral increase. The type-species of the genus, *E. columellata* from the upper Viséan of S. Spain, shows 23-25 major septa for a mean diameter of 6.5 mm (Rodríguez & Hernando, 2005). *Espielia columellata* with similar dimensions is also known from the Asbian of the Béchar Basin, N Africa (Aretz, 2011) and from the Montagne Noire, S France (Aretz, 2002). The Turkish specimen is two times smaller than this species and have less septa. Consequently, the *Espielia* of Kongul Yayla is considered as a new distinct species.

Family Lithostrotionidae d'Orbigny, 1852

Genus *Lithostrotion* Fleming, 1828

Lithostrotion araneum (McCoy 1844)
(Fig. 7D)

See Poty (1981) and Aretz (2010) for synonymy.

Diagnosis. Large *Lithostrotion*, maximum 5.3 mm in tabularium diameter and having 26 to 31 major septa. Minor septa short. Dissepimentarium large, made of numerous rows of simple interseptal, V-shaped, herringbone dissepiments and occasional transeptal dissepiments.

Material. Fragments of two colonies, 60 cm in diameter (KY.13.1 and KY.13.2).

Description. The specimens have a mean tabularium diameter of 6.25 mm for 22 major septa in average (max. 23). The major septa are long, some are connected to the columella, the other show

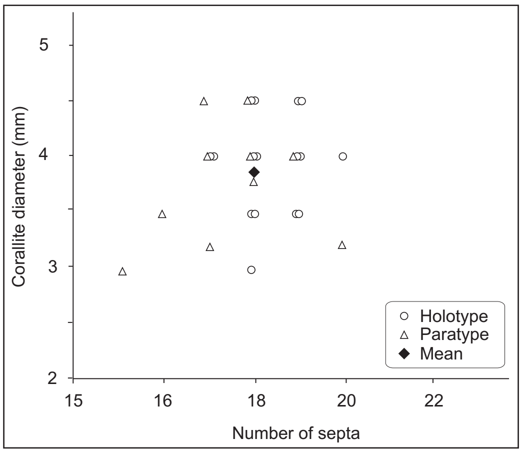

Figure 6. Statistical data for *Espielia tauridensis* sp. nov. Plot of number of septa versus external diameter (analyses on 64 corallites).

usually a slightly curved axial end. They are undulating in the dissepimentarium. The minor septa are short (1/3-1/2 length of the major), thin and undulating. They rarely enter the tabularium. The columella is a simple plate variably thickened (0.5 mm large, 2 mm long). There 4-8 rows of simple, concentric, V-shaped and herringbone dissepiments. The wall is thin (0.2-0.4 mm) and straight.

Discussion. The Turkish specimens are larger than typical Western European *L. araneum* (6.25 mm versus 5.3 mm) but show less major septa (max. 23 versus 28), but these differences are considered to be part of the normal variability.

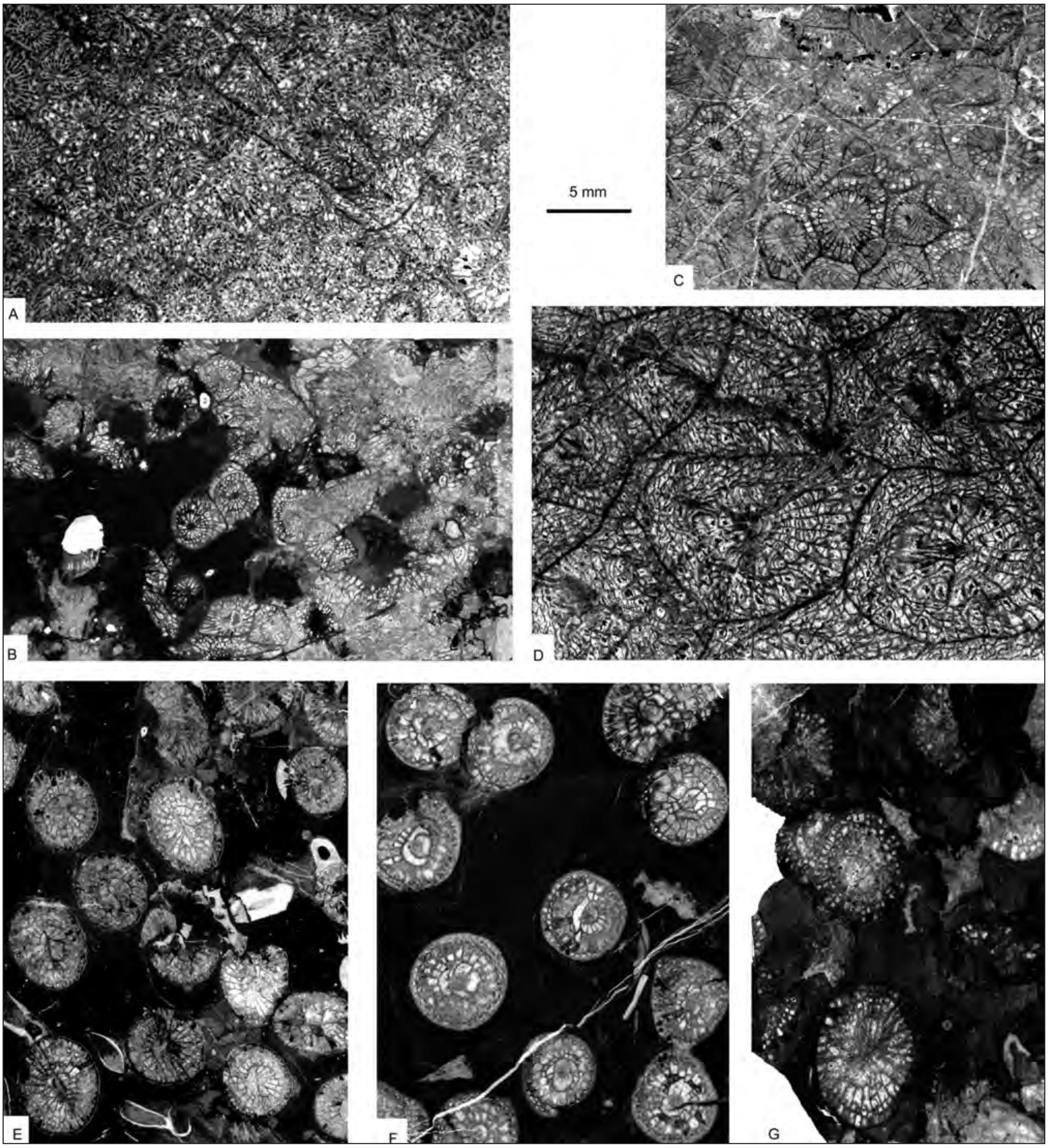

Figure 7. Colonial rugose corals form Kongul Yayla. A: *Lithostrotion maccoyanum* (specimen KY.3.5.a, transverse section, x3); B: *Lithostrotion maccoyanum* showing sub-fasciculate trends and transeptal dissepiments due to sediment fouling on the top of the colony (specimen KY.3.3.b, transverse section, x3); C: *Lithostrotion decipiens* (specimen KYB.2, transverse section, x3); D: *Lithostrotion araneum* (specimen KY.13.2.a, transverse section, x2); E: *Siphonodendron pauciradiale* (specimen KY.1.1, transverse section, x3); F: *Siphonodendron* cf. *intermedium* (specimen KY.2.4.b, transverse section, x3); G: S*iphonodendron irregulare* (specimen KY.1.3.a, transverse section, x3).

Distribution. *L. araneum* is known in the Livian of Belgium, N France, British Isles (Poty, 1981) and in NW Turkey (Denayer, 2011), in the Asbian of S Spain (Gómez-Herguedas & Rodríguez, 2005) and N Africa (Said et al., 2007; Aretz, 2010a). In Kongul Yayla, it is known only form one level (KY.11) topping the oolithic limestone of the NLU.

Lithostrotion decipiens **(McCoy 1849)**
(Fig. 7C)

See Poty (1981) and Aretz (2011) for synonymy.

Diagnosis. Medium-sized *Lithostrotion* maximum 3 mm in tabularium diameter and having maximum 18 major septa.

Material. One colony from an isolated block (KY.B.2).

Description. This single specimen has a mean tabularium diameter of 3.5 mm for 16 major septa in average (max. 19). The major septa are straight, long, usually connected to the columella, but are withdrawn where the columella is absent. The minor septa are long enough to enter the tabularium. The columella is a simple plate variably thickened (0.5 mm large, 1.2 mm long). It is always connected to cardinal and counter septa and often to other septa. There are 2-4 rows of simple dissepiments, the inner usually thickened. Some diphymorphic corallites show unusual irregular transeptal dissepiments. The wall is thin (0.1-0.3 mm) and straight.

Discussion. The Turkish specimens are very similar to typical Western European *L. decipiens* but are slightly larger (3.5 mm in average, *versus* 2.5 mm in Belgian specimens). This difference is not incompatible with intraspecific variability.

Distribution. *L. decipiens* is known in the Asbian of Belgium, N France and British Isles (Poty, 1981; Somerville & Rodríguez, 2007). In Kongul Yayla, it is known in the NLU.

Lithostrotion maccoyanum **Milne-Edwards & Haime, 1851**
(Fig. 7A-B)

See Poty (1981) and Aretz (2010a) for synonymy.

Diagnosis. Small *Lithostrotion* maximum 2 mm in tabularium diameter and having maximum 14 major septa.

Material. Parts of three large colonies, 60 cm in height and more than 1 m in diameter (KY.3.3, KY.3.5 and KY.3.8).

Description. The Turkish specimens have a mean tabularium diameter of 2 mm for 13 major septa in average. The major septa are long, usually connected to the columella, and thickened in the dissepimentarium. The minor septa are short (half length of the major) or longer and enter the tabularium. They are undulating in some corallites. The columella is thick, elliptical (0.3 mm large, 0.5 mm long) and bears small spines. There are 1-3 rows of simple dissepiments, the inner being usually thickened. Some corallites of the border of the colony show several irregular transeptal dissepiments and sub-fasciculate trend. The wall is variable in thickness, 0.15 mm in average but is sometimes thicker and sometimes partly absent. The tabulae are complete and bell-shaped with a peripheral gutter. Rare axial tabellae occur. There are 20-24 tabulae in 1 cm. In longitudinal section, the dissepiments are declined toward the tabularium and their height varies between 0.2 to 0.5 mm. There are up to 30 dissepiments in 1 cm.

Discussion. The Turkish specimens fit with the definition of *L. maccoyanum* as known in Europe. The upper surface of the colony is usually fouled with fine argillaceous material and the corals seem to have fought against this detrial influx (ragged borders, rejuvenescence features, Fig. 7B), some corallites getting a fasciculate trend and a circular section.

Distribution. *L. maccoyanum* is known in the upper Asbian of Belgium and N France (Poty, 1981), British Isles (Rodríguez & Somerville, 2007), S Spain (Gómez-Herguedas & Rodríguez, 2005), S France (Aretz, 2002) and in equivalent strata in N Africa (Said et al., 2007; Aretz, 2010a). In Kongul Yayla, it was collected from the crest facies of the microbial bioherm, upper Asbian in age.

Genus *Siphonodendron* McCoy, 1849

Siphonodendron **cf. *intermedium*** **Poty, 1981**
(Fig. 7F)

Material. 3 fragments of colonies (KY.2.4, KY.B.1 and KY.2.6).

Description. Phacelloid colonies showing small corallites with a mean diameter of 5.8 mm and having 21-23 major septa (max. 26). Major septa long, reaching the axis and connected to the columella. Minor septa short. Columella made of a short axial plate, strongly thickened, elliptical to circular in transverse section. 1-4 (usually 2) rows of small concentric dissepiments. Wall straight and thick (0.8-1 mm). Tabulae complete, bell-shaped or tent-shaped, upturned toward the axis. There are 12-14 tabulae in 1 cm. Dissepiments small (0.8-1.2 mm long, 0.5 mm high) and almost vertically disposed.

Discussion. The specimens are very similar to *S. intermedium* but are smaller and the dissepimentarium is narrower. The strongly thickened columella reminds *Espielia* (particularly *E. columellata* of similar dimensions) but the tabulae are clearly those of *Siphonodendron*.

Distribution. *S. intermedium* is known in the upper Viséan of Belgium, N. France and British Isles (Poty 1981), S. Spain (Rodríguez et al. 2002). The Turkish material was collected in the microbial facies of the bioherm of Kongul Yayla and is upper Asbian in age.

Siphonodendron irregulare **(Phillips, 1836)**
(Fig. 7G)

See Poty (1981) and Aretz (2010) for synonymy.

Diagnosis. Dendroid to phaceloid colonies. Corallites mean diameter 4.5 mm for 21-23 major septa (max. 26). Usually 1 row of dissepiments, but commonly up to 4.

Material. 2 fragments of colonies (KY.1.3 and KY.B.3).

Description. Phacelloid colonies of cylindrical corallites, 5 mm in mean diameter (max. 6 mm) for 20-22 major septa. Major septa long but rarely reaching the axis and connected to the columella. Minor septa long, entering the tabularium on 0.5-0.8 mm. Columella made of a simple axial plate, usually thin, connected to the counter septum, rarely to other. There are 0-1 rows of simple concentric dissepiments, some corallites show another incomplete row.

Discussion. These corals fit with the definition of *S. irregulare*. They are similar but larger than *S. pauciradiale* and have less septa than *S. intermedium*. Unfortunately, their bad preservation does not allow further discussion.

Distribution. *S. irregulare* is known in the upper Livian and Warnantian of Belgium and N France (Poty, 1981), British Isles (Somerville & Rodríguez, 2007), NW Turkey (Denayer, 2011), S Spain (Herbig & Mamet, 1985; Herbig, 1986; Gómez-Herguedas & Rodríguez, 2005) and in equivalent strata in N Africa (Said et al., 2007; Aretz, 2010a). In Kongul Yayla, it was collected in the bioherm, upper Asbian in age.

Siphondendron pauciradiale **(McCoy, 1844)**
(Fig. 7E)

See Poty (1981) and Aretz (2010a) for synonymy.

Diagnosis. Dendroid to phaceloid colonies. Corallites mean diameter 4 mm for 18-20 major septa (max. 22). 1-2 rows of dissepiments, rarely up to 4.

Material. 3 fragments of colonies (KY.1.1, KY.B.1 and KY.B.4).

Description. Phacelloid colonies with small corallites, 4-4.5 mm in diameter and having 18-20 major septa (max. 23). Major septa long, usually reaching the axis but some corallites have withdrawn major septa. Minor septa short, never overcrossing the inner edge of the dissepimentarium. Major counter septa longer, connected to the columella. Columella made of a long axial plate, often undulating, more or less thickened and connected to some of the major septa (usually the peri-counter septa). 1-2 rows of small concentric dissepiments, thickened or not. Wall straight and thick (0.5-1 mm). Tabulae incomplete, dome-shaped, downturned toward the dissepimentarium, forming a peripheral gutter. There are 10-14 tabulae in 1 cm. Dissepiments small (0.7-1 mm long, 0.5 mm high) and strongly downturned toward the tabularium (75°-80°).

Discussion. The Turkish specimens fit with the definition of *S. pauciradiale* as known in Europe. They are close to *S. intermedium* and *S. irregulare* but are smaller and have less septa.

Distribution. *S. pauciradiale* is known in the Warnantian of Belgium and N France (Poty, 1981), in the Asbian of British Isles (Somerville & Rodríguez, 2007), NW Turkey (Denayer, 2011), S Spain (Herbig & Mamet, 1985; Herbig, 1986; Gómez-Herguedas & Rodríguez, 2005) and in equivalent strata in N Africa (Said et al., 2007; Aretz, 2010a). In Kongul Yayla, it was collected in the microbial facies of the bioherm and are upper Asbian in age.
Family Antiphyllidae Iljina, 1970

Genus *Rotiphyllum* Hudson, 1942

Rotiphyllum cf. *densum* (Carruthers, 1908)

(Fig. 4O, 4Q)

Material. Many specimens in gregarious clusters included in microbial texture (KY.3.9, KY.3.12).

Description. Small solitary coral with a mean diameter of 4 mm having in average 17 septa (max. 22). Major septa long and reaching the axis, fusing by group of 4-5 septa before joining the axis, forming a more or less thickened axial structure. Base of the septa thickened, especially in cardinal quadrant. Minor septa not developed but sometimes present in the stereoplasma of the wall. The direction cardinal-counter is shown by the symmetry of the axial structure and sometimes by a shorter cardinal septum withdrawn in the fossula. Alar fossulae present in some specimens but often inconspicuous. Wall extremely thick (0.4 mm in juvenile corallites, up to 1.2 mm in mature).

Discussion. The Turkish specimens are close to *R. densum* by their characters but are smaller (4 mm in average, versus 8-19 mm). They share a very thick wall with *R.* aff. *costatum* figured by Rodríguez & Falces (1994) but are larger.

Distribution. *R. densum* is known in the strata around the Tournaisian-Viséan boundary in Belgium, N France and British Isles (Mitchell et al., 1986), in the Asbian in England (Hudson, 1944) and upper Viséan of S Spain (Rodríguez & Falces, 1994). In Kongul Yayla, *Rotiphyllum* cf. *densum* is present in the upper part of the bioherm, associated with lithistid sponges and microbial boundstone.
Family Laccophyllidae Grabau, 1928

Genus *Amplexocarinia* Soshkina, 1941

Amplexocarinia aff. *cravenensis* Smith, 1955

(Fig. 4P)

Material. One specimen encrusted by microbial mats (KY.8.2).

Description. Small solitary coral, 6.5 mm in diameter for 15 septa. Septa short (2 mm) and thick (0.25 mm) with dilated axial ends. Base thickened, continuous with the wall. No minor septa. Cardinal (?) septum slightly shorter. Aulos incomplete, 2.5 mm in diameter, formed by the axial ends of septa and upturned tabulae. Rare small dissepiments.

Discussion. This coral belongs incontestably to *Amplexocarinia*. It is close to *A. cravenensis* by its dimension and number of septa. The presence of dissepiments also reminds *A. smithi* but the latter is smaller.
Distribution. *Amplexocarinia* comprises species ranging from the Middle Devonian to the Upper Permian. In the Mississippian, *Amplexocarinia* is often found in microbial facies of reefs as in the upper Tournaisian and upper Viséan of the British Isles (Smith, 1925; Bancroft et al., 1988; Mundy, 1994). Our specimen was collected in a blocs with microbial facies, coming from the upper part of the bioherm.

Family Polycoeliidae de Fromentel, 1861

Genus *Soshkineophyllum* Grabau, 1928

Soshkineophyllum? sp.

(Fig. 4N)

Material. 4 specimens, crushed and eroded (KY.5.1, KY.5.3, KY.5.4, KY.5.5).

Description. Large solitary coral with a maximum diameter of 18 mm having in average 32 septa. Major septa unequal in length, the longer reaching the axis and fusing by groups, forming a more or less twisted axial structure. Usually four major septa are thicker and longer than the others, except in highly mature stages. Minor septa short, more developed in the counter quadrants. Minor

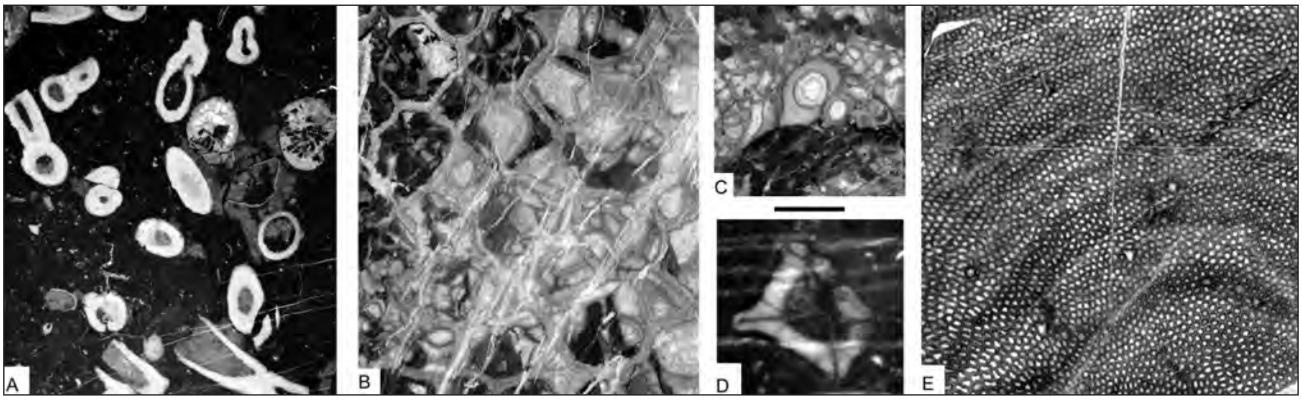

Figure 8. Tabulate corals, Heterocorals and Chaetetidae from Kongul Yayla. A: Cladochonids tabulate coral (specimen KY.1.2, transverse and tangential sections, x2); B: Micheliniid tabulate coral (specimen KY.3.2, transverse section, x2); C: Auloporid tabulate coral covered by stenoporid bryozoan (specimen KY.2.8, transverse section, x6); D: *Hexaphyllia* sp. (specimen KY.3.1, transverse section, x8); E: *Chaetetes* sp. (specimen KY.3.4, transverse section, x4). Scale bar: 5 mm for a and b, 2.5 mm for E, 1.75 mm for C, 1.25 mm for D.

and major septa extremely thick (up to 1.2 mm) and contiguous. Cardinal septum short and thick, withdrawn in a large fossula. The wall is 1.6-2 mm thick.

Discussion. The specimens are attributed to *Soshkineophyllum* with a query because they share with this genus the dominating four major septa, the other septa being of various length, and the reduced development of minor septa in cardinal quadrants. Nevertheless, *Soshkineophyllum* is not so thickened and have rhopaloid major septa. Moreover, the Turkish specimens are very close to Gen. et sp. indet. of Rodríguez & Falces (1992) by having the same septal pattern and dimensions. Aretz (2011) attributed similar taxa to "*Streptelasmina* gen. et sp. unknown". These three taxa are probably the same (same morphology, age and occurrence in similar facies) and seem to belong to a new genus.

Distribution. Gen. et sp. indet. of Rodríguez & Falces (1992) comes from the upper Viséan of S. Spain, Gen. et sp. unknown of Aretz (2011) is from equivalent strata of N. Africa. In Kongul Yayla, *Soshkineophyllum ?* sp. was collected at the base of the shaly unit capping the bioherm.

3. Discussions

3.1. Faunal association

In the bioherm of Kongul Yayla and related facies, four faunal associations of corals and other organisms can be recognized.

1) The bioclastic facies includes all the lateral facies the BLU (flanking facies KY.5, sole facies KY.1). These facies yielded many specimens of *Axophyllum,* and *Palaeosmilia* and, in a lesser abundance, colonies of *Siphonodendron* and *Espielia*. This facies is also very rich in lithistid and calcareous sponges, in bryozoans (fenestellids, fistuliporids, stenoporids, rhabdomesids), brachiopods, gastropods, crinoids, tabulate corals (cladochonids, Fig. 8A) and heterocorals (*Hexaphyllia*, Fig. 8D). The corals are rarely in living position and are mostly reworked and encrusted by other organisms. This first association correspond to B2-Patchy coral meadow (low biodiversity coral meadow) and D1-Bioherm dwellers (moderate biodiversity bioherm environment) in the classification of Aretz (2010a). After Somerville & Rodríguez (2007)'s classification, it corresponds to the Rugose Coral Association RCA2 (*Palaeosmilia-Axophyllum-Clisiophyllum* association) with a moderate biodiversity in low energy wackestone-packstone facies; and to RCA5 (*Dibunophyllum-Axophyllum-Siphonodendron* association) with a moderate biodiversity in low energy wackestone-packstone facies. This association is also typical of the Zones 5 and 6 of Madi et al. (1996), respectively corresponding to the crinoid-fenestellid assemblage and sponge-fenestellid assemblage. Said et al. (2011) described such an association in their Assemblage 2 but the latter is richer and more diversified.

Facies	Main components	Classifications		
		Aretz 2010a	Somerville & Rodriguez 2007	Madi et al. 1996
Bioclastic facies	*Axophyllum* aff. *pseudokirsopianum* *Palaeosmilia multiseptata* *Clisiophyllum* aff. *keyserlingi* *Amygdalophyllum* sp. *Siphonodendron* cf. *Intermedium* *Siphonodendron irregulare* *Siphonodendron pauciradiale* *Espielia tauridensis* cladochonids syringoporids	B2 & D1	RCA2 & RCA5	Zones 5 & 6
Microbial facies	*Axophyllum* aff. *pseudokirsopianum* *Rotiphyllum* cf. *densum* *Amplexocarinia* aff. *cravenensis* micheliniids auloporids heterocorals	D3	RCA6 (part)	Zone 4
Reef-crest	*Lithostrotion maccoyanum* chaetetids	D2	RCA7	
Silts.	*Soshkineophyllum* ? sp.	D2 (part)	RCA8	

Figure 9. Summarized corals associations of the Kongul Yayla bioherm and their equivalents in various classifications. The classification of Aretz (2010a) was established mainly on Western European corals. Somerville & Rodríguez (2007) based their classifications on British and Spanish associations. Madi et al. (1996) based their study on Algerian corals (Béchard Basin). See also Denayer & Aretz (2012) for comparison of facies with other reefs.

2) The microbial framework of the core facies is rich in clusters of small undissepimented rugose corals (*Rotiphyllum, Amplexocarinia*), micheliniid and auloporid tabulate corals (Fig. 8B-C), associated with lithistid sponges and microbial mats. The diversity is lesser and no colonial rugose corals was observed. Similar association of solitary rugose corals standing in microbial texture were described from northern England by Mundy (1994) and in the Béchard Basin by Madi et al. (1996) in their Zone 4 (coral-microbialite assemblage). It corresponds also partly to the D3 (supporting framestone builders) category of Aretz (2010a) and partly to the microbial boundstone association (RCA6) of Somerville & Rodríguez (2007). The coral association 5 described by Said et al. (2011) form the Adarouch area (Morocco) is also very similar.

3) The reef-crest facies composed of large colonies of *Lithostrotion maccoyanum* and chaetetid sponges in upright growth position (Fig. 8E) and rare solitary rugose corals (*Axophyllum*). The biodiversity is also low but the rugose corals and chaetetid sponges form large colonies, up to 80 cm in diameter. They are commonly ragged and show rejuvenescence features, probably due to sediment fouling. It is typically the high energy facies of the capping beds association described as D2 in Aretz (2010a). Somerville & Rodríguez (2007) included such facies in their RCA7 (*Lithostrotion-Siphonodendron* association) characterized by densely packed cerioid colonies, typical of high energy environment. These associations are comparable to the Assemblage 1 of Said et al. (2011).

4) The siltstones facies (KY.5) yielded a monospecific association of solitary rugose coral (*Soshkineophyllum* ? sp.). It is comparable to the level-bottom community A1 of Aretz (2010a) with its low diversity of solitary corals embedded in marly facies. Somerville and Rodríguez (2007) included this association in their RCA8 (*Cyathaxonia-Rylstonia-Rotiphyllum*) typical of low energy environments. Said et al. (2011) described similar association (Assemblage 4) in the Adarouch Area.

The non-reefal associations include the fossiliferous facies of the NLU (oolithic grainstone, bioclastic packstone, etc.) but are not detailed further here. Theses association are dominated by solitary rugose corals (*Axophyllum, Clisiophyllum, Palaeosmilia, Amygdalophyllum*). Colonial corals are locally abundant (*Lithostrotion, Siphonodendron*). Tabulate corals are also common (cladochonids, syringoporids). The diversity is not high but the organisms are usually abundant. Figure 9 summarizes the distribution of corals associations in the bioherm and their equivalent in other classification.

3.2. Biostratigraphy

Based on the identification of a few foraminifers (*Endostafella, Eostafella, Archaediscus, Neoarchaediscus, Permodiscus, Pseudoglomospira, Millerella*), Özgül (1997) and Altıner & Özgül (2001) attributed a Viséan to Serpukhovian age to the Zindancık Formation (considered by this author as a Member of their "Kongul Formation"). Ekmekçi & Kozur (1999) indicated a Moscovian age for the entire formation based on four conodonts (juvenile *of Idiognathodus incurvus*, of *Idiognathodus* ? cf. *suberectus* and of *Neognathodus columbienis* and fragments of *Idioprioniodus* sp.) from one single sampled locality. Turan (2000) identified as well some foraminifers and macrofossils and indicated a Carboniferous age for one olistolith of the Zindancık Formation. Other olistoliths are supposed to be Permian based on the occurrence of microfossils (*Stafella* sp., *Pseudovermiporella* sp., *Nagatoella* sp., *Ungdarella* sp., *Eolasiodiscus* sp., *Baisalina pulchra*). The siltstones are surprisingly supposed to be Triassic but this age is not argued by this author and remains questionably.

The identification of rugose corals allows us to indicate a more precise age. The northern limestone unit olistolith (NLU) provided few corals, among them *Axophyllum* aff. *pseudokirsopianum* and *Lithostrotion araneum*, which both have rather long stratigraphic ranges through the Livian and Warnantian. The NLU is thus not precisely dated. The occurrence of *Siphonodendron pauciradiale* at the base of the biohermal unit (BLU) and of *Lithostrotion maccoyanum* at the top, and without younger fauna, is sufficient to indicate a late Asbian age (RC7β biozone of Poty et al., 2006) of this bioherm. The bioclastic rudstone and (?) parts of the siltstones above the BLU seems to be also Viséan because it yielded *Soshkineophyllum*? sp. which is apparently analogous to yet unnamed taxa from that time slice. Further investigation of foraminifers should allow a more precise dating of each block as well as the whole Zindancık Formation.

3.3. Palaeobiogeography

Despite the preliminary and discontinuous aspect of the sampling, the Kongul Yayla bioherm yielded many taxa useful for palaeobiogegraphy. The occurrence of *Lithostrotion, Siphonodendron, Axophyllum* and *Palaeosmilia* indicates relationships with the Eurasian Fauna. The absence of *Kueichouphyllum* excludes the Bolkar Dağı unit from the "*Kueichouphyllum* zone" of Minato & Kato (1977) extending from eastern Asia up to Iran and neighbouring tectonostratigraphic units of Taurides (in the Aladağ Unit; Kato, 1979). All of the corals genera present in Kongul Yayla are known from similar environments in S Spain: Ossa Morena (Rodríguez & Falces, 1992, 1994; Gómez-Herguedas & Rodríguez, 2005; Rodríguez et al., 2001), Bétic Cordillera (Herbig, 1986), S France (Montagne Noire: Aretz, 2002) and N Africa: Azrou-Khenifra Basin of the Moroccan Meseta (Aretz & Herbig, 2010), Jerada Massif (Aretz, 2010a, 2010b), Adarouch Area (Said & Rodríguez, 2008, Said et al. 2010, 2011), Béchar Basin (Semenoff-Tian-Chansky, 1974) and Algerian Sahara (Aretz, 2011). Like all these regions, the Bolkar Dağı unit belongs to the southern branch of the Western Europe Coral Province of Sando (1990). The absence of typical taxa (e. g. *Kizilia, Dibunophyllum*) indicates that the Kongul Yayla is most similar to the southern part of this palaeogeographic zone (North Africa), but it could be local anomalies based on limited material from these areas (I. Somerville, personal communication, 2012). However, the richness in axophyllids seems to be a typical feature of the Béchar Basin (Semenoff-Tian-Chansky, 1974). Further comparison and additional material should lead to a precise understanding of the palaeobiogegraphical relationship of the Turkish corals.

4. Conclusions

The coral fauna collected in and near the microbial-sponge-bryozoan-coral bioherm of Kongul Yayla in the Taurides includes three genera (seven species) of colonial rugose corals, seven genera of solitary rugose corals, and additional tabulate corals and heterocorals. The colonial corals are dominated by *Siphonodendron* (*S. irregulare, S. pauciradiale* and *S.* cf. *intermedium*) and *Lithostrotion* (*L. araneum, L. decipiens* and *L. maccoyanum*). *Espielia tauridensis* sp. nov. is described here for the first time. Among the solitary corals, *Axophyllum* aff. *pseudokirsopianum* and *Palaeosmilia multiseptata* are the most common. *Clisiophyllum* cf. *keyserlingi, Amygdalophyllum* sp., *Palaeosmilia murchisoni, Amplexocarinia* aff. *cravenensis, Rotiphyllum densum* and *Soshkineophyllum* ? sp. are the other solitary corals. The tabulate corals are represented by cladochonids, syringoporids, micheliniids and auloporids. This coral assemblage and particularly the guide taxa *L. maccoyanum* and *S. pauciradiale* indicate a late Asbian (lower Warnantian) age (RC7β biozone, upper Viséan). The coral fauna is very similar to the assemblages known in the Asbian strata of S. Europe and N. Africa belonging to the southern branch of the Western Europe Coral Province of Sando (1990).

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Late Viséan to Early Serpukhovian Rugose Corals from the Yashui Section, Guizhou, South China

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ABSTRACT. Abundant rugose corals are recorded in the Yashui Section in Huishui County of Central Guizhou, South China. The section is mainly composed of light-coloured bioclastic limestone with intercalations of some beds of dolomitized limestone and punctuated by a certain number of unconformities. Totally 20 species belonging to 13 genera are recognized. The composition of the fauna shows resemblance to the Western European faunas of latest Viséan to early Serpukhovian age. Many well-known European taxa such as *Dibunophyllum bipartitum*, *Palaeosmilia murchisoni*, *Lithostrotion decipiens*, *Siphonodendron pauciradiale* and *Aulina rotiformis* appear in Yashui, but with different stratigraphic ranges. There are also some endemic taxa such as *Arachnolasma sinense*, *Yuanophyllum kansuense*, *Kueichouphyllum sinense* and *Stylostrotion petalaxoidae* which can be used for correlations throughout South China. The coral diversity of the Yashui section shows: (1) a diversity decrease in the uppermost part of the Viséan, and (2) a poorly renewed fauna in the Serpukhovian, which is the similar pattern recorded in Palaeotethys. Therefore, a coral based biostratigraphic succession to separate the early Serpukhovian from latest Viséan is difficult to establish. Among the 20 species, 18 are described and illustrated, including 2 in open nomenclature. Two species are omitted from the description due to their bad preservation.

KEY WORDS: Rugose corals, Biostratigraphy, Mississippian, Viséan-Serpukhovian boundary.

1. Introduction

Mississippian rugose corals are relatively diversified and have received much attention in the past decades. Generalized distributional patterns and biostratigraphic successions of the Mississippian rugose corals have been developed and summarized (e.g. Sando, 1990; Sando & Bamber, 1985; Fedorowski, 1981; Mitchell, 1989; Poty et al., 2006; Somerville, 2008). In general, limited information on the temporal and spatial distribution of rugose corals is available for the Serpukhovian. This is probably due to the decrease in coral occurrences caused by sudden change of sedimentary facies from carbonate to siliciclastic near the Viséan/Serpukhovian boundary (Poty et al., 2006) or/and frequent appearances of subaerial exposure surfaces in shallowing-upwards cycles (Smith & Read, 2000; Al-Tawil et al., 2003). These lithofacies changes are probably linked to global scale glacial and tectonic events. As a result, the rugose corals are often rare in Serpukhovian strata, and furthermore, it is relatively difficult to recognize the Viséan/Serpukhovian boundary by rugose corals.

During the Mississippian, South China had a tropical archipelago layout (Scotese et al., 1979; Scotese & McKerrow, 1990; Torsvik & Van der Voo, 2002). The Mississippian in

Yu(1931)		Wu (1964)			Lo (1984)			Xu and Poty (1997)		Poty et al. (2006)	
Visean	Y.	Visean	Y.	*Lophophyllum lophophylloides*	Nam.	Y.	*Aulina carinata*	Visean	*Yuanophyllum*	Serp.	*Yuanophyllum*
				Neoclisiophyllum yengtzeense-Koninckophyllum stelletum	Visean					Visean	
				Arachnolasma sinense-Heterocaninia tholusitabulata			*Heterocaninia tholusitabulata*				
				Thysanophyllum.-Kueichouphyllum sinense							
	T.						*Thysanophyllum asiaticum*		*Thysanophyllum (Dorlodotia)*		*Dorlodotia*
								Tournaisian	Interval zone		Interval zone
Tournaisian	P.	Tournaisian		P.	Tournaisian		*Pseudouralinia gigantea*		*Keyserlingophyllum*	Tournaisian	*Keyserlingophyllum*
									Uralinia tangpakouensis		*Uralinia tangpakouensis*
									C-U interval zone		C-U interval zone
							Cystophrentis kolaohoensis	Famenian		Famenian	C.
	C.			C.							
							Caninia dorlodoti				*Eocarinophyllum yizhangensis*
							Ceriphyllum elegantum				

Table 1. Mississipian coral zonations in China. *C.: Cystophrentis*; *P.: Pseudouralinia*; *T.: Thysanophyllum*; *Y.:Yuanophyllum*; *U.: Uralinia*; Nam.: Namurian; Serp.: Serpukhovian.

most parts of South China consists of shallow-water carbonates intercalated with some terrigenous clastics. Abundant rugose corals occur in the Mississippian, especially in Tournaisian and Viséan strata, which have been intensively studied, starting with the early taxonomic work of Yabe & Hayasaka (1915, 1920) and Grabau (1922, 1928). Yu (1931, 1933, 1937) proposed the first biostratigraphic zonation of rugose corals of the Fengningian System (= Lower Carboniferous) on the basis of collections from southern Guizhou, central Hunan and western Gansu (with additional data by Chi, 1931, 1935). Within the Fengningian System, he established four rugose coral zones in ascending order which are *Cystophrentis* zone, *Pseudouralinia* zone, *Thysanophyllum* zone and *Yuanophyllum* zone. This biostratigraphic zonation has been applied in other parts of South China (Wu, 1964; Luo, 1984; Xu & Poty, 1997; Poty et al., 2006) with some modifications (Table 1). However, despite the relative frequent occurrences of rugose corals during the Mississippian, the resolution of the zonation is still rather low, e.g. the *Yuanophyllum* zone covers a very long range from the middle Viséan to the Serpukhovian.

The main aim of this paper is to describe and illustrate the coral fauna from the Yashui Section in Huishui County of Central Guizhou, which displays a continuous succession from the Upper Viséan through the entire Serpukhovian in shallow water facies.

2. Geological setting and materials

In the Carboniferous, a large carbonate platform developed on the Yangtze Block (South China), with the Upper Yangtze Old Land to the northwest and the Cathaysia Old Land to the east, together with numerous small intra-continental basins in the western part. The northern part of the Guizhou province belongs to the southern Upper Yangtze Old Land. The Carboniferous sediments in central and southern Guizhou can be subdivided into three distinctive lithostratigraphic regions representing carbonate platform to slope-basin: the Dushan-Weining region, the Puan-Mawei region, and the Langdai-Luodian region.

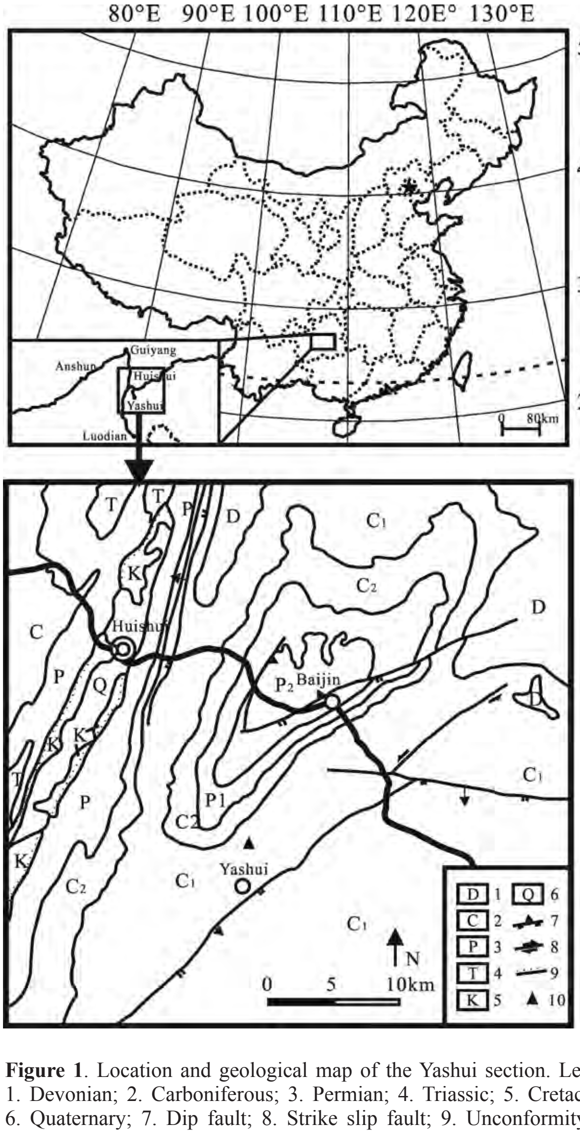

Figure 1. Location and geological map of the Yashui section. Legend: 1. Devonian; 2. Carboniferous; 3. Permian; 4. Triassic; 5. Cretaceous; 6. Quaternary; 7. Dip fault; 8. Strike slip fault; 9. Unconformity; 10. Location of the section (GPS 26°00′47.6″N, 106°45′28″E).

The Yashui section is located in the south-eastern part of the Huishui County, about 90 km south of the city of Guiyang (Fig. 1). It is mainly composed of light-coloured bioclastic limestone with intercalations of some beds of dolomitized limestone, which is typical for the Dushan-Weining lithostratigraphic region. A certain number of unconformities associated with palaeokarst features and terrigeneous clastic deposits that should be considered as palaeosol punctuate the section. Most of the limestone beds of the section are rich in fossils such as corals, brachiopods, chaetetid sponges, foraminifers and calcareous algae.

The Yashui section was first presented during the 11th International Congress on the Carboniferous stratigraphy and geology in 1987. It was selected as the stratotype of the local Chinese stage Dewuan (Wu, 2003). Although the section is a typical representative of the shallow water carbonate facies, it has not been studied in detail in terms of sedimentological and paleontological aspects. Wu (2003) and Wu et al. (2009) published some data of foraminifers from Viséan/Serpukhovian boundary interval, but only few specimens were illustrated. A more recent study on foraminifers in the Yashui section by Groves et al. (in press) uses the first appearance datum (FAD) of *Janischewskina delicata* to suggest a provisional Viséan/Serpukhovian boundary at 41.6m from the base of the section. Other fossil groups have not been studied yet from the section.

The Yashui section was measured in 2008 and permanent markers (metal pins) have been installed throughout the whole section meter by meter. Rugose corals were sampled for the first time in 2008 and were additionally sampled in 2010 and 2011. All specimens were numbered by the true thickness from the base of the section. The material presented in this study is from the collections of the first sampling, which includes nearly 300 thin sections made from 68 specimens.

3. Composition of rugose coral fauna and discussion

20 rugose species belonging to 13 genera of the families Aulophyllidae, Lithostrotionidae, Palaeosmilidae and Axophyllidae were identified. Seven genera are solitary and six are colonial. In the latter group, three genera are massive and three are fasciculate. The rugose coral association is composed of several endemic taxa and more abundant taxa known in the Palaeotethys. The common abrasion of the dissepimentarium of solitary corals and the fragmentation of the compound corals indicates a shallow water environment with relatively high energy.

Most of the rugose samples were collected from the lower part of the Yashui section (0-25 m). Locally, corals are concentrated at the bottom or top of limestone beds. The rugose coral association in the lower part of the section is dominated by large dissepimented solitary corals such as *Palaeosmilia murchisoni*, *Kueichouphyllum sinense*, *Axophyllum* cf. *lonsdaleiforme*, *Arachnolasma sinense*, *Dibunophyllum bipartitum* and "*Dibunophyllum*" *tingi*, accompanied by some colony fragments of *Siphonodendron pauciradiale*, *Diphyphyllum fasciculatum* and *Palastraea* sp. (Fig. 2). *Aulina rotiformis* is not present in the first sampling from the lower part, but it was found 6 m below the base of the measured section based on the preliminary observation of the later samplings. The occurrence of *Palastraea*, *Dibunophyllum bipartitum*, *Siphonodendron pauciradiale* and *Aulina rotiformis* indicate a late Viséan and early Serpukhovian age. Similar association can be found in zone RC8 (Belgium, France) and RC9 (South France, Poty et. al., 2006), faunal divisions H-K in Britain (Mitchell, 1989) and the upper Viséan in North Africa (Aretz, 2010, 2011).

In the middle part of the Yashui section (25-35 m), the abundance of colonial corals increases rapidly with a dominant

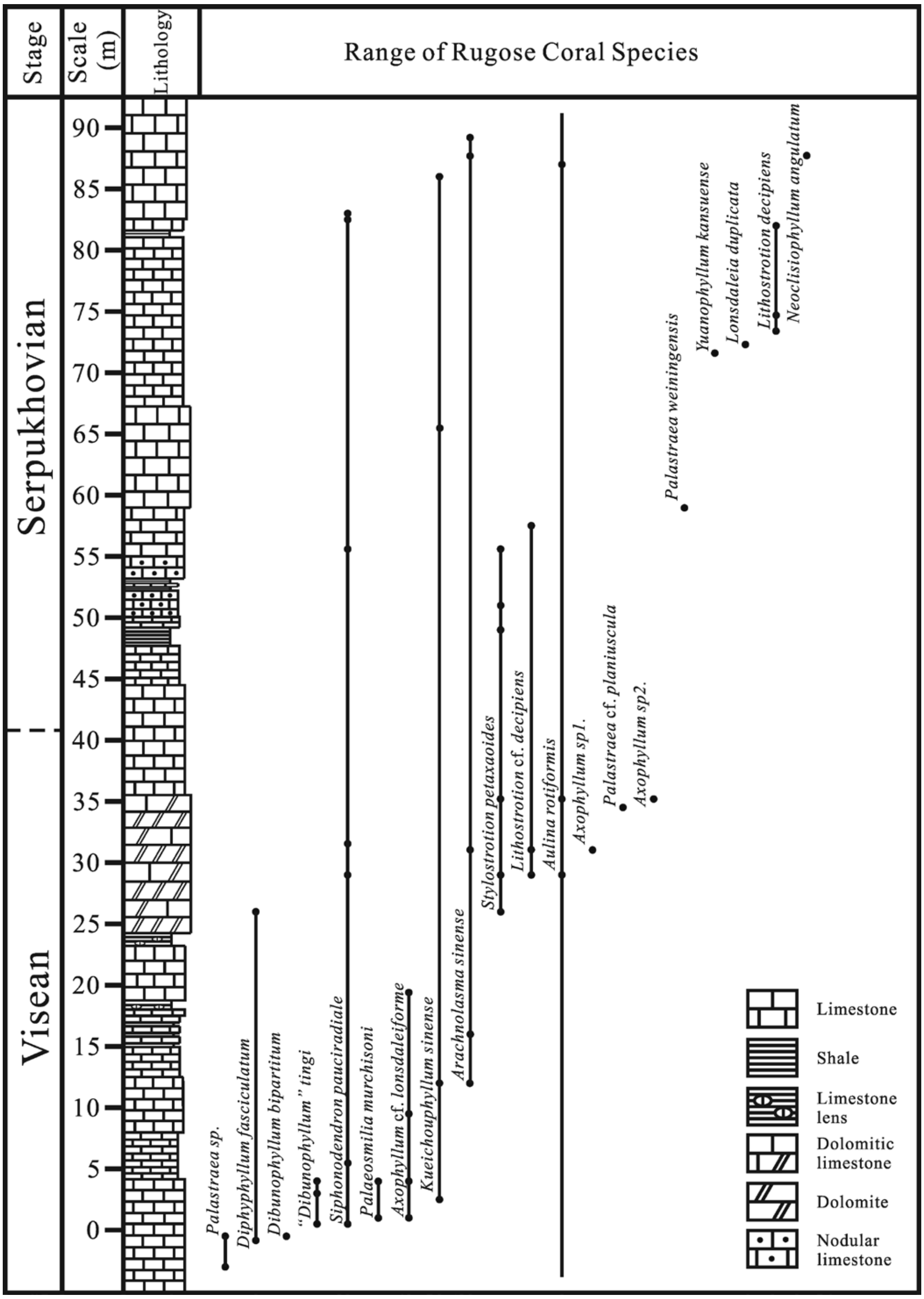

Figure 2. Vertical range of rugose corals from the Yashui section.

occurrence of *Stylostrotion petaxaoides* and *Siphonodendron pauciradiale* in several coral beds. They are often preserved as broken branches. Other associated rugose corals are some small colonies of *Lithostrotion* cf. *decipiens*, *Aulina rotiformis*, and *Palastraea* cf. *planiuscula*, together with some badly preserved *Axophyllum* and *Arachnolasma sinense*. It is important to note that *Aulina rotiformis* is known from the lower Namurian in Britain (Hill, 1940; Smith & Yu, 1943), but already in the uppermost Viséan of South China (Poty et al., 2011) and in the Yashui section.

Coral abundance decreases slightly in the upper part of the Yashui section (above 35 m). *Palastraea weiningensis*, *Yuanophyllum kansuense*, *Lonsdaleia duplicata*, *Lithostrotion decipiens* and *Neoclisiophyllum angulatum* are for the first time recorded in the section (Fig. 2). *Siphonodendron pauciradiale*, *Kueichouphyllum sinense* and *Arachnolasma sinense* have already been found in the underlying beds. *Lonsdaleia duplicata* occurs fairly late in the Yashui section compared to Western Europe (Poty et al., 2011). In Belgium (Poty et al., 2006) and Britain (Mitchell, 1989), it is the index fossil for the latest Viséan. The genus *Yuanophyllum,* represented by *Yuanophyllum kansuense*, also occurs very late in the Yashui section. Elsewhere in South China it is known from the middle Viséan onward (e.g. Wu, 1964; Wu & Zhao, 1989; Yan 1982). In most parts of Western Europe the Viséan-Serpukhovian boundary is usually marked by a prominent change in the sedimentation style (from carbonate dominated to siliciclastic dominated) resulting in the total disappearance of rugose corals in the lower Serpukhovian. In places where carbonate deposition persisted, a decrease in rugose coral diversity can be seen around the Viséan-Serpukhovian boundary. Earliest Serpukhovian coral associations comprise mainly taxa from late Viséan and only some new taxa, which established the rugose coral Zone 9 of Poty et al. (2006). On the East European Platform and in the Urals, Hecker (2001) defined a Serpukhovian coral assemblage characterized by the appearance of *Turbinatocaninia*, *Actinocyathus borealis* and *Paralithostrotion*. The Yashui section shows similar patterns for the coral diversity around the Viséan/ Serpukhovian boundary to the western Palaeotethys: (1) a diversity decrease in the uppermost part of the Viséan, and (2) a poorly renewed fauna in the Serpukhovian.

Aulina rotiformis, though not present in the first collections concerned in this paper, is found as high as 120 m above the base of the Yashui section based on the preliminary observation of later samplings. Since its range covers the whole Yashui section which represents the time interval from uppermost Viséan to early Serpukhovian, it is not as usefully marking the Viséan/Serpukhovian boundary in South China as in Britain. In fact, the exact FAD of *A. rotiformis* in Europe is not well known (see Hill, 1940). In Central Hunan, South China, *Aulina rotiformis* was also found together with many other Viséan rugose corals (Wu, 1964). Thus the FAD of *A. rotiformis* in South China is confirmed as the uppermost Viséan

4. Systematic description

Nearly all the samples collected from the Yashui section are embedded in limestone blocks and lack well-preserved external structures. Therefore, the external characters will not be described in this paper. Among 20 recognized species, 18 are described and illustrated. The other two species are too badly preserved and are not described here. Specimens are housed in the palaeontological collection of the Nanjing Institute of Geology and Palaeontology (China Academy of Science), under numbers YSR-.

Suborder Aulophyllina Hill, 1981
Family Aulophyllidae Dybowski, 1873
Subfamily Clisiophyllinae Nicholson, 1889

Genus *Neoclisiophyllum* Wu, 1963

***Neoclisiophyllum angulatum* Wu & Zhao, 1989**
(Pl.1, Figs A-B)

Material. One specimen: YSR-87.7-1-1. One transverse section (ts) and one longitudinal section (ls).

Description. Solitary coral. In transverse section, corallum oval in shape, with a longer axis of 24 mm. 45 septa in two orders. Major septa thin in the dissepimentarium and thickened in the tabularium. The axial ends of some major septa bend to one side and connect to the axial column margin. Minor septa about 1/3 length of major septa. Axial structure occupies 1/3 of the coralla diameter, consisting of a straight median plate with 3.5 mm in length, 37 septal lamellae and numerous concentrically arranged axial tabellae. Dissepiments concentric or herringbone, with the innermost series dilated. Cardinal septum short. Cardinal fossula distinct and narrow.

The longitudinal section does not strictly pass the axial centre. Axial tabellae steeply ascend to the axis. Periaxial tabellae slightly convex, gently descend to the tabularium. Usually there are 6 tabellae per 5 mm. Dissepimentarium partly preserved. Dissepiments convex, deeply incline towards the centre and various in size.

Subfamily Dibunophyllinae Wang, 1950

Genus *Dibunophyllum* Thomson & Nicholson, 1876

***Dibunophyllum bipartitum* (McCoy), 1849**
(Pl. 1, Figs C-D)

Material. One specimen: YSR-(0.5)-1-1; (3 ts, 1 ls).

Description. Large solitary coral. In transverse section, corallum nearly circular, with a diameter of 28 mm. 48 septa of each orders. Major septa thick and thinning at axial ends. Minor septa thin and short, sometimes discontinuous. Axial structure occupies about 1/3 of the coralla diameter. Median plate thin, slightly thickened in the middle. Septal lamellae semi-radially arranged 9, in number, mostly intercept by the axial tabellae and not connected with the median plate. Tabularium wide, about 1/2 of corallite diameter. Dissepiments herringbone.

In longitudinal section, the boundary of the axial column is distinct from the periaxial tabellae. In inner tabularium, the large vesicular tabellae steeply ascend to the median plate. In periaxial area, the tabellae incline gently to the margin, sometimes becoming concave near the dissepimentarium. There are 8 tabellae per 5 mm. Vesicular dissepiments various in size, counting 7-9 rows.

Discussion. Dibunophyllum bipartitum has a very wide intraspecific variation (Hill, 1938-1941; Poty, 1981). This species has been reported from other locations of China, some of them may not strictly in accordance with the diagnosis of *Dibunophyllum*, or their assigning is not very convincing due to poor photographing and simple description.

"*Dibunophyllum*" *tingi* (Yu, 1933)
(Pl. 1, Figs E-G)

Material. Four specimens: YSR-0.5-1-1, YSR-3, YSR-4-1-1 and YSR-4-2-1; (11 ts, 6 ls).

Description. Large solitary coral. 44 and 48 septa in two orders, at diameter of 20 mm and 28 mm. Major septa thickened in the middle, bending to one side at axial ends. Minor septa never extend beyond the tabularium. Both series of septa become flexuous near the wall. The spider-web-like axial column occupies about 1/3 of corallite diameter. Median plate dilated in the middle, straight or slightly curved, with short "spines" at both sides. Septal lamellae 6-8 in each side of median plate, some discontinuous and become series of spines on the axial tabellae. Dissepimentarium broad, about 1/2 of corallite diameter. Dissepiments concentrically arranged or herringbone when minor septa are short.

In longitudinal section, axial tabellae ascend towards the columella. Periaxial tabellae horizontal or slightly concave, sometimes incomplete and large vesicle shaped, numbering 6-8 per 5 mm. Dissepiments vesicular shape, large, elongated and incline steeply at axial side and small, globose at adaxial side.

Discussion. The appearance of "spines" at each side of median plate is the diagnostic character of this species. The specimens from Yashui differ from Yu's specimens in having much thicker median plates. Though originally assigned to *Dibunophyllum*, this group of rugosa might be a whole new genus. They differ from the typical *Dibunophyllum* in that the latter usually has a long, thin median plate and rudimentary or none minor septa.

Distribution: Uppermost Viséan. At 0.5 m, 3 m and 4 m of the Yashui section.

Genus *Arachnolasma* Grabau, 1922

***Arachnolasma sinense* (Yabe & Hayasaka, 1920)**
(Pl. 1, Figs H-I)

Material. Five specimens: YSR-12-1-1, YSR-16-1-1, YSR-31.2, YSR-87.7-2 and YSR-89.2; (12 ts, 5 ls).

Description. Solitary coral. In transverse section, coralla circular, with diameter of 14-17 mm. 34-26 septa in two orders. Major septa thickened in the middle, attenuating at both ends, slightly flexuous. Minor septa short, about 1/4-1/3 length of major septa. Axial structure occupies 1/5 of the diameter of corallite, consisting of a lens shaped median plate, irregularly arranged septal lamellae and axial tabellae. Dissepiments angulo-concentrically arranged, with the innermost series thickened.

In the longitudinal section, the incomplete, vesicular tabellae ascend to the thick median plate, numbering 7 per 5 mm. Dissepiments 3-6 rows, various in size, inclining steeply towards the tabularium. The innermost series thickened and nearly vertical.

Discussion. The specimens from Yashui are smaller in size and less in septa number than the holotype (Yabe & Hayasaka, 1920; Grabau, 1922), and specimens from Guizhou (Yu, 1933), Poland (Fedorowski, 1971) or Spain (Rodríguez et al., 2001).

Genus *Yuanophyllum*Yu, 1931

***Yuanophyllum kansuense* Yu, 1931**
(Pl. 1, Figs J-K)

Material. Three specimens: YSR-71.6-1-1, YSR-71.6-1-2 and YSR-71.6-1-3; (8 ts, 5 ls).

Description. Solitary coral. Wall of the coralla are missing in many transverse sections due to abrasion. The diameter of the preserved part is not less than 30 mm in mature stage. 46-52 septa in two orders. Major septa thin in the dissepimentarium, thickened in tabularium and attenuate adaxially. Minor septa are fairly short, about 1/5 length of major septa. Median plate thickened in younger stage and thin in mature stage, sometimes connect with the counter septum. Cardinal septum shortened and an open cardinal fossula can be observed. Dissepimentarium broad, with width of 1/2 length of major septa. Dissepiments mostly herringbone or angulo-concentric. Thick layer of stereoplasm coat the innermost series, more obvious in counter quadrant.

In longitudinal section, tabulae incomplete, ascend (more steeply and densely arranged in the axial area) towards the flexuous, sometimes discontinuous columella, numbering 7-10 per 5 mm in the axial part and 4-7 per 5 mm in periaxial part. Dissepiments large, elongated, vesicle shape and incline steeply adaxially. The innermost row nearly perpendicular.

Discussion. The specimens from Yashui are more complex in axial structure compared with the holotype (Yu 1931, 1933). Yu (1937) observed that the axial structure of this species differs considerably in transverse section in different individuals due to irregular arrangement of elongated major septa and tabellae in axial area. Thus the Yashui specimens can be assigned to *Y. kansuense*. Sometimes, the transverse section of this species may resemble *Arachnolasma*, but the latter has a much thicker or oval shaped columella which normally is not connected with the counter septum in mature stage.

Subfamily Heterocariniinae Hill 1981

Genus *Kueichouphyllum* Yu, 1931

***Kueichouphyllum sinense* Yu, 1931**
(Pl. 1, Figs L-M)

Material. Four specimens: YSR-2.4, YSR-12-1-2, YSR-65.5 and YSR-86.2; (10 ts, 5 ls).

Description. Large solitary coral. Wall was missing in all thin sections due to abrasion. 137 septa in two orders in a relatively well preserved specimen with a corallite diameter of 48 mm. Major septa long, thin in dissepimentarium, thickened in the tabularium of cardinal quadrant. Some major septa reach the centre and are flexuous at their axial ends. Minor septa about the 1/3 length of major septa, not extend into the tabularium. Dissepimentarium occupies about 1/5 of diameter of the corallite. Dissepiments dense, concentrically arranged. Cardinal fossula closed, not very prominent.

In longitudinal section, tabular incomplete, large vesicle shaped and slightly ascend to the centre. Dissepiments mostly uniform, incline more steeply inward, numbering 13-15 rows. The innermost series nearly upright.

Discussion. This species strongly resembles *Heterocaninia tholusitabulata* Yabe & Hayasaka, 1920 except the latter has much shorter minor septa. This species also differs from another species of same genus, *K. heishikuanense*, in having (1) a broader dissepimentarium, (2) thickened major septa in cardinal quadrant.

Family Palaeosmiliidae Hill, 1940

Genus *Palaeosmilia* Milne-Edwards & Haime, 1848

***Palaeosmilia murchisoni* Milne-Edwards & Haime, 1848**
(Pl. 1, Figs N-O)
Material. Two specimens: YSR-1-1-2 and YSR-4; (4 ts, 3 ls).

Description. Solitary coral. In transverse section, coralla circular. 71-74 septa in two orders and a diameter of 30-33 mm. Major septa long, straight or slightly sinuous, reach the centre and curved at the axial end. Minor septa about 1/2 length of major septa, extend beyond the dissepimentarium. Dissepiments mostly concentrically arranged. Cardinal fossula narrow, prominent in one specimen (YSR-1-1-2) but not in another one.

In longitudinal section, tabularium occupies 2/5 of the corallites diameter. Tabulae incomplete, depressed in the axis and upturned at edges. The boundary between tabularium and dissepimentarium not very distinct. Dissepiments globose or elongated, incline more steeply towards the axis, 15-16 rows.

Genus *Palastraea* McCoy, 1851

***Palastraea* cf. *planiuscula* Wu & Zhao, 1989**
(Pl. 1, Figs P-Q)

cf. 1989 *Palastraea planiuscula*, Wu & Zhao: p. 103, pl. XXI, figs. 4a-b, 6a-b.

Material. One colony fragment: YSR-34.5; (2 ts, 2 ls)

Description. Cerioid to aphroid coral. In transverse section, the largest corallite has a diameter of 18 mm. Adjacent corallites are bounded by multilayered, wave shaped wall or without distinct boundary. 29 septa in two orders at diameter of 15 mm. Major septa thin, do not reach the centre, open central space of 1.5-2 mm in diameter. Minor septa about 1/2-3/5 length of the major septa. Both orders of septa not reach the outer wall and intercepted by transeptal dissepiments. Dissepiments concentrically arranged. Cardinal fossula not distinct.

In longitudinal section, tabularium occupies 1/3 of the corallite diameter. Tabulae domed, flat in axial part (about 15 per 5 mm) and vesicular, adaxially inclined at each side. Dissepiments globose, steeply inclined at the inner series, and elongated, arched upward at the outer series. The outmost series may ascend steeply outwards where corallites are bounded by wall.

Discussion. The specimens from Yashui are similar to the holotype of *P. planiuscula*, but differ in having a narrower dissepimentarium and broader axial tabellae.

***Palastraea weiningensis* Wu & Zhao, 1989**
(Pl. 2, Figs A-B)

Material. Two colony fragments: YSR-58~59-1-1 and YSR-58~59-1-2; (6 ts, 7 ls).

Description. Cerioid coral. Corallites diagonal length 12-15 mm. Outer wall are mostly complete. 27-29 septa in two orders. Major septa thin and straight in the tabularium, not reach the centre. Minor septa about 1/2 length of the major septa. Both orders may connect to the wall or intercepted by transeptal dissepiments. They may become flexuous in the dissepimentarium. Dissepiments mostly concentrically arranged.

In longitudinal sections, tabularium occupies 1/2 of the corallite diameter. Tabulae incomplete, flat or slightly depressed at the axis and vesicular, adaxially inclined at each side, with edges upturned, numbering 14 per 5 mm at the axial part. Dissepiments 4-7 row, vesicle shaped and not very uniform in size.

Discussion. Yashui specimens are identical to the holotype of *P. weiningensis* except some small variations: (1) slightly smaller in corallite size and fewer in septal number; (2) more densely arranged axial tabellae. This species differs from *P. planiuscular* in having a more complete wall, wider tabularium and without upwardly arched dissepiments.

***Palastraea* sp.**
(Pl. 2, Figs C-D)

Material. Three colony fragments: YSR-(3), YSR-(0.5)-2-1, YSR-(0.5)-2-2 and YSR(-0.5)-2-3; (6 ts, 4 ls).
Description. Astreoid coral. Wall between corallites usually badly preserved and broken. Corallite diameter 20-30 mm. 33-38 septa in two orders. Major septa long, reach the axis and sometimes meet each other. Minor septa about 2/3 length of major septa. Both orders of septa may thicken slightly at the inner dissepimentarium

and the thickening is more conspicuous in the cardinal quadrant. Dissepiments concentrically arranged in the inner tabularium. Lateral dissepiments usually occur at the outer tabularium.

In longitudinal sections, tabularium narrow, occupies 1/4 of the corallite diameter. The axial tabellae densely arranged, 12-14 per 5 mm. they are flattened in the centre and abruptly turned 90 degree at both ends and rest on the tabellae below. The periaxial tabellae are horizontal or gently inclined outwards, and each may or may not develop an up-turned ends. Dissepiments mostly globose, steeply inclined at the inner part and arched upwards near the margin.

Discussion. The specimens from Yashui resemble *Palastraea regia* (Phillips) in transverse section, but differ from the later in having abruptly turned edges in axial tabellae. This character also distinguishes the Yashui specimens from other species of the same genus, and erection of a new species may be applicable. However, the snapped axial end of major septa and broken corallites boundaries indicate bad preservation of the material, so this species is placed in open nomenclature.

Suborder Lithostrotionina Spasskiy & Kachanov, 1971
Family Lithostrotionidae d'Orbigny, 1852
Subfamily Lithostrotioninae d'Orbigny, 1852

Genus *Lithostrotion* Fleming, 1828

***Lithostrotion* cf. *decipiens* (McCoy), 1849**
(Pl. 2, Figs E-F)

Material. Three colony fragments: YSR-28~29-2-2, YSR-31.2-1-2 and YSR-57.7; (5 ts, 7 ls)

Description. Cerioid coral, lateral offsetting. Corallites polygonal, usually 5-6 sided. The length of the longest diagonal vary from 7 mm to 10 mm in mature stage. 16-19 septa in two orders. Major septa thin, slightly flexuous and sometimes dilated a little in tabularium and/or at the adaxial end. They usually connect to the lens shaped columella but, in less common cases, retreat from the centre. Minor septa about 1/2-2/3 length of major septa, sometimes discontinuous. In rare cases, lonsdaleoid septa occur. Tabularium 2.5 to 4 mm in diameter. Dissepimentarium about as wide as the length of minor septa. Dissepiments concentrically to angulo-concentrically arranged. Very few lateral dissepiments may occur.

In longitudinal sections, axial tabellae ascend to the thickened columella, with downward turned sides which rest on the lower axial tabellae or flat periaxial tabellae (numbered 7-8 per 5 mm). Occasionally, amplexoid septa may occur. Dissepiments vary in size, globose or elongated, numbering 2-4 rows.

Discussion. Although the specimens from Yashui are slightly larger in corallite size compared to most European specimens (Nudds, 1980; Poty 1981, 1993), they are at the limit of the range of variation of *L. decipiens*.

***Lithostrotion decipiens* (McCoy), 1849**
(Pl. 2, Figs G-F)

Material. Four colony fragments: YSR-73.4, YSR-74.7-1-2, YSR-82-1-1 and YSR-82-1-2; (9 ts, 9 ls)

Description. Cerioid coral. Corallites polygonal, 4-7 sided. The length of the longest diagonal vary from 3-8 mm. 15-18 septa in two orders. Major septa connect to the lens shaped columella. Minor septa long, about 1/2-3/4 length of major septa. Both orders of septa may be thickened, reach the outer wall, and no lonsdaleoid form can be observed. Dissepiments concentrically arranged. Diameter of tabularium 2.5-3.2 mm.

In longitudinal section, tabularium occupies about 2/3 of the corallite diameter. Tabulae mostly complete, gently ascend to the columella, numbered 18 per 5 mm. Dissepiments mostly globose, numbering 2-3 rows.

Discussion. The specimens do not differ from specimens of *L. decipiens* in having small corallite size and are assigned to it.

Genus *Siphonodendron* McCoy, 1849

***Siphonodedron pauciradiale* (McCoy), 1844**
(Pl. 2, Figs. I-K; Pl. 3, Figs A-B)

Material. Eight limestone blocks containing colony fragments: YSR-0.5-2-1, YSR-0.5-2-2, YSR-5.5-1-3, YSR-28~29-2-3, YSR-31.5, YSR-55.6-2-1, YSR-82.5 and YSR-83. (38 thin sections) (due to the fragmentation of the coral colonies, some thin sections include both transverse and longitudinal sections of the corallite. The number given here refers to the total amount of the thin sections made. It is the same in the following descriptions if the number of ts and ls are not given separately.)

Description. Fasciculate coral, lateral increase. In transverse section, corallite diameter 3-5 mm. 15-22 septa in two orders. Major septa thin, sometimes connected with the columella, but mostly intercepted by the downward turned edges of tabulae. Minor septa short, or just spine-shaped. Columella often thickened. Dissepiments concentrically arranged.

In longitudinal section, the conical tabula ascend to the columella and bend downward at both edges. Columella thick, straight and continuous. Dissepiments 1-2 rows, vesicular and the innermost series often thickened.

Discussion. The specimens from Yashui can be assigned to *S. pauciradiale* applying Poty's standard (1981, 1993). Though samples from 82.5 m and 83 m have lesser septa number, about 15-17 in average. And they also differ from the specimens from lower part of the section in that their major septa rarely extend into the pseudo-aulos formed by the tabulae.

Genus *Stylostrotion* Chi, 1935

***Stylostrotion petalaxoidae* (Yu), 1933**
(Pl. 2, Figs L-N)

Material. Eleven limestone blocks containing colony fragments: YSR-26-1-1, YSR-28.45-1-2, YSR-28.45-2-1, YSR-28.2, YSR-28~29, YSR-28~29-1-1, YSR-28~29-1-2, YSR-35.2-2-1, YSR-49.1, YSR-50.9, YSR-55.6-1-1; (62 sections).

Description. Fasciculate coral, axial increase. Corallites diameter 5-10 mm. Major septa long, slightly thickened, numbering 20-24. Minor septa rudimentary or not present. Columella long, dilated, usually continuous with cardinal septum and counter septum. Dissepiments concentrically arranged or herringbone.

In longitudinal section, the conical tabulae ascend to the thickened columella, numbering 8 per 5 mm. They incline more steeply outward and upturned near the dissepimentarium. Dissepiments large, elongated, vesicle shape, 1-2 rows, the innermost series may be coated by stereoplasm.

Discussion. This genus was established by Chi (1935). According to the text figure and the photos of the genotype, many resemblances present between this genus and *Siphonodendron*, except that no minor septa are present in Chi's specimens. This character is also present in other specimens from China (Yu, 1933; Wu, 1964; Xu & Poty, 1997). However, the name *Stylostrotion* rarely appears in literatures and this group was always identified as *Siphonodendron*. Fedorowski (2004) questions the validity of this genus name because the definition of this genus does not have a good basis and lack convincing reinvestigation. He points out the Heterocorallia-like arrangement of septa in this genus and suggests using *Donophyllum* for corals with such septal patterns if synonymy of these two names is proven. In the present author's opinion, it is still questionable if the resemblance in septal arrangement truly represents the similar developing pattern, and considering the priority of *Stylostrotion* over *Donophyllum*, the former genus name is applied for the Yashui specimen in this paper.

Subfamily Diphyphyllinae Dybowski, 1873

Genus *Diphyphyllum* Lonsdale, 1845

***Diphyphyllum fasciculatum* (Flaming), 1828**
(Pl. 3, Figs C-D)

Material. Two limestone blocks containing colony fragments: YSR-(0.8)-1-1 and YSR-26; (6 sections).

Description. Fasciculate coral, axial increase. Corallite diameter 5-6 mm. 20-23 septa in two orders. Major septa about half of the corallite radius, mostly not extend to the pseudo-aulos formed by the axial tabellae. Minor septa fairly short, not extended into the tabularium. Dissepiments concentrically arranged.

In longitudinal section, the domed axial tabellae overlapping the preceding one, with sub-horizontal periaxial tabellae on both sides. Dissepiments elongated, vesicle shaped, 1-2 rows.

Subfamily Aulinae Hill, 1981

Genus *Aulina* Smith, 1917

***Aulina rotiformis* Smith, 1917**
(Pl. 3, Figs E-F)

Material. Three colony fragments: YSR-28.45-1-1, YSR-28~29-2-1 and YSR-35.2-1-1; (6 ts, 8 ls)

Description. Astreoid coral. Distance between the adjacent corallites centre 3-6 mm. 10-16 septa in two orders. Major septa intercepted by an aulos of 1-1.5 mm in diameter. Minor septa about 3/4-4/5 length of major septa, extend slightly into tabularium. Carinae may be present on the septa, which sometimes are dilated.

In longitudinal section, tabulae divided in axial and periaxial tabellae. Axial tabellae flat or slightly domed, overlapping the preceding one, numbering 13-15 per 5 mm. The downward turned edges of axial tabellae form an aulos. Periaxial tabellae gently inclined to the dissepimentarium. Dissepiments vesicle-shaped, mostly arch upward. No distinct boundaries between adjacent corallites.

Discussion. The diameter of tabularium and aulos of Yashui specimens is between English specimens of *Aulina rotiformis* and *A. senex*. They more resemble to *A. rotiformis* in having continuous aulos which is a diagnostic character of the later.

Distribution. In the Yashui section, this species range from top to bottom. They are found at 28~29 m and 35.2 m in the first sampling, and at 6 m below the measured base, 87 m and 110 m in the following two samplings. The FAD of this species may extent to the latest Viséan.

Suborder Lonsdaleiina Spaskkiy, 1974
Family Axophyllidae Milne-Edwards & Haime, 1851

Genus *Axophyllum* Milne-Edwards & Haime, 1850

***Axophyllum* aff. *lonsdaleiforme* Salée, 1912**
(Pl. 3, Figs G-H)

Material. Five samples: YSR-1, YSR-4-3-1, YSR-9.4-1-1, YSR-9.4-1-2 and YSR-19.3-1-3; (17 ts, 3 ls)

Description. Solitary coral. In younger stage, transeptal dissepiments and columella not developed. In mature stage, septa in two orders, 28 at diameter of 12 mm, and 34 at diameter of 20 mm. Major septa thickened and thinning adaxially. Minor septa become septal crests, resting on the adaxial surfaces of dissepiments of inner series. Axial structure consists of a thickened, flexuous columella, several irregularly curved septal lamellae and some concentrically arranged axial tabellae. Dissepiments transeptal near the thickened outer wall and concentric at the inner tabularium, with the innermost series coated with stereoplasmic layer.

In longitudinal sections, the three-zonal-structure can be clearly observed. Axial tabellae irregularly ascend to the flexuous median plate. Periaxial tabellae horizontal or incline to the axial region column. Dissepiments very large, vesicle shaped and thickened.

Discussion. The specimens have affinities with *Axophyllum lonsdaleiforme*, but have an axial structure less developed and a wider dissepimentarium.

Genus *Lonsdaleia* McCoy, 1849

***Lonsdaleia duplicata* (Martin), 1809**
(Pl. 3, Figs I-L)

Material. One colony fragment: YSR-72.3; 8 sections.

Description. Fasciculate coral. The colony may show subcerioid habit while corallites are in contact with each other. Corallite diameters from 10 to 20 mm. Wall undulating and thickened by stereoplasm. 28 septa in two orders at a diameter of 10 mm, 32 at a diameter of 15 mm and 36 at a diameter of 20 mm. The major septa are dilated in their middle part and attenuate to both ends. Most of them do not connect with the axial column, which consists of a median plate, several incomplete septal lamellae and concentrically arranged axial tabellae. Minor septa thin, usually as septal crests. The outer dissepiments are transeptal, very large vesicle shaped; there are some inner rings of simple or second-order transeptal dissepiments.

In longitudinal sections, the three-zonal-structure can be clearly observed. Axial tabellae ascend to the flexuous median plate, numbered 8 per 5 mm. Periaxial tabellae inclined to the axis and slightly concave. Dissepimentarium consists of very large vesicular dissepiments and clearly bounded by an inner wall from the tabularium.

5. Conclusions

The rugose coral fauna in the Yashui section indicate a latest Viséan to Early Serpukhovian age and shows resemblance to the Western European fauna. Many well-known European taxa such as *Dibunophyllum bipartitum*, *Palaeosmilia murchisoni*, *Lithostrotion decipiens*, *Siphonodendron pauciradiale* and *Aulina rotiformis* appear in Yashui, but with different stratigraphic ranges. For example, the FAD of *Aulina rotiformis* is usually regarded in earliest Namurian (early Serpukhovian) in Britain while in Yashui, it first appears in latest Viséan strata. There are also some endemic taxa such as *Arachnolasma sinense*, *Yuanophyllum kansuense*, *Kueichouphyllum sinense* and *Stylostrotion petalaxoidae* which can be used for correlations throughout South China. The coral diversity of the Yashui section shows: (1) a diversity decrease in the uppermost part of the Viséan, and (2) a poorly renewed fauna in the Serpukhovian, which is the similar pattern recorded in the Palaeotethys Therefore, a coral biostratigraphic succession which distinguish early Serpukhovian from latest Viséan is difficult to establish.

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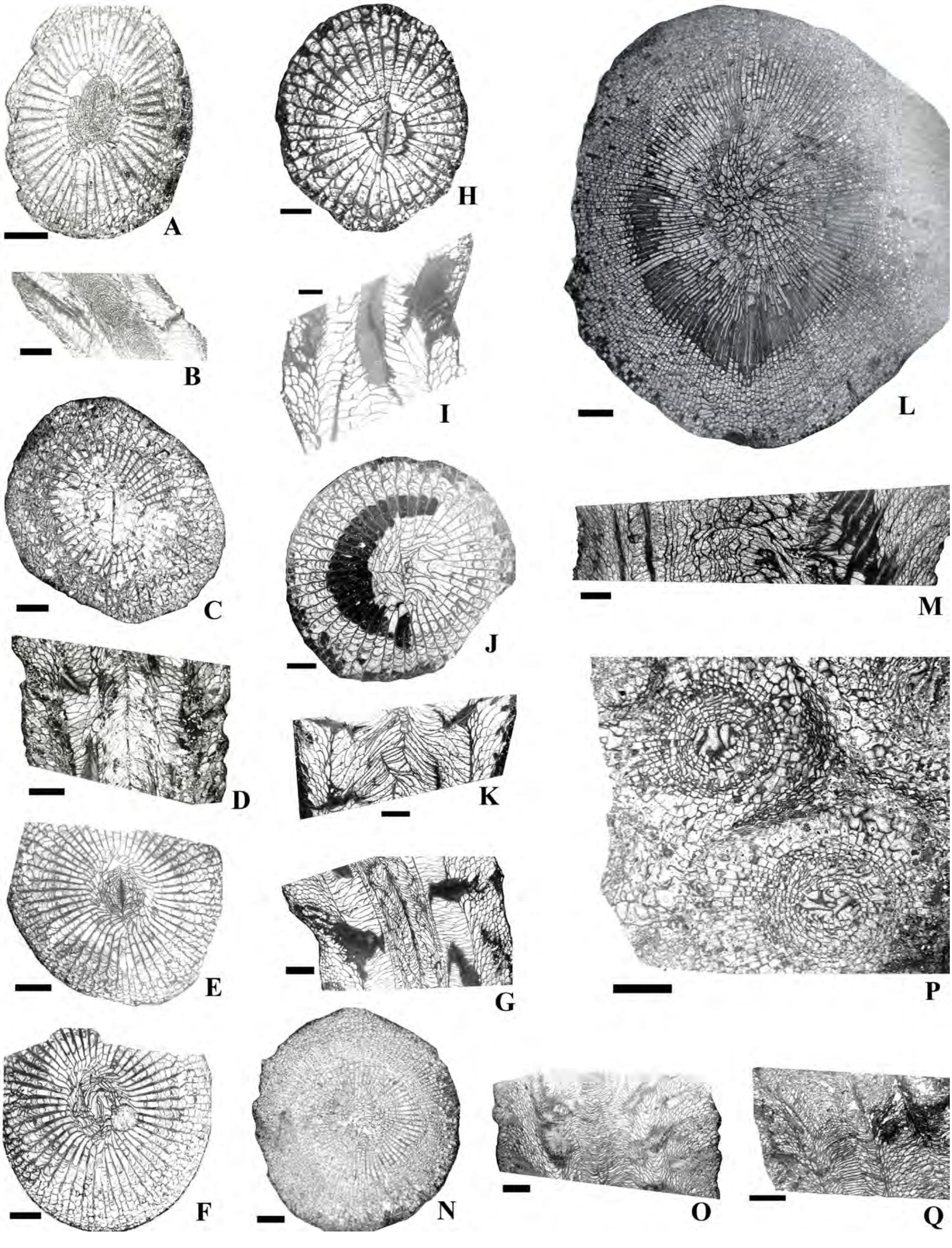

Plate 1. A-B: *Neoclisiophyllum angulatum* Wu & Zhao, 1989. Sample YSR-87.1-1-1, ts and ls. C-D: *Dibunophyllum bipartitum* (McCoy), 1849. Sample YSR-(-0.5)-1-1, ts and ls. E-G: "*Dibunophyllum*" *tingi* (Yu), 1933. Sample YSR-3, ts and ls. H-I: *Arachnolasma sinense* (Yabe and Hayasaka), 1920. Sample YSR-89.2, ts and ls. J-K: *Yuanophyllum kansuense* Yu, 1931. Sample YSR-71.6-1-1, ts and ls. L-M: *Kueichouphyllum sinense* Yu, 1931. Sample YSR-65.5, ts and ls. N-O: *Palaeosmilia murchisoni* Milne-Edwards & Haime, 1848. Sample YSR-4, ts and ls. P-Q: *Palastraea* cf. *planiuscula* Wu & Zhao, 1989. Sample YSR-34.5, ts and ls. All the scale bars are 4 mm except H and I, which are 2mm.

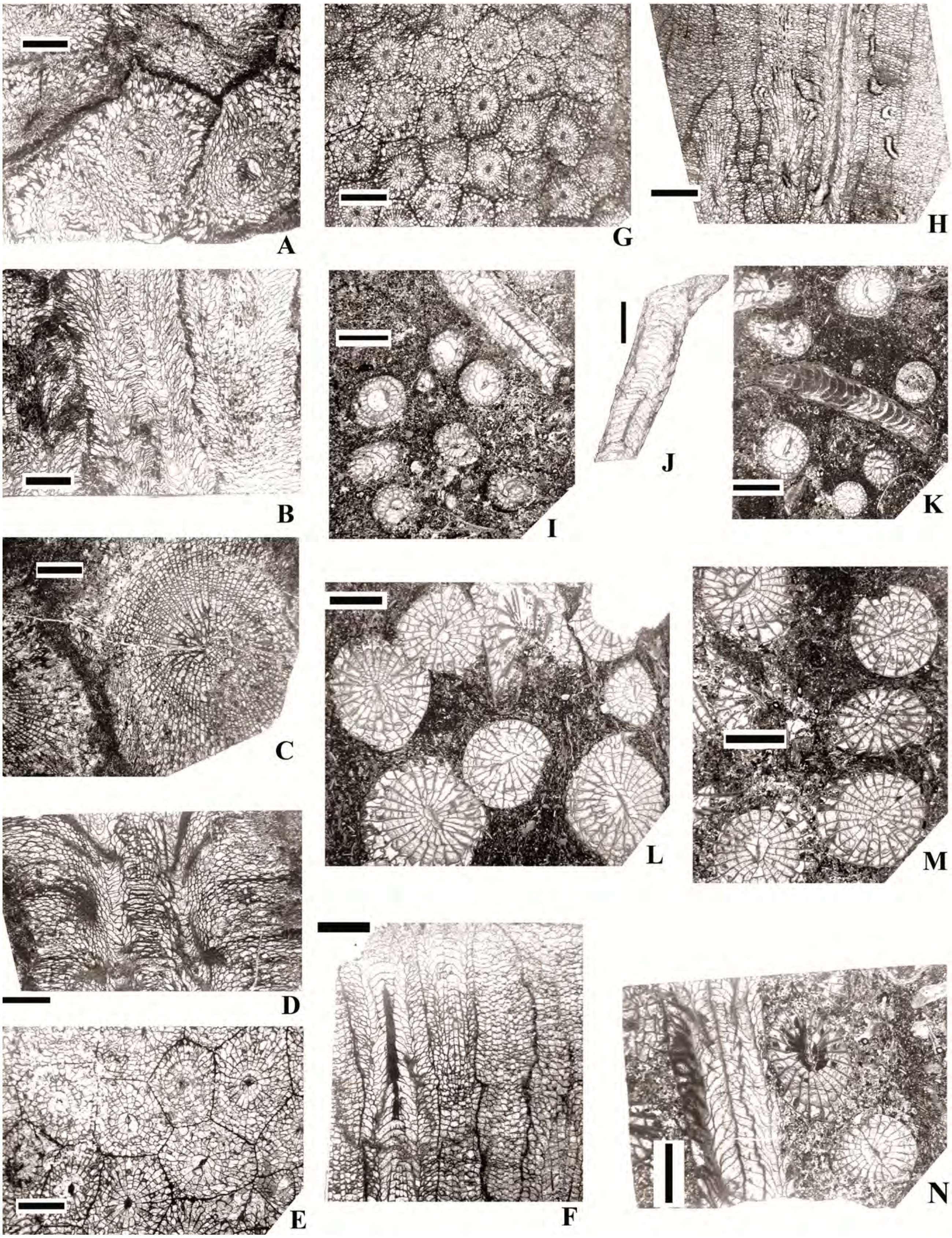

Plate 2. A-B: *Palastraea weiningensis* Wu & Zhao, 1989. Sample YSR-58~59-1-1, ts and ls. C-D: *Palastraea* sp. Sample YSR-(-0.5)-2-1, ts and ls. E-F: *Lithostrotion* cf. *decipiens* (McCoy), 1849. Sample YSR-28~29-2-2, ts and ls. G-H: *Lithostrotion decipiens* (McCoy), 1849. Sample YSR-82-1-2, ts and ls. I-K: *Siphonodedron pauciradiale* (McCoy), 1844. I-J: sample YSR-0.5-2-2, ts and ls. K: sample YSR-5.5-1-3, ts and ls in one slide. L-N: *Stylostrotion petalaxoidae* (Yu), 1933. L: sample YSR-28.45-1-2, ts. M-N: sample YSR-28.45-2-1, ts and ls. All the scale bars are 4 mm.

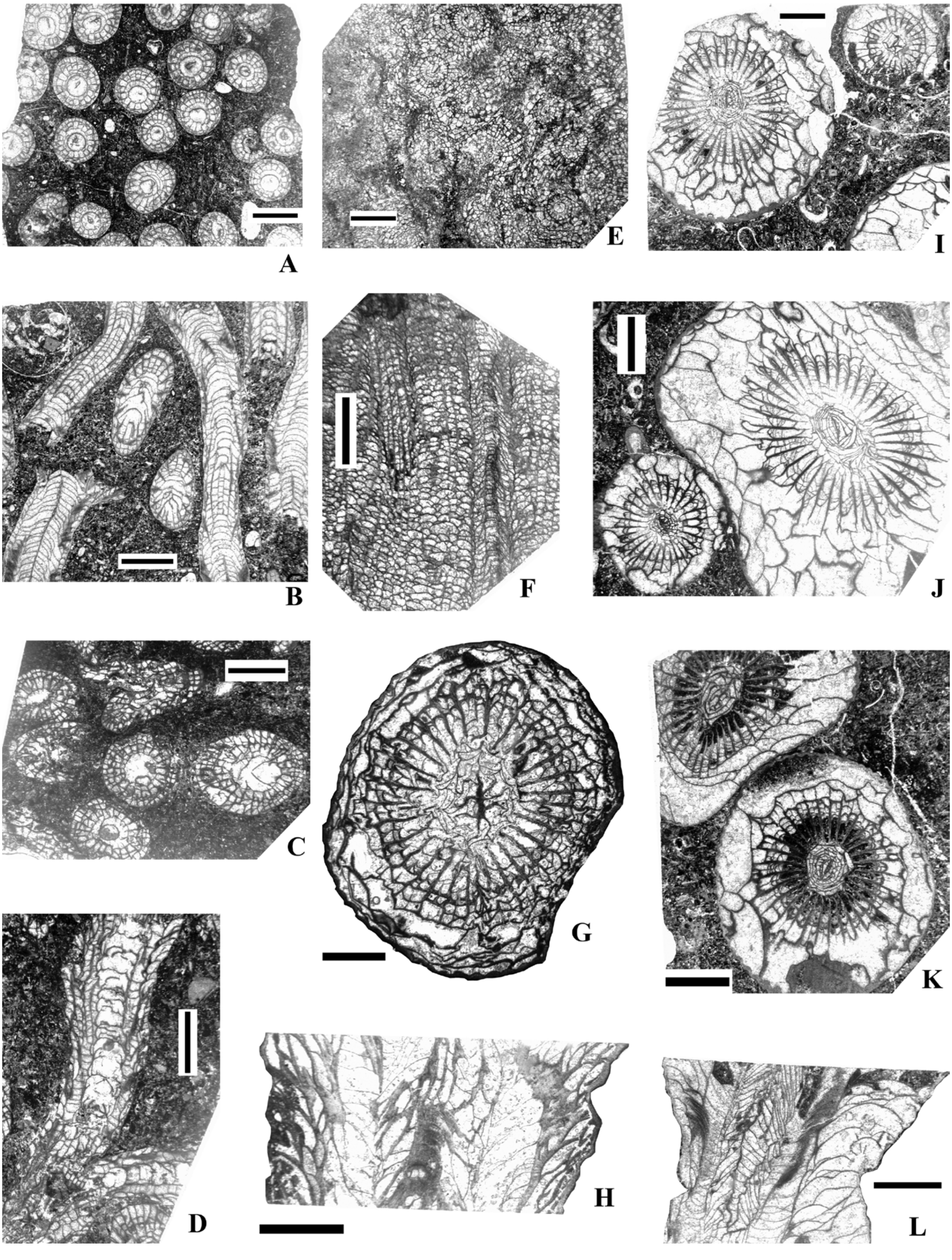

Plate 3. A-B: *Siphonodedron pauciradiale* (McCoy), 1844. Sample YSR-83, ts and ls. C-D: *Diphyphyllum fasciculatum* (Flaming), 1828. Sample YSR-(0.8)-1-1, ts and ls. E-F: *Aulina rotiformis* Smith, 1917. Sample YSR-28~29-2-1, ts and ls. G-H: *Axophyllum* aff. *lonsdaleiforme* Salée, 1912. Sample YSR-19.3-1-3, ts and ls. I-L: *Lonsdaleia duplicata* (Martin), 1809. Sample YSR-72.3, ts and ls. All the scale bars are 4 mm.

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Carboniferous buildups in the Donets Basin (Ukraine)

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ABSTRACT. The Carboniferous (Mississippian and Pennsylvanian) of the Donets Basin contains bioherms and biostromes in several stratigraphic levels. The study of buildups of this region and their comparison with other areas allows to suggest that the composition of reef-building organisms changed during the Carboniferous. Up to the late Viséan, they were formed on a shallow water carbonate platform, whereas younger bioconstructions are restricted to distinctive limestone horizons of cyclothems. Viséan shallow-marine bioconstructions are represented by *Siphonodendron*-biostromes which are typical for the Late Viséan of many areas of the Paleothetys. In the unstable conditions of the paralic basin with frequent environmental changes bioconstructions formed during transgressive phases. The late Serpukhovian buildups were complex coral-chaetetid biostromes and bioherms. In Bashkirian times appeared chaetetid and coral-chaetetid biostromes as well as algal bioherms. In the early Moscovian coral and coral-chaetetid biostromes were the most common. During the middle Moscovian dominated bioherms probably of microbial origin, and at the end of Moscovian time chaetetid biostromes were typical. At the earliest Gzhelian time algae-sponge bioherms appeared in the Donets Basin.

KEY WORDS: Mississippian, Pennsylvanian, bioconstructions, coral biostrome, chaetetid biostrome, bioherm, Donets Basin.

1. Introduction

The Donets Basin together with the Dnieper-Donets Depression is part of the Don-Dnieper Downwarp. The Carboniferous bioconstructions of the Donets Basin can be used as outcrop analogous for oil and gas fields in the subsurface of the Dnieper-Donets Depression. There such structures are only known in greater depths, and their studies are based mainly on seismological and geophysical data, since only very limited core material is available.

Only fragmentary data on Carboniferous bioconstructions of the Donets Basin were obtained. Except the detailed study of Poljakova (1986) on Upper Serpukhovian coral bioherms, information is limited to briefly described and mentioned horizons rich in bioconstructors as corals (Fomichev, 1953), chaetetids (Vassiljuk, 1959) and palaeoaplysins (Vassiljuk, 1974).

It is the aim of this paper to summarize all available data of bioconstructions based on the previous studies and personal observations (Fig. 1). During field works a focus was laid on the spatial distribution of rugose and tabulate corals, chaetetids, and "stromatoporoid"-like fossils in order to determine their role as a reef builders. The comparisons of studied buildups with those described in other areas of the world can help to identify the most common patterns in their evolution during the Carboniferous period.

2. Geological setting and stratigraphy

The Donets Basin is part of a Paleozoic fold belt near the southern part of the East–European Platform between the Ukrainian Shield and the Voronezh Massif (Fig. 2). The Carboniferous deposits are dislocated here in folds with north-western direction of axes and complicated by faults of the same direction. The Golovna Anticline occupies the central position in the structure of the Donets Basin. In the northern part of the Donets Basin younger sediments cover the "Zone of Small Folds". It forms a transition zone between the Folded Donets Basin and the southern slope of the Voronezh Massif and is widely known as the Northern Outskirts of the Donets Basin.

The study area is located within the Donetsk and Lugansk regions of Ukraine (Fig. 1). Carboniferous deposits of

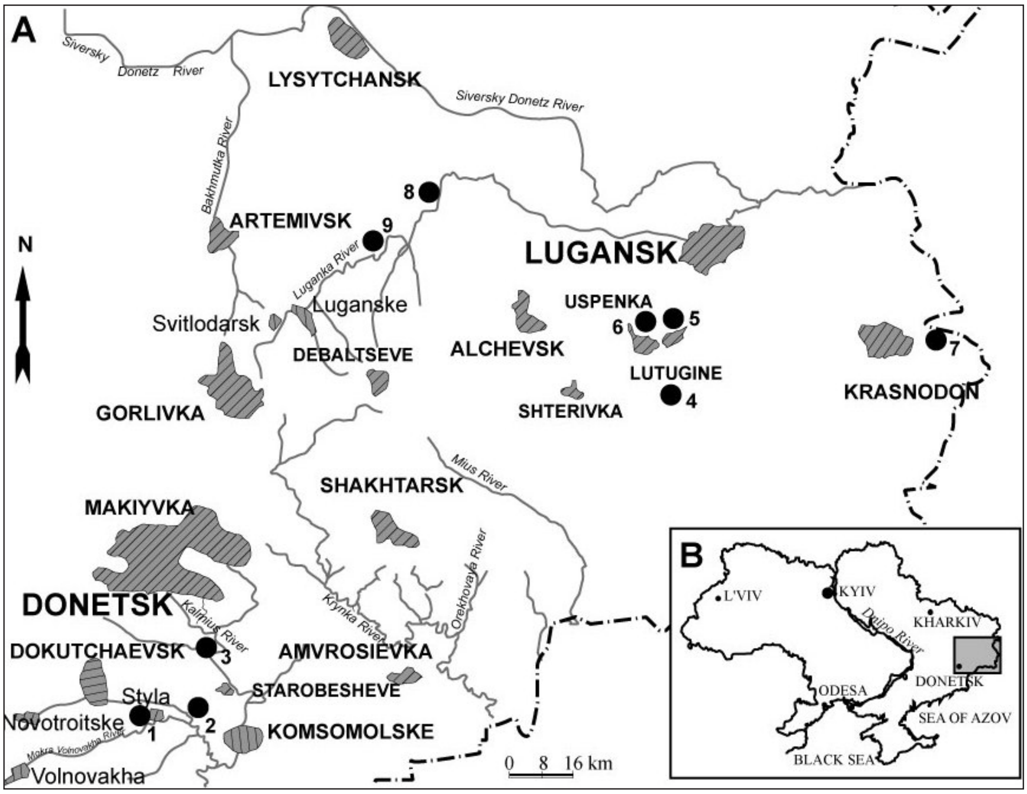

Figure 1. Location map of studied sections. 1: Mokra Volnovakha River near the village Styla, 2: Kypucha Krynytsa village, 3: Starobesheve village, 4: Volnukhino village, 5: Karahuz ravine, 6: Pashenna ravine, 7: Izvarine railway station, 8: Golubovka railway station, 9: Kalynove village.

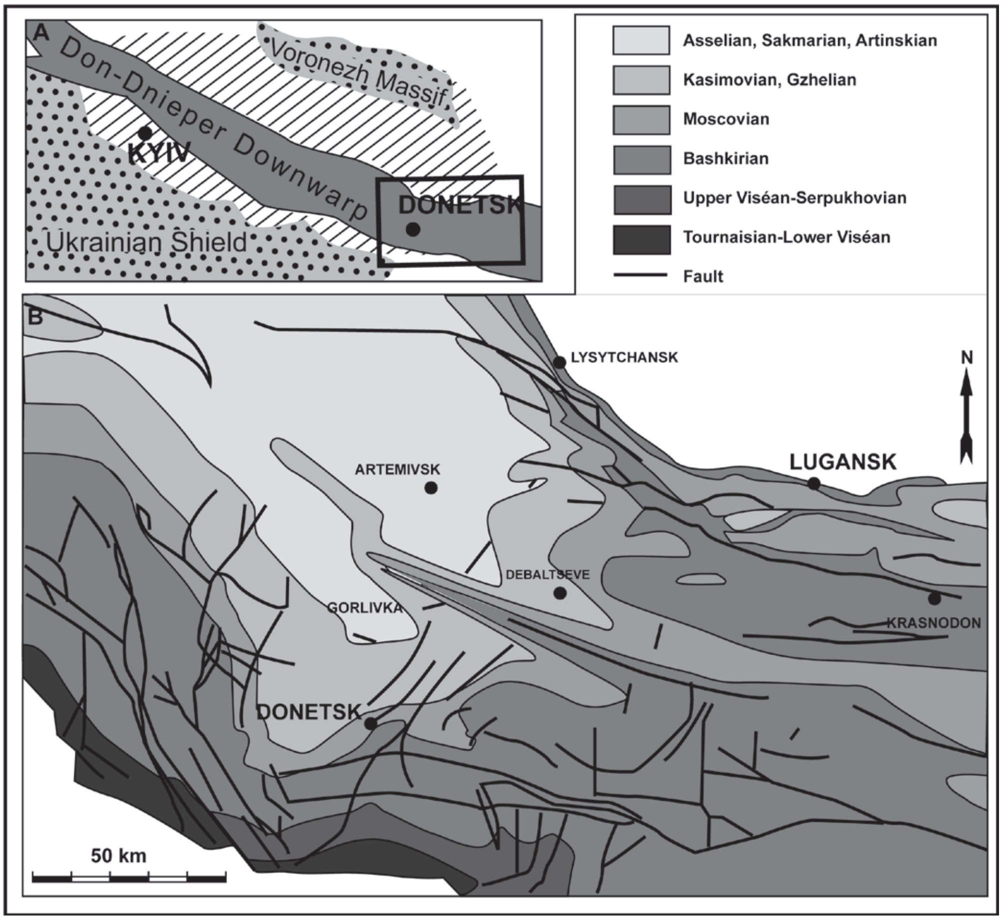

Figure 2. A: Sketch of the Don-Dnieper Downwarp B: Geological map of the Donets Basin (modified after Aizenverg et al., 1975).

Global Stratigraphic Scale				Regional Stratigraphic Scale					
System	Subsystem	Series	Stage	Series	Regional Stage	Regional Substage (Horison)	Zone	Suite	Limestone
CARBONIFEROUS	PENNSYLVANIAN	UPPER	GZHELIAN	Upper Carboniferous	Myronovkian	Vyskrivskian		Kartamysh (Q)	Q_7 Q_1
						Luganskian		Araukaritova C_3^3 (P)	P_5^0
					Kalynovian	Troizkian			P_3
						Kluchovian		Avilovka C_3^2 (O)	O_5
			KASIMOVIAN		Toretzian	Svitlanovkian			O_4^1
						Kartanashkian		Isaivka C_3^1 (N)	N_5-N_5^1
		MIDDLE	MOSCOVIAN	Middle Carboniferous	Lomovatkian	Sanzharivkian	C_2^m e	Gorlivka C_2^7(M)	M_8
						Sabivkian	C_2^m b-d		M_1
					Lozovian	Marjivkian		Almazna C_2^6 (L)	L_1
						Kamenkian	C_2^m a	Kamenka C_2^5 (K)	K_3
		LOWER	BASHKIRIAN		Kayalian	Krasnodonian	C_2^b e	Bilokalytvenka C_2^4 (I)	I_2
						Makijivkian	C_2^b d	Smolyanynovka C_2^3 (H)	H_4
						Zujevian	C_2^b b-c	Mospinska C_2^2 (G)	G_1
					Mandrykinian	Blagodatnian	C_2^b a	Mandrykinka C_2^1 (F)	F_1
						Manuilivian		Amvrosiivka C_2^0(E)	E_8
					Olmezivkian	Feninian			E_1
						Voznesenskian	C_1^s g	Kalmiuska C_1^4(D)	D_5^{8u}
	MISSISSIPPIAN	UPPER	SERPUKHOVIAN	Lower Carboniferous	Starobeshevian	Zapaltyubian	C_1^s e-f		D_3
						Novolyubivkian	C_1^s d		D_1^{5l}
						Prokhorovian	C_1^s b-c	Samara C_1^3(C)	C_5
					Efremovian	Samarian	C_1^s a		C_1
		MIDDLE	VISEAN			Mezhevian	C_1^v g	Mezha C_1^2(B)	B_1
						Donetsian	C_1^v f	Mokrovolnovakha Siries C_1^1(A) Donetsk	
					Olenivkian	Stylian	C_1^v e	Styla	
						Sukhian	C_1^v b-d	Skelyuvatka	
						Glybokian			
		LOWER	TOURNAISIAN		Upper Buzinivian	Dokuchaevskian	C_1^v a	Karpivka	
						Karpovkian	C_1^t d		
						Volnovakhian	C_1^t c	Volnovakha	
					Lower Buzinivian	Karakubian	C_1^t b^u	Karakuba	
						Bazaliivian	C_1^t b^l	Bazaliivka	

Figure 3. General stratigraphic chart of the Carboniferous of the Donets Basin (after Mening et al., 2006; Poletaev et al., 2011).

the Donets Basin have been studied since the 18th century. The early history of their study was described by Novick et al. (1960). Since then, a very detailed stratigraphic subdivision was achieved (Lissitzin, 1925, 1929; Aizenverg et al., 1963; Rotai, 1975). Foraminifers are the main biostratigraphic tools and have been used to define horizons, but detailed biostratigraphic charts for other group of fossils exist also (Poletaev et al., 2011).

According to the lithological differences, the Carboniferous of the Donets Basin is divided into two parts. The lower part, Mokrovolnovakha Series, is predominantly composed of limestone, which formed on a carbonate platform during the Tournaisian and most of the Viséan. The series is well exposed in the Southern Donets Basin and has a thickness of 500 m. Carboniferous carbonate strata unconformably overlies the Devonian carbonate deposits. The latter had been considered as being Carboniferous in age (C_1^ta), but detailed biostratigraphic studies showed their Late Devonian age. The Uppermost Devonian and Lower Carboniferous limestones are mined by numerous quarries for flux material used in steel industry.

A much larger thickness is found in the upper part of the Carboniferous deposits. Cyclothems accumulated to a total thickness of 7-10 km in a paralic basin from the end of the Viséan to the top of the Carboniferous. These deposits are exposed in the central and northern parts of the Donets Basin and often contain industrial coal seams. The Fig. 3 shows a general stratigraphic chart of the Carboniferous of the Donets Basin. Stratigraphic correlations of the Carboniferous of the Donets Basin to neighbouring regions have been established, but remain partly controversial (Mening et al., 2006).

3. Stratigraphic distribution and structure of the buildups

3.1. Lower Viséan

Corals become abundant in the Upper Tournaisian strata. The Volnovakha Suite (Zone C_1^tc) contains a number of large solitary rugose corals *Cyathoclisia* and *Keyserlingophyllum* as well as numerous tabulate corals *Syringopora, Roemeripora, Michelinia,*

Figure 4. Viséan coral-rich limestones. A: The Lower Viséan coral rudstones. The base of the Skelyuvatka Suite ($C_1^{v}b$). B: The Upper Viséan coral biostrome is composed of fasciculate colonies of *Siphonodendron junceum* (Fleming). Middle part of the Donetsk Suite ($C_1^{v}f$).

and *Volnovakhipora*. Corals are found in bioclastic limestones. There are some features of transportation and they do not form significant accumulations.

The role of corals in carbonate sedimentation increases markedly with the appearance of colonial rugose corals as *Siphonodendron*, *Dorlodotia* and *Eolithostrotionella* in the lower part of the Viséan. This is clearly seen in the outcrop "Pigeons Rock" on the left bank of the Styla reservoir (Mokra Volnovakha River). Here at the bottom of the Skelyuvatka Suite (Olenivskian Regional Stage, Zone $C_1^{v}b$) fragments of *Siphonodendron affine* var. *tanaicum* Vassiljuk, and *Syringopora* form a coral-rich bed (Vassiljuk, 1960). Its thickness is 0.3-0.5 m (Fig. 4A). Coral debris is cemented by bioclastic material and forms coral rudstones.

In the western extension of the Donets Basin and Dnieper-Donets Depression a Tournaisian-Viséan reef complex is described (Lukin & Vakarchuk, 1999). The authors stressed that corals did not play a significant role in the structure of this complex. But its reef nature, in our opinion, has not been studied in enough detail.

3.2. Upper Viséan

The first real bioconstructions are found in Upper Viséan deposits. These simplest buildups occur in the middle part of the Donetsk Suite (Zone $C_1^{v}f$, Efremovian Regional Stage) in the outskirts of Styla and Kypucha Krynica villages.

These bioconstructions are composed of large fasciculate colonies of *Siphonodendron junceum* (Fleming), each of which has a height of 15 cm to 40 cm and in some cases up to 80 cm. Colonies grow one by one, touching or placing at a distance of 10-30 cm, both vertically and horizontally forming coral biostromes. The length of these constructions is 2-3 m and a height of 80 cm (Fig. 4B, Pl. 1A).

The biostromes are intercalated between coarse-grained bioclastic limestone beds and argillaceous limestone with inclusions of black chert of irregular shape. The limestone includes the debris of *Dibunophyllum*, clusters of gigantoproductid brachiopods, and flat chaetetid colonies (*Chaetetipora* and *Caetetiporella*).

3.3. Upper Serpukhovian

The Upper Serpukhovian buildups (the Starobeshevian Regional Stage, the Kalmiuska Suite, C_1^{4} (D) are more complex in composition and structure than the Upper Viséan. They are exposed around the Starobesheve village on the banks of Kalmius River and studied in detail by Poljakova (1986), who related them to shore reefs. These coral-rich structures were observed by the author in two outcrops.

The first outcrop is located on the left bank of the Kalmius River near the former village Novolyubivka. Here two thick limestone levels of the group D_1^{5} (Novolyubivkian Horizon) are separated by a 10 m thick shale interval containing plant remains. Several interbedded thin layers of yellow clay limestone contain numerous fragments of small solitary rugose corals, brachiopods, bryozoans, and crinoids (Poletaev et al., 2011).

The lower limestone level is 11.2 m thick. It is a dark-brown bioclastic limestone, with abundant remnants of various macrofauna and biolithites. Corals are abundant in bafflestones and framestones. They form separate lenses (coral bioherms) with a thickness of about 0.7 m, composed of large colonies of rugose corals *Lithostrotion, Siphonodendron* and *Aulina.* Among colonial rugose corals the fasciculate *S. asiatica* are predominant. They form the framework that can accommodate solitary rugose corals mainly *Dibunophyllum*, as well as calcareous algae, bryozoans, foraminifers, brachiopods, gastropods, bivalves, and the debris of other organisms. The upper limestone level is 9.2 m thick. The light-gray micritic clotty massive limestone contains many stromatolites, and thus is probably microbial in origin. Fauna is rare in this limestone.

The second outcrop is located on the right bank of the Kalmius River in the outskirts of the Starobesheve village. On the eastern slope of the Zapal-Tube mountain the coral-chaetetid limestone D_5 (the Zapaltyubian Horizon) is exposed. The chaetetids *Chaetetiporella* and *Chaetetes* (*Boswellia*) and "stromatoporoid"-like fossils *Kyklopora* are presented along with colonial and solitary rock-forming rugose corals. Often there are also calcareous algae, bryozoans, brachiopods and remains of other organisms. Colonies of rugose corals, "stromatoporoid"-like fossils and chaetetids form several layers (Fig. 5). The lower layer is composed of flat colonies of *Kyklopora* and *Chaetetiporella* (bindstone). At the top of the bed, they are replaced by spherical colonies of *Chaetetes*, *Actinocyathus*, *Lonsdaleia*, *Siphonodendron*, *Lithostrotion* (Pl. 1B) and *Aulina* (Pl. 1C) forming bafflestones and framestones. The thickness of the buildup is 1.75 m, the visible length reaches 12 m.

Limestones D_1^{5} and D_5 are much persistent in the area. But near the former village Novolyubivka (D_1^{5}) and on the eastern slope of the Zapal-Tube Mountain (D_5) they reach their maximum thickness, which also indirectly indicates to their reef origin. Drilling results show that the thickness of some Serpukhovian limestones can reach several tens of meters, but reef genesis of these thickening limestones has not been studied and is only supposed.

3.4. Bashkirian

The Bashkirian is characterized by the arrival of a new coral community, and among corals, the typical reef builders of the Serpukhovian have become extinct.

On the right bank of Kalmius River in the limestone D_5^{9} (the lowermost of the Bashkirian; the upper part of the Kalmiuska Suite; Voznesenskian Horizon), are exposed many nodules of *Chaetetes (Boswellia)* with sizes up to 1 m and placed among bioclastic limestones. They belong to chaetetid sponge biostromes. Up-section, in the Amvrosiivka Suite (limestone E_1, E_2; Feninian Horizon), *Chaetetes* (*Boswellia*) *boswelli* Heritsch and *Multithecopora sokolovi* Vassiljuk form biostromes. Large

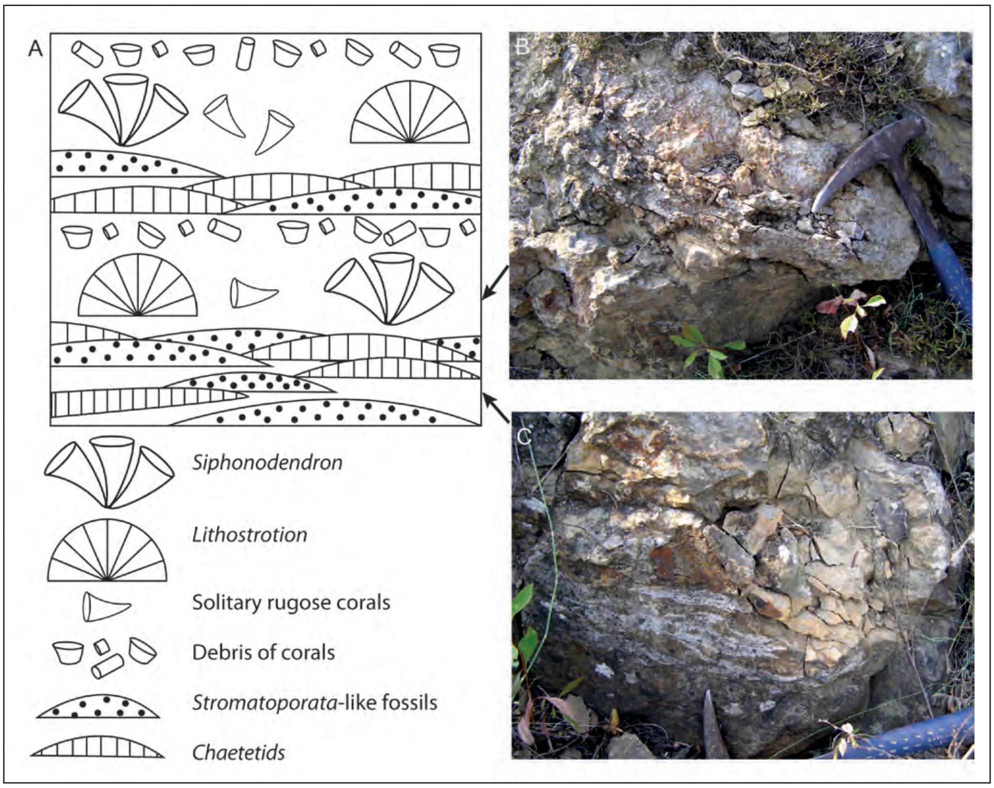

Figure 5. The Upper Serpukhovian coral bioherms near Starobesheve village, Limestone D_5. A: Sketch of the bioherm. B: *Siphonodendron rossicum* (Stuckenberg) colony (upper layer). C: Chaetetids *Chaetetiporella* and "stromatoporoid"-like fossils *Kyklopora* (lower layer).

Figure 6. Pennsylvanian bioherms. A, D: Moscovian microbial? bioherm, Pashenna section, limestone L_7. A: General view, D: tubes of *Tubulus*. B, C, E: Moscovian microbial? bioherm, Golubivka railway station, limestone L_6. B: General view. C: crinoidal limestone. E: fragment of stromatolite. F: Moscovian microbial? bioherm, Karahuz section, limestone L_7, tube of *Tubulus*. G: Gzhelian algal-sponge bioherm, "Stone Gate" outcrop near the village Kalinove, limestone O_6^1.

colonies of ?*Lytvophyllum dobrolyubovae* Vassiljuk with widths and heights of both 50 cm (Vassiljuk, 1960) occur dispersed in the biostrome. They do not form any significant clusters and thus did not contribute to biostrome formation.

In a quarry near the Volnukhino village lenticular structures crop out in the limestone F$_1$ (Mandrykinka Suite, C$_2^1$ (F); Blagodatnian Horizon). The quarry exposes two parts of this limestone. The lower, thicker part is composed of bluish-gray massive possibly phylloid algae dominated bafflestone (Pl. 2A). This part is covered by a 1.5-2 m thick layer of dark-gray bioclastic and clayish limestone with numerous red algae, which according to D. Vachard (pers. com.) possibly belong to *Archaeolithophyllum lamellosum* Wray, 1964 (Pl. 2B), fragments of crinoids, brachiopods, bryozoans, bivalves and solitary rugose corals. Limestone F$_1$ is evenly distributed in this area, due to its persistence distinctly manifested in the landscape. Usually, it is only few meters thick, but near the Volnukhino village its thickness reaches 10-12 m (Aizenverg et al., 1975; Poletaev et al., 2011).

3.5. Moscovian

Probably microbial-mediated lenticular structures (bioherms) are particularly well developed in the middle part of the Moscovian in the northern part of the Donets Basin (Ogar, 2007). These bioherms are associated with limestone L$_6$ and L$_7$ (Lozovian Regional Stage, Almazna Suite C$_2^6$ (L). Microbial origin of these buildups is very probable, but not completely proven.

In the Pashenna section, located in the northern outskirts of Chelyuskinets, limestone L$_7$ is exposed near the mine in an old quarry (Fig. 6A). Light-gray massive limestone is overlain by a crinoidal layer with thickness 30 cm. The limestones include in some cases chaetetid colonies and massive colonies of the rugose corals *Ivanovia*. The thickness of the bioherm exceeds 3 m and its length reaches several tens of meters.

The largest buildup is the Holubivka bioherm. It is located in the northern part of Kirov (opposite to the railway station Holubivka) on the right bank of the Luganka River near the heap of coal mine No.100 (Fig. 6B). The bioherm is associated with the limestone L$_6$. It has the shape of a lens and 200×300 m as viewed from the top. The central part of this bioherm is almost mined by the quarry. Only a marginal part is preserved and the thickness exceeds 3 m. The bioherm is composed of light-gray thick-layered and massive wackestone-packstone. Macrofauna is rare and represented by brachiopods, chaetetids, solitary rugose corals (*Yuanophylloides*), and massive colonial corals (*Petalaxis*). Stromatolites are frequently found (Fig. 6E).

The upper part of the bioherm is composed of light-brown crinoidal rudstone (encrinite) with a thickness of 30 cm (Fig. 6C). The diameter of the largest crinoid fragments reaches 1.5 cm. Debris of chaetetids and solitary rugose corals are commonly found in these crinoidal limestones.

A smaller bioherm is found in the Karahuz section. It is located at a distance of about 2 km to the east of the Pashenna section and it also occurs in limestone L$_7$. The limestone lens reaches a thickness of 6 m and a length of 12-15 m. The central part of the bioherm (core) is composed of massive light-gray limestone with poorly preserved texture. The microphotograph (Pl. 2C) illustrates recrystallized probably primary microbial origin mudstone with scattered foraminifers and dark round tubes. The upper part of the buildup consists of crinoidal limestones, which contain the solitary rugose corals *Axolithophyllum*, *Yuanophylloides* and *Monophyllum*, the tabulate corals *Cladochonus* and bryozoans. A crinoidal layer is distributed locally and thinned along strike. Towards the marginal parts the thickness of the limestone L$_7$ is reduced to 2.5-3 m.

A characteristic feature of the Moscovian bioherms is the presence of cylindrical tubes (Figs 6D, F; Pl. 2C). Their diameter varies from 0.6 to 4 mm and maximum length is 3 cm. Most tubes are straight; curved tubes connected with straight ones are only occasionally observed. They can form clusters in which the tubes may be in contact to each other, but do not intersect, and are located within a distance of 5 mm. Most of these tubes are oriented perpendicular to the surface layers. Thus the characteristic feature of limestone texture is the presence of cylindrical channels, which are probably the traces of unknown borrowing organisms possibly worms for which the name *Tubulus* was proposed (Ogar, 2007). Similar structures are described in the Pennsylvanian of the South China, where they regarded as probably worm tubes (Zhang et al., 2010).

Coral and chaetetid limestones are very common in the lower part of the Moscovian; the top of the Kamenka Suite, C$_2^5$(K), limestone K$_8$, and in the middle part of the Almazna Suite,C$_2^6$(L), limestone L$_5$. They have been studied in outcrops on the Karahuz, Pashenna sections and near the railway station Izvaryne. These bioconstructions are considered to be coral and coral-chaetetid biostromes because there are no significant changes in the thickness of these limestones along strike.

Limestone K$_8$ is composed mainly of colonies of the fasciculate rugose coral *Donophyllum* (Pl. 1E) and chaetetids. Individual *Donophyllum* colonies have significant size - up to 30 cm in height and up to 1 m in diameter. Limestone L$_5$ comprises massive colonies of the rugose coral *Petalaxis* (Pl. 1D) and chaetetids. They are mentioned by Fomichev (1953), who indicates that in the section near the railway station Maryivka, limestone L$_5$ has a thickness of 10 m and contains *Petalaxis maccoyanum*. Dimensions of the colonies reach 0,75-1 m in diameter (Fomichev, 1953). The biostromes have an even surface. Their central part (core) is composed of coral boundstone including calcareous algae, crinoids, brachiopods, foraminifers. Along their strike they are replaced by packstone-wackestone with foraminifers and calcareous algae.

To the top of the Moscovian deposits of the Donets Basin (the Isaivka Suite, C$_3^1$(N), limestones N$_2$ and N$_3$) chaetetids form biostromes. Vassiljuk (1959) named them chaetetid beds. In the biostrome in the outskirts of the Kalynove key-section *Chaetetes mosquensis* Stuckenberg (Pl. 1F) reaches 30-40 cm in height and 1.2 m in width.

3.6. Gzhelian

The Gzhelian buildup is located in the northern part of the left bank of Lugan River, near the village Kalinove (Avilovka Suite, C$_3^2$(O). In the “Stone Gate” outcrop a bioherm has a lenticular shape with a maximum thickness of 5.2 m that decreases along the strike to 0.7-1.0 m (Aizenverg et al., 1975). It is confined to limestone O$_6^1$. Vassiljuk (1974) considered that it consists of *Palaeoaplysina*.

According to our data this buildup is an algal-sponge bioherm. It is composed primarily of phylloid algae (Pl. 3H). D. Vachard (pers. com.) identified also primitive forms of *Tubiphytes* and perhaps cyanobacteria (Pl. 2D, E, H). Some parts of the bioherm also consist of aggregates of spicules of siliceous sponges (Pl. 2F). Spicules are in some cases scattered in the dark mass of primitive *Tubiphytes*, probably trapped in the growth process (Pl. 2D). Often there are also bryozoans, and foraminifera. Sponge spicules dominant limestone is similar to those described from the Late Viséan of NE Morocco (Aretz & Herbig, 2008).

The solitary rugose corals *Amplexus* and *Sestrophyllum* are rare in this limestone. Along the strike these limestone are replaced by dark-grey clayey limestone with different macrofauna. In the quarry on the eastern outskirts of Luganske (section Buchkov Yar) a coral rudstone bed about 30 cm thick is observed in the same limestone O$_6^1$. It consists of large debris of solitary rugose corals *Bothrophyllum* and *Arctophyllum*. It seems that these coral accumulations were deeper than algal-spicule bioherms.

4. Interpretation

Reef structures have not been found in the Tournaisian deposits. Perhaps favourable conditions for their formation may occur on the western extension of the Donets Basin and in the Dnieper-Donets Depression. In the Donets Basin first bioconstructions appeared only in the Viséan with the emergence of a wide variety of colonial rugose corals. Moreover, the maximum development of buildups is during the Late Viséan and Late Serpukhovian. At late Viséan time formed coral biostromes, at late Serpukhovian occured coral and coral-chaetetid biostromes and bioherms. The abundance of remains of various organisms occurring in association with reef builders, the rock textures and the encasing deposits show that buildups are formed under favourable

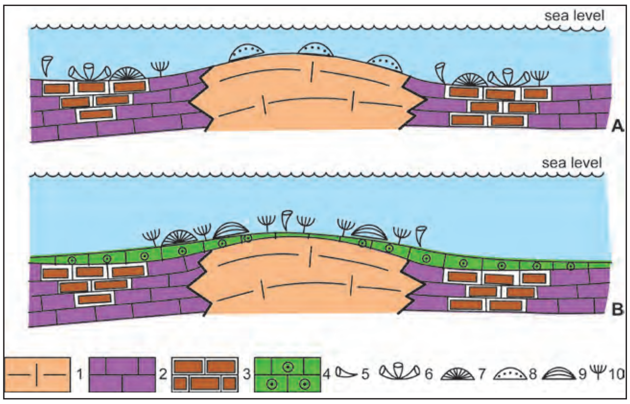

Figure 7. Model for the development of the shallow water shelf with microbial buildup: to deepen (A) and after the deepening of the basin (B). Limestones: 1: microbial, 2: bioclastic, 3: coral-chaetetid boundstone, 4: crinoidal rudstone. Fauna and Flora: 5: solitary rugose corals, 6: colonial rugose corals, 7: chaetetid sponge, 8: microbial organisms, 9: stromatolites, 10: crinoids.

conditions of the shallow water shelf. The coral buildups do not reach a significant thickness due to reduced accommodation space of a slowly sinking shelf. But, it is possible that they could achieve considerable thickness, if such bioconstructions are located on the border of the shelf edges and deeper basins (Aretz & Chevalier, 2007). Then the steady subsidence of the shelf edge could be compensated by the growth of colonial organisms. Such areas may be found in the deep parts of the Donets Basin and Dnieper-Donets Depression.

So, only the Upper Viséan *Siphonodendron* biostromes are interbedded into limestone facies. Carbonate sedimentation during this period occurred in a shallow-water shelf environment with slow sea-level fluctuation.

The most parts of the studied bioconstructions are located in the Donets Basin coal-bearing rocks of the Upper Serpukhovian and Pennsylvanian. They are also predominantly shallow-water biostromes and bioherms. But due to periodic interruption of carbonate sedimentation in the cyclothems, the bioconstructions did not reach important heights.

During Pennsylvanian times calcareous algae and probably microbial organisms played an important role in the formation of buildups. In Bashkirian times coral and coral-chaetetid biostromes as well as algal bioherms formed. But chaetetid sponges were involved as reef builders only since late Viséan up to the end of the Moscovian. During Moscovian time along with the coral and coral-chaetetid biostromes were common bioherms, a probably microbial origin is still not enough studied. An algal-sponge origin can be postulated for Gzhelian bioherms in the Donets Basin.

The studied Pennsylvanian bioconstructions of the Donets Basin formed in shallow water. Locally the interaction of a variety of bioconstructors (algae, probably microbial communities, algal-sponge associations) resulted in the appearance of mounds resistant to the destruction by waves. Ecospace between the mounds was populated by a variety of benthic organisms, among which were especially numerous brachiopods, bryozoans, crinoids as well as colonial and solitary rugose corals and chaetetid sponge forming underwater thickets. But even during a small increase in the deepening of the basin growth of builders was stopped, and crinoid thickets on the mounds developed.

The simplified hypothetical model for the development of the Moscovian shallow shelf with microbial buildup (limestones L_{6-7}) is shown in Figure 7. Further deepening of the basin led to a complete stop of carbonate sedimentation and burial of the carbonate rocks by clayey sediments. As a result, at different stratigraphic levels buildups are covered by clayey or crinoidal facies. Along strike the buildups facies are replaced by bioclastic limestones or in some cases coral rudstones or coral and chaetetid sponge biostromes.

5. Comparison with other areas

Similarly to the Donets Basin, Carboniferous buildups occur at various stratigraphic levels in other regions (see recent reviews of Wahlman (2002), Kuznetsov & Antoshkina (2006) and Aretz &Vachard (2007).

Tournaisian-Lower Viséan reefs were found in the Dnieper-Donets Depression by seismic surveys and drilling (Lukin & Vakarchuk, 1999; Machulina, 1996). But the nature of this carbonate structures has not been investigated in details yet. Most wells cut through predominantly bioclastic Tournaisian-Viséan rocks.

Most common are Upper Viséan buildups. In addition to the Donets Basin, they occur in similar stratigraphic levels of the Lvov-Volyn basin (Shul'ga & Ogar, 2009), are known in Western Europe, Urals, Japan and many other places of the world (Aretz, 2002a, 2002b; Aretz & Chevalier, 2007; Aretz & Webb, 2007; Aretz & Herbig, 2003a, 2003b, 2008; Kuznezov & Antoshkina, 2006; Somerville et al., 2003). Similar to coral biostromes of the Donets Basin these formations are also known in Western Europe - Belgium, north-west of Ireland, Spain and other countries, as well as in North Africa where framework are formed by *Siphonodendron* colonies (Aretz, 2001, 2002; Aretz & Herbig, 2008; Somerville et al., 2009; Aretz et al., 2010). Most similar to the Donetsk ones are biostromes described in Belgium from the Royseux area (Aretz, 2001, 2002). They are built mainly by the colonial rugose corals *Siphonodendron* and *Lithostrotion.*

The Late Serpukhovian-Early Bashkirian buildups are known on the Northern Outskirts of the Donets Basin (Lukin et al., 1979), the Caspian depression (Kuznezov, 1998; Konyukhov et al., 2006) and in the Urals (Kulagina et al., 2009). Contemporaneous reefal facies was discovered in wells in the northern outskirts of the Donets Basin (Lukin et al., 1979), but they were not studied in detail.

The same situation can be applied to the Caspian Basin and the Urals, where the bioherm facies composed barrier reef mounds (Kuznezov, 1998; Konyukhov et al., 2006). Serpukhovian-Early Bashkirian bioherm facies of the Southern Urals are documented in details (Kulagina et al., 2009). These are mainly small algal bioherms, which have dimensions of 10-15 m and height of 3-5 m.

Coral biostromes and bioherms are known from the Upper Moscovian deposits of the Moscow Basin. Massive colonies of the massive corals *Ivanovia* and chaetetids form small bioherms in the middle part of the Podolskian Horizon (Makhlina et al., 2001). Algal bioherms are described in the Podolskian Horizon of the western part of the Moscow Basin (Ilhovsky, 1975). Their thickness is 1-5 m. Persistent along strike coral-chaetetid beds (biostrome), comprising chaetetids colonies and massive rugosan *Petalaxis* and *Ivanovia,* are distinguished at the base of the Myachkovian Horizon (Makchlina et al., 2001).

In Western Europe Pennsylvanian bioconstructions are described in the Cantabrian Mountains (northern Spain). Here various bioconstructions built by calcareous algae, chaetetids, rugose and tabulate corals, and bryozoans are documented (Minwegen, 2001; Samankassou, 2001). Very similar to the Bashkirian algae bioherms of the Donets Basin (limestone F_1) were described as *Donezella* buildups from the San Emiliano Formation of Cantabrian Mountains (Samankassou, 2001).

The chaetetid buildups at the top of the Moscovian Stage, were studied in south-eastern Kansas (Marmaton Group) (West & Clark, 1984), Central Texas and New Mexico (Late Atokan) (Sutherland, 1984) and Mexico (Almazán-Vázquez et al., 2007).

In the central parts of the Caspian basin synchronous deposits are made of thin (a few tens of meters) deep clay-carbonate rocks of the uncompensated basin, among which are the individual reef tracts that have arisen within the various paleoshallow sites in the Caspian Sea (Kuznezov, 1998). In the eastern part of the depression are found microbial-algal "carbonate mounds" similar to Donetsk ones which are believed to have emerged in parts of the paleoshelf edge (Konyukhov et al., 2006).

The most studied Upper Carboniferous reefs are located in the Uralian Foredeep. They can be traced along the eastern margin of the East European Platform in the area of its junction with the Uralian Foredeep (Shcherbakov & Shcherbakova, 1986; Vennin, 1997). Most of them were discovered by wells, but some are exposed to the surface and carefully studied. Among them are Voskresenka Reef, Plakunsky Reef, and Ust-Koyvynskian bioherms. Along with calcareous algae and bryozoans, palaeoaplysins also played a significant role in the construction of these buildings. Unlike the Upper Carboniferous buildups of the Donets Basin, these are typical reefs. One of them, Voskresenka Reef is exposed in the form of elongated hill of about 80 m in height, with length of 2.0 km and width of 200 m. Its frame is constructed mainly bryozoans and calcareous algae (Alexandrov & Einor, 1984).

Upper Carboniferous-Lower Permian buildups very similar to the Gzhelian bioherms of the Donets Basin are described from Carnic Alps, where they are composed of phylloid algal and calcisponge-*Shamovella* boundstone (Samankassou, 2003). The large Pennsylvanian (Gzhelian) coral reef described recently in Guizhou (South China, Zhang et al., 2010) is so far rather unique and nothing comparable has been found in the Donets Basin.

6. Conclusions

Coral, coral-chaetetid, chaetetid biostromes and coral-sponge, calcareous algae, calcareous algae-sponge and probably microbial bioherms can be identified in the Donets Basin. Carbonate bioconstructions as well as coral and chaetetid sponge rudstones occur in the Donets Basin during Carboniferous time only in specific stratigraphic levels. They are confined to the Lower Viséan (probably), upper parts of the Viséan, Upper Serpukhovian, Lower Bashkirian, Upper Moscovian and Gzhelian sediments (Fig. 8). However, the composition of the bioconstructors in the Donets Basin has changed over time. The coral biostromes appeared in late Viséan. Coral, chaetetid sponge and "stromatoporoid"-like fossils formed biostromes and bioherms during the late Serpukhovian. At Bashkirian time along with coral, coral-chaetetid and chaetetid biostromes, developed also algae bioherms. Coral and coral-chaetetid biostromes were also common at Moscovian time, but along with them were also the bioconstructions formed probably by microbial communities. At the end of Moscovian time in the Donets Basin extend the chaetetid biostromes. At the similar stratigraphic levels they were studied in many areas of the world. At Gzhelian time in the Donets Basin appeared algae-sponge bioherms.

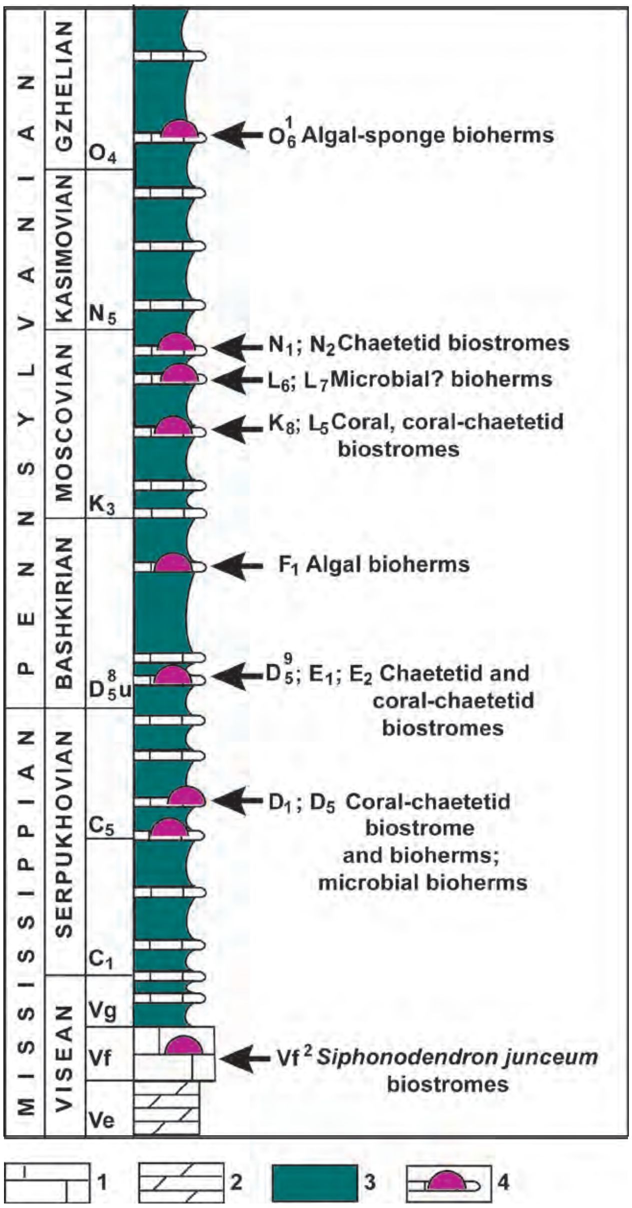

Figure 8. Distribution of the Carboniferous buildups in the Donets Basin. Legend: 1: limestone, 2: marl, 3: alternation of sandstones, siltstone, shale and coals, 4: limestone with buildups.

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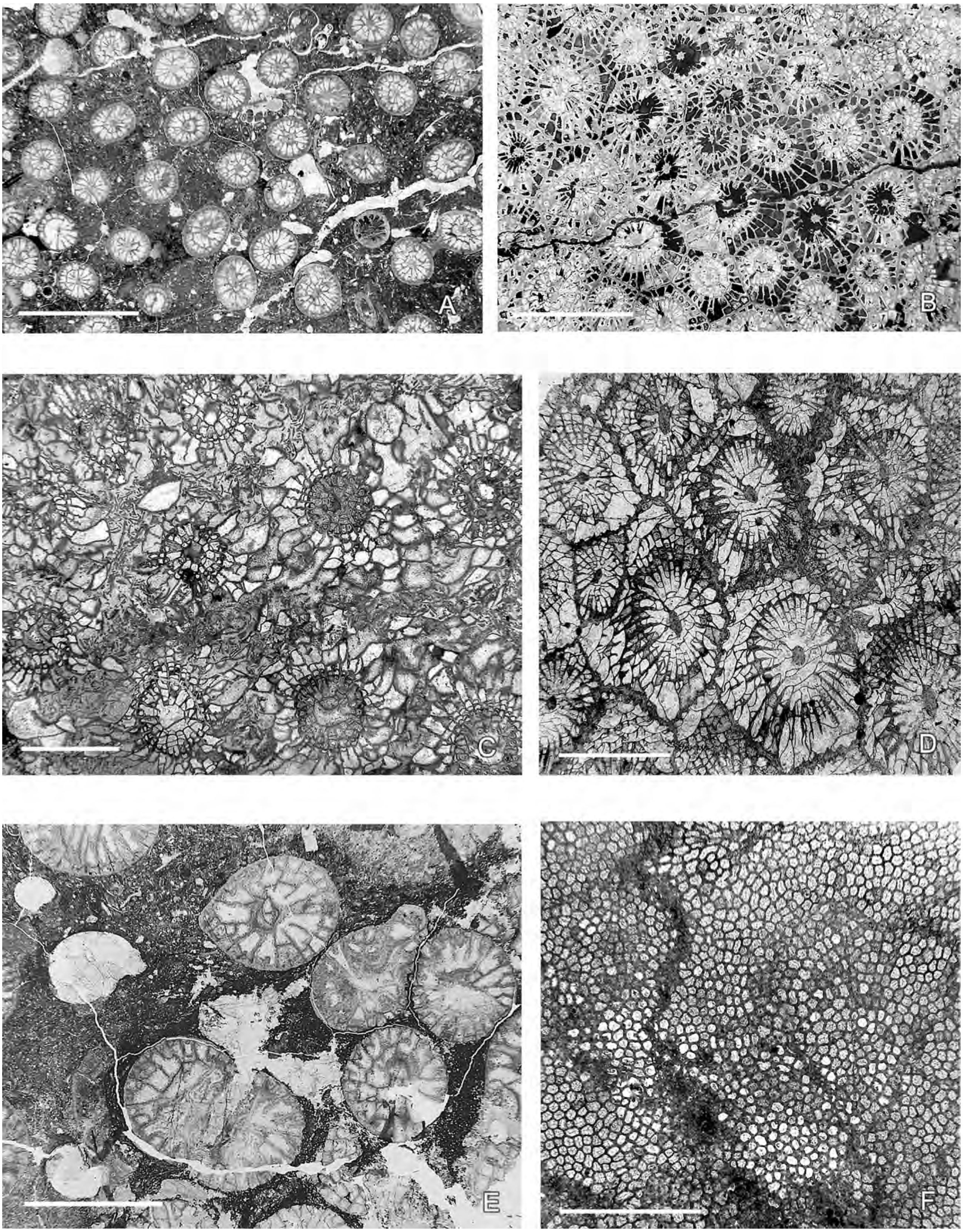

Plate 1. Typical Carboniferous coral and sponge boundstones of the Donets Basin (scale: 5 mm). A: *Siphonodendron junceum* (Fleming) (coral bafflestone, village Kypucha Krynytsa, Donetsk Suite ($C_1^v f$). B: *Lithostrotion maccoyanum* (Edwards & Haime), coral framestone, village Starobesheve, Kalmiuska Suite, limestone D_5. C: *Aulina parasenex* Vassiljuk; coral framestone, village Starobesheve, Kalmiuska Suite, limestone D_5. D: *Petalaxis donbassicus* (Fomichev), coral framestone, railway station Izvarine, Almazna Suite, limestone L_5. E: *Donophyllum intermedium* Fomichev, coral bafflestone, Karaguz section, Almazna Suite, limestone L_5. F: *Chaetetes mosquensis* Stuckenberg, chaetetid-sponge framestone, village Kalynove, Isaivka Suite, limestone N_3.

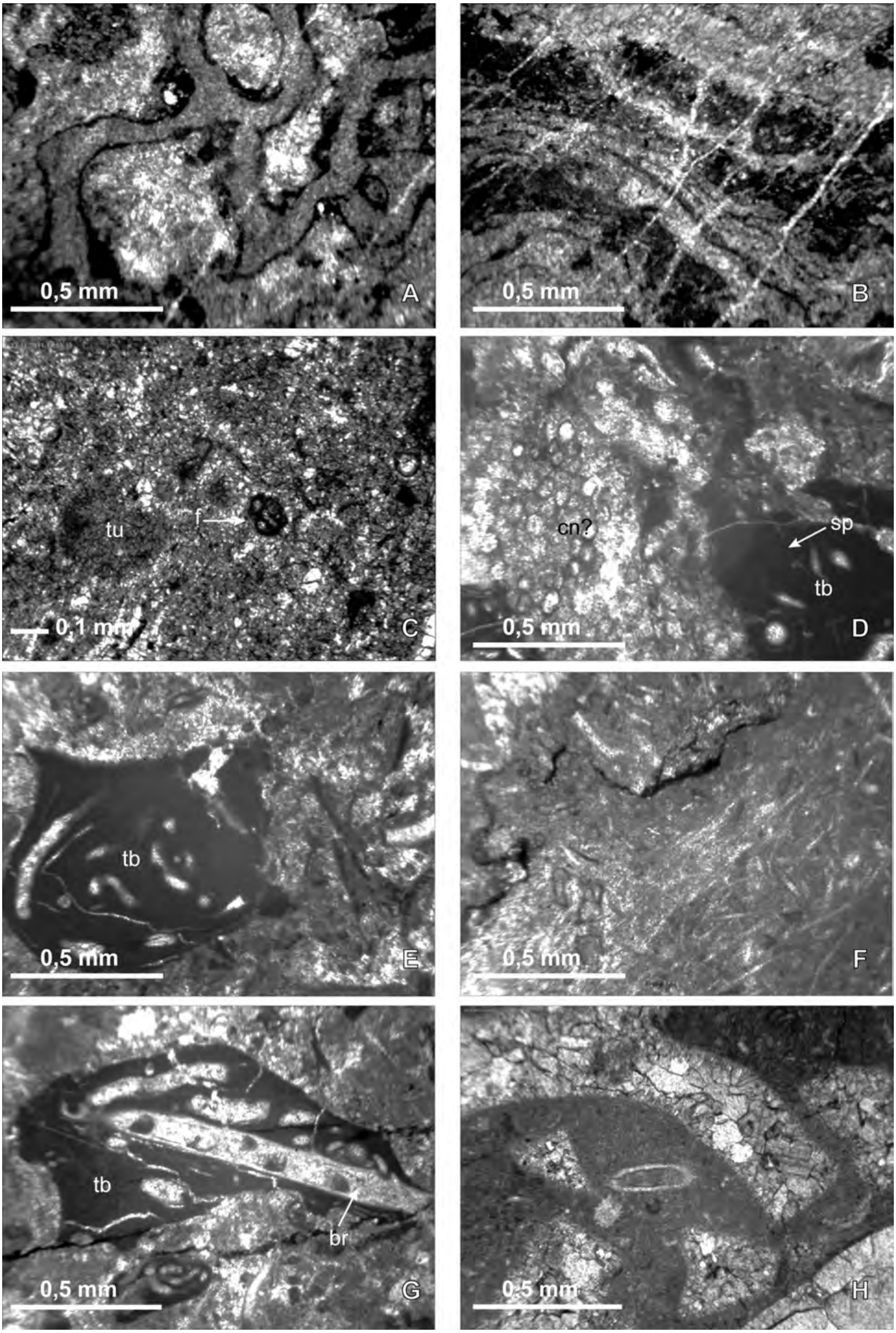

Plate 2. Microfacies of the Pennsylvanian limestones of the Donets Basin. A: Algae bafflestone, composed of possibly phylloid algae or "*Contortiporidium*" Maslov, 1973, limestone F_1, village Volnukhino, Mandrykinska Suite. B: Algae boundstone consisting probably *Archaeolithophyllum lamellosum* Wray, 1964 village Volnukhino, Mandrykinska Suite. C: Recrystallized probably primary microbial limestone with scattered in it foraminifers (f), dark round tube (tu), Karahuz section, limestone L_7. D-H: Algae-sponge bioherm, "Stone Gate" outcrop near the village Kalinove, limestone O_6^1. D, E, G: Algae boundstone consisting of cyanobacteria (cn?) or red algae, primitive *Tubiphytes* (tb) with inclusions of sponge spicules (sp) and bryozoans (br). F: Sponge spicule packstone. H: Probably phylloid algae boundstone.

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Paleobiogeographic significance of Bashkirian (Pennsylvanian) rugose corals from northernmost Ellesmere Island, Arctic Canada

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ABSTRACT. The oldest known Carboniferous rugose coral fauna in the Canadian Arctic Islands occurs on the northwestern margin of the Sverdrup Basin, in the Yelverton Inlet area of northern Ellesmere Island. It was collected from Bashkirian carbonates of the lower Nansen and Otto Fiord formations and includes representatives of the genera *Dibunophyllum* Thomson & Nicholson, *Lonsdaleia* McCoy, *Palaeosmilia* Milne-Edwards & Haime and ?*Tizraia* Said & Rodríguez. Such a combination of genera is unknown elsewhere above the Serpukhovian and in this sense it is unique in the world. It is typical, however, for coral faunas in the Upper Viséan of Europe, North Africa and China. In those areas, genera of this assemblage range into the Upper Serpukhovian and individual genera such as *Dibunophyllum* in the Donets Basin and *Palaeosmilia* in Northern Timan and Novaya Zemlya continue into the Lower Bashkirian. The Yelverton Inlet fauna shows limited similarity to Serpukhovian faunas of several other basins but differs from the Bashkirian faunas of those basins. It is remarkable because of its unusual taxonomic content, high stratigraphic position, and remote geographic location. Faunal comparisons suggest Novaya Zemlya as the most likely source for the Yelverton Inlet fauna. Northern Timan may qualify as another possible source when its Viséan to Bashkirian coral fauna is described in detail.

KEY WORDS: Rugosa, mid-Carboniferous, paleobiogeography, Sverdrup Basin.

1. Introduction

The rugose corals described in this paper were collected from the Yelverton Inlet area in northernmost Ellesmere Island. They occur on the northwestern margin of the Sverdrup Basin, a southwest-northeast trending rift basin underlying the northern islands of the Canadian Arctic Archipelago (Fig. 1). Within the basin, the Carboniferous succession comprises a marginal facies dominated by siliciclastic rocks, passing basinward into platform carbonates, siliciclastics and basinal deposits (Beauchamp et al., 1989, p. 106). The stratigraphic interval yielding the Yelverton Inlet corals consists of outer shelf, Bashkirian carbonates of the lower Nansen Formation, passing southeastward into the subaqueous evaporite deposits and interbedded, fossiliferous limestone beds of the lower Otto Fiord Formation (Mayr, 1992, fig. 16; Fig. 2, Table 1). The coral specimens available for this study are limited in number (see below) because they were obtained from remote localities (Fig. 1) under arctic conditions, with no opportunity for further collecting.

Our oldest collection [Geological Survey of Canada (GSC) locality C-45455], from the lower Otto Fiord Formation, contains the first newcomers to the Sverdrup Basin (Fig. 2, coral collection 2; Fig. 3). The material available from this locality includes one specimen of *Tizraia*? sp. aff. "*Diphyphyllum*" *carinatum* Gorsky, 1951, five specimens of *Palaeosmilia murchisoni* Milne Edwards & Haime, 1848 and three specimens of *Lonsdaleia duplicata* (Martin, 1809). Such an occurrence at this biostratigraphic level is unusual, because this association of species is typical for much older, Upper Viséan strata. In addition to this lowest fauna, a single specimen of *Dibunophyllum bipartitum* (McCoy, 1849), also characteristic of the Viséan and Serpukhovian, was found in slightly younger Bashkirian limestone of the Nansen Formation (Fig. 2, coral collection 1; GSC locality C-45420; Fig. 3). The youngest coral in our collection is a single specimen of *Paraheritschioides* Sando, 1985, which was collected still higher in the Nansen Formation, from beds of probable late Bashkirian age (Fig. 2, coral collection 1; GSC locality 45444; Fig. 3).

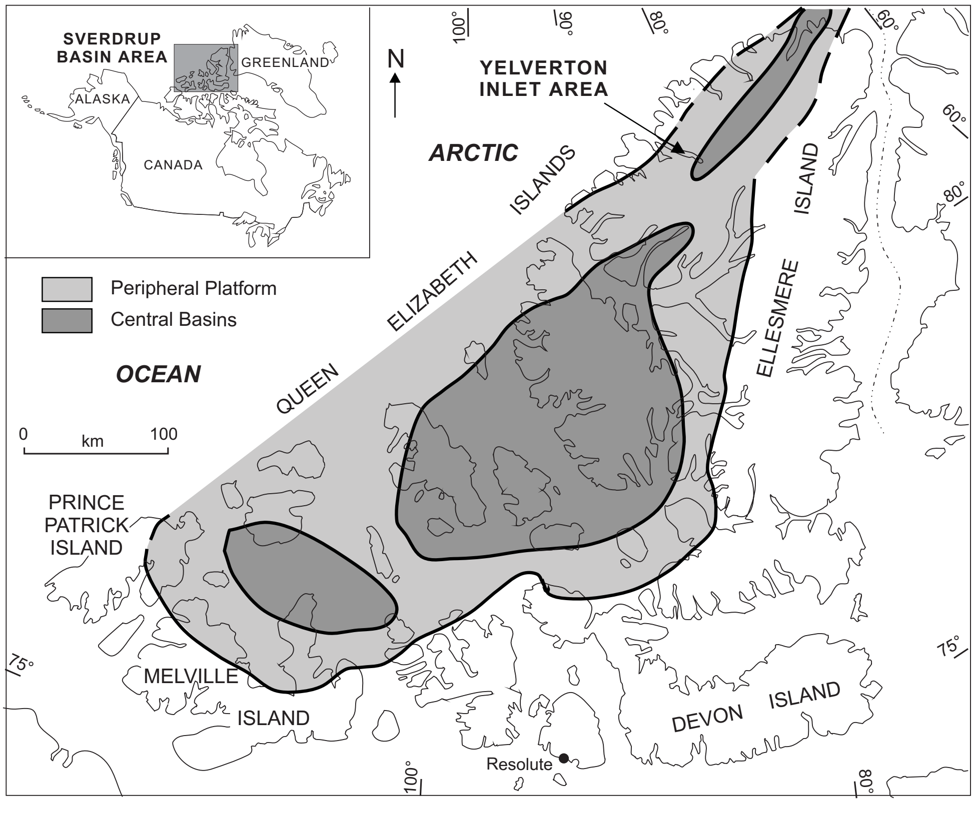

Figure 1. Sverdrup Basin, Canadian Arctic Archipelago; after Beauchamp et al. (1989, fig.1).

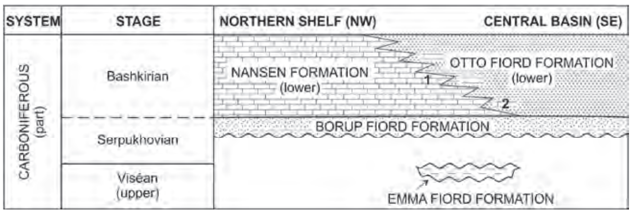

Figure 2. Stratigraphic relationships, Upper Viséan-Bashkirian formations, northwestern side of Sverdrup Basin; after Mayr (1992, fig. 16). Coral collections: 1 (GSC localities C-45444, C-45420), 2 (GSC locality C-45455).

The Bashkirian age assignment for our corals was derived from associated foraminiferal faunas first identified by B. L. Mamet and C. A. Ross (Mayr, 1992, p. 110, GSC localities C-45383 and C-45421). This age was confirmed by subsequent foraminiferal studies by D. Baranova (appendix in Fedorowski & Bamber, in review), who identified several species of the genera *Pseudostaffella* Thompson, 1942 (e.g., *P. timanica* Rauser, 1951) and *Parastaffella* Rauser-Chernousova, 1941 in consultation with E. I. Kulagina and N. B. Gibshman.

2. Faunal analysis

The Yelverton Inlet rugose coral fauna is significant for several reasons. First, it is the oldest coral fauna in the Sverdrup Basin, with several newly arrived taxa. Second, three species listed below either belong to or are closely comparable to the uppermost Viséan-Serpukhovian coral fauna of the Western European Province. Third, the species in common with that province suggest the development of open marine communication between western Europe and western North America around the northern margin of Euramerica. Communication around its southern margin has been confirmed by Bamber et al. (in preparation). Finally, our specimen of *Paraheritschioides* represents the oldest known occurrence of that genus in the world.

Late Viséan (Brigantian) rugose coral faunas diminished markedly on a world-wide scale near the end of that substage or soon afterward as a result of early Variscan orogenic movements and subsequent drastic environmental changes. Areas inhabited by corals were either uplifted or subjected to shallow water clastic sedimentation preventing both temporary settlement by larvae and permanent colonization by corals. Western and Central Europe exemplifies such changes. Extremely rich and diversified Late Viséan (Asbian and Brigantian) coral faunas were drastically reduced at the end of the Viséan (Fedorowski, 1981), with only a few dissepimented solitary and colonial genera, accompanied by small, nondissepimented taxa, surviving in the British Isles and continuing into the Serpukhovian. In the context of this paper, *Dibunophyllum bipartitum* (McCoy, 1849), *Palaeosmilia murchisoni* Milne Edwards & Haime, 1848 and *Lonsdaleia duplicata* (Martin, 1809) are the most important of these survivors. However, all of them disappeared from the Western European Province before the end of the Serpukhovian. Thus, that area was eliminated as a source area for our fauna.

Representatives of Late Viséan/Serpukhovian faunas continued to develop in several scattered parts of the world (Fig. 4) until the end of the Serpukhovian or slightly longer. The most important of those sites are:

1. The Donets Basin, which occupies the westernmost part of the Eastern European Province. It has yielded diversified coral faunas (Vasilyuk, 1960), which partly resemble the Upper Viséan fauna of Western European Province, but generally range higher in the section, into the Upper Serpukhovian. A few taxa range into the Lower Bashkirian. The Donets Basin species of greatest importance for our study are *D. bipartitum, P. murchisoni* and a probable representative of *L. duplicata*. However, none of those species extended to the Bashkirian in that area. *D. finalis*, known from the upper part of the *Reticuloceras-Bashkortoceras* Biozone (upper Kinderscoutian or upper Krasnopoljan) is a morphologically simplified species endemic to the Donets Basin.

2. North Africa, in which several basins developed during Carboniferous time in various areas presently occupied by the Sahara Desert. Very rich collections have been described from these areas by several authors (e.g., Menchikoff & Hsu, 1935; Semenoff-Tian-Chansky, 1974, 1985; Said & Rodríguez, 2007), but neither *Dibunophyllum bipartitum* nor *Palaeosmilia murchisoni* has been described above the top of the Serpukhovian, either in the listed papers or in the most recent study by Rodriguez et al. (2011). The latter publication contains the first confirmed report of *Lonsdaleia* in North Africa, from the northern Tindouf Basin, southern Morocco. In that occurrence, however, only the genus is listed, but not the species *L. duplicata*. Also, representatives of *Lonsdaleia* disappear in bed M, i.e., well below the top of the Brigantian, whereas representatives of other taxa continued to develop (Rodriguez et al., fig. 2). Only *Palaeosmilia*, not yet identified to species level, has been reported in the Bashkirian of the area by Semenoff-Tian-Chansky (1974) and I. D. Somerville (pers. comm., 2012). Specimens included by Semenoff-Tian-Chansky (ibid.) in Carruthers' (1909) species "*Campophyllum*" *carinatum* from Novaya Zemlya have been excluded by us from that northern taxon (Fedorowski & Bamber, submitted). Despite the few faunal similarities listed above, it would be difficult to find routes leading directly from the scattered Lower Carboniferous basins of North Africa to the northern part of the Sverdrup Basin.

3. Novaya Zemlya, where strata of probable Late Viséan/Serpukhovian age have yielded highly diversified coral faunas, described by Gorsky (1938, 1951). Unfortunately, collections from this area, which were gathered in conjunction with geological mapping and prospecting, are incomplete and the number of specimens is restricted. As a result, some of the described species are based on insufficient data. Nevertheless, the presence of *Dibunophyllum bipartitum, Palaeosmilia murchisoni* and *Lonsdaleia duplicata* can be accepted with a reasonable degree of certainty. In addition, these three species are associated with corals most probably related to *Tizraia* Said & Rodriguez, 2007, described by Gorsky (1951) as his new species *Diphyphyllum carinatum*. Lonsdaleoid dissepiments, which are variably developed in *Tizraia*, are absent from the Novaya Zemlya specimens and those from the Sverdrup Basin. This is the only significant difference between the northern specimens and *Tizraia*, and is adequate for no more than a subgeneric distinction.

4. The northern Timan area, located south-west of Novaya Zemlya (Fig. 4, locality 4) has yielded various Carboniferous rugose coral faunas from Brigantian, Serpukhovian and younger strata. Unfortunately, neither the old taxonomic paper by Stuckenberg (1895) nor the more recent paper by Kossovaya (1996) dealing with the question of the mid-Carboniferous rugose coral recovery offers modern and comprehensive, illustrated information on those faunas. Thus, we consider northern Timan as only a potential but still unproven source for the Bashkirian rugose corals of the Sverdrup Basin.

5. The Upper Viséan/Serpukhovian coral faunas of China should also be mentioned here as having potential significance for the Yelverton Inlet fauna. Among many species described from that area, at least *Dibunophyllum bipartitum* and *Palaeosmilia murchisoni* should be listed as almost certainly present. *Lonsdaleia duplicata* is mentioned as well (Fan et al., 2003) but the occurrence of that species cannot be confirmed from the published illustrations. During late Viséan-Bashkirian time, however, the Chinese microcontinents, like North Africa,

GSC locality	Map location	Formation	Interval
C-45444	81°54.59'N, 79°24'W	Nansen	368 m above base
C-45420	81°54.59'N, 79°24'W	Nansen	206.5-207.5 m above base
C-45455	81°56.72'N, 79°12'W	Otto Fiord	Lower

Table 1. Register of Geological Survey of Canada (GSC) localities.

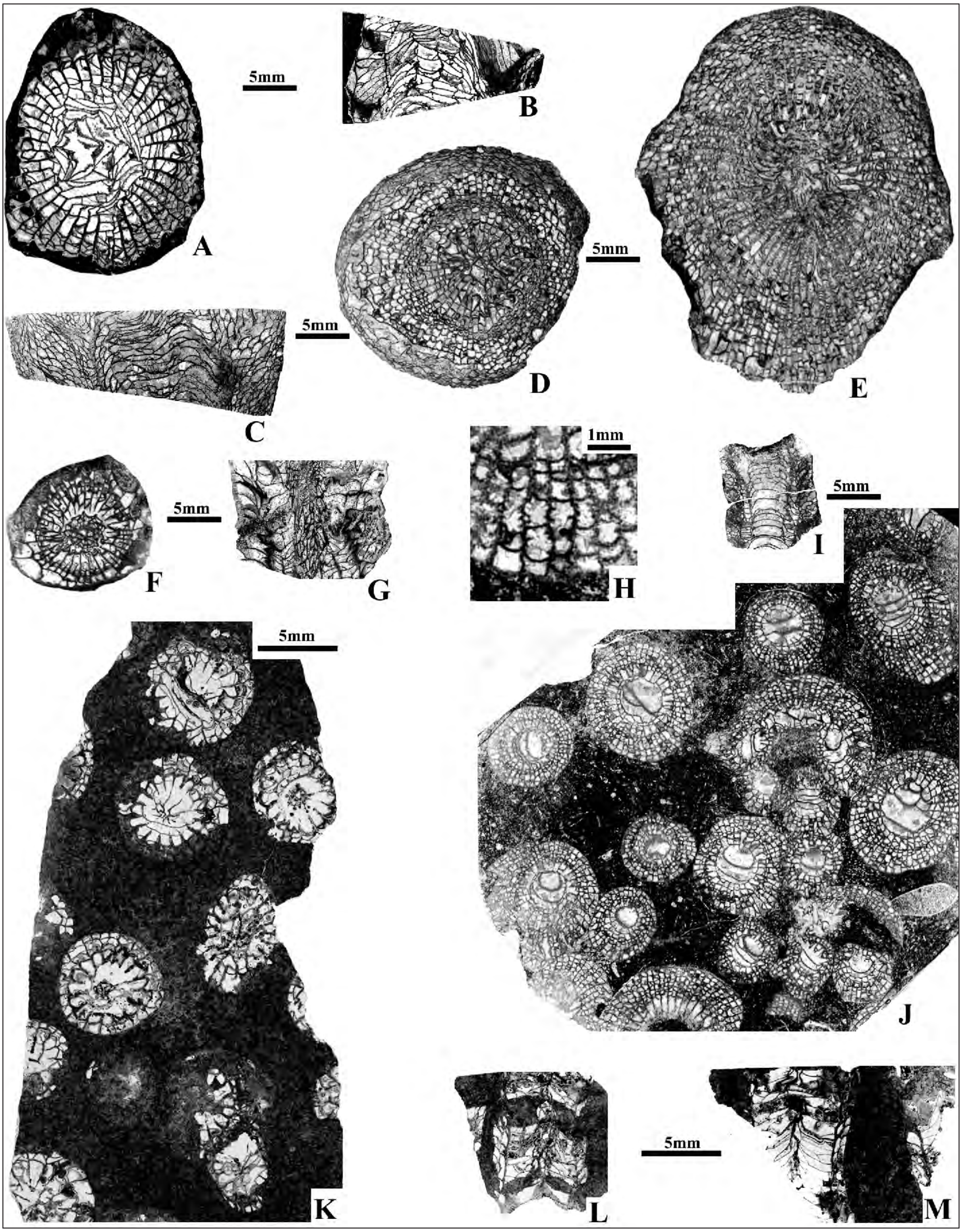

Figure 3. Examples of coral specimens studied. All specimens were collected from the Nansen and Otto Fiord formations in the Yelverton Inlet area of northernmost Ellesmere Island (see locality register). All figured specimens are stored in the Geological Survey of Canada type collection, Ottawa; illustrations are from thin sections. In transverse sections of solitary specimens, the cardinal protoseptum is orientated downward. A-B: *Dibunophyllum bipartitum* (McCoy, 1849); hypotype GSC 133208, Geological Survey of Canada (GSC) locality C-45420, Nansen Formation. A: Transverse section. B: Longitudinal section. C-E: *Palaeosmilia murchisoni* Milne-Edwards & Haime, 1851; Otto Fiord Formation. C, D: hypotype GSC 133209, GSC locality C-45455, specimen G. C: Longitudinal section. D: Transverse section. E: Hypotype GSC 133210, GSC locality C-45455, specimen A; transverse section. F, G: *Lonsdaleia duplicata* (Martin, 1809); hypotype GSC 133211, GSC locality C-45455, specimen F; Otto Fiord Formation. F: Transverse section. G: Longitudinal section. H-J: *Tizraia* sp. aff. "*Diphyphyllum*" *carinatum* Gorsky, 1951; hypotype GSC 133212, GSC locality C-45455, specimen C; Otto Fiord Formation. H: Fragment of colony, transverse section. I: Longitudinal section. J: Transverse section showing carinae well preserved (left) and diagenetically altered (right). K-M: *Paraheritschioides* sp.; hypotype GSC 133213, GSC locality C-45444; Nansen Formation. K: Fragment of colony, transverse section. L, M: Longitudinal sections.

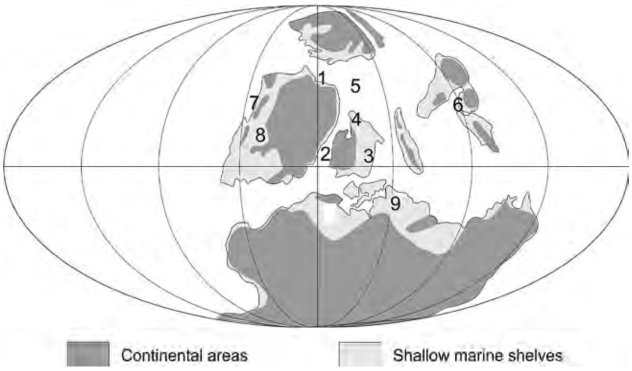

Figure 4. Bashkirian paleogeography and coral distribution, simplified and slightly modified after Fedorowski (1981, fig. 2). Legend: 1: Sverdrup Basin, 2: Western European Province, 3: Eastern European Province, 4: Northern Timan, 5: Novaya Zemlya, 6: Chinese microcontinents, 7: Stikine terrane, 8: southern Canadian Rocky Mountains, 9: North Africa.

were located much farther from the Sverdrup Basin than were Northern Timan and Novaya Zemlja. Therefore, an influence from China on our fauna is unlikely.

Our analysis of all important sites in the world yielding Serpukhovian rugose coral faunas (Fedorowski & Bamber, submitted) has eliminated most of them as potential sources for the Yelverton Inlet fauna. Their faunas became extinct too early (Western European Province), differ in their general content (e.g. the Voronezh Uplift, Moscow Basin), or there is doubt concerning the age and number of species in common with the arctic Canadian fauna (China).

Two western North American areas - the cratonal southern Canadian Rocky Mountains and the accreted Stikine terrane - have both yielded many European Upper Viséan and Serpukhovian coral taxa and should be of special value for comparison with the Yelverton Inlet fauna. However, the Rocky Mountain fauna contains no species in common with the arctic fauna (Bamber et al., in preparation) and only a single corallite from the Stikine terrane was identified by the present authors as *Dibunophyllum bipartitum* (Fedorowski & Bamber, in preparation).

3. Concluding remarks

Our brief analysis of the main areas of Upper Viséan/Serpukhovian rugose coral occurrences with rare species extending into the Lower Bashkirian allows some general conclusions to be drawn. (1) Faunas of that age, derived from the widely separated sites discussed above, may be comparable in having several taxa in common, but they differ considerably when their entire contents are analyzed. This may have resulted not only from isolation of these sites, but also from the influence of living conditions. Compared to the other faunas discussed above, the Yelverton Inlet fauna contains relatively few taxa. However, from their low stratigraphic occurrence it may be concluded that the Yelverton Inlet corals were undoubtedly pioneers in the Sverdrup Basin. (2) The almost complete absence from the Rocky Mountains and Stikine terrane of species in common with the Yelverton Inlet fauna suggests there was no direct marine communication between these northern and western regions through northwestern Euramerica. Northward migration from the western areas must have been prevented by physical or sedimentological barriers presently unknown to us (Fig. 4). (3) From faunal comparisons it appears that Novaya Zemlya and perhaps Northern Timan are the most likely sources for the Yelverton Inlet fauna. Unfortunately, the late Viséan/early Bashkirian rugose coral faunas of Northern Timan cannot be reliably assessed without an up-to-date, completely illustrated study. We have drawn our conclusion on the source of our fauna despite some reservations concerning the indefinite Late Viséan/Early Namurian age assignments given by Gorsky (1951). In our opinion there is a good possibility that the corals identified by that author as *Dibunophyllum bipartitum, Palaeosmilia murchisoni, Lonsdaleia duplicata* and "*Diphyphyllum*" *carinatum* belong to those species and are in common with the Yelverton Inlet fauna. Thus, it appears that these corals must have migrated to the northwestern Sverdrup Basin along the northern margin of Euramerica. This conclusion may change when the Northern Timan rugose coral faunas are better known, but it is presently supported by the geographic positions of both areas - the northern limit of the Eastern European Province for Novaya Zemlya and the northern part of the Sverdrup Basin in northernmost Euramerica for the Yelverton Inlet area. Both of those areas were located at relatively low latitudes in mid-Carboniferous time and appear to have been connected by open marine seaways with conditions suitable for coral migration. It is important to note, however, that the age of our fauna has been determined as Bashkirian, possibly middle Bashkirian, whereas the Novaya Zemlya corals were assigned an indefinite Late Viséan/Early Namurian age by Gorsky (1951). If the latter age is correct, then the fauna must have survived in a refuge of unknown location during the intervening time interval.

4. Acknowledgements

We wish to thank U. Mayr, who collected corals from Yelverton Inlet for the Geological Survey of Canada during the field seasons of 1975 to 1982. The numerous thin sections used in our study were prepared by G. Martin and M. Bartkowiak, M.Sc., and the digital drafting of our text-figures was completed by D. Then. Foraminiferal studies by D. V. Baranova (University of Calgary), in consultation with E. I. Kulagina (Ufa Research Center) and N. B. Gibshman (Paleontological Institute, Moscow), provided valuable information on the age of our collections. Helpful observations and suggestions were given by the reviewers of our manuscript, I. D. Somerville, K. E. Dewing and G. E. Webb. Geological Survey of Canada contribution number 20110228. The paper was also granted by the National Science Centre, Grant number NN 307 074140.

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Gregarious growth versus colonial habit in the rugose coral family Geyerophyllidae Minato, 1955

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ABSTRACT: The family Geyerophyllidae Minato, 1955 includes corals having clinotabulae, lonsdaleoid dissepiments and a variable complex axial structure formed as an extension of the cardinal septum. Included in the family are four genera originally considered to have a colonial (fasciculate) growth habit - *Carniaphyllum* Heritsch, *Carinthiaphyllum* Heritsch, *Lonsdaleoides* Heritsch, and *Darwasophyllum* Pyzhyanov. More recent studies and a review of the type specimens of *Carniaphyllum, Carinthiaphyllum* and *Lonsdaleoides* have shown them to be solitary corals with a gregarious growth habit. In its original description and in all subsequent works, *Darwasophyllum* has consistently been referred to as a fasciculate coral, but the presence of offsets has not been illustrated in the genus and a colonial growth habit has not been clearly demonstrated. Early Serpukhovian specimens of *Darwasophyllum* from the Etherington Formation (Mississippian) in Canada were initially regarded as fasciculate colonies with long, sub-parallel, closely spaced corallites. When they were studied in detail by means of serial sections, however, these corals were found to be solitary individuals grouped into gregaria, without shared structures or offsets. Thus, true colonies are unknown in the Geyerophyllidae and all genera described as colonial in that family consist of gregarious, solitary corals.

KEYWORDS: Solitary corals, Colonialism, *Darwasophyllum*, *Axolithophyllum* Carboniferous, Rugosa.

1. Introduction

Rugose corals show a large amount of variation in growth form, occurring as solitary individuals or as various types of colonies. There is a great deal of diversity in the size and shape of colonial corals, which range in morphology from incipient colonies through branching, fasciculate colonies to various types of massive colonies. Detailed descriptions of the different types of colonies and their methods of development have been published by many authors (e.g., Fedorowski, 1978; Hill, 1981; Scrutton, 1998; Poty, 2010) and are not treated further in this paper. It should be noted, however, that the formation of colonies may be confused with the development of a gregarious growth habit – i.e., the tendency for solitary corallites to grow in groups of closely spaced but separate individuals and form large populations. This is a tendency observed not only in corals, but also in many other invertebrate groups (e. g., brachiopods, rudists, etc.). Because of their contrasting growth forms, massive colonies and gregaria may easily be distinguished from each other. It may be more difficult to distinguish gregarious corals from fasciculate colonies, however, because both may have sub-parallel corallites completely or partly separated by matrix. When these corals occur in growth position and are well preserved, their growth form can be determined by checking for the presence of budding corallites, but this may be difficult if the relationship between corallites is obscured by reworking or poor preservation. Consequently, the growth habits of some taxa have not been accurately described, or colonialism has been inferred only from the presence of individuals either growing together or occurring together in reworked groups. This is especially true in the family Geyerophyllidae, where solitary corals commonly have a gregarious growth habit.

2. Gregarious growth habit *vs.* colonialism in Geyerophyllidae

The family Geyerophyllidae was erected by Minato (1955) for corals having variable, complex axial structures, lonsdaleoid dissepiments and clinotabulae. In a comprehensive review of the taxonomic history and morphology of the family, Minato & Kato (1975) presented a revised diagnosis and emphasized that the axial structures in these corals are connected to the cardinal septum. They also enlarged the list of genera assigned to the family to include 9 genera: *Kionophyllum* Chi, 1931, *Carinthiaphyllum* Heritsch, 1936, *Carniaphyllum* Heritsch, 1936, *Geyerophyllum* Heritsch, 1936 (=*Kionophyllum)*, *Lonsdaleoides* Heritsch, 1936, *Amygdalophylloides* Dobrolyubova & Kabakovich, 1948, *Axolithophyllum* Fomichev, 1953, *Paracarruthersella* Yoh, 1961 and *Darwasophyllum* Pyzhyanov, 1964. Other genera showing the basic morphology of the Geyerophyllidae have been described in later studies: *Chuanshanophyllum* Yü, 1977 (?= *Kionophyllum*), *Ramiphyllum* Wu & Zhang, 1979, *Majiaobaphyllum* Fan, 1980, *Qinglongshanophyllum* Yü, 1980, *Naoticophyllum* Shi, 1982, *Geyeronaotia* Rodríguez, 1984, *Protonaoticophyllum* Xu & Chen in Xu et al., 1987 (?= *Geyeronaotia*), and *Pseudoaxolithophyllum* Xu, Ding & Chen, *In* Lin *et al.*, 1995 (?= *Axolithophyllum*) (Table 1).

It may be concluded from the description by Heritsch (1936) that he considered *Carniaphyllum* and *Carinthiaphyllum* to be solitary corals, but this growth form was later questioned by Hill (1981), who regarded *Carinthiaphyllum* as possibly fasciculate. Heritsch (1936) did not specify a solitary or colonial growth form for his new genus *Lonsdaleoides,* but from his comparisons with colonial corals (*Lonsdaleia, Waagenophyllum*) it could be inferred that he was describing a colonial coral. Minato & Rowet (1967, p. 178), re-describing *Lonsdaleoides nishikawai* Hayasaka and Minato, 1966, stated that the collected specimens were free of matrix and widely separated, and therefore could not form part of a fasciculate coral. They also noted that the three paratypes show no sign of budding, but the holotype has several small

Table 1. List of genera included in Geyerophyllidae Minato.

Genus	Author	Year	Habit
Kionophyllum	Chi	1931	Solitary
Carinthiaphyllum	Heritsch	1936	Fasciculate?
Lonsdaleoides	Heritsch	1936	Fasciculate?
Carniaphyllum	Heritsch	1936	Fasciculate?
Geyerophyllum (= Kionophyllum)	Heritsch	1936	Solitary
Koninckocarinia	Dobrolyubova	1937	Solitary
Amygdalophylloides	Dobrolyubova & Kabakovitch	1948	Solitary
Axolithophyllum	Fomichev	1953	Solitary
Paracarruthersella	Yoh	1961	Solitary
Darwasophyllum	Pyzhanov	1964	Fasciculate?
Chuanshanophyllum	Yü	1977	Solitary
Ramiphyllum	Wu & Zheng	1979	Solitary
Majiaobaphyllum	Fan	1980	Solitary
Qinglongshanophyllum	Yü	1980	Solitary
Naoticophyllum	Shi	1982	Solitary
Geyeronaotia	Rodríguez	1984	Solitary
Protonaoticophyllum	Xu & Chen	1987	Solitary
Pseudoaxolithophyllum	Xu, Ding & Chen	1995	Fasciculate?

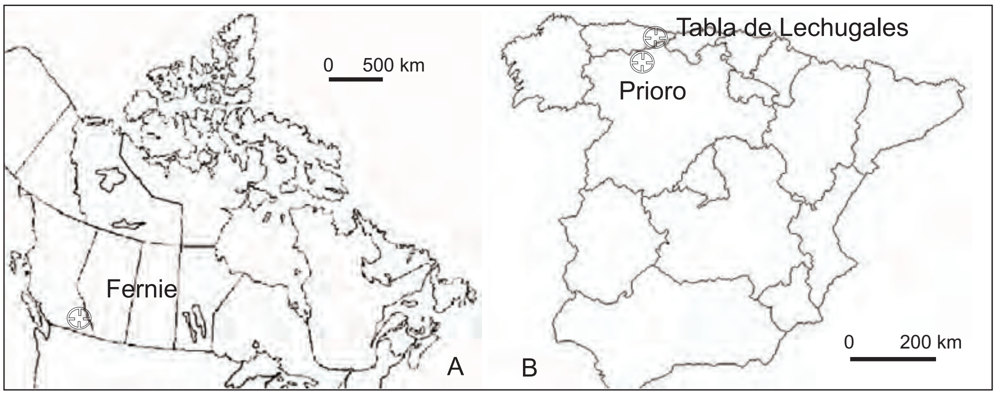

Figure 1. Localities yielding studied specimens. A. Outcrops near Fernie, British Columbia, in the southern Rocky Mountains, Canada. B. Prioro and Tabla de Lechugales outcrops in the Cantabrian Mountains, Spain.

offsets in the peripheral part of its lonsdaleoid dissepimentarium. Lower Permian specimens of *Carinthiaphyllum* from the Glass Mountains of Texas were shown to be solitary corals with gregarious growth habit by Fedorowski (1980, p. 435, pl. 26, fig. 2). Rodríguez (1985) analysed the relationships between various solitary geyerophyllids and questioned the colonialism of some of the genera described by Heritsch (1936). A review of the type material of *Carniaphyllum*, *Carinthiaphyllum* and *Lonsdaleoides* during the IX Symposium on Fossil Cnidaria by one of the authors (S. R.) confirmed that they are solitary corals with gregarious growth habit. Consequently, *Darwasophyllum* is the only remaining genus within the family Geyerophyllidae that may still be regarded as a colonial coral.

3. Growth habit in *Darwasophyllum*

Authors dealing with *Darwasophyllum* have consistently described it as a colonial coral, using such terms as "branching" (Pyzhyanov, 1964, p. 170; type species, *D. irregulare*), "loosely fasciculate" (Rowett and Kato, 1968, p. 39) and, most commonly,

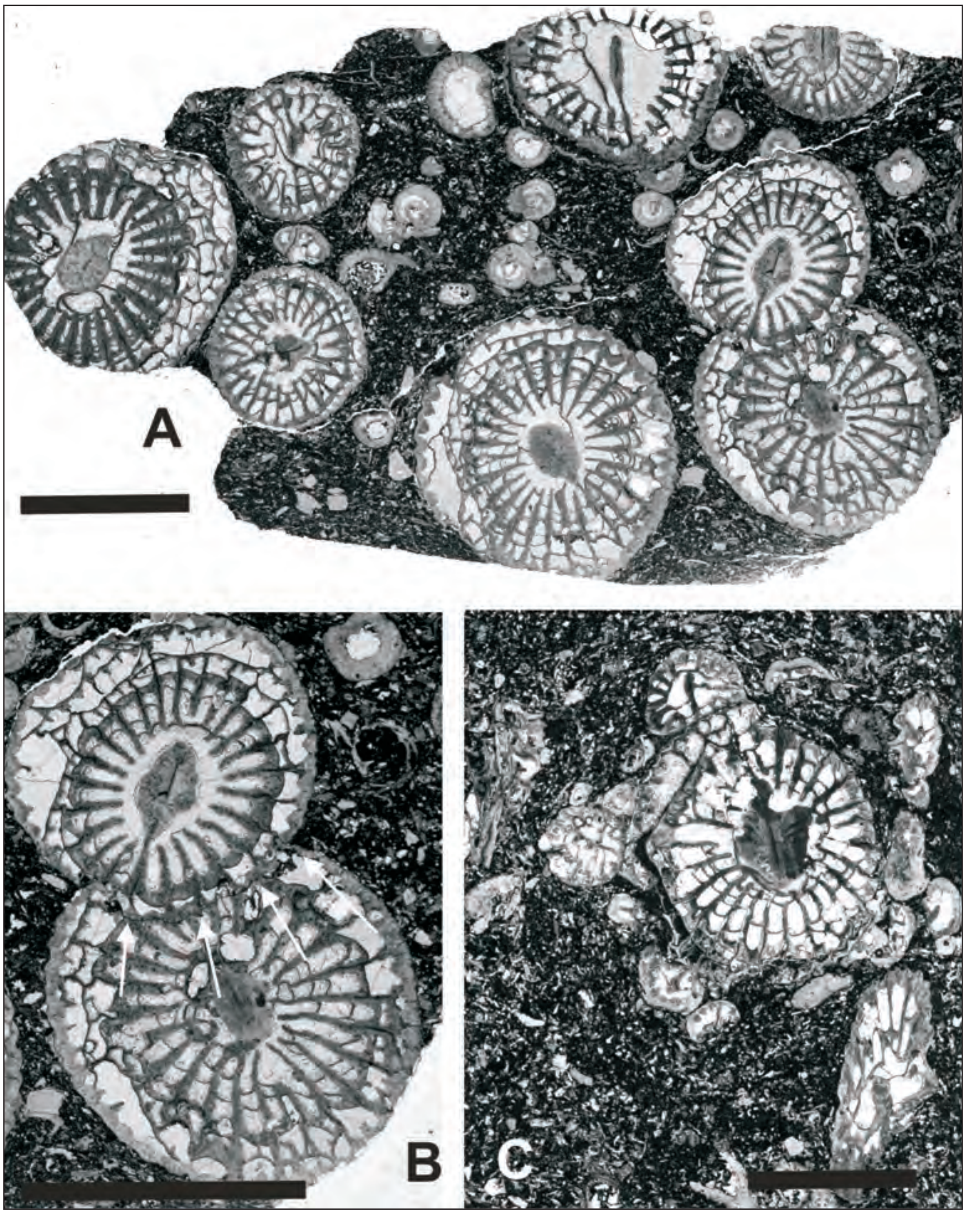

Figure 2. Gregarious growth form in *Darwasophyllum* sp. from the Etherington Formation. A. Several individuals growing together (hypotype GSC 133206; Geological Survey of Canada (GSC) locality C-409092, specimen 7). Note that the corallites in the lower right appear to share some structures. B. Close-up of figure A, showing a stylolite producing the false impression of structures common to adjacent corallites. C. Numerous young corallites surrounding an adult corallite (hypotype GSC 133207; GSC locality C-409092, specimen 15); some are attached to the wall of the adult, but none of them is an offset.
Locality information: Both specimens collected from GSC locality C-409092; Latitude 49°27'57"N, Longitude 115°07'45"W; Cedar Bowl section, Lizard Range, near Fernie, southeastern British Columbia, Canada (Fig 1A) ; 56.91-57.59 m. below stratigraphic top of inverted section. Scale bars = 5 mm.

"fasciculate" [e.g., Fan (1978, p. 180), Hill (1981, p. F407), Yu & Wang (1987, p. 83), Lin et al. (1995, p. 536)]. In no instance, however, has a colonial growth habit been clearly demonstrated for the genus. The descriptions of Rowett & Kato (1968, p. 40) and Wu & Zhao (1989, p. 158) are each based on a single corallite, and all published illustrations, including those of the type species, show separate corallites, none of which appear as definite offsets or share internal structures with other corallites.

Our specimens of *Darwasophyllum*, collected from the middle part of the Etherington Formation (Upper Viséan-Lower Serpukhovian, Canada), were also first regarded as colonial, with a close relationship between corallites. They occur in a single, laterally extensive, packstone bed that was traced over a considerable distance at the Fernie Alpine Resort in the Lizard Range of south-eastern British Columbia (Fig. 1A). The corallites are located in the upper part of this bed and appear to have been concentrated, in part, by re-working. Most of them occur as separate coral fragments, but locally they form groups of closely spaced, sub-parallel individuals, which resemble colonies but show no evidence of offsetting or shared structures. We have interpreted these groups as gregaria, based on observed relationships between immature specimens and associated, larger corallites of *Darwasophyllum* and other taxa.

The most convincing evidence for a solitary, gregarious growth habit was derived from serial transverse acetate peels and thin sections through a small specimen from our collection (Fig. 2C; hypotype GSC 133207). It consists of a mature corallite surrounded by numerous, closely spaced, immature corallites in various stages of development. New corallites appear at several levels within the growth interval studied. For the most part they lie very near or are in contact with the central mature corallite or other larger immature corallites. The new corallites are consistently oriented with their cardinal quadrants facing the corallites to which they are attached. Along the contacts between attached corallites, their external walls and other peripheral skeletal elements may show local damage caused by compaction and pressure solution. Where they have not been affected by this process, however, their external walls are distinct and well developed at all observed stages of development, and are commonly separated from each other by a thin layer of limestone matrix or crystalline calcite. These contact relationships persist over significant growth intervals with no evidence for sharing of walls or internal skeletal elements to indicate that the younger corallites originated as offsets from their neighbouring, more mature specimens.

In other gregaria of *Darwasophyllum* used for this study (Fig. 2A, B; hypotype GSC 133206), the contact relationships between corallites are consistent with those described above. No evidence of offsetting was found in our entire collection, which comprises more than 100 specimens. It is interesting to note that our collection contains two specimens in which the initial stages of young corallites are attached to taxa other than *Darwasophyllum*. These include a tabulate coral to which a small, doubly curved corallite is attached by its proximal end, and an incomplete cyathopsid coral bearing two very young, attached corallites of *Darwasophyllum* with diameters of 1.5 and 2 mm and no septa developed other than the cardinal septum. Thus, it appears that the preferred attachment sites for larvae of the Etherington corals were not entirely restricted to corallites of *Darwasophyllum*, but also included those of completely unrelated coral taxa.

4. Growth habit in *Axolithophyllum*

Although the genus *Axolithophyllum* has generally been regarded as solitary, some occurrences of Pennsylvanian specimens from the Cantabrian Mountains suggest the possibility of a colonial habit (Fig. 1B). These specimens show corallites that are in contact and share some septa in at least two different outcrops: close to Prioro village (Upper Moscovian, Figs 3 C, D) (De Groot in Van Loon, 1971) and Tabla de Lechugales peak (Lower

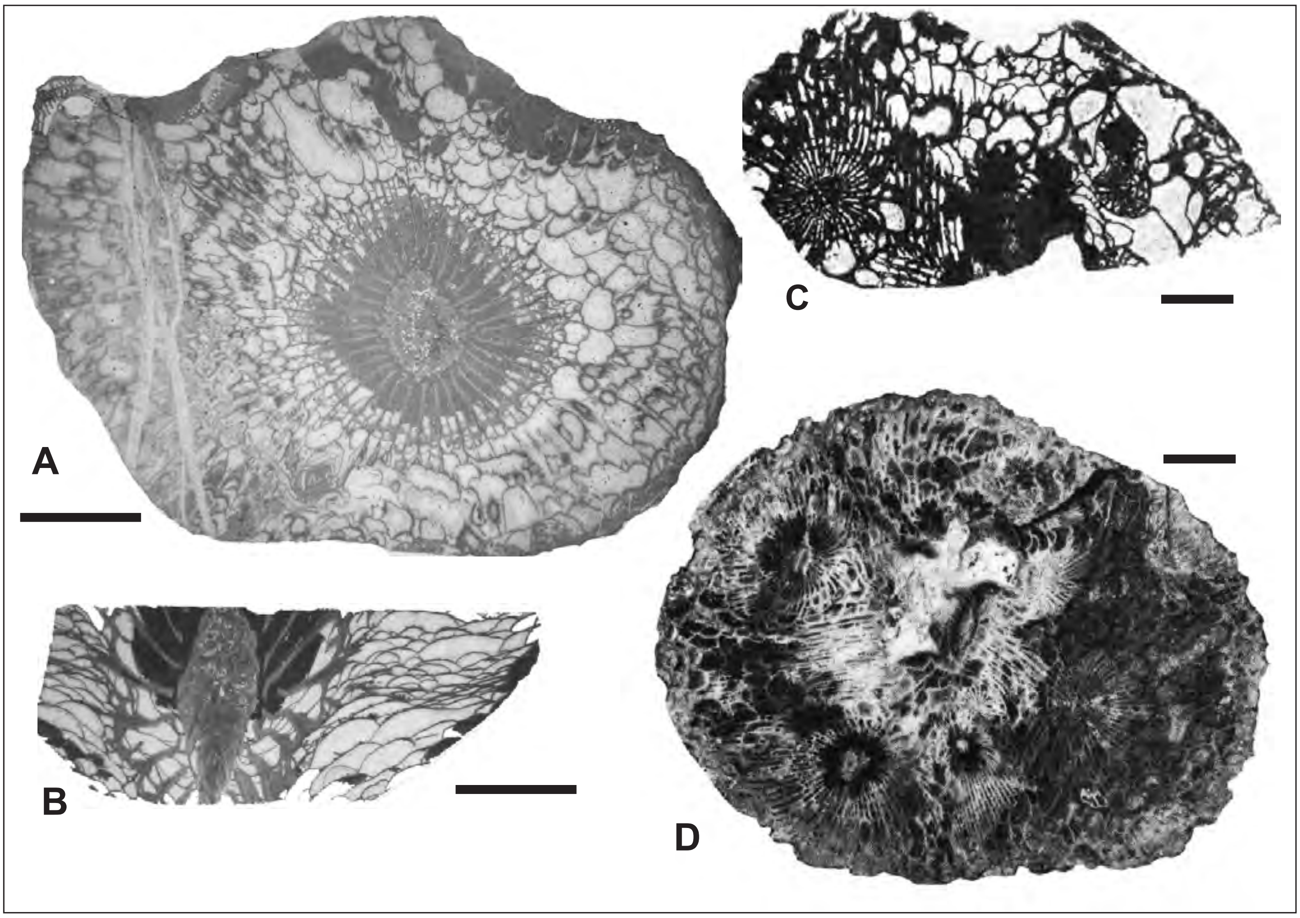

Figure 3. Protocolonialism in *Axolithophyllum*. A. *Axolithophyllum quiringui* from Tabla de Lechugales, specimen TLE1/73. Transverse section, showing contact between two adjacent corallites (upper right and left). B. Longitudinal section of the same specimen, showing it to be a solitary coral. C. cf. *Axolithophyllum* from Prioro (Escalada Formation), taken from Van Loon (1971, plate 6, fig. 4); two solitary corallites in contact. D. cf. *Axolithophyllum* from Prioro (Escalada Formation), take from Van Loon (1971, plate 6, fig. 6); solitary coral showing several offsets in calice. Scale bars = 5 mm.

Kasimovian, Figs 3A, B). In longitudinal section, however, it can be seen that they are separate individuals that are joined as a result of crowding caused by diameter increase during growth. This indicates a high degree of affinity between these individual corallites, but they do not form part of a colony formed by asexual budding. Elsewhere in the Upper Moscovian of the Cantabrian Mountains (Escalada Formation; De Groot in Van Loon, 1971), *Axolithophyllum* has been found with several corallites budding from the calice of a single corallum, but without further development. These specimens do not form true colonies, but only protocolonies or pseudocolonies. The original description by De Groot indicates: "obvious budding in solitary forms" (De Groot in Van Loon, 1981, p.247). They display the maximum degree of colonialism observed in the Geyerophyllidae.

The genus *Pseudoaxolithophyllum* was erected by Xu, Ding & Chen in Lin et al. (1995) for corals identical to *Axolithophyllum*, but developing small colonies. However, the original figures show only several closely spaced corallites with no evident budding.

5. Conclusions

The geyerophyllid genera *Carniaphyllum* and *Carinthiaphyllum*, described by Heritsch (1936) as solitary corals, but later regarded as colonial, are now known to be solitary corals having a gregarious growth habit. The same gregarious habit is shown in *Lonsdaleoides*, described by Heritsch (1936) as being colonial.

The genus *Darwasophyllum* has been consistently described as colonial (fasciculate), but our review of the original illustrations and our detailed study of a large, Early Serpukhovian population from the Etherington Formation of British Columbia have shown it to be solitary with a gregarious growth habit.

With the possible exceptions of the genera *Axolithophyllum* and *Lonsdaleoides*, which show a minor tendency to form protocolonies, it can be demonstrated that all geyerophyllid corals are solitary, with a strong tendency in some taxa toward the formation of gregaria.

6. Acknowledgements

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Sloveniaxon, a new genus of ahermatypic Rugosa (Anthozoa) from the basal Permian (Asselian) of Slovenia

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ABSTRACT. The proposal of the new genus is based on *Sloveniaxon asseliensis* sp. nov. from the late Early Asselian of the Dovžanova Soteska section NNE of Tržič (Karavanke Mts.), in a *Cyathaxonia* facies assemblage with *Cyathaxonia* and *Lophophyllidium*. Together with *Variaxon* Fedorowski, 2010, the taxon is classified as Variaxoninae Fedorowski, 2010 of Antiphyllidae Iljina, 1970 (suborder Zaphrentoidina Schouppé & Stacul, 1959), descending from *Rotiphyllum* Hudson, 1942. *Sloveniaxon* was widely distributed in Eurasia (Spain, Hungary, Russia, Ukraine, Iran, Timor, China) during Late Bashkirian, Moscovian, Asselian, Sakmarian?, Late Artinskian, Capitanian, Dzhulfian? times; there it had been mostly misidentified as really quite homoeomorphic *Cyathaxonia* Michelin, 1847 or *Cyathocarinia* Soshkina, 1928 (suborder Cyathaxoniina Spasskiy, 1977). The diagnostic difference is a true aseptal columella (Cyathaxoniinae Milne-Edwards & Haime, 1850) against a massive septal pseudocolumella (Variaxoninae), best visible in cross sections of the calice. For unambiguous identification, often neglected studies of the calicular phase are demanded to see the axial boss in *statu nascendi* without later stereoplasmatic thickening and diagenetic recrystallisations.
Future modern revisions (including intensive serial sectioning) should verify the proposed transfer of the following previous species into *Sloveniaxon*: *Cyathaxonia* (*Cyathocarinia*) *multituberculata* Soshkina, 1928, *Cyathaxonia angularis* Fomichev, 1953, *Cyathaxonia archangelskyi* Fomichev, 1953, *Cyathaxonia lomonossovi* Fomichev, 1953, *Cyathocarinia crassata* Guo, 1980, *Cyathaxonia degrootae* Rodríguez, 1984, *Cyathaxonia pinguis* Rodríguez & Kullmann, 1999, *Cyathaxonia* sp.n.B, Rodríguez & Kullmann, 1999.

KEYWORDS: Variaxoninae, *Cyathaxonia*-homoeomorphs, Karavanke-Mts., Eurasia-distribution, Bashkirian-Capitanian.

1. Introduction

Traditionally, aphotic coral communities of cold and deeper waters are named as the *Cyathaxonia* facies (according to Hill, 1938: *Cyathaxonia* fauna). This originally Lower Carboniferous term is in common use for all such Rugosa faunas (from Ordovician to Permian times). The name-giving genus *Cyathaxonia* Michelin, 1847 (lower Famennian-Early Permian) seems to be well defined, but a partially homoeomorphic, phylogenetically unrelated taxon which sometimes caused misidentifications was recognized recently.

The best material was jointly collected in 2010 in the Asselian of the Karavanke Mountains (Southern Alps, Slovenia), where Heritsch (1933, 1938) had already described some ahermatypic Rugosa. Additional records - mainly among so-called *Cyathaxonia* species - from Iran (Sakmarian?), Indonesia (Timor island, Capitanian), Hungary (Dzhulfian?), Russia (Late Artinskian), Ukraine (Late Bashkirian-Moscovian), Spain (Late Bashkirian-Late Moscovian), and China (Moscovian-Cisuralian) indicate a much wider stratigraphical and regional distribution in Eurasia.

An older record of the new genus is the misinterpreted "*Cyathaxonia cornu cornu* Michelin, 1847 ?" of Flügel (1972, 84, fig. 17, pl. 3/7) from the Early Permian (Sakmarian?) basal Jamal Formation of East Iran (Kuh-e-Bagh-e-Vang section south of Shirgest), here determined as *Sloveniaxon* sp. The determination was repeated correctly by Flügel (1995, 39), but incorrectly by Flügel & Hubmann (1993, 36, fig. 9A, omitting the indispensable "?"). The preliminary determination of that specimen was *Cyathaxonia khmeriana* Fontaine, 1961 (cited in Ruttner et al., 1968, 70).

Quite unexpectedly, also a part of *Cyathaxonia* (*Cyathocarinia*) Soshkina, 1928 from the Late Artinskian of the Russian Ural Mountains is not a member of the family Cyathaxoniidae Milne-Edwards & Haime, 1850. The illustrations of *Cyathaxonia* (*Cyathocarinia*) *multituberculata* Soshkina, 1928 demonstrate a septal pseudocolumella in the lectotype (Soshkina, 1928, fig. 18, Soshkina et al., 1941, 43, pl. 1/3), but not in some hypotypes (Soshkina, 1932, figs. 4, 5, 8, obviously with an aseptal columella characterizing real *Cyathaxonia*).

Some of the *Cyathaxonia* species described by Rodríguez (1984: pl.3/7, "*Cyathaxonia cornu* Michelin, 1847" Upper Bashkirian) and Rodríguez & Kullmann (1999, *Cyathaxonia* sp. n. B, *Cyathaxonia degrootae* Rodríguez, 1984, *Cyathaxonia pinguis* Rodríguez & Kullmann, 1999) might also belong to *Sloveniaxon* gen. nov. Their illustrations of specimens from the upper Picos de Europa Formation (Late Moscovian, Myachkovian) in the Cantabrian Mountains do not include calicular stages, where a septal or aseptal columellar structure is more easily visible. Probably, Falces & Rodríguez (1994) observed such differences in the columellar microstructure, suitable to differentiate "two species groups", but unfortunately this idea (published only in an unillustrated abstract) was not applied later in Rodríguez & Kullmann (1999).

Ukrainian Late Carboniferous *Cyathaxonia* species of the Donez Basin (Fomichev, 1953) demonstrate the same (and in Moscovian-Cisuralian times usual) co-occurrence of both true *Cyathaxonia* and *Sloveniaxon* gen. nov. in one assemblage. Our reinterpretation concerns *Sloveniaxon angularis* (Fomichev, 1953) (Moscovian), *Sloveniaxon*? *archangelskyi* (Fomichev, 1953), and *Sloveniaxon*? *lomonossovi* (Fomichev, 1953) (both late Bashkirian-early Moscovian). Finally, we dispose of two further isolated specimens of *Sloveniaxon*, an undescribed one from the Hungarian Bükk Mountains (Dzhulfian?), the other one from Indonesia (Timor island, Capitanian), already mentioned by Schouppé & Stacul (1959, 348, pl.13/73-75) as "Pterocorallia *incertae sedis* Form II".

In addition, *Sloveniaxon* gen. nov. occurs certainly throughout China (hitherto misidentified as *Cyathocarinia*). Correct determinations require intensive revisions of all these insufficiently sectioned, shortly described, and not well illustrated materials; therefore we select only some few citations, which should be excluded from the Cyathaxoniidae: Liao et al. (1987, pl. 5/6 - *Cyathocarinia tuberculata* Soshkina, 1928, Moscovian), Guo (1980, 114, pl. 63/10 - *Cyathocarinia crassata* Guo, 1980, Cisuralian), Wu (1975, 97, pl. 2/11-12 - *Cyathocarinia tuberculata* Soshkina, 1928, Cisuralian), Yu et al. (1981, 20, pl. 1/7 - *Cyathocarinia multituberculata* Soshkina, 1928, Cisuralian).

It is strange, that such a remarkable case of homoeomorphy between two totally unrelated, either columellate or pseudocolumellate taxa of different suborders (Cyathaxoniina Spasskiy, 1977, Zaphrentoidina Schouppé & Stacul, 1959) could survive up to present days. Steps to overcome these misidentifications started with Falces & Rodríguez (1994: observation of different microstructures in the "columella" of "*Cyathaxonia*"), Weyer (2001: interpretation of the aseptal columella in *Cyathaxonia* as an everted "aulos" = circulotheca, in the simple phylogenetic line *Laccophyllum* Simpson, 1900 → *Cyathaxonia* Michelin, 1847), Fedorowski & Vasilyuk (2011, affirmation of the unique aseptal columellar structure in

Figure 1. Locality map of the Dovžanova Soteska section, Karavanke Mts., Slovenia.

Cyathaxonia by complete ontogenetic studies), and Berkowski & Weyer (2012, this volume: redefinition of the terms columella and pseudocolumella for Rugosa in the original, already morphogenetic sense of their authors Milne-Edwards & Haime 1848).

2. Locality and stratigraphy in Slovenia

The *Sloveniaxon* material comes from Dovžanova Soteska (Dovžan's Gorge), written as Dolžanova in older publications and known as Teufelsschlucht (Devil's Gorge) in German-language literature. Dovžanova Soteska, 3.5 km NNE of the town of Tržič (Neumarktl in German-language literature) is known since Schellwien (1898, 1900) as a classical locality of fossil-rich Upper Carboniferous to Lower Permian sections (Fig. 1). Outcrops with corals are exposed along the forest path crossing the steep eastern slope of the gorge (NW slope of mount Vratni vrh) high above the Dolžanov bridge on the river Tržiška Bistrica. The section is indicated in Forke (2002, pl. 35/2, profile DSE).

The outcrops are exposed in three adjoining horizons (no. 130, 131 and 133 of Novak, 2007a) within a distance of ca. 5 m, Fig. 2) in the upper part of the Dovžanova Soteska Formation (a new lithostratigraphic term proposed by Forke, 2002, 210). Here, the sedimentological description of Novak (2007b) indicates a deepening phase of the reef mound expressed by an 80 cm thick horizon of thin-bedded brownish-grey calcareous siltstones, marlstones, and marly limestones (locality 130). Besides corals, rare brachiopods, sponge spicules and trilobite fragments occur. This short-term drowning sequence is followed by the re-establishment of the reef growth. Approximately 4 metres of dark-red thin-bedded grainstones to microbreccia composed predominantly of reworked bioclasts indicate deposition in the upper slope facies belt. Almost every limestone bed is capped by a thin violet-red stained silty crust (horizons 131 and 133). The diverse biotic association is predominantly composed of crinoidal columns, phylloid algae and bryozoan debris, accompanied by some small, often corroded corals, brachiopods, gastropods and fusulinid foraminifera. *Sloveniaxon* is found together with other small solitary Rugosa of the *Cyathaxonia* facies (*Cyathaxonia*, *Lophophyllidium*), and with the Tabulata *Sutherlandia* (attached to crinoid stems).

Based on lithological similarity and the distinctive red colour, this limestone was traditionally (since Schellwien, 1900) regarded as an equivalent of the Trogkofel Limestone of Artinskian age in the Carnic Alps. However, later studies of conodonts and fusulinids, which occur in several levels (Buser & Forke, 1996; Forke, 2002; Novak, 2007a, 2007b), indicated the late Early Asselian age (Kholodnolozhian of the Southern Ural Mountains). The difference in microfacies types to the predominant *Shamovella*-*Archaeolithoporella*-cement boundstone type of the Trogkofel Limestone in addition to the age difference led Buser and Forke (1996) to introduce a new name - Dovžanova Soteska Limestone Member - to the upper part of the Dovžanova Soteska Formation (named by Forke, 2002), an approx. 140 m thick succession overlying Upper Carboniferous beds.

Index fossils among conodonts and fusulinids in the uppermost part are *Streptognathodus bellus* Chernykh & Ritter, 1997, *S.* aff. *nodulinearis* Chernykh & Reshetkova, 1987, *S.* aff. *isolatus* Chernykh, Ritter & Wardlaw, 1997, *Hindeodus minutus* (Ellison, 1941), and *Diplognathodus* sp., *Dutkevitchia complicata* (Schellwien, 1898), *Pseudoschwagerina* aff. *uddeni* (Beede & Kniker, 1924), *Sphaeroschwagerina carniolica* (Kahler & Kahler, 1937), and *S. citriformis* (Kahler & Kahler, 1941).

Corals described by Heritsch (1933, 1938, ahermatypic taxa of the genera *Amplexocarinia*, *Tachylasma*, *Sinophyllum*, *Lopholasma*) bear no precise locality data, but came clearly also from the late Early Asselian Dovžanova Soteska Formation.

3. Systematic Palaeontology

Abbreviations: CS cross section, LS longitudinal section, TS thin section, P peel, R remaining part of corallum, n number of major septa, N number of all septa, D diameter.

The studied coral materials are deposed in the Museum of Natural History at Humboldt University, Berlin (department of palaeontology, coral numbers MB.K….), and in the Chernyshev Museum of the All-Russian Geological Survey Institute (VSEGEI), St.Petersburg (E. D. Soshkina collection).

Suborder Zaphrentoidina Schouppé & Stacul, 1959

Synonyms: Metriophyllina Spasskiy, 1965, Stereolasmatina Hill, 1981, Hapsiphyllina Nudds in Nudds & Löser, 2001.

Family Antiphyllidae Iljina, 1970
Subfamily Variaxoninae Fedorowski, 2010

Genera included. *Variaxon* Fedorowski, 2010; *Sloveniaxon* gen. nov.

Diagnosis. Descendants of *Rotiphyllum* acquiring an axial boss (pseudocolumella), at first with short free catasepta, finally with long contratingent catasepta and a biform tabularium.

Remarks. Now, the subfamily is not longer a monophyletic taxon, and a phylogenetic line *Rotiphyllum* → *Variaxon* → *Sloveniaxon* seems acceptable. Fedorowski (2010) did not

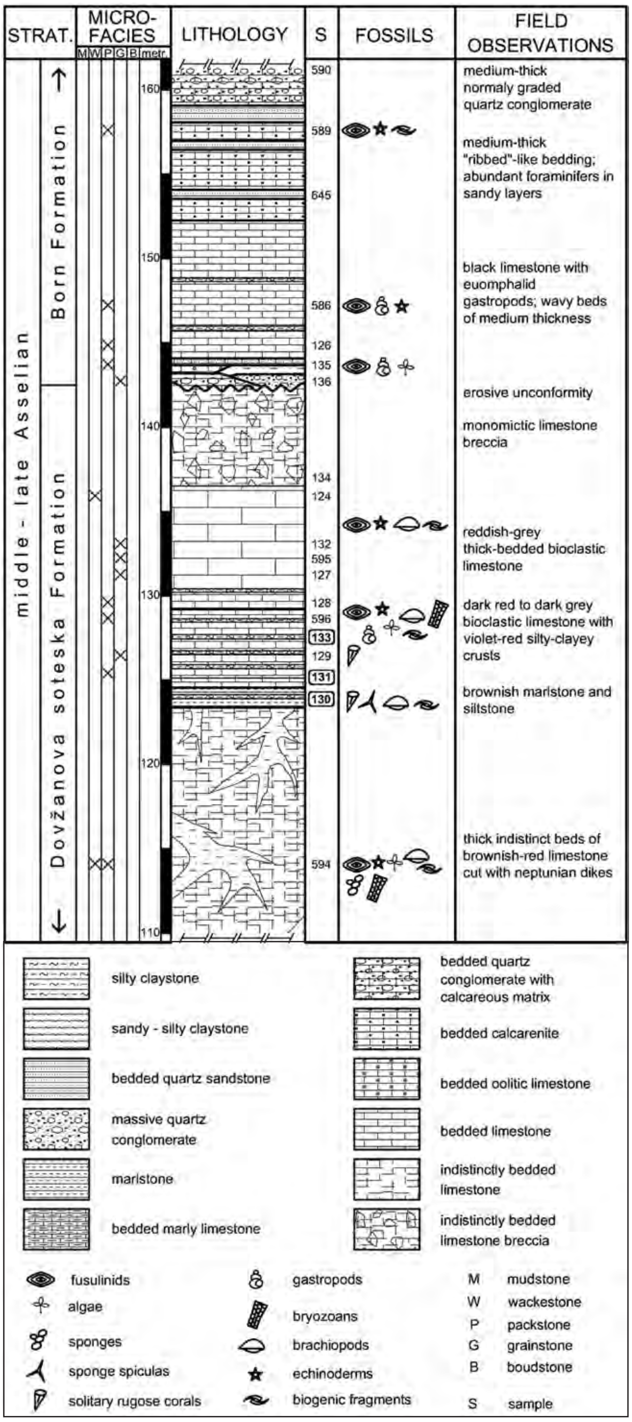

Figure 2. Lithostratigraphic section of the Sloveniaxon occurrences in the upper Dovžanova Soteska Formation (sample beds 130,131,133, late Early Asselian).

propose a family assignment, but was thinking about a "distant" ancestor *Rotiphyllum* Hudson, 1942. A first revision (Weyer, 1977) of the type species of *Variaxon*, *Fasciculophyllum repressum* Schindewolf, 1952, had shown the presence of an axial boss; the resulting transfer to *Lophophyllidium*? was proposed only with reservation, already speculating about a future separate new genus descending directly from *Rotiphyllum*.

Fedorowski (2010, 181) preferred to classify *Antiphyllum* Schindewolf, 1952 (plesiomorph: short and free catasepta, normal tabulae) and *Claviphyllum* Hudson, 1942 (apomorph: longer contratingent catasepta, tabulae biform) perhaps in different families. We consider these features as a general trend (*sensu* Lang, 1923) appearing within many Rugosa families, frequently and independently repeated through Ordovician-Permian times, and high enough valued as a generic or even only subgeneric criterion as in the case of *Lophophyllidium* (*Lophbillidium*) Fedorowski, 1986.

Distribution. Late Serpukhovian-Capitanian (Dzhulfian?).

Genus *Sloveniaxon* gen. nov.

Derivation of name. From the type area of the genus, Slovenia.

Type species. *Sloveniaxon asseliensis* sp. nov.

Diagnosis. Small long-conical, archaeothecate, diaphragmatophorous, with deep calice bearing a prominent massive pseudocolumella of few, slightly twisted septal lamellae (nearly without tabulae, no dominance of any antiseptal prolongation). Major septa radially arranged, reaching the axial boss in lower calice; cardinal septum slightly shorter than metasepta. Length of contracline or mostly contratingent minor septa amounts to 40-70% of that of major septa. Antiseptal triad equal to other catasepta, or a little more prominent. All septa with smooth, non-trabecular internal margin; their flanks are smooth or bear a weak to strong spiny ornament which disappears towards the calicular base after continuous stereoplasmatic thickening of the complete septal apparatus. Subtabular stages without (especially in the youth) or with only tiny open interseptal spaces. Simple tabulae strongly biform; horizontal or slightly axially inclined in position I, domed in position II.

Species included. *Cyathaxonia* (*Cyathocarinia*) *multituberculata* Soshkina, 1928, *Cyathaxonia angularis* Fomichev, 1953. ?*Cyathaxonia archangelskyi* Fomichev, 1953, ?*Cyathaxonia lomonossovi* Fomichev, 1953, ?*Cyathaxonia degrootae* Rodríguez, 1984, ?*Cyathaxonia pinguis* Rodríguez & Kullmann, 1999, ?*Cyathaxonia* sp. n. B, Rodríguez & Kullmann, 1999, ?*Cyathocarinia crassata* Guo, 1980, *Sloveniaxon* sp. A ("*Cyathaxonia cornu cornu* Michelin, 1847 ?" of Flügel 1972, 84, fig.17, pl.3/7), *Sloveniaxon* sp. B (1 unpublished specimen from the Dzhulfian? of the Bükk Mountains, Hungary), *Sloveniaxon* sp. C ("Pterocorallia *incertae sedis* Form II" of Schouppé & Stacul, 1959, 348, pl.13/73-75).

Discussion. *Sloveniaxon* differs from its assumed ancestor *Variaxon* in one apomorphic feature: the longer catasepta have changed towards a contratingent structure which is – as usual – connected with a marked biform tabularium. Further distinct characteristics (*Cyathaxonia*-like juvenile subtabular regions with strongly thickened septa leaving nearly no interseptal spaces, less shortened cardinal septum) might be only specific criteria. Both genera share the sometimes present, strong or weak spiny ornament of the septal flanks, appearing strange within the Antiphyllidae.

This reminds the partly homoeomorphic subgenus *Cyathaxonia* (*Cyathocarinia*) Soshkina, 1928, representing another suborder of Rugosa (Cyathaxoniina Spasskiy, 1977). Several times (Soshkina, 1928, 1932, Fomichev, 1953, Flügel, 1972, Rodríguez, 1984, Rodríguez & Kullmann, 1999), both taxa had been mixed. For sure identifications, often neglected studies of the calice are demanded to see the columella/pseudocolumella in *statu nascendi* without later stereoplasmatic thickening and diagenetic recrystallisations – then the differences between the circular aseptal columella of *Cyathaxonia* (genetically derived from tabulae after an everted growth of a former aulos (circulotheca) in the phyletic line *Laccophyllum* → *Cyathaxonia* in the Early Famennian; Weyer, 2001) and the septal pseudocolumella of *Sloveniaxon* are striking.

Temporarily, it seemed possible that *Cyathocarinia* is the valid name for the new genus *Sloveniaxon*. This was based on an incorrect designation of the type species in Ivanovskiy (1976, 50 - *C. multituberculata* Soshkina, 1928, said to be a questionable synonym of *C. rushiana* Vaughan, 1906), following Soshkina et al. (1941, 43 - genotype *C. rushiana* Vaughan, 1906, including as a subspecies *C. multituberculata* Soshkina, 1928 with synonym *C. tuberculata* Soshkina, 1928). The real type species is *Cyathaxonia* (*Cyathocarinia*) *tuberculata* Soshkina, 1928, designated by Lang et al. (1940, 43), surely an unfortunate (but valid) choice because this species was known by only one rather juvenile specimen; its original illustrations (Soshkina, 1928, 376, figs. 17) look like a

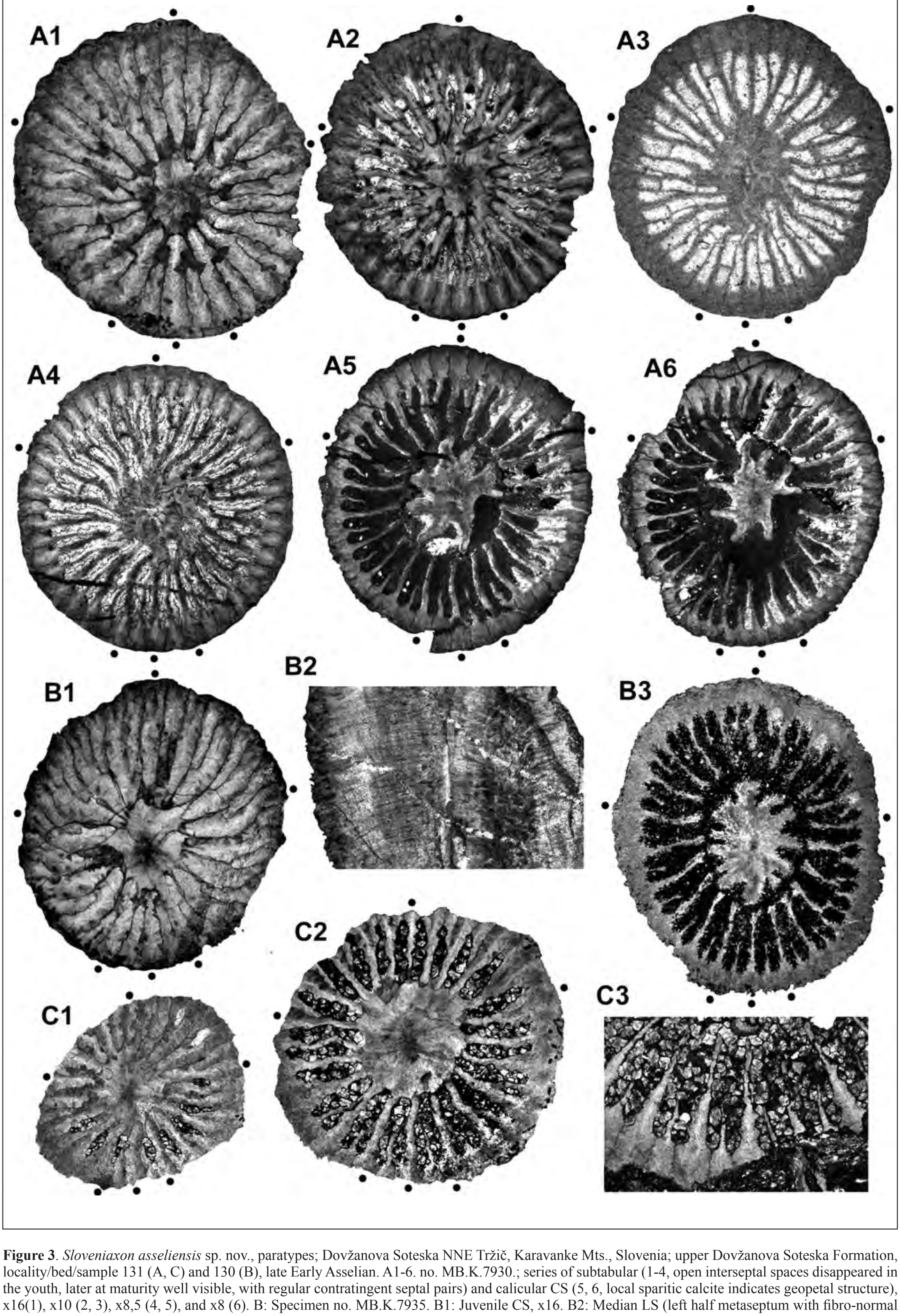

Figure 3. *Sloveniaxon asseliensis* sp. nov., paratypes; Dovžanova Soteska NNE Tržič, Karavanke Mts., Slovenia; upper Dovžanova Soteska Formation, locality/bed/sample 131 (A, C) and 130 (B), late Early Asselian. A1-6. no. MB.K.7930.; series of subtabular (1-4, open interseptal spaces disappeared in the youth, later at maturity well visible, with regular contratingent septal pairs) and calicular CS (5, 6, local sparitic calcite indicates geopetal structure), x16(1), x10 (2, 3), x8,5 (4, 5), and x8 (6). B: Specimen no. MB.K.7935. B1: Juvenile CS, x16. B2: Median LS (left half metaseptum with fibro-normal = lamellar microstructure, without trabeculae; right half pseudocolumella with domed growth lines), x16. B3: Lower calicular CS (pseudocolumella with ca. 16 septal lamellae), x10. C: Specimen no. MB.K.7928. C1: basal calicular CS, x12. C2: lower calicular CS, x15. C3: septa with spinous flank ornamentation in a middle calicular CS, x20.

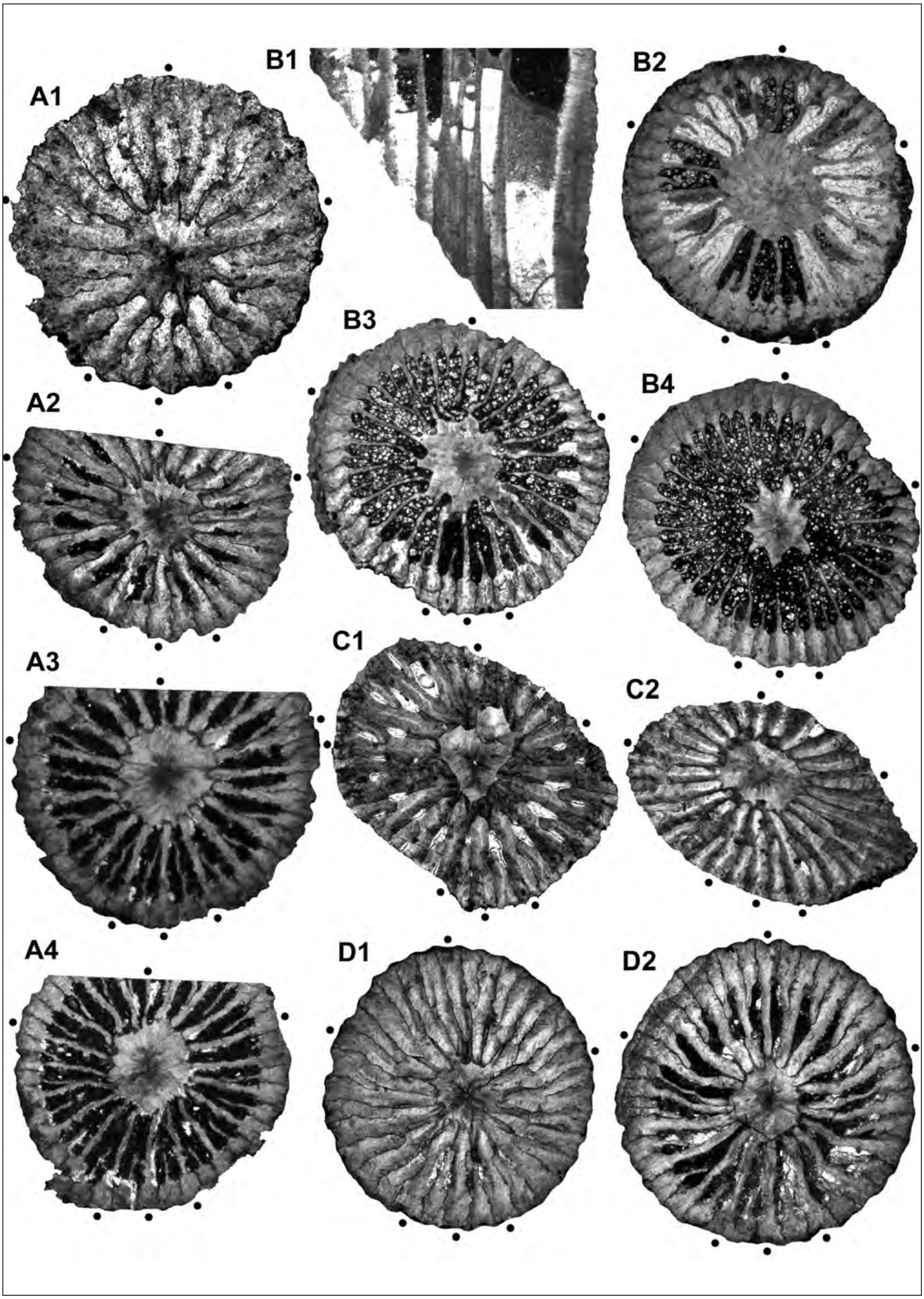

Figure 4. *Sloveniaxon asseliensis* sp. nov., holotype (B) and paratypes (A, C, D); Dovžanova Soteska NNE Tržič, Karavanke Mts., Slovenia; upper Dovžanova Soteska Formation, locality/bed/sample 130 (A,D) and 131 (B,C), late Early Asselian. A: Specimen no. MB.K.7934. A1: juvenile subtabular CS without open lumina, x25. A2-4: lower calicular CS, x14 (2, 3) and x12 (4). B: Specimen no. MB.K.7924. B1: eccentric LS, x12. B2-4: CS in the basal, lower and middle calice, x10 (appearance of biform tabulae in B3). C: Specimen no. MB.K.7929. C1: Juvenile subtabular CS showing unusual unclosed lumina, x15. C2: Subtabular later CS of a middle growth phase where lumina almost disappeared, x10. D1-2: Specimen no. MB.K.7936.; subtabular and lower calicular CS with well visible septal lamellae inside the pseudocolumella, x14.

normal *Cyathaxonia*. We can not provide a more comprehensive revision based on additional collections, as nobody has topotypes from the Northern Urals (river Ilytch).

Epiphanophyllum Iljina, 1970 (Middle Permian, Murgabian, Pamirs, Tajikistan) with its dominant antiseptal pseudocolumella (comparable to *Lophophyllidium* Grabau, 1928) is not related to *Sloveniaxon*. The original orientation of Iljina (1970) was reversed in Weyer (1979, 13, axial boss not of cardinal, but of antiseptal origin, as common in Rugosa).

Cyathaxonella Stuckenberg, 1895 remained unrevised, at present still a nomen dubium. The probably upper Viséan monotypic type species *C. gracilis* Stuckenberg, 1895 has short, obviously not contratingent catasepta. A lectotype designation (Ivanovskiy, 1976, 50) was done without any re-description; he simply declared the genus to be a synonym of *Cyathaxonia* Michelin, 1847, clearly an unjustified opinion against the better diagnosis of Stuckenberg (1895, "columella" with septal lamellae). In vain, we tried to restudy this specimen; it seems to be lost in the collections of the Chernychev Museum (VSEGEI, St.-Petersburg). Topotypes in calcareous preservation would be necessary for a modern analysis; perhaps *Cyathaxonella* is a senior synonym of *Variaxon*? But interesting are the determinations given as a faunal list in Schellwien (1898a, 1898b, *Cyathaxonella* nov. sp.) from the Dovžanova Soteska Formation (his "Trogkofel Limestone") - very probably this was the here described *Sloveniaxon asseliensis* sp. nov. and then an extraordinary precise determination for those times.

Distribution. Late Carboniferous (late Bashkirian-upper Moscovian), Ukraine (Donez Basin), Spain (Cantabrian Mountains), China, Early Permian (Asselian - Slovenia, Sakmarian? - Iran, Late Artinskian - Russia, Ural Mountains, Cisuralian - China), Middle Permian (Capitanian) - Indonesia (Timor), Late Permian (Dzhulfian)? - Hungary (Bükk Mountains).

***Sloveniaxon asseliensis* sp. nov.**

(Figs 3-6)

? 1898a *Cyathaxonella* nov. sp. –Schellwien: 697.
? 1898b *Cyathaxonella* nov. sp. –Schellwien: 361.

Derivation of name. After the Asselian age of the new species.

Holotype. Specimen no. MB.K.7924. [9CS (5P, 4TS), 2LS (TS), 2R] - Fig. 4/B1-4, 6/A1-6.

Paratypes. 14 specimens - 7 from the type locality/sample 131 (no. MB.K.7925.-7931., coll. Kossovaya, Novak & Weyer 2010), 2 from the locality/sample 133 (no. MB.K.7932.-7933., coll. Novak 2005), 5 from the locality/sample 130 (no. MB.K.7934.-7938., coll. Kossovaya, Novak & Weyer 2010). Altogether, 79 CS and 8 LS were prepared from 11 specimens (Figs 5-6).

Type locality and horizon. Dovžanova Soteska section NNE Tržič (locality 131, Novak, 2007a - forest path at the steep eastern slope of the gorge high above the Dolžanov bridge on the river Tržiška Bistrica). Upper Dovžanova Soteska Formation (level about 125 m above its base - see Fig. 2), late Early Asselian.

Diagnosis. Small corallum (up to 29 mm length and 8 mm calice diameter) with 44 septa and a high massive pseudocolumella consisting of 9-17 well developed septal lamellae (occupying 24-34 % of the diameter). Septal flanks weakly spinose in the upper calice; deeper (and subtabular) smooth after strong stereoplasmatic thickening leaving no free interseptal spaces in the youth. Long catasepta contratingent.

Description. The small solitary, straight to very slightly cornute corallum reaches 15-20 mm length and 6-8 mm calicular diameter. A basal talon was never observed (even at the minimal preserved diameter of 1,6 mm). Mostly, there occurs corrosion before the final sedimentation (proximal and distal ends broken away, upper calice compressed, archaeotheca damaged, only sometimes showing the well developed regular interseptal longitudinal ribbing without hyposeptal furrows - Figs 4D, 5A3). Weak rejuvenescense is very rare (Fig. 6A3). All the material could not be freed from the sediment and was mainly collected by splitting the stones at right angle to the bedding plane (then looking for cross sections).

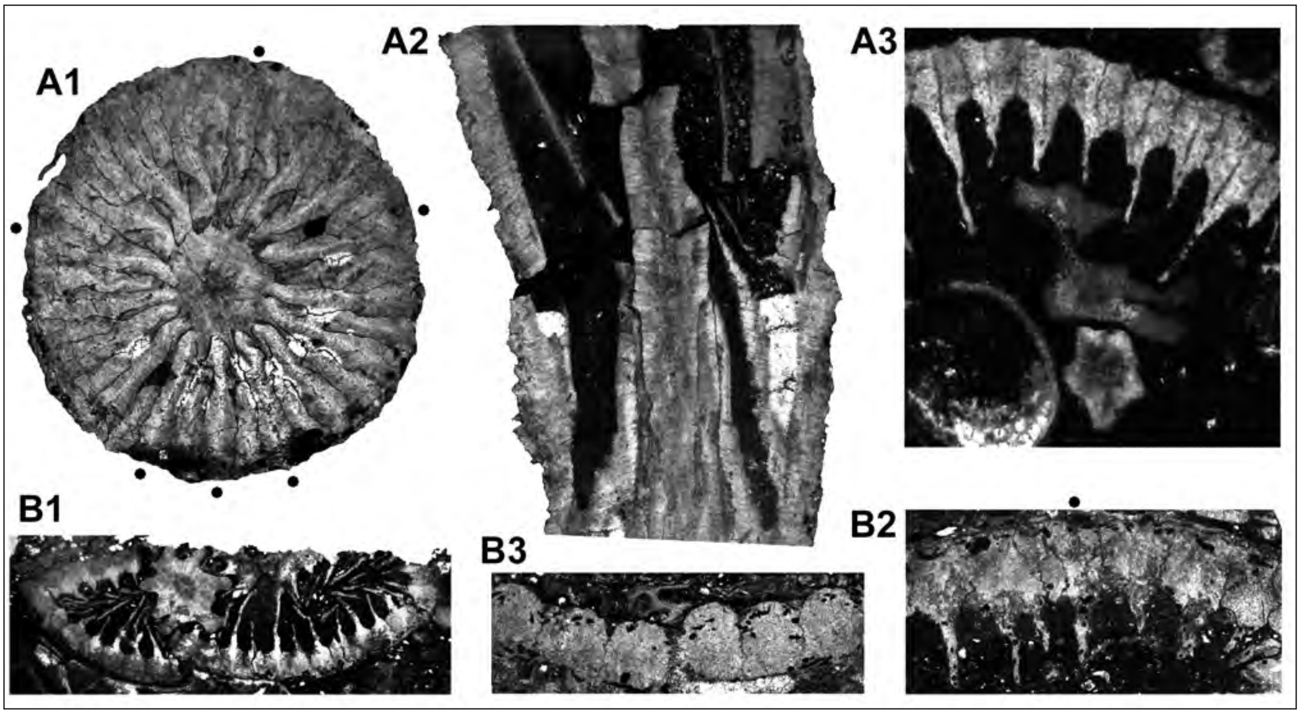

Figure 5. *Sloveniaxon asseliensis* sp. nov., paratypes; Dovžanova Soteska NNE Tržič, Karavanke Mts., Slovenia; upper Dovžanova Soteska Formation, locality/bed/sample 131, late Early Asselian. A: Specimen no. MB.K.7925. A1: Subtabular CS, with most septa strongly thickened by stereoplasma, x15. A2: median calicular LS, with tabulae only in contratingent lumina (position I), x10. A3: part of middle calicular CS, with still free metasepta and catasepta, and with top of pseudocolumella bearing 5 septal lamellae, x20. B: Specimen no. MB.K.7926. B1: Crushed middle calicular CS with pseudocolumella bearing 10 septal lamellae, x8. B2: cardinal septum, metasepta, and catasepta in a middle calicular CS showing weak ornamentation of septal flanks, x20. B3: undifferentiated, broadly rounded septa near the upper calicular margin, x20.

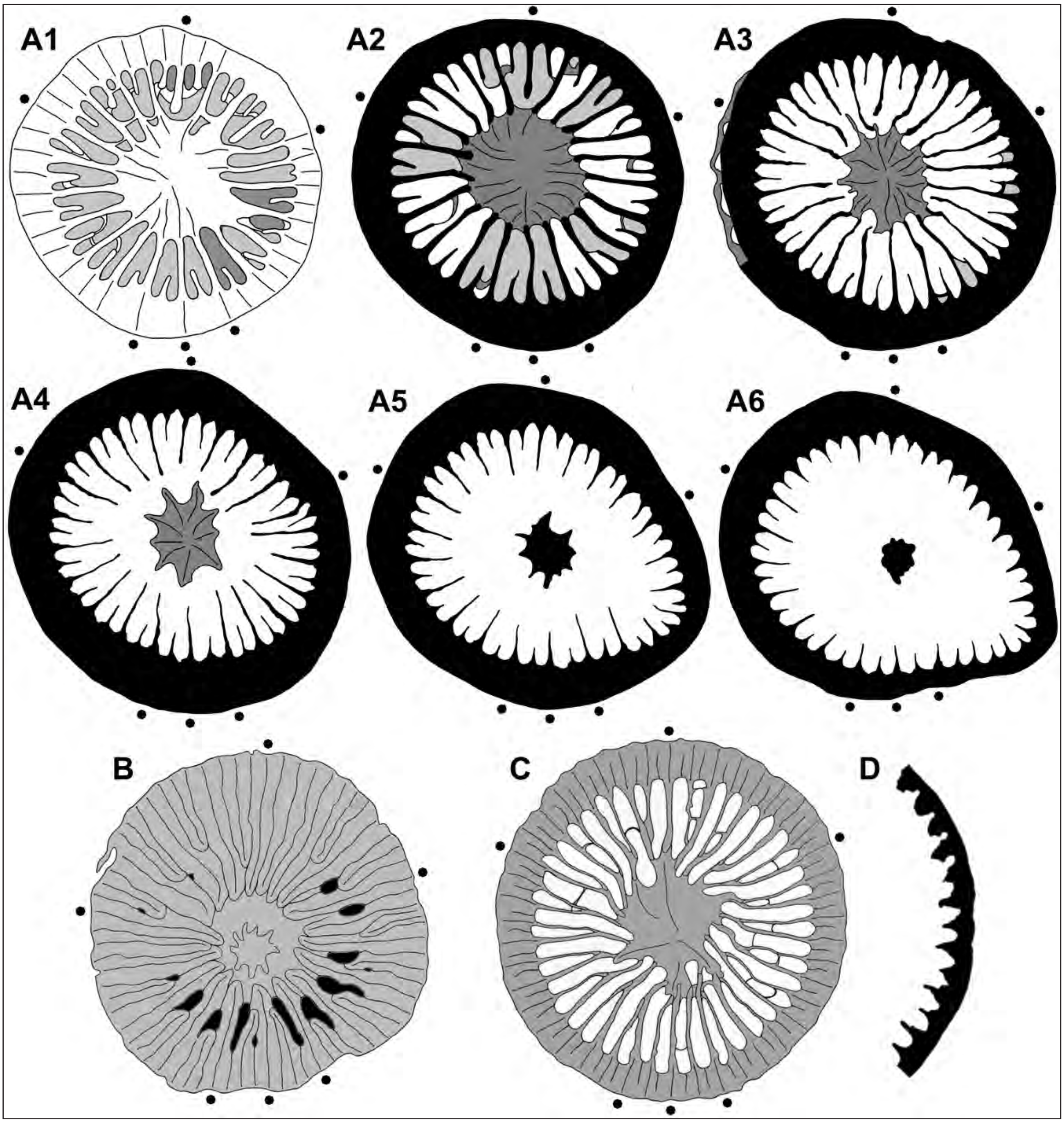

Figure 6. *Sloveniaxon asseliensis* sp. nov., holotype (A) and paratypes (B-D); Dovžanova Soteska NNE Tržič, Karavanke Mts., Slovenia; upper Dovžanova Soteska Formation, locality/bed/sample 131 (A-C) and 130 (D), late Early Asselian. A1-6: Specimen no. MB.K.7924. series of calicular CS, well demonstrating the change of free to contracline and finally (at the calicular base) to contratingent catasepta, x10 (subtabular regions light grey in 1, white in 2). B: Specimen no. MB.K.7925.; subtabular CS, x15. C: Specimen no. MB.K.7930.; mature subtabular CS, x9. D: Specimen no. MB.K.7935.; septa with irregular flank ornamentation in the upper calice, x10.

The deep calice contains a high and massive pseudocolumella built of axially fused septal lamellae. Their peripheral free ends are well visible in middle calicular cross sections, but nearly disappear slowly against the calicular base after strong stereoplasmatic thickening. The microstructure may show their former presence (Figs 4A3, 6A2, 6B), even in most subtabular cross sections, where regular concentric growth lines as in Cyathaxonia are never seen. There is no dominant antiseptal participation and no prominent cardinal/counter lamella. A small lumen within the pseudocolumella (caused by an isolated tabula) occurs only once.

The adult septal apparatus (D 5-7 mm) has 44 radially arranged septa: 26 major septa (21 of equal length, cardinal septum only slightly shortened, 4 last metasepta of the four quadrants mostly appearing like minor septa), and 18 catasepta (of variable length amounting 30-80%, but mostly about 50% of the length of major septa). Septal formulae of the smallest and of the larger cross section:

3|3 n 17	**5|5 n 26**	**4|4 n 26**
4|4 N 28	**6|6 N 44**	**7|7 N 44**
D 2.3 mm	**D 5.2 mm**	**D 5.0-6.3 mm**
Fig. 4A1	Fig. 3B3	Fig. 3A4-6, 6A

Catasepta are free in the upper and middle calice; later (in the lower calice, when major septa join the pseudocolumella) they become contraclined and finally contratingent. The antiseptal triad has no longer minor septa. Septal flanks may bear weak and irregular tiny spines (Figs 3C3, 6D) which disappear in the deeper calice after continuous stereoplasmatic thickening of the complete septal apparatus. Subtabular regions of juvenile and middle growth stages have completely lost their interseptal lumina (thus much resembling the homoeomorphic genus *Cyathaxonia*) which are left still widely open at maturity (Figs 6A1-2, 6C). Interseptal spaces of position I are closed first (Fig. 4A3, 4D2).

The septal microstructure (Fig. 3B2) is lamellar (Schindewolf, 1942, with synonymous term fibronormal of Kato, 1963); there are no trabeculae or tiny spines at the upper septal margins which have a special broadly rounded appearance (without a multitrabecular zone) near the upper rim of the calice (Fig. 5B3).

A strongly developed biform tabularium is visible in longitudinal sections (Fig. 5A2), in a series of calicular cross sections (Fig. 6A2-3), and in subtabular cross sections with interseptal lumina (Fig. 6C) demonstrating the contrary inclination of tabular intersections in position I (adaxially inclined) and position II (inclined towards the archaeotheca). A very weak cardinal fossula is indicated in Figs 6A1-2.

Discussion. The majority of definitely/probably included species (especially those from Bashkirian-Moscovian) is imperfectly studied and can be compared only after intensive revisions (including the hitherto neglected calicular morphology). No further record of Asselian times is known. Well differentiated are the Late Artinskian *Sloveniaxon multituberculatus* (Soshkina, 1928) by its much stronger spine ornament at the septal flanks, and the Capitanian *Sloveniaxon* sp. C (Pterocorallia *incertae sedis* Form II, Schouppé & Stacul, 1959) with smooth septal flanks. Obviously, there exist only very minor specific differences which are rather difficult to discriminate, as in *Cyathaxonia*. There, some authors (starting with Soshkina, 1932 and Schindewolf, 1951) proclaimed only few, extremely long-living species - an biologically improbable hypothesis not followed here.

Distribution. For the moment, only at the type locality/bed and two immediately neighbouring outcrops.

4. Acknowledgments

The authors thank Nina Mikhaylovna Kadlets (St.Petersburg) for her assistance to study the Stuckenberg and Soshkina coral collections in the Chernyshev Museum (All-Russian Geological Survey Institute, VSEGEI), and Sergio Rodríguez (Madrid) and Julien Denayer (Liège) for their detailed reviews.

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The scleractinian corals: a perspective

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ABSTRACT. Though scientific interest in scleractinian corals originated in the 16th century, the knowledge base continues to grow and is far from complete. The progress of the research on these organisms is represented here as an exponential process and its history may be divided into three periods. In the beginning, Plant period (1576-1727), these organisms were interpreted as plants. The Animal period (1727-2007) brought in their consideration as animals and includes three phases that introduce new research approaches (phase 1: variability, microstructure, transplantation; phase 2: multiple skeletal characters, global spatial and temporal attention; phase 3: life history, molecular biology). Recently, the number of sources of scleractinian knowledge has increased to five: morphology, paleobiology, ecology, life history and molecular biology. Scleractinian corals are no longer considered alone but as holobionts, along with their symbiotic zooxanthallae and other associated microbiota. The accumulated multidisciplinary data and new integrative concepts urge a holistic interpretation and have been indicating (since 2007) the commencement of the present, Holistic period. This analysis of the current status of scleractinian knowledge provides a list of proposed directions for future research.

KEYWORDS: Taxonomy, morphology, paleobiology, ecology, life history, molecular biology.

1. Introduction

Scleractinian corals have been of interest to scientists since the 16th century and yet our understanding of them remains far from satisfactory. Scientists forming the international Scleractinia Working Group recognized “that existing classification systems for scleractinians are inadequate, and a revised system that better reflects new molecular results needs to be adopted as soon as possible” (Budd et al., 2010). In addition to the higher classification, “generic definition of the Scleractinia remain[s] in chaos” (Stolarski et al., 2006). Though new research approaches over the past half century have contributed considerably to resolution of the taxonomy of this group, the existing concepts are being challenged and accumulated data are in need of new interpretations. Presently, “the combined use of morphological and molecular tools holds great promise for ending confusion in scleractinian systematics” (Budd et al., 2010). Studies of life history and ecology also are contributing to the holistic understanding of the Scleractinia. This article reviews the progress of scleractinian knowledge and its current status and provides suggestions for future work.

2. History

The goal here is not to present a detailed history of scleractinian studies but rather to trace the progress and timing of research.

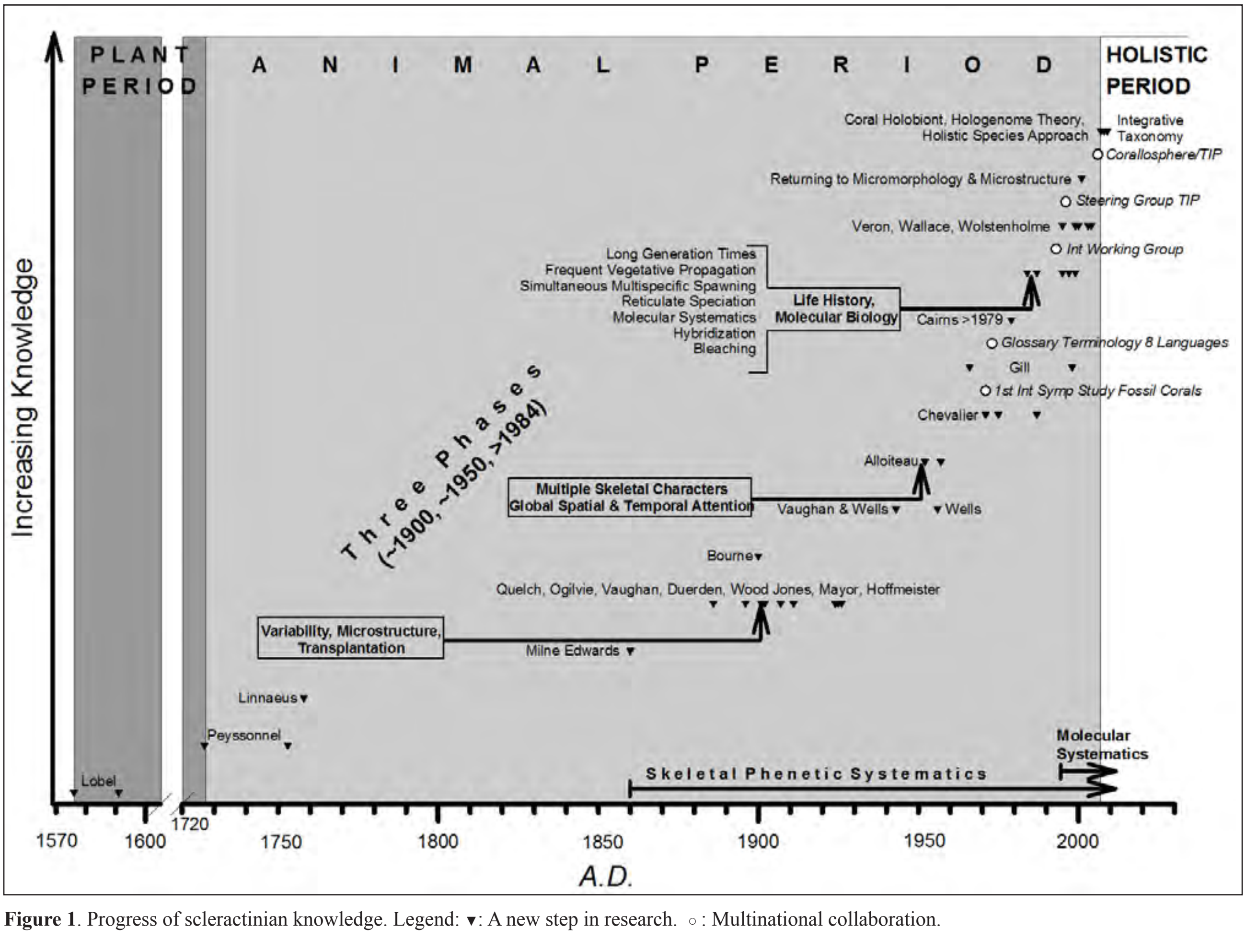

Figure 1. Progress of scleractinian knowledge. Legend: ▾: A new step in research. ○: Multinational collaboration.

The history of research on scleractinian corals may be divided into three periods. A graphical presentation of the progress of scleractinian knowledge reveals here an exponential growth (Fig. 1).

The **First period** (1576-1727) may be named the **Plant period**. During this time, scleractinian corals were interpreted as plants. M. Lobel illustrated two scleractinians, *Dendrophyllia ramea* and *Madrepora oculata* in 1576 and in 1591 (Vaughan & Wells, 1943), and naturalists illustrated many scleractinians as botanical objects.

The **Second period** (1727-2007) may be called the **Animal period**, during which scleractinian corals were considered animals. Peyssonnel was the first, in 1727 and 1753 (Vaughan & Wells, 1943), to maintain that they are not plants but animals. In 1758, the 10th Edition of Linnaeus's "Sistema Naturae" marked the starting point of zoological nomenclature. Initially, studied coralla were found fortuitously. The taxonomy was purely typological. Milne Edwards published "Histoire naturelle des Coralliaires" (1857-1860) based on living and fossil species.

This period includes three phases that introduce new research approaches. They are not applicable to the azooxanthellate representatives of the order because their predominantly deep-sea distribution made *in situ* access for study difficult, and those azooxanthellate corals living in shallow water are small and frequently cryptic. The time around the end of the 19th and beginning of the 20th centuries was marked by the **first phase (variability, microstructure**, **transplantation)**, which (except for microstructure) resulted from entrance into the natural coral habitat. During this phase, the extraordinarily rich variability of coralla was established, the species problem was considered and formae were introduced (Quelch, 1886; Vaughan, 1901, 1907; Hoffmeister, 1925, 1926). Aggregated colonies (Duerden, 1902) and growth forms (Wood Jones, 1907) were described. The new knowledge prompted transplantation experiments (Vaughan, 1911; Mayor, 1924; Mayor's work reviewed in Stephens & Calder, 2006). In addition, skeletal microstructure was applied as the basis of higher classification (Ogilvie, 1896). The order Scleractinia was created by Bourne in 1900. During the first half of the 20th century, paleontologists were leading the research and synthesized the results on scleractinians (Vaughan & Wells, 1943; Wells, 1956).

A **second phase of the second period** (**multiple skeletal characters, global spatial and temporal attention)** of research on Scleractinia marked the middle of the last century. By paying special attention to micromorphology and microstructure, the paleontologist J. Alloiteau (1952, 1957) founded a Parisian coral school whose members studied Scleractinia of all geological periods beginning with those of the Triassic (Sorauf et al., in this volume). His successor Chevalier (1971, 1975, 1987) started in situ research on living corals and published the most complete descriptions on skeletal variability ever produced. Gill (1966-1998 in: Lathuilière & Barta-Calmus, 1999) pioneered the study of functional micromorphology. SCUBA made the euphotic and the upper part of the mesophotic habitat accessible for research (Zlatarski & Martinez Estalella, 1982; Zlatarski, 2008, 2009). Since the 1970s, Cairns (2007) and Zibrowius (1980) published revisions of museum material and new collections of azooxanthellates.

A **third phase of the second period (life history, molecular biology)** began in 1984 as a series of discoveries of new aspects of scleractinian nature including: evolutionary consequences of long generation times and frequent propagation through vegetative fragmentation (Potts, 1984), the existence of simultaneous multispecific spawing (Harrison et al., 1984 ; Oliver & Willis, 1987), the possibility for reticulate speciation (Veron, 1995), the usage of molecular systematics (Chen et al., 1995), the presence of introgressive hybridization (Willis et al., 1997), the impact of bleaching (Hoeg-Guldbgerg, 1999) and unusual growth forms in aquaria (Carlson, 1999). Veron (1995, 2000, 2003) summarized his worldwide observations on zooxanthellate Scleractinia. Both mitochondrial and DNA markers revealed incongruence with the conventional gross-morphology-based taxonomy when traditionally defined families were shown to be polyphyletic (Chen et al., 1995; Romano & Palumbi, 1997). Wallace (1999) published a revision of *Acropora*, the most speciose scleractinian genus in the world, using the contemporary approaches. The returning of attention to the micromorphological and microstructural characters suggested a possibility for harmonizing skeletal and molecular data (Stolarski & Roniewicz, 2001). Difficulty in finding molecular markers suitable for differentiating species-level relationships compounded the problem of large-scale polyphyly. Scleractinian corals were shown to have slowly evolving mitochondrial genomes (Shearer et al., 2002). After analysis of morphological, molecular and reproductive criteria, Wolstenholme (2004) concluded that hybridization events of corals occur in nature but are not frequent. In the late 1980s Hoeksema began publishing on the taxonomy, ecology, phylogeny and biogeography of mushroom corals (Fungiidae) (Gittenberger et al., 2011).

At the beginning of this century we "have a greatly improved toolbox for studying scleractinian evolution" (Budd et al., 2010), but the knowledge about this group is coming in from different disciplines. As a consequence, results concerning morphology, paleobiology, ecology, life history and molecular biology need a holistic approach for analysis. The notion of the coral holobiont no longer considers the coral animal alone, but with its symbiotic zooxanthellae and all associated microbiota in connection with coral health, and has led to the theory of hologenome evolution (Rosenberg et al., 2007). These changes together with the holistic species approach (Zlatarski, 2007) and the increasingly integrative character of scleractinian research (Zlatarski, 2008, 2009) indicate the commencement of a **Third period** (2007-present), which may be named the **Holistic period**.

Multinational collaboration started with the First International Symposium on the Study of Fossil Corals in 1971 in Novosibirsk (Russia), where the International Committee on Fossil Corals was elected and the International Newsletter of ICFC (now Fossil Cnidaria & Porifera) was started. A glossary of equivalent terms for scleractinian studies in eight languages followed (Zlatarski, 1973), as well as the International Working Group on Scleractinian Corals (Löser & Rosen, 1993), the Steering Group for Revision of Scleractinia for the Treatise on Invertebrate Paleontology (TIP) (since 1996, led by Rosen), the Corallosphere (since 2006, http://www.corallosphere.org) and TIP Project (Stolarski et al., 2006).

3. Current status

The species richness of Scleractinia has not even approximately been calculated. Recently 1,482 valid extant species were recognized, a little more than half of them zooxanthellate (Cairns, 2007). The higher taxonomic categories are pending revisions. Currently, "[c]oral taxonomy and systematics continue to be plagued by a host of problems" (Huang et al., 2009).

The sources of scleractinian knowledge today are various: morphology, paleobiology, ecology, life history and molecular biology. Their combined use for studying azooxanthellate scleractinians indicates the evolutionary origin of the Order deep in the Paleozoic (Stolarski et al., 2011).

Skeletal **morphology** has been studied since the dawn of scleractinian research and until less than two decades ago was the exclusive basis for scleractinian classification, but it still lacks information about variability and microarchitecture. Where sampling is insufficient (e.g., collecting only clear representatives of different phenotypes and ignoring specimens showing intermediate characters or bimorphic colonies), it presents an impediment for obtaining a more objective taxonomy because it shows only part of the phenotypes' picture. Neglected, the variability in different levels of biological organization (a structural element, corallite, colony, etc., Zlatarski & Martinez Estalella, 1982) also introduces a typological component into taxonomic practice and hinders understanding of intraspecific polymorphism, plasticity and the process of speciation. Study of taxonomically "atypical" portions of coralla may indicate that coral life is under stress (Nothdurft & Webb, 2009). Nanostructure data are promising for phylogeny analysis (Janiszewska et al., 2011). Information on skeletogenesis has shown to be important for conclusions on past and future climates, as well as for coral taxonomy (Clode et al., 2011). A novel non-destructive technique based on micro-computed tomography was introduced for measuring skeletal growth (Roche et al., 2010). Existing museum collections may be useful for determining long-time biodiversity changes (Hoeksema & Koh, 2009; Hoeksema et al., 2011). However, no large extant coralla collections are realized recently, and the old are not always available or digitally documented, with the exception of the Dana types digitized on the Smithsonian Institution web pages and the Cuban collection of 4,980 SCUBA-collected specimens from the early 1970s available in multimedia format with digital photos of all specimens.

Paleobiology continues to contribute knowledge on past biodiversity and coral evolution, and is now also contributing to examinations of ecology, climatology, biological interaction, life strategies and reef building. Paleoecological analysis of assemblages under sediment input (Sanders & Baron-Szabo, 2005), paleoenvironmental implications of free-living colonies (Sorauf & Harries, 2009, 2010; Harries & Sorauf, 2010), the roles of clone-clone interactions in building reef framework (Fagerstrom & West, 2011), fossil clonal fusion (Helm & Schülke, 2000), conspecific and heterospecific interactions in nonextant material (West et al., 2011), and the evolutionary importance of hybridization in the geological past (Budd, 2010; Zlatarski, 2010) have received attention. Paleoecology is placing the modern biodiversity crisis in an historical context (Pandolfi, 2011). Scleractinian evidence contributes to paleoclimatology by no supporting permanent El Niño (ENSO) during the Pliocene warm period (Watanabe et al., 2011). Caribbean paleontological records are being used for identifying analogues to 21st century Earth conditions (Klaus et al., 2011). Caribbean coral reef development over the last 28 million years was shown to be independent of scleractinian diversity and this poses a question for researchers and reef managers, to choose between encouraging reef development or maximizing diversity of reef-corals (Johnson et al., 2008). Data of fossil corals were used for the analysis of generation, senescence and "hopping" of paleobiodiversity hotspots (Renema et al., 2008). There are indications of repeated loss of coloniality and symbiosis in scleractinian evolution (Barbeitos et al., 2010). The skeletal growth information is under-exploited (Lough, 2008). The coral "fossil record remains a largely untapped resource for understanding evolutionary rates and patterns" (Knowlton et al., 2006).

The migration of species farther from the equator, phase shifts and alternative states on coral reefs are changing our knowledge of scleractinian **ecology** and have implementation in paleoecological interpretations (Precht & Aronson, 2004, Norström et al., 2009; Yamano et al., 2011). The research is focused predominantly on shallow waters. Experiments demonstrated the functional significance of light-induced morphological plasticity (Ow & Todd, 2010) and environmental control on corallite morphology (Klaus et al., 2007). The latter work showed that the characters in thin sections are more useful for species identification while the characters of calical surface provide information for interpreting the adaptive significance of species differences. The phenotypic differences between ecomorphs were found to be maintained in sympatry despite evidence of hybridization (Carlon & Lippé, 2011). The studies of mesophotic habitat noted high biodiversity and endemism, but the mechanisms for these patterns have not been established (Lesser et al., 2009). Also, the expected recruitment of larvae of deep water origin into shallow habitats was not always confirmed (van Oppen et al., 2011). The effect of ocean acidification on corals is presently the focus of study (Erez et al., 2011).

Recent years have brought considerable contributions to scleractinian **life history**. "The ongoing global renaissance in coral reproduction research" (Harrison, 2011) established data on sexual reproduction for 444 species. Of them, 64.5% are hermaphroditic broadcast spawners, 19.5% gonochoric spawners, with fewer hermaphroditic and gonochoric brooders and a number of species demonstrating mixed sexual patterns/sex change. Multispecific spawning was recorded in many reef regions. Pioneering achievements include: analysis of systematic and biogeographical patterns in the reproductive biology (Baird et al., 2009), correlated evolution of sex (gonochorism/hermaphrodism) and reproductive mode (brooding/spawning) (Kerr et al., 2011) and observations that hybrids can be more fit than both parents, occupy new econiches and have a bioconstructive role (Budd, 2010; Zlatarski, 2010). The questions of coral allorecognition and xenorecognition (Rinkevich, 2004), chimerism (Puill-Stephan et al., 2009), skeletal calcification (Allemand et al., 2011) and diseases (Rosenberg & Kushmaro, 2011) received attention. The established evolutionary significance of hybridization is now posing a serious challenge to conservation policy and legislation because of the ignoring of the hybrids (Richards et al., 2010). The finding that climate change induces demographic resistance to disease in novel coral assemblages is important for projections concerning ecosystems under climate change (Yakob & Mumby, 2011).

Molecular biology has changed the way we think about the systematics and the evolution of the Scleractinia, although we are just beginning to realize its full potential. The lack of diversity in mitochondrial DNA makes it more difficult to establish intraspecific relationships with this type of genetic marker. Molecular analyses revealed that while the extant Scleractinia are monophyletic, families within the order are not (Fukami et al., 2008). Even more striking than the general lack of congruence within families is the amount of gross-morphological convergence between species in geographically distinct ocean basins (Fukami et al., 2004). Studies are focused on exploring the use of micromorphological, microstructural and nanostructural skeletal characteristics along with genetic data to present a more complete picture of the Scleractinia (Cuif et al., 2003; Benzoni et al., 2007; Budd & Stolarski, 2009, 2011; Budd et al., 2010, Kitahara et al., 2010; Gittenberger et al., 2011; Huang et al., 2011; Janiszewska et al., 2011). Molecular data also contribute to understanding reef connectivity by demonstrating historic and current patterns of connectivity between populations (Hellberg, 2007), the developmental and regulatory pathways in corals (Grasso et al., 2008; Schwarz et al. 2008), the innate immunity and resistance to infection (Vollmer & Kline, 2008), and the hologenome's response to environmental change and coral-specific gene families with predicted roles in calcification (Shinzato et al., 2011).

4. Future directions

Recent progress in scleractinian research has accumulated a considerable base of temporal and spatial information pending new interpretation and urging efficient holistic, multidisciplinary scientific collaboration. The following is a list of proposed directions for further attention, and serves as an appeal for discussion and steps toward future research in these areas:

- Material – expand the sample size of material collected to tap the phenotypic and genotypic diversity, the geological past, and the ecological distribution of species (Hoeksema et al., 2011), photo-digitizing collections in multimedia format, using the Coral Virtual Microscope Database System of the Coral Disease and Health Consortium, strong partnership between natural history collections holders and global change biologists (Johnson et al., 2011), develop standards for holistic collection of material and photodocumentation and organize virtual species museum (idea of Dr. V. Kosmynin, personal communication);
- Phenotypic variation – study variability at multiple levels, exploring plasticity (Shaish et al., 2007), intraspecific polymorphism and hybrids;
- Ontogeny – gain further insight into reproduction, septal insertion, astogeny, pathology and senescence and exploit skeletal growth records;
- Functional macro- and micromorphology – bring to light these important aspects of morphology;
- Paleobiology – focus research on temporal morphological diversification, reversed actuopaleontology (Zlatarski, 2010), forecasts from the past, sea-level changes as speciation "pumps", species reshufle for biodiversity conservation (Precht & Aronson, 2004), the importance of hybridization in the geological past and fossil behavior;
- Molecular biology – connect new molecular findings with taxonomic revision, engage in more integrative collaborations and maximize the potential of molecular techniques in life history, physiology, ecology and skeletogenesis;
- Skeletogenesis – further explore the interrelation between

animal and skeleton, and how the genes of soft organisms control the formation of an extracellular 3D-skeleton, particularly the physiology of skeletogenesis (ion transport, organic matrix characterization);

- Mesophotic and deep-sea habitats – prompt scleractinian research and evaluate their conservational and evolutionary potential;
- Speciation – better understand hybridization, histocompatibility and chimeras;
- Coral holobiont and reef ecosystem – direct attention to their coevolution in temporal and spatial dimensions;
- Integrative approach to harmonize the data of all sources of knowledge;
- Preparation of specialists – workshops of the International Association for the Study of Fossil Cnidaria and Porifera, the Projects Corallosphere/TIP and the Integrative Graduate Education and Research Traineeship;
- The importance of coral hybridization urges re-evaluation of species and ecosystem conservation approaches and including scleractinian hybrids in conservation policy and legislation.

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Early Jurassic corals of the Pamir Mountains - a new Triassic-Jurassic transitional fauna

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ABSTRACT. Four microstructural groups of corals representing the orders Scleractinia and Hexanthiniaria are known in the Triassic and in the Early Jurassic of the Tethys realm. In the south-eastern Pamir Mountains, Lower Jurassic corals occur from the Hettangian to Toarcian sediments. Hettangian?-Sinemurian and Sinemurian coral faunas discussed in this paper come from the Gurumdy and Mynkhajir facies zones. Coral associations are composed of classical Early Jurassic West European and North African (Moroccan) taxa, accompanied by several genera previously unknown in the West Tethys. After the end-Triassic extinction, the Early Jurassic recovery faunas of the Pamir Mountains contain *Stylophyllopsis, Eocomoseris*, a genus related to *Elysastrea,* and a large number of Jurassic genera: *Oppelismilia, Archaeosmilia, Archaeosmiliopsis, Stylosmilia, Proaplophyllia, Cylismilia, Intersmilia, Prodonacosmilia, Pachysmilia, Placophyllia* and *Stephanastrea.* More or less fragmented corals and complete skeletons are found in detrital carbonate, oolitic, or micritic limestone facies. Phaceloid growth forms prevail over solitary and massive ones.

KEYWORDS: Scleractinia, Hexanthiniaria, Tethys, Central Asia, recovery fauna.

1. Introduction

Hettangian?-Sinemurian corals from the south-eastern Pamir Mountains occur soon after the end-Triassic mass extinction and while incompletely known represent the most taxonomically differentiated coral faunas of that time. This recovery fauna is composed of new taxa of relic Triassic groups as well as of newly evolved coral groups. The purpose of this paper is to present a summary of the fauna and its palaeogeographic relationships to the west Tethyan corals.

The earliest coral-bearing sediments in the south-eastern Pamir Mountains belong to strata of the late Hettangian? to Sinemurian age (Dronov & Melnikova, 1987, 2007; Melnikova, 2006, p. 173). These widely distributed sedimentary rocks composed of bedded, dark limestones of variable lithology, occur at the lower part of two structural zones (Fig. 1): south-west Gurumdy Zone and north-east Mynkhajir Zone, separated by the Istyk Uplift, directed NW-SE with marine transgressive facies of the Aalenian-early Bajocian (Andreeva & Dronov, 1972), all lying discordantly upon Triassic sedimentary strata. In each zone a number of sedimentary series were differentiated, each having a characteristic lithology, named with informal terms: suite (svita: Dronov & Melnikova, 1987), or formation (Melnikova, 2006).

Some of these finds were described in the past (Melnikova, 1975, 1989; Melnikova & Roniewicz, 1976; Melnikova et al., 1993), providing a more complete insight in the coral recovery after the Triassic-Jurassic faunal crisis (Melnikova, 2006). This crisis was preceded by the intra-Norian decrease in coral diversity observed in the west Tethys, as documented by comparisons of faunas of the late Carnian-early Norian with those of the late Norian-Rhaetian time (Roniewicz, 2010, 2011). During the late Norian and Rhaetian bloom the coral fauna reached a different taxonomic composition in comparison with that of the preceding stage (Fig. 2).

Stage	Structural Zones		
	Gurumdy Zone at the SW of the Istyk Uplift	Istyk Zone Istyk Uplift	Mynhadjir Zone at the NE of the Istyk Uplift
Late Sinemurian-Bajocian	Sedek Formation **A**	Karauldyn Formation	Zormynkhadjir Formation
Sinemurian	Ghurumdy Formation ** **A**	[land]	Mynkhadjir Formation **
Hettangian?--Sinemurian	** **A** *Cardinia* sp.sp.	Shahtesay Formation	** *Cardinia* sp.sp.
Hettangian	Darbazatash Formation		Kyzylbeles Formation
Upper Triassic deposits discordantly overlain by Lower-Jurassic conglomerates			

Figure 1. Structural-facies zonation of the lowest Early Jurassic strata in the South-East Pamir Mountains with distribution of Early Jurassic corals and ammonites. Legend: ** corals of Triassic and Jurassic relationships, **A** Early Jurassic ammonites.

A well known late Norian-Rhaetian fauna (e.g. Roniewicz 1989, Roniewicz & Michalik 1998, Melnikova, 2001) forms a basis for comparison of diversity between Late Triassic and Early Jurassic faunas. Dramatic diversity decrease of Rhaetian coral families after the T/J boundary is comparable to that of other marine organisms (Hallam, 1995). Knowledge of the composition of the Early Jurassic coral fauna is far from complete, but new finds from the south-eastern Pamir Mountains allow us to understand the proportion of Triassic corals to typical Jurassic genera in this Early Jurassic fauna. In defining the changes in coral fauna diversity at the level of high rank taxonomical units, a microstructural criterion has been used (Roniewicz & Morycowa, 1989, 1993).

2. Material

The characteristics provided herein are based on corals collected by G.K. Melnikova and on field observations that V.I. Dronov and G.K. Melnikova made between 1958 and 1980 (Institute of Geology, Dushanbe, Tadjik Republic). The material has been prepared in the form of thin sections. While the skeletons are recrystallized, they retain recognizable traces of the septal microstructure.

The collection of thin sections is housed at the Institute of Paleobiology of the Polish Academy of Sciences in Warsaw, Poland, under the repository number ZPAL H26.

3. World distribution of the Early Jurassic corals

From all Early Jurassic occurrences in the world, those from the West Europe, North Africa (Morocco) and the south-eastern Pamir Mountains in Central Asia are recognized the best. First taxonomic descriptions from the early Early Jurassic and middle Early Jurassic are these from the Belgium, Luxemburg, France (d'Orbigny, 1850; Chapuis & Dewalque, 1853; Fromentel, 1862; Dumortier, 1864; Terquem & Piette, 1865; Fromentel & Ferry, 1865-1869) and British Isles (Duncan, 1867-1868; Tomes, 1878, 1882, 1888). In the 20th century, this literature was increasing (Alloiteau, 1958; Weyer, 1965; Turnšek et al., 1975; Beauvais, 1976; Roniewicz & Michalik, 1998; Turnšek & Buser, 1999; Turnšek & Košir, 2000; Stolarski & Russo, 2002; Turnšek et al., 2003; Kiessling et al., 2009).

Microstructural group	Family	LC - EN	LN - R	H - S
1st	Stylophyllidae	—	▬	▬
	Gigantostylidae		—	
2nd	Volzeiidae	▬		
	Protoheterastraeidae	—		
	Archeosmiliidae			▬
	Coryphylliide	—	—	
	Reimaniphylliidae	—	▬	
	Distichoflabellidae		—	
	Margarophylliidae	▬	—	
	Procyclolitidae		—	
	Alpinophylliidae		—	
3rd	Actinastraeidae	—	—	▬
	Stylinidae			—
	Placophylliidae			—
	Conophyllidae	▬		
	Cycliphylliidae	—	—	
	Gablonzeridae	—	—	
	Curtoseriidae	—	—	
	Cuifastraeidae	—	▬	
	Thamnasteriidae	—	—	●●●●●▶
	Pamiroseriidae		▬	
	Tropiastraeidaea	▬		
	Astreomorphidae	—	▬	
	Microsolenidae	—	—	▬
	Latomeandridae			—
	Furcophylliidae	—		
4th	Zardinophyllidae	—	—	—
	Amphiastraeidae	—	●●●●●▶	●●●●●▶
	Donacosmiliidae			—
	Intersmiliidae			—
Corals of poorly preserved microstructure belonging to the 2nd or 3rd microstructural group	family A: *Hydrasmilia*	—		
	family B: *Thamnasterites*	—		
	family C: forking coral	—		
	family D: solitary dwarfish coral	—		
	No. of families/genera	24/ca.50	18/ca.40	10/>11

Figure 2. Coral families documenting the post-Early Norian and post-Rhaetian drops of faunal diversity. Legend: microstructural groups 1st fascicular; 2nd minitrabecular; 3rd thick-trabecular; 4th pachythecal after Roniewicz & Morycowa (1993); LC-EN families of the late Carnian-early Norian fauna; LN-R families of the late Norian-Rhaetian fauna, both observed in the Northern Calcareous Alps; H-S families in the Hettangian?-Sinemurian and Sinemurian fauna in the Pamir Mountains (after Roniewicz, 2010, 2011, modified).

The literature covers other Tethyan regions including Morocco with Early Jurassic fauna described by Beauvais (1986), and earlier results (Le Maitre, 1935; see also Melnikova et al., 1993), and the south-eastern Pamir Mountains with early Early Jurassic corals (Melnikova, 1975, 1989, 2006; Melnikova & Roniewicz, 1976; Melnikova et al., 1993; Dronov & Melnikova, 1987).

Early Jurassic corals also were described form the North America from the deposits of the Sinemurian from British Columbia (Beauvais 1982; Stanley & Beauvais, 1994), and from the Lower Jurassic of the South America: Peru (Wells, 1953; Senowbari-Daryan & Stanley, 1994), from the Hettangian to Pliensbachian of Chile (Prinz, 1991), and from the Pliensbachian of Argentina (Morsch, 2001). Although these other faunas will not be addressed in the comparisons, a common presence of stylophylline corals seems clear. Global changes in coral generic diversity during the Late Triassic and Early Jurassic as connected with reefal environment development were analyzed by Lathuilière & Marchal (2006) who presented range charts.

4. Early Jurassic coral environments

In the Recent reef ecosystem, scleractinians are important components of the fauna on continental shelves and volcanic islands in subtropical and tropical zones, in the depth range of storm wave base, in oligotrophic, transparent, well aerated water, settled on hard bottom, in presence of green algae of similar preferences. The picture for Mesozoic coral environments is different when we consider the type of sedimentation, bottom conditions and associated organisms, among which are cyanobacteria.

The earliest Jurassic corals found in situ, formed associations of a few taxa, contained in fine detrital facies, so, they were developed on soft sediment bottom. In comparison to Triassic conditions, corals lost their significance in reef-building and as an influence on sedimentation, because high growing, bushy growth form, frequent in the Triassic, became replaced by solitary forms incapable of reef-building. Phaceloid corals developed only locally. Later in the Hettangian and Sinemurian, coral diversity was augmented by discoid, fungiform and incrusting colonial growth forms as well as rare cerioid or thamnasterioid branching colonies, but their influence on sedimentation as potential bafflers was restricted as well.

Early Jurassic coral-bearing deposits were described from many regions (Joly, 1936; Turnšek et al., 1975; Buser & Debeljak, 1996; Kiessling et al., 2009). In the Hettangian and Sinemurian of Europe, corals occur, as fragments or complete skeletons, in marls, mudstones, sandstones etc; in the Pliensbachian, corals are known in the limestones (Slovenia). In the south eastern Pamir Mountains, early Early Jurassic corals occur in limestones: micritic through oolitic to pelletal-bioclastic or in marls and sandy marls; commonly, corals are associated with structures of cyanobacterian origin. In Europe and in the Pamir Mountains, early Jurassic corals settled on unstabilized sediment bottom; if branching (mostly phaceloid), corals formed meadow-like thickets at most, without making upward-growing bioconstructions.

The post-Triassic time was characterized with a global decrease of carbonate production in general and a rarity of reefs in particular. So, the corals, although present in Early Jurassic shallow seas, rarely developed reefs. The so called "Elmi Reef" in southern France, represents the only known example of an Early Jurassic reefal body, up to 20 meters thick, traceable laterally for 200 m and with smaller bodies in the immediate vicinity. It was described as coral-microbial reef, developing at a moderately deep water, but in range of storm-wave base (Kiessling et al., 2009).

5. Four evolutionary lines of Mesozoic corals

Micromorphology and microstructural aspects of the coral skeleton may be traced throughout the stratigraphical column, allowing us to recognize specific microstructural coral groups corresponding to high systematic units. This allows us to recognize the pressing problems of homeomorphy that is a troubling issue in taxonomic studies. Thanks to the microstructural studies, it was subsequently possible to differentiate four groups of corals by particular details of their skeletal structure (some detectable also in the micromorphology of septa).The recognition of these groups can be made from the Triassic throughout the Jurassic and three of the microstructural groups represent evolutionary stems. These are coral groups with the following skeleton microstructure types: 1st fascicular, 2nd minitrabecular, 3rd thick-trabecular (heterogeneous group) and 4th pachythecal (terminology: Roniewicz & Morycowa, 1989; 1993). Each group embraces one or more units of suprafamilial rank belonging to the orders Scleractinia (1st - 3rd groups) or Hexanthiniaria (4th group). In addition, an informal, heterogeneous scleractiniamorph-group, to which some Ladinian-Carnian corals were ascribed, defined by trabecular microstructure and broom-like arrangement of septa (Stolarski et al., 2004, Melnikova & Roniewicz, 2007). The microstructural groups exemplify evolutionary lines which are to be traced throughout the Mesozoic. The contents of the groups in the Early Jurassic will be characterized in the section 8.

Participation of these coral groups in the fauna of different geological periods allows us to differentiate a number of stages and developmental phases in scleractinian history (Roniewicz & Morycowa, 1989, 1993). The stages are determined by a share of given families in composition of fauna; phases differ from each other by a generic content of the families, changeable in time, thus, expressed in the faunistic spectrum, which is typical of a given time slice. The fauna considered in this paper developed during the Hettangian-Pliensbachian phase of the Early Mesozoic.

6. Characteristics of Early Jurassic corals from the West Tethys

Instability of environmental conditions and a collapse of coral development at the Rhaetian/Hettangian boundary was followed early in the Jurassic by the start of a coral recovery in the Tethys and neighbour epicontinental seas (West Europe, southern Europe, Carpathians, North Africa). Although corals are known from numerous localities, coral bearing sediments do not represent a significant volume within the early Jurassic column. The "Elmi Reef" is perhaps the exception to this (Kiessling et al. 2009).

In the western Tethys, the decline of the coral fauna at the T/J boundary is in both taxonomic and morphologic contrast between a rich end-Triassic fauna and that, impoverished one of the early Hettangian. A majority of Triassic families are missing during the Early Jurassic record (Fig. 2).

The descriptions of the earliest Jurassic corals from the British Isles, Luxemburg, and France (early Hettangian: *Psiloceras planorbis recte* - *Psiloceras spelae* ammonoid Zone) were not yet taxonomically revised. Judging from illustrations, this fauna is formed, first of all, from genera thriving from the Triassic, the most numerous corals from the fascicular microstructural group (the 1st group): *Stylophyllopsis* Duncan, (1867-1868; described as *Montlivaltia* in part), *Phacelostylophyllum* (in Duncan: *Thecosmilia* in part), *Heterastraea* (in Duncan: *Septastraea* and *Isastrea),* and from thick-trabecular group (the 3rd group): small-calicular, colonial corals, apparently were diversified taxonomically (described in the Duncan monograph as *Astrocoenia* and *Cyathocoenia)*, among others containing *Chondrocoenia* of Triassic derivation under these names. In southern France, these groups are the best represented in the "Elmi Reef" (Kiessling et al., 2009), including subglobular *Rhaetiastraea,* another Triassic holdover. Stylophyllid genera from the *Oppelismilia*-group are frequent in the earliest Jurassic, as a novelty presenting septal apparatus made of isomorphic septal spines: *Oppelismilia* (Flügel, 1964), *Heterastraea* (Beauvais, 1976) and *Haimeicyclus* (Stolarski & Russo, 2002).

European corals of the minitrabecular and pachythecal (hexanthiniarian) groups (the 2nd and 4th groups) have not been mentioned in the literature as yet, although among *Thecosmilia, Montlivaltia,* or a coral erroneously attributed to *Elysastrea* in Duncan's monograph, are possible their representations. Their presence in the western Europe is expected as the minitrabecular archeosmiliids, in addition to those from the south-eastern Pamirs, are present in Morocco (Beauvais, 1986), and the pachythecal corals occur in the Pamirs.

A lack of Triassic, ecological conditions of coral habitats in the Early Jurassic may account for the observed changes in taxonomic character of coral fauna. This is evidenced by widespread solitary growth forms (terminology of Coates & Jackson, 1987), locally disc-like (British Isles, Luxemburg, Spain, Morocco, Sicily), in a smaller share of pseudocolonial phaceloid corals, than it was in the Late Triassic, and in appearance of small, disc-like and fungi-form cerioid colonies (Beauvais, 1976).

7. Early Jurassic corals in the South-East Pamir Mountains

The microstructural differentiation of Early Jurassic corals still relates to that of the preceding, late Norian-Rhaetian fauna (Roniewicz & Morycowa, 1993). However, the Pamirian corals differ from the latter fauna in taxonomic variability, i.e., in a different generic representation of Triassic families, and in appearance of typically Jurassic taxa that were ancestors of new families.

7.1. Geological characteristics of coral distribution

7.1.1. The Gurumdy Zone

In the Gurumdy Zone (Fig. 1), three superposed lithological units have been observed (Dronov & Melnikova, 1987, Melnikova, 1989, 2006): (a) the Darbazatash Formation estimated to be of the Hettangian age, transgressive, composed of terrigenic sediments overlying discordantly Permo-Triassic strata; (b) the Gurumdy Formation which will be discussed below as the only in this zone containing coral-bearing limestones; its stratigraphic position is determined by late Hettangian-Sinemurian ammonites, a schlotheimiid shell fragment, at its lower part, and an imprint of a Sinemurian ammonite *Angulaticeras* or *Gleviceras*, in its limits; (c) the Sedek Formation, overlying concordantly the preceding one, composed of bedded limestone and marls with abundant, taxonomically diversified ammonites from late Sinemurian at its lower part, through Pliensbachian up to Aalenian age at the top.

Lower Jurassic sediments of the Gurumdy Formation (from 40 m up to 400 m thick, depending the place) may be observed along the Alichur and Gurumdy rivers in the creeks ("*says"*) opening to these river valleys and in the easternmost site, in the Gunyabay Say in the Teshiktash Massif.

In the creeks at the right side of the Alichur River, the sequence is composed of limestones of variable lithology. Its lower member (20-100 m thick) is composed of bioclastic limestones with frequent coral debris, limy shales, and marls with frequent corals, layers rich in bivalves *Cardinia* sp., and a peculiar, layered limestone bed of algal origin. In the upper part of the member, there are gray, micritic limestones with corals, especially phaceloid ones. The upper member (in a whole 20 m up to 300 m thick) is composed of oolitic and micritic limestones interbedded with oncolitic-bioclastic limestones of variable thickness, and of massive, thick-bedded limestone. The corals are represented by colonies of heavily recrystallized skeletons, rendering them difficult to determine taxonomically.

7.1.2. The Mynkhadjir Zone

Lower Jurassic sediments are observed in the valley of the Kizylbeles River, on the Kizylbeles Pass and in the West and East Mynkhadjir massif. Two Lower Jurassic lithological units were distinguished (Dronov & Melnikova, 1987, Melnikova, 2006): (a) the Kizylbeles Formation (30-50 m thick) discordantly overlying Norian-Rhaetian strata with transgressive facies, its tentative age is Hettangian; (b) the Mynkhadjir Formation (200 m) concordantly overlying the latter, composed of limestones, marls and limy shales, and divided into three parts; its tentative age is late Hettangian to Sinemurian. The formation is concordantly overlain by dark, well bedded limestone of (c) the Zormynkhadjir Formation (20-50 m), corresponding in lithology and fauna to the Sedek Formation of the Gurumdy Zone; its age being tentatively assigned as early Middle Jurassic.

The Mynkhajir Formation, in the most complete development is observed in the Kizylbeles Valley: the lower part (50 m) is composed of dark micritic limestones of the late Hettangian?-Sinemurian age. A peculiar, layered limestone bed of algal origin and *Cardinia* beds correspond to those known from the Gurumdy lower member. On the Kizylbeles Pass, in the lower member, there are coral-bearing limestones; the middle member (50 m) mostly dolomitic in the upper part, contains limestone with corals in the lower part; the upper member (100 m) contains thick-bedded, grey, bioclastic limestone with oolites and oncolitic structures. In the Kizylbeles Valley, Sinemurian corals were observed.

7.2. General characteristics of the Pamirian coral fauna

In comparison with the fauna of the west Tethys, the ecological character of the Pamirian fauna is different, because pseudocolonial, phaceloid genera (8-9) dominated over solitary genera (4). Nine genera with 12 species from the Hettangian?-Sinemurian of the south-eastern Pamir Mountains already were described (Melnikova, 1975, 1989, Melnikova & Roniewicz, 1976, Melnikova et al., 1993), and other seven taxa have been here identified on the generic level (Fig. 3). The list is not yet complete as the collection contains a number of genera awaiting description.

Microstructural groups	Taxa	growth forms			
		s	**ph**	**c**	**t**
1st	*Stylophyllopsis* sp.	■	■		
	Oppelismilia sp.	■			
	Pinacophyllum? sp.		■		
2nd	***Archeosmilia beata***	■			
	Archaeosmiliopsis densus		■		
3rd	***Stylosmilia alitschurica***		■		
	Stylosmilia decemseptata		■		
	Proaplophyllia basardaraensis		■		
	Placophyllia sp.		■		
	Stephanastraea sp.			■	
	Cyathocoenia? sp.			■	
	Elysastrea? sp.			■	
	Eocomoseris gurumdyensis				■
	Eocomoseris lamellata				■
4th	***Pachysmilia prima***		■		
	Prodonacosmilia dronovi		■		
	Cylismilia brevis	■			
	Cylismilia longa	■			
	Intersmilia djartyrabatica		■		

Figure 3. Hettangian?-Sinemurian and Sinemurian corals recognized in the Pamir Mountains. Legend: microstructural groups 1st fascicular; 2nd minitrabecular; 3rd thick-trabecular; 4th pachythecal after Roniewicz & Morycowa (1993); growth forms: s solitary, ph phaceloid, c cerioid, t thamnasterioid after Coates & Jackson (1987); in bold style are marked taxa described in earlier papers (Melnikova, 1975, 1989; Melnikova & Roniewicz, 1976; Melnikova et al., 1993).

In the taxonomical spectrum of this fauna, Late Triassic genera of the stylophyllid, volzeioidean and hexanthiniarian (pachythecal) corals are present, as well as microsolenids. Corals of the suborder Stylophyllina, highly differentiated taxonomically in the Rhaetian, are represented by Triassic solitary/phaceloid genera *Stylophyllopsis,* and by Jurassic genus *Oppelismilia,* known also from the faunas of the west Tethys. The superfamily Volzeioidea contain two genera with a straight midseptal line, *Archaeosmilia* and *Archaeosmiliopsis,* from the family Archaeosmiliidae (originally attributed to the sub-order Amphiastraeina) which is close to the Carnian Protoheterastraeidae. Hexanthiniarian corals are represented by the zardinophyllid genus *Pachysmilia* (originally attributed to the Amphiastraeidae), by intersmiliid genus *Intersmilia* (originally treated as of unknown attribution in Eliášová, 1974, or considered to be linked with archaeosmiliids in Roniewicz & Morycowa, 1993), and by donacosmiliid genera *Cylismilia* and *Prodonacosmilia*.

From the thick-trabecular group of corals abundantly represented in the Triassic, two colonial genera with pennulae and meniana are present: regularly porous *Eocomoseris* and a coral related to *Elysastrea* Laube, 1865, having no common characters with corals described by Duncan, 1867 under this name. This links the Triassic fauna with two Jurassic groups: the first, the microsolenids and the second, the latomeandrids.

The remaining Early Jurassic corals of the south-eastern Pamirs belong to groups which, appeared for the first time in the Jurassic, then became typical of the Late Jurassic: phaceloid *Stylosmilia* and *Proaplophyllia* (Stylinidae) described in Melnikova (1989), and corals determined herein to the generic level as phaceloid *Placophyllia* sp. (Rhipidogyrina), colonial, lamellar *Stephanastrea* sp. (Actinastraeidae), and a coral determined provisionally herein as *Cyathocoenia?* sp. (Actinastraeidae?).

8. Discussion

The composition of the Pamirian coral fauna is especially interesting because the abundant fossils allow us to more accurately consider the familial composition of a transitional Triassic/Jurassic character with a slant towards those of the Jurassic.

With application of the microstructure as a taxonomical guide, differentiation of corals into four microstructural groups was possible (Roniewicz & Morycowa, 1989). Two drops of coral diversity have been recognized during the Late Triassic: the intra-Norian (post-early Norian) and the second at the Triassic/Jurassic boundary (Roniewicz, 2010, 2011). Interestingly, this shows different responses of each of corals groups (Fig. 2).

Late Norian-Rhaetian coral fauna, composed of 19 families, at least, and approximately of 40 genera (Roniewicz, 2011), most frequently occur in meadow-like associations (*constratal growth fabric* of Insalaco, 1998). These corals were well differentiated morphologically, abounding in solitary, phaceloid, high-growing, bushy forms and colonial forms of a variable corallite integration: cerioid, meandroid, thamnasterioid, astreoid, plocoid, kuhnastreoid (Roniewicz, 1989). Septal micromorphology (pennulae, meniana) of many Late Triassic corals was connected with their feeding specialization as was clarified using modern agariciid corals as the homology (compare Schlichter, 1992).

Such faunal composition changed by extinction of genera and families at the T/J boundary. During Early Jurassic, this fauna was replaced by a new one, exemplified by Pamirian corals, supplemented with new genera, but still composed of four microstructural groups (Fig. 3), each of them evolved at their own pace, as follows:

The first group: fascicular microstructure (sub-order Stylophyllina). The relic Triassic genera (*Stylophyllopsis, Phacelostylophyllum, Pinacophyllum*-like coral) are the most widely distributed palaeogeographically with occurrences in west Europe, north-western Africa, and the south-eastern Pamir Mountains. In addition, a new morphological trend appeared in this group with the formation, for example, of septa of thin, homogeneous septal spines that are observed in corals of diverse growth forms. In solitary corals this structure is known in taxa with ecologically conditioned ceratoid or discoid shapes of corallum connected with unloving on unstable sediment bottom: the first in *Oppelismilia* Duncan (re-described in Flügel, 1964), recognized also in the Pamirian fauna, and the second in *Haimeicyclus* Alloiteau (re-described in Stolarski & Russo, 2002).

The second group: minitrabecular microstructure (superfamily Volzeioidea). In the Hettangian-Sinemurian of the south-eastern Pamir Mountains, this group is represented by *Archaeosmilia* and *Archaeosmiliopsis*. Well illustrated, published photos allow us to recognize genus *Archaeosmilia* among the fauna of the upper Sinemurian of Spain, described as *Montlivaltia polymorpha* and *M. doriai* (Turnšek et al., 1975). Among Domerian corals of Morocco, five species of *Archaeosmilia* have been determined (Beauvais, 1986).

The third group: thick-trabecular diverse microstructures (heterogeneous group) The corals of this microstructural group were present during Hettangian and Sinemurian in the Tethys and also in the Pamirs. During Hettangian?-Sinemurian time in the south-eastern Pamir Mountains, the genera *Stylosmilia* (known also from the lower Domerian of Morocco) and *Proaplophyllia* occurred (described in Melnikova, 1989), as well as other Jurassic genera: *Eocomoseris* (described in Melnikova et al., 1993), *Placophyllia*, *Stephanastrea, Cyathocoenia* -like coral, and others, stated within the Pamirian collection. A rich representation of colonial genera makes this fauna similar to that of the Rhaetian time: however, abounding in different colonial taxa.

In this early Jurassic spectrum, genus *Eocomoseris* is especially interesting (described from Morocco as *Spongiomorpha crassa* by LeMaitre, 1935): the coral defined by a regular septal porosity, meniana-type micromorphology and a monotrabecular columella. It is a genus appearing during early Norian time (Roniewicz, 2011) and originally was described from the Rhaetian of the Alps as *Spongiomorpha ramosa* Frech, 1890. It was recognized among Early Jurassic corals of the south-eastern Pamir Mountains (Melnikova et al., 1993), and among Cenomanian, Late Cretaceous corals (Löser in Melnikova et al., 1993). Together with pennular coral resembling late Carnian *Elysastrea*, they may profitably be compared with the recent deep-water *Leptoseris fragilis* by a similar micromorphology of septa. In *Leptoseris fragilis*, septal sides bear meniana to support coelenteron ramifications provided with perforations related to the unusual anatomical adaptation by this coral to a filtering mode of feeding (Schlichter, 1992).

The fourth group: pachythecal microstructure (order Hexanthiniaria). During the Hettangian?-Sinemurian in the south-eastern Pamir Mountains, this coral group diversified into zardinophyllids, represented by phaceloid *Pachysmilia* (Melnikova, 1989), donacosmiliids, represented by solitary *Cylismilia* and phaceloid *Prodonacosmilia*, and intersmiliids represented by phaceloid *Intersmilia* (see Melnikova & Roniewicz, 1976), the latter attributed to the archaeosmiliid group in Roniewicz & Morycowa, 1993. Outside the Pamirs, this group has not been reported from the Lower Jurassic. It thus is thought to have migrated much later in the Upper Jurassic of the Tethys realm.

9. Conclusions

a) Early Jurassic coral faunas developed in ecological conditions different from those of the Late Triassic. They display a different taxonomic composition. West European, North-West African and south-east Pamirian corals of the Early Jurassic, show that the groups which characterized Late Triassic assemblages (solitary and phaceloid corals with minitrabecular septal microstructure), like *Retiophyllia, Distichophyllia, Margarosmilia* (see Roniewicz, 1989; Melnikova, 2001) or colonial corals of the Pamiroseriidae and Cuifastraeidae with thick-trabecular septa, were absent from the Jurassic.

b) In Europe, the earliest Jurassic corals (early Hettangian) have simple morphologies: that most frequently are solitary with ceratoid or patelloid shapes, as well as phaceloid. More complex colonial corals are rare, and these include small colonies of cerioid type, or very rare corals of thamnasterioid type. Solitary and phaceloid growth forms are typical of each of the four microstructural groups. This is a veritable “fauna of survival”.

c) Meniana-bearing, regularly porous microsolenid *Eocomoseris* and the pennular, non-porous skeleton of the *Elysastrea* -like genus, both displaying Triassic micromorphological patterns typical of the Pamir fauna, showed the ability to adjust to varying environmental conditions and to pass through the end-Triassic mass extinction also characterized by a major drop of sea level at the T/J boundary. Following the extinction they then adapted to new conditions of the Early Jurassic.

d) Stylophyllid group, relatively rich morphologically during the Rhaetian, crossed the Rhaetian/Hettangian boundary with the most simple morphologies, and then diversified morphologically and taxonomically in the Early Jurassic.

e) Early Jurassic Pamirian and Moroccan faunas contain genera which later gave rise to coral lineages during the Late Jurassic and Early Cretaceous recovery of calcareous platforms. These corals evolved into the microsolenids, latomeandrids, stylinids, rhipidogyrinas (the 3rd group), and pachythecal amphiastreids (the 4th group). In contrary, minitrabecular corals, (the 2nd group) disappeared from shallow waters. This microstructural line renewed itself in deep water environments (see also Roniewicz & Morycowa, 1993). The stylophylline coral lineage (the 1st group), presented throughout the Tethys during the Early Jurassic as well as Panthalassa, did not crossed the boundary of the Middle/Late Jurassic. It occurred up to the Callovian. This is illustrated by a coral from Israël, determined as *Epistreptophyllum* (Gill, 1982*)* which shows all features of septal structure typical of the Stylophyllina.

f) A high ecological specialization of early Jurassic in particular and Mesozoic corals in general, is expressed in their evolution of skeleton structures adjusted to the following environmental characteristics: i) a soft-sediment bottom for corals settlement; ii) lowered water transparency resulting from intense precipitation of calcium carbonate, a part of which must remain temporarily in suspension; iii) a high nutrient content indicated by the relative abundance of the microbial development; iv) a strong paleoecological specialization of some coral genera in a filtering mode of feeding as indicated by their septal micromorphology (i.e., pennulae and meniana); v) a frequency of high-growing corals of phaceloid, uniserial form, which were different from many modern multiserial branching corals. This indicates that these Mesozoic corals preferred zones of less energetic water than those living in Recent reefs (Roniewicz & Stolarski, 1999).

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Intraspecific variation in the genus *Stelidioseris* (family Actinastraeidae, suborder Archeocaeniina, order Scleractinia; Jurassic-Cretaceous)

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ABSTRACT. The genus *Stelidioseris* (= *Actinastrea* s.l.) is one of the most common genera in the Late Jurassic and Early Cretaceous and has a high number of species. Species separation is generally based on calicular dimensions, septal symmetry, and septal number. To obtain better insight into intraspecific variation and results for species separation, systematic measurements of the corals were taken and statistically analysed. As a preliminary study, ten type specimens were selected for analysis. In thin sections a large number of calices (up to 200) were measured, including their diameter, distance and the thickness of the wall and coenosteum. For all values, the arithmetic mean, standard deviation and the coefficient of variation were calculated. In *Stelidioseris*, the calicular diameter is the character with the lowest variation. The distance of the calicular centres, the thickness of the wall, and the number of calices per a given area show a much higher variation and are therefore less suitable for distinguishing samples within a population or species of different faunas. It was found that about 70% of all values of the lumen diameter fall in the first interval (range of the arithmetic mean ± standard deviation). Hence, the first interval is a good representation for most types of measured values in fossil corals. The results are compared to traditional methods by remeasuring published material. It is concluded that the application of systematic measuring should be extended to other species rich coral genera.

KEYWORDS: Corals, statistics.

1. Introduction

The Late Jurassic to Cretaceous *Stelidioseris* Tomes, 1893 (= *Actinastrea* s.l., see Löser, 2012) belongs to the most common genera in the Late Jurassic and Early Cretaceous. The large number of 120 described species (Löser, 2012) reflects the abundance of the genus in the fossil record. Most species were established on the base of complete unsectionned specimens and / or without proper comparison to existing species. *Stelidioseris* taxa are generally distinguished by their calicular dimensions and the number of septal systems and septal cycles. To handle the high number of taxa and to create a base for a revision of the genus, type material of ten species has been systematically examined. Various statistical methods were applied to understand the variation of the calicular dimensions within individual colonies and obtain a better idea about the limits of species.

2. Abbreviations

BGS, The British Geological Survey, Keyworth (England);
ERNO, Instituto de Geología, Estación Regional de Noroeste, Universidad Nacional Autónoma de México, Hermosillo

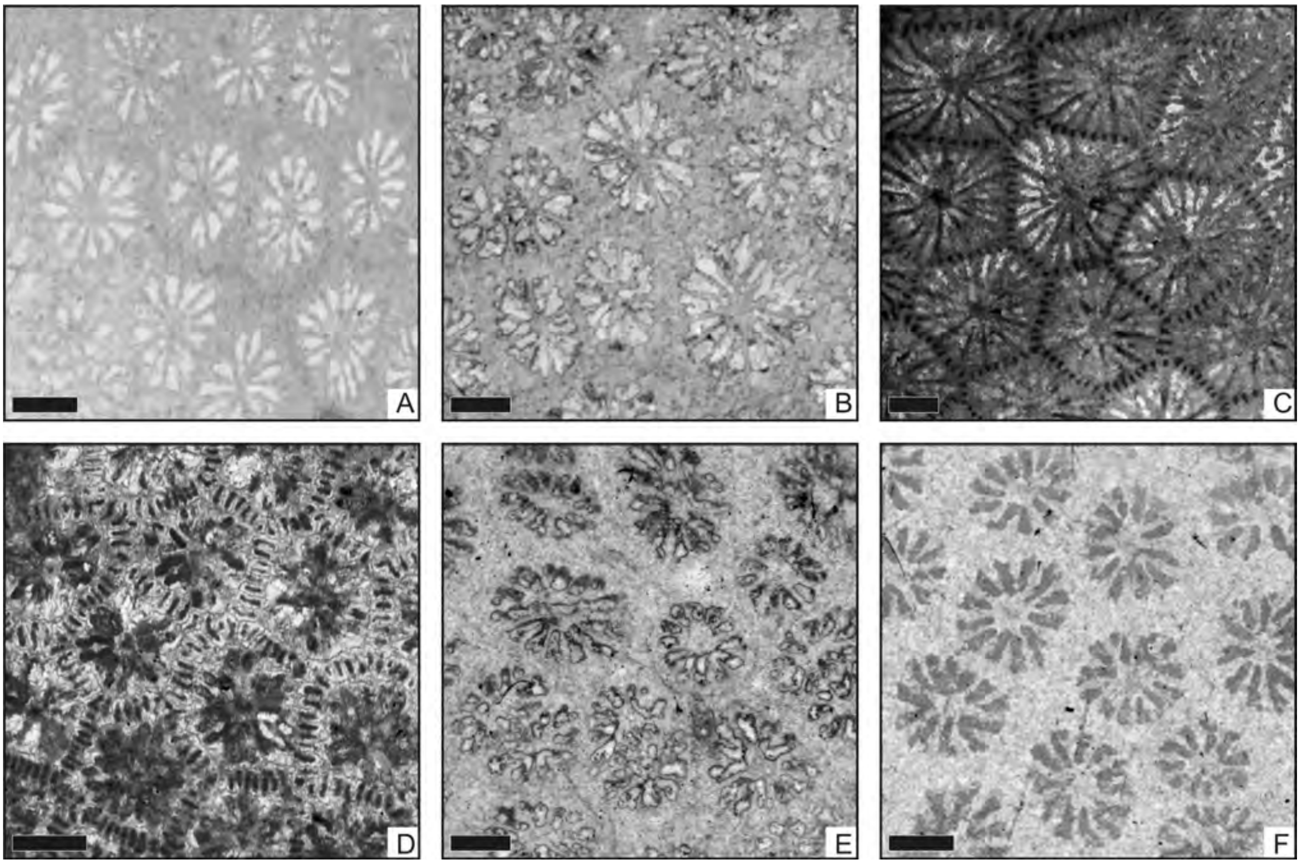


Figure 1. A: *Astrocoenia bernensis explanata* Dietrich, 1926, holotype MB K1330, thin section. B: *Astrocoenia bernensis sphaeroidalis* Dietrich, 1926, lectotype MB K1328, thin section. C: *Thamnasteria harrisoni* Gregory, 1927, lectotype GLAHM C4140, thin section. D: *Astrocoenia japonica* Eguchi, 1951, lectotype TUM 56502, thin section. E: *Holocoenia polymorpha* Prever, 1909, lectotype PU 18062, acetate peel. F: *Astrea ruvida* Prever, 1909, holotype PU 17933, acetate peel. Scale 1 mm.

(Mexico);
GLAHM, Hunterian Museum, Glasgow (England);
MB, Museum für Naturkunde der Humboldt-Universität Berlin (Germany);
PU, Museo di Geologia e Paleontologia dell' Università di Torino (Italy);
TUM, Tohoky University Museum, Sendai (Japan);
UJ, Jagiellonian University, Instytut Nauk Geologicznych, Kraków (Poland).

3. Material

Numerous *Stelidioseris* samples were examined in preparation of this study. The following ten type specimens of *Stelidioseris* species were selected for detailed examination to demonstrate the methods:

- *Astrocoenia bernensis explanata* Dietrich, 1926, holotype (by monotypy) MB K1330 (Fig.1A);
- *Astrocoenia bernensis sphaeroidalis* Dietrich, 1926, lectotype (here designated) MB K1328 (Fig.1B);
- *Stelidioseris gibbosa* Tomes, 1893, lectotype (by subsequent designation) BGS 5161;
- *Thamnasteria harrisoni* Gregory, 1927, lectotype (here designated) GLAHM C4140 (Fig.1C);
- *Astrocoenia japonica* Eguchi, 1951, lectotype (here designated) TUM 56502 (Fig.1D);
- *Actinastrea minima irregularis* Morycowa, 1964, holotype (by original designation) UJ 4P7#1;
- *Columastrea paucipaliformis* Baron-Szabo & González-León, 1999, holotype (by original designation) ERNO 2153;
- *Holocoenia polymorpha* Prever, 1909, lectotype (here designated) PU 18062 (Fig.1E);
- *Astrea ruvida* Prever, 1909, holotype (by monotypy) PU 17933 (Fig.1F);
- *Astrocoenia tendagurensis* Dietrich, 1926, (lectotype by subsequent designation) MB K1337.

4. Methods

The distinction of species in Mesozoic scleractinian corals is almost entirely based on (1) dimensions of the corallites, distance of corallites, and width of calicular rows in meandrinoid corals, respectively, (2) the number of regular septal systems (if present), and (3) the number and/or density of septa. Corallite dimensions indicated in the literature, or their ranges between a lower and an upper value, are generally not based on statistically significant measurements. While skeletal dimensions are indispensable for species determination, almost nothing is known about the variation of these dimensions within single colonies, species or populations of Mesozoic corals apart from a few empiric studies (Lathuilière, 1988, 1990; Lathuilière & Gill, 1998; Pandey et al., 1999) on mainly Jurassic corals. In contrast to Tertiary corals where systematic measurements of skeletal dimensions serve as an important tool for understanding taxonomy, phenotypic plasticity and palaeoecology (for instance Budd Foster, 1979, 1980, 1983, 1984), the dimensions of the coral skeleton are generally not systematically measured in Mesozoic corals.

The Mesozoic coral genus *Stelidioseris* and its synonyms, which are the subject of this study, counts according to the literature with up to 120 species (Lathuilière, 1989; Löser, 2000; Löser, 2012). These species were established during the previous 150 years, based on different ideas and concepts. The species are generally distinguished by (1) calicular dimensions, (2) the number of septal systems and cycles, (3) number of septa, and (4) number of septa reaching the columella. Whereas septal systems and the number of septa remain relatively constant within one colony, the calicular dimensions (calicular diameter, distance and thickness of wall) vary within one colony. The knowledge about the ranges and variation of these dimensions and consequences for the separation of species is limited. For this reason, more attention is paid to skeletal dimensions in the framework of this study.

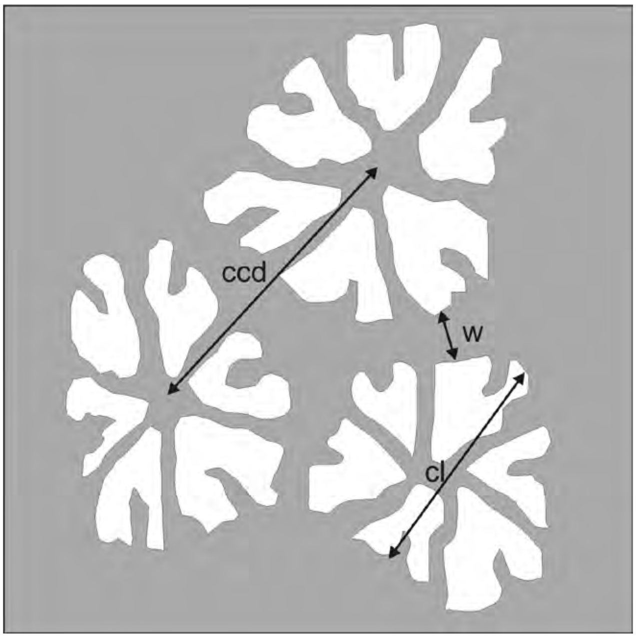


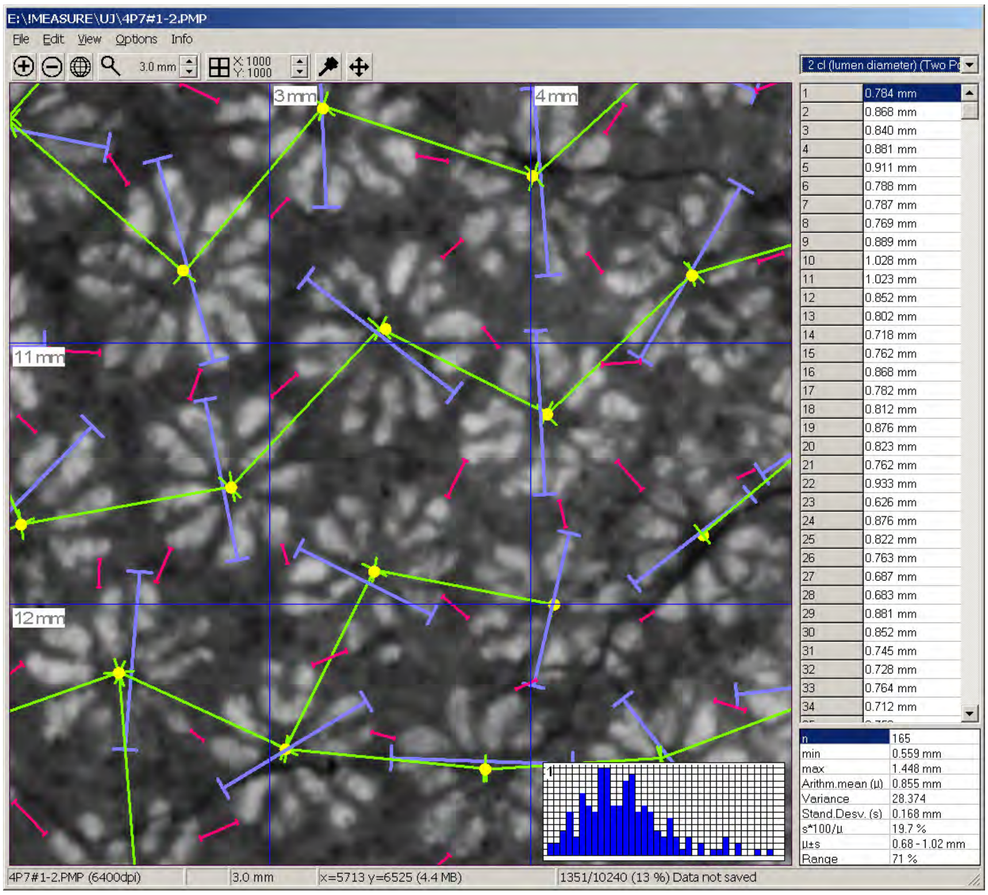
Figure 2. Schematic illustration showing how the calicular diameter (cl), distance (ccd) and wall thickness (w) values were measured.

To gain more insight into the intraspecific variation of genus *Stelidioseris* and to obtain a better strategy for separating species, selected thin sections and peels were systematically measured. The smaller calicular diameter (cl; inner calicular diameter), the distance between the four to five nearest calicular centres (ccd; from columella to columella) and wall thickness (w) were measured (Fig. 2). To achieve statistical significance, the largest number of possible measurements was taken. This number was mainly determined by the size and quality of the thin section. For each type of measurement (calicular diameter and distance, thickness of the walls) in one thin section the following values were obtained:

n	number of measurements
v_{min}	lowest measured value
v_{max}	highest measured value
μ	arithmetic mean (average)
σ	standard deviation
ν	coefficient of variation

The coefficient of variation (ν) according to K.Pearson (Weber, 1986) is calculated for all values to be able to compare the variability of the values cl, ccd and w. A low coefficient of variation indicates a lower variation of the values and makes them more suitable for the distinction of samples (species, populations). When there were more than 50 measurements, values were classified into ranges of 50µm or 100µm and converted into a graph to observe the distribution and asymmetry of the measured values. In addition to this, the number of calices per 25 square millimetres was counted for each thin section where possible. Thin sections were measured and values were calculated using the Palaeontological Database System PaleoTax, module PaleoTax/Measure (version 1.2; http://www.paleotax.de/measure; Fig. 3).

Coral species in the fossil record are strictly morpho species that are separated on the basis of their respective calicular diameters, septal symmetry and number of septal cycles and/or septal density. The comparison of skeletal dimensions is up to now the only method to distinguish fossil species. Although some attention has been paid to intraspecific variation and a certain variation of measured values has always been admitted, there exists no quantification of this variation. In descriptions of Cretaceous corals, ranges are provided for the calicular diameter,



1	0.784 mm
2	0.868 mm
3	0.840 mm
4	0.881 mm
5	0.911 mm
6	0.788 mm
7	0.787 mm
8	0.769 mm
9	0.889 mm
10	1.028 mm
11	1.023 mm
12	0.852 mm
13	0.802 mm
14	0.718 mm
15	0.762 mm
16	0.868 mm
17	0.782 mm
18	0.812 mm
19	0.876 mm
20	0.823 mm
21	0.762 mm
22	0.933 mm
23	0.626 mm
24	0.876 mm
25	0.822 mm
26	0.763 mm
27	0.687 mm
28	0.683 mm
29	0.881 mm
30	0.852 mm
31	0.745 mm
32	0.728 mm
33	0.764 mm
34	0.712 mm

n	165
min	0.559 mm
max	1.448 mm
Arithm.mean (µ)	0.855 mm
Variance	28.374
Stand.Desv. (s)	0.168 mm
s*100/µ	19.7 %
µ±s	0.68 - 1.02 mm
Range	71 %

Figure 3. Screen shot of the program used to measure the dimensions of the corals (PaleoTax/Measure).

but it is not clear how these ranges are defined. Here, the ranges are defined as an interval of µ±σ. It has been found - not only for corals but for all normally distributed values - that any observation is rarely more than a few standard deviations away from the mean (Chebyshev's inequality; Krengel, 2003). In the values observed here, about 70% of all values fit into the interval of two standard deviations (µ±σ). This allows the calculation of ranges that (1) accurately reflect the measured values and (2) are comparable to values not obtained through systematic measurements.

5. Results

Table 1 gives for the measured samples the dimensions of the lumen diameter, the distance of the calices and the wall thickness, and the quantity of calices per 25 mm^2. In all specimens the calicular diameter (lumen) has the lowest variation, followed by the calicular distance and the thickness of the wall (after normalisation using the coefficient of variation v). The high standard deviation of the wall thickness corresponds to the high standard deviation of the calicular distance. These are correlated since the calicular distance corresponds to the sum of the values cl and w. The standard deviation of both the calicular distance and the thickness of the wall is low where the wall is thin and both are higher where the wall is thick. A thin wall can be a constant character within one colony, but in colonies where a thick wall is found, the thickness of the wall generally varies. Studies about intraspecific variation carried out on extant and Neogene corals with comparable morphology (Budd Foster, 1979, 1980, 1984) confirm that the wall thickness is a character that varies greatly depending on the palaeoecological conditions. The higher variation of the calicular distance is also shown by the different distribution of the calicular diameter and calicular distance for eight samples (Fig. 4).

6. Discussion

6.1. Variation through ontogenesis

Varying calicular diameters are due to the ontogenesis of the individuals on the one hand and due to a certain variation, perhaps depending on the position in the colony and in relation to other individuals, on the other. Budding is mainly intracalicinal, which means that adult (large) calices divide into two or more new individuals whose calicular diameter is at first much smaller than that of the mother calice. Depending on the resulting number of new calices, these calices start with a diameter that can be very small to only slightly smaller than the average. The distribution of the calicular diameters in eight measured colonies (Fig. 4) shows that new calices relatively quickly reach the average calicular diameter, and the number of calices that are larger than average decrease with increasing diameter, because they obviously divide into new calices. All colonies show a positive skewness of the distribution of calicular diameter, so the maximum of counts in any class lies below the average.

6.2. Sample and species distinction

For more than 200 years, Cretaceous corals have been described and illustrated and new genera and species created. Examination methods and ideas about what constitutes a species have changed over that time. During this period, new species have been erected based on different ideas, giving importance to different macromorphological or micromorphological features. When new species were established, already existing species were rarely considered under the specific aspects used to distinguish the new material. This procedure has produced a high number of synonymous species (from today's point of view). Another source of synonyms is that it is often easier to establish a new species than compare one's own material to all existing species of the same genus or species group (Lathuilière, 1988). The genus *Stelidioseris* is unfortunately a genus with - from today's point of view - a high number of species including many synonyms. As statistical analysis has shown, the separation of samples (populations, species) in *Stelidioseris* species should mainly be based on the dimension of the lumen in addition to the septal symmetry and number of septal cycles. The calicular distance shows a larger variation, which confirms the low importance of this value for the distinction of samples (populations, species). The density of calices per x square millimetres is controlled not only by the calicular diameter, but also by wall thickness and

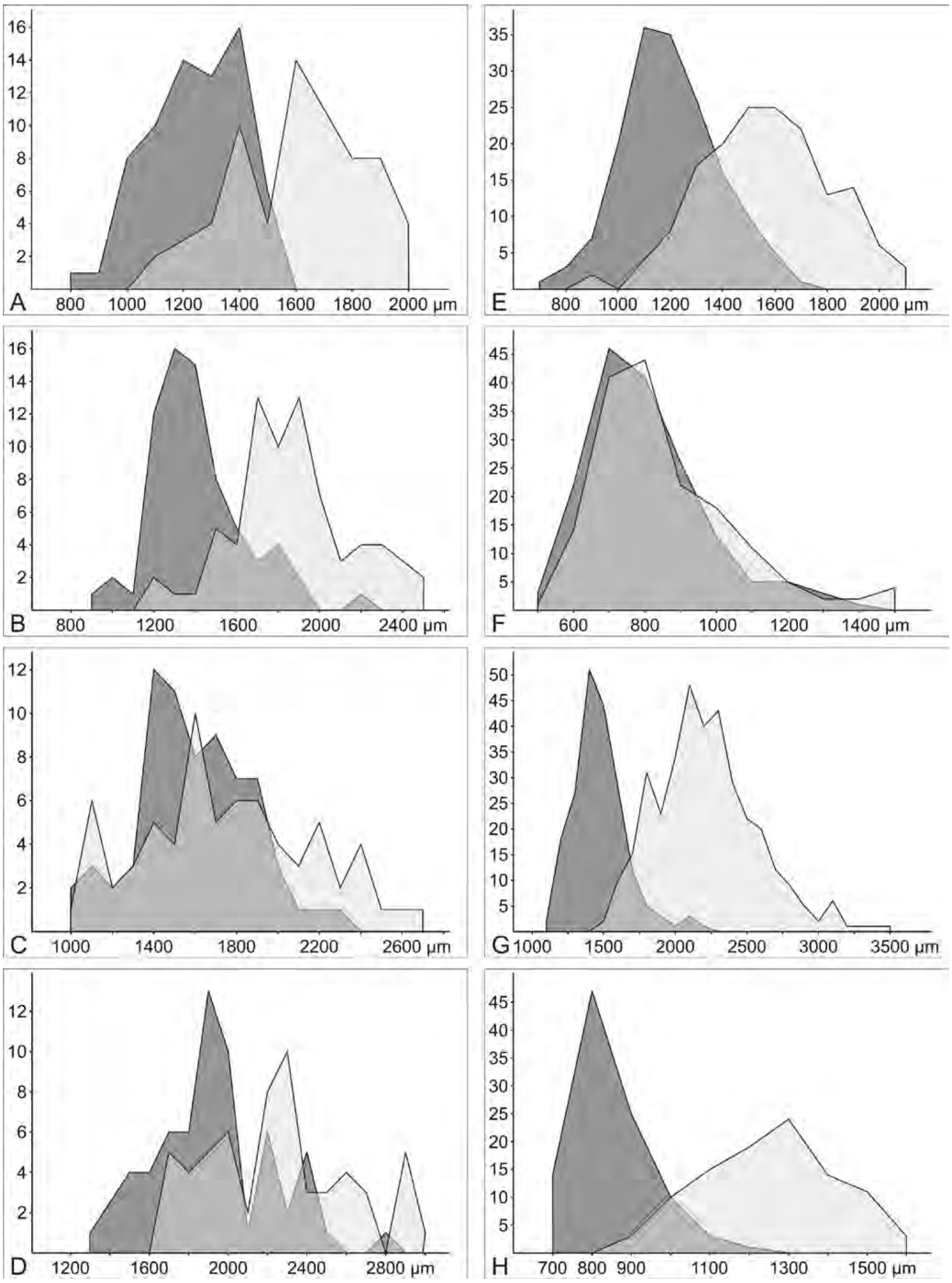


Figure 4. Distribution of the calicular diameters (dark grey) and distance (light grey) in eight *Stelidioseris* species. Size of classes is 100µm. A: MB K1330. B: MB K1328. C: BGS 5161. D: GLHAM C4140. E: TUM 56502. F: UJ 4P7#1. G: ERNO 2153. H: MB K1337.

therefore distance of the calices. The density of calices varies over a large range and will not help distinguish samples (populations, species) from each other.

6.3. Methods

This study presents results obtained from a large number of systematic measurements of colonial corals of the genus *Stelidioseris* in order to better understand intraspecific variation and the limits of species. The method is new in Mesozoic corals and two questions arise: 1) what is the optimal number of measurements and 2) how are the newly obtained values comparable to calicular dimensions obtained through traditional methods that did not quantify their obtained values?

6.3.1. Number of measurements

In fossil scleractinian corals, few previous studies have systematically measured individual colonies in order to understand the ranges of dimensions of single colonies and therefore also species. Even in previous statistical approaches, the number of measurements of the calicular diameter and distance within one colony has been low. Six calices per colony were measured by Budd Foster (1979), five to ten in Budd & Johnson (1996), ten in Budd Foster (1985) and Budd Foster (1980), and two to three in Budd Foster (1979). No quantity of measurements is provided in Lathuilière (1988), Lathuilière & Gill (1998) and Pandey et al. (1999). Whereas Scott & Aleman (1984) give the results of detailed measuring, the number of values taken is unknown. The data presented here shows that variation of important coral dimensions within one colony can be very high. Figure 5 shows the oscillations of the arithmetic mean, the standard deviation and the resulting first interval in steps of ten values for one characteristic in one colony. Whereas the oscillation is low in the arithmetic mean, it is high in the standard deviation and the first interval. To obtain a representative value for the arithmetic mean, a low number of measurements is required (< 25), but in order to obtain representative values for the standard deviation, the coefficient of variation and the first interval more values are necessary (> 50). This is the case for studies on variation in dependence on environmental factors on the one hand, and for taxonomic interpretations on the other.

6.3.2. Comparison of values

In the literature, the dimensions of coral calices are generally given as minimum-maximum value, often also based on various specimens. It is often not indicated whether these values represent the respective smallest and largest value measured

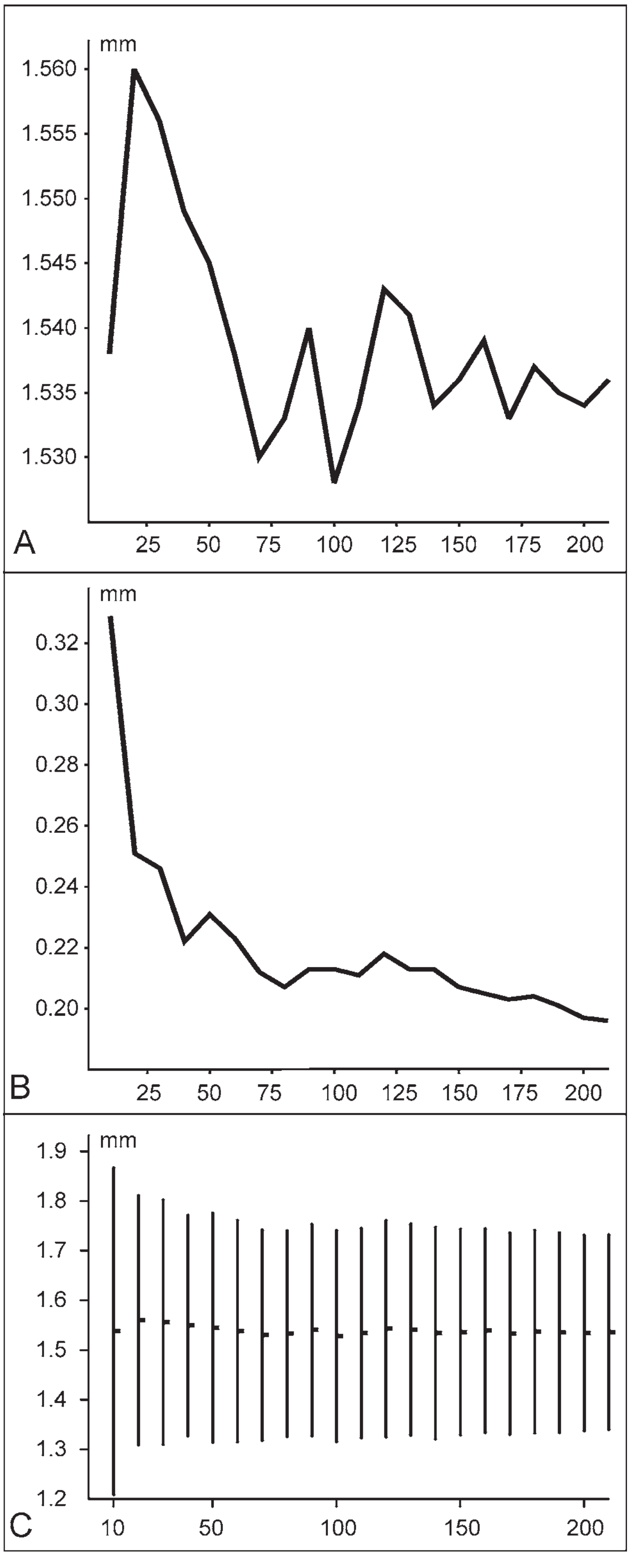


Figure 5. Variation of the arithmetic mean (A) standard deviation (B) and the first interval (C) in order of increasing number of measured values. The sequence of values is random. Sample ERNO 2153.

or the average range of the measured values. In order to value dimensions given in the literature, some published samples were measured systematically on the base of the originally published material. The result is given in Table 2. The general tendency is that systematically measured values limit the variation more than the published values, though not for all samples. In some samples, the obtained absolute value was higher than indicated in the literature, in some cases it was lower. Higher values obtained from recent measurements can be explained by the higher precision achieved with the computer application. Lower values are probably due to the fact that the wall in the plocoid corals is sometimes measured together with the calice by some authors. The difference between the smallest and highest value is of course higher in the measured values than in the values found in the literature because of the higher number of measurements obtained and probably also because obvious juvenile calices were discarded by other authors because they are not considered to be representative of the species.

7. Conclusions

Systematic statistical investigation of the Cretaceous plocoid coral genus *Stelidioseris* helps elucidate its intraspecific variation, ontogeny and taxonomy. Systematically measuring scleractinian corals can greatly assist with distinguishing species both within and between collections. The method allows for a more precise quantification of important characters because it makes a difference if only five or 50 calices are measured. It is recommended that future publications at least provide the number of measurements (n), the absolute lowest and highest value, the arithmetic mean and the standard deviation, for instance in the form “ERNO 2153, cl: (210) 1.172-2.304 (1.536, 0.196)” which allows the calculation of the first interval and the coefficient of variation. It is further recommendable to give dimensions for single specimens, not for species or populations. This makes the constitution of the given population or the separation of species within a fauna much more transparent to readers. Whereas the limits for specimens will not change, the limits of an abstract unit such as a population or species may change.

Apart from including more sample material in future studies it would also be useful to extend this research method to species of other Mesozoic species rich genera, such as *Cryptocoenia* or *Stylina* to gain more insight into intraspecific variation and to obtain more stable criteria for the separation of species. Comparisons to studies on extant corals show that non-overlapping first intervals of the calicular diameter in different samples or populations do not necessarily indicate different species, but may only represent ecotypes. This may have influence upon studies of biodiversity changes: the fossil coral species is probably not an appropriate unit to be counted and compared to extant diversity values.

The presented methods help only to analyse the variation of the calicular dimensions within one colony.

A transparent and comprehensive concept of the separation of species does not exist for fossil corals. So far species have been distinguished on the basis of their calicular dimensions, septal symmetry, septal counts, or septal density. The method of obtaining these values is not standardised nor is the process of comparing samples (populations, species) controlled by mathematical models. If fossil coral species are understood as units based on quantitative characteristics, it should be possible to apply statistical methods for easier comparison.

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Acroporidae of the Caribbean

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ABSTRACT. The scleractinian family Acroporidae reaches its greatest diversity in the Indo-Pacific region, where it has six extant genera and around 250 valid species, and dominates coral species composition on many reefs. Only one genus, *Acropora*, represented by only two species, survives in the Caribbean, although at least four other genera, *Astreopora*, *Alveopora*, *Dendracis* and *Isopora* are present in the Caribbean fossil record. Using fossil specimens from museum collections, this study reviews the Caribbean genera and species of Acroporidae and their relevance to the evolution and biogeography of the family. Two turnover periods (late Oligocene/early Miocene and Plio-Pleistocene) have been recognised as major influences on the post-Tethyan fossil history of Caribbean reef-building Scleractinia. Because of the importance of Acroporidae in the Indo-Pacific today, the successive origination and loss of taxa as well as unique taxon characteristics in the Caribbean setting are of interest in assessing the challenges faced by extant taxa under a regime of global climate change.

KEYWORDS: Coral reefs, Oligocene/Miocene turnover, biogeography, evolution, climate change, fossils, Scleractinia.

1. Introduction

The history of fossil Caribbean corals and reefs has been documented for at least 150 years (e.g. Duncan, 1863, 1864, 1873; Vaughan, 1919; Vaughan & Hoffmeister, 1926; Weisbord, 1973; Frost & Langenheim, 1974), but with particular vigour in recent decades (e.g. Budd et al., 1994, 1995, 1998; Stemann, 2004; Johnson et al., 2009). These efforts have resulted in collections representing a wide range of taxa, stratum ages and locations. As a result of this body of work, significant events in the history of the Caribbean coral fauna have been identified and quantified in terms of biodiversity (e.g. Edinger & Risk, 1994; Budd, 2000; Johnson & Kirby, 2006). The Caribbean has been home to at least 66 genera of Scleractinia, of which 25 are extant there (Budd, 2000). The consensus is that a cosmopolitan Tethyan fauna existed in the Caribbean from the late Cretaceous to the end of the Eocene (Edinger & Risk, 1994; Budd, 2000). Following this, two intervals of pronounced turnover are documented (a) an Oligocene/ early Miocene turnover (OMT), which represented "the early divergence of a distinctive western Atlantic fauna from the previous pan-tropical Tethyan fauna" (Johnston & Kirby, 2006) and (b) a Plio-Pleistocene turnover (PPT), when loss of many genera led to establishment of the modern Caribbean fauna, distinguished by strong representation from certain families, especially Mussidae and Faviidae, and region-wide domination by a few genera and species (Budd, 2000; Johnston & Kirby, 2006).

This paper reports on the Caribbean history of one particular Scleractinian family, the Acroporidae. The family has been placed within the "Complex" clade by molecular phylogenetic analyses (e.g. Romano & Cairns, 2000; Fukami et al., 2008) and is characterised by the entire colony skeleton, including thecae, septa and coenosteum, being an open synapticulate framework (Wells, 1956; Veron & Wallace, 1984). This family of purely reef-building corals reaches its living zenith in the Indo-Pacific, where it has six extant genera and around 250 valid species (Veron & Wallace 1984; Veron, 2000; Dai & Horng, 2009). Frequently, numerous species co-exist, making Acroporidae a dominant contributor to coral biodiversity in shallow-water coral assemblages. One genus, *Acropora*, often forms the major framework of whole reef zones and has a rapid branching growth mode, allowing many species to be superior competitors for space on the reef (Connell et al., 2004; Wallace, 1999), and it also plays a major role in mass spawning events (Harrison, 2011). Outside the Indo-Pacific today, Acroporidae is represented only in the Caribbean, where just a single species group of *Acropora* with two biological species occurs (along with an F1 hybrid of these: Volmer & Palumbi, 2002; Van Oppen et al., 2000). In contrast to the extant Caribbean fauna, five genera (*Dendracis, Astreopora, Acropora, Isopora* and *Alveopora*) have a fossil history in the region (references above, Budd & Wallace, 2008). All these genera except *Isopora* are also present in the fossil record of Europe, the Mediterranean and the Middle East, making Acroporidae one of the most global families, with a rich evolutionary and biogeographic history (Table 1).

The future of the taxon richness of Acroporidae in the current scenario of rapid global climate change is of great concern, as many species are limited to the upper photic zone, and thus subject to the impact of coral bleaching events resulting, in particular, from elevated sea temperatures (e.g. Hoegh-Guldberg, 1999; Donner et al., 2005) and also to the impacts of human exploitation and disturbance (e.g. Fabricius, 2005; Wilkinson, 2008). While the loss of Acroporidae from the European region is associated with a general loss of all reef-building Scleractinia by the end of the Miocene (Perrin, 2002), the history of the genera in the Caribbean has not been explored. This paper is a first attempt to assess the Caribbean record of Acroporidae for information relevant to the phylogeny and biogeography of the family. The following questions are posed for initial response and future study:

1) How do Caribbean occurrences of Acroporidae genera relate to the two major turnover events?
2) Was the Caribbean sojourn of these genera a dead-end, or did it contribute to or even benefit from Indo-Pacific lineages?
3) Does the Caribbean record include any new first appearance records for the purpose of molecular clock interpretations?
4) Are there points of interest, such as characters that might inform interpretations of the evolution and phylogeny of the family?

Table 1. Number of documented species for each genus in each geographical area. Numbers for genera still extant within an area are underlined.

Genus	Geological range	Caribbean	Europe & Middle East	Indo-Pacific
Dendracis	upper Cretaceous to Miocene	2	10	2
Astreopora	upper Cretaceous to Recent	3-6	27	17
Acropora	Paleocene to Recent	7	19	~150
Alveopora	Eocene to Recent	2	3	14
Isopora	Miocene to Recent	2	0	6
Montipora	Eocene to Recent	1 record	0	76
Anacropora	Recent	0	0	7

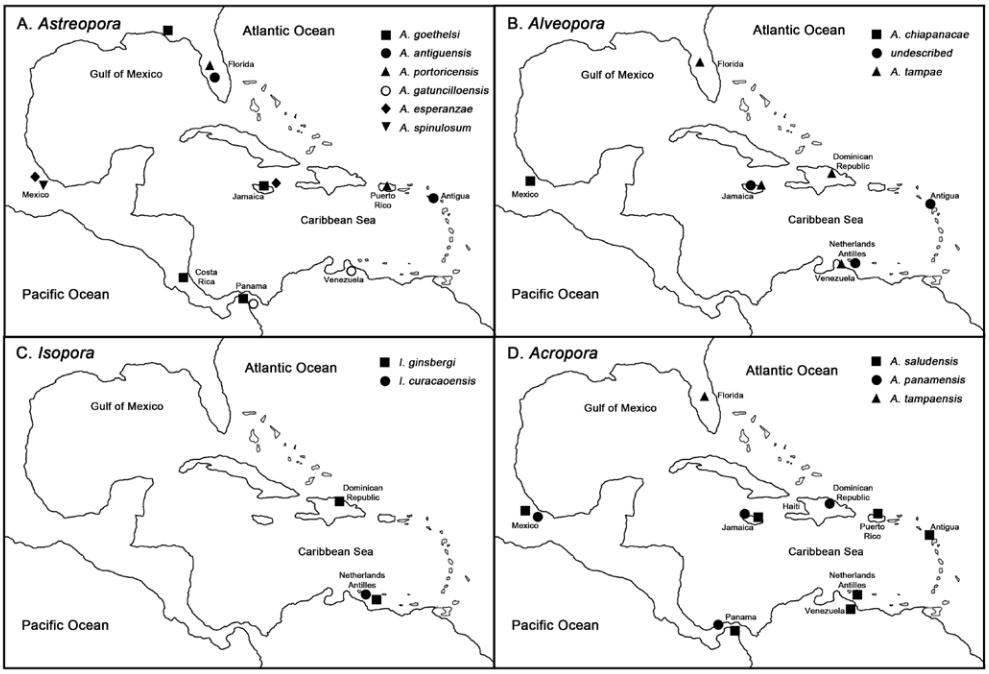

Figure 1. Distribution records for extinct Caribbean species of four Acroporidae genera (A) *Astreopora* (B) *Alveopora* (C) *Isopora* (D) *Acropora*.

Figure 2. Examples of extinct genera and/or species of Caribbean Acroporidae, represented by NMNH specimens, except where noted. A: *Astreopora antiguensis* Vaughan, 1919 paratype from Antigua NMNH 325609. B: *Isopora ginsbergi* Budd and Wallace, 2008 holotype from Curaçao (University of Iowa Paleontology Repository SUI 102751). C: *Alveopora tampae* Weisbord, 1973 holotype from Tampa, Florida, USA NMNH 66160 lower Miocene. D: *Dendracis cantabrigiensis* Vaughan, 1899 NMNH 44292 from Jamaica. E, I, J: Undescribed *Acropora* species from: (E) Cuba; (I) Antigua and (J) Tampa, Florida. F: *Acropora saludensis* Vaughan, 1919 from Panama NMNH 64046. G: *Acropora tampaensis* Weisbord, 1973 from Tampa, Florida, USA holotype NMNH 68313. H: *Acropora panamensis* Vaughan, 1919 NMNH 325041 from Panama. Scale bar 10 mm.

2. Materials and methods

The study is based on examination of fossil specimens at the National Museum of Natural History of the Smithsonian Institution, Washington DC (NMNH). The NMNH collection includes types and published material from Vaughan (1919), Weisbord (1973), Frost and Langenheim (1974) and others including papers of A.F. Budd and colleagues and J.W. Wells, an unpublished manuscript of J.E. Hoffmeister, and specimens collected by numerous authors, researchers and NMNH staff during exploration and/or research on other taxa or geological topics. *Isopora* was studied in Neogene deposits in Curaçao and from specimens from Budd et al. (1998) from the University of Iowa Paleontology Repository. Material was studied using light microscopy, scanning electron microscopy and thin sections. Potential new species mentioned in the text were often represented by only one or a few specimens, and further study is required before these can be published. Literature records for other taxonomic and stratigraphical surveys of Caribbean locations are given in the text.

3. Results and discussion

3.1. Astreopora

Astreopora has a distinctive coenosteal structure of sturdy spinules, which makes identification of fossil specimens relatively straightforward. It is recorded from the late Cretaceous in Jamaica (Baron-Szabo, 2006), the middle Eocene of Mexico (*A. esperanzae* and *A. spinulosum*) and Oligocene to early Miocene in Florida, Panama, Antigua and elsewhere (*A. antiguensis, A. goethelsi, A. portoricensis and A. gatuncilloensis*) (Fig.1A). Some of the latter group of species may be synonyms, as they share a striking general colony form, not seen elsewhere in *Astreopora*. *A. goethelsi* has thick columnar branches, *A. antiguensis* has similar branches that are expanded at the tips (Fig. 2A) and the others have variants of these forms. These sturdy branches are similar in general outline to those of some species of *Isopora* and this is discussed below.

Astreopora is rarely dominant or diverse in living assemblages (Lamberts, 1982; Veron, 2000). Despite this, the genus is proving to be more diverse than previously thought, with novel characters recently found in two new species from western Papua (Wallace et al., 2011). *Astreopora* is usually interpreted as basal to the family in molecular phylogenies (Fukami et al. 2000, 2008). Most *Astreopora* are non-branching as are many *Montipora* and *Alveopora*, however the new species are branching. One has a dendritic branching mode, shared with branching *Montipora*, and another has axial growth, previously found only in the clade containing *Acropora* and *Isopora*. We proposed that these characters might be due to a historical constraint that causes the same condition to originate more than once, but in different character settings, within a lineage (Wallace et al., 2011). The sturdy branching units of the Oligocene-Miocene Caribbean *Astreopora* may offer another example of this phenomenon, being similar to the branching type seen in some *Isopora* (Fig. 3).

Astreopora disappears from the Caribbean record in the OMT (Fig. 4A). It is likely that its sojourn in the Caribbean was a dead-end, as there are no indications of the thick-branching lineage elsewhere. Its post-Eocene species, with their large, sturdy skeletons, probably contributed substantially to Caribbean reef development. They also offer an insight into evolutionary novelty and parallelism in the family.

3.2. Alveopora

Alveopora was transferred from Poritidae to Acroporidae by Dai & Horng (2009) following molecular phylogenies which indicated affinity with the family (e.g. Fukami et al. 2000, 2008). The disparity with other Poritidae genera had previously been noted (e.g. Wells, 1956; Veron & Wallace, 1984). *Alveopora* has the Acroporidae characteristic of synapticulothecate skeleton but does not have coenosteum. Its minimalist skeletal architecture offers few skeletal features for taxonomic comparison or identification, and biologists sometimes seek to use polyp features to distinguish species (Kitano et al., submitted).

Alveopora is known from the middle Eocene of Mexico (*Alveopora chiapanecae* Frost & Langenheim 1974) and Oligocene to early Miocene in Florida, Dominican Republic, Venezuela and elsewhere (*Alveopora tampae* Weisbord 1973, see Fig. 2C) as well as an undescribed species. On modern Indo-Pacific reefs, *Alveopora* is usually difficult to find, as species mostly occur deeper than the intertidal, in sheltered habitats. This may also be so for the fossil species, as the genus is infrequent in collections, but it is found frequently enough to indicate a broad distribution (Fig. 1B). From the specimens available to date it is not possible to say whether or not the Caribbean species contributed to Indo-Pacific evolution of this genus.

Alveopora is found in the fossil history of the Caribbean from the Eocene and disappears in the OMT at around the same time as *Astreopora* (Fig. 4A).

3.3. Isopora

Previously a subgenus of *Acropora*, *Isopora* was elevated to genus level based on genetic distance as well as differences in axial corallite development, skeletal microstructure and reproductive mode (Wallace et al., 2007). It is a distinctive genus with sturdy

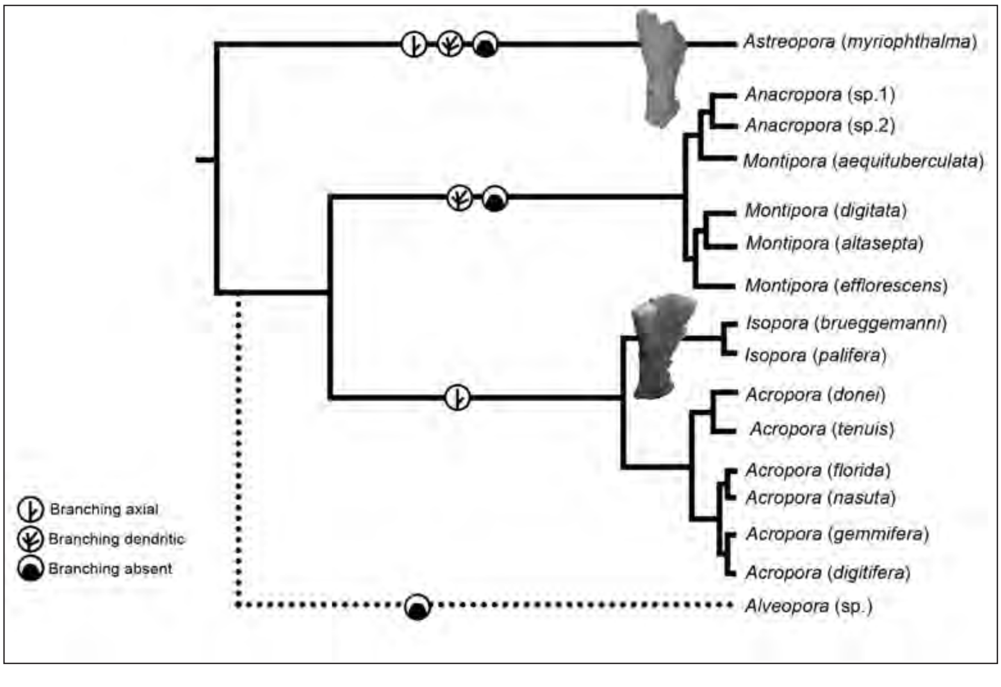

Figure 3. Colony form characters shared by the basal Acroporidae genus *Astreopora*, with other genera in the family, indicated on a composite cladogram of Acroporidae phylogeny based on molecular studies of Fukami et al. (2000, 2008). Sturdy branch character from Caribbean Astreopora superimposed.

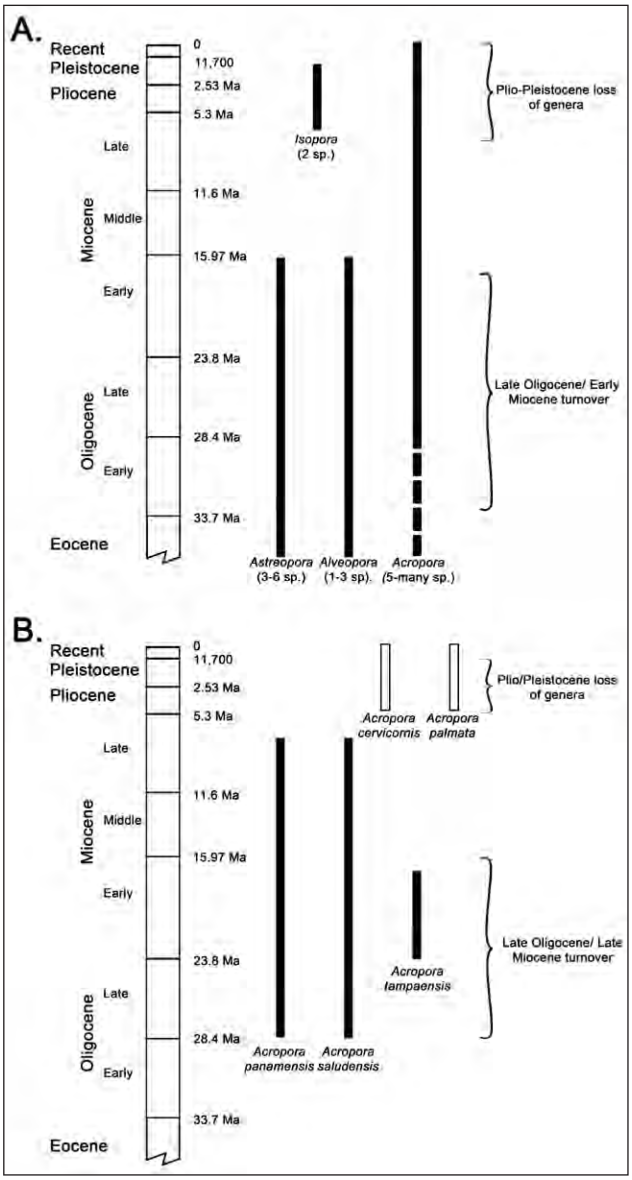

Figure 4. Timelines for Acroporidae from the Caribbean and relationship to major turnover events. A: Genera *Astreopora*, *Alveopora*, *Isopora* and *Acropora*. B: Described species of *Acropora*, extinct and extant.

skeleton, whose species can form extensive colonies and play a dominant role in reef-building, especially on reef fronts (Wallace, 1999). It has a characteristic coenosteal microstructure with meandroid spinules, and occurs in two main growth forms: either with thick club-shaped or cuneate branches and numerous axial corallites, or with a single main axial supported by one or more supplementaries (Wallace et al., 2007).

Thought to be absent from the Caribbean, *Isopora* was found from late Miocene to Pliocene reefs of Curaçao by Budd et al. (1998), who initially interpreted it as very thick *Acropora* (Budd & Wallace, 2008). Two species, *Isopora ginsbergi* Budd & Wallace, 2008 (Fig. 2B) and *I. curacaoensis* Budd & Wallace 2008, occurred as an ecological dominant, second only to *Stylophora*, and would have been important in reef-building, as indicated particularly by the abundance of the thick club-shaped branches of *I. ginsbergi* at the type locality (Budd et al., 1998). The second species, *I. curacaoensis* has the growth form based around a main axial corallite (Wallace & Budd, 2009). The NMNH collection also includes two small, *Isopora*-like specimens from the Dominican Republic and these suggest a broader distribution for *Isopora* (Fig. 1C).

Isopora is not found in European deposits (Table 1). At the time of discovery, the Curaçao species were the earliest global records for *Isopora*: but the genus was reported subsequently from the middle Miocene of Fiji by Bromfield & Pandolfi (2011). Curaçao is quite close to the Panama region which would have provided access to and from the Pacific Ocean and it seems a reasonable hypothesis that *Isopora* might have invaded the Caribbean from the Pacific, then become extinct due to events associated with the closure of the isthmus of Panama. Because of its reproductive mode, *Isopora* is quite vulnerable to local extinction (Paulay & Wallace, 2000)

For the present, indications are that *Isopora* had a brief sojourn in the Caribbean, disappearing in the Plio-Pleiostocene event, having appeared only 4-5 million years before (Fig. 4A). The location of origination of the genus, whether Atlantic or Indo-Pacific, is as yet unknown, but the Atlantic record has already more than doubled the origination date of two million years ago previously used for *Isopora* in molecular clock calibrations (Fukami et al., 2000).

3.4. Acropora

This genus is distinguished by its exclusively axial branching mode, and differentiation of two types of corallites: axial and radial, with associated coenosteal differentiation, such that 20 species groups have been recognised using these characters (Wallace, 1999). In the Caribbean today only the *cervicornis* species group is extant (Fig. 2B). This has two widespread species *A. cervicornis* (Lamarck, 1816) and *A. palmata* (Lamarck, 1816), which are considered to be highly endangered, as evidenced by their listing on the US endangered wildlife list (Gardner et al. 2003).

Three species of extinct *Acropora* are described and recorded from the Caribbean: *Acropora saludensis* Vaughan, 1919 and *A. panamensis* Vaughan, 1919 are broadly distributed in Oligocene to late Miocene deposits from Mexico, Panama, and several other locations, while *A. tampaensis* Weisbord, 1973 is recorded only in the early Miocene of Florida (Fig. 1D).

Following a finding of up to 10 of the 20 currently recognized extant species groups of *Acropora* in the Eocene of England and France (Wallace & Rosen, 2006; Wallace, 2008; White et al., 2010), it could be predicted that species groups additional to the *cervicornis* group might also be represented in the fossil history of Caribbean *Acropora*. This does seem to be the case from the characteristics of the species, although further study will be required to place the fossil material in putative species groups. *A. tampaensis* (Fig. 2G) has characters suggestive of the *cervicornis* group. *Acropora saludensis* (Fig. 2F), well represented in the NMNH collections has characteristics of the *muricata* species group. *A. panamensis* (Fig. 2H), does not align with either of these groups, suggesting at least a third species group is represented in the Caribbean.

In addition to these described species of living and fossil *Acropora*, there appear to be at least five undescribed species in the Smithsonian records, three of which from Cuba, Barbados and Florida are shown in Figure 2 (E, I, J). This material, once examined and described, will greatly add to the information about the diversification and history of *Acropora* in the Caribbean.

Even from the currently available information, it can be seen that *Acropora* has been involved in both turnover events (Fig. 4B). *Acropora tampaensis* disappeared in the first event, at least two other species existed up until the Plio-Pleistocene turnover, which was also the time of origination of the modern species. The extant species *Acropora cervicornis* and *A. palmata* are present in the Caribbean record from the early Pliocene (Fig. 4B). The ancestor of these two species, which are extremely similar in skeletal features other than colony form, is unknown at present, but *A. tampaensis* Weisbord, 1973 is suggested as a possibility. The species group is thought to be represented in the Eocene of Europe (Wallace, 2008) and if this is the case it would be expected to be present in the pan-Tethyan fauna, possibly along with other species groups as mentioned above.

3.5. Dendracis

This globally extinct genus is represented by *Dendracis cantabrigiensis* Vaughan 1899 (type locality Cambridge, Jamaica). *Dendracis* disappeared from the Caribbean at the end of the Eocene (Budd, 2000) and globally in the Miocene (Wells, 1964), so is not included in the timeline considered for this paper.

3.6. Montipora

One record of *Montipora* has been reported for the Caribbean: Johnson & Kirby (2006) mention "*Montipora* sp. A" from Antigua. At present there do not appear to be other specimens for examination. *Montipora* is not reliably known from the European region (*M. danielli* Reig, 1990 from the Eocene of Spain is *Actinacis cognata* (G. Alvarez-Perez, pers. com.)).

4. Conclusions

This preliminary study examines published and museum evidence of Caribbean Acroporidae, in relation to current taxonomic grouping from molecular phylogeny of the extant genera. Some findings are:

1) *Astreopora*, basal genus, distributed through the region possibly from the late Cretaceous, and especially Oligocene to Miocene, demonstrates a unique branching form in some Caribbean members, which finds a possible homologue in a later genus, *Isopora*. *Astreopora* became extinct in the Caribbean in the late Oligocene/early Miocene turnover and probably did not contribute to an Indo-Pacific lineage.

2) *Alveopora* (recently moved to this family from Poritidae), also a basal genus, and present from the Eocene, also became extinct in the Caribbean in the OMT, but little can be said on any lineage in the Pacific, as fossils are infrequent and no unique skeletal features occur in the Caribbean species.

3) *Isopora*, apparently restricted to the Netherlands Antilles but possibly more widely distributed, dominated reef-front assemblages during a period of about 3.9 Ma in the late Miocene to late Pliocene. This genus, now widespread on reefs throughout the Indo-Pacific but never recorded in Europe, probably originated in either the Caribbean or Indo-Pacific. The Curaçao species, when published, were the earliest record for *Isopor*a, and made it possible to extend back its date of origination for molecular clock purposes by three million years. A recently published middle Miocene record of *Isopora* in the Pacific Ocean extends this record and raises an obvious hypothesis, that this genus entered the Caribbean from the Pacific and briefly had great ecological success in a localised setting.

4) *Acropora* is now restricted to a single living species group with two main species that are widespread and ecologically abundant from the late Miocene or Plio-Pleistocene to the present. This genus has been represented in the Caribbean by other species and species groups, described and undescribed, up to the late Miocene, indicating a more diverse history for this genus, which will be potentially very informative once studied. Several new species of extinct Caribbean *Acropora* remain to be described, representing additional species groups.

5) The position of *Montipora* as a purely Indo-Pacific genus remains unchallenged by the evidence of this initial study of Caribbean Acroporidae.

These findings indicate that, in particular, detailed study and description of new *Acropora* species and a search for further specimens providing broader distribution of *Isopora*, would enhance understanding of the evolution and biogeography of the family in the region and globally. Extinction of three genera of Acroporidae (*Astreopora*, *Alveopora* and *Isopora*) in the Caribbean appears to have the same root cause as that of other genera lost in the relevant turnover event: OMT in the case of the first two species and PPT in the case of *Isopora*. For *Acropora*, the situation is different, in that it appears that only one of a number of species groups survived through to the present, and the reason for this could be examined in relation to the environmental preferences of the species groups involved.

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Fusion or non fusion of coral fragments in *Acropora*

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ABSTRACT. Corals inhabit high energy environments where frequent disturbances result in physical damage to coralla, including fragmentation, as well as generating and mobilizing large sediment clasts. The branching growth form common in the *Acropora* genus makes it particularly susceptible to such disturbances and therefore useful for study of the fate of large sediment clasts. Living *Acropora* samples with natural, extraneous, broken coral branches incorporated on their living surface and dead *Acropora* skeletons containing embedded clasts of isolated branch sections of *Acropora* were observed and/or collected from the reef flat of Heron Reef, southern Great Barrier Reef and Bargara, Australia respectively. Here we report three different outcomes when pebble-sized coral branches became lodged on living coral colonies during sedimentation events in natural settings in *Acropora*: 1) Where live coral branches produced during a disturbance event come to rest on probable genetic clone-mate colonies they become rapidly stabilised leading to complete soft tissue and skeletal fusion; 2) Where the branch and underlying colony are not clone-mates, but may still be the same or similar species, the branches still may be stabilised rapidly by soft tissue, but then one species will overgrow the other; and 3) Where branches represent dead skeletal debris, they are treated like any foreign clast and are surrounded by clypeotheca and incorporated into the corallum by overgrowth. The retention of branch fragments on colonies in high energy reef flat settings may suggest an active role of coral polyps to recognise and fuse with each other. Also, in all cases the healing of disturbed tissue and subsequent skeletal growth is an adaptation important for protecting colonies from invasion by parasites and other benthos following disturbance events and may also serve to increase corallum strength. Knowledge of such adaptations is important in studies of coral behaviour during periods of environmental stress.

KEYWORDS: scleractinian coral, coral reef, biomineralisation, skeletogenesis, clypeotheca, disturbance.

1. Introduction

Modern reef-building corals inhabit high energy environments near sea level where waves and currents commonly cause physical damage to colonies, including fragmentation, and generate and mobilize large sediment clasts that may come to rest on in situ colonies. Hence, corals in shallow reef environments frequently undergo sedimentation and clearance (re-suspension) of fine and coarse sediment. Many corals have apparently adapted to frequent disturbance and increase their distribution through vegetative reproduction and dispersal of broken fragments (Tunnicliffe, 1981; Bothwell, 1981; Highsmith, 1982). However, although fragmentation is a useful strategy for dispersal in some corals, many shallow reef corals have developed defensive mechanisms to adapt to sedimentation events, including both morphological and behavioural adaptations (e.g., Hubbard & Pocock, 1972; Hubbard, 1973; Barnard et al., 1974; Bak & Elgerschuizen, 1976; Lasker, 1980; Stafford-Smith & Ormond, 1992; Stafford-Smith, 1993; Riegl, 1995). Most studies of coral responses to sedimentation have involved the reaction of corals to finer sediment (mud-sand-granule size ranges), and in some cases that sediment is incorporated into the skeleton (e.g., Davies 1992). The effects of deposition of coarse clasts on corals are more poorly documented despite the common occurrence of coral communities in high energy settings, including gravel-cobble-dominated environments (e.g., Braga et al., 1990; Perry & Smithers, 2009). In particular, very little research has been conducted on the incorporation into scleractinian coral skeletons of coarse foreign material that cannot be dislodged from the coral colony, despite such occurrences presumably being common in nature. Cases of fused, broken branches have been observed in nature in some corals (e.g., *Acropora*, Collins, 1978; *Madracis mirabilis* and *Oculina diffusa*, Logan, 1985), but such interactions have rarely been documented in detail. Experimental work on reactions between mature coral branches from different colonies has been undertaken mostly to investigate competitive interactions and histocompatibility behaviour (Potts, 1976; Collins, 1978; Neigel and Avise, 1983).

Most of the gravel-sized sediment produced in clean reef environments consists of broken skeletal material, including live or dead coral branches. Such branches may be difficult to dislodge from a particular corallum by biological means or by subsequent physical energy (e.g., wave action), especially where the in situ corallum has irregular surface and branching morphology (e.g., Stafford-Smith & Ormond, 1992), such as is common in *Acropora*. Coral debris deposited on a living colony can represent one of four classes of relationships with the underlying colony: (1) dead coral fragment possibly encrusted by other biota (live-dead relationship of Fagerstrom & West, 2011); (2) living fragment from the same colony or clone (conspecific and isogenic); (3) living fragment from another colony of the same species (conspecific but anisogenic), or (4) living fragment from a different species or genus (heterospecific and anisogenic) (see West et al., 2011 figure 1). Here we report three different observed outcomes when pebble-sized coral debris became lodged on living coral colonies during sedimentation events in natural settings.

2. Materials and methods

Two field sites were chosen to allow observation of biological interactions in both live collected and dead coral skeletons so as to evaluate preservation potential in fossil material. Living *Acropora* samples with natural, extraneous, broken coral branches incorporated on their living surface were observed and/or collected from the reef flat of Heron Reef, southern Great Barrier Reef (~E151º55.53', S23°26.07'). Dead *Acropora* skeletons containing embedded clasts, including isolated branch sections of *Acropora*, were collected from beach cobbles at Bargara, central coast of Queensland, Australia (~E 152°27'22.56"; S 24°48'17.30"). Heron Reef is a clean carbonate environment ~70 km off shore, whereas the Bargara corals occur in a rocky-pebble shore setting with abundant, shore-worked carbonate and fluvial-derived siliciclastic gravel.

Samples were analysed using x-ray computer tomography (µCT) and then cut for microstructural analysis on polished and etched sections and blocks using scanning electron microscopy (SEM). The corals were scanned with a micro computed tomography scanner (µCT 40, Scanco Medical, Brüttisellen, Switzerland), at an energy of 70 kVp and intensity of 114 µA with 200 ms integration time. The scans resulted in an isotropic nominal resolution of 30 µm. The reconstructed cross sectional images were exported as stacks of TIFF images with 1024 x 1024 pixels for further visualisation with DRISTI©. Polished sections were etched in 2% formic acid for approximately 20 s. Samples for observation using SEM were gold coated and were analysed on either a FEI QUANTA 200 Environmental scanning electron microscope (SEM) or a FEI QUANTA 3D SEM.

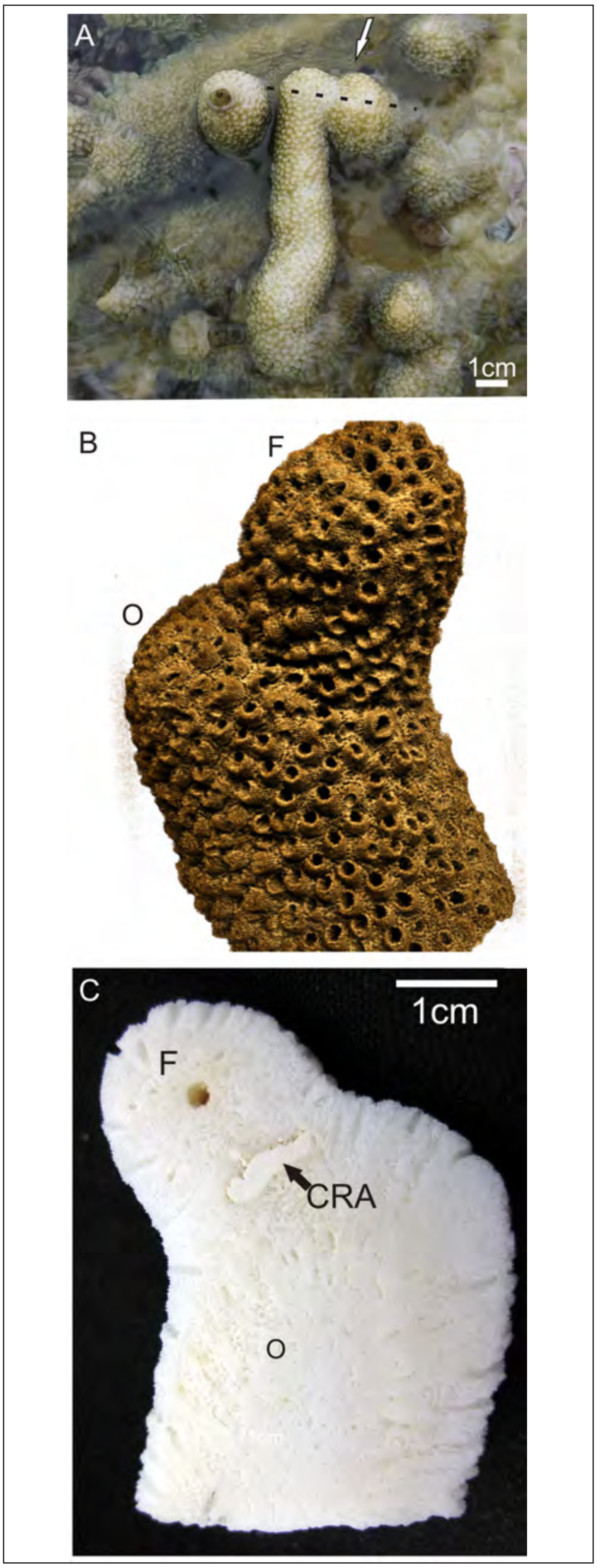

Figure 1. A: Fused branch of *Acropora sp*. on the reef flat of Heron Reef, Southern GBR. The dashed line represents a vertical line of section for Fig. 1C. The arrow shows the direction of view of µCT image (upper right) in Fig. 1B. B: 3D reconstruction of µCT images of the outer surface of the fused branch of *Acropora*. C: Photograph of the cut surface of the fused branch. The fused branch is shown by the letter F and the original in situ branch by the letter O. The cut section contains a grain of coralline red algae (CRA) at the junction between the branches.

3. Results

Pebble sized *Acropora* branch sections were observed enclosed within the skeletons of subfossil *Acropora* coralla from Bargara (Plate 1A). They are encased within the skeleton in the same way as other - non-carbonate clasts, which include basalt and quartzite. The clasts range in size from 3 to12 mm. In all cases (i.e., both for coral clasts and for siliciclastic pebbles), the cavities were lined by obvious clypeotheca (see Nothdurft & Webb, 2009), thus separating the clasts from living coral tissues as the clasts were incorporated (Plate 1B-D). Clypeotheca surrounding the *Acropora* branch is stained dark in appearance, but the source of the staining is unknown. Otherwise, the clypeotheca developed around the clast is constructed in the same way as clypeotheca previously reported on external corallum surfaces around the external bases of branches (Nothdurft & Webb, 2009). Hence, it represents a surface produced by the amalgamation of flanges

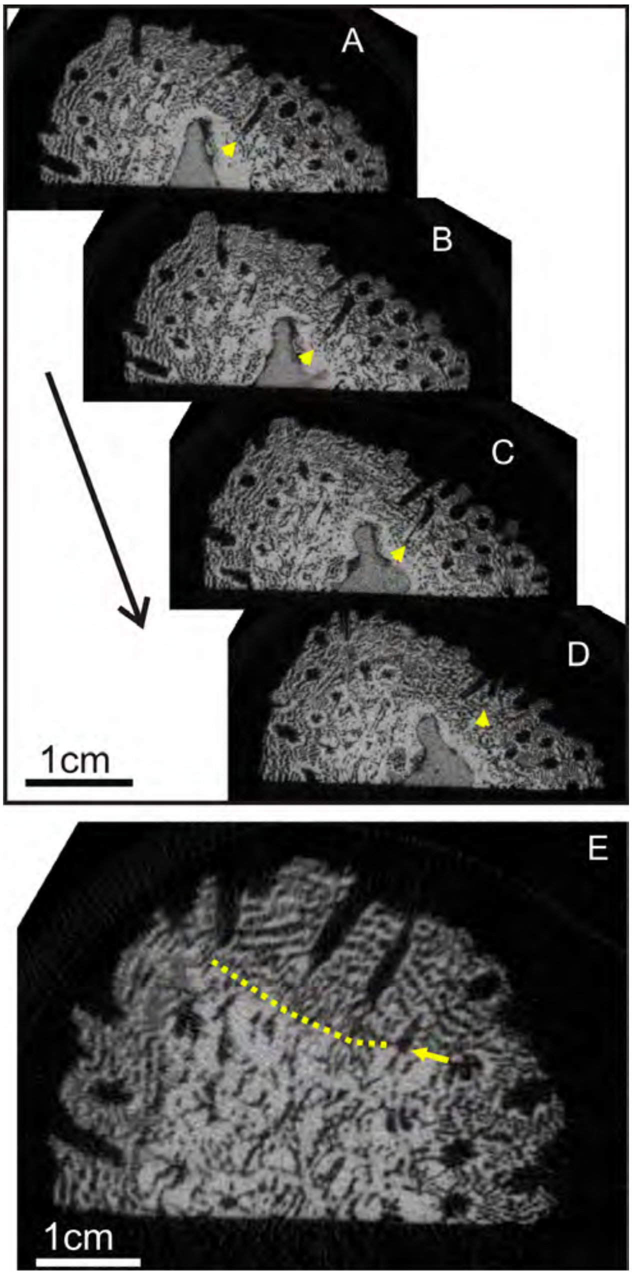

Figure 2. X-ray images of slices collected during µCT analysis. A to D: Sections through the junction between the two *Acropora* branches in Fig. 1. The yellow arrows track the location of an individual corallite through the section. The corallite, which initiated from the broken branch, had a straight growth direction initially, but the trajectory changed around a neighbouring corallite from the other branch. This competition for space resulted in a high density of corallites on the surface and changes to their size and shape. E: X-ray section through the broken branch. There is a large density difference between the inner and outer areas. The junction on the upper side of the image (dashed yellow line) is an apparent fracture surface on which the coral has been able to regenerate. No corallites are continuous through this surface and the yellow arrow shows the apparent initiation point of one corallite on the upper side of the junction.

produced from near the tips of coenosteal spines with centripetal growth (Plate 1E), and covers over corallite apertures much like upside-down dissepiments. The clypeotheca completely sealed off coenosteum and corallites alike from the cavity containing the entrapped clast. The extent to which polyps beneath the clast were able to deflect and grow around the clast or rather ceased growing to be abandoned and covered by clypeotheca is still somewhat unclear because it is very difficult to track an individual corallite through its entire trajectory of growth. However, some corallites certainly appear to have been abandoned and sealed over.

In samples from the reef flat on Heron Reef, clearly broken and redeposited *Acropora* branch fragments were found to have been incorporated onto existing colonies (Fig. 1, Plate 2). In one example, a clearly broken and displaced coral branch consisting of a broken end and distal tip came to rest more or less horizontally on top of in situ, predominantly upright branches on the underlying colony. The branch was then fused into place by continued skeletal growth, both from the underlying colony and from the displaced branch itself. The axial corallites of the horizontal clast and the upright branches to which it became fused are perpendicular to each other (Fig. 1A). Both ends of the broken branch were completely covered with living polyps of similar architecture and colour to those in the rest of the underlying colony. Corallites over the top of the fused branch appear to originate both from the branch and from the underlying colony with no discernable juncture and the broken end of the branch has been completely overgrown by new coral growth. At the depressed junction between the fused branches, closely-spaced smaller corallites occur with no lips (Fig. 1B; Plate 2A, B). Underlying and overlying corallites directed toward the junction of the branch and corallum do not appear to change direction and must terminate, but the exact nature of the process is not clear.

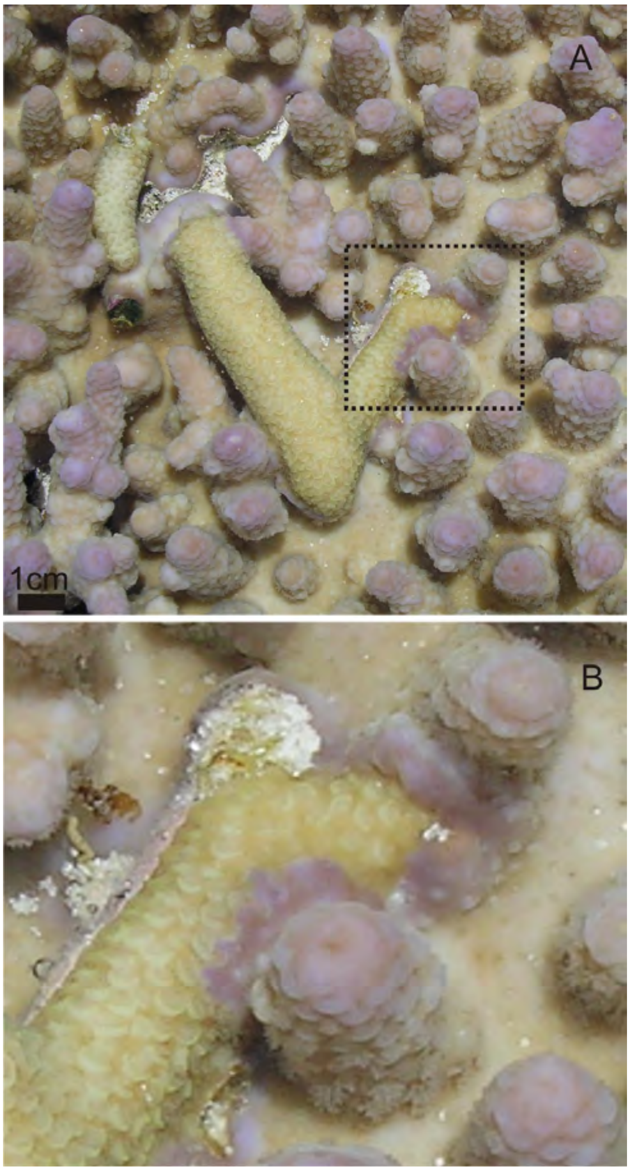

Figure 3. Photograph of probable anisogenic interaction between the host colony of *A. hyacithus* and an incorporated branch of *Acropora sp*. The location of the higher magnification image in B is shown on A with a dashed box.

The polished and etched sections (Plate 2B, C) show that there is no obvious skeletal junction between the branches, but several coarse clasts of coralline red algae (CRA) have lodged between the opposing branches and become incorporated at the approximate location of the junction (Fig. 1C). Embedded clasts that are visible in section include an elongate pebble approximately 7 mm long and 3 mm wide adjacent to numerous other loosely packed grains of mixed carbonate origin, including CRA, mollusc and coral fragments ranging in size from 100 to 500 µm. The coral skeletal has encased the clasts with new skeletal growth not in contact with the grains in some places and with coral skeleton moulded to the surface of the grain in intricate detail in other places (Plate 2F).

Within the broken branch and the *in situ* branch to which it fused, there appears to be a large amount of skeletal thickening deposits where synapticulae have completely filled areas between septa, costae and ceonosteum (Fig. 2, Plate 2E). This thickening occurs in areas of the branches that initially formed prior to the fusion. The skeletal formation on the outer 2.5 to 3 mm of the branches is much less dense where septal and costal structures rarely exceed 50 µm in thickness.

In another example where an *Acropora sp.* branch fragment was deposited more or less horizontally on a colony of *A. hyacithus* (Fig. 3A) The branch also became fused to the underlying corallum, but in this case, the polyps of the branch and the host colony are different in colour and there is a clear junction between the live polyps of the branch and those of the underlying colony (Fig. 3B). The junction is irregular in outline and is white, apparently with a thin region of dead tissue. The margin stands higher in relief on the in situ colony side of the junction. A purple pigmentation was observed in the tissue of the underlying *A. hyacinthus* and is consistent with the colour of new tissue growth at the ends of branches. The internal characteristics of the junction are unknown as the sample could not be collected.

4. Discussion

In the case of the incorporated coral branches found within *Acropora* coralla at Bargara, Queensland, the branches are interpreted to have been dead when deposited on the living coral surface because they are moderately abraded (Plate 1A, C) and must have been abraded before being embedded in the living colony. The living coral colony treated them as foreign clasts that could not be dislodged passively or by means of soft tissue manipulation, and they were simply grown around and incorporated into the corallum. If the dead branches of an adjacent colony were grown over and encrusted *in situ*, Fagerstrom & West (2011) would have termed it quasi-fusion. Regardless, in the case of the clasts, they apparently served as irritants, and the colony withdrew soft tissues from the area immediately beneath and adjacent to the foreign clast and secreted a clypeotheca to isolate living coral tissues from the cavity containing the clast. The sealing off of individual polyps beneath the clast, rather than their diversion around the clast, may suggest that they were damaged by abrasion or it may simply reflect normal resorption of non-viable polyps consistent with the high levels of colonial integration in *Acropora*. In other cases of clypeotheca production individual polyps appear to have been readily 'sacrificed' and sealed over in order for the overall colony to have protection, apparently from invasion where soft tissues were stressed by adjacent sediment (Nothdurft & Webb, 2009) or in this case damage from an individual clast. This is consistent with the previous interpretation of clypeotheca as a protective skeletal adaptation to a localised stress (Nothdurft & Webb, 2009).

Although coral branch clasts observed in coralla at Bargara appear to have been dead upon deposition, clypeotheca also apparently was observed at the junctions between non-clone branches of *A. formosa* in allograft (anisogenic) experiments

(Collins, 1978, his figure 30). Collins (1978, p.108) noted the formation of 'epithecal morphology, a consistent feature noted at all mature allogeneic interfaces' where non-clonal branches were forced to interact with each other. Potts (1976, p. 84) also may have referred to clypeotheca in describing the formation of 'a growing edge similar to the expanding edge of the basal disk of a colony,' developing where two non-clonal branches of '*A. palifera*' (now *Isopora palifera,* Wallace et al., 2007) grew against each other without fusion of soft tissues. Clypeotheca was described at the junction between two colonies of *I. palifera* by Nothdurft &Webb (2009). Hence, clypeotheca production may in some cases also be a response to stress from interactions with more aggressive coral species.

The broken branch that fused seamlessly to the underlying colony on Heron Reef developed no clypeotheca and demands a different interpretation. In this case, the polyps on the branch were still clearly alive at the time of deposition, and they remained alive when collected, well after fusion took place. We interpret the fused branch as most likely representing a clone-mate (i.e., the same genotype - isogeneic) of the underlying colony. Although no genetic analyses have so far been carried out to test that hypothesis, previous studies of interspecific aggression (Lang, 1971; Shepard, 1979) and soft part and skeletal fusion (Hildemann et al., 1975; Logan, 1984; Neigel & Avise, 1983; Frank et al., 1997) in scleractinian corals suggest that it is unlikely that two mature non-clone mates would have fused so readily at both the soft tissue and skeletal levels. Although allogenetic fusion occurs in some very young coral colonies where spats settle very close to each other (Hidaka, 1985; Hidaka et al., 1997), presumably owing to delayed development of the histocompatability mechanism (Frank et al., 1997; Raymundo & Maypa, 2004), allogeneic fusion of mature colonies is rare (Chornesky, 1991; Fagerstrom & West, 2011). Significantly, the coral branch did not appear obviously to have been broken off of the host colony, although that possibility exists. The branch differs from the underlying colony in that it has significantly thickened skeletal structure, but that could represent a stress response wherein polyps limited their own extension, so as to reduce interference with other proximal polyps while continuing to deposit skeletal aragonite. Some of the polyps appear to have changed their growth trajectories (Fig. 2). It is difficult to track an individual corallite through its entire trajectory, but interestingly, some may have stopped growing and entire corallites were abandoned where they interfered with opposing polyps. This observation differs from that of Collins (1978) who suggested that all polyps survived at the sites of experimental fusions between *Acropora* branches, but that they diverted significantly away from the contact zone. However, polyp abandonment apparently occurred in an example illustrated by Neigel & Avise (1983, their figure 1A) and polyp abandonment is consistent with the stress reaction of *Acropora* where clypeotheca is formed (Nothdurft & Webb, 2009).

Regardless, of the morphological response, the apparent clone-mate branch may have been transported laterally from a different, but clone-mate colony. Fragmentation is an important mode of reproduction for branching corals, such as *Acropora* (Tunnicliffe, 1981; Highsmith 1982), in shallow reef settings and large storm events can break and distribute corals over 100s of meters of reef surface. Hence, clone-mates can be distributed over a wide area of reef flat and then come into contact again with lateral transport of broken branches during subsequent disturbance events. The likelihood of such a process depends on the morphology of the colony and recurrence rate of the disturbance events that cause physical damage to the colonies.

Irrespective of the exact source of the branch, it was not washed off of the colony subsequently. As its position was not particularly obstructed by underlying morphology, it is interesting to speculate that it may have been in some part anchored initially by soft tissues, perhaps partly by interaction between the polyps in the underlying corallum and the branch. That soft tissues responded relatively quickly to the clast is suggested by the fact that the broken end of the branch was not colonised by other benthos before being overgrown by new coral skeleton. Hence, soft tissue from the larger colony may have expanded over the broken branch end relatively quickly and this may have helped anchor the branch into place before full soft tissue and skeletal fusion occurred. Such ability would aid fragile colonies in these high energy settings by fostering rapid development of rigid buttresses where colonies were damaged and branches fell into contact with each other. The relatively fragile *Agaricia tenuifolia* developed the ability to fuse with non-clone-mates as a possible means to produce such buttresses and increase strength across adjacent colonies (Chornesky, 1991). Rapid response of polyps to anchor to a clone-mate fragment could serve the same purpose. However, some branching corals (e.g., *Stylophora pistillata*) appear to have a chemical response between adjacent branches that signals their proximity and limits their mutual interference and presumably fusion during normal growth (Rinkevich & Loya, 1985). That type of response would be at odds with any active role for polyps in anchoring a fragment to the colony. Regardless, Fagerstrom & West (2011) highlighted the importance of processes involving clone interaction in the formation and rigidity of skeletal reef framework and early interaction and or fusion of soft tissues could be an advantageous adaptation for framework forming corals.

Finally, there is the third case, also from Heron Reef, wherein a transported branch was actively being overgrown by the underlying colony. In that case, the apparent fusion was clearly the result of competitive overgrowth (Neigel & Avise, 1983; Hidaka et al., 1985) wherein the underlying colony was dominant. Such reactions have been observed in cases of anisogenic fusion (Hidaka, 1985; Rinkevich & Loya, 1985; Chadwick-Furman & Rinkevich, 1994; Frank et al., 1997) and suggest that the transported branch was not a clone-mate of the underlying colony. A variety of stressful interaction circumstances are associated with discoloured tissues pink, purple or blue. This cellular inflammation and the melanin-producing signalling pathway are two mechanisms employed by invertebrates to remove foreign organisms (e.g., Palmer et al., 2008; Willis et al., 2004 and references therein). No discoloured tissue was observed in the example of clone mate interaction (Fig. 1A). Although the sample was not collected, it is unlikely that any skeletal fusion would be observed, but as with the previous example, there may have been early interaction of soft tissues before the overgrowth reaction began. It is unknown if the host colony deposited a clypeotheca around the branch like that observed by Nothdurft & Webb (2009) between two colonies of *Isopora palifera*. Regardless, continued growth of the underlying colony would eventually encapsulate the branch entirely within the corallum and produce an embedment similar to those documented above from Bargara, but in this case as a live-live ecological association.

In summary, we have demonstrated three different behaviours regarding the interaction between coral colonies and broken coral branches that become lodged on their surfaces in natural settings. Where live coral branches produced during a disturbance event come to rest on probable genetic clone-mate colonies they become rapidly stabilised leading to complete soft tissue and skeletal fusion. Where the branch and underlying colony are not clone-mates, but may still be the same or similar species, the branches still may be stabilised rapidly by soft tissue, but then one species will overgrow the other. Where the underlying colony is dominant, the smaller branch will eventually become embedded within the host corallum. Where branches represent dead skeletal debris, they are treated like any foreign clast and are surrounded by clypeotheca and incorporated into the corallum.

The retention of branch fragments on colonies in high energy reef flat settings may suggest an active role of coral polyps to recognise and fuse with each other. This ability may represent an adaptation to help heal damaged colonies where branches were broken, but not removed from the host colony, so as to increase corallum strength. Many reef framework forming invertebrates have developed the ability to fuse with clone-mates and non-clonemates to provide rigidity in high energy settings (Fagerstrom & West, 2011). Where non-clone-mate branches are involved, they do not become fused with the underlying colony at both soft tissue and skeletal levels, but the corals may compete at the site of contact and the branch may be engulfed forming a quasi-fusion. In such cases, the encrustation formed by new skeletal growth may still be very firm. Where dead coral branches come to rest on a colony, the colony isolates the clasts in cavities lined by clypeotheca. Such an adaptation may be important for protecting colonies from invasion by parasites and other benthos following disturbance events. In both cases, individual polyps may be abandoned and resorbed by the colony. This provides strong evidence of the very high level of colonial integration in *Acropora*.

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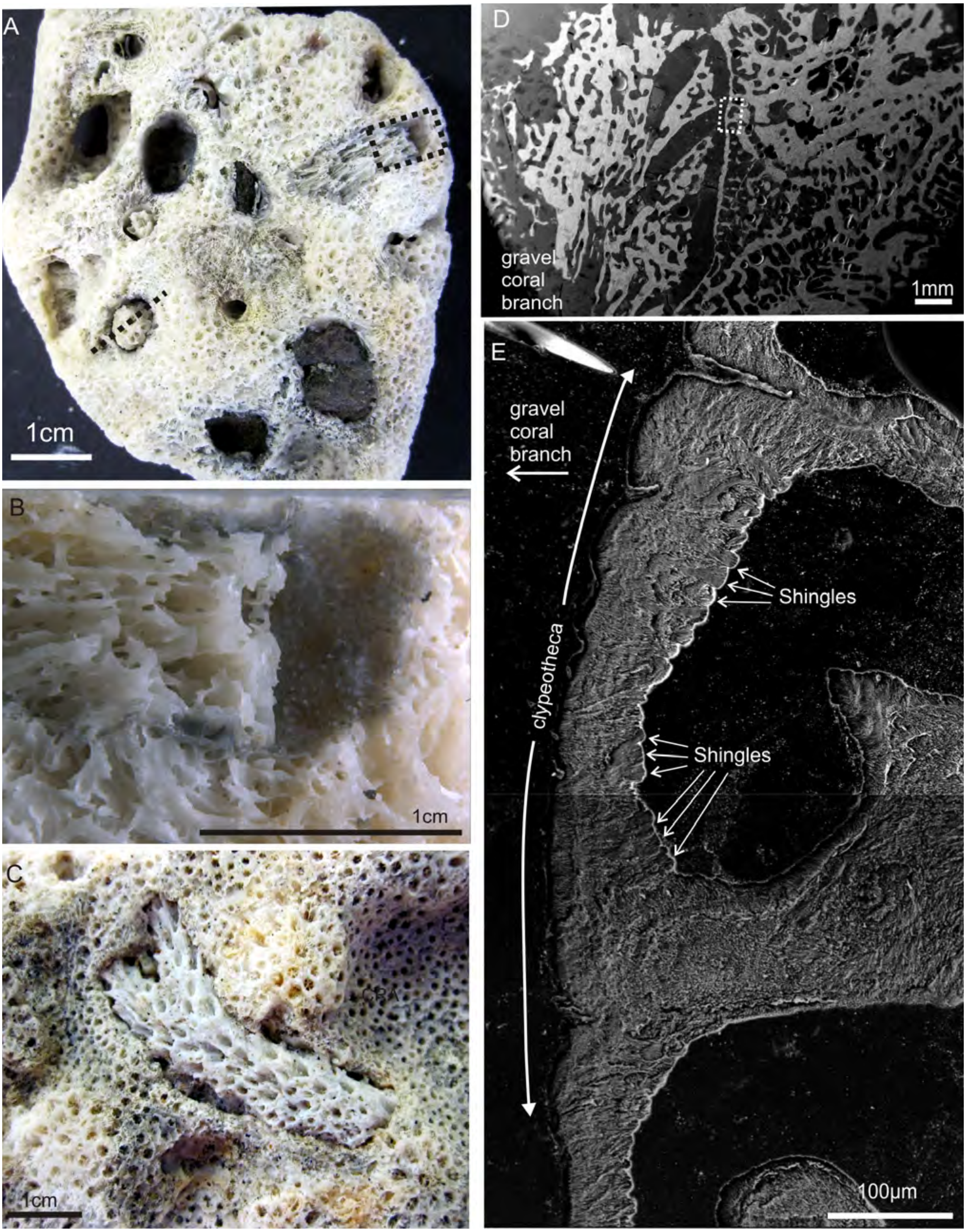

Plate 1. Photographs and SEM images of coral rubble washed up on a beach around the rocky headlands at Bargara, Queensland. A: *Acropora* fragment containing encased gravel fragments including coral branches and noncarbonate clasts. B: Photograph of a gravel clast consisting of an *Acropora* branch contained within the larger corallum. The branch was encased in clypeotheca (stained area). The location of this image is shown in Plate 1-A by the dashed box. C: Photograph of another example of sediment (*Acropora* branch) that was incorporated into the larger skeleton. Note how the skeleton is modified to wrap around the sediment grain. D: SEM image of a branch from Plate 1-A (sectioned vertically at the location of the dashed line) that is surrounded by clypeotheca. The embedded clast is on the left side. E: Higher magnification stitched image showing typical clypeotheca in cross section (location shown by dashed box in Plate 1-D). The walled structure has a shingle microstructure on the surface away from the grain (to the right) indicating clypeotheca growth away from the grain into the living coral tissue.

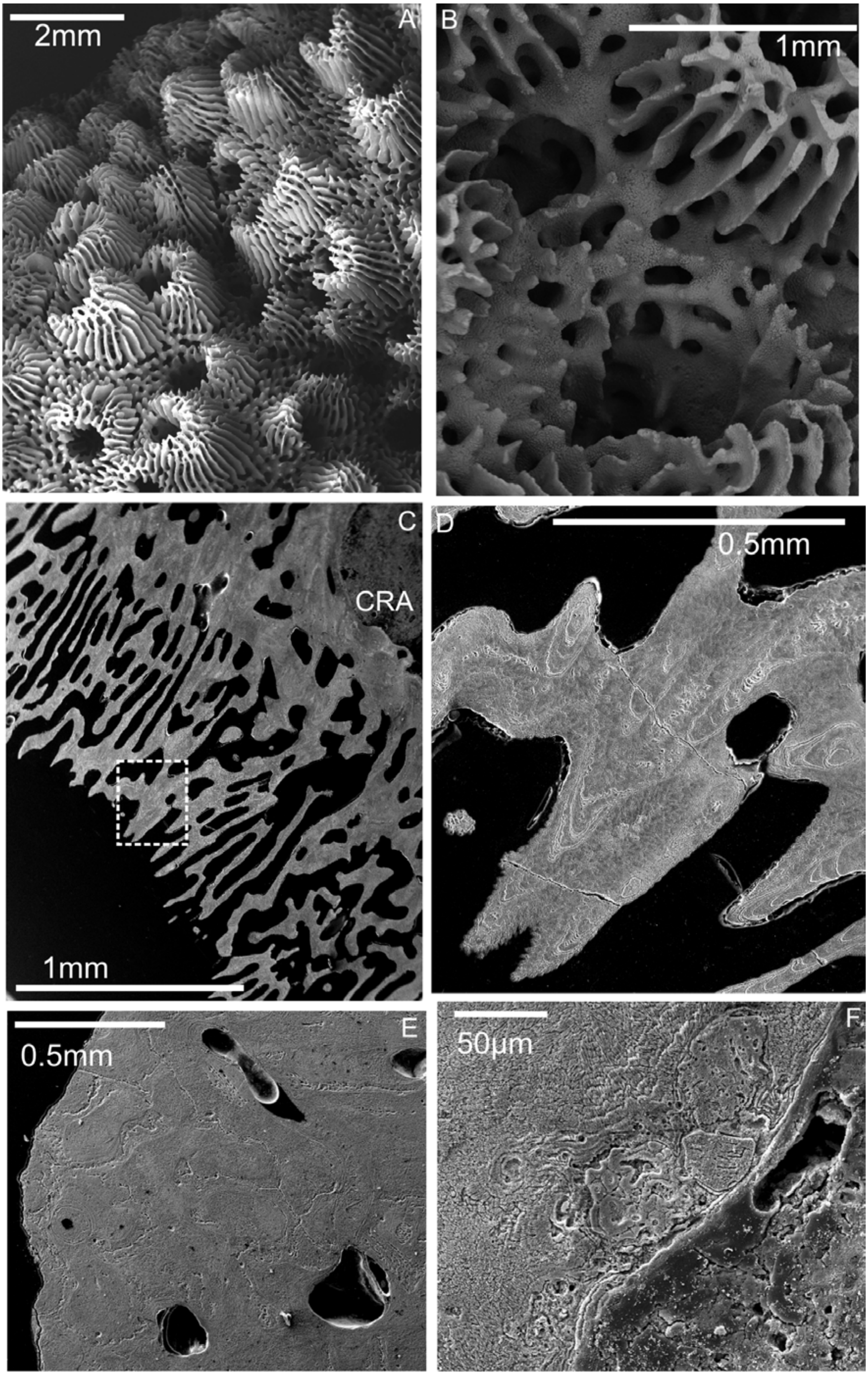

Plate 2. SEM images of external surfaces and polished and etched sections of junction between the two branches in Figure 1. A and B: External surfaces of the junction between the two branches showing complete skeletal fusion, but variability between corallite size, shape and orientation. C: Image of polished and etched section at the approximate junction between the branches illustrating an essentially seamless skeletal fusion. Note the difference in thickening of skeletal material prior to the fusion compared to post fusion skeletal deposition and the grain of coralline red algae (CRA) at the junction between the branches. D: Close-up view of Plate 2-C (dashed box) showing no skeletal demarcation at site of fusion between branches. E: Polished and etched section of part of original broken branch that has a large degree of skeletal thickening deposits. F: Polished and etched section of the contact between coral and encased sediment grains of mixed carbonate material showing the intricate contouring of the skeletal surface by what is presumably clypeotheca around and against the sediment grains.